COMBINING ABILITY, GENOME-WIDE ASSOCIATION STUDIES AND GENOMIC PREDICTION FOR MAIZE RESISTANCE TO *STRIGA (Striga hermonthica* (DEL.) BENTH)

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DECLARATION

I hereby declare that except for references duly cited herein, this is my original research work and that neither part nor whole has been presented elsewhere for the award of a degree.

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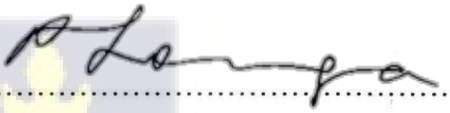

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ABSTRACT

One of the major biotic stresses affecting maize production in SSA is the parasitic weed *Striga hermonthica* (Del.) Benth. Breeding for *Striga* resistance is decades old and some progress has been made despite the complex nature of its inheritance. Progress in developing high-yield *Striga* resistant germplasm has been hampered by the narrow genetic base, lack of breeder-ready molecular markers for selection and limited phenotyping capacity for *Striga* resistance breeding programs in SSA.

The objectives of this study were to:

i) investigate gene action for resistance to *Striga hermonthica* in mid-altitude adapted tropical maize;

ii) identify genomic regions associated with *Striga* resistance among early maturing mid-altitude maize inbred lines

iii) predict performance of tested and untested doubled haploid (DH) lines under artificial *Striga* infested conditions.

Three independent studies were conducted to gain understanding of the genetics of *Striga* resistance in mid-altitude tropical maize germplasm.

In the first experiment, 132 hybrids were generated from 12 inbred lines through a diallel mating design. The inbred lines and the hybrids were phenotyped under artificial *Striga* infestation at Kibos and Alupe for two seasons and under optimal conditions in 2022 and 2023. An alpha lattice experimental design was used for hybrid evaluation, with two replicates at four trial locations under optimal conditions and two trial locations under artificial *Striga* infestation. Data were collected on grain yield, agronomic traits and *Striga* resistance parameters. Analysis of variance, variance components estimates, and heritability were carried using AsREML in R. Combining ability analysis of the hybrids and lines following Griffing's Method 3, Model 1 was carried out using AGD-R software. Results showed that the inbred lines and the test hybrids varied significantly with broad sense heritability >73% for grain yield, agronomic and *Striga* resistance parameters under the two management schemes. Fifteen (15) hybrids outperformed the checks by 32.1% in grain yield under *Striga* infestation. The study revealed that additive and non-additive gene effects influenced grain yield, agronomic traits and *Striga* resistance parameters. Based on Baker's ratio, additive gene effects were more important than non-additive gene effects indicating that the traits are genetically controlled. Maternal effects were not significant for most traits. Five parental lines namely: DL171342,

DL17535, DL17611, DL17933 and TZISTR1163 had positive GCAs effects for grain yield and negative GCA for *Striga* resistance under *Striga* infestation.

In the second experiment, 163 F_6 early maturing inbred lines were used in a genome-wide association study. The 163 lines were testcrossed to generate 459 hybrids that were phenotyped under artificial *Striga* infested conditions at two locations (Kibos and Alupe) and natural *Striga* infestation at two locations (Madeya and Teso). The inbred lines were genotyped with 955,670 single nucleotide polymorphic (SNP) markers. After quality control 155 inbred lines and 151, 670 high quality SNP markers were retained for association analysis. Analysis of variance, variance components estimates, adjusted means and heritability were computed using AsREML in R. The FarmCPU model was used to identify significant SNPs associated with grain yield, *Striga* resistance parameters and agronomic traits using GAPIT package in R. The putative candidate genes linked to significant SNPs were obtained from the Maize Genetics and Genomics Database (MaizeGDB; http://maizegdb.org) using BedTools. Gene functions were obtained from MaizeMine. Analysis of variance revealed that hybrids varied significantly showing moderate broad sense heritability for all *Striga* resistance parameters except *Striga* damage rating whose heritability was high (62−64%). High significant negative correlations were observed between grain yield and *Striga* damage rating (-0.47***–-0.56***). A total of 42 significant SNPs, which accounted for 0.1–38.9% of the phenotypic variation for *Striga* resistance parameters, were identified. Eight loci in chromosomes 2 (S2_44331849, S2_87827811), 3 (S3_175540577, S3_8219084) and 6 (S6_159470193, S6_107754561, S6_96337848 and S6_109282273) accounted for 11.9−38.9% phenotypic variance in *Striga* resistance parameters. The significant SNPs were near several putative genes that coded for proteins, transcription factors, metabolic enzymes among other factors involved in plant growth and defense against pathogens.

For the third objective, 606 doubled haploid (DH) lines were used for genomic prediction. A training population of 116 lines was phenotyped in hybrid combination by crossing the lines with two testers to generate 232 test cross hybrids. The testcrosses were phenotyped at Kibos, Alupe and Siaya under artificial *Striga* infestation in 2020. The 606 DH lines were genotyped with 8,439 rAmpSeq markers. After quality control, 5,380 high quality rAmpSeq markers were retained and used for genomic prediction. Analysis of variance was carried out to estimate components of variance and heritability. AsReml was used in generating the best linear unbiased estimates (BLUEs), best linear unbiased predictions (BLUPs), estimates of variance components and heritability. The BLUEs of the training population and the 5,380 rAmpSeq

markers were used in genomic prediction of the 606 inbred lines. A genomic relationship matrix was computed and incorporated in the genomic prediction using the reaction norm model. Three cross validation schemes (CV0, CV1 and CV2) were used to estimate the prediction accuracy of the model. The model was then used to predict the performance of the tested and untested DH lines. Genomic estimated breeding values (GEBVs) were computed for various *Striga* resistance parameters. Genetic variance was larger than the G×E variance. Heritability was low to moderate (38–65%) for *Striga* resistance parameters while that of grain yield was 54%. Prediction accuracy based on cross validation (CV) was low to moderate (0.24 to 0.53) for CV0 and CV2 (0.20 to 0.37). For GY, the prediction accuracies were 0.59 and 0.56 for CV0 and CV2, respectively. Using the reaction norm model, 300 DH lines with desirable GEBVs for reduced number of emerged *Striga* plants (STR) at 8, 10, and 12 weeks after planting were identified. The GEBVs of DH 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 for *Striga* resistance breeding in maize.

In conclusion, the study findings indicate that additive gene effects were preponderant based on Baker's ratio. Five inbred lines that can potentially be used as valuable sources of favourable alleles in *Striga* resistant hybrid breeding programs were identified. Additionally, the study identified 10 significant SNPs that can be considered for fine mapping and development breeder-ready markers for selection in *Striga* breeding programs. The application of GS where a large set is genotyped and phenotyping only a limited subset helps to reduce phenotyping costs due to limited land and the need for artificial *Striga* infestation. The integration of genomic-assisted strategies and DH technology for line development coupled with forward breeding for major adaptive traits will enhance genetic gains in breeding for *Striga* resistance in maize. The estimation of the GEBVs should be part of the standard operation procedures for *Striga* resistance breeding programs.

DEDICATION

I dedicate this research to God and to my entire family. Special thanks to my Dad, Jacob Beles, I would not manage without you. My sister Cosy, you know this road way too well, thanks! To my family, The Shimbas, I dedicate this work to you, for your patience and perseverance!! You are all my support structure.

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LIST OF ABBREVIATIONS

AsReml	Residual Maximum Likelihood
AUDPC	Area under Disease Progress Curve
BGLR	Bayesian Generalized Linear Regression
BLUEs	Best Linear Unbiased Estimates
BLUPs	Best Linear Unbiased Predictions
CAN	calcium ammonium nitrate
CIMMYT	International Maize and Wheat Improvement Centre
CV	Cross Validation
DAP	Di-Ammonium Phosphate
DH	Doubled Haploid
FAO	Food and Agriculture Organization
FAOSTAT	Food and Agriculture Organization Corporate Statistics Database
FarmCPU	fixed and random model circulating probability unification
FAW	Fall armyworm
FEM	Fixed Effect Model
GBLUP	Genomic Best Linear Unbiased Prediction
GBS	Genotyping-by-Sequencing
GCA	general combining ability
GEBVs	Genomic estimated breeding values
GMP	Global Maize Program
GP/S	Genomic Prediction/Selection
GRM	Genomic Relationship Matrix
GWAS	Genome Wide Association Studies
IITA	International Institute of Tropical Agriculture
IMAS	Improved Maize for African Soils
IPM	integrated pest management
MABC	Marker Assisted Backcrossing
MAF	Minor Allele Frequency
MaizeGDB	Maize Genetics and Genomics Database

MAS	Marker Assisted Selection
META-R	Multi-Envrironment Trial Analysis in R
MLN	Maize lethal necrosis
MSV	Maize streak virus
NERICA	New rice for Africa
OPV	Open pollinated variety
PAV	Present-Absent Variant
QC	Quality Control
QTLs	Quantitative Trait Loci
rAmSeq	Random Amplicon Sequencing
REM	Random Effect Model
SCA	specific combining ability
SNPs	Single Nucleotide Polymorphisms
SSA	Sub Saharan Africa
TASSEL	Trait Analysis by aSSociation, Evolution
TLB	Turcicum leaf blight
TRN	Training population
TST	Testing population

CHAPTER ONE

INTRODUCTION

Maize (*Zea mays* L.) is one of the staple foods to a vast population in Africa providing key dietary sources of starch, protein, vitamins, minerals as well as phytochemical compounds including carotenoids, phytosterols and phenolic compounds (Siyuan *et al.,* 2018). Maize further provides feed for livestock in form of silage, crop residue and grains besides being a major ingredient in industrial food products for starch and oil extraction. In Africa, maize is grown on over 38.4 million ha of land forming 16.4% increase in production area from 2013 to 2017 (FAOSTAT, 2020). Although maize is grown on 2.15 million ha in Kenya, production is low, (average of 1.77 t ha^{-1}) (FAO, 2023), which is attributed to biotic and abiotic stresses. Other challenges include loss of soil fertility, land degradation, lack of farm inputs such as fertilizers and pesticides as well as rural transformation. The situation is further worsened by climate change that has direct impact on production and the general stability of food systems (Kornher, 2018). Biotic stresses such as pests, diseases, and weeds have also been detrimental to food production in SSA. *Striga hermonthica* (Del.) Benth. also called the purple witchweed, is one of the major parasitic weeds affecting maize production in SSA. Cereal yield losses due to *Striga* negatively impact food security in SSA since the weed affects major staple food crops including maize, rice, sorghum and millet (Dechassa & Abate, 2021).

Striga hermonthica competes with maize for water, nutrients and sunlight in agricultural ecosystems thus inducing reductions of crop biomass leading to diminished yields. Weeds have been reported to lead to an estimated 37% of global maize losses (Shiferaw *et al.,* 2011; Cerrudo *et al.,* 2012). *Striga hermonthica* has been found to be of greater economic importance to maize farmers in SSA among other parasites (Atera *et al.,* 2012; Mbogo *et al.,* 2016). *Striga* seed often germinates as soon as the host or non-host plants produce chemical cues called strigolactones (Brun *et al.,* 2018). Successful connection nourishes the parasite and ensures it grows to produce flowers and numerous seeds (about 200,000 per plant) which remain in the soils for several years (Kanampiu and Friesen, 2004). The weed infestation adversely affects maize resulting in poor growth, retardation, and yield losses estimated at US$ 7-10 billion yearly with heavy parasitic attack leading to up to 100% loss (Berner *et al.,* 1996; M'mboyi *et al.,* 2010; Kanampiu *et al.,* 2018; Kebede & Ayana, 2018; Gowda *et al.,* 2021).

Striga control strategies including cultural, biological, chemical control and host plant resistance have been proposed (Kanampiu *et al.,* 2003; Makumbi *et al.,* 2015). However, no

single management strategy aimed at either prevention, containment or depletion of the *Striga* seed bank has been effective in reducing *Striga* associated yield losses (Kebede & Ayana, 2018). Therefore, an integrated management approach that combines two or more control options is required to control *Striga* in the farmers' fields (Kanampiu *et al.*, 2018; Mwangangi *et al.*, 2021; Jamil *et al.*, 2021). Host plant resistance coupled with other control strategies could be a more affordable, sustainable and environmentally friendly *Striga* management approach. Consequently, research efforts have contributed to the development of improved maize varieties with *Striga* tolerance/resistance (Badu-Apraku *et al*, 2007; Menkir *et al.*, 2012). In Kenya, the Kenya Agriculture and Livestock Research Organization (KALRO) developed a *Striga* tolerant OPV KSTP94 in 1994.

Yield losses impact food security in SSA since the weed affects major staple food crops including maize, rice, sorghum and millet. The lifecycle of *Striga*, which is intimately synchronized with that of its host, renders control methods difficult. Conventional control methods have been less effective in managing the effects of *Striga* on crop plants. This is attributed to the intricate parasitic life cycle, which is synchronized to that of the host, production of numerous seeds by *Striga* which remain viable for extended periods, low soil nitrogen, financial constraints among the smallholder farmers and lack of resistant germplasm that can provide a long-term and more sustainable strategy for *Striga* control. Besides, integrated management strategies aimed at either prevention, containment or depletion of the parasites are extremely costly to the smallholder farmers (Jamil *et al.*, 2021). Host resistance coupled with other *Striga* control methods could offer a more affordable and sustainable control strategy.

Despite these challenges significant progress has been made in developing and deploying *Striga* resistant maize varieties in West Africa by the 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} yr^{-1} (Menkir and Meseka, 2019) and 101 kg ha^{-1} yr^{-1} (Badu-Apraku *et al.*, 2020b) 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, 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).

Striga resistance has been reported in wild relatives of maize, *Tripsacum dactyloides* and *Zea diploperennis* (Amusan *et al.*, 2008; Menkir, 2006; Gurney *et al.*, 2003). Exploiting these germplasms through breeding programs has been a step in the right direction towards developing germplasm that have complete resistance to the noxious weed. Consequently, research efforts have had success in development of improved crop varieties in relation to *Striga* resistance with great milestones for sorghum (Gobena, 2017; Mbuvi *et al.*, 2017; Ejeta, 2007b), millet (Sattler *et al.*, 2018; Kountche *et al.*, 2013), rice (Rodenburg *et al.*, 2017; Jamil *et al.*, 2012), and maize (Badu-Apraku *et al.*, 2020a, c; Mutinda *et al.*, 2018; Shayanowako *et al.*, 2018). Several milestones have been achieved in maize in regards to *Striga* resistance, i.e., the development of inbred lines that can be utilized in breeding programs (Badu-Apraku *et al.*, 2020a, c; Gowda *et al.*, 2021). Besides, population improvement and development of hybrids that show improved resistance to *Striga* have been reported (Menkir & Kling, 2007; Badu-Apraku *et al.*, 2009; 2010). In Kenya for example, an open pollinated variety was developed by KALRO in 1994 and has since been in cultivation among the smallholder farmers (Mutinda *et al.*, 2018). Since then, *Striga* control strategies have been the key management approach (Abdallah *et al.*, 2015; Kanampiu *et al.*, 2018; Mwangangi *et al.*, 2021). Few studies have utilized molecular techniques such as linkage analysis or QTL mapping and genome wide association mapping (GWAS) in an effort to identify molecular markers for marker assisted selection (MAS) in *Striga* breeding programs.

While these studies identified QTLs closely linked to the genes involved in defense mechanism of the maize plants under *Striga* infestation, they are yet to be validated and deployed for MAS in *Striga* breeding programs (Singh & Singh, 2015). Additionally, the International Institute of Tropical Agriculture (IITA) in West and Central Africa has conducted most of these studies with limited advancements in East Africa where *Striga* infestation remains a critical issue. *Striga* exhibits high phenotypic plasticity, adapting quickly to different environmental conditions and hosts. This adaptability makes it challenging to develop maize varieties with

consistent resistance across diverse agro-ecological zones. This underscores the need for the development of well-adapted *Striga* resistant germplasm suitable for East Africa's agro-ecologies.

To build and widen the genetic base, IITA donor lines have been utilized for the introgression of *Striga* resistance genes to the International Maize and Wheat Improvement Center (CIMMYT) elite germplasm (Menkir *et al.*, 2012; Makumbi *et al.*, 2015; Kanampiu *et al.*, 2018). However, the breeding cycle for developing *Striga*-resistant maize cultivars require multiple generations of crossing, selection, and testing. Whereas initial studies made use of bi-parental populations derived from inbred lines developed following pedigree breeding method, which takes 6 – 8 generations, CIMMYT has employed doubled haploid (DH) technology in the development of inbred lines. This technology has been further reported to enhance genetic diversity thus accelerating the rate of genetic gains in *Striga* breeding programs (Chaikam *et al.*, 2019). Consequently, several inbred lines with *Striga* resistance background have been developed.

Some of the key challenges encountered in *Striga* breeding programs include the polygenic nature of the trait making it difficult to identify and combine all necessary resistance genes into a single variety. The interactions between these genes and their environment further complicate breeding efforts. Multiple studies have underscored the significant impact of the environment on *Striga*-related parameters (Makumbi *et al.*, 2015; Stanley *et al.*, 2021). Whereas multi-locational screening has been reported to reduce environmental influence, germplasm screening for *Striga* resistance is labor intensive and costly. Besides, screening for *Striga* resistance requires artificial inoculation for uniform infestation. This limits multi-locational trials due to avoidance of introducing the weed to new sites free of the weed.

Several studies have proposed the use of combining ability studies for genetic dissection of *Striga* inheritance (Menkir *et al.*, 2007; Yallou *et al.*, 2009; Badu-Apraku *et al.*, 2011; Rwiza *et al.*, 2011; Badu-Apraku *et al.*, 2013). Besides, combining ability studies are important in the heterotic grouping and selection of suitable parental lines for the development of superior hybrids. Therefore, understanding the genetic control of *Striga* resistance in CIMMYT germplasm is critical in the identification of parental lines for the development of hybrids with high yields coupled with *Striga* resistance. Besisdes, some studies have employed GWAS in the identification of significant SNPs that confer resistance to *Striga* in IITA germplasm, the

results of most of which are applicable to West and Central Africa, with little impact on East Africa, particularly in areas where mid-altitude adapted tropical maize dominates. There is, therefore, need to investigate the genetics of *Striga* resistance genes among CIMMYT germplasm for maize yield improvement in *Striga* resistance breeding programs. The development of double haploid (DH) lines at CIMMYT opens avenues to speed up the production of inbred lines for use in the development of *Striga* resistant hybrids. Genomic prediction, on the other hand, has been reported to enhance selection accuracy without the need to phenotype large number of plant materials (Meuwissen *et al.*, 2001; de los Campos *et al.*, 2009; Crossa *et al.*, 2010; Pérez-Rodríguez *et al.*, 2012). Beyene *et al.* (2019) for example reported on the practical application of genomic selection in CIMMYT's breeding program in Kenya using the test half and predict all method. This method reduces the dependency on extensive and costly field trials and enables the selection of superior lines more efficiently. Therefore, to overcome the workload and inconsistencies in the prediction of genotypes based on phenotype, phenotyping challenges including limited trial locations and costs, genomic prediction and/or selection offers promising alternatives. So, despite progress in the development of *Striga* resistant maize, especially in SSA, the current techniques of DH and genomic selection are likely to speed up research for product development. The main goal of this study was to provide information through recent advances in genetics towards improving *Striga* resistance in maize. The study was guided by the following objectives:

i. To determine gene action responsible for resistance to *Striga hermonthica* in mid-altitude adapted tropical maize
ii. To identify genomic regions linked to *Striga* resistance among early maturing mid-altitude adapted maize inbred lines
iii. To predict performance of tested and untested DH lines under artificial *Striga* infested conditions

CHAPTER TWO

LITERATURE REVIEW

2.1 Maize production in Kenya

Maize belongs to the grass family and serves as a staple food crop for most of Kenyan households providing a vital source of calories and nutrition. Annually, Kenya produces approximately 3–4 million metric tons of maize, accounting for about 40% of the country's total cereal production (FAO, 2023). Maize cultivation in Kenya encompasses approximately 2.15 million hectares annually, making it one of the most extensively grown crops in the country. Maize occupies nearly 40% of the total cultivated land. Major maize-producing regions include the Rift Valley, Western, Nyanza, and parts of Eastern Kenya. Smallholder farmers, who collectively contribute the bulk of the national maize output (Santpoort, 2020), predominantly drive the cultivation of maize. These small-scale farmers, typically cultivating less than two hectares each, play a crucial role in sustaining maize production and ensuring food availability for both rural and urban populations.

Despite its widespread cultivation, maize yields in Kenya average around 1.77 metric tons per hectare (FAO, 2020). The production volumes are, however, inconsistent due to various factors such as climatic conditions (Mumo *et al.*, 2018), biotic and abiotic stresses as well as agricultural practices. Therefore, achieving optimal yields remains a challenge due to the crop's susceptibility to pests and diseases, climate variability characterized by droughts and irregular rainfall patterns, and low soil fertility stemming from degraded soils and insufficient fertilizer use. Addressing these challenges is essential to improving maize productivity and enhancing food security for millions of Kenyans who rely on maize as a dietary staple and income source. The sale of surplus maize can provide cash for other household needs and investments. Additionally, maize farming provides employment opportunities for rural populations, both directly on farms and indirectly through related activities such as transportation, marketing, and processing.

Maize remains a fundamental crop in Kenya's agricultural landscape, essential for food security, economic stability, and rural livelihoods. Despite facing several challenges, both in production and post-harvest, continued efforts in research, policy support and sustainable farming practices are vital to enhance maize production and ensure the well-being of millions of Kenyans who depend on this crucial crop.

2.2 Overview of maize production constraints

Maize production in Kenya is adversely affected by socioeconomic factors coupled with abiotic and biotic constraints. Socio-economic constraints such as lack of access to quality agricultural inputs is a major issue, with many farmers unable to afford or access high-quality seeds, fertilizers, pesticides and herbicides. The availability of substandard or counterfeit inputs further exacerbates the problem, leading to poor crop performance. Limited access to agricultural extension services means many farmers lack the knowledge and support needed to implement best practices for maize cultivation, pest and disease management and soil fertility improvement (Gido *et al.*, 2015).

Financial constraints form a significant hurdle for maize farmers in Kenya (Ali-Olubandwa *et al.*, 2011; Onono *et al.*, 2013). Limited access to credit and financial services prevents many farmers from investing in necessary inputs and technologies that could improve maize productivity. The high cost of credit and stringent lending requirements often exclude smallholder farmers from obtaining loans (Olwande & Mathenge, 2011). Additionally, the lack of crop insurance options leaves farmers vulnerable to losses due to unpredictable climatic conditions, pests, and diseases (Ntukamazina *et al.*, 2017). This financial instability discourages investment in maize farming and perpetuates a cycle of low productivity. Policy and institutional constraints also play a crucial role in limiting maize production in Kenya. For example, inconsistent or poorly implemented subsidy programs for agricultural inputs can undermine farmers' efforts to achieve sustainable productivity. Insufficient investment in agricultural research and development limits the introduction and adoption of improved maize varieties and technologies that could enhance productivity and resilience to biotic and abiotic stresses (Byerlee & Heisey, 1996). Moreover, the gap between research institutions and farmers need to be bridged to ensure that new innovations reach the end-users effectively and are adopted at scale.

Major abiotic constraints include climate variability which result in either prolonged dry spells leading to drought or excessive rainfall and flooding especially in rain-fed farming systems (Bozzola *et al.*, 2018; Ochieng *et al.*, 2016; Singh *et al.*, 2013; Cairns *et al.*, 2012). While drought can lead to total crop loss, flooding results in waterlogging, root rot, and increased disease incidence. Extreme temperatures especially during flowering negatively affect pollination and grain filling leading to reduced yields. Low soil fertility attributed to continuous mono-cropping

and lack of farm inputs among smallholder farmers also contribute to diminished crop yields. High soil acidity levels in some regions limit nutrient availability and maize growth while lack of essential nutrients like nitrogen, phosphorus, and potassium can severely limit maize productivity.

Some of the biotic stresses include pests such as stem borers like African maize stalk borer (*Busseola fusca*) and the spotted stem borer (*Chilo partellus*) (de Groote, 2002); and fall armyworm (FAW) (*Spodoptera frugiperda*) (Kamweru *et al.,* 2023). Foliar diseases such as gray leafspot (GLS), Turcicum leaf blight (TLB), maize streak virus (MSV) and maize lethal necrosis (MLN) have been reported to cause significant yield losses in maize (Boddupalli *et al.,* 2020; Ward *et al.,* 1999; Njuguna, 1996). Common weeds in maize fields include *Striga* (witchweed), which parasitizes maize roots, and various other crops in the grass family, competes for essential resources such as nutrients, water, and sunlight, leading to reduced crop growth and yields (Kanampiu *et al.,* 2018; Makumbi *et al.*, 2015, Atera *et al.*, 2013). *Striga hermonthica*, an obligate hemi-parasitic weed not only reduces maize yields but also increases the cost of production as farmers must invest time and resources in manual or chemical weed control methods.

2.3 Parasitic weeds and their economic importance

Parasitic weeds pose significant challenges to crop production particularly in regions where staple cereals and legumes are cultivated. The most problematic species are *Striga hermonthica* and *Striga asiatica* infesting crops like maize, sorghum, millet, and rice. These parasitic weeds attach to the roots of host plants, depriving them of essential nutrients, water, and carbohydrates. The effects are detrimental, leading to stunted growth, reduced vigor, and ultimately, significant yield losses (Kanampiu *et al.,* 2018; Fig. 2.1).

The economic importance of *Striga hermonthica* in Sub-Saharan Africa cannot be overstated, as it exerts a significant toll on agricultural productivity and rural livelihoods (Berner *et al.,* 1996). *Striga* infestations cause substantial yield losses in staple cereal crops which are crucial for food security in the region. The direct impact of reduced yields translates into diminished income for farmers, who often rely on these crops for subsistence and income generation. Additionally, the indirect costs associated with *Striga* management further strain farmers' resources. In this context, addressing *Striga* infestations is not only essential for enhancing agricultural productivity but also

for promoting socio-economic development and improving the overall well-being of communities in SSA.

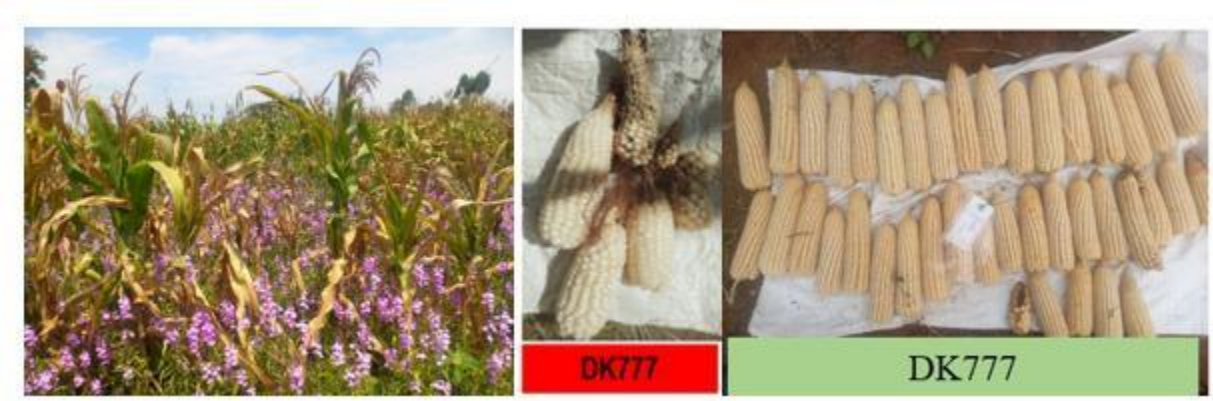


Fig. 2. 1 Striga infested fields; DK777 under Striga infestation; and under optimum conditions

In Kenya, the impact of parasitic weeds on crop production extends beyond yield losses to encompass socio-economic consequences for farmers and rural communities (Atera *et al.*, 2012). Yield losses diminish food availability and increase the vulnerability of communities to food insecurity and malnutrition. *Striga* infestations on maize fields compromise the quality and quantity of harvests, perpetuating the cycle of hunger and poverty among vulnerable populations. In addition to direct yield losses and economic hardships, farmers incur additional costs for weed management, including labor, chemical control methods, and the implementation of cultural practices to mitigate infestations. These expenses strain already limited resources and reduce farmers' profitability. Moreover, the persistent presence of *Striga* weeds can lead to the abandonment of affected farmlands, further diminishing agricultural productivity (Ejeta, 2007a). The adverse effects of parasitic weeds underscore the urgency of effective management strategies to alleviate the burden on farmers, promote sustainable agricultural practices, and enhance food and nutrition security.

2.4 Geographical distribution of *Striga*

Striga comprises of up to 42 species worldwide (Kountche *et al.*, 2016). The most widespread species are *Striga hermonthica* and *Striga asiatica* which majorly affect cereal crops and *Striga gesnerioides* which affects cowpea (Spallek, 2013). The distribution of *Striga* species is influenced by climatic conditions, soil types, and the presence of suitable host crops. The distribution of *Striga* underscores the weed's adaptability to different environmental conditions and its potential to

spread further, highlighting the importance of integrated management strategies to curb its impact on agriculture globally. *Striga* is predominantly distributed across SSA, where it causes a significant threat to agricultural productivity (Fig. 2.2). The most prevalent and destructive species, *Striga hermonthica* and *Striga asiatica*, thrive in warm, semi-arid to sub-humid climates, which are typical of the African savannas. *Striga hermonthica***,** reported to have originated from Ethiopia and Sudan**,** is especially prevalent in the savanna regions of West Africa, including Nigeria, Ghana, and Mali (Ejeta, 2007a). Severe infestations, particularly in the western and coastal regions of East African countries have been reported due to suitable climatic and soil conditions that favor *Striga* proliferation (Gethi *et al.*, 2005).

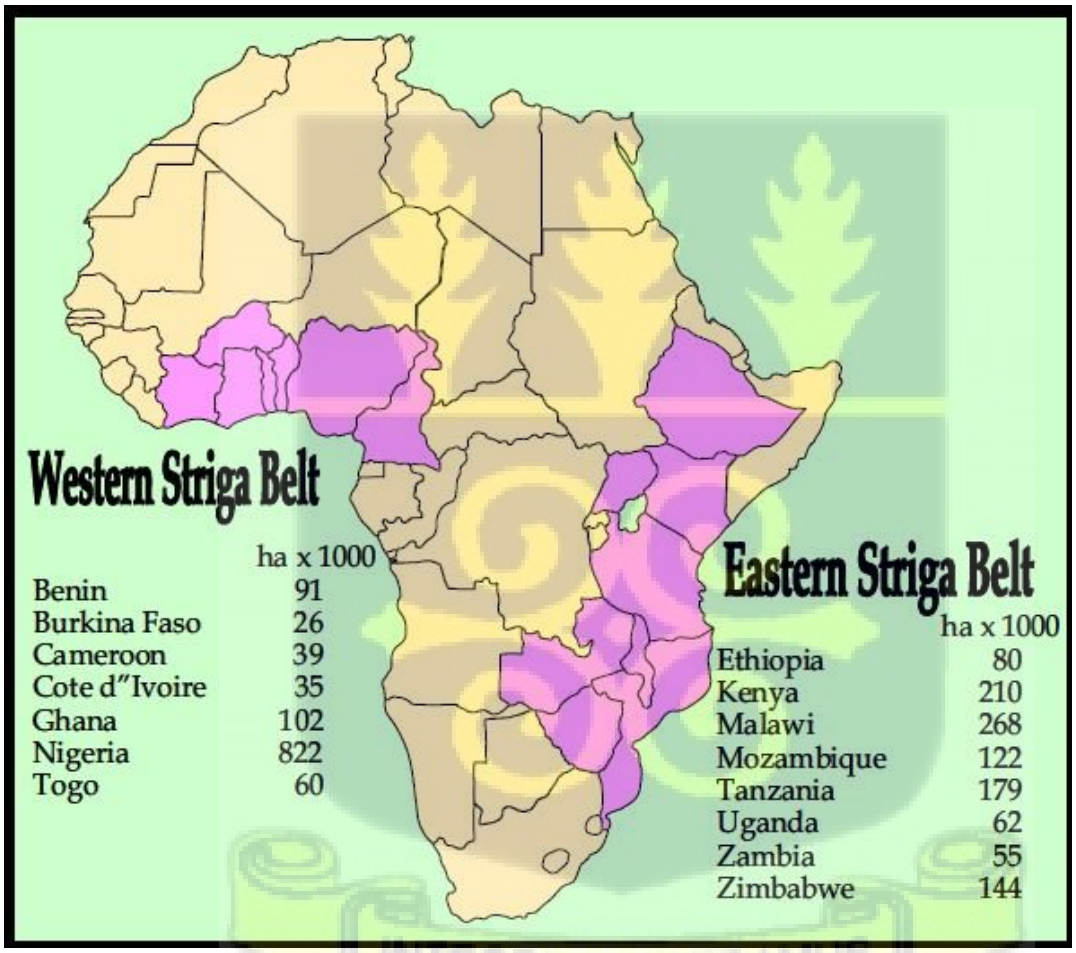


Fig. 2. 2 Striga distribution in Africa

In Kenya, *Striga* is widely distributed in approximately eight counties in the Rift Valley and western parts of the country (Fig.2.3) (Atera *et al.*, 2013). These areas are major smallholder maize

and sorghum growing regions. *Striga*'s impact in these regions is compounded by continuous mono cropping of susceptible cereals and inadequate soil fertility management practices, which contribute to the persistence and spread of the weed. The coastal regions of Kenya further experience considerable *Striga* infestations, affecting both smallholder and commercial farming operations.

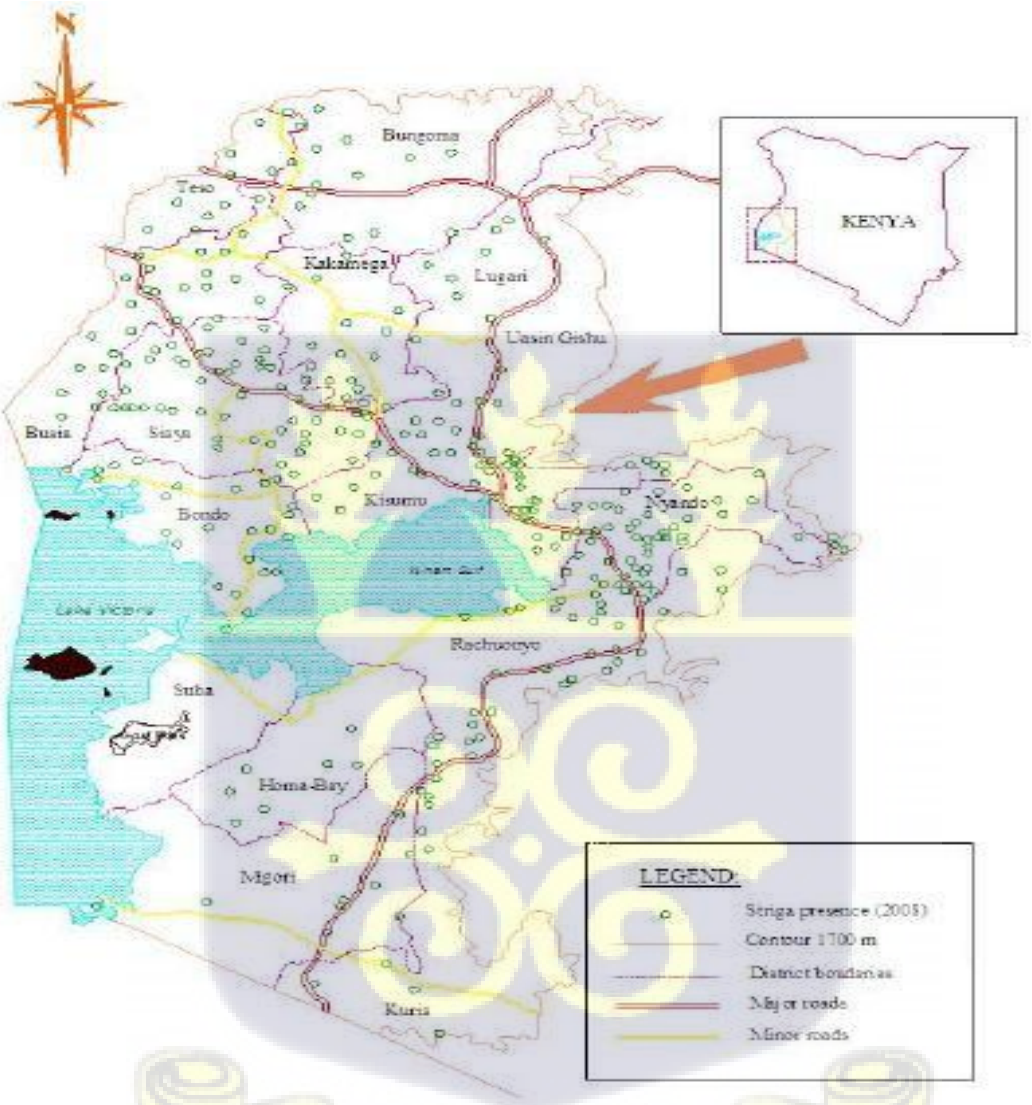


Fig. 2. 3 Striga hermonthica distribution in Western Kenya (Atera et al., 2013)

The prevalence of *Striga* in major agricultural regions poses a serious threat to food security and economic stability. This underscores the importance of *Striga* management in the region.

2.5 Biology of *Striga*

Striga is a genus of obligate hemi-parasitic plants of Orobanchaceae family. These plants are notorious for their parasitic relationship with the roots of host plants, particularly cereals and legumes. *Striga* completes its life cycle in four main stages: seed germination, host attachment, growth and development and reproduction (Spallek, 2013). *Striga* seeds are exceptionally small and can remain viable in the soil for many years, often over a decade, waiting for the right conditions to germinate. *Striga* seeds must go through a 7–14 days preconditioning (exposure to moisture and high temperatures) before breaking dormancy. Seed dormancy is broken when the seeds detect chemical signals called strigolactones, which are exuded by potential host plant roots, otherwise the seeds undergo secondary seed dormancy (Gbèhounou *et al.*, 2000). This biochemical interaction between *Striga* seeds and germination stimulants initiate the germination process, allowing *Striga* to synchronize its life cycle with that of its host. With tiny seeds, *Striga* endosperm can only sustain life for 3–7 days after which *Striga* can only survive if it is attached to the host plant (Spallek, 2013).

Once germinated, the *Striga* seedling attaches itself to the host plant's roots using a specialized organ called a haustorium (Fig. 2.4). The haustorium establishes connection with the host's roots thus extracting water, nutrients, and photoassimilates. This parasitic relationship significantly weakens the host plant, leading to symptoms such as stunted growth, wilting, chlorosis (yellowing of leaves), and reduced photosynthetic efficiency. *Striga*'s aggressive extraction of resources severely impacts the host plant's ability to thrive, often resulting in substantial yield losses.

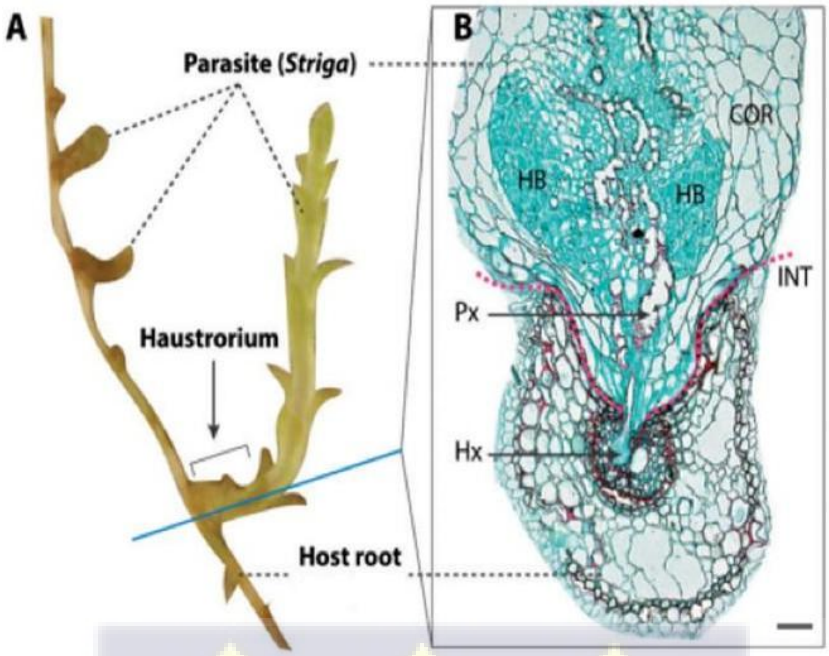


*Fig. 2. 4 Striga attachment (A) and penetration (B) into the host vascular tissues (*Ichihashi *et al.*, 2015*)*

Striga plants exhibit a high reproductive capacity, producing thousands of microscopic seeds that are dispersible by wind, water, animals, and human activities. These seeds can infest new areas rapidly, contributing to the widespread prevalence of *Striga* in the African savannas. The lifecycle of *Striga* involves a vegetative stage, where the parasite remains underground attached to the host roots (1–23 days), followed by an above-ground flowering stage (Fig. 2.5) (Berner *et al.*, 1997). During the flowering stage, *Striga* produces bright, colorful flowers that attract pollinators, ensuring the continuation of its reproductive cycle. After pollination, the flowers develop into seed pods that release numerous seeds back into the soil, perpetuating the cycle of infestation.

The ecological adaptability of *Striga*, combined with its efficient reproductive strategies, makes it a daunting pest in agricultural systems. The weed thrives in diverse environmental conditions but is particularly problematic in warm, semi-arid to sub-humid climates, where many staple crops are grown. *Striga*'s ability to parasitize a wide range of host plants, its long-lived seed bank, and the difficulty in detecting early infestations contribute to the challenges in managing this parasitic weed. Effective control measures require integrated management strategies to reduce the seed bank and limit the spread of *Striga*. In general, The *Striga* fecundity, seed longevity, ease of spread and

the life-cycle synchronized with that of the host present great challenges in pest management. Host resistance is, therefore presents the most promising way to overcome *Striga* challenges.

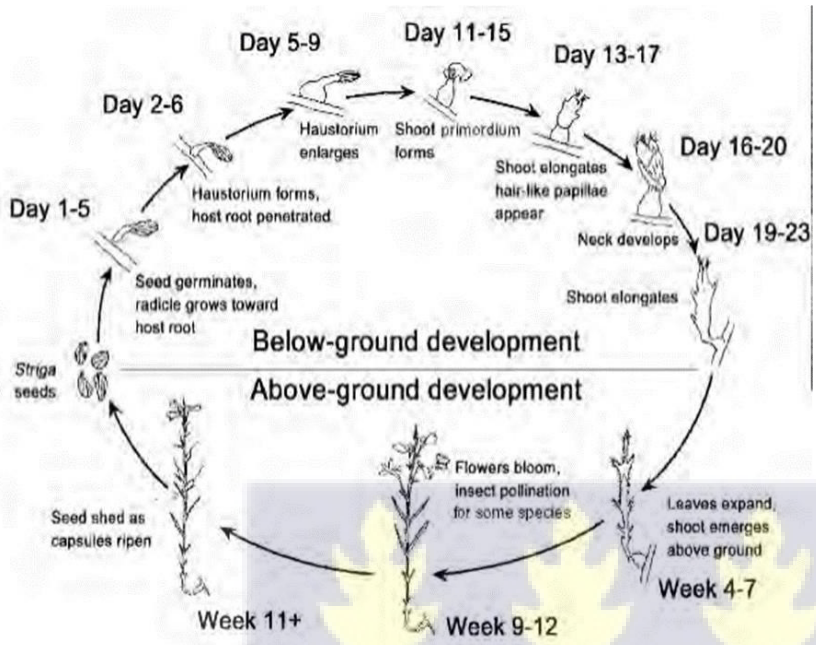


Fig. 2. 5 Striga life cycle (Berner et al., 1997)

2.6 *Striga* Control Strategies

Striga presents a formidable challenge to maize production necessitating the implementation of diverse control strategies. Several control strategies including cultural and agronomic practices, biological and chemical control options including host resistance have been proposed (Fig. 2.6; Jamil *et al.*, 2021). Several control strategies have been proposed to reduce the burden of *Striga* for farmers in SSA. These include crop rotation (Oswald and Ramson, 2001), intercropping (Khan *et al.*, 2002), push-pull technology (Khan *et al.*, 2008a), 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 in SSA. 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).

Cultural practices play a crucial role in managing *Striga* infestations, with crop rotation and intercropping being widely practiced. Alternating maize with non-host crops like *Desmodium* species, groundnut and soybean disrupts the weed's life cycle, while intercropping creates a physical barrier that inhibits *Striga* germination and attachment to maize roots (Khan *et al.*, 2008b). Additionally, timely planting before the *Striga* germination period can help minimize weed infestation levels, reducing the weed's impact on maize yields. Agronomic practices focused on enhancing maize growth and competitiveness against *Striga* contribute to effective weed management (Schulz *et al.*, 2003). Improving soil fertility through application of organic and inorganic fertilizer stimulates maize growth and suppresses *Striga* germination (Jamil *et al.*, 2014; Sarmiso, 2016). Moreover, implementing effective weed control measures, such as hand weeding or mechanical cultivation, suppresses *Striga* and reduces its competition with maize for resources.

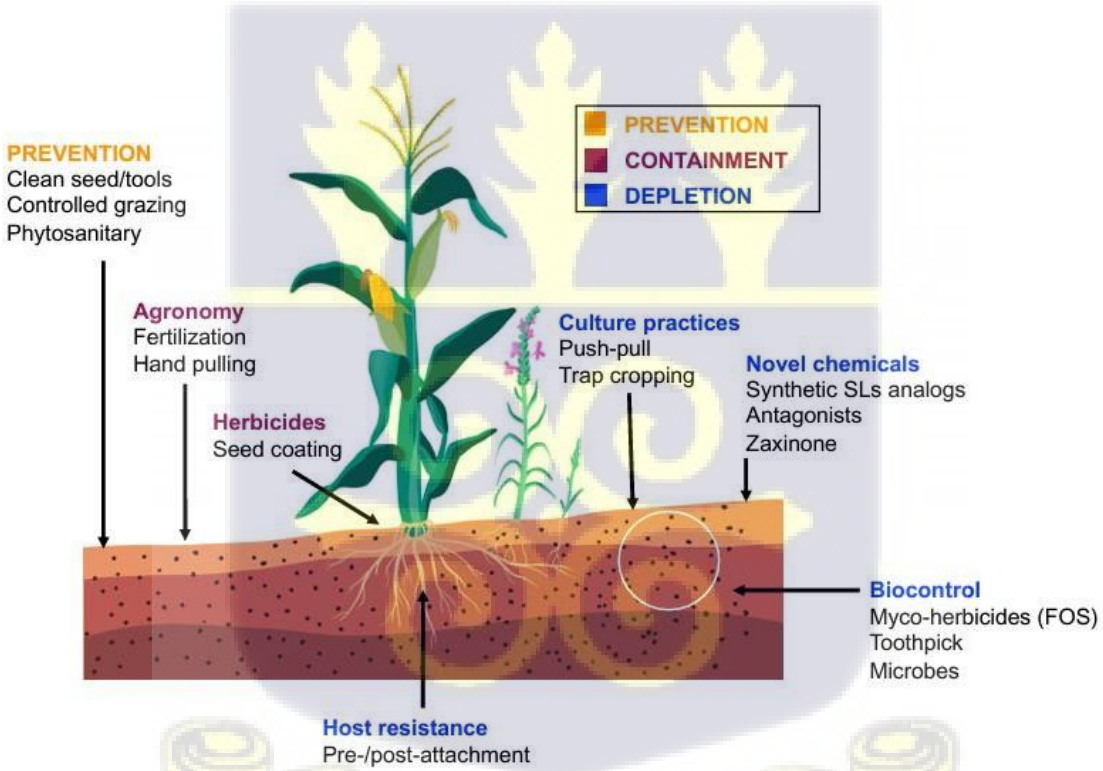


*Fig. 2. 6 Striga control Strategies (*Jamil *et al.*, 2021*)*

Biological control methods harness the power of natural enemies to suppress *Striga* populations. Microorganisms for instance *Fusarium oxysporum f.sp.Strigae*, AM fungi and *Pseudomonas*

fluorescens and *Pseudomonas putida* (Ahonsi *et al.,* 2002; Lendzemo *et al.,* 2007; Babalola and Odhiambo, 2008) in the soil exhibit antagonistic effects against *Striga*, either by inhibiting its germination or damaging its seeds and seedlings. Promoting the proliferation of these beneficial organisms through soil management practices can enhance *Striga* control. Allelopathic crops, such as sorghum with low germination stimulant (lgs) (Gobena *et al.*, 2017) or sunflower (Sun *et al.*, 2007), release compounds that inhibit *Striga* germination or growth, offering another avenue for biological control.

Chemical control is a common approach for managing *Striga* infestations. Selective herbicides containing active ingredients like imazapyr or mesotrione are used in controlling *Striga* when applied either pre-emergence or post-emergence. Seed treatments, involving the coating of maize seeds with systemic herbicides or biocontrol agents, provide early protection to young maize seedlings against *Striga* attachment and germination (Makumbi *et al., 2015*).

Despite the *Striga* control strategies (Jamil *et al.,* 2021; David *et al.,* 2022), they have been less efficient due to the prolificacy of the pest, large seed banks, ease of spread, seed longevity and favorable environmental conditions (moisture and temperature). Besides, several control strategies have had low rate of adoption, scalability, and amenability (Hearne, 2009). Improved soil nitrogen has been reported to suppress *Striga* germination by substantially diminishing the amount of strigolactones produced by the host plant roots but its impact on plant performance under *Striga* infestation is still variable coupled with constrained resources among the smallholder farmers (Pieterse, 1991; Mumera & Below, 1993; Cechin & Press, 1993; Igbinnosa *et al.,* 1996; Ayongwa *et al.,* 2006). Another example is the use of herbicide resistance (IR maize) that has been challenged by the fact that not all maize varieties are resistant to imidazolinines making it difficult to scale this technology (de Groote *et al.,* 2008; Hearne, 2009). Further, the use of non-host crops to elicit suicidal germination of *Striga* has been defied by the possibility of secondary seed dormancy in case of absence of the host plant after seed preconditioning (Spallek *et al.,* 2013). Other challenges include seasonal variability in *Striga* effects which encourage inconsistencies in the application of *Striga* control strategies (Berner *et al.,* 1996); vast genetic variation among *Striga* sub-populations which limits chances of complete host resistance (Rodenburg *et al.,* 2017). The situation is further augmented by lack of *Striga* resistant maize varieties in the region.

No single *Striga* control method has been successful in managing *Striga* related yield loses in maize. Host plant resistance is the most promising strategy. By adopting integrated pest management (IPM) principles including host plant resistance, farmers can effectively manage *Striga* infestations, minimize yield losses, and improve maize productivity in Kenya.

2.7. Breeding for *Striga* Resistance

Developing maize cultivars with inherent resistance to *Striga* attachment is a promising strategy for managing *Striga* infestations sustainably (Teka, 2014). Host plant resistance involves breeding maize cultivars that possess genetic effects conferring resistance to *Striga*, thereby reducing the weed's impact on crop productivity. Various techniques have been employed to identify and incorporate desirable traits into maize germplasm, with the aim of enhancing resistance mechanisms against *Striga*.

Resistance mechanisms in maize can target different stages of the *Striga* life cycle, including germination, attachment, and establishment (Rich & Ejeta, 2008). *Striga* resistance mechanisms in various crops has been classified as pre- or post-attachment (Mutinda *et al.,* 2018; Jamil *et al.,* 2011; Amusan *et al.,* 2008). Pre-attachment resistance has been associated with low production and/or the insensitivity of the pest receptors to *Striga* germination stimulants as well as low production of initiation factors leading to failed haustorial development (Mutinda *et al.,* 2018). Pre-attachment resistance has been reported for NERICA rice (Samejima *et al.,* 2016; Jamil *et al.,* 2012) and sorghum (Mallu *et al.,* 2021) among others. It has been reported that pre-attachment resistance largely depends on the quality and quantity of strigolactones produced by the host plants as well as the sensitivity of the pest receptor cells to the germination stimulants (Gwatidzo *et al.,* 2020; Mutinda *et al.,* 2018; Jamil *et al.,* 2011). For example, SRN39, a sorghum breeding line was found to produce a type of strigolactone called orobanchol which inhibits *Striga* germination (Gobena *et al.,* 2017). Post-attachment resistance on the other hand has been attributed to the presence of physiological and biochemical barriers that prevent successful xylem-xylem connections between the parasite and the host and upon attachment (Jamil *et al.,*2011; Mutinda *et al.,* 2018; Fishman & Shirasu, 2021). Additionally, post attachment resistance results from the host production of secondary metabolites that induce host immune responses leading to blockage of parasitic attachment. Post-attachment can also result from incompatibility in which the host fails

to support pest attachment and sometimes through avoidance or escape via root structures and early maturity (Rich & Ejeta, 2008). Pre- and post-attachment resistance to *Striga* in some crops such as sorghum providing more durable resistance to *Striga* have been reported (Gwatidzo *et al.*, 2020; Jamil *et al.*, 2011). The mechanisms of resistance indicate that various genes could be responsible in controlling *Striga* resistance in crop plants. This could be exploited in breeding programs for the improvement of crop resistance to *Striga*.

Identifying and incorporating these different types of resistance into maize breeding programs requires thorough screening of diverse germplasm to identify sources of resistance to *Striga*. This involves evaluating maize genotypes under controlled conditions and in *Striga*-infested fields to assess their performance and identify promising candidates for further breeding efforts. By leveraging genetic diversity, various breeding techniques and resistance mechanisms, identification and introgression of resistance genes into elite maize lines has been possible for accelerated breeding process. *Striga* breeding programs are, however, challenged by the complex genetic architecture of *Striga* resistance, limited sources of resistance and germplasm pool, low phenotyping capacity, slow breeding cycle and lack of molecular markers for the selection of *Striga* resistant maize lines.

2.8 Population improvement for *Striga* resistance

To overcome the challenges of narrow germplasm pool and lack of resistance sources, earlier research in *Striga* breeding made use of *Zea diploperennis*, a wild relative of maize to introgress *Striga* resistance genes to maize followed by population improvement (Menkir & Kling, 2007). Population improvement through recurrent selection aims at accumulating favorable alleles and enhancing genetic variability for subsequent selections (Hallauer & Darrah, 1985). Population improvement in *Striga* breeding has been applied to augment the genetic pool of maize for the development of varieties with improved resistance to *Striga* while maintaining or improving other desirable traits like yield, drought tolerance, and disease resistance (Badu-Apraku *et al.*, 2007a). This has been made possible through recurrent selection which is a cyclical process of selecting and intercrossing individuals with desirable traits to accumulate favorable alleles over successive generations (Menkir & Kling, 2007; Badu-Apraku *et al.*, 2007b; 2009; 2010; 2012). The new populations are then evaluated in *Striga*-infested environments to assess the level of resistance and

other agronomic traits. Evaluations result in re-selection of the best-performing individuals for further breeding cycles. This approach increases the frequency of resistance alleles in the population, progressively improving the overall resistance. For example, Menkir and Kling (2007) reports -5 and -9% gain per cycle for *Striga* damage rating and emerged *Striga* plants in a breeding population exposed to six cycles of selection.

2.9 Combining Ability Studies in Maize Breeding

For population improvement through recurrent selection, combining ability studies provide valuable insights into the genetic architecture of *Striga* inheritance thus facilitating the development of high-performing maize hybrids (Menkir *et al.,* 2007; Yallou *et al.,* 2009; Badu-Apraku *et al.,* 2011; Rwiza *et al.,* 2011). Combining ability studies contribute to better understanding of the genetic mechanisms underlying *Striga* resistance by dissecting the contributions of additive and non-additive genetic effects to the phenotypic expression of *Striga* resistance. The identification of gene effects controlling *Striga* resistance have enhanced the identification and selection of parental lines with favorable GCAs for *Striga* resistance (Zebire *et al.,* 2020). Further, combining ability studies have been resourceful in hybrid prediction, heterotic grouping and exploitation of heterosis (Akinwale *et al.,* 2014; Abimiku *et al.,* 2020; Adu *et al.,* 2022).

In maize breeding for *Striga* resistance, understanding the nature of gene action is critical for designing effective improvement strategies. Additive gene effects involve the cumulative action of individual alleles, where each contributes a predictable and heritable portion to the phenotype. These effects are particularly valuable for polygenic traits, such *Striga* resistance, because they can be fixed through selection and exploited in recurrent selection or population improvement programs. In contrast, non-additive gene effects arise from dominance and epistatic interactions between alleles, leading to hybrid vigor or heterosis. These effects are especially important for developing high-yielding and *Striga* resistant hybrids, as specific combinations of alleles can enhance resistance expression beyond the average parental performance. On the other hand, maternal effects, resulting from cytoplasmic inheritance or the influence of the female parent during seed development, also play a vital role affecting early seedling vigor, nutrient reserves, and physiological readiness to withstand parasite attachment. Genetic effects guide in the choice

of appropriate parents and breeding strategies. A balanced understanding of the genetic control of *Striga* resistance is therefore essential for sustainable development of stable, high-performing, and *Striga*-resistant maize varieties.

Different studies have resulted in variable reports of gene action in *Striga* resistance. Early studies by Yallou *et al*. (2009) used a diallel among inbred lines carrying genes from Zea diploperennis, reported that additive gene effects largely control *Striga* resistance. Using line × tester designs Zebire *et al*. (2020) evaluated testers differing in resistance levels and demonstrated that resistant and tolerant testers had positive GCA for yield and negative GCA for *Striga* damage, confirming that additive genetic variance plays a dominant role in resistance inheritance. However, significant SCA effects were also detected for yield and damage ratings, showing that non-additive gene effects contribute to hybrid performance and should be exploited through hybrid breeding. In more recent studies, Okunlola *et al*. (2023) and Makinde *et al*. (2023) analyzed extra-early and provitamin A maize inbreds under *Striga* and low-nitrogen stress, both studies revealed the importance of additive × environment interactions, where additive effects predominated under optimal conditions, but non-additive effects were more influential under *Striga* infestation. These results highlight the need for environment-specific selection and evaluation across multiple stress conditions. Similarly, Adu *et al*. (2022) and Sangaré *et al*. (2018) reported that both GCA and SCA effects significantly influenced grain yield and *Striga*-related traits, recommending the use of heterotic grouping and multi-trait combining ability for efficient hybrid development. A few studies have also noted maternal effects and reciprocal differences in *Striga* resistance expression (Abu *et al*., 2021), implying a role for cytoplasmic and seed-developmental factors in early seedling vigor and host tolerance. Studying maternal effects in diallel or reciprocal crosses enables breeders to identify superior female parents, select the optimal crossing direction, and improve the efficiency of hybrid seed production. Ultimately, understanding maternal influence enhances the predictability, stability, and effectiveness of breeding strategies aimed at developing *Striga*-resistant maize varieties.

The varied reports have been attributed to relative contribution of additive, dominance, and epistatic effects depends on the genetic material, environment, trait complexity, stage of selection, and analytical methods used (Falconer & Mackay, 1996; Hallauer *et al*., 2010; Acquaah, 2012).

Yallou *et al*. (2009) for example demonstrated variability in genetic control of *Striga* resistance traits due to environment and parental combinations. Badu-Apraku *et al*. (2011) on the other hand emphasized that gene action and combining ability can differ across environments, reflecting genotype × environment interactions. Combining ability studies facilitate the selection of superior parental lines, prediction of hybrid performance, and exploitation of heterosis. Maternal influences further refine crossing direction and seed quality, making combining ability studies a cornerstone of sustainable *Striga* resistance breeding in maize.

2.10 Linkage analysis (QTL mapping) and Association Mapping

Quantitative trait loci (QTL) mapping (Amusan *et al.,* 2010; Badu-Apraku *et al.,* 2020a, c; 2023) and association mapping (Adewale *et al.,* 2020; Stanley *et al.,* 2021; Gowda *et al.,* 2021; Okunlola *et al.,* 2022) are two approaches used in genetic studies to identify genomic regions associated with complex traits such as *Striga* resistance in maize. While both methods are beneficial, association mapping offers the advantage of high mapping resolution, greater allelic diversity, reduced population size requirements, enhanced population structure control and genome-wide coverage over QTL mapping in *Striga* breeding programs (Singh & Singh, 2015). Association mapping identifies marker-trait associations that can directly be utilized in MAS to expedite the development of *Striga*-resistant maize varieties. It allows for the identification of smaller genomic regions or even individual genes underlying resistance traits, enhancing precision in marker-assisted selection.

The application of molecular breeding technologies including QTL mapping (Amusan, 2010; Badu-Apraku *et al.,* 2020a, c; 2023) and GWAS (Adewale *et al.,* 2020; Stanley *et al.,* 2021; Gowda *et al.,* 2021; Okunlola *et al.,* 2022) have yielded significant results in relation to maize resistance to *Striga*. Earlier on, Amusan (2010) mapped two QTLs on chromosome 6 of maize which explained 55% of the phenotypic variation in relation to *Striga* tolerance in a maize inbred line. Badu-Apraku *et al.* (2020 a, b) used linkage analysis in the identification of QTLs controlling *Striga* resistance and grain yield in yellow and white tropical maize inbred lines. In one study, using 194 F_2 derived F_3 families as a mapping population, QTLs mapped for resistance to *Striga* in yellow maize inbred lines were found to explain 14.2% and 3.2% phenotypic variation in *Striga* damage and emerged *Striga* plants respectively (Badu-Apraku *et al.,* 2020a). A different study

utilized 198 BC_1S_1 families and identified seven QTLs associated with *Striga* damage in white inbred lines (Badu-Apraku *et al.*, 2020c). Adewale *et al.* (2020) performed GWAS for agronomic traits under *Striga* infestation. The study findings revealed 24 SNPs associated with yield and yield parameters including ears per plant and ear aspect of maize under *Striga* infestation. In the same study, they identified a locus in chromosome 9 (S9_154, 978, 426) in close proximity to ZmCCD1 gene involved in strigolactone reduction in maize roots. In a more recent study Gowda *et al.* (2021) identified 57 SNPs associated with grain yield and nine candidate genes two of which were closely linked with the emerged *Striga* plants at 10 and 12 weeks after planting. A total of 32 genes were involved in plant defense during *Striga* stress (Gowda *et al.*, 2021).

Extensive application of linkage and genome-wide association analyses in *Striga* breeding programs have been carried out at IITA. While several QTLs that confer resistance to *Striga* parameters and yield related traits have been identified, molecular markers are yet to be identified and deployed for MAS in *Striga* breeding programs. The availability of genomic technologies enables the deployment of marker-assisted breeding strategies for selecting and stacking favorable alleles associated with *Striga* resistance, accelerating genetic gains in breeding programs.

2.11 Genomic Prediction in *Striga* Breeding Programs

Genomic prediction, also known as genomic selection, is a powerful tool in modern plant breeding that utilizes genomic information to predict the genetic value of individuals for complex traits such as *Striga* resistance in maize (Gowda *et al.*, 2021). While genomic prediction is paramount for enhanced selection accuracy, early selection, exploitation of genetic variability, adoption of genomic-based breeding strategies, accelerated breeding progress, and adaptive breeding in dynamic environments, limited application has been reported in *Striga* breeding programs (Badu-Apraku *et al.*, 2019; Gowda *et al.*,2021).

To overcome the phenotyping challenges experienced in *Striga* resistance breeding, genomic prediction/ or selection is the most promising approach. Screening for *Striga* resistance requires artificial inoculation which limits the number of screening sites since this endemic pest cannot be introduced to new sites. Genomic prediction therefore allows for phenotyping of smaller numbers of inbred lines in hybrid combinations (training population). This phenotypic information coupled

with genotypic information of the training population is useful in predicting the performance on genotyped but untested lines (testing population) thus managing not only challenges on phenotyping capacity but also reducing phenotyping costs. Genomic prediction accelerates breeding progress and shortens the time required to develop *Striga*-resistant maize varieties (Crossa *et al.*, 2017). Genomic prediction enables the early selection of superior genotypes based on their genomic estimated breeding values (GEBVs) rather than waiting for multiple years of phenotypic evaluation. This approach has been successfully applied in wheat, rice, barley and maize among other crops. In wheat, the integration of genomic prediction with high-throughput phenotyping at CIMMYT has resulted in up to a 30% increase in genetic gain per cycle compared with conventional methods (Juliana *et al*., 2018). Similarly, in rice and barley, genomic prediction has been used to accelerate recurrent selection schemes, achieving more rapid accumulation of favorable alleles (Spindel *et al*., 2015; Poland *et al*., 2012). In maize, genomic selection has led to the identification of high-yielding hybrids in early generations, reducing the time per breeding cycle from about 8–10 years to 5–6 years (Beyene *et al*., 2015; Technow *et al*., 2021). Predicting performance before field testing, therefore, enable faster decision-making, more efficient use of resources, and sustained genetic gain per unit time.

Genomic selection, however, depends on both the population and the environment. High predictive accuracy is achieved when the training population is large, genetically diverse, and closely related to the breeding population, ensuring consistent linkage disequilibrium between markers and QTLs (Habier *et al*., 2007: Heffner *et al*., 2009; Crossa *et al*.,2017). Population characteristics such as genetic structure, relatedness, and heritability of the target trait strongly influence the accuracy of genomic predictions. Daetwyler *et al*. (2008) further quantifies how prediction accuracy depends on the number of markers, training population size, and heritability. Environmental factors and genotype × environment interactions, can alter marker effects and reduce transferability of prediction models across environments (Crossa *et al*., 2017). Therefore, a training population that captures both genetic and environmental diversity, combined with accurate phenotyping, adequate marker density, and suitable statistical models, is crucial for achieving reliable and robust genomic selection outcomes (Heffner *et al*., 2009; Crossa *et al*., 2017; Jannink *et al*., 2010).

CHAPTER THREE

COMBINING ABILITY FOR RESISTANCE TO *STRIGA HERMONTHICA* IN MID-ALTITUDE ADAPTED TROPICAL MAIZE

3.1 Introduction

Maize, a cereal of great economic importance and a cornerstone of global food security, is a versatile crop used for food, animal feed, and industrial purposes (Erenstein *et al.,* 2022; Shiferaw *et al.,* 2011). However, maize production among smallholder farm systems is greatly challenged by abiotic stresses such as drought and low soil nitrogen affect maize production in SSA (Makumbi *et al.,* 2018). Of critical importance among the biotic stresses is *Striga*, a parasitic weed majorly affecting food crops in the grass family including maize, sorghum, rice, sugarcane and millet and is found to thrive well under low soil nitrogen (Makumbi *et al.,* 2015; Menkir *et al.,* 2012).

Striga hermonthica (Del.) Benth. adversely affects maize production in the African Savannas leading to up-to 100% yield losses (Stanley *et al.,* 2021). *Striga* is entirely host dependent for growth and survival especially at pre-emergence and early development stages, estimated to be up-to 2 months (Okunlola *et al.,* 2022). It is at this stage that the pest causes extensive damage to the host by depriving it of water and photoassimilates thus ravaging the hosts' growth and development. This leads to reduced maize biomass resulting from *Striga* effects such as impaired photosynthesis due to chlorosis, stunted growth, reduced ear height and often a total collapse of the host (Akaogu *et al.,* 2020). Although several control strategies have been developed and deployed, *Striga* life-cycle that is synchronized with that of the host, its photosynthetic capacity, seed bank and seed longevity, ease of dispersion and spread pose a great challenge (Ejeta, 2007a; Atera, 2012). Integrated pest management combining two or more approaches including cultural, chemical and biological practices are quite effective in managing *Striga* effects. Host resistance to *Striga* coupled with these approaches could be more promising in enhancing maize productivity in *Striga* prone areas of the Savannas (Rich and Ejeta, 2008).

The initial stages of research at the West Africa by the IITA involved population improvement through recurrent selection procedures for the accumulation of desirable alleles (Menkir & Kling, 2007; Badu-Apraku *et al.,* 2007a; 2008; 2009; 2010; 2013; Menkir and Meseka, 2019; Badu-Apraku *et al*. 2020a). In these studies, recurrent selection was preceded by introgression of *Striga* resistance genes from the wild relative of maize, *Zea diploperennis*, to IITA elite lines. Further

research sought to understand the genetic architecture of *Striga* resistance and its inheritance. This was made possible through the establishment of combining abilities of both lines and hybrids following hybridization procedures between donor and elite lines (Gethi *et al.*, 2004; Menkir *et al.*, 2007; Kim *et al.*, 1994; Yallou *et al.*, 2009; Badu-Apraku *et al.*, 2011). IITA has, therefore, made significant progress in *Striga* resistance breeding strategies for which the impact is largely applicable to the West Africa. CIMMYT identified a critical need in East and Southern Africa, where *Striga* remains a serious challenge. Through the introgression of *Striga* resistance genes from the IITA donor lines to the CIMMYT germplasm, a breeding strategy was designed. This led to the development of a huge number of inbred lines with *Striga* resistance background.

To further streamline the breeding strategy, it is important to understand the genetic control of *Striga* resistance in this germplasm, a critical step in the selection of parental lines for hybrid development. This is achieved by estimating gene effects controlling the inheritance of *Striga* (Sprague & Tatum, 1942). Combining ability studies of maize under *Striga* infested conditions have yielded variable results. For example, Akaogu *et al*. (2020) reported that GCA accounted for 65% of variability in grain yield and >60% of *Striga*-related traits, pointing to strong additive control. Besides, Adu *et al*. (2022) reported that SCA contributed more to most traits than GCA, suggesting the importance of non-additive effects while Makinde *et al*. (2023) found both GCA and SCA to be important emphasizing that maternal GCA effects were dominant for many traits in extra early pro-vitamin A maize. Additive gene effects contribute to improved selection response while non-additive effects contribute to resistance heterosis and can be harnessed in hybrid breeding. The determination of gene effects controlling *Striga* can enable breeders to prioritize crosses that are likely to produce the most resistant and high-yielding progeny. The application of combining ability analysis in *Striga* resistance breeding programs is further justified by the need to enhance the genetic base of maize germplasm. Narrow genetic diversity in breeding materials can limit the progress of breeding programs and reduce the adaptability of new varieties to changing environmental conditions (Harlan, 1975; Cooper *et al.*, 2001; Rauf *et al.*, 2010). The objectives of this study were to: i) determine gene effects for grain yield, agronomic traits and *Striga* resistance under optimal and artificial *Striga* infested conditions; ii) identify parental lines with suitable agronomic traits and *Striga* resistance and hybrids that show heterosis; and iii) investigate the importance of maternal effects in the inheritance of *Striga*.

3.2 Materials and methods

3.2.1 Genetic material

This study utilized 12 inbred lines; eight (CIMMYT, Kenya), three (IITA, Nigeria) and one from Mexico. The eight CIMMYT Kenya Lines (CKLs) were developed by CIMMYT Kenya under the Global Maize Program (GMP) while the IITA lines were developed in Nigeria. The details of the inbred lines used in the diallel are provided in Table 3.1.

Table 3. 1 Names, origin and the characteristics of the inbreds used in the diallel breeding nursery at Kiboko in 2021

Entry	Name	Origin	Background/characteristics
1	TZISTR1163	IITA-Nigeria	Resistant to *Striga* based on field tests in Nigeria
2	TZMI1240	IITA-Nigeria	Resistant to *Striga* based on field tests in Nigeria
3	TEISTR1159	IITA-Nigeria	Resistant to *Striga* based on field tests in Nigeria
4	CKL17933	CIMMYT-Kenya	Tolerant to *Striga* based on field tests in Kenya; Tolerant to Turcicum leaf blight
5	CKL17535	CIMMYT-Kenya	Resistant to *Striga* based on field tests in Kenya
6	CKL 171145	CIMMYT-Kenya	Resistant to *Striga* based on field tests in Kenya; Resistant to Turcicum leaf blight
7	CKL 171342	CIMMYT-Kenya	Resistant to *Striga* based on field tests in Kenya; Tolerant to Turcicum leaf blight
8	CKL 172791	CIMMYT-Kenya	Tolerant to *Striga* based on field tests in Kenya; Tolerant to Turcicum leaf blight
9	CKL 17495	CIMMYT-Kenya	Tolerant to *Striga* based on field tests in Kenya
10	CKL 17611	CIMMYT-Kenya	Tolerant to *Striga* based on field tests in Kenya
11	CML312	Mexico	Susceptible to *Striga*
12	CKL14546	CIMMYT-Kenya	Susceptible; Tolerant to Turcicum leaf blight

CKL, CIMMYT Kenya line

The CML line is a CIMMYT maize line that has been released for use by the maize breeding pipelines.

3.2.2 Nursery and Pollination

The twelve inbred lines were crossed following Griffing's method 3 at the Kenya Agricultural and Livestock Research Organization (KALRO) Kiboko, (2°15'S, 37°75' E; 975 masl and 530mm of rainfall), in the year 2021. The parental lines were alternated in rows to allow for efficient

pollination. The lines were then crossed in all possible combinations (Each parental line used both as a male and a female) to generate single and reciprocal crosses. During nursery establishment, the lines were sown in single 4 meter rows, spaced at 0.75 m × 0.20 m between and within rows. Di-ammonium phosphate fertilizer (DAP, 18:46:0) was applied during planting and calcium ammonium nitrate (CAN, 26%) fertilizer was used for topdressing a fortnight after planting at the rate of 125 kg ha^{-1}. Agronomic practices including weeding and drip irrigation were done. At flowering, shoots were covered using shoot bags as soon as they emerged to control pollination. Tassels were also covered using tassel bags which served to collect pollen. Pollen was collected from all plants in a plot and bulked for the pollination of the female parent. A total of 132 hybrids resulted from this nursery and were evaluated in 12 environments in 2022 and 2023.

3.2.3 Experimental sites and trial evaluations

The hybrids were evaluated at Kibos, Alupe, Kakamega and Embu (Table 3.2). Generally, the 132 hybrids together with 4 checks were phenotyped under *Striga* infested conditions at Kibos and Alupe during the long rain seasons of 2022 and 2023; under optimal conditions at Kibos and Alupe in 2022 and 2023 and Kakamega and Embu in 2023; and under managed drought at Kiboko in 2022and 2023. The parental lines were evaluated for *per se* performance under artificial *Striga* infestion and optimal conditions at Kibos and Alupe and under managed drought at Kiboko in 2022 and 2023. For hybrid evaluation, two genetic gain checks developed at CIMMYT (TZSTR184/CKL17622//CKL192608 and TZSTR184/CKL17633//CKL192608) and two commercial check hybrids (UH5354 and DK777) were included in the evaluation. The pedigrees of the 136 hybrids are shown in Appendix Table 1. The trial was laid down in 34 x 4 (34 incomplete blocks with 4 plots each) alpha lattice design with two replicates. Each plot composed of a single 4m row. The plants were spaced at 25 cm within rows and 75 cm between rows. Two separate trials were set at Kibos and Alupe; *Striga* infested and optimum trials while only optimal trials were set up at Embu and Kakamega. The trial locations and trial management are shown in Table 3.2.

Table 3. 2 Experimental sites used in the evaluation of the hybrids under artificial *Striga* infestation and optimal conditions in 2022 and 2023.

Trial location	Management	Year	Latitude	Longitude	Altitude (m asl)	Mean annual rainfall (mm)
Kibos	Artificial *Striga* infestation and optimal conditions	2022,2023	0º2'S	34º48'E	1193	865
Alupe	Artificial *Striga* infestation and optimal conditions	2022,2023	0º30'N	34º7'E	1250	1400
Kakamega	Optimal conditions	2023	0°16'N	34°49'E	1585	1916
Embu	Optimal conditions	2023	0°30'S	37°27'E	1504	1200

For artificial *Striga* infested trials, *Striga* inoculum was supplied in each planting hole using a calibrated spoon to ensure uniform exposure of the plants to *Striga*. *Striga* inoculum was prepared by mixing 10 g of *Striga* seeds with 5 kg of sand. The DAP and CAN fertilizers were applied at half the normal rate (30 kg ha^{-1}) during planting and topdressing, respectively. This was to support plant establishment without suppressing *Striga* germination. Hand weeding was employed to eradicate all other weeds except *Striga* plants. For the optimal trials DAP and CAN fertilizers were used at the rate of 60 kg ha^{-1} during planting and top dressing, respectively, to enhance optimal performance of the crop. All agronomic practices were carried out as required.

Fig 3. 1 Preparation and supply of Striga inoculum to the experimental units in the field, Kibos 2022

3.2.4 Data collection

Data was collected from all the plants in an experimental unit excluding the end plants. Data was collected for all the grain yield, agronomic traits and *Striga* resistance parameters (Table 3.3).

Table 3. 3 Grain yield, agronomic traits and *Striga* resistance parameters collected in the field

Parameter	**Explanation**
Days to Anthesis (AD)	Number of days from planting to the day when 50% the plants in a plot have shed pollen
Ear height	The height of a plant in centimeters from the base of the plant to the point of the upper cob taken using a ruler calibrated in cm.
Plant height	Height from the ground to the point of flag leaf measured with a ruler calibrated in cm.
Number of emerged *Striga* plants (STR)	The total number of *Striga* plants 15 cm away from either side of each experimental unit. The number of emerged *Striga* plants were counted and recorded at 8, 10 and 12 weeks after planting (WAP)
Striga damage rating (SDR)	Recoded at 10 and 12WAP using a 1–9 rating scale (Kim, 1991; Kim *et al.*, 1994). Where: 1 = a healthy plant with no visible symptoms of *Striga* damage (resistant) and 9 = highly susceptible to *Striga* with totally scorched leaves, absent ears and untimely death of the host plant (Fig. 3.2)
Turcicum leaf blight (TLB)	Recoded on 1–9 rating scale (Kim, 1991; Kim *et al.*,1994).
AUSNPC (Area under *Striga* number progress curve)	AUSNPC was computed based on the number of emerged *Striga* plants at 8, 10 and 12WAP following the formula for computing area under disease progress curve (AUDPC) as suggested by Shaner and Finney (1977), $\text{AUSNPC} = \sum_{i=1}^{n} \left(\frac{y_i + y_{i-1}}{2}\right)(t_i - t_{i-1})$, Where: y_i = the number of *Striga* plants at the ith observation, t_i = the time point in days after planting at the *i*th observation and n = the total number of observations.
Grain yield (based field)	$\text{Grain yield (t/ha)} = \frac{Fresh\ ear\ weight\ (Kg/plot) \times 10 \times (100 - MC) \times 0.8)}{((100 - 12.5) \times Plot\ area)}$ Assuming 80% Shelling percentage and 12.5 adjusted grain moisture (ASTM, 2001; Vivek *et al.*, 2001).

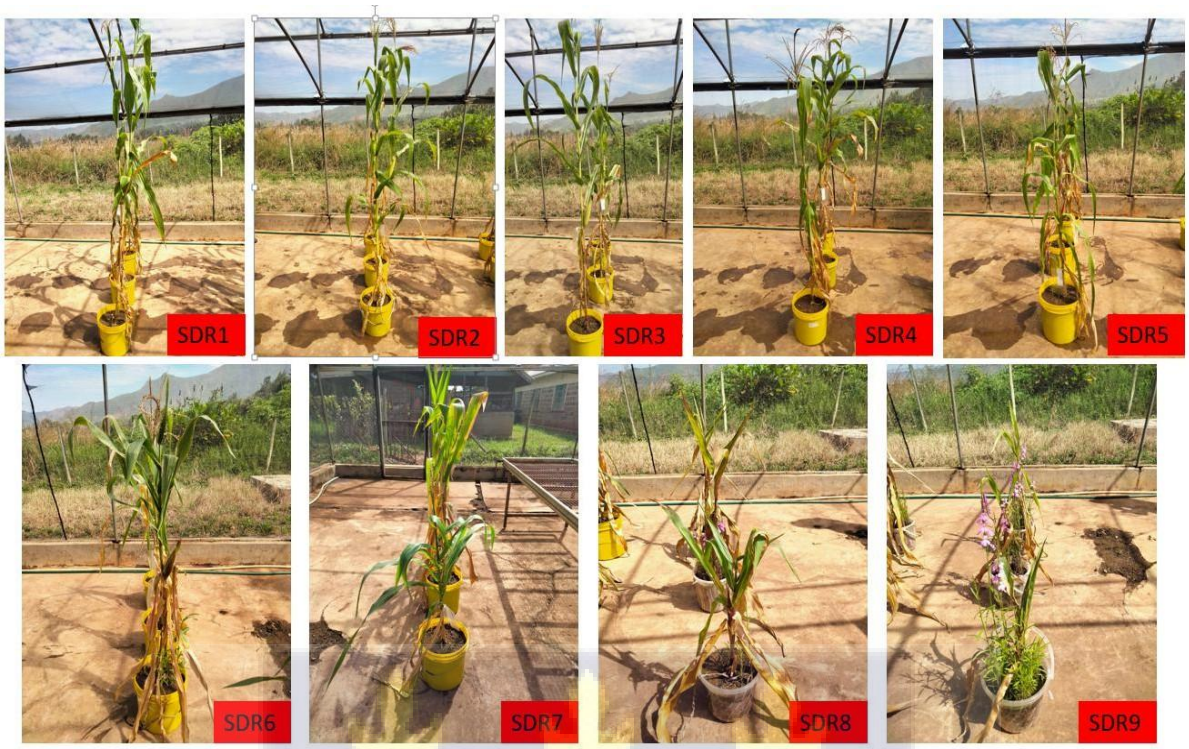


Fig 3. 2 Striga damage rating, scale 1−9, Kibos 2023

3.2.5 Statistical Analysis

3.2.5.1 Phenotypic analysis

AsReml-R package in R (v. 4.2) was used for phenotypic analysis for all traits (Butler *et al.*, 2009). For the computation of BLUEs, the genotypes were considered as fixed effects with all other parameters as fixed. The best linear unbiased predictions (BLUPs) together with the components of variance were also computed by considering all the factors as random in the linear mixed model. Multi-environment analysis was carried out as follows:

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

Where:

y_{ijkl} = the response variable of the *i*th genotype in *j*th environment, *k*th replicate and lth block;

μ = an intercept

G_i = the effect of the *i*th genotype

E_j = the effect of the *j*th environment

$R_k(E_j)$ = the effect of the *k*th replicate in the *j*th environment

$B_l(ER)_{jk}$ = the effect of the *l*th block within the *k*th replicate at the *j*th environment

GE_{ij} = the effect of the interaction between the *i*th genotype and the *j*th environment

ε_{ijkl} =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 and independently distributed (NID) with mean zero and homoscedastic variance σ^2_{ε}.

Broad sense heritability was estimated for combined environments (Hallauer *et al.*, 2010):

$$H^2 = \frac{\sigma^2_G}{\left[\sigma^2_G + \frac{\sigma^2_{GE}}{E} + \frac{\sigma^2_{\varepsilon}}{ER}\right]}$$

where:

H^2 = the broad sense heritability for combined environments,

σ^2_G = the genotypic variance,

σ^2_{GE} = the variance of the interaction between the genotype and the environment,

E = the number of environments,

R = the number of replicates,

σ^2_{ε} = the error variance (experimental error).

3.2.5.2 Combining ability

This study utilized Griffing (1956) diallel method III in which single and reciprocal crosses were included excluding the parental lines. Both general and specific combing ability were computed for the 132 test hybrids following Griffing (1956) method III and model 1. In this analysis, the parental lines were considered as fixed effects since prior information of the lines was available and they were not selected from random populations. In order to estimate the GCA and SCA gene effects, the following formula was adopted:

$$y_{ijk} = \mu + g_i + g_j + s_{ij} + r_{ij} + b_k + \varepsilon_{ijk}$$

where:

y_{ijk}= the response variable

μ= the overall mean

g_i =the GCA of the *i*th parent

g_j =the GCA of the *j*th parent

s_{ij} = the SCA of the cross between *i*th and *j*th parental lines

r_{ij} = the reciprocal effects of the cross between *i*th and *j*th parental lines

b_k =the replication effects

ε_{ijk} =the residual effect

The sources of variation in this analysis include GCA, SCA and reciprocal effects. The reciprocal effects were further partitioned into maternal and non-maternal effects

$$r_{ij} = m_i + m_j + nm_{ij}$$

where:

r_{ij} = the reciprocal effect of the cross between *i*th and *j*th parental lines

m_i= the maternal effect of the *i*th parental line

m_j= the maternal effect of the *j*th parental line

nm_{ij} = the nonmaternal effect of the cross between *i*th and *j*th parental lines

In order to determine genetic effects controlling grain yield, agronomic traits and *Striga* resistance parameters, Baker's ratio was used to determine the relative importance of GCAs and SCAs across all traits (Baker, 1978):

$$Baker'sratio = \frac{2\sigma^2_{GCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA}}$$

3.3 Results

3.3.1 Inbred line performance

A total of 12 inbred lines and 136 hybrids were phenotyped across 4 trial locations under artificial *Striga* infestation and optimal conditions. The inbred lines were evaluated for *per se* performance at Kibos and Alupe in the year 2022 and 2023 (Table 3.4). Under optimal conditions, the grain yield of the inbred lines was 0.7–2.2 t ha^{-1} with a mean of 1.2 t ha^{-1}. Three inbred lines (TZISTR1163, DL17933 and DL17611) had high yield under optimum and *Striga* infested

conditions. Generally, the best yielding inbred lines under optimal conditions were not the best under *Striga* infestation. The inbred lines had a plant height (PH) of 99.4–166.6 cm with 48.5–93.6 cm ear heights (EH). Turcicum leaf blight (TLB) ranged from 2.5–3.7. Under *Striga* infestation, grain yield was 0.3–2.2 t ha^{-1} with a mean of 0.9 t ha^{-1} while emerged number *Striga* of ranged from 7−94 for emerged number of *Striga* plants at 10−12WAP. *Striga* damage rating was 1.2–7.0 while the AUSNPC was 11–71.7 cm^2. In general, the inbred lines varied significantly under both management schemes and genetic variance was higher than the G×E variance. G×E variance was significant for all traits except EH. Broad sense heritability was high (0.73–0.97) for all traits across the management schemes. The aerial view of the inbred lines evaluated under *Striga* infestation is shown in Fig. 3.3.

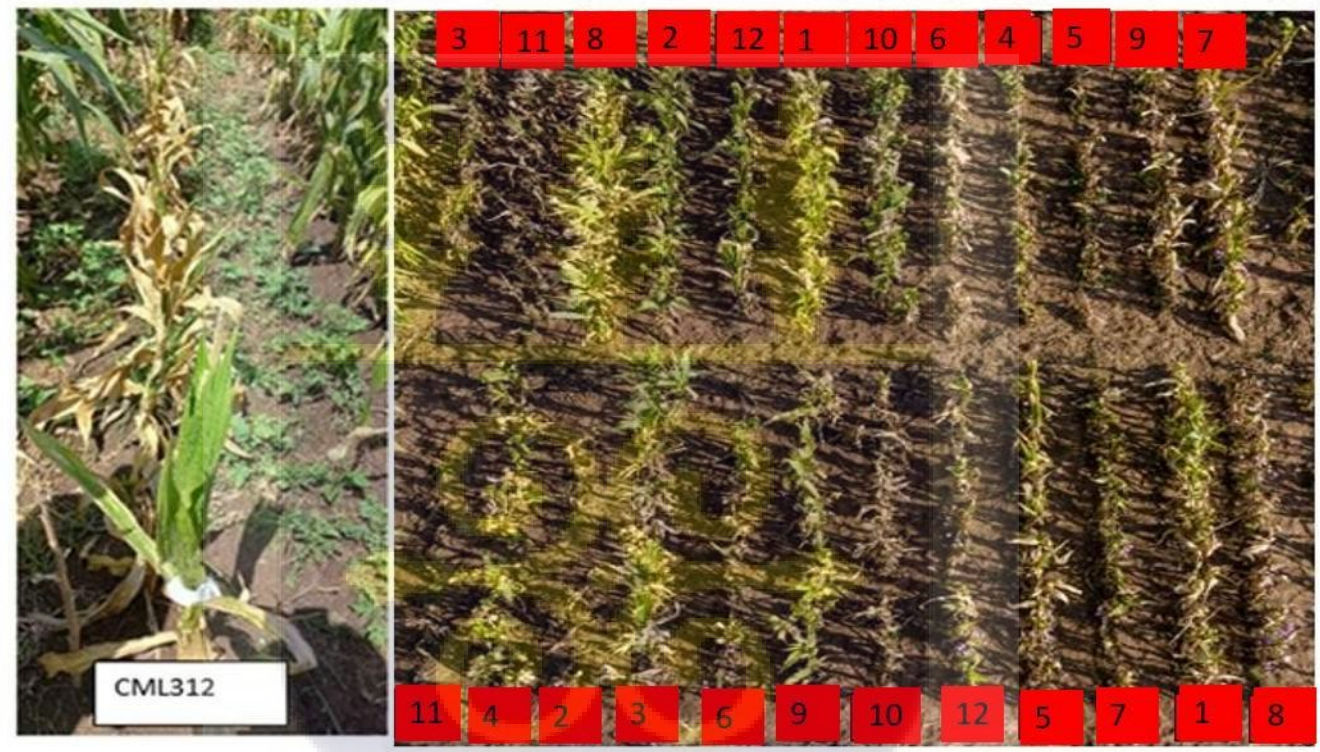


Fig 3. 3 Aerial view of the parental lines at Kibos, 2022

Table 3. 4 *Per se* performance of the parental lines, variance component estimates, heritability and summary statistics for the 12 parental lines evaluated in several locations in 2022 and 2023

Genotype	Optimal conditions				Artificial *Striga* infested conditions				
	GY	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR	AUSNPC
TZISTR1163	1.6	130.8	68.7	2.5	2.0	12	18	3.0	16.9
TZMI1240	1.0	112.9	66.4	2.3	0.8	22	29	6.7	27.5
TEISTR1159	1.0	166.6	93.6	2.9	0.5	43	94	5.2	70.5
DL17933	1.1	139.5	78.6	3.4	0.9	7	11	3.8	11.0
DL17535	1.0	158.8	85.7	3.1	1.3	23	39	2.1	32.8
DL171145	0.9	136.6	82.8	2.7	0.6	19	40	3.7	31.4
DL171342	0.9	106.6	51.4	3.6	0.8	10	13	4.6	13.6
DL172791	0.7	99.4	48.5	3.7	0.3	31	38	7.0	36.4
DL17495	0.8	142.4	67.8	3.6	0.5	12	24	3.3	19.9
DL17611	1.6	178.1	87.1	3.1	2.2	18	24	1.2	23.1
CML312	1.2	164.6	62.6	3.5	0.6	58	83	6.7	72.7
DL14546	2.2	136.1	77.2	2.6	0.8	54	69	6.0	63.8
$\hat{\sigma}_G^2$	0.3**	633.0***	211.9***	0.3***	0.4***	358.6***	879.7***	3.8***	568.0***
$\hat{\sigma}_{GE}^2$	0.3***	55.5**	0.01	0.2*	0.1**	176.3***	391.9***	0.2*	278.2*
$\hat{\sigma}_\varepsilon^2$	0.2	109.5	136.7	0.3	0.1	188.5	386.7	0.5	237.7
Mean	1.2	139.4	72.5	3.1	0.9	26	40	4.4	35.0
LSD	0.8	13.8	10.4	0.7	0.7	21.7	32.2	1.1	26.4
CV	37.0	7.5	16.1	18.7	39.8	53.2	49.0	15.5	44.1
H^2	0.73	0.97	0.94	0.81	0.90	0.84	0.86	0.97	0.85

***, **, ***: Significant at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively.**

GY, grain yield; PH, plant height; EH, ear height; TLB, Turcicum leaf blight; STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR, *Striga* damage rating at 12 WAP; AUSNPC, Area under *Striga* number progress curve; H^2, broad-sense heritability; $\hat{\sigma}_G^2$, genotypic variance; $\hat{\sigma}_{GE}^2$, genotype by environmental variance; $\hat{\sigma}_\varepsilon^2$, error variance.

The phenotypic data of the 132 test hybrids and four (4) checks are shown in Appendix (Table 2). The yield of the test hybrids ranged from 3.0–7.6 t ha^{-1} and 1.3–4.1 t ha^{-1} with a mean of 5.3 t ha-1 and 2.6 t ha^{-1} under optimal and *Striga* infested conditions respectively. The hybrids generally flowered earlier (60–69 days) under *Striga* infested conditions than under optimal conditions (61−72 days). Under optimal conditions, the hybrids had an average of 238.0 cm and 135.3 cm plant and ear heights, respectively. Under *Striga* infestation, the number of emerged *Striga* plants

ranged from 30–214 while *Striga* damage rating ranged from 1.3–6.6 with a mean of 3.0 (SDR1) and 3.9 (SDR2). On average, the area under *Striga* number progress curve was 214.0 cm^2.

The best yielding, the least yielding and the check hybrids were compared (Table 3.6). One hybrid (CML312 × DL14546) yielded better than the best yielding check while 37 test hybrids yielded better than the average yield of the checks under optimal conditions. On the other hand, 15 hybrids had 32.1% yield advantage over the mean of the checks under *Striga* infested conditions. Two hybrids, TZISTR1163/DL17933 and DL17933/DL17611 had a mean yield of 4 t ha^{-1} under *Striga* infestation. Additionally, the test hybrids flowered earlier than the checks under optimal conditions but flowered later under *Striga* infested conditions. Under *Striga* conditions, the best yielding hybrids yielded more than the checks while the least yielding hybrids had worse yields than the checks. The best yielding hybrids sustained few number of emerged *Striga* plants (32–147) compared to the least yielding hybrids (91–168) and the checks (55–214). The least yielding hybrids had high *Striga* damage rating as well as the checks. The best yielding hybrids under optimal conditions were not necessarily the best yielding under *Striga* infested condition. The best yielding hybrid under *Striga* infested conditions was entry 5 and 71 which are TZISTR1163/DL17933 and DL17933/DL17611, respectively (Appendix Table 2; Table 3.4)

In general, the hybrids varied significantly ($P<0.001$) across all traits under optimal and artificial *Striga* infested conditions (Table 3.5). The genetic variance was higher than the G×E variance in all traits except for TLB under optimal conditions. The hybrids showed high heritability under optimal (69–95%) and under *Striga* infested conditions (81–92%). Fig. 3.4 show variable response of the check and the test hybrids in the field.

Fig 3. 4 The reaction of the test hybrids and a check (DK777, also used as a guard row) at Kibos, 2022

Table 3. 5 A comparison between the best and the least yielding hybrids and the checks under optimal and *Striga* infested conditions

	Entry	Optimal conditions					Entry	Artificial *Striga* infested conditions						
		GY	AD	PH	EH	TLB		GY	AD	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
Best yielding	131	7.6	65	229.6	133.9	2.1	5	4.1	65	32	52	1.7	2.5	94.2
	19	7.2	65	248.2	133.9	1.9	71	4.0	66	42	74	1.6	1.8	132.6
	60	7.1	69	241.8	142.9	1.9	20	3.9	63	103	147	3.1	3.7	285.2
	74	7.1	65	258.1	145.9	2.3	65	3.8	65	30	52	1.7	3.0	92.2
	57	7.0	67	258.2	144.7	2.1	18	3.8	65	49	65	1.7	2.3	131.3
Low yielding	63	3.7	71	238.8	144.6	2.2	117	1.5	62	103	146	5.1	6.0	283.4
	68	3.7	65	221.9	126.4	2.6	23	1.4	68	109	168	4.4	5.7	311.5
	104	3.5	63	190.2	104.5	2.5	48	1.4	68	92	167	2.9	5.0	296.4
	7	3.4	69	223.6	130.6	2.3	132	1.4	65	126	163	5.4	6.4	336.2
	79	3.0	68	202.6	114.9	2.4	101	1.3	68	91	133	4.5	5.9	253.0
Checks	CKH212346	4.6	66	241.9	149.5	2.4		3.4	63	72	100	2.1	2.7	197.1
	CKH212241	4.6	68	242.4	146.9	2.3		3.5	65	55	86	2.2	2.7	157.7
	UH5354	7.3	67	251.8	131.7	1.9		3.3	65	90	144	2.7	3.9	269.9
	DK777	6.7	64	233.9	117.9	2.2		1.3	63	170	214	5.4	6.6	458.8
	Mean	5.3	67	238.0	135.3	2.3		2.6	65	74	113	3.0	3.9	214.0
	LSD	1.1	1.5	13	10.9	0.4		1	2.2	31.4	43.7	0.9	1.1	82
	σ_G^2	1.1***	5.1***	317.2***	171.5***	0.1***		0.5***	3.7***	703.0***	1211.9***	1.1***	1.4***	4890.8***
	σ_{GE}^2	0.5***	0.5***	35.8***	16.4**	0.1***		0.2***	0.4	178.1***	438.4***	0.2***	0.3***	1446.2***
	σ_ε^2	1.1	1.6	123.1	112.1	0.2		0.6	4.6	691.4	1219.7	0.4	0.6	4172.4
	H^2	0.87	0.95	0.94	0.92	0.69		0.81	0.84	0.84	0.82	0.92	0.91	0.85
	n Env	6	5	5	5	6		4	4	4	4	4	4	4

***, **, ***: Significant at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively.**

GY, grain yield; AD, days to 50% anthesis; PH, plant height; EH, ear height; TLB, Turcicum leaf blight; STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1, *Striga* damage rating at 10 WAP; SDR2, *Striga* damage rating at 12 WAP; AUSNPC, Area under *Striga* number progress curve; H^2, broad-sense heritability; $\hat{\sigma}^2_G$, genotypic variance; $\hat{\sigma}^2_{GE}$, genotype by environmental variance; $\hat{\sigma}^2_e$, error variance; nEnv, number of environments

3.3.2 Combining ability

The GCAs and SCAs varied significantly (P<0.001) for all traits under optimal and *Striga* infested conditions (Table 3.6). The reciprocal effects were of lower magnitude compared to the GCA and SCA effects. Reciprocal effects were significant for all the traits under the two management regimes. The maternal effects were significant for grain yield and agronomic traits under optimal conditions whereas under *Striga* infested conditions, maternal effects were significant for grain yield (P<0.05) and *Striga* damage rating at 12WAP (P<0.001). The maternal effects were not significant for emerged number *Striga* plants and AUSNPC. All other interactions were significant but of lower magnitude compared to the GCA, SCA and REC effects. Baker's ratio ranged from 0.98–0.99 for all traits under optimal and *Striga* infested conditions.

Table 3. 6 Mean squares for combined ANOVA for *Striga* resistance parameters and grain yield across seasons (2022, 2023)

Source of variation	Optimal conditions						*Striga* infested conditions					
	Df	GY	AD	PH	EH	TLB	Df	GY	STR10WAP	STR12WAP	SDR2	AUSNPC
E	4	138.1***	8065.5***	10239.2***	21438.3***	148***	3	163.0***	4975.9***	50499***	29.2***	73509.8***
REP(E)	5	8.8***	27.0***	2582.4***	1537.3***	0.2***	4	15.2***	19036.6***	18137.7***	18.3***	71767.3***
Cross	131	11.4***	55.2***	3673.5***	1927.0***	1.6***	131	5.2***	6711.2***	12534.1***	12.6***	36652.3***
GCA	11	104.1***	581.9***	36343.4***	19084.5***	14.6***	11	45***	66950.9***	126864.9***	125.8***	374555***
SCA	54	4.0***	6.0***	1259.2***	576.9***	0.7***	54	2.0***	1324.0***	2352.8***	3.6***	6470.5***
REC	66	2.1***	6.6***	203.8**	172.1**	0.2	66	1.0**	1078.9**	1809.1**	1.1***	5029.4***
MAT	11	2.5*	21.5***	286.0**	314.7**	0.2	11	1.4*	1049.3	1433	1.6***	4241.9
NM	55	2.0**	3.7***	187.3*	143.5	0.2	55	0.9*	1084.8**	1884.3**	1.0***	5186.9***
Cross × E	524	2***	3.2***	260.5***	172.7***	0.5***	383	1.3***	1335.1***	2711.1***	1.7***	7109.4***
GCA × E	44	8***	10.4***	526.6***	476.4***	2.5***	33	6.2***	2911.0***	7384.1***	4.4***	17794.8***
SCA × E	216	1.5*	3***	256.7***	147.6**	0.4***	162	1.2***	1216.0***	2279.1***	1.9***	6253.2***
REC × E	264	1.5*	2.4**	219.2***	142.6*	0.2*	198	0.8*	1169.9***	2285.8***	1.0***	6029.0***
MAT × E	44	1.8*	2.1	280.8***	170.7*	0.2	33	1.2**	1182.3**	2715.3***	1.3***	6819.1***
NM × E	220	1.4	2.5***	206.9***	137*	0.2*	165	0.7	1167.4***	2199.9***	1.0***	5871.0***
Residual	325	1.2***	1.7***	122.1***	109.5***	0.2***	232	0.6***	643.3***	1076.7***	0.5***	2773.9***
Baker's ratio		0.98	0.99	0.98	0.99	0.98		0.98	0.99	0.99	0.99	0.99

***, **, ***: Significant at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively.**

GY, grain yield; AD, days to 50% anthesis; PH, plant height; EH, ear height; TLB, Turcicum leaf blight; STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR2, *Striga* damage rating at 12 WAP; AUSNPC, Area under *Striga* number progress curve; E, environment; GCA, general combining ability; SCA, specific combining ability; REC, reciprocal effects; MAT, maternal effects; NM, non-maternal effects.

Table 3. 7 General combining ability (GCA) estimates for the 12 parental lines evaluated under *Striga* infested and optimal conditions in 2022 and 2023

Inbred line	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
TZISTR1163	-0.2	0.2	-7.4***	-5.4***	-0.3***	0.5***	-17.4***	-24.6***	-0.3***	-0.4***	-42.0***
TZMI1240	0.6***	0.5*	-4.8***	0.4	-0.2***	-0.2***	5.0*	4.8	0.9***	1.0***	9.7*
TEISTR1159	0.2	2.2***	15.8***	14.2***	-0.2***	-0.7***	29.1***	49.4***	0.01	0.6***	78.6***
DL17933	-0.5*	1.7***	7.7***	8.9***	0.3***	0.8***	-26.7***	-35***	-0.9***	-1.0***	-61.6***
DL17535	-0.6***	1.4***	6.8***	9.0***	0.01	0.2*	-10.3***	-14.5***	-1.0***	-1.1***	-24.8***
DL171145	-0.4*	2.0***	4.5*	9.0***	-0.4***	-0.4***	-3.5	6.0*	-0.1*	0.1*	2.5
DL171342	-0.5***	-2.2***	-27.3***	-16.1***	0.2***	0.3***	-19.4***	-28.3***	0.1	0.01	-47.7***
DL172791	-0.7***	-3.1***	-20.0***	-16.6***	0.3***	-0.8***	12.8***	10.2***	1.1***	1.1***	23.0***
DL17495	-0.4*	-0.8***	5.7***	-5.9***	0.2***	0.1	-10.8***	-14.4***	-0.7***	-0.7***	-25.2***
DL17611	-0.1	-0.4*	13.1***	2.7*	0.3***	0.7***	-13.8***	-18.9***	-1.0***	-1.3***	-32.7***
CML312	1.6***	-1.6***	12.5***	-0.8	0.01	-0.1	38.3***	49.8***	0.9***	0.8***	88.1***
DL14546	1.0***	0.1	-6.5***	0.6	-0.3***	-0.3***	16.8***	15.3***	0.9***	1.0***	32.1***

***, **, ***: Significant at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively.**

GY, grain yield; AD, days to 50% anthesis; PH, plant height; EH, ear height; TLB, Turcicum leaf blight; STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1, *Striga* damage rating at 10 WAP; SDR2, *Striga* damage rating at 12 WAP; AUSNPC, Area under *Striga* number progress curve; GCA, general combining ability; SCA, specific combining ability.

The GCA of the twelve inbred lines are shown in Table 3.7. Five inbred lines namely: DL171342, DL17535, DL17611, DL17933 and TZISTR1163 showed positive GCAs for grain yield and most agronomic traits under *Striga* infestation. These lines showed negative GCAs for emerged *Striga* plants, *Striga* damage rating and AUSNPC. CML312, DL14546 and TZMI1240 had significant positive GCAs for grain yield under optimal conditions but negative GCAs for grain yield under *Striga* infested conditions.

Twelve (12) best performing test hybrids were compared with the check hybrids for grain yield and number of emerged *Striga* plants at 10 and 12WAP (Fig. 3.5). The inbred line DL17933 contributed to the highest number of best hybrids (6) followed by DL17611 (5) and TZISTR1163 (5). All the inbred lines with favorable GCAs (positive GCA for grain yield and negative GCA for *Striga* resistance parameters) formed the highest number of the best hybrids (7) except DL17535. A total of five hybrids, DL171342 × DL17611, DL171342 × DL17933 (DL17933 × DL171342), DL17611 × TZISTR1163 (TZISTR1163 × DL17611), DL17933 × DL17611 and TZISTR1163 × DL17933, were combinations of parental lines with favorable GCAs.

Generally, the hybrids of the susceptible inbred lines (CML312 × TZISTR1163 & DL14546 × DL17933) sustained high number of emerged *Striga* plants like the commercial checks but had better yield. On the other hand, the test hybrids compared favorably with the genetic gain checks (TZSTR184/CKL17622//CKL192608 and TZSTR184/CKL17633//CKL192608) in terms of emerged *Striga* plants and grain yield.

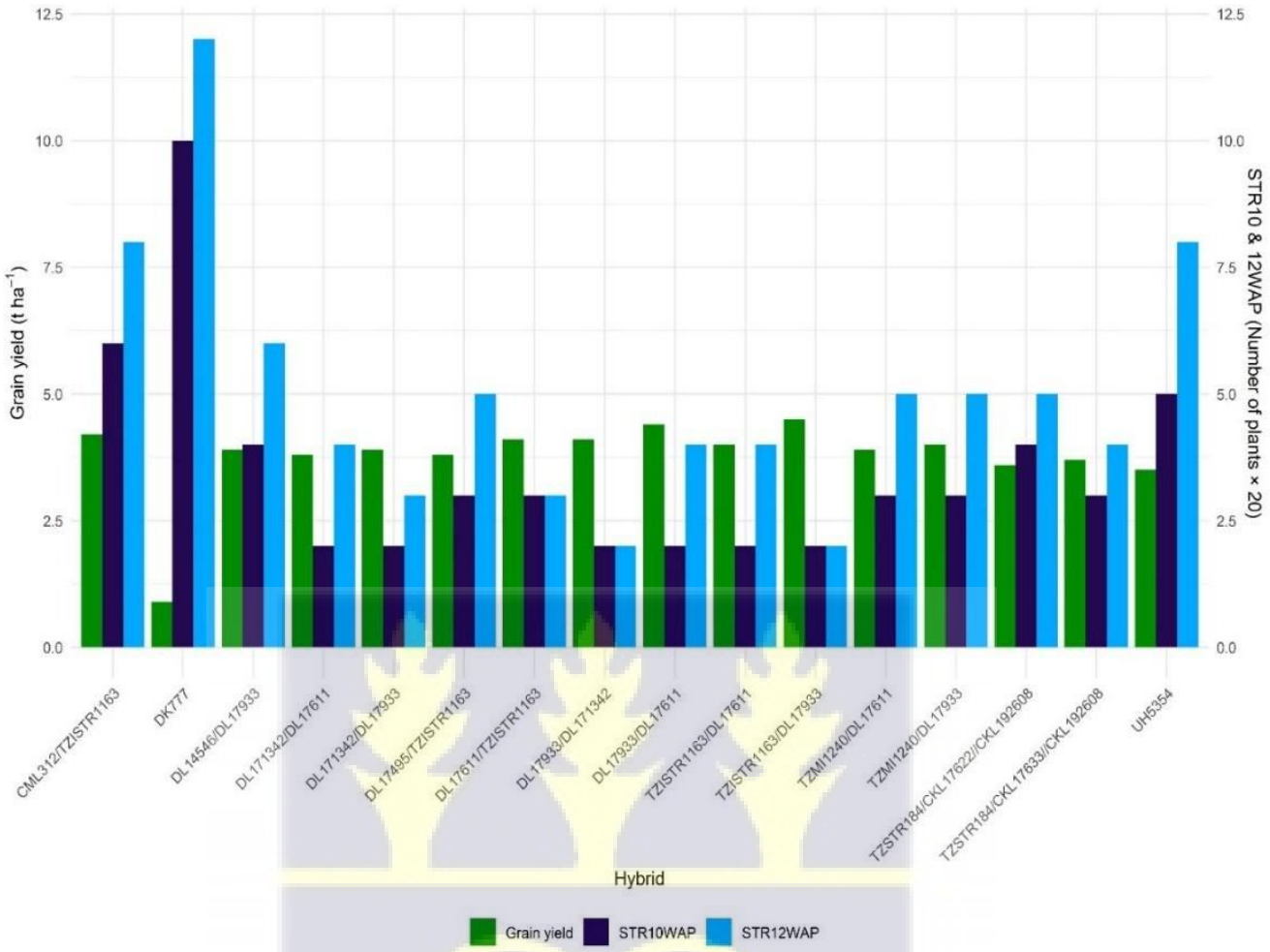


Fig 3. 5 Combined graph showing the performance of the best 12 hybrids, genetic gain and commercial checks.

The SCAs of the 66 hybrids are shown in Appendix Table 3. The best ten (10) specific combiners are shown on Table 3.8. The inbred line DL17535 was the best specific combiner. Although crosses between DL171145 × DL17495 and DL14546 × TZISTR1163 had no significant SCA for grain yield and most agronomic traits under optimal conditions, they consistently showed significant positive SCA for grain yield and significant negative SCAs for all the *Striga* resistance parameters under *Striga* infestation. Other hybrids, CML312 × DL17535, CML312 × TZISTR1163, TEISTR1159 × TZISTR1163 and DL17611 × TZMI1240 had positive significant SCA for grain yield and negative significant SCA for *Striga* damage rating (Table 3.8).

Table 3. 8 Ten hybrids with significant SCAs for various traits under optimal and *Striga* infested conditions

HYBRID	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR1	SDR2	AUSNPC
CML312 × DL14546	-0.2	0.3	-12.6***	-1.3	0	-0.94***	1.15	8.48	0.65***	0.83***	9.63
DL171342 × DL17535	-1**	1.1*	-18.2***	-15.6***	0.1	-0.66***	-9.03	-7.22	0.85***	0.65***	-16.25
DL171145 × DL17495	-0.1	-0.9	-0.2	0.2	-0.3*	0.48**	-13.41*	-27.51***	-0.57***	-0.83***	-40.92***
CML312 × DL17535	0.3	0.1	5.6	6.1*	0.1	0.55**	8.62	12.03	-0.8***	-1.05***	20.65
DL14546 × DL17535	-0.1	0	15.6***	6.9*	-0.1	0.37*	-9.81	-5.13	-0.14	-0.21	-14.94
DL17495 × DL17535	1**	0.4	0.7	2.4	0	0.36*	1.77	2.16	-0.04	0.2	3.93
CML312 × TZISTR1163	0.6	-0.7	4.8	1.2	0	0.66***	0.39	4.26	-0.7***	-0.62***	4.65
DL14546 × TZISTR1163	0.3	-0.1	10**	3.6	-0.1	0.46*	-11.35*	-15.08*	-0.86***	-0.97***	-26.44*
TEISTR1159 × TZISTR1163	0.1	-0.1	-3.2	3.3	0.2	0.52**	2.8	2.37	-0.31*	-0.46**	5.17
DL17611 × TZMI1240	-0.3	0.3	0.4	-0.5	0.1	0.65***	-8.93	-11.65	-0.7***	-0.89***	-20.58

***, **, ***: Significant at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively.**

GY, grain yield; AD, days to 50% anthesis; PH, plant height; EH, ear height; TLB, Turcicum leaf blight; STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1, *Striga* damage rating at 10 WAP; SDR2, *Striga* damage rating at 12 WAP; AUSNPC, Area under *Striga* number progress curve; GCA, general combining ability; SCA, specific combining ability.

3.4 Discussion

3.4.1 Inbred line and hybrid performance

The inbred lines and the hybrids had significantly reduced yields under *Striga* infested conditions as opposed to optimal conditions. This aligns with previous studies which have reported significant yield losses resulting from *Striga* infestation (Berner *et al.*, 1996; Kim *et al.*, 2002). The reduced yield could be attributed to large numbers of emerged *Striga* plants sustained by the inbred lines and the hybrids as well as high *Striga* damage rating. Several studies have reported negative correlations between grain yield and *Striga* resistance parameters (Adewale *et al.*, 2020, Stanley *et al.*, 2021; Gowda *et al.*, 2021).

The inbred lines and hybrids varied significantly under optimal and artificial *Striga* infested conditions pointing to the possibility of broadening the germplasm pool for *Striga* resistance breeding and subsequent selection for the improvement of *Striga* resistance in maize (Cooper *et al.*, 2001). Additionally, genetic variance was higher than the G×E variance suggesting that the traits are genetically determined leading to more predictable and stable outcomes in breeding programs (Mulder *et al.*, 2007; Hill & Mulder., 2010). This is further substantiated by the high broad sense heritability observed across all traits. Genetic variance and high heritability have been associated with high selection efficiency and success of breeding programs (Habib *et al.*, 2007).

3.4.2 Gene effects controlling *Striga* resistance

Significant GCA and SCA effects were revealed through Griffing's diallel analysis indicating that both additive and non-additive gene effects were important in the inheritance of grain yield, agronomic traits and *Striga* resistance parameters under the two management schemes. The reciprocal effects were of lower magnitude in comparison to the cross effects indicating that cytoplasmic inheritance was less influential for all the traits under study. Based on Baker's ratio, additive gene effects were more important than non-additive gene effects for all the traits. This implies that these traits are genetically controlled and therefore highly heritable (Baker, 1978). This implies that recurrent selection and population improvement can be effective in *Striga* breeding programs. Although similar results have been reported Akaogu *et al*. (2019) indicates that gene action for *Striga* resistance in maize has been variable depending on the germplasm used.

The significant positive GCAs for grain yield and significant negative GCAs for the *Striga* parameters in five parental lines (DL171342, DL17535, DL17611, DL17933 and TZISTR1163)

indicate that these lines could be useful in improving yield under *Striga* stressed conditions. Additionally, the findings suggest that these parental lines possess favorable alleles for breeding *Striga* resistant maize. Additive gene effects contribute to the trait in a predictable and linear manner enhancing predictability for more accurate selections on the performance of offspring based on the genetic contributions from parents. Besides, additive effects accumulate over generations thus each selection cycle can build on the previous one, leading to steady and continuous genetic improvement in the desired traits. Studies have shown that traits governed by additive gene effects have high selection response and therefore recurrent selection can be employed in the continuous accumulation of *Striga* resistance alleles in maize (Geber *et al.*, 2003; Hill *et al.*, 2008). The findings align with Simon *et al.* (2018) who found that additive gene action governed *Striga* resistance in maize. However, the findings contrast with those of Badu-Apraku *et al.* (2007) who reported the importance of dominance variance over additive variance. These variations can be attributed to various factor including the geneti variation in the germplasm background, environmental influence, epistasis (gene -by-gene interaction), experimental design etcetra. Bernardo (2002) for example explains that different genetic control in different studies can be due to environmental effects, sampling, and genetic heterogeneity. On the other hand, Acquaah (2012) states that population structure, environment, and selection methods affect detection of gene action.

Superior hybrids were often found to be combination of parental lines with favorable GCAs indicating that it is possible to intercross the selected lines in hybrid development. This is however possible if the line belongs to a different heterotic group thus exhibiting heterosis (Moll *et al.*, 1965; Datta *et al.*, 2004). This study identified hybrids with significant positive SCA for grain yield and significant SCA for *Striga* resistance parameters.

3.5 Conclusion

Understanding the genetic architecture of crop resistance to biotic and abiotic stress factors is key to the success of breeding programs. This study identified 15 hybrids which out yielded the mean of the checks by 32.1%. Additionally, five parental lines were identified three (TZISTR1163, DL17611 and DL17933) of which had outstandingly high significant favorable GCAs for grain yield and *Striga* parameters and can be utilized in maize improvement for *Striga* resistance. Of the five, all were among good general combiners except DL17933. Five (5) hybrids including

DL171342 × DL17611, DL171342 × DL17933 (DL17933 × DL171342), DL17611 × TZISTR1163 (TZISTR1163 × DL17611), DL17933 × DL17611 and TZISTR1163 × DL17933 were combinations of parental lines with favorable GCAs for grain yield and *Striga* resistance parameters. These hybrids can be advanced by testing widely. Two hybrids, DL17933 × DL171342 and TZISTR1163 × DL17611, and their reciprocal crosses performed well under *Striga* infestation. These hybrids can be considered for further testing

CHAPTER FOUR

GENOME WIDE ASSOCIATION STUDY FOR *STRIGA* RESISTANCE IN EARLY MATURITY TROPICAL MAIZE

4.1 Introduction

Maize, has been reported to encounter up to 100% yield loss with reported annual yield losses of 7-10 billion dollars in the African Savannas due to *Striga* (Berner *et al.,* 1996). *Striga* seed banks in affected areas, continuous mono-cropping and depreciating soil fertility complicate *Striga* control. Consequently, excessive *Striga* effects coupled with new invasions in previously unaffected fields emanating from lack of proper phytosanitary activities have led to the abandonment of the farm fields by farmers (Ejeta, 2007a).

Both classical and molecular techniques have been applied in an effort to enhance host resistance to *Striga* in maize. Earlier studies reported yield improvement through population development preceded by hybridization followed by several cycles of recurrent selection under *Striga* infestation (Menkir & Kling, 2007; Badu-Apraku *et al.*, 2007b). Combining ability studies on the other hand have led to the identification of suitable parental lines by estimating their general combining ability (GCA) and subsequent heterotic grouping based on specific combining ability (SCA) as well as determination of the gene effects that control *Striga* resistance in maize. The application of quantitative trait loci (QTL) mapping for the identification of genes associated with *Striga* resistance have been conducted in quality protein maize (QPM) and early and extra early maize varieties suitable for the West African ecologies (Badu-Apraku *et al.,* 2020 a, c; 2023). These studies have identified genes linked to *Striga* resistance and yield under *Striga* infested conditions. For example, 7, 8 (Badu-Apraku *et al.,* 2020 a, c) and 17 QTLs associated with *Striga* resistance (Badu-Apraku *et al.,* 2023) have been reported. However, QTL mapping makes use of bi-parental population with limited recombination events and low mapping resolution. Genome wide association studies (GWAS) also known as association mapping which exploit recombination frequencies in natural breeding populations (Singh & Singh, 2015) are more promising approaches in accelerating *Striga* resistance breeding. Association mapping has led to the identification of 32 (Adewale *et al.,* 2020), 13 (Stanley *et al.,* 2021) and 17 (Okunlola *et al.*,2022) significant single nucleotide polymorphisms (SNPs) associated with *Striga* damage rating and emerged *Striga*

In an effort to mitigate the *Striga* menace within the East and Central Africa, CIMMYT, earlier developed herbicide resistant (IR) open pollinated varieties (OPVs) which were found to have higher yields compared to the checks and significantly reduced *Striga* seed banks (Makumbi *et al., 2015*). Additionally, a genome wide association study on Improved Maize for African Soils (IMAS) mapping population of 380 lines identified 57 SNPs associated with emerged *Striga* counts, *Striga* damage rating, area under *Striga* number progress curve and grain yield (Gowda *et al.,* 2021). However, these materials had no background in *Striga* resistance. Using IITA germplasm as donor lines, the Global Maize Program (GMP) at CIMMYT has introgressed *Striga* resistant genes into elite germplasm followed by a series of artificial *Striga* infestation and selection of plant materials with low number of emerged *Striga* plants coupled with low *Striga* damage rating. In order to develop molecular markers that can enhance effective selection thus ensuring timely line and product development and reduction of phenotyping costs, this study aims to: i) determine the genetic variability of 163 F_6 early maturing maize CIMMYT germplasm under *Striga* infested conditions; ii) identify genomic regions linked to *Striga* resistance parameters, grain yield and agronomic traits; and iii) identify putative candidate genes underlying *Striga* resistance, grain yield and agronomic performance of early tropical maize germplasm.

4.2 Materials and methods

4.2.1 Genetic material

A set of 163 F_6 lines developed at CIMMYT were used in this study. The lines were developed from biparental populations between early maturity *Striga* resistant lines from the IITA and adapted lines from CIMMYT (Fig. 4.1). The *Striga* resistance donor lines from IITA were TZEI1, TZEI2, TZEI3, TZEI4, TZEI6 and TZEI18 (Badu-Apraku, 2010). The adapted lines from CIMMYT were of the early maturity category and were described by Mageto *et al.* (2017). The F_2 populations were selfed and subsequently F_6 lines were developed through pedigree selection. The segregating F_2 populations were subjected to artificial *Striga* infestation and choice of F_2 populations for advancement was based on lower *Striga* plant germination relative to the check entries. The check entries were *Striga* susceptible single cross hybrids from CIMMYT. In subsequent generations, advancement to the next generations was based on lower *Striga* plant count per individual plant under artificial *Striga* infestation. Between F_3 to F_6, two donor lines from IITA (TZEI1 and TZEI4) were used as controls. These early segregating lines showed varied reactions to *Striga* under artificial *Striga* infested conditions. Through this process, 163 F_6 lines

were selected and used for this study. The 163 F_6 lines were testcrossed to three tester inbred lines from IITA: TZEE-WPop×LDS6Inb.44, TZEE-WSRBC5×1368STRS7Inb.27 and TZE-W Pop×1368STRS7Inb.2 (Badu-Apraku and Lum, 2007). The crossing plan resulted in 459 testcross hybrids which were evaluated at two locations each under artificial *Striga* infestation and natural *Striga* infestation in 2016 (Fig. 4.1).

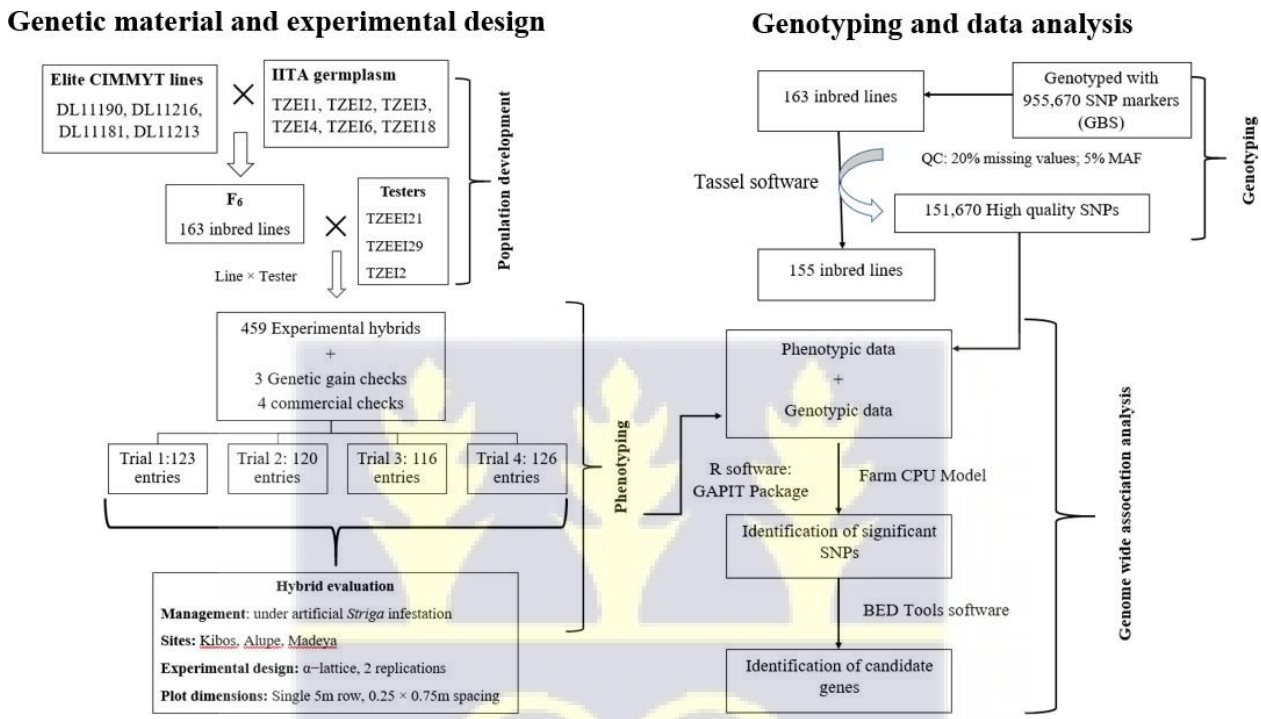


Fig. 4. 1 A schematic diagram showing the process of population development, phenotyping, genotyping and GWAS for 155 lines evaluated under artificial and natural Striga infested conditions in 2016

4.2.2 Experimental Design and Test locations

The 459 testcross (TC) hybrids alongside seven early maturity commercial checks were evaluated in four trial sets. There were 123, 120, 116 and 126 testcross hybrids in Trials 1, 2, 3 and 4 respectively. The experimental design was 3 × 41, 4 × 30, 4 × 29 and 3 × 42 alpha lattice for trials 1, 2 3, and 4, respectively. There were two replications in each trial. 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 (0º2'S, 34º48E, 1193 masl) and Alupe (0º30'N,

34º7E, 1250 masl). The same set of trials were planted under natural *Striga* infestation at Madeya (0º8'N, 34º24E; 1344 masl) and Teso (0º48'N, 34º13E; 1199 masl), the hotspot areas. All locations have a bimodal rainfall distribution (March–July and September–November).

4.2.3 *Striga* Infestation

At Kibos and Alupe artificial *Striga* infestation was ensured by exposing each plant to ~3,000 *Striga* seeds supplied in form of inoculum to up to 10 cm deep planting holes (Makumbi *et al.*, 2015). *Striga* inoculum was prepared by mixing *Striga* seeds with sand in the ratio of 1:500. 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. Two maize seeds were planted per hole and thinning was carried out three weeks after germination. The trials at Madeya and Teso were planted in farmers' fields which historically have had *Striga* infestation and hence a large *Striga* seed bank. These two locations are in the *Striga* belt of Kenya (Gethi *et al.*, 2005). One of the on-farm locations (Teso) has been used previously (Kanampiu *et al.*, 2018). Half dose (125 kg ha^{-1}) of di-ammonium phosphate (DAP, 18:46:0) and calcium ammonium nitrate (CAN, 26%) (60 kg ha^{-1}) fertilizer was applied during planting and topdressing, respectively. Half the recommended fertilizer application rate was used to enhance plant establishment but avoid suppressing *Striga* germination. Hand weeding, supplemental irrigation and other agronomic practices were carried out as per site recommendation. The trials undertaken under on-farm conditions were entirely rainfed.

4.2.4 Data Collection

4.2.4.1 Phenotypic data

Data was collected on *Striga* parameters including the number of emerged *Striga* plants (STR) at 8, 10 and 12 weeks after planting (WAP) and *Striga* damage rating at 12WAP (SDR2) as explained by Makumbi *et al.* (2015), Kanampiu *et al.* (2018) and Gowda *et al.* (2021). In brief, the number of emerged *Striga* plants were counted fifteen centimeters away from each experimental unit and recorded at 8, 10 and 12 WAP. *Striga* damage rating was recorded using a 1–9 scale as proposed by Kim (1991) and as described by Gowda *et al.* (2021). The area under *Striga* number progress curve was computed based on the formula for estimating the area under disease progress curve (AUDPC) as stipulated by Shaner and Finney (1977) and as described by Gowda *et al.* (2021). Grain yield (t ha^{-1}) was calculated using the fresh ear weight per plot considering 80% shelling

percentage and 12.5% adjusted grain moisture (ASTM, 2001; Vivek *et al.*, 2001). Agronomic traits such as days to anthesis (AD), days to silking (SD), plant height (PH), ear height (EH) and husk cover were also recorded. Days to anthesis and days to silking were recorded as the number of days from planting to the time when 50% of the plants per plot had shed pollen and produced silks respectively. Plant height and ear height were measured in centimeters using a ruler as the height from the base of the plant to the flag leaf and the upper cob, respectively. Husk cover (HC) was recorded as a percentage of the number of plants with bare tips relative to the number of plants per plot.

4.2.4.2 Genotyping

Three weeks after planting, fresh leaf samples from 2,022 maize inbred lines were collected at the KALRO, Kiboko station and exported to Intertek Labs, Sweden for DNA extraction and subsequent genotyping using genotyping-by-sequencing (GBS) marker platform, at Cornell Life Science Core Laboratory Center, Ithaca, NY, USA. The genomic libraries were constructed in 96-plex while ApeK1 restriction enzyme was used to digest genomic DNA before sequencing on a single Illumina flow cell (Edriss *et al.*, 2017). SNPs were discovered by aligning the raw reads and sequence tags to maize reference genome, B73 version 2 using TASSEL 4.0 SNP GBS Discovery Pipeline giving rise to a total of 955, 960 SNP markers for each inbred line. The quality control process eliminated SNPs with 20% missing values, less than 5% minor allele frequency (MAF) and SNPs with unknown chromosomes. After the quality control process, 151, 670 SNP markers distributed across the ten maize chromosomes were retained for association analysis (Fig. 4.2).

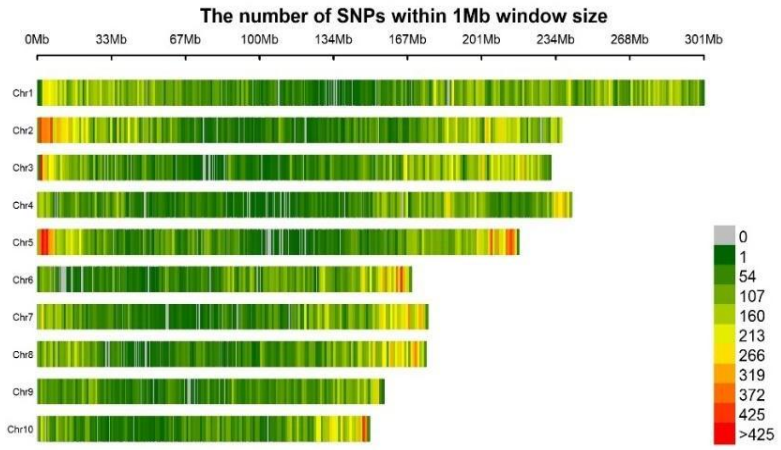


Fig. 4. 2 Chromosome wise SNP density plot representing number of SNPs within 1 Mb window size.

The horizontal axis shows the chromosome length (Mb); the different colors depicts SNP density

4.2.5 Data Analyses

4.2.5.1 Phenotypic Data

Summary statistics, component of variance estimates and broad sense heritability for *Striga* resistance parameters, grain yield and selected agronomic traits were computed based on the phenotypic performance of the 466 hybrids. Mixed linear model was applied to generate the BLUEs and the best linear unbiased predictions (BLUPs) by adjusting the trial means for trials and block effects using AsReml in R version 4.2 (Butler *et al.*, 2009). The four trials and locations were considered as environments but some traits in some environments were omitted due to low trait heritability (<10%). Combined analysis was carried out as:

$$y_{jklm} = \mu + G_j + E_k + R_l(E_k) + B_m(ER)_{kl} + GE_{jk} + \varepsilon_{jklm},$$

where y_{jklm} is the intercept; μ is the mean; $G_j$is the effect of the *j*th genotype; $E_k$is the effect of the *k*th environment; $R_l(E_k)$is the effect of the *l*th replicate in the *k*th environment; $B_m(ER)_{kl}$is the effect of the *m*th block within the *k*th replicate at the *j*th environment; $GE_{jk}$is the effect of the interaction between the *j*th genotype and the *k*th environment; while ε_{jklm} is the experimental error associated with the *j*th genotype, *k*th environment, *l*th replicate and *m*th block. The error term is considered to be normally and independently distributed with mean zero and variance σ^2_ε.

Additionally, variance components and broad-sense heritability across the 12 environments were estimated. Phenotypic distribution histograms were generated using R software. Genetic

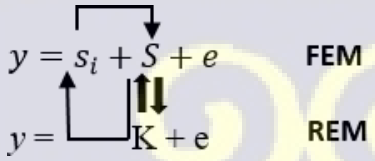
correlation among the 12 measured traits was carried out using ggplot2 and reshape2 packages installed in R.

The broad sense heritability across environments was computed as: $H^2 = \sigma_G^2 / [\sigma_G^2 + \frac{\sigma_{GE}^2}{E} + \frac{\sigma^2}{E \times R}]$,

where H^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 error variance. BLUPs obtained from the combined phenotypic analysis were used to calculate Pearson's correlation coefficients among the different traits.

4.2.5.2 Association analysis

After quality control, 151, 670 SNP markers were retained for marker trait association analysis. Marker trait association analysis was carried out using fixed and random model circulating probability unification (FarmCPU) implemented in GAPIT package installed in R. The FarmCPU model as proposed by Liu *et al.* (2016) uses both fixed and random models iteratively to completely remove confounding factors.



The FEM contains the testing marker (Si) and the associated markers (S), herein referred to as covariates, to control false positives. The S are selected from associated markers and evaluated by the random effect model, with K defined by the S. The FEM and REM are used iteratively until a merge is attained, i.e., when no new covariates are added (Liu *et al.*, 2016).

The model is broken down as follows:

i) In the FEM, markers are tested, one at a time while using the rest of the associated markers as covariates.

$$y_i = g_{i1}s_1 + g_{i2}s_2 \ldots\ldots g_{it}s_t + k_{ij}m_j + e_i \ldots\ldots\ldots FEM\ldots\ldots Equation\ 1$$

where y is the response variable of the ith individual; g_{i1}, g_{i2},....., g_{it} are the genotypes of t covariates (associated markers); s_1, s_2,...., s_t are the corresponding effects of the covariates; k_{ij} is the genotype of the ith individual and jth genetic marker; m_j is the corresponding effect of the jth genetic marker; ei is the residual with zero mean and σ_e^2 variance.

ii) Running the FEM leads to the computation of the most significant P values for the covariates which are then assigned to the corresponding markers (substitution). While using the associated markers as covariates controls for false positives, the FEM tends to over fit the model. Hence the REM is used to estimate the covariates using SUPER algorithm as follows:

$$y_i = u_i + e_i \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots REM \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots Equation\ 2$$

where y is the response variable of the ith individual; u is the total genetic effect of the ith individual; and e is the residual of the ith individual with mean distribution of zero and σ_e^2 variance.

Generally, the covariates are used to define kinship in the REM as follows;

$$G = 2K\sigma_a^2 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots Equation\ 3$$

where G is variance and covariance matrix of the individual's total genetic effect; K is kinship defined by the covariates and σ_a^2 is an unknown genetic variance.

The model has been reported to improve computational efficiency by eliminating confounding factors, controlling for false negatives and preventing model overfitting (Liu *et al.,* 2016). Manhattan plots for *Striga* parameters, grain yield and agronomic traits were generated using GAPIT package in R. The Bonferroni threshold was set at $-\log_{10}$ (5e-6) = 5.3. The candidate genes were identified based on the LD decay and computed BedTools (Quinlan & Hall, 2010; Dale *et al.*, 2011). Gene functions were obtained from MaizeGDB (https://www.maizegdb.org/).

4.3 Results

4.3.1 Hybrid performance

The combined analysis of variance of the 466 hybrids across the twelve environments and under artificial and natural *Striga* infested conditions are shown in Table 4.1. The number of emerged

Striga plants ranged from 8–159 with a mean of 18, 78 and 109 emerged *Striga* plants at 8, 10 and 12 WAP, respectively. *Striga* damage rating was 1.6 to 3.2 at 10–12WAP.

Grain yield across the nine environments and across the management schemes varied from 2.5–4.1 t ha^{-1} with a mean of 3.3 t ha^{-1}. Flowering occurred between 53 to 70 days while plant and ear heights were 162.1 cm and 83.4 cm on average, respectively. There were high significant (P<0.001) genotypic and G × E interactions variations for almost all traits. The G × E variances were 2–4 times greater than the genetic variances for *Striga* parameters. For agronomic traits, the G × E variances were greater than the genetic variances for all traits except for the flowering dates. Genetic variances were 6 and 10 times greater for STR10WAP and STR12WAP than for STR8WAP. The AUSNPC had the highest variances whereas *Striga* damage rating (SDR1 and SDR2) had the lowest. The broad sense heritability was moderate (0.48–0.53) for most *Striga* parameters except *Striga* damage rating which showed high heritability (0.62–0.64). Grain yield showed 39% heritability across nine environments. Generally, the testcrosses yielded more than the genetic gain and commercial check hybrids (Fig. 4.3). Additionally, the test hybrids had fewer attached *Striga* plants, less severe damage and flowered early in relation to the checks.

Table 4. 1 Summary statistics, variance component estimates, and heritability for *Striga* resistance parameters, grain yield, and agronomic traits across twelve locations under artificial and natural *Striga* infested conditions.

Trait	Mean	Range	$LSD_{0.05}$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_{GE}$	$\hat{\sigma}^2_s$	H^2	No. Env
STR8WAP	18	8–25	7.6	12.76***	29.22***	186.44	0.48	9
STR10WAP	78	40–104	18.4	79.26***	350.55***	993.88	0.51	11
STR12WAP	109	65–159	22.8	124.43***	459.82***	1642.34	0.52	11
SDR1	2.2	1.6–2.7	0.4	0.05***	0.10***	0.32	0.62	9
SDR2	2.6	1.9–3.2	0.4	0.05***	0.10***	0.42	0.64	10
AUSNPC	282.5	144.2–385.4	63.8	995.39***	3992.97***	11398.86	0.53	11
Grain yield	3.3	2.5–4.1	0.5	0.04**	0.19***	0.75	0.39	9
AD	58	53–68	1.6	1.95***	2.72***	1.83	0.85	11
SD	60	56–70	1.9	2.85***	3.37***	3.39	0.86	11
PH	162.1	152.3–173.9	7.2	11.10***	44.86***	149.23	0.46	9
EH	83.4	72.8–91.1	5.4	6.51***	33.16***	86.09	0.46	10
HC	13.3	5.9–27.1	8.6	23.61***	106.15***	82.09	0.62	10

, *: Significant at P < 0.01 and P < 0.001, respectively.

STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; AUSNPC, area under *Striga* number progress curve; AD, days to 50% anthesis; SD, days to 50% silking; PH, plant height; EH, ear height; HC, husk cover; H^2 broad-sense heritability; $\hat{\sigma}^2_G$, genotypic variance; $\hat{\sigma}^2_{GE}$, genotype by environmental variance; $\hat{\sigma}^2_\varepsilon$, error variance; nEnv, number of environments

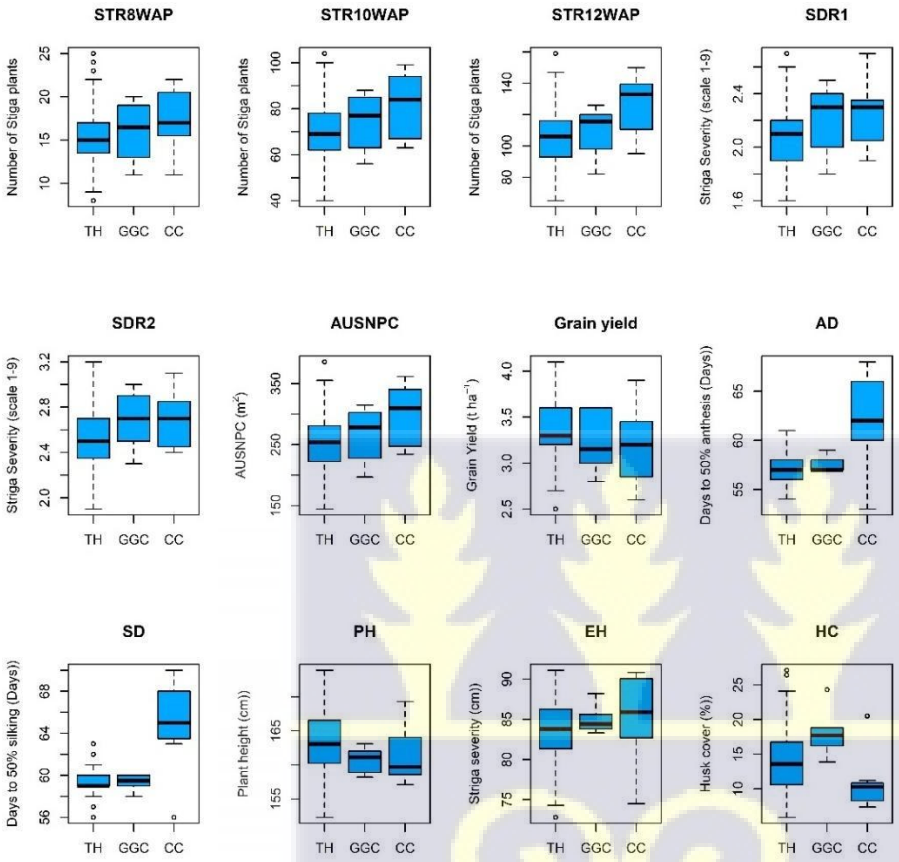
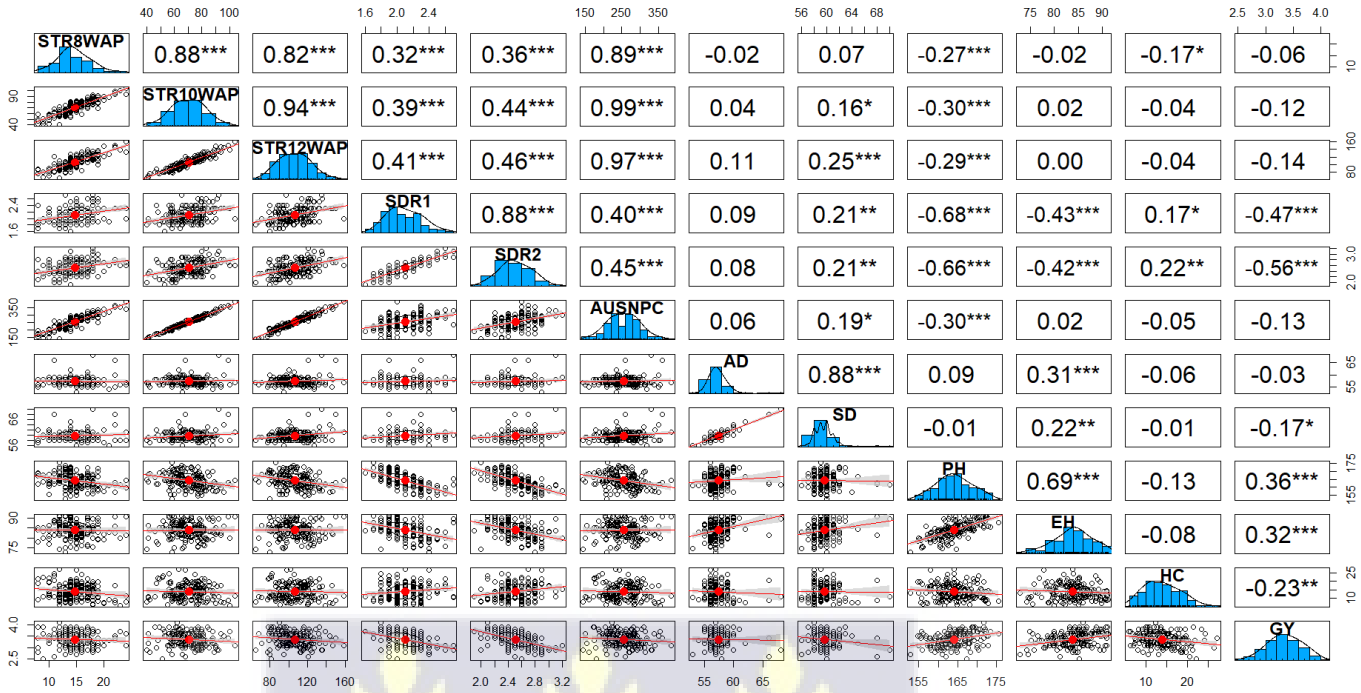


Fig. 4. 3 Boxplots of Striga resistance parameters, grain yield and agronomic traits for test hybrids (TH), genetic gain checks (GGC) and commercial checks (CC) evaluated under natural and artificial Striga infested conditions.

STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; AUSNPC, Area under *Striga* number progress curve (m^2), AD, days to 50% anthesis; SD, days to 50% silking; PH, plant height (cm); EH, ear height (cm); HC, percentage of plants with poor husk cover

The results show strong positive correlation (P<0.001) among *Striga* resistance parameters (Fig. 4.4). *Striga* parameters were strongly (P<0.001) and negatively correlated with plant height (r = -0.27 to -0.68). Notably, *Striga* damage rating at 10 and 12WAP had strong (P<0.001) negative correlation with plant height (r = -0.66*** – -0.68***), ear height (r = -0.42*** – -0.43***) and grain yield (-0.47*** – -0.56***). Grain yield showed strong positive association with EH (r = 0.32***) and PH (r = 0.36***).



*, **, ***: Significant at P < 0.05, P < 0.01 and P < 0.001, respectively.

STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12 WAP; SDR1 and 2, *Striga* damage rating at 10 and 12 WAP, respectively; AUSNPC, area under *Striga* number progress curve AD, days to 50% anthesis; SD, days to 50% silking; PH, plant height; EH, ear height; HC, husk cover; GY, grain yield.

Fig. 4. 4 Genetic correlations between Striga resistance parameters, agronomic traits and grain yield of 466 hybrids evaluated under Striga infestation in four trials in Kenya in 2016.

4.3.2 Marker-trait associations

4.3.2.1 Striga parameters

Following the genome-wide association analysis using FarmCPU model, 42 significant SNPs underlying *Striga* resistance with putative genes were identified (Fig. 4.5; Table 4.2). These SNPs were found in all the maize chromosomes and accounted for 0.1–38.9% phenotypic variation. Chromosome 2 had the highest number of significant SNPs (8) while chromosome 10 had the least (1 SNP). The largest number of significant SNPs were identified for STR10WAP and the least were associated with AUSNPC. Chromosome 2 was very important for all the *Striga* resistance parameters with the highest number of significant SNPs across the traits. Generally, chromosomes 1, 2, 6, 7 and 8 had 5–8 significant SNPs across the *Striga* resistance parameters.

A total of 24 significant SNPs underlying the number of emerged *Striga* plants at 8–12WAP explained 0.1 to 26.8% of the phenotypic variation. The SNPs occupied all the maize chromosomes except chromosome 10. At eight weeks after planting, seven (7) SNPs found in chromosomes 1, 2, 3, 6 and 8 explained between 2.8–26.8% of the total phenotypic variation. Two SNPs in chromosome 3 (S3_175540577 & S3_8219084) accounted for 26.8 and 12.2% of the variations observed in the number of emerged *Striga* plants at 8WAP. Additionally, two SNPs in chromosomes 2 (S2_44331849) and 6 (S6_159470193) explained 9.5 and 16.9% phenotypic variations, respectively. For STR10WAP, nine (9) significant SNPs were identified and occupied six out of ten chromosomes. These SNPs explained 2.6–24.4% phenotypic variation among the hybrids. A SNP located at chromosome 6 (S6_107754561) explained the highest (24.4%) phenotypic variation followed by S2_44331849 in chromosome 2 which accounted for 13.1% variation among the hybrids. Notably, two SNPs, S2_44331849 and S6_159470193 were associated with the number of emerged *Striga* plants at 8 and 10WAP. At 12WAP, eight (8) significant SNPs that accounted for 0.1–15.3% phenotypic variation were identified for emerged *Striga* plants. Three SNPs, S2_87827811, S4_153521908 and S6_71449430 in chromosomes 2, 4 and 6 explained 8.1–15.3% of the differences observed among the hybrids. In general, chromosomes 1, 2 and 6 consistently showed significant SNPs for emerged *Striga* plants at 8, 10 and 12WAP. However, significant SNPs in chromosome 1 accounted for low phenotypic variance (2.7–3.3) compared to chromosome 2 (2.6–15.3%) and chromosome 6 (7.2–24.4%) for emerged *Striga* plants at 8–12 WAP.

Fourteen (14) SNPs associated with *Striga* damage rating at 10 (SDR1) and 12 (SDR2) WAP occupied all the maize chromosomes except 3, 4 and 10 and explained 1.7–38.9% of the phenotypic variation. Three SNPs accounted for more than 10% phenotypic variation in *Striga* severity damage. A SNP in chromosome 7, S7_103945810, explained the highest (18.2%) phenotypic variations for SDR1 whilst S6_96337848 accounted for 38.9% of the observed differences among the hybrids in SDR2. Chromosomes 2 and 8 showed significant SNPs associated with both SDR1 and SDR2. One SNP in chromosome 8 (S8_149982616) was commonly associated with *Striga* damage rating at 10 and 12 WAP explaining 3.7 and 5.2% differences observed among the hybrids, respectively. Four SNPs explaining 1.2–11.9% phenotypic variation were identified for AUSNPC. The SNPs were located in chromosomes 2, 6, 7 and 10 with a SNP located in chromosome six (S6_109282273) explaining the highest (11.9%)

phenotypic variation. In general, chromosome 6 consistently showed significant SNPs explaining high phenotypic variation in all the *Striga* resistance parameters except SDR1.

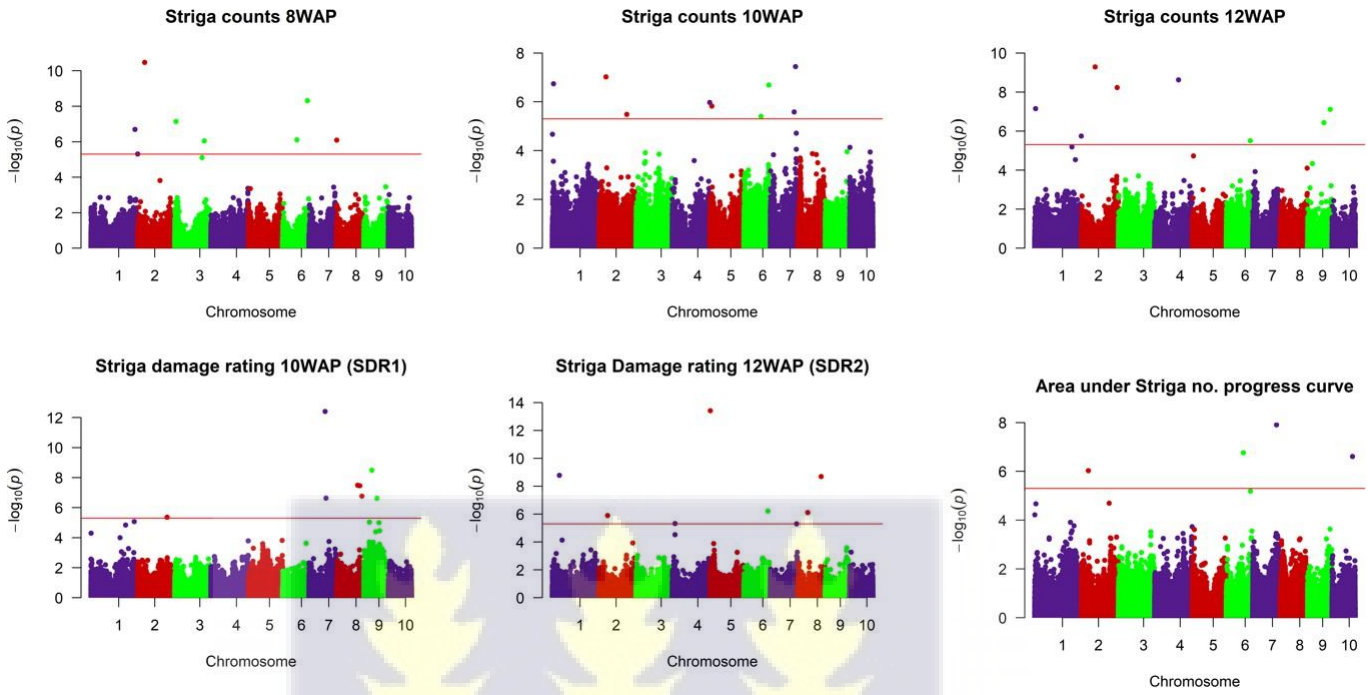


Fig. 4. 5 Manhattan plots of GWAS scans for Striga resistance parameters in 155 maize inbred lines using the FarmCPU model.

The y-axis represents the *P*-value of the marker–trait association on a −log10 scale, and the x-axis represents the 10 chromosomes of maize. The significantly associated SNPs are distinguished by the red threshold line.

4.3.2.2 Grain yield and agronomic traits

The significant SNPs associated with grain yield and agronomic traits and candidate genes are shown in Fig. 4.6 and Table 4.3. Six and 43 significant SNPs were identified for grain yield and agronomic traits respectively. For grain yield, the significant SNPs occupied 5 chromosomes; 2, 3, 4, 8 and 9 and accounted for 3.9–22.4% of the yield differences observed among the hybrids. Two SNPs in chromosomes 2 (S2_71314591 & S2_184536913) accounted for 10 and 22.4% variation in yield among the hybrids whereas a SNP in chromosome 3 (S3_156434858) explained 12.8% variation.

The significant SNPs identified for agronomic traits occupied all the maize chromosomes except chromosome 6. Specifically, 20, 10, 5 and 8 SNPs were significant for flowering dates (AD & SD), PH, EH and HC, respectively. Days to 50% silking (SD) had the highest number of significant

SNPs while ear height (EH) had the least. The highest number of significant SNPs occupied chromosomes 3 and 5 whereas the least occupied chromosome 7. Twenty SNPs associated with flowering dates occupied all the maize chromosomes except 4, 6 and 7 and accounted for 0.5–31.8% of the differences observed. Five SNPs accounted for >10% of differences in days to 50% anthesis with S8_16444445 explaining the highest (31.8%). For days to 50% silking (SD), S2_96784848 and S8_11920667 explained 11.3 and 19.1% of the differences observed respectively. Generally, chromosomes 1, 2, 3, 8 and 10 were important for the flowering dates with 75% of the significant SNPs. A single SNP, S2_184536913, was significant for grain yield and days to anthesis explaining 10% phenotypic variation in both traits.

Ten significant SNPs associated with PH accounted for 1.4–14.7% phenotypic variation with S1_56929946, S2_139077719 and S9_86203364 in chromosomes 1, 2 and 9 explaining 7.2, 14.7 and 8.2% variation respectively. On the other hand, five significant SNPs were associated with EH and occupied chromosomes 1, 3, 4 and 9. A SNP in chromosome 4 (S4_160460503) underlying EH accounted for the highest (47.4%) phenotypic variations among the hybrids. Chromosomes 1, 3, 4 and 9 were important for both PH and EH with 11 out of the 15 significant SNPs identified for the two traits. Eight significant SNPs were found to be associated with HC and explained between 2.5–25.3% phenotypic differences among the hybrids. Two SNPs in chromosomes 5 (S5_197606529) and 9 (S9_5004370) explained the highest (12.8 & 25.3%) phenotypic variation. In general, chromosome 3 was important for all the agronomic traits.

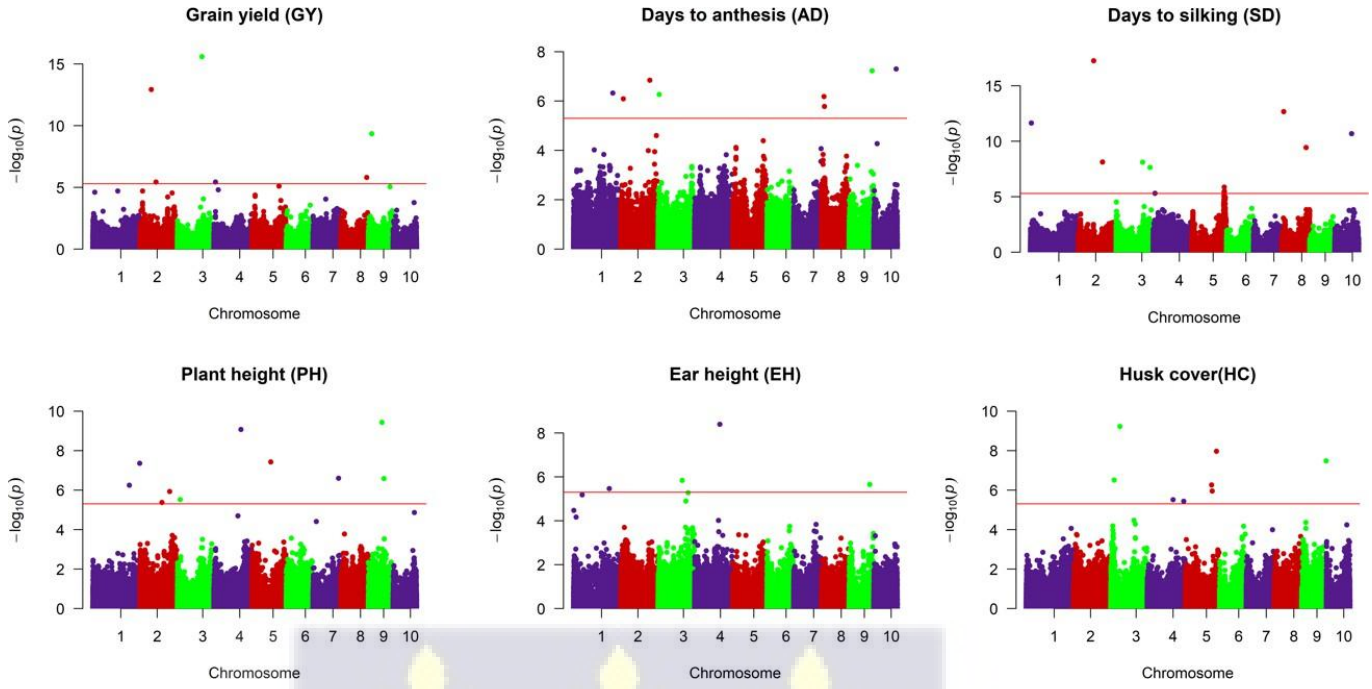


Fig. 4. 6 Manhattan plots of GWAS scans for grain yield and agronomic traits in 155 maize inbred lines using the FarmCPU model.

The y-axis represents the *P*-value of the marker–trait association on a −log10 scale, and the x-axis represents the 10 chromosomes of maize. The significantly associated SNPs are distinguished by the red threshold line.

4.3.3 Identification of putative genes

According to genomic information of maize reference genome, B73 RefGen_v2, 112 candidate genes were in close proximity to the significant SNPs associated with *Striga* parameters. Specifically, there were 58, 43 and 11significant SNPs for the number of emerged *Striga* plants, *Striga* damage rating and AUSNPC, respectively (Table 4.2). On the other hand, 14 candidate genes surrounded six significant SNPs underlying grain yield while 119 candidate genes were close to the significant SNPs underlying agronomic traits. A total of 22, 34, 34, 11 and 19 candidate genes were in close proximity to significant SNPs associated with 50% days to anthesis (AD), 50% days to silking (SD), plant height (PH), ear height (EH) and husk cover (HC) respectively (Table 4.3). The candidate genes close to the significant SNPs were identified within the LD window (Fig. 4.7).

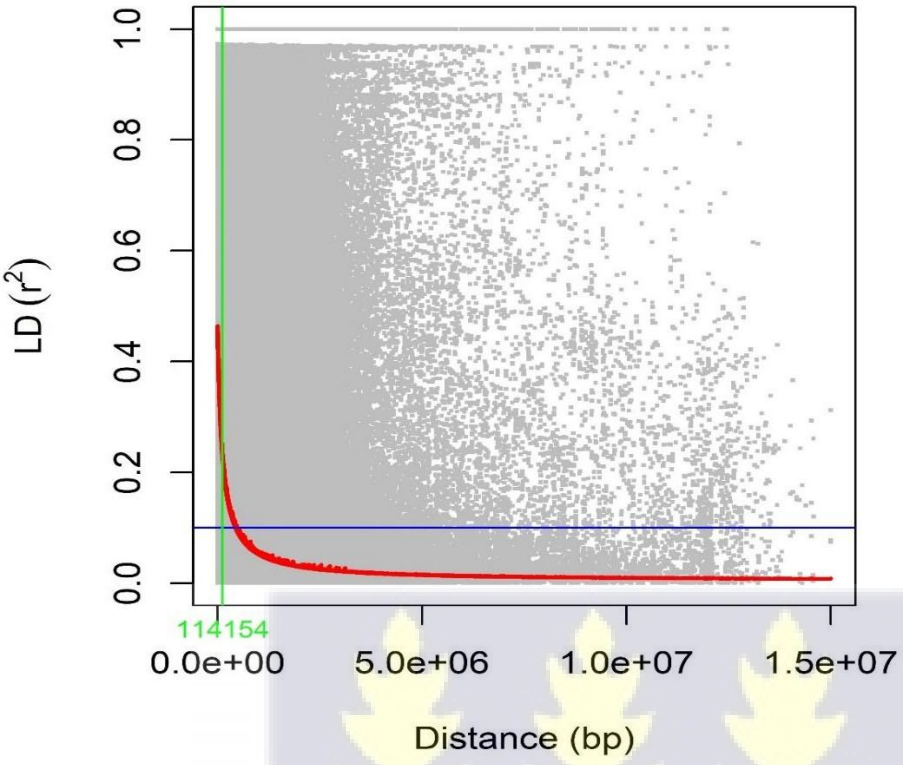


Fig. 4. 7 Visual presentation of linkage disequilibrium (LD) decay plotted based on r^2 values and genetic distance in base pairs using TASSEL

4.3.3.1 Gene identification for Striga resistance parameters

The significant SNPs were found to be located close to several proteins, transcription factors and/or enzymes involved in plant defense. For example, 13 candidate genes were found to be close to the seven significant SNPs associated with STR8WAP. The highest number of candidate genes were in chromosome 3 followed by chromosomes 2 and 6. A gene model, GRMZM2G149756, found in chromosome 3 upstream of S3_175540577 encoded for ethylene-responsive transcription factor ABR1. Additionally, GRMZM2G475984 and GRMZM2G176489 located close to S3_8219084 encoded for WRKY domain-containing protein while GRMZM2G108898 coded for cysteine dioxygenase. On chromosome 6, two candidate genes (GRMZM2G033971 & GRMZM2G331833) close to S6_159470193 coded for putative membrane protein YuiD and CLP protease regulatory subunit CLPX1 (CLPX) respectively.

Twenty-nine candidate genes were close to nine significant SNPs that governed STR10WAP. Chromosomes 2 and 7 had the highest number of candidate genes followed by chromosome 6. Around 50% of the candidate genes encoded for various proteins while the remainder encoded for enzymes and transcription factors. Two candidate genes, GRMZM5G827810 and

GRMZM2G470309, in chromosome 1 close to S1_9664956 encoded for Xyloglucan galactosyltransferase KATAMARI1 and Exostosin domain-containing protein, respectively. Three candidate genes found close to S2_44331849 coded for two proteins (FSH1 domain- containing protein & Signal recognition particle 19 kDa protein) and an enzyme (protein- serine/threonine phosphatase). Further, two candidate genes (GRMZM2G040095 and GRMZM2G045049) located downstream of S2_4162808 encoded for lipoxygenase and formylglycinamide ribonucleotide amidotransferase enzymes. In chromosome 6, GRMZM2G033971 and GRMZM2G331833 that are 4 kb apart and located upstream of S6_159470193, coded for putative membrane protein YuiD and CLP protease regulatory subunit CLPX1 (CLPX), respectively. Further, GRMZM2G156986, GRMZM5G846719 and GRMZM2G012276 encoded for nucleolar GTP-binding protein 1, adrenodoxin-like protein 2 and thioredoxin-dependent peroxiredoxin, respectively.

Table 4. 2 List of significant single-nucleotide polymorphisms (SNPs) and associated genes revealed through GWAS, chromosomal positions and percentage phenotypic variance explained (PVE) for *Striga* resistance parameters of hybrids evaluated under artificial and natural *Striga infestation.*

SNP	chr	*P* value	MAF	PVE (%)	Gene model	Gene description
***Striga* plant count 8 weeks after planting (STR8WAP)**						
S1_283196822	1	2.04734E-07	0.33	2.8	GRMZM2G472827	GYF domain-containing protein
					GRMZM2G046900	FSH1 domain-containing protein
S2_44331849	2	3.40009E-11	0.33	9.5	GRMZM2G167262	Signal recognition particle 19 kDa protein
					GRMZM2G015610	Protein-serine/threonine phosphatase
S3_175540577	3	9.43921E-08	0.41	26.8	GRMZM2G149756	Ethylene-responsive transcription factor ABR1
					GRMZM2G475984	WRKY domain-containing protein
S3_8219084	3	7.22139E-08	0.22	12.2	GRMZM2G108898	Cysteine dioxygenase
					GRMZM2G176489	WRKY domain-containing protein
S6_159470193	6	9.11986E-08	0.20	16.9	GRMZM2G033971	Putative membrane protein YuiD
					GRMZM2G331833	CLP protease regulatory subunit CLPX1 (CLPX)
S6_92611059	6	7.87E-07	0.16	3.5	GRMZM2G164835	twinkle homolog protein
S8_2111497	8	7.23099E-10	0.29	5.8	GRMZM2G082214	Phosphoribosyl-AMP cyclohydrolase
					GRMZM2G052875	Glucosidase 2 subunit beta
***Striga* plant count 10 weeks after planting (STR10WAP)**						

S1_9664956	1	1.82264E-07	0.15	2.7	GRMZM5G827810	Xyloglucan galactosyltransferase KATAMARI1
					GRMZM2G470309	Exostosin domain-containing protein
					GRMZM2G046900	FSH1 domain-containing protein
S2_44331849	2	1.69103E-10	0.33	13.1	GRMZM2G167262	Signal recognition particle 19 kDa protein
					GRMZM2G015610	Protein-serine/threonine phosphatase
					GRMZM2G039345	Ribulose bisphosphate carboxylase/oxygenase activase
					GRMZM2G039588	Glucose-6-phosphate 1-epimerase
S2_4162808	2	2.06E-11	0.09	2.6	GRMZM2G040095	Lipoxygenase
					GRMZM2G039532	XS domain-containing protein
					GRMZM2G045049	Formylglycinamide ribonucleotide amidotransferase
S4_177434367	4	2.34344E-07	0.25	3.5	GRMZM2G165991	Growth-regulating factor
					GRMZM2G165961	Protein trichome birefringence
					GRMZM2G415491	RNA helicase
S5_1946440	5	4.70E-07	0.12	8.3	GRMZM2G003109	Anthranilate synthase
					GRMZM2G398668	XPGI domain-containing protein
					GRMZM2G100419	Organic solute transporter Ost-alpha
					GRMZM2G033971	Putative membrane protein YuiD
S6_159470193	6	2.03592E-07	0.20	7.2	GRMZM2G331833	CLP protease regulatory subunit CLPX1 (CLPX)
					GRMZM2G156986	Nucleolar GTP-binding protein 1
S6_107754561	6	1.73092E-07	0.25	24.4	GRMZM5G846719	Adrenodoxin-like protein 2
					GRMZM2G012276	Thioredoxin-dependent peroxiredoxin
					GRMZM2G475148	auxin eflux carrier
S7_115182646	7	1.56328E-10	0.33	4.3	GRMZM2G027563	Transcription factor bHLH66
					GRMZM2G171408	U-box domain-containing protein 12
					GRMZM2G057247	Formin-like protein 13
					GRMZM2G057260	Transcription factor bHLH85
S7_162068277	7	3.62823E-08	0.11	3.9	GRMZM2G057023	IFRD domain-containing protein
					GRMZM2G057176	Pentatricopeptide repeat-containing protein
					GRMZM2G357734	Phytoene dehydrogenase
***Striga* plant count 12 weeks after planting (STR12WAP)**						
S1_182283458	1	6.93591E-15	0.37	3.8	GRMZM2G136313	RING-type E3 ubiquitin transferase
S1_22439668	1	8.00037E-10	0.44	3.3	GRMZM2G077127	probable strigolactone esterase DAD2
S2_229130712	2	5.93583E-09	0.16	5.3	GRMZM2G041549	RING-type E3 ubiquitin transferase
S2_87827811	2	5.20466E-10	0.09	15.3	GRMZM2G159678	Putative carbohydrate esterase
S4_153521908	4	2.40515E-09	0.14	8.1	GRMZM2G010488	E3 ubiquitin ligase

					GRMZM2G080842	Mitochondrial substrate carrier family protein
					GRMZM2G310410	U-box domain-containing protein 33
					GRMZM2G007489	Acyl-[acyl-carrier-protein] hydrolase
S6_71449430	6	2.88E-10	0.45	8.7	GRMZM2G155662	single-stranded DNA-binding protein WHY1
					GRMZM2G105787	Squalene monooxygenase
					GRMZM2G021573	AP2-like ethylene-responsive transcription factor ANT
S9_144795453	9	7.76748E-08	0.18	2.3	GRMZM2G105834	Homeobox-leucine zipper protein HOX19
					GRMZM2G407119	BHLH domain-containing protein
					GRMZM2G099101	Endoglucanase
S9_131916087	9	3.05E-08	0.43	0.1	GRMZM2G045467	Hexosyltransferase
					GRMZM2G086614	Zinc finger CCCH domain-containing protein 53
***Striga* damage rating 10 weeks after planting (SDR1)**						
					GRMZM2G137541	Transcription factor bHLH49
S2_188405867	2	3.49E-13	0.18	8.4	GRMZM2G137558	1-phosphatidylinositol 4-kinase
					GRMZM2G058862	metallo-dependent hydrolases superfamily protein pseudogene
					GRMZM2G061620	Ubiquitin receptor RAD23
S7_109722251	7	2.30089E-07	0.12	2.2	GRMZM2G362131	SprT-like domain-containing protein Spartan
					GRMZM2G175910	Glycosyltransferase
S7_103945810	7	3.96614E-13	0.09	18.2	GRMZM2G315431	RING-type E3 ubiquitin transferase
					GRMZM2G014066	Drought-induced 19
					GRMZM2G014346	Putative homeodomain-like transcription factor superfamily protein
S8_149982616	8	3.47625E-08	0.19	3.7	GRMZM2G160990	DUF1421 domain-containing protein (Fragment)
					GRMZM2G115828	Ubiquitin-conjugating enzyme E2 36
					GRMZM2G061419	Ceramide glucosyltransferase
					GRMZM2G065893	E3 ubiquitin-protein ligase RGLG1
S8_163374573	8	1.70829E-07	0.26	3.1	GRMZM2G065971	Magnesium transporter
					GRMZM2G066024	Fructose-bisphosphate aldolase
					GRMZM2G061396	BCL-2 binding anthanogene-1
					GRMZM2G100146	Histone deacetylase102
					GRMZM2G113078	Ethylene-responsive transcription factor WRI1
S8_136048049	8	3.24022E-08	0.21	1.7	GRMZM2G001243	Protein-serine/threonine phosphatase

					GRMZM2G437575	Protein-serine/threonine phosphatase
					GRMZM2G137802	Description WRKY domain-containing protein
					GRMZM2G100229	Mitochondrial outer membrane porin
					GRMZM2G463953	MAPK kinase substrate
S9_84242391	9	2.34847E-07	0.36	1.9	GRMZM2G163641	protein OVEREXPRESSOR OF CATIONIC PEROXIDASE 3
S9_51352331	9	3.24652E-09	0.21	7.1	GRMZM2G354610	feruloyl-arabinoxylan b-1,2- xylosyl transferase
***Striga* damage rating 12 weeks after planting (SDR2)**						
					GRMZM2G104464	Polynucleotide 5'-hydroxyl-kinase nol9 isoform X1
S1_46550390	1	1.66085E-09	0.21	4.0	GRMZM2G104534	Protein SCAR2
					GRMZM2G104373	26S proteasome regulatory subunit 4 homolog A
					GRMZM5G820287	Acyl-coenzyme A oxidase
S2_55037582	2	1.28E-06	0.24	4.8	GRMZM2G079323	WD repeat-containing protein 44-like
					GRMZM2G079298	Elicitor-inducible cytochrome P450
					GRMZM2G144109	PPM-type phosphatase domain-containing protein
S5_2259980	5	3.90404E-14	0.15	10.7	GRMZM2G143998	MFS domain-containing protein
					GRMZM2G144042	Protein kinase APK1A chloroplastic
					GRMZM2G144020	TOG domain-containing protein
					GRMZM2G144008	RAB GTPase homolog A2D
S6_96337848	6	1.19E-07	0.11	38.9	GRMZM5G848603	Lysosomal Pro-X carboxypeptidase
S8_63553299	8	7.88E-07	0.36	2.5	GRMZM2G568912	suppressor of disruption of TFIIS isoform X2
					GRMZM2G119693	Transcription factor MYB86
					GRMZM2G014066	Drought-induced 19
					GRMZM2G014346	Putative homeodomain-like transcription factor superfamily protein
S8_149982616	8	2.03397E-09	0.19	5.2		
					GRMZM2G160990	DUF1421 domain-containing protein (Fragment)
					GRMZM2G115828	Ubiquitin-conjugating enzyme E2 36
Area under *Striga* number progress curve (AUSNPC)						
S2_55905285	2	2.15E-08	0.36	7.1	GRMZM2G369792	Pentatricopeptide repeat-containing protein
					GRMZM2G134389	Tyrosine-protein like
S6_109282273	6	1.73817E-07	0.26	11.9	GRMZM2G048161	Aspartic proteinase nepenthesin-1
					GRMZM2G048194	LysM domain-containing GPI-anchored protein 1

S7_152810004	7	1.24557E-08	0.41	8.7	GRMZM2G108874	LRAT domain-containing protein
					GRMZM2G108849	Cathepsin B
					GRMZM2G320135	ATP-dependent Clp protease proteolytic subunit
					GRMZM5G812538	Putative metal-nicotianamine transporter YSL11
S10_131887753	10	2.45465E-07	0.26	1.2	GRMZM5G893444	Putative metal-nicotianamine transporter YSL12
					GRMZM2G400570	Putative metal-nicotianamine transporter YSL12
					GRMZM5G854655	Glycosyltransferase

Chr, chromosome; MAF, minor allele frequency.

Sixteen candidate genes were located close to eight significant SNPs that were associated with STR12WAP. Up to 50% of candidate genes encoded for several enzymes. Chromosome 9 had the highest number of candidate genes whereas chromosomes 1 and 2 had the least. Four candidate genes: GRMZM2G136313, GRMZM2G041549, GRMZM2G010488 and GRMZM2G310410 encoded for ubiquitin-related enzymes and a protein. Two candidate genes, GRMZM2G077127 and GRMZM2G021573 encoded for probable strigolactone esterase DAD2 and AP2-like ethylene-responsive transcription factor ANT, respectively. Three other candidate genes including GRMZM2G105834, GRMZM2G407119 and GRMZM2G086614 coded for Homeobox-leucine zipper protein HOX19, BHLH domain-containing protein and Zinc finger CCCH domain-containing protein 53, respectively. A gene on chromosome 2, GRMZM2G159678 located close to S2_87827811 encoded for putative carbohydrate esterase. Two candidate genes close to a locus on chromosome 2 (S2_87827811) encoded for putative carbohydrate esterase and E3 ubiquitin ligase. On chromosome 6, two candidate genes located close to S6_71449430 encoded for acyl-[acyl-carrier-protein] hydrolase and single-stranded DNA-binding protein WHY1.

Forty-three candidate genes were found around 14 significant SNPs governing *Striga* damage rating at 10 and 12WAP (SDR1 & SDR2). Chromosome 8 had the highest number of candidate genes for SDR1 (15) and SDR2 (6). For SDR1, three candidate genes found close to S2_188405867 in chromosome 2 encoded for Transcription factor bHLH49, 1-phosphatidylinositol 4-kinase and metallo-dependent hydrolases superfamily protein pseudogene. Besides, two candidate genes (GRMZM2G175910 & GRMZM2G315431) located close to S7_103945810 encoded for two enzymes: glycosyltransferase and RING-type E3 ubiquitin

transferase. Other key candidate genes: GRMZM2G113078, GRMZM2G137802 and GRMZM2G119693 found in chromosomes 8 and 9 encoded for ethylene-responsive transcription factor WRI1, WRKY domain-containing protein and MAPK kinase substrate respectively. For SDR2, five candidate genes: GRMZM2G144109, GRMZM2G143998, GRMZM2G144042, GRMZM2G144020 and GRMZM2G144008, found close to S5_2259980 on chromosome 5 encoded for 4 proteins and an enzyme. One gene model found close to S6_96337848 coded for lysosomal Pro-X carboxypeptidase.

There were 11 candidate genes located close to 4 significant SNPs underlying AUSNPC. Three candidate genes, GRMZM2G134389, GRMZM2G048161 and GRMZM2G048194, found close to S6_109282273 in chromosome 6 encoded for tyrosine-protein like, aspartic proteinase nepenthesin-1 and lysM domain-containing GPI-anchored protein 1, respectively. Other candidate genes coded for transporters and metabolic enzymes.

4.3.3.2 Gene identification for grain yield and agronomic traits

Several genes surrounded significant SNPs underlying grain yield and agronomic traits (Table 4.3). Specifically, 14 candidate genes were close to the six significant SNPs underlying grain yield while 119 genes were identified for agronomic traits.

For grain yield, all chromosomes had 3 candidate genes close to the significant SNPs except chromosome 4 which had 2. The significant SNPs in chromosome 2 (S2_71314591 & S2_184536913) encoded for protein indeterminate-domain 16 and Serine/threonine-protein kinase STY463 while a SNP in chromosome 3 (S3_156434858) had 3 candidate genes, GRMZM2G338259, GRMZM2G173534 and GRMZM2G300862 which encoded for auxin response factor, inducer of CBF expression 2 and aspartate kinase, respectively. Other key candidate genes were GRMZM2G407605, GRMZM2G172001, GRMZM2G472991, and GRMZM2G144421 which encoded for proteins and enzymes.

Fifty-six candidate genes were found to be close to SNPs linked to flowering dates, AD and SD. More specifically, 21 candidate genes and one uncharacterized protein were found close to eight SNPs underlying days to 50% anthesis. Seven candidate genes were found close to significant SNPs in chromosome 8 followed by chromosome 2 which had five candidate genes. Some of the candidate genes in chromosomes 1 (GRMZM2G532387), 2 (GRMZM2G073661, GRMZM2G459854, GRMZM2G158629 & GRMZM2G158679) and 3 (GRMZM2G152370)

encoded for usp domain-containing protein, serine/threonine-protein kinase STY46, enoyl-CoA hydratase 2, rop guanine nucleotide exchange factor 1 and zinc finger CCCH domain-containing protein 59. Serine/threonine-protein kinase STY46 was coded for by two candidate genes, GRMZM2G073661 and GRMZM2G459854, located upstream of S2_184536913 and S2_196865748 in chromosome 2, respectively. In chromosome 8, GRMZM2G380414 found close to S8_16444445 coded for Ultraviolet-B-repressible protein while other genes (GRMZM2G136158, GRMZM2G035595, GRMZM2G007057 and GRMZM2G136121) close to S8_3240791 encoded for peroxidase, hydroxyproline O-arabinosyltransferase, ubiquitin-conjugating enzyme E2 20 and 1-phosphatidylinositol 4-kinase, respectively.

A total of 34 candidate genes inclusive of uncharacterized proteins were found close to 12 significant SNPs associated with 50% days to silking. Fifteen candidate genes were found in chromosome 5 while the rest were close to significant SNPs in chromosomes 1, 2 3, 8 and 10. Several of these candidate genes encoded for enzymes involved in metabolic functions. A gene model, GRMZM2G171830, found upstream of S2_96784848 encoded for Protein TIFY 10B whereas GRMZM2G051491, GRMZM2G051534 and GRMZM2G353024 in close proximity with S2_151568759 encoded for cysteine desulfurase 1 chloroplastic, Mannan endo-1 and Root phototropism protein 2, respectively. Three candidate genes (GRMZM2G006277, GRMZM2G177220 and GRMZM2G113264) located close to S3_166013552 in chromosome 3 encoded for SANT/Myb domain-containing protein, two-component response regulator and protein ACTIVITY OF BC1 COMPLEX KINASE 8. Out of the fifteen candidate genes found in chromosome 5, GRMZM2G075158 and GRMZM2G075562 encoded for Calcium-dependent protein kinase 14 and Zinc finger protein CONSTANS-LIKE 9, respectively. At chromosome 8, two candidate genes (GRMZM2G111898 and GRMZM2G095964) close to S8_152440663 encoded for putative LRR receptor-like serine/threonine-protein kinase and homeobox protein Hox-D11-like. Further, GRMZM2G065538 close to S8_152440663 coded for AP2/ERF and B3 domain-containing transcription repressor TEM1.

For plant height, 33 candidate genes close to 10 significant SNPs were identified. Chromosomes 1, 3 and 7 had 8, 6 and 6 candidate genes, respectively. Two candidate genes, GRMZM2G131443 and GRMZM5G854138, close to significant SNPs in chromosome 2 encoded for SCD domain-containing protein and abscisic stress ripening, respectively. Eleven candidate genes were close to

five SNPs associated with EH. Chromosomes 1 and 9 had four candidate genes each. A gene in chromosome 4, GRMZM2G029573, found close to S4_160460503 encoded for Carbamoyl phosphate synthetase A isoform 2. Nineteen candidate genes were found close to 8 significant SNPs associated with HC with 8 and 6 candidate genes found in chromosomes 4 and 5, respectively. Two candidate genes in chromosome 5 (GRMZM2G029850 & GRMZM2G057766) encoded for HTH myb-type domain-containing protein and chitinase 2, respectively, while GRMZM5G862101 found close to S9_5004370 in chromosome 9 encoded for HVA22-like protein A.

Table 4. 3 List of significant SNPs, chromosomal positions, percentage PVE and associated genes for grain yield and agronomic traits of hybrids evaluated under artificial and natural *Striga* infestation.

SNP	chr	*P* value	MAF	PVE (%)	Gene model	Gene description
Grain yield						
S2_71314591	2	1.15689E-13	0.19	22.4	GRMZM2G096048	protein indeterminate-domain 16
S2_184536913	2	1.44376E-07	0.27	10.0	GRMZM2G073661	Serine/threonine-protein kinase STY46
					GRMZM5G820822	Oryzain gamma chain
S3_156434858	3	2.49774E-16	0.20	12.8	GRMZM2G338259	Auxin response factor
					GRMZM2G173534	Inducer of CBF expression 2
S4_10697227	4	3.65E-06	0.39	3.8	GRMZM2G300862	Aspartate kinase
					GRMZM2G133757	CCR4-NOT transcription complex subunit 11
					GRMZM2G407605	Protein-serine/threonine phosphatase
S8_164741092	8	3.00885E-07	0.20	8.0	GRMZM2G172001	PHD finger protein ALFIN-LIKE 6
					GRMZM2G472991	Non-specific serine/threonine protein kinase
					GRMZM2G172829	AAA ATPase domain
S9_21721916	9	4.48799E-10	0.38	3.9	GRMZM2G144440	Aspartic proteinase A1
					GRMZM2G144421	auxin-induced protein 15A-like
					GRMZM2G376918	Protein-methionine-S-oxide reductase
Days to 50% anthesis (AD)						
S1_248750895	1	3.20286E-07	0.10	10.6	GRMZM2G532387	Usp domain-containing protein
					GRMZM2G083437	Nucleolar protein 14
S2_184536913	2	1.44376E-07	0.27	10.0	GRMZM2G073661	Serine/threonine-protein kinase STY46
					GRMZM5G820822	Oryzain gamma chain
S2_196865748	2	4.65214E-12	0.10	14.4	GRMZM2G158629	enoyl-CoA hydratase 2

					GRMZM2G459854	Serine/threonine-protein kinase STY46
					GRMZM2G158679	Rop guanine nucleotide exchange factor 1
S3_7606050	3	5.39E-07	0.38	13.4	GRMZM2G152370	Zinc finger CCCH domain-containing protein 59
S8_16444445	8	4.72859E-09	0.10	31.8	GRMZM2G380414	Ultraviolet-B-repressible protein
					GRMZM2G136158	Peroxidase
					GRMZM2G035595	Hydroxyproline O-arabinosyltransferase
					GRMZM2G007057	ubiquitin-conjugating enzyme E2 20
S8_3240791	8	6.12913E-08	0.25	4.4	GRMZM2G136121	1-phosphatidylinositol 4-kinase
					GRMZM2G007258	uncharacterized protein LOC100192752
					GRMZM2G036070	Putative 26S proteasome complex subunit sem1-1
					GRMZM2G045981	Somatic embryogenesis receptor kinase 5-like
S9_146336181	9	5.97644E-08	0.12	3.2	GRMZM2G051782	Tubulin alpha chain
					GRMZM2G051689	Random slug protein 5
					GRMZM2G150901	Polyadenylate-binding protein-interacting protein 3
S10_143174294	10	5.04773E-08	0.43	0.5	GRMZM2G021885	Myosin heavy chain-related
					GRMZM2G326066	60S ribosomal protein L27
					GRMZM2G096107	SIT4 phosphatase-associated family protein
Days to 50% silking (SD)						
					GRMZM2G096020	4-coumarate--CoA ligase-like 4
					GRMZM2G057158	Ubiquitin family protein
S1_7297183	1	2.22763E-12	0.28	4.0	GRMZM2G040887	Putative plant ubiquilin
					GRMZM2G132019	Calcium-dependent protein kinase 23 isoform 4
S2_96784848	2	5.48876E-18	0.24	11.3	GRMZM2G171830	Protein TIFY 10B
					GRMZM2G051491	Cysteine desulfurase 1 chloroplastic
S2_151568759	2	7.33682E-09	0.08	8.0	GRMZM2G051534	Mannan endo-1
					GRMZM2G353024	Root phototropism protein 2
S3_212155729	3	2.22941E-08	0.10	3.4	GRMZM2G070360	V-type proton ATPase subunit E
					GRMZM2G117851	G-box-binding factor 3
					GRMZM2G006277	SANT/Myb domain-containing protein
S3_166013552	3	7.72732E-09	0.16	9.3	GRMZM2G177220	Two-component response regulator
					GRMZM2G113264	Protein ACTIVITY OF BC1 COMPLEX KINASE 8
S5_203211045	5	1.36E-06	0.42	3.9	GRMZM2G038375	Outer envelope pore protein 16-3

					GRMZM2G024211	Alpha/beta-Hydrolases superfamily protein
					GRMZM2G012213	Pentatricopeptide repeat-containing protein
S5_204318058	5	3.18E-06	0.41	4.3	GRMZM2G012044	Cellulose synthase-like protein E1
					GRMZM2G011951	Uclacyanin-2
					GRMZM2G494600	Aquaporin SIP1-1
					GRMZM5G845775	Pumilio homolog 24
					GRMZM2G075158	Calcium-dependent protein kinase 14
S5_204229832	5	3.30E-06	0.42	3.2	GRMZM2G075372	TPT domain-containing protein
					GRMZM2G075562	Zinc finger protein CONSTANS-LIKE 9
					GRMZM2G012213	Pentatricopeptide repeat-containing protein
					GRMZM2G494600	Aquaporin SIP1-1
S5_204331742	5	1.99665E-08	0.34	4.7	GRMZM2G012044	Cellulose synthase-like protein E1
					GRMZM2G011951	Uclacyanin-2
					GRMZM5G845775	Pumilio homolog 24
					GRMZM2G111898	Putative LRR receptor-like serine/threonine-protein kinase
S8_11920667	8	2.70659E-11	0.10	19.1	GRMZM2G095964	homeobox protein Hox-D11-like
					GRMZM2G077187	acidPPc domain-containing protein
S8_152440663	8	3.60124E-10	0.21	3.9	GRMZM2G065538	AP2/ERF and B3 domain-containing transcription repressor TEM1
					GRMZM2G139407	Nuclear transport factor 2 (NTF2) family protein with RNA binding (RRM-RBD-RNP motifs) domain
S10_106429588	10	2.07694E-11	0.30	3.9	GRMZM2G139512	Chloroplastic quinone-oxidoreductase
Plant height (PH)						
					GRMZM2G123527	Transmembrane protein 70
					GRMZM5G832651	GCFC domain-containing protein
					GRMZM2G100020	Brevis radix-like domain-containing protein
S1_298963206	1	4.3668E-08	0.18	4.6	GRMZM2G422670	Non-specific phospholipase
					GRMZM2G422671	Expressed in cucumber hypocotyls
					GRMZM2G099987	Ribonuclease P protein subunit P38-related
					GRMZM2G353147	GTP diphosphokinase
S1_56929946	1	1.52438E-07	0.16	7.2	GRMZM2G069618	Sperm-associated antigen 1A
					GRMZM2G453008	Unknown
S2_230358799	2	1.05482E-09	0.22	4.6	GRMZM2G131443	SCD domain-containing protein

					GRMZM2G134559	2-oxoglutarate and Fe(II)-dependent oxygenase superfamily protein
S2_139077719	2	4.64434E-08	0.18	14.7	GRMZM5G854138	Abscisic stress ripening
					GRMZM2G380195	Chlororespiratory reduction 2
					GRMZM2G384090	uncharacterized protein LOC100276757
S3_18015666	3	3.00E-06	0.46	2.8	GRMZM2G085713	glucose-induced degradation protein 4 homolog
					GRMZM2G100881	Transcription factor IIS
					GRMZM2G100898	Factor of DNA methylation 1
					GRMZM2G079625	Scarecrow-like transcription factor 11 (SCL11)
					GRMZM2G084984	Haloacid dehalogenase-like hydrolase domain-containing protein
					GRMZM2G402319	Nicotinamide-nucleotide adenylyltransferase
S4_171665338	4	8.47711E-10	0.39	4.3	GRMZM2G099097	Aldehyde oxygenase (deformylating)
					GRMZM2G102163	Receptor-like serine/threonine-protein kinase ALE2
					GRMZM2G384780	Anther-specific proline-rich protein APG
S5_119136457	5	3.71E-08	0.10	3.2	GRMZM5G823524	Unknown
					GRMZM2G056143	integral component of membrane
					GRMZM2G119705	rRNA N-glycosidase
					GRMZM2G056075	DNA mismatch repair protein MSH2
S7_162758515	7	2.52054E-07	0.50	1.4	GRMZM2G418899	Scarecrow-like protein 6
					GRMZM2G008468	Golgi transport 1 protein B
					GRMZM2G119740	Putative transcriptional regulator UXT
S9_86203364	9	3.69311E-10	0.32	8.2	GRMZM2G114672	ACB domain-containing protein
					GRMZM2G443728	Potassium transporter
S9_98687413	9	2.57904E-07	0.27	2.9	GRMZM2G144142	Pentatricopeptide repeat-containing protein
					GRMZM2G443715	Glucomannan 4-beta-mannosyltransferase 9
Ear height (EH)						
					GRMZM2G077780	Bifunctional fucokinase/fucose pyrophosphorylase
S1_3197144	1	2.12913E-07	0.43	3.3	GRMZM2G077669	Molybdate-anion transporter
					GRMZM2G092232	kinesin-like protein KIN-14R
					GRMZM2G124550	serine/threonine-protein kinase sid1 isoform X1

S3_146251234	3	2.99703E-08	0.28	7.4	GRMZM2G309512	Receptor-like serine/threonine-protein kinase
S3_143698441	3	2.56795E-07	0.16	4.8	GRMZM2G102174	Tudor/PWWP/MBT superfamily protein
S4_160460503	4	3.98638E-09	0.29	47.4	GRMZM2G029573	Carbamoyl phosphate synthetase A isoform 2
					GRMZM2G005869	Non-specific serine/threonine protein kinase
S9_131567877	9	2.20E-06	0.28	1.9	GRMZM2G006080	Protein kinase domain-containing protein
					GRMZM2G006178	Putative molybdate-transporting ATPase
					GRMZM2G027499	uncharacterized LOC100275583
Husk cover (HC)						
S3_58669935	3	5.94384E-10	0.28	4.7	GRMZM2G080262	Replicase polyprotein 1a
					GRMZM2G378547	Pto-interacting protein 1
S3_22388359	3	3.12458E-07	0.50	2.5	GRMZM2G362949	Heavy metal-associated isoprenylated plant protein 26-like
					GRMZM2G007615	Translation initiation factor IF-2-like
					GRMZM2G091044	PLATZ transcription factor
S4_157482501	4	5.08906E-09	0.41	4.3	GRMZM2G091069	Ubiquitin carboxyl-terminal hydrolase
					GRMZM2G091003	Transcription factor FAMA
					GRMZM2G428027	Nitrate reductase
					GRMZM2G126732	1-aminocyclopropane-1-carboxylate oxidase
S4_177653268	4	1.72536E-07	0.42	4.8	GRMZM2G126765	Putative tyrosine-protein phosphatase
					GRMZM2G126646	Homeobox-leucine zipper protein ROC8
					GRMZM2G126795	CopI
					GRMZM2G062151	Cytochrome P450
S5_193534899	5	8.24382E-10	0.19	6.5	GRMZM2G465957	Unknown
					GRMZM2G061938	Copper ion binding
S5_216836829	5	1.77E-05	0.40	3.6	GRMZM2G043331	beta-catenin-like protein 1
S5_197606529	5	2.31082E-08	0.34	12.8	GRMZM2G029850	HTH myb-type domain-containing protein
					GRMZM2G057766	Chitinase 2
S9_5004370	9	3.31705E-08	0.47	25.3	GRMZM5G862101	HVA22-like protein a

Chr, chromosome; MAF, minor allele frequency.

4.4 Discussion

4.4.1 Phenotypic performance of the hybrids

There were variable number of emerged *Striga* plants among the hybrids and the severity of *Striga* damage was equally variable. Significant genetic variations observed across the traits indicate that there was successful introgression of *Striga* resistance genes into the CIMMYT elite lines from the IITA donor lines. Hence, the broadened *Striga* genetic pool allow for selection and improvement of desirable traits in maize breeding programs. Genetic variability has been reported among tropical early and extra early white and yellow maize lines with *Zea diploperennis* background (Badu-Apraku *et al.*, 2020a, c; Adewale *et al.*, 2020; Stanley *et al.*, 2021). There was, however, high significant G×E interaction variances across traits suggesting that environmental factors such as variable temperature and rainfall patterns and soil types could have played a critical role in determining the performance of maize hybrids under *Striga* stress. As a complex trait, *Striga* resistance has been reported to exhibit high environmental influence leading to relatively low to moderate trait heritability (Ejeta & Butler, 1993).

The observed genotypic variance and moderate heritability for most *Striga* resistance parameters suggest that genetic improvement for *Striga* resistance is feasible. The moderate to high heritability of *Striga* resistance traits indicates that these traits are genetically controlled and can be improved through selection. Further, the higher heritability for *Striga* damage ratings compared to the number of emerged *Striga* plants suggests that selection based on damage ratings may be a more reliable selection criterion for breeding *Striga*-resistant maize. This is aligned with the findings of Adewale *et al.* (2020) and Gowda *et al.* (2021), who reported high (67–84%) broad sense heritability for *Striga* damage rating and moderate to high heritability for emerged number of *Striga* plants (47–68%). Badu Apraku *et al.* (2020b) also reported moderate (48%) and low (8%) heritability for *Striga* damage rating and emerged number of *Striga* plants respectively. However, the findings of this study contrast with studies that have reported either similar (Okunlola *et al.*, 2022) heritability for the two traits or lower heritability for *Striga* damage rating than the emerged number of *Striga* plants (Badu-Apraku *et al.*, 2020a). These discrepancies could be attributed to variations in the genetic background of the germplasm (Badu-Apraku & Fakorede., 2017), densities of *Striga* seed banks as well as environmental and G × E interactions. The extent of genetic diversity within a population strongly influences heritability, as populations with broader genetic bases tend to exhibit greater additive genetic variance (Hallauer et al., 2010; Falconer & Mackay, 1996).

Testcross hybrids demonstrated superior performance in terms of grain yield and *Striga* resistance compared to the commercial check hybrids. This suggests that the testcrosses possess favorable alleles for these traits, making them valuable for developing *Striga*-resistant and high-yielding maize varieties. The high performance of the testcross hybrids in relation to the checks can also be attributed to fewer *Striga* plants and less severe damage exhibited by the test hybrids. Strong positive correlations were found among *Striga* resistance parameters which negatively correlated with plant height (PH) and ear height (EH). The negative correlations between *Striga* resistance parameters and plant/ear height imply that taller plants tend to be more resistant to *Striga* and can indirectly improve yield under *Striga* infestation. The strong negative correlations of *Striga* damage ratings with grain yield further highlight the detrimental impact of *Striga* on maize productivity. Previous studies have reported similar results with r=-0.58**– -0.75** (Adewale *et al.,* 2020; Badu-Apraku *et al.,* 2020 a, c; Gowda *et al.,* 2021; Okunlola *et al.,* 2022; Badu-Apraku *et al.,* 2023). Badu-Apraku *et al.* (2020 b) computed genotypic correlations with the same trends, r=-0.96** for *Striga* damage rating at 12WAP and r=-0.05 for emerged *Striga* plants. However, the positive correlation between *Striga* damage rating and emerged *Striga* plants alludes to the importance of using the two traits as selection criteria in *Striga* breeding programs (Gowda *et al.,* 2021).

4.4.2 Marker trait associations

Association analysis was carried out using phenotypic and genotypic data (151, 670 SNP markers) of 155 early maturing F_6 maize inbreds. Significant *Striga* resistance SNP identification provides valuable information on putative markers for breeding programs. In the present study, important genomic regions were identified in several loci on chromosomes 1, 2, 3, and 6 marked by significant SNPs associated with emerged *Striga* plants. Similar findings have been reported (Gowda *et al.,* 2021; Stanley *et al.,* 2021; Badu-Apraku *et al.,* 2023). For *Striga* damage rating, the most important genomic regions were found in several loci on chromosomes 5, 6 and 7 which aligns with the findings of Stanley *et al.* (2021) and Okunlola *et al.* (2022). From the present study, SNPs on chromosome 6 accounted for high phenotypic variation for *Striga* resistance parameters, making it a key target for breeding efforts. Important genomic regions with significant SNPs associated with grain yield were located in chromosomes 2 and 3 highlighting these regions as important for yield improvement. Previous studies have also reported similar findings (Badu-Apraku *et al.,* 2020a, c; Gowda *et al.,* 2021; Badu-Apraku *et al.,* 2023). On the other hand, chromosomes 1, 2, 3 and 8 were important for flowering dates while chromosomes 2 and 4 accounted for high %PVE for PH and EH, respectively. The genetic architecture of agronomic traits has not been studied before.

4.4.3 Candidate genes

The identified genes associated with *Striga* resistance, grain yield and agronomic traits can be broadly categorized into several functional groups, each providing insights into various mechanisms that contribute to the plant's defense against this parasitic weed. These groups include transcription factors, hormone signaling, signal transduction, protein modification and degradation, and stress response and maintenance. The interplay between different genes and their respective pathways highlights a complex network of responses activated during *Striga* parasitism. These genes are involved in a range of functions, from stress signaling and hormone regulation to protein modification and metabolic adjustments.

The transcription factors (TFs) are part of complex signaling networks that allow plants to perceive and respond to a variety of stress signals. By regulating the expression of genes involved in stress tolerance, TFs play vital roles in modulating the expression of stress-responsive genes. The current study reports some genes that are directly involved in recognizing *Striga* attack and triggering immediate defense responses (e.g., WRKY transcription factors), while others modulate hormone signaling pathways (e.g., ethylene-responsive transcription factors) or maintain cellular homeostasis (e.g., CLP protease regulatory subunit CLPX1). WRKY domain-containing proteins, for example, located 1.1 and 5.9 kb upstream of a gene locus on chromosome 3 (S3_8219084), were found to regulate the expression of genes involved in plant defense, stress responses, and hormone signaling. In assessing gene expression under *S. hermonthica* and *S. gesnerioides* infestation, Swarbrick *et al.* (2009) and Huang *et al.* (2012) reported upregulation of WRKY TFs on rice and cowpea roots, respectively. These proteins were found to be essential in modulating the plant's response to *Striga* infestation by activating defense genes involved in stress signaling pathways including salicylic acid pathway and jasmonic acid pathway in rice (Mutuku *et al.,* 2015). A more recent study underscored the activation of WRKY-dependent signaling pathway resulting in hypersensitive response of sorghum under *Striga* infestation (Mutinda *et al.,* 2023). In maize, WRKY TFs have been implicated in *Striga* resistance (Badu-Apraku *et al.,* 2020a, c; Stanley *et al.,* 2021; Badu-Apraku *et al.*, 2023).

Similarly, ethylene-responsive transcription factor ABR1 mediates responses to ethylene, a hormone involved in stress signaling by regulating genes that enhance the plant's defensive capabilities under pathogen attack (Chaffai *et al.,* 2024). Other transcription factors such as bHLH66, bHLH85, and bHLH49, part of the basic helix-loop-helix family, play roles in various stress responses, including those against pathogens, potentially activating genes

involved in reinforcing cell walls and producing defensive compounds (Badu-Apraku *et al.*, 2020a, c; Stanley *et al.*, 2021; Gowda *et al.*, 2021; Badu-Apraku *et al.*, 2023). AP2-like ethylene-responsive transcription factor ANT, similar to ABR1, is involved in ethylene signaling and may regulate genes that bolster the plant's defenses. Homeodomain-like transcription factors and MYB86 are also involved in regulating developmental processes and stress responses, which can be crucial in mitigating *Striga*'s impact, while WRI1 helps in adjusting metabolic processes during *Striga* stress to maintain cellular functions (Huang *et al.*, 2012; Mutuku *et al.*,2015; Badu-Apraku *et al.*, 2020a, c; 2023). Transcription factors like Inducer of CBF expression 2 and Ultraviolet-B-repressible protein help the plant adapt to environmental stresses by regulating the expression of stress-responsive genes.

Hormone signaling pathways are also pivotal, with genes like drought-induced 19 and the ethylene-responsive transcription factor WRI1, as well as the protein OVEREXPRESSOR OF CATIONIC PEROXIDASE 3, indicating that hormonal regulation and oxidative stress response are significant components of the plant's defense mechanisms (Verma *et al.*, 2016). These genes likely contribute to the modulation of physiological and biochemical processes that help the plant manage the adverse effects of *Striga* parasitism. Signal transduction pathways are essential for perceiving stress signals and activating appropriate responses (Kacperska, 2004). Proline-Rich Receptor-Like Protein Kinase PERK4, for instance, is involved in recognizing external signals and initiating downstream signaling pathways that activate defense mechanisms against the pathogen. Signal recognition particle 19 kDa protein aids in targeting newly synthesized proteins to their proper cellular locations, which is crucial during stress responses to ensure that defense proteins are correctly localized. Protein-serine/threonine phosphatases play a critical role in dephosphorylating target proteins, thus modulating their activity in stress signal transduction pathways. The CLP protease regulatory subunit CLPX1 (CLPX) is involved in protein quality control, ensuring that damaged or misfolded proteins are degraded, thus maintaining cellular homeostasis during stress. Xyloglucan galactosyltransferase KATAMARI1 and Exostosin domain-containing protein are both components of salicylic acid mediated signaling pathway. Signal transduction factors, including Serine/threonine-protein kinase STY46 and Putative LRR receptor-like serine/threonine-protein kinase, are essential for transmitting external signals to elicit appropriate cellular responses, coordinating growth, development, and defense mechanisms.

Furthermore, genes involved in protein modification processes such as ubiquitination play crucial roles in maintaining cellular homeostasis under stress conditions (Gowda *et al.*, 2021;

Stanley *et al.*, 2021). Protein modification and degradation systems are vital for maintaining protein homeostasis under stress conditions (Karve & Cheema, 2011). Ubiquitin-related proteins, such as the ubiquitin receptor RAD23, RING-type E3 ubiquitin transferase, E3 ubiquitin ligase, ubiquitin-conjugating enzyme E2 36, Usp domain-containing protein and E3 ubiquitin-protein ligase RGLG1are key players in tagging damaged or misfolded proteins for degradation. This process helps in removing proteins that could potentially accumulate and cause cellular toxicity under stress conditions. The involvement of these ubiquitin-related proteins suggests a robust protein quality control system is crucial for managing *Striga*-induced stress. For example, protein ubiquitination for cellar homeostasis has recently been reported in cowpea (Su *et al.*, 2020; Koura *et al.*, 2024).

Stress response and maintenance proteins ensure that cellular functions continue under adverse conditions. Cysteine dioxygenase and Thioredoxin-dependent peroxiredoxin aid in maintaining cellular redox balance thus managing oxidative stress by detoxifying reactive oxygen species (ROS) while Adrenodoxin-like protein 2 is involved in P450-containing electron transport chain, ensuring energy production and overall cellular health during stress. Putative membrane protein while YuiD is an integral member of the membrane known for cellular oxidant detoxification and peroxidase activity. Lysosomal Pro-X Carboxypeptidase participates in protein degradation and turnover, helping manage cellular protein quality under stress conditions.

Moreover, several enzymes identified, such as lipoxygenase, formylglycinamide and anthranilate synthase ribonucleotide amidotransferase enzymes are involved in oxidoreductase activity and stress response. These enzymes help produce molecules such as leukotrienes and lipoxins that can directly inhibit pest growth or signal other parts of the plant to bolster their defenses. Similar findings have been reported in sorghum (*Sorghum bicolor*) (Hiraoka & Sugimoto, 2008) and barrelclover (*Medicago truncatula*) (Dita *et al.*, 2009) in response to the parasitic weeds, *S. hermonthica, O. crenata*, respectively. The involvement of carbohydrate-active enzymes, like Putative carbohydrate esterase, xyloglucan galactosyltransferase KATAMARI1 and hexosyltransferase, indicates an active modification of the cell wall structure, making it more difficult for *Striga* to penetrate and establish itself. Signaling pathways and kinases, represented by genes like 1-phosphatidylinositol 4-kinase and MAPK kinase substrate, are vital for transducing stress signals and initiating appropriate cellular responses. These genes play a role in the activation of downstream effectors that mediate stress adaptation. Metabolic enzymes, including glycosyltransferase, ceramide glucosyltransferase,

fructose-bisphosphate aldolase, and feruloyl-arabinoxylan b-1,2-xylosyl transferase, are involved in various biochemical pathways that modulate the plant's metabolism during stress. These enzymes likely contribute to the synthesis and modification of essential biomolecules that support cell structure, energy production, and signaling. Finally, protein phosphatases and hydrolases, including protein-serine/threonine phosphatases and the metallo-dependent hydrolases superfamily protein pseudogene, play a role in the reversible phosphorylation of proteins, a key mechanism in regulating protein function and signaling pathways.

4.5 Conclusion

Genetic and G×E variances were significant for all traits. G×E variances were higher than the genetic variances. Heritability was moderate to high for *Striga* resistance parameters (48−64% with *Striga* damage rating showing higher heritability (62−64%). Broad sense heritability for grain yield was 39% while that of agronomic traits was 46−86%. The test hybrids performed better than the checks in all traits i.e. the test hybrids yielded more, sustained fewer *Striga* plants and showed less damage compared to all the checks. *Striga* parameters were negatively associated with plant height. There were strong negative correlations between *Striga* resistance parameters and plant height (r=-0.27—0.68). *Striga* damage rating negatively affected, plant height (r = -0.66*** – -0.68***), ear height (r = -0.42*** – -0.43***) and grain yield (-0.47*** – -0.56***). Association analysis identified 42, 6 and 43 significant SNPs associated with *Striga* resistance parameters, grain yield and agronomic traits with 10, 3 and 8 SNPs explaining more that 10% phenotypic variance for these traits, respectively. Consequently, the study identified 112, 14 and 119 putative genes associated with *Striga* resistance parameters, grain yield and agronomic traits, respectively. The candidate genes were associated with molecular functions and biological processes involved in plant growth and development and modulation of plant defense against stress. WRKY domain-containing proteins, for example, located 1.1 and 5.9 kb upstream of a gene locus on chromosome 3 (S3_8219084), were found to regulate the expression of genes involved in plant defense, stress responses, and hormone signaling. The results point to the feasibility of identifying molecular markers that can be applied in marker assisted breeding in *Striga* resistance maize breeding programs.

CHAPTER FIVE

GENOMIC PREDICTION OF THE PERFORMANCE OF TROPICAL DOUBLED HAPLOID MAIZE LINES UNDER ARTIFICIAL *STRIGA HERMONTHICA* (DEL.) BENTH. INFESTATION

5.1 Introduction

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. 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.

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 (QTLs) related to *Striga* resistance have been reported (Badu-Apraku *et al.,* 2020a, c; 2023). Genome-wide association studies (GWAS) 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.,* 2022). 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 non-additive effects of lines (Crossa *et al.*, 2017; Bonnett *et al.*, 2022). Estimation of additive gene effects allows for selection in early generations such as F_2 (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 is 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 non-parametric statistical and computational models that account for both genetic and non-genetic effects have been developed to estimate genomic breeding values (GEBVs) (Crossa *et al.*, 2017). Additionally, linear and non-linear kernels that are based on genomic relationship matrices have been reported to be better than the conventional methods (Crossa *et al.*, 2022). Non-linear 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. 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 *Striga hermonthica* still presents a major challenge. The objectives of this study were to (i) estimate variance components and heritability among the hybrids used in the study; (ii) assess the efficiency of genomic prediction for *Striga* resistance associated traits and grain yield using the reaction norm model, and (iii) predict the genetic values of field tested and untested DH lines.

5.2 Materials and methods

5.2.1 Genetic material

This study utilized 606 DH lines developed by CIMMYT at the Maize DH Facility in Kiboko, Kenya (Appendix, Table 4). The DH lines were developed from induction of F_2 and BC_1F_2 populations formed by crossing *Striga* resistant donor lines from IITA with elite mid-altitude tropical maize lines developed by CIMMYT (Fig. 5.1). 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 (imazaypr) resistance. Some F_1 crosses were advanced to F_2 while others were planted alongside either the IITA donor lines or the adapted CIMMYT lines and crossed to form BC_1F_1. The BC_1F_1 were selfed to form BC_1F_2 populations which were then submitted for DH induction. There were 171 and 435 DH lines developed from F_2 and BC_1F_2 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 two inbred line testers from IITA to form 232 testcross hybrids.

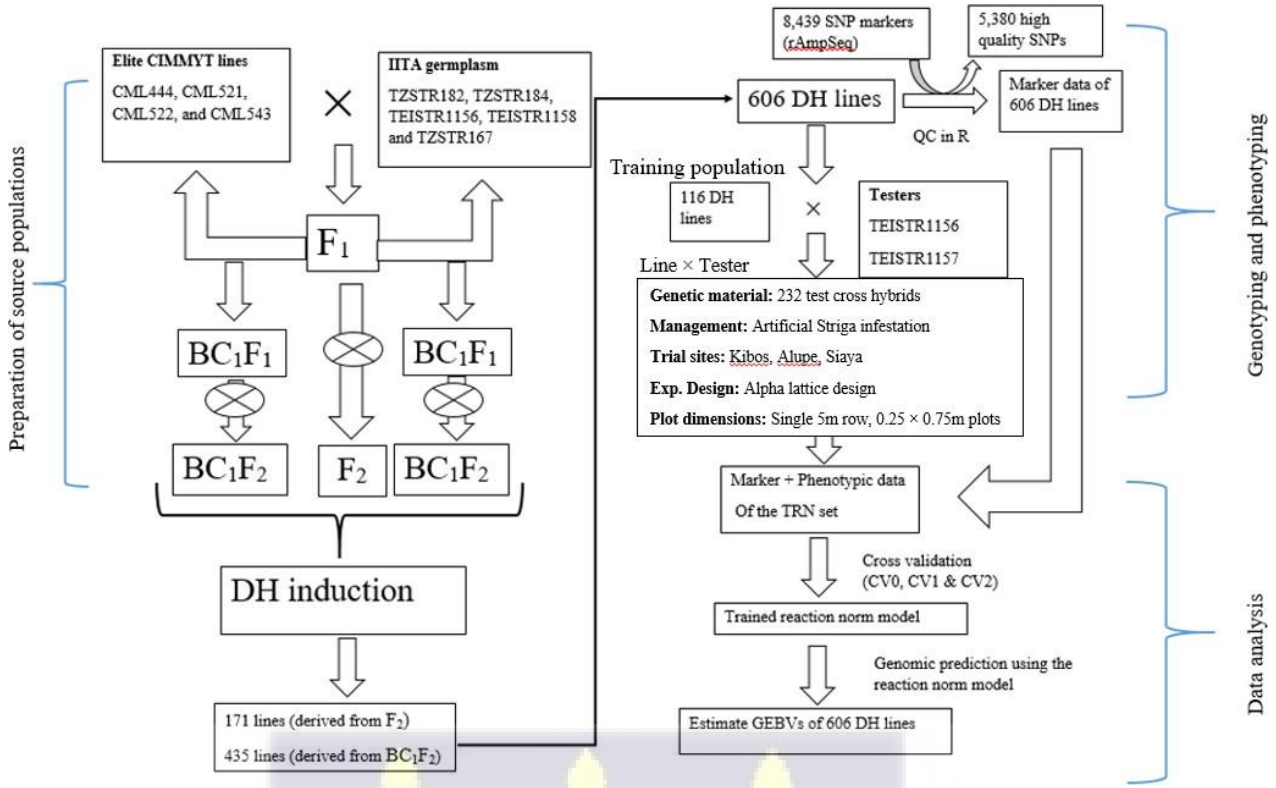


Fig. 5. 1Breeding scheme followed in the development of DH populations, testcross formations, phenotyping, genotyping and subsequent genomic prediction following reaction norm model.

5.2.2 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 two 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 two internal genetic gain checks and six commercial checks while Trial 2 had two internal genetic gain checks and seven commercial checks. The experimental design was 4 × 47 and 4 × 45 alpha-lattice with two 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, Alupe and Siaya, Table 5.1. All locations have a bimodal rainfall distribution (March–July and September–November), with most of the rain falling between March–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 (Alister and Kogan, 2005) kills *Striga* seed in the soil.

Table 5. 1 Characteristics of the trial locations used in the phenotyping of the training population in 2020

Location	Latitude	Longitude	Altitude (m)	Soil type
Kibos	0º2'S	34º48E	1193	Eutric Cambisol
Alupe	0º30'N	34º7E	1250	Orthic Ferralsol
Siaya	03º10'N	34º17E	1288	Plinthic Ferralsol

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 10g 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 to 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 topdressing at 4 weeks after planting. Agronomic practices including hand weeding were performed at all locations during the growth seasons.

5.2.3 Data collection

5.2.3.1 Phenotypic data

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 weeks after planting (WAP). The SDR was recorded at 10 (SDR1) and 12WAP (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.*, 1994). The area under *Striga* number progress curve (AUSNPC) was computed from the three STR plant counts (8, 10, and 12 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 ith 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.

5.2.3.2 Genotypic data

Leaf samples of the 606 DH inbred lines were collected three weeks after planting 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 (PAV) format where one (1) and zero (0) denoted present or absent, respectively. For the 606 DH lines, 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 (MAF) <0.05 and those whose variances were equal to zero 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.

5.2.4 Statistical analysis

5.2.4.1 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). A linear mixed model in which genotype effect was considered as fixed and random

was used to compute the best linear unbiased estimates (BLUEs) and the best linear unbiased

predictions (BLUPs), 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 factors in the model were considered as random effects. Single site analysis using linear mixed model was performed as;

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

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. It was assumed that $\varepsilon \sim NIID(0, \sigma^2)$, where *NIID* is normal independent and identically distributed random variables, σ^2 is the associated variance parameter.

After individual analysis, data was analyzed combined across locations with a linear mixed model using ASREML-R version 4.2 (Butler *et al.*, 2009). After here, 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 zero and homoscedastic variance σ_s^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:

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

where H_a^2 the broad sense heritability for individual environments is, 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:

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

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 and 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.

5.2.4.2 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; $\boldsymbol{G} = \boldsymbol{M}/p$, where $\boldsymbol{M}$ is the matrix of markers centered and standardized by column (mean and variance zero 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 three 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:

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

where $\boldsymbol{y}$ is the BLUEs of the response vector (number of emerged *Striga* plants, *Striga* damage rating, AUSNPC or grain yield), $\boldsymbol{Z}_E$ is a design matrix for environments (locations), $\boldsymbol{\beta}_E$ is the vector effect of the environments, $\boldsymbol{\beta}_E \sim MN(\boldsymbol{0}, \sigma_E^2\boldsymbol{I})$, where MN is multivariate normal distribution, $\boldsymbol{0}$ is a vector or zeros, σ_E^2 is the variance parameter associated with environments and $\boldsymbol{I}$ is the identity matrix; $\boldsymbol{Z}_g$ is a matrix that connects phenotypes with genotypes, and $\boldsymbol{g}$ is the vector of random effects of genotypes. We assumed $\boldsymbol{g} \sim MN(\boldsymbol{0}, \sigma_g^2\boldsymbol{G})$ with σ_g^2 the variance associated to the genotypes, $\boldsymbol{G}$ is a genomic relationship matrix (López-Cruz *et al.*, 2015); $\boldsymbol{u}$ represents the interaction, we assumed $\boldsymbol{u} \sim MN(\boldsymbol{0}, \sigma_{g\times E}^2 \boldsymbol{Z}_g\boldsymbol{G}\boldsymbol{Z}_g^t \# \boldsymbol{Z}_E\boldsymbol{Z}_E^t)$, with $\sigma_{g\times E}^2$ the variance parameter associated to the interaction and # representing the element-wise product of two matrices. Finally, $\boldsymbol{e}$ represents the error, assuming $\boldsymbol{e} \sim MN(\boldsymbol{0}, \sigma_e^2\boldsymbol{I})$, with σ_e^2 the variance associated to the error. Furthermore, we also assumed that $\boldsymbol{\beta}_E, \boldsymbol{g}, \boldsymbol{u}$ and $\boldsymbol{e}$ 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.

5.2.4.3 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), two 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 (CV0) involving use of phenotypic data from two 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).

5.3 Results

5.3.1 Analysis of variance and testcross performance

Analysis of variance at individual locations showed significant variation among the hybrids for all the traits measured (Table 5.2). 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 two locations. The mean number of emerged *Striga* plants at 8WAP was the lowest at Alupe (7), but the same location recorded the highest mean number of emerged *Striga* plants at 10WAP and 12WAP (Fig. 5.2). The *Striga* damage rating (SDR), at 10WAP, 12WAP, and the average SDR were highest at Siaya and lowest at Alupe (Fig. 2). The AUSNPC was lowest at Kibos and Siaya (190 m^2). Mean grain yield was highest at Alupe (5.3 t ha^{-1}) and lowest at Siaya (3.3 t ha^{-1}).

Table 5. 2 Variance component estimates and heritability for different *Striga* resistance parameters and grain yield at three locations under artificial *Striga* infestation in 2020

Trait	KIBOS			ALUPE			SIAYA		
	$\hat{\sigma}_G^2$	$\hat{\sigma}_\varepsilon^2$	H_a^2	$\hat{\sigma}_G^2$	$\hat{\sigma}_\varepsilon^2$	H_a^2	$\hat{\sigma}_G^2$	$\hat{\sigma}_\varepsilon^2$	H_a^2
STR8WAP	16.75***	63.51	0.35	25.20***	77.05	0.4	16.23***	75.76	0.3
STR10WAP	136.66***	334.54	0.45	133.56***	325.07	0.45	44.14**	303.14	0.23
STR12WAP	275.95***	632.55	0.47	189.14***	408.31	0.48	194.70***	510.89	0.43
SDR1	0.13***	0.37	0.42	0.17***	0.29	0.54	0.20***	1.05	0.28
SDR2	0.19***	0.55	0.41	0.20***	0.49	0.46	0.19***	0.99	0.27
SDR	0.15***	0.38	0.44	0.18***	0.31	0.53	0.19***	0.94	0.29
AUSNPC	1912.02***	4475.35	0.46	1696.94***	3507.76	0.49	925.27***	3844.05	0.32
Grain yield	0.45***	1.47	0.38	0.37***	1.61	0.31	1.01***	1.76	0.53

*, **, ***: Significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

H_a^2, broad-sense heritability; $\hat{\sigma}_G^2$, genotypic variance; $\hat{\sigma}_s^2$, error variance; STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; 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)

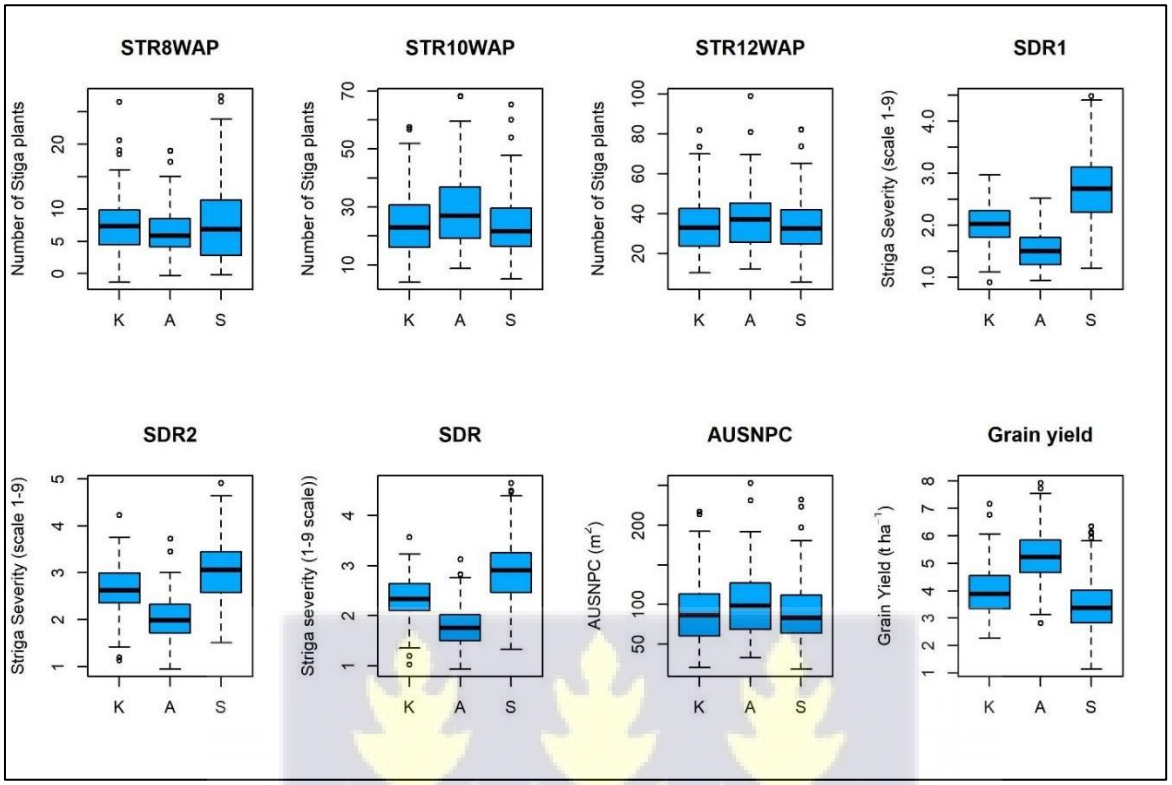


Fig. 5. 2 Boxplots of Striga resistance parameters and grain yield at the three trial locations in Kenya (K, Kibos; A, Alupe; S, Siaya) in 2020.

STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; 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)

Combined analysis of variance under artificial *Striga* infestation revealed highly significant ($P < 0.001$) variation among hybrids for all traits (Table 3). The G × E interaction was significant for all the traits. The $\hat{\sigma}^2_G$ was 3 and 5 times larger than $\hat{\sigma}^2_{GE}$ 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 m^2 with a mean of 102.2 m^2 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 three *Striga* resistance parameters were found (Fig. 3). The correlations between the number of emerged *Striga* plants at 8, 10 and 12WAP, and AUSNPC were high (r = 0.73–0.98). *Striga* damage rating showed significant negative correlation with grain yield (r = -0.73 – -0.79).

Table 5. 3 Summary statistics, variance component estimates and heritability for different Striga resistance parameters and grain yield across three locations under artificial Striga infestation in 2020

Trait	Mean	Range	$LSD_{0.05}$	$\hat{\sigma}^2_G$	$\hat{\sigma}^2_{GE}$	$\hat{\sigma}^2_s$	H^2_b
STR8WAP	8	4–32	6.3	9.24***	9.94***	72.39	0.38
STR10WAP	27	16–82	14.1	80.02***	22.65**	322.99	0.57
STR12WAP	39	21–126	18.4	181.61***	32.99*	520.38	0.65
SDR1	2.1	1.5–3.9	0.6	0.12***	0.05***	0.57	0.51
SDR2	2.6	1.8–4.4	0.6	0.13***	0.06***	0.68	0.49
SDR	2.3	1.6–4.2	0.5	0.11***	0.05***	0.55	0.51
AUSNPC	102.2	59.5–331.0	50.0	1182.87***	295.5**	3966.04	0.61
Grain yield	4.5	3.1–6.1	1.0	0.40***	0.22***	1.61	0.54

*, **, ***: Significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

H^2_b, broad-sense heritability; $\hat{\sigma}^2_e$, error variance; $\hat{\sigma}^2_G$, genotypic variance; $\hat{\sigma}^2_{GE}$, genotype by environmental variance; STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; 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.

Phenotypic correlations

STR8WAP	**1**	0.66***	0.64***	0.35***	0.27***	0.32***	0.73***	-0.19***
STR10WAP	0.97***	**1**	0.92***	0.10ns	0.02ns	0.06ns	0.98***	0.08
STR12WAP	0.94***	0.99***	**1**	0.13*	0.07	0.10	0.96***	0.05
SDR1	0.65***	0.61***	0.61***	**1**	0.87***	0.97***	0.15*	-0.73
SDR2	0.44***	0.39***	0.41***	0.89***	**1**	0.97***	0.07	-0.79***
SDR	0.54***	0.51***	0.51***	0.97***	0.98***	**1**	0.11*	-0.79***
AUSNPC	0.94***	0.99***	0.99***	0.60***	0.41***	0.51***	**1**	0.04
GY	0.11ns	0.08ns	0.08ns	-0.69***	-0.74***	-0.75***	-0.17*	**1**
	STR8WAP	**STR10WAP**	**STR12WAP**	**SDR1**	**SDR2**	**SDR**	**AUSNPC**	**GY**

Genetic correlations

Fig. 5. 3 Genetic and phenotypic correlation coefficients between different Striga resistance parameters and grain yield for testcrosses evaluated under artificial Striga infestation across three test locations in Kenya (Kibos, Alupe, and Siaya) in 2020.

STR8WAP, emerged *Striga* plants 8 weeks after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; 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.

5.3.2 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 4). For individual locations, Alupe showed better prediction accuracies for most traits across the three CV schemes while Siaya had the lowest prediction accuracies for the *Striga* resistance parameters but the highest for grain yield with CV0 (0.59) and 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 12WAP (Table 4). 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.

Table 5. 4 Prediction accuracies for *Striga* resistance parameters and grain yield using three cross validation schemes (CV0, CV1 and CV2) for Kibos, Alupe and Siaya and across locations under artificial *Striga* infestation.

	CV0				CV1				CV2			
Trait	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 10WAP; 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.

5.3.3 Genomic estimated breeding values

The genomic estimated breeding values (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 three trial locations are presented in Fig. 5.4. The results indicated that there was a close relationship between the GEBVs in TRN and TST sets (Fig. 5.5). The mean GEBVs were either equal in the TRN and the 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 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 lower number of emerged *Striga* plants than the mean GEBVs at 8, 10 and 12WAP, respectively.

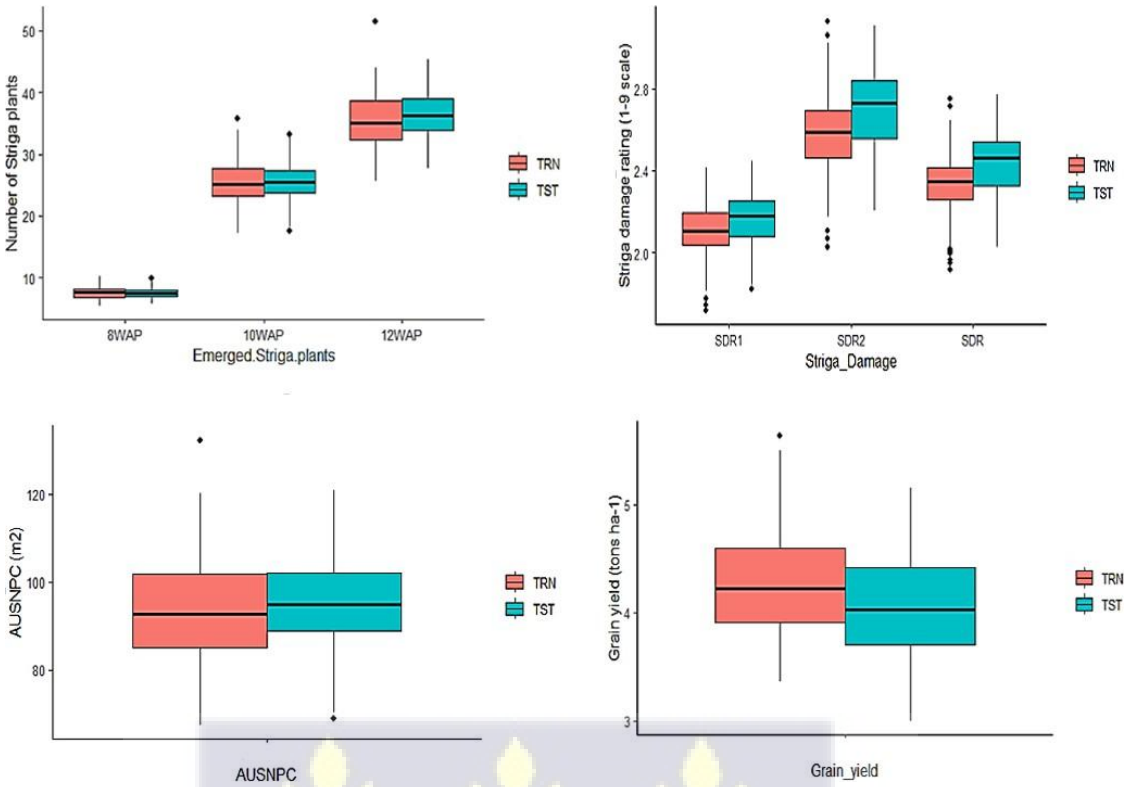


Fig. 5. 4 Boxplots of mean GEBVs for Striga resistance parameters and grain yield for the training (TRN) and testing (TST) sets across the trial locations.

8WAP, emerged *Striga* plants 8 weeks after planting (WAP); 10WAP, emerged *Striga* plants 10WAP; 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.

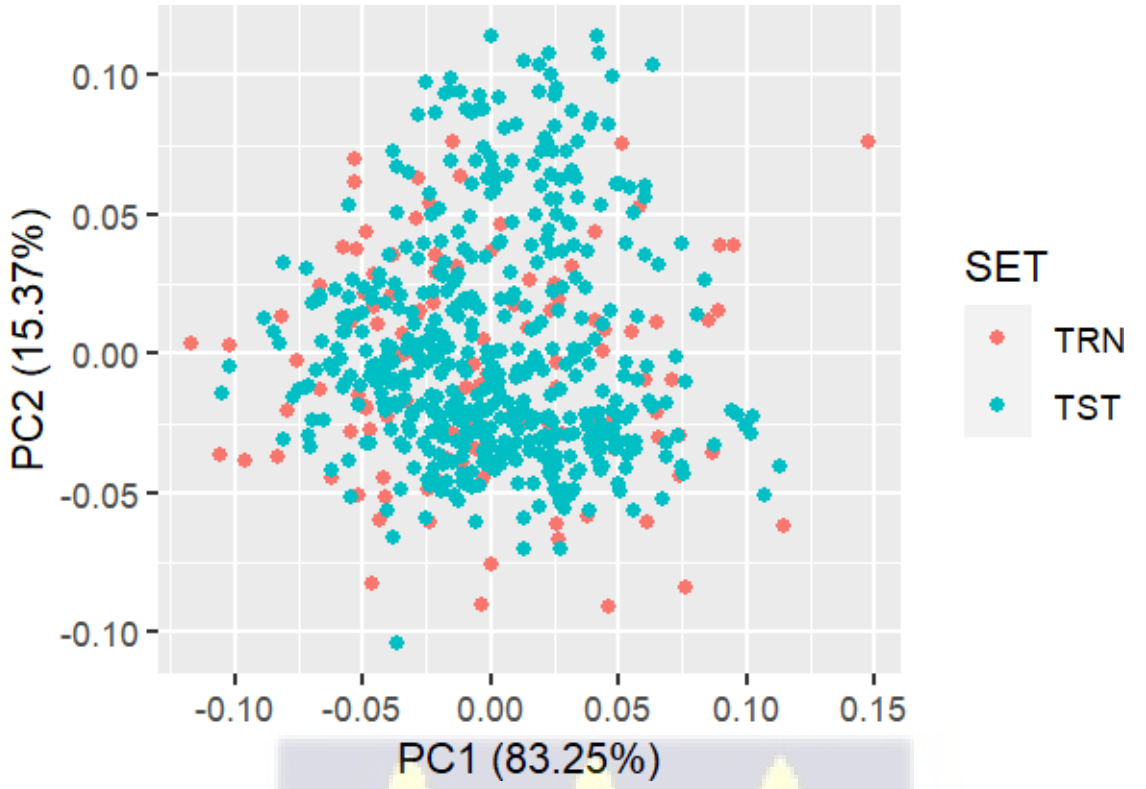


Fig. 5. 5 Principal component analysis of the GEBVs for the TRN and TST sets. The x and the y-axes are the first and the second principal components, respectively. TRN, training population, TST, testing population.

5.4 Discussion

5.4.1 Genetic variability 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 × 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 10WAP and 12WAP, respectively, than at 8WAP 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 8WAP. The genetic variance recorded in this study was larger than G × 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.*, 2022) 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 non-significant. This corroborates the findings by Adewale *et al.* (2020), Stanley *et al.* (2021) and Okunlola *et al.* (2022) 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. Parents of the inbred lines used in the present study show significant negative correlation between SDR and STR, and between grain yield under infestation and SDR, and STR. As SDR and STR are controlled by many genes with small effects, the lines derived from crosses between IITA and CIMMYT lines may not carry all the favorable alleles derived from these lines leading to weak correlation among these traits. 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.

5.4.2 Genomic prediction

Genotype × environment interactions significantly influence phenotypic performance and ultimate selection potential in crops (Des *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 three 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). Gowda *et al*. (2021) reported a similar finding 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; Ornella *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 & Bernardo, 2019). In this study, 300 lines with desirable GEBVs for fewer emerged *Striga* plants at 10 and 12WAP were identified. 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 ones 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.

5.5 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 overcomed 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).

The 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 could 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 (Jarquin *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.

5.6 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 two cross validation schemes (CV0 and CV2), the findings revealed moderate prediction accuracies for three key *Striga* resistance traits, (STR10WAP, STR12WAP and AUSNPC), and grain yield (GY) at two out of the three locations under artificial *Striga* infestation. The reaction norm model sufficiently modeled the interactions among genotypes, environments, markers, and G × E effects, to obtain accurate genomic 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.

CHAPTER SIX

CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

Striga hermonthica threatens food security in SSA with its devastating effects on maize and other cereal crops like sorghum and millet. *Striga* control through host plant resistance could mitigate over $7 billion worth annual yield losses in maize production due to *Striga* (Berner *et al.,* 1996). Breeding for host plant resistance is challenged by the complexity of *Striga* inheritance, narrow germplasm base, lack of breeder-ready molecular markers and limited phenotyping capacities. Understanding the genetics of trait inheritance coupled with diversity within germplasm are fundamental in crop improvement. The application of genomic tools such as marker-assisted selection (MAS) and genomic selection improves breeding efficiency while reducing costs and time. The general objective of this study was to understand the genetics of *Striga* resistance in CIMMYT's tropical maize germplasm.

The results from the study indicate that there is significant variability in CIMMYT's tropical maize germplasm. The combining ability studies showed that both additive and non-additive gene effects influence grain yield, agronomic traits and *Striga* resistance parameters. The high magnitude of additive over the non-additive gene effects indicates that the traits are highly heritable and therefore selection procedures such as pedigree, recurrent selection, marker assisted selection and genomic selection can be utilized for effective and efficient breeding programs in the maize germplasm. Five parental lines (DL171342, DL17535, DL17611, DL17933 and TZISTR1163) had significant negative GCAs for *Striga* resistance parameters and positive significant GCA for grain yield suggesting that they could posses favourable allels for *Striga* resistance. This study identified 15 test hybrids which out yielded the mean of the checks by 32.1%. Five (5) hybrids including DL171342 × DL17611, DL171342 × DL17933 (DL17933 × DL171342), DL17611 × TZISTR1163 (TZISTR1163 × DL17611), DL17933 × DL17611 and TZISTR1163 × DL17933 were combinations of parental lines with favorable GCAs for grain yield and *Striga* resistance parameters. Negative correlation between grain yield and *Striga* damage rating coupled with moderate to high heritability suggests that this trait can be used as a selection criterion in *Striga* breeding programs. In this study, 42 SNPs significantly associated with *Striga* resistance parameters were identified on all the maize chromosomes. Ten SNPS located on chromosomes 2, 3, 5, 6 and 7 accounted for >10% phenotypic variation in *Striga* resistance traits. The study identified 10 highly significant SNPs (S2_44331849, S2_44331849, S2_87827811, S2_188405867, S3_175540577, S3_8219084,

S6_159470193, 6_107754561, S6_96337848 and S6_109282273). These 10 SNPS are candidates for fine mapping in developing molecular markers for selection in *Striga* breeding programs. The significant SNPs and the associated putative genes identified for the *Striga* resistance parameters point to the potential of molecular marker development if fine mapping is carried out in the target regions identified and validation done in a large sample of lines. Use of molecular markers in MAS and marker assisted backcrossing (MABC) enhances the efficiency of breeding programs. Despite the small training population, genomic prediction was efficient in estimating GEBVs for reduced number of emerged *Striga* plants thus highlighting its potential in breeding for *Striga* resistance in maize. Together, the determination of inheritance through combining ability studies; identification of candidate genes associated with grain yield and *Striga* resistance through genome wide association studies (GWAS), and the application of genomic prediction could be instrumental in enhancement of *Striga* breeding programs for improved food security at the SSA.

6.2 Recommendations

Based on the findings of this study, it is recommended that:

(i) the genetic variability in grain yield and response to *Striga* infestation in maize should be exploited in *Striga* resistance breeding programs. For example, the high genetic variability observed in the number of emerged *Striga* plants at 10 and 12 weeks after planting (WAP) provides sufficient genetic information, hence STR8WAP can be omitted in *Striga* screening programs.

(ii) the information on *Striga* inheritance should be exploited in developing *Striga* resistant maize genotypes. The inbred lines identified based on desirable GCA effects can be incorporated in other breeding programs in SSA.

(iii) the information on trait correlations should be utilized in the selection of quantitative traits for maize improvement against *Striga*, with emphasis on the strength and direction of trait correlations. It is recommended that strong emphasis be placed on *Striga* damage rating selection for improved grain yield under *Striga* infestation.

(iv) fine mapping of important genomic regions should be undertaken to develop breeder-ready markers. Marker assisted selection for *Striga* resistance should then be routine in maize breeding programs targeting *Striga* resistance once the markers have been validated.

(v) adoption of genomic prediction should be considered by breeding programs to circumvent challenges on phenotyping capacity and save on phenotyping costs while contributing to improved genetic gains in *Striga* breeding programs.

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APPENDICES

Appendix Table 1 Entry numbers, stock ID, name and pedigree of 136 hybrids phenotyped across several locations under optimal and artificial *Striga* infested conditions in 2022 and 2023.

Entry	Stock ID	Name	Pedigree
1	D1834-1	CKSTRH2201	TZISTR1163/TZMI1240
2	D1834-2	CKSTRH2202	TZMI1240/TZISTR1163
3	D1834-3	CKSTRH2203	TZISTR1163/TEISTR1159
4	D1834-4	CKSTRH2204	TEISTR1159/TZISTR1163
5	D1834-5	CKSTRH2205	TZISTR1163/DL17933
6	D1834-6	CKSTRH2206	DL17933/TZISTR1163
7	D1834-7	CKSTRH2207	TZISTR1163/DL17535
8	D1834-8	CKSTRH2208	DL17535/TZISTR1163
9	D1834-9	CKSTRH2209	TZISTR1163/DL171145
10	D1834-10	CKSTRH2210	DL171145/TZISTR1163
11	D1834-11	CKSTRH2211	TZISTR1163/DL171342
12	D1834-12	CKSTRH2212	DL171342/TZISTR1163
13	D1834-13	CKSTRH2213	TZISTR1163/DL172791
14	D1834-14	CKSTRH2214	DL172791/TZISTR1163
15	D1834-15	CKSTRH2215	TZISTR1163/DL17495
16	D1834-16	CKSTRH2216	DL17495/TZISTR1163
17	D1834-17	CKSTRH2217	TZISTR1163/DL17611
18	D1834-18	CKSTRH2218	DL17611/TZISTR1163
19	D1834-19	CKSTRH2219	TZISTR1163/CML312
20	D1834-20	CKSTRH2220	CML312/TZISTR1163
21	D1834-21	CKSTRH2221	TZISTR1163/DL14546
22	D1834-22	CKSTRH2222	DL14546/TZISTR1163
23	D1834-23	CKSTRH2223	TZMI1240/TEISTR1159
24	D1834-24	CKSTRH2224	TEISTR1159/TZMI1240
25	D1834-25	CKSTRH2225	TZMI1240/DL17933
26	D1834-26	CKSTRH2226	DL17933/TZMI1240
27	D1834-27	CKSTRH2227	TZMI1240/DL17535
28	D1834-28	CKSTRH2228	DL17535/TZMI1240
29	D1834-29	CKSTRH2229	TZMI1240/DL171145
30	D1834-30	CKSTRH2230	DL171145/TZMI1240
31	D1834-31	CKSTRH2231	TZMI1240/DL171342
32	D1834-32	CKSTRH2232	DL171342/TZMI1240
33	D1834-33	CKSTRH2233	TZMI1240/DL172791
34	D1834-34	CKSTRH2234	DL172791/TZMI1240
35	D1834-35	CKSTRH2235	TZMI1240/DL17495
36	D1834-36	CKSTRH2236	DL17495/TZMI1240
37	D1834-37	CKSTRH2237	TZMI1240/DL17611
38	D1834-38	CKSTRH2238	DL17611/TZMI1240
39	D1834-39	CKSTRH2239	TZMI1240/CML312
40	D1834-40	CKSTRH2240	CML312/TZMI1240
41	D1834-41	CKSTRH2241	TZMI1240/DL14546

Entry	Stock ID	Name	Pedigree
42	D1834-42	CKSTRH2242	DL14546/TZMI1240
43	D1834-43	CKSTRH2243	TEISTR1159/DL17933
44	D1834-44	CKSTRH2244	DL17933/TEISTR1159
45	D1834-45	CKSTRH2245	TEISTR1159/DL17535
46	D1834-46	CKSTRH2246	DL17535/TEISTR1159
47	D1834-47	CKSTRH2247	TEISTR1159/DL171145
48	D1834-48	CKSTRH2248	DL171145/TEISTR1159
49	D1834-49	CKSTRH2249	TEISTR1159/DL171342
50	D1834-50	CKSTRH2250	DL171342/TEISTR1159
51	D1834-51	CKSTRH2251	TEISTR1159/DL172791
52	D1834-52	CKSTRH2252	DL172791/TEISTR1159
53	D1834-53	CKSTRH2253	TEISTR1159/DL17495
54	D1834-54	CKSTRH2254	DL17495/TEISTR1159
55	D1834-55	CKSTRH2255	TEISTR1159/DL17611
56	D1834-56	CKSTRH2256	DL17611/TEISTR1159
57	D1834-57	CKSTRH2257	TEISTR1159/CML312
58	D1834-58	CKSTRH2258	CML312/TEISTR1159
59	D1834-59	CKSTRH2259	TEISTR1159/DL14546
60	D1834-60	CKSTRH2260	DL14546/TEISTR1159
61	D1834-61	CKSTRH2261	DL17933/DL17535
62	D1834-62	CKSTRH2262	DL17535/DL17933
63	D1834-63	CKSTRH2263	DL17933/DL171145
64	D1834-64	CKSTRH2264	DL171145/DL17933
65	D1834-65	CKSTRH2265	DL17933/DL171342
66	D1834-66	CKSTRH2266	DL171342/DL17933
67	D1834-67	CKSTRH2267	DL17933/DL172791
68	D1834-68	CKSTRH2268	DL172791/DL17933
69	D1834-69	CKSTRH2269	DL17933/DL17495
70	D1834-70	CKSTRH2270	DL17495/DL17933
71	D1834-71	CKSTRH2271	DL17933/DL17611
72	D1834-72	CKSTRH2272	DL17611/DL17933
73	D1834-73	CKSTRH2273	DL17933/CML312
74	D1834-74	CKSTRH2274	CML312/DL17933
75	D1834-75	CKSTRH2275	DL17933/DL14546
76	D1834-76	CKSTRH2276	DL14546/DL17933
77	D1834-77	CKSTRH2277	DL17535/DL171145
78	D1834-78	CKSTRH2278	DL171145/DL17535
79	D1834-79	CKSTRH2279	DL17535/DL171342
80	D1834-80	CKSTRH2280	DL171342/DL17535
81	D1834-81	CKSTRH2281	DL17535/DL172791
82	D1834-82	CKSTRH2282	DL172791/DL17535
83	D1834-83	CKSTRH2283	DL17535/DL17495
84	D1834-84	CKSTRH2284	DL17495/DL17535
85	D1834-85	CKSTRH2285	DL17535/DL17611
86	D1834-86	CKSTRH2286	DL17611/DL17535

Entry	Stock ID	Name	Pedigree
87	D1834-87	CKSTRH2287	DL17535/CML312
88	D1834-88	CKSTRH2288	CML312/DL17535
89	D1834-89	CKSTRH2289	DL17535/DL14546
90	D1834-90	CKSTRH2290	DL14546/DL17535
91	D1834-91	CKSTRH2291	DL171145/DL171342
92	D1834-92	CKSTRH2292	DL171342/DL171145
93	D1834-93	CKSTRH2293	DL171145/DL172791
94	D1834-94	CKSTRH2294	DL172791/DL171145
95	D1834-95	CKSTRH2295	DL171145/DL17495
96	D1834-96	CKSTRH2296	DL17495/DL171145
97	D1834-97	CKSTRH2297	DL171145/DL17611
98	D1834-98	CKSTRH2298	DL17611/DL171145
99	D1834-99	CKSTRH2299	DL171145/CML312
100	D1834-100	CKSTRH22100	CML312/DL171145
101	D1834-101	CKSTRH22101	DL171145/DL14546
102	D1834-102	CKSTRH22102	DL14546/DL171145
103	D1834-103	CKSTRH22103	DL171342/DL172791
104	D1834-104	CKSTRH22104	DL172791/DL171342
105	D1834-105	CKSTRH22105	DL171342/DL17495
106	D1834-106	CKSTRH22106	DL17495/DL171342
107	D1834-107	CKSTRH22107	DL171342/DL17611
108	D1834-108	CKSTRH22108	DL17611/DL171342
109	D1834-109	CKSTRH22109	DL171342/CML312
110	D1834-110	CKSTRH22110	CML312/DL171342
111	D1834-111	CKSTRH22111	DL171342/DL14546
112	D1834-112	CKSTRH22112	DL14546/DL171342
113	D1834-113	CKSTRH22113	DL172791/DL17495
114	D1834-114	CKSTRH22114	DL17495/DL172791
115	D1834-115	CKSTRH22115	DL172791/DL17611
116	D1834-116	CKSTRH22116	DL17611/DL172791
117	D1834-117	CKSTRH22117	DL172791/CML312
118	D1834-118	CKSTRH22118	CML312/DL172791
119	D1834-119	CKSTRH22119	DL172791/DL14546
120	D1834-120	CKSTRH22120	DL14546/DL172791
121	D1834-121	CKSTRH22121	DL17495/DL17611
122	D1834-122	CKSTRH22122	DL17611/DL17495
123	D1834-123	CKSTRH22123	DL17495/CML312
124	D1834-124	CKSTRH22124	CML312/DL17495
125	D1834-125	CKSTRH22125	DL17495/DL14546
126	D1834-126	CKSTRH22126	DL14546/DL17495
127	D1834-127	CKSTRH22127	DL17611/CML312
128	D1834-128	CKSTRH22128	CML312/DL17611
129	D1834-129	CKSTRH22129	DL17611/DL14546
130	D1834-130	CKSTRH22130	DL14546/DL17611
131	D1834-131	CKSTRH22131	CML312/DL14546
132	D1834-132	CKSTRH22132	DL14546/CML312

Entry	Stock ID	Name	Pedigree
133	D1827-65	CKH212346	TZSTR184/CKL17622//CKL192608
134	D1827-136	CKH212241	TZSTR184/CKL17633//CKL192608
135	SSYT	UH5354	UH5354
136	MON	DK777	DK777

Appendix Table 2 Adjusted means for grain yield, agronomic traits and *Striga* resistance parameters of 136 maize hybrids evaluated for combining ability in six trial locations under optimal and artificial *Striga* infestation in 2022 and 2023

	Optimal conditions					Artificial *Striga* infested conditions							
Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
1	5.2	67	217.6	124.6	1.9	2.3	64	26	65	95	4.0	4.7	179.9
2	5.0	68	214.9	125.2	2.0	2.6	65	22	58	100	4.0	4.8	177.9
3	6.0	69	247.5	151.5	2.1	3.0	65	25	92	138	2.3	3.6	258.3
4	5.4	69	243.6	142.9	2.1	3.0	66	25	74	123	2.5	3.5	222.3
5	4.5	68	227.8	133.0	2.3	4.1	65	17	32	52	1.7	2.5	94.2
6	4.5	68	234.2	139.4	2.2	3.1	66	17	46	76	1.9	3.0	137.8
7	3.4	69	223.6	130.6	2.3	2.8	65	23	56	93	2.4	3.0	169.6
8	4.1	68	221.7	127.5	2.1	2.9	65	18	61	83	2.6	3.4	163.5
9	5.1	69	240.2	141.7	1.8	2.9	66	25	57	96	2.8	3.6	184.0
10	4.8	69	237.9	142.1	1.9	2.5	66	23	53	91	2.4	3.5	164.3
11	4.0	65	210.7	116.0	2.2	2.9	63	17	42	68	3.5	3.7	123.6
12	4.3	64	206.2	116.2	2.2	3.1	63	19	46	72	3.5	4.1	133.0
13	4.3	64	217.9	116.6	2.1	2.4	62	21	57	95	3.7	4.7	174.0
14	4.2	64	212.8	115.4	2.2	2.4	63	25	71	101	3.7	4.6	194.7
15	5.1	66	249.4	132.0	2.2	3.0	64	21	55	87	2.0	2.0	161.2
16	5.2	66	248.6	132.7	2.1	3.6	64	20	57	90	1.9	2.7	163.6
17	4.6	67	244.8	131.6	2.3	3.7	64	23	47	78	1.7	2.4	142.2

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
18	4.7	68	246.2	134.1	2.0	3.8	65	21	49	65	1.7	2.3	131.3
19	7.2	65	248.2	133.9	1.9	3.3	63	42	87	134	2.5	3.4	262.5
20	6.8	65	244.6	126.8	2.2	3.9	63	31	103	147	3.1	3.7	285.2
21	6.8	67	241.2	135.5	1.8	3.4	65	27	67	97	2.8	3.4	192.7
22	5.9	67	230.6	134.0	1.8	3.0	65	33	70	98	3.2	4.1	198.1
23	6.0	70	245.5	142.4	2.0	1.4	68	31	109	168	4.4	5.7	311.5
24	6.3	68	251.9	147.7	2.2	1.5	67	35	101	139	4.6	6.1	278.5
25	5.4	69	248.4	145.3	2.3	3.7	67	19	58	96	2.8	3.6	171.2
26	5.0	69	246.1	149.0	2.3	2.8	67	35	66	109	3.2	3.9	203.3
27	5.7	68	240.6	147.7	2.1	3.0	66	22	79	112	2.5	3.3	216.1
28	5.6	67	233.8	143.0	2.1	2.4	66	26	72	93	3.1	3.9	190.9
29	5.7	68	238.6	148.1	1.9	2.6	60	27	84	121	3.7	4.9	234.1
30	5.5	68	231.7	144.0	1.9	2.1	66	32	79	136	3.5	5.1	245.1
31	5.9	65	214.6	128.5	2.2	2.9	64	25	67	98	3.7	4.9	189.1
32	5.5	65	209.4	125.5	2.2	2.8	62	32	72	113	3.7	4.8	213.8
33	4.9	65	219.0	121.6	2.4	1.8	64	33	95	137	4.8	5.5	263.2
34	4.9	65	223.3	122.1	2.3	2.1	64	37	91	120	4.0	4.9	246.0
35	5.6	67	245.3	133.2	2.3	2.9	65	24	72	106	2.5	3.5	199.7
36	5.1	67	240.5	131.6	2.3	2.3	65	30	66	99	3.4	4.1	192.0

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
37	5.6	68	252.0	142.9	2.4	3.7	65	28	62	99	2.4	2.8	182.5
38	5.3	66	242.7	134.3	2.4	3.5	65	22	59	94	2.4	3.0	174.1
39	6.1	67	244.7	131.4	2.0	2.3	66	32	78	119	4.6	5.8	223.7
40	6.2	65	243.4	130.1	2.1	2.0	65	38	93	111	5.0	5.9	233.2
41	6.4	68	221.9	134.9	1.9	2.2	66	31	79	128	4.8	5.8	235.0
42	6.4	67	220.0	133.7	2.0	2.1	65	32	83	108	4.5	5.9	219.4
43	6.3	69	257.3	157.3	2.3	3.0	67	24	66	125	1.9	3.4	210.8
44	4.6	71	245.8	146.5	2.2	2.5	68	22	60	115	2.3	3.4	199.9
45	4.7	70	262.8	164.4	2.1	2.2	67	22	87	137	1.8	3.2	255.5
46	5.2	71	272.1	169.4	2.2	1.8	67	31	100	159	2.0	3.6	292.8
47	4.9	71	247.5	151.6	2.0	1.8	67	27	83	151	2.7	4.4	268.8
48	4.8	72	242.6	153.1	1.9	1.4	68	30	92	167	2.9	5.0	296.4
49	5.5	66	235.6	138.9	2.2	2.8	64	26	82	124	2.2	3.5	235.5
50	5.0	65	219.8	123.2	2.2	2.6	63	24	89	119	3.4	4.4	230.1
51	4.4	66	238.4	133.1	2.7	1.7	64	59	129	186	4.2	5.6	370.8
52	4.2	66	236.7	130.0	2.6	1.7	65	33	97	152	4.2	5.2	286.9
53	5.0	68	264.8	150.6	2.3	2.5	66	23	80	138	1.9	3.1	252.0
54	4.6	69	260.4	139.6	2.3	1.8	65	25	78	141	1.7	3.3	246.6
55	6.4	68	274.9	162.8	2.3	2.5	66	37	106	151	2.0	3.1	295.9

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
56	5.4	69	268.9	149.4	2.3	2.6	65	27	69	112	2.0	3.0	211.8
57	7.0	67	258.2	144.7	2.1	2.0	65	48	123	174	3.9	5.2	341.5
58	6.9	67	262.9	141.5	2.1	1.9	65	45	139	191	4.1	5.2	381.6
59	6.6	69	247.8	146.5	1.9	1.9	67	35	110	172	4.0	5.5	318.3
60	7.1	69	241.8	142.9	1.9	2.0	67	44	118	158	4.2	5.7	316.9
61	4.9	70	253.9	147.6	2.4	3.3	67	15	53	80	1.3	2.0	153.2
62	4.9	70	259.4	156.1	2.4	3.3	67	17	40	71	1.6	1.9	127.7
63	3.7	71	238.8	144.6	2.2	2.6	68	17	35	79	2.1	3.0	128.6
64	3.8	71	241.9	147.1	2.3	2.9	68	21	55	88	2.2	3.4	167.5
65	4.4	67	223.8	130.7	2.5	3.8	65	11	30	52	1.7	3.0	92.2
66	4.3	66	226.4	133.1	2.5	3.6	64	12	32	60	2.2	2.8	99.4
67	3.8	65	219.6	123.8	2.7	2.4	62	19	59	80	3.5	4.2	155.6
68	3.7	65	221.9	126.4	2.6	2.5	63	20	61	89	3.3	4.2	168.6
69	4.7	67	256.9	143.4	2.7	3.0	65	20	45	70	1.8	2.6	132.2
70	5.2	67	251.0	142.5	2.7	3.5	64	20	56	83	1.9	2.7	159.0
71	4.5	68	256.5	146.4	2.6	4.0	66	17	42	74	1.6	1.8	132.6
72	4.7	68	255.6	144.8	2.9	3.5	66	17	44	67	1.4	2.1	127.0
73	6.5	67	262.1	146.0	2.4	3.3	64	23	80	135	2.9	3.9	242.3
74	7.1	65	258.1	145.9	2.3	3.1	63	36	102	151	2.6	3.4	291.1

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
75	5.7	69	240.6	139.8	2.2	2.9	66	24	60	86	2.7	3.5	168.2
76	6.3	68	240.8	146.9	2.2	3.6	65	29	77	115	2.8	3.4	215.5
77	4.2	70	252.1	150.6	2.2	2.5	68	19	53	101	1.9	2.8	177.9
78	4.7	70	253.9	156.9	2.1	2.7	67	23	61	116	1.6	2.9	203.1
79	3.0	68	202.6	114.9	2.4	2.6	65	14	45	82	3.2	3.7	140.3
80	3.8	65	203.1	115.7	2.5	2.7	63	13	36	61	2.5	3.2	105.8
81	3.9	65	226.7	129.0	2.4	2.1	62	27	79	97	2.9	3.9	199.9
82	4.4	65	232.8	135.3	2.5	2.5	62	21	74	123	2.7	3.5	221.6
83	5.4	68	247.5	141.5	2.5	3.1	65	16	57	95	1.5	2.4	170.6
84	5.3	67	253.4	140.1	2.3	3.0	64	24	58	91	1.6	2.5	172.4
85	5.5	67	246.4	138.8	2.3	3.3	64	24	57	88	1.4	2.2	163.7
86	4.8	67	248.9	137.5	2.5	3.2	65	23	47	78	1.6	2.2	145.6
87	6.3	67	261.9	150.6	2.3	2.9	65	33	106	151	2.4	3.1	289.1
88	7.0	66	262.1	145.7	2.3	3.3	63	29	102	153	2.1	2.6	285.4
89	5.0	69	254.3	150.0	2.0	2.3	66	25	59	97	3.0	3.7	177.2
90	6.7	67	249.0	149.7	2.1	3.0	65	33	76	108	2.5	3.2	212.2
91	4.1	66	224.9	130.5	2.3	2.8	65	17	49	85	2.7	3.6	153.7
92	4.3	67	222.7	127.5	2.3	2.6	64	33	61	97	2.6	3.4	187.1
93	3.8	65	227.7	129.2	2.4	1.8	63	24	83	128	4.1	4.9	243.6

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
94	4.5	65	224.3	129.4	2.1	1.8	63	25	68	107	3.8	4.9	195.6
95	4.2	67	245.8	136.5	2.1	2.9	65	17	52	91	1.8	2.6	162.1
96	5.0	67	250.8	140.7	2.1	2.3	65	19	54	89	1.7	3.0	158.9
97	5.1	69	260.6	150.2	2.2	2.8	66	32	63	106	1.8	2.6	201.3
98	4.9	68	259.4	149.3	2.1	2.9	66	29	70	114	2.0	3.2	213.0
99	6.4	68	258.0	141.9	1.9	1.8	66	34	121	164	4.2	5.3	322.0
100	6.9	67	258.2	142.3	2.0	2.3	65	47	102	164	3.6	4.5	312.2
101	5.5	69	229.3	139.8	2.1	1.3	68	23	91	133	4.5	5.9	253.0
102	5.5	69	224.4	140.2	2.0	1.6	69	24	81	107	4.4	5.2	211.4
103	4.3	61	188.9	107.1	2.5	2.1	61	22	64	92	4.5	5.1	177.4
104	3.5	63	190.2	104.5	2.5	2.3	62	23	59	105	4.2	4.8	182.7
105	4.9	63	216.3	115.6	2.5	2.8	62	23	55	83	2.3	3.2	158.7
106	4.5	64	212.2	114.2	2.6	3.2	62	18	57	82	2.4	3.3	156.4
107	5.3	64	230.4	126.0	2.6	3.5	62	19	44	73	2.1	2.6	133.7
108	4.9	65	226.5	125.4	2.6	3.4	63	19	44	79	2.2	3.1	138.5
109	5.6	62	226.5	117.7	2.5	2.8	63	31	86	119	3.5	4.2	236.8
110	6.0	63	227.0	125.9	2.4	2.8	62	41	98	146	3.8	4.3	284.6
111	6.1	64	212.1	122.4	2.3	2.7	63	23	72	100	3.6	4.5	195.2
112	5.6	65	210.7	127.9	2.3	2.8	63	30	85	117	3.7	4.7	229.9

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
113	3.8	63	218.4	109.2	2.5	1.9	61	36	88	120	3.4	4.2	242.9
114	4.3	63	218.0	110.5	2.6	1.8	61	25	75	110	3.5	4.4	209.8
115	4.5	63	233.8	128.5	2.6	2.4	62	23	67	88	3.1	4.1	172.3
116	4.5	63	238.7	128.8	2.5	2.6	62	37	72	107	3.2	3.8	208.7
117	5.6	63	228.3	118.2	2.1	1.5	62	35	103	146	5.1	6.0	283.4
118	5.7	61	220.9	112.2	2.2	1.7	61	44	108	135	4.7	5.5	277.6
119	4.8	65	208.0	119.7	2.5	1.7	63	36	99	141	4.8	5.6	272.0
120	5.9	62	211.6	118.3	2.4	1.6	62	33	99	124	4.7	5.6	253.2
121	4.1	65	245.4	122.1	2.5	2.6	63	21	54	90	2.0	2.8	165.0
122	4.4	67	247.3	122.9	2.6	3.2	64	25	55	96	2.0	2.5	174.9
123	6.0	65	250.1	131.4	2.6	2.4	63	32	85	123	3.2	4.2	237.5
124	5.9	65	255.1	127.0	2.7	2.4	64	36	101	144	3.1	4.1	282.5
125	5.5	64	237.6	124.5	2.2	2.3	63	28	84	121	3.3	4.6	236.0
126	5.5	66	235.7	127.5	2.3	2.6	64	34	78	124	2.8	3.9	231.3
127	6.2	66	260.2	134.2	2.5	3.1	63	37	86	136	2.9	3.1	254.9
128	7.0	64	254.2	136.7	2.6	3.2	63	46	106	145	3.1	3.5	291.1
129	6.4	67	249.1	139.8	2.2	2.6	64	41	93	124	3.0	3.5	254.7
130	6.2	65	241.9	142.0	2.4	3.3	63	31	77	113	2.5	2.9	221.1
131	7.6	65	229.6	133.9	2.1	1.5	64	54	112	174	4.9	6.1	333.5

Entry	GY	AD	PH	EH	TLB	GY	AD	STR8WAP	STR10WAP	STR12WAP	SDR1	SDR2	AUSNPC
132	7.0	66	229.4	132.6	2.1	1.4	65	56	126	163	5.4	6.4	336.2
133	4.6	66	241.9	149.5	2.4	3.4	63	34	72	100	2.1	2.7	197.1
134	4.6	68	242.4	146.9	2.3	3.5	65	23	55	86	2.2	2.7	157.7
135	7.3	67	251.8	131.7	1.9	3.3	65	32	90	144	2.7	3.9	269.9
136	6.7	64	233.9	117.9	2.2	1.3	63	77	170	214	5.4	6.6	458.8
H^2	0.87	0.95	0.94	0.92	0.69	0.81	0.84	0.70	0.84	0.82	0.92	0.91	0.85
σ_G^2	1.1***	5.1***	317.2***	171.5***	0.1***	0.5***	3.7***	144.9***	703.0***	1211.9***	1.1***	1.4***	4890.8***
σ_{GE}^2	0.5***	0.5***	35.8***	16.4**	0.1***	0.2***	0.4	38.0*	178.1***	438.4***	0.2***	0.3***	1446.2***
σ_s^2	1.1	1.6	123.1	112.1	0.2	0.6	4.6	170.0	691.4	1219.7	0.4	0.6	4172.4
Mean	5.3	66.7	238.0	135.3	2.3	2.6	65	28	74	113	3.0	3.9	214.0
LSD	1.1	1.5	13.0	10.9	0.4	1.0	2.2	19.4	31.4	43.7	0.9	1.1	82.0
CV	19.8	1.9	4.7	7.8	18.0	30.6	3.3	46.9	35.4	31.0	22.5	19.3	30.2
n Env	6	5	5	5	6	4	4	2	4	4	4	4	4

Appendix Table 3 Specific combining ability (SCAs) for grain yield, agronomic traits and *Striga* resistance parameters for maize hybrids evaluated in six trial locations under optimal and artificial *Striga* infestation in 2022 and 2023

Hybrid	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR1	SDR2	AUSNPC
CML312 × DL14546	-0.2	0.3	-12.6***	-1.3	0	-0.9***	1.1	8.5	0.6***	0.8***	9.6
CML312 × DL171145	0.5	0.3	6.5	-0.2	-0.1	-0.1	18.2**	19.3*	0.5**	0.5**	37.5**
DL14546 × DL171145	-0.4	0.5	-9.6*	-4.1	0.2	-0.5**	5.4	-4.2	0.8***	0.8***	1.2
CML312 × DL171342	-0.4	-0.3	2.9	2.6	0.2	0.3	3.1	2.6	-0.2	-0.4*	5.7
DL14546 × DL171342	0.4	-0.2	5.6	4.8	0.1	0	7.3	5	-0.2	-0.2	12.4
DL171145 × DL171342	0	-0.1	8.9*	1.5	0.2	0.2	1.1	-2.8	-0.3	-0.4**	-1.7
CML312 × DL172791	-0.2	0.1	-6.6	-4.6	-0.5***	-0.2	-6.2	-12.3	0.1	0.2	-18.5
DL14546 × DL172791	-0.1	-0.3	-2.3	-0.7	0.4**	-0.1	3.2	3.3	0	0	6.5
DL171145 × DL172791	0	-0.3	2.2	0.9	0	0.2	-8	-9.9	0	-0.3	-17.9
DL171342 × DL172791	0	0.7	-6.5	-0.3	-0.1	0	-12.9*	-2.4	0.1	0.1	-15.3
CML312 × DL17495	-0.4	0.3	1	2.2	0.4***	-0.1	-9.6	-11.9	0.2	0.2	-21.5
DL14546 × DL17495	-0.5	-0.9	-1.5	-4.9	0	0.3	0.5	9.4	-0.1	0.1	10
DL171145 × DL17495	-0.1	-0.9	-0.2	0.2	-0.3*	0.5**	-13.4*	-27.5***	-0.6***	-0.8***	-40.9***
DL171342 × DL17495	0.1	-0.2	-8*	-2.2	-0.1	-0.1	13.8*	17.6*	0.1	0.3	31.4**
DL172791 × DL17495	-0.1	-0.2	-7.2	-5.2	0	-0.4*	15.7**	12.7	0.3*	0.4**	28.4*
CML312 × DL17535	0.3	0.1	5.6	6.1*	0.1	0.6**	8.6	12	-0.8***	-1.1***	20.6
DL14546 × DL17535	-0.1	0	15.6***	6.9*	-0.1	0.4*	-9.8	-5.1	-0.1	-0.2	-14.9
DL171145 × DL17535	-0.1	-0.1	5.1	2	0.1	0.2	-13.1*	-6.7	-0.4**	-0.3	-19.8

Hybrid	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR1	SDR2	AUSNPC
DL171342 × DL17535	-1**	1.1*	-18.2***	-15.6***	0.1	-0.7***	-9	-7.2	0.8***	0.7***	-16.2
DL172791 × DL17535	0.3	0	4.6	3.9	0	0.3	2.7	0.7	-0.3*	-0.2	3.5
DL17495 × DL17535	1**	0.4	0.7	2.4	0	0.4*	1.8	2.2	0	0.2	3.9
CML312 × DL17611	-0.1	0.1	-5.2	-2.4	0.3*	0	3.7	12.3	0.1	-0.1	16
DL14546 × DL17611	0.2	-0.5	1.3	2.2	0	0.1	7.3	3.6	-0.1	-0.5**	10.9
DL171145 × DL17611	0.4	-0.1	5.3	4.1	-0.2	-0.2	11.8*	18.6*	0.1	0.2	30.3*
DL171342 × DL17611	0.4	-0.3	2.5	3.2	0	0.1	-9.8	-10.1	-0.3*	-0.2	-19.9
DL172791 × DL17611	0	-0.4	6.3	7*	-0.2	0	3.1	6.7	0.1	0.3	9.8
DL17495 × DL17611	-0.7	0.7	-10.4**	-10.5***	0	-0.4*	-2.9	1.3	0.5***	0.7***	-1.5
DL17535 × DL17611	0.3	-0.8	-8.6*	-8.4**	-0.1	-0.2	-5.7	-4.9	0.2	0.4*	-10.6
CML312 × DL17933	0.5	-0.7	5.7	3.6	-0.1	0.1	6.3	19.5**	-0.2	0	25.8*
DL14546 × DL17933	0	0.5	2.2	-0.5	-0.2	0.3	2.5	5.6	-0.3	-0.3	8.1
DL171145 × DL17933	-0.6	0.8	-9.2*	-6.2*	0	-0.2	-7.2	-12.3	0.1	0.1	-19.4
DL171342 × DL17933	0	0.2	6.7	3.9	-0.1	0.2	-4.4	-5.9	-0.3	0	-10.2
DL172791 × DL17933	-0.2	-0.5	-7.5*	-4.5	0.1	-0.1	0.6	-6	0.1	0.1	-5.5
DL17495 × DL17933	0.5	-0.6	4.1	6.2*	0.2	-0.1	3.2	-6.7	0.2	0.1	-3.4
DL17535 × DL17933	0.4	0.3	7.9*	0.9	-0.1	-0.3	2.3	-3.7	0.4*	0.2	-1.5
DL17611 × DL17933	-0.4	0.2	-1.7	-0.8	0.3*	0.1	-1.4	-5.5	0.2	0.1	-6.9
CML312 × TEISTR1159	0.2	0	-3.4	-3.4	-0.1	-0.2	1.4	-15.7*	0.2	0.1	-14.3
DL14546 × TEISTR1159	0.5	0.4	-0.4	-4	-0.2	0.2	3.1	-5.7	0.2	0.3	-2.6

Hybrid	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR1	SDR2	AUSNPC
DL171145 × TEISTR1159	-0.3	0.8	-12.1**	-3.6	0.1	-0.2	-3.3	15.2*	-0.2	0.2	11.9
DL171342 × TEISTR1159	0	-1	-0.4	-3.3	-0.2	0.3	5.3	-4.1	-0.3	-0.3*	1.2
DL172791 × TEISTR1159	-0.3	0.5	5.4	0	0.5***	0.3	3.3	10	0.2	0	13.4
DL17495 × TEISTR1159	-0.2	0.4	5.5	2.3	-0.1	0	-14.6*	-2.3	-0.5**	-0.6***	-16.9
DL17535 × TEISTR1159	-0.5	-0.1	9*	12.1***	-0.1	-0.3	6.7	8	-0.2	0	14.7
DL17611 × TEISTR1159	0.4	-0.2	7.4*	5.7	-0.1	-0.1	1.4	-6.1	-0.1	-0.2	-4.7
DL17933 × TEISTR1159	0	-0.2	-8.1*	-5.1	-0.1	0.1	-12.1*	-6.6	0	-0.1	-18.6
CML312 × TZISTR1163	0.6	-0.7	4.8	1.2	0	0.7***	0.4	4.3	-0.7***	-0.6***	4.6
DL14546 × TZISTR1163	0.3	-0.1	10**	3.6	-0.1	0.5*	-11.4*	-15.1*	-0.9***	-1***	-26.4*
DL171145 × TZISTR1163	0.2	0.1	3.8	3.2	0	-0.1	2.5	3.3	0	0	5.8
DL171342 × TZISTR1163	-0.3	0.1	0.8	-1	0	-0.5**	-2.5	-5.7	0.6***	0.5**	-8.2
DL172791 × TZISTR1163	0.2	0	4.3	1.8	-0.2	-0.1	-7.9	-7.4	0.2	0.3*	-15.3
DL17495 × TZISTR1163	0.5	0.2	13.9***	8.6**	0	0	8.8	11.5	0.1	-0.2	20.3
DL17535 × TZISTR1163	-1.1**	0.2	-17***	-11.5***	0.2	-0.4*	6.9	6.8	0.8***	0.7***	13.7
DL17611 × TZISTR1163	-0.3	0.8	2.7	0.5	-0.1	0	1.3	-4.2	0	0.2	-2.9
DL17933 × TZISTR1163	0	-0.5	-8.4*	-2.5	0.1	-0.1	-2.5	-4.5	-0.3	0	-7
TEISTR1159 × TZISTR1163	0.1	-0.1	-3.2	3.3	0.2	0.5**	2.8	2.4	-0.3*	-0.5**	5.2
CML312 × TZMI1240	-1*	0.6	1.3	-3.8	-0.1	-0.2	-27.1***	-38.5***	0.1	0.3*	-65.6***
DL14546 × TZMI1240	-0.1	0.3	-8.3*	-1.9	0	-0.1	-9.5	-5.1	0.1	0.3	-14.6
DL171145 × TZMI1240	0.3	-1.1*	-0.7	2.2	0	0.3	6	7.1	-0.1	0.1	13

Hybrid	Optimal conditions					*Striga* infested conditions					
	GY	AD	PH	EH	TLB	GY	STR 10WAP	STR 12WAP	SDR1	SDR2	AUSNPC
DL171342 × TZMI1240	0.7	0	5.5	6.3*	-0.1	0.2	7.9	12.9	-0.1	0.1	20.8
DL172791 × TZMI1240	0.4	0.3	7.3	1.8	0	0.2	6.2	4.6	-0.7***	-0.8***	10.9
DL17495 × TZMI1240	0	0.7	2.3	1.1	0	0	-3.4	-6.4	-0.2	-0.3	-9.8
DL17535 × TZMI1240	0.4	-1.2*	-4.6	1.2	-0.1	0.1	8.6	-2.1	-0.3	-0.3	6.5
DL17611 × TZMI1240	-0.3	0.3	0.4	-0.5	0.1	0.6***	-8.9	-11.6	-0.7***	-0.9***	-20.6
DL17933 × TZMI1240	-0.2	0.6	8.3*	5	0	0	12.7*	25.9***	0.1	-0.1	38.6**
TEISTR1159 × TZMI1240	0.1	-0.5	0.2	-4	0.1	-0.6**	5.9	4.8	1***	1***	10.7
TZISTR1163 × TZMI1240	-0.4	0	-11.6**	-7.2*	0	-0.5**	1.6	8.5	0.6***	0.6***	10.1

Appendix Table 4. List, names, pedigrees and the role of 606 DH lines used in the study and the role as the TRN or the TST sets.

Entry	Name	Pedigree	Role
1	DL17834	((TZSTR182/CML444-IR)-B)DH1-B-B-B-B-B	Training (TRN)
2	DL17835	((TZSTR182/CML444-IR)-B)DH2-B-B-B-B-B	TRN
3	DL17836	((TZSTR182/CML444-IR)-B)DH3-B-B-B-B-B	TRN
4	DL17837	((TZSTR182/CML444-IR)-B)DH4-B-B-B-B-B	TRN
5	DL17838	((TZSTR182/CML444-IR)-B)DH6-B-B-B-B-B	TRN
6	DL17839	((TZSTR182/CML444-IR)-B)DH8-B-B-B-B-B	TRN
7	DL17840	((TZSTR182/CML444-IR)-B)DH9-B-B-B-B-B	TRN
8	DL17841	((TZSTR182/CML444-IR)-B)DH11-B-B-B-B-B	TRN
9	DL17842	((TZSTR182/CML444-IR)-B)DH13-B-B-B-B-B	TRN
10	DL17843	((TZSTR182/CML444-IR)-B)DH14-B-B-B-B-B	Testing (TST)
11	DL17845	((TZSTR182/CML444-IR)-B)DH17-B-B-B-B-B	TRN
12	DL17846	((TZSTR182/CML444-IR)-B)DH18-B-B-B-B-B	TRN
13	DL17847	((TZSTR182/CML444-IR)-B)DH19-B-B-B-B-B	TRN
14	DL17848	((TZSTR182/CML444-IR)-B)DH22-B-B-B-B-B	TRN
15	DL17849	((TZSTR182/CML444-IR)-B)DH23-B-B-B-B-B	TRN
16	DL17850	((TZSTR182/CML444-IR)-B)DH25-B-B-B-B-B	TRN
17	DL17852	((TZSTR182/CML444-IR)-B)DH27-B-B-B-B-B	TRN
18	DL17854	((TZSTR182/CML444-IR)-B)DH33-B-B-B-B-B	TRN
19	DL17855	((TZSTR182/CML444-IR)-B)DH34-B-B-B-B-B	TRN
20	DL17856	((TZSTR182/CML444-IR)-B)DH35-B-B-B-B-B	TRN
21	DL17857	((TZSTR182/CML444-IR)-B)DH36-B-B-B-B-B	TRN
22	DL17858	((TZSTR182/CML444-IR)-B)DH38-B-B-B-B-B	TRN
23	DL17859	((TZSTR182/CML444-IR)-B)DH39-B-B-B-B-B	TRN
24	DL17860	((TZSTR182/CML444-IR)-B)DH41-B-B-B-B-B	TRN
25	DL17861	((TZSTR182/CML444-IR)-B)DH42-B-B-B-B-B	TRN
26	DL17862	((TZSTR182/CML444-IR)-B)DH43-B-B-B-B-B	TRN
27	DL17863	((TZSTR182/CML444-IR)-B)DH44-B-B-B-B-B	TRN
28	DL17864	((TZSTR182/CML444-IR)-B)DH45-B-B-B-B-B	TRN
29	DL17865	((TZSTR182/CML444-IR)-B)DH47-B-B-B-B-B	TRN
30	DL17866	((TZSTR182/CML444-IR)-B)DH49-B-B-B-B-B	TST
31	DL17867	((TZSTR182/CML444-IR)-B)DH51-B-B-B-B-B	TRN
32	DL17868	((TZSTR182/CML444-IR)-B)DH52-B-B-B-B-B	TRN
33	DL17869	((TZSTR182/CML444-IR)-B)DH53-B-B-B-B-B	TRN
34	DL17870	((TZSTR182/CML444-IR)-B)DH54-B-B-B-B-B	TRN
35	DL17871	((TZSTR182/CML444-IR)-B)DH55-B-B-B-B-B	TRN
36	DL17872	((TZSTR182/CML444-IR)-B)DH56-B-B-B-B-B	TRN
37	DL17873	((TZSTR182/CML444-IR)-B)DH57-B-B-B-B-B	TRN
38	DL17875	((TZSTR182/CML444-IR)-B)DH59-B-B-B-B-B	TST
39	DL17877	((TZSTR182/CML444-IR)-B)DH63-1-B-B-B-B	TRN
40	DL17878	((TZSTR182/CML444-IR)-B)DH63-2-B-B-B-B	TRN
41	DL17879	((TZSTR182/CML444-IR)-B)DH63-3-B-B-B-B	TRN

Entry	Name	Pedigree	Role
42	DL17880	((TZSTR182/CML444-IR)-B)DH64-B-B-B-B-B	TRN
43	DL17881	((TZSTR182/CML444-IR)-B)DH65-B-B-B-B-B	TRN
44	DL17882	((TZSTR182/CML444-IR)-B)DH66-B-B-B-B-B	TRN
45	DL17883	((TZSTR182/CML444-IR)-B)DH67-B-B-B-B-B	TRN
46	DL17884	((TZSTR182/CML444-IR)-B)DH68-B-B-B-B-B	TRN
47	DL17886	((TZSTR182/CML444-IR)-B)DH75-B-B-B-B-B	TST
48	DL17887	((TZSTR182/CML444-IR)-B)DH76-B-B-B-B-B	TRN
49	DL17888	((TZSTR182/CML444-IR)-B)DH78-B-B-B-B-B	TRN
50	DL17890	((TZSTR182/CML444-IR)-B)DH80-B-B-B-B-B	TRN
51	DL17891	((TZSTR182/CML444-IR)-B)DH81-B-B-B-B-B	TRN
52	DL17893	((TZSTR182/CML444-IR)-B)DH86-B-B-B-B-B	TRN
53	DL17894	((TZSTR182/CML444-IR)-B)DH87-B-B-B-B-B	TRN
54	DL17895	((TZSTR182/CML444-IR)-B)DH89-B-B-B-B-B	TRN
55	DL17896	((TZSTR182/CML444-IR)-B)DH90-B-B-B-B-B	TRN
56	DL17897	((TZSTR182/CML444-IR)-B)DH92-1-B-B-B-B	TRN
57	DL17898	((TZSTR182/CML444-IR)-B)DH92-2-B-B-B-B	TRN
58	DL17899	((TZSTR182/CML444-IR)-B)DH93-B-B-B-B-B	TRN
59	DL17900	((TZSTR182/CML444-IR)-B)DH95-B-B-B-B-B	TRN
60	DL17901	((TZSTR182/CML444-IR)-B)DH96-B-B-B-B-B	TRN
61	DL17902	((TZSTR182/CML444-IR)-B)DH98-B-B-B-B-B	TRN
62	DL17904	((TZSTR182/CML444-IR)-B)DH103-B-B-B-B-B	TRN
63	DL17905	((TZSTR182/CML444-IR)-B)DH104-B-B-B-B-B	TRN
64	DL17906	((TZSTR182/CML444-IR)-B)DH105-B-B-B-B-B	TRN
65	DL17907	((TZSTR182/CML444-IR)-B)DH108-B-B-B-B-B	TRN
66	DL17909	((TZSTR182/CML444-IR)-B)DH110-B-B-B-B-B	TRN
67	DL17910	((TZSTR182/CML444-IR)-B)DH113-B-B-B-B-B	TRN
68	DL17912	((TZSTR182/CML444-IR)-B)DH115-B-B-B-B-B	TRN
69	DL17913	((TZSTR182/CML444-IR)-B)DH116-B-B-B-B-B	TRN
70	DL17914	((TZSTR182/CML444-IR)-B)DH118-B-B-B-B-B	TRN
71	DL17915	((TZSTR182/CML444-IR)-B)DH119-B-B-B-B-B	TRN
72	DL17918	((TZSTR182/CML444-IR)-B)DH125-B-B-B-B-B	TRN
73	DL17919	((TZSTR182/CML444-IR)-B)DH127-B-B-B-B-B	TRN
74	DL17920	((TZSTR182/CML444-IR)-B)DH128-B-B-B-B-B	TRN
75	DL17921	((TZSTR182/CML444-IR)-B)DH130-B-B-B-B-B	TRN
76	DL17922	((TZSTR182/CML444-IR)-B)DH131-B-B-B-B-B	TRN
77	DL17923	((TZSTR182/CML444-IR)-B)DH134-B-B-B-B-B	TRN
78	DL17924	((TZSTR182/CML444-IR)-B)DH135-B-B-B-B-B	TRN
79	DL17925	((TZSTR182/CML444-IR)-B)DH136-B-B-B-B-B	TRN
80	DL17926	((TZSTR182/CML444-IR)-B)DH137-B-B-B-B-B	TRN
81	DL17927	((TZSTR182/CML444-IR)-B)DH139-B-B-B-B-B	TRN
82	DL17928	((TZSTR182/CML444-IR)-B)DH140-B-B-B-B-B	TRN
83	DL17929	((TZSTR182/CML444-IR)-B)DH141-B-B-B-B-B	TRN
84	DL17930	((TZSTR182/CML444-IR)-B)DH142-B-B-B-B-B	TRN
85	DL17931	((TZSTR182/CML444-IR)-B)DH143-B-B-B-B-B	TRN
86	DL17932	((TZSTR182/CML444-IR)-B)DH144-B-B-B-B-B	TRN
87	DL17933	((TZSTR182/CML444-IR)-B)DH145-B-B-B-B-B	TRN

Entry	Name	Pedigree	Role
88	DL17934	((TZSTR182/CML444-IR)-B)DH146-B-B-B-B-B	TRN
89	DL17935	((TZSTR182/CML444-IR)-B)DH147-B-B-B-B-B	TRN
90	DL17936	((TZSTR182/CML444-IR)-B)DH148-B-B-B-B-B	TRN
91	DL17937	((TZSTR182/CML444-IR)-B)DH149-B-B-B-B-B	TRN
92	DL17938	((TZSTR182/CML444-IR)-B)DH150-B-B-B-B-B	TRN
93	DL17939	((TZSTR182/CML444-IR)-B)DH151-B-B-B-B-B	TRN
94	DL17940	((TZSTR182/CML444-IR)-B)DH152-B-B-B-B-B	TRN
95	DL17942	((TZSTR182/CML444-IR)-B)DH156-B-B-B-B-B	TRN
96	DL17944	((TZSTR182/CML444-IR)-B)DH158-B-B-B-B-B	TRN
97	DL17945	((TZSTR182/CML444-IR)-B)DH159-B-B-B-B-B	TRN
98	DL17946	((TZSTR182/CML444-IR)-B)DH160-B-B-B-B-B	TRN
99	DL17947	((TZSTR182/CML444-IR)-B)DH162-B-B-B-B-B	TRN
100	DL17948	((TZSTR182/CML444-IR)-B)DH163-B-B-B-B-B	TST
101	DL17949	((TZSTR182/CML444-IR)-B)DH164-B-B-B-B-B	TRN
102	DL17950	((TZSTR182/CML444-IR)-B)DH165-B-B-B-B-B	TRN
103	DL17951	((TZSTR182/CML444-IR)-B)DH166-B-B-B-B-B	TRN
104	DL17952	((TZSTR182/CML444-IR)-B)DH167-B-B-B-B-B	TRN
105	DL17953	((TZSTR182/CML444-IR)-B)DH168-B-B-B-B-B	TRN
106	DL17954	((TZSTR182/CML444-IR)-B)DH169-B-B-B-B-B	TRN
107	DL17955	((TZSTR182/CML444-IR)-B)DH170-B-B-B-B-B	TRN
108	DL17956	((TZSTR182/CML444-IR)-B)DH171-B-B-B-B-B	TRN
109	DL17957	((TZSTR182/CML444-IR)-B)DH173-B-B-B-B-B	TRN
110	DL17958	((TZSTR182/CML444-IR)-B)DH174-1-B-B-B-B	TRN
111	DL17959	((TZSTR182/CML444-IR)-B)DH174-2-B-B-B-B	TRN
112	DL17960	((TZSTR182/CML444-IR)-B)DH175-B-B-B-B-B	TRN
113	DL17961	((TZSTR182/CML444-IR)-B)DH177-B-B-B-B-B	TRN
114	DL17963	((TZSTR182/CML444-IR)-B)DH179-B-B-B-B-B	TRN
115	DL17964	((TZSTR182/CML444-IR)-B)DH182-B-B-B-B-B	TRN
116	DL17965	((TZSTR182/CML444-IR)-B)DH183-B-B-B-B-B	TRN
117	DL17966	((TZSTR182/CML444-IR)-B)DH184-B-B-B-B-B	TRN
118	DL17969	((TZSTR182/CML444-IR)-B)DH190-B-B-B-B-B	TRN
119	DL17970	((TZSTR182/CML444-IR)-B)DH191-B-B-B-B-B	TRN
120	DL17971	((TZSTR182/CML444-IR)-B)DH193-B-B-B-B-B	TRN
121	DL17973	((TZSTR182/CML444-IR)-B)DH196-B-B-B-B-B	TRN
122	DL17974	((TZSTR182/CML444-IR)-B)DH197-B-B-B-B-B	TST
123	DL17976	((TZSTR182/CML395-IR)-B)DH1-B-B-B-B-B	TST
124	DL192340	((TZSTR167/CML444-IR//TZSTR167)-B)DH218-B	TST
125	DL192341	((TZSTR167/CML444-IR//TZSTR167)-B)DH219-B	TST
126	DL192342	((TZSTR167/CML444-IR//TZSTR167)-B)DH222-B	TST
127	DL192343	((TZSTR167/CML444-IR//TZSTR167)-B)DH224-B	TST
128	DL192344	((TZSTR167/CML444-IR//TZSTR167)-B)DH228-B	TST
129	DL192345	((TZSTR167/CML444-IR//TZSTR167)-B)DH231-B	TST
130	DL192346	((TZSTR167/CML444-IR//TZSTR167)-B)DH232-B	TST
131	DL192347	((TZSTR167/CML444-IR//TZSTR167)-B)DH239-B	TST
132	DL192348	((TZSTR167/CML444-IR//TZSTR167)-B)DH240-B	TST
133	DL192349	((TZSTR167/CML444-IR//TZSTR167)-B)DH241-B	TST

Entry	Name	Pedigree	Role
134	DL192350	((TZSTR167/CML444-IR//TZSTR167)-B)DH245-B	TST
135	DL192351	((TZSTR167/CML444-IR//TZSTR167)-B)DH249-B	TST
136	DL192352	((TZSTR167/CML444-IR//TZSTR167)-B)DH252-B	TST
137	DL192353	((TZSTR167/CML444-IR//TZSTR167)-B)DH253-B	TST
138	DL192354	((TZSTR167/CML444-IR//TZSTR167)-B)DH256-B	TST
139	DL192355	((TZSTR167/CML444-IR//TZSTR167)-B)DH261-B	TST
140	DL192356	((TZSTR167/CML444-IR//TZSTR167)-B)DH262-B	TST
141	DL192357	((TZSTR167/CML444-IR//TZSTR167)-B)DH268-B	TST
142	DL192358	((TZSTR167/CML444-IR//TZSTR167)-B)DH269-B	TST
143	DL192359	((TZSTR167/CML444-IR//TZSTR167)-B)DH275-B	TST
144	DL192360	((TZSTR167/CML444-IR//TZSTR167)-B)DH276-B	TST
145	DL192361	((TZSTR167/CML444-IR//TZSTR167)-B)DH281-B	TST
146	DL192362	((TZSTR167/CML444-IR//TZSTR167)-B)DH282-B	TST
147	DL192363	((TZSTR167/CML444-IR//TZSTR167)-B)DH289-B	TST
148	DL192364	((TZSTR167/CML444-IR//TZSTR167)-B)DH292-B	TST
149	DL192365	((TZSTR167/CML444-IR//TZSTR167)-B)DH299-B	TST
150	DL192366	((TZSTR167/CML444-IR//TZSTR167)-B)DH307-B	TST
151	DL192367	((TZSTR167/CML444-IR//TZSTR167)-B)DH308-B	TST
152	DL192368	((TZSTR167/CML444-IR//TZSTR167)-B)DH312-B	TST
153	DL192369	((TZSTR167/CML444-IR//TZSTR167)-B)DH318-B	TST
154	DL192370	((TZSTR167/CML444-IR//TZSTR167)-B)DH319-B	TST
155	DL192371	((TZSTR167/CML444-IR//TZSTR167)-B)DH320-B	TST
156	DL192372	((TZSTR167/CML444-IR//TZSTR167)-B)DH321-B	TST
157	DL192373	((TZSTR167/CML444-IR//TZSTR167)-B)DH322-B	TST
158	DL192374	((TZSTR167/CML444-IR//TZSTR167)-B)DH326-B	TST
159	DL192375	((TZSTR167/CML444-IR//TZSTR167)-B)DH329-B	TST
160	DL192376	((TZSTR167/CML444-IR//TZSTR167)-B)DH333-B	TST
161	DL192377	((TZSTR167/CML444-IR//TZSTR167)-B)DH344-B	TST
162	DL192378	((TZSTR167/CML444-IR//TZSTR167)-B)DH346-B	TST
163	DL192871	((TZSTR167/CML444-IR//TZSTR167)-B)DH48-B	TST
164	DL192872	((TZSTR167/CML444-IR//TZSTR167)-B)DH226-B	TST
165	DL192873	((TZSTR167/CML444-IR//TZSTR167)-B)DH288-B	TST
166	DL192874	((TZSTR167/CML444-IR//TZSTR167)-B)DH303-B	TST
167	DL192889	((TZSTR167/CML444-IR//TZSTR167)-B)DH158-B	TST
168	DL192890	((TZSTR167/CML444-IR//TZSTR167)-B)DH194-B	TST
169	DL192891	((TZSTR167/CML444-IR//TZSTR167)-B)DH283-B	TST
170	DL192892	((TZSTR167/CML444-IR//TZSTR167)-B)DH287-B	TST
171	DL192929	((TZSTR167/CML444-IR//TZSTR167)-B)DH31-B	TST
172	DL192930	((TZSTR167/CML444-IR//TZSTR167)-B)DH34-B	TST
173	DL192931	((TZSTR167/CML444-IR//TZSTR167)-B)DH127-B	TST
174	DL192932	((TZSTR167/CML444-IR//TZSTR167)-B)DH338-B	TST
175	DL192962	((TZSTR167/CML444-IR//TZSTR167)-B)DH33-B	TST
176	DL192963	((TZSTR167/CML444-IR//TZSTR167)-B)DH177-B	TST
177	DL192965	((TZSTR167/CML444-IR//TZSTR167)-B)DH234-B	TST
178	DL192966	((TZSTR167/CML444-IR//TZSTR167)-B)DH247-B	TST
179	DL192990	((TZSTR167/CML444-IR//TZSTR167)-B)DH22-B	TST

Entry	Name	Pedigree	Role
180	DL192991	((TZSTR167/CML444-IR//TZSTR167)-B)DH86-B	TST
181	DL192992	((TZSTR167/CML444-IR//TZSTR167)-B)DH112-B	TST
182	DL192993	((TZSTR167/CML444-IR//TZSTR167)-B)DH175-B	TST
183	DL192994	((TZSTR167/CML444-IR//TZSTR167)-B)DH211-B	TST
184	DL193027	((TZSTR167/CML444-IR//TZSTR167)-B)DH6-B	TST
185	DL193028	((TZSTR167/CML444-IR//TZSTR167)-B)DH21-B	TST
186	DL193029	((TZSTR167/CML444-IR//TZSTR167)-B)DH114-B	TST
187	DL193030	((TZSTR167/CML444-IR//TZSTR167)-B)DH140-B	TST
188	DL193031	((TZSTR167/CML444-IR//TZSTR167)-B)DH164-B	TST
189	DL193032	((TZSTR167/CML444-IR//TZSTR167)-B)DH181-B	TST
190	DL193033	((TZSTR167/CML444-IR//TZSTR167)-B)DH250-B	TST
191	DL193034	((TZSTR167/CML444-IR//TZSTR167)-B)DH341-B	TST
192	DL193071	((TZSTR167/CML444-IR//TZSTR167)-B)DH70-B	TST
193	DL193072	((TZSTR167/CML444-IR//TZSTR167)-B)DH97-B	TST
194	DL193073	((TZSTR167/CML444-IR//TZSTR167)-B)DH102-B	TST
195	DL193074	((TZSTR167/CML444-IR//TZSTR167)-B)DH109-B	TST
196	DL193075	((TZSTR167/CML444-IR//TZSTR167)-B)DH131-B	TST
197	DL193076	((TZSTR167/CML444-IR//TZSTR167)-B)DH135-B	TST
198	DL193077	((TZSTR167/CML444-IR//TZSTR167)-B)DH202-B	TST
199	DL193078	((TZSTR167/CML444-IR//TZSTR167)-B)DH277-B	TST
200	DL193115	((TZSTR167/CML444-IR//TZSTR167)-B)DH79-B	TST
201	DL193116	((TZSTR167/CML444-IR//TZSTR167)-B)DH176-B	TST
202	DL193117	((TZSTR167/CML444-IR//TZSTR167)-B)DH223-B	TST
203	DL193118	((TZSTR167/CML444-IR//TZSTR167)-B)DH270-B	TST
204	DL193153	((TZSTR167/CML444-IR//TZSTR167)-B)DH74-B	TST
205	DL193154	((TZSTR167/CML444-IR//TZSTR167)-B)DH129-B	TST
206	DL193155	((TZSTR167/CML444-IR//TZSTR167)-B)DH157-B	TST
207	DL193156	((TZSTR167/CML444-IR//TZSTR167)-B)DH295-B	TST
208	DL193157	((TZSTR167/CML444-IR//TZSTR167)-B)DH331-B	TST
209	DL193158	((TZSTR167/CML444-IR//TZSTR167)-B)DH334-B	TST
210	DL193191	((TZSTR167/CML444-IR//TZSTR167)-B)DH151-B	TST
211	DL193192	((TZSTR167/CML444-IR//TZSTR167)-B)DH260-B	TST
212	DL193193	((TZSTR167/CML444-IR//TZSTR167)-B)DH328-B	TST
213	DL191005	(TZSTR184/CML444-IR/TZSTR184)DH1-B	TST
214	DL191006	(TZSTR184/CML444-IR/TZSTR184)DH2-B	TST
215	DL191007	(TZSTR184/CML444-IR/TZSTR184)DH3-B	TST
216	DL191008	(TZSTR184/CML444-IR/TZSTR184)DH6-B	TST
217	DL191009	(TZSTR184/CML444-IR/TZSTR184)DH7-B	TST
218	DL191010	(TZSTR184/CML444-IR/TZSTR184)DH9-B	TST
219	DL191011	(TZSTR184/CML444-IR/TZSTR184)DH11-B	TST
220	DL191012	(TZSTR184/CML444-IR/TZSTR184)DH12-B	TST
221	DL191013	(TZSTR184/CML444-IR/TZSTR184)DH13-B	TST
222	DL191014	(TZSTR184/CML444-IR/TZSTR184)DH15-B	TST
223	DL191015	(TZSTR184/CML444-IR/TZSTR184)DH17-B	TST
224	DL191016	(TZSTR184/CML444-IR/TZSTR184)DH20-B	TST
225	DL191017	(TZSTR184/CML444-IR/TZSTR184)DH21-B	TST

Entry	Name	Pedigree	Role
226	DL191018	(TZSTR184/CML444-IR/TZSTR184)DH23-B	TST
227	DL191019	(TZSTR184/CML444-IR/TZSTR184)DH24-B	TST
228	DL191020	(TZSTR184/CML444-IR/TZSTR184)DH28-B	TST
229	DL191021	(TZSTR184/CML444-IR/TZSTR184)DH29-B	TST
230	DL191022	(TZSTR184/CML444-IR/TZSTR184)DH32-B	TST
231	DL191023	(TZSTR184/CML444-IR/TZSTR184)DH33-B	TST
232	DL191024	(TZSTR184/CML444-IR/TZSTR184)DH39-B	TST
233	DL191025	(TZSTR184/CML444-IR/TZSTR184)DH40-B	TST
234	DL191026	(TZSTR184/CML444-IR/TZSTR184)DH41-B	TST
235	DL191027	(TZSTR184/CML444-IR/TZSTR184)DH45-B	TST
236	DL191028	(TZSTR184/CML444-IR/TZSTR184)DH46-B	TST
237	DL191029	(TZSTR184/CML444-IR/TZSTR184)DH49-B	TST
238	DL191030	(TZSTR184/CML444-IR/TZSTR184)DH64-B	TST
239	DL191031	(TZSTR184/CML444-IR/TZSTR184)DH65-B	TST
240	DL191032	(TZSTR184/CML444-IR/TZSTR184)DH67-B	TST
241	DL191033	(TZSTR184/CML444-IR/TZSTR184)DH70-B	TST
242	DL191034	(TZSTR184/CML444-IR/TZSTR184)DH72-B	TST
243	DL191035	(TZSTR184/CML444-IR/TZSTR184)DH74-B	TST
244	DL191036	(TZSTR184/CML444-IR/TZSTR184)DH75-B	TST
245	DL191037	(TZSTR184/CML444-IR/TZSTR184)DH76-B	TST
246	DL191038	(TZSTR184/CML444-IR/TZSTR184)DH79-B	TST
247	DL191039	(TZSTR184/CML444-IR/TZSTR184)DH80-B	TST
248	DL191040	(TZSTR184/CML444-IR/TZSTR184)DH82-B	TST
249	DL191041	(TZSTR184/CML444-IR/TZSTR184)DH87-B	TST
250	DL191042	(TZSTR184/CML444-IR/TZSTR184)DH90-B	TST
251	DL191043	(TZSTR184/CML444-IR/TZSTR184)DH91-B	TST
252	DL191044	(TZSTR184/CML444-IR/TZSTR184)DH92-B	TST
253	DL191045	(TZSTR184/CML444-IR/TZSTR184)DH93-B	TST
254	DL191046	(TZSTR184/CML444-IR/TZSTR184)DH94-B	TST
255	DL191047	(TZSTR184/CML444-IR/TZSTR184)DH96-B	TST
256	DL191048	(TZSTR184/CML444-IR/TZSTR184)DH97-B	TST
257	DL191049	(TZSTR184/CML444-IR/TZSTR184)DH98-B	TST
258	DL191050	(TZSTR184/CML444-IR/TZSTR184)DH99-B	TST
259	DL191051	(TZSTR184/CML444-IR/TZSTR184)DH100-B	TST
260	DL191052	(TZSTR184/CML444-IR/TZSTR184)DH101-B	TST
261	DL191053	(TZSTR184/CML444-IR/TZSTR184)DH102-B	TST
262	DL191054	(TZSTR184/CML444-IR/TZSTR184)DH103-B	TST
263	DL191055	(TZSTR184/CML444-IR/TZSTR184)DH105-B	TST
264	DL191056	(TZSTR184/CML444-IR/TZSTR184)DH106-B	TST
265	DL191057	(TZSTR184/CML444-IR/TZSTR184)DH107-B	TST
266	DL191058	(TZSTR184/CML444-IR/TZSTR184)DH111-B	TST
267	DL191059	(TZSTR184/CML444-IR/TZSTR184)DH113-B	TST
268	DL191060	(TZSTR184/CML444-IR/TZSTR184)DH115-B	TST
269	DL191061	(TZSTR184/CML444-IR/TZSTR184)DH116-B	TST
270	DL191062	(TZSTR184/CML444-IR/TZSTR184)DH117-B	TST
271	DL191063	(TZSTR184/CML444-IR/TZSTR184)DH125-B	TST

Entry	Name	Pedigree	Role
272	DL191064	(TZSTR184/CML444-IR/TZSTR184)DH126-B	TST
273	DL191065	(TZSTR184/CML444-IR/TZSTR184)DH129-B	TST
274	DL191066	(TZSTR184/CML444-IR/TZSTR184)DH130-B	TST
275	DL191067	(TZSTR184/CML444-IR/TZSTR184)DH131-B	TST
276	DL191068	(TZSTR184/CML444-IR/TZSTR184)DH133-B	TST
277	DL191069	(TZSTR184/CML444-IR/TZSTR184)DH139-B	TST
278	DL191070	(TZSTR184/CML444-IR/TZSTR184)DH144-B	TST
279	DL191071	(TZSTR184/CML444-IR/TZSTR184)DH146-B	TST
280	DL191072	(TZSTR184/CML444-IR/TZSTR184)DH152-B	TST
281	DL191073	(TZSTR184/CML444-IR/TZSTR184)DH153-B	TST
282	DL191074	(TZSTR184/CML444-IR/TZSTR184)DH155-B	TST
283	DL191075	(TZSTR184/CML444-IR/TZSTR184)DH156-B	TST
284	DL191076	(TZSTR184/CML444-IR/TZSTR184)DH157-B	TST
285	DL191077	(TZSTR184/CML444-IR/TZSTR184)DH158-B	TST
286	DL191078	(TZSTR184/CML444-IR/TZSTR184)DH159-B	TST
287	DL191079	(TZSTR184/CML444-IR/TZSTR184)DH160-B	TST
288	DL191080	(TZSTR184/CML444-IR/TZSTR184)DH165-B	TST
289	DL191081	(TZSTR184/CML444-IR/TZSTR184)DH166-B	TST
290	DL191082	(TZSTR184/CML444-IR/TZSTR184)DH167-B	TST
291	DL191083	(TZSTR184/CML444-IR/TZSTR184)DH168-B	TST
292	DL191084	(TZSTR184/CML444-IR/TZSTR184)DH169-B	TST
293	DL191085	(TZSTR184/CML444-IR/TZSTR184)DH178-B	TST
294	DL191086	(TZSTR184/CML444-IR/TZSTR184)DH179-B	TST
295	DL191087	(TZSTR184/CML444-IR/TZSTR184)DH183-B	TST
296	DL191088	(TZSTR184/CML444-IR/TZSTR184)DH184-B	TST
297	DL191089	(TZSTR184/CML444-IR/TZSTR184)DH185-B	TST
298	DL191090	(TZSTR184/CML444-IR/TZSTR184)DH186-B	TST
299	DL191091	(TZSTR184/CML444-IR/TZSTR184)DH187-B	TST
300	DL191092	(TZSTR184/CML444-IR/TZSTR184)DH188-B	TST
301	DL191093	(TZSTR184/CML444-IR/TZSTR184)DH189-B	TST
302	DL191094	(TZSTR184/CML444-IR/TZSTR184)DH192-B	TST
303	DL191095	(TZSTR184/CML444-IR/TZSTR184)DH193-B	TST
304	DL191096	(TZSTR184/CML444-IR/TZSTR184)DH198-B	TST
305	DL191097	(TZSTR184/CML444-IR/TZSTR184)DH199-B	TST
306	DL191098	(TZSTR184/CML444-IR/TZSTR184)DH200-B	TST
307	DL191099	(TZSTR184/CML444-IR/TZSTR184)DH202-B	TST
308	DL191100	(TZSTR184/CML444-IR/TZSTR184)DH207-B	TST
309	DL191101	(TZSTR184/CML444-IR/TZSTR184)DH208-B	TST
310	DL191102	(TZSTR184/CML444-IR/TZSTR184)DH209-B	TST
311	DL191103	(TZSTR184/CML444-IR/TZSTR184)DH210-B	TST
312	DL191104	(TZSTR184/CML444-IR/TZSTR184)DH212-B	TST
313	DL191105	(TZSTR184/CML444-IR/TZSTR184)DH214-B	TST
314	DL191106	(TZSTR184/CML444-IR/TZSTR184)DH217-B	TST
315	DL191107	(TZSTR184/CML444-IR/TZSTR184)DH218-B	TST
316	DL191108	(TZSTR184/CML444-IR/TZSTR184)DH219-B	TST
317	DL191109	(TZSTR184/CML444-IR/TZSTR184)DH221-B	TST

Entry	Name	Pedigree	Role
318	DL191110	(TZSTR184/CML444-IR/TZSTR184)DH223-B	TST
319	DL191111	(TZSTR184/CML444-IR/TZSTR184)DH224-B	TST
320	DL191112	(TZSTR184/CML444-IR/TZSTR184)DH225-B	TST
321	DL191113	(TZSTR184/CML444-IR/TZSTR184)DH228-B	TST
322	DL191114	(TZSTR184/CML444-IR/TZSTR184)DH229-B	TST
323	DL191115	(TZSTR184/CML444-IR/TZSTR184)DH234-B	TST
324	DL191116	(TZSTR184/CML444-IR/TZSTR184)DH235-B	TST
325	DL191117	(TZSTR184/CML444-IR/TZSTR184)DH237-B	TST
326	DL191118	(TZSTR184/CML444-IR/TZSTR184)DH238-B	TST
327	DL191119	(TZSTR184/CML444-IR/TZSTR184)DH239-B	TST
328	DL191120	(TZSTR184/CML444-IR/TZSTR184)DH240-B	TST
329	DL191121	(TZSTR184/CML444-IR/TZSTR184)DH241-B	TST
330	DL191122	(TZSTR184/CML444-IR/TZSTR184)DH243-B	TST
331	DL191123	(TZSTR184/CML444-IR/TZSTR184)DH244-B	TST
332	DL191124	(TZSTR184/CML444-IR/TZSTR184)DH247-B	TST
333	DL191125	(TZSTR184/CML444-IR/TZSTR184)DH248-B	TST
334	DL191126	(TZSTR184/CML444-IR/TZSTR184)DH249-B	TST
335	DL191127	(TZSTR184/CML444-IR/TZSTR184)DH254-B	TST
336	DL191128	(TZSTR184/CML444-IR/TZSTR184)DH256-B	TST
337	DL191129	(TZSTR184/CML444-IR/TZSTR184)DH257-B	TST
338	DL191130	(TZSTR184/CML444-IR/TZSTR184)DH258-B	TST
339	DL191131	(TZSTR184/CML444-IR/TZSTR184)DH259-B	TST
340	DL191132	(TZSTR184/CML444-IR/TZSTR184)DH260-B	TST
341	DL191133	(TZSTR184/CML444-IR/TZSTR184)DH261-B	TST
342	DL191134	(TZSTR184/CML444-IR/TZSTR184)DH263-B	TST
343	DL191135	(TZSTR184/CML444-IR/TZSTR184)DH264-B	TST
344	DL191136	(TZSTR184/CML444-IR/TZSTR184)DH265-B	TST
345	DL191137	(TZSTR184/CML444-IR/TZSTR184)DH266-B	TST
346	DL191138	(TZSTR184/CML444-IR/TZSTR184)DH270-B	TST
347	DL191139	(TZSTR184/CML444-IR/TZSTR184)DH271-B	TST
348	DL191140	(TZSTR184/CML444-IR/TZSTR184)DH275-B	TST
349	DL191141	(TZSTR184/CML444-IR/TZSTR184)DH276-B	TST
350	DL191142	(TZSTR184/CML444-IR/TZSTR184)DH277-B	TST
351	DL191143	(TZSTR184/CML444-IR/TZSTR184)DH278-B	TST
352	DL191144	(TZSTR184/CML444-IR/TZSTR184)DH279-B	TST
353	DL191145	(TZSTR184/CML444-IR/TZSTR184)DH280-B	TST
354	DL191146	(TZSTR184/CML444-IR/TZSTR184)DH281-B	TST
355	DL191147	(TZSTR184/CML444-IR/TZSTR184)DH283-B	TST
356	DL191148	(TZSTR184/CML444-IR/TZSTR184)DH285-B	TST
357	DL191149	(TZSTR184/CML444-IR/TZSTR184)DH288-B	TST
358	DL191150	(TZSTR184/CML444-IR/TZSTR184)DH289-B	TST
359	DL191151	(TZSTR184/CML444-IR/TZSTR184)DH290-B	TST
360	DL191152	(TZSTR184/CML444-IR/TZSTR184)DH292-B	TST
361	DL191153	(TZSTR184/CML444-IR/TZSTR184)DH293-B	TST
362	DL191154	(TZSTR184/CML444-IR/TZSTR184)DH294-B	TST
363	DL191155	(TZSTR184/CML444-IR/TZSTR184)DH295-B	TST

Entry	Name	Pedigree	Role
364	DL191156	(TZSTR184/CML444-IR/TZSTR184)DH297-B	TST
365	DL191157	(TZSTR184/CML444-IR/TZSTR184)DH301-B	TST
366	DL191158	(TZSTR184/CML444-IR/TZSTR184)DH302-B	TST
367	DL191159	(TZSTR184/CML444-IR/TZSTR184)DH303-B	TST
368	DL191160	(TZSTR184/CML444-IR/TZSTR184)DH304-B	TST
369	DL191161	(TZSTR184/CML444-IR/TZSTR184)DH305-B	TST
370	DL191162	(TZSTR184/CML444-IR/TZSTR184)DH309-B	TST
371	DL191163	(TZSTR184/CML444-IR/TZSTR184)DH311-B	TST
372	DL191164	(TZSTR184/CML444-IR/TZSTR184)DH317-B	TST
373	DL191165	(TZSTR184/CML444-IR/TZSTR184)DH322-B	TST
374	DL191166	(TZSTR184/CML444-IR/TZSTR184)DH325-B	TST
375	DL191167	(TZSTR184/CML444-IR/TZSTR184)DH328-B	TST
376	DL191168	(TZSTR184/CML444-IR/TZSTR184)DH329-B	TST
377	DL191169	(TZSTR184/CML444-IR/TZSTR184)DH330-B	TST
378	DL191170	(TZSTR184/CML444-IR/TZSTR184)DH332-B	TST
379	DL192761	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH7-B	TST
380	DL192762	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH17-B	TST
381	DL192763	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH31-B	TST
382	DL192764	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH34-B	TST
383	DL192765	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH36-B	TST
384	DL192766	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH42-B	TST
385	DL192767	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH63-B	TST
386	DL192768	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH66-B	TST
387	DL192769	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH70-B	TST
388	DL192770	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH73-B	TST
389	DL192771	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH75-B	TST
390	DL192772	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH79-B	TST
391	DL192773	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH90-B	TST
392	DL192774	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH99-B	TST
393	DL192775	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH101-B	TST
394	DL192776	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH103-B	TST
395	DL192777	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH104-B	TST
396	DL192778	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH108-B	TST
397	DL192779	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH111-B	TST
398	DL192780	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH116-B	TST
399	DL192781	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH117-B	TST
400	DL192782	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH125-B	TST
401	DL192783	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH126-B	TST
402	DL192784	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH127-B	TST
403	DL192785	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH129-B	TST
404	DL192786	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH130-B	TST
405	DL192787	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH131-B	TST
406	DL192788	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH134-B	TST
407	DL192789	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH135-B	TST
408	DL192790	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH136-B	TST
409	DL192791	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH138-B	TST

Entry	Name	Pedigree	Role
410	DL192792	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH139-B	TST
411	DL192793	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH141-B	TST
412	DL192794	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH142-B	TST
413	DL192795	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH143-B	TST
414	DL192796	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH144-B	TST
415	DL192797	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH145-B	TST
416	DL192798	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH146-B	TST
417	DL192799	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH149-B	TST
418	DL192800	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH152-B	TST
419	DL192801	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH153-B	TST
420	DL192802	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH155-B	TST
421	DL192803	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH161-B	TST
422	DL192804	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH166-B	TST
423	DL192805	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH167-B	TST
424	DL192806	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH171-B	TST
425	DL192807	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH174-B	TST
426	DL192808	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH183-B	TST
427	DL192809	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH185-B	TST
428	DL192810	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH187-B	TST
429	DL192811	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH188-B	TST
430	DL192886	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH53-B	TST
431	DL192887	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH159-B	TST
432	DL192919	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH54-B	TST
433	DL192920	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH105-B	TST
434	DL192921	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH154-B	TST
435	DL192954	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH95-B	TST
436	DL192955	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH132-B	TST
437	DL192981	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH29-B	TST
438	DL193014	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH10-B	TST
439	DL193015	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH13-B	TST
440	DL193016	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH19-B	TST
441	DL193017	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH122-B	TST
442	DL193018	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH128-B	TST
443	DL193019	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH163-B	TST
444	DL193060	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH83-B	TST
445	DL193061	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH193-B	TST
446	DL193104	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH60-B	TST
447	DL193105	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH80-B	TST
448	DL193106	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH81-B	TST
449	DL193107	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH94-B	TST
450	DL193108	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH177-B	TST
451	DL193109	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH199-B	TST
452	DL193142	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH14-B	TST
453	DL193143	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH20-B	TST
454	DL193144	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH22-B	TST
455	DL193182	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH51-B	TST

Entry	Name	Pedigree	Role
456	DL193183	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH118-B	TST
457	DL193184	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH140-B	TST
458	DL193185	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH151-B	TST
459	DL193186	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH179-B	TST
460	DL193202	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH165-B	TST
461	DL193203	((TEISTR1158/CML444-IR//TEISTR1158)-B)DH176-B	TST
462	DL192608	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH13-B	TST
463	DL192609	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH20-B	TST
464	DL192610	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH21-B	TST
465	DL192611	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH24-B	TST
466	DL192612	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH27-B	TST
467	DL192613	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH28-B	TST
468	DL192614	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH35-B	TST
469	DL192615	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH36-B	TST
470	DL192616	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH44-B	TST
471	DL192617	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH51-B	TST
472	DL192618	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH52-B	TST
473	DL192619	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH53-B	TST
474	DL192620	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH55-B	TST
475	DL192621	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH68-B	TST
476	DL192622	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH71-B	TST
477	DL192623	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH75-B	TST
478	DL192624	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH76-B	TST
479	DL192625	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH78-B	TST
480	DL192626	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH81-B	TST
481	DL192627	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH102-B	TST
482	DL192628	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH108-B	TST
483	DL192629	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH113-B	TST
484	DL192630	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH114-B	TST
485	DL192631	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH119-B	TST
486	DL192632	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH122-B	TST
487	DL192633	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH126-B	TST
488	DL192634	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH128-B	TST
489	DL192635	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH135-B	TST
490	DL192636	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH136-B	TST
491	DL192637	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH137-B	TST
492	DL192638	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH145-B	TST
493	DL192639	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH149-B	TST
494	DL192640	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH166-B	TST
495	DL192641	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH168-B	TST
496	DL192642	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH169-B	TST
497	DL192643	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH174-B	TST
498	DL192644	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH193-B	TST
499	DL192645	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH194-B	TST
500	DL192646	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH202-B	TST
501	DL192647	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH203-B	TST

Entry	Name	Pedigree	Role
502	DL192648	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH205-B	TST
503	DL192649	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH206-B	TST
504	DL192650	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH212-B	TST
505	DL192651	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH213-B	TST
506	DL192652	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH215-B	TST
507	DL192653	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH216-B	TST
508	DL192654	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH217-B	TST
509	DL192655	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH229-B	TST
510	DL192656	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH231-B	TST
511	DL192882	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH59-B	TST
512	DL192883	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH198-B	TST
513	DL192908	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH63-B	TST
514	DL192909	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH91-B	TST
515	DL192910	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH134-B	TST
516	DL192911	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH175-B	TST
517	DL192949	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH38-B	TST
518	DL192950	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH118-B	TST
519	DL192973	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH45-B	TST
520	DL192974	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH72-B	TST
521	DL192975	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH73-B	TST
522	DL192976	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH192-B	TST
523	DL193011	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH144-B	TST
524	DL193012	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH178-B	TST
525	DL193048	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH74-B	TST
526	DL193049	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH90-B	TST
527	DL193050	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH155-B	TST
528	DL193051	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH189-B	TST
529	DL193091	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH34-B	TST
530	DL193092	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH232-B	TST
531	DL193133	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH15-B	TST
532	DL193134	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH85-B	TST
533	DL193135	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH123-B	TST
534	DL193136	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH195-B	TST
535	DL193176	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH3-B	TST
536	DL193177	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH64-B	TST
537	DL193178	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH96-B	TST
538	DL193199	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH9-B	TST
539	DL193200	((TEISTR1156/CML444-IR//TEISTR1156)-B)DH26-B	TST
540	DL171396	((TZSTR184/CML444-IR)-B)DH1-B-B-B-B-B	TST
541	DL171398	((TZSTR184/CML444-IR)-B)DH8-B-B-B-B-B	TST
542	DL171407	((TZSTR184/CML444-IR)-B)DH23-B-B-B-B-B	TST
543	DL171408	((TZSTR184/CML444-IR)-B)DH25-B-B-B-B-B	TST
544	DL171409	((TZSTR184/CML444-IR)-B)DH26-B-B-B-B-B	TST
545	DL171410	((TZSTR184/CML444-IR)-B)DH27-B-B-B-B-B	TST
546	DL171411	((TZSTR184/CML444-IR)-B)DH29-B-B-B-B-B	TST
547	DL171412	((TZSTR184/CML444-IR)-B)DH32-B-B-B-B-B	TST

Entry	Name	Pedigree	Role
548	DL171415	((TZSTR184/CML444-IR)-B)DH38-B-B-B-B-B	TST
549	DL171416	((TZSTR184/CML444-IR)-B)DH39-B-B-B-B-B	TST
550	DL171422	((TZSTR184/CML444-IR)-B)DH48-B-B-B-B-B	TST
551	DL171423	((TZSTR184/CML444-IR)-B)DH49-B-B-B-B-B	TST
552	DL171424	((TZSTR184/CML444-IR)-B)DH50-B-B-B-B-B	TST
553	DL171425	((TZSTR184/CML444-IR)-B)DH53-B-B-B-B-B	TST
554	DL171426	((TZSTR184/CML444-IR)-B)DH54-B-B-B-B-B	TST
555	DL171427	((TZSTR184/CML444-IR)-B)DH61-B-B-B-B-B	TST
556	DL171428	((TZSTR184/CML444-IR)-B)DH62-B-B-B-B-B	TST
557	DL171429	((TZSTR184/CML444-IR)-B)DH63-B-B-B-B-B	TST
558	DL171432	((TZSTR184/CML444-IR)-B)DH67-B-B-B-B-B	TST
559	DL171433	((TZSTR184/CML444-IR)-B)DH68-B-B-B-B-B	TST
560	DL171434	((TZSTR184/CML444-IR)-B)DH72-B-B-B-B-B	TST
561	DL171436	((TZSTR184/CML444-IR)-B)DH75-B-B-B-B-B	TST
562	DL171440	((TZSTR184/CML444-IR)-B)DH82-B-B-B-B-B	TST
563	DL171441	((TZSTR184/CML444-IR)-B)DH83-B-B-B-B-B	TST
564	DL171442	((TZSTR184/CML444-IR)-B)DH85-B-B-B-B-B	TST
565	DL171443	((TZSTR184/CML444-IR)-B)DH86-B-B-B-B-B	TST
566	DL171446	((TZSTR184/CML444-IR)-B)DH92-B-B-B-B-B	TST
567	DL171447	((TZSTR184/CML444-IR)-B)DH93-B-B-B-B-B	TST
568	DL171450	((TZSTR184/CML444-IR)-B)DH97-B-B-B-B-B	TST
569	DL171454	((TZSTR184/CML444-IR)-B)DH107-B-B-B-B-B	TST
570	DL171455	((TZSTR184/CML444-IR)-B)DH108-B-B-B-B-B	TST
571	DL171457	((TZSTR184/CML444-IR)-B)DH113-B-B-B-B-B	TST
572	DL171458	((TZSTR184/CML444-IR)-B)DH114-B-B-B-B-B	TST
573	DL171459	((TZSTR184/CML444-IR)-B)DH115-B-B-B-B-B	TST
574	DL171460	((TZSTR184/CML444-IR)-B)DH121-B-B-B-B-B	TST
575	DL171462	((TZSTR184/CML444-IR)-B)DH124-B-B-B-B-B	TST
576	DL171464	((TZSTR184/CML444-IR)-B)DH129-B-B-B-B-B	TST
577	DL171466	((TZSTR184/CML444-IR)-B)DH133-B-B-B-B-B	TST
578	DL171468	((TZSTR184/CML444-IR)-B)DH138-B-B-B-B-B	TST
579	DL171469	((TZSTR184/CML444-IR)-B)DH143-B-B-B-B-B	TST
580	DL171473	((TZSTR184/CML444-IR)-B)DH152-B-B-B-B-B	TST
581	DL171476	((TZSTR184/CML444-IR)-B)DH163-B-B-B-B-B	TST
582	DL171478	((TZSTR184/CML444-IR)-B)DH165-B-B-B-B-B	TST
583	DL171482	((TZSTR184/CML444-IR)-B)DH170-B-B-B-B-B	TST
584	DL171484	((TZSTR184/CML444-IR)-B)DH175-B-B-B-B-B	TST
585	DL171485	((TZSTR184/CML444-IR)-B)DH177-B-B-B-B-B	TST
586	DL171486	((TZSTR184/CML444-IR)-B)DH178-B-B-B-B-B	TST
587	DL171487	((TZSTR184/CML444-IR)-B)DH181-B-B-B-B-B	TST
588	DL192260	((TZSTR182/CKL05003//CKL05003)-B)DH5-B	TST
589	DL192261	((TZSTR182/CKL05003//CKL05003)-B)DH21-B	TST
590	DL192262	((TZSTR182/CKL05003//CKL05003)-B)DH27-B	TST
591	DL192263	((TZSTR182/CKL05003//CKL05003)-B)DH30-B	TST
592	DL192264	((TZSTR182/CKL05003//CKL05003)-B)DH37-B	TST
593	DL192265	((TZSTR182/CKL05003//CKL05003)-B)DH38-B	TST

Entry	Name	Pedigree	Role
594	DL192266	((TZSTR182/CKL05003//CKL05003)-B)DH39-B	TST
595	DL192267	((TZSTR182/CKL05003//CKL05003)-B)DH50-B	TST
596	DL192268	((TZSTR182/CKL05003//CKL05003)-B)DH52-B	TST
597	DL192269	((TZSTR182/CKL05003//CKL05003)-B)DH56-B	TST
598	DL192270	((TZSTR182/CKL05003//CKL05003)-B)DH57-B	TST
599	DL192271	((TZSTR182/CKL05003//CKL05003)-B)DH88-B	TST
600	DL192961	((TZSTR182/CKL05003//CKL05003)-B)DH44-B	TST
601	DL192989	((TZSTR182/CKL05003//CKL05003)-B)DH75-B	TST
602	DL193026	((TZSTR182/CKL05003//CKL05003)-B)DH40-B	TST
603	DL193069	((TZSTR182/CKL05003//CKL05003)-B)DH41-B	TST
604	DL193070	((TZSTR182/CKL05003//CKL05003)-B)DH67-B	TST
605	DL193151	((TZSTR182/CKL05003//CKL05003)-B)DH47-B	TST
606	DL193152	((TZSTR182/CKL05003//CKL05003)-B)DH66-B	TST