GENOTYPIC RESPONSE TO STRIGA (*Striga hermonthica*) INFESTATION IN WILD RELATIVES AND LANDRACES OF SORGHUM (Sorghum bicolor) AND THE INTROGRESSION OF THE RESISTANCE INTO CULTIVATED VARIETIES

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Department of Plant Science and Crop Protection

Faculty of Agriculture

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2022

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I declare that this thesis is my original work and has not been submitted elsewhere for examination, award of a degree or publication. Where other people's work, or my own work has been used, this has properly been acknowledged and referenced in accordance with the University of Nairobi's requirements.

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DEDICATION

This work is dedicated to my parents Mr. and Mrs. Muchira. Thank you for your tremendous love, support, and guidance throughout my life. Thank you both for always believing in me and encouraging me to follow my dreams.

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LIST OF ABBREVIATIONS

ASNPC: Area under Striga Number Progress Curve

DTF: Days to Flowering

NSFC: Number of Striga Forming Capsules

NSmax: Maximum Striga Count

PNH: Panicles Harvested

DPW: Dry Panicle Weight

HGW: Hundred Grain Weight

YLD: Yield

GBK: Gene Bank of Kenya

KALRO: Kenya Agricultural and Livestock Research Organization

ICRISAT: International Crops Research Institute for the Semi-Arid Tropics

FAO: Food and Agriculture Organization

DNA: Deoxyribonucleic acid

QTL: Quantitative Trait Loci

SSR: Simple Sequence Repeat

DArT: Diversity Array Technology

GS: Genomic Selection

TASSEL: Trait Analysis by association, Evolution and Linkage

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ABSTRACT

Sorghum is the second most important cereal crop in Kenya after maize, grown on an area of 117000 ha -1 with about 144000 tonnes being produced annually. *Striga hermonthica* is among the major causes of sorghum yield loss especially in Western and Nyanza regions of the country. Farmers have traditionally managed *Striga* using cultural methods but the most `effective and practical solution to poor smallholder farmers is to develop *Striga* resistant varieties. A field trial consisting of Sixty-four sorghum genotypes comprising of wild relatives, landraces, improved varieties and F_4 progenies were evaluated in a sickplot (field with Striga inoculum capable of causing up to 100% incidence in susceptible sorghum genotypes) and in a potted trial at KALRO-Kenya Agricultural and Livestock Research Organization Alupe during the 2019 rainy season. The experiment was laid out in a square lattice design with three replications. These accessions were also genotyped using Diversity Array Technology markers to assess their diversity. In another experiment, Marker Assisted Selection (MAS) was used to transfer *Striga* resistance quantitative trait loci into adapted farmer preferred varieties Gadam and Kari-Mtama-1. Crosses were also made between known *Striga* resistance namely N13, Framida, SRN39 and Hakika as donor sources and Gadam and Kari- Mtama-1 as the female parents to obtain F_1 and BC_1F_1 generations. Backcross generation crosses were genotyped using DArT markers to trace heterozygous alleles and to confirm successful backcrossing. The (ASNPC) selection criteria was used to identify resistant genotypes in the trials. Wild genotypes GBK045827, GBK044336, GBK047293 and GBK048921, improved varieties F6YQ212, ICSV III_IN and F4 population F6YQ212 × B35, B35 × Lodoka and B35 × ICSVIII_IN had lower ASNPC values than N13, the resistant check under sickplot conditions. Four wild genotypes GBK016109, GBK016085, GBK045827, GBK048152, one improved variety F6YQ212 and three F_4 population crosses F6YQ212 × B35, LODOKA × Landiwhite, ICSVIII_IN × E36-1 had lowest ASNPC values in the potted trial. Genotypes SRN39, F6YQ212, GBK045827 and F6YQ212 × B35 were the most resistant to *Striga* in both field and potted trials. MACIA, B35, E36-1, OKABIR × AKUOR-ACHOT and LODOKA × ICSVIII_IN were the most tolerant to *Striga* recording superior yield performance in both trials. Negative correlation was observed between yield traits (100 grain weight, dry panicle weight, yield (t/ha) and *Striga* related traits across both trials while *Striga* response related traits (ASNPC, NSmax, NSFC) significantly (<0.001) correlated positively with each other in both trials. Days to flowering and plant height were also negatively correlated to yield and *Striga* resistance.

The overall best performing genotypes in terms of *Striga* resistance and yield in both trials were Macia, SRN39,GBK 045827 and GBK 016085. SNPs generated from DArT-sequencing grouped the genotypes into three major clusters, with all resistant checks grouping in the same cluster except N13. The results from this analysis revealed successful backcrosses for the crosses Gadam × N13 × Gadam, Gadam × Framida × Gadam and Gadam × SRN39 × Gadam with heterozygous allele percentages ranging from 63% to 77%. High heritability values for yield and ASNPC suggest additive gene action and selection for improvement of these trait will be beneficial. Demonstrated genetic gain for *Striga* tolerance points the possibility of development of *Striga* tolerant varieties that give substantial yield under *Striga* pressure. The study showed that *Striga* resistance and *Striga* tolerance alleles are available within the local wild relatives, in local landraces and in improved sorghum genotypes and there is need tap into this potential to improve sorghum production in the crop.

CHAPTER ONE: INTRODUCTION

1.1 Sorghum production and importance

Sorghum is a cereal grass of the *Gramineae* family commonly found in the tropical regions. Its domestication dates back to around 1000 BC in northern parts of Africa along the Nile river or Ethiopian regions (Kimber, 2000). Sorghum genotypes are widely adapted to ecological and climatic conditions and can tolerate high salinity, drought, water logging as well as poor soil fertility. At a global scale, sorghum is ranked fifth after maize, rice, wheat and barley with respect to its importance as cereal staple(Kiprotich et al., 2015). In Africa, sorghum had an annual production of 27,219,117 tonnes in 2019 ranking it second with maize leading in terms of importance for cereal consumption (FAOSTAT, 2019).

The major sorghum growing regions in Africa include countries in west Africa like Nigeria and Burkina Faso and Eastern African countries like Sudan and Ethiopia and these account for approximately 70% of Africa's total production (Taylor, 2004). In Kenya, sorghum is placed second after maize in tonnage and the area under sorghum production amounts to 144,000 ha (FAO STAT, 2019). Sorghum is mainly cultivated in the Eastern, Nyanza and Coast Provinces that experience little rainfall annually and are prone to drought. The crop performs best in regions with an altitude of 500 to 1700 meters above sea level and minimum rainfall of 300mm per season (Grain production report in Kenya, 2005).

Sorghum is a versatile in terms of its applicability and has been used for both commercial and subsistence purposes for food and non-food products. It is used as a major ingredient in the baking industry to make bread, cakes and biscuits (CFC and ICRISAT, 2004). Industrial products prepared from sorghum include alcohol (Seetharama et al., 2002), malt (Jaya et al., 2001) starch and by-products glucose, high fructose syrup (Anonymous 2002; 2003), modified starches, maltodextrins, sorbitol (Rainer and Silveira, 2003) and citric acid. Sweet stalk sorghum is a potential raw material for preparation of jaggery, syrup as well as ethanol. Process of making jaggery from sorghum is identical to production from sugarcane and the jaggery obtained is comparable to sugarcane jaggery (CFC and ICRISAT, 2004). However, grain yield of sorghum in farmer fields has remained at low at 954.6 kilograms per hectare (FAO STAT, 2019).

Figure 1. Global area harvested and production of cereal food crops in order of importance (FAO, 2020)

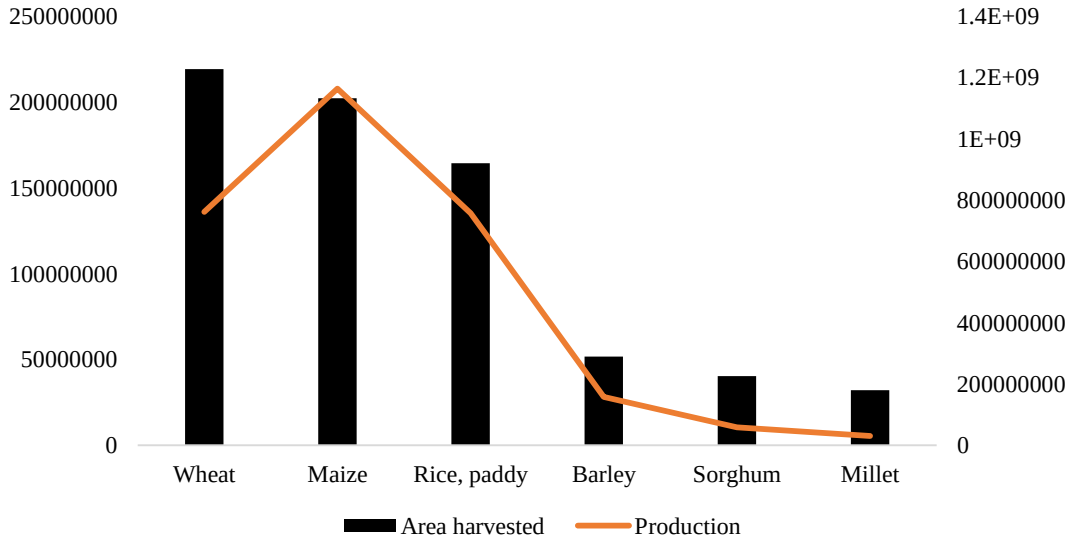

Table 1. Importance of sorghum in Africa and Kenya (FAO, 2019)

Crop	Africa (ton)	Kenya(ton)
Maize	84,152,626	3,186,000
Rice	36,560,295	81,198
Sorghum	27,219,117	144,000
Wheat	27,153,529	165,200
Millet	12,872,964	54,000
Barley	6,609,790	77,000

1.2: Constraints in sorghum production

Sorghum is a C4 plant with high photosynthetic efficiency; however, its physiological growth and production parameters are impaired under drought stress, *Striga* stress and poor soil fertility limiting grain yield. Approximately one-third of 1.5 billion hectares of the world's agricultural land are affected by drought which leads to low yield and poverty (James, 2002). In the arid and semi-arid areas drought accounts for approximately 70% yield loss (Ejeta et al., 2007). *Striga* is the most important biotic factor affecting sorghum production in Sub-Saharan Africa (Rodenburg et al., 2005). *Striga* problem is associated with degraded environments and highly affects subsistence farming systems that have little resources to address the weed. Sorghum farmers are undoubtedly in need of both short and long term affordable solutions to *Striga* problems.

1.2.1 **Striga in Sorghum**

Striga species is an obligate parasitic weed that is a major biotic stress in sorghum cultivation especially in areas with poor soil fertility (Baptiste et al., 2012). The weed germinates upon stimulation by a strigolactone (Bouwmeester et al., 2019; Aliche et al., 2020) induced by the host, or in some cases, non-host plants. The germinated *Striga* then attaches to the host plant roots, by means of a special invasive organ, haustorium (Yoshida et al., 2016). The haustorium enables water and nutrients uptake from the host plants for growth and development of *Striga*, as well as the introduction of phytotoxins to the host (Hast et al., 2000). Consequently, the growth and development of the host plants become severely affected resulting in yield losses of up to 100% (Kim et al., 2002; Ejeta, 2007). A fully-grown *Striga* plant is estimated to produce up to 100,000 tiny seeds that can remain viable in the soil for more than 20 years (Pieterse and Pesch 1983; Gurney et al., 2005), making it extremely difficult to control.

Striga species are believed to have evolved alongside sorghum in the grasslands of the old world and semiarid tropics, mainly in Ethiopia (Kroschel, 1999). It has since spread to other parts of the world with severe infestation occurring in sub-Saharan Africa (Mohammed et al., 2006). The most important *Striga* species affecting cereals are: *S. hermonthica, S. aspera, S. densiflora, S. passargei Engle, S. asiatica, S. angustifolia, S. forbesii Benth, S. laterica Vatke, S. multiflora Benth, S. parviflora Benth and S. curviflora Benth.* Striga *hermonthica* and S. *asiatica* are the most notorious (Dafaallah et al., 2019). Over 21 million ha of land under cereal crops have been reported to be affected by *Striga hermonthica* (Sauerborn, 1991), amounting to 20-80% yield loss, equal to 4.1 million tons of grain per year. These losses affect livelihoods of approximately 100 million people (Kanampiu et al., 2002).

Striga asiatica (L.) Kuntze and *Striga hermonthica* (Del.) Benth are the main *Striga* species found in Kenya. *Striga hermonthica* is widely spread in western Kenya, while *Striga asiatica* is distributed in the coastal region of the country (Odhiambo, 1998). On average, 76% of land planted to maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench) in western Kenya is *Striga hermonthica* infested, ensuing annual losses projected at 40.8 million dollars (Kanampiu et al., 2002). *Striga asiatica* is not widely distributed in Kenya, and its occurrence has only been recorded along the Indian Ocean coast (Frost,1994). Genetic diversity studies within *S. hermonthica* populations parasitizing crops in west, east and central Africa reported existence of biotypes within the species with diversity levels of up to 6.8% (Olivier et

al.,1998). These biotypes are believed to be responsible for the breakdown of *Striga* resistance in previously resistant crops (Doggett, 1952).

Wild sorghum genotypes have demonstrated resistance to *Striga* over the years and are believed to harbor novel resistance genes that if exploited they can help in improvement of adapted sorghum varieties for *Striga* resistance.

1.3 **Wild relatives of Sorghum**

Domesticated sorghum genotypes are often susceptible to *Striga* (Ejeta, 2007). This is a result of domestication in which the bottleneck effect has limited the genetic diversity (Papa et al., 2005). Wild sorghums belong to the subsp. *Verticilliflorum*, comprised of the races arundinaceum, verticilliflorum virgatum and aethiopicum (Harlan and de Wet, 1972). Semien Mountains of Ethiopia and the Nubian Hills of Sudan are believed to be the centers of domestication of *Sorghum*, the host on which monocot-parasitizing *Striga* species have evolved and spread throughout Africa and Asia (Vasudeva-Rao and Musselman, 1987). Its therefore most likely that wild relatives of sorghum have *Striga* resistance genes that have enabled them to survive amidst *Striga* pressure. Wild relatives of sorghum as *Striga* resistance sources have been reported in the past. Mbuvi et al. (2017) reported three wild sorghum genotypes, (WSE-1,WSA-1 and WSA-2) exhibited a resistance response significantly higher than N13, which is a known *Striga* resistant landrace. The use of wild sorghum genotypes in future breeding programmes is justified by the reports of successful interspecific hybridization occurring naturally between cultivated and wild sorghum.

Interspecific hybridization between cultivated sorghum and its wild relatives has been reported and the progenies of this process are classified as *drummondii* (Paterson et al., 2013). The interspecific hybridization between sorghum wild relatives and cultivated sorghum results in disruptive selection which is responsible for the gene-flow into the local landraces (Magomere et al., 2015). Increased genetic diversity and allelic heterozygosity within domesticated and wild sorghum populations, has been reported in the past in Kenya (Mutegi et al., 2007). Given the complex mechanisms of genetic resistance to *Striga* in sorghum, there is need to widen the genetic base in the wild relatives. This study aimed at screening wild relatives along landraces and adapted sorghum for *Striga* resistance with the hope to discover new sources of *Striga* resistance that can be used in future breeding research.

1.4 Statement of the problem

Striga hermonthica has been a major problem in production of sorghum in western regions of Kenya (Khan et al., 2006). Increased population pressure has subsequently increased pressure on land and continuous land use coupled with cereal monoculture has aggravated the *Striga* problem in these regions (Ogutu et al., 1993). A study by Woomer and Savala (2009) reported about 217,000 ha in Kenya to be infested with *Striga* leading to losses of US $53 million annually. The study also revealed that out of 83 farms under the study, *Striga* infestation was at 73%. *Striga* is responsible for approximately 1.15, 1.10 and 0.99 tons yield loss per hectare for maize, sorghum and millet, respectively (Mac Opiyo et al., 2010). The severity of destruction caused by *Striga* depends on Striga population size, affected species and genotype, cropping system, amount of nutrients in the soil and rainfall regime in the area of agriculture (Atera et al., 2012). *Striga* form a complex parasitic relationship with the host by producing haustoria that penetrate the host and extract nutrients from the host plant. This relationship leads to malnutrition of the plant and subsequent death or stunted growth. Poor soil fertility aggravates the *Striga* problem because the plant is unable to get additional nutrients to compensate the nutrients deficiency caused by uptake by the parasitic *Striga* weed. Previous studies have reported *Striga* seed and plant densities in western Kenya at about 1,188 seeds per mature Striga seed capsule (Van Delft et al., 1997) and about 14 plants per m2 (Mac-Opiyo et al., 2010) respectively. In Kenya, the three crops most devastated by *Striga hermonthica* are maize, finger millet and sorghum.

Conventionally, farmers manage *Striga* in sorghum using cultural and mechanical methods including hand weeding (Frost, 1994), intercropping and crop rotations with edible legumes such as common bean *(Phaseolus vulgaris L.)*, pigeonpea (*Cajanus cajan* (L) Millsp.) and mung bean (*Vigna radiata* (L.) R. Wilczek) (Aasha et al., 2017, Oswald and Ransom 2001). Effective bioherbicide activity of *Fusarium oxysporum* f. sp. *strigae* isolates has been reported, particularly when combined with other control practices (Rebeka et al.,2013) but has received low adoption due to cost implications. Push-pull technology has also been used and it involves planting of cereals alongside a trap crop (pull), usually Napier grass (*Pennisetum purpureum*), and a push forage legume crop, usually desmodium (*Desmodium* spp.) (Khan et al., 2011) but has resulted in low adoption due to lack of alternative use for desmodium by farmers. “Suicidal death” of *Striga*, which is achieved by inducing

germination of *Striga* by non-host legumes has been employed in the reduction of *Striga* seed banks (Rubiales, 2012) but the strategy is not yet ready for direct application.

Chemical control has been tested in maize (Menkir et al., 2010) and sorghum (Dembele et al., 2005: Tuinstra et al., 2009) but are not environmentally friendly besides being unaffordable for the average sorghum farmer in Kenya.

Although genes controlling *Striga* resistance in sorghum have been identified, advances in incorporating these genes into susceptible sorghum backgrounds have remained minimal. This partly due to the recessive nature of inheritance of some of these genes especially the low germination stimulus production genes (*lgs*) that makes the breeding process lengthy and tedious as well as lack of adequate understanding of the action of hypersensitive response genes (Rodenburg et al., 2005). The complex interaction between host genotype and *Striga* populations in different environments lead to differences in *Striga* virulence levels and specificity due to adaptation to different host plant resistance mechanisms further complicating the process of evaluation for *Striga* resistance in field trials (Fantaye, 2018). Breakdown of resistance in previously resistant varieties due to the many *Striga* ecotypes has also been a worrying occurrence (Muchira et al., 2021).

1.5 Justification

The most effective and practical solution to the smallholder sorghum farmers is to develop *Striga* resistant sorghum varieties. Sorghum germplasm screening against *Striga* is the first step towards the identification of *Striga* resistant genotypes. *Striga* resistance has been reported to be abundant among the sorghum wild and landrace gene pool and evidence of gene transfer from wild to cultivated sorghum genotypes has been documented in Kenya (Maiti et al.,1984; Mutegi et al., 2010; Mutegi et al., 2012), Ethiopia and Niger (Tesso et al., 2008), northern Cameroon (Barnaud et al., 2009), and western Africa (Sagnard et al., 2011). Wild relatives of sorghum as superior sources of *Striga* resistance have been reported with significantly higher resistance than N13, a known *Striga* resistant landrace (Mbuvi et al., 2017) and it provides a strong justification for more screening of sorghum wild and landraces towards the identification of additional sources of resistance to *Striga*.

Further studies have identified the specific genes conferring *Striga* resistance and these are the *Hrs1* and *Hrs2* genes for hypersensitive response to *Striga* (Haussmann et al., 2000) and *Lgs* gene for low germination stimulus production as a mechanism of *Striga* resistance (Ramaiah et al., 1990). As a result, several sorghum genotypes with *Striga* resistance including N13, SRN39, Framida, IS9830 and Hakika have been documented as *Striga* resistance donor sources and can be used in breeding programmes for *Striga* resistance improvement.

Five genomic regions (QTLs) associated with stable *Striga* resistance from resistant variety N13 have been identified based on screening across a series of field trials in Mali and Kenya. The use of molecular markers in breeding for *Striga* resistance in sorghum is made possible by the availability of identified molecular markers linked to these *Striga* resistance QTLs. These advances in MAS techniques and use of markers for diversity studies have led to reliable estimation of genetic diversity and relatedness among populations and accelerated the introgression of genes of interest into adapted cultivars.

The use of molecular markers for genetic analysis and manipulation of important agronomic and stress-tolerance traits has gained increased acceptance in sorghum improvement. Transfer of these traits into susceptible sorghum background through marker assisted backcrossing (MABC) will provide a solid foundation to improve *Striga* resistance in farmers preferred lines. With the use of high throughput marker technology like Diversity Array Technology markers, lines which will be used as parents in next generation are selected.

This is made possible with the aid of molecular markers that are closely linked or flanking already detected and validated QTLs.

The outcrossing nature of *Striga* that results in different ecotypes with mixed response to different genotypes (Fantaye, 2015) would require the pyramiding of multiple alleles from diverse sources into farmer-preferred varieties if the resistance were to be durable.

1.6 General objective

To enhance sorghum productivity in *Striga* prone areas by identifying novel sources of *Striga* resistance genes followed by introgression of the genes in to cultivated farmer preferred sorghum varieties through Marker Assisted Backcrossing.

1.6.1 Specific objectives

1. To screen sorghum wild relatives, landraces and improved genotypes for *Striga* resistance using morphological and molecular markers to identify resistance sources.

2. To transfer *Striga* resistance QTLs from known donor sources to susceptible farmer preferred varieties using marker assisted backcrossing with DArT molecular markers.

1.6.2 Hypotheses

1. Wild, landrace and improved sorghum varieties do not vary in terms of, yield, agronomic and commercially desirable traits.
2. Genetic variability for *Striga* resistance cannot be transferred from known donors into cultivated farmer preferred sorghum varieties through hybridization and Marker assisted Backcrossing.

CHAPTER TWO: LITERATURE REVIEW

2.1 Taxonomy of sorghum

Sorghum (*Sorghum bicolor* (L.) Moench) is a diploid (2n=2x=20) cereal grass of the Gramineae family native to Africa. It is classified in the genus sorghum, which is composed of 52 species where 31 are cultivated, 17 are wild and 4 are weedy species (Tesshome et al., 1997). The genus *Sorghum* is further divided into five sections; *sorghum*, *stiposorghum heterosorghum*, *parasorghum* and *chaetosorghum* (Ejeta et al., 2005). The genus is very complex, as indicated by differences in number of chromosomes for species in the different subgenera. Subgenera *Parasorghum* and *Stiposorghum* have the lowest haploid chromosome of five and most polyploid species arising from these two sub generas are autopolyploids in which chromosome number is built by units of ten (i.e., 2n=10,20,30). The lowest haploid chromosome number in *Eusorghum* is ten and polyploid species arising from this subgenera are allopolyploids with chromosome numbers built by units of twenty (i.e. 2n = 20, 40). *Chaetosorghum* and *Heterosorghum* are 2n = 40 allopolyploids (Celarier, 1958). Figure 2. Shows the classification of sorghum.

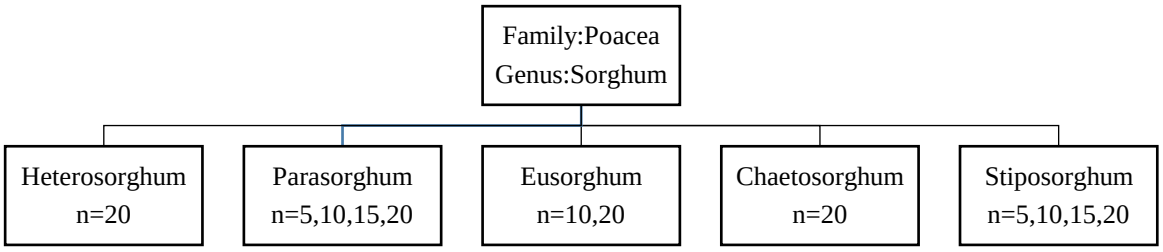

Figure 2. Subgenera of Sorghum.' n' denotes haploid chromosome number.

The *sorghum* section comprises of three species: *Sorghum halepense, Sorghum bicolor and Sorghum propinquum* (Deu et al., 1994). The species *Sorghum bicolor* has three sub-species; *drummondii* which is a weed, *bicolor* which is cultivated and *arundinaceum* which is a wild type. The cultivated *bicolor* subspecies is sub-divided into five races including *bicolor, durra ,caudatum, , guinea* and *kafir* and an additional 10 intermediate races (Harlan et al., 1972). The most commonly found wild subspecies *arundinaceum* races include *aethiopicum, verticilliflorum, arundinaceum* and *virgatum* (Deu et al., 1994). Subspecies *drummondii* is a diverse group composed of all the intermediate forms between wild and cultivated sorghums across the African continent (Okeno et al., 2012).

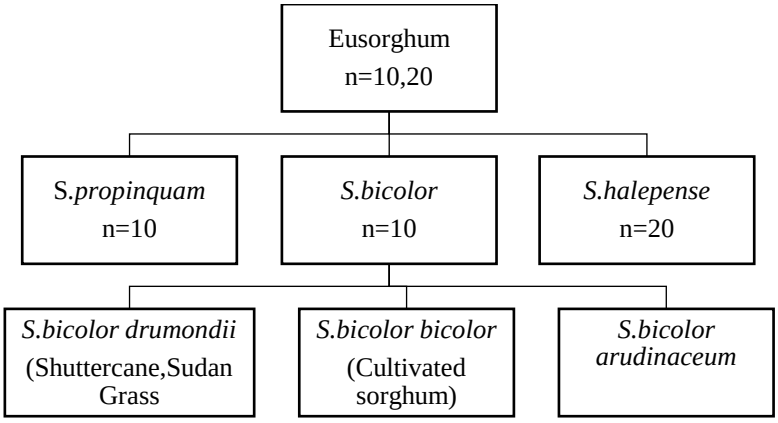

Figure 3: Species and subspecies of subgenus Eusorghum.' n' represents haploid chromosome number**.**

Sorghum originated in northeast Africa where it is believed to have been first domesticated over 3000–5000 years ago (Ejeta et al., 2005). Modern sorghums have been reported to have diverse origins. It has been proposed that the cultivated subspecies *bicolor* arose from the wild subspecies *verticilliflorum*, wild race *aethiopicum* gave rise to *durra* and *bicolor* cultivated races, while wild races *arundinaceum* and *verticilliflorum* gave rise to *guinea* and *kafir* types of sorghum, respectively (Mann et al., 1983).

Disruptive selection where traits beneficial for cultivation are favoured is believed to be the process through which early domestication of sorghum occured (Doggett, 1988). Later on, geographic isolation and genetic recombination in different environments led to the creation of many varieties and races of sorghum. Disruptive selection, geographical isolation and genetic recombination resulted in three wide clusters of *S. bicolor* namely cultivated and improved types, wild types, and intermediate types (Kimber, 2000). Cultivated sorghums were selected for various phenotypic traits such as plant height, inflorescence characters, seed characters, resistance to biotic and abiotic stresses as well as suitability for food, fodder, fiber and as building materials (Dillon et al., 2007b).

2.2 Morphology of sorghum plant

Sorghum grows as monocot crop and is similar morphologically to maize and sugarcane. Sorghum has stout and erect stems, 0.5m to 6m tall (Habindavyi, 2009). The stem can be thin or very stocky measuring 5 - 50 mm in diameter. Internal structure of the stem is composed of a hard cortex shielding a softer inner pith that may be sugary or tasteless, juicy or dry giving it a solid texture (House, 1985).

Stem nodes contain root bands and growth rings that give rise to new stems in case of damage of upper part of the stem. The bottommost nodes in the stem contain buds that produce axillary tillers whereas basal tillers are formed at the first node of the stem (Doggett, 1988). The plant has wide glossy leaves with serrated margins. The leaves are wide and rough, linear to lanceolate in shape and resemble maize leaves. They measure 90 - 100cm in length and approximately 10 - 12 cm in width (House, 1985). The coleoptile which emerges as the first leaf has a rounded leaf tip which makes it different from the other leaves. At full development of the leaves the leaf collar emerges marking the junction between leaf blade and sheath. Each leaf sheath emerges at its own node on the plant stalk. The last leaf to emerge is the flag leaf which is usually smaller than the other leaves on the plant (Dogget, 1988). Some sorghum varieties have leaves concentrated near the base of the plant while others have leaves evenly distributed along the stem. The leaves display an alternate leaf arrangement where a single leaf is borne at each node along the stem interchangeably in an ascending spiral. A sorghum plant at flowering stage usually has 14 – 18 leaves (House, 1985).

Sorghum inflorescence is a panicle that vary in compactness from open and loose to compacted and is borne at the top of the plant. Panicle sizes vary but they have been reported to be up 50 - 60 cm long and 30 cm wide (Doggett, 1988). Inflorescence is composed of primary and secondary branches bearing spikelets which hold the flowers. Number of flowers in mature panicle varies from 1600 – 4000 (Stephens et al., 1934). Blooming starts when yellow anthers appear at the tip of the panicle 5 to 7 days after panicle exertion and continue for 4 to 9 days where anthers continue to develop progressively down the panicle (Gerik et al., 2003). Sorghum grains have a variety of colours ranging from brown, white, yellow, red, orange and other with transitional colours.

2.3 Reproduction in Sorghum

Sorghum is a sexually reproducing crop that reproduces by means of seeds. Onset of flowering in sorghum varies dependent on variety and growing conditions but most genotypes take an average of 60-70 days (Spenceley et al., 2005). Flowering occurs within three days after the development of panicle from the flag leaf. The optimal flowering temperatures are 21 - 35°C and temperatures outside this range may result in delayed flowering (Schertz et al., 1980).

Stigmas are receptive from 2 days before anthesis and continue being receptive for 5 - 16 days depending on the cultivar (Stephens et al., 1934). For best results, pollination should be carried out within the first three days of blooming (Doggett, 1988).

Pollen germination requires light and is reported to only germinate on the stigma after daybreak (Artschwager et al., 1949). Fertilization occurs within two hours after pollen germination (Doggett, 1988). Sorghum cannot reproduce vegetatively but can be propagated vegetatively from stem cuttings since root primordia are present at the nodes (Schertz et al., 1980). Most sorghum genotypes are non-rhizomatous but a few, especially forage sorghums produce short rhizomes that enable local spread within a region (Parsons et al., 2001a).

2.4 Striga hermonthica

2.4.1 Biology

Striga hermonthica (Del.) Benth is classified in the Orobanchaceae family. The plant is an annual angiosperm which is also regarded a hemi-parasite as it has capacity to carryout photosynthesis (Spelleck et al., 2013). There are approximately 30 species in *Striga* genus, and all are parasitic to plants in the Poaceae family except *Striga gesnerioides* (Willd.)Vatke which exhibits virulence behavior to dicots. *Striga hermonthica, Striga asiatica* and *Striga gesnerioides* are the most destructive of the striga species (Parker, 2009). Several studies using different *Striga* plant tissues have been conducted to determine chromosome numbers in various *Striga* species. Chromosome numbers counted from anther squashes were reported as n = 20 for *Striga asiatica* and n = 30, 40 for *Striga hermonthica* depending on geographic location (Iwo et al., 2008). Another study that utilized pollen mother cells reported chromosome numbers of n = 27 for *Striga aspera* and n = 32 for *Striga hermonthica* (Musselman et al., 1991). Chromosome counts using shoot tips reported haploid n =18 for *Striga aspera* and n= 19 for *Striga hermonthica* (Aigbokhan et al., 2000). The great inconsistencies in reported chromosome counts for *Striga* species in these studies indicates weak understanding of chromosome composition in *Striga* species that needs to be addressed on further study.

Striga is believed to have originated from an area between the Semien Mountains of Ethiopia and the Nubian Hills of Sudan which is also the center of origin for sorghum (Atera et al., 2011). *Striga* species thrive in regions with annual rainfall ranging from 25-150 cm and severity of infestation being low in areas of high rainfall (Mohamed et al., 1998). It is

believed that striga is endemic to Africa with approximately 80% of the described Striga species occurring in Africa (Berner et al., 1995).

Striga hermonthica is extensively distributed in sub-Saharan Africa, with its occurrence being documented from West African countries to Ethiopia, Uganda and Kenya in East Africa (Mohamed et al., 2001). *Striga hermonthica* is mainly harmful to sorghum, maize and millet, but is also gradually being found in sugarcane and rice fields (Atera et al., 2011).

2.4.2 Morphology of *Striga hermonthica* plant

Striga hermonthica in particular is an obligate root parasite and its lifecycle is closely related to that of its host (Haussmann et al., 2000). The plant spends nearly all its life underground and only emerges to the surface for reproduction purposes. The height of the mature plant ranges from 15–20 cm. Stem have a square cross-section and diameter ranging between 1-2.5mm. These stems are light green in colour and are lightly covered with coarse, short, white, bulbous-based pubescence. The underground stems start off round and white in colour then change in to blue when exposed to air. The leaves are oriented perpendicular to one another and are narrowly lanceolate with a length of about 1–3 cm. Their round and succulent roots grow attached to the host root system and they do not have root hairs. Flowers are small and borne directly on the stalk at the axial of the leaf. *Striga* flowers may be white, yellow, pink, orange, red or purple in colour. Striga produces a capsule that has five edges and narrow wings and inside the capsule about 250-500 seeds are borne (Ejeta et al., 2007).

Striga hermonthica can easily be distinguished from *Striga asiatica* by the colour of the inflorescence. *Striga hermonthica* has purple flowers while *Striga asiatica* produces red flowers. *Striga hermonthica* shares a very close resemblance with *Striga aspera* in that both produce purple flowers and cases of misidentification have been reported before. However, in *Striga aspera* has the walls of the corolla tube are covered by glandular pubescence, which is bent well above the calyx. *Striga hermonthica* has no glandular pubescence on corolla tube and is bent just above the calyx (Ramaiah et al., 1983). Ratio of Corolla tube length below and above the bend has been reported to be 1.5:1 in *S. aspera* and 0.9:1 in *S. hermonthica* (Parker, 1991). In addition to that, *Striga aspera* usually affects wild grasses and it often occur in moist transient habitats along roadsides while *Striga hermonthica* invades cereal crops like maize, sorghum and millet on poor and disturbed soils (Mohammed et al., 2006).

2.4.3 Striga etiology

Striga is an obligate parasite, and it has a growth cycle that is intimately related to growth cycle of its host plant (Haussmann et al., 2000). Mature *Striga* seeds can stay dormant in the soil for a number of months or years until a suitable host is present and they also avoid sprouting in the last rains of the season (Berner et al., 1997). Germination in *Striga* seeds is triggered by presence of germination stimuli produced by host roots (Satish et al., 2011). For germination to take place the seeds need to be preconditioned by exposure for a number of days to optimal moisture and temperature conditions following production of the germination stimuli (Gobena et al., 2017). These stimulants have been described as strigolectones. Strigol was the first to be identified and was isolated from cotton roots (Cook et al., 1966). Sorgolactone is produced by sorghum roots while alectrol is exuded from roots of cowpea (Matusova et al., 2005). Ethylene is the hormone that prompts germination of *Striga* seeds leading to suicidal germination hence reduction in their numbers in the soil (Mohamed, 2002).

These chemicals are unstable hence degrade quickly in soil and therefore are produced in concentrations enough to trigger germination of seeds within a few millimeters from the roots of host plant (Fate et al., 1990). Upon germination, the radicle grows in the direction of the host's root and develops haustoria that connect it to the host root. Using the haustoria the weed is able to absorb water, minerals, carbohydrates as well as amino acids from the affected plant resulting in underdeveloped shoots, leaf chlorosis and subsequent decline in photosynthesis rate in the host (Ejeta and Butler, 2000). *Striga* weeds spend most of its life cycle underground and only emerge to the soil surface to flower and reproduce seeds.

2.4.4 Haustorium Development

Upon initiation of germination, an initial root develops from the *Striga* seed towards the host root. Haustoria development starts once the radicle is in contact with the host's roots and it may be initiated at various locations on the root including root tip, at the radicle and on the sides of the fully developed root (Kujit, 1977). The cells in the dermatogen or the outer layer of tissue and underlying tissues enlarge and haustorial hairs start to develop (Riopel et al., 1987). Cells in the tip become specialized for penetration and undergo cell division as well as

cell elongation very rapidly. The haustorium develops into a wedge shape that aids in the penetration of the host root by mechanical force as well as breakdown of root tissues using chemicals such as an oxidizing enzymes (Hood et al., 1997).

Oscula, which are small finger-like projections from the haustorium infiltrate the host xylem via open spaces in the membrane and swell so that they can fit perfectly in their position inside the xylem membrane (Dorr et al., 1996). This is followed by development of *Striga* sieve tubes within eight cells layer from the host phloem allowing passage of nonspecific nutrients from the host to *Striga* (Dorr et al., 1995). *Striga* cotyledons emerge from the seed a day after establishment of connection with the vascular tissues.

2.5 Effects of *Striga* weeds on sorghum production in Kenya

Striga is reported to infest over 60% of cultivable land in sub-Saharan Africa affecting lives of over 300 million farmers in more than 25 countries causing yield losses of over seven billion dollars (Ejeta, 2007). Approximately 50 million hectares of land under cereal production in sub-Saharan Africa are reported to be infested with *Striga* (Westwood et al., 2010). In East Africa, approximately 1.4 million hectares of farmland is affected by *Striga*, with over 340,000 hectares of farmland affected in Kenya alone. The total area of land harvested with sorghum in Kenya is approximately 301,705 hectares which amounts to an annual production of 288,000 tonnes per hectare (FAOSTAT, 2019). This is considerably low compared to the global average production of 57 million tonnes per hectare (FAOSTAT, 2019).

Striga, as the main biotic constraint in production of sorghum and maize in Africa and is responsible for approximately 8 million tons in grain loss annually (Sauerborn et al., 2009). A survey by (Woomer et al., 2009) reported about 217,000 ha in Kenya to be infested with *striga* leading to crop loss valued at 53 million dollars annually. *Striga* accounts for loss of yield approximated to 1.15, 1.10 and 0.99 tons per hectare for maize, sorghum and millet, respectively (Mac Opiyo et al., 2010). Extent of damage caused by *Striga* depends on *Striga* densities, the affected plant species and genotype, cultural practices during cultivation, nutrients amount in the soil and rainfall regimes of the agricultural area (Atera et al., 2012).

In recent years, food security in Kenya has been on the decline. A survey carried out by (Kenya: Integrated food security Phase Classification, Food Security & Nutrition Snapshot) reported that nearly 1.8 million people in Kenya's rural and arid and semi-arid land areas faced high levels of acute food insecurity between August and September of 2020. Strategies

of reverting this food shortage trends including improving soil quality, use of superior seeds to improve yield, employing good agricultural practices (GAPs), reducing quantity of weed seedbanks in the soil as well as integrated management of common disease and pests (Bruce, 2010) need to be popularized.

Population increase coupled with rise in demand for food has led to increased land use, monocropping for cash crops and subsequent deterioration of soil quality and fertility has caused an increase in *Striga* prevalence (Ransom, 1996). Sorghum is a hardy crop and is tolerant to various abiotic and edaphic stresses such as drought, infertile soil, saline or alkaline soils, water logging and high temperatures (Muui et al., 2013). It can therefore be used to supplement the food shortage. However, most sorghum varieties that are grown by farmers do not have *Striga* resistance genes and this has led to the low yield recorded for this crop. Efforts to improve Sorghum varieties for *Striga* resistance will greatly boost food security in the country.

2.6 Resistance to *Striga* in sorghum

Resistance mechanisms against *Striga* are categorized as pre-attachment or post attachment resistance (Michael et al., 2012). Pre-attachment mechanisms enable a would-be host to evade or prevent parasite attachment. Some of the mechanisms included in this category include lack of germination stimuli, production of low quantities of germination stimulant, inhibition of germination, prevention or reduction of haustorium formation, partial inhibition of haustorium development, and thickened host root cell-walls resulting in a mechanical barrier to infection (Michael et al., 2012).

Low germination stimulant activity in sorghum is the most studied of the pre-attachment mechanisms of *Striga* resistance in sorghum (Satish et al., 2011). The mechanism was described over 50 years ago and is believed to have resulted from a mutation event where mutants produced low quantities of germination stimulants in root exudate (Williams, 1959). Sorghum genotypes that either do not produce the stimulants or produce it in very low amounts have been observed to be resistant to *Striga* in field experiments (Hess et al., 1992). Low *Striga* germination activity is controlled by a single gene and is recessively inherited (Ramaiah et al., 1990).

Post attachment mechanisms include constitutive or induced resistance mechanisms that occur as the haustorium tries to gain access to the root tissues of the host and link to the vascular system. Post attachment resistance mechanisms are characterized by the production

and release of compounds that are toxic to living cells, mechanical barriers, programmed cell death expressed in form of hypersensitive reaction (HR) and incompatible responses (Haussmann et al., 2000). These cytotoxic compounds include phenolic acids and phytoalexins (Timko et al., 2013).

These cytotoxic compounds are produced inside the host root cells in a physiological process called abiosis and once they are produced, they destroy the haustoria cells preventing further germination of the haustoria (Timko et al., 2013). Formation of physical barriers such as lignified cell wall to prevent possible haustorium entrance and growth, rapid death of cells at the area of haustoria attachment (hypersensitive response) preventing further haustoria growth hence hindering penetration into the root, as well as inability of the haustorium to create a connection with the host vascular system have been described as post attachment resistance mechanism to *Striga* (Michael et al., 2012). Hypersensitive reaction response is controlled by two dominant genes with dominant inheritance (Mohammed et al., 2010). Due to its dominance nature and simple inheritance, hypersensitive reaction is best suited for breeding research to improve Striga resistance in susceptible sorghum genotypes.

2.7 Physiological and biochemical basis of resistance

Several cellular response mechanisms are employed following infection of the roots by *Striga*. An experiment carried out by Olivier et al., (1991) revealed that within a duration of between 24 and 72 hours after haustoria has attached to the host root there was accumulation of polyphenolic compounds at the host-parasite interface of *Striga hermonthica* and sorghum. This electron build up often results in the development of physical barriers such as cell wall thickening brought about by deposition of complex organic polymers such as suberin, callose, or lignin at the parasite penetration point (Botanga et al., 2005). This has been defined as a hypersensitive reaction to *Striga* attack at the parasite attachment point and has been observed in some cultivated and wild species of sorghum (Mohamed et al., 2003).

Host resistance may as well occur after the parasites have established connection to the vascular system of a susceptible host. The mechanisms involved include obstruction of vascular vessels using gels or gummy elements preventing passage of minerals, nutrients and water from the affected plant to the parasite (Scholes et al., 2008). Another mechanism involves production and transport of harmful substances to the host vascular system resulting in their translocation into the parasite through the haustorium (Scholes et al., 2008).

Striga germination is triggered by strigolactones produced as sorghum root exudates. The main strigolactones found in sorghum root exudates include; sorgolactone, strigol, 5-deoxystrigol, and sorgomol (Gobena et al., 2017). These share a common stereochemistry with respect to the β-orientation of their C rings but differ from each other by various substitutions on A and B rings (Xie et al., 2013).

These strigolactones however have opposite stereochemistry, displaying high and low *Striga* germination stimulant activities, respectively. Sorghum genotypes expressing high *Striga* resistance have reduced 5-deoxystrigol but increased orobanchol levels. However, the change in the type of strigolactone does not change other strigolactone functions, such as related to tillering or symbiosis with arbuscular mycorrhizal (Lyu et al., 2017). *Striga* is very sensitive to these strigolactones and is able to germinate at concentrations as low as 10−11M (Cook et al., 1966) depending on the particular strigolactone being produced (Nomura et al., 2013).

2.8 Genetic basis of resistance mechanisms to *Striga* in sorghum

Sorghum genotypes that produce insufficient quantities of exudates essential for *Striga* seed germination have been found to be resistant to *Striga* while genotypes that show high susceptibility to *Striga* produce high amounts of stimulant that trigger germination of striga seeds (Ejeta, 2007). In a study by Ejeta, (2007) sorghum cultivars SRN39, Framida, 555, IS9830, ICSV1006 and the wild *S. bicolor* subspecies *drummondii* were found to exhibit the low germination stimulant character as their mechanism of resistance to *Striga*. This resistance is controlled by one major gene and several minor genes (Haussmann et al., 2000). Through diallel and line x tester analysis, it was pointed out that in sorghum, germination of *Striga hermonthica* seeds is inherited in a quantitative manner with additive effects (Haussmann et al., 2000). However, in other studies, this mechanism of resistance was proposed to be controlled by a single recessive gene (Olupot, 2011). It is therefore necessary to carry out more studies to determine the inheritance of this character.

In plants with low production of haustoria inducing factors, germinated *Striga* seeds do not develop haustoria and consequently die because they are unable to create an association with the host roots hence cannot gain nutrients from the host. Apart from germination stimuli, an additional signal to induce haustoria development is required (Ejeta, 2007). This mechanism of resistance has been observed in the wild species *Sorghum bicolor* subspecies *drummondii* and P78. The resistance is conditioned by a single dominant gene (Mohammed 2002). To verify this information, crosses were made involving a mutant sorghum genotype P78, that

has low production of haustoria inducing factors and the sorghum cultivars PP34 and Shanqui Red, both having high haustoria initiation capacity, the F1 exhibited the low production of haustoria inducing factors while the F2 segregated in 3:1 ratio for low to high haustoria initiation character (Olupot, 2011).

Host resistance involves a hypersensitive reaction where there is localized death of host tissues around infection site together with a release of phytoalexins to prevent further attachment of the *Striga* weed. This resistance mechanism has been reported in sorghum wild relatives *S. bicolor* subspecies *drummondii*, *S.hewisonni* and *S.b.verticilliflorum* cultivars such as Dobbs, Framida and Serena (Patrick et al., 2004). In a study by Mohamed, (2002) it was reported that two nuclear genes with dominant gene action conditioned a hypersensitive reaction to *Striga*. In the study, crosses were made between sorghum lines, KP33 and CK32 which had a strong hypersensitive response with two sorghum cultivars, TX430 and TX2737, with no hypersensitive response. A hypersensitive response to *Striga* attack was observed on all the F1 progeny. Segregation at F2 for all the crosses was in the ration 15:1 (HR: no HR) while be BC1 populations segregated in the ratio 3:1 (HR: no HR). The two genes were assigned the symbols *Hrs1* and *Hrs2*.

In incompatible response mechanism, development of *Striga* after attachment is discouraged and the seedlings do not develop beyond emergence of first leaves (Olupot, 2011). Those that manage to develop show signs of stunted growth (Ejeta, 2007). Some of the sorghum cultivars that exhibit this form of resistance to *Striga* attack include SRN39, ICSV761 and the wild accession *S. b. verticilliflorum* (Patrick et al., 2004). However, it is not clear how this resistance mechanism is inherited.

2.9 DNA markers and markers assisted selection in Sorghum

A DNA (deoxyribonucleic acid) marker is a DNA segment that co-segregates with the trait of interest and its inheritance can be traced in a Mendelian fashion. These markers are based on DNA sequence variation which may either be single nucleotide polymorphisms, insertion of nucleotides and deletion of nucleotides or variation in the numbers of tandem repeats. The different ways in which polymorphism is revealed have led to the grouping of markers into three categories; hybridization based polymorphisms, Polymerase Chain Reaction (PCR)-based markers and sequence- based markers (Gupta et al., 2002). Polymorphic markers reveal variability for a particular trait among genotypes within a species or across different species. DNA markers have been used in selection for superior traits at early developmental stages of

plants, in identifying donor parents in backcrossing, speeding up recovery of recurrent parent genotype in backcrossing, characterization of germplasm for future use and other uses in plant breeding (Varshney et al., 2009). DNA markers are useful in MAS for tracking genes of interest whether dominant or recessive across generations.

This allows identification of the most appropriate individuals amid the segregating progeny based on composition of alleles across the entire genome or part of the genome.

2.9.1 Hybridization-based molecular markers

2.9.1.1 Restriction fragment length polymorphism (RFLP)

These are markers that reveal differences in length of DNA fragments cut using restriction enzymes. The differences in restriction fragment lengths may be due to mutation at a particular point, insertion or deletion of nucleotides, translocation, inversion and duplication of DNA segments resulting in addition, loss or repositioning of restriction enzyme recognition sites hence the varying number and size fragments among individuals. RFLP markers are co-dominant, and no sequence information is required for synthesis. However, high quality and quantity of DNA is required, and the level of polymorphism is low. Since the technique cannot be automated, it is time consuming, labor intensive; expensive in addition to requiring radioactively labelled probes (Tanksley et al., 1989, Kochert, 1994).

2.9.2 Markers based on the Polymerase Chain Reaction process

2.9.2.1 Random amplified polymorphic DNA (RAPD)

RAPD markers reveal differences in DNA sequences that have been amplified using random oligonucleotide primers (Fevzi, 2000). Sequence information of target DNA or the primer is not required. The technique can be automated and has high level of polymorphism. However, these markers are dominant and have low reproducibility within and between laboratories (Welsh et.al., 1990).

2.9.2.2 Amplified fragment length polymorphism (AFLP)

AFLP markers combine the Restriction Fragment Length Polymorphism (RFLP) procedure and PCR technology. Specific fragments of genomic DNA that has been digested using restriction enzymes are multiplied using PCR. The sequence information of the border sections of the target DNA must be identified in order to design specific primers. Polymorphism in AFLP markers is revealed by differences in restriction sites. These markers

are dominant as one cannot make a distinction between homozygous genotypes and heterozygous genotypes (Vos et al., 1995).

2.9.2.3 Single Nucleotide Polymorphism (SNP)

Single Nucleotide Polymorphism (SNP) markers arise due to single nucleotide differences among individuals .They are the most abundant markers as they occur throughout the genome. Allele specific primers are used to amplify the trait of interest hence sequence information is required in order to develop these markers. The markers are co-dominant and highly reproducible.

2.9.2.4 Diversity Array Technology (DArT)

This is micro-array hybridization based technique that allows the simultaneous assessment of several hundred polymorphic loci spread over the genome. The method detects the presence as well as absence of individual fragments in genomic DNA. This requires the availability of genetic sequence data. High automation of the technique allows for fast results. The technique allows for genotyping of species regardless of previous advances in genomic resources of the particular species. Thus, it is the most appropriate for polyploidy species (Peter et al., 2015).

2.9.2.5 Simple Sequence Repeats (SSRs)

Simple Sequence Repeats markers also known as microsatellites arise from DNA sequences of 2 to 6 units recurring not more than 100 times in the genome (Mohapatra et al., 2003). Polymorphism in SSR markers is caused by the variable number of tandem repeats. SSR markers are most preferred for the assessment of molecular diversity since a large number of polymorphisms can be detected in a relatively simple protocol (Park et al., 2009). They are codominant, greatly reproducible and only require a small quantity of DNA for analysis. Large populations can be mapped using the SSR markers as the markers allow analysis of multiple loci in the same lane using different primers in a process called multiplexing (Park et al., 2009). Simple Sequence Repeats (SSRs) markers are also useful in identification and protection of varieties, assessment of germplasm and population genetics, assessment of purity of seed and quality of hybrid seed, gene tagging and forensics studies (Ahmed, 2005). However, analysis of SSR markers requires DNA sequence information for the designing of primers for PCR amplification. Several protocols for analyzing SSR markers have been developed and these include analysis using agarose gel, analysis using PAGE and silver staining, analysis using radio labels and analysis using fluorescent dinucleotide triphosphates

(Ahmed, 2005). Analysis using agarose gel is fast and is efficient but PAGE and silver staining gives better resolution though it requires more labor than agarose gel. The use of fluorescent dinucleotides for SSR analysis is most appropriate for size and band density estimation and allows large scale analysis since multiple loci can be multiplexed (Ahmed, 2005).

2.10 *Striga* resistance QTLs in sorghum

A Quantitative Trait Locus is a section in the genome that influences a trait that is quantitative in nature. Useful QTL should be intimately connected to the trait of importance to avoid chances of genetic recombination as this causes loss of the QTL. Quantitative trait locus (QTL) analysis is a statistical process that describes the genetic basis of variation in complex traits by establishing the relationship between phenotypic data and genotypic data (Falconer et al., 1996). This is achieved by identifying the action, interaction, number, and precise location of the QTLs.

In an effort to identify QTL associated with resistance to *Striga* weed in sorghum, recombinant inbred populations were established following the crossing of the lines IS9830 × E36-1 and N13 × E36-1 (Haussmann et al., 2004). The parental genotypes used in the crosses have different *Striga* resistance mechanisms. Genotype IS9830 which is a Sudanese feterita race caudatum exhibits production of low quantities of stimulants that trigger *Striga* seed germination. N13 which is Indian durra sorghum, encourages high germination of *Striga* seeds; however, parasite penetration is prevented by formation of a mechanical barrier. In each of the two Recombinant Inbred Populations, five stable QTL were expressed on chromosomes A, B, I and J across test sites, years and independent mapping population samples (Haussmann et al., 2004). The genes for resistance expressed in these stable QTLs came from the resistant parents identified as N13 and IS9830. The two recombinant inbred populations (RIP1 and RIP 2) both showed two sets of 11 QTLs and 9 QTLs in the two sites which was equivalent to 79% and 81% of the genetic variance for AUSPC respectively. The effects of these QTLs were confirmed by testing across many environments, years and independent recombinant inbred population samples and therefore they can be used in marker assisted selection for *Striga* resistance in sorghum (Haussmann et al., 2004).

Quantitative trait loci analysis to identify genes influencing low germination stimulant production trait in sorghum showed a single main QTL peak exactly on the *lgs* locus on chromosome five (Satish et al., 2011). The study utilized a high density genetic map

developed using 367 markers (DArT and SSRs) and an in vitro assay for germination stimulant activity towards *Striga asiatica* in 354 recombinant inbred lines derived from SRN39 (low stimulant) x Shanqui Red (high stimulant). The *lgs* QTL was finely mapped between two tightly linked microsatellite markers SB3344 and SB3352 at a distance of 0.5 and 1.5 cM, respectively (Satish et al., 2011). The study supported the suggestion that the trait is controlled by a single major gene.

2.11 Marker Assisted Backcrossing for *Striga* resistance in sorghum

Marker Assisted Backcrossing is a selection technique that uses DNA markers to isolate individuals for use as parents in subsequent generations in breeding (Semagn, 2006). Intimate connection between the markers and the trait of interest is important in marker assisted backcrossing as it hastens the process of selection. A study by Lee, (1995) indicated that the ideal distance between an introgressed gene and its flanking markers should be as close as 2cM.

Several selection strategies are employed in marker assisted backcrossing and these include foreground selection, background selection and recombinant selection. In foreground selection, foreground markers linked to the target gene are used to trace its introgression into the elite germplasm.

This strategy is suitable for traits whose screening procedures are laborious and take a lot of time and in addition it allows for selection of recessive alleles and also allows selection of traits that appear at the reproductive stage when the plants are just seedlings. Background selection involves the use of background markers which are makers that are linked to the preferred parent genome. These markers therefore identify individual backcrosses that possess the greatest proportion of the preferred parent genome (Semagn, 2006). Recombinant selection involves the selection of progenies from the backcrossing that contain the gene of interest as well as exhibiting recombination between the target locus and the flanking markers (Bertrand, 2007). Due to linkage drag, the rate at which the donor chromosome segment is decreased at the target locus is lower than at the unlinked sections and therefore recombinant selection is used to hasten the selection process (Hospital, 2005).

2.12 Wild relatives of sorghum

Due to its diversity and complexity, *Sorghum bicolor* is divided in three subspecies including *Sorghum bicolor* ssp *Bicolor, Sorghum bicolor* ssp *Verticilliflorum* and *Sorghum bicolor* ssp *Drummondii* (Evans et al., 2009). The subspecies *bicolor* comprises of the five main races of

sorghum which is cultivated including bicolor, caudatum, durra, guinea and kafir. *Sorghum bicolor* subspecies *verticilliflorum* includes close wild relatives of cultivated sorghum while the hybridization between subspecies bicolor and verticilliflorum gives rise to the heterogeneous *Sorghum bicolor* ssp *Drummondii* which grows as a weed (Evans et al., 2009).

Sorghum wild relatives are classified into four botanical groups which include *Sorghum arundinaceum, Sorghum verticilliflorum, Sorghum virgatum* and *Sorghum aethiopicum*.

Sorghum arundinaceum is a robust tall forest grass which has big leaves and a wide loose panicle with overhanging branches. *Sorghum verticilliflorum* is morphologically similar to *Sorghum arundinaceum* but its panicle is compact. *Sorghum aethiopicum* is shorter and its panicle is small with stiff or sub-erect branches. *Sorghum virgatum* is grass commonly found in deserts with slender leaves and it occurs along riverbanks and irrigation sites (Hariprasanna et al., 2015).

Wild sorghum species mature faster than the cultivated species but their prolonged seed dormancy and high tillering ability leads to synchronization of the onset of anthesis and this scenario has led to hybridization between these two (Doggett et al., 1968). In a study by Magomere, (2014) to investigate hybridization between *S. bicolor* and its wild relatives in Western Kenya, interspecific hybridization between *S. halepense* and *S. bicolor* and *S. sudanense* and *S. bicolor* was observed. Although the phenotypic traits of F1 progenies varied depending on the wild parents involved in the crosses significant heterosis in the F1 progenies was evident as they showed prolific tillering and branching when compared to the parental populations. The F1 progenies also showed a ratooning ability that was equal or lesser than that of the wild parents. However, although these hybrids had more seeds compared to the parents, these seeds showed high levels of dormancy and poor germination.

2.13 Flowering and fertilization in sorghum

Flower formation starts 30-40 days after sprouting but some genotypes start forming flowers as early as from 19 days while others flower as late as at 70 days or more. Active growth due to meristematic activity stops with the onset of floral initiation. This is followed by a period of rapid cell elongation where the inflorescence develops. The boot forms as a protrusion from the covering of the flag leaf approximately six to ten days before flowering. Sorghum generally starts to flower in fifty five to seventy days in warm environments although the duration may vary from thirty to a hundred or more days (House, 1985).

Flowering starts from the tip of the sorghum head and proceeds successively down in a 4 to 5 day period. Flowering is marked by the opening of the glumes where three anthers fall free and two stigmas stick out while still attached on firm styles. Flowering normally occurs just before sunrise or just after sunrise. However, during cloudy and damp mornings flowering may be delayed. Pollen is released from the anthers in to the air when the anthers are dry (House, 1985). Viable pollen is normally shed up to until noon.

Sorghum undergoes self- pollination but natural outcrossing of about 2 - 10% occurs. Once the pollen has landed on the sticky stigma it forms a structure known as pollen tube which has two nuclei and starts germinating down through the style. This pollen tube continues germinating until it reaches the ovule sac and enters via the micropyle. Once in the ovule sac, one sperm cell fuses with an egg cell and fertilization occurs resulting in a diploid zygote. The remaining sperm cell fuses with the two polar nuclei resulting in the formation of a triploid endosperm. The glumes close soon after pollination. Cleistogamy may occur in some of the very long glumed sorghum genotypes where the glume does not open and therefore fertilization takes place in the closed florets (House, 1985). Cytoplasmic male sterility is also present in sorghum where plants that are male sterile do not develop anthers and in case they do develop anthers, the anthers do not have viable pollen or have very little amount of pollen compared with other plants (House, 1985)

2.13.1 Strategies for controlled pollination in sorghum.

The purpose of carrying out hybridization in sorghum is to create segregation for breeding and selection. Four strategies have been suggested that can be used for controlled pollination in sorghum.

2.13.1.1 Hand emasculation

Emasculation refers to the removal male component of a flower which is the stamen in order to prevent self-pollination. Emasculation is done a day before anthesis. Normally the florets to be emasculated occurs about 3cm from the already opened florets on a panicle. Once the florets to be emasculated have been located all the other florets are removed. Emasculation is done using sharp equipment like a sharpened pencil or any other pointed instrument. Using a sharp pointed tool, the anthers are exposed from the enclosing lemma and palea and are removed. After emasculation the panicle is covered with a paper bag for 1-2 days where they are later pollinated by dusting with pollen from the male lines (Rooney, 2004).

2.13.1.2 Genetic male sterility

Several nuclear recessive male sterility genes have been characterized in sorghum and designated *ms1* to *ms7*. Male sterility is important as it eliminated the need to carryout emasculation and therefore large numbers of seed can be produced more easily. This strategy is however not used in hybrid seed production due to the inability to produce true breeding progeny. Genetic male sterility is therefore used in sorghum population improvement programmes (Rooney, 2004). The male sterile lines are used as the females.

A genetically male sterile plant can be identified at the flowering stage .Their anthers are smaller, thinner and produce pollen that is not viable. Male sterile plants are covered with pollination bags for 3-5 days to avoid open pollination and are then fertilized with pollen from designated male parents.

2.13.1.3 Cytoplasmic male sterility

Cytoplasmic male sterility system was developed to bring down hybrid seed production cost making this practice economically viable. The method is based on male sterile alleles in the cytoplasm and complementary fertility restorer alleles located in the nuclear genome. These genetic factors are inherited independent of each other. It is the interaction of the male sterile system and the fertility restorer system that determines whether the progeny will be fertile or sterile. There are several cytoplasmic male sterility systems but the A1 system is most common in hybrid seed production (Rooney, 2004).

The system requires a male sterile A-line, a B-line known as the maintainer and R-line which is a fertility restorer line. The maintainer line is used to propagate and maintain the A-line and the two should be genetically identical except for the fact that the A-line is genetically male sterile. The R-line carries the dominant fertility restoration genes and is genetically different from the A-line. During hybrid seed production, the A-line is fertilized with pollen from the R-line. The male fertile lines are maintained by bagging to ensure self -pollination (Rooney, 2004).

2.13.1.4 Hot water emasculation

This emasculation method was developed by Stephens and Quinby, (1934) before the discovery of the cytoplasmic male sterility. The method was developed so as to aid in production of large number of F1 seeds. Once a panicle has been selected, the open florets are removed and the entire panicle is covered with a waterproof sleeve and securely knotted round the peduncle. The panicle is then immersed for ten minutes in water that has been

heated to 42-48 degree Celsius. Panicle is allowed to dry and then covered with a paper bag for 3-4 days after which the pollination is done by dusting the panicle with pollen from the male lines. Heat treatment kills majority of the pollen grains but not all of them hence some amount of self-pollination is expected. The heat does not damage the ovary.

2.13.1.5 Anther dehiscence control

The method aims to control the opening of anthers by use of the moisture generated due to covering the panicle using a plastic bag preceding flowering (Schertz and Clark, 1967).

The plants to be used as females are selected and their panicles should have flowered approximately 2.5-5cm from the tip of the panicle. This section of the panicle that has already flowered together with florets in the bottom section are removed such that only 3-5 cm of the panicle remains.

Two bags a plastic bag and a pollinating bag are used where the plastic bag covers the panicle while the pollinating bag is used to provide shade to the panicle and reduce the temperature under the plastic bag. The panicle is covered for 2-3 days and then fertilized with pollen from chosen male plants. The highly humid atmospheres created by the two bags prevent anther dehiscence. However, some self-pollination may occur because the anthers are not removed and therefore it is necessary to carry out a progeny test to identify the selfs and the hybrids (Schertz and Clark, 1967).

CHAPTER THREE: SCREENING OF SORGHUM WILD RELATIVE, LANDRACES AND IMPROVED GENOTYPES FOR *STRIGA* RESISTANCE USING MORPHOLOGICAL AND MOLECULAR MARKERS

3.0 Abstract

Striga hermonthica is the most important parasitic weed in sub-Saharan Africa and causes yield losses amounting approximately 1.15 tonnes per hectare in Western regions of Kenya. Control methods including herbicides and agronomic practices have proven ineffective hence genetic resistance remains the only control option. In this study phenotypic screening in the field coupled with genotyping using diversity array technology markers (DArT) were used to screen diverse sorghum accessions for Striga resistance and identify genetic relatedness of the accessions. The 64 sorghum genotypes composed of wild, landraces, improved varieties, and F_4 generation crosses were evaluated in a sickplot and a potted trial at KALRO Alupe during the 2019 short rain season. The trials were laid in an alpha lattice design with three replications.

The accessions were also planted in a greenhouse and leaf sampling for DNA extraction was done at two weeks. Library construction and DArT-sequencing (DArTseq) was done at Integrated Genotyping Service and Support (IGSS) at the Bioscience eastern and central Africa (BecA) Lab at the International Livestock Research Institute (ILRI) hub. Four genotypes SRN39, F6YQ212, GBK045827 and F6YQ212xB35 were among the most resistant to Striga in both trials. Five genotypes MACIA, B35, E36-1, OKABIR × AKUOR-ACHOT and LODOKA × ICSVIII IN were the most tolerant to Striga recording superior yield performance in both trials. The overall best performing genotypes in terms of Striga resistance and yield in both trials were Macia, SRN 39, GBK 045827 and GBK 016085. SNPs generated from DArT-sequencing grouped the genotypes into three major clusters, with all resistant checks grouping in the same cluster except N13.There exists novel sources of striga resistance within the wild relatives and cultivated sorghum gene pool and these can be tapped to improve Striga resistance in susceptible sorghum varieties.

3.1 Introduction

Striga hermonthica is the most important parasitic weed in sub-Saharan Africa and remains one of the most devastating biotic factors affecting sorghum production in Kenya (Muchira et al., 2021).Woomer & Savala (2009) reported about 217,000 ha in Kenya to be infested with *Striga*. *Striga* density in these areas has increased over the last years and it is now estimated that on average 1188 seeds are produced per mature striga seed capsule (Van Delft et al., 1997). *Striga* density in Western Kenya is approximately 14 plants per m^2 and it is associated with an average yield loss of 1.10 tons per hectare for sorghum (Mac Opiyo et al., 2010). Severity of destruction caused by *Striga* depends on *Striga* population size, the affected species and genotype, cropping system, amount of nutrients in soil and rainfall regime in the area of agriculture (Atera et al., 2012).

Traditionally, farmers have managed *Striga* in sorghum fields using cultural and mechanical methods including hand weeding (Frost, 1994), intercropping (Aasha et al., 2017) and crop rotations with edible legumes (Oswald and Ransom, 2001). Chemical control has been used but it's not environmentally friendly besides being unaffordable for the average sorghum farmer in Kenya (Dembele et al., 2005: Tuinstra et al., 2009). The most effective and practical solution to the smallholder sorghum farmers is to develop *Striga* resistant sorghum varieties.

Sorghum germplasm screening against *Striga* is the first step towards the identification of Striga resistant genotypes. Resistance has been reported among cultivated sorghum varieties including N13 (Haussmann et al., 2004), SRN 39, Framida and IS9830 (Rodenburg et al., 2005). The resistance mechanism in N13 is a hypersensitive reaction characterised by thickening of the cell wall and silica deposition that limits xylem-xylem connection with the host (Maiti et al., 1984). N13 has been used extensively as a source of resistance (Ngugi et al., 2015; Yohannes et al., 2015; Ali et al., 2016) and the QTLs responsible for resistance have been mapped (Haussmann et al., 2004). The outcrossing nature of Striga that results in different ecotypes with mixed response to different genotypes (Fantaye, 2015) would require the pyramiding of multiple alleles from diverse sources into farmer-preferred varieties for durable resistance. Crop wild relatives of sorghum as superior sources of Striga resistance have been reported with significantly higher resistance than N13 (Mbuvi et al., 2017). Such

reports provide strong justification for more screening of wild relatives and landraces towards the identification of additional sources of resistance to Striga.

Screening sorghum germplasm for *Striga* resistance is complicated by its outcrossing nature that results in different ecotypes with mixed response to different genotypes (Fantaye, 2015). Recommended methodologies for effective field screening include artificial inoculation with *Striga* seeds, suitable experimental designs with sufficient replications, quantitative data scoring and inclusion of susceptible and resistant checks at regular intervals (Haussmann et al., 2000; Rodenburg et al., 2005). A quantitative measure such as "Area under Striga Number Progress Curve" (ASNPC) alongside *Striga* count, *Striga* vigor and yield have been used in past studies (Haussmann et al., 2015; Abate et al., 2016) with great success.

The objective of this study was to screen for novel sources of resistance to *Striga* using sorghum wild and landrace accessions, improved varieties, selected F4 progenies as well as known *Striga* resistance donors, N13, FRAMIDA, HAKIKA, IS9830 and SRN39, as checks. This study made use of an existing *Striga* sick plot with supplemented artificial inoculation to establish the performance of a diverse set of sorghum germplasm alongside their F4 progenies. A pot trial with artificial *Striga* inoculation was used to represent a second environment. While the pot trial was not an ideal environment to mimic field conditions, it was necessary to avoid adding any more *Striga* to the soil while providing a second environment with more uniform *Striga* infestation.

3.2 Materials and Methods

3.2.1 Field trials

A field trial was established in KALRO Alupe, which is situated at 1189meters above sea level 00o29′latitude and 34 o 08′E longitudes along Busia-Malaba road approximately 8 kms from Busia town (Haussmann et al., 2004). The research centre falls within lower medium 1 agro-ecological zone with annual mean temperature from 20.5 to 21.7 °C and annual rainfall of 1800-2000 mm. The centre also has shallow to deep, ferralo-orthic acrisols and ferralsol soils. The site is in a *Striga* hotspot zone hence its appropriate for screening materials for *Striga* resistance.

3.2.2 Planting material and experimental layout

The planting materials comprised 64 genotypes consisting of sorghum wild relatives, elite breeding lines, improved genotypes and F_4 generation crosses. The accessions were sown in a *Striga* sickplot in a square lattice design with three replications in the rainy season of between May 2019 and August 2019. Each block consisted of eight plots. Each plot consisted of two rows 2 m long with a between plant spacing of 30cm and between row spacing of 75cm. A Striga inoculum of 15g was spread along each row during planting to supplement on the *Striga* seed load already in the sickplot. The inoculum was prepared by mixing 5kg of sand with 10g of *Striga* seeds. Phosphorus (P) was applied at the rate of 90 Kg ha-^{1} after thinning while Nitrogen (N) was applied at the rate of 92 Kg ha-^{1} when the plants were 45 to 50 cm tall at 30 days after germination. Chemical control using Chlorantraniliprole and Abamectin was used to control insects, especially fall armyworm (*Spodoptera frugiperda*) and cutworms (*Agrotis* spp, *Spodoptera* spp and *Schizonycha* spp.). The field experiment was purely rain-fed.

For the potted experiment, pots of 30cm diameter were filled with *Striga* free soil obtained from a *Striga* free field which has never shown any *Striga* germination. Each pot was used to represent a plot. Each block consisted eight plots with a between plot spacing of 75cm. To each pot, 15g *Striga* seed inoculum prepared as earlier described was added followed by the planting of the sorghum seeds. Phosphorus (P) was applied at the rate of 90 Kg ha-^{1} after thinning while Nitrogen (N) was applied at the rate of 92 Kg ha-^{1} when the plants were were 45 to 50 cm tall at 30 days after germination. Chemical control using Chlorantraniliprole and

Abamectin was used to control insects, especially fall armyworm (*Spodoptera frugiperda*) and cutworms (*Agrotis* spp, *Spodoptera* spp and *Schizonycha* spp). For the genotyping activities, the 64 accessions were germinated in germination trays in the greenhouse at the World Agroforestry centre. Leaf sampling for DNA extraction was done at two weeks on ice.

Table 2. Planting materials used in the study.

	GENOTYPE	SOURCE	CLASSIFICATION
1	GEN 016109	GeRRI	Wild
2	GEN 048152	GeRRI	Wild
3	GEN 048917	GeRRI	Wild
4	GEN016085	GeRRI	Wild
5	GEN016114	GeRRI	Wild
6	GEN040577	GeRRI	Wild
7	GEN044058	GeRRI	Wild
8	GEN044063	GeRRI	Wild
9	GEN044120	GeRRI	Wild
10	GEN044336	GeRRI	Wild
11	GEN044448	GeRRI	Wild
12	GEN045827	GeRRI	Wild
13	GEN047293	GeRRI	Wild
14	GEN048156	GeRRI	Wild
15	GEN048916	GeRRI	Wild
16	GEN048921	GeRRI	Wild
17	GEN048922	GeRRI	Wild
18	GEN 044054	GeRRI	Landrace
19	GEN043565	GeRRI	Landrace
20	GEN044065	GeRRI	Landrace
21	AKUOR-ACHOT	ICRISAT	Landrace
22	B35	ICRISAT	Improved variety
23	B35_1	ICRISAT	Improved variety
24	E36-1	ICRISAT	Improved variety
25	F6YQ212	ICRISAT	Improved variety
26	GADAM	ICRISAT	Improved variety
27	ICSV III IN	ICRISAT	Improved variety
28	KARI MTAMA 1	ICRISAT	Improved variety
29	KAT/ELM/2016 PL1 SD15	ICRISAT	Improved variety
30	KAT/ELM/2016 PL82 KM32-2	ICRISAT	Improved variety
31	LODOKA	ICRISAT	Landrace
32	MACIA	ICRISAT	Improved variety
33	OKABIR	ICRISAT	Landrace
34	N13	ICRISAT	Landrace (Striga resistance source)
35	SRN39	ICRISAT	Improved variety (Striga resistance source)
36	IS 9830	ICRISAT	Landrace (Striga resistance source)
37	FRAMIDA	ICRISAT	Improved variety (Striga resistance source)
38	HAKIKA	ICRISAT	Improved variety (Striga resistance source)

39	AKUOR-ACHOT X ICSV III IN	UoN	F4 Population
40	B35 X AKUOR ACHOT	UoN	F4 Population
41	B35 X E36-1	UoN	F4 Population
42	B35 X F6YQ212	UoN	F4 Population
43	B35 X ICSV III IN	UoN	F4 Population
44	B35 X LANDIWHITE	UoN	F4 Population

Table 2. Planting materials used in the study.

	GENOTYPE	SOURCE	CLASSIFICATION
45	B35 X LODOKA	UoN	F4 Population
46	E36-1 X MACIA	UoN	F4 Population
47	F6YQ212 X B35	UoN	F4 Population
48	F6YQ212 X LODOKA	UoN	F4 Population
49	IBURSAR X E36-1	UoN	F4 Population
50	IBURSAR X LANDWHITE	UoN	F4 Population
51	IBUSAR X ICSV III IN	UoN	F4 Population
52	ICSV III IN X B35	UoN	F4 Population
53	ICSV III IN X E36- 1	UoN	F4 Population
54	ICSV III IN X LANDWHITE	UoN	F4 Population
55	ICSV III IN X LODOKA	UoN	F4 Population
56	ICSV III IN X MACIA	UoN	F4 Population
57	LANDIWHITE X B35	UoN	F4 Population
58	LANDIWHITE X MACIA	UoN	F4 Population
59	LODOKA X ICSV III IN	UoN	F4 Population
60	LODOKA X LANDWHITE	UoN	F4 Population
61	LODOKA X OKABIR	UoN	F4 Population
62	OKABIR X AKUOR ACHOT	UoN	F4 Population
63	OKABIR X B35	UoN	F4 Population
64	OKABIR X ICSV III IN	UoN	F4 Population

GRRI-Genetic Resources Research Institute; F_4. Fourth filial generation; ICRISAT-International Crops Research Institute for the semi-Arid Tropics; UoN- University of Nairobi; *Resistant checks

3.2.3 Data collection

Striga infestation count on the sickplot and pot trial was recorded at two-week intervals from the 42nd day after planting when First Striga germination is expected. Six plants sampled randomly from the plants in each plot were selected for agronomic data collection. The data collected included:

i. Seedling vigor score-Scored 14 days after emergence with a score of 3 for low,5 for intermediate and 7 for high.
ii. Days after planting to *Striga* emergence was recorded as the day the first plant was observed in a plot.
iii. *Striga* count; was recorded per plot at two weeks intervals after the first Striga emergence in a plot.

iv. Number of *Striga* forming capsules was counted per plot at 105 days after sowing.

v. Days to 50 % anthesis of sorghum; was recorded when half the plants in a plot had flowered.

vi. Plant height: was measured in meters using a tape measure from the ground level to the tip of the panicle when the panicles ate fully exerted.

vii. Dry panicle weight: Recorded as the weight of all mature panicles harvested in a plot.

viii. Total grain weight: measured in grams as weight of threshed sundried grain from the panicle heads in each plot.

ix. 100 seed weight-measured in grams as weight of a sample of 100 seeds from each plot.

3.2.4 Extraction of DNA for Sequencing

DNA for sequencing was extracted using the ISOLATE II Plant DNA Kit to ensure high quality. To the ground samples 300ul of Lysis Buffer PA1 was added and the mixture vortexed thoroughly. 10µLl of RNAse A was added in the mixture and mixed thoroughly. These were incubated at 65ºc for 10 minutes. The samples were centrifuged for 5 minutes to separate the plant debris from the lysate. The lysate was place in the ISOLATE 11 Filter (violet) and centrifuged for two minutes after which the clear flow through in the collection tube was collected and the ISOLATE 11 Filter was discarded. 450µl of binding buffer PB was added to the flow-through and mixed thoroughly by pipetting up and down five times. The sample was then loaded into the ISOLATE II Plant DNA Spin column (green) with a collection tube and centrifuged for one minute. The flow through was the discarded. 400µl of Wash Buffer PAW 1 was added to the column and centrifuged, for one minute and the flow-through was discarded.

To the column another 700µl of Wash Buffer PAW2 was added and sample was centrifuged for one minute after which the flow-through was discarded. The columns containing the samples were then centrifuged for two minutes to remove the wash buffers completely and to dry the silica membrane. The ISOLATE II Plant DNA Spin column was placed in a 1.5 ml microcentrifuge tube. 50µl of Elution Buffer PG pre-heated at 65ºC was placed on the silica membrane and centrifuged for one minute. This step was done two times and the DNA collected on the microcentrifuge tube was stored at 4ºC. After DNA quality and quantity check through carrying out a gel electrophoresis, the samples were plated in a 96 well plate, sealed and sent to the Integrated Genotyping Service and Support (IGSS) at the Bioscience

eastern and central Africa (BecA) Lab at the International Livestock Research Institute (ILRI) hub, for library construction and DArT-sequencing (DArTseq).

3.3 Data analysis

3.3.1 ANOVA and Striga data analysis

The maximum above ground *Striga* (NSmax) was calculated as per (Rodenburg et al., 2006). The Area under *Striga* Number Progress Curve (ASNPC) was calculated by summing the product of *Striga* plant counts and the number of days between observations through the season in the formula as described by (Haussman et al., 2000) using the formula;

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{Y_i + Y_{(i+1)}}{2}\right](t_{(i+1)} - t_i)$$

Where *n* is the number of *Striga* assessment dates, Y_i the *Striga* count at the *i*th assessment date, t_i the days after sowing at the *i*th assessment date.

Analysis of variance (ANOVA) and means for quantitative traits were performed/generated in alpha lattice design using GenStat v19.1 (VSN International, 2011). Treatment means were compared using Fisher's protected least significant differences at P≤0.05. The estimates of phenotypic and genotypic variance, genotypic and phenotypic coefficients of variation were done based on the formula proposed by Syukur et al. (2012).

Genotypic variance;

$$\sigma_g^2 = \frac{MS_g - MS_e}{r}$$

Phenotypic variance;

$$\sigma_p^2 = \sigma_g^2 + \sigma_e^2$$

where: σ_g^2= Genotypic variance; σ_p^2 = Phenotypic variance; σ_e^2 = environmental variance (error mean square from the analysis of variance);

MS_g = mean square of genotypes; MS_e = error mean square; r = number of replications.

Genotypic coefficient of variation;

$$[GCV] = \left[\left\{ \sqrt{\sigma_g^2} \right\} \Big/ \bar{x} \right] \times 100$$

Phenotypic coefficient of variation;

$$[PCV] = \left[\left\{ \sqrt{\sigma_P^2} \right\} \Big/ \bar{x} \right] \times 100$$

where: σ_g^2 = Genotypic variance; σ_P^2 = Phenotypic variance; $\bar{x}$ is grand mean of a character.

Simple linear correlation coefficients (Pearson, 1986) were calculated to understand the relationship among the studied agronomic traits as below

$$PX, Y = \frac{cov(x, y)}{\sigma_x \sigma_Y}$$

Where cov is the covariance, σ_x is the standard deviation of x, σ_y is the standard deviation of Y.

3.3.2 Heritability estimates

Estimations of broad sense (H^2) of all traits were calculated based on parental and family means respectively according to the formula described by Allard (1960):

$$H^2\, bs = \left[\sigma_g^2 / \sigma_p^2 \right] \times 100$$

$H^2\, bs$ = heritability in broad sense; σ_g^2 = Genotypic variance; σ_p^2 = Phenotypic variance.

Estimation of broad sense heritability (H^2) assuming selection intensity of 5% for individual and combined analysis of variance were computed using the formula adopted from (Johnson et al., 1955). H^2 scores were classified according to (Robinson et al., 1949) as follows: 0 – 30% = low; 30 – 60% = moderate; > 60% = high.

Estimation of genetic diversity was performed using TASSEL (Trait Analysis by aSSociation, Evolution and Linkage) 5.2.63 software and the results were visualized by generating archaeopteryx tree.

3.4 Results

3.4.1 Evaluation of *Striga* resistance in a sickplot at KALRO Alupe.

Figure 4. Response to *Striga* at the sick plot

Figure 5. Tolerance and resistance response to *Striga* in Sick plot

3.4.1.1 Agronomic performance of genotypes in *Striga* sickplot at KALRO Alupe

Wild genotypes GBK016109, GBK044448, GBK047293, GBK048921, GBK048156, GBK016085 and GBK048922 had highest vigor with a score of 5 compared to N13 with 4, an indication that these genotypes are very vigorous at seedling stage (Table 3). Dry panicle weight and yield had high CV of 46% and 49%, respectively, indicating great variability for the two traits while days to flowering showed the least variability having low CV of 12.6% (Table 3).

Earliest flowering was noted on improved variety Macia which flowered at 65 days while F_4 population cross IBURSAR×ICSVIII_IN took the longest time of 134 days (Table 3). Wild and landrace genotypes recorded the highest values in height as compared to the cultivated and elite breeding genotypes. Tallest genotype was LODOKA×LANDIWHITE with mean height of 3.24 m, the shortest genotype was B35 with 0.88 m while resistant check, N13, was 1.37 m (Table 3). Significant variation was observed for vigor, agronomic score and overall pest and disease score where most genotypes had their scores closely dispersed around the grand mean for the particular traits (Table 3).

The most prevalent diseases in the field were fungal, namely leaf blight, leaf ladder spot, zonate spot and anthracnose. GEN044336, IBUSAR × LANDIWHITE, ICSV IIIN × B35 and OKABIR × ICSVIII IN had the lowest disease scores of 3.67 each compared to N13 with 4.33 (Table 3). Apart from Striga weeds, other prevalent pests in the field were birds feeding on sorghum seeds, mites, sorghum midge and sorghum shoot fly. With regards to pests, F_4 populations LODOKA × OKABIR and LODOKA × ICSVIII_IN had the lowest overall pest score of 2 indicative of multiple pest resistance (Table 3). It was necessary to score for overall disease and pest scores to account for the variation that may be caused by pressure created by other pests and diseases not part of the study and to discover genotypes that may be performing well under both Striga pressure, other diseases and pests occurring in farmer fields.

ICSVIII_IN × LANDWHITE and IBURSAR × LANDIWHITE recorded high yields of 4.96 and 4.51 t/ha^{-1} compared to N13, yield of 0.68 t/ha^{-1} (Table 3). Wild genotype GBK016085 recorded the highest yield among the wild accessions with 3.27 t/ha^{-1} while GBK 048156 gave the poorest yield of 0.03 t/ha^{-1} (Table 3).

Top 10 ranking with high yielding genotypes in the sick plot revealed six genotypes being F4 progenies (IBUSAR × LANDI-WHITE (4.51 t/ha), LODOKA×ICSV III IN (3.55 t/ha), OKABIR × AKUOR-ACHOT (3.55 t/ha), OKABIR × ICSV III IN (3.00 t/ha), ICSV III IN × B35 (3.53 t/ha), ICSV III IN × LANDIWHITE (4.96 t/ha), three being improved varieties (FRAMIDA (3.54 t/ha), E36-1 (2.29 t/ha) and MACIA (2.88 t/ha) and one wild accession GBK016085 (3.28 t/ha) (Table 3).

The 100 seed weight for GBK016085 (least) and ICSVIIIN × E36-1 (highest) was 0.3 and 3.9 g, respectively, compared to 2.83 g for N13 (Table 3). Top 10 genotypes with high 100 grain weight were ICSVIII_IN × LODOKA (3.97 g), ICSVIII_IN × E361 (3.67 g), LANDWHITE × B35 (3.63 g), F6YQ212 × B35 (3.6 g), E36-1 × Macia (3.53 g), AKUOR-ACHOT (3.5 g), HAKIKA (3.433 g), OKABIR × ICSVIII_IN (3.37 g), E36-1 (3.3 g) and ICSVIII_IN × B35 (3.3 g). F_4 populations OKABIR × ICSVIII_IN and ICSVIII_IN × B3 and improved variety E36-1 had both high yield and high 100 grain weight values.

Wild accessions have the tendency of producing multiple panicles per plant which is as a result of their high tillering capacity. In this study, as would be expected, wild accessions recorded the highest number of panicles harvested with only one F4 population cross ranking number 10 in this category. GBK047293 recorded the highest harvested panicles at 58 panicles with OKABIR × ICSVIII_IN ranked number 10 with 23 panicles harvested per plot (Table 3). Genotypes with highest number of harvested panicles were GBK047293 (58.33), GBK044336 (56), GBK044054 (54), GBK016114 (39), GBK044120 (30), GBK016109 (28), GBK048922 (24), GBK044065 (23), OKABIR×ICSVIII_IN (23) and GBK040577 (23) (Table 3).

The F4 populations had highest dry panicle weight values where the top 10 genotypes were ICSVIII_IN×B35 (1170.7 g), ICSVIII_IN×Landiwhite (1089 g), OKABIR × AKUORACHOT (953 g), IBUSAR × LANDWHITE (952.3 g), LODOKA × ICSVIII_IN (920.3 g), GBK045827 (858.3 g), B35 × AKUOR-ACHOT (847.3 g), FRAMIDA (788.7 g), F6YQ212 × B35 (734.3 g) and E36-1 × MACIA (726.3 g) (Table 3). Most of these genotypes were also ranked as high yielding which indicated a high correlation between the total yield and dry panicle weight.

Table 3. Means for agronomic traits for selected sorghum genotypes sown in a sickplot during the long rains of 2019 at KARLO, Alupe.

GENOTYPE	100GW (gm)	AGS	DPW	DTF	ODS	OPS	PNH	PH	PV	YIELD (t/ha)
AKUOR-ACHOT	3.50	4	263	83	6.67	6.67	17	188.7	3.33	0.92
B35	2.00	4.67	49	83	8	6	6	87.7	3.33	0.20
B35xAKUOR-ACHOT	2.57	3	847	81	6.67	6.67	21	145	3.33	2.72
E36-1	3.30	2.67	652	80	4.67	5.33	19	167	3.33	2.92
E36-1xMACIA	3.53	3	726	89	5.67	4	18	184	3.33	2.49
F6YQ212	1.87	3.67	170	83	8	6.33	18	114.7	3.33	0.44
F6YQ212xB35	3.60	4.17	734	89	5.33	6	21	193.7	3.67	2.85
FRAMIDA	3.13	4.32	789	74	6.1	6.01	12	189.4	3.33	3.54
GBK016085	2.97	5.33	548	75	6	7.33	20	168	5.00	3.28
GBK016109	0.33	5	164	87	7.33	6	28	195	5.00	0.36
GBK016114	2.27	4.67	289	70	6	4	39	200.3	4.67	0.44
GBK040577	2.57	5.33	308	82	4.67	6.67	22	206.3	4.67	1.16
GBK044065	1.70	4.38	301	83	5.43	6.04	23	235	3.91	1.01
GBK044120	1.60	5	90	86	7	5	30	266.7	4.67	0.17
GBK044336	1.13	5	270	80	3.67	3.33	56	226.3	4.67	0.48
GBK044448	1.80	4.67	14	85	6	6.67	7	182	5.00	0.06
GBK045827	2.60	3.33	858	74	5.33	5	20	182.7	3.33	2.86
GBK047293	2.43	4.02	244	84	5.85	5.36	58	184.1	5.00	1.28
GBK048156	1.00	4.33	7	80	5.59	6.01	3	227.1	5.00	0.03
GBK048921	2.57	4.67	377	84	5	6.33	20	179.7	5.00	1.77
GBK048922	2.03	5	114	96	5	4.33	24	194.7	5.00	0.30
HAKIKA	3.43	3.67	599	82	6.67	5.33	15	119.7	4.00	2.68
LODOKAxICSVIII_IN	1.60	2	920	78	5.33	2.33	16	148.3	2.33	3.55
LODOKAxLANDWHITE	1.50	5.33	325	95	5.33	5	8	324	3.33	1.11
LODOKAxOKABIR	2.33	2	334	78	4.67	2.33	8	184	2.67	1.50
MACIA	2.60	3.89	708	65	6.33	5.67	18	135	2.00	2.88
N13	2.83	4	217	97	4.33	4.33	9	137.3	4.33	0.68
OKABIRxAKUOR-ACHOT	1.07	2.67	953	68	4.67	4.33	18	183.7	2.67	3.55
OKABIRxICSVIII_IN	3.37	4.67	708	95	3.67	5	23	275.3	3.33	3.00
MEAN	2.30	4.02	392	84	5.85	5.36	17	184.1	3.56	1.54
CV (%)	31.90	12.2	45.8	8	12.6	13.5	24	9.9	15.00	49.40
LSD	1.19	0.79	290	11	1.19	1.17	7	29.4	0.86	1.23
Fpr	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

GW-Seed weight, AGS-Agronomic Score, DPW-Dry Panicle Weight, DTF-Days to Flowering, ODS-Overall Disease Score, OPS-Overall Pest Score, NPH-Number of Panicles Harvested, PV-Plant vigor, Yield is in tonnes per hectare.

3.4.1.2 Response of sorghum genotypes to Striga at KALRO Alupe

Wild genotypes GBK 045827, GBK 044336, GBK 047293 and GBK 048921, improved varieties F6YQ212, ICSV III_IN, *Striga* resistance donor lines Macia, SRN 39, Hakika and IS9830 and F_4 population F6YQ212×B35, B35×Lodoka and B35×ICSVIII_IN had ASNPC values lower than N-13,the resistant check (Table 4).

ASNPC values for GBK 045827, GBK 044336, GBK 047293 and GBK 048921 were 523, 926, 994 and 838 respectively, compared to N13 with 1034 while susceptible varieties (Kari Mtama-1, 3232, and Gadam, 1190) had higher values (Table 4). SRN 39 had lowest ASNPC values (299) an indication that it was the most resistant. Improved variety F6YQ212 had ASNPC value of 434 making it the third most resistant genotype in the trial (Table 4).

ICSVIII_IN had ASNPC value of 406 making the second most resistant genotype in the trial. F4 population crosses involving either these two as parents also showed low ASNPC values with F6YQ212×B35(714) and B35×ICSVIII_IN (922) ranking among top resistant genotypes (Table 4). The maximum *Striga* count per plot ranged from 7 to 168 in the trial. SRN39 had the lowest maximum *Striga* count of 7 followed by ICSVIII_IN, F6YQ212, GBK045827 and B35 × Lodoka with 12, 13, 14, and 19 *Striga* plants respectively which was lower than *Striga* count of 20 for N13 (Table 4). Wild accessions and landrace genotypes generally recorded very high maximum *Striga* counts with GBK044058 having the highest count of 168 (Table 4).

Improved varieties that recorded high maximum *Striga* counts included B35 (128), KariMtama_1 (94) and KAT/ELM/2016PL82KM32-2 (99) (Table 4). SRN39 had the lowest number of *Striga* plants forming capsules with an average of 1 plant per plot. Wild accessions and landraces had high number of *Striga* plants forming capsules per plot ,which is an indication of their ability to support full *Striga* growth cycle (Table 4). With a maximum *Striga* count of 117, 168 and 150 respectively, GBK044063, GBK044058 and GBK016109 recorded high number of *Striga* plants that formed capsules with each having a count of 51, 55 and 69 respectively (Table 4).

Table 4. Response of selected sorghum genotypes to *Striga* in the sick plot sown during long rains and short rains 2019 at KARLO, Alupe.

GENOTYPE	NSFC	NSmax	ASNPC
B35	42	128.67	5269
B35xICSVIII_IN	8	20.33	922
B35xLODOKA	11.67	19	824
F6YQ212	3.67	13	434
F6YQ212xB35	6.33	24.67	714
GADAM	16.67	27.33	1190
GBK044058	54.67	168.33	5698
GBK044063	51.33	117.67	4492
GBK045827	6.33	14.33	523
HAKIKA	13.33	28	1008
ICSVIII_IN	3	12.33	406
IS9830	10	22.33	882
KAT/ELM/2016PL82KM32-2	28.33	99	3936
N13	9	20	1034
SRN39	1.33	7	299
MEAN	22	62.1	2250
CV	50.7	53.8	60.6
LSD	81.034	53.97	2204.3
Fpr	<0.01	<0.01	<0.01

NSmax-Maximum *Striga* Count, SPFC-Number of *Striga* Plants Forming Capsules, ASNPC-Area under *Striga* Number Progress Curve

3.4.1.3 Genotypic and phenotypic coefficients of variations and trait heritability measured in the sickplot

High genotypic and phenotypic variation was observed among traits measured in the field trial with the highest variation being expressed on dry panicle weight and maximum *Striga* count per plot (Table 5). All traits presented high broad sense heritability values that ranged from (0.66) for 100 grain weight to (0.94) for plant height (Table 5). *Striga* response related traits, such as , maximum *Striga* count , total ASNPC, and number of *Striga* plants forming capsules recorded high heritability values at 0.82, 0.75 and 0.75 respectively (Table 5). All traits gave higher PCV than GCV an indication of presence of environmental effects on the phenotypic expression of these traits. PCV and GCV values for days to flowering, days to maturity and plant height were closer hence the high heritability values for these traits (Table 5).

Table 5. Genotypic and phenotypic coefficients of variations and heritability of traits measured in the field trial.

TRAITS	RANGE	σ^2 G	σ^2 P	GCV (%)	PCV (%)	H^2 bs (%)
100 GRAIN WEIGHT	0.33-3.967	0.53	0.79	31.05	37.99	66.85
DRY PANICLE WEIGHT	14-1171	72697	88022	66.73	73.44	82.59
DTF	65-134	89.47	106.42	11.21	12.23	84.08
DTM	99-157	50.31	53.84	5.84	6.04	93.46
NSFC	1 to 71	140.23	185.87	54.31	62.52	75.45
PLANT HEIGHT	87.7-324	2020.30	2145.43	24.78	25.54	94.17
ASNPC	17.5-355.8	5509.33	7262.67	58.56	67.24	75.86
NSmax	7-168	28283.33	34267.67	279.73	307.91	82.54
YIELD(t/ha)	0.004-4.96	1.13	1.41	72.66	81.19	80.07

DTF-Days to flowering, DTM-Days to Maturity, ASNPC-Area Under Striga Number Progress Curve, NSFC-Number of Striga plants Forming Capsules, NSmax-Maximum Striga Count

3.4.1.4 Relationship among agronomic, yield and *Striga* related traits measured in sickplot.

Negative correlation was observed between 100 grain weight and all *Striga* related traits where the correlation with maximum *Striga* count (r = -0.287) was significant (Table 6). Grain yield gave a significant positive correlation with dry panicle weight (r = 0.9438), grain weight (r = 1) and stand after thinning (r = 0.4045) (Table 6). A significant negative correlation was also observed between grain yield and agronomic score (r = -0.4893), overall disease score (r = -0.3102) and overall pest score (r = -02769). Agronomic score was significantly negatively correlated to dry panicle weight (r = -0.4749), and positively correlated with overall pest score (r = 0.4535), plant height (r = 0.2826) and plant vigor (r = 0.5716) (Table 6).

Dry panicle weight was significantly negatively correlated with days to flowering (r = -0.3074), overall disease score (r = -3249), overall pest score (r = -0.3337) and plant vigor (r = -0.3584) (Table 6). Days to flowering was positively correlated with plant height (r=0.2679) and negatively with dry panicle weight (r=-0.3008) and grain weight (r=-0.3107) (Table 4). Other positive correlations included number of panicles harvested with plant stand after thinning (r = 0.3169) and plant vigor (r = 0.3808), and overall disease score and overall pest score (r = 0.4856) Negative correlations were observed between overall disease score and plant height (r = -0.3472) while overall pest score correlated significantly positively with plant vigor(r = 0.3338) (Table 6). All *Striga* related traits were significantly positively correlated with each other. ASNPC correlated positively with maximum *Striga* count (r = 0.828) and number of *Striga* plants forming capsules (r = 0.7686) (Table 6). Maximum

Striga count and number of *Striga* plants forming capsules were correlated significantly positively (r = 7998) (Table 6).

Table 6. Correlations between agronomic, yield and *Striga* related traits in the sick plot.

	100GW	AGS	ASNPC	DTF	DPW	GW	NSmax	NSFC	ODS	OS	PNH	PH	SAT	PV
100GW	-													
AGS	0.1316	-												
ASNPC	-0.1341	-0.1613	-											
DTF	-0.0063	0.135	0.2081	-										
DPW	0.1645	-0.4749***	-0.1377	-0.3008*	-									
GW	0.2287	-0.4902***	-0.1384	-0.3107**	0.9441***	-								
NSmax	-0.287*	-0.0457	0.828***	0.0716	-0.2259	-0.2171	-							
NSFC	-0.165	-0.0126	0.7686***	0.111	-0.1928	-0.1879	0.7998***	-						
ODS	0.0112	0.1078	-0.0481	,-0.2031	-0.3249**	-0.3103**	-0.109	-0.0556	-					
OS	0.1672	0.4535***	-0.2014	-0.0485	-0.3337**	-0.278*	-0.1893	-0.1743	0.4888***	-				
PNH	-0.2303	0.2187	-0.0325	-0.1161	0.0856	0.0059	-0.0476	-0.0721	-0.1411	-0.1245	-			
PH	-0.2201	0.2826*	0.1278	0.2679*	0.0402	0.0265	0.168	0.0712	-0.3472**	-0.0764	0.2059	-		
SAT	0.0577	-0.1467	-0.0748	-0.2008	0.4525***	0.4042***	-0.2501*	-0.0921	0.0025	-0.2022	0.3169**	-0.155		
PV	-0.2166	0.5716***	-0.2077	0.0615	-0.3584**	-0.3693***	-0.0189	-0.0803	0.0055	0.3338**	0.3808**	0.207	-0.3057**	-
YIELD_t_ha	0.2288	-0.4893***	-0.1389	-0.3109	0.9438***	1***	-0.2177	-0.1883	-0.3102**	-0.2769*	0.0059	0.0264	0.4045***	-0.3682**

* Significant at <0.05, **Significant at <0.01, ***Significant at< 0.001, GW-Grain weight, DPW-Dry Panicle Weight, DTF-Days to Flowering, GW-Grain Weight, ODS-Overall Disease Score, OPS-Overall Pest Score, PH-Panicles Harvested, ASNPC-Area under Striga Number Progress Score, NSFC-Number of Striga Plants Forming Capsules, NSmax-Maximum Striga Count, PNH-Panicles Harvested, SAT-Stand after Thinning, PV-Plant Vigor

3.4.2 Evaluation of *Striga* resistance in a potted trial during the long and short rains of 2019 at KARLO, Alupe

3.4.2.1 Agronomic performance of genotypes in potted trial at KALRO Alupe

All agronomic traits in the study showed significant variation apart from plant vigor. Genotypes B35 × ICSV III IN and SRN39 had highest 100 seed weight with 4.9 and 4.97 g while the wild genotype GBK 048152 had the lowest 100 seed weight of 0.588 g (Table 7). Wild accessions generally recorded low 100 grain weight values although some had good performance with the highest performer GBK085016 recording 3.887 g (Table 7). Dry panicle weight ranged from 2.5 g for wild genotype GBK 048156 and 287 g for LODOKA × ICSVIII_IN (Table 7). Wild accessions still recorded low values for dry panicle weight with most of them ranking bottom of the list. GBK085016 record the highest dry panicle weight among wild accessions weighing at 151 g (Table 7).

The F4 population crosses had very high dry panicle weight where 8 out of 10 top ranked were F4 populations; LODOKA × ICSVIII_IN (287g), OKABIR × AKUOR-ACHOT (260 g), ICSVIII_IN × LANDIWHITE (246 g), IBUSAR × ICSVIII_IN (214 g), OKABIR × B35 (195.4 g), E36-1 × MACIA (187 g), B35 × E36-1 (186.8 g) and B35 × ICSVIII_IN (187 g). MACIA (274 g) and KAT/ELM/2016 PL82 KM32-2 (198 g) were the only other genotypes in the top ten list (Table 7). Most F4 populations with high dry panicle weight were also among genotypes with highest number of panicles harvested per plot. These included OKABIR × AKUOR ACHOT (12), ICSVIII_IN × LANDIWHITE (11), IBUSAR × ICSVIII_IN (9), B35 ×LANDIWHITE (8), ICSVIII_IN×MACIA (7), LODOKA× ICSVIII_IN (6), LANDIWHITE × B35 (6) and AKUOR-ACHOT × ICSVIII_IN (6) (Table 7).

Other genotypes that recorded high number of harvested panicles include; KAT/ELM/2016 PL1 SD15 (8), KAT/ELM/2016PL82 KM32-2 (7) LODOKA (6), GBK045827 (6), GBK048921 (6), F6YQ212 (6), HAKIKA (6), GBK047293 (6) ,GBK048922 (6) (Table 7).A similar trend was observed for overall grain yield where the F4 population crosses had the highest yield values. Macia and KAT/ELM/2016 PL82 KM32-2 were the only improved varieties that ranked among the top ten best yielders with 28 and 21 t/ha respectively (Table 7). Other top yielding genotypes in the trial included LODOKA × ICSVIII_IN (30.44t/ha), OKABIR × AKUOR-ACHOT (29.06 t/ha), IBUSAR × ICSVIII_IN (24.05 t/ha), LODOKA

× OKABIR (21.3 t/ha), OKABIR × B35 (20.33 t/ha), B35 × E36-1 (20.04 t/ha), E36-1 × MACIA (19.9 t/ha), ICSVIII_IN × B35 (18.66t/ha) (Table 7).

Wild accessions performed poorly in terms of yield with most ranking at the bottom of the list with seven out of 19 recording yield of less than one tonne per hectare. Wild genotype GBK 044448 was the earliest flowering as it flowered in 45 days while OKABIR × ISCVIII_IN took the longest time of 95 days (Table 7). The second earliest flowering genotypes were F6YQ212, GBK016114, B35 × LANDIWHITE, ICSVIII_IN × LANDIWHITE and GBK043565 which flowered in 65 days, 10 days after the earliest flowering genotype. N13, a known *Striga* resistant genotype flowered in 66 days making it one of the earliest flowering materials in the trial (Table 6).

Wild sorghum genotypes were tall as most of them measured more than two meters in height. The tallest of the wild accessions was GBK044054 with a height of 257cm while the shortest was GBK045827 with 141 cm (Table 7). Overall OKABIR × B35 recorded the highest height (278 cm) while B35 × F6YQ212 recorded lowest height of 96 cm (Table 7). The agronomic score was taken to quantify the general performance of the genotypes in the season. Most genotypes had agronomic score of above average with the least performers having a score of 2 (Table 7). Wild genotypes had particularly good agronomic scores where almost all of them had the highest score of 5. N13 and Kari Mtama-1 are the only other genotypes that achieved an agronomic score of 5 (Table 7).

Similarly, wild accessions had high vigor scores with GBK 043565 recording highest vigor score of 5 in the trial (Table 7). N13 also ranked among highly vigorous genotypes with a score of 3 (Table 7). However, the high agronomic scores and high vigor for wild accessions did not translate to high yields as illustrated earlier in the text.

The accessions showed significant variation in overall pest and disease scores. IBURSAR × E36-1 and IBURSAR × LANDIWHITE had lowest disease score of 2.5 while B35 and F6YQ212 had the highest score of 8 indicative of high susceptibility to multiple diseases (Table 7). Resistant donor N-13, as well as F4 populations B35 × F6YQ212 and LODOKA × ICSVIII_IN showed good tolerance to pests with overall pest score of 3. Other genotypes with possible resistance to multiple pests included; E36-1×MACIA, LANDIWHITE× MACIA, GEN044065 and Macia (Table 7). There was a large variation in the days to anthesis with the potted trial genotypes flowering earlier (72 days) than those in the field trial (84 days) (Tables 3 and 7)

Table 7. Means for agronomic traits for selected sorghum genotypes sown in a potted trial during the long rains of 2019 at KARLO, Alupe.

GENOTYPE	10GW (gm)	AGS	DPW (gm)	DTF	ODS	OPS	PNH	PH(cm)	PV	YIELD (t/ha)
B35xE36-1	3.967	3.333	187	73	4.333	4	4	163.3	2	20.04
B35xF6YQ212	3.667	4	145	67	3.667	3	2.67	95.7	2.333	11.94
B35xICSVIII_IN	4.9	3.333	154	67	6.333	4.67	5	166.3	2.667	15.1
B35xLANDIWHITE	4.433	3.333	87.9	65	5.333	5.33	7.67	139.3	3	10.01
E36-1xMACIA	4.2	3	187	81	5.333	3.33	5.33	168.7	3	19.9
F6YQ212	4.167	4.333	107	65	8	6	5.67	103.3	3	11.48
GBK016114	2.5	4.667	126	65	7	4.33	4	222.7	3	10.12
GBK043565	1.6	4.667	7.3	65	7.667	6.67	4	201.3	3.667	0.7
GBK044054	1.367	4.667	111	67	5	4.67	4.67	257	3	4.59
GBK044058	0.667	4.333	7.6	82	4.333	4.67	5.33	238	2.333	0.6
GBK045827	3.833	3.167	120	71	5.667	5.33	5.67	141.3	2.667	12.86
GBK048921	2.667	5	116	75	6.667	5.67	5.67	240	3	12
GBK048922	3.533	4.667	58.8	75	4.667	4.67	6	225	3.333	5.62
HAKIKA	4.167	3	103	72	7	6.33	5.67	118.7	3	9.05
ICSVIII_IN	4.267	3.167	111	72	4	5.33	5.33	143.7	2.333	12.62
ICSVIII_INxB35	2.533	2.667	187	80	4.333	4.33	4.33	158.3	1.667	18.66
ICSVIII_INxLANDIWHITE	3.433	3.667	246	65	3.667	5	11	203.7	2.667	18.08
ICSVIII_INxMACIA	2.233	3	150	74	5	5.67	6.67	140.3	3	14.75
KAT/ELM/2016 PL1 SD15	4.5	3.667	86.5	69	6.333	5	8.33	133.7	2.667	8.81
KAT/ELM/2016 PL82 KM32-2	4.133	2.333	198	80	5.667	4.67	7	138.7	2	21.31
LANDIWHITExB35	3.733	3.333	113	66	7.031	5.67	6.33	176.3	2.333	10.33
LANDIWHITExMACIA	3.167	2.667	152	71	4.333	3.33	4.33	191.3	2.333	11.8
LODOKA	3.2	3	139	66	5.333	5	5.67	153	2.333	12.45
LODOKAxICSVIII_IN	2.9	2.333	287	72	4	3	6.33	123.7	1.333	30.44
LODOKAxOKABIR	4.633	3	184	67	7	4.33	4	187	2.333	21.3
MACI	3.033	3	274	77	3.333	3.33	4	114.3	2	27.59
N13	2.733	4.5	58.3	66	7.333	3	2.67	148.3	3.333	5.18
OKABIRxAKUOR-ACHOT	3.467	2.333	260	79	3.333	4.33	12.3	189	2	29.06
OKABIRxB35	3.8	3.333	195	94	5.333	4.33	4.67	277.7	1.667	20.33
OKABIRxICSVIII_IN	3.433	3.513	110	95	3.48	3.85	5	217.3	2	10.45
SRN39	4.967	3.333	120	67	5	5	2.67	138	2.667	12.31
Grand mean	3.148	3.774	115	72	5.646	4.91	4.86	177	2.732	10.53
CV(%)	27.9	17.6	54.8	9	18.9	20.8	39	13.5	22.9	60.4
LSD	1.421	1.075	102	11	1.725	1.65	3.07	38.62	1.01	10.29
P value	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001

GW-Grain weight, AGS-Agronomic Score, DPW-Dry Panicle Weight, DTF-Days to Flowering, ODS-Overall Disease Score, OPS-Overall Pest Score, PNH-Panicles Harvested, PV-Plant vigor.

3.4.2.2 Response of sorghum genotypes to *Striga* in Potted trial at KALRO Alupe

Four wild genotypes ; GBK016109, GBK016085, GBK045827, GBK048152, three improved varieties; SRN39, F6YQ212, Hakika and three F_4 population crosses; F6YQ212 × B35, LODOKA × Landiwhite, ICSVIII_IN × E36-1 had lowest ASNPC values (Table 8).

Genotype F6YQ212 was the most resistant with ASNPC value of 40 compared to N13, ASNPC value of 579 (Table 8). Wild genotypes GBK045827, GBK016085, GBK048152 and GBK016109 had low ASNPC values of 226, 154, 77 and 149, respectively compared to ASNPC values of 579 and 684 for N-13 and for susceptible genotype, Kari Mtama-1, respectively (Table 8). N13 performed poorer than all other known *Striga* resistance donor sources in the trial such as SRN39 (131), Hakika (273), Framida (359),and IS9830 (527) (Table 8).

Genotypes with low ASNPC values also recorded low maximum *Striga* count values. For instance, F6YQ212 had only 2 germinated *Striga* plants while LODOKA×LANDIWHITE, GBK016109 and F6YQ212 × B35 each had a maximum *Striga* count of three (Table 8). Wild GBK048058 had the highest maximum *Striga* count with an average of 25 *Striga* plants per pot (Table 8).The number of *Striga* plants forming capsules per genotype ranged from 0 to 8. F6YQ212, ICSVIII_IN × E36-1, B35 × ICSVIII_IN, HAKIKA, GBK048152, GBK016109, AKUOR-ACHOT and B35 × E36-1 each had a score of zero for number of *Striga* plants forming capsules making them the best performers in this category. N13 had a score of 2 while GBK 048058 recorded a total of 8 *Striga* plants forming capsules, the highest score in the trial (Table 8).

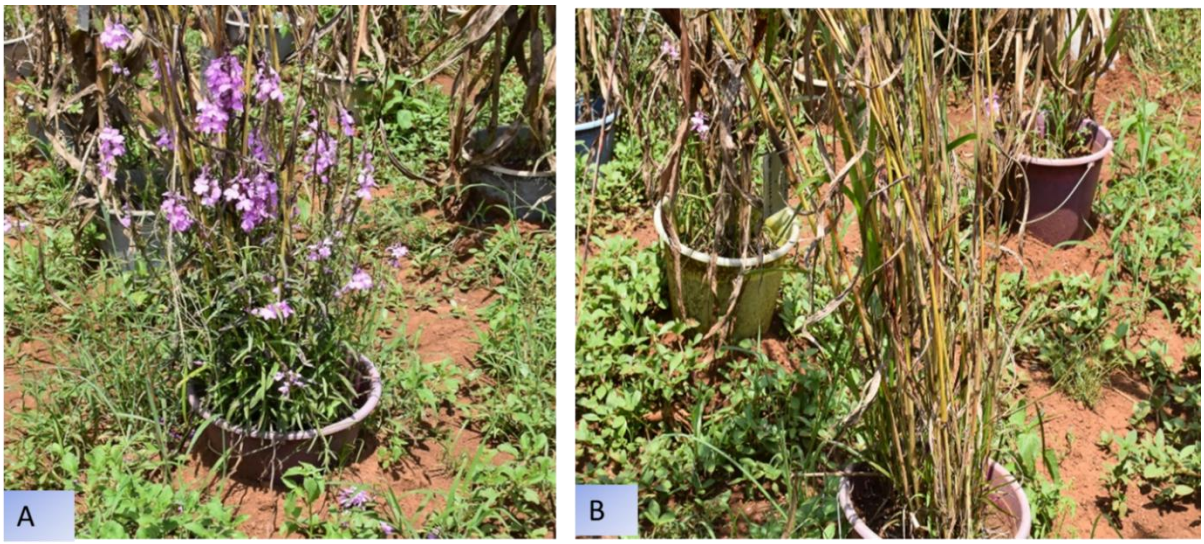

Figure 6. Response to *Striga* in potted trial. A., Susceptible response B., Resistance response

Table 8. Response of selected sorghum genotypes to *Striga* in the potted trial in 2019 long rain season at KARLO, Alupe

GENOTYPE	NSFC	Nsmax	ASNPC
AKUOR-ACHOT	0	9	471
B35xE36-1	0	12	588
B35xICSVIII_IN	0	9	296
F6YQ212	0	2	40
F6YQ212xB35	1	3	175
FRAMIDA	1	5	359
GBK016085	1	6	154
GBK016109	0	3	149
GBK044058	8	25	1647
GBK045827	2	4	226
GBK048152	0	11	77
HAKIKA	0	9	273
ICSVIII_INxE36-1	0	4	166
IS 9830	2	10	527
KARI MTAMA 1	1	21	684
LODOKAxLANDIWHITE	1	3	142
N13	2	8	579
SRN39	2	4	138
Grand mean	2.48	10.09	566
CV(%)	80	33	53
LSD	3.206	5.387	482
P value	<.001	<.001	<0.01

NSmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsules, ASNPC-Area under Striga Number Progress Curve

3.4.2.3 Heritability estimates for traits in the potted trial.

High broad sense heritability was observed in most traits with plant height having the highest heritability of 91% (Table 9). Overall disease score, panicles harvested and number of *Striga* plants forming capsules had moderate heritability (58%, 55% and 56%) respectively (Table 9). All traits gave higher PCV than GCV an indication of presence of environmental effects on the phenotypic expression of these traits. PCV and GCV values for days to flowering, and plant height were closer hence the high heritability values for these traits (Table 9).

Table 9. Heritability estimates for traits in the potted trial at KALRO Alupe.

TRAIT	RANGE	MEAN	MSG	MSE	σ2 G	σ2 P	PCV	GCV	H^2 bs
100 GW (gm)	0.414 - 4.967	3.136	3.5156	0.7931	0.91	1.17	34.52	30.38	0.77
DPW (gm)	2.5-287	114.8	13633	3992	3213.67	4544.33	58.72	49.38	0.71
DTF	45 - 95	72.12	176.6	45.15	43.82	58.87	10.64	9.18	0.74
YIELD (t/ha)	0.16 - 30.44	10.47	171.17	40.33	43.61	57.06	72.15	63.08	0.76
ODS	2.5 -8	5.639	5.767	1.132	1.55	1.92	24.59	22.04	0.8
OPS	3 - 6.667	4.913	2.635	1.108	0.51	0.88	19.08	14.52	0.58
PNH	2.67 - 12.33	4.85	10.78	4.876	1.97	3.59	39.08	28.92	0.55
HEIGHT (cm)	95.7 - 277.7	176.8	6286.3	562.4	1907.97	2095.43	25.89	24.71	0.91
Nsmax	2.0 - 25.0	10.07	73.2	16.59	18.87	24.4	49.05	43.14	0.77
NSFC	0 -8	2.48	8.87	3.94	1.64	2.96	69.33	51.69	0.56
ASNPC	40 - 1647	28	543.7	128.7	138.33	181.23	48.08	42.01	0.76

GW-Grain weight, DPW-Dry Panicle Weight, DTF-Days to Flowering, ODS-Overall Disease Score, OPS-Overall Pest Score, PNH-Panicles Harvested.

3.4.2.4 Correlations among traits in the potted trial at KALRO Alupe

100 grain weight correlated negatively with agronomic score (r = -0.5132), plant height (r = -0.4913) and maximum *Striga* count (r = -0.2817) and positively with yield (r =0.5339), dry panicle weight (r = 0.4788) and grain weight (r = 0.5516) (Table 10). Agronomic score correlated negatively with all yield related traits where correlation with dry panicle weight (r = -0.6595), Grain weight (r = -0.7107) and yield (r = -0.6894) was highly significant at < 0.001 and that between the same trait and panicles harvested (r = - 0.2502), stand after thinning (r = -0.2449) being significant at < 0.05 (Table 10).

Plant height, plant vigor and overall disease score correlated significantly positively with agronomic score with values r = 0.5138, r = 0.4957 and r = 0.3279 respectively (Table 10). Days to flowering correlated negatively with overall disease score (r = -0.3164), overall pest score (r = -0.2702) and plant vigor (r = -0.2638) and positively with plant height (r = 0.3301). Dry panicle weight was correlated significantly positively with all yield related traits including yield (r=0.9232), grain weight (r = 0.9535), panicles harvested (r = 0. 3465) and negatively with *Striga* and disease related traits; Overall disease score (r = -0.3936), overall pest score (r = -0.4104), ASNPC (r = -0.2696) and Maximum *Striga* count (r = -0.2722) (Table 10). Overall disease score and overall pest score were positively highly correlated with the correlation being significant at < 0.001.

Overall disease score also positively correlated with plant vigor (r = 0.3413) and negatively with panicles harvested (r = -0.2448) and yield (r = -0.263) (Table 10). Overall pest score, similarly, correlated positively with plant vigor and negatively with panicles harvested (r = 0.3305) and yield (r = -0.3458). Other significant correlations included the positive correlation between panicles harvested and stand after thinning (r = 0.2874), panicles harvested and yield (r = 0.3288) and the negative correlation between yield and plant height (r = -0.3345) and plant vigor (r = -0.5138) (Table 10). All *Striga* related traits were highly significantly correlated with each other with the correlation being significant at < 0.001 (Table 10)

Table 10. Correlation coefficients between traits in the Potted trial.

	100 GW	AGS	DTF	DPW	GW	ODS	OPS	PNH	PH	SAT	PV	YIELD t/ha	ASNPC	NSmax
100 GW	-													
AGS	-0.5132***	-												
DTF	-0.1279	-0.0972	-											
DPW	0.4788***	-0.6595***	0.1142	-										
GW	0.5516***	-0.7107***	0.0898	0.9535***	-									
ODS	-0.0548	0.3279**	-0.3164**	-0.3936**	-0.3764**	-								
OPS	-0.0609	0.1832	-0.2702*	-0.4104***	-0.357**	0.4585***	-							
PNH	0.0884	-0.2502*	0.1509	0.3465**	0.3378**	-0.2448*	-0.0352	-						
PH	-0.4913***	0.5138***	0.3301**	-0.2696*	-0.3442**	-0.0855	-0.0937	0.0651	-					
SAT	0.1873	-0.2449*	-0.0004	0.1292	0.1358	0.1601	0.0312	0.2874*	-0.208	-				
PV	-0.2154	0.4957***	-0.2638*	-0.505***	-0.5355***	0.3413**	0.3305**	-0.2126	0.0694	-0.2073	-			
YIELD t/ha	0.5339***	-0.6894***	0.0877	0.9232***	0.9684***	-0.263*	-0.3458**	0.3288**	-0.3345**	0.1662	-0.5138***	-		
ASNPC	-0.2262	0.1725	0.0557	-0.2696*	-0.2088	-0.0999	-0.1277	0.118	0.2062	-0.0419	0.099	-0.182	-	
NSmax	-0.2817*	0.23	0.041	-0.2722*	-0.215	0.0327	0.0155	0.0983	0.1177	0.0063	0.053	-0.1886	0.8451***	-
NSFC	-0.2027	0.0626	0.0199	-0.1909	-0.1694	-0.2347	-0.0762	0.1497	0.2189	-0.0676	0.034	-0.1647	0.7388***	0.5545***

* Significant at <0.05, **Significant at <0.01,***Significant at< 0.001, GW-Grain weight, DPW-Dry Panicle Weight, DTF-Days to Flowering, GW-Grain Weight, ODS-Overall Disease Score, OPS-Overall Pest Score, PH-Panicles Harvested, ASNPC-Area under Striga Number Progress Score, NSFC-Number of Striga Plants Forming Capsules, NSmax-Maximum Striga Count, PNH-Panicles Harvested, SAT-Stand after Thinning, PV-Plant Vigor

3.4.3 Agronomic mean performance of the genotypes between the two trials

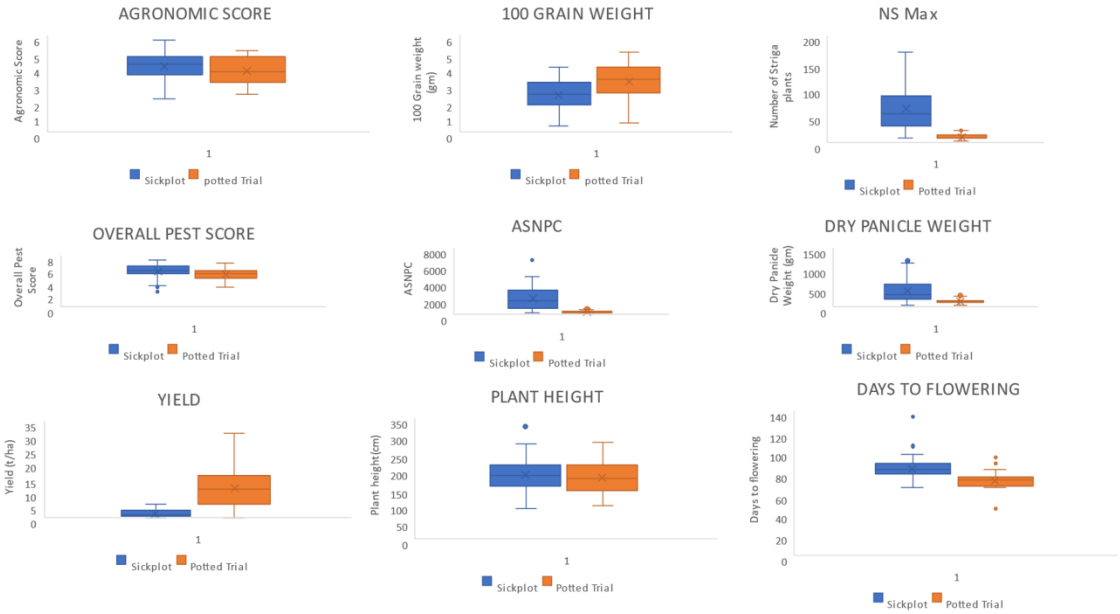

Figure 7. Boxplots showing the performance of genotypes in the sickplot and potted trial

Genotypes recorded higher mean values for 100 grain weight and yield in the potted trial (3.148 and 10.53) than in the sickplot (2.30 and 1.54) respectively (Figure 7). Dry panicle weight was also higher in the sickplot (392 g) compared to the same trait in the potted trial (115 g). Materials in the sickplot had a better agronomic score compared to the potted trial as indicated by the higher agronomic score mean of 4 in the sickplot (Figure 7). A tendency for earliness was observed in the potted trial where average days to flowering were lower than that of the same accessions in the sickplot. Means for days to flowering was 74 for potted trial and 84 for the sickplot (Figure 7). Plant height under *Striga* infestation was not affected by environment as the genotypes maintained a relatively constant mean height in both trials (177cm in potted trial and 184 cm in sickplot) (Figure 7). The overall pest score was slightly higher in the sickplot (5.4) compared to the potted trial (4.9) as shown by the higher pest score in the sickplot leading to higher mean pest score. As would be expected, maximum *Striga* count was higher in the sickplot than in the potted trial owing to the larger plot sizes in the sickplot. ASNPC values were also much higher in the sickplot compared to the potted trial as this values are calculated using the *Striga* counts observed in the trials. The same trend was observed for number of Striga plants forming capsules where more counts were made in the sickplot (22) compared to the potted trial (2).

3.4.4 Rank Summation Index for yield and ASNPC in Potted trial and Sickplot

Improved variety Macia was the overall best performing genotype in the potted trial as it combined both high yield and low ASNPC values (Table 11). This indicates that Macia is not only considerably *Striga* resistant but also high yielding (Table 11). Adapted variety F6YQ212 was the second best performing genotype in both trials. *Striga* resistant donor line SRN39 was ranked as 5th best making it the best performing resistant checks included in this study (Table 11). KAT/ELM/2016PL82KM32-2 another improved variety exhibited good performance and was ranked 10th best genotype in the trial (Table 11). Wild genotypes GBK 016085 and GBK 045827 yielded higher with the rank summation index performed ranking them higher than existing improved and adapted varieties in the trial (Table 11). GBK 016085 was ranked third best while GBK 045827 was ranked eighth best in terms of *Striga* resistance and yield potential (Table 11). Most wild accessions were ranked at the bottom of the list due to their high ASNPC values and low yields (Table 11). Four F4 population crosses that were ranked among the top ten best genotypes in the trial included the crosses between; B35 × ICSVIII_IN, F6YQ212 × LODOKA, LODOKA × OKABIR and OKABIR × B35 (Table 11). *Striga* resistance donor line N13 was raked at number 43 out of 64 an indication that although the line is a good source *Striga* resistance genes, it is an extremely poor performer in terms of yield (Table 11).

Wild genotype GBK045827 was the overall best performing genotype in the sickplot in terms of *Striga* resistance and yield potential (Table 11). The genotype outperformed all the adapted varieties, landraces, F4 populations and *Striga* resistance donor lines as it was able to express *Striga* resistance while still maintaining high grain yield (Table 11). GBK048917, GBK044065 and GBK016085 also performed well in the sickplot being ranked sixth, nineth and ten best respectively (Table 11). F4 population crosses between F6YQ212 × B35 and ICSVIII_IN × B35 also performed really well and were ranked among the top ten best genotypes in the rank summation index (Table 11). It is important to note that both F6YQ212 and ICSVIII_IN were among the most *Striga* resistant genotypes in the trial while B35 is a known donor source for Stay green genes for drought tolerance (Table 11). This means that these are very superior crosses that should be advanced for possible release as both *Striga* and drought resistant varieties (Table 11). *Striga* resistance donor lines Hakika, Macia, SRN39 and Framida also performed well and were ranked among the top ten best genotypes in the sickplot rank summation index for yield and *Striga* resistance (Table 11).

Two wild genotypes (GBK 016085, GBK 045827) and two *Striga* resistance donor lines (SRN39 ,Macia) were the most consistent in performance as they were ranked top ten best genotypes in rank summation index for yield and *Striga* resistance both in the sickplot and in the potted trial (Table 11). GBK 044058 was ranked last in both the sickplot and the potted trial making it the poorest performing genotype in the entire trial when *Striga* resistance and yield potential was considered (Table 11).

Table 11. Rank Summation Index in ASNPC and yield for genotypes in the potted trial

	SICKPLOT			POTTED TRIAL	
RANK	GENOTYPE	RSI	RANK	GENOTYPE	RSI
1	GBK045827	23.67	1	MACIA	23.67
2	F6YQ212xB35	24	2	F6YQ212	28
3	MACIA	27.67	3	GBK016085	28.33
4	GBK048917	29.33	4	B35xICSVIII_IN	33
5	HAKIKA	29.33	5	SRN39	33.67
6	FRAMIDA	30.67	6	F6YQ212xLODOKA	34.33
7	SRN39	30.67	7	LODOKAxOKABIR	34.67
8	ICSVIII_INxB35	33	8	GBK045827	35.67
9	GBK044065	33.67	9	OKABIRxB35	36.67
10	GBK016085	34.33	10	KAT/ELM/2016PL82KM32-2	40
11	B35xLODOKA	34.67	11	ICSVIII_INxB35	42.67
12	GBK048921	35.33	12	ICSVIII_INxE36-1	43
13	ICSVIII_IN	36.67	13	LODOKA	43
14	B35xAKUOR-ACHOT	44	14	FRAMIDA	43.67
15	ICSVIII_INxLANDWHITE	44.33	15	IBUSARxLANDWHITE	44.33
16	E36-1	45.33	16	F6YQ212xB35	46.67
17	LODOKAxICSVIII_IN	47	17	OKABIRxAKUOR-ACHOT	46.67
18	OKABIRxAKUOR-ACHOT	48.33	18	AKUOR-ACHOT	47
19	KAT/ELM/2016PL1SD15	48.67	19	LANDIWHITExMACIA	48
20	GBK047293	49.33	20	B35xF6YQ212	49.33
21	OKABIRxICSVIII_IN	49.33	21	E36-1xMACIA	50
22	GADAM	50.33	22	GBK044336	50
23	IS9830	52	23	HAKIKA	50.67
24	GBK040577	54.67	24	GBK 016109	51.67
25	B35xF6YQ212	55.67	25	B35xE36-1	53.67
26	ICSVIII_INxMACIA	56	26	LODOKAxICSVIII_IN	54
27	B35xLANDWHITE	58	27	ICSVIII_IN	56
28	F6YQ212	60	28	LODOKAxLANDIWHITE	58
29	ICSVIII_INxE36-1	60.67	29	ICSVIII_INxMACIA	59.33
30	B35xICSVIII_IN	61	30	E36-1	59.67
31	GBK048156	61.67	31	ICSVIII_INxLANDIWHITE	59.67
32	B35_1	62.33	32	B35xAKUOR-ACHOT	60.67
33	KARI MTAMA 1	63	33	GBK044448	61.67
34	E36-1xMACIA	63.33	34	IS 9830	64.67

SICKPLOT			POTTED TRIAL		
RANK	GENOTYPE	RSI	RANK	GENOTYPE	RSI
35	ICSVIII_INxLODOKA	66	35	B35xLODOKA	68
36	N13	66	36	ICSVIII_INxLODOKA	68.67
38	GBK044336	69	38	GBK 048152	69.67
39	IBUSARxICSVIII_IN	69	39	GBK048921	69.67
40	GBK043565	72	40	B35_1	70.67
41	OKABIR	73.67	41	OKABIRxICSVIII_IN	71.67
42	GBK048916	77.67	42	B35	73.33
43	F6YQ212xLODOKA	79.33	43	GBK048916	75.67
44	AKUOR-ACHOT	80	44	AKUOR-ACHOTxICSVIII_IN	76.33
45	LANDWHITExMACIA	80.67	45	LANDIWHITExB35	78
46	GBK044448	81.67	46	IBUSARxE36-1	80.67
47	GBK044120	84.33	47	N13	80.67
48	LODOKAxOKABIR	84.33	48	OKABIR	83.33
49	LODOKA	84.67	49	GBK 044054	83.67
50	KAT/ELM/2016PL82KM32-2	85.67	50	GBK040577	85.33
51	LANDWHITExB35	87.33	51	B35xLANDIWHITE	86
52	GBK048152	90.33	52	KAT/ELM/2016PL1SD15	87.33
53	GBK044054	91	53	GADAM	88.67
54	GBK048922	91.67	54	GBK047293	88.67
55	B35xE36-1	93.33	55	KARI MTAMA 1	89.67
56	AKUOR-ACHOTxICSVIII_IN	94.33	56	GBK043565	92.67
57	GBK044063	95.33	57	GBK048922	97.67
58	IBUSARxE36-1	102	58	GBK016114	99
59	OKABIRxB35	104.67	59	GBK048156	100.33
60	GBK016114	105.67	60	IBUSARxICSVIII_IN	105.67
61	IBUSARxLANDWHITE	106.33	61	GBK048917	107.67
62	GBK016109	108.33	62	GBK044065	110.67
63	B35	109.67	63	GBK044063	111.33
64	GBK044058	118	64	GBK044058	118.33
	MEAN	65		MEAN	65
	CV (%)	24.6		CV (%)	27
	LSD	25.8		LSD	29
	Fpr	<0.01		Fpr	<0.01

3.5 Genotyping and Diversity Estimation

3.5.1 Genetic relatedness among sorghum accession

Six randomly tagged F_4 plants were genotyped alongside all parental lines, bringing to a total 153 genotypes. A total of 26,291 raw SNPs were generated for the 153 diverse genotypes in TASSEL software. Filtering was performed using a site minimum count of 70%,and a minimum allele frequency of 0.05. After filtering, 7,075 SNPs were recovered, and these were used to assess genetic diversity within the 153 genotypes. Three major clusters were observed with the F_4 populations being evenly distributed across the accessions (Figure 8). In cluster 1, *Striga* resistance donors SRN39, Framida, IS9830 and Hakika clustered together in a subcluster alongside the resistant F_4 cross F6YQ212 × B35 (Figure 8). Resistant F_4 crosses with B35 as the female parent B35 × ICSVIII_IN (sickplot and potted trial), B35 × LODOKA (Sickplot), B35 × LANDIWHITE(sickplot) and LODOKA × LANDIWHITE (potted trial)) clustered together with resistant donor line N13 in a subclade as shown in (Figure 8). In the second cluster ICSVIII_IN × E36_1 which exhibited a resistance response in the potted trial clustered with the *Striga* resistant improved line ICSVIII_IN. IBUSAR × E36_1 was the only *Striga* resistant cross that did not cluster with any known *Striga* resistance source (Figure 8). The genotype was found in the third cluster which had Macia as the only improved genotype. Macia is a high yielding genotype, and other genotypes in this cluster that exhibited high yields in the sickplot were ICSVIII_IN × Macia and B35 × Akuor-Achot. Another trend of clustering based on yield capacity was observed in cluster 2 where high yielding genotypes; ICSVIII_IN, E36-1, ICSVIII_IN × Landiwhite and ICSVIII_1N × E36-1 were found in the same cluster (Figure 8).

In terms of breeding status, wild accessions showed the highest level of relatedness with most clustering together in one subclade with resistant donor source N-13. The only wild genotypes that clustered away from the rest were GBK048917 and GBK0444448 in Cluster 2, as well as GBK047293 in Cluster 3 (Figure 8). Landrace accessions were also distributed in different subclades within Cluster 1 with LODOKA and GBK044054 (Cluster 3) being the only landrace genotypes that clustered away from the rest. Improved varieties as well as the F4 population crosses were distributed within the population which is an indication of low genetic relatedness hence high diversity.

Most F_4 crosses clustered together with each other or with either of the parents used in the cross. However, some crosses grouped away from their siblings and parents and this suggest possibility of them being off types (Figure 8).

These include B35 × Akuor-Achot_6 and B35 × Landiwhite which clustered in completely different clusters from their parents and siblings (Figure 8).

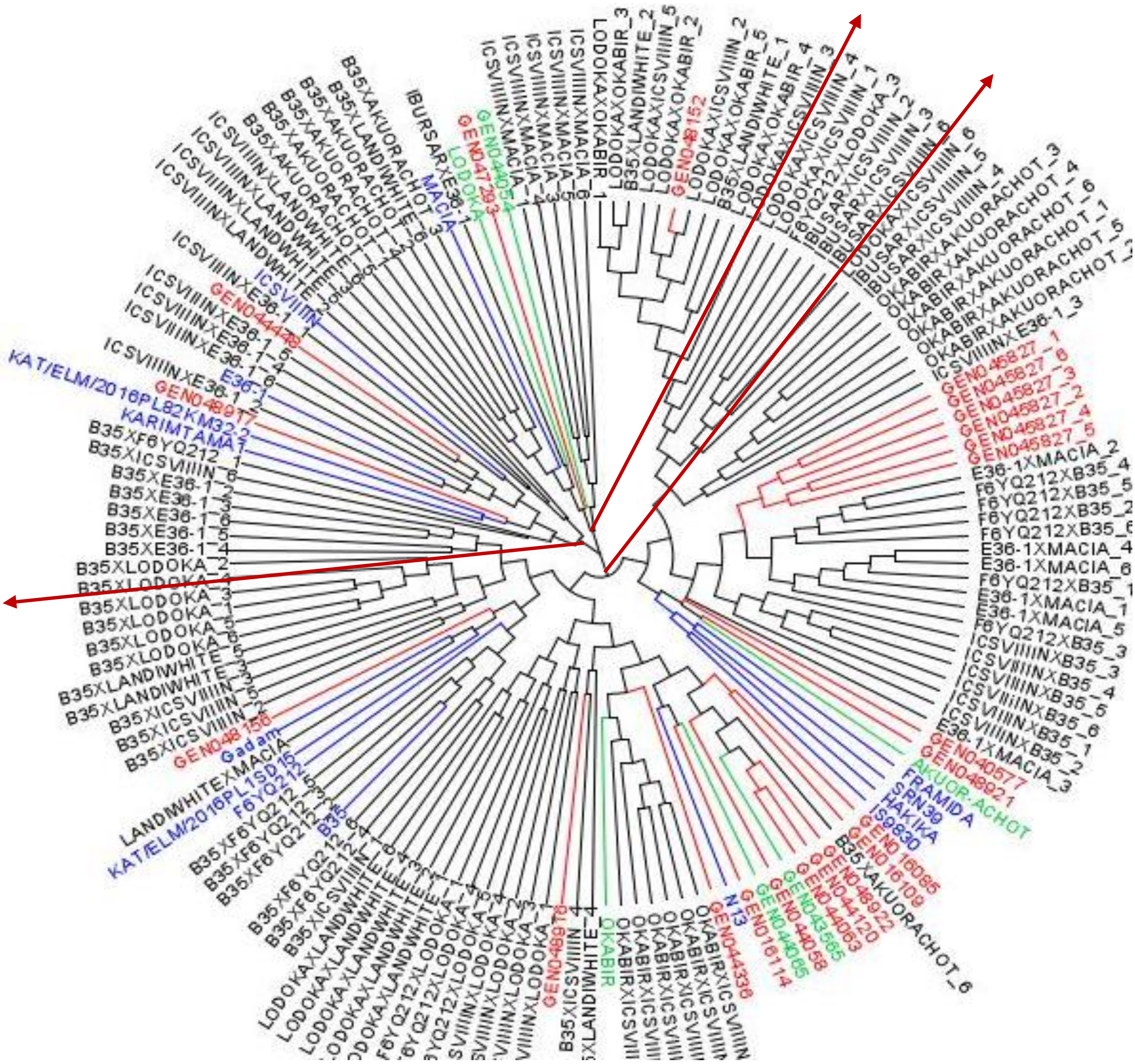

Figure 8.**Dendrogram showing the clustering of 153 accessions used in this study. Red-wild accession, Green-landrace, Blue-improved variety and Black -F4 population. The arrows originate from the root of the cluster.**

3.5.2 Parental genotype relatedness

Molecular data for 37 parental genotypes that consisted of 17 wild accessions, 8 landraces and 12 improved varieties was generated for genetic diversity analysis. The Neighbor Joining dendrogram drawn resulted in three major clusters (Figure 9). The first cluster (A) (Figure 9) comprised of *Striga* resistant genotypes including the four resistant checks, IS9830, SRN39, FRAMIDA and HAKIKA. Other genotypes in cluster A that were recorded as resistant to *Striga* in the current experiment included GBK048156 (sick plot), GBK048152 (potted trial), F6YQ212 (sickplot and potted trial) and GBK045827 (sick plot and potted trial). The only susceptible genotype in this cluster was the improved variety KAT/ELM/2016PL1SD15 (Figure 9). Cluster B comprised mostly of wild accessions and landraces, although two improved varieties, B35 and MACIA were also in the same cluster but different sub-clusters (Figure 9). The only *Striga* resistant check in this cluster was N13, which was grouped in the same sub-cluster with the staygreen genotype, B35. Both B35 and N13 are known to have wild pedigrees. Two wild genotypes (GBK016109 and GBK016085) which were among the most resistant in the potted trial, as well as one landrace (GBK044065) that was among the most resistant in the sickplot were also grouped in cluster B (Figure 9).

Cluster C was composed of four improved varieties, two landraces and four wild accessions. Two genotypes (KAT/ELM/2016PL82KM32-2 and GBK044054) were recorded among the most susceptible and another two (GBK048917 and ICSVIII IN) were among the topmost resistant genotypes in the sickplot trial. Genotype E36-1, a well-known drought tolerant (staygreen) material that was also among the best yielders in the sick plot trial, was grouped in cluster C in the same sub-cluster with a landrace GBK044054, which recorded one of the highest ASNPC values and lowest yields in the sickplot trial (Figure 9).

Landrace and wild accessions exhibited close relatedness as they clustered together. The only improved varieties that clustered together with wild and landrace accessions were B35 and Macia (Figure 9). Wild accessions that clustered with improved varieties include GBK 048156, GBK 048152 and GBK 045827 (Figure 9).

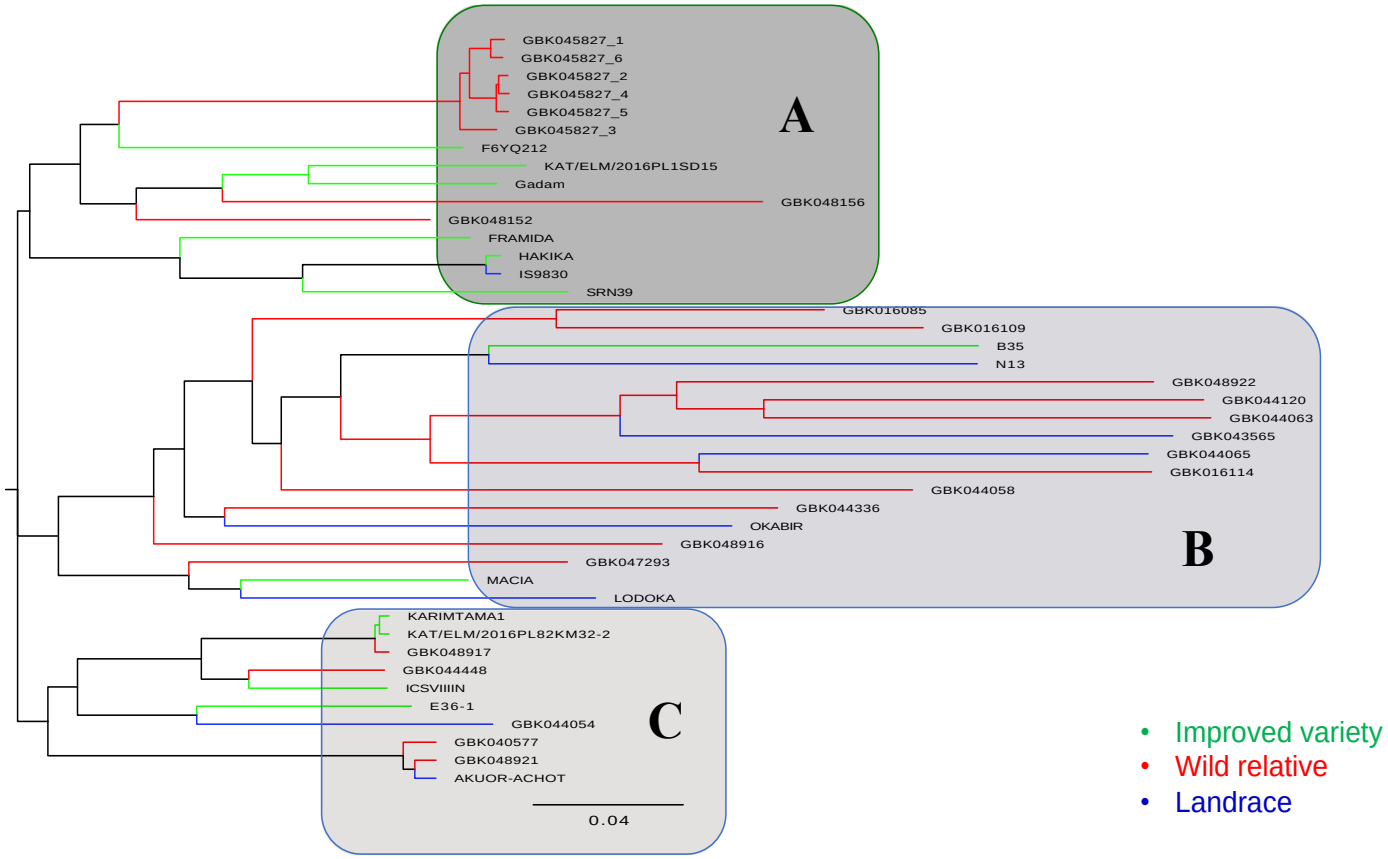

Figure 9. Dendrogram showing the clustering of Striga resistance donors among 39 parental accessions used in this study. Red-wild accession, Green- improved variety ,Blue- landrace.

3.6 Discussion

In identifying the resistant genotypes, the selection criteria used in these trials, was the ASNPC. ASNPC values have been reported as the most discriminative, comprehensive and unbiased measure of identifying *Striga* response because they take into account both infection time and length of growth period of a genotype (Rodenburg et al., 2005, Omanya et al., 2004, Haussmann et al., 2001). From the results reported here, 10 genotypes F6YQ212, GBK045827, GBK048921, ICSVIII_IN, Macia, IS9830, SRN39, B35 × ICSVIII_IN, F6YQ212 × B35 and F6YQ212 × Lodoka gave the highest *Striga* resistance response as depicted by low ASNPC values in the sick plot. The ten most resistant genotypes in the potted trial as indicated by their ASNPC values included F6YQ212, LODOKA× LANDIWHITE, GBK016109, SRN39, F6YQ212 × B35, ICSV III IN × E36-1, GBK016085, GBK045827, Hakika and GBK048152. Four genotypes GBK045827, F6YQ212, SRN39, and F6YQ212 × B35 showed a consistent resistance response in both the potted trial and the sickplot as they were ranked among top ten resistant genotypes both in the sickplot and in the potted trial.

GBK045827, GBK048921, GBK016109, GBK016085 and GBK048152 are all wild accessions that demonstrated *Striga* resistance. *Striga* resistance in wild relatives of sorghum has been reported to be due to either the low germination stimulant production, hypersensitive response and incompatible response (Ejeta et al., 2001). Additional *Striga* resistance mechanisms of germination inhibition and low haustorial initiation activity have been observed in sorghum wild accessions (Rich et al., 2004). (Mbuvi et al., 2017) reported three wild sorghum genotypes that had marked resistance to *Striga* and described their resistance mechanism as a qualitative hypersensitive reaction similar to that of N13, a known *Striga* resistant landrace. The biological mechanisms underpinning this form of resistance in *Striga* include thickening of cell walls in the pericycle, lignification and silica deposition (Maiti et al., 1984). Low germination stimulant production as a mechanism of *Striga* resistance has been widely studied with SRN39 as the donor line. Genetic studies on the trait have revealed that it is controlled by a single gene with recessive inheritance (Ramaiah et al., 1990). Other genotypes in this study that have been reported to have the low germination stimulant production as a means of *Striga* resistance include Framida and IS9830 (Rodenburg et al., 2005). The resistance mechanisms conferring resistance in the wild genotypes and improved varieties discovered in this study will need to be determined in future studies.

Significant difference was observed in performance of genotypes within the two trials in terms *Striga* response and yield. This can be explained by the differential *Striga* infestation levels within the two trials where high infestation intensity was present in the sickplot compared to the potted trial. Response to *Striga* stress can be classified as either tolerance or resistance. Tolerance to *Striga* is a defense mechanism demonstrated when *Striga* infestation levels are low, whereas resistance response is exhibited at high infestation levels. (Mbuvi et al., 2017, DeVries, 2000, Pierce et al., 2003). Tolerant genotypes have ability to germinate and support as many *Striga* plants as other genotypes without the same severity of yield reductions (Rodenburg et al., 2005). In the potted trial, where *Striga* infestation levels were lower, genotypes that were able to record high yields despite *Striga* pressure included E36-1 × Macia, LODOKA × ICSVIII_IN and B35 × LODOKA. In the sickplot, *Striga* resistance was an important determinant of yield hence no genotype was able to produce considerable yields if it was not expressing *Striga* resistance since *Striga* infestation lowers yield.

One disadvantage of using potted trials in *Striga* studies is that potted trial data may not be expected to correspond to that of the field trial because of the large environmental effect on the few number of plants scored and therefore this may account for the discrepancies in the data despite the number of replications (Rodenburg et al., 2005; Haussmann et al., 2000). The unit area for *Striga* germination was smaller in the potted trial than in the field trial, therefore data on potted trial might not adequately explain the differences in *Striga* response and grain yield potential. Estimation of genotypic effects of quantitative traits, require an optimal plot size that takes into consideration the environmental effects on the genotype as well. Nevertheless, ASNPC values and yield scored in both sickplot and potted trials, demonstrated consistent association at all levels despite the shortcoming in plot size. SRN39, F6YQ212, GBK045827, F6YQ212 × B35, MACIA, B35 × ICSVIII_IN and GBK044336 showed consistent low ASNPC values in both trials regardless of the *Striga* infestation levels. Genotypes Framida, B35 × Lodoka, GBK045827, GBK016085, ICSV III IN × Landiwhite and Macia consistently recorded high grain yield irrespective of the environment.

A negative correlation was observed between yield traits and *Striga* related traits across the two trials which is an illustration of the yield reduction effects of *Striga* on sorghum. All *Striga* response related traits correlated positively significantly (< 0.001) with each other in both trials which implies that either of these traits can be used to estimate *Striga* resistance.

Similarly, high significant association between grain yield and panicles harvested, dry panicle weight and grain weight suggests that these can be considered as a secondary trait when selecting for improved grain yield in sorghum breeding.

Negative correlation between ASNPC and plant height observed in this study has been reported in studies by (Omanya et al., 2004) and (Afolayan et al., 2020) where they suggested that the negative correlation is due to the fact that *Striga* infestation affects normal plant development leading to stunted growth which later affect grain yield. The same conclusion can be drawn to explain the negative correlation between overall disease score and plant height.

Days to flowering was significantly positively associated with plant height at (<0.05) and similar observations have been reported by (Mangesha et al., 2019). The positive correlation between plant height and days to flowering and their negative effect on yield has been reported in numerous studies. Most adapted sorghum genotypes are of determinate growth habit with short maturity duration hence tend to flower early compared to the traditional indeterminate landrace and wild types. This explains the positive association between plant height and days to flowering . High yielding cultivars undergo a process of high dry matter accumulation before forming heads and increase translocation rate after heading to ensure high yields (Ranawake et al.,2014). Most wild and landrace genotypes are not as genetically advanced and evolutionally complex as the adapted varieties, hence they lack the physiological complexity that allow high dry matter accumulation and high translocation rates leading to high yields. Since most of these genotypes are inherently very tall, this leads to the negative correlation between yield and plant height. The same conclusion can be drawn to explain the negative correlation between agronomic score and yield traits since wild and landrace genotypes had higher agronomic scores compared to adapted genotypes.

Grain weight, grain yield, plant height, dry panicle weight, days to 50% flowering, ASNPC, maximum *Striga* count had high broad-sense heritability estimates which indicate the presence of additive gene action hence quantitative inheritance of these traits. High broad-sense heritability estimates for sorghum traits under *Striga* infestation have been reported before by (Warkad et al., 2008; Haussmann et al., 2000b). Heritability estimates for traits were higher for parental accessions compared to those of their respective F4 progenies and this can be attributed to uniformity of parental accessions at genetic level which has been reported to increase the heritability of traits. F4 progeny accessions are still segregating hence still unstable at genetic level reducing the chances of a trait being passed on from one generation to the next. The role of additive genetic effects in the inheritance of *Striga*

resistance, Days to flowering, plant height and yield has also been reported by (Obilana, 1984).

Estimation of heritability of traits in *Striga* resistance trials is important as it shows the amount of genetic variation present among the accessions. Low broad sense heritability estimates indicate low genetic variation which leads to slow genetic gain since *Striga* infestation stress affects both genetic and phenotypic components of the accessions (Afolayan et al., 2020). Results of this study revealed adequate genetic variability among genotypes for traits measured and (Dhliwayo and Pixley, 2003), suggested that such genetic variability is important in introgression of important traits that are deficient in elite crop varieties via conventional breeding and molecular breeding approaches.

Seven new genotypes; two improved varieties F6YQ212 and ICSVIII_IN, three wild genotypes GBK045827, GBK047293, GBK044336, and two F_4 population crosses B35 × ICSVIII_IN and F6YQ212 × B35 that gave a consistent *Striga* resistance response across the two trials with ASNPC values lower than those of the resistant check N13 were identified. F6YQ212 was the best performer in the potted trial, with ASNPC values lower than all the other genotypes including all the known resistant donors in the trial. The wild genotypes discovered in this study have not been reported in any other *Striga* resistance studies as resistant donors.

ICSV III_IN, was first released as a *Striga* resistant variety in Ghana and Togo in west Africa in 1991 WCASRN (ICRISAT, 1991) but its response to *Striga* biotypes in Kenya has not been tested. F6YQ212 has been included in sorghum studies for phenotypic and biochemical analysis of grain storage pest resistance (Mwendwa, 2019) but no study has reported its inclusion in *Striga* resistance studies. Resistant donors IS9830 and SRN 39 though high in *Striga* resistance, have been reported to have adoption problems in various parts of sub-Saharan Africa due to small grain size and low grain yield (Lagoke et al., 1994) hence more breeding trials to improve them on these qualities are necessary. Wild GBK045827 demonstrated a combination of *Striga* resistance and good yield across the two trials. Although it could be genetically related to the resistant donors, it is superior to them due to this ability to combine resistance and yield across variable *Striga* infestation levels.

Estimation of genetic diversity and relatedness among genotypes is a key aspects to consider in germplasm management and utilisation, genetic fingerprinting, and genotype selection (Blakeney, 2002; IBPGR, 1993; Bucheyeki et al., 2009). Due to the influence of environment on morphological markers, molecular markers have proven to be a more reliable approach

for assessment of genetic diversity as they are not affected by the environment (Gerrano et al., 2014).

Molecular makers have been used in defining genetic relationships and population structure as well as establishing the distribution of variation among individuals within populations aiding in designing germplasm management strategies (Westman and Kresovich, 1997; Dje`et al., 1999).

The current study successfully employed the use of DArT markers to estimate genetic diversity and relatedness of sorghum accessions with the aim to further select superior genotypes to be incorporated in future studies. The variation among the sorghum accessions in this study was primarily demonstrated by agromorphological traits rather than their geographical distribution. Molecular markers further confirmed the existence of this variation and further grouped the accessions into groups depending on their hierarchical relationships.

The clustering together of four (Framida, Hakika, IS9830 and SRN39) out of the five resistant checks in the same sub-clade suggests a narrow genetic base for *Striga* resistant sources that are currently being used in breeding programmes in eastern Africa (Mohamed et al., 2010). Genotype F6YQ212 provides a good alternative source of resistance as it was grouped in a different sub-clade with the current known resistant sources. F6YQ212 has been previously screened for response to grain storage pest (Mwendwa, 2019) but has not been screened for its resistance to *Striga*. The mechanism of resistance in Framida, IS9830 and SRN39 is reported to be low germination stimulation production (Haussman et al., 2000; Mohamed et al., 2010; Gobena et al., 2017), which is the most widely studied mechanism of resistance to *Striga* in sorghum.

Wild genotype GBK 045827 which showed resistance in both sickplot and potted trial, closely clustered with F6YQ212. This observation strongly suggests that the resistance observed in F6YQ212 may have been introgressed from GBK045827. *Striga* resistance is more abundant among wild relatives (Rich et al., 2004; Mbuvi et al., 2017), which tend to cross-pollinate with cultivated genotypes in open fields (Ohadi et al., 2018). This assumption will however need to be further investigated.

The only other resistant check that clustered differently was N13, a durra sorghum from India, which is known to stimulate *Striga* germination but forms a mechanical barrier to *Striga* penetration (Maiti et al., 1984; Mohemed et al., 2016; Mbuvi et al., 2017). Genotype

N13 grouped together with B35, a drought tolerant variety, which has its origins in Ethiopia (Ochieng et al., 2020).

N13 has been reported to be a landrace (Mbuvi et al., 2017) and this could explain the clustering with wild and landrace genotypes in this study. ICSVIII_IN also clustered in a different group from all the resistant checks that were used in the current study, suggesting its source of resistance may be different.

A majority of the best yielding (most tolerant) genotypes were crosses, especially those with ICSVIII_IN as the common parent. ICSVIII_IN was first released as a *Striga* resistant variety in Ghana and Togo in West Africa in 1991 (ICRISAT, 1991). The genotype has in this study proved to be a good combiner for yield.

F_4 population crosses that exhibited a resistance response in either the sickplot or potted trial had either one of the parents exhibiting *Striga* resistance and they clustered together with either of the parents. Ibusar × E36-1 was the only resistant F_4 cross that both clustered away from known donor sources and none of its parents was a resistant genotype. This cross may therefore possess a novel form of *Striga* resistance or have resistance from a novel source that will need to be further investigated. The results of this study showed a clear distribution of variation among the genotypes studied and these results will be used in designing future crop improvement for *Striga* resistance.

3.10 Conclusion

Genotypes F6YQ212, ICSVIII_IN, GBK045827, GBK047293, GBK044336, B35× ICSVIII_IN and F6YQ212 × B35 gave a consistent *Striga* resistance response across the two trials with ASNPC values lower than those of the resistant check N13. Estimation of genetic relatedness of these genotypes revealed three clusters where F6YQ212 and GBK 045827 clustered away from known *Striga* resistance donors. N13 clustered away from all other resistant checks in the trial. High broad sense heritability was observed for yield and *Striga* resistance related traits which suggests their additive nature. The identified *Striga* resistant genotypes are likely to become important sources of resistance in future *Striga* breeding research.

CHAPTER FOUR: TRANSFER OF STRIGA RESISTANCE QTL FROM KNOWN DONORS INTO CULTIVATED FARMER PREFERRED SORGHUM VARIETIES THROUGH MARKER ASSISTED BACKCROSSING

4.0 Abstract

Advances in MAS techniques have led to invention of MAB scheme where DNA markers are used trace the introgression of genes of interest into adapted cultivars. The MAS was used to transfer *Striga* resistance QTL into adapted farmer preferred varieties Gadam and Kari-Mtama1 from N13, Framida, SRN-39 and Hakika all of which are elite *Striga* resistance donor sources. The materials were crossed in a North Carolina Design II mating design to generate F_1 progenies that were later advanced to BC_1F_1. The BC_1F_1 progenies were generated by backcrossing the F_1s to their respective female parents. These were genotyped using DArT markers to trace heterozygous alleles confirming successful backcrossing. Genomic DNA extraction and quality check was done at International Centre for Research in Agroforestry (ICRAF) Genomic laboratory while DArT sequencing was done at Integrated Genotyping Service and Support (IGSS) at the Bioscience eastern and central Africa (BecA) Lab at the International Livestock Research Institute (ILRI) hub. The results from this analysis revealed successful backcrosses for the crosses Gadam × N13 × Gadam, Gadam × Framida × Gadam and Gadam × SRN39 × Gadam with heterozygous allele percentages ranging from 63% to 77%. High heritability values for yield and *Striga* resistance was observed both in the parents and progenies for both trials. High genetic gain for *Striga* tolerance (Yield) was observed in both trials while gain for *Striga* resistance was low. Molecular marker-assisted backcrossing is widely recommended for transferring favourable alleles from a donor to an elite variety. The demonstrated gain in *Striga* tolerance and resistance is great news for breeding programmes as it shows the huge potential of enhancing the performance of varieties in response to *Striga* through improved genetics.

4.1 Introduction

Sorghum genome mapping based on DNA markers started in the early 1990s and numerous genetic linkage maps based initially on RFLP, AFLPs and SSRs and very recently, Diversity Array Technology (DArT) markers have been published (Mace et al., 2009). Diversity Arrays Technology (DArT™) is a high-through put hybridization-based marker technology that offers a high multiplexing level while being independent of sequence information (Gawroński et al., 2016). The first DArT markers for *Sorghum bicolor* were developed in 2008 and were reported to be suitable for diversity analyses and construction of medium-density genetic linkage maps (Mace et al., 2008). DArT assays generate whole-genome fingerprints by scoring the presence versus absence of DNA fragments in genomic representations generated from genomic DNA samples through the process of complexity reduction (Mace et al., 2008). High level of polymorphism is a key trait for molecular markers that are suitable for fingerprinting and marker assisted selection (Smith et al., 2000).

Marker-Assisted Selection entails selection of plants that carry genes for traits of interest by use of molecular markers (Babu et al., 2004). MAS is used to trace the transfer of the target genomic regions as well as to hasten the recovery of the backcross parent genome in breeding programmes (Robert et al., 2001). The technique is also used to significantly improve screening effectiveness for complex traits (Kassahun, 2006). Incorporation of MAS in *Striga* resistance breeding can significantly accelerate the breeding progress since field screening is difficult, complex, and often unreliable. Some *Striga* resistance genes like the *Lgs* genes for low germination stimulus production are recessively inherited, increasing the time required for introgression and difficulty of convectional backcross schemes (Rasha et al., 2016). The molecular marker density around these *Striga* QTLs has been increased in sorghum in order to improve the accuracy of Marker Assisted Selection (Haussmann et al., 2000).

Cultivated sorghum is self-pollinating although cross pollination by wind and insects may occur (Schmidt and Bothma, 2005). Hand emasculation which refers to the removal of male component of a flower which is the stamen in order to prevent self-pollination is commonly employed in crossing self -pollinated crops. Different mating designs are used in breeding programmes in order to generate a breeding population for selection and development of

potential varieties, provide information on the genetic control of traits of interest, estimate genetic gain and to evaluate the parents used in the breeding programme (Acquaah, 2012).

North Carolina II mating design is a diallel mating design in which each member of a group of parents designated as males is mated to each member of another group of parents designated as females. The design is therefore a factorial mating scheme which is mostly used for plants that have multiple flowers that are enough for same plant to be used repeatedly as both male and female (Acquaah, 2012). The design can be used to estimate combining ability of genotypes in the study. The design is basically a two-way ANOVA in which the variation may be separated into difference between males (m) and females (f) and their interaction.

Understanding the genetic control of economic traits through quantitative traits locus analysis allows the identification of distinct chromosome segments controlling complex traits (Frova et al., 1999). Heritability is defined as the amount of the phenotypic variance associated to genetic causes and provides an estimate of genetic advance a breeder can anticipate from selection applied to a population in a particular environment (Songsri et al., 2008). The higher the heritability estimates, the simpler are the selection procedures (Khan et al., 2008). However, adequate improvement though selection in advanced generations require the incorporation of heritability accompanied by substantial amount of genetic advance (Eid, 2009). The usefulness of heritability therefore increases when it is used to calculate genetic advance (Shukla et al., 2004).

Genetic advance describes the degree of gain obtained in a character under a particular selection pressure (Ogunniyan et al., 2014). High genetic advance together with high heritability estimates present the most fitting condition for selection (Nwangburuka et al., 2012). It indicates the presence of additive genes in the trait and further suggest reliable crop improvement through selection of such traits (Hess et al., 1992). Estimates of heritability with genetic advance are more reliable and meaningful than individual consideration of the parameters.

4.2 Materials and Methods

4.2.1 Hybridization of the sorghum genotypes

The hybridization programme was performed in a greenhouse at the University of Nairobi Upper Kabete Campus field station. Gadam and Kari Mtama-1 are superior farmer preferred

lines that are *Striga* susceptible and were used as the female parents. The elite *Striga* resistance donor lines used in this study were N13, SRN 39, Framida and Hakika. The mating design used was North Carolina design II.

The F_1s were advanced by backcrossing each cross to its respective susceptible female parents either Gadam or KariMtama-1 for one generation producing BC_1F_1 progenies.

Table 12. North Carolina Design II mating scheme between N13, Framida, SRN39 and Hakika as male parents and Gadam and Kari Mtama 1 as female parents.

MALES	FEMALES	PROGENY
N13	Gadam	Gadam x N13
	KariMtama-1	KariMtama-1 x N13
Framida	Gadam	Gadam x Framida
	KariMtama-1	KariMtama-1 x Framida
SRN 39	Gadam	Gadam x SRN 39
	KariMtama-1	KariMtama-1 x SRN 39
Hakika	Gadam	Gadam x Hakika
	KariMtama-1	KariMtama-1 x Hakika

4.2.2 Greenhouse Activities

In the green house, seeds were sown directly in buckets containing a mix of manure, soil and sand in a ratio of 2:1:1 respectively. Planting was staggered to avoid synchronous flowering and reduce the workload of hand emasculation. Emasculation was carried out a day before anthesis and pollinating bags were used to cover the panicle to prevent pollination by foreign pollen from neighboring plants. Pollen harvesting was done in the morning. Pollination was done a day after emasculation when the emasculated flowers had opened. The F_1 seeds were harvested as single plants at physiological maturity stage.

For the backcrossing activity, F_1 progenies seed as well as female parent per cross were sown alongside each other in buckets containing a mix of manure, soil and sand in a ratio of 2:1:1 respectively. Pollen was harvested from the F_1 plants and introduced into the recurrent female

parent. After harvesting, the BC_1F_1 seeds were sown in germination trays at World Agroforestry Centre greenhouse where leaf sampling was done after two weeks.

Leaf sampling was done on ice and the fresh leaf tissues were collected in 2ml Eppendorf tubes awaiting DNA extraction.

4.2.3 DNA extraction for DArT sequencing.

Two steel beads were put into each Eppendorf tube containing approximately 50mg of leaf sample and the Eppendorf tube was later submerged in liquid nitrogen for one minute. These were put in a Geno grinder set at 1500 revolutions per minute to allow thorough grinding of the leaf samples. The samples were then stored at -20 degrees for five minutes to allow them to thaw. DNA for DArT sequencing was extracted using the ISOLATE II Plant DNA Kit. To the ground samples 300ul of Lysis Buffer PA1 was added and the mixture vortexed thoroughly. 10µLl of RNAse A was added in the mixture and mixed thoroughly. These were incubated at 65ºc for 10 minutes. The samples were centrifuged for 5 minutes to separate the plant debris from the lysate. The lysate was place in the ISOLATE II Filter (violet) and centrifuged for two minutes after which the clear flow through in the collection tube was collected and the ISOLATE II Filter was discarded. 450µl of Binding Buffer PB was added to the flow-through and mixed thoroughly by pipetting up and down five times. The sample was then loaded into the ISOLATE II Plant DNA Spin column (green) with a collection tube and centrifuged for one minute. The flow through was then discarded. 400µl of Wash Buffer PAW 1 was added to the column and centrifuged, for one minute and the flow-through was discarded. To the column another 700µl of Wash Buffer PAW2 was added and sample was centrifuged for one minute after which the flow-through was discarded. The columns containing the samples were then centrifuged for two minutes to remove the wash buffers completely and to dry the silica membrane. The ISOLATE II Plant DNA Spin column was placed in a 1.5 ml microcentrifuge tube. 50µl of Elution Buffer PG pre-heated at 65ºC was placed on the silica membrane and centrifuged for one minute. This step was done two times and the DNA collected on the microcentrifuge tube was stored at 4ºC. DNA quality and quantity assessed by gel electrophoresis and a Qubit 2.0 Fluorometer (Life Technologies, Carlsbad, CA) respectively and the samples were standardized by making a final dilution of 50 ng/µl for all.

The diluted DNA was sent to the Integrated Genotyping Service and Support (IGSS) at the Bioscience eastern and central Africa (BecA) Lab at the International Livestock Research

Institute (ILRI) hub, for library construction and DArT-sequencing (DArTseq) (https://www.diversityarrays.com/products-and-services/applications/), as detailed in (Wójcik-Jagła et al., 2018).

4.3 Data Analysis

Data analysis was performed using TASSEL (Trait Analysis by association, Evolution and Linkage) 5.2.63 software. Each backcross was analyzed separately from the others. Preliminary analysis involved first creating a pedigree file for each cross specifying the male and female parents as well as the progenies and indicating the expected genetic contribution of each individual to the cross. This was followed by creating two text files each containing the name of the male and female parent used in the cross (Parent 1 and parent 2).

The resulting raw SNPs from DArT-sequencing for each backcross were further sorted in TASSEL software creating a sorted HapMap file. The sorted HapMap file was then further filtered using a minor allele frequency of ≥ 0.05 and maximum missing data of 30% to remove unwanted SNPs.

To undertake hybridity confirmation for Backcross populations that were generated in the greenhouse, the filtered SNP variant call file for the backcross progenies genotyped alongside their parents was parsed through the GenosToABHPlugin in TASSEL 5.2.67 alongside the corresponding parents to obtain informative biallelic SNPs in the ABH format (female parent alleles as "A", male parent allele as "B", and heterozygotes as "H"). The proportions of Parent A alleles, Parent B alleles and Heterozygous alleles was determined using output file from this analysis.

4.3.1 Heterosis and Genetic gain in response to *Striga* infestation

For this analysis F_4 generation crosses that were included in the *Striga* sickplot and potted trial screening were used. The backcrosses generated were not included in the sickplot trial because as the sickplot trial was growing, the backcross programme was taking place in the greenhouse hence the backcrosses were not ready by the time the sickplot trial was being set up. Therefore, phenotype data for the response of the backcrosses to *Striga* was not collected. However, estimation of genetic gain in response to *Striga* infestation was still possible since the accessions screened in the *Striga* sickplot and potted trial included F_4 populations and their parents.

To undertake hybridity confirmation for F_4 populations that were screened in the sickplot, the filtered SNP variant call file for the F_4 progenies genotyped and their parents was parsed

through the GenosToABHPlugin in TASSEL 5.2.67 alongside the corresponding parents to obtain informative biallelic SNPs in the ABH format (female parent alleles as "A", male parent allele as "B", and heterozygotes as "H") as described earlier.

Crosses involving parental lines Ibusar and Landiwhite were not included in this analysis as both parents failed to germinate in *Striga* sickplot trial. Hybridity of 16 F_4 progenies was confirmed using bi-allelic SNP markers ranging from 1204 to 2868 that had been called from DArT-sequencing.

Chi-Square goodness of fit test was performed using the following formula:

$$x^2 = \left[\frac{(O-E)^2}{E}\right]$$

Where,

x^2= Chi-Square goodness of fit test, O= observed value , E= expected value

Null hypothesis: There is no significant difference between the observed and the expected value.

Alternative hypothesis: there is a significant difference between the observed and the expected value.

The percent increase or decrease of F_4 cross over mid-parent was calculated to observe heterotic effects for Yield and ASNPC. The average F_4 values per cross were used for estimation of heterosis expressed in percentage over mid parent (MP) as described in (Turner, 1955).

Where;

Mid parent (MP) value = (P1+P2)/2

Relative heterosis = [(F_4-MP)/MP] x 100

4.4 Results

4.4.1 Hybridization Process

Figure 10. The hybridization process; (A) Panicle that with ready pollen, (B) Hand emasculation using a needle, (C) Emasculated panicle ready for pollination, (D) Pollinated panicle with successful seed set.

A total of five backcrosses (Gadam × N13 × Gadam, Gadam × Framida × Gadam, Gadam × SRN39 × Gadam, Gadam × Hakika × Gadam, Karimtama-1 × N13 × Karimtama-1) and their progenies were analyzed in this study. The results from this analysis revealed successful backcrosses for the crosses Gadam × N13 × Gadam, Gadam × Framida × Gadam and Gadam × SRN39 × Gadam.

Percentage of heterozygous alleles in the backcross Gadam × Framida × Gadam ranged from 11-75% for the nine plants that were analyzed (Table 13). The backcross Gadam × SRN39 × Gadam had a percentage of heterozygous allele range of 5 – 75% (Table 14) while Gadam × N13 × Gadam had a percentage heterozygous allele ranging from 77% to 54% (Table 15). There were no successful backcrosses for Gadam × Hakika × Gadam and Karimtama-1 × N13 × Karimtama-1 as the percentage of heterozygotes in each cross was extremely low (Table 16 and 17). The percentage of the female parent alleles in these two crosses was more than 90 % which indicates that the original F_1 crosses used to generate the backcrosses were most probably not true F_1s or they were off types (Table 16 and 17). The total number of bi-allelic markers that was used in this analysis ranged from 664 markers for the cross Karimtama-1 × N13 × Karimtama-1 to 2452 markers for the cross Gadam × N13 × Gadam.

Table 13. Progeny analysis for Gadam × Framida × Gadam in the BC_1F_1 generation.

Plant	Total no. of Loci	A	% of Parent A alleles	B	% of Parent B alleles	H	% Heterozygous Alleles
1	1144	317	27.71	14	1.22	813	71.07
2	1144	565	49.39	36	3.15	543	47.47
3	1144	411	35.93	34	2.97	699	61.10
4	1144	298	26.05	11	0.96	835	72.99
5	1144	265	23.16	18	1.57	861	75.26
6	1144	342	29.90	15	1.31	787	68.79
7	1144	316	27.62	17	1.49	811	70.89
8	1144	682	59.62	23	2.01	439	38.37
9	1144	948	82.87	70	6.12	126	11.01

Table 14. Progeny analysis for Gadam × SRN 39 × Gadam in the BC_1F_1 generation

Plant	Total no. of Loci	A	% of Parent A alleles	B	% of Parent B alleles	H	% of Heterozygous Alleles
1	1688	547	32.41	73	4.32	1068	63.27
2	1688	628	37.20	73	4.32	987	58.47
3	1688	396	23.46	171	10.13	1121	66.41
4	1688	447	26.48	2	0.12	1239	73.40
5	1688	418	24.76	171	10.13	1099	65.11
6	1688	480	28.44	2	0.12	1206	71.45
7	1688	649	38.45	174	10.31	865	51.24
8	1688	427	25.30	75	4.44	1186	70.26
9	1688	425	25.18	2	0.12	1261	74.70
10	1688	472	27.96	73	4.32	1143	67.71
11	1688	1435	85.01	172	10.19	81	4.80
12	1688	1536	91.00	73	4.32	79	4.68

Table 15. Progeny analysis for Gadam × N13 × Gadam in the BC_1F_1 generation

Plant	Total no. of Loci	A	% of Parent A alleles	B	% of Parent B alleles	H	% Heterozygous Alleles
1	2451	691	28.19	87	3.55	1673	68.26
2	2452	665	27.12	76	3.10	1711	69.78
3	2451	772	31.50	88	3.59	1591	64.91
4	2451	1013	41.33	113	4.61	1325	54.06
5	2451	630	25.70	56	2.28	1765	72.01
6	2451	572	23.34	34	1.39	1845	75.28
7	2451	532	21.71	29	1.18	1890	77.11

Table 16. Progeny analysis for Gadam × Hakika × Gadam in the BC_1F_1 generation

Plant	Total no. of Loci	A	% of Parent A alleles	B	% of Parent B alleles	H	% Heterozygous Alleles
1	1873	1856	99.09	3	0.16	14	0.75
2	1873	1855	99.04	4	0.21	14	0.75

Table 17. Progeny analysis for Karimtama-1 × N13 × Karimtama-1 in the BC_1F_1 generation

Plant	Total no. of Loci	A	% of Parent A alleles	B	% of Parent B alleles	H	% Heterozygous Alleles
1	664	660	99.4	0	0	4	0.6
2	664	659	99.25	0	0	5	0.75
3	664	659	99.25	0	0	5	0.75
4	664	662	99.7	0	0	2	0.3

4.4.2 Chi-square test for the observed genotypic proportions

A Chi-Square goodness of fit test was performed to determine whether the observed female and heterozygous allele frequencies are significantly different from the expected frequencies. Chi-Square goodness of fit tests are used in genetics to compare the observed sample distribution with the expected probability distribution and determine how well theoretical distribution fits the empirical distribution. In performing the Chi-Square goodness of fit test the data was divided into two categories which included Female parent allele frequency and heterozygous allele frequencies. The null hypothesis was that there is no significant difference between the observed and the expected value while the alternative hypothesis was that there is a significant difference between the observed and the expected value.

Since the crosses were in the $BC_1 F_1$ generation, the expected female parent allele frequency was 25 % while the expected heterozygous allele frequency was 75%. The test results showed that all crosses with heterozygous allele frequency of less than 63% were not true backcross progenies. Out of the nine plants tested for the backcross Gadam × Framida × Gadam five were confirmed to be true backcross progenies (Table 18). For Gadam × N13 × Gadam, five out of the seven tested plants were confirmed to be true backcrosses while for Gadam × SRN39 × Gadam, eight out of thirteen tested plants were confirmed to be true backcross progenies (Table 19 and Table 20). The heterozygous allele frequencies for the confirmed successful backcross progenies was 68-75% for Gadam × Framida × Gadam, 68-77% for Gadam × N13 × Gadam and 63-74% for Gadam × SRN39 × Gadam.

Table 18. Chi-Square test for successful backcross progenies for Gadam × Framida × Gadam

Plant	Total no. of Loci	A	% of Parent A alleles	H	% Heterozygous Alleles	P. Value	Test Statistic
1	1144	317	27.70979	813	71.06643	0.01677	5.72028
4	1144	298	26.04895	835	72.98951	0.289908	1.120047
5	1144	265	23.16434	861	75.26224	0.212774	1.552448
6	1144	342	29.8951	787	68.79371	4.07E-05	16.84033
7	1144	316	27.62238	811	70.89161	0.016759	5.721445

Table 19. Chi-Square test for successful backcross progenies for Gadam × N13 × Gadam

Plant	Total no. of Loci	A	% of Parent A alleles	H	% Heterozygous Alleles	P. value	Test Statistic
1	2451	691	28.19	1673.00	68.26	6.20E-07	2.48E+01
2	2452	665	27.12	1711.00	69.78	2.71E-04	1.33E+01
5	2451	630	25.70	1765.00	72.01	6.50E-02	3.40E+00
6	2451	572	23.34	1845.00	75.28	9.82E-02	2.73E+00
7	2451	532	21.71	1890.00	77.11	5.05E-04	1.21E+01

Table 20. Chi-Square test for successful backcross progenies for Gadam × SRN39 × Gadam

Plant	Total no. of Loci	A	% of Parent A alleles	H	% Heterozygous Alleles	P.value	Test Statistic
1	1688	547	32.41	1068	63.27	1.64E-16	67.396
3	1688	396	23.46	1121	66.41	1.98E-05	18.209
4	1688	447	26.48	1239	73.40	0.151521	2.057
5	1688	418	24.76	1099	65.11	2.63E-06	22.067
6	1688	480	28.44	1206	71.45	0.001007	10.815
8	1688	427	25.30	1186	70.26	0.023726	5.115
9	1688	425	25.18	1261	74.70	0.839395	0.041

10	1688	472	27.96	1143	67.71	2.36E-05	17.874

4.5 Genetic gain for striga resistance and yield

4.5.1 Confirmation of hybridity for the crosses screened in the *Striga* filed trials.

A total of sixteen crosses were assessed to establish the gain in *Striga* resistance and yield. The highest proportion (22 – 46%) of heterozygous alleles were recorded in the progenies of the cross B35 × E36-1, while the lowest (<1%) were recorded in the crosses, Okabir × Akuor-Achot and Lodoka × Okabir. B35 and E36-1 are improved varieties derived from wild backgrounds while Lodoka and Akuor-Achot are landraces (Table 21). The total number of Bi-allelic alleles analysed ranged from 1204 -2868. An average of six plants was analysed for each cross.

Table 21. Confirmation of hybridity among the F_4 progenies using SNP markers.

Cross	Plants tested	Average no. of bi-allelic markers	Proportion of heterozygous alleles (%)
1. B35 x ICSVIII IN	6	2806	<1 - 33
2. B35 x F6YQ212	6	2774	15 - 43
3. B35 x AKUOR-ACHOT	6	2699	1 - 4.5
4. E36-1 x MACIA	6	1485	<1 - 29
5. F6YQ212 x LODOKA	5	1947	2 - 13
6. B35 x ICSVIII IN	6	2806	<1 - 33
7. B35 x E36-1	6	2868	22 - 46
8. B35 x LODOKA	6	2467	9 - 25
9. F6YQ212 x B35	5	2695	<1 - 10
10. ICSVIII IN x E36-1	6	1313	14 - 33
11. LODOKA x ICSVIII IN	6	1825	<1 - 15
12. OKABIR x ICSVIII IN	6	2339	<1 - 2
13. OKABIR x AKUOR-ACHOT	6	2174	<1
14. LODOKA x OKABIR	6	2357	<1
15. ICSVIII IN x MACIA	6	1204	10 – 17
16. ICSVIII IN x LODOKA	4	1764	4 – 13

4.5.2 Gain in tolerance and resistance to *Striga* in the F_4 progenies

Table 22 below shows heterosis values for yield and response to *Striga* in each of the crosses in the sick plot and potted trial. Crosses of improved varieties B35 and ICSVIII_IN were the best and worst gainers respectively for yield in both sickplot and potted trials(Table 19). The highest gain in yield recorded in the sick plot (790%; F6YQ212 × B35) also corresponded with a high gain in response to *Striga* (75%). The reciprocal cross (B35 × F6YQ212) was also among the top six crosses recording high gain in yield (197%) and resistance to *Striga* (58%) in the sickplot. There were significant gains in resistance to *Striga* for the same cross (F6YQ212 × B35) in the potted trial but not for yield (Table 22). All the seven crosses that recorded the highest gain in yield (194 – 790%) also recorded gains in resistance to *Striga* in the sickplot. The only two landrace × landrace crosses (Okabir × Akuor-Achot and Lodoka × Okabir) recorded gains in yield in both trials. Okabir × Akuor-Achot also recorded a slight gain in resistance to *Striga* (17% ASNPC) in the sickplot (Table 22).

The lowest yielding genotype in both trials was Akuor-Achot × ICSVIII_IN, which also recorded increased susceptibility to *Striga* (Table 22). Three (B35 × E36-1, ICSVIII_IN × Lodoka, B35 × ICSVIII_IN) out of the five lowest gainers in yield in the sickplot recorded enhanced resistance to *Striga*. Four crosses (F6YQ212 × B35, B35 × ICSVIII_IN, Okabir × B35, ICSVIII_IN × B35), all of which involved B35 as a common parent, showed enhanced resistance to *Striga* in both trials revealing their relative stability in response to *Striga* across the two environments (Table 22).

Table 22. Proportion of gain in tolerance and resistance to *Striga* in the sick plot and pot trial with a ranking of the crosses from the highest to the lowest yielding

Sick Plot			**Pot trial**		
Crosses	**Gain in tolerance (%)**	**Gain in resistance (%)**	**Crosses**	**Gain in tolerance(%)**	**Gain in resistance (%)**
1. F6YQ212xB35	790	75	1. OKABIRxB35	346	35
2. B35xLODOKA	456	79	2. LODOKAxOKABIR	205	3
3. B35xAKUOR-ACHOT	385	65	3. OKABIRxAKUOR-ACHOT	204	-19
4. OKABIRxAKUOR-ACHOT	302	17	4. B35xE36-1	183	-28
5. ICSVIII INxB35	207	53	5. LODOKA xICSVIII IN	143	-124
6. B35xF6YQ212	197	58	6. ICSVIII INxB35	85	33

Sick Plot			Pot trial		
Crosses	**Gain in tolerance (%)**	**Gain in resistance (%)**	**Crosses**	**Gain in tolerance(%)**	**Gain in resistance (%)**
7. OKABIRxB35	194	38	7. B35xICSVIII IN	49	41
8. LODOKAxICSVIII IN	170	-54	8. OKABIRxICSVIII IN	48	-41
9. LODOKAxOKABIR	119	-140	9. B35xAKUOR-ACHOT	44	-25
10. OKABIRxI CSVIII_IN	104	-40	10. F6YQ212xLODOKA	42	-99
11. F6YQ212xLODOKA	76	-63	11. B35xLODOKA	29	-147
12. ICSVIII IN x MACIA	8	-272	12. B35xF6YQ212	25	-16
13. ICSVIII IN x E36-1	0	-73	13. E36-1xMACIA	16	-144
14. E36-1 x MACIA	-14	-108	14. ICSVIII INxE36-1	-5	55
15. B35 x ICSVIII IN	-35	68	15. F6YQ212xB35	-11	45
16. ICSVIII IN x LODOKA	-40	19	16. ICSVIII INxLODOKA	-23	-87
17. B35 x E36-1	-69	25	17. ICSVIII INxMACIA	-27	-87
18. AKUOR-ACHOT x ICSVIII IN	-71	-72	18. AKUOR-ACHOTxICSVIII IN	-70	-5

Heritability estimates were generally lower in the potted trial compared to the values in the sickplot. The lowest heritability estimates (40%) were observed for 100 grain weight among progenies in the sickplot and overall pest score (28%) among progenies in the potted trial. The pattern of heritability of traits among parents and progenies were similar across the two environments, with parents recording higher heritability values for ASNPC, Maximum *Striga* count ,plant height, overall disease score, number of panicles harvested, 100 grain weight and yield (Tables 23,24,25,26). Progenies expressed higher heritability for days to flowering compared to parental genotypes in both trials (Tables 23,24,25,26). In the sickplot, heritability of yield trait for parents was 87% while that of the progenies was 65% (Table 23,24). In the potted trial, heritability estimates for yield in parents and progenies was 75% and 65% respectively.

Heritability for *Striga* resistance as denoted by ASNPC values was 75% and 71% for parents and progenies respectively in the Sickplot and 78% and 58% for parent and progenies respectively in the potted trial (Tables 23,24,25,26).

Table 23. Broad sense heritability estimates among parents measured under the Sickplot for yield and *Striga* related traits.

	RANGE	MEAN	MSG	MSE	σ2 G	σ2 P	PCV	GCV	H2 bs
100 GW	0.33 - 3.5	2.092	4.20	0.34	1.29	1.40	56.56	54.23	0.92
DPW	14 - 858	305	149443.00	17096.00	44115.67	49814.33	73.18	68.86	0.89
DTF	64.67 - 105.33	83.67	218.80	42.12	58.89	72.93	10.21	9.17	0.81
DTM	98.67 - 125.33	119.1	95.40	9.18	28.74	31.80	4.73	4.50	0.90
YIELD	0.05 -3.54	0.921	2.86	0.36	0.83	0.95	106.03	99.11	0.87
ODS	3.67 - 8	6.041	3.56	0.71	0.95	1.19	18.04	16.16	0.80
OPS	3.33 - 7.33	5.459	2.70	0.74	0.66	0.90	17.39	14.83	0.73
PNH	2.50 - 58.33	19.87	610.76	25.58	195.06	203.59	71.81	70.29	0.96
PH	87.70 -266.7	170.2	5559.70	304.00	1751.90	1853.23	25.29	24.59	0.95
NSmax	7 - 168	50.8	5623.00	1532.00	1363.67	1874.33	85.22	72.69	0.73
NSFC	1 TO 71	20.9	848.30	140.90	235.80	282.77	80.46	73.47	0.83
ASNPC	0-5698	2012	7863173.00	1966274.00	1965633.00	2621057.67	80.47	69.68	0.75

100 GW-100 Grain Weight(gm), DPW-Dry Panicle Weight, DTF-Days To Flowering, DTM-Days to Maturity, ODS-Overall Disease Score, OPS-Overall Pest Score, Nmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsules, ASNPC-Area Under Striga Number Progress Curve

Table 24. Broad sense heritability estimates among progenies measured under the Sickplot for yield and *Striga* related traits.

	RANGE	MEAN	MSG	MSE	σ2 G	σ2 P	PCV	GCV	H2 bs
100 GW	1.07 - 3.97	2.66	2.329	1.387	0.31	0.78	33.12	21.07	0.40
DPW	81 - 1171	530	342926	844.7	114027.10	114308.67	63.79	63.71	0.99
DTF	68 -133.67	85.22	463.62	61.74	133.96	154.54	14.59	13.58	0.87
DTM	103 - 157.33	123.7	223.81	12.4	70.47	74.60	6.98	6.79	0.94
YIELD	0.43 -4.96	2.1	187.82	65.48	40.78	62.61	376.78	304.09	0.65
ODS	3.67 - 7.33	5.65	3.608	0.4183	1.06	1.20	19.41	18.25	0.88
OPS	2 -6.67	5.143	5.1505	0.366	1.59	1.72	25.48	24.56	0.93
PNH	6 TO 23	14.05	85.52	16.67	22.95	28.51	38.00	34.10	0.81
PH	133.7 - 324	195.3	6738	466	2090.67	2246.00	24.27	23.41	0.93
NSmax	19 -148	61.8	3061	1128	644.33	1020.33	51.69	41.07	0.63
NSFC	6 TO 46	23.1	298.2	133.8	54.80	99.40	43.16	32.05	0.55
ASNPC	714- 6225	2599	6E+06	2E+06	1474638.33	2067703.67	55.33	46.72	0.71

100 GW-100 Grain Weight(gm), DPW-Dry Panicle Weight, DTF-Days To Flowering, DTM-Days to Maturity, ODS-Overall Disease Score, OPS-Overall Pest Score, Nmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsule

Table 25. Broad sense heritability estimates among parents measured under the potted trial for yield and *Striga* related traits.

	RANGE	MEAN	MSG	MSE	σ2 G	σ2 P	PCV	GCV	H2 bs
100 GW	0.414 - 4.967	2.88	4.22	0.82	1.13	1.41	41.13	36.93	0.81
DPW	2.5 - 274	89.90	10351.00	2982.00	2456.33	3450.33	65.34	55.13	0.71
DTF	44.67 - 89	70.97	140.58	59.32	27.09	46.86	9.65	7.33	0.58
YIELD	0.133- 27.59	8.06	120.14	25.16	31.66	40.05	78.51	69.81	0.79
ODS	3.333 - 8	6.13	4.56	0.91	1.22	1.52	20.11	17.99	0.80
OPS	3 - 6.667	5.12	2.64	0.81	0.61	0.88	18.35	15.27	0.69
PNH	2.33 -8.33	4.40	5.90	2.15	1.25	1.97	31.87	25.41	0.64
PH	95.3 - 257	178.60	7008.20	541.90	2155.43	2336.07	27.06	25.99	0.92
Nsmax	2 TO 25	10.68	83.99	13.60	23.46	28.00	49.54	45.35	0.84
NSFC	0 -8	2.60	10.35	3.88	2.16	3.45	71.45	56.52	0.63
ASNPC	39.7-1647.3	590.00	448828.00	100110.00	116239.33	149609.33	65.56	57.79	0.78

100 GW-100 Grain Weight(gm), DPW-Dry Panicle Weight, DTF-Days To Flowering, DTM-Days to Maturity, ODS-Overall Disease Score, OPS-Overall Pest Score, NSmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsules, ASNPC-Area Under Striga Number Progress Curve

Table 26. Broad sense heritability estimates among progenies measured under the potted trial for yield and *Striga* related traits.

	RANGE	MEAN	MSG	MSE	σ2 G	σ2 P	PCV	GCV	H2bs
100 GW	2.033 - 4.9	3.55	1.61	0.77	0.28	0.54	20.64	14.89	0.52
DPW	42.5 -287	154.70	11527.00	5651.00	1958.67	3842.33	40.07	28.61	0.51
DTF	65 - 95.33	73.91	224.72	26.41	66.10	74.91	11.71	11.00	0.88
YIELD	1.59 - 30.44	14.04	187.82	65.48	40.78	62.61	56.36	45.48	0.65
ODS	2.5 -7.667	4.90	4.98	1.50	1.16	1.66	26.30	22.00	0.70
OPS	3 TO 6	4.59	2.23	1.61	0.21	0.74	18.79	9.95	0.28
PNH	2.67 - 12.33	5.62	16.21	7.36	2.95	5.40	41.36	30.55	0.55
PH	95.7 - 277.7	173.90	5335.40	605.70	1576.57	1778.47	24.25	22.83	0.89
Nsmax	2 TO 22	9.29	56.79	11.61	15.06	18.93	46.83	41.77	0.80
NSFC	0 -6	2.31	6.83	4.16	0.89	2.28	65.30	40.84	0.39
ASNPC	142.3 -1113	531.00	169309.00	75477.00	31277.33	56436.33	44.74	33.31	0.55

100 GW-100 Grain Weight(gm), DPW-Dry Panicle Weight, DTF-Days To Flowering, DTM-Days to Maturity, ODS-Overall Disease Score, OPS-Overall Pest Score, NSmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsules, ASNPC-Area Under Striga Number Progress Curve

4.6 Discussion

Backcross breeding approach is used to introgress genes of interest from a donor genotype, often poor agronomic performance, into a recipient elite genotype. The resultant F_1 progeny of this cross is then crossed back to the recurrent parent, usually the female recipient genotype. This process is repeated for as many backcrosses as are necessary to create a line as identical as possible to the recurrent parent with the addition of the gene of interest from the donor line. In this study, only one backcross was performed necessitating further advancement of the generated backcrosses.

Advancement of backcross populations is dependent on the nature of inheritance of the gene of interest. The resistant donors used in the backcrossing programme (N13, SRN39 and Framida) have different resistance genes that are inherited differently. SRN39 and Framida possess the *Lgs* gene that is responsible for low germination stimuli production (Hess et al., 1992) which is inherited as a single recessive gene (Mohammed et al., 2010). N13 on the other hand, possess the *Hrs1* and *Hrs2* gene (hypersensitive response to *Striga*) which is dominantly inherited (Mohammed et al., 2010).

Genes with recessive inheritance are only carried in the heterozygous progenies and would not be detected throughout the backcross programme since they are only expressed in the homozygous recessive state (Miko, 2008).

To deal with this problem, when working with recessive traits, such as low germination stimulus production in sorghum, (Allard, 1960) suggested advancing the first backcross to the F_2 generation (BC_1 F_2) followed by selection for the trait of interest from the donor parent and the general features of the recurrent parent. The second and third backcrosses are then made in succession after which the inbreeding with selection phase for homozygous recessive individuals is repeated (Miah et al., 2015). This is followed by the fourth and fifth backcrosses in succession. The fifth backcross (BC_5F_2) that are resistant (homozygous recessive) are crossed to recurrent parent producing a BC_6 F_1 which is resistant. For traits controlled by a dominant gene such as the *Hrs1* and *Hrs2* for hypersensitive response to *Striga*, the backcrossing process involves four rounds of backcrossing within which the proportion of donor genome is reduced at each generation, except on the chromosome holding the gene of interest (Vogel, 2009).

Chi-Square goodness of fit test is a non- parametric test used to establish whether the observed value is significantly different from the expected value in a given test. The test compares the observed sample distribution with the expected probability distribution. The $\chi 2$ test is a way of quantifying the various deviations expected by chance if a hypothesis is true (Griffith et al., 2000). The expected proportions of parental genes in the BC_1F_1 have been reported in a study by (Frisch et al., 2005) where in backcrossing without selection, the expected donor genome proportion in generation BC_n is $1/2^{n+1}$.

This is equivalent to a ratio of 1:3 observed in the successful crosses in this study. The proportions of recurrent parent genome at BC_1F_1 generation are 75% while that of the donor parent which in this case is the susceptible parent is 25% (Collard et al., 2005).This is consistent with the results observed in this study where an average of 75% was observed for heterozygous alleles and 25% for the female parent alleles.

High quality DArT markers for *Sorghum bicolor* have been developed and have been used for diversity analyses as well as to construct medium-density genetic linkage maps (Mace et al., 2008). The high quantity of DArT markers generated in a single test and their even distribution over the genome provides a comprehensive estimate of genetic relationships among genotypes (Sansaloni et al., 2011). While there are several studies reporting the use of DArT-seq for diversity analysis in sorghum (Kotla et al., 2019; Allan et al., 2020; Mengistu et al., 2020), ours is the first study to use DArT-seq for hybridity testing. The unique SNP markers from this study will be useful for Genome Selection and for incorporation into marker panels that aim at the identification of successful hybrids from new crosses involving any of the parents.

Parental genotypes expressed high heritability compared to progenies for most traits because they are genetically more stable than the progenies which are still undergoing segregation. Heritability values alone do not offer much practical importance in selection based on phenotypic appearance (Eid et al., 2009). Therefore, both heritability and genetic advance should be considered in breeding programmes for successful selection results. High heritability values for yield and *Striga* resistance was observed both in the parents and progenies for both trials. Genetic gain for *Striga* tolerance (Yield) was high in both trials while genetic gain for *Striga* resistance was lower. High heritability and genetic gain values for *Striga* tolerance (Yield) is indicative of the additive nature of inheritance for the trait and that this trait was successfully transferred from parents to the progenies. This also suggest

that this trait can easily be fixed in the genotypes by selection in early generations (Hassan, 2004).

In addition ,the high heritability values recorded suggested that there is an opportunity for further improvement for this trait (Songsri et al., 2008). High heritability values accompanied by low genetic advance for *Striga* resistance suggested that non-additive gene action was predominant. This mode of gene action could be exploited through heterosis breeding (Eid et al., 2009). High heritability and low genetic gain may also suggest lack of sufficient genetic variability within the germplasm (Sardana et al., 2007).

The demonstrated gain in *Striga* tolerance and resistance is great for breeding programmes as it shows the huge potential of enhancing the performance of varieties in response to *Striga* through improved genetics. Given the high variation in the biotypes of *Striga* across different environments, the best breeding strategy would be genomic selection (GS) (Goddard, 2009). This is a good basis for designing a GS strategy for developing *Striga* resistant and *Striga* tolerant sorghum varieties that will be suitable for the harsh environments typical of *Striga* - endemic ecologies. The available genomic resources in sorghum public databases will enhance the ease with which GS is implemented in sorghum.

4.7 Conclusion

The test results showed that progenies of three crosses were true backcrosses with heterozygous allele frequency of above 63%. Progenies of remaining crosses did not reach the required heterozygous allele frequencies which was attributed to failure of backcrossing programme either at initial F_1 generation stage or at the backcrossing stage.

An assessment of genetic gain for *Striga* resistance and *Striga* tolerance in F_4 progenies showed that that genetic gain for yield also expressed as tolerance was high in both sickplot and potted trial. Genetic gain for *Striga* resistance was generally low in both trials with only a few progenies exhibiting higher resistance than either parents. The demonstrated gain in *Striga* tolerance and resistance is indicative of the huge potential of enhancing the performance of varieties in response to *Striga* through improved genetics.

CHAPTER FIVE: GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

5.1 General discussion

This study aimed to identify new sources new sources of resistance to parasitic weed *Striga hermonthica*. Total of 64 genotypes consisting of wild relatives, landraces, improved varieties and F_4 lines were included in the study. The study took place in Kenya using one field trial and one potted trial both of which were carried out within the same year. The study resulted in identification of genotypes both more resistant and higher yielding than currently used conventional checks. Seven new genotypes; two improved varieties F6YQ212 and ICSVIII_IN, three wild genotypes GBK045827, GBK047293, GBK044336, and two F4 population crosses B35 × ICSVIII_IN and F6YQ212 × B3 gave a consistent *Striga* resistance response across the two trials with ASNPC values lower than those of the resistant check N13. Estimation of genetic relatedness of these genotypes revealed three clusters where F6YQ212 and GBK 045827 clustered away from known Striga resistance donors in the trial which shows that they possess unique genes. N13 clustered with GBK 047293 and GBK044336 suggesting that they may possess resistance from a common source.

The best yielding genotypes were predominantly F_4 crosses in both experiments, all of which yielded better than resistant checks, except Framida in the sickplot. Crosses involving improved variety ICSVIII_IN were among the best yielding in both trials. Among the top yielding genotypes were MACIA, B35 and E36-1, all of which are drought tolerant improved varieties that have been used for decades in the region. Other genotypes that have been reported to be drought tolerant and showed high yielding potential under *Striga* included OKABIR, AKUOR-ACHOT and LODOKA. These results indicate a possible correlation between drought and *Striga* tolerance.

Introgression of *Striga* resistance genes from known donors to susceptible sorghum varieties yielded successful BC_1F_1 progenies for three crosses with resistant donors N13, SRN39 and Framida as one of the parents. Further investigation of heritability and genetic gain for *Striga* resistance and tolerance indicated high heritability for the two traits. Genetic gain for *Striga* tolerance was high in both sickplot and potted trial. Genetic gain for *Striga* resistance was generally low in both trials with only a few progenies exhibiting higher resistance than either parents.

5.2 Conclusions

Striga is one of the major causes of yield loss especially in Western and Nyanza regions of the country which are the major sorghum growing regions and therefore the need to screen diverse sorghum genotypes, to identify novel sources of *Striga* resistance that can be used in crop improvement. Field trial conducted in a sickplot and a potted trial at KALRO Alupe station in Busia County identified seven novel resistant genotypes including; two improved varieties F6YQ212 and ICSVIII_IN, three wild genotypes GBK045827, GBK047293, GBK044336, and two F_4 population crosses B35 × ICSVIII_IN and F6YQ212 × B35.

Estimation of genetic diversity of these genotypes revealed three clusters where all resistant checks clustered together apart from N13. F6YQ212 and GBK 045827 clustered together with known *Striga* resistance donors but in a separate sub-clade which shows that they possibly possess unique genes. N13 clustered with resistant wild genotypes GBK047293 and GBK044336 suggesting that they may possess resistance from a common source. Successful marker assisted backcrossing was achieved . Genetic gain for *Striga* tolerance was high in both sickplot and potted trial while genetic gain for *Striga* resistance was generally low in both trials.

The study thus concluded that genetic diversity for *Striga* resistance is abundant in local landrace and wild sorghum genotypes. DArT markers were successfully used to assess the diversity of accessions and confirm the hybridity of the Backcrosses that were generated with the intention to introgress *Striga* resistance Quantitative Trait Loci (QTL) into a Kenyan adapted farmer preferred sorghum varieties, Gadam and Karimtama-1.

5.3 Recommendations

- The newly identified *Striga* resistant genotypes should be studied further to confirm their resistance and to establish their exact mechanism of resistance to *Striga* before being incorporated in breeding programmes as resistance donors.
- Successful backcrosses should advanced in a striga field trial to assess their response to striga under natural infestation.
- The identified F_4 generation plants with *Striga* resistance QTL should be selfed to fix the QTL and then be released as *Striga* resistant varieties.
- Screening of wild and landrace genotypes should be intensified to accelerate discovery more resistance genes.
- Future field trials should also include Striga-free plots besides the infested plots to enable estimation of the extent to which Striga affects particular traits.
- Farmers should also be advised to practise use of integrated *Striga* management options to curb *Striga* problem

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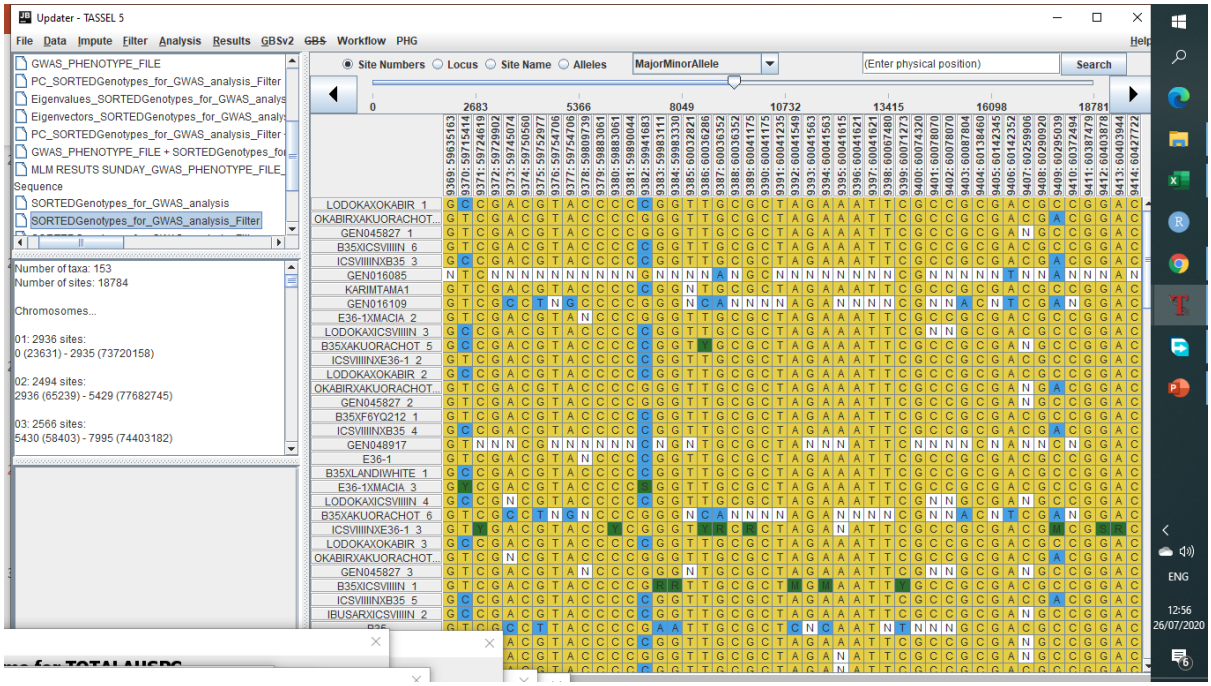
APPENDIXES

Appendix 1.Generation of backcrosses in a greenhouse at the University of Nairobi field Station

Appendix 2. Laying out the Potted trial at KALRO Alupe Station

Appendix 3. Fully established Potted trial at KALRO Alupe Station.

Appendix 4. Two weeks old sorghum seedlings in a screenhouse at ICRAF ready for leaf sampling for DNA extraction.



Appendix 5. Diversity analysis in TASSEL

Appendix 6. Means for agronomic traits for all sorghum genotypes sown in the field trial during the long rains of 2019 at KARLO, Alupe

GENOTYPE	100GW (gm)	AGS	DPW	DTF	ODS	OPS	PNH	PH	PV	YIELD (t/ha)
AKUOR-ACHOT	3.50	4	263	83	6.67	6.67	17	188.7	3.33	0.92
AKUOR-ACHOTxICSVIII_IN	3.27	4.33	81	97	5.67	5	9	142.3	3.33	0.43
B35	2.00	4.67	49	83	8	6	6	87.7	3.33	0.20
B35_1	2.23	4	152	78	7	5.67	10	96	3.33	0.78
B35xAKUOR-ACHOT	2.57	3	847	81	6.67	6.67	21	145	3.33	2.72
B35xE36-1	3.30	4.33	193	81	6.67	5	7	159.7	2.33	0.48
B35xF6YQ212	2.43	3.67	331	80	6.67	6.33	13	133.7	3.00	0.95
B35xICSVIII_IN	1.87	5	247	85	7	5.67	15	150.7	3.00	0.75
B35xLANDWHITE	2.50	4.33	290	89	5.33	5	7	175	3.00	1.26
B35xLODOKA	2.60	3.67	556	88	5	6	19	203.7	3.00	2.03
E36-1	3.30	2.67	652	80	4.67	5.33	19	167	3.33	2.92
E36-1xMACIA	3.53	3	726	89	5.67	4	18	184	3.33	2.49
F6YQ212	1.87	3.67	170	83	8	6.33	18	114.7	3.33	0.44
F6YQ212xB35	3.60	4.17	734	89	5.33	6	21	193.7	3.67	2.85
F6YQ212xLODOKA	3.10	5	239	91	7.33	6.67	13	235.3	2.67	0.85
FRAMIDA	3.13	4.32	789	74	6.1	6.01	12	189.4	3.33	3.54
GADAM	2.30	4.17	337	89	7.33	6	11	116.2	3.33	1.29
GBK016085	2.97	5.33	548	75	6	7.33	20	168	5.00	3.28
GBK016109	0.33	5	164	87	7.33	6	28	195	5.00	0.36
GBK016114	2.27	4.67	289	70	6	4	39	200.3	4.67	0.44
GBK040577	2.57	5.33	308	82	4.67	6.67	22	206.3	4.67	1.16
GBK043565	1.60	5.67	308	87	5.67	6.33	20	180.7	4.67	1.16
GBK044054	0.93	5	244	75	6.67	5.33	54	216.7	4.00	0.58
GBK044058	1.03	4.33	33.3	94	5	6	17	227.7	3.00	0.14
GBK044063	0.47	5	393	92	5.33	5	22	224.7	4.67	0.73
GBK044065	1.70	4.38	301	83	5.43	6.04	23	235	3.91	1.01
GBK044120	1.60	5	90	86	7	5	30	266.7	4.67	0.17
GBK044336	1.13	5	270	80	3.67	3.33	56	226.3	4.67	0.48
GBK044448	1.80	4.67	14	85	6	6.67	7	182	5.00	0.06
GBK045827	2.60	3.33	858	74	5.33	5	20	182.7	3.33	2.86
GBK047293	2.43	4.02	244	84	5.85	5.36	58	184.1	5.00	1.28
GBK048152	1.84	4.43	156	84	5.72	6.37	3	234.1	4.92	0.40
GBK048156	1.00	4.33	7	80	5.59	6.01	3	227.1	5.00	0.03
GBK048916	2.17	3.5	124	95	5.67	4.67	4	186	3.00	0.72
GBK048917	1.77	4.5	308	82	5.73	6.14	20	166.9	4.96	1.16
GBK048921	2.57	4.67	377	84	5	6.33	20	179.7	5.00	1.77
GBK048922	2.03	5	114	96	5	4.33	24	194.7	5.00	0.30
HAKIKA	3.43	3.67	599	82	6.67	5.33	15	119.7	4.00	2.68
IBUSARxE36-1	2.30	5	392	81	7	6.67	17	247	4.00	1.54
IBUSARxICSVIII_IN	2.30	2.33	392	134	5	5	17	260.3	3.00	1.54
IBUSARxLANDWHITE	1.67	2.33	952	78	3.67	3.67	18	172.7	2.33	4.51

GENOTYPE	100GW (gm)	AGS	DPW	DTF	ODS	OPS	PNH	PH	PV	YIELD (t/ha)
ICSVIII_IN	3.07	3.5	538	73	7	6.33	17	189	4.00	2.10
ICSVIII_INxB35	3.30	3	1171	82	3.67	3	18	168.3	2.67	3.53
ICSVIII_INxE36-1	3.77	3.5	329	77	5	5.67	18	166.7	3.33	2.51
ICSVIII_INxLANDWHITE	1.17	3	1089	71	6.33	5	16	260.7	3.00	4.96
ICSVIII_INxLODOKA	3.97	4	140	86	7.33	6	7	198	4.00	0.79
ICSVIII_INxMACIA	2.07	4.33	572	81	5	3.33	13	232.3	2.33	2.69
IS9830	2.17	3.83	300	86	6.67	6.33	13	118.3	3.67	1.12
KARI MTAMA 1	2.57	3	358	88	6.67	4.33	13	151.7	2.67	1.51
KAT/ELM/2016PL1SD15	1.63	2	563	82	6.33	3.33	12	178.7	3.00	2.76
KAT/ELM/2016PL82KM32-2	2.03	3.5	259	85	6	5.67	17	148.3	3.00	0.82
LANDWHITExB35	3.63	4.67	200	80	5.33	6.67	8	173	3.00	0.77
LANDWHITExMACIA	3.07	2.67	190	71	7	6.33	7	177.7	2.33	0.96
LODOKA	1.40	2.67	155	78	6.33	5.33	11	107.7	2.67	0.53
LODOKAxICSVIII_IN	1.60	2	920	78	5.33	2.33	16	148.3	2.33	3.55
LODOKAxLANDWHITE	1.50	5.33	325	95	5.33	5	8	324	3.33	1.11
LODOKAxOKABIR	2.33	2	334	78	4.67	2.33	8	184	2.67	1.50
MACIA	2.60	3.89	708	65	6.33	5.67	18	135	2.00	2.88
N13	2.83	4	217	97	4.33	4.33	9	137.3	4.33	0.68
OKABIR	1.77	5	168	105	4	4.33	14	217.7	3.00	0.84
OKABIRxAKUOR-ACHOT	1.07	2.67	953	68	4.67	4.33	18	183.7	2.67	3.55
OKABIRxB35	2.30	5	392	90	6	6.33	17	195.3	4.00	1.54
OKABIRxICSVIII_IN	3.37	4.67	708	95	3.67	5	23	275.3	3.33	3.00
SRN39	2.43	4.67	353	89	7	5.33	20	144.3	3.00	1.37
MEAN	2.30	4.02	392	84	5.85	5.36	17	184.1	3.56	1.54
CV (%)	31.90	12.2	45.8	8	12.6	13.5	24	9.9	15.00	49.40
LSD	1.19	0.79	290	11	1.19	1.17	7	29.4	0.86	1.23
Fpr	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

GW-Seed weight, AGS-Agronomic Score, DPW-Dry Panicle Weight, DTF-Days to Flowering, ODS-Overall Disease Score, OPS-Overall Pest Score, NPH-Number of Panicles Harvested, PV-Plant vigor, Yield is in tonnes per hectare.

Appendix 7.Response of sorghum genotypes to *Striga* in the field trial sown during long rains of 2019 at KARLO, Alupe.

GENOTYPE	NSFC	NSmax	ASNPC
AKUOR-ACHOT	36	85	3607
AKUOR-ACHOTxICSVIII_IN	34	104.67	3446
B35	42	128.67	5269
B35_1	29.67	53	1806
B35xAKUOR-ACHOT	20.67	36.33	1575
B35xE36-1	33	69.67	3064
B35xF6YQ212	10.33	34.67	1195
B35xICSVIII_IN	8	20.33	922
B35xLANDWHITE	18	33.33	1318
B35xLODOKA	11.67	19	824
E36-1	28.33	76	2910
E36-1xMACIA	22.33	89.67	3843
F6YQ212	3.67	13	434
F6YQ212xB35	6.33	24.67	714
F6YQ212xLODOKA	22.33	54.33	2522
FRAMIDA	11.67	26	1267
GADAM	16.67	27.33	1190
GBK016085	16	33.33	1300
GBK016109	69.3	150.67	4881
GBK016114	45	107.67	4797
GBK040577	6.67	24.33	1225
GBK043565	18.33	67.67	2490
GBK044054	8.33	87.67	4041
GBK044058	54.67	168.33	5698
GBK044063	51.33	117.67	4492
GBK044065	21	60	0
GBK044120	15	64.67	1195
GBK044336	10.33	29.33	926
GBK044448	14	34.67	1113
GBK045827	6.33	14.33	523
GBK047293	11.67	34	994
GBK048152	10	156.67	3334
GBK048156	21	59.8	0
GBK048916	19.33	47.33	1976
GBK048917	2.33	60	0
GBK048921	7.33	21.67	838
GBK048922	46.67	100.33	2210
HAKIKA	13.33	28	1008
IBUSARxE36-1	32	78.67	2844
IBUSARxICSVIII_IN	26	66.33	6118
IBUSARxLANDWHITE	37.67	148	3414
ICSVIII_IN	3	12.33	406

GENOTYPE	NSFC	NSmax	ASNPC
ICSVIII_INxB35	15	35.67	1328
ICSVIII_INxE36-1	26.33	60	2875
ICSVIII_INxLANDWHITE	16.33	54	3101
ICSVIII_INxLODOKA	22	38.33	1244
ICSVIII_INxMACIA	24.67	74.67	2212
IS9830	10	22.33	882
KARI MTAMA 1	34	94.33	3232
KAT/ELM/2016PL1SD15	16.33	36.67	1181
KAT/ELM/2016PL82KM32-2	28.33	99	3936
LANDWHITExB35	46	93.33	4251
LANDWHITExMACIA	20.67	89	3502
LODOKA	19.33	54	2665
LODOKAxICSVIII_IN	20	54.33	2364
LODOKAxLANDWHITE	13.67	36.67	1652
LODOKAxOKABIR	49.67	157	6225
MACIA	17	26	784
N13	9	20	1034
OKABIR	22.33	74.33	2527
OKABIRxAKUOR-ACHOT	26	65.67	2536
OKABIRxB35	21.67	49.67	2427
OKABIRxICSVIII_IN	27.33	62	2046
SRN39	1.33	7	299
MEAN	22	62.1	2250
CV	50.7	53.8	60.6
LSD	81.034	53.97	2204.3
Fpr	<0.01	<0.01	<0.01

NSmax-Maximum *Striga* Count, SPFC-Number of *Striga* Plants Forming Capsules, ASNPC-Area under *Striga* Number Progress Curve

Appendix 8. Means for agronomic traits for all sorghum genotypes sown in the potted trial during the long rains of 2019 at KARLO, Alupe.

GENOTYPE	10GW (gm)	AGS	DPW (gm)	DTF	ODS	OPS	PNH	PH(cm)	PV	YIELD (t/ha)
AKUOR-ACHOT	4.667	3.667	166	73	6.333	5.67	2.33	184.7	3	17.59
AKUOR-ACHOTxICSVIII_IN	2.3	4.333	42.5	69	7.667	5.33	6	169.7	2.333	4.6
B35	3.833	3	79.8	68	8	6.33	2.67	95.3	2.667	7.59
B35_1	3.333	3.833	116	67	8	5.33	2.67	150	3	11.67
B35xAKUOR-ACHOT	3.333	2.667	175	76	5.333	5	2.67	128.7	3.333	18.17
B35xE36-1	3.967	3.333	187	73	4.333	4	4	163.3	2	20.04
B35xF6YQ212	3.667	4	145	67	3.667	3	2.67	95.7	2.333	11.94
B35xICSVIII_IN	4.9	3.333	154	67	6.333	4.67	5	166.3	2.667	15.1
B35xLANDIWHITE	4.433	3.333	87.9	65	5.333	5.33	7.67	139.3	3	10.01
B35xLODOKA	3.8	4	134	69	5	5	4.67	177	3	12.95
E36-1	2.7	2.5	83.9	76	4	5.67	2.67	153.7	3.333	6.58
E36-1xMACIA	4.2	3	187	81	5.333	3.33	5.33	168.7	3	19.9
F6YQ212	4.167	4.333	107	65	8	6	5.67	103.3	3	11.48
F6YQ212xB35	4.133	4.333	78.2	74	5.333	5.33	4.33	150.7	2.667	8.48
F6YQ212xLODOKA	4.1	3.833	159	66	5	6	4	203.7	3.333	17.03
FRAMIDA	4.267	3	141	67	5.667	3.67	3	148	3	14.25
GADAM	4.133	3.667	90.7	68	7	6.33	3.67	107	3	10.67
GBK016085	3.867	5	151	68	5.667	5	3	219.3	2.667	15.31
GBK016109	1.567	4.667	115	73	7	4.33	5.33	224.7	3.333	3.06
GBK016114	2.5	4.667	126	65	7	4.33	4	222.7	3	10.12
GBK040577	3.067	4.667	16.4	71	6.667	6	5	198	2.667	3.9
GBK043565	1.6	4.667	7.3	65	7.667	6.67	4	201.3	3.667	0.7
GBK044054	1.367	4.667	111	67	5	4.67	4.67	257	3	4.59
GBK044058	0.667	4.333	7.6	82	4.333	4.67	5.33	238	2.333	0.6
GBK044063	2.933	5	21.3	76	5.333	4	4.33	253.7	3.333	0.61
GBK044065	1.6	4.667	10.5	75	3.667	3.33	5	232	3	0.75
GBK044120	3.267	4.667	133	89	7.333	4.67	4.67	212	3	7.21
GBK044336	1.7	5	121	68	5.667	4.33	4.33	208	3.333	10.64
GBK044448	3.233	3.833	85.2	45	7	5	3	165	2.667	9.3
GBK045827	3.833	3.167	120	71	5.667	5.33	5.67	141.3	2.667	12.86
GBK047293	1.967	4	42.5	73	6.667	4.33	5.67	202.3	3	2.02
GBK048152	0.588	4.968	17	72	7.031	6.3	5.27	226.3	2.855	0.133
GBK048156	0.8	5	2.5	70	6	5.67	4.33	226.3	3.333	0.16
GBK048916	2.333	4.667	89.8	73	6.333	6.33	4	191	3	4.75
GBK048917	1.567	4.667	3.7	69	6.333	6.33	3	159.7	3.333	0.4
GBK048921	2.667	5	116	75	6.667	5.67	5.67	240	3	12
GBK048922	3.533	4.667	58.8	75	4.667	4.67	6	225	3.333	5.62
HAKIKA	4.167	3	103	72	7	6.33	5.67	118.7	3	9.05
IBUSARxE36-1	3.148	3.774	115	72	2.48	4.91	4.86	177	3	0.14
IBUSARxICSVIII_IN	3.467	2.667	214	75	5.333	4.33	8.67	164	2.333	24.05
IBUSARxLANDIWHITE	3.148	3.774	115	72	2.48	4.91	4.86	177	2.333	0.14
ICSVIII_IN	4.267	3.167	111	72	4	5.33	5.33	143.7	2.333	12.62

GENOTYPE	10GW (gm)	AGS	DPW (gm)	DTF	ODS	OPS	PNH	PH(cm)	PV	YIELD (t/ha)
ICSVIII_INxB35	2.533	2.667	187	80	4.333	4.33	4.33	158.3	1.667	18.66
ICSVIII_INxE36-1	4.033	3.833	115	70	6	5.33	5	136.7	3	9.08
ICSVIII_INxLANDIWHITE	3.433	3.667	246	65	3.667	5	11	203.7	2.667	18.08
ICSVIII_INxLODOKA	3.833	3.167	118	67	6	5.33	4.33	183	2.667	9.63
ICSVIII_INxMACIA	2.233	3	150	74	5	5.67	6.67	140.3	3	14.75
IS 9830	2.4	3.333	94.2	75	6.667	5.67	5.33	130.3	3.333	9.19
KARI MTAMA 1	2.5	4.667	48.8	76	7.333	4.67	3	128.3	2.667	2.01
KAT/ELM/2016 PL1 SD15	4.5	3.667	86.5	69	6.333	5	8.33	133.7	2.667	8.81
KAT/ELM/2016 PL82 KM32-2	4.133	2.333	198	80	5.667	4.67	7	138.7	2	21.31
LANDIWHITExB35	3.733	3.333	113	66	7.031	5.67	6.33	176.3	2.333	10.33
LANDIWHITExMACIA	3.167	2.667	152	71	4.333	3.33	4.33	191.3	2.333	11.8
LODOKA	3.2	3	139	66	5.333	5	5.67	153	2.333	12.45
LODOKAxICSVIII_IN	2.9	2.333	287	72	4	3	6.33	123.7	1.333	30.44
LODOKAxLANDIWHITE	2.033	4.333	44.8	89	5	4	5	275.7	3	1.58
LODOKAxOKABIR	4.633	3	184	67	7	4.33	4	187	2.333	21.3
MACIA	3.033	3	274	77	3.333	3.33	4	114.3	2	27.59
N13	2.733	4.5	58.3	66	7.333	3	2.67	148.3	3.333	5.18
OKABIR	1.967	4.013	41.1	72	6.48	5.85	2.67	256	1.667	1.52
OKABIRxAKUOR-ACHOT	3.467	2.333	260	79	3.333	4.33	12.3	189	2	29.06
OKABIRxB35	3.8	3.333	195	94	5.333	4.33	4.67	277.7	1.667	20.33
OKABIRxICSVIII_IN	3.433	3.513	110	95	3.48	3.85	5	217.3	2	10.45
SRN39	4.967	3.333	120	67	5	5	2.67	138	2.667	12.31
Grand mean	3.148	3.774	115	72	5.646	4.91	4.86	177	2.732	10.53
CV(%)	27.9	17.6	54.8	9	18.9	20.8	39	13.5	22.9	60.4
LSD	1.421	1.075	102	11	1.725	1.65	3.07	38.62	1.01	10.29
P value	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001

Appendix 9. Response of sorghum genotypes to *Striga* in the potted trial during the long rains of 2019 at KARLO, Alupe

GENOTYPE	NSFC	Nsmax	ASNPC
AKUOR-ACHOT	0	9	471
AKUOR-ACHOTxICSVIII_IN	1	8	464
B35	1	12	597
B35_1	3	13	742
B35xAKUOR-ACHOT	2	11	667
B35xE36-1	0	12	588
B35xF6YQ212	2	7	371
B35xICSVIII_IN	0	9	296
B35xLANDIWHITE	3	22	915
B35xLODOKA	4	15	1113
E36-1	3	5	320
E36-1xMACIA	4	9	735
F6YQ212	0	2	40
F6YQ212xB35	1	3	175
F6YQ212xLODOKA	1	4	343
FRAMIDA	1	5	359
GADAM	6	17	1057
GBK016085	1	6	154
GBK016109	0	3	149
GBK016114	2	15	1013
GBK040577	3	13	751
GBK043565	2	9	562
GBK044054	3	11	600
GBK044058	8	25	1647
GBK044063	3	19	1318
GBK044065	6	19	1617
GBK044120	3	9	481
GBK044336	3	9	322
GBK044448	3	8	474
GBK045827	2	4	226
GBK047293	4	10	562
GBK048152	0	11	77
GBK048156	3	11	793
GBK048916	1	9	441
GBK048917	5	20	842
GBK048921	2	15	674
GBK048922	6	15	1146
HAKIKA	0	9	273
IBUSARxE36-1	1	6	308
IBUSARxICSVIII_IN	2	13	621
IBUSARxLANDIWHITE	4	10	509
ICSVIII_IN	3	6	413
ICSVIII_INxB35	1	5	341

GENOTYPE	NSFC	Nsmax	ASNPC
ICSVIII_INxE36-1	0	4	166
ICSVIII_INxLANDIWHITE	6	12	679
ICSVIII_INxLODOKA	4	8	672
ICSVIII_INxMACIA	3	9	651
IS 9830	2	10	527
KARI MTAMA 1	1	21	684
KAT/ELM/2016 PL1 SD15	4	10	849
KAT/ELM/2016 PL82 KM32-2	1	9	436
LANDIWHITExB35	4	15	730
LANDIWHITExMACIA	4	6	525
LODOKA	3	7	306
LODOKAxICSVIII_IN	3	15	805
LODOKAxLANDIWHITE	1	3	142
LODOKAxOKABIR	3	7	399
MACIA	2	9	282
N13	2	8	579
OKABIR	3	8	513
OKABIRxAKUOR-ACHOT	2	9	586
OKABIRxB35	2	7	359
OKABIRxICSVIII_IN	3	12	651
SRN39	2	4	138
Grand mean	2.48	10.09	566
CV(%)	80	33	53
LSD	3.206	5.387	482
P value	<.001	<.001	<0.01

NSmax-Maximum Striga Count, NSFC-Number of Striga plants Forming Capsules, ASNPC-Area under Striga Number Progress Curve