Integrated *Striga* Management in Sorghum through Resistance Breeding and Biocontrol in the Semi-Arid Regions of Tanzania

By

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy (PhD) in Plant Breeding

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Republic of South Africa

November 2017

Thesis Abstract

Sorghum [*Sorghum bicolor* (L.) Moench] is an important food, feed, and bioenergy crop widely grown in arid and semi-arid parts of sub-Saharan Africa, including Tanzania. In this region sorghum productivity is often low as a result of biotic and abiotic stresses, as well as socio-economic constraints. *Striga* is one of the major biotic constraints, which typically causes yield losses of 30 to 90% in Tanzania. Both *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*) are widely distributed in the country and severely impact on crop yields of sorghum, millet, maize and rice. Several cultural, biological, chemical and host resistance measures have been recommended to control *Striga*. However, these measures need to be integrated for effective control of the parasite and to improve sorghum productivity. The overall aim of this study was to improve sorghum yield by integrating host resistance and the use of a biological control agent, *Fusarium oxysporum* f.sp. *strigae* (*FOS*) to control *Sh* and *Sa* in the semi-arid parts of Tanzania.

The specific objectives of this study were: 1) to investigate the constraints affecting sorghum production, and to document farmers' approaches to *Striga* management in the semi-arid regions of Tanzania; 2) to screen and select farmers-preferred sorghum genotypes for *Sh* and *Sa* resistance, and for *FOS* compatibility, for resistance breeding under western Tanzanian conditions; 3) to identify promising sorghum parents and crosses that demonstrated *FOS*-compatibility and *Striga* resistance and displayed high combining ability for grain yield and yield components for Integrated *Striga* Management (ISM); 4) to determine the gene action and inheritance of *Striga* resistance using genetically diverse populations of sorghum involving *FOS* treatment; and 5) to determine the gene action controlling maximum germination distance in sorghum genotypes.

A participatory rural appraisal (PRA) study was also conducted involving three selected districts across six villages in semi-arid regions of Tanzania. The study identified *Striga* infestation, drought, storage pests, damage by birds, a lack of access to improved varieties, and a lack of access to production inputs, such as fertilizers, insecticides, fungicides and herbicides as the major constraints affecting sorghum production in these study areas.

To achieve the second objective, 60 sorghum genotypes were evaluated under screen-house conditions using *Sh and Sa* infested field soils with controlled seed infestation, with or without treatment of the sorghum seeds with *FOS.* Inoculation of sorghum seeds with *FOS* significantly enhanced sorghum growth and productivity, and supressed *Sh and Sa* growth and allowed for the selection of *FOS* compatible sorghum genotypes.

To address objective three, one hundred sorghum families were developed through controlled crosses using the North Carolina Design II, which involved 10 female parents selected for their *FOS* compatibility and excellent agronomic performances, and 10 male parents selected for high levels of *Striga* resistance. The F1s and their parents were field evaluated at three locations in Tanzania known for their severe *Striga* infestation using a lattice experimental design with two replications. The following genotypes were identified as the best general combiners for yield and yield components 675 and 3424 (female parents), and AS426 and AS430 (male parents) Genotypes 672, AS436 and AS429 (male parents) and 3984 (female parents) were the best general combiners for *Striga* resistance, displaying smaller GCA effects in a desirable direction. Three promising families, 675 x 654, 3424 x 3933 and 4567 x AS426, were selected for further breeding as they displayed larger SCA effects for grain yield. Crosses selected with small SCA effects for *Striga* counts were 4567 x AS424 and 3984 x 672.

To address objective four, gene action and inheritance of *Striga* resistance were investigated using genetically diverse populations of sorghum involving *FOS* treatment. Twelve sorghum parents were selected for *Striga* resistance, *FOS* compatibility or superior agronomic performances. These were crossed using a bi-parental mating scheme. The selected male and female parents and their F_1 progenies, backcross derivatives and the F_2 segregants were field evaluated at three locations in Tanzania known for their severe *Striga* infestations using a lattice experimental design with two replications. Results from the generation mean analysis (GMA) on days-to-50% flowering (DFL), seed yield per plant (SYP) and number of *Striga* plants per plant (SN) showed the preponderance of additive genetic action contributing to the total genetic variation in the evaluated sorghum populations. The additive genetic effect for DFL, SYP and SN, with and without *FOS* treatments, ranged from 72.02 to 86.65% and 41.49 to 95.44%, 75.62 to 91.42% and 71.83 to 91.89%, and 77.35 to 93.56% and 72.86 to 95.84%, in that order. The contribution of non-additive genetic effects was minimal and varied among generations. *FOS* application reduced DFL and SN, and improved SYP in most of the tested sorghum populations. DFL of the sorghum populations was reduced by a mean of 8 days under *FOS* treatment compared to the untreated control in families such as 675 x 654, AS435 x AS426 and 1563 x AS436. *FOS* treatment improved SYP with a mean of 6.44 g $plant^{-1}$ in 4567 x AS 426, 3424 x 3993 and 3984 x 672. The numbers of *Striga* plants were reduced with a mean of 16 plants due to *FOS* treatment in the crosses of 675 x 654, 1563 x AS436, 4567 x AS424, and 3984 x 672. The study demonstrated that additive genes were predominantly responsible for the inheritance of *Striga* resistance in sorghum.

The last objective of this study was to determine the gene action controlling maximum germination distance (MGD) among sorghum families, with and without *FOS*, in an agar-gel assay. In this study additive, dominance and epistatic genetic action contributed significantly to the total genetic variation. The relative contribution of the additive, additive-by-additive and dominance-by-dominance genetic effect for MGD, with *FOS,* contributed to 20%, 33% and 36% in treatments involving *Sh,* respectively. In a set with *Sa*, the relative contribution of additive, additive-by-additive and dominance-by-dominance genetic effect were 21%, 32% and 35% with *FOS* treatment, respectively. The influence of dominance and the interaction of additive-by-dominance genetic effects were minimal. A mean MGD of 10 mm was reduced by *FOS* application in both *Sh* and *Sa*. In a pot experiment to evaluate the efficacy of *FOS* among sorghum families using roots and soil samples, *FOS* was abundantly detected on sorghum root and soil samples with variable colony forming unit (CFU) among the tested sorghum genotypes.

Overall, these study determined constraints affecting sorghum production, farmers' preference quality traits, and their perceptions on *Striga* management. It also identified the, gene actions controlling *Striga* resistance and inheritance. This is important for the implementation of ISM for the improvement of sorghum productivity. It also identified a number of useful parents and crosses for effective sorghum breeding to control *Striga* in the semi-arid areas of Tanzania. Cultivar development targeting reduced MGD, reduced *Striga* counts and famers' traits of preferences in the selected populations, combined with compatibility with *FOS* could provide the basis available for integrated *Striga* management programme.

Declaration

I, Emmanuel Justine Mrema, declare that

1. The research reported in this thesis, except where otherwise indicated is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons‟ data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

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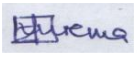
……  ……..

Emmanuel Justine Mrema

As the candidate‟s supervisors, we agree to the submission of this thesis:

……

Prof. Shimelis Hussein (Supervisor)

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Prof. Mark Laing (Co-Supervisor)

Acknowledgements

The achievements of this work were possible through the help rendered so kindly by many institutions and people that I believe deserve earnest acknowledgment. Hence, I owe a great gratitude to all those who helped me generously in one way or another for the accomplishment of this thesis.

I would like to extend my sincere thanks and gratitude to my main supervisor, Professor Shimelis Hussein for giving me genuine and regular advice to this study and thesis write up from its inception to culmination. I am also grateful for his gracious approach throughout my study.

I am thankful to my co-supervisor Professors Mark Laing. He has played crucial role on the mass production of the biocontrol agent and for his thoughtful guidance and creative suggestions during the research execution and evaluation of manuscripts. Dr. Learnmore Mwadzingeni is acknowledged for providing insights and comments to some of the draft chapters.

I would like to express my gratitude to my in country co-supervisor Dr. Tulole Lugendo Bucheyeki for his wholehearted assistance to facilitate the research activities whenever required.

My study would not be fruitful without the financial support from the Alliance for a Green Revolution in Africa (AGRA) through scholarship support. All members of the academic and administrative staff at the African Centre for Crop Improvement (ACCI) in general and Mrs. Rowelda Donnelly in particular deserve many thanks for administrative support during my study.

Thanks are due to the Permanent Secretary, Ministry of Agriculture, Livestock and Fisheries, and the Government of Tanzania, for offering me the study leave. It is my pleasure to say thank you to Mr. Deusdedit Byamungu, the zonal director of Agriculture Research Institute Tumbi (ARI-Tumbi) for providing me leave of absence and for access to facilities during the study. Thanks are extended to the staff of ARI-Tumbi for their support and follow up during the field experiments.

I would like to thank the International Crops Research Institute for the Semi-Arid Tropics/India (ICRISAT), Institute of Biodiversity Conservation (IBC) of Ethiopia, Sirinka Agricultural

Research Centre/Ethiopia (SARC), African Centre for Crop Improvement (ACCI); Pannar Seed Company (PSC) and Tanzania National Gene Bank for providing the required germplasm. The African Seed Health Centre Laboratory, at the Crop Science Department of Sokoine University of Agriculture/ Tanzania is sincerely acknowledged for allowing the maximum germination distance study.

My deepest gratitude goes to my family, especially to my wife, Mrs. Happyness Mrema, my sons, Justine and Samuel, my daughter Wittiness and all members of the family. Thank you for your unconditional love and endless support, not only during the course of completing this thesis, but throughout the years. Most of all, I offer my gratitude to God, with Him everything is possible. May his name be glorified.

Dedication

This thesis work is humbly dedicated to my late father Justine Issack Mrema and my mother Echikael Mrema, for their overall support during my studies.

Table of Contents

Abbreviations

aa	Additive x additive gene interaction
ACCI	African Centre for Crop Improvement
ad	Additive x dominance gene interaction
AGRA	Alliance for a Green Revolution in Africa
ANOVA	Analysis of variance
BCP_1	Backcross to parent one
BCP_2	Backcross to parent two
BM	Biomass
CFU	Colony forming unit
CV	Coefficient of variation
dd	Dominance x dominance gene interaction
DF	Degrees of freedom
DFL	Days to flowering
Env	Environment
F_1	Filial generation one
F_2	Filial generation two
FOS	*Fusarium oxysporum* f.sp. *strigae*
GCA	General combining ability
GCA_f	General combining ability of females
GCA_m	General combining ability of males
GMA	Generation mean analysis
H^2	Broad sense heritability
H^2_F	Heritability due to female effects
H^2_M	Heritability due to male effects
HSW	Hundred seed weight
IBC/Ethiopia	Institute of Biodiversity Conservation/Ethiopia
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics/India
ISM	Integrated *Striga* management
LHF	Low haustorium initiation factor
LSD	Least significance difference
MGD	Maximum germination distance
NCD II	North Carolina Design II
P_1	Parent one
P_2	Parent two

PDA	Potato dextrose agar
PH	Plant height at 50% flowering
PPA	Peptone-pentachloronitrobenzene agar
PRA	Participatory rural appraisal
PSC	Pannar Seed Company
PW	Panicle weight
R^2	Coefficient of determination
Sa	*Striga asiatica*
SARC/Ethiopia	Sirinka Agricultural Research Centre/Ethiopia
SCA	Specific combining ability
Sh	*Striga hermonthica*
SN	Number of *Striga* plants
SNA	Special nutrient agar
SSA	Sub-Saharan Africa
$SSGCA_F$ %	Percentage sum square of the general combining ability of females
$SSGCA_m$ %	Percentage sum square of the general combining ability of males
SSSCA %	Percentage sum square of the specific combining ability
SV	*Striga* vigour
SYP	Seed yield per plant
VAM	Vesicular arbuscular mycorrhizal
δ^2_A	Additive variance
δ^2_{AF}	Additive variance contributed by females
δ^2_{AM}	Additive variance contributed by males
δ^2_D	Dominance variance
δ^2_{EW}	Environmental variance
δ^2_{GCA}	Additive variance of females and males
δ^2_{GCAF}	Additive variance of females
δ^2_{GCAM}	Additive variance of males
δ^2_{SCA}	Additive variance for female by male interaction
δ^2_T	Total variance

Introduction to Thesis

Importance of sorghum

Sorghum (*Sorghum bicolor* [L.] Moench, 2n=2x=20) is a multi-purpose cereal crop serving as a source of food, feed, bioenergy, vegetable oil, waxes, dyes and alcohol (Doggett, 1988). It is well adapted to arid and semi-arid environments under poor soil fertility and high temperature conditions, where other cereal crops, such as maize and wheat, fail to produce grain (Blum, 2004). Worldwide, sorghum is cultivated on an area of 42 million ha with a total production of 61.5 million tonnes of grain, of which 80% is produced in Africa and Asia. In East Africa, an area of 5 million ha is devoted to sorghum cultivation, with a mean productivity of 1.3 tonnes ha^{-1}. In Tanzania, an area of 6.2 million ha is used for cereal crop production, of which 0.9 million ha (15%) is under sorghum cultivation (FAOSTAT, 2013). However, mean grain yields of less than 1.0 tonnes ha^{-1} have been reported for Tanzania which is considerably below the mean yield of 1.3 tonnes ha^{-1} reported for east Africa as a whole (FAOSTAT, 2013).

Sorghum production constraints

The yield potential of sorghum is constrained by both abiotic and biotic stresses (Wortmann et al., 2006). Infestation by *Striga*, storage pests, damage by birds, a lack of access to improved varieties, and a lack of access to production inputs such as fertilizers, insecticides, fungicides and herbicides, and recurrent drought have been among the major identified production constraints affecting sorghum in the semi-arid areas of Tanzania. However, *Striga* infestation is the most important problem in these regions (Mrema et al., 2017). Therefore, this study focused on developing an integrated *Striga* management option in order to enhance sorghum productivity in Tanzania.

Striga infestation

Striga species belong to the family Orobanchaceae. Forty one species have been reported, and, 11 of these causes significant yield losses in cereal crops (Mohamed et al., 2007). *Striga hermonthica* (Del.) Benth and *S. asiatica* (L.) Kuntze have been reported to infest nearly one million ha of sorghum, and to cause severe yield losses of 20 to 80% worldwide (Hearne, 2009). Yield losses reported from around the world tend to be lower than the losses of 30 to 90% reported in Tanzania (Riches, 2003). The most severe infestations have been found along Lake Victoria in the Mwanza, Mara, Shinyanga, and Simiyu regions, in the western zone

including the Igunga in Tabora region, and in the central parts of Tanzania, such as in Dodoma and Singida.

Striga infestation is intensified by poor soil fertility, use of a single management method, cereal mono-cropping, and the growing of susceptible varieties (Parker, 1991). Furthermore, *Striga* produces large quantities of small seeds estimated at 50,000 per *Striga* plant (USDA, 2011) that remain viable in the soil up to 20 years (Parker, 1991).

Control options

Several control methods have been recommended to reduce *Striga* infestations. These include the use of resistant varieties, biological agents, cultural practices, application of fertilizers and chemical control (Hearne, 2009). These methods can be effective in retarding germination and growth of juvenile *Striga* plants and improving host growth and development (Redda and Verkleij, 2004). However, the costs of implementing some of these measures are high, and this hinders their adoption by smallholder farmers. Furthermore, no single option on its own has proven to be effective and durable for sorghum production for resource poor farmers. The best options for successful *Striga* control lies in an integrated *Striga* management (ISM) approach (Hearne, 2009). That could include the use of resistant sorghum genotypes and a biological control agent (Rebeka et al., 2013; Mrema et al., 2017), among others.

Rationale for integrated *Striga* management (ISM)

Host resistance is potentially the acceptable control measure for resource-poor farmers (Rich et al., 2004). The method is affordable, and is more environmentally friendly than chemical control practices (Marley et al., 2004). However, reliance on host resistance alone is not ideal because complete resistance against *Striga* has not yet been attained through breeding (Gurney et al., 2002). Most of the improved sorghum varieties that have been developed so far have not been widely adopted by farmers, usually because they lack critical quality traits that farmers' insist on, such as tall stems (Adugna, 2007; Mrema et al., 2017). One of the problems is that, sorghum landraces that posses the farmer preferred traits have not been used as a primary source of breeding material. In order to develop a viable ISM program, plant breeder will need to use information on farmers' perceptions of sorghum production constraints, their *Striga* control practices, the quality traits of their preference and the variability present among the existing sorghum genotypes.

Biological control using *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, is potentially an important component of ISM. The effectiveness of the pathogenic isolates of *FOS* in controlling *Striga* has been reported when the method is integrated with host resistance (Mrema et al., 2017). Sorghum seeds treated with *FOS* were reported to yield better and to have reduced *Striga* numbers and parasitic vigour relative to untreated sorghum plants (Rebeka, 2007). However, when applied individually these control options were not effective. The combined use of resistant varieties with the application of *FOS* was reported to be effective in controlling *Striga* (Mrema et al., 2017). Thus several options need to be integrated in order to achieve sustained and successful *Striga* control.

An evaluation of potential ISM practices would involve the use of sorghum genotypes that are compatible with *FOS*, *Striga* resistant and with farmers preferred traits. Subsequently the sorghum genotypes compatible to *FOS* and with farmers' traits of preference would be used as parents to be crossed with varieties with *Striga* resistance to generate progeny to be used in the ISM program. However, information related to the general and specific combining abilities and the mode of gene action responsible for controlling *Striga* resistance and yield of the selected parental lines is needed for this study. Therefore, there was need to study the combining ability, generation mean analysis (GMA) and maximum germination distances (MGD) after systematic crossing of selected parents using different mating designs, using family evaluations with and without *FOS* application, in several *Striga* infested environments. This would enable selection of promising parents and families for further breeding.

Research aim and objectives

The overall aim

The overall aim of this study was to integrate host resistance to *Striga* spp. and the use of a biological control agent, *Fusarium oxysporum* f.sp. *strigae* (*FOS*), for the control of both *Sh* and *Sa* on sorghum in the semi-arid parts of Tanzania.

The specific objectives

The specific objectives of this study were:

1. To investigate the constraints affecting sorghum production and farmers' approaches to *Striga* management in the semi-arid regions of Tanzania.

2. To screen and select farmers-preferred sorghum genotypes for *Sh* and *Sa* resistance and *FOS* compatibility, to be used as parents for resistance breeding under Tanzanian conditions.
3. To identify promising sorghum parents and crosses with *FOS*-compatibility and *Striga* resistance displaying high combining ability for grain yield and yield components for Integrated *Striga* Management (ISM).
4. To determine the gene action and inheritance of *Striga* resistance using genetically diverse populations of sorghum, including *FOS* treatment.
5. To determine the gene action controlling the maximum germination distance in sorghum genotypes.

Research hypotheses

1. It also identified Sorghum farmers in Tanzania have various perceptions of the challenges that they face, have varied quality preferences, and a range of ideals towards problem resolution and adoption of new technologies for *Striga* control in sorghum crop.
2. Sorghum genotypes exist that have resistance to *Striga* infestations, and are compatible with a biocontrol agent, *FOS*.
3. Crosses between selected sorghum genotypes will exhibit different levels of combining ability effects for *Striga* resistance.
4. Crosses between selected sorghum genotypes will differ in gene action for the control of *Striga* resistance
5. Crosses between selected sorghum genotypes will differ in gene action controlling maximum germination distances of *Striga* seed

Outline of thesis

This thesis consists of six distinct chapters in accordance with a number of activities related to the above objectives (Table 0.1). Chapters 2-6 are written in the form of discrete research chapters, each following the format of a stand-alone research paper. This is the dominant thesis format adopted by the University of KwaZulu-Natal. As such, there is some unavoidable repetition of references and some introductory information between chapters.

The referencing system used in the chapters of this thesis is based on the Crop Science referencing system. The exception to this are Chapters 2, 3, 5, and 6 which have been already published in the journal of “International Journal of Pest Management”, “Acta Agriculturae

Scandinavica, Section B - Soil & Plant Science", "Euphytica" and "Journal of Integrative Agriculture", respectively.

Table 0.1. Outline of thesis

Chapter	Title
-	Introduction to thesis
1	A review of the literature
2	Farmers' perceptions of sorghum production constraints and *Striga* control practices in semi-arid areas of Tanzania
3	Screening of sorghum genotypes for resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*
4	Combining ability of yield and yield components among *FOS*-compatible and *Striga*-resistant sorghum genotypes
5	Gene action controlling *Striga* resistance among sorghum genotypes
6	Genetic analysis of maximum germination distance of *Striga hermonthica* and *S. asiatica* in sorghum with *FOS*

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CHAPTER ONE

A Review of the Literature

1.1 Abstract

In the semi-arid agro-ecologies of Tanzania potential yield of sorghum [*Sorghum bicolor* (L.) Moench] is curtailed due to several biotic and abiotic stresses and socio-economic constraints. *Striga* is one of the major biotic constraints that cause yield losses of 30 to 90% in Tanzania. *Striga* species, *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*), are widely distributed in the country severely affecting yields of sorghum, millet, maize and rice. Integrated *Striga* management (ISM), which involves the use of sorghum genotypes resistant to *Striga* and compatible to *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, has been advocated as an option to control *Striga*. This strategy is yet to be explored in Tanzania and most sub-Saharan Africa countries where sorghum is the staple crop of millions of households. The objective of this chapter was to provide a review of the literature on the major constraints affecting sorghum production and productivity, management of *Striga* in sorghum production, breeding sorghum for *Striga* resistance including a search for *Striga* resistant sorghum genotypes with compatibility to *FOS*, combining ability analysis, generation mean analysis, farmers' preferences of sorghum varieties and participatory variety development. The literature presented supports the thesis research work and will provide background information for breeders emphasising the development of sorghum cultivars with *Striga* resistance, *FOS* compatibility and the inclusion of traits of farmers' preferences.

Keywords: *Striga* resistance, *Fusarium oxysporum* f.sp. *strigae*, integrated *Striga* management, sorghum, gene action

1.2 Introduction

Sorghum (*Sorghum bicolor* [L.] Moench, 2n=2x=20) is a multi-purpose cereal crop serving as a source of food, feed, bioenergy, vegetable oil, waxes, dyes and alcohol (Doggett, 1988). Sorghum thrives under harsh growing conditions including those of arid and semi-arid regions, low soil fertility and high temperature conditions where maize and wheat fail to grow (Blum, 2004; Rwebugisa, 2008). Sorghum is believed to have originated in the drier parts of eastern Africa, mainly in Ethiopia and Sudan (Doggett, 1988). In terms of total production and consumption, sorghum is ranked as the fifth leading cereal crop in the world after wheat (*Triticum aestivum* L), rice (*Oryza sativum* L), maize (*Zea mays* L) and barley (*Hordeum vulgae*) (Murty et al., 1994). In Tanzania sorghum is a key crop supporting millions of smallholder farmers, and is widely grown in the semi-arid areas including the Dodoma, Singida, Tabora, Shinyanga and Mwanza regions (Msambichaka, 1999).

Globally an estimated area of 42 million ha of agricultural land is devoted to sorghum production. This provides a total production of 61.5 million tonnes of grain annually, of which 80% is produced in Africa and Asia (FAOSTAT, 2014). In east Africa, an area of 5 million ha is allocated to sorghum cultivation with an average productivity of 1.3 t ha^{-1} (FAOSTAT, 2013). In Tanzania alone, an area of 6.2 million ha is being used annually for cereal crop production of which 0.9 million ha (15%) is under sorghum cultivation (FAOSTAT 2013). However, in the country a mean grain yield of 1.0 t ha^{-1} is achieved, which is far below the attainable yields of the crop, such as is achieved in other east African countries (FAOSTAT, 2014).

1.3 Constraints to sorghum production and productivity

Sorghum production is affected by abiotic stresses (e.g. poor soil fertility, drought) as well as biotic stresses [e.g. infestations by *Striga*, stem borers, and shoot fly (*Atherigona soccata*)] (Wortmann et al., 2006). Mrema et al. (2017) reported *Striga* infestation, recurrent drought, storage pests, damage by birds, a lack of access to improved varieties, and a lack of access to production inputs such as fertilizers, insecticides, fungicides and herbicides to be among the major production constrains of sorghum in the semi-arid areas of Tanzania.

Among abiotic factors, poor soil fertility and drought are the main constraints limiting sorghum production and productivity (Roose, 1994). Most sorghum fields are poor in soil nutrition, due to soil erosion, mono-cropping, a lack of fertilizer application, a total removal of the crop's biomass by farmers for diverse uses, overgrazing, and increased population pressure, among

others. In sub-Saharan Africa, frequent torrential rains cause movement of soil nutrients and fertile soils from slopes and hillsides to valley bottoms, where crop cultivation is often impossible. This has led to decreased cation exchange capacity and weakened soil physical structure, leading to inhanced soil infertility (Roose, 1994). An estimated 30% of global crop productivity is lost due to soil infertility (Cerdà, 2000). In Tanzania, most agricultural lands have been reported to have of low to moderate soil fertility (Lamboll et al., 2001). Interestingly, infertile soils where sorghum, maize and rice are cultivated are also heavily infested by *Striga* spp [*Striga hermonthica* (Del.) Benth (*Sh*) and *S. asiatica* (L.) Kuntze (*Sa*)] (Johnson et al., 1997). Therefore, improved farming technologies that enhance soil fertility are critically required to boost sorghum yields and to minimize damage caused by *Striga*. Yield improvement in sorghum fields infested by *Striga* can be realised through application of recommended levels of inorganic fertilizers based on targeted soil tests. However, inorganic fertilizers are not accessible or affordable for most smallholder farmers, suggesting the need to develop innovative solutions to boost sorghum productivity under smallholder farming systems.

Drought or limited water availability is an important abiotic stress factor affecting sorghum production and productivity. The frequency of drought occurrence and associated yield losses are pronounced in the semi-arid agro-ecologies. Sorghum is a relatively drought tolerant crop providing good yields under high temperature conditions ranging from 26 to 34°C (Maiti, 1996; Taylor, 2003). However, extreme drought and heat stress can reduce both vegetative and reproductive traits in sorghum. A yield loss of 7.8 to 8.4% has been reported due to a rise in temperature by 1°C above 34°C (Hatfield et al., 2008).

In the semi-arid regions of Tanzania drought was the second most important yield limiting factor of sorghum after *Striga* infestation reported by 70%–75% of the respondent farmers (Mrema et al., 2016). Mixed farming systems, avoiding use of newly introduced sorghum varieties, and abandoning some landraces, particularly the late-maturing ones that fail to produce yield under reduced rainfall, were among the mitigation strategies adopted by smallholder farmers in Tanzania.

The next major constraints to sorghum production are biotic factors, notably *Striga* infestation, storage pests, birds, lack of improved varieties with drought tolerance, and diseases. Among these stresses*, Striga* has been reported to be the main constraint affecting sorghum yields in the semi-arid regions of Tanzania (Riches, 2003; Mrema et al., 2016). Yield losses of 90 % have been reported due to infestation by *Striga* species [*S. hermonthica* and *S. asiatica*] (Riches 2003). The two weed species (Figure 1.1) are persistently present in cereal fields in

the Tabora, Mwanza and Shinyanga regions as reported by Riches (2003) and Mrema et al. (2016). *Striga* species belong to the family Orobanchaceae, damaging wild grasses and cereal crops such as rice (*Oryza glaberrima* Steudel and *O. sativa* L.), pearl millet (*Pennisetum glaucum* L. R. Br. or 16 *P*. *americanum* [L.] K. Schum), maize (*Zea mays* L.), and sorghum (*S.bicolor* [L.] Moench) (Johnson et al., 1997).

Figure 1.1. The top two photos: sorghum (left) and maize (right) fields infested by *Striga hermonthica* at Mwanagwa village farm of Misungwi District, Mwanza Region in the Lake Victoria Zone of Tanzania. The bottom pictures show sorghum fields infested mostly by *Striga asiatica* at Mbutu village farm of Igunga District, Tabora Region in the Western Zone of Tanzania.

Striga species are found in most sorghum and maize fields in semi-arid regions of Tanzania. *Striga* spp spread effieciently owing to their ability to produce many seeds (10,000 – 500,000 seeds per plant). Moreover, their seeds are microscopic and they remain viable in dry soil for 15 to 20 years (Koichi et al., 2010). *Striga* seeds can easily disperse by wind, water, cattle, man and farm machinery (Enserink, 1995). *Striga* seed germination may happen only when

there is a stimulant produced by the host plant. Also, some non-host species have been reported to produce stimulus for germination of *Striga* seed (Matusova et al., 2005). For instance, strigol, exuded by roots of cotton a non-host plant, induced germination of *Striga* seeds (Garcia-Garrido et al., 2009). Sorgolactone and alectrol the analogs of strigol which are produced from sorghum and cowpea roots, respectively, reportedly induced *Striga* germination (Matusova et al., 2005). Ethylene initiates *Striga* seed germination and can be used as *Striga* management technology where selective pre- or post-emergent herbicides cannot be applied to destroy the weed. *Striga* seedlings can die back owing to a lack of its host crops (Mourik et al., 2011). *Striga* seed germinates after passing a period of primary dormancy followed by seed preconditioning under humid condition (30 to 50% relative humidity) and warm temperatures (25-35°C) for two weeks (Parker and Riches, 1993). Also, secondary metabolites (xenognosins) released as root exudates from their hosts, is one of the requirements for *Striga* seed germination (Yoder, 2001). These metabolites are reported to direct the radicle of the *Striga* seedling towards the host root (Williams, 1961a, b).

The amount of exudate produced by sorghum genotypes can be studied in agar-gel assays as developed by Hess et al. (1992). In their studies, preconditioned *Striga* seeds were dispersed in agar in petri dish, followed by inserting a sterilised sorghum seed at a centre of each dish. After 5 days the maximum germination distance (MGD) between the sorghum seed and a distantly germinated *Striga* were measured. Entries with a germination distance below 10 mm were classified as *Striga*-resistant. This technique is useful in screening sorghum genotypes for *Striga* resistance.

Striga is an obligate parasite that requires host synthesized water and nutrients (Mohamed et al., 2001). After *Striga* seed germination is initiated by the host plant exudates, the radicle of the parasite seedling makes contact with the host root and enlarges to form a haustorium. This structure provides attachment of the parasite to the host. Using the haustorium, *Striga* penetrates the host and establish an intimate contact with the host, from which to derive nutrients and metabolites (Patrick and Ejeta, 2007). Failure of haustorium formation and or its development leads to the death of the parasite. The parasitic mode of life between *Striga* and sorghum enables the *Striga* to extract water, mineral nutrients and synthesized food from the vascular system of sorghum (Press and Stewart, 1987). The rate of absorption of nutrients in *Striga* is facilitated by its high transpiration rate that is greater than that of the host. This process speeds up the flow of food, water and nutrients from the host (Stewart et al., 1991). Furthermore, *Striga* is reported to produce a pathological effect through toxin production that retards growth and development of sorghum (Stewart and Press, 1990). Production of the toxin is associated with decreased cytokinin and gibberellins concentrations with a substantial

increase in abscisic acid in damaged plant tissues (Drennan and El Hiweris, 1979). Fischer et al. (1986) found that the rate of ribulose biphosphate carboxylation is reduced when the rate of abscisic acid in the xylem tissue is high.

The ultimate outcome of *Striga* invasion in sorghum fields is decrease in growth rate, yellowing and wilting, failure of panicle formation and yield loss. Apart from the parasite competing with the host plant for natural resources such as water and nutrients, it also exerts its allelopathic effect to the host plant. These limit the ability of susceptible sorghum genotypes to express their genetic potential in yield performance. Understanding of the conditions required for *Striga* seed dispersal, germination, infection parasitism, and interaction with their hosts will allow plant breeders to develop varieties for the semi-arid areas of Tanzania. Knowledge on the association of the parasite with the host and non-host species will also help in designing cropping patterns and crop choices.

1.4 Management of *Striga* in sorghum production

1.4.1 Cultural practices

Several cultural methods have been recommended to manage *Striga* in sorghum fields. The techniques have been reported to reduce the *Striga* seed bank in the soil and at the same time, improve soil fertility (Reda and Verkleij, 2007). Cultural practices facilitate the sorghum growth rate, and at the same time retards parasite seed germination and seedling development (Reda and Verkleij, 2007). Some of these practices include crop rotation (Oswald and Ransom, 2001); mixed cropping (Udom et al., 2007); transplanting (Oswald et al., 2001); water management (Reda and Verkleij, 2007), fertilization (Jamil et al., 2011) and weeding (Ransom 2000). Mrema et al. (2016) reported that early planting following the main rains, and the use of early maturing sorghum varieties, to be among farmers adopted practices for minimizing *Striga* in the semi-arid regions of Tanzania. Early planting using early maturing sorghum varieties was reported to escape heavy *Striga* infestation, which was reported to happen almost two months after planting (Mrema at al., 2017).

Regardless of the nominal effectiveness of the cultural methods in *Striga* management, the methods were poorly adopted by smallholder farmers. The methods were not accessible, nor were they understood by the majority of smallholder farmers, and their implementation cost was higher in resources, time and labour. The poor performance of introduced sorghum varieties for critical traits such as resistance to bird and storage pest attack were among the

reasons for the poor adoption of most previously released early maturing, sorghum varieties in the semi-arid regions of Tanzania (Mrema et al., 2016). Their susceptibility to drought stress and their need for fertilizer were other negative attributes reported by farmers. Proper application rates and timing of fertilizer applications have not been adopted by the majority of sorghum growers in Tanzania. Development of a viable integrated *Striga* management program aiming at minimizing *Striga* and improving sorghum yield will require an understanding of the potential and limitations of the currently available management approaches.

1.4.2 Chemical control

Several herbicides are reported to control *Striga* infestation in sorghum (Kanampiu et al., 2003). Among selective herbicides reported are 2,4-D and MCPA (2-methyl-4-chlorophenoxyacetic acid) (Ejeta et al., 1996). Many herbicides have a residual effect in the soil but they are not effective in managing the parasite prior to emergence (Kanampiu et al., 2003). Chemicals that allow *Striga* germination but subsequently kill the weed before attachment to the host would be extremely valuable for the control of *Striga.* Studies conducted in sorghum and maize has shown that treatment of sorghum seeds with 2, 4-D provides good control of *Striga* (Dembele et al., 2005). Development of transgenic herbicide resistant sorghum genotypes is an alternative approach (Kanampiu et al., 2003). Ndungu (2009) reported the effectiveness of sulfosulfuron herbicide seed coating applied to mutant sorghum lines for control of *Striga*. He reported that herbicide seed coating is a low cost treatment that is affordable for small-scale farmers, due to the requirement of only a small quantity of herbicide for seed dressing. However, this approach has not been adopted widely in the semi-arid regions of Tanzania.

The high price of herbicides, their limited availability, and the lack of technical knowledge on the use of agrochemicals for weed and pest management were identified as the main reasons for their limited use in sorghum production (Mrema et al., 2017). To improve sorghum yield under smallholder farmers conditions there is a need to develop a *Striga* management programme that is cheap enough for the farmers to adopt, and should involve technologies that they are willing to adopt. Among them is an integrated approach that involves the use of sorghum genotypes that are partially resistant to *Striga*, and at the same time, are compatible to *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, which has been advocated as an option to control *Striga* (Rebeka et al., 2013; Mrema et al., 2017).

1.4.3 Biological control

Biological agents are beneficial organisms that parasitize pest, pathogens or weeds (Templeton, 1982). Among the biological agents, microbes are host specific, highly aggressive, easly to mass produce and show maximum diversity (Ciotola et al., 2000). A biological agent has no residual effect in the soil or plant system, and is therefore more environmentally friendly than chemical control (Abbasher et al., 1998). *FOS* is an experimental biocontrol agent that has been reported to control *Striga* infestation in sorghum (Ciotola et al., 2000). It was reported to be effective in improving sorghum biomass and in controlling the parasite by 90% (Ciotola et al., 2000). Franke et al. (2006) reported an increase in sorghum yield of 50%, and reduction of *Striga* of 95% by using *Striga* resistant sorghum genotypes and seeds coated with *FOS*. *Striga* numbers can be significantly reduced by coating sorghum seeds with *FOS* (Rebeka et al., 2013; Mrema et al., 2017). These authors also reported a significant reduction in days to flowering and maturity for sorghum seed coated with *FOS* compared to their untreated controls. The use of *FOS* in *Striga* management in sorghum fields in Tanzania has not been reported previously, let alone implemented as a practical measure. There is no opportunity for integrated management of the parasite through host resistance and application of *FOS* to enhance production and productivity of sorghum and related cereals affected by *Striga.*

1.4.4 Host resistance

Striga management through the use of resistant cultivars has been reported in several crops including sorghum (Ejeta et al., 1992). Resistant cultivars were reported to reduce *Striga* emergence and subsequent *Striga* seed production. Also these genotypes supported fewer *Striga* plants and yielded better than susceptible counterparts under *Striga* infested fields (Doggett, 1988; Ejeta et al., 1992). Lower levels of production of germination stimulants, the presence of mechanical barriers, the inhibition of germ tube exoenzymes by root exudates, phytoalexin synthesis, *Striga* incompatibility, antibiosis, insensitivity to *Striga* toxins, and the avoidance of *Striga* infection through root growth habit are some of the reported *Striga* resistance mechanisms in sorghum (Ejeta et al., 1992; Ejeta and Butler, 1993; Berner et al., 1995; Wegmann1996; Mrema et al., 2017).

Hypersensitive reaction or necrotic tissue development, and phytoalexin production by sorghum plants are among the mechanisms for *Striga* resistance. Host tissues die at the point of attachment by the parasite, an event that limits the supply of water and nutrients to the parasite. A hypersensitive reaction like this is reported to be associated with the secretion of

phytoalexins that kills the parasite (Patrick et al., 2004). Genes for the hypersensitive response and for phytoalexin production have been reported in some sorghum genotypes (Mohamed, 2002). A wild sorghum genotype, P47121, has been reported to have a stronger hypersensitive response to *Striga* infestation than cultivated sorghum genotypes (Mohamed et al., 2003).

An incompatible response in some sorghum genotypes towards *Striga* infestation has been reported (Ejeta, 2007). Incompatible genotypes do not show any response towards *Striga* infestation at the time of attachment, is unable to infect the host tissue following initial host penetration (Grenier et al., 2001). This case, *Striga* plants are reported to die before the formation of the first leaf, or show sign of stunted growth, and do not survive beyond the early growth stages (Matusova et al., 2005).

Sorghum varieties differ in root morphology due to difference in the amount of lignin formation (Mati et al., 1984), layers of cellulose deposition (Oliver et al., 1991), and encapsulation (Labrousse et al., 2001). Fewer *Striga* haustora penetrate the tougher roots of resistant sorghum genotypes than susceptible cultivars with tender roots. Developing sorghum genotype with tougher root systems that act as a developmental barrier, in addition to other resistance mechanisms, can reduce *Striga* infestation. However, the ability of *Striga* to damage the host plant before emergence and development makes the development of mechanical management impractical (Ejeta, 2007).

The selection for a low haustorium initiation factor (LHF) present in some sorghum genotypes is one of the more effective methods reported in supressing *Striga* (Lynn and Chang, 1990). The presence of LHF (sorgolactones) has been reported from agar gel assay studies (Hess et al., 1992). Several wild and cultivated sorghum genotypes were verified to have gene mediated LHF. A recessive gene conditioning LHF has been reported in a wild sorghum accession, P47121, in which resistance was manifested before the parasite attachment (Mohamed et al., 2003). Haussmann et al. (2000) reported a set of genes controlling LHF. A single dominant gene was reported to control LHF by Mohamed (2002). Haustoria do not form when the sorghum root carries the LHF gene, blockading infection by the parasite (Ejeta, 2007). The LHF gene can be introgressed into high yielding and broadly-adapted sorghum cultivars (Ejeta et al. 1997). Therefore, exploring the mode of gene action and inheritance of candidate *Striga* resistance genes is imperative to develop promising sorghum genotypes with multiple resistance genes adapted in the semi-arid environments of Tanzania.

1.4.5 Integrated *Striga* management (ISM)

Striga management using a single control method is not very effective in sorghum production (Rebeka et al., 2013). A combination of several options can be more efficient and economical with better control of *Striga* (Tesso et al., 2007). The use of trap-cropping, fertilizer application and resistant genotypes are some of the effective tools in *Striga* management (Tesso, et al., 2007). Also, several *Fusarium* spp. and vesicular arbuscular mycorrhizal (VAM) fungi have been reported to kill *Striga* and to enhance biomass production of hosts when integrated with resistance genes (Franke et al., 2006). The integrated use of *Striga* resistant sorghum genotypes compatible to *FOS* was reported to reduce *Striga* numbers and at the same time, to improve grain yield (Rebeka et al., 2013). Therefore, ISM should be developed as an effective way of managing *Striga* under smallholder farming systems for popularisation and ultimate adoption. An ISM that combines the use of *Striga* resistant sorghum varieties compatible with *FOS* should be cost effective, environmentally friendly and easily be adopted by smallholder farmers (Joel, 2000; Hearne, 2009).

1.5 Breeding sorghum for *Striga* resistance

1.5.1 Search for sorghum genotypes with *Striga* resistance and compatibility with *FOS*

In sub-Saharan Africa (SSA) breeding for *Striga* resistance in sorghum started in 1953 in South Africa (Mohamed, 2002). This study identified several sorghum genotypes that were resistant to *S. asiatica* (Riches et al., 1987). Screening for *Striga* resistance was also conducted in 1970 at the Institute for Agricultural Research (IAR) in Samaru, Nigeria (Lagoke et al., 1991). In 1991, the International Crop Research Institute for the Semi-arid Tropics (ICRISAT) reported sorghum genotypes that were resistant to *S. hermonthica* in SSA (Obilana and Ramaiah, 1992). ICRISAT released some sorghum varieties with resistance to *S. asiatica* in Botswana, Tanzania and Zimbabwe (Mabasa, 1996). Doggett (1953) and Haussmann et al. (2000) reported several genotypes that were resistant to both *S. asiatica* and *S. hermonthica*.

Efforts in *Striga* resistance breeding were initiated in Tanzania in the East African Regional Sorghum Improvement Program, which started in 1958 (Obilana, 2004). From 1999 to 2003 some preliminary evaluation studies were conducted on the control of *Striga* infestation through integrating resistant sorghum genotypes and improving the fertility status of soils (Riches, 2000). Two introduced sorghum varieties, namely, ‘’Hakika’’ and ‘’Wahi’’ were

identified as expressing adequate levels of *Striga* resistance when grown in fertile soils (Riches, 2000). The present performance of these genotypes is not adequate, particularly in areas with poor soil fertility and high levels of *Striga* infestation. Macia, a widely grown, high yielding variety with excellent seed quality, is highly susceptible under farmers' field conditions and during screening trials (Mrema et al., 2016, 2017). Further studies are required in Tanzania to identify sorghum varieties with durable *Striga* resistance, expressed in low fertility soils, and which carry essential farmer preferred traits.

The need to develop sorghum varieties with a combination of durable *Striga* resistance and compatibility with *FOS* is crucial in areas of high *Striga* infestation. Some sorghum genotypes are compatible with *FOS* (Mrema et al., 2017). Coating seeds of *FOS* incompatible sorghum genotypes has no significant influence on *Striga* management or yield improvement (Rebeka et al., 2013). Conversely, treating seeds of *FOS* compatible sorghum genotypes result in good control of the parasite which wilts, and dies soon after the host penetrated (Grenier et al., 2001). Rebeka et al. (2013) reported several sorghum genotypes that were compatible to *FOS* among a diverse population of sorghum screened for *FOS* compatibility in Ethiopia. Presence of incompatible and compatible sorghum genotypes towards *FOS* has also been reported by Ejeta, (2007). However, there have been no prior reports of evaluation for *FOS* compatibility among cultivated sorghum genotypes in Tanzania.

1.5.2 Combining ability studies in sorghum

Integrated *Striga* management can involve the use of host resistance and *FOS*. This requires screening of sorghum genotypes for their combining ability for these two traits. The combining ability of parents is critical and determines their breeding value in cultivar development to enhance yield, and abiotic and biotic stress tolerance. General combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in conditioning economic traits (Stoskopf et al., 1993). GCA is reported to represent mainly the additive and additive x additive types of genetic variance (Chapman et al., 2000; Kenga et al., 2004), while SCA is mainly due to genes with dominance and/or epistatic effects. The North Carolina Design II (NCD II) is one of the commonly used genetic mating designs used to determine of the combining ability of genotypes for yield and yield-related traits, and pest and disease resistance. The technique helps to identify suitable parents and families from targeted crosses which can then be advanced in a breeding programme. It will also indicate optimal selection procedure to follow when breeding for *Striga* resistant sorghum genotypes.

1.5.3 Generation mean analysis

Knowledge on the mode of gene action controlling *Striga* resistance among sorghum genotypes assists in determining the breeding method and the selection procedure to follow during ISM. The mode of gene action and the selection procedure to follow during ISM is not yet known in Tanzania. Generation mean analysis (GMA) is a useful technique for estimating gene effects (Anderson and Kempthorne, 1954; Mather and Jinks, 1971). The method requires male and female parents (P_1 and P_2), F_1 progenies, F_2 segregants, and backcrosses to parent one generation (BCP_1) and parent two generation (BCP_2) (Hayman, 1958). The mean response of these generations allows estimation of genetic effects such as additive, dominance and epistatic components, or their interactions. The technique is mostly used when the parents are divergent, possessing complementary and favourable alleles. GMA has been widely used to study gene action controlling biotic or abiotic stress tolerance or resistance, and yield and yield related traits in sorghum (Gamble, 1962), maize (Badu-Apraku et al., 2013) and rice (Gurney et al., 2006).

1.5.4 Farmers' preferences and participatory variety development

Development of sorghum varieties with traits of farmer' preferences require involvement of farmers at all breeding stages. Involvement of farmers' in a breeding program should allow breeders to identify the constraints affecting sorghum production, traits preferences, and strategies for effective *Striga* management in the major sorghum production of the semi-arid regions of Tanzania. Understanding of the current farming systems, including the prevailing farming practices, farmer constraints, and the overall socio-economic aspects is needed as a basis for developing a strategy for managing the parasite. Successful development, release and adoption of new plant varieties are dependent on the quality of engagement with farmers' and stakeholders.

Participatory rural appraisal (PRA) is a set of multidisciplinary research techniques used to identify farmers' perceived production constraints, preferred crop varieties, and required quality traits as a basis for deployment of production packages and crop varieties with a high potential for adoption by a farmers concerned. The techniques enable plant breeders to understand farmers' knowledge, experience, and needs, and the crop constraints, and the preferred traits (Chambers, 1992). Over many years, sorghum varieties released in Africa have been poorly adopted by smallholder farmers because they lacked quality traits that farmers demand from

a successful variety (Ceccarelli et al., 2001; Mrema et al., 2016). To improve the level of adoption of newly released sorghum varieties, and to enhance the productivity of sorghum in Tanzania, it is essential to investigate farmers' production constraints, and the traits of critical preference, before variety development is initiated.

1.6 Conclusions

Sorghum is an important multipurpose crop in the semi-arid parts of SSA where other cereal crops, such as maize, cannot perform due to parasitic weeds, and adverse environmental conditions, especially drought and heat stress. The yield of sorghum in SSA is low due to biotic and abiotic factors, including *Striga*. Several cultural practices and chemical control measures have been recommended by national and international agencies for the control of *Striga*. However, these have been poorly adopted by smallholder farmers due to the unavailability and unaffordability of herbicides, delayed hand weeding, lack of varieties with both *Striga* resistance and farmer preferred traits, land scarcity that prevents crop rotation and fallowing, and intercropping of crop species with similar growth requirements. Most of the previously bred and released sorghum varieties have lacked key traits of farmers' preference. Consequently, they have not been adopted. Diverse local sorghum germplasm is already available in Tanzania, which could be screened for their *Striga* resistance and compatibility with *FOS*.

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CHAPTER TWO

Farmers' perceptions of sorghum production constraints and *Striga* control practices in semi-arid areas of Tanzania

This chapter has been already published by:

Emmanuel Mrema, Hussein Shimelis, Mark Laing and Tulole Bucheyeki (2017)

Farmers' perceptions of sorghum production constraints and *Striga* control practices in semi-arid areas of Tanzania, International Journal of Pest Management (2017), 63 (2): 146-156, DOI:10.1080/09670874.2016.1238115

CHAPTER TWO

Farmers' perceptions of sorghum production constraints and *Striga* control practices in semi-arid areas of Tanzania

2.1 Abstract

Sorghum [*Sorghum bicolor* (L.) Moench] is an important food, feed, and bioenergy crop widely grown in arid and semi-arid parts of sub-Saharan Africa, including Tanzania. In this region sorghum productivity is low owing to biotic and abiotic stresses, as well as socio-economic constraints. The objectives of this study were to investigate constraints affecting sorghum production and farmers' approaches of *Striga* management in the semi-arid regions of Tanzania. The study involved three selected districts across six villages. Focus group discussions based on a semi-structured questionnaire and observations following transect walks were used for data collection. About 65% of the farmers grew sorghum landraces and had not adopted newly released varieties. Only 35, 15, and 10% of the farmers from Igunga, Kishapu, and Meatu Districts, respectively, reported growing newly released varieties. The major constraints affecting sorghum production in the study areas included *Striga* infestation, drought, storage pests, damage by birds, a lack of access to improved varieties, and a lack of access to production inputs, such as fertilizers, insecticides, fungicides and herbicides. Hand weeding, crop rotation, fallowing, intercropping, and organic manure application were the most common practices of farmers for reducing S*triga* infestations, but most farmers (79.7%) had little knowledge of the best recommended *Striga* management practices. About 65% of the farmers did not use fertilizers and herbicides for soil fertility improvement and weed management, respectively, creating favourable conditions for *Striga* infestation, and for severe yield losses in sorghum. A systematic breeding program aiming at improving sorghum varieties for *Striga* resistance, including farmers' preferred traits, should be designed and implemented to increase the adoption of these new varieties by the farmers.

Key words: agro-ecology; pest control; survey, preferences; resistant varieties

2.2 Introduction

Sorghum [*Sorghum bicolor* (L.) Moench, 2n=2x=20] is the fifth important cereal crop after wheat, rice, maize, and barley worldwide (FAOSTAT 2014). This crop is well adapted in arid and semi-arid environments under poor soil fertility and high temperature conditions, where other cereal crops, such as maize and wheat, fail to produce grain (Blum 2004). Globally, sorghum is grown for food, feed, and bioenergy on an area of 42 million ha, with a total production of 61.5 million tonnes of grain, of which 80% is produced in Africa and Asia. In East Africa, an area of 5 million ha is devoted to sorghum cultivation, with a mean productivity of 1.3 tonnes ha^{-1}. In Tanzania, sorghum is grown in almost all the semi-arid areas by subsistence farmers for food, feed, and beer. An area of 6.2 million ha is used for cereal crop production, of which 0.9 million ha (15%) is under sorghum cultivation (FAOSTAT 2013). However, low grain yield of less than 1.0 tonnes ha^{-1} has been reported, which is considerably below the mean yield of 1.3 tonnes ha^{-1} reported in east Africa (FAOSTAT 2013).

The low yields of sorghum in Tanzania have been attributed to both abiotic stresses (e.g. poor soil fertility, drought) as well as biotic stresses [e.g. *Striga* infestation, stem borers, and shoot fly (*Atherigona soccata*)] (Wortmann et al., 2006). Among the biotic stresses*, Striga* [*Striga hermonthica* (Del.) Benth *and S. asiatica* (L.) Kuntze] often causes severe yield losses (Riches 2003). *Striga* spp*.* are parasitic on the host plant (Press et al., 1996) and can infest a wide range of crops, including rice (*Oryza glaberrima* Steudel and *O. sativa* L.), pearl millet (*Pennisetum glaucum* L.), and maize (*Zea mays* L.) (Krittika & Adam 2008). There are 41 *Striga* species belonging to the family Orobanchaceae, and of these, 11 are documented to cause significant yield losses in tropical cereals (Mohamed et al., 2007). Ejeta (2007) estimated that *Striga* affected 100 million ha in cereal fields in Africa. In Tanzania, *Striga* infestation has been reported in most parts of the country. The most severe infestations are found along Lake Victoria in the Mwanza, Mara, Shinyanga, and Simiyu regions, in the western zone, including Igunga Tabora region, and in the central parts of Tanzania, such as Dodoma and Singida. These are semi-arid parts of Tanzania, where sorghum cultivation remains the main farming activity. In these areas, sorghum and maize fields are severely infested by both *Striga* species (Riches 2003). Globally, nearly one million ha of sorghum fields has been reported to be infested with *Striga,* resulting in yield losses ranging from 20 to 80% (Hearne 2009). *Striga* infestation is exacerbated by poor soil fertility, use of a single management method, cereal mono-cropping, and growing susceptible varieties (Parker 1991). *Striga* plants produce large quantities of small seeds that remain viable in the soil up to 20 years. A single plant can produce up to 500,000 seeds, which mature at different times (Koichi et al., 2010).

In the semi-arid areas of Tanzania, yield losses of sorghum have been estimated to be between 30% and 90% due to *Striga* infestation (Riches 2003). Doggett (1953) reported 70% to 100% yield losses in sorghum due to *Striga* infestation. The magnitude of yield losses depends on the extent of infestation, the prevailing climatic conditions, and the control measures implemented (Tesso et al., 2007). Understanding the biological and metabolic relations of the host and parasite may provide strategies for integrated control measures of *Striga* spp. (Ejeta, 2007). However, managing *Striga* spp. is difficult for smallholder farmers because they have limited access to production inputs.

Several control practices have been recommended for reducing *Striga* infestation. These include the use of resistant varieties, cultural practices, and chemical control methods (Hearne 2009). Cultural practices, such as the cultivation of different crops in the same piece of land in successive years, application of fertilizers, soil moisture management, and manual weeding, help to reduce *Striga* seed bank (Reda & Verkleij 2004). These strategies improve the soil structure and fertility, promote growth and development of the host plant, and retard growth and development of juvenile *Striga* plants (Reda & Verkleij 2004). However, the costs of implementing these measures are high and this fact hinders adoption by smallholder farmers. Some herbicides, such as 2,4-D, have been reported to be effective in reducing the buildup of *Striga* (Ejeta et al., 1996), while other herbicides were found less effective in controlling the effect of the parasite after emergence (Carsky et al., 1994). Furthermore, the cost of herbicides and spray units make this approach unaffordable for most smallholder farmers. An approach to the integrated management of *Striga* involves a combination of farmers' knowledge, a bio-control agent, and the use of resistant sorghum varieties. This is a relatively cheap option for smallholder farmers in the semi-arid regions of Tanzania.

Little information exists on production constraints of sorghum, traits preferences, and strategies for effective *Striga* management in the major sorghum production regions of the semi-arid Tanzania. A research strategy for improving sorghum productivity requires detailed information regarding sorghum farming systems, including the prevailing farming practices, farmers' constraints, and the overall socio-economic aspects. In turn, this strategy requires documenting current circumstances and constraints through farmers' participatory methods across the farming systems. A sorghum improvement program should focus on the needs of smallholder farmers and their value chains to satisfy their demands, and to ensure the successful release and adoption of newly bred cultivars and production technologies, to deliver on the goal of securing production and improving livelihoods.

Participatory rural appraisal (PRA) is a set of multidisciplinary research techniques used to identify farmers' perceived production constraints, preferred crop varieties, and traits for the deployment of production packages and suitable crop varieties. PRA is a useful method to understand farmers' knowledge, experiences, constraints, preferred traits, and needs (Chambers 1992). Technologies to improve sorghum yields that neglect farmers' needs and preferences have largely been ignored (Singh & Morris 1997). To improve adoption of newly released sorghum varieties and enhance productivity, it is important to investigate farmers' production constraints and their traits of preference, before variety development is initiated (Ceccarelli et al., 2001). Therefore, the objective of this study was to investigate farmers' production constraints and perceptions of *Striga* management practices by sorghum farmers in the semi-arid regions of Tanzania.

2.3 Materials and methods

2.3.1 Description of study sites

The study was conducted in three regions: Tabora, Shinyanga, and Simiyu. These regions represent the semi-arid parts of Tanzania, where sorghum cultivation is constrained by both *S. hermonthica* and *S. asiatica* (Figure 2.1). The Tabora region was represented by the Igunga District, which is found in the western part of Tanzania. The area receives unimodal rainfall, with a mean of 880 mm per year that falls between November and April. It has a long dry season of about 5-6 months and temperatures ranging from 14.6^{o}C in June to 32.5^{o}C in October. The site is characterized by sandy to loamy soils.

The Shinyanga and Simiyu regions were represented by Kishapu and Meatu Districts, respectively, which are located in the lake zone, 3°39′43″S and 33°25′23″E, with altitudes of 1000 to 1200 m above sea level. The areas are characterized by the presence of undulating plains with rocky hills and low scarps. The regions have well drained soils with low fertility and a growing season running from December to March. The two sites experience temperatures ranging from a mean of 16^{o}C in June to a mean of 33^{o}C in October, with prolonged warm conditions.

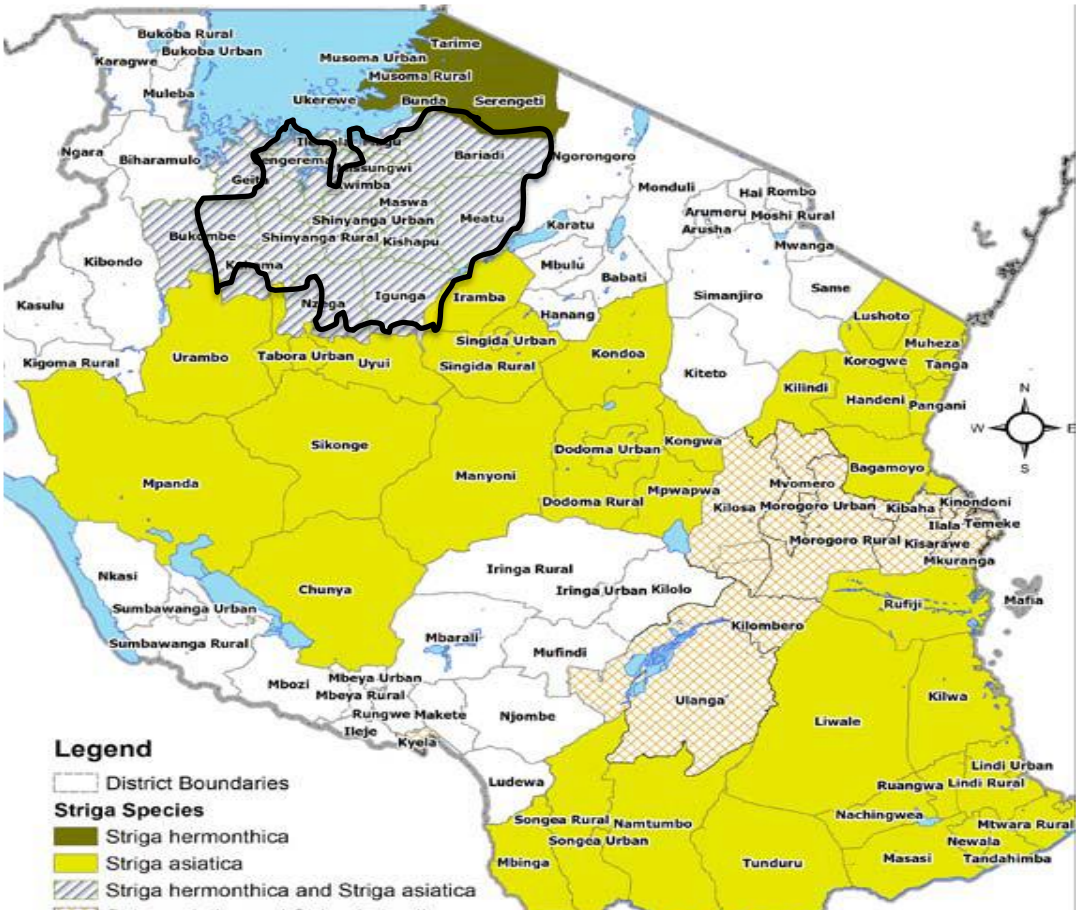

Figure 2.1. *Striga* distribution map within the boundaries of Tanzania (MacOpiyo et al. 2009) and location of the three study districts.

2.3.2 Sampling method

Purposive sampling was used for the study to increase the likelihood of including relevant sites and samples. Briefly, three districts were sampled, including Igunga (from Tabora region), Kishapu (from Shinyanga region) and Meatu (from Simiyu region), all situated in the semi-arid areas of northern Tanzania. The following six wards were sub-sampled: Mbutu and Isakamaliwa (from Igunga District), Mwataga and Kishapu (from Kishapu District), Mamshali and Mwagwila (from Meatu District). Each ward was represented by the following six villages: Mbutu, Kidalu, Lubaga, Isoso, Itongolyagamba, and Mwanyahina, in that order. The three districts, the six wards and the six villages were selected because of the type and severity of *Striga* infestation and the scale of sorghum production. In each village, twenty farmers were randomly sampled. This procedure provided a total of 120 farmers who were interviewed using a semi-structured questionnaire. Additionally, focus group discussions (FGDs) were held, involving eight focus groups comprising farmers, local leaders, and key informants. Each focus

group composed of eight representative farmers who were sampled based on their experience in sorghum production. A total of 48 farmers participated in the FGDs across the three districts.

2.3.3 Data collection and analysis

Data were collected through face-to-face interviews, observations made through transect walks across selected villages, and discussions with focus groups. The semi-structured questionnaire was formulated based on factors related to farmers' preferences on sorghum traits, the socio-economic status of the households, the varieties grown and their performance, production constraints, *Striga* infestation, and control practices. Farmers' varieties were identified by their local names, along with their merits and demerits. Farmers` preferred traits of sorghum were described and ranked using a pair-wise matrix technique. Identified traits were labelled and tallied in a matrix, both in rows and columns. Each trait was weighed and prioritized relative to the other based on one-on-one comparisons. Consequently, the values 1 and 0 were assigned to the most and least preferred trait, respectively. Finally, the scores were counted and traits were ranked based on relative values.

Key informant interviews were held with experienced sorghum farmers and community leaders. Forty eight farmers (16 from each district) who are known for their rich indigenous and technical knowledge on sorghum production, management, and utilization were selected and interviewed in all selected sites for secondary data collection. They were also involved in the FGDs, in which their observations and comments were recorded. Personal observations on land characteristics of sorghum fields and the importance of sorghum, were made during transect walks in the selected districts to provide complementary data.

Quantitative and qualitative data collected through the questionnaire were coded and subjected to statistical analyses using the Statistical Package for Social Sciences software (SPSS Inc. 2005). Cross-tabulations tables were constructed and descriptive statistics were calculated to summarise data from the questionnaires or the FGDs. To make statistical inferences, contingency chi-square tests were computed at a given level of significance to analyse relationships between variables. This allowed empirical analyses and description of associations between the collected parameters across the three study districts.

2.4 Results and discussion

2.4.1 Description of households

A total of 120 smallholder farmers interviewed during the study and all indicated that their sorghum fields were affected by *Striga* infestation in 2014. Table 2.1 summarises the basic socio-demographic profile of the respondents.

Table 2.1. Basic socio-demographic profile of the farmers

Variable	Class	District			Mean
		Igunga	Kishapu	Meatu	
Gender	Male	87.5	87.5	82.5	85.8
	Female	12.5	12.5	17.5	14.2
Age (years)	≥ 18	30.0	35.0	35.0	33.3
	≤ 17	70.0	65.0	65.0	66.7
Family size (number of individuals per family)	≤ 3	22.5	35.0	30.0	29.2
	4-6	72.5	55.0	60.0	62.5
	≥7	5.0	10.0	10.0	8.3
Education level	Primary	72.5	72.5	70.0	71.7
	Secondary	7.5	5.0	2.5	5.0
	Illiterate	20.0	22.5	27.5	23.3

The proportion of males (85.8%) was greater than females (14.2%) in all the study districts. Male and female farmers usually differ in priority and ownership for some of the crops, land access, and management practices. Female farmers cultivate a range of crops, mostly for feeding their family and for sale to cater for some of their social needs, whereas the males owned fertile lands and grow crops mostly for selling.

The mean family size in the study sites was 7.1 individuals. About 30% of the farmers had four children. Thirst percent of the farmers were older than 18 years in Igunga, whereas the respective proportion in Meatu and Kishapu Districts was 35%. Individuals older than 18 have decision-making power on the crop and variety to cultivate, the size of land to cultivate and the date of planting, which in turn have an impact on sorghum production. The number of

individuals per household influences farming operations that need human labour. Households with more than four family members were more efficient in sorghum farming than families with fewer members, which predominantly required outsourcing their labour needs from their communities. During the peak production events (e.g. planting, weeding, and harvesting) labour was one of the most important constraints affecting sorghum production.

Most respondents (71.7%) had attended primary school and were able to read and write with the local language Kiswahili only, while 5% had attended secondary education and were able to read and write in both English and Kiswahili. The remaining 23.3% had not attended school (Table 2.1). The low level of education in the study areas indicated that extension and research service providers or 'change agents' are needed to verbally communicate the nature and value of any new technologies or agricultural inputs to these communities. The educated individuals (5%) could be useful agents in gathering information regarding farmers' constraints, needs and priorities, who could act as facilitators of adoption of the new technologies of value to the smallholder farming communities in the study areas.

2.4.2 Main socio-economic activities in the study districts

Economic activity

The roles of farmers in various economic activities are summarised in Table 2.2. Major economic activities identified in all surveyed districts were crop production, livestock production, and small businesses. There were non-significant (X^2 = 3.533; P = 0.475) differences in the percentage of individuals engaged in different economic activities among the surveyed districts. About 75% of the farmers engaged in crop production, reflecting a greater contribution to the local economy compared with animal production (17.5%), and small business (7.5%) across the study districts.

Table 2.2. Major economic activities of the farmers

Economic activity	District			Mean	Df	Chi-square	P-value
	Igunga	Kishapu	Meatu				
Crop production	82.5	77.5	65.0	75.0			
Livestock production	12.5	15.0	25.0	17.5	4	3.533	0.475
Small businesses	5.0	7.5	10.0	7.5			

Df = degrees of freedom

Crop production

Farmers practiced both crop and livestock production as major sources of food, feed, and cash income. The area of land being cultivated by each household during the interview period ranged from 0.4 to 12 ha, with a mean of 3.0 ha (SD = 5.8). Crops grown in the study districts included sorghum, maize, cotton, green gram, sunflower, rice, and beans (Figure 2.2). The majority of the farmers allocated most of their land to sorghum (33%), followed by cotton (23%), and maize (21%). Rice, green gram, and sunflower were each allocated about 5% of the cultivated land (Figure 2.2).

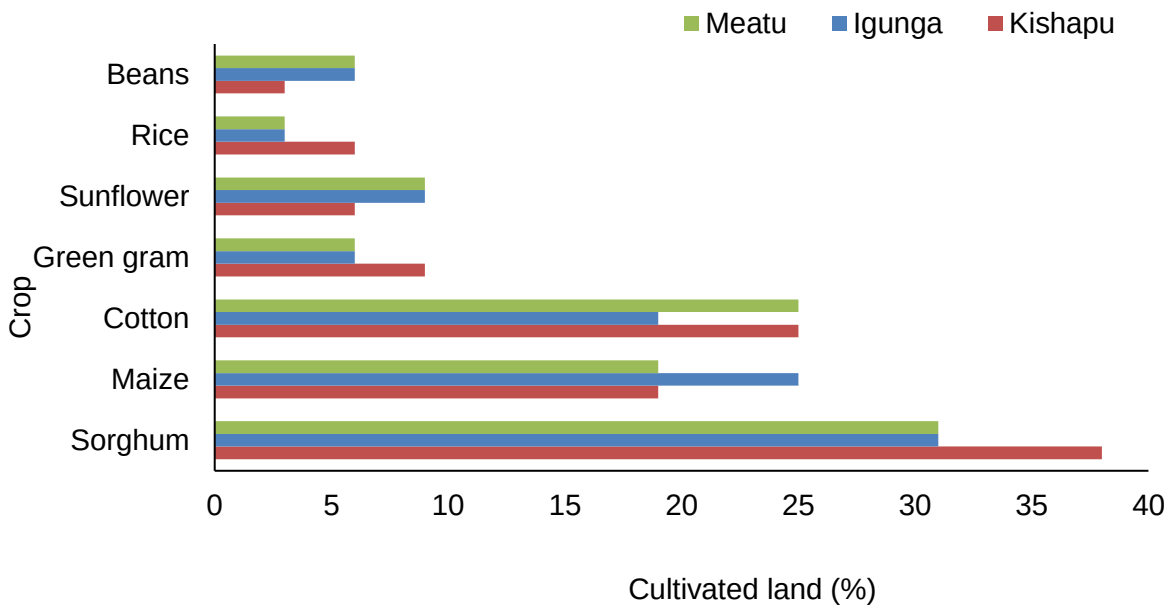

Figure 2.2. Different crops grown in 2013/2014 cropping season.

Mono-cropping, mixed cropping, and crop rotation were the major cropping systems practiced by most farmers in all study districts. Mono-cropping of sorghum was practiced by 70.5% of the farmers in Igunga, 67.0% in Kishapu, and 59.6% in Meatu. The remaining farmers intercropped sorghum with beans or sorghum with maize and green gram or sorghum with sunflower. Crop rotation was practiced by few individuals who had enough land for implementing this practice. Cropping systems that involve mono-cropping or mixed cropping using related crop species with similar growth requirements, such as soil moisture and fertilizers, are not sustainable because they draw nutrients without replacement. Such cropping systems contribute to the build-up of *Striga* infestation, pests and diseases, soil infertility, and thus yield reduction. By contrast, recommended cultural and chemical methods for the control of *Striga* may not be well adopted (Hearne 2009). This may be due to the high costs of the recommended technologies, a lack of information transfer about the new technologies, and also because these practices may not be compatible with farmers` preferred practices. The use of partially resistant sorghum lines, such as Wahi and Hakika, has not been effective in areas with high levels of *Striga* infestation in Tanzania. These lines were also reported to be low yielding, while the high-yielding varieties Pato and Tegemeo are susceptible to *Striga* (Hearne 2009). Introduced varieties, such as Macia and Serena, have not been adopted mostly because they are susceptible to *Striga*, birds, storage pests, and harsh environmental conditions, such as low rainfall and poor soil fertility. Low levels of adoption of introduced cultivars that lack some farmers' preferred traits have been reported in Ethiopia (McGuire 2008; Sinafkish et al., 2010). To facilitate adoption of new sorghum varieties, it is important to select for farmers' preferred traits during the breeding stages.

Data from the group discussions revealed that early planting following the main rains, the use of early maturing and *Striga* resistant sorghum varieties, and the use of good agronomic practices were the main practices adapted to ensure high yields in all study areas. Planting was done in the middle of the main rainy season (December) to utilize the available moisture at the early stages of the plant development and to allow the crop to escape drought stress during grain filling in January.

Observations made during transect walks were that farmers who planted early-maturing sorghum varieties in the beginning of the rains in mid-October achieved better yields than farmers who planted late in January. The latter group of farmers reported to lose much of their crop to drought and *Striga* infestation. Low yields were reported during group discussions, especially by the farmers who grew late-maturing varieties during 2013 to 2014. Planting times differed among farmers, depending on choice of variety, time of land preparation, and the onset of rain. Late-maturing landraces were grown by the majority of the smallholder farmers. These

were planted between December and early January, while improved early-maturing varieties that were grown by few farmers were planted in mid-October to November, following early seasonal rains. The need to replace late-maturing landraces with early-maturing ones, and *Striga* resistant introduced varieties was seen as a priority by most smallholder farmers. This was because late-maturing varieties have a long growing period, and they are therefore susceptible to drought events often occurring in most seasons in the semi-arid areas of Tanzania.

2.4.3 Sorghum production

The use of various inputs for the production of the primary crops is summarized in Table 2.3. Significant differences ($X^2 = 8.75$; $P = 0.013$) were detected among respondents on the use of production inputs. The predominant seed sources used by most smallholder farmers were landraces, selected and kept by the farmers themselves from previous harvests. Only 35, 15, and 10% of the farmers in Igunga, Kishapu, and Meatu Districts, respectively, used seeds of introduced sorghum varieties from research institutes. The poor adoption of new varieties was most probably because of their susceptibility to *Striga* infestation, attack by birds, damage by storage pests, and susceptibility to drought.

There were no significant differences ($X^2 = 6.867$; $P = 0.143$) among farmers concerning the use of fertilizers in sorghum production across the surveyed districts (Table 2.3). About 66% of the farmers in all three districts did not apply fertilizers. Some farmers (24%) were aware of the need for the application of inorganic fertilizers in sorghum production. Application of such fertilizers was reported by farmers who mentioned that this practice increased stress to plants due to extreme drought that affect most of the late-maturing landraces. Other factors that limited the use of inorganic fertilizers in sorghum production were the high costs of inorganic fertilizers that made them unaffordable for smallholder farmers; the poor response of some landraces to these fertilizers; and a lack of information on optimising the application of inorganic fertilizers. Some farmers: 35, 25, and 35% in Igunga, Kishapu, and Meatu Districts, respectively, applied organic fertilizers, such as farmyard manure, boma manure or compost, as an alternative way of improving soil fertility (Table 2.3). Pesticide use was low in all surveyed districts: 22.5% in Igunga, 25.0% in Kishapu and 30.0% in Meatu. Few farmers (5, 14, and 8.0% in Igunga, Kishapu and Meatu, respectively) applied pesticides in sorghum production. The high price of pesticides, their limited availability, and the lack of technical knowledge on the use of agrochemicals for pest management were identified as the main reasons for the limited use of pesticides in sorghum production, during the FGDs.

Table 2.3. Use of various inputs for cereal crop production

Input	Type/use	District			Mean	Df	Chi-square	P-value
		Igunga	Kishapu	Meatu				
Fertilizers	Inorganic	0.0	7.5	0.0	2.5	4	6.867	0.143
	Organic	35.0	25.0	35.0	31.7			
	None	65.0	67.5	65.0	65.8			
Varieties	Local	65.0	85.0	90.0	80.0	2	8.750	0.013
	Improved	35.0	15.0	10.0	20.0			
Crop protection chemicals	Yes	22.5	25.0	30.0	25.8	2	0.609	0.738
	No	77.5	75.0	70.0	74.2			

D.f =degrees of freedom

Table 2.4 presents the mean seeding rates and the mean yields of sorghum cultivated in the surveyed districts. Variations in sorghum yields could be ascribed to differences in soil type, weather conditions, management practices, farming systems, tillering ability of the varieties, and varietal tolerance to stresses. The overall mean and standard deviation of the seeding rate of sorghum used by the farmers was 13.2 ± 3.8 kg ha^{-1}. The seeding rate used in the study areas was slightly higher than the recommended seeding rate of 12.5 kg ha^{-1} (FAOSTAT 2013). The higher seeding rates used by the smallholder farmers were attributed to the inefficiency of seed broadcasting, efforts to maximize the probability of seed germination, and efforts to compensate losses by seed damage due to soil-borne diseases. In the study areas, farmers practiced 'songa mbele', a planting technique where the seeds are hand broadcasted followed by trampling the soil with oxen. This method requires more seed per unit area. A lack of knowledge about improved agronomic practices, such as row planting, is a significant limiting factor for sorghum production in the study areas.

The mean sorghum yield achieved by the farmers during 2014 was 815.3 kg ha^{-1}, which was lower than the estimated national yield of 1000 kg ha^{-1} for the same season (FAOSTAT 2014). Yields ranged from 786.0 to 837.5 kg ha^{-1} due to differences in sorghum varieties grown, variations in the extent of the environmental stresses (e.g. drought), soil types, inputs used, weeds, pests and diseases. In spite of the economic importance of sorghum in the study areas, yields remain low. These findings concur with the reports of Fisher and Wilson (1975), Dogget (1988), and Wortmann et al. (2006) who documented low yields of sorghum across Africa, despite its economic importance. Despite low yields, sorghum landraces are still widely cultivated by the smallholder farmers due to better adaptation to semi-arid environments, good grain quality, dual purpose uses (for food and brew), and resistance to pre- and post-harvest pests, birds, and fungal diseases.

Table 2.4. Seeding rate and grain yield of sorghum during the survey season

District	Mean ± standard deviation	
	Seed rate (kg ha^{-1})	Yield (kg ha^{-1})
Igunga	12.4±4.4	837.5±157.9
Kishapu	12.8±2.6	822.3±110.5
Meatu	14.5±3.9	786.0±166.0
Overall	13.2±3.8	815.3±147.2

2.4.4 Constraints to sorghum production

The major production constraints of sorghum in the study districts are summarized in Table 2.5. These constraints included both biotic and abiotic stresses. Among the challenges that contributed to low yields, drought, low soil fertility, *Striga* infestation, storage pests, damage by birds, lack of improved varieties, lack of production inputs (fertilizers, insecticides, herbicides, fungicides, and improved seeds) as well as diseases were included.

Farmers' ranking of production constraints across districts showed that 75 to 85% of the respondents ranked *Striga* infestation as a highly important constraint. *Striga* caused serious yield losses in sorghum in all studied districts. The importance of this parasitic weed may be attributed to high occurrence due to the production of large numbers of seeds that remain viable for many years and the multiple dispersal mechanisms of the seeds by water, wind, cultivation equipment and animal movement (Koichi et al., 2010). Moderate infestations (15 to 25%) were reported by some farmers, probably those who used fertilizers or who practiced regular weeding (at least three times in a season). The ranking of *Striga* infestation did not show significant differences (X^2 = 1.781; P = 0.410) among districts. High severity of *Striga* was estimated at 85, 85, and 75% in Igunga, Kishapu, and Meatu, respectively. Such variation was rather expected due to differences in the levels of soil infertility, rainfall distribution, drought conditions, animal movement, *Striga* control methods, weeding events, and the farming system implemented. These all have a significant impact on *Striga* seed bank and seed movement in the soil. Generally, all the studied districts are *Striga* infested areas with low soil fertility. Such environmental conditions agree with the observations of Wortmann et al. (2006) who reported that low sorghum yields in eastern Africa was associated with nutrient deficiencies, drought, *Striga*, stem borers, and shoot fly.

After *Striga* infestation, the second most yield-limiting factor for sorghum production in the study areas was drought (Table 2.5). High severity of drought was reported by 70 to 75% of the respondents across all studied districts. Drought is associated with frequent changes of weather conditions in almost all semi-arid parts of Tanzania. To mitigate drought stress,

farmers adopted various strategies, such as mixed farming systems, use of a portion of the farmland, avoiding use of newly introduced sorghum varieties, and abandoning some landraces, particularly the late-maturing ones that fail to produce yield under reduced rainfall. Other constraints to sorghum production were storage pests, birds, lack of improved varieties with drought tolerance, lack of production inputs, low soil fertility, and diseases. The severity of these constraints varied from district to district and within a district (Table 2.5).

Table 2.5. Major constraints to sorghum production

		District						
Constraints	Severity	Igunga	Kishapu	Meatu	Mean	Df	Chi-Square	P-value
Drought	HS	75.0	75.0	70.0	73.3			
	MS	15.0	15.0	25.0	18.3	4	2.345	0.673
	LS	10.0	10.0	5.0	8.3			
Storage pests	HS	15.0	20.0	30.0	21.7			
	MS	85.0	75.0	65.0	75.0	4	5.221	0.265
	LS	0.0	5.0	5.0	3.3			
Striga	HS	85.0	85.0	75.0	81.7	2	1.781	0.410
	MS	15.0	15.0	25.0	18.3			
Birds	HS	10.0	20.0	20.0	17.0			
	MS	85.0	75.0	75.0	78.0	4	1.940	0.747
	LS	5.0	5.0	5.0	5.0			
Lack of improved varieties	HS	20.0	0.0	10.0	10.0			
	MS	25.0	15.0	20.0	20.0	4	11.571	0.021
	LS	55.0	85.0	70.0	81.7			
Poor soil fertility	HS	10.0	0.0	5.0	5.0			
	MS	20.0	5.0	15.0	13.3	4	132.277	0.000
	LS	70.0	95.0	80.0	81.7			
Lack of production inputs	HS	5.0	0.0	15.0	7.0			
	MS	25.0	90.0	65.0	60.0	4	170.287	0.000
	LS	70.0	10.0	20.0	33.0			
Diseases	HS	0.0	0.0	5.0	1.7			
	MS	95.0	0.0	80.0	58.3	4		
	LS	5.0	100.0	15.0	40.0		219.628	0.000

HS = high severity, MS = moderate severity and LS = low severity

Df = degrees of freedom

2.4.5 *Striga* infestation and control strategies

Farmers in all surveyed districts reported *Striga* infestation as the major limiting factor for sorghum production, particularly when the crop is cultivated alone. The extent of infestation did not vary significantly (X^2 = 1.781; P = 0.410) among districts. A high severity (75 to 85%) was reported in all surveyed districts (Table 2.5). At Igunga farmers used small quantities of inorganic and organic fertilizers and did not apply herbicides. This may be the reason for the high levels of *Striga* infestation in this district. Other crops cultivated in the study areas included green gram and beans, which have the ability to fix atmospheric nitrogen. These crops were cultivated in a mixed cropping system with sunflower and cotton in several areas. In these farming systems, there were lower levels of *Striga* infestation due to improved levels of soil fertility and inability of *Striga* seeds to germinate in soils with low levels of a germination

stimulus (e.g. strigol) released from the roots of sorghum plants (Parker 1991). The level of *Striga* infestations was reported to be increasing in sorghum crops in all surveyed areas (Table 2.6). Previously, yield losses of 30 to 100% had been reported when sorghum was grown alone under severe *Striga* infestations. Tesso et al. (2007) reported yield loss of 65% under severe *Striga* infestation. In the three study areas, farmers indicated that *Striga* had been present for more than 30 years, but with no information as to the original source of the infestation. Farmers reported the emergence of the weed about 1 to 2 months after the emergence of sorghum seedlings. They also reported that the weed affected the host plants immediately after its emergence from the ground. According to farmers, the major symptoms of sorghum affected by *Striga* infestation were stunted growth, yellowing of the leaves, and death of the plant.

Table 2.6. Farmers' assessment of the levels of *Striga* infestation in sorghum

	District						
Infestation	Igunga	Kishapu	Meatu	Mean	Df	Chi-Square	P-value
None	0.0	0.8	2.5	1.1			
Mild	10.0	11.7	10.0	10.6	4	2.629	0.622
Severe	90.0	87.5	87.5	88.3			

Df = degrees of freedom

Hand weeding, crop rotation, fallowing, intercropping, and organic manure application were some of the coping mechanisms reported by the farmers for reducing S*triga* infestations (Table 2.7). About 25 to 30% of the farmers used hand weeding in their sorghum fields to reduce *Striga* infestation. Farmers tried to manage *Striga* without consideration of the growth stage of the parasite; some weeded before flowering, while others after flowering. Weeding after flowering of the parasite may contribute to a substantial increase in *Striga* seed bank in the soil and thus increase subsequent infestations. Most farmers (86, 79, and 76%) in Igunga, Kisapu, and Meatu Districts, respectively, reported that hand weeding was not very effective for the control of *Striga*. Woomer et al. (2004) reported that under high *Striga* infestation, traditional *Striga* management practices, such as hand weeding, were insufficient to protect cereal crops.

Most farmers (79.7%) had little knowledge of the best recommended *Striga* management practices. Few farmers (15.8%) adopted *Striga* reducing practices, such as the use of organic and inorganic fertilizers, fallowing, intercropping of host plants with legumes, crop rotation, and the use of herbicides, such as 2,4-D (Table 2.7). Farmers were asked the main reasons why

they did not apply integrated *Striga* management systems. They reported the following limitations: i) little knowledge about *Striga* management, ii) land shortage, iii) little access to herbicides, iv) positive traits in *Striga* susceptible landraces, or v) limited access to seeds of improved varieties with resistance to birds, storage pests, and drought.

Table 2.7. Farmers' coping mechanisms for *Striga* management in sorghum

Strategy	District			Mean	Df	Chi-Square	P-value
	Igunga	Kishapu	Meatu				
Hand weeding	30.0	25.0	30.0	28.3	8	2.231	0.973
Crop rotation	12.5	15.0	10.0	12.5			
Fallowing	10.0	15.0	15.0	13.3			
Organic manure	35.0	30.0	25.0	30.0			
Intercropping	12.5	15.0	20.0	15.8			

Df = degrees of freedom

2.4.6 Farmers' perceptions of *Striga* management options

The level of *Striga* infestation and crop losses was considered to be increasing across the study districts. Farmers perceived that the use of fertilizers, fallowing, crop rotation, timely weeding, and intercropping sorghum with legumes may help in *Striga* management when used singly or in combination. However, farmers rarely adopt *Striga* control methods mainly due to limitations associated with the technology itself or because the technology is not available or affordable to them or because of a lack of detailed information about these control options. Most farmers followed sole cropping of sorghum and cultivated *Striga* susceptible and late-maturing varieties, resulting in an increasing *Striga* seed bank in the soil. Adoption of *Striga* resistant varieties has been slow, primarily due to a lack of i) farmers` preferred traits, ii) effective seed production, and iii) marketing mechanisms. This poor level of adoption requires the development of sorghum varieties with resistance to *Striga* including farmers` preferred traits, such as improved yield, and tolerance to drought stress, bird, and disease damages.

2.4.7 Sorghum varieties grown in the study areas

A description of the most popular cultivated sorghum varieties within the surveyed districts was recorded using their vernacular names (Table 2.8). Farmers reported several sorghum landraces that had been grown and maintained within and outside the districts. Macia, Serena,

Tegemeo, and Wahi are introduced sorghum varieties that had been grown by some farmers. Presently, these varieties were being cultivated by only few farmers. Various landraces were reported to be cultivated in a particular district, while others were grown in several districts. Most of the named landraces were maintained by the farmers from crop to crop. The reasons for the diversity of landraces in the study areas were for several specific traits, such as adaptability to environmental stresses, limited input requirements for growth, resistance to birds and storage pests, drought tolerance, weed tolerance, a high market value, good cooking quality, seed availability, and differences in climatic conditions among the studied zones of the semi-arid regions of Tanzania. The presence of diverse sorghum landraces in Ethiopia was found to be due to genetic variation, environmental adaptation, and farmers' selections in a range of agro-ecologies (Tesso et al., 2007).

Although there were several introduced high-yielding varieties developed within and outside the country, only few were mentioned by the farmers. These were Macia, Serena, Wahi, Pato, and Tegemeo. Low levels of adoption of the introduced varieties were reported probably because these varieties failed to match with farmers` preferred traits (Table 2.8). Macia, one of the introduced high-yielding sorghum varieties, is reported to be susceptible to birds, storage pests, and *Striga* infestation. The variety Wahi was meant to have *Striga* tolerance, but it was found to have no longer tolerance, especially under high levels of *Striga* infestation recorded in Tanzania.

Rebeka et al. (2013) reported the adoption of a novel sorghum variety, Emahoy, which was selected for its high yield and resistance to *Striga*. Teshome et al. (2007) reported that the strong preference for landraces by smallholder farmers in Ethiopia was because the landraces matched with farmers' preferred traits and had good adaptability to field conditions. For these reasons, it is important to include landraces in a breeding program to capture their valuable traits and to ensure the maximum adoption of newly developed varieties.

Table 2.8. Sorghum varieties grown and their associated characteristics

Districts	Local names of varieties	Suggested traits	
		Preferred	Non-preferred
Igunga	Kakula, Kenya, Mbiti, Gumi, Kombituna	Drought tolerant and bird resistant	Susceptible to *Striga* and late maturing
	Macia, Serena	Early maturing, high yielding, and good food quality	Susceptible to *Striga*, birds, and storage pests
Kishapu	Bukula/Miningamela, Selemani, Kombituna, Mwanangudungu	Drought tolerant and bird resistant	Susceptible to *Striga*
	Wahi, Macia, Serena	Early maturing, high yielding, and good food quality	Susceptible to *Striga*, birds, and storage pests
Meatu	Galolo, Miningamela, Selemani,	Drought tolerant and bird resistant	Susceptible to *Striga*
	Pato, Macia, Tegemeo	Early maturing, high yielding, and good food quality	Susceptible to *Striga*, birds, and storage pests

Farmers' ranking of the traits of preference in sorghum varieties in the study regions is presented in Table 2.9. The preferences were related to *Striga* infestations, earliness, drought tolerance, grain yield, resistance to pests and diseases as well as resistance to bird attacks, all of which occur in the studied areas. In all districts, resistance to *Striga* was rated as the number one trait of preference. In Igunga District, farmers rated early maturity and drought tolerance as the second and third traits of preference, respectively. This was similar to preferences in Kishapu and Meatu Districts, in which drought tolerance and earliness were ranked as the second and third most preferred traits, respectively (Table 2.9). Mean ranks in all districts showed that grain yield, pest and disease resistance, bird repellence, and grain quality were the fourth, fifth, sixth, and seventh most preferred traits, respectively. The differences in the ranks between the districts could be attributed to variations in soil type, levels of annual rainfall, sorghum varieties grown, and the duration of dry spells.

To cope with the situation, farmers prefer early maturing varieties that could escape drought period, high *Striga* infestations, and damage by birds. Most of the cultivated landraces were late-maturing ones and were susceptible to *Striga.* Developing sorghum varieties that perform better in harsh and un-predictable environments, with traits of farmers' preference will maximize the adoption of such varieties in the study areas. Lacy et al. (2006) and Sinafkish et al. (2010) reported that farmers usually grew sorghum varieties with wide environmental adaptability and yield stability, and had other traits of preference. Yield improvement by

introducing new varieties that lack most of the traits preferred by the farmers did not work in most parts of Africa (Ouédraogo 2005). Incorporation of farmers' knowledge, preferences, and use of their landraces as a basis for breeding programs will maximize the adoption of newly developed varieties (Mekbib. 2006; Gyawali et al., 2007; Nkongolo et al., 2008).

Table 2.9. Farmers' traits of preference (%) for sorghum varieties

	District			
Traits	Igunga	Kishapu	Meatu	Mean
Striga resistance	45.0	42.5	52.5	46.7
Earliness	17.5	15.0	13.5	15.3
Drought tolerance	12.5	17.5	15.0	15.0
Resistance to bird attack	11.0	5.0	2.5	6.2
Pest and disease resistance	4.5	10.0	7.5	7.3
Grain yield	6.0	7.5	9.0	7.5
Grain quality	3.5	2.5	0.0	2.0

2.5 Conclusions

Sorghum is a valuable food security crop in the semi-arid regions of Tanzania owing to its ability to thrive under harsh growing environments. Its low production and productivity in the semi-arid regions of Tanzania can be attributed to both biotic and abiotic factors as well as socio-economic constraints. In the study areas, *Striga* infestation was the major biotic constraint limiting sorghum production. Unavailability and unaffordability of herbicides, delayed hand weeding, lack of *Striga* resistant, and farmers` preferred varieties, land scarcity to practice crop rotation and fallowing, and intercropping of crop species with similar growth requirements were the main reasons limiting the effectiveness of *Striga* management. Further, sole cropping of sorghum, low soil fertility, drought stress, and the limited use of fertilizers and herbicides were additional constraints in *Striga* management. These constraints can be solved through integrated research approaches by various disciplines and institutions. Other constraints may need further interventions, such as access to credit and entrepreneurship.

Previously released *Striga* resistant varieties achieved a low level of adoption due to a lack of match to farmers' preferred traits. Therefore, there should be a systematic breeding program aiming at improving sorghum varieties for *Striga* resistance, including farmers' preferred traits, to increase the adoption of these new varieties by the farmers. There should be also other strategies, such as technology transfer to farmers through training on the importance of *Striga*

management options, to limit the spread and impact of this parasitic weed. This will help to increase the adoption of *Striga* resistant varieties and management options by the local communities to successfully fight this parasitic weed in sorghum production in the semi-arid regions of Africa. In the next chapter, sorghum genotypes were evaluated to identify varieties resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*

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CHAPTER THREE

Screening of sorghum genotypes for resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*

This chapter has been published by:

Emmanuel Mrema, Hussein Shimelis, Mark Laing and Tulole Bucheyeki (2017)

Screening of sorghum genotypes for resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*, Acta Agriculturae Scandinavica, Section B - Soil and Plant Science (2017), 67 (5): 395-404, DOI: 10.1080/09064710.2017.1284892

CHAPTER THREE

Screening of sorghum genotypes for resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*

3.1 Abstract

In the semi-arid areas of Tanzania yield losses of sorghum [*Sorghum biocolor* (L.) Moench] is estimated to be 30 to 90% due to *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*) infestations. The use of resistant sorghum varieties compatible with *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, may supress the weed and enhance productivity of the crop. The objective of this study was to screen and select farmers-preferred sorghum genotypes for *Sh* and *Sa* resistance and *FOS* compatibility for resistance breeding under Tanzanian conditions. Sixty sorghum genotypes were evaluated. Evaluations were conducted under screen house conditions using *Sh and Sa* infested field soils with controlled seed infestation, with or without inoculation of the sorghum seeds with *FOS.* The experiment was laid out using a split-plot design; *FOS* being the main-plot and sorghum genotypes as the sub-plot treatments. Data on crop growth and grain yield parameters, and *Striga* incidence were collected. Inoculation of sorghum seeds with *FOS* significantly enhanced sorghum growth and productivity, and supressed *Sh and Sa* growth and development. Twenty eight sorghum genotypes evaluated in *Sh* infested soil had increased seed yields of 9 g per plant; 30 genotypes screened under *Sa* infestation had increased seed yields of 10 g per plant after *FOS* inoculation of the sorghum seeds compared to untreated controls. There were reductions of 1 to 4 *Sh and Sa* plants when sorghum seeds were inoculated with *FOS*. Overall, the present study selected 25 promising sorghum lines resistance to *Sh* and/or *Sa,* and *FOS* compatibility. The selected sorghum lines are valuable genetic resources for the development of *Striga* management in sorghum through the integrated use of host resistance and *FOS* inoculation.

Keywords: bio-agent, integrated *Striga* management, genotypes, parasitic weed, host resistance

3.2 Introduction

Striga species [*Striga hermonthica* (Del.) Benth and *S. asiatica* (L.) Kuntze], are obligate root parasites that cause severe yield losses of 30 to 90% in sorghum in Tanzania (Riches 2003). *Striga* spp. derives their nutrients from host plants and exert phytotoxic effects to their host. These retard growth and lowers sorghum yields (Press et al., 1996). *Striga* spp. also attack rice (*Oryza glaberrima* Steudel & *O. sativa* L.), pearl millet (*Pennisetum glaucum* L.) and maize (*Zea mays* L.) (Rodenburg et al., 2015). There are 41 *Striga* species in the family Orobanchaceae. Of these, 11 are documented to cause significant yield losses in tropical cereals (Mohamed et al., 2001; Mohamed et al., 2006). Ejeta (2007) reported that *Striga* affects some 100 x 10^6 ha of cereal fields in Africa. An on-going expansion of the areas affected by *Striga* spp. have been attributed to poor soil fertility, the use of a single method of *Striga* management and cereal mono-cropping (Parker 2009; Parker, 2012). *Striga* is perpetually occurring because of its ability to produce large quantities of very small seeds that remain viable in the soil for up to 20 years. A single plant can produce up to 500,000 seeds, which mature and germinate at different times (Rodenburg et al., 2006; van Mourik et al., 2008).

Striga hermonthica (*Sh*) and *S. asiatica* (*Sa*) occur in several cereal crop growing parts of Tanzania. Both species are economically important in the Lake Victoria and the western zones of Tanzania. In these areas the weeds damage several crops including maize, sorghum, millet and upland rice across extensive agro-ecological areas (Rodenburg et al., 2015; Schut et al., 2015). Doggett (1953) reported 70 to 100% yield losses in sorghum due to *Striga* infestation in Tanzania. Yield losses of 40% have been reported in other parts of Africa (Lagoke 1991; Parker 2009). The magnitude of yield losses depends on the extent of infestation, climatic conditions and control measures used (Tesso et al., 2007). Combined use of various *Striga* management option based on understanding of biological and metabolic relations of the host and parasite, may provide strategies to control the parasite (Ransom 2000; Tesso & Ejeta 2011). However, managing *Striga* sp. is difficult for smallholder farmers because they have limited access to production inputs such as fertilizers and herbicides.

Several control strategies have been recommended to reduce *Striga* infestations. These include the use of resistant varieties, biological agents, cultural practices and chemical control methods (Hearne 2009). Cultural practices such as the cultivation of several crops in the same piece of land in successive years, application of fertilizers, soil moisture management and manual weeding all help to reduce the *Striga* seed bank (Tesso & Ejeta 2011). These strategies improve the soil structure and fertility, promote growth and development of the host plant, and retard germination and growth of juvenile *Striga* plant (Redda & Verkleij 2004). However, their

costs of implementing these measures are high, and this hinders their adoption by smallholder farmers. Some herbicides such as 2,4-D are reported to be effective in reducing the build-up of *Striga* (Ejeta et al., 1996). But they are less effective in controlling the effect of the parasite after emergence (Carsky et al., 1994; Hearne 2009; Haussmann et al., 2000a). Furthermore, the cost of herbicides and spray units make this approach unaffordable for smallholder farmers. The use of resistant varieties is the cheapest and most environmentally friendly *Striga* management option for the smallholder farmers in the semi-arid regions, who depend on sorghum production for food security.

Striga resistant sorghums can be a major component of integrated *Striga* control approaches if resistance is incorporated into well-adapted and productive cultivars (Haussmann et al., 2000a). Resistant cultivars can reduce both new *Striga* seed production and the *Striga* seed bank in infested soils. The genotypes, when grown under conditions of *Striga* infestation, support significantly fewer *Striga* plants and have a higher yield than a susceptible cultivar (Doggett 1988; Ejeta et al., 1992). Several *Striga* resistance mechanisms have been reported, these involves low production of germination stimulant, mechanical barriers, inhibition of germ tube exoenzymes by root exudates, phytoalexine synthesis, incompatibility, antibiosis, insensitivity to *Striga* toxin, avoidance through root growth habit (Ejeta et al., 1992; Ejeta & Butler 1993; Berner et al., 1995; Wegmann1996).

Integrated *Striga* management practices that encompass the use of resistant sorghum genotype and a biological control is one way of managing root parasitic weeds. This involves the use of microbes to control *Striga* as part of an integrated control strategy for smallholder farmers (Kroschel & Müller-Stöver 2004; Sauerborn et al., 2007). The method is affordable, and is more environmentally friendly than chemical control practices (Marley et al., 2004). Changes in biotic and abiotic conditions due to the presence of microbes surrounding the rhizosphere have been reported to retard the efficacy of *Striga* parasitism on the host plant (Kroschel & Müller-Stöver 2004; Sauerborn et al., 2007) and may stimulate plant growth (Kroschel & Müller-Stöver 2004; Sauerborn et al., 2007). Different microbial communities have been reported to have different impacts on *Striga* and the host (Sauerborn et al., 2007). Pathogenic isolates of *Fusarium oxysporum* f.sp. *strigae* (*FOS*) are reported to be effective bio-herbicides for management of *Striga* infestation in sorghum, particularly when the method is integrated with other control practices (Rebeka et al., 2013). Rebeka (2007) reported the ability of the biocontrol fungus to destroy *Striga* before it penetrates the roots of sorghum under Ethiopian conditions. The *FOS* biocontrol agent is reported to be host specific, highly aggressive against *Striga*, easy to mass produce and shows high level of genetic diversity (Ciotola et al., 2000). When sorghum seeds are treated with *FOS*, the fungus grows well in the

rhizosphere of the sorghum plants. It parasitizes *Striga* sp. inhibiting their growth and development stopping them from parasitizing the roots of host plants (Rebeka 2007). Breeding sorghum varieties for farmer-preferred traits, resistance to *Striga* infestation, and compatibility with *FOS*, would make a major contribution to the sorghum yields of farmers in the semi-arid parts of Tanzania. The potential for adoption of these improved varieties by small scale farmers would be high. Further, this approach contributes to the reduction of *Striga* infestations and will result in sorghum improved yields. Therefore, the objective of this study was to screen and select farmers-preferred sorghum genotypes for *Sh* and *Sa* resistance, and for *FOS* compatibility as the basis for effective breeding for Tanzania conditions.

3.3 Materials and methods

3.3.1 Plant materials

The study used 60 sorghum genotypes consisting of landraces and introduced varieties. The genotypes were collected from varied sources such as farmers' fields in Tanzania, the Tanzania National Gene Bank, the Institute of Biodiversity Centre (IBC)/Ethiopia and the International Crop Research Institute for the Semi-arid Tropics (ICRISAT)/India (Table 3.1). The sorghum genotypes acquired from ICRISAT were reported to be *Striga* resistant. An introduced sorghum variety, 'Macia,' which is widely grown in Tanzania, was included as, a susceptible control. The landraces were included because of their wide adaptability to varied growing environments, and because they have agronomic and quality traits preferred by smallholder farmers.

Table 3.1. List and sources of sixty sorghum genotypes used in the study.

Entry	Accession number	Source	Entry	Accession number	Source
1	77	Sumbawanga/Tanzania	31	AS 429	ACCI
2	203	Sumbawanga/Tanzania	32	3424	Igunga/Tanzania
3	476	Kondoa/Tanzania	33	5275	Kishapu/Tanzania
4	483	Kondoa/Tanzania	34	AS 433 (Birhan)	SARC/Ethiopia
5	501	Dodoma rural/Tanzania	35	3904	Nachingwea/Tanzania
6	536	Dodoma rural/Tanzania	36	2255	Meatu/Tanzania
7	550	Manyoni/Tanzania	37	308	Manyoni/Tanzania
8	207	Manyoni/Tanzania	38	3933	Serengeti/Tanzania
9	575	Singida rural/Tanzania	39	3937	Serengeti/Tanzania
10	AS 426	ACCI/South Africa	40	1580	Iramba/Tanzania
11	594	Iramba/Tanzania	41	3984	Musoma/Tanzania
12	612	Iramba/Tanzania	42	3993	Musoma/Tanzania
13	630	Serengeti/Tanzania	43	AS 422	ACCI/South Africa
14	654	Bunda/Tanzania	44	4023	Ukerewe/Tanzania
15	672	Musoma rural/Tanzania	45	4027	Ukerewe/Tanzania
16	675	Tarime/Tanzania	46	4031	Ukerewe/Tanzania
17	AS 425	ACCI/South Africa	47	AS 423	ACCI/South Africa
18	104	Kishapu/Tanzania	48	4396	Lindi/Tanzania
19	AS 424 (Hormat)	SARC/Ethiopia	49	4368	Ngara/Tanzania
20	AS 431	ACCI/South Africa	50	4543	Liwale/Tanzania
21	714	Tarime/Tanzania	51	4572	Magu/Tanzania
22	1563	Bukoba/Tanzania	52	AS 421	ACCI/South Africa
23	P 40281	IBC/Ethiopia	53	4567	Magu/Tanzania
24	AS 71	ACCI/ South Africa	54	4643	Misungwi/Tanzania
25	2246	Kilwa Masoko/Tanzania	55	2379	Tarime/Tanzania
26	AS 436	ICRISAT/India	56	105	Mwanza/Tanzania
27	AS 434	IBC/Ethiopia	57	AS 427	Framida/ICRISAT
28	AS 428	IBC/Ethiopia	58	AS 435	ACCI/South Africa
29	2357	Mtwara/Tanzania	59	AS 432	ACCI/South Africa
30	AS 430	ACCI/South Africa	60	PAN 8816	PSC/South Africa

IBC = Institute of Biodiversity Conservation/Ethiopia; SARC = Sirinka Agricultural Research Centre/Ethiopia; ICRISAT = International Crop Research Institute for the Semi-arid Tropics/India; ACCI=African Centre for Crop Improvement; PSC = Pannar Seed Company

3.3.2 Inoculation preparation

A pathogenic strain of *F. oxysporum* f.sp. *strigae* (*FOS*), originally isolated from sorghum fields infested with *Striga* in north eastern lowlands of Ethiopia, was used (Rebeka et al., 2013). The taxonomic identification of *FOS* was confirmed by the Phytomedicine Department of Humboldt University in Berlin, Germany. Rebeka (2007) confirmed the pathogenicity and host specificity of the *FOS* isolate to *Striga*. The isolate was maintained on special nutrient agar (SNA) (Rebeka et al., 2013) medium kept at -40^{o}C. Pure *Fusarium* spores were mass produced and formulated by Plant Health Products (pty) Ltd, Kwazulu-Natal, South Africa.

3.3.3 Study sites, experimental design and trial establishment

A trial was established at the Agriculture Research Institute - Tumbi (ARI-Tumbi), situated in the Western Zone of Tanzania. The experiment was laid out in a split plot design, with *FOS* being main-plot, and sorghum genotypes being the sub-plot treatment, with three replications.

A hole measuring 30 cm deep and 25 cm wide and positioned along the drip pipeline was dug in the screen house ground. A total of 1440 holes were divided in to two sets. A set of 720 holes were allocated for *S. hermonthica* (*Sh*) and the other 720 for *S. asiatica* (*Sa*) screenings. Each hole was filled with field soils initially collected from two sites known for their heavy infestation by both *Striga* species. The soil was a mixture of forest top soil and sand soil in a ratio of 4:2, respectively. To ensure *Striga* infestation, top soil was uniformly infested with 25 mg of *Sh* seeds, which was evenly distributed and planted 1 to 1.5 cm deep and covered with a thin layer of soil. Similarly, the remaining holes were infested with seeds from *Sa*. The *Striga* seeds were collected from *Striga* plants grown in the farmers' fields. The fields were previously used for sorghum and maize production and had heavy and recurrent infestation by *Sh* and *Sa*. The collected seeds were stored in the Crop Science laboratory at ARI-Tumbi.

After a ten days delay to precondition the *Striga* seed, sorghum seeds were planted. One set of the holes were planted with sorghum seeds dressed with 75 mg of *FOS* spores*,* while the other half was planted without *Fusarium* inoculation. After emergence the sorghum plants were thinned to one seedling per hole. Apart from *Striga*, other weeds were hand weeded when observed. Watering was done using a drip irrigation system for 30 minutes 4 times per week in the evening during the first and the second month of the trial establishment. The number of irrigations was then reduced to two per week. Other agronomic practices were done following recommendation for the areas.

3.3.4 Data collection and analysis

Data on both sorghum and *Striga* parameters were collected. Data on sorghum included days to 50% flowering, panicle weight (g/main panicle), fresh biomass (g/plant), seed yield (g/plant) and weight of 100 seeds (g/100 seed). *Striga* vigor was recorded on a scale of 0 to 9 (Haussmann et al., 2000b). Collected data were assembled in Excel and subjected to analysis of variance (ANOVA) using the split-plot procedure of GENSTAT 14th Edition (Payne et al., 2011). Independent samples t-test was used to assess the significance difference between *FOS* coated and uncoated sorghum genotypes' performances and *Striga* vigour. Treatment means were separated using the Fisher's Least Significant Difference procedure at the 5% probability level.

3.4 Results and discussion

3.4.1 The effect of *FOS* on sorghum and *Striga hermonthica* growth and development

Table 3.2 summarises the analysis of variance when 60 sorghum genotypes were evaluated under *Sh* infestation with and without *FOS* application. Sorghum genotypes differed significantly in yield, yield components and *Sh* counts among treated and untreated sets. Treating sorghum seeds with *FOS* significantly affected both crop and *Striga* parameters (Table 3.2).

Table 3.3 summarises the response of tested sorghum genotypes with and without *FOS* application under *Striga hermonthica* infestation. *FOS* markedly suppressed the establishment and vigour of the parasite such that the number of *Striga* plant and mean *Striga* vigour were significantly ($p<0.05$) reduced compared to the non-inoculated treatments. Likewise, sorghum grain yields were significantly higher from holes with *FOS* treatment, yielding 5 g plant^{-1}, which was higher than the untreated control and the susceptible check. This concurs with Rebeka et al. (2013) who found the yields were higher when sorghum seeds were treated with *FOS*. Crop maturity for some varieties was shortened by 7 days and weight of fresh biomass per plant increased by 31 g after *FOS* treatment (Table 3.3).

Table 3.2. *Mean squares and significance tests of the effect of Striga hermonthica and FOS treatment on sorghum and Striga parameters.*

Sources of variation	D.F	Sorghum parameters					*Striga* parameters	
		DFL	PW	BM	SYP	HSW	SV	NS
Replication	2	573.35	395.93	4104	1870.41	2.51	9.98	6.61
FOS	1	190.14**	1880.19*	172416.00*	4601.57**	68.84**	528.73*	789.61*
Error (a)	2	25.84	1569.51	106130	2762.96	5.8	7.3	26.56
Variety	59	322.92***	1550.32***	127429.00***	956.62***	2.43***	1.76	4.12*
FOS x Variety	59	154.99*	422.6*	33053*	487.16**	0.72*	1.51	3.2**
Error (b)	236	141.08	419.77	38665	511.77	0.55	1.33	2.88
Total	719							

*, and ***= denote significant differences at 0.05, and 0.01 probability levels, respectively; D.F = degrees of freedom; DFL = days to flowering; PW = panicle weight; BM = sorghum biomass; SYP = seed yield per plant; HSW = hundred seed weight; SV= *Striga* vigour; NS = number of *Striga* plants and *FOS* = *Fusarium oxysporum* f.sp. *strigae*

Treatment of sorghum seeds with *FOS* in *Striga* control provided various responses among sixty sorghum genotypes (Table 3.3). The following genotypes such as 3933, 3993, 4031,

4643, AS 433 and AS 435 flowered 5 days earlier than untreated control. Seed treatment reduced days to flowering in 27 sorghum varieties varying from 1 to 12 days. Delayed flowering was observed in 29 sorghum genotypes with a mean of 7 days and ranged from 1 to 22 days. Conversely, no treatment effect on days to flowering was observed in 4 sorghum genotypes such as 203, 2246, 4572 and AS 424 where both treated and untreated seeds flowered at the same time (Table 3.3). The influence of *FOS* on days to flowering has been reported by Rebeka et al. (2013) who indicated that *FOS* treated sorghum genotypes matured 13 days earlier than untreated controls.

Mean biomass and panicle weight, and seed yields of sorghum genotypes differed significantly due to *FOS*. Mean biomass weight gain of 66.75 g plant^{-1} was recorded for 24 sorghum genotypes. Panicle weight of 8.67g plant^{-1} for 22 sorghum genotypes was recorded through *FOS* application. Mean hundred seed yield and seed yield plant^{-1} of 0.73 and 12.21 for 54 and 38 sorghum genotypes were observed due to *FOS* treatment, respectively (Table 3.3). Genetic differences and incompatibly of the host to *FOS* could be the results of lower productivity observed in some of the tested sorghum genotypes. *FOS* is reportedly host specific showing maximum genetic diversity and improving growth to some sorghum genotypes while retarding growth in others (Ciotola et al., 2000).

Treating sorghum seeds with *FOS* significantly ($P< 0.01$) reduced *Striga* vigour and number. *FOS* application significantly reduced *Striga* vigour and rated from 1 to 4 in all sorghum genotypes (Table 3.3). Mean reduction of at least two *Striga* plants per sorghum plant in *FOS* treated plants has been counted in 58 genotypes (Table 3.3). A reduced *Striga* vigour and number were observed in the majority of sorghum genotypes evaluated in the present study. This could have been attributed to both genetic resistance present in some genotypes and the ability of the *FOS* in infecting the parasite and retarding its subsequent growth and development. Wilting and weakening *Striga* in holes treated with *FOS* was observed. Overall, the present study identified the following genotypes: 1563, 3937, 3984, 3993, 4031, 4390, 4567, 4643, 630, 654, 672, 675, AS 422, AS 424, AS 426, AS 429, AS 430, AS 433, AS 435 and AS 436 (Table 3.3). These genotypes showed better compatibility to *FOS*, supporting no or few *Striga*, with relatively higher seed yield and biomass.

Table 3.3. Mean agronomic characters among 60 sorghum genotypes, and *Striga* parameters, with (+) and without (-) *FOS* application under *Striga hermonthica* infestation

Variety	DF (d)		PW (g)		BM (g)		SYP (g)		HSW (g)		SV (1-9)		NS	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-
104	**60**	**56**	**53.43**	**54.98**	**211**	**296**	**44.95**	**27.80**	**2.69**	**1.82**	**1**	**3**	**1**	**4**
105	**61**	**52**	**34.68**	**20.34**	**94**	**63**	**17.36**	**16.22**	**2.25**	**1.32**	**1**	**2**	**1**	**3**
1563	**54**	**60**	**24.93**	**24.53**	**154**	**328**	**34.23**	**29.08**	**1.95**	**1.87**	**1**	**2**	**2**	**3**
1580	**61**	**51**	**47.19**	**50.40**	**217**	**288**	**39.55**	**26.87**	**2.80**	**2.19**	**1**	**3**	**2**	**4**
203	58	58	39.60	30.39	162	216	30.78	18.52	2.45	2.41	1	3	2	3
207	50	53	20.01	19.26	250	120	19.61	11.32	2.42	1.81	1	3	1	4
2246	65	65	17.86	26.63	160	118	28.02	37.54	2.27	1.29	1	4	3	5
2255	58	59	30.68	31.00	183	254	30.34	20.34	1.98	1.80	1	3	1	4
2357	63	67	39.14	57.60	303	433	49.35	57.19	3.04	2.17	1	2	2	3
2379	65	70	19.36	20.85	299	225	29.25	24.36	2.79	1.63	1	3	2	5
308	51	61	47.55	37.12	180	164	35.46	40.17	2.46	2.00	1	4	2	5
3424	**61**	**60**	**20.79**	**16.30**	**262**	**143**	**18.33**	**31.03**	**2.32**	**1.73**	**1**	**3**	**2**	**4**
3904	70	62	16.95	37.51	393	363	15.51	26.94	2.66	2.18	1	4	2	6
3933	**57**	**67**	**42.64**	**63.44**	**364**	**441**	**39.64**	**38.20**	**3.50**	**2.75**	**1**	**3**	**2**	**4**
3937	**64**	**57**	**52.67**	**41.34**	**135**	**301**	**47.84**	**30.69**	**2.40**	**1.93**	**1**	**3**	**2**	**4**
3984	**69**	**56**	**55.90**	**48.49**	**236**	**372**	**50.74**	**36.22**	**2.69**	**1.49**	**1**	**3**	**1**	**4**
3993	**54**	**65**	**43.16**	**43.66**	**516**	**304**	**44.23**	**49.19**	**2.49**	**2.10**	**1**	**2**	**2**	**3**
4023	72	63	24.40	28.16	189	374	17.55	16.29	2.39	1.23	1	3	1	5
4027	53	58	32.13	34.43	149	239	33.82	30.45	2.24	1.63	1	4	2	5
4031	**51**	**63**	**30.38**	**26.99**	**257**	**281**	**52.41**	**21.57**	**3.12**	**2.62**	**1**	**3**	**2**	**4**
4368	71	61	20.67	27.96	240	431	25.42	26.49	2.30	1.80	1	2	2	3
4396	**65**	**57**	**59.93**	**38.17**	**234**	**220**	**49.44**	**30.72**	**2.58**	**1.47**	**1**	**2**	**2**	**3**
4543	58	60	31.73	42.77	268	404	67.88	38.71	2.57	1.90	1	3	2	4
4567	**66**	**63**	**49.63**	**36.14**	**205**	**185**	**41.47**	**23.70**	**2.43**	**1.77**	**1**	**3**	**2**	**4**
4572	65	65	23.63	29.59	154	195	31.21	24.74	2.35	1.67	1	2	2	3
4643	**56**	**63**	**44.84**	**57.30**	**243**	**272**	**43.59**	**37.19**	**2.85**	**2.44**	**1**	**3**	**1**	**4**
476	61	69	41.35	37.18	428	202	20.23	30.85	2.73	2.49	1	2	1	2
483	68	60	18.19	36.84	329	512	24.67	11.45	2.50	2.49	2	3	4	5
501	67	55	29.31	49.64	353	550	23.52	23.69	2.69	1.84	1	3	2	4
5275	64	69	35.50	23.85	456	340	29.83	20.57	3.12	2.71	1	4	1	5
536	64	66	22.80	26.09	389	552	28.98	35.30	2.77	1.90	1	2	1	2
550	62	68	30.01	34.55	328	449	27.11	25.14	2.37	2.00	1	3	2	4
575	60	67	17.87	29.50	305	207	26.12	17.29	2.66	2.76	2	3	2	3
594	69	64	22.87	22.42	277	184	38.78	13.92	2.98	2.31	1	2	1	3
612	57	71	40.14	37.74	427	481	41.32	21.83	3.42	2.40	1	2	2	3
630	**63**	**57**	**61.86**	**38.09**	**278**	**301**	**41.57**	**24.52**	**3.50**	**2.27**	**1**	**4**	**1**	**5**
654	**58**	**59**	**41.07**	**28.90**	**332**	**216**	**36.64**	**22.53**	**2.61**	**1.21**	**1**	**3**	**2**	**4**
672	**69**	**67**	**56.23**	**60.37**	**242**	**248**	**46.02**	**46.91**	**2.81**	**1.89**	**1**	**3**	**2**	**5**
675	**58**	**52**	**24.21**	**37.19**	**71**	**187**	**29.34**	**24.85**	**2.13**	**1.26**	**1**	**3**	**1**	**4**
714	71	62	32.19	34.98	163	224	35.09	23.67	2.27	1.70	1	4	2	5
77	62	55	8.67	22.62	518	490	19.43	26.37	1.65	1.91	1	2	3	2
AS421	62	54	22.06	22.77	242	132	29.32	23.31	2.70	1.76	1	4	2	5
AS422	**40**	**44**	**31.43**	**22.89**	**81**	**74**	**23.58**	**24.60**	**2.36**	**1.72**	**1**	**2**	**2**	**2**
AS423	54	51	49.43	45.40	274	255	36.59	43.79	3.97	3.42	1	2	1	3
AS424	**50**	**54**	**42.34**	**53.53**	**205**	**208**	**40.20**	**16.06**	**2.56**	**2.28**	**1**	**2**	**2**	**3**
AS425	65	53	13.35	48.29	111	278	15.22	49.51	3.19	2.69	1	5	2	6
AS426	**63**	**54**	**30.81**	**34.89**	**191**	**173**	**29.50**	**27.73**	**2.65**	**2.77**	**1**	**4**	**2**	**5**
AS427	64	54	38.34	57.70	136	297	32.67	40.43	3.27	1.87	1	3	1	3
AS428	65	60	43.22	66.10	277	317	38.46	44.21	3.35	2.47	1	2	1	2
AS429	**54**	**56**	**41.12**	**43.09**	**218**	**190**	**36.46**	**35.47**	**3.87**	**2.43**	**1**	**3**	**2**	**4**
AS430	**52**	**59**	**44.45**	**60.53**	**293**	**312**	**45.41**	**53.58**	**2.89**	**3.49**	**1**	**4**	**2**	**5**
AS431	62	64	33.11	27.76	152	449	54.45	20.23	2.51	3.28	1	4	1	4
AS432	62	48	39.02	42.78	164	197	26.47	26.52	3.14	2.62	1	2	2	3
AS433	**55**	**63**	**19.46**	**33.10**	**97**	**81**	**22.29**	**32.94**	**2.83**	**1.66**	**1**	**4**	**1**	**5**
AS434	65	65	33.41	39.50	139	203	29.16	29.73	3.16	2.59	1	2	1	3
AS435	**51**	**56**	**29.00**	**52.41**	**146**	**230**	**23.14**	**31.19**	**3.55**	**2.43**	**1**	**2**	**2**	**3**
AS436	**52**	**50**	**34.46**	**24.38**	**153**	**133**	**31.39**	**25.45**	**4.13**	**2.73**	**1**	**2**	**2**	**3**
AS71	52	56	11.86	23.38	94	75	15.06	14.03	2.12	2.71	1	3	2	4
P40281	58	48	29.79	18.56	134	135	42.28	13.50	2.61	1.71	1	3	1	3
PAN8816	57	54	17.09	21.47	111	119	26.36	8.55	2.58	1.72	1	2	2	3
Significance	*		***		***		***		***		***		***	
LSD	1.19		14.98		19.60		2.18		0.09		0.13		0.18	

*, **and ***= denote significant differences at 0.05, 0.01, and 0.001 probability levels, respectively; DF = days to flowering; PW = panicle weight; BM = biomass; SYP = seed yield per plant; HSW = hundred seed weight; MGD = Maximum germination distance; SV= *Striga* vigour; and NS = number of *Striga*

Bold text denotes selected genotypes.

The impact of *FOS* application on sorghum seed yield and number of *Sh* plant per hole in the 60 sorghum genotypes is displayed in Figure 3.1. Count and vigour of *Sh* on hole without *FOS* inoculation was higher than in the treated holes (Figure 3.1). The *FOS* treated sorghum genotypes yielded significantly more than untreated controls. These could be the result of fewer *Sh* infestations and weak *Striga* vigour on the *FOS* treated holes. More *Sh* counts and robust *Striga* vigour were observed in holes grown with sorghum seeds without *FOS* treatment. This finding is supported by Fen et al (2007) who reported the effectiveness of the fungus (*FOS*) in managing *Striga* by surrounding the rhizosphere of sorghum root and retarding *Striga* parasitism to the host plant. Rebeka (2007) reported the ability of the fungus to destroy *Striga* before it penetrates the roots of sorghum.

A few of the treated sorghum genotypes (105, 3424, 207, 3904, 4023, 77, AS 71 and AS 425) had yield performances that were not substantially different from some of the untreated genotypes (203, 575, P 40281, and PAN 8816), despite *FOS* treatment (Figure 3.1). This could be explained by the genotypes being not compatible with *FOS* and thus there was less colonization of *FOS* in the rhizosphere and therefore high *Sh* populations. The ability of *FOS* to work efficiently with some sorghum genotypes has been reported in earlier studies. Ciotola et al (2000) reported strains of *FOS* to be cultivar specific showing considerable genetic diversity and varying in aggressiveness against *Striga.* With some sorghum genotypes (77, 476, 536, AS 422 and AS 428) there was a low *Sh* continuum with plants not treated with the *FOS*, which may reflect varietal resistance against the parasite (Figure 3.1). This was confirmed by poor *Striga* vigour and number of *Sh* observed.

The number of days taken to flowering has a direct relationship with days to maturity. Early flowering genotypes may escape harsh environmental conditions such as drought stress and heavy *Striga* infestation at late stages of the crop. The number of days to flowering and maturity were observed to be negatively correlated to the number of germinated *Striga*. Any technique that reduces the number of *Striga* per plant will accelerate flowering, and indirectly improves seed yield in sorghum. Overall, breeding ideal sorghum genotypes with improved seed yields and *Striga* resistance requires selection of host genotypes with relatively heavy panicles and high seed yield, few and weak *Striga* counts (Table 3.3).

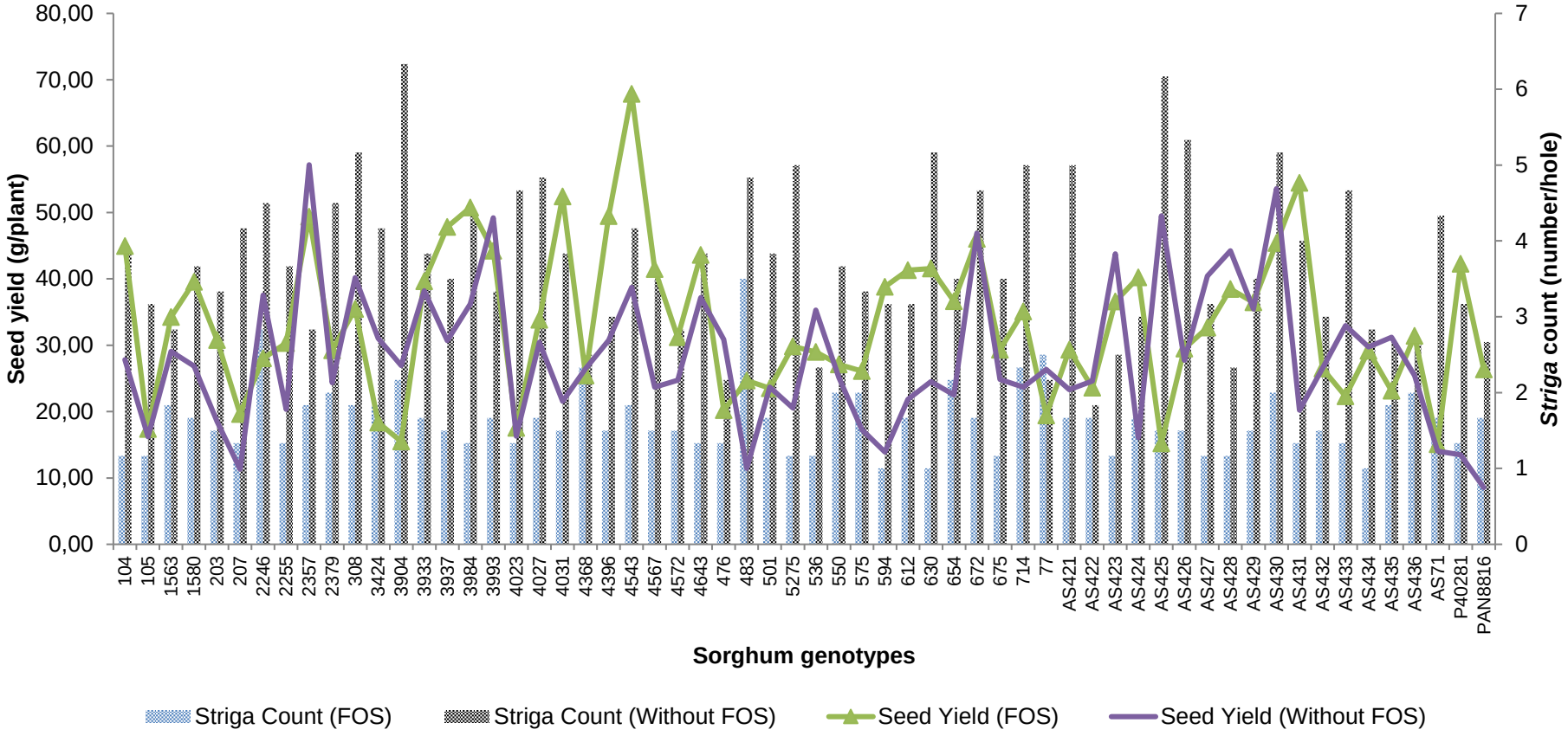

Figure 3.1. Effects of *Fusarium oxysporum* f.sp. *strigae* (*FOS*) application on sorghum grain yield (g/plant) and *Striga hermontica* count per hole on 60 sorghum genotype.

3.4.2 The influence of *FOS* on sorghum growth and yield, and *Striga asiatica* management

The ANOVA of 60 sorghum genotypes evaluated under *Sa* infestation, with and without *F. oxysporum* application, is presented in Table 3.4. Sorghum genotypes differed significantly ($p<0.001$) in yield, yield components and *Sa* counts, under *FOS* treated and untreated conditions. The number of emerged *Striga* counts and mean *Striga* vigour were significantly ($p<0.05$) reduced as the result of inoculation with *FOS* (Table 3.5). Maturity of 31 sorghum genotypes was shortened by 6 days and biomass weight per plant increased by 69 g due to *FOS* inoculation when compared to the untreated plants (Table 3.5). This suggests that *FOS* adversely affected the parasite, improving sorghum growth and development, and improving seed yields (Table 3.5). Sorghum seed yields were significantly higher from holes planted to *FOS* treated seeds, providing seed yields of 15.13 to 64.85 g plant^{-1} .The yield harvested from untreated plants were relatively low, varying from 11.82 to 40.60 g plant^{-1}. Previously Rebeka et al. (2013) reported that sorghum yields from *Sh* infested plots were higher when seeds were treated with *FOS* than in untreated plots. The lower seed yield and increased number of *Striga* associated with some sorghum varieties were due to incompatibility of the genotypes with *FOS* (Ciotola et al. (2000).

Table 3.4. Mean square and significance tests of sorghum and *Striga asiatica* parameters when tested with and without *FOS* application.

Sources of variation	D.F	Sorghum parameters					*Striga* parameters	
		DFL	PW	BM	SYP	HSW	SV	NS
Replication	2	302.49	426.58	47573.2	4451.57	0.2576	40.58	80
FOS	1	116.81*	806.05*	289799.6*	10931.32**	120.42*	288.8	464.01**
Error (a)	2	350.8	908.37	61348.9	1997.5	6.18	45.34	58.94
Variety	59	451.01***	1094.58***	130014.70***	637.68**	2.40***	1.11	1.94
FOS x Variety	59	161.40*	514.73*	30531.2	370.47*	0.72*	1.38	2.67*
Error (b)	236	117.47	518.19	24780.9	385.5	0.65	1.16	2.44
Total	719							

*, **and ***= significantly different at 0.05, 0.01 and 0.001 probability levels, respectively; DF = degrees of freedom; DFL = days to flowering; PW = panicle weight; BM = biomass; SYP = seed yield per plant; HSW = hundred seed weight; SV= *Striga* vigour and NS = number of *Striga*

Growing of sorghum seeds treated with *FOS* in the holes treated resulted in various responses among 60 sorghum genotypes tested (Table 3.5). Thirty one genotypes flowered 6 days earlier than the untreated control (Table 3.5). Delayed flowering was observed in 29 sorghum genotypes with a mean of 5 days. The influence of *FOS* on days to flowering in some sorghum genotypes was reported by Rebeka et al. (2013), who found that, some treated sorghum genotypes matured 13 days earlier than untreated genotypes. Compared to untreated seeds,

FOS dressing improved mean sorghum plant and panicle length by 29 cm for 20 genotypes and 2.9 cm for 29 genotypes, respectively (data not shown). The study recorded decreased mean plant and panicle lengths of 42 cm for 40 genotypes and 2.9 cm for 31 genotypes, respectively (Table 3.5).

Mean biomass, panicle, and grain yields responses of sorghum genotypes differed significantly with *FOS* treatment. The mean biomass was 67 g plant^{-1} recorded in 17 sorghum genotypes. Increased panicle weights by 9 g plant^{-1} were observed for 26 sorghum genotypes due to *FOS* application. The *FOS* treatment caused higher mean hundred seed weight and seed yields plant^{-1} of 0.84 g and 11 g for 59 and 48 sorghum genotypes, respectively.

Striga vigour and number were considerably reduced due to *FOS* application. *Striga* vigour was rated from 1 to 3 in all sorghum genotypes (Table 3.5). About 52 genotypes had two *Striga* plants per sorghum plant following *FOS* treatment. Reduction in *Striga* vigour and number were recorded for the majority of the sorghum genotypes due to both genetic resistance present in some genotypes and the ability of *FOS* to reduce the effect of the parasite. Overall, the present study identified the genotypes 104, 105, 1563, 1580, 3424, 3933, 3937, 3984, 3993, 4031, 4390, 4567, 4643, 630, 654, 672, 675, AS 422, AS 424, AS 426, AS 429, AS 430, AS 433, AS 435 and AS 436 showing good compatibility to *FOS*, supporting no or few *Sa* plants and improved seed yields and biomass (Table 3.5).

Table 3.5. Mean values of sorghum agronomic characters among 60 sorghum genotypes with (+) and without (-) *FOS* application under *Striga asiatica* infestation.

Variety	DF (d)		PW (g)		BM (g)		SYP (g)		HSW (g)		SV (1-9)		NS	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-
104	**62.83**	**52.67**	**31.97**	**38.06**	**172**	**200**	**28.08**	**22.46**	**2.62**	**1.86**	**1.17**	**1.67**	**2**	**3**
105	**56.00**	**53.00**	**38.91**	**15.86**	**231**	**78**	**33.44**	**13.07**	**2.76**	**2.13**	**1.17**	**2.67**	**1**	**3**
1563	**55.83**	**53.83**	**32.52**	**23.78**	**186**	**145**	**35.40**	**11.82**	**3.63**	**0.94**	**1.17**	**3.17**	**2**	**4**
1580	**57.00**	**52.17**	**47.52**	**42.15**	**312**	**332**	**39.94**	**27.18**	**3.26**	**2.75**	**1.00**	**1.67**	**2**	**2**
203	52.67	52.33	24.63	26.48	125	136	23.28	22.03	2.35	1.80	1.17	1.83	1	2
207	56.83	49.67	30.89	18.29	91	155	20.86	20.34	2.15	1.27	1.33	2.00	2	2
2246	56.67	66.50	16.91	24.90	76	203	25.09	25.84	2.28	1.27	0.83	3.00	1	4
2255	60.33	54.33	30.14	27.51	218	268	27.79	26.10	2.05	1.85	1.33	2.50	2	3
2357	63.67	74.67	43.41	40.69	399	342	42.86	26.61	2.87	1.87	1.33	3.50	2	4
2379	65.00	65.83	29.18	36.08	305	501	33.49	26.29	2.90	2.18	1.33	2.17	2	3
308	52.83	54.67	44.60	39.69	128	183	30.28	31.69	2.40	1.80	1.17	1.83	2	2
3424	**62.00**	**64.00**	**27.12**	**21.69**	**284**	**250**	**24.89**	**22.17**	**2.40**	**1.52**	**1.00**	**2.17**	**2**	**3**
3904	64.50	58.67	27.53	30.90	397	328	35.29	21.46	2.79	1.98	1.00	3.83	2	5
3933	**67.33**	**65.83**	**31.88**	**40.69**	**215**	**313**	**16.51**	**26.67**	**3.08**	**2.85**	**1.17**	**1.83**	**2**	**3**
3937	**62.83**	**62.83**	**22.01**	**40.12**	**85**	**263**	**28.78**	**28.16**	**2.99**	**1.88**	**1.00**	**3.00**	**2**	**4**
3984	**62.00**	**68.33**	**29.74**	**59.93**	**238**	**286**	**45.03**	**37.97**	**3.10**	**1.81**	**1.00**	**3.00**	**1**	**4**
3993	**57.83**	**63.33**	**54.89**	**60.73**	**318**	**292**	**47.48**	**40.40**	**2.83**	**1.63**	**1.00**	**2.33**	**1**	**3**
4023	60.67	70.17	22.86	35.19	337	241	36.45	21.23	2.29	1.31	1.17	2.17	2	4
4027	59.00	54.50	33.69	43.04	153	169	26.01	32.97	1.90	1.68	1.17	3.17	2	5
4031	**61.00**	**59.50**	**37.43**	**31.89**	**240**	**244**	**30.08**	**23.92**	**2.96**	**2.57**	**1.17**	**2.33**	**2**	**4**
4368	66.67	72.50	31.74	35.67	457	535	57.69	20.41	3.11	2.22	1.00	2.00	2	3
4396	**54.50**	**59.33**	25.98	33.26	**208**	**246**	**26.49**	**21.54**	**2.77**	**1.53**	**1.17**	**2.17**	**2**	**3**
4543	69.00	66.67	48.75	51.27	369	356	51.33	36.57	2.66	1.95	1.00	2.17	2	3
4567	**55.00**	**61.00**	28.75	55.89	**179**	**304**	**36.16**	**36.12**	**2.32**	**2.12**	**1.17**	**2.17**	**2**	**3**
4572	63.83	69.17	43.73	23.60	128	163	21.85	19.13	2.31	1.60	1.33	3.00	2	4
4643	**57.17**	**54.17**	68.96	44.61	**295**	**200**	**55.89**	**31.29**	**2.84**	**1.78**	**1.33**	**2.00**	**2**	**3**
476	68.17	71.17	30.74	35.24	171	245	44.01	17.81	2.78	1.88	1.17	2.50	2	4
483	58.67	69.33	18.87	27.87	295	550	15.86	22.78	2.56	1.32	1.17	2.00	2	3
501	65.00	59.00	25.16	62.47	342	398	24.04	20.15	2.84	2.02	1.17	1.67	2	2
5275	67.00	67.50	25.09	28.61	517	461	23.51	21.08	2.76	2.21	1.00	2.00	1	3
536	64.67	71.33	16.68	44.17	354	629	21.06	24.22	3.21	2.15	1.00	2.50	2	3
550	50.50	63.33	31.85	37.36	277	345	25.74	25.19	2.83	1.99	1.17	1.33	2	2
575	58.83	71.67	41.66	31.25	188	520	26.99	16.87	2.73	2.39	1.17	2.83	2	4
594	55.67	60.50	19.97	30.64	323	333	22.71	17.10	2.66	1.87	1.17	1.83	3	2
612	59.83	68.83	38.67	37.79	341	403	30.08	29.14	3.85	2.75	1.00	3.00	2	5
630	**58.17**	**69.17**	**36.13**	**44.44**	**186**	**222**	**29.97**	**18.39**	**3.13**	**2.39**	**1.00**	**2.17**	**1**	**3**
654	**55.50**	**54.67**	**35.36**	**24.20**	**145**	**202**	**31.44**	**27.01**	**2.73**	**1.60**	**1.17**	**2.33**	**2**	**3**
672	**60.67**	**68.50**	**38.30**	**64.23**	**246**	**300**	**32.77**	**40.60**	**2.82**	**1.73**	**1.00**	**3.67**	**1**	**5**
675	**55.50**	**51.67**	**35.50**	**33.10**	**137**	**184**	**23.00**	**30.51**	**2.48**	**1.72**	**1.00**	**2.33**	**2**	**3**
714	63.83	71.00	28.25	34.76	232	277	27.89	24.77	2.52	1.74	1.00	1.83	2	3
77	61.83	65.67	31.84	20.58	337	641	24.33	18.61	1.84	1.72	1.33	2.83	2	4
AS421	53.83	53.50	34.09	24.25	224	192	32.76	24.69	2.45	1.90	1.00	1.50	2	2
AS422	**39.83**	**31.17**	**25.63**	**22.91**	**51**	**89**	**21.47**	**13.23**	**2.97**	**1.81**	**1.00**	**2.50**	**1**	**4**
AS423	57.50	57.17	31.22	43.56	269	346	39.02	30.73	3.54	3.23	1.17	2.33	2	3
AS424	**54.83**	**49.83**	**33.87**	**36.18**	**119**	**274**	**32.08**	**24.22**	**3.74**	**2.78**	**1.17**	**2.83**	**1**	**4**
AS425	53.33	52.17	30.02	32.25	287	136	58.46	22.30	3.34	1.47	1.00	2.17	2	3
AS426	**66.50**	**49.67**	**33.02**	**26.55**	**215**	**165**	**29.55**	**21.08**	**3.19**	**2.48**	**2.67**	**2.00**	**2**	**2**
AS427	62.00	48.50	37.29	13.02	135	150	34.71	12.17	3.15	2.80	1.17	2.17	2	3
AS428	62.50	69.83	34.77	50.13	248	342	28.86	29.33	3.37	2.78	1.00	1.67	1	2
AS429	**50.50**	**54.00**	**27.66**	**46.64**	**191**	**323**	**43.04**	**27.31**	**3.96**	**2.47**	**1.17**	**2.33**	**2**	**4**
AS430	**64.33**	**59.00**	**62.51**	**59.44**	**353**	**275**	**64.85**	**27.14**	**3.07**	**2.57**	**1.17**	**2.33**	**1**	**3**
AS431	68.67	49.33	20.76	26.05	142	196	16.81	25.94	3.28	1.82	1.00	3.00	2	4
AS432	49.50	53.67	40.15	35.90	195	257	36.98	31.79	3.92	3.27	1.00	2.17	2	3
AS433	**55.67**	**53.00**	**38.66**	**28.10**	**271**	**165**	**43.25**	**20.37**	**2.67**	**2.35**	**1.00**	**2.33**	**2**	**3**
AS434	60.67	63.50	34.88	52.93	225	361	33.40	28.18	2.81	3.29	1.33	2.67	2	3
AS435	**58.67**	**58.83**	**11.42**	**14.66**	**310**	**258**	**21.26**	**14.92**	**3.19**	**2.53**	**0.83**	**3.67**	**1**	**4**
AS436	**52.50**	**68.67**	35.26	31.06	**130**	**140**	**36.97**	**31.55**	**3.31**	**2.07**	**1.33**	**1.83**	**2**	**2**
AS71	53.50	60.00	17.29	8.80	144	79	28.94	32.50	2.18	2.10	1.00	4.00	1	5
P40281	64.17	53.83	41.23	24.17	176	140	51.51	25.11	3.81	1.92	1.00	2.67	1	3
PAN8816	55.50	50.50	28.43	29.61	99	101	15.13	15.13	2.18	1.18	1.00	1.83	2	3
Significance	***		***		***		***		***		**		***	
LSD	8.195		16.47		113.7		14.408		0.7325		1.0318		1.346	

*, **and ***= significantly different at 0.05, 0.01, and 0.001 probability levels, respectively; DF = days to flowering; PW = panicle weight; BM = biomass; SYP = seed yield per plant; HSW = hundred seed weight; SV = *Striga* vigour and NS = number of *Striga*

Bold text denotes selected genotypes.

The *Sa* count on holes without *FOS* inoculation was higher than in the *FOS* treated holes (Figure 3.2). The impact of *FOS* application on sorghum grain yield and number of *Sa* plant per hole is depicted in Figure 3.2. Low *Sa* counts were observed for several sorghum genotypes with *FOS* application. The following genotypes 4396, AS431, 2357 and P40281, were relatively good seed yielders with *FOS* compatibility. The *FOS* treated sorghum genotypes yielded significantly higher (15.13 to 64.85 g plant^{-1}) than the untreated genotypes (11.82 to 40.6 g per plant^{-1}). The following genotypes: 3904, 4027. 612, 672, and AS 71, displayed higher numbers of *Sa* and robust *Striga* vigour in holes without *FOS* treatment. Fen et al. (2007) reported the effectiveness of *FOS* in supressing *Striga* infestation. The fungus surrounds the rhizosphere of sorghum root, subsequently retarding the efficacy of *Striga* parasitism to the host plant. Ciotola et al. (2000) pointed out that *FOS* is a highly host specific fungus with high levels of genetic diversity and varied levels of aggressiveness against *Striga.*

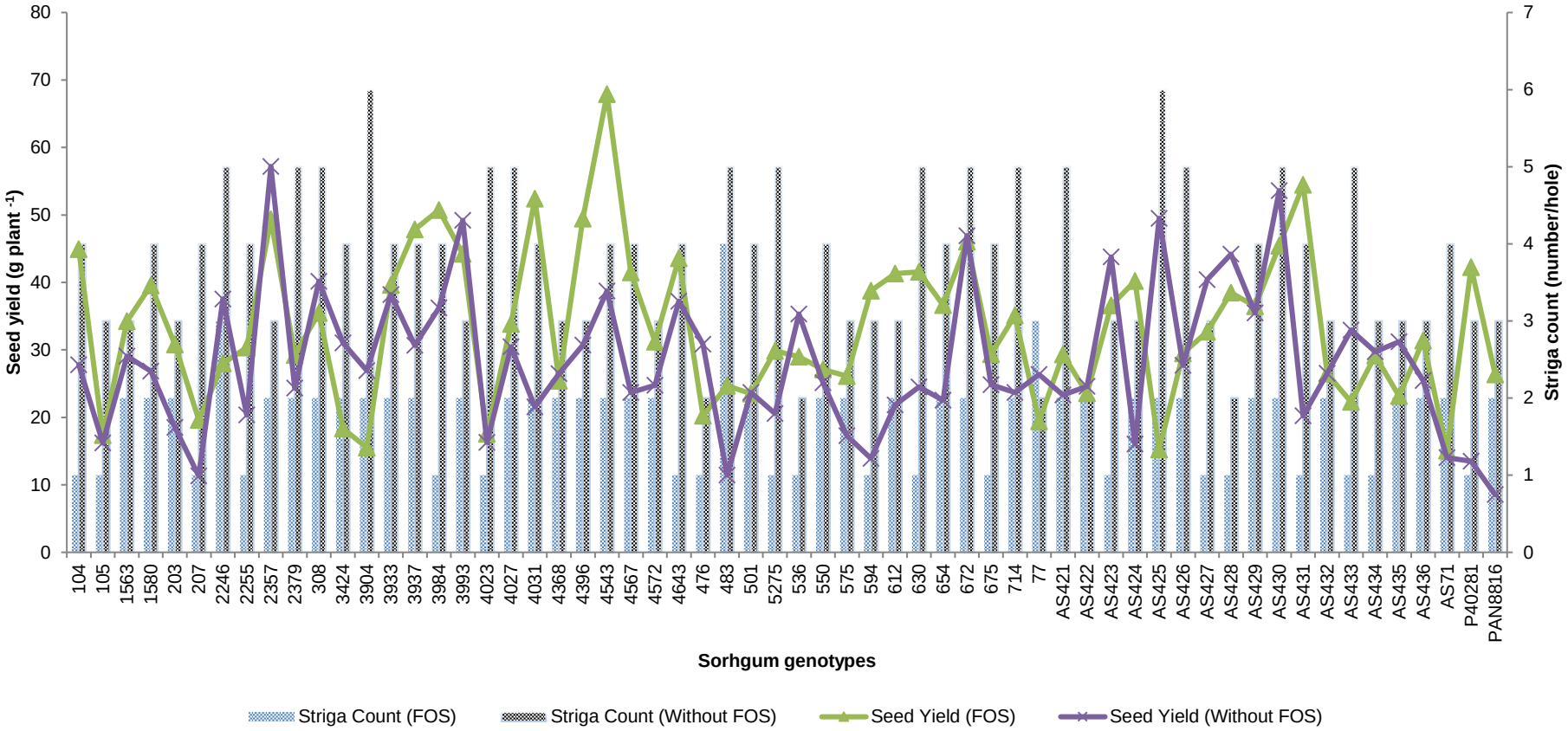

Figure 3.2. Effects of *Fusarium oxysporum* f.sp. *strigae* (*FOS*) application on sorghum grain yield (g/plant) and *Striga asiatica* count per hole on 60 sorghum genotypes.

3.5 Conclusions

The present study found a significant reduction of *Striga* count by 1 to 4 per sorghum plant due to a sorghum seed dressing with the bio-agent, *F. oxysporum* f.sp. *strigae* (*FOS*). Ten sorghum genotypes were identified with significant *Striga* resistance, while 15 genotypes had good seed yield and agronomic traits, when the genotypes were grown under controlled conditions with application of the bio-agent. The following sorghum genotypes: 3937, 3993, 630, 654, 672, AS 424, AS 426, AS 429, AS 430 and AS 436 expressed resistance to both *S. hermonthica* and *S. asiatica*. The *FOS* strain used in the current study was also effective in improving sorghum yield and yield components, simultaneously reducing the number and vigour of both *S. hermonthica* and *S. asiatica.* The present study demonstrated the potential of an integrated *Striga* management strategy that incorporates host plant resistance and biological control using *FOS* as a means to control *S. hermonthica* and *S. asiatica*. Further evaluations of selected sorghum genotypes and their families in the semi-arid ago-ecologies of Tanzania infested with *Striga* species with and without *FOS* application are required to develop sorghum varieties with *FOS* compatibility, *Striga* resistance and enhanced yield levels. In the next chapter, the combining ability of yield and yield components among *FOS*-compatible and *Striga*-resistant sorghum genotypes was investigated to find out promising families and parents for further breeding.

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CHAPTER FOUR

Combining ability of yield and yield components among *FOS*-compatible and *Striga*-resistant sorghum genotypes

4.1 Abstract

Striga hermonthica (*Sh*) and *S. asiatica* (*Sa*) infestation is the leading yield limiting factor of sorghum [*Sorghum biocolor* (L.) Moench] production in the semi-arid areas of Tanzania. The use of *Striga* resistant sorghum varieties compatible with *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, is a novel strategy to control the weed and to enhance sorghum production and productivity. The objective of this study was to identify promising sorghum parents and crosses with *FOS*-compatibility and *Striga* resistance displaying high combining ability for grain yield and yield components for Integrated *Striga* Management (ISM). Hundred sorghum families were developed through controlled crosses using the North Carolina Design II involving 10 female parents selected for their *FOS* compatibility and high agronomic performances, and 10 male parents possessing *Striga* resistance. The F1s and their parents were field evaluated at three locations in Tanzania known for their severe *Striga* infestation using a lattice experimental design with two replications. Significant ($p<0.05$) general combining ability (GCA) and specific combining ability (SCA) effects were recorded among the tested sorghum genotypes at both sites. The following genotypes: 675 and 3424 (female parents), AS426 and AS430 (male parents) were identified as the best general combiners for yield and yield components. Genotypes 672, AS436 and AS429 (male parents) and 3984 (female parents) were the best general combiners for *Striga* resistance, displaying smaller GCA effects in a desirable direction. The following promising families: 675 x 654, 3424 x 3933 and 4567 x AS426 were selected for further breeding because they displayed larger SCA effects for grain yield. Crosses selected with small SCA effects for *Striga* counts were 4567 x AS424 and 3984 x 672. The selected sorghum parents and crosses are useful genetic resources for breeding, and for the implementation of ISM in sorghum.

Keywords: biocontrol *Striga* control, combining ability, *Fusarium oxysporum* f.sp.*strigae*, resistance breeding, sorghum

4.2 Introduction

Striga infestation is one of the main challenges affecting sorghum production in sub-Saharan Africa (Watson et al., 2007). *Striga hermonthica* [Del.] Benth and *S. asiatica* [L.] Kuntze, are the two main obligate parasitic weeds that inflict severe yield losses reaching up to 100% in susceptible sorghum varieties (Doggett, 1953; Lagoke et al., 1991; Riches, 2003). However, the level of yield losses depends on the level of infestation, climatic conditions and control measures (Tesso et al., 2007). Both *Striga hermonthica* and *S. asiatica* parasitize several cereal crops including maize, sorghum, millet, and upland rice across extensive agro-ecological areas in sub-Saharan African countries including Tanzania. Poor soil fertility, use of a single method in *Striga* management and cereal mono-cropping are among the major causes of *Striga* perpetuation, and high yield losses in sorghum (Parker, 1991). *Striga* is highly productive, with each plant plant producing up to 5,000 to 84,000 seeds that remain viable in the soil for up to 20 years (van Mourik et al., 2008). *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*) infestation has reached endemic proportions in the semi-arid areas of the Lake, Western, and Central Zones of Tanzania where the parasite is a serious threat to sorghum production. In these areas farmers are often compelled to abandon their farm lands to *Striga*, and switch to cultivation of non-host crop species. In some localities farmers grow unimproved sorghum landraces that are less susceptible to *Striga* (Mrema et al., 2016)

The use of resistant varieties, biological agents, cultural practices and chemical control methods are important strategies to manage *Striga* infestation (Kenga et al., 2004). These strategies promote growth and development, and reduce germination and development of the juvenile *Striga* plants (Kenga et al., 2004). Combined use of various *Striga* management options, and understanding the biological and metabolic relationships between the host and parasite are important pre-requisites for the implementation of Integrated *Striga* Management (ISM) (Reda and Verkleij, 2004). The development use of resistant varieties is the most environmentally friendly and economical *Striga* management option for millions of smallholder farmers in sub-Saharan Africa who depend on sorghum production for their livelihoods.

Biological control involves the use of microbes to control *Striga* and can be applied to smallholder farming systems (Rebeka et al., 2013). The method is more affordable and environmentally friendly than chemical control practices (Abbasher et al., 1998). Changes in biotic and abiotic conditions due to the presence of microbes surrounding the rhizosphere have been reported to retard the efficacy of *Striga* parasitism of the host plant (Beed et al., 2007) and may stimulate host growth, development and productivity (Rebeka et al., 2013). Different microbial communities have been reported to have different impacts on *Striga* and

the host (Beed et al., 2007). Pathogenic isolates of *Fusarium oxysporum* f.sp. *strigae* (here after referred to as *FOS*) are reported to be effective bio-herbicides to manage *Striga* infestation in sorghum, particularly when the method is integrated with other control practices (Rebeka et al., 2013). The biocontrol fungus destroy *Striga* before it penetrates the roots of sorghum. *FOS* is reported to be host specific, its inoculum can be mass-produced easily and it shows high levels of genetic diversity (Ciotola et al., 2000). When sorghum seeds are treated with *FOS*, the fungus grows well in the rhizosphere of the sorghum plants. It infects and inhibits growth and development of *Striga*, stopping it from parasitizing the roots of the host plant (Rebeka, 2007).

One of the main goal of sorghum breeding program is to develop sorghum genotypes that are resistant or tolerant to *Striga* with farmers' trait of preferrence and compatible with *FOS* (Shayonowako et al., 2017). This requires an understanding of the genetics of sorghum parents and their crosses in order to devise an effective selection procedure. Crosses between parents from genetically unrelated populations or different heterotic groups may result in suitable genetic recombinants and superior transgressive segregants (Makanda et al., 2009; Konate et al., 2017). Equally important is the nature of gene action affecting the inheritance of quantitative and qualitative traits of economic importance.

Both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in conditioning economic traits (Stoskopf, 1993). General combining ability represents mainly the additive and additive x additive type of genetic variance as reported by Kenga et al. (2004), while SCA is mainly due to genes with dominance and/or epistatic effects. Combining ability tests based on mating designs such as the North Carolina Design II (NCD II) and diallel methods, are useful in selecting suitable parents and transgressive segregants of given crosses to use in breeding programmes and to determine the subsequent selection procedure to follow.

In an attempt to select *Striga* resistant and *FOS* compatible sorghum lines, promising genotypes were identified through controlled evaluations (Chapter 3). Some of the selected landraces were relatively poor yielders but adapted to the drier regions of Tanzania and possessed farmers-preferred traits. In contrast, some of the introduced sorghum genotypes had better yield potential and *FOS* compatibility, but they lacked farmers preferred traits. Previous studies employed several genetic parameters of sorghum genotypes under *Striga* infestation. The study reported the influence of additive and no-additive gene actions on the expression of *Striga* resistance, as well as the differential expression of heterosis and heritability of economictraits among varied populations (Mutengwa et al., 1999; Haussmann et

al., 2001). However, there is limited work that elucidate the genetic effect of *Striga* resistance in sorghum when integrating *FOS* as a biocontrol method of the parasite. This knowledge would serve as a selection guide for both *Striga* resistance and *FOS* compatibility to enhence integrated *Striga* management. Therefore, the objective of this study was to identify the nature of gene action controlling grain yield and yield components and to select promising sorghum crosses with *FOS*-compatibility and *Striga* resistance displaying high combining ability for these traits under *Striga* infestation with and without *FOS* application. The hypothesis being tested was that additive genetic effect could be important in controlling *Striga* resistance and that the new families could be selected with farmers preferred traits.

4.3 Materials and methods

4.3.1 Plant materials and crosses

Hundred single cross hybrids developed using 10 female and 10 male sorghum lines and two checks were evaluated in the present study. Crosses were performed using the North Carolina Design II. A description of the 20 varieties used to generate the crosses is shown in Table 4.1. The genotypes were selected from previous evaluation studies (Chapter 3). These materials had different levels of reaction to both *S. hermonthica* and *S. asiatica*. Resistant lines exhibited less *Striga* counts, while tolerant lines yielded well under heavy *Striga* infestation compared to their comparative control. Other genotypes were *FOS* compatible, manifesting *FOS* proliferation and reduced *Striga* count under *FOS* treatment (Chapter 3). Further, the selected lines had most of the farmers' preferred traits in the semi-arid areas of Tanzania.

Table 4.1. List and descriptions of parental sorghum genotypes used in crosses

Entry	Name	Source	Attributes	Entry	Name	Source	Attributes
1	4567	Magu/Tanzania	High yielding, medium maturing and *FOS* compatible	11	AS 436	ICRISAT/India	Early maturing, medium yielding and *Striga* resistant
2	675	Tarime/Tanzania	Early maturing and *FOS* compatible	12	AS 426	ACCI/South Africa	Medium maturing and yielding, and *Striga* tolerant
3	1563	Bukoba/Tanzania	*FOS* compatible, early maturing and high yielding	13	672	Musoma Rural/Tanzania	Medium maturing and *Striga* resistant
4	AS 435	ACCI/South Africa	High yielding and late maturing	14	3933	Serengeti/Tanzania	Early flowering and *Striga* tolerant
5	4643	Misungwi/Tanzania	*FOS* compatible and early maturing	15	AS 430	ACCI/South Africa	Early maturing and *Stiga* tolerant
6	104	Kishapu/Tanzania	*Striga* susceptible, early maturing and high yielding	16	AS 429	ACCI	Early maturing, *Striga* resistant, and medium yielding
7	4031	Ukerewe/Tanzania	Early flowering and high yielding	17	3937	Serengeti/Tanzania	*Striga* resistant
8	3424	Igunga/Tanzania	*FOS* compatible and medium maturity	18	630	Serengeti/Tanzania	*Striga* resistant
9	AS 422	ACCI/South Africa	High yielding and early maturing	19	654	Bunda/Tanzania	*Striga* resistant
10	3984	Musoma/Tanzania	*FOS* compatible, high yielding and late maturing	20	AS 424	SARC/Ethiopia	Early maturing and *Striga* tolerant

Entries 1 to 10 were used as female parents and 11 to 20 as male parents.

SARC = Sirinka Agricultural Research Centre in Ethiopia; ICRISAT = International Crop Research Institute for the Semi-arid Tropics/India and ACCI=African Centre for Crop Improvement

4.3.2 Bio-control agent and inoculation preparation

A pathogenic strain of *F. oxysporum* f.sp. *strigae* (*FOS*) originally isolated from sorghum fields infested with *Striga* in north eastern lowlands of Ethiopia was used (Rebeka et al., 2013). The strain was positively diagnosed at Humboldt University's Phytomedicine Division and isolates were maintained at -40^{o}C on Special Nutrient Agar (SNA). Previous reports confirmed the pathogenicity and host specificity of the *FOS* isolate to *Striga* (Rebeka et al., 2013; Mrema et al., 2017). Cultures were grown on potato dextrose agar (PDA) and pure chlamydospores were extracted and mass produced at Plant Health Products (pty) Ltd, South Africa and stored at the University of KwaZulu-Natal's Plant Pathology Division. About 500 seeds of each sorghum genotype were surface sterilized using 70% ethanol and soaked in 1% sodium hypochlorite solution for 30min. The seed were dried under a laminar airflow. Dry seed were then coated with *FOS* using the procedure described by Elzein et al. (2006), involving film coating of each seed with a mixture of 40% Arabic gum and fresh spores and dried under a laminar airflow.

4.3.3 Experimental sites

One hundred sorghum hybrids and two standard check varieties were evaluated at three locations namely: Igunga, Misungwi and Kishapu of Tabora, Mwanza and Shinyanga Regions, respectively (Table 4.2). Evaluations were conducted during the main cropping season of December 2015 to April 2016. Field evaluations were conducted with and without *FOS* application. The study sites represent the semi-arid areas of Tanzania and known for their sorghum production and *Striga* infestation both by *S. hermonthica* and *S. asiatica*. However *S. hermonthica (Sh)* was the dominant species. An introduced sorghum variety 'Macia' widely grown in Tanzania and AS436 from ICRISAT India were included as susceptible and *Striga*, which is resistant checks, respectively.

Table 4.2. Descriptions of the three locations used for evaluation of crosses and standard checks

Location/site name	Region	Latitude (^{0}South)	Longitude (^{0}East)	Altitude (m)	Rainfall (mm)	Temp (Min, ^{0}C)	Temp (Max, ^{0}C)
Mbutu	Tabora	4.23	33.91	1060	134	17.50	29
Mwanangwa	Mwanza	2.96	33.16	1176	235	19.33	28
Isoso	Shinyanga	3.62	33.84	1126	234	19.33	28

Min=minimum; Max=maximum

4.3.4 Experimental design and trial establishment

The crosses were field evaluated using a 10 x 10 alpha lattice experimental design, running separately for two *FOS* treatments, with two replications at each location using three row plots. Each row was 0.9m wide with total plot width of 2.7m and length of 5.1m. Each replication consisted of the 100 hybrids randomly allocated across 10 incomplete blocks, each with 10 genotypes. However, the two parental genotypes were established in separated plots with two replications as comparative controls. The *FOS* treatments involved seeds treated with *FOS,* and a set planted without *FOS* inoculation. To ensure even distribution of *Striga* population, artificial *Striga* infestation was done according to Berner et al. (1997) by using a scoop of 1:99 ratio of seed and sand mixture, respectively. This ensured delivery of about 5000 viable *Striga* seeds. This was done after preconditioning the seeds by drenching the mixture in water and incubating it for a week at room temperature. Sorghum genotypes were planted with inter-row spacing of 90 cm and intra-row spacing of 30 cm. Two seeds per hill were sown and later thinned to one seedling per hill, two weeks after planting, to have a plant density of 37,037 ha^{-1}. Also, 60 $kgha^{-1}$ of NPK 20-10-5 fertiliser was applied three weeks after sowing. The crops were raised under rain-fed conditions. Apart from *Striga*, other weeds were hand weeded immediately when observed. To control stem borer, Attakan C344SE, a systemic insecticide, was mixed with water at a ratio of 15 ml of Attakan C344SE to 20 liters of water, and sprayed to the crop at a rate of 1 liter per 50 m^2. During seed set and grain filling stages fungal diseases were controlled through two scheduled applications of Hexaconazole 5 EC, a systemic fungicide, at a rate of 30 ml per 20 litres of water. Bird scares were implanted at the middle and corner sections of each field to prevent bird damage.

4.3.5 Data collection

Data on sorghum and *Striga* parameters were collected. Seven sorghum plants from the middle rows on each plot were tagged for data collection. Data on sorghum parameters included days to 50% flowering (expressed in days [d]), plant height (expressed in cm) measured at 50% flowering, seed yield (g/plant) and weight of 100 seeds (g/100 seed). A quadrant of 0.09 m^2 was placed around sample plants and the number of *Striga* plants in the quadrant were counted and recorded as *Striga* counts.

4.3.6 Data analysis

Data collected were analysed using an alpha lattice procedure of the SAS (SAS, 2011). Combined analysis of variance (ANOVA) was performed following tests for normality of the data and homogeneity of variances. Genotypes are treated as fixed factors, while location, replication and incomplete blocks were treated as random factors.

Estimation of combining ability effects

Both the GCA and SCA effects were estimated from parental varieties and crosses, respectively. The standard checks were excluded while analysing combining abilities. The GCA effects of females and males, the SCA effect of crosses, and their interactions with the environment were determined following the NCD II mating design and using the following model: *Yijk* = μ + *gi* + *gj* + *Sij* +*ek* + (*ge*)ik +(*ge*)jk +(*se*)ijk, where *Yijk* = the performance of the hybrid developed with *ith male* and *jth female*, in the *kth* location, μ = the overall mean; gi = the effect of the i*th* male; gj = the effect of the jth female; sij = the interaction of the ith male with the jth female; ek = the effect of the kth environment; (ge)ik = the interaction of the gi and ek; (ge)jk = the interaction of the gj and ek; (se)ijk = the interaction of sij and ek.

According to Hallauer and Miranda (1988), male (M) and female (F) main effects represent two independent estimates of GCA, which are designated GCA_M and GCA_F, respectively. The F x M component is equivalent to the SCA effect. The significance of GCA mean squares of males [GCA (M)] and that of the females [GCA (F)] in each location was determined using the M x F interaction as the error term while the significance of the M x F interaction (SCA) was determined using the error mean square as error term. Since the combining ability mean squares were calculated based on cross means of each genotype from each location, error mean squares calculated for crosses above were used to test the significance of GCA and SCA interactions with location (Singh and Chaudary, 1985). The proportional contributions of Males (GCA_M), Females (GCA_F), and their interaction (SCA_{MxF}) to the sum of squares of crosses were calculated as the ratio between the sum of squares of each component and the cross sum of squares (Singh and Chaudary, 1985). The GCA effects of females and males were calculated as a deviation of the male and female mean from all hybrids mean as per Singh and Chaudary (1985). The SCA effects were calculated as a deviation of each cross mean from all hybrid means adjusted for corresponding GCA effects of parents, as suggested by Singh and Chaudary (1985).

Components of variance was partitioned from the mean square as follows: error variance (σ_w^2) = total variance (δ^2_P) - covariance of full sibs (Cov_{FS}) = ½ δ^2_A+ ¾ δ^2_D + δ^2_{EW}; female and male variance σ^2_{FM} = cov_{FS} – 2covariance of half sibs (cov_{HS}) = ¼ δ^2_D; male variance σ^2_m = female variance σ^2_F = $Cov_{(HS)}$ = ¼ δ^2_A; total variance (δ^2_P) = σ^2_W + σ^2_{FM} + [(σ^2_F + σ^2_M)/2]; male additive variance (δ^2_{AM}) = 4σ^2_M; female additive variance (δ^2_{AF}) = 4σ^2_F; dominance variance (δ^2_D) = 4σ^2_{FM}, environmental variance (δ^2_{EW}) = σ^2_w – (½δ^2_A + ¾ δ^2_D); heritability h^2 = 2(σ^2_F + σ^2_M)/σ^2_P = δ^2_A/δ^2_P; heritability in male (h_M^2) = 4σ^2_M/σ^2_P = δ^2_{AM}/δ^2_P; and heritability in female (h_F^2) = 4σ^2_F/σ^2_P = δ^2_{AF}/δ^2_P (Muhammad et al., 2010).

4.4 Results and discussion

4.4.1 Combined analysis of variance

The analysis of variance across location showed highly significant (P<0.01) differences among the crosses for both sorghum and *Striga* parameters (data not shown). The results from combined analyses of variance for grain yield, yield related traits and *Striga* count are presented in Table 4.3. Highly significant differences (P<0.01) were detected among females, males, and females x males interaction with and without *FOS* application. These sources of variations had significant interactions with the testing sites for grain yield, hundred seed weight and *Striga* count. There were also highly significant differences (P<0.01) among females, males and females x males x environment interaction effects on plant height and days to flowering (Table 4.3).

The significance of the mean squares of the GCA effects of females and males and the SCA effects of F x M indicated the importance of both additive and non-additive gene effects, respectively. This concurs with the findings reported by Hallauer and Miranda (1988). The GCA sum of squares of the interaction effects of females and males were greater than the GCA sum of squares of the main effects of females and males for all traits respectively, indicating that non-additive gene effects contributed more favourable genes towards high values for these traits. Significant mean squares (P<0.01) of environments for the traits revealed that the responses of the genotypes across the testing environments were different. The significance of mean squares due to genotypes (P<0.01) indicated the existence of genetic variability for breeding.

Table 4.3. Mean squares and significant tests of yield and yield related traits and *Striga* count of 100 sorghum hybrids derived from 10 x 10 NCDII and evaluated with (+) and without (-) *Fusarium oxysporum* application in three environments in Tanzania

		Sorghum parameters									
		DFL		PH		SYP		HSW		NS	
Source	**DF**	**+**	**-**	**+**	**-**	**+**	**-**	**+**	**-**	+	-
Env	2	1729.13**	2454.07**	116933.92**	38545.10**	2027.53**	1019.46**	14.60**	21.35**	35290.51**	84653.56**
Rep(Env)	3	5.83**	26.56**	221.59*	309.07**	262.72**	164.13**	1.77**	1.27**	2.43	17.71
GCAf	9	149.35**	165.72**	4958.92**	2234.51**	1181.62**	970.91*	2.78**	1.89**	935.04**	884.45**
GCA_M	9	102.76**	114.16**	3361.30*	612.11**	525.66**	556.76**	2.12**	1.95**	2477.42**	3192.39**
SCA	81	104.54**	107.33**	2271.78**	1184.85**	786.44**	747.08	2.86**	1.78**	567.63**	1254.55**
GCA_F*Env	18	33.52**	29.49**	8565.46**	2960.94**	402.89**	297.40**	1.05**	1.01**	1171.08**	1419.31**
GCA_M*Env	18	37.33**	28.33**	1826.00**	1264.30**	538.78**	481.26**	1.92**	1.64**	2309.97**	3066.36**
SCA*Env	162	36.93**	42.68**	2119.17**	1268.31**	307.22**	239.38**	1.56**	1.16**	564.12**	1233.46**
Error	297	1.31	1.84	53.46	31.31	15.14	4.75	0.02	0.06	9.95	27.22
$SSGCA_F$ %		12.52	13.30	17.24	16.54	13.45	11.77	9.06	9.48	10.97	5.76
$SSGCA_M$ %		8.61	9.16	11.68	4.53	5.98	6.75	6.93	9.82	29.07	20.77
SSSCA %		78.87	77.54	71.08	78.93	80.57	81.49	84.01	80.69	59.95	73.47

* = significant at 0.05 probability level, ** = significant at 0.01 probability level, DF = degrees of freedom, DFL = days to flowering; PH = plant height at 50% flowering; SYP = seed yield per plant; HSW = hundred seed weight; NS = number of *Striga* plants

Env = environment; Rep (Env) = replication within environment; GCAf = general combining ability of female; GCAm = general combining ability of male; SCA = specific combining ability; GCAf*Env = general combining ability of female x environment interaction; GCAm*Env = general combining ability of male x environment interaction; SCA*Env = specific combining ability x environment interaction; SSGCAF % = percentage sum square of the general combining ability of female; SSGCAm % = percentage sum square of the general combining ability of male; and SSSCA % = percentage sum square of the specific combining ability

4.4.2 Mean response of crosses and checks for agronomic traits and *Striga* resistance with and without *Fusarium* application

The mean values of the 100 crosses and two standard checks for days to flowering, plant height, seed yield, hundred seed yield and number of *Striga* with and without *FOS* applications across three environments are presented in Table 4.4. Treatment of sorghum seeds with *FOS* for *Striga* control provided various responses among 100 crosses and standard check sorghum genotypes (Table 4.4)

Seeds of sorghum crosses treated with *FOS* flowered earlier than the untreated control. *FOS* treatment enhanced early flowering by 1 to 9 days with a mean of 4 days. The following *FOS* treated sorghum crosses: 1563 x AS426, 675 x AS430 and 4643 x 630 flowered 9 days earlier than the untreated control. Early flowering has significance implications because early maturity provides for an escape mechanism against terminal drought and heavy *Striga* infestation, which typically occurs during the late stages of plant development. The influence of *FOS* on reducing days to flowering in some sorghum genotypes has been reported by Rebeka et al. (2013). The authors found that that *FOS* treated sorghum genotypes matured 13 days earlier than untreated controls. Selection of early maturing genotypes has been considered as one of the options to mitigate the negative effects of *Striga* and drought. Farmers' preferences for early maturing genotypes has also been reported in earlier studies where moisture stress and variability were a common phenomenon (Kriegshauser et al., 2006; Rebeka et al., 2013; Mrema et al., 2016).

FOS treated sorghum crosses had variable plant height that ranged from 18.67 to 145.67 cm with a mean of 65 cm. The crosses showing long plant heights due to *FOS* application included 3984 x AS430, 3984 x AS426 and 3424 x AS424 measuring 132.67, 136 and 145.67 cm, respectively. This indicated the highest level of compatibility of the crosses with *FOS* resulted in taller plants. All plants have a positive relationship with improved biomass production, which is one of the most important farmer preferred attributes in sub-Saharan Africa (Kriegshauser et al., 2006). In the region sorghum is grown both for multiple uses with the grain for food and the stalk for animal feed, fire wood or construction material.

Variation in seed yield and hundred seed weight was observed among families, with and without *FOS*. Mean grain yield plant^{-1} of 52.62, 77.44 and 82.98 gplant^{-1} were achieved by *FOS* treated crosses including 675 x AS430, 4567 x AS426 and 104 x AS429, respectively. The yield response of these crosses was markedly higher than AS436, the *Striga* resistant

check which provided 52.17 gplant^{-1} with *FOS* application. Such crosses could have suitable gene combination for high yield, *Striga* tolerance and *FOS* compatibility. Therefore, these are useful genetic stocks to be used for further selection and progeny evaluation. The mean hundred seed weight of 98 crosses increased from 0.05 to 1.58 g due to *FOS* treatment. Marked differences in genetic constitution and incompatibility of the sorghum crosses to *FOS* could have contributed to the observed variation in seed yield and hundred seed weight. *FOS* was found to be host specific, consequently differential responses and genetic plasticity noted among the tested genotypes. These resulted in positive responses towards some sorghum genotypes, while growth was retarded in others (Ciotola et al., 2000).

Treating sorghum seeds with *FOS* significantly ($P< 0.01$) reduced the number of *Striga* per plant in the tested population. A mean reduction of 13 *Striga* plants per sorghum plant was recorded due to *FOS* treatment. A reduced number of *Striga* plants were observed in 99 sorghum crosses (Table 4.4). Only 1 to 2 *Striga* per plants sorghum plant were counted for the following crosses: 3424 x AS430, 1563 x 3937, 4567 x 654, 104 x 630, 3984 x 630, 4567 x 3993 and 3424 x 654. A mean of 4 *Striga* plants were counted in the resistant check, AS436, when its seeds were treated with *FOS*. The above experimental hybrids are useful genetic resources for direct production in *Striga* infested sorghum areas of Tanzania. Reduced *Striga* count in sorghum genotypes treated with *FOS* was also reported by Rebeka et al. (2013).

Table 4.4. Mean grain yield and yield components and number of *Striga* per plant under artificial *Striga* infestation with (+) and without (-) *Fusarium oxysporum* application among sorghum hybrids evaluated at three locations in Tanzania

Genotypes	DFL (d)		PH (cm)		SYP (g)		HSW (g)		NS	
	+	-	+	-	+	-	+	-	+	-
Crosses										
AS422 x 654	59.67	66.67	144.00	109.33	19.88	13.99	2.88	1.55	13.33	26.67
4567 x AS424	52.00	57.33	161.50	124.00	16.84	12.86	1.50	1.18	5.17	14.17
675 x 630	68.17	71.33	140.17	112.17	24.90	21.33	1.25	0.75	12.67	43.67
AS422 x 672	67.17	73.33	111.17	92.50	27.62	23.41	2.60	2.00	10.50	20.00
AS422 x AS429	66.00	67.83	115.50	66.83	29.13	23.54	1.73	1.43	4.00	13.83
AS422 x AS436	67.67	71.17	111.67	75.17	24.77	20.15	2.22	1.65	4.67	12.00
4567 x AS426	61.67	65.00	129.50	79.00	52.62	58.08	1.85	1.93	17.00	64.83
4567 x 672	68.17	72.50	85.33	60.50	17.52	12.63	1.47	1.02	10.00	25.67
4567 x AS430	67.33	69.83	105.17	59.33	41.41	31.58	2.10	1.58	19.83	25.17
1563 x 3937	68.67	72.00	132.83	64.17	21.40	16.54	2.22	1.69	1.50	2.83
4567 x 654	62.33	66.67	114.17	63.83	28.66	23.62	1.60	1.07	2.33	4.33
4567 x 630	68.00	72.00	146.00	70.33	31.61	23.89	1.92	1.30	11.67	18.17
3424 x AS426	68.50	72.33	123.00	61.50	24.38	19.38	3.58	2.87	7.83	19.33
4567 x 3937	71.50	73.83	148.83	72.33	31.71	23.23	4.23	2.65	24.67	34.00
104 x 672	70.00	72.83	149.83	60.00	31.02	26.17	1.67	1.10	24.50	40.67
3424 x AS436	55.67	60.67	117.17	66.67	33.16	27.96	2.93	1.95	7.17	13.17
1563 x 672	69.00	72.67	142.00	85.83	23.08	18.99	1.78	1.23	13.17	26.00
AS422 x AS430	68.33	72.67	124.33	90.83	27.81	21.37	1.45	1.00	7.67	14.50
4643 x 630	69.83	78.67	120.67	98.00	27.27	19.70	1.72	1.28	9.67	14.33
104 x 3937	69.00	73.00	120.83	85.17	28.04	23.09	2.28	1.23	23.00	46.17
3424 x 430	67.17	69.67	162.83	106.17	27.93	18.86	1.73	1.25	1.17	3.67
1563 x 630	58.83	62.50	143.00	79.00	32.24	25.94	2.12	1.68	5.83	11.67
1563 x 436	70.33	74.83	134.83	65.50	28.91	22.15	2.73	2.27	13.00	38.33
AS435 x AS426	64.83	72.67	113.00	81.50	21.33	19.37	2.68	1.83	20.83	28.67
675 x 654	64.17	66.50	126.50	77.50	49.16	40.30	3.03	2.43	19.83	22.67
1563 x AS426	56.33	65.00	156.83	72.33	40.81	32.51	2.98	1.85	1.17	2.50
AS435 x AS429	67.17	71.50	100.33	63.00	24.98	20.46	1.77	1.20	14.67	35.67
1563 x AS430	71.00	75.67	99.33	73.33	19.28	15.07	1.57	1.00	12.00	21.50
4643 x 430	65.00	69.67	130.00	76.67	31.15	23.13	1.52	0.97	8.00	38.67
AS435 x 630	68.67	71.67	94.17	70.83	30.38	24.13	2.23	1.25	25.17	33.67
104 x AS424	63.00	70.17	136.33	94.17	30.21	23.45	3.85	3.13	5.33	14.67
104 x AS436	63.33	69.00	129.33	69.50	29.69	24.52	1.72	0.92	8.33	35.33
104 x 630	62.33	66.00	119.83	72.17	31.68	27.12	1.80	1.22	1.17	3.50
AS435 x 3993	65.00	69.17	128.83	98.33	32.56	29.42	2.23	2.02	13.50	19.33
AS435 x 672	71.00	74.50	129.33	87.00	23.58	17.61	1.82	1.38	31.17	42.50
4031 x 630	65.00	69.50	135.50	91.17	25.30	20.34	2.18	1.63	3.83	12.17
4031 x 654	64.50	70.83	136.67	105.50	50.09	42.18	2.33	1.67	10.17	26.67
4031 x AS426	69.67	74.17	134.67	83.50	44.06	41.47	2.82	1.95	8.00	19.50
4031 x 3937	68.33	72.00	162.50	80.00	37.43	27.35	4.58	3.62	20.00	38.00
AS422 x 3993	63.50	64.67	124.17	78.83	20.75	12.95	1.73	1.15	25.67	41.67
AS422 x 630	54.00	60.33	128.67	63.00	24.96	19.64	2.23	1.30	8.50	36.67
AS422 x 3937	58.67	60.50	145.17	65.00	28.11	21.55	2.10	1.25	8.17	17.00
AS422 x AS424	58.50	61.00	170.33	86.17	23.32	17.63	1.73	1.58	3.83	8.83
AS435 x 3937	70.33	74.33	141.50	85.17	26.74	21.37	1.87	1.27	7.67	10.17
3424 x 672	70.33	73.17	143.00	87.17	27.60	23.60	1.88	1.40	15.17	42.83
3424 x 3937	62.33	66.83	154.00	92.33	32.45	27.59	1.85	1.27	7.83	14.50
3424 x AS429	53.33	55.83	152.17	95.50	51.39	53.19	2.50	1.55	4.67	18.83
104 x AS426	70.00	71.67	143.83	99.50	49.84	42.59	2.88	2.28	20.50	34.50
104 x AS429	63.33	65.83	124.83	79.00	82.98	65.50	2.95	1.73	4.50	13.33
104 x 3993	66.17	70.33	133.67	73.67	24.35	16.63	1.42	0.93	20.00	31.67
4031 x AS430	68.67	73.33	142.00	75.83	20.71	12.12	1.38	1.02	5.17	10.00
3424 x 630	67.83	72.33	156.33	80.00	20.19	14.45	1.80	1.42	5.67	20.67
3424 x 3993	59.33	63.00	149.00	83.00	22.74	15.26	1.62	1.13	2.17	5.50
3984 x 3937	56.50	62.00	168.67	67.67	20.92	16.96	1.53	1.05	20.67	23.17
3984 x 672	54.50	56.17	179.67	52.17	41.77	33.08	2.10	1.37	13.00	27.33
3984 x 630	54.83	56.50	179.33	59.33	27.94	21.56	2.98	2.25	1.50	3.67
3984 x AS430	65.83	71.50	194.00	61.33	28.26	25.10	1.98	1.48	9.17	16.00
3984 x AS436	66.50	69.83	199.17	69.83	45.14	38.18	2.60	1.95	16.67	22.83
3984 x AS429	64.17	64.50	113.17	66.83	24.95	19.15	1.68	1.23	9.83	16.67
3984 x AS424	66.00	69.00	166.67	64.00	25.79	19.32	1.68	1.35	46.17	50.17

Table 4.4. Continued.

Cross	DFL (d)		PH (cm)		SYP (g)		HSW (g)		NS	
	+	-	+	-	+	-	+	-	+	-
3984 x AS426	64.67	67.00	195.83	59.83	29.71	22.51	2.45	2.40	5.83	10.67
4643 x 654	68.17	71.17	196.33	79.83	30.18	25.42	1.58	1.35	28.50	33.50
4643 x AS426	69.33	73.67	174.50	65.67	22.38	18.05	2.03	1.53	7.50	15.83
4643 x 3937	64.00	66.67	134.67	71.00	28.28	21.17	1.53	1.13	15.50	22.50
4643 x AS436	67.17	70.33	102.17	72.50	34.84	34.83	2.12	1.87	14.33	26.50
4643 x 672	64.33	67.33	156.00	86.17	39.04	29.17	2.60	1.95	3.33	7.50
4643 x AS424	67.00	70.50	139.83	79.67	22.99	19.66	1.83	1.40	13.33	16.83
4396 x 3993	61.50	65.33	163.33	87.00	20.65	17.10	1.73	1.18	10.00	17.33
AS435 x AS424	63.50	65.50	122.50	53.50	23.16	17.81	1.67	1.15	18.17	21.00
AS435 x AS430	68.33	72.00	125.17	75.33	25.28	18.37	1.60	1.37	22.17	26.67
AS435 x 654	70.67	74.17	127.83	80.00	20.31	14.87	1.58	1.03	4.67	9.67
675 x 3993	62.17	64.50	173.00	72.83	35.90	27.71	2.47	1.55	24.00	34.17
675 x 429	64.00	70.17	141.00	76.17	32.42	27.26	1.95	1.40	2.83	7.50
675 x AS424	64.67	72.17	166.67	80.50	25.93	18.91	2.40	2.68	61.17	72.50
675 x AS430	60.00	69.33	160.67	62.67	77.44	65.05	2.10	1.33	18.17	29.33
675 x 3937	66.83	72.33	118.17	67.83	36.22	32.07	2.10	1.62	6.83	12.83
675 x AS426	73.17	74.17	153.50	58.33	37.57	28.10	1.70	1.10	24.00	41.33
675 x 672	64.83	70.67	147.83	75.67	51.71	40.48	2.20	1.45	59.17	69.33
4031 x 3993	65.00	67.00	162.83	65.83	29.22	20.04	1.90	1.08	10.83	16.67
4031 x AS436	63.83	71.17	155.17	58.00	17.66	13.11	1.30	0.85	12.33	16.83
4031 x AS429	65.83	72.50	145.67	67.50	25.91	16.97	2.20	1.68	2.17	5.00
4031 x 672	65.17	71.67	147.17	55.50	27.89	20.80	3.73	2.80	9.50	16.00
4567 x 3993	56.33	63.00	156.50	58.33	21.58	16.77	1.48	1.12	1.83	4.00
1563 x 654	66.33	70.67	123.83	61.33	31.60	33.90	2.90	1.95	55.50	62.67
1563 x 3993	51.67	54.67	152.33	50.33	20.73	13.12	1.62	0.85	24.67	34.17
1563 x AS 429	62.33	66.67	123.33	57.83	26.37	20.47	1.52	1.23	7.17	17.50
4567 x AS 436	65.00	68.00	121.17	62.17	26.88	19.81	1.53	1.13	13.50	20.17
1563 x 654	65.00	68.67	102.50	64.83	27.26	20.93	1.68	0.92	7.50	11.33
AS 435 x AS 436	68.67	71.50	115.50	64.00	31.74	21.66	1.97	1.27	3.83	10.67
4643 x AS429	69.00	72.33	136.67	82.83	29.25	24.98	1.68	1.25	6.17	9.17
104 x 654	77.00	79.83	117.17	59.00	30.02	21.44	1.77	1.37	6.33	10.33
104 x AS 430	73.83	75.83	123.50	68.33	33.41	25.54	2.13	1.38	4.00	10.83
3424 x 654	74.67	77.67	125.17	74.00	25.59	22.90	2.22	1.35	2.00	4.83
3424 x AS 424	54.67	57.33	189.17	43.50	37.30	27.71	2.23	1.47	12.33	21.83
4567 x AS 429	75.33	75.67	126.83	71.33	27.08	20.98	1.82	1.23	7.17	12.67
675 x AS 436	73.33	76.00	114.67	61.33	32.27	29.82	1.75	1.45	5.67	13.00
4031 x AS 424	64.17	67.17	142.50	67.50	24.68	20.94	2.10	1.35	11.83	19.33
AS 422 x AS 426	56.17	57.67	174.00	87.83	26.85	22.99	2.02	1.77	6.33	14.67
3984 x 3993	65.83	68.67	171.00	86.67	22.52	16.00	2.42	1.45	9.50	64.00
3984 x 654	65.17	68.00	132.67	53.83	31.27	26.83	2.53	1.68	7.83	11.17
Checks										
Macia (104)	73.41	75.12	161.67	100.00	33.14	28.24	1.81	1.52	8.33	59.67
AS 436	65.51	67.23	167.17	127.50	52.17	43.61	3.07	2.52	4.17	6.83
Cross mean	65.08	68.99	139.85	74.56	30.46	24.50	2.11	1.52	12.78	22.76
CV (%)	1.76	1.97	5.23	7.50	12.78	8.89	7.23	16.15	24.69	22.92
LSD (0.05)	9.23	10.097	76.88	54.01	23.31	20.22	1.63	1.52	17.14	24.15
F-Test	***	***	***	***	***	***	***	***	***	***
Maximum	77.00	79.83	199.17	127.5	82.98	65.50	4.58	3.62	61.17	72.50
Minimum	51.67	54.67	85.33	43.50	16.84	12.12	1.25	0.75	1.17	2.50

***= significantly different at 0.001 probability level; DFL = days to 50% flowering; PH = plant height at 50% flowering; SYP = seed yield per plant; HSW = hundred seed weight; and NS = number of *Striga* per plant

4.4.3 General combining ability effects of females

The GCA effects of ten female parents for sorghum and *Striga* parameters are summarized in Table 4.5**.** All female parents had positive and variable GCA effects for all the tested parameters, with and without *FOS* inoculation. This suggests that female parents were good

general combiners for most agronomic traits but not for *Striga* resistance. The genotypes 4643 and AS435 had relatively low GCA values (4) for days to 50% flowering in a desirable direction, with and without *FOS*. The GCA effect for days to flowering was reduced and ranged from 0.33 to 1.77 for eight female sorghum genotypes due to *FOS* application. Therefore, these parents are good combiners when breeding for early maturity. *FOS* application had no influence on days to flowering on the sorghum genotype 1563 but it delayed flowering in 675. Early maturing sorghum lines may easily escape from harsh environmental conditions such as drought and *Striga* infestation. Except genotype 675, *FOS* application improved the GCA values for plant height in a desirable direction. Female parents such as 3984, 1563 and 4643 had significantly larger GCA values of 42.99, 42.37 and 44.13 under *FOS* treatment, respectively. Therefore, they are good combiners for plant height improvement. Tall sorghum genotypes are highly preferred by sorghum growers in Tanzania for their dual purposes, its grain for food and stalk for animal feed.

Female parents 675 and 3424 had a significantly large positive GCA effect for grain yield per plant and hundred seed weight, with and without *FOS* treatment. These genotypes are good combiners for grain yield. Also they displayed relatively low GCA effects (14.57 to 44.16) for *Striga* count. Lower GCA values of 6.14 and 28.57 were observed in sorghum genotype 3984 with and without *FOS*. Female sorghum parents with high GCA for seed yield and low GCA values for days to flowering and *Striga* count are promising candidates for developing novel progenies possessing high yield potential, early maturity and significant levels of *Striga* tolerance. This will allow for the application of integrated *Striga* management in sorghum using *Striga* tolerant genotypes and seed treatment with *FOS*. In line with the current study, several authors have reported positive significant GCA effects for agronomic attributes of sorghum affecting its seed yield (Kenga et al., 2004; Tadesse et al., 2008; Makanda et al., 2009).

Table 4.5. Estimates of the GCA effects of ten sorghum genotypes used as female parents on days to flowering, plant height at flowering, seed yield per plant, hundred seed weight and number of *Striga* with (+) and without (-) *FOS* dressing in three environments.

Female	DFL (d)		PH (cm)		SYP (g)		HSW (g)		NS	
	+	-	+	-	+	-	+	-	+	-
4567	6.91	7.01	45.97	35.09	18.94	17.64	1.21	1.02	12.66	36.13
675	5.02	4.69	26.04	27.44	26.31**	24.22**	0.57	0.88	14.83	24.32
1563	7.19	7.19	42.37	18.29	11.90	10.96	0.65	0.55	16.27	28.05
AS 435	4.08**	4.61	38.57	21.11	8.59	7.48	0.51	0.45	19.42	30.05
4643	3.96**	4.3	44.13	18.16	10.11	10.78	0.60	0.58	14.12	28.04
104	5.37	5.56	41.21	33.93	8.97	6.80	1.30	1.12	23.06	24.46
4031	4.90	6.67	40.54	38.92*	16.16	17.27	1.83**	1.49*	17.59	19.55
3424	7.88	7.62	42.55	29.27	22.82**	18.78**	1.18	1.06	44.98	52.51
AS 422	6.49	7.31	42.93	30.65	10.83	10.19	0.69	0.47	29.85	32.32
3984	5.80	6.64	42.99	20.39	10.07	9.02	0.61	0.58	6.14	28.57

DFL = days to flowering; PH = plant height at flowering; SYP = seed yield per plant; HSW = hundred seed weight; NS = number of *Striga* per plant

4.4.4 General combining ability effects of males

The GCA effects of the male parents for days to flowering, plant height, seed yield, hundred seed weight and *Striga* counts, with and without *FOS* application, are presented in Table 4.6. Significant positive GCA effects were observed for all measured traits. Genotype 3937 had lower GCA value for days to flowering under *FOS* treatment. The GCA value of days to flowering was found to be low after *FOS* treatment in seven genotypes. These genotypes are favourable candidates for breeding early maturing sorghum. The genotypes AS426 and AS430 had significantly large positive GCA effects for plant height.

All tested male parents showed positive GCA effects for seed yield. However, genotypes 672 and 3933 had significantly large GCA values for grain yield, with and without *FOS* application. Interestingly, these genotypes expressed good GCA for early maturity and *Striga* resistance, with and without *FOS* application. Similarly, genotypes 672, AS 436 and AS 429 had low GCA values for the number of *Striga*, and therefore, they are good combiners for breeding for *Striga* resistance. Conversely, genotypes such as 3937 and 672 with low GCA effects for days to flowering and AS429 and AS436 with lower *Striga* count are good general combiners for *Striga* resistance and breeding for early maturity, and therefore, they were selected for future breeding program.

Table 4.6. Estimates of the GCA effects of ten sorghum genotypes used as male parents on days to flowering, plant height at flowering, seed yield per plant, hundred seed weight and number of *Striga* with (+) and without (-) *FOS* dressing evaluated in three environments

	DFL (d)		PH (cm)		SYP (g)		HSW (g)		NS	
Male	+	-	+	-	+	-	+	-	+	-
AS 436	7.06	6.82	39.05	29.73	10.58	10.99	0.56	0.55	8.57	20.98
AS 426	6.11	6.91	44.74	26.42	21.18	21.18	1.15	1.04	18.37	26.97
672	4.79	5.50	39.08	26.91	23.32	22.13	1.30	1.08	7.23	23.71
3933	5.19	5.47	42.35	24.70	22.22	18.37	0.60	0.49	43.10	47.46
AS 430	5.44	5.48	43.52	29.21	12.21	10.73	0.57	0.40	20.97	30.49
AS 429	6.28	5.70	37.95	18.89	7.95	6.67	0.56	0.39	3.48	7.71
3937	4.34	5.54	42.31	31.66	9.21	6.96	1.80	1.47	13.93	35.84
630	6.52	6.18	41.47	32.07	14.16	13.27	0.79	0.75	31.07	35.29
654	6.26	6.38	41.11	35.21	19.32	17.23	0.59	0.48	12.03	33.34
AS 424	6.94	8.65	41.57	28.68	8.94	7.62	1.30	1.32	26.49	31.73

DFL = days to flowering; PH = plant height at flowering; SYP = seed yield per plant; HSW = hundred seed weight; NS = number of *Striga* per plant

4.4.5 Specific combining ability effects

Estimates of the SCA effects of the 100 sorghum crosses averaged across three test locations for days to flowering, plant height, seed yield, hundred seed weight and number of *Striga* plants is presented in Table 4.7. All sorghum crosses had positive SCA values for the tested parameters at different levels when treated with *FOS*. Treatment of sorghum seeds with *FOS* contributed to the significantly lower positive SCA for days to flowering in the crosses of 1563 x AS436 and AS435 x AS426. These are suitable cross combinations ideal for breeding for early maturity with *FOS* application. Most of the farmers in semi-arid region of Tanzania prefer early maturing crop genotypes because of poor and erratic rainfall distribution during the cropping season. Also, early flowering crosses may escape heavy *Striga* infestation, the leading problem affecting sorghum production in drier regions of Tanzania (Mrema et al., 2016). Therefore these crosses can be recommended for further breeding.

All tested crosses showed positive SCA values for plant height. Families including 1563 x AS426 and 3424 x AS424 had relatively significantly large SCA values when treated with *FOS*. Therefore, these families are a good source of improved and plant height, which is a key trait preferred by farmers for grain and feed stalk production. Relatively large and positive SCA values were recorded for seed yield in the following families: 675 x 654, 3424 x 3933 and 4567 x AS426 with *FOS* application. Also, these crosses had large SCA values for hundred seed weight, making them ideal candidates for further breeding.

The newly developed sorghum crosses had relatively low SCA values for the number of *Striga* plants. This was recorded in the families of 4567 x AS424 and 3984 x 672 with *FOS* application. Therefore, these crosses are *Striga* tolerant and compatible to *FOS* application. Such crosses would be useful for cultivation in farmers' fields infested by *Striga*. Families with high SCA effects for grain yield and yield components exhibited dominance genetic effects, but the expression of heterosis though epistasic genetic effects may not be ruled out (Kenga et al., 2004).

Table 4.7. Estimates of specific combining ability effects of 100 sorghum hybrids for days to flowering, plant height, seed weight per plant, hundred seed weight and Striga count with (+) and without (-) Fusarium oxysporum (FOS) evaluated in three environments

.Cross	DFL (d)		PH (cm)		SWP (g)		HSW (g)		NS	
	+	-	+	-	+	-	+	-	+	-
4567 x AS 436	4.34	6.62	19.77	53.30	3.69	2.91	0.42	0.28	23.91	44.76
4567 x AS 426	4.80	4.52	60.09	39.44	44.77	35.90	0.73	0.73	1.60	4.40
AS 4567 x 672	5.61	5.61	27.12	19.68	1.76	1.20	0.12	0.06	11.62	44.81
4567 x 3933	6.22	3.08	31.15	11.02	9.53	6.59	0.57	0.16	8.69	9.34
4567 x AS 430	6.28	7.66	21.52	14.77	23.78	16.65	0.33	0.22	1.26	11.07
4567 x AS 429	5.19	1.03	31.15	22.78	3.46	3.85	0.18	0.40	3.27	8.58
4567 x 3937	2.99	1.03	55.53	33.49	6.11	2.12	2.32	2.30	17.54	80.71
4567 x 630	6.89	6.28	54.66	45.67	12.53	10.56	0.10	0.42	8.29	26.73
4567 x 654	4.23	8.96	57.99	43.15	18.18	13.46	0.52	0.50	18.14	20.44
4567 x AS 424	2.32	4.17	38.28	6.71	4.11	3.90	0.15	0.08	0.55	0.98
675 x AS 436	1.38	0.89	10.60	15.35	5.90	6.79	0.48	0.59	1.37	1.86
675 x AS 426	2.86	1.41	9.56	19.73	11.26	8.23	0.31	0.15	5.57	4.88
675 x 672	1.63	3.33	23.31	10.01	2.75	3.62	0.24	0.33	4.22	3.98
675 x 3933	2.43	3.76	33.94	16.73	6.11	5.86	0.35	0.38	23.97	21.45
675 x AS 430	5.27	2.48	16.79	15.78	7.63	10.94	0.69	0.10	25.93	41.58
675 x AS 429	4.59	6.47	22.95	19.79	11.61	9.71	0.24	0.27	3.87	8.16
675 x 3937	1.97	2.32	6.12	20.85	3.00	1.37	0.38	0.44	17.33	34.52
675 x 630	5.27	4.68	39.77	58.29	10.74	9.30	0.57	0.29	3.61	5.89
675 x 654	1.17	1.17	30.72	29.93	40.91	36.10	0.77	0.87	5.16	5.13
675 x AS 424	5.33	3.31	17.57	15.78	6.63	3.00	0.32	2.45	15.56	38.74
1563 x AS 436	0.84	1.21	39.31	5.49	2.65	1.89	0.42	0.51	0.75	0.82
1563 x AS 426	9.58	6.79	72.93	9.18	31.07	24.04	0.82	0.38	4.07	6.92
1563 x 672	4.03	4.59	43.67	40.44	4.22	3.70	0.71	0.40	14.44	46.64
1563 x 3933	8.25	9.33	45.50	13.00	2.68	3.44	0.12	0.21	27.12	32.99
1563 x AS 430	1.10	2.34	10.31	12.21	4.83	3.12	0.47	0.62	22.25	21.32
1563 x AS 429	6.35	5.61	25.22	7.38	2.52	5.41	0.53	0.46	0.75	1.87
1563 x 3937	1.94	4.23	64.02	11.09	7.05	5.25	0.61	0.66	17.43	37.55
1563 x 630	7.51	7.63	31.39	7.80	6.71	4.04	0.20	0.22	3.10	4.28
1563 x 654	7.64	6.85	16.19	22.08	4.01	3.89	0.31	0.08	7.04	37.63
1563 x AS 424	5.35	6.63	43.95	16.19	3.38	1.17	0.36	0.27	23.97	24.92
AS 435 x AS 436	5.27	5.85	11.30	12.48	2.99	2.82	0.14	0.10	4.18	14.15
AS 435 x AS 426	0.89	0.82	46.01	28.27	10.79	9.56	0.46	0.40	11.52	50.49
AS 435 x 672	2.37	2.59	41.00	27.09	12.11	9.12	0.77	0.53	0.75	2.07
AS 435 x 3933	1.41	1.47	53.47	33.27	10.62	9.94	0.47	0.44	14.76	16.10
AS 435 x AS 430	2.93	3.27	7.15	11.39	2.83	3.08	0.39	0.45	37.91	49.63
AS 435 x AS 429	1.60	1.63	43.75	6.13	5.51	4.75	0.52	0.24	1.72	8.30
AS 435 x 3937	3.06	5.05	25.99	8.41	3.06	2.82	0.24	0.20	8.98	28.33
AS 435 x 654	3.58	4.56	24.51	18.02	12.17	10.17	0.74	0.38	2.97	6.80
AS 435 x 630	1.47	2.23	35.92	16.09	2.52	3.50	0.20	0.34	21.74	34.86
AS 435 x AS 424	4.71	6.62	30.35	5.20	2.65	3.11	0.24	0.23	32.04	32.56
4643 x AS 436	3.58	3.76	2.94	8.99	19.14	24.84	0.46	0.97	7.87	40.27
4643 x AS 426	2.42	2.45	17.33	6.51	5.85	6.41	0.84	0.69	5.34	7.56
4643 x 672	2.34	3.08	64.96	6.99	9.50	8.87	0.78	0.67	1.83	4.36
4643 x 3933	5.19	4.26	45.21	19.32	13.65	12.58	0.29	0.17	9.97	10.42
4643 x AS 430	4.04	5.24	24.64	31.05	5.30	5.08	0.36	0.29	17.75	48.44
4643 x AS 429	5.46	4.23	16.41	9.00	5.77	5.34	0.18	0.31	3.54	7.42
4643 x 3937	3.31	2.26	26.32	6.08	4.87	2.86	0.12	0.13	5.82	25.10
4643 x 630	0.89	1.79	52.37	16.16	10.84	6.91	0.23	0.32	25.24	33.72
4643 x 654	2.17	3.69	36.34	13.60	8.81	9.15	0.21	0.56	4.85	15.00
4643 x AS 424	1.05	1.38	32.22	36.04	6.01	3.10	0.55	0.18	26.78	37.87
104 x AS 436	2.10	3.39	37.50	41.87	2.55	2.70	0.44	0.15	3.97	4.56
104 x AS 426	3.54	3.43	26.07	20.44	5.05	4.01	0.18	0.20	4.23	18.04
104 x 672	4.03	4.84	40.89	47.23	3.86	4.69	0.14	0.11	1.17	1.52
104 x 3933	4.08	4.76	18.59	20.56	9.53	4.44	0.49	0.37	29.34	30.54
104 x AS 430	8.71	7.42	65.91	22.61	4.21	4.76	0.34	0.14	9.86	15.20
104 x AS 429	3.51	5.78	56.91	36.06	4.61	2.55	0.39	0.10	1.38	1.63
104 x 3937	4.08	4.37	52.69	59.55	12.00	8.06	0.66	0.34	8.59	12.08
104 x 630	3.08	5.40	12.59	11.70	2.73	5.02	0.11	0.22	18.10	18.08
104 x 654	7.99	7.40	41.20	10.13	12.62	10.04	0.49	0.39	6.91	11.29
104 x AS 424	4.84	4.55	19.12	8.35	11.65	8.51	3.35	3.04	54.39	55.17
4031 x AS 436	4.17	4.97	46.09	10.94	12.99	11.45	0.69	0.34	4.17	5.01
4031 x AS 426	6.09	6.68	43.01	42.44	22.14	24.92	0.40	0.24	42.24	46.89
4031 x 672	1.38	2.76	35.57	5.06	2.53	2.19	3.06	2.63	5.36	9.00
4031 x 3933	2.40	4.13	45.52	32.98	9.97	8.01	0.13	0.25	14.10	14.04
4031 x AS 430	2.10	1.47	47.77	51.54	2.53	6.68	0.28	0.43	8.19	7.84
4031 x AS 429	5.65	2.48	39.12	5.39	6.76	6.77	0.27	0.38	1.21	2.88
4031 x 3937	1.38	4.54	41.28	51.35	9.74	4.37	3.64	3.09	9.09	8.66
4031 x 630	4.96	6.28	22.42	6.79	10.14	7.97	0.70	0.54	13.59	21.35
4031x 654	2.04	4.71	57.68	68.99	29.39	25.72	0.20	0.18	8.64	10.33

Table 4.7. Continued.

	DFL (d)		PH (cm)		SYP (g)		HSW (g)		NS	
	+	-	+	-	+	-	+	-	+	-
4031 x AS 424	4.26	9.28	32.55	43.58	3.51	4.05	0.23	0.19	23.89	25.23
3424 x AS 436	8.43	9.20	29.30	17.20	5.61	5.20	0.41	0.70	4.37	8.87
3424 x AS 426	6.63	7.47	57.35	31.68	7.03	5.31	2.96	2.71	34.49	47.65
3424 x 672	1.41	1.87	10.53	32.04	10.25	10.61	0.45	0.78	1.33	4.04
3424 x 3933	4.96	5.12	45.45	11.62	43.52	36.47	0.75	0.28	92.83	107.68
3424 x AS 430	4.46	6.37	21.02	45.29	8.69	4.59	0.22	0.27	23.35	31.97
3424 x AS 429	3.78	5.35	49.37	26.92	5.18	4.15	0.55	0.52	4.79	6.97
3424 x 3937	1.75	0.52	23.67	18.78	6.73	7.12	0.51	0.24	26.62	40.93
3424 x 630	3.58	2.66	39.15	39.28	23.53	20.65	0.95	0.86	85.88	93.92
3424 x 654	1.41	1.67	26.76	12.22	1.68	3.58	0.12	0.08	15.33	21.65
3424 x AS 424	11.00	12.63	78.78	24.32	3.65	1.86	0.17	0.19	17.27	21.85
AS 422 x AS 436	3.78	5.27	54.45	20.69	10.97	7.29	0.65	0.16	0.98	2.00
AS 422 x AS 426	5.47	6.66	28.59	15.46	3.36	2.32	0.22	0.21	5.24	8.81
AS 422 x 672	1.33	1.03	26.64	28.50	11.73	11.39	1.09	0.93	1.17	1.10
AS 422 x 3933	5.47	5.87	42.42	20.04	6.76	6.04	0.33	0.16	81.92	85.99
AS 422 x AS 430	5.61	7.12	31.34	24.03	17.44	18.27	1.04	0.66	28.14	34.90
AS 422 x AS 429	1.10	1.60	52.38	22.83	16.31	12.38	0.62	0.29	3.37	10.84
AS 422 x 3937	1.21	2.66	48.96	10.26	1.28	1.84	0.43	0.17	9.44	10.87
AS 422 x 630	7.06	1.75	39.92	24.69	3.42	3.39	0.64	0.37	1.64	3.83
AS 422 x 654	7.23	8.87	48.78	49.19	3.06	1.25	0.32	0.34	0.98	3.78
AS 422 x AS 424	2.53	3.33	14.79	54.16	6.71	7.01	0.11	0.08	1.83	3.60
3984 x AS 436	5.61	4.14	57.44	17.40	11.75	10.13	0.62	0.53	5.09	5.05
3984 x AS 426	3.60	5.75	39.87	11.92	12.30	11.78	0.50	0.49	1.26	5.53
3984 x 672	9.97	12.56	39.70	13.95	9.26	7.68	0.29	0.36	0.63	0.75
3984 x 3933	2.14	3.50	48.13	33.60	2.44	1.86	0.19	0.19	6.15	9.28
3984 x AS 430	2.25	1.52	47.95	30.85	4.45	2.92	0.50	0.51	5.15	4.80
3984 x AS 429	1.41	2.88	43.45	13.32	2.47	2.92	0.18	0.17	0.82	2.83
3984 x 3937	7.63	8.86	42.96	15.03	2.68	1.81	0.14	0.27	5.42	9.44
3984 x 630	9.83	9.78	44.79	16.06	14.97	12.52	0.41	0.36	5.99	6.86
3984 x 654	1.47	2.83	33.40	18.56	2.36	2.44	0.30	0.16	8.24	78.26
3984 x AS 424	4.36	3.94	32.11	10.65	9.77	7.08	0.52	0.36	10.25	12.80

DFL = days to flowering; HFL = plant height at flowering; SYP = seed yield per plant; HSW = hundred seed weight; and NS = number of *Striga* per plant

4.4.6 Estimates of genetic variance components and contribution of sorghum genotypes to the total phenotypic variance

Estimates of genetic variance components and contribution of sorghum genotypes and their interaction to total variance with and without *FOS* are summarised in Table 4.8. Significant differences in variances among treatments with and without *FOS* were observed for days to flowering, plant height at flowering, seed yield per plant, hundred grain weight and number of *Striga* per plant with and without *FOS* application. Significant variance (δ^2) among parents indicated that crosses differed from the parents significantly. Therefore, it can be inferred that traits could be transmitted to progenies as indicated by high value of broad sense heritability for each character. The value of variance of GCA (σ^2_{GCA}) was less than variance of SCA (σ^2_{SCA}) for all traits showing the preponderance of non-additive gene action. It was further supported by the ratio of $\sigma^2_{GCA}/\sigma^2_{SCA}$ being less than unity one and degree of dominance, i.e., ratio of dominance variance (σ^2_D) to additive variance (σ^2_A) being greater than one. Preponderance of non-additive gene action for days to flowering, plant height, seed yield per plant, hundred seed weight and number of *Striga* per plant in sorghum have been reported by Kenga et al. (2004).

Table 4.8. Estimates of variance components for yield and yield related traits, and *Striga* count of 100 sorghum hybrids derived from a 10 x 10 NCDII and evaluated with (+) and without (-) *Fusarium oxysporum* application in three environments in Tanzania

Parameter	Sorghum parameters								Number of *Striga*	
	DFL		PH		SYP		HSW			
	+	**-**	**+**	**-**	**+**	**-**	**+**	**-**	+	-
δ^2_{GCAF}	0.45	0.58	26.87*	10.50	3.95	2.24	-0.001	0.001	3.67	-3.70
δ^2_{GCAM}	-0.02	0.07	10.90	-5.73	-2.61	-1.90	-0.01	0.002	19.1*	19.38*
$\delta^2_{GCA(GCAF+GCAM)}$	0.43	0.65	37.77	4.77	1.34	0.34	-0.01	0.003	22.77	15.68
δ^2_{SCA}	5.16**	5.27**	110.92**	57.68**	38.57**	37.12**	0.14	0.09	27.88**	61.37**
$\delta^2_{W\ (Error)}$	1.31	1.84	53.46*	31.31*	15.14	4.75	0.02	0.06	9.95	27.22
$\delta^2_{GCA}/\delta^2_{SCA}$	0.08	0.12	0.34	0.08	0.03	0.01	-0.08	0.03	0.82	0.26
δ^2_A	0.86	1.30	75.54	9.54	2.68	0.68	-0.02	0.01	45.54	31.36
δ^2_D	20.64**	21.08**	443.68	230.72	154.28	148.48	0.56	0.36	111.52	245.48
$(\delta^2_D/\delta^2_A)^{1/2}$	4.90	4.03	2.42	4.92	7.59	14.78	-5.29	6.00	1.56	2.80
δ^2_{AM}	-0.08	0.28	43.60	-22.92	-10.44	-7.60	-0.04	0.01	76.40	77.52
δ^2_{AF}	1.80	2.32	107.48	42.00	15.80	8.96	0.004	0.004	14.68	-14.80
δ^2_{EW}	-14.6**	-14.62**	-317.07**	-146.5**	-101.91**	-106.95**	-0.01	-0.22	-96.46**	-172.57**
δ^2_T	6.69	7.44	183.27	91.38	54.38	42.04	0.15	0.15	49.22	96.43
H^2 (δ^2_A/δ^2_T)	0.13	0.17	0.41*	0.10	0.05	0.02	-0.13	0.07	0.93**	0.33
$H^2_M(\delta^2_{AM}/\delta^2_T)$	-0.01	0.04	0.24	-0.25	-0.19	-0.18	-0.27	0.07	1.55**	0.80**
$H^2_F(\delta^2_{AF}/\delta^2_T)$	0.27	0.31	0.59*	0.46*	0.29	0.21	0.03	0.03	0.30	-0.15

* = significant at 0.05 probability level, ** = significant at 0.01 probability level DFL = days to flowering; PH = plant height at flowering; SYP = seed yield per plant; HSW = hundred seed weight; NS = number of *Striga* per plant; δ^2_{GCAF} = additive variance of female; δ^2_{GCAM} = additive variance of male; δ^2_{GCA} = additive variance of female and male; δ^2_{SCA} = additive variance for female and male interaction; δ^2_A = additive variance in the population; δ^2_D = dominance variance; δ^2_{AM} = additive variance in males; δ^2_{AF} = additive variance in female; δ^2_{EW} = environmental variance; δ^2_T = Total variance; H^2 = broad sense heritability; H^2_M = heritability due to males and H^2_F = heritability due to female effect

4.5 Conclusions

The present study found promising sorghum crosses with significance levels of compatibility with *FOS*, *Striga* resistance and good agronomic performances. The levels of *FOS* compatibility was reflected by the diferential suppression of *Striga* infestation and varied performance of sorghum genotypes under *FOS* treatment when compared to the control grown under *Striga* infestation without *FOS* treatment. *FOS* application had a significant ($p<0.05$) influence on number of *Striga*, days to flowering, plant height and grain yield. Genotypes showed significant interactions with the testing environments. Also there were variations in the GCA and SCA effects of some lines across locations for sorghum and *Striga* parameters. Four genotypes; 672, AS436, AS429 and 3984, were identified as good combiners for *Striga* resistance, while another four, 675, 3424, AS426, AS430, had good GCA effects for grain yield when evaluated at three sites of the semi-arid regions of Tanzania. Three families were found to have relatively high SCA effects for grain yield, namely 675 x 654, 3424 x 3933 and 4567 x AS426. The study identified *Striga* resistant hybrids, such as 4567 x AS424 and 3984 x 672, with low SCA effects in a desirable direction. This implies the presence of both additive and non-additive genetic effects influencing these traits in the selected parents and crosses, in that order. Overall, the study identified promising sorghum parents and crosses useful for integrated *Striga* management breeding that combine the use of the resistant sorghum genotypes and hybrids with good agronomic traits that are compatible with *FOS*, a bio-control agent. Further stability tests and farmers participatory evaluation of the selected genotypes across representative growing environments are, however, needed for release and large scale production.

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CHAPTER FIVE

Gene action controlling *Striga* resistance among sorghum genotypes

This chapter has been published by:

Emmanuel Mrema, Hussein Shimelis, and Mark Laing (2017)

Genetic effect of *Striga* resistance in sorghum genotypes, Euphytica (2017) 213:280, https://doi.org/10.1007/s10681-017-2073-3

CHAPTER FIVE

Gene action controlling *Striga* resistance among sorghum genotypes

5.1 Abstract

Striga is an important parasitic weed causing substantial economic losses in cereal and legume crop production in sub-Saharan Africa. Integrated *Striga* management approaches such as a combined use of *Striga* resistant varieties and *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, are an option to control the parasite and to boost sorghum productivity. Understanding the gene action influencing *Striga* resistance, with or without *FOS* treatment, is key to developing improved sorghum varieties with durable resistance and high yield. The objective of this part of study was to determine the gene action and inheritance of *Striga* resistance using genetically diverse populations of sorghum involving *FOS* treatment. Twelve sorghum parents selected for *Striga* resistance, *FOS* compatibility or superior agronomic performances were crossed using a bi-parental mating scheme. The selected male and female parents and their F_1 progenies, backcross derivatives and the F_2 segregants were field evaluated at three locations in Tanzania known for their severe *Striga* infestations using a lattice experimental design with two replications. The following data were collected and subjected to generation mean analysis (GMA): days-to-50% flowering (DFL), seed yield per plant (SYP) and number of *Striga* per plant (SN). GMA showed the preponderance of additive genetic action contributing to the total genetic variation in the evaluated sorghum populations. The additive genetic effect for DFL, SYP and SN, with and without *FOS* treatments, ranged from 72.02 to 86.65% and 41.49 to 95.44%, 75.62 to 91.42% and 71.83 to 91.89%, and 77.35 to 93.56% and 72.86 to 95.84%, in that order. The contribution of non-additive genetic effects was minimal and varied among generations. *FOS* application reduced DFL and SN and improved SYP in most of the tested sorghum populations. DFL of sorghum populations was reduced by a mean of 8 days under *FOS* treatment compared to the untreated control in families such as 675 x 654, AS435 x AS426 and 1563 x AS436. *FOS* treatment improved SYP with a mean of 6.44 g $plant^{-1}$ in 4567 x AS 426, 3424 x 3993 and 3984 x 672. The numbers of *Striga* plants were reduced with a mean of 16 plants due to *FOS* treatment in the crosses of 675 x 654, 1563 x AS436, 4567 x AS424, and 3984 x 672. The study demonstrated that additive genes were predominantly responsible for the inheritance of *Striga* resistance in sorghum. Pure line cultivar development targeting reduced DFL, SN and high SYP in the

selected populations may provide enhanced response to selection for integrated *Striga* management (ISM) programme.

Key words: *Fusarium oxysporum* f.sp *strigae*, generation mean analysis, genetic effect, integrated *Striga* management, sorghum

5.2 Introduction

Striga damage is one of the main constraints to sorghum production in sub-Saharan Africa (Watson et al., 2007). *Striga hermonthica* [Del.] Benth (*Sh*) and *S. asiatica* [L.] Kuntze, (*Sa*) are obligate root parasites inflicting yield losses of 30 to 90% in sorghum in Tanzania (Riches, 2003). Integrated *Striga* management (ISM) is a system that involves the use of resistant sorghum varieties, biological agents, cultural practices and chemical control methods to minimize losses incurred by *Striga* species (Hearne, 2009). Breeding *Striga* resistant sorghum is the cheapest and most environmentally friendly management option (Ejeta, 2007). Wegmann (1996) reported the following components of *Striga* resistance in sorghum: minimum production of *Striga* stimulants; mechanical barriers, inhibition of germtube exoenzymes by root exudates; phytoalexine synthesis; incompatibility, antibiosis, insensitivity to *Striga* toxins and avoidance through root growth habit. Reduced production of the germination stimulus for *Sa* has been reported to be controlled by a single recessive gene (Vogler et al., 1996). Single major gene and several minor genes have been reported to stimulate germination of *Sh* (Vogler et al., 1996).

In contrast, Haussmann et al. (1996) reported the presence of quantitative genetic variation with a preponderance of additive genetic effects influencing stimulation of *Sh* seed germination. Significant genotype by environment interaction on *Striga* count was reported by Omanya et al. (2000). Heterosis for *Striga* resistance was also reported to be genotype-dependent (Haussmann et al., 2000a). Partial or complete dominant genes for *Striga* susceptibility was also reported for sorghum hybrids derived from crosses between resistant and susceptible parents (Obilana, 1984).

Based on the modes of gene action, gene effects are broadly classified into additive, dominance and epistasis. Further, additive x additive (aa), additive x dominance (ad) and dominance x dominance (dd) gene interaction effects are theoretically possible, affecting trait expression. The nature and type of gene action is important in designing an effective breeding

and gene deployment strategy in a *Striga* resistance breeding program (Falconer and McKay, 1996).

Generation mean analysis (GMA) is a useful technique for estimating gene effects (Anderson and Kempthorne, 1954; Mather and Jinks, 1971). The method requires the following six generations: male and female parents (P_1 and P_2), F_1 progenies, F_2 segregants, backcrosses to parent one (BCP_1) and parent two (BCP_2) (Hayman, 1958). The mean response of these generations allows estimation of genetic effects such as additive, dominance and epistasis components or their interactions. The technique is mostly used when the parents are divergent, possessing complementary and favourable alleles. GMA has been widely used to study gene action controlling biotic or abiotic stress tolerance or resistance, and yield and yield related traits in sorghum (Gamble, 1962), maize (Badu-Apraku et al., 2013) and rice (Gurney et al., 2006).

The mode of gene action responsible for controlling *Striga* resistance in sorghum in the semi-arid regions of Tanzania has not been established previously. Integrated *Striga* management practices involving a combined use of resistant sorghum genotypes compatible with *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, is an option to control the parasite and to boost sorghum productivity (Rebeka et al., 2013). Pathogenic isolates of *FOS* have been reported to be effective bio-herbicides in managing *Striga* infestation in sorghum, particularly when the method is integrated with other control practices (Rebeka et al., 2013). The *FOS* has been shown to be host specific, pathogenic and highly destructive against *Striga*, easy to mass produce and shows maximum genetic diversity (Ciotola et al., 2000). When sorghum seeds are treated with *FOS*, the fungus grows well in the rhizosphere of the young and developing sorghum plants, followed by parasitizing and inhibiting growth and development of *Striga*, barring it from attacking the roots of the host plant (Rebeka, 2007).

Breeding sorghum varieties with farmer-preferred traits and possessing *Striga* resistance, and compatibility with *FOS,* could improve grain yield and reduce *Striga* infestation in the semi-arid parts of Tanzania. These could improve adoption of newly released varieties by farmers. The effectiveness of the *FOS* application to the selected compatible sorghum populations across *Striga* infested fields of the semi-arid areas of Tanzania is yet to be explored. Selection of desirable parents, their crosses and backcross derivatives with high yield and improved yield components and *Striga* resistance across the main agro-ecologies of sorghum may provide a foundation for a *Striga* management program. This requires understanding of the genetic variability and inheritance of *Striga* resistance and other traits of importance for effective selection in sorghum (Mrema et al., 2017).

In an effort to select *Striga* resistant and *FOS* compatible sorghum lines, promising genotypes were identified through controlled evaluations (Mrema et al., 2017). Some of the selected landraces were relatively poor yielders but were well adapted to the drier regions of Tanzania and possessed farmers-preferred traits (Mrema et al., 2016). In contrast, some of the newly released sorghum genotypes had better yields and *FOS* compatibility but lacked essential farmers preferred traits. Detailed information on the performance of the selected complementary parents, F1s, backcross derivatives and F_2 populations were needed to establish the gene action influencing *Striga* resistance, with or without *FOS* treatment. Therefore, the objective of this part of the study was to determine the gene action and inheritance of *Striga* resistance using genetically diverse populations of sorghum involving *FOS* treatment. The hypothesis being tested was that additive, dominance or epistatic genetic effects were important in controlling *Striga* resistance and that the new families could be systematically selected to develop resistant pure line cultivars with *FOS* compatibility. Findings of this study may guide the sorghum breeding programme in Tanzania in deciding on parental sorghum genotypes to be used, the best selection technique to employ when breeding for *Striga* resistance and *FOS* compatibility with farmers preferred traits.

5.3 Materials and methods

5.3.1 Plant materials and crosses

The study used 12 selected parents (Table 5.1) that were identified to have good general and specific combining ability effects for days-to-50% flowering, seed yield per plant and *Striga* resistance (Mrema et al., 2017). Also the selected parents were found to be resistant to both *Sh* and *Sa*, compatible to *FOS* and had most of the farmer preferred traits required for semi-arid areas of Tanzania (Mrema et al., 2016). The 12 parents were divided into two sets (Set I consisting of six female parents and Set II into six male parents). The two sets were crossed using a bi-parental mating design providing the following 7 F_1 and 7 F_2 populations: 675 x 654, AS435 x AS426, 4567 x AS 426, 3424 x 3993, 1563 x AS436, 4567 x AS424 and 3984 x 672. Each F_1 progeny was backcrossed to their corresponding parents to generate BCP_1 and BCP_2 derivatives. The 7 F_1 progenies were then selfed to develop F_2 families. These constituted the six generation (P_1, P_2, F_1, BCP_1, BCP_2 and F_2) required for the present GMA study. The description of the parents used in generating the populations is shown in Table 5.1.

Table 5.1. Description of parental sorghum genotypes used in the bi-parental crosses for generation mean analysis

Entry	Name	Source	Attributes	Parentage in the cross
1	4567	Magu/Tanzania	High yielding, medium maturing and *FOS* compatible	P_1
2	675	Tarime/Tanzania	Early maturing and *FOS* compatible	P_1
3	1563	Bukoba/Tanzania	*FOS* compatible, early maturing and high yielding	P_1
4	AS 435	ACCI/South Africa	High yielding, late maturing and *FOS* compatible	P_1
5	3424	Igunga/Tanzania	*FOS* compatible and medium maturity	P_1
6	3984	Musoma/Tanzania	*FOS* compatible, high yielding and late maturing	P_1
7	AS 436	ICRISAT/India	Early maturing, medium yielding and *Striga* resistant	P_2
8	AS 426	ACCI/South Africa	Medium maturing and yielding, and *Striga* tolerant	P_2
9	672	Musoma Rural/Tanzania	Medium maturing and *Striga* resistant	P_2
10	AS 424	SARC/Ethiopia	Early maturing and *Striga* resistant	P_2
11	654	Bunda/Tanzania	*Striga* resistant	P_2
12	3993	Musoma/Tanzania	*Striga* tolerant	P_2

Entries 1 to 6 were used as female parents (P_1) and 7 to 12 were male parents (P_2).
SARC = Sirinka Agricultural Research Centre in Ethiopia; ICRISAT = International Crop Research Institute for the Semi-arid Tropics/India and ACCI = African Centre for Crop Improvement
FOS= *Fusarium oxysporum* f.sp. *strigae*

5.3.2 Bio-control agent and inoculum preparation

A pathogenic strain of *F. oxysporum* f.sp. *strigae* (*FOS*) originally isolated from sorghum fields infested with *Striga* in north eastern lowlands of Ethiopia was used as a bio-control agent for *Striga* management (Rebeka et al., 2013). Taxonomic identification of *FOS* was confirmed by the Phytomedicine Department of Humboldt University in Berlin, Germany. Rebeka, (2007) confirmed the pathogenicity and host specificity of the *FOS* isolate to *Striga*. The isolate was maintained on Special Nutrient Agar (SNA) medium at -40^{o}C. Pure *Fusarium* chlamydospores from cultures grown on potato dextrose agar (PDA) were sampled and mass produced at Plant Health Products (Pty) Ltd, Kwazulu-Natal, South Africa and preserved by the Discipline of Plant Pathology, University of KwaZulu-Natal.

5.3.3 Experimental sites

The six sorghum generations consisting of 6 P_1, 6 P_2, 7 F_1, 7 F_2, 6 BCP_1, and 6 BCP_2 were planted during the main cropping season of December 2015 to April 2016 at three locations, namely; Igunga situated in Tabora Region, Misungwi of Mwanza region and Kishapu of Shinyanga Region (Table 5.2). Field evaluations were conducted with and without *FOS* treatment. The three study sites represent the semi-arid areas of Tanzania known for their high levels of sorghum production and heavy *Striga* infestations, both by *Sh* and *Sa,* species. Therefore, natural infestation in the *Striga* hotspot areas was used for the study.

Table 5.2. Descriptions of the three study sites used for evaluation of the sorghum populations

Location/site name	Region	Latitude (^{0}South)	Longitude (^{0}East)	Altitude (m)	Rainfall (mm)	Temp (Min, ^{0}C)	Temp (Max, ^{0}C)
Igunga	Tabora	4.23	33.91	1060	134	17.50	29
Misungwi	Mwanza	2.96	33.16	1176	235	19.33	28
Kishapu	Shinyanga	3.62	33.84	1126	234	19.33	28

Min=minimum; Max=maximum

5.3.4 Experimental design and trial establishment

The six generations were planted using a randomized complete blocks design with 2 replications in each site. Each plot consisted of three rows of 2.7 m in width and 5.1 m length. Sorghum genotypes were planted at a spacing of 30 cm and 90 cm between plants and rows, respectively. Two sets of plots were prepared and used as follows: one set was planted with sorghum seeds treated with 75 mg of *Fusarium* chlamydospores, while the other set was planted to each genotype without *Fusarium* treatment. Two seeds per hill were initially sown and later thinned to one seedling per hill, two weeks after planting. This provided a plant density of 37,037ha^{-1}. Fertilizer was applied at a dose of 60 kgha^{-1} NPK 20-10-5 by side dressing three weeks after sowing. Apart from *Striga*, other weeds were hand weeded immediately when observed. Other management practices were done according to the recommendations of the specific areas.

5.3.5 Data collection

Data on sorghum and *Striga* parameters were collected. Seven sorghum plants from the middle rows on each plot were selected at random and tagged for data collection. Data on sorghum parameters included days-to-50% flowering (expressed in days [d]) and seed yield (g/plant). Days taken from sowing to when 50% of the sorghum plants in a plot had completed flowering were counted from each plot for each tagged plant. Seeds separated from the panicle of each plant were weighed and the weight of the seeds was recorded and expressed in grams. A quadrant of 0.09 m^2 (0.3 m width x 0.3 m length) was used for each sampled plant to determine its *Striga* count. This was done by counting the number of *Striga* that germinated within a quadrant of each plant two months after sorghum sowing, when 50% of the *Striga* from each plot germinated.

5.3.6 Data analysis

Following separate analysis of variance and homogeneity of variance tests on the collected data on sorghum and *Striga* parameters, the data were subjected to combined analysis of variance using the general linear model procedure (PROC GLM) in SAS version 9.3 (SAS Institute, 2011) to determine significance differences. The following model was used for data analysis Yijk = μ + Gi + Ej + G × E + rk (E) + eijk. Where Yijk = response on days-to- 50% maturity or seed yield per plant or *Striga* count of i^{th} generation in j^{th} environment of k^{th} replication, μ = overall mean, Gi = generation mean, Ej = j^{th} environment, G × E = generation × environment interaction, rk = k^{th} replication within E environment and eijk = residual factor. Mean separation between generations was done in SAS version 9.3 (SAS Institute, 2011) using the least significance difference (LSD) procedure for pair-wise comparisons (P≤ 0.05), as suggested by Kang (1994).

Data was subjected to GMA using the methodology proposed by Mather and Jinks (1971) following analysis of variance. GMA was performed using PROC GLM and PROC REG procedures in accordance with SAS macros described by Kang (1994). The genetic model used was: $Y = m + \alpha a + \beta d + \alpha^2 aa + 2\alpha\beta ad + \beta^2 dd$ where; α and β are the coefficients for a and d, respectively, Y = generation mean, m = mean of the F_2 generation as the base population and intercept value, a = additive genetic effect, d = dominance genetic effect, aa = additive x additive gene interaction effect, ad = additive x dominance gene interaction effect and dd = dominance x dominance gene interaction effect.

A stepwise linear regression model was used to estimate the additive and dominance parameters. The regression analysis was carried out using PRO REG macros in SAS developed by Kang (1994). The regression analysis was weighted based on the inverse of the variance of means and matrix parameter (Checa et al., 2006). To establish the parameters that were acceptable within the model, R^2 and F-test (goodness of- fit) were calculated (Ceballos et al., 1998). The F-test was calculated using the sums of squares (ss) and degrees of freedom (df) as used by Checa et al. (2006):

$$FC = \frac{(SS\ general\ model) - (SS\ reduced\ model)\ /difference\ in\ df}{SS\ residual\ from\ the\ general\ model\ /\ df\ residual\ from\ the\ general\ model}$$

Where, FC = F calculated, SS = sums of squares and df = degrees of freedom

To determine the magnitude of additive, dominance and epistatic genetic effects, the model's parameters were tested sequentially, one at a time, starting with additive effects and then in

combination with other parameters of the model (Ceballos et al., 1998). The importance of the gene effect estimates was based on the ratio between the sums of squares of each component and the total sums of square. Significance of the genetic estimates was also determined by dividing the estimated parameter values with their standard errors; if the value exceeded 1.96 then it was considered significant (Singh and Chaudhary, 1995).

Variance components (additive, dominance or environmental) were estimated as described by Mather and Jinks (1982) using the following equations: additive genetic variance = $(2\sigma^2F_2) - \sigma^2BCP_1 + \sigma^2BCP_2$, dominance genetic variance = $\sigma^2G\ (F_2) - \sigma^2A\ (F_2)$ and environmental variance = $1/4\ (\sigma^2P_1 + \sigma^2P_2 + (2\sigma^2F_1)$. Where: σ^2P_1 = variance of P_1; σ^2P_2 = variance of P_2; σ^2F_1 = variance of F_1; σ^2F_2 = variance of F_2; σ^2BCP_1 = variance of backcross to P_1; σ^2BCP_2 = variance of backcross to P_2.

5.4 Results and discussion

5.4.1 Combined analysis of variance of days to flowering, seed yield per plant and number of *Striga* per plant evaluated with and without *FOS* treatment in families of sorghum evaluated in three environments

The analysis of variance for seven crosses (675 x 654, AS435 x AS426, 4567 x AS 426, 3424 x 3993, 1563 x AS436, 4567 x AS424 and 3984 x 672) and six generations evaluated across three locations showed highly significant (P<0.01) differences (Table 5.3). The results from analyses of variance for DFL, SYP and NS are presented in Table 5.3. DFL in sorghum crosses 675 x 654 and 3984 x 672 differed significantly (P<0.01), with and without *FOS* treatments, across the environments. Marked variations were recorded among generations in all test populations, which was confirmed by their larger percentage generation sum of squares (SSG %) (Table 5.3).

SYP differed significantly (P<0.01) in crosses of 675 x 654 and 3424 x 3993. SYP significantly differed between test environments in the crosses of 3984 x 672, 1563 x AS436 and 675 x 654 due to *FOS* treatment. Further, the families AS435 x AS426 and 4567 x AS424 showed significant differences for SYP across test environments without *FOS* treatment. SYP showed significant difference (P<0.01) among generations in all the test populations. This difference was attributed to a larger generation sum of squares (Table 5.3). Generation by environment interaction showed significant difference, with and without *FOS* treatments, in populations of 3984 x 672 and 675 x 654, respectively.

SN differed significantly ($P<0.01$) in populations of 675 x 654 and AS435 x AS426, with and without *FOS* treatments. Significant differences were further observed in the population 3424 x 3993 with *FOS* treatment, while 675 x 654, 675 x 654, 4567 x AS424 and 3984 x 672 exhibited significant differences without *FOS* treatment. Generations showed variable responses for SN owing to their larger percentage sums of squares when compared to their interaction with the environment.

The significant variation revealed by sorghum genotypes among generations for DFL, SYP and SN in the testing environments indicated the presence of considerable genetic variation for DFL, SYP and *Striga* resistance. Difference in response of the genotypes across the testing environments may have partly contributed to the influence of the environment on expression of the genes controlling DFL, SYP and *Striga* resistance. These findings concurred with Ramaiah (1987) and Haussmann et al. (2000a) who reported variation in DFL, SYP and SN among sorghum genotypes grown under *Striga* infestation across varied environments.

Table 5.3. Mean squares and significant tests of days to flowering, seed yield per plant and number of *Striga* per plant evaluated with (+) and without (-) *Fusarium oxysporum* application in 7 families of sorghum across three environments

Cross and source of variation	DF	Days to flowering		Seed yield per plant		Number of *Striga* per plant	
		+	-	+	-	+	-
675 x 654							
ENV	2	18.11**	35.03***	16.41**	16.58*	44.19***	516.19***
REP (ENV)	3	34.33***	12.39***	9.40*	10.39^{ns}	2.50^{ns}	14.83**
Gen	5	202.31***	104.44***	94.25***	138.93^{ns}	200.51***	777.71***
Gen x ENV	10	2.61^{ns}	0.63^{ns}	1.42^{ns}	1.02^{ns}	1.36^{ns}	1.03^{ns}
SSEV%	2	3.37	11.70	6.33	4.49	8.00	20.94
SSG%	5	94.20	87.24	90.92	94.13	90.77	78.86
SSG x EV%	10	2.43	1.05	2.74	1.38	1.23	0.21
Error	15	53.00	11.83	2.42	3.59	1.77	1.50
Overall mean		58.94	63.89	59.63	60.5	13.39	46.78
CV (%)		3.19	1.39	2.61	3.13	9.93	2.62
R^2 (%)		0.97	0.98	0.94	0.93	0.98	0.99
AS435 x AS426							
ENV	2	4.75^{ns}	6.25*	1.19^{ns}	17.19**	30.53***	35.36*
REP(ENV)	3	4.58^{ns}	5.72*	6.58^{ns}	3.25	1.36^{ns}	10.25^{ns}
Gen	5	161.18***	53.87***	79.69***	138.89^{ns}	186.36***	261.03***
Gen x ENV	10	16.38^{ns}	1.32^{ns}	2.39^{ns}	2.89^{ns}	3.69^{ns}	4.29^{ns}
SSEV%	2	0.97	4.24	0.56	4.54	5.93	4.98
SSG%	5	82.30	91.30	93.80	91.64	90.48	91.99
SSSG x EV%	10	16.73	4.46	5.64	3.82	3.59	3.03
Error	15	9.58	1.52	2.78	1.78	1.49	5.65
Overall mean		59.42	69.50	24.64	22.64	19.36	22.13
CV (%)		5.21	1.78	6.77	5.90	6.31	10.74
R^2 (%)		0.87	0.93	0.91	0.97	0.98	0.94
4567 x AS 426							
ENV	2	1.00^{ns}	156.00**	8.08*	3.69^{ns}	12.58^{ns}	60.86**
REP (ENV)	3	5.64^{ns}	13.33^{ns}	3.47^{ns}	2.06^{ns}	23.72^{ns}	1.69^{ns}
Gen	5	128.18***	56.53*	114.18***	63.98***	318.40***	512.09***
Gen x ENV	10	3.23^{ns}	18.03^{ns}	1.82^{ns}	17.59***	15.68^{ns}	9.83^{ns}
SSEV%		0.30	40.26	2.67	1.47	1.42	4.38
SSG%		94.92	36.47	94.33	63.57	89.74	92.09
SSG x EV%		4.79	23.27	3.00	34.96	8.84	3.53
Error	15	3.51	17.67	1.67	1.86	20.86	7.29
Overall mean		59.92	60.67	49.58	43.28	18.00	18.97
CV (%)		3.12	6.93	2.61	3.15	25.37	14.24
R^2 (%)		0.93	0.75	0.96	0.95	0.86	0.96
3424 x 3993							
ENV	2	14.78^{ns}	24.69**	62.69*	38.11**	2.69**	1.19^{ns}
REP(ENV)	3	17.00^{ns}	26.61**	6.14^{ns}	1.22ns	0.50ns	2.92^{ns}
Gen	5	131.11***	104.04***	395.03***	146.98***	9.18***	18.23***
Gen x ENV	10	6.68^{ns}	2.69^{ns}	10.29^{ns}	5.38^{ns}	0.56^{ns}	0.96^{ns}
SSEV%		3.93	8.27	5.69	8.81	9.47	2.32
SSG%		87.19	87.2	89.64	84.97	80.66	88.37
SSSG x EV%		8.88	4.52	4.67	6.22	9.86	9.32
Error	15	9.33	2.74	15.27	4.09	0.30	1.05
Overall mean		57.56	57.89	27.52	18.94	2.44	4.31
CV (%)		5.31	2.86	14.2	10.67	22.41	23.8
R^2 (%)		0.85	0.94	0.91	0.93	0.93	0.88
1563 x AS436							
ENV	2	13.08^{ns}	16.75*	37.03**	18.86^{ns}	6.58^{ns}	23.58^{ns}
REP (ENV)	3	13.50^{ns}	10.06^{ns}	4.14^{ns}	3.06^{ns}	8.50^{ns}	32.47^{ns}
Gen	5	312.47***	331.67***	130.09***	95.18**	79.47***	1196.72***
Gen x ENV	10	29.05*	4.32^{ns}	2.03^{ns}	5.23^{ns}	2.85^{ns}	51.35^{ns}
SSEV%		1.39	1.931	9.94	6.67	3.00	0.72
SSG%		83.15	95.581	87.33	84.10	90.51	91.43
SSSG x EV%		15.46	2.488	2.72	9.24	6.49	7.85
Error	15	10.97	4.19	2.34	11.26	5.97	34.21
Overall mean		62.33	67.33	27.86	24.06	10.00	26.58
CV (%)		5.31	3.04	5.49	13.95	24.43	22.00
R^2 (%)		0.92	0.97	0.96	0.77	0.84	0.93

Table 5.3. Continued.

Cross and source of variation	DF	Days to flowering		Seed yield per plant		Number of *Striga* per plant	
		+	-	+	-	+	-
4567 x AS424							
ENV	2	7.19	64.19**	84.19^{ns}	46.69**	1.75^{ns}	21.33**
REP (ENV)	3	50.39	5.03^{ns}	26.14^{ns}	14.58^{ns}	3.39**	16.22**
Gen	5	132.78***	341.89***	181.29**	173.89***	43.73***	125.27***
Gen x ENV	10	3.56	6.36^{ns}	38.06^{ns}	4.29^{ns}	0.98^{ns}	3.40^{ns}
SSEV%		2.02	6.75	11.57	9.28	1.51	6.07
SSG%		93.00	89.90	62.28	86.45	94.25	89.09
SSSG x EV%		4.99	3.35	26.15	4.27	4.24	4.84
Error	15	2.66	5.89	31.81	4.45	0.52	2.69
Overall mean		53.44	55.53	21.03	20.64	4.33	8.00
CV (%)		3.05	4.37	26.82	10.22	16.68	20.50
R^2 (%)		0.96	0.96	0.76	0.94	0.97	0.95
3984 x 672							
ENV	2	24.69**	27.44**	20.08*	16.03^{ns}	54.53**	259.19*
REP (ENV)	3	0.81^{ns}	8.53*	33.92**	14.58^{ns}	13.50*	31.39^{ns}
Gen	5	112.56***	134.23***	169.52***	94.09***	303.24***	154.64^{ns}
Gen x ENV	10	8.49*	8.21**	78.65***	3.29^{ns}	35.56***	51.79^{ns}
SSEV%		7.08	6.79	2.40	5.99	5.51	28.65
SSG%		80.73	83.05	50.62	87.86	76.54	42.73
SSSG x EV%		12.18	10.16	46.98	6.15	17.95	28.62
Error	15	2.27	2.13	4.45	6.38	3.30	64.39
Overall mean		56.19	56.19	37.92	33.47	9.56	18.89
CV (%)		2.68	2.60	5.56	7.55	19.01	42.48
R^2 (%)		0.95	0.96	0.96	0.86	0.98	0.66

* = significant at the 0.05 probability level, ** = significant at the 0.01 probability level, *** = significant at the 0.001 probability level, DF = degrees of freedom,
Env = environment; Rep (Env) = replication within environment; Gen = generation; Gen x Env = generation by environment interaction; SSEV % = percentage sum square of the environment; SSG % = percentage sum square of the generation; SSG % x Environment = percentage sum square by environment interaction
CV= coefficient of variation; R^2=coefficient of determination

5.4.2 Response of test populations for sorghum and *Striga* parameters

Days-to-50% flowering

Mean performances and pair-wise contrasts on DFL among sorghum populations evaluated, with and without *FOS* treatments, in three environments are presented in Table 5.4. *FOS* application significantly reduced DFL in crosses 675 x 654, AS435 x AS426 and1563 x AS436. In these families, *FOS* treated entries flowered earlier, with a mean of 7 days less than their untreated controls. Reduced DFL was observed in *FOS* treated genotypes in all generations. Therefore, selection of individual plants with desirable characteristics within these families is important where early flowering is considered to be one of the *Striga* resistance components (Rebeka et al., 2013). Early flowering and *FOS* treated genotypes tended to escape *Striga* damage. Management of *Striga* through early maturing genotypes and *FOS* application of compatible sorghum genotypes was reported by Rebeka et al. (2013). *FOS* application did not exert a significant impact on sorghum families 3424 x 3993 and 3984 x 672, where the mean DFL was similar among treated and untreated plots. These genotypes had *FOS* compatibility based on field observation of some generations (Table 5.4). Differential response to *FOS* application on sorghum parameters has been reported by

Rebeka et al. (2013). The authors showed a significant reduction in DFL for some sorghum genotypes compatible with *FOS*.

Sorghum seed yield

SYP varied among test genotypes evaluated with and without *FOS* treatments in three environments (Table 5.4). Increased seed yield with a mean SYP of 6 g plant^{-1} was observed due to *FOS* treatment when compared to untreated controls of sorghum families 4567 x AS 426, 3424 x 3993 and 3984 x 672. The effect of *FOS* was variable across test generations of all crosses. The present findings support the report of Rebeka et al. (2013) and Mrema et al. (2017) who found significant increase in SYP in sorghum genotypes treated with *FOS*.

Number of *Striga* plants per sorghum plant

FOS treatment significantly reduced SN in sorghum family 675 x 654, 1563 x AS 436 and 3984 x 672 (Table 5.4). The treatment led to a reduction of up to 20 *Striga* plants per sorghum plant in the test families. Selection of sorghum genotypes with farmers preferred traits and minimal SN among these families may improve SYP in areas infested by *Striga*. *FOS* treatment had no marked influence in the sorghum family 4567 x AS 426, where a mean of 18 *Striga* plants were counted per sorghum plant in both treated and untreated plots. A synergistic effect of *FOS* on some sorghum genotypes for reduced SN was observed by Mrema et al. (2017). The authors reported a significant reduction in SN in some *FOS* treated sorghum genotypes, while there were slight or no SN reduction in sorghum genotypes that were not compatible to *FOS*.

Table 5.4. Tukey's multiple mean comparison and significant tests for days to flowering (DFL), seed yield per plant (SYP) and number of *Striga* per plant (SN) evaluated with (+) and without (-) *FOS* treatment for seven pair-wise crosses and six generations evaluated in three environments in Tanzania.

Cross and generation	Days to 50% flowering		Seed yield per plant		Number of *Striga* plant	
	+	**-**	**+**	**-**	**+**	**-**
675 x 654						
P1	66.33a	70.33a	64.50a	6600a	21.83a	60.33a
F1	65.00a	61.83c	61.45b	64.33a	15.50b	59.67a
BCP1	60.3b	67.83b	62.83ab	61.83b	15.00cb	49.17b
F2	54.67c	61.50c	58.67c	61.50b	13.50c	39.17c
BCP2	54.50c	62.00c	55.67d	54.67c	9.83d	38.33c
P2	52.83c	59.83d	54.67d	54.67c	4.67e	34.00c
Mean	58.94	63.89	59.63	60.5	13.39	46.78
LSD (5%)	2.3132	1.09	1.92	2.33	1.64	1.51
AS435 x AS426						
P1	53.17b	73.33a	21.17d	31.00a	28.00a	32.00a
F1	63.83a	71.50b	22.33cd	18.17d	19.17c	24.67b
BCP1	54.67b	71.67b	22.50cd	24.67b	24.00b	26.00b
F2	56.83b	67.00c	23.67c	22.50cb	15.50d	19.17c
BCP2	62.50a	67.00c	27.67b	21.33c	15.67d	16.50cd
P2	65.50a	66.50c	30.50a	18.17d	13.83e	14.50d
Mean	59.42	69.50	24.64	22.64	19.36	22.13
LSD (5%)	3.8095	1.52	2.053	1.64	1.5044	2.9251
4567 x AS 426						
P1	55.17c	59.50ab	45.00e	40.17c	30.67a	32.83a
F1	63.83ab	63.33a	47.83d	41.83c	18.33bc	22.67b
BCP1	55.67c	55.83b	45.33e	40.33c	21.17b	24.50b
F2	56.83c	59.00ab	50.67c	44.00b	14.83cd	14.00c
BCP2	62.00b	63.17a	52.50b	44.50b	11.83d	10.83cd
P2	66.00a	63.17a	56.17a	48.83a	11.17d	9.00d
Mean	59.92	60.67	49.58	43.28	18.00	18.97
LSD (5%)	2.30	5.17	1.59	1.68	5.62	3.32
3424 x 3993						
P1	52.17d	55.17c	18.67c	13.67d	4.33a	7.00a
F1	58.67bc	61.00b	22.83cb	15.50cd	2.17c	4.83b
BCP1	55.00cd	53.67c	22.83cb	17.50c	3.50b	5.33b
F2	54.50d	54.17c	26.00b	17.00c	2.00c	3.50c
BCP2	59.83b	59.50b	35.33a	23.67b	1.67cd	2.50c
P2	65.17a	63.83a	39.50a	26.33a	1.00d	2.67c
Mean	57.56	57.89	27.52	18.94	2.44	4.31
LSD (5%)	3.76	2.04	4.81	2.49	0.67	1.26
1563 x AS436						
P1	73.50a	75.00a	34.17a	30.17a	15.33a	43.17a
F1	66.67b	72.17b	25.83b	21.83b	11.00bc	36.17ab
BCP1	63.33cb	70.17cb	33.00a	27.83a	12.50ab	33.67cb
F2	60.67c	69.33c	26.00b	21.33b	8.50cd	27.33c
BCP2	56.17d	62.67d	25.83b	22.83b	5.50d	10.50d
P2	53.67d	54.67e	22.33cd	20.33b	7.17d	8.67d
Mean	62.33	67.33	27.86	24.06	10.00	26.58
LSD (5%)	4.08	2.52	1.88	4.13	3.00	7.20

Table 5.4. Continued.

Cross and generation	Days to 50% flowering		Seed yield per plant		Number of *Striga* plant	
	+	-	+	-	+	-
4567 x AS424						
P1	61.83a	65.17a	26.83ab	29.83a	8.83a	15.67a
F1	51.67c	57.17c	18.17c	19.67c	4.67b	10.67b
BCP1	55.33b	61.00b	28.33a	24.17b	5.50b	7.67c
F2	52.33c	56.50c	21.33cb	17.50cd	3.67c	6.50c
BCP2	51.33c	47.50d	15.83c	16.50d	1.83d	3.67d
P2	48.12d	45.83d	15.67c	16.17d	1.50d	3.83d
Mean	53.44	55.53	21.03	20.64	4.33	8.00
LSD (5%)	2.01	2.99	6.94	2.60	0.89	2.02
3984 x 672						
P1	63.83a	63.17a	45.50a	39.67a	22.50a	26.67a
F1	53.83c	55.50c	32.67d	34.33b	11.17b	19.67ab
BCP1	59.00b	60.33b	42.33b	35.17b	9.50cb	22.00ab
F2	53.83c	55.17c	38.67c	33.17b	7.50c	17.83ab
BCP2	53.50c	52.00d	36.17c	33.17b	4.00d	14.17b
P2	53.17c	51.00d	32.17d	28.67c	2.67d	13.00b
Overall mean	56.19	56.19	37.92	33.47	9.56	18.89
LSD (5%)	1.86	1.80	2.60	3.11	2.24	9.87

DF = degrees of freedom; P_1 = parent one; P_2 = Parent two; F_1 = first filial generation (P1 x P2); BCP_1 = Back cross to P_1; BCP_2 = back cross to P_2; F_2 = second filial generation
Generation means for each cross and trait in a column followed by the same letter are not significantly different at p=0.05.

5.4.3 Generation mean analysis

Generation mean analysis for DFL, SYP and SN, with and without *FOS* treatment, is presented in Table 5.5. Additive genetic effect made highly significant (P<0.001) contributions to DFL in both treatments for all families. Dominant and epistatic effects exerted small contribution to genetic variation of families for DFL. Significant contributions of dominance genetic effect with *FOS* treatment was recorded in families 675 x 654, 4567 x AS 426, 4567 x AS424 and 3984 x 672. In 3984 x 672 and 4567 x AS424, the additive-by-additive gene effect was significant (P<0.05) due to *FOS* treatment. An additive-by-dominance interaction effect was the main contributor of genetic variation for DFL in 4567 x AS424 with *FOS* treatment. Dominance-by-dominance interaction had non-significant (P>0.05) effects on DFL with *FOS* treatment for all test populations. This genetic effect had a significant influence on DFL in families 675 x 654 and 1563 x AS436 without *FOS* treatment

Additive gene effects were the most significant contributor (P<0.001) of genetic variation for SYP in all sorghum families. Also there were minimal or non-significant effects of epistatic genetic effects for SYP. Therefore SYP may be improved in these families through selection of high yielding sorghum genotypes in early generations. Dominance genetic effects were the significant genetic determinant (P<0.05) affecting SYP with *FOS* treatment in AS435 x AS426, 3424 x 3993 and 4567 x AS 426. An additive-by-additive gene effect was noted in the cross

675 x 654 with *FOS* treatment. Additive-by-dominance showed a significant effect in the cross of AS435 x AS426 without *FOS* treatment. Dominance-by-dominance genetic effects were significant (P>0.05), with and without *FOS* treatment, in populations of 3424 x 3993 and 1563 x AS436, and for 675 x 654 without *FOS* application.

Additive genetic effects were the most significant (P<0.001) form of genetic variation in most test families, with and without *FOS* treatments. Significant dominant genetic effects were recorded in AS435 x AS426 with, and 675 x 654 and 1563 x AS436 without *FOS*. Additive × additive gene effects had significant effects (P<0.05) in AS435 x AS426, 1563 x AS436 and 4567 x AS424 with *FOS*. Additive × dominance gene effects were significant (P<0.05) in 675 x 654 and 1563 x AS436 with *FOS* treatment, whilst this genetic effect was significant (P > 0.05) in 1563 x AS436 without *FOS*.

Table 5.5. Sum of squares and significant tests and genetic effects controlling days-to-50% flowering (DFL), seed yield per plant (SYP) and *Striga* number (SN) of sorghum genotypes evaluated in three environments in Tanzania with (+) and without (-) *FOS* treatment

	DFL		SYP		NS	
Cross and genetic effect	+	-	+	-	+	-
675 x 654						
Replication	93.44***	32.11**	16.91*	28.44**	7.11ns	44.44^{ns}
Additive (a)	646.82***	432.02***	432.02***	534.02***	936.15***	2419.35***
Dominance (d)	48.34**	41.83**	7.71^{ns}	36.76**	12.08^{ns}	310.61**
Additive × additive (aa)	306.35**	5.31^{ns}	18.56*	22.88*	9.86^{ns}	1099.59***
Additive × dominance (ad)	2.02^{ns}	0.82^{ns}	12.15^{ns}	5.40^{ns}	28.02**	13.07^{ns}
Dominance × dominance (dd)	8.03^{ns}	42.25**	0.82^{ns}	95.60***	16.45^{ns}	45.94^{ns}
Mean	58.94	63.89	59.63	60.50	13.39	46.77^{ns}
R^2 (%)	0.90	0.86	0.84	0.89	0.89	0.77
CV (%)	3.52	2.81	3.03	3.07	15.75	12.96
AS435 x AS426						
Replication	12.25^{ns}	9.00*	0.25^{ns}	8.03^{ns}	3.36^{ns}	10.03^{ns}
Additive (a)	633.75***	201.67***	340.82***	504.60***	806.67***	1188.15***
Dominance (d)	44.49^{ns}	2.88^{ns}	46.67**	148.04***	23.14*	0.20^{ns}
Additive × additive (aa)	118.24**	59.40***	0.01^{ns}	10.97^{ns}	68.00**	114.75**
Additive × dominance (ad)	6.67^{ns}	3.75^{ns}	0.60^{ns}	22.82*	3.75^{ns}	1.35^{ns}
Dominance × dominance (dd)	2.77^{ns}	1.63^{ns}	10.38^{ns}	8.03^{ns}	30.25*	0.69^{ns}
Mean	59.42	69.50	24.64	22.64	19.36	22.14
R^2 (%)	0.72	0.83	0.82	0.88	0.89	0.86
CV (%)	5.58	2.01	7.05	7.86	10.56	12.42
4567 x AS 426						
Replication	12.25^{ns}	28.44^{ns}	0.25^{ns}	1.78^{ns}	0.11^{ns}	0.03
Additive (a)	470.40***	129.07***	522.15***	277.35***	1401.67***	2257.07***
Dominance (d)	14.13*	3.76^{ns}	29.78**	32.03*	64.06^{ns}	0.08ns
Additive × additive (aa)	151.01***	67.56^{ns}	5.56^{ns}	0.77^{ns}	122.08^{ns}	295.60***
Additive × dominance (ad)	2.02^{ns}	72.60^{ns}	6.02^{ns}	0.07^{ns}	0.42^{ns}	7.35^{ns}
Dominance × dominance (dd)	3.36^{ns}	9.68^{ns}	7.41^{ns}	9.68^{ns}	3.78^{ns}	0.37^{ns}
Mean	59.92	60.67	49.58	43.28	18.00	18.97
R^2 (%)	0.88	0.29	0.89	0.60	0.74	0.88
CV (%)	2.97	8.49	3.12	6.30	24.54	17.90
3424 x 3993						
Replication	2.78^{ns}	53.78**	0.25^{ns}	2.78^{ns}	0.44^{ns}	8.03**
Additive (a)	570.42***	322.02***	1760.42***	595.35***	43.35***	79.35***
Dominance (d)	2.61^{ns}	0.03^{ns}	129.02**	65.36**	1.10^{ns}	0.59^{ns}
Additive × additive (aa)	70.92*	190.00***	6.76^{ns}	0.92^{ns}	0.37^{ns}	9.69**
Additive × dominance (ad)	6.67^{ns}	5.40^{ns}	10.42^{ns}	0.07^{ns}	0.07^{ns}	1.07^{ns}
Dominance × dominance (dd)	4.94^{ns}	2.78^{ns}	68.52*	73.20**	1.00^{ns}	0.44^{ns}
Mean	57.56	57.89	27.52	18.94	2.44	4.31
R^2 (%)	0.70	0.80	0.81	0.79	0.74	0.78
CV (%)	5.44	3.84	14.71	13.59	30.91	23.01
1563 x AS436						
Replication	0.44^{ns}	4.00^{ns}	4.69^{ns}	1.00^{ns}	25.00*	38.03^{ns}
Additive (a)	1316.02***	1392.02***	570.42***	365.07***	326.67***	5096.82***
Dominance (d)	7.12^{ns}	204.76***	16.67^{ns}	45.03*	4.76^{ns}	252.37*
Additive × additive (aa)	150.68**	0.04^{ns}	0.00	6.15^{ns}	40.79**	191.50*
Additive × dominance (ad)	18.15^{ns}	17.07^{ns}	3.75^{ns}	0.02^{ns}	20.42*	84.02^{ns}
Dominance × dominance (dd)	70.37^{ns}	44.44**	59.63**	59.63*	4.69^{ns}	358.89**
Mean	62.33	67.33	27.86	24.06	10.00	26.58
R^2 (%)	0.75	0.91	0.83	0.64	0.76	0.84
CV (%)	6.80	3.55	7.81	12.61	21.31	23.51

Table 5.5. Continued.

Cross and genetic effect	DFL		SYP		NS	
	+	-	+	-	+	-
4567 x AS424						
Replication	136.11***	1.36ns	56.25^{ns}	3.36^{ns}	1.78^{ns}	4.00^{ns}
Additive (a)	589.07***	1632.82***	728.02***	735.00***	201.67***	459.27***
Dominance (d)	50.61**	6.08^{ns}	23.14^{ns}	68.67**	3.76^{ns}	1.47^{ns}
Additive × additive (aa)	3.16^{ns}	1.93^{ns}	23.14^{ns}	58.16*	10.46**	105.42**
Additive × dominance (ad)	19.27*	35.27^{ns}	114.82^{ns}	1.67^{ns}	0.00^{ns}	8.82^{ns}
Dominance × dominance (dd)	1.78^{ns}	33.38^{ns}	17.36^{ns}	5.98^{ns}	2.78^{ns}	51.36**
Mean	53.44	55.53	21.03	20.64	4.33	8.00
R^2 (%)	0.88	0.85	0.48	0.78	0.88	0.80
CV (%)	3.56	5.74	28.59	14.04	23.30	29.51
3984 x 672						
Replication	0.25^{ns}	8.03^{ns}	0.03^{ns}	17.36^{ns}	40.11^{ns}	1.00^{ns}
Additive (a)	432.02***	640.27***	646.82**	448.27***	1224.02***	742.02**
Dominance (d)	102.94**	12.94^{ns}	106.25^{ns}	0.59^{ns}	41.83^{ns}	2.61^{ns}
Additive × additive (aa)	16.67^{ns}	4.42^{ns}	64.27^{ns}	11.17^{ns}	142.20**	22.62^{ns}
Additive × dominance (ad)	0.07^{ns}	12.15^{ns}	0.60^{ns}	0.07^{ns}	46.82^{ns}	2.40^{ns}
Dominance × dominance (dd)	11.11^{ns}	1.36^{ns}	29.64^{ns}	10.38^{ns}	61.36^{ns}	3.57^{ns}
Mean	56.19	56.19	37.92	33.47	9.56	18.89
R^2 (%)	0.77	0.78	0.46	0.72	0.75	0.27
CV (%)	4.32	4.51	15.45	7.59	44.08	45.00

* = significant at 0.05 probability level; ** = significant at 0.01 probability level; DF = degrees of freedom; CV = coefficient of variation; R^2=coefficient of determination

5.4.4 Relative contribution of genetic effects to sorghum and *Striga* parameters

The relative contributions of gene effects following GMA for DFL, SYP and SN, with and without *FOS* treatment are presented in Table 5.6. The relative contribution of gene effect showed that the additive genetic effect was significant, with and without *FOS* treatment, for all test populations. Additive genetic effects contributed to 75% and 74% of the total genetic variation for DFL, with and without *FOS*, respectively. Dominance and epistatic genetic effects made small contributions to the total genetic variation for DFL. A dominance genetic effect (18%) was recorded with *FOS* treatment in families 3984 x 672. In 675 x 654 and 4567 x AS426, additive-by-additive gene effects contributed to 28% and 23% of the total genetic variation associated with *FOS* treatment, in that order. Additive-by-dominance and dominance-by-dominance interactions made little contribution to the total genetic variation for DFL in all test populations.

Likewise, the additive gene effect (83%) contributed the most to the total genetic variation for SYP in all sorghum families. Mean relative contributions of 85% and 81% of additive genetic variance was recorded for SYP in test populations, with and without *FOS* treatments, respectively. Dominance and epistatic genetic effects made relatively small contributions to the genetic variation of families for SYP. In some families such as AS435 x AS426, 4567 x AS 426 and 3984 x 672 dominance genetic effects made significant contributions with the *FOS* treatment.

Also, the additive genetic effect provided a significant proportion of the genetic variation present for SN in most test families, with and without *FOS* treatments. This contribution amounted to 87% and 82%, with and without *FOS*, respectively. Dominance and epistatic genetic effects made relatively small contributions to SN. Overall, additive genetic effects contributed the most to the total genetic variation for DFL, SYP and SN. This outcome suggests the possibility of fixing additive genes through individual plant selection in the early segregating generation followed by pure line or single descent selection methods in advanced generations.

Table 5.6. Relative contribution of gene effect (%) for days to flowering (DFL), seed yield per plant (SYP) and *Striga* number (SN) of sorghum populations evaluated with (+) and without (-) *FOS* in three environments in Tanzania

	Days to 50% flowering		Seed yield per plant		Number of *Striga*	
Cross and genetic effect	+	-	+	-	+	-
675 x 654						
Replication	0.86	5.79	3.46	3.93	0.70	1.13
Additive (a)	58.54	77.93	88.5	73.85	92.72	61.51
Dominance (d)	4.370	7.55	1.58	5.08	1.20	7.90
Additive × additive (aa)	27.72	0.96	3.80	3.16	0.98	27.96
Additive × dominance (ad)	0.18	0.15	2.49	0.75	2.77	0.33
Dominance × dominance (dd)	0.73	7.62	0.17	13.22	1.63	1.17
AS435 x AS426						
Replication	1.50	3.23	0.06	1.14	0.36	0.76
Additive (a)	77.46	72.46	85.48	71.83	86.26	90.34
Dominance (d)	5.44	1.04	11.70	21.07	2.47	0.02
Additive × additive (aa)	14.45	21.34	0.00	1.56	7.27	8.72
Additive × dominance (ad)	0.81	1.35	0.15	3.25	0.40	0.10
Dominance × dominance (dd)	0.34	0.59	2.60	1.14	3.23	0.05
4567 x AS 426						
Replication	1.88	9.14	0.04	0.55	0.01	0.00
Additive (a)	72.02	41.49	91.42	86.22	88.04	88.15
Dominance (d)	2.16	1.21	5.21	9.96	4.02	0.00
Additive × additive (aa)	23.12	21.71	0.97	0.24	7.67	11.54
Additive × dominance (ad)	0.31	23.34	1.05	0.02	0.03	0.29
Dominance × dominance (dd)	0.51	3.11	1.30	3.01	0.24	0.01
3424 x 3993						
Replication	0.42	9.37	0.01	0.38	0.96	8.10
Additive (a)	86.65	56.10	89.12	80.71	93.56	80.02
Dominance (d)	0.40	0.00	6.53	8.86	2.38	0.59
Additive × additive (aa)	10.77	33.1	0.34	0.12	0.79	9.77
Additive × dominance (ad)	1.01	0.94	0.53	0.01	0.14	1.08
Dominance × dominance (dd)	0.75	0.48	3.47	9.92	2.16	0.45
1563 x AS436						
Replication	0.03	0.24	0.72	0.21	5.92	0.63
Additive (a)	84.21	83.74	87.06	76.55	77.35	84.64
Dominance (d)	0.46	12.32	2.54	9.44	1.13	4.19
Additive × additive (aa)	9.64	0.00	0.00	1.29	9.66	3.18
Additive × dominance (ad)	1.16	1.03	0.57	0.00	4.83	1.40
Dominance × dominance (dd)	4.50	2.67	9.10	12.50	1.11	5.96
4567 x AS424						
Replication	17.01	0.08	5.84	0.39	0.81	0.63
Additive (a)	73.63	95.44	75.62	84.21	91.48	72.86
Dominance (d)	6.33	0.36	2.40	7.87	1.71	0.23
Additive × additive (aa)	0.40	0.11	2.40	6.66	4.74	16.72
Additive × dominance (ad)	2.41	2.06	11.93	0.19	0.00	1.40
Dominance × dominance (dd)	0.22	1.95	1.8	0.68	1.26	8.15
3984 x 672						
Replication	0.04	1.18	0.00	3.56	2.58	0.13
Additive (a)	76.73	94.27	76.31	91.89	78.65	95.84
Dominance (d)	18.28	1.91	12.54	0.12	2.69	0.34
Additive × additive (aa)	2.96	0.65	7.58	2.29	9.14	2.92
Additive × dominance (ad)	0.01	1.79	0.07	0.01	3.01	0.31
Dominance × dominance (dd)	1.97	0.20	3.50	2.13	3.94	0.46

* = significant at 0.05 probability level, ** = significant at 0.01 probability level, DF = degrees of freedom

5.5 Conclusions

The present study examined the genetic effects controlling *Striga* resistance in a sorghum population. Additive genetic effects were responsible for most of the genetic variation present for DFL, SN and SYP in seven sorghum populations evaluated at three environments in Tanzania. Dominance and epistatic genetic effects made minor contributions in the test populations and environments. *FOS* treatment enhanced the expression of additive genes, which had a complementary effect on improved SYP, reduced SN and DFL. *FOS* application accelerated the primary contribution of additive genetic effect raising the possibility of breeding for *Striga* resistant sorghum genotypes with *FOS* compatibility. This may allow deployment of superior pure line sorghum cultivars adapted to *Striga* prone environments in Tanzania. The following crosses had improved levels of *Striga* resistance: 675 x 654, 1563 x AS436, 4567 x AS424 and 3984 x 672. Families 675 x 654, AS435 x AS426 and 1563 x AS436 had reduced DFL. Crosses 4567 x AS 426, 3424 x 3993 and 3984 x 672 were selected with higher SYP. These crosses are useful genetic resources to advance integrated *Striga* management (ISM) in the semi-arid regions of Tanzania. Following this chapter is a study on the maximum germination distance (MGD) aimed to determine gene action influencing MGD of *Striga hermonthica* and *S. asiatica* among selected sorghum genotypes treated with a biocontrol agent, *Fusarium oxysporum* f. sp. *strigae* (*FOS*) for effective breeding with *Striga* resistance and *FOS* compatibility

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CHAPTER SIX

Gene action controlling maximum germination distance of *Striga hermonthica* and *S. asiatica* in sorghum

This chapter has been published by:

Emmanuel Mrema, Hussein Shimelis, Mark Laing and Learnmore Mwadzingeni (2017)

Genetic analysis of the maximum germination distance of *Striga* under *Fusarium oxysporum* f. sp. *strigae* biocontrol in sorghum, Journal of Integrative Agriculture 2017, 16(0): 60345-7, doi: 10.1016/S2095-3119(17)61790-8

CHAPTER SIX

Gene action controlling maximum germination distance of *Striga hermonthica* and *S. asiatica* in sorghum

6.1 Abstract

Maximum germination distance (MGD) of *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*) is one the important components of *Striga* resistance in sorghum. However, there is a lack of information on gene action controlling MGD of *Striga*, especially with the combined use of host resistance and *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of the parasitic weed. Knowledge about the host gene action conditioning MGD of *Striga*, with or without *FOS* treatment, could be valuable for the development of improved sorghum varieties with *Striga* resistance and high yields. The objective of this part of study was to determine gene action controlling MGD of *Sh* and *Sa* in selected sorghum genotypes with *FOS* treatment. Twelve sorghum parents selected for *Striga* resistance, *FOS* compatibility or superior agronomic performances were crossed using a bi-parental mating design. The selected male and female parents and their F_1 progenies, backcross derivatives and the F_2 segregants were evaluated for their low haustorium initiation factor (LHF) on agar-gel assay in two sets. One set had *Sh* seed and the other set had *Sa* seed, both with and without *FOS*. Genotypes were evaluated using a split-plot design with three replications. MGD, was recorded for each treatment as the most distantly germinated *Striga*. This was followed by a pot experiment intended to evaluate the presence of *FOS* on sorghum roots and soil. Generation mean analysis showed the preponderance of additive, dominance and epistatic gene actions controlling MGD in the evaluated sorghum populations. In the set inoculated with *Sh*, the relative contribution of the additive, additive-by-additive and dominance-by-dominance genetic effect for MGD with *FOS* were 20%, 33% and 36%, respectively. In the set with *Sa*, the relative contribution of additive, additive-by-additive and dominance-by-dominance genetic effect were 21%, 32% and 35% with *FOS,* respectively. The influence of a dominance genetic effect and the interaction of an additive-by-dominance genetic effect were minimal. MGD was reduced by a mean of 1 cm due to *FOS* treatment in both sets involving *Sh* and *Sa*. There were varied *FOS* levels on sorghum root and soil samples, indicating variable colony forming units associated in the tested sorghum genotypes. This study demonstrated that additive, additive-by-additive and dominance-by-dominance genes were predominantly responsible for the inheritance of MGD of *Sh* and *Sa* in sorghum. Cultivar development exploiting these genetic effects contributing to

reducing MGD in the selected populations with *FOS* may provide enhanced response to selection for integrated *Striga* management (ISM) programme.

Key words: *Fusarium oxysporum* f.sp *strigae*, genetic effect, integrated *Striga* management, Maximum germination distance, sorghum

6.2 Introduction

Productivity of sorghum [*Sorghum bicolour* (L.) Moench] is affected by various biotic and abiotic stresses notably by *Striga* infestation, drought, storage pests and damage by birds. Further, a lack of access to seeds of improved varieties, and a lack of access to production inputs, such as fertilizers, insecticides, fungicides and herbicides are the most important yield limiting factors of sorghum in sub-Saharan Africa (Mrema et al., 2017). *Striga* [*Striga hermonthica* (Del.) Benth and *S. asiatica* (L.) Kuntze] are obligate root parasites cause severe yield losses in cereal crops including sorghum, rice (*Oryza glaberrima* Steudel and *O. sativa* L.), pearl millet (*Pennisetum glaucum* L.) and maize (*Zea mays* L.) (Riches, 2003; Rodenburg et al., 2015).

Integrated *Striga* management (ISM) in sorghum is a system that involves the use of resistant varieties, biological control agents, cultural practices and chemical control methods to minimize losses (Hearne, 2009). Breeding for *Striga* resistant sorghum is the cheapest and most environmentally friendly management option (Ejeta, 2007). Low haustorium initiation factor (LHF) reduced *Striga* germination stimulation, mechanical barriers, inhibition of germ tube exoenzymes by root exudates, phytoalexin synthesis, incompatibility, antibiosis, insensitivity to *Striga* toxins, and avoidance through root growth habits are reported to be important components of *Striga* resistance in sorghum (Wegmann,1996).

The use of sorghum varieties that exude low levels of *Striga* germination factors or LHF is reported to be one of the most effective methods for *Striga* management (Lynn and Chang, 1990). Sorghum genotypes with LHF have been reported to support few or no *Striga* at all (Hess et al., 1992; Ejeta et al., 1997). The agar-gel assay developed by Hess et al. (1992) is an effective tool for screening host genotypes for reduced levels of *Striga* germination factors. In this system, preconditioned *Striga* seeds are spread onto agar in petri dishes followed by sowing of sorghum seeds. The emerging radicles trigger the germination of *Striga* seed. The maximum distance between sorghum rootlets and germinated *Striga* seeds is referred to as maximum germination distance (MGD), one of the important components of *Striga* resistance.

Sorghum genotypes with a germination distance below 10 mm are classified as low germination stimulant types (Ejeta, 2000).

Gene effects are broadly classified into additive, dominance and epistasis. Further, additive x additive (aa), additive x dominance (ad) and dominance x dominance (dd) interaction effects of genes govern trait expression. The nature and type of gene action is important in designing an effective breeding program and in the subsequent gene deployment strategy in a *Striga* resistance breeding program. Several minor genes have been reported to enhanced germination of *Striga* (Vogler et al., 1996). Haussmann et al. (1996) reported the presence of quantitative genetic variation with a preponderance of additive genetic effects influencing stimulation of *Sh* seed germination. Partial or complete dominant genes for *Striga* susceptibility were also reported for sorghum hybrids derived from crosses between resistant and susceptible parents (Obilana, 1984).

Generation mean analysis (GMA) has been widely used for estimating gene effects. The method is based on the following six generations: female parent (P_1) and male parent (P_2), F_1 progenies, F_2 segregants, backcrosses to P_1 (BCP_1) and P_2 (BCP_2) (Anderson and Kempthorne, 1954; Hayman, 1958). The mean response of these generations allows estimation of genetic effects such as additive, dominance and epistasis components or their interactions. The technique is mostly used when the parents are divergent, possessing complementary and favourable alleles. GMA has been widely used to study gene action controlling *Striga* resistance in sorghum (Gamble, 1962), maize (Badu-Apraku et al., 2013) and rice (Gurney et al., 2006). The mode of gene action responsible for controlling MGD of *Striga* in sorghum has not been widely reported. This information is necessary to exploit the nature of genetic effects in *Striga* resistance breeding or integrated s*triga* management (ISM) programs.

Integrated S*triga* management (ISM) that combines the use of resistant sorghum genotypes compatible with *Fusarium oxysporum* f.sp. *strigae* (*FOS*), a biocontrol agent of *Striga*, is an option to control the parasite and to bolster sorghum productivity (Rebeka et al., 2013). Pathogenic isolates of *FOS* have been reported to be effective bio-herbicides in managing *Striga* infestation in sorghum, particularly when the method is integrated with other control practices (Rebeka et al., 2013). *FOS* has been shown to be host specific, pathogenic and highly destructive against *Striga*, and easy to mass produce (Ciotola et al., 2000). When sorghum seeds are treated with *FOS*, the fungus grows well in the rhizosphere of the young and developing sorghum plants, and subsequently parasitizes *Striga* plant stopping them from successfully attacking the roots of the host plant (Rebeka, 2007).

Breeding sorghum varieties with the traits of *Striga* resistance combined with compatibility with *FOS* could improve grain yield and reduce *Striga* infestation. This could improve the adoption of newly released varieties by farmers. The effect of *FOS* application on the selected compatible sorghum parents as measured by MGD is yet to be explored. Selection of desirable parents, their crosses and backcross derivatives with reduced MGD and compatibility with *FOS* would provide the basis for an ISM. This requires understanding of the genetic variability and inheritance of MGD of *Striga* for effective selection in sorghum breeding programs (Mrema et al., 2017).

In an effort to select *Striga* resistant and *FOS* compatible sorghum lines, promising genotypes were identified under controlled evaluation conditions (Mrema et al., 2017). Some of the selected landraces were relatively poor yielders but were well adapted to the drier regions of Tanzania and possessed farmers-preferred traits (Mrema et al., 2016). In contrast, some of the newly released sorghum genotypes had better yields and *FOS* compatibility but lacked essential farmer preferred traits. Detailed information on MGD of *Striga* of the selected complementary parents, F1s, backcross derivatives and F_2 populations were needed to establish the gene action influencing MGD of *Striga*, with or without *FOS* treatment. Therefore, the objective of this study was to determine the gene action controlling the maximum germination distance of *Sh* and *Sa* of sorghum genotypes combined with *FOS* treatment. The hypothesis being tested was that additive, dominance or epistatic genetic effects were important in controlling MGD of *Striga* and that the new families could be systematically selected to develop resistant cultivars with *FOS* compatibility.

6.3 Materials and methods

6.3.1 Plant materials and crosses

The study used 12 selected parents that were identified to have good general and specific combining ability effects for days-to-50% flowering, seed yield per plant and *Striga* resistance. Deatail descriptions of these materials are summarised in Chapter 4, Section 4.3.1

6.3.2 Bio-control agent and inoculum preparation

A pathogenic strain of *F. oxysporum* f.sp. *strigae* (*FOS*) originally isolated from sorghum fields infested with *Striga* in north eastern lowlands of Ethiopia was used as a bio-control agent for *Striga* management (Rebeka et al., 2013). The detail of the bi-control agent and inoculum preparation are outlined in Chapter 4, Section 4.3.2

6.3.3 Experimental site

The six breeding generations consisting of six female parents (P_1) and six male parents (P_2), F_1 progenies, F_2 segregants, backcrosses to P_1 (BCP_1) and backcrosses to P_2 (BCP_2) were evaluated to determine the MGD of *Sh* and *Sa* and their compatibility to *FOS*. The study was conducted at the Plant Pathology screen-house facility and the African Seed Health Centre laboratory in the Crop Science Department of Sokoine University of Agriculture in Tanzania.

6.3.4 Experimental design and trial establishment

Screening of sorghum genotypes for LHF and compatibility with *FOS*

Screening of sorghum genotypes to determine the MGD of *Sh* and *Sa* was carried out in two sets of experiments using an agar-gel assay developed by Hess et al. (1992). The two sets involved *Sh* or *Sa*, and both were with and without *FOS* treatment. The experiments were laid out in a split plot design with three replications. *FOS* was used as the main-plot factor and sorghum genotypes as the sub-plot factor.

MGD was screened using the procedure developed by Hess et al. (1992). The *Striga* seeds require pre-treatment, they were first surface sterilized by soaking in a 1% sodium hypochlorite solution for 5 minutes and then washed with distilled water on filter paper on a funnel until the chlorine odour disappeared. Two layers of circular filter paper were placed in a Petri dish base of 9 cm diameter and wetted with distilled water. Five mm Discs of filter paper were made by a core of 5 mm diameter and arranged on the moist paper in the Petri dish base. The sterilized, dried *Striga* seeds were sprinkled on the discs and the Petri dishes were covered with the lid. The Petri dishes were kept under dark conditions by covering the Petri dish with aluminium foil. The *Striga* seeds were then incubated at 25°C for 15 days. For the MGD study involving sorghum seeds treated with or without *FOS*, the preconditioned *Striga* seeds were randomly sown onto water agar in Petri dishes followed by planting one sterilised sorghum seed in each Petri dish. Another dish was sown with *Striga* seed and one sorghum seed dressed with 75 mg of *FOS* spores. Both sorghum and *Striga* seeds were left to germinate for 15 days. The maximum germination distance (MGD) was determined after 5 days by measuring the distance between the most distant germinated *Striga* and sorghum root.

Determination of the presence of *FOS* on sorghum roots and in soil

The above six generations were planted in plastic pots in screen house conditions using a randomized complete design with 3 replications. Plastic pots of 4 kg capacity were filled with soil and arranged on benches of 1.5 m height. Each replication had 42 pots arranged in 6 lines, each with 7 pots. Each pot was randomly allocated to each genotype. Two seeds coated with 75 mg of *FOS* product per variety were planted in each pot. Thinning was done after germination and one seedling per pot was allowed to grow. Fifty days after planting, soil and plant root samples were taken to monitor changes in *FOS* population and to determine the persistence of the *FOS* propagules in sorghum rhizosphere environments. The *FOS* propagules per gram of soil were determined using a modified serial dilution plate technique as described by Stapleton and Devay (1982). A cylindrical corer, 10 cm in depth and 1 cm in diameter, was used to remove sub-samples of soil from the infested top soil of each pot. Three subsamples, one from the centre and two from opposite sides of each pot were collected and mixed together to form a composite sample. The samples collected from each pot were air dried, crushed, mixed thoroughly and sieved using a 600 mm mesh. The samples were then diluted in 0.05% water agar and 1 ml aliquots were spread onto three peptone-pentachloronitrobenzene agar (PPA). The cultures were incubated for 7 days, and then the concentration of colony forming units (CFU) per gram of sample was determined.

The compatibility of *FOS* with sorghum roots was studied using root samples collected from each pot. The roots were cut into small pieces and surface sterilized in 5% sodium hypochlorite for 3 minutes. Then the samples were placed into petri dishes containing potato dextrose agar (PDA). The plates were incubated at 25^{o}C for seven days for visible fungal growth. After the incubation period, microscopic observation was carried out to observe the number of CFU.

6.3.5 Data analysis

Separate analysis of variance and homogeneity of variance tests were conducted, followed by combined analysis of variance (ANOVA) using the general linear model procedure (PROC GLM) in SAS version 9.3 (SAS Institute, 2011) to determine significance differences. The following model was used for data analysis: $Yijk = \mu + Gi + Ej + G \times E + rk (E) + eijk$. Where Yijk = response on MGD of ith generation in jth *FOS* interaction of kth replication, μ = overall mean, Gi = generation mean, Ej = jth *FOS* interaction, G × *FOS* interaction = generation × *FOS* interaction, rk = kth replication within FOS and eijk = residual factor. Independent samples t-test was used to assess the significance difference between *FOS* coated and uncoated sorghum genotypes' on MGD. Mean separation between generations for MGD and number of

CFU was done in SAS version 9.3 (SAS Institute, 2011) using the least significance difference (LSD) procedure for pair-wise comparisons (P≤ 0.05), as suggested by Kang (1994).
To determine gene action, data was subjected to generation mean analysis (GMA) using the methodology proposed by Mather and Jinks (1971), following ANOVA. GMA was performed using PROC GLM and PROC REG procedures in accordance with SAS macros described by Kang (1994). The genetic model used was: $Y = m + \alpha a + \beta d + \alpha^2 aa + 2\alpha\beta ad + \beta^2 dd$, where α and β are the coefficients for a and d, respectively; Y = generation mean; m = mean of the F_2 generation as the base population and intercept value; a = additive genetic effect, d = dominance genetic effect; aa = additive x additive gene interaction effect; ad = additive x dominance gene interaction effect; and dd = dominance x dominance gene interaction effect. A stepwise linear regression model was used to estimate the additive and dominance parameters. The parameters of the model were tested sequentially, starting with additive effects in order to determine the magnitude of additive, dominance and epistatic genetic effects as described by Ceballos et al. (1998). The importance of the gene effects was estimated as the ratio of the sums of squares of each component over the total sums of square. Significance of the genetic estimates was determined by dividing the estimated parameter values with their standard errors and was considered significant if the value exceeded 1.96 (Singh and Chaudhary, 1995).

To determine the magnitude of additive, dominance and epistatic genetic effects, the model's parameters were tested sequentially, one at a time, starting with additive effects and then in combination with other parameters of the model (Ceballos et al., 1998). The importance of the gene effect estimates was based on the ratio between the sums of squares of each component and the total sums of square. Significance of the genetic estimates was also determined by dividing the estimated parameter values with their standard errors; if the value exceeded 1.96, then it was considered significant (Singh and Chaudhary, 1995).

6.4 Results and discussion

6.4.1 Evaluation of mean germination distance (MGD) of *Striga hermonthica* in sorghum, with and *Fusarium oxysporum* f.sp. *strigae* (*FOS*)

Analysis of variance of MGD among sorghum families, with and without *FOS*

The analysis variance of the MGD among six sorghum crosses (675 x 654, AS435 x AS426, 3424 x 3993, 1563 x AS436, 4567 x AS424 and 3984 x 672) and six generations, evaluated with and without *FOS* application differed, significantly (P<0.01) (Table 6.1). Except for the

following crosses: AS435 x AS426 and 4567 x AS 426, other families interacted significantly ($P<0.01$), with *FOS* application affecting MGD.

The significant variation revealed by sorghum genotypes among generations for MGD indicated the presence of considerable genetic variation for LHF, which is an essential factor for *Striga* germination. These findings concurred with Hess et al. (1992) who reported variation in MGD for sorghum genotypes evaluated for *Sh* susceptibility in an agar-gel assay. Interaction between sorghum genotypes with *FOS* application indicated the variability in *FOS* compatibility among the sorghum genotypes. The presence of sorghum genotypes compatible with *FOS* was also reported in earlier studies conducted by Mrema et al. (2017).

Table 6.1. Mean squares and significance tests of the effect of *FOS* on germination distance between sorghum seed and the most distantly germinated *Sh* in six families of sorghum

Source of Variation	DF	Families					
		675 x 654	AS435 x AS426	3424 x 3993	1563 x AS436	4567 x AS424	3984 x 672
Replication	2	0.50	0.37	0.20	1.08	1.21	1.19
FOS	1	49.88***	6.85***	18.35***	14.19*	12.02**	12.84*
Error (a)	2	0.32	0.02	0.01	0.18	0.10	0.42
Generation	5	2.21***	11.24***	15.59***	20.48***	15.79***	17.06***
FOS x Generation	5	7.43***	0.10^{ns}	0.74**	1.22***	1.17***	1.05*
Error (b)	20	0.17	0.09	0.18	0.13	0.23	0.31
Total	35						

DF = degrees of freedom; *FOS* = *Fusarium oxysporum* f.sp. *strigae*.
*Significant difference at .05 probability level.
**Significant difference at .01 probability level.

***Significant difference at .001 probability level.

6.4.2 Responses of the tested sorghum population in relation to MGD of *Striga* and *FOS* treatment

Mean responses and pair-wise contrasts in relation to MGD of *Striga* among sorghum families evaluated, with and without *FOS* treatments, are presented in Table 6.2. Except for the sorghum family AS435 x AS426, *FOS* application significantly reduced MGD in all other crosses. In these families, *FOS* treated entries had reduced MGD measures as compared to their untreated controls. Sorghum genotypes with an MGD below 10 mm were reported to be *Striga* resistant (Ejeta, 2000). These genotypes were reported to support few or no *Striga* (Ejeta et al., 1997). Therefore, selection of individual plants with desirable characteristics within families with a reduced MGD and compatibility with *FOS* would control *Striga* infestation (Ejeta, 2000; Mrema et al., 2017).

Table 6.2. Mean maximum germination distance (MGD) of *Sh* among six sorghum families, with (+) and without (−) *FOS* application

	675 x 654		AS435 x AS426		3424x3993		1563xAS436		4567xAS424		3984x672	
Generation	+	-	+	-	+	-	+	-	+	-	+	-
P1	5.23	7.67	3.70	4.77	4.43	6.97	3.73	6.43	3.40	6.13	3.63	6.00
P2	0.60	1.03	0.30	1.43	1.07	2.63	0.43	0.83	0.33	0.67	0.50	1.27
F1	3.27	5.90	1.83	2.43	2.33	3.40	0.93	1.70	2.77	4.23	1.30	2.20
F2	2.97	3.80	2.47	3.10	1.27	2.37	0.87	1.93	1.20	2.37	1.30	1.90
BCP1	4.10	4.77	3.17	4.30	3.03	4.83	2.73	4.73	2.27	3.07	3.13	5.27
BCP2	1.53	2.00	0.77	1.43	1.30	1.80	0.30	0.90	0.67	1.10	0.87	1.27
Mean	2.95	4.20	2.04	2.91	2.24	3.67	1.50	2.75	1.77	2.93	1.79	2.99
Significance test	***	***	***	***	***	***	***	***	***	***	***	***
LSD (5%)	0.93	0.74	0.44	0.63	0.67	0.85	0.27	0.89	0.79	0.94	0.50	1.34

***Significant difference at .001 probability level

6.4.3 Generation mean analysis of MGD of *Sh*

Generation mean analysis for MGD of *Sh*, with and without *FOS*, is presented in Table 6.3. Additive, dominant and epistatic effect contributed significantly to the outcomes of the MGD for sorghum population, evaluated with and without *FOS*. Additive genetic effect made highly significant (P<0.001) contributions to MGD in both treatments for all families. Dominant and epistatic effects also contributed to genetic variation among families for MGD. Significant contributions of dominance genetic effects with *FOS* treatment were recorded for families 675 x 654, 3424 x 3993, 1563 x AS436 and 4567 x AS424. In all crosses, the additive-by-additive gene effect was significantly (P<0.001) higher after the *FOS* treatment. Additive-by-dominance interaction effects were the main contributor of genetic variation for MGD in AS435 x AS426,

3424 x 3993, 1563 x AS436, and 3984 x 672 with *FOS* treatment. Dominance-by-dominance interaction had significant (P<0.001) effects on MGD for all tested populations, with and without *FOS* treatments.

Table 6.3. Mean squares and significance tests for maximum germination distance between the sorghum seed, and the most distantly germinated *Sh*, evaluated with (+) and without (-) *Fusarium oxysporum* application for six families of sorghum

Source/gene effect	Families											
	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 x AS424		3984 x 672	
	+	**-**	**+**	**-**	**+**	**-**	**+**	**-**	**+**	**-**	**+**	**-**
Replication	0.78	1.15	0.11	0.28	0.13	0.07	0.25	1.01	0.70	0.61	0.13	1.48
Additive	7.11***	6.08***	5.29***	6.53***	5.90***	11.91***	8.97***	27.27***	0.77***	5.38***	7.60***	17.33***
Dominance	2.23*	22.46***	0.11^{ns}	0.00^{ns}	2.36**	3.69**	0.20*	0.44^{ns}	4.79***	20.24***	0.00^{ns}	0.00^{ns}
Additive x additive	10.87***	24.19***	4.08***	6.29***	12.96***	24.19***	11.12***	26.24***	9.60***	16.52***	9.59***	29.74***
Additive x dominance	0.00^{ns}	0.01^{ns}	0.26***	1.63**	0.80*	8.22***	2.82***	6.35***	0.00^{ns}	0.32^{ns}	0.77**	4.33*
Dominance x dominance	22.30***	38.04***	16.95***	15.56***	3.95***	7.69***	6.32***	18.81***	7.35***	19.85***	6.64***	14.58***
R 2	0.94	0.98	0.98	0.96	0.95	0.96	0.99	0.97	0.93	0.96	0.97	0.93
CV (%)	17.30	9.69	11.73	11.91	16.38	12.74	9.96	17.68	24.35	17.68	15.26	24.72

*Significant difference at .05 probability level.
**Significant difference at .01 probability level.

***Significant difference at .001 probability level.

R^2= coefficient of determination

CV= coefficient of variation

6.4.4 Relative contribution of the genetic effects on MGD of *Sh*

The relative contributions of gene effects on MGD of *Sh* in treatments with and without *FOS* are presented in Table 6.4. The relative contribution of gene effect showed that additive, dominance and epistatic genetic effect were significant, with and without *FOS* treatment, for some of the tested families. Additive genetic effects contributed to 20% and 21% of the total genetic variation for MGD, with and without *FOS*, respectively. However, contribution was lower than the respective contribution from additive-by-additive and dominance-by-dominance gene effects. Dominance and an additive-by-dominance genetic effect made small contributions to the total genetic variation. A significant dominance genetic effect of 20% and 32% was recorded for the cross 4567 x AS424 with and without *FOS,* respectively. Additive-by-additive gene effects contributed to 33% and 32% of the total genetic variation for families with and without *FOS*, respectively. Additive-by-dominance interaction made little contribution to the total genetic variation for MGD for all tested families. Dominance-by-dominance interaction made higher contributions of 36% and 31% to the total genetic variation for MGD in all tested families with and without *FOS*, respectively.

Overall, additive, dominance and non-additive genetic effects each contributed about 20-30% to the total genetic variation for MGD. Additive and epistasis gene effects have been found to make more significant contribution than dominance gene action in breeding for *Striga* resistance in sorghum (Kulkarni and Shinde, 1985). This study concurs with Kulkarni and Shinde (1985), who reported that *Striga* resistance was controlled by both additive and non-additive gene action. This outcome suggests the possibility of fixing additive genes through individual plant selection in the early segregating generation, followed by pure line or single seed descent selection methods in advanced generations.

Table 6.4. Relative contribution of genetic effect (%) for maximum germination distance between the sorghum seed and the most distant germinated *Sh* evaluated with (+) and without (-) *FOS* in six sorghum populations

Source/gene effect	Families											
	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 x AS424		3984 x 672	
	+	-	+	-	+	-	+	-	+	-	+	-
Replication	3.55	2.48	0.80	1.85	1.02	0.26	1.64	2.48	5.87	1.91	1.02	4.30
Additive	16.13	6.53	19.67	21.37	22.47	21.32	29.97	33.61	3.21	8.46	30.58	25.13
Dominance	5.05	24.13	0.42	0.00	9.01	6.61	0.66	0.54	20.05	31.87	0.00	0.00
Additive × additive	24.66	25.99	15.16	20.57	49.38	43.32	37.17	32.35	40.14	26.01	38.58	43.14
Additive × dominance	0.01	0.01	0.97	5.34	3.05	14.71	9.43	7.83	0.00	0.50	3.09	6.28
Dominance × dominance	50.6	40.87	62.98	50.88	15.06	13.78	21.13	23.19	30.72	31.24	26.72	21.15

6.4.5 Evaluation of MGD of *Sa* for sorghum populations, with and without *FOS*

Analysis of variance of MGD of *Sa* for sorghum families, with and without application of *FOS*

The analysis of variance for six sorghum crosses (675 x 654, AS435 x AS426, 3424 x 3993, 1563 x AS436, 4567 x AS424 and 3984 x 672), and six generations, evaluated with and without *FOS* application for MGD were highly significantly ($P<0.05$) different (Table 6.5). Sorghum crosses such as 675 x 654, 1563 x AS436 and 4567 x AS424 interacted significantly ($P<0.05$) with *FOS* application.

The significant variation revealed for sorghum genotypes among generations for MGD indicated the presence of considerable genetic variation for LHF secretion. These findings concurred with Hess et al. (1992) who reported variation in MGD among sorghum genotypes evaluated for *Striga* infestation on agar-gel assay. Interaction of sorghum genotypes with *FOS* application indicated variable compatibility among sorghum genotypes for *FOS*. The presence of certain sorghum genotypes compatible with *FOS* was reported in earlier studies conducted by Mrema et al. (2017).

Table 6.5. Mean squares and significance tests of the effect of *FOS* on the germination distance between sorghum seed and the most distant germinated *Sa* in six families of sorghum

Source of Variation	DF	Families					
		675 x 654	AS435 x AS426	4567 x AS 426	1563 x AS436	4567 x AS424	3984 x 672
Replication	2	0.80	0.29	0.01	0.73	1.19	0.65
FOS	1	11.45*	6.85*	0.87*	11.33*	12.84*	10.56*
Error (a)	2	0.40	0.22	0.02	0.29	0.42	0.17
Generations	5	14.68***	9.43***	3.63***	12.04***	17.06***	12.31***
FOS x Generations	5	1.02*	0.12^{ns}	0.02^{ns}	0.59*	1.05*	0.39^{ns}
Error (b)	20	0.28	0.14	0.06	0.15	0.31	0.24
Total	35						

Notes: DF = degrees of freedom; *FOS* = *Fusarium oxysporum* f.sp. *strigae*.
*Significant difference at .05 probability level.
**Significant difference at .01 probability level.

***Significant difference at .001 probability level.

Response of sorghum populations for MGD of *Sa*, with and without *FOS* application

Mean performances and pair-wise contrasts for MGD among the sorghum population evaluated, with and without *FOS* treatments, are presented in Table 6.6. There were significance (P<0.001) differences in mean MGD for the sorghum generation, with and without *FOS*. The significant variation on the sorghum genotypes among generations for MGD indicated the presence of considerable genetic variation for production of LHF which is essential for *Striga* germination. Ejeta (2000) showed that sorghum genotypes on MGD less than 10 mm were effectively *Striga* resistant, supporting few or no *Striga* infestations (Ejeta et al., 1997).

Except for the sorghum families AS435 x AS426, *FOS* applications significantly reduced the MGD for other crosses. Selection of individual plants with desirable characteristics within families with minimum MGD, and compatible with *FOS*, should result in control *Striga* infestations (Ejeta, 2000; Mrema et al., 2017).

Table 6.6. Mean maximum germination distance among six sorghum families with (+) and without (−) *FOS* application under *Sa* infestation

	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 x AS424		3984 x 672	
Generation	+	-	+	-	+	-	+	-	+	-	+	-
P1	4.37	6.50	3.63	4.63	4.80	6.60	3.10	5.17	3.07	5.33	3.33	5.23
P2	0.87	1.30	0.40	1.47	1.10	2.70	0.53	1.00	0.43	0.83	0.40	1.27
F1	2.67	4.90	2.10	2.33	2.30	3.47	0.83	1.83	2.63	4.00	1.27	2.30
F2	2.57	3.27	1.90	2.97	1.40	2.37	0.83	1.80	1.27	2.20	1.20	1.87
BCP1	3.47	4.20	2.80	4.00	3.17	4.47	2.40	4.07	2.10	2.83	2.87	4.33
BCP2	1.53	2.07	0.80	1.47	1.33	2.03	0.47	1.03	0.70	1.33	0.70	1.27
Mean	2.58	3.71	1.94	2.81	2.35	3.61	1.36	2.48	1.70	2.75	1.63	2.71
Significance	***	***	***	***	***	***	***	***	***	***	***	***
LSD	0.76	1.14	0.76	0.58	1.03	1.06	0.51	0.87	0.62	0.85	0.55	1.13

***Significant difference at .001 probability level

6.4.6 Generation mean analysis of MGD of *Sa* in sorghum families

Generation mean analysis for MGD with and without *FOS* treatments is presented in Table 6.7. Additive, dominant and epistatic effect contributed significantly in MGD among sorghum populations evaluated with and without *FOS*. Additive genetic effect made a significant (P<0.001) contribution to MGD in both treatments for all families. Significant contributions of dominance genetic effect with *FOS* treatment were recorded in families 675 x 654, 3424 x 3993 and 4567 x AS424. In all crosses, the additive-by-additive gene effect was significantly

higher (P<0.001) due to *FOS* application. Additive-by-dominance interaction effect was the main contributor of genetic variation for MGD in 4567 x AS426, 1563 x AS436, and 3984 x 672 with *FOS* treatment. Dominance-by-dominance interaction had significantly higher (P<0.001) effects on MGD in both treatments.

Table 6.7. Mean squares and significance tests for maximum germination distance between the sorghum seed and the most distantly germinated *Sa* evaluated with (+) and without (-) *Fusarium oxysporum* application in six families of sorghum

Source/gene effect	Families											
	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 x AS424		3984 x 672	
	+	-	+	-	+	-	+	-	+	-	+	-
Replication	0.16	1.05	0.10	0.40	0.57	0.46	0.17	0.85	0.41	0.63	0.09	0.74
Additive	4.96***	4.72**	4.49***	6.35***	8.22***	9.41***	5.99***	13.47***	0.39^{ns}	3.01**	5.90***	10.33***
Dominance	1.04*	12.93***	0.67^{ns}	0.03^{ns}	2.61*	4.21**	0.03^{ns}	0.21^{ns}	3.82***	14.85***	0.01^{ns}	0.25^{ns}
Additive × additive	6.12***	15.88***	4.44***	5.18***	13.60***	19.01***	7.08***	16.61***	6.82***	12.07***	8.42***	18.81***
Additive × dominance	0.04^{ns}	0.01^{ns}	0.26^{ns}	1.59**	1.24^{ns}	5.99**	1.73***	3.20**	0.00^{ns}	0.03^{ns}	0.65*	2.58*
Dominance × dominance	11.91***	20.91***	12.06***	12.67***	4.81**	5.05**	3.62***	11.20***	6.05***	12.72***	6.40***	10.18***
R 2	0.93	0.93	0.93	0.96	0.91	0.93	0.96	0.95	0.94	0.95	0.96	0.92
CV (%)	16.30	16.92	21.67	11.39	24.03	16.08	20.68	19.33	19.89	16.86	18.62	22.85

*Significant difference at .05 probability level.
**Significant difference at .01 probability level.

***Significant difference at .001 probability level.

R^2= coefficient of determination

CV= coefficient of variation

6.4.7 Relative contribution of genetic effects

The relative contributions of gene effects following MGD for sorghum families, with and without *FOS*, application are presented in Table 6.8. Additive, dominance and epistatic genetic effect were significant, with and without *FOS* treatment, for some of the tested population. Additive genetic effects contributed to 22% and 20% of the total genetic variation for MGD, with and without *FOS*, respectively. However, its contribution was lower than the contributions from additive-by-additive and dominance-by-dominance gene effects. Dominance and additive-by-dominance genetic effects made small contributions to the total genetic variation. Significant dominance genetic effects of 21% and 34% were recorded for 4567 x AS424, with and without *FOS*, respectively. Additive-by-additive gene effects contributed to 32% and 33% of the total genetic variation associated with and without *FOS* treatment, respectively. Additive-by-dominance interaction made little contribution to the total genetic variation for MGD in all test populations with *FOS*. Dominance-by-dominance interaction contributed to 35% and 30% of the total variation in all test populations, with and without *FOS*, respectively.

Additive, dominance and non-additive genetic effects contributed the most to the total genetic variation for MGD. The current result agrees to the report of Kulkarni and Shinde (1985), who found that *Striga* resistance, was controlled by both additive and non-additive gene action. This outcome suggests the possibility of fixing additive genes through individual plant selection in the early segregating generation followed by pure line or single seed descent selection methods in advanced generations.

Table 6.8. Relative contribution of genetic effect (%) for maximum germination distance between the sorghum seed and the most distant germinated *Sa* of evaluated with (+) and without (-) *FOS* in six sorghum populations

Source/gene effect	Families											
	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 x AS424		3984 x 672	
	+	**-**	**+**	**-**	**+**	**-**	**+**	**-**	**+**	**-**	**+**	**-**
Replication	1.29	3.72	0.91	3.04	3.61	2.07	1.78	3.67	4.60	2.88	0.84	3.38
Additive	20.36	8.35	20.28	23.85	25.96	21.10	31.89	29.02	2.15	6.85	27.35	23.67
Dominance	4.25	22.87	3.02	0.10	8.39	9.45	0.17	0.46	21.36	33.78	0.05	0.58
Additive × additive	25.11	28.08	20.08	19.45	42.95	42.63	37.70	35.8	38.08	27.46	39.07	43.12
Additive × dominance	0.17	0.00	1.18	5.96	3.92	13.42	9.21	6.90	0.02	0.08	2.99	5.92
Dominance × dominance	48.82	36.98	54.53	47.6	15.18	11.32	19.26	24.14	33.79	28.95	29.69	23.33

6.4.8 Presence of *FOS* on sorghum roots and in the rhizosphere

Quantification of *FOS* on sorghum roots and in the sorghum rhizosphere is summarised in Table 6.9.The numbers of colony forming units (CFU) found in soil and plant samples varied significantly ($p<0.001$) among sorghum families. This variation indicated the differential response of *FOS* to the sorghum genotypes. The multiplication of *FOS* was confirmed by the CFU counts recorded on the soil samples. Mean CFU values of 5.21 and 3.99 were recorded on sorghum roots and in soil samples, respectively. The number of CFU indicated the persistence of *FOS* on sorghum roots and on the rhizosphere. Its presence reduced the chances of successful attachment of *Striga* to its host, reducing the number of *Striga* infestations on treated plants.

Table 6.9. Tukey's multiple mean comparison and significant tests for the number of CFU on sorghum root and soil for seven sorghum families

Generation	675 x 654		AS435 x AS426		3424 x 3993		1563 x AS436		4567 xAS424		3984 x 672	
	Plant	Soil	Plant	Soil	Plant	Soil	Plant	Soil	Plant	Soil	Plant	Soil
P1	4.33	2	3.00	2.00	2.33	1.33	2.33	1.67	2.33	2.33	1.67	1.00
P2	11.00	9	8.00	5.67	5.67	3.67	9.00	5.67	11.33	11.33	7.33	5.33
F1	4.67	3	4.33	2.67	5.00	2.67	7.00	5.00	2.00	2.00	3.67	2.67
F2	4.33	4	4.00	4.67	6.33	5.00	7.00	5.00	3.67	3.67	4.00	2.67
BCP1	2.33	2	5.67	4.00	6.00	4.33	4.00	3.00	3.00	3.00	2.67	2.00
BCP2	4.33	3	6.33	6.33	4.67	3.00	6.00	4.67	9.00	9.00	6.33	4.67
Mean	5.17	3.83	5.22	4.22	5.00	3.33	5.89	4.17	5.22	5.22	4.28	3.06
Significance	***	***	***	**	***	**	***	***	***	***	***	***
LSD (5%)	1.66	1.73	1.81	1.93	1.45	1.49	1.09	1.37	1.90	1.90	1.62	1.32

CFU = colony forming units

6.5 Conclusions

The present study examined the genetic effects controlling maximum germination distance (MGD) among sorghum genotypes. Additive, additive-by-additive, and dominance-by-dominance genetic effects were responsible for most of the genetic variation present for MGD in the evaluated sorghum families. Dominance and additive-by-dominance genetic effects made minor contributions in the test populations. *FOS* treatment enhanced the expression of additive, additive-by-additive and dominance-by-dominance genes, which had a complementary effect on reducing MGD. *FOS* application accelerated the primary contribution of additive genetic effect raising the possibility of breeding for *Striga* resistant sorghum genotypes with *FOS* compatibility. This will allow deployment of superior pure line sorghum cultivars with reduced MGD and compatible with the bioagent for ISM in *Striga* prone environments in Tanzania. The following crosses were identified to have reduced MGD in set with *Sh* and *Sa* through *FOS* application: 1563 x AS436, 4567 x AS424, and 3984 x 672. These crosses are useful genetic resources to advance in ISM in the semi-arid regions of Tanzania.

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CHAPTER SEVEN

An overview of the research findings

7.1 Introduction and objectives of the study

Sorghum [*Sorghum bicolor* (L.) Moench] is an economic crop supporting some 500 million people predominantly in arid and semi-arid parts of sub-Saharan Africa (SSA). In SSA including Tanzania sorghum production and productivity is affected by diverse biotic and abiotic stresses, as well as socio-economic constraints. *Striga* is one of the major biotic constraints that causes yield losses of 30 to 90% in sorghum in Tanzania. Cultural, biological, chemical and host resistance measures have been recommended to control *Striga*. However, these measures need to be integrated for effective control of the parasite and to improve sorghum productivity, especially under the smallholder farming systems. A biological control agent based on *Fusarium oxysporum* f.sp. *strigae* (*FOS*) has shown promise in controlling *Striga* in SSA and can be integrated with resistant sorghum genotypes. Treatment of seeds of resistant sorghum genotypes with *F. oxysporum* reduces *Striga* numbers and vigour, and improves the agronomic performance and productivity of sorghum. A systematic breeding program aimed at improving sorghum varieties for *Striga* resistance, and which specifically includes farmers' preferred quality traits, may be the best option for developing new sorghum varieties that will be adopted by the farmers. This chapter highlights the objectives of the study followed by concise summary of major findings of each objective. Lastly, the inferences of the findings are presented for integrated *Striga* management (ISM) programme in the semi-arid parts of Tanzania.

7.1.1 The objectives of this study were:

1. To document the constraints affecting sorghum production and farmers' approaches of *Striga* management in the semi-arid regions of Tanzania.
2. To screen and select sorghum genotypes for *Striga hermonthica* (*Sh*) and *S. asiatica* (*Sa*) resistance and *FOS* compatibility for resistance breeding under Tanzanian conditions, including farmers-preferred quality traits.
3. To identify promising sorghum parents and crosses with *FOS*-compatibility and *Striga* resistance, with a high combining ability for grain yield and yield components for ISM.
4. To determine the gene action and inheritance of *Striga* resistance using genetically diverse populations of sorghum, including the interactions with *FOS* treatment.
5. To determine the gene action controlling the maximum germination distance of *Striga* using diverse sorghum genotypes, combined with *FOS* treatment.

7.2 Research findings in brief

Farmers' perceptions of sorghum production constraints and *Striga* control practices in semi-arid areas of Tanzania

This study was conducted across three selected districts and six villages involving 120 farmers in western Tanzania. Further focus group discussions based on a semi-structured questionnaire and observations following transect walks were used for data collection. The main findings of the study were:

- About 65% of the farmers grew sorghum landraces and had not adopted newly released varieties. Only 35, 15, and 10% of the farmers from Igunga, Kishapu, and Meatu Districts, respectively, reported growing newly released varieties.
- The major constraints affecting sorghum production in the study areas included *Striga* infestation, drought, storage pests, damage by birds, a lack of access to improved varieties, and a lack of access to production inputs such as fertilizers, insecticides, fungicides and herbicides.
- Hand weeding, crop rotation, fallowing, intercropping, and organic manure application were the most common practices of farmers for reducing S*triga* infestations.
- Most farmers (79.7%) had little knowledge of the best recommended *Striga* management practices.
- About 65% of the farmers did not use fertilizers and herbicides for soil fertility improvement and weed management, respectively, creating favourable conditions for *Striga* infestation, and for severe yield losses in sorghum.
- A systematic breeding program aiming at improving sorghum varieties for *Striga* resistance, including farmers' preferred traits, should be designed and implemented to increase the adoption of these new varieties by the farmers.

Screening of sorghum genotypes for resistance to *Striga hermonthica* and *S. asiatica* and compatibility with *Fusarium oxysporum* f.sp. *strigae*

Sixty sorghum genotypes were evaluated under screen house conditions using *S. hermonthica* (*Sh*) and *S. asiatica* (*Sa*) infested field soils with controlled seed infestation, with or without inoculation of the sorghum seeds with *FOS*. The experiment was laid out using a split-plot design; *FOS* being the main-plot and sorghum genotypes as the sub-plot treatments. Data on crop growth and grain yield parameters, and *Striga* incidence were collected. The core findings of the study were:

- Inoculation of sorghum seeds with *FOS* significantly enhanced sorghum growth and productivity, and supressed *Sh* and *Sa* growth and development.
- Compared to untreated controls, 28 sorghum genotypes evaluated in *Sh* infested soil had increased seed yields of 9 g per plant; 30 genotypes screened under *Sa* infestation had increased seed yields of 10 g per plant after *FOS* inoculation of the sorghum seeds.
- There were reductions of 1 to 4 *Sh* and *Sa* plants when sorghum seeds were inoculated with *FOS*.
- Overall, the present study selected 25 promising sorghum lines resistant to *Sh* and/or *Sa*, and *FOS* compatibility.
- The selected sorghum lines are a valuable genetic resources for the development of *Striga* management in sorghum through the integrated use of host resistance and *FOS* inoculation.

Combining ability of yield and yield components among *FOS*-compatible and *Striga*-resistant sorghum genotypes

One hundred sorghum families were developed through controlled crosses using the North Carolina Design II, involving 10 female parents selected for their *FOS* compatibility and high agronomic performances, and 10 male parents possessing *Striga* resistance. The F1s and their parents were field evaluated at three locations in Tanzania known for their severe *Striga* infestation, using a lattice experimental design with two replications. Significant general combining ability (GCA) ($p<0.05$) and specific combining ability (SCA) effects were recorded among the tested sorghum genotypes at both sites. The main findings of the study were:

- The best female parents were 675 and 3424 and the best male parents were AS426 and AS430 for general combining ability for yield and yield components.
- Genotypes 672, AS436 and AS429 (male parents) and 3984 (female parents) were the best general combiners for *Striga* resistance, displaying smaller GCA effects in a desirable direction.
- The families 675 x 654, 3424 x 3933 and 4567 x AS426 were selected for further breeding as they had the greatest SCA effects for grain yield.
- Crosses selected with small SCA effects for *Striga* counts were 4567 x AS424 and 3984 x 672. These were found to have high levels of *FOS* compatibility, *Striga* resistance and good agronomic traits.
- The selected sorghum parents and crosses are useful genetic resources for breeding, and for the implementation of ISM in sorghum.

Gene action controlling *Striga* resistance among sorghum genotypes

Twelve sorghum parents selected for *Striga* resistance, *FOS* compatibility or superior agronomic performances were crossed using a bi-parental mating scheme. The selected male and female parents and their F_1 progenies, backcross derivatives and the F_2 segregants were field evaluated at three locations in Tanzania known for their severe *Striga* infestations using a lattice experimental design with two replications. The following data were collected and subjected to generation mean analysis (GMA): days-to-50% flowering (DFL), seed yield per plant (SYP) and number of *Striga* per plant (SN). The main findings of the study were:

- GMA showed the preponderance of additive genetic action contributing to the total genetic variation in the evaluated sorghum populations.
- The additive genetic effect for DFL, SYP and SN, with and without *FOS* treatments, ranged from 72.02 to 86.65% and 41.49 to 95.44%, 75.62 to 91.42% and 71.83 to 91.89%, and 77.35 to 93.56% and 72.86 to 95.84%, in that order.
- The contribution of non-additive genetic effects was minimal and varied among generations. *FOS* application reduced DFL and SN and improved SYP in most of the tested sorghum populations.
- The DFL of sorghum populations was reduced by a mean of 8 days under *FOS* treatment compared to the untreated control in families such as 675 x 654, AS435 x AS426 and 1563 x AS436.
- *FOS* treatment improved SYP with a mean of 6.44 g plant^{-1} in 4567 x AS 426, 3424 x 3993 and 3984 x 672.
- The numbers of *Striga* plants were reduced with a mean of 16 plants due to *FOS* treatment in the crosses of 675 x 654, 1563 x AS436, 4567 x AS424, and 3984 x 672.
- The study demonstrated that additive genes were predominantly responsible for the inheritance of *Striga* resistance in sorghum.
- Cultivar development targeting reduced DFL, SN and high SYP in selected populations may provide an enhanced response to selection for ISM in western Tanzania.

Genetic analysis of maximum germination distance of *Striga hermonthica* and *S. asiatica* in sorghum treated with *Fusarium oxysporum*

Twelve sorghum parents selected for *Striga* resistance, *FOS* compatibility or superior agronomic performances were crossed using a bi-parental mating design. The selected male and female parents and their F_1 progenies, backcross derivatives and the F_2 segregants were evaluated for their low haustorium initiation factor (LHF) in an agar-gel assay in two sets. One set had *Sh* seed and the other set had *Sa* seed, both with and without *FOS*. Genotypes were evaluated using a split-plot design with three replications. MGD, was recorded for each

treatment as the most distantly germinated *Striga* plant. This was followed by a pot experiment to evaluate the presence of *FOS* on sorghum roots and soil. Data were subjected to generation mean analysis (GMA). The core findings of the study were:

- A generation mean analysis showed the preponderance of additive, dominance and epistatic gene actions controlling MGD in the evaluated sorghum populations.
- In the set inoculated with *Sh*, the relative contribution of the additive, additive-by-additive and dominance-by-dominance genetic effect for MGD with *FOS* were 20%, 33% and 36%, respectively.
- In the set with *Sa*, the relative contribution of additive, additive-by-additive and dominance-by-dominance genetic effects were 21%, 32% and 35% with *FOS*, respectively.
- The influence of a dominance genetic effect and the interaction of an additive-by-dominance genetic effect were minimal.
- MGD was reduced by a mean of 1 cm due to *FOS* treatment in both sets involving *Sh* and *Sa*.
- There were varied *FOS* levels on sorghum root and soil samples, indicating variable colony forming units associated with the tested sorghum genotypes.
- The study demonstrated that additive, additive-by-additive and dominance-by-dominance genes were predominantly responsible for the inheritance of MGD of *Sh* and *Sa* in sorghum.
- Cultivar development with a reduced MGD in the selected populations, combined with *FOS*, may provide enhanced responses to selection for integrated Striga management.

7.3 Implications of the study for breeding and integrated *Striga* management

- The PRA study showed that farmers preferred to grow landraces than improved introduced varieties dictating targeted breeding using both germplasm sets. There is a need of improving farmers preferred varieties rather than relying on introduced new varieties that lack most of the farmers' traits of preferences like *Striga* resistance, days to maturity and drought tolerance.
- Farmers' identified *Striga* infestations, earliness, drought tolerance, grain yield resistance to pests and diseases as well as resistance to bird attacks as their traits of preference. This shows the need to have a combined breeding objective aimed at integrating these traits of farmers-preference into developed varieties.
- Inoculation of sorghum seeds with *FOS* significantly enhanced sorghum growth and productivity, and supressed *Sh* and *Sa* growth and development for *FOS* compatible

sorghum genotypes. Therefore, integration of this biocontrol agent with resistant sorghum genotypes could play a pivotal role in reducing *Striga* and improving sorghum productivity

- Sorghum genotypes compatible with *F. oxysporum* were identified among the farmers preferred varieties collections of the semi-arid areas of Tanzania, providing an opportunity of exploiting the genetic resources for breeding towards ISM.
- Both additive, dominance and epistatic genetic actions were detected as controlling sorghum agronomic traits and *Striga* resistance related parameters which is useful for further selection and in hybridization programs aiming to develop transgressive segregants and improved cultivars. A future hybrid sorghum breeding program could exploit heterosis displayed by some sorghum genotypes.

7.4 Challenges in the implementation of ISM in sorghum

- Access to the Bio-Control Agent (*F. oxysporum* f.sp *strigae*). There is a need to develop local capacity to mass produce the biocontrol agent (*FOS*) for effective and large scale application of the technology in Tanzania. Altenatively, there need to be the efficient transport of a formulated *FOS* product from an established biocontrol company with large scale production capacilty in another country.
- Registration Requirements: regulatory requirements by Tanzania must be completed to allow for the introduction of *FOS* as a bio-herbicide to control *Striga* in sorghum and maize in Tanzania.
- Distribution Network: one or more agents need to be appointed to manage the distribution and sale of the biocontrol agent in Tanzania. Delivery System: the seed coating delivery system is an efficient method for uniform application of *Fusarium* and can be done on-farm by the farmers immediately before planting. Farmers should be educated about the technology through formal local extension services. Also, the seed delivery system should be integrated with this novel approach.
- Introduction of New Cultivars: Farmers should be educated about the new *Striga* resistant sorghum cultivars through the local extension services, using farmers' days, and demonstration plots.