Genetic Analysis of *Striga hermonthica* Resistance in Sorghum (*Sorghum bicolor*) Genotypes in Eastern Uganda

By

Olupot John Robert
BSc. Hons (Botany & Zoology), MSc. (Crop Science), Makerere University, Kampala, Uganda

A thesis submitted in partial fulfilment of the requirements for the degree of

Doctor of Philosophy (PhD) in Plant Breeding

School of Agricultural, Earth and Environmental Sciences
Faculty of Science and Agriculture
University of KwaZulu-Natal
Pietermaritzburg
South Africa.

December 2011

Thesis Abstract

Sorghum (*Sorghum bicolor*) is the third most important cereal food crop in Uganda. However, the parasitic weed *Striga hermonthica* severely constraints its production. The use of *Striga* resistant sorghum varieties may be one of the most feasible ways of managing the *Striga* problem. A series of studies were carried out with the overall objective to develop new sorghum genotypes that are resistant to *Striga* and high yielding in Eastern Uganda. Initially, a participatory rural appraisal (PRA) was carried out with the main objectives to study the current constraints faced by farmers in sorghum production and determine their preferences for new sorghum varieties. Secondly, fifty different African sorghum accessions were evaluated to determine phenotypic and genotypic variability for *Striga* resistance and identify suitable parents to be used in breeding for new *Striga* resistant and high yielding sorghum genotypes. Thirdly, a genetics study was conducted to determine gene action responsible for *Striga* resistance and sorghum yield in new sorghum genotypes. Finally, laboratory studies were carried out to identify specific mechanisms of *Striga* resistance available in new sorghum genotypes and their parents.

During the PRA, S*triga* was identified as the main constraint limiting sorghum production in Eastern Uganda, followed by insect pests. Farmers indicated preference for red gain sorghum with erect and compact heads, a plant height of 1.5m and a maturity period of around three months, as well as *Striga* resistance and drought tolerance. From farmers' own assessments, the individual field surveys and soil seed bank analyses that were carried out, the degree of *Striga* infestation in farmers' fields was found to be high.

Both phenotypic and genotypic factors contributed significantly to the variability observed among the African sorghum accessions with respect to *Striga* resistance and sorghum crop performance indicating that *Striga* resistance can be improved through selection. However, techniques that minimise environmental effects need to be employed in order to improve on heritability. The values for genetic coefficient of variation (GCV) and genetic advance (GA) indicated that genetic gain for *Striga* resistance could be achieved by selection based on area under *Striga* severity progress curve (AUSVPC), area under *Striga* number progress curve (AUSNPC) and individual *Striga* emergence counts. The sorghum accessions SRN39, Brhan, Framida, Gubiye, Wahi, P9407 and N13 were found to be resistant to *Striga hermonthica*.

These accessions consistently showed low AUSNPC, AUSVPC, and individual *Striga* emergence, *Striga* vigour and severity indices. These accessions could be used as sources of *Striga* resistance genes when breeding for *Striga* resistance in sorghum.

In the study to determine gene action responsible for *Striga* resistance and sorghum yield, significant genetic variation for *Striga* resistance and sorghum yield parameters was observed among the new sorghum genotypes and their parents. The sorghum parental lines: Brhan, SRN39, Hakika and Sekedo consistently had negative GCA effects for AUSNPC and AUSVPC, while SRN39 and Hakika additionally had negative GCA effects for *Striga* vigour, indicating that they were effective in transferring *Striga* resistance into their progeny. The new genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108, SRS2908, SRS2609, SRS609 and SRS1708 had negative SCA effects for AUSNPC, AUSVPC and *Striga* vigour meaning that they were resistant to *Striga*. Sorghum parental lines: Sekedo, Brhan, Framida and Hakika had positive GCA effects for head length, meaning that they increased head length in their crosses. The genotypes: SRS3408, SRS5309, SRS1608 and SRS2908 derived from the above parents had the longest heads compared to other progenies, which were on average, 20% longer than their parents. The genotypes: SRS609, SRS1408, SRS2608 and SRS3408 were the highest grain yielders and yielded 11-51% better than the highest yielding parent (Sekedo) under the non *Striga* environment. The parental lines; Sekedo, Brhan and Framida had positive GCA effects for grain yield indicating that they could act as sources of genes for grain yield increase. The genotypes; SRS609, SRS4609 and SRS2908 had large positive SCA effects for grain yield. The relative contributions of GCA effects to the observed genotypic variances were 80.5%, 43.3%, 65%, 92.6% and 53.2% for AUSNPC, AUSVPC, *Striga* vigour, sorghum head length and plant height respectively. This shows that additive gene action was important in controlling *Striga* resistance, sorghum head length and plant height in the present sorghum populations.

Laboratory studies aimed at investigating the specific mechanisms of *Striga* resistance available in new sorghum genotypes found that two new sorghum genotypes, SRS1608 and SRS1208 expressed both the low germination stimulant character and low haustoria initiation as mechanisms of resistance to *S. hermonthica*. The sorghum genotypes, SRS2808 and SRS1108, and two fixed lines, Brhan and Hakika expressed only the low germination stimulant character, while the genotypes, SRS608, SRS3408, SRS4109 and SRS2308 expressed only the low haustoria initiation mechanism. The inheritance patterns of the low germination stimulant character in the present sorghum genotypes varied. In some genotypes, it appeared to

be controlled by a single gene while in others; it appeared to be controlled by more than one gene.

Declaration

I, Olupot John Robert, hereby declare that;

- (i) The research reported in this thesis, except where otherwise indicated, is my original research.
- (ii) This thesis has not been submitted for any degree or examination at any other university.
- (iii) This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from those persons.
- (iv) This thesis does not contain other authors' writing, unless specifically acknowledged as being sourced from other authors. Where other written sources have been quated, then:
    - a) their words have been re-written but the general information attributed to them has been referenced;
    - b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced.
- (v) This thesis does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the references section.

Signed:……………………………………………Date……………………………………….

Olupot John Robert (Candidate)

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

Signed:……………………………………………Date………………………………………….
Prof. Pangirayi Tongoona (Principal Supervisor)

Signed:…………………………………………..…..Date…………………………………………
Prof. John Derera (Co-Supervisor)

Dedication

This thesis is dedicated to my eldest brother, the late Dr. John Peter Esele (1953-2011). He dearly took care and educated me right from primary one up to University level.

Acknowledgements

I would like to extend my sincere thanks and gratitude to my supervisors, Prof. P. Tongoona and Prof. J. Derera of the African Center for Crop improvement (ACCI), University of Kwazulu-Natal, and my in-country supervisor Dr. T.E.E. Areke of the National Semi-Arid Resources Research Institute, Serere, for their guidance and supervision during the entire course of this study. The additional support and guidance provided by Dr. Julia Sibiya during the study is greatly acknowledged.

I would also like to thank the Aliance for a Green Revolution in Africa (AGRA) for providing financial support that enabled the accomplishment of this study. I thank the Director of ACCI, Prof. Mark Laing for admitting me into the programme. The logistical support provided by Ms. Felicity de Stadler and Lesley Brown that enabled me to get into the programme and my stay in South Africa is greately acknowledged.

My thanks also go to the Director General of the National Agricultural Research Organisation (NARO), Uganda for granting me a study leave. Special thanks go to the Principal Human Resource Officer at NARO secretariat, Mr. R. Bagonza for facilitating the process to enable me acquire the study leave. I greatly appreciate the staff of the National Semi-Arid Resources Research Institute, Serere for the support rendered during this research. Specifically, I would like to thank Mr. A.P. Okello, Mr. J. Adoku, Mr. M. Epiku and Ms. S. Adiango for the assistance they offered in the course of this research.

Last, but not least, I would like to thank my dear children, Otialuk, Esele, Adie and Adong for the sacrifice they went through in my absence during this study. May the Almighty God bless you all. Amen.

Table of contents

GENERAL INTRODUCTION

Background

Sorghum (*Sorghum bicolor* (L.) Moench) originated in Eastern Africa, in the region bordering Sudan and Ethiopia (House, 1996; Doggett 1988). It is the fifth leading cereal crop in the world in total production and utilization, after wheat (*Triticum aestivum*), rice (*Oryza sativum*), maize (*Zea mays*) and barley (*Hordeum vulgae*) (Doggett, 1988; House, 1996; Murty et al., 1994; Quinton, 1985). It is grown in the tropical and sub-tropical parts of the world. In Uganda, sorghum is the third most widely grown cereal crop after finger millet and maize. The crop is grown in the northern, eastern and western parts of the country, occupying an average land area of 286,000ha annually (FAOSTAT, 2007).

Sorghum production in Uganda

Sorghum is one of the most important staple food crops in Uganda particularly in the northern and eastern parts. It is used for making bread and for brewing alcoholic beverages (Akwang et al., 1998). The nutritional composition of sorghum is 68-74% carbohydrate, 8-15% protein, 2-5% fat, 8-16% water, 1-3% fibre and 1.5-2.0% ash (Perseglove, 1975). It therefore has most of the main daily diet requirements of the human body. Sorghum is normally a drought tolerant crop usually yielding well even under marginal conditions. Therefore with the persistent droughts in the northern and north-eastern parts of Uganda, sorghum forms an important food security crop. In the north-eastern region of Uganda, sorghum occupies over 80% of the total crop acreage. Sorghum in Uganda is predominantly a peasant farmers' crop. Yields of up to 1527 kg ha^{-1} are obtainable with well-managed local varieties (Table i). However, improved varieties yield up to 5000 kg ha^{-1}. Hybrids on the other hand may yield 25% higher than improved open pollinated varieties, especially under conditions of low rainfall (Ebiyau and Oryokot, 2001).

From 2000 to 2005, sorghum occupied an average of 286,000 ha of arable land in Uganda producing an average of 413,000 metric tonnes of grain annually (Tables ii and iii). Whereas maize and millet occupy considerably more land compared to sorghum, the mean yields in kg ha^{-1} for the three crops were not significantly different in the period 2000 – 2005.

Table i: Yield (kg ha^{-1}) of major cereal crops in Uganda (2000 – 2005)

Crop	2000	2001	2002	2003	2004	2005	Mean
Maize	1742	1800	1800	1831	1440	1500	1685
Finger millet	1390	1501	1490	1600	1599	1600	1530
Sorghum	1289	1500	1498	1452	1400	1527	1444

Source: FAO Statistics Division 2007/10th July 2007

Table ii: National production ('000MT) of major cereal crops in Uganda (2000 –2005)

Crop	2000	2001	2002	2003	2004	2005	Mean
Maize	1096	1174	1217	1300	1080	1170	1173
Finger millet	534	584	590	640	659	672	613
Sorghum	361	423	427	421	399	449	413

Source: FAO Statistics Division 2007/10th July 2007

Table iii: Area harvested ('000Ha) under major cereal crops in Uganda (2000 – 2005)

Crop	2000	2001	2002	2003	2004	2005	Mean
Maize	629	652	676	710	750	780	699
Finger millet	384	389	396	400	412	420	400
Sorghum	280	282	285	290	285	294	286

Source: FAO Statistics Division 2007/10th July 2007

Despite the importance of sorghum, its production is characterized by low on-farm yields ranging from 800 to 1500 kg ha^{-1}(Omanya et al., 2004). The national average annual yield for the period 2000 to 2005 in Uganda was 1444 kg ha^{-1}(FAOSTAT, 2007). Sorghum yields are frequently lower than other cereals such as maize and millet. The realized yields are far below the potential yield of 5000 kg ha^{-1} in improved varieties under high levels of management in the absence of pests and diseases. One of the most important constraints that has been identified as contributing to this low yield is high *Striga* infestation in most of the sorghum growing areas (Akwang et al., 1998; Akwang et al., 1999).

Constraints to sorghum production in Uganda

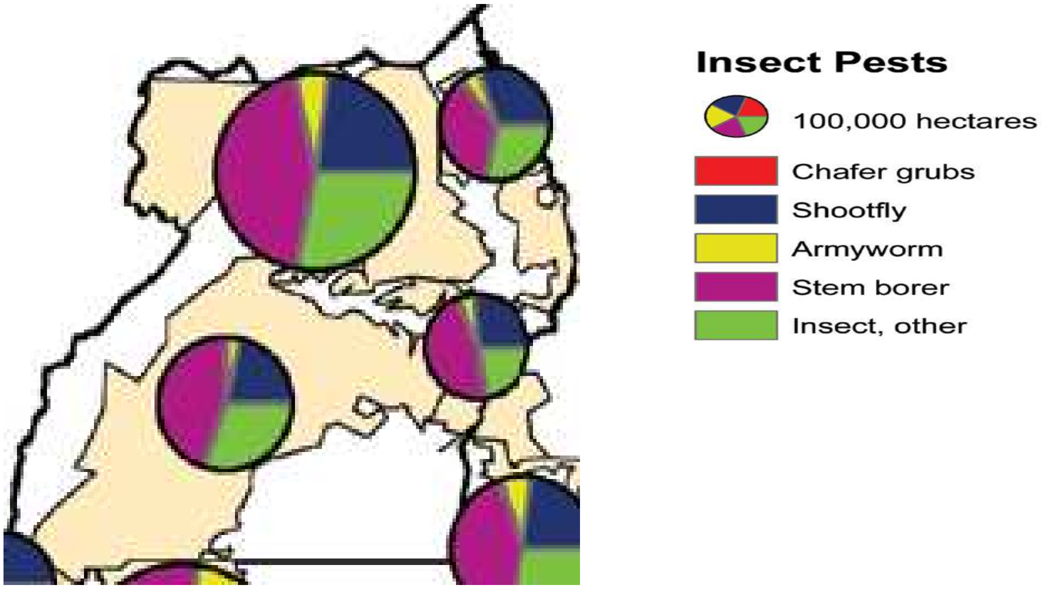
Table iv below presents yield losses attributed to the first eleven constraints limiting sorghum production in Uganda. Insect pests particularly stem borers and shootflies cause the greatest yield loss. These insect pests occur in all the five agro-ecological zones where sorghum is produced but are more destructive in the Eastern and Northern zones (Figure i). *Striga* and other weeds are the second most important constraints that cause yield reduction in sorghum. The *Striga* problem is experienced in Northern, Eastern and North-Eastern zones but is absent in the South-Western highlands (Figure ii).

Sorghum grain yield is also reduced due to poor soil fertility (in terms of nitrogen and phosphorous deficiency) and bird damage especially Quelea. While they are not among the first eleven constraints listed, sorghum diseases like grain mold, anthracnose and head smut also cause considerable yield reductions in sorghum productivity in Uganda.

Table iv: Estimated losses of grain sorghum due to the 11 most important constraints in Uganda

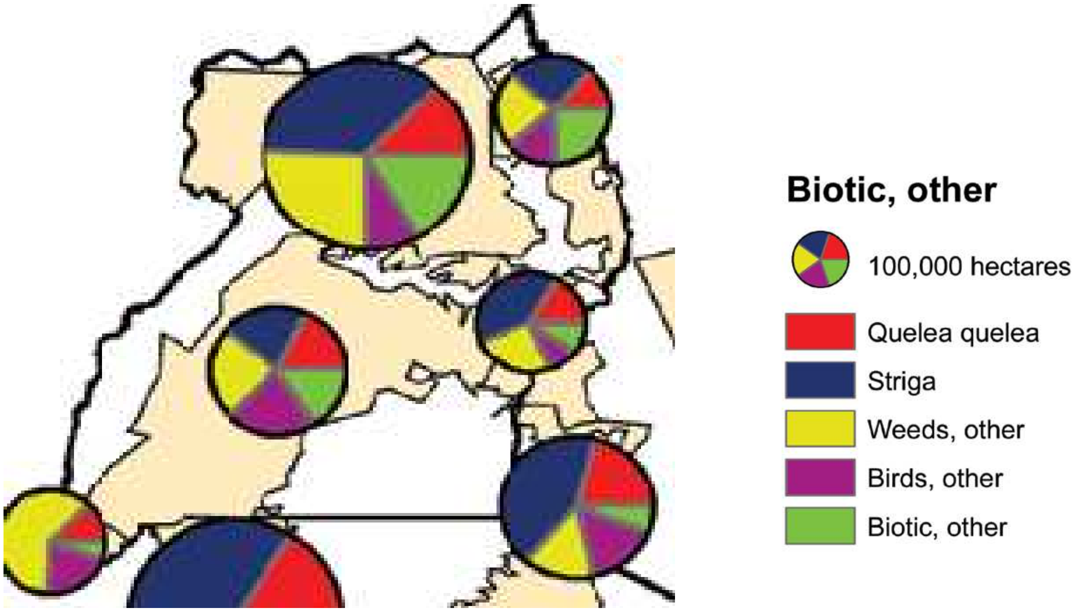
Constraint	Grain loss (Mg yr^{-1})
Stem borers	130,000
Striga	118,000
Other weeds	100,000
Nitrogen deficiency	81,000
Shootfly	76,000
Quelea	61,000
Other birds	55,000
Phosphorous deficiency	45,000
Late water deficit	30,000
Mid-season water deficit	59,000
Early water deficit	37,000

Adapted from: Atlas of sorghum production. INTSORMIL



Adapted from: Atlas of sorghum production. INTSORMIL

Figure i: Distribution of insect pests in major sorghum production zones in Uganda



Adapted from: Atlas of sorghum production. INTSORMIL

Figure ii: Prevalence of *Striga* and other biotic stresses in major sorghum production zones in Uganda

The *Striga* problem

Striga Spp. (witchweeds), are notorious root parasites of cereals including among many, sorghum, millet and maize grown in most semi-arid and tropical regions of the world. These parasites are increasingly reported to be a menace to crop production particularly in the savannah regions of sub-Saharan Africa. In Uganda, *S. hermonthica* (Del.) Benth. poses a serious threat to sorghum production causing average yield losses of up to 95%. This species is the most widely distributed in Uganda, and as reported by Kim (1991), in Africa as a whole. Sorghum producers in Uganda are largely peasant farmers who lack the resources to purchase and apply high quantities of fertilizers, herbicides, and mechanical tillage equipment, which have facilitated *Striga* control in developed countries. These farmers still await *Striga* management options that will be relevant to their needs and capacities.

Striga has been recognized as a major constraint to the production of sorghum since the 1940s (Enserink, 1995). In 1965, Doggett reported that grain yield loss of susceptible sorghum varieties in East Africa was 59%. This figure has steadily increased and to date total crop failure due to *Striga* infestation is frequent. A survey carried out in eastern Uganda, for example, found *Striga* to infest 83% and 50% of fields in Pallisa and Tororo districts respectively, causing sorghum grain yield losses estimated at 60 – 100% (Ebiyau and Ouma, 1995). The losses in yield vary depending on the cultivar, with resistant cultivars sustaining less yield loss. For example, Obilana (1983) recorded, among three groups of sorghum, a range of 5% loss in resistant cultivars to 95% in susceptible ones, with tolerant cultivars losing 45 – 63% of their potential yield.

The current cropping practices in East and Northern Uganda have led to a rapid decline in soil fertility and a build-up of *Striga* seed in the soil seed bank. These practices are characterized by intensive cultivation of small pieces of land with shortened or no fallow (Webb et al., 1993), and collapse of previous rotations that included cotton, cereals and legumes.

Recent research efforts in Uganda came up with some promising options for the management of *Striga* in farmers' fields. These are: (i) inter-planting sorghum with a *Striga* 'chaser' C*elosia argentea* (Olupot et al., 2003); (ii) growing sorghum in rotation with trap crops (Olupot, 2002); and (iii) use of the tolerant sorghum variety, Seredo, coupled with fertilizer application and weeding (Olupot et al., 1999). However, effective management of *Striga* at farm level has not been achieved in the country.

The way forward

The use of *Striga* resistant sorghum cultivars could be a key to an effective *Striga* control programme as it would be compatible with the low cost input requirements of subsistence farmers. Resistant cultivars effectively reduce *Striga* emergence and enhance the efficiency of other control measures (Haussmann et al., 2000a). The effectiveness of this strategy is enhanced when resistance is available in adapted, productive germplasm (Haussmann et al., 2000b). In a number of countries in Africa, USA and India, considerable effort has, over the years, been put into breeding for *Striga* resistance in sorghum (Kapran et al., 2007; Ezeaku and Gupta, 2004; Grenier et al., 2001; Ejeta, 2000; Ejeta et al., 1997; Ransom et al., 1997, Mabasa, 1996; Obilana and Ramaiah, 1992). The earlier breeding programmes had limited success because resistance frequently broke down (Ejeta et al., 1993; Kim, 1991). This is probably because the breeding was done without an understanding of the mechanisms of resistance to *Striga* operating in the sorghum genotypes, coupled with inefficient screening techniques. Even of recent, breeding has been slow due to inadequate knowledge about the genetics of *Striga* resistance, difficulty in evaluating the trait in segregating progeny, heterogeneity of natural infestations, micro-variability in soils and large environmental effects on *Striga* emergence (Ejeta, 2007; Patrick et al.,2004; Haussmann et al., 2000b; Haussmann et al., 2000a).

Another problem that has been reported to constrain breeding for *Striga* resistance is the existence of high variability within the same *Striga* species (Gethi and Smith, 2004; Ejeta et al., 1991), which probably leads to differences in virulence. This is particularly so for *S. hermonthica*, which is an outcrossing species. Further more, the difficulty in clearly identifying resistant variants from segregating germplasm in the field could be due to complex interactions between the host, parasite and environment (Patrick and Ejeta, 2008; Ejeta, 2007; Haussmann et al., 2000a).

Additionally, it is widely recognised that most of the *Striga* resistant sorghum lines so far developed have poor agronomic characteristics particularly low grain yield. For example, Framida, a West African sorghum line known to be resistant to *S. hermonthica*, was found to yield lower than some of the local farmers' varieties in Uganda, and to possess undesirable grain characteristics such as high tannin content. In Tanzania, varieties like Wahi, Hakika and SRN 39, were found to yield between 1800-2300 kgha^{-1} in a *Striga* free site (Ilonga) in trials conducted between 2001 and 2002. Such yield is actually lower than the potential yield of the current improved varieties in Uganda (3000-5000 kg ha^{-1}). It is necessary to develop varieties that combine *Striga* resistance with high grain yield, which could be acceptable to farmers in Uganda.

The existence of different mechanisms of resistance to *Striga* in sorghum

Some individual mechanisms conferring resistance to *Striga* in sorghum have so far been identified through laboratory studies (Patrick and Ejeta, 2008; Ejeta, 2007, Mutengwa 2004, Patrick et al., 2004;; Mohamed et al., 2003; Mohamed, 2002; Ejeta, 2001; Ejeta et al., 2000; Hess et al., 1992;). These are:

- low production of germination stimulants,
- low production of haustoria initiation factors,
- hypersensitive response/antibiosis, and
- incompatible response.

The same authors have also suggested the type of gene action and the nature of inheritance of the above mechanisms of *Striga* resistance in sorghum (see literature review). Other mechanisms that have been suggested with limited emphasis are presence of mechanical barriers in sorghum roots and parasite avoidance mechanisms such as deep rootedness (Mutengwa, 2004, Ejeta et al., 1991). Identification and understanding of these specific mechanisms in resistant sources is crucial for designing a breeding programme aimed at achieving multiple resistance that could be more effective against the parasite. It may be necessary to introgress genes for different mechanisms of resistance into a common background by producing a population involving diverse sources and improved resistant lines using specific mating designs (Kim, 1991). Therefore, through using an appropriate mating design such as the North Carolina II, crosses could be made between the different *Striga* resistant sources and locally adapted high yielding backgrounds in order to come up with sorghum genotypes that carry two or more mechanisms of resistance.

Field screening and evaluation of materials for *Striga* resistance

The efficiency of field screening and evaluation for *Striga* resistance could be improved by including one or several of the following practices: field inoculation with *Striga* seeds, appropriate experimental design with increased replications, specific plot layout, use of appropriate susceptible and resistant checks, evaluation in adjacent infested and uninfested plots; and the use of selection indices derived from emerged *Striga* counts, *Striga* vigour and grain yield or host damage scores (Haussmann et al., 2000b). Extreme variability in the parasite and significant genotype x environment interaction effects may be overcome through multi-locational testing of advanced germplasm to obtain materials with stable performance. Additional strategies could include; careful definition of the target environments, determination of the most important selection traits in each target environment, characterisation of crop germplasm and improvement of available sources of resistance for better agronomic performance.

Furthermore, the efficiency of evaluating germplasm for *Striga* resistance could be improved by initially partitioning the observed phenotypic variability into the heritable component (genetic) and the non-heritable component (environmental). This is because crop improvement may not only be dependent on the magnitude of phenotypic variability but also on the extent to which the desirable characters are inherited. During development of new germplasm, the genetic component of variability could be partitioned into the additive and the non-additive genetic component. The additive genetic component is the fixable part of genetic variation on which selection for the desirable attributes can be based on.

Farmer perceptions about new sorghum varieties and the *Striga* problem

In the past, the sorghum breeding programme in Uganda has made considerable achievements in developing high yielding and high grain quality sorghum varieties. However, most of these varieties have had limited adoption by farmers. This is probably because farmers' perceptions on the types of new sorghum varieties were not captured in a participatory rural appraisal before the varieties were developed. It is necessary to initially interact with farmers in a participatory rural appraisal at the beginning of a breeding programme so as to capture their specific preferences for new varieties. The breeder could then take such views into consideration right at the inception of the breeding programme. In a series of earlier surveys (Akwang et al., 1999, 1998; Ebiyau and Ouma, 1995; Webb et al., 1993) farmers in Eastern Uganda have pointed out the *Striga* problem as a leading constraint to the production of cereal crops. While research has attempted to investigate agronomic options to control *Striga*, there is an apparent need to develop *Striga* resistant varieties that additionally incorporate farmers' preferred traits. To meet this, farmers need to be engaged in discussions in order to understand their current perceptions of the *Striga* problem vis-a-vis use of resistant sorghum varieties.

Objectives of the study

The overall objective of this study was to develop sorghum genotypes with multiple mechanisms of resistance to *Striga hermonthica* in Uganda. The specific objectives were:

(i) To determine the current constraints faced by farmers in sorghum production in Eastern Uganda.
(ii) To determine farmers' preferences for new sorghum varieties in Eastern Uganda.
(iii) To assess the current cropping practices and determine the infestation levels and impact of *Striga* on sorghum production in Eastern Uganda.
(iv) To determine the phenotypic and genotypic variability of African sorghum accessions for *Striga* resistance and estimate its heritability.
(v) To determine the gene action effects of different sorghum cultivars and new genotypes for *Striga* resistance.
(vi) To investigate the existence of two or more mechanisms of resistance to *Striga* in new genotypes of sorghum.

Research hypotheses

Based on the above objectives, the following hypotheses were tested in this study:

(i) *Striga* is not a major constraint to sorghum production in Eastern Uganda.
(ii) Farmers have no specific preferences for new sorghum varieties in Eastern Uganda.
(iii) The current cropping practices in Eastern Uganda do not favour *Striga* infestation.
(iv) There are no available sources of *Striga* resistance in sorghum.
(v) Heritability of *Striga* resistance in African sorghum accessions is low.
(vi) The additive genetic effects are not important in the inheritance of *Striga* resistance in sorghum.
(vii) The present sorghum germplasm do not possess more than one mechanism of resistnace to *Striga* in a single genotype.

Outline of the thesis

Chapter one of this thesis is a review of literature. The history, current status and constraints to sorghum production in Uganda are reviewed. Previous information on the *Striga* problem in Uganda, the nature of damage and its biology is described. Attempts to breed sorghum for resistance to *Striga* carried out elsewhere are reviewed. The possible mechanisms of *Striga* resistance available in sorghum and their inheritance (for cases that have been studied) are also reviewed. Chapter two is a participatory rural appraisal in which the current constraints to sorghum production and farmers' preferences for new sorghum varieties are discussed. The current cropping practices, infestation levels and impact of *Striga* on sorghum production in Eastern Uganda are also presented in this chapter. In chapter three, the phenotypic and genotypic variability of a set of African sorghum accessions for *Striga* resistance in Eastern Uganda was investigated. Both the environmental and genetic factors were found to contribute significantly to the variability observed among the sorghum accessions for *Striga* resistance. Resistant sorghum lines that can be used as parents when breeding for new *Striga* resistant sorghum varieties are identified. The most effective selection criteria that could be used when screening or evaluating materials for *Striga* resistance are suggested. In chapter four, the gene action effects of sorghum parental lines and their crosses for *Striga* resistance and sorghum yield parameters were investigated. The best parental lines that can act as sources of genes for *Striga* resistance and sorghum yield are identified and discussed. Additionally, the new crosses that are resistant to *Striga* and high yielding are identified and discussed in the chapter. In the fifth chapter, the mechanisms of *Striga* resistance available in the new sorghum crosses were analysed. Specifically, the expression of low germination stimulant production and low haustoria initiation were investigated. The new sorghum crosses expressing both mechanisms of resistance to *S. hermonthica* are identified and discussed. The general discussion and overview of the present study, including opportunities and the way forward are presented in chapter seven.

References

Akwang, A.A., S. Okalebo, and J. Oryokot. 1998. Needs assessment for agricultural research in the Teso farming system, ‘Aijul Eode’: Main report. NARO/DFID, Kampala,Uganda

Akwang, A.A., J.P. Obuo, J. Okwadi, and J. Oryokot. 1999. Needs assessment for agricultural research in the Teso farming system: Summary report. NARO/DFID, Kampala, Uganda.

Doggett, H. 1988. Sorghum. 2nd ed. John Wiley & sons, New York, NY.

Ebiyau, J., and E. Ouma. 1995. *Striga* survey in Eastern Uganda. Serere Agricultural and Animal Production Research Institute/National Agricultural Research Organisation.

Ebiyau,J. and J.O.E. Oryokot. 2001. Sorghum (*Sorghum bicolor* (L.) Moench). In: Mukiibi, J.K.(ed.). Agriculture in Uganda, Vol.II. National Agricultural Research Organization 2001, Fountain Publishers Ltd, Kampala, Uganda.

Ejeta, G. 2007. Breeding for *Striga* resistance in sorghum: Exploitation of an intricate host-parasite biology. Crop Science 47:216-227.

Ejeta, G. 2001. *Striga* biotechnology development and technology transfer. 2001 Annual Report. INTSORMIL.

Ejeta, G. 2000. Molecular mapping of *Striga* resistance genes in sorghum, *In* B. I. G. Haussman, et al., (eds.) Breeding for Striga resistance in cereals. Proceedings of a Workshop held at IITA, Ibadan, Nigeria. Margraf Verlag, Weikersheim, Germany.

Ejeta, G., L.G. Butler, and A.G.T. Babiker. 1993. New approaches to the control of *Striga*: *Striga* research at Purdue University. Agricultural Experiment Station, Purdue University, USA.

Ejeta, G., L.G. Butler, D.E. Hess, and R.K. Vogler. 1991. Genetic and breeding strategies for *Striga* resistance in sorghum, pp. 539-544, *In* J. K. Ransom, et al., (eds.) Proceedings of the Fifth International Symposium on Parasitic Weeds, Nairobi, Kenya.

Ejeta, G., L.G. Butler, D.E. Hess, T. Obilana, and B.V. Reddy. 1997. Breeding for *Striga* resistance in Sorghum, pp. 504-516. *In* Proceedings of the international conference on genetic improvement of sorghum and pearl millet. INTSORMIL, ICRISAT, Holiday Inn Plaza, Lubbock, Texas.

Ejeta, G., L.G. Butler, D.E. Hess, T. Obilana, and B.V. Reddy. 2000. Breeding for *Striga* resistance in Sorghum, *In* B. I. G. Haussman, et al., (eds.) Breeding for Striga resistance in cereals. Proceedings of a Workshop held at IITA, Ibadan, Nigeria. Margraf Verlag, Weikersheim, Germany.

Enserink, H.J. 1995. Sorghum agronomy in West Kenya: Investigations from a farming systems perspective. Royal Tropical Institute, Amsterdam.

Ezeaku, I.E. and S.C. Gupta. 2004. Development of sorghum populations for resistance to *Striga hermonthica* in the Nigerian Sudan Savannah. African Journal of Biotechnology 3(6): 324-329.

FAOSTAT. 2007. Production statistics [Online]. Available by Food and Agriculture Organisation of the United States, Statistics division. http://faostat.fao.org/

(verified 10th July).

Gethi, J.G., and M.E. Smith. 2004. Genetic responses of single crosses of maize to *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze. Crop science 44: 2068-2077.

Grenier, C., P.J. Rich, A. Mohamed, A. Ellicot, C. shaner, and G. Ejeta. 2001. Independent inheritance of LGS and IR genes in sorghum. *In*: Fer et al. (ed.) Proceedings of the 7th International Parasitic Weed Symposium, Nantes, France.

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, H.G. Welz, and H.H. Geiger. 2000b. Improved methodologies for breeding *Striga* resistant sorghums. Field Crops Research 66(3):195-211.

Hess, D.E., G. Ejeta, and L.G. Butler. 1992. Selecting genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga.* Phytochemistry 31:493-497.

House, L.R. 1996. Inaugural address. *In* Proceedings of the international conference on genetic improvement of sorghum and pearl millet. INTSORMIL, ICRISAT, Holiday Inn Plaza, Lubbock, Texas.

Kapran, I., C. Grenier, and G. Ejeta. 2007. Introgression of genes for *Striga* resistance into African landraces of sorghum. *In*: Ejeta and Gressel, (eds.) Integrating New Technologies for Striga Control. World Scientific Publishing Co. Pte. Ltd.

Kim, S.K. 1991. Combating *Striga* in Africa, *In* S. K. Kim, (ed.) Proceedings of the International Workshop, IITA, Ibadan, nigeria.

Mabasa, S. 1996. Screening sorghum genotypes for resistance to witchweed (*Striga asiatica*) in Zimbabwe, *In* K. Leuschner and C. S. Manthe, (eds.) Drought tolerant crops for southern Africa: Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, Gaborone, Botswana.

Mohamed, A.H. 2002. Identification and characterization of genetic variants in sorghum for specific mechanisms of *Striga* resistance. PhD thesis, Purdue University, USA.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43: 1320-1324.

Murty, D.S., R. Tabo, and O. Ajayi. 1994. Sorghum hybrid seed production and management. Information Bulletin no.41. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andra Pradesh, India.

Mutengwa, C.S. 2004. The search for molecular markers, parental characterisation and inheritance studies of witchweed (*Striga asiatica*(L.) Kuntze) resistance in sorghum (*Sorghum bicolor* (L.) Moench). PhD Thesis, University of Zimbabwe

Obilana, A.T. 1983. Socio-economic impact of *Striga* in cereal crops in West Africa. Paper presented at the International training course on the control of *Striga* in cereal crops. August 1983, Raleigh, NC, USA: North Carolina State University.

Obilana, A.T., and K.V. Ramaiah. 1992. *Striga* (Witchweeds) in sorghum and millet: Knowledge and future research needs, pp. 187-207, *In* W. A. J. deMilliano, et al., (eds.) Sorghum and millet diseases, a second world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andra Pradesh, India.

Olupot, J.R. 2002. Development of an integrated *Striga* management strategy for small-scale sorghum growers in Uganda. Msc. Thesis, Makerere University, Kampala, Uganda.

Olupot, J.R., D.S.O. Osiru, J. Oryokot, and B. Gebrekidan. 1999. Development of an integrated *Striga* management strategy for Ugandan conditions, *In* A. O. Chivinge, et al., (eds.) Proceedings of the 17th Biennial Weed Science Society Conference for Eastern Africa. WSSEA, Harare Zimbabwe.

Olupot, J.R., D.S.O. Osiru, J. Oryokot, and B. Gebrekidan. 2003. The effectiveness of *Celosia argentia* ("*Striga* Chaser") to control *Striga* on sorghum in Uganda. Crop Protection 22:463 – 468.

Omanya, G.O., B.I.G. Haussmann, D.E. Hess, B.V.S. Reddy, M. Kayentao, H.G. Welz, and H.H. Geiger. 2004. Utility of indirect and direct selection traits for improving *Striga* resistance in two sorghum recombinant inbred populations. Field Crops Research 89(2-3):237-252.

Patrick, J.R., and G. Ejeta. 2008. Towards effective resistance to *Striga* in African maize. Plant signal Behaviour 3(9): 618-621.

Patrick, J.R., C. Grenier, and G. Ejeta. 2004. *Striga* resistance in the wild relatives of sorghum. Crop Science 44: 2221-2229.

Perseglove, J.W., (ed.) 1975. Tropical crops: Monocotyledons, Vol. 1 and 2. Longman group Ltd.

Quinton, J.R. 1985. Characterization of sorghum for genes affecting pericarp color and polyphenols. Ph.D. thesis, Texas A&M University, USA.

Ransom, J.K., G.D. Odhiambo, G. Abayo, and A. Oswald. 1997. An update of *Striga* control research in Africa, pp. 215-219, *In* E. Adipala, et al., (eds.) Proceedings of the 16th Biennial Weed Science Society Conference for Eastern Africa. WSSEA, Kampala, Uganda.

Webb, M., C. Conroy, D. Baguma, and R. Kabanyoro. 1993. Survey of the socio-economics of weed control on smallholder farms in three districts of Uganda. Report R 2014 (S), Natural Resources Institute, Chatham, UK.

CHAPTER ONE: LITERATURE REVIEW

1.1 Introduction

This review covers areas that provide relevant literature deemed necessary to guide research into breeding for *Striga* resistance in sorghum in Uganda. The history and current status of sorghum production in the country are described. Previous information on the *Striga* problem in Uganda, the nature of damage and its biology is reviewed. Attempts to breed sorghum for resistance to *Striga* carried out elsewhere are also reviewed. The specific mechanisms of *Striga* resistance identified in some sorghum lines as well as the suggested modes of inheritance are briefly described.

1.2 History and distribution of sorghum in Uganda

Sorghum is known to have originated in East Africa, in the region bordering Sudan and Ethiopia. This region, being the centre of diversity of sorghum and millet contains tremendous sorghum genetic variability (Doggett, 1965; Ebiyau and Oryokot, 2001). Sorghum was introduced into Uganda by the pastoral and Bantu peoples around AD 350, who entered the country from the north and western parts and moved east and southwards along the rift valley and extensive trade routes, on land and rivers (Doggett 1970). It has been indicated that up to 204 landraces of sorghum have so far been collected from farmers' fields in Uganda (Ebiyau and Oryokot 2001). The collections include both cultivated and wild types. The Caudatum race was found in South-Western Uganda, Guinea-Caudatum in the extreme North-Western and Guinea in the Eastern and Central parts of the country. The other races such as Kafir, Bicolor and Dura seem not to be recorded in the country. Generally, five basic races of cultivated sorghum have been recognised (House, 1996). These are: Bicolor, Kafir, Guinea, Caudatum and Durra. The Bicolor race is characterized by open inflorescences and long, clasping glumes that usually enclose the grain at maturity. It is widely distributed in Africa and Asia. Kafir is found south of the equator in Africa, and exhibits symmetrical and nearly spherical grains with glumes shorter than the grain. Guinea is predominant in West Africa and is easily recognized by long and obliquely twisted, gaping glumes revealing grains at maturity. Grains of the race Caudatum are asymmetrical with a turtleback, pointed beak and short glumes. This race is distributed throughout Central Africa and is of recent origin. Durra exhibits obovate grains which are wedge-shaped at the base but slightly broad above the middle. During the collection in Uganda, the wild sorghum types, *S.halepense* (L) Pers. and *S.arundinaceum* (Desv.) Stapf were also found abundantly on field boundaries in all regions of Uganda.

Sorghum is grown in five different agro-ecological zones in Uganda, which vary according to length of growing season, rainfall, temperature and altitude (Table 1.1). Over 80% of the crop is grown in the dry and hot lowland areas of Eastern, Northern and Western parts with only 12% in the highland areas of the South-West. The dry and hot lowland areas are characterized by short rainy seasons with low and erratic rainfall. Over 90% of farmers still grow their indigenous varieties which possess extensive genetic variability, and they produce and preserve their own seed for planting. The farmers of South and South-Western region grow the Caudatum race which is used for making porridge, *Obushera* and local beer, *Omuramba* and *Marwa*. *Obushera* is thick porridge made out of sorghum flour in South-Western Uganda while *Omuramba* and *Marwa* are names given to local beer made from sorghum in South-Western and Eastern Uganda respectively. In the North and North-Western parts of the country, the race Guinea-Caudatum with lax panicles is grown and used for thick porridge (*Ugali).* Most farmers in Central and Eastern Uganda grow the Guinea race and use it for *Ugali* and brewing beer, *Mwengge* or *Ajon*. *Ugali* is a local name for bread while *Mwengge* or *Ajon* are local names given to the local alcoholic beer made from sorghum in Central and Eastern Uganda.

Table 1.1: Characteristics of sorghum production zones in Uganda

Zone	**Area under sorghum ('000 ha yr^{-1})**	**Altitude (masl)**	**Latitude (degrees north of equator)**	**Climatic characteristic of main sorghum production season**		
				Mean temperature (^{o}c)	Rainfall (mm month^{-1})	Duration of the rain period (months)
Northern	112	1100	2	23	130	4*
North-east (Karamoja)	37	1250	3	26	82	3*
Eastern	31	1170	1	22	98	3*
Central and West	51	1160	0	22	98	4*
South West highlands	32	1900	-1	18	110	6

Source: Atlas of sorghum Production. INTSORMIL.

* The 3-4 months of rainfall occur in two different seasons in a year.

1.3 Sorghum breeding in Uganda

Breeding to improve the sorghum crop in Uganda started in 1958 under the East African Agriculture and Forestry Research Organization (EAAFRO), which was a department under the East African Community (EAC) (Ebiyau and Oryokot, 2001). Since then, the breeding programme has been geared towards increased yield, resistance to insect pests, drought tolerance, high grain quality, and hybrid development.

The breeding programme has made considerable achievements in the above areas. Several high yielding varieties have so far been developed and released to farmers (Table 1.3). The most recent releases are Seredo, Sekedo and Epuripur. Seredo and Sekedo are high yielding brown seeded varieties that are currently recommended for lowland areas below 1,530 masl. Epuripur is a high grain quality variety that was developed for industrial purposes. It is being used by Nile Breweries Ltd to produce bottled beer called *Eagle Lagger*. All the three varieties are tolerant to stem borers and shootfly but Epuripur is susceptible to bird damage at the soft dough stage due to its sweet taste.

Three hybrids were developed and released three decades ago (Table 1.4). These were Hijack, Himidi and Hibred. Having the same maturity length as Serena, Seredo and Sekedo, the hybrids yield 20 – 25% more than the open pollinated varieties, especially under conditions of low rainfall. They are however susceptible to the central shootfly due to CK-60A background (Doggett, 1970).

Table 1.3: Improved synthetic sorghum varieties released to farmers in Uganda

Sorghum variety	Year of release	Plant height (cm)	Days to maturity	Yield (kg/ha)	Grain colour
Serena	1966	150	95-100	3000-4000	Light brown
Lulu D	1972	120	110	2500-3000	White/corneous
Lulu T	1972	150	110	2500-3000	White/corneous
Dobbs	1973	150	100	2000-3000	Light brown
Seredo	1982	140	100	3500-5000	Light brown
Sekedo	1995	140	100	3000-5000	Light brown
Epuripur	1995	150	110	2500-3000	White/corneous

Source: NARO/SAARI Sorghum Growers Guide 1995

Table 1.4: Hybrid sorghum varieties released in Uganda

Hybrid name	Female parent	Male parent	Year of release	Plant height (cm)	Days to flower	Yield (kg/ha)
Hijack	CK60A	SB 65	1969	155	59	2900-6500
Himid	CK60A	Lulu D	1969	157	60	2400-5800
Hibred	CK60A	Simila	1972	155	62	3000-6000

Adapted from: Agriculture in Uganda, Vol. II, Crops. Sorghum.

1.4 The problem of *Striga* on sorghum in Uganda and farmer perceptions

Striga spp. or witchweed (Scrophulariaceae) is the second most important constraint limiting sorghum production in Uganda. *Striga* has been recognised as a constraint to cereal crop production since the early 1940s. The first systematic survey of *Striga* distribution in East Africa was reported in 1971 and it was indicated to be a particular problem causing serious cereal crop loss (Greathead and Milner, 1971). A national survey in 1993 (Baguma, 1996) confirmed the widespread occurrence of witchweeds in northern and eastern Uganda. During a study on the impact of weeds in selected cropping systems, Webb et al. (1993) reported that farmers in Soroti district (eastern Uganda) considered *Striga* to be an increasing problem in both finger millet and sorghum fields.

By 1995, *Striga* was found to infest 83% and 50% of sorghum fields surveyed in Pallisa and Tororo districts respectively causing yield losses estimated at 60-100% (Annon, 1995). In a recent needs assessment conducted by the National Agricultural Research Organisation (NARO), *Striga* was confirmed as the leading production constraint in both the Lango and Teso farming systems (Akwang et al., 1998, 1999).

The above review shows that farmers have recognised *Striga* as a constraint to sorghum production for over six decades. However, the problem has persisted and actually increasing. Either this shows that there are no control options being practiced or if they are practiced, they are not effective in combating the problem. It could also be due to progressive loss of fertility of the soil. Recently, during discussions with some Kenyan scientists (Woyengo, pers.com.), it was revealed that during the colonial administration in Kenya (1950s), a byelaw for farmers to uproot emerged *Striga* plants in their fields was instituted. However, the communities used to view it as a punishment from government. This indicated that farmers lacked the basic knowledge about

Striga. In the present time, there is need to sensitize farmers about the *Striga* problem and closely involve them in designing effective control strategies.

In Uganda, there are two species of economic importance; *Striga hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze. In the survey conducted in Pallisa and Tororo districts, the most devastating and widely distributed species was reported to be *S. hermonthica. S.asiatica* was observed to be common in low-lying areas and moist areas like valleys (Annon, 1995). Where it occurs, it is reported to have a more serious effect on yield than the more common *S. hermonthica*. *S. hermonthica* is an erect herb (50 – 70cm) with bright purple flowers while *S. asiatica* is a slender erect herb with bright red flowers reaching a height of 20 – 30cm. However, white and pink flowered *S. asiatica* have also been reported in Zimbabwe (Mutengwa, 2004).

1.5 Ecology and germination biology of *Striga*

Striga, commonly known as witchweed is a genus of 28 species of parasitic plants that occur naturally in parts of Africa, Asia and Australia (Koichi et al., 2010). Witchweeds are characterised by bright-green stems and leaves and small, brightly coloured flowers. The genus is classified in the family Orobanchaceae although earlier classifications place it in the Scrophulariaceae (Nelson et al., 1999).

1.5.1 The seed

Striga seeds are minute, with the average seed size being 200µ wide and 300µ long (Koichi et al., 2010; Berner et al., 1997). A single *Striga* plant can produce up to 10,000 – 500,000 seeds in one season (Koichi et al., 2010; Ariga et al., 1997; Berner et al., 1997). The seeds are dispersed by wind, water, cattle, man and farm machinery like tractors (Enserink, 1995). *Striga* seeds can stay viable in the soil for 15 – 20 years (Berner et al., 1997). Viability is longest in soils which are usually dry (Ariga et al., 1997; Enserink, 1995). Only a fraction of the seed germinates in any season in the presence of a host (Berner et al., 1995).

1.5.2 Germination

Striga seeds only germinate in response to stimulants exuded by the host roots. A number of these stimulants have been reported by several authors (Garcia-Garrido et al., 2009; Matusova et al., 2005; Ejeta et al., 1993; Hauk et al., 1992; Muller et al., 1992), but their nature and mechanism of operation is not well understood. The first natural stimulant to be identified was **Strigol**, exuded by roots of cotton, which is not a host of *Striga* but can stimulate its germination. Other germination stimulants have been identified as **Sorgolactone** and **Alectrol**, which are analogs of **Strigol** and are produced from root exudates of sorghum and cowpea respectively (Matusova et al., 2005; Hauk et al., 1992; Muller et al., 1992). Ethylene on the other hand, is a synthetic chemical that has been found to effectively induce germination of *Striga* seeds (Mourik et al., 2011; Obilana and Ramaiah, 1992). It has been used to induce suicidal germination of *Striga* seeds and reduce their numbers in the soil (Mohamed, 2002; Ransom and Njoroge, 1991).

1.5.3 Attachment and establishment on host roots

Following germination, the radical tip of the parasite seedling makes contact with the host root and enlarges giving rise to a structure known as the Haustorium. The haustorium has three functions, attachment, penetration and nutrient acquisition from the host (Patrick and Ejeta, 2007; Patrick et al., 2004; Mohamed, 2002; Stewart, 1990). The initiation of this haustorium is dependent on yet another signal from the host’s root, which has been identified as a simple degradation product of the host root lignin, known as 2,6- dimethoxybenzoquinone (Yoder et al., 2007; Lynn and Chang, 1990). This is one of the weakest points in the life cycle of *Striga* because if the haustorium does not form, parasitism fails and the weed dies.

1.6 How *Striga* damages its cereal host

The early symptoms of *Striga* damage on cereal hosts include stunted growth, bleaching/yellowing and wilting. These are often evident even before the emergence of the parasite. Under severe infestation, failure of panicle formation may occur resulting in total crop loss. More specifically, *Striga* reduces sorghum yields in two main ways:

(i) By direct parasitism in which *Striga* derives water, mineral nutrients and photosynthetic assimilates from sorghum root vascular system and thus retarding its growth and development (Press and Stewart, 1987). Although *Striga* is chlorophyllous, its rate of photosynthesis is reported to be low and as much as 60% of its carbon is host-derived (Graves et al., 1989). The nutrients flow from the host’s vascular system to the parasite via the feeding apparatus of the parasite, the haustorium, which penetrates the host roots. This flow of nutrients is facilitated by the high rate of transpiration in *Striga*, which exceeds that of its host like sorghum (Stewart et al., 1991). However, according to Patrick et al., 2004 and Berner et al., 1997, *Striga* inflicts most of the damage to its host while still underground. Therefore, while nutrient flow, as it is facilitated by transpiration, contributes to damage, it may not be taken as the main contributing factor.

(ii) By pathological effect in which *Striga* is known to produce toxins affecting sorghum growth and development (Stewart and Press, 1990). This effect can be seen from the imbalance in the amounts of growth regulators, which occur in infected sorghum. Drennan and El Hiweris (1979) reported decreases in the concentrations of cytokinins and gibberellins, coupled with increases in abscisic acid in the sap of sorghum plants infected with *Striga*. High concentrations of abscisic acid inhibit growth by reducing the rate of photosynthesis. Fischer et al. (1986) found that introduction of abscisic acid to the xylem stream of plants affects photosynthesis by suppressing ribulose biphosphate carboxylation. Therefore the increased concentrations of abscisic acid occurring during *Striga* infestation retards sorghum growth and development.

1.7 Breeding for resistance to *Striga* in sorghum

Breeding for resistance to *Striga* in sorghum is reported to have started in South Africa around 1920 (Mohamed, 2002). Saunders (1933) reported on one of the first comprehensive studies to select sorghum varieties for resistance to *Striga* in South Africa. His work led to the identification of several cultivars that were resistant to *Striga asiatica*, one of which was ‘Radar’, with reportedly complex resistance (Riches et al., 1987; Saunders, 1942).

In 1953, Doggett reported that sorghum varieties, Dobbs and P41 were resistant to *Striga* in East Africa (Doggett, 1953). Early research in Sudan confirmed that the sorghum varieties Dobbs, Framida, Serena and Najjad were resistant to *Striga* (Mohamed, 2002). In Kenya, breeding sorghum for *Striga* resistance started in 1965, when the variety, Dobbs, was found to be resistant in western Kenya (Kiriro, 1991). The same author explains that Dobbs was later crossed with a Swaziland variety, P127 to produce Serena. Further crossing of Serena with CK60A produced Seredo. Both Serena and Seredo have some resistance to *Striga* (Kiriro, 1991). Additionally, some sorghum landraces like MY134, MY183 and MY95-Z were found to be resistant to *Striga* infestation in Western Kenya (Ochanda and Njeru, 1984). However, the exact mechanisms of resistance in these genotypes have not been studied.

In West Africa, it is reported that since 1970, the Institute for Agricultural Research (IAR) in Samaru, Nigeria, has screened over 200 sorghum lines for resistance/tolerance to *Striga*

(Lagoke et al., 1991). The sorghum lines SPV103 and IS6961 were identified to exhibit high levels of resistance. Other resistant varieties reported by the same institute are L-187 (long-season variety), RZI and YG5760 (medium-season), and BES (short-season). Still in West Africa, another series of sorghum lines, ICSV1002, ICSV1005, ICSV1006 and ICSV1007 have been reported to show good levels of resistance (Carson, 1986; Lagoke, 1987; Ramaiah, 1986).

In 1991, ICRISAT reported seven sorghum varieties; Framida, IS6961, IS7777, IS7739, IS14928, IS14825 and IS9830 to be the most promising varieties resistant to *Striga hermonthica* in Africa (Obilana and Ramaiah, 1992; Ramaiah, 1991). In Zimbabwe, the SADC/ICRISAT regional sorghum and pear millet improvement programme screened a series of sorghum cultivars and identified SAR29, SAR33, SAR35, SAR37 and SAR16 as resistant to *Striga asiatica* (Mabasa, 1996). According to the same author, these SAR cultivars were reported to be resistant to either *S. asiatica* or *S. forbesii* in Botswana, Tanzania and Zimbabwe indicating that they probably have stable resistance. However, in a more recent study in the University of Zimbabwe (Mutengwa, 2004), SAR16 was found not to be resistant.

More recently, Haussmann et al. (2000b), quoting several authors, listed thirty-two sorghum cultivars that have been reported to be resistant to *Striga asiatica* and *Striga hermonthica* in various parts of the world. These are Dobbs, Radar, Framida (SRN 4841), Seguetana sorghums from Mali, 555, N13, IS9830, Najjad, ICSV1002BF (a cross between Framida and E35-1), ICSV1007BF, CS54, CS95, KSV4, SSV6, SRN39 and SRN6838. They also listed the SAR (*Striga asiatica* resistant) cultivars developed by ICRISAT such as SAR16, SAR19 and SAR33. Another series was IS1005, IS1006, IS7777, IS7739, IS6961, IS1260, IS8140, IS9934, IS14825, IS14829, IS14907, IS14928 and IS15401. Resistance to *Striga* has also been reported from some wild relatives of sorghum such as *Sorghum versicolor* (Lane et al., 1995) and *Sorghum drummondii* (Ejeta, 2000). Therefore, it can be seen that some considerable efforts have been put over the years to breed for *Striga* resistance in sorghum in Africa but tangible outcomes have not yet been achieved, such as release of varities with durable resistance. There is need to develop varieties that carry multiple mechanisms of resistance that could be durable.

1.8 Mechanisms of *Striga* resistance and their inheritance in sorghum

Little has been published about the actual host defence mechanisms in sorghum that discourage the growth and establishment of *Striga*. Such information could be very useful for designing effective breeding strategies for *Striga* resistance in sorghum. A number of possible defence reactions that could operate singly or in various combinations have been suggested (Gethi and Smith, 2004; Kroschel, 2001; Ejeta et al., 1991). These include:

- Low production of germination stimulants;
- Low production of haustoria inducing factors;
- Presence of mechanical barriers in host roots (e.g., lignification of cell walls or radicular cortex structure);
- Inhibition of germ tube exoenzymes by root exudates;
- Phytoalexin synthesis;
- Post-attachment hypersensitive reactions;
- Prevention of vascular connection between vessels of host and parasite;
- Disturbed internal flow of nutrients to the young parasite;
- Antibiosis;
- Unfavourable phytohormone supply by the host;
- Insensitivity to *Striga* “toxin” e.g. maintenance of photosynthetic efficiency; and
- Avoidance through root growth habit (e.g., fewer roots in the upper 15-20cm soil layer).

Using *in vitro* laboratory techniques, research at Purdue University has recently elucidated four specific mechanisms of resistance to *Striga* in a series of cultivated sorghums and some wild accessions (Ejeta, 2007; Rich et al., 2004; Mohamed et al., 2003; Mohamed, 2002; Ejeta, 2001; Ejeta et al., 2000). These are low production of germination stimulant (LGS), low production of the haustoria initiation factor (LHF), hypersensitive response (HR), and incompatible response (IR). Initial genetic studies at the same institution have also hinted on the inheritance of some of these resistance mechanisms in sorghum. For example the low germination stimulant production was said to be inherited as a single recessive gene.

Low germination stimulant genotypes of sorghum produce insufficient amounts of the exudates required for germination of conditioned *Striga* seed. Sorghum genotypes that produce very low levels of the germination stimulants have been found to be resistant to *Striga* in field tests (Hess et al., 1992; Ramaiah, 1987). All highly susceptible sorghum genotypes appear to be high producers of the germination stimulant (Ejeta, 2007). The sorghum cultivars SRN39, Framida, 555, IS9830, ICSV1006 and a wild accession *S. bicolor subspecies drummondii* have been reported to exhibit the LGS character as their mechanism of resistance to *Striga* (Ejeta et al., 2007). It was earlier reported that the LGS character is controlled by a single recessive gene in sorghum (Vogler et al., 1996). However, in agar-gel studies conducted with a recombinant inbred population derived from a cross of IS9830 (resistant) and E 36-1 (susceptible line), and F_2 populations from crosses of Framida, 555, and IS 9830 with E 36-1, Haussmann et al. (2000b) reported that one major gene and several minor genes were involved in the stimulation of *S. hermonthica* seed germination. In other studies on general combining ability (GCA) effects for germination distance in agar-gel assay, it was found that different sets of alleles were responsible for stimulation of *S. hermonthica* seed germination in each of the sorghum cultivars Framida, IS9830 and 555 (Haussmann et al., 2000a). Furthermore, through diallel studies and line x tester analysis, it was indicated that quantitative genetic variation with more of additive effects is present for stimulation of *S. hermonthica* seed germination in sorghum (Haussmann et al., 2000a). These findings suggest that there is still need for additional studies to fully understand the inheritance of the LGS character as a mechanism of *Striga* resistance in sorghum. Such studies need to focus on additional new genetic materials from different sources that may exhibit resistance to Striga. For example, some authors report single gene inheritance while others report quantitative gene inheritance for LGS production. Does the nature of inheritance vary between different genetic backgrounds? These types of observations necessitate more studies into the actual inheritance of the LGS production.

In resistance based on LHF, germinated *Striga* near the roots of sorghum possessing this trait normally do not form haustoria and therefore die because they are unable to attach to their potential host. As pointed out earlier, the haustorium is the penetrating and feeding apparatus of *Striga*. While the need for chemical signals exuded by host plants to elicit *Striga* germination has been known for many years, evidence for the requirement of an additional host signal to encourage production of the haustorium to facilitate attachment to host roots only emerged recently (Ejeta, 2007). This trait has not been clearly identified among cultivated sorghums but was found in the wild accessions *S. bicolor subspecies drummondii* (Patrick et al., 2004) and P78 (Mohamed et al., 2003; Mohamed, 2002). Mohamed, (2002) employed an extended agar-gel assay to study the inheritance of LHF. He concluded that a single dominant gene conditioned the LHF character. In crosses involving a mutant sorghum genotype P78, known to posses the LHF, and the sorghum cultivars PP34 and Shanqui Red, both with high haustoria initiation capacity, the F_1 exhibited the LHF character. The F_2 segregated 3:1 for low to high haustoria initiation character. These observations led the author to suggest that a single nuclear gene with dominant gene action controlled the haustoria initiation trait, and proposed the gene symbol L*hf* for low haustoria initiation factor. It can be noted that most of the studies on the LHF have been based on wild sorghum accessions. Little or no studies have been done on cultivated sorghum genotypes. There is need to explore this trait and understand its genetic behaviour in cultivated sorghum genotypes that may exhibit resistance to *Striga*. Furthermore, the above case studies were based on resistance to *Striga asiatica*. Probably no information is available regarding the LHF in relation to *Striga hermonthica*.

Resistance based on the HR involves localised necrosis of host tissues surrounding the site of attempted parasite attachment, presumably coupled with a release of phytoalexins that kill the attached *Striga*. Hypersensitive response has been extensively studied in a wide range of host-parasite associations, where it is generally characterized by the appearance of a necrotic zone around the site of attempted infection. In its case, host cell death results in unsuccessful establishment of the parasite and leads to its ultimate demise. Hypersensitive response has been observed in sorghum cultivars Dobbs, Framida, Serena and wild accessions *S. bicolor subspecies drummondii*, *S.hewisonni* and *S.b.verticilliflorum* (Patrick et al., 2004). In studying the inheritance of HR, Mohamed, (2002) crossed two sorghum lines, CK32 and KP33 that possessed a strong HR response with two sorghum cultivars, TX430 and TX2737, which possessed no HR response. All the F_1 progeny showed HR when subjected to *Striga* attack. The F2 from all crosses segregated 15:1 (HR: no HR), while the BC1 populations segregated 3:1 (HR: no HR). It was suggested, based on the segregation ratios that two nuclear genes with dominant gene action conditioned hypersensitive response to Striga infection in the sorghum genotypes. Anthony et al. (2000) explain that 15:1 ratio results from an epistatic gene interaction called duplicate gene action. In this case, genes located at two different loci control a particular trait, and the presence of a dominant allele from either of the two loci is required to produce the effect. The gene symbols Hrs_1 and Hrs_2 were proposed for hypersensitive response to *Striga* infection in sorghum. These findings provide a basis for further studies on different sorghum genotypes and different *Striga* populations in order to fully understand the genetics of *Striga* resistance in sorghum. Such knowledge will enhance effective breeding for resistance to this notorious parasite in cereal crops.

On the other hand, the principle underlying IR is similar to HR in that parasite development beyond attachment is discouraged. In host genotypes whose *Striga* resistance is based on IR, *Striga* seedlings that succeed in penetrating host tissue may not develop beyond emergence of the first leaves (Mohamed, 2002). Some *Striga* will be observed to develop normally at first but later show signs of stunted growth (Ejeta 2007). The reaction is similar to that observed when

Striga unsuccessfully infests non-host plants. Patrick et al. (2004) mention the sorghum cultivars SRN39, ICSV761 and the wild accession *S.b.verticilliflorum* to possess this trait. However, its inheritance is so far not clear.

1.9 Effort so far made to pyramid *Striga* resistance genes in sorghum

A series of authors have over the years pointed out the need to pyramid *Striga* resistance genes in order to achieve effective resistance against the parasite (Rodenburg et al., 2005; Patrick et al., 2004; Grenier et al., 2001; Haussmann et al., 2000b; Ejeta et al., 1997). Using marker-mediated pyramiding, Grenier et al. (2001) reported some progress in pyramiding *Striga* resistance genes in a sorghum cultivar developed from a cross between SRN39 and Framida. Progenies that exhibited low germination stimulant production, hypersensitive response and incompatible reaction were recovered. The same authors also report gene pyramiding on a sorghum population derived from a cross between an Ethiopian adapted sorghum variety, SEPON82 and two *Striga* resistant parents, SRN39 and PQ434. Evaluation is reported to be in progress (Grenier et al., 2001). The critical idea in pyramiding the genes would be to bring together the genes conferring pre-attachment resistance mechanisms and those conferring the post-attachment resistance mechanisms (Patrick et al., 2004). This will equip the host with multiple lines of defence against the parasite. Since most of the individual *Striga* resistance mechanisms that have been reported so far appear to be simply inherited, this could indicate that effective pyramiding of genes for *Striga* resistance with multiple mechanisms could be achieved through conventional breeding and introgression. Kim (1991) explains that an indirect approach to inserting genes for different mechanisms of resistance into a common background may be to produce a population, involving diverse sources and improved resistant lines, using standard random mating procedures. Later, recurrent selection procedures may be employed to recombine and reconstitute through progressive cycles and extract stable *Striga* resistant derivatives. However more studies on the genetics of *Striga* resistance are required in order to design an effective strategy to pyramid genes for *Striga* resistance.

In summary, from the present literature review, it can be concluded that:

(i) Sorghum is one of the most widely grown staple cereal food crop in Uganda.

(ii) *Striga* is one of the most important constraints limiting sorghum production in Eastern and Northern Uganda.

(iii) The *Striga* problem in Uganda was initially reported in 1971 but it has apparently persisted and is observably increasing.

(iv) While farmers seem to have long recognised *Striga* as a constraint to cereal crop production, they seem to have lacked the basic knowledge of the weed particularly its spread and ways to control it.

(v) There has been limited progress in breeding for *Striga* resistant sorghum varieties in Africa, and probably none in Uganda.

(vi) Information about specific mechanisms of resistance to *Striga* in cultivated sorghum is still scanty, particularly their occurrence and type of genetic control.

(vii) Gene pyramiding for *Striga* resistance could be a useful approach to get genotypes that carry multiple mechanisms of resistance.

References

Akwang, A. A., J.P. Obuo, J. Okwadi and J. Oryokot. 1999. Needs assessment for agricultural research in the Teso farming system: Summary report. NARO/DFID. Kampala, Uganda.

Akwang, A. A., S. Okalebo and J. Oryokot. 1998. Needs assessment for agricultural research in the Teso farming system, *'Aijul Eode'*: Main report. NARO/DFID. Kampala , Uganda.

Anonymous. 1995. *Striga* survey in Eastern Uganda. Serere Agricultural and Animal Production Research Institute/National Agricultural Research Organisation.

Anthony, J.F.G., J.H. Miller, D.T. Suzuki, R.C. Lewontin, and W.M. Gelbart (eds.). 2000. An introduction to genetic analysis, 7th edition. W.H. Freeman, New York.

Ariga,E.S., J.K. Ransom, G.D. Odhiambo, G. Abayo and D.K. Ndungu. 1997. Potential of using cotton and other trap crops for *Striga hermonthica* management in cereals in Kenya. *In:* Adipala,E., G. Tusiime and P. Okori (eds.),*Proceedings of the 16th Biennial Weed Science Society Conference for Eastern Africa*. Kampala: WSSEA. Pp 247-254.

Baguma, S.D. 1996. *Striga* research activities in Uganda, 1994 – 1995. *Striga* Newsletter ,6, 5-6.

Berner, D.K., J.G. Kling, and B.B. Singh. 1995. *Striga* research and control: a perspective from Africa. Plant disease. 79, 652-660.

Berner, D.K., M.D. Winslow, E.A. Award, K.F. Cardwell, D.R. Mohan Raj, and S.K. Kim. 1997. *Striga* research methods: A manual. 2nd Ed. International Institute of Tropical Agriculture. Ibadan, Nigeria.

Carson, A.G. 1986. Research and development strategies for the control of *Striga hermonthica* in the Gambia. *In:* Proceedings of the FAO/OAU All-African Government Consultation on *Striga* Control, 20-24 October 1986, Maroua, Cameroon.

Doggett, H. 1953. Sorghum improvement in Tanganyika. East African Agricultural Journal 18:155-159

Doggett, H. 1965. *Striga hermonthica* on sorghum in East Africa. Journal of Agricultural Science, Cambridge 65: 183-194.

Doggett, H. 1970. Sorghum. Longmans, Harlow, England, 403 pp.

Drennan,D.S.H. and S.O. El Hiweris. 1979. Changes in growth regulatory substances in *Sorghum vulgae* infected with *Striga hermonthica*. *In:* Musselman,L.J., A.D.Worsham and R.E. Eplee (eds.), Second International Symposium on Parasitic Weeds. North Carolina State University, Raleigh, USA. Pp 144-155.

Ebiyau,J. and J.O.E. Oryokot. 2001. Sorghum (*Sorghum bicolor* (L.) Moench). In: Mukiibi, J.K.(ed.). Agriculture in Uganda, Vol.II. National Agricultural Research Organization 2001, Fountain Publishers Ltd, Kampala, Uganda.

Ejeta, G. 2007. Breeding for *Striga* resistance in sorghum: Exploitation of an intricate host-parasite biology. Crop Science 47:216-227.

Ejeta, G. 2001. *Striga* biotechnology development and technology transfer. 2001 Annual Report. INTSORMIL.

Ejeta, G. 2000. Molecular mapping of *Striga* resistance genes in sorghum. *In:* Haussman, B.I.G., D.E. Hess, M.L. Koyama, L. Grivet, H.F.W. Rattunde, and H.H. Geiger (Eds.), Breeding for *Striga* resistance in cereals. *Proceedings of a Workshop held at IITA, Ibadan, Nigeria, August 1999*. Margraf Verlag, Weikersheim, Germany.

Ejeta, G., L.G. Butler and A.G.T. Babiker. 1993. New approaches to the control of *Striga*, *Striga* research at Purdue University. Agricultural experiment station, Purdue University, USA, pp 27.

Ejeta, G., L.G. Butler, D.E. Hess, and R.K. Vogler. 1991. Genetic and breeding strategies for *Striga* resistance in sorghum, pp. 539-544, *In* J. K. Ransom, et al., (eds.) Proceedings of the Fifth International Symposium on Parasitic Weeds, Nairobi, Kenya.

Ejeta, G., L.G. Butler, D.E. Hess, T. Obilana, and B.V. Reddy. 2000. Breeding for *Striga* resistance in Sorghum, *In* B. I. G. Haussman, et al., (eds.) Breeding for Striga resistance in cereals. Proceedings of a Workshop held at IITA, Ibadan, Nigeria. Margraf Verlag, Weikersheim, Germany.

Enserink, H.J. 1995. Sorghum Agronomy in West Kenya: Investigations from a farming systems perspective. Royal Tropical Institute, Amsterdam.

FAOSTAT. 2007. Food and Agriculture Organization of the United Nations, Statistics Division. http://faostat.fao.org/.

Fischer, E., K. Raschke and M. Stitt. 1986. Effects of Abscisic acid on photosynthesis in whole leaves: Changes in carbondioxide assimilation, levels of carbon-reduction-intermediates and activity of ribulose-1,5-bisphosphate carboxylase. Planta 169, 536-545.

Garcia-Garrido, J.M., V. Lendzemo, V. Castellanos-Morales, S. Steinkellner, and H. Vierheilig. 2009. Strigolactones, signals for parasitic plants and arbuscular mycorrhizal fungi. Mycorrhiza 19(7): 449-459.

Gethi, J.G., and M.E. Smith. 2004. Genetic responses of single crosses of maize to *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze. Crop Science 44: 2068-2077.

Graves, J.D., M.C. Press and G.R. Stewart. 1989. A carbon balance model of the sorghum-*Striga hermonthica* host-parasite association. Plant cell and Environment 12: 101-109.

Greathead, D.J. and J.E.D. Milner. 1971. A survey of *Striga* species (Scrophulariaceae) and their insect natural enemies in East Africa with a discussion of the possibilities of biological control. Tropical Agriculture, 48: 111-124.

Grenier, C., P.J. Rich, A. Mohamed, A. Ellicott, C. Shaner, and G. Ejeta. 2001. Independent inheritance of LGS and IR genes in sorghum. *In*: Fer et al., (ed.) Proceedings of the 7th International Parasitic Wee Symposium, Nantes, France.

Hauk, C., S. Muller and H. Shildknecht. 1992. A germination stimulant for parasitic flowering plants from Sorghum bicolor, a genuine host plant. Journal of plant physiology 139: 474-478.

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, H.G. Welz, and H.H. Geiger. 2000b. Improved methodologies for breeding *Striga* resistant sorghums. Field Crops Research 66(3):195-211.

Hess, D.E., G. Ejeta, and L.G. Butler. 1992. Selecting genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga.* Phytochemistry 31:493-497.

House, L.R. 1996. Inaugural address. *In* Proceedings of the international conference on genetic improvement of sorghum and pearl millet. INTSORMIL, ICRISAT, Holiday Inn Plaza, Lubbock, Texas.

Kiriro, F.H. 1991. The *Striga* problem in Kenya. In: Kim, S.K. (ed.), Proceedings of the International Workshop on Combating *Striga* in Africa, 22-24 August 1988. IITA, Ibadan, Nigeria.

Koichi, Y., A.A. Awad, X. Xiaonan, Y. Kaori, and Y. Takeuchi. 2010. Strigolactones as germination stimulants for root parasitic plants. Plant Cell Physiology 51(7): 1095-1103.

Kroschel, J., (ed.) 2001. A technical manual for parasitic weed research and extension. Kluwer Academic Publishers, 3300 AA Dordrecht, Netherlands.

Lagoke, S.T.O. 1987. Evaluation of sorghum varieties for resistance to *Striga*. Cereals Research Program: Cropping Scheme Report 1987. Institute for Agricultural Research, ABU, Zaria, Nigeria.

Lagoke, S.T.O., V. Parkinson and R.M. Agunbiade. 1991. Parasitic weeds and control methods in Africa. In: Kim, S.K. (ed.), Proceedings of the International Workshop on Combating *Striga* in Africa, 22-24 August 1988. IITA, Ibadan, Nigeria.

Lane, J.A., D.V. Child, T.H.M. Moore and J.A. Bailey. 1995. Wild relatives of cereals as new sources of resistance to *Striga*. In: Parasitic plants: Biology and Resistance. International Workshop, IACR-Long Ashton Research Station, Bristol, UK, 30 May-2 June 1995, p 13.

Lynn, D.G. and M. Chang. 1990. Phenolic signals in cohabitation: Implications for plant development. Annual review of plant physiology 41: 497-526.

Nelson, D.Y., E.S. Kim, and C.W. dePamphilis. 1999. The evolution of parasitism in Scrophulariaceae/Orobanchaceae: Plastid gene sequences refute an evolutionar transition series. Annals of the Missouri Botanical Garden 88 (4): 876-893.

Mabasa,S. 1996. Screening sorghum genotypes for resistance to witchweed (*Striga asiatica*) in Zimbabwe. *In*: Leuschner,K.and Manthe,C.S.(eds.) Drought tolerant crops for Southern Africa: Proceedings of the SADC/ICRISAT Regional sorghum and pearl millet workshop,25-29 July 1994,Gaborone,Botswana.

Matusova, R., K. Rani, F.W.A. Verstappen, C.R. F. Maurice, M.H. Beale, and H.J. Bouwmeester. 2005. The Strigolactone germination stimulants of the plant-parasitic *Striga* and Orobanche spp. are derived from the carotenoid pathway. Plant Physiology 139(2): 920-934.

Mohamed, A. H. 2002. Identification and characterization of genetic variants in sorghum for specific mechanisms of *Striga* resistance. PhD thesis. Purdue University, USA.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43: 1320-1324.

Mourik, T.A.V., T.J. Stomph, and A.J. Murdoch. 2011. Purple witchweed (Striga hermonthica) germination and seed bank depletion under different crops, fallow, and bare soil. Weed Biology and Management 11: 100-110.

Muller,S., C. Hauck and H. Schildknecht. 1992. Germination stimulants produced by *Vigna unguiculata* (Walp.) cv Saunders,upright. Journal of plant growth regulation 11: 77-84.

Mutengwa, C.S. 2004. The search for molecular markers, parental characterisation and iheritence studies of witchweed (*Striga asiatica*(L.) Kuntze) resistance in sorghum (*Sorghum bicolor* (L.) Moench). PhD Thesis, University of Zimbabwe.

Obilana,A.T. and K.V. Ramaiah. 1992. *Striga* (witchweeds) in sorghum and millet: Knowledge and future research needs*. In*: deMilliano,W.A.J., R.A., Frederikson and G.D.,Bengston (eds.) Sorghum and millet diseases, a second world review, ICRISAT. Pp 187-207.

Ochanda, N.W. and E.S. Njeru. 1984. *Striga* research in Alupe Agricultural Research Station. Kenya Agricultural Research Institute, Kenya.

Patrick J.R., and G. Ejeta. 2007. Biology of host-parasite interactions in *Striga* species. *In*: Ejeta and Gressel (eds.) Integrating New Technologies for *Striga* Control. World Scientific Publishing Co. Pte. Ltd.

Patrick, J.R., C. Grenier, and G. Ejeta. 2004. *Striga* resistance in the wild relatives of sorghum. Crop Science 44: 2221-2229.

Press, M.C., and G.R. Stewart. 1987. Growth and photosynthesis in sorghum bicolor infected with *Striga asiatica*. Annals of Botany 60: 657-662.

Ransom, J.K. and K. Njoroge, 1991. Seasonal variation in ethylene induced germination of Striga hermonthica in Western Kenya. In: Adipala, E., G. Tusiime and P. Okori (eds.) Proceedings of the 16th Biennial Weed Science Society Conference of Eastern Africa, Kampala: WSSEA. Pp 391-396.

Ramaiah, K.V. 1991. Breeding for *Striga* resistance in sorghum and millet. *In:* Kim, S.K. (ed.) Proceedings of the International Workshop on Combating *Striga* in Africa, 22-24 August 1988. IITA, Ibadan, Nigeria.

Ramaiah, K.V. 1987. Breeding cereal grains for resistance to witchweed. In: Musselman, L.J. (ed.) Parasitic weeds in Agriculture. Vol. 1. Striga. CRC Press, Boca Raton. Pp 227-242.

Ramaiah, V. 1986. Status of ICRISAT's *Striga* resistance breeding in sorghum and millet in Africa. In: Proceedings of the FAO/OAU All-African Government Consultation on Striga Control, 20-24 October 1986, Maroua, Cameroon.

Riches, C.R., W.A.J. de Milliano, A.T. Obilana and L.R. House. 1987. Witchweeds (*Striga* spp.) of sorghum and pearl millet in the SADCC region: Distribution and control. *In* proceedings of the third regional SADCC/ICRISAT sorghum and millet improvement, project workshop, Lusaka, Zambia, 20-25 September 1986.

Rodenburg, J., L. Bastiaans, E. Weltzien, and D.E. Hess. 2005. How can field selection for *Striga* resistance and tolerance in sorghum be improved? Field Crops Research 93:34-50.

Saunders, A.R. 1933. Studies on phanerogamic parasitism with particular reference to *Striga lutea*. Department of Agricultural Science, South Africa. Bulletin No. 128. Pretoria, South Africa. Pp56.

Saunders, A.R. 1942. Field experiments at Potchestroom. A summary of investigations conducted during the period 1903-1940. South African Department of Agriculture and Forestry Science Bulletin 214: 19-31, 49-50.

Siame, B., K. Wood, G. Ejeta and L.G. Butler .1993. Isolation of Strigol, a germination stimulant for *Striga asiatica*, from natural host plants. J. Agric. Food Chem., in review.

Stewart, G. 1990. Witchweed: a parasitic weed of grain crops. Outlook on Agriculture 19: 115-117.

Stewart, G.R. and M.C. Press. 1990. The physiology and biochemistry of parasitic angiosperms. Plant molecular biology 41: 127-151.

Stewart, G.R., M.C. Press, J.D. Graves, J.J. Nour and A. Wylde. 1991. Physiological characterization of the Host-Parasite Association between *sorghum bicolor* and *Striga hermonthica* and its implications for *Striga* control. *In:* Kim,S.K.(ed.), Combating *Striga* in Africa, Proceedings, International Workshop organised by IITA, ICRISAT and IDRC, 22-24 August 1988. IITA, Ibadan, Nigeria. Pp 48-54.

Vogler, R.K.., G. Ejeta and L.G. Butler. 1996. Inheritence of low production of Striga germination stimulant in sorghum. Crop Science 36, pp. 1185-1191.

Webb, M., C. Conroy, D. Baguma, and R. Kabanyoro. 1993. Survey of the socio-economics of weed control on smallholder farms in three districts of Uganda. Report R 2014 (S), Natural Resources Institute, Chatham, UK, 26 pp.

Yoder, J.I., R. Russell, A. Tomilove, N. Tomilova, and M. Torres. 2007. Host detection by root parasites: Insights from transcription profiles. *In*: Ejeta and Gressel (eds.) Integrating New Technologies for *Striga* Control. World Scientific Publishing Co. Pte. Ltd.

CHAPTER TWO: PARTICIPATORY RURAL APPRAISAL ON SORGHUM PRODUCTION CONSTRAINTS AND VARIETAL PREFERENCES IN EASTERN UGANDA

Abstract

Sorghum productivity in Uganda is constrained by several factors, of which *Striga hermonthica* infestation is one of the most important. A participatory rural appraisal was carried out in four districts of Eastern Uganda in December 2008 to January 2009. The main objectives were to study the current constraints faced by farmers in sorghum production and determine their preferences for new sorghum varieties. Group discussions guided by a checklist were used to document the constraints to sorghum production and farmers' preferences for new sorghum varieties. A semi-structured questionnaire coupled with field inspections were also used for data collection. S*triga* was identified as the main constraint limiting sorghum production in Eastern Uganda, followed by insect pests. Farmers indicated preference for red grain sorghum with erect and compact heads, a plant height of 1.5 m and a maturity period of around three months, as well as *Striga* resistance and drought tolerance. From farmers' own assessments, the individual field surveys and soil seed bank analyses that were carried out, the degree of *Striga* infestation in farmers' fields was found to be high. This study further found that while farmers were adequately aware of the *Striga* problem in their fields, they had considerably limited knowledge of the factors that lead to *Striga* increase and the possible ways of controlling it. Therefore, there is urgent need to sensitise farmers about the biology and control of *Striga*, and develop new *Striga* resistant sorghum varieties that are endowed with other farmer preferred attributes in order to improve sorghum production in Eastern Uganda.

2.1 Introduction

The production of sorghum, one of the most important staple food crops in Uganda, is characterized by low on-farm yields ranging from 800 to 1500kg ha^{-1}(Ebiyau and Oryokot, 2001). The national average annual yield for the period 2000 to 2005 was 1444kg ha^{-1} (FAO, 2007). This yield is far below the potential yield of 5000kg ha^{-1} in improved varieties when grown under high level of management in the absence of pests and diseases. One of the factors contributing to this low yield is continued use of unimproved varieties that are low yielding and susceptible to pests and diseases.

Over 90% of sorghum farmers in Uganda still grow their indigenous varieties irrespective of the poor yield (Akwang et al., 1998). Since the beginning of sorghum improvement in Uganda, in 1958 (Ebiyau and Oryokot, 2001), more than ten improved and high yielding varieties have been produced but these have had limited acceptance and or adoption by the small-scale farmers, who are the main sorghum growers in the country. There could be some reasons why farmers stick to unimproved varieties and breeders may not have been keen to understand them. Hence breeders have developed new varieties with limited or no consideration of the special preferences of farmers particularly those in marginal areas (Bazinger and Cooper, 2001). Effective plant breeding probably needs to be based on clear understanding of farmers' preferences for new cultivars and their perceived production constraints. Sperling et al. (2001) cited by Derera et al. (2006) indicated that farmers can provide vital information on plant types, desired traits and insight into trade-offs they are willing to make among traits in designing cultivar types. Therefore, through close researcher-farmer interaction and collaboration farmers can be engaged to provide such information that could be incorporated by the plant breeder in developing acceptable new crop cultivars.

The second factor responsible for low sorghum yields in Uganda is infestation by pests and diseases, of which *Striga* is among the most important ones (Akwang et al., 1998, 1999). This weed highly infests most of the sorghum growing areas in the country. A survey carried out in eastern Uganda, 14 years ago; found *Striga* to infest 83% and 50% of fields in Pallisa and Tororo districts respectively, causing sorghum grain yield losses estimated at 60 – 100% (Ebiyau and Ouma, 1995). *Striga* has been recognized as a major constraint to the production of sorghum since the 1940s (Enserink, 1995). In 1965, Doggett reported that grain yield loss of susceptible sorghum varieties in East Africa was 59% (Enserink, 1995). This figure has steadily increased and to date total crop failure due to *Striga* infestation is frequent (Ebiyau and Oryokot, 2001). Furthermore, the spread of the weed seems to be favoured by the current cropping practices such as continous cereal cropping and allowing animals to graze in infested fiels after the sorghum crop has been harvested.

The use of *Striga* resistant sorghum cultivars could be a key to an effective *Striga* control programme as it would be compatible with the low cost input requirements of subsistence farmers. Resistant cultivars effectively reduce *Striga* emergence and enhance the efficiency of other control measures (Haussmann et al., 2000a). However, the effectiveness of this strategy is enhanced when resistance is available in adapted, productive and farmer preferred varieties (Haussmann et al., 2000b).

It is widely recognised that most of the *Striga* resistant sorghum lines so far developed have poor agronomic characteristics particularly low grain yield. For example, Framida, a West African sorghum line known to be resistant to *S. hermonthica*, was found to yield lower than some of the local farmers' varieties in Uganda, and to possess undesirable grain characteristics such as high tannin content. In Tanzania, varieties like Wahi, Hakika and SRN 39, were found to yield between 1800-2300 kg ha^{-1} in a *Striga* free site (Ilonga) in trials conducted between 2001 and 2002 (Mbwaga et al., 2007). Such yield is actually lower than the potential yield of the current improved varieties in Uganda (3000-4500kg ha^{-1}) (Ebiyau and Oryokot, 2001). It is necessary to develop varieties that combine *Striga* resistance with high grain yield, which could be acceptable to farmers in Uganda.

Furthermore, information about farmer perceptions and preferences for new improved sorghum varieties is necessary so that *Striga* resistant or tolerant varieties that may be developed should be endowed with farmer preferred characteristics. This could enhance the acceptance and adoption of such varieties by the farmers. In order to achieve this, the initial step is to carry out a participatory rural appraisal among local communities that are engaged in sorghum production and discuss with the farmers. Therefore, the objectives of this study were; (i) to study the current constraints faced by farmers in sorghum production, (ii) determine farmers' preferences for new sorghum varieties, (iii) assess the current cropping practices, and (iv) determine farmer perceptions on infestation levels and impact of *Striga* on sorghum production in eastern Uganda.

2.2 Materials and Methods

The study was divided into two components: a study of farmers' constraints to sorghum production and determination of their preferences for new sorghum varieties; and an assessment of the cropping practices, infestation levels and impact of *Striga* on sorghum production in Uganda.

2.2.1 Farmers' constraints to sorghum production and determination of their preferences for new sorghum varieties.

Group discussions were held with five farmer groups in the districts of Kaberamaido, Kumi, Bukedea and Pallisa in Eastern Uganda. Two group discussions were held in Kaberamaido district and one in each of Kumi, Bukedea and Pallisa districts. In these districts sorghum is one of the most important staple food crops and the survey focused on farmers who grew sorghum at least every year. The objective of the group discussions was to determine farmers' main constraints to sorghum production and identify their preferences for new sorghum varieties. Using a checklist, farmers were asked to list the current constraints they faced in sorghum production. The constraints were subsequently ranked using pair-wise ranking. Following that, farmers were requested to outline the qualities they would wish new sorghum varieties to possess. In this case, the farmers were guided through a series of attributes ranging from agronomic field performance, post harvest processing, marketing to consumption. The characteristics were also ranked according to their relative importance using pair-wise ranking. The goup discussions covered 172 famers of which 97 were males and 75 were females.

2.2.2 Assessment of the cropping practices, infestation levels and impact of *Striga* on sorghum production in Eastern Uganda.

A survey was carried out in Kaberamaido, Kumi and Bukedea districts of Eastern Uganda in December 2008. The objective was to derive information about the cropping practices, infestation levels, history of existence and the extent of damage by *Striga* on sorghum. In this survey, it was deemed necessary to assess the cropping practices because they could have influence on *Striga* infestation. In each district, two sub-counties were selected and in each sub-county two villages were identified with the help of key informants. In each village 7-9 farmers who grew sorghum were randomly selected. This resulted in a total of 95 farmers successfully interviewed in the three districts. A semi-structured questionnaire was administered to each selected farmer in his/her own homestead. At the same time field visits were made to each farmer's sorghum field where the history of *Striga* presence and extent of crop damage were discussed utilising the farmer's own experience. Additionally, the on-spot above ground *Striga* infestation and crop density in each field were assessed. This was done by randomly placing a quadrant measuring 1m^{-2} five times in each field, and the numbers of emerged *Striga* plants as well as sorghum plants within the quadrant were counted. Furthermore, soil samples were taken from each field visited in order to determine the soil *Striga* seed bank. This was done by taking five soil cores in each field along an 'M' and composting these into one sample per field (Olupot, 2002). The soil samples were analysed for *Striga* seed concentration in the laboratory at Serere research station using the sucrose extraction method as described by Berner et al. (1997).

2.2.3 Data analysis

The data on farmers' constraints to sorghum production, their preferences for new sorghum varieties, cropping practices and impact of *Striga* on sorghum production were analysed using SPSS (Statistical package for social science) version 19 (SPSS, 2010). The data on *Striga* infestation levels (emerged *Striga* and soil seed bank), as well as sorghum crop intensity were analysed using Genstat release 14.1 statistical package (Payne et al., 2011).

2.3 Results

2.3.1 Attendance in the group discussions

A total of 172 farmers participated in the group discussions (Table 2.1). The number of farmers per group discussion ranged from 22-41 and both males and females were present in each group discussion. In Kaberamaido district, there were slightly more females (67%) than males while in the other three districts, there were more males than females with an average male: female ration of 3:1. In total, more males attended than females in the four districts.

Table 2.1: PRA attendance

District	No. of farmers	Males	Females
Kaberamaido	76	25	51
Pallisa	33	27	6
Bukedea	22	15	7
Kumi	41	30	11
Total	**172**	**97**	**75**

2.3.2 Constraints to sorghum production in Eastern Uganda

A total of 14 different constraints affecting sorghum production were listed by farmers in Eastern Uganda (Tables 2.2 and 2.3). The constraints were both biotic and abiotic with the biotic constraints being the most important. In three out of four districts, *Striga* was ranked as the number one constraint to sorghum production. Second in importance in most districts were insect pests such as shootfly, stem borers and sorghum midge. Specific to Pallisa district was that lack of seed of improved varieties was ranked as the main constraint to sorghum production, followed by shortage of land. In general, *Striga* ranks as the most important constraint to sorghum production in the four districts. The main abiotic constraints identified were drought and poor soil fertility.

Table 2.2: Constraints to sorghum production in Kaberamaido and Kumi districts

Kaberamaido		**Kumi**	
Constraint	**Rank**	**Constraint**	**Rank**
Striga	1	*Striga*	1
Shoot fly	2	Stem borer	2
Drought	3	Poor soil fertility	3
Smuts	4	Termites	4
Poor soil fertility	5	Smuts	5
Midge	6	Drought	6
Termites	7		
Other weeds	8		

Table 2.3: Constraints to sorghum production in Bukedea and Pallisa districts

Bukedea		Pallisa	
Constraint	**Rank**	**Constraint**	**Rank**
Striga	1	Lack of seed of improved varieties	1
Smuts	2	Shortage of land	2
Stem borers	3	*Striga*	3
Tall varieties, difficult to harvest	4	Smuts	4
Ergort	5	Midge	5
		Stem borers	6
		Storage pests	6

2.3.3 Farmers' preferences for new sorghum varieties

Tables 2.4, 2.5 and 2.6 show a list of farmers' preferences for new sorghum varieties in Eastern Uganda. The main attributes that came out across the districts were grain colour, head shape, plant height, maturity time, *Striga* resistance and drought tolerance. Red grain colour, erect and compact heads, short plants of 1.5m, a maturity period of three months, *Striga* resistance and drought tolerance were the main attributes preferred in all the districts (Table 2.4). The relative ranking of these attributes however, varied from district to district. In Kaberamaido district, resistance to *Striga* was the first ranked attribute, while in Kumi it was red grain coloured sorghum (Table 2.5). In Bukedea district, sorghum with compact and erect long heads was preferred most while in Pallisa district it was drought tolerant sorghum (Table 2.6). Early maturity of around three months featured as the second most important attribute preferred in three out of the four districts. The least important attributes also varied from district to district.

Table 2.4: The main sorghum attributes preferred by farmers across the 4 districts

Sorghum attribute	Farmers' preference
Grain colour	Red
Head shape	Erect and compact
Plant height	Short (1.5m)
Maturity time	Early (3 months)
Striga and drought	Resistant/tolerant

Table 2.5: Farmers' preferences for new sorghum varieties in Kaberamaido and Kumi districts

Kaberamaido			**Kumi**		
Attribute	**Reason(s)**	**Rank**	**Attribute**	**Reason(s)**	**Rank**
Resistance to *Striga*	Very poor harvest is got from infested fields	1	Red grains	- Mixes well with cassava to make good flour - Resistant to birds	1
Early maturity (2-2.5 months)	Rain season is short	2	Early maturity (3 months)	- Rain season is short - Saves early from hunger	2
Short plant	Easy to harvest	3	Compact head	- Gives high grain output after threshing	3
Drought tolerant	Drought is common	4	Big grains	- Yields high	3
Red grains	- Sells better in market - Mixes well with cassava to make good flour for bread	5	Heavy grain weight	- Fetches more money	3
Big seeds	Yields are high	6	Tolerance to pests and diseases	-	3
Compact head	Yields are high	7	Medium height (1.5m)	- Easy to harvest	4

Table 2.6: Farmers’ preferences for new sorghum varieties in Bukedea and Pallisa districts

Bukedea			Pallisa		
Attribute	**Reason(s)**	**Rank**	**Attribute**	**Reason(s)**	**Rank**
Compact erect and long head, large grains	-Yields high - Easy to thresh	1	Tolerant to drought	- Drought is common	1
Red grains	- Good for bread/*Kalo* - Resistant to birds - Easy to market	2	Early maturity	- Short rain season	2
Short plant	- Resistant to lodging - Easy to harvest	3	Big compact heads	- Yields high	3
Resistant to smuts	-	4	Short plants	- Easy to harvest	4
Resistant to *Striga*	-	5	Resistant to *Striga*	-	5
Ease of storage	-	6	Red grains	- Good for bread - Marketable	6
Ease of grinding	-	7			

2.3.4 Cropping practices: Soil types, sources of sorghum seed and time of planting sorghum

There was little variation in soil type among the one hundred and five farmers’ fields surveyed in the three districts (Table 2.7a). Sandy-loam soil appeared to be more common followed by loam soil and lastly sandy soil. Regarding the sources of sorghum seed for planting, it was found that more than half of the farmers planted their own home saved seed. A fair proportion of the farmers bought seed from the local markets, and others got seed from friends/relatives. Only two farmers reported having received sorghum seed from Non Governmental Organisations (NGOs). It was also found during this survey that most farmers in Eastern Uganda planted their sorghum crops at the beginning of the second rain season (August). A few farmers planted either earlier in July or late in September. Those who planted late indicated that the oxen were not readily available for land preparation, while those who planted earlier owned their oxen.

Table 2.7a: Cropping practices: Soil types, seed sources and planting times

	Responses	Frequency	Percentage
Soil type	Loam soil	29	30.5
	Sandy soil	26	27.4
	Sandy-loam soil	60	42.1
Source of sorghum seed	Own saved	53	56.4
	Friends/relatives	16	17.0
	Local market	23	24.5
	NGO	2	2.1
Month of planting sorghum	June	3	3.2
	July	18	18.9
	August	61	64.2
	September	13	13.7

2.3.5 Cropping practices: Field operations

The majority of farmers interviewed (81%) prepared their land using ox-plough and only 18% prepared using hand hoes (Table 2.7b). All the farmers interviewed planted sorghum by broadcasting by hand. Over 92% of the farmers weeded sorghum fields only once and only six reported weeding twice. Almost all the farmers (98.9%) weeded their sorghum fields using hand hoes. It was also realised that some few farmers (13.8%) used inorganic fertilizers in sorghum production. However, the majority of farmers (86%) did not use inorganic fertilizers in sorghum production. In terms of field management after the sorghum crop was harvested, it was found that 70% of the farmers allowed animals (cattle and goats) to graze in the fields. A small proportion of farmers immediately ploughed under the sorghum stalks. Cereal-legume (sorghum-groundnuts or cowpea) rotation system was the most common crop rotation system, but a considerable proportion of the farmers (33.7%) practiced cereal-cereal (sorghum-millet or sorghum-maize) rotation system. The least common among the three crop rotation systems identified was cereal-root crop rotation. The most common intercropping system mentioned was sorghum and finger millet.

Table 2.7b: Cropping practices: Field operations

Cropping practices	Responses	Frequency	Percentage
Method of land preparation	Hand hoe	18	18.9
	Ox-plough	77	81.1
Method of planting	Broadcasting	95	100
	Row planting	0	0
Number of weedings	Once	87	92.6
	Twice	6	6.4
	No weeding	1	1.1
Method of weeding	Hand hoe	92	98.9
	None	1	1.1
Fertilizer application	Yes	13	13.8
	No	81	86.2
Field management after harvest	Leave animals to graze	67	70.5
	Burn	1	1.1
	Plough under	5	5.3
	Leave to fallow	1	1.1
	Animals graze and plough under	5	5.3
	Others	16	16.8
Crop rotation system	Cereal-Cereal	32	33.7
	Cereal-Legume	53	55.8
	Cereal-Root crop	10	10.5

2.3.6 Farmers' knowledge about the *Striga* problem

Through discussions with individual farmers, this survey revealed that farmers in Eastern Uganda have some knowledge about the *Striga* problem in their fields (Table 2.8). It was discovered that about 37% of the farmers had observed *Striga* in their fields for over 10 years while 43.7% had observed it in less than 10 years. A few farmers (19.5%) saw *Striga* in their fields in the past 3 years. The survey also found that over 95% of the farmers recognised *Striga hermonthica* as the only *Striga* species infesting their fields and damaging cereal crops. Three farmers reported *S. asiatica* and only one farmer identified both species. About 64% of farmers indicated the degree of *Striga* infestation in their fields to be high while 22.7% perceived the degree of infestation to be low. A series of factors were identified by farmers as contributing to the increase in *Striga* but the most common factor that was reported was continuous cereal cropping (45%). It was however surprising to find that a relatively equal proportion of farmers (44%) had no idea about the factors that led to *Striga* increase. Similarly, while a fair proportion of farmers (36.8%) rated the crop losses caused by *Striga* as high, a relatively equal proportion (35.8%) had no idea about the level of crop losses caused by *Striga*. Another finding was that 62% of the farmers had no idea of any methods of controlling *Striga* and completely no farmer mentioned the use of resistant varieties. A few farmers reported the use of crop rotation and manure application (15.8% each). Furthermore, in terms of the best control methods as perceived by farmers, 70.6% of the farmers had no idea. A small proportion of farmers (12.6%) suggested manure application and 11.6% suggested crop rotation.

Table 2.8: Farmers’ knowledge about the *Striga* problem

Knowledge aspect	Response	Frequency	Percentage
Number of years *Striga* has existed in his/her field	Over 10 years	32	36.8
	Less than 10 years	38	43.7
	Less than 3 years	17	19.5
Striga species present in the field	*S. hermonthica*	84	95.5
	S. asiatica	3	3.4
	Both species	1	1.1
Degree of *Striga* infestation in the field	High	56	63.6
	Moderate	12	13.6
	Low	20	22.7
Factors that increase *Striga*	Continuous cereal cropping	43	45.3
	Exhausted soils	6	6.3
	Animal grazing	2	2.1
	Wind dispersal	1	1.1
	Water dispersal	1	1.1
	No idea	42	44.2
Crop losses due to *Striga*	High	35	36.8
	Moderate	13	13.7
	Low	13	13.7
	No idea	35	35.8
Current control methods practiced	Crop rotation	15	15.8
	Intercropping	1	1.1
	Manure application	15	15.8
	Fertilizer application	5	5.3
	Resistant varieties	0	0
	None	59	62.1
Perceived best control method	Crop rotation	11	11.6
	Manure application	12	12.6
	Fertilizer application	5	5.3
	No idea	67	70.6

2.3.7 Crop density and *Striga* incidence in three districts of Eastern Uganda

Table 2.9 shows the mean squares from the analysis of variance for crop density and *Striga* incidence for eight sub-counties of three districts in Eastern Uganda, while Figure 2.1 shows the mean values. The differences in crop density were not significant between the various sub-counties in the three districts. However, in all sub-counties, sorghum crop density was generally lower than the locally recommended of at least 18 sorghum plants per square meter. Numbers of emerged *Striga* plants in individual farmers' fields differed significantly ($P<0.05$) between the different sub-counties in the three districts (ranging from 3-16 *Striga* plants m^{-2}). It was observed that the number of emerged *Striga* plants in farmers' fields was highest in Kumi sub-county of Kumi district followed by Anyara sub-county in Kaberamaido district. It was lowest in Ngero and Atutur sub-counties of Kumi and Bukedea districts respectively. On the other hand, the differences in *Striga* soil seed bank were highly significant ($P<0.001$) between the various sub-counties in the three districts. The highest *Striga* soil seed bank was recorded in Kumi sub-county of Kumi district followed by Anyara sub-county of Kaberamaido district. *Striga* soil seed bank was lowest in Mukura sub-county of Kumi district. The two sub-counties of Bukedea district had equal amounts of *Striga* seed in their soils, which were on average lower than other districts. The correlation between the *Striga* soil seed bank and the number of emerged *Striga* plants in farmers' fields was highly significant ($P<0.001$) and positive ($r=0.43$). This indicates that the more the *Striga* seed in the soil, the more the *Striga* plants that emerge above ground in the presence of a host crop.

Table 2.9: Mean squares from analysis of variance for crop density and *Striga* incidence for 8 sub-counties in 3 districts of Eastern Uganda

Crop intensity and *Striga* incidence	Source of variation	d.f.	Mean squares
No. sorghum plants m^{-2}	Sub-county	7	37.77
	Residual	88	21.02
	Total	95	
No. *Striga* plants m^{-2}	Sub-county	7	171.79*
	Residual	88	78.94
	Total	95	
No.*Striga* seeds kg^{-1} soil	Sub-county	7	134699**
	Residual	88	12057
	Total	95	

*Significant at $P<0.05$. ** Significant at $P<0.001$

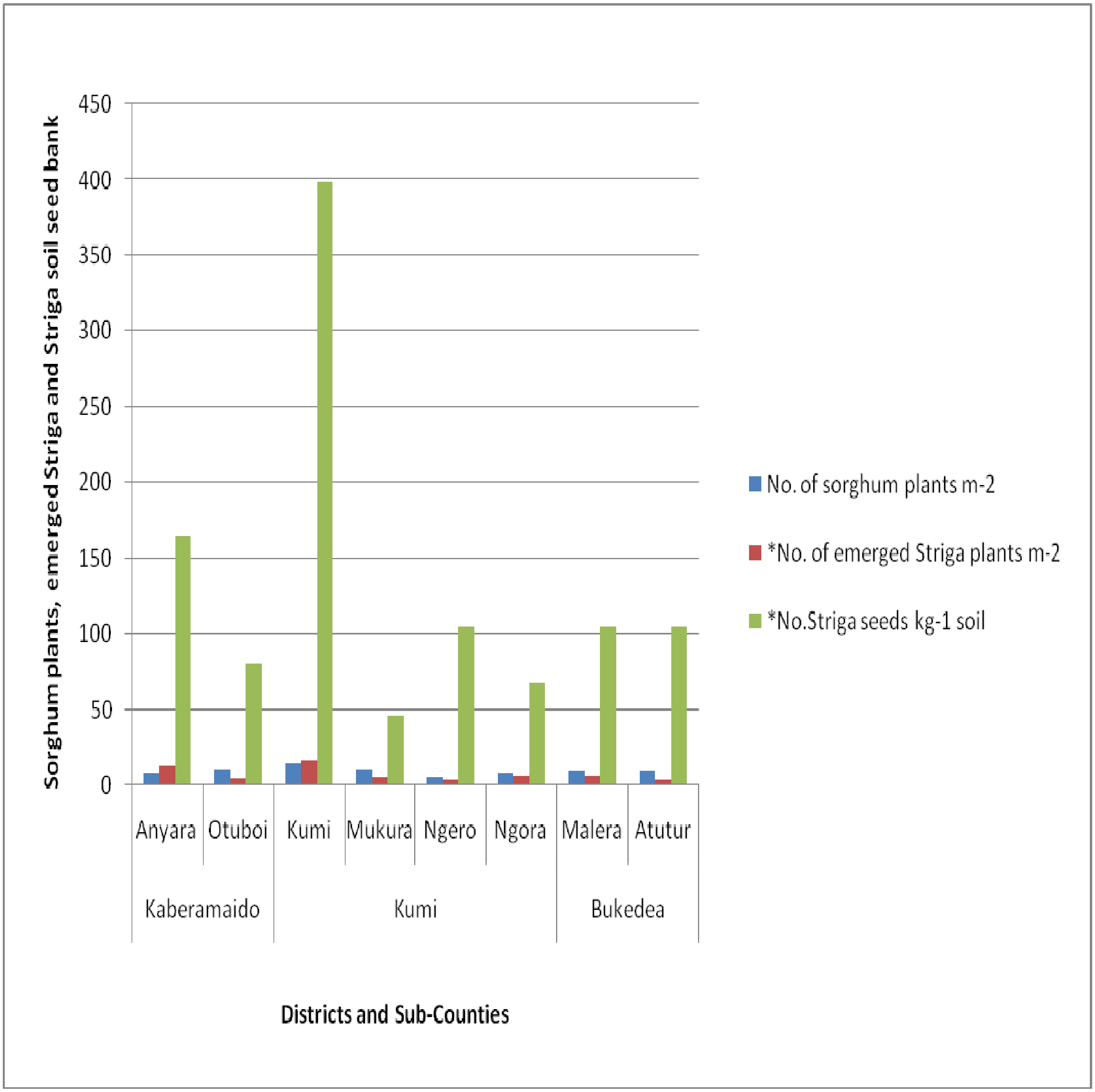


Figure 2.1: Mean values for crop density and *Striga* incidence in 8 sub-counties of 3 districts of Eastern Uganda

2.4 Discussion

2.4.1 Constraints to sorghum production and farmers' preferences for new sorghum varieties

In the present survey, farmers have identified *Striga* as the leading constraint affecting sorghum production in Eastern Uganda. This finding is consistent with earlier surveys carried out in the region (Ebiyau and Ouma, 1995, Akwang et al., 1998, 1999) in which farmers had earlier on pointed out the *Striga* problem in cereal cultivation. This survey has confirmed the persistence of the *Striga* problem and in fact with evidence of an increase in infestation. The evidence of increase was shown by the high proportion of farmers who had newly observed *Striga* in their fields in both less than three years and ten years. Exceptionally in Pallisa district, *Striga* was not considered a main threat to sorghum production. It was observed that in this district, farmers frequently grew cotton and cowpea in rotation with their cereal crops. In a series of studies over the years (Traore et al., 2011, Schulz et al., 2003, Olupot et al., 2003, Olupot, 2002, Ariga et al., 1997, Parker and Riches, 1993), cotton and cowpea have been found to effectively suppress *Striga* infestation when grown in rotation with cereal crops by inducing suicidal germination of its seeds in the soil. This therefore probably explains why *Striga* does not feature as a main constraint to sorghum production in Pallisa district.

In terms of preference for new sorghum varieties, farmers included in this survey preferred red grain sorghum, with compact and erect heads, maturing in about three months, a plant height of 1.5m in addition to being *Striga* resistant and drought tolerant. Red grain sorghum was preferred because it reportedly mixes well with dry cassava chips to produce flour that is used for making the local bread (*Atap*). This probably indicates that one of the main uses of sorghum in this region is for food preparation because the breweries normally use white grain sorghum. For example, Epuripur sorghum that is currently used by Nile breweries Ltd for making Eagle lager beer is a white grained sorghum variety. Farmers also pointed out that the red grain sorghum fetches more money since it is bought by traders even from Western Kenya. Additionally, red grained sorghum was said to be resistant to bird damage compared to white grained sorghum. Red grained sorghum is therefore important in these communities for both food and cash income. However, most if not all of the previous improved varieties released were either brown seeded or white.

Compact and erect sorghum heads were associated with higher yields. Sorghums with compact and erect heads belong to the *Kafir* race (Bantilan et al., 2004). According to the same authors, the genes contributing to yield in sorghum are found in the races *Kafir, Caudatum* and *Durra*. It can therefore be observed that farmers in this survey were correctly associating compact and erect heads to increased sorghum yields. Early maturity on the other hand was being associated with drought escape and early relief from hunger. This indicates that drought is also a major problem in Eastern Uganda, and additionally demonstrates the importance of sorghum as a food security crop in the region. While there are two growing seasons in a year for Eastern Uganda, the rain period is hardly more than three months in each.

2.4.2 Soil types and sources of sorghum seed for planting

The problem of *Striga* has previously been reported to increase under conditions of light soils with low soil fertility among others (Oswald, 2005; Olupot, 2002; Ariga et al., 1997, Enserink, 1995). This survey found that most of the soils in Eastern Uganda were sandy-loam, loam or sandy soils that were visibly light and seemingly infertile or exhausted. This observation may partly explain the increased *Striga* infestation in Eastern Uganda. One other factor that has previously been found to contribute to increase in *Striga* infestation is planting sorghum seed already contaminated with *Striga* seeds (Kamal et al., 2007, Olupot et al., 2005, Berner et al., 1994). Most of the farmers interviewed during this survey planted their own home saved seed, which they had previously harvested from their already infested fields. This probably leads to increase in *Striga* levels in their fields. Buying sorghum seed from the local markets within the same area also does the same because most of the surrounding area is infested with *Striga*. Most of the sorghum sold in the local markets is probably grown within the surrounding villages.

2.4.3 Field operations

In a number of earlier investigations (Kamal et al., 2007, Olupot et al., 2005, Ransom et al., 1997, Berner et al., 1994 and Kim, 1991), animal grazing has been pointed out as one of the main channels through which *Striga* seed is dispersed. The present survey found that 70% of the farmers open their fields for animals to graze on the stover after the sorghum grain has been harvested. From field observations, it was at that stage that most of the *Striga* shoots also matured and shed their seed. Therefore, through grazing, the animals (cattle and goats) move mature *Striga* seeds from infested fields to un-infested ones thereby spreading the weed from field to field and resulting in increased *Striga* infestations. In the case of weeding, it was found that almost all the farmers encountered (92%) carry out weeding of their sorghum crop only once, presumably 3-4 weeks after crop emergence. At that stage, the *Striga* plants may not have emerged, as it has been observed to start emerging around six weeks after crop emergence. In this case, *Striga* escapes the first weeding operation, and since farmers generally do not carry out a second weeding, *Striga* is left to mature and shed thousands of its seed back into the soil therefore building up its soil seed bank. This is also probably the reason why many sorghum fields show thousands of *Striga* plants flowering at the end of the season in these districts (personal observation). Whereas it has been reported by several authors (Fasil Reda and Verkleij, 2007; Olakojo and Olaoye, 2007; Grenier et al., 2004; Mohamed et al, 2003; Aflakpui et al., 1994; Parker and Riches, 1993) that inorganic fertilizers, particularly nitrogenous fertilizers minimise *Striga* damage on sorghum, it was realised in this survey that a majority of the farmers (86%) did not use inorganic fertilizers in sorghum production. This indicates that farmers are probably not able to apply the technology of inorganic fertilizers to control *Striga*. It may also suggest that farmers are not aware of the positive effects of inorganic fertilizers as shown by only 5% who applied fertilizers as a method to minimise Striga damage. Awareness creation on the positive effects of fertilization and the use of *Striga* resistant sorghum varieties might be some of the options that could be applicable to control Striga infestation.

2.4.4 Farmers' knowledge about the *Striga* problem

Basing on the farmers knowledge about the problem of *Striga* in Eastern Uganda, it could be seen that *Striga* is spreading into new fields. This is evidenced by a total of 63.2% of farmers having recently seen *Striga* in their fields within the last 10 years, more so the 19.5% who have recently seen it within the last 3 years. The fact that a considerable proportion of farmers (44%) have no idea about the factors that lead to increase in *Striga* infestation and the associated crop losses (35.8%) could be considered as a challenge to cereals research in Uganda. In addition, a large proportion of farmers (70.6%) having no idea about possible control options that could be used to manage *Striga* is also a challenge to research and extension. It probably indicates the need for research and extension workers to carry out adequate farmer sensitisation about *Striga* biology and its control. Even more challenging, particularly to sorghum breeding, is that farmers have no idea about the possibility of having *Striga* resistant sorghum varieties. It brings out the urgent need to develop and evaluate *Striga* resistant sorghum varieties because this is the option that is likely to be applicable to the resource poor farmers who are the majority of sorghum growers in Eastern Uganda.

2.4.5 The level of *Striga* infestation in farmers' fields

It was found out from this study that the soils in farmers' fields are heavily loaded with *Striga* seed. Pieterse and Verkleij (1991) indicated that in heavily infested fields, only about 30% of the available *Striga* seed may germinate in a season in the presence of the host. Enserink (1995) reported that in case of heavy infestation, it may take several years even with trap crops to bring the *Striga* population under control. For example in Kumi sub-county of Kumi district where the highest soil seed bank (399 seeds kg^{-1} of soil) was recorded, only about 4% of this *Striga* (15.8 plants m^{-2}) had emerged above ground. The indication here is that while it may be possible probably through trap cropping to reduce *Striga* seed load in the soil; it may take several years for farmers to achieve it in the case of heavily infested fields. In the mean time therefore, farmers may need to grow resistant sorghum varieties in order to get sufficient grain from the infested fields. Although the new *Striga* resistant sorghum cultivars may be challenged by the enormous seed bank (Kamal et al., 2007, Mohamed et al., 2003), this could be mitigated by evaluating the new materials in such fields so that only those materials that are resistant/tolerant enough for such levels of infestation could be passed out to farmers. Large differences in *Striga* soil seed bank were observed within and between districts. This shows the high variability in *Striga* distribution under natural conditions. It indicates that when evaluating new sorghum genotypes for *Striga* resistance, the evaluation needs to be done in many sites and probably many replications within the site.

2.5 Conclusions

This participatory rural appraisal has revealed that:

i. *Striga hermonthica* is one of the most important constraints limiting sorghum production in Eastern Uganda, followed by insect pests such stalk borers and sorghum midge.

ii. Sorghum farmers in eastern Uganda mostly preferred red grained sorghum with compact and erect heads, short plant height of 1.5m, and maturing in about three months in addition to being *Striga* resistant and drought tolerant.

iii. The level of *Striga* infestation in farmers' fields is high judged by the soil seed bank levels. There were large differences in *Striga* soil seed bank levels between and within districts indicating the high variability of *Striga* distribution under natural conditions.

iv. There is need to sensitise farmers about *Striga* biology and control in order to reduce its spread and institute control measures.

v. There is urgent need to develop and evaluate *Striga* resistant and high yielding sorghum varieties for the farmers in Eastern Uganda in order to contribute to the food security of the region.

References

Aflakpui, G.K.S., G. Bolfrey, F.R. Arias, and P.Y.K. Sallah. 1994. *Striga* control research in 1990 and future perspectives in Northern Ghana. *In* Lagoke, et al., (eds.) Improving *Striga* management in Africa, Proceedings, 2nd General Workshop of the Pan-African *Striga* Control Network (PASCON), 23-29 June 1991, Nairobi, Kenya. Accra, (Ghana): FAO. pp. 131-134.

Akwang, A. A., J.P. Obuo, J. Okwadi and J. Oryokot. 1999. Needs assessment for agricultural research in the Teso farming system: Summary report. NARO/DFID. Kampala, Uganda.

Akwang, A. A., S. Okalebo and J. Oryokot. 1998. Needs assessment for agricultural research in the Teso farming system, *'Aijul Eode'*: Main report. NARO/DFID. Kampala , Uganda.

Ariga,E.S., J.K. Ransom, G.D. Odhiambo, G. Abayo and D.K. Ndungu. 1997. Potential of using cotton and other trap crops for *Striga hermonthica* management in cereals in Kenya. *In* Adipala, et al., (eds.) *Proceedings of the 16th Biennial Weed Science Society Conference for Eastern Africa*. Kampala: WSSEA. Pp 247-254.

Bantilan, M.C.S., U.K. Deb, C.L.L. Gowda, B.V.S. Reddy, A.B. Obilana, and R.E. Evenson (eds.). 2004. Sorghum genetic enhancement: research process, dissemination and impacts. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Bazinger, M. and Cooper, M. 2001. Breeding for low input conditions and consequences for participatory plant breeding: examples from tropical maize and wheat. *Euphytica* 122: 503-519.

Berner, D.K., K.F. Cardwell, B.O. Faturoti, F.O. Ikie, and A.O. Williams, 1994. Relative roles of wind, crop seeds and cattle in dispersal of *Striga* spp. Plant Disease 78: 402-406.

Berner, D.K., M.D. Winslow, E.A. Award, K.F. Cardwell, D.R. Mohan Raj, and S.K. Kim. 1997. *Striga* research methods: A manual. 2nd Ed. International Institute of Tropical Agriculture. Ibadan, Nigeria.

Derera, J. P. Tongoona, A. Langyintou, M.D. Laing, and B. Vivek. 2006. Farmer perceptions on maize cultivars in the marginal eastern belt of Zimbabwe and their implications for breeding. African Crop Science Journal.14 (1): 1-15.

Ebiyau, J., and E. Ouma. 1995. *Striga* survey in Eastern Uganda. Serere Agricultural and Animal Production Research Institute/National Agricultural Research Organisation.

Ebiyau,J., and J.O.E. Oryokot. 2001. Sorghum (*Sorghum bicolor* (L.) Moench*). In* Mukiibi, J.K. (ed.) Agriculture in Uganda, Vol.II. National Agricultural Research Organization 2001, Fountain Publishers Ltd, Kampala, Uganda.

Enserink, H.J. 1995. Sorghum Agronomy in West Kenya: Investigations from a farming systems perspective. Royal Tropical Institute, Amsterdam.

FAOSTAT. 2007. Food and Agriculture Organization of the United Nations, Statistics Division. http://faostat.fao.org/.

Fasil Reda and J.A.C. Verkleij. 2007. Cultural and cropping systems approach for *Striga* management- a low cost alternative option in subsistence farming. *In* Ejeta, G. and Gressel, J. (eds.) Integrating new technologies for *Striga* control: Towards ending the witch-hunt. World Scientific Publishers Co. Pte.Ltd.

Grenier, C., A. Deressa, Z. Gutema, G. Gebeyehu, H. Desmae, and Shewayrga. 2004. Integrated *Striga* management (ISM) in East Africa. *In* Proceedings Consultation Workshop on Millet and Sorghum-Based systems in West Africa. Niamey, Niger, 27-30 January 2004.

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, H.G. Welz, and H.H. Geiger. 2000b. Improved methodologies for breeding *Striga* resistant sorghums. Field Crops Research 66(3):195-211.

Kamal, I.M., J.F. Bolin, L.J. Musselman, and A.T. Peterson. 2007. Genetic diversity of *Striga* and implications for control and modelling future distributions. *In* Ejeta, G. and Gressel, J. (eds.) Integrating new technologies for *Striga* control: Towards ending the witch-hunt. World Scientific Publishers Co. Pte.Ltd.

Kim, S.K. 1991. Combating *Striga* in Africa, *In* S. K. Kim, (ed.) Proceedings of the International Workshop, IITA, Ibadan, Nigeria.

Mbwaga, A.M., Riches, C. and Ejeta, G. 2007. Integrated *Striga* management to meet sorghum demand in Tanzania. *In* Ejeta, G. and Gressel, J. (eds.) Integrating new technologies for *Striga* control: Towards ending the witch-hunt. World Scientific Publishers Co. Pte.Ltd.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43: 1320-1324.

Olakojo, S.A., and G. Olaoye. 2007. Response of maize (*Zea mays* L) to different nitrogen fertilizer formulations under *Striga lutea* (Lour) artificial infestation. Tropical and Subtropical Agroecosystems, 7 (2007): 21-28.

Olupot, J.R. 2002. Development of an integrated *Striga* management strategy for small-scale sorghum growers in Uganda. Msc. Thesis, Makerere University, Kampala, Uganda.

Olupot, J.R., D.S.O. Osiru, J. Oryokot, and B. Gebrekidan. 2003. The effectiveness of *Celosia argentia* ("*Striga* Chaser") to control *Striga* on sorghum in Uganda. Crop Protection 22:463 – 468.

Olupot, J.R., I. Abaijuka, F. Dradiku, P. Edema, and J. Mukalazi. 2005. *Striga* infestation in the West Nile Agro-Ecological Zone of Uganda: The socio-economic perspective and the way forward. *In* p. 1507-1511. African Crop Science Conference Proceedings. African Crop Science Society.

Oswald, A. 2005. *Striga* control technologies and their dissemination. Crop Protection 24 (2005) 333-342.

Parker, C., and C.R. Riches. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.

Payne, R.W., D.A. Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2011. An introduction to GenStat for Windows (14th edition). VSN International, Hemel, Hemstead, UK.

Pieterse, A.H. and J.A.C. Verkleij. 1991. Effect of soil conditions on Striga development – A review. In: Ransom, J.K., L.J. Musselman, A.D. Worsham and C. Parker (eds.) Proceedings of the 5th International Symposium of Parasitic Weeds, Nairobi: CIMMYT. Pp 329-339.

Ransom, J.K., G.D. Odhiambo, G. Abayo, and A. Oswald. 1997. An update of *Striga* control research in Africa, pp. 215-219, *In* E. Adipala, et al., (eds.) Proceedings of the 16th Biennial Weed Science Society Conference for Eastern Africa. WSSEA, Kampala, Uganda.

Schulz, S., M.A. Hussaini, J.G. Kling, D.K. Berner, and F.O. Ikie. 2003. Evaluation of integrated *Striga hermonthica* control technologies under farmer management. Experimental Agriculture, 39, pp. 99-108.

Sperling, L., J.A. Ashby, M.E. Smith, E. Weltzien, and S. McGuire. 2001. A framework for analysing participatory plant breeding approaches and results. *In* Hocde, H., J. Lancon and G. Trouche. (eds.) *Selection participative, Montpellier, 5-6 Septembre 2001*. pp. 106-119

SPSS Inc. 2010. Statistical package for social sciences-Users guide. SPSS Inc., Chicago, II.

Traore, H., D. Yonli, and P. Sereme. 2011. Suicidal germination of *Striga hermonthica* (Del.) Benth. by cotton, cowpea and groundnut genotypes in Burkina Faso. International Journal of Agricultural Research, 6, pp. 49-57.

CHAPTER THREE: PHENOTYPIC AND GENOTYPIC VARIABILITY AMONG AFRICAN SORGHUM ACCESSIONS FOR *STRIGA* RESISTANCE IN EASTERN UGANDA

Abstract

Striga infestation severely constraints sorghum productivity in semi-arid lowland areas of Uganda. Fifty different African sorghum accessions were evaluated in the field for resistance to *Striga hermonthica* in Eastern Uganda. The objectives were to determine phenotypic and genotypic variability among African sorghum accessions for *Striga* resistance and identify suitable sources of resistance that could be used in breeding *Striga* resistant sorghum varieties in Ugandan. The accessions were evaluated for two seasons in a naturally infested field that was augmented using one year old *S. hermonthica* seed, so as to improve on the uniformity of *Striga* distribution in the experimental field. *Striga* emergence, *Striga* vigour and severity, the area under *Striga* number progress curve (AUSNPC), area under *Striga* severity progress curve (AUSVPC) and sorghum crop performance were used to assess resistance. Both phenotypic and genotypic factors contributed significantly to the variability observed among the African sorghum accessions with respect to *Striga* resistance and sorghum crop performance. This indicates that *Striga* resistance could be improved through selection. Broad sense heritability estimates were relatively low probably due to the large seasonal effects. Therefore, techniques that minimise environmental effects need to be employed when selecting for *Striga* resistance in sorghum in order to improve on heritability. The values for genetic coefficient of variation (GCV) and genetic advance (GA) indicate that genetic gain for *Striga* resistance could be achieved through selection based on AUSVPC, AUSNPC and *Striga* emergence. The sorghum accessions SRN39, Brhan, Framida, Gubiye, Wahi, P9407 and N13 consistently showed low AUSNPC, AUSVPC, *Striga* emergence, *Striga* vigour and severity. The above accessions were consequently classified as resistant and it is therefore suggested that they could be used as reliable sources of resistance when breeding for *Striga* resistant sorghum varieties in Uganda. Most of the accessions from Serere breeding programme (Seredo, Sekedo, Epuripur, Sila and Hakika) were moderately resistant together with one landrace from Northern Uganda (Ar2) and one accession from South Africa (AS17). The rest of the 37 accessions, mostly landraces were susceptible to *S. hermonthica*.

3.1 Introduction

The development of *Striga* resistant sorghum cultivars has previously been slowed down by the lack of reliable and rapid screening and evaluation techniques (Mohamed, 2002). Field evaluation for *Striga* resistance is hampered by several factors including extreme variability in the distribution of *Striga* seed under natural infestation and complex genotype x environment interactions. The efficiency of field evaluation for *Striga* resistance in sorghum could be improved by including one or several of the following practices: field inoculation with *Striga* seeds, appropriate experimental design with increased replications, specific plot layout, use of appropriate susceptible and resistant checks, evaluation in adjacent infested and un-infested plots; and the use of selection indices derived from emerged *Striga* counts, *Striga* vigour and grain yield or host damage score (Haussmann et al., 2000b). Extreme variability in the parasite and significant genotype x environment interaction effects may be overcome through multi-location testing of advanced germplasm to obtain materials with stable performance. Additional strategies could include; careful definition of the target environments, determination of the most important selection traits in each target environment, characterization of crop germplasm and improvement of available sources of resistance for better agronomic performance.

Showemimo and Kimbeng (2005) report that preliminary and confirmed studies have shown the importance of some agronomic traits in response to *Striga*. Such traits may serve as resistance traits or selection criteria on the basis of their significant genetic variability and correlations. Knowledge of inheritance of resistance to *Striga*, genetic variance components and phenotypic performance would therefore be useful in developing *Striga* resistant sorghum genotypes. Kroschel (2001) indicated that estimates of broad sense heritabilities for *Striga* counts ranged between 0.1 and 0.58 in a pot trial, compared to a laboratory study where heritabilities ranged from 0.91 to 0.97 for low germination stimulant production, which is one of the mechanisms of *Striga* resistance that can be investigated in the laboratory. Heritability estimates for *Striga* resistance under field conditions might be lower due to environmental effects.

Crop improvement is not only dependent on the magnitude of phenotypic variability but also on the extent to which the desirable characters are heritable (Tesfaye, 2002). It is therefore essential to partition the observed variability into its heritable (genetic) and non-heritable (environmental) components using appropriate genetic analysis. The aim of this study was to determine phenotypic and genotypic variability among a series of African sorghum accessions for *Striga* resistance and identify resistant lines that could be used in breeding new sorghum varieties that are resistant to *Striga* as well as being adapted to the local conditions in Eastern Uganda.

3.2 Materials and Methods

Fifty different sorghum accessions were screened for *Striga* resistance in Eastern Uganda for two seasons (March- July 2009 and 2010). In 2009, fourty eight sorghum accessions comprising of 15 elite lines from the National Semi-Arid Resources Research Institute (NaSARRI) breeding programme, 11 landraces from Eastern Uganda, 15 landraces from Northern Uganda, three accessions from Ethiopia and another three from South Africa were screened. In 2010, two more landraces from Eastern Uganda were included adding up to 50 accessions. Screening was done in one site that was naturally infested with *Striga hermonthica* in Eastern Uganda. In order to improve on the uniformity of *Striga* distribution, the experimental area was augmented using *S. hermonthica* seed that was collected in Eastern Uganda in 2007 on sorghum hosts. The augmentation was done by applying approximately 3000 *Striga* seeds in each planting hole using a bottle top just before dropping sorghum seed. *Striga* seed was measured following the procedure described by Berner et al. (1997). The sorghum entries were planted in two-row plots measuring two meters in length and plots were separated by one empty row. Sorghum was spaced at 60cm between rows and 20cm between plants. In 2009, the 48 entries were laid in 24x2 lattice design and replicated three times. In 2010, the 50 entries were laid in 25x2 lattice design again replicated three times. The experiment was weeded twice, at two and four weeks after sorghum emergence before *Striga* started to emerge.

3.2.1 Data Collection and Analysis

The data that were collected were number of emerged *Striga* plants in each plot, *Striga* vigour, sorghum damage, plant height at maturity and number of sorghum panicles formed in each plot. The number of emerged *Striga* plants was determined by physically counting all the emerged *Striga* plants in each plot. Three *Striga* counts were taken at two weeks intervals starting 7 weeks after crop emergence in each season. *Striga* vigour was scored using a scale of 0-9 as described by Haussmann et al. (2000b) and Kroschel (2001), where 0= no emerged *Striga* plants and 9= very vigorous *Striga* plants (average height >40cm with >10 branches). Scoring for *Striga* vigour was done each time the counts were taken. Sorghum damage was rated on a 1-9 scale as described by Ezeaku and Gupta (2004), where 1= normal sorghum growth with no visible symptoms of *Striga* damage, and 9= virtually all leaf area is scorched with two-thirds or more reduction in plant height, no useful panicles formed, plants dead or nearly dead. This was also done each time the *Striga* counts data were collected. Sorghum plant height was determined at maturity by measuring ten plants selected randomly in each plot using a tape measure. Sorghum plant height was measured only during the 2010 season. The numbers of panicles formed in each plot were counted at maturity. Sorghum grain formation was severely affected by sorghum midge infestation, and attempts to spray twice in 2010 season could still not save the grain. It was therefore considered unreasonable to measure sorghum grain yield. Before analysis, the data were initially tested for normality. The data which had skewed distribution such as *Striga* counts were first transformed using square root transformation before analysis of variance was done. In addition to the above parameters, two indices were calculated that give a measure of the overall *Striga* growth and development throughout the season; area under *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC) (Haussmann et al., 2000a; Rodenburg et al., 2005). The AUSNPC was calculated as follows:

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

where n is the number of *Striga* assessment dates, Y_i the *Striga* number at the *i*th assessment date, t_i the days after planting at the *i*th assessment date, t the days after planting to *Striga* emergence minus 1, and Y is 0. The AUSVPC was calculated similarly, with Y_i representing the *Striga* severity score. *Striga* severity score is a product of the *Striga* vigour and the number of *Striga* plants at each assessment date, as shown below:

Striga severity at *i*th assessment date = *Striga* vigour x *Striga* number at *i*th date

In order to determine genotypic and phenotypic variability among the different sorghum accessions, the data on each of the above parameters were subjected to analysis of variance using REML procedure in Genstat release 14.1 statistical package (Payne et al., 2011). The gross phenotypic variability was partitioned into components due to genetic (hereditary) and non-genetic (environmental) factors and the magnitudes of these were also estimated. In this case, genotypic variance is taken as that part of the phenotypic variance attributed to genotypic differences among the sorghum accessions, while the phenotypic variance is the total variance observed among the accessions when grown in different environments (seasons). Therefore the variance components were estimated using the formulae described by Tesfaye (2002) as follows:

$Vg = [MSG-MSE/r]$
$Vp = [MSG/r]$
$Ve = [MSE/r]$
where MSG, MSE and r are the mean squares of genotypes, mean squares of error and number of replications respectively. Phenotypic (PCV) and genotypc (GCV) coefficients of variation were derived using the formulae below:

$PCV = (\sqrt{vp}/\mu) \times 100$
$GCV = (\sqrt{vg}/\mu) \times 100$
Where vp, vg and µ are phenotypic variance, genotypic variance and grand mean per site respectively for the parameter under consideration. Broad sense heritability (H^2) was calculated and expressed as a percentage of the ratio of the genotypic variance (vg) to the phenotypic variance (vp).

Genetic advance expected was calculated and expressed as percent of the mean assuming a selection intensity of 5% for the superior genotypes using the following formulae:

$GA = K(Sp)H^2$
$GA \text{ (as \% of the mean)} = (GA/ \mu) \times 100$
Where K is a constant, which varies depending on the selection intensity, and at a selection intensity of 5%, K=2.06. Sp is the phenotypic standard deviation ($\sqrt{vp}$), H^2 is the heritability ratio and µ is the site mean of the parameter. The heritability ratio was calculated as follows:

$H^2 = Vg/Vp$

Correlation analysis was also applied in order to assess the relationship between *Striga* resistance parameters (*Striga* emergence, vigour, severity, AUSNPC and AUSVPC) and sorghum performance parameters (number of panicles formed and plant damage rating).

3.3 Results

3.3.1 Phenotypic and genotypic variability among sorghum accessions for *Striga* resistance and sorghum performance

Table 3.1 shows the analysis of variance for *Striga* resistance and sorghum performance parameters measured during the evaluation. Both genotypic and seasonal (environmental) variances were highly significant ($P \leq 0.001$, $P < 0.005$) for all the parameters measured. Genotype x season variation was only significant ($P = 0.001$) for number of sorghum panicles formed. This shows that the sorghum accessions responded similarly to *Striga* infestation between the two seasons of evaluation except in number of panicles formed. This is inspite of the significant difference between the two seasons.

Phenotypic variances (vp) were generally larger than the genotypic variances (vg) for all the traits (Table 3.2) indicating that the environmental effects constituted a major portion of the total phenotypic variability in the expression of *Striga* resistance among the sorghum accessions. However, there were relatively small differences between the phenotypic and genotypic variances for *Striga* vigour and sorghum damage. Large differences were observed between phenotypic and genotypic variances for *Striga* emergence, *Striga* severity, AUSNPC, AUSVPC and number of sorghum panicles formed. The error variance (ve) was large conceivably due to significant differences between the two seasons in terms of *Striga* infestation.

Table 3.1: Analysis of variance for *Striga* resistance and sorghum performance parameters for 48 African sorghum accessions

Source of variation	Wald statistic	df	F statistic	P value
***Striga* emergence**				
Season	173.14	1	173.14	<0.001
Genotype	97.02	47	2.06	<0.001
Season x Genotype	44.25	47	0.94	0.584
***Striga* vigour**				
Season	126.41	1	126.41	<0.001
Genotype	110.85	47	2.36	<0.001
Season x Genotype	42.12	47	0.90	0.663
***Striga* severity**				
Season	158.08	1	158.08	<0.001
Genotype	91.75	47	1.95	0.001
Season x Genotype	46.94	47	1.00	0.485
AUSNPC				
Season	134.47	1	134.47	<0.001
Genotype	87.73	47	1.87	0.002
Season x Genotype	38.64	47	0.82	0.782
AUSVPC				
Season	141.57	1	141.57	<0.001
Genotype	90.6	47	1.93	0.001
Season x Genotype	46.45	47	0.99	0.502
Sorghum damage				
Season	15.18	1	15.18	<0.001
Genotype	89.63	47	1.91	0.001
Season x Genotype	52.59	47	1.14	0.266
No. of sorghum panicles formed				
Season	9.26	1	9.26	0.003
Genotype	94.62	47	2.01	<0.001
Season x Genotype	79.18	47	2.08	0.001

Table 3.2: Estimates of phenotypic (vp), genotypic (vg) and error (ve) variances for *Striga* resistance and sorghum performance parameters in 48 african sorghum accessions.

Parameter	vp	vg	ve	s.e
Striga emergence	998.9	118.2	880.7	61.1
Striga vigour	1.537	0.324	1.213	0.132
Striga severity	92223	9312	82911	6928
AUSNPC	174734	24427	150307	15110
AUSVPC	17480890	1909787	15571103	1444279
Sorghum damage	0.406	0.227	0.179	0.168
No. of panicles	1289307977	220097735	1069210242	206313703

AUSNPC = area under *Striga* number progress curve.

AUSVPC = area under *Striga* severity progress curve.

The phenotypic coefficients of variability (PCV) were generally higher than the genotypic coefficients of variability (GCV) in all the parameters measured (Table 3.3). However, the differences were relatively small for *Striga* damage on sorghum and *Striga* vigour. The PCV ranged from 10.7, for *Striga* damage to 112.9, for *Striga* severity. The GCV ranged from 8.9 to 36.6 for *Striga* damage and AUSVPC respectively. Heritability estimates were mostly low ranging from 10.1% to 55.9% for *Striga* severity and *Striga* damage to sorghum respectively. Genetic advance as a percentage of the mean ranged from 11.8% to 27.4% for *Striga* vigour and AUSNPC respectively. The GA results seem to suggest that when selecting for *Striga* resistance, reasonable genetic advance may be achieved by selection based on AUSNPC and AUSVPC. The heritability estimates seem to indicate that selection based on ratings of *Striga* damage on sorghum may be more useful.

Table 3.3: Estimates of phenotypic coefficient of variability (PCV), genotypic coefficient of variability (GCV), heritability (H^2) and genetic advance (GA) as a per cent of the mean for *Striga* resistance and sorghum performance parameters among African sorghum accessions

Parameter*	Trial mean	PCV	GCV	H^2 (%)	GA (% of mean)
Striga emergence	31.7	99.7	34.4	11.8	24.3
Striga vigour	4.4	27.3	13.6	21.1	11.8
Striga severity	269.1	112.9	35.9	10.1	23.5
AUSNPC	439.0	95.2	35.6	14.0	27.4
AUSVPC	3772.0	110.8	36.6	10.9	24.9
Sorghum damage	5.6	10.7	8.9	55.9	12.3
No. of panicles	63267.0	56.8	23.4	17.1	20.0

AUSNPC = area under *Striga* number progress curve.
AUSVPC = area under *Striga* severity progress curve.
* Data for *Striga* parameters is based on the average of 3 *Striga* counts

3.3.2 The effect of different sorghum accessions on *Striga* emergence, vigour and severity in 2009

3.3.2.1 *Striga* emergence

During the early stages of infection (7 weeks after crop emergence), *Striga* emergence did not significantly differ between the different sorghum accessions (Table 3.4). However, eight elite lines (SRN39, Brhan, Wahi, N13, Seredo, Hakika, Gubiye and P9407) and two local landraces (MA2 and KA4) had relatively low *Striga* emergence. The highest *Striga* emergence at this early stage was observed mainly on landraces from two districts of Northern Uganda, Ar1-5 from Arua district and YU1-3 from Yumbe district. Two Ethiopian lines ABEt and ABEw, and two South African lines AS20 and AS7 where moderately infected while one landrace from Kumi district of Eastern Uganda, Ku3 and another from Maracha district of Northern Uganda, MA7 also experienced relatively high infestation at seven weeks after crop emergence.

At the ninth week after crop emergence, there was a progressive increase in the number of *Striga* plants emerging on all accessions. At this stage, statistically significant differences (P<0.05) in *Striga* emergence were observed between accessions. *Striga* emergence was highest mainly among the local landraces such as YU2 and MA5 and lowest on some improved lines such as Wahi, Epuripur and P9407. Most of the accessions experienced moderate infection. Between the ninth week and the eleventh week after crop emergence, while there was a progressive increase in the numbers of emerged *Striga* plants, some lines such as SRN39, Brhan, N13 and Framida showed a reduction. In another case, some lines such as Gubiye, Hakika and one landrace Ar2, maintained a constantly low number of emerged *Striga* plants. On average, SRN39, Wahi, Gubiye and P9407 had low *Striga* infection across the season while Brhan, N13, Framida, Sila and Hakika were moderately infected. The highest infections were observed mainly on the landraces both from Eastern and Northern Uganda and also on the introductions from Ethiopia and South Africa.

3.3.2.2 *Striga* vigour

At the ninth week after crop emergence, *Striga* vigour was generally low with no significant differences observed between the different sorghum accessions (Table 3.4). Between the ninth week and the eleventh week after crop emergence, there was an increase in *Striga* vigour in most of the accessions, but SRN39, P9407 and Gubiye did not experience an increase in *Striga* vigour. The highest vigour score of 8 was recorded mainly on the local landraces and on one Ethiopian line, ABEw.

3.3.2.3 *Striga* severity

The differences in *Striga* severity between the sorghum accessions were not statistically significant at nine weeks after crop emergence (Table 3.4). However, Epuripur, Wahi, Gubiye, P9407 and Sila experienced considerably low *Striga* severity. The highest severity scores of more than 200 were recorded on many of the landraces and some introductions. At the eleventh week after crop emergence, while there was a tremendous increase in *Striga* severity on most of the accessions, SRN39 and Brhan showed a reduction in *Striga* severity. The lowest severities of less than 100 were recorded on SRN39, Brhan, P9407 and Gubiye.

Table 3.4: Mean *Striga* incidence and severity on different sorghum accessions in 2009

Sorghum accession	**Striga* number (7 w. a.c.e)	**Striga* number (9 w. a.c.e)	**Striga* number (11 w a.c.e)	Average *Striga* emergence	*Striga* vigour (9 w.a.c.e)	*Striga* vigour (11 w.a.c.e)	**Striga* severity (9 w.a.c.e)	*Striga* severity (11 w.a.c.e)
SRN39	0.7	26.0	5.0	10.6	3	3	99	18
Brhan	1.0	34.3	15.7	17.0	3	5	111	78
Wahi	0.7	12.3	19.7	10.9	3	5	38	110
N13	0.7	40.7	38.0	26.4	3	7	150	266
Framida	5.0	40.7	30.3	25.3	3	6	146	226
Gubiye	2.0	16.7	16.7	11.8	3	4	56	99
Dobbs	5.2	59.9	105.8	57.0	4	7	147	384
Sila	2.7	26.3	54.7	27.7	3	6	58	328
Hakika	0.7	42.0	42.7	28.4	4	5	163	317
Seredo	2.3	57.3	99.7	53.1	3	6	176	653
Sekedo	4.7	49.0	59.7	37.8	3	5	194	405
Epuripur	6.3	8.8	77.7	39.7	3	7	28	571
IS9830	3.7	36.7	62.3	34.2	3	6	127	404
P9407	2.0	16.7	21.0	13.2	3	3	55	62
ABEr	9.3	62.3	63.3	45.0	4	6	239	397
ABEt	3.3	35.3	95.3	44.7	3	6	120	659
ABEw	6.7	89.3	117.7	71.2	4	8	402	895
Ar1	18.3	88.3	121.0	74.6	4	7	285	1083
Ar2	11.0	47.3	47.0	35.1	4	6	209	282
Ar3	8.3	62.3	96.0	55.6	4	8	249	793
Ar4	21.3	84.3	136.3	80.7	4	8	388	1172
Ar5	13.0	55.3	149.7	72.7	4	7	221	1157
AS14	7.0	45.0	83.0	45.0	4	7	203	566
AS17	9.0	29.3	75.3	38.7	3	6	76	470
AS20	4.7	43.0	101.7	49.8	4	7	161	712
AS7	6.3	31.3	85.0	40.9	3	7	113	647
BU1	7.3	42.0	116.3	55.2	4	7	165	820
KA1	10.3	82.0	184.0	92.1	4	8	316	1366
KA2	3.3	43.3	93.7	46.6	3	7	123	695
KA3	5.7	29.3	122.7	52.6	4	7	117	859
KA4	2.3	27.0	123.0	50.8	3	8	81	992
Karimtama	10.3	31.7	81.0	41.0	4	8	119	623
Ku1	2.7	35.6	138.7	59.0	3	7	132	983
Ku2	8.0	83.3	122.3	71.2	3	8	281	1012
Ku3	14.0	65.0	117.3	65.4	4	7	298	976
Ku4	12.0	59.7	158.3	76.7	3	7	226	1110
L1	9.0	43.3	136.7	63.0	3	7	158	987
L2	8.0	54.0	113.7	58.6	4	7	198	815
MA1	9.0	49.3	130.3	62.9	4	8	197	1126
MA2	2.0	53.7	130.7	62.1	3	7	174	1010
MA3	5.0	83.0	190.3	92.8	4	9	332	1713
MA4	13.0	44.7	80.0	45.9	4	7	179	572
MA5	10.0	117.3	122.3	76.8	4	8	320	1043
MA6	10.3	64.7	165.7	80.2	4	8	246	1301
MA7	15.0	59.3	134.7	69.7	4	7	228	996
YU1	6.0	40.7	207.3	84.7	4	7	154	1572
YU2	24.7	125.0	133.0	94.2	4	8	500	1105
YU3	15.0	89.8	153.0	82.7	3	8	247	1317
Mean	**7.5**	**51.3**	**99.5**	**52.7**	**3.5**	**6.7**	**187.6**	**744.7**
l.s.d	ns	58.9	97.73	48.91	ns	2.24	ns	858.3

*Analysis based on transformed data, means presented as original figures. w.a.c.e.: Weeks after crop emergence. *Striga* vigour rating (0-9 scale): 0 = no emerged *Striga* plants; 9 = average height of *Striga* plants > 40cm, with > 10 branches.

3.3.3 The effect of different sorghum accessions on *Striga* emergence, vigour and severity in 2010

3.3.3.1 *Striga* emergence

In 2010 season, *Striga* emergence was generally low across the season compared to 2009 (Table 3.5). However, the differences in emergence were statistically significant (P<0.05) between accessions at seven, nine and eleven weeks after crop emergence. At seven weeks after crop emergence, some sorghum lines such as Brhan, Framida, Gubiye, Sekedo, AS20, AS7, Karimtama and Ku3 had no *Striga* plants emerged on them. One of the landraces, Ar4 had the highest emergence (26 *Striga* plants) while others such as ABEt, YU1, MA6 and MA7 had few (6) *Striga* plants emerged.

At nine weeks after crop emergence, there was a progressive increase in *Striga* emergence on all accessions but at different magnitudes. The highest progressive increase was observed mainly on landraces while improved lines such as Brhan, Framida, Wahi, Hakika, ABEw and AS17 had minimal increase. By the eleventh week after crop emergence, some lines such as SRN39, Gubiye, Seredo, IS9830 and landraces (Ar2, Ar4, KA3, Ku2, MA2, MA7, YU2 and YU3) showed a reduction in the number of emerged *Striga* plants, contrary to an increase in the rest of the accessions. On average, Framida, Brhan, Wahi, AS14 (South African accession), KA1 and Ku2 (local landraces) had the lowest *Striga* emergence across the season, while most of the landraces experienced the highest emergence.

Table 3.5: Mean *Striga* incidence and severity on different sorghum accessions in 2010

Sorghum accession	**Striga* number (7 w. a.c.e)	**Striga* number (9 w. a.c.e)	**Striga* number (11 w a.c.e)	*Average *Striga* emergence	**Striga* vigour (7 w.a.c.e)	*Striga* vigour (9 w.a.c.e)	*Striga* vigour (11 w.a.c.e)	Average *Striga* vigour	*Striga* severity (7 w.a.c.e)	*Striga* severity (9 w.a.c.e)	*Striga* severity (11 w.a.c.e)
SRN39	1.0	4.3	3.3	2.9	0.3	2.7	6.0	3.0	5.7	5.7	7.7
Brhan	0.0	0.7	1.0	0.6	0.0	1.3	3.7	1.7	7.7	8.0	8.6
Wahi	0.7	1.3	3.0	1.7	0.3	3.7	3.0	2.3	7.3	7.1	8.1
N13	0.3	3.0	4.0	2.4	0.3	3.0	5.0	2.8	6.3	6.7	7.3
Framida	0.0	0.3	0.3	0.2	0.0	0.7	2.0	0.9	6.3	6.7	7.0
Gubiye	0.0	5.3	4.7	3.3	0.0	1.3	3.0	1.4	7.0	6.0	7.7
Dobbs	0.3	23	35.3	19.6	0.7	4.0	6.3	3.7	4.3	6.0	7.7
Sila	1.0	5.0	7.0	4.3	1.0	3.7	7.0	3.9	4.3	4.3	7.0
Hakika	1.3	3.3	6.3	3.7	0.3	2.7	4.7	2.6	4.3	6.0	6.7
Seredo	2.0	11.0	3.0	5.3	0.3	2.7	7.3	3.4	4.3	6.7	7.7
Sekedo	0.0	3.0	11.0	4.7	0.0	2.0	5.3	2.4	5.3	7.3	7.0
Epuripur	2.0	9.3	8.9	6.6	0.3	1.2	3.9	1.8	2.5	3.0	4.8
IS9830	0.7	6.0	4.3	3.7	0.3	3.0	4.3	2.6	6.0	6.3	8.0
P9407	2.3	3.0	3.7	3.0	0.3	2.0	4.3	2.2	5.3	6.0	7.3
ABEr	4.3	21.7	20.7	15.6	1.0	4.7	7.7	4.4	4.3	5.0	5.3
ABEt	8.0	23.4	25.7	19.1	0.8	5.4	7.6	4.6	1.7	2.0	3.1
ABEw	1.1	1.7	4.7	3.1	0.2	3.3	5.3	3.9	3.9	7.1	9.1
Ar1	1.0	56.7	61.0	39.6	0.7	3.7	7.3	3.9	3.3	6.0	8.7
Ar2	3.3	61.0	38.3	34.2	1.3	4.7	6.7	4.2	4.0	6.0	9.0
Ar3	4.0	32.7	57.7	31.4	1.3	5.7	8.0	5.0	5.7	7.0	9.0
Ar4	26.0	104.3	65.0	65.1	2.0	6.3	7.3	5.2	5.3	8.3	9.0
Ar5	1.0	32.3	44.3	25.9	0.3	3.3	6.3	3.3	4.7	5.7	8.7
AS14	0.3	0.7	3.7	1.6	0.3	1.7	6.3	2.8	6.0	6.3	8.0
AS17	1.3	1.3	3.3	2.0	0.7	2.0	5.0	2.6	6.7	7.0	7.7
AS20	0.0	3.3	3.7	2.3	0.0	4.3	6.3	3.6	3.3	6.7	7.7
AS7	0.0	8.7	8.3	5.7	0.0	3.3	4.7	2.7	4.7	5.0	6.3
BU1	2.0	3.3	4.3	3.2	0.3	2.3	4.3	2.3	5.0	4.7	5.3
KA1	0.3	2.0	2.7	1.7	0.3	2.7	5.7	2.9	4.7	7.1	6.6
KA2	2.3	10.0	10.3	7.6	1.3	5.0	7.7	4.7	5.3	6.3	6.7
KA3	0.3	10.3	8.7	6.4	0.3	3.3	7.0	3.6	4.0	5.3	4.7
KA4	0.3	26.0	40.7	22.3	0.3	4.0	7.0	3.8	3.0	4.7	6.0
Karimtama	0.0	5.3	9.7	5.0	0.0	2.7	4.7	2.4	3.7	7.6	7.6
Ku1	1.3	17.3	13.7	10.8	0.7	4.3	6.3	3.8	3.7	5.3	6.0
Ku2	3.0	7.2	2.3	1.2	0.5	1.0	4.4	2.5	4.8	5.6	6.9
Ku3	0.0	2.7	6.3	3.0	0.0	3.7	6.7	3.4	5.2	5.1	5.0
Ku4	1.0	9.7	10.3	7.0	1.0	3.3	5.0	3.1	5.7	4.6	4.1
L1	2.3	7.3	7.7	5.8	0.3	2.3	6.0	2.9	4.0	5.3	6.7
L2	3.0	8.3	16.7	9.3	2.0	4.0	7.3	4.4	4.7	4.3	5.7
MA1	0.3	10.7	18.0	9.7	0.3	3.7	7.0	3.7	5.0	3.7	5.7
MA2	1.5	4.7	2.5	2.9	0.2	4.0	4.0	2.8	6.7	4.6	5.1
MA3	1.5	15.7	24.0	13.7	0.2	5.5	8.5	4.8	4.2	5.6	9.6
MA4	1.0	19.3	10.0	10.1	0.3	3.0	5.0	2.8	5.0	5.3	7.0
MA5	2.0	23.7	38.0	21.2	0.7	6.0	8.5	5.1	4.2	5.6	9.6
MA6	6.7	9.3	11.0	9.0	1.7	4.3	5.3	3.8	4.7	4.7	7.0
MA7	6.3	14.0	12.7	11.0	1.7	6.0	7.7	5.1	5.7	5.0	5.7
YU1	8.0	15.0	9.3	10.8	1.7	6.0	7.7	5.1	4.0	5.0	6.0
YU2	6.0	14.7	13.7	11.4	0.3	2.7	4.7	2.6	6.3	6.3	7.3
YU3	1.7	25.3	12.7	13.2	0.3	2.7	5.0	2.7	4.7	6.7	7.3
At1	4.0	25.0	22.3	17.1	1.7	5.3	7.7	4.9	3.0	3.0	5.0
At2	2.3	16.7	26.3	15.1	1.3	5.0	7.0	4.4	2.7	2.7	4.3
Mean	**2.4**	**14.6**	**15.3**	**10.7**	**0.6**	**3.5**	**5.9**	**3.4**	**4.8**	**5.6**	**6.9**
l.s.d	2.6	6.5	5.86	2.49	1.15	3.1	ns	2.4	2.66**	2.49**	2.19**

*Analysis based on transformed data, means presented as original figures. ** Highly significant ($P<0.01$). w.a.c.e.: Weeks after crop emergence. *Striga* vigour rating (0-9 scale): 0 = no emerged *Striga* plants; 9 = very vigorous, average height of *Striga* plants > 40cm, with > 10 branches. ns: not significant

3.3.3.2 *Striga* vigour

The differences in *Striga* vigour between the sorghum accessions were only significant (P<0.05) at the seventh and ninth week after crop emergence (Table 3.5). At the eleventh week, the differences in *Striga* vigour were not significant. Except for Wahi and MA2, there was a steady increase in *Striga* vigour from the seventh to the ninth week after crop emergence on all accessions. Framida, Gubiye, Brhan and Epuripur had the lowest average *Striga* vigour across the season while the landraces, Ar3, MA5, MA7, YU1, At1 and MA3 recorded the highest *Striga* vigour.

3.3.3.3 *Striga* severity

Differences in severity of *Striga* attack between the sorghum accessions were highly significant (P<0.01) throughout the season in 2010 (Table 3.5). At the seventh week after crop emergence, the lowest severity scores (1-2.7) were recorded on ABEt, Epuripur and At2, while 17 accessions registered relatively high severity (>6). At nine weeks after crop emergence, ABEt and At2 maintained low *Striga* severity. The same two accessions maintained low *Striga* severity even at the eleventh week of crop growth. Between the seventh and the ninth week after crop emergence there was generally little increase in *Striga* severity while from nine to eleven weeks, the increase in *Striga* severity was considerably high.

3.3.4 The area under the *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC) on the various sorghum accessions during the growing season of 2009

As indicated earlier in the data collection and analysis section, the AUSNPC and AUSVPC are indices that give a measure of the overall *Striga* growth and development on its hosts throughout the season. The AUSNPC did not significantly differ between the sorghum accessions at nine weeks after crop emergence in 2009 (Figure 3.1). However, Wahi and Epuripur had the lowest AUSNPC while some landraces such as YU2 and Ar4 had the highest AUSNPC values. At eleven weeks after crop emergence, there were statistically significant (P<0.05) (figures not shown) differences between the sorghum accessions in AUSNPC. Accessions: SRN39, Wahi and Gubiye had the lowest AUSNPC, and again most landraces had the highest. From nine to eleven weeks after crop emergence, there was generally an increase in AUSNPC for each sorghum accession. In total, SRN39, Wahi and Gubiye had the lowest AUSNPC across the season while most of the landraces showed the highest AUSNPC. The

AUSVPC was calculated at the eleventh week after crop emergence, with significant differences observed between the sorghum accessions (Figure 3.2). SRN39, P9407, Wahi and Gubiye experienced the smallest AUSVPC while almost all the landraces had remarkably high AUSVPC figures.

3.3.5 The area under the *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC) on the various sorghum accessions during the growing season of 2010

The values for the AUSNPC and AUSVPC were relatively lower in 2010 compared to 2009 season (Figures 3.3 and 3.4). This originates from lower *Striga* emergence and vigour in the 2010 season. However, the differences in AUSNPC between the sorghum accessions were statistically significant (P<0.05) (figures not shown) across the season. At nine weeks after crop emergence, Framida, Brhan, AS14 and two landraces (Ku2 and MA2) had the smallest AUSNPC while Wahi, ABEw, AS17, AS20, Sekedo and another two landraces had moderate AUSNPC. The rest of the sorghum accessions recorded considerably high values for AUSNPC. A similar trend was observed at eleven weeks after crop emergence and consequently in mean AUSNPC over the season.

The sorghum accession also differed significantly (P<0.05) in AUSVPC throughout the season in 2010. Framida, Brhan, Ku2 and MA2 had the smallest AUSVPC at nine weeks after crop emergence. AS14, KA1, ABEw and Sekedo showed moderate AUSVPC, but many of the landraces had remarkably high AUSVPC values. Again the same trend was observed at eleven weeks after crop emergence and eventually in mean AUSVPC.

3.3.6 The response of various sorghum accessions to *Striga* infestation in 2009

3.3.6.1 Plant damage due to *Striga* infestation

Plant damage due to *Striga* infestation varied on the different sorghum accessions during 2009 season (Table 3.6). However, the differences were only statistically significant at eleven weeks after crop emergence and on the average damage throughout the season. At nine weeks after crop emergence, Framida, Hakika, IS9830, ABEw and two landraces, L1 and KA3, were the least damaged (<3). Most of the sorghum accessions showed moderate damage (4-6). At eleven weeks after crop emergence, there was an increase in plant damage on each accession but at different magnitudes. Twenty six accessions could be rated as moderately damaged, while the rest of them were highly damaged (≥7). In terms of the average damage throughout the season, 30 accessions could be rated as moderately damaged, 18 as highly damaged while none showed little damage.

Table 3.6: The response of various sorghum accessions to *Striga* infestation in 2009

Sorghum accession	Damage rating (9 w.a.c.e)	Damage rating (11 w.a.c.e)	Average damage	No. of panicles ha^{-1} ('000')
SRN39	4	6	5	78
Brhan	3	5	4	94
Wahi	4	7	6	30
N13	4	7	6	25
Framida	2	6	4	122
Gubiye	4	7	6	83
Dobbs	3	5	4	47
Sila	3	7	5	39
Hakika	2	6	4	64
Seredo	3	6	5	125
Sekedo	4	6	5	53
Epuripur	4	6	5	44
IS9830	2	6	4	69
P9407	4	7	6	67
ABEr	3	5	4	56
ABEt	2	7	5	33
ABEw	5	8	7	0
Ar1	4	7	6	17
Ar2	6	8	7	3
Ar3	5	8	7	17
Ar4	5	9	7	0
Ar5	4	8	6	53
AS14	4	6	5	58
AS17	4	6	5	81
AS20	4	5	5	94
AS7	4	7	6	75
BU1	4	6	5	58
KA1	3	5	4	108
KA2	3	6	5	11
KA3	2	7	5	33
KA4	4	6	5	53
Karimtama	3	6	5	47
Ku1	4	6	5	92
Ku2	3	5	4	86
Ku3	4	6	5	64
Ku4	3	4	4	100
L1	2	5	4	128
L2	3	4	4	147
MA1	3	8	6	33
MA2	4	6	5	31
MA3	4	7	5	0
MA4	3	6	5	31
MA5	4	7	6	0
MA6	3	8	6	14
MA7	3	8	6	0
YU1	4	8	6	50
YU2	3	8	6	0
YU3	5	8	7	0
Mean	**3.5**	**6.5**	**5.3**	**52.4**
l.s.d	ns	1.9**	1.5**	61.0**

w.a.c.e.: Weeks after crop emergence. ** Highly significant (P<0.01).
Damage rating (1-9 scale): 1=no damage symptoms; 9= complete damage, plants dead
ns: not significant

3.3.6.2 Number of panicles formed

There was a highly significant (P<0.01) variation in the number of panicles formed in different sorghum accessions (Table 3.6). Framida, Seredo, L1 and L2 are the only accessions that formed relatively higher numbers of panicles. Accessions; ABEw, Ar4, MA3, MA5, MA7, YU2, and YU3 (mostly landraces from northern Uganda) hardly formed any panicles, probably due their relatively high susceptibility to *Striga*. Under severe *Striga* infestation, panicle formation may be impaired in susceptible sorghum varieties. However, most of the accessions could be considered as moderate in terms of panicle formation.

3.3.7 The response of various sorghum accessions to *Striga* infestation in 2010

3.3.7.1 Plant damage due to *Striga* infestation

During the 2010 growing season, plant damage rating was started earlier at seven weeks after crop emergence and continued up to the eleventh week. With the damage symptoms being clearly visible at the seventh week, variation between the sorghum accessions was observed (Table 3.7). Seven accessions were rated as less damaged (≤3), most of them being landraces. Five accessions were highly damaged (≥7) and thirty eight being moderately damaged (4-6). At the ninth week, while there was an observed increase in damage for most of the accessions, eighteen of them did not show a change in damage level, with ABEt being the least damaged. At the same time, there was a significant decrease in damage rating for one of the landraces, MA2, which could indicate possible recovery from early damage. At the eleventh week after crop emergence, only ABEt remained less damaged, fifteen accessions rated as moderately damaged while the rest were highly damaged. In terms of the average damage over the season, only two accessions (ABEt and At2) were less damaged.

3.3.7.2 Sorghum plant height and number of panicles formed

There were no statistically significant differences in plant height between the sorghum accessions (Table 3.7). A few lines such as Brhan, Framida, Sekedo and IS9830 grew close to their potential height of 130cm; otherwise, most of the accessions were dwarfed. The variation in number of panicles formed was statistically significant (P<0.05) between the accessions. Only three accessions (ABEr, MA1 and Ar2) produced more than 100,000 panicles per hectare. All the accessions that were rated as totally damaged (rate 9) at the eleventh week after crop emergence did not produce any panicles.

Table 3.7: The response of various sorghum accessions to *Striga* infestation in 2010

Sorghum accession	Damage rating (7 w.a.c.e)	Damage rating (9 w.a.c.e)	Damage rating (11 w.a.c.e)	Average damage	Plant height (cm)	No. of panicles ha^{-1} ('000')
SRN39	6	6	8	6	87.9	50.0
Brhan	8	8	8	8	126.6	8.3
Wahi	7	7	8	7	59.4	53.0
N13	6	7	7	7	58.9	36.1
Framida	6	7	7	7	107	47.2
Gubiye	7	6	8	7	88.4	39.0
Dobbs	4	6	8	6	63.6	53.0
Sila	4	4	7	5	38.5	55.6
Hakika	4	6	7	6	77.0	55.6
Seredo	4	7	8	6	87.8	58.3
Sekedo	5	7	7	6	111.3	16.7
Epuripur	3	3	5	4	96.3	12.7
IS9830	6	6	8	7	115.6	30.6
P9407	5	6	7	6	88.6	39.0
ABEr	4	5	5	5	73.0	105.6
ABEt	2	2	3	2	115.8	89.0
ABEw	4	7	9	7	83.0	0.0
Ar1	3	6	9	6	72.2	0.0
Ar2	4	6	9	6	110.9	0.0
Ar3	6	7	9	7	32.8	0.0
Ar4	5	8	9	7	58.1	0.0
Ar5	5	6	9	6	132.4	0.0
AS14	6	6	8	7	119.3	39.0
AS17	7	7	8	7	76.7	22.2
AS20	3	7	8	6	71.1	25.0
AS7	5	5	6	5	123.2	66.7
BU1	5	5	5	5	46.9	86.1
KA1	5	7	6	6	123.6	33.3
KA2	5	6	7	6	74.0	64.0
KA3	4	5	5	5	220.3	61.1
KA4	3	5	6	4	93.2	58.3
Karimtama	4	7	7	6	98.9	16.7
Ku1	4	5	6	5	93.1	86.1
Ku2	5	5	7	6	94.9	0.0
Ku3	5	5	5	5	94.7	47.2
Ku4	6	4	4	5	107.6	72.2
L1	4	5	7	5	103.3	64.0
L2	5	4	6	5	77.4	69.4
MA1	5	4	6	5	114.9	105.6
MA2	7	4	5	5	78.5	25.0
MA3	4	5	9	6	109.3	0.0
MA4	5	5	7	6	94.3	86.1
MA5	4	5	9	6	85.1	0.0
MA6	5	5	7	5	71.9	47.2
MA7	6	5	6	5	74.7	58.3
YU1	4	5	6	5	98.4	72.2
YU2	6	6	7	6	87.7	36.1
YU3	5	7	7	6	82.0	36.1
At1	3	3	5	4	98.6	97.2
At2	3	3	4	3	106.1	113.9
Mean	**4.8**	**5.6**	**6.9**	**5.7**	**92.1**	**44.8**
l.s.d	ns	2.5**	2.2**	1.9**	ns	63.7

w.a.c.e.: Weeks after crop emergence. ** Highly significant (P<0.01).
Damage rating (1-9 scale): 1=no damage symptoms; 9= complete damage, plants dead
ns: not significant

3.3.8 Correlation between *Striga* parameters and sorghum performance parameters

There was a significantly (P<0.05) negative correlation between all the *Striga* parameters measured and the number of sorghum panicles formed (Table 3.8). This shows that panicle formation in sorghum was significantly affected by *Striga* infestation. There was a significantly (P<0.05) positive correlation between *Striga* numbers and severity with sorghum damage, indicating that the more the *Striga* emergence, the more the sorghum was damaged. However, this relationship was only significant (P<0.05) at 7 weeks after crop emergence (early stages of crop growth).

Table 3.8: Correlation coefficients between *Striga* parameters and sorghum performance parameters

Striga parameters	Sorghum parameters	
	No. of panicles formed	Average damage score
Striga number (7 w. a.c.e)	-0.2194*	0.2135*
Striga number (9 w. a.c.e)	-0.2033*	0.1220
Striga number (11 w a.c.e)	-0.1879*	0.0705
Average *Striga* emergence	-0.2139*	0.1187
Striga vigour (7 w.a.c.e)	-0.1440	0.0650
Striga vigour (9 w.a.c.e)	-0.1493	0.0375
Striga vigour (11 w.a.c.e)	-0.0617	-0.0814
Average *Striga* vigour	-0.1234	-0.0105
Striga severity (7 w.a.c.e)	-0.1730*	0.1723*
Striga severity (9 w.a.c.e)	-0.1904*	0.1365
Striga severity (11 w.a.c.e)	-0.1845*	0.0736
AUSNPC (9 w. a.c.e)	-0.2179*	0.1449
AUSNPC (11 w. a.c.e)	-0.2034*	0.10260
Mean AUSNPC	-0.2113*	0.1205
AUSVPC (9 w. a.c.e)	-0.1929*	0.1413
AUSVPC (11 w. a.c.e)	-0.1991*	0.1150
Mean AUSVPC	-0.1990*	0.1265

* Significant (P<0.05). w.a.c.e.: Weeks after crop emergence.

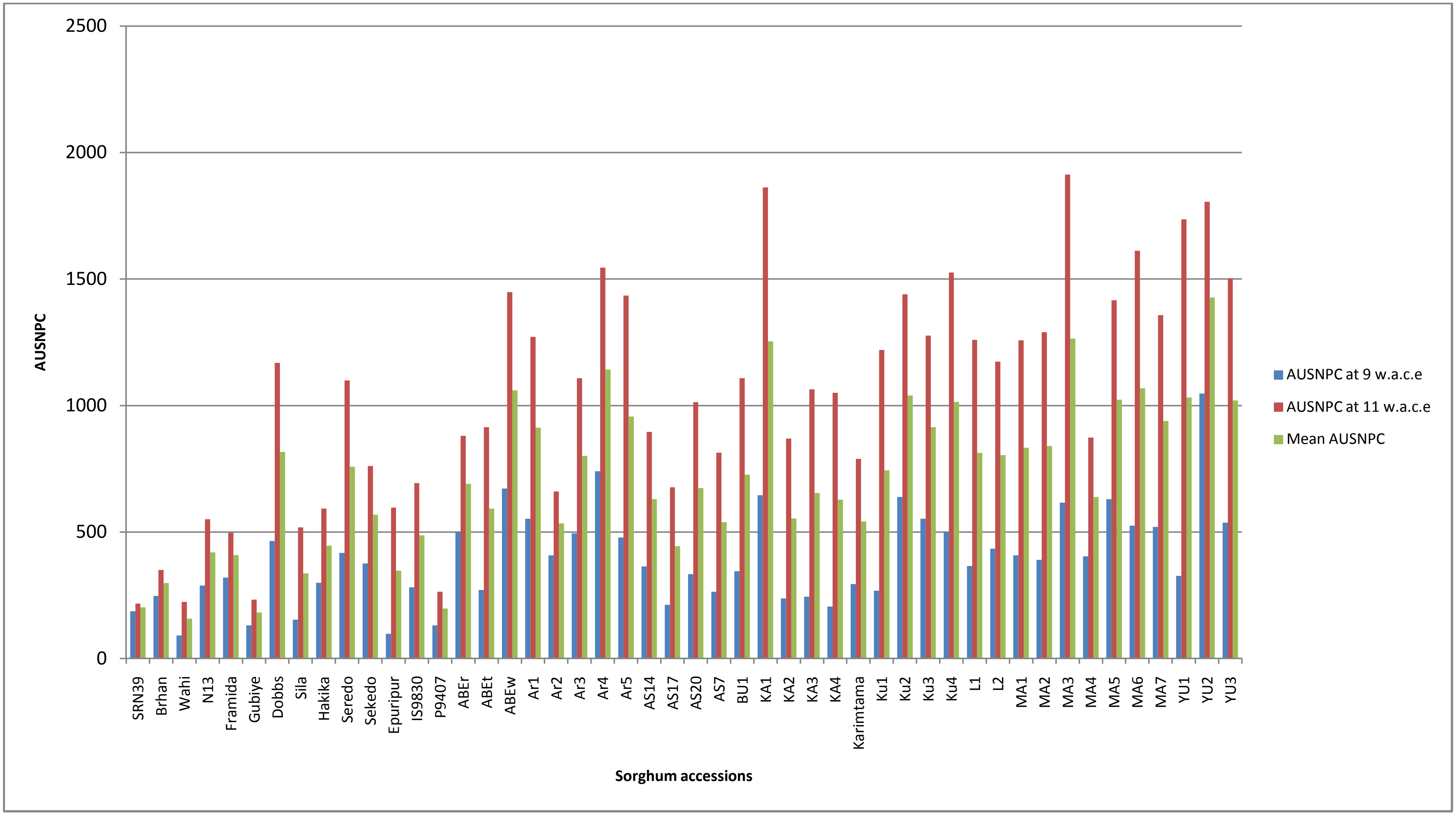


Figure 3.1: The area under *Striga* number progress curve (AUSNPC) on different sorghum accessions in 2009 season

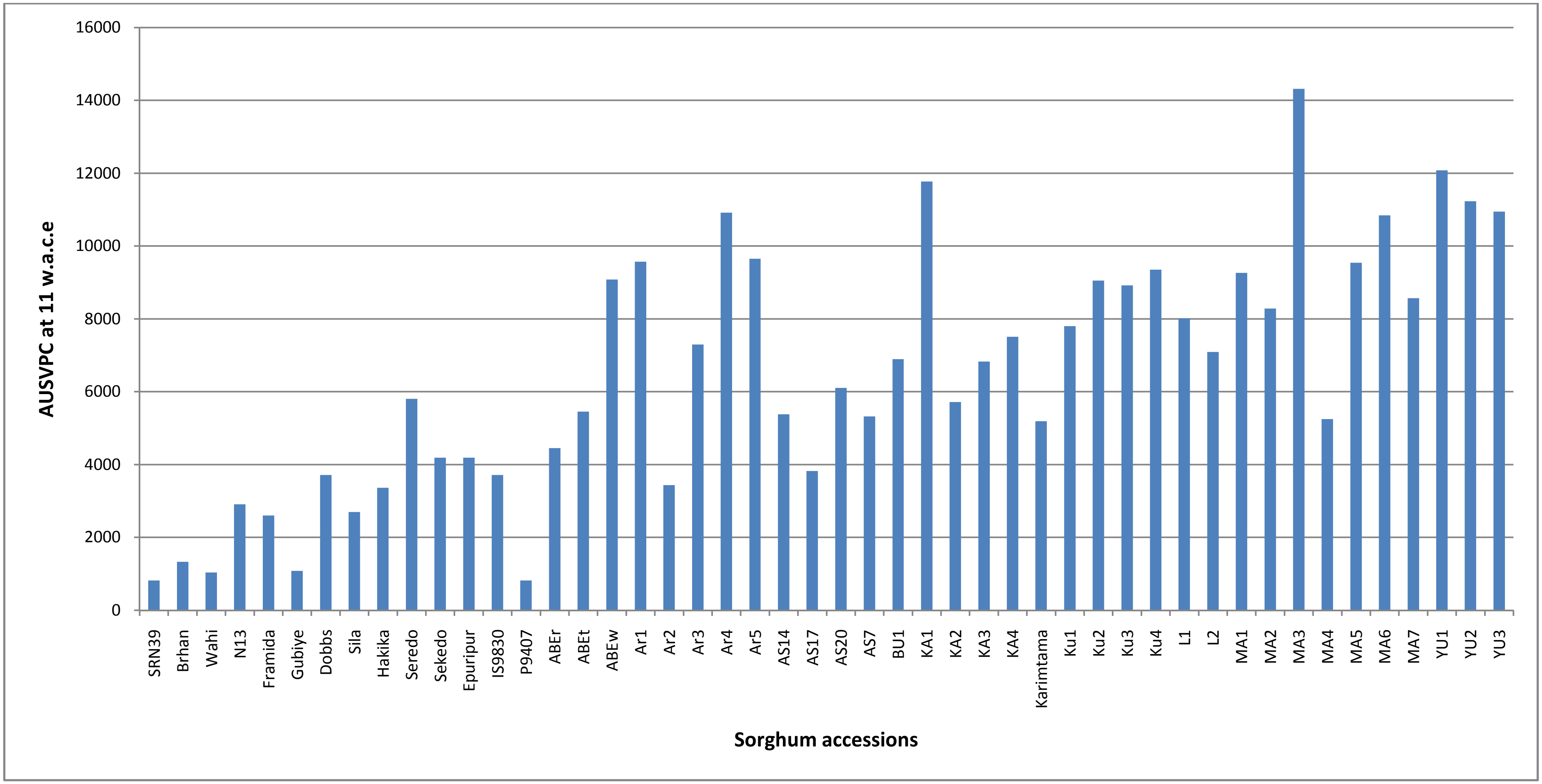


Figure 3.2: Area under *Striga* severity progress curve (AUSVPC) on different sorghum accessions in 2009 season

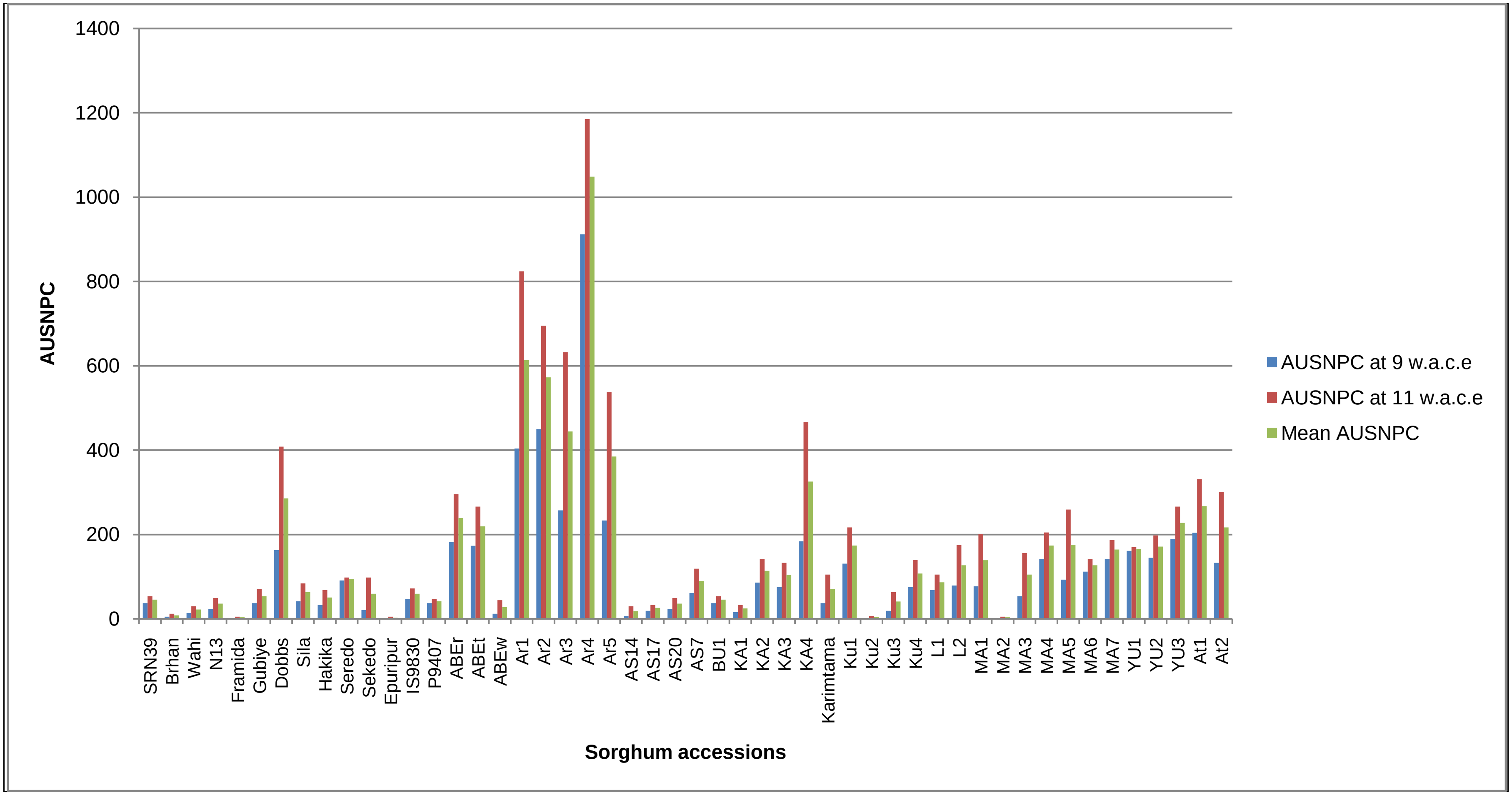


Figure 3.3: The area under *Striga* number progress curve (AUSNPC) on different sorghum accessions in 2010 season

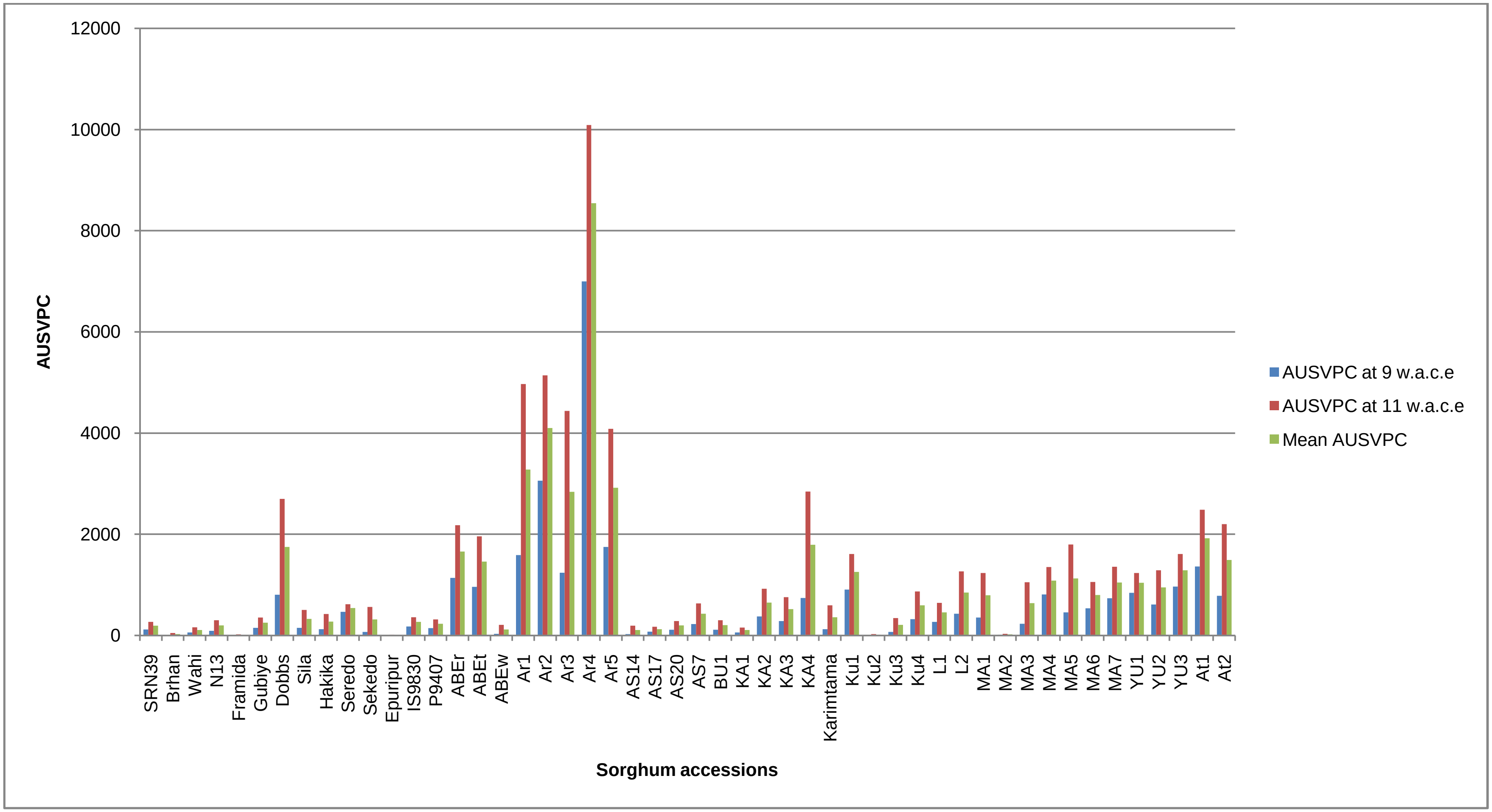


Figure 3.4: The area under *Striga* severity progress curve (AUSVPC) on different sorghum accessions in 2010 season

3.4 Discussion

3.4.1 Phenotypic and genotypic variability among the sorghum accessions for *Striga* resistance

Both phenotypic and genotypic factors contributed significantly to the variability observed among the African sorghum accessions with respect to *Striga* resistance and sorghum crop performance. The fact that genotypic factors were significant indicates that improvement can be achieved through selection but techniques that could minimise the environmental variance need to be devised and employed in order to improve on heritability and genetic advance. Basing on the genotypic coefficient of variation, broad sense heritability estimates and genetic advance, selection based on area under *Striga* severity progress curve (AUSVPC), area under *Striga* number progress curve (AUSNPC) and individual *Striga* emergence counts could be more useful. Tesfaye (2002) recorded GA values ranging from 1.1% to 56.5% for 17 characters in *Vernonia galamensis*. In the present study, the GA values for AUSVPC, AUSNPC and *Striga* emergence were 24.9%, 27.4% and 24.3% respectively. This indicates that reasonable genetic advance can be achieved when suitable selection criteria are employed. Tesfaye (2002) further reasoned that improvement efficiency is related to the magnitude of the genetic coefficient of variability (GCV), heritability and genetic advance (GA). Presently, the above traits with high GA values also correspondingly have moderate GCV values hence suggesting that improvement could be achieved through selection based on these traits.

3.4.2 *Striga* emergence

Striga emergence in the field is not only influenced by host genotypic differences but by a number of other factors such as variation of natural infestation, complex interactions between the parasite and the host as well as edaphic and environmental factors (Kroschel, 2001; Ejeta et al., 1991). In this particular study, an effort was made to cater for the above factors by infesting with additional *Striga* seed (augmentation), screening in the same field for two seasons, using a balanced lattice experimental design and replicating three times in each season. During this study, it was observed that in the early stages of infection, in this case seven weeks after crop emergence, some sorghum genotypes had either few or no *Striga* plants emerged on them while others had considerably high numbers of *Striga* plants emerged. The first level of interaction between *Striga* and its host is stimulation of *Striga* seed germination by the host root exudates (Berner et al., 1997; Ejeta et al., 1993; Hauk et al., 1992; Muller et al., 1992). This therefore indicates that the sorghum genotypes that had few or no *Striga* plants emerged on them at early stages of infection probably produced very little of *Striga* seed germination stimulants. These genotypes could be characterized as resistant with the possible mechanisms being low germination stimulant production and low haustoria initiation. In this study, these genotypes were SRN39, Brhan, Framida, Gubiye, Wahi, P9407 and Hakika.

It was also observed in this study that, while some sorghum genotypes experienced a progressive increase in *Striga* emergence from the seventh week to the eleventh week of crop growth, other genotypes showed a reduction in emerged *Striga* plants particularly between the ninth and eleventh weeks, and others maintained constantly low numbers. For successful and sustainable parasitism to exist, a series of other interactions occur between *Striga* and its host beyond emergence and attachment. These interactions should ensure that the parasite continues to derive its nourishment from the host and there should be no incompatible reactions from the host. A reduction in the number of emerged *Striga* plants on some sorghum genotypes or constant maintenance of low numbers meant that the parasitism was not progressing. This points to the existence of some incompatible reactions from the hosts and therefore these sorghum genotypes could also be classified as resistant with incompatibility being the possible mechanism of resistance. In this study, these genotypes were SRN39, Brhan, Framida, N13, Gubiye, Hakika, Seredo and IS9830 and some landraces such as Ar2. These observations are in agreement with those made by Haussmann et al. (2000b), Grenier et al. (2001), Mohamed et al. (2003), Omanya et al. (2004) and Ejeta et al. (2007). In these investigations, sorghum genotypes such as Framida, SRN39 and N13 were reported to exhibit some incompatible response to *Striga* infestation. According to Ejeta et al. (2007), the overall effect of an incompatible reaction is that a small portion of attached parasites proceed to slowly establish on the resistant host, but most of the attached show diminished growth and delayed emergence above ground. It can be noted that most of the sorghum genotypes listed above had also shown low Striga emergence. This could be a sign of the existence of more than one mechanism of resistance. These genotypes might be possessing low germination stimulant production, low haustoria initiation as well as incompatible reactions to *Striga* infestation.

3.4.3 *Striga* vigour and severity

As in *Striga* numbers, *Striga* vigour and severity are a reflection of the level of successful parasitism. The *Striga* vigour score offers a quick, effective, non-destructive approximation of *Striga* development and average biomass in each field plot by taking into account morphological features of the *Striga* plant such as height and branching (Omanya et al., 2004). Highly vigorous

Striga plants indicate successful parasitism where the parasite is deriving adequate nourishment from its host with probably no incompatible reactions coming from the host. This could be what happens in susceptible sorghum varieties. Less vigorous *Striga* plants probably indicate that the parasitic weed is not deriving adequate nourishment from its host and there could be some incompatible reactions from the host. This could be what happens in some resistant sorghum genotypes. From this study, the genotypes that maintained low *Striga* vigour were SRN39, Brhan, Framida, Gubiye and P9407. The recurrence of these same genotypes as resistant under different measures of *Striga* resistance probably points to a fact that the genotypes are strongly resistant to *S. hermonthica*.

Striga severity on the other hand, is a product of *Striga* number and vigour, which is an indication of the severity of infestation. The *Striga* severity index provides a proportional estimate of the total *Striga* biomass in the plot (Omanya et al., 2004). According to these authors, *Striga* severity index is highly heritable and therefore provides a reliable screening trait. High *Striga* severity shows successful parasitism in susceptible genotypes while low severity indicates low or unsuccessful parasitism, which probably happens in resistant genotypes. In this study, SRN39, Brhan, P9407 and Gubiye showed low *Striga* severity, indicating resistance in these genotypes. Additionally, SRN39 and Brhan experienced a reduction in *Striga* severity between the ninth and eleventh weeks, further pointing to the existence of some incompatibility reaction in the genotypes. In addition the same genotypes were showing low *Striga* severity and more so even a reduction in severity with time. This could strengthen the speculation of the existence of resistance to *S. hermonthica* in these sorghum genotypes.

3.4.4 The area under *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC)

The AUSNPC and AUSVPC were derived from individual emerged *Striga* counts and *Striga* severity indices respectively. Omanya et al. (2004) and Haussmann et al. (2000b) concurrently found that the AUSNPC and AUSVPC were under strong genetic control and therefore offered useful measures of progressive *Striga* development in the field and therefore reliable screening parameters. This study found the sorghum genotypes SRN39, Wahi, Gubiye, P9407, Framida and Brhan to show both low AUSNPC and AUSVPC. Since these parameters were previously found to be under strong genetic control, these sorghum genotypes may offer useful sources of field resistance to *Striga*.

3.4.5 Relationship between *Striga* resistance parameters and sorghum performance parameters

In this study, a significantly negative correlation was observed between all the *Striga* parameters measured and number of sorghum panicles formed. This shows that panicle formation in sorghum was significantly reduced by *Striga* infestation. Kroschel (2001) indicates that under severe *Striga* infestation, panicle formation may either be reduced or completely failed in sorghum. A significant positive correlation was observed between *Striga* infestation and sorghum damage during the early stages of crop growth (in this case 7 weeks after crop emergence). It has been widely observed that *Striga* inflicts most of its damage to its hosts before it emerges above ground. The present findings seem to support the previous observations by a significant positive correlation being observed between *Striga* infestation and sorghum damage at early stages of growth. This correlation was not significant at later stages of sorghum growth.

3.5 Conclusions

- Both phenotypic and genotypic factors contributed significantly to the variability observed among the African sorghum accessions with respect to *Striga* resistance and sorghum crop performance indicating that *Striga* resistance can be improved through selection.
- Heritability estimates for *Striga* resistance traits were generally low. This indicates that environmental factors largely contributed to the observed phenotypic variation in *Striga* resistance among the sorghum accessions. It therefore implies that when evaluating sorghum genotypes for *Striga* resistance, techniques that minimise environmental effects need to be employed in order to improve on heritability.
- The GCV and GA values indicate that genetic gain for *Striga* resistance can be achieved by selection based on AUSVPC, AUSNPC and *Striga* emergence.
- Basing on AUSNPC, AUSVPC and individual *Striga* counts, vigour and severity indices, it can be concluded that the sorghum genotypes SRN39, Brhan, Framida, Gubiye, Wahi, P9407 and N13 showed resistance to *Striga hermonthica* in Eastern Uganda. These genotypes could therefore act as useful sources of resistance to *Striga* and be used as donor parents in breeding for *Striga* resistant sorghum varieties in Uganda.

- The significantly negative correlation between all the *Striga* parameters measured and number of panicles formed in sorghum indicates that panicle formation in sorghum was significantly reduced due to *Striga* infestation.
- The significant positive correlation between *Striga* infestation and sorghum damage at 7 weeks after crop emergence (early stages of crop growth) re-affirms the fact that *Striga* inflicts most of its damage to sorghum even before it emerges above ground.

References

Berner, D.K., M.D. Winslow, E.A. Award, K.F. Cardwell, D.R. Mohan Raj, and S.K. Kim. 1997. *Striga* research methods: A manual. 2nd ed. International Institute of Tropical Agriculture, Ibadan, Nigeria.

Ejeta, G., L.G. Butler, and A.G.T. Babiker. 1993. New approaches to the control of *Striga*: *Striga* research at Purdue University. Agricultural Experiment Station, Purdue University, USA.

Ejeta, G., L.G. Butler, D.E. Hess, and R.K. Vogler. 1991. Genetic and breeding strategies for *Striga* resistance in sorghum, pp. 539-544, *In* J. K. Ransom, et al., (eds.) Proceedings of the Fifth International Symposium on Parasitic Weeds, Nairobi, Kenya.

Ejeta, G., P. Rich, and A. Mohamed. 2007. Dissecting a complex trait to simpler components for effective breeding of sorghums with high level of resistance to *S. hermonthica*, *In* G. Ejeta and J. Gressel, (eds.) International Symposium on Integrating New Technologies for *Striga* Control: Towards Ending the Witch-hunt, Addis Ababa, Ethiopia.

Ezeaku, I.E. and S.C. Gupta. 2004. Development of sorghum populations for resistance to *Striga* hermonthica in the Nigerian Sudan Savannah. African Journal of Biotechnology 3(6): 324-329.

Grenier, C., P.J.Rich, A. Mohamed, A. Ellicot, C. Shaner, and G. Ejeta. 2001. Independent inheritance of LGS and IR genes in sorghum p.220-223. In A. Feretal. (ed). Proc. 7th Int. Parasitic Weed Symp., Nantes, France. 5th – 8th June 2001. Universite de Nantes, France.

Hauk, C., S. Muller, and H. Shildknecht. 1992. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a genuine host plant. Journal of plant physiology 139:474-478.

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, H.G. Welz, and H.H. Geiger. 2000b. Improved methodologies for breeding *Striga* resistant sorghums. Field Crops Research 66(3):195-211.

Kroschel, J., (ed.) 2001. A technical manual for parasitic weed research and extension. Kluwer Academic Publishers, 3300 AA Dordrecht, Netherlands.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43:1320-1324.

Mohamed, A.H. 2002. Identification and characterization of genetic variants in sorghum for specific mechanisms of *Striga* resistance. PhD thesis, Purdue University, USA.

Muller, S., C. Hauck, and H. Schildknecht. 1992. Germination stimulants produced by *Vigna unguiculata* (Walp.) cv Saunders,upright. Journal of plant growth regulation 11:77-84.

Omanya, G.O., B.I.G. Haussmann, D.E. Hess, B.V.S. Reddy, M. Kayentao, H.G. Welz, and H.H. Geiger. 2004. Utility of indirect and direct selection traits for improving *Striga* resistance in two sorghum recombinant inbred populations. Field Crops Research 89(2-3):237-252.

Payne, R.W., D.A. Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2011. An introduction to GenStat for Windows (14th edition). VSN International, Hemel, Hemstead, UK.

Rodenburg, J., L. Bastiaans, E. Weltzien, and D.E. Hess. 2005. How can field selection for *Striga* resistance and tolerance in sorghum be improved? Field Crops Research 93:34-50.

Showemimo, F.A., and C.A. Kimbeng. 2005. Genetic studies of sorghum cultivars under *Striga* infestation in northern guinea savannah of Nigeria. Agricultura Tropica Et Subtropica 38(2): 91-96.

Tesfaye, B. 2002. Genotypic and phenotypic variability in *Vernonia galamensis* germplasm collected from Eastern Ethiopia. Journal of Agricultural Science 139: 161-168.

CHAPTER FOUR: COMBINING ABILITY FOR *STRIGA* RESISTANCE AND SORGHUM YIELD IN NEW SORGHUM GENOTYPES IN UGANDA

Abstract

A study was carried out to determine the gene action effects of selected sorghum parental lines and their crosses for *Striga* resistance and yield. Four *Striga* resistant sorghum lines used as males were crossed to four locally adapted and high yielding sorghum lines used as females in a North Carolina II mating design. The F_1s were advanced up to F_3 generation through selfing and bulking before subjecting to field evaluation. Field evaluation was done in three sites. Significant genotypic differences were found among the new sorghum genotypes for area under *Striga* number progress curve (AUSNPC), area under *Striga* severity progress curve (AUSVPC), *Striga* vigour, sorghum head length and plant height. The sorghum parental lines: Brhan, SRN39, Hakika and Sekedo consistently had negative GCA effects for AUSNPC and AUSVPC, while SRN39 and Hakika additionally had negative GCA effects for *Striga* vigour. This indicates that these parental lines were effective in transferring *Striga* resistance into their progeny. The new genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108, SRS2908, SRS2609, SRS609 and SRS1708 had negative SCA effects for AUSNPC, AUSVPC and *Striga* vigour meaning that they were resistant to *Striga*. Parental lines: Sekedo, Brhan, Framida and Hakika had positive GCA effects for head length, meaning that they increased head length in their crosses. The genotypes: SRS3408, SRS5309, SRS1608 and SRS2908 derived from the above parents had the longest heads, which were on average, 20% longer than their parents. The mean values for grain yield showed that the genotypes: SRS609, SRS1408, SRS2608 and SRS3408 were the highest yielders and yielded 2951-4028 kg ha^{-1}, which was 11-51% better than the yield of the highest yielding parent, Sekedo (2659 kg ha^{-1}) under the non *Striga* environment. The parental lines; Sekedo, Brhan and Framida had positive GCA effects for grain yield indicating that they could act as sources of genes for grain yield increase. The specific crosses; SRS609, SRS4609 and SRS2908 had large positive SCA effects for grain yield. The relative contributions of GCA effects to the observed genotypic variances were 80.5%, 43.3%, 65%, 92.6% and 53.2% for AUSNPC, AUSVPC, *Striga* vigour, sorghum head length and plant height respectively. This shows that additive gene action was important in controlling *Striga* resistance, sorghum head length and plant height in the present sorghum populations. It is

therefore suggested that selection could be effectively employed to improve *Striga* resistance, sorghum head length and plant height in these genetic materials.

4.1 Introduction

Striga is an obligate parasitic weed that significantly limits cereal crop production in most of Sub-Saharan Africa. In Uganda, sorghum productivity is severely affected by *Striga hermonthica*, which causes yield losses ranging from 60-100% in individual farms (Olupot et al., 2005; Ebiyau and Oryokot, 2001; Akwang et al., 1998, 1999). Crop damage due to *Striga* is most severe where drought and low soil fertility already limit crop productivity (Mohamed et al., 2003; Parker and Riches 1993). Control of *Striga* is complicated due to its enormous seed reserve in the soil that can be triggered to germinate and damage crops even before the *Striga* plants emerge above ground (Patrick et al., 2004; Mohamed et al., 2003).

A majority of sorghum growers in Uganda are subsistence farmers who are unable to adopt expensive chemical control or use of modern cultural practices. The use of *Striga* resistant and high yielding sorghum cultivars is perhaps the most feasible means that could be used by such farmers to minimize crop losses due to *Striga* (Patrick et al., 2004; Mohamed et al., 2003; Ejeta et al., 1997). Omanya et.al. (2004) further advise that, in order for *Striga* resistance to be useful as a control option, the resistance should be incorporated in locally adapted and productive germplasm. Elsewhere, significant progress has been made in breeding for *Striga* resistance in sorghum (Omanya et al., 2004; Mohamed, 2002; Haussman et al., 2000a, 2000b). However, there has been no deliberate effort to breed for *Striga* resistance in sorghum in Uganda.

The concept of combining ability is useful to study and compare the performance of various lines in hybrid combinations (Mutengwa et al., 1999). It provides the plant breeder with important genetic information to enable development of effective breeding strategy. The North Carolina II mating design is a factorial mating design whereby each member of a group of parents designated as males is mated to each member of another group of parents used as females. The design is used to estimate genetic variances and to evaluate inbred lines for combining ability (Stuber, 1980). The analysis of variance for the North Carolina II mating design gives the magnitude of significance of General Combining Ability (GCA), Specific Combining Ability (SCA). The parental main effects (males and females) and their interactions are estimated, as independent GCA effects attributable to males and females respectively, while the interaction effects estimate the SCA effects.

Omanya et al. (2004) found highly significant genetic variation for a series of *Striga* resistance traits when studying *Striga* resistance in two recombinant inbred populations of 456 $F_{3:5}$ sorghum lines. These findings indicate that it is possible to improve *Striga* resistance in sorghum using conventional breeding techniques. There is need to study gene action responsible for *Striga* resistance and sorghum yield parameters in new sorghum genotypes in order to design the most appropriate selection techniques for improvement of *Striga* resistance and sorghum yield. Therefore, the objective of the present study was to determine the gene action responsible for *Striga* resistance and sorghum yield parameters in selected sorghum parental lines and their crosses in Uganda. The hypothesis being tested was that additive genetic effects were not important in controlling *Striga* resistance and sorghum yield in the new sorghum genotypes. It is expected that the findings of this study will guide the sorghum breeding programme in Uganda in future to decide on which parental sorghum lines to use, the specific crosses to advance in future generations, and the best selection techniques to employ when breeding for *Striga* resistant and high yielding sorghum varieties.

4.2 Materials and methods

4.2.1 Development of the new sorghum genotypes

Four *Striga* resistant sorghum lines used as males were crossed with four locally adapted and high yielding sorghum lines used as females according to the North Carolina II mating design. The *Striga* resistant lines were Brhan, N13, SRN39 and Framida. Brhan was received from the International Sorghum and Millets Collaborative Research Support Programme (INTSORMIL CRSP) (courtesy of Prof. Gebisa Ejeta), while N13, SRN39 and Framida were received from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (courtesy of Dr. Mary Mgonja and Mr.Eric Manyasa). The locally adapted lines were Sekedo, Hakika, Dobbs and Karimtama, picked from the local breeding programme at the National Semi-Arid Resources Research Institute, Serere. Crossing was manually done at Serere (33^0 27'E, 1^0 31'N; 1000 metres above sea level) using hand emasculation and pollination at the end of 2008. Seed of the successful crosses were harvested and planted in March 2009 to raise the F_1 plants. The

F_1s were advanced up to F_3 generation through selfing and bulking all the seed of each cross in order to raise enough seed for field evaluation.

4.2.2 Field evaluation

Field evaluation was carried out during the second rain season (September-December) of 2010 in three sites, Serere (on-station under no *Striga* infestation), and Kumi and Bukedea (under *Striga* infestation). The evaluation in Kumi and Bukedea was done in farmers' fields that were naturally infested with *Striga hermonthica*. The entries consisted of 16 crosses and their 8 parents totalling 24. The 24 entries were laid out in a 12x2 simple lattice design replicated three times in each site. The entries were planted in three row plots measuring 4m in length and plots were separated by 1m paths. The spacing was 60cm between rows and 20cm between hills, and thinned two weeks after crop emergence to leave two plants per hill (giving 132 plants per plot). At Serere, the experiment was weeded three times while in Kumi and Bukedea, the experiment was weeded two times (at two and four weeks after crop emergence, before *Striga* started to emerge).

4.2.3 Data collection and analysis

The data collected were number of emerged *Striga* plants in each plot, *Striga* vigour, sorghum damage, plant height at maturity, head length at maturity and grain yield. The number of emerged *Striga* plants was determined by physically counting all the emerged *Striga* plants in each plot. Two *Striga* counts were taken at two weeks interval starting 9 weeks after crop emergence. *Striga* vigour was scored using a scale of 0-9 as described by Haussmann et al. (2000b) and Kroschel (2001), where 0= no emerged *Striga* plants and 9= very vigorous *Striga* plants (average height >40cm with >10 branches). Scoring for *Striga* vigour was done each time the counts were taken. Sorghum damage was rated on a 1-9 scale as described by Ezeaku and Gupta (2004), where 1= normal sorghum growth with no visible symptoms of *Striga* damage, and 9= virtually all leaf area is scorched with two-thirds or more reduction in plant height, no useful panicles formed, plants dead or nearly dead. Sorghum damage was rated at 11 weeks after crop emergence. Sorghum plant height and head length were measured at maturity by measuring ten plants selected randomly in each plot using a tape measure and ruler, respectively. The *Striga* data were recorded in Kumi and Bukedea while the sorghum yield data were collected at Serere and Bukedea sites. Sorghum yield in Kumi was severely affected by midge infestation and it was therefore considered unreasonable to record it. In addition to the above parameters, two indices were calculated that give a measure of the overall *Striga* growth and development throughout the season; area under *Striga* number progress curve (AUSNPC) and area under *Striga* severity progress curve (AUSVPC) (Haussmann et al., 2000a; Rodenburg et al., 2005). The AUSNPC was calculated as follows:

$$\text{AUSNPC} = \sum_{i=0}^{n-1}\left[\frac{Y_i + Y(i+1)}{2}\right]\{t(i+1) - t_i\}$$

Where n is the number of *Striga* assessment dates, Y_i the *Striga* number at the *i*th assessment date, t_i the days after planting at the *i*th assessment date, t the days after planting to *Striga* emergence minus 1, and Y is 0. The AUSVPC was calculated likewise, with Y_i representing the *Striga* severity score. *Striga* severity score is a product of the *Striga* vigour and the number of *Striga* plants at each assessment date, as shown below:

Striga severity at *i*th assessment date = *Striga* vigour x *Striga* number at *i*th date

Data were analyzed using REML procedure in Genstat release 14.1 statistical package (Payne et al., 2011) using the following fixed effects model:

$$Yijkl = \mu + s_i + g_i + m_k + f_l + mf_{kl} + s_i{*}m_k + s_i{*}f_l + s_i{*}mf_{kl} + eij_{kl}$$

Where: Yijk = observed response of the genotypes;
μ = overall population mean;
s_i = effect of the ith environment;
g_i = effect of the i_{th} cross genotype;
m_k = effect of the kth male parent;
f_l = effect of the lth female parent;
mf_{kl} = interaction effect of the kth male and the lth female parents;
$s_i{*}m_k$ = interaction effect of the ith environment and the kth male;
$s_i{*}f_l$ = interaction effect between the ith environment and lth female;
$si{*}mf_{kl}$ = interaction effect of the ith environments and the interaction effects between the kth male and the lth female parents; and
eij_{kl} is the experimental error.

From the analysis of variance, where the variance due to the crosses was significant, this variance was partitioned into male and female parent main effects giving two independent estimates of GCA effects, while the male × female interaction estimated the SCA effects, according to the procedure described by Hayman (1954). The standard error (SE) and standard error of a difference (SED) for male and female GCA effects were calculated according to Dabholkar (1992). The relative contribution of GCA effects to genotypic variance was calculated using the formula below:

$$\% \text{ GCA} = \frac{SSGCA_m + SSGCA_f}{SSGCA_m + SSGCA_f + SSSCA} \text{ X } 100$$

Where: $SSGCA_m$ = sums of squares for male GCA; $SSGCA_f$ = sums of squares for female GCA and SSSCA = sums of squares for the SCA effects.

4.3 Results

4.3.1 The area under *Striga* number progress curve (AUSNPC)

The genotypic differences for AUSNPC were highly significant ($P<0.001$) among the new genotypes of sorghum (Table 4.1). Both the male and female parent general combining ability (GCA) effects contributed significantly to the genotypic differences with the male GCA effects being more significant than the female GCA effects. This indicates that additive genetic effects were important in the expression of AUSNPC. The interaction between the male and female GCA effects with environment, and the specific combining ability (SCA) effects were not significant. Also, while the individual environmental effects were significant ($P<0.005$), the genotype by environment interaction effects were not significant. Further analysis revealed that the parental lines: Brhan, SRN39, Hakika and Sekedo had negative GCA effects indicating that they contributed to reduction of AUSNPC in their progeny (Table 4.2). The ratio of female GCA effects to male GCA effects was less than one indicating that the effects of the paternal genotypes were more important than the maternal effects in AUSNPC. The crosses: Brhan x Dobbs (SRS3108), Brhan x Karimtama (SRS4609), N13 x Sekedo (SRS609), N13 x Dobbs (SRS1708), N13 x Karimtama (SRS2609), SRN39 x Sekedo (SRS3408), SRN39 x Hakika (SRS2408) and Framida x Hakika (SRS1608) had negative SCA effects meaning that these specific crosses reduced the AUSNPC. From the mean values shown in Figure 4.1, it can be seen that genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108 and SRS2908 had the lowest values for AUSNPC, which were 9-31% lower than the value for the most resistant parental line (Brhan), and 58-68% lower than the value for the most susceptible parent (N13). Therefore, based on the AUSNPC, SRS1608, SRS3408, SRS2408, SRS4609, SRS3108 and SRS2908 could be classified as resistant to *Striga hermonthica* in the field.

Table 4.1: Mean squares for *Striga* resistance parameters[a] in sorghum genotypes for Bukedea and Kumi sites

Source of variation	df	AUSNPC	AUSVPC	*Striga* vigour
Environment	1	1.1218**	1.0946*	0.111242***
Genotype	15	0.4430***	1.0391***	0.018111*
GCA_m	3	1.0700***	1.4094***	0.017535
GCA_f	3	0.3473*	0.6552*	0.018994*
SCA	9	0.1143	0.9008***	0.006567
Genotype x Environment	15	0.1692	0.1028	0.008109
GCA_m x Environment	3	0.1059	0.1020	0.004240
GCA_f x Environment	3	0.0492	0.0932	0.010925
SCA x Environment	9	0.2304	0.1062	0.008460
Error	46	0.1182	0.2155	0.008386
$MSGCA_f/MSGCA_m$		0.32	0.46	1.08
% GCA to genotype ss		80.50	43.30	65.00

[a] analysis based on transformed data. GCA_m = GCA for males. GCA_f = GCA for females

***, **, * Data significant at $P<0.001$, $P<0.005$ and $P<0.05$ respectively

MS = Mean square. ss = sums of squares

Table 4.2: GCA effects for male and female sorghum parents for selected *Striga* resistance parameters

	AUSNPC	AUSVPC	*Striga* vigour
Male parents			
Brhan	-0.215**	-0.131	0.0095
N13	0.205**	0.312**	0.0280
SRN39	-0.146	-0.241**	-0.0363
Framida	0.155	0.061	-0.0013
SE	0.0729	0.09	0.01881
SED	0.1031	0.1273	0.0266
Female parents			
Sekedo	-0.048	-0.053	0.0287
Hakika	-0.145	-0.209	-0.0361
Dobbs	0.071	0.106	-0.0068
Karimtama	0.122	0.155	0.0142
SE	0.0729	0.09	0.01881
SED	0.1031	0.1273	0.0266

** Significant at P<0.001

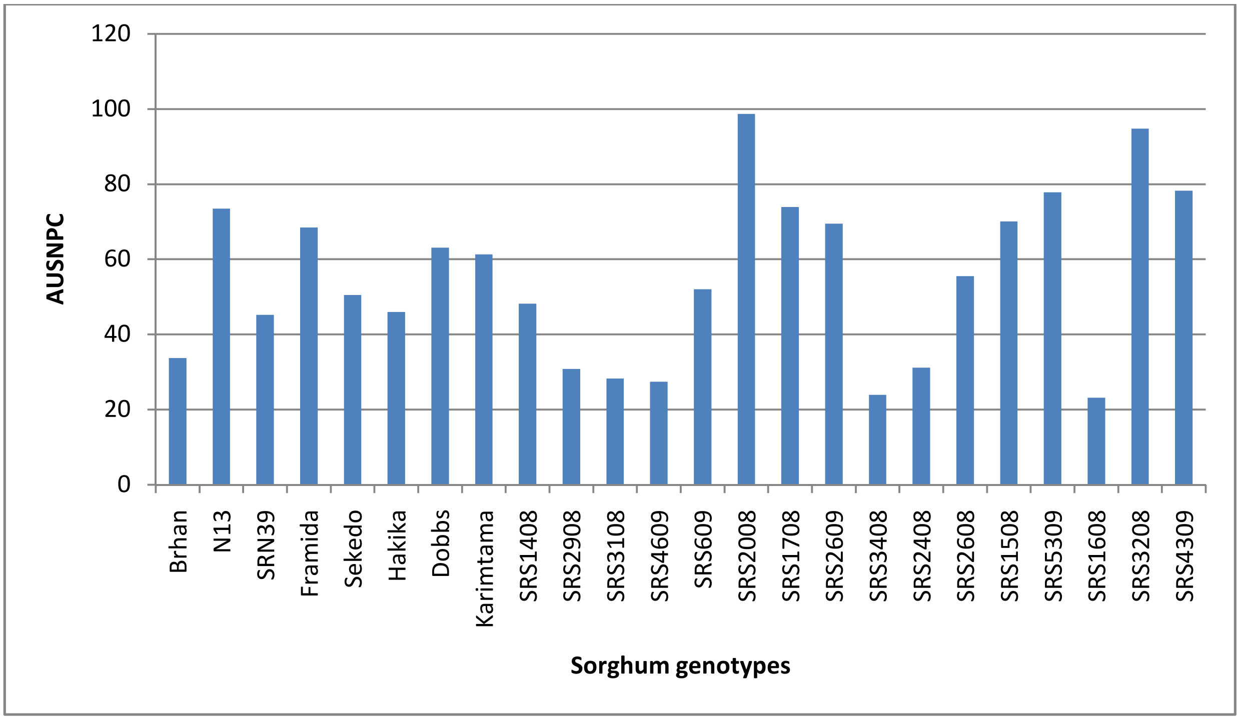


Figure 4.1: Mean values for AUSNPC on sorghum parental lines and their crosses

4.3.2 The area under *Striga* severity progress curve (AUSVPC)

Genotypic differences for AUSVPC were also highly significant (P<0.001) among the new sorghum genotypes (Table 4.1). The GCA effects for both male and female parents and the SCA effects of the crosses all contributed significantly to the genotypic differences, with the GCA effects for the males and SCA effects of the crosses being significant. The environmental effects were significant but the genotype by environment interaction effects were not significant for AUSVPC. The same parental lines; Brhan, SRN39, Hakika and Sekedo had negative GCA effects for AUSVPC indicating that they contributed to reduction of AUSVPC in their crosses (Table 4.2). The ratio of female GCA effects to male GCA effects was less than one indicating that the effects of the paternal genotypes were more important than the maternal effects in AUSVPC.Crosses; Brhan x Dobbs (SRS3108), Brhan x Karimtama (SRS4609), N13 x Dobbs (SRS1708), N13 x Karimtama (SRS2609), SRN39 x Sekedo (SRS3408) and Framida x Hakika (SRS1608) had reduced AUSVPC. Figure 4.2 shows the mean values for the AUSVPC. It is observed that the same genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108 and SRS2908 had the lowest values for AUSVPC. Their values ranged 16-89% lower than the value for the most resistant parental line (Brhan), and 69-96% lower than the value for the most susceptible parent (N13). Therefore, also based on the AUSVPC, SRS1608, SRS3408, SRS2408, SRS4609, SRS3108 and SRS2908 can be classified as resistant to *Striga hermonthica* in the field.

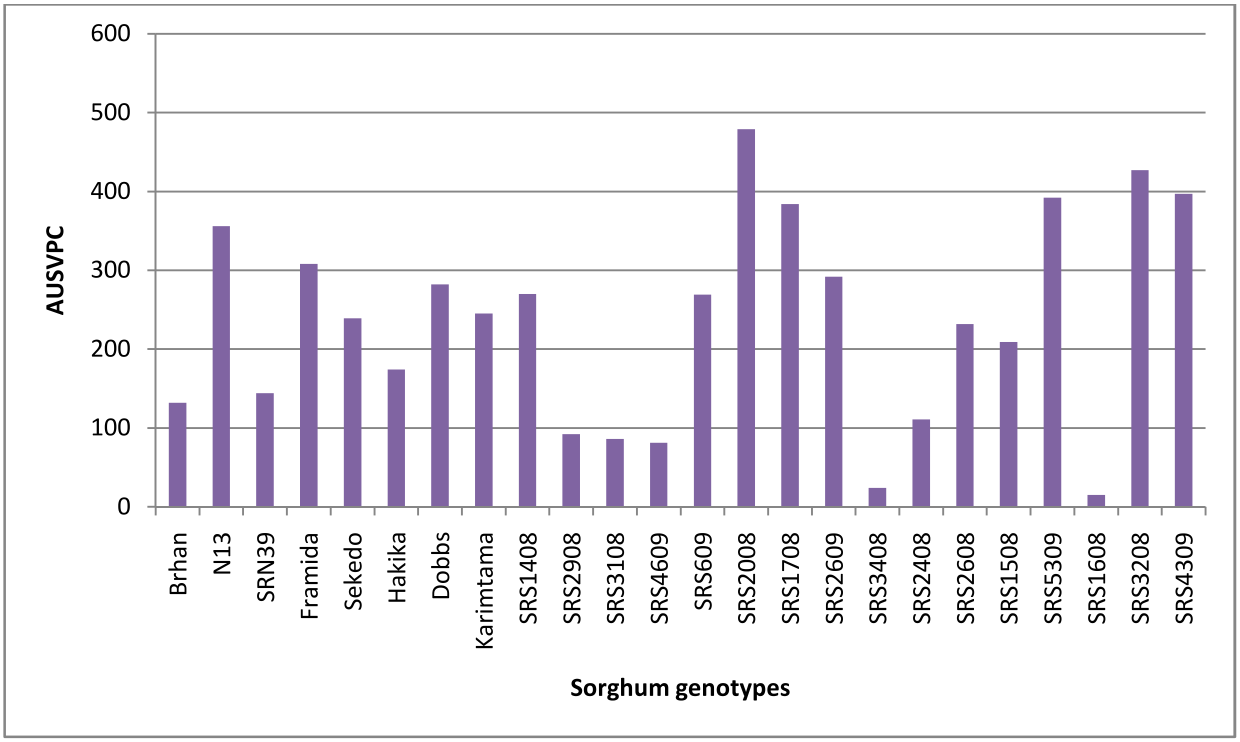


Figure 4.2: Mean values for AUSVPC on sorghum parental lines and their crosses

4.3.3 *Striga* vigour

Significant genotypic differences among genotypes were observed on *Striga* vigour (Table 4.1). In this case, the contribution was mainly from the female parents as indicated by significant (P<0.05) GCA effects for the female parents. The male parent GCA effects were not significant. The environmental effects were highly significant (P<0.001) but the genotype by environment interaction effects were not significant. This indicates that there were large environmental differences in *Striga* vigour but this did not influence genotypic differences with respect to *Striga* vigour. For *Striga* vigour, the ratio of female GCA effects to male GCA effects was equal to one indicating that both maternal and paternal effects were equally important in determining *Striga* vigour. Six crosses; Brhan x Sekedo (SRS1408), Brhan x Karimtama (SRS4609), N13 x Sekedo (SRS609), N13 x Karimtama (SRS2609), SRN39 x Dobbs (SRS1708) and Framida x Hakika (SRS1608) expressed negative GCA effects hence reduced *Striga* vigour (Table 4.2). However, from the mean values displayed in Figure 4.3, the genotypes: SRS1608, SRS3408, SRS2408, SRS2608 and SRS2908 had the lowest values for *Striga* vigour. Among the parental lines, SRN39 and Hakika had the lowest *Striga* vigour. *Striga* vigour on SRS1608, SRS3408, SRS2408, SRS2608 and SRS2908 was 5-23% lower than for the most resistant parental lines and 28-42% lower than for the most susceptible parental line (N13). This further confirms the presence of *Striga* resistance in the above genotypes.

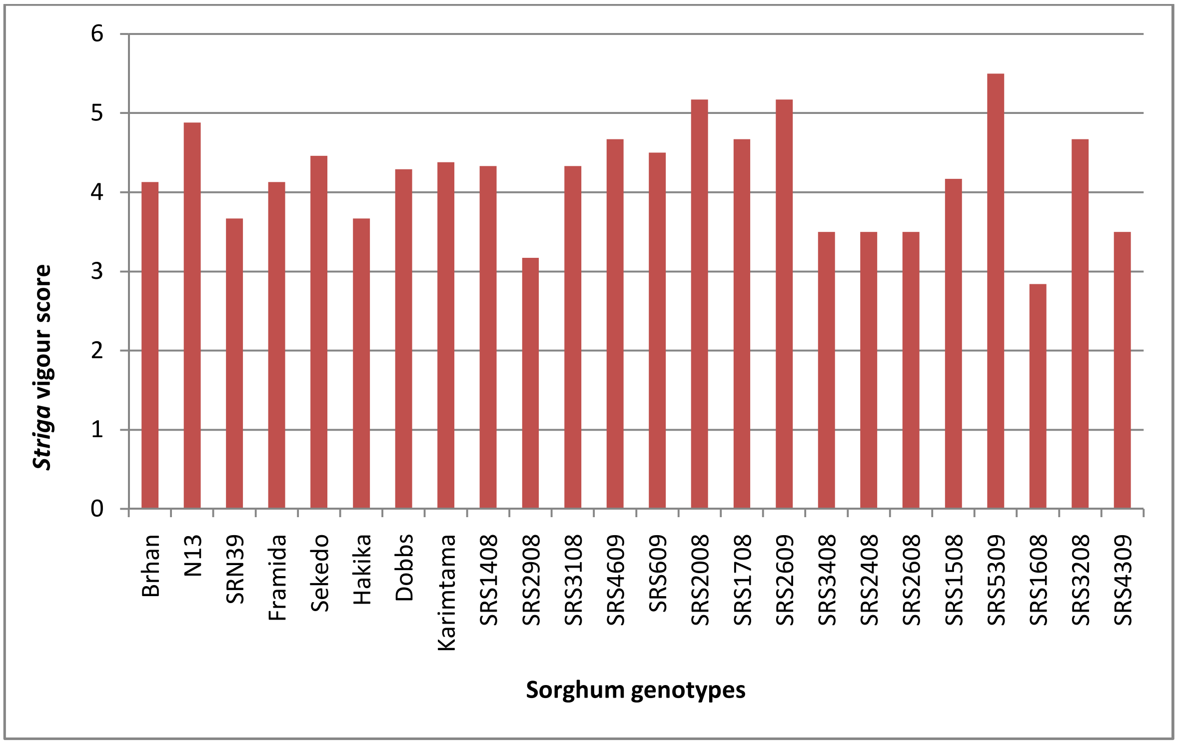


Figure 4.3: Mean values of *Striga* vigour scores on sorghum parental lines and their crosses

4.3.4 *Striga* emergence

While the genotypic differences in individual *Striga* emergence counts were not statistically significant, the mean values displayed in Figure 4.4 show a closely similar trend as in AUSNPC, AUSVPC and *Striga* vigour. The genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108 and SRS1508 had the lowest *Striga* emergence. Among the parental lines, Brhan, SRN39 and Hakika had the lowest *Striga* emergence. The parasite emergence on the above genotypes was 17-43% lower than the above most resistant parents and 53-68% lower than the most susceptible parent (N13).

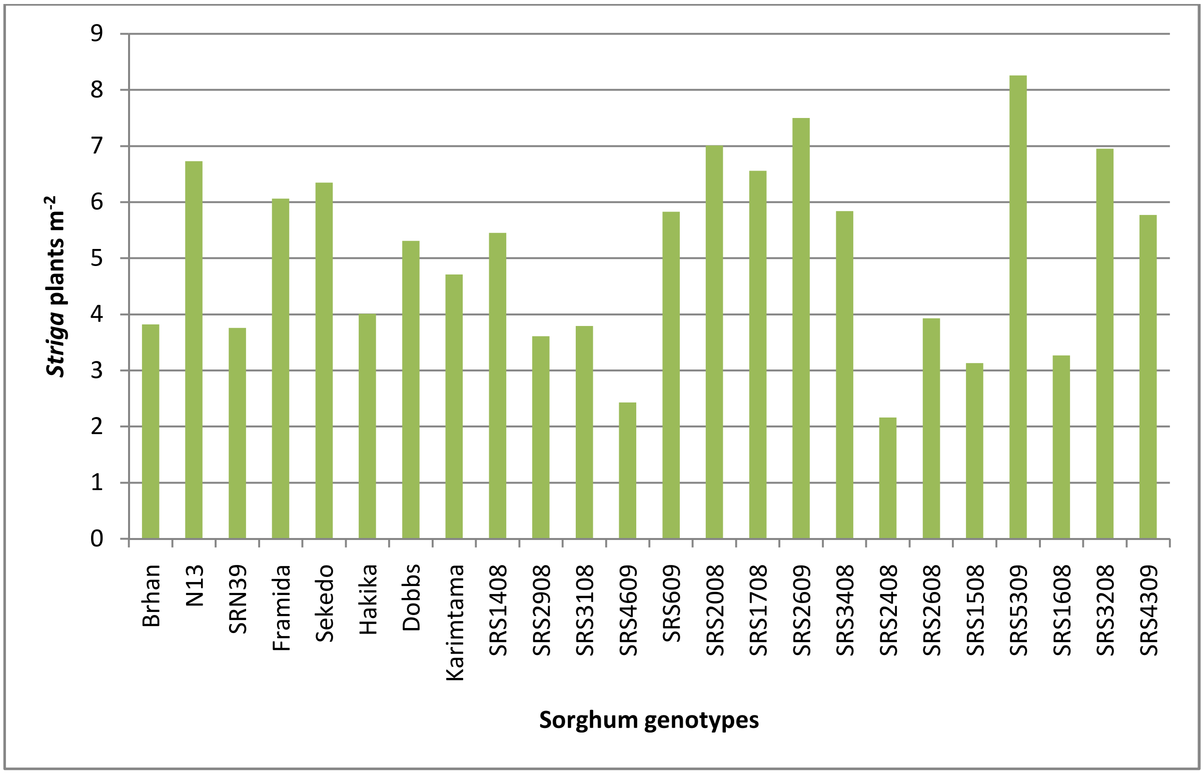


Figure 4.4: Mean values of *Striga* emergence on sorghum parental lines and their crosses

4.3.5 Genetic control of selected agronomic performance traits in the new genotypes of sorghum

The genetic effects were found to be significant in plant height, head length, and 1000 seed weight and grain yield. This was evidenced by the significant genotypic effects for each of the above traits in the analysis of variance (Table 4.3). However, the relative contributions of specific genetic effects varied from trait to trait as described below:

Table 4.3: Mean squares for sorghum agronomic performance data for Serere and Bukedea sites

Source of variation	df	Plant height (cm)	Head length (cm)	1000 seed weight (g)	Grain yield (kgha^{-1})
Environment	1	81369.4***	923.490***	10110.82***	91638887***
Genotype	15	2116.8***	41.990***	132.29*	1395042*
GCA$_m$	3	4412*	120.05***	30.2	527858
GCA$_f$	3	1214	74.43**	119.7	2613167
SCA	9	1653	5.15	170.5	1278062
Genotype x Environment	15	719.5**	14.078***	61.80*	1140135*
GCA$_m$ x Environment	3	1851.6***	20.244***	14.93	509798
GCA$_f$ x Environment	3	762.0*	24.083***	44.76	1979359*
SCA x Environment	9	328.0	8.688*	83.11	1070505
Error	62	257.3	3.441	77.40	622035
MSGCA$_f$/MSGCA$_m$		0.27	0.62	3.96	4.95
% GCA to genotype ss		53.2	92.6	23	17

GCA$_m$ = GCA for males. GCA$_f$ = GCA for females

***, **, * Data significant at $P<0.001$, $P<0.005$ and $P<0.05$ respectively

MS = Mean square. ss = sums of squares

4.3.5.1 Sorghum plant height

Genotypic differences in plant height were highly significant ($P<0.001$) between the new sorghum genotypes (Table 4.3). The male parent GCA effects were significant ($P<0.05$) while the female parent GCA effects were not significant. The interactions between the male and female GCA effects with the environment were both significant (at $P<0.001$ and $P<0.005$ respectively). In addition, both the environment and genotype by environment interaction effects were highly significant (at $P<0.001$ and $P<0.005$ respectively). The parental lines: Brhan, SRN39, Hakika and Dobbs, having negative GCA effects, contributed to reduced plant height in their crosses (Table 4.4). The parents: N13, Framida, Sekedo and Karimtama with positive GCA effects contributed to increased plant height. The ratio of the female GCA effects to the male GCA effects was less than one, meaning that paternal effects were more important in controlling plant height than maternal effects in the present set of genotypes. The specific genotypes: Brhan x Sekedo (SRS1408), Brhan x Hakika (SRS2908), N13 x Sekedo (SRS609), SRN39 x Karimtama (SRS1508), Framida x Hakika (SRS1608) and Framida x Dobbs (SRS3208) had reduced plant height. On the other hand, genotypes: Brhan x Dobbs (SRS3108), Brhan x Karimtama (SRS4609), N13 x Hakika (SRS2008), N13 x Dobbs (SRS1708), N13 x Karimtama (SRS2609), SRN39 x Sekedo (SRS3408), SRN39 x Hakika (SRS2408), SRN39 x Dobbs (SRS2608), Framida x Sekedo (SRS5309) and Framida x Karimtama (SRS4309) had increased plant height. Table 4.5 presents the mean values for selected sorghum agronomic traits. It shows that some of the genotypes derived from the parents contributing to reduced plant height above, such as SRS1408, SRS1508, SRS2408, SRS2608 and SRS2908 had short plant heights ranging from 109.1cm to 138.8cm under the no *Striga* environment, and this was 12-24% shorter than their parents. During the PRA, conducted at the beginning of this study, farmers pointed out their preference for short sorghum plant height of around one and half meters. Therefore the above five genotypes can be said to be within the farmers' expectations hence meeting the preference for plant height.

Table 4.4: GCA effects for male and female sorghum parents for selected sorghum performance parameters

	Plant height (cm)	Head length (cm)	1000 seed weight (g)	Grain yield (kgha^{-1})
Male parents				
Brhan	-5.6	1.96	-1.6	163
N13	6.3	-3.00	0.9	-124
SRN39	-15.8	-0.39	0.6	-127
Framida	15.1	1.43	0.0	88
SE	7.60	0.849	2.91	280.5
SED	10.75	1.2	4.11	396.7
Female parents				
Sekedo	7.4	2.29*	-1.0	484
Hakika	-8.9	0.40	-2.6	-123
Dobbs	-2.1	-1.72	2.4	-100
Karimtama	3.7	-0.97	1.3	-260
SE	7.60	0.849	2.91	280.5
SED	10.75	1.2	4.11	396.7

* Significant at P≤0.05

4.3.5.2 Sorghum head length

The genotypic differences together with specific interactions were highly significant ($P \leq 0.001$) for head length (Table 4.3). The specific interactions that were significant were male GCA by environment ($P=0.001$), female GCA by environment ($P<0.001$), genotype by environment ($P<0.001$) and SCA by environment that was significant at $P<0.05$. The male GCA effects were highly significant ($P<0.001$) while the female GCA effects were significant at $P<0.05$. The environmental main effect was also highly significant ($P<0.001$). Parental lines: Brhan, Framida, Sekedo and Hakika had positive GCA effects hence contributed to increased head length in their crosses (Table 4.4). Parents: N13, SRN39, Dobbs and Karimtama reduced head length in their crosses as indicated by their negative GCA effects. The ratio of the female GCA effects to the male GCA effects was less than one, indicating that paternal effects were more important than maternal effects in controlling head length in these sorghum parental lines. Genotypes: SRS2908, SRS3108, SRS2609, SRS3408, SRS2608, SRS1508, SRS5309 and SRS1608 had increased head length while the rest of the crosses had reduced head length. The mean values on Table 4.5 show that genotypes: SRS3408, SRS5309, SRS1608 and SRS2908 derived from the parents contributing to increased head length above, had the longest heads, which were on average, 20% longer than those of their parents.

4.3.5.3 One thousand seed weight

Genotypic differences contributed slightly to the variation in 1000 seed weight (Table 4.3). Most of the variation in 1000 seed weight seemed to be contributed by environmental effects, which were highly significant ($P<0.001$). Genotype by environment interaction effects were also significant ($P=0.05$). Maternal effects contributed more to seed weight than the parternal effects. This is indicated by the ratio of female to male GCA effects being greater than one. The mean values of the crosses show that SRS1708, SRS4309, SRS2608, SRS2408 and SRS3408 had seed weights that were 19-42% greater than the parent values (Table 4.5).

4.3.5.4 Grain yield

The new sorghum genotypes showed significant ($P<0.05$) genotypic differences in grain yield (Table 4.3). The interaction effect between the GCA for the female parents and the environment was significant ($P<0.05$). The environmental effects on grain yield were highly significant ($P<0.001$). Genotype by environment interaction effects were significant at $P=0.05$. The individual GCA effects of the parents were not significant. Although the GCA effects of the parents were not statistically significant, the results show that parents: Sekedo, Brhan and Framida contributed to yield increase in their crosses as indicated by their positive GCA effects

(Table 4.4). The other remaining five parents contributed to yield reduction as shown by their negative GCA effects. The ratio of female GCA effects to male GCA effects is greater than one meaning that the maternal effects contributed more (by more than four times) to grain yield than the paternal effects. Mean values from Table 4.5 show that the genotypes: SRS609, SRS1408, SRS2608 and SRS3408 yielded highest under the non *Striga* environment. These genotypes yielded 11-51% above the highest yielding parent (Sekedo), which is also currently the most popular improved variety for food sorghum in the area. There was variation in genotype ranking in yield in such a way that genotypes that ranked high in the non-*Striga* environment did not necessarily rank the same in the *Striga* environment. This indicates significant genotype x environment interaction effect on sorghum yield.

4.3.6 Reduction in crop performance under the *Striga* environment

Figures presented in Table 4.5 show that there was a reduction in all the sorghum performance parameters measured in the *Striga* environment (Bukedea) compared to the non-*Striga* environment (Serere). Sorghum grain yield was reduced by a range of 55% for SRS1708 to 92% for SRS609. The average reduction in grain yield was 87%. Seed weight was reduced in the range of 25% (SRS1608) to 59% (SRS2408), with the average reduction in seed weight being 49%. Sorghum head length was reduced by a range of 11% for SRS1708 to 50% for SRS3108, the average reduction in head length being 30.7%. Furthermore, sorghum plant height was also reduced by a range of 15% for SRS2408 to 50% for SRS1708. The average reduction in sorghum plant height was 38%. These figures portray the negative implications of *Striga* infestation on sorghum productivity.

4.3.7 Relationship between sorghum grain yield and other performance parameters

Table 4.6 shows a correlation analysis between sorghum grain yield and other crop performance parameters in the non-*Striga* environment (Serere) a *Striga* environment (Bukedea). A significant ($P<0.05$) positive correlation was observed between sorghum grain yield and, head length ($r=0.2079$) and plant height ($r=0.1882$) at Serere. The correlation between grain yield and 1000 seed weight was negative but not significant. Under the *Striga* environment, the correlations were all not significant but positive. Generally, the correlation coefficients in both environments indicate that head length was more positively related to grain yield than seed weight and plant height.

Table 4.5: Mean values for sorghum plant height, head length, 1000 seed weight and grain yield for sorghum parental lines and their crosses in Serere and Bukedea

Sorghum Genotype	Serere (no *Striga* infestation)				Bukedea (under *Striga* infestation)			
	Plant height (cm)	Head length (cm)	1000 seed weight (g)	Grain yield (kgha^{-1})^{r}	Plant height (cm)	Head length (cm)	1000 seed weight (g)	Grain yield (kgha^{-1})^{r}
Parental lines								
Brhan	148.2	20.9	42.3	2325^{10}	100.2	13.4	20.4	203^{16}
N13	161.7	18.9	40.7	2112^{14}	86.6	15.4	22.0	416^{5}
SRN39	143.6	20.4	42.2	2124^{13}	104.7	13.9	20.5	404^{6}
Framida	159.7	20.8	41.2	2403^{9}	88.7	13.5	21.4	124^{22}
Sekedo	151.7	20.9	40.5	2659^{6}	96.7	13.4	22.2	131^{20}
Hakika	146.1	20.9	40.8	2198^{11}	102.3	13.4	21.9	330^{12}
Dobbs	158.4	20.4	41.6	2071^{15}	90.0	13.9	21.1	457^{4}
Karimtama	157.1	18.8	43.5	2036^{16}	91.3	15.5	19.2	492^{3}
Parent mean	**153.3**	**20.3**	**41.6**	**2241**	**95.1**	**14.1**	**21.1**	**319.6**
Crosses								
SRS1408	138.8	23.8	46.7	3021^{2}	98.6	16.3	20.7	382^{8}
SRS1508	118.2	17.9	36.4	937^{21}	74.1	14.0	17.1	125^{21}
SRS1608	143.0	25.0	28.9	2708^{4}	99.0	14.2	21.6	160^{19}
SRS1708	189.5	12.8	52.4	799^{22}	93.6	11.4	29.2	356^{10}
SRS2008	168.1	17.6	38.6	1806^{17}	97.0	11.3	19.4	285^{14}
SRS2408	109.1	18.3	50.2	1076^{20}	92.0	13.1	20.3	174^{18}
SRS2608	132.2	18.3	47.6	3021^{2}	80.9	11.8	24.2	494^{2}
SRS2609	181.4	15.2	44.9	1319^{19}	95.3	12.1	23.3	194^{17}
SRS2908	128.4	24.1	34.9	2708^{4}	85.5	16.5	15.9	208^{15}
SRS3108	147.7	23.4	37.0	1528^{18}	88.4	12.9	19.3	368^{9}
SRS3208	155.6	20.3	38.8	2535^{8}	88.5	12.5	21.1	208^{15}
SRS3408	151.6	25.5	36.9	2951^{3}	108.7	14.9	22.8	312^{13}
SRS4309	188.1	18.2	53.5	2153^{12}	104.9	16.2	22.0	100^{23}
SRS4609	155.3	19.9	44.3	2694^{5}	105.7	15.8	19.1	507^{1}
SRS5309	212.6	25.4	43.8	2569^{7}	122.9	16.7	21.2	383^{7}
SRS609	133.1	18.0	30.5	4028^{1}	86.0	14.7	19.9	333^{11}
Mean of crosses	**153.3**	**20.2**	**41.6**	**2240.8**	**95.1**	**14.0**	**21.1**	**286.8**
Trial mean	**153.3**	**20.2**	**41.6**	**2241**	**95.1**	**14.0**	**21.07**	**287**
l.s.d	21.9***	2.6***	18.39**	1517.2**	22.0*	3.3*	ns	ns
C.V. (%)	8.6	7.6	26.5	40.6	13.9	14.3	27.4	64.5

*** Significant at P<0.001, ** Significant at P<0.005, *Significant at P<0.05

ns=not significant

r= Values in superscript represent the genotype rank in terms of yield in the site

Table 4.6: Correlation analysis between sorghum grain yield (kg ha^{-1}) and other crop performance parameters at Serere and Bukedea

	Serere (no *Striga* infestation)		Bukedea (under *Striga* nfestation)	
	Correlation coefficient	F probability	Correlation coefficient	F probability
1000 seed weight (g)	-0.0919	0.2479	0.0705	0.4971
Head length (cm)	0.2079	0.0083	0.1584	0.1253
Plant height (cm)	0.1882	0.0172	0.0210	0.8400

4.4 Discussion

4.4.1 The genetic control of *Striga* resistance

The genetic control of *Striga* resistance in the present new genotypes of sorghum was revealed in area under *Striga* number progress curve (AUSNPC), area under *Striga* severity progress curve (AUSVPC) and *Striga* vigour. The AUSNPC is a measure of progressive *Striga* emergence across the season. On the other hand, AUSVPC is a measure of progressive *Striga* severity across the season, whereby severity is a product of *Striga* number and vigour at each assessment date. The AUSNPC, being a measure of *Striga* numbers alone, may be used to assess *Striga* resistance based on mechanisms that operate at the initial stages of host-parasite interaction, such as low germination stimulation and low haustoria initiation. The AUSVPC on the other hand combines *Striga* numbers and vigour hence could assess other mechanisms of resistance that operate beyond attachment and penetration such as incompatible response and hypersensitive responses. In previous studies, Omanya et al. (2004) and Hausmann et al. (2000b) concurrently found strong genetic control for AUSNPC and AUSVPC in the field. They observed that the two parameters were useful measures of progressive *Striga* development in the field. However, Hausmann et al. (2000a) additionally found that individual *Striga* emergence count was also under genetic control from experiments conducted in pots. The findings of the present study seem to add to the above observations and additionally find that *Striga* vigour was also under strong genetic control. Significant genotypic differences were found for AUSNPC, AUSVPC and *Striga* vigour in the new sorghum genotypes. The relative contributions of GCA effects to the observed genotypic variances were 80.5%, 43.3% and 65% for AUSNPC, AUSVPC and *Striga* vigour, respectively. This shows that additive gene action was more important than the non-additive gene action in controlling *Striga* resistance in the present sorghum populations. It is therefore suggested that selection could be effectively employed to improve *Striga* resistance in these genetic materials.

The sorghum parental lines: Brhan, SRN39, Hakika and Sekedo consistently had negative GCA effects for AUSNPC and AUSVPC, while SRN39 and Hakika additionally had negative GCA effects for *Striga* vigour. This indicates that these parental lines were effective in transferring *Striga* resistance into their progeny and therefore could be considered as sources of *Striga* resistance genes when breeding for new *Striga* resistant sorghum varieties. The mean values for AUSNPC, AUSVPC and *Striga* vigour also show that the same lines had the lowest values among the eight parents further supporting the point that they could be used as sources of resistance to *Striga* in a breeding programme. The specific crosses: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108, SRS2908, SRS2609, SRS609 and SRS1708 showed resistance to *Striga hermonthica*. It can be suggested that these genotypes could be used in two ways: (i) the genotypes selected and moved to advanced generations and, with the application of suitable selection criteria developed into new *Striga* resistant sorghum varieties, or (ii) the genotypes could be utilised in backcross programmes to develop high yielding and *Striga* resistant sorghum varieties.

4.4.2 Genetic control for sorghum agronomic parameters

The genetic control of sorghum agronomic parameters was shown in head length and plant height. This was indicated by the significant effects of both male and female GCA effects for head length and male GCA effects for plant height. The relative contributions of GCA effects to genotypic variances were 92.6% and 53.2% for head length and plant height respectively. This shows that the additive gene action was more important than the non-additive gene action in controlling the above two traits, suggesting that selection can be effectively employed to improve head length and plant height in the population.

Kenga et al. (2004) reported highly significant GCA and SCA effects for grain yield, head length, plant height, seed weight, days to anthesis and threshing percentage in F_1 sorghum hybrids. While there are similarities in the findings, the present study differs from the previous study in two ways; (i) the present study used F_3 sorghum populations while Kenga et al. (2004) used F_1 sorghum hybrids, (ii) the GCA and SCA effects presented in this study were generated under both *Striga* infested and non-*Striga* infested environments, while the former study worked under no *Striga* infestation. Grain yield and seed weight in the present study were highly affected by environmental differences between the *Striga* environment and the non-*Striga* environment.

This is shown by the highly significant effects of the environment in the analysis of variance and the mean values of these traits as presented in Table 4.5. The mean values show that grain yield for example was reduced by more than 80% in the *Striga* environment compared to the non-*Striga* environment. However, this yield reduction may not have been due to *Striga* infestation alone but a combination of factors including sorghum midge damage, stalk borers and drought whose effects were actually observed in the field. Despite the above, mean values for grain yield under the non *Striga* environment show that the genotypes: SRS609, SRS1408, SRS2608 and SRS3408 yielded highest under the non *Striga* environment. These genotypes yielded 11-51% above the highest yielding parent (Sekedo), which is also currently the most popular food sorghum variety in the area. The two studies however arrive at the same findings for head length and plant height.

During the participatory rural appraisal (PRA) carried out at the initial stages of this study, farmers indicated preference for short sorghum varieties of 1.5m, and erect/long and compact heads. The study found that sorghum parental lines: Brhan, SRN39, Hakika and Dobbs had negative GCA effects for plant height they can act as sources of genes for reduction of plant height. The specific crosses derived from the above parents, such as SRS1408, SRS1508, SRS2408, SRS2608 and SRS2908 had plant heights ranging from 109.1cm to 138.8cm under the no *Striga* environment, and this was 12-24% shorter than their parents. These genotypes are within the farmers' preferred plant height of one and half meters, hence the study could be said to have met the farmers' preference in terms of plant height. Regarding head length, the parents: Sekedo, Brhan, Framida and Hakika had positive GCA effects, meaning that they increased head length in their crosses. These lines can be considered as sources of genes for increased head length. The genotypes: SRS3408, SRS5309, SRS1608 and SRS2908 derived from the above parents had the longest heads, which were on average, 20% longer than their parents. Therefore, there was an improvement in head length in the new genotypes, which was another requirement that was suggested by farmers during the PRA. The correlation analysis showed that head length was more positively related to grain yield than seed weight and plant height, in both the *Striga* environment and the non-*Striga* environment. This indicates that selection for sorghum grain yield could as well be done based on head length.

4.5 Conclusions

Generally, from the results of the present study, it can be concluded that:

- There was significant genetic variation for *Striga* resistance in the new sorghum genotypes generated.
- The additive gene action was important in controlling *Striga* resistance, indicating that resistance can be effectively improved through selection.
- There was also significant genetic control for sorghum head length and plant height, with preponderance of additive genetic effects indicating that improvement can be achieved through selection.
- The sorghum parental lines: Brhan, SRN39, Hakika and Sekedo displayed negative GCA effects for *Striga* resistance hence can be used as sources of *Striga* resistance genes when breeding for new *Striga* resistant sorghum varieties.
- The new sorghum genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108, SRS2908, SRS2609, SRS609 and SRS1708 were resistant to *Striga hermonthica* in the field.
- The parental lines; Sekedo, Brhan and Framida could be used as sources of genes for grain yield increase in a breeding programme.
- The highest yielding sorghum genotypes were SRS609, SRS1408, SRS2608 and SRS3408. Selections for high yield could be done on advanced generations of these genotypes.

References

Akwang, A. A., J.P. Obuo, J. Okwadi and J. Oryokot. 1999. Needs assessment for agricultural research in the Teso farming system: Summary report. NARO/DFID. Kampala, Uganda.

Akwang, A. A., S. Okalebo and J. Oryokot. 1998. Needs assessment for agricultural research in the Teso farming system, *'Aijul Eode'*: Main report. NARO/DFID. Kampala , Uganda.

Dabholkar, R.R. 1992. Elements of biometrical genetics. Asholk Kumar Mittal Concept Publishing Company, New Delhi, India.

Ebiyau,J., and J.O.E. Oryokot. 2001. Sorghum (*Sorghum bicolor* (L.) Moench*). In* Mukiibi, J.K. (ed.) Agriculture in Uganda, Vol.II. National Agricultural Research Organization 2001, Fountain Publishers Ltd, Kampala, Uganda.

Ejeta, G., L.G. Butler, D.E. Hess, T. Obilana, and B.V. Reddy. 1997. Breeding for *Striga* resistance in Sorghum, pp. 504-516. *In* Proceedings of the international conference on genetic improvement of sorghum and pearl millet. INTSORMIL, ICRISAT, Holiday Inn Plaza, Lubbock, Texas.

Ezeaku, I.E. and S.C. Gupta. 2004. Development of sorghum populations for resistance to *Striga* hermonthica in the Nigerian Sudan Savannah. African Journal of Biotechnology 3(6): 324-329.

Haussmann, B.I.G., A.B. Obilana, P.O. Ayiecho, A. Blum, W. Schipprack, and H.H. Geiger. 1999. Quantitative-genetic parameters of sorghum [*Sorghum bicolour* (L.) Moench] grown is semi-arid areas of Kenya. *Euphytica* 105:109-118.

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, H.G. Welz, and H.H. Geiger. 2000b. Improved methodologies for breeding *Striga* resistant sorghums. Field Crops Research 66(3):195-211.

Hayman, B.I. 1954. The theory and analysis of diallel crosses. Genetics 39: 787-809.

Kenga, R., S.O. Alabi, and S.C. Gupta. 2004. Combining ability studies in tropical sorghum (*Sorghum bicolour* (L.) Moench). Field Crops Research 88: 251-260.

Kroschel, J., (ed.) 2001. A technical manual for parasitic weed research and extension. Kluwer Academic Publishers, 3300 AA Dordrecht, Netherlands.

Mohamed, A.H. 2002. Identification and characterization of genetic variants in sorghum for specific mechanisms of *Striga* resistance. PhD thesis, Purdue University, USA.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43: 1320-1324.

Mutengwa, C.S., P. Tongoona, S. Mabasa, and O.A. Chivinge. 1999. Resistance to *Striga asiatica* (L.) Kuntze in sorghum: Parent characterisation and combining ability analysis. African Crop Science Journal 4: 321-326.

Olupot, J.R., I. Abaijuka, F. Dradiku, P. Edema, and J. Mukalazi. 2005. *Striga* infestation in the West Nile Agro-Ecological Zone of Uganda: The socio-economic perspective and the way forward. *In* p. 1507-1511. African Crop Science Conference Proceedings. African Crop Science Society.

Omanya, G.O., B.I.G. Haussmann, D.E. Hess, B.V.S. Reddy, M. Kayentao, H.G. Welz, and H.H. Geiger. 2004. Utility of indirect and direct selection traits for improving *Striga* resistance in two sorghum recombinant inbred populations. Field Crops Research 89(2-3):237-252.

Parker, C., and C.R. Riches. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.

Patrick, J.R., C. Grenier, and G. Ejeta. 2004. *Striga* resistance in the wild relatives of sorghum. Crop Science 44: 2221-2229.

Payne, R.W., D.A. Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2011. An introduction to GenStat for Windows (14th edition). VSN International, Hemel, Hemstead, UK.

Rodenburg, J., L. Bastiaans, E. Weltzien, and D.E. Hess. 2005. How can field selection for *Striga* resistance and tolerance in sorghum be improved? Field Crops Research 93:34-50.

Stuber, C.W. 1980. Mating designs, field nursery layouts, and breeding records. *In*: Fehr, W.R. and H. Henry (eds.). *Hybridisation of crop plants*, pp 83-104.

CHAPTER FIVE: RESISTANCE TO *STRIGA HERMONTHICA* BASED ON LOW GERMINATION STIMULANT PRODUCTION AND LOW HAUSTORIA INITIATION IN TEN NEW GENOTYPES AND SEVEN SORGHUM LINES IN UGANDA

Abstract

Information about specific mechanisms conferring resistance to *Striga* in sorghum is still scanty. There is need to understand these specific mechanisms in order to develop *Striga* resistant sorghum varieties that carry two or more resistance mechanisms for durable resistance. The main objective of the present study was to investigate the mechanisms of resistance to *Striga* available in the new sorghum genotypes recently generated in Uganda. The genetic materials for the study were selected based on their field reaction to *Striga*. They were categorized as very resistant, moderately resistant and susceptible. Based on this, ten new genotypes and seven fixed sorghum lines were selected for the laboratory studies. Two bio-assays were conducted: agar-gel assay, to detect low germination stimulant production and extended agar-gel assay, to detect low haustoria initiation, as mechanisms of resistance to *Striga*. Two new sorghum genotypes: SRS1608 and SRS1208 expressed both low germination stimulant production and low haustoria initiation mechanisms of *Striga* resistance. The genotypes: SRS2808 and SRS1108, and two fixed sorghum lines; Brhan and Hakika expressed only the low germination stimulant production mechanism while genotypes: SRS608, SRS3408, SRS4109 and SRS2308 expressed only the low haustoria initiation mechanism. The inheritance patterns of low germination stimulant production in the new sorghum genotypes varied. In some genotypes, it appeared to be controlled by a single gene while in others; it appeared to be controlled by more than one gene. There is need to conduct more studies to better understand the inheritance of the low haustoria initiation mechanism.

5.1 Introduction

Striga hermonthica (Del.) Benth. is a major constraint to sorghum production in Uganda. *Striga* is an obligate parasitic weed that presents a particular threat to sorghum production because most of its damaging action occurs underground before the parasite emerges above ground. This phenomenon basically makes it out of reach of most control measures. Furthermore, each *Striga* plant is capable of producing up to 500,000 minute seeds that can remain viable in the soil for more than 14 years (Kroschel, 2001, Bebawi et al., 1984). Often mechanical and chemical control options are too expensive or ineffective against *Striga*, and farmers may have no option than to either change their crop or abandon the infested fields. A more practical control option for subsistence farmers to ensure productivity in *Striga* infested fields is to grow crops with resistance to *Striga* (Patrick et al., 2004).

The sorghum host participates in the parasitic association with *Striga* at many levels: exuding the stimulus that induces *Striga* seed germination, providing the haustoria initiation signal, allowing penetration to its vascular system and producing assimilates and possibly other factors in forms usable by the parasite (Patrick et al., 2004). Opportunities for genetic resistance to *Striga* in sorghum may exist in each of these areas of cooperation. There is need to explore these interactions and carry out precise genetic studies that may provide avenues for genetic improvement of sorghum for resistance to *Striga*.

As early as 1992, Hess and Ejeta (1992) studied the inheritance of resistance to *Striga* in the sorghum genotype SRN39 and observed that the variation in resistance was controlled by both additive and dominance components. Mutengwa et al. (2005) while studying inheritance of *Striga* resistance in selected sorghum cultivars found that a single recessive gene controlled the low germination stimulant production trait in the sorghum cultivars SAR19 and SAR29. Patrick et al. (2004) found low germination stimulant production, germination inhibition and low haustoria initiation activity as mechanisms of *Striga* resistance present in a collection of wild relatives of sorghum and some cultivated sorghum lines. Mohamed (2002) reported that the low haustoria initiation factor in the wild sorghum genotype, P78, was inherited as a single dominant gene, while hypersensitive response was conditioned by two dominant genes. Furthermore, Mohamed et al. (2003) found the sorghum genotypes SRN39, IS9830 and 555 to possess the low germination stimulant character, while P47121, Framida and Dobbs exhibited hypersensitive response as their mechanisms of resistance to *Striga asiatica*. The above studies show that some progress has been made towards identifying specific mechanisms of *Striga* resistance but their genetric inheritance still needs to be studied for more clearity in cultivated sorghum. This knowledge is necessary so that in future, *Striga* resistant sorghum varieties possessing multiple mechanisms of resistance could be developed for more durable resistance. The objective of the present study was to determine the mechanisms of *Striga* resistance present in the new genotypes of sorghum generated in Uganda and study their inheritance.

5.2 Materials and methods

5.2.1 Genetic materials

The genetic materials used in this study comprised of ten new sorghum genotypes (SRS..) of F_3 generation and seven fixed lines. These were specifically selected based on their field performance under *Striga* infestation in the previous season. For convenience, the materials were categorised as resistant (R), moderately resistant (MR) and susceptible (S) as shown in Table 5.1 below:

Table 5.1: Field response of 17 sorghum genotypes to *Striga* infestation

Entry	No. of emerged *Striga* plants m^{-2}	Field score
Parental lines		
N13	8.9	S
EPURIPUR	4.9	MR
BRHAN	2.4	R
SILA	5.6	S
HAKIKA	5.0	MR
DOBBS	17.0	S
SRN 39	8.6	S
Crosses		
SRS1908	14.0	S
SRS 2808	2.9	R
SRS 1608	2.6	R
SRS 3108	2.8	R
SRS 608	7.0	S
SRS 1108	10.6	S
SRS 3408	4.0	MR
SRS 1208	4.0	MR
SRS 4109	5.2	S
SRS 2308	4.0	MR
l.s.d	3.1	
C.V. (%)	41.3	

For convenience, R = <3 *Striga* plants m^{-2}, MR = 4-5 *Striga* plants m^{-2}, S = >5 *Striga* plants m^{-2}

5.2.2 The laboratory procedures

The laboratory procedures followed in this study are those described by previous researchers, specifically, Mutengwa (2004), Patrick et al. (2004), Omanya et al. (2004), Mohamed et al. (2003), Mohamed (2002), and Haussmann et al. (2000b). Two bio-assays were concurrently run in the laboratory, the agar-gel assay and the extended agar-gel assay. The agar-gel assay was used to detect low germination stimulant production, while the extended agar-gel assay, being a modification of the former, allows examination of haustoria formation. The details of all the laboratory procedures are briefly described below:

5.2.2.1 Surface sterilization of sorghum seeds

Twenty grams (approximately 500 seeds) of each of the sorghum genotypes were separately soaked in 10ml of 2.62% sodium hypocloride (NaOCl) solution (50% commercial bleach) for 30 minutes and rinsed three times with double distilled water (ddH_20). The seeds were soaked in a 0.5% solution of Captan50-W for 24 hours. The seeds were again washed three times in ddH_20 and then transferred to Petri dishes that contained moist filter papers and incubated in the dark at 28^0C for 24 hours. Only healthy germinated seeds were selected for the analysis.

5.2.2.2 Surface sterilization and conditioning of *Striga* seeds

The *Striga hermonthica* seeds that were used in these experiments were 3 years old and had been harvested from sorghum hosts in Eastern Uganda. A sample of *Striga* seeds was put in a 50ml flask containing ddH_20 and 3 drops of Tween 20. Sand and other debris were removed using a pipette. The seeds were sonicated for 2 minutes with occasional swirling in order to settle down. After sonicating, the remaining sand/debris and water were removed using a pipette. The seeds were rinsed 3 times with ddH_20. The clean seeds were pipetted into a flask containing mancozeb that was diluted 10 times. The seeds were again sonicated and rinsed three times using 10ml of ddH_20. After that, 4ml of ddH_20 and 1.5ml of 0.01% benomyl solution were added to the flask followed by additional 10ml of sterile water. The flask was then placed into an incubator set at 28^0C to begin conditioning. After every 3-4 days, the seeds were pipetted into a fresh sterile flask containing 15.5ml of benomyl solution and returned to the incubator. The *Striga* seeds were conditioned for 14 days before being used in the agar-gel assays (Haussmann et al., 2000b).

5.2.2.3 The agar-gel assay (AGA)

One hundred and fifty micro-litres of settled *Striga* seeds were pipetted into each of 68 90mm petridishes. The 68 petridishes represented the 17 sorghum genotypes each replicated 4 times. The petridishes were thus labelled according to the genotypes and replications. A solution of 0.7% water agar was autoclaved for 15 minutes and cooled to 50^0C for one hour. Twenty millilitres of the agar solution was poured into each petridish just before it solidified in order to achieve a uniform distribution of *Striga* seeds within the agar. Four pre-germinated sorghum seeds for each genotype were picked and placed at equal intervals around the edges of the respective petridishes. The seedlings were placed in the petridishes in such a way that the radicles just penetrated the gels. The petridishes were covered and placed into an incubator set at 28^0C. After 3 days (72 hours), the petridishes were observed for germination of *Striga* seeds under a stereo microscope at x25 magnification (Figure 5.1). The maximum germination distance, i.e. the distance between the host root and the most distant germinated *Striga* seed was recorded in mm for 3 seedlings in each plate.

5.2.2.4 The extended agar-gel assay (EAGA)

About 1500 conditioned *Striga* seeds (4 drops of settled seeds) were placed into each of 68 150mm petridishes. A solution of 0.7% water agar was autoclaved for 15 minutes and cooled to 50^0C for one hour. The agar solution was poured into each petridish containing the conditioned *Striga* seeds to produce an even distribution of the seeds. Four pre-germinated sorghum seeds for each genotype were picked and placed at equal intervals around the edges of each dish so that the radicles just penetrated the gel. The dishes were covered and placed in an incubator set at 28^0C.

After 3 days, the dishes were observed for germination, parasitic attachment and host root development under a stereo microscope at x25 magnification. To remove the host genotypic differences in inducing *Striga* seed germination, the experimental set-up was treated with ethylene. To do this, the dishes were placed in a dosing chamber located in a bio-safety cabinet and a 30 second burst of ethylene gas was applied to them (Mohamed, 2002). The idea was to germinate all the viable *Striga* seeds. The dishes were left in the chamber for 2 days. After the 2 days, the dishes were aerated in front of the bio-safety cabinet in order to remove any residual ethylene and later placed under light for 12 hours. The dishes were then observed under a stereo microscope at x25 magnification, scanning through entire host roots for haustoria initiation in germinated *Striga* seedlings. A *Striga* seedling was counted as having developed a haustorium either when hair-like projections (tubercles) were observed on its radical or when it was observed attaching to the sorghum root (Figure 5.2). The furthest distance between the three primary host roots and *Striga* seedlings with haustoria was measured in mm.

Each of the above experiments was carried out in two rounds. During the first round, the experiments were replicated four times, and in the second round they were replicated six times. The experiment was arranged in a completely randomised design. In each replication, measurements were taken from three sorghum seedlings for each genotype. This therefore means that measurements were taken from a total of thirty seedlings for each sorghum genotype.

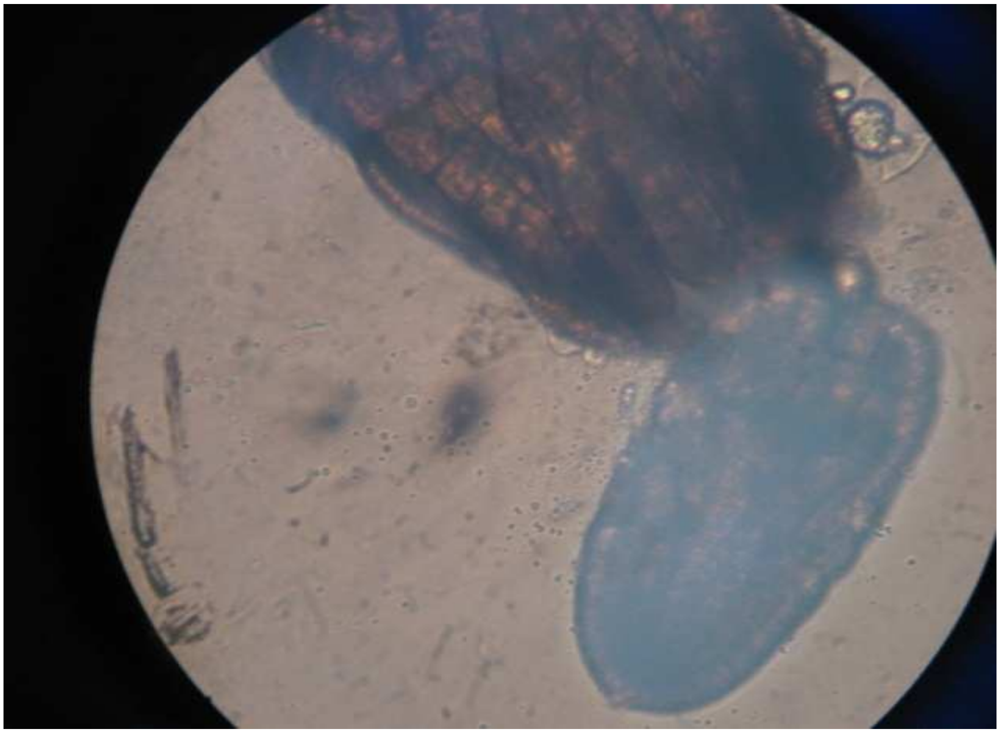


Figure 5.1: A germinating *Striga* seedling as observed under a stereo microscope

Figure 5.2: *Striga* seedlings attached to sorghum root-haustoria formed

5.2.3 Data analysis

Data for number of germinated *Striga* seeds, maximum germination distance in the AGA, and maximum haustoria initiation distance in the EAGA were analysed using Genstat release 14.1 statistical package (Payne et al., 2011). A correlation analysis was carried out to assess the relationship between the number of *Striga* seeds that germinate in a gel and the average maximum *Striga* germination distance. Frequency distributions for mean maximum *Striga* germination distances were plotted for the individuals of each sorghum genotype. In this case, the germination distances (0 – 29mm) were grouped into six classes; with a class interval of 5mm. Individuals falling into the various classes for each genotype were then counted and plotted. Additionally, a chi-square test was conducted to test the observed data for goodness-of-fit to the hypothesis that a single recessive gene controlled the inheritance of low germination stimulant production, in the four sorghum genotypes that showed low germination stimulant production. Since the F_2 progeny were expected to segregate 1:3 for low germination stimulant: high germination stimulant under the hypothesis of a single recessive gene, the F_3 generation was expected to segregate 3:5 for low germination stimulant (ls): high germination stimulant (hs), as exemplified below:

F_2 segregation: AA + Aa (hs): aa (ls)
3 : 1
F_3 segregation: ½(1/4 AA + ½ Aa + 1/4aa): 1/8 aa
(1/4 + 1/8 + ¼) : 1/8 + ¼
5(hs) : 3 (ls)

Therefore the observed frequency values were tested against the expected F_3 ratio of 3:5.

5.3 Results

5.3.1 *Striga* germination distances in the agar-gel assay

Generally, seeds of all the sorghum genotypes evaluated readily germinated in the moist filter papers and grew with adequate vigour in the agar-gel. The average number of *Striga* seeds that germinated on each sorghum genotype and maximum germination distances between the primary host roots and the most distant germinated *Striga* seed, measured from three sorghum seedlings in a gel are shown in Table 5.2. The differences in the number of germinated *Striga* seed and the maximum germination distances were highly significant (P<0.001) between the sorghum genotypes evaluated. The number of germinated *Striga* seeds associated with the sorghum genotypes ranged from 13 – 24. The maximum *Striga* germination distances ranged from 6mm – 20.3mm. The correlation between the number of germinated *Striga* seeds and the average maximum germination distance, though relatively low, was positive (r=0.37) and highly significant (P<0.001). The sorghum genotypes that had the average maximum *Striga* germination distance of <10mm were rated as low germination stimulant producers while those with the maximum *Striga* germination distances of ≥10mm were rated as high germination stimulant producers (Mutengwa, 2004; Patrick et al., 2004). The new sorghum genotypes: SRS1108, SRS1608, SRS4109 and SRS2808, and the fixed lines Brhan and Hakika had average maximum *Striga* germination distances ranging from 6.9-9mm. These genotypes were therefore classified as having the low germination stimulant character as a mechanism of resistance to *Striga*. The rest of the genotypes had average maximum germination distances of ≥10mm hence were classified as high germination stimulant producers meaning they lacked the low germination stimulant character for *Striga* resistance.

Table 5.2: Analysis of sorghum genotypes for *Striga* germination stimulant production

Sorghum genotype	No. *Striga* seeds germinated	D1	D2	D3	Average maximum germination distance
Parental lines					
N13	14.5	16.7	17.1	20.3	18.0
EPURPUR	20.5	12.3	14.6	16.1	14.3
BRHAN	14.5	7.3	8.2	8.2	7.9
SILA	16.0	9.0	10.2	11.8	10.3
HAKIKA	15.9	9.3	9.0	8.6	9.0
DOBBS	20.6	10.6	11.0	11.1	10.9
SRN 39	23.5	14.0	14.6	13.5	14.0
Crosses					
SRS1908	24.2	11.0	13.0	13.4	12.5
SRS 2808	17.3	9.8	8.9	9.0	9.2
SRS 1608	13.6	6.5	7.6	7.6	7.2
SRS 3108	13.9	10.4	10.1	10.8	10.4
SRS 608	18.0	10.7	9.6	10.7	10.3
SRS 1108	16.5	6.0	7.3	7.5	6.9
SRS 3408	13.5	10.8	10.6	9.7	10.4
SRS 1208	15.0	6.4	7.9	8.1	7.5
SRS 4109	15.8	12.6	12.9	15.1	13.5
SRS 2308	13.3	10.8	9.9	9.5	10.1
l.s.d	5.4	2.6	2.7	2.7	2.7
C.V.(%)	34.8	28.6	28.4	27	28.0

D1-D3 represents germination distances (mm) measured from 3 sorghum seedlings in a gel
Genotypes marked in red are classified as low germination stimulant producers
Germination distance<10mm classified as low germination stimulant production
Germination distance≥10mm classified as high germination stimulant production (Patrick et al., 2004; Mutengwa, 2004)

The chi-square test (Table 5.3) showed a significant (P<0,001 and P=0.005) deviation from the expected F_3 segregation ratio of 3:5 low germination stimulant: high germination stimulant in genotypes; SRS1108, SRS1208 and SRS1608 respectively, for the case of a single recessive gene inheritence. The segregation pattern in the three genotypes above seems to suggest a single dorminant gene action for low germination stimulant production. While the deviation was not statistically significant in genotype SRS2808, the observed figures deviated from the expected ratio. The chi-square tests for genotypes: SRS1908 and SRS4109 seem to support a single recessive gene inheritance. In the other genotypes (SRS3108, SRS608, SRS3408 and

SRS2308), the chi-square test does not support either single dominant gene inheritance or single recessive gene inheritance, suggesting the involvement of several genes in the inheritance of low germination stimulant production. Therefore these results appear to differ from those of the previous studies that indicated that the low germination stimulant character was controlled by a single recessive gene.

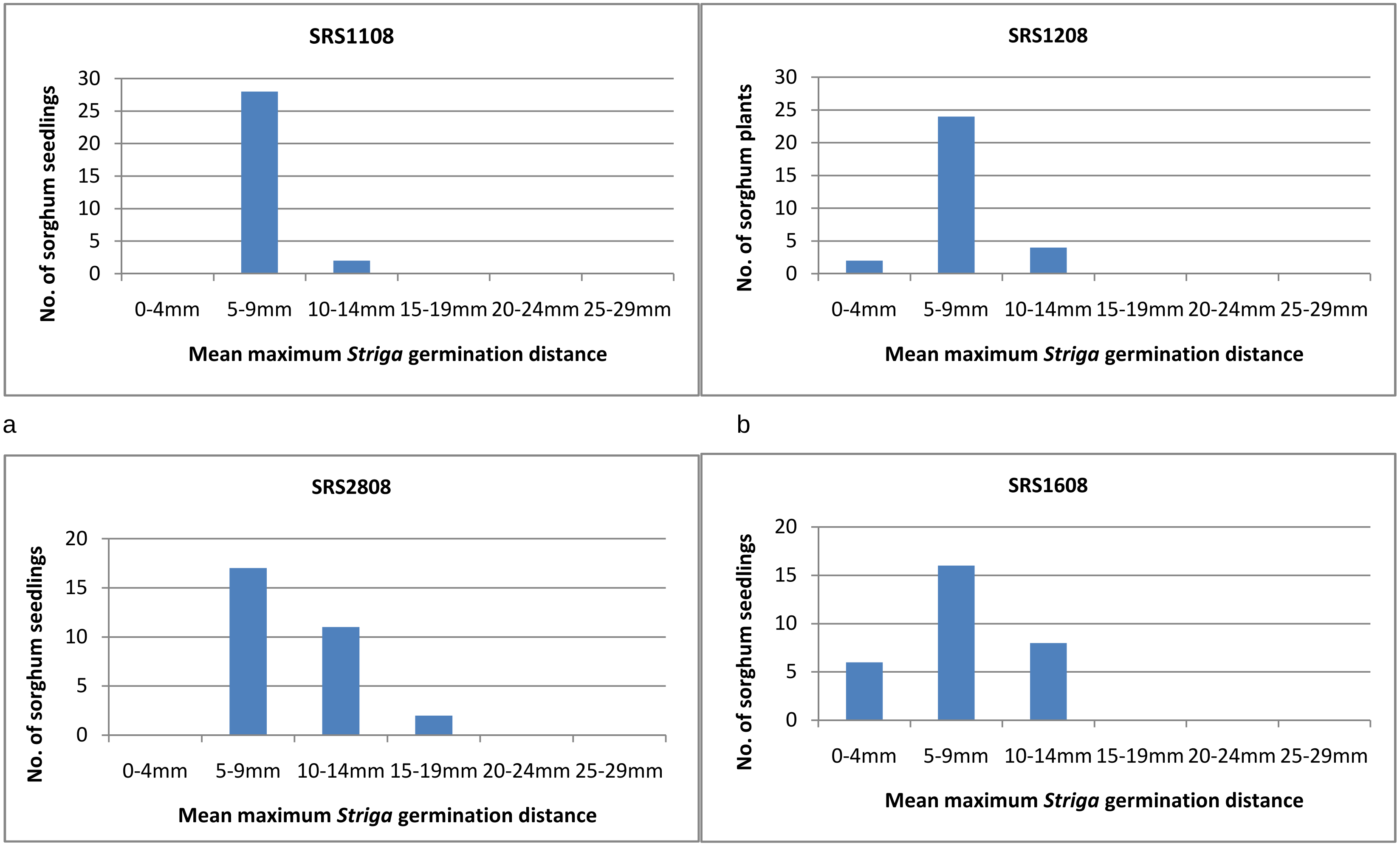
Table 5.3: Chi-square test for deviations from a 3:5 low (LS): high (HS) ratio in four F_3 sorghum genotypes for maximum germination distance in the agar-gel assay

Genotype	Observed ratio		X^2	P
	LS	HS		
SRS1108	28	2	20.67	<0.001
SRS1208	26	4	15.40	<0.001
SRS2808	17	13	2.21	0.137
SRS1608	22	8	7.80	0.005
SRS1908	3	27	6.26	0.012
SRS3108	11	17	0.02	0.889
SRS608	12	18	0.04	0.842
SRS3408	12	18	0.04	0.842
SRS4109	5	25	3.30	0.069
SRS2308	8	22	0.81	0.369

LS=Low germination stimulant HS=High germination stimulant

5.3.2 Frequency distribution for maximum *Striga* germination distances

Figures 5.3 to 5.6 show the frequency distributions for mean maximum *Striga* germination distances for the different sorghum genotypes. Among the four genotypes that were classified as resistant (low germination stimulant producers), the individuals in SRS1208 and SRS1608 fitted a normal distribution, while for SRS1108 and SRS2808, a bimodal frequency distribution was observed. These frequency distributions seem to indicate the presence of more than one gene in the control of low germination stimulant production. The bimordal frequency distribution points to the existence of two gene classes, while the normal distribution would suggest the presense of several genes with quantitative effects. For the above resistant genotypes, the proportion of individuals scoring resistant ranged from 57 to 93%. For the six genotypes that were classified as susceptible (high germination stimulant producers), SRS3108 and SRS3408 showed a normal distribution with 37% and 40% of their respective individuals showing resistance. Frequency distributions in SRS609, SRS4109, SRS1908 and SRS2308 were skewed towards the susceptible side but with some resistant individuals (10-40%) appearing. Among the fixed sorghum lines, frequency distributions were generally skewed. For the lines classified as resistant (Brhan and Hakika), distribution was skewed towards the resistance side and the individuals fell into only two distinct classes; 5-9mm (resistant) and 10-14mm (susceptible). The rest of the other five lines had distributions skewed towards the susceptible side with individuals appearing in various classes.



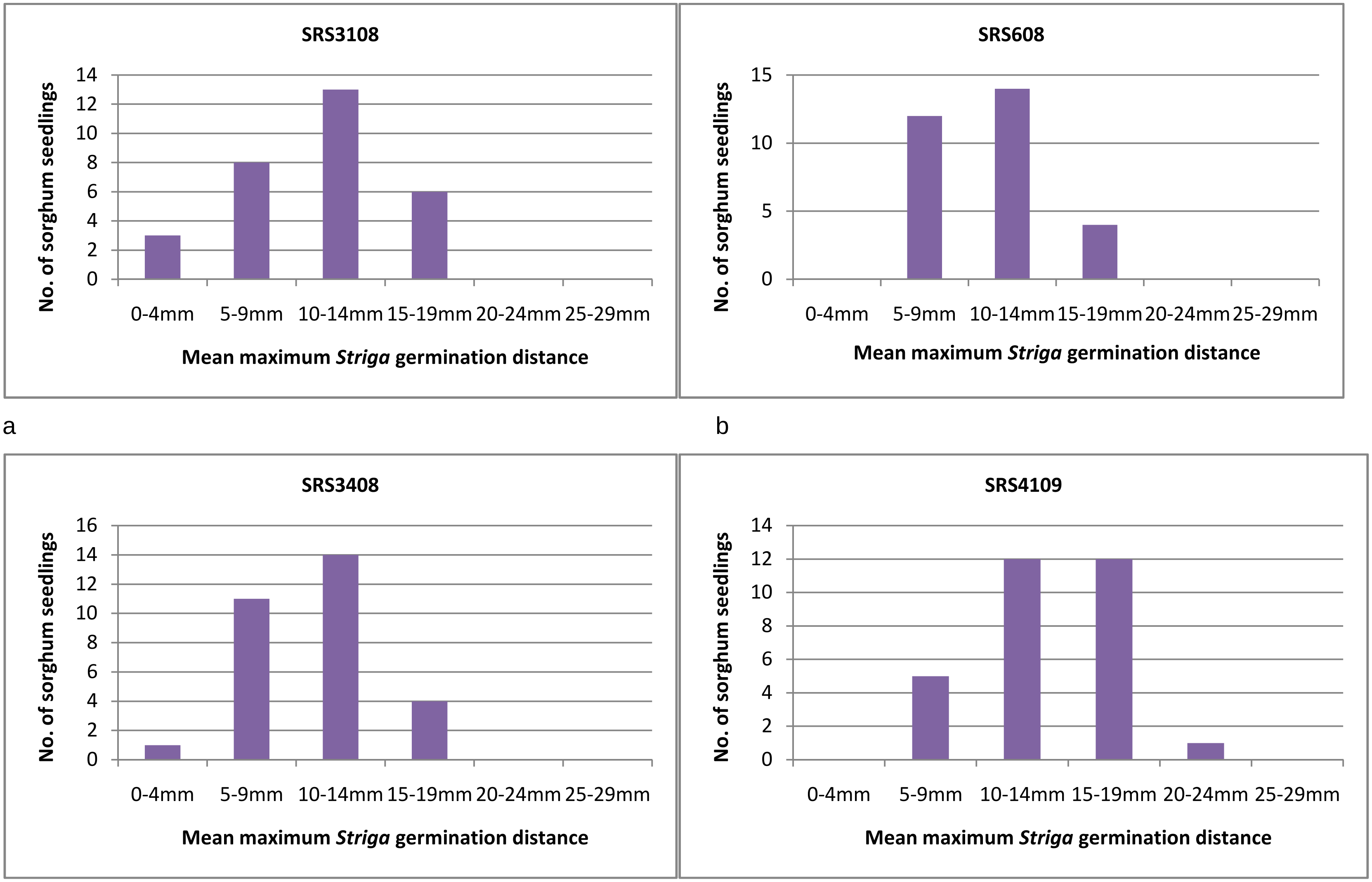
a

b

c

d

Figure 5.3: Frequency distribution for mean maximum *Striga* germination distances on four sorghum genotypes (a-d) that exhibited low germination stimulant character in the agar-gel assay



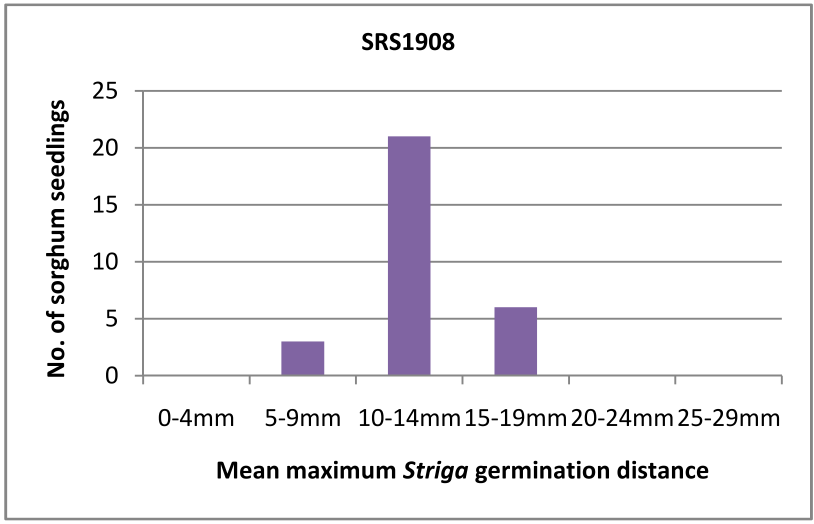
a

b

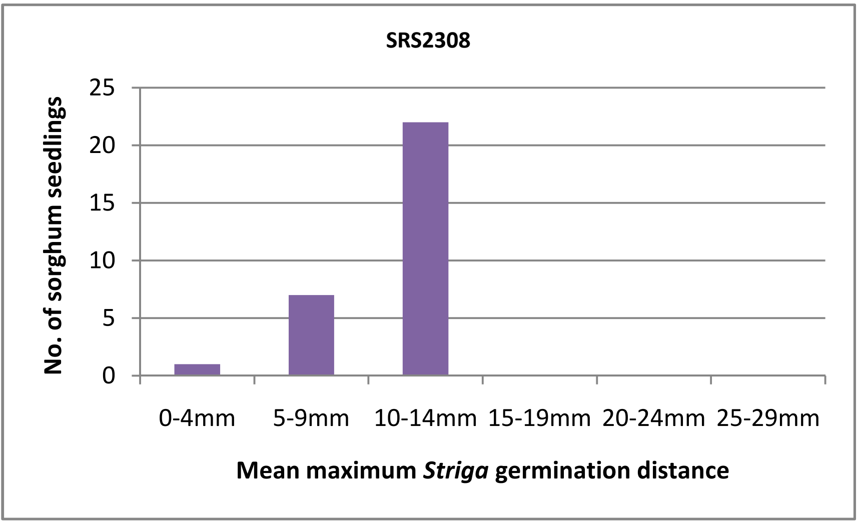
c

d

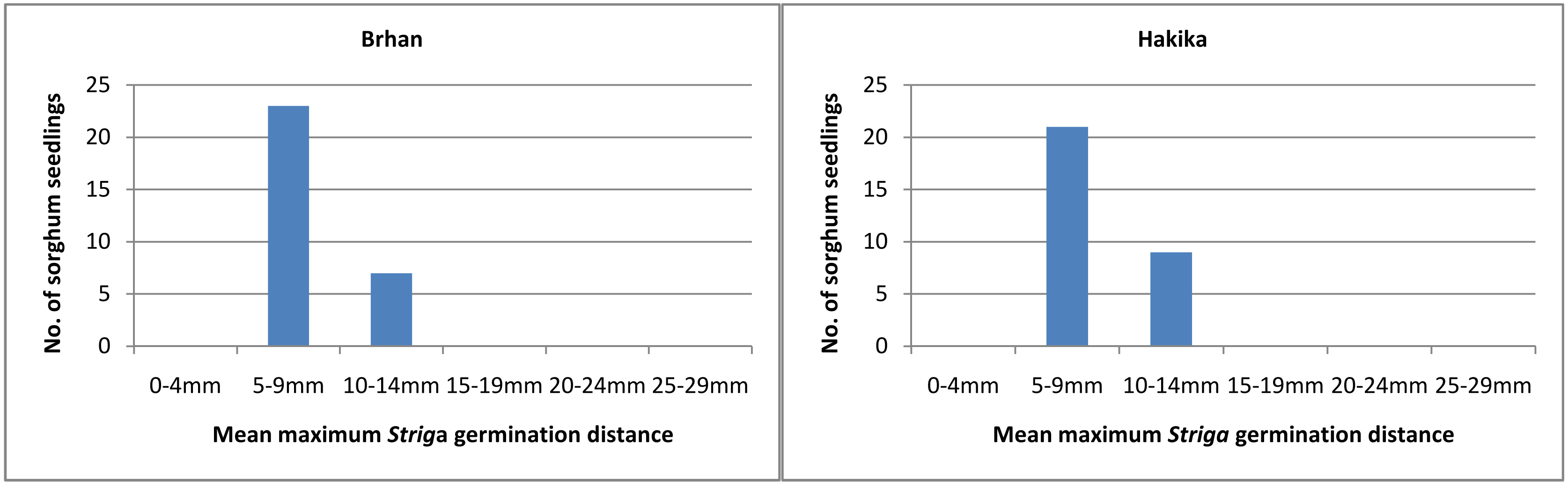
Figure 5.4: Frequency distribution for mean maximum *Striga* germination distances on six sorghum genotypes (a-d above and e-f below) that exhibited high germination stimulant production in the agar-gel assay


SRS1908
No. of sorghum seedlings
25
20
15
10
5
0
0-4mm
5-9mm
10-14mm
15-19mm
20-24mm
25-29mm
Mean maximum *Striga* germination distance

e


SRS2308
No. of sorghum seedlings
25
20
15
10
5
0
0-4mm
5-9mm
10-14mm
15-19mm
20-24mm
25-29mm
Mean maximum *Striga* germination distance

f



a

b

Figure 5.5: Frequency distribution for mean maximum *Striga* germination distances on two fixed sorghum lines (a-b) that exhibited low germination stimulant character in the agar-gel assay

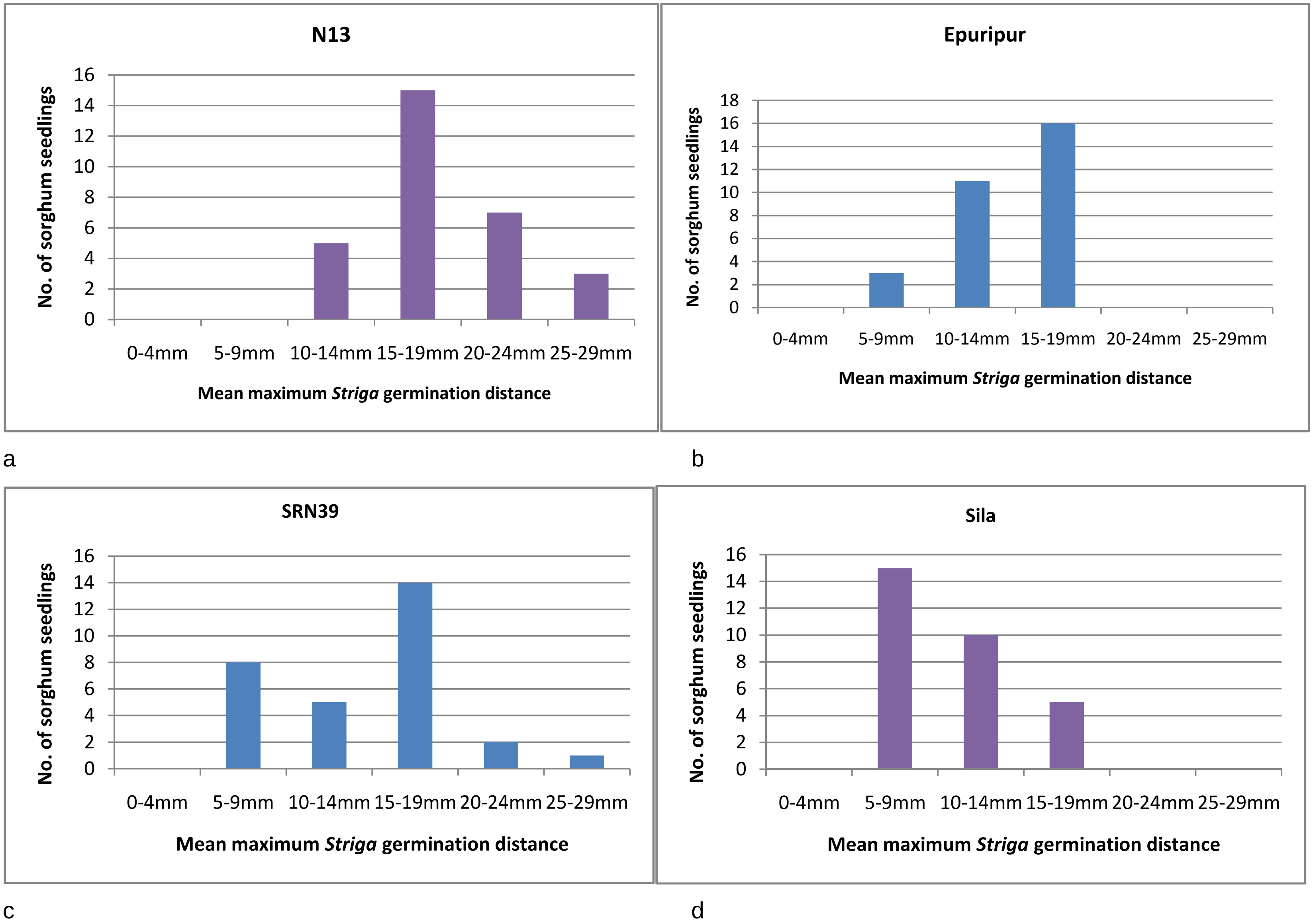
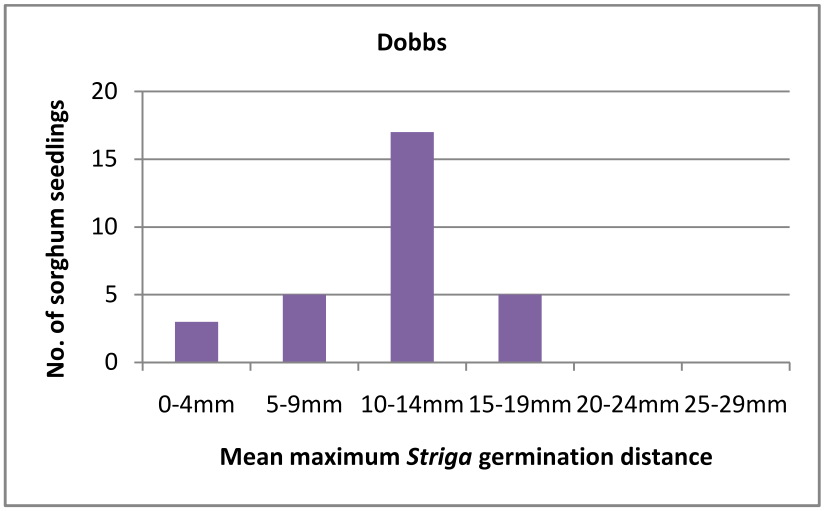


Figure 5.6: Frequency distribution for mean maximum *Striga* germination distances on five fixed sorghum lines (a-d above and e below) that exhibited high germination stimulant production in the agar-gel assay



e

5.3.3 Haustoria initiation in the extended agar-gel assay

The sorghum genotypes differed significantly (P<0.001) in their capacities to induce haustoria formation in germinated *Striga* seedlings (Table 5.4). The number of *Striga* seeds germinating on the sorghum genotypes in the EAGA ranged from 14 – 30 seeds, and the maximum haustoria initiation distances ranged from 1.4mm – 3.4mm. Sorghum genotypes recording maximum haustoria initiation distances of <2mm were considered as producing low haustoria initiation signals, while those with haustoria initiation distances of ≥2mm were considered as producing high haustoria initiation signals (Patrick et al., 2004). Sorghum genotypes: SRS608, SRS3408, SRS2308, SRS4109, SRS1208 and SRS1608 recorded average maximum haustoria initiation distances ranging from 1.4mm – 1.9mm. These genotypes were rated as producing low haustoria initiation signals hence possessing the low haustoria initiation trait as a mechanism of resistance to *Striga*. SRS608 and SRS3408 particularly had the lowest maximum haustoria initiation distance. All the fixed sorghum lines and the other four cross genotypes initiated haustoria formation in *Striga* seedlings at distances ≥2mm. They were therefore rated as producing high haustoria initiation signals hence lacking the low haustoria initiation mechanism of *Striga* resistance. Dobbs had the highest maximum haustoria initiation distance of 3.4mm among the fixed lines while for the genotypes SRS1108 had the highest haustoria initiation distance of 2.6mm.

Table 5.4: Analysis of sorghum genotypes for low haustoria initiation distance

Sorghum genotype	No. *Striga* seeds germinated	D1	D2	D3	Average maximum haustoria distance
Parental lines					
N13	30.0	2.7	1.6	2.0	2.1
EPURPUR	22.4	3.0	1.7	3.4	2.7
BRHAN	17.6	2.5	2.2	2.7	2.5
SILA	14.2	2.3	2.0	2.0	2.1
HAKIKA	24.6	2.5	2.1	2.9	2.5
DOBBS	20.8	2.4	4.1	3.6	3.4
SRN 39	26.6	2.5	1.5	2.0	2.0
Crosses					
SRS1908	29.0	2.4	1.4	2.9	2.2
SRS 2808	18.8	3.2	1.9	2.3	2.5
SRS 1608	19.8	1.9	1.9	2.0	1.9
SRS 3108	17.6	2.1	1.8	2.8	2.2
SRS 608	21.6	2.0	1.3	0.9	1.4
SRS 1108	25.8	2.3	2.7	2.9	2.6
SRS 3408	22.6	1.1	1.8	1.3	1.4
SRS 1208	23.3	2.1	2.4	0.7	1.7
SRS 4109	28.4	1.7	1.6	1.6	1.6
SRS 2308	15.4	2.2	1.3	0.9	1.5
l.s.d	5.6	0.6	0.8	1.0	0.8
C.V.(%)	27.0	29.0	43.0	39.0	37.0

D1-D3 represents haustoria initiation distances (mm) measured from 3 sorghum seedlings in a gel
Genotypes marked in red are classified as producing low haustoria initiation factors
Haustoria initiation distance<2mm classified as low haustoria initiation
Haustoria initiation distance≥2mm classified as high haustoria initiation (Patrick et al., 2004)

5.4 Discussions

5.4.1 The low germination stimulant production in the agar-gel assay

Information about individual mechanisms conferring resistance to *Striga* and their genetic control in affected crops is still scanty. However, in spite of that, the low germination stimulant character in sorghum has been most widely studied. In the present study, low germination stimulant production was found in four sorghum genotypes: SRS1108, SRS1208, SRS1608 and SRS2808, and two fixed lines; Brhan and Hakika. Chi-square studies conducted indicated a significant deviation from the expected F_3 segregation ratio of 3:5 low germination stimulant: high germination stimulant for the case of a single recessive gene, in genotypes SRS1108, SRS1208 and SRS1608. However, the segregation in genotypes SRS1908 and SRS4108 seemed to fit into the ratio of a single recessive gene inheritance. Segregation in genotypes SRS3108, SRS608, SRS3408 and SRS2308 shows involvement of several genes. This indicates that the low germination stimulant character in some sorghum genotypes could be controlled by more than one gene. Frequency distributions for maximum *Striga* germination distances showed a bimodal distribution for genotypes, SRS1108 and SRS2808 and a normal distribution for SRS1208 and SRS1608. This further suggests the presense of more than one gene, perhaps several genes in the control of low germination stimulant production. The significant variation in frequency distributions observed in the rest of the sorghum genotypes, and the appearance of few resistant individuals among the genotypes classified as susceptible (high stimulant producers) probably points to the presence of quantitative gene action in the inheritance of low germination stimulant character in the present sorghum genotypes.

Mutengwa et al. (2005) pointed out that a single recessive gene largely controlled low germination stimulant production in sorghum cultivars; SAR19 and SAR29, which were resistant to *S. asiatica*. Haussmann et al. (2001), when investigating the inheritance of the low germination stimulant production character in sorghum progenies derived from crosses of Framida and IS9830 (low stimulant producers) with E36-1 (high stimulant producer), concluded that the inheritance of the low germination stimulant character was recessive but with involvement of both major and minor genes. Haussmann et al. (2000a) reported that the low germination stimulant trait was quantitatively inherited with predominance of additive gene effects in sorghum genotypes that exhibited resistance to *S. hermonthica*.

Some of the case studies cited above suggested a single recessive gene inheritance for low germination stimulant production with probable modifications by minor genes in various sorghum genetic materials. However, based on the chi-square studies and frequency distributions observed, findings from the present study seem to differ and suggest that low germination stimulant production in the present sorghum genotypes was controlled by more than one gene in some sorghum genotypes.

5.4.2 Haustoria initiation in the extended agar-gel assay

Relatively few studies have been carried out to explore the low haustoria initiation as another mechanism of resistance to *Striga* in sorghum (Patrick et al., 2004; Mohamed et al., 2003; Mohamed, 2002). In the present study, low haustoria initiation was detected in six new sorghum genotypes namely; SRS1608, SRS608, SRS3408, SRS1208, SRS4109 and SRS2308. All the fixed sorghum lines and the remaining four genotypes were found to be high haustoria initiators. Patrick et al. (2004) found low haustoria initiation in 16 wild sorghum accessions and one cultivated sorghum; SRN39. However, Mohamed et al. (2003) and Mohamed (2002) classify SRN39 as a high haustoria initiator. The present study also found SRN39 to be a high haustoria initiator. Mohamed (2002) found low haustoria initiation only in the wild sorghum accession; P78. These limited and seemingly inconsistent findings demonstrate the need for more studies to fully understand haustoria initiation as a mechanism of resistance to *Striga* particularly in cultivated sorghum. Mohamed (2002) further indicated that maximum haustoria initiation distance was influenced by time and temperature, again indicating the need for more studies.

While Mohamed (2002) indicated that low haustoria initiation in the wild sorghum accession; P78 was controlled by a single dominant gene, no attempt was made in the present study to investigate the inheritance of low haustoria initiation in the current sorghum genotypes. This is because the numbers of sorghum seedlings that induced haustoria formation in each sorghum genotype were considerably low, presumably due to the short time in which the investigation was carried out. However, looking at both results for germination stimulant production and haustoria initiation, it can be observed that two genotypes; SRS1608 and SRS1208 had both the low germination stimulant production and low haustoria initiation mechanisms for *Striga* resistance.

5.5 Conclusions

In summary therefore, the following conclusions can be derived from this study:

- Two new sorghum genotypes; SRS1608 and SRS1208 expressed both the low germination stimulant character and low haustoria initiation as mechanisms of resistance to *S. hermonthica*.
- The sorghum genotypes; SRS2808 and SRS1108, and two fixed lines; Brhan and Hakika expressed only the low germination stimulant character, while the genotypes; SRS608, SRS3408, SRS4109 and SRS2308 expressed only the low haustoria initiation mechanism.
- The inheritance of low germination stimulant character in the present sorghum genotypes varied but seems to be controlled by more than one gene.
- There is need to carry out more studies to better understand low haustoria initiation in cultivated sorghum and investigate the genetics of its inheritance.

References

Bebawi, F.F., R.E. Eplee, C.E. Harris, and R.S. Norris. 1984. Longevity of witchweed (*Striga asiatica*) seed. Weed Research 32: 494-497.

Hess, D.E., and G. Ejeta. 1992. Inheritance of resistance to *Striga* in sorghum genotype SRN39. Plant Breeding 109: 233-241

Haussmann, B.I.G., D.E. Hess, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2000a. Analysis of resistance to *Striga hermonthica* in diallel crosses of sorghum. Euphytica 116:33-40.

Haussmann, B.I.G., D.E. Hess, G.O. Omanya, B.V.S. Reddy, H.G. Welz, and H.H. Geiger. 2001. Major and minor genes for stimulation of *Striga* hermonthica seed germination in sorghum, and interaction with different *Striga* populations. Crop Science 41: 1507-1512.

Haussmann, B.I.G., D.E. Hess, M.L. Koyama, L. Grivet, H.F.W. Rattunde, and H.H. Geiger (eds.). 2000b. Breeding for *Striga* resistance in cereals. In: Proceedings of a workshop held at IITA, Ibadan, Nigeria, 18-20 August 1999. Margraf Verlag, Weikersheim, Germany.

Kroschel, J., (ed.) 2001. A technical manual for parasitic weed research and extension. Kluwer Academic Publishers, 3300 AA Dordrecht, Netherlands.

Mohamed, A.H. 2002. Identification and characterization of genetic variants in sorghum for specific mechanisms of *Striga* resistance. PhD Thesis, Purdue University, USA.

Mohamed, A., A. Ellicott, T.L. Housley, and G. Ejeta. 2003. Hypersensitive response to *Striga* infection in sorghum. Crop Science 43: 1320-1324.

Mutengwa, C.S., P.B. Tongoona, and I. Sithole-Niang. 2005. Genetic studies and a search for molecular markers that are linked to *Striga asiatica* resistance in sorghum. African Journal of Biotechnology 4: 1355-1361.

Mutengwa, C.S. 2004. The search for molecular markers, parental characterisation and inheritance studies of witchweed (*Striga asiatica*(L.) Kuntze) resistance in sorghum (*Sorghum bicolor* (L.) Moench). PhD Thesis, University of Zimbabwe.

Omanya, G.O., B.I.G. Haussmann, D.E. Hess, B.V.S. Reddy, M. Kayentao, H.G. Welz, and H.H. Geiger. 2004. Utility of indirect and direct selection traits for improving *Striga* resistance in two sorghum recombinant inbred populations. Field Crops Research 89(2-3):237-252.

Patrick, J.R., C. Grenier, and G. Ejeta. 2004. *Striga* resistance in the wild relatives of sorghum. Crop Science 44: 2221-2229.

Payne, R.W., D.A. Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2011. An introduction to GenStat for Windows (14th edition). VSN International, Hemel, Hemstead, UK

CHAPTER SIX: GENERAL OVERVIEW

6.1 Introduction

Sorghum is presently the third most widely grown cereal crop in Uganda. Despite its importance, particularly in the semi-arid regions of the country, its production is severely constrained by *Striga hermonthica* infestation. Most of the low-land sorghum growing districts of the country are infested by this notorious weed. A majority of sorghum farmers in Uganda are subsistence farmers who are unable to apply high input *Striga* control options such as use of chemicals or mechanical means. The use of *Striga* resistant sorghum cultivars could be the most feasible control options for such farmers. The main objective of this research was to develop *Striga* resistant and high yielding sorghum genotypes for the resource poor subsistence farmers in Eastern Uganda.

6.2 The specific objectives were:

- To determine the current constraints faced by farmers in sorghum production in Eastern Uganda.
- To determine farmers' preferences for new sorghum varieties in Eastern Uganda.
- To assess the current cropping practices and determine the infestation levels and impact of *Striga* on sorghum production in Eastern Uganda.
- To determine the phenotypic and genotypic variability of African sorghum accessions for *Striga* resistance in Eastern Uganda.
- To estimate heritability for *Striga* resistance among a collection of African sorghum accessions.
- To determine the gene action effects of different sorghum cultivars and new genotypes for *Striga* resistance and grain yield.
- To investigate the existence of two or more mechanisms of resistance to *Striga* in new genotypes of sorghum.

6.3 Summary of research findings and their implications

6.3.1 Literature review

The literature review established that:

- Sorghum is one of the most widely grown staple cereal food crops in Uganda. Therefore constraints that tend to limit its productivity need to be addressed by research.
- *Striga* is one of the most important constraints limiting sorghum production in Eastern and Northern Uganda. It is now fourty years since the *Striga* problem was first reported in Uganda. The problem has persisted and is notably increasing. This indicates that there has been limited knowledge about its biology and control, and if any control options were devised, they have been ineffective.
- There has been limited progress in breeding for *Striga* resistant sorghum varieties in Africa, and probably none in Uganda. For many of the biological constraints affecting crop production, host plant resistance is one of the most feasible options of control. There is need to develop *Striga* resistant sorghum varieties if the impact of the parasitic weed on sorghum productivity is to be minimised.
- Information about specific mechanisms of resistance to *Striga* in cultivated sorghum is scanty, particularly their occurrence and type of genetic control. In order to effectively breed for *Striga* resistance in sorghum, there is need to identify the specific mechanisms of resistance that could occur in the course of host-parasite interaction, and once identified, their genetic control needs to be studied.

6.3.2 Constraints to sorghum production and farmers' varietal preferences for new sorghum cultivars

During the PRA study, it was established that:

- *Striga* is one of the most important constraints limiting sorghum production in Eastern Uganda, and it has high soil seed bank levels in infested fields. This further confirms what is reported in the literature and echoes the need for research attention to minimise crop losses due to *Striga* infestation.
- Sorghum farmers in eastern Uganda mostly preferred red grained sorghum with compact and erect heads, short plant height of 1.5m, and maturing in about three months in addition to being *Striga* resistant and drought tolerant. This probably explains the limited adoption of most of the previously released improved varieties because most of them were either white seeded or brown seeded. It therefore shows the importance of

initially interacting with farmers and understand their varietal preferences at the beginning of the breeding programme. Farmers' views can now be considered when selecting the parental lines for crossing.

- There is need to sensitise farmers about *Striga* biology and control in order to reduce its spread and institute control measures. When farmers understand the biology of *Striga*, for example the ways by which it spreads, it may be possible to institute control measures that could combat its spread, for example by uprooting before it flowers in the field.
- There is urgent need to develop and evaluate *Striga* resistant and high yielding sorghum varieties for the farmers in Eastern Uganda in order to contribute to the food security of the region.

6.3.3 The phenotypic and genotypic variability of African sorghum accessions for *Striga* resistance

Through evaluating a series of African sorghum accessions for *Striga* resistance, it was found that:

- Both phenotypic and genotypic factors contributed significantly to the variability observed among the African sorghum accessions with respect to *Striga* resistance and sorghum crop performance indicating that *Striga* resistance can be improved through selection. However, techniques that minimise environmental effects need to be employed in order to improve on heritability.
- The genotypic coefficient of variation (GCV) and genetic advane (GA) values indicated that genetic gain for *Striga* resistance can be achieved by selection based on area under *Striga* severity progress curve (AUSVPC), area under *Striga* number progress curve (AUSNPC) and *Striga* emergence.
- The sorghum genotypes SRN39, Brhan, Framida, Gubiye, Wahi, P9407 and N13 showed resistance to *Striga hermonthica* in Eastern Uganda because they consistently had low values of AUSNPC, AUSVPC and individual *Striga* counts, vigour and severity indices. These genotypes could therefore act as useful sources of resistance to *Striga* and be used as donor parents in breeding for *Striga* resistance in sorghum in Uganda.
- Panicle formation in sorghum was significantly affected by *Striga* infestation. This was shown by significantly negative correlations between all the *Striga* parameters measured and number of panicles formed in individual sorghum accessions.

- The significant positive correlation between *Striga* infestation and sorghum damage at 7 weeks after crop emergence (early stages of crop growth) re-affirms the fact that *Striga* inflicts most of its damage to sorghum even before it emerges above ground.

6.3.4 Gene action controlling *Striga* resistance and sorghum yield in new genotypes

The genetics study found that:

- There was significant genetic variation for *Striga* resistance in the new sorghum genotypes generated. This shows that it is possible to genetically improve *Striga* resistance in sorghum.
- The additive gene action was important in controlling *Striga* resistance, indicating that resistance can be effectively improved through selection.
- There was also significant genetic control for sorghum head length and plant height, with preponderance of additive genetic effects indicating that improvement can be achieved through selection. During the participatory rural appraisal (PRA) carried out at the initial stages of this study, farmers indicated preference for short sorghum varieties of 1.5m, and erect/long and compact heads. The new sorghum genotypes: SRS1408, SRS1508, SRS2408, SRS2608 and SRS2908 had plant heights ranging from 109.1cm to 138.8cm when grown at Serere. These genotypes are closer to the farmers' preferred plant height of 1.5m, hence the study could be said to have met the farmers' expectation for plant height. Furthermore, the genotypes SRS3408, SRS5309, SRS1608 and SRS2908 had the longest heads, which were on average, 20% longer than the available sorghum varieties in the region. Therefore, there was an improvement in head size in the new genotypes, which was another expectation from farmers during the PRA.
- The sorghum parental lines: Brhan, SRN39, Hakika and Sekedo can be used as sources of *Striga* resistance genes when breeding for new *Striga* resistant sorghum varieties.
- The new sorghum genotypes: SRS1608, SRS3408, SRS2408, SRS4609, SRS3108, SRS2908, SRS2609, SRS609 and SRS1708 were resistant to *Striga hermonthica* in the field. These genotypes can now be either backcrossed to high yielding parents to improve on their yield, or forwarded to advanced generations where deliberate selection can be done for *Striga* resistance and high yield.
- The parental lines; Sekedo, Brhan and Framida could be used as sources of genes for grain yield increase in a breeding programme.

- The highest yielding sorghum genotypes were SRS609, SRS1408, SRS2608 and SRS3408. These genotypes could be forwarded to advanced generations where, through careful selection, the genes for high yield can be fixed in them.

6.3.5 Expression of the low germination stimulant production and low haustoria initiation traits as mechanisms of *Striga* resistance in new sorghum genotypes

The laboratory investigation revealed that:

- Two new sorghum genotypes; SRS1608 and SRS1208 expressed both the low germination stimulant character and low haustoria initiation as mechanisms of resistance to *S. hermonthica*. Resistance in these genotypes is expected to be more durable than those with single mechanisms of resistance. Under field evaluation, the two genotypes supported very few *Striga* plants (2 and 4 *Striga* plants m^{-2} respectively). SRS1608 was particularly scored as resistant under field conditions.
- The sorghum genotypes; SRS2808 and SRS1108, and two fixed lines; Brhan and Hakika expressed only the low germination stimulant character, while the genotypes; SRS608, SRS3408, SRS4109 and SRS2308 expressed only the low haustoria initiation mechanism.
- The inheritance of low germination stimulant character in the present sorghum genotypes varied and appeared to be controlled by more than one gene in some of the genotypes. This supports the quantitative gene action model in the control of low germination stimulant production. This implies that *Striga* resistance can be improved through acquiring resistance from different sources and application of suitable selection criteria.
- There is need to carry out more studies to better understand low haustoria initiation in cultivated sorghum and investigate the genetics of its inheritance.

6.4 The way forward

Development of *Striga* resistant sorghum varieties needs to be prioritized in order to improve sorghum productivity in Uganda. In breeding for *Striga* resistance, individual mechanisms conferring resistance in the course of the host-parasite interactions, and their genetic control need to be understood. Emphasis should then be geared towards developing varieties carrying multiple mechanisms of resistance. Such resistance is expected to be more durable than single mechanism resistance. When resistant varieties are available, they can be used in an integrated strategy with other control options to effectively minimize the effects of *Striga* on sorghum productivity.