# Genetic analysis of upland rice for grain yield and some agronomic traits under *Striga hermonthica* infestation in Uganda

By

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# Abstract

Rice (*Oryza sativa* L.*)* has become a major food and cash crop grown in many districts in Uganda. However, its productivity is low due to an array of biotic and abiotic constraints including infestation by the weed *Striga hermonthica*. This parasite is endemic in Uganda, and affects all forms of cereal production, especially in areas where soils are degraded, prone to adverse effects and it is common to find yield losses ranging from 30 to 100%. Breeding of resistant varieties could offer a long-term sustainable solution to the *Striga* problem affecting rice production in Uganda. Consequently, the overall objective of this research was to develop high yielding and adaptable upland rice varieties with resistance to *Striga hermonthica*. The specific objectives were: (i) to assess genetic diversity of upland rice germplasm in Uganda, (ii) to determine genetic variability, correlations, direct and indirect effects of various attributes on yield of upland rice under *Striga* infestation, (iii) to determine the gene action responsible for yield and other performance traits under *Striga* infestation, and (iv) to test the effect of genotype x environment (GE) interaction on yields of upland rice under *Striga* infestation.

Assessment of genetic diversity was conducted in central Uganda at the Namulonge Agricultural Research Institute. One-hundred and sixty genotypes were laid out in a 10 x 16 alpha lattice design with two replications. After 3 weeks, leaf samples of 157 genotypes (three genotypes did not germinate) were sent to Nairobi (the BecA Laboratory) for genotyping using 30 simple sequence repeats (SSR) markers. Data were analysed using Power Marker and DARwin software, and showed that moderate genetic diversity existed in the population (50.98%). It divided the genotypes into three major clusters with several subgroups. Two-hundred and seventy-four alleles were detected with a mean of 9.13 alleles per locus. Polymorphism information content (PIC) values ranged from 0.11 (RM324) to 0.86 (RM257) with a mean of 0.48 per marker, indicating that the chosen markers were usefully informative. This analysis will guide future choices of unrelated parent material for breeding while avoiding inbreeding.

To establish genetic variability, correlations and other relationships; all of the 160 genotypes used in the diversity study were subjected to attack by *Striga hermonthica* in three fields considered to be *Striga* hotspots and were scored for resistance. At each of the three sites, Bukedea, Kumi and Pallisa the trials were conducted for 2 seasons in 10 x 16 alpha lattice design with two replications. Agronomic data of the crop as well as developmental data of *Striga* was recorded and analysis of variance was conducted to explore variability through mean performance and coefficients of variation. Furthermore, correlations, direct and indirect effects of some upland rice agronomic traits and effect of *Striga* resistance traits on grain yield

were estimated. Highly significant differences ($p<0.001$) were observed for all the characters studied. The mean performance of the genotypes revealed the highest yielding genotypes were NERICA 10 (5545.07 kg $ha^{-1}$), Faro 39 (4684.51 kg $ha^{-1}$) and ART16-21-5-12-3-1-2-1 (4635.58 kg $ha^{-1}$). Estimates of phenotypic coefficient of variability were generally higher than the corresponding genotypic coefficients of variability for all characters studied implying a substantial environmental influence on the performance of the traits. Heritability estimates were generally low (a mean of 30.56%) for most of the traits studied. Grain yield recorded the highest genetic advance (GA) (65.77) followed by area under *Striga* number progressive curve (AUSNPC) (54.05), number of grains per pod (NGPP) (31.88), Number of pods per plant (NPPP) (6.24) and a thousand grain weight (TGW) (4.59); meaning that it is beneficial to select for these traits. The highest direct phenotypic and genotypic effects to grain yield per hectare were obtained from number of grains per panicle (0.830, 0.882), number of panicles per plant (0.380, 0.438) and 1000-grain weight (0.250, 0.285). The phenotypic direct effects of these three traits were positive and slightly greater or equal to their phenotypic correlations with yield, that is, 0.83 > 0.8, 0.38 > 0.27 and 0.25 = 0.25 for NGPP, NPPP and TGW respectively. These results mean that NGPP, NPPP and TGW are the traits $ha^{-1}$ that can be used for direct selection for improved grain yield in rice.

For determination of gene action responsible for yield and other performance traits under *Striga* infestation, ten *Striga hermonthica* resistant and ten *Striga hermonthica* susceptible genotypes were crossed in a North Carolina II (NCD II) mating design. Sixty $F_2$ crosses together with their 20 parents were evaluated at two sites; Bukedea and Pallisa under *Striga* infestation. However, only 35 crosses fitted a complete 5 x 7 NCDII and together with their parents were used for determination of gene action. Using yield under *Striga* infestation as a resistance trait' the study revealed that resistance to *Striga hermonthica* was controlled by both additive and non-additive gene action with the non-additive effects being stronger than the additive effect. Some of the $F_2$ progeny outperformed the parents in grain yields under *Striga* infestation. The $F_2$ progeny that gave the highest yields were NERICA 8 x NERICA 3, NERICA 12 x NERICA 10, NERICA 7 x NERICA 1, and NERICA 9 x NERICA 5 and NERICA 11 x NERICA 5, NERICA 12 x NERICA 3; IR 64 x NERICA 6 gave the lowest yields. Yield, plant height at maturity, syndrome damage score and days to flowering were under the control of additive gene action. On the other hand, yield, plant height at maturity and days to flowering also exhibited significant female by male interaction effects indicating presence of non-additive gene action as well. However, estimates of relative contributions to General combining ability (GCA) sums of squares revealed preponderance of the additive gene action in the inheritance of *Striga* resistance in upland rice. The study identified parents NERICA 3, NERICA 10, NERICA 5, IG10, NERICA 8, NERICA 12 and WAB56-50 as exceptionally good sources of

genes for resistance to *Striga hermonthica* since they gave the lowest negative GCA effect for *Striga* syndrome damage score. While on the other hand NERICA 12, WAB56-104, NERICA 10, NERICA 14 and IR 64 are good sources of genes for higher grain yield since they gave the highest GCA effect for grain yield. Conclusively NERICA 10 and NERICA 12 have combined genes for both resistance and high grain yields. The favourable GCA inbred parents and superior $F_2$ progeny will provide a basis for future development of *Striga* resistance genotypes for use in *Striga* prone areas.

To test the effect of GE interactions on yield of upland rice under *Striga* infestation, 156 genotypes and 4 check varieties were grown in three sites under artificial infestation of *Striga hermonthica* for two seasons. At each site, the experiments were laid out in 10 x 16 alpha lattice designs with two replications. Analysis of GE was conducted for yield and days to *Striga* emergence (DSE). The study revealed the most stable high yielding and thus ideal genotypes as SCRID006-2-4-3-4, ART3-3L7P1-B-B-3, WAB706-3-4-K4-KB-3 and NERICA 10. Genotypes such as SCRID079-1-5-4-2, NERICA 14 and P29 1 (14), were high yielding but quite unstable. The most stable and *Striga* resistant genotypes were WAB706-3-4-K4-KB-3, NERICA 10, WAB880-1-38-19-23-P1-HB and ART3-3L7P1-B-B-3. Genotypes such as FARO 39, NERICA 8, ART10-1L12E2-1-B-1 and ART12-1L4P7-21-4-B-3 were resistant to *Striga* but highly unstable. Genotypes ART3-3L7P1-B-B-3, WAB706-3-4-K4-KB-3 and NERICA 10 combined both high yield and days to *Striga* emergence

# Declaration

I, Mary Teddy Asio, declare that:

1. The studies reported in this thesis except where otherwise indicated, is my original work.

2. This thesis has not been submitted to any university for any degree or examination.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

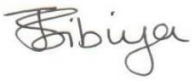
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then their words have been paraphrased and summarised but the general information attributed to them referenced.

5. Finally, the thesis present herein 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 sections

Sign  4/92018

Mary Teddy Asio Date

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

Sign  4/9/2018

Dr. Julia Sibiya Date

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Prof. John Derera Date

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Prof. Pangirayi Tongoona Date

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# Dedication

**TO GOD**

For whom all things are possible!

The author and finisher of all that is!

The Lion of Judah!

**Who enabled me to finish this thesis.**

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# Acronyms

GDP: Gross Domestic Product

SSA: Sub Saharan Africa

FAO: Food and Agricultural Organization

FAOSTAT: The Statistical Data Base for the Food and Agricultural Organisation

IRRI: International Rice Research Institute

NARO: National Agricultural Research Organisation

NACRRI: National Agricultural Crop Resources Research Institute

NASARRI: National Semi-Arid Resources Research Institute

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# Thesis Introduction

## Background to the study

Rice is a major food and cash crop grown in many districts of Uganda. Its cultivation increased particularly after the introduction of upland varieties that are high yielding and resistant to most of the biotic and abiotic stresses (Ahmed, 2012). The government of Uganda has specifically identified rice production as a major intervention in the fight against food insecurity and poverty, because it improves incomes of the rural households (Kijima et al., 2006; MAAIF, 2009). Upland rice in particular has been promoted in preference to the irrigated rice (Lamo et al., 2007); because irrigation is expensive for the subsistence farmers, who dominate the sector and paddy rice has aroused cultural, health and environmental concerns (Odogoola, 2006). Consequently, upland rice production in Uganda currently covers 71% of total area under rice production (Gitau et al., 2011; Ahmed, 2012).

In spite of becoming a staple crop with a per capita consumption that is increasing because of changes in patterns of consumption, population growth and urbanization (FAOSTAT, 2010; Ahmed, 2012); Uganda is a net importer of rice and will continue to do so unless domestic rice production improves significantly (Kijima et al., 2012; Kikuchi et al., 2014). Numerous constraints contribute to low yields in upland rice production in Uganda, including biotic, abiotic and socioeconomic factors (Biruma et al., 2003; Odogoola, 2006). However, among the biotic factors; weeds are the most significant factor reducing yield in rice (Waddington et al., 2010). This is because rice is a weak competitor against weeds in infertile dry land soils (WARDA, 2009; Balasubramanian et al., 2007). Several weed species cause losses to rice production but the genus that poses the greatest threat to rice production is *Striga* (Rodenburg et al., 2010; Jamil et al., 2011).

## Problem statement

An estimate of 107,799 ha of arable land in Uganda are infested by *Striga* spp. (MacOpiyo et al., 2010). The two primary species, *Striga hermonthica* and *Striga asiatica* are endemic in Uganda and pose some of the most severe biological constraints to cereal production (Olupot et al., 1999; Ejeta, 2010). *Striga* damage is more severe in low potential areas, and areas where farmers apply limited fertilisers. At these sites, it is common to find yield losses up to 100% of the crop (Dugje et al., 2006; Rodenburg et al., 2010; Spallek et al., 2013). Infestation can become so severe that farmers abandon their fields (Badu-Apraku et al., 2010; Kountche et al., 2013).


**Figure 1.1: Distribution of Striga weeds in Uganda (Adapted from MacOpiyo et al., 2010)**

Yield losses caused by *Striga* in rice production in Uganda have not been established. However, Atera et al. (2012) reported yield losses of 33 to 90% in upland rice due to *Striga hermonthica* infestation in Western Kenya, and yield losses of up to 60 to 100% due to heavy infestation of *Striga* in sorghum have been reported in Uganda (Ebiyau and Ouma, 1995; NARO, 1997). Furthermore, previous agricultural needs assessments conducted in Uganda have also identified *Striga* to be a widespread constraint to cereal production in the Lango and Teso farming systems of the north and eastern Uganda (Riches, 2000), as well as in the west Nile region and some districts in western Uganda (Fig 1) where cereals are grown (MacOpiyo et al., 2010).

## Justification of the study

Upland rice, which is mainly grown as a subsistence crop in Africa, plays a big role in the local food security of poor communities that do not have access to wetland fields (Balasubramanian et al., 2007). In Uganda, the government has shifted emphasis from promoting paddy rice to promoting cultivation of upland varieties in a deliberate effort to prevent the fragile wetland ecosystem (Lamo et al., 2010). In addition, a careful appraisal of available strategies revealed that upland rice is easier to cultivate compared to traditional paddy varieties, most varieties are resistant to pests and diseases, have shorter growing periods, respond well to low rainfall as long as it is well distributed during the growing phase with less risks of health problems like bilharzia and paddy yields are significantly lower than those reportedly obtained by growing upland varieties (Oonyu, 2011). Consequently, the above reasons have led to more research attention being drawn towards upland rice; resulting in the increase of rice production in Uganda. Upland rice constitutes over 71% of total area under rice production in Uganda (Gitau et al., 2011)

Since the introduction of NERICA, rice production has shown an upward trend both in acreage and in volume of production (Ahmed, 2012). However, adequate production of rice in Uganda and the rest of Africa is seriously hampered by parasitic weeds among other factors (Jamil et al., 2011; Rodenburg et al., 2015). In particular, *Striga hermonthica* is a critical constraint to production for subsistence upland rice production (Rodenburg et al., 2010; Spallek et al., 2013). Hence, control of this weed would contribute substantially to rural food security and poverty alleviation in Uganda. Furthermore, to meet the growing food needs and overcome malnutrition, rice varieties with higher yield potential and multiple resistance to biotic and abiotic stresses as well as improved nutritional qualities are needed (Khush et al., 2003). In areas where *Striga* is endemic, the immediate answer to successful crop production lies in good farming practices, i.e. with adequate inputs. However, resource-poor subsistence farmers cannot afford the level of inputs that are required. Therefore, they need low input technologies that are easy to apply. Several methods have been advanced for the control of *Striga* and these include cultural, chemical, host resistance and biological control methods. However, previous evaluations of these methods has revealed that no single method is effective on its own, and that they need to be used in an integrated approach (Oswald, 2005; Rodenburg et al., 2010; Kountche et al., 2013; Rich and Ejeta, 2008). Host plant resistance is the most economically feasible and environmentally friendly means of *Striga* control (Haussmann et al., 2000; Swarbrick et al., 2009; Atera et al., 2012) and therefore it is imperative to include host resistance in the mixture of approaches adopted in any Integrated *Striga* Management (ISM) regime.

For resource-poor farmers who usually cannot afford to apply mineral fertilizers, incorporation of host plant resistance into *Striga* management is more likely to be adopted as a means to control the parasite. Consequently, identification and utilisation of *Striga* resistant / tolerant cultivars is required for all of the important cereals such as sorghum, finger millet, maize and upland rice. However, in Uganda previous efforts in this regard have only concentrated on sorghum and to date *Striga* tolerant sorghum lines like Seredo and Epuripur are available in the country (Olupot et al., 1999; Riches, 2000). Nevertheless, there are no reports on previous attempts to control parasitic weeds with relevance to upland rice production in Uganda. Consequently, the current study or investigation was targeting to develop suitable high yielding and *Striga* resistant upland rice cultivars through improving associated quantitative and qualitative traits.

Previous assessments on interaction of *Striga hermonthica* with some rice genotypes including the interspecific upland New RICe for Africa (NERICA) cultivars which are popular amongst subsistence farmers (Kaewchumnong and Price, 2008; Cissoko et al., 2011; Jamil et al., 2011); have revealed variable reactions, ranging from high susceptibility to good tolerance and resistance. This indicates that genes for *Striga* resistance or tolerance exist in the rice germplasm and these can be further studied to enhance knowledge on the resistance trait and promote breeding for *Striga* – resistant genotypes. In addition, a successful breeding program requires a high degree of genetic diversity among the progeny (Ukalska et al., 2006; Manyasa et al., 2015). This can be achieved by using unrelated and diverse parents in hybridisation to minimise inbreeding but boost genetic advance since genetic distance between parents is reported to be positively correlated to heterosis of the hybrids (Adedze et al., 2012). Thus the need to conduct diversity analysis to measure genetic distances among the available collections. The rice program in Uganda holds germplasm obtained from various sources, which is a good resource for breeding; but their genetic distances were unknown.

A couple of studies in Sub–Saharan Africa (SSA) and elsewhere have documented instances of resistance to *Striga hermonthica* in upland rice (Cissoko et al., 2011; Jamil et al., 2011; Atera et al., 2012). However, the genetics of host plant resistance in rice is still limited, hence the need to explore genetic studies to aid in determining traits for enhancement of yield potential (Jagadeesan and Ganesan, 2006). Most of the resistance to *Striga* in cereals appears to be polygenic (Kim, 1994; Amusan, 2010), however, some studies have found resistance to *Striga* to be controlled by both major and minor genes (Volgler et al., 1996; Kaewchumnong and Price, 2008).

Development of varieties having high yield as well as good yield determining attributes requires information regarding the nature and magnitude of heritable variation in the available germplasm (Kumar and Senapati, 2013). This information is applicable in selection of parents among inbred lines or selection of advanced lines prior to release. Selection based on a single trait may not always be effective, yet on the other hand, it is not practical to select for a large number of traits concurrently in one selection scheme. The solution here is to use correlation analysis to identify those traits, which greatly contribute to yield. Better still path coefficient analysis provides an effective tool for partitioning the correlation coefficient into direct and indirect effects of cause and effect nature (Soni et al., 2013). In order to achieve meaningful response to selection in a given breeding program, assessment of genetic variability is indispensable; because estimates of genetic parameters of variation are specific for a particular population and the phenotypic expression of the quantitative characters may be altered by environmental stress that affect plant development and growth (Idahosa et al., 2010).

Furthermore, the issue of adaptation to wide or specific environments needs to be addressed through multi- environment trials (Mohammadia et al., 2015). Rice genotypes would respond differently to *Striga* infestation as influenced by different environmental factors such as soil nutrients, climate and agronomic practices (Bose et al., 2014). Genotype x environment interaction (GE) and yield-stability analysis are important in measuring varietal suitability and stability for cultivation across seasons and ecological zones (Nassir and Ariyo, 2011). Genotype x environment interaction analysis in rice, especially the upland-rain fed cultivation in *Striga* prone areas has not received adequate attention comparable to the crops' importance. The ultimate goal of this research is to develop varieties that are high yielding, resistant to *Striga hermonthica*, adapted to a wide range of environments and adoptable by farmers. Adaptability of a genotype to diverse environments is tested by its level of interaction with the target environments and a genotype is said to be stable if it has a high mean performance for the measured traits with less fluctuation across environments (Tariku et al., 2013). Therefore, evaluation of the genotypes, environments and their interactions on yield and resistance traits of upland rice grown under *Striga* infestation is imperative.

## Objectives of the research

The overall objective was to enhance rice productivity in Uganda by developing *Striga* resistant rice varieties that are high yielding and adaptable in Uganda.

The specific objectives were to:

(i) assess genetic diversity in some upland rice germplasm in Uganda using SSR markers,

(ii) determine genetic variability, correlations, direct and indirect effects of various secondary traits on yield of upland rice under *Striga* infestation,

(iii) study the gene action responsible for yield and some other performance traits under *Striga* infestation,

(iv) assess the effects of genotype x environment interaction (GE) on yield of upland rice under *Striga* infestation, and identify genotypes with stable high yield potential under *Striga* infestation.

## Research hypotheses

(i) There is significant genetic diversity in upland rice germplasm collection in Uganda.

(ii) There are important relationships between secondary traits and grain yield in upland rice grown under *Striga* infestation.

(iii) Additive gene action is responsible for yield and some other performance traits under *Striga* infestation.

(iv) Performance of upland rice under *Striga* infestation can be affected by genotype x environment interaction (GE) which complicates selection of new genotypes that combine high yield potential with high stability under *Striga* infestation.

## Structure of the thesis

This thesis is organized into six chapters as follows:

**Chapter one:** Literature review

This chapter outlines relevant literature related to the study of genetic analysis of upland rice under *Striga hermonthica* infestation. It covers origin and domestication of rice, taxonomy, importance and constraints of rice. Followed by important aspects of *Striga hermonthica*; its occurrence and distribution as a constraint in upland rice, biology, its economic losses, control options, host plant resistance mechanisms, gene action and inheritance of host plant resistance and a few other topics; pointing out the critical gaps that gave rise to this study.

**Chapter Two:** Assessment of Genetic Diversity of Upland Rice Germplasm Using SSR Markers.

With an objective of estimating the nature and magnitude of genetic diversity present among some of the available upland rice genotypes in Uganda; this chapter outlines how 157 genotypes of upland rice were evaluated using 30 simple sequence repeat (SSR) markers. A total of 274 alleles were detected with an average of 9.13 alleles per locus. Based on this, genetically diverse groups were identified.

**Chapter Three:** Genetic and path coefficient analysis of yield of upland rice under *Striga* infestation in Uganda.

This chapter attempts to estimate genetic variability among rice genotypes and study relationships among traits under *Striga* infestation using path coefficient analysis. The overall aim of the study was to obtain information that could be useful in upland rice improvement for increased yield and resistance to *Striga hermonthica*. The highest direct phenotypic and genotypic effects to grain yield per hectare were obtained from number of grains per panicle, followed by number of panicles per plant and 1000-grain weight. This meant that these traits could be used for direct selection for grain yield in rice under *Striga* infestation.

**Chapter Four:** Gene action for grain yield and associated traits in upland rice under *Striga hermonthica* infestation in Uganda.

This chapter explains how gene action for grain yield and associated traits in upland rice under *Striga hermonthica* infestation in Uganda was assessed by crossing resistant and susceptible upland rice genotypes in a North Carolina Design II mating design. The key findings of this study were that grain yield of upland rice was under the control of both additive and non-additive gene action, while the study revealed preponderance of the additive gene action in the inheritance of *Striga* resistance in upland rice. The study identified parents NERICA 3, NERICA 10, NERICA 5, IG10, NERICA 8, NERICA 12 and WAB56-50 as exceptionally good sources of genes for resistance to *Striga hermonthica* since they gave the lowest negative GCA effect for *Striga* syndrome damage score. While on the other hand NERICA 12, WAB56-104, NERICA 10, NERICA 14 and IR 64 are good sources of genes for higher grain yield since they gave the highest GCA effect for grain yield. In conclusion, NERICA 10 and NERICA 12 have combined genes for both resistance and high grain yields.

**Chapter Five:** GGE-biplot and non-parametric analysis of genotype x environment interaction on yield of upland rice grown under *Striga hermonthica*

This chapter presents findings of a study aimed at analysing effects of genotype x environment interaction on yield of upland rice under *Striga* infestation, and identifying suitable genotypes for use in breeding high yielding and stable varieties that could be deployed in *Striga* infested areas. This was done through GGE–biplot analysis and non-parametric stability analyses. Two traits; grain yield and days to *Striga* emergence (DSE) as an indicator of resistance were found to be significantly sensitive to GE and for both traits, the nature of GE detected was the crossover type which implied selection of genotypes for specific adaptation. The most stable and high yielding and thus ideal genotypes included 30 (SCRID006-2-4-3-4), 35 (ART3-3L7P1-B-B-3), 94 (WAB706-3-4-K4-KB-3) and 46 (SCRID079-1-5-4-2). Genotypes such as 68 (NERICA 10), 105 (NERICA 14) and 113 (P29 1 (14)), were high yielding but unstable and would be selected for specific adaptation. GGE biplot analysis for DSE revealed the most stable and *Striga* resistant genotypes as 125 (ART10-1L12E2-1-B-1), 85 (NERICA 16), 160 (WAB880-1-38-19-23-P1-HB) and 53 (ART2-9L3P3-B-B-4

**Chapter Six:** Research overview and recommendations

This last chapter summarizes the findings from the different studies in the thesis.

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# Chapter 1 : Literature Review

## 1.0 Introduction

This chapter consists of an overview of relevant literature related to the study of genetic analysis of upland rice under *Striga hermonthica* infestation. The chapter covers origin and domestication of rice, taxonomy, importance and constraints of rice. It then dwells on important aspects of *Striga hermonthica*; its occurrence and distribution as a constraint in upland rice, its economic losses, biology, control options, host plant resistance mechanisms, gene action and inheritance of host plant resistance. Other topics reviewed include genetic diversity studies, genetic diversity of rice, use of molecular markers in diversity studies of rice, correlations, path analysis and effects of genotype by environmental interaction in breeding; pointing out the critical gaps that gave rise to this study.

## 1.1 Origin and domestication of rice

Two cultivated species were domesticated under different environmental conditions (Fiskesjö and Hsing, 2011). *Oryza sativa* was domesticated in South and Southeast Asia and has *O. rufipogon* and *O. nivara* as its direct progenitors (Jiang and Liu, 2006; Xu et al., 2012 ). *O. glaberrima* comes from tropical West Africa and has *O. barthii* as progenitor (Khush, 1997). *Oryza sativa* was first domesticated in Asia possibly 10,000 to 15,000 years ago (Jiang and Liu, 2006; Wei et al., 2012). Molecular evidence suggests it was domesticated at least twice independently in widely different locations from different ecotypes of the wild ancestors of the *O. rufipogon* and *O. nivara* (Fuller, 2011). Two mega centres of diversity are observed: one centred in Yunnan province of China and stretching west to Nepal and east to the Red river delta of northern Vietnam; and the second centred in northern India and Bangladesh (Ting, 1957; Fuller et al., 2009; Wei et al., 2012). *O. glaberrima* is indigenous to the upper valley of the Niger River in West Africa where it was domesticated from *O. barthii* (Chang, 1976; Ruaraidh, 2010). However, *O. sativa* is more widely grown throughout all the rice growing environments around the world including the indigenous home of *O. glaberrima,* which did not spread outside its region of origin (Hill, 2010).

## 1.2 Taxonomy of rice

Rice belongs to the grass (*Gramineae* or *Poacae*) family. The genus *Oryza* classified under the tribe *Oryzeae*, subfamily *Oryzoideae* is a complex but relatively small genus with two (*Oryza sativa* Lour. and *Oryza glaberrima* Steud) cultivated and 22 wild species distributed throughout the tropics and subtropics (Khush, 1997; Ge et al., 1999; Vaughan et al., 2004).

Morphological, cytological, and molecular divergence studies have classified the species of *Oryza* into ten genome groups, namely AA, BB, CC, BBCC, CCDD, EE, FF, GG, HHJJ, and HHKK (Aggarwal et al., 1997; Khush, 1997; Ge et al., 1999). The basic chromosome number of the genus *Oryza* is 12, but within the genus, genome size varies several-fold (Iyengar and Sen, 1978; Martinez et al., 1994; Uozu et al., 1997) polyploidy exists, and there are structural chromosomal changes between species (Huang and Kochert, 1994; Jena et al., 1994; Hass et al., 2003). The cultivated species, *O. sativa* and *O. glaberrima* are both designated as AA genome diploids (2*n* = 2x = 24). However because *O. glaberrima* does not pair well with *O. sativa* it has been given a genome formula AgAg (Sleper and Poehlman, 2006a). *O. rufipogon* the progenitor of *O.sativa* together with *O. longistaminata* and *O. sativa* form the *O.sativa* complex (Takeoka, 1962). The comparative ease of interspecific crosses within this complex has resulted in the effective use of the wild species for transferring new traits into *O. sativa*, particularly for disease and pest resistance and also a number of other genes, including CMS (cytoplasmic male sterility) genes used to start the hybrid rice industry (Ruaraidh, 2010).

## 1.3 Importance of rice

Rice (*Oryza sativa* L.*)* is one of the most important food crops in the world, providing 20% of the per capita energy and 13% of the per capita protein worldwide (Yamamoto et al., 2009; Soni et al., 2013). It is a staple diet in many Asian countries as well as many developing countries in Africa (IRRI, 2013). According to Soni et al. (2013), more than 91% of the world's rice is grown and consumed in Asia. Furthermore, the origins of *Oryza sativa* are also traced to Asia (Sharma et al., 1997; Sleper and Poehlman, 2006b). However, several other developing countries in Latin America, the Caribbean and sub-Saharan Africa (SSA) grow rice and it plays an important role in the national economies of those countries (FAO, 2015). The major role of rice in developing countries is its contribution to the Gross Domestic Product (GDP) through foreign currency earning or reduction of the import bill as well as being a staple food. In those countries, rice accounts for 715 kcal/capita/day; 27% of dietary energy supply, 20% of dietary protein and 3% of dietary fat (FAO, 2004; Yuliar, 2014).

Rice has become a highly strategic and priority commodity for food security in Africa. It is the fourth most important cereal grown in Africa following maize, sorghum and millet based on area under cultivation (Table 1.1). In addition, rice consumption is growing faster than that of any other major staple on the continent because of high population growth, rapid urbanization and changes in eating habits (Seck et al., 2013).

**Table 1.1**: Area and Production of selected cereal crops in Africa

| Crop | Africa (2012) | |
|---|---|---|
| | **Area (ha)** | **Production (t)** |
| Maize | 34, 075, 972 | 70, 076, 591 |
| Millet | 19, 998, 008 | 16, 008, 838 |
| Rice, Paddy | 11, 206, 813 | 28, 798, 202 |
| Sorghum | 23, 142, 595 | 23, 350, 064 |
| Wheat | 10, 224, 952 | 24, 704, 201 |
| **Total** | **98, 226, 080** | **162, 422, 507** |

**Source: FAOSTAT (FAO Statistics Division 2015)**

With a harvested area increase of 105% and a production growth of 170%, rice is the fastest growing cereal commodity in this region than anywhere in the world (FAO, 2008). In SSA alone, rice is grown and consumed in more than 40 countries where it is perceived as the most suitable crop in the fight against hunger and poverty (Nwanze et al., 2006). However, on the contrary, local rice production cannot meet the increasing demand in many SSA countries; consumption of rice in the subcontinent exceeds its production (IRRI, 2013; Nasrin et al., 2015). Consequently, SSA accounts for 25% of global rice imports at a cost of more than US$1.5 billion per year (Lançon and Erenstein, 2002). The major reason for this deficit is that the average rice yields in SSA are the lowest in the world: 1.4 t $ha^{-1}$ compared to Asia's average of 4.0 t $ha^{-1}$ and more than 6.0 t $ha^{-1}$ in China alone (Nwanze et al., 2006). Moreover, small-scale farmers constrained by low resource inputs (Moukoumbi et al., 2011) mainly grow it.

**Table 1.2**: Rice production area in Uganda 4

| Area (ha) '000' | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Year | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | Average |
| Maize | 780 | 819 | 844 | 862 | 942 | 1032 | 1063 | 1094 | 1000 | 899.6 |
| Sorghum | 294 | 308 | 314 | 321 | 340 | 355 | 364 | 373 | 350 | 326.7 |
| Millet | 420 | 429 | 437 | 200 | 192 | 167 | 172 | 175 | 180 | 289.5 |
| Rice | 102 | 113 | 119 | 128 | 86 | 87 | 90 | 92 | 93 | 99 |
| Wheat | 9 | 10 | 11 | 11 | 12 | 12 | 13 | 14 | 14.2 | 11.3 |

**Source: FAOSTAT, 2015**

## 1.4 Rice production and consumption in Uganda

In Uganda today, rice is a major food security crop as well as a cash crop grown in many districts of the country. Its cultivation has particularly increased after the introduction of upland varieties (Ahmed, 2012). With an average area coverage of 99,000, ha in the last decade (Table 1.2) together with an estimated annual output of 185,073 tonnes, rice has had a steady increase in area planted and output (UBOS, 2004; FAOSTAT, 2015). Previously, rice was grown on a small scale on lowlands until recently when the country adopted upland rice varieties after the release of NERICA 1, 4 and 10 by the National Agricultural Research Organization in 2002 (Anon, 2009). Although rice ranks fourth (Table I.2) amongst the cereals grown in the country, the government of Uganda has identified rice production as a major intervention in the fight against food insecurity and poverty in the country, since it improves incomes of the rural households (Kijima et al., 2006; MAAIF, 2009). Because of this, land is being brought under rice production at a rate of 4,000 ha per year (Imanywoha, 2001; FAOSTAT, 2015).

Upland rice in particular is being promoted in preference to the irrigated rice (Lamo et al., 2007). This is because irrigation is expensive and out of reach of the subsistence farmers who dominate the sector and paddy rice has aroused cultural, health and environmental concerns (Odogoola, 2006). Consequently, upland rice production in Uganda currently

constitutes 71 percent of total area under rice production (Gitau et al., 2011; Ahmed, 2012). As a cereal cash crop, rice has been found to give the best economic return to the peasant farmers based on labor per man/day/ha (Imanywoha, 2001). Rice has the highest returns on investment among cereals grown in the country (APC, 1997; NAADS, 2003; Jagwe et al., 2005). For example, Kijima et al. (2006) reported that rice grown in Uganda had an output to input ratio of 1.83 while other common cereals such as maize hybrids and sorghum stood at 1.2 and 1.6 respectively. However, in spite of becoming a staple crop with a per capita consumption that is increasing because of changes in patterns of consumption, population growth and urbanization (FAOSTAT, 2010; Ahmed, 2012); available statistics show that Uganda is a net importer of rice and will continue to do so unless domestic production improves significantly (WorldBank, 1993; Hyuha, 2006). Domestic production is still running below the demand, implying that Uganda may continue to be a net importer of rice for a while.

The major cause of this deficit is attributable to yield gaps. NERICA varieties, which are widely adopted in Uganda, have got a yield potential of 4.5 -5.0 t $ha^{-1}$ with good agricultural practices, but on farmers' fields, it is just 1.5 - 2.2 t $ha^{-1}$(WARDA, 2001). Furthermore, like most countries in SSA, the challenge with rice production in Uganda is that production is increasing at a lower rate than the population growth (Anon., 2009). Thus, Uganda is not self-sufficient. Although production is increasing because of expansion of land area, productivity per unit area is still unsatisfactory (Ogwang, 2002).

## 1.5 Constraints of rice production in Uganda

Numerous constraints contribute to the yield gap in rice production in Uganda. Constraints that persistently jeopardize rice productivity in Uganda include biotic, abiotic and socio-economic factors. The problematic biotic factors include weeds, diseases such as rice yellow mottle virus and rice blast (Biruma et al., 2003), pests such as African rice gall midge (Abong, 1999) and stem borers (Obaa et al., 2005). Abiotic factors include drought (Lamo et al., 2007), eroded and infertile soils, high temperatures and erratic rainfall (Diiro et al., 2015). In addition, Uganda is vulnerable to climate change because of the over-dependence on rain-fed agriculture and the high incidence of poverty (CGIAR, 2007). Other constraints such as poor cultural practices (NARO, 2005) and lack of inputs (Odogoola, 2006) are the socio-economic issues arising from poverty and lack of knowledge by subsistence farmers.

Among the biotic factors, weeds are the most significant yield reducing factor (Johnson et al., 1997b). This is so because rice is a weak competitor against weeds in infertile dry land soils (WARDA, 2009; Balasubramanian et al., 2007). Damage caused by weeds is usually immense and estimated yield losses due to weeds range from slight to total loss. Although the actual yield losses inflicted by weeds to rice production in Uganda is not yet quantified; elsewhere in West Africa, weeds have been reported to cause grain yield losses of 28-54% in transplanted lowland rice and 28-65% in direct seeded lowland rice (Akobundu, 1980; Diallo and Johnson, 1997; Becker et al., 2003; Johnson et al., 2004). Very few effective and suitable weed control options are known or accessible to farmers in SSA (Demont et al., 2009). Where they are known farmers are not taking them up (Oswald, 2005), due to associated monetary, labour and skills costs, as well as variable or limited reliability of the technologies (Hearne, 2009; Rodenburg et al., 2010). Several weed species cause losses to rice production but the species that poses the greatest threat to rice production is *Striga* spp. (Jamil et al., 2011).

## 1. 6 *Striga hermonthica* weed as a constraint

Among other factors, adequate production of rice is hampered by *Striga* infestation in Uganda and elsewhere*. Striga hermonthica* is one of the 28 species of the *Striga* parasitic weeds, which is seriously constraining cereal production in SSA (Oswald, 2005; Atera et al., 2011). In Uganda, *Striga hermonthica* is the most abundant species whose incidence and severity is steadily increasing and threatening food production in the country. It occurs on fields of maize, sorghum, millet and upland rice that are the major cereals grown in the country (Olupot et al., 2005; Ejeta, 2010). In upland rice, *Striga hermonthica* has been reported to cause yield losses of between 33–90% (Atera et al., 2012). This weed draws water and nutrients from the crop causing it to wither, stunt and thus reduce grain yield, and hence it is commonly known as witch weed (Khan et al., 2007). *Striga* is highly adapted to its environment and will only germinate in response to specific chemical stimulants produced by the host. Once germinated, *Striga* integrates itself with the host plant, attaching to the vascular system within the root structure from where it draws water and nutrients, wounds the outer root tissue, and weakens the host plant's ability to maintain its normal growth patterns by impairing photosynthesis (Gurney et al., 1995; Joel 2000). *Striga* exerts a potent phytotoxic effect on its host causing severe stunting and a characteristic "bewitched" and chlorotic whorl (Ransom et al., 1996). As a result, plant

performance is severely disrupted by *Striga* with a large reduction in host plant height, biomass, and ultimately grain yield (Parker and Riches, 1993; Gurney et al., 1999). In severe cases of *Striga* parasitism, the whole plant dies (Haussmann et al., 2000b). A single *Striga* plant produces thousands of seeds which are capable of remaining dormant for up to 20 years in the soil (Parker and Riches, 1993; Webb and Smith, 1996).

## 1.7 Occurrence and distribution of *Striga* spp

*Striga* spp. of family *Orobanchaceae* (formerly *Scrophulariaceae*) are parasitic weeds which attack all dry land cereals including sorghum (*Sorghum bicolor* [L.]), pearl millet (*Pennisetum glaucum* [L.]), and finger millet (*Eleusine coracana* [L.] Gaertn), maize (*Zea mays* [L.]), and upland rice (both *Oryza glaberrima* [Steudel] and *O. sativa* [L.]) (Rodenburg et al., 2006; Scholes and Press, 2008; Rodenburg et al., 2010). They have been reported among the most harmful weeds in many of the rice growing countries in SSA (Mohamed et al., 2006). Several species of the genus *Striga* have been identified in Africa but the most important in upland rice are *Striga hermonthica, Striga asiatica, and S. aspera* (Mohamed et al., 2006; Rodenburg et al., 2010). *Striga* can be found in many regions south of the Sahara except areas where rainfall is too high or temperatures too low for its development. It is found from sea-level up to 1600 m altitude in production systems with rainfall from 500 up to 2000 mm and in almost all soil types; *Striga* is found to be highly adapted to its environment (Lagoke et al., 1988; Sauerborn, 1991).

*Striga* damage is more prominent in areas where soil fertility and rainfall are low; factors highly associated with poverty (Khan et al., 2001; Oswald, 2005). In other words, parasitic weeds flourish in production systems with degraded soils and uncontrolled water, which are typically the realm of poor subsistence farmers who have the lowest resilience to those problems because they are limited by lack of capacity and access to control options. Yet on the other hand, they lack alternative economic activities (Rodenburg et al., 2010).

## 1.8 *Striga* biology

*Striga* is an obligate hemiparasitic weed species, which is endemic in the African continent (Jamil et al., 2010; Rodenburg et al., 2010). It attaches to the roots of grasses and major cereal crops (Rodenburg et al., 2006; Scholes and Press, 2008). *Striga* obtains nutrients and water from its host causing incapacitating effects, which have resulted to it being

named as a witch weed (Ransom et al., 1996). The witch weed produces very many tiny seeds, which can remain viable in the soil for up to 20 years, and those seeds only germinate when there is a host plant growing near it because they require specific plant exudates to trigger germination (Bouwmeester et al., 2003; Jamil et al., 2010). However, prior to germination, a metabolic process known as conditioning is required. This is a preparatory process, which necessitates exposure of the *Striga* seed to warm and moist conditions before the seed responds to chemical stimulants. It is presumed that during this process essential metabolic processes take place, resulting in production of proteins and hormones involved in parasitism (Joel et al., 2007). In the event when no host stimulus is available, *Striga* seed has got the ability to enter wet dormancy (Mohamed et al., 1998).

The limited energy reserves found in the small *Striga* seeds can only support the germinated seed for a short period, and then continued survival is derived from the host plant through a specialised organ known as the haustorium. Formation of the haustorium triggered by another root derived signal marks the beginning of parasitism in which *Striga* attaches itself to the vascular system within the root structure, competes with the host plant for water and nutrients, and weakens the host plant by impairing photosynthesis (Joel 2000; Yoder, 2001). As a result, plant performance is severely degraded by *Striga* with a large reduction in host plant height, biomass, and ultimately grain yield (Parker and Riches, 1993; Gurney et al., 1999).

*Striga* depends on the host for its survival and its life cycle is linked to that of its host (Haussmann et al., 2000c). Therefore, development of resistance to *Striga* should target the relation between the *Striga* and its host. Nonetheless, development and growth of *Striga* is controlled by a complex exchange of chemical stimulants. During germination for example; there are several classes of germination stimulants but strigolactones are the most common ones (Matusova et al., 2005). After germination, haustorial inducing factors are required (HIF). Pre-attachment mechanisms (factors) include germination stimulants and HIF; post-attachments mechanisms include development cues and nutrient flux from host to parasite and hypersensitive response (Ejeta et al., 2000). However, *Striga* causes effects that are more devastating to its hosts in soils of low fertility (Khan et al., 2007; Atera et al., 2011). Currently in SSA population, pressures are going up and more land is being brought under cropping as people try to grow more food to overcome the looming food insecurity. As a result, soils are being depleted, *Striga* seed bank is increasing in the soil,

its effects on the crop are becoming more severe, and the result will be reduction of yields (Badu-Apraku and Akinwale, 2011).

## 1.9 Economic losses caused by Striga

*Striga* has become the greatest biological constraint to food production in SSA (Rodenburg et al., 2010) because it inflicts yield losses in cereals in general (Gurney et al., 2002; Rodenburg et al., 2005). In rice, *Striga* does not affect flooded rice, but serious losses in upland rice have been reported as caused by *Striga* species including *Striga hermonthica* (Mohamed et al., 2006). Reliable estimates of the percentage of the area infested with parasitic weeds and resulting yield loses are lacking but according to FAO as reported by Rodenburg et al. (2010), *Striga* infests more than 40% of all cereal production areas in SSA. Across the African continent, *Striga's* economic damage is estimated to reach $7 billion per year, negatively affecting the welfare and livelihoods of 300 million people (Ejeta, 2007).

## 1.10 *Striga* control options

Several control options against *Striga* have been suggested (Parker, 1991). These include agronomic practices such as improving soil fertility (Cechin and Press, 1993; Showemimo et al., 2002), intercropping cereals with the legume *Desmonium uncinatum* (Khan et al., 2002) and use of trap crops (Doggett, 1988; Hess and Dodo, 2004). The other options involve chemical control or soil fumigation (Eplee and Norris, 1987; Carsky et al., 1994), biological control (Kroschel and Muller-Stover, 2004; Lendzemo et al., 2005) and host plant resistance (Johnson et al., 1997b; Kim et al., 1998). However, in spite of these suggested measures, this menace continues ravaging cereal crops in the semi-arid tropics (Ogborn, 1987).

Hand weeding and cultivation, the most prevalent control practices, are conducted after the parasite emerges above ground and has already inflicted significant damage to the crop (Ejeta, 2007). Consequently, farmers with crop fields severely infested with *Striga* resort to abandoning their fields contributing to an already severe pressure on availability of farmlands. Therefore, measures that minimize impact on crop losses, deplete the *Striga* seed bank in the soil, reduce further *Striga* seed production, and diminish the spread of *Striga* to un-infested fields are needed. Host plant resistance, when effectively deployed,

offers many of these benefits with an insignificant increase in cost, as the technology is embedded in the genetics of the seed of the crop cultivars to be planted (Ejeta, 2005). Genetic control thus either offers a practical and economically feasible measure (Parker and Riches, 1993; Ejeta et al., 1997), independently or as a part of an integrated *Striga* control approach.

## 1.11 Host resistance mechanisms to *Striga*

Resistance against *Striga* has been defined as the ability of the host plant to reduce or prevent infection and reproduction of the parasite (Shew and Shew, 1994). Host resistance is believed to reduce *Striga* seed production through a reduction in *Striga* development rate or *Striga* numbers (Weber et al., 1995; Haussmann et al., 2000b). Resistance to parasitic plants is exhibited at different stages of the parasite lifecycle, before attachment to the host (Pre-attachment), during penetration of the root (Parasite establishment), or after establishment (Post-establishment maturation) of vascular connections (Yonder 1998; 2010). These mechanisms are in a way similar to those employed by host plants against fungal and bacterial pathogens (Yonder, 2010).

Host plants have been observed to display resistance to *Striga* infection with mechanisms that include reduced host plant exudates that suppress *Striga* germination, and post germination barriers that prevent *Striga* from attaching to the host plant (Williams, 1959; Ramaiah, 1991; Harahap et al., 1993; Johnson et al., 2000b; Ejeta, 2007). Examples of such mechanisms include low production of the haustorial initiation factor, avoidance mechanisms, presence of physical barriers, and antibiosis (Ejeta et al., 1999). However low germination stimulant production is the only mechanism that has been studied and exploited for breeding purposes (Hess et al., 1992; Ejeta et al., 1999). Some cultivars with good level of *Striga* resistance have been identified in sorghum (Ejeta, 1995), maize (Kim et al., 1998), and rice (*Oryza sativa*) (Johnson et al., 1997b). Genotypes that consistently support fewer emerged *Striga* plants, sustain less *Striga* damage and produce higher grain yields under infestation are considered resistant (Badu-Apraku et al., 2010). Resistance is manifested as (i) significantly fewer attachments to the roots of the host (ii) delayed parasitic development and (iii) higher mortality of attached parasites while susceptibility is seen from substantial internal haustorial development.

## 1.12 Genetic diversity studies

Although rice is a rich crop based on its genetic diversity, several studies have reported that some varieties released by breeding programs in various parts of the world have a narrow genetic base (Guimarães, 2000; Mishra, 2002). That narrow genetic base limits genetic gains and may cause the crop to reach a grain yield plateau very quickly (Flinn et al., 1982; Carmona, 1990). However, genetic diversity only becomes usable after characterisation and evaluation of germplasm as a selection guide for parents with adequate variability and thus good genetic advance or gain (Lapitan et al., 2007a; Guimarães, 2009). Several studies have already been conducted to assess diversity in rice. For example, Semagn et al. (2006) reported a wide range of genetic variability in all rice genotypes used except Nerica 8 and 9. They found a distinct separation of Nerica 1 and 7 from Nerica 8 and 18. Lapitan et al. (2007b) used simple sequence repeats (SSRs) to assess genetic diversity of Philippine rice and found an overall genetic diversity of 0.71 indicating a high level of genetic variation among those cultivars.

Therefore, studies about genetic diversity, genetic variation and genetic relationships in the gene pool need to be conducted as a prerequisite in adopting an efficient and valuable breeding approach (Lapitan et al., 2007a; Ghneim et al., 2008). Once genetic diversity is known, then informed breeding strategies can be developed and utilized in a manner that will broaden the genetic base (Esuma et al., 2012). In addition, genetic distance has been found to correlate positively to heterosis of some hybrids in rice (Xu et al., 2002; Phetmanyseng et al., 2010), maize (Lariepe, 2012) and carrot (Jagoz, 2011).

## 1.13 Gene action and inheritance of host plant resistance to *Striga*

Gene action is specific for a character, and it comprises of three components: additive, dominant and epistatic variance (Sleper and Poehlman, 2006a). Genes exert their influence either singly or in combination with other genes and in conjunction with the environment (Hallauer and Miranda, 2010). To establish gene action of a specific character, specific mating designs are used to estimate the general combining ability (which includes both additive and additive x additive components) and specific combining ability (non-additive which includes both dominance and components of all sources of epistatic effects) in different environments (Kulembeka et al., 2012).

Most of the resistance to *Striga* appears to be polygenic; however, some studies have found resistance to *Striga* to be controlled by both major and minor genes (Kaewchumnong and Price, 2008a). In maize, Kim (1994) found tolerance and resistance to *Striga* to be polygenic and quantitatively inherited. In addition, Amusan (2010) found both additive and dominance effects to be important for resistance to *Striga* in maize. However, that analysis established presence of more dominance genetic effects for the expression of major *Striga* resistance QTLs. In sorghum, Vogler et al. (1996) found that a major recessive gene and some minor genes controlled resistance to *Striga* as well. For rice, Gurney et al. (2006a) and Swarbrick et al. (2009) identified several QTLs for post–attachment resistance to *Striga hermonthica*, which are useful findings for upland rice improvement by marker assisted selection. Consequently, more studies need to expound on the analysis of gene action of *Striga* resistance in rice through analysis of combining ability and or use of molecular methods.

Combining ability studies aid in determining traits for enhancement of yield potential as well as providing a criterion for selecting elite parents that make the highest contributions to hybrid performance (Qi, 2013). The current investigation was targeting to develop suitable high yielding *Striga* resistant cultivars by improving quantitative and qualitative traits. Nonetheless, understanding the genetics underlying performance of a genotype for specific trait of interest is crucial because it informs the breeder on how to choose procedures and promising parents for effective improvement and selection in a breeding program (Sharma et al., 2013; Dawud, 2017). For example, combining ability analysis provides information on additive and dominance variance, which is useful in choosing parents, crosses and appropriate breeding procedure for selecting desirable segregants (Salgotra et al., 2009; Sharma et al., 2013).

## 1.14 Use of molecular markers in diversity studies in rice

The use of molecular markers has played an important role in improving rice breeding and genetics (Miah et al., 2013). Molecular markers have proved to be valuable tools in the characterization and evaluation of genetic diversity within and between species and populations (Nagy et al., 2012). In rice breeding, the availability of a map-based sequence resulting from successful genome sequencing of both *Oryza sativa* (International Rice Genome Sequencing Project, 2005) and *Oryza glaberrima* (Wang et al., 2014); has made it possible to understand the genetics and functional diversity of rice. Once the locus

identities of the genes are outlined, gene organization and structure can be analyzed to determine unique features of genes and their products. Similarly, evolutionary and phylogenetic analyses help classify the family members into distinct classes and define their origin (Agarwal et al., 2014).

Molecular or DNA-based markers have been found to be the most effective and reliable tools in the assessment of genetic diversity and study of evolutionary relationships (Benali et al., 2011). Unlike morphological traits, molecular markers reveal profuse differences among genotypes at DNA level, thus presenting a more direct, reliable and efficient tool for germplasm characterization, management and conservation with environmental influence excluded (Prabakararo et al., 2010).

Several PCR based markers do exist, and up to the recent past before the introduction of single nucleotide polymorphism (SNP) markers; simple sequence repeat markers (SSRs) also known as microsatellite markers have been more popular in rice breeding because they are highly informative, mostly monolocus, codominant, easily analyzed and cost effective (Gracia et al., 2004). Microsatellite markers have been widely used to screen, characterize and evaluate genetic diversity in cereal species (Kalia et al., 2011) and they have been the most suitable markers for genotyping a highly self-pollinated crop like rice (Manyasa et al., 2015). Several researchers have employed SSRs to study diversity in rice (Jin et al., 2010; Choudhury et al., 2013; Das et al., 2013; Sow et al., 2014). However currently, SNPs have become the most common form of variation; they have become the markers of choice due to their relative abundance, presence of many platforms for SNP genotyping (Mammadov et al., 2012) and precision (Kumari and Pande, 2010). A number of studies have utilized SNPs to study diversity in rice (Zhao et al., 2011; Courtois et al., 2012).

## 1.15 Relationship among economically important traits of rice

Grain yield of rice is a complex character resulting from interaction of a number of components and understanding the relationship between these components and grain yield aids selection (Ekka et al., 2011). First because it forms the basis for selection of suitable parents for crop improvement (Dutta et al., 2013), and secondly it facilitates understanding of mode of inheritance of quantitative traits which guides in choosing an effective selection procedure for improvement (Hasanuzzaman and Golam, 2011).

Character association conducted through correlation coefficient indicates relative influence of various component characters on grain yield; thus aiding selection (Ekka et al., 2011).

Selection based on a single trait may not always be effective; however, it is also not practical to select for a large number of traits concurrently in one selection scheme (Govindaraji et al., 2011; Ezeaku et al., 2015). That therefore necessitates the use of correlation analysis to identify those traits, which greatly contribute to yield. Furthermore, path coefficient analysis in rice breeding provides an effective tool for partitioning the correlation coefficient into direct and indirect effects of cause and effect nature and presents the relationships in a more meaningful way (Prasad et al., 2001; Soni et al., 2013). For example, karim et al. (2014) conducted path coefficient analyses on aromatic rice and found that 1000-grain weight showed the highest positive direct effect on grain yield, while panicle length and spikelet sterility showed negative negligible direct effect. In addition, they reported the highest positive indirect effect was observed for 1000-grain weight via plant height and the highest negative indirect effect for 1000-grain weight via number of filled grains per panicle. Breeding for improvement in yield is reinforced with information of breeding value of potential parents as well as interrelationships among the plant characters (Prasad et al., 2001). For instance, Pandey et al. (2009) reported high heritability along with high genetic advance for grain yield, plant height, number of tillers per hill and number of spikelet per panicle among other traits, which suggests preponderance of additive gene action in the expression of those characters in rice. In this case a modified bulk selection procedure would be effective to target late generation improvement of those traits in rice (Hasanuzzaman and Golam, 2011). Consequently, for any rice-breeding program to achieve meaningful response to selection, assessment of genetic variability is indispensable. In any case, estimates of genetic parameters such as heritability and genetic advance are specific for a particular population of rice and the phenotypic expression of the quantitative characters may be altered by environmental stress that affect rice development and growth (Idahosa et al., 2010).

## 1.16 Genotype by environment interaction

The general breeding procedure involves testing a number of genotypes at different stages and evaluating the selected ones at various locations to obtain superior genotypes (Uphoff et al., 2015). However, a genotype cultivated in separate environments will often express

significant variations in yield performance (Mohammadi and Amri, 2012). These fluctuations are caused by different environmental conditions and are referred to as genotype by environment interactions (GE) (Kamutando et al., 2013; Tariku et al., 2013). Presence of GE complicates interpretation of results obtained from multi-environment trials (METs) and reduces accuracy of selection of new genotypes for diverse environments (Akcura et al., 2005; Mortazavian and Azizi-nia, 2014; Makumbi et al., 2015).

The common target of many plant breeders therefore is to develop new varieties, which show high and stable performance for yield and other crucial agronomic traits that show minimal interaction over a wide range of environments (Yan et al., 2007; Kamutando et al., 2013). Consequently, analysis of GE has become one of the major subjects of study in breeding; allowing generation of different practices for genetic improvement and identification of genotypes with general and specific stability or adaptation to environments (Nassir and Ariyo, 2011; Gasura et al., 2015). Breeders have to utilize the available options to deal with GE, such as identification of mega-environments to reduce negative GE, and identification of ideal testing locations within mega-environments as well as identification of superior genotypes with either broad or specific adaptation to different environments (Tariku et al., 2013; Gasura et al., 2015).

There are several examples of previous studies that were undertaken to investigate GE in different traits in rice. These have included rice starch properties (Bao et al., 2004), yield (Tariku et al., 2013; Bose et al., 2014) and bacterial leaf blight resistance (Lussewa et al., 2016). For a complex quantitative trait like yield, performance is greatly influenced by environmental fluctuations; thus selection for superior genotypes for yield *per se* at one location in one year would not be effective (Shrestha et al., 2012). Furthermore, it is not yet well known whether yield performance of upland rice grown under *Striga* infestation and or its resistance varies with different seasons and locations and it would be of interest to find this out. Analyzing the magnitude of the effects of environmental conditions on yield grown under *Striga* is what will provide stimulus in rice breeding on determining when, where and how best to select for yield and *Striga* resistance.

Studies on GE have employed both parametric and non-parametric approaches (Lin et al., 1986; Crossa et al., 1990; Hussein et al., 2000; Mohammadi et al., 2010; Bose et al., 2014). However the most commonly used approach is the parametric which involves

relating observed phenotypic responses to a section of environmental conditions under statistical assumptions of normality, independence of observations as well as homogeneity of error variances all in the absence of outlier influence (Liu et al., 2010; Mortazavian and Azizi-nia, 2014). Nonetheless, when these assumptions are not fulfilled; parametric methods based on absolute data fail and the non-parametric tests based on ranks become a better alternative for defining environments and genotypes relative to biotic and abiotic factors (Liu et al., 2010; Karimizadeh et al., 2012). The rank eliminates the main effect of the environment and genotype and only considers GE and error effects (Mortazavian and Azizi-nia, 2014). In breeding and testing programs, the rank orders of the genotypes are the most significant information in selection for yield stability. Genotypes with similar ranking across environments are considered stable (Yan et al., 2007; Mortazavian and Azizi-nia, 2014).

There are several statistical techniques that have been presented for studying of GE effects and analysis of stability (Mohammadi et al., 2010; Bose et al., 2014; Tadege et al., 2014). However, the two powerful and widely used tools are the additive main effects and multiplicative interaction (AMMI) (Gauch, 2013) and the genotype plus genotype by environment (GGE) (Yan, 2011). The AMMI procedure utilizes an analysis of variance for effects due to genotypes and environments and principal component analysis for the GE (Bose et al., 2014). However when the normality assumption is not fulfilled, then AMMI cannot be used and GGE biplot remains the most suitable tool for multi environment trials (MET) data analysis (Yan et al., 2000; Yan, 2001; Yan et al., 2001). The GGE biplot analysis enables genotype evaluation for their performance in specific environments and across several environments, mean performance and stability, and general or specific adaptations (Mohammadi and Amri, 2012). In addition, GGE biplot can reveal the which-won–where pattern of mega environment investigation and specific genotypes can be recommended to specific mega-environments (Yan and Tinker, 2005; Yan, 2011); environment evaluation to identify the best environment for cultivar evaluation: the most discriminating and representative environment; and redundant environments can be eliminated (Cooper et al., 1997; Yan and Rajcan, 2002). GGE is reportedly handy and efficient in selection of suitable genotypes for locations and hence guides varietal development for stable environmental based selection (Gauch, 2006; Nassir and Ariyo, 2011).

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# Chapter 2 : Assessment of genetic diversity of upland rice germplasm in Uganda using SSR markers


## Abstract

The national rice-breeding program in Uganda responsible for development of high yielding varieties holds a large number of introductions and breeding lines, providing possibility of genetic divergence that is needed in the production of better varieties. However, genetic diversity of this germplasm is largely unknown. Consequently, the objective of this study was to estimate the nature and magnitude of genetic diversity present among some of the available upland rice genotypes in Uganda. One hundred fifty seven genotypes were evaluated for genetic diversity using 30 simple sequence repeat (SSR) markers. A total of 274 alleles were detected with an average of 9.13 alleles per locus. The major allele frequency revealed was 64.27% on average. Genetic diversity ranged from 9.37% (RM 324) to 86% (RM 257) with a mean genetic diversity of 50.93% that is a moderate level of genetic variation. Polymorphism information content (PIC) values of the markers ranged from 0.11 (RM324) to 0.86 (RM257) with an average of 0.48 per marker meaning the markers were reasonably informative. Cluster analysis enabled identification of three main groups at 60% level of dissimilarity with additional sub clusters within each group. This study revealed that SSR markers facilitated grouping or classification of these cultivars accordingly and that genetic diversity present in these germplasm was about 50% calling for careful considerations when selecting parents for improvement in this program. Consequently, the successful separation of the genotypes into different clusters will facilitate selection of distantly related parents for the breeding program.



**Key words:** Genetic diversity, Polymorphism, SSR markers, Upland rice.

## 2.0 Introduction

Rice is an important cereal crop in the world and is one of the major crops grown in Uganda (Soni et al., 2013). However, in spite of becoming a staple crop with increased production and consumption, productivity of this crop in Uganda is low. One of the solutions to this deficit is production of improved varieties with good resistance to a number of pests (Ahmed, 2012). The rice breeding program in Uganda is already releasing improved varieties; however, there is a strong need to ascertain presence of diversity in the germplasm with an aim of broadening the gene pool for future utilization in breeding of high yield, superior quality and stable varieties in the country. Assessment of genetic diversity of rice germplasm is a precondition for conservation and breeding (Lin et al., 2012). Genetic diversity is the heritable difference among germplasm, which forms the starting point for crop improvement and offers a basis for genetic analysis of complex traits (Liang et al., 2010; Soni et al., 2013). Once genetic diversity is known, informed breeding strategies can be formulated and implemented. Therefore, to facilitate effective selection of parental lines for breeding; it becomes imperative to establish the genetic diversity of the germplasm (Esuma et al., 2012). Furthermore, in this era where improved cultivars are rapidly replacing the more diverse but less productive indigenous landraces, the diversity of most crops is threatened. Consequently, any breeder contemplating improvement of local germplasm must consider assessment of genetic diversity of the parent stock; because the more diverse the parents, the more are the chances of increased range of variability among the offspring (Banumathy et al., 2010).

Breeding for improvement of yield and other traits in rice, will always require selection of parents with a wide genetic diversity. This is because the latter enables breeders to obtain high heterotic crosses and transgressive segregants, thus boosting genetic gains. Research has shown that the magnitude of heterosis in crop plants depends on the degree of genetic divergence between the parents, and this can be used as an indicator of the inherent yielding capacity of the progeny (Medhabati et al., 2013). Presented here, is the molecular or genetic diversity analysis of upland rice germplasm assembled at the national rice program in Uganda. The current study sought to assess genetic diversity as a prerequisite in identifying distant parents that would lead to production of superior segregants and thus limit production of narrow base varieties. The latter would cause the crop to reach a grain yield plateau very quickly (Flinn et al., 1982; Carmona, 1990). On the other hand, however, a wider variability is important for adaptability to climate change. The

objective of this study was to quantify genetic diversity that exists in the plant material that could be utilized for further improvement of the local upland rice varieties in Uganda.

## 2.1 Materials and Methods

### 2.1.1 Plant Material

One-hundred and sixty rice genotypes comprising of 120 advanced lines being evaluated for adaptation to upland conditions, 16 NERICA (1–16) varieties and 24 cultivars commonly grown in the country were used in this study. Appendix 1 shows the list of germplasm used. However, some three genotypes did not germinate and only 157 genotypes were characterized.

### 2.1.2 Field experiment

The experiment was set up at the National Crops Resources Research Institute of Uganda, NACCRI, located in Namulonge, 28km north of Kampala, Wakiso District, (32$^{o}$ 34'E,0$^{0}$32'N) at 1200 m above sea level. The area receives an average rainfall of 1300 mm, average annual temperature of 22$^{0}$C with annual minimum and maximum temperatures of 16 and 28$^{0}$C, respectively. The genotypes were planted in an alpha lattice design of 10 x 16 with two replications. Each genotype was planted directly by drilling method in a plot size of 1 m$^{2}$ with both in-row and inter-row spacing of 20 cm. Each block consisting of 16 plots was spaced at 40 cm from the other and the two replications had 1 m space between them. This arrangement produced six rows per plot and six plants per row, giving a total number of 36 plants per plot. Weeds were controlled mechanically by hand weeding regularly. Other standard agronomic practices were followed and after 21 days, leaf samples were harvested and sent to BecA – ILRI hub in Nairobi for genotyping.

### 2.1.3 Genotyping and PCR procedure

Three weeks after planting, 157 leaf tissue samples were sent to the BecA laboratory for genotyping. Three genotypes did not germinate. DNA was extracted by solvent method and its quality confirmed by OD reading using a Nanodrop ND-8000 and agarose gel electrophoresis. A total of 2 µl of DNA was loaded in a 0.8% agarose gel and electrophoresed at 100 volts/hour to check the overall sample quality. Most of the samples were of good quality with intact DNA without degradation. The concentrations were used to guide the normalization of each sample at a concentration of 50 ng/µl. Additionally, the purity of the samples was determined from the ratio 260/280 provided by the Nanodrop. The ratio was within the acceptable range for subsequent analysis (Appendix 2). All the

markers amplified well with an exception of RM2887, which failed and was replaced with RM1125. The PCR fragments were resolved on the genetic analyzer, the ABI 3730xl. The markers used were directly labelled. The choice of 30 SSR markers used was determined by their known suitability, availability and the available budget for the work. A total of 4616 data points were achieved out of the expected 4710 data points giving an overall success rate of 98.00%.

A standard Polymerase Chain Reaction (PCR) protocol optimized for rice SSR markers was used. PCR was conducted in a reaction solution of 10 µl containing 50 ng of template DNA, 2.0 pmoles/µl 1.0 µl of each forward and reverse primer, 2.5 nM 0.8 µl of each dNTPs, 10 x 1.0 µl reaction buffer, 10 mM $MgCl_2$, 5U/µl 0.05 µl Taq polymerase and 4.35 µl $H_2o$. The thermocycler process was programmed for initial denaturation at 95$^oC$ for 3 minutes, followed by 35 cycles of 30 sec denaturation at 95$^oC$, 1 minute denaturation at 56$^oC$, 2 minute annealing at 72$^oC$, then 30 minute extension at 72$^oC$ and finally held at 4$^oC$.

### 2.1.4 Data handling

Data was captured using the Genscan®software and the amplified DNA fragments or alleles were scored using the Genemapper®software version 4.1 (Applied Biosystems). The data was then compiled into a spreadsheet as a standard Genemapper output file. With Sample ID and marker found in the first two columns to identify each genotype. The reference dyes used were; Ned (Y) Pet (R) 6-FAM (B) and Vic (G). The sizes for each detected allele were indicated in base pairs. Parameters considered for data quality were indicated in the genotyping quality (GQ) column of the excel file.

## 2.2 Data Analysis

The data was first transposed to show marker data for each genotype. Then statistical analysis of the marker data was conducted using PowerMarker V 3.25 software (Liu and Muse, 2005) and Dissimilarity Analysis and Representation for Windows (DARwin V 5.0) software package developed for diversity and phylogenetic analysis on the basis of evolutionary dissimilarities (Perrier et al., 2003). PowerMarker enabled estimation of genetic diversity parameters which included number of alleles per locus, polymorphism information content (PIC); a measure of discriminatory power of each SSR locus (Anderson et al., 1993), frequency of the major allele, genetic diversity (expected

heterozygosity) and unexpected heterozygosity for the 30 polymorphic markers. Cluster analysis was performed on the dissimilarity matrix using the Neighbour - Joining algorithm to build dendrograms by unweighted pair-group method with arithmetic average (UPGMA) at a bootstrapping value of 10 000 in DARwin (Saitou and Nei, 1987). In addition, principal coordinate analysis (PCA) which gives spatial representations of genetic distances was also achieved using DARwin 5.0 software. A two-dimension scatter plot was plotted for all genotypes using scores of the first two principal components.

## 2.3 Results

### 2.3.1 Marker summary statistics

Two-hundred and seventy-four alleles were detected among the 157 rice genotypes (Table 2.1). The average number of alleles per locus was 9.13 with a range of three alleles (RM38) to as many as 24 alleles (RM1812). PIC values of the SSR markers used, ranged from a low value of 0.11 (RM324) to a high value of 0.86 (RM 257) with an average of 0.48 per marker (Table 2.1). Forty three percent of the markers had PIC values above 0.5 to the maximum of 0.86 and 40% had PIC values between 0.3 and 0.5, whereas only 16.7% had PIC values below 0.3. Major allele frequency on average was 0.642 and ranged from 0.242 (RM257) to 0.9395 (RM324). This means that 64.2% of the 157 genotypes shared a common allele and it is one of the measures used to depict genetic diversity. Genetic diversity (GD) ranged from 9.37 (RM324) to 86% (RM257) with an average genetic diversity of 51% revealed. Fifty three percent (53.3%) of the loci revealed GD higher than 0.5; 33.3% of the loci revealed GD between 0.3 and 0.5, and diversity below 0.3 was revealed by 13.3% of the markers. On average, heterozygosity was 14.71%; however, it ranged from zero percent (RM242) to 78.34% (RM256). Twenty-nine out of 30 SSRs exhibited heterozygosity.

**Table 2.1**: Summary statistics for the 30 SSR loci screened across 157 rice genotypes

| Marker | PIC | Major.Allele.Frequency | GeneDiversity | Heterozygosity | Allele No per locus | Genotype No |
|---|---|---|---|---|---|---|
| RM1 | 0.2681 | 0.8439 | 0.2796 | 0.0127 | 9 | 9 |
| RM101 | 0.6775 | 0.5287 | 0.6933 | 0.3822 | 15 | 21 |
| RM11 | 0.4457 | 0.7197 | 0.4642 | 0.0318 | 9 | 12 |
| RM1125 | 0.3871 | 0.6783 | 0.4604 | 0.0318 | 5 | 7 |
| RM1377 | 0.374 | 0.7452 | 0.4112 | 0.0637 | 5 | 7 |
| RM1812 | 0.8203 | 0.3121 | 0.8364 | 0.4395 | 24 | 28 |
| RM19 | 0.4811 | 0.535 | 0.5661 | 0.0382 | 7 | 8 |
| RM202 | 0.5987 | 0.5605 | 0.6333 | 0.0701 | 8 | 13 |
| RM204 | 0.443 | 0.7261 | 0.4583 | 0.4586 | 14 | 18 |
| RM214 | 0.6138 | 0.4873 | 0.6627 | 0.0637 | 9 | 15 |
| RM242 | 0.1211 | 0.9363 | 0.1225 | 0 | 7 | 7 |
| RM253 | 0.522 | 0.6019 | 0.5716 | 0.0701 | 6 | 10 |
| RM257 | 0.8648 | 0.242 | 0.8753 | 0.7834 | 19 | 23 |
| RM259 | 0.3799 | 0.7166 | 0.434 | 0.0446 | 5 | 7 |
| RM26 | 0.6709 | 0.4331 | 0.7109 | 0.121 | 11 | 16 |

**Table 2.1: Continued**

| Marker | PIC | Major.Allele.Frequency | GeneDiversity | Heterozygosity | Allele No per locus | GenotypeNo |
|---|---|---|---|---|---|---|
| RM324 | 0.1148 | 0.9395 | 0.1164 | 0.0127 | 6 | 7 |
| RM334 | 0.5659 | 0.4299 | 0.6348 | 0.8535 | 9 | 12 |
| RM335 | 0.6988 | 0.4936 | 0.7182 | 0.1146 | 15 | 23 |
| RM341 | 0.3757 | 0.758 | 0.4024 | 0.0382 | 9 | 11 |
| RM349 | 0.4871 | 0.6433 | 0.5322 | 0.0446 | 8 | 12 |
| RM3510 | 0.5655 | 0.6051 | 0.5949 | 0.2548 | 10 | 17 |
| RM38 | 0.3282 | 0.7771 | 0.3655 | 0.0382 | 3 | 4 |
| RM5 | 0.3528 | 0.7898 | 0.3658 | 0.0255 | 8 | 10 |
| RM50 | 0.6044 | 0.5605 | 0.6367 | 0.0446 | 9 | 12 |
| RM518 | 0.4922 | 0.672 | 0.5191 | 0.0764 | 7 | 12 |
| RM5434 | 0.6575 | 0.4713 | 0.6957 | 0.121 | 13 | 18 |
| RM561 | 0.2692 | 0.8217 | 0.3012 | 0.0127 | 4 | 5 |
| RM569 | 0.5302 | 0.6465 | 0.554 | 0.1274 | 11 | 17 |
| RM85 | 0.2145 | 0.879 | 0.2223 | 0.0127 | 4 | 5 |
| Mean | 0.4776 | 0.6427 | 0.5093 | 0.1471 | 9.1333 | 12.4 |

## 2.4 Cluster analysis

Genetic dissimilarity values between the genotypes calculated in DARwin software were used to produce a cluster tree analysis (dendrogram, Fig 2.1) and a two dimensional scale diagram (PCA (Fig 2.2) which portrayed the main groups as well as the subsets among the 157 upland rice genotypes. Using 60% dissimilarity as the threshold for UPGMA clustering, three major groups or clusters were observed. Each cluster contained both cultivars and advanced lines. The new rice for Africa (NERICA) varieties were scattered into different clusters.

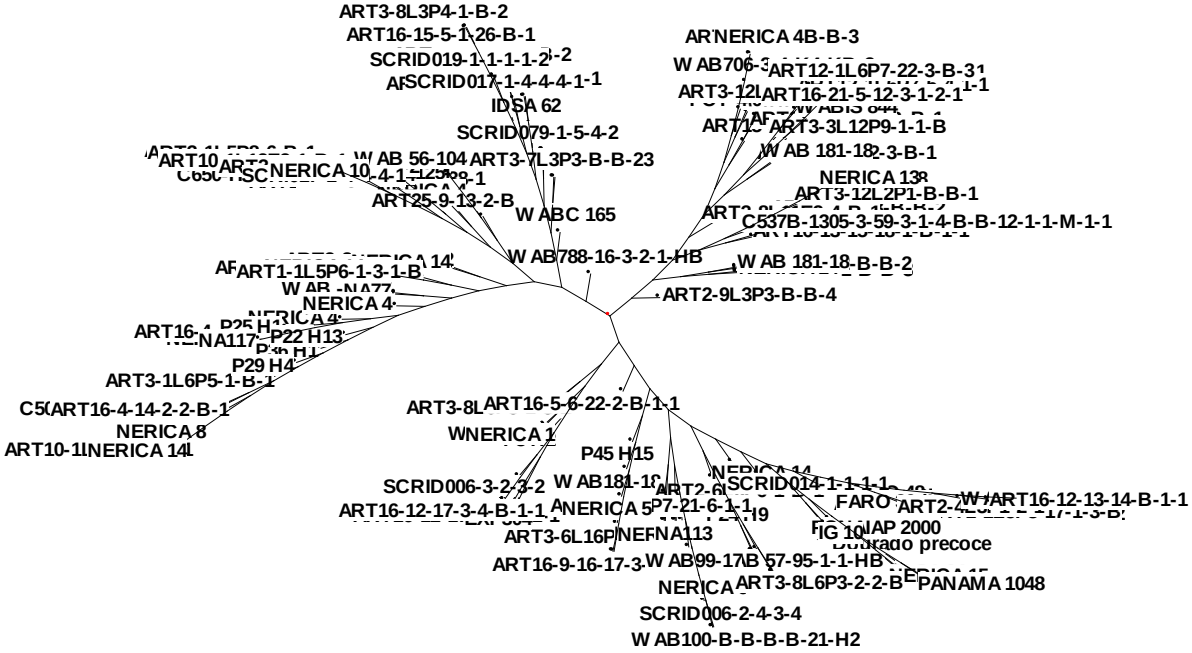


**Figure 2.1:** Dendrogram of 157 upland rice genotypes showing three major clusters with several subgroups on each cluster

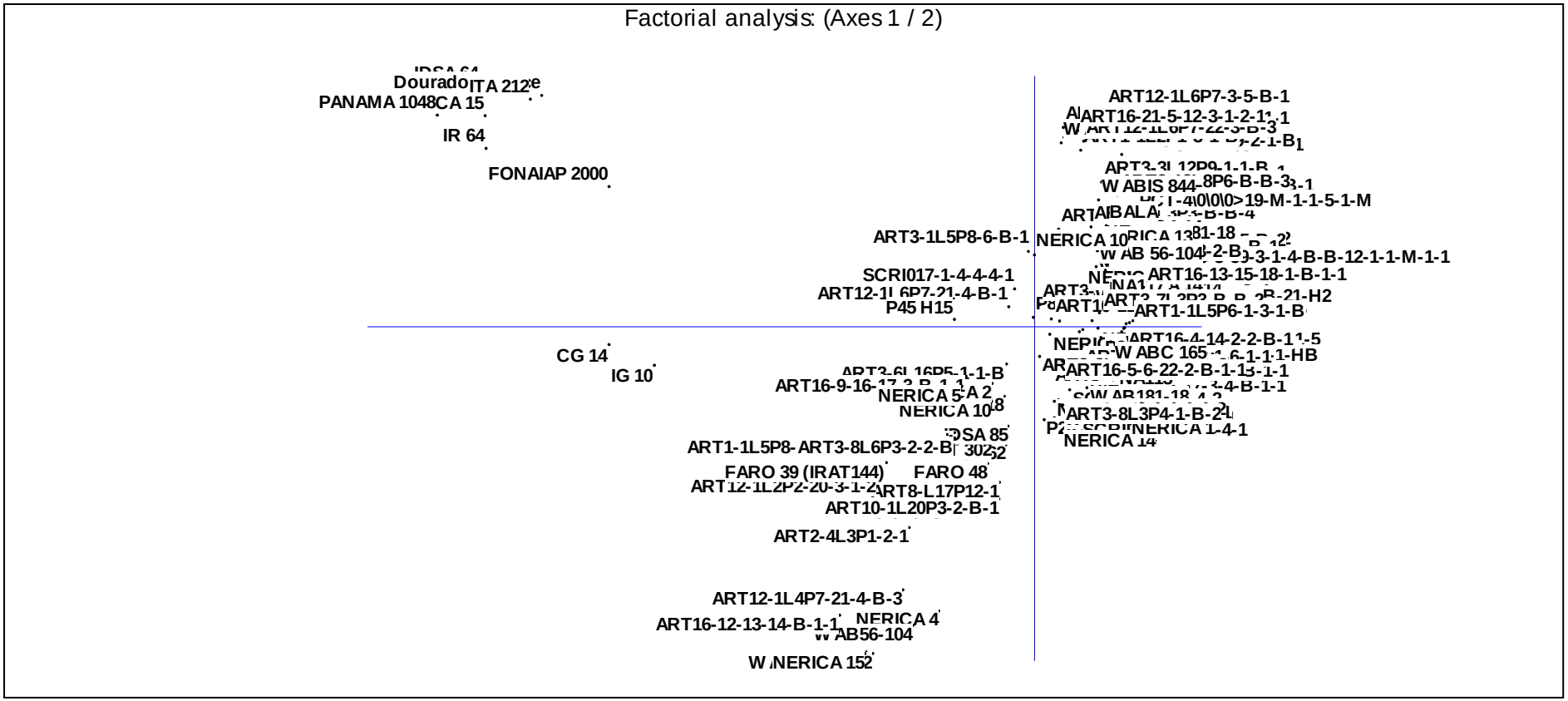


**Figure 2.2**: A scatter plot of axes 1 and 2 derived through PCA based on dissimilarity of 30 SSR markers across 157 loci.

## 2.5 Discussion

The rice breeding program in Uganda is already releasing improved varieties; however, there was a strong need to ascertain presence of diversity in the germplasm with an aim of broadening the gene pool for future utilization in breeding of high yielding, superior quality and better-adapted varieties in the country. The presence of molecular markers, which distinguish genotypes held at any breeding program, is of interest to all breeders because it facilitates testing of varietal purity and enables broadening of genetic diversity. All the microsatellites used in this study could readily distinguish one rice genotype from the other with none having a zero PIC value, and all at an average PIC value of 0.48 were reasonably informative according to the first application of PIC by Botstein et al. (1980) in human genetics. This result is in line with the findings of Sunita et al. (2004) and Lapitan et al. (2007); who also found SSR markers to be very informative in diversity studies of rice. However, on the other hand these results contradict the findings of Chuan-Guang and Gui-Quan (2010) who reported low PIC values of SSR markers used to test diversity in rice cultivars from China. Generally, markers with multiple alleles and or alleles of equal allelic frequencies within the population have higher PIC values; in other words more informative and useful for establishing linkage with a gene of interest (Hildebrand et al., 1992). In this study, the most powerful marker for discriminating among closely related genotypes was RM1812 where 24 distinct alleles were detected. The hyper variable nature of this marker makes it highly informative but such markers are suspected to be mutagenic and potentially unstable (Sunita et al., 2004). The solution is to combine them with other moderate markers.

The PIC values of loci provide an estimate of the discriminatory power of loci, considering the number of alleles and their relative frequencies. Forty three percent of the loci used in this study had PIC values of more than 0.5, indicating that these loci have high discriminatory powers that distinctively classified most of the genotypes. The polymorphism values reported in this study were higher than those reported by Chuan-Guang and Gui-Quan (2010). In general, the current results concur with the results of Sunita et al. (2004) and Lapitan et al. (2007a) who also showed that even markers with moderate PIC values could classify most of the inbred lines and detect the polymorphism rate at a specific locus. Markers with higher PIC values have great use in validating the variation between alleles and they are useful in testing genetic variability (Andersen and Lubberstedt, 2003).

The average number of alleles per DNA locus in this study was 9.13 with a range of 3-24. This is higher than the average range of 7.8 and 3-22 respectively reported by Sunita et al. (2004) or 7.4

and 3-17 respectively reported by Olufowote et al. (1997). The large number of alleles generated by the SSRs is a useful indicator of genetic diversity for subsequent breeding (Petit et al., 1998). Genetic diversity appears to resonate directly with PIC. This is in agreement with Chuan-Guang and Gui-Quan (2010) that the higher the PIC value the higher the Genetic diversity and vice versa. The average genetic diversity of 51% indicated that the germplasm had moderate diversity among the genotypes.

Rice being self-pollinating should be genetically homozygous, however the probable explanations of presence of heterozygous loci among rice germplasm include simple remnant heterozygosity in some varieties, probably because many lines in the germplasm used were not yet fully inbred lines but were advanced lines heading towards homozygosity. A few of the SSR markers may be located in the noncoding regions of the rice genome, which belong to neutral variation without selection pressure, hence maintaining heterozygous pattern in a few loci. On the other hand, during selection, a few heterozygous loci for non-target traits are retained and thus the population does not become completely homozygous (Chuan-Guang and Gui-Quan, 2010). Heterozygosity in rice was first reported in American rice (Olufowote et al., 1997) and later Xu et al. (2004) and Chuan-Guang and Gui-Quan (2010) reported the same finding. Presence of some level of genetic heterogeneity in rice is not all disadvantageous and can be explored for improvement since it is known to contribute to yield stability of plant populations (Zhu et al., 2000). In this study, presence of reasonable heterozygosity in the germplasm might be arising from the fact that many lines used were not fully inbred lines, but were advanced lines heading towards homozygosity. Twenty-nine out of 30 SSRs exhibited heterozygosity, thus reflecting presence of good genetic diversity as indicated by Agrama and Tuinstra (2003).

## 2.6 Conclusion and recommendation

Cluster analysis enabled identification of three main groups at 60% level of dissimilarity with additional sub clusters within each group. This study revealed that SSR markers facilitated grouping or classification of these cultivars accordingly and that genetic diversity present in these germplasm was about 50% calling for careful considerations when selecting parents for improvement in this program. Consequently, the successful separation of the genotypes into different clusters will facilitate selection of distantly related parents for the breeding program.

Several workers have emphasized the importance of genetic divergence for the selection of desirable parents. This information may be used to facilitate selection of diverse parents, broaden the germplasm base in the future rice breeding programs and formulate efficient strategies for the

sustainable management of the genetic resources of rice crops. Hybridization involving genetically diverse parents belonging to different clusters would provide an opportunity for bringing together gene patterns of diverse nature.

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**Appendix 2.1:** Genotypes used in the diversity analysis

| ID | Entry Name | Type | ID | Entry Name | Type | ID | Entry Name | Type |
|---|---|---|---|---|---|---|---|---|
| 1 | ART16-15-5-1-26-B-1 | Advanced line | 56 | NERICA 14 | Cultivar | 111 | ART3-12L2P1-B-B-1 | Advanced line |
| 2 | WAB96-1-1 | Advanced line | 57 | EXP304 | Cultivar | 112 | FONAIAP 2000 | Cultivar |
| 3 | ART15-4-14-63-2-B-1 | Advanced line | 58 | P24 H9 | Advanced line | 113 | P29 1 (14) | unknown |
| 4 | P29 H1 | unknown | 59 | NERICA 4 | unknown | 114 | C650-H.T.-lignée 1 p14-6-4 | Advanced line |
| 5 | ART10-1L7P2-3-B-1 | Advanced line | 60 | CG 14 | Cultivar | 115 | WAB56-104 | Cultivar |
| 6 | ART3-2L4-P19-2-1-B | Advanced line | 61 | ART3-12L11P1-B-B-1 | Cultivar | 116 | NERICA 15 | Cultivar |
| 7 | ART15-11-8-5-2-B-1 | Advanced line | 62 | ART12-1L2P2-20-3-1-2 | Advanced line | 117 | NA117 | unknown |
| 8 | IDSA 64 | Cultivar | 63 | Dourado precoce | Advanced line | 118 | ART2-4L3P1-2-1 | Advanced line |
| 9 | ART12-1L6P7-21-4-B-1 | Advanced line | 64 | WAB638-1 | Cultivar | 119 | WAB 181-18 | Cultivar |
| 10 | P45 H15 | unknown | 65 | NERICA 11 | cultivar | 120 | SCRID014-1-1-1-1 | Advanced line |
| 11 | P8 H2 | unknown | 66 | OS 6 | Cultivar | 121 | ART16-9-16-17-3-B-1-1 | Advanced line |
| 12 | ART10-1L15P1-4-B-1 | Advanced line | 67 | WAB181-18 | Cultivar | 122 | ART3-12L8P6-B-B-3 | Advanced line |
| 13 | ART3-9L6P2-B-B-3 | Advanced line | 68 | NERICA 10 | Cultivar | 123 | ART12-1L4P7-21-6-1-1 | Advanced line |
| 14 | ART12-1L6P7-22-9-B-1 | Advanced line | 69 | NERICA 8 | Cultivar | 124 | WABIS 844 | Cultivar |
| 15 | ART3-6L16P5-1-1-B | Advanced line | 70 | ART16-4-11-13-4 | Cultivar | 125 | ART10-1L12E2-1-B-1 | Advanced line |
| 16 | ART3-3L10P1-1-B-2 | Advanced line | 71 | ART3-3L12P9-1-1-B | Advanced line | 126 | ART16-13-15-18-1-B-1-1 | Advanced line |
| 17 | EXP304 | Advanced line | 72 | ART3-8L4P1-2-1-3 | Advanced line | 127 | ART3-7L3P3-B-B-2 | Advanced line |

| ID | Entry Name | Type | ID | Entry Name | Type | ID | Entry Name | Type |
|---|---|---|---|---|---|---|---|---|
| 18 | C507-1373-1-B-2-M-1-5 | Advanced line | 73 | IR 64 | Cultivar | 128 | WAB99-17 | Cultivar |
| 19 | IDSA 62 | Cultivar | 74 | NERICA 4 | Cultivar | 129 | ART2-9L9P6-1-B-3 | Advanced line |
| 20 | ART8-L17P12-1 | Advanced line | 75 | ART2-6L6P6-1-B-1 | Cultivar | 130 | NERICA 1 | Cultivar |
| 21 | ART25-3-29-2-B | Advanced line | 76 | SCRID017-1-4-4-4-1 | Advanced line | 131 | ART3-12L11P2-B-B-1 | Advanced line |
| 22 | ART12-1L6P7-2-2-1-1 | Advanced line | 77 | NA77 | Advanced line | 132 | BALA | Cultivar |
| 23 | ART3-8L6P3-1-3-B | Advanced line | 78 | P27 H1 | unknown | 133 | NERICA 15 | Cultivar |
| 24 | ART121L6P7-11-6-B-2 | Advanced line | 79 | ART3-5L20P5-B-B-3 | unknown | 134 | NERICA 14 | Cultivar |
| 25 | ART2-4L3P1-2-2 | Advanced line | 80 | NERICA 14 | Advanced line | 135 | ART3-4L18P3-2-6 | Advanced line |
| 26 | SCRID006-3-2-3-2 | Advanced line | 81 | FARO 48 | Cultivar | 136 | C537B-1305-3-59-3-1-4-B-B-12-1-1-M-1-1 | Advanced line |
| 27 | ART16-12-17-3-4-B-1-1 | Advanced line | 82 | ART3-7L3P3-B-B-2 | Cultivar | 137 | ART3-8L6P3-2-2-B | Advanced line |
| 28 | NERICA 6 | Cultivar | 83 | SCRID019-1-1-1-1-2 | Advanced line | 138 | NERICA 13 | Cultivar |
| 29 | NERICA 9 | Cultivar | 84 | WAB 56 – 104 | Advanced line | 139 | ART3-3L13P2-2-B-B-2 | Advanced line |
| 30 | SCRID006-2-4-3-4 | Advanced line | 85 | NERICA 16 | Cultivar | 140 | ITA 212 | Cultivar |
| 31 | NERICA 8 | Cultivar | 86 | WAB 57-95-1-1-HB | Cultivar | 141 | ART25-9-13-2-B | Advanced line |
| 32 | ART12-1L4P7-21-4-B-3 | Advanced line | 87 | ART16-12-17-3-4-B-1-1 | Cultivar | 142 | IG 10 | Cultivar |
| 33 | IDSA 85 | Cultivar | 88 | WAB181-18 | Advanced line | 143 | ART16-12-17-29-2-B-1-1 | Advanced line |
| 34 | IRAT 302 | Cultivar | 89 | ART3-8L11E2-4-B-1 | Cultivar | 144 | PANAMA 1048 | Cultivar |
| 35 | ART3-3L7P1-B-B-3 | Advanced line | 90 | WAB891-SG12 | Advanced line | 145 | WAB 56-104 | Cultivar |
| 36 | ART16-5-2-28-2-2-1 | Cultivar | 91 | ART1-1L5P8-17-1-3-B | Cultivar | 146 | ART3-8L3P4-1-B-2 | Advanced line |

| ID | Entry Name | Type | ID | Entry Name | Type | ID | Entry Name | Type |
|---|---|---|---|---|---|---|---|---|
| 37 | ART3-9L6P1-B-B-1 | Advanced line | 92 | ART12-1L6P7-3-5-B-1 | Advanced line | 147 | ART16-4-14-2-2-B-1 | Advanced line |
| 38 | ART3-8L6P3-2-4-B | Advanced line | 93 | WAB100-B-B-B-B-21-H2 | Advanced line | 148 | SCRI017-1-4-4-4-1 | Advanced line |
| 39 | ART1-1L2P1-3-1-B | Advanced line | 94 | WAB706-3-4-K4-KB-3 | Cultivar | 149 | ART12-1L6P7-5-4-1-1 | Advanced line |
| 40 | ART3-1L5P8-6-B-1 | Advanced line | 95 | NERICA 4 | Advanced line | 150 | ART16-12-13-14-B-1-1 | Advanced line |
| 41 | NERICA 7 | Cultivar | 96 | NERICA 14 | Cultivar | 151 | NERICA 5 | Cultivar |
| 42 | ART3-1L6P5-1-B-1 | Advanced line | 97 | ART16-9-4-16-3-B-1 | Cultivar | 152 | ART3-6L3P9-B-B-4 | Cultivar |
| 43 | P36 H1 | unknown | 98 | P29 H4 | Advanced line | 153 | WABC 165 | Cultivar |
| 44 | TOX 1857-3-2-201-1 | Cultivar | 99 | FARO 39 (IRAT144) | unknown | 154 | ART1-1L5P6-1-3-1-B | Advanced line |
| 45 | WAB788-16-3-2-1-HB | Advanced line | 100 | NERICA 4 | Cultivar | 155 | ART12-1L6P7-22-3-B-3 | Advanced line |
| 46 | SCRID079-1-5-4-2 | Advanced line | 101 | WAB56-125 | Cultivar | 156 | ART16-21-5-12-3-1-2-1 | Advanced line |
| 47 | ART10-1L20P3-2-B-1 | Advanced line | 102 | NERICA 12 | Cultivar | 157 | WAB 56-50 | Cultivar |
| 48 | WAB -56-77 | Cultivar | 103 | NERICA 14 | Cultivar | 158 | ART12-1L4P7-22-5-B-2 | Advanced line |
| 49 | ART2-5L8P2-B-B-2 | Advanced line | 104 | NERICA 14 | Cultivar | 159 | ART16-5-6-22-2-B-1-1 | Advanced line |
| 50 | ART3-8L6P6-5-B-2 | Advanced line | 105 | NERICA 14 | Cultivar | 160 | WAB880-1-38-19-23-P1-HB | Advanced line |
| 51 | P5 H2 | unknown | 106 | NERICA 6 | Cultivar | | | |
| 52 | Moroberekan | Cultivar | 107 | PCT-4\0\0\0>19-M-1-1-5-1-M | Cultivar | | | |
| 53 | ART2-9L3P3-B-B-4 | Advanced line | 108 | NERICA 4 | Advanced line | | | |
| 54 | NERICA 3 | Cultivar | 109 | P25 H1 | unknown | | | |
| 55 | NERICA 2 | Cultivar | 110 | P22 H13 | unknown | | | |

## Appendix 2.2 Nanodrop reading

| Sample ID | Conc. | Units | 260/280 | | Sample ID | Conc. | Units | 260/280 |
|---|---|---|---|---|---|---|---|---|
| 1 | 226.6 | ng/µl | 2.02 | | 27 | 545.8 | ng/µl | 2 |
| 3 | 303.5 | ng/µl | 1.92 | | 28 | 825 | ng/µl | 2.03 |
| 4 | 284.6 | ng/µl | 1.98 | | 29 | 730.4 | ng/µl | 2.07 |
| 5 | 317.2 | ng/µl | 1.99 | | 30 | 460.5 | ng/µl | 2.04 |
| 6 | 348.7 | ng/µl | 2.02 | | 31 | 659.2 | ng/µl | 2.16 |
| 7 | 400.8 | ng/µl | 2.05 | | 32 | 678.6 | ng/µl | 2.05 |
| 8 | 438.4 | ng/µl | 2.04 | | 33 | 424.6 | ng/µl | 2 |
| 9 | 282.7 | ng/µl | 2.05 | | 34 | 0.0744 | ng/µl | -0.1 |
| 10 | 428.9 | ng/µl | 2.05 | | 35 | 551.6 | ng/µl | 1.97 |
| 11 | 358.5 | ng/µl | 1.99 | | 36 | 18.23 | ng/µl | 2.05 |
| 12 | 632.5 | ng/µl | 2.01 | | 37 | 797.8 | ng/µl | 2.03 |
| 13 | 541.2 | ng/µl | 2.01 | | 38 | 447.9 | ng/µl | 2.01 |
| 14 | 458.7 | ng/µl | 2.01 | | 39 | 540.6 | ng/µl | 2.03 |
| 15 | 393.7 | ng/µl | 2.07 | | 40 | 233.1 | ng/µl | 2 |
| 16 | 376.5 | ng/µl | 2.06 | | 41 | 445.2 | ng/µl | 1.99 |
| 17 | 451.3 | ng/µl | 1.93 | | 42 | 311.8 | ng/µl | 1.99 |
| 18 | 462.3 | ng/µl | 1.93 | | 43 | 634.5 | ng/µl | 2.06 |
| 19 | 407.4 | ng/µl | 1.97 | | 44 | 589.4 | ng/µl | 2.01 |
| 20 | 558.2 | ng/µl | 1.99 | | 45 | 407.5 | ng/µl | 1.98 |
| 21 | 388.7 | ng/µl | 2.03 | | 46 | 413.9 | ng/µl | 2.01 |
| 22 | 546.5 | ng/µl | 1.98 | | 47 | 379.2 | ng/µl | 1.99 |
| 23 | 561.6 | ng/µl | 2.03 | | 48 | 297 | ng/µl | 2.06 |
| 24 | 729.8 | ng/µl | 2 | | 49 | 403.1 | ng/µl | 2.09 |
| 25 | 526.4 | ng/µl | 2.05 | | 50 | 426.7 | ng/µl | 2.06 |
| 26 | 256.8 | ng/µl | 1.96 | | | | | |

# Chapter 3 : Genetic variability and path coefficient analysis of yield and related traits of upland rice under *Striga* infestation in Uganda


## Abstract

Genetic variability and relationships between traits and yield in rice grown under *Striga* infestation has not been studied. Hence, the objective of this study was to establish genetic variability, correlations, direct and indirect effects of various attributes to yield of upland rice under *Striga* infestation. One hundred and fifty six test genotypes and four check varieties were grown in three sites under artificial infestation of *Striga hermonthica* for two seasons. At each site, the experiments were laid out in 10 x 16 alpha lattice designs with two replications. Agronomic data of the crop as well as developmental data of *Striga* were recorded and analysis of variance conducted to explore variability through mean performance and coefficients of variation. Secondly, correlations, direct and indirect effects of some upland rice agronomic traits as well as *Striga* resistance traits on grain yield were estimated. Highly significant differences ($p<0.001$) were observed for all the characters studied. Estimates of phenotypic coefficient of variability were generally higher than the corresponding genotypic coefficients of variability for all characters studied implying substantial environmental influences on the performance of the traits. Broad sense heritability estimates were generally low (an average of 30.56%) for most of the traits studied. Grain yield (65.77) recorded the highest genetic advance (GA) followed by area under *Striga* number progress curve (54.05), number of grains per panicle (31.88), number of panicles per plant (6.24) and thousand grain weight (4.59); meaning that it is beneficial to select for these traits. The highest direct phenotypic and genotypic effects to grain yield per hectare were obtained from number of grains per panicle (0.830, 0.882), followed by number of panicles per plant (0.380, 0.438) and 1000-grain weight (0.250, 0.285). This meant that these traits could be used for direct selection for grain yield in rice under *Striga* infestation.



**Key words:** Correlations, Direct and Indirect effects, *Striga hermonthica*, Variability, Yield.

## 3.1 Introduction

Rice is an important food and cash crop in Uganda. Its consumption has increased so much so that domestic production is unable to meet the demand and the country relies on imports to cover the deficit (Kikuchi et al., 2013; Tokida et al., 2014). Like other cereals in Africa, the parasitic weeds and *Striga hermonthica* in particular, heavily threaten upland rice grown under rain fed ecologies in Uganda (Parker, 2012; Kibiri et al., 2015; Rodenburg et al., 2015). Using a specialized organ known as haustorium, these weeds extract water, nutrients and metabolites and alter the plant growth regulators of the host, leading to stunted growth and losses in reproductive output of the host plant (Westwood, 2013). Consequently, there is need to devote efforts towards development of rice genotypes that yield highly under *Striga* infestation as an attempt to meet the fastest growing demand for rice grain.

Development of varieties having good yield determining attributes requires knowledge of the nature and magnitude of heritable variation in the available germplasm (Semagn et al., 2012; Kumar and Senapati, 2013). In addition, being a complex character, breeding for improvement in yield is supported with knowledge of breeding value of potential parents as well as interrelationships among the plant characters (Prasad et al., 2001). For upland rice in Uganda and or Africa at large, genetic variability and relationships between traits and yield in rice grown under *Striga* infestation has not been studied. Hence, the objective of this study was to establish genetic variability, correlations, direct and indirect effects of various attributes to yield of upland rice under *Striga* infestation

The above information enables breeders to achieve maximum efficiency in selection of parents among inbred lines and or selection of advanced lines prior to release (Semagn et al., 2012). However, selection based on a single trait may not always be effective; and yet at the same time it is not practical to select for a large number of traits concurrently in one selection scheme (Govindaraji et al., 2011; Ezeaku et al., 2015). The solution here is to use correlation analysis to identify those traits, which greatly contribute to yield. Better still, path coefficient analysis provides an effective tool for partitioning the correlation coefficient into direct and indirect effects of cause and effect nature and presents the relationships in a more meaningful way (Prasad et al., 2001; Soni et al., 2013).

Path coefficient analysis refers to a statistical procedure of partitioning of correlation index into direct and indirect effects through genotypic pathway associations of yield attributing characters (Kumar and Senapati, 2013). The relevance of this analysis lies in the identification of traits that

can be directly or indirectly selected for during improvement of yield. Otherwise, the practice of unilateral selection alone does not meet the optimum requirements for improvement. Consequently, for any breeding program to achieve meaningful response to selection, assessment of genetic variability is indispensable. In any case, estimates of genetic parameters such as heritability and genetic advance are specific for a particular population and the phenotypic expression of the quantitative characters may be altered by environmental stress that affect plant development and growth (Idahosa et al., 2010).

Broad sense heritability ($H^2$) of a trait is an estimate which gives an idea of the extent of genetic control for the expression of a particular character and it also provides an indication of the reliability of phenotypic variability in the selection program hence influencing its success (Chopra, 2000; Idahosa et al., 2010). Genetic advance (GA) measures the magnitude of the expected genetic gain from one cycle of selection (Hamdi, 1992). However, it is more meaningful to use both heritability and genetic advance in prediction of the resulting effects of selection of the best individuals (Dutta et al., 2013). Consequently, the present study was designed to estimate genetic variability, heritability, genetic advance and relationships between yield and its contributing characters of upland rice under *Striga* infestation. The overall aim of the study was to obtain information that could be useful in upland rice improvement for increased yield and resistance to *Striga hermonthica*.

## 3.2 Materials and Methods

### 3.2.1 Study area and experimental design

The trials were conducted under *Striga* infestation during the first (March to June) rain seasons of 2012 and 2013 in three districts of Bukedea, Kumi and Pallisa all found in the eastern region of Uganda, which is a hotspot area for *Striga hermonthica*. The trials were laid out in 10 x 16 alpha lattice design with two replications as recommended by Cochran and Cox, (1957) for large entry experiments. The materials consisted of 160 genotypes (156 experimental material plus 4 checks) which were the same materials used for diversity study in Chapter 2. The seed was planted directly by drilling method at a spacing of 20 cm within row and 30 cm between rows in $1m^2$ plots. In addition, artificial inoculation was done to ensure uniform infection. Artificial inoculation using a mix of *Striga hermonthica* seed and sand providing approximately 4000 *Striga* seed inoculum per hole as recommended by Kaewchumnong and Price (2008). To arrive at this recommended inoculum; the method outlined by Berner et al. (1997) was applied. This *Striga* seed was obtained from previous season fields of sorghum and using a bottle top estimated to have a 5 g capacity

of a sand *Striga* seed mixture estimated to contain 4000 *Striga* for every planting hole was inoculated shortly before placing 3-5 seeds of rice genotypes to the planting hole. Recommended agricultural practices were implemented in order to obtain a good plant stand to enable season long study of the effect of *Striga* on the crop without killing the crop prematurely.

### 3.2.2 Data collection

Important agronomic traits for both the crop and weed development were recorded and computed accordingly for 20 randomly selected plants per plot; following procedures described by. Haussmann et al. (2000). Traits studied were: days to maturity (DM) determined by counting number of days from date of planting to date when 80% of the panicles were ripe for harvest, plant height at maturity (PHM) measured in centimetres (cm) from the ground level to the top of the panicle (excluding awn) at 80% maturity, number of tillers per plant (TNPP) counted on a plant basis, flag leaf length (FLL) measured in cm from the base to the tip of the leaf below the panicle (flag leaf), flag leaf width (FLW) in cm measured as the breadth of the central part of the flag leaf, number of panicles per plant (NPPP) counted as per plant basis, number of grains per panicle (NGPP), grain breadth in mm (GB), grain length in mm (GL), 1000-grain weight in grams (TGW), and days to *Striga* emergence (DSE). Damage rating score (DS) was estimated based on extent of damage inflicted on the crop while grain yield in kg/ha (YIELD) was calculated from the grain weight per plot. The average number of *Striga* plants per plot (SN) was used to calculate the area under *Striga* number progress curve (AUSNPC) using the formula similar to that of AUDPC; Successive *Striga* counts were then used to calculate the "Area under *Striga* number progress curve" (AUSNPC) (Kountche et al., 2013).

$$AUSNPC = \sum_{i=0}^{n-1} \left[\frac{yi + y_{(i+1)}}{2}\right](t_{(i+1)} - ti$$

Where: n is the number of *Striga* assessment dates, $y_i$ the *Striga* count at the $i^{th}$ assessment date, $t_i$ the days after sowing at the $i^{th}$ assessment date, t are the days after planting to *Striga* emergence minus 1 and $y_i$ is 0. Low AUSNPC mean values indicate resistance, and high values indicate susceptibility to *Striga*.

### 3.2.3 Data analysis

Analysis of variance (ANOVA) was conducted using REML in Genstat 17$^{th}$ version (Payne et al., 2014) to assess performance of the genotypes. The mixed model used for analysis of data was: Constant + Site + season + Site.season + Site.season.Rep + Site.season.Rep.Bloc + Entry + Site.Entry + season.Entry + Site.season.Entry. To obtain direct and indirect effects of agronomic

characters on yield; path coefficient analysis was conducted using SAS for phenotypic effects and Minitab in combination with excel for genotypic effects.

Phenotypic and genotypic coefficients of variation were estimated according to the method suggested by Burton and De Vane (1953) as follows:-

Environmental variance ($\sigma^2 e$) = MSe

Genotypic variance ($\sigma^2 g$) = [MSg - MSe] / r

Phenotypic variance ($\sigma^2 p$) = $\sigma^2 g + \sigma^2 e$

Phenotypic coefficient of variation (PCV) = $\frac{\sqrt{\sigma^2 Ph} \times 100}{\text{Grand mean}}$

Genotypic coefficient of variation (GCV) = $\frac{\sqrt{\sigma^2 g} \times 100\%}{\text{Grand mean}}$

Broad sense heritability ($H^2$) expressed as the percentage of the ratio of the genotypic variance ($\sigma^2 g$) to the phenotypic variance ($\sigma^2 p$) was estimated on genotype mean basis as described by Allard (1960) as: $H^2 = [\sigma^2 g] / \sigma^2 p \times 100$

Genetic advance in absolute unit (GA) assuming selection of superior 5% of the genotypes was estimated in accordance with the methods illustrated by Johnson et al. (1955 ) as: $GA = K\sigma p H^2$

Where K = the standardized selection differential at 5 % selection intensity (K = 2.063), $H^2$ = Heritability in broad sense, σp = Phenotypic standard deviation.

## 3.3 Results

### 3.3.1 Performance of the genotypes

The analysis of variance revealed presence of highly significant differences ($p< 0.001$) among the entries for fourteen traits (Table 3.1). Estimates of phenotypic coefficient of variability (PCV) were generally higher (Table 3.1) than the corresponding genotypic coefficients of variability (GCV) for all traits studied. However, for %CV, %GCV and %PCV; AUSNPC (98.00, 36.53 and 121.07, respectively) had the highest variability coefficients, followed by DS (88.72, 38.12 and 106.46), YIELD (72.75, 20.19, and 76.09), NGPP (67.67, 57.16 and 73.79), DSE (62.00, 25.44 and 75.06) and TNPP (48.24, 30.94, and 57.31) with at least one or more coefficients above 50%. Nonetheless, traits like NPPP (34.23, 36.88, and 37.21) and TGW (20.30, 16.81, and 24.02) had values of all the three coefficients below 50% with the least being realized from DM (8.86, 5.50, and 10.43) and PHM (9.95, 2.84, and 12.43). Other traits, which also produced low coefficients of variation, were FLL (18.46, 10.90, and 21.44), FLW (17.58, 11.06, and 20.77), GB (12.96, 8.54, and 15.52) and GL (11.56, 8.23, and 14.19).

Heritability realized in this study was generally low (an average of 30.56%) for most of the traits under study (Table 3.1). The traits with the highest heritability were NPPP (98.23%), NGPP (59.99%), TGW (48.95%), GL (33.61%) and GB (30.25%), followed by TNPP (29.15%), FLW (28.34%) and DM (27.87). The traits with the lowest heritability were PHM (5.21%), and YIELD (7.04%). Grain yield (65.77) recorded the highest genetic advance (GA) followed by AUSNPC (54.05), NGPP (31.88), NPPP (6.24) and TGW (4.59).The lowest GA was produced in FLW (0.10), GB (0.17), DS (0.28) and PHM (0.30). The highest estimates of genetic advance coupled with the corresponding broad sense heritability were recorded in YIELD (65.77, 7.04), AUSNPC (54.05, 9.1), NGPP (31.88, 59.99), NPPP (6.24, 98.23) and TGW (4.59, 48.95) followed by DM (4.05, 27.87), TNPP (2.9, 29.15), DSE (2.49, 11.49) and FLL (58.18, 25.83). The traits with the least importance for genetic advance and heritability were FLW (0.10, 28.34,) GB (0.17, 30.25) and DS (0.28, 12.82).

**Table 3.1**: Analysis of variance and estimates of variability

| | | | Trait mean squares | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fixed term/DF | AUSNPC | DM | DS | DSE | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
| Site (2) | 2.76* | 229.46*** | 30.98*** | 500.48*** | 57.57*** | 60.13*** | 125.06*** | 131.69*** | 3.28** | 18.05*** | 192.92*** | 48.27*** | 12.2*** | 133.72*** |
| season (1) | 1.88ns | 162.44*** | 22.19*** | 2281.31** | 769.79*** | 804.01*** | 1672.12** | 1760.73** | 93.2*** | 216.67*** | 1.54 | 13.53*** | 100.45*** | 1787.94*** |
| Site.season (2) | 0 | 0.15ns | 0.17ns | 6.83*** | 0.71ns | 0.74ns | 1.54ns | 1.63ns | 2.39* | 0.06ns | 0 | 0.27ns | 0.63ns | 1.65ns |
| Site.season.Rep (6) | 25.08*** | 18.24*** | 16.36*** | 10.49*** | 0.8ns | 0.04ns | 0.04ns | 10.06*** | 24.28*** | 9.81*** | 9.11*** | 5.75*** | 11.58*** | 10.21*** |
| Site.season.Rep.Bloc (108) | 9.84*** | 0.97ns | 3.17*** | 2.64*** | 3.33*** | 2.06*** | 2.54*** | 1.58*** | 5.74*** | 3.43*** | 2.6*** | 3.18*** | 1.88*** | 1.61ns |
| Entry (159) | 3.53*** | 5.84*** | 3.12*** | 1.29** | 4.8*** | 5.6*** | 7.42*** | 6.59*** | 2.11*** | 2.58*** | 2.45*** | 2.45*** | 6.2*** | 1.08*** |
| Site.Entry (318) | 0 | 0.01ns | 0.04ns | 1.09ns | 0 | 0.01ns | 0.01ns | 0.01ns | 0.74ns | 0.4ns | 0 | 0.06ns | 0.08ns | 1.16* |
| season.Entry (159) | 3*** | 0.02ns | 2.67*** | 1.12ns | 0.06ns | 0.07ns | 0.09ns | 0.08ns | 1.56*** | 0.31ns | 3.74*** | 2.97*** | 0.05ns | 1.1ns |
| Site.season.Entry (318) | 0 | 0 | 0.04ns | 1.3** | 0 | 0 | 0 | 0 | 0.76ns | 0.16ns | 0 | 0.06ns | 0.03ns | 1.19** |
| ***% CV*** | **98.00** | **8.86** | **88.72** | **62.00** | **18.46** | **17.58** | **12.96** | **11.56** | **67.67** | **34.23** | **9.95** | **20.30** | **48.24** | **72.75** |
| ***% GCV*** | **36.53** | **5.50** | **38.12** | **25.44** | **10.90** | **11.06** | **8.54** | **8.23** | **57.16** | **36.88** | **2.84** | **16.81** | **30.94** | **20.19** |
| ***% PCV*** | **121.07** | **10.43** | **106.46** | **75.06** | **21.44** | **20.77** | **15.52** | **14.19** | **73.79** | **37.21** | **12.43** | **24.02** | **57.31** | **76.09** |
| ***Heritability ($H^2$)*** | **9.10** | **27.87** | **12.82** | **11.49** | **25.83** | **28.34** | **30.25** | **33.61** | **59.99** | **98.23** | **5.21** | **48.95** | **29.15** | **7.04** |
| ***Genetic Advance*** | **54.05** | **4.05** | **0.28** | **2.49** | **1.50** | **0.10** | **0.17** | **0.45** | **31.88** | **6.24** | **0.30** | **4.59** | **2.90** | **65.77** |

KEY: AUSNPC - Area under *Striga* number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha. % - percentage, CV – coefficient of variation, GCV – Genotypic coefficient of Variation, PCV- Phenotypic coefficient of Variation.

The mean performance of the genotypes (Table 3.2) revealed the highest yielding genotypes as NERICA 10 (5545.07 kg/ha), followed by Faro 39 (4684.51 kg/ha) and ART16-21-5-12-3-1-2-1 (4635.58 kg/ha).These genotypes and many others yielded higher than the mean of the four checks (2874.19 kg/ha). Among the top ten genotypes, NERICA 14 was shown to mature earlier (115.76 days), as well as show early susceptibility to *Striga,* in 66.38 days to *Striga* emergence. The lowest yielding genotypes were ART3-12L2P1-B-B-1 (835.84 kg/ha), PCT-4\0\0\0>19-M-1-1-5-1-M (867.08 kg/ha), ART12-1L4P7-21-4-B-3 (934.21 kg/ha) and SCRID079-1-5-4-2 (1029.10 kg/ha).

### 3.3.2 Correlation analysis

The phenotypic correlation coefficients (Table 3.3) were generally lower in magnitude than the corresponding genotypic correlation coefficients (Table 3.4). There were strong positive correlations at both phenotypic and genotypic levels between YIELD and NGPP (0.800, 0.818), followed by NPPP (0.270, 0.296), TGW (0.250, 0.271) and TNPP (0.140, 0.175). The *Striga* development traits had high positive correlation to one another for instance AUSNPC was highly correlated to DSE (r = 0.70), DS (r = 0.58) and the latter is highly correlated to DSE (r = 0.73). These three *Striga* development traits did not show any tangible correlation to yield (Table 3.3), however they showed significant negative correlations to NGPP, NPPP, and PHM. This suggests that the three *Striga* development traits; AUSNPC, DSE and DS are likely to exert indirect effect on grain yield through negative correlations with NGPP, NPPP and PHM. For example DSE exhibited negative correlations with NGPP (r = - 0.020), NPPP (R = - 0.140) and PHM (r = -0.130).

**Table 3.2**: Overall mean performance of top ten and bottom five varieties

| Genotypes | AUSNPC | DSE | DM | DS | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **TOP TEN HIGH YIELDING ENTRIES** | | | | | | | | | | | | | | |
| NERICA 10 | 1025.29 | 76.34 | 142.49 | 0.38 | 22.71 | 1.58 | 2.92 | 11.09 | 39.15 | 7.97 | 94.97 | 26.75 | 24.28 | 5545.07 |
| FARO 39 (IRAT144) | 1128.47 | 74.96 | 120.64 | 4.06 | 25.91 | 1.50 | 3.90 | 9.37 | 46.08 | 8.74 | 99.94 | 25.96 | 13.08 | 4684.51 |
| ART16-21-5-12-3-1-2-1 | 816.08 | 79.16 | 128.61 | 2.06 | 28.46 | 1.51 | 2.90 | 9.27 | 54.51 | 6.12 | 96.64 | 26.25 | 12.85 | 4635.58 |
| NERICA 14 | 607.74 | 66.38 | 115.76 | 2.30 | 25.87 | 1.62 | 3.30 | 9.20 | 43.10 | 11.15 | 94.50 | 26.18 | 13.79 | 4602.32 |
| NERICA 15 | 668.58 | 73.48 | 120.21 | 2.43 | 28.06 | 1.78 | 3.36 | 8.88 | 45.80 | 6.11 | 98.09 | 27.80 | 8.98 | 4441.92 |
| ART12-1L2P2-20-3-1-2 | 2070.48 | 74.23 | 127.17 | 5.11 | 22.73 | 1.40 | 3.33 | 8.88 | 62.65 | 7.52 | 99.26 | 23.97 | 21.86 | 4437.89 |
| WABC 165 | 500.39 | 74.66 | 156.10 | 2.69 | 30.78 | 1.43 | 3.14 | 8.87 | 28.84 | 8.37 | 115.26 | 27.37 | 12.50 | 4434.12 |
| ITA 212 | 570.74 | 68.72 | 140.47 | 0.98 | 28.36 | 1.48 | 3.29 | 8.81 | 53.18 | 8.23 | 102.29 | 26.39 | 18.79 | 4407.20 |
| NERICA 4 | 867.08 | 72.14 | 123.25 | 3.78 | 18.58 | 1.29 | 3.74 | 8.72 | 45.85 | 7.39 | 98.38 | 27.58 | 14.41 | 4358.25 |
| WAB891-SG12 | 213.42 | 80.39 | 144.94 | 0.82 | 23.75 | 1.39 | 3.48 | 8.67 | 49.76 | 7.91 | 105.01 | 24.90 | 11.30 | 4333.74 |
| **BOTTOM FIVE LOW YIELDING ENTRIES** | | | | | | | | | | | | | | |
| OS 6 | 709.88 | 72.68 | 121.77 | 2.40 | 23.51 | 1.54 | 2.86 | 6.37 | 32.03 | 8.76 | 99.20 | 29.47 | 13.53 | 2182.99 |
| SCRID079-1-5-4-2 | 1112.73 | 74.70 | 127.93 | 3.01 | 21.64 | 1.56 | 3.16 | 6.06 | 35.15 | 6.04 | 98.71 | 25.40 | 11.88 | 1029.10 |
| ART12-1L4P7-21-4-B-3 | 463.66 | 76.59 | 144.62 | 2.97 | 22.56 | 1.60 | 3.01 | 5.87 | 21.10 | 10.08 | 102.03 | 22.99 | 17.96 | 934.21 |
| PCT-4\0\0\0>19-M-1-1-5-1-M | 784.94 | 75.28 | 126.59 | 2.23 | 29.27 | 1.45 | 3.48 | 5.73 | 45.82 | 8.83 | 100.28 | 25.47 | 13.43 | 867.08 |
| ART3-12L2P1-B-B-1 | 913.49 | 69.28 | 118.68 | 3.18 | 26.21 | 1.56 | 2.90 | 5.67 | 30.27 | 10.19 | 97.70 | 33.06 | 14.37 | 835.84 |
| **CHECK ENTRIES** | | | | | | | | | | | | | | |
| Moroberekan | 74.81 | 2.05 | 137.29 | 0.52 | 26.13 | 1.24 | 3.76 | 6.67 | 44.00 | 11.79 | 110.69 | 28.54 | 21.15 | 2938.45 |
| IRAT 302 | 649.90 | 50.62 | 134.34 | 2.23 | 25.75 | 1.51 | 3.62 | 7.25 | 48.89 | 9.41 | 99.53 | 27.33 | 17.28 | 2876.47 |
| ITA 212 | 570.74 | 36.91 | 140.47 | 0.98 | 28.36 | 1.48 | 3.29 | 8.81 | 53.18 | 8.23 | 102.29 | 26.39 | 18.79 | 2863.24 |
| IDSA 85 | 684.68 | 47.16 | 123.30 | 1.63 | 27.06 | 1.37 | 3.35 | 7.60 | 56.02 | 8.02 | 99.52 | 27.51 | 11.71 | 2818.58 |
| ***Standard error*** | ***362.00*** | ***27.00*** | ***6.10*** | ***0.27*** | ***1.00*** | ***0.00*** | ***0.01*** | ***0.04*** | ***33.90*** | ***0.37*** | ***4.42*** | ***1.28*** | ***2.57*** | ***901.00*** |
| ***Grand mean*** | ***787.90*** | ***41.37*** | ***127.90*** | ***2.78*** | ***25.90*** | ***1.52*** | ***3.22*** | ***7.84*** | ***45.06*** | ***8.35*** | ***99.42*** | ***27.03*** | ***15.61*** | ***2244.00*** |
| ***Range*** | ***3267.00*** | ***115.10*** | ***116.74*** | ***9.00*** | ***68.75*** | ***5.08*** | ***3.32*** | ***9.88*** | ***126.40*** | ***27.52*** | ***108.40*** | ***53.33*** | ***106.80*** | ***6780.00*** |

KEY: AUSNPC - Area under *Striga* number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha.

**Table 3.3**: Phenotypic correlation coefficients between *Striga* development traits and agronomic traits with grain yield of upland rice

| | AUSNPC | DM | DS | DSE | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AUSNPC | - | | | | | | | | | | | | | |
| DM | -0.030 | - | | | | | | | | | | | | |
| DS | 0.580 | -0.060 | - | | | | | | | | | | | |
| DSE | 0.700 | -0.090 | 0.730 | - | | | | | | | | | | |
| FLL | -0.070 | -0.020 | 0.010 | -0.070 | - | | | | | | | | | |
| FLW | -0.090 | -0.160 | -0.020 | -0.040 | 0.230 | - | | | | | | | | |
| GB | 0.000 | -0.020 | 0.040 | 0.070 | -0.040 | -0.140 | - | | | | | | | |
| GL | 0.140 | 0.060 | 0.060 | 0.140 | -0.040 | -0.030 | 0.090 | - | | | | | | |
| NGPP | -0.020 | -0.030 | -0.070 | -0.020 | -0.030 | -0.090 | 0.010 | -0.070 | - | | | | | |
| NPPP | -0.070 | -0.080 | -0.080 | -0.140 | 0.150 | 0.070 | 0.010 | -0.060 | -0.100 | - | | | | |
| PHM | -0.120 | 0.530 | -0.050 | -0.130 | 0.380 | 0.070 | 0.060 | -0.040 | -0.020 | 0.050 | - | | | |
| TGW | 0.200 | -0.110 | 0.170 | 0.170 | 0.030 | -0.010 | -0.020 | -0.090 | 0.020 | -0.050 | 0.040 | - | | |
| TNPP | 0.110 | -0.050 | 0.050 | 0.010 | -0.180 | -0.120 | 0.040 | 0.030 | 0.120 | 0.140 | -0.290 | -0.110 | - | |
| YIELD | 0.030 | -0.070 | 0.000 | 0.030 | 0.020 | -0.030 | 0.040 | -0.080 | 0.800 | 0.270 | 0.010 | 0.250 | 0.140 | - |

KEY: AUSNPC - Area under striga number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha..+

**Table 3.4**: Genotypic correlation coefficients of *Striga* development traits and agronomic traits with grain yield in upland rice

| | AUSNPC | DM | DS | DSE | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AUSNPC | 1.000 | | | | | | | | | | | | | |
| DM | -0.052 | 1.000 | | | | | | | | | | | | |
| DS | 0.634 | -0.067 | 1.000 | | | | | | | | | | | |
| DSE | 0.748 | -0.116 | 0.782 | 1.000 | | | | | | | | | | |
| FLL | -0.088 | -0.024 | 0.016 | -0.081 | 1.000 | | | | | | | | | |
| FLW | -0.107 | -0.172 | -0.022 | -0.029 | 0.232 | 1.000 | | | | | | | | |
| GB | 0.009 | -0.018 | 0.061 | 0.091 | -0.050 | -0.150 | 1.000 | | | | | | | |
| GL | 0.165 | 0.044 | 0.078 | 0.166 | -0.046 | -0.020 | 0.092 | 1.000 | | | | | | |
| NGPP | -0.035 | -0.050 | -0.096 | -0.014 | -0.002 | -0.136 | 0.009 | -0.090 | 1.000 | | | | | |
| NPPP | -0.076 | -0.076 | -0.091 | -0.164 | 0.167 | 0.078 | 0.012 | -0.082 | -0.120 | 1.000 | | | | |
| PHM | -0.213 | 0.626 | -0.103 | -0.202 | 0.481 | 0.062 | 0.071 | -0.066 | -0.026 | 0.068 | 1.000 | | | |
| TGW | 0.269 | -0.149 | 0.199 | 0.210 | 0.040 | -0.009 | -0.011 | -0.121 | 0.029 | -0.079 | 0.025 | 1.000 | | |
| TNPP | 0.125 | -0.064 | 0.057 | 0.005 | -0.205 | -0.130 | 0.055 | 0.028 | 0.171 | 0.119 | -0.368 | -0.133 | 1.000 | |
| YIELD | 0.049 | -0.094 | 0.013 | 0.047 | 0.057 | -0.040 | 0.056 | -0.119 | 0.818 | 0.296 | 0.000 | 0.271 | 0.175 | 1.000 |

KEY: AUSNPC - Area under *Striga* number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha

### 3.3.3 Path coefficient analysis

Path coefficient analysis (Tables 3.5 and 3.6) revealed ten traits with positive phenotypic and genotypic direct effects to yield. Namely: DM, DS, DSE, FLW, GB, GL, NGPP, NPPP, TGW and TNPP whereas AUSNPC and FLL showed negative direct effects. The highest direct phenotypic and genotypic effects to grain yield per hectare was obtained from number of grains per panicle (0.830, 0.882), followed by number of panicles per plant (0.380, 0.438) and 1000-grain weight (0.250, 0.285). The phenotypic direct effects of these three traits were positive and slightly greater or equal to their phenotypic correlations with yield, that is, 0.83 > 0.8, 0.38 > 0.27 and 0.25 = 0.25 for NGPP, NPPP and TGW respectively.

**Table 3.5**: Phenotypic direct effects of agronomic traits to grain yield of upland rice grown under *Striga* infestation

| | AUSPC | DM | DS | DSE | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **AUSPC** | **-0.030** | 0.000 | 0.020 | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 | -0.020 | -0.020 | 0.000 | -0.050 | 0.000 | **0.030** |
| **DM** | 0.000 | **0.020** | 0.000 | 0.000 | 0.000 | -0.010 | 0.000 | 0.000 | -0.020 | -0.030 | 0.000 | -0.030 | 0.000 | **-0.070** |
| **DS** | -0.020 | 0.000 | **0.030** | 0.040 | 0.000 | 0.000 | 0.000 | 0.000 | -0.060 | -0.030 | 0.000 | 0.040 | 0.000 | **0.000** |
| **DSE** | -0.020 | 0.000 | 0.020 | **0.050** | 0.000 | 0.000 | 0.000 | 0.000 | -0.010 | -0.050 | 0.000 | 0.040 | 0.000 | **0.030** |
| **FLL** | 0.000 | 0.000 | 0.000 | 0.000 | **-0.010** | 0.010 | 0.000 | 0.000 | -0.020 | 0.060 | 0.000 | 0.010 | 0.000 | **0.020** |
| **FLW** | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | **0.040** | 0.000 | 0.000 | -0.080 | 0.030 | 0.000 | 0.000 | 0.000 | **-0.030** |
| **GB** | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | -0.010 | **0.030** | 0.000 | 0.010 | 0.000 | 0.000 | 0.000 | 0.000 | **0.040** |
| **GL** | 0.000 | 0.000 | 0.000 | 0.010 | 0.000 | 0.000 | 0.000 | **0.010** | -0.060 | -0.020 | 0.000 | -0.020 | 0.000 | **-0.080** |
| **NGPP** | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | **0.830** | -0.040 | 0.000 | 0.010 | 0.000 | **0.800** |
| **NPPP** | 0.000 | 0.000 | 0.000 | -0.010 | 0.000 | 0.000 | 0.000 | 0.000 | -0.080 | **0.380** | 0.000 | -0.010 | 0.000 | **0.270** |
| **PHM** | 0.000 | 0.010 | 0.000 | -0.010 | -0.010 | 0.000 | 0.000 | 0.000 | -0.010 | 0.020 | **0.000** | 0.010 | 0.000 | **0.010** |
| **TGW** | -0.010 | 0.000 | 0.000 | 0.010 | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | -0.020 | 0.000 | **0.250** | 0.000 | **0.250** |
| **TNPP** | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.100 | 0.050 | 0.000 | -0.030 | **0.010** | **0.140** |

KEY:AUSNPC - Area under *Striga* number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha

**Table 3.6**: Genotypic direct effect of agronomic traits to grain yield of upland rice grown under *Striga* infestation

| | AUSNPC | DM | DS | DSE | FLL | FLW | GB | GL | NGPP | NPPP | PHM | TGW | TNPP | YIELD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **AUSNPC** | -0.042 | -0.003 | 0.049 | 0.030 | 0.002 | -0.008 | 0.000 | 0.003 | -0.031 | -0.033 | 0.003 | -0.077 | 0.000 | **0.490** |
| **DM** | -0.002 | 0.065 | -0.005 | -0.005 | 0.001 | -0.013 | -0.001 | 0.001 | -0.044 | -0.033 | -0.008 | -0.043 | 0.000 | **-0.094** |
| **DS** | 0.027 | -0.004 | 0.078 | 0.032 | 0.000 | -0.002 | 0.003 | 0.001 | -0.085 | -0.040 | 0.001 | 0.057 | 0.000 | **0.013** |
| **DSE** | 0.032 | -0.008 | 0.061 | 0.040 | 0.002 | -0.002 | 0.004 | 0.003 | -0.013 | -0.072 | 0.002 | 0.060 | 0.000 | **0.047** |
| **FLL** | -0.004 | -0.002 | 0.001 | -0.003 | -0.021 | 0.017 | -0.002 | -0.001 | -0.001 | 0.073 | -0.006 | 0.011 | 0.000 | **0.057** |
| **FLW** | -0.005 | -0.011 | -0.002 | -0.001 | -0.005 | 0.074 | -0.007 | 0.000 | -0.120 | 0.034 | -0.001 | -0.003 | 0.000 | **-0.040** |
| **GB** | 0.000 | -0.001 | 0.005 | 0.004 | 0.001 | -0.011 | 0.048 | 0.001 | 0.008 | 0.005 | -0.001 | -0.003 | 0.000 | **0.056** |
| **GL** | 0.007 | 0.003 | 0.006 | 0.007 | 0.001 | -0.002 | 0.004 | 0.015 | -0.080 | -0.036 | 0.001 | -0.034 | 0.000 | **-0.119** |
| **NGPP** | -0.001 | -0.003 | -0.008 | -0.001 | 0.000 | -0.010 | 0.000 | -0.001 | 0.882 | -0.052 | 0.000 | 0.008 | 0.000 | **0.818** |
| **NPPP** | -0.003 | -0.005 | -0.007 | -0.007 | -0.004 | 0.006 | 0.001 | -0.001 | -0.105 | 0.438 | -0.001 | -0.022 | 0.000 | **0.296** |
| **PHM** | -0.009 | 0.041 | -0.008 | -0.008 | -0.010 | 0.005 | 0.003 | -0.001 | -0.023 | 0.030 | -0.012 | 0.007 | -0.001 | **0.000** |
| **TGW** | 0.011 | -0.010 | 0.015 | 0.008 | -0.001 | -0.001 | -0.001 | -0.002 | 0.026 | -0.034 | 0.000 | 0.285 | 0.000 | **0.271** |
| **TNPP** | 0.005 | -0.004 | 0.004 | 0.000 | 0.004 | -0.010 | 0.003 | 0.000 | 0.151 | 0.052 | 0.004 | -0.038 | 0.002 | **0.175** |

KEY: AUSNPC - Area under *Striga* number progress curve, DM - Days to maturity, DS - Damage rating score, DSE - Days to *Striga* emergence, FLL - Flag leaf length (cm), FLW - Flag leaf width (cm), GB - Grain breadth (mm), GL - Grain length, NGPP - Number of grains per panicle, NPPP – Number of panicles per plant, PHM – Plant height at maturity, TGW – Thousand grain weight, TNPP – Tiller number per plant, YIELD – Grain yield kg/ha.

## 3.4 Discussion

### 3.4.1 Variability

Presence of highly significant differences among the entries portrayed considerable amount of variability in the entries. The higher PCVs in comparison with GCVs obtained for all traits are a reflection of greater environmental influence on the expression of the characters. Traits like days to maturity, plant height at maturity, grain breadth and grain length, which showed small PCVs as well as small CVs, had a smaller environmental influence on their expression. High heritability coupled with high genetic advance as seen in number of grains per panicle, number of panicles per plant and thousand grain weight is a revelation of high genetic influence. Such characters can be improved through selection as suggested by Kumar and Senapati, (2013). Likewise high heritability associated with low genetic advance such as observed in grain length, grain breadth, tiller number per plant, flag leaf width, flag leaf length and days to maturity means high environmental variance. Thus cannot be improved through selection. On the other hand, low heritability coupled with low genetic advance observed for plant height at maturity, *Striga* damage score and days to *Striga* emergence; as well as low heritability coupled with high genetic advance as registered by grain yield and area under *Striga* number progress curve is an indication of high interference of environmental influence, thus direct selection would be ineffective for those traits. These findings are in agreement with the study of Jha et al. (2014) who also reported additive gene action for number of grains per panicle; arising from high heritability and high genetic advance; as well as non-additive gene action for grain yield and thousand1000-grain weight arising from high heritability and low genetic advance.

The traits that exhibited high variability coefficients included area under *Striga* number progress curve, damage syndrome, grain yield, number of grains per panicle, days to Striga emergence and tiller number per plant while number of panicle per plant, thousand grain weight, grain breadth and grain length had low coefficients of variation. These findings are similar to the findings of other workers for one or more characters for example Kumar and Senapati (2013), for grain yield, number of panicles per plant and number of grains per panicle; Anjaneyulu et al. (2010), and Raut et al. (2009) for grain yield and number of grains per panicle.

Heritability realized in this study was generally low for most of the traits under study. The traits with the highest heritability were number of panicles per plant , number of grains per panicle, thousand grain weight, grain length and grain breath followed by tiller number per plant, flag leave width and days to maturity, whereas the traits with the lowest heritability were plant height at

maturity, and grain yield. A similar result was reported by Kumar and Senapati (2013) for number of grains per panicle, grain yield, grain length, grain breath and days to maturity. Grain yield recorded the highest genetic advance followed by area under Striga progress curve, number of grain per plant, number of panicles per plant and thousand-grain weight. The lowest genetic advance was produced in flag leave width, grain breadth, damage rating score and plant height at maturity. This is in agreement with Kumar and Senapati (2013) for grain breadth; and while plant height at maturity produced a low genetic advance in this study, these authors reported a high genetic advance for plant height at maturity in their study.

### 3.4.2 Correlation

The phenotypic correlation coefficients (Table 3.3) were generally lower in magnitude than the corresponding genotypic correlation coefficients (Table 3.4). This is in agreement with the report of Soni et al. (2013) who observed a similar comparison. The probable cause of the higher magnitude of genotypic correlation coefficients compared with the corresponding phenotypic correlation coefficient could be due to the modifying effect of the gene and environment in genetic association between characters (Swain and Reddy, 2006). The strong positive correlations at both phenotypic and genotypic levels between grain yield and number of grains per panicle, followed by number of panicles per plant, 1000-grain weight and number of tillers per plant shows that grain yield, number of grains per panicle, number of panicles per plant and 1000-grain weight can be improved simultaneously as also reported by Seyoum et al., (2012).

### 3.4.3 Path coefficient analysis

The value of direct effects (both phenotypic and genotypic) between number of grains per panicle, number of panicles per plant and 1000-grain weight and their correlation coefficients with yield were almost equal, therefore correlation explained a true relationship and direct selection through one or all the three traits would be effective. These traits were also reported by Soni et al. (2013) as well as Prasad et al. (2001) as traits that can be included in the selection criterion to develop high yielding new rice varieties in a given breeding program although their studies were not done under *Striga* infestation. Similarly, NGPP, NPPP and TGW are the traits, which can be used for direct selection of grain yield in rice under *Striga* infestation. Traits with small, zero or negative phenotypic and or genotypic direct effects, such as AUSNPC (-0.03, -0.04), FLL (-0.01, -0.02), TNPP (0.01, 0.00) and PHM (0.00, -0.01) did not seem to have direct effects on grain yield but affected it indirectly through other traits. For example AUSNPC seems to be affecting yield through negative effects inflicted on TGW (-0.05), NGPP (-0.020) and NPPP (-0.02). FLL indirectly affects yield through NPPP (0.06) and TNPP appears to indirectly affect yield through NGPP. The

traits whose direct effects were positive and yet their correlations with yield were negative: DM (0.02, -0.07), FLW (0.04, -0.03) and GL (-0.080) did have direct effects on yield but their effects were being interfered with by other indirect effects.

## 3.5 Conclusion

There were high significant differences ($p<0.001$) for all the characters studied, with phenotypic coefficient of variability being generally higher than the corresponding genotypic coefficients of variability for all characters studied. This implied presence of substantial environmental influences on the performance of the traits and consequently the reason for the generally low heritability estimates observed in most of the traits studied. However, since grain yield followed by area under *Striga* number progressive curve, number of grains per pod, number of panicles per plant and a thousand grain weight recorded the highest genetic advance which meant that it is reasonably beneficial to select for these traits. In addition, since the highest direct phenotypic and genotypic effects to grain yield per hectare was obtained from number of grains per panicle, followed by number of panicles per plant and 1000-grain weight, this meant that these traits could be used for direct selection for grain yield in rice under *Striga* infestation.

## References


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# Chapter 4 : Gene action for grain yield and associated traits in upland rice under *Striga hermonthica* infestation in Uganda


## Abstract

Breeding rice for resistance and or tolerance to *Striga hermonthica* will significantly reduce yield loss due to *Striga* in Uganda. However, the nature of inheritance of yield in upland rice under *Striga* infestation in the field was unknown; yet it is an important ingredient of breeding. Thus, there was need to select parents on the basis of their combining ability for grain yield and other agronomic traits under *Striga* infestation. Not many studies, if any have used combining ability in breeding for rice under *Striga* infestation. Consequently, the study used North Carolina Design II (NCDII) to determine gene action for grain yield and improved agronomic traits under *Striga* infestation. NCDII crosses were made from 10 resistant varieties used as males and 10 susceptible varieties used as females of upland rice genotypes. As a result, 60 successful crosses (F1s) were generated, advanced to the $F_2$ generation through selfing and bulking before subjecting to field evaluation together with their parents under artificial infestation of *Striga hermonthica* at two hotspot locations; Bukedea, and Pallisa in Uganda. The experimental material totalling 80 genotypes (60 crosses + 20 parents) were planted on two sites named above with two replications in a 10 x 8 alpha lattice design. However only 35 crosses fitted a complete NCDII and these were the ones used for the study of gene action of resistance of upland rice to *Striga* using yield performance as the index for resistance. Data analysis was conducted using Genstat. Some of the $F_2$ progeny outperformed the parents in grain yields under *Striga* infestation. The $F_2$ that gave the highest yields were N8 x N3, N12 x N10, N7 x N1, and N9 x N5 and N11 x N5, N12 x N3, IR 64 x N6 gave the lowest yields. Yield, plant height at maturity, syndrome damage score and days to flowering were under the control of additive gene action. On the other hand; yield, plant height at maturity and days to flowering also exhibited significant female by male interaction effects indicating presence of non-additive gene action as well. However estimates of relative contributions to GCA sums of squares revealed preponderance of the additive gene action in the inheritance of *Striga* resistance in upland rice. The study identified parents NERICA 3, NERICA 10, NERICA 5, IG10, NERICA 8, NERICA 12 and WAB56-50 as exceptionally good sources of genes for resistance to *Striga hermonthica* since they gave the lowest negative GCA effect for *Striga* syndrome damage score. While on the other hand NERICA 12, WAB56-

104, NERICA 10, NERICA 14 and IR 64 are good sources of genes for higher grain yield since they gave the highest GCA effect for grain yield. Conclusively NERICA 10 and NERICA 12 have combined genes for both resistance and high grain yields. The favourable GCA inbred parents and superior $F_2$ will provide a basis for future development of *Striga* resistance genotypes for use in *Striga* prone areas.

**Key Words:** GCA, Gene action, SCA, *Striga hermonthica*, *Striga* resistance, Rice.

## 4.0 Introduction

Rice has become a preferred cash crop in Uganda and its consumption in the country has rapidly increased. This trend is most likely to continue at an accelerated rate as the economic development improves the income levels of consumers. However, the only snag with this rosy increase in consumption is that the country is not able to satisfy demand and is therefore forced to rely on imports of rice to meet the deficit. The major cause of this deficiency is an array of biotic and a biotic constraints; key to rice is the parasitic weed infestation.

An estimate of 107,799 ha of arable land in Uganda is infested by *Striga* spp. (MacOpiyo et al., 2010) which is now endemic in the country and poses one of the most severe biological constraints to cereal production (Oswald, 2005; Ejeta, 2010). The most abundant species of *Striga* in Uganda is *Striga hermonthica* whose incidence and severity is steadily increasing and threatening food production in the country. It occurs on fields of maize, sorghum, millet and upland rice which are the major cereals grown in the country (Olupot et al., 2005; Ejeta, 2010). In rice, *Striga* does not affect flooded rice, but serious losses of between 33–90% in upland rice have been reported (Mohamed et al., 2006; Atera et al., 2012). This weed draws water and nutrients from the crop causing it to wither, stunt and thus reduce grain yield, and hence the name witch weed (Khan et al., 2007).

The witch weed can be controlled in many ways; however, host resistance to *Striga* is the most relevant trait for adoption of rice to upland environmental conditions which are now largely degraded in Uganda (Akello, 2002; Bigirimana, 2012). This complex trait which in some cases is reported to be controlled by both minor and major genes is massively influenced by environmental factors (Badu-Apraku et al., 2010); thus requiring specific studies that expound on the understanding of the inheritance of the trait and ascertain which actual gene action was present in the current material. This will aid in identification of the most appropriate strategy for improvement (Fasahat et al., 2016). The objectives of this study were to evaluate field performance of crosses for some agronomic traits; determine the gene action responsible for yield and other agronomic traits in $F_2$ rice genotypes grown under *Striga hermonthica*, and to identify promising upland rice parents with high combining ability for grain yield and other good performance traits for future use in *Striga* endemic ecologies.

## 4.1 Materials and Methods

### 4.1.1 Study Location

A crossing block was set up at the National Crops Resources Research Institute of Uganda, NACCRI,, located in Namulonge, 28 km north of Kampala, Wakiso District, (32$^{o}$ 34'E, 0$^{0}$32'N) at 1200 m above sea level. The area receives an average rainfall of 1300 mm, average annual temperature of 22$^{0}$C with annual minimum and maximum temperatures of 16 and 28$^{0}$C, respectively. Field evaluation was later conducted in two hotspot districts; Bukedea (34$^{o}$ 2'E, 1$^{o}$ 22'N; 1080 m above sea level) and Pallisa (33$^{o}$ 54'E, 1$^{o}$ 15'N, 1070 m above sea level) both located in eastern Uganda.

### 4.1.2 Experimental material

The experimental material of the study comprised of 20 rice cultivars used as parents and their $F_2$ progeny. The parents were selected on the basis of resistance and / or susceptibility as reported by previous studies (Table 4.1). Parents were crossed in a 5 x 7 factorial mating of mainly resistant x susceptible genotypes; but some susceptible x susceptible and resistant x resistant genotypes were also crossed. Several replications of the crossing block were made to increase number of crosses. Direct crosses were made at flowering through emasculation and pollen transfer from male plants to female plants. Susceptible genotypes were used as females while the resistant ones provided the pollen. Sixty successful crosses were obtained from this process but only 35 crosses fitted into a complete 5 x 7 NCDII mating design and these were used for gene action analysis. All the $F_1$ seed were harvested at maturity and dried in the sun before advancing to $F_2$ generation through selfing. Individual plants were left to self before field testing in *Striga* prone areas.

### 4.1.3 Field evaluation

The treatments for field evaluation comprised 35 crosses from the factorial mating scheme, other 25 experimental crosses, 12 parents used in the factorial mating and 8 pure lines used as controls. These 80 genotypes were evaluated for performance under artificial *Striga* infestation. This was evaluated at two sites: Bukedea and Pallisa with two replications in a 10 x 8 alpha lattice design. Plots that had previously been infested with *Striga* by previous researchers for sorghum research were used. In addition, artificial inoculation providing approximately 4000 *Striga* seed inoculum per hole as recommended by Kaewchumnong and Price (2008b) and calculated following the method outlined by Berner et al. (1997) was applied. *Striga* seeds were mixed with sieved sand which acts as

a carrier material to provide adequate volume for rapid and consistent infestation (Kountche et al., 2013). Using a bottle top which carries about 5 g of the mixture each hole was inoculated before planting was done on the same day. Four to five seeds of rice genotypes were then planted into *Striga* inoculated holes. Each genotype was planted in a plot of 1 $m^2$ at spacing of 20 cm between rows and 20 cm between plants. The replications were spaced 1 m apart and within each replication, the plots had 60 cm distance between them.

**Table 4.1**: Genotypes that were used as parents in the NCDII

| Genotype | Species | Known reaction to *Striga* | Parent status | Source of seed |
|---|---|---|---|---|
| N1 | Interspecific | Resistant (Cissoko et al., 2011) | Male | JICA |
| N2 | Interspecific | Resistant (Cissoko et al., 2011) | Male | JICA |
| N3 | Interspecific | Resistant (Cissoko et al., 2011) | Male | JICA |
| N4 | Interspecific | Tolerant (Atera et al., 2012) | Male | JICA |
| N5 | Interspecific | Resistant (Cissoko et al., 2011) | Male | JICA |
| N6 | Interspecific | Resistant | Male | JICA |
| N10 | Interspecific | Resistant (Cissoko et al., 2011) | Male | JICA |
| WAB 56-104 | *Oryza sativa* | Resistant (Cissoko et al., 2011) | Male | ARC-Benin |
| CG 14 | *O. glaberrima* | Tolerant (Johnson et al., 1997a; 2000a; Atera et al., 2011) | Male | ARC-Benin |
| IG 10 | *O. glaberrima* | Tolerant (Johnson et al., 1997a; 2000a; Atera et al., 2011) | Male | ARC-Benin |
| N7 | Interspecific | Susceptible (Cissoko et al., 2011) | Female | JICA |
| N8 | Interspecific | Susceptible (Cissoko et al., 2011) | Female | JICA |
| N9 | Interspecific | Susceptible (Cissoko et al., 2011) | Female | JICA |
| N11 | Interspecific | Susceptible (Cissoko et al., 2011) | Female | JICA |
| N12 | Interspecific | Susceptible | Female | JICA |
| N14 | Interspecific | Susceptible (Cissoko et al., 2011) | Female | JICA |
| Douradoprecoce | | Susceptible (Gurney et al., 2006b; Atera et al., 2011) | Female | NACRRI |
| IR 64 | *O. sativa* | Susceptible (Gurney et al., 2006b; Atera et al., 2011) | Female | NACRRI |
| Bala | *O. sativa* | Susceptible | Female | ARC-Benin |
| WAB 56-50 | *O.sativa* | Susceptible | Female | ARC-Benin |

### 4.1.4 Data collection

At each site, data was collected on a plot basis for parameters related to *Striga* tolerance and or resistance, rice phenology, growth, and yield components, which were grouped as *Striga* resistance traits and crop performance traits. Data were taken on 20 randomly selected plants from 1 $m^2$ plot. The *Striga* resistance parameters scored included the number of *Striga* plants emerged, *Striga* vigour score (scored using a scale of 0-9 as described by Haussmann et al. (2000) and Kroschel (2001)) where 0 = no emerged *Striga* plants and 9 = very vigorous, *Striga* plants (average height >40cm with >10 branches); scored at intervals of two weeks beginning from anthesis and from which area under *Striga* severity progress curve (ASVPC) and area under *Striga* number progress curve (ASNPC) were calculated from successive *Striga* counts using the formula adapted from that of 'area under the disease progress curve' (AUDPC); (Kountche et al., 2013).

$$ASNPC = \sum_{i=0}^{n-1} \left[\frac{yi + y_{(i+1)}}{2}\right] (t_{(i+1)} - ti$$

Where n is the number of *Striga* assessment dates, $y_i$ the *Striga* count at the $i^{th}$ assessment date, $t_i$ the days after planting at the $i^{th}$ assessment date, $t_0$ is 0 and $Y_0$ is 0. Low ASNPC values indicate resistance and High values indicate susceptibility to *Striga*. Similarly an "area under the *Striga* severity progress curve" (ASVPC) can be computed by using the *Striga* severity values as Yi. *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

The crop syndrome rating on a scale of 1-9 (with 1 being minimal damage and 9 being severe damage) was also recorded. The rice performance traits were; dates to flowering and maturity, height at flowering and maturity, yield components that were used to calculate yield. Rice yield components recorded were number of ripened grains per panicle, number of panicles per hill and 1000 grain weight. Then with a known number of hills per square meter as determined by the crop spacing used in a known area planted; yield was calculated from the formula: Yield (kg/ha) = weight of the grain x number of grains per panicle x number of panicles per hill x number of hills per square meter x 10,000 $m^2$/ha.

### 4.1.5 Data handling and analysis

Data was analysed using restricted maximum likelihood (REML) procedure in Genstat 17th version (Payne et al., 2014). The data was first tested for violation of normality and traits like counts of *Striga*, were log transformed before general analysis of variance was conducted using the following fixed effects model:

Yijkl = μ + si + gi + mk + fl + mfkl + si*mk+ si*fl +si*mfkl + eijkl

Where: Yijk = observed response of the genotypes;

μ = overall population mean;

si = effect of the $i^{th}$ environment;

gi = effect of the $i^{th}$ cross genotype;

mk = effect of the $k^{th}$ male parent;

fl = effect of the $l^{th}$ female parent;

mfkl = interaction effect of the $k^{th}$ male and the $l^{th}$ female parents;

si*mk = interaction effect of the $i^{th}$ environment and the $k^{th}$ male;

si*fl = interaction effect between the $i^{th}$ environment and $l^{th}$ female;

si*mfkl = interaction effect of the $i^{th}$ environments and the interaction effects between the $k^{th}$ male and the $l^{th}$ female parents; and eijkl is the experimental error.

General combining ability was computed for the 19 inbred parents (one parent Bala had poor stand and data was not collected). Specific combining ability was not computed since the objective was to select suitable inbred parents and not rice hybrids. Relative contribution of sum of squares of GCA effects (additive effects) to genotypic variance was calculated from the ratio of each component sum of squares to the total of the sum of squares of GCA female, GCA male and SCA.

$$\%\ Additive\ effect = \frac{SSGCAm + SSGCAf}{SSGCAm + SSGCAf + SSSCAmf} X\ 100$$

The above equation is modified from Hung and Holland (2012) Where: SSGCAm = sums of squares for GCA of the males; SSGCAf = sums of squares for GCA of the female main effects, and SSSCAmf = sums of squares for the SCA of crosses or male x female interaction effects. The significance of effects of the GCA and SCA were tested by a two tailed t-test procedure.

## 4.2 Results

### 4.2.1 General analysis of variance

Table 4.2 presents analysis of variance (ANOVA) for the parent GCA and $F_2$ progeny SCA effects. The rice entries showed highly significant ($P<0.001$) genotypic differences in grain yield as well as the interaction effects between the entries and sites. Site effects were also highly significant ($P\leq0.01$) for grain yield. The GCA main effects of both the females ($P\leq0.01$) and males ($P<0.05$) as well as their interaction effect Female x male ($P\leq0.01$) SCA effects were significant for grain yield. Furthermore, the mean squares for yield were highly significant for the site and SCA effect ($P\leq0.01$) as well as site x female GCA interaction effect at 5 % significance. The site x male GCA interaction effect was not significant.

The genotypic differences for plant damage score (syndrome rating score) were significant ($P<0.05$) among the upland rice entries used in this study. Both male and female GCA effects were significantly different ($P<0.05$) among the new rice genotypes in response to damage by *Striga*. But the SCA effect was not significant. Site differences for plant damage score were not revealed, however site x entries interaction was significant at 5% level of significance, while female x male SCA and site x female x male interactions were not significant ($P<0.05$).

**Table 4.2**: Mean squares for GCA and SCA for yield and other parameters scores in upland rice genotypes for Bukedea and Pallisa sites under *Striga* infestation

| **Source of Variation** | **DF** | **Mean squares** | | | | | |
|---|---|---|---|---|---|---|---|
| | | Days to Flowering | Damage score | Days to Maturity | Plant height at Maturity | *Striga* numbers | Yield (kg/ha) |
| Site | 1 | 86.19** | 3.23 | 17.66** | 48.08** | 76.7** | 55.16** |
| Site/Rep | 2 | 0.22 | 0.10 | 5.11** | 5.06** | 1.73 | 5.51** |
| Site/Rep/Blk | 36 | 2.43** | 2.34** | 1.24 | 3.15** | 1.56* | 1.54* |
| Entries | 46 | 2.37** | 1.33* | 2.24* | 3.29* | 0.69* | 1.66*** |
| Site x Entries | 46 | 1.41* | 1.32* | 1.62** | 1.99** | $1.08^{ns}$ | 1.73*** |
| GCAf | 4 | 2.4** | 1.70* | 4.13** | 5.24** | $0.61^{ns}$ | 1.38** |
| GCAm | 6 | $1.5^{ns}$ | 1.71* | 1.95* | 2.57** | $0.55^{ns}$ | 1.72* |
| SCAfxm | 24 | 2.62** | 1.02* | $1.41^{ns}$ | 2.55** | 0.75* | 1.66** |
| Site x GCAf | 4 | 1.28 | 1.5 | 2.93** | 1.8 | 0.92 | 2.06* |
| Site x GCAm | 6 | 1.86* | 1.14 | 1.94* | 1.91* | 0.68 | 1.26 |
| Site x SCAfxm | 24 | 1.29 | 1.37 | 1.21 | 2.28** | 1.23 | 1.73** |
| Error | | 41.68 | 2.91 | 32.82 | 69.38 | 312.6 | 82 |

*****, ** and * data is significant at <0.001, <0.01 and <0.05; ns – Not significant.**

Key: DF–Degrees of Freedom, GCAf –General combining ability for female parents, GCAm-General combining ability for male parents, ASNPC-Area under *Striga* number progress curve, ASVPC-Area under *Striga* severity progress curve.

For days to flowering (Table 4.2), the site, entry and female differences were highly significant ($p < 0.01$). In addition, some interactions such as site by entries, site by male and SCA effect were also highly significant ($p < 0.01$). However, the male GCA and site by female effects were not significant.

Genotypic differences in plant height (Table 4.2) at maturity of the new rice genotypes were significant ($P<0.05$). The male, female GCA main effects as well as SCA effects and site x female x male interaction were highly significant ($P<0.01$). Site and site x entries interactions were also significant ($P<0.01$). Site x male effects were significant ($P<0.05$); while Site x female effects were not significant.

### 4.2.2 The general combining ability effect

General combining ability (GCA) effect of the parent inbreds for *Striga* and rice agronomic traits under artificial infestation inoculation are presented in Table 4.3. GCA effects for *Striga* count and the damage rating score were generally low with some parents having negative values such as NERICA 3, NERICA 10, NERICA 5 and IG10 with negative GCAs of -6.115, -5.929, -4.115 and -3.857 respectively. GCAs for their *Striga* counts were also relatively low i.e. 7.95, 4.424, -58.05, and -8.48 respectively. On the other hand the susceptible parents that supported low damage score and low *Striga* count included NERICA 8, NERICA 12, and WAB56-50 with negative GCA effects of -5.115, -2.036 and -1.712 respectively for *Striga* syndrome damage score and -22.95, -5.38 and -8.89 respectively for *Striga* count.

**Table 4.3:** General combining ability (GCA) in *Striga* and rice agronomic traits under artificial *Striga hermonthica* infestation

| GENOTYPES | FLO | DS | DM | PHM | SN | YIELD |
|---|---|---|---|---|---|---|
| NERICA 4 | 0.211** | -0.364 | 0.147* | -0.332 | 0.762 | -.982** |
| NERICA 7 | 24.893 | 2.643 | 2.821** | 6.32 | -3.64 | -745 |
| NERICA 8 | -0.462** | -5.115 | 7.115 | -26.33 | -22.95** | -998* |
| NERICA 9 | 22.786 | 2.286** | 12.143 | -26.04 | -5.38 | 1497* |
| NERICA 11 | 0.571* | 1.071 | 1.286** | -23.82 | -17.57 | 1306** |
| NERICA 12 | -2.286 | -2.036 | -2.143 | 3.7 | 55.95 | 3329 |
| NERICA 14 | -2.286 | 0.464* | 0.857 | 1.95 | 58.62*** | 2610** |
| IR 64 | 16.214** | 6.214* | 4.857* | -24.3 | 40.29* | 2379** |
| WAB65-50 | 0.404 | -1.712 | 5.462** | 7.39 | -8.89 | 811 |
| NERICA 1 | 2.393 | -1.357 | -3.679** | -0.93 | 4.02** | 510 |
| NERICA 2 | 1.643* | 0.143 | 2.571 | -5.01 | 13.52 | -144 |
| NERICA 3 | -7.462 | -6.115** | 4.115 | -30.13 | 7.95* | -1057* |
| NERICA 5 | -4.462 | -4.115** | 10.115** | -42.33 | -58.05* | -1952 |
| NERICA 6 | 22 | 1.5 | 16 | 22.68** | 47 | 2340* |
| NERICA 10 | -5.571* | -5.929* | 7.714* | -22.18 | 4.24** | 2724** |
| WAB56-104 | 1.786 | 0.071 | 10.143 | 16.86** | -0.29* | 2776* |
| IG 10 | 8.643 | -3.857* | 4.571 | -3.61 | -8.48* | -358 |
| CG-14 | 5.5** | -0.5 | 10 | -7.75 | 13 | -182* |

KEY: FLO- Number of days to flowering, DS - Damage rating score, DM - Days to maturity, PHM – Plant height at maturity, SN- *Striga* numbers, YIELD – Grain yield kg/ha.

Similarly, parents such as NERICA 12, WAB56-104, NERICA 10 and NERICA 14 gave the highest GCA effect for grain yield. The above genotypes gave positive GCAs as 3329, 2776, 2724 and 2610.

### 4.2.3 Relative performance of crosses vs. parents

In general, some crosses performed better than the pure line parents as indicated by their dominance of the top 10 list (Table 4.4). However, some crosses also performed poorly as indicated in the bottom 5 category. Analysis revealed that crosses N8 x N3, N12 x N10, N7 x N1 and N9 x N5 produced the best yields (Table 4.4) under *Striga* infestation while IR 64 x N6, N12 x N11, and N11 x N5 were the least yielders. The best yielding crosses performed higher than the best parent NERICA 10 which is one of the most popular improved rice varieties of upland rice in the area.

**Table 4.4**: Performance of top ten and worst five genotypes

| Top 10 high yielding genotypes | | | | | |
|---|---|---|---|---|---|
| **Genotype** | **FLO** | **DS** | **DM** | **PHM** | **Yield** |
| N8 x N3 | 79.85 | 3.682 | 112.2 | 78.57 | 4052 |
| N12 x N10 | 90.63 | 2.131 | 122 | 77.33 | 3009 |
| N7 x N1 | 88.75 | 2.146 | 117.8 | 72.91 | 2872 |
| N9 x N5 | 85.16 | 2.637 | 122.9 | 81.65 | 2571 |
| NERICA 10 | 85.86 | 3.435 | 129.5 | 56.2 | 2448 |
| N9 x N10 | 89.56 | 2.828 | 127.5 | 72.27 | 2333 |
| N8 x WAB56-104 | 94.78 | 2.89 | 121.3 | 55.55 | 2190 |
| N12 x N11 | 90.14 | 0.491 | 118.8 | 62.64 | 2121 |
| NERICA 1 | 80.89 | 3.407 | 119.8 | 72.32 | 2028 |
| **Bottom 5 low yielding genotypes** | | | | | |
| NERICA 9 | 104.3 | 4.343 | 123.6 | 50.77 | 562 |
| N11 x N5 | 94.76 | 6.063 | 114.1 | 55.71 | 523 |
| N12 x N3 | 86.15 | 4.706 | 124.1 | 63.18 | 512 |
| NERICA 7 | 96.69 | 5.152 | 130.3 | 67.89 | 337 |
| IR 64 x N6 | 88.73 | 7.032 | 127.5 | 75.47 | 158 |
| P Significance | * | * | * | * | * |

KEY: FLO- Number of days to flowering, DS - Damage rating score, DM - Days to maturity, PHM – Plant height at maturity, SN- *Striga* numbers, YIELD – Grain yield kg/ha.

N12 x N11 had the least damage score (0.49) followed by N12 x N10 (2.13) and N7 x N1 (2.146). Genotypes N8 x N3 (79.85 days), NERICA 1 (80.89 days), N9 x N5 (85.16 days) and NERICA 10 flowered earlier and genotypes NERICA 9 (104.3 days), N8 x WAB 56-104 (94.78 days), N11 x N5 (94.76 days) and NERICA 7 (96.69 days) flowered later. Genotypes N9 x N5 (81.65 cm), N8 x N3 (78.57 cm) and N12 x N10 (77.33 cm) produced the tallest plants whereas NERICA 9 (50.77 cm), N8 x WAB 56-104 (55.55 cm) and N11 x N5 (55.71 cm) produced the shortest plants.

### 4.2.4 Relative genetic contributions of GCA and SCA to the crosses

Proportional or relative genetic contributions of GCA and SCA to the crosses are presented in Table 4.4. Contribution of the female GCA was greater than the male GCA for days to flowering, days to maturity, plant height at maturity and *Striga* numbers. While on the other hand, the male GCA was greater than the female GCA for grain yield and more or less equal in syndrome damage score.

The combined effects of the male and female parent GCA effects for *Striga* damage score (54.87%), days to maturity (60.91%) and plant height at maturity (52.52%) were greater than the interaction effects of 45.13%, 39.09% and 47.48% for the same traits respectively; hence suggesting the importance of additive gene action in the control of syndrome rating, days to maturity and plant height at maturity.

The SCA effect of female x male for days to flowering (64.98%), *Striga* numbers (64.31%) and grain yield (59.64%) were higher than the total parent GCA effects 35.02%, 35.69% and 40.35% respectively for the same traits; indicating prevalence of non-additive gene action in controlling days to flowering, *Striga* numbers and grain yield.

**Table 4.5**: Relative genetic contributions of GCA and SCA to the crosses

| Source of Variation | Days to Flowering | Damage score | Days to Maturity | Plant height at Maturity | *Striga* numbers | Yield (kg/ha) |
|---|---|---|---|---|---|---|
| % Female (GCA) | 21.58 | 27.38 | 41.40 | 35.23 | 18.81 | 18.00 |
| % Male (GCA) | 13.44 | 27.49 | 19.51 | 17.29 | 16.88 | 22.36 |
| % Female x Male (SCA) | 64.98 | 45.13 | 39.09 | 47.48 | 64.31 | 59.65 |
| Total GCA effects. | 35.02 | 54.87 | 60.91 | 52.52 | 35.69 | 40.35 |
| | 21.58 | 27.38 | 41.40 | 35.23 | 18.81 | 18.00 |

## 4.3 Discussion

The abundance of significant GCA for most of the traits shows significant variability of the materials used. GCA is owing to the activity of genes, which are largely additive in their effects or additive by additive interactions. According to Karaya et al. (2014), the desirable genotypes would show negative GCA effects for syndrome damage score and *Striga* count and a positive GCA effects for grain yield under *Striga* infested conditions. The low values for *Striga* counts and syndrome damage score in some parents shows that they are good combiners for tolerance and or resistance. Consequently, NERICA 3, NERICA 10, NERICA 5, IG10, NERICA 8, NERICA 12 and WAB56-50 were exceptionally good sources of genes for resistance to *Striga hermonthica.* While on the other hand NERICA 12, WAB56-104, NERICA 10, NERICA 14 and IR 64 are good sources of genes for higher grain yield. Conclusively NERICA 10 and NERICA 12 are able to combine genes for resistance and high grain yields. Genotypes that consistently support fewer emerged *Striga* plants, sustain less *Striga* damage and produced higher grain yields under infestation are considered resistant. The combined effects of the male and female parent GCA effects for *Striga* damage score (54.87%), days to maturity (60.91%) and plant height at maturity (52.52%) were greater than the interaction effects of 45.13%, 39.09% and 47.48% for the same traits respectively; hence suggesting the importance of additive gene action in the control of syndrome rating, days to maturity and plant height at maturity.

In general genetic gain was realized from some new crosses such as N8 x N3, N12 x N10, and N7 x N1. These results indicated that yield of rice varieties under *Striga* infestation can be improved by hybridization of promising parents because in this study some crosses performed better than the pure line parents as seen from their dominance of the top 10 list (Table 4.4). This perhaps depends on the genetic distance between pairs of parents selected for crosses. For some crosses such as N11 x N5, N12 x N3 and IR 64 x N6 that performed poorly as indicated in the bottom 5 category (Table 4.4); there is a possibility of presence of small genetic distances between those parents as indicated in Fig 1 of Chapter two where each pair of those parents were located in one cluster.

In this study all the best performing progenies combined reduced *Striga* damage syndrome rating with high grain yields and these included: N8 x N3, N12 x N10, N7 x N1 and N9 x N5 which can be considered as resistant. This trend indicates that productive varieties can be developed for *Striga* infested environments.

The significance of mean squares of males as well as females provides a direct test of significance of additive genetic variance. According to Hallauer and Miranda (2010) significant main effects mean additive gene action is preponderant while significant F x M represent non-additive gene action. Therefore, yield, plant height at maturity, syndrome damage score and days to flowering which displayed significant GCA effects as well as significant female by male interaction effects indicated the presence of both additive and non-additive gene action. However estimates of relative contributions (Table 4.4) revealed that total GCA effects were greater than SCA effects for these traits, indicating preponderance of the additive gene action in *Striga* resistance and tolerance traits.

Genetic variances can be directly estimated from the mean squares of females, males and crosses (Hallauer and Miranda, 2010). Significant mean squares of males and females provide a direct test of significance of additive genetic variance, while significance of mean squares of male x female provides a direct test of significance of dominance variance. Gene action was determined using yield performance as an index for resistance to *Striga and* damage symptom rating as an index for tolerance as suggested by Kim (1994) and Badu-Apraku et al. (2010).

## 4.4 Conclusion

Yield (being used as an index of *Striga* resistance), plant height at maturity, syndrome damage score and days to flowering were under the control of additive gene action. However, yield, plant height at maturity and days to flowering also exhibited presence of non-additive gene action. But nonetheless, estimates of relative contributions revealed preponderance of the additive gene action in *Striga* resistance and other traits; meaning that selection would be effective for improving yield under *Striga* infestation in the upland rice germplasm.

Parents such as NERICA 10 and NERICA 12 that combine good performance for both *Striga* resistance and high grain yield production are recommended for future work on improvement of upland rice varieties for use in *Striga* prone areas. Otherwise, other parents like NERICA 3, NERICA 5, IG10, NERICA 8, and WAB56-50 which were exceptionally good sources of genes for resistance to *Striga hermonthica* and WAB56-104, NERICA 14 and IR 64 which are good sources of genes for higher grain yield can be used for breeding.

Although the crosses are still segregating, the study indicated possible significant genetic gains for yield under *Striga* infestation, since the new crosses dominated the top 10 list thus winning most of their parents. The four best cross combinations: N8 x N3, N12 x N10, N7 x N1 and N9 x

N5 which outperformed the best pure line parent NERICA 10 would be recommended for use as breeding materials for programs that emphasize high yield potential under *Striga* infestation.

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# Chapter 5 : GGE biplot and non-parametric analysis of genotype x environment interaction on yield of upland rice grown under *Striga hermonthica* infestation


## Abstract

Information on effects of genotype x environment interaction (GE) on resistance of upland rice grown under *Striga* infestation in Uganda is still limited. Thus it was necessary to explore GE and stability of upland rice in *Striga* prone areas, in order to facilitate cultivar selection for general or specific environments. The objectives of this study were to analyse effects of GE on yield of upland rice under *Striga* infestation, and identify suitable genotypes for use in breeding high yielding and stable varieties that could be deployed in *Striga* infested areas. One hundred and fifty six genotypes and four check varieties were grown at three sites under artificial infestation of *Striga hermonthica* for two seasons. The experiments were laid out in 10 x 16 alpha lattice design with two replications at each site. Seed was planted at a spacing of 20 cm x 30 cm in 1 $m^2$ plots. Data on days to *Striga* emergence (DSE) and grain yield was collected and subjected to non-parametric stability analyses i.e. rank analysis, cultivar superiority index, and GGE biplot analysis. For both traits, the nature of GE detected was the crossover type which implied selection of genotypes for specific adaptation. Both traits were significantly influenced by environment. The second season performance was generally poor compared to the first season performance; thus indicating significant season x genotype interaction. The most stable and high yielding and thus ideal genotypes included 30 (SCRID006-2-4-3-4), 35 (ART3-3L7P1-B-B-3), 94 (WAB706-3-4-K4-KB-3) and 46 (SCRID079-1-5-4-2). Genotypes such as 68 (NERICA 10), 105 (NERICA 14) and 113 (P29 1 (14)), were high yielding but unstable and would be selected for specific adaptation. GGE biplot analysis for DSE revealed the most stable and *Striga* resistant genotypes as 125 (ART10-1L12E2-1-B-1), 85 (NERICA 16), 160 (WAB880-1-38-19-23-P1-HB) and 53 (ART2-9L3P3-B-B-4).



**Key words:** GE, GGE biplot analysis, Grain yield, Non-parametric analysis, Stability analysis.

## 5.1 Introduction

In Uganda, *Striga hermonthica* is the most abundant species of *Striga* weeds whose incidence and severity is steadily increasing and threatening production of upland rice, maize, sorghum, and millet which are the major cereals grown in the country (Olupot et al., 2005; Ejeta, 2010). Upland rice is a favourable host of *Striga hermonthica* that is reported to cause yield losses of between 33–90% in East Africa and elsewhere (Atera et al., 2012; Samejima et al., 2016). This weed commonly known as witch weed; draws water and nutrients from the crop causing it to wilt, stunt and ultimately reduces grain yield (Khan et al., 2007). Developing crop varieties that are resistant (minimise *Striga* attachment or growth) or tolerant (produce acceptable yields despite *Striga* attack) is found to be the most suitable and highly effective method for its control (Ejeta, 2007; Rodenburg et al., 2015; Samejima et al., 2016). Genetic resistance is reported to be the most feasible and environmentally friendly method for small-holder farmers to control *Striga* (Rodenburg et al., 2015). However, the ability for breeders to identify resistant varieties is made complicated by presence of genotype x environment interaction (GE) in *Striga* prone environments (Shrestha et al., 2012; Uphoff et al., 2015).

GE results into varying performance of genotypes in different environments, thus prompting its study in breeding programs to curb its negative effects in the development of new cultivars that are high yielding and stable over a range of environments (Yan et al., 2007; Efisue and Derera, 2012). It has become inevitable to evaluate genotypes in many environments so as to test their suitability and stability in different locations (Mohammadi and Amri, 2012). Presence of genotype x environmental interaction makes it difficult and expensive to select and recommend new genotypes for different environments (Gasura et al., 2015), because of the variable performance of the genotypes. In addition presence of GE reduces the correlation between phenotype and genotype which in return lowers response to selection (Yan and Kang, 2002). Thus raising the need to identify stable and high yielding genotypes (Kamutando et al., 2013). Nonetheless, very few studies have been directed towards exploration of the effects of GE on resistance of upland rice to *Striga hermonthica*. Only the studies of Atera et al. (2012) and Rodenburg et al. (2015) have attempted to investigate some upland rice varieties for adaptability to *Striga* prone areas in Kenya and Tanzania. However, the two studies have concentrated mainly on the NERICA varieties and their parents; whereby N1 and N10 were reported to be widely adapted and yielding between 1.7 – 2.5 t $ha^{-1}$ under *Striga hermonthica* infestation.

Studies of GE can be aided by the use of several statistical modelling methods; both parametric and non-parametric (Bose et al., 2014). These include linear formulations, such as joint-regression (Yates and Cochran, 1938; Eberhart and Russell, 1966), multivariate clustering techniques (Lin and Butler, 1990), multiplication approaches, such as additive main effects and multiplicative interaction (AMMI) (Nassir and Ariyo, 2011), genotype main effect plus genotype by environment (GGE) biplot analysis (Yan, 2001), and parametric and non-parametric stability methods (Huehn, 1979). All these modelling procedures help to determine phenotypic stability of genotypes. Consequently, growing numbers of stability measures have been developed (Lin et al., 1986; Hussein et al., 2000; Mohammadi et al., 2010; Mohammadi and Amri, 2012). However, GGE is reported to be the most versatile in selecting appropriate genotypes for different locations (Nassir and Ariyo, 2011).

The GGE biplot analysis is utilised to address many questions regarding genotype and test environment evaluation (Yan and Tinker, 2006). For example Makumbi et al. (2015) used GGE biplot analysis to assess GE for grain yield of IR Maize and number of emerged *Striga* plants across 17 environments under *Striga* infested and *Striga* free conditions in East Africa. They were able to evaluate genotypes for their performance in individual environments as well as across environments. In addition, mean performance, stability, and general or specific adaptations can be assessed with GGE biplot (Yan, 2011). Simultaneously, environments can be visualised and grouped on the basis of their ability to discriminate among genotypes and their representativeness of other test environments. Furthermore, a GGE biplot reveals the ‘‘which-won where’’ pattern of a multi environment trial (MET) data, which is important for mega-environment identification and for recommendations of specific genotypes to each mega-environment (Mohammadi and Amri, 2012). In addition, nonparametric stability procedures (NPSPs) such as those proposed by Huehn (1979), Nassar and Huehn (1987), Kang (1988) and Fox et al. (1990 ) have been embraced in identification of stable genotypes in many breeding schemes. NPSPs do not need any assumptions, but are based on the ranks of genotypes in each environment whereby the genotypes with similar ranking across environments are classified as stable (Akcura and Kaya, 2008).

In comparison with parametric stability methods, NPSPs reduce the bias caused by outliers and no assumptions are needed about the distribution of observed values. They are easy to use and interpret, and deletions or additions of one or a few genotypes have little effect on the results (Huehn, 1990a; Tariku et al., 2013). Furthermore, where a breeder is only interested in the existence of rank order differences over different environments, the non-parametric statistics for

GE based on ranks provide a useful alternative to parametric statistics approaches which are based on absolute data (Mohammadi and Amri, 2012). In that case, the relative characteristics and comparisons of the genotypes are considered more important than absolute characterization and comparisons. The objectives of the current study were to analyse the patterns of genotype x environment interaction (GE) effect on yield of upland rice under *Striga* infestation, and identify suitable genotypes for use in breeding high yielding and stable varieties that can be deployed in *Striga* infested areas.

## 5.2 Materials and Methods

The materials consisted of 160 genotypes (156 experimental material plus 4 checks) which were the same materials used for variability study in Chapter three. It comprised of 120 advanced lines that were being evaluated for adaptation to upland conditions, 16 NERICA (1 – 16) varieties and 24 cultivars commonly grown in the country. The list of this germplasm is shown in Appendix 1 of chapter two.

### 5. 2.1 Field experiment

The trials were conducted under *Striga* infestation during the first and second rainy seasons of 2012 and 2013 respectively (Table 1.1). These experiments were carried out in three districts of Bukedea, Kumi and Pallisa all found in the eastern region of Uganda which is a hotspot area for *Striga hermonthica*. The environments were defined as seasons x sites combinations, hence three sites and two seasons resulted to six (E1-E6) test environments (Table 5.1).

**Table 5.1**: Description of the six test environments where the genotypes were evaluated in the two seasons between 2012 and 2013

| Site | Season | Environment | Altitude (m.a.s.l) | Latitude | Longitude | Total Rainfall (mm) |
|---|---|---|---|---|---|---|
| Bukedea | 2012A* | E1 | 1123 | 01°21'88N | 034°02'48E | 481.8 |
| Bukedea | 2013B** | E2 | 1123 | 01°21'88N | 034°02'48E | 389.4 |
| Kumi | 2012A | E3 | 1138 | 01°27'39N | 033°57'10E | 490.7 |
| Kumi | 2013B | E4 | 1138 | 01°27'39N | 033°57'10E | 475.4 |
| Pallisa | 2012A | E5 | 1066 | 01°15'48N | 033°54'02E | 582.0 |
| Pallisa | 2013B | E6 | 1066 | 01°15'48N | 033°54'02E | 484.5 |

A* represents first season of the year (February to May) and B** represents second season of the year (July to October)

Trials were laid out in 10 x 16 alpha lattice design with two replications. The seed was planted at a spacing of 20 cm between plants and 30 cm between rows in1 $m^2$ plots. Shortly before placing the seed; artificial inoculation providing approximately 4000 *Striga* seed inoculum per hole as recommended by Kaewchumnong and Price (2008) and calculated following the method outlined by Berner et al. (1997) was applied. The inoculum was constituted by mixing *Striga* seed with sieved sand which acts as a carrier material to provide adequate volume for rapid and consistent infestation (Kountche et al., 2013). Using a bottle top which carries about 5g of the mixture each hole was inoculated before planting was done on the same day. Four to five seeds of rice genotypes were then planted into *Striga* inoculated holes. Recommended agricultural practices were implemented in order to obtain a good plant stand to enable season long study of the effect of *Striga* on the crop without killing the crop prematurely.

### 5.2.2 Data collection and analysis

Two traits of relevance to this study were days to *Striga* emergence (DSE) and grain yield. DSE used as a *Striga* resistance measure was estimated by counting the number of days from planting to the day when the first *Striga* plants are observed on each plot and grain yield was estimated on plot basis at 80% maturity. GE of the two traits was analysed using GGE biplot, non-parametric rank analysis and cultivar superiority index. GGE biplot analysis uses a biplot to show the effects

of G and GE (the sources of variation in GE analysis) in genotype evaluation of MET data (Yang et al., 2009). This analysis was conducted using the Breeding View (BV), a statistical tool of the Breeding Management System - BMS (The Breeding Management System, 2015); first as a field trial analysis to obtain the best linear unbiased estimates (BLUEs) of the traits, which were used in the subsequent analysis of GE in the BV. The GGE biplot model described by Yan (2011) was employed to analyse the GE of DSE and yield. It is based on the formula:

$$Yij=\mu+\beta j+\lambda 1\xi i1\eta j1+\lambda 2\xi i2\eta j2+\varepsilon ij$$

Where: $Yij$ = mean yield of $ith$ genotype in $jth$ environment, $\mu$ = grand mean, $\beta j$ = main effect of environment $j$, $\mu+\beta j$ = mean yield across all genotypes in environment $j$, $\lambda 1$ = singular value for PC1, $\lambda 2$ = singular value PC2, $\xi i1$ = eigenvector of genotype $i$ for PC1, $\xi i2$ = eigenvector of genotype $i$ for PC2, $\eta j1$ = eigenvector of environment $j$ for PC1, $\eta j2$ = eigenvector of environment $j$ for PC2, and $\varepsilon ij$ is the residual associated with genotype $i$ in environment $j$.

Consequently, GGE biplot was constructed by plotting the PC1 scores against the PC2 scores for each genotype and each environment. These biplots were used to visually analyse the upland rice MET data to rank genotypes based on performance and stability in individual environments as well as across environments and generate “which won where” patterns and mega environment analysis. Secondly four rank-based nonparametric stability parameters proposed by Huehn (1979), Nassar and Huehn (1987) and Lin and Binns (1988) were employed and these included $Si^{(1)}$, $Si^{(2)}$, $Si^{(3)}$ and Pi which are defined and calculated as follows:

$Si^{(1)}$ – The genotype absolute rank difference mean as tested over m environments (Huehn, 1979).

$$Si^{(1)} = \sum_{j=1}^{m} \sum_{j\prime=j+1}^{m} |rij - rij'| \quad / \, [m\,(m-1)]$$

$Si^{(2)}$ – Variance among ranks over environments (Huehn, 1979)

$$Si^{(2)} = \sum_{j=1}^{m} (rij - \overline{ri.})^2 \,/(m-1)$$

$Si^{(3)}$ – Sum of squares of ranks for each genotype relative to the mean of ranks (Nassar and Huehn, 1987)

$$Si^3 = \sum_{j=1}^{m} \left( rij - \overline{ri.} \right)^2 / \overline{ri.}$$

Pi – superiority of cultivar performance measured by the distance mean squares from the maximum responses across all locations (Lin and Binns, 1988).

$$\text{Pi} = \sum_{j=1}^{m}(Xij - Mj)^2 /(2m)$$

For all the above formulae;

Genotypes were identified by i and environments by j. Thus rij is the rank of the $i^{th}$ genotype in the $j^{th}$ environment, $\overline{ri.}$ is the mean rank across all environments for the $i^{th}$ genotype, m is the total number of the environments used. In the calculation of cultivar superiority measure (Pi); Xij denotes the yield of the $i^{th}$ cultivar grown in the $j^{th}$ location and Mj is the maximum response among all cultivars in the $j^{th}$ location.

## 5.3 Results and Discussion

### 5.3.1 GE pattern for grain yield and DSE

The analysis revealed heterogeneity of variance for both yield and DSE at each environment (Fig 5.1); the range of variation in good (higher yield) environments (E1, E3, and E6) was higher than the range in poor (low yield) environments (E2, E4 and E6).

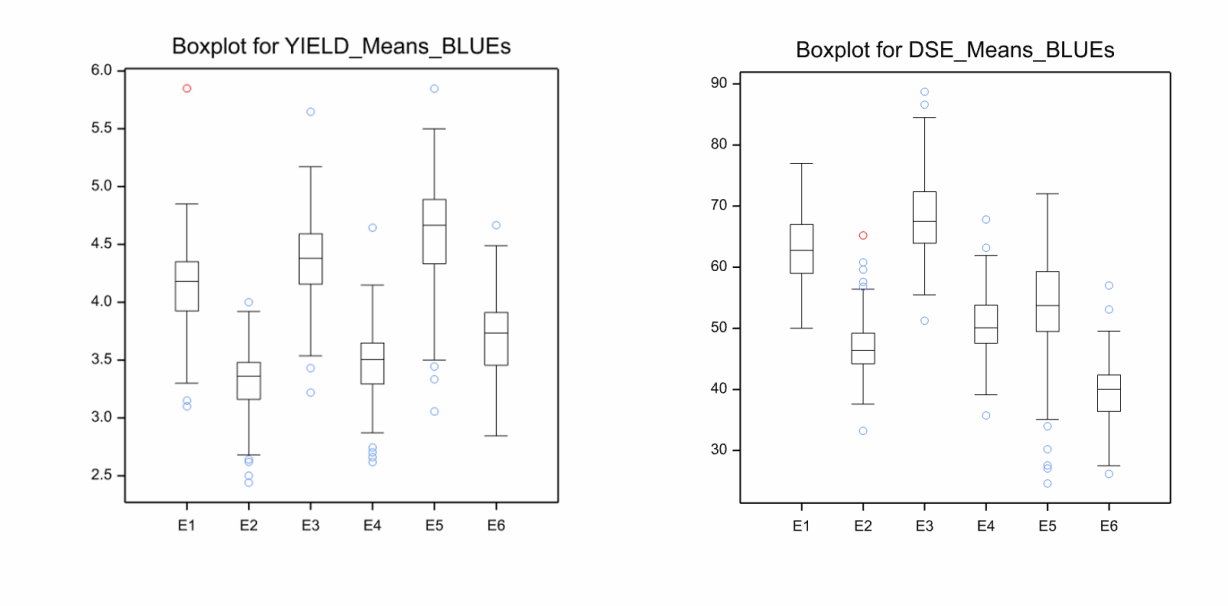


**Figure 5.1**: Boxplots of yield and DSE of upland rice, displaying total range, interquartile range (box) and median (line) for all environments

Key: Environments E1=2012 first rains in Bukedea, E2=2013 second rains in Bukedea, E3=2012 first rains in Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa

The analysis revealed minimal correlations between environments used in this study as represented in the correlation plots (Fig 5.2) with mainly green colour (representing very low correlation ~ 0), and blue colour represents small negative correlation < -0.5) while yellow shows a weak positive correlation ~ 0.25.

Heterogeneity of variance represents presence of GE influencing yield and DSE of upland rice. GE was initially described in terms of the relative differences between genotypic means that occurs when the performance of the genotypes changes from one environment to another (Segherloo et al., 2008). However, GE can also be considered in terms of heterogeneity of genetic variance and correlation. In the presence of GE, the genetic variance realized within individual environments changes from one environment to the other and genetic correlations between environments is high (Malosetti et al., 2013). Although the environmental conditions for the study areas were not readily available the probable reason for these low correlations between the study environments might be mainly due to differences in total rainfall and soil fertility during the study period. Similarity in environmental conditions elicits similar phenotypic response (indicative of low GE) and thus a stronger genetic correlation.

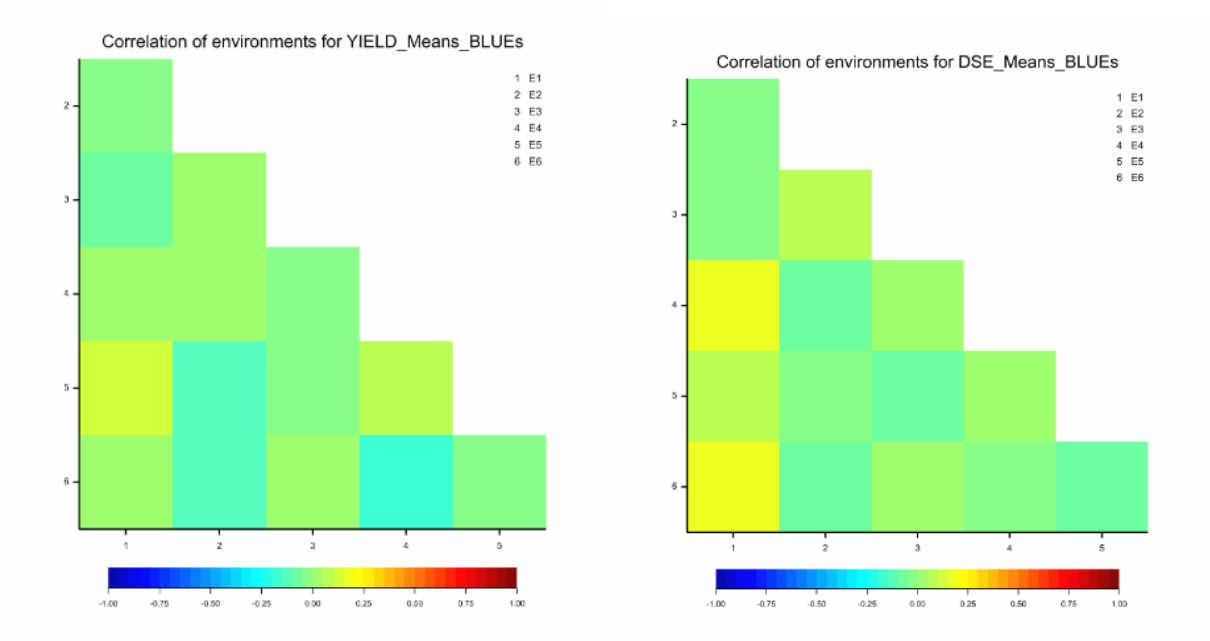


**Figure 5.2**: Correlation plots of yield and DSE for all environments

Key: Environments E1=2012 first rains in Bukedea, E2=2013 second rains in Bukedea, E3=2012 first rains in Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa

In addition, Table 5.2, showed variable ranking of the best ten genotypes at different environments for both yield and DSE. For example NERICA 10 the highest yielding genotype was ranked 1, 124, 87, 60, 49 and 21 in environments E1, E2, E3, E4, E5 and E6 respectively. Whereas for DSE it was ranked 17, 126, 21, 6, 43, 29, and 2 respectively in environments named above.

Variable ranking or relative difference between genotypic means of genotypes occurs when the performance of the genotypes change from one environment to another (Segherloo et al., 2008). This type of GE is the crossover type which implies the need for selection towards specific adaptation (Kamutando et al., 2013). In addition to variable ranking used for description of GE patterns; GE was also considered in terms of heterogeneity of genetic variances; and correlations. Heterogeneity of variance, in itself, represents presence of GE. In the presence of GE, the genetic variance realized within individual environments changes from one environment to the other, with the genetic variance tending to be larger in better environments than in poorer environments (Malosetti et al., 2013). GE also influences the correlations between genotypic performances in different environments.

**Table 5.2**: Variable ranking of top ten genotypes for yield and DSE at different locations

| | | | E1 | | E2 | | E3 | | E4 | | E5 | | E6 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Traits | Entries | Genotypes | Mean | Rank | Mean | Rank | Mean | Rank | Mean | Rank | Mean | Rank | Mean | Rank | Overall Mean | Overall Rank |
| YIEL | | | | | | | | | | | | | | | | |
| D | 68 | NERICA 10 | 5.85 | 1 | 3.1 | 124 | 4.35 | 87 | 3.59 | 60 | 4.81 | 49 | 4 | 21 | 4.28 | 1 |
| | 119 | WAB 181-18 | 3.95 | 119 | 3.52 | 31 | 4.96 | 6 | 3.88 | 13 | 4.94 | 28 | 4.04 | 14 | 4.22 | 2 |
| | 48 | WAB -56-77 | 4.4 | 32 | 3.76 | 5 | 4.96 | 6 | 3.63 | 48 | 4.72 | 65 | 3.8 | 67 | 4.21 | 3 |
| | 66 | OS 6 | 4.25 | 61 | 3.56 | 22 | 4.86 | 12 | 3.63 | 48 | 5.11 | 11 | 3.78 | 72 | 4.2 | 4 |
| | 28 | NERICA 6 | 4.55 | 14 | 3.46 | 48 | 4.54 | 48 | 3.68 | 32 | 5 | 18 | 3.87 | 48 | 4.18 | 5 |
| | 126 | ART 16-13-15-18-1-B-1-1 | 4.7 | 5 | 3.4 | 65 | 4.35 | 87 | 2.93 | 152 | 4.97 | 22 | 4.67 | 1 | 4.17 | 6 |
| | 147 | ART 16-4-14-2-2-B-1 | 4.43 | 27 | 3.56 | 22 | 4.37 | 84 | 3.76 | 22 | 4.89 | 39 | 4 | 21 | 4.17 | 7 |
| | 113 | 29 1 (14) | 4.35 | 41 | 3 | 133 | 5.65 | 1 | 3.17 | 139 | 4.94 | 28 | 3.88 | 44 | 4.16 | 8 |
| | 146 | ART 3-8L3P4-1-B-2 | 4.45 | 22 | 3.4 | 65 | 4.33 | 94 | 3.97 | 4 | 5 | 18 | 3.78 | 72 | 4.15 | 9 |
| | 35 | ART 3-3L7P1-B-B-3 | 3.8 | 129 | 3.4 | 65 | 4.43 | 72 | 3.88 | 13 | 5.5 | 2 | 3.8 | 67 | 4.14 | 10 |
| DSE | 53 | ART 2-9L3P3-B-B-4 | 65 | 54 | 60.8 | 2 | 76.06 | 24 | 49.67 | 89 | 65.41 | 11 | 47.34 | 7 | 60.71 | 1 |
| | 68 | NERICA 10 | 70.75 | 17 | 43.6 | 126 | 76.58 | 21 | 60.22 | 6 | 59.07 | 43 | 43.34 | 29 | 58.93 | 2 |
| | 120 | SCRIDO14-1-1-1-1 | 77 | 1 | 50.8 | 28 | 76.58 | 21 | 48.82 | 99 | 55.03 | 70 | 41.97 | 45 | 58.37 | 3 |
| | 143 | ART16-12-17-29-2-B-1-1 | 64.5 | 60 | 54.4 | 15 | 74.47 | 32 | 49.67 | 89 | 64.79 | 18 | 40.47 | 70 | 58.05 | 4 |
| | 51 | P5 H2 | 67 | 40 | 48.4 | 52 | 66.56 | 89 | 53.04 | 48 | 55.24 | 68 | 57 | 1 | 57.87 | 5 |
| | 116 | NERICA 15 | 63.5 | 67 | 55.6 | 11 | 67.61 | 77 | 56 | 25 | 54.78 | 72 | 48.84 | 4 | 57.72 | 6 |
| | 135 | ART3-4L18P3-2-6 | 70.5 | 19 | 46.8 | 72 | 72.89 | 37 | 56 | 25 | 60.92 | 31 | 38.82 | 93 | 57.65 | 7 |
| | 83 | SCRID019-1-1-1-1-2 | 72 | 11 | 45.6 | 90 | 67.61 | 77 | 49.67 | 89 | 65.8 | 8 | 45.23 | 11 | 57.65 | 8 |
| | 74 | NERICA 4 | 71 | 15 | 51.6 | 23 | 75 | 29 | 56.42 | 20 | 50.86 | 106 | 40.82 | 63 | 57.62 | 9 |
| | 11 | P8H2 | 75.5 | 2 | 44.8 | 106 | 58.64 | 154 | 53.47 | 44 | 69.74 | 4 | 42.94 | 33 | 57.51 | 10 |

Key: Environments E1=2012 first rains in Bukedea, E2=2013 second rains in Bukedea, E3=2012 first rains in Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa

### 5.3.2 GGE biplot analysis for grain yield

The GGE biplot analysis was used to elucidate genotype performance in individual environments and across environments; which-won-where pattern, mean performance and stability, and mega environment identification. In general, the GGE biplot explained 75.74% of the G and GE interaction whereby IPCA 1 contributed 56.46% and IPCA 2 accounted for 19.28% of GE.

### 5.3.3 Mean performance and stability

The genotype centred GGE comparison biplot (Fig 5.4) reveals genotype performance in terms of both mean yields and stability. The single arrowed line which passes through the biplot origin is the average environment coordinate (AEC) defined by the average PC1 and PC2 scores of all environments (Yan and Kang, 2003). It points to the high mean yield with the highest yielding genotypes appearing on the right hand side of the graph and the lowest genotypes on the left hand side. The second line that also passes through the origin but perpendicular to the AEC represents the stability of the genotypes. That is the most unstable genotypes for grain yield were those located farther away from either side of the origin on this axis where GE is high.

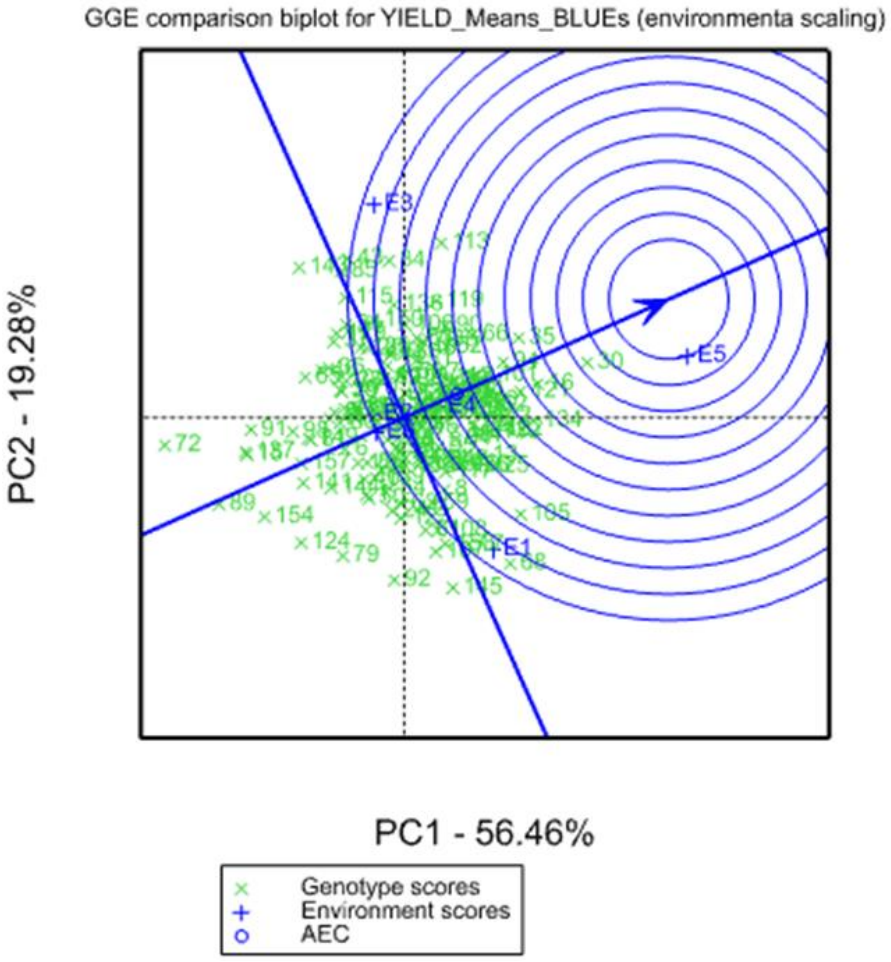

**Figure 5.4**: GGE biplot showing grain yield means and stability of 160 genotypes in six environments

Key: Environments E1=2012 first rains in Bukedea, E2=2013 second rains in Bukedea, E3=2012 first rains in Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa. Details of genotype codes 1-160 are found on appendix 1 of chapter two.

From Fig 5.4, the most stable high yielding and thus ideal genotypes included 30 (SCRID006-2-4-3-4), 35 (ART3-3L7P1-B-B-3), 94 (WAB706-3-4-K4-KB-3) and 46 (SCRID079-1-5-4-2). Genotypes such as 68 (NERICA 10), 105 (NERICA 14) and 113 (P29 1 (14)), were high yielding but quite unstable. E2, E3 and E4 were not important for discriminating genotypes since they were close to the origin and were grouped in one mega environment in Fig 5.5. They were the most unstable and lowest yielding environments and may be the probable source of crossover interactions. The low yielding and stable genotypes included 89 (ART3-8L11E2-4-B-1), 141 (ART25-9-13-2-B), 154 (ART1-1L5P6-1-3-1-B) and 137 (ART3-8L6P3-2-2-B), whereas genotypes 72 (ART3-8L4P1-2-1-3), 124 (WABIS 844), 79 (ART3-5L20P5-B-B-3) and 92 (ART12-1L6P7-3-5-B-1) were low yielding and unstable. The most stable and *Striga* resistant genotypes were WAB706-3-4-K4-KB-3, NERICA 10, WAB880-1-38-19-23-P1-HB and ART3-3L7P1-B-B-3. Genotypes such as FARO 39, NERICA 8, ART10-1L12E2-1-B-1 and ART12-1L4P7-21-4-B-3 were resistant to *Striga* but highly unstable. Genotypes ART3-3L7P1-B-B-3, WAB706-3-4-K4-KB-3 and NERICA 10 combined both high yield and high DSE.

### 5.3.5 GGE biplot analysis for days to *Striga* emergence (DSE)

The GGE-biplot analysis (Fig 5.6) for days to *Striga* emergence explained 72.76% of the G and GE interaction. In the environment centred GGE biplot, IPCA 1 contributed 43.06% and IPCA 2 accounted for 29.70% of GE.

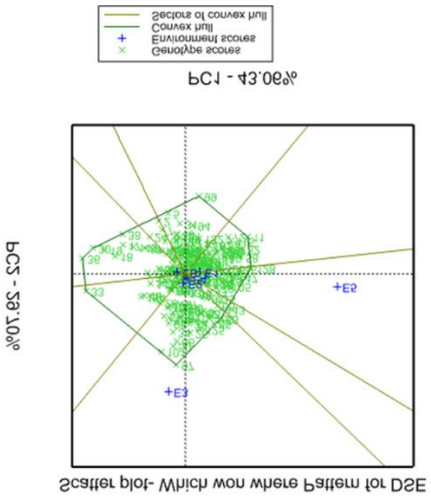


**Figure 5.6**: Polygon view of "Which won where" GGE biplot for DSE of 160 upland rice genotypes in six environments

IDSA 85Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa. Details of genotype codes 1-160 are found on appendix 1 of chapter two

This GGE biplot revealed the discriminatory environments as E3 and E5 with E5 with a longer vector from the origin of the biplot being the most discriminatory environment. It is in these two environments that DSE values were higher implying that some genotypes exhibited resistance to *Striga* by delaying its (*Striga*) emergence in the field.

In E3 the most *Striga* resistant genotypes included 97 (ART16-9-4-16-3-B-1), 102 (NERICA 12), 66 (OS 6), 26 (SCRID006-3-2-3-2) and 125 (ART10-1L12E2-1-B-1). In E5 genotypes 128 (WAB99-17), 17 (EXP304), 95 (NERICA 4), 58 (P24 H9) and 82 (ART3-7L3P3-B-B-2) were resistant to *Striga hermonthica*. The most susceptible genotypes included: 33 (IDSA 85), 36 (ART16-5-2-28-2-2-1), 30 (SCRID006-2-4-3-4), 19 (C507-1373-1-B-2-M-1-5), 18 (IDSA 62), and 38 (ART3-8L6P3-2-4-B).

### 5.3.6 Mean performance and stability for DSE of upland rice

The environment centred GGE-biplot (Fig 5.7) for DSE revealed the most stable and *Striga* resistant genotypes as 125 (ART10-1L12E2-1-B-1), 85 (NERICA 16), 160 (WAB880-1-38-19-23-P1-HB) and 53 (ART2-9L3P3-B-B-4) as seen from those genotypes close to the horizontal line with arrow head and appearing on the right hand side of the graph. E3 was the ideal environment with the most stable and resistant genotypes: followed by E5 and lastly E1. According to the performance shown in Table 5.2, E1 was indeed associated with genotypes having good resistance, but Fig 5.7 has shown it to be very unstable. Genotypes such as 99 (FARO 39), 31 (NERICA 8), 94 (WAB706-3-4-K4-KB-3) and 132 (ART12-1L4P7-21-4-B-3) were resistant to *Striga* but highly unstable. E2, E3 and E4 were not important for discriminating genotypes since they were close to the origin and were grouped in one mega environment (Fig 5.8).

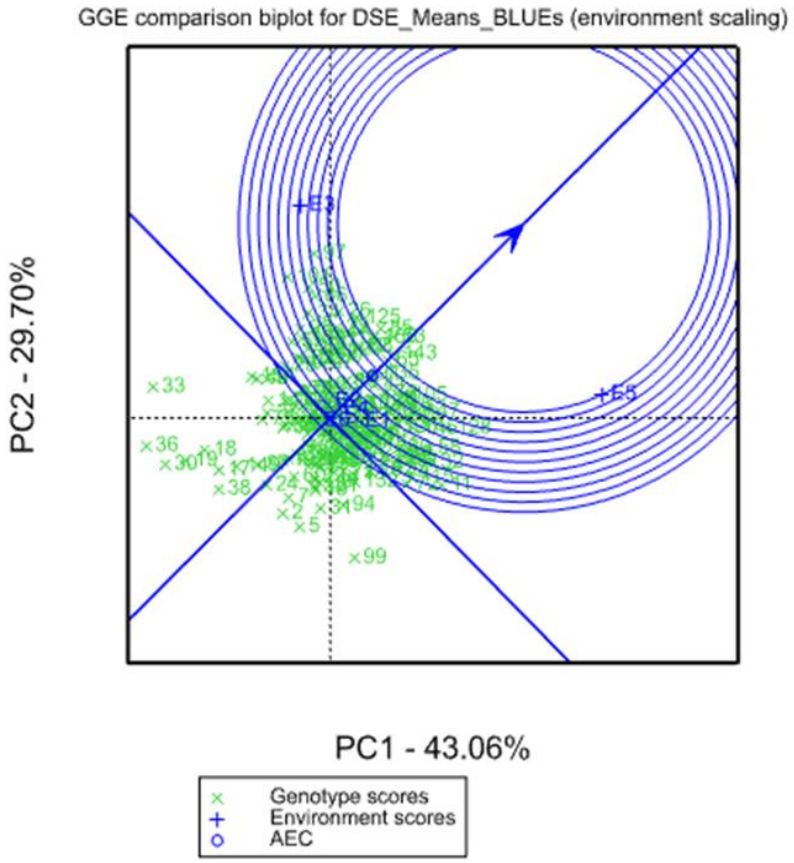


**Table 5.7**: GGE genotype centered comparison biplot for DSE in 160 genotypes in six environments

Key: Environments E1=2012 first rains in Bukedea, E2=2013 second rains in Bukedea, E3=2012 first rains in Kumi, E4=2013 second rains in Kumi, E5=2012 first rains in Pallisa and E6=2013 second rains in Pallisa

## 5.4 Non-parametric Measures of Stability

The estimates of non-parametric stability statistics for ten upland rice genotypes that were consistently sorted among the best 20 genotypes by each of the statistical measure used are presented in Table 5.3. The $Si^{(1)}$ (mean absolute rank differences) and $Si^{(2)}$ (variance of ranks) statistics of Hu¨ehn (1979) are based on adjusted ranks of the genotypes across environments and they give equal weight to each environment.

**Table 5.3**: Non-Parametric stability measures for grain yield of ten most stable upland rice genotypes as determined by all the four non-parametric measures

| | Entry | Yield | $Si^{(1)}$ | $Si^{(2)}$ | $Si^{(3)}$ | Pi |
|---|---|---|---|---|---|---|
| WAB 96-1-1 | 2 | 8.187 | 28.9 | 610.4 | 50.92 | 2.286 |
| ART8-L17P12-1 | 20 | 8.236 | 26.3 | 557.1 | 50.08 | 2.071 |
| NERICA 6 | 28 | 8.366 | 18.1 | 234.5 | 33.58 | 1.83 |
| ART10-IL20P3-2-B-1 | 47 | 8.266 | 33.33 | 733.5 | 47.17 | 2.176 |
| WAB 56-77 | 48 | 8.425 | 32.73 | 721.4 | 36.33 | 1.891 |
| NERICA 14 | 56 | 8.255 | 25.17 | 535.5 | 48.75 | 2.119 |
| OS 6 | 66 | 8.395 | 32.27 | 713.9 | 38.17 | 1.913 |
| P27H1 | 78 | 8.235 | 32.4 | 728 | 51 | 2.204 |
| WAB 181-18 | 119 | 8.435 | 33.43 | 872.2 | 35.75 | 2.03 |
| ART 16-4-14-2-2-B-1 | 147 | 8.333 | 24.67 | 591 | 35.33 | 2.004 |
| | Entry | Ranks | Ranks | Ranks | Ranks | Ranks |
| WAB 96-1-1 | 2 | 22 | 8 | 7 | 11 | 16 |
| ART8-L17P12-1 | 20 | 14 | 6 | 5 | 10 | 9 |
| NERICA 6 | 28 | 5 | 1 | 1 | 1 | 2 |
| ART10-IL20P3-2-B-1 | 47 | 12 | 14 | 14 | 8 | 11 |
| WAB 56-77 | 48 | 3 | 13 | 12 | 4 | 3 |
| NERICA 14 | 56 | 13 | 5 | 4 | 9 | 10 |
| OS 6 | 66 | 4 | 11 | 10 | 5 | 4 |
| P27H1 | 78 | 15 | 12 | 13 | 12 | 13 |
| WAB 181-18 | 119 | 2 | 15 | 16 | 3 | 7 |
| ART 16-4-14-2-2-B-1 | 147 | 7 | 4 | 6 | 2 | 5 |

$Si^{(1)}$ – The genotype absolute rank difference mean as tested over 6 environments, $Si^{(2)}$ – Variance among ranks over 6 environments, $Si^{(3)}$ – Sum of squares of ranks for each genotype relative to the mean of ranks, Pi – superiority of cultivar performance measured by the distance mean squares from the maximum responses across all locations

Genotypes with fewer changes in rank are considered to be more stable (Becker and Le´on 1988). NERICA 6, NERICA 14, ART16-4-14-2-2-B-1 and ART8-L17P12-1 were selected by both statistics as the most stable genotypes and WAB-181-18 and ART10-1L20P3-2-B-1 as the least stable genotypes though high yielding.

Based on $Si^{(3)}$, genotypes NERICA 6, ART16-4-14-2-2-B-1, WAB 181-18, and WAB 56-77 were the most stable while genotypes P27H1, WAB 96-1-9 and ART8-L17P12-1 were the least stable. Genotypes NERICA 6, ART16-4-14-2-2-B-1, WAB 56-77 and OS 6 were the most stable according to the pi parameter, whereas WAB 96-1-1, P27H1 and ART10-1L20P3-2-B-1 were the most unstable.

Non parametric statistics measure stability in units of the mean rank of each genotype. The lowest value for each of these statistics indicates maximum stability for a given genotype. Genotypes with similar ranking across environments are said to be stable (Mohammadi and Amri, 2012) and comparing NPSM with GGE biplot analysis the two methods produce a similar

ranking of genotypes based on yield and stability performance, however exact matches should not be expected. However, the idea of using both npsm and the parametric (multivariate) measures is to enable recommendations based on actual data and not assumptions, thus more credible recommendations.

## 5.5 Conclusion

The completed study indicated high level of crossover type of GE and environment main effects contribution to both yield and DSE in upland rice, accounting for 65 to 75% of the total variation. Although there is no G x E work that has been done before on rice under *Striga* infestation, the observed level of G x E contribution is comparable to previous studies under different conditions. The study was effective in identifying superior genotypes from both yield and DSE. The lines ART3-3L7P1-B-B-3, WAB706-3-4-K4-KB-3 and NERICA 10 were consistently ranked among the top 5 out 160 genotypes qualifying them as potential candidates for use in breeding rice for *Striga* resistance without compromising yield.

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# Chapter 6 : Overview of the Research

## 6.1 Introduction

Upland rice production in Uganda has increased substantially over the last two decades following the introduction of the NERICA varieties in the country. Rice production is envisaged to play a crucial role in the local food security and income generation for the small-scale farmers who in most cases have no access to wetland fields. Local production is not able to meet the domestic demand and the country has continued to be a net importer of rice. This is partly so because upland rice production in Uganda is seriously hampered by infestation of weeds among other factors. *Striga hermonthica* in particular is the species of *Striga* that is widespread and endemic in most of the arable land of Uganda. Given the fact that host plant resistance is the most economically feasible and environmentally friendly means of *Striga* control; the ultimate goal of this research was to develop varieties that are high yielding, resistant to *Striga hermonthica* and adapted to a wide range of environments.

The study commenced with assessment of genetic diversity as a prerequisite for successful breeding to minimise inbreeding and boost genetic advance, since heterosis of hybrids is reported to be correlated to the genetic distance between the parents. Secondly, the study explored the nature and magnitude of heritable variation in the available germplasm through path coefficient and correlation analyses to identify critical yield determining attributes to target for the improvement of yield for upland rice grown under *Striga* infestation. Furthermore, due to limited information regarding the genetics of host plant resistance in rice; there was need to elucidate this phenomenon to facilitate choice and design of improvement procedures. Finally, the issue of adaptation to wide or specific environments of production was investigated through multi-environment trials to measure varietal suitability and stability of cultivation of genotypes across seasons and ecological zones. This chapter outlines the research objectives and summarises the major findings and implications for breeding of upland rice.

## 6.2 The specific objectives were:

(i) To assess genetic diversity in some upland rice germplasm in Uganda using SSR markers.

(ii) To establish genetic variability, correlations, direct and indirect effects of various secondary traits on yield of upland rice under *Striga* infestation.

(iii) To determine the gene action responsible for yield and some other performance traits under *Striga* infestation.

(iv) To assess the effect of genotype x environment interaction (GE) on yield of upland rice and identify potential genotypes with high stable yield potential under *Striga* infestation.

## 6.3 Summary of the major findings

### 6.3.1 Diversity study

- A total of 274 alleles were detected with an average of 9.13 alleles per locus.
- The major allele frequency revealed was 64.27% on average.
- Genetic diversity ranged from 9.37% (RM 324) to 86% (RM 257) with an overall genetic diversity of 50.93%, which is an average level of genetic variation.
- Polymorphism information content (PIC) values of the markers ranged from 0.11 (RM324) to 0.86 (RM257) with an average of 0.48 per marker meaning the markers were reasonably informative.
- Cluster analysis enabled identification of 3 main clusters at 60% level of dissimilarity with additional sub clusters within each group.
- This study revealed that SSR markers facilitated grouping or classification of these cultivars accordingly and that genetic diversity present in these germplasm was about 50% calling for careful considerations when selecting parents for improvement in this program.

### 6.3.2 Genetic and path coefficient analysis

- Highly significant differences ($p<0.001$) were observed for all the characters studied.
- The mean performance of the genotypes revealed the most high yielding genotypes such as NERICA 10 (5545.07 kg/ha) followed by Faro 39 (4684.51 kg/ha) and ART16-21-5-12-3-1-2-1 (4635.58 kg/ha).
- Estimates of phenotypic coefficients of variability were generally higher than the corresponding genotypic coefficients of variability for all characters studied implying substantial environmental influence on the performance of the traits.
- Heritability estimates were generally low (an average of 30.56%) for most of the traits studied. Grain yield (65.77) recorded the highest genetic advance (GA) followed by AUSNPC (54.05), NGPP (31.88), NPPP (6.24) and TGW (4.59); meaning that it is beneficial to select for these traits.

- The highest direct phenotypic and genotypic effects to grain yield per hectare was obtained from number of grains per panicle (0.830, 0.882), followed by number of panicles per plant (0.380, 0.438) and 1000-grain weight (0.250, 0.285).
- The phenotypic direct effects of these three traits were positive and slightly greater or equal to their phenotypic correlations with yield, that is, 0.83 > 0.8, 0.38 > 0.27 and 0.25 = 0.25 for NGPP, NPPP and TGW respectively. That means these traits can be used for direct selection of grain yield in rice.

### 6.3.3 Gene action of yield and associated traits

- Yield, plant height at maturity, syndrome damage score and days to flowering were under the control of additive gene action.
- On the other hand; yield, plant height at maturity and days to flowering also exhibited significant female by male interaction effects indicating presence of non-additive gene action as well.
- However, estimates of relative contributions revealed preponderance of the additive gene action in *Striga* resistance and tolerance traits.
- Some of the $F_2$ progeny outperformed the parents in grain yields under *Striga* infestation. The $F_2$ that gave the highest yields were N8 x N3, N12 x N10, N7 x N1, and N9 x N5 and N11 x N5, N12 x N3, IR 64 x N6 gave the lowest yields.
- The study identified parents NERICA 3, NERICA 10, NERICA 5, IG10, NERICA 8, NERICA 12 and WAB56-50 as exceptionally good sources of genes for resistance to *Striga hermonthica* since they gave the lowest negative GCA effect for *Striga* syndrome damage score.
- While on the other hand NERICA 12, WAB56-104, NERICA 10, NERICA 14 and IR 64 are good sources of genes for higher grain yield since they gave the highest GCA effect for grain yield.
- Conclusively NERICA 10 and NERICA 12 have combined genes for both resistance and high grain yields.
- The favorable GCA inbred parents and superior $F_2$ will provide a basis for future development of *Striga* resistance genotypes for use in *Striga* prone areas.

### 6.3.4 GGE biplot and non-parametric analysis

- The nature of GE found present for grain yield and days to *Striga* emergence, was of the crossover type, which necessitated selection for specific adaptation.

- The GGE biplot for grain yield explained 75.74% of the G and GE; whereby IPCA 1 contributed 56.46% and IPCA 2 accounted for 19.28% of GE.
- For days to *Striga* emergence, GGE biplot explained 72.76% of the G and GE interaction whereby; IPCA 1 contributed 43.06% and IPCA 2 accounted for 29.70% of GE.
- The most stable high yielding and thus ideal genotypes included 30 (SCRID006-2-4-3-4), 35 (ART3-3L7P1-B-B-3), 94 (WAB706-3-4-K4-KB-3) and 46 (SCRID079-1-5-4-2).
- E5 was the ideal environment with the most stable high yielding genotypes, followed by E3 and E1.
- Genotypes such as 68 (NERICA 10), 105 (NERICA 14) and 113 (P29 1 (14)), were high yielding but quite unstable and would be selected for specific adaptation.
- The poorer environments E2, E3 and E4 were grouped in one mega environment and may have been the probable source of crossover interaction.
- The low yield and yet stable genotypes included 89, 141, 154 and 137, whereas genotypes 72, 124, 79 and 92 were low yield as well as unstable.
- GGE biplot analysis for DSE revealed the most stable and *Striga* resistant genotypes as 125 (ART10-1L12E2-1-B-1), 85 (NERICA 16), 160 (WAB880-1-38-19-23-P1-HB) and 53 (ART2-9L3P3-B-B-4).
- E3 was the ideal environment with the most stable and resistant genotypes; followed by E5 and E1. However, E1 was shown to be very unstable, less discriminatory and it could be the source of cross over interaction for DSE.
- Genotypes such as 99, 31, 94 and 132 were resistant to *Striga* but highly unstable**.**

## 6.5 Implications of the findings

- Parents should be selected from distant groups to avoid inbreeding during genetic improvement, genetic mapping or application of marker–assisted selection (MAS) in the program. Parents with desirable characters should be selected from different clusters to bring together gene patterns of diverse nature.
- Number of grains per pod was found to be the most yield determining attribute.
- With preponderance of additive gene action in *Striga* resistance and tolerance traits, improvement can be achieved through selection.
- The crossover type of GE calls for selection for specific adaptation. Crossover GEs can be a significant barrier to selection strategies that aim to improve broad adaptation. Where some aspects of GE are repeatable – it is possible to select for components of specific adaptation to the target environments. This study provides a basis for defining

breeding strategies that would contribute to higher and more stable grain yields for variable *Striga* infested environments thereby reducing farmers' risk and uncertainty while increasing productivity.

- The result implied that both grain yield and the measure of *Striga* resistance were significantly influenced by environment. The second season performance was generally poor compared to first season performance; thus indicating significant season x genotype interaction.
- The favorable GCA inbred parents and superior $F_2$ will provide a basis for future development of *Striga* resistance genotypes for use in *Striga* prone areas.