Genetic analysis and improvement of pearl millet for rust resistance and grain yield in Uganda

By

Geofrey Lubadde

BSc (Hons.) Agriculture, Makerere University
MSc (Crop Sci.), Makerere University

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African Centre for Crop Improvement
School of Agricultural, Earth and Environmental Sciences
College of Agriculture, Engineering and Science
University of KwaZulu-Natal
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Abstract

Pearl millet is a sustainable food security crop for people living in areas with extreme drought and heat conditions. Like in many countries where it is grown, in Uganda the crop grows in semi-arid zones characterised by low average annual rainfall and hot conditions. Despite saving many from hunger, not much is known about the crop. Studies were therefore initiated to generate information on the production characteristics of pearl millet in Uganda, genetic improvement and to assess gene action for grain yield and rust resistance. A survey and experiments were conducted in two predominantly pearl millet growing areas with four objectives: 1) to establish production determinants of the pearl millet cropping system with related uses, constraints and desirable traits, 2) to determine the response to S_1 progeny recurrent selection for rust resistance and grain yield in two local populations, 3) to study the inheritance and gene action for grain yield and rust resistance in improved pearl millet germplasm, and 4) to determine the stability of improved pearl millet lines and crosses for grain yield and rust resistance.

The first objective was achieved by conducting a participatory rural appraisal in four districts (Kumi and Katakwi in the east and Kitgum and Lamwo in the north), where data was collected from 160 households. The second objective was achieved by subjecting two commonly grown rust susceptible populations (Omoda from east and Lam from north) to two cycles of S_1 progeny recurrent selection and the cycles evaluated in randomised complete blocks design with three replications, three locations and one season. Objective three was achieved by crossing six rust resistant male parents with ten rust susceptible female lines in a North Carolina design II scheme. The parents and crosses were evaluated in four environments in a 4 x 19 alpha-lattice design. Additionally, data from the same experiment were used to achieve objective four.

The survey findings indicated that pearl millet was mainly grown for food and income. The production environment was low input, where farmers used family labour, planted unimproved genotypes and used no chemicals nor manure to enhance productivity. The majority of the households had minimal access to credit, agricultural trainings or extension services. The households identified the most desirable variety traits as stay green, tall, high tillering, high yield, early maturity and ergot resistant. The constraints were ergot and rust susceptibility, short genotypes, low yielding, low tillering, late maturity, and sterile panicles. Lack of markets, low prices and price fluctuation were the most important market constraints. Farmers also lacked knowledge about rust. Regression analysis showed that area planted, age of spouse and experience in pearl millet cultivation were the most important factors enhancing grain yield, while age of the household head, amount of seed planted and distance to the market negatively affected grain yield.

The findings from the recurrent selection suggested a possibility to improve grain yield and rust resistance of locally adapted populations through two cycles of S_1 progeny recurrent selection. The Lam population responded faster than the Omoda population leading to respective net genetic gains of 72% and 36%, respectively. The effect was an increase in grain yield from 611 kg ha^{-1} to 1047 kg ha^{-1} in Lam population and 693 kg ha^{-1} to 943 kg ha^{-1} in Omoda population. The genetic gain for rust resistance was -55% and -71% achieved in populations Lam and Omoda, respectively; leading to improvement in rust resistance from 30% to 14% in Lam and 57% to 17% in Omoda.

The genetic analysis results indicated predominance of additive gene action for grain yield and rust severity at 50% physiological maturity while non-additive gene action was predominant for area under disease progress curve. Better-parent heterosis was significantly high for all the traits. For mid-parent heterosis the best crosses had heterosis of 12%-28%. One cross (ITMV8001 x SDMV96053) performed exceptionally well with better-parent heterosis of 93%. The better-parent heterosis for rust severity at 50% physiological maturity was higher than the better-parent heterosis for area under disease progress curve for all the crosses. The genotype by environment (GxE) interaction was important for grain yield, rust severity at 50% physiological maturity and area under disease progress curve. The GGE biplot identified the crosses ICMV3771 x SDMV96053 and Shibe x Okollo as the winners for grain yield and rust resistance respectively. These crosses will be advanced in the programme in Uganda.

Declaration

I, Geofrey Lubadde, declare that:

1. This thesis, except where otherwise indicated, is my original development.

2. It 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.

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

Sign

Dr. Julia Sibiya (Major supervisor) | Date

Sign | 19/11/2014

Prof. John Derera (Co-supervisor) | Date

Sign | 18/11/2014

Prof. Pangirai Tongoona (Co-supervisor) | Date

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Dedication

To my lovely family and all my descendants yet to come; my father Mr. Moses Bukenya and my mother Ms Noeline Bwesige; and the Sekitooleko family.

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Acronyms

IAPP: International Association for the Plant Protection Sciences
IBP-BMS: Integrated Breeding Platform Breeding Management System
IBPGR: International Board for Plant Genetic resources
ICRISAT: International Crops Research Institute for the Semi-Arid Tropics
IFAD: International Fund for Agricultural Development
IRRI: International Rice Research Institute
FAO: Food and Agriculture Organisation of the United Nations
NRC: National Research Council

Introduction

Importance of pearl millet

Pearl millet, *Pennisetum glaucum* (L.) R. Br., is a widely grown and distributed (Figure 1.0) (Andrews, 1990) multipurpose cereal. It is grown for food, feed, fodder, fuel and mulch (Gulia et al., 2007). The crop has been grown mainly in West Africa since prehistoric times, from where its cultivation subsequently spread to eastern and southern Africa and to southern Asia, where a secondary centre of diversity exists in India. Research findings by Kumar (2002) indicate that India produces most of the world's pearl millet from approximately 10 million hectares. On the contrary, in the American continents pearl millet is a relatively new crop grown mainly for forage and feed since the 1850s. In Africa, the cereal is now grown on approximately 14 million hectares in the dry areas of Africa with an annual production of 10.5 million tonnes (Kumar, 2002). In East Africa, it is grown in Tanzania, Kenya, Rwanda and Uganda (Table 1.0) (FAO, 2000). The widespread cultivation of pearl millet is mainly due to its ability to adapt to marginal areas with below average amounts of rainfall and poor soil conditions (Agdag et al., 2001).

Figure 1.0: The world's millet growing areas (in red marks)
Source: FAO (2002)

Table 1.0: Area, yield and production of pearl millet in Eastern and Southern Africa

	Yield (kg ha^{-1})			Production (Mt)		
Country	1980-2	1990-92	2000-2	1980-2	1990-92	2000-2
East Africa						
Uganda	1497	1487	1534	569333	446667	590000
Tanzania	1062	1110	919	241833	336667	220926
Kenya	465	807	542	44749	57427	63023
Rwanda	800	583	389	4000	1991	1000
Southern Africa						
Zimbabwe	220	445	393	33526	138570	97317
Angola	523	654	510	124162	52333	68167
Namibia	287	249	269	66018	35333	39667
Zambia	737	652	607	40830	15897	35044
Malawi	592	583	422	20274	7667	7099
Mozambique	561	250	265	53857	5000	5000
Botswana	174	163	162	1067	1777	1150

Source: FAO (2000)

The conditions under which pearl millet is grown are characterized by drought and unpredictable low rains (200-600 mm), high temperature, and soils with low fertility and high salinity (Singh, 1993). Due to the inherent ability to tolerate such harsh growing conditions, pearl millet is found in areas where competing cereals such as maize and sorghum do not survive (Kumar, 1989). Thus drought and heat tolerance, coupled with its capacity for rapid grain filling under stress, makes pearl millet a major crop adaptable to intensely hot and dry zones of the world. The adaptability also enables pearl millet roots to extract mineral nutrients and water from poor soils (Mangat et al., 1999)**.** The compounded result is a crop with good quality fibre stover and grain of high nutritional value (Hall et al., 2004), which makes all parts of pearl millet important to marginalized and food insecure communities (Singh, 1993).

In addition to being food to 500 million people living in dry regions of India and Africa (Vetriventhan et al., 2008), pearl millet is also a fodder crop for livestock in such regions (FAO, 1996; FAO, 2000; FAO, 2002). As a food grain, about 95% of pearl millet produced is consumed in steamed form as soft porridge or gruel, or as leavened bread. In flour form, the grain is used as an ingredient in many bakery products like flat breads, commonly known as roti in India, or mixed (up to 25%) with wheat flour for use in yeast bread. The flour, when used to make pan cakes, cookies, gives the crunchy texture which is a desired quality of such bakery products (Baltensperger, 2002). In developing countries, the stover is chopped after harvest and fed directly to animals as forage or processed into hay which is fed to livestock during the dry season (Davis et al., 2003). On the contrary, in developed countries the crop is mainly grown for fodder and feed grain (Khairwal et al., 1999; Davis et al., 2003).

The low production cost of pearl millet increases its potential of being a major source of income in developing countries as it is in developed countries (Andrews et al., 1996). In the USA and Europe, the grain has become a substitute for corn in feed manufacturing industries because of the high nutrient value and low levels of feed-utilisation inhibitors like tannins (Gulia et al., 2007). These qualities greatly lower the production costs in the manufacture of animal feeds and fuel ethanol production. This increases the marginal income levels, which results in higher economic return from pearl millet than from maize or sorghum (Wu et al., 2006). Wu et al. (2006) further noted that the lowering of production costs and rapid fermentation rate makes pearl millet a better candidate crop in beer making at industrial level; thus competing with sorghum which has relatively high tannin levels. Therefore, the economic potential of pearl millet and its drought tolerance qualities make it a suitable cereal for the study area and population; which is characterised by drought and chronic food insecurity. Despite being adapted to harsh conditions, the average productivity of pearl millet of 600 kg ha^{-1} at farm level is low when compared with the established average potential yield of over 3000 kg ha^{-1} obtained from research experiments. The low productivity is a combined effect of several production constraints (Baltensperger, 2002), which were investigated in the current study.

Constraints to pearl millet production

Pearl millet productivity suffers from many production constraints, which include socio-economic, abiotic and biotic. However, specific information about pearl millet production constraints in Uganda is not available as of now, due to low research hence no publications available. Therefore, most of the information is general and based on experiences from other countries. The low budgetary allocation to research activities aimed at developing and promoting pearl millet is the major socio-economic constraint to the production of the crop. As a result, there is a low rate of developing new technologies (Onyewotu et al., 1998). Conversely, where new technologies for crop improvement have been developed, adoption rate has been low, partly because of inadequate funding of the extension service delivery system (Bidinger et al., 2009). In addition, the crop attracts minimal financial support for research from profit-oriented organisations, due to low returns to investment when compared with non-farm enterprises (Zarafi, 2005). Furthermore, many new technologies may not be designed to suit farmers' resource-constrained circumstances, because no financial support is allocated to induce farmers at the technology development phase (Bidinger et al., 2009). As a result, the crop lags behind the other major grains, such as maize and sorghum in yield improvement research. For instance, its average yield is barely 600 kg ha^{-1} (Rai et al., 1999) when compared with the other major grains (Table 2.0). Thus, more funding is needed for yield-related research particularly for management of abiotic and biotic stresses (Winkel et al., 2001).

Table 2.0: Mean productivity of major cereal crops

Crop	Mean yield (kg ha^{-1})
Maize	4859
Rice	3970
Wheat	2869
Barley	2720
Sorghum	1357
Pearl millet	600

Source: FAO (2004) database

Drought is the major abiotic factor affecting the ultimate productivity of pearl millet (Yadav, 2010). Pearl millet productivity is reduced by low rainfall amount of about 600 mm received in the growing areas relative to major cereal crops like barley, wheat, sorghum, maize and rice, which are grown in areas with well distributed rainfall (Zarafi, 2005). The low amount and poor distribution of rainfall leads to less available soil moisture for crop utilisation and thus reducing productivity (Mahalakshmi et al., 1988). In most pearl millet growing areas, the onset of the rainy season is highly variable while the end of the rains is unpredictable. This further reduces soil moisture availability (Mahalakshmi and Bidinger, 1985). The intermittent breaks and low amounts of rainfall also lead to low soil moisture availability at sowing time (Bacci et al., 1998), which reduces seedling emergence, thus leading to poor crop growth, development, and establishment of the crop (Baltensperger, 2002). However, flowering and grain filling are the most sensitive stages to moisture deficits and therefore stress at these stages leads to serious reduction in grain productivity (Mahalakshmi et al., 1988). A compounded low productivity is realised if other abiotic factors affect the crop in combination. Such factors include air and soil temperatures, photoperiodism, radiation and wind. However, the impact of these factors on productivity is much lower unless the crop is severely affected by major biotic stresses like crop pests and diseases (Anderson et al., 2005).

In pearl millet production, pests and diseases cause yield losses (Gulia et al., 2007) of about 20% annually in developing countries (Anderson et al., 2005). Striga, downy mildew, ergot, and rust are among the main biotic production constraints of pearl millet in many parts of Africa and

Asia (Gulia et al., 2007)**.** Twenty-one million hectares of the crop in Africa are estimated to be infested by various striga species, especially *Striga hermonthica* (Del.) Benth (MacOpiyo et al., 2010). This leads to an estimated annual grain loss of over four million tonnes per year (Anderson et al., 2005). Striga weed invades the root system and directly competes with pearl millet for water and nutrients leading to low grain yield (IAPPS, 2007). Unfortunately, the low soil fertility and drought experienced in the marginal areas, where pearl millet is grown, also favour striga infestations. However, resistance genes to various striga species exist in the wild progenitors of pearl millet, but are yet to be transferred to farmer-acceptable varieties (Panwar and Wilson, 2001). Combined with striga, plant diseases cause yet a more devastating effect to pearl millet productivity. Among the diseases downy mildew, ergot, smut, and rust are the most devastating in Africa with their effect greatly influenced by the highly susceptible varieties, especially hybrids and exotic breeding lines, currently grown (IAPPS, 2007).

The introduction of hybrid and exotic breeding lines has greatly increased the severity of downy mildew, smut, ergot, and rust diseases in many parts of Africa (Panwar and Rathi, 1997; Morgan et al., 1998). Rust (Figure 2), caused by *Puccinia substriata* var *indica* (L.) R. Br., is a widespread and highly destructive foliar disease throughout pearl millet growing regions of Africa. It leads to grain yield loss of over 50% and greatly lowers forage quality. Unfortunately, most of the local germplasm materials are susceptible to the disease (Table 3.0). The rust affects pearl millet at all growth and development stages, but mostly occurs in severe form at/or after the soft dough stage. When the disease strikes at the seedling stage, substantial reduction in grain and forage yield and quality is observed (Wilson et al., 1995a). All local and commercial cultivars have persistently remained susceptible to rust even though a single dominant gene for resistance is available. The use of a single dominant resistant gene against rust has not been effective due to the high mutation rate of the pathogen population (Eboh, 1986; Tapsoba and Wilson, 1996). Therefore, multiple loci for rust resistance need to be incorporated into the locally adapted cultivars for sustainable control of pearl millet rust. A sustainable control of rust may be achieved through breeding for partial resistance through recurrent selection.

Figure 2.0: Rust disease taken from farmer's field during germplasm collection

Table 3.0: Characteristics and rust resistance levels of Ugandan pearl millet accessions

IP No.	Identity	DFL	PLH	TOT	SPL	SPT	GC	TGWT	Rust (%)
4940	Serere	54	148	4.2	20	18.4	6	8.13	1
4941	Serere	58	165	3	20	27.2	6	9.17	1
4945	Serere	55	152	3.8	22.6	19.7	6	9.14	1
4947	Serere	63	182	3	30.3	20	6	7.35	2
4951	Serere	58	187	3.4	26.4	21.4	6	6.86	2
4966	Serere	68	203	2	22.5	27.8	6	6.99	1
4967	SC 1 (S4)	70	235	1.8	27.8	21.2	6	9.46	1
4971	SC 13 (M)	76	232	2.2	27.4	23.4	6	8.2	2

Source: ICRISAT 1976-94 Database (Singh et al., 1997)
Key: DFL=days to flowering, PLH=plant height (cm), TOT=number of tillers, SPL=spike length, SPT=spike thickness (cm), GC=grain colour (1=deep gray, 2=mixture of white and gray grains), TGWT=1000 grain weight (g)

Rationale for improving locally adapted pearl millet germplasm

The role of resource poor farmers in variety development has shifted from providing local germplasm to being active participants in variety development and selection. On-farm trials have enabled farmers to appreciate differences between their local germplasm materials and those improved (Sharma et al., 2011). This comparison has enabled the farmers to have preferences for particular traits which creates flexibility in the breeding programmes to target the important traits preferred by farmers (Weltzien and Fischbeck, 1990). Therefore, by involving farmers through participatory breeding their preferences are considered leading to successful adoption of the improved varieties (Makanda, 2009). A participatory rural appraisal was conducted in the dry zones of Uganda to establish the farmers' preferences, constraints and production determinants in the pearl millet cropping system. Findings from the appraisal will help to design a better breeding programme that shall include traits that are preferred by farmers. In many breeding programmes, knowing the farmers' preferences has greatly reduced the time required to develop a breeding line. This is because the farmers' preferred traits can easily be identified early in the breeding process and genotypes with such traits selected rather than waiting until the on-farm trials are conducted (Maurya, 1989). In addition, it helps to understand farmers' agronomic practices, storage, processing, marketing and other preferences as a major step in addressing their needs (Danial et al., 2007). As mentioned earlier, a wide spread rust infection and drought has already been highlighted as major pearl millet productivity constraints in many developing countries (Hammond-Kosack and Jones, 2000). Thus, improvement of grain yield of the local genotypes will be addressed by breeding for rust resistance.

Many areas in Uganda have increasingly become semi-arid and some have become totally arid due to changes in global climatic conditions that lead to the ever expanding desertification (Sundquist, 2004). The desertification has resulted in reduced arable land for agriculture. However, the ever increasing population forces farmers to cultivate in the marginalised hot and dry lands (Sharma et al., 2011) not suitable for crop production (Fatondji et al., 2006). As a result many crops, such as maize and sorghum, increasingly fail to adapt to the changes and subsequently succumb to drought (Kumar, 2002). Thus the drought tolerant crop that can withstand such stress extremes is pearl millet which has increasingly become an important food security crop (Sharma et al., 2011). Despite being an important food security crop, the on-farm yield is very low (600 kg ha^{-1}) as compared with the potential of over 3000 kg ha^{-1} due to the little research attention aimed at improving the locally adapted materials (Yadav, 2010). The local germplasm is fairly adapted to drought (Yadav et al., 2003) and readily accepted by farmers (Khairwal et al., 2009), but potentially low yielding and poor at utilising available resources under favourable conditions (Bidinger et al., 2006). In addition, hybrids are high yielding under favourable conditions, but not adapted to drought conditions (Bidinger et al., 2008). Thus, improving local germplasm was adopted as a breeding strategy to generate rust resistant germplasm (Yadav, 2007; Yadav, 2008).

The rust pathogen, *Puccinia substriata* var *indica* (L.) R. Br., has a high mutation rate producing new pathotypes within a relatively short period of time (Singh and King, 1991; Wilson et al., 1995b; Wilson and Gates, 1999). The high mutation rate implies that breeding for rust resistance is a prerequisite for successful and sustainable control of the disease. However, breeding for resistance by introducing resistance genes into the acceptable local materials may provide control against the disease, but it is not sustainable because of the high mutation rate of the pathogen (Tapsoba and Wilson, 1996). The best option, therefore, is to breed for partial resistance achievable through recurrent selection, for a sustainable and long lasting control of pearl millet rust (Bidinger et al., 1982; Crampton et al., 2009). This can be achieved through a better understanding of the mode of gene action and inheritance of rust resistance genes and conducting stability analysis to assess the effect of genotypes by environment interaction. To achieve the foregoing, the under listed objectives were pursued.

Research objectives

The goal of the research was to enhance the food security of smallholder farmers in north and eastern Uganda through increased productivity of pearl millet through improving locally adapted populations for grain yield and resistance to rust. This will improve grain food availability in the chronically dry zones of Uganda.

Specific objectives

The specific objectives of the study were:

1. To establish the importance of pearl millet in Uganda, production constraints and farmers' preferred traits and to identify the production determinants through participatory rural appraisal.
2. To determine the response to S_1 progeny recurrent selection for rust resistance and grain yield in pearl millet populations.
3. To study the inheritance and gene action for grain yield and rust resistance in locally adapted and improved pearl millet germplasm.
4. To determine the stability of pearl millet rust resistance in different agro-ecologies in Uganda.

Research hypotheses

The research objectives were tested through the following hypotheses:

1. Pearl millet is an important crop in Uganda, but adequate production is hampered by production constraints which have not been prioritised by the programme. In addition farmers have preferred traits in their diversified locally adapted materials, which breeders might not know
2. Pearl millet resistance to rust is governed by additive gene action and therefore the populations will respond to S_1 progeny recurrent selection
3. Inheritance of grain yield and rust resistance in pearl millet is controlled by additive gene effects
4. The pearl millet rust resistance is quantitative and thus stable across environments

Structure of the thesis

The thesis consists of six chapters based on the activities related to the specific objectives. Some overlap and repetition may exist between the chapters as they were written as independent journal papers. The thesis is laid out as follows:

- Introduction
- Chapter One: Literature Review
- Chapter Two: Production determinants of the pearl millet cropping system with related uses, traits and constraints: A case of Uganda
- Chapter Three: Response of locally adapted pearl millet populations to modified S1 progeny recurrent selection for grain yield and resistance to rust
- Chapter Four: Combining ability and heterosis for grain yield and rust resistance in pearl millet
- Chapter Five: Analysis of genotype by environment interaction of improved pearl millet genotypes for grain yield and rust resistance
- Chapter Six: Overview of research findings

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Chapter One

Literature Review

1.1 Introduction

The literature review includes information relevant to the research conducted in this study. The importance of participatory rural appraisal in identifying the farmers' desired traits and constraints is highlighted. The role of recurrent selection in population improvement is established. In addition, the importance of knowledge of gene action in deciding on a breeding strategy is discussed while the importance of genotype by environment interaction in also included.

1.2 Taxonomy and genetics of pearl millet

Pearl millet nomenclature has undergone several changes due to the difficulty in classification of the genus *Pennisetum* (Kumar, 2002). It has had the greatest changes in the naming than any other crop in the family Gramineae (Brunken, 1977). This resulted in several species names like; *americanum, penicillariae, spicatum, typhoides* and *glaucum* (Kumar, 2002). Currently the accepted nomenclature of pearl millet is; Family: Gramineae, sub-family: Panicoideae, tribe: Paniceae, and section: *Penicillaria*, genus: *Pennisetum*, and species: *glaucum* and the generally accepted taxonomic name of pearl millet is *Pennisetum glaucum* (L) R. Br. Pearl millet is a simple diploid (2n=2x=14) C_4 plant with a a basic chromosome number of x=7 (Terrell, 1976). It is allogamous due to the protogynous nature of its spikelets in addition to immense genetically diverse gene pools; which makes crossing easy in case of crop genetic improvement. Detailed genetic maps of some 3000 loci spread over 7 linkage groups are available (Liu et al., 1994). Despite this potential, pearl millet research for increased yield is inadequately supported by politics and science in developing countries. This is shown by the fact that, over the last two decades, production in West Africa has only increased by 0.7% per year, the lowest growth rate of any food crop in the region (NRC, 1996). Further, pearl millet has maintained the global position of being the sixth most important cereal for the last four decades (Burton, 1983). However, with the increasing scarcity and unpredictability of rains, pearl millet still has a place in many farming systems (Kumar, 2002).

1.3 Gene pool and sources of diversity

Kumar (2002) subdivided the genus *Pennisetum* into five sections namely; *Pennisetum, Brevivalvuva, Gymnothrix, Heterostycha,* and *Penicillaria*. All the five groups provide inter-specific and intra-specific sources of variation as there has been minimal inter-mating barriers observed when crossed (Amoukou and Marchais, 1993). These variations provide breeding opportunities for improving pearl millet to the advantage of the rural poor communities in order to avert food insecurity. However, criticism of this classification led to suggestions of more acceptable grouping systems of three gene pools namely; primary, secondary and tertiary gene pools (Harlan, 1992).

The primary gene pool comprises of the i) cultivated species *Pennisetum galucum* subsp. *Glaucum* (AA genome), ii) the wild species, *Pennisetum galucum* subsp. *monodii* (Maire) Brunken, and iii) weedy species, *Pennisetum galucum* subsp. *stenostachyum* Kloyzcsh ex. A. Br. and Bouche, which has intermediate morphology between *glaucum* and *monodii*. The subspecies form a single reproductive unit but remain distinct because of prezygotic and postzygotic barriers (Sarr et al., 1988). However, despite the presence of such inter-mating barriers, *monodii* and *stenostachyum* have been noted as valuable sources of genetic diversity for sterile cytoplasm, pest and disease resistance, fertility restoration and heterosis (Hanna, 1987). Nevertheless, if the primary gene pool does not provide the desired characteristic, it may be sought from the secondary gene pool.

The secondary gene pool includes all the species which cross with the primary gene pool but may result in sterile hybrids. Members of this category are Napier grass (*Pennisetum purpureum*) and *Pennisetum squamulatum* Fresen. Napier grass (2n=4x=28) is a highly valuable possible source of sterile male genes. The grass is a good source of forage traits so it can be a superior candidate for forage improvement in pearl millet. Napier grass (A'A'BB genomes) and pearl millet have the A genome in common and the two readily cross to produce sterile triploid hybrids whose fertility can be restored through doubling the chromosome number of the triplods to form hexaploids. The B genome is dominant over the A genome and this masks the genetic variability of the A' genome (Hanna, 1987). Hanna (1987) suggested that masking has resulted in accumulated mutations over time with low selection pressure. As such Napier grass should be a good source of genetic variability. However, the secondary gene pool having only one candidate may not create a diverse availability of novel traits but these may be sought from the tertiary gene pool which seems to be more diverse (Kumar, 2002).

The tertiary gene pool has both sexual and apomictic species that are both diploids and polyploids and the majority belong to the x=9 group. Annual, perennial, rhizomatous and non-rhizomatous species exist in this group. Hybrids developed through crossing members of this gene pool with the primary gene pool members are usually anomalous, sterile, or lethal and gene transfer is complicated. But Hanna (1987) suggested that the tertiary gene pool can be a good source of resistance genes for striga resistance (Wilson et al., 2001) and utilised for apomictic production, perennial growth habit, drought tolerance, cold resistance, pest resistance and cytoplasm diversity. The tertiary, secondary, and primary gene pools provide a wide genetic base for sources of traits for crop improvement. Simmonds (1983) outlined ways of creating variation in pearl millet improvement. Suggestion was made to use locally adapted varieties produced by breeding in similar conditions as some of those local materials may be closely related. Unadapted varieties from within a region like the highly photoperiod sensitive varieties from Guinea zone may also have specific attributes such as high grain quality (Simmonds, 1987). However, for better general adaptation the landraces were recommended more but they do not contribute much to grain yield (Hanna, 1987). Hanna (1987) further reported that inter-specific hybridization with wild species may provide unique attributes such as sterile cytoplasm and factors for apomixes and specific genetic sources for particular characters like cytoplasmic male sterility, dwarfing, brown midrib and trichome characters may be sought for as sources of genetic variation (Kumar, 2002).

1.4 Pearl millet diseases

In developing countries pearl millet is affected by many diseases but five diseases warrant international attention due to their effect on grain and stover yield (Hash et al., 1997). These are; downy mildew, smuts, ergot, pyricularia leaf spot and pearl millet leaf rust. Downy mildew [*Sclerospora graminicola* (Sacc.) J. Schroet.] is a wide spread disease in India and West Africa. It is economically important causing 60-70% yield loss in susceptible hybrids (Singh, 1995).

Smuts [*Moesziomyces penicillariae* (Bref.) Vanky.] and ergot [*Claviceps fusiformis* (Loveless).] are the two major seed-bone diseases limiting the production of pearl millet seed (Gaur et al., 2003). The panicle diseases are widely distributed in many pearl millet growing areas of the world and cause considerable yield and quality loss to grain (Hash et al., 1997). The introduction of hybrid and exotic breeding lines has greatly increased the severity of these diseases in India and Africa (Panwar and Rathi, 1997).

Pyricularia leaf spot [*Pyricularia grisea* (Cke.) Sacc] and pearl millet leaf rust [*Puccinia substriata* Ell. & Barth. var *indica* Ramachar & Cumm.] are the two most destructive foliar diseases of pearl millet (Morgan et al., 1998) and have a capability to evolve new virulent host-specific pathotypes (Hash et al., 1997). Pyricularia appears to be limited to India, Singapore and United States whereas rust is fairly widespread throughout the Americas, Asia and Africa. Disease resistance to both pyricularia leaf spot and pearl millet leaf rust has been transferred to agronomically acceptable grain and forage cultivars. However, the diverse nature of *Puccinia substriata* var *indica* has slowed the effort to breed for increased biomass production (Wilson and Gates, 1999). As a result, pearl millet leaf rust has become an important limiting factor for grain and forage production. Despite its importance and prevalence being reported in Uganda and other countries of eastern Africa, little or no effort has been undertaken to lower the effect of rust which seems to greatly lower pearl millet yield (Johnson et al., 1999).

Other diseases, but of minor economic importance to pearl millet production, include viral, bacterial, fungal leaf spots (*Cercospora, Curvularia* and *Exserohilum*) and nematodes (King, 1992). The effects of the minor diseases are virtually not documented although a few studies have been done about nematodes (Wilson, 2000). The studies indicated differences in resistance of improved materials to nematode species *Melodogyne incognita* Chitwood and *Paratrichodorus minor* (Colbran) Sidiqi (Singh, 1995; Johnson et al., 1999). However, such studies are yet to be conducted in Uganda especially on local landraces since the prevalence of hybrids is almost negligible.

1.4.1 History of pearl millet rust nomenclature and research

Pearl millet rust was first recorded in India as being caused by *Puccinia penniseti* Zimm.(Ramakrishnan and Soumini, 1948), but later the fungus was recorded in the USA as *Puccinia substriata* (Ramachar and Cummins, 1965). Among the races *indica* and *penicillariae* are closely related and the distinction between them is doubtful (de Carvalho et al., 2006). Comments about *indica* being the common rust in India and different from *penicillariae* by having small dehiscent telia and narrower and usually paler teliospores have often been cited (Ramachar and Cummins, 1965). However, de Carvalho et al. (2006) demonstrated that *indica* was a late synonym of *penicillariae* and they argued that a subspecies could not only be differentiated basing on telial size and dehiscence as these factors could also be determined by variability in hosts. Their argument was based on observations by Wilson et al. (1996) that telial size and dehiscence were not important in differentiating subspecies in rust classification. This may further be corroborated by reports that only one race (*indica*) has been observed to occur in the USA, Africa and Brazil (de Carvalho et al., 2006).

Research on pearl millet leaf rust started after a severe epidemic was reported in the USA in 1972, and since then rust epidemics have occurred regularly in pearl millet growing areas (de Carvalho et al., 2006). The importance of pearl millet rust has been documented in many countries, including Brazil, where the crop is relatively new, but not much has been done in Uganda to highlight the importance of the disease. Despite rust being important, relatively little research has been published about the disease and the fungus in many developing countries. For *P. substriata* var *indica*, studies have proven that *Solanum melongena* L., *S. aethiopicum* L. (Solanum gilo Raddi), and several members of *Solanacaea* are hosts for the aecial stage (Wilson et al., 1996). Although there are reports of solanaceus hosts for aecial stage of *P. substriata* var *indica* on *S. melongena* and *S. aethiopicum* (Paz Lima et al., 2002), such reports are just hypothetical since they were solely based on field observations, without cross-inoculations experiments (de Carvalho et al., 2006). The uredial and telial stages occur on *Pennisetum* spp while spermogonial and aecial stages occur on *Solanum* spp (de Carvalho et al., 2006). It is, therefore, important to document the importance of the rust disease in Uganda in order to develop effective control measures.

1.4.2 Symptoms of pearl millet rust

Pearl millet rust is a long-cycle pathogen that needs two distinct host plants to complete its life cycle. Five spore forms (basidiospores, pycniospores, aeciospores, urediniospores, and teliospores) are produced and appear in a definite succession. All spores except basidiospores are produced in well-defined sori and these are; pycnia, aecia, uredinia, and telia (Singh et al., 1997). Uredinia on pearl millet are small green to yellow randomly distributed lesions that occur on leaf surface but more abundant adaxially, turning brown with yellow edges, and eventually forming elliptic shiny brown uredinial and dark brown to shiny black telial pustules. Uredinia are amphigenous, sub-epidermal, erumpent non-paraphysate and pale brown. Urediniospores are ovoid to elipsoidal with uniformly thick, golden yellow, echniculate, 3-4 equatorial germ spores which are sometimes irregularly distributed. The distal end of the leaf is initially infected and as severity increases the leaf tissues become necrotic from the distal to the basal part. Necrosis rarely forms around uredinia, and chlorosis is generally not associated with rust infection in pearl millet.

Under severe cases and on susceptible genotypes, uredinia may occur on leaf sheaths, stem, and culm. Telia appear late in the season and are black, elliptical, and sub-epidermal and may develop within uredinia or independently on leaf blades, leaf sheaths, or culm thereby requiring special screening techniques (Ramakrishnan, 1963). Telia are more abundant on older basal leaves of young plants or on old plants, coalescing and leading to foliage blight. Telia are also amphigenous, irregularly distributed, sub-epidermal, erumpent, paraphysate, dark-brown to black while teliospores are bicellular, pedicelate oblong-ellipsoidal to clavate with chestnut brown walls (de Carvalho et al., 2006). Telia coalesce to form foliage blight (de Carvalho et al., 2006).

1.4.3 Screening techniques for pearl millet rust

Urediniospores are used to inoculate pearl millet. For general screening purposes, urediniospores are collected from field-grown plants with a vacuum spore collector or by scraping (Singh et al., 1997). They are spread into waxed paper or aluminium foil overnight in an air-conditioned room to allow evaporation of excess moisture. The urediniospores are transferred into individual self-sealing plastic bags that are dated and stored at -80^0C (Wilson, 1994). Prior to use, plastic bags containing urediniospores are placed in a water bath at 40^0C for about 10 minutes. They are then suspended in water. A surfactant is added to ensure uniform distribution of spores in water.

Harvesting urediniospores by scrapping with a scalpel and suspended in sterile water is suitable when application is to be effected immediately by brushing on the leaf surfaces (de Carvalho et al., 2006). However, this method is not appropriate for large scale screening of materials. Another short-coming of this method is that the spores cannot be stored and applied at a later time. For certain precise studies, single uredinial isolates are needed. To obtain useful isolates, bulk urediniospores are used to inoculate resistant pearl millet genotypes. More urediniospores can be regenerated by inoculating on susceptible varieties (Singh et al., 1997).

In the greenhouse, seeds are sown in pots or in flats and conditions for promoting optimum seedling growth maintained for accurate assessment of resistance. A known susceptible genotype should be inoculated as a control. At the 3-5-leaf stage, seedlings are inoculated with a water suspension of $1x10^5$ urediniospores ml^{-1} water using a sprayer. Inoculated seedlings are maintained in a moist chamber (95% RH, 25-27^0C) for about 18 hours and adequate moisture maintained on leaf surfaces for successful infection. After incubation the moisture on the leaves is allowed to dry and the pots are transferred to greenhouse benches. Under optimal conditions, uredinia develop in about 8 days after inoculation and rust score should begin as soon as symptoms appear and infection type scale of 0-4 may be used (Singh et al., 1997). If conditions are suboptimal rust assessment may begin 15 days after inoculation. On the modified scale the infection types 0, 1, and 2 indicate resistance, and infection types 3, and 4 indicate susceptibility. Modification of the scale is required when describing moderately resistant infection types 1 and 2. Well-developed chlorosis or necrosis rarely forms around the uredinia. Instead host tissue usually turns dark, reddish-brown and the eruption of small uredinia is delayed. Infection types 3 and 4 usually indicate susceptibility and slow-rusting resistance (Wilson, 1994).

Greenhouse screening is useful to identify resistance in large populations in a small space, but field screening is necessary to identify resistance that is effective against the variable pathogen populations that occur in the field (Wilson et al., 1993). In the field, the best inoculation technique involves spraying crops twice with urediniospores at 25 and 40 days after sowing. The method of inoculation is used to promote rust infection under field conditions to achieve adequate screening for resistance. For effective production of urediniospores border rows of susceptible genotypes can be planted surrounding the field under study. Border rows are inoculated about 30 days after sowing with a water suspension of $5x10^5$ urediniospores ml^{-1}. The 3-5 ml of inoculum is dispensed into the whorls of the plants in the border rows at approximately 10 m intervals. In large fields, two or more additional spreader rows can be sown to subdivide the field and supply adequate inoculum within the field. Inoculating into whorls ensures that some moisture is retained with inoculum during the infection process and using high concentration increases the infection probability. The success of inoculation is examined within 7-10 days. If uredinia are observed no further inoculation should be done (Singh et al., 1997).

1.4.4 Infection and colony development of *Puccinia substriata* var *indica*

The pearl millet rust pathogen, *Puccinia substriata* var *indica*, is heteroecious and macrocyclic affecting both pearl millet and eggplant, the former being the primary host. Monson et al. (1986) reported that the pathogen causes severe effects ranging from plant death, when attacked at early stage (Wilson et al., 1996), to premature desiccation or death of leaves if attack occurs at latter stages of the plant growth and development. The disease initiates from urediniospores (Thakur et al., 2011).Taylor and Mims (1991) reported that for *Puccinia substriata* var *indica* development, all the infection stages (spore germination, appressorium development, infection peg and substomatal vesicle formation) are fully observed on susceptible and resistant cultivars; implying that genotypes cannot be characterised basing on stages of pathogen infection but tissue colonisation and hypersensitive reaction. It appears that tissue colonisation is intense in susceptible genotypes as opposed to resistant genotypes which exhibit hypersensitive reaction (dominant gene action) and rapid cell death at the point of infection (Littlefield and Heath, 1979).

Taylor and Mims (1991) further confirmed the observation by Littlefield and Heath (1979) that moderately susceptible genotypes may be identified as those supporting fairly considerable fungal growth resulting in formation of macroscopic flecks. Wilson (1997) characterised elements of partial resistance as; longer latent period (time taken to 50% uredinia formation), longer incubation period, short uredinium length and width (most important at seedling stage), reduced uredinium area (3.14 x length x width)/4, reduced number of uredinia per unit area of leaf (frequency of uredinia per unit leaf area), low percentage leaf area affected by uredinia (disease severity), reduced uredospore production and low rust index of up to 3%. Similar observations were reported by Sokhi and Singh (1984) but they noted a variation in reaction of some varieties to the components of slow rusting. This indicates that some components are variety-specific suggesting that studies be conducted to identify which components are important in the available germplasm.

1.4.5 Gene action for pearl millet rust resistance

Pearl millet rust resistance has been reported to be conferred by several gene effects. Rust resistance is reported to be controlled by dominant genes, recessive genes or a combination of both dominant and recessive genes, depending on the plant genotype. Panna et al. (1996) noted that in one set of germplasm some crosses showed dominant gene action (high resistance levels) while others showed presence of durable resistance conferred by a combination of both dominant and recessive genes. These observations were further supported by Godasara et al. (2010) and Wilson (1997) through generation mean analysis experiments where different gene actions were identified in specific crosses. Further, Wilson (1997) observed presence of additive, dominance and dominance x dominance epistatic gene actions, depending on the type of resistance gene in the parents used in making crosses and growth stage. Wilson (1997) also reported that additive and partial recessive gene actions were more predominant at seedling stage; implying that partial rust resistance may be observed even at early stages of plant growth. These observations indicate that type of gene action greatly depended on a given set of germplasm used to make crosses and thus a need to carry out genetic studies to establish type of gene action present in a particular set of germplasm.

1.5 Recurrent selection

Genetic worth of a plant is always reflected by its progeny and the selection based on progeny evaluation is progeny recurrent selection. Methods for determining genetic worth include; self-pollinated progeny testing, full-sib progeny testing (Bidinger et al., 2006) and half-sib progeny testing (Fehr, 1987; Bidinger et al., 2006). Self-pollinated progeny testing has superior attributes like exposing deleterious recessive genotypes in a population, exploiting more of the additive gene action, generating between progeny variation for efficient selection, easy to operate because it does not involve any crossing, final selection can be done at harvest, being effective for selecting desired phenotypes, providing better opportunity for further selection for highly heritable traits and saving time if selected progenies are to be developed to inbred lines (Rai and Virk, 1999).

Several recurrent selection methods have been adopted with great success to improve pearl millet populations where polygenically controlled traits like grain yield are targeted. They include; simple recurrent selection, recurrent selection for combining ability (GCA and SCA), reciprocal recurrent selection, full sib family recurrent selection, half sib family recurrent selection, S_1 and S_2 progeny recurrent selection. Of these; half-sib, full-sib and S_1 progeny recurrent selection methods have been reported to result in dramatic genetic advance. However, S_1 progeny recurrent selection has proved to be more effective for improving many polygenic traits. Dutt and Nirania (2005) compared the effectiveness of the three selection methods and reported that S_1 consistently gave higher response to selection for grain yield and many traits. It was observed that maximum response to selection for grain yield can be achieved in two cycles. On the other hand half-sib recurrent selection was the most effective for forage traits. Basing on the consistency and reproducibility of S_1 recurrent selection for grain yield, it was adopted for this study.

1.6 Gene action for grain yield and yield components

Grain is the major product of pearl millet production systems in developing countries. The component is influenced by many yield-related traits among which are; number of productive tillers, panicle length, panicle width, panicle area, grain density, days to 50% flowering, plant height, 1000 grain weight, leaf area, panicle weight, harvest index and rust index. These yield components are controlled by gene actions (Bidinger et al. 2003; Bhoite et al., 2008) which affects the selection procedure for trait improvement. Kapoor et al (1979) reported that additive gene action was predominant in the inheritance of productive tillers, while Tomar et al. (2008) reported low heritability and low genetic gain. This indicates that the trait may be improved through recurrent selection. However, Gandhi et al. (1999) reported presence of both additive and dominant genetic effects in crosses within the same experiment, indicating that the gene action is dependent on the genotypes of the parents involved in making the crosses. They also observed significant negative additive gene action for some crosses. However, Vagadiya et al. (2010) reported that number of productive tillers was controlled by non-additive genetic effects and thus indicating that dominance and epistasis were also important in the inheritance of number of productive tillers. The observations confirm that number of productive tillers is quantitatively inherited but dependent on the parents used to make crosses.

Panicle-related parameters also significantly contribute to grain yield. Dominance and additive x additive gene effects have been reported to control the inheritance of panicle length (Ghandhi et al., 1999). Ghandhi et al. (1999) also observed a variation in gene action depending on the parents used in the crosses. They noted that in some crosses inheritance of panicle length was controlled by dominance and additive x additive gene action, while in other crosses duplicate dominance was predominant for the same trait (Shinde and Patil, 1987). Similar observations were reported by Vagadiya et al. (2010) when using cytoplasmic male sterile lines. However, Sandhu and Phul (1984) reported predominance of additive genetic effects controlling the inheritance of the trait. It implies that panicle length may be improved through recurrent selection or hybrid breeding depending on the parents used in the breeding programme. In addition, panicle width and panicle weight inheritance has been reported to be controlled by additive gene effects (Chotaliya et al., 2010). The same observations were reported by Ghodasara et al. (2008) when they observed non-significant heterosis and heterobeltiosis for panicle width and length and suggested that these traits can be improved through recurrent selection.

Plant height is a quantitatively inherited trait that greatly influences grain yield. Shanmuganathan et al. (2005) reported dominant genetic effects for plant height; confirming findings by Mahawar et al. (2003) that the trait is predominantly controlled by non-additive genetic effects. However, Rasal and Patil (2003) and Rathore et al. (2004) observed additive gene action when diverse restorer genotypes were used, but reported low heritability and thus low genetic advance due to the high response to the environment (Mahawar et al., 2003). They suggested improving the trait through indirect selection. These observations indicate that the quality of materials used in the breeding programme and testing for stability across environments is crucial in order to achieve high genetic advance.

Days to 50% flowering, determined by approximately 50% of the panicles having stigma, is another component that affects grain yield. Rasal and Patil (2003) reported that the trait is highly influenced by additive gene effects, while Rathore et al. (2004) reported that both additive and non-additive gene action operated concurently. Contrary, Azhaguvel and Jayaraman (1998) and Lakshmana and Guggari (2001) had earlier reported non-additive gene action as being predominant when they observed a high heritability, but low genetic gain for days to 50% flowering.

1.7 Heterosis

Heterosis measures the superiority of the hybrid relative to the parents. It has been identified as the most important breeding approach for improving grain yield in pearl millet (Hanna and Gupta, 1999; Ramamoorthi and Nadarajan, 2001). It has been exploited to improve adaptability of elite materials to drought stress and to improve grain yield of landraces (Bidinger et al., 1994; Yadav et al., 2000; Presterl and Weltzien, 2003). However, this necessitates selection of suitable parents whose combination results in the desired genotype (Vetriventhan et al., 2008). A survey conducted by Virk (1988) showed a 40% average better parent heterosis for grain yield. Various studies have shown high level of heterosis for grain yield and harvest index (Chavan and Nerkar, 1994; Yadav and Nijhawan, 1994), and standard high level of heterosis for grain yield (49.3%), number of productive tillers (63.3%), panicle length (49.3%), panicle girth (22.1%), panicle weight (76.6%), and 1000-grain weight (86.7%) (Karthigeyan, 1994). The analysis shows that heterosis breeding is ideal for increasing yield in pearl millet (Ramaamoorthi and Nadarajan, 2001). However, much as heterosis has been widely accepted as a crop improvement approach, the physiological and genetic basis by which it is defined is not well understood, even though considerable evidence has been the accumulation of dominance genes hypothesis; whose interpretation is complicated by the fact that disease infection and mechanisms for drought resistance may elicit production of growth hormones that may increase yields (Konzak, 1989).

1.8 Correlation analysis

In pearl millet breeding for increased grain and stover yield correlation analysis is important in identifying traits that influence yield. This helps to make a better selection combination of traits (Izge et al., 2006). Some traits have a consistently positive correlation with grain yield (Vengadessan, 2008). Number of tillers is consistently and positively related and has a direct influence on grain and stover yield under optimum and stress conditions (Ram et al., 2007; Maman et al., 2004). Patil et al. (2006) reported a strong positive association between days to 50% flowering under terminal water stress. In addition, Patil et al. (2006) observed that plant height was negatively correlated to grain yield under stress environments; indicating the importance of type of materials used in the study. However, Salunke et al. (2006) reported a small, but positive association with grain yield for local germplasm under optimum conditions. This indicates that association of some traits with grain yield is dependent on the environment. Harvest index has been reported to have a positive association with grain yield under drought condition and negatively correlated under highly productive environments (Maman et al., 2004). Number of days to maturity is also positively associated with grain yield under stress condition, but negatively correlated under optimum conditions (Patil and Jadeja, 2006).

1.9 Genotype x environment analysis

Differential performance of genotypes across environments (genotype by environment interaction, GEI) complicates selection of genotypes with superior performance (DeLacy et al., 1996). This necessitates that genotypes be tested across many environments and statistical analyses done to establish which ones win where (Yan et al., 2000). Statistical analyses are often done to characterise the genotypes relative to environments, but they are rarely correlated with the physiological characters. Thus a combined analysis of GEI and physiological analysis for plant adaptation is necessary to adequately characterise genotypes (Byth and Mungomery, 1981). Several methods have been used to analyse GEI in pearl millet improvement programmes. Among them is linear/joint regression analysis, multivariate techniques like principle components analysis (PCA), Additive Main effects and Multiplicative Interaction (AMMI) analysis, pattern analysis, cluster analysis, GGE biplots (Yan et al., 2000), and shifted multiplicative model (SHMM) (Seyedsadr and Cornelius, 1992).

Mgonja et al. (2003) used linear regression to assess stability of varieties across environments in eastern and southern Africa. The linear component of the regression accounted for the greatest variation and genotypes were adequately charaterised basing on “what won where” comparison. However, when Yahaya et al. (2006) used linear regression to characterise hybrids in Nigeria, based on yield, the non-linear component accounted for the greatest variation. Although Leon and Becker (1988) reported linear regression as the best estimate for stability and widely used in pearl millet breeding, it has many faults which make it inadequate for sole use to discriminate environments (Bramel-Cox et al., 1986). These may to a greater extent be overcome by the use of non-parametric methods (Nasser and Huhn, 1987) and pattern analysis (Byth et al., 1976) which are based on both classification and ordination techniques (Bramel-Cox et al., 1986). AMMI could be used to select for yield and stability for grain yield using the Yield-Stability index (YSi) (Kang, 1993). However, this method has a weakness of being over-reliant on yield performance rather than arbitrariness in the scoring procedure (Bajpai and Prabhakaran, 2000). The SHMM method is more sensitive than AMMI, because it incorporates all variance components in the analysis (G, E, and GE) which makes it more precise, but has not been explored in pearl millet that much. On the other hand, the SHMM is also more appropriate when micro-environments are to be characterised, but may not be effective for characterizing mega environments (Seyedsadr and Cornelius, 1992).

1.10 Participatory rural appraisal in pearl millet breeding

Farmers are the important primary end-user of new breeding technologies and also provide local germplasm in addition to being active participants in variety development, multiplication, selection and distribution of improved seed (Danial et al., 2007). On-farm trials have enabled farmers to appreciate differences between their local germplasm and improved materials in relation to their preferred traits (Sharma et al., 2011). This enhances adoption of new varieties (Sperling et al., 1993) and the need for flexibility in the breeding programmes to target the important traits preferred by farmers (Weltzien and Fischbeck, 1990; Makanda, 2009). However, the farmers' preferences and constraints faced can only be identified through conducting participatory rural appraisal studies (Oduori, 2009). This creates a close interaction with the farmers and appreciating their challenges and needs and thus design breeding programmes targeted at meeting the needs and solving problems (Maurya, 1989).

Participatory rural appraisal studies conducted reveal variations in farmers' preferences depending on the type of production environments. For farmers in high production environments, high yielding varieties are given first priority whereas farmers in low production environments prefer varieties which can stand the harsh condition. Studies conducted by Omanya et al. (2007) in West Africa showed that farmers preferred high yielding varieties which were relatively late maturing (80-100 days), with many productive tillers and long panicles in addition to tasting more like the local varieties. However, in southern Africa, farmers' preferences were not high grain yield per se, but rather earliness, drought tolerance, grain size and colour (Mwa'ngombe and Mushonga, 1996). In addition to the above traits, farmers in Eritrea also preferred long storage varieties with high and strong straw yield for use in thatching their houses as there are no reliable alternative grass sources for roofing (Roden et al., 2006). Interestingly, through PRA studies in Namibia, it was observed that farmers grow improved early maturing varieties concurrently with local late maturing varieties (Uno, 2005). Uno (2005) further reported that this is done to minimise risk of yield loss in case drought occurs. Despite the high variability in farmers' preferences established through participatory rural appraisal, such studies have not been conducted in Uganda. Thus there is need to conduct participatory rural appraisal studies in Uganda in order to develop pearl millet varieties with farmers' desired characters.

1.11 Research gaps identified from the review of the literature

The literature review herein shows that; suitable breeding methods, including heterosis, for pearl millet improvement need to be established in order to produce high yielding cultivars for the semi-arid to arid regions; use of modern techniques as an integral part for hastening production of improved germplasm with desired traits needs to be explored; information about the rust epidemiology in Uganda is lacking; the relationship between grain yield components and rust resistance has not been established in the pearl millet germplasm in Uganda; and genotype x environment studies need to be explored in order to develop germplasm suitable for the agroecological zones in Uganda and finally the farmers ability to participate in the development of improved pearl millet germplasm needs to be established.

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Chapter Two

Production determinants of the pearl millet cropping system with related uses, traits and constraints: A case of Uganda

Abstract

Although pearl millet is an important food and source of income for the rural communities living in environmentally marginalized areas in Uganda, not much is known about the production environment. A survey was therefore conducted in eastern and northern regions of Uganda to characterise the pearl millet cropping system in order to identify the most important determinants of production. Using questionnaires, data was collected from 160 households through face-to-face interviews with the respondents. Results showed that pearl millet was mainly grown for food and source of income. The production environment was low input as farmers planted landraces, used no artificial chemicals or manure, and had minimal access to credit or agricultural trainings or extension services. The production was also characterised by planting in the second rains, poor optimal use of important resources like family labour and seed due to adoption of planting method of broadcasting. This led to wastage of seed in addition to requiring a lot of labour for weeding and thinning. Additionally, farmers grew landraces with traits such as being tall, grey grain colour, early maturity, late maturity, stay green, high tillering, small grains and brown grains; though the most desirable were stay green, being tall, high tillering, high yield, early maturity and being ergot resistant, respectively. The most important constraints were ergot susceptibility, being short, rust susceptibility, low yielding, low tillering, late maturity, sterile panicles; while lack of market, low prices and price fluctuation were the important market constraints. Results further showed that farmers lacked knowledge about the common diseases like rust and ergot. The regression analysis showed area planted, age of spouse and years of pearl millet cultivation as the important factors enhancing production while age of household head, amount of seed planted and distance to the market were the negative factors affecting grain yield.

Key words: Pearl millet, production determinants, desired traits, constraints, rural appraisal

2.1 Introduction

Pearl millet is the world's hardiest warm season cereal (Reddy et al., 2012) and a primary food grain for millions of people living in drought-prone areas of Africa (Ndjeunga and Nelson, 2005) and India (Roden et al., 2007). Under rain-fed production conditions (FAO, 2007), it is the sixth most important cereal in terms of cultivated area after rice, wheat, maize, barley and sorghum (Khairwal et al., 2007a). It accounts for 42% of total world cereal production (Ramesh et al.,2006). In India, the highest producer, pearl millet is the fourth most important cereal (Yadav et al., 2011) while in Africa the crop ranks high in terms of importance in many countries. For example in Niger, the crop is the most important in terms of total cereal cultivation and production (Ndjeunga and Nelson, 2005) while in Namibia it is the most important cereal food (Ipinge, 1998; FAO, 2008). In Eritrea it ranks as the second most important staple cereal after sorghum (Roden et al., 2007). Nutritionally, it is better than common cereals like sorghum, maize, and rice in terms of proteins (Roden et al., 2007), fats, iron, energy and carotene (Singh et al., 1987).

Pearl millet is important forage for livestock (Basavaraj et al., 2010) and food for humans (Vetriventhan et al., 2008). Humans consume the grain as porridge, cakes known as masa (Izge and Song, 2013), or steamed granulated product or is used as a source of yeast in the brewing industry (Murty and Kumar, 1995). The various forms of food use have particular standards set by the users, which leads to varietal preferences. The different preferences form a basis for pearl millet breeders to develop varieties that have the desired qualities needed by the users. However, until recently plant breeders have not involved pearl millet users, especially farmers, when developing varieties with users' desirable characteristics. The result has been many varieties not being adopted by the intended beneficiaries (Ndjeunga et al., 2000). The low adoption may partially be explained by the poor seed supply system, production constraints and failure to identify desirable cooking qualities (Ndjeunga and Nelson, 2005). This implies that knowledge of traits preferred by the pearl millet beneficiaries and establishing constraints is important for designing an effective breeding strategy (Ndjeunga et al., 2000). However, appropriate approaches should be adopted in order to effectively characterise the pearl millet production environment in terms of desirable attributes and constraints.

Participatory rural appraisal techniques have successfully been used to characterise the production environment of different crops; leading to identification of desirable features and production constraints. Mergeai et al. (2001) reported that informal appraisal techniques help to elucidate the relevant local knowledge which improves the precision of the formal techniques. Through participatory surveys, Brocke et al. (2003) established farmers' selection criteria of new pearl millet varieties in stress environments based on adaptability and productivity, while Weltzien et al. (1998) showed that farmers were important in the evaluation of new pearl millet varieties before release. In addition, Paris et al. (2008) showed that integration of gender issues in participatory research was important in varietal selection and dissemination while Camara et al. (2006) successfully adopted participatory rural appraisals to assess the impact of sorghum and millet research in West Africa. Much as it was noted by Paris et al. (2008) that for increased technology adoption farmers should be involved at all technology development stages, most of the participatory rural appraisal approaches involve farmers at variety selection stage.

This study aimed at seeking farmers' views in order to design an effective breeding programme in Uganda. This is important because scanty information about pearl millet research exists in Uganda; production characteristics being combined with those of finger millet. A participatory rural appraisal baseline study was then conducted to establish pearl millet production characteristics like demography, productivity, uses/importance, important factors of production, constraints, desired traits, and establishing the importance of production determinants. Thus, the information from the baseline study will be used to develop an effective participatory plant breeding programme which considers the pearl millet users' views.

The major objective was therefore to characterise the pearl millet cropping system in Uganda. The specific objectives included; 1) establishing the importance and utilisation of pearl millet, 2) assessing the extent to which improved inputs and improved technologies were used to increase productivity, 3) highlighting the agronomic factors, 4) identifying farmers' desirable and undesirable pearl millet traits, 5) pearl millet production and marketing constraints, and 6) identifying the most important determinants of production and their effect on grain yield.

2.2 Methodology

2.2.1 Study area

A baseline survey was conducted in January 2012 in the eastern and northern regions in Uganda where pearl millet is predominantly grown. Both regions are characterised by rearing of cattle and production of annual crops such as cotton, sorghum, millets, cassava, sweet potato, ground nuts, sun flower and sesame (Ronner and Giller, 2013). The eastern region has a bimodal rainfall pattern with long dry seasons and infertile sandy-loam soils while the northern region has less pronounced bimodal rainfall pattern, which reduces to unimodal pattern with long dry intervals in the far north and north-eastern Uganda (Mwebaze, 2006). The location of the study areas and soil texture is as indicated in the Table 2.1

In the east the study was conducted in Kumi and Katakwi districts. In Kumi district 40 households were covered in three villages namely; Olupe, Asinge and Okouba while in Katakwi still 40 households were covered in Olera and Usuku villages. In Kitgum district the study was conducted in Kitgum town council, Mucwini and Kitgum Matidi villages covering 38 households while in Lamwo data were collected from Rudi and Pobar villages covering 22 households.

Table 2.1: Location, mean rainfall and soil types of the study districts

Region	District	Latitude	Longitude	Altitude (m.a.s.l)	Mean rainfall (mm)	Soil types
Eastern	Kumi	01° 30′N	033° 57′E	1138	1270	Sandy loam
	Katakwi	01°54′N	034°00′E	1107		Sandy loam
Northern	Kitgum	03°13′N	032°47′E	969	1130	Sandy loam
	Lamwo	03°32′N	032°48′E	1100		Sandy loam

Source: http://en.wikipedia.org/wiki/Districts of Uganda, accessed on 19/03/2011.

2.2.2 Selection of farmers and enumerators

Pearl millet production is localised in a few places in northern, eastern and northeastern Uganda. Therefore, purposive selection of the study area and respondents was done basing on how widely the crop was grown in the districts. In eastern Uganda, the farmers were selected basing on the fact that they had grown pearl millet in the last two consecutive years. However, in northern Uganda some respondents who had grown the crop in the last one year were considered as long as they had some experience of growing pearl millet. This is because most farmers in the northern region were still settling for normal farming after over 20 years of being in a zone associated with insecurity. In all the four districts a five-stage stratified selection criteria was adopted in order to identify respondents. The strata were 1) cropping system, 2) district, 3) sub-county, 4) village, and 5) respondents. For the respondents' stratum households were randomly selected with the help of local council leaders who had a register of all the village members. After selecting about one hundred households that grew pearl millet, random selection of those to participate in the study was done. This number varied by village depending on the willingness of households to participate in the study.

2.2.3 Data collection

Data were collected using various participatory rural appraisal techniques. The techniques included; transect walks, problem listing, ranking and analysis (Lelo et al., 1995) with key informants (Figure 2.1) and were corroborated by household formal interviews using a semi-structured questionnaire (Figure 2.2). In addition, informal data collection techniques like observations were adopted in order to better understand the pearl millet cropping system at the household level. Two three-member teams collected the data with the help of the village local council leaders and the extension workers. One team worked in the east covering eighty households while the second team worked in north covering sixty households. The household crop and animal productivity in the last twelve months was estimated using the 'farmer recall' (Fermont et al., 2009; Smale et al., 2010) and 'prediction' methods (Singh, 2003).

Figure 2.1: Key informants using charts to identify pearl millet diseases in Kitgum district


Figure 2.2: Enumerator interviews household head

2.2.4 Data analysis

Data collected from the focus groups discussion and household interviews were entered and analysed using the statistical package for social scientists version 20 (IBM-SPSS, 2011) where average scores and ranks were calculated from the quantitative and qualitative data collected. Descriptive statistics were used for analysis to identify general patterns (Pender et al., 2002) and tests, regression, analyses of variance and means comparisons were computed.

2.3 Results

2.3.1 Importance and utilisation of pearl millet

2.3.1.1 Importance of pearl millet in terms of cultivation frequency and being food security crop

The majority (56%) of the farmers (Figure 2.3) indicated that they planted the crop 3-4 times in the last five consecutive years. Results in Figure 2.4 show that farmers in Kumi district (35%) had grown the crop more often than farmers in the other three districts in the last five years; while Figure 2.5 indicates the importance of pearl millet as a food security crop.

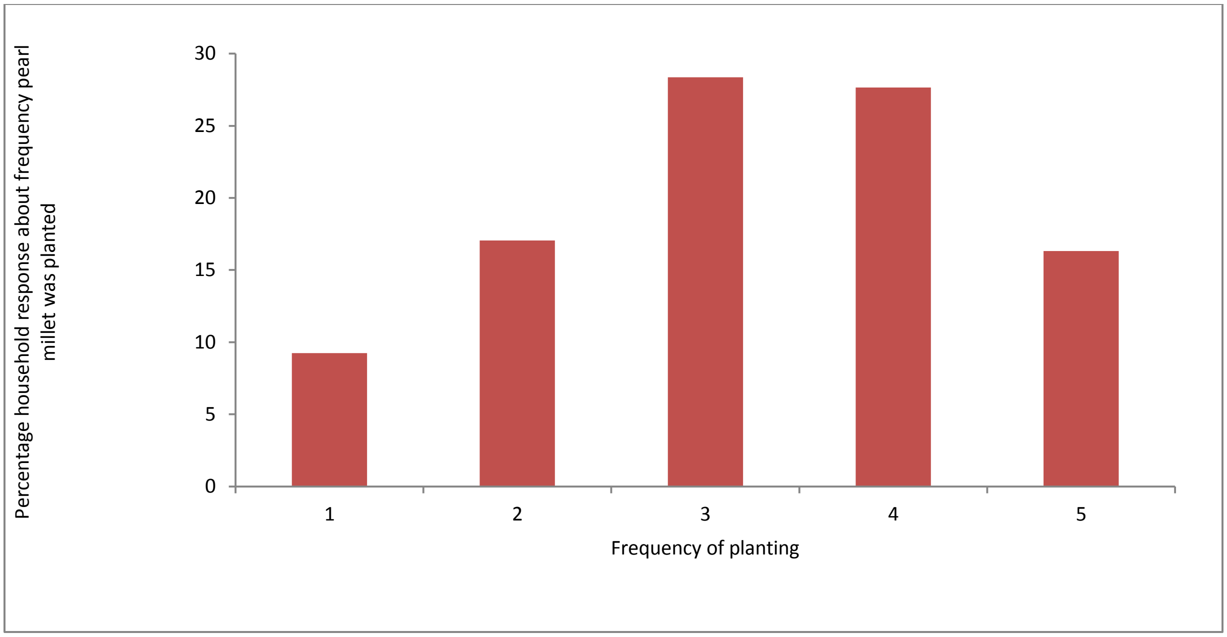

Figure 2.3: Frequency pearl millet was planted in the last five years

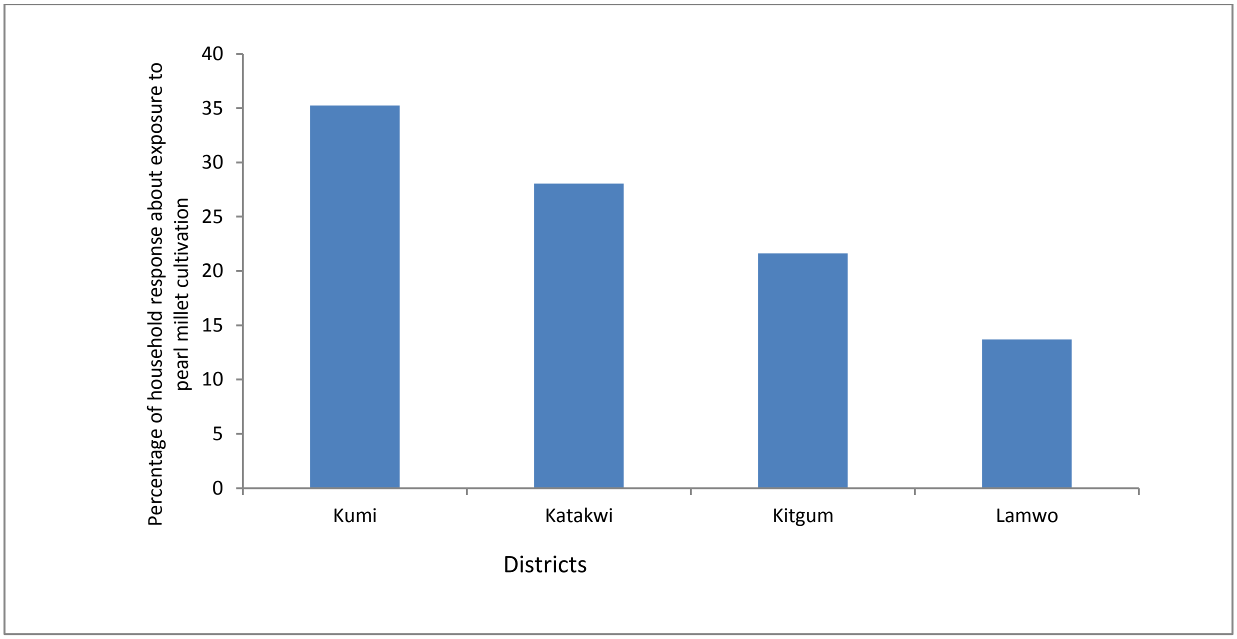

Figure 2.4: Level of exposure to pearl millet cultivation in the last five years

The majority (98%) of the households responded that pearl millet was an important food security crop, mainly because it could easily be sold to buy other preferred foods in addition to readily being accepted as a food. Results in Figure 2.5 also show that pearl millet was preferred as a food security crop because it had a high multiplier effect when eaten, had no market and was nutritious. Easily sold was a response mainly from Kumi district where the crop was mostly grown for sale while having no market was a response from the other districts where pearl millet was mainly grown for food.

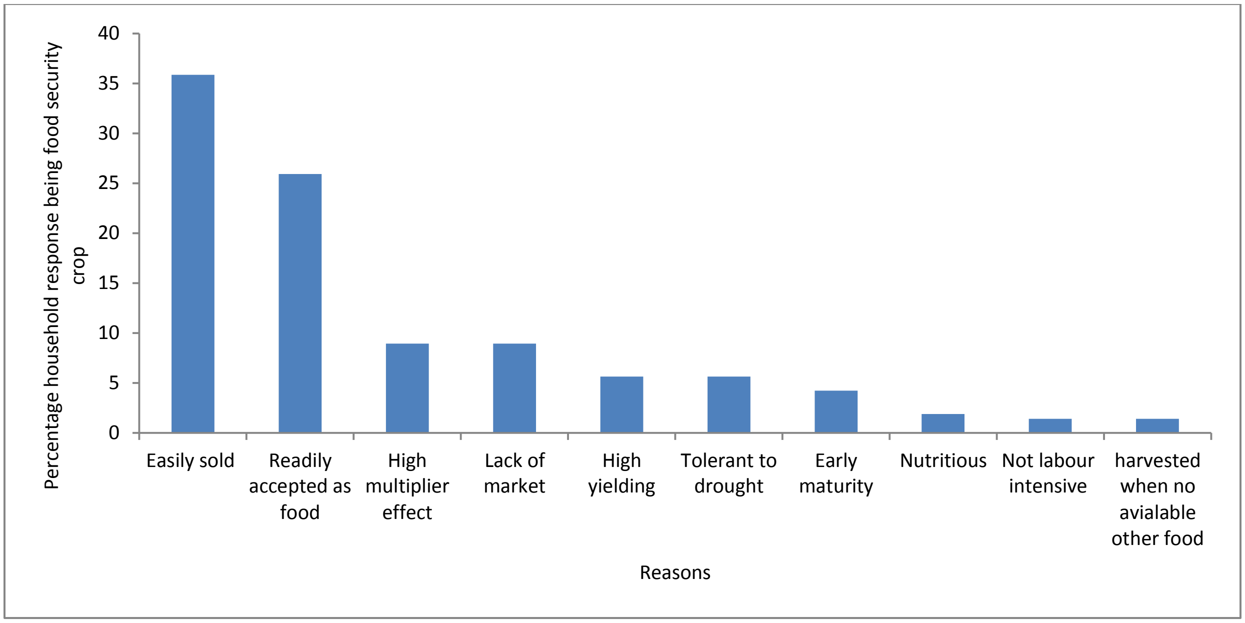

Figure 2.5: Reasons for growing pearl millet as food security crop

2.3.1.2 Ranking of pearl millet relative to other crops

The pearl millet cropping system was characterised by crops such as sorghum, maize, cassava, groundnuts, cowpea, pigeonpea, finger millet, green gram, sesame, beans, cotton, rice, sweet potato, field peas and sunflower. Generally the crops were grown for food, income and because they were adaptable to drought conditions (Figure 2.6). Basing on the importance of the crops as a source of income and being food, a ranking system was developed to establish the importance of pearl millet relative to other crops. The rank was an average of the rank of the pearl millet as a food crop and the rank as a source of income. The ranking showed groundnuts as the most important crop to the farmers in terms of food and income (Table 2.2). Pearl millet was the fourth most important crop, being ranked higher than sorghum, maize, finger millet, green gram and sweet potato. Figure 2.7 shows that the rank could change if changes in palatability, being source of income, marketability and readily being accepted as food exist.

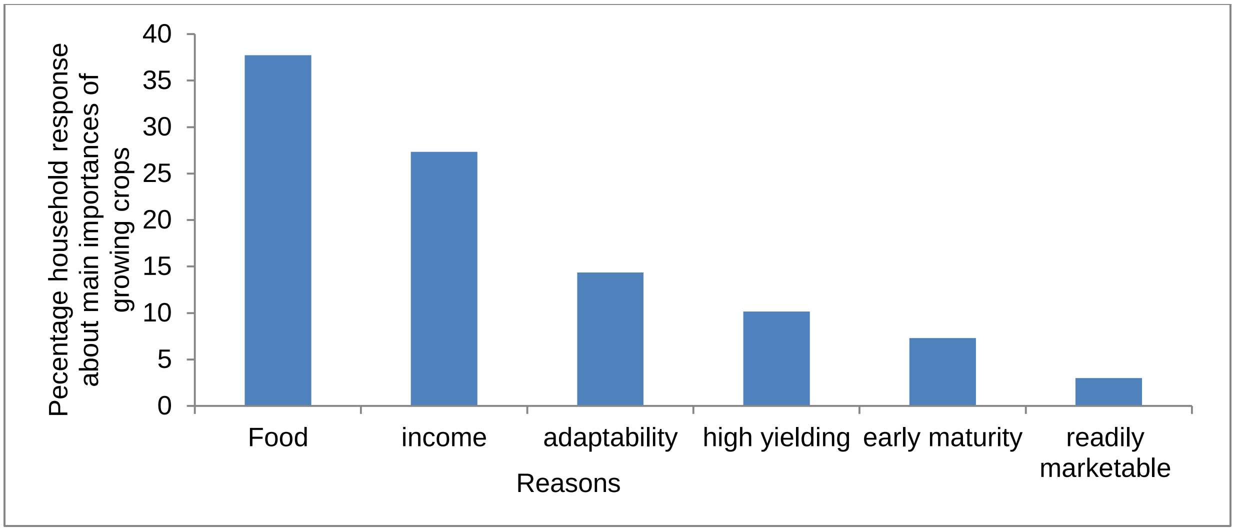

Figure 2.6: Reasons for growing crops

Table 2.2: Ranking of the nine most important crops

Crop	Mean percent	Rank*
Groundnuts	26.59	1
Sesame	18.24	2
Cassava	16.82	3
Pearl millet	9.47	4
Sorghum	9.10	5
Maize	8.65	6
Finger millet	4.99	7
Green gram	3.24	8
Sweet potato	2.88	9

*Rank=average of the rank as a food crop and the rank as a source of income

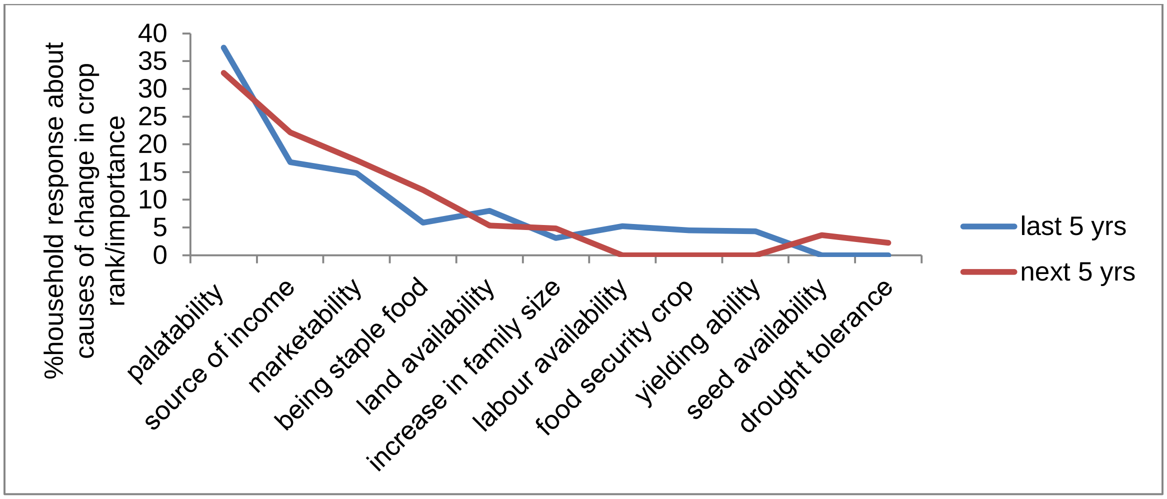

Figure 2.7: Causes of change in crop rank/importance

2.3.1.3 Uses and utilisation of pearl millet

Pearl millet has numerous uses in Uganda (Table 2.3). The grain was mostly used as food (44%), source of income (36%) and in brewing as yeast (17%). On a small scale, the grain was also bartered for other food commodities or fed to poultry (Figure 2.8) while stover was fed to livestock. Bartering the grain for other food stuffs was one of the coping strategies for using pearl millet as food security crop. Farmers also claimed that pearl millet was strategically grown to control striga and to increase honey production. The use of pearl millet to control striga was confirmed by there being no striga in the pearl millet fields visited during the survey. Pearl millet was more of a source of income and food in eastern region than in the northern region where food was the main use (Table 2.3). In addition, no household reported the use of pearl millet stover as building materials or as fuel for cooking; an indicator that these may not be important uses for the stover in Uganda.

Table 2.3: Uses of pearl millet in Uganda

District	%household response about uses and importance of pearl millet							
	Food	Income	Yeast for brewing	Barter trade	Livestock stover	Poultry feed	Killing striga	Honey production
Katakwi	12.82	14.29	3.66	0.00	0.37	0.00	0.00	0.37
Kumi	8.79	13.55	6.96	0.00	0.37	0.00	0.37	0.00
Kitgum	13.92	5.13	4.03	1.10	0.00	0.37	0.00	0.00
Lamwo	8.42	2.56	2.56	0.37	0.00	0.00	0.00	0.00
Total percent	43.95	35.53	17.21	1.47	0.74	0.37	0.37	0.37

Figure 2.8: Poultry feeding on pearl millet

As food, pearl millet is consumed in many different ways. The whole grain (not decorticated) is pounded to make flour, which is then used to make either soft porridge or posho (Table 2.4). In the northern region the grains may be consumed when boiled, while in the eastern region the pearl millet flour is mixed with cassava flour and tamarind to improve on the taste of posho (Table 2.4). The results also showed that consumption of pearl millet as food was district-specific with Katakwi in eastern and Kitgum in northern region being the leading consumers.

Table 2.4: Percent household response about different ways pearl millet is used as food

	%household response about ways pearl millet is eaten				
District	Plain posho	Plain porridge	Grains boiled like rice	Cassava+ pearl millet posho	Pancake /bread
Katakwi	11.93	6.88	2.75	2.75	0.00
Kumi	7.34	6.88	0.46	1.38	0.00
Kitgum	12.84	15.60	8.26	0.00	0.92
Lamwo	8.72	7.80	4.59	0.00	0.92
Total percent	40.83	37.16	16.06	4.13	1.83

2.4 Use of improved inputs and improved technologies

2.4.1 Access to improved seed and sources of seed

The Figure 2.9 shows that majority of the farmers did not use or access services such as improved inputs and technologies. In terms of planting materials, almost all households planted unimproved seed which was either saved from previous harvests or bought from local markets (Figure 2.10). Results in Figure 2.9 further indicate that all the households in the north planted local unimproved genotypes while only 2% planted improved varieties, which they could not identify by name. The most important reason for planting local unimproved varieties was that there were no alternative seeds (23%) (Fig. 2.11). Other reasons were that genotypes planted were drought tolerant, early maturing and high yielding. However, early maturity and high yielding were reasons that came from farmers in the east.

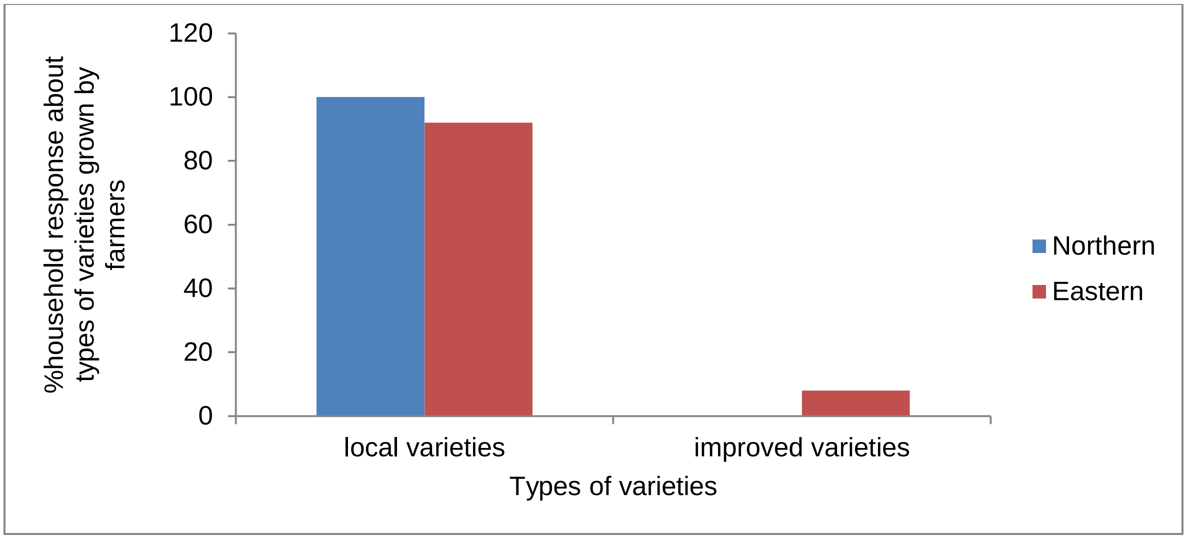

Figure 2.9: Types of planting materials grown by farmers

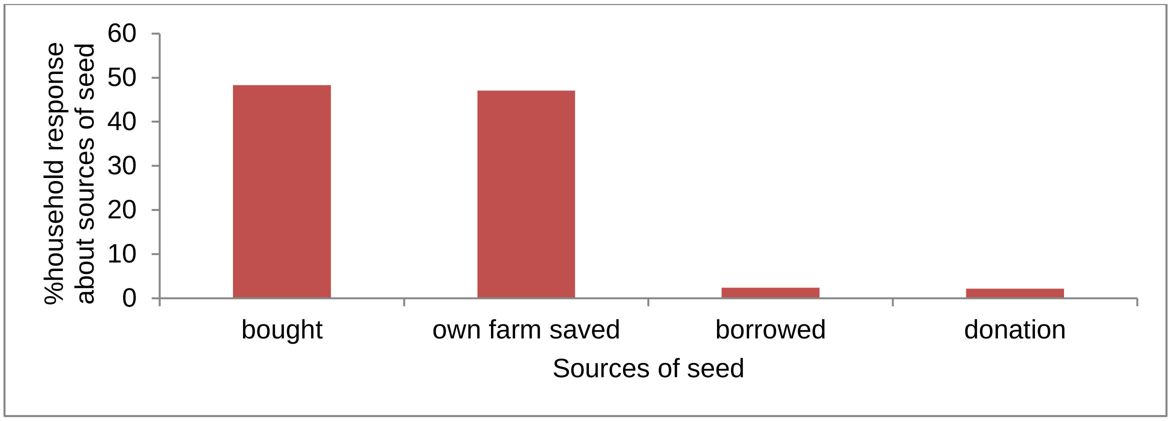

Figure 2.10: Common sources of pearl millet seed

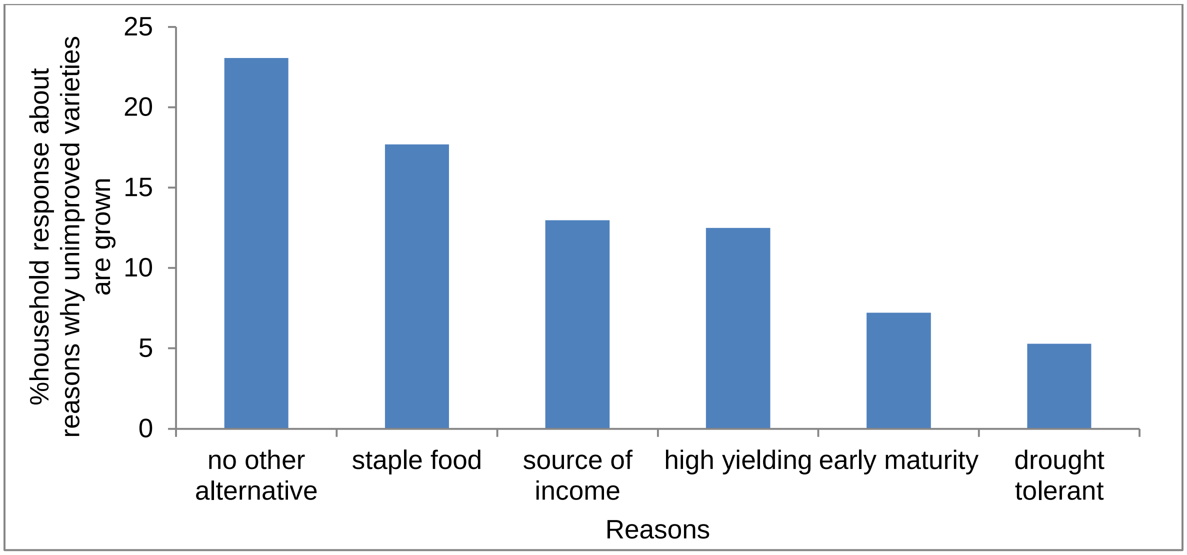

Figure 2.11: Reasons for growing local unimproved varieties

2.4.2 Access to fertilisers, manure, pesticides and herbicides

Information about use of external inputs like fertilisers, manure, herbicides, pesticides and soil and water conservation measures was sought. Results in Figure 2.12 showed that the majority (96%) of the farmers did not use the external inputs mentioned to enhance pearl millet yield. They relied on inputs like unimproved seeds, family labour and to a lesser extent other social services like agricultural trainings, extension services and rain water.

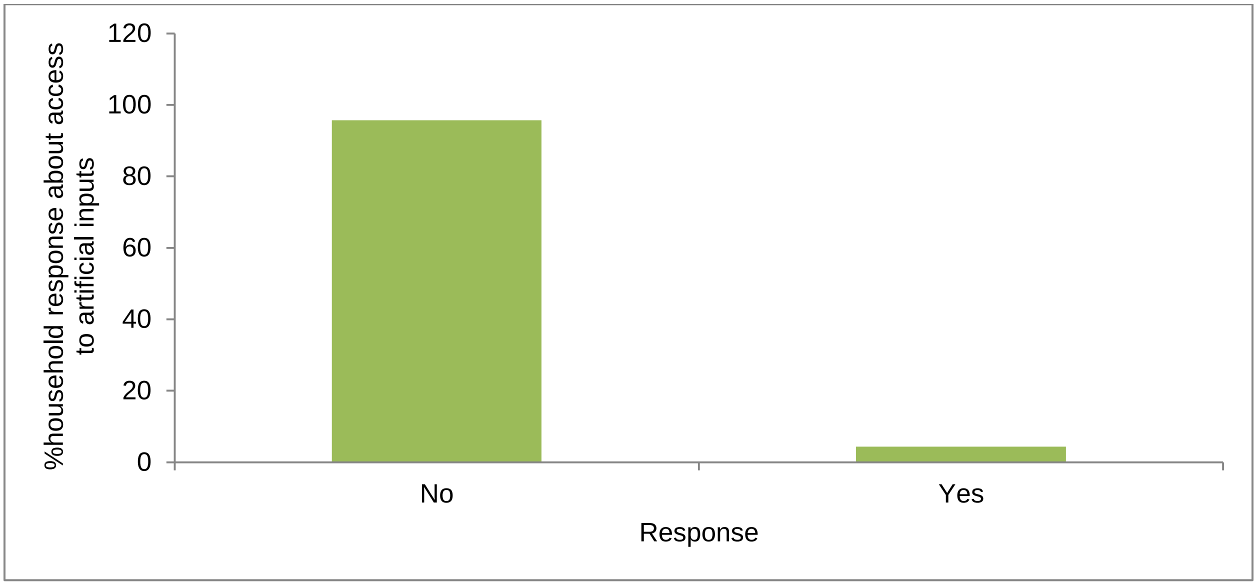

Figure 2.12: Response about use of artificial inputs

2.4.3 Access to social services

Figure 2.13 shows that the majority of the respondents did not have access to important social services which would enhance productivity. More than 86% did not keep financial and production records while more than 84% did not have access to credit. In addition, more than 55% did not have access to extension services or agricultural training nor were they members in any community based groups.

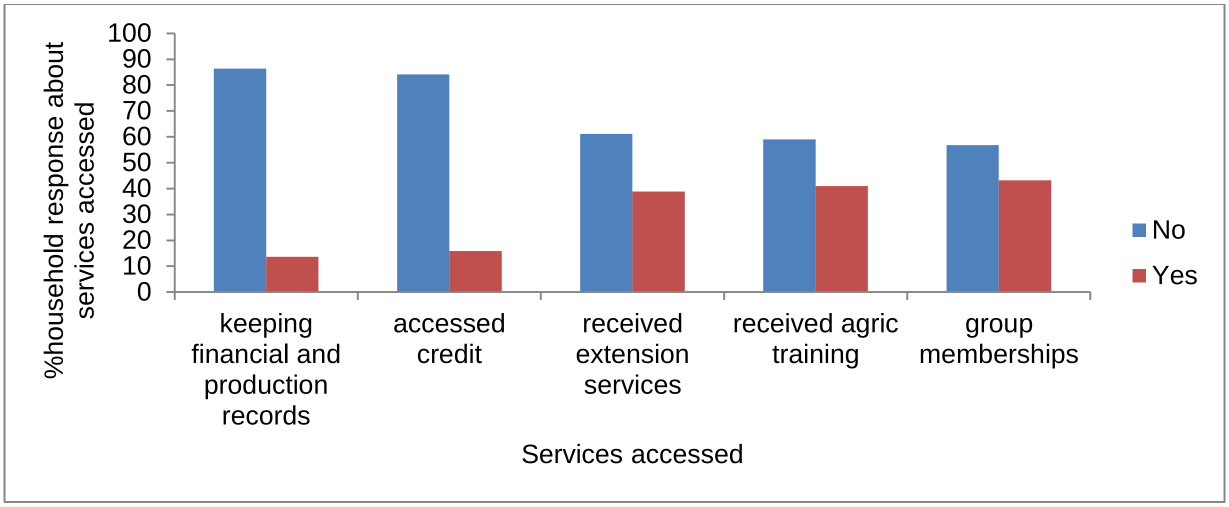

Figure 2.13: Services accessed by farmers

2.5 Agronomic factors

2.5.1 Farming activities

Agronomic issues assessed included season/time of the year pearl millet was planted, methods of planting, frequency of weeding and labour availability. Labour provision by gender was assessed for farm activities like land preparation, planting, weeding, bird scaring, harvesting and threshing. Results in Figure 2.14 show that men were mostly involved in land preparation and planting, while women were much involved in weeding, harvesting and threshing. The main task for children was bird scaring.

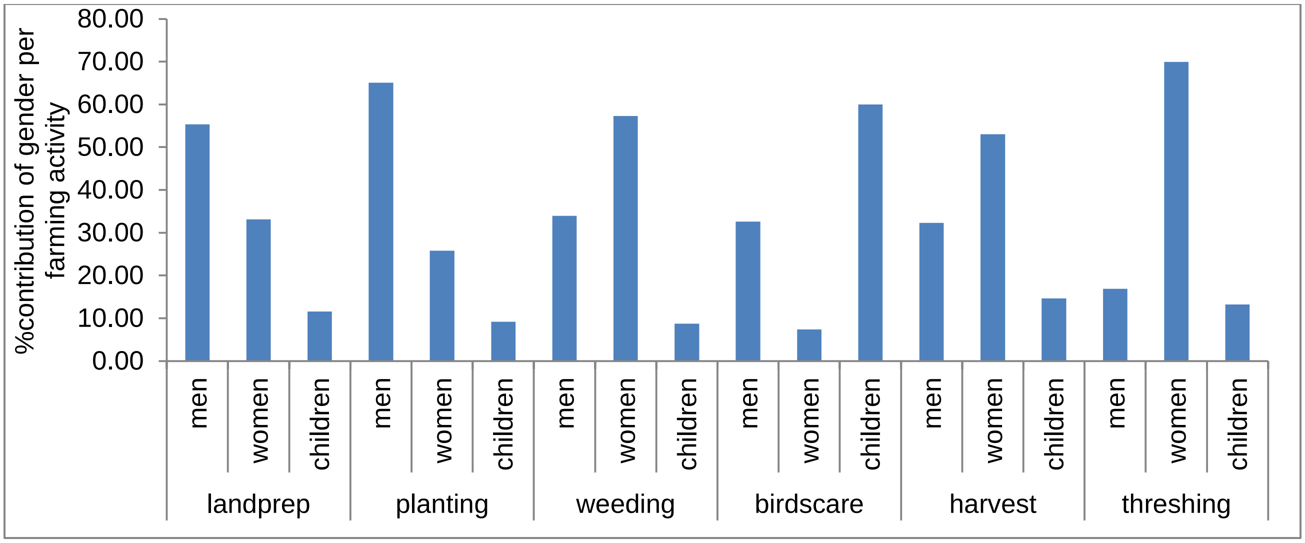

Figure 2.14: Farming activity by gender

2.5.2 Cropping systems, planting methods and season of planting

The farmers practiced mainly sole cropping system and seed broadcasting as the mode of sowing (Figure 2.15). During planting farmers may either first broadcast the seed in a weedy field and later plough or they first ploughed and then sowed the grain. The quality of fields determined how often and soon weeding was done but in this case majority (74.10%) weeded only once (Figure 2.16). However, because most farmers planted pearl millet in the second rainy season (Figure 2.17), weeds may not be too much of a problem since normally less rainfall is received in that season.

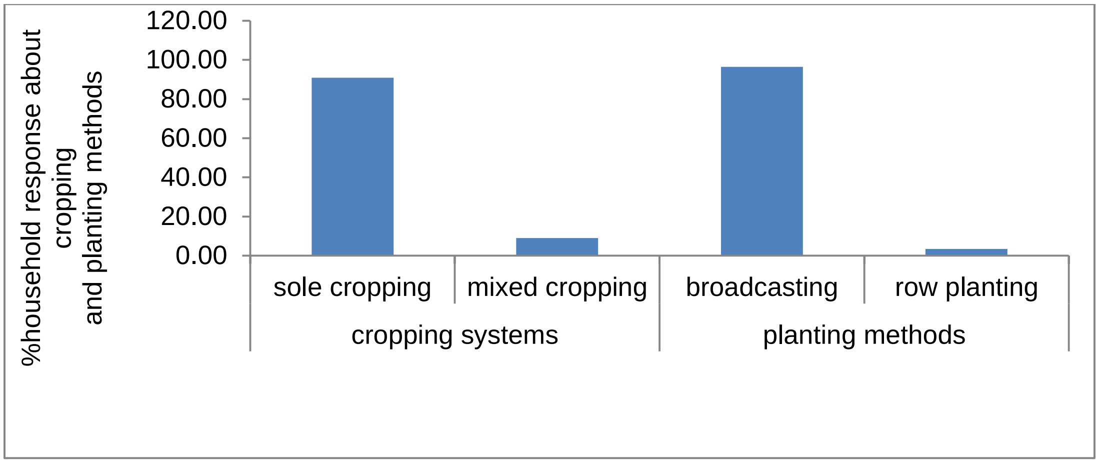

Figure 2.15: Cropping and planting methods

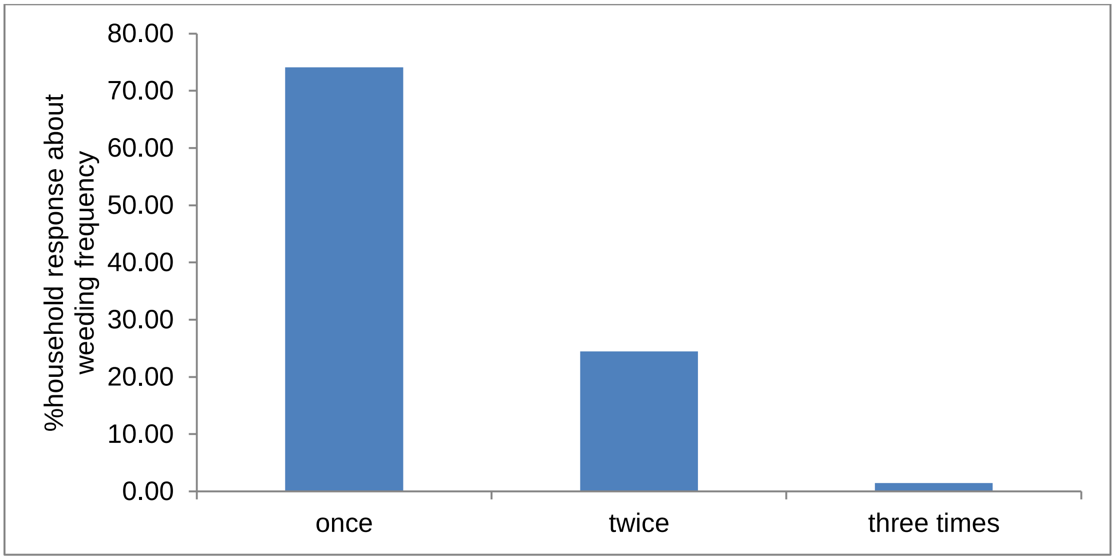

Figure 2.16: Weeding frequency

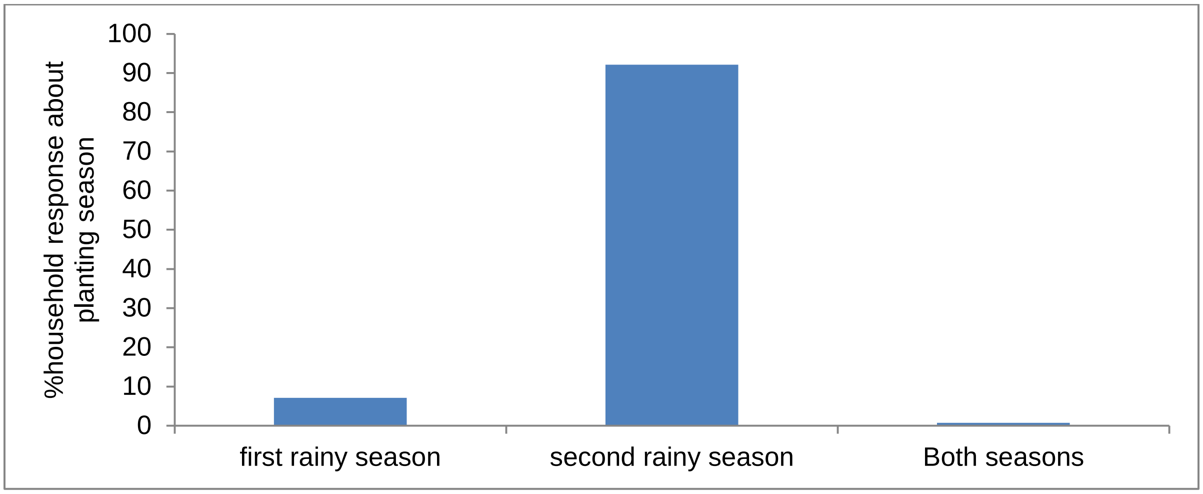

Figure 2.17: Seasons when pearl millet is planted

2.6 Farmers’ desirable and undesirable pearl millet traits

The pearl millet farmers listed the common traits of the pearl millet genotypes currently grown. The desirable traits, undesirable traits, and traits to be improved or introduced were also identified.

2.6.1 Traits of the farmers’ pearl millet genotypes

The genotypes grown by farmers were tall, early or late maturing, stay green, high yielding, big grain size, highly tillering, with small grains and strong thick stems. Being tall was the most common trait reported by farmers followed by white/grey coloured grains (Figure 2.18). However, unique to the northern region were traits like late maturity, small grain size and stay green which are associated with drought tolerance.

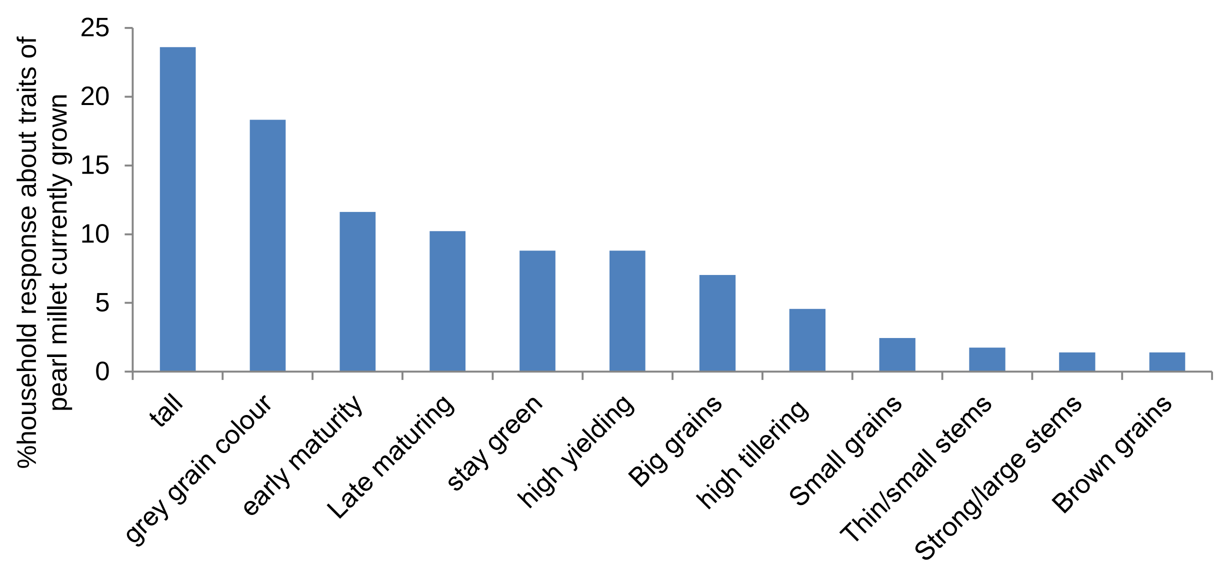

Figure 2.18: Traits of currently grown pearl millet

2.6.2 Desirable traits

The desirable traits were stay green, being tall, high tillering ability, high yielding, early maturity and ergot resistance (Figure 2.19). Traits like small grain size (Figure 2.20), thin/small stems and brown seed colour are among the traits in currently grown pearl millet which were not mentioned among the desirable traits; an indication that these traits may not be desirable.

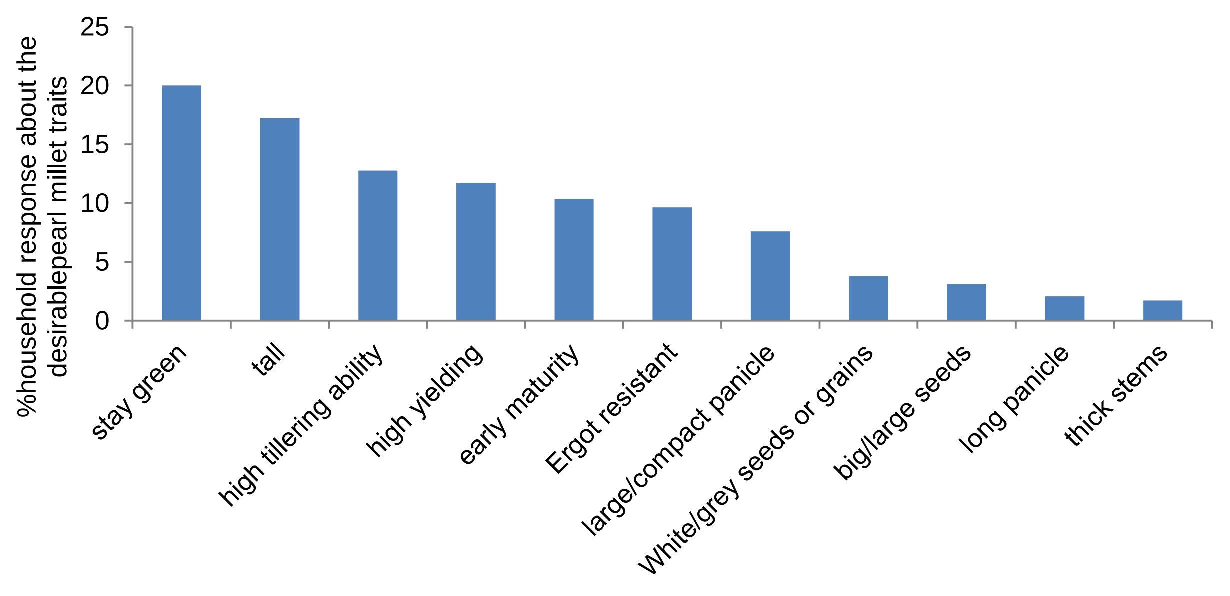

Figure 2.19: Desirable pearl millet traits

Figure 2.20: Variation in grain size of improved and farmers' unimproved genotypes

2.6.3 Undesirable traits in the farmers' pearl millet genotypes

The majority of the farmers reported ergot susceptibility as the most undesirable trait followed by varieties being short and susceptibility to rust (Figure 2.21). Low tillering ability, late maturity and sterile panicles also ranked high among the undesirable traits, especially in the northern region. Other less important undesirable characteristics are also shown in Figure 2.21.

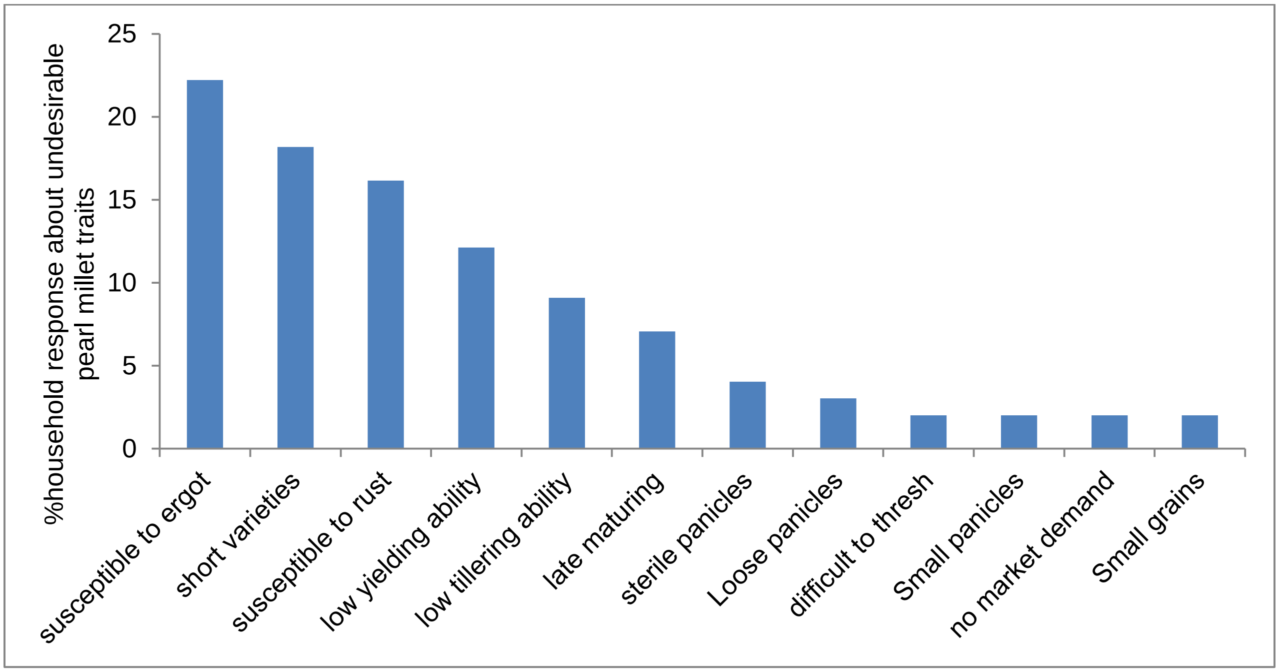

Figure 2.21: Undesirable pearl millet traits

2.6.4 Attributes to be introduced or improved with related information for pearl millet improvement

Farmers described the preferred ideal pearl millet plant they wanted to grow. They noted that the pearl millet varieties should have traits like being ergot resistant, high yielding varieties with large white grains and early maturing. However, other important factors to consider should be; introducing appropriate pesticides and providing stable market for grain, training in fertliser/manure use, and developing non-itchy varieties (Figure 2.22). Ergot susceptibility is one trait that farmers talked about mostly as the single most important determining factor leading to late planting in the second season and predisposing the crop to drought and rust.

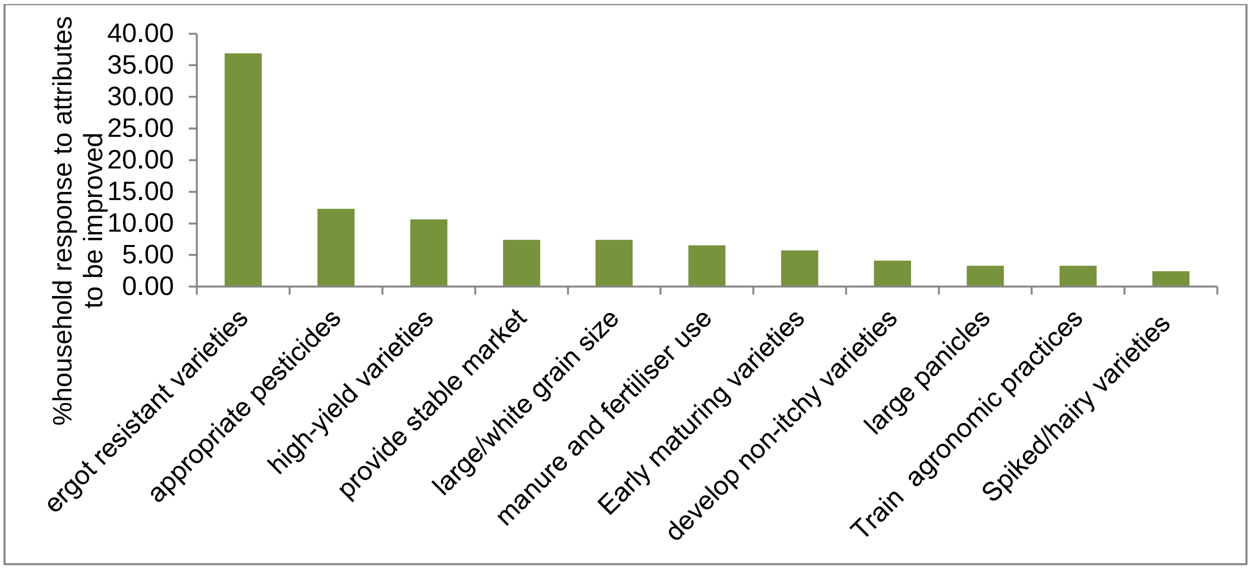

Figure 2.22: Pearl millet attributes to be introduced or improved

2.7 Pearl millet production and marketing constraints

2.7.1 Field constraints and control adopted strategies

Results in Figure 2.23 show that ergot (*Claviceps fusiformis*) (Figure 2.25) was the most important field production constraint (33%) reported by farmers followed by birds, weeds (not striga), rust and insect pests (Figure 2.26). Other field constraints included; low yield, animal destruction, drought (Figure 2.27) and itching during field operations like weeding and harvesting. In the field it was observed that smut was another disease affecting pearl millet but not mentioned by farmers. Although ranked rust was fourth, majority of (77%) of the farmers confessed that they did not know the symptoms of the disease, while 10% made a wrong diagnosis (Figure 2.24). Many farmers thought the rusty appearance was a trait unique to some genotypes. Results further showed that ergot and insect pests were more prevalent in northern region especially in Kitgum district whereas in the east they were more prevalent in Katakwi district than in Kumi district. Birds and weeds were reported mostly in the east than in the north.

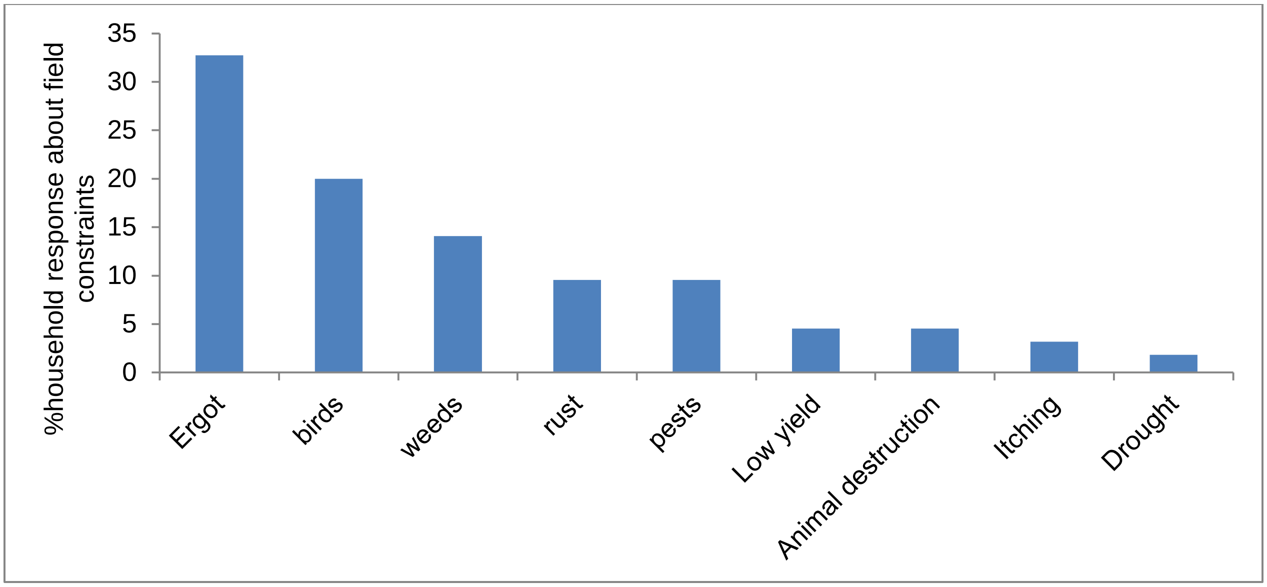

Figure 2.23: Pearl millet field production constraints

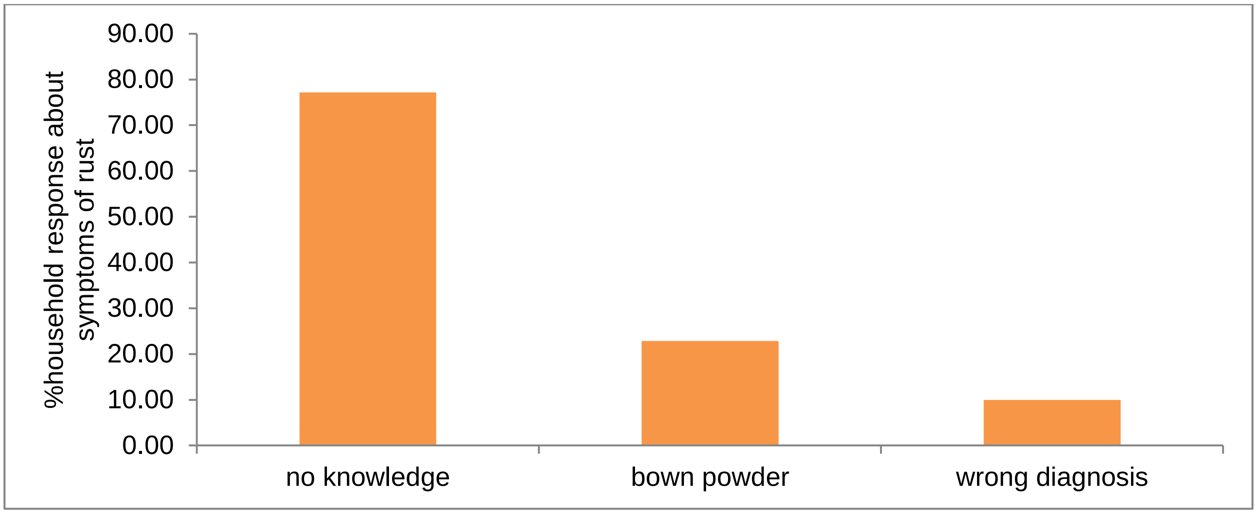

Figure 2.24: Knowledge about pearl millet rust symptoms

The majority (66%) of the farmers had no control strategy for ergot while 34% planted late in the second season to control the disease and birds. Drought effect resulted in panicles with low seed set as shown in Figure 2.28.

Figure 2.25: Panicles infected with ergot

Figure 2.26: Pearl millet destroyed by stem borer (inset)

Figure 2.27: Panicles with poor seed set due to drought

Crop damage by birds was ranked as the second most important field constraint destroying pearl millet at all grain development stages. The Quelea quelea birds were destructive at milk stage while the weaver birds destroyed the crop at all grain development stages. The birds were mainly reported in the eastern region especially in Kumi district. Most farmers had no control over the birds although some claimed that planting in the second rains minimised their effect. Early weeding was noted as the best control strategy against weeds whereas farmers had no control measures against rust and insect pests.

2.7.2 Storage and taste constraints and adopted control strategies

Storage constraints, which equally affected pearl millet farmers in eastern and northern regions, are shown in Figure 2.28. Rodents (36%), especially rats, were the most important storage constraint followed by rotting or moulding. Most farmers (38%) used poison to solve the constraint of rodents while many used traps (31%) and others (31%) did nothing to control rodents. Rotting and moulding was ranked second among the storage constraints. Majority of the farmers (67%) controlled rotting/moulding by proper drying of the grain before storage while 20% sold their grain produce as soon as it was threshed and 13% did nothing to control the loss. Other constraints with no control strategy included; insects (especially termites and ants), weevils and moths and poultry (especially chicken).

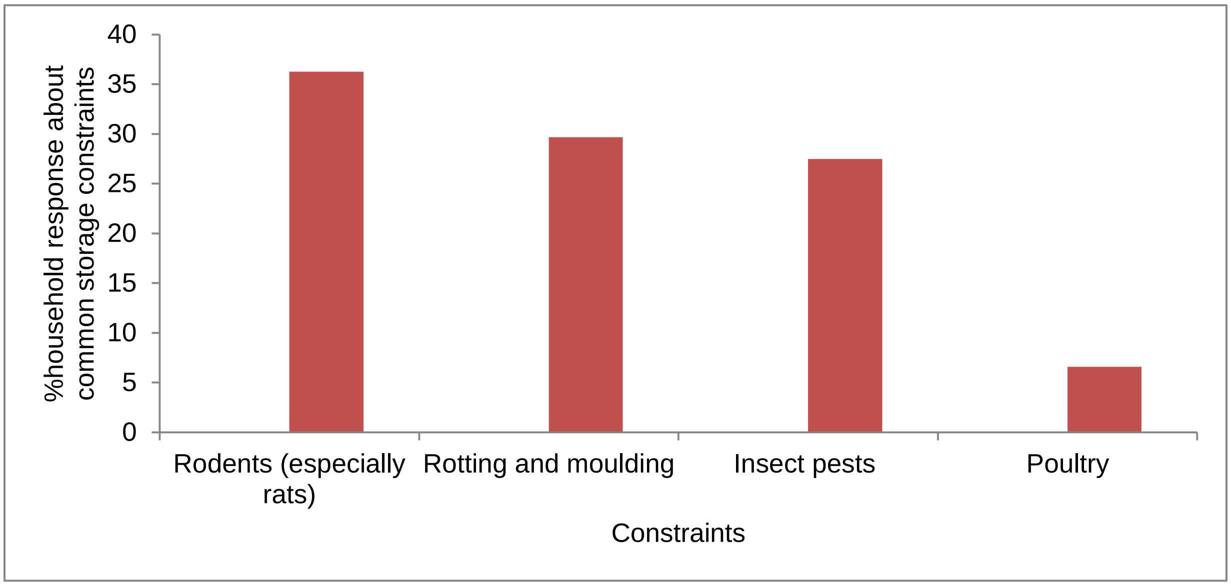

Figure 2.28: Storage constraints

2.7.3 Marketing constraints, control strategies and access to markets

The most frequently reported market constraint was lack of markets (29%), followed by low prices, and price fluctuation (Fig 2.29). Other market constraints of minor importance included; far away markets, high transport costs, and poor road conditions. To assess whether distance to markets was an important constraint, farmers estimated the distance and time taken to the nearest market. Majority (67%) indicated 0.03-1 km and taking 1-60 minutes. Others (30%) indicated covering 1-3 km in 60-120 minutes and the rest covering more than 3 Km and taking more than 120 minutes to the nearest market place.

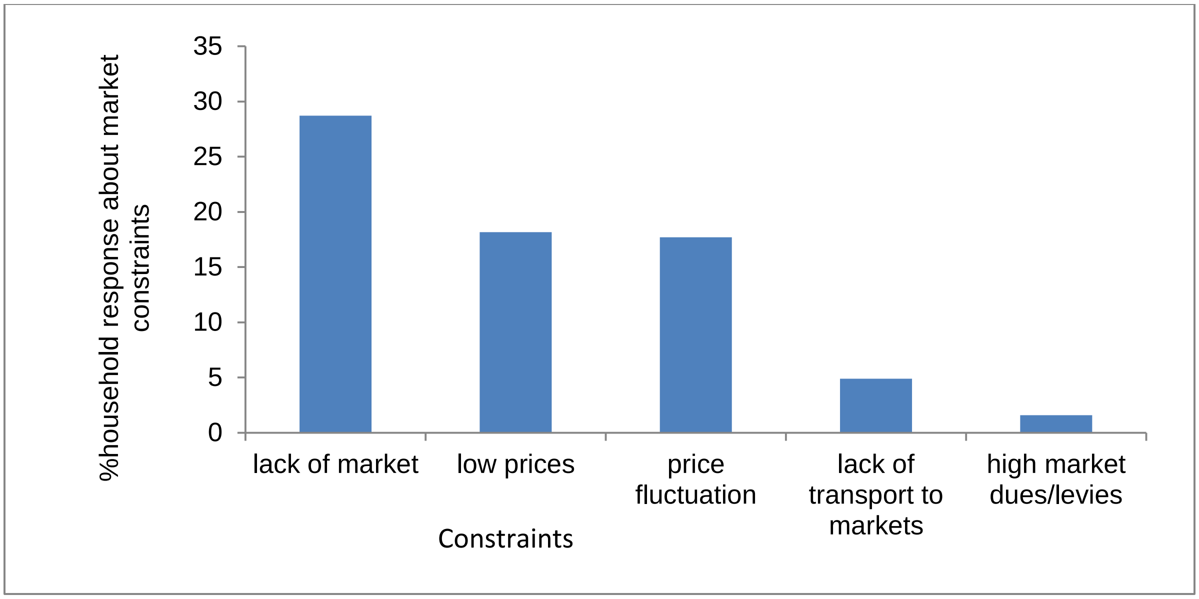

Fig 2.29: Market constraints

Some pearl millet farmers suggested possible solutions to the major marketing constraints but many had no idea (Table 2.5). Some farmers suggested government intervention by fixing prices for pearl millet annually (40%) and carrying out market research to create more markets for the produce in addition to forming farmer groups for collective marketing (Table 2.5). However, majority of the farmers had no idea (54%) on how to control the high market taxes although a few suggested carrying out market research before imposing the market taxes. Still on lack of transport to markets, majority of the farmers had no idea on how to fix the constraint but 31% suggested provision of bicycles at reduced prices and promoting buying on-farm to minimise the need for transportation to markets. About lack of markets for pearl millet grain produce, majority (47%) of the farmers suggested carrying out market search to create more markets for pearl millet although still many had no idea on how the constraint could be managed. Some farmers suggested longer storage of produce till good market is got but this had cost implications of investing in control of storage constraints. The solution to cheating by unscrupulous middlemen could be solved by using well calibrated weighing scales standardised by Uganda National Bureau of Standards (UNBS) but still the rest had no idea on how to solve the constraint.

Table 2.5: Percentage of household response about possible solutions to market constraints

Market constraints	Responses									
	No idea	Carryout market research	Gov't should fix prices annually	Road repairs needed	Using UNBS calibrated weighing scales	Providing bicycles at reduced cost	Promote buying on-farm at good prices	Form farmer groups for collective marketing	Open nearby markets in villages	Storage of produce for longer periods
Low prices for produce	28.00	16.00	40.00	4.00	0.00	0.00	2.00	10.00	0.00	0.00
High market taxes	53.85	46.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lack of transport to markets	34.62	0.00	0.00	0.00	0.00	30.77	11.54	3.85	19.23	0.00
Lack of market	41.67	47.22	2.78	2.78	0.00	0.00	2.78	0.00	0.00	2.78
Unscrupulous middlemen	20.00	0.00	0.00	0.00	80.00	0.00	0.00	0.00	0.00	0.00

2.8 Important production determinants of pearl millet

Age of spouse, average seed amount, average area planted, average distance to land cultivated with pearl millet, average person hours, distance to the nearest market, education experience of household head, education experience of spouse, household population, pearl millet production experience and walking time to the market (Table 2.6) were modeled to determine their effect on grain yield. The statistical test showed that the factors significantly ($p<0.05$) affected grain yield (Table 2.7). However, a stepwise reduced model (Table 2.8) showed that area planted to pearl millet, distance to market, number of years (experience) of pearl millet production, seed amount planted, age of household head and age of spouse were the important quantitative determinants with a significant direct effect on pearl millet grain yield. The coefficient of determination (R^2=26.4%) showed that the model accounted for less than 27% of the variation observed; an indicator that other factors may also contribute to variation in grain yield but not accounted for in the model. These may include agronomic issues, desirable traits, undesirable traits, constraints and qualitative factors.

Table 2.6: Factors used to model determinants of pearl millet production

	Statistics			
Factor	Minimum	Maximum	Mean	standard error
Average production (kg)	6.25	825.00	178.55	13.82
Average area of planted (ac)	0.17	5.00	0.78	0.05
age of household head (years)	21.00	89.00	45.39	1.20
Age of spouse (years)	12.00	70.00	34.91	1.03
Education experience of household head (years)	0.00	13.00	5.68	0.33
Education experience of spouse (years)	0.00	13.00	3.88	0.28
Experience of pearl millet production (years)	1.00	50.00	6.96	0.60
Number of people in household	1.00	15.00	7.47	0.23
Distance to the garden (km)	0.00	50.00	2.66	0.50
Seed amount planted (kg)	0.16	770.00	13.01	5.97
Average person hours	24.50	231115.00	2214.15	1716.30
Distance to market (km)	0.03	11.00	3.08	0.20
Walking time to market (mins)	1.00	240.00	60.15	3.89

Table 2.7: Analysis of variance for the reduced model

Source of Variation	DF	Sum of squares	Mean squares	F-value	P-value	%R2	%AdjR2
Regression	5	1106.27	221.25	9.11	.0001*	26.4	23.5
Residual	127	3083.62	24.28				
Total	132	4189.89					

*significant at α=0.05

The most important factor, with a positive effect, was the amount of land available for pearl millet cultivation (Table 2.8). Other important factors with positive effect were age of spouse (who comprised 87% female), followed by years of pearl millet cultivation. Results in table 2.8 further show that distance to the markets where the grain was sold or grain seed bought and age of the heads of households were significantly important but had a negative effect to pearl millet production. The rest were non-significant (Table 2.9) and hence excluded from the model.

Table 2.8: Most important quantitative factors in pearl millet production

variable	Coefficients	Standard. error	t-value	P-value
(Constant)	2.417	3.593	0.673	0.502^{ns}
Area planted (ac)	9.05	1.768	5.118	<0.001*
Age of spouse (years)	1.164	0.537	2.169	0.032*
Years of pearl millet growing	1.056	0.388	2.724	0.007*
Distance to market (km)	-0.424	0.145	2.925	0.004*
Seed amount (kg)	-0.21	0.009	-2.277	0.024**
Age of household head (years)	-1.548	0.531	-2.917	0.004*

Testing done at α=0.05 *significant≤0.05, **significant≤0.01, ns=non-significant p>0.05

Table 2.9: Factors excluded from the model

Excluded Factors	coefficient	standard errors	t-value	p-value
Number of people in household	1.034	0.986	1.048	0.297^{ns}
Education experience of household head (years)	0.224	0.488	0.459	0.647^{ns}
Labour hours (person hours)	-0.006	0.011	-0.557	0.579^{ns}
Education experience of spouse (years)	-0.049	0.470	-0.104	0.917^{ns}
walking time market (minutes)	-0.233	0.259	0.900	0.370^{ns}
distance to the garden (km)	-0.531	0.404	-1.314	0.191^{ns}

ns=non-significant at α=0.05

2.9 Discussion

2.9.1 Importance and utilisation of pearl millet

Indirect indicators of pearl millet importance that may affect production included frequency of cultivation, rank relative to other crops, and change in importance with time. The high frequency of cultivation in the last five years showed that pearl millet was important to the farmers; one of the reasons why almost all households grew the crop every year. Being the fourth most important crop and its demand projected to increase in the next five years further emphasizes the importance of pearl millet to the farmers. This is because it is a food security crop with diverse uses. Farmers noted that pearl millet was a food security crop partly because it was drought tolerant; a reason why it is grown in the drought-prone areas of the east, north and north-east. The same applies in other countries where the crop is grown. For example in southern Africa, pearl millet is the most important cereal in the hot zones of Namibia (Rohrbach, 2000) and also the most important in Sahel countries like Niger while in India it is grown on fringes of the Thar desert (Vadez et al., 2012). This makes pearl millet indispensable (Reddy et al., 2012) and the most important cereal in the dry areas (Ramesh et al., 2006); thus the best candidate for promotion in the drought-prone areas of Uganda to abate food insecurity.

In developed countries pearl millet is used as mulch, forage and feed ingredient in animal feed industries (Basavaraj et al., 2010). However, in developing countries the crop is used for food and the stover is fed to livestock (Kelley et al., 1996) or used for building or fuel for cooking (Vetriventhan et al., 2008). Like in other developing countries, in Uganda the crop is also used for food and stover is fed to livestock while grain is sometimes fed to poultry. In addition, the grain is also used as yeast in brewing, source of income and suppressing striga. Unlike in other developing countries, pearl millet is neither utilised as building materials nor fuel for cooking in Uganda. The grain also has diverse uses as food in Asian countries like India, unlike in African countries where use is limited. Thus, diverse use of pearl millet should be explored to promote wider cultivation and more production.

2.9.2 Use of improved inputs and technologies and access to social services

Improved inputs enhance grain yield. Improved seed, source of seed, access to and use of artificial inputs like fertilisers, pesticides, herbicides, soil and water conservation technologies and access to social and cultural services may define the production environment (Soleri et al., 2002) and thus promote adoption of new technologies (Amarender-Reddy et al., 2013). Majority of the farmers in Uganda grew local unimproved genotypes with grain yield of about 658 kg ha^{-1} under low input environment. Under comparable conditions this productivity is much higher than the 150-200 kg ha^{-1} realised in Namibia (Matanyaire, 1996) or 300-400 kg ha^{-1} harvested by many farmers in India (Khairwal et al., 2007b). However, under improved production environment (Yadav et al., 2011), involving use of artificial inputs, farmers in Uganda would increase productivity if they grew hybrids or improved open pollinated varieties (OPVs) (Shakoor and Naeem, 1999). Under optimal production conditions hybrids perform better than OPVs, yielding up to 4000-5000 kg ha^{-1} (Khairwal et al., 2007b). However, optimal growth conditions rarely exist in Africa, a reason why OPVs are mostly grown in Africa. Having no access to improved varieties is another reason why farmers in Uganda continuously grow unimproved seed. Thus increasing access to improved seed would lead to higher production and productivity of pearl millet in Uganda. This seed should be bought from certified seed dealers and not home saved or bought from open markets as is the case currently. In addition a proper seed distribution chain should be developed.

2.9.3 Agronomic factors

Agronomic factors like; time of planting, cropping system, plating methods, weeding frequency also affected pearl millet production and productivity. In Uganda, the production environment is dominated by planting once in the second rains, sole cropping, broadcasting seed and weeding once. In the second season, there is always less rainfall when compared with the first rainy season. Proper time of planting being important in determining the pearl millet yield (Hancock and Durham, 2010) where planting in the first season would be the ideal time of the year to achieve high yield. However, farmers plant late in the second season to minimise the effect of ergot disease and birds but exposing the crop to drought and late season diseases and pests. Winkel et al. (1997) reported that drought negatively affected grain yield, number of grains per tiller, single grain mass, number of productive tillers and booting time. In addition, effect of insect pests and diseases is pronounced under drought conditions (Ali et al., 2013). Thus, to achieve maximum yield farmers should plant early than late (Deshmukh et al., 2009) to avoid the combined negative effect of late planting.

Optimizing soil nutrient use is important to achieve high yield. Namara et al. (2005) reported that crop production systems had an effect on the rate of nutrient uptake in the soil. Latha and Singh (2003) observed that nitrogen and phosphorous uptake was higher in the sole cereal cropping system. In addition, yield advantage and improvement in soil nutrients have been reported in the pearl millet-legume cropping system where cluster been, cowpea and mung beans were components (Sarr et al., 2008; Singh and Joshi, 1994). Other beneficial legumes include; pigeon pea, green gram, soybean, groundnuts (Paraniappan and Sirivaman, 1996). However, in Uganda a sole cropping system is practiced and as such no optimal use of soil nutrient is achieved, a factor leading to low yield. Thus beneficial cropping systems, especially cereal-legume, should be promoted in Uganda for increased yield.

Sowing/planting methods also affect the pearl millet yield (Bakht et al., 2007). Farmers in this study adopted broadcasting method of planting. The method does not optimise grain yield compared with row planting (De Gautam and Kaushir, 1988). This is because under broadcasting there is uneven plant spacing which results in reduced number and size of panicles (Soman et al., 1987). In addition, it was observed in this study that broadcasting led to seed wastage since farmers planted 20 kg ha^{-1} instead of the recommended 2-5 kg ha^{-1} (Murty et al., 2007). Thus, farmers should adopt planting methods like row planting either on ridges or in furrows to minimise seed wastage and to obtain higher grain yield (Fromme et al., 2010).

Weeding under broadcast planting method is done manually and thus labour-intensive (Klaij et al., 1996); one of the reasons why farmers in Uganda weeded pearl millet once in a season. However, higher grain yield is obtained when weeding is done more than once (Tenebe et al., 2012). Weeding once is not an effective control of weeds; the result is all yield components of pearl millet being negatively affected. The number of grains per panicle is the most severely affected component under weed infestation (Limon-Ortega et al., 1998). Thus, Limon-Ortega et al. (1998) concluded that grain yield is enhanced under adequate weed control, narrow row spacing, use of nitrogen fertiliser and adequate availability of water.

2.9.4 Farmers' desirable traits and undesirable traits

Pearl millet local genotypes are defined by traits which may be desirable or not (Ndjeunga and Nelson, 2000). In Uganda, the genotypes currently grown had desirable and undesirable traits. Among the desirable traits stay green was the most important trait needed by farmers. This was followed by being tall, high tillering ability, high yielding and early maturity; all of which are related to drought tolerance. However, in countries like India, the order of importance differs; where high yield and good taste are the most important attributes for variety adoption (Asare-Marfo et al., 2010). High yielding ability, early maturity and large grains are among the traits with visual appeal (Khairwal et al., 2007a) used in plant breeding programmes to improve varieties

(Rai et al. 1999). In this study the traits ranked fourth and fifth respectively; an indicator that farmers may not focus on yield per se but stability under high-risk environments as also noted by Haussman et al. (2010). This is reflected in the farmers' most desirable traits being related to drought adaptability. Same observation was made by Brocke et al. (2003) where farmers selected varieties with stable yielded under stress conditions rather than those with high grain yield under favourable conditions. Thus breeding programmes should involve the target beneficiaries in problem identification in order to develop technologies for effective adoption.

2.9.5 Production and marketing constraints

The most important field production constraint reported by farmers was ergot disease followed by birds, weeds, rust and insect pests especially the stem borers, moths and red flour beetle. Smut and blast were other field constraints not mentioned by farmers but observed in the pearl millet fields (Lubadde et al., 2014). Though not seen to be important by farmers, smut is a potential cause of epidemics (Wilson et al., 1990) while blast has of recent become a serious disease in major pearl millet producing areas of the world (Sharma et al., 2013). Drought negatively affects vegetative and reproductive growth stages of pearl millet thereby reducing grain yield (Maqsood and Azam-Ali, 2007) by more than 45% (Fussel et al., 1991; Radhouane, 2013). Radhouane (2013) reported that drought effected grain yield through reduction of number of grains per panicle, plant height and panicle weight with yield reduction being severe in high-input environments. The yield components are also severely affected when drought sets in before and after flowering of the main panicle (Winkel et al., 1997). The probability that drought severely affected grain yield of pearl millet in Uganda is high because farmers always planted late as a coping strategy against ergot disease and birds, but predisposing the crop to drought and late diseases like rust and pests. Thus drought may be one of the major factors reducing grain yield, a reason 'stay green' was their most desirable trait.

Ergot is a widely distributed fungal disease affecting pearl millet mostly in Africa. In Uganda, the disease was first reported in 1980 (Rachie and Majmudar, 1980) but no studies establishing its effect on grain yield are reported although in West Africa it was reported as one of the important diseases causing considerable yield loss (Nutsuga et al., 2006). Ergot being the most important field constraint reported by farmers calls for immediate attention because the pathogen produces alkaloids that cause ergotism in humans and other animals when contaminated grains are consumed (Thakur and King, 1988).

Birds affect pearl millet right from germination stage through milk stage to physiological maturity. In some Asian countries like India the Blue Rock Pigeon, House Crow and Grey Francolin are the most destructive at germinating stage (Patel, 2011). However, in many African countries (Ali et al., 2013) and in Uganda the *Quelea quelea ethiopica* is the most destructive bird affecting peal millet. In Uganda it affects the crop at milk stage while the weaver bird affects the crop at soft dough and physiological maturity stages. The only coping strategy for bird control by farmers in Uganda is through planting late in the second rainy season because that is the time when cereals like rice, finger millet and sorghum are also in the field.

Other field constraints affecting pearl millet grain yield in pearl millet producing areas, but not observed in Uganda, are downy mildew and striga. The two constraints are some of the world's most destructive constraints of pearl millet (Kumar and Manga, 2010). In major pearl millet producing countries, downy mildew is the most important constraint of production (Thakur et al., 2008) which reduces grain yield by 60% (Thakur et al., 2011) under favourable conditions for disease development and spread (Thakur, 2008). On the contrary, striga was not reported as a constraint in Uganda. However, it is a major persistent threat (Kountche et al., 2013) that is widespread and destructive affecting pearl millet production and productivity in Africa (Wilson et al., 2004). A grain yield loss of up to 100% has been reported in susceptible genotypes under drought conditions (Ejeta, 2007; Amusan et al., 2008).

Farmers did not emphasize insect pests as serious yield constraints and thus could not name any pest. However, through observation in the farmers' fields and stored grain, conclusion was made that stem borer, red flour beetle, grain weevils and Indian meal moth were the common insect pests affecting pearl millet. The stem borer is also one of the major pests in West Africa (Nwanze, 1991) and India causing significant grain loss to pearl millet while the red flour beetle and Indian meal moth cause significant losses in stored grain (Yadav et al., 2011). In Uganda the stem borer was observed mostly in the northern region which is also characterised by drier conditions.

The most important market constraints were lack of market for pearl millet grain, low prices and price fluctuation of grain respectively. The distance covered by the majority of the pearl millet farmers to markets did not seem to be inhibitory and may be that is why it was ranked low among the market constraints. Much as Baba and Maina (2013) reported high transport costs as being the major constraint among traders, it ranked low among the farmers in Uganda; implying that those involved in the value chain may have different constraints. Low prices for grain was identified as a major factor limiting the commercial viability of pearl millet in Africa (Rohrbach, 2000). Rohrbach (2000) suggested exploring larger market opportunities to increase the marketability of pearl millet; a reason also suggested by farmers in Uganda. However, the market value chain of pearl millet in Uganda has not been studied as yet so the importance of the marketing constraints could not effectively be explored.

2.9.6 Modelling for important determinants of production

The important factors with significant effect on pearl millet grain yield were; area planted, seed amount planted, years of pearl millet growing, age of spouse, age of household head and distance to markets. All factors, except age of household head and distance to the markets, had a positive effect on grain yield. Area planted to pearl millet was the most important determinant of grain yield. The factor has also been reported as being important in determining agricultural profitability (Cornia, 1985) and technology adoption (Gabre-Madhin and Haggblade, 2001). Research findings by Feder et al. (1985) showed that farmers with large areas of land were likely to adopt advanced technologies such as irrigation although this may lead to decreased yield due to reduction in returns to scale (Cornia, 1985). On the contrary, majority of the farmers in this study generally had small areas of land cultivated to pearl millet which compares well with pearl millet farmers in other developing countries like Nigeria (Idrisa et al., 2012). This implies that they are less likely to adopt advanced technologies but most likely to operate profitably. This is based on findings by Nkonya et al. (2002) and Pender et al. (2004) that households in Uganda with less land were more productive and earned more crop income per unit area of land than those with more land available for cultivation. Thus input-intensive or land-saving technologies may be the best alternatives to increase productivity (Yaron et al., 1992). This implies that technologies that increase productivity, such as use of fertilisers, should be promoted rather than those that encourage cultivation of more land; as is currently the practice in Uganda (Pender et al., 2002). In addition, Singh and Joshi (2008) reported that to get positive returns, the marginalised small scale farmers should mainly use family labour; which was the case in this study where family labour accounted for more than 76% of the labour used in pearl millet cultivation. The years of pearl millet cultivation by a household had a positive significant effect on grain yield. This implies that the higher the experience of pearl millet cultivation the more the production. However, this may apply to the spouses but not the head of household as age of head of household had a negative effect on yield. To the contrary Mustapha and Dangaladima (2008) reported that years of pearl millet cultivation and age of the farmers were not important determinants grain yield in Nigeria.

Studies by Nkonya et al (2005) showed the importance of distance from the homestead to the cultivated land and market had a negative and significant effect on the use of farm resources and crop productivity. Results in this study concur with the Nkonya et al. (2005) findings as distance to the market had a significant negative effect on grain yield while that to the cultivated land had a negative effect but not significantly important. It implies that the further away the land for cultivation or the market the more farmers lose interest to grow the crop. Seed amount planted was important in determining grain yield but had a negative effect. This is because high seed rates result in high plant population which reduces number of tillers per plant (Newman et al., 2014). On the contrary, low seed rates result in high number of productive tillers (Newman et al., 2006); a component that contributes to high grain yield.

2.10 Conclusion

The study highlighted the pearl millet production characteristics in the four districts of Katakwi, Kumi, Kitgum and Lamwo. The high cultivation frequency, uses and rank relative to other crops indicate that pearl millet is important to the farmers. The crop is limited to use as food and source of income; with diverse use yet to be explored. However, the future for pearl millet is bright as farmers indicated continued cultivation as long as the production environment improves and market for grain is available. The production environment was typical of low input which does not lead to high productivity. Farmers hardly used modern technologies like improved seed, fertilisers, pesticide or any soil amendment strategy. The lack of a seed supply chain compels farmers to regularly plant unimproved genotypes, which are inherently low yielding and susceptible to ergot disease and drought. The low input environment, when combined with constraints and lack of a supportive social environment, leads to the observed low grain yield. In addition, the cultural myths attached to field disease constraints show that farmers did not have much knowledge about the diseases. Thus, farmers should be trained in disease identification. The social environment is also inhibitory to increased productivity because the farmers lacked access to credit, lacked training in keeping financial records, majority had no access to agricultural training or extension services; yet these are aspects also enhance adoption rate of new technologies. Further, factors of production like area planted, production experience and age of spouses enhanced yield, while some important factors like family labour and number of people in household were not limiting. Thus creating a supportive environment like training farmers and increasing access to new technologies like improved seed and use of fertilisers would promote increased productivity of pearl millet in Uganda.

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Chapter Three

Response of locally adapted pearl millet populations to modified S_1 progeny recurrent selection for grain yield and resistance to rust

Abstract

Pearl millet (*Pennisetum glaucum*) is an important cereal grown in semi-arid zones of Uganda mainly for food and income. However, productivity is constrained by many factors leading to a low on-farm grain yield of about 658 kg ha^{-1}. The main objective of the study was therefore to genetically improve the grain yield by increasing rust resistance of two locally adapted pearl millet populations (Lam and Omoda) through two cycles of phenotypic S_1 progeny recurrent selection. Evaluation of the cycles C_0, C_1 and C_2 was done in a randomised complete block design, three replications, three locations and one season. Results showed a significant variation in the two cycles for grain yield and rust resistance. A significant net genetic gain for grain yield of 72% and 36% was achieved for the Lam and Omoda populations, respectively. This led to grain yield of 1047 kg ha^{-1} from 611 kg ha^{-1} in Lam population and 943 kg ha^{-1} from 693 kg ha^{-1} in Omoda population. Significant improvement in rust resistance was also registered in the two populations with a net genetic gain of -55% and -71% achieved in Lam and Omoda populations, respectively. The selection resulted in reduction of rust severity from 30% to 14% in Lam population and 57% to 17% in Omoda population after two cycles of selection. A net positive genetic gain of 68% and 8% was also achieved for 1000 grain weight in Lam and Omoda, respectively. The traits with a net negative genetic gain in both populations were days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, flower-anthesis interval, plant height, leaf area and biological yield. In both populations, grain yield had a positive correlation with 1000-grain weight, while its correlation with rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, leaf area and biological yield was negative. Thus the genetic improvement of grain yield and rust resistance was achieved in two cycles of phenotypic S_1 progeny recurrent selection in the two local populations.

Key words: Pearl millet, recurrent selection, grain yield, rust, genetic gain, heritability

3.1 Introduction

Pearl millet is an important cereal worldwide ranking sixth after wheat, rice, maize, barley and sorghum (FAO, 2007). It is a multipurpose cereal crop performing well under both high input and low input conditions (Izge, 2006). In the high input environments, especially in developed countries, pearl millet is grown mainly for forage (Basavaraj et al., 2010) whereas in the low input conditions it is grown for food and stover used as cooking fuel, building material or fed to livestock (Vetriventhan et al., 2008). Under the low input conditions, the crop is adapted to environmentally marginalized conditions; the reason why it is grown by millions of poor people living in drought-prone zones where other cereals would hardly survive, and thus making it the world's hardiest crop (Reddy et al., 2012). In India and Africa, where more than 90% of the grain is produced, pearl millet is mainly grown in the driest areas like the Thar desert and the Sahel region (Vadez et al., 2012), respectively. In addition, in many zones of Africa the cereal is still grown in hot and dry environments. For example, in southern Africa, it is grown in the Namibia desert while in east Africa pearl millet is mainly grown in the hot and dry areas of central Tanzania (Rohrbach and Kiriwaggulu, 2001). The same applies to Uganda where the cereal is grown in the semi-arid to arid zones in the east, north and northeast.

Despite the multipurpose importance and resilience to adverse conditions, pearl millet on-farm productivity has remained low (400-600 kg ha^{-1}) (FAO, 1981) in the last two decades when compared with the potential of over 3000 kg ha^{-1} achieved under research environments (Rai et al., 1999). This is partly due to the numerous biotic constraints, among them being downy mildew, striga, blast, ergot, birds, smut and rust (Anderson et al., 2005; Baltensperger, 2002). However, in Uganda, all except downy mildew and striga have been reported to affect pearl millet yield. Rust is one of the major diseases reducing grain yield in Uganda (Lubadde et al., 2014) and worldwide (Bidinger et al., 2006; Lakshmana et al., 2010). It reduces yield and quality of grain and forage (Wilson and Gates, 1999; Timper et al., 2002). The grain yield is lowered through reduction of the leaf photosynthetic area while forage quality is lowered through reduction of digestible dry matter yield (Wilson et al., 1991).

However, the effect of rust on yield components may be minimised under controlled conditions; but being a low value crop, use of artificial inputs like chemicals is not viable for the economically marginalized farmers. The best option to control rust is therefore to breed for resistance (Singh, 1990). However, Tapsoba and Wilson (1996) observed that breeding for monogenic resistance had not been effective in controlling rust because of the multiple races of the pathogen that exist. Their suggestion was to develop varieties with many small-effect genes as the most effective approach to control rust. This may be achieved through recurrent selection because it leads to accumulation of many small-effects gene loci (Menkir and Kling, 2007). The result is an improved population with maintained genetic variability which enables response to further improvement (Baskaran et al., 2009). Recurrent selection has the advantage of increasing the frequency of favorable alleles and decreasing the frequency of unfavorable alleles through additive, partial dominance, dominance or over dominance gene effects (Hallauer, 1985).

Several recurrent selection schemes have been adopted by pearl millet breeders to improve populations. Through full-sib recurrent selection Bidinger et al. (2006) improved grain yield and stover quality while significant increase in grain yield and striga resistance was achieved through five successive cycles of both full-sib phenotypic recurrent selection and phenotypic S_1 progeny recurrent selection (Kountche et al., 2013). In addition, successful improvement in downy mildew resistance was achieved through full-sib and S_1 progeny recurrent selection by Weltzien and King (1995). Although full-sib recurrent selection has the advantage of the improved populations being in their natural highly heterozygous state, there is less probability to identify and move forward desirable recessive alleles compared to S_1 progeny recurrent selection (Kountche et al., 2013). In addition, the S_1 progeny recurrent selection is shown to be superior to either half-sib or full-sib recurrent selection schemes for improving grain yield, because it leads to increased panicle length and surface area (Dutt and Bainiwal, 2005). Basing on its superiority to other recurrent selection schemes, the phenotypic S_1 progeny recurrent selection scheme was adopted to improve two locally adapted pearl millet populations in Uganda. The objective of this study therefore was to improve resistance to rust of two locally adapted and commonly grown pearl millet populations through two cycles of phenotypic S_1 progeny recurrent selection; with the assumption that improved resistance would lead to increased grain yield. The objective was achieved through modified S_1 recurrent selection.

3.2 Materials and Methods

The study was conducted between 2012 and 2014 during which cycles C_1 and C_2 were developed through modified phenotypic S_1 progeny recurrent selection. The modification was that of rogueing plants with rust severity above 20% and leaving those with desirable rust severity level for recombination instead of planting another season for gene recombination. In addition, due to time constraints evaluation was done once but in three locations and three replications.

3.2.1 Experimental materials

The two experimental populations used in the study were selected from the predominantly pearl millet growing regions in northern and eastern Uganda. The populations were Lam from the north and Omoda from the east; named after the locations where they were collected for easy identification. They were both described by farmers as being low grain yielding and rust susceptible but drought tolerant with good taste. The farmers described the population from the east (Omoda) as early maturing and short (125 cm) while that from the north (Lam) was late maturing and tall and these were used to constitute C_0 for each population and consequently develop the C_1 and C_2 cycles through phenotypic S_1 progeny recurrent selection.

3.2.2 Developing the S_1 progeny recurrent selection cycles

The selection and recombination trials were done at the National Semi-Arid Resources Research Institute (NaSARRI) located in Serere district in eastern Uganda. At the Institute about 2000 C_0 plants were grown for each population and 500 plants (20% selection pressure) with rust severity of less than 20% were selected from each population and selfed. The selfed seed was bulked and half acre plots were planted for each population for recombination to form cycle one (C_1) seed. Rogueing was done before flowering leaving plants with less than 20% rust severity for recombination. The same process was adopted to form cycle two (C_2) where about 2000 plants were grown for each population and 500 plants with less than 20% rust severity were selected and selfed. The selfed seed was bulked and half acre plots established and rogueing done to leave plants with less than 20% rust severity for recombination to form C_2 seed. A summary of the recurrent selection scheme indicating the time frame is shown in the Table 3.1.

Table 3.1: Phenotypic S_1 progeny recurrent selection scheme for rust resistance

Season	Activity
First season Feb-June 2012	-Planting 2000 plants for each of the two selected populations (C_0 populations) and keeping remnant seed -Inoculation with rust urediniospores -Selecting (S_0) and self-pollinating 500 plants (S_1 progeny) showing low severity (10-20%) from each population and bulking the seed
Second season Aug-Nov 2012	-Planting 2000 plants of each population and inoculating with rust urediniospores -Rogueing was done before flowering to leave 500 plants with less than 20% rust severity for recombination. -Bulking of selected C_0 plants was done to form C_1 seed and remnant seed kept
First season Feb-June 2013	-Planting 2000 plants from each of the two C_1 populations -Inoculation with rust urediniospores -Selecting and self-pollinating 500 plants with less than 20% rust severity to form S_1 progeny
Second season Aug-Nov 2013	-Planting 2000 of S_1 progeny from the C_1 populations and inoculation with rust urediniospores -Rogueing was done before flowering to leave 500 plants with less than 20% rust severity for recombination -Bulking seed to form C_2 seed
First season Feb-June 2014	-Evaluating the C_0, C_1, and C_2 for each population in three hot spot environments (Serere, Kitgum and Katakwi)

3.2.3 Field evaluation of the experimental materials (C_0, C_1 and C_2)

The evaluation of the cycles C_0, C_1 and C_2 of the two populations was conducted in 2014 at three sites, namely Serere (1°32'N, 33°27'E, 1140 m.a.s.l) at the National Semi Arid Resources Research Institute (NaSARRI), Kitgum (03°13′N, 032°47′E, 969 m.a.s.l) at Ngetta Zonal Agricultural Research and Development Institute (NgettaZARDI) and Katakwi (01°54′N, 034°00′E, 1107 m.a.s.l) at Olera village, Katakwi subcounty in Katakwi district. All the three sites are characterised as rust hot spots and located in areas where pearl millet is predominantly grown. Table 3.2 shows rainfall received during the evaluation season.

The materials were planted in 5 m x 5 m plots in a completely randomised block design with three replicates and spacing of 60 cm x 30 cm. This resulted in each plot having 8 rows of 16 plants per row and a population of 128 plants per plot. Fertiliser application at rates of N 40 kg ha^{-1}, P 30 kg ha^{-1} and K 35 kg ha^{-1} applied in two splits (Khairwal et al., 2007), was adopted and hand weeding done twice in a season. For easy data collection and to establish the tillering ability of the populations, a wider spacing was adopted instead of the 60 cm x 15 cm recommended by Rai et al. (2009).

Table 3.2: Rainfall amount for the experimental sites during evaluation period

Site	Months in 2014							
	Jan	Feb	Mar	Apr	May	Jun	Jul	Total
Kitgum	3.2	38.3	127.3	60.0	229.7	229.8	113.5	801.8
Serere	26.8	3.8	178.6	158.8	257.1	75.8	47.2	748.1
Katakwi	14.5	5.9	73.7	145.6	161.7	74.9	93.6	569.9

Source: Department of Meteorology, Ministry of Water and Environment, Uganda

3.2.4 Data collection and analysis

Data were collected on at least 36 plants per plot. The data collected included; rust severity using the modified Cobb's disease severity scale (0-100%) at 50% physiological maturity, panicle length (cm), panicle girth (cm), panicle area (cm^2) calculated, 1000-grain weight (g), plant height (cm), days to 50% flowering, days to 50% anthesis, flower-anthesis interval calculated (days), days to 50% physiological maturity, total number of tillers, number of productive tillers, biological yield per plant, grain yield per plant, harvest index, leaf length and leaf breadth (cm) of third leaf from plant top, leaf area (cm^2) and grain productivity (kg ha^{-1}).

Data for each population was separately analysed using SAS computer software, version 9.2 (SAS Institute. Inc., 2012), where analyses of variance for the measured traits were determined based on Proc GLM. Pearson correlation analysis was done using Proc Corr to establish the relationship among all traits measured. The separate analysis done for each population was based on the model: Y = μ + cycle + site + rep(site) + site*cycle + random error

Where; Y = observed value; μ = grand mean; rep = replication effect with 3 levels; cycle = cycle effect with 3 levels (C_0, C_1 and C_2); site = site effect with 3 levels (Serere, Kitgum and Katakwi).

Response to selection was determined using the means of the cycles C_0, C_1 and C_2 for the two populations (Lam and Omoda).

Broad sense heritability was calculated using the formula H^2=Vg/Vp*100.

The gain per cycle was determined using differences between cycle means as:

($\mu C_2 - \mu C_0$), ($\mu C_2 - \mu C_1$), and ($\mu C_1 - \mu C_0$).

Where; H^2= Broad sense heritability, Vg= genetic variance,

Vp= phenotypic variance (Vg + interaction variances + estimated error mean square)

3.3 Results

3.3.1 Analysis of variance of the three cycles

The mean squares results for the two cycles (Table 3.3) of the two populations (Lam and Omoda) were significantly different ($p \leq 0.05$) for grain yield, rust and other selected agronomic traits. The main effects of cycle and site were the most important sources of variation. In population Lam, the main effects of cycles were significant ($p \leq 0.05$) for grain yield, flower-anthesis interval, number of productive tillers, panicle area, biological yield, harvest index and highly significant ($p \leq 0.001$) for rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, percentage of productive tillers, leaf area, 1000-grain weight, but no significant variation for total number of tillers. Additionally, the sites main effects were significant for days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity and biological yield, while cycles x sites effects were significant for grain yield, days to 50% flowering, panicle area, biological yield and highly significant ($p \leq 0.001$) for days to 50% anthesis.

Results in Table 3.3 further show that the cycles of population Omoda also had varying trait response. Except for flower-anthesis interval, panicle area and harvest index, the cycles had significant variation ($p \leq 0.05$) for grain yield, days to 50% physiological maturity, plant height, percentage of productive tillers, total number of productive tillers, leaf area, 1000-grain weight and highly significant ($p \leq 0.001$) for rust severity at 50% physiological maturity, days to 50% flowering and days to 50% anthesis. The site main effects were also significant ($p \leq 0.05$) for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, panicle area, leaf area and biological yield, but not significant for flower-anthesis interval, total number of productive tillers, percentage of productive tillers, 1000-grain weight and harvest index. The cycles x sites interaction effects were significant for grain yield, rust severity at 50% physiological maturity, days to 50% physiological maturity, total number of productive tillers and highly significant ($p \leq 0.001$) for days to 50% flowering and days to 50% anthesis. No significant effects were registered for flower-anthesis interval, plant height, percentage of productive tillers, panicle area, leaf area, 1000-grain weight, biological yield and harvest index.

Generally there was significant variation for total number of productive tillers in the Lam population while it was detected for Omoda population under main cycle effects and cycle*site interaction effects; and there was no significant variation for harvest index for Omoda population while it was detected for Lam population due to the cycle main effects and cycles x sites interaction.

3.3.2 Broad sense heritability estimates

The broad sense heritability estimates for the phenotypic S_1 progeny recurrent selection for the two populations (Lam and Omoda) under rust infection are presented in Table 3.4. The broad sense heritability was generally high for all the traits in both populations and the estimates for Omoda were generally lower than those of Lam. The estimates for population Lam showed that the heritability for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, flower-anthesis interval and days to 50% physiological maturity were 74%, 90%, 98%, 98%, 62% and 87%, respectively. The broad sense heritability estimates for plant height, productive tillers, percentage of productive tillers, panicle area and leaf area were 99%, 79%, 92%, 33% and 91%, respectively; while the estimates for 1000-grain weight, biological yield and harvest index were 94%, 47% and 63% respectively. The days to 50% flowering, days to 50% anthesis, plant height, percentage of productive tillers and leaf area had broad sense heritability estimates of more than 90% while relatively low estimates were recorded for panicle area and biological yield.

The heritability estimates for Omoda population for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, flower-anthesis interval and days to 50% physiological maturity were 57%, 93%, 79%, 79%, 6% and 47%, respectively. In addition, the heritability estimates for plant height, number of productive tillers, percentage of productive tillers, panicle area and leaf area were 59%, 72%, 39%, 4% and 42%, respectively; while those for 1000-grain weight, biological yield and harvest index were 52%, 60%, 21%, respectively. The flower-anthesis interval, panicle area and harvest index had relatively low heritability estimates for the Omoda population while rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis and number of productive tillers had heritability estimates of more than 71%.

Table 3.3: Mean squares for analysis of variance for Lam and Omoda populations

Source of variation	DF	Traits														
		GY	RUST	FLO50	ANT50	FAI	PSM50	PLH	TOT	PRO	PRT	PAR	LAR	1000GWT	BY	HI
Lam																
site	2	4809.28ns	21.61ns	17.12*	11.91*	0.53ns	36.84*	89.47ns	8.62ns	38.24ns	6.30ns	42.45ns	7149.27ns	0.91ns	0.02*	24.47ns
rep(site)	6	58293.61ns	21.26ns	0.45ns	1.78ns	1.80*	5.35ns	105.25ns	6.89ns	40.29ns	6.04ns	584.04ns	9471.32ns	0.35ns	0.02*	24.39ns
cycle	2	429526.41*	678.33**	1297.20**	1468.22**	5.39*	1694.16**	28549.41**	3.76ns	2804.68**	72.15*	1055.50*	352848.12**	36.14**	0.06*	121.87*
site*cycle	4	7528.26*	5.43ns	11.96*	15.09**	0.57ns	207.05**	29.80ns	1.99ns	123.14ns	2.56ns	1268.45*	11185.65ns	0.60ns	0.02*	11.79*
Error	12	78472.58	25.03	0.94	0.85	0.46	4.79	124.99	5.00	53.63	4.33	257.40	644.05	0.34	0.01	10.88
R-Square		0.57	0.84	0.90	0.90	0.82	0.99	0.98	0.55	0.91	0.80	0.78	0.91	0.95	0.82	0.79
%cv		34.03	24.95	10.01	9.21	16.27	13.40	39.92	17.03	10.65	22.85	9.41	8.87	8.52	16.24	35.94
Omoda																
site	2	74213.35*	206.25*	13.01*	12.44*	0.06ns	27.34*	377.87*	5.29ns	3.69ns	4.83ns	4059.42*	36607.64*	0.83ns	0.01*	56.06ns
rep(site)	6	8208.28ns	16.10ns	1.04ns	0.66ns	0.42ns	10.54*	33.46ns	1.48ns	535.89*	3.06ns	479.93ns	2395.63ns	0.37ns	0.01ns	29.73ns
cycle	2	150882.87*	4090.45**	180.21**	185.80**	0.07ns	82.93*	777.06**	54.43*	462.72*	4.22*	262.81ns	39324.63*	2.64*	0.02*	34.23ns
site*cycle	4	28904.22*	69.01*	32.05**	35.88**	0.52ns	52.77*	95.35ns	10.12*	31.87ns	5.59ns	688.70ns	10197.63ns	0.34ns	0.01ns	21.59ns
Error	12	5027.53	12.98	1.33	1.03	0.21	4.27	38.75	2.86	156.45	3.36	451.60	4745.50	0.86	0.01	23.78
R-Square		0.91	0.98	0.97	0.98	0.66	0.91	0.86	0.83	0.70	0.77	0.73	0.78	0.51	0.79	0.61
%cv		8.88	11.08	16.69	11.42	15.07	21.14	38.80	17.93	14.753	23.04	19.84	15.09	8.85	16.81	34.30

Testing done at α=0.05, *=significant p≤0.05, *=significant p≤0.0001, ns=non-significant p>0.05.
Key: : GY=grain yield (Kg plant^{-1}), RUST= rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), LAR=leaf area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (Kg plant^{-1}), HI=%harvest index

Table 3.4: Estimates for genetic variance, phenotypic variance and broad sense heritability for Lam and Omoda populations

Variance	Traits														
	GY	RUST	FLO50	ANT50	FAI	PSM50	PLH	TOT	PRT	PRO	PAR	LAR	1000GWT	BY	HI
Lam															
Vg	429526.41	678.33	1297.21	1468.22	5.39	1694.16	28549.41	3.76	72.15	2804.68	1055.50	352848.12	36.13	0.06	121.87
VP	578630.13	751.66	1327.67	1497.85	8.74	1948.18	28898.92	26.26	91.37	3059.98	3207.84	387091.41	38.34	0.13	193.40
(%H^2)	74.23	90.24	97.71	98.02	61.62	86.96	98.79	14.32	78.96	91.66	32.90	91.15	94.26	46.84	63.02
Omoda															
Vg	150882.86	4090.45	180.21	185.80	0.07	82.93	777.05	54.43	43.22	462.72	262.81	39324.63	2.64	0.02	34.28
VP	267236.24	4394.79	227.63	235.81	1.28	177.84	1322.49	74.18	60.06	1190.62	5942.46	93271.01	5.04	0.03	165.44
(%H^2)	56.46	93.08	79.17	78.79	5.49	46.63	58.76	73.38	71.96	38.86	4.42	42.16	52.31	59.85	20.72

Key: GY=grain yield (Kg plant^{-1}), RUST= rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), LAR=leaf area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (Kg plant^{-1}), HI=%harvest index

3.3.3 Mean performance of the three cycles

The means for grain for cycle two (C_2) of the two populations Lam and Omoda were significantly ($p \leq 0.05$) higher than those of cycles one (C_1) and cycle zero (C_0) while the C_1 and C_0 means had no significant differences across locations but C_1 performed better than C_0. However, varying trends were observed for other traits (Table 3.5). The population Lam had significantly lower rust severity at 50% physiological maturity and flower-anthesis interval means for C_2 and C_1 than C_0 while significant variation in cycle means was recorded for days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity and plant height. The C_2 means for Lam population were significantly higher for harvest index, 1000-grain weight, percentage of productive tillers and number of productive tillers than for C_1 and C_0 while C_1 and C_0 showed no significant differences in the means for the same traits. In addition, means for biological yield, leaf area, panicle area and plant height were significantly lower for C_2 when compared with those of C_1 and C_0 for the Lam population. For the Omoda population the means for rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis and plant height were significantly lower than those of C_1 and C_0 yet C_1 and C_0 means were also significantly different ($p \leq 0.05$). The Omoda population cycles had no significant variation in means for flower-anthesis interval, panicle area and harvest index. Cycles C_2 and C_1 did not significantly differ for total number of tillers, number of productive tillers and percentage of productive tillers while C_1 and C_0 were significantly different for the same traits as shown in Table 3.5.

Table 3.5: Means for selected traits of cycles for Lam and Omoda pearl millet populations

Traits	Lam					Omoda				
	C2	C1	C0	Standard error	$lsd_{(0.05)}$	C2	C1	C0	Standard error	$lsd_{(0.05)}$
GY	1047.10a	811.70b	610.60b	280.13	287.72	943.10a	761.18b	692.54b	70.91	72.83
RUST	13.45a	16.83a	29.89b	5	5.14	16.76a	23.99b	56.77c	3.6	3.7
FLO_{50}	85.22a	95.11b	109.12c	0.97	1	64.61a	67.22b	73.32c	1.15	1.19
ANT_{50}	88.74a	99.07b	114.14c	0.92	0.95	67.52a	70.29b	76.40c	1.02	1.04
FAI	3.52a	3.96a	5.02b	0.68	0.7	2.92a	3.07a	3.08a	0.46	0.47
PSM_{50}	141.10a	160.64b	167.55c	2.19	2.25	92.95a	97.63b	98.64b	2.07	2.12
PLH	222.52a	301.33b	331.63c	11.18	11.48	154.78a	163.27b	173.34c	6.23	6.39
TOT	13.82a	12.53a	13.06a	2.24	2.3	7.87a	8.16a	12.27b	1.69	1.74
PRT	12.37a	7.49b	7.45b	2.08	2.14	6.02a	7.51a	10.34b	1.83	1.88
PRO	89.11a	59.68b	57.51b	7.32	7.52	77.35a	85.35ab	91.65b	12.51	12.85
PAR	158.67a	179.99ab	172.63b	16.04	16.48	112.37a	107.46a	101.58a	21.25	21.83
LAR	675.81a	1025.73b	1011.34b	80.23	82.41	381.21a	482.63b	505.36b	68.89	70.76
1000GWT	9.14a	5.95b	5.44b	0.58	0.6	10.70ab	10.89a	9.87b	0.93	0.95
BY	0.42a	0.52b	0.59b	0.08	0.09	0.21a	0.20a	0.28b	0.04	0.04
HI	13.04a	8.77b	5.72b	3.3	3.39	14.31a	12.22a	16.12a	4.88	5.01

Means with the same letter are not significantly different at p=0.05

Key: GY=grain yield (kg plant^{-1}), RUST= rust severity at 50% physiological maturity, FLO_{50}=days to 50% flowering, ANT_{50}=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM_{50}=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^{2}), LAR=leaf area (cm^{2}), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index

3.3.4 Genetic gains from two cycles of S_1 progeny recurrent selection

Results in Table 3.6 show a positive net genetic gain for grain yield from cycle C_0 to cycle C_2 where 72% and 36% gain were achieved in two cycles of phenotypic S_1 progeny recurrent selection in Lam and Omoda populations, respectively. In addition, a positive net genetic gain was achieved in both populations for 1000-grain weight. For both populations, a desirable negative net genetic gain was observed for rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height, leaf area and biological yield. However, the net genetic gain for rust severity at 50% physiological maturity of -54% and -71% achieved in Lam and Omoda populations, respectively is desirable because it reflects an improvement in rust resistance in the two populations. Table 3.6 also shows contrasting net genetic responses for some traits. In Lam population a net positive gain was achieved for total number of tillers, number of productive tillers, percentage of productive tillers and harvest index. In contrast a net negative genetic gain was achieved in Omoda for the same traits. The panicle area was increased in Omoda population while decreased in Lam population.

Table 3.6: Genetic gain for Lam and Omoda pearl millet populations

	Lam population						Omoda population					
	Response to selection			Genetic gain			Response to selection			Genetic gain		
trait	C2-C1	C1-C0	Net response C2-C0	(C2-C1)/C0*100	(C1-C0)/C0*100	Net gain(C2-C0)/C0*100	C2-C1	C1-C0	Net response C2-C0	(C2-C1)/C0*100	(C1-C0)/C0*100	Net gain (C2-C0)/C0*100
GY	235.40	201.10	436.50	29.00	32.94	71.49	181.92	68.64	250.56	23.90	9.91	36.18
RUST	-3.38	-13.06	-16.44	-20.06	-43.70	-55.00	-7.23	-32.78	-40.01	-30.13	-57.74	-70.47
FLO$_{50}$	-9.89	-14.01	-23.89	-10.40	-12.84	-21.90	-2.62	-6.10	-8.72	-3.90	-8.32	-11.89
ANT$_{50}$	-10.33	-15.07	-25.39	-10.43	-13.20	-22.25	-2.77	-6.11	-8.88	-3.94	-8.00	-11.62
FAI	-0.44	-1.07	-1.50	-11.10	-21.22	-29.96	-0.15	-0.01	-0.16	-4.79	-0.40	-5.16
PSM$_{50}$	-19.54	-6.91	-26.45	-12.17	-4.13	-15.79	-4.68	-1.01	-5.69	-4.80	-1.02	-5.77
PLH	-78.81	-30.30	-109.11	-26.15	-9.14	-32.90	-8.48	-10.08	-18.56	-5.20	-5.81	-10.71
TOT	1.29	-0.52	0.76	10.25	-4.01	5.83	-0.29	-4.11	-4.40	-3.61	-33.46	-35.86
PRT	4.88	0.04	4.92	65.22	0.52	66.09	-1.49	-2.83	-4.32	-19.82	-27.34	-41.74
PRO	29.43	2.17	31.60	49.32	3.77	54.95	-8.01	-6.30	-14.31	-9.38	-6.87	-15.61
PAR	-21.32	7.36	-13.97	-11.85	4.26	-8.09	4.91	5.88	10.80	4.57	5.79	10.62
LAR	-349.92	14.39	-335.53	-34.11	1.42	-33.18	-101.42	-22.73	-124.15	-21.01	-4.50	-24.57
1000GWT	3.19	0.51	3.70	53.55	9.40	67.97	-0.19	1.02	0.83	-1.74	10.31	8.40
BY	-0.10	-0.07	-0.16	-18.505	-11.77	-28.08	0.01	-0.08	-0.07	3.35	-28.40	-26.00
HI	4.28	3.05	7.33	48.77	53.31	128.28	2.09	-3.90	-1.81	17.07	-24.19	-11.25

Key: GY=grain yield (kg plant^{-1}), RUST= rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), LAR=leaf area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index

3.3.5 Correlations for selected traits with grain yield

The results in Table 3.7 show that in the Lam population grain yield had a positive significant correlation ($p \leq 0.05$) with total number of productive tillers, percentage of productive tillers, 1000-grain weight and a highly significant ($p<0.001$) correlation with number of productive tillers. The results further show that grain yield had a significant negative correlation with rust at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height and leaf area. In addition, panicle area, biological yield and harvest index had no significant correlation with grain yield. Table 3.7 also indicates the rust severity correlation with other traits. It had a highly significant positive correlation with days to 50% flowering and days to 50% anthesis while plant height had a positive significant correlation with flower-anthesis interval, days to 50% physiological maturity, leaf area and biological yield and a negative significant correlation with number of productive tillers, percentage of productive tillers, 1000-grain weight and harvest index was observed. Table 3.7 further shows the correlation among the other traits.

The correlation results for Omoda population are in Table 3.8. The grain yield had no positive significant correlation with any trait, but a weak positive correlation with flower-anthesis interval, panicle area and 1000-grain weight. However, grain yield had a negative significant correlation with rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, total number of productive tillers, number of productive tillers, percentage of productive tillers, leaf area and biological yield. The rust severity at 50% physiological maturity had a positive highly significant correlation with days to 50% flowering, plant height, total number of productive tillers and number of productive tillers; its correlation with days to 50% anthesis, days to 50% physiological maturity, leaf area, biological yield and harvest index was also positive and significant. The days to 50% flowering had a positive highly significant correlation with days to 50% anthesis and total number of productive tillers while a positive significant correlation existed with days to 50% physiological maturity, plant height, number of productive tillers, leaf area and biological yield. The days to 50% anthesis had a positive correlation with days to 50% physiological maturity, plant height, total number of productive tillers, number of productive tillers, leaf area and biological yield. The flower-anthesis interval had no significant correlation with any trait while the days to 50% physiological maturity had a positive significant correlation with percentage of productive tillers. The plant height had a positive significant correlation with total number of productive tillers, number of productive tillers, panicle area, leaf area, biological yield and HI while the total number of productive tillers had a positive significant correlation with number of productive tillers, leaf area, biological yield and harvest index. The number of productive tillers had a positive significant correlation with percentage of productive tillers, panicle area, leaf area and biological yield. The percentage of productive tillers was positively and significantly correlated with panicle area and leaf area, but had a negative significant correlation with harvest index. The panicle area had a positive highly significant correlation with leaf area and 1000-grain weight, while the leaf area only had a positive significant correlation with biological yield.

Table 3.7: Pearson's correlation coefficients for Lam population

Traits	RUST	FLO50	ANT50	FAI	PSM50	PLH	TOT	PRT	PRO	PAR	LAR	GWT1000	BY	HI
GY	-0.44*	-0.61*	-0.61*	-0.44*	-0.50*	-0.51*	0.50*	0.77**	0.62*	-0.28ns	-0.46*	0.61*	-0.09ns	0.18ns
RUST	1.00	0.82**	0.82**	0.53*	0.66*	0.71**	-0.20ns	-0.48*	-0.51*	0.26ns	0.58*	-0.57*	0.34*	-0.44*
FLO50		1.00	0.99**	0.56*	0.84**	0.91**	-0.07ns	-0.60*	-0.77**	0.13ns	0.66*	-0.80**	0.57*	-0.64*
ANT50			1.00	0.63*	0.83**	0.90**	-0.06ns	-0.60*	-0.78**	0.15ns	0.67*	-0.80**	0.57*	-0.64*
FAI				1.00	0.46*	0.45*	0.08ns	-0.29ns	-0.47*	0.30ns	0.44*	-0.43*	0.33*	-0.31s
PSM50					1.00	0.85**	-0.25ns	-0.71**	-0.80**	0.06ns	0.68*	-0.89**	0.47*	-0.48*
PLH						1.00	-0.17ns	-0.68**	-0.83**	0.32ns	0.84**	-0.91**	0.53*	-0.62*
TOT							1.00	0.71**	0.19ns	-0.29ns	-0.18ns	0.35*	0.28ns	-0.33ns
PRT								1.00	0.82**	-0.27ns	-0.64*	0.80*	-0.17ns	0.20ns
PRO									1.00	-0.18ns	-0.77**	0.83**	-0.48*	0.54*
PAR										1.00	0.60*	-030ns	0.045ns	-0.22ns
LAR											1.00	-0.79**	0.42*	-0.54*
GWT1000												1.00	-0.34*	0.46*
BY													1.00	-0.82**

Correlation at α=0.05, *=significant $p<0.05$, **= highly significant $p<0.01$, ns=non-significant correlation $p>0.05$

Key: GY=grain yield (kg plant^{-1}), RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), LAR=leaf area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index

Table 3.8: Pearson’s correlation coefficients for Omoda population

Traits	RUST	FLO50	ANT50	FAI	PSM50	PLH	TOT	PRT	PRO	PAR	LAR	GWT1000	BY	HI
GY	-0.53*	-0.51*	-0.48*	0.20ns	-0.64*	-0.18ns	-0.20ns	-0.30ns	-0.23ns	0.14ns	-0.11ns	0.09ns	-0.28ns	-0.07ns
RUST	1.00	0.67**	0.66*	-0.03ns	0.33*	0.70**	0.70**	0.71**	0.14ns	0.21ns	0.50*	-0.33*	0.65*	0.37*
FLO50		1.00	0.99**	0.10ns	0.512*	0.54*	0.75**	0.66*	0.03ns	-0.12ns	0.34*	-0.49*	0.43*	-0.02ns
ANT50			1.00	0.21ns	0.51*	0.54*	0.73**	0.66*	0.01ns	-0.13ns	0.36*	-0.48*	0.40*	-0.024ns
FAI				1.00	0.05ns	0.14ns	0.11ns	-0.01ns	-0.19ns	-0.10ns	0.17ns	-0.02ns	-0.14ns	-0.02ns
PSM50					1.00	0.13ns	0.03ns	0.26ns	0.43*	-0.05ns	0.32ns	-0.07ns	0.25ns	-0.26ns
PLH						1.00	0.78**	0.80**	0.17ns	0.47*	0.70**	-0.06ns	0.44*	0.42*
TOT							1.00	0.85**	-0.10ns	0.15ns	0.43*	-0.29ns	0.35*	0.48*
PRT								1.00	0.43*	0.36*	0.59*	-0.21ns	0.38*	0.26ns
PRO									1.00	0.42*	0.39*	0.10ns	0.12ns	-0.36*
PAR										1.00	0.75**	0.42*	0.29ns	0.11ns
LAR											1.00	0.21ns	0.42*	0.11ns
GWT1000												1.00	-0.22ns	0.07ns
BY													1.00	0.14ns

Correlation at α=0.05, *=significant $p<0.05$, **= highly significant $p<0.01$, ns=non-significant correlation $p>0.05$

Key: GY=grain yield (kg plant^{-1}), RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^{2}), LAR=leaf area (cm^{2}), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index

3.4 Discussion

3.4.1 Analysis of variance of the three cycles

In this study, the results from the analysis of variance showed significant differences in grain yield, rust and other traits among the three cycles (C_0, C_1, C_2) in the two local populations evaluated in three locations. The variation in all the traits was due to the main effects of cycles in both populations except for the Omoda population where main effects of cycles were not significant for flower-anthesis interval (days), panicle area and harvest index as also reported by Bidinger et al. (2006). These traits also had very low broad sense heritability estimates and thus needed more cycles of S_1 progeny recurrent selection to increase heritability. The improvement is achieved without affecting important traits like yield and rust resistance (Bidinger et al. 2006; Pannu et al., 1996). The possibility of trait improvement through S_1 progeny recurrent selection was also reported by Kannan et al. (2013) in their study to quantify response to recurrent selection using SSR markers for grain yield and related traits. They further noted that the possibility was due to pearl millet being a highly cross pollinating crop with a high level of genetic variability for important traits among and within populations; exploiting the variability may thus lead to trait improvement and stability in a wide range of environments.

The significant main effects of cycles for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, total number of tillers, number of productive tillers, leaf area, 1000-grain weight, biological yield; and the non-significant effects of site and the cycle*site interaction for most traits indicates that selection for genetic improvement in diverse environments is possible for such traits. This shows the suitability of the phenotypic S_1 progeny recurrent selection to improve the quantitative traits, as proposed by Hallauer and Darrah (1985). The improvement can be achieved in diverse environments with minimal antagonistic interaction (Bidinger and Raju, 2000). Main effects of cycles were significant for rust severity in both populations; an indication that selection for rust resistance was effective in reducing rust severity in both populations. Similar observations were made by Tapsoba et al. (1997) when they improved rust resistance in pearl millet through four cycles of simple recurrent selection.

For the Lam population the cycles had a significant effect on grain yield where C_2 was better than C_1 and C_0. The effect of two cycles of phenotypic S_1 progeny recurrent selection led to a net increase in grain yield of 436.50 kg ha^{-1}. The main effect of sites had no significant effect on grain yield for the Lam population; an indication that the sites were not important in determining the performance of the cycles. However, the site x cycle interaction significantly varied showing that G x E had an effect and was important in determining the realised yield and thus site specific selection was important for grain yield improvement. Similar observations were reported by Dutt and Nirania (2005). The observed increase in grain yield was due to a cumulative improvement in 1000-grain weight, increase in total number of tillers and productive tillers, increase in percentage of the productive tillers and increase in harvest index realised through the cycles of the S_1 recurrent selection. The positive significant effects of these traits and a significant reduction in rust severity led to the increase in grain yield realised in C_2 in the Lam population as a result of the phenotypic S_1 progeny recurrent selection.

In the Lam population cycles reacted differently to rust infection where C_2 had the lowest final disease severity score of 13.5% at 50% physiological maturity, leading to a net negative genetic response of -16.4% and net genetic gain of 55.0% rust reduction. The main effects of sites and cycles x sites interaction were not important for improvement of rust resistance. This may imply that the observed reduction in rust severity was mainly due to genetic improvement in resistance due to phenotypic S_1 progeny recurrent selection and not due to disease escape. As shown by Tapsoba et al. (1997), rust resistance was increased through the increase of favourable genes as a result of recurrent selection which largely depends on the quality of the population being improved. The response of the two cycles to phenotypic S_1 progeny recurrent selection also had negative significant effects on many traits in the Lam population. There was a significant effect in days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, flower-anthesis interval, plant height, panicle area, leaf area and biological yield. This effect was also reported by Dutt and Nirania (2005) when they compared performance of three recurrent selection schemes on grain yield.

In the Omoda population, the same trend was observed for grain yield and rust resistance but the levels were different. The cycles, sites and cycles x sites effects had a significant effect on grain yield and thus important in determining grain yield unlike in the Lam population where sites were not. This highlights the importance of the quality of the original populations used in the S_1 progeny recurrent selection scheme; thus response may be population specific. The effect of phenotypic S_1 recurrent selection led to an increase in grain yield by 250.6 kg ha^{-1}, a

36.2% net genetic gain compared with the original population. However, the increase in grain yield was lower in the Omoda population compared with the Lam population; another indicator that the two populations probably had a varying genetic background. The realised increase in grain yield was due to the increase in the panicle area and a significant improvement in 1000-grain weight and improvement in rust resistance (genetic gain of -70.5%); since the phenotypic S_1 progeny recurrent selection had negative significant effects on the other yield-related traits. Unlike in Lam population, the site main effects had a significant effect on the performance of the cycles for grain yield, rust severity at 50% physiological maturity, plant height, panicle area, leaf area and biological yield; an indicator that the selection for cycles of the population should be site-specific unlike for the Lam population. In addition, the main effects of sites were not important for flower-anthesis interval, total number of tillers, percentage of productive tillers, number of productive tillers, 1000-grain weight and harvest index; showing that these traits could be selected for diverse environments. The cycle x site interaction was important for grain yield, rust severity, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity and total number of tillers; an indicator that genotype by environment interaction affected the traits and this further confirms that selection for these traits should be site-specific.

3.4.2 Broad sense heritability

Results in this study showed high broad sense heritability estimates for grain yield (H^2=74%), rust resistance at 50% physiological maturity (H^2=90%), days to 50% flowering (H^2=98%), days to 50% anthesis (H^2=98%), 1000-grain weight (H^2=94%) for the Lam population. For the Omoda population most traits also had relatively high broad sense heritability estimates; an indicator that the S_1 progeny recurrent selection was effective in improving these populations. However, the low broad sense heritability estimates achieved for flower-anthesis interval (H^2=6%), panicle area (H^2=4%) and harvest index (H^2=21%) shows that these traits needed more than two selection cycles for improvement; the low heritability being an indicator for a possibility for genetic improvement through recurrent selection as reported by Burton (1983). The high heritability estimates imply that for most of the traits the phenotypic variation observed was due to genetic effects rather than environmental or genotype by environment effects; an indicator as reported by Abulai et al. (2012) and Ezeaku and Mohammed (2006), that these traits may be improved in diverse environments. The high heritability estimates have been reported for many traits. Dutt and Bainiwal (2005) reported high heritability estimates of 80% and 53% for grain yield and panicle area, respectively. Similarly Virk (1988) reported high heritability estimates

(H^2=50-70%) for grain yield achieved through recurrent selection. In addition, high broad sense heritability estimates have been reported for panicle area dimensions (length and diameter) (Lakshmana and Guggari, 2001; Varu et al. 2005) while Kountche et al. (2013) reported a 71% heritability estimate for days to 50% flowering after five cycles of recurrent selection; although in this study more than 79% was achieved after only two cycles of recurrent selection. However, for grain yield, Bidinger and Raju (2000) reported low heritability estimates of 16% while Hash (1986) through literature review made an estimate of 20%. The high broad sense heritability for 1000-grain weight was also reported by Borkhataria et al. (2005) and Solanki et al. (2002) although Sachan and Singh (2001) reported moderate broad sense heritability for the same trait. Therefore findings from the current study are consistent with previous investigations.

3.4.3 Mean performance of the cycles

The mean grain yield for the cycles for the two populations differed significantly across locations; where C_2 performed better than C_1, and the mean for the original populations (C_0) being the lowest. This indicates a positive response to phenotypic S_1 progeny recurrent selection. Lam population had grain yield improved from 611 kg ha^{-1} to 1047 kg ha^{-1} compared with Omoda which had a mean grain yield improved from 693 kg ha^{-1} to 943 kg ha^{-1}. The improvement in grain yield shows that the phenotypic S_1 progeny recurrent selection was effective. Bidinger and Raju (2000) reported that, if high genetic variation exists in selected progeny, increase in grain yield may be due to recombination effects due to the cycles. However, in this study the highest grain yield attained was still low compared with the potential of over 3000 kg ha^{-1} (Rai et al., 1999) or 4154 kg ha^{-1} recorded by Kountche et al. (2013) after five cycles of recurrent selection. This implies that further improvement in grain yield may be possible through more selection cycles. But further selection for grain yield should be done concurrently with selection for rust resistance as the mean rust severity attained after two cycles was still above the resistance severity level of ≤ 10% (Singh et al., 1997) in both populations. In this study rust severity was reduced to 14% severity from about 30% recorded in the base population for Lam; while a reduction to 16.8% rust severity from 57% was observed in the Omoda population. This shows an improvement in rust resistance attained through the two cycles of phenotypic S_1 progeny recurrent selection; but still above the resistance severity level of ≤ 10% at which materials are said to be resistant (Singh et al., 1997).

3.4.4 Genetic gains per cycle

A net positive genetic gain for grain yield (72% and 36%) and 1000 grain weight (68% and 8%) was achieved, while a net negative genetic gain was attained for days to 50% flowering (-10% and -12%) and plant height (-33% and -11%), respectively, in Lam and Omoda populations after two cycles of phenotypic S_1 progeny recurrent selection. The results differ from those reported by Dutt and Bainiwal (2005) where a 20% genetic gain was achieved for grain yield through recurrent selection. Dutt and Bainiwal (2005) further reported a genetic gain of 21% for panicle area while in this study a net negative genetic gain of 8% and net positive genetic gain of 11% was recorded for Lam and Omoda populations, respectively. For 1000-grain weight, a high genetic gain of 68% was reported in Lam population while a much lower gain of 8% was achieved for Omoda population; showing variation in response to selection in the two populations. A comparable trend of results was reported by Govil et al. (1985) under the full-sib recurrent selection; but differing in magnitude of genetic gain. This further emphasises the importance of S_1 progeny recurrent selection as an effective scheme for improving pearl millet populations.

As expected a negative net genetic gain for rust resistance was achieved in both populations; indicating a genetic improvement for rust resistance of the populations through two cycles of phenotypic S_1 progeny recurrent selection. However, differences in net genetic gain were attained for the same traits in the two populations. A positive net genetic gain was achieved in the Lam population for total number of tillers, productive tillers, percentage of productive tillers and harvest index, while a net genetic loss was realised in the Omoda population for the same traits. In addition the two cycles of phenotypic S_1 progeny recurrent selection resulted in a net genetic loss in both populations for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height and leaf area; an indicator that some traits may be improved while a loss may be realised for others, as also observed by Govil et al. (1985). The loss in genetic gain may be attributed to the effect of inbreeding depression as a result of two cycles of selfing. The flower-anthesis interval has not received attention in pearl millet breeding improvement yet it is important in determining the number of grains per panicle, another yield related trait (Saini and Westgate, 2000). Saini and Westgate (2000) noted that reducing the flower-anthesis interval improves pollination rate in cereals which, results in high number of grains per panicle; an adaptation to drought conditions (de Wet et al., 1992) but may also promote undesirable selfing. In addition, the rapid change in genetic gain for grain yield and rust resistance and other traits after only two cycles of selection indicates that the two traits were controlled by a relatively large number of small-effects genes (Geiger and Heun, 1989) although Pannu et al. (1996) also reported that rust was controlled by both dominant and recessive genes in other breeding schemes.

3.4.5 Correlations for selected traits with grain yield

The significant correlation of grain yield with most traits showed a strong dependency of grain yield on other traits and thus selection for grain yield leads to a simultaneous change in the other yield-related traits as also observed by Vengadessan (2008). In both populations, grain yield had a positive significant correlation with 1000-grain weight, and negative significant correlation with days to 50% flowering and plant height; as also reported by Govil et al. (1985) under full-sib recurrent selection studies. This confirms that selection for these traits leads to reduced yield except for 1000-grain weight. The results further show a need to always establish the relationship and strength for grain yield with the contributing traits in order to determine the direction for improvement for a particular set of germplasm (Abuali et al., 2012).

However, varying levels existed between populations for the other traits. In the Lam population, grain yield had a strong significant association with all traits except panicle area, biological yield and harvest index where a non-significant association was recorded. The important traits with a positive contribution to grain yield were; number of productive tillers (r=0.77), percentage of productive tillers (r=0.62) and 1000-grain weight (r=0.61). Abuali et al. (2012) reported similar results for number of productive tillers and total number of tillers, but a significant negative correlation for 1000-grain weight. The variation in correlation sign may be due to the genetic and environmental sources of variation affecting the traits through different physiological mechanisms (Falconer, 1980). Grain yield had a negative significant correlation (r=-0.51) with plant height due to more nutrients being partitioned into the stem. This is contrary to findings by Vagadiya et al. (2010) who reported a significant positive correlation. Thus, simultaneous selection for the positively correlated traits may lead to increased grain yield. Traits with a significant negative association with grain yield in the Lam population were days to 50% flowering (r=-0.61), days to 50% anthesis (r=-0.61), plant height (r=-0.51), flower-anthesis interval (r=0.44), days to 50% physiological maturity (r=-0.50) and leaf area (r=0.46). A similar pattern was reported by Bashir et al. (2014) and da Costa et al. (2009) for association between grain yield and the above traits. Thus selection for these traits leads to low grain yield due to reduced time in grain filling as observed by de Rouw (2004) that late maturing varieties yielded more than early maturing varieties.

In addition grain yield had a desirable significant negative association with rust severity. This is an indication that increasing rust resistance would greatly increase grain yield in the Lam population. Leaf area had strong negative association with grain yield. This conforms to findings by van Oosterom et al. (2001) that age and area of the leaf relative to grain filling stage was important. The younger the leaves at grain filling the more they positively contributed to grain yield. In this study data for leaf area was collected on the third leaf from the top which at physiological maturity may no longer have a positive contribution to grain yield but becomes a sink for assimilates. Still in the Lam population rust had a positive significant association with days to 50% flowering (r=0.82), days to 50% anthesis (r=0.82), plant height (r=0.53), flower-anthesis interval (r=0.44), days to 50% physiological maturity (r=0.66), leaf area (r=0.58) and biological yield (r=0.34). This trend is expected because rust is mostly a late season disease (Taylor and Mims, 1991; Wilson, 1994); being more severe at later stages of crop development. The positive association between rust with leaf area and plant height is an indicator that selecting for a larger leaf area promotes rust development in susceptible genotypes.

The days to 50% flowering had a strong positive association with days to 50% anthesis (r=0.99), flower-anthesis interval (r=0.56) and days to 50% physiological maturity (r=0.84); indicating a strong dependency of these traits on days to 50% flowering. Plant height had a strong negative association with 1000-grain weight (r=-0.91); an indicator that high plant height becomes a sink at grain filling stage leading to low grain yield; this relationship may be desirable for forage production than grain yield. In addition a strong positive association of 1000-grain weight with number of productive tillers (r=0.80) shows that the more the productive tillers the higher the grain yield. This has also been reported by Bashir et al. (2014). The harvest index is a component of grain yield and biological yield. A strong negative correlation with biological yield (r=-82) indicates that lowering biological yield through reduction of plant height and leaf area would lead to increased grain yield and a higher harvest index. Almost the same pattern of association was observed in the Omoda population though significant grain yield was contrastingly correlated with panicle area; being positive in Omoda and negative in Lam. This shows that the two populations had contrasting genetic backgrounds and thus varying correlation of yield-related traits; another indicator that quality of the populations in S_1 progeny recurrent selection (Ferreira et al., 2006). However, it is desirable that selection for positive correlation of panicle area with grain yield is promoted, because this promotes higher grain yield under optimal conditions as reported by van Oosterom et al. (2006). The results in this study, in relation with reported findings, show that correlation of grain yield may have a strong link with some yield-related traits, like 1000-grain weight than others. This is an indication that selection specificity is important.

3.5 Conclusion

Significant increases in grain yield and rust resistance were achieved through two cycles of phenotypic S_1 progeny recurrent selection. Results showed that genetic variability existed for low grain yield in the rust susceptible populations and phenotypic S_1 progeny recurrent selection was effectively exploited to improve the yield and resistance to rust in the two local populations Lam and Omoda. The improvement in the grain yield and rust resistance are reflected in the significant desirable genetic gains for the two traits. The improvement of the two traits is further confirmed by the higher grain yield and lower rust severity achieved in the second cycle of selection. This is an indicator that through the two cycles of phenotypic S_1 recurrent selection genetic improvement for grain yield and rust resistance was achieved. However, higher broad sense heritability estimates were observed in the Lam population relative to Omoda population. This indicates that the two populations had differing potential for genetic improvement. In addition, low heritability was registered for traits like flower-anthesis interval, panicle area and harvest index in Omoda population; implying that these traits needed more cycles of recurrent selection to achieve better genetic improvement. Correlations between grain yield and other yield-related traits were established. A rapid change in genetic gain for grain yield and rust resistance and other traits, after only two cycles of selection, in the two populations indicates that the phenotypic S_1 progeny recurrent selection was effective in achieving genetic improvement of the two traits and thus improving rust resistance and grain yield of the two locally adapted populations Lam and Omoda. Results from this study also showed the response to recurrent selection depends on the genetic background of the population and the target traits.

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Chapter Four

Combining ability and heterosis for grain yield and rust resistance in pearl millet

Abstract

Pearl millet is an important dual-purpose crop for dwellers in semi-arid zones of Uganda. In such environments, it is constrained by unpredictable inadequate rainfall and rust disease which lowers yields. No studies have been conducted to determine the gene effects for yield and yield-related traits and rust resistance in these environments; yet this knowledge is important in improving grain yield and rust resistance. A North Carolina II mating design was adopted to study the genetic effects for rust resistance, grain yield and yield-related traits of improved pearl millet genotypes. The study was conducted in an alpha-lattice design at two sites, two seasons and two replications. A higher proportion of general combining ability (GCA) effect was observed for grain yield, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height, total number of tillers, number of productive tillers, percentage of productive tillers, panicle area, leaf area, 1000-grain weight, biological yield and harvest index. The specific combining ability (SCA) effect was predominant for area under disease progress curve while equal GCA and SCA effect was observed for number of productive tillers. Eleven crosses performed better than the best male parent and five crosses performed better than the best female parent for grain yield while all the fifteen selected best crosses performed better than all parents for area under disease progress curve. Ten crosses were more resistant to rust than the best male parent and all the crosses were more resistant to rust than the female parents. The additive gene action was predominant for grain yield, rust severity at 50% physiological maturity, days to 50% flowering, days to 50% anthesis, total number of tillers, percentage of productive tillers, panicle area, 1000-grain weight, biological yield, harvest index and leaf area. High better-parent heterosis was also observed for most traits including grain yield and rust resistance. The traits were also characterized by relatively low levels of narrow sense heritability and high broad sense heritability estimates.

Key words: Combining ability, genetic analysis, gene action, heritability, heterosis, rust

4.1 Introduction

Pearl millet is a staple crop in the crop-livestock production systems of the arid and semi-arid zones (Sharma and Pareek, 1993). The crop is grown worldwide mainly for food and forage (Girgi et al., 2006). Relative to other cereals, it performs well under stressful conditions of drought and acidic soils (FAO, 2004); though it also does competitively well in favorable environments (Bhatnagar et al., 1998; Christinck, 2002). In the stressful environments, farmers stick to growing low yielding landraces characterized by yield stability rather than high grain yield per se. It implies that minimizing risk to crop failure is a major priority than high grain yield (Kelley et al., 1996; van Oosterom et al., 1996). However, stress-adapted varieties with high grain yield have been developed through hybrid breeding (van Oosterom et al., 1996) but are not available in Uganda; a reason why low yielding rust susceptible genotypes (Lubadde et al., 2014) are perpetually grown. The disease causes high annual grain and forage loss (Wilson, 2000) in the production system. There is then a dire need to develop and provide improved pearl millet varieties with high grain yield and resistance to rust.

Grain yield improvement can be achieved through improving the local populations or developing improved varieties. However, to develop high yielding varieties, knowledge about genetic factors responsible for the inheritance of important traits is essential for a successful applied breeding programme. This is achieved through identifying the predominant genetic components (Vengadessan, 2008) and establishing the magnitude of their effects on trait expression. The genetic analysis of the improved materials should also be done to elucidate the combining ability of the lines in order to employ an appropriate crop improvement strategy. The combining ability assessment of the available materials helps to identify the best parent combinations that result in superior performing hybrids (Banziger and Cooper, 2001). The combining ability of inbred lines also helps to determine the potential value of the variety development programme (Legesse et al., 2009). Through combining ability analysis the nature of gene action (additive or non-additive) involved in expression of traits is also established. The additive gene action is related to general combining ability while specific combining ability is associated with non-additive genetic effects (Falconer, 1989)..

To assess combining ability an appropriate crossing design should be adopted. With the help of crossing designs, genetic variance analysis is used to characterise genotypes into those with additive or non-additive gene action. Commonly used crossing designs (Hallauer and Miranda,

1988) in pearl millet breeding include; diallel, line x tester, generation mean analysis, triple test cross, and the North Carolina mating designs. The diallel crossing design has been widely used in pearl millet breeding to assess nature of gene action for yield-related traits. The design has been used to assess type of gene action for grain yield (Bhadalia et al., 2012; Bhadalia et al., 2014), 1000-grain weight (Izge et al., 2007), phytate acid content (Satija and Thukral., 1985; Shanmuganathan et al., 2006), zinc and iron content (Rai et al., 2013; Velu et al., 2011), salt tolerance (Ali et al., 2006; Venkata et al., 2012,) and assessing gene action for napier grass x pearl millet crosses (Pereira et al., 2006). The line x tester has been adopted to assess the combining ability of inbred parents (Arulselvi et al., 2009) in order to establish their potential to develop superior hybrids for grain quality traits (Parmar et al., 2013). It has also been used to assess gene action and heterosis for micronutrients like zinc and iron content (Govindaraj et al., 2013), heterosis for early maturity (Kumhar, 2007), combining ability for dry fodder yield (Chaudhary et al., 2012) and male sterile lines (Rasal and Patil, 2003). Generation mean analysis and triple test cross designs have been used to assess nature of gene action for grain sink size (Vengadessan, 2008) and physiological traits in pearl millet (Singh et al., 1991).

The North Carolina II mating design has been widely used in genetic assessment to identify the best parents for hybrid development and identify superior hybrids for specific traits (Hallauer and Miranda, 1988). In pearl millet breeding the design has been used to assess gene action for downy mildew (Angarawai et al., 2008). Basing on the quality of the available improved lines tested for resistance to rust, the design was used to assess the nature of gene action predominantly governing the expression of the traits and other yield-related traits in Uganda. The objectives of the genetic analysis study were to establish i) the combining ability effects, ii) nature of gene action and iii) levels of heterosis for grain yield, rust resistance and selected yield-related traits.

4.2 Materials and Methods

The study was conducted between 2012 and 2014 during which crosses between improved rust resistant and susceptible varieties were made in a North Carolina II design mating scheme.

4.2.1 Experimental materials

In order to conduct genetic analysis for grain yield and rust resistance, 16 improved varieties (Table 4.1) were used as parents and crossed in a North Carolina II design. Six rust resistant male parents were crossed with ten susceptible female parents resulting in 60 F_1 crosses. In order to ensure synchromy during the crossing staggering of the planting dates was done basing on the days to 50% flowering, days to 50% anthesis and days to 50% physiological maturity. To avoid undesirable pollination the plant heads were coverd at boot stage. To minimise selfing which occurs due to stigmas that may emerge later after the crossing, the lower quarter and upper quarter of the panicle were cut off before threshing. In addition, roguing of off-types was done during evaluation.

Table 4.1: The parental materials used to make crosses

Experimental materials	Role in crosses	Rust reaction	Source
ICMV3771	Male	Resistant	ICRISAT-ESA
Manganara	Male	Resistant	UKZN
Okashana2	Male	Resistant	ICRISAT-ESA
ITMV8001	Male	Resistant	ICRISAT-WSA
SDMV94001	Male	Resistant	ICRISAT-ESA
Shibe	Male	Resistant	ICRISAT-ESA
Exbornu	Female	Susceptible	ICRISAT-WSA
CIVT9206	Female	Susceptible	ICRISAT-WSA
GGB8735	Female	Susceptible	ICRISAT-WSA
ICMV221	Female	Susceptible	ICRISAT-ESA
ICMV221white	Female	Susceptible	ICRISAT-ESA
KatPM1	Female	Susceptible	ICRISAT-ESA
OKOA	Female	Susceptible	UKZN
SDMV96053	Female	Susceptible	ICRISAT-ESA
Sosank	Female	Susceptible	UKZN
Okollo	Female	Susceptible	UKZN

4.2.2 Experimental sites and field layout

The crosses were developed at the National Semi Arid Resources Research Institute (NaSARRI)-Serere in the first rains of 2012 (2012A). The 10 female x 6 male resulted in 60 crosses and, including parents (16), 76 genotypes were evaluated at Serere and Kitgum. Both sites were characterised as hot spots for rust, with sandy soils and being in semi-arid zones. The Kitgum site is an extension of the Ngeta Zonal Agricultural and Research Development Institute (NgetaZARD) with GPS coordinates (03°13′N, 032°47′E, 969 m.a.s.l.). The Serere site is a location at the National Semi Arid Resources Research Institute (NaSARRI) with GPS coordinates (01°32’N, 033°27’E, 1140 m.a.s.l.). The crosses and parents were replicated twice and planted in a 4 x 19 alpha-lattice design. The materials were planted in 8 m x 5 m plots spacing of 60 cm x 30 cm. This resulted in each plot having 8 rows of 26 plants per row and a population of about 213 plants per plot. A nutrient regime of N 40 kg ha^{-1}, P 30 kg ha^{-1} and K 35 kg ha^{-1} recommended for seed production under rain fed conditions (Khairwal et al., 2007), applied in two splits, was adopted and hand weeding done twice in a season. A wider spacing was adopted, instead of the 60 cm x 15 cm adopted by Rai et al. (2009), for ease of data collection and to establish the tillering ability of the test materials. The plants were inoculated with freshly harvested uredospores from earlier planted susceptible genotypes.

4.2.3 Data collection

Data was collected on at least 36 randomly selected plants per plot using the ‘Descriptors of pearl millet’ (IBPGR and ICRISAT. 1993). The traits on-which data was collected are shown in Table 4.2.

Table 4.2: Traits and how they were determined

Trait	How it was determined
Panicle length, L_p (cm)	measured with a metre ruler from the panicle base to the tip
Panicle girth W_p (cm)	measured at the mid-point of the panicle using vannier caliper
Panicle area PAR (cm^2)	calculated from panicle length and width (π x L_p x W_p)
1000-grain weight (g)	measured using weighing scale
Plant height PLH (cm)	measured using measuring tape from the ground level to the top of the plant
Days to 50% flowering FLO_{50}	determined at plot level from day of planting to 50% stigma emergence
Days to 50% anthesis ANT_{50}	determined at plot level from day of planting to 50% anther emergence
Flower-anthesis interval calculated (days) FAI	as difference between ANT_{50} and FLO_{50}
Days to 50% physiological maturity PSM_{50}	determined at plot level from day of planting to 50% physiological maturity
Total number of tillers TOT	counted per plant
Number of productive tillers PRT	counted at physiological maturity of the main tiller
Percentage of productive tillers, PRO	number of productive tillers expressed as percentage of Total number of tillers (PRT/TOT*100)
Biological yield per plant, BY (kg)	determined by weighing all the harvested materials per plant
Grain yield per plant, G_pY(g)	determined by weighing the harvested grain from main and secondary tillers
Harvest index, HI	percentage of grain yield to biological yield (G_pY/BY*100)
Leaf length of third leaf from plant top, L_f (cm)	measured with meter ruler from leaf base to the apex
Leaf breadth (cm) of third leaf from plant top	measured with meter ruler at the widest part of the leaf
Grain productivity, GY (kg ha^{-1})	weighed at plot level and converted to yield per hectare
Rust severity	using the modified Cobb's disease severity scale (0-100%) at 50% physiological maturity

Where: π = 3.14

Table 4.3: Modified Cobb rust disease rating scale

Disease severity (%)	Description
0	Highly resistant=lower leaves being infected
1-10	Resistant=lower and upper leaves covered by pustules
11–20	Moderately resistant=lower and upper leaves covered with pustules
21–30	Susceptible=lower, middle and boot leaf, and stalk covered by pustules
>30	Highly susceptible=entire plant covered by pustules and at times may cause premature death

4.2.4 Calculation of AUDPC and data analysis

Area under disease progress curve for rust, AUDPC= $\sum [(x_{i+1} + x_i)/ 2] * [t_{i+1} - t_i]$ calculated according to Singh and King (1991) from severity data. The data was collected using modified Cobb's disease severity scale (Table 4.3) at five-day interval from day of first identifying the rust on the plant (Tooley and Grau, 1984).

Where: x_i is the cumulative disease severity or percentage of infected plants at the i^{th} observation; t_i is the time (days after planting) at the i^{th} observation; n is the total number of observations.

Data analysis was done using the SAS computer software, version 9.2 (SAS Institute Inc., 2012), with analyses of variance for the measured traits determined based on Proc GLM. Using the same model, the components of variance for estimating gene action were determined in SAS with Proc varcomp. The variances for the male (GCA_m) parents, female (GCA_f) parents and crosses (SCA_{mf}) were used as direct estimates for additive and non-additive gene actions for the parents and crosses, respectively as suggested by Dabholkar (1992). The variance components were also used to estimate the narrow sense and broad sense heritability for the traits. In the model, the parents, crosses and sites were fixed factors, while the random factors were; seasons, replications, blocks (nested within reps and seasons and sites) and the interactions of parents with seasons and sites. A modification of the Arunachalam (1974) fixed effects model was used to estimate the effects of the test materials across the two seasons and two sites.

The model: $Yijk = \mu + gi + gj + sij + e_k + (ge)_{ik} + (ge)_{jk} + (se)_{ijk}\ b_{(rek)} + (gi*gj*sij*e_k)eijk + Єijk$

where;

$Yijk$ = performance of the cross made with ith male line and jth female line in the kth environment

- μ = overall mean
- gi = effect of ith male line
- gj = effect of jth female line
- sij = interaction of the ith male line with the jth female line
- e_k = effect of the kth environment
- $(ge)_{ik}$ = interaction of g_i and e_k;
- $(ge)_{jk}$ = interaction of gj and ek
- $(se)_{ijk}$ = the interaction of sij and ek.
- $b_{(rek)}$ = effect of blocks nested in reps, season and location
- $(gi*gj*sij*e_k)eijk$ = four-way interaction of parents, crosses and sites
- $Єijk$ = random error

The general combining ability (GCA) effects for the male and female parents were determined using parental means inter se while the specific combining ability (SCA) effects were estimated using the means of the progeny (Singh and Chaudhary, 1985; Kurt and Evans, 1998). The GCA effects of the male and female parents were estimated as the difference between the grand mean and the mean of the parents for the trait. The SCA effects of each cross were calculated as a deviation of the cross mean from the grand mean of all the crosses adjusted for corresponding GCA effects of parents.

Calculation of the combining ability effects;

$$GCA_{male} = X_{male} - \mu;\ GCA_{female} = X_{female} - \mu;\ SCA_{male\ x\ female} = X_{male\ x\ female} - E(X_{male\ x\ female})$$

Where:

GCA_{male} and GCA_{female} are the general combining of the male and female parents, respectively

$SCA_{malexfemale}$ is the specific combining ability for the crosses

X_{male} and X_{female} are the means for male and female parents, respectively

μ is the overall mean,

X_{male}, X_{female} and $X_{male\ x\ female}$ are respective observed means for the male, female parents and the crosses,

$E(X_{\text{male x female}})$ is the predicted or expected mean value of the cross given by $E(X_{\text{male x female}}) = [GCA_{\text{male}} + GCA_{\text{female}} + \mu]$

The percentage of heterosis and better parent heterosis were computed using the means of the parents and the crosses as shown in the formulae;

Mid-parent heterosis (MP) = $[(X_{\text{male x female}} - MP) \times 100]/MP$
Better-parent heterosis (BP) = $[(X_{\text{male x female}} - BP) \times 100]/BP$
Where,
$MP = (X_{\text{male}} + X_{\text{female}})/2$

Broad sense heritability was calculated as: $\sigma^2_{(g)} / \sigma^2_{(P)} \times 100$
Narrow sense heritability was calculated as: $\sigma^2_{(A)} / \sigma^2_{(P)} \times 100$
Where; $\sigma^2_{(P)} = \sigma^2_{(A)} = \sigma^2_{\text{female(A)}} + \sigma^2_{\text{male(A)}} + \sigma^2_{\text{male x female}}$ + random error (all variance components determine from Proc varcomp anova table.
$\sigma^2_{(g)} = \sigma^2_{\text{female(A)}} + \sigma^2_{\text{male(A)}} + \sigma^2_{\text{male x female(D)}}$, $\sigma^2_{(A)} = \sigma^2_{\text{female(A)}} + \sigma^2_{\text{male(A)}}$

4.3 Results

4.3.1 Pooled analysis of variance

For grain yield, significant ($p \leq 0.05$) effects were observed for parents and crosses (Table 4.4). In addition, the site and season x male interactions also had significant effects on grain yield, while site and season x female interactions had no significant ($p > 0.05$) effect on grain yield. Table 4.4 further shows a relatively high coefficient of determination ($R^2 = 0.64$) although the coefficient of variance was relatively high. The site effects were highly significant for rust severity at 50% physiological maturity and AUDPC. Only female x season and female x site interactions were significant for rust severity. The main effects of male parents, site and season x male interactions were also significant. Significant effects were also observed for the three way interaction of male, site and seasons. Highly significant ($p \leq 0.001$) to significant ($p > 0.05$) variations were observed for the male main effects for all the traits (Table 4.4) with exception of panicle area, percentage of productive tillers, thousand grain weight, total number of tillers and number of productive tillers. For the female main effects all the traits were highly significant to significant except for 1000-grain weight and harvest index. The interactions between female and male parents were also significant for all the traits except for days to 50% anthesis, panicle area, 1000-grain weight, leaf area and harvest index.

Table 4.4: Analysis of variance mean squares for traits pooled across sites

Source of variation	DF	Traits related to reproductive phase							
		GY	RUST	AUDPC	FLO$_{50}$	ANT$_{50}$	FAI	PSM$_{50}$	PAR
Site	1	3458486.61*	60915.32**	4261084.66**	798.30**	123.57*	344.70**	698.27*	22043305.41**
Block(Season x site x rep)	8	7901438.01**	20212.08**	166698.27**	334.88**	532.88**	27.21**	753.18**	6177113.57**
Male	5	1989356.55*	8684.55**	102987.234*	90.90**	116.64**	2.80*	225.99**	138303.49ns
Female	9	1211649.81*	7961.73ns	29573.76ns	69.16**	91.22**	2.48*	192.37**	292797.32*
Female x male	44	1507374.04*	11684.94*	36526.30ns	23.21*	27.75ns	2.06*	51.24*	154816.01ns
Site x female	9	1865350.94ns	8576.45ns	24592.02ns	11.29ns	21.63ns	1.99*	94.64*	71555.90ns
Season x female	10	1656209.21ns	13264.62**	18311.32ns	59.51**	74.00**	2.67*	139.56**	807846.56**
Season x site x female	10	2496250.39*	13216.13**	27401.45ns	34.93*	35.51*	4.01*	129.23*	1344518.02**
Site x male	5	2211695.22*	5409.24**	183630.86*	17.35ns	32.27*	2.51ns	60.99ns	350640.57*
Season x male	5	1844002.59*	10299.35*	175076.06*	13.34ns	8.19ns	0.31ns	69.89ns	214997.17*
Season x site x male	5	1874388.21ns	12104.17ns	189210.51**	30.42*	24.13ns	1.45	78.57ns	166708.48ns
Site x female x male	44	1330138.85ns	11175.11ns	28751.53ns	22.04*	28.24*	1.59ns	60.98ns	310099.14**
Season x female x male	44	1679336.79*	10665.09*	23525.27ns	18.13ns	23.87ns	1.92*	61.93ns	199953.43**
Season x site x female x male	44	1518669.84ns	10247.94ns	32329.43ns	18.29ns	22.02ns	1.18ns	65.89ns	193304.52*
Error	233	1171949.2	10819.23	44161.85	15.47	18.73	1.38	64.02	160987.7
Total mean square		33716296	215235.98	5343860.5	1557.21	1180.65	398.25	2746.76	32626947
R-square		0.64	0.8	0.62	0.73	0.73	0.76	0.71	0.85
%CV		36.37	11.67	17.68	6.85	6.94	22.74	9.08	9.73

LSD testing at α=0.05; **=significant with p≤0.001, *=significant with p≤0.05, ns=non-significantKey: GY=grain yield (Kg plant^{-1}), AUDPC=Area under disease progress curve, RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^{2}), 1000GWT=thousand grain weight (g), BY=biological yield (Kg plant^{-1}), HI=%harvest index, LAR=leaf area (cm^{2})

Table 4.4: continued

Source of variation	DF	Traits related to vegetative phase							
		PLH	TOT	PRT	PRO	LAR	1000GWT	HI	BY
Site	1	18905.18**	703.36**	1.17**	44667.57**	670535.50**	214.13**	12691.96**	6.06**
Block(Season x site x rep)	8	10068.14**	20.12**	122.59**	13857.06**	201922.16**	206.88**	3339.71**	25.42**
Male	5	1182.15*	11.54ns	45.21ns	3032.60ns	90107.01*	1.76ns	641.56*	37.72ns
Female	9	2017.24*	14.49*	41.24*	3757.12*	47850.02*	6.73ns	558.35ns	31.52*
Female x male	44	1322.63*	10.26*	66.64*	4271.56*	50117.64ns	5.75*	915.58ns	20.69*
Site x female	9	1189.24ns	16.08*	59.72ns	3755.11ns	24633.81 ns	2.18 ns	550.22ns	16.68ns
Season x female	10	884.48*	12.05*	52.00ns	3125.42ns	70556.28*	12.15*	1146.23*	14.30*
Season x site x female	10	2621.20**	5.74ns	50.86*	3142.20*	143684.47**	11.24*	1127.345*	36.84ns
Site x male	5	1280.28ns	9.86 ns	56.45ns	2491.81ns	44563.826*	27.60**	169.37*	11.82ns
Season x male	5	899.84*	11.59ns	61.58ns	3141.75ns	87594.60*	41.17**	1239.76*	48.27*
Season x site x male	5	836.35ns	14.60*	82.03*	2271.54*	41205.20ns	34.73**	585.28*	9.86*
Site x female x male	44	1035.75ns	10.57*	55.92*	4441.56*	57943.27ns	5.68ns	757.46*	27.58ns
Season x female x male	44	1119.25*	7.23ns	55.18ns	3870.99ns	61417.44*	4.06ns	913.577*	23.73ns
Season x site x female x male	44	1596.45**	8.40ns	55.09*	3819.39ns	63255.42*	4.67ns	700.43*	22.45ns
Error	233	819.66	6.94	52.97	3847.65	45821.23	5.55	744.35	24.1
Total mean square		45777.82	862.79	383.11	103493.34	1701207.90	584.27	26081.15	357.04
R-square		0.71	0.67	0.65	0.63	0.69	0.77	0.72	0.66
%CV		17.96	18.1	19.41	20.76	14.52	16.75	27.72	29.62

LSD testing at α=0.05; **=significant with p≤0.001, *=significant with p≤0.05, ns=non-significant

Key: GY=grain yield (Kg plant^{-1}), AUDPC=Area under disease progress curve, RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (Kg plant^{-1}), HI=%harvest index, LAR=leaf area (cm^2)

4.3.2 General combining ability effects for the male parents

The estimates of general combining ability (GCA) effects for the male parents are shown in Table 4.5. The male parent ITMV8001 had the highest positive combining ability effects for grain yield. The same male parent had positive general combining ability estimate for days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height, total number of tillers and harvest index; but showed negative GCA effects for days to 50% flowering, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, biological yield and leaf area. ITMV8001 also had desirable negative GCA effects for area under disease progress curve (AUDPC) and rust severity at 50% physiological maturity. The male parents with the worst and negative GCA effects were ICMV3771 and Manganara and this was observed for grain yield. The two parents also had negative GCA effects for days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity and plant height. In addition, the two parents had positive GCA effects for days to 50% flowering and undesirable positive GCA, for AUDPC. The parent ICMV3771 also had positive GCA effects for rust severity at 50% physiological maturity, days to 50% flowering, total number of tillers, number of productive tillers, percentage of productive tillers, 1000-grain weight, harvest index and leaf area while the GCA effects were negative for Manganara except for panicle area.

Okashana2 and SDMV94001 had positive general combining ability effects for AUDPC and plant height; and negative GCA effects for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, percentage of productive tillers and leaf area. Shibe was respectively a good combiner for grain yield, panicle area, percentage of productive tillers, plant height, harvest index, number of productive tillers, days to 50% physiological maturity and days to 50% anthesis and the best general combiner for AUDPC followed by Okashana2. Only two male parents (Okashana2 and ITMV8001) had desirable GCA effects for AUDPC and rust severity at 50% physiological maturity. Three male parents (ITMV8001, SDMV94001 and Shibe) were good combiners for grain yield and only ICMV3771 and SDMV94001 combined well for 1000-grain weight. One male parent (SDMV94001) combined well for biological yield and only one parent (ICMV3771) had a positive and relatively high general combining ability effect for leaf area. In addition, most male parents had positive GCA effects for harvest index.

4.3.3 General combining ability effects for the female parents

The results for GCA effects for the female parents are shown in Table 4.6. All the female parents had desirable positive GCA effects for days to 50% flowering, days to 50% anthesis, number of productive tillers and 1000-grain weight biological yield and majority had desirable negative GCA effects for AUDPC and rust severity at 50% physiological maturity. However, many female parents also expressed undesirable negative GCA effects for grain yield, flower-anthesis interval, days to 50% physiological maturity, plant height, total number of productive tillers, percentage of productive tillers, panicle area, harvest index and leaf area. The highest GCA effect was registered in SDMV96053 for grain yield followed by Sosank for panicle area. Other female parents with desirable positive GCA effects were CIVT9206, GGB8735 and Sosank. Female parents with desirable negative GCA effects for AUDPC were GGB8735, SDMV96053, Sosank, KatPM1, Okollo and Okoa; while ICMV221white and GGB8735 were the worst combiners for the trait. Most female parents were good general combiners for rust severity at 50% physiological maturity but Okollo, GGB8735 and CIVT9206 were the worst general combiners for the trait. Relatively high desirable positive GCA effects were observed in CIVT9206 and ICMV221 for panicle area and leaf area. For the other traits the female parents had either low positive or negative GCA effects for most traits, as shown in Table 4.6.

Table 4.5: Estimates of general combining ability for male parents

Male parents	Traits															
	GY	AUDPC	RUST	FLO$_{50}$	ANT$_{50}$	FAI	PSM$_{50}$	PLH	TOT	PRT	PRO	PAR	1000GWT	BY	HI	LAR
ICMV3771	-142.38	2.33	9.95	1.27	-0.65	-0.09	-0.58	-0.37	0.18	0.71	6.85	-39.42	0.28	-0.07	0.39	63.68
Manganara	-143.79	7.79	-7.15	0.52	-1.19	-0.02	-2.27	-7.15	-0.01	-0.69	-4.93	55.11	-0.18	-0.40	-2.99	-31.06
Okashana2	-75.12	53.87	-11.02	-1.69	-0.26	-0.02	-0.9	5.18	-0.56	-1.01	-3.63	27.92	-0.06	-0.39	-3.04	-5.16
ITMV8001	248.32	-21.92	-9.31	-0.15	2.33	0.37	2.77	0.93	0.52	-0.04	-4.11	-21.71	-0.03	-0.40	0.05	-2.31
SDMV94001	19.17	13.42	8.16	-2.17	-0.32	-0.10	0.74	0.04	0.17	0.80	-2.82	-45.51	0.17	1.30	4.16	-15.30
Shibe	93.79	-55.48	9.40	-0.77	0.09	-0.12	0.22	1.40	-0.3	0.23	8.65	23.59	-0.16	-0.07	1.42	-9.86

Key: GY=grain yield (kg plant^{-1}), AUDPC=Area under disease progress curve, RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index, LAR=leaf area (cm^2)

Table 4.6: Estimates of general combining ability for female parents

Female parents	Traits															
	GY	AUDPC	RUST	FLO$_{50}$	ANT$_{50}$	FAI	PSM$_{50}$	PLH	TOT	PRT	PRO	PAR	1000GWT	BY	HI	LAR
Exbornu	-113.93	2.68	-9.57	1.42	1.80	0.42	1.14	4.11	-0.65	-1.10	-1.48	-25.15	0.29	0.38	-4.41	-10.74
CIVT9206	28.33	30.03	15.19	0.67	0.69	-0.04	2.49	4.12	-0.17	0.81	-8.02	31.61	-0.86	1.28	4.04	15.02
GGB8735	31.50	-30.61	19.63	-1.54	-1.66	-0.18	-0.31	-13.04	0.01	1.55	17.78	-92.60	-0.26	2.83	4.31	-51.24
ICMV221	-94.73	25.08	-8.46	0.01	0.01	-0.06	-0.65	-2.63	-0.47	-0.93	-2.45	33.65	0.06	0.37	-2.93	59.00
ICMV221white	-24.43	32.72	-7.84	-2.02	-1.93	0.03	-3.80	-1.61	0.40	0.03	-1.25	-76.15	0.35	0.47	-1.27	-28.01
KatPM1	-54.45	-8.85	-7.04	-0.62	-1.01	-0.45	-1.44	-2.68	-0.46	-0.94	-4.99	51.20	0.31	0.34	-0.11	-15.98
Okoa	-32.70	-3.57	-6.89	0.15	0.63	0.34	-0.19	5.27	0.67	0.33	-1.16	5.39	0.60	0.41	-2.51	12.20
SDMV96053	380.89	-20.13	-6.76	-0.65	-1.29	-0.08	-1.40	2.82	1.04	0.43	-2.89	-46.79	-0.31	0.37	-2.29	-13.03
Sosank	44.28	-19.43	-9.99	1.35	1.40	-0.01	0.84	-4.60	-0.22	-0.92	-8.42	176.65	0.04	0.35	-0.75	-19.46
Okollo	-164.77	-7.88	21.79	1.26	1.35	0.04	3.27	8.29	-0.16	0.74	12.93	-57.85	-0.18	1.04	5.91	52.24

Key: GY=grain yield (kg plant^{-1}), AUDPC=Area under disease progress curve, RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tillers, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index, LAR=leaf area (cm^2)

4.3.4 Specific combining ability effects for fifteen best selected crosses

Results for the specific combining ability (SCA) for grain yield, rust and other selected traits are shown in Table 4.7. The selected best fifteen crosses, all had desirable positive SCA effects for grain yield, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, total number of tillers, plant height, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, harvest index and leaf area. The cross 4 x 14 (ITMV8001 x SDMV96053) showed the highest SCA effect for grain yield while crosses 1 x 9 (ICMV3771 x GGB8735) and 5 x 16 (SDMV94001 x Okollo) exhibited the highest desirable negative SCA effects for AUDPC and rust severity at 50% physiological maturity, respectively. In addition, desirable negative SCA effects were observed for AUDPC and severity at 50% physiological maturity for the other crosses.

Table 4.7: Estimates of specific combining ability effects for the best fifteen crosses

Crosses and traits															
Cross	GY	Cross	AUDPC	Cross	RUST	Cross	FLO_{50}	Cross	ANT_{50}	Cross	FAI	Cross	PSM_{50}	Cross	PLH
4x14	1941.46	1x9	-149.45	5x16	-38.36	5x7	3.98	5x7	4.36	6x13	1.00	5x8	5.03	3x11	24.90
3x11	559.10	5x13	-123.61	6x9	-38.35	3x14	2.70	3x14	3.39	5x12	0.77	1x9	4.23	1x12	24.80
6x10	553.43	6x16	-104.49	5x9	-37.23	3x9	2.59	1x12	3.00	4x10	0.65	1x12	4.16	6x8	23.17
3x12	432.67	5x11	-101.13	1x16	-36.05	1x12	2.56	3x9	2.64	6x11	0.56	2x13	4.10	5x9	21.12
5x12	403.79	6x8	-88.40	6x8	-33.40	1x14	2.33	1x14	2.53	2x10	0.54	3x14	3.94	1x13	16.35
2x16	346.91	4x12	-70.44	1x8	-33.36	3x16	2.30	2x15	2.13	3x10	0.54	1x14	3.50	4x16	14.77
2x15	315.04	1x13	-64.32	4x16	-23.00	6x8	1.74	3x16	2.12	1x12	0.51	6x16	3.25	6x15	11.79
6x8	311.04	5x15	-59.78	2x9	-22.75	6x9	1.69	4x10	2.00	4x13	0.51	5x7	3.01	5x14	11.34
4x16	307.25	4x10	-59.77	4x9	-21.15	2x15	1.69	6x8	1.93	2x15	0.49	4x7	2.48	5x7	11.2
6x9	292.30	3x10	-54.12	2x16	-20.39	4x10	1.35	1x16	1.60	5x13	0.48	3x9	2.10	2x8	10.82
5x13	269.98	1x12	-51.11	3x9	-20.24	3x11	1.32	6x11	1.43	1x16	0.46	2x15	1.82	1x15	10.51
6x7	215.86	6x10	-49.61	4x8	-19.17	1x16	1.20	6x9	1.29	1x7	0.38	6x11	1.72	4x10	9.73
5x15	212.96	3x7	-46.7	3x16	-16.72	1x13	1.16	4x13	1.25	1x9	0.36	4x12	1.56	3x16	9.60
3x16	209.15	2x9	-46.62	2x8	-14.85	2x7	1.13	5x13	1.15	1x8	0.34	2x7	1.40	6x9	9.40
2x11	185.33	2x7	-46.58	3x8	-14.72	6x11	1.05	5x11	0.97	3x14	0.31	5x10	1.30	1x7	9.40

Table 4.7: Continued

Crosses and traits															
Cross	TOT		PRT	Cross	PRO	Cross	PAR	Cross	1000GWT	Cross	BY	Cross	HI	Cross	LAR
1x7	2.27	1x9	10.85	1x9	99.83	3x15	289.61	5x9	1.83	5x9	7.98	5x8	39.00	1x10	369.91
5x13	2.25	5x8	9.66	6x16	84.53	4x12	284.24	1x8	1.83	5x8	2.83	6x16	37.14	5x9	103.25
4x14	2.09	6x16	6.69	5x8	17.67	1x16	223.48	4x16	1.47	6x16	2.81	1x9	27.41	5x13	96.22
5x9	2.08	4x14	3.10	5x12	12.63	2x8	221.54	3x15	1.25	3x14	0.58	2x11	7.28	3x11	74.56
4x11	1.56	4x11	2.06	3x15	10.73	5x12	193.44	1x16	1.01	1x9	0.58	3x10	6.64	4x14	70.92
2x10	1.47	2x10	1.36	2x11	10.32	6x10	184.57	2x13	0.96	4x11	0.56	4x7	4.96	1x12	65.47
1x15	1.13	2x7	1.30	4x10	10.03	1x11	179.68	6x14	0.79	2x7	0.51	4x10	4.14	2x7	65.03
4x13	1.11	4x13	1.25	4x14	9.70	3x10	161.71	3x7	0.76	2x10	0.50	1x15	3.86	3x15	57.72
1x9	1.05	3x12	1.01	5x15	8.78	3x14	127.25	4x13	0.73	3x11	0.46	3x13	3.70	3x7	55.52
6x10	0.89	5x13	0.91	4x7	8.44	5x7	123.43	1x12	0.72	4x15	0.44	2x14	3.69	5x14	40.79
3x11	0.86	3x11	0.9	3x12	7.88	2x9	121.08	1x7	0.65	2x15	0.43	4x15	3.21	4x12	40.26
2x7	0.83	3x15	0.77	2x14	7.77	1x13	117.6	3x11	0.61	3x7	0.41	5x14	2.59	2x8	39.15
6x12	0.82	2x15	0.76	4x11	7.46	6x15	114.74	5x14	0.59	4x14	0.39	2x13	2.50	6x16	34.25
2x16	0.60	4x10	0.73	2x8	7.24	6x8	92.24	2x11	0.57	3x15	0.38	4x12	2.13	4x11	34.18
6x7	0.58	1x15	0.69	2x13	6.98	4x13	88.42	5x12	0.50	2x11	0.38	1x12	2.07	5x11	32.22

Key: 1-6= male parents; 7-16=female parents; 1=ICMV3771, 2=Manganara, 3=Okashana2, 4=ITMV8001, 5=SDMV94001, 6=Shibe, 7=Exbornu, 8=CIVT9206, 9=GGB8735, 10=ICMV221, 11=ICMV221white, 12=KatPM1, 13=Okoa, 14=SDMV96053, 15=Sosank, 16=Okollo

4.3.5 Gene action and heritability

The types of gene action, narrow sense heritability and broad sense for grain yield and other selected traits under the influence of rust are presented in Table 4.8. Figure 4.1 shows the percentage contribution of each type of gene action to total genetic variation. For grain yield, additive gene action due to female parents ($\sigma^2_{female(A)}$) accounted for 32% of the total variation as well as additive gene action due to the male parents ($\sigma^2_{male(A)}$) (32%), the non-additive gene action ($\sigma^2_{female\ x\ male(D)}$) accounted for 36%. The sum of additive gene action for male and female parents was 64%. For rust severity at 50% physiological maturity the order existed $SCA > GCA_{male} > GCA_{female}$ The graphical presentation in Figure 4.1 further shows the strength of gene action contribution of GCA and SCA in following order $GCA_{female(A)} > GCA_{male(A)} > SCA_{female\ x\ male(D)}$ for days to 50% flowering, days to 50% anthesis, plant height and number of productive tillers. However, non-additive gene action ($SCA_{female\ x\ male(D)}$) was predominant over the additive gene actions ($GCA_{female(A)}$ and $GCA_{male(A)}$) for grain yield, AUDPC, rust severity at 50% physiological maturity, panicle area, harvest index and leaf area. Additive gene action due to female parent was predominant for 1000-grain weight and leaf area while additive gene action due to male parents was predominant for flower-anthesis interval, days to 50% physiological maturity and biological yield. The expression of total number of productive tillers was controlled mainly by additive gene action due to the female parent and dominance, with minimal effect of the male parents. Narrow sense heritability was much lower than the broad sense heritability for most traits (Table 4.8). Traits with narrow sense heritability of less than 10% were AUDPC, total number of productive tillers and biological yield while rust severity at 50% physiological maturity, flower-anthesis interval and harvest index had narrow sense heritability of less than 20%. The majority of the traits had narrow sense heritability higher than 20% and these included grain yield, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, harvest index and leaf area.

Table 4.8: Components of gene action and heritability for the selected traits

Traits	Variance components			h^2 (%)	H^2 (%)
	$\sigma^2_{male(A)}$	$\sigma^2_{female(A)}$	$\sigma^2_{female*male(D)}$		
GY	40859.40*	42196.80*	45911.80*	22.33	47.02
RUST	1.68**	0.71ns	1.76*	11.26	27.82
AUDPC	91.08*	482.79ns	718.08**	3.02	10.56
FLO50	1.11**	1.87**	0.29n*	34.43	41.05
ANT50	1.21**	1.87**	0.08ns	31.27	32.84
FAI	0.13*	0.07*	0.09*	16.13	29.54
PSM50	3.53**	2.62**	0.81*	38.51	48.64
PLH	152.70*	186.76*	88.75*	37.42	56.98
PRT	0.28ns	0.48*	0.09*	30.96	38.19
TOT	0.01ns	0.13*	0.13*	4.74	14.34
PRO	25.08ns	29.87*	45.54*	23.9	63.52
PAR	65408.00ns	78742.00*	87434.50ns	32.16	71.17
1000GWT	1.37ns	1.77ns	1.76*	26.61	56.47
BY	0.05ns	0.02*	0.04*	7.2	33.64
HI	4.71*	6.87ns	8.25ns	19.29	46.79
LAR	4200.50*	5297.10*	4965.20ns	35.18	71.96

Key: GY=grain yield (kg plant^{-1}), AUDPC=Area under disease progress curve, RUST=rust severity at 50% physiological maturity, FLO$_{50}$=days to 50% flowering, ANT$_{50}$=days to 50% anthesis, FAI=flower-anthesis interval (days), PSM$_{50}$=days to 50% physiological maturity, PLH=plant height (cm), TOT=total number of tiller, PRT=number of productive tillers, PRO=%productive tillers, PAR=panicle area (cm^2), 1000GWT=thousand grain weight (g), BY=biological yield (kg plant^{-1}), HI=%harvest index, LAR=leaf area (cm^2)

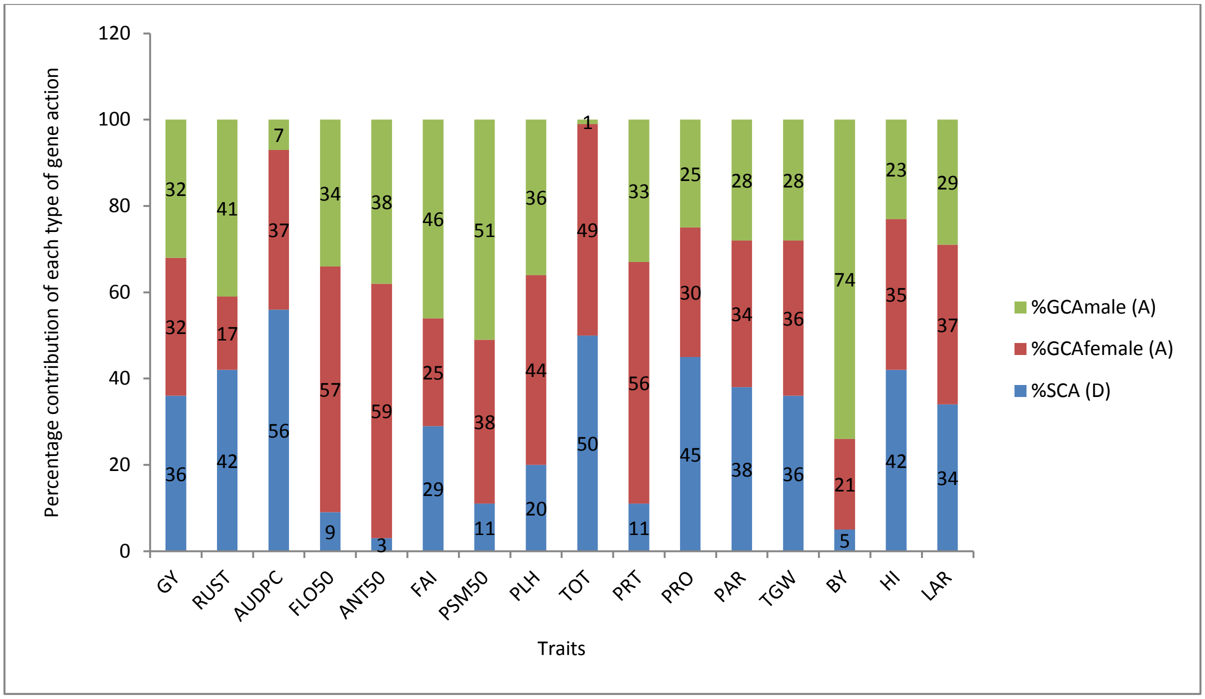

Figure 4.1: Percentage contribution of type of gene action for each trait

4.3.6 Better-parent heterosis

Trait-specific results for fifteen crosses showing superior performance relative to the better performing parents are shown in Table 4.9. The cross 4 x 14 (ITMV8001 x SDMV96053) exhibited very high better parent heterosis (92.72%) for grain yield relative to other crosses which also had positive better parent heterosis. The crosses 3 x 11 (Okashana2 x ICMV221white) and 6 x 10 (Shibe x ICMV221) also performed better than their better parents increasing grain yield by more than 22%. The other crosses had levels of better-parent heterosis of less than 20%; with crosses 5 x 8 (SDMV94001 x CIVT9206) and 6 x 7 (Shibe x Exbornu) showing the lowest heterosis of less than 5% for grain yield. Desirable negative better parent heterosis was observed for rust severity at 50% physiological maturity and AUDPC. In addition, relatively high heterosis was registered for rust severity at 50% physiological maturity (48-59%) when compared with AUDPC (10-29%). All the fifteen selected crosses performed much better than their better parents for rust resistance. Generally, crosses involving male parents 4 (ITMV8001), 5 (SDMV94001) and 6 (Shibe) dominated the list of better performers for most of the traits. In addition, relatively low better parent heterosis (<7%) was observed for days to 50% flowering, days to 50% anthesis and days to 50% physiological maturity for most of the crosses (Table 4.9). The results in Table 4.9 show that low levels of heterosis were registered for AUDPC while relatively high better-parent heterosis for rust was observed in all the fifteen crosses selected. Results for mid-parent heterosis showed the same pattern.

Table 4.9: Better-parent heterosis for the best fifteen crosses per trait

Crosses and traits															
Cross	GY	Cross	AUDPC	Cross	RUST	Cross	FLO50	Cross	ANT50	Cross	FAI	Cross	PSM50	Cross	PLH
4x14	92.72	1x9	-28.79	3x9	-59.21	5x7	6.85	5x7	6.29	6x13	15.91	5x8	6.37	6x8	15.03
3x11	25.09	6x16	-25.87	4x16	-59.20	3x14	3.83	3x14	3.38	4x13	15.38	5x7	4.20	3x11	14.16
6x10	22.19	6x8	-22.12	4x8	-58.88	4x15	3.54	4x15	3.30	4x10	10.86	4x16	4.19	1x12	13.97
3x12	18.83	5x13	-20.06	4x9	-57.70	1x12	3.42	1x12	3.29	4x14	10.62	1x9	4.15	1x13	9.70
5x12	17.71	6x10	-16.28	2x9	-56.64	6x8	3.27	6x8	3.20	3x10	9.49	4x7	3.99	4x16	9.34
6x8	16.37	4x12	-15.10	5x16	-55.4	3x16	3.11	4x10	3.11	2x10	9.45	6x16	3.75	3x16	8.79
6x9	15.62	5x11	-13.43	5x9	-55.06	1x14	2.95	3x16	2.95	2x15	9.25	1x12	3.14	5x14	7.00
5x13	12.03	4x10	-12.65	6x9	-54.83	4x7	2.70	4x13	2.92	6x11	8.43	3x14	2.91	5x7	6.87
5x15	11.34	5x15	-12.5	3x8	-53.22	4x8	2.70	4x8	2.53	1x16	7.32	1x14	2.43	3x14	6.68
2x16	9.99	2x9	-12.41	3x16	-50.96	4x10	2.28	4x7	2.14	5x13	6.82	2x13	2.09	1x7	5.52
2x15	8.30	6x11	-11.81	2x16	-50.61	4x13	1.64	1x14	2.07	5x12	6.17	4x15	2.06	5x9	5.07
5x9	6.83	1x13	-10.74	1x15	-49.89	6x10	1.60	3x9	1.57	3x14	5.70	3x9	1.36	3x7	4.92
4x16	6.47	2x14	-10.69	6x8	-49.63	5x10	1.57	1x16	1.52	4x7	5.22	4x8	1.10	6x15	4.53
6x7	4.80	6x7	-10.66	1x8	-48.41	3x9	1.54	2x15	1.48	3x7	5.22	6x8	0.99	4x10	4.43
5x8	4.71	1x12	-9.47	1x16	-48.02	4x16	1.01	5x13	1.32	1x7	5.22	5x9	0.73	6x10	4.02

Key: 1-6= male parents; 7-16=female parents; 1=ICMV3771, 2=Manganara, 3=Okashana2, 4=ITMV8001, 5=SDMV94001, 6=Shibe, 7=Exbornu, 8=CIVT9206, 9=GGB8735, 10=ICMV221, 11=ICMV221white, 12=KatPM1, 13=Okoa, 14=SDMV96053, 15=Sosank, 16=Okollo

Table 4.9: Continued

Crosses and traits															
Cross	TOT	Cross	PRT	Cross	PRO	Cross	PAR	Cross	1000GWT	Cross	BY	Cross	HI	Cross	LAR
1x7	37.08	6x16	95.84	6x16	92.59	3x15	43.10	5x9	12.48	3x14	41.78	6x16	98.93	1x10	89.16
4x14	31.42	4x14	44.53	5x8	11.45	4x12	42.27	4x16	10.44	4x11	33.04	1x9	75.06	4x14	13.90
5x9	31.00	4x11	31.31	1x9	10.72	2x8	40.37	3x15	9.45	5x9	32.50	2x11	13.65	5x9	12.89
5x13	30.59	4x13	17.94	5x12	9.07	6x10	34.50	1x12	7.88	6x16	26.35	3x10	12.08	3x11	11.26
4x11	27.14	5x13	17.05	4x10	7.00	1x16	31.76	1x8	7.71	2x7	23.87	5x8	11.68	1x16	10.97
2x10	21.54	1x9	14.80	4x14	6.71	3x10	31.43	1x7	7.34	2x10	19.45	1x15	9.29	3x7	10.82
4x13	20.51	5x8	14.44	2x11	6.28	5x12	23.84	1x16	6.63	1x9	17.82	4x15	7.50	1x12	10.41
1x9	16.97	2x10	7.63	4x7	5.06	1x11	20.02	2x13	6.00	3x11	15.55	4x12	6.18	3x15	9.25
2x7	12.35	1x13	3.92	4x11	3.90	6x8	19.29	3x7	5.51	5x8	15.27	1x12	5.81	4x12	5.83
1x15	12.27	2x7	3.68	5x7	3.80	6x15	19.02	4x13	5.40	3x7	1.32	4x10	3.70	6x7	3.15
4x12	9.77	6x14	1.20	3x12	3.46	2x7	17.71	5x12	5.25	4x15	-0.90	2x14	2.36	6x14	2.09
6x10	8.67	3x12	-0.08	2x14	3.44	5x7	14.34	3x11	4.34	2x15	-3.94	3x13	2.17	4x11	1.48
6x12	7.58	6x11	-0.90	3x15	2.76	1x13	13.63	6x14	3.89	2x11	-4.06	4x7	1.70	5x11	1.05
4x8	7.20	3x11	-1.66	5x14	2.45	3x14	13.50	5x10	3.82	2x13	-7.99	4x9	0.94	5x13	0.19
2x16	6.18	2x14	-2.23	2x13	2.39	4x13	11.64	2x11	3.08	4x14	-8.25	5x14	0.80	2x7	0.08

Key: 1-6= male parents; 7-16=female parents; 1=ICMV3771, 2=Manganara, 3=Okashana2, 4=ITMV8001, 5=SDMV94001, 6=Shibe, 7=Exbornu, 8=CIVT9206, 9=GGB8735, 10=ICMV221, 11=ICMV221white, 12=KatPM1, 13=Okoa, 14=SDMV96053, 15=Sosank, 16=Okollo

4.4 Discussion

4.4.1 General performance of the parents and crosses

The pooled analysis of variance results indicated a highly variable environment in which the genotypes were tested. The significantly different effects of genotypes and environment interactions indicate a high level of environmental variation for expression of heterosis. This implies that stability analysis was important in order to identify which environments were suitable for particular crosses. Similar effects of strong environmental influence were also reported by Bidinger et al. (2003) and Sharma and Shrikant (2006) when testing materials for heterosis. More importantly, they indicated why selection for improved grain yield in marginal environments has been primarily based on selection for a higher harvest index rather than increased productivity. The significantly different variation observed for female and male parents, crosses and their interaction with the environment shows that high variability existed in tested genotypes; and thus genotype by environment analysis is necessary to identify which genotypes are suitable for which particular environments. No significant differences were observed for grain yield in all the ten female parents while differences existed in the male parents and the crosses.

However differences were observed in the per se performance of all the genotypes tested. Eleven best selected crosses yielded more than the best male parents while five crosses performed better than the best female parent. In addition, one cross (ITMV8001 x SDMV96053) yielded almost twice more than the best female and male parent making it the best performer. This variation expresses the effect of heterosis. Similar effects of crosses outperforming the parents have been reported in many studies. Penthani et al. (2004) and Chavan and Nerkar (1994) reported crosses performing better than parents while Yadav et al. (2000) reported the same observation for top cross hybrids.

In terms of rust-related traits all the selected best crosses had lower AUDPC relative to the best parents, while all the crosses were more resistant than the female parents and ten crosses were better than the male parents. Observations of crosses being more resistant to rust than the parents have also been reported by Lakshmana et al. (2010). The crosses performing better than their parents has been reported for 1000-grain weight, plant height and days to 50% flowering (Ouendeba et al., 1993). The 1000-grain weight (Kelley et al., 1996; van Oosterom et al., 1996) and harvest index (Bidinger et al 2003) are some of the most important traits determining grain yield; indicating that selection for the traits may increase grain yield. In this study all the parents and crosses had relatively high harvest index (HI>28%) (Yagya and Bainiwal, 2001; van Oosterom et al. (2006) and thus this set of materials could be advanced to breed for high harvest index, a trait also largely associated with resistance to drought.

The significant difference in the flower-anthesis interval for the parents and crosses emphasises the importance of the trait. All the crosses had lower flower-anthesis interval relative to all the female and male parents; and since they yielded better than the parents it implies that selecting for flower-anthesis interval would lead to higher grain yield. The trait has been reported to have a strong positive correlation with number of grains per panicle (Bidinger and Raju, 2000a) which is a function of maximum number of surviving florets (Miralles et al., 1998) at anthesis (Saini and Westgate, 2000); thus selecting for low flower-anthesis interval will greatly increase grain yield.

4.4.2 Combining ability effects and gene action

The analysis of variance showed significant differences in combining ability of the parents and crosses under the influence of rust. Variation was observed for both male and female parents for grain yield, days to 50% flowering, flower-anthesis interval, days to 50% physiological maturity and plant height. The results indicated that the parents used for genetic analysis were diverse; as also reported by Naik et al. (1996) when they studied the combining ability for grain yield and its components. The GCA was higher than SCA for grain yield, rust severity at 50% physiological maturity, plant height, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, total number of tillers, percentage of productive tillers, panicle area, leaf area, 1000-grain weight, harvest index, and biological yield. These traits can be improved through simple selection schemes such as pedigree or recurrent selection because it is easy to predict short-term response to selection (Vengadessan, 2008). The AUDPC had SCA higher than general combining ability, and thus improvement can be achived through breeding for hybrids.. Similar observations were reported for some traits. Bhadalia et al. (2012) reported additive gene action for grain yield, plant height and harvest index while Izge et al. (2007) reported additive gene action for 1000-grain weight. Contrasting results have been reported for panicle dimension (Singh and Sagar, 2001) and 1000-grain weight (Gotmare and Govila, 1999; Sheoran et al., 2000; Pethani et al., 2004; Bhadalia et al., 2012). Pannu (et al., 1996) reported predominance of non-additive gene action for 1000-grain weight.

In addition, based on Hallauer and Miranda (1988) classification of heritability, relatively high broad sense heritability estimates were observed for most traits including grain yield. Similar reports were also made by Borkhataria et al. (2005) and Solanki et al. (2002) though Sachan and

Singh (2001) indicated the contrary for 1000-grain weight. It implies that the the non-additive and environmental effects may be important in the expression of the traits (Vengadessan, 2008). However, as also reported in this study, Pethani et al. (2004) reported additive gene action for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, plant height and number of productive tillers; though contrary to Bhadalia et al. (2012) findings. Bhadalia et al. (2012) reported preponderance of non-additive gene action for days to 50% flowering and days to 50% physiological maturity. In addition, there was high narrow sense heritability for the traits, as also noted by Bhoite et al. (2008). This may indicate simple inheritance of the traits as reported by Azhaguvel et al. (2003). Thus the traits may be improved through schemes like recurrent selection or pedigree selection. Likewise inbred lines with improved levels of the traits may be developed as suggested by Vengadessan (2008).

4.4.3 Heterosis

Results showed that the magnitude of heterosis was cross-dependent for all the traits considered for the fifteen best selected crosses. For grain yield, positive heterosis was recorded for the best selected fifteen crosses. Most of the best crosses had better-parent heterosis of 11% to 25%, though few were within the range (20 to 30%) at which a hybrid is considered to be good (Axtell et al., 1999); and one cross (ITMV8001 x SDMV96053) had very high better-parent heterosis of 93%. The high positive heterosis for grain yield in cross ITMV8001 x SDMV96053 may be due to the high positive heterosis expressed for days to 50% flowering, total number of tillers, number of productive tillers and leaf area under better-parent heterosis. Relatively high levels of heterosis for grain yield have been reported in many findings. Yadav et al. (2000) first reported high heterosis of 88% though in later studies Yadav (2006) reported lower levels of 42% while Davda et al. (2012) reported 41% standard heterosis and presence of heterobeltiosis. In addition, Karthigeyan (1994) reported 49% heterosis for grain yield, while Ouendeba et al. (1993) reported 36-81% for better-parent heterosis. On the contrary, Bidinger et al. (2003) reported negative heterosis for grain yield. This implies that exploiting heterosis for grain yield largely depends on specific parent combinations.

Heterosis was exploited by Wilson et al. (2001) to produce hybrids with increased levels of resistance to pearl millet rust. Findings in this study also reveal that crosses with high levels of heterosis could be developed and thus minimise grain yield loss due to rust effects. Results in the current study showed high levels of heterosis for rust at 50% physiological maturity for better parent heterosis (-48% to -59%); reflecting the importance of non-additive gene action also as suggested by Pannu et al. (1996). However, lower levels were recorded for better-parent heterosis (-10% to -29%) for AUDPC. Lower AUDPC has also been reported in other studies (Lal Ahamed et al., 2004.); indicating that selecting for AUDPC may not be a reliable trait for increasing resistance to rust relative to selecting for rust severity at 50% physiological maturity. However, the non-significant correlation between rust severity at 50% physiological maturity and AUDPC may indicate a possibility for independent selection for each trait. For other traits, various levels of heterosis were achieved. Relatively higher levels of better-parent heterosis were achieved for panicle area, total number of tillers as also reported by Pethani et al. (2004), percentage of productive tillers, number of productive tillers as reported by Karthigeyan (1994), biological yield, harvest index as also reported by Bidinger et al. (2003) and leaf area. A high harvest index in hybrid seed parents is desirable because it is a measure of grain filling and fodder production strength of the seed parent (Bidinger et al., 2003).

Lower levels of better-parent heterosis were recorded for plant height, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, grain yield and 1000-grain weight; though non-additivity was predominant in the last two traits. It shows that the traits could be improved through population improvement schemes that exploit additive gene action. However, contrasting reports have been published about direction and magnitude of heterosis for some traits. For example, Pethani et al. (2004) and Karthigeyan (1994) reported high heterosis for plant height and 1000-grain weight while in this study lower heterosis levels have been reported. Karad and Harer (2004) reported high levels of heterosis for days to 50% flowering while findings in this study indicate very low levels. However, they tested different materials in different environments. These variations in heterosis indicate the importance of specific combining ability for grain yield when breeding for hybrids.

4.5 Conclusion

The significantly important interactions of the genotypes with the environment showed the relevance to characterise the test materials across environments. The male parents ITMV8001, SDMV94001 and Shibe and female parents SDMV96053, Sosank, CIVT9206 and GGB8735 had high and positive GCA effects for grain yield. These parents could be used in breeding schemes like recurrent selection that target population improvement. The male parents Manganara and Okashana2 and female parents Exbornu, ICMV221 and ICMV221white were the best general combiners for rust and thus could be used to breed for rust resistance. The crosses ITMV8001 x SDMV96053, Okashana2 x ICMV221white, Shibe x ICMV221, Okashana2 x KatPM1 and

SDMV94001 x KatPM1 were the best genotypes for grain yield. Crosses ICMV3771 x GGB8735, SDMV94001xOkoa, ShibexOkollo, SDMV94001 x ICMV221white, Shibe x CIVT9206 were the best specific combiners for rust resiatnce.

The preponderance of additive gene action for days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, number of productive tillers and plant height means these traits could be improved through schemes like recurrent selection. On the other hand traits including grain yield, 1000-grain weight, panicle area and leaf area had preponderance to both additive and non-additive gene action and could thus be improved through schemes like recurrent selection and hybrid breeding. In contrast, traits like rust severity at 50% physiological maturity, AUDPC, biological yield, total number of tillers and percentage of productive tillers had preponderance to non-additive gene action, relatively low narrow sense heritability and low genetic coefficient of variation. Thus these traits could be improved through hybrid breeding.

Crosses ITMV8001 x SDMV96053, ITMV8001 x SDMV96053, Okashana2 x ICMV221white, Shibe x ICMV221, Okashana2 x KatPM1 and SDMV94001 x KatPM1 that expressed high better-parent for grain yield could be promoted for high grain yield. Crosses Shibe x GGB8735, SDMV94001 x GGB8735, ICMV3771 x Okollo, ITMV8001 x GGB8735, Manganara x GGB8735, Okashana2 x GGB8735, ITMV8001 x Okollo, ITMV8001 x CIVT9206, ICMV3771 x CIVT9206, Shibe x CIVT9206 and SDMV94001 x Okollo had heterosis for rust resistance above 41% and could thus be deployed as resistant hybrids.

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Chapter Five

Analysis of genotype by environment interaction of improved pearl millet genotypes for grain yield and rust resistance

Abstract

In Uganda pearl millet is an important crop for those living in the semi-arid zones which are characterized by low annual rainfall and highly unpredictable climatic conditions. Due to the unpredictable climatic conditions the genotype by environment interaction makes it hard to select and recommend improved cultivars to farmers. The study objectives were therefore; i) to analyse the patterns of genotype by environment interaction effect for grain yield and rust resistance in four environments, and ii) to identify genotypes suitable for each environment. Seventy six improved genotypes were planted in the four environments in a 4 x 19 alpha-lattice experimental design with two replications. The genotype and genotype x environment (GGE) biplot was adopted to assess the genotype by environment interaction effects for grain yield and rust resistance. The GGE biplot analysis revealed that the environments associated with 2012 second rains for both sites (Kitgum and Serere) were highly productive for grain yield and suitable for rust resistance screening. The environments associated with 2013 first rains performed poorly for both grain yield and had high rust disease pressure. The winning hybrid in the best environment for grain yield was ICMV3771 x SDMV96053 while Okashana2 x KatPM1, Shibe x CIVT9206, Shibe x GGB8735 were the best for rust resistance and area under disease progress curve.

Key words: Pearl millet, GGE biplot, grain yield, rust resistance, genotype by environment

5.1 Introduction

Pearl millet is adapted to marginal environments where conditions are extremely variable and erratic (IFAD, 1999; Bashir et al., 2014), with low annual rainfall (Sharma and Pareek, 1993). Despite the advantage of being adapted to marginal conditions, farm level pearl millet average productivity is low. Although, high yielding genotypes adapted to low input and drought-prone environments have been developed (Serraj et al., 2003; Vadez et al., 2012); their potential performance under marginal conditions is always obscured by the effect of genotype by environment interaction (GEI) (Gauch and Zobel, 1988, Gauch and Zobel, 1996; Yan and Racjan, 2002). Due to the GEI effect, inconsistent performance of genotypes across environments has been reported (Delacy et al., 1996; Matus-Cadiz et al., 2003; Alberts, 2004). This may result in inappropriate selection for particular environments or a change in relative rank of genotypes (Falconer, 1990; Crossa, 1990; Cooper and Delacy, 1994). It is therefore important to assess genotypes for adaptability and stability, a process which may slow selection for specific environments in breeding programmes (Yau, 1991).

There are two types of stability: static and dynamic. For static stability, stable genotypes maintain constant yield across different environments, while for dynamic stability genotype performance is parallel to the mean response of all genotypes (Bridge, 1989). The smallholder farmers in drought-prone environments would prefer genotypes with a stable minimum yield over years than genotypes with high yielding potential which is attainable only under adequate rainfall conditions (Haussmann et al., 2012). However, genotypes that maintain high yielding ability over a wide range of environments may be desirable (Yahaya et al., 2006). In order to identify the genotypes with desirable stability in pearl millet, it is thus important to conduct GEI trials (Gupta and Ndoye, 1991). Several approaches have been adopted in order to assess GEI in pearl millet breeding, but the commonly used methods include; conventional analysis of variance (ANOVA), stability analysis [Regression coefficient (b_i) (Finlay and Wilkinson, 1963), deviation mean square, coefficient of determination (r_i^2) (Pinthus, 1973), ecovalence (Wi) (Wricke, 1964), cultivar performance measure (P_i) (Lin and Binns (1988a)], Additive Main effects and Multiplicative Interactions (AMMI) models (Gauch, 1988) and Genotype and Genotype x Environment (GGE) biplot (Yan and Hunt, 2002) which is a graphical analysis. Inadequacy though has been reported about most of the stability measures used to assess GEI.

The ANOVA is used to identify sources of variation due to GEI effect and to estimate variance components used to calculate heritability and predicted gain of traits (Crossa, 1990); but it is not able to explore the underlying structure within the GEI. This may mask the true performance of some genotypes in certain environments (Crossa, 1990). The regression approach is one of the most widely used methods for assessing GEI effect across environments (Westcott, 1986). However, genotype's response to environments is intrinsically multivariate yet regression transforms it into a univariate variable (Lin et al., 1986). Crossa (1990) also noted that the parameters of regression (mean, slope, and deviation) make it difficult to determine which genotypes are superior for particular environments (Freeman and Perkins, 1971; Virk et al., 1985).

On the other hand the AMMI model (Gauch, 1992; Gauch, 2006; Gauch et al., 2008) combines the ANOVA for the genotype and environment main effects with principal components analysis along with prediction assessment, which helps to obtain better yield estimates under complex GEIs (Alberts, 2004; Gruneberg et al., 2005). The main drawback of the AMMI method is the difficulty in interpretation of the interaction when there is a poor explanation of the first principal component, which could indicate false statistical stability of the genotypes and/or environments (Lavoranti et al., 2007). Much as both the AMMI and the GGE biplot analysis combine genotype (G) and genotype by environment (GE) in mega environment analysis and evaluation, the GGE biplot is superior to the AMMI in graphical analysis since it explains more G+GE than AMMI (Yan et al., 2007). In addition, GGE biplot is more efficient in discriminating genotypes (Yan et al., 2007). The GGE biplot was therefore adopted to analyze the patterns of GEI effects for grain yield, rust resistance and area under disease progress curve (AUDPC) for rust and to identify the winning genotypes in each of the four environments.

5.2 Materials and methods

5.2.1 Experimental layout and germplasm

In order to conduct G x E analysis 6 male and 10 female parents and their 60 F_1 hybrids, developed from North Carolina design II, were evaluated in a 4 x 19 alpha-lattice experimental design in four environments. The male parents were ICMV3771, Manganara, Okashana2, ITMV8001, SDMV94001 and Shibe. The female parents were Exbornu, CIVT9206, GGB8735, ICMV221, ICMV221white, KatPM1, Okoa, SDMV96053, Sosank and Okollo. Details of the source of germplasm, field lay out and data collection process are in materials and methods in Chapter Four.

Table 5.1 shows the rainfall amount received in each environment during the time of conducting the field experiment. The environments are defined as seasons x sites combinations, i.e. two sites x two seasons, resulting in four test environments.

Table 5.1: Rainfall pattern for the test environments

Site			2012 (E1)					2013 (E2)			
Kitgum	Oct	Nov	Dec	Jan	Feb		May	Jun	Jul	Aug	Sep
	220.1	63.1	30.3	74.9	2.3		110	105.5	139.7	348.5	112.85
Total (mm)			390.7						816.55		
Serere			2012 (E3)						2013(E4)		
	Sep	Oct	Nov	Dec	Jan	Apr	May	Jun	Jul	Aug	
	226.4	74.9	116	44.2	37.8	217.5	130.8	73.2	50.5	117.3	
Total (mm)			499.3					589.3			

Source: Department of Meteorology, Ministry of Water and Environment, Uganda
Key: E1 = Kitgum 2012 second rains, E2 = Kitgum 2013 first rains, E3 = Serere 2012 second rains and E4 = Serere 2013 first rains

5.2.2 Data collection and analysis

The data collection process for grain yield, rust severity at 50% physiological maturity and area under disease progress curve is as described in materials and methods in Chapter Four. However, the analysis was done using the Breeding View in the Breeding Management System version 3.0 (IBP-BMS, 2014) software and Genstat version 14 (Payne et al., 2011). The IBP-BMS (2014) was used to rank genotypes and environments while Genstat was used to characterize the environments and to identify which genotypes won where.

Environment-centred data was used in GGE biplot analysis to visualise the relationship of the enironments and the genotypes (Yan et al., 2000). This method exploits the singular value decomposition of genotype and environment scores principle (Yan and Tinker, 2006) to generate principle components (PCs) that explain the variation observed in the genotype x environment interaction (Yan and Hunt, 2002). The ideal genotype is one with high mean performance and high stability across environments and should be at the centre of the concentric rings and on the average environment axis (AEA) (Yan and Tinker, 2006). Yan and Tinker (2006) further noted that the closer the genotype is to the ideal genotype the more desirable and the closer it is to the AEA the more stable the genotype is across environments. in addition, the environements with longer vetors from the origin are more discriminating than those with shoter vectors (Yan et al., 2007).

The GGE biplot model (Yan, 2002) used was:

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

Where: Yij = mean yield of ith genotype in jth environment, μ = grand mean, βj = 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, $\xi i1$ = eigen vector of genotype i for PC1, $\xi i2$ = eigen vector of genotype i for PC2, $\eta j1$ = eigen vector of environment j for PC1, $\eta j2$ = eigen vector of environment j for PC2, and εij is the residual associated with genotype i in environment j

5.3 Results

5.3.1 Performance of environments and best five genotypes

Results in Table 5.2 show performance of genotypes in the four environments. environment E1 was associated with high levels of grain yield, rust severity at 50% physiological maturity and AUDPC. Environment E3 was the second best performer in terms of grain yield but the best in terms of rust severity at 50% physiological maturity and area under disease progress curve. Environments E2 and E4 were associated with poor performance for grain yield. Table 5.3 shows the best five performing genotypes in each environment for the three traits.

Table 5.2: Performance of environments for selected traits

Traits	Means and CV	Environments			
		E1	E2	E3	E4
Grain (yield kg ha^{-1})	Mean	2361.00(1)	1397.00(4)	1997.00(2)	1902.00(3)
	%cv	21.95	6.67	28.82	30.05
RUST	Mean	23.40(3)	30.94(1)	17.51(4)	25.52(2)
	%cv	7.23	9.61	32.60	25.98
AUDPC	Mean	778.90(1)	666.20(2)	512.20(4)	536.60(3)
	%cv	5.75	21.49	29.38	22.14

Environment ranks in parentheses

Table 5.3: Performance of the best five genotypes per environment

Rank	Environments							
	E1		E2		E3		E4	
	Genotype	Mean	Genotype	Mean	Genotype	Mean	Genotype	Mean
	Grain yield (t ha^{-1})							
1	5x12	3395	6x10	1950	1x14	3576	6x9	3630
2	5x9	3387	6x9	1924	5x13	3523	2x15	3475
3	6x12	3335	3x11	1894	6x10	3051	4x13	3272
4	3x15	3295	6x8	1859	5x15	3005	3x8	3108
5	5x8	3282	5x12	1819	4x14	2993	1x8	2996
	RUST							
2	2x15	19.44	2x15	23.76	1x16	6.53	3x15	5.57
3	4x8	20.57	6x10	24.37	6x12	7.64	2x9	9.39
4	3x8	20.8	6x11	25.21	3x9	8.35	1x15	12.97
5	6x12	20.8	6x16	25.7	2x12	9.67	3x7	13.6
	6x10	20.83	4x7	27.01	1x10	11.11	4x14	15
	AUDPC							
1	1x9	647.9	4x16	441.5	2x9	158	2x14	330.1
2	2x14	659	5x11	452.5	1x13	187.9	1x9	332.3
3	6x10	671.9	6x14	463.8	4x16	250.5	2x11	333.1
4	4x12	675.9	6x11	464.3	4x14	286.3	1x12	372.3
5	1x12	677.5	5x12	482.2	5x13	295.9	3x16	390.3

Key: RUST=rust severity at 50% physiological maturity, AUDPC=area under disease progress curve for rust

5.3.2 GGE biplots for grain yield

The environment-centred biplots for grain yield are shown in Figures 5.1A and 5.1B where PC1 accounted for 39.10% and PC2 accounted for 34.34% of the total variation. Figure 5.1A shows the comparison of genotypes and environments based on means and stability. E1 was the ideal environment while E3 was desirable. Both environments were positively correlated and associated with high grain yield and grouped as one mega environment (Figure 5.1B). Figure 5.1A further shows that E2 was not important in discriminating genotypes since it was close to the origin while E4 was the most unstable and low yielding and source of crossover interaction. On the other hand the genotypes 5 x 12 (SDMV94001 x KatPM1; 2322 kg ha^{-1}) and 6 x 8 (Shibe x CIVT9206; 2387 kg ha^{-1}) were the most ideal genotypes for grain yield; but SDMV94001 x KatPM1 was also the average performing genotype as it appeared on the arrow head of the average environment coordinate (AEC). They were also the most stable genotypes and high yielding. The crosses 1 x 14 (ICMV3771 x SDMV96053; 2355 kg ha^{-1}) and 5 x 13 (SDMV94001 x Okoa; 2210 kg ha^{-1}) were high yielding and desirable though SDMV94001 x Okoa was relatively unstable. The high yielding genotypes were also associated with the high yielding environments E1 and E3 though SDMV94001 x Okoa was not associated with any environment. Figure 5.1B shows characterisation of mega environments. The polygon view shows the four environments grouped into three mega environments namely E1 E3, E2 and E4. E1 E3 was associated with high grain yield while E4 was associated with high grain yield but highly unstable and E2 did not provide good information since it was at the origin of the biplot. The winner in E1 E3 was 1 x 14 (ICMV3771 x SDMV96053; 2355 kg ha-1) while 6 x 9 (Shibe x GGB8735; 2371 kg ha^{-1}) won in E4 but highly unstable.

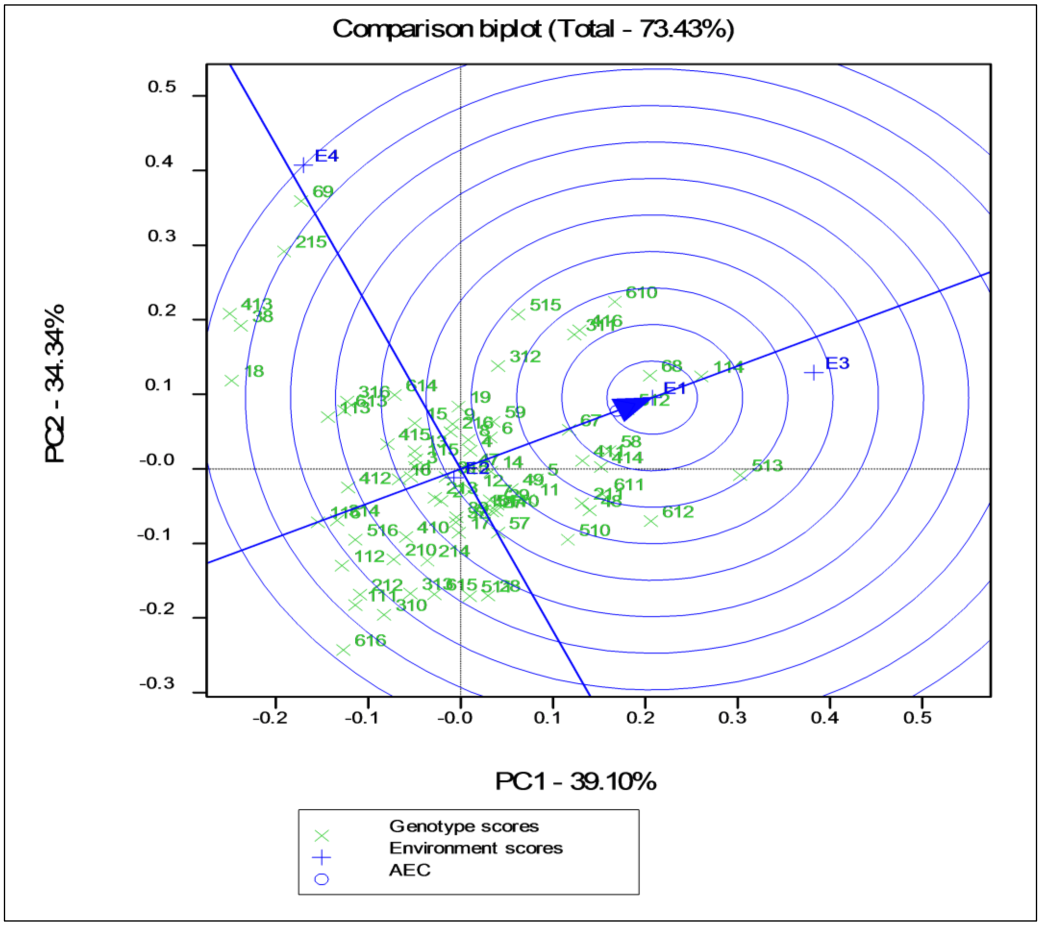

Fig 5.1A: Genotype means and stability for grain yield. Environments E1 = 2012 second rains in Kitgum, E2 = 2012 second rains in Serere, E3 = 2013 first rains in Kitgum, and E4 = 2013 first rains in Serere

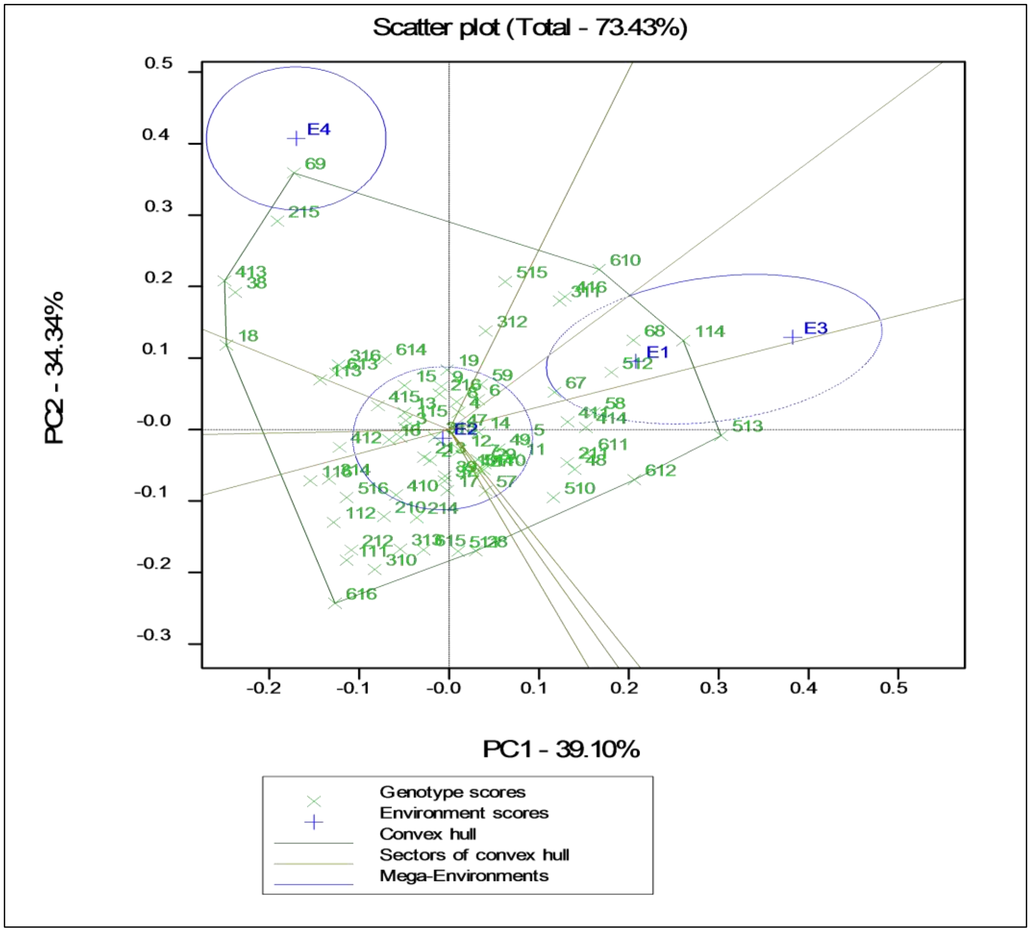

Fig 5.1B: ‘Which won where’ genotype for grain yield. Environments as defined in Fig 5.1A

5.3.3 Rust severity at 50% physiological maturity

Figure 5.2A shows the means and stability of the environments and genotypes for rust severity at 50% physiological maturity. PC1 accounted for 37.32% and PC2 accounted for 26.02% of the total variation. E1 was the most ideal environment with a relatively closer association to E3. The two environments formed a mega environment E1/E3 (Figure 5.2B) which was unfortunately favourable for rust development. Unlike for grain yield, E2 was extremely discriminatory as well as E4 and were associated with low rust development. The environments E2 and E4 were in this case the sources of crossover GEI relative to E1 and E3. The genotype 4 x 14 (ITMV8001 x SDMV96053; RUST=25.33%) was the ideal while 3 x 10 (Okashana2 x ICMV221; RUST=21.12%) was the average performer for rust severity at 50% physiological maturity. The genotype associated with the ideal environment was also susceptible to rust. The winning genotype in mega environment E1/E3 was 6 x 16 (Shibe x Okollo; RUST=24.73%) while 1 x 7 (ICMV3771 x Exbornu; RUST=24.16%) won in E2 and 6 x 11 (Shibe x ICMV221white; RUST=27.58%) won in E4.

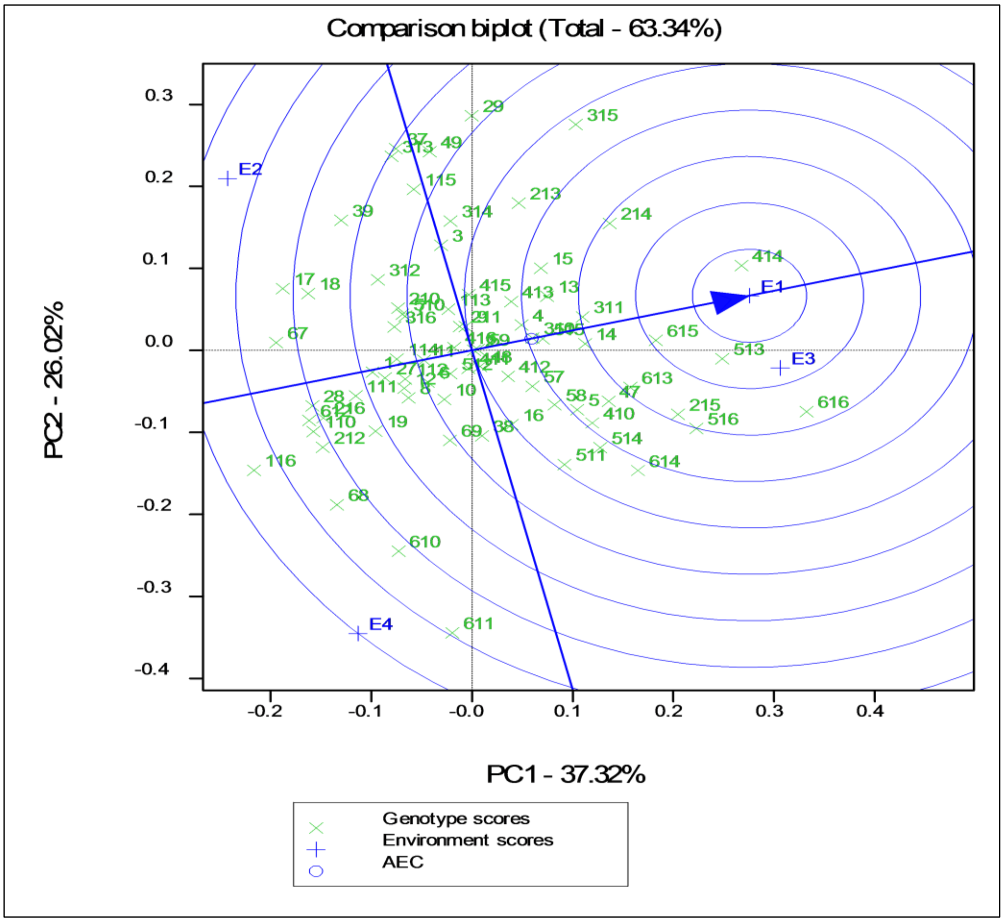

Fig 5.2A: Association between environments for rust severity at 50% physiological maturity. Environments as defined in Fig 5.1A

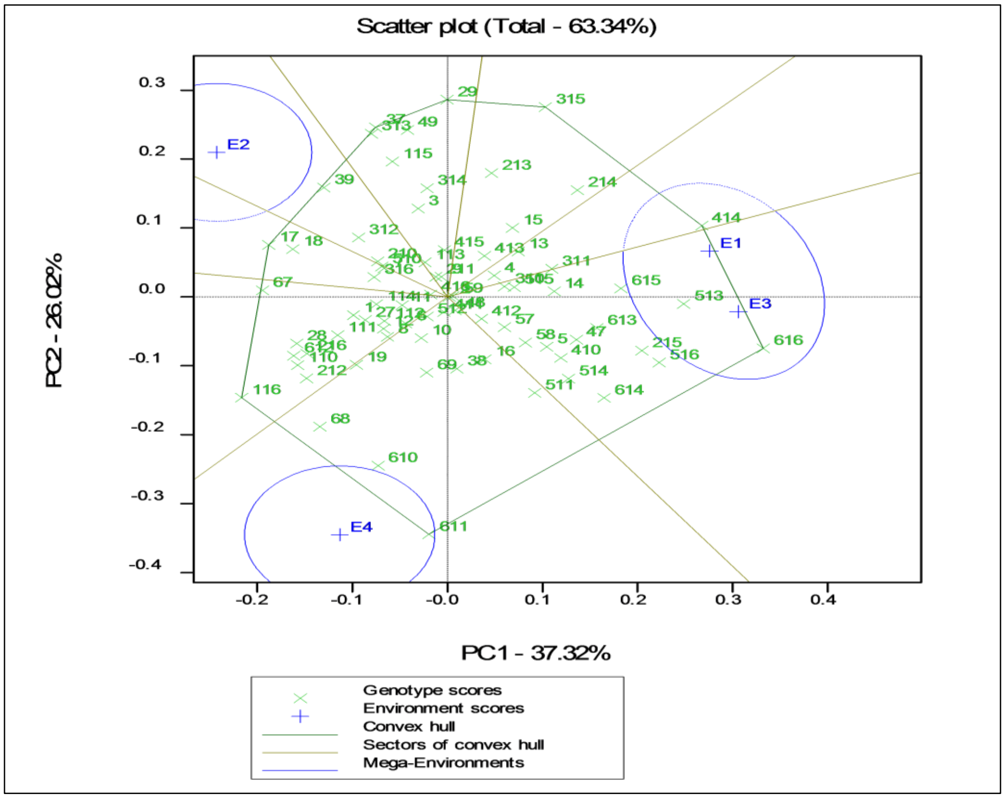

Fig 5.2B: Genotype performance for rust severity at 50% physiological maturity. Environments as defined in Fig 5.1A.

5.3.4 Area under disease progress curve

The PC1 accounted for 43.94% and PC2 accounted for 26.64% of the total variation for area under disease progress curve (AUDPC). Figure 5.3A shows mean and stability of the environments and genotypes for AUDPC. E1 was the ideal environment and 4 x 7 (ITMV8001 x Exbornu; AUDPC=647.5) as the ideal genotype. Genotype 5 x 14 (SDMV94001 x SDMV96053; AUDPC=613.4) was the most desirable and relatively stable. All the four environments, including the ideal, were unstable; with E2 negatively correlated with the other three and the source of crossover GEI. The association resulted in three mega environments (E1, E2, and E3/E4). The winner in E1 mega environment was 4 x 7 (ITMV8001 x Exbornu) while 3 x 14 (Okashana2 x SDMV96053; AUDPC=622.0) won in E2 and genotype 4 x 13 (ITMV8001 x Okoa; AUDPC=734.2) won in E3/E4.

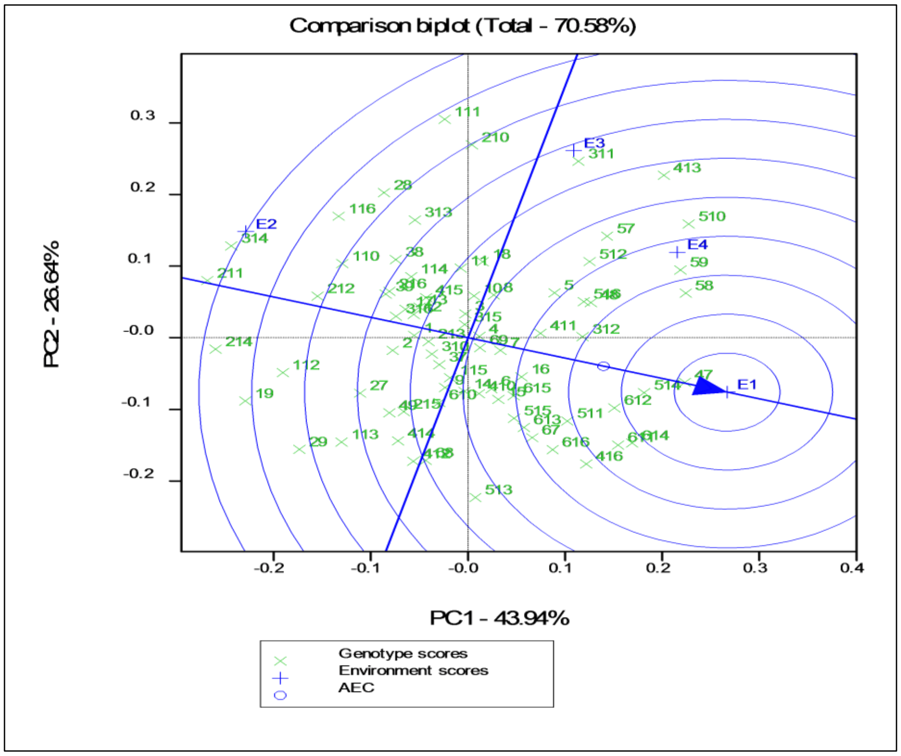

Fig 5.3A: Association between environments for area under progress curve disease. Environments as defined in Fig 5.1A

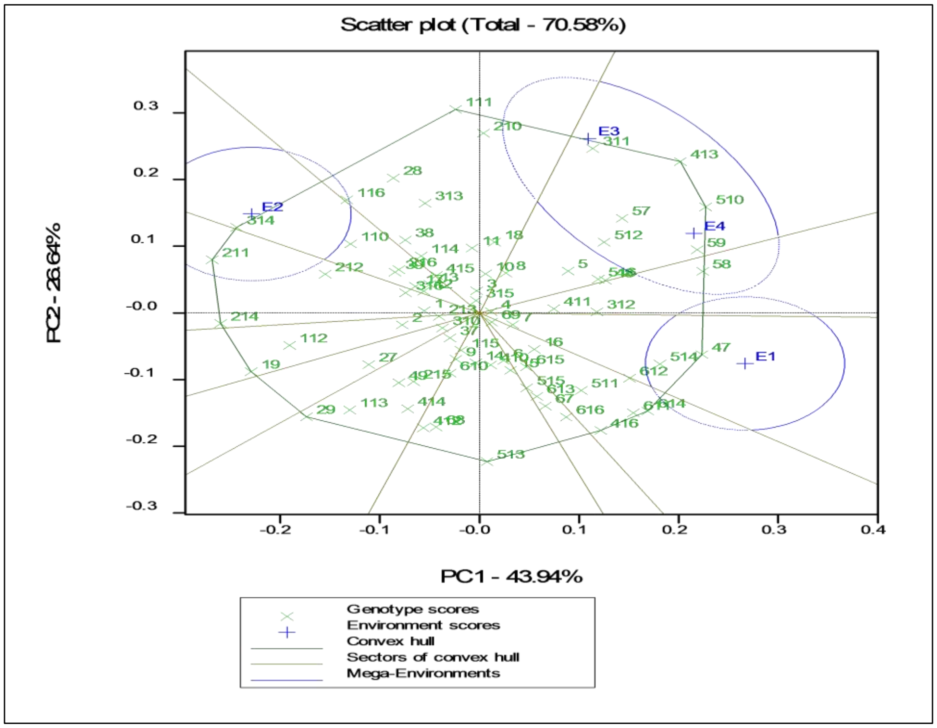

Fig 5.3B: Genotype performance for area under disease progress curve. Environments as defined in Fig 5.1A

5.4 Discussion

The GGE biplot analysis successfully classified the four environments and showed that GEI was important in performance of genotypes. The winners in particular environments differed across the four environments. The GGE biplot helped to establish the type of interaction for each trait. It was observed that crossover GEI existed for grain yield, rust severity at 50% physiological maturity and area under disease progress curve; an indicator of specific adaptability and thus selection of genotypes should be environment-specific. These observations emphasize the importance of GEI. However, as shown by many genotypes not associated with any environment, testing in more environments is necessary to obtain conclusive information about the stability and adaptability of these genotypes. In some pearl millet studies, the GGE biplot has also been used to identify pearl millet mega environments; leading to a reduction in the number of test environments with minimal information loss (Gupta et al., 2013; Ishaq et al., 2014). Adoption of the method has also led to identification of stable and high yielding genotypes (Bashir et al., 2014; Mashiri et al., 2014). Gebre (2014) and Mustapha and Bakari (2014) used the GGE biplot analysis to identify high yielding pearl millet genotypes adapted to arid conditions. Thus, the practicability in using the GGE biplot merits its use in selecting for stable and high yielding pearl millet genotypes.

5.5 Conclusion

The study focused on establishing the importance of genotype by environment interaction effect on genotype performance in the four environments for grain yield, rust resistance and area under disease progress curve. The GGE biplot was useful in characterising the environments and the genotypes; identifying many genotypes not associated with any of the environments an indicator that they were stable. It characterised the environments in terms of stability, adaptability, productivity potential and correlation; where a weak correlation (negative in most cases) was observed for all the traits. This resulted in grouping of mega environments and led to identification of ICMV3771 x SDMV96053 as the most stable and high yielding, and ICMV3771 x Exbornu and Okashana2 x SDMV96053 as the best for rust resistance. However, many genotypes were not associated with any environment, especially for rust resistance indicating that they were stable

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Chapter Six

Overview of research findings

6.1 Introduction

The study focused on characterising the pearl millet cropping system in Uganda, through participatory rural appraisal, and exploiting the diverse variation to improve grain yield and rust resistance through S_1 recurrent selection scheme. However, effective improvement can better be achieved through understanding the mode of gene action and establishing level of heterosis of the traits. This should be supported by assessing the stability and adaptability of the improved genotypes across locations for effective selection. This is essential due to genotype by environment interaction effect in obscuring the potential performance of genotypes, which slows the selection process. All the activities were conducted with a major goal of increasing pearl millet productivity and production through improving populations for grain yield and resistance to rust, which would ultimately increase food availability in the chronically dry zones of Uganda. This focus was thus based on to formulate the study objectives and the tested hypotheses. The overview highlights the research findings and implications to pearl millet breeding.

The specific objectives were;

1. To establish production determinants of the pearl millet cropping system with related uses, traits and constraints
2. To determine the response to S_1 progeny recurrent selection for rust resistance and grain yield in pearl millet populations.
3. To study the inheritance and gene action for grain yield and rust resistance in newly introduced improved pearl millet germplasm.
4. To determine the stability of improved pearl millet lines and crosses for grain yield and rust resistance in two predominantly pearl millet growing zones of Uganda.

6.2 Summary of the major findings

6.2.1 Participatory rural appraisal

- Pearl millet was mainly grown for; food, income, brewing, and fed to poultry.
- It was ranked fourth after cassava, sesame, and groundnuts and was better than sorghum, maize and finger millet.
- 92% of the households had never grown any improved variety of pearl millet and the local grain used as seed was either bought from communal markets or saved from the previous harvests. In addition no household used fertilisers, manure nor any chemical input to enhance productivity.
- The majority did not have access to credit, training in agriculture, record keeping or financial management but many were members of local community groups whose main role was to provide mutual support.
- In most cases household labour was used for farming activities with women majoring in the weeding, harvesting and threshing while men were key participants in land preparation and planting and children involved in bird scaring. The planting was mainly done during the second rains (Sept-Nov) where sole cropping was predominant and broadcasting as a method of planting.
- Farmers preferred the stay green trait, tall, high tillering, high yielding, early maturing and ergot resistant genotypes while the undesirable traits included ergot susceptibility, short varieties, rust susceptibility, low yielding, low tillering, late maturity, sterile and loose panicles.
- Attributes to be introduced or improved included ergot resistance, high yield, large white grains, early maturity, appropriate pesticides, stable market access and trainings in agronomic aspects.
- Constraints identified were ergot disease, bird damages, weeds, rust, insect pests (especially Indian meal moth, weevil, and red flour beetle), lack of market for grain, low prices for grain, price fluctuation. In addition the majority did not consider rust as a disease; as shown by majority making wrong diagnosis and many testifying that they thought it was a character unique to particular varieties.
- Important production determinants included amount of land available for pearl millet cultivation, age of household members (spouse and head), experience in pearl millet cultivation, and amount of seed available for planting.

6.2.2 Recurrent selection

The study on the response of two local pearl millet populations to two cycles of S_1 recurrent selection for grain yield and rust resistance improvement revealed. Expectations were that different populations will show desired responses to selection.

- A net genetic gain of 72% and 36% for grain yield in the Lam and Omoda populations respectively, after the two cycles of S_1 recurrent selection. This resulted in a respective net grain yield improvement of 436 kg ha^{-1} and 250 kg ha^{-1}.
- A net genetic gain of -55% and -70% was attained for rust resistance which resulted in rust severity reduction of 30% and 13% for Lam and Omoda populations, respectively
- The two populations responded differently to the two cycles of phenotypic S_1 progeny recurrent selection under the effects of rust with higher genetic gains for grain yield and rust resistance attained in the Lam than Omoda population.
- Heritability estimates were high in both populations for most traits including grain yield and rust resistance but still higher heritability estimates were noted in the Lam population than Omoda population.
- A significant negative correlation between grain yield and rust resistance was noted for the two populations.

6.2.3 Combining ability and heterosis

The study on the combining ability and heterosis showed that:

- Most crosses performed better than the best parents for grain yield, rust resistance other other yield-related traits.
- The type of gene action was trait and parent dependent and most traits were predominantly controlled by the additive gene action.
- Traits where additive gene action due to male parent was predominant included; grain yield, area under diseases progress curve, rust severity at 50% physiological maturity, total number of tillers, percentage of productive tillers, panicle area, thousand grain weight and harvest index.
- Traits where the additive gene action was due to female parents were days to 50% flowering, days to 50% anthesis, number of productive tillers and leaf area.
- Area aunder disease progress curve was predominantly controlled by non-additive gene action while number of productive tillers was controlled by both additive and non-aditive gene action.

- Better-parent heterosis was significantly high for all the traits but trait specific.
- For grain yield, the best five crosses had better-parent heterosis in the range 11-25%.
- The ITMV8001 x SDMV96053 performed exceptionally well with better-parent heterosis being 93%. The grain yield for the cross was equally high.
- The better-parent heterosis for rust severity at 50% physiological maturity (-48% to -59%; -33% to -50%) was much higher than the respective better-parent for area under disease progress curve (-9% to -27%; -8% to -27%) for all the traits.

6.2.4 Genotype by environment interaction analysis

The study aimed at evaluating the stability of genotyoes for grain yield and resistance to rust across environments and identifying the best performing materials for wide and specific adaption per environment.

- The first PCs explained 39%, 37% and 44% and second PCs explained 34%, 26% and 27%, respectively for grain yield, rust severity at 50% physiological maturity and area under disease progress curve for rust.
- The environments E1 and E3 were the best perfoming for the traits which also received less amount of rainfall most of which was received during the vegetative phase
- Generally the crosses were more stable, adapted and high yielding than the parents.
- GGE biplot characterised the sites into three mega environments for grain yield E1E3 with cross 1 x 14 (ICMV3771 x SDMV96053) as the winner and 6 x 8 (Shibe x CIVT9206), 5 x 12 (SDMV94001 x KatPM1) and 6 x 7 (Shibe x) and 6 x 8 (Shibe x CIVT9206) as being stable and high yielding.
- The winner for rust resistance was 1 x 7 (ICMV3771 x Exbornu) while 6 x 7 (Shibe x Exbornu), while 1 x 16 (ICMV3771 x Okollo) and 1 x 8 (ICMV3771 x CIVT9206) considered stable.
- For area under disease progress curve for rust geotype 3 x 14 (Okashana2 x SDMV96053) was the winner while 2 x 11 (Manganara x ICMV221white) and 2 x 14 (Manganara x SDMV96053) were stable.

6.3 Implications of the findings for pearl millet breeding

The participatory rural appraisal study characterised the pearl millet cropping system. Results showed that pearl millet was an important food and as well as a source of income and relevance of the crop was reflected in the majority growing it every year and attesting that it was a food security crop. However, the production environment is low input with minimal use of improved technologies to enhance productivity. There is common use of unimproved seed which is mostly purchased or saved from previous harvests. There is no soil fertility improvement, minimal access to social services like credit or agricultural training or extension. An effective breeding programme aimed at producing improved varieties should consider developing a seed delivery system since none currently exists. A poor seed delivery system is one of the key factors hindering adoption of improved pearl millet varieties in Africa (Ndjeunga et al., 2000). In addition, the productivity should be enhanced by linking farmers to social services as they also hasten technology adoption (Soleri et al., 2002) and considering their preferred traits and minimising effects of constraints. Farmers preferred varieties with stay green, tall, high tillering and early maturing traits. These are traits generally associated with drought tolerance (Vadez et al., 2012); an indicator that the improved varieties should be adapted to the farmers' drought conditions. Since in Uganda pearl millet is grown in areas associated with drought, a breeding programme should target these traits in order to hasten the adoption rate of the new materials. The programme should also consider the constraints which include ergot, rust, blast and smut diseases, Red flour beetle and Indian meal moth. Most of these constraints can be controlled through breeding for resistance. Priority should be on improving resistance to ergot and rust. Marketing and utilisation of pearl millet should be emphasised in order to hasten adoption of new technologies. The strength of the cropping system depends on the availability of household labour although other important production factors like land and seed availability, age of farmers and their education level may be limiting.

The two cycles of phenotypic S_1 progeny recurrent selection scheme were effective in improving the grain yield, rust resistance and selected yield-related traits of the two local pearl millet populations. The improved populations will further be improved for traits that had low heritability by introducing more variation for the traits which exhibited low narrow sense heritability. The improved populations will released as open pollinated varieties. The scheme can be exploited to improve traits of local populations in a relatively short time. Significant negative correlation between grain yield and rust resistance indicates a possibility of improving grain yield through selecting against rust.

For traits with predominant additive gene action, improvement can be achieved through simple selection methods or pedigree breeding. Such traits include grain yield, rust resistance, flower-anthesis interval, days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, plant height, total number of productive tillers, percentage of productive tillers, panicle area, 1000-grain weight, biological yield, harvest index and leaf area. The area under disease progress curve had non-additive gene action being predominant and can be reduced through breeding for dominance. In this case heterosis should be exploited and GxE analysis done for selected genotypes.

The multiplicative effect of GEI is a reality in obscuring the potential performance of improved genotypes and thus testing should always be done in many environments to establish their potential as being stable and adapted; for GEI obscures the potential performance of improved genotypes and thus slows the selection process for best performing genotypes. The GGE biplot may be adopted in stability assessment and identification of environment-specific genotypes because of its ease to interprete due to the three dimensional viewing of the G, GE, and the environments in one plane

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