A study of the diversity, adaptation and gene effects for blast resistance and yield traits in East African finger millet *(Eleusine coracana* (L.) Gaertn) landraces.

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Thesis Abstract

Finger millet (*Eleusine coracana*) productivity in East Africa has remained low in all production agro-ecologies for decades owing to the low yielding potential of existing that are susceptible to the blast disease caused by the fungus Magnaporthe grisea (Hebert) Barr. and the limited research on the crop. The region holds large finger millet germpasm collections whose value is not yet been fully exploited. However, with the ongoing breeding efforts through hybridization, there is a need to comprehensively characterize the germplasm to identify valuable traits to address biotic and abiotic stresses that affect finger millet productivity. Studies on gene action and inheritance of key traits that contribute to yield improvement are also required to help formulate an effective breeding strategy for finger millet improvement. The objectives of this study were to (i) determine the genetic diversity in a set of germplasm from East Africa (ii) determine association between grain yield and its component traits (iii) identify genotypes for target production agro-ecologies (iv) identify blast resistant finger millet genotypes for use in breeding and production and (v) generate information on the inheritance of blast, grain yield and yield components for the development of an effective breeding strategy.

A total of 340 finger millet accessions were collected from three countries in East Africa: Kenya, Tanzania and Uganda and 80 global minicore accessions sourced from ICRISAT-India. High phenotypic variability in the germplasm was recorded for 23 quantitative traits, blast reaction and five qualitative traits. Both morphological and molecular characterization (using SSR markers) of the 340 accessions revealed higher diversity within than among the countries Kenya, Tanzania and Uganda. Seven morphological clusters and three major genetic clusters were detected. Morphological diversity delineation was largely influenced by leaf sheath length, plant height, peduncle length, panicle exertion and grain yield. The mean polymorphic information content (PIC) of 19 polymorphic markers was 0.606 with mean alleles of 195 with sizes that ranged from 148-474 base pairs. The Kenyan and Tanzanian accessions had higher diversity than the Ugandan with the Kenyan and Ugandan, and the Kenyan and Tanzanian accessions being closely related than the Tanzanian and Ugandan. The low diversity in the Ugandan accessions could be attributed to higher research intervention in the country leading to the promotion and use of improved cultivars. Efforts have to be directed towards collection and conservation of valuable diversity before it is lost. The diversity in plant height, maturity, yield and blast reaction and the cluster groups detected in the germplasm should provide a basis for finger millet improvement through hybridization and selection.

Higher genotypic than phenotypic correlations were recorded for most of the traits studied with grain yield having high positive correlations with finger width, grains per spikelet, threshing percent, peduncle length and panicle exertion. Both grain yield and days to flowering had negative correlations with all three blast types (leaf, neck and finger). Path coefficient analysis revealed that productive tillers per plant, 1000 grain mass, grains per spikelet and threshing percent had positive direct genetic effects on grain yield with strong indirect effects from several of the other traits which necessitates simultaneous selection for those traits with strong direct effects and those with strong indirect effects for grain yield improvement. High broad sense heritability estimates and high genetic advance as percent of mean were recorded in fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, peduncle length, panicle exertion, number of leaves per plant and leaf sheath length probably indicating the predominance of additive gene effects in controlling these traits hence the potential for improvement through selection.

Adaptation and stability analysis using the GGE biplot model identified Lanet 2012 long rains, Serere 2012 long rains and Miwaleni 2012 long rains as the most discriminating environments for the low temperature, sub-humid mid altitude and dry lowland areas, respectively. Alupe 2012 long rains was the ideal environment for genotype discrimination for blast while Lanet 2012 long rains was best for grain yield. Genotypes G3, G5, G17, G25, G28, G36 and G71 were identified as being stable across environments and G1, G18, G19, G37, G54, G61, G74, G75, and G77 were found ideal for specific adaptation.

Disease severity scores were highly negatively ($P \leq 0.01$) correlated with days to flowering and grain yield suggesting that early lines suffered more disease damage leading to reduced yield. Resistant genotypes were slow blasting (probably associated with horizontal resistance) which may enable them to withstand blast pathogen variability for longer periods. Nine genotypes were identified with high resistance to blast and will be useful for breeding as blast resistance sources. Resistant genotypes had low AUDPC values and disease severity rating for the three blast types and vice-versa for susceptible genotypes. Further investigations need to be carried out to determine the possibility of the three blast types being controlled by the same genes. Early maturing blast susceptible genotypes with good yield potential could be utilized in areas with low blast prevalence.

To understand the gene action for inheritance of the various traits 16 F_2 families plus their four female and four male parents were evaluated at Alupe and Kakamega western Kenya under artificial blast inoculation. Significant additive genetic effects were recorded for all traits (except for finger width and grains per spikelet) meaning that improvement for these traits would be possible through the common

selection methods for self pollinating crops. Parent lines KNE 392, and KNE 744 and IE 11 were found to be suitable for blast resistance breeding while Okhale 1 was found to be suitable for high grain yield and blast resistance improvement due to their high desirable GCA effects. Most of the F_2 families showed transgressive segregation for the three blast types in either direction which gives hope for the development new pure lines with better blast resistance than the parents. Crosses IE 3104 x KNE 796, KAT FM 1 x Okhale 1, IE 11 x Okhale, IE 11 x P 224 and KNE 744 x KNE 392 have potential to generate lines with blast resistance due to their high desirable SCA effects. The F_2 segregation distributions for blast indicated quantitative inheritance. However the one to four minimum number of genes (effective factors) detected for resistance control in all the three blast types was not in sync with the segregation patterns in the F_2 families and further investigations are required. There were differences in segregation patterns between crosses which may suggest the presence of different resistance genes in the different parents used. This would call for gene pyramiding for durable resistance.

These results confirm the potential of sourcing valuable parental stocks in the local germplasm for the development of genotypes to improve finger millet productivity in East Africa. Already some of the high yielding and blast resistant genotypes identified here have been incorporated in the regional cultivar trials. The diversity information generated will facilitate effective conservation and utilization of this germplasm. Results of gene action for inheritance of the various traits from this study will enable breeders to develop sound breeding strategies for finger millet improvement in the region.

Declaration

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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Signed

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Eric Okuku Manyasa

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

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Dr. Paul Shanahan (Co-Supervisor)

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Prof. Githiri Mwangi (Co-Supervisor)

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Dedication

This thesis is dedicated to my dear parents, Mwalimu Gershom Manyasa (Late) and Mama Florence Nawesia and to all those who saved my life.

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Introduction to Thesis

1. Background

Finger millet (*Eleusine coracana* (L.) Gaertn) together with tef (*Eragrostis tef (*Zucc.) Trotter) belong to the grass subfamily, the Chloridoideae. It is a short day crop with the C4 photosynthetic pathway and thus has wide adaptability in diverse agro-ecologies of the tropics (Holt, 2000). It is largely a subsistence crop cultivated without supplementary irrigation by small-scale farmers and it plays an important role in the dietary needs and economy of these farmers. Africa is reported to produce 2 000 000 of the global 4 500 000 tonnes (National Research Council (NRC), 1996). Although still cultivated under traditional shifting cultivation systems in Zambia, Malawi and southern Tanzania, cultivation under modern agronomic practices is taking root in Kenya and Uganda (Oduori, 2008; Wanyera, 2007). Like any other crop finger millet in East Africa is subject to a number of constraints along the value chain. These constraints have to be addressed to improve finger millet production and productivity in the region. The potential to address abiotic and biotic constraints lies in the crop's reported significant morphological and genetic diversity (Hilu and de Wet, 1976; Kumari and Pande, 2010; Upadhyaya et al., 2010) that can be exploited in breeding new genotypes with desirable traits.

2. Importance of finger millet

The importance of finger millet lies in its long storability without insect damage and its superior nutritional value compared to other cereals. Finger millet is mainly consumed as a stiff porridge (*ugali*-in East Africa), thin porridge (*uji- in* East Africa) and to make local beer. The grain is exceptionally high in calcium (358mg kg^{-1}), iron (46mg kg^{-1}) and protein (7.4%) and has good digestibility (NRC, 1996; Serna-Saldivar and Rooney, 1995) which makes it an important food for expectant women, breast feeding mothers, children, the sick and diabetics. The main protein fraction eleusinin has significant amounts of tryptophan (1.3 g per 16g N), cystine (1.7g per 16g N), methionine (2.9g per 16g N) and total aromatic amino acids (phenylalanine and tyrosine) (NRC, 1996). White seeded types have higher protein levels than brown and red types which contain higher levels of tannins. The grain is also used in malting and brewing because of its high amylase enzymes which convert starch into sugar and as an adjunct in beers made from maize (*Zea mays*) and sorghum (*Sorghum bicolor*) (Obilana and Manyasa, 2002a). Foods made from sprouted grain (malt) are easily digestible and provide good nutrition for children and the elderly (NRC, 1996). Finger millet foods also have a high satiety value derived from the high fibre

content (3.6% of crude fibre) which slows the digestion rate. The husks have fibre and are valuable in poultry feed. Being gluten free, finger millet has a global potential in sub-regions where demand for gluten free products is increasing (Lenné et al., 2007). The straw can be used as feed/fodder for livestock and contains up to 60% total digestible nitrogen (NRC, 1996). Commercialization of finger millet in East Africa is steadily increasing. There are a number of small, medium and large commercial millers who mill the grain into acceptable flours (pure finger millet, composite flour and porridge mixture) that are readily available in leading supermarket outlets (Obilana, 2002; Lenné et al., 2007). However for commercialization to grow sustainably, effort must be put into increasing the productivity and production of finger millet.

3. Finger millet production in East Africa

In East Africa, finger millet covers 50% of the area cultivated to both finger and pearl millets (Riley et al., 1993; Obilana, 2002). Regional domestic demand for finger millet grain coupled with increased regional trade and higher market prices relative to other cereals has seen a 25% rise in production over the last 30 years (Lenné et al., 2007). Finger millet is grown in over 800 000 ha in the three East African countries with Uganda having about 470 000 ha, Tanzania about 350 000 ha and Kenya about 77 890 ha (Table 0.3-1) (ICRISAT, 2013). In Uganda, the districts of Tororo, Iganga, Kamuli and Soroti in the East and Apac, Lira, Gulu and Kitgum in the North produce about 60% of the total production (Waswa and Odelle, 1995; Wanyera. 2007). These are also the districts where finger millet is the staple food. In Tanzania more than half of the production is from southern highlands sub-regions of Mbeya, Iringa, Ruvuma and Rukwa (Kisandu et al., 2007). In Kenya the crop is mainly grown west of the Rift Valley in Teso, Busia, Kakamega, Kisii and Rongai districts (Oduori, 2008). Average grain yields in Kenya and Tanzania are about 0.6 t ha^{-1}, but yields are slightly higher in Uganda at 1.8 t ha^{-1} (Table 0.3-1). However, in the major finger millet producing districts of Kenya and Tanzania, yields of over 2.5 t ha^{-1} have been realized (Oduori and Kanyenji, 2007). The higher yields in Uganda are largely due to earlier research on finger millet that led to the release of several improved high yielding and blast resistant cultivars and the high regard for finger millet as a staple food in the main producing districts. However, the low attention given to the crop by the national and international research systems as well as indifferent government policies have contributed greatly to its productivity potential not being fully realized. With appropriate research and extension interventions, it is possible for farmers to realize the grain yields of 3-4 t ha^{-1} reported from on-station and on-farm testing in Kenya and Uganda (Odelle, 1993; Odouri and Kanyenji, 2007) and in Ethiopia and India (Mulatu and Kebede, 1993; Bondale, 1993). Amidst these low production volumes,

finger millet demand in East Africa is growing. One major finger millet processor in Kenya has a monthly throughput of 500-800 tonnes and 90% of this is imported mostly from Tanzania (Lenné et al., 2007).

Table 0.3-1. National finger millet production in Kenya, Uganda and Tanzania during 2007-2011

Country	**Year**	**Area (hectares)**	**Production (metric tonnes)**	**Yield (t ha^{-1})**
Tanzania				
	2007	270243	218897	0.81
	2008	213972	149780	0.70
	2009	398506	310835	0.78
	2010	345855	349314	1.01
	2011	350000	234500	0.67
Kenya				
	2007	89680	83719	0.93
	2008	37209	26897	0.72
	2009	73203	39492	0.54
	2010	69387	37717	0.54
	2011	77890	51377	0.66
Uganda				
	2007	437000	732000	1.68
	2008	448000	783000	1.75
	2009	460000	841000	1.83
	2010	470000	850000	1.81
	2011	-	-	-

Source- ICRISAT, 2013.

Most of the finger millet in East Africa is sold through local markets where prices are unstable depending on supply and demand conditions. Even where large processors are involved, grain is sourced through middlemen who buy from local markets or individual farmers. Ironically prices offered by the formal markets like the National Cereals and Produce Board in Kenya are usually lower than what the local markets offer (Mitaru et al., 1993). If the constraints along the production to consumption chain are adequately addressed, finger millet could form an integral part of the agricultural cash economy in the finger millet farming systems of East Africa.

4. Constraints to finger millet production and productivity

In spite of its salient role in the livelihoods of millions of households in East Africa for food security, nutrition and cash income generation, several constraints inhibit the crop's potential productivity. Key among these constraints are limited understanding and utilization of the genetic diversity of the region's germplasm, lack of high yielding improved cultivars for the different finger millet production agro-ecologies, high levels of blast disease caused by the fungus *Magnaporthe grisea* (Herbert) Barr, poor crop husbandry, infestation by the striga weed (*Striga hermontheca* (Del.) Benth) and lack of adequate policy support (Sreenivasaprasad et al., 2007). In East Africa blast was first recorded in Uganda in 1933 (Emechebe, 1975) and has subsequently been reported to occur in all finger millet growing areas of East Africa (Obilana and Manyasa, 2002b; Wanyera, 2007; Kisandu et al., 2007). It is the major biotic constraint in finger millet productivity in the three East African countries. Most cultivated landraces are susceptible with grain yield losses of up to 60% (Pande, 1992; Obilana and Manyasa, 2002b). Most of the cultivars grown by farmers are un-improved, with low grain yields and are susceptible to blast disease. Research support for finger millet in the region has been dismal relative to what is accorded to maize, sorghum, rice (*Orza sativa*), wheat (*Triticum aestivum*) and industrial crops. Likewise international donor support has been negligible (Lenné et al., 2007) possibly because of the regard for finger millet as a low 'value' crop.

5. Way forward

The possibility of addressing finger millet productivity constraints through breeding has been demonstrated via selection for blast resistance and high yields in the local germplasm in East Africa. This has led to the release of a few blast resistant high yielding cultivars in the last two decades. Apart from the 5844 finger millet accessions kept in the global finger collection at ICRISAT (Upadhyaya et al., 2007), Kenya holds about 1000 accessions (Bennetzen, 2003) and Uganda was reported to hold over 2000 accessions by 1993 (Odelle, 1993). No official figures are available from Tanzania but based on reports by Chambo (1993), Kisandu et al. (2007) and Manyasa and Kisandu (2010), the national genebank could be holding up to 352 accessions. These germplasm banks are a repository from which to access key traits to address biotic and abiotic stresses that affect finger productivity like blast, low yield and poor agro-ecological adaptation. However, the germplasm held by the three East African countries remain largely unutilized due to limited characterization and evaluation. There is an urgent need to characterize the conserved germplasm as well as the new collections to understand the degree of genetic diversity and

value of the germplasm for use in breeding. Understanding variability should also be coupled with knowledge of the associations between traits that contribute to finger millet yield through well designed breeding. Knowledge of the diversity in the germplasm will also help in identification of diverse potential parents for hybridization to generate new cultivars with desired traits. However, understanding of gene action and trait inheritance of the target traits will be required to help formulate an effective breeding strategy.

6. Statement of the problem and justification

For a long time finger millet has been neglected by mainstream research and earned the name 'orphan crop'. However, the crop's growing importance in East Africa has enhanced its importance to researchers and other stakeholders along the production-supply chain. Socioeconomic surveys in Kenya and Uganda in 2002 and the Stakeholders Workshop in 2005 (Mgonja et al., 2007) did provide insight into finger millet production systems including farmers/industry practices and preferences, patterns of use, blast disease incidence/severity and other value chain constraints (Obilana and Manyasa, 2002b; Mgonja et al., 2007). Among the priority constraints were the poor understanding of the value of the region's germplasm and limited or lack of blast resistant high yielding cultivars for the different finger millet agro-ecologies. Although a large number of finger millet collections have been made, only a small fraction of the total available collections have been characterized and evaluated or used in breeding programmes. The value of the region's finger millet germplasm is therefore not well understood. To help formulate an effective breeding strategy, an understanding of the breeding value of the landraces and the mode of gene action for the key traits is essential. Studies on inheritance and gene action for finger millet traits are limited in the region with the only study reported being that of Oduori (2008).

This study involved phenotypic and molecular characterization of finger millet germplasm from different production agro-ecologies in Kenya, Tanzania and Uganda as well as evaluation for adaptation, trait association, productivity and blast resistance. A genetic study to understand gene systems responsible for blast resistance, grain yield and yield components inheritance was also undertaken to help in the development of an effective breeding strategy.

7. Research Objectives

The specific objectives of the study were to:

- determine the genetic variation in the germplasm for effective conservation and utilization;

- determine the association between grain yield and its components and levels of heritability of traits;
- identify blast resistant finger millet genotypes for use in breeding;
- determine adaptation and stability of finger millet genotypes across contrasting production agro-ecologies,
- determine inheritance of blast, grain yield and yield components in finger millet; and
- determine combining ability for blast and grain yield and its components in East African finger millet germplasm.

8. Hypotheses

- There is genetic variation among the finger millet landraces cultivated in East Africa.
- There is differential productivity potential and reaction to blast disease among the landraces.
- There is high association between grain yield and its components that could be utilized for indirect selection for grain yield.
- Performance of finger millet for agronomic traits is stable across environments.
- Genetic systems controlling blast and grain yield traits in finger millet are predominantly additive.

9. Thesis structure

The specific objectives were addressed in the various chapters that make up this thesis. Each chapter is an independent, potential manuscript for journal publication hence there may be some overlap in content and references. The chapters appear as follows:

1. Introduction to thesis
2. Chapter 1: Literature review
3. Chapter 2: Morphological diversity in East African finger millet landraces
4. Chapter 3: Genetic diversity in East African finger millet landraces based on SSR markers and some qualitative traits
5. Chapter 4: Correlations, path coefficient analysis, heritability and genetic advance for quantitative traits in finger millet landraces
6. Chapter 5: Genotype x Environment interaction, yield stability and blast reaction in East African finger millet landraces
7. Chapter 6: Gene action for blast resistance and grain yield traits in finger millet
8. Chapter 7: Overview of the research findings

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Chapter 1

Literature review

1.1 Finger millet origin, botany and taxonomy

Finger millet (*Eleusine coracana (L.)* Gaertn) has its centre of origin in eastern Africa and is thought to have been domesticated in areas extending from western Uganda to the highlands of Ethiopia (Harlan, 1971; de Wet, 1995). It later spread to Asia reaching India about 3000 years ago. It then spread to southwest India in the Himalayas, Nepal and along the hills of southern Asia and east China. It belongs to the family Poaceae and subfamily Chlorodoidae. There are two known sub-species, the cultivated *Eleusine coracana* subsp. c*oracana* (L.) Gaertn and the wild type *E. coracana* subsp. a*fricana* (Kenn.-O'Byrne) (Upadhyaya, 2006). It is a tetraploid (2n = 4x = 36; AABB) (Dida et al., 2008). Two diploid species *Eleusine indica* (L.) Gaertn (AA) and either *E. tristacya* (Lam.) Lam or *E. floccifolia* (Forssk.) Spreng (BB) were thought to be the genome donors (Hilu and de Wet, 1976a; Hiremath and Salimath, 1992; Gupta et al., 2010). However, de Wet (2006) suggested that *E. coracana* was descended from *E. africana*, a tetraploid, through mutation since the two species do cross to form fertile hybrids. Although genomic data has confirmed a close genetic relationship between *E.coracana* and *E. indica*, no evidence of genetic association with *E. floccifolia* has been found (Neves et al., 2005) thus strengthening the theory of mutation from *E. africana*. Based on vegetative, floral and seed morphology, Hilu and de Wet (1976b) classified finger millet into three eco-geographical races viz: African highland race that is found in the East African highlands, lowland race found in the lowlands of Africa and south India and the Indian race found in north east India.

Finger millet is an annual grass that grows to a height of 40-130 cm producing numerous tillers with diverse maturity periods ranging from two and half to six months [National Research Council (NRC), 1996]. This diversity attests to the versatility of finger millet in terms of production agro-ecolgies. The stems are prominently flattened, erect and hairy. Leaf blades are linear and tapering with ciliated margins. The culms are typically green in colour with green or purple nodes. The inflorescence consists of spike-like main branches that are open, incurved or compact and arranged like fingers on a hand (Rachie and Peters, 1977). Purple plants with compact panicles have been associated with resistance to blast disease caused by *Magnaporthe grisea* (Herbert) Barr in finger millet (Takan et al., 2004). Florets are completely covered by glumes leading to near complete self-pollination. The florets are very small making manual

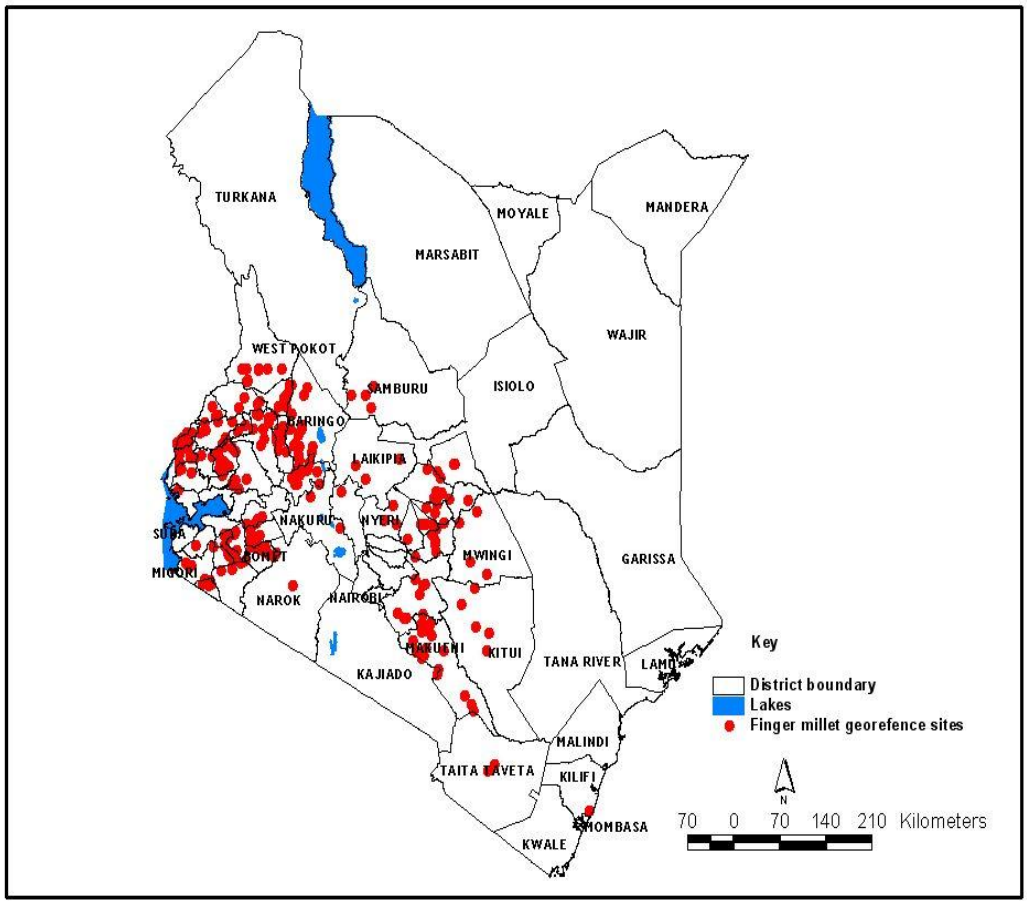
emasculation difficult which has over the years limited hybridization to generate new cultivars (Hilu and de Wet, 1980; NRC, 1996). Seeds are largely non-dormant although seeds of *Eleusine indica* (wild relative) exhibit dormancy and can remain viable in the soil for up to two years (Kulkarni and Basavaraju, 1976; Chuah et al., 2004). The grain is spherical with a pericarp that is not fused to the seed coat and varies from almost black, orange red to white in colour (NRC, 1996**).** Breeding success will largely depend on the genetic variability in the crop. High diversity for the various traits is expected in the East African germplasm since the region is the primary centre of origin of the crop. Success in finger millet improvement in the region through selection and hybridization of appropriate genotypes should be achievable.

1.2 Crop adaptation

Finger millet has a wide adaptation and is cultivated from 0-2 400 m above sea level within annual precipitation range of 500 to 1000 mm (Rachie and Peters, 1977) thus making it suitable for areas with short and long seasons and low and high temperatures (18-35°C). Differential adaptation to temperature has also been reported with two distinct classifications of lowland and highland races (NRC, 1996). However, good rainfall distribution over the growing period with dry weather at harvesting for grain drying are essential. Heavy rains at flowering reduce seed set. The crop does best on lateritic and well drained alluvial soils and tolerates some degree of alkalinity but not water logging (Obilana and Manyasa, 2002a; de Wet 2006). In East Africa the finger millet production agro-ecologies have different biotic and abiotic stresses to finger millet productivity. In the Lake Victoria zone and southern highlands of Tanzania (close to Lake Tanganyika), high rainfall, humidity and temperatures favour blast disease development (Chambo, 1993; Kisandu et al., 2007; Wanyera, 2007; Oduori, 2008). These sub-regions require cultivars that are not only high yielding but also resistant to blast. In the cool high elevation production areas in the Rift valley, low temperatures at flowering affect pollen viability leading to poor seed set. These areas require cultivars that are cold tolerant. In the lowland areas of eastern Kenya, rainfall is low and erratic and the crop suffers moisture stress. These areas require cultivars that are early maturing. These limitations call for concerted breeding efforts to identify suitable cultivars for the various agro-ecologies for finger millet productivity. This requires use of sufficient test locations that reveal adaptive characteristics needed for target production areas (Andrews, 1993).

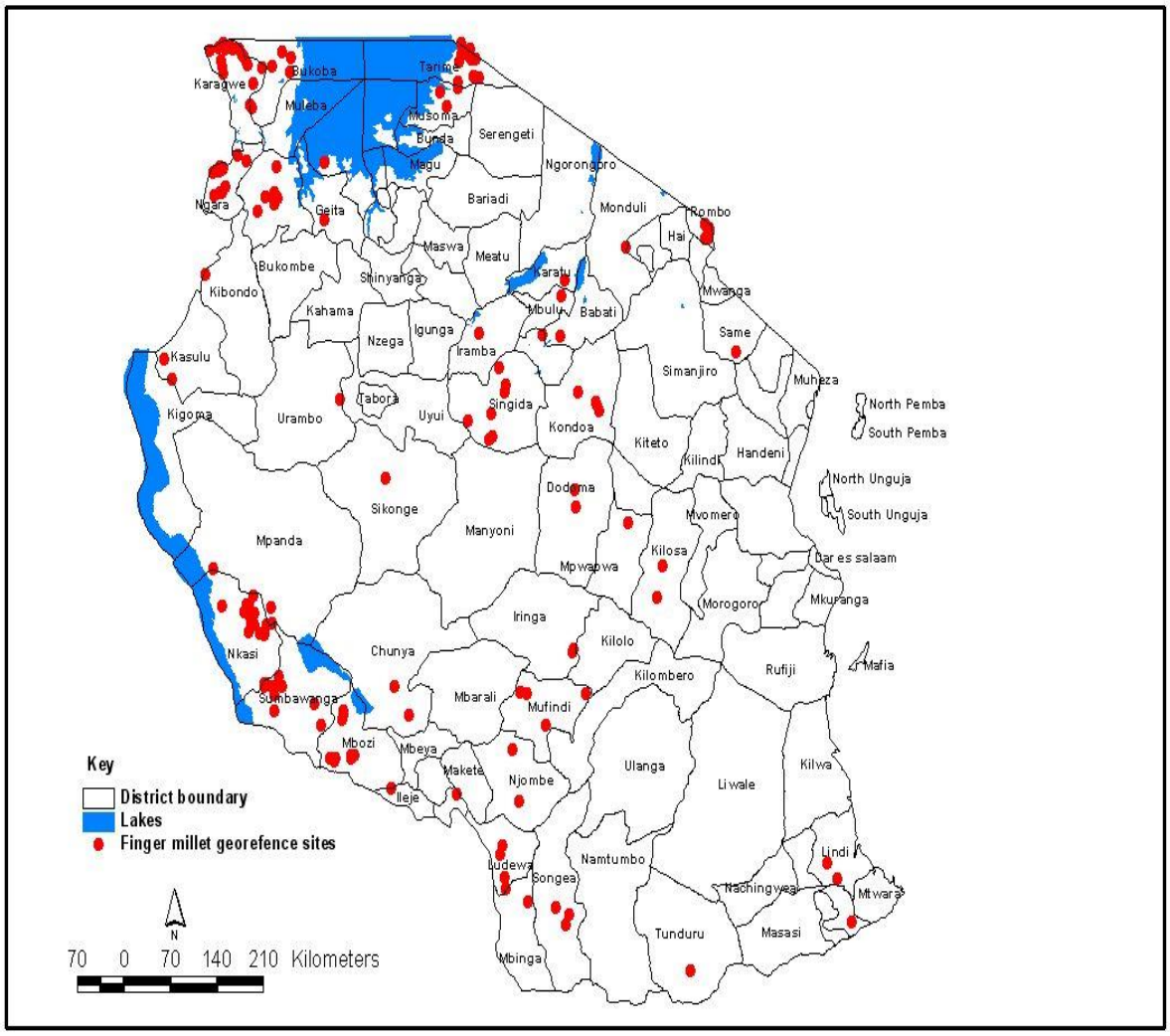
1.3 Finger millet breeding and research in East Africa

Finger millet research in East Africa started in the 1940s at Ukiriguru, Tanzania but regional research picked up in the 1960s at Serere research station in Uganda (Chambo, 1993; Odelle, 1993). Extensive germplasm collections were carried out in Kenya and Uganda in the 1980s but less so in Tanzania (Kisandu et al., 2007; Oduori, 1993; Wanyera, 2007) (Figures 1.3-1, 1.3-2, 1.3-3). Additional collections were made in 2010 in Tanzania and Uganda. However, much of this germplasm remains largely uncharacterized and hence its genetic value is not well understood. Crop improvement activities have largely been based on selection from farmer materials and introductions through regional crop networks in East Africa and from ICRISAT-India except in Uganda where both selection and hybridization have been used successfully (Odelle, 1993). Hybridization work in Kenya started in 2001 (Oduori, 2008). Much of the success in selection and/or hybridization efforts were realized in the Ugandan program where a few high yielding cultivars with blast resistance among them P 224, Gulu E and U 15 were identified and have been released in the three East African countries. However, these cultivars have been in cultivation for a long time and are starting to succumb to blast (personal observation). There have been limited or no studies carried out to understand the association, inheritance and gene action for finger millet traits in the region that would help formulate an effective breeding strategy. Due to limited resources much of the selection and evaluation is confined to specific test sites without multi-environment testing thus limiting the realization of the potential of more general adaptation in some of the genotypes.



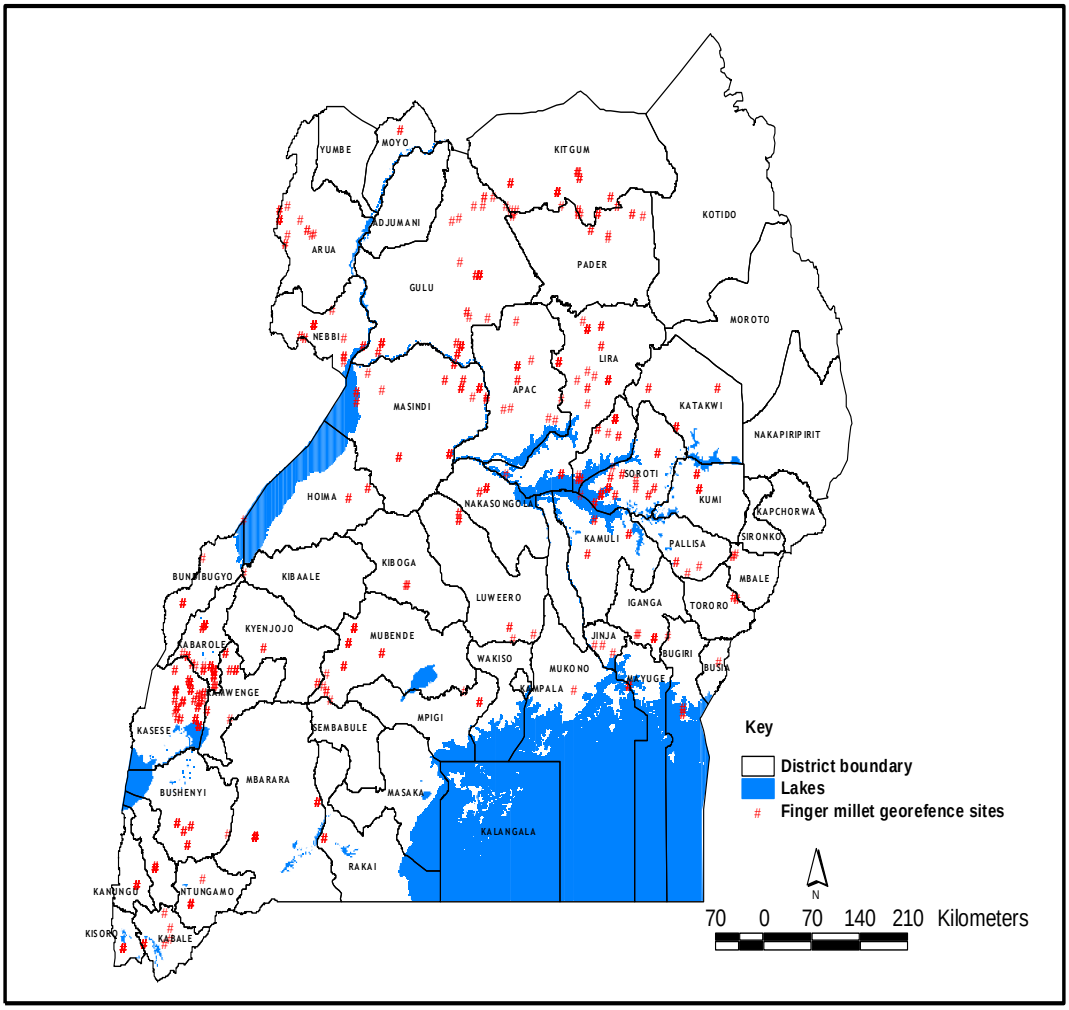
Source: ICRISAT (2010)

Figure 1.3-1. Map of Kenya showing geo-referenced sites of finger millet collections



Source: ICRISAT (2010)

Figure 1.3-2. Map of Tanzania showing geo-referenced sites of finger millet collections



Source: ICRISAT (2010)

Figure 1.3-3. Map of Uganda showing geo-referenced sites of finger millet collections

1.4 Genetic diversity

The role of genetic variation from traditional landraces and wild species in the improvement of cultivated plants has been well recognized (Thomas and Mathur, 1991; Rao and Bramel, 2000). However, the value of plant genetic resources largely depends on richness of the collection, extent of characterization/evaluation and access to information and the germplasm itself. Evaluation of germplasm for response to biotic and abiotic stresses and identification of farmer and market preferred traits are key factors in its effective utilization for improved crop productivity (Manyasa et al., 2008). Investment in studies to determine the genetic diversity is important, for this knowledge enables proper organization and

development of improved parents and new cultivars. Morphological and agronomic traits have been widely used in the characterization and evaluation of various crops (Rick and Holle, 1990; Kaemer et al., 1995) and help understand the agronomic value of the germplasm and define potential divergent heterotic groups for use in hybridization (Ortiz et al., 1998). Use of morphological traits therefore increases the understanding of genetic variability within the germplasm thus enabling its proper management and utilization for breeding and production. Morphological characterization is relatively easy, reliable and low in cost. Genetic markers have become useful in enhancing the understanding of the diversity of natural variation especially in species where appropriate polymorphic markers are available. Over the last decade, a number of DNA markers have been developed and used in the study of crop genes, genome and genetic diversity. Therefore, agro-morphological evaluation and molecular analysis of germplasm are useful in diversity determination because they provide complementary information and increase the resolution of genetic diversity analysis (Dida et al., 2008).

1.4.1 Diversity studies in finger millet

The East African region being the primary centre of finger millet diversity boasts of a wider genetic base for the crop and large germplasm collections are held in the countries' genebanks. These East African germplasm pools however, remain largely uncharacterized and hence unutilized (Kisandu et al., 2007; Oduori and Kanyenji, 2007; Wanyera 2007). In Uganda, the civil strife in the 1970s and early 1980s led to loss of some landraces (Wanyera personal Communication). The *ex-situ* collection at the National Semi-Arid Research Institute (NASARRI) has been reduced from the original 2000 to 1000 accessions due to circumstances beyond the breeder's control (Wanyera, personal **c**ommunication). Even at global level, Upadhyaya (2010) reported that only 1% of the total germplasm has been used in crop improvement largely due to lack of data and information yet many germplasm lines evaluated have been found to be superior for specific traits and utilized either for breeding or direct release as cultivar. Moreover, to be able to discern and appreciate diversity and adaptation for production and productivity of the germplasm, there is need to characterize and evaluate the germplasm within countries of collection and/or in similar target production agro-ecologies.

Cultivated finger millet is reported to have a narrow genetic base (Dida et al., 2007). However, phenotypic variation has been observed by many authors in a number of germplasm collections assessed. Using 150 accessions from Africa and Asia, Hilu and de Wet (1976a) reported variability in vegetative, floral and seed morphology based on eco-geographical origin and were able to distinguish three eco-geographical races namely African highland race, lowland race and the Indian race. The variability

observed was mainly contributed by flag leaf sheath length, flowering culm branches, culm diameter and seed colour. In Ethiopia, Bezaweletaw et al. (2006) characterized 66 accessions and found high variability among the accessions for all agronomic traits. High variability for productive tillers was also reported by Ganapathy et al. (2011) and Reddy et al. (2009). Phenotypic diversity was recorded in 2000 accessions from East Africa and India and effectively used to group the material into six races namely africana, spontenea-wild types, elongate, plana, compacta and vulgaria (Reddy et al., 2009). The variability reported indicates the potential for finger millet improvement through selection.

The use of molecular markers to study diversity in finger millet has been limited due to the limited understanding of the finger millet genome and unavailability of adequate polymorphic markers (Dida et al., 2007). The finger millet genome has only recently been studied and a few markers identified. Upadhyaya et al. (2008) used 20 Simple Sequence Repeat (SSR) markers to characterize over 900 finger millet accessions at ICRISAT-India, revealing 231 alleles and identifying unique alleles distinguishing accessions from East Africa, southern Africa and south Asia. Although Dida et al. (2008) reported the availability of more than 200 SSR markers in finger millet suitable for mapping critical traits, they only reported the successful use of 45 of the markers for finger millet diversity studies. The 45 markers were used together with phenotypic data on 79 accessions from India and Africa and found three groups based on origin namely African, Asian and African x Asian hybrids with low variability in Asian accessions suggesting that they originated from a small genepool. Sinha and Pande (2010) using six homologous and seven heterologous SSR primer pairs found homologous primer sets more appropriate as they revealed high polymorphic alleles. Random amplified polymorphic DNA (RAPD) markers have also been used in finger millet diversity studies revealing high polymorphism in African landraces and low polymorphism in Indian landraces and improved lines (Fakrudin et al., 2000). The low diversity in improved types could be due to genetic loss through selection over time. Other researchers among them Gupta et al. (2010), Das et al. (2006), Salimath et al. (1995), Babu et al. (2007) and Kumari and Pande (2010) also reported successful use of RAPD markers to study diversity in finger millet. Because of low variability within cultivated finger millet types a large number of highly variable markers such as SSRs are required for molecular analysis (Dida et al., 2007). The SSRs have a high level of allelic diversity as a result of the variable number of repeat units within their structure, making them valuable tools for diversity studies (Morgante and Olivieri, 1993). They are often multi-allelic and can be multiplexed and automated for high-throughput genotyping (Tommasini et al., 2003). They are also characterized by hyper-variability, abundance and reproducibility and are co-dominant hence are able to identify heterozygotes which makes them a suitable option for mapping and molecular characterization (Morgante and Olivieri, 1993; Saghai-Maroof et al., 1994).

1.5 Association between traits

Although many trait relationships are useful in selection, grain yield with associated desirable traits form a key consideration for all crop breeders. Trait associations are always explained by correlation estimates with observed and true relationships being explained by phenotypic and genotypic correlations, respectively (Sonnad, 2005). However, yield is a complex trait and it is influenced by its various components directly as well as indirectly by other traits (Wolie and Dessalegn, 2011). Correlation coefficients alone do not elucidate precisely the nature of association between traits or how change in a trait affects the associated trait (Dabholker, 1992). To address this deficiency, path correlation coefficient, a standardized regression coefficient developed by Wright (1921) disaggregates the correlation coefficient into direct and indirect effects of various traits towards a dependent variable (Das et al., 2004; El-Din et al., 2012). Though not extensive, several studies have reported on the correlations and path coefficients of traits in finger millet. Gupta and Mushonga (1992) found high correlations between grain yield and days to 50% flowering, 1000 grain mass and threshing percent. In Ethiopia and India, respectively, Wolie and Dessalegn (2011) and Thakur and Saini (1995) reported that grain yield was positively correlated with finger length, fingers per panicle and panicles per plant but negatively correlated with plant height and days to maturity. Using path analysis Shanthakumar (1988) found grain yield to be more influenced by panicle mass per plant. Bendale et al. (2002) recorded direct effects on grain yield from days to 50 % flowering, date of finger emergence and finger length and width, whereas Bharathi (2011) reported high direct effects on yield from number of basal tillers, flag leaf blade width and panicle length. Ravikumar (1988), Wolie and Dessalegn (2011) and Bharathi (2011) reported correlations and direct and indirect effects of various traits on yield in finger millet. In East Africa, other than the study by Oduori (2008), no other literature is available on association and path coefficient analysis for finger millet traits. Understanding trait associations is useful in designing a selection strategy to improve finger millet productivity, hence more comprehensive studies are needed to generate information based on the region's germplasm and environments.

1.6 Heritability and genetic advance

Response to selection is mainly influenced by heritability and selection intensity (Allard, 1960). Better understanding and management of the genotype–environment complex are essential to the breeder to maximize actual gain from selection. Heritability specifies the proportion of total variability due to genetic causes (Allard, 1960) and heritability estimates for a trait are usually specific to a particular

population raised in a specific environment (Falconer, 1981). Broad sense heritability is due to the influence of both additive and non-additive gene effects (Johnson et al., 1955; Ganapathy et al., 2011). Traits with high heritability (in broad and narrow sense) are less influenced by the environment and will respond better to selection. According to Johnson et al. (1955) broad sense heritability estimates alone do not give an indication of response to selection hence the importance of using heritability together with genetic advance expressed as percent of parental mean. Estimates of broad sense heritability and genetic advance as percent of the parental mean are important statistics that provide an indication of the progress that potentially will be realized through selection in a breeding programme (Adewale et al., 2010). Several studies in finger millet have found high heritability (> 50%) and genetic advance as percent of mean (> 20%) in finger length and width (Bezawelataw, 2006), productive tillers per plant, fingers per panicle and dry mass (John , 2006), days to 50% flowering, days to maturity and plant height (Thakur and Saini, 1995), days to flowering, plant height, productive tillers per plant, fingers per panicle, finger length and grain yield per plant (Ganapathy et al., 2011) and in days to 50% flowering, productive tillers per plant, days to maturity and finger length (Mishra et al., 1980) among others. The large finger millet germplasm stocks held by the national genebanks in East Africa have least been subjected to heritability and genetic gain studies to better understand the potential of using selection for trait improvement.

1.7 Blast disease of finger millet

1.7.1 Blast pathogen variability and distribution

Out of the sixteen fungal, three viral, and one bacterial pathogen reported to infect finger millet (Rachie and Peters 1977) blast caused by *Magnaporthe grisea* (Herbert) Barr is the most destructive (Pande, 1992). Blast is endemic to all finger millet growing sub-regions of Asia and Africa (Seetharam and Ravikumar, 1994). Roumen et al. (1997) and Takan et al. (2012) have reported on the genetic variability of the blast pathogen isolates from both rice and finger millet. Studies by Takan et al. (2012) on genetic diversity of East African blast populations in finger millet found a wide range of haplotypes with a continuous genetic variation pattern and a strong sexual reproductive potential. Srivastava et al. (2009) found high probability for male and female sterile *M. grisea* isolates in pathogen populations in finger millet from southern and northern India but detected probability for sexual reproduction in the populations of *M. grisea* from central Himalayas. Earlier reports by Uddin (2000) had found sexual reproduction to be rare in the blast pathogen in rice. Takan et al. (2012) also found common haplotypes in Kenya and Tanzania. According to McDonald and Linde (2002), pathogens with a mixed reproductive system as reported in finger millet pose the greatest risk of breaking down resistance genes. On the basis

of presence or absence of the grasshopper DNA repeat element (*grh*) found only in Asian haplotypes, Tanaka et al. (2009) suggested that *Eleusine* isolates could be divided into two genetically distinct subgroups viz. African and Asian types. However, Takan et al. (2012) detected a few haplotypes in East Africa carrying the *grh* element and they attributed this to recent germplasm exchanges. Pande (1992) and Takan et al. (2004) also found isolates causing leaf, neck and finger blast to be genetically similar suggesting the role of the same strain in different blast types. In India Ramakrishnan (1948) found similarity in morphological characters among four isolates of *M. grisea* from rice, finger millet and *Digitaria indiginata*. Pande et al. (1995) reported *M. grisea* to be seed borne but the pathogen was confined to the pericarp and not in the embryo. The findings by Takan et al. (2012) on the predominance of sexual reproduction provides a new dimension and calls for a rethink on breeding strategies to counter the rapid evolution of the pathogen that would otherwise lead to quicker breakdown of host resistance. Breeding for blast resistance would therefore have to focus on horizontal resistance to counter pathogen variability. Success in managing blast using genetic resistance will also have to be complimented by effective control of blast pathogen host weeds, debris management and appropriate finger millet seed treatment.

1.7.2 Conditions for blast disease development and disease symptoms

The source of blast infection in the field is from seed and previous seasons' crop debris. Many weedy relatives like *E. indica* and *E. africana, Digitaria spp., Setaria spp*. and *Doctylocterium spp*. are alternate hosts of the blast pathogen and play an important role in disease epidemiology since these serve as primary sources of inoculum (Sreenivasprasad et al., 2007). The seed borne nature of the pathogen is largely confined to the pericarp (Pande, 1992; Hayden 1999). Blast infection is promoted by cloudy skies, frequent rain and drizzles, which support accumulation of dew on leaves for a long time. The rate of sporulation increases with increasing relative humidity >89% and for pathogen germination, the optimum temperature should be 25-28 °C. The fungus also establishes better on plants grown in soils with high levels of nitrogen (Sreenivasaprasad et al., 2007, Hayden, 1999). Nitrogen supply influences branching and leaf expansion leading to a large canopy that is conducive to spore transfer and pathogen infection (Kurschner et al., 1992). Finger millet blast is characterized by the appearance of lesions on the leaves, nodes and heads. On the leaves, lesions are typically spindle-shaped, wide in the centre and pointed towards either end [Figure 1.7-1 (i)]. Large lesions usually develop a grayish centre, with a brown margin on older lesions. Under blast disease-conducive conditions, lesions on the leaves of susceptible lines expand rapidly and tend to coalesce, leading to complete drying of infected leaves. Resistant plants may develop minute brown specks, indicative of a hypersensitive reaction. When the area between the leaf

blade and leaf sheath (leaf collar) is infected, the collar turns brown and dies. The fungus also attacks the neck (section between the ligule of flag leaf and the base of the inflorescence) causing neck rot [Figure 1.7-1 (ii)]. When the neck is infected, all parts above the infected section may die (Sreenivasaprasad 2004). When this occurs, yield losses may be large because grain formation is inhibited and/or formed grains may be shriveled. In such cases yield losses may be as high as 90% (Ekwamu, 1991). The panicle phase of the disease is the most destructive causing non-formation of grain or poorly filled shriveled grain (Pande, 1992; Takan et al., 2012). One, several or all fingers could be affected [Figure 1.7-1 (iii)]. The fungus infects the panicle as seeds form causing gray brown lesions on the fingers.

(i) (ii) (iii)

Figure 1.7-1: (i) Leaf blast (ii) Neck blast and (iii) Finger blast symptoms

The major finger millet production agro-ecologies in East Africa fall within the sub-humid environments where conditions favour blast pathogen development and wild relatives of finger millet are present as alternate hosts of the pathogen. Several options are available for the management of blast among them: use of clean seed; use of optimum plant populations (very high densities enhance blast development due to high dew accumulation on leaves); weed management to eliminate alternate hosts; planting resistant cultivars; and chemical control using fungicides e.g. Benlate, Bavistin, Dithane M45 and Mancozeb (Prqdhanang and Abington, 1993; Bua and Adipala, 2008). Chemical blast control, though effective to a reasonable level, is a very expensive option for the resource poor farmer and use of resistant cultivars (where available) is the most viable and cost effective approach for blast control in finger millet. So far a few cultivars with blast resistance have been identified through selection and released in the region and more need to be developed to manage the pathogen variability as reported by Takan et al. (2012). Screening the sub-regions germplasm needs to be a priority to identify blast resistant sources for breeding and direct utilization.

1.7.3 Blast screening

The key to disease resistance breeding is dependent on availability of sources of resistance to the disease. These sources could be cultivated genotypes or wild relatives of the crop. Blast resistance is often evaluated in the field in hot spot areas under natural infection (Nagaraja, 2010). This sometimes provides opportunity for escapes leading to spurious resistance being identified (Thakur et al., 2009). To avoid disease escape artificial inoculation either in the field or in the greenhouse is carried out. However field inoculation is more appropriate as it helps the breeder know whether the results from artificial inoculation are consistent with those obtained under natural infection conditions (Lübberstedt et al., 1999). Blast research through host resistance in East Africa was reported in Uganda as early as 1958 when a finger millet line, Mozambique 359 was used as a source of resistance in a breeding program to transfer resistance to local Uganda lines (Rachie and Peters, 1977). Subsequent research activities have seen several blast resistant lines developed for example Gulu E, Seremi 1, Seremi 2, Pese 1, SX 8, and SEC 915 and subsequently released in East Africa (Lenné et al., 2007; ICRISAT, 2013). Several authors have also reported on blast resistant sources in finger millet germplasm evaluations. Somasekhara et al. (1991) found no cultivar to be resistant to leaf blast but identified line IE 1012 to be immune to neck and finger blast under field screening. Fakrudin et al. (2000) identified lines IE 2912, IE 2885 and IE 2912 to be resistant to both leaf and finger blast. Partial or slow blasting resistance has also been reported in both finger millet and rice (Parlevliet, 1988; Pande, 1992; Sunil and Anilkumar, 2003; Wu et al., 2005). Slow blasting cultivars were found to have low levels of neck and finger blast. Partial resistance has been reported to be horizontal thus long lasting and more stable (van Der Plank, 1963). Several plant qualitative traits have also been associated with blast resistance. Pigmented plants with compact panicles and dark seed have been associated with blast resistance (Pande, 1992; Takan, 2004; Krishnappa, 2009a). Reports by Takan et al. (2004) and Obilana and Manyasa (2002b) from surveys in Uganda and western Kenya indicated that cultivars with dark coloured seeds and compact heads had less blast than lighter coloured and open headed cultivars. Plant pigmentation (reddish brown or brown pigments) has been useful in crossing as a marker in identification of F_1 plants (Krishnappa et al., 2009b). The identification of blast resistance through germplasm screening in Uganda is an indication of the existing potential of the region's finger millet germplasm which needs to be exploited for enhanced finger millet productivity. More blast resistant sources need to be identified to counter chances of resistance breakdown in the few improved resistant cultivars due to blast pathogen variability.

1.8 Genotype x environment Interaction

Genotypes will perform differently from one agro-ecology to the other and likewise within a location, performance will vary across seasons. Time to flowering is dependent on photoperiod and temperature. According to Turner and Turner (2009) high temperatures lead to shortened time to flowering and maturity in photoperiod insensitive crops until an optimum temperature is reached above which days to flowering increases with increasing temperature. High temperatures have been found to reduce time to flowering in both short and medium duration sorghum (*Sorghum bicolor*) and pigeonpea (*Cajanus cajan*) genotypes but prolonged the time to flowering in long duration pigeonpea types (Silim et al., 2006; Manyasa et al., 2008). Finger millet blast is prevalent in areas of high rainfall, humidity and temperatures, causing grain yield losses of up to 60 - 90% (Ekwamu, 1991; Pande, 1992). These challenges call for scientists and farmers to find and adopt strategies to have similar or more sustainable yields in accordance with the envisaged erratic changes in temperature and rainfall. The breeder therefore has to understand the influence of environment on phenotype and separate it from genotypic expression. Since genotype x environment interactions (GxE) have been defined as the failure of genotypes to achieve the same relative performance in different environments (Baker, 1988), the best genotype for one environment may not necessarily perform well in another. These effects usually influence quantitative traits expression (Yan and Tinker, 2006) and will be manifested by changes in the relative performance of the genotype in the different environments (Kandus et al., 2010). Cross-over GxE interaction effects are manifested in the differential ranking of genotypes in different environments (Ding et al., 2007). Selection of genotypes with desirable traits has to take into consideration the effect of the environment on the relative performance of the genotypes for the traits under consideration, hence the need for multi-environment testing of genotypes to identify genotypes for target production agro-ecologies (Manrique and Hermann, 2000; Yan and Tinker, 2006). However, many researchers who carry out GxE trials eventually base their selection on the mean performance of the genotypes across environments with total disregard for GxE interactions (Yan and Tinker, 2006) which compromises the effectiveness of cultivar selection. A number of statistical techniques for the analysis of stability and multi-environment data are available and include the regression models of Eberhart and Russell (1966), Perkins and Jinks (1968) and Freeman and Perkins (1971) and the biplot models using Additive Main effects and Multiplicative Interactions (AMMI) (Gauch, 1992) and Genotype and Genotype x Environment interaction (GGE) (Yan and Tinker, 2006).

In finger millet, significant GE interactions on grain yield and finger number have been reported by Misra et al. (2010) and Joshi et al. (2005) with the latter identifying cultivars suitable for specific environments and those suitable for early and late sowing. In Ethiopia, Bezaweletaw et al. (2006) found significant GxE

on most agronomic traits except productive tillers, finger width, leaf blade length, number of fingers and yield per plant. With the reality of global climate change there is a need to exploit the variation in the germplasm in order to develop genotypes adapted to these changes. This requires breeding and selection of crops at strategically selected locations along a rainfall/temperature gradient to ensure that a range of cultivars are available to farmers. In East Africa, no GxE studies have been reported in finger millet and most cultivar selections have been based on individual location testing. Multi-environment testing of elite germplasm and breeding lines is necessary in order to speed up regional cultivar release that would take advantage of the harmonized seed and cultivar release policy that has been implemented in East Africa.

1.9 Inheritance of blast resistance, yield and yield components in finger millet

Resistance to blast and high yield are key factors in the release of finger millet cultivars. Limited information on gene action for most traits in finger millet is available especially on East African germplasm due to little breeding having been done. In order to respond to existing and new changes in crop growing conditions, finger millet breeders have to device a breeding strategy that produces cultivars to respond to these changes. Controlled crosses have been successfully used by the Ugandan and Kenyan finger millet breeding programs to develop pure lines in finger millet (Odelle, 1993; Oduori, 2008). An effective crossing programme requires selection of the right parents and a good understanding of gene effects/actions and their interactions controlling traits of interest (Hallauer and Miranda; 1988; Krishnappa et al., 2009a). Combining ability is used in discriminating between suitable parents especially to combine target traits into high yielding backgrounds (Sumathi et al., 2005). In finger millet combining ability studies for various traits have been reported by Sumathi et al. (2005), Shailaja et al. (2010), Krishnappa et al. (2009b), Parashuram et al. (2011), Priyadharashini et al. (2011) and Nimalakumar et al. (2010). Blast resistance in finger millet has been described as being polygenic and complex with all types of genic effects reported. He et al. (1989) and Bonman (1992) have suggested the involvement of both minor and major genes with complimentary or additive effects plus environment interactions. Seetharam and Ravikumar (1993) reported significant additive gene effects for neck and finger blast resistance with non-additive component being predominant. Similar studies on inheritance of leaf blast in rice (caused by *M. grisea*) found dominance genetic effect (Mackill and Bonman, 1992; Selvaraj et al., 2011). Takan et al. (2004) found blast resistance for the three blast types in finger millet to be mainly quantitatively expressed and was therefore deemed to be durable over time. However, as suggested by (Paul et al., 2003) mechanisms of resistance may be different in the parental sources. Blast pathogen isolates causing leaf, neck and head blast on finger millet have been reported to be genetically similar suggesting the role of the same pathotypes in different types of blast, hence the host resistance identified could be effective against all expressions of blast in general (Takan et al., 2004).

The few studies available on finger millet have reported the significance of both additive and non-additive gene effects for grain yield and most of the yield components (productive tillers, days to flowering, days to maturity, plant height, fingers per ear, finger length and width and 1000 grain mass). Among these are studies by Krishnappa et al. (2009b), Sumathi et al. (2005), Shailaja et al. (2010) and Oduori (2008). Predominance of additive gene effects in finger length was reported by Priyadharshini et al. (2011) and Nimalakumar et al. (2010). Crossing utilizing appropriate and sufficiently diverse finger millet germplasm can be used effectively to control blast and improve yield. Traits with a predominance of additive gene effects will be improved relatively faster through selection. Combining ability information is specific to the genotypes used and environments in which they were tested (Falconer and Mackay (1996). Therefore, to facilitate development of an effective breeding strategy it is important to understand the mode of inheritance (gene action) of the target traits in the parental lines in East African germplasm and under East African environments.

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Chapter 2

Morphological diversity in East African finger millet landraces

Abstract

This study was conducted at four locations in Kenya to assess the morphological diversity in 340 finger millet accessions collected from Kenya, Tanzania and Uganda plus 80 minicore accessions from the global collection using 24 quantitative and five qualitative traits. Significant ($P \leq 0.05$) variability was detected between accessions for 23 of the 24 quantitative traits studied. The highest Shannon diversity indices were recorded for grains per spikelet (H' = 0.87) and panicle shape (H' = 0.85). The highest diversity in most traits was detected within country with the highest recorded in Tanzanian and the least in Ugandan accessions. The minicore accessions had higher diversity for most traits than the accessions from the three countries. Cluster analysis separated the accessions into seven groups strongly influenced by leaf sheath length, plant height, peduncle length, panicle exertion and grain yield. Overall though there were no patterns of delineation as observed from the cross clustering of the three countries' accessions implying that the germplasm is probably closely related. The low diversity in Ugandan accessions could be due to the high research intervention in that country that has led to promotion and adoption of few improved cultivars. The high diversity detected at country level heightens the need for concerted efforts to characterize germplasm held in genebanks to determine useful traits for finger millet improvement. There was very low-representation of the minicore accessions in three clusters of the seven clusters of the entire germplasm which is an indication of potential room to enrich the global collection.

Key words: East Africa, cluster analysis, finger millet, phenotypic diversity

2.1 Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn) has its center of origin in the highlands of eastern Africa and was domesticated in areas extending from western Uganda to the highlands of Ethiopia (Harlan, 1971). It was introduced into tropical and sub-tropical Australia, America and south East Asia as a weed (de Wet, 1984). de Wet (1984) suggested that racial evolution occurred before the crop was introduced into India hence the Indian and African finger millets have similar morphology and adaptation. Finger millet is highly valued in East Africa as it plays an important role in the dietary requirements and economy of the small holder farmers. The crop's high importance lies in its superior nutritional value [calcium (358mg kg^{-1}), iron (46mg kg^{-1}) and protein (7.4%)] compared to other cereals and long storability without insect damage. In spite of its important role in the livelihoods of millions of households in East Africa in terms of food security, nutritional value and cash incomes, productivity is low mainly due to the use of low yielding blast susceptible cultivars.

The three East African countries (Kenya, Tanzania and Uganda) hold large finger millet germplasm collections but only very limited diversity studies have been undertaken on the germplasm hence the degree of genetic diversity and the value of the germplasm are not well understood. Developing an effective breeding strategy requires knowledge and understanding of the variability present in the crop which enables careful selection of parents with a wide genetic base to enhance genetic gain (Lapitan et al., 2007).

Morphological characterization has been effectively applied in many crops to generate germplasm references that are genetically diverse (Lapitan et al., 2007) and these classical methods of estimating plant diversity are still utilized in crop species (Rao and Hodgkin, 2002) more so in finger millet where information on molecular markers for diversity studies is limited. According to Abu-Alrub et al. (2004) and Ortiz (1997), even when genotype by environment interactions are significant, morphological traits are often used in a natural system of classification. However, this is enhanced by assessing the genotypes in several environments and using the mean values (Goodman and Paterniani, 1969). Morphological descriptors help in studying similar adaptation patterns and also help to define potential divergent heterotic gene pools for purposes of hybridization (Ortiz, 2000).

In finger millet there has been limited use of genetic variability to develop improved cultivars with response to biotic and abiotic stresses with only 1% of the available global germplasm being utilized (Upadhyaya et al., 2010). Several investigators have reported varying diversity levels and patterns in

finger millet based on morphological traits. For example Naik et al. (1993) characterised African and Asian accessions and reported that African accessions were more diverse than Asian accessions in both quantitative and qualitative traits. Hilu and de Wet (1976) identified three distinct races in African and Asian germplasm based on morphological traits. In Ethiopia Bezawelataw et al. (2007) and Lule et al. (2012) reported high regional variability in Ethiopian finger millet landraces with the few accessions from Kenya, Uganda and Tanzania assessed being closely related. Other than diversity studies done in India and Ethiopia, there are none reported in the three countries on East African finger millet germplasm based on morphological traits.

This study was conducted with the aim of assessing genetic diversity in finger millet germplasm collected from Kenya, Tanzania and Uganda using morphological traits to generate information for use in germplasm management and in breeding programs for target trait improvement.

2.2 Materials and methods

2.2.1 Experimental material

The study was conducted using 420 finger millet accessions (340 landraces collected across agro-ecologies in East Africa, viz. Kenya (154), Tanzania (81) and Uganda (105): and 80 global minicore accessions) and five checks (Appendix 2.1). The five checks were Nakuru FM 1-released in cool highlands of Kenya; Seremi 2 (U 15)-released in Kenya and Uganda for sub-humid Lake Victoria zone; Kahulunge-a popular local cultivar from southern Tanzania; KNE 814-a blast resistant check and KNE 479-a blast susceptible check. The minicore comprises 1% of the global collection at ICRISAT-genebank representing the total global diversity, constituted by Upadhyaya et al. (2010). The East African collection areas were divided into nine sub-sub-regions based on length of growing period (LGP) in days: eastern Uganda, mid altitude (1024-1156 metres above sea level-masl), sub humid with 240-269 length of growing period-LGP in days, western Uganda-mid altitude (1090-1150 masl) with 270-299 days, northern Uganda-mid altitude (1018-1155 masl) with 210-230 days, western Kenya-mid-altitude sub humid (1154-1230 masl) with 240-269 days, Rift Valley Kenya-high altitude (1400-2400 masl) low temperature with 120-209 days, eastern Kenya-semi-arid mid to low altitude (850-1296 masl), western Tanzania-mid altitude (1025-1200 masl) with 210-239 days, northern Tanzania-mid altitude sub humid (1100-1400 masl) with 90-149 days, and Rukwa sub-region southern Tanzania, mid to high altitude (1000-2165 masl) with 120-209 days. These sub-regions also have differential ethnic representation with

occasional overlaps. However most of the accessions collected earlier than 2010 lacked altitude, latitude and longitude information.

2.2.2 Test locations

The trials were grown at four locations in Kenya which represent the finger millet production agro-ecologies in East Africa: Alupe-sub-humid Lake Victoria zone, Lanet – low temperature (cool) highland, Kiboko-dry lowland and Mtwapa-sea level humid coast (Table 2.2-1).

Table 2.2-1. Characteristics of the four test locations in Kenya

Location	Altitude (m)	Latitude	Longitude	Soil type	Mean annual temperatures (°C)			Mean annual rainfall (mm)	Rainfall during study cropping season (mm)
					Min	Max	Mean		
Alupe	1189	0° 28'N	34° 7'E	Sandy loam	17.7	30.3	24.0	1100	736.4
Lanet	1920	0°30'S	36°0'E	Sandy loam	10.0	20.0	15.0	850	NA
Kiboko	960	2°20'S	37° 45'E	Sandy clay loam calcareous	16.6	29.4	23.0	604	243.7
Mtwapa	21	4° 25'S	39°44'S	Deep sandy clay loam	22.5	30.2	26.4	1049	479.0

NA-Not available

2.2.3 Experimental design and crop management

At all the four locations, the accessions were planted in 2011 long rains season (starting March/April) in an augmented design comprising 20 blocks of 26 plots each. The entries were sown in single row plots of 4 m length and inter-row spacing of 0.40 m. Seed was manually drilled in furrows (2.5-3.0 cm deep) and plants were thinned two weeks after emergence to one plant per hill after every 0.10 m. Each check entry was planted once in each block to obtain an estimate of error and of blocking effects. Double Ammonium Phosphate (18:46:0) at the rate of 20 kg N and $\simeq$ 20 kg P_2O_5 per hectare was applied as basal fertilizer at planting time and Urea (46%N) at the rate of 20 kg N per hectare was applied as top dressing three weeks after sowing. Data were collected on five qualitative and 24 quantitative traits from five randomly selected plants per accession according to descriptors for finger millet (IBPGR[1], 1985) (Table 2.2-2). Leaf, neck and finger blast scores were taken at Alupe on plot basis on a scale of 1-9 (1 = no infection; 2 = 1-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75% and 9 = >75% leaf area covered with lesions for leaf and severity of infection for neck and finger blast). The mean of five

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plants per accession were used for statistical analysis of the quantitative data. Qualitative data were recorded at Kiboko location only. Due to very low rainfall at Kiboko supplementary irrigation was applied during very dry periods up to the crop flowering stage. Moisture stress was experienced at this location at grain filling stage. Harvesting was done manually at Alupe, Kiboko and Mtwapwa in July/August and in September/October at Lanet and the panicles sun dried before threshing.

Table 2.2-2. Description and measurements for traits used in the study

Trait	Description/scoring
Culm thickness (mm)	Diameter of internode between third and fourth nodes from top at dough stage
Days 50% flowering	Days from sowing to when 50% of plants in the plot were in flower
Plant height (cm)	From ground level to tip of panicle at dough stage
Plant colour	At flowering (0-tan; 1-pigmented)
Growth habit	Tillering attitude 40 days after sowing (3-decumbent; 5-erect; 7-prostrate)
No. of productive basal tillers	Basal tillers with mature panicles at maturity
No. of Leaves	Number of leaves on main tiller at flowering
Flag leaf blade length (cm)	From ligule to leaf tip at flowering
Flag leaf blade width (cm)	Across centre of flag leaf at flowering
Leaf blade length (cm)	From ligule to tip of fourth leaf blade from top at flowering
Leaf blade width (cm)	Across centre of fourth leaf blade from top
Leaf sheath length (cm)	From node to ligule of fourth leaf from top at flowering
Leaf sheath width (cm)	Across centre of fourth leaf sheath from top
Peduncle length (cm)	From top most node to base of the thumb finger
Panicle exertion (cm)	From flag leaf ligule to base of the thumb finger
Panicle shape	Shape of panicle at dough stage (1-droopy; 2-open; 3-semi-compact; 4-compact; 5-fisted)
No. of Fingers	On main panicle at dough stage
Finger length (cm)	From base to tip of longest finger at dough stage
Finger width (cm)	Distance across centre of longest finger at dough stage
Glume covering	Proportion of grain covered by the glume at maturity (3-exposed; 5-intermediate; 7-enclosed
Grains per spikelet	At maturity
Agronomic score	Overall agronomic performance of an accession taken on 1-5 scale (1-very good, 5-very poor
Grain yield (t ha^{-1})	Plot weight at 12.5% moisture content converted to t ha^{-1}
Threshing percent	Grain weight expressed as percent of panicle weight
1000 grain mass (g)	Mass of 1000 grains at 12.5% moisture content
Grain colour	Post-harvest (1-white; 2-light brown; 3-copper brown; 4-purple brown; 5-others)

Source: IBPGR (1985). All data were recorded on 5 plants except agronomic score, days to flowering, 1000 grain mass and threshing percent taken on plot basis.

2.3 Data analyses

2.3.1 Qualitative diversity

Shannon-Weaver diversity indices (*H´)* as described by Jain et al. (1975) were calculated based on phenotypic frequencies (proportions) of each trait category to estimate phenotypic diversity between the accessions, across the countries and within each country as:

$$H = \Sigma P_i \log_e P_i$$

where: H = Shannon diversity index, P_i = proportion of accessions in the i^{th} class of an n class trait in a population. The H value was standardized by dividing it by its natural log, $\log_e$ n (n = number of phenotypic classes in the trait) to give H´. Frequencies of occurrence of each trait category in the germplasm expressed as a percent of total number of accessions in the entire germplasm collection and in each country and in the entire germplasm were also calculated.

2.3.2 Descriptive statistics

Quantitative data were analysed using the augmented random model of residual maximum likelihood (REML) (Federer and Wolfinger, 2003) in SAS (SAS, 2008) as follows:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$$

where:

Y_{ij} = Observation of i^{th} entry in j^{th} block.

α_i = i^{th} entry effect.

β_j = j^{th} block effect.

ε_{ij} = Random error component

The block effects were estimated from the repeated check means and then removed from the means of the test entries (Federer and Wolfinger, 2003). A two way location (random) by accessions (fixed) analysis was performed. An estimate of the error variance over locations was obtained by computing the average effective error variance at each location and then averaging these over locations as suggested by Cochran and Cox (1957).

2.3.3 Principal components analysis

Patterns of variation and major quantitative traits contributing to the delineation were determined from principal component analyses (PCA) (Fundora Mayor et al., 2004) using combined data. Before the correlations between the traits were determined the data set for each trait was standardized to account for the different scales of measurement of the various traits by subtracting the trait mean from each data value and dividing by the standard deviation. Only PCs with eigenvalues >1.0 were considered in determining the variability in the accessions based on the criterion established by Kaiser (1960) as there are no tests to evaluate the significance of latent roots (Rojas et al., 2000) and below 1.0 very little of random

variability is left. The first two PCs were presented in biplots to graphically enhance the dispersion of the accessions based on the quantitative traits.

2.3-4 Cluster analysis

Cluster analysis was carried out based on 19 quantitative traits for the 420 accessions and the five checks using unweighted pair group method with arithmetic mean (UPGMA) based on Euclidean distance matrix (Spark, 1973; Fundora Mayor et al., 2004) in Genstat 15.0 (http://www.genstat.co.uk). The phenotypic distance matrix was created by calculating the distance between each pair of accessions for each quantitative trait. The distance between two quantitative traits was determined by averaging all the distances in the phenotypic value for each trait divided by the respective range as described by Gower (1985). The phenotypic distances for these traits were transformed into a 0-1 scale. A dendrogram was constructed to present the overall similarity between clusters with the between and within cluster distances estimated using Mahalanobis genetic distance (D^2) (Bedrick et al., 2000).

2.4 Results

2.4.1 Qualitative traits variability

A wide range of variability was recorded in the qualitative traits among the accessions (Table 2.4-1 and Figure 2.4-1). The pigmented plant types (68.6%) were the most predominant in the entire population with the highest proportion in the Tanzanian accessions (85.5%). The population had 93.2% erect plants and 6.8% decumbent with all Kenyan accessions being erect. Most of the decumbent plant types were found in Tanzanian accessions (19.5%). The predominant panicle shapes in the population were the compact types (48.7%) largely contributed by Ugandan accessions, followed by the semi-compact types (38.1%), fisted types (8.4%), open types (3.4%) and droopy types (2.4%). Semi-compact types were most prevalent in Kenyan (48.6%) and Tanzanian (46.4%) accessions. Most of the accessions (>50%) had exposed grain. A range of grain colours were present in the germplasm with brown being dominant both in the entire population (73.2%) and within countries (Kenya-76.1%, Tanzania-62.7%, Uganda-81.0%). The least prevalent grain colour was white (0.6%) and was absent in Ugandan accessions. Shannon-Weaver diversity indices (H') showed an overall moderate allelic richness in the qualitative traits with a mean $H' = 0.66$ across countries (Table 2.4-1). The highest overall diversity across the countries was recorded in panicle shape ($H' = 0.85$) and the least in growth habit ($H' = 0.27$). The highest overall diversity within country was in Tanzania ($H' = 0.76$) and least in Uganda ($H' = 0.55$).

Figure 2.4-1. Morphological variability in the germplasm at Lanet test location

Table 2.4-1. Proportion of qualitative traits categories among finger millet accessions (%) per country and Shannon diversity indices

		Proportion (%)					Diversity index (*H'*)	
Trait	Category	Kenya	Tanzania	Uganda	Overall (3 countries)	Minicore	Across 3 countries	Minicore
Plant colour	0	68.8	85.5	51.4	68.6	62.5	0.58	0.65
	1	31.2	14.5	48.6	31.4	37.5		
Growth habit	3	0.0	19.5	1.0	6.8	10.0	0.27	0.25
	5	100	80.5	99.0	93.2	90.0		
Panicle shape	1	0.0	7.2	0.0	2.4	2.5	0.85	0.82
	2	2.9	7.2	0.0	3.4	2.5		
	3	47.6	46.4	19.4	37.8	33.8		
	4	41.8	36.2	67.0	48.3	57.4		
	5	7.7	2.9	13.6	8.1	3.8		
Glume cover	3	53.3	46.0	61.9	50.1	32.5	0.40	0.50
	5	42.2	38.2	38.1	43.1	55.0		
	7	4.5	15.8	0.0	6.8	12.5		
Grain colour	1	0.6	1.3	0.0	0.6	3.8	0.81	0.77
	2	9.7	30.7	10.5	17.0	8.8		
	3	76.1	62.7	81.0	73.3	65.2		
	4	13.6	5.3	8.5	9.1	22.2		
	Diversity index (*H'*)	0.67	0.76	0.55			0.66	0.74

Plant colour: 0-Tan, 1-Pigmented; Growth habit: 3-Decumbent, 5-Erect; Panicle shape: 1-Droopy, 2-Open, 3-Semi-compact, 4-Compact, 5-Fisted; Glume cover: 3-Exposed, 5-Intermediate, 7-Enclosed; Grain colour: 1-White, 2-Light brown, 3-Brown, 4-dark brown

2.4.2 Quantitative traits variability

2.4.2.1 Performance of accessions at individual and across locations

Trait means and mean squares at individual and across the four test locations for the entire germplasm are presented in Table 2.4-2. Significant variation ($P \leq .05$) was recorded in all traits at all the locations except in threshing percent at Alupe, flag leaf blade width at Lanet, leaf blade width at Kiboko and 1000 grain mass at Mtwapa. Alupe recorded the widest culms, longest panicle exertions, and lowest threshing percent. A total of 26 accessions (four from Kenya, ten from Uganda, three from Tanzania and ten from the minicore accessions) showed moderate to high resistance to blast (leaf, neck and finger) (Table 2.4-3). At Lanet the accessions took longer to flower and were shorter in height relative to other test locations. This location recorded the lowest mean minimum temperature (10.0^0C) during the cropping season. Due to the prolonged rains at Lanet, the material had the highest mean number of productive tillers per plant (ten) and mean grain yields (3.63 t ha^{-1}). Partial sterility was also detected in some accessions especially on check accession KNE 479. The highest mean leaf sheath width (1.9 cm) and lowest mean 1000 grain mass (2.4g) were recorded at Kiboko where some moisture stress was experienced during maturity especially on late maturing accessions. Relative to Alupe, Kiboko and Lanet, the accessions were generally earlier to flower at Mtwapa (67 days). This location also recorded the highest mean plant height (97 cm), the lowest mean number of productive tillers per plant (one) and widest and longest fingers (1.6 cm and 8.3 cm, respectively).

Table 2.4-2. Mean squares and CV% for 24 quantitative traits of finger millet accessions evaluated over four locations

	Mean					Sum of squares					CV%				
Trait	**Across**	**Loc 1**	**Loc 2**	**Loc 3**	**Loc 4**	**Across**	**Loc 1**	**Loc 2**	**Loc 3**	**Loc 4**	**Across**	**Loc 1**	**Loc 2**	**Loc 3**	**Loc 4**
1	1.35	2.8	2.2	1.4	2.8	3.76***	0.39***	13.94**	0.063*	16.31***	14.1	11.6	10.6	14.7	10.8
2	84.0	80.0	116.5	75.3	67.0	28.95***	183.69***	7.71**	95.57	31.42***	5.1	4.4	5.9	3.9	3.4
3	9.6	10.9	8.4	9.47	9.3	4.46***	13.44**	2.16**	12.56***	12.90***	21.6	19.5	21.1	22.4	23.6
4	8.0	8.0	7.8	7.9	8.0	8.14***	1.45**	1.43**	2.31***	2.48***	9.6	9.8	9.6	9.3	9.8
5	6.8	6.2	5.2	7.6	8.3	12.55***	1.39**	0.02**	3.04***	2.09***	10.2	8.1	9.9	9.3	11.5
6	1.1	1.0	0.9	1.1	1.6	3.36***	0.02**	1.70**	0.01*	0.13***	12.4	8.0	9.2	9.06	15.2
7	10.5	9.9	10.3	10.56	11.6	7.18***	2.21**	0.03**	2.41***	3.54***	8.9	12.1	6.9	6.9	9.0
8	1.2	1.1	0.9	1.28	1.5	3.75***	0.01***	0.33ns	0.04ns	0.05***	12.9	5.8	21.9	15.5	8.0
9	6.0	5.6	4.9	5.8	6.0	2.79***	1.03**	0.62**	0.48**	1.83***	12.6	11.2	12.6	8.2	16.3
10	2.6	2.5	2. 9	2.47	2.5	2.37***	0.32**	0.33**	0.22**	0.21ns	16.2	19.1	13.2	16.1	16.6
11	2.38	1.84	3.63	2.54	1.52	3.68***	0.78**	4.74**	0.64**	0.30***	32.3	30.7	27.0	22.8	19.1
12	48.0	49.9	34.9	50.2	57.1	6.39***	39.21***	18.63**	49.42***	54.15***	7.9	7.4	8.8	7.7	7.9
13	1.3	1.3	1.0	1.3	1.7	6.80***	0.02***	0.01**	0.05ns	0.178***	13.3	5.4	7.9	24.1	7.0
14	14.0	16.2	11.8	16.3	13.0	9.44***	5.22**	2.60**	8.98***	6.00***	8.9	6.1	8.8	9.2	11.6
15	11.3	10.3	10.3	11.3	13.3	8.04***	1.96***	1.71**	1.84***	2.38***	6.7	6.3	6.7	7.4	6.4
16	1.6	1.5	1.30	1.9	1.7	4.46***	0.03***	0.06**	0.07***	0.04***	8.9	7.2	11.9	9.1	7.3
17	19.9	20.7	18.6	19.8	20.4	30.18***	19.25**	9.93**	20.98***	18.19***	8.9	9.9	10.0	11.8	11.5
18	84.5	92.7	58.7	89.0	97.0	9.50***	275.18**	156.90**	176.11***	197.37***	8.2	7.8	11.2	8.3	6.8
19	71.3	65.3	74.59	70.2	74.7	2.83***	99.49ns	152.99**	123.31*	42.60***	10.8	16.1	7.27	13.1	5.3
20	4.0	2.6	9.9	2.5	1.0	5.36***	2.80**	18.6**	1.44**	0.85***	33.9	33.2	24.8	32.8	37.2
21†	-	3.3	-	-	-	-	2.32**	-	-	-	-	17.5	-	-	-
22†	2.9	3.1	-	-	-	-	2.87**	-	-	-	-	24.4	-	-	-
23†	4.3	4.0	-	-	-	-	2.87**	-	-	-	-	17.9	-	-	-
24	3.2	3.2		2.8	3.3	0.88***	0.75**	0.73**	0.50ns	0.5**	21.9	12.9	18.9	23.8	16.6

Key: Across-Across locations values, Loc 1-Alupe, Loc 2-Lanet, Loc 3-Kiboko, Loc 4-Mtwapa; 1-Culm thickness, 2-days to flowering, 3-Panicle exertion, 4-Fingers per panicle , 5-Longest finger length, 6-Longest finger width, 7-Flag leaf blade length, 8-Flag leaf blade width, 9-Grains per spikelet, 10-1000 grain mass, 11-Grain yield (t ha^{-1}), 12-Leaf blade length, 13-Leaf blade width, 14-Number of leaves, 15-Leaf sheath length, 16-Leaf sheath width, 17-Peduncle length, 18-Plant height, 19-Threshing %, 20-Productive tillers/plant, 21-Leaf blast score, 22-Neck blast score, 23-Finger blast score, 24-Agronomic score. ***-significant at P≤0.001, **-significant at P≤0.01, ns-not significant, †-data at Alupe only

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Table 2.4-3. Twenty six accessions with the best blast tolerance at Alupe under natural infection ranked according to finger blast severity scores

Acc. #	Acc. Name	Country	Grain yield (t ha^{-1})	Days to flower	Fingers /panicle	finger length (cm)	Finger width (cm)	1000 grain mass (g)	Leaf blast score (1-9)	Neck blast score (1-9)	finger blast score (1-9)	Agrono mic. score (1-5)	Plant height (cm)	Plant colour	Panicle shape	Grain colour
211	GBK-029673A	Kenya	2.30	86	7	7.1	1.0	1.5	2.1	1.7	1.4	2.3	98.0	P	SC	B
311	IE 4797	Minicore	2.36	86	7	6.8	0.9	1.6	2.1	1.7	1.4	2.3	113.0	P	SC	B
351	Acc # 2968	Tanzania	1.77	81	8	8.1	1.1	2.2	2.1	1.7	1.4	2.8	106.3	P	SC	B
47	Cirogal	Uganda	0.68	73	7	7.1	1.0	2.6	2.1	3.7	1.4	2.3	88.8	P	C	B
274	IE 2619	Minicore	1.41	69	9	6.9	1.0	2.6	3.9	3.2	1.5	3.1	101.5	T	SC	B
93	Otara chilgal	Uganda	3.62	74	7	6.2	1.0	2.8	1.7	2.0	1.5	1.8	103.5	P	C	B
336	IE 7018	Minicore	2.83	74	8	7.1	1.0	1.9	1.9	2.0	1.7	2.9	113.9	P	C	DB
95	Kal	Uganda	4.21	64	10	7.0	1.2	2.8	1.9	3.0	1.7	2.9	106.7	T	C	B
165	GBK-011136A	Kenya	2.79	77	8	7.1	1.0	3.3	2.5	2.2	1.8	1.4	102.2	T	C	B
333	IE 6473	Minicore	2.36	80	10	4.7	1.0	2.1	1.3	3.0	1.8	3.3	106.3	T	C	DB
63	Kal atari	Uganda	2.48	71	7	5.6	1.0	2.4	2.5	2.2	1.8	1.9	70.4	P	C	B
202	GBK-029650A	Kenya	1.31	90	7	9.0	0.8	3.1	1.7	2.6	2.0	3.1	92.6	T	SC	DB
206	GBK-029667A	Kenya	0.81	83	9	6.2	1.0	3.5	1.9	1.8	2.0	2.5	92.2	T	C	W
315	IE 5106	Minicore	2.38	84	8	4.3	1.0	2.9	2.3	2.2	2.0	2.9	89.2	P	F	B
287	IE 3392	Minicore	2.33	77	6	4.4	1.1	3.6	2.1	2.6	2.0	3.3	75.1	T	C	LB
298	IE 4121	Minicore	1.63	73	8	6.6	1.0	1.8	2.3	3.2	2.0	1.9	81.8	P	C	B
328	IE 6294	Minicore	1.37	87	8	5.6	1.0	1.4	1.9	2.8	2.0	2.5	78.0	T	C	B
324	IE 6154	Minicore	1.32	88	9	6.8	0.9	1.0	2.3	2.2	2.0	4.4	69.8	T	SC	B
335	IE 6533	Minicore	0.56	72	9	11.1	1.5	2.4	1.9	1.8	2.0	3.5	99.6	T	D	DB
408	Namakonta	Tanzania	1.15	83	11	7.6	0.9	3.7	3.5	1.0	2.0	3.7	101.2	T	SC	B
96	Kal	Uganda	3.11	68	8	6.2	1.0	2.4	1.7	3.6	2.0	2.1	96.6	P	C	B
1	Unknown	Uganda	2.67	74	8	5.4	1.0	3.2	1.7	2.6	2.0	2.6	109.8	T	C	DB
105	RW 127 (IE 6613)	Uganda	2.18	85	9	6.6	1.1	2.4	1.9	1.8	2.0	1.0	104.0	T	C	B
59	Kal-purple	Uganda	1.87	73	7	5.8	0.9	3.2	1.9	2.8	2.0	2.0	109.6	P	SC	B
64	Kal atari	Uganda	1.86	76	7	5.8	0.9	2.6	1.7	2.6	2.0	2.1	101.0	P	C	B
3	Purple	Uganda	1.07	71	7	7.0	1.2	2.1	2.3	3.2	2.0	2.4	93.2	P	C	DB
Checks	Nakuru FM1		3.18	81	6	8.2	1.3	2.9	4.1	4.1	4.4	3.1	97.1	P	SC	DB
	U 15		2.14	75	9	7.0	1.1	2.5	3.6	3.4	3.7	3.0	74.6	P	SC	B
	Kahulunge		2.37	90	8	7.0	1.1	2.8	2.6	2.2	3.2	3.0	83.4	T	C	B
	KNE 479		1.70	67	7	6.1	1.1	2.5	5.3	7.3	7.0	3.8	81.7	P	SC	DB
	KNE 814		2.05	86	7	7.4	1.1	2.6	2.1	2.2	2.2	2.9	90.3	P	SC	B
	Mean (N=425)		**1.84**	**80**	**8**	**6.2**	**1.0**	**2.5**	**3.3**	**3.1**	**4.0**	**3.2**	**92.7**	**-**	**-**	**-**
	SE±		**0.57**	**3.44**	**0.76**	**0.51**	**0.08**	**0.48**	**0.58**	**0.79**	**0.71**	**0.42**	**7.24**	**-**	**-**	**-**
	$LSD_{0.05}$		**1.73**	**10.51**	**2.33**	**1.55**	**0.24**	**1.48**	**1.78**	**2.42**	**2.16**	**1.28**	**22.10**	**-**	**-**	**-**
	CV%		**30.7**	**4.4**	**9.8**	**8.1**	**8.0**	**19.1**	**17.5**	**24.4**	**17.9**	**13.0**	**7.8**	**-**	**-**	**-**

Acc. #-Accession number, Plant colour: P-Purple, T-Tan; Panicle shape: SC-Semi compact, C-Compact, D-Droopy; Grain colour: LB-Light brown, B-Brown, DB-Dark brown, W-White

The genotype x environment interaction effects were significant ($P \leq 0.01$) for all the quantitative traits studied. Accessions from Kenya had the highest mean values for six traits (grain yield 2.58 t ha^{-1}), 1000 grain mass (2.6 g), leaf sheath length (11.6 cm) and plant height (88.8 cm). The highest mean values for days to flowering (92), finger width (7.1 cm), number of leaves per plant (16) and number of productive tillers per plant (5) were recorded by the Tanzanian accessions. Ugandan accessions had the highest mean values for panicle exertion (10.4 cm), finger width (1.2 cm), peduncle length (20.8 cm) and threshing percent (72.5%). The lowest mean scores were for leaf blast (2.7), neck blast (2.2), finger blast (3.3) plus best agronomic score of 3.0 (Table 2.4-4). The minicore accessions had the highest mean values for only two traits (flag leaf blade length-16 cm and number of grains per spikelet-5). However, mean number of fingers per panicle (8) and grains per spikelet (six) were relatively stable across environments. The widest ranges for grain yield (0.006-3.415 t ha^{-1}), panicle exertion (3.1-335.2 cm), leaf sheath width (1.2-2.1 cm), agronomic score (2.0-5.0), threshing % (32.7-85.4) and finger blast score (1.3-7.8) were recorded in the Tanzanian accessions. The Ugandan accessions had the lowest range for all traits studied. Most of the accessions were classified in the medium maturity group for flowering in 81-90 days after sowing (Figure 2.4-2). There was high yield potential in the germplasm with 55.3% and 0.7% of the accessions attaining grain yields of 2.00-3.00 t ha^{-1} and > 4.00 t ha^{-1}, respectively (Figure 2.4-3). A total of 54 accessions had grain yields higher than the best commercial check cultivar (Nakuru FM 1) and the top 20 of these are presented in Table 2.4-5.

Table 2.4-4. Mean, minimum, maximum and ranges of 24 quantitative traits for three accession groups (based on country of origin) and the minicore across four test locations

Trait	Kenya		Tanzania		Uganda		Minicore	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Grain yield (t ha^{-1})	2.58	1.265-4.39	2.12	0.01-3.14	2.43	1.39-5.53	2.25	0.34-4.23
Days to flowering	84.0	41.0-105.0	92.0	66.0-114.0	81.0	72.0-95.0	85.0	59.0-109.0
Panicle exertion (cm)	9.2	3.9-15.0	8.7	3.1-13.4	10.4	6.3-13.7	8.6	4.2-13.6
Fingers per panicle	8.0	6-10	8.0	6.0-12.0	8.0	6.0-11.0	8.0	6.0-13.0
Finger length (cm)	7.0	4.6-9.5	7.1	4.4-12.7	6.5	4.6-8.5	6.6	4.6-17.2
Finger width (cm)	1.2	0.7-1.4	1.1	0.8-1.4	1.2	0.9-1.6	1.1	0.8-1.5
Flag leaf blade length (cm)	10.7	8.2-13.5	10.0	8.3-13.5	10.5	8.6-13.1	11.0	8.1-14.5
flag leaf blade width (cm)	1.2	0.8-1.6	1.1	0.9-1.4	1.2	1.0-1.4	1.2	0.8-2.0
Grains per spikelet	6.0	3.0-7.0	6.0	4.0-8.0	6.0	4.0-7.0	5.0	4.0-7.0
1000 grain mass (g)	2.6	1.6-3.6	2.5	1.9-3.4	2.5	1.8-3.1	2.5	1.8-3.4
Leaves per plant	14.6	10.3-18.4	15.6	10.2-19.7	14.0	11-17	14.1	6.7-19.4
Leaf sheath length (cm)	11.6	9.0-14.0	10.7	7.7-13.6	11.4	9.7-13.0	11.1	8.3-15.1
Leaf sheath width (cm)	1.6	1.2-2.0	1.5	1.2-2.1	1.6	1.3-2.0	1.5	1.2-2.0
Leaf blade length	49.2	38.1-58.9	45.9	40.3-55.8	49.1	40.0-58.2	45.3	26.3-59.1
Leaf blade width	1.3	0.9-1.9	1.3	0.9-1.7	1.3	1.0-2.7	1.3	1.1-2.7
Culm thickness	2.4	0.8-4.2	2.2	0.8-4.3	2.3	0.9-4.1	2.2	0.5-4.4
Leaf blast score (1-9)*	3.0	1.7-5.4	3.0	1.5-5.0	2.7	1.8-4.3	3.5	1.7-6.4
Neck blast score (1-9)*	2.5	1.0-6.9	2.4	0.9-5.0	2.2	0.9-5.2	3.0	1.1-7.7
Finger blast score (1-9)*	3.5	1.5-7.4	3.6	1.3-7.8	3.3	2.0-6.4	4.4	1.8-8.5
Agronomic score (1-5)	3.1	2.2-4.5	3.5	2.0-5.0	3.0	2.1-4.3	3.4	2.0-25.3
Peduncle length (cm)	19.7	13.2-27.0	18.6	12.6-25.7	20.8	15.4-26.6	19.4	12.7-25.3
Plant height (cm)	88.8	49.2-115.6	82.1	62.2-103.4	84.4	67.0-99.3	77.3	41.6-103.8
Threshing %	72.0	51.8-88.8	68.5	32.7-85.4	72.5	61.7-81.3	69.3	45.6-81.4
Productive tillers/plant	4.0	1.0-9.0	5.0	2.0-11.0	4.0	2.0-7.0	4.0	2.0-9.0

*-Data from Alupe location only.

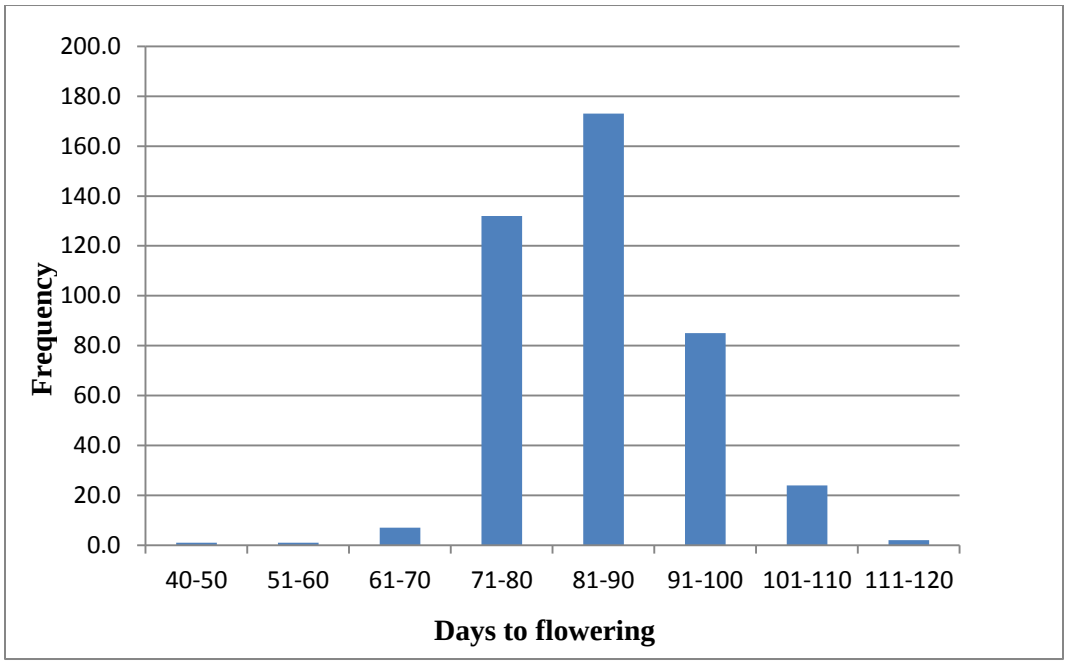

Figure 2.4-2. Frequency of Days to flowering across four locations and four accession groups

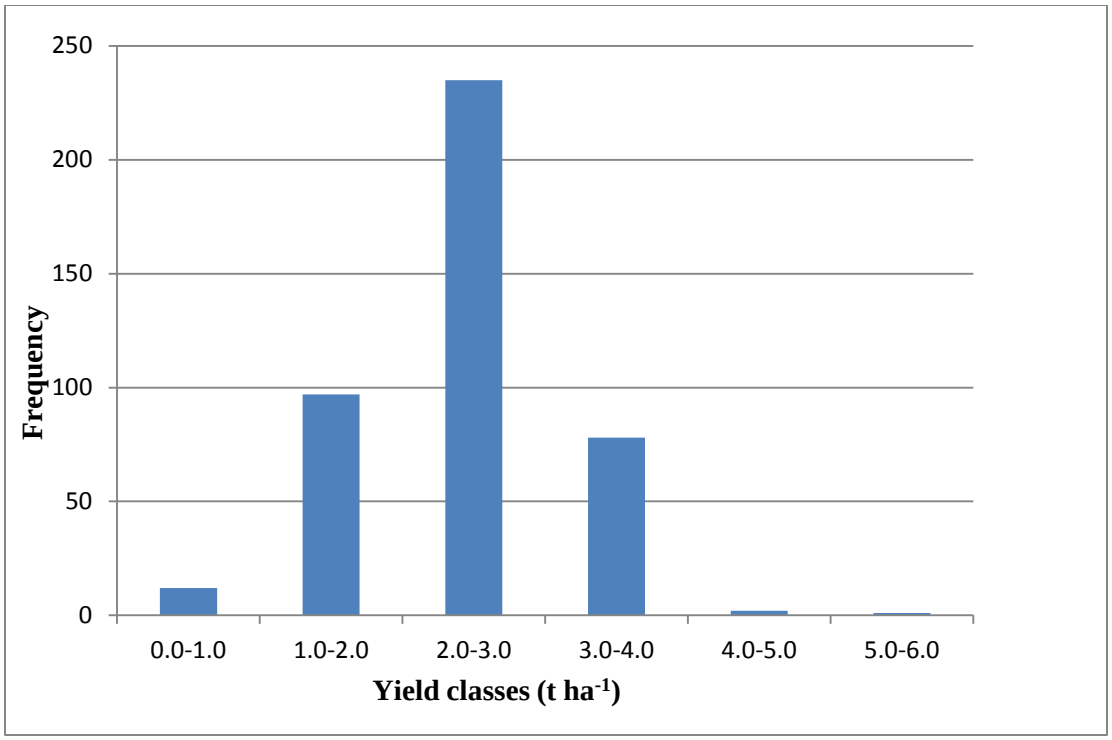

Figure 2.4-3. Frequency of grain yield classes across four locations and four accession groups

Table 2.4-5. Top 20 accessions ranked for grain yield (t ha^{-1}) and their leaf, neck and finger blast scores, threshing% and agronomic scores across four test locations

Acc #	Name	Country of origin	Sub-region	Gyld	Rank	% above best check	Daf	LB†	NB†	FB†	Thresh	Ag. score
31	Ekama-white	Uganda	eastern Uganda	**5.53**	**1**	**43**	85.0	2.6	1.9	3.0	78.7	2.7
299	IE 4329	Minicore	Minicore	**4.22**	**2**	**25**	87.0	3.3	2.4	3.3	70.4	2.5
142	GBK-008328A	Kenya	western Kenya	**3.78**	**3**	**16**	101.0	2.5	2.3	2.4	74.9	2.8
144	GBK-008336A	Kenya	western Kenya	**3.76**	**4**	**15**	90.0	2.0	1.8	3.3	76.4	2.7
187	GBK-027165A	Kenya	Rift valley	**3.69**	**5**	**14**	97.0	3.6	3.2	3.6	80.0	3.3
254	Acc. # 76	Kenya	Rift valley	**3.68**	**6**	**14**	94.0	2.7	2.0	3.3	88.7	2.8
103	Rwemereza (IE 6591)	Uganda	eastern Uganda	**3.67**	**7**	**13**	94.0	3.9	2.6	3.1	73.4	2.9
258	Acc. # 80	Kenya	Rift valley	**3.66**	**8**	**13**	99.0	3.6	4.0	3.9	74.6	3.5
107	GBK-000349A	Kenya	Rift valley	**3.66**	**9**	**13**	97.0	3.9	2.8	4.0	75.7	2.9
334	IE 6514	Minicore	Minicore	**3.66**	**10**	**13**	80.0	3.8	1.5	1.8	75.4	2.5
246	GBK-043165A	Kenya	western Kenya	**3.60**	**11**	**12**	82.0	2.6	2.4	3.8	71.4	3.0
53	Kal	Uganda	northern Uganda	**3.56**	**12**	**11**	89.0	2.4	2.0	3.2	75.2	3.2
136	GBK-008278A	Kenya	western Kenya	**3.51**	**13**	**9**	96.0	2.7	2.4	3.5	55.2	3.1
190	GBK-027189A	Kenya	Rift valley	**3.41**	**14**	**7**	93.0	3.1	2.2	3.1	75.4	2.9
301	IE 4497	Minicore	Minicore	**3.39**	**15**	**6**	78.0	3.1	1.6	2.6	66.7	2.8
330	IE 6337	Minicore	Minicore	**3.39**	**16**	**6**	72.0	2.7	1.3	2.5	68.1	2.7
146	GBK-008365A	Kenya	western Kenya	**3.38**	**17**	**6**	95.0	2.7	2.0	3.0	73.4	2.9
376	Acc # 3927	Tanzania	northern Tanzania	**3.38**	**18**	**6**	96.0	3.5	2.3	3.0	79.0	2.9
217	GBK-029680A	Kenya	western Kenya	**3.38**	**19**	**6**	84.0	3.6	3.6	5.0	72.8	2.8
404	Kaulunge	Tanzania	southern Tanzania	**3.37**	**20**	**6**	80.0	2.5	1.8	3.1	69.2	3.5
421	Nakuru FM 1	Check		3.18	48		97	4.1	4.1	4.4	3.1	3.18
423	Kahulunge	Check		2.37	197		83	2.6	2.2	3.2	3.0	2.37
425	KNE 814**	Check		2.15	254		90	2.1	2.2	2.2	2.9	2.15
422	Seremi 2 (U 15)	Check		2.14	261		75	3.6	3.4	3.7	3.0	2.14
424	KNE 479*	Check		1.70	340		82	5.3	7.3	7.0	3.8	1.7
	Checks											
Mean (N = 425)				**2.38**			**84.0**	**2.8**	**2.9**	**0.3**	**71.3**	**3.2**
SE±				**1.19**			**10.44**	**1.08**	**1.39**	**1.43**	**9.46**	**0.70**
CV%				**32.3**			**5.1**	**35.4**	**54.4**	**38.4**	**10.8**	**21.9**
$LSD_{0.05}$				**1.6**			**15.8**	**1.7**	**2.5**	**2.4**	**14.5**	**1.1**

Gyld-Grain yield (t ha^{-1}), Daf-Days to flowering, LB-Leaf blast score (1-9), NB-Neck blast score (1-9), FB-Finger blast score (1-9), Thresh-Threshing%, Ag. score-Agronomic score (1-5). *-Susceptible check to the three blast types, **-Resistant check to the three blast types; †-Alupe location only

2.4.2.2 Sub-regional variability in performance

Significant ($P \leq 0.05$) differences between sub-regions were recorded for the 24 traits. At the low temperature high elevation Lanet location, the highest mean grain yield (5.48 t ha^{-1}) was recorded in accessions from Kenyan Rift Valley followed by accessions collected from western and northern Tanzania with grain yields of 4.59 and 4.54 t ha^{-1}, respectively (Appendix 2.2). The lowest yielding accessions with mean grain yield of 2.57 t ha^{-1} were from northern Uganda. At Alupe accessions from northern Uganda attained the highest mean grain yield (2.62 t ha^{-1}) followed by accessions from eastern Uganda with mean grain yield of 2.32 t ha^{-1} which were also among the earliest to flower (mean 75 days) (Appendix 2.3) . The best performing Kenyan accessions at Alupe were those from western Kenya with mean grain yield of 2.00 t ha^{-1}. Eastern Tanzania collections were the latest to flower (104 days). The best finger blast tolerance was recorded in western and northern Uganda accessions with a mean score of 3.1 (1-9 scale) while collections from western Tanzania were the most susceptible (mean score 4.9). At Mtwapa, accessions from northern Uganda performed best attaining mean grain yield of 1.73 t ha^{-1} and the least mean yield (1.26 t ha^{-1}) was recorded in accessions from the Rift Valley sub-region which are adapted to cooler environments (Appendix 2.4). At Kiboko the best performing accessions were from eastern Uganda with mean grain yield of 3.00 t ha^{-1} which were also earliest to flower (mean 71 days) (Appendix 2.5). Accessions from eastern Tanzania were the last to flower (mean 93 days) and the shortest in height (mean 82.0 cm).

2.4.3 Trait variances and diversity indices

Trait variances differed significantly between countries, and between sub-regions of collection (Tables 2.4.6 and 2.4.7). Between the three countries, the most heterogeneous accessions were from Tanzania (mean variance 60.4) with the highest variances in 13 traits (among them days to 50% flowering, panicle exertion, finger blast, productive tillers per plant, length of longest finger and grains per spikelet) (Table 2.4-6). Ugandan accessions were the least heterogeneous (mean variance 48.7) with highest variances in culm thickness, finger width, plant height, leaf blade length and width. Kenyan accessions attained the highest variances in grain yield and 1000 grain mass, flag leaf blade length, leaf sheath length and neck blast scores (mean variance 54.4). The minicore accessions had the highest variability (mean 65.3) in 13 out of the 24 quantitative traits. Differences were also found in variances between sub-regions of the three countries where western Tanzania collections had the highest variability (mean variance 14.24) followed by southern Tanzania (mean variance 11.48) (Table 2.4-7). The least variance was recorded in accessions from eastern Uganda (mean variance 4.47) followed by western Uganda (mean variance 4.95). As expected there was higher variability at country level (mean variance 57.20) than at sub-regional level

(mean variance 7.95). High overall mean Shannon diversity index (*H′* = 0.80*)* was recorded for the quantitative traits with the highest index recorded by the accessions from Tanzania (*H′* = 0.82*)*, followed by Kenya (*H′* = 0.82*)*, Uganda (*H′* = 0.80) and the lowest by the minicore (*H′* = 0.77*)* (Table 2.4-8). The highest diversity indices were recorded in grains per spikelet (*H′* = 0.87), finger length (*H′* = 0.83), panicle exertion (*H′* = 0.83*)* and 1000 grain mass (*H′* = 0.80), all traits that have a major contribution to grain yield.

Table 2.4-6. Variances of 24 traits for the three accession groups (based on country of origin) and the minicore across four test locations

Country	1	2	3	4	5	6	7	8	9	10	11	12	13
Kenya	2.839	0.297	469.5	10.20	3.008	1.515	95.05	0.104	146.0	2.523	1.021	3.772	0.093
Tanzania	2.442	0.289	609.7	11.36	3.905	2.026	78.89	0.089	126.3	2.249	1.569	3.664	0.123
Uganda	1.214	0.291	362.2	9.746	3.322	1.465	100.30	0.155	147.3	2.137	0.752	2.593	0.085
Minicore	2.054	0.280	651.5	11.37	5.903	3.476	115.50	0.215	135.9	3.624	3.059	3.476	0.119

Country	14	15	16	17	18	19	20	21	22	23	24	Mean
Kenya	7.829	2.423	0.576	15.06	408	115.7	15.97	3.186	0.106	0.0753	1.034	54.4
Tanzania	11.010	1.71	0.629	16.94	384.4	156.6	30.32	4.425	0.089	0.0677	1.289	60.4
Uganda	6.202	1.371	0.549	12.94	427.9	70.89	12.62	2.74	0.141	0.0821	1.241	48.7
Minicore	10.98	4.634	0.8	17.74	416	151.8	21.03	5.124	0.101	0.104	1.308	65.3

Table 2.4-7. Variances of 24 traits for ten accession groups (based on the sub-regions of the three countries of origin) and the minicore across four test locations

Sub-region	1	2	3	4	5	6	7	8	9	10	11	12
eastern Kenya	0.350	0.135	61.440	4.566	1.554	0.541	42.540	0.191	0.061	1.308	0.436	1.251
eastern Uganda	0.435	0.075	22.730	3.183	0.560	0.443	29.430	0.023	0.066	1.231	0.231	0.432
eastern Tanzania	0.261	0.026	0.040	0.130	0.253	1.299	3.640	0.001	0.000	0.039	0.758	0.045
Minicore	0.557	0.109	86.870	4.623	3.137	1.905	54.150	0.028	0.070	1.682	0.974	1.366
northern Uganda	0.213	0.064	24.620	2.397	0.243	0.769	15.000	0.017	0.038	0.536	0.220	0.433
northern Tanzania	0.339	0.023	30.580	3.256	0.473	0.549	6.370	0.025	0.059	0.566	0.283	0.424
Rift valley	0.354	0.089	65.370	2.906	0.896	1.144	43.570	0.028	0.056	1.235	0.452	1.111
southern Tanzania	0.560	0.122	70.390	4.186	1.675	1.321	32.220	0.020	0.059	0.901	0.447	1.140
western Kenya	0.390	0.106	79.850	3.928	0.584	0.873	29.630	0.037	0.041	0.917	0.263	1.214
western Uganda	0.177	0.042	41.910	2.990	0.296	0.422	28.230	0.019	0.070	0.470	0.240	0.480
western Tanzania	0.678	0.161	171.200	2.142	3.661	0.895	19.830	0.071	0.061	2.343	0.547	2.541

Sub-region	14	15	16	17	18	19	20	21	22	23	24	Mean
eastern Kenya	2.960	1.335	0.189	8.198	122.490	21.550	2.093	1.029	0.013	0.015	0.368	11.040
eastern Uganda	1.465	0.449	0.125	5.037	39.750	15.110	1.245	1.013	0.019	0.014	0.201	4.465
eastern Tanzania	0.031	0.074	0.000	6.661	9.240	15.180	0.087	0.003	0.000	0.004	0.053	1.628
Minicore	5.330	2.060	0.335	7.643	150.030	41.090	2.366	2.839	0.017	0.025	0.305	14.919
northern Uganda	1.069	0.328	0.079	4.049	60.750	13.220	1.131	0.564	0.009	0.007	0.224	5.283
northern Tanzania	1.081	0.172	0.047	4.323	24.760	60.960	2.080	0.291	0.004	0.006	0.240	6.213
Rift valley	2.692	1.095	0.196	4.612	96.930	40.700	1.474	1.169	0.010	0.013	0.289	10.607
southern Tanzania	3.331	0.859	0.338	6.794	71.550	71.220	3.459	2.422	0.014	0.010	0.378	11.483
western Kenya	1.739	0.376	0.120	6.668	74.640	26.430	1.744	1.098	0.018	0.011	0.337	9.587
western Uganda	0.757	0.314	0.154	3.606	27.150	22.850	1.413	0.414	0.011	0.010	0.240	4.950
western Tanzania	4.591	1.070	0.290	2.682	60.990	41.800	1.422	1.391	0.004	0.009	0.682	14.244

Traits key: 1-grain yield, 2-1000 grain mass, 3-days to flowering, 4-Panicle exertion, 5-finger blast, 6-fingers/panicle, 7-leaf blade length, 8-leaf blade width, 9-culm thickness, 10-flag leaf blade length, 11-leaf blast, 12-leaf sheath length, 13-leaf sheath width, 14-leaves/plant, 15-neck blast, 16-agronomic score, 17, peduncle length, 18-plant height, 19-threshing%, 20-productive tillers/plant, 21-finger length, 22-finger width, 23-flag leaf blade width, 24-grains per spikelet

Table 2.4-8. Shannon Weaver diversity indices (*H'*) for 20 quantitative traits for three accession groups (based on the country of origin) and the minicore across four test locations

Trait	1	2	3	4	5	6	7	8	9	10	11
Kenya	0.87	0.83	0.68	0.81	0.84	0.82	0.79	0.74	0.77	0.79	0.81
Minicore	0.87	0.70	0.36	0.81	0.79	0.72	0.83	0.82	0.79	0.82	0.81
Tanzania	0.85	0.94	0.69	0.87	0.83	0.79	0.77	0.84	0.78	0.83	0.82
Uganda	0.74	0.81	0.37	0.83	0.83	0.85	0.85	0.82	0.79	0.86	0.80
Mean	0.83	0.82	0.53	0.83	0.82	0.80	0.81	0.81	0.78	0.83	0.81

Trait	12	13	14	15	16	17	18	19	20	Mean±SE	CV%
Kenya	0.88	0.80	0.83	0.78	0.89	0.92	0.80	0.85	0.81	0.82±0.012	6.5
Minicore	0.83	0.64	0.67	0.90	0.81	0.84	0.69	0.80	0.82	0.77±0.26	15.1
Tanzania	0.87	0.85	0.78	0.79	0.66	0.69	0.89	0.94	0.84	0.82±0.017	9.2
Uganda	0.76	0.75	0.85	0.86	0.71	0.86	0.83	0.89	0.85	0.80±0.25	13.8
Mean	0.84	0.76	0.78	0.83	0.77	0.83	0.80	0.87	0.83		

1-Grain yield, 2-Leaf blade length, 3-Leaf blade width, 4-Leaf sheath length, 5-Leaf sheath width, 6-Leaves per plant, 7-Peducnle length, 8-Plant height, 9-Threshing%, 10-Productive tillers per plant, 11-Culm diameter, 12-Flag leaf blade length, 13-flag leaf blade width, 14-Days to flowering, 15-Panicle exertion, 16-Fingers per panicle, 17-Longest finger length, 18-Longest finger width, 19-Grains per spikelet, 20-1000 grain mass

2.4.4 Principal component analysis

The first six PCs were significant and accounted for 66.1% of the total variability in the 340 accessions (Table 2.4-9). The traits that mainly contributed to the variation accounted for in PC1 were panicle exertion, leaf sheath length, peduncle length, grain yield, plant height and leaf blade length. Flag leaf blade width, leaf blade width, leaf sheath width and productive tillers per plant contributed to the variation accounted for in PC2. The highest contribution to the variation accounted for in PC3 was from culm thickness, days to flowering, number of fingers per panicle, and leaves per plant. The highest contribution to variation accounted for in PC4 was made by number of fingers per panicle, leaves per plant and plant height whereas number of fingers per panicle, finger width, grain yield and productive tillers per panicle contributed the most to variation accounted for in PC5. Number of fingers per panicle, finger length, grain yield and productive tillers per plant contributed the most to variation accounted for in PC6 delineation. There was no defined delineation pattern between the accessions along the first two axes.

Table 2.4-9. First six principal components and the respective eigenvalues of the contributing 19 quantitative traits across country of origin and test locations

	Principal components					
	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	4.685	2.449	1.387	1.228	1.095	1.023
Proportion of variance (%)	26.09	13.64	7.72	6.84	6.1	5.7
Total variance (%)	26.1	39.7	47.5	54.3	60.4	66.1
	Eigenvalues (Loadings)					
Culm thickness	-0.05344	-0.17423	0.35121	0.29311	-0.09472	0.18684
Days to flowering	-0.24670	0.07725	0.32325	0.06942	0.22804	-0.13432
Panicle exertion	0.33542	-0.24703	0.04798	-0.20946	0.04798	-0.12498
Fingers per panicle	0.07260	0.19637	-0.39483	0.43129	-0.32997	0.11430
Finger length	0.13630	0.22226	0.22304	0.04920	0.53708	0.16967
Finger width	0.25783	0.01516	0.28763	-0.21003	-0.04253	0.00927
Flag leaf blade length	0.25813	-0.12945	-0.26357	0.24645	0.17241	0.15430
Flag leaf blade width	0.09592	0.43672	0.01857	-0.02166	-0.22120	0.02497
Grains per spikelet	0.21626	0.03100	0.34880	-0.19784	-0.21164	0.01997
1000 grain mass	0.05943	0.06829	-0.06271	-0.35230	-0.02227	0.84764
Grain yield	0.30822	-0.17112	0.16118	0.08791	-0.33903	-0.03216
Leaf blade length	0.29325	0.21013	-0.01013	0.10527	0.18527	-0.23880
Leaf blade width	0.17222	0.46418	0.09087	-0.00319	-0.22380	-0.04206
Leaves per plant	-0.07577	0.12240	0.45814	0.50625	0.03917	0.21739
Leaf sheath length	0.31347	-0.02461	-0.28024	0.11564	0.18919	-0.00493
Leaf sheath width	0.24936	0.37693	-0.02598	-0.13972	-0.05167	-0.18061
Peduncle length	0.36143	-0.25239	0.01065	-0.09116	0.06967	-0.07726
Plant height	0.31782	-0.08322	0.10668	0.33938	0.19268	0.16521
Productive tillers per plant	0.04117	-0.33841	0.27294	0.25062	-0.37588	0.08994

2.4.5 Cluster analysis

Cluster analysis based on across locations data delineated the accessions into seven clusters with accessions from each country represented in each cluster (Table 2.4-10 and Figure 2.4-4). Most of the accessions (53.4%) were placed in clusters one and two. Cluster one had 125 accession with 33 from Kenya, 56 from Uganda 15 from Tanzania and 20 from the minicore accessions. The accessions in this cluster were generally high yielding (mean 2.57 t ha^{-1}), early to medium flowering (mean 79 days) with broad fingers (1.2 cm) and wide flag leaves (1.2 cm). The 102 accessions in cluster two (40 from Kenya, 21 from Uganda, 25 from Tanzania, and 14 from the minicore) had the widest leaf blades (1.4 cm). The highest mean grain yield (2.86 t ha^{-1}), high grains/spikelet (six), longest leaf blades (50.7 cm), longest flag leaf blade lengths (12.3 cm) longest peduncles (22.1 cm) and longest panicle exertion (10.9 cm) were recorded in cluster three. This cluster had 54 accessions: 34 from Kenya, 13 from Uganda, three from Tanzania and three from the minicore. Cluster four had 33 accessions with eight from Kenya, five from Uganda, four from Tanzania and 15 from the minicore accessions. Accessions in this cluster were

characterized by early flowering (75 days), least mean finger length (2.4 cm), least mean leaf blade length (42.7 cm) and least mean number of leaves per plant (13). Cluster five with 29 accessions: 12 from Kenya, four from Uganda, ten from Tanzania and three from the minicore had the highest mean productive tillers per plant (5), lowest mean 1000 grain mass (2.4 g). Cluster six had 27 accessions: 18 from Kenya, three from Uganda, four from Tanzania and two from the minicore accessions. This cluster had the tallest plants (mean 100.4 cm) that flowered the latest (mean 95 days) with the highest mean 1000 grain mass (2.7g). Cluster seven had 55 accessions: nine from Kenya, three from Uganda, 20 from Tanzania and 23 from the minicore that had the lowest mean grain yield (2.07 t ha^{-1}), lowest mean leaf sheath length (10.3 cm), shortest peduncles (17.4 cm), lowest mean plant height (72.7 cm) with shortest mean flag leaf blade length (10.1 cm), shortest mean panicle exertion (mean 7.5 cm) and lowest mean grains per spikelet (5). Minicore accessions were least represented in clusters three (three accessions), five (three accessions) and six (two accessions). Based on Mahalanobis genetic distance (D^2) the widest separation (D^2 = 39.58) was between clusters four and six and whereas clusters two and five were the closest (D^2 = 11.3) (Table 2.4-11). Within cluster variability was highest in cluster seven (D^2 = 11.53) and least in cluster two (D^2 = 11.64).

In terms of within country clustering, seven clusters were detected in Kenya, five in Uganda and three in Tanzania (Table 2.4-12). For the Kenya clusters, the widest genetic distance (D^2 = 60.88) was between cluster six and seven and the least (D^2 = 12.5) between clusters one and three whereas within cluster distance was highest (D^2 = 9.64) in cluster one and least in cluster six. For the Uganda clusters, the widest distance (D^2 = 21.81) was between clusters one and five and the least (D^2 = 8.29) between clusters one and two. Within cluster distance was highest (D^2 = 7.86) in cluster four and least (D^2 = 6.17) in cluster five. Although there were only three clusters in the Tanzanian accessions, they had the widest diversity relative to the Kenyan and Ugandan accessions. For the Tanzania clusters, the widest (D^2 = 10.71) distance was between clusters one and three and the least (D^2 = 12.18) between cluster one and two whereas within cluster diversity was highest (D^2 = 10.71) in cluster two and least (D^2 = 8.53) in cluster one. There were three clusters in the minicore with relatively higher between cluster distances where the widest (D^2 = 48.82) distance was between clusters two and three. The highest (D^2 = 12.47) within cluster diversity in the minicore was in cluster one which was higher than all within cluster distances in the three countries of origin

Table 2.4-10. Means of 24 traits within clusters determined from cluster analysis across country of origin of accessions and test locations

	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5	Cluster 6	Cluster 7
	Number of accessions from each country						
Kenya	33	40	34	8	12	18	9
Uganda	56	21	13	5	4	3	3
Tanzania	15	25	3	4	10	4	20
Minicore	20	14	3	15	3	2	23
Checks	1	2	1	1	0	0	0
	Trait means of accessions in each cluster						
Grain yield (t/ha)	2.57	2.35	2.86	2.14	2.11	2.32	2.07
Leaf blade length (cm)	48.1	50.1	50.7	42.7	47.3	48.3	44.7
Leaf blade width (cm)	1.3	1.4	1.3	1.3	1.3	1.3	1.3
Leaf sheath length (cm)	11.7	11.3	12.3	11.1	11.2	10.8	10.3
Leaf sheath width (cm)	1.6	1.6	1.6	1.5	1.5	1.5	1.5
Leaves per plant	14.0	15.0	14.0	13.0	15.0	17.0	15.0
Peduncle length	20.6	19.0	22.1	19.0	20.3	19.8	17.4
Plant height (cm)	82.5	88.2	96.9	67.3	87.7	100.4	72.7
Productive tillers/plant	4.0	4.0	4.0	4.0	5.0	4.0	5.0
Culm diameter (cm)	13.3	14.1	13.6	13.1	12.6	14.1	13.1
Flag leaf blade length (cm)	10.9	10.3	11.2	11.0	10.7	10.2	10.1
Flag leaf blade width (cm)	1.2	1.2	1.2	1.1	1.1	1.2	1.2
Days 50% flowering	79.0	88.0	80.0	75.0	88.0	95.0	92.0
Panicle exertion (cm)	10.0	8.9	10.9	8.4	9.6	9.6	7.5
Fingers per plant	8.0	8.0	8.0	8.0	8.0	8.0	8.0
Longest finger length (cm)	6.7	6.9	7.0	6.2	6.6	7.4	6.4
Longest finger width (cm)	1.2	1.2	1.2	1.1	1.1	1.1	1.1
Grains per spikelet	6.0	6.0	6.0	6.0	5.0	6.0	5.0
1000 grain mass (g)	2.5	2.6	2.6	2.5	2.4	2.7	2.5

.

Table 2.4-11. Inter and Intra-cluster distances based on Mahalanobis genetic distance (D^2) determined across country of origin of accessions and test locations

	Cluster distances						
Cluster	1	2	3	4	5	6	7
1	**8.199**	11.64	14.90	16.86	15.48	24.61	18.76
2		**9.10**	12.59	26.14	11.33	14.33	17.89
3			**7.99**	31.51	17.94	16.32	29.28
4				**10.98**	27.41	39.58	19.87
5					**9.89**	17.28	17.24
6						**10.26**	28.45
7							**11.53**

NB. Diagonal values in bold are within cluster distances

Table 2.4-12. Inter and Intra-cluster distances based on Mahalanobis genetic distance (D^2) determined within the four accession groups across test locations

Kenya								Tanzania			
	Cluster distances								Cluster distances		
Cluster	1	2	3	4	5	6	7	Cluster	1	2	3
1	**9.64**	13.60	12.50	13.75	12.51	20.35	42.27	1	**8.53**	12.18	25.38
2		**8.94**	23.36	14.08	15.72	31.26	30.54	2		**10.71**	13.38
3			**8.38**	20.15	17.21	16.80	50.58	3			**10.02**
4				**9.55**	23.71	32.78	32.86				
5					**7.89**	18.50	45.65				
6						**7.63**	60.88				
7							**8.64**				
	Uganda							Minicore			
	Cluster distances								Cluster distances		
Cluster	1	2	3	4	5			Cluster	1	2	3
1	**6.47**	8.29	14.98	12.45	21.81			1	**12.47**	21.50	29.72
2		**7.14**	11.93	13.51	15.48			2		**9.99**	48.82
3			**7.01**	21.30	16.64			3			**7.86**
4				**7.86**	18.69						
5					**6.17**						

NB. Diagonal values in bold are within cluster distances

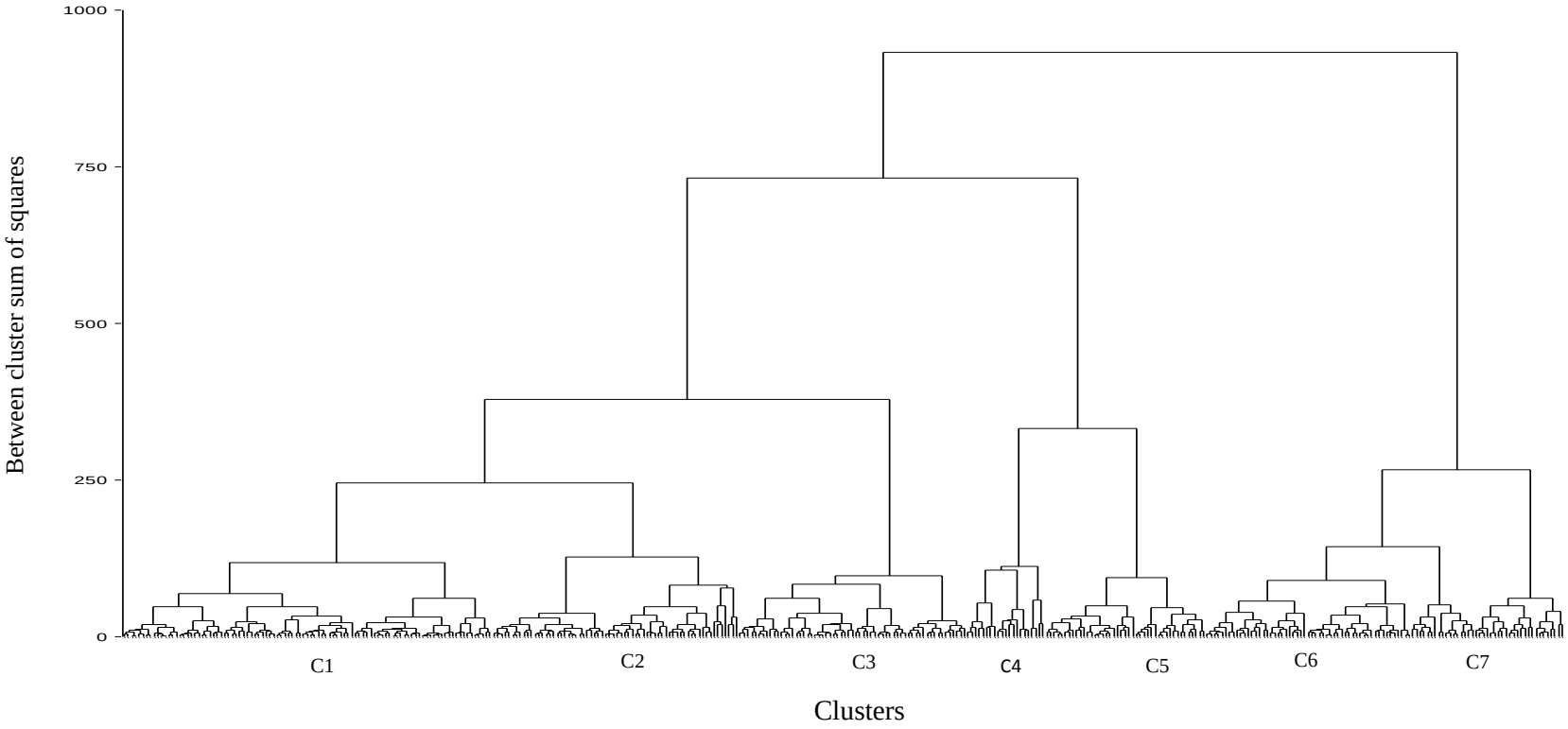

Figure 2.4-4. Dendrogram based on cluster analysis of quantitative traits across country of origin of accessions and locations at which they were evaluated (see appendix 2.1 for accessions in each cluster)

2.5 Discussion

2.5.1 Qualitative traits variability

The most valuable qualitative traits are those that show variability between the accessions. In this study the germpasm had high diversity indices for panicle shape and grain colour. Panicle shape and grain colour are often used by farmers in cultivar differentiation (de Wet et al., 1984). The predominance of brown grain types is based on quality requirements dictated by farmer and industry preferences. During a survey carried out in Kenya and Uganda in 2002 (Sreenivasaprasad et al., 2004), it was established that brown/red grain types were the most preferred because they make good beer and blend well with cassava for *ugali* (a stiff porridge prepared in East Africa). They are also the most preferred by industry/processors for making composite and pure flours for weaning foods and porridges. Choice of cultivar in finger millet being based on consumer and market preferences was also reported by Oduori (2008) in Kenya and Tsehaye and Kebebew (2002) in Ethiopia. Environmental adaptation dictates cultivar choice as evidenced from the predominance of pigmented plant types with brown grain and compact/fisted panicle types which have been reported to be resistant to blast and grain mold (Pande, 1992; Takan et al., 2004).These types are therefore preferred in sub-humid finger millet production agro-ecologies in the Lake Victoria zone where blast disease prevails. The very low frequency of white grain types recorded in this study was also reported by Tsehaye and Kebebew (2002) and Bezawelataw et al. (2007). The susceptibility of these white seeded types to bird attack and grain mold in humid environments may have contributed to their low frequency. The overall diversity index for the qualitative traits of 0.68 was higher than the 0.57 reported by Gopal Reddy et al. (2009) in India but lower than the 0.82 reported by Bezawelataw et al. (2007) in Ethiopia.

2.5.2 Quantitative traits variability

Significant variability ($P \leq 0.05$) were recorded in the three blast types, grain yield and yield components across all the accessions and between accessions based on countries of origin and their sub-regions. This confirms the genetic variability in the entire collection hence its value for finger millet improvement. Morphological traits are vulnerable to environmental influences (Smith and Smith (1992). Days to flowering in the germplasm were quite variable across the test locations with accessions from southern Tanzania taking over 95 days to 50% flowering and maturing late. In this regard, the behavior of these accessions is a reflection of the long mono-modal growing season in southern Tanzania where they are cultivated which starts in November and could extend to May. The cultivars preferred by farmers in this

region are long season types that mature when the rains are ending; a key trait as drying and threshing are usually done in the fields. This is corroborated by Gopal Reddy et al. (2009) in studies done in India who found accessions from Tanzania to be the latest maturing among collections from East Africa. Production areas in Kenya and Uganda have bimodal rainfall patterns with each season lasting three to four months hence cultivars used are relatively early and drying and harvesting are done in the homesteads. Specific agro-ecological adaptation was detected in the germplasm. At Alupe the best yielding accessions were from northern Uganda, eastern Uganda, and western Kenya. The similarity in these accessions was in their duration to flowering (they flowered in about 75 days) and had good resistance to leaf, neck and finger blast. The relatively high blast tolerance in Ugandan accessions could be as a result of farmer awareness about the disease (hence selection against susceptible cultivars) coupled with research intervention leading to promotion and adoption of improved blast tolerant cultivars.

At the low altitude Kiboko research station, accessions from the eastern and western sub-regions of Uganda performed best and were relatively early (71-77 days to flower). The lower 1000 grain mass at Kiboko could be attributed to moisture stress especially at grain filling particularly in late maturing accessions. The best performing accessions at the cool high altitude Lanet location were from the Rift valley sub-region where Lanet is also situated. Genotypes adapted to this location are usually late flowering but importantly they are also cold tolerant as low temperatures usually occur at the crop flowering stage thus affecting pollen viability. In finger millet low temperature has been reported to affect pollination and fertilization processes (Bandyopadhyay, 2009). This was evident at Lanet where partial sterility was recorded in early maturing check cultivar KNE 479 and several other accessions which effectively reduced grain yield. This is not unique to finger millet. Low temperatures have been reported to affect many crops at various stages of growth and development. In sorghum (*Sorghum bicolor*) low night temperatures (<13°C) during flag leaf formation induce male sterility and reduce pollen viability (McLaren, 1997) and possibly stigma receptivity (Osuna-Ortega et al., 2000).

Uganda is presumed to be the centre of origin for finger millet (Hilu et al., 1979) hence higher variability was expected to be found in the country's collections. However the variability in these accessions was relatively lower across most of the quantitative traits compared to accessions from Kenya and Tanzania. This trend could be attributed to: low variability in finger millet production agro-ecologies hence cultivars used are relatively similar (Personal observation in 210 during collection of the germplasm used in this study); more research intervention relative to Kenya and Tanzania hence more use of improved cultivars (ICRISAT, 2013) leading to a narrow genetic base; more commercialization of finger millet with end-users preferring specific cultivars; and diversity loss during the war in the 1970s (N. Wanyera

personal communication). Conversely, more variability was detected in the Tanzanian accessions where there has been less research intervention and so most of the cultivars currently used are unimproved landraces and are expected to have a wider variability. The high overall mean diversity indices detected in this study for quantitative traits reflects the potential breeding value of the germplasm. Gopal Reddy et al. (2009) reported lower diversity indices (0.492) for quantitative traits of germplasm sourced from East Africa but also recorded high diversity in finger length, plant height and days to flowering. The low diversity detected could have been due to the germplasm used and/or the environment under which evaluation was carried out. Overall Ugandan accessions performed better agronomically across locations than the other accessions which could be due to the more improved genotypes in the collection compared to the Tanzanian accessions for instance which were mostly landraces.

2.5.3 Principal component and cluster analyses

Based on differential traits loadings on PC1 and PC2 the delineation of the variability in the accessions was based on peduncle length, panicle exertion, plant height, leaf sheath length, grain yield and leaf blade length. Earlier research by Bezawelataw et al. (2006) and Bharathi (2011) also corroborated these findings. High contribution of grain yield to the variability between accessions was also reported by Lule et al. (2012) while Dhanakodi (1988) found most contribution to be from leaf length. The 66.1% of total variability accounted for by the six PCs was higher than the 59.63% reported by Bharathi (2011) on seven PCs but less than 91.5% by three PCs reported by Gopal Reddy et al. (2009). However, lack of a distinct delineation pattern between the countries of origin for the first two PCs was indicative of the close relationship between the three countries' germplasm. This finding agrees with earlier studies by Gopal Reddy et al. (2009) and Lule et al. (2012) who analyzed a set of finger millet accessions from Burundi, Ethiopia, Kenya, Tanzania and Uganda and found that accessions from East Africa, viz. Kenya, Tanzania and Uganda were closely related. Quantitative traits play a key role in adaptation to environments. Most of the agro-ecologies where finger millet is grown in East Africa receive above average rainfall. This therefore means that a number of different genotypes could be grown in a single agro-ecology which essentially explains the similarity in adaptation for several of the genotypes assessed. However from the Shannon diversity indices, trait variances and cluster distances, it was evident that higher diversity exists in Tanzanian accessions relative to Kenyan and Ugandan accessions. This diversity must be exploited for finger millet improvement. Since most of the germplasm in the Tanzanian genebank remains uncharacterized (Kisandu et al., 2007), efforts should be made to characterize the germplasm to ascertain its true value for effective conservation and utilization. Inter-and intra-cluster distances obtained

could form a basis for selection of diverse parents for target trait improvement. Accessions with similar agronomic traits will always group together irrespective of region of origin. The cross country and sub-region cluster patterns could also be as a result of seed exchanges between farmers either through relatives, markets and/or relief food/seed coupled with cross cutting agro-ecologies, cultures and end uses. However, selections within countries and sub-regions for agro-ecological adaptation and end use could be the reason for the high variability recorded within countries and sub-regions. The high frequency of similarity in accession names across the sub-regions in Uganda also suggested that probably the landraces used were fairly similar thus narrowing the genetic diversity. In the cluster analysis, the low representation of minicore accessions in clusters three, five and six may be an indication of the existence of diversity in this germplasm collection not yet represented in the global collection which should be carefully identified and included in future minicore constructions.

2.6 Conclusion

The significant ($P \leq 0.05$) genotypic differences in quantitative traits were recorded both within and across the locations is a manifestation of the diversity in the germplasm that could be exploited to produce cultivars for the different finger millet production agro-ecologies. The high variability found in qualitative traits, blast reaction, yield and yield related traits provides the opportunity for producing high yielding disease resistant cultivars with consumer and market acceptability. High diversity indices were recorded in grains per spikelet, finger length, panicle exertion and 1000-grain mass, traits that make major contributions to grain yield, indicating the potential for yield improvement in finger millet through selection. Low diversity was detected in Ugandan accessions a situation that is likely to occur in the other countries as promotion and use of improved cultivars takes root and calls for concerted efforts to collect and conserve valuable diversity before it is lost. There is need to promote further characterization of the germplasm held in genebanks to determine available diversity (useful traits) for finger millet improvement. Based on Mahalanobis genetic distance (D^2), distinct clusters were detected within the entire germplasm and within countries. The inter and intra-cluster distances obtained could form a basis for selection of diverse parents for target trait improvement. Much of the diversity recorded was to a greater extent well captured by the minicore except for three clusters of the germplasm collection in which the minicore accessions were poorly represented more so cluster three which had accessions mainly from cool high elevation agro-ecologies in Kenya) an indication of room to enrich the global diversity collection.

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Appendix 2.1. The 425 accessions phenotyped study and their cluster groups based on quantitative data across four locations

Accession #	Name	Country	Sub-region	Cluster	Accession #	Name	Country	Sub-region	Cluster
1	Unknown	Uganda	Eastern	3	49	Turi-open	Uganda	Northern	3
2	Unknown	Uganda	Eastern	1	50	Turi-closed	Uganda	Northern	2
3	Purple	Uganda	Eastern	1	51	Kal	Uganda	Northern	1
4	Ekama	Uganda	Eastern	1	52	Kal	Uganda	Northern	2
5	Ebega	Uganda	Eastern	3	53	Kal	Uganda	Northern	1
6	Engenyi	Uganda	Eastern	1	54	bulk market	Uganda	Northern	3
7	Ekama	Uganda	Eastern	1	55	bulk market	Uganda	Northern	1
8	Emoru	Uganda	Eastern	1	56	Fama atar	Uganda	Northern	1
9	Emiroit/Engeny	Uganda	Eastern	1	57	Kal	Uganda	Northern	4
10	Emaru	Uganda	Eastern	3	58	Kal-white	Uganda	Northern	3
11	Etiyo-brown	Uganda	Eastern	7	59	Kal-purple	Uganda	Northern	3
12	Etiyo-White	Uganda	Eastern	1	60	Kal	Uganda	Northern	2
13	Emiroit	Uganda	Eastern	1	61	Kal	Uganda	Northern	7
14	Ekwangapel	Uganda	Eastern	1	62	Kal	Uganda	Northern	2
15	Unknown	Uganda	Eastern	1	63	Kal atari	Uganda	Northern	4
16	Emorumoru (rock)	Uganda	Eastern	2	64	Kal atari	Uganda	Northern	1
17	Obeet	Uganda	Eastern	1	65	Kal atari	Uganda	Northern	3
18	Unknown	Uganda	Western	1	66	Ekamo	Uganda	Eastern	6
19	Etiyo	Uganda	Eastern	1	67	Unknown	Uganda	Eastern	1
20	Acomomcomo	Uganda	Eastern	4	68	Gulu E	Uganda	Northern	1
21	Eteke	Uganda	Eastern	1	69	Anyandri	Uganda	Northern	2
22	Ochom	Uganda	Eastern	3	70	Unknown	Uganda	Western	5
23	Emodigoit	Uganda	Eastern	1	71	Unknown	Uganda	Western	5
24	Namata	Uganda	Eastern	2	72	Unknown	Uganda	Western	1
25	Unknown	Uganda	Eastern	1	73	Bulo	Uganda	Western	5
26	Namakala	Uganda	Eastern	2	74	Bulo	Uganda	Western	2
27	Tanzakira	Uganda	Eastern	4	75	Bulo	Uganda	Western	2
28	Lowa	Uganda	Eastern	1	76	Bulo	Uganda	Western	2
29	Ekwangapel	Uganda	Eastern	1	77	Bulo	Uganda	Western	6
30	Emiroit/unknown purple	Uganda	Eastern	5	78	Bulo	Uganda	Western	1
31	Ekama-white	Uganda	Eastern	1	79	Unknown	Uganda	Western	2
32	Adalaka	Uganda	Western	3	80	Unknown	Uganda	Western	1
33	Emorumoru (rock)	Uganda	Eastern	2	81	Unknown	Uganda	Western	1
34	Ekama	Uganda	Eastern	1	82	Unknown	Uganda	Western	2
35	Ebati	Uganda	Eastern	1	83	Unknown	Uganda	Western	7
36	Omunga	Uganda	Eastern	3	84	Unknown	Uganda	Western	2
37	Emiroit	Uganda	Eastern	2	85	Unknown	Uganda	Western	2
38	Otunduru	Uganda	Eastern	3	86	Unknown	Uganda	Western	1
39	Kal (millet)	Uganda	Northern	1	87	Unknown	Uganda	Western	1
40	Kal (millet)	Uganda	Northern	1	88	Unknown	Uganda	Western	1
41	Kal (millet)	Uganda	Northern	1	89	Otara chilgal	Uganda	Northern	6
42	Kal (millet)	Uganda	Northern	1	90	Otara chilgal	Uganda	Northern	1
43	Kal (millet)	Uganda	Northern	2	91	Otara chilgal	Uganda	Northern	1
44	Otim cherigar/ceruget	Uganda	Northern	1	92	Otara chilgal	Uganda	Northern	1
45	Kal Lango	Uganda	Northern	4	93	Otara chilgal	Uganda	Northern	1
46	Kal	Uganda	Northern	1	94	Otara chilgal	Uganda	Northern	1
47	Cirogal	Uganda	Northern	1	95	Kal	Uganda	Northern	1
48	Oturi Aweri	Uganda	Northern	1	96	Kal	Uganda	Northern	1

Accession #	Name	Country	Sub-region	Cluster	Accession #	Name	Country	Sub-region	Cluster
97	Kal	Uganda	Northern	1	147	GBK-011107A	Kenya	Eastern	1
98	Kal	Uganda	Northern	1	148	GBK-011109A	Kenya	Eastern	2
99	Obeet	Uganda	Eastern	1	149	GBK-011110A	Kenya	Eastern	4
100	Ekoma-Okwa (IE 6555)	Uganda	Eastern	1	150	GBK-011111A	Kenya	Eastern	4
101	Quteke (IE 6557)	Uganda	Eastern	3	151	GBK-011112A	Kenya	Eastern	2
102	Eito (IE 6575)	Uganda	Eastern	1	152	GBK-011113A	Kenya	Eastern	2
103	Rwemereza (IE 6591)	Uganda	Eastern	2	153	GBK-011114A	Kenya	Eastern	5
104	Oburo (IE 6592)	Uganda	Eastern	2	154	GBK-011116A	Kenya	Eastern	1
105	RW 127 (IE 6613)	Uganda	Eastern	2	155	GBK-011117A	Kenya	Eastern	7
106	GBK-000347A	Kenya	Rvalley	3	156	GBK-011118A	Kenya	Eastern	4
107	GBK-000349A	Kenya	Rvalley	3	157	GBK-011119A	Kenya	Eastern	5
108	GBK-000350A	Kenya	Rvalley	3	158	GBK-011120A	Kenya	Eastern	7
109	GBK-000351A	Kenya	Rvalley	1	159	GBK-011129A	Kenya	Eastern	1
110	GBK-000352A	Kenya	Rvalley	3	160	GBK-011130A	Kenya	Eastern	6
111	GBK-000361A	Kenya	Rvalley	2	161	GBK-011131A	Kenya	Eastern	3
112	GBK-000364A	Kenya	Rvalley	3	162	GBK-011133A	Kenya	Eastern	6
113	GBK-000368A	Kenya	Rvalley	3	163	GBK-011134A	Kenya	Eastern	7
114	GBK-000369A	Kenya	Rvalley	3	164	GBK-011135A	Kenya	Eastern	6
115	GBK-000370A	Kenya	Rvalley	2	165	GBK-011136A	Kenya	Eastern	2
116	GBK-000371A	Kenya	Rvalley	3	166	GBK-011137A	Kenya	Eastern	3
117	GBK-000372A	Kenya	Rvalley	6	167	GBK-011138A	Kenya	Eastern	2
118	GBK-000373A	Kenya	Rvalley	3	168	GBK-011139A	Kenya	Eastern	2
119	GBK-000375A	Kenya	Rvalley	3	169	GBK-011140A	Kenya	Eastern	5
120	GBK-000379A	Kenya	Rvalley	6	170	GBK-011141A	Kenya	Eastern	4
121	GBK-000399A	Kenya	Western	3	171	GBK-013126A	Kenya	Eastern	1
122	GBK-000405A	Kenya	Western	2	172	GBK-013139A	Kenya	Eastern	6
123	GBK-000410A	Kenya	Western	1	173	GBK-013144A	Kenya	Eastern	7
124	GBK-000414A	Kenya	Western	1	174	GBK-013161A	Kenya	Eastern	3
125	GBK-000415A	Kenya	Western	2	175	GBK-013183A	Kenya	Eastern	5
126	GBK-000584A	Kenya	Eastern	1	176	GBK-027127A	Kenya	Rvalley	1
127	GBK-000587A	Kenya	Eastern	1	177	GBK-027128A	Kenya	Rvalley	3
128	GBK-000590A	Kenya	Eastern	2	178	GBK-027130A	Kenya	Rvalley	6
129	GBK-000591A	Kenya	Eastern	2	179	GBK-027133A	Kenya	Rvalley	6
130	GBK-000592A	Kenya	Eastern	3	180	GBK-027134A	Kenya	Rvalley	5
131	GBK-000594A	Kenya	Eastern	5	181	GBK-027135A	Kenya	Rvalley	6
132	GBK-000596A	Kenya	Eastern	2	182	GBK-027141A	Kenya	Rvalley	5
133	GBK-000597A	Kenya	Eastern	1	183	GBK-027145A	Kenya	Rvalley	4
134	GBK-000599A	Kenya	Eastern	2	184	GBK-027149A	Kenya	Rvalley	3
135	GBK-008277A	Kenya	Western	1	185	GBK-027155A	Kenya	Rvalley	3
136	GBK-008278A	Kenya	Western	5	186	GBK-027158A	Kenya	Rvalley	6
137	GBK-008279A	Kenya	Western	3	187	GBK-027165A	Kenya	Rvalley	3
138	GBK-008280A	Kenya	Western	3	188	Ikhulule	Kenya	Western	1
139	GBK-008281A	Kenya	Western	1	189	GBK-027185A	Kenya	Rvalley	2
140	GBK-008301A	Kenya	Western	1	190	GBK-027189A	Kenya	Rvalley	2
141	GBK-008321A	Kenya	Western	3	191	GBK-027193A	Kenya	Rvalley	6
142	GBK-008328A	Kenya	Western	3	192	GBK-027194A	Kenya	Rvalley	6
143	GBK-008329A	Kenya	Western	4	193	GBK-027200A	Kenya	Rvalley	3
144	GBK-008336A	Kenya	Western	1	194	GBK-027201A	Kenya	Rvalley	1
145	GBK-008352A	Kenya	Western	1	195	GBK-028546A	Kenya	Western	3
146	GBK-008365A	Kenya	Western	2	196	GBK-028588A	Kenya	Rvalley	3

Accession #	Name	Country	Sub-region	Cluster	Accession #	Name	Country	Sub-region	Cluster
197	GBK-028589A	Kenya	Rvalley	3	246	GBK-043165A	Kenya	Western	1
198	GBK-028590A	Kenya	Rvalley	3	247	GBK-043166A	Kenya	Western	3
199	GBK-029646A	Kenya	Western	1	248	GBK-043212A	Kenya	Eastern	1
200	GBK-029648A	Kenya	Western	5	249	GBK-043213A	Kenya	Eastern	5
201	GBK-029649A	Kenya	Western	2	250	GBK-044007A	Kenya	Rvalley	3
202	GBK-029650A	Kenya	Western	2	251	GBK-044008A	Kenya	Rvalley	1
203	GBK-029663A	Kenya	Western	2	252	GBK-044009A	Kenya	Rvalley	2
204	GBK-029664A	Kenya	Western	7	253	GBK-044047A	Kenya	Rvalley	2
205	GBK-029666A	Kenya	Western	7	254	Acc. # 76	Kenya	Rvalley	3
206	GBK-029667A	Kenya	Western	7	255	Acc. # 77	Kenya	Rvalley	3
207	GBK-029668A	Kenya	Western	7	256	Acc. # 78	Kenya	Rvalley	1
208	GBK-029670A	Kenya	Western	6	257	Acc. # 79	Kenya	Rvalley	3
209	GBK-029671A	Kenya	Western	2	258	Acc. # 80	Kenya	Rvalley	3
210	GBK-029672A	Kenya	Western	2	259	Acc. # 81	Kenya	Rvalley	1
211	GBK-029673A	Kenya	Western	2	260	IE 501	India	Minicore	4
212	GBK-029674A	Kenya	Western	2	261	IE 518	India	Minicore	7
213	GBK-029676A	Kenya	Western	6	262	IE 1055	Unknown	Minicore	1
214	GBK-029677A	Kenya	Western	2	263	IE 2034	India	Minicore	7
215	GBK-029678A	Kenya	Western	2	264	IE 2042	India	Minicore	1
216	GBK-029679A	Kenya	Western	5	265	IE 2217	India	Minicore	7
217	GBK-029680A	Kenya	Western	1	266	IE 2296	India	Minicore	7
218	GBK-029681A	Kenya	Western	1	267	IE 2312	India	Minicore	2
219	GBK-029682A	Kenya	Western	2	268	IE 2430	Kenya	Minicore	1
220	GBK-029754A	Kenya	Western	2	269	IE 2437	Kenya	Minicore	2
221	GBK-029755A	Kenya	Western	3	270	IE 2457	Kenya	Minicore	1
222	GBK-029756A	Kenya	Western	1	271	IE 2572	Kenya	Minicore	1
223	GBK-029758A	Kenya	Western	2	272	IE 2589	USA	Minicore	6
224	GBK-029763A	Kenya	Western	2	273	IE 2606	Malawi	Minicore	7
225	GBK-029766A	Kenya	Western	2	274	IE 2619	Malawi	Minicore	4
226	GBK-029767A	Kenya	Western	7	275	IE 2710	Unknown	Minicore	1
227	GBK-029768A	Kenya	Western	2	276	IE 2790	unknown	Minicore	4
228	GBK-029769A	Kenya	Western	2	277	IE 2821	Nepal	Minicore	7
229	GBK-040436A	Kenya	Rvalley	2	278	IE 2871	Zambia	Minicore	2
230	GBK-040459A	Kenya	Rvalley	1	279	IE 2872	Zambia	Minicore	7
231	GBK-040463A	Kenya	Rvalley	4	280	IE 2911	Zambia	Minicore	4
232	GBK-040468A	Kenya	Rvalley	4	281	IE 2957	Germany	Minicore	4
233	GBK-040555A	Kenya	Rvalley	6	282	IE 3045	India	Minicore	6
234	GBK-040556A	Kenya	Rvalley	6	283	IE 3077	India	Minicore	7
235	GBK-040559A	Kenya	Rvalley	6	284	IE 3104	India	Minicore	4
236	GBK-040568A	Kenya	Rvalley	5	285	IE 3317	Zimbabwe	Minicore	2
237	GBK-040569A	Kenya	Rvalley	1	286	IE 3391	Zimbabwe	Minicore	7
238	GBK-043153A	Kenya	Western	2	287	IE 3392	Zimbabwe	Minicore	4
239	GBK-043154A	Kenya	Western	1	288	IE 3470	India	Minicore	7
240	GBK-043155A	Kenya	Western	1	289	IE 3475	India	Minicore	7
241	GBK-043159A	Kenya	Western	2	290	IE 3614	Unknown	Minicore	3
242	GBK-043161A	Kenya	Western	1	291	IE 3721	Uganda	Minicore	5
243	GBK-043162A	Kenya	Western	6	292	IE 3945	Uganda	Minicore	2
244	GBK-043163A	Kenya	Western	1	293	IE 3952	Uganda	Minicore	1
245	GBK-043164A	Kenya	Western	2	294	IE 3973	Uganda	Minicore	1

Accession #	Name	Country	Sub-region	Cluster	Accession #	Name	Country	Sub-region	Cluster
295	IE 4028	Uganda	Minicore	3	348	Acc # 2920	Tanzania	Southern	7
296	IE 4057	Uganda	Minicore	2	349	Acc # 2924	Tanzania	Southern	7
297	IE 4073	Uganda	Minicore	2	350	Acc # 2954	Tanzania	Southern	7
298	IE 4121	Uganda	Minicore	1	351	Acc # 2968	Tanzania	Southern	5
299	IE 4329	Zimbabwe	Minicore	1	353	Acc # 2999	Tanzania	Southern	2
300	IE 4491	Zimbabwe	Minicore	1	354	Acc # 3016	Tanzania	Southern	5
301	IE 4497	Zimbabwe	Minicore	1	355	Acc # 3027	Tanzania	Southern	6
302	IE 4545	Zimbabwe	Minicore	5	356	Acc # 3030	Tanzania	Southern	5
303	IE 4565	Zimbabwe	Minicore	7	357	Acc # 3040	Tanzania	Southern	2
304	IE 4570	Zimbabwe	Minicore	2	358	Acc # 3063	Tanzania	Southern	7
305	IE 4622	Zimbabwe	Minicore	7	359	Acc # 3081	Tanzania	Southern	2
306	IE 4646	Zimbabwe	Minicore	7	360	Acc # 3083	Tanzania	Southern	2
307	IE 4671	India	Minicore	4	361	Acc # 3114	Tanzania	Western	5
308	IE 4734	India	Minicore	4	362	Acc # 3135	Tanzania	Western	4
309	IE 4757	India	Minicore	7	363	Acc # 3163	Tanzania	Western	7
310	IE 4795	Zimbabwe	Minicore	4	364	Acc # 3574	Tanzania	Western	5
311	IE 4797	Maldives	Minicore	2	365	Unknown	Tanzania	Western	2
312	IE 4816	India	Minicore	7	366	Acc # 3656	Tanzania	Southern	1
313	IE 5066	Senegal	Minicore	3	367	Acc # 3721	Tanzania	Southern	4
314	IE 5091	Zimbabwe	Minicore	7	368	Acc # 3724	Tanzania	Southern	1
315	IE 5106	Zimbabwe	Minicore	7	369	Acc # 3779	Tanzania	Southern	5
316	IE 5201	India	Minicore	5	370	Acc # 3849	Tanzania	Southern	2
317	IE 5306	Zimbabwe	Minicore	2	371	Acc # 3865	Tanzania	Southern	2
318	IE 5367	Kenya	Minicore	1	372	Acc # 3902	Tanzania	Southern	1
319	IE 5537	Nepal	Minicore	4	373	Acc # 3910	Tanzania	Southern	3
320	IE 5817	Nepal	Minicore	4	374	Acc # 3919	Tanzania	Northern	3
321	IE 5870	Nepal	Minicore	1	375	Acc # 3924	Tanzania	Northern	1
322	IE 6059	Nepal	Minicore	1	376	Acc # 3927	Tanzania	Northern	2
323	IE 6082	Nepal	Minicore	1	377	Acc # 3944	Tanzania	Northern	2
324	IE 6154	Nepal	Minicore	1	378	Acc # 3953	Tanzania	Northern	1
325	IE 6165	Nepal	Minicore	4	379	Acc # 3960	Tanzania	Northern	1
326	IE 6221	Nepal	Minicore	4	380	Acc # 3962	Tanzania	Northern	2
327	IE 6240	Zimbabwe	Minicore	7	381	Acc # 3989	Tanzania	Northern	1
328	IE 6294	Zimbabwe	Minicore	7	382	Acc # 3995	Tanzania	Northern	5
329	IE 6326	Zimbabwe	Minicore	7	383	Acc # 4225	Tanzania	Western	3
330	IE 6337	Zimbabwe	Minicore	1	384	Acc # 4263	Tanzania	Western	1
331	IE 6350	Zimbabwe	Minicore	7	385	Kahulunge	Tanzania	Southern	2
332	IE 6421	Uganda	Minicore	2	386	Sansamula	Tanzania	Southern	1
333	IE 6473	Uganda	Minicore	2	387	Nameka	Tanzania	Southern	7
334	IE 6514	Zimbabwe	Minicore	2	388	Mautila	Tanzania	Southern	7
335	IE 6533	Nigeria	Minicore	7	389	Anguumi	Tanzania	Southern	2
336	IE 7018	Unknown	Minicore	2	390	Unknown	Tanzania	Southern	4
337	IE 7079	Unknown	Minicore	4	391	Nameka	Tanzania	Southern	2
338	IE 7320	Unknown	Minicore	1	392	Chikufi	Tanzania	Southern	7
339	IE 7508	Unknown	Minicore	1	393	Nameka	Tanzania	Southern	7
340	Acc # 2292	Tanzania	Southern	2	394	Ngumi	Tanzania	Southern	2
341	Acc # 2361	Tanzania	Southern	5	395	Kaulunge (Ngumi)	Tanzania	Southern	1
342	Acc # 2369	Tanzania	Southern	2	396	Katila	Tanzania	Southern	2
343	Acc # 2457	Tanzania	Southern	2	397	Kauhulunge	Tanzania	Southern	7
344	Acc # 2502	Tanzania	Southern	7	398	Chikwekwele	Tanzania	Southern	7

Accession #	Name	Country	Sub-region	Cluster
399	Kaulunge (Makazi)	Tanzania	Southern	2
400	Kafumbata/Sanzamula mix	Tanzania	Southern	2
401	Sansamula	Tanzania	Southern	1
402	Kafumbata/Kaulunge	Tanzania	Southern	7
403	Sansamula	Tanzania	Southern	5
404	Kaulunge	Tanzania	Southern	7
405	Unkown	Tanzania	Southern	2
406	Kafumbata	Tanzania	Southern	1
407	Kaulunge	Tanzania	Southern	1
408	Namakonta	Tanzania	Southern	2
409	Magasi	Tanzania	Southern	2
410	Katila	Tanzania	Southern	7
411	Magas/Kaulunge mix	Tanzania	Southern	2
412	Katila	Tanzania	Southern	1
413	Kaulunge	Tanzania	Southern	7
414	Naupule/Ng'ombe mix	Tanzania	Southern	1
415	Ng'ombe	Tanzania	Southern	4
416	Katila	Tanzania	Southern	7
417	Mautila (white)	Tanzania	Southern	7
418	Solila	Tanzania	Southern	2
419	Katila	Tanzania	Southern	7
420	Ng'ombe	Tanzania	Southern	7
421	Nakuru FM 1	Kenya	Check	3
422	U 15	Uganda	Check	4
423	Kahulunge	Tanzania	Check	2
424	KNE 479	ICRISAT-Nairobi	Check	1
425	KNE 814	ICRISAT-Nairobi	Check	2

Appendix 2.2. Means for 24 traits for the 420 accessions based on sub-regions evaluated at Lanet

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
eastern Kenya	3.64	2.2	117	8.6	8	5.3	0.9	10.4	0.9	5	5	2.9	35.7	1.0	12	2.4	10.5	1.4	2.6	3.6	18.7	61.7	74.6	11
eastern Uganda	2.86	2.3	111	8.4	7	4.7	1.0	10.5	0.9	6	5	2.8	34.1	0.9	11	2.5	10.6	1.3	2.6	3.8	18.8	52.1	71.1	9
eastern Tanzania	2.50	1.8	144	9.6	7	4.9	0.9	8.8	0.8	6	5	2.4	31.8	0.9	11	1.9	8.8	0.9	3.3	4.0	19.1	54.7	74.9	21
Minicore	3.20	2.1	120	7.4	8	4.9	0.9	10.3	0.9	6	5	2.8	33.1	1.0	12	2.4	10.3	1.2	2.8	3.9	17.4	55.0	70.3	10
northern Uganda	2.57	2.1	109	7.5	7	4.8	0.9	10.0	0.9	5	5	2.9	34.2	1.0	11	2.6	9.9	1.4	2.2	3.9	17.3	52.8	73.0	7
northern Tanzania	4.55	2.2	111	8.4	8	5.0	1.0	10.7	0.9	3	5	2.7	34.5	1.0	12	2.3	10.7	1.3	2.0	2.9	19.1	59.2	72.5	10
Rift valley	5.48	2.3	113	9.4	8	5.6	1.0	11.0	0.9	4	5	3.1	37.5	1.0	12	2.2	11.0	1.3	2.2	2.9	20.3	68.9	82.2	10
southern Tanzania	3.67	2.2	130	8.4	8	5.6	0.9	9.7	0.9	5	5	2.7	34.8	1.0	13	2.1	9.7	1.2	2.7	3.8	18.3	60.1	75.9	13
western Kenya	4.02	2.2	117	8.2	8	5.0	0.9	10.7	0.9	4	5	2.9	35.5	1.0	12	2.2	10.7	1.3	1.8	3.5	18.8	60.0	7.05	10
western Uganda	3.28	2.0	119	9.3	7	4.6	0.9	10.2	0.9	5	5	2.8	35.9	1.0	12	2.3	10.2	1.3	2.3	3.6	19.3	59.1	76.6	10
western Tanzania	4.59	1.9	124	9.4	8	5.3	0.9	10.0	1.1	6	5	2.5	34.1	0.9	12	2.2	10.0	1.1	3.9	3.7	19.5	66.4	75.4	12
Mean	3.63	2.1	119	8.6	8	5.1	0.9	10.2	0.9	5	5	2.8	34.7	1.0	12	2.3	10.2	1.3	2.5	3.6	18.8	59.0	69.0	11
SE±	1.96	3.5	12.8	2.6	1.3	1.1	0.1	1.2	0.2	1.9	0.7	0.5	4.0	0.1	1.4	0.7	1.2	0.2	1.5	0.8	2.9	10.9	11.2	3.82
CV (%)	34.3	15.9	11.0	30.0	17.4	21.0	14.3	11.5	18.2	32.0	15.2	18.4	11.5	10.4	12.3	29.0	11.5	17.4	33.0	21.8	15.6	18.7	15.1	30.0
$LSD_{0.05}$	1.37	2.5	9.0	1.8	0.9	0.7	0.1	0.8	0.1	1.4	0.5	0.4	2.8	0.1	1.0	0.4	0.8	0.1	1.1	0.5	2.0	7.7	7.8	2.7

See appendix 2.5 for trait names

Appendix 2.3. Means for 24 traits for the 420 accessions based on sub-regions evaluated at Alupe

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
eastern Kenya	1.73	2.9	79	9.6	8	6.4	1.0	9.3	1.1	4.3	5	2.6	49.6	1.3	16	3.7	10.2	1.5	3.3	3.3	19.1	90.6	63.5	2
eastern Uganda	2.32	2.6	75	12.7	8	6.1	1.0	10.3	1.1	3.6	6	2.6	51.2	1.3	16	2.8	10.7	1.5	2.8	2.9	22.7	97.9	65.8	3
eastern Tanzania	1.83	2.4	104	9.6	7	5.7	0.9	7.6	1.1	*	6	2.6	48.6	1.3	20	2.1	9.4	1.3	2.4	*	18.5	76.7	65.2	2
Minicore	1.64	2.8	80	9.7	8	6.0	1.0	10.2	1.0	4.1	5	2.5	47.0	1.3	16	4.0	10.0	1.4	3.8	3.6	19.8	83.9	61.4	3
northern Uganda	2.62	2.7	75	12.9	8	6.4	1.0	9.6	1.1	3.1	6	2.6	53.4	1.3	16	2.3	10.6	1.6	2.7	2.5	22.3	97.2	69.3	3
northern Tanzania	1.97	2.8	75	10.9	7	6.5	1.0	9.2	1.1	4.6	6	2.3	48.4	1.3	17	3.7	10.3	1.5	4.0	3.3	20.3	96.4	66.2	3
Rift valley	1.74	2.8	78	11.2	8	6.7	1.0	10.5	1.1	4.5	6	2.6	51.2	1.3	16	3.8	10.9	1.5	3.6	3.5	21.6	103.0	65.1	2
southern Tanzania	1.24	2.9	89	8.7	8	6.0	0.9	9.5	1.1	4.3	5	2.5	45.8	1.3	17	3.3	9.3	1.4	2.6	3.6	18.0	86.1	66.4	3
western Kenya	2.00	2.9	77	10.1	8	6.2	1.0	10.0	1.1	3.7	6	2.5	50.1	1.3	17	2.8	10.1	1.5	2.9	3.0	19.6	96.5	65.9	3
western Uganda	1.76	2.8	82	10.9	8	5.9	0.9	9.3	1.1	3.1	5	2.2	50.1	1.3	16	2.5	9.8	1.4	2.3	2.8	20.4	91.0	66.5	2
western Tanzania	1.58	2.4	91	12.1	8	5.7	0.9	9.0	1.0	4.9	5	2.4	46.3	1.1	18	3.1	10.3	1.3	2.2	4.0	20.2	85.1	61.4	3
Mean	1.84	2.7	81	10.9	8	6.2	1.0	9.5	1.1	4.0	6	2.5	49.5	1.3	17	3.1	10.2	1.5	3.0	3.2	20.4	91.7	65.3	3
SE±	0.76	0.58	12.5	3.2	1.1	1.1	0.1	1.4	0.1	1.5	0.9	0.5	5.5	0.1	2.0	1.3	1.2	1.1	1.5	0.7	3.8	14.3	9.7	1.5
CV (%)	33.0	21.0	15.9	28.0	14.6	16.8	12.8	14.1	10.4	32.1	16.4	21.5	11.0	9.7	12.5	34.0	12.1	10.8	35.0	22.8	18.6	15.3	14.9	35.0
$LSD_{0.05}$	0.5	0.4	9.8	2.2	0.8	0.7	0.1	0.9	0.1	0.8	0.6	0.4	3.8	0.1	1.4	1.1	0.8	0.1	1.1	0.4	2.7	9.9	6.8	1.1

See appendix 2.5 for trait names

Appendix 2.4. Means for 21 traits for the 420 accessions based on sub-regions evaluated at Mtwapa

Trait	1	2	3	4	5	6	7	8	9	11	12	13	14	15	17	18	20	21	22	23	24
eastern Kenya	1.47	28.9	67	7.9	9	8.5	1.6	11.4	1.6	6	2.5	58.5	1.7	13	13.1	1.7	3.4	18.7	97.0	74.4	1
eastern Uganda	1.78	29.3	64	10.3	8	8.1	1.7	11.8	1.5	6	2.3	57.9	1.8	13	13.5	1.7	3.0	21.5	96.1	76.0	2
eastern Tanzania	0.91	21.7	78	14.0	9	7.0	1.3	10.1	1.2	8	2.7	46.6	1.5	13	10.5	1.5	3.7	21.1	90.1	60.3	2
Minicore	1.60	26.6	65	8.5	9	8.1	1.5	12.5	1.4	6	2.5	54.6	1.8	13	13.0	1.7	3.5	20.4	88.7	74.6	2
northern Uganda	1.73	29.2	65	11.1	8	8.2	1.7	10.9	1.6	6	2.4	58.0	1.7	13	13.2	1.7	2.9	21.9	96.4	76.4	1
northern Tanzania	1.68	29.2	65	8.5	9	9.4	1.8	11.0	1.5	6	2.4	58.6	1.6	13	13.7	1.7	3.1	19.2	99.3	77.4	1
Rift valley	1.26	26.9	67	9.8	8	8.4	1.5	11.4	1.5	6	2.7	57.9	1.7	13	14.0	1.7	3.4	20.7	104.1	73.7	1
southern Tanzania	1.38	25.6	69	9.3	9	8.8	1.5	11.0	1.4	6	2.7	54.7	1.7	14	12.7	1.7	3.4	19.8	96.0	73.5	1
western Kenya	1.54	28.5	67	8.4	8	8.2	1.6	11.7	1.5	6	2.5	59.2	1.7	14	13.9	1.7	3.2	19.8	101.5	74.6	1
western Uganda	1.54	28.3	66	9.7	8	7.8	1.6	11.7	1.5	6	2.4	60.1	1.7	14	13.5	1.7	3.2	21.0	102.4	76.0	1
western Tanzania	1.36	25.3	72	9.1	9	7.8	1.5	9.8	1.5	7	2.3	54.8	1.6	15	12.5	1.6	4.0	19.0	99.6	72.2	1
Mean	1.52	27.3	67	9.8	9	8.2	1.6	11.2	1.5	6	2.5	56.5	1.7	13	13.1	1.7	3.3	20.4	97.3	73.7	1
SE±	0.49	3.7	4.9	3.3	1.4	1.6	0.3	1.7	0.2	1.3	0.4	6.8	0.4	2.2	1.4	0.2	0.7	3.9	12.5	6.1	0.9
CV (%)	32.1	13.4	7.4	32.0	17.2	19.2	21.2	14.5	13.8	21.7	17.4	11.9	22.0	17.3	10.5	10.9	20.3	19.3	12.9	8.2	25.0
$LSD_{0.05}$	0.4	2.6	3.4	2.3	0.9	1.2	0.2	1.2	0.2	0.9	0.3	4.8	0.3	1.6	0.9	0.1	0.4	2.8	8.8	4.3	0.6

See appendix 2.5 for trait names

Appendix 2.5. Means for 21 traits for the 420 accessions based on sub-regions evaluated at Kiboko

Trait	1	2	3	4	5	6	7	8	9	11	12	13	14	15	17	18	20	21	22	23	24
eastern Kenya	2.55	1.4	75	8.3	8	7.8	1.1	10.3	1.2	6	2.4	49.9	1.4	16	11.4	1.9	2.8	19.0	88.9	68.3	2
eastern Uganda	3.00	1.4	71	10.9	8	6.9	1.1	10.8	1.2	6	2.4	50.1	1.3	16	11.3	1.9	2.5	21.6	91.4	74.0	3
eastern Tanzania	1.85	1.4	93	5.5	9	7.0	1.0	9.1	1.1	5	1.8	47.1	1.1	20	9.5	1.6	3.1	13.9	85.3	55.5	4
Minicore	2.53	1.4	73	9.1	8	7.4	1.1	11.2	1.2	6	2.3	47.1	1.3	16	11.0	1.8	2.8	20.2	82.2	70.5	3
northern Uganda	2.82	1.4	72	10.3	8	7.6	1.1	10.1	1.2	6	2.4	52.6	1.3	16	11.2	2.0	2.6	20.6	89.5	75.2	2
northern Tanzania	2.77	1.5	72	10.4	8	7.3	1.1	10.2	1.1	6	2.4	50.2	1.3	17	11.8	1.9	2.9	20.6	93.2	71.3	2
Rift valley	2.49	1.5	76	9.9	8	8.0	1.1	10.8	1.2	6	2.5	52.4	1.3	16	12.0	1.9	2.8	20.5	97.7	71.9	2
southern Tanzania	1.75	1.5	87	6.6	8	8.1	1.1	9.5	1.1	6	2.3	47.8	1.3	19	10.4	1.8	3.1	16.5	82.0	60.2	3
western Kenya	2.68	1.5	77	8.3	8	7.5	1.1	10.6	1.2	6	2.5	51.7	1.3	17	11.6	1.9	2.6	18.5	91.6	72.3	2
western Uganda	2.84	1.5	77	10.4	8	7.4	1.1	10.4	1.2	6	2.2	53.4	1.3	16	11.3	2.0	2.8	21.1	92.9	69.4	2
western Tanzania	1.51	1.2	83	8.6	9	6.4	1.0	9.8	1.0	6	2.2	46.8	1.2	17	10.9	1.6	3.4	18.8	86.9	59.0	4
Mean	2.54	1.4	77	9.1	8	7.5	1.1	10.3	1.2	6	2.3	50.0	1.3	17	11.2	1.8	2.9	19.4	89.3	68.3	3
SE±	0.7	0.2	7.8	3.1	1.3	1.6	0.1	1.4	0.2	0.7	0.5	6.4	0.2	2.6	1.2	0.3	0.7	4.1	11.6	9.9	1.1
CV (%)	27.1	17.0	10.4	32.01	17.6	20.9	10.6	13.2	16.4	11.3	19.1	12.7	17.6	15.9	10.9	13.2	14.4	20.5	13.2	14.1	33.4
$LSD_{0.05}$	0.5	0.2	5.5	2.2	0.9	1.1	0.1	0.9	0.1	0.4	0.3	4.5	0.2	1.8	0.8	0.2	0.5	2.8	8.2	6.9	0.8

1-Grain yield (t ha^{-1}), 2-Culm diameter (cm), 3-Days to flowering, 4-Panicle exertion (cm), 5-Fingers per panicle, 6-Finger length (cm), 7-Finger width (cm), 8-Flag leaf sheath length (cm), 9-Flag leaf sheath Width (cm), 10-Finger blast (1-9), 11-Grains per spikelet, 12-1000 grain mass, 13-Leaf blade length (cm), 14-Leaf blade width (cm), 15-Leaves per plant, 16-Leaf blast, 17-Leaf sheath length (cm), 18-Leaf sheath width (cm), 19-Neck blast score (1-9), 20-Agronomic (1-5), 21-Peduncle lenth (cm), 22-Plant height (cm), 23-Threshing %, 24-Productive tillers per plant

Chapter 3

Genetic diversity in East African finger millet landraces based on SSR markers and some qualitative traits

Abstract

Genetic diversity in 340 finger millet accessions from Kenya, Tanzania and Uganda and 15 minicore accessions was assessed using 23 SSR markers and five qualitative traits. Nineteen markers were polymorphic with mean PIC value of 0.606 (range of 0.035 to 0.889) with allele size range of 148-478. A total of 195 alleles were detected (range of 3-23 and an average of 10.3 alleles per locus) with 57.7% being rare and 17.4% being private. Differentiation between the three countries' accessions was weak with most of the genetic variability explained within country and sub-region than among country and sub-region levels. The highest genetic diversity was observed in Kenyan accessions (0.638±0.283) and the least in Ugandan accessions (0.583±0.264). The widest differentiations based on Wight's fixation index were between Ugandan and Tanzanian accessions (F_{ST} = 0.117: $P \leq 0.001$). There was no association between the morphological traits assessed and the genetic classes observed. The low variability between the countries could be attributed to a shared genepool since the crop originated from the East African region. Farmers' selection for adaptation and end use could have contributed to the high diversity within countries. Concerted efforts need to be made to characterize the large germplasm stocks in the region for its effective conservation and utilization. Lack of representation of the three countries accessions in all minicore diversity clusters points to the need to explore the regions germplasm to identify the diversity not earlier captured to be included in the global repository.

Key words: East Africa, genetic diversity, *Eleusine coracana*, molecular characterization, SSR markers

3.1 Introduction

Finger millet (*Eleusine coracana*) accounts for about 4 million ha (10%) of the 38 million ha sown to millets globally and in East Africa it covers 50% of the millet area (Obilana, 2002). The importance of finger millet lies in its superior nutritional value compared to other cereals and long storability without insect damage and [National Research Council (NRC), 1996]. The grain is exceptionally high in Ca^{2+} (358 mg kg^{-1}) and Fe^{2+} (46 mg kg^{-1}) which makes it an important food for expectant women, breast feeding mothers, children, the sick and diabetics (NRC, 1996). Being gluten free, finger millet has a global potential in regions where demand for gluten free products is increasing (Lenné et al., 2007). East Africa, specifically Uganda being the primary center of finger millet diversity, is presumed to have a wider and richer genetic base for the crop than other regions (Harlan, 1971; de Wet, 1995).

Effective breeding for target traits requires careful selection of parents with a wide genetic base to enhance genetic gain (Lapitan et al., 2007). Both morphological and molecular characterization approaches have been effectively applied in many crops to identify germplasm references that are genetically diverse. The complementarity of phenotypic and molecular characterization helps to understand not only the variability in the germplasm but also the value of the variability observed. Hilu and de Wet (1976) reported variability in vegetative, floral and seed morphology in finger millet based on eco-geographical origin and were able to distinguish three eco-geographical races, namely: African highland race; lowland race; and Indian race. In Ethiopia, Lule et al. (2012) distinguished two clusters in germplasm from Ethiopia, Kenya, Eritrea, Zambia and Zimbabwe based on growth habit, ear type, glume color, glume covering, spikelet density and seed colour. Using morphological data, Upadhyaya et al. (2010) were able to develop a core collection (10% of total collection) and a minicore (10% of the core collection) to represent the total global diversity held at the ICRISAT genebank.

Molecular characterization is useful to eliminate deficiencies in morphological classification of genotypes (Kumari and Pande, 2010). For molecular characterization, it is imperative that the markers used are polymorphic. This avoids spurious clustering of genotypes. Previous studies of finger millet diversity using molecular approaches are limited. This is due to the limited understanding of the finger millet genome compared to other cereals like maize (Z*ea mays*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), rice (*Oryza sativa*) and sorghum (*Sorghum bicolor*). Both hybridization and Polymerase Chain Reaction (PCR) based markers have been used in finger millet diversity studies though not extensively. Panwar et al. (2010) compared Random Amplified Polymorphic DNA (RAPDs) and Single Sequence Repeats (SSRs) and found the highest polymorphic information content (PIC) with SRRs (0.89)

compared to RAPDs (0.280). Using SSR markers Sinha and Pande (2010) found homologous primer sets more suitable for finger printing as they revealed a greater number of polymorphic alleles. Dida et al. (2008) used 45 SSR markers on 79 finger millet accessions from Africa and Asia and distinguished three sub-populations where those from Africa and Asia (*E. coracana*) were clearly differentiated from a wild subpopulation (*E. africana*). Upadhyaya et al. (2008) used 20 SSR markers to characterize over 959 finger millet accessions at ICRISAT-India revealing 231 alleles and identifying unique alleles distinguishing accessions from East Africa, southern Africa and south Asia. The SSR markers are the most suitable for genotyping a highly self-pollinating crop ($\geq$ 99%) with a narrow genetic base such as finger millet (Dida et al., 2007). They are characterized by a high degree of length polymorphism and are single-locus co-dominant markers (Sharma et al., 2010). To date, a large number of finger millet collections have been made in Kenya, Tanzania and Uganda but only a small fraction of the total available collections have been characterized and/or used in breeding programs.

This study was conducted to assess the genetic differentiation among 340 East African finger millet accessions from Kenya, Tanzania and Uganda using five qualitative and 23 previously documented SSR markers to inform appropriate conservation and utilization strategies for the germplasm.

3.2 Materials and Methods

3.2.1. Germplasm

A total of 340 samples (Appendix 3.1) which included 301 accessions from Kenya, Uganda and Tanzania, 15 selections from the global minicore set [minicore set being 1% (80) of the global finger millet collection at ICRISAT genebank-India constituted by Upadhyaya et al. (2010)] and 24 checks (elite and blast resistant/susceptible lines from ICRISAT Nairobi breeding program) were used in this study. The 301 accessions represented nine sub-regions viz: eastern Uganda-mid altitude, sub humid with 240-269 length of growing period (LGP in days); western Uganda-mid altitude with 270-299 LGP; northern Uganda-mid altitude with 210-230 LGP; western Kenya – mid altitude sub humid with 240-269 LGP; Rift Valley Kenya-high altitude low temperature with 120-209 LGP; eastern Kenya-semi-arid mid to low altitude; western Tanzania-mid altitude with 210-239 LGP; northern Tanzania-mid altitude sub humid with 90-149 LGP; and Rukwa region southern Tanzania high altitude with 120-209 LGP. These sub-regions also have differential ethnic representation with occasional overlaps. The 15 minicore accessions

were selected based on the diversity groups established by Upadhyaya et al. (2010) and were included in order to ascertain if the minicore set adequately captured the total global diversity.

3.2.2. Growing plants

Finger millet seeds were planted in an 8 x 12 well format in plastic trays in soil that was sterilized at 140°C for 30 minutes, and placed in an incubator at 30^{o}C for 24 hours to germinate. The seedlings were then transferred to a greenhouse at the University of Nairobi field station for 2 weeks and were watered regularly.

3.2.3 DNA extraction

Leaf samples of similar size were taken from 10-14 day-old plants from five seedlings in each accession and bulked per accession. The leaf tissue was placed in 12 x 8 well strip tubes with strip caps (Marsh Biomarket, USA) together with two 4 mm stainless steel grinding balls (Spex CertiPrep, USA). To each sample 450 µL of preheated (65°C) extraction buffer (100mM Tris-HCL [pH 8), 1.4 M NaCl, 20 mM EDTA, CTAB [3% w/v], β-mercaptoethanol (0.15% v/v) were added and secured with 8-strip caps (Marsh Biomarket). Grinding of the samples was done in a Spex Certi-prep Inc. Geno/grinder 2000® at 500 strokes/min for 10 min. The samples were then incubated for 30 min at 65°C in a water bath with occasional mixing. DNA extraction was then carried out following the protocol by Mace et al. (2013) with the exclusion of the phenol-chloroform step (de Villiers S, unpublished) where 450 µL of chloroform-isoamylalcohol (24:1) was added to each sample and then inverted twice to mix. The samples were then centrifuge plated at 6200 *g* for 10 min (Sigma centrifuge model 4K15C with QIAGEN rotor model NR09100: 2 × 1120 g SW). A fixed volume (400 µL) of aqueous layer was transferred to fresh strip tubes (Marsh Biomarket) and 0.7 vol isopropanol (stored at –20°C) added to each sample and inverted once to mix and the centrifuge plated at 6200 *g* for 15 min. Supernatant from each sample was decanted and the pellet air dried for 30 min. To each sample 200 µL low-salt TE (10 mM Tris, 0.1 mM EDTA [pH 8]) plus 3 µL RNase A (10 mg/mL) were added and incubated at 37°C for 30 min. To each sample 200 µL chloroform-isoamylalcohol (24:1) was added and the sample was inverted twice to mix then centrifuge plated at 4000 *g* for 15 min. A fixed volume of aqueous layer was transferred to a fresh 96 deep-well plate (Marsh Biomarket). To each sample 315 µL ethanol-acetate solution (30mL EtOH, 1.5mL 3 M NaOAc [pH 5.2]) was added and placed in –20°C for 5 min then centrifuge plated at 4000 *g* for 15 min. Supernatant was decanted from each sample and the pellets washed with 70% EtOH and centrifuge plated at 4000 *g* for 5 min then washed again with 70% EtOH. Supernatant from each sample was decanted and air dried for approximately 1 h and the pellet resuspended in 100 µL low-salt TE and stored

at 4°C. DNA quality and quantity for all samples was determined by agar gel electrophoresis (0.8% w/v) and spectrophotometry (Nano-drop® 1000-Thermo Scientific, USA) then diluted to 10ng/µl in TE buffer (10 mM Tris, 0.1 mM EDTA at PH 8.0).

3.2.4 PCR

The PCR procedure was carried out according to Roux (2009). A 10 µL reaction mix containing ddH_2O, *Taq* buffer (20 mM Tris-HCl (pH 7.6); 100 mM KCl; 0.1 mM EDTA; 1 mM DTT; 0.5% (v/v) Triton X-100; 50% (v/v) glycerol), 2 mM $MgCl_2$, 0.16 mM dNTPs, 0.16 µM of a labeled M13-sequence 0.04 µM forward primer, 0.2 µM reverse primer and 0.2 units of Taq DNA polymerase (SibEnzyme Ltd, Russia) was prepared. In an optical 384 well reaction plate (Applied Biosystems, USA), 7 µL of the reaction mix was added to 30 ng of template DNA and amplified in a PCR machine (Thermocycler-GeneAmp PCR system 9700®, Applied Biosystems, USA). Amplification consisted of initial denaturation of the template DNA at 94°C for 5 min, followed by 35 cycles of 94°C for 30 sec, annealed at 59°C for 1 min, with first extension at 72°C for 2 min and final extension at 72°C for 20 min. To verify amplification, PCR products were electrophoresed on a 2% agarose gel. The amplified DNA was visualized under UV light after staining with GelRed® (Biotium, USA). The DNA samples described above for each accession were subsequently subjected to SSR genotyping using the best 23 markers selected from a reference microsatellite kit of 82 markers which were evaluated across ten finger millet cultivars at ICRISAT-Nairobi molecular lab (de Villiers S, unpublished) to determine their amplification efficiency, polymorphism and ability to discern genetic diversity in finger millet. All the forward primers contained an M13-tag (5'-CACGACGTTGTAAAACGAC-3′) on the 5' end that was fluorescently labeled to allow detection of amplification products (Sheulke, 2000). Depending on the efficiency of amplification, 1.5-3.5µL of three different amplification products were co-loaded together with a size standard that ranged from 50-500 bp (GeneScan™ -500 LIZ® Applied Biosystems) and Hi-Di™-Formamide (Applied Biosystems) and amplified fragments separated by capillary electrophoresis using an ABI Prism® 3730 Genetic analyser (Applied Biosystems) (Kuomi et al., 2004). Gene Mapper 4.0 (Applied Biosystems) was used to score allele sizes in base pairs.

3.2.5 Phenotypic characterization

A total of 420 finger millet accessions (301 genotyped from Kenya, Uganda and Tanzania genotyped as above, plus an additional 39 accessions from the three countries, 80 global minicore accessions and five checks) were phenotyped at Kiboko (a dry lowland location 960 meters above sea level, 2°20’S 37° 45’E)

in eastern Kenya. The five checks were 'Kahulunge'-farmer preferred in Tanzania, 'Nakuru FM1'- released in Kenya for cool high altitudes, 'Seremi 2'-released in Kenya and Uganda for mid-altitudes, 'KNE 479'-blast susceptible check, and 'KNE 814'-blast resistant. The materials were planted in an augmented design in single row plots of 4 m length with inter-row spacing of 0.40 m. The trial was arranged in twenty blocks of twenty six plots each with all check cultivar replicated once in each block. Seed was manually drilled in furrows 2.5-3 cm deep and plants were thinned to one plant per hill at intervals of 0.10 m two weeks after emergence. Standard fertilizer rates were applied. Qualitative data (plant colour, growth habit, ear shape, ear size, and grain colour) were collected according to morphological descriptors for finger millet (IBPGR[2], 1985) (Table 3.2-1) from five randomly selected plants in each plot.

Table 3.2-1. Description and scoring for phenotypic traits

Trait	Description/scoring
Plant colour	At flowering (0-tan; 1-pigmented)
Growth habit	Tillering attitude 40 days after sowing (3-decumbent; 5-erect; 7-prostrate)
Panicle shape	Shape of panicle at dough stage (1-droopy; 2-open; 3-semi-compact; 4-compact; 5-fisted)
Glume covering	Proportion of grain covered by glume at maturity (3-exposed; 5-intermediate; 7-enclosed
Grain colour	Post-harvest (1-white; 2-light brown; 3-copper brown; 4-purple brown; 5-others)

3.3 Data analysis

3.3.1 Marker statistics and clustering

Polymorphic information content (PIC) which measures the discriminatory power of each SSR locus (Anderson et al., 1993), number of alleles per locus, frequency of the major allele, observed and expected heterozygosity for the 19 polymorphic markers were calculated using PowerMarker 3.2.5 (Liu and Muse, 2005). Principal coordinates analyses (PCoA) were performed using pairwise genetic dissimilarity coefficients of accessions using simple matching of Unweighted Pair Group Method with Arithmetic Mean with DARwin v.5.0.158 software (Perrier and Jacquemoud-Collet, 2006). Neighbouring trees were generated based on the matrix of genetic distances with a bootstrapping value of 10 000 (Saitou and Nei, 1987).

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3.3.2 Genetic diversity

Standard parameters of genetic diversity viz: total number of alleles (A_t), number of rare alleles (A_r, with allele frequency <5%), private alleles (A_p, alleles unique to a group), observed heterozygosity (H_o), and expected heterozygosity (or gene diversity, H_e) were computed using Arlequin 3.1.1 (Excoffier et al., 2005). These parameters were compared pairwise for the germplasm at country and regional levels and tested for their significance using 10 000 permutations (Belkhir et al., 2002).

3.3.3 Analysis of molecular variance (AMOVA)

The analysis of molecular variance (AMOVA) was used to estimate population differentiation directly from molecular data by using genetic distances as deviations from a group mean position and the squared deviations as variances (Excoffier et al., 2005). Wright's fixation index (F) was calculated according to Wright (1965) as follows:

$$F_{ST} = (H_T - H_S)/H_T$$

where: H is the mean percent of heterozygous individuals per locus, H_T is the sum of population heterozygosities and H_S is sum of sub-population heterozygosities divided by the total number of sub-populations. The significance of the F_{ST} was tested using Fisher's Exact Test (Guo and Thompson, 1992) in Arlequin 3.1.1 (Excoffier et al., 2005). To test the null hypothesis of no population structure within and between groups, the F_{ST} values were compared on a pairwise basis to determine the level of genetic differentiation at country and regional levels (Fitzpatrick, 2009). Based on the F_{ST} values the differentiation between sub-populations was classified as little (0.0-0.05), moderate (0.05-0.15), great (0.15-0.25) and very great (>0.25) (Wright, 1965).

3.3.4 Phenotypic traits

Shannon-Weaver diversity indices (*H´)* as described by Jain et al. (1975) were calculated based on phenotypic frequencies (proportions) of each trait category to estimate phenotypic diversity between the accessions, across the countries and within each country:

$$H = \Sigma P_i \log_e P_i$$

where*:* H = Shannon diversity index, P_i = proportion of accessions in the i^{th} class of an n class trait in a population. The H value was standardized by dividing it by its natural log $\log_e$ n (n = number of phenotypic classes in the trait) to give H´. Frequencies of occurrence of each trait category in the

germplasm expressed as a percent of total number of accessions in the entire germplasm collection and in each country and in the entire germplasm were also calculated. To understand the association of the phenotypic traits with the SSR based tree derived in DARwin, the phenotypic values (for similar entries) scored for each trait category were overlaid on the SSR generated tree and the relative importance assessed by comparing the SSR tree grouping with distribution of these traits in each group (Sharma et al., 2010).

3.4 Results

3.4.1 Marker summary statistics

Four markers (UGEP5, UGEP68, UGEP98 and UGEP96) failed to amplify in PCR across most samples and were eliminated. One marker (UGEP110) appeared to amplify duplicate loci and was scored as two separate markers leading to 19 markers amplifying 20 loci. The 19 markers amplified PCR products across 337 accessions with amplification failing in three accessions. Allele sizes ranged from 148 base pairs (bp) (allele from UGEP20) to 474 bp (from UGEP57) (Table 3.4-1). Marker UGEP33 was monomorphic. The number of alleles per marker ranged from three (UGEP110 and UGEP106) to 23 (UGEP24) with an average of 10.3 alleles per marker (Table 3.4-1). Average gene diversity for the 337 accessions was 0.604 with a range of 0.035 (UGEP110) to 0.898 (UGEP67) and the PIC values for the 19 polymorphic markers ranged from 0.035 (UGEP110) to 0.889 (UGEP67) with a mean of 0.606.

Table 3.4-1. Summary statistics for the 20 polymorphic SSR loci screened across 337 genotypes

SSR marker	Repeat sequence	Allele size range	Major allele frequency	PIC	Availability	Heterozygosity	No. of Alleles
UGEP67	$(TC)_{22}$	227-243	0.167	0.889	0.837	0.358	12
UGEP53	$TT(GT)_5$ $(AG)_{26}$	220-240	0.168	0.877	0.938	0.513	14
UGEP66	$(AG)_{29}$	207-237	0.234	0.876	0.956	0.227	20
UGEP12	$(CT)_{22}$	226-244	0.265	0.825	0.973	0.000	10
UGEP46	$(GA)_{14}$	176-192	0.234	0.819	0.914	0.046	13
UGEP24	$(GA)_{26}$	164-204	0.310	0.800	0.932	0.239	23
UGEP64	$(CT)_{23}$	192-196	0.331	0.759	0.941	0.000	14
UGEP95	$(TC)_{14}$	209-231	0.403	0.734	0.979	0.209	10
UGEP31	$(GA)_{12}$	239-261	0.317	0.722	0.712	0.000	10
UGEP27	$(GA)_{19}$	209-235	0.455	0.716	0.994	0.275	12
UGEP57	$(GA)_{16}$	460-474	0.531	0.613	0.858	0.010	8
UGEP20	$(GA)_{20}$	148-170	0.598	0.574	0.985	0.078	9
UGEP79	$(CT)_{12}$	183-191	0.604	0.502	1.000	0.131	6
UGEP56	$(GT)_{12}$	157-183	0.517	0.491	0.861	0.238	5
UGEP84	$(CT)_{24}$	166-188	0.775	0.375	0.896	0.248	13
UGEP110-1	$(CT)_{12}$	195-215	0.673	0.365	0.979	0.000	5
UGEP106	$(AC)_{12}$	182-194	0.752	0.339	0.988	0.018	3
UGEP73	$(CT)_4$	242-248	0.889	0.197	0.988	0.012	5
UGEP110	$CC(CT)_{10}$ $(CT)_{12}$	165-173	0.982	0.035	0.991	0.000	3
Max		474	0.982	0.889	1.000	0.513	20
Min		148	0.167	0.035	0.712	0.000	3
Mean		-	0.485	0.606	0.933	0.137	10.3

Neighbour joining (NJ) tree was constructed based on the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) to visualize the genetic dissimilarities detected across the 20 SSR loci and it differentiated the accessions into three major genetic groups or clusters and eight sub-clusters

(Figure 3.4-1). Cluster one had 43 accessions from Kenya, 52 from Tanzania, seven from Uganda, seven from the minicore (four originally from Uganda, one from Kenya and two from Zambia) and 16 checks (elite and blast resistant parents). Cluster two had 77 Kenyan accessions, 13 from Tanzania, 89 from Uganda, eight from the minicore (one originally from Kenya, three from Zimbabwe, one from Nigeria, two from India and one from Nepal) and five checks. Cluster three (made up mainly of the accessions from high altitudes) had eight accessions from Kenya (seven from the high altitude Rift valley sub-region), eight from Tanzania (seven from the southern high altitudes sub-region), one from Uganda, zero from the minicore and three blast resistant checks. Sub-cluster 1A had 17 accessions from Kenya, two from Uganda, 33 from Tanzania, two from the minicore (one originally from Uganda and one from Kenya) and three checks (two blast resistant). Sub-cluster 1B had 12 accessions from Kenya, zero from Uganda, seven from Tanzania, four from the minicore (two originally from Zambia, one from Zimbabwe and one from Kenya) and four checks (three blast resistant). Sub-cluster 1C had 14 accessions from Kenya, five from Uganda, 12 from Tanzania, three from the minicore (all originally from Uganda) and nine checks (seven blast susceptible). Sub-cluster 2A had ten accessions from Kenya, 34 from Uganda, two from Tanzania, zero from the minicore and two checks (all blast susceptible). Sub-cluster 2B had 21 accessions from Kenya, 29 from Uganda, one from Tanzania, one from the minicore (originally from Kenya) and one blast susceptible check. Sub-cluster 2C had 14 accessions from Kenya, ten from Uganda, eight from southern Tanzania, two from the minicore (one originally from Nigeria and two originally from Zimbabwe) and one blast resistant check. Sub-cluster 2D had 32 accessions from Kenya, 16 from Uganda, two from Tanzania, three from the minicore (two originally from India and one originally from Nepal) and one blast resistant check. There was a close association between Kenyan and Tanzanian accessions in Clusters one and three, and between Kenyan and Ugandan accessions in Cluster two (Figure 3.4-1).

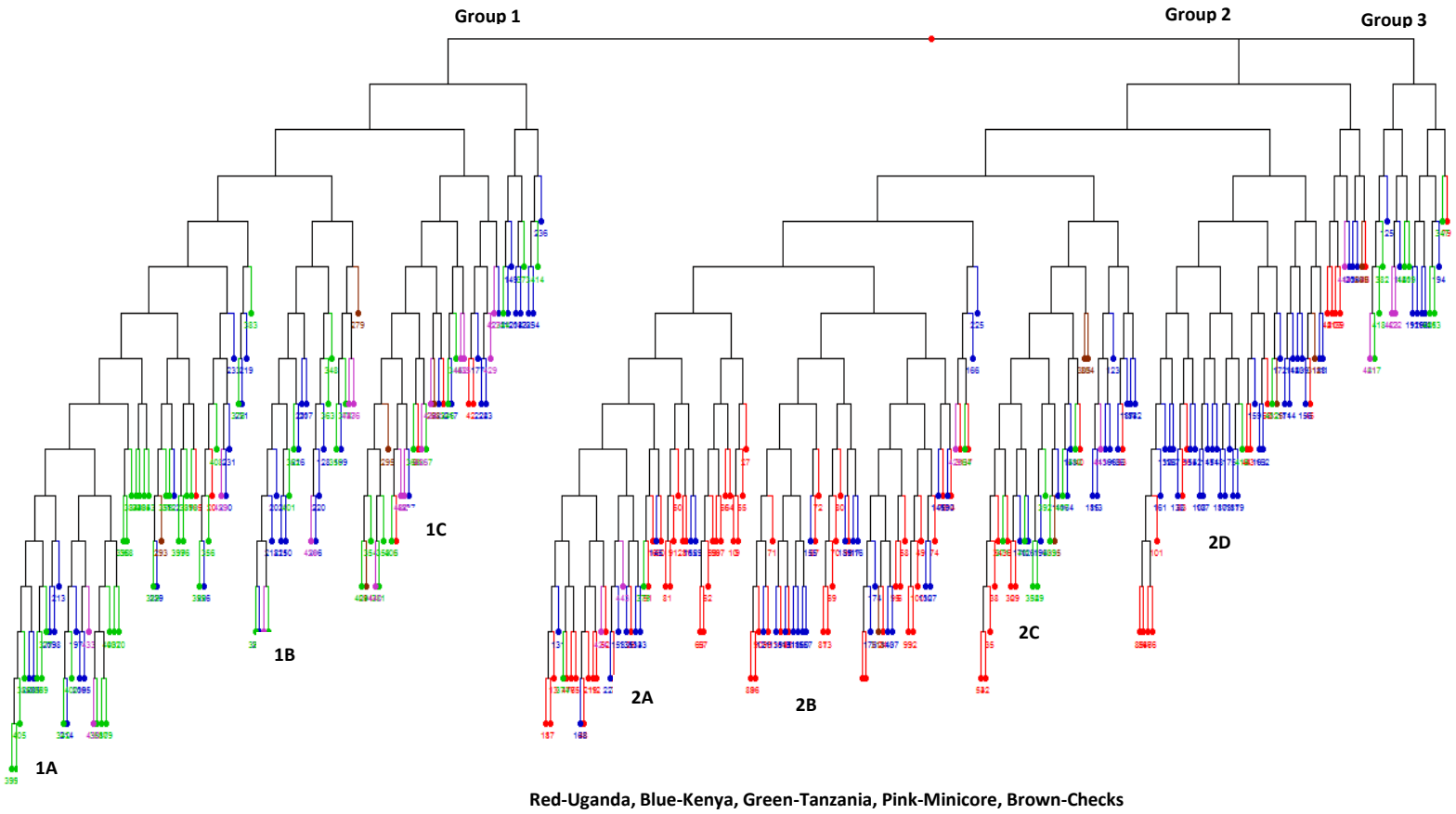

Figure 3.4-1. Neighbour joining tree based on UPGMA genetic disimilarities for the 337 accessions (See appendix 3.1 for accessions in each cluster)

3.4.2 Genetic relationships between countries and between sub-regions

A biplot of the first two axes accounted for 11.13% of the total variation. However, there was no clear separation of accessions on the two axes based on country and sub-region of collection. A total of 195 alleles were detected in the 337 accessions out of which 123 (57.7%) were rare (alleles with frequency <5%) and 37 (17.4%) were private (alleles that appear in individuals from only one subpopulation). Most of the private alleles (21 or 56.8%) occurred in the Kenyan accessions (Table 3.4-2). The highest genetic diversity (0.639 ±0.283) was recorded in Kenyan accessions followed by those from Tanzania (0.636 ±0.262) (both countries with a wider agro-ecology) and the least was in accessions from Uganda (0.583±0.264). The minicore accessions had a mean genetic diversity of 0.638±0.224. At sub-regional level, the highest genetic diversity (0.596±0.280) was detected in accessions from eastern Uganda and the lowest in accessions from western Tanzania (0.049±0.335) (Table 3.4-2).

Table 3.4-2. Genetic diversity estimates for the 337 finger millet accessions at country and sub-regional levels

Structural factor	Total alleles (A^t)	Rare alleles (A^r)	Private alleles (A^p)	Expected heterozygosity (Gene diversity) (H_e)	Observed heterozygosity (H_o)
Countries					
Kenya	188	96	21	0.639	0.115
Tanzania	159	72	5	0.636	0.114
Uganda	142	82	11	0.583	0.127
Minicore	104	19	0	0.638	0.148
Checks	105	28	0	0.598	0.099
Sub-regions					
eastern Kenya	124	46	5	0.578	0.124
eastern Kenya	133	42	8	0.592	0.138
Rift Valley	131	50	4	0.562	0.150
western Tanzania	53	0	0	0.490	0.140
northern Tanzania	72	0	0	0.542	0.141
southern Tanzania	136	54	10	0.577	0.133
eastern Uganda	129	43	3	0.596	0.160
western Uganda	105	22	3	0.545	0.166
northern Uganda	119	46	6	0.553	0.122

3.4.3 Genetic differentiation

There was moderate but highly significant genetic differentiation between and within countries (F_{ST} = 0.054: P≤0.001) and sub-regions (F_{ST} = 0.049: P≤0.001). At country level within country variability accounted for 76.0% of the genetic differences whereas between countries and within accessions in each country accounted for 5.4% and 18.5%, respectively (Table 3.4-3). Pairwise comparison of variability between the three countries detected the highest variability between Ugandan and Tanzanian accessions (F_{ST} = 0.119: P≤0.001) and the least between Kenyan and Ugandan accessions (F_{ST} = 0.031) (Table 3.4-5). The Ugandan accessions (F_{ST} = 0.092: P≤0.001) had the widest variability from the minicore and the Tanzanian the least (F_{ST} = 0.041: P≤0.001). Between sub-regions variability accounted for 4.9%, among accessions in the sub-regions 73.7% and within accessions in each sub-region 21.4% of the genetic diversity (F_{ST} = 0.049: P≤0.001) (Table 3.4-4). The widest diversity was observed between accessions from northern Tanzania and northern Uganda (F_{ST} = 0.139: P≤0.001) and the least between northern Uganda and western Tanzania (F_{ST} = 0.013: P≤0.001) (Table 3.4-5).

Table 3.4-3. AMOVA for between and within country variability of finger millet accessions obtained from three East African countries

Source of variation	Sum of squares	Variance components	Percentage variation
Between countries	214.440	0.358	5.434
Within countries	3675.390	5.010	76.033
Within accessions	406.500	1.221	18.533
Total	4296.332	6.590	

Table 3.4-4. AMOVA for between and within sub-region variability of finger millet accessions obtained from nine sub-regions of three East African countries

Source of variation	Sum of squares	Variance components	Percentage variation
Between sub-regions	263.920	0.299	4.916
Within sub-regions	3063.559	4.490	73.681
Within accessions	405.000	1.304	21.403
Total	3738.479	6.094	

Table 3.4-5. Pairwise F_{ST} estimates for East African finger millet accessions between countries and sub-regions of collection

	Between countries		
	Tanzania	Uganda	Minicore
Kenya	0.048	0.031	0.046
Tanzania	-	0.118	0.041
Uganda		-	0.092
Minicore			-

	Between sub-regions									
	EK	WK	RV	EU	NU	WU	NT	WT	ST	Mc
eastern Kenya (EK)	-	0.030	0.033	0.017	0.088	0.048	0.088	0.058	0.079	0.064
western Kenya (WK)		-	0.031	0.039	0.064	0.0578	0.036	0.014	0.026	0.051
Rift valley (RV)			-	0.060	0.066	0.061	0.094	0.033	0.066	0.064
eastern Uganda (EU)				-	0.029	0.039	0.029	0.083	0.081	0.066
northern Uganda (NU)					-	0.048	0.139	0.011	0.134	0.105
western Uganda (WU)						-	0.113	0.084	0.126	0.113
northern Tanzania (NT)							-	0.054	0.039	0.094
western Tanzania (WT)								-	0.042	0.071
southern Tanzania (ST)									-	0.064
Minicore (Mc)										-

3.4.4 Diversity based on qualitative traits

A wide range of variability was observed in qualitative traits among the accessions (Table 3.4-6). The tan plant types (68.6%) were the most predominant across the three countries with a higher proportion in the Tanzanian accessions (85.5%). Overall, the accessions had 93.2% erect plants and 6.8% decumbent with all Kenyan accessions being erect. Most of the decumbent plant types were found within the Tanzanian accessions (19.5%). The predominant panicle shape in all the accessions was the compact type (48.3%) largely contributed by Ugandan accessions, followed by the semi-compact (37.8%), fisted (8.1%), open (3.4%) and droopy types (2.4%). Semi-compact types were most prevalent in Kenyan (47.6%) and Tanzanian (46.4%) accessions. A range of grain colours was observed with brown being dominant in all the accessions (73.3%) and within countries of origin. The least prevalent grain colour was white in all the accessions (0.6%) with none observed in the Ugandan accessions. There was a near even distribution of the different trait categories in the three countries germplasm and the minicore accessions except in glume cover and grain colour. The minicore accessions had a proportionately lower number of exposed grain types (32.5%) and more dark seeded types (22.2%) relative to the total across the three countries' germplasm. Shannon-Weaver diversity indices showed an overall moderate allelic richness in the qualitative traits ($H' = 0.66$). Relatively though, the highest diversity was observed in panicle shape ($H' = 0.85$) and the least in growth habit (0.27) (Table 3.4-6).

Table 3.4-6. Relative percentage representation per country and Shannon diversity indices (*H'*) of qualitative traits

		Percentages						
Trait	Category	Kenya	Tanzania	Uganda	Overall (3 countries)	Minicore	Diversity index (*H'*) overall (3 countries)	Diversity index (*H'*) minicore
Plant colour	0	68.8	85.5	51.4	68.6	62.5	0.58	0.65
	1	31.2	14.5	48.6	31.4	37.5		
Growth habit	3	0.0	19.5	1.0	6.8	10.0	0.27	0.25
	5	100.0	80.5	99.0	93.2	90.0		
Panicle shape	1	0.0	7.2	0.0	2.4	2.5	0.85	0.82
	2	2.9	7.2	0.0	3.4	2.5		
	3	47.6	46.4	19.4	37.8	33.8		
	4	41.8	36.2	67.0	48.3	57.4		
	5	7.7	2.9	13.6	8.1	3.8		
Glume cover	3	53.3	46.0	61.9	50.1	32.5	0.40	0.50
	5	42.2	38.2	38.1	43.1	55.0		
	7	4.5	15.8	0.0	6.8	12.5		
Grain colour	1	0.6	1.3	0.0	0.6	3.8	0.81	0.77
	2	9.7	30.7	10.5	17.0	8.8		
	3	76.1	62.7	81.0	73.3	65.2		
	4	13.6	5.3	8.5	9.1	22.2		
	Overall diversity index (*H'*)	0.67	0.76	0.55	-	-	0.66	0.74

Plant colour: 0-Tan, 2-Pigmented; Growth habit: 3-Decumbent, 5-Erect; Panicle shape: 1-Droopy, 2-Open, 3 Semi-compact, 4-Compact, 5-Fisted; Glume covering: 3-Exposed, 5-Intermediate, 7-Enclosed; Grain colour: 1-White, 2-Light brown, 3-Brown, 4-Dark brown

The highest diversity was recorded in Tanzanian accessions ($H' = 0.76$) followed by minicore ($H' = 0.74$) and the least in Ugandan accessions ($H' = 0.55$). The scores for growth habit, ear shape, grain colour and plant colour were associated with the SSR-based genetic diversity results of similar accessions in the neighbour-joining tree constructed using DARwin 5.0 (Figure 3.4-1). When used to assess their importance/value in delineating the diversity detected in the 340 accessions based on molecular data, these morphological traits played no role.

3.5 Discussion

3.5.1 Marker summary

According to Smith et al. (2000), PIC values of markers do provide an estimate of the discriminating power of the markers in a given set of accessions. The polymorphic information content (PIC) and gene diversity values obtained using the 19 primer pairs showed high diversity in the germplasm. An average of 60.6% polymorphism revealed by the 19 SSR markers compares with 70.2% reported by Panwar et al. (2010), whereas the mean genetic diversity, 0.636 and mean number of alleles per locus, 10.3 across the 340 accessions is higher than the 0.330 and 3.4, respectively reported by Dida et al. (2008) across 79 accessions drawn from Africa. The differences in diversity and alleles could be attributed to population type and size used and marker polymorphism, respectively. The lowest number of alleles per locus (1.0) was reported by Naga et al. (2011) using 20 SSR primers. With a heterozygosity range of 0.0-0.5 in the germplasm in this study, it is likely that some markers may have detected/amplified more than a single locus or they amplified segments on two different genomes considering that finger millet is an allotetraploid with two genomes (AA and BB) (Dida et al., 2008). The high percentage of rare alleles in the germplasm (57.5%) coupled with a high number of private alleles in the Kenyan germplasm (56.8%) confirm the existing potential in the germplasm for selection of genetically diverse parental lines for breeding.

3.5.2 Genetic differentiation

Genetic distances based on UPGMA clustering and PCoA showed no distinct differentiation among the countries and sub-regions of collection. The three major clusters observed were made up of a mix of accessions from all countries and sub-regions. This undefined clustering was supported by AMOVA where a higher level of variability was detected among accessions within countries and sub-regions than among countries and sub-regions. This could be attributed to agro-ecological and length of growing period differences within countries and sub-regions. Non-differentiation of the sub-regions could also be attributed to the lack of a link between political boundaries and ecological separation. In addition, there is a similarity in ethnic communities occupying both sides of neighbouring countries such as the *Luhya* and *Teso* ethnic groups who occupy western Kenya and eastern Uganda. These communities retain their cultures and food habits irrespective of the political borders and regularly share seed and grain markets. Lack of separation of accessions relative to region of collection was also reported by: Naga et al. (2011) using 20 SSR primers on 15 finger millet accessions from Africa and Asia: Bezawelataw (2011) using 15

RAPD primers on 66 Ethiopian finger millet landraces and Vetriventhan et al. (2012) in 155 accessions (a core collection) of foxtail millet (*Setaria italica*) using 84 SSR markers in India. Earlier genetic diversity studies by Dida et al. (2008) using isozyme and DNA markers also revealed limited genetic variation in finger millet among cultivated genotypes from varying agro-ecological adaptation. This finding is further supported by molecular diversity studies in other crops where an overlap of accessions from different geographic regions was reported by Kimani et al. (2012) using 15 RAPD primer pairs on 50 lablab bean (*Lablab purpureus)* accessions collected in Kenya. In Mali, Barro-Kodombo et al. (2010) found a weakly stratified diversity in sorghum germplasm that could not be explained by any biophysical criteria with higher variability within populations as opposed to regions/zones. However, these findings differ from those of Fakrudin et al. (2004) who found variability based on regional origin in 12 finger millet accessions in India using 35 RAPD primers. Pairwise comparisons of countries and sub-regions clearly showed that the highest variability resided within countries and sub-regions compared to between countries and sub-regions of collection. Cluster analysis, F_{ST} and PCoA did not correlate the diversity detected by the 19 SSR markers to country of origin. The high genetic diversity observed within the Kenyan accessions and the least differentiation between the Tanzanian accessions from minicore is indicative of the potential in this germplasm for finger millet improvement.

The low genetic differentiation observed between the countries in the East African finger millet germplasm could be historical in nature due to the crop's origin from the eastern African region hence these accessions share a common gene pool. The role and impact of seed mediated gene flow, as evidenced by the regular cross border finger millet trade and grain market seed sourcing, could explain the close relationship between most of the Kenyan and Ugandan, and the Kenyan and Tanzanian accessions in addition to the close similarity in agro-ecologies between western Kenya and the three finger millet production sub-regions of Uganda. However, selections within countries and sub-regions for agro-ecological adaptation and end use play a key role in the variability observed within countries and sub-regions. Conversely, the overall wide diversity observed between Uganda and Tanzania germplasm could be explained by the wide geographic separation, hence any genetic commonality is largely due to farmer to farmer interaction in terms of seed exchanges and grain trade. The surprisingly low variability in Ugandan accessions (despite the country being the primary centre of finger millet diversity) is a pointer to potential genetic erosion that could be due to adoption of improved cultivars, high selection pressure to satisfy a growing commercial market (leading to genetic drift) and/or diversity loss during the recent period of war. Low polymorphism was also reported among highly inbred cultivated finger millet types in India by Fakrudin et al. (2004). There was almost an even distribution of the eight sub-clusters of major clusters one and two in the selected global minicore set groupings in the DARwin tree clusters but no

genotypes from cluster three were represented in the minicore accessions pointing to a possibility of unique accessions in this germplasm not captured in the global germplasm at ICRISAT genebank. This agrees with conclusions by Upadhyaya et al. (2006) that the composition of the core collection is subject to change as additional accessions become available. According to Ramu et al. (2013), effective genetic differentiation assessment depends on the type of markers and how representative they are across the crop's genome. Since only seven of the markers used in this study have been fully mapped, it is not known to what extent they provided adequate genome coverage across the linkage groups, which likely limited the ability to fully capture the existing variability in the germplasm.

3.5.3 Qualitative traits

Panicle shape and grain colour are often used by farmers in cultivar differentiation (de Wet et al., 1984). The predominance of brown grain types is based on quality acceptance dictated by farmer and industry preferences. During a survey carried out in Kenya and Uganda in 2002 (Sreenivasaprasad et al., 2004), it was established that brown/red grain types were the most preferred because they made good beer and blended well with cassava for *ugali*. They were also the most preferred by industry/processors for making composite and pure flours for weaning foods and porridges. These types also suffer less bird damage compared to the white grain types. Brown grain types with compact panicles have been reported to have resistance to finger blast (Pande, 1992; Takan et al., 2004; Krishnappa et al., 2009). The very low frequency of occurrence of white grain types observed in this study was also reported by Tsehaye and Kebebew (2002) and Bezawelataw et al. (2007). The susceptibility of the white seeded types to bird attack and grain mold (*Fusarium* spp.) in humid environments especially in Ugandan and Kenyan agro-ecologies where finger millet is mainly grown may have contributed to their low frequency. However, the morphological (qualitative) traits of panicle shape and both grain and plant colour seemed not to play a role in the delineation of diversity in this germplasm as there was no correlation between genetic variability and phenotypic traits. This, however, was not unexpected since the 19 markers used in the study are not known to be linked to any of these morphological traits. This was similarly observed in fonio (*Digitaria exilis)* by Adoukonou-Sagbadja et al. (2007).

3.6 Conclusion

This study has shown that although there is close relationship between the three East African countries' finger millet germplasm, substantial diversity exists within each county's germplasm. Kenyan germplasm is more closely related to Ugandan and Tanzanian germplasm with wide variability between Ugandan and

Tanzanian germplasm. This could be attributed to geographical proximities and ethnic similarities and cross border seed exchanges between neighbouring communities. Low diversity observed in Ugandan accessions could point to genetic diversity loss due to the promotion and use of a few improved cultivars. The genetic diversity and high number of rare and private alleles detected could be attributed to the high diversity in the germplasm considering that East Africa is the primary centre of finger millet diversity. The lack of representation of cluster three accessions (largely represented by accessions adapted to cool high elevation agro-ecologies) in the minicore accessions could provide an opportunity to enrich the global finger millet germplasm. No correlations between qualitative traits and genotypic diversity were observed. The diversity revealed in this germplasm will be valuable for conservation and for breeding programs to develop diverse populations and lines to respond to prevalent abiotic and biotic stresses. The extent of the variability measured in the accessions of this study corresponds with that of the few other studies that have been conducted and overall these studies provide incentive to develop more robust, trait associated markers in finger millet.

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Appendix 3.1. Passport information of the 337 germplasm lines with successful marker amplification

Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster
Unknown	Uganda	Eastern	2A	Otim cherigar/ceruget	Uganda	Northern	2D	Unknown	Uganda	Western	2B
Unknown	Uganda	Eastern	1C	Kal Lango	Uganda	Northern	2D	Unknown	Uganda	Western	2B
Purple	Uganda	Eastern	1C	Kal	Uganda	Northern	2D	Otara chilgal	Uganda	Northern	2B
Ekama	Uganda	Eastern	1C	Cirogal	Uganda	Northern	2A	Otara chilgal	Uganda	Northern	2B
Ebega	Uganda	Eastern	1C	Oturi Aweri	Uganda	Northern	2A	Otara chilgal	Uganda	Northern	2A
Engenyi	Uganda	Eastern	2B	Turi-open	Uganda	Northern	2B	Otara chilgal	Uganda	Northern	2B
Ekama	Uganda	Eastern	2A	Turi-closed	Uganda	Northern	2A	Otara chilgal	Uganda	Northern	2B
Emoru	Uganda	Eastern	2A	Kal	Uganda	Northern	2A	Kal	Uganda	Northern	2B
Emiroit/Engeny	Uganda	Eastern	2A	Kal	Uganda	Northern	2A	Kal	Uganda	Northern	2B
Emaru	Uganda	Eastern	2A	Kal	Uganda	Northern	2C	Kal	Uganda	Northern	2A
Etiyo-brown	Uganda	Eastern	2A	bulk market	Uganda	Northern	2C	Kal	Uganda	Northern	2A
Etiyo-White	Uganda	Eastern	2A	bulk market	Uganda	Northern	2A	Obeet	Uganda	Eastern	2B
Emiroit	Uganda	Eastern	2A	Fama atar	Uganda	Northern	2D	Ekoma-Okwa (IE 6555)	Uganda	Eastern	2B
Emorumoru (rock)	Uganda	Eastern	2A	Kal	Uganda	Northern	2A	Rwemereza (IE 6591)	Uganda	Eastern	2D
Obeet	Uganda	Eastern	2A	Kal-white	Uganda	Northern	2B	Oburo (IE 6592)	Uganda	Eastern	2B
Unknown	Uganda	Western	2A	Kal-purple	Uganda	Northern	2A	RW 127 (IE 6613)	Uganda	Eastern	1A
Etiyo	Uganda	Eastern	2A	Kal	Uganda	Northern	2A	GBK-000347A	Kenya	Rift valley	2C
Acomomcomo	Uganda	Eastern	1A	Kal	Uganda	Northern	1C	GBK-000349A	Kenya	Rift valley	2D
Eteke	Uganda	Eastern	2A	Kal	Uganda	Northern	2A	GBK-000350A	Kenya	Rift valley	2D
Ochom	Uganda	Eastern	2B	Kal atari	Uganda	Northern	2A	GBK-000351A	Kenya	Rift valley	2D
Emodigoit	Uganda	Eastern	2B	Kal atari	Uganda	Northern	2A	GBK-000352A	Kenya	Rift valley	2C
Unknown	Uganda	Eastern	2B	Kal atari	Uganda	Northern	2A	GBK-000361A	Kenya	Rift valley	2D
Namakala	Uganda	Eastern	2A	Ekamo	Uganda	Eastern	2D	GBK-000364A	Kenya	Rift valley	1C
Tanzakira	Uganda	Eastern	2A	Unknown	Uganda	Eastern	2D	GBK-000368A	Kenya	Rift valley	2C
Lowa	Uganda	Eastern	2A	Gulu E	Uganda	Northern	2D	GBK-000369A	Kenya	Rift valley	3
Ekwangapel	Uganda	Eastern	2C	Anyandri	Uganda	Northern	2B	GBK-000370A	Kenya	Rift valley	2B
Emiroit/unknown purple	Uganda	Eastern	2C	Unknown	Uganda	Western	2B	GBK-000371A	Kenya	Rift valley	2B
Ekama-white	Uganda	Eastern	2B	Unknown	Uganda	Western	2B	GBK-000372A	Kenya	Rift valley	2B
Adalaka	Uganda	Eastern	2C	Unknown	Uganda	Western	2B	GBK-000373A	Kenya	Rift valley	2B
Ekama	Uganda	Eastern	2C	Bulo	Uganda	Western	2B	GBK-000375A	Kenya	Rift valley	2B
Ebati	Uganda	Eastern	2C	Bulo	Uganda	Western	2B	GBK-000379A	Kenya	Rift valley	3
Omunga	Uganda	Eastern	2C	Bulo	Uganda	Western	2A	GBK-000399A	Kenya	Western	2B
Emiroit	Uganda	Eastern	2B	Bulo	Uganda	Western	2A	GBK-000405A	Kenya	Western	1A
Otunduru	Uganda	Eastern	2C	Bulo	Uganda	Western	2B	GBK-000410A	Kenya	Western	123
Kal (millet)	Uganda	Northern	2D	Unknown	Uganda	Western	3	GBK-000415A	Kenya	Western	3
Kal (millet)	Uganda	Northern	2C	Unknown	Uganda	Western	2B	GBK-000584A	Kenya	Eastern	2C
Kal (millet)	Uganda	Northern	2D	Unknown	Uganda	Western	2B	GBK-000587A	Kenya	Eastern	2B
Kal (millet)	Uganda	Northern	2D	Unknown	Uganda	Western	2D	GBK-000590A	Kenya	Eastern	1B
Kal (millet)	Uganda	Northern	2D	Unknown	Uganda	Western	2D	GBK-000591A	Kenya	Eastern	2A
Unknown	Uganda	Western	2D	Unknown	Uganda	Western	2D	GBK-000592A	Kenya	Eastern	2B

Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster
GBK-000594A	Kenya	Eastern	2A	GBK-013161A	Kenya	Eastern	2B	GBK-029680A	Kenya	Western	1C
GBK-000596A	Kenya	Eastern	2D	GBK-013183A	Kenya	Eastern	2D	GBK-029681A	Kenya	Western	1B
GBK-000597A	Kenya	Eastern	2A	GBK-027127A	Kenya	Rift valley	2B	GBK-029682A	Kenya	Western	1A
GBK-000599A	Kenya	Eastern	2A	GBK-027128A	Kenya	Rift valley	1C	GBK-029754A	Kenya	Western	1B
GBK-008277A	Kenya	Western	2B	GBK-027130A	Kenya	Rift valley	2D	GBK-029755A	Kenya	Western	1A
GBK-008278A	Kenya	Western	2A	GBK-027133A	Kenya	Rift valley	2D	GBK-029756A	Kenya	Western	1C
GBK-008279A	Kenya	Western	2B	GBK-027134A	Kenya	Rift valley	2D	GBK-029758A	Kenya	Western	1C
GBK-008280A	Kenya	Western	2D	GBK-027135A	Kenya	Rift valley	2D	GBK-029763A	Kenya	Western	1C
GBK-008281A	Kenya	Western	2C	GBK-027141A	Kenya	Rift valley	2C	GBK-029766A	Kenya	Western	2B
GBK-008301A	Kenya	Western	2B	GBK-027145A	Kenya	Rift valley	1C	GBK-029767A	Kenya	Western	1A
GBK-008321A	Kenya	Western	2D	GBK-027149A	Kenya	Rift valley	2C	GBK-029768A	Kenya	Western	2A
GBK-008328A	Kenya	Western	2D	GBK-027155A	Kenya	Rift valley	2C	GBK-029769A	Kenya	Western	1A
GBK-008329A	Kenya	Western	2D	GBK-027158A	Kenya	Rift valley	2C	GBK-040436A	Kenya	Rift valley	1A
GBK-008336A	Kenya	Western	2D	GBK-027165A	Kenya	Rift valley	2C	GBK-040459A	Kenya	Rift valley	1A
GBK-008352A	Kenya	Western	2A	Ikhulule	Kenya	Western	2D	GBK-040463A	Kenya	Rift valley	1A
GBK-008365A	Kenya	Western	2B	GBK-027185A	Kenya	Rift valley	2B	GBK-040468A	Kenya	Rift valley	1C
GBK-011107A	Kenya	Eastern	2D	GBK-027189A	Kenya	Rift valley	2B	GBK-040555A	Kenya	Rift valley	1A
GBK-011109A	Kenya	Eastern	2D	GBK-027193A	Kenya	Rift valley	3	GBK-040556A	Kenya	Rift valley	1C
GBK-011110A	Kenya	Eastern	1C	GBK-027194A	Kenya	Rift valley	3	GBK-040559A	Kenya	Rift valley	1C
GBK-011111A	Kenya	Eastern	2D	GBK-027200A	Kenya	Rift valley	3	GBK-040568A	Kenya	Rift valley	1C
GBK-011112A	Kenya	Eastern	2D	GBK-027201A	Kenya	Rift valley	3	GBK-040569A	Kenya	Rift valley	1C
GBK-011113A	Kenya	Eastern	2D	GBK-028546A	Kenya	Western	1A	IE 2457	Kenya	Minicore	1B
GBK-011114A	Kenya	Eastern	2A	GBK-028588A	Kenya	Western	2C	IE 2872	Zambia	Minicore	1B
GBK-011116A	Kenya	Eastern	2D	GBK-028589A	Kenya	Western	1A	IE 2911	Zambia	Minicore	1B
GBK-011117A	Kenya	Eastern	2B	GBK-028590A	Kenya	Western	1A	IE 3475	India	Minicore	2D
GBK-011118A	Kenya	Eastern	2D	GBK-029646A	Kenya	Western	1B	IE 3952	Uganda	Minicore	1A
GBK-011119A	Kenya	Eastern	2B	GBK-029648A	Kenya	Western	1A	IE 3973	Uganda	Minicore	1C
GBK-011120A	Kenya	Eastern	2C	GBK-029650A	Kenya	Western	1B	IE 4028	Uganda	Minicore	1C
GBK-011129A	Kenya	Eastern	2D	GBK-029663A	Kenya	Western	1A	IE 4121	Uganda	Minicore	1C
GBK-011130A	Kenya	Eastern	2B	GBK-029664A	Kenya	Western	1C	IE 4545	Zimbabwe	Minicore	2C
GBK-011131A	Kenya	Eastern	2D	GBK-029666A	Kenya	Western	1A	IE 4570	Zimbabwe	Minicore	2C
GBK-011133A	Kenya	Eastern	2D	GBK-029667A	Kenya	Western	1B	IE 4622	Zimbabwe	Minicore	1B
GBK-011134A	Kenya	Eastern	2D	GBK-029668A	Kenya	Western	1B	IE 4816	India	Minicore	2D
GBK-011135A	Kenya	Eastern	2C	GBK-029670A	Kenya	Western	2D	IE 5367	Kenya	Minicore	2B
GBK-011137A	Kenya	Eastern	2B	GBK-029672A	Kenya	Western	1B	IE 6165	Nepal	Minicore	2D
GBK-011138A	Kenya	Eastern	2D	GBK-029673A	Kenya	Western	1B	IE 6533	Nigeria	Minicore	2C
GBK-011139A	Kenya	Eastern	2A	GBK-029674A	Kenya	Western	1B	Acc # 2292	Tanzania	Southern	1A
GBK-011141A	Kenya	Eastern	2C	GBK-029676A	Kenya	Western	1A	Acc # 2361	Tanzania	Southern	1A
GBK-013126A	Kenya	Eastern	2D	GBK-029677A	Kenya	Western	1A	Acc # 2369	Tanzania	Southern	1A
GBK-013139A	Kenya	Eastern	2D	GBK-029678A	Kenya	Western	1B	Acc # 2457	Tanzania	Southern	1A
GBK-013144A	Kenya	Eastern	2D	GBK-029679A	Kenya	Western	1B	Acc # 2502	Tanzania	Southern	1C

Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster	Accession name	Country of origin	Region	Cluster
Acc # 2706	Tanzania	Eastern	1C	unknown	Tanzania	Southern	1A	KNE 1124	ICRISAT	Check	1C
Acc # 2720	Tanzania	Eastern	1C	Chikufi	Tanzania	Southern	2C	KNE 741	ICRISAT	Check	1C
Acc # 2879	Tanzania	Southern	3	Nameka	Tanzania	Southern	1A	KNE 689	ICRISAT	Check	1A
Acc # 2920	Tanzania	Southern	3	Ngumi	Tanzania	Southern	1B	P 224	Uganda	Check	1C
Acc # 2924	Tanzania	Southern	2C	Kaulunge (Ngumi)	Tanzania	Southern	1A	KNE 814	ICRISAT	Check	1C
Acc # 2954	Tanzania	Southern	1B	Katila	Tanzania	Southern	1A	KNE 796	ICRISAT	Check	1B
Acc # 2968	Tanzania	Southern	1A	Kauhulunge	Tanzania	Southern	1A	KNE 1149	ICRISAT	Check	1B
Acc # 2974	Tanzania	Southern	2C	Chikwekwele	Tanzania	Southern	1A	KNE 392	ICRISAT	Check	1B
Acc # 2999	Tanzania	Southern	1C	Kaulunge (Makazi)	Tanzania	Southern	1A	Okhale 1	KARI-Kakamega	Check	2D
Acc # 3016	Tanzania	Southern	1C	Kafumbata/Sanzamula mix	Tanzania	Southern	1A	KNE 620	ICRISAT	Check	1C
Acc # 3027	Tanzania	Southern	1A	Sansamula	Tanzania	Southern	1B	KNE 1034	ICRISAT	Check	2C
Acc # 3030	Tanzania	Southern	1A	Kafumbata/Kaulunge	Tanzania	Southern	1A	Nanjala brown	KARI-Kakamega	Check	1C
Acc # 3040	Tanzania	Southern	1C	Sansamula	Tanzania	Southern	1A	IE 1012	ICRISAT	Check	2A
Acc # 3063	Tanzania	Southern	1A	Kaulunge	Tanzania	Southern	1C	Okhale 1	KARI-Kakamega	Check	2D
Acc # 3081	Tanzania	Southern	1A		Tanzania	Southern	1A				
Acc # 3114	Tanzania	Western	1B	Kafumbata	Tanzania	Southern	1C				
Acc # 3135	Tanzania	Western	1B	Kaulunge	Tanzania	Southern	2C				
Acc # 3163	Tanzania	Western	1B	Namakonta	Tanzania	Southern	1A				
Acc # 3574	Tanzania	Western	2B	Magasi	Tanzania	Southern	2C				
Acc # 3656	Tanzania	Southern	1C	Katila	Tanzania	Southern	2C				
Acc # 3849	Tanzania	Southern	1A	Magas/Kaulunge mix	Tanzania	Southern	2C				
Acc # 3865	Tanzania	Southern	2C	Katila	Tanzania	Southern	2D				
Acc # 3902	Tanzania	Southern	1A	Kaulunge	Tanzania	Southern	3				
Acc # 3910	Tanzania	Southern	1C	Naupule/Ng'ombe mix	Tanzania	Southern	1C				
Acc # 3919	Tanzania	Northern	2A	Ng'ombe	Tanzania	Southern	2D				
Acc # 3924	Tanzania	Northern	2A	Katila	Tanzania	Southern	3				
Acc # 3927	Tanzania	Northern	1A	Mautila (white)	Tanzania	Southern	3				
Acc # 3944	Tanzania	Northern	1A	Solila	Tanzania	Southern	3				
Acc # 3953	Tanzania	Northern	1B	Katila	Tanzania	Southern	3				
Acc # 3960	Tanzania	Northern	1A	Ng'ombe	Tanzania	Southern	3				
Acc # 3962	Tanzania	Northern	1A	IEL 6	ICRISAT	Check	3				
Acc # 3989	Tanzania	Northern	1C	KNE 479	ICRISAT	Check	3				
Acc # 3995	Tanzania	Northern	3	IE 11	ICRISAT	Check	3				
Acc # 4225	Tanzania	Western	3	VL 520	ICRISAT	Check	2A				
Acc # 4263	Tanzania	Western	1A	IE 2522	ICRISAT	Check	2B				
Kahulunge	Tanzania	Southern	1A	IE 2285	ICRISAT	Check	1C				
Sansamula	Tanzania	Southern	1A	KAT FM 1	KARI-Kiboko	Check	1C				
Nameka	Tanzania	Southern	1A	KNE 755	ICRISAT	Check	1B				
Mautila	Tanzania	Southern	1A	Acc # 100007	Ethiopia	Check	1C				
Anguumi	Tanzania	Southern	1A	KNE 744	ICRISAT	Check	1A				

Chapter 4

Correlations, analyses of path coefficients, heritability and genetic advance for quantitative traits in finger millet germplasm

Abstract

Knowledge of association between traits, heritability and genetic advance is important in breeding for purposes of effective trait selection. Such information on finger millet in East Africa is very limited. This study was intended to determine the association, heritability and genetic advance for 23 quantitative traits of 340 finger millet landraces from Kenya, Tanzania and Uganda and 80 global minicore accessions sourced from ICRISAT Genebank in India. Significant ($P \leq 0.01$) differences were recorded between genotypes for the traits studied. Genotypic correlations were higher than phenotypic correlations for most of the traits studied with grain yield having high, positive correlations with finger width, grains per spikelet, threshing percent, peduncle length and panicle exertion. Negative genotypic correlations were detected between grain yield and days to flowering and between both grain yield and days to flowering with all blast disease types (leaf, neck and finger). Path coefficient analysis revealed that productive tillers per plant (0.473), 1000 grain mass (0.136), grains per spikelet (0.131) and threshing percent (0.118) had positive, direct effects on grain yield. Due consideration should be placed on them while selecting for grain yield improvement in finger millet. However, there were strong, positive indirect effects contributed to grain yield by several other traits. It will be necessary to simultaneously select for these traits together with those with strongly positive, direct effects on grain yield in order to improve grain yield in finger millet. High broad-sense heritability and high genetic advance (as a percent of the mean) estimates were recorded for fingers per panicle, flag leaf blade length, 1000 grain mass, productive tillers per plant, finger length, peduncle length and panicle exertion indicating the potential for their improvement through selection.

Key words: Correlations, path analysis, heritability, genetic advance, finger millet

4.1 Introduction

Although many trait relationships are useful in selection, the associations between yield and other component traits would be of key consideration for all crop breeders. Observed and true associations between traits may be quantified in terms of simple phenotypic and genotypic correlation coefficients, respectively (Dewey and Lu, 1959). However, yield is a complex trait and is influenced directly as well as indirectly by its various components. Correlation coefficients alone do not elucidate the complexity of the associations between traits or how change in a trait affects an associated trait (Dabholker, 1992; Dewey and Lu, 1959). To address this deficiency, path coefficient, a standardized regression coefficient developed by Wright (1921), disaggregates the correlation coefficient into the direct and indirect effects of various variables (traits) on a dependent variable (Das et al., 2004; El-Din et al., 2012). Direct effects are where a variable directly affects another without being influenced by other variables whereas indirect effects occur when the relationship between two variables is mediated by one or more variables (Tyagi and Lal, 2007). Knowledge of the associations between yield and its component traits and among the component traits themselves would allow for more effective selection for yield (Izge et al., 2006; Salahuddin et al., 2010). In finger millet, grain yield has been reported to be highly directly associated with: panicle mass and straw yield per plant (Sonnad et al., 2008); productive tillers and 1000 grain mass (Bezawelataw et al., 2006; Lule et al., 2012); biomass yield, finger length and number of fingers per panicle (Ganapathy et al., 2011; Wolie and Dessalegn, 2011); and basal tillers, flag leaf blade length, and panicle length and width (Bharathi, 2011). Studies which have generated such information on finger millet in East Africa are limited.

As much as progress in a crop improvement programme will depend on the amount of genetic variability in the target trait in the base population (Ganapathy et al., 2011), variability alone will not indicate the degree of improvement through selection (Priyadharshini et al., 2011). Estimates of broad-sense heritability (H^2) and genetic advance (GA), expressed as a percent of the parental mean, are important genetic statistics that provide an indication of the potential progress that will be made through selection in a breeding programme. The salient function of heritability is in expressing the reliability of the phenotypic value for a trait as a guide to the breeding value for that trait in a population (Falconer, 1981). In its broadest sense it specifies the proportion of the total phenotypic variability that is due to genetic causes (Allard, 1960). Traits with high percent heritability are less affected by the environment in their expression and quantitative traits usually have low heritability estimates due to their sensitivity to the environment (Allard, 1960). Genetic gain which is the product of the selection differential (k), the phenotypic standard deviation and the heritability estimate (broad or narrow) estimates the expected gain

from a cycle of selection (Johnson et al., 1955). For effective selection, Falconer (1981) proposes using a combination of genetic parameters, genetic and phenotypic coefficients of variation, heritability and genetic advance. This study was conducted to determine the associations between grain yield and related quantitative traits, the degree and direction of association, heritability and genetic advance in finger millet for the effective formulation of a breeding strategy/selection scheme to generate higher yielding lines.

4.2 Materials and methods

The genotypes assessed in this study were 340 finger millet landraces collected across agro-ecologies in Kenya (154), Tanzania (81) and Uganda (105), 80 global minicore accessions sourced from ICRISAT Genebank in India and five known checks (Nakuru FM 1 released in cool highlands of Kenya, Seremi 2 (U 15) released in Kenya and Uganda for sub-humid Lake Victoria zone, Kahulunge a popular local cultivar in southern Tanzania, KNE 814 a blast resistant check and KNE 479 a blast susceptible check). The trials were conducted in four diverse agro-ecologies in Kenya: Alupe – sub-humid Lake Victoria zone, 1189 meters above sea level (masl), 0°28'N and 34°7'E and a blast hot spot; Lanet – cool highland, 1920 masl, 0°30'S and 36°0'E; Kiboko – dry lowland, 960 masl, 2°20'S and 37°45'E; and Mtwapa – near sea level humid coast, 21 masl, 4°25'S and 39°44'S. These locations represent the finger millet production agro-ecologies in East Africa. At all four locations, the accessions were planted in an augmented design comprising 20 blocks of 26 plots each. Each check entry was planted once in each block to obtain an estimate of error and of blocking effects. The block effects were estimated from the repeated check means and then removed from the means of the test entries (Federer and Wolfinger, 2003). The entries were sown in single row plots, 4 m in length at inter-row and intra-row spacings of 0.40 m. Seed was drilled in furrows (2.5-3 cm deep) and plants were thinned two weeks after emergence to one plant per hill after every 0.10 m. At planting, Double Ammonium Phosphate fertilizer (18:46:0) was applied at the rate of 20 kg N and 20 kg P_2O_5 per hectare. After thinning, the trials were top dressed with Urea (46% N) at the rate of 20 kg N per hectare. Data were collected on 23 quantitative traits based on the descriptors for finger millet (IBPGR[3], 1985) as presented in Table 4.2-1.

Data were taken on five randomly selected plants in each plot and the means of the five plants from each plot were used for statistical analysis except for grain yield and 1000 grain mass which were done on plot basis. Blast data were recorded at Alupe (blast hot spot) where natural blast occurrence is high.

[3] International Board for Plant Genetic Resources

Table 4.2-1. Descriptions and measurements for traits

Trait	Description/scoring
Days 50% flowering	Days from sowing to when 50% of plants in the plot were in flower
Plant height (cm)	From ground level to tip of panicle at dough stage
No. of productive tillers	Basal tillers with mature panicles at maturity
No. of Leaves per plant	Number of leaves on main tiller at flowering
Flag leaf blade length (cm)	From ligule to leaf tip at flowering
Flag leaf blade width (cm)	Across centre of flag leaf at flowering
Leaf blade length (cm)	From ligule to tip of fourth leaf blade from top at flowering
Leaf blade width (cm)	Across centre of fourth leaf blade from top
Leaf sheath length (cm)	From node to ligule of fourth leaf from top at flowering
Leaf sheath width (cm)	Across centre of fourth leaf sheath from top
Peduncle length (cm)	From top most node to base of the thumb finger
Panicle exertion (cm)	From flag leaf ligule to base of the thumb finger
No. of Fingers per panicle	On main panicle at dough stage
Finger length (cm)	From base to tip of longest finger at dough stage
Finger width (cm)	Distance across centre of longest finger at dough stage
Grains per spikelet	At maturity
Grain yield (t ha^{-1})	Plot weight at 12.5% moisture content converted to t ha^{-1}
1000 grain mass	Weight of 1000 grains at 12.5% moisture content
Threshing percent	Grain weight as percent of panicle weight
Agronomic score	Overall appearance of genotype including yield potential 1-5 scale (1-very good; 5-very poor)
Leaf blast severity score	1-9 scale: 1 = no infection; 2 = 1-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75%; and 9 = >75% leaf area covered with lesions. At milky grain stage
Neck blast severity score	1-9 scale: 1 = no infection; 2 = 1-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75%; and 9 = >75% leaf area covered with lesions. At physiological maturity
Finger blast severity score	1-9 scale : 1 = no infection; 2 = 1-5%; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75%; and 9 = >75% leaf area covered with lesions. At physiological maturity

Source: IBPGR (1985); Pande (1992)

4.3 Data analysis

4.3.1 REML

Quantitative data were analysed using the augmented random model of residual maximum likelihood (REML) (Federer and Wolfinger, 2003) in SAS (SAS, 2008) as follows:

$$Yij = \mu + \alpha i + \beta j + \varepsilon ij$$

where:

Yij = Observation of i^{th} entry in j^{th} block.

αi = i^{th} entry effect.

βj = j^{th} block effect.

εij = Random error component

The block effects were estimated from the repeated check means and then removed from the means of the test entries (Federer and Wolfinger, 2003). A two way location (random) by accessions (fixed) analysis was performed. An estimate of the error variance over locations was obtained by computing the average effective error variance at each location and then averaging these over locations as suggested by Cochran and Cox (1957).

4.3.2 Correlation and path coefficient analyses

Phenotypic and Genotypic correlation coefficients were calculated in SAS (SAS, 2008) according to Kwon and Torrie (1964) as follows:

Phenotypic correlations

$$r_p = \mathrm{COV}_P(X1, X2) / \sqrt{V_P(X1) * V_P(X2)}$$

where: r_p = phenotypic correlation, X1 is independent variable and X2 is dependent variable, V_P and COV_P are the phenotypic variance and phenotypic covariance, respectively.

Genotypic correlations coefficients

$$r_g = \mathrm{COV}_G(X1, X2) / \sqrt{V_G(X1) * V_G(X2)}$$

where: r_g = genotypic correlation, V_G and COV_G are the genotypic variance and genotypic covariance, respectively.

Path coefficients were calculated according to Dewey and Lu (1959) to determine direct and indirect effects of the yield components on grain yield per ha^{-1}:

$$r_{ij} P_{ij} + \sum r_{ik} p_{kj}$$

where: r_{ij} = mutual association between independent trait *i* and dependent trait; $j; P_{ij}$ = direct effect of independent trait *i* on dependent trait *j* as measured by the corresponding path coefficient; and $\sum r_{ik} p_{kj}$ = summation of the components of the indirect effect of independent trait *i* on dependent trait *j* via all other independent traits *k*.

Estimation of residual effect:

$$\sqrt{(1 - R^2)}$$

where: $R^2 = \sum P_{ij} r_{ij}$, and P_{ij} and r_{ij} are as before. Scales for path coefficients have been suggested by Lenka and Mishra (1973) where 0.00-0.09 is negligible association effects, 0.01-0.19 is low, 0.20-0.29 is moderate, 0.30-0.99 is high and >1.0 is very high. Score data (agronomic score and blast scores) were not used in path analysis.

4.3.3 Phenotypic, genotypic and environmental coefficients of variation; broad sense heritability and genetic advance as percent of mean

Phenotypic coefficient of variation (PCV), genotypic coefficients of variation (GCV) and environmental coefficients of variation (ECV) were calculated according to Burton (1952) as follows using combined data:

$$PCV = \frac{\sqrt{\sigma_p^2}}{\bar{x}} \text{ x } 100$$

where: σ^2_p = phenotypic variance; and $\bar{x}$ = phenotypic trait population mean.

$$GCV = \frac{\sqrt{\sigma_g^2}}{\bar{x}} \text{ x } 100$$

where: σ^2_g = genotypic variance; and $\bar{x}$ phenotypic trait population mean

$$ECV = \frac{\sqrt{\sigma_e^2}}{\bar{x}} \text{ x } 100$$

where: σ^2_e = random error variance

Shivasubramanian and Menon (1973) have given PCV and GCV scales as 0-10% low, 10-20% moderate and >20% high.

Broad-sense heritability per location was estimated according to Hanson et al. (1956) as follows:

$$H^2 = (\sigma^2_g / \sigma^2_p) \text{ x } 100$$

where: σ^2_g = genotypic variance; and σ^2_p = phenotypic variance.

Broad sense heritability for combined analysis across locations was calculated as follows:

$$H^2 = \sigma^2_g / \sigma^2_{g+} \sigma^2_{Gl} / l + \sigma^2_e / rl$$

where: σ^2_{Gl} is variance due to genotype x location interaction, l and r are the numbers of environments and replications per environment, respectively.

Robinson et al. (1949) classified heritability values into 0-30%-low, 31-60%-medium and >61%-high.

Expected (predicted) genetic advance using broad-sense heritability under a selection intensity of 5% was computed following Johnson et al. (1955) using combined data as follows:

$$GA = (k)\ (\sigma_p)\ (H^2)$$

where: GA = expected genetic advance; k = selection differential in standardized units which for a selection intensity of 5% = 2.056; σ_p = phenotypic standard deviation; and H^2 = broad-sense heritability.

Genetic advance was then expressed as a percent of the mean of the unselected parental population

$$GA\% = \frac{GA}{\bar{x}} \text{ x } 100$$

where: GA% = Genetic advance as percent of mean, $\bar{x}$ = Population mean for the trait considered

Scales for GA% given by Johnson et al. (1955) as 0-10%-low, 10-20%-moderate and >20%-high were used.

4.4 Results

4.4.1 Correlation coefficients

For the data collected at Alupe, negative and significant ($P \leq 0.01$) Spearman's rank correlations were detected between days to flowering and: leaf blast (r_p = -0.265); neck blast (r_p = -0.440); and finger blast (r_p = -0.167). Similar correlations were recorded between grain yield and: leaf blast (r_p = -0.278); neck blast (r_p = -0.134); and finger blast (r_p = -0.347) (Table 4.4-1).

Table 4.4-1. Spearman's rank correlation coefficients for blast severity with selected finger millet yield components at Alupe.

	Correlation coefficients										
Blast type	**Days to flower**	**Grain yield**	**Plant height**	**Leaf blade width**	**Leaf blade length**	**Finger width**	**Finger length**	**Grains per spikelet**	**1000 grain mass**	**Threshing %**	**Agronomic score**
Leaf blast	-0.265***	-0.278***	-0.106***	-0.105*	-0.178***	-0.110**	0.140*	-0.155***	0.007ns	-0.140***	0.666***
Neck blast	-0.440***	-0.134***	-0.058*	-0.048ns	-0.078*	-0.106***	0.048ns	-0.023ns	0.099ns	-0.081**	0.448***
Finger blast	-0.167***	-0.347***	-0.153***	-0.102**	-0.246***	-0.153***	0.0064ns	-0.233***	0.08ns	-0.157***	0.661***

***- Significant at P≤0.001, **- Significant at P≤0.01, *-Significant at P≤0.05, ns-Non significant

Tall accessions had lower blast scores as reflected by the negative correlations between plant height and blast score. Blast was also highly positively correlated with agronomic score thus accessions with high blast were poor agronomically. There was some moisture stress during the end of the crop reproductive phase hence low humidity and this could have reflected negatively on blast pathogen prevalence and blast reaction of late maturing genotypes.

Phenotypic and genotypic correlation coefficients were determined between 19 quantitative traits across locations excluding score data (Table 4.4-2). Low but significant ($P \leq 0.01$) positive phenotypic correlations were recorded between grain yield and finger width ($r_p = 0.134$), peduncle length ($r_p = 0.272$), panicle exertion ($r = 0.281$), grains per spikelet ($r_p = 0.255$) and threshing percent ($r_p 0.459$) (Table 4.4-2). The same trend was recorded in genotypic correlations but with higher correlation values between grain yield and finger width ($r_g = 0.876$), peduncle length ($r_g = 0.517$), panicle exertion ($r_g = 0.571$), grains per spikelet ($r_g = 0.623$) and threshing percent ($r_g = 0.677$). The highest phenotypic correlation was recorded between peduncle length and panicle exertion ($r_p = 0.853$). The highest genotypic correlation was recorded between finger width and 1000 grain mass ($r_g = 1.207$). The phenotypic and genotypic correlations between grain yield and days to flowering were both negative at $r_p = -0.357$ and $r_g = -0.450$, respectively. Very high negative genotypic correlations were recorded between productive tillers and: 1000grain mass ($r_g = -1.000$); flag leaf blade width ($r_g = -1.000$); leaf sheath width ($r_g = -0.927$); and finger width ($r_g = -0.768$).

Table 4.4-2. Phenotypic and genotypic (bold) correlation coefficients between 19 quantitative traits of finger millet evaluated across four locations

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	1.000	-0.248	-0.028	0.022	0.036	-0.326	-0.021	0.022	0.023	-0.111	-0.405	0.4620	-0.3710	-0.063	-0.085	-0.111	-0.001	-0.210	-0.357
	1.000	**-0.417**	**0.056**	**0.180**	**0.140**	**-0.532**	**-0.059**	**0.135**	**0.039**	**-0.663**	-0.571	**0.813**	**-0.516**	**0.138**	**-0.200**	**-0.410**	**-0.373**	**-0.420**	**-0.450**
2		1.000	0.169	0.366	0.060	0.335	0.060	0.072	0.109	0.114	0.155	-0.078	0.063	0.334	-0.015	0.092	0.044	0.036	0.127
		1.000	**0.087**	**0.401**	**-0.068**	**0.502**	**0.033**	**-0.050**	**0.189**	**0.216**	**0.386**	**-0.360**	**0.315**	**0.503**	**-0.297**	**0.223**	**0.089**	**0.323**	**0.144**
3			1.000	0.504	0.362	-0.072	0.344	0.156	0.192	0.185	-0.011	0.134	0.024	0.152	-0.231	0.130	0.078	0.081	0.160
			1.000	**0.795**	**0.752**	**-0.587**	**1.000**	**0.090**	**0.322**	**0.851**	**-0.281**	**0.180**	**-0.014**	**0.146**	**-0.927**	**0.502**	**0.102**	**0.451**	**0.215**
4				1.000	0.278	-0.101	0.317	0.073	0.293	0.163	0.034	0.184	0.095	0.411	-0.215	0.151	0.092	0.093	0.210
				1.000	**0.679**	**-0.389**	**0.776**	**-0.046**	**0.432**	**0.643**	**-0.036**	**0.111**	**0.194**	**0.556**	**-0.792**	**0.429**	**0.075**	**0.385**	**0.214**
5					1.000	-0.124	0.328	0.186	0.090	0.170	-0.130	0.107	-0.053	0.054	-0.135	0.077	0.051	0.001	0.064
					1.000	**-0.369**	**0.763**	**0.218**	**0.267**	**0.380**	**-0.275**	**0.190**	**-0.125**	**0.224**	**-0.962**	**0.126**	**0.266**	**0.018**	**0.081**
6						1.000	-0.185	0.077	-0.069	-0.037	0.405	-0.206	0.109	0.142	0.180	0.036	-0.059	0.016	0.135
						1.000	**-0.581**	**0.061**	**-0.198**	**-0.270**	**0.698**	**-0.475**	**0.361**	**0.028**	**0.502**	**-0.299**	**-0.329**	**-0.028**	**0.175**
7							1.000	0.097	0.173	0.231	-0.017	-0.001	0.060	0.061	-0.128	0.074	0.095	0.002	0.023
							1.000	**0.132**	**0.443**	**0.441**	**-0.207**	**0.059**	**0.008**	**0.060**	**-1.000**	**0.338**	**0.375**	**0.357**	**0.235**
8								1.000	0.014	-0.064	-0.153	0.141	-0.206	-0.004	-0.027	-0.026	-0.028	-0.09	-0.01
								1.000	**-0.049**	**-0.394**	**-0.230**	**0.166**	**-0.280**	**-0.129**	**-0.116**	**-0.213**	**-0.264**	**-0.273**	**-0.192**
9									1.000	0.185	-0.04	0.100	-0.02	0.201	-0.13	0.185	0.062	0.009	0.058
									1.000	**0.349**	**-0.087**	**0.157**	**-0.024**	**0.296**	**-0.377**	**0.564**	**0.391**	**-0.059**	**-0.098**
10										1.000	0.007	-0.010	0.034	0.073	-0.027	0.160	-0.013	0.029	0.134
										1.000	**0.326**	**-0.207**	**0.525**	**0.186**	**-0.768**	**1.000**	1.000	**0.912**	**0.876**
11											1.000	-0.267	0.853	0.385	0.141	0.112	-0.022	0.161	0.272
											1.000	**-0.479**	**0.910**	**0.305**	**0.459**	**0.401**	**-0.360**	**0.462**	**0.517**
12												1.000	-0.260	0.226	-0.077	0.064	0.008	-0.086	-0.004
												1.000	**-0.416**	**0.275**	**-0.261**	**0.058**	**0.333**	**-0.191**	**-0.174**
13													1.000	0.384	0.084	0.109	0.018	0.187	0.281
													1.000	**0.369**	**0.291**	**0.605**	**-0.366**	**0.560**	**0.571**
14														1.000	-0.020	0.121	0.039	0.097	0.252
														1.000	**-0.237**	**0.264**	**-0.084**	**0.179**	**0.119**
15															1.000	-0.004	-0.070	-0.071	0.140
															1.000	**-0.398**	**-1.000**	**-0.290**	**0.098**
16																1.000	-0.026	0.037	0.255
																1.000	**-0.429**	**0.476**	**0.623**
17																	1.000	0.100	0.078
																	1.000	**0.416**	**-0.294**
18																		1.000	0.459
																		1.000	**0.677**

1-days to flowering, 2-Leaf sheath length, 3-Leaf sheath width, 4-leaf blade length, 5-Leaf blade width, 6-Flag leaf blade length, 7-Flag leaf blade width, 8-Fingers/panicle, 9-Finger length, 10-Finger width, 11-Peducnle length, 12-Leaves/plant, 13-Panicle exertion, 14-Plant height, 15-Productive tillers/plant, 16-Grains/spikelet, 17-1000 grain mass, 18-Threshing%, 19-Grain yield.

4.4.2 Path coefficients

For the 18 quantitative traits, genotypic correlations were determined and direct and indirect path coefficients were estimated (Table 4.4-3). The path coefficients revealed that threshing percent (2.864), leaf blade width (2.523), leaves per plant (1.229), leaf blade length (1.119), grains per spikelet (0.760), leaf sheath length (0.601), and finger length (0.448) had high positive direct effects on grain yield. Negative direct effects were contributed by leaf sheath width (-2.938), plant height (-1.545), finger length (-1.260) and days to flowering (-1.183). Indirect genotypic effects of traits on grain yield through other traits were high. Some of the traits that had positive direct effects recorded overall negative effects on grain yield due to their negative indirect effects on grain yield through other traits and vice versa. Finger length which had a positive direct effect (0.448) had an overall negative effect on grain yield due to its high indirect negative effects via leaf sheath width (-0.945), flag leaf blade width (-0.318), finger width (-0.439) and plant height (-0.457). Leaves per plant with a positive direct effect (1.229) on grain yield gave a negative overall effect contributed by its high indirect negative effects via days to flowering (-0.962), leaf sheath width (-0.529) plant height (-0.425), and threshing percent (-0.547). Traits which had negative direct effects on grain yield but with an overall positive effect included leaf sheath width, flag leaf blade length, finger width, peduncle length, panicle exertion plant height as a results of high indirect positive effects via other traits. The efficiency of the genotypic path coefficients was high with R = 0.935 and a very low residual of 0.255.

Table 4.4-3. Genotypic path coefficients showing direct (diagonal) and indirect genetic effects of 18 quantitative traits on grain yield

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Overall path coefficients
1	**-1.183**	-0.251	-0.165	0.201	0.352	0.378	0.042	-0.043	0.018	0.836	0.242	0.999	0.084	-0.213	-0.019	-0.312	-0.216	-1.202	-0.450
2	0.493	**0.601**	-0.257	0.449	-0.172	-0.357	-0.024	0.016	0.085	-0.273	-0.163	-0.442	-0.051	-0.777	-0.028	0.169	-0.052	0.926	0.144
3	-0.067	0.053	**-2.938**	0.889	1.898	0.417	-0.727	-0.029	0.144	-1.073	0.119	0.221	0.002	-0.225	-0.086	0.381	-0.059	1.293	0.215
4	-0.213	0.241	-2.336	**1.119**	1.713	0.276	-0.557	0.015	0.194	-0.810	0.015	0.136	-0.032	-0.858	-0.073	0.326	-0.044	1.102	0.214
5	-0.165	-0.041	-2.210	0.759	**2.523**	0.262	-0.547	-0.069	0.120	-0.479	0.117	0.234	0.020	-0.347	-0.089	0.096	-0.154	0.052	0.081
6	0.629	0.301	1.724	-0.435	-0.931	**-0.711**	0.417	-0.019	-0.089	0.341	-0.295	-0.584	-0.059	-0.043	0.046	-0.227	0.190	-0.081	0.175
7	0.070	0.020	-2.979	0.868	1.926	0.413	**-0.717**	-0.042	0.198	-0.556	0.087	0.073	-0.001	-0.093	-0.096	0.257	-0.217	1.023	0.235
8	-0.160	-0.030	-0.266	-0.051	0.549	-0.043	-0.095	**-0.316**	-0.022	0.497	0.097	0.204	0.046	0.199	-0.011	-0.162	0.152	-0.781	-0.192
9	-0.046	0.114	-0.945	0.483	0.674	0.141	-0.318	0.016	**0.448**	-0.439	0.037	0.192	0.004	-0.457	-0.035	0.429	-0.226	-0.169	-0.098
0	0.785	0.130	-2.502	0.719	0.960	0.192	-0.316	0.125	0.156	**-1.260**	-0.138	-0.254	-0.086	-0.287	-0.071	0.809	-0.697	2.611	0.876
11	0.676	0.232	0.825	-0.041	-0.695	-0.497	0.148	0.073	-0.039	-0.410	**-0.423**	-0.589	-0.148	-0.472	0.043	0.304	0.208	1.322	0.517
12	-0.962	-0.216	-0.529	0.124	0.48	0.338	-0.043	-0.052	0.070	0.261	0.203	**1.229**	0.068	-0.425	-0.024	0.044	-0.192	-0.547	-0.174
13	0.610	0.189	0.042	0.218	-0.314	-0.256	-0.006	0.089	-0.011	-0.662	-0.385	-0.511	**-0.163**	-0.570	0.027	0.460	0.211	1.604	0.571
14	-0.163	0.302	-0.428	0.622	0.566	-0.020	-0.043	0.041	0.133	-0.234	-0.129	0.338	-0.060	**-1.545**	-0.022	0.200	0.048	0.513	0.119
15	0.237	-0.178	2.724	-0.886	-2.426	-0.357	0.746	0.037	-0.169	0.967	-0.194	-0.321	-0.047	0.366	**0.093**	-0.303	0.640	-0.830	0.098
16	0.485	0.134	-1.474	0.48	0.317	0.212	-0.242	0.067	0.253	-1.340	-0.169	0.071	-0.098	-0.407	-0.037	**0.760**	0.248	1.364	0.623
17	-0.442	0.054	-0.300	0.084	0.672	0.234	-0.269	0.083	0.175	-1.521	0.152	0.409	0.060	0.130	-0.103	-0.326	**-0.578**	1.192	-0.294
18	0.496	0.194	-1.326	0.431	0.045	0.020	-0.256	0.086	-0.026	-1.149	-0.195	-0.235	-0.091	-0.276	-0.027	0.362	-0.240	**2.864**	0.677

1-days to flowering, 2-Leaf sheath length, 3-Leaf sheath width, 4-leaf blade length, 5-Leaf blade width, 6-Flag leaf blade length, 7-Flag leaf blade width, 8-Fingers/panicle, 9-Finger length, 10-Finger width, 11-Peduncle length, 12-Leaves/plant, 13-Panicle exertion, 14-Plant height, 15-Productive tillers/plant, 16-Grains/spikelet, 17-1000 grain mass, 18-Threshing%; R Square = 0.935 Residual effect = 0.2552

4.4.3 Phenotypic, genotypic and environmental coefficients of variation

For the 19 quantitative traits estimates of PCV, GCV and ECV across locations were determined (Table 4.4-4). The PCV estimates were higher than GCV estimates for all the traits. High PCV were recorded for finger per panicle, flag leaf blade length, finger length, peduncle length, number of leaves per plant, leaf sheath length, plant height, leaf blade length, grains per spikelet, days to flowering and number of productive tillers per plant. There were no high GCV estimates recorded but medium GCV were recorded for finger length, peduncle length, number of leaves per plant, threshing percent and number of productive tillers per plant. The ECV estimates were relatively low ranging from 2.4% for grain yield to 23.8% in peduncle length.

4.4.4 Heritability and genetic advance

At Alupe, H^2 ranged between 0.0% in threshing percent to 92.4% in days to flowering and at Lanet the lowest H^2 was recorded in flag leaf width (3.6%) and the highest in finger length (81.4%) (Table 4.4-4). Leaf blade width (7.6%) and days to flowering (88.4%) had the lowest and highest H^2, respectively at Kiboko and at Mtwapa, 1000 grain mass had the lowest H^2 (19.2%) and leaf blade width (91.8%) had the highest. Heritability estimates across locations were lower than for individual locations. The highest H^2 estimate across locations was recorded in fingers per plant (83.0%) while the least (10.0%) was recorded for finger width. High H^2 ($\geq$60%) was recorded for fingers per panicle, flag leaf blade length, 1000 grain mass, productive tillers per plant, finger length, peduncle length and panicle exertion. Number of leaves per plant, Plant height, days to flowering, leaf blade length, grains per spikelet, leaf sheath length and width and threshing percent had moderate H^2 (33.9-59.8%). Genetic advance (%) varied from 6.2% for grain yield to 44.1% for panicle exertion (Table 4.4-4). Moderate H^2 estimates and high GA% were recorded in plant height leaf sheath length, number of leaves per plant and days to flowering. All the traits with high H^2 also had high GA%.

Table 4.4-4. Genotypic, phenotypic and error coefficients of variability, heritability and genetic advance (expressed as a percent of the population mean) of 19 quantitative traits in finger millet

Trait	Means across locations	GCV across locations	PCV across locations	ECV across locations	H^2 Alupe	H^2 Lanet	H^2 Kiboko	H^2 Mtwapa	H^2 across locations	GA* Across locations (% of mean)
1	7.94	9.57	25.02	8.02	52.5	73.5	72.6	68.2	83.0	30.3
2	10.53	8.71	26.50	8.25	38.3	70.3	76.7	65.2	77.8	25.4
3	2.59	1.64	11.70	7.44	14.6	54.8	33.6	19.2	68.5	30.0
4	4.08	17.61	54.56	5.00	72.2	65.1	54.4	72.2	66.0	30.4
5	6.85	15.50	56.19	7.85	78.1	81.4	82.1	66.7	65.1	38.3
6	19.91	17.57	79.20	23.77	76.1	63.9	69.3	63.3	64.2	26.3
7	9.56	2.12	11.58	4.39	63.8	58.6	59.0	55.0	61.6	44.1
8	14.32	16.72	72.43	11.36	79.0	47.9	69.9	58.7	59.8	27.7
9	11.31	7.50	35.48	5.41	78.6	72.3	60.9	63.5	56.7	20.7
10	84.51	8.92	57.78	6.04	79.1	71.9	64.6	75.3	45.3	24.3
11	48.00	2.68	24.93	3.00	58.8	45.6	60.3	53.4	35.6	16.7
12	71.34	10.27	16.68	8.50	0.0	80.6	31.5	44.7	35.2	11.1
13	5.60	1.45	21.73	9.60	61.2	38.0	47.3	36.2	34.2	13.9
14	1.59	0.70	7.35	1.31	60.7	60.0	56.6	50.7	34.2	15.1
15	2.38	0.94	10.11	2.36	54.2	78.4	44.6	68.4	34.0	14.2
16	84.31	8.04	72.86	21.99	92.4	77.0	88.4	80.6	33.9	20.5
17	1.17	0.54	8.14	1.92	73.2	3.6	16.3	68.4	27.1	14.7
18	1.33	0.65	11.41	2.48	72.2	48.2	7.6	91.8	23.6	14.2
19	1.15	0.25	11.35	2.14	65.5	50.0	22.9	44.1	10.0	6.5

GCV-Genotypic coefficient of variation, PCV-Phenotypic coefficient of variation, ECV-Environment coefficient of variation, H^2-Broad-sense heritability, GA%-Predicted genetic advance as percent of the mean; 1-Fingersper panicle, 2-Flag leaf blade length, 3-1000 grain mass, 4-Productive tillers per plant, 5-Finger length, 6-Peduncle length, 7-Panicle exertion, 8-Leaves per plant, 9-Leaf sheath length, 10-Plant height, 11-Leaf blade length, 12-Threshing percent, 13-Grains per spikelet, 14-Leaf sheath width,15-Grain yield, 16-Days to flowering, 17-Flag leaf blade width, 18-Leaf blade width, 19-Finger width.

4.5 Discussion

4.5.1 Associations between traits

Knowledge of correlation among traits is important to breeders in that improvement of one trait may impact positively or negatively on an associated trait. For effective simultaneous improvement of the key traits in crop productivity it is necessary to determine the magnitude of associations between the traits. In this study, correlation coefficient analysis indicated the magnitude and direction (positive or negative) of the associations between the traits. Through path analysis, however, it was possible to partition and quantify the complex associations between the various traits and grain yield into direct and indirect effects on grain yield. Correlation analysis of the Alupe data revealed significant ($P \leq 0.01$) negative correlations between all blast types (leaf, neck and finger) with days to flowering and grain yield. These findings agree with those of Dida and Devos (2006) and Takan et al. (2004). The high positive correlations among leaf, neck and finger blast lend support to the conclusions of Pande (1992). The negative correlations between finger blast and panicle shape, grains per spikelet and threshing percent showed that lax panicles were more susceptible than compact and tight fisted types similar to findings by

Sreenvasaprasad et al. (2005) and Pande et al. (1995). Higher blast scores contributed to fewer and lighter grains per spikelet and low threshing percent leading to low grain yields. Leaf blast reduces the photosynthetic capacity of the plant, whereas early neck blast reduces or completely impairs flow of nutrients to the panicle and finger blast reduces or completely impairs grain filling (Rath and Mishra, 1975). Low blast scores in tall accessions could be due to their higher clearance from the ground (inoculum levels could be higher near the ground due to debris and rain drops splashes), or due to the negative correlation between days to flowering and blast since most of the tall plants were late and flowered in lower humidity when rains had reduced.

Across locations, the genotypic correlations were higher than phenotypic correlations for most of the traits studied indicative of the inherently strong genetic relationships among the traits once the non-heritable influence of the environment was removed. This was also reported by Chaudhari and Acharya (1969) and Wolie and Desalegn (2011). However, the same authors found grain yield to be positively correlated with finger width, peduncle length, panicle exertion, grains per spikelet, and threshing percent. Sonnad et al. (2008) and Priyadharshini et al. (2011) reported similar results except for threshing percent. Days to flowering had high negative genotypic and phenotypic correlations with the key yield related traits of finger width, peduncle length, panicle exertion grains per spikelet, and threshing percent, corroborating results reported by Bezawelataw et al. (2006). Late maturing accessions, therefore, had narrow fingers, shorter peduncles, shorter exertions, fewer grains per spikelet and poor threshing percent. These high negative correlations negated the positive effects of higher number of leaves per plant in late maturing plants and hence were not translated into higher grain yield. The negative association between plant height and number of productive tillers per plant in this study was also reported by Sonnad et al. (2008). However, Suyambulingam and Jebarani (1977) reported positive significant correlations between plant height and finger length and number of fingers per panicle. Finger width recorded the highest positive genotypic correlations (r_g = 1.00) with grains per spikelet, 1000 grain mass (r_g = 1.00) and threshing percent (r_g = 0.91) but had high negative genotypic correlation with productive tillers per plant (r_g = -0.77) which agrees with findings of Bezawelataw et al. (2006) save for threshing percent. Therefore, many tillers will give many panicles but with narrow fingers hence fewer grains. The negative correlations between grain yield and fingers per panicle (r_g = -0.019) was contrary to that recorded by Ravikumar and Seetharam (1993). The negative correlation between grains per spikelet and 1000 grain mass could be from the high competition for assimilates between the two traits as was also reported by Dewey and Liu (1959).

4.5.2 Path coefficients

The highest direct positive effects on grain yield were contributed by number of leaves per plant, leaf blade length, leaf blade width, leaf sheath blade length, finger length, grains per spikelet, and threshing percent. When compared to the path coefficient scales suggested by Lenka and Mishra (1973) where 0.00-0.09 is negligible, 0.0 1-0.19 low, 0.2 0-0.29 moderate, 0.30-0.99 high and >1.0 very high, threshing percent (2.864), leaf blade width (2.523), number of leaves per plant (1.229) and leaf blade length 1.119) had very high direct effects whereas grains per spikelet (0.760), leaf sheath length (0.601) and finger length (0.448) had high direct effects. Productive tillers per plant had a positive but low direct effect (0.093) on grain yield. This basically means that accessions with a high number of long, wide leaves and long fingers with many grains and a high grain to panicle ratio will give more grain yield per unit area. The high yields achieved by accessions with a high number of long and wide leaves could be attributed to their high capacity to intercept more light thereby increasing photosynthesis (Dewey and Lu 1959). By implication this would require a strong source-sink relationship. Dependence of grain yield on sink size in finger millet was reported by Subedi and Budhathoki (1996). Although plant height had a negative direct effect on grain yield, it had an overall positive effect due to positive indirect effects via leaf blade length and width, leaves per plant and threshing percent. In pearl millet (*Pennisetum glaucum* (L.) R.Br) though, Chaudhry et al. (2003) found positive direct effects of plant height on grain yield. Threshing percent has been found to be useful as a selection criterion for terminal drought tolerance in pearl millet and is used to indirectly select for grain yield (Bidinger and Mukuru 1995). The results of this study confirm the value of threshing percent in yield selection based on its very high direct positive effects on yield. The negative direct effects of days to flowering on grain yield were contributed largely via the number of leaves per plant and 1000 grain mass. Late accessions had lower 1000 grain mass due to limited moisture at grain filling. Very leafy accessions were also late to flower meaning much of the assimilates went into leaf maintenance at the expense of grain development.

In previous studies positive direct effects on grain yield have been reported by Bendale et al. (2002) and Ganapathy et al. (2011) from finger length, Dhanakodi (1988) from number of leaves per plant and leaf length and Bezawelataw et al. (2006) from number of leaves per plant. Positive direct effects of grains per spikelet on grain yield detected in this study were also reported by Lule et al. (2012) in finger millet. and Eldin et al. (2012) in sorghum (*Sorghum bicolor* (L.) Moench). Negative direct effects of plant height and days to flowering on grain yield in finger millet have been reported by Wolie and Dessalagn (2011) and from plant height in wheat by Pandey et al. (2012). However, Bezawelataw et al. (2006) reported positive direct effects from 1000 grain mass and negative direct effects from grains per spikelet. Although

Ravikumar and Seetharam (1993) and Sonnad et al. (2008) reported positive direct effects of productive tillers per plant on grain yield, this study found a negligible direct effect (0.093) which could be attributed to the negative indirect effects of this trait via leaf blade length and threshing percent on grain yield.

Finger length had negative indirect contribution via leaf sheath width, finger width, and plant height. These traits should therefore be used with caution when selecting for grain yield. On the contrary, although finger width, peduncle length, panicle exertion and leaf sheath width had high negative direct effects on grain yield their overall effects were significantly positive due to their positive indirect effects via days to flowering, leaf blade length and width, grains per spikelet and threshing percent (for finger width), days to flowering, leaf sheath width and threshing percent (for peduncle length), leaf blade length and width, flag leaf blade length, grains per spikelet and threshing percent (for leaf sheath width). Number of fingers per panicle had negative direct effects on grain yield which contradicts findings of Priyadharshini et al. (2011) and Ganapathy et al. (2011) who reported direct positive effects.

Grain yield is influenced by many independent traits and understanding the nature and magnitude of the association of these traits with grain yield and among themselves is vital for effective selection for grain yield. Findings of this study show that threshing percent, leaf blade width, number of leaves per plant, leaf blade length, grains per spikelet, leaf sheath length and finger length had high positive direct effects on grain yield and could be the ideal traits to select for in finger millet for grain yield improvement. Simultaneous selection for the improvement of those traits with strong direct and those with strong indirect effects on grain yield would be the best approach. However, constraints of negative trait associations in plants are an important consideration when selecting for any components of yield individually. The magnitude of the other component traits may often compensate downwards in order to allow for the increase in the fixed pool of assimilate partitioned to the improved component trait (Slafer et al., 1996). For example high direct effects were detected from grains per spikelet but this was negatively correlated with 1000 grain mass meaning having more grains per spikelet will use more photo-assimilates at the expense of grain filling leading to low grain weights hence reduced yield. In essence selection for a trait must be coordinated with selection for the other trait so that an optimum level maximizes the net effect of the system (Yan and Wallace, 1995).

The variability in grain yield in finger millet was well captured by the 18 traits studied based on the very low residual effect obtained (0.255) and a high coefficient of determination (R^2 = 0.935) for path coefficients.

4.5.3 Phenotypic and genotypic coefficients of variation

Phenotypic coefficient of variation and GCV are useful in obtaining a measure of the genetic variability in the expression of the target traits. Higher GCV than PCV estimates would suggest that the phenotypic expression of the trait is more influenced by genes than the environment whereas higher PCV estimates would mean the trait is more influenced by the environment. From the results, PCV estimates were higher than GCV estimates for all traits suggesting high environmental influence. However, in fingers per panicle, flag leaf blade length, finger length, number of leaves per plant, leaf sheath length, productive tillers per plant, plant height and threshing percent, the effects of the environment were relatively lower than those for the other traits as evidenced by the low ECV estimates. Likewise, the relatively closer estimates of PCV and GCV in threshing percent suggest low environmental effects for this trait thus high heritability. Improvement of these will be achievable through selection. However very high environmental effects were recorded in finger length, number of leaves per plant, plant height, days to flower and productive tillers per plant owing to the very high PCV (>50%) estimates obtained suggesting low heritability. In Ethiopia, Bezawelataw et al. (2006) found influence of both genes and environment on most of the finger millet traits he studied owing to the high PCV and GCV estimates. In India though, Ganapathy et al. (2011) found high PCV and GCV only in productive tillers per plant. Lule et al. (2012) reported low PCV in days to flowering with low GCV in grains per spikelet and finger width while Nandini et al. (2010) found a narrow difference between PCV and GCV for fingers per panicle.

4.5.4 Heritability and genetic advance

Trait variability for yield and yield components, heritability and genetic advance are key factors for selection progress in crop improvement. Although heritability estimates across locations/environments are usually lower than the component single location estimates (Falconer, 1981; Mudler and Bijma, 2005), as was detected in this study, they provide a more realistic estimate for genetic gain predictions in the absence of narrow sense heritability that estimates the additive effects. For single location data GxE interaction effects are confounded with genotypic effects and consequently the magnitude of the heritability estimates is inflated. High H^2 across locations were recorded in fingers per panicle, flag leaf blade length, 1000 grain mass, productive tillers per plant, finger length, panicle exertion, and peduncle length indicating that these traits are influenced more by genetic than environmental effects. Because of their high H^2 improvement of these traits through selection should theoretically be achieved quickly. High H^2 was also reported by Daba (2000), Sumathi et al. (2007), Gananapathy et al. (2011),

Priyadharshini (2011) and Lule et al. (2012) in fingers per panicle and finger length with Sumathi et al. (2007) also reporting high H^2 in 1000grain mass.

Low H^2 in number of productive tillers per plant, finger width and grain yield implies high environmental effects on expression of these traits. Low H^2 has also been reported by Patnaik (1968) for productive tillers per plant. Satish et al. (2007) and Kadam et al. (2008) found high H^2 in grain yield. Trait H^2 estimates varied between locations with lowest estimates in nine traits recorded at Kiboko, a dry lowland location with limited and erratic rainfall. This was not surprising since the degree of genetic influence on trait development is dependent on the environment (Robinson et al., 1949) and, as reported by Falconer (1981), H^2 increases with reduced variability in test conditions and vice versa. Rosielle and Hamblin (1981) also found H^2 in grain yield to be correlated with the availability of water and Eid (2009) found low H^2 in drought stress conditions in wheat.

In inbred lines dominance effects diminish rapidly with inbreeding and the variance component estimated provides an estimate of additive genetic variance (Hallauer and Miranda, 1998). Finger millet being a highly self-pollinating crop means each line will be highly inbred with much of the genetic variance estimates close to additive. Traits which recorded high H^2 and GA% in this study (number of fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, productive tillers per plant, peduncle length, panicle exertion) would be presumed to be under additive genetic control hence can be improved through selection. These traits also had high heritability estimates. Similar findings of high H^2 estimates and GA% in finger millet traits were reported by John (2006) for fingers per panicle; Bezawelataw (2006) for finger length; Satish et al. (2007) and Nandini et al. (2010) for fingers per panicle and finger length; and Lule et al. (2012) for finger length and 1000 grain mass. Whereas Satish et al. (2007) found high H^2 and GA% in days to flowering, Daba (2000), Ganapathy et al. (2011) reported high H^2 estimates and low GA%. Finger width had low H^2 estimates and GA% an indication of high environmental effects on this trait hence very slow progress through direct selection is expected. The slow rate of progress in yield improvement in breeding programs has always been due to its low heritability (though moderate in this study) rendering direct selection difficult. Using traits with high heritability, positive direct effects on yield and highly correlated with yield would help hasten the selection for yield. In this case grains per spikelet though with moderate heritability had high correlation and high positive direct effects on grain yield and would be a key trait for yield selection.

4.6 Conclusion

High potential for finger millet improvement to address the different biotic and abiotic stresses in varied agro-ecologies exists owing to the ample variability recorded in the quantitative traits. This variability could be utilized in direct selection and for hybridization. Genotypic correlations were higher than phenotypic correlations for most traits. Grain yield was significantly ($P \leq 0.01$) positively correlated with grains per spikelet, threshing percent, peduncle length and panicle exertion. These traits could be used to indirectly select for grain yield. The identification of the key yield components, namely: threshing percent, , number of leaves per plant, leaf blade length, grains per spikelet, leaf sheath length and finger length with direct effects on grain yield will inform indirect selection for grain yield, a complex trait with low heritability. But due consideration should also be given to traits with strong indirect effects on grain yield during selection factoring in the constraints of photo-assimilates for the components of yield individually. Though there were high environmental influences on most traits, the high heritability and genetic advance as percent of mean recorded in fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, peduncle length, panicle exertion, number of leaves per plant and leaf sheath length gives hope for faster improvement through selection in early generations as these traits are under additive gene effects.

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Chapter 5

Genotype x environment interaction, yield stability and blast reaction in East African finger millet landraces

Abstract

Eighty one finger millet germplasm selections from East Africa were evaluated in eight environments for adaptation, grain yield stability using the additive main effects and multiplicative interaction (AMMI) ANOVA and Genotype and Genotype x Environment (GGE) models and blast reaction under artificial and natural inoculation. Lanet 2012 long rains (Lan12LR), Serere 2012 long rains (Ser12LR) and Miwaleni 2012 long rains (Miw12LR) were found to be the most discriminating environments for the low temperature, sub-humid mid-altitude and dry lowland areas, respectively. Alupe 2012 long rains was identified as the ideal environment for blast selection. Seven genotypes were identified for yield stability across the eight environments whereas nine genotypes had specific adaptation. Nine genotypes were identified with resistance to three blast types. However, one and two genotypes had high resistance only to leaf and neck blast, respectively. Two resistant and 12 moderately resistant genotypes to blast attained the highest grain yields and had varied maturity, plant heights and grain colour. This will provide farmers the opportunity to select genotypes appropriate to their target agro-ecologies with desired end-uses. Disease severity scores were highly negatively correlated with days to flowering and grain yield suggesting that early lines suffered more disease damage leading to reduced yield. Resistant genotypes were slow blasting (probably associated with horizontal resistance) which may enable them to withstand blast pathogen variability for a longer time. The East African finger millet germplasm has high potential as a source of high yielding and blast resistant genotypes for direct production or breeding.

Key words: blast resistance, finger millet, GGE, yield stability

5.1 Introduction

Finger millet in East Africa is mainly grown in the sub-humid to humid Lakes Victoria and Tanganyika zones where blast disease (caused by the fungus *Magnaporthe grisea*) thrives, the cool highlands with low temperatures and to a lesser extent in the low rainfall lowlands that suffer from moisture stress/drought. Finger millet has been reported to be sensitive to temperature extremes. Very high temperatures (38°/28°C compared to 32° /22°C), decrease panicle emergence, number of seeds per panicle, grain yield and harvest index (Opole, 2012) whereas low temperatures have been reported to affect pollination and fertilization processes (Bandyopadhyay, 2009). The improved cultivars available in the region have been derived mainly from germplasm selections (Oduori, 2008). The extent of significant genotype by environment (G x E) interactions determine the consistency of performance of genotypes across locations and seasons. The analysis of a multi-environmental trial (MET) data set enables partitioning of G x E interaction into Genotype x Locations and Genotype x Years within Locations. The determination of the extent and nature of GxE interactions distinction is essential in order to identify genotypes with specific adaptation to an environment or with wide adaptability (; Yan and Tinker, 2006; Das et al., 2011). In East Africa, no GxE studies have been reported in finger millet and most cultivar selections have been based on individual location testing. This limits the appreciation of the performance potential of many cultivars in other agro-ecologies not used as test sites. Significant GxE interactions for grain yield and yield components in finger millet have been reported in India by, among others, Misra et al. (2010) and Joshi et al. (2005) and in Ethiopia by Bezaweletaw et al. (2006) and Adugna et al. (2011)

The accuracy with which GxE is measured and interpreted will determine choice of genotypes and identification of ideal test locations and recommendations for regional cultivar releases (Yan, 2001). Although there are a number of statistical models for analysis of stability and multi-environment data, Additive and Main effects and Multiplicative Interactions (AMMI) (Gauch, 1992) and Genotype and Genotype x Environment interaction (GGE) biplot analyses (Yan and Tinker, 2006) are most commonly used. Both AMMI and GGE biplots graphically display the main effects and the genotype x environment effects based on principal component analysis (Gauch, 1992; Ding et al., 2007). However, the GGE biplot analysis has been reported to be more informative as it uses a combination of some of the functions of the methods of GxE analysis (Ding et al., 2007) and it is more effective in identifying the best performing cultivars in a specific mega-environment ('which won where' pattern) (Yan, 2001). It is also more effective in discriminating the stability of genotypes and test environments (Yan, 2001).

Finger millet blast is the most important disease in all finger millet growing areas of East Africa and causes yield losses of between 10-68% (Takan et al., 2004). Most cultivars grown by farmers are susceptible to the disease and although fungicides for the control of the disease are available, they are beyond the reach of the farmers relative to the economic returns from finger millet (Sunil and Anilkumar, 2003). Host plant resistance therefore remains the most viable option in the management of the disease. Previous studies in finger millet (Pande, 1992; Sunil and Anilkumar, 2003) and in rice (*Oryza sativa*) (Kumar et al., 2010; Kapoor, 2010) found partial (slow blasting) resistance in blast resistant genotypes. Due to reported existence of different blast pathotypes (Takan et al., 2012) any finger millet improvement program should consider horizontal resistance in the breeding programme especially targeting humid and sub-humid finger millet production agro-ecologies where the disease thrives. Partial resistance is known to be relatively long lasting and more stable (van der Plank, 1963) than race specific resistance. Evaluation of partial resistance is best done by characterizing the sequential observations (scoring) of the disease from initiation to the end of the epidemic using the area under disease progress curves (AUDPC) (Mohapatra et al., 2008). Due to the favourable weather and presence of alternate host plants (wild grasses) in East Africa, the disease occurs throughout the year (Mackill and Bonman, 1992; Pande et al., 1995). This study was conducted to evaluate the GxE interaction, yield stability and blast reaction of 81 finger millet genotypes selected from an East African germplasm pool.

5.2 Materials and methods

5.2.1 Experimental material

For this study a total of 81 genotypes (including five checks-U 15, KNE 814, KNE 479, Nakuru FM 1 and Kahulunge) with high productivity potential and blast resistance (Table 5.2-1) were selected from 420 accessions (340 landraces and 80 minicore set) previously phenotyped across four locations in Kenya (Chapter 2).

Table 5.2-1. The 81 finger millet genotypes selected for G x E evaluation

Genotype	Name	Origin	Genotype	Name	Origin	Genotype	Name	Origin
G1	Emiroit/Engeny	Uganda	G28	Gulu E	Uganda	G55	GBK-040468A	Kenya
G2	Ekama-white	Uganda	G29	GBK-011110A	Kenya	G56	GBK-043163A	Kenya
G3	Kal	Uganda	G30	GBK-011141A	Kenya	G57	Acc # 79	Minicore
G4	Kal	Uganda	G31	GBK-027145A	Kenya	G58	Acc # 3924	Minicore
G5	Kal Atari	Uganda	G32	GBK-027201A	Kenya	G59	P 224	Uganda
G6	Kal Atari	Uganda	G33	IE 4497	Minicore	G60	Unknown	Uganda
G7	Kal atari	Uganda	G34	Ekama	Tanzania	G61	Etiyo -brown	Uganda
G8	Ekamo	Uganda	G35	IE 5306	Minicore	G62	Ekama	Uganda
G9	Unknown	Uganda	G36	IE 6154	Minicore	G63	Kal	Uganda
G10	RW 127 (IE 6613)	Uganda	G37	KNE 1034	Kenya	G64	Otara chigal	Uganda
G11	GBK-008301 A	Kenya	G38	Acc # 3989	Minicore	G65	GBK-000352A	Kenya
G12	GBK-011116A	Kenya	G39	Eteke	Uganda	G66	GBK-011113A	Kenya
G13	GBK-011136A	Kenya	G40	Adalaka	Uganda	G67	GBK-011119A	Kenya
G14	GBK-029681A	Kenya	G41	Kal	Uganda	G68	GBK-027200A	Kenya
G15	Acc # 2954	Minicore	G42	GBK-000347A	Kenya	G69	GBK-029646A	Kenya
G16	Acc # 3656	Minicore	G43	GBK-000351A	Kenya	G70	GBK-029672A	Kenya
G17	Acc # 3779	Minicore	G44	GBK-000368A	Kenya	G71	GBK-029768A	Kenya
G18	Kafumbata	Tanzania	G45	GBK-000373A	Kenya	G72	GBK-043166A	Kenya
G19	Kaulunge	Tanzania	G46	GBK-000410A	Kenya	G73	IE 2430	Minicore
G20	3953	Tanzania	G47	GBK-011111A	Kenya	G74	IE 4121	Minicore
G21	Purple	Uganda	G48	GBK-011129A	Kenya	G75	Ngome	Uganda
G22	Engenyi	Uganda	G49	GBK-011133A	Kenya	G76	Katila	Uganda
G23	Unknown	.Uganda	G50	GBK-011137A	Kenya	G77	KNE 479	Kenya
G24	Acomomcomo	Uganda	G51	GBK-027149A	Kenya	G78	KNE 814	Kenya
G25	Lowa	Uganda	G52	GBK-027155A	Kenya	G79	Nakuru FM 1	Kenya
G26	Omunga	Uganda	G53	GBK-028590A	Kenya	G80	U 15	Uganda
G27	Kal	Uganda	G54	GBK-040463A	Kenya	G81	Kahulunge	Tanzania

5.2.2 Test environments

The genotypes were evaluated for two seasons at Alupe and Kiboko (Kenya) and in one season each at Lanet (Kenya), Miwaleni and Uyole (Tanzania) and Serere (Uganda) (Table 5.2-2).

Table 5.2-2. Characteristics of the eight test environments used in the evaluation of 81 finger millet accessions in 2011 and 2012

Location	Environments	Codes	Altitude (m)	Latitude	Longitude	Temperatures (°C)			Mean annual rainfall (mm)	Rainfall during cropping season (mm)
						Min	Max	Mean		
Alupe (Kenya)	Alupe 2011 short rains	Alu11SR, Alu12LR Alu12LR-IN	1189	0°28'N	34°7'E	17.7	30.3	24.0	1100	439.0
	Alupe 2012 long rains									715.5
Lanet (Kenya)	Lanet 2012 long rains	Lan12LR	1920	0°30'S	36°0'E	10.0	20.0	15.0	850	693.1
Kiboko (Kenya)	Kiboko 2011 short rains	Kib11SR,	960	2°20'S	37°45'E	16.6	29.4	23.0	604	252.2
	Kiboko 2012 long rains	Kib12LR								277.7
Serere (Uganda)	Serere 2012 long rains	Ser12LR	1000	1°31'N	33°27'E	18.0	30	24.0	1378	Not available
Miwaleni (Tanzania)	Miwaleni 2012 long rains	Miw12LR	500	3°25'S	37°27'E	16.5	27.0	21.7	650	300.0
Uyole (Tanzania)	Uyole 2012	Uyol12	1800	8°55'S	33°34'E	7.9	19.3	13.5	870	764.7

Alu12LR – Natural infection, Alu12LR-IN –Artificial inoculation

5.2.3 Experimental design and crop management

The trials were planted in a 9 x 9 square lattice design with two replications per environment with each experimental plot comprising three 4 m length rows with inter-row and intra-row spacing of 0.4 m and 0.1 m, respectively. Seed was manually drilled in furrows and thinned at two weeks after emergence to 41 plants per row. Weeding and pest control were done according to recommended practices. Double Ammonium Phosphate (18:46:0) at the rate of 20 kg N and ca. 20 kg P_2O_5 per hectare was applied as basal fertilizer at planting time and Urea (46%N) at the rate of 20 kg N per hectare was applied as top dressing three weeks after sowing. Data collected were: days to 50% flowering (when half of the plants in the plot had started flowering); plant height (from the base of the stem to the tip of the panicle at hard dough stage in cm), grain yield (at 12.5% moisture content in t ha^{-1}); leaf, neck and finger blast scores

(scored as indicated in next paragraph). The trials in four environments (Alu11SR, Alu12LR, Alu12LR-IN, Ser12LR and Lan12LR) were screened for blast reaction under natural blast infection and artificial inoculated under Alu12LR-IN. Blast screening was not possible at Uyol12 due to logistical reasons and disease levels at Kib12LR, Kib11SR and Miw12LR (dry lowlands) are usually very low. The GxE trials were conducted under rain grown conditions at all environments except at Kiboko and Miwaleni where supplementary irrigation was applied during very dry periods up to flowering. However, irrigation for Alu12LR-IN was applied as described in the protocol below.

For the artificial inoculation in Alu12LR-IN, a technique using crop debris, infector rows, spray application of a spore suspension and supplemental irrigation was implemented (Pande et al., 1995; Kiran Babu et al., 2013). An infector row (using susceptible line GBK-011118A) was planted alternately to every four test rows (every 1.6 m) and infected finger millet debris collected from the previous season was spread in between test rows on moist soil (15-20 d after sowing). To create the required high humidity for disease development, irrigation was applied at least once a day from 11h00-12h00 on rain-free days up to the start of grain filling. Inoculum was prepared from a single-spore culture of *Magnaporthe grisea* (isolated from blast infected samples collected from the finger millet fields in the previous season at Alupe) on oat meal agar (OMA) medium at 26±1ºC for 10 days. Spores were harvested by flooding the plates with sterilized distilled water and then scraping the culture off the surface of the medium using a spatula. The spore suspension was adjusted to the desired concentration (1×10^5 spores/ml) with the aid of a hemocytometer (Kiran Babu et al., 2013). The spore suspension was sprayed on 20 day old seedlings and at pre-flowering stage using a knapsack sprayer. All blast data were recorded on five randomly selected plants which were tagged in each plot. The leaf blast severity was recorded at 30, 51, 61, and 71 days after sowing (coinciding with tillering, booting, flowering and milky stages of most genotypes) using a 1 to 9 scale (Pande et al., 1995) where: 1 = no lesions to small brown specks of pinhead size (0.1-1.0 mm), less than 1% leaf area affected; 2 = typical blast lesions covering 1-5% leaf area covered with lesions; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75% and many leaves dead; and 9 = typical blast lesions covering >75% leaf area or all the leaves dead. The 1 to 9 disease rating scale was divided into four general categories of reaction: (1.0-3.0) moderately resistant; (3.1-5.0) susceptible (5.1-7.0); and highly susceptible (7.1-9.0) (Pande et al., 1995). Neck blast severity was scored using neck blast rating scale developed for finger millet at ICRISAT-India (Kiran Babu et al., 2013). This is based on the relative lesion size on the neck using a 1 to 5 scale where: 1 = no lesions to pinhead size of lesions on the neck region (<10% damage); 2 = 0.1 to 2.0 cm size of typical blast lesion on the neck region (10-20% damage); 3 = 2.1 to 4.0 cm (20-50% damage); 4 = 4.1 to 6.0 cm (50-70% damage); and 5 = >6.0 cm size of typical blast lesion (>70% damage) on the neck region. The

scale was divided into four categories of reaction: resistant (1.0-2.0); moderately resistant (2.1-3.0); susceptible (3.1-4.0); and highly susceptible (4.1-5.0). The finger blast severity was scored using a 1 to 9 disease rating scale (Pande et al., 1995) where: 1 = no disease on all panicles; 2 = 1-5% severity on infected panicles; 3 = 6-10% severity; 4 = 11-20% severity; 5 = 21-30% severity; 6 = 31-40% severity; 7 = 41-60% severity; 8 = 61-80% severity; and 9 = 81-100% severity. The scale was divided into four general categories of reaction as for leaf blast. For neck and finger blast, scoring was done at 61, 71, 81, 91 and 101 days after sowing and these coincided respectively with flowering, milky, soft dough, hard dough and physiological maturity stages of most genotypes. Due to high cost and logistical problems of inoculum preparation, the artificial inoculation of the trial at Alupe was conducted for one season only. Data were also recorded on days to flowering, plant height and grain yield as described earlier in this section. Only finger blast severity scores under natural infection were used for GGE discrimination of environments. Spearman's rank correlations between traits were also determined.

5.3 Data analysis

5.3.1 AMMI ANOVA

The additive main effects and multiplicative interaction (AMMI) model of Gauch (1988) was used to explain the significant GxE interaction for grain yield, days to flowering, plant height neck and finger blast:

$$Y_{ger} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \theta_{ge} + \varepsilon_{ge}$$

where: Y_{ger} is the observed yield of genotype g in environment e for replicate r. The additive parameters μ = grand mean; α_g = the deviation of genotype g from the grand mean; β_e = the deviation from environment e. The multiplicative parameters λ_n = singular value for interaction principal component axis (IPCA) n; γ_{gn} = the genotype eigenvector for axis n; δ_{en} = environment eigenvector for axis n; θ_{ge} = residual accounting for the unfitted IPCAs; and ε_{ge} = random error. The AMMI analysis was done in Genstat Genstat 15.0 (http://www.genstat.co.uk). Since the error variances of the environments were found to be heterogeneous using Bartlett's test (Bartlett, 1937), the AMMI analyses were done after data values of each environment were standardized by subtracting the general mean and dividing by the standard error (square root of the random error mean square) of the respective environment. Leaf blast severity scores were not taken at Ser12LR due to logistical problems and were therefore not used for the combined analysis.

5.3.2 GGE biplot analysis

For GGE biplot analysis, Yan (2002) model based on the singular value decomposition (SVD) of the first two principal components was used in Genstat 15.0 (http://www.genstat.co.uk).

$$Y_{ij} - \mu - \beta_j = \lambda 1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

where: Y_{ij} is the measured mean yield or finger blast severity of genotype *i* in environment *j*; μ is the grand mean; β_j is the main effect of environment *j*; λ_1 and λ_2 are the singular values (SV) for the first and second principal components (PC1 and PC2), respectively; ξ_{i1} and ξ_{i2} are eigenvectors of genotype *i* for PC1 and PC2, respectively; η_{1j} and η_{2j} are eigenvectors of environment *j* for PCl and PC2, respectively; εij is the residual associated with genotype *i* in environment *j*.

The GGE biplots were interpreted according to Yan et al. (2001) and Yan (2002) where ideal genotypes were those with high yield and low finger blast severity, high PC1 values (higher yield) and PC2 values close to zero (more stable) whereas ideal environments were those with high PC1 values (better genotype discrimination). Using a polygon that enclosed all genotypes, those furthest from the origin were specifically adapted to a group of environments with similar magnitude and sign. Environments enclosed within two perpendicular lines drawn from the biplot origin formed an environmental group. Using vectors drawn from the origin to each environment, the distance between two environments indicated their dissimilarity in discriminating the genotypes and the furthest environment from the origin had the most discriminating ability. Average environment coordination axis (AEC) is a line that passes through the origin and the coordinate point defined by the average PC1 and PC2 scores of all environments. The AEC was used to indicate the ranking of genotypes by mean yield and stability. Stability of a genotype was determined by the AEC passing through the biplot origin and another line perpendicular to it representing genotype stability. The distance of a genotype away from the biplot origin on the AEC axis in either direction indicated greater G x E interaction hence reduced stability. GGE biplots were also used to discriminate four environments (Alu11SR, Alu12LR, Lan12LR and Ser12LR) based of finger blast severity scores.

5.3.3 Area under disease progress curves (AUDPC)

Area under disease progress curve (AUDPC) was calculated for disease severity scores (at milk-dough stage for leaf blast and physiological maturity for neck and finger blast) for each genotype following Wilcoxson et al. (1975) formula:

$$AUDPC = \sum_{i=1}^{k-1} 1/2\,(S_i + S_{i+1})(t_{i+1} - t_i)$$

where: S_i = severity scores at days *i*; *k* = number of scores; t_i = time at *i* days

The AUDPC values are not easily interpreted which somewhat limits their utility in comparing cultivars. To aid in the interpretation of AUDPC values, AUDPC susceptibility scale values as suggested by Yuen and Forbes (2009) were calculated as follows:

$$Sx = Sy\,(Dx/Dy)$$

where: Sx = susceptibility scale value; Sy = severity score of susceptible check; Dx = AUDPC value for the genotype in question; Dy = AUDPC value of susceptible check. Low AUDPC susceptibility scale values mean resistance whereas high values mean susceptibility of the genotype to the disease.

5.4 Results

5.4.1 ANOVA across environments

The first four IPCAs were significant in the AMMI ANOVA for grain yield (Table 5.4.1). Treatments sum of squares (SS) comprised 76.4% of total sum of squares with 9.1%, 19.9% and 47.3% from the respective SS for genotypes, environments and their interaction. Genotypes comprised 12.0%, environments 26.0% and their interaction 62.0% of the treatment sum of squares. A total of 80.9% of the interaction SS was accounted for by the four significant IPCAs with IPCA1 and IPCA2 contributing a total of 53.8%. The grand mean for grain yield across environments was 2.32 t ha^{-1} with a range of 1.66 t ha^{-1} (G70) to 3.16 t ha^{-1} (G74). Forty three accessions attained means higher than the grand mean and 21 accessions attained means above the best check Nakuru FM 1 (2.50 t ha^{-1}) across environments. Only the first two IPCAs were significant for finger blast severity scores and contributed 87.0% of total interaction sum of squares with IPCA1 contributing 64.7% and IPCA2 22.3% (Table 5.4-2) . Genotypes comprised 27.4%, environments 46.8% and their interaction 25.9% of the treatment sum of squares. Mean days to flowering were significant ($P \leq 0.001$) (Table 5.4.3) and ranged from 64-91, whereas plant height

(significant at P≤0.001) ranged from 74.6 cm-105.5 cm environments. Neck blast severity scores were also significant (P≤0.001) and ranged from 1.5-5.0 across environments while finger blast severity scores ranged from 2.0-6.3.

Table 5.4-1. AMMI ANOVA for grain yield (t ha^{-1}) across eight environments

Source	df	SS	MS	% total SS explained	% treat SS explained	% interaction SS explained
Rep(ENV)	8	36.0	4.499***	-	-	-
Treatments	647	1025.3	1.585***	76.4	-	-
Environments	7	267.0	38.15***	19.9	26.0	-
Genotypes	80	122.6	1.533***	9.1	12.0	-
Interaction	560	635.6	1.135***	47.3	62.0	-
IPCA1	86	190.3	2.213***	-	-	29.9
IPCA2	84	152.2	1.812***	-	-	23.9
IPCA3	82	110.1	1.342***	-	-	17.3
IPCA4	80	62.0	0.775**	-	-	9.8
Residuals	228	121.1	0.531ns	-	-	-
Error	629	281.3	0.447	21.0	-	-
Total	1295	1342.6	1.037	.-	-	-

*** Significant at: P≤0.001, **P≤0.01; ns-non significant

Table 5.4-2. AMMI ANOVA for finger blast severity across four environments

Source	df	SS	MS	% total SS explained	% treat SS explained	% interaction SS explained
Rep(Env)	4	14.2	3.54***			
Treatments	323	1587	4.91***	86.3		
Environments	3	742	247.34***	40.3	46.8	
Genotypes	80	434.7	5.43***	23.6	27.4	
Interactions	240	410.3	1.71***	22.3	25.9	
IPCA	82	265.6	3.24***			64.7
IPCA	80	91.6	1.14**			22.3
Residuals	78	53.1	0.68ns			
Error	319	238.4	0.75	13.0		
Total	647	1839.7	2.84			

*** Significant at: P≤0.001, **P≤0.01

Table 5.4-3. Mean, minimum, maximum, mean squares, CV% and SE± for three traits

Trait	Mean	Min	Max	Ms	CV%	SE
Plant height (cm)[a]	86.7	74.6	105.5	852***	12.4	±10.62
Days to flowering[a]	78.0	64.0	91	484***	6.2	±4.80
Neck blast (1-5)[†]	3.0	1.5	5.6	8.08***	18.3	±0.99

[a] - Across eight environments; [†] -Across four environments; *** Significant at: P≤0.001

5.4.2. Genotype ranking and environments rank correlations based on grain yield

Based on untransformed location means the frequency of appearance of genotypes among the top 25 varied from one to six times (Table 5.4-4). The highest frequency was in genotypes G1, G3, G28 and G74 which appeared among the top 25 in six environments, genotypes G32, G71 and G41 in five environments and genotypes G40, G62 and G17 in four environments. Based on AMMI ranking for grain yield, no genotype appeared among the top four in more than two environments except G3 (Table 5.4-5). Genotype 13 was ranked in the top four in environments four and six, G17 in environments three and six, G3 in environments one, three and six, G32 in environments five and seven and G51 in environments seven and eight. Significant ($P \leq 0.05$) positive correlations were detected between environments Kib11SR and Kib12LR (r = 0.25), Kib11SR and Alu11SR (r = 0.34), Ser12LR and Alu12LR (r = 0.30), Miw12LR and Kib12LR (r = 0.32) and between Lan12LR and Uyol12 (r = 0.27) (Table 5.4-6). However, there was a significant (P = 0.05) negative correlation between Lan12LR and Alu11SR (r = -0.27).

Table 5.4-4. Ranking of the best 25 genotypes at each environment based on grain yield (t ha^{-1})[a]

	Alu11SR		Alu12LR		Kib11SR		Kib12LR		Lan12LR		Miw12LR		Uyol12		Ser12LR		Across	
	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld	Gen	Gyld
	G1	2.57	G33	4.13	G17	4.44	G3	4.70	G37	4.84	G20	4.64	G32	4.69	G44	4.34	G74	3.16
	G41	2.45	G34	3.72	G39	3.78	G30	4.46	G72	4.12	G43	4.16	G2	4.56	G51	3.29	G32	2.94
	G64	2.45	G23	3.60	G63	3.75	G79	4.45	G51	4.03	G42	3.99	G59	4.21	G32	3.25	G28	2.90
	G21	2.43	G36	3.58	G40	3.72	G12	4.43	G35	3.95	G1	3.61	G6	4.12	G74	3.21	G3	2.89
	G10	2.42	G74	3.37	G30	3.66	G36	4.32	G18	3.82	G13	3.47	G74	4.07	G31	2.96	G71	2.78
	G26	2.42	G60	3.29	G3	3.58	G14	4.21	G34	3.74	G45	3.46	G21	3.96	G5	2.93	G1	2.75
	G23	2.29	G3	3.25	G29	3.48	G13	4.19	G52	3.71	G71	3.43	G37	3.95	G67	2.85	G5	2.75
	G22	2.27	G39	3.24	G71	3.43	G28	4.11	G44	3.65	G41	3.34	G28	3.74	G18	2.78	G17	2.73
	G62	2.25	G9	3.18	G13	3.33	G29	4.08	G74	3.61	G25	3.28	G23	3.69	G64	2.78	G23	2.70
	G8	2.24	G81	3.17	G49	3.22	G74	4.02	G19	3.30	G17	3.23	G75	3.53	G58	2.71	G41	2.67
	G63	2.22	G10	3.12	G64	3.21	G40	3.98	G75	3.18	G46	3.20	G43	3.47	G3	2.71	G13	2.66
	G52	2.15	G20	3.12	G80	3.17	G66	3.97	G50	3.14	G24	3.15	G68	3.41	G76	2.70	G21	2.63
	G15	2.15	G32	3.08	G38	3.15	G47	3.97	G71	3.13	G29	3.14	G1	3.38	G2	2.69	G36	2.63
	G34	2.12	G67	3.07	G8	3.09	G75	3.88	G53	3.09	G3	3.13	G25	3.32	G26	2.69	G10	2.62
	G39	2.09	G17	3.06	G24	3.08	G31	3.87	G46	2.90	G21	3.07	G57	3.31	G19	2.67	G20	2.62
	G5	2.08	G5	3.01	G41	3.06	G5	3.85	G32	2.88	G23	2.96	G14	3.24	G62	2.56	G8	2.60
	G20	2.07	G4	3.00	G1	3.05	G50	3.77	G17	2.81	G60	2.96	G63	3.21	G79	2.52	G62	2.59
	G60	2.06	G1	2.91	G69	3.05	G41	3.76	G79	2.80	G22	2.88	G7	3.20	G20	2.52	G2	2.58
	G4	2.03	G70	2.89	G72	3.00	G35	3.73	G55	2.77	G56	2.87	G71	3.17	G4	2.50	G6	2.58
	G58	2.03	G21	2.87	G32	2.98	G49	3.72	G28	2.72	G6	2.83	G58	3.11	G50	2.49	G14	2.57
	G40	1.99	G27	2.86	G28	2.98	G77	3.72	G73	2.67	G12	2.82	G41	3.05	G69	2.47	G25	2.52
	G30	1.95	G14	2.85	G33	2.93	G71	3.72	G42	2.66	G73	2.80	G67	3.01	G28	2.46	G79	2.50
	G59	1.94	G59	2.84	G12	2.93	G1	3.68	G10	2.62	G74	2.71	G18	3.01	G7	2.42	G51	2.49
	G38	1.94	G62	2.83	G78	2.92	G54	3.67	G45	2.56	G36	2.67	G62	3.01	G10	2.39	G40	2.45
	G3	1.94	G40	2.76	G26	2.90	G6	3.66	G3	2.47	G28	2.66	G22	3.00	G56	2.39	G30	2.45
Mean (N = 81)		1.62		2.39		2.52		3.29		2.01		2.15		2.48		2.14		2.32
Min		0.53		0.90		0.25		1.82		0.20		0.18		0.67		1.00		3.16
Max		2.57		4.13		4.44		4.70		4.85		4.64		4.69		4.34		1.66
SE±		0.42		0.59		0.66		0.60		0.57		1.09		0.48		0.95		0.76

Al11SR - Alupe 2011 short rains, Alu12LR - Alupe 2012 long rains, Kib11SR - Kiboko2011 short rains, Kib12LR - Kiboko 2012 long rains, Lan12LR - Lanet 2012 long rains, Miw12LR - Miwaleni 2012 long rains, Uyol12 - Uyole 2012, Ser12LR - Serere 2012 long rains; Gen and G – Genotype, Gyld – Grain yield (t ha^{-1}), Across – Across 8 environments; [a]based on untransformed location means

Table 5.4-5. AMMI ranking of the best four genotypes per environment based on mean grain yield

Environment	Mean grain yield (t ha^{-1})	PCA Score	Rank 1	2	3	4
Miw12LR	2.16	1.0332	G20	G42	G13	G43
Kib11SR	2.52	0.9691	G17	G3	G49	G40
Alu11SR	1.62	0.5329	G3	G40	G74	G5
Kib12LR	3.29	0.5151	G3	G17	G13	G1
Alu12LR	2.39	0.1605	G33	G34	G23	G60
Ser12LR	2.48	0.0142	G32	G2	G59	G6
Lan12LR	2.14	-0.6194	G74	G44	G32	G51
Uyol12	2.01	-2.6056	G37	G72	G18	G51

Al11SR - Alupe 2011 short rains, Alu12LR - Alupe 2012 long rains, Kib11SR - Kiboko2011 short rains, Kib12LR - Kiboko 2012 long rains, Lan12LR - Lanet 2012 long rains, Miw12LR - Miwaleni 2012 long rains, Uyol12 - Uyole 2012, Ser12LR – Serere 2012 long rains

Table 5.4-6. Rank order correlations between environments for grain yield (t ha^{-1})

	Alu11SR	Alu12LR	Kib11SR	Kib12LR	Lan12LR	Miw12LR	Ser12LR
Alu11SR	-						
Alu12LR	0.207	-					
Kib11SR	0.334**	-0.009	-				
Kib12LR	0.001	0.033	0.253*	-			
Lan12LR	-0.265*	-0.135	-0.115	-0.014	-		
Miw12LR	0.053	-0.059	0.239	0.317**	-0.019	-	
Ser12LR	0.136	0.301**	-0.059	0.105	-0.060	0.105	-
Uyol12	0.006	0.005	0.028	0.052	0.273*	-0.044	0.155

Al11SR - Alupe 2011 short rains, Alu12LR - Alupe 2012 long rains, Kib11SR - Kiboko2011 short rains, Kib12LR - Kiboko 2012 long rains, Lan12LR - Lanet 2012 long rains, Miw12LR - Miwaleni 2012 long rains, Uyol12 - Uyole 2012, Ser12LR - Serere 2012 long rains; *Significant at P = 0.05; ** significant at P = 0.01

5.4.3 GGE

5.4.3.1 Discriminatory ability and representativeness of test environments

The GGE biplot explained 46.1% of the total G x E interaction for grain yield (Figure 5.4-1). Since the correlation between environments is determined by the angles between them (<90°-high correlation, 90°-no correlation and >90- negative correlation), high correlations were detected between Miw12LR, Kib11SR, Kib12LR, Alu11SR and Alu12LR and between Lan12LR and Uyol12. The biplot rays divided the plot into eight sections with environments falling in three of the sections. The environments were thus placed in three groups based on inter-environment distances (Figure 5.4-2). Group one comprised the Alu11SR, Alu12LR, Kib11SR, Kib12LR and Miw12LR, group two comprised the two cool highlands

environments Lan12LR and Uyol12, and Ser12LR stood alone. Although Ser12LR grouped alone, it was significantly ($P \leq 0.01$) positively correlated to Alu12LR. All the environments had PC1 scores between -0.1 and 0.2 except Lan12LR (>-0.3) whereas Kib11SR, Kib12LR, Alu11SR Alu12LR and Uyol12 had PC2 scores less than 0.1 except. Environments Lan12LR, Ser12LR and Miw12LR had PC2 scores between 1.5 and close to 2.5. The shortest vector from the biplot origin was for Alu12LR whereas Lan12LR had the longest. Thus the most discriminative environment for grain yield was Lan12LR and the least was Alu12LR. Lan12LR and Uyol12 had negative PC1 scores hence fell on the left side of the mean axis (low mean grain yield values). Based on (AEC, Ser12LR had the smallest angle with the AEC whereas Alu11SR and Lan12LR had the widest angle. The best performing genotypes for grain yield per mega-environment (and furthest from the biplot origin) were G74, G32, G71 and G28 for Ser12LR (G74 best adapted), G1, G21, G20, G23 for Alu11SR, Alu12LR, Kib11SR, Kib12LR and Miw12LR (G1 best adapted), and G37, G35, G71 and G75 for Lan12LR and Uyol12 (G37 best adapted) (Figure 5.4-2).

The GGE biplot accounted for 86.2% (PC1-71.8% and PC2-14.4%) of the total GxE interaction for finger blast severity (Figure 5.4-3). The four environments were placed in one quadrant out of the eight formed with very high correlation between Alu11SR, Alu12LR and Ser12LR. The most discriminative environment for finger blast was Alu12LR and the least was Ser12LR. The highest blast severity scores were recorded in genotypes G77, G29, G49, G47 and G48 whereas genotypes G43, G78, G9, G67, G10 and G17 had the lowest disease severity scores.

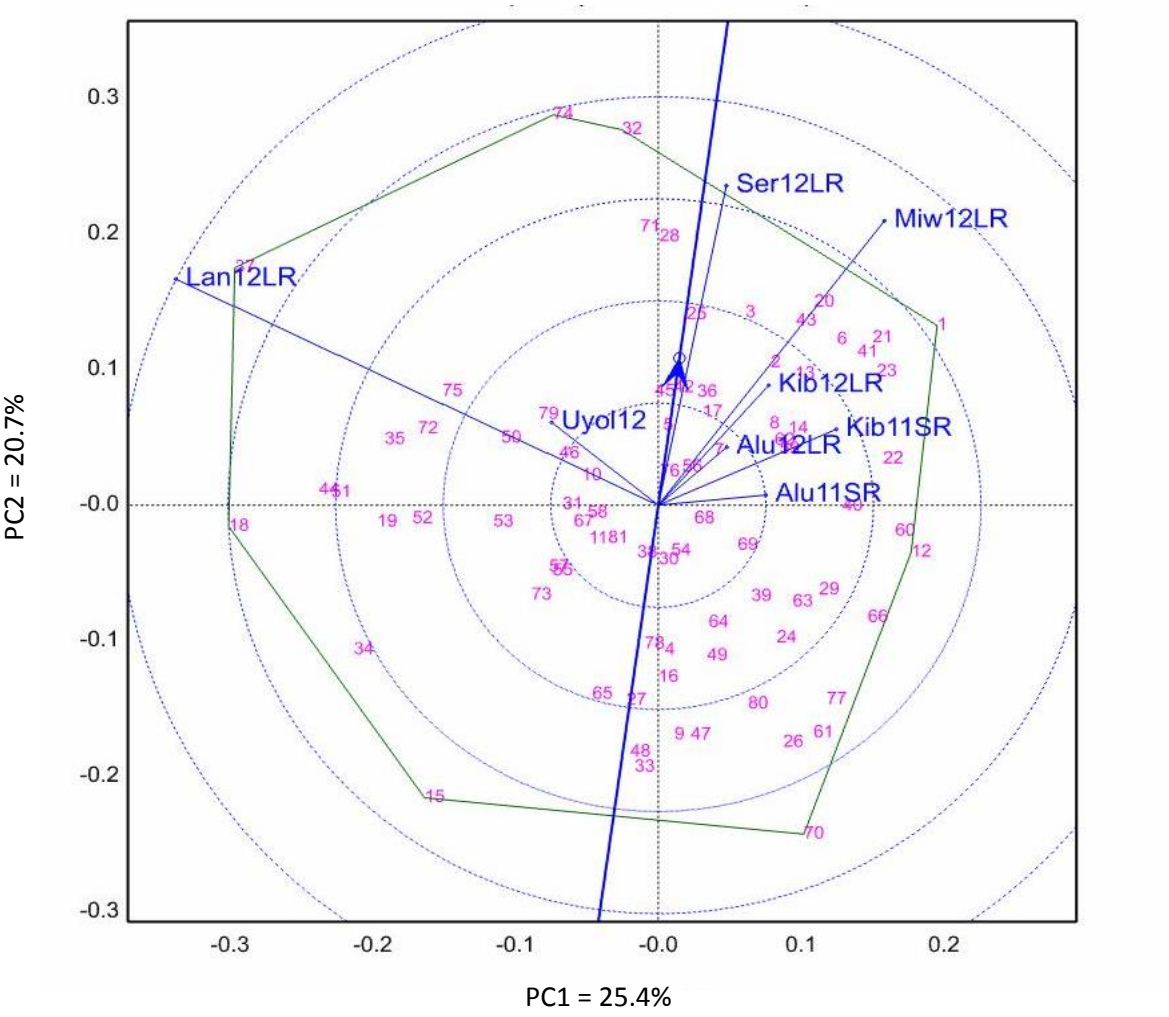

Figure 5.4-1. Discriminatory ability and representativeness of the eight test environments for grain yield (t ha^{-1})

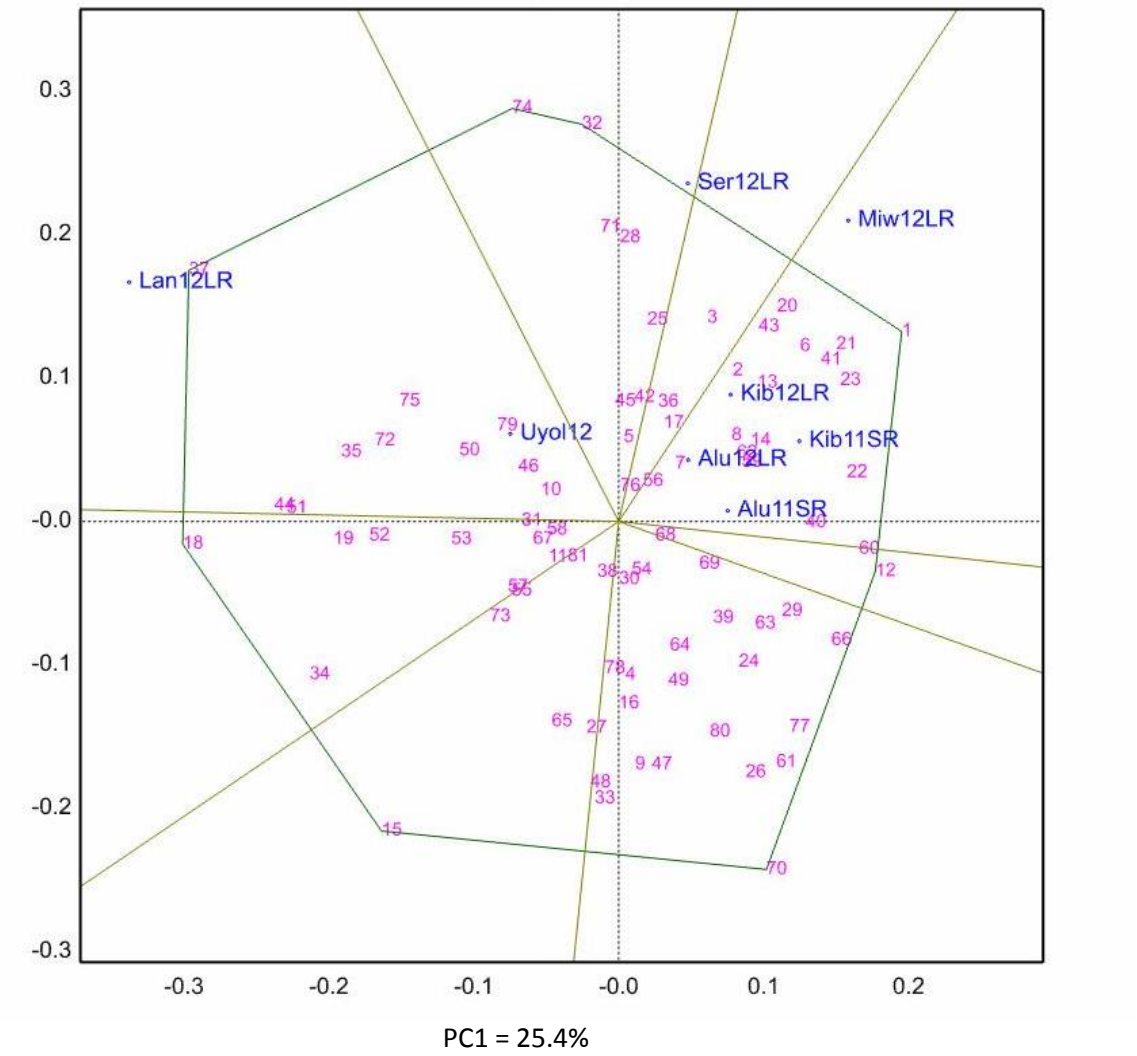

Figure 5.4-2. Polygon view of the GGE biplot for grain yield (t ha^{-1})

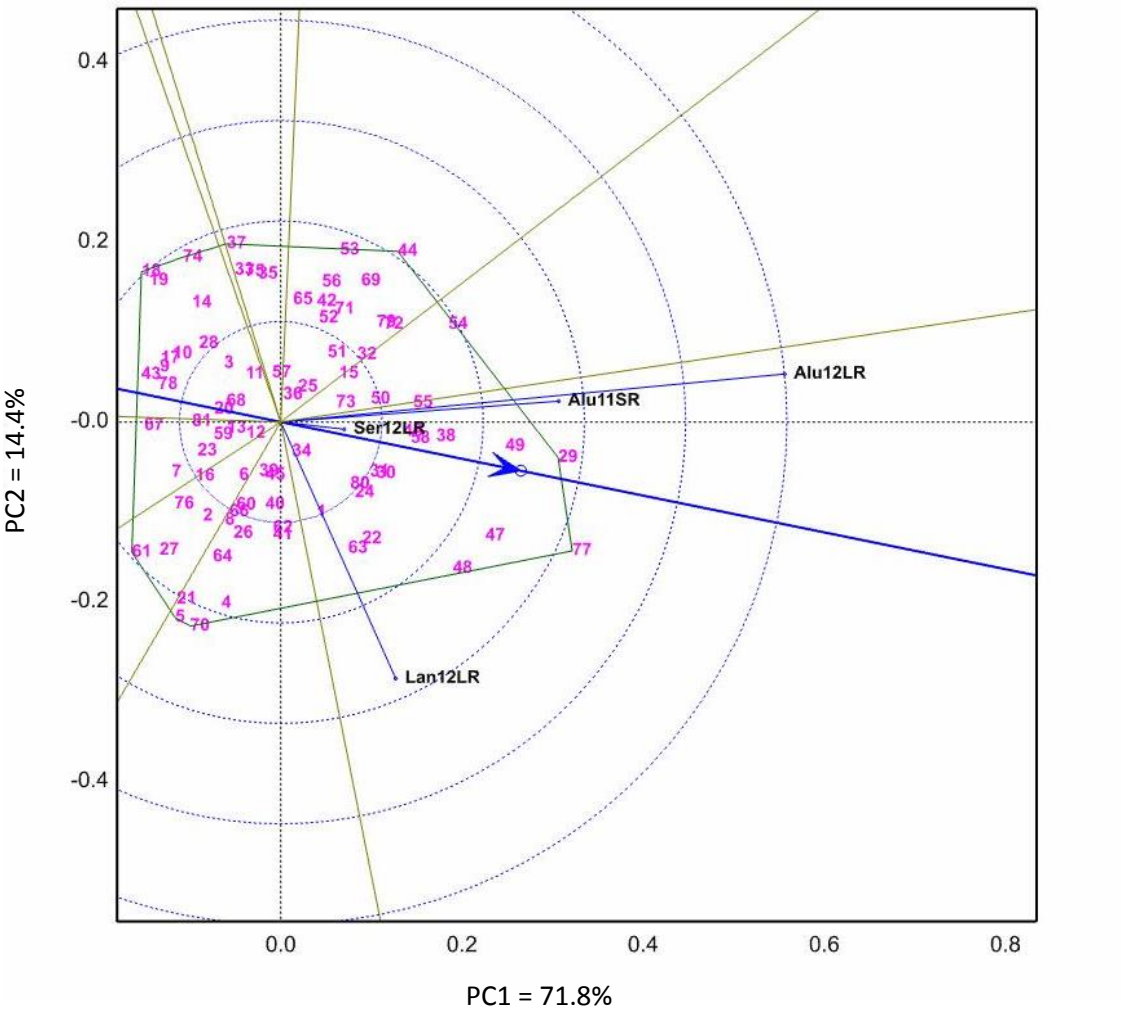

Figure 5.4-3. Discrimination of environments based on finger blast severity scores

5.4.3.2 Genotype ranking based on mean grain yield and stability

The AEC arrow points in the direction of higher grain yield while the line perpendicular to the AEC is the AEC ordinate and depicts greater variability in either direction (Figure 5.4-4). Therefore high yielding and stable genotypes were placed further along the AEC but close to the AEC on either side. On this basis, therefore, genotypes G74, G32, G71 and G28 had the highest mean yield regardless of stability and G5, G12, G25, G27, G30, G33, G458, G48, G56 and G76, were most stable regardless of yield. Genotypes G5, G17, G25, G28, G36, G42, G45, G56 and G71 were highly stable with grain yield above the grand mean across environments whereas genotypes G18 and G37 were the most unstable regardless of yield. Genotypes G15 and G70 were unstable with the lowest grain yield whereas genotypes G27, G30, G33, G48, G54, G65 and G78 were stable with low yield.

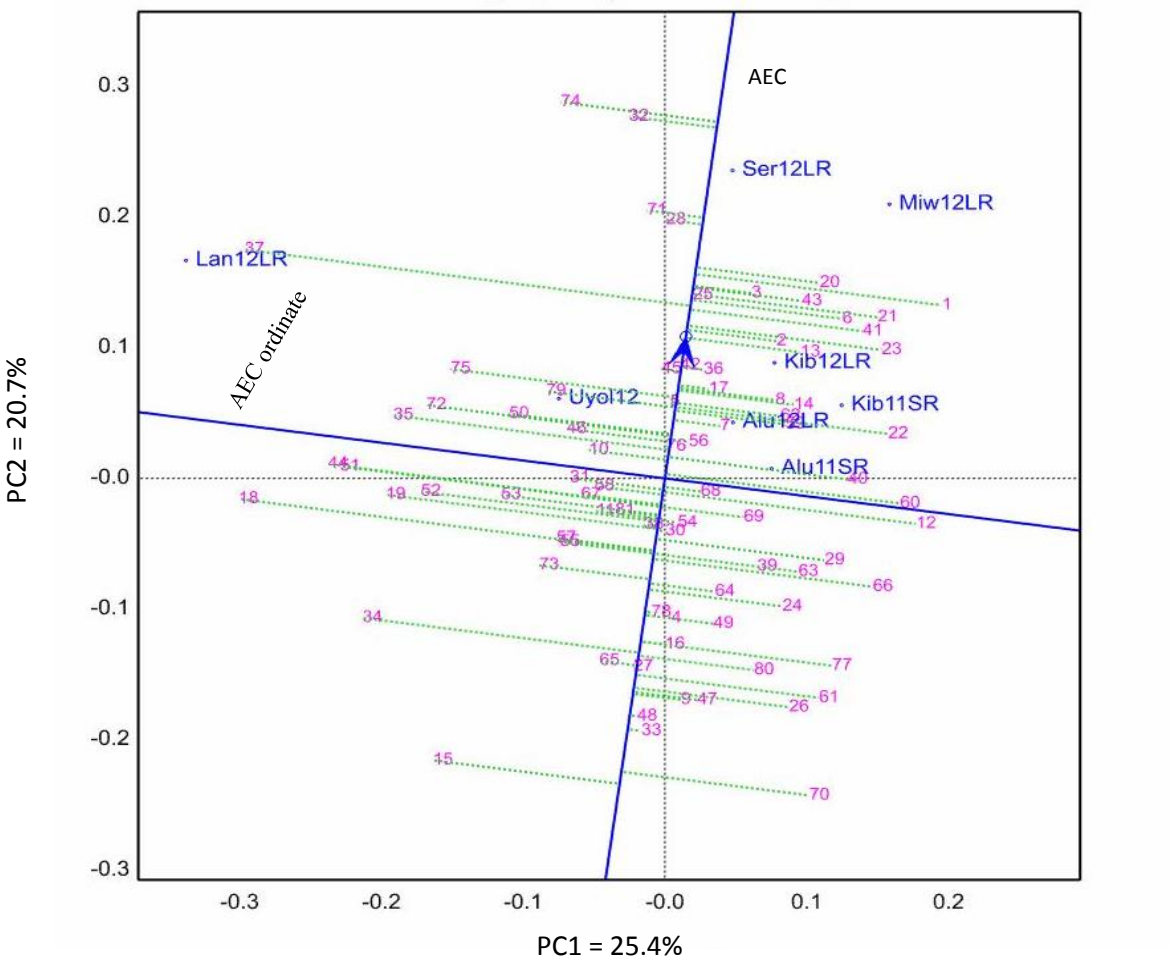

Figure 5.4-4. Genotype ranking based on mean grain yield and stability across environments

5.4.4 Blast screening

High and well distributed rainfall during the cropping season ensured optimum relative humidity hence pathogen proliferation and disease development in Alu12LR and Lan12LR which was higher than at Ser12LR and Alu11SR which were all under natural infection. Disease pressure was higher under artificial inoculation relative to all environments under natural infection.

5.4.4.1 Disease severity and genotype reaction type under artificial inoculation

Based on disease severity scores in Alu12LR-IN, leaf blast scores (1-9 scale) at milky grain stage ranged from 2.8 to 7.0, neck blast (1-5 scale) at physiological maturity ranged from 1.9 to 5.0 and finger blast (1-9 scale) at physiological maturity ranged from 1.5 to 9.0 (Table 5.4-7). No genotype exhibited complete immunity to blast. Grouped into resistant, moderately resistant, susceptible and highly susceptible the number of genotypes that fell into these classes were 3, 67, 11 and zero, respectively for leaf blast (Figure 5.4-5). Fifteen genotypes were resistant, 37 moderately resistant, 21 susceptible and 8 highly susceptible to neck blast. Ten genotypes were resistant, 56 were moderately resistant, nine were susceptible and six were highly susceptible to finger blast (Figure 5.4-5). The most resistant genotypes were G18, G67, and G43 for all three blast types; G9, G7, G8, G2 and G6 for leaf and neck blast; and G27, G78, G76 and G81 for neck and finger blast. Genotype G3 presented high resistance to leaf blast only whereas G16, G15, G60 and G70 had high resistance to neck blast only. Using six resistant and six susceptible genotypes to finger blast for comparison, there was a progressive reduction in grain yield associated with an increase in disease severity (Figure 5.4-6). Disease pressure was apparently low under Ser12LR environment and scoring may therefore not have been done with necessary attention to detail. Inoculation (Alu12LR-IN) increased disease severity by 12.9-40% for leaf blast, 0.0-52.8% for neck blast and 0.0-64.4% for finger blast (compared to Alu12LR-natural infection) (Table 5.4-7). Resistant genotypes identified under artificial infection had low blast scores across the other four environments (Table 5.4-8). Stable genotypes (G3, G5, G17, G25, G28, G30, G36 and G71) had moderate resistance under both artificial and natural infection across environments.

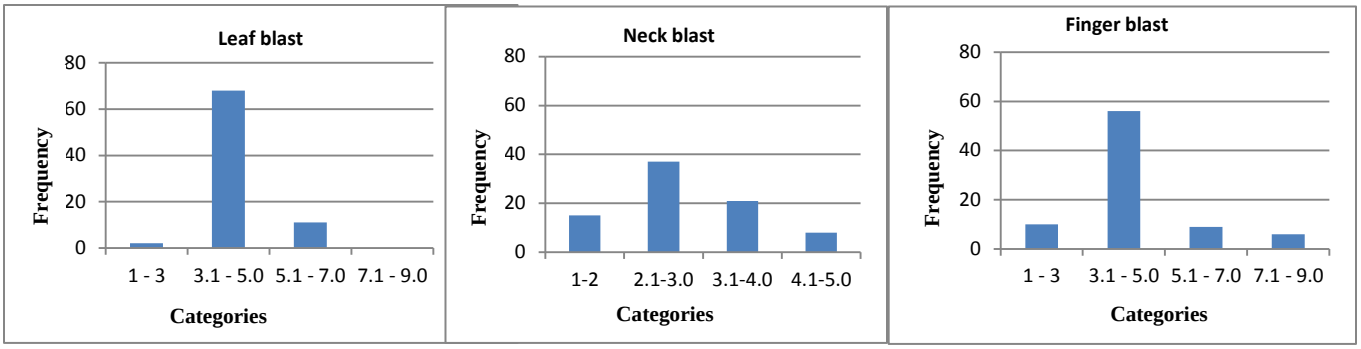

Figure 5.4-5. Frequency distributions for leaf, neck and finger blast reaction categories

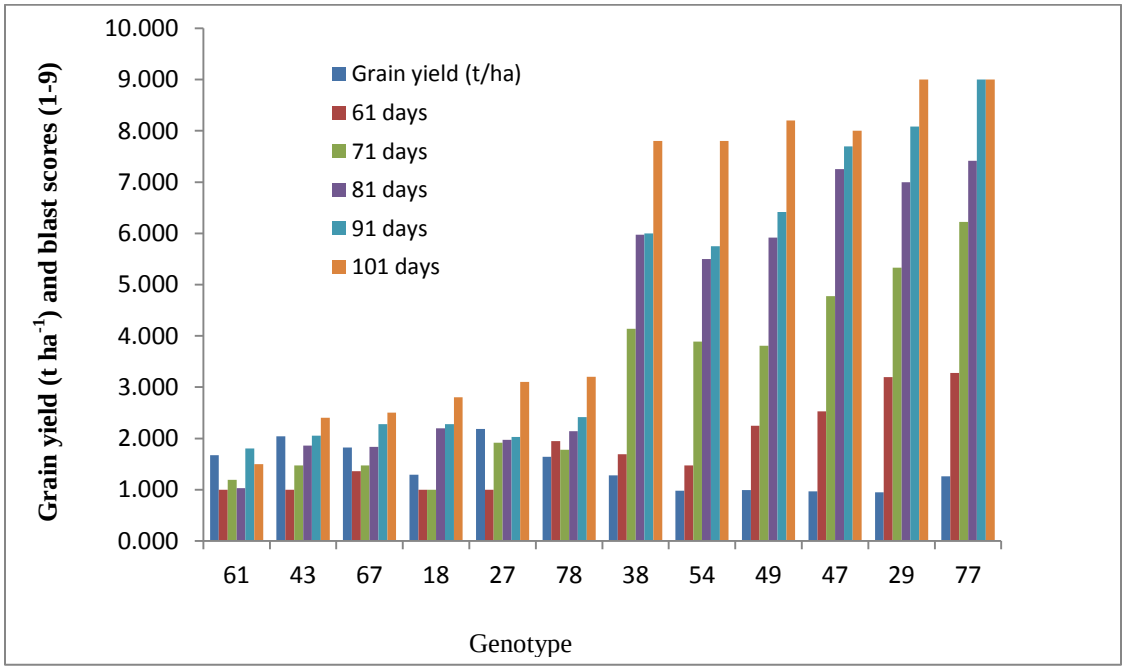

Figure 5.4-6. Grain yield and finger blast scores (at different days after sowing) for the most resistant (61-78) and the most susceptible (38-77) genotypes

Table 5.4-7. Blast severity differences under natural (Alu12LR) and artificial (Alu12LR-IN) inoculation

Severity	Blast type		
	Leaf (1-9 scale)	Neck (1-5 scale)	Finger (1-9 scale)
Range severity score natural infection	2.0-6.2	1.5-4.5	1.4-9.0
Mean severity score	3.3	2.7	4.6
Range severity score inoculated	2.8-7.0	1.9-5.0	1.5-9.0
Mean severity score	4.0	3.1	5.0
Range % severity increase	12.9-40.0	0.0-52.8	0.0-64.4
Mean % severity increase	25.1	14.9	11.6

Table 5.4-8. Grain yield, plant height, days to flowering and blast reaction of resistant, susceptible and stable genotypes

Genotype	Grain yield (t ha^{-1})[a]	Plant height (cm)[a]	Days to flowering[a]	Finger blast severity score					
				Alu12LR-IN	Alu12LR	Alu11SR	Ser12LR	Lan12LR	Across environs ‡
Resistant									
G61	1.67	79.7	85	1.5	1.4	1.4	1.1	4.1	2.0
G43	2.04	87.9	79	2.4	2.2	2.0	1.1	3.3	2.2
G67	1.82	95.3	86	2.5	2.4	2.0	1.1	3.6	2.3
G18	1.29	88.8	86	2.8	2.8	2.6	1.0	1.7	2.0
G27	2.19	91.8	86	3.1	2.3	2.0	1.9	4.3	2.6
G78	1.64	93.0	84	3.2	3.1	3.0	1.8	3.4	2.8
Susceptible									
G38	1.28	82.2	72	7.8	6.0	3.1	2.4	4.1	4.7
G54	0.98	78.1	72	7.8	6.0	4.3	1.0	4.0	4.3
G49	0.99	81.8	71	8.2	7.0	4.1	1.7	4.6	5.2
G47	0.97	77.5	70	8.0	7.5	4.4	2.6	5.1	5.3
G29	0.95	83.0	66	9.0	9.0	3.3	3.8	4.7	5.8
G77	1.26	79.1	64	9.0	9.0	1.3	3.8	6.0	6.3
Stable									
G3	3.13	71.5	81	4.8	4.2	3.1	1.0	2.9	2.8
G5	2.75	75.0	76	3.8	3	2.5	1.7	5.1	3.0
G17	2.79	83.0	82	3.8	3.0	2.4	1.0	2.6	3.0
G25	2.52	78.0	82	5.8	5.0	2.3	1.2	3.3	3.4
G28	2.90	81.7	87	4.3	3.8	6.0	1.7	2.6	2.6
G30	2.45	74.4	75	6.8	4.8	4.6	1.2	4.4	4.0
G36	2.51	78.5	81	4.7	4.5	2.8	1.8	3.2	3.4
G56	2.34	79.5	83	5.5	5.0	3.5	2.2	2.6	3.5
G71	2.66	81.0	97	6.6	4.8	4.8	1.4	2.8	3.5
Grand mean (N = 81)	**2.14**	**86.7**	**78**	**5.0**	**4.6**	**3.1**	**1.8**	**3.7**	**3.4**

[a]Across eight environments, ‡across four environments (Natural infection); Alu12LR-IN–Alupe 2012 long rains inoculated, Alu2012LR-Alupe 2012 long rains natural infection, Alu11SR-Alupe 2011 short rains, Ser12LR-Serere 2012 long rains, Lan12LR-Lanet 2012 long rains

5.4.4.2 Disease progress curves for blast severity under artificial inoculation

There were differential disease progress rates among the genotypes in disease severity for the three blast types. Blast symptoms appeared as early as 24 days after sowing on the susceptible check G77 (KNE 479) compared to 30 days after sowing in resistant genotypes. To facilitate graphic comparisons, the six most resistant and six most susceptible genotypes to finger blast were used. These genotypes also had the same

disease reaction to neck blast (Table 5.4-9). Leaf blast severity was relatively lower for genotypes that were resistant and susceptible to both neck and finger (Table 5.4-9). There was a general decline in disease development progress for leaf blast 51 days after sowing (Figure 5.4-7). Resistant genotype G18 had the slowest leaf blast disease progress rate and minimum severity score of 2.8 (<5% damage). Severity in neck blast (Table 5.4-9) in the six susceptible genotypes was higher than for finger blast (Figure 5.4-8) as all six reached the maximum severity of 5.0 (>6.0 cm size lesions or >70% severity) for neck blast at 101 days after sowing. Slow rate of progress in neck blast severity was recorded in resistant genotypes. By 81 days after sowing finger blast severity in the most susceptible genotypes was >6.0 (>30%) whereas it was <2.5 (about 5%) in the most resistant genotypes. At 101 days after sowing, the six susceptible genotypes had finger blast severity scores >7.0 (>40%) with the two most susceptible genotypes at the maximum severity score of 9.0 (>80%) (Table 5.4-9 and Figure 5.4-9) although the most susceptible genotype G77 leveled off at 91 days after sowing (Figure 5.4-9). In the resistant genotypes, the maximum finger blast severity at 101 days after sowing was <3.5 ($\leq$10%) with the most resistant genotype (G61) attaining the lowest severity with a score of <2.0 (<5%) leveling off at 91 days after sowing (Figure 5.4-9). A sharp increase in finger blast severity in the susceptible genotypes was recorded between 61 and 81 days after sowing with a slowed rate towards maturity. All six susceptible genotypes flowered early (59-64 days). The six resistant genotypes were mostly pigmented whereas the six highly susceptible types (which included susceptible check KNE 479-G77) were mostly tan coloured. Susceptible genotypes G38 and G77 exhibited reasonable levels of tolerance attaining yields >1.00 t ha^{-1} in spite of their high neck and finger blast scores (Table 5.4-9).

Table 5.4-9. Blast scores and grain yield for six resistant and six susceptible genotypes to neck and finger blast at different stages after sowing under artificial inoculation

	Leaf blast (1-9)				Neck blast (1-5)					Finger blast (1-9)						
Days after sowing	30	51	61	71	61	71	81	91	101	61	71	81	91	101	Grain yield (t ha^{-1})	Plant colour[a]
Genotypes																
Resistant																
G61	3.2	3.2	4.7	4.7	1.5	1.9	2.4	2.6	2.6	1.0	1.2	1.2	1.5	1.5	1.67	P
G43	1.9	1.9	3.3	3.4	1.0	1.2	1.8	1.9	1.9	1.0	1.5	1.9	2.1	2.4	2.04	P
G67	2.7	2.7	3.2	3.3	1.0	1.5	1.9	2.4	2.4	1.4	1.5	1.8	2.3	2.5	1.82	P
G18	1.3	1.3	1.9	2.8	1.0	1.0	2.0	2.0	2.0	1.0	1.0	2.2	2.3	2.8	1.29	P
G27	2.5	2.5	3.1	3.6	1.1	1.4	1.9	1.9	2.7	1.0	1.9	2.0	2.0	3.1	2.19	T
G78	2.6	2.6	4.3	4.7	1.0	2.0	2.0	2.4	2.4	1.5	1.8	2.1	2.4	3.2	1.64	P
Susceptible																
G38	2.4	2.4	3.3	4.2	1.1	1.9	2.9	3.8	5.0	1.7	4.1	6.0	6.0	7.8	1.28	T
G54	2.1	2.1	3.4	3.9	1.1	2.6	3.6	3.9	4.9	1.5	3.9	5.5	5.8	7.8	0.98	T
G49	3.2	3.2	3.9	4.6	1.4	2.1	3.6	4.7	5.0	2.3	3.8	5.9	6.4	8.2	0.99	T
G47	2.7	2.7	3.9	6.0	2.1	3.7	4.0	4.7	4.9	2.5	4.8	7.3	7.7	8.0	0.97	T
G29	2.7	2.7	3.8	4.8	2.1	3.2	3.9	4.4	5.0	3.2	5.3	7.0	8.1	9.0	0.95	T
G77	3.1	3.1	5.6	7.0	2.1	3.1	4.6	5.0	5.0	3.3	6.2	7.4	9.1	9.0	1.26	P

Plant colour: P-purple, T-Tan, [a]Data taken from Chapter 2

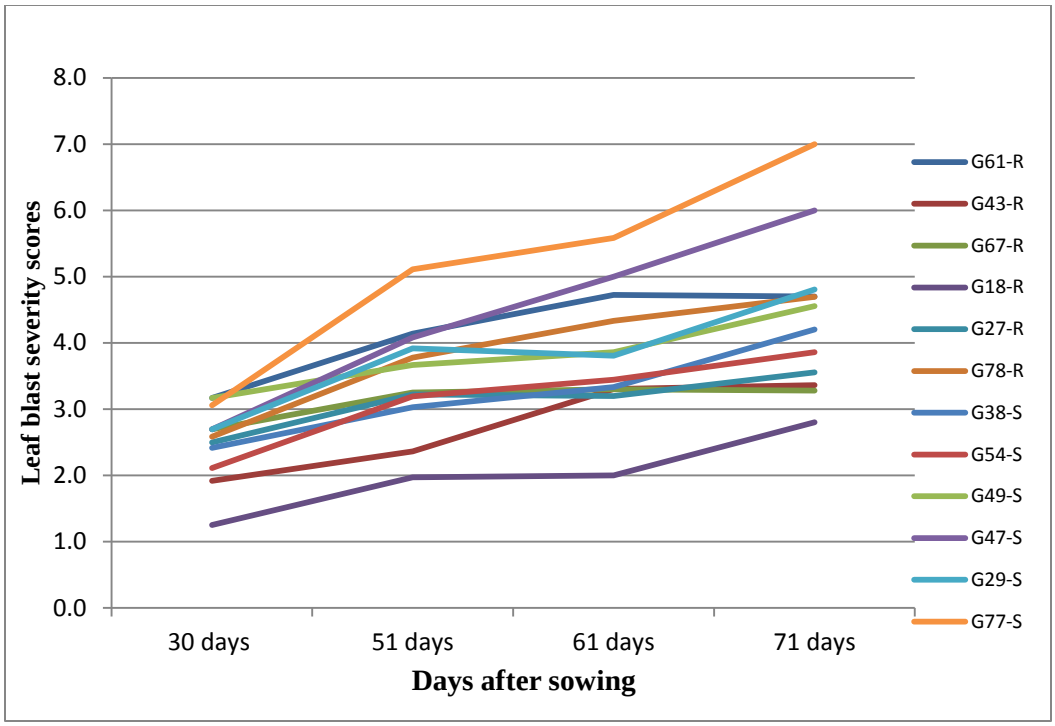

Figure 5.4-7. Leaf blast disease progress (severity scores) of six resistant and six susceptible genotypes to neck and finger blast under artificial inoculation at different intervals after sowing. R-Resistant, S-Susceptible

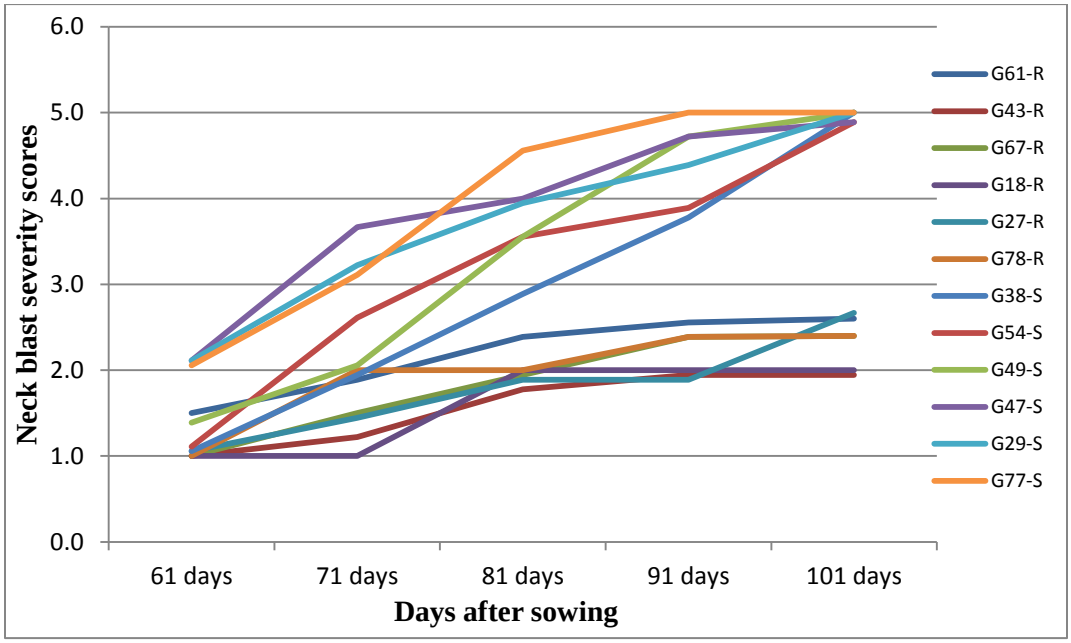

Figure 5.4-8. Neck blast disease progress (severity scores) of six resistant and six susceptible genotypes to neck and finger blast under artificial inoculation at different intervals after sowing R-Resistant, S-Susceptible

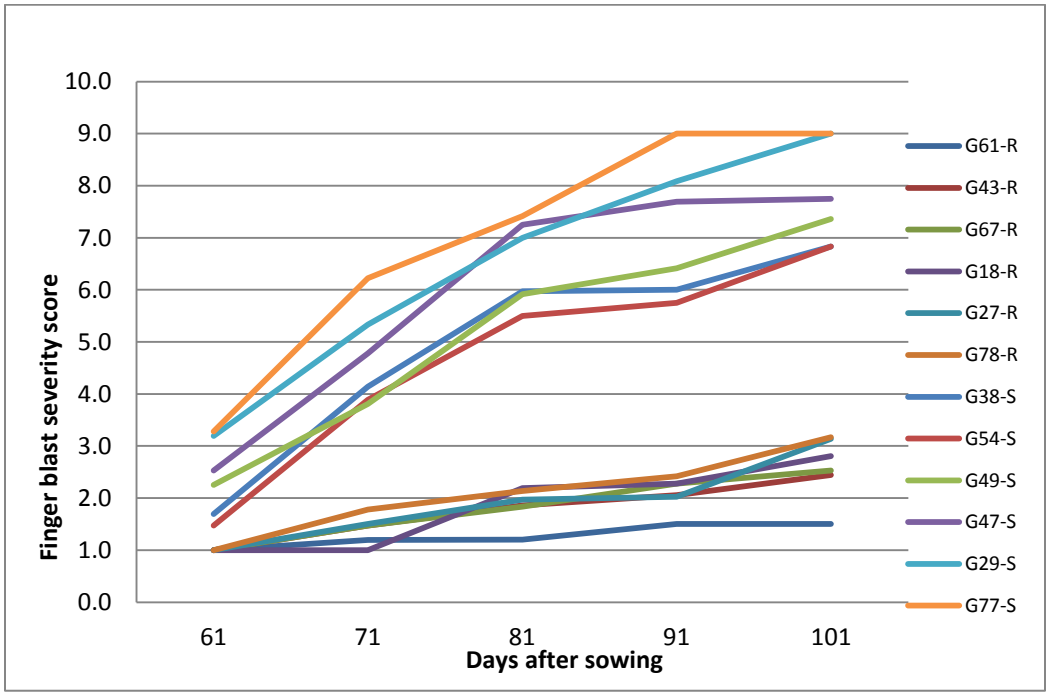

Figure 5.4-9. Finger blast disease progress (severity scores) of six resistant and six susceptible genotypes to neck and finger blast under artificial inoculation at different intervals after sowing. R-Resistant, S-Susceptible

5.4.4.3 Area under disease progress curves for blast severity

Area under disease progress curves (AUDPC) were highly significant ($P \leq 0.01$) for the three blast types under artificial and natural infection. Resistant genotypes had lower AUDPC values for all the three blast types with higher values recorded in susceptible genotypes. However, the AUDPC values for resistant and susceptible genotypes were almost similar for leaf blast. Leaf blast appeared to have larger AUDPC values than neck and finger blast. The lowest AUDPC values were recorded in G18 (leaf blast), G43 (neck blast) and G61 (finger blast) (Table 5.4-10 and 5.4-11). Genotype G77 (susceptible check) had the highest AUDPC for all the three blast types. There were similarities in genotype ranking based on AUDPC susceptibility values and disease severity scores at physiological maturity for neck and finger blast (Tables 5.4-10 and 5.3-11) in both Alu12LR and Alu12LR-IN.

Table 5.4-10. Area under disease progress curve (AUDPC) for final leaf, neck and finger blast severity scores for six resistant and six susceptible genotypes under artificial inoculation (Alu12LR-IN)

Genotype	AUDPC Leaf blast	Leaf blast severity score (1-9)	AUDPC susceptibility value	AUDPC Neck blast	Neck blast severity score (1-5)	AUDPC susceptibility value	AUDPC Finger blast	Finger blast severity score (1-9)	AUDPC susceptibility value
Resistant									
G18	78.5	2.8R	3.0R	66.5	2.0R	1.8R	75.2	2.8R	2.0R
G27	111.8	3.6MR	4.4MR	71.5	2.7MR	2.0R	74.6	3.1MR	2.0R
G43	80.7	3.4MR	3.6MR	65.8	1.9R	1.8R	71.8	2.4R	2.0R
G61	138.4	4.7.8MR	5.2S	92.7	2.6MR	2.6MR	47.9	1.5R	1.0R
G67	128.1	3.3MR	4.6MR	72.0	2.4MR	2.0R	71.1	2.5R	2.0R
G78	143.4	4.7MR	5.5S	76.6	2.4MR	2.1MR	85.0	3.2MR	2.0R
Susceptible									
G29	143.7	4.8MR	5.5S	172.5	5.0HS	5.0HS	278.5	9.0HS	8.0HS
G38	128.9	4.2MR	5.0MR	122.4	4.9HS	5.0S	214.8	6.8S	6.0S
G47	144.1	6.0S	6.2S	179.8	5.0HS	4.9HS	265.9	7.8HS	8.0HS
G49	142.6	4.6MR	5.6S	147.9	4.9HS	5.0HS	221.1	7.4HS	6.0S
G54	123.0	3.9MR	4.9MR	133.5	5.0HS	4.9S	208.2	6.8S	6.0S
G77	173.5	7.0S	7.0S	181.2	5.0HS	5.0HS	311.7	9.0HS	9.0HS
Mean (N = 81)	260.5	4.0	4.1	93.3	3.1	2.6	128.9	5.0	4.5
CV (%)	10.7	18.3	-	11.8	18.3	-	12.8	19.40	-
$LSD_{0.05}$	26.3	1.36	-	23.2	1.36	-	35.2	2.10	-

R = Resistant, MR = Moderately resistant, S = Susceptible, HS = Highly susceptible. Final scores used for Leaf blast –milk stage, Neck and finger blast-physiological maturity

Table 5.4-11. Area under disease progress curve (AUDPC) for final leaf, neck and finger blast severity scores for six resistant and six susceptible genotypes under natural infection (Alu12LR)

Genotype	AUDPC Leaf blast	Leaf blast severity score (1-9)	AUDPC susceptibility value	AUDPC Neck blast	Neck blast severity score (1-5)	AUDPC susceptibility value	AUDPC Finger blast	Finger blast severity score (1-9)	AUDPC susceptibility value
Resistant									
18	70.0	2.0R	2.6R	57.4	2.0R	1.6R	58.8	2.8R	1.9R
27	86.2	2.8R	3.2MR	50.2	2.0R	1.4R	66.1	2.3R	2.2R
43	77.5	2.6R	2.9R	65.8	1.5R	1.9R	78.1	2.2R	2.6R
61	131.2	3.9MR	4.9MR	63.1	2.0R	1.8R	66.4	1.4R	2.2R
67	115.0	2.5R	4.3MR	46.3	2.0R	1.3R	61.8	2.0R	2.0R
78	106.2	3.9MR	4.0MR	66.8	2.0R	1.9R	75.8	2.2R	2.5R
Susceptible									
29	137.5	4.0MR	5.2S	162.3	4.5HS	4.6HS	279.7	9.0HS	9.0HS
38	115.0	3.4MR	4.3MR	153.1	4.5HS	4.3HS	238.9	6.0S	7.9HS
47	133.7	5.2S	5.0MR	170.3	4.5HS	4.8HS	246.3	7.5HS	8.2HS
49	128.8	3.8MR	4.8MR	151.2	4.5HS	4.3HS	250.3	7.0HS	8.3HS
54	112.5	3.1MR	4.2MR	152.3	4.5HS	4.3HS	265.8	6.0S	8.8HS
77	164.9	6.2S	6.2S	159.5	4.5HS	4.5HS	271.5	9.0HS	9.0HS
Mean (N = 81)	101.8	3.5	3.8	94.8	2.5	2.6	130.8	4.6	4.3
CV (%)	10.5	16.1	-	15.4	20.5	-	13.3	19.4	-
$LSD_{0.05}$	21.3	1.6	-	28.9	1.4	-	34.9	2.1	-

R = Resistant, MR = Moderately resistant, S = Susceptible, HS = Highly susceptible; Final scores used for leaf blast –milk stage, neck and finger blast-physiological maturity

5.4.5 Correlations

Based on Spearman's rank correlation, leaf, neck and finger blast had significant ($P \leq 0.05$) negative correlation with grain yield (r = -0.233, -0.481, and -0.486, respectively), with days to flowering (r = -0.431, -0.381, -0.440, respectively) and with panicle shape (r = -0.201, -0.192, -0.189, respectively) (Table 5.4-12). Though not significant, plant colour was also negatively correlated with neck (r = -0.012) and finger (r = -0.134) blast. High significant ($P \leq 0.01$) positive correlations between leaf and neck (r = 0.436), leaf and finger (r = 0.458), neck and finger (r = 0.754) blast were recorded.

Table 5.4-12. Spearman's rank correlations between final blast scores, grain yield, days to flowering, plant colour and panicle shape based on artificial inoculation data

Finger blast	-						
Grain colour[a]	0.083	-					
Grain yield	-0.486**	-0.035	-				
Leaf blast	0.458**	0.149	-0.233**	-			
Neck blast	0.754**	0.100	-0.481**	0.436**	-		
Panicle shape[a]	-0.189*	-0.182*	0.146	-0.201*	-0.192*	-	
Days to flowering	-0.440**	-0.159*	0.230**	-0.431**	-0.381**	-0.008	-
Plant colour[a]	-0.134	0.341**	-0.005	0.142	-0.026	-0.050	-0.059
	Finger blast	**Grain colour**	**Grain yield**	**Leaf blast**	**Neck blast**	**Panicle shape**	**Days flowering**

[a]-Data taken from Chapter 2.

5.5 Discussion

5.5.1 General performance and ranking of genotypes

Based on the AMMI analysis, the GxE interaction had the greatest effect accounting for 47.3% and 62.0% of the total and treatment sum of squares, respectively for grain yield. This contributed to the differential genotype responses across environments but there was a lower variability among the genotypes (9.1 and 12.0% contribution to total and treatment sum of squares, respectively). For finger blast, the greatest contribution to both total and treatment sum of squares was from environments (40.3 and 46.8%, respectively). Genotypes therefore had high differences in responses for finger blast across environments. The highly significant ($P \leq 0.01$) differences among the genotypes at each environment and across environments is an indication of genetic variability in blast reaction, grain yield, maturity duration and plant height which can be utilized for genetic improvement through hybridization. The higher grain yields realized at the lower altitude moisture stressed environments of Kib11SR, Kib12LR and Miw12LR was attributed to the supplementary irrigation applied. High elevation, low temperature environments (Lan12LR and Uyol12) had delayed flowering and short plants. Temperature is one of the major environmental factors that influence adaptation of crops through their effects on days to flowering and plant height (McPherson et al., 1985). High temperatures in plants have been found to slow height growth, rate of leaf formation and delay flowering (Sonsteby and Heide, 2009). The sensitivity of finger millet to low temperature has been reported by Bandyopadhyay (2009) and Opole (2012). The AMMI ranking of the best four genotypes at each environment varied. The change in rank order of genotypes across environments is an indication of cross-over interactions and possible existence of distinct groups within the environments. The higher yields realized at Lan12LR and Uyol12 in spite of the low temperatures could be linked to high precipitation, the high number of productive tillers per plant and a

longer reproductive phase. The low yields in the sub-humid environment Alu12LR could be attributed to high rainfall hence high humidity leading to high blast disease severity which resulted in grain yield loss. Loss in yield due to blast is a result of a reduction in canopy photosynthesis due to the effects of the lesions on leaf photosynthetic rate caused by leaf blast (Bastiaans and Kropff, 1993) and reduction or inhibition of nutrient flow to the panicle and poor grain filling due to neck and finger blast (Takan et al., 2004; Pande, 1992). Genotypes G74, G32, G28, and G3 performed well across the environments in G x E analysis ranking but individual environments differed in the best top yielders.

5.5.2 Correlation between environments

The significant positive rank correlations between Lan12LR and Uyol2 and between Alu12LR and Ser12LR implies that either of the two environments in each pair could be used for genotype selection as they had similar discriminating power. The environments Lan12LR and Uyol12 are in the cool, high elevation region and had seven common genotypes among the top 25 while Al12LR and Ser12LR are in the sub-humid mid-altitude Lake Victoria zone with similar mean annual rainfall and had nine common genotypes among the top 25. The Lan12LR and Alu11SR environments differ in annual rainfall and mean minimum temperatures with Lan12LR having higher rainfall and lower minimum temperatures than Al1211SR hence the negative correlation between them.

5.5.3 GGE

5.5.3.1 Discriminatory power and representativeness of test environments

The most discriminating environment will give the most information about the genotypes and it is characterized by long vectors from the biplot origin (Yan and Tinker, 2006). For grain yield, Lan12LR followed by Miw12LR and Ser12LR were the most informative environments whereas Alu12LR and Alu11SR were the least informative. Based on polygon biplot, there were three mega-environment groups with the cool high elevation environments Lan12LR and Uyol12 in one mega-environment; Alu11SR, Alu12LR (sub-humid, mid-altitude), Kib11SR, Kib12LR and Miw12LR (dry lowlands) in another group; and Ser12LR (sub humid mid-altitude) on its own. However, the grouping of Kib12SR, Kib12LR and MIW12LR with the two Alupe environments is probably as a consequence of the supplementary irrigation applied to the former environments. Although Ser12LR formed its own mega-environment, its significant positive correlation with Alu12LR was more realistic as these two environments fall within the same sub-humid zone with similar mean temperatures and rainfall. Yan (2001) has defined a representative environment as having the smallest angle with the AEC axis. In this case, Ser12LR was the

most representative test environment in terms of average interaction effects with the genotypes in terms of PC1 and PC2 and relative to environments and genotypes evaluated whereas Lan12LR and Alu12SR were the least representative for grain yield. Ser12LR was also highly discriminating for grain yield and hence useful for carrying out selection for both general and specific adaptation to sub-humid environments. However, although Lan12LR would be ideal for low temperature genotype discrimination, it should be utilized separately from Uyol12 when selecting for specific and general adaptation considering the differences in latitude (5°) between the two environments. Hopkins (1938) alluded to the fact that phenological development of plants can differ by four days for every degree of latitude. Alu12LR could be the best environment for finger blast selection as the location was the best discriminator of the genotypes for blast reaction. Blast thrives best under high humidity and temperatures, conditions that occur at Alupe especially during the long rains season and use of the location as a blast hot spot is only effective during that time as the short rains season receives less rainfall hence low humidity. The poor discrimination for blast under Ser12LR, an environment similar to Alu12LR and where most of the blast resistant releases in the region were selected, could simply be due to inefficiency in scoring and/or poor disease pressure during that season as rainfall (hence humidity) was relatively lower than the normal seasonal mean.

5.5.3.2 Genotype ranking based on mean yield and stability indices

The winning (vertex) genotype and best genotypes in each mega-environment were identified by the polygon and polygon rays of the GGE biplots. The vertex genotypes were: G1 in the mega-environment grouping of Alu11SR Alu12LR, Kib11SR, Kib12LR and Miw12LR environments, genotype G74 in Ser12LR and genotype G37 in Lan12LR and Uyol12. Although they 'won', they were also the most unstable but with high grain yield compared to the unstable and poorest yielding genotypes G15 and G70. The highest yielding genotypes in each of the three mega-environment were G74, G32, G71 and G28 in Ser12LR; G1, G21, G20, and G23 in Alu11SR, Alu12LR, Kib11SR, Kib12LR and Miw12LR; and G37, G35, G71 and G75 in Lan12LR and Uyol12. The blast susceptible G77 had better performance in Alu11SR when blast pressure was low due to low and erratic rainfall hence low humidity. Selection of suitable genotypes is based on both yield *per se* and stability. Yan and Kang (2003) described an ideal genotype as one having the highest mean and stability represented by the longest vector from origin and short AEC ordinate and zero GEI in a GGE biplot. High stability and above average mean grain yields were recorded in genotypes G3, G5, G17, G25, G28, G36, and G71. These genotypes were early to medium in flowering, had average height and moderate resistance to blast. However genotypes G25, G30,

and G71 may be best utilized in environments with low incidence of blast as they were susceptible to all three blast types.

5.5.4 Blast screening

5.5.4.1 Genotype reaction type, area under disease progress curves (AUDPC) and disease severity

Although significant variability in reaction to the three blast types was recorded among the genotypes, over 50% presented resistance to leaf blast, neck and finger blast under artificial inoculation. This high percentage of resistance could have been a result of the preliminary selection against blast during the evaluation of the initial germplasm set (Chapter 2 of this thesis) from which the 81 genotypes were selected. There was similarity between AUDPC susceptibility values and disease severity scores in ranking of genotypes for reaction to blast. The relatively slow disease progress in leaf blast after 51 days could be due to changes in the physiological status of the plant hence the expression of mature resistance as reported by Li et al. (2007) in rice. Resistant genotypes were slow blasting and had low AUDPC susceptibility values and disease severity rating for the three blast types and vice-versa for susceptible genotypes. This may indicate the cross infectivity and similarity in pathotypes causing the three blast types as reported by Pande et al. (1995) and Takan et al. (2004) in finger millet and Meena (2005) in rice. This also suggests similar gene responses/expression for the three blast types. But this contrasts with findings of Wu et al. (2005) in rice who reported differential gene responses for blast at seedling and reproductive stages. Slow blasting in leaf diseases has been associated with horizontal resistance (polygenic control) (Van der Plank, 1963). If this is true then the slow blasting genotypes identified in this study stand to have long term resistance and may withstand the high blast pathogen variability reported by Takan et al. (2012). Genotype G78 (KNE 814-resistant check) presented as resistant and slow blasting in this study similar to the reaction reported by Pande (1992). This genotype is currently undergoing on-farm testing in East Africa with promising preliminary results and it will also be valuable in blast resistance breeding. Genotypes with low and moderate blast scores recorded the highest grain yield whereas most susceptible genotypes had low grain yield and flowered early. No genotype was completely immune to any of the three blast types in this germplasm set. Blast resistant genotypes had diversity in grain yield, days to flowering, plant height and grain colour which will provide farmers with options to select for their target agro-ecologies and end use. Most farmers' early lines are blast susceptible (Personal observation) hence the relatively early and medium maturity and blast resistant genotypes G39, G43, G27, G16, and G60 identified in this study should result in increased finger millet productivity. Genotypes G18, G43 and

G67 with high resistances to the three blast types and genotypes G27, G78, G76 and G81 with resistance to both neck and finger blast were also identified. The resistant genotypes will be useful parents in breeding new lines with blast resistance and high grain yield. Blast pathogen races have been reported to differ between seasons in rice (Nelson, 1973) and between agro-ecologies in finger millet (Sreenivasaprasad, 2005). It is therefore essential that these genotypes are adequately screened for blast across seasons and agro-ecologies to ascertain stability of their resistance especially in humid and sub-humid finger millet production agro-ecologies where blast is prevalent. The relatively stable resistance across environments recorded in some genotypes enhances the possibility of using a representative location for blast screening which saves on cost and time. This is corroborated by the fact that the few blast resistant cultivars released in East Africa were all screened and identified at Serere and are stable across the sub-humid environments. Due to reported pathogen variability and appearance of pathotypes initially confined to Asia in East Africa (Takan et al., 2012), there is a need for regular monitoring of the pathogen populations. This will enable the breeders and pathologists to determine if new pathotypes have been introduced into the region and also if frequencies of certain pathotypes change over time and then design appropriate breeding approaches.

5.5.4.2 Correlations

Significant ($P \leq 0.05$) correlations were recorded between scores for the three blast types thus genotypes with high leaf blast also had high neck and finger blast. Results of this study agree with those reported by Ou and Nuque (1963) who found positive correlations between leaf blast and neck and finger blast. However, Somasekhara et al. (1991) and Kiran Babu et al. (2013) found weak correlation between leaf and both neck and finger blasts whereas Oduori (2008) found no correlation between leaf and neck blast suggesting differential gene expression. The different findings could be attributed to variation in weather conditions during the cropping season that could influence disease expression as reported by Esele (2002). It was also noted that some resistant genotypes that were resistant to neck and finger blast and were agronomically superior had high leaf blast AUDPC values. Bonman et al. (1989) also reported a few cases in rice where cultivars susceptible to leaf blast exhibited resistance to neck blast and attributed this to non-linkage of leaf and neck blast resistance in the cultivars involved. Therefore, using leaf blast to select for neck and finger blast resistance should be done with caution. Since the scores for the three blast types were highly correlated in most of the genotypes in this study, the high AUDPC and blast severity scores at physiological maturity when blast severity is at maximum indicates the possibility of a single selection at this growth stage for all the three blast types in finger millet.

Resistance to blast has been linked to phenolic compounds found in pigmented plants (Seetharam and Ravikumar, 1993; Jain and Yadav, 2003) and to semi-compact/compact panicle shape (Pande et al., 1995); Takan et al., 2004) which corroborates the predominance of pigmented plant types with semi-compact and compact panicles among the resistant genotypes detected in this study. Since the most vulnerable stages for neck and finger blast in finger millet is at the pre-flowering stage, high inoculum levels early in the season could be the cause of high susceptibility in early flowering genotypes as reported by Kiran Babu et al. (2013) and Esele (2002). The negative correlation between the three blast types with grain yield was due to reduced photosynthetic area on affected leaves, poor or no nutrient flow to the panicle when necks are affected and poor grain filling and sterility due both neck and finger infection. All these elements led to reduced grain yield. Similar observations were also reported by Rath and Mishra (1975) and Takan et al. (2004).

5.6 Conclusion

The high elevation low temperature finger millet production environments were distinctly separated from the warmer mid-altitudes and lowlands environments. Lan12LR was identified as an ideal environment to discriminate low temperature adapted genotypes, Ser12LR for sub-humid environments and Miw12LR for the dry lowlands for grain yield while Alu12LR was ideal for blast selection. Adaptation testing for the low temperature environments Lan12LR and Uyol12 may be handled separately considering large differences in latitude between them. Genotypes G3, G5, G17, G25, G28, G36 and G71 were identified to be stable across the eight environments based on grain yield. Genotypes G1, G18, G19, G37, G54, G61, G74, G75 and G77 were identified for specific adaptation. Disease severity scores were highly negatively correlated with days to flowering and grain yield suggesting that early lines suffer more disease damage leading to reduced yield. The slow blasting resistance recorded in the identified genotypes in this study may provide more durable resistance given the high variability associated with the blast pathogen. Qualitative traits like plant colour and panicle shape that were found associated with blast resistance could be useful as selectable markers in early breeding generations. Genotypes G43, G39 (resistant), G33, G20, G66, G23, G81, G7, G31, G74, G11, G36 and G3 (moderately resistant) with yields above 2.00 t ha^{-1} will be further evaluated for direct commercialization whereas genotypes G61, G67, G70, G18, G16, G60, G27 and G78 have potential for use as sources of resistance to blast.

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Chapter 6

Gene action of blast disease reaction and grain yield traits in finger millet

Abstract

Gene action of blast reaction, yield and yield associated traits in finger millet were studied using a 4x4 North Carolina Design II mating scheme. The four female and four male parents and their 16 crosses were evaluated at Alupe and Kakamega in western Kenya in a randomized complete block design under artificially induced high disease pressure. A separate control experiment with the same genotypes exposed to natural disease pressure was conducted at each site. Data were recorded on leaf, neck and finger blast, grain yield and its associated traits. General combining ability (GCA) and specific combining ability (SCA) estimates of the various traits were calculated to determine the breeding values of the genotypes. The GCA and SCA variances were significant for all traits (except for finger width and grains per spikelet) at each location and across them. The GCA variance predominated over SCA variance for all traits except finger width. Therefore, other than finger width, the traits can be improved relatively fast through selection due to the prevalence of additive gene effects. With high, desirable GCA effects, male parent KNE 392 and female parents KNE 744 and IE 11 are suitable parents for blast resistance breeding while male parent Okhale 1 is suitable for grain yield improvement. Transgressive segregation was evident in many of the crosses for the three blast types and in particular, crosses IE 3104 x KNE 796, KAT FM 1 x Okhale 1, IE 11 x Okhale, IE 11 x P 224 and KNE 744 x KNE 392 which indicates the possibility of generating lines with blast resistance. The frequency distribution for the segregating F_2 generation for the three blast types differed between crosses. The differences in segregation patterns detected between crosses could be due to the differences in gene numbers or gene combinations being expressed in the different parents used which would call for convergent crossing or gene pyramiding for durable resistance.

Key words: **Combining ability, effective genetic factors, blast resistance, finger millet, NCD II**

6.1 Introduction

Finger millet production in East Africa is largely for subsistence with grain yields as low as 0.60 t ha^{-1} in Tanzania to as high as 1.80 t ha^{-1} in Uganda. The low productivity of the crop has been linked to the use of low yielding blast susceptible cultivars and the labour intensiveness of its production (Oduori and Kanyenji 2007; Wanyera, 2007; Kisandu et al., 2007). Finger millet blast caused by the fungus *Magnaporthe grisea* (anamorph *Pyricularia oryzae*) is the major biotic constraint in finger millet productivity in East Africa (Wanyera, 2007; Oduori and Kanyenji, 2007; Kisandu et al., 2007). Most cultivated landraces are susceptible to the disease with grain yield losses of up to 60% having been reported (Pande et al., 1995; Obilana and Manyasa, 2002). Blast affects finger millet at all stages of growth from seedling to grain formation. Panicle blast (neck and finger) is the most destructive phase of the disease and causes failure of seed to set or leads to formation of shriveled seeds (Pande et al., 1995). Takan et al. (2004) reported the same pathotype to cause the three blast types. Chemical control of blast, though only effective to a reasonable level, is an expensive option for the resource poor farmers and so the use of resistant cultivars is the most viable and cost effective alternative. Screening of germplasm at Serere (Uganda), Kakamega (Kenya) and Uyole (Tanzania) has identified several accessions with significant blast tolerance and good agronomic and grain quality traits (Wanyera, 2007; Oduori and Kanyenji, 2007; Kisandu et al., 2007). Thelargely unexploited genetic potential of the region's finger millet germplasm must be intensively characterized and utilized for increased crop productivity. Improvement through hybridization has been limited by difficulties in crossing owing to the floral morphology of the crop (Rachie and Peters 1977). In the recent past, however, efforts have been directed towards developing and perfecting emasculation techniques to enable hybridization and successes have been reported from covering the inflorescence with a plastic bag to the use of the gametocide, ethrel (Oduori, 2008; Wanyera, 2010).

For an effective breeding strategy, knowledge of the nature of gene action determining inheritance of target traits is necessary (Krishnappa et al., 2009). Information on mode of inheritance of blast and agronomic traits in East African germplasm is very limited and the only reported attempt is that by Oduori (2008). Determination of parents with good combining ability has been effectively used in various breeding programmes especially in order to introduce target traits into high yielding backgrounds (Sumathi et al., 2005). Combining ability is divided into general combining ability (GCA) which estimates additive genetic variance and specific combining ability (SCA) which estimates non-additive (dominance and epistasis) genetic variance (Sprague and Tatum, 1942; Sumathi et al., 2005; Selvaraj et al., 2011). This helps determine whether trait improvement can be achieved through recurrent selection or

convergent crossing (if GCA effects are predominant) or in hybrid breeding to exploit heterosis (especially for open pollinated crops if SCA effects are predominant) (Makanda, 2010). The general prediction ratio (GPR) which is the relative importance of GCA and SCA variances is useful in determining the value of additive gene effects in trait inheritance (Baker, 1978). The closer the GPR value to unity the greater the predictability of additive gene effects based on GCA alone.

Combining ability studies in finger millet have been reported by Seetharam and Ravikumar (1993), Sumathi et al. (2005), Krishnappa et al. (2009), Shailaja et al. (2010), Nirmalakumari et al. (2010), Parashuram et al. (2011) and Priyadharashini et al. (2011). All these researchers found both additive and non-additive gene effects to be important in the inheritance of most finger millet traits. Using the relationship of the difference in the means of two parents to the variance of their F_2 populations, Wright (1968) developed a formula to estimate the minimum number of genes controlling a trait and is the most used for this purpose due to its simplicity (Zeng et al., 1990). There is no published information on estimates of number of genes controlling inheritance of blast in finger millet. However, in rice Leung et al. (2003) and Padmavathi et al. (2005) have reported on more than 30 genes controlling blast inheritance. The objectives of this study were to generate information on the combining ability and trait inheritance of eight finger millet parental lines and their progenies to determine their suitability for use as parents in finger millet improvement or for selection.

6.2 Materials and methods

6.2.1 Experimental material

The basic characteristics of the four blast resistant lines used as males: Okhale 1, KNE 796, KNE 392 and P 224; and the four blast susceptible lines used as females: KAT FM 1, IE 3104, KNE 744 and IE 11 were determined in previous ICRISAT blast screening trials except for Okhale 1 which was sourced from Kenya Agricultural Research Institute, Kakamega (Table 6.2-1).

Table 6.2-1: Characteristics of eight finger millet genotypes used in the NCD II mating scheme in this study

Parent	Parent category	Plant colour	Panicle shape	Blast reaction	Yield potential
KAT FM 1	Female	Tan	Open	Susceptible	High
IE 3104	Female	Purple	Semi-compact	Very susceptible	Medium
KNE 744	Female	Tan	compact	moderately susceptible	High
IE 11	Female	Tan	Open	Susceptible	Medium
Okhale 1	Male	Purple	Open (in-fold tips)	Resistant	High
KNE 796	Male	Purple	Open	Resistant	High
KNE 392	Male	Tan	Open	Resistant	High
P 224	Male	Tan	Semi-compact	Resistant	High

The female and male lines were crossed in a 4 x 4 North Carolina Design II (NCD II) mating scheme (Comstock and Robinson, 1952) conducted at KARI/ICRISAT Kiboko station during the 2011 short rainy season generating 16 crosses. Florets were emasculated before flowering by covering each panicle with a transparent plastic bag (75 microns, 76 mm x 127 mm) and tying the bottom of the bag closed around a cotton wool plug (Wanyera, 2010). The high humidity created inside the plastic bag retards dehiscence of the anthers (House, 1985). After three to four days the bag was removed, the undehisced anthers shaken off and pollen from the male parent, either collected in quarter size brown paper bags or applied directly from excised panicles, was dusted onto the emasculated panicle. The pollinated panicles were immediately covered with standard pollination bags which were removed after seed set. The first filial generation (F_1) seed was planted at Kiboko and true hybrids were identified through comparison with the maternal parent based on plant colour, plant height, panicle shape and days to flowering (Oduori, 2008). Bulked F_1 seed of each cross was used to plant the F_2 families. A total of 16 F_2 families were obtained.

6.2.2 Evaluation trial locations

The evaluation trials were planted at Alupe and Kakamega in western Kenya in the sub-humid Lake Victoria zone during the 2012 short rains season. Alupe is 1189 meters above sea level (masl), 0°28'N and 34°7'E with mean annual rainfall of 1100 mm and mean temperature of 24.0°C (mean minimum 17.7°C, mean maximum 30.3°C). Kakamega is 1535 masl, 00°20'N and 34°46'E, with mean annual rainfall of 1921 mm, and mean temperature of 20.5°C (mean minimum 10.3°C, mean maximum 30.8°C).

6.2.3 Experimental design and crop management

The 16 F_2 families and their parents including three checks (KNE 479-susceptible to blast, U 15-released resistant and Ikhulule – local landrace) were evaluated. Separate inoculated and non-inoculated field trials were planted at each of the two locations. Blast reaction levels in the inoculated trial were compared to those in the control or non-inoculated trial at each location to ascertain the effectiveness of artificial inoculation in enhancing disease pressure. The trials at both locations were planted in a Randomized Complete Block Design (RCBD) in three replications with two rows per plot each 3 m in length with 0.4 m between rows. Seeds were drilled in furrows 2.5-3 cm deep and plants were thinned two weeks after emergence to one plant per hill after every 0.1 m maintaining 30 plants per row. Double Ammonium Phosphate (DAP-18:46:0) fertilizer at the rate of 20 kg N ha^{-1} and $\underline{\sim}$ 20 kg P_2O_5 ha^{-1} was applied at planting time. Trials were top dressed with Urea (46% N) three weeks after sowing at the rate of 20 kg N ha^{-1}; however, in the inoculated trial an extra 10 kg N ha^{-1} was applied to boost blast infection as suggested by Kurschner et al. (1992). The plots were manually kept weed free.

6.2.4 Enhancing epiphytotic conditions

To infect plants with blast a broad-based inoculation technique incorporating crop debris, infector rows, artificial inoculation and supplemental irrigation (Pande et al., 1995; Kiran Babu et al., 2013) was implemented. A single infector row (using susceptible line GBK-011118A) was planted after every four test rows and also a two row border around the trial. Infected finger millet debris collected during the previous season was spread in-between test rows on moist soil (15-20 days after sowing). To create the required high humidity, irrigation was applied at least once a day (at 11h00-12h00) on rain free days up to grain filling stage. Due to logistical problems irrigation could not be applied twice a day as recommended on rain free days. Inoculum was prepared from a single-spore representative culture of *M. grisea* (Figure 6.2-1) isolated from blast infected samples collected from the finger millet fields in the previous season at Alupe and cultured on oat meal agar (OMA) medium at 26±1ºC for ten days (Kiran Babu et al., 2013). Spores were harvested by flooding the plates with sterilized distilled water and scraping the culture off the surface of the agar with a spatula. The spore suspension was adjusted to 1×10^5 spores/ml with the aid of a hemocytometer before inoculating the plants in the field at Alupe and Kakamega. Foliage of twenty day old seedlings and plants at pre-flowering were spray inoculated using a Knapsack sprayer during the early evening hours.

Figure 6.2-1. An eight day old culture of *Magnaporthe grisea*, the pathogen that causes blast in finger millet

6.2.5 Disease severity scoring

Leaf blast severity was scored at ten days after inoculation using a 1-9 scale (Pande et al., 1995; Kiran Babu et al., 2013), where: 1 = no lesions to small brown specks of pinhead size (0.1-1.0 mm), less than 1% leaf area affected; 2 = typical blast lesions covering 1-5% leaf area; 3 = 6-10%; 4 = 11-20%; 5 = 21-30%; 6 = 31-40%; 7 = 41-50%; 8 = 51-75% and many leaves dead; and 9 = >75% leaf area covered or all leaves dead (Pande et al., 1995). The 1-9 scale was divided into four general groups or categories of reaction: resistant (1.0-3.0); moderately resistant (3.1-5.0); susceptible (5.1-7.0); and highly susceptible (7.1-9.0). Neck blast severity was scored at physiological maturity based on the relative lesion size on the neck using a 1-5 scale developed for finger millet by ICRISAT (Kiran Babu et al., 2013) where: 1 = no lesions to pin head size of lesions on the neck region; 2 = 0.1-2.0 cm size of typical blast lesion, 3 = 2.1-4.0 cm, 4 = 4.1-6.0 cm, and 5 = >6.0 cm size of typical blast lesion. The 1-5 scale was divided into four general categories of reaction: resistant (1.0-2.0); moderately resistant (2.1-3.0); susceptible (3.1-4.0); and highly susceptible (4.1-5.0). Finger blast severity was scored at physiological maturity using a 1-9 scale (Pande et al., 1995), where: 1 = no disease on all panicles; 2 = 1 – 5% severity on infected panicles; 3 = 6-10% severity; 4 = 11-20% severity; 5 = 21-30% severity; 6 = 31-40% severity; 7 = 41-60% severity; 8 = 61-80% severity; and 9 = 81-100% severity. The 1-9 scale was divided into four categories of reaction as for leaf blast. Data were also recorded for other traits (Table 6.2-2) that are used as descriptors for finger millet (IBPGR[4], 1985). Data were recorded from 30 plants per plot (total of 90 plants across three

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replications) for each cross whereas data were recorded from five plants per plot (total of 15 plants across three replications) for each parent except for days to flowering, grain yield ha^{-1} and 1000 grain mass which were taken on whole plot basis.

Table 6.2-2. Description and measurement for traits

Trait	Description/measurement
Days to 50% flowering	Days from sowing to when 50% of plants in the plot were in flower
Days to maturity	Days from sowing to when 50% of main tillers had mature panicles
Plant height (cm)	From ground level to tip of panicle at dough stage
No. of productive tillers	Basal tillers with mature panicles at maturity
No. of fingers	On main panicle at dough stage
Finger length (cm)	From base to tip of longest finger at dough stage
Finger width (cm)	Distance across centre of longest finger at dough stage
No. of grains per spikelet	At maturity
Grain yield per plant (g)	Dry grain mass of single plant plus tillers (mean of 15plants)
Grain yield (t ha^{-1})	Dry grain mass per plot at 12.5% moisture content converted to tonnes per hectare
1000-grain mass (g)	Mass of 1000 grains at 12.5% moisture content

Source: IBPGR (1985)

6.3 Data analysis

6.3.1 ANOVA

All analyses were done using PROC GLM procedures (SAS, 2008) for individual location first then across the two locations. Since variance among the environments were found to be heterogeneous using the Bartlett test (Bartlett, 1937), the G x E data were transformed by subtracting the environment mean and dividing by standard errors of the corresponding environment. The following model was used in across locations analysis (SAS, 2008):

$$Y_{ijr} = \mu + G_i + E_j + (GE)_{ij} + R_j + e_{ijr}$$

Y_{ijr} is the observation of any variable in the r^{th} replication in the j^{th} location of the i^{th} genotypes; μ is the general mean; G_i and E_j are effects of i^{th} genotype and j^{th} location; $(GE)_{ij}$ are genotype location interactions, R_j is the replication effect at j^{th} location; e_{ijr} are random errors associated with r^{th} replication of the i^{th} genotypes at the j^{th} location. Locations were considered as random effects and entries/treatments as fixed effects. Entry main effect and their interactions were partitioned into various components: parent, crosses, parent x crosses, females x males, location x entry, location x parents, location x females,

location x males and location x females x males. Analysis of variance for combining ability was done using mean values of the two locations following procedure by Kempthorne (1957). Crosses sum of squares were partitioned into variation due to females and males.

6.3.2 Combining ability

General combining ability (GCA) effects were determined as:

$$GCA_f = \bar{x}_f - \mu, \text{ and } GCA_m = \bar{x}_m - \mu$$

where: GCA_f and GCA_m = General combining ability estimates of female and male parents, respectively

$\bar{x}_m$ and $\bar{x}_{mf}$ = Mean of male and female parents, respectively $\bar{x}_f$

μ = Overall mean of crosses in the trial

Specific combining ability (SCA) effects were determined as:

$$SCA_{fm} = \bar{x} - E(\bar{x}) = \bar{x} - [GCA_f + GCA_m + \mu]$$

where: SCA_{fm} = specific combining ability of the cross between female, f and male, m

$\bar{x}$ = Observed mean value of the cross

$E(\bar{x})$ = Expected mean value of a cross based on the two GCAs of its parents

Random error terms were used to generate the F-tests for each of the mean squares (GCA and SCA) generated in the analysis. These were done automatically in SAS (2008).

6.3.3 General predicted ratio (GPR)

The general predicted ratio which gives the relative importance of GCA and SCA was estimated using the formula by Baker (1978):

$$GPR = 2\sigma^2_{GCA} / (2\sigma^2_{GCA} + \sigma^2_{SCA})$$

where: GCA MS and SCA MS are mean squares for GCA and SCA, respectively.

6.3.4 Minimum number of genes (effective factors) controlling blast resistance

The minimum number of genes controlling resistance to leaf and neck blast were estimated according to Wright's (1968) formula:

$$N = (x_1\text{-}x_2)^2/8 * (\sigma^2F_2\text{-}\sigma^2_e)$$

where:
N = number of genes
x_1 = mean resistance of parent1
x_2 = mean resistance of parent2
$\sigma^2F_2\text{-}\sigma^2_e = \sigma^2_g$
σ^2F_2 = variance of F_2 generation
σ^2_e = environmental variance within each respective F_2 family

The following assumptions are made:
- all genes controlling the trait are unlinked
- the genes affect the trait equally in size and direction
- there are no dominance or epistatic effects involved
Segregation patterns were also determined for the three blast types only and not for the other traits.

6.3.5 Narrow sense heritability

Estimates of narrow sense heritability by genotype-environment interaction and based on the means across locations was calculated according to Hallauer and Miranda (1988):

$$h^2 = 4\sigma^2_m /[\sigma^2/(rl) + 4\sigma^2_{fml} /e + 4\sigma^2_{ml}/e + 4\sigma^2_{mf} + 4\sigma^2_m]$$

where: $4\sigma^2_m$ = male variance, f = females, l = locations, σ^2 = pooled error variance, $4\sigma^2_{fml}$ = variance due to female x male x location, $4\sigma^2_{ml}$ = male x location variance, $4\sigma^2_{mf}$ = male x female variance,

6.4 Results

6.4.1 Blast reaction of the parents

Significant differences ($P \leq 0.05$) for the three blast types were recorded among the parents across locations (Table 6.4-1, 6.4-3). There was a significant increase in leaf, neck and finger blast under artificial inoculation relative to natural infection (Table 6.4-1). The mean percent increase across the two locations was 32.3% for leaf blast, 19.4% for neck blast and 26.4% for finger blast. Male parent Okhale 1 had low percent disease increase suggesting a high/stable resistance. The highest increase in disease

meaned across locations (50.0%) was for leaf blast and was recorded by female parents KNE 744 and IE 11 whereas female parent KAT FM 1 and male parent P 224 had the highest increase in mean finger blast (40%). Female parents IE 3104, IE 11 and susceptible check KNE 479 had high disease levels under both inoculation and natural infection. Male parent Okhale 1 was the most resistant to all the three blast types. However, differences between males across locations for leaf, neck and finger blast were not significant but they were significant ($P \leq 0.05$) between females. Parents and crosses differed significantly ($P \leq 0.05$) for the three blast types.

Table 6.4-1: Reaction to blast for parents in inoculated and non-inoculated conditions across two test locations

	Mean disease score								
	Leaf		**Neck**		**Finger**		**% change**		
Parents	**Inoc**	**Non-inoc**	**Inoc**	**Non-inoc**	**Inoc**	**Non-inoc**	**Lblast**	**Nblast**	**Fblast**
Females									
KAT FM 1	**6.0**	4.5	4.5	3.5	7.0	5.0	33.3	28.6	40.0
IE 3104	**7.0**	5.0	5.0	4.0	8.0	7.0	40.0	25.0	14.3
KNE 744	**6.0**	4.0	4.0	3.0	6.0	4.5	50.0	33.3	33.3
IE 11	**6.0**	4.0	4.0	3.0	8.0	6.5	50.0	33.3	23.1
Males									
Okhale 1	**3.0**	2.5	2.0	2.0	2.2	2.0	20.0	0.0	10.0
KNE 796	**3.0**	2.5	2.2	2.0	3.0	2.3	20.0	10.0	30.4
KNE 392	**2.5**	2.0	2.0	2.0	3.0	2.5	25.0	0.0	20.0
P224	**3.0**	2.5	2.5	2.0	3.5	2.5	20.0	25.0	40.0
Mean	**4.6**	**3.4**	**3.3**	**2.7**	**5.1**	**4.0**	**32.3**	**19.4**	**26.4**
SE±	**0.619****	**0.774***	**0.531****	**0.495***	**0.808****	**0.571****			
CV%	**1.5**	**21.8**	**17.5**	**19.0**	**17.1**	**15.9**			
$LSD_{0.05}$	**1.004**	**1.255**	**0.861**	**0.803**	**1.309**	**0.926**			
Checks									
KNE 479 (Susceptible)	6.0	5.1	5.0	4.0	8.5	7.0	17.6	25.0	21.4
U 15 (resistant)	4.2	3.9	3.0	2.0	4.5	3.9	6.8	50.0	15.1
Ikhulule (Farmer line)	3.7	3.2	3.0	2.0	3.5	2.8	16.1	50.0	27.1

Inoc = inoculated, Non-inoc = non-inoculated, Lblast = leaf blast, Nblast = neck blast, Fblast = finger blast; * $P \leq 0.05$, **-$P \leq 0.01$

6.4.2 Yield and yield components

The best yielding male parent was Okhale 1 (2.14 t ha^{-1}) whereas the poorest yield was recorded in female parent IE 3104 (0.75 t ha^{-1}) that was most susceptible to blast and early (table 6.4-2). Mean days to flowering ranged from 65-88 with a mean of 76 days. The earliest parent to flower was IE 3104 at 66

days whereas KNE 744 (female) and KNE 392 (male) took the longest to flower at 84 days after sowing. The earliest check cultivar U 15 had mean flowering time of 71 days. Days to maturity followed a similar pattern to days to flowering. Plant heights ranged from 53.1-89.7 cm. Check cultivar U 15 attained a mean height of 69.1 cm. Mean number of fingers per panicle ranged from 3-8 whereas male parent Okhale 1 had the longest fingers (9.3cm). Finger widths ranged from 0.9 – 1.1 cm. Productive tillers per plant with range of 2–5 were highest in female parents IE 11 and IE 3104. Grains per spikelet had little variability with parents attaining a mean of seven grains per spikelet slightly higher than check cultivar U 15 (6 grains per spikelet). Mean 1000 grain mass varied from 1.6–2.4 g with parents attaining a mean of (2.0g) and was highest in male parent P 224. Parents and crosses differed significantly ($P \leq 0.05$) for plant height, fingers per panicle, for both finger length and width and grain yield.

Table 6.4-2: Mean performance of parents and checks for different traits across two test locations

Entry	Grain yield (t ha^{-1})	Days to flowering	Days to maturity	Fingers/ panicle	Finger length (cm)	Finger width (cm)	No. of grains/ spikelet	1000 grain mass (g)	Plant height (cm)	Plant yield (g)	Tillers/ plant
Parents											
KAT FM 1	1.59	66	108	7	7.3	1.1	7.2	2.1	75.1	9.9	4
IE 3104	0.75	71	106	7	4.0	0.9	5.7	1.9	53.1	4.4	5
KNE 744	1.29	84	120	6	4.6	1.0	6.5	1.6	68.1	8.2	3
IE 11	1.01	72	109	6	6.2	0.9	5.2	1.9	55.1	6	5
Okhale	2.14	78	119	7	9.3	1.1	7.7	2.1	87.7	12.5	3
KNE 392	1.59	84	120	7	7.2	1.0	6.8	2.0	86.6	9.1	2
KNE 796	2.05	81	118	7	6.7	1.0	6.5	1.9	89.7	12.1	3
P224	1.52	76	120	3	8.1	1.1	7.2	2.4	81.1	9.1	2
Mean	**1.49**	**77**	**115**	**6**	**6.7**	**1.0**	**6.6**	**2.0**	**74.6**	**8.9**	**3**
Checks											
U 15	1.88	71	109	8	6.8	1.0	6	2.3	69.1	9.9	3
Ikhulule	1.45	83	118	7	6.7	1.0	6	1.9	84.8	7.8	2
KNE 479	0.90	66	103	7	5.6	1.0	5	2.4	70.7	7.2	6
Grand Mean	1.47	76.0	114.0	7.0	6.6	1.0	6.0	2.0	74.6	8.7	4.0
SE±	0.43	5.37	3.99	0.81	0.90	0.07	1.08	0.29	5.22	2.56	1.20
CV%	27.1	7.1	3.5	11.3	13.3	7.1	16.2	14.4	6.9	26.4	34.7
$LSD_{0.05}$	0.69	8.71	6.465	1.29	1.52	0.12	1.75	0.47	8.46	4.15	2.00

6.4.3 Combining ability

6.4.3.1 Mean sums of squares for combining ability

Differences between parents and between crosses were significant ($P \leq 0.05$) for 13 of the 14 traits, the exceptions being number of fingers and grains per spikelet, respectively (Table 6.4-3). Differences were significant ($P \leq 0.05$) between females for ten traits and between males for six traits; the female x male interaction was significant ($P \leq 0.05$) for 13 traits. Interactions were significant ($P \leq 0.05$) for location x parents for four traits, location x crosses for seven traits, location x females for four traits, location x males for two traits and location x female x males for four traits.

6.4.3.2 Leaf, neck and finger blast

Significant ($P \leq 0.05$) GCA (females) and SCA variances were recorded for leaf, neck and finger blast (Table 6.4-3). The general prediction ratio values were 0.8, 0.8 and 0.9 for leaf, neck and finger blast, respectively. Based on the GPR values there was higher additive than non-additive gene effects for the three blast types. Location x crosses interactions were significant ($P \leq 0.05$) for leaf and neck blast whereas location x parents interaction was significant ($P \leq 0.05$) for finger blast only with similar reaction for leaf and neck blast across the two locations. The highest contribution to the total SS was from female x male interaction with 65.4% for neck and finger blast and 56.8% for leaf blast (Table 6.4-4).

6.4.3.3 Yield and associated traits

Based on across locations data, significant GCA and SCA variances were recorded for grain yield ha^{-1}, grain yield $plant^{-1}$, days to flowering, days to maturity, plant height, finger length and finger width and 1000-grain mass (Table 6.4-3). The general prediction ratio values ranged from 0.4 (fingers per panicle) to 0.9 for plant height, finger width and grains per spikelet. Based on GPR values, GCA estimates, hence additive gene effects were predominant for days to flowering and maturity, plant height, productive tillers per plant, finger length and width, grains per spikelet, grain yield ha^{-1}, grain yield per plant and 1000-grain mass. Significant interactions for location x crosses were observed for days to maturity, productive tillers per plant, grain yield per plant, plant height, and fingers per ear. Parent x location interactions were significant for productive tillers per plant, grain yield per plant and fingers per panicle. Female x male interaction contributed most to total variance in all traits except for productive tillers per plant (Table 6.4-4).

Table 6.4-3: Mean squares for combining ability for 14 traits of finger millet across two test locations

Source	Df	Lblast	Nblast	Fblast	Gyld	Tillers	Plyld	Daf	Dam	Pht	Fingers	Fin length	Fin width	Grains	1000 mass
Loc	1	5.25**	66.02**	41.71**	52.84**	7.56*	3826.45**	3239.50**	2558.67**	26490.28**	166.84**	113.96**	0.22**	4.34	8.11**
Rep/loc	4	2.46**	2.85*	1.82*	1.25**	3.31	28.66**	81.08*	30.36	101.93**	0.74	0.16	0.03**	0.76	0.49**
Treat	23	1.90**	10.30**	12.19**	1.18**	5.84**	37.62**	200.92**	185.09**	491.17**	2.25**	10.12**	0.02**	2.16*	0.25**
Parents	7	2.42*	16.69**	22.63**	1.35**	9.04**	45.97**	262.04**	235.05**	1261.74**	1.04	17.78**	0.04**	4.10**	0.33**
Crosses	15	1.53**	7.65**	7.95**	1.15**	4.74**	33.28**	183.79**	174.08**	155.18**	2.57**	6.53**	0.01*	1.39	0.24**
Parents x Crosses	1	3.90*	5.28*	2.80*	0.45*	0.01	44.348**	30.03	0.42	136.95*	5.84**	10.31**	0.05**	0.28	0.02
Female (GCA_f)	3	2.885**	9.27**	12.71**	0.25	13.68**	2.76	284.04**	289.98**	191.27**	2.43*	17.89**	0.01	2.59	0.39**
Male (GCA_m)	3	0.412	0.38	1.02	1.12**	2.71	27.94**	37.96	68.51**	194.22**	3.96**	5.64**	0.01	1.04	0.05
Female*Male (SCA)	9	1.44**	9.54**	8.67**	1.46**	2.44*	45.23**	198.98**	170.64**	130.14**	2.16**	3.04**	0.01	1.10	0.25**
Loc x Treat	23	0.72*	1.37	1.37*	0.27*	4.35**	20.53**	30.22	26.57*	52.58*	1.96**	1.17	0.01	0.88	0.10
Loc x Parents	7	0.83	2.12	3.11*	0.32	6.38**	23.79*	57.33	26.19	37.86	1.42*	1.26	0.01	0.62	0.15
Loc x Crosses	15	0.70**	1.08*	0.59	0.26	3.67**	19.60**	19.02	28.13*	62.87*	2.14**	1.11	0.01	0.93	0.08
Loc x Females	3	0.27	0.39	0.23	0.13	5.32**	17.07*	22.04	23.46	130.35**	6.68**	1.80	0.03	0.87	0.06
Loc x Males	3	0.60	0.82	1.00	0.38	2.34	10.88	3.68	46.59*	23.28	0.26	0.74	0.04	0.71	0.02
Loc x Female x Male	9	0.87*	1.40*	0.57	0.26	3.56*	23.34**	23.13	23.54	53.58	1.26	1.01	0.01	1.03	0.10
Error	92	0.33	1.05	0.74	0.15	1.49	6.20	27.21	14.98	27.11	0.65	0.90	0.01	1.17	0.06
General predicted ratio (GPR)		0.8	0.8	0.9	0.7	0.8	0.7	0.7	0.7	0.9	0.4	0.8	0.9	0.9	0.7

Df-Degrees of freedom; Lblast-Leaf blast;, Nblast-Neck blast; Fblast-Finger blast; Gyld-Green yield (t ha^{-1}); Pyld-Plant yield; Daf-Days to flowering; Dam-Days to maturity; Pht-Plant height; Finlength-Finger length; Finwidth-Finger width; Grains-Grains per spikelet; 1000 mass-1000-grain mass. ** Significant at $P \leq 0.01$; * Significant at $P \leq 0.05$

Table 6.4-4: Percent contribution (%) of females, males and female x male to the total sum of squares

Trait	Females	Males	Female x Male	Trait	Females	Males	Female x Male
Leaf Blast	37.8	5.4	56.8	Days to maturity	33.3	7.9	58.8
Neck blast	32.0	2.6	65.4	Plant height	24.7	25.0	50.3
Finger blast	32.0	2.6	65.4	Fingers per ear	18.9	30.8	50.4
Grain yield	4.4	19.5	76.1	Finger length	54.8	17.3	28.0
Productive tillers/plant	57.7	11.4	30.9	Finger width	25.8	13.6	60.6
Grain yield/Plant	1.7	16.8	81.5	Grains per spikelet	37.4	15.0	47.7
Days to flowering	30.9	4.1	65.0	1000-grain mass	32.8	4.2	63.0

6.4.3.4 General combining ability effects

6.4.3.4.1 Leaf blast, neck and finger blast

The GCA effects varied among the parents (Table 6.4-5). Among the female parents, KNE 744 had significant ($P \leq 0.05$), desirable negative GCA effects for leaf blast (-0.36), neck (-0.67) and finger blast (-1.04). Female parents IE 3104 and IE 11 had negative GCA effects for at least one of the blast types. Female parent KAT FM 1 had significant ($P \leq 0.05$) positive GCA effects for the three blast types (0.47, 0.77 and 0.55 for leaf, neck and finger blast, respectively). Among the male parents no significant positive nor negative GCA effects were recorded but male parent KNE 392 had negative GCA effects for the three blast types whereas Okhale 1 and P 224 had negative GCA effects, each for one blast type.

6.4.3.4.2 Yield and associated traits

General combing ability effects for the traits varied among the parents exhibiting both positive (desirable) and negative (undesirable) sign for the various yield traits (Table 6.4-5). Significant ($P \leq 0.05$) positive GCA effects in females ranged from 0.11 for 1000-grain mass (KAT FM 1) to 1.03 (IE 3104) for productive tillers per plant. Female parents KAT FM 1 and IE 3104 recorded significant ($P \leq 0.05$) negative GCA effects of -2.70 and 4.36 for flowering and maturity, respectively. Among the male parents, Okhale 1 had significant ($P \leq 0.05$) positive GCA effects for grain yield ha^{-1} (0.27), fingers per panicle (0.41) and finger length (0.72). Male parent KNE 392 had significant ($P \leq 0.05$) desirable negative GCA effects for days to maturity (-1.74) and plant height (-2.24).

Table 6.4-5: General combining ability effects of parents

	Leaf Blast	Neck blast	Finger blast	Gyld	Tillers	Pyld	Daf	Dam	Pht	Fingers	Fin length	Fin width	Grains	1000 mass
GCA females														
KAT FM 1	0.47**	0.77**	0.55**	0.13	0.07	0.35*	-3.03**	-4.36**	3.70**	0.11	0.30	0.01	0.28	0.11*
IE 3104	-0.07	0.19	0.46**	0.00	1.03**	0.20	-2.70**	0.3	-2.56*	0.36*	-0.17	-0.03*	-0.47*	-0.16**
KNE 744	-0.36**	-0.67**	-1.04**	-0.02	-0.43	-0.15	4.01**	4.14**	-1.80	-0.09	-1.09**	0.02	0.03	-0.05
IE 11	-0.05	-0.29	0.03	-0.12	-0.68**	-0.4	1.72	-0.07	0.66	-0.39*	0.96**	-0.01	0.16	0.10
GCA males														
OKHALE 1	0.04	-0.06	0.03	0.27**	0.11	1.50**	0.34	1.51*	4.06**	0.41*	0.72**	0.02	0.16	-0.04
KNE 796	0.06	0.17	0.28	0.03	0.03	-0.48	-1.41	-1.16	-0.15	0.16	-0.31	-0.01	0.03	0.03
KNE 392	-0.19	-0.13	-0.10	-0.04	0.32	-0.02	-0.49	-1.74*	-2.24*	-0.01	-0.21	-0.02	-0.30	-0.03
P 224	0.10	0.02	-0.20	-0.26**	-0.47*	-1.00*	1.55	1.39	-1.67	-0.55**	-0.21	0.00	0.11	0.05
SE (gi)	0.101	**0.156**	**0.148**	0.078	**0.222**	**0.459**	**0.918**	**0.745**	**1.079**	**0.170**	**0.193**	**0.015**	**0.231**	**0.051**
SE(gij)	0.142	**0.220**	**0.209**	0.110	**0.314**	**0.649**	**1.298**	**1.053**	**1.526**	**0.240**	**0.273**	**0.021**	**0.326**	**0.072**

Gyld-Grain yield (t ha^{-1}), Pyld-Plant yield, Daf-Days to flowering, Dam-days to maturity, Pht-Plant height, Fin length-Finger length, Fin width-Finger width, Grains-Grains per spikelet, 1000 mass – 1000-grain mass**.** ** Significant at P≤0.01; * Significant at P≤0.05

6.4.3.5 Specific combining ability effects

6.4.3.5.1 Leaf blast, neck and finger blast

Significant ($P \leq 0.05$) desirable negative SCA effects for at least two blast types were recorded in five crosses with a range of -0.40 for leaf blast in KNE 744 x Okhale 1 to -1.75 for neck blast in IE 3104 x KNE 796. Crosses KAT FM 1 x Okhale 1, IE 11 x P 224 and IE 3104 x KNE 796 had significant ($P \leq 0.05$) negative SCA effects for all the three blast types (Table 6.4-6). Significant ($P \leq 0.05$) desirable negative SCA effects were also recorded in KAT FM 1 x P 224 (-0.65) and IE 3104 x KNE 392 (-0.92) for finger blast and in IE 11 x Okhale 1 (-0.77) and IE 11 x KNE 392 (-0.67) for neck blast. Crosses IE 3104 x P 224 and IE 11 x KNE 796 exhibited significant ($P \leq 0.05$) undesirable positive SCA effects for all the three blast types.

6.4.3.5.2 Yield and yield associated traits

Specific combining ability effects differed among crosses for each trait (Table 6.4-6). Significant $P \leq 0.05$) SCA effects in the desirable direction were recorded in the crosses for the various traits. Positive SCA effects were desirable except for days to flowering, maturity and plant height. Crosses KAT FM1 x P 24, IE 3104 x KNE 796 and KNE 744 x KNE 392 had significant ($P \leq 0.05$) positive SCA effects for grain yield whereas IE 3104 x KNE 392 and KNE 744 x P 244 had significant ($P \leq 0.05$) positive SCA effects for 1000 grain mass. Significant ($P \leq 0.05$) positive SCA effects for finger length were recorded in KAT FM1 x P 224 and IE 3104 x KNE 796, and in KNE 744 x KNE 796 for productive tillers per plant. Significant ($P \leq 0.05$) negative SCA effects were recorded in IE 3104 x P 44 and IE 11 x KNE 796 for days to flowering and maturity, and in IE 3104 x KNE 392 and IE 3104 x P 224 for plant height.

Table 6.4-6: Specific combining ability effects of the 16 crosses

Crosses	Leaf Blast	Neck blast	Finger blast	Gyld	Tillers	Pyld	Daf	Dam	Pht	Fingers	Fin length	Fin width	Grains	1000 mass
KAT FM 1 x Okhale 1	-0.43*	-0.69*	-0.63*	0.07	-0.16	0.72	3.03	1.57	3.24	-0.41	-0.25	-0.03	-0.61	0.14
KAT FM 1 x KNE 796	0.21	-0.10	0.12	-0.49**	-0.41	-2.62**	-0.55	-1.43	-1.85	-0.16	0.33	0.05	0.01	0.01
KAT FM 1 x KNE 392	0.21	0.67*	1.16**	-0.32*	-0.2	-2.17*	-1.3	-0.18	1.42	-0.16	0.22	0.01	0.68	-0.08
KAT FM 1 x P 224	0.01	0.13	-0.65*	0.73**	0.76	4.07**	-1.18	0.03	-2.82	0.72*	-0.30	-0.03	-0.07	-0.06
IE 3104 x Okhale 1	-0.14	0.58	-0.13	0.19	0.22	1.80*	1.86	1.91	4.02	0.34	0.47	0.03	0.47	0.09
IE 3104 x KNE 796	-0.49*	-1.75**	-1.21**	0.58**	-0.70	2.18*	6.78**	7.57**	5.68**	0.43	0.83*	-0.07*	-0.24	0.00
IE 3104 x KNE 392	-0.24	0.10	-0.92**	-0.27	0.51	0.41	0.36	-0.84	-5.12*	-0.41	-0.72	0.01	-0.41	0.25*
IE 3104 x P 224	0.88**	1.06**	2.27**	-0.50**	-0.03	-4.40**	-9.01**	-8.64**	-4.58*	-0.36	-0.58	0.04	0.18	-0.34**
KNE 744 x Okhale 1	0.40*	0.88**	0.45	-0.40*	-0.66	-2.73**	-2.68	-1.93	-3.96	-0.36	0.19	0.03	0.3	-0.08
KNE 744 x KNE 796	-0.12	-0.54	0.12	-0.14	0.93*	0.13	-2.26	0.57	-3.01	-0.61	-0.09	-0.01	0.09	-0.03
KNE 744 x KNE 392	0.05	-0.1	-0.34	0.32*	-0.03	1.76	4.32*	0.66	3.47	0.55	-0.21	-0.03	-0.41	-0.18
KNE 744 x P 224	-0.33	-0.23	-0.23	0.22	-0.24	0.84	0.61	0.70	3.5	0.43	0.11	0.01	0.01	0.29**
IE 11 x Okhale 1	0.17	-0.77*	0.31	0.13	0.59	0.22	-2.22	-1.55	-3.3	0.43	-0.41	-0.03	-0.16	-0.14
IE 11 x KNE 796	0.40*	2.40**	0.97**	0.06	0.18	0.30	-3.97*	-6.72**	-0.82	0.34	-1.07**	0.04	0.14	0.02
IE 11 x KNE 392	-0.02	-0.67*	0.1	0.26	-0.28	0.00	-3.39	0.36	0.23	0.01	0.71	0.01	0.14	0.01
IE 11 x P 224	-0.56**	-0.96**	-1.38**	-0.45**	-0.49	-0.51	9.57**	7.91**	3.89	-0.78*	0.77*	-0.02	-0.11	0.11
SE (gi)	**0.202**	**0.295**	**0.295**	0.155	0.444	**0.918**	**1.836**	**1.490**	**2.158**	**0.339**	**0.386**	**0.030**	**0.462**	**0.102**
SE(gij)	**0.856**	**1.252**	**1.252**	0.658	1.884	**3.894**	**7.788**	**6.319**	**9.156**	**1.440**	**1.638**	**0.129**	**1.959**	**0.433**

Gyld-Grain yield (t ha^{-1}), Pyld-Plant yield, Daf-Days to flowering, Dam-days to maturity, Pht-Plant height, Fin length-Finger length, Fin width-Finger width, Grains-Grains per spikelet, 1000 mass –1000-grain mass. ** Significant at $P \leq 0.01$; * Significant at $P \leq 0.05$

6.4.4 Segregation patterns based on blast severity and minimum number of genes (effective factors) controlling blast resistance

For all three blast types, continuous variation was evident in the frequency distributions of the severity scores of the F_2 progeny of most of the crosses. Distributions of some of the crosses were skewed either towards resistance or susceptibility, especially for neck and finger blast while others were near normally distributed (Figures 6.4-1, 6.4-2 and 6.4-3). Most of the distributions for leaf blast were near normal. Crosses that had high severity scores such as IE 11 x KNE 796 and KAT FM 1 x KNE 392 had relatively skewed distribution towards susceptibility for finger and neck blast, respectively whereas those with low severity scores like IE 11 x P 224 were skewed towards resistance. Some of the plants in crosses like KAT FM 1 x Okhale 1 and KNE 744 x Okhale 1 exhibited disease severity scores either above the susceptible or below the resistant parent for leaf and finger blast with the same being observed in crosses KNE 744 x KNE 392 and KNE 744 x P 224 for leaf and neck blast. This was indicative of transgressive segregation. Differences were also observed in the frequency distribution patterns of the three blast types for the same cross, for example the frequency distribution of the progeny of cross IE 3104 x Okhale 1 was skewed towards resistance for leaf blast, towards susceptibility for neck blast and near normal for finger blast (Figure 6.4-3). Although there was no distinct pattern among the crosses in the ratio of resistant to susceptible transgressive segregants for the three blast types, some of the crosses involving female parent KNE 744, which had significant negative GCA effects, recorded the highest number of resistant transgressive segregants. The highest number of susceptible transgressive segregants especially for neck and finger blast were recorded in some of the crosses where KAT FM 1, which had a significant positive GCA effects, was the female parent. In both these situations, the male parents in the crosses were P 224 (positive GCA effects for leaf and neck blast), KNE 392 (negative GCA effects for the three blast types) and KNE 796 (positive GCA effects for three blast types).

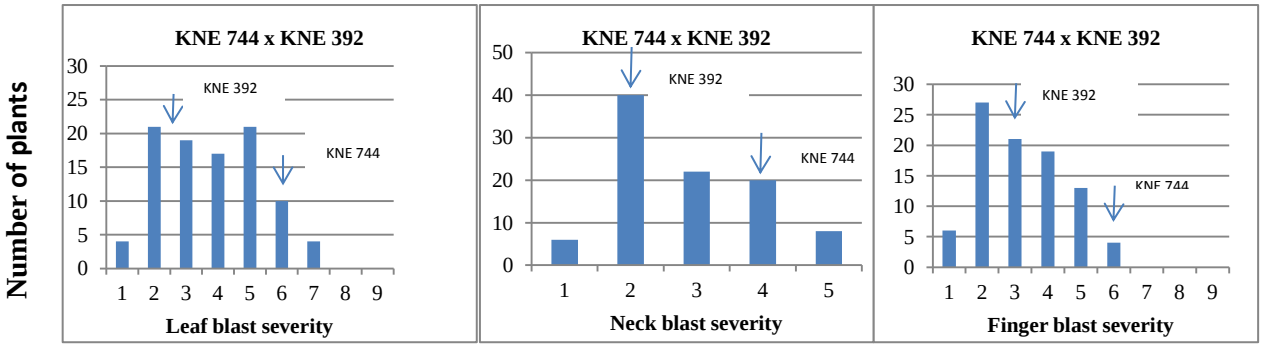

Figure 6.4-1 Frequency distribution of blast scores (leaf, neck and finger) in the F_2 generation of cross KNE 744 x KNE 392

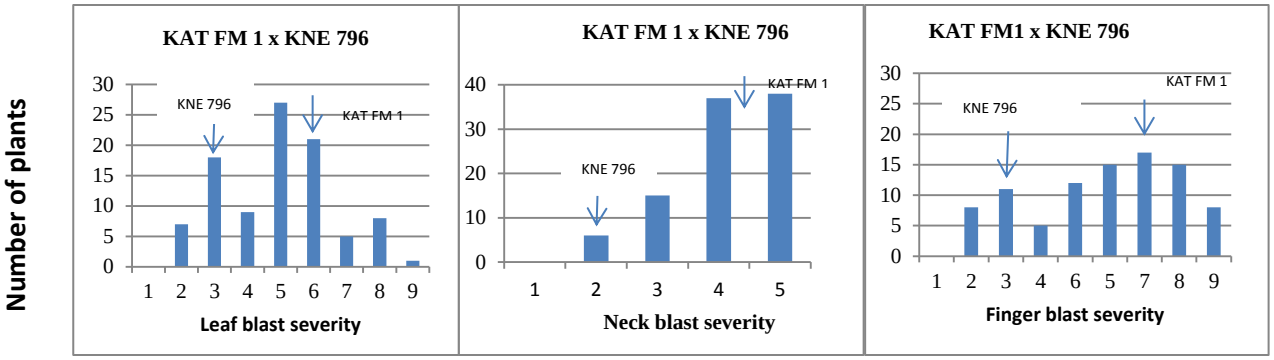

Figure 6.4-2 Frequency distribution of blast scores (leaf, neck and finger) in the F_2 generation of cross KAT FM 1 x KNE 796

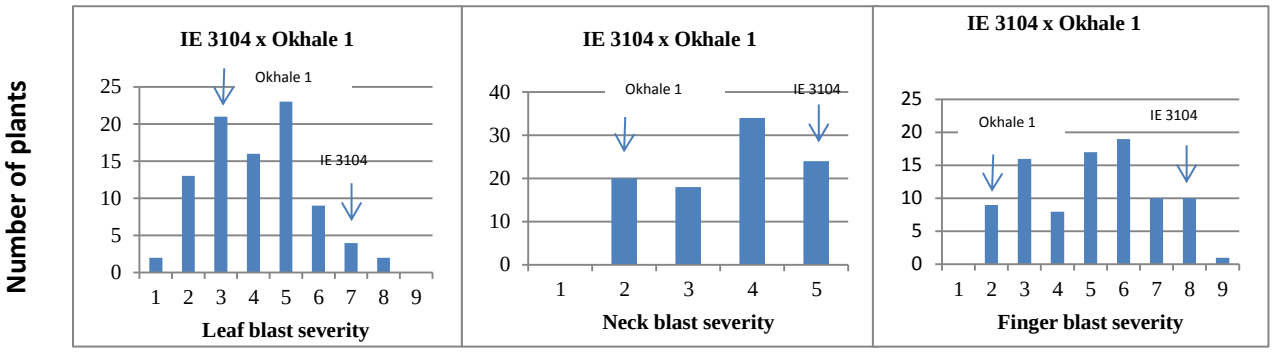

Figure 6.4-3 Differential frequency distribution of blast scores (leaf, neck and finger) within an F_2 generation of cross IE 3104 x Okhale 1

NB: Arrows in all graphs indicate the parental scores

The minimum number of genes controlling the three blast types varied from one to four (Table 6.4-7). Cross IE 3104 x Okhale 1 had the highest minimum number of genes expressed for controlling the three blast types (four for leaf and neck and three for finger blast) whereas the least was found in crosses KAT FM 1 x P 224 (three for leaf and one each for neck and finger blast) and KNE 744 x KNE 392 and KNE 744 x KNE 796 (two for leaf and finger and one for neck blast). Table 6.4-7.

Table 6.4-7. Minimum number of genes (effective factors) controlling blast resistance per F_2 parent pair

	Minimum number of genes (effective factors)				Minimum number of genes (effective factors)		
Cross	Leaf blast	Neck blast	Finger blast	**Cross**	Leaf blast	Neck blast	Finger blast
KAT FM 1 x Okhale 1	2	1	3	KNE 744 x Okhale 1	1	1	4
KAT FM 1 x KNE 796	4	1	4	KNE 744 x KNE 796	2	1	2
KAT FM 1 x KNE 392	4	2	1	KNE 744 x KNE 392	2	1	2
KAT FM 1 x P 224	3	1	1	KNE 744 x P 224	3	3	4
IE 3104 x Okhale 1	4	4	3	IE 11 x Okhale 1	3	2	4
IE 3104 x KNE 796	4	1	4	IE 11 x KNE 796	2	4	2
IE 3104 x KNE 392	4	1	3	IE 11 x KNE 392	1	1	4
IE 3104 x P 224	3	2	2	IE 11 x P 224	4	1	3

6.4.5 Narrow sense heritability

The narrow-sense heritability for the 14 traits ranged from 5.0-65% (Table 6.4-8). High heritability estimates (> 60%) were recorded for grains per spikelet only whereas moderate heritability estimates (31-60%) were recorded for productive tillers per plant, finger length, plant height, fingers per panicle, days to maturity and leaf blast. The lowest heritability estimates (5.0%) were recorded for finger width.

Table 6.4-8. Narrow sense heritability for 14 traits in the F^2 generation

Trait	h^2 (%)	Trait	h^2 (%)
Grain yield (t ha^{-1})	15.5	Days to maturity	34.5
Finger blast	26.1	Plant height (cm)	44.5
Neck blast	16.5	Fingers per panicle	43.4
Leaf blast	31.4	Finger length (cm)	51.5
Productive tillers per plant	55.0	Finger width (cm)	5.0
Grain yield per plant	10.5	Grains per spikelet	65.0
Days to flowering	28.0	1000 grain mass	19.0

6.5 Discussion

6.5.1 Gene action

Both additive and non-additive gene effects influenced inheritance of blast and all yield traits studied except fingers per panicle which was controlled mainly by non-additive gene effects and grains per

spikelet which was controlled mainly by additive gene effects. Breeding gains in these traits could therefore be achieved relatively fast through selection due to additive gene effects. All the traits had GPR values close to unity (one) except fingers per panicle, implying that inheritance for these traits is mainly under additive gene effects providing optimism for their improvement through selection. The predominance of non-additive gene effects in fingers per panicle would delay selection to later generations in order to accumulate fixable (additive) genes. The few studies conducted on gene action in finger millet have reported the significance of both additive and non-additive gene effects in most of the traits with a high frequency of non-additive effects predominating over additive effects. Among the studies are those by Krishnappa et al. (2009), Sumathi et al. (2005), Shailaja et al. (2010) and Oduori (2008). This study also observed greater influence of non-additive gene effects on fingers per panicle and additive genes for grains per spikelet. According to Paul et al. (2003) these varied observations could be attributed to parental differences. The predominance of additive gene effects in finger length observed in this study agrees with what was reported by Priyadharshini et al. (2011) and Nirmalakumar et al. (2010).

There were higher maternal than paternal influences for leaf, neck and finger blast observed in this study. Lunsford et al. (1974) attributed susceptibility to plant disease to maternal influence. The predominance of female over male contribution indicates that success in blast resistance breeding could be achieved more easily where a less susceptible female parent is used. This explains the higher success in crosses with KNE 744 which had the lowest blast scores of the female parents. Proof of maternal influence would however require reciprocal crossing. As observed by Derera et al. (2008), a breeder has to take precaution when maternal effects go beyond the F_1 as this may not be ideal for selection since they tend to inflate heritability estimates. The significant location x parent interaction for finger blast, productive tillers per plant, fingers per panicle and plant yield indicates the need for location specific breeding for these traits.

6.5.2 Combining ability effects

6.5.2.1 GCA effects

A decreasing GCA effect would be desirable in disease scores or in maturity while an increasing effect would be desirable in grain yield. As observed in surveys conducted in Kenya and Uganda (Oduori, 2008; Takan et al., 2004; Audi et al., 2003), earliness, high yield potential, early maturity and resistance to blast disease are some of the desirable traits preferred by most of the finger millet farmers when selecting a cultivar. Desirable significant negative GCA estimates for leaf, neck and finger blast were detected in

female parent KNE 744 and significant high negative GCA effects were detected in male parents KNE 392 for leaf and neck blast, P 224 for finger blast and Okhale 1 for neck blast. According to Baker (1978), prediction for GCA effects can be used to identify and select potential parents for desired traits hence the best crosses could be obtained from parents with high desirable GCA effects. This was reflected in the best four crosses with low leaf, neck and finger blast mean scores which had KNE 744 (with desirable GCA for blast) as female parent. Female lines KAT FM 1 and IE 3104, and male lines KNE 392 and KNE 796 had the best desirable negative GCA effects for imparting earliness. Desirable positive GCA effects for grain yield ha^{-1} were exhibited only by male parent Okhale 1 and correspondingly the best crosses with high mean grain yield ha^{-1} had Okhale 1 as male parent. Female parent KAT FM 1 with desirable significant GCA effects for 1000-grain mass would be ideal for breeding for improvement of this trait.

To address difficulties in harvesting and grain spoilage due to lodging, preference is given to medium and short statured cultivars. Female parents IE 3104 and male parent KNE 392 which recorded significant negative GCA effects for plant height were the best for breeding for height reduction. Productive tillers per plant, fingers per panicle and length of longest finger have been associated with high grain yield in finger millet (Patnaik, 1968; Sonnad et al., 2008; Wolie and Dessalegn, 2011) hence parents exhibiting high positive GCA effects for these traits would be desirable. Male parent Okhale 1 would be ideal for the improvement of fingers per panicle and finger length while female parents IE 3104 and IE 11 would be ideal for productive tillers per plant and fingers per panicle and finger length, respectively. All eight parents used did not have significant positive GCA effects for finger width and grains per spikelet and more parents need to be evaluated for desirable GCA effects for these traits

With a large unexploited regional finger millet gene pool, it is possible to find better parents to generate genotypes with resistance to blast, high yield and early to medium maturity as this study has shown.

6.5.2.2 Specific combining ability effects

Although SCA estimates provide invaluable information on F_1 hybrid development, their value in a self-pollinating species like finger millet would be in informing the selection of target traits in the case of transgressive segregation. According to Krishnappa et al. (2009), selection from crosses with higher mean expression and variance at the F_2 generation leads to better performance in subsequent generations while retaining higher variance hence giving a better chance for further selection. Selection of a cross will therefore depend on it's *per se* yield, high SCA effects, additive variance of the parents and positive effects of yield components. On this basis, crosses KAT FM 1 x Okhale 1, IE 3104 x KNE 796, IE 3104 x

KNE 392, IE 11 x KNE 796 and KAT FM 1 x P 224 with significant negative SCA effects would be advanced for leaf, neck and finger blast selection. Crosses KAT FM 1 x P 224, IE 3104 x KNE 796, would be the best for selection for grain yield whereas cross IE 3104 x P 224 would be the best for earliness and short plant stature. Number of fingers per panicle could be improved through advancement and selection in cross KAT FM 1 x P 224 and finger length in cross IE 3104 x KNE 796. With ongoing efforts to find cytoplasmic male sterility in finger millet, the hope is that the findings of this study will lay a foundation for future F_1 hybrid development in finger millet as has been utilized in rice (Parvez, 2006). However, the success of hybrids would depend on the yield advantage over the pure line cultivars, the appropriate seed system and seed cost.

6.5.3 Segregation patterns for blast severity and minimum number of genes (effective factors) controlling blast resistance

The F_2 segregating families showed continuous variation for the three blast types. The frequency distributions appeared normal or relatively skewed towards resistance or susceptibility. The presence of plants more resistant than their parents was evident in the transgressive segregation observed in many of the crosses for the three blast types, especially in crosses where at least one parent had desirable negative GCA effects. The low frequency of transgressive effects observed in some crosses may be due to similar gene frequencies in the parents. The difference in segregation patterns between crosses may indicate the presence of different resistance genes in the different parents used which would call for gene pyramiding for durable resistance (Sridhar and Singh, 2001). The differences in segregation patterns for leaf, neck and finger blasts within the cross IE 3104 x Okhale 1 may suggest that resistance to each of the blast types was influenced by the developmental stage of the plants as reported in rice by Li et al. (2007) who opined that genes are expressed selectively at different plant growth stages. Although there is no literature on minimum number of genes (effective factors) determining blast resistance, these findings suggest that a minimum of one to four genes are involved. Cross IE 3104 x Okhale 1 with a high number of genes (effective factors) expressed for all the three blast types may have durable resistance.

6.5.4 Narrow-sense heritability (h^2)

Productive tillers per plant, finger length and grains per spikelet had h^2. Traits with high h^2 are known to be mainly under additive genetic control (Allard, 1960) and will therefore respond to selection. In finger millet, literature on narrow sense heritability estimates is quite limited. The moderate h^2 recorded in this study for days to flowering and plant height and low h^2 for yield agree with findings of Shanthakumar and

Gowda (1997) in an F_2 generation. However the same authors reported low h^2 for number of fingers per panicle, finger length, productive tillers and grains per spikelet contrary to findings of this study. Krishnappa et al. (2009) using F_1 generation found low h^2 for days to flowering (8%), plant height (7%), productive tillers per plant (18%) and plant yield (11%) with higher non-additive genetic effects. However, fingers per panicle had moderate h^2 (36%) close to the moderate value (43.4%) recorded in this study. Based on findings of this study improvement through selection will be faster for productive tillers per plant, finger length and grains per spikelet. Grain yield is a complex quantitatively inherited trait and its expression varies with environment hence the low h^2 recorded in this study for the trait was expected. Therefore improvement of this trait and of those traits with low h^2 (finger blast, neck blast, 1000 grain mass and finger width) will be slow.

6.6 Conclusion

This study has demonstrated the potential of utilizing a relevant mating design to identify potential parents to generate crosses with blast resistance and high yield. Although both additive and non-additive genetic effects were significant additive genetic effects predominated over non-additive effects in thirteen out of the fourteen traits studied meaning that most of the traits can be improved relatively fast through selection. Male parent KNE 392 and female parents KNE 744 and IE 11 would be considered for blast resistance breeding while male parent Okhale 1 was found suitable for grain yield improvement due to their respective high desirable GCA effects. The significant desirable GCA effects for earliness in female parents KAT FM 1 and IE 3104, for productive tillers per plant and number of fingers per panicle in female parent IE 3104 and male parent Okhale 1, for finger length in female parent IE 11 and male parent Okhale 1 and for 1000-grain mass in female parent KAT FM 1 are positive indications of the potential for yield improvement in finger millet. The F_2 segregation patterns for the three blast types differed between crosses. This may suggest the presence of different resistance genes in the different parents used which would call for gene pyramiding for durable resistance. However, this will require proper characterization of the genes to be used. The possibility of identifying resistant plants was demonstrated by the transgressive segregation observed in many of the crosses for the three blast types. With the presented transgressive segregation, crosses IE 3104 x KNE 796, KAT FM 1 x Okhale 1, IE 11 x Okhale and KNE 744 x KNE 392 have the potential to generate lines with blast resistance. Blast resistance was found to be controlled by a minimum of one to four genes (effective factors) with no clear link to segregations patterns detected. The high h^2 detected in productive tillers per plant, finger length and grains per spikelet means that these traits can be improved through selection.

These results confirm the potential in the local germplasm for sourcing valuable parental stocks for development of high yielding and blast resistant finger millet genotypes in East Africa and will help formulate an effective breeding strategy.

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Chapter 7

Overview of the research findings

7.1 Introduction

Finger millet in East Africa is cultivated in varying agro-ecologies and the poor yields realized by farmers are largely attributed to the low yielding blast susceptible cultivars grown. The aim of this study was to explore the diversity in selected East African finger millet accessions, determine blast reaction and adaptation, and understand gene action for blast and key agronomic traits to enable the formulation of a sound breeding strategy for productivity improvement. This chapter is an overview of the study in terms of the hypotheses tested, the resultant findings and their implications in informing the way forward for finger millet improvement in eastern Africa.

Hypotheses tested

- There is genetic variation among the finger millet landraces cultivated in East Africa.
- There is differential productivity potential and reaction to blast disease among the landraces.
- There is high association between grain yield and its components that could be utilized for indirect selection for grain yield.
- Performance of finger millet for agronomic traits is stable across environments.
- Genetic systems controlling blast and grain yield traits in finger millet are predominantly additive.

7.2 Summary of the major findings

7.2.1 Genetic diversity in selected East African finger millet germplasm

Both morphological and molecular characterization of the germplasm revealed significant variation in most of the traits.

- There was greater diversity within than between the Kenyan, Tanzanian and Ugandan accessions.
- There was a close relationship between Kenyan and Ugandan and Kenyan and Tanzanian accessions than between Ugandan and Tanzanian accessions. Low variability was observed in Ugandan accessions relative to the Tanzanian and Kenyan accessions.

- Nineteen of the 23 markers used in the diversity study were polymorphic with polymorphic information content (PIC) of 0.606 for the 195 alleles detected with a range of 3-23 alleles per locus.
- Tanzanian accessions were later in maturing than Kenyan and Ugandan accessions
- Blast incidence was lower in the Ugandan than the Kenyan and Tanzanian accessions.
- Semi-compact and compact brown grain types were predominant across the countries.
- Accessions from Uganda had better grain yields in low and mid-altitudes whereas accessions from the Rift valley region of Kenya did better in the cool high elevation environment.
- Seven diversity clusters were observed with variability contributed largely by peduncle length, plant height, panicle exertion, grain yield, leaf blade length and leaf sheath length.
- There was evidence of some diversity in the three countries' germplasm not being captured in the global minicore set. This agrees with conclusions by Upadhyaya et al. (2006b) that the composition of the core collection is subject to change as additional accessions become available.

7.2.2 Trait association, path coefficient analysis, heritability and genetic advance

Correlation estimates and path coefficients were carried out on 23 quantitative traits to explain trait associations in finger millet and to determine direct and indirect effects of the various traits on grain yield. Broad sense heritability (H^2) and genetic gain as percent of the mean (GA%) were also calculated to estimate the potential for traits improvement through selection.

- Genotypic correlations were higher than phenotypic correlations for most of the traits studied
- Grain yield was positively correlated with finger width, grains per spikelet, threshing percent, peduncle length and panicle exertion and negatively correlated with days to flowering, leaf blast, neck blast and finger blast.
- Early flowering/maturing accessions were more blast susceptible than the late maturing ones.
- Productive tillers per plant, 1000 grain mass, grains per spikelet and threshing % had positive direct effects on grain yield.
- As expected, higher phenotypic coefficients of variation (PCV) than genotypic coefficients of variation (GCV) were observed for all traits.
- Lower environmental coefficients of variation (ECV) than GCV were recorded for fingers per panicle, leaf blade width, flag leaf blade length, finger length, leaves per plant, leaf sheath length and plant height.

- High heritability and genetic advance as percent of mean were recorded in fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, peduncle length, panicle exertion, leaves per plant and leaf sheath length with low H^2 and GA% observed in finger width and grain yield.

7.2.3 Genotype x environment interaction, yield stability and blast reaction in finger millet landraces

Adaptation and yield stability studies were carried out using 81 accessions (selected from the 420 accessions phenotyped in Chapter 2) across eight environments and screening for blast disease reaction under artificial and natural infection done at one and four environments, respectively.

- Based on AMMI results the interaction had the greatest effect accounting for 47.3% and 62.0% of the total and treatment sum of squares, respectively for grain yield. This contributed to the differential genotype responses across environments.
- The greatest contribution to both total and treatment sum of squares for finger blast was from environments (40.3 and 46.8%, respectively).
- GGE biplot analyses revealed Lan12LR, Ser12LR and Miw12LR to be the most discriminating environments for low temperature, sub-humid mid altitude and dry lowland areas, respectively.
- Seven genotypes G3 G5, G17, G25, G28, G36 and G71 were found to be stable across environments whereas genotypes G1 (for Kib11SR) G37 and G18 (for Lan12LR) G61 (for Alu12LR), G77 (for Alu11SR), G74 (for Ser12LR) and G19 and G75 (for Uyol12) had specific adaptation.
- Resistant genotypes were slow blasting and had low AUDPC susceptibility values and disease severity rating for the three blast types and vice-versa for susceptible genotypes
- Disease severity scores were highly negatively correlated with days to flowering and grain yield suggesting that early lines suffered more disease damage leading to reduced yield.
- Genotypes G16, G18, G27, G43, G61, G67, G70, G60 and G78 were resistant to all the three blast types.
- Genotypes with high rates of disease progress had poor grain yield.

7.2.4 Gene action for blast resistance and grain yield traits in finger millet

To understand the combining ability and gene action for blast resistance and grain yield and related traits, 16 F_2 families plus their four male and four female parents were evaluated at Alupe, and Kakamega in western Kenya under artificial inoculation and under natural infection.

- General combining ability and SCA variances were significant for all traits except for finger width and grains per spikelet with higher GCA than SCA variances recorded for leaf, neck and finger blast, plant height, productive tillers per plant, days to flowering, days to maturity, finger length and width and 1000 grain mass. Improvement for these traits is achievable through selection.
- Parents KNE 744, KNE 392 and P 224 had desirable negative GCA effects for blast resistance
- Parent Okhale 1 had desirable positive GCA effects for grain yield
- Frequency distributions in the F_2 families for three blast types represented that for quantitative inheritance but segregation patterns varied between families indicating gene differences in the parents.
- A minimum of one to four genes (effective factors) were detected for resistance control in all the three blast types but this was at variance with the frequency distributions detected in the F_2 families that represented quantitative inheritance. Further investigations are required.
- Based on the transgressive segregation evident in the F_2 progeny populations of crosses IE 3104 x KNE 796, KAT FM 1 x Okhale 1, IE 11 x Okhale, IE 11 x P 224 and KNE 744 x KNE 392 they have potential to generate lines with blast resistance.

7.3 Implications of the findings for germplasm conservation and utilization, breeding for high yield and blast resistance

Diversity analysis indicated the existence of considerable variability for almost all the traits studied. The high variability observed attests to the genetic value of the region's germplasm which needs to be conserved and utilized.

- Low productivity and production of finger millet in East Africa has been largely attributed to the use of low yielding blast susceptible cultivars. The variability recorded in the germplasm will be utilized to address this problem.
- Collected and conserved germplasm urgently needs to be characterized to determine its value for breeding and commercial utilization.

- Low diversity in Ugandan accessions calls for urgent action to collect and conserve the untapped diversity.
- There is a need to include the diversity not captured in the global minicore set to enrich the global finger millet repository.
- Finger millet genome studies should be enhanced to develop robust and trait specific markers for diversity studies and marker assisted selection.
- Genetic evaluation of the germplasm to identify more genotypes with desirable general combining ability for target traits is required.
- Genotypes identified with specific and general adaptation need to be further evaluated for possible release. The diversity of these lines for agronomic and grain traits provides farmers with the opportunity to choose genotypes appropriate for their target production areas and desired end use.
- Cultivars with general adaptation will be useful in the harmonized regional seed system and hasten the release process.
- Blast resistant genotypes with high grain yield need to be considered for further evaluation and release whereas genotypes with high resistance and average to low grain yield will be utilized as sources of genes for blast resistance breeding. Slow blasting has been associated with horizontal or durable resistance and therefore genotypes with this form of resistance should withstand variation in blast pathogen biotypes for a longer time than genotypes with vertical resistance.
- For faster yield improvement, emphasis needs to be placed on traits with high H^2 and GA% which may be selected for in a relatively early generations.
- Since additive gene effects were significant and predominated over non-additive effects for blast, grain yield related traits improvement of these traits can be achieved through selection.
- Indications of gene differences in the parents for blast inheritance need to be further investigated and if confirmed gene pyramiding will be required in breeding for durable blast resistance.

7.4 Challenges

Cross-pollination was difficult in parents with poor pollen shed. Distinct morphological markers expression in the F_1 generation was occasionally absent which made it difficult to rely on them for true F_1 identification. Obtaining a balanced mating design was difficult as some crosses were not successful and a number of crosses could not be included in the analysis. Lack of a laboratory at the Alupe location for blast inoculum preparation raised costs as inoculum had to be prepared in Nairobi and transported to Alupe 500 km away. Limited project funds reduced the desired frequency of visits to trial locations

outside Kenya and compromised the effectiveness of data collection. Scant literature on many finger millet breeding aspects limited comprehensive comparisons of the results obtained. A motor vehicle accident which left the author temporarily incapacitated from December 2012 to March 2013 slowed progress in the third year of this study.

7.5 Looking ahead

This study has demonstrated the potential for blast resistance and yield improvement in finger millet based on the diversity recorded in the germplasm. This diversity could be utilized for breeding and/or direct use through selection. The significant and predominant additive genetic effects indicate that blast resistance and grain yield could be improved through selection. Genetic studies to understand gene action for key traits for finger millet improvement should be enhanced. The value of finger millet for nutrition and income generation is increasingly being appreciated by East African countries and globally. Finger millet has been included in the East African countries' strategic grain reserves and given high priority in the research agenda of the Association for Strengthening Agricultural Research in Eastern and Central Africa (ASARECA). Much effort has been invested in developing breeding methodologies in finger millet (Oduori, 2008; Wanyera, 2010) and finger millet genome studies with comparative analysis with the rice genome to map out traits of interest (Dida et al., 2007) is on-going. At ICRISAT enhanced studies have been carried out to identify trait specific genotypes from the core finger millet germplasm collection to address biotic and abiotic tresses (Upadhyaya, 2006). With a fast growing population, African global policy advisors are now echoing the need for Africa to embrace more productive, nutritious and pest resistant crops in order to be self sufficient in food production (Orengo, 2013). For this to be realized, however, Africa must invest more in technological research in agriculture rather than socio-economic research. Increasing finger millet productivity and production is more important now than ever before.

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