Genetic Variation Diversity and Genotype by Environment Interactions of Nutritional Quality traits in East African Sweetpotato

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Declaration

I wish to declare to the best of my knowledge that that the research presented in this thesis is original and conducted by myself and has not been presented for a degree award before.

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The thesis has been submitted for examination with our approval as University supervisors

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Dedication

To my loving family, parents, sisters and brothers for their support during the study.

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Acronyms

AMMI	Additive Multiplicative Main Interactions
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
CIAT	International Centre for Tropical Agriculture
CIMMTY	International Maize and Wheat Research Centre
CIP	International Potato Centre
CV	Coefficieint of Variation
DM	Dry matter
EA	East Africa
ECA	East and Central Africa
HPLC	High Performance Liquid Chromatography
IARC	International Agricultural Research Centres
IITA	International Institute of Tropical Agriculture
NaCRRI	National Crops Resources Research Institute
ng	Nanogram
NIRS	Near Infra-red Reflectance Spectroscopy
OFSP	Orange-fleshed sweetpotato
PC	Principal Component
PCR	Polymerase Chain Reaction
PLABSTAT	Plant Breeding Statistical program
RDA	Recommended Daily Allowance
SSA	Sub-Saharan Africa
SSR	Simple Sequence Repeats
UPGMA	Unweighted Pair Group Method Analysis
UBOS	Uganda Beareau of Statistics
VAD	Vitamin A dificiency
WFSP	White/cream-fleshed sweetpotato

Abstract

Sweetpotato is one of the staples that have been earmarked by the global initiatives to fight micronutrient deficiency, particularly vitamin A deficiency. The present study sought to contribute to the pre-breeding knowledge base required for the improvement of sweetpotato nutritional quality targeting β-carotene, dry matter, starch, sucrose and minerals (i.e Fe, Zn, Ca and Mg) as a sustainable strategy to reduce the problems associated with the micronutrient deficiencies and malnutrition among people in developing countries. The specific objectives of the study were to i) characterize selected East African sweetpotato accessions for storage root quality (dry matter, protein, starch, sucrose, ß-carotene, iron, zinc, calcium and magnesium) ii) determine the magnitude of GxE variation in orange-fleshed sweetpotato (OFSP) varieties of East African origin for yield and nutritional traits conducted across ecogeograhic zones of Uganda; and iii) study genetic relationships among and between OFSP and white-fleshed sweetpotato (WFSP) farmer varieties gene pools, and how these two phenotypic groups compare with non-African OFSP and WFSP accessions. For the micronutrient profiling study, 89 (White/cream- and orange-fleshed) landraces, plus one introduction, Resisto, were evaluated at Namulonge and Kachwekano research stations in Uganda. Roots were analyzed for β-carotene, iron, zinc, calcium, magnesium, protein and starch content using the Near Infrared Refractance Spectroscopy (NIRS) procedure. The σ_G^2 variance was significant ($p < 0.01$) for all the traits except sucrose content. Overall, the farmer varieties had higher dry matter, higher starch, and lower sucrose contents than the check. It is these qualities that make sweetpotato attractive as a starchy staple in EA. A low population's mean of β-carotene content was observed. However, deep orange-fleshed farmer varieties, 'Carrot_C', 'Ejumula', 'Carrot Dar', 'Mayai' and 'Zambezi' had β-carotene content that can meet ≥350% of recommended daily allowance (RDA) with 250 g serving to a 5 – 8 year old child. More, but light orange-fleshed farmer varieties 'ARA244 Shinyanga', 'HMA493 Tanzania', 'K-118', 'K-134', 'K-46', 'PAL161', 'Sowola6', 'SRT52', and 'Sudan' can provide 50 - 90% RDA of the child. The root minerals' content was generally low except for magnesium, the content of which can meet ≥ 50% RDA in many farmer varieties. However, in areas with high sweetpotato consumption, varieties 'Carrot_C', 'Carrot Dar', 'KRE Nylon', 'MLE163 Kyebandula' and 'SRT49 Sanyuzameza' can improve iron, zinc, calcium, and magnesium intake. In conclusion, some EA farmer varieties can contribute greatly to alleviation of vitamin A deficiency and meaningful mineral intakes.

The GxE analysis was conducted with regression, and additive main effects and multiplicative interaction (AMMI). The environment effects were significant ($p < 0.05$; or < 0.01) for root yield, harvest index, and all quality traits except dry matter. The genotypic effects were significant ($p < 0.05$; or < 0.01) for all traits except root yield, iron and magnesium. Accessions, 'Ejumula', 'SPK004/6', and 'SPK004/6/6' had higher root yields

than the check, Resisto, while 'Naspot_5/50' had the lowest root yields. The former three accessions are released in Uganda, and represent the potential gains in breeding for orange-fleshed sweetpotato clones with high root yields, dry matter and β-carotene. The σ^2_{GxE} components were not significant ($p>0.05$) for β-carotene and starch root content. The σ^2_{GxE} components were highly significant ($p<0.01$) for dry matter but fractional (0.4) compared to the corresponding σ^2_G component. These results suggest traits can be improved with high selection efficiency in the early stages of a sweetpotato breeding program. The σ^2_{GxE}: σ^2_G ratio was close to 1 for harvest index and sucrose content, and large (> 2) for storage root yields and all mineral contents. Like for yield, the results suggest that breeding for elevated mineral levels in sweetpotato is complex and requires information about the causes of GxE interactions before the breeder can embark on enhancing these minerals. However, medium to high positive correlations among mineral traits simplify selection aiming at elevated mineral contents in sweetpotato and it merits research if the trait complex of minerals can be improved more efficiently by an index.

For the genetic diversity study, eighty five East African farmer varieties (29 OFSPs and 56 WFSPs) and 7 varieties of non-African origin as check clones were analyzed using 26 simple sequence repeat (SSR) markers. A total 158 alleles were scored with an average of 6.1 alleles per SSR loci. The mean of Jaccard's similarity coefficients was 0.54. The unweighted pair group method analysis (UPGMA) revealed a main cluster for EA germplasm at a similarity coefficient of 0.52. At a similarity coefficient of about 0.56 sub clusters within the EA germplasm were observed, but these were neither country nor flesh color specific. Analysis of molecular variance (AMOVA) found a significant difference between EA and non-African germplasm, and a non significant difference between OFSP and WFSP germplasm. In conclusion, the EA germplasm appears to be distinct from non-African germplasm, and OFSP and WFSP farmer varieties from EA are closely related. OFSP farmer varieties from EA might show similar adaptation to SSA environments as WFSP and a big potential in alleviating vitamin A deficiency (VAD).

Introduction

Origin and Importance of Sweetpotato

Sweetpotato *[Ipomoea batatas* (L.) Lam] belongs to the family Convolvulaceae. It is hexaploid, and usually considered the only species of Ipomoea of economic importance. It is of neotropical origin and crossed the Pacific via Polynesia before the discovery of the new world (Huaman *et al*., 1999; Zhang et al., 2000). In Africa it was introduced by explorers from Spain and Portugal during the 16th century (O'Brien, 1972; Zhang *et al*., 2000; Zhang *et al*., 2004). Based on the presence of large numbers of varieties, East Africa, is one of the areas suggested as secondary centres of diversity (Gichuki *et al*., 2003). With an annual production of 124 million tones, sweetpotato is the world's seventh most important food crop after wheat, rice, maize, potato, barley and cassava (FAOSTAT, 2007), and the third most important tuberous root crop (Gibson *et al*., 2002). It is widely adapted in the tropics, sub-tropical and warm temperate regions where it is grown by smallholder farmers on marginal land with minimal inputs (Bashasha *et al*., 1995; Kapinga et al., 1995). Developing countries account for 98% of the world's sweetpotato production. Africa produces only about 6% of the world crop, and almost all the crop is consumed directly by humans, hence the crop has a relatively large nutritional impact (Gibson *et al*., 2002). Indeed in East and Central Africa where over 70% of the Sub-Saharan Africa (SSA) regional sweetpotato is produced and daily per capita intake is high [e.g. about 240g in Uganda (FAOSTAT, 2007)], the potential to contribute to solving the problem of VAD has been shown to be greatest (Low *et al*., 2001).

Micronutrient Deficiency Problems

The pro-vitamin A and minerals (Fe, Zn, Ca, and Mg) are critical and deficient in human food supply (Frossard *et al*., 2000). Worldwide 100 million (Black, 2003) children under the age of five are vitamin A deficient and suffer high death rates due to diarrhea, measles and malaria. Also, 2 billion people, mostly infants, children and women of childbearing age in developing countries, are anemic (Frossard *et al*., 2000) due to Fe deficient diets. In the developing world, Fe and Zn deficiencies are implicated in 700,000 and 800,000 deaths per year, respectively (Black, 2003; WHO, 2002). According to Black (2003) 2.4%, 1.8% and 1.9% of the global disease burden is attributable to Fe deficiency, vitamin A deficiency (VAD) and Zn deficiency, respectively. In Uganda, about 20% of children and 19% of women are vitamin A deficient; and 73% of children and 49% of women are anemic (UBOS and Macro International Inc., 2007). The levels of anemia are higher among pregnant (64%) and breast feeding (53%) mothers. Overall, severe micronutrient malnutrition damages the cognitive development, lowers disease resistance in children and reduces the likelihood that mothers survive childbirth (Frossard *et al*., 2000).

Control strategies for Micronutrient Deficiencies

Three broad strategies, namely; supplementation with pharmaceutical preparations, food fortifications, and dietary diversification have been adopted worldwide to avert the effects of micronutrient malnutrition (Frossard *et al*., 2000). Although notable reductions in prevalence levels have been achieved due to the above interventions, malnutrition remains high in remote areas of developing countries. The strategies have proved costly and less sustainable (Bouis, 2003; HarvestPlus, 2003). Food staples enriched with micronutrients through plant breeding have been adopted as a new but complementary strategy to avert the effects of micronutrient malnutrition by many International Agricultural Research Centers (IARC) and their partners in developing countries including SSA (Bouis, 2003; and HarvestPlus, 2003; Welch and Graham, 2004). The strategy is potentially sustainable because the staples are already part of the diets of the majority of the people (Frossard, *et al*., 2000; Harvest Plus, 2003) and high levels of the micronutrients have been identified in the staples. For example, high contents of Fe and Zn have been observed in the edible parts of such staple foods as rice, maize, beans and wheat (Gregorio, *et al*., 1999; Gregorio, 2002). It is within this IARC's main framework to improve the nutritional quality of major staples that International Potato Centre (CIP) and its partners are aiming at improvement of sweetpotato nutritional quality, targeting β-carotene, starch, dry matter, protein, sucrose and minerals (i.e Fe, Zn, Ca and Mg) (Grüneberg *et al*., 2009).

Problem Statement

The breeding goals for nutrition quality in sweetpotato cannot be fully met with the current pre-breeding knowledge gaps (Grüneberg et al., 2005). For example whereas cultivars rich in β-carotene have been identified (Hagenimana *et al*., 1999; Laurie 2008; Mwanga et al., 2007; Mwanga *et al*., 2009), scanty information exists on the sources of mineral nutrients (Fe, Zn, Ca and Mg) among sweetpotato germplasm. Woolfe (1992) on average reported up to 0.69 and 0.24 mg/100g amounts of Fe and Zn, respectively. These levels are very low and comprehensive screening studies are required (Grüneberg *et al*., 2005 unpublished) to identify cultivars with higher levels. At the same time there is conflicting information on the extent to which this genetic variation of these micronutrients in sweetpotato germplasm interacts with environment (GxE). Previous studies (Woolfe, 1992; Ngeve, 1993, Ravindran *et al*., 1995) on several traits have shown that sweetpotato is sensitive to environmental variation, despite wide adaptability to harsh growing conditions. Preliminary findings (Grüneberg *et al*., 2005) show extremely low GxE interactions for the quality traits, β-carotene, Fe and Zn while Manrique and Hermann (2000) observed increased concentrations of ß-carotene at high altitudes among the studied clones. GxE interactions are of great importance when evaluating the stability of breeding clones under different environmental conditions. Of additional importance, especially to multi-trait breeding objectives of the micronutrients in sweetpotato, is the understanding of the genetic correlations of the target quality traits. All this information is currently lacking.

CIP's overall goal of multi-trait selection for nutrient dense sweetpotato varieties, builds on the progress so far registered in the development of sweetpotato cultivars rich in ß-carotene. In SSA, breeding for ß-carotene rich cultivars has been faced with moderate rates of acceptability (due to low dry matter) and high susceptibility to viruses and drought of the introduced OFSP varieties. At the same time, CIP and partners in the region have identified what are considered as African ß-carotene rich farmer varieties, which are more adapted and are looked at as important gene pool to enhance the breeding objectives for quality sweetpotato in Africa. However, the genetic variation and distinctiveness of this group of OFSP farmer varieties are not understood. This knowledge is important for efficient rationalization and utilization of this germplasm (Zhang *et al*., 1998; LaBonte *et al*., 1997), designing appropriate plant breeding programs, as well as in making choice of parent genotypes for population development.

Justification of the Study

It has already been demonstrated that micronutrient enrichment traits are available within genomes of the major staple food crops including sweetpotato. However, research to identify accessions high in different nutritional qualities (dry matter, protein, starch, sucrose, ß-carotene, Fe, Zn, Ca and Mg) has been initiated by CIP for germplasm in genebank and breeding. But such characterization needs to be done for the germplasm from the Eastern Africa sub-region. The identified accessions could be promoted as superior varieties to farmers or used as parents in a comprehensive breeding program for improved nutrition in sweetpotato varieties without negatively impacting crop yields (Grüneberg *et al*., 2005). Apart from identifying varieties rich in the nutrients, there is a need to understand the GxE as well as the stability of the nutrient traits across diverse environments to guide future choice and use of appropriate breeding strategies for the improvement of sweetpotato (Grüneberg *et al*., 2005). Such an understanding would also allow making informed choices regarding which locations and input systems to be used in breeding efforts for improved nutrient levels in sweetpotato. Stability for β-carotene in sweetpotato cultivars has been reported (Manrique and Hermann, 2000) while no reports exists for mineral traits (Fe, Zn, Ca and Mg). African OFSP farmer varieties are a new sweetpotato population whose genetic diversity and distinctiveness are not understood. This is crutial if such varieties are to be maximally utilized for breeding.

Objectives of the Study

A study was therefore undertaken with the overall objective of contributing to the pre-breeding knowledge base required for the improvement of sweetpotato nutritional quality targeting β-carotene, dry matter, starch, sucrose and minerals (i.e Fe, Zn, Ca and Mg) as a sustainable strategy to reduce the problems associated with the deficiencies. The specific objectives of the study were to i) characterize selected East African sweetpotato accessions for storage root quality (dry matter, protein, starch, sucrose, ß-carotene, iron, zinc, calcium and magnesium); ii) determine the magnitude of GxE variation in OFSP varieties of East African origin for yield and nutritional traits conducted across ecogeograhic zones of Uganda; and iii) study

genetic relationships among and between OFSP and WFSP farmer varieties gene pools, and how these two phenotypic groups compare with non-African OFSP and WFSP accessions.

Literature review

Sweetpotato Germplasm

Sweetpotato is one of the major world staples with rich germplasm diversity (He et al., 1995). Nearly 8000 accessions of sweetpotato have been collected and maintained at various gene banks worldwide (Zhang *et al*., 2000) though this may represent a fraction of existing diversity. The majority of the accessions (5526) are being maintained in vitro at the CIP gene bank in Peru and these have been collected from 57 countries (Huaman and Zhang, 1997; Huaman *et al*., 1999; Zhang *et al*., 2000). A total of 2589 accessions have been collected from Latin America most of which are landraces and farmers' varieties. In Papua New Guinea alone, there are about 5000 estimated cultivars (Takagi, 1988). Other sizable collections exist in China, Indonesia (CIP, Bogor) and the United States (National Plant Germplasm System collection, Griffin Georgia).

Genetic Diversity Studies of the Sweetpotato Germplasm

Genetic diversity studies have enhanced greater understanding of the extent of variation within the germplasm collections and required management practices. The information has been crucial in the development of core collections of different crops (Zhang *et al*., 2000) and tailoring germplasm exploration to focus on those areas with maximal genetic diversity (Wilde *et al*., 1992; Graner *et al*., 1994). The information has also been useful for the optimal design of plant breeding programs, influencing the choice of genotypes to cross for development of new populations (Zhang *et al*., 2000). In sweetpotato, a lot of germplasm diversity assessments have been based on morphological and agronomic traits as well as reaction to pests, diseases and other stresses (CIP/AVRDC/IBPGR, 1991). These traits, however, vary a lot with cultivars, environment, stage of growth, and cultural practices (Jarret *et al*., 1992; Gichuru, 2003) and hence unreliable when correct identification of germplasm is desired. Molecular markers supplant morphological characterization for traits that are environmentally unstable. They are powerful and reliable tools for discerning variation within crop germplasm and studying evolutionary relationships (Jarret *et al*., 1992; Gepts, 1993). Although, no practical use of molecular markers exists in sweetpotato improvement to date, studies in phylogenetics and gene pool evaluation, (Jarret et al., 1992; Jarret and Bowen, 1994; He et al., 1995; Zhang *et al*., 1998; Zhang *et al*., 2001), genomic characterization (Villordon and La Bonte, 1995), finger printing (Conolloy *et al*., 1994), map-making strategies (Krienger *et al*., 2001), and a marker for root-knot nematode resistance (Ukoskit et al., 1997) are reported. Zhang *et al*. (2001) studied genetic diversity of 113 accessions from Latin America using SSR markers. Results showed that three regions, Mesoamerica (Guatemala, Mexico, Nicaragua, Panama, El Salvador), Peru and Ecuador, and Colombia and Venezuela, were distinct from one another based on alleles unique in each of the three areas. Mesoamerica was found to possess the most allelic diversity and hence warrants consideration as the primary source of genetic

diversity in sweetpotato. Earlier, dispersal studies by Zhang et al. (1998) showed that Pupua New Guinea sweetpotato cultivars were distinct from those in Peru. On the other hand Rossel et al. (2001) showed that accessions from Oceania are likely to have originated from Mesoamerica and not from Peru Ecuador. Based on molecular classification, Fajardo (2000) identified a core collection of 12 genotypes from a collection of 141 genotypes from Papua New Guinea.

High genetic diversity has been observed among the sweetpotato germplasm in East African region (Gichuki *et al*., 2003; and Gichuru, 2003; Abdelhameed *et al*., 2007; Yada *et al*., 2010) with the majority being farmers' varieties (Bashasha *et al*., 1995; Kapinga *et al*., 1995; Abidin, 2004) existing under different names. None of these studies has reported genetic diversity of OFSP farmer varieties. Under this study, a sample of what is considered African OFSP farmer varieties was assessed for genetic relatedness with counterpart white or cream-fleshed cultivars.

Germplasm Characterization for Quality Traits among Staple Crops

Germplasm characterization studies for quality traits are reported by various Consultative Group on International Agricultural Research centres for different staple crops. CIAT (International Centre for Tropical Agriculture) scientists have characterized various bean (for Fe and Zn) and cassava (for β-carotene) accessions. In over 1000 bean accessions evaluated, Fe concentrations ranging between 34 and 89 µg/g (average = 55 µg/g) and Zn concentrations ranging between 21 and 54 µg/g (average = 35 µg/g) are reported (Graham *et al*., 1999; Beebe et al., 2000). In cassava, β-carotene levels ranging between 0.1 and 2.4 mg/100 are reported for 630 core cassava genotypes from about 5500 CIAT's global collection (Iglesias *et al*., 1997). The genotypes containing the highest levels of β-carotene were collected from the Amazon region of Brazil and Colombia, where the indigenous farmers prefer yellow root lines.

At CIMMYT (International Maize and Wheat Improvement Centre), accessions of wheat and maize have been assessed for Fe and Zn. Monasterio and Graham (2000), revealed wheat grain Fe and Zn concentrations ranging between 28 to 56.5 µg/g (average 37.3 µg/g) and 25.2 – 53.3 µg/g (average 35.0 µg/g), respectively. The species *Triticum doccum* had the highest concentrations of Fe and Zn. On the other hand Fe and Zn concentrations in maize kernels seem not to be as high as in other cereals though improvement is possible (Welch and Graham, 2004). Twenty lines from South African germplasm showed a range between 16.4 and 22.9 µg/g (mean 19 µg/g) for Fe, and between 14.7 and 24.0 µg/g (mean of 19.8 µg/g) for Zn (Bazinger and Long, 2000). At IITA (International Institute of Tropical Agriculture), scientists observed Fe and Zn concentration ranges between 15.5 – 19.1 µg/g and 16.5 – 20.5 µg/g, respectively, among a number of early maturing lines of maize in Nigeria. Additional 1814 accessions from CIMMTY and evaluated in Zimbabwe and Mexico between 1994 and 1999 (Bazinger and Long, 2000), showed Fe and Zn concentrations ranges of 9.6 to 63.2 µg/g (average 23.76 µg/g) and 12.9 to 57 µg/g (average 33.27µg/g), respectively.

In sweetpotato germplasm, considerable variability of different nutritional traits has been reported (Woolfe, 1992; Ravindran *et al*., 1995; Saad, 1996; Laurie, 2008; Grüneberg *et al*., 2009b). Also extreme high genetic variation has been observed for ß-carotene among orange-fleshed types by CIP and partners (Manrique and Hermann, 2000; Grüneberg *et al*., 2005). Up to 8000 μg of ß-carotene per 100g of fresh weight have been recorded in some sweetpotato varieties tested by CIP (Hagenimana *et al*., 1999; Grüneberg *et al*., 2009b). However, scanty preliminary studies (Grüneberg *et al*., 2005) show low to medium values and high genetic variation for Fe, Zn, and Ca content in sweetpotato storage roots. More characterization studies have been recommended.

Application of Near Infrared Reflectance Spectroscopy (NIRS) in Rapid Screening of Quality Traits in Staple Crops

Successful selection for quality traits in plants and animals require adequate analytical procedures to measure them. Chemical analyses are expensive and often a few samples can be analyzed per unit time (Zum Felde *et al*., 2009). Yet breeding studies involve large populations that must be analyzed. NIRS has proven an accurate, precise, and rapid alternative to wet chemistry procedures for determining concentrations of major classes of chemical compounds in organic materials (Baye and Becker, 2004). It is a non-destructive, reliable and rapid method to determine quality traits simultaneously as an early screening method in many agricultural products. The method utilizes reflectance signals resulting from bending and stretching vibrations in molecular bonds between carbon, nitrogen, hydrogen and oxygen. Calibration is required to correlate the spectral response of each sample at individual wavelengths to known chemical concentrations from laboratory analyses. The technique has had a broad range of analytical applications. NIRS has been used to measure protein, oil and starch content in agricultural and food industries due to its convenience and easy sampling. In breeding studies the technique has equally had a broad range of applications. It has been effectively used to achieve rapid screening of germplasm (Baillères *et al*., 2002; Baye and Becker, 2004), assessing genetic control and heritability studies (Raymond, 2002) as well as prediction of disease/pest resistance (Cao *et al*., 2002). In sweetpotato, preliminary studies have been done to screen sweetpotato germplasm for micronutrients Fe, Zn and β-carotene concentrations (Grüneberg *et al*., 2009b).

Genetic and Environmental Interactions for Micronutrient Traits

Genotype by environment (GxE) interaction is the differential response of crop genotypes to changing environmental conditions. Such interactions complicate testing and selection in breeding programs and result in reduced overall genetic gains of the desired traits (Shafii and Price, 1998). They are of great interest when evaluating the stability of breeding clones under different environmental conditions. Understanding of GxE therefore, allows making of informed choices regarding which locations and input

systems to be used in the breeding efforts (Grüneberg *et al*., 2005). In spite of wide adaptability to harsh growing conditions, GxE studies on several traits (Collins et al., 1987; Bacusmo *et al*., 1988; Woolfe, 1992; Ngeve, 1993, Ravindran *et al*., 1995; Grüneberg et al., 2005, Ndirigwe, 2005) have shown that sweetpotato is sensitive to environmental variation. For example, sweetpotato root yield and yield components have been shown to be highly sensitive to changes in environment (Bacusmo *et al*., 1988; Manrique and Hermann, 2000; Grüneberg *et al*., 2005). GxE interactions for quality traits such as dry matter, starch, total protein, sugar and ß-carotene have been studied with contrasting findings. Li (1976) observed environmental influence on protein, sugar, and ß-carotene contents of sweetpotato, and none for dry matter. Contrastingly, Jones *et al*. (1986) observed that breeding for quantitative traits like root dry matter in hexaploid sweetpotato has partly been inhibited by the significant GxE interactions. In Rwanda, Ndirigwe (2005) observed significant GxE interactions for β-carotene levels with the increasing trend in the high altitudes. Zhang and Collins (1995) found significant GxE interactions for trypsin inhibitor activity, crude protein, and true protein. However, a significant proportion of the GxE interaction could be explained by linear environment effect. Recent studies (Grüneberg et al., 2009b, Grüneberg *et al*., 2005) agree with some studies and disagree with others depending on the quality traits. Grüneberg et al. (2005) showed general low GxE interaction effects for nutritional traits root dry matter, starch, root and leaf ß-carotene content, as well as chlorophyll content. Earlier, Manrique and Hermann (2000) equally reported low GxE interaction effects of ß-carotene content in sweetpotato. However, it is important to observe that few GxE studies are reported for mineral nutrients (e.g. Fe and Zn) in sweetpotato. Yet mineral nutrients are part of the breeding targets for sweetpotato by CIP and partners. In other staple crops significant GxE for both Fe and Zn are reported in beans (Beebe *et al*., 2000) and wheat grains (Monasterio and Graham, 2000).

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CHAPTER ONE 01

Evaluation of Dry Matter, Protein, Starch, ß-carotene, Iron, Zinc, Calcium and Magnesium in East African Sweetpotato [*Ipomoea batatas* (L.) Lam] Germplasm

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Additional Index words: Biofortified crops, protein, starch, sucrose, β-carotene, iron, zinc, calcium, and magnesium contents, Near infrared reflectance spectroscopy (NIRS) technology, *Ipomea batatas*.

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Abstract

The present study evaluated selected East African (EA) sweetpotato varieties for storage root dry matter and nutrient content, and obtained information on the potential contributions of the varieties to alleviate vitamin A and mineral deficiencies. Roots obtained from 89 farmer (white- and orange-fleshed) varieties and one introduced variety ('Resisto'), were analyzed for storage root quality using Near Infrared Reflectance Spectrometry. Location differences were only significant for starch content. The σ_G^2 variance was significant ($p < 0.01$) for all the traits except sucrose content. Overall, the farmer varieties had higher dry matter, higher starch, and lower sucrose contents than the check, 'Resisto'. It is these qualities that make sweetpotato attractive as a starchy staple in EA. A low population's mean β-carotene content (19.0 ppm) was observed. However, deep orange-fleshed farmer varieties, 'Carrot_C', 'Ejumula', 'Carrot Dar' 'Mayai' and 'Zambezi' had β-carotene content that can meet 350% or greater recommended daily allowance (RDA) with 250 g serving to a 5 – 8 year old child. More but light orange-fleshed farmer varieties K-118', 'K-134', 'K-46', 'KMl61', 'MLE162 Nakahi', 'PAL161', 'Sowola6', 'Sponge', 'SRT34 Abuket2', 'SRT35 Anyumel', 'SRT52' and 'Sudan' can provide 50 - 90% RDA of the child. The root minerals' content was generally low except for magnesium whose content can meet 50% or greater RDA in many farmer varieties. However, in areas with high sweetpotato consumption, varieties 'Carrot_C', 'Carrot Dar', 'KRE Nylon', 'MLE163 Kyebandula' and 'SRT49 Sanyuzameza' can make good intakes of iron, zinc, calcium, and magnesium. In conclusion, some EA farmer varieties can contribute greatly to alleviation of vitamin A deficiency and substantial mineral intakes.

Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam] ranks fifth in importance for its caloric contribution in developing countries after rice, wheat, maize and cassava (CIP, 2005). In some areas of East Africa (EA) the crop has become a staple (Scott et al., 2000). For example, in Uganda the daily intake of sweetpotato is estimated to be 240 g per day per person (FAOSTAT, 2007). Information about quality attributes of African sweetpotato germplasm is very limited. The average storage root dry matter (DM) of the cultivated sweetpotato clones of the world is ≈30% (Woolfe, 1992; Bradbury and Holloway, 1988). Two main taste groups can be distinguished: (i) white- and cream-fleshed sweetpotatoes usually with DM contents of ≈25 to 35% and (ii) orange-fleshed, sweetpotatoes (OFSP) with DM of ≈20 to 30% and high provitamin A carotenoids (Grüneberg *et al*., 2009; Martin and Jones, 1986). The taste preference in Sub-Saharan Africa is clearly the dry and low sweet type, which is nearly exclusively white-fleshed.

Carotenoid pigments provide OFSP storage roots the orange flesh color. More than 60 mg total carotenoids in 100 g DM have been reported (Woolfe, 1992). A constant high proportion (≈90%) of β-carotene in relation to total carotenoids in OFSP has been known for decades (Ezell and Wilcox, 1958; Purcell, 1962; Purcell and Walter, 1968; Haggenimana *et al*., 1998), and currently OFSP is considered a complementary food approach to alleviate vitamin A deficiency (VAD) in the world (Low *et al*., 2001, 2007). Modern OFSP varieties that are more adapted to African consumer preferences than traditional moist and sweet OFSP have been bred and released in Uganda (Mwanga *et al*., 2007, 2009). Also, OFSP farmer varieties that meet local consumer preferences have been found in EA (Tumwegamire *et al*., 2004; CIP, 2005). Approximately 80 to 90% of sweetpotato storage root DM is made up of carbohydrates, mainly starch (≈60 to 70% of DM) and sugars (≈15 to 20% of DM with a wide range from ≈5 to 40% of DM), and lesser amounts of pectins, hemicelluloses and cellulose (Woolfe, 1992). Usually white- and cream-fleshed varieties have higher starch (≈50 to 80% of DM) and lower sugar contents (≈5 to 15 % of DM) compared with OFSP genotypes, which have lower starch (≈45 to 55 % of DM) and higher sugar contents (≈10 to 20 % of DM) (Woolfe, 1992). Additionally, the storage root of sweetpotato also contains reasonable amounts of protein [≈5% of storage root DM] (Woolfe, 1992). Studies on sweetpotato storage root mineral contents (especially trace minerals)

are limited, particularly for African sweetpotato germplasm. Bradbury and Holloway (1988) reported storage root mineral content ranges of ≈75 to 740 ppm calcium, ≈180 to 350 ppm magnesium, ≈1.6 to 9.4 ppm iron, and ≈2.7 to 18.9 ppm zinc in sweetpotato accessions from the South Pacific. Courtney (2007) observed up to ≈10 ppm iron and ≈6.4 ppm zinc in fresh storage roots for North American breeding material.

The pro-vitamin A and minerals (Fe, Zn, Ca, and Mg) are critical and deficient in human food supply (Frossard et al., 2000; Munoz et al., 2000). In Uganda, ≈20% of children and 19% of women are vitamin A deficient; and 73% of children and 49% of women are anemic (UBOS and Macro International Inc., 2007). The levels of anemia are higher among pregnant (64%) and breast feeding (53%) mothers. Worldwide, 127 million preschool children and more than 7.2 million pregnant women in developing countries suffer from vitamin A deficiency (VAD) (Bouis, 2003; West, 2002) and approximately 2 billion people are anemic (Frossard *et al*.; 2000). Another 13.5 million pregnant women have low vitamin A status (West, 2002). Globally, 800,000 and 700,000 deaths per year are attributed to Fe and Zn deficiencies, respectively (Black, 2003). According to Black (2003) 2.4%, 1.8% and 1.9% of the global disease burden is attributable to Fe deficiency, vitamin A deficiency and Zn deficiency, respectively. OFSPs have been demonstrated to have a great potential to alleviate VAD around the Lake Victoria region and East African highlands (Low *et al*., 2001). However, the majority of sweetpotato varieties consumed in EA are white-fleshed. Also, the traditional OFSP with their moist and sweet taste are unlikely to be accepted on a broad basis in EA. Fortunately, African OFSP farmer varieties and modern breeding lines have been identified and are currently being promoted by CIP and HarvestPlus in Uganda and Mozambique (Mwanga et al., 2009). The present study evaluated selected East African sweetpotato accessions for storage root quality (dry matter, protein, starch, sucrose, ß-carotene, iron, zinc, calcium and magnesium), and obtained information on the potential contributions of the accessions to alleviate vitamin A and mineral deficiencies in EA region.

Materials and Methods

Ninty sweetpotato accessions were used in this study (Table 1.1). All varieties were farmer varieties from EA, except the modern variety 'Resisto' from the United States of America. Non-Ugandan accessions had been introduced for regional trials during early 2005. The variety, 'Resisto', was used in this study as a check to compare OFSP varieties of African origin with the typical moist and sweet OFSP type of non-African origin. It should be noted that several nutritional studies have used 'Resisto' to investigative effects on human vitamin A status due to OFSP consumption (Low *et al*. 2007; van Jaarsvield *et al*., 2005). Thirty-two of the farmer varieties were OFSP cultivars, with varied intensities of orange flesh color. One cultivar, 'Kwezikumwe', was purple-fleshed. The remaining accessions were cream, white or yellow-fleshed varieties. Sixty five farmer varieties were from Uganda, 19 from Kenya, four from Tanzania and one from Zambia.

The field trials were planted at the National Crops Resources Research Institute (NaCRRI) at Namulonge close to lake Victoria (1150 m.a.s.l), and Kachwekano Zonal Agricultural Research Institute (2220 m.a.s.l) in the south western highlands of Uganda (Table 1.2). Namulonge has a bimodal rainfall pattern of 1270 mm per year, annual mean temperature of 22.2 ^{o}C (mean maximum temperature = 28.4^{o}C, mean minimum temperature = 15.9^{o}C), ferralitic soils (red sandy clay loams) and soil pH 4.9 to 5.0. Kachwekano has a bimodal rainfall of 1319 mm per year, annual mean temperature of 18^{o}C, latosolic soils (sandy clay loam), and soil pH 5.8 – 6.2. During the second rain season of 2005 (starting in October), each variety was planted on two-row plots using 20 vines placed 30 cm apart. The rows were 1 m apart and each variety was planted with two plot replications in a randomized complete block design. The plots were kept weed free and no fertilizer or other agro-chemicals were applied. Harvest was carried out five months after planting at Namulonge and seven month after planting at Kachwekano, using the local practice of sweetpotato crop duration in these different eco-geographic zones.

Table 1.1. List of Sweetpotato varieties used for quality characterization at Namulonge and Kachwekano in Uganda during 2005/06.

Variety name	CIP code	Plant type	Country Origin	Cultivar Type	Storage root		
					Flesh color	Skin colour	Form
Obuogo1	i.p.	n.a	Kenya	FV	Cream	Cream	n.a
KBL640 Africare	No	Semi-erect	Uganda	FV	LO	Cream	Long elliptic
APA343	No	Semi-erect	Uganda	FV	LO	Cream	Round elliptic
APA348 Liralira	No	Semi-erect	Uganda	FV	Cream	Purple red	Elliptic
APA352 Oketodede	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Round elliptic
APA365 Anam Anam	i.p.	Erect	Uganda	FV	Cream	Cream	Elliptic
ARA208 Ombivu	i.p.	Semi-erect	Uganda	FV	Cream	Purple red	Round elliptic
ARA214	i.p.	Semi-erect	Uganda	FV	LO	Cream	Round elliptic
ARA244 Shinyanga	i.p.	Semi-erect	Uganda	FV	LO	Cream	Long elliptic
Bunduguza	i.p.	Spreading	Uganda	FV	Cream	Purple red	Round elliptic
Bungoma	No	Semi-erect	Uganda	FV	Cream	Purple red	Elliptic
Carrot_C	i.p.	Spreading	Tanzania	FV	DO	Cream	Long irregular
Carrot Dar	i.p.	Semi-erect	Tanzania	FV	DO	Cream	Long elliptic
Dimbuka	No	Semi-erect	Uganda	FV	Cream	Cream	Obovate
Ejumula	No	Spreading	Uganda	FV	DO	Cream	Long irregular
HMA490 Kawogo	No	Semi-erect	Uganda	FV	Cream	Brown	Ovate
HMA493 Tanzania	i.p.	Spreading	Uganda	FV	LO	Cream	Long elliptic
IGA963 Nyongerabarenzi	No	Erect	Uganda	FV	Cream	Cream	Round elliptic
K-118	i.p.	Semi-erect	Kenya	FV	LO	Cream	Long elliptic
K-134	No	Erect	Kenya	FV	LO	Purple red	Round elliptic
K-207	No	n.a	Kenya	FV	Yellow	Cream	n.a
K-37	i.p.	n.a	Kenya	FV	LO	Cream	Elliptic
K-46	i.p.	Semi-erect	Kenya	FV	Orange	Purple red	Round elliptic
KBL627 Mukazi	i.p.	Spreading	Uganda	FV	Cream	Cream	Long elliptic
KBL632 Nyinakamanzi	No	Spreading	Uganda	FV	Cream	Purple red	Round
KMI56 Opira	No	Erect	Uganda	FV	Cream	Brown	Long irregular
KMI59 Kampala	i.p.	Semi-erect	Uganda	FV	Cream	Purple red	Long elliptic
KMI61	i.p.	Semi-erect	Uganda	FV	Orange	Cream	Long elliptic
KMI78 Osukari	No	Semi-erect	Uganda	FV	Cream	Purple red	Obovate
KMI81 Ikala	i.p.	Semi-erect	Uganda	FV	LO	Cream	Round elliptic
KMI83 Ikala2	i.p.	Semi-erect	Uganda	FV	LO	Cream	Elliptic
KML883 Silkempya	No	Semi-erect	Uganda	FV	White	Cream	Elliptic
KRE716 Nylon	No	Spreading	Uganda	FV	Cream	Cream	Ovate
KRE726 Kwezikumwe	No	Semi-erect	Uganda	FV	Purple	Purple red	Elliptic
KRE733 Kitambi	i.p.	Spreading	Uganda	FV	Cream	Purple red	Round
KSR673Mabereikumi	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Ovate
KSR652 Mugumire	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Long elliptic
KSR662 Kakoba	i.p.	Semi-erect	Uganda	FV	Yellow	Purple red	Elliptic
KSR664 Mulerabana	No	Semi-erect	Uganda	FV	Cream	Pink	Long elliptic
KSR675 Norall	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Round
Kunykubiongo	No	Erect	Kenya	FV	Cream	Purple red	Elliptic
Kyabafuriki	No	Spreading	Uganda	FV	Cream	Cream	Round elliptic
LIR257 Otada	No	Semi-erect	Uganda	FV	Cream	Cream	Round elliptic
LIR296	i.p.	Semi-erect	Uganda	FV	PY	Purple red	Round elliptic

Table 1.1. Continued.

Variety name	CIP code	Plant type	Country Origin	Cultivar Type	Storage root		
					Flesh color	Skin colour	Form
Mayai	No	Semi-erect	Tanzania	FV	DO	Cream	Long elliptic
MBR 539 Kitekamaju	i.p.	Semi-erect	Uganda	FV	White	Cream	Elliptic
MBR524 Nkwasahansi	i.p.	Semi-erect	Uganda	FV	Cream	Purple red	Long irregular
MBR536 Karebe	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Elliptic
MBR552 Kahungezi	No	Semi-erect	Uganda	FV	Cream	Purple red	Ovate
MBR560 Mugurusi	No	Semi-erect	Uganda	FV	Cream	Cream	Long irregular
MBR580 Nylon	No	Semi-erect	Uganda	FV	Cream	Purple red	Long elliptic
MBR600 Kisakyabikiramaria	No	Semi-erect	Uganda	FV	Cream	Cream	Long elliptic
MLE166	No	Semi-erect	Uganda	FV	LO	Purple red	Round
MLE162 Nakahi	No	n.a	Uganda	FV	LO	Cream	n.a
MLE163 Kyebandula	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Long elliptic
MLE165 Namafumbiro	No	Semi-erect	Uganda	FV	Cream	Cream	Elliptic
MLE173 Kijovu	i.p.	Semi-erect	Uganda	FV	Cream	Purple red	Long irregular
MLE184 Manafayereta	No	Semi-erect	Uganda	FV	White	Pink	Long irregular
MSK1025 Bitambi	i.p.	Erect	Uganda	FV	Cream	Brown	Long irregular
MSK1047 Bwanjure	i.p.	Semi-erect	Uganda	FV	White	Purple red	Long irregular
Nyaguta	i.p.	n.a	Kenya	FV	Cream	Pink	Long elliptic
Nyandere	i.p.	n.a	Kenya	FV	PY	Purple red	Elliptic
Nyathiodiewo	No	Spreading	Kenya	FV	LO	Purple red	Round
Nyatonge	i.p.	n.a	Kenya	FV	Cream	Cream	n.a
Obuogo2	No	n.a	Kenya	FV	White	Purple red	n.a
Oguroiwe	i.p.	Semi-erect	Kenya	FV	Cream	Cream	Long elliptic
PAL153 Abukoki	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Elliptic
PAL161	i.p.	Semi-erect	Uganda	FV	LO	Cream	Elliptic
Pipi	i.p.	n.a	Tanzania	FV	LO	Cream	n.a
Resisto	440001	Semi-erect	USA	MV	DO	Brown	Ovate
Sowola (389A)	No	Semi-erect	Uganda	FV	Cream	Brown	Elliptic
Sowola 6	No	Semi-erect	Uganda	FV	LO	Cream	Long irregular
Sponge	No	Semi-erect	Kenya	FV	LO	Purple red	Round elliptic
SRT14 Nora	No	Erect	Uganda	FV	Cream	Purple red	Elliptic
SRT01 Osapat	i.p.	Erect	Uganda	FV	Yellow	Cream	Obovate
SRT02 Araka White	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Ovate
SRT30 Nyara	No	Semi-erect	Uganda	FV	LO	Cream	n.a
SRT33 Abuket1	i.p.	Semi-erect	Uganda	FV	Orange	Pink	Long elliptic
SRT34 Abuket2	i.p.	Semi-erect	Uganda	FV	LO	Cream	Elliptic
SRT35 Anyumel	No	Erect	Uganda	FV	LO	Cream	Round elliptic
SRT39 Rwanda	No	Semi-erect	Uganda	FV	Orange	Cream	Round elliptic
SRT40 Mary	No	Semi-erect	Uganda	FV	Cream	Cream	Long elliptic
SRT49 Sanyuzameza	No	Erect	Uganda	FV	Yellow	Purple red	Long oblong
SRT52	No	Erect	Uganda	FV	Orange	Cream	Oblong
Sudan	No	Spreading	Uganda	FV	LO	Cream	Long elliptic
Tororo 3	i.p.	Semi-erect	Uganda	FV	Cream	Cream	Long elliptic
Ukerewe	i.p.	Semi-erect	Tanzania	FV	Yellow	Purple red	Elliptic
Wagaborige	i.p.	Spreading	Uganda	FV	Cream	Cream	Round
Wera	i.p.	n.a	Kenya	FV	Yellow	Cream	n.a
Zambezi	i.p.	Semi-erect	Zambia	FV	DO	Purple red	Round elliptic

i.p. = designation of CIP code in process, No = no acquisition from the gene bank at CIP.
FV = Farmer variety; MV Modern variety.
DO = Deep orange, LO = Light orange, PY = Pale yellow.

Plots were harvested by uprooting the center of each row, leaving a plant at both ends of each row. The harvested roots were collected into a composite pile and a sample of five roots each between 100 and 300 g weight was taken for dry matter, protein, starch, sucrose, β-carotene, Fe, Zn, calcium, and magnesium determination. The roots were washed of soil particles and rinsed with abundant tap water, peeled, and each root cut longitudinally into four sections. Two opposite sections of each of the sectioned roots were taken to prepare a 100 g compound sample that was placed in transparent polythene bags, and freeze dried at -31°C for 72 hours. Dry samples were weighed, milled into flour in a stainless steel mill and stored in Kraft paper bags.

Percent root dry matter was calculated from flesh and dry weight estimates. Near infrared reflectance spectroscopy (NIRS) technology (Shenk and Westerhaus, 1993) was used to determine protein, starch, sucrose, β-carotene, Fe, Zn, calcium and magnesium in milled samples of freeze dried storage root samples. NIRS technology has been used to screen for macro-nutrients in root and tuber crops (Haase, 2006; Young *et al*., 1997; Mehrübeoglu and Coté, 1997) including sweetpotato (Lebot *et al*., 2009; Lu *et al*., 2006), and has been tested for minerals in agricultural commodities (Cozzolino and Moron, 2004, Halgerson *et al*., 2004). Also the technology has become a standard fast screening method for mirco-nutrients (pro-vitamins A, iron and zinc) (Zum Felde *et al*., 2009; Pfeiffer and McClafferty, 2007). Each milled sample material (two times 3 g) was analysed by NIRS within the range of 400 to 2500 nm on a NIRS monochromator model 6500 (NIRSystems, Inc. Silver spring, MD) using small ring cups with sample autochanger. Near-infra-red spectra of each sample were stored in a computer file and in 2009 these spectra were again used to determine protein, starch, sucrose, β-carotene, Fe, Zn, calcium and magnesium with the latest calibration version for sweetpotato freeze dried samples (Zum Felde, 2009). In this version the correlations in cross validation

Table 1.2. Description of locations used for the evaluation of farmer varieties.

Location	Ecogeographic region	Soil types	Altitude (m.a.s.l)	Rainfall† (mm)	Temperature† °C	
					Mean	Range
Namulonge	Tropical rain forest	Sandy clay soils (pH 4.9 to 5.0)	1150	359.0	23.1	16.1 - 30.1
Kachwekano	Tropical mountain region	Sandy clay Loam (pH 5.8 to 6.2)	2220	423.1	18.1	11.9 - 24.2

†Rainfall (mm) and temperature experienced during the crop growing period: Oct. 2005 to Feb. 2006 at Namulonge; Oct. 2005 to Apr. 2006 at Kachwekano.

between standard laboratory reference methods and NIRS are 0.95, 0.96, 0.80, 0.97, 0.80, and 0.89, for protein, starch, sucrose, β-carotene, iron, and zinc, respectively (Zum Felde, 2009) and 0.92 and 0.78 for calcium and magnesium, respectively (Zum Felde pers. Comm.). The reference methods for NIRS calibration were Dumas according to Sweeney and Rexroad (1987) for crude protein, polarimetrically by hydrochloric acid dissociation according to ICC No. 123/1 (ICC, 1994) for starch, high performance liquid chromatography (HPLC) according to Rodriguez-Amaya and Kimura (2004) for β-carotene, inductively coupled plasma argon optical emission spectrometer (ICP-OES), according to Bridger and Knowles (2000) and reviewed by Aceto et al (2002) for Fe, Zn, calcium and magnesium. For sucrose determination we used a procedure in which a water extract of the freeze-dried samples (0.1 g in 100 mL) was used: (i)The samples were incubated in a water bath at 60°C for 1 h and afterwards, they were treated with each 0.2 mL Carrez I and Carrez II solution to remove proteins. (ii) Samples were purified by centrifugation (Sorvall RC-5B Refrigated Superspeed, GMI, Ramsay, USA) for 10 min and 20°C with 10000 rpm, total sugars were determined from the membrane-filtered supernatant (pores size 0.45 µm), and sucrose, glucose, fructose, maltose and galactose were separated using a LiChrospher 100 NH2 (5 µm) 4 x 4 mm pre-column in combination with a LiChrospher 100 NH2 (5 µm) 4 x 250 mm separation column (Merck KGaA, Darmstadt, Germany) and an acetonitrile - pure water solution (80:20 v/v) as mobile phase (flow rate 1.0 mL min^{-1}) at 20 °C and an injection volume of 20 µL. Sugars were detected with a Knauer differential refractometer 198.00 (Knauer, Berlin, Germany).

Statistical analyses were conducted using PLABSTAT (Plant Breeding Statistical Program) computer package (Utz, 2001) and SAS6.12 (SAS Institute 1988; 1997). Data were classified relative to varieties or genotypes (G), locations (L), and blocks or replications (R). In an analysis of variance (ANOVA), each trait xi (namely, protein, starch, sucrose, ß-carotene, Fe, Zn, calcium and magnesium) was analyzed from each experimental site separately to determine outliers, experimental means, coefficients of variation, minimum and maximum values using the SAS procedure GLM and the model statement X_i = G + R, which corresponds to the statistical model

$$Y_{ijl} = \mu_i + g_{ij} + bl_{il} + \varepsilon_{ijl},$$

where Y_{ijl} is the plot value of the *i*th trait of the *j*th genotype and the *l*th block, μ_i is the trial mean of the *i*th trait, g_{ij}, is the effect of genotypes, bl_{il} is the effect of blocks, and ε_{ijl} is the plot error. For the analysis across locations an ANOVA was carried out for each trait x_i using PLABSTAT, with the model statement X_i = G + L + GL + R: L + RGL, which corresponds to the statistical model

$$Y_{ijkl} = \mu_i + g_{ij} + l_{ik} + gl_{ijk} + bl(l)_{il(k)} + \varepsilon_{ijkl}$$

where l_{ik} and gl_{ijk} are the effects of locations and genotype-location interactions, respectively, and other effects as designated above. In the first analysis all effects were considered random in order to use the ANOVA to estimate the magnitude and significance of variance components for σ^2_G, σ^2_L, σ^2_{GxL}, and

σ^2_ε. In a second analysis the effects g_{ij}, l_{ik} and gl_{ijk} were considered as fixed to estimate the least significant difference (LSD) to compare means among varieties and locations for each trait.

Correlations among traits were carried out by SAS procedure CORR and the optional statement PEARSON. The correlations were calculated for each location and replication separately, followed by calculating the average correlation between each trait pair across locations and replications using the statement BY in SAS procedure CORR. These correlations are still phenotypic correlations, but can be considered as a good approximation of genotypic correlation estimates (Hill *et al*., 1998).

In the final analysis the contribution of sweetpotato to the recommended daily allowance (RDA) for β-carotene, Fe, Zn, calcium and magnesium were calculated by assuming an intake of 250 g fresh sweetpotato storage root per day (comparable to the consumption estimates for Uganda). The RDAs for school age children from five to eight years were based on the Institute of Medicine in the United States (National Academy of Sciences, 2004) statistics. These RDA per day are: 400 µg Retinol, which corresponds to 4.8 mg β-carotene, 10 mg iron, 5 mg zinc, 800 mg calcium, and 130 mg magnesium. For each, β-carotene, Fe, Zn, calcium and magnesium data value, the corresponding % RDA were calculated by: % RDA = nutrient content in 250 g fresh weight basis (fwb) / RDA * 100. To compare varieties for their value in RDA contribution the LSDs were calculated for % RDA as described for other traits above.

Results

Differences in the experimental means between locations were not large for all the traits, except storage root starch content (Table 1.3). Storage root yield means were 7.5 t ha^{-1} for Namulonge and 10.0 t ha^{-1} for Kachwekano. However, some accessions had higher storage root yields than respective means at both locations. At Kachwekano, storage root starch and sucrose contents were respectively higher and lower than at Namulonge (Table 1.3). The lowest storage root sucrose contents for farmer varieties were 4.3% and 4.7% at Namulonge and Kachwekano, respectively.

Table 1.3. Experimental means ($\bar{x}$), coefficient of variation (CV %), minimum (min) and maximum (max) genotypic values for observed traits at locations.

Trait	Namulonge				Kachwekano			
	$\bar{x}$	CV %	Min	Max	$\bar{x}$	CV %	Min	Max
Storage root yield, t ha^{-1}	7.5	47.8	0	18.1	10.0	56.0	0.2	21.3
Dry matter content of storage roots, %	32.3	5.5	19.4	38.3	31.7	6.8	20.8	36.7
Protein content of storage roots, % DM	6.8	13.4	4.0	9.2	6.5	16.0	3.8	9.5
Starch content of storage roots, % DM	60.5	3.2	30.1	68.2	68.2	3.2	62.2	73.4
Sucrose content of storage roots, % DM	11.4	14.6	4.3	48.7	9.4	18.0	4.7	13.8
β-carotene content of storage roots, ppm DM	36	40.6	0	338	24	65.9	0	295
Iron content of storage roots, ppm DM	23.7	8.9	17.3	33.2	19.5	11.1	14.7	26.9
Zinc content of storage roots, ppm DM	12.3	11.0	9.5	17.8	9.5	12.1	5.9	12.7
Calcium content of storage roots, ppm DM	1980	21.2	929	4411	1880	18.0	1029	3795
Magnesium content of storage roots, ppm DM	569	25.4	169	1416	676	25.12	363	1392

DM = dry matter

At Namulonge, means for protein, β-carotene, Fe, Zn, and calcium were slightly higher than at Kachwekano. Maximum values for β-carotene were high at both locations, while the mean values for β-carotene were low (approximately two-thirds of the farmer varieties used in the study were white-fleshed). The CV (CV given as a percentage) values for observed traits were low to moderate, except storage root yield and β-carotene content of storage roots (greater than 30%).

Table 1.4. Estimated variance components, variance component ratios in brackets, and operational broad-sense heritabilities of observed traits†.

Trait	σ^2_G	σ^2_L	σ^2_{GL}	σ^2_ε	h^2
Storage root yield,	8.01**	-4.56	4.83*	22.05	0.50
t ha^{-2}	(1)	(-0.56)	(0.60)	(2.75)	
Dry matter content of storage roots, %	4.94**	-0.97	3.62**	3.89	0.64
	(1)	(-0.20)	(0.73)	(0.79)	
Protein content of storage roots, % DM	0.32**	0.06	0.34**	0.94	0.44
	(1)	(0.18)	(1.05)	(2.94)	
Starch content of storage roots, % DM	5.31**	29.78**	13.88**	4.24	0.40
	(1)	(5.61)	(2.62)	(0.80)	
Sucrose content of storage roots, % DM	1.30	1.86*	12.09**	2.81	0.16
	(1)	(1.44)	(9.32)	(2.16)	
β-carotene content of storage roots, ppm DM	4362**	60**	430**	183	0.94
	(1)	(0.01)	(0.10)	(0.04)	
Iron content of storage roots, ppm DM	1.97**	8.72**	2.63**	4.54	0.45
	(1)	(4.42)	(1.33)	(2.30)	
Zinc content of storage roots, ppm DM	0.81**	3.80**	0.64**	1.59	0.53
	(1)	(4.70)	(0.79)	(1.97)	
Calcium content of storage roots, ppm DM	52643*	-23551	137272**	145497	0.33
	(1)	(-0.45)	(2.61)	(2.76)	
Magnesium content of storage roots, ppm DM	15008**	4306	15355**	24607	0.52
	(1)	(0.29)	(1.02)	(1.64)	

* Significant at the 0.05 level.
** Significant at the 0.01 level.

† Variance components: σ^2_G = genotypes, σ^2_L = locations, σ^2_{GxL} = genotype-location interactions, σ^2_ε = error; h^2 = operational broad-sense heritability.
‡ DM dry matter.

The σ^2_G, variance component was significant ($p < 0.01$) for all traits, except storage root sucrose content (Table 1.4). For several observed traits the σ^2_L, variance component was not significant ($p>0.05$), except starch, β-carotene, Fe and Zn. In contrast the σ^2_{GxL} variance component was significant ($p < 0.01$) for all traits. The σ^2_G : σ^2_{GxL} ratios were high (1: 0.1 for β-carotene content) to extremely low (1: 9.32 for sucrose content). It should be noted that the $\sigma^2_G : \sigma^2_{GxL}$ ratio for sucrose is extreme for a quality trait. Mainly due to the magnitude of $\sigma^2_G : \sigma^2_{GxL}$ ratios within the interval 1 : 0.5 and 1 : 3.0 for most traits as well as the number of locations (2) the operational broad sense heritabilities (h^2) were moderate (0.3 to 0.6) for most traits, and only high for β-carotene content of storage roots (0.94).

The population means (across varieties, locations and replications) for storage root yield were low (8.6 t.ha^{-1}) (Table 1.5), but higher than the national average of 4.2 t.ha^{-1}(Yanggen and Nagujja, 2006). Compared with averages given for cultivated sweetpotato clones of the world, higher population means for storage root dry matter (32.1%) and starch content (64.4%) were observed. In contrast, sucrose population's mean (10.3%) was clearly low. The population mean values observed for storage root Fe, Zn, calcium, and

magnesium were 21.6 ppm, 10.9 ppm, 1950 ppm, and 626 ppm, respectively. However, an important finding was that nearly all light to deep OFSP farmer varieties clearly contain pro-vitamin A β-carotene. For the OFSP check ('Resisto') a storage root β-carotene content of 271 ppm was observed.

Table 1.5. Clone means of farmer varieties for observed traits across locations.

Farmer variety	Observed traits[†]									
	YLD (tha^{-1})	DM (%)	PRO (%)	STA (%)	SUC (%)	BC (ppm)	Fe (ppm)	Zn (ppm)	Ca (ppm)	Mg (ppm)
APA343	5.3	32.5	5.7	63.9	11	12	19.7	9.7	1582	523
APA348 Liralira	11.2	39.0	6.8	69.9	-	0	20	9.7	1748	607
APA352 Oketodede	13.9	32.4	5.9	65.8	10.1	0	19.6	10.3	1587	478
APA365 Anam Anam	12.3	33.0	5.7	67.1	8.9	0	20.1	10.4	1789	540
ARA208 Ombivu	12.2	29.6	8.2	66.3	9.9	0	23.2	12.4	1550	401
ARA214	8.4	31.9	6.2	64.3	9.6	27	19.9	10.3	1500	520
ARA244 Shinyanga	14.3	24.7	5.3	57.7	14	64	20.2	9.3	1685	561
Bunduguza	5	35.3	6	66.6	10.7	0	19.8	8.6	2033	660
Bungoma	11.9	33.4	6.2	67.5	6.4	0	20.8	10.1	1699	644
Carrot C	5.5	33.2	8.2	58.7	13.7	259	26.1	12.7	2591	924
Carrot Dar	7.8	31.1	8	58.2	13.7	272	28.4	14.4	2232	981
Dimbuka	16.8	32.2	7.5	67.1	8.3	0	21.2	11.3	1778	539
Ejumula	8.4	32.7	7.4	58	13.4	240	23.8	11.4	2263	848
HMA 490 Kawogo	1.3	32.6	6.1	65.5	8.6	0	20.1	10.4	1709	456
HMA493 Tanzania	1.8	33.4	6.1	65.8	8.4	29	20.2	9.7	1996	682
IGA963 Nyongerabarenzi	15.5	30.7	6.6	66.2	9.5	1	20.6	10.8	1525	374
K-118	5.5	30.7	7.2	62.8	11.6	38	21.4	11.5	1350	470
K-134	10.3	31.9	6.7	64.5	10.5	40	21.1	11.1	1885	616
K-207	5.8	37.4	5.8	67.5	7.4	0	20.4	9.7	2888	857
K-37	2.8	34.1	4.7	66.6	7.4	25	18	8.2	2426	665
K-46	4.5	33.7	6.6	62.9	11.3	48	21.3	10.7	2522	730
KBL627 Mukazi	8.1	35.8	6.6	64.4	12.4	0	22.7	10.9	2053	747
KBL632 Nyinakamanzi	7.1	31.3	6.6	68	7.4	1	20.9	11.4	2128	694
KBL640 Africare	15.3	30.2	6.5	63.6	11.4	15	20.2	9.9	1392	467
KMI56 Opira	10.6	31.3	6.8	65	9.5	0	22.9	11.2	1978	763
KMI59 Kampala	11.6	32.6	7.1	63.8	9.8	0	22.9	10.1	1904	651
KMI61	7.9	33.4	7.4	64.4	10.5	75	23	11.3	1333	496
KMI78 Osukari	6.5	31.5	8.4	66.1	8.6	0	22	11.8	1543	531
KMI81 Ikala	11.7	25.6	7.3	60	12.1	28	22.7	12.6	1594	495
KMI83 Ikala2	11.9	29.9	7.4	63.2	11.7	11	21.2	10.8	1620	507
KML883 Silkempya	13.8	35.1	6.2	68.7	8	0	20.1	9.4	1931	485
KRE716 Nylon	2.5	36.1	6.9	66.7	8.3	-1	22.8	11.6	2569	816
KRE726 Kwezikumwe	16.6	31.7	5.9	69.3	8.3	9	19.2	10.7	1426	445
KRE733 Kitambi	3.8	35.2	6.3	66.4	8.6	0	21.9	11	1977	661
KSR673 Mabereikumi	6.6	33.5	6.2	67.4	7.5	0	21.1	11.3	1505	365
KSR652 Mugumire	1.9	34.9	7.5	66.9	8.9	1	21.1	10.9	2029	412
KSR662 Kakoba	7.5	32.7	4.8	68	7.9	1	18.3	9.6	2313	568
KSR664 Mulererabana	5.8	31.4	7.5	66.8	8.4	1	22.7	10.9	2056	738

Table 1.5. Continued.

Farmer variety	Observed traits†									
	YLD (tha^{-1})	DM (%)	PRO (%)	STA (%)	SUC (%)	BC (ppm)	Fe (ppm)	Zn (ppm)	Ca (ppm)	Mg (ppm)
KSR675 Nora II	7.2	33.2	6.9	64.7	10.5	0	24	11.1	1897	730
Kunykubiongo	15	29.3	6.2	63.4	10.1	0	21.3	10.2	1866	565
Kyabafuriki	10.3	27.4	7.5	63.4	10.2	0	22.8	12.4	1969	492
LIR257 Otada	11.7	32.7	6.7	67.8	6.7	0	20.3	9.5	1810	582
LIR296	15.5	32.6	6.5	63.2	11.6	0	19.4	9.7	1742	564
Mayai	6.8	33.2	7.3	66.6	9.8	264	22.5	10.8	2177	761
MBR539 Kitekamaju	6.5	32.5	6.7	69.3	5.6	1	20.8	11.5	1934	530
MBR524 Nkwasahansi	1.1	31.5	7.5	62.1	12.1	1	25.2	11.7	1904	639
MBR536 Karebe	15	31.3	5.1	65.3	10.7	0	19.4	10.7	2120	633
MBR552 Kahungezi	9.3	33.9	7.3	66.8	9.8	0	21.2	11.2	1986	644
MBR580 Nylon	4.8	27.4	6.5	58.4	13.7	0	27.4	14.8	3290	1152
APA343	5.3	32.5	5.7	63.9	11	12	19.7	9.7	1582	523
PAL161	6.8	35.5	6.8	65.2	9.3	33	20.2	10.5	1609	602
Pipi	7.7	33.2	6.4	65	10.2	13	19	10	1903	602
Resisto	7.8	24.8	7.6	53.5	15.7	271	24.1	12.7	1821	646
Sowola (389 A)	13.2	33.3	7.2	66.4	9.8	0	21.1	11.1	1603	469
Sowola6	9.9	30.6	8	62.2	10.3	54	24.6	12.5	2302	770
Sponge	11.4	32.4	6	65.1	10	48	19.7	10.2	2039	595
SRT 14 Nora	14.1	32	6.6	62.8	11.7	0	21.2	9.5	2156	593
SRT01 Osapat	9.5	33.6	6.2	66.8	9.6	0	19.5	10	1660	525
SRT02 Araka white	10.3	33	7.3	65.8	9.6	0	22.5	11.5	1608	440
SRT30 Nyara	13.9	29	7.6	58.3	13.8	22	22.9	11.7	1891	644
SRT33 Abuket1	11.6	27.7	7.1	58.2	14.6	159	23.1	12.4	1938	670
SRT34 Abuket2	13.2	31	6.6	59.5	14.5	51	20.3	10.1	1762	587
SRT35 Anyumel	9.4	31.6	6.9	63.8	10.6	82	22.7	11.2	1871	636
SRT39 Rwanda	12.2	20.1	5.4	51.1	17	169	22.7	10.7	2179	771
SRT40 Mary	10.6	35.9	6.4	64.7	10.7	-1	22.1	10.8	2916	918
SRT49 Sanyuzameza	5.8	35.3	8	65.7	9.3	0	24.3	12.3	2414	976
SRT52	4.1	32.5	7.5	64.2	11	35	23.4	11.7	2644	892
Sudan	6.1	32.2	6.3	64.6	10.6	44	20.6	10.2	1571	646
Tororo3	5.1	32.9	5.2	65.2	9.3	0	18.1	7.9	2238	537
Ukerewe	13.7	34.6	5.7	65.7	11.2	0	18.4	9.6	1536	421
Wagaborige	7.3	32.2	6	65.2	11.9	0	19.9	8.7	1493	498
Wera	4.2	29.9	7	50.1	28.5	1	26.1	13.1	2544	1004
Zambezi	6.7	29.5	7	62	11.1	233	22.9	12.9	2631	884
LSD (0.05)	6.6	2.8	1.4	2.9	2.5	19	3.0	1.8	534	219
Population mean	8.6	32.1	6.7	64.4	10.3	30.6	21.6	10.9	1950	628

† Observed traits: YLD = Storage root yield, t ha^{-1}; DM = dry matter content of storage roots, %; PRO = protein content of storage roots, % DM; STA = starch content of storage roots, % DM; SUC = sucrose content of storage roots, % DM; BC = β-carotene content of storage roots, ppm DM; Fe = iron content of storage roots, ppm DM; Zn = zinc content of storage roots, ppm DM; Ca = calcium content of storage roots, ppm DM; Mg = magnesium content of storage roots, ppm DM.

Several OFSP farmer varieties, namely 'Carrot_C' (259 ppm), 'Carrot Dar' (272 ppm), 'Ejumula' (240 ppm), 'Mayai' (264 ppm), and 'Zambezi' (233 ppm) exhibited similar or slightly different β-carotene contents as the check. For these OFSP accessions high storage root dry matter contents (≈33%), elevated storage root starch contents (≈58% to 66.6 % dry weight basis), and low to moderate sucrose contents (≈9.8 and 13.7% dry weight basis) were also observed. However, low storage root sucrose contents (6.4 to 7.4%) were also observed in several white-fleshed varieties such as 'Bungoma', 'K-207', 'K-37', and 'KBL632 Nyinakamanzi'. Two OFSP varieties ('Rwanda' = 169 ppm; 'Abuket1' = 159 ppm) were observed with moderately high β-carotene contents. It should be noted that for these two varieties, only low to medium storage root DM contents were observed [in the case of 'Rwanda' significantly ($P<0.05$) lower than 'Resisto']. Additional 12 farmer varieties ['K-118', 'K-134', 'K-46', 'KMI61', 'MLE162 Nakahi', 'PAL161', 'Sowola6', 'Sponge', 'SRT34 Abuket2', 'SRT35 Anyumel', 'SRT52' and 'Sudan'] were observed with significant but low β-carotene contents, and high to very high storage root DM contents. Relative high values for minerals were observed in OFSP (e.g. 'Carrot Dar' with values that correspond to 8.8 ppm Fe, 4.5 ppm Zn, 695 ppm calcium and 305 ppm magnesium on fresh weight basis) as well as white-fleshed farmer varieties (i.e. 'MBR580 Nylon' with values that correspond to 7.5 ppm Fe, 4.1 ppm Zn, 901.5 ppm calcium and 315.6 ppm magnesium on fresh weight basis).

Moderate to high positive correlations were observed between trait pairs for dry matter and starch (r = 0.620), protein and Fe (r = 0.810), protein and Zn (r = 0.796), Fe and Zn (r = 0.859), Fe and magnesium (r = 0.633), and calcium and magnesium (r = 0.837) in storage roots on basis of all accessions (N=90) used in the study (Table 1.6).

Table 1.6. Pearson correlation coefficients among observed traits in East African sweetpotatoes.

	YLD	DM	PRO	STA	SUC	BC	Fe	Zn	Ca
				Estimates based on all farmer varieties (N=89)					
DM	-0.178								
PRO	-0.095	0.018							
Sta	-0.015	0.620	-0.265						
Suc	-0.023	-0.472	0.147	-0.885					
BC	-0.061	-0.275	0.131	-0.467	0.351				
Fe	-0.188	-0.176	0.810	-0.505	0.368	0.232			
Zn	-0.123	-0.205	0.796	-0.361	0.231	0.205	0.859		
Ca	-0.299	0.088	0.228	-0.214	0.163	0.149	0.428	0.276	
Mg	-0.276	0.067	0.397	-0.301	0.234	0.232	0.633	0.433	0.837
				Estimated based on orange fleshed farmer varieties (N =32)					
DM	-0.258								
PRO	-0.148	0.064							
Sta	-0.071	0.708	-0.199						
Suc	0.050	-0.586	0.181	-0.917					
BC	-0.188	-0.209	0.213	-0.521	0.470				
Fe	-0.172	-0.205	0.805	-0.493	0.429	0.446			
Zn	-0.140	-0.167	0.855	-0.375	0.325	0.379	0.899		
Ca	-0.355	0.050	0.315	-0.137	0.061	0.374	0.469	0.324	
Mg	-0.350	0.006	0.505	-0.232	0.151	0.428	0.705	0.560	0.857

† Observed traits: YLD = Storage root yield, t ha^{-1}; DM = dry matter content of storage roots, %; PRO = protein content of storage roots, % DM; STA = starch content of storage roots, % DM; SUC = sucrose content of storage roots, % DM; BC = β-carotene content of storage roots, ppm DM; Fe = iron content of storage roots, ppm DM; Zn = zinc content of storage roots, ppm DM; Ca = calcium content of storage roots, ppm DM; Mg = magnesium content of storage roots, ppm DM.

A high negative correlation was observed for starch and sucrose (r = -0.885) on basis of all accessions used in the study. A separate analysis with only OFSP varieties (N=32 clones) revealed that there are positive correlations between β-carotene and mineral (Fe r = 0.446; Zn r = 0.379; Mg r = 0.374; Ca r = 0.428) and sucrose (r = 0.470) contents although these are not strong (Table 1.6). Also a moderate negative correlation between β-carotene and starch (r = -0.521) was observed.

The %RDA under the condition of a high intake (250 g fresh storage roots) and consumers 5 to 8 years old was high for β-carotene (350 to 450) in deep OFSP farmer varieties [i.e. 'Carrot_C', 'Carrot Dar', 'Ejumula', 'Mayai', and 'Zambezi']. It should be noted that the estimated %RDA β-carotene for the check clone ('Resisto') was 350%. Estimates of ≈50% (results not presented) for %RDA β-carotene were obtained with small intakes (≈30 g fresh storage roots per day) of deep OFSP farmer varieties (variety names given above). Many OFSP farmer varieties with light orange color and high dry matter and starch contents in storage roots were observed with %RDA β-carotene estimates of 50 to 90% ('Shinyanga', 'HMA493 Tanzania', 'K-118', 'K-134', 'K-46', 'PAL161', 'Sowola6', 'SRT52', and 'Sudan'). On average, low to medium %RDA were observed for Fe and Zn (17.5%), calcium (20%), and magnesium (40%) (Table 1.7). Several accessions were observed with %RDA between 20 and 22% for Fe and Zn, 25 to 33% for calcium, 50 to 66% for magnesium, which were significantly different from accessions below the population mean (LSD test).

Table 1.7. Clone means of farmer varieties for contribution to recommended daily intake (RDA) of micro-nutrients based on 250 g fresh sweetpotato root consumption per day.

Farmer varieties	RDA contribution (%)				
	β-carotene	Iron	Zinc	Calcium	Magnesium
APA343	21	16	15.7	16	32.7
APA348 Liralira	0	19.5	18.9	21.3	45.5
APA352 Oketodede	0	15.9	16.6	16.1	29.8
APA365 Anam Anam	0	16.6	17.1	18.4	34.3
ARA208 Ombivu	-0.1	17.2	18.4	14.4	22.9
ARA214	44.4	15.8	16.3	14.9	31.8
ARA244 Shinyanga	82.7	12.4	11.5	13	26.6
Bunduguza	-0.2	17.5	15.2	22.4	44.8
Bungoma	0	17.3	16.8	17.7	41.3
Carrot C	447.6	21.6	21	26.8	58.9
Carrot Dar	440.7	22.1	22.4	21.7	58.7
Dimbuka	-0.2	17.1	18.2	17.9	33.4
Ejumula	409.4	19.5	18.7	23.1	53.4
HMA490 Kawogo	0	16.4	16.9	17.4	28.6
HMA493 Tanzania	50.9	16.8	16.2	20.8	43.7
IGA963 Nyongerabarenzi	1.5	15.8	16.6	14.6	22
K-118	60.3	16.4	17.7	12.9	27.7
K-134	65.6	16.8	17.7	18.8	37.8
K-207	-0.2	19	18.2	33.8	61.7
K-37	45.1	15.4	13.9	25.8	43.5
K-46	83.2	17.9	17.9	26.5	47.3
KBL627 Mukazi	0	20.3	19.5	23	51.4
KBL632 Nyinakamanzi	1.5	16.4	17.8	20.8	41.7
KBL640 Africare	23.6	15.2	15	13.2	27.1
KMI56 Opira	0	17.9	17.6	19.3	45.9
KMI59 Kampala	0	18.6	16.4	19.4	40.7
KMI61	130.2	19.2	18.8	13.9	31.9
KMI78 Osukari	0.1	17.3	18.6	15.2	32.2
KMI81 Ikala	37.4	14.6	16.1	12.8	24.4
KMI83 Ikala2	16.7	15.8	16.1	15.1	29.1
KML883 Silkempya	0	17.7	16.5	21.2	32.8
KRE716 Nylon	-1.7	20.6	20.9	29.0	56.7
KRE726 Kwezikumwe	14.2	15.2	16.9	14.1	27.1
KRE733 Kitambi	0	19.2	19.3	21.7	44.7
KSR673 Mabereikumi	0	17.6	18.8	15.7	23.5
KSR652 Mugumire	1.7	18.4	19.0	22.1	27.6
KSR662 Kakoba	1.7	14.9	15.7	23.6	35.7
KSR664 Mulererabana	1.5	17.8	17.0	20.2	44.6
KSR675 Nora II	0	19.9	18.3	19.7	46.5
Kunykubiongo	0	15.6	14.9	17.1	31.8
Kyabafuriki	0	15.6	17.0	16.9	25.9
LIR257 Otada	-0.2	16.6	15.4	18.5	36.6
LIR296	0	15.8	15.8	17.7	35.4
Mayai	456.5	18.6	17.9	22.6	48.6
MBR539 Kitekamaju	1.4	16.9	18.6	19.6	33.2
MBR524 Nkwasahansi	1.5	19.8	18.3	18.7	38.7
MBR536 Karebe	0	15.2	16.7	20.7	38.1
MBR552 Kahungezi	0	18.0	18.9	21.0	42.0
MBR560 Mugurusi	0	18.2	18.9	19.0	37.1
MBR580 Nylon	-0.1	18.7	20.3	28.1	60.6
MBR600 Kisakyabikiramaria	0	18.1	19.0	15.5	30.9
MLE166	9.8	18.8	18.9	24.4	49.8
MLE162 Nakahi	77.1	17.0	16.6	18.5	38.7
MLE163 Kyebandula	-1.7	22.3	22.0	27.3	60.8
MLE165 Namafumbiro	0.1	16.8	17.7	22.4	44.6
MLE173 Kijovu	-1.4	17.6	16.9	17.2	28.8
MLE184 Manafayereta	0	18.8	21.7	18.3	25.7
MSK1025 Bitambi	0	17.1	17.9	27.7	51.1
MSK1047 Bwanjure	0	17.0	17.1	15.8	25.8
Nyaguta	0	20.6	18.8	27.6	66.8
Nyandere	0	17.0	18.2	16.6	31.7

Table 1.7. Continued.

Farmer varieties	RDA contribution (%)				
	β-carotene	Iron	Zinc	Calcium	Magnesium
Nyathiodiewo	0	14.8	15.3	15.5	32.8
Nyatonge	0	16.3	16.5	20.9	40.6
Obuogo1	0	20.7	18.3	23.5	54.5
Obuogo II	0	18.9	16.8	18.9	43.6
Oguroiwe	0	16.7	17.6	12.9	23.2
PAL153 Abukoki	-1.4	12.3	13.4	15.2	17.7
PAL161	60.7	17.9	18.7	17.9	41.1
Pipi	22.5	15.8	16.6	19.7	38.4
Resisto	350.1	14.9	15.7	14.1	30.8
Sowola (389A)	0	17.5	18.4	16.7	30.0
Sowola_6	86.3	18.8	19.1	22.0	45.3
Sponge	80.6	16.0	16.6	20.6	37.1
SRT14 Nora	-0.1	17.0	15.2	21.5	36.5
SRT01 Osapat	0	16.4	16.8	17.4	34.0
SRT02 Araka white	-0.2	18.5	18.9	16.6	27.9
SRT30 Nyara	32.5	16.6	16.9	17.2	35.9
SRT33 Abuket_1	228.8	16.0	17.1	16.7	35.6
SRT34 Abuket_2	82.2	15.7	15.6	17.0	35.0
SRT35 Anyumel	134.7	17.9	17.7	18.4	38.6
SRT39 Rwanda	176.5	11.4	10.7	13.7	29.7
SRT40 Mary	-1.7	19.9	19.3	32.7	63.4
SRT49 Sanyuzameza	0	21.5	21.8	26.7	66.3
SRT52	59.3	19.0	19.0	26.8	55.7
Sudan	72.9	16.6	16.4	15.8	39.9
Tororo3	0.2	14.9	13.0	23.0	33.9
Ukerewe	0	15.9	16.6	16.6	28.0
Wagaborige	0	16.0	14.0	15.0	30.8
Wera	1.4	19.5	19.6	23.8	57.7
Zambezi	357.6	16.9	19.1	24.3	50.2
LSD (0.05)	27.8	2.7	3.0	6.0	14.9
Population mean	47.9	17.3	17.4	19.6	38.9

Discussion

This study focused on β-carotene, DM, sucrose, protein, starch, and minerals contents in EA sweetpotato against the background of the contribution of sweetpotato to food supply. Whereas levels of root β-carotene and DM contents are fairly well documented for African germplasm, other quality traits are not, thus making results of this study the first of its kind. The more pronounced differences between locations for starch content in our study (Table 1.3) extend our knowledge by documenting the magnitude of this variability (Saad, 1996; Grüneberg *et al.*, 2005) but could have also resulted from small plots used in the present study. Experiments with large plots would be needed to generate reliable data for root yield performance of the accessions. The CV for all traits at both locations were low (Table 3), except storage root yields and storage root β-carotene contents. High CV values for storage root yield have been previously reported for sweetpotatoes (Grüneberg *et al.*, 2005). The high CV values for storage root β-carotene contents in this study can be explained by the low population mean (for all accessions including white- and cream-fleshed), whereas mean estimates for β-carotene contents varied considerably between accessions. The variance component σ^2_{GxL} was unexpectedly higher for starch and sucrose content of storage roots (Table 1.4). However, CV values for both traits at each location were low. The locations belong to different agro-ecological zones and differ greatly in altitude and crop duration for harvest (Table 1.2), which might be the reason for high σ^2_{GxL} estimates for starch (Grüneberg *et al.*, 2005) and sucrose. Such extreme locations, which are useful in testing accessions' adaptability and resistance to pests and diseases, might be less useful for nutritional quality breeding (Grüneberg *et al.*, 2009). The extreme locations result in lower heritabilities in programs focusing on improvement of quality traits, which was also observed in this study (Table 1.4). This merits further studies with a fraction of the varieties used in this study. Nevertheless, the variance component σ^2_G was significant ($p < 0.01$) for all the observed traits except storage root sucrose contents, which indicates significant differences between accession means. Owing to the magnitude of σ^2_{GxL} estimates and that locations were in distinct eco-geographical zones, genotype and location were set as fixed factors for a multiple comparison of accessions by the LSD-test. Hence, LSD values at the 0.05 level might be under estimated, which does not affect the evidence that differences below the LSD values given (Table 1.5) are not significantly different.

In contrast to germplasm from other regions (Woolfe, 1992), the EA accessions have clearly higher DM (≈32 to 33%), higher starch, (≈65% DM), and lower sucrose (≈10% DM) contents in storage roots. It appears that sweetpotato in EA has on average a moderate sweetness and several accessions, such as 'Bungoma', 'K-207', 'K-37', and 'KBL632 Nyinakamanzi' have very low sucrose (≈7.5% DM) content. These quality attributes make the crop more attractive to be used as a starchy staple in East Africa compared to such other regions of the world as South Asia and Central and South America where sweetpotato is consumed in low amounts. However, sweetness after cooking or boiling is determined by enzymatic conversion of starch to maltose (Kays *et al.*, 2005) and not by the sucrose content we observed in fresh storage roots.

The study found 5 OFSP farmer varieties ['Carrot_C', 'Carrot Dar', 'Ejumula', 'Mayai', and 'Zambezi'] with high storage root β-carotene contents similar to the check variety 'Resisto' (Table 1.5). The β-carotene estimates compare well with those reported for OFSP accessions with low storage root DM (Grüneberg *et al.*, 2005; Purcell, 1962; Purcell and Walter, 1968). β-carotene content of 'Resisto' in the present study is lower than previous estimates (Laurie, 2008). The variety 'Resisto' is typical for the taste group "OFSP moist and sweet" (Martin and Jones, 1986), and had a storage root DM content of 24.8% and a storage root starch content of 53.5% (Table 1.5). Varieties such as 'Carrot_C', 'Carrot Dar', 'Ejumula', 'Mayai', and 'Zambezi' cannot be classified as "OFSP moist and sweet" but rather propose to be designated as "OFSP dry and starchy". These five OFSP farmer varieties all had storage root DM content greater than a 29.5% and storage root starch content greater than 62.0% (attributes close to those observed in many white-fleshed African farmer varieties). OFSP varieties with high DM and high starch contents in storage roots might make OFSP attractive to a much wider range of taste preferences. The 12 light OFSP accessions ['K-118', 'K-134', 'K-46, 'KMI61', 'MLE162 Nakahi', 'PAL161', 'Sowola6' 'Sponge' 'SRT34 Abuket2', 'SRT35 Anyumel', 'SRT52' and 'Sudan'] with meaningful β-carotene (Table 1.5) are also important. The storage root DM and starch contents of these accessions were high whereas sucrose contents were low, and thus have attributes close to white-fleshed farmer varieties.

The results of this study are the first description of OFSP accessions which are high in storage root DM and high in storage root starch contents. This leads to the question where these "OFSP dry and starchy" are coming from in crop evolution. A molecular characterization of this material (Tumwegamire *et al.*, 2011) has shown close clustering of African OFSP with their sister WFSP accessions and clear genetic distances between African OFSP and non-African OFSP germplasm. Breeders in Africa have observed that open pollinated white-fleshed accessions results in segregation of OFSP at low frequencies (Mwanga *et al.*, 2003).

The potential to alleviate VAD through use of accessions 'Carrot_C', 'Carrot Dar', 'Ejumula', 'Mayai', and 'Zambezi' is high in Uganda and other areas where daily sweetpotato consumption is high. These accessions showed at least 350% RDA β-carotene for the age group 5 to 8 years old with routine intake quantities found in Uganda (Table 1.7). This suggests that these varieties could address VAD in many other

areas across the world, including south and East Asia and north Eastern states of Brazil where VAD prevalence is high but with low per capita consumption of sweetpotato. For example 'Carrot_C' could provide 100% of RDA pro-vitamin A intake with modest 70 g of cooked roots per day. The potential to alleviate VAD using OFSP has been demonstrated (Low *et al.*, 2001, 2007; van Jaarsveld *et al.*, 2005). However, the challenge has been reluctance by farmers to grow and consume 'OFSP moist and sweet" varieties, a situation that should possibly change given the "OFSP dry and starchy" accessions found in this study. Additionally, the light orange-fleshed accessions have been found to contribute significantly to RDA β-carotene in the range between 50 to 90% (Table 1.7).

The storage root mineral (Fe = 21.6 ppm, Zn = 10.9 ppm, calcium = 1950 ppm and magnesium = 626 ppm) and protein (6.7%) contents observed in the present study are in the range previously reported by Bradbury and Holloway (1988), Woolfe (1992), Courtney (2007) and Grüneberg *et al.* (2009). Percent RDA for magnesium is notably higher and approaches 50% of daily needs (250 g roots) in many accessions. Iron, Zn and calcium had mean %RDA of 17.3, 17.4 and 19.6, respectively. In areas with high sweetpotato consumption, farmer varieties like 'Carrot_C', 'Carrot Dar', 'KRE Nylon', 'MLE163 Kyebandula' and 'SRT49 Sanyuzameza' can contribute to the intake of Fe, Zn, calcium, and magnesium (Table 1.7), but cannot alleviate respective mineral deficiencies at the current storage root concentrations. Breeding efforts, particularly in areas with high sweetpotato consumption, have to double iron, zinc, and calcium contents in storage roots to reach %RDA of ≈50% to achieve impact. In regions with low sweetpotato consumption and high VAD breeders should mainly target high β-carotene content and consumer acceptance.

The correlation matrix (Table 1.6) is consistent with those reported for sweetpotato (Grüneberg *et al.*, 2009; Courtney, 2007; Saad, 1996; Collins and Walter, 1982). The positive correlations between β-carotene and mineral and sucrose contents suggest possibility of an indirect improvement of the latter through selection for higher β-carotene (Grüneberg *et al.*, 2009). The challenge, however, is simultaneous improvement of DM and β-carotene levels among the sweetpotato germplasm. Whereas starch and DM were positively correlated, they were both negatively correlated to β-carotene content. Similar observations are reported by Grüneberg *et al.* (2009).

In conclusion East African sweetpotato germplasm is clearly higher in storage root DM and storage root starch contents, and clearly lower in storage root sucrose contents compared to the cultivated sweetpotato of the rest of the world, especially the traditional OFSP. The study revealed that African OFSP farmer varieties such as 'Carrot_C' 'Ejumula' 'Carrot Dar', 'Mayai' and 'Zambezi' contain moderate to high levels of storage root DM with high levels of β-carotene and might be useful for better acceptance of OFSP in Africa as well as other regions of the world. Moreover, sweetpotato significantly adds to the mineral contribution in food supply (i.e. Fe, Zn, calcium, and magnesium) when sweetpotato is consumed frequently. The new OFSPs described in this study justify a category (or group) termed "OFSP dry and starchy" and this group

may enhance consumer appeal towards a more nutritious sweetpotato, which increases the potential of OFSP to contribute to the alleviation of VAD.

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CHAPTER TWO 02

Genotype x Environment Interactions for East African Orange-fleshed Sweetpotato Clones Evaluated across Varying Ecogeograhic Conditions in Uganda

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Abstract

The understanding of GxE interactions, stability parameters, and genetic correlations for root yield and nutritional traits is needed for an informed choice of appropriate breeding strategies for sweetpotato. The present study assessed: i) the magnitude of GxE variation in OFSP varieties of East African origin for yield and nutritional traits conducted across four ecogeograhic zones of Uganda; ii) the "genetic correlations" (on basis of means of phenotypic correlations) among traits in the "OFSP dry and starchy" gene pool from East Africa; and iii) the breeding options for sweetpotato of the category "OFSP dry and starchy". Ten OFSP varieties including six farmer varieties ('Ejumula', 'Zambezi', 'Carrot_C', 'Kakamega', 'KMI61', and 'Abuket_1'), three modern varieties ('SPK004/6/6', 'SPK004/6' and 'Naspot_5/50') of African origin and one modern variety ('Resisto') of American origin were evaluated in replicated trials at four sites during 2006 first and second rainy seasons. The GxE analysis was conducted with regression, and additive main effects and multiplicative interaction (AMMI). The environment effects were significant ($p < 0.05$; or < 0.01) for root yield, harvest index, and all quality traits except dry matter (DM). On the other hand the genotypic effects were significant ($p < 0.05$; or < 0.01) for all traits except root yield, iron and magnesium. Accessions, 'Ejumula', 'SPK004/6', and 'SPK004/6/6' had root yields significantly greater than the check, Resisto, while 'Naspot_5/50' had lowest root yields. The former three varieties are released in Uganda, and represent the potential gains in breeding for high DM orange-fleshed sweetpotato clones. The σ^2_{GxE} components were not significant ($p>0.05$) for β-carotene and starch root content. The σ^2_{GxE} components were highly significant ($p<0.01$) for dry matter but fractional (0.4) compared to the corresponding σ^2_G component. These results suggest it is feasible to improve these traits with high selection efficiency in the early stages of the sweetpotato breeding program. The σ^2_{GxE} : σ^2_G ratio was close to 1 for harvest index and sucrose content, and large (> 2) for storage root yields and all mineral contents. Like for yield, our findings suggest that breeding for elevated mineral levels in sweetpotato is complex and requires information about the causes of GxE interactions before the breeder can embark on enhancing these minerals. However, medium to high positive correlations among mineral traits are clearly in favor of selection aiming at elevated mineral contents in sweetpotato simulteneously and it merits research if the trait complex minerals can be improved more efficiently by an index.

Key words: GxE variance, Iron, Zinc, ß-carotene and AMMI

Introduction

Sweetpotato is cultivated in East and Central Africa (ECA) on 1.5 million hectares (FAOSTAT, 2008). This excludes vast acreage occupied in home gardens in thousands of villages that never make entry into statistics. The crop like no other contributes to the food security in ECA. The crop is a staple in some areas of ECA e.g. in Uganda the average daily intake of sweetpotato per person is estimated to be 240 g (FAOSTAT, 2007). Sweetpotato is high in carbohydrates and can produce more edible energy ha^{-1} day^{-1} than wheat, rice or cassava (Woolfe, 1992). Unfortunately, the crop has often been considered a mere subsistence crop and ignored in terms of its nutritional value and huge potential for genetic enhancement. However, this image is changing due to the increasing awareness among policy makers, nutritionists, breeders, farmers and consumers of: (i) the vitamin A malnutrition and its effect on public health in the world (Pfeiffer and McClafferty, 2007); (ii) the high β-carotene contents in storage roots of OFSP (Grüneberg *et al*., 2009b); and (iii) the great genetic variation for β-carotene among existing high yielding sweetpotato varieties (Laurie, 2008, Grüneberg *et al*., 2009b; Mwanga *et al*., 2007; Tumwegamire *et al*., 2011).

The levels and effects of pro-vitamin A, iron (Fe) and zinc (Zn) malnutrition on public health are well documented (Frossard *et al*., 2000; Black, 2003; Bouis, 2003; Welch and Graham, 2004), and noted as "The Hidden Hunger" (Harvest Plus, 2003; Bouis, 2003). It affects billions of people by lowering IQ, causing stunting and blindness in children, lowering immunity to disease in both children and adults, and increasing risks during pregnancy and childbirth. The use of fortified food supplements has not greatly reduced the effects of micronutrient malnutrition around the world (Bouis, 2003). Food staples enriched with micronutrients through plant quality breeding, designated by nutritionist as biofortification, have been adopted as a complementary strategy to avert the effects of pro-vitamin A, Fe, and Zn malnutrition (Bouis, 2003; Lönnerdal, 2003; Harvest Plus, 2003; Welch and Graham, 2004). Sub-Saharan Africa (SSA) is one of the primary targets of this strategy to alleviate vitamin A deficiency using OFSP (Low *et al*., 2001, 2007).

Many OFSP varieties in the category "OFSP moist and sweet", mainly from breeding programs in the USA (Mwanga, *et al*., 2007; Grüneberg *et al*., 2009a) are not desired given preference in SSA for high DM content, similar to commonly consumed white-fleshed sweetpotato. A few OFSP varieties categorized as "OFSP dry and starchy" have been found among East African farmer varieties (CIP, 2005; Mwanga, *et al*., 2007b; Tumwegamire *et al*., 2011). Also, three modern varieties of this category have been released in Uganda (Mwanga *et al*., 2009). Apart from identifying varieties that are rich in the nutrients and meet farmer and consumer preferences, there is a need to understand the GxE interactions and stability of yield and

nutritional traits across diverse environments. Whereas information on GxE interactions for β-carotene is contradictory, little has been reported for other nutrients in sweetpotato. While Grüneberg *et al*. (2005) and Manrique and Hermann (2000) found extremely low environment interaction effects on levels of β-carotene, K'osambo *et al*. (1998); Ndirigue (2005) report significant effects. Grüneberg et al. (2005) also reported extremely low GxE interactions for other quality traits, like dry matter and starch. Less known is genetic correlations between nutritional traits in sweetpotato. Grüneberg *et al*. (2009b) has reported genetic correlation among yield and nutritional traits. Given difficulty in estimating genetic correlations, means of phenotypic correlations (estimated separately by environments) have been useful as genetic correlation estimates. Phenotypic correlations among sweetpotato traits including mineral contents of storage roots have been previously reported by Courtney (2007) and Tumwegamire *et al*. (2011). The combined understanding of GxE interactions, stability parameters, and genetic correlations for root yield and nutritional traits is needed for informed choice of appropriate breeding strategies for sweetpotato (Shafii and Price, 1998; Grüneberg *et al*., 2005). The present study assessed: i) the magnitude of GxE variation in OFSP varieties of East African origin for yield and nutritional traits conducted across ecogeograhic zones of Uganda; ii) the "genetic correlations" (on basis of means of phenotypic correlations) among traits in the "OFSP dry and starchy" gene pool from East Africa; and iii) the breeding options for "OFSP dry and starchy" sweetpotato.

Materials and Methods

Ten OFSP varieties were used for the study (Table 2.1). These included six farmer varieties ('Ejumula', 'Zambezi', 'Carrot_C', 'Kakamega', 'KMI61', and 'Abuket_1') and three modern varieties ('SPK004/6/6', 'SPK004/6' and 'Naspot_5/50') of African origin. All these OFSP can be designated as "OFSP dry and starchy". Additionally, one modern variety ('Resisto') of American origin was used as a check, which clearly falls into the category "OFSP moist and sweet".

Table 2.1. Description of clones used for the GxE analysis (CT, Cultivar type; FV, Farmer variety; MV, Modern variety; IO, Intermediate orange; DO, Deep orange; LO, Light orange; SPVD, sweetpotato virus disease)

Cultivar	CT	Origin	Flesh colour	Skin colour	Root Shape	SPVD Resistance
Kakamega	FV	Kenya	IO	Pink	Long irregular	Resistant
Resisto	MV	USA	DO	Brown	Ovate	Susceptible
Ejumula	FV	Uganda	DO	Cream	Long irregular	Susceptible
SPK004/6/6	MV	Uganda	DO	Pink	Long irregular	Resistant
Naspot_5/50	MV	Uganda	LO	Purple red	Long elliptic	Resistant
Zambezi	MV	Zambia	DO	Purple red	Round elliptic	Susceptible
KMI61	FV	Uganda	IO	Cream	Round elliptic	Susceptible
Carrot_C	FV	Tanzania	DO	Cream	Long irregular	Susceptible
Abuket_1	FV	Uganda	IO	Purple red	Long elliptic	Susceptible
SPK004/6	MV	Uganda	DO	Pink	Obovate	Resistant

The materials are diverse in origin, root shape, skin color, and flesh color (Table 2.1). The latter has been shown to be correlated with the levels of β-carotene in sweetpotato (Takahata *et al*., 1993). Four locations representing the major sweetpotato agro-ecologies in Uganda were used for the study (Table 2.2). These include: i) Kachwekano Zonal Agricultural Research Institute characterized by high altitude (2220 m.a.s.l), bimodal rainfall average of 1319 mm annually, sandy clay loam, and soil pH 5.8 – 6.2; ii) National Crops Resources Research Institute (NaCRRI) – Namulonge, which is characterized by mid altitude (1150 m.a.s.l) a bimodal rainfall (1270 mm annually), annual mean temperature of 22.2 ^{o}C, red sandy clay loams, soil pH 4.9 – 5.0, and high pressure sweetpotato virus disease; iii) Serere, characterized by mid altitude (1140 m.a.s.l), a low rainfall (900 -1300 mm annually), annual temperature (26 ^{o}C), sandy loam soils, soil pH 5.2 – 6.0, and high weevil infestation levels; and (iv) Mobuku, a low altitude site (900 m.a.s.l) with annual rainfall less than

1000 mm, annual temperature ranging between 23.9 and 30.0 °C, alluvial soil types, soil pH 5.5 – 6.1, and high evapotransipiration (crops survive with supplementary irrigation).

Table 2.2. Description of locations used for the GxE analysis.

Sites	**Characteristics of the agro-ecologies**					
	Altitude (m.a.s.l)	**Soil pH**	**Soil type**	**Rainfall (mm)**	**Vegetation**	**Temp °C**
Namulonge	1150	4.9 - 5.0	Sandy clay loam	1270	Tropical rain forest	22.2
Kachwekano	2220	5.8 – 6.2	Sandy clay loam	1319	Montane	17.5
Serere	1140	5.2 – 6.0	Sandy loam	900 - 1300	Tall savanna	26.0
Mobuku	900	5.5 – 6.1	Alluvial soils	≤1000	Grass savanna	23.9–30.0

The entries were planted at all sites during the first rains (March/April/) in 2006 and again during the second rains (October/November) of the same year. Unlike at Namulonge where final ridging of the plots was done using a tractor other sites were manually ridged using hand hoes. At Mobuku the crop was irrigated (using fallow irrigation) periodically through the growth cycle. Plots were made of three ridges and arranged in a randomized complete block design with two plot replications. Each ridge was 3 m long and 1 m away from the next ridge. On each ridge ten vines were planted at a distance of 0.3 m from each other. The trials were kept weed free and no fertilizers or pesticides were applied. After five months, plots at Mobuku, Namulonge, and Serere were harvested. At Kachwekano the trial was harvested after seven months (note: at Kachwekano the cool temperate conditions of the West Ugandan highlands slow the growth of sweetpotato). Yield was measured for vines and roots and recorded in tha^{-1}. From a composite pile of the harvested roots of the center ridge, a sample of 4 or 5 roots (each between 100 g and 300 g weight) were taken to prepare a 100 g sub-sample for dry matter and micronutrient analysis. The sub-sample was freeze dried at -31°C for 72 hours, using a vacuum freeze drier YK-118, and weighed to obtain the dry weight (g). The dry samples were then milled into flour using a stainless steel mill and used to estimate β-carotene, Fe, Zn, Ca, Mg, % protein, and % starch of storage roots using near infrared reflectance spectroscopy (NIRS) (Cozzolino and Moron, 2004; Halgarson *et al*., 2004; Zum Felde, 2009).

Different seasons were considered as different environments. Statistical analyses were done using PLABSTAT (Utz, 1997) and R (R Development Core Team, 2009) considering varieties, environments and blocks as random. The variance components σ^2_G, σ^2_E, σ^2_{GxE} and σ^2_e were estimated with the model statement $X_i = L + R{:}L + G + GL + RGL$ which correspond to the statistical model

$$Y_{ijkl} = \mu_i + g_{ij} + e_{ik} + ge_{ijk} + bl(e)_{il(k)} + \varepsilon_{ijkl}$$

where Y_{ijkl} is the plot value of the ith trait of the *j*th genotype, *k*th environment and the *l*th block, μ_i is the trial mean of the *i*th trait, g_{ij}, is the effect of genotypes, e_{ik}, is the effect of environments, ge_{ijk} is the effect of genotype by environment interactions, $bl(e)_{il(k)}$ is the effect of blocks within environments, and ε_{ijkl} is the plot error.

Operational broad-sense heritabilities of observed traits were calculated by,

$$h^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{GxE}^2}{k} + \frac{\sigma_{error}^2}{kl}}$$

where k the number of environments and l the number of replications.

For all traits for which σ^2_{GxE} was significantly and considerably larger than σ^2_G and σ^2_E the static as well as the dynamic concept of stability was applied (Becker and Leon, 1988). The static concept was applied by calculating variance of genotype *j* across environments, variance of environment *k* across genotypes, and ecovalence (Wricke and Weber, 1986). The dynamic concept was applied by sub-dividing the interaction term into heterogenity due to regression and residual deviations. The stability parameters were calculated with respect to genotypes and environments. In order to assess the usefulness of these stability parameters the heritability of stability was determined by calculating the parameters separately for season 1 and season 2. In addition to a stability analysis by the classical ANOVA an AMMI (Additive Main Effect Multiplicative Interaction) analysis (Gollob, 1968) was performed to visualize the GxE structure, following the R function developed by Onofri and Ciriciofolo (2007).

Correlations among traits were carried out by SAS procedure CORR (SAS Institute, 1988) and the optional statement PEARSON. The correlations were calculated for each location and replication separately, followed by calculating the average correlation between each trait pair across locations and replications using the statement BY in SAS procedure CORR. These correlations are still phenotypic correlations, but can be considered as a good approximation of genotypic correlation estimates (Hill *et al*., 1998).

Results

Environment effects were significant ($p<0.05$) for all the traits except DM (Table 2.3). Differences in the experimental mean among environments were extremely large for storage root yield, and harvest index. The mean storage root yields ranged between 6.6 and 33.9 t.ha^{-1} with NM1 as the highest yielding (33.9 t.ha^{-1}) environment followed by MBK2 (23.1 t.ha^{-1}) while NM2 was the poorest yielding (6.6 t.ha^{-1}) environment. This was associated with low and high means for harvest indices, respectively. The ranges for nutritional traits across environments were 13.4 to 18.9 ppm for Fe, 6.4 to 10.7 ppm for Zn, 192.2 to 264.9 ppm for β-carotene, 61.4 to 69.9% for starch, 1627.2 ppm to 2250.3 ppm for calcium, 305.1 ppm to 903.1 ppm for magnesium, and 7.4 to 12.0% for sucrose. Both Fe (19.0 ppm) and Zn (10.7 ppm) contents were highest at environment NM2 and lowest at environment MBK2. β-carotene (264.9 ppm) and sucrose (12.0%) levels were highest at environment MBK2 and lowest at environments NM1 and KA1, respectively. Starch, calcium, magnesium were highest at KA1 and lowest at MBK2, NM2 and SR2, respectively. Genotype effects were significant for all traits except storage root yields, iron and magnesium content of storage roots (Table 2.4). Though not significant, the mean root yields across genotypes ranged between 7.7 and 18.8 t.ha^{-1}. Accessions 'Ejumula' (18.8 t.ha^{-1}), 'SPK004/6/6' (17.8 t.ha^{-1}), 'SPK004/6' (17.7 t.ha^{-1}), 'Abuket_1' (16.9 t.ha^{-1}), and 'Kakamega' (16.3 t.ha^{-1}) yielded above the check variety 'Resisto' (15.8 t.ha^{-1}) while 'Naspot_5/50' (7.7 t.ha^{-1}) had the lowest

Table 2.3. Environmental means for observed traits across genotypes [harvest index (HI), % dry matter (DM), Iron (Fe), Zinc (Zn), β-carotene (BC), Calcium (Ca), Magnesium (Mg) and Sucrose (SUC)].

Environment†	Root yield t.ha^{-1}	HI (%)	DM (%)	Fe‡ (ppm)	Zn‡ (ppm)	BC‡ (ppm)	Starch‡ (%)	Ca‡ (ppm)	Mg‡ (ppm)	SUC‡ (%)
MBK1‡‡	17.6	38.7	33.0	15.3	9.3	220.6	66.0	2139.3	452.2	10.3
MBK2‡‡‡	23.1	59.0	32.7	13.6	6.4	264.9	61.4	1636.9	376.3	12.0
NM1	33.9	48.3	32.4	16.1	9.1	192.2	68.3	1844.9	514.6	8.1
NM2	6.6	29.3	33.2	19.0	10.7	232.1	65.8	1627.2	482.7	7.6
SR1	13.1	32.1	32.2	18.5	10.7	208.3	65.4	1899.2	504.0	9.0
SR2	9.0	34.2	32.6	17.2	10.2	260.8	66.1	1894.7	305.1	10.6
KA1	10.5	49.5	32.1	18.0	10.3	224.6	69.9	2250.3	903.1	7.4
KA2	8.4	37.0	32.1	18.9	10.5	225.4	68.5	1737.9	587.9	8.5
Mean	15.3	41.0	32.5	17.1	9.6	228.6	66.4	1878.8	515.7	9.2
LSD (0.05)	6.6**	12.2**	1.5	2.1**	1.4**	37.9*	1.8**	332.6**	102.5**	1.2**

† MBK = Mobuku, NM = Namulonge, SR = Serere, KA = Kachwekano
‡ on storage root dry weight basis
‡‡ season 1 and ‡‡‡ season 2
* Significant at the 0.05 level and ** significant at the 0.01 level.

root yields (Table 2.4). However, the highest yielding accession 'Ejumula' and lowest yielding accession 'Naspot_5/50' did not consistently rank as the highest and lowest yielding across all environments (Figure 2.1). 'Ejumula' ranking changed from 1st for storage root yields to 7th for harvest index (HI), the ranking of other accessions did not change greatly for storage root yields and HI. 'SPK004/6/6' and 'SPK004/6' changed from rank 2 and 3 for root yield to 1 and 2 for HI, respectively. 'Kakamega', 'KMI61' and 'Naspot_5/50' had similar ranks for yields and HI. No accession was consistently highest in all the nutritional traits measured.

Table 2.4. Clone means for observed traits across environments [harvest index (HI), % dry matter (DM), Iron (Fe), Zinc (Zn), β-carotene (BC), Calcium (Ca), Magnesium (Mg) and % Sucrose (SUC)].

	Root yield $t.ha^{-1}$	HI (%)	DM (%)	Fe‡ (ppm)	Zn‡ (ppm)	BC‡ (ppm)	Starch‡ (%)	Ca‡ (ppm)	Mg‡ (ppm)	SUC‡ (%)
Resisto	15.8	47.2	28.0	17.0	9.2	343.9	60.3	1895.0	493.8	11.6
Kakamega	16.3	41.2	33.5	15.3	9.0	169.4	68.4	1669.3	469.5	8.4
Ejumula	18.8	38.5	34.1	17.0	9.3	282.9	66.4	1994.6	514.3	9.4
SPK004/6/6	17.8	52.7	32.3	17.8	10.5	229.6	66.1	1967.6	461.8	9.2
Naspot_5/50	7.7	24.6	32.1	17.4	9.3	132.1	67.2	1823.9	489.5	9.4
Zambezi	14.2	40.2	32.0	16.7	9.6	238.2	67.1	2002.6	572.7	9.1
KMI61	12.6	32.3	32.7	16.7	9.3	191.6	69.5	1521.9	429.5	7.0
Carrot_C	14.9	47.3	35.7	17.8	9.7	278.9	65.5	2153.6	595.0	10.1
Abuket_1	16.9	35.8	32.0	17.7	10.1	184.4	66.4	1899.3	532.3	9.3
SPK004/6	17.7	50.3	32.8	17.1	10.2	235.0	67.3	1860.3	498.8	8.6
Mean	15.3	41.0	32.5	17.1	9.6	228.6	66.4	1878.8	515.7	9.2
LSD (0.05)	7.0	12.1**	1.7**	1.8	0.9*	34.7**	2.1**	295.4**	125.1	1.0**

‡ On storage root dry weight basis
* Significant at the 0.05 level and ** Significant at the 0.01 level.

However, 'Ejumula' and 'Carrot_C' showed nutritional levels higher than respective averages while 'Kakamega', 'KMI61' and 'Naspot_5/50' had lower nutritional levels than respective averages. Despite low contents of most of the nutrients, the starch contents for 'Kakamega', 'KMI61' and 'Naspot_5/50' were significantly above average. 'Resisto' had the highest β-carotene (343.9 ppm) and sucrose (11.6%) contents, and lowest DM (28.0%) and starch (60.3%) contents. Other varieties SPK004/6, SPK004/6/6, and Zambezi all had β-carotene and starch contents above the average but differ for other traits with some higher or lower than their respective averages.

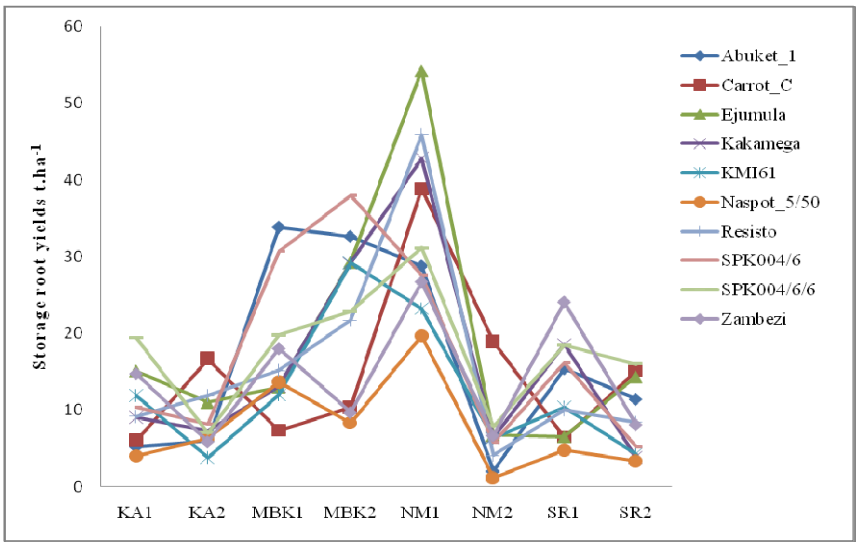

Figure 2.1. Storage root yield of ten clones of sweetpotato used for analysis of genotype x environment interactions across eight environments: KA = Kachwekano, S = Serere, NM = 1 Namulonge, MBK = Mobuku, S1 = season 1, and S2 = season 2.

The σ^2_G variance component was significant for all traits, except storage root yield, Fe and magnesium content of storage roots (Table 2.5). The σ^2_E variance component was significant for all traits, except storage root DM. Non significant σ^2_{GxE} were observed for starch and β-carotene contents of storage roots, whereas all remaining traits showed significant σ^2_{GxE} variance component due to genotype by environment interactions. Among the traits with significant genotype by environment interactions the ratio $\sigma^2_{GxE} : \sigma^2_G$ was close to 1 for harvest index and sucrose content of storage roots, and close to 2 for Zn and calcium content of storage roots. The ratios of $\sigma^2_{GxE} : \sigma^2_G$ were larger than 2 for storage root yield, Fe, Zn, calcium and magnesium content of storage roots with values of 6.2, 8, 2.1, 2.2, and 13.2, respectively.

Table 2.5. Variance components and operational broad-sense heritabilities for observed traits.

Traits	σ^2_G	σ^2_E	σ^2_{GxE}	σ^2_{error}	h^2
Storage root yield	4.3	81.2**	26.5**	46.0	
	(1)	(18.9)	(6.2)	(10.7)	0. 41
Harvest Index	57.3**	88.7**	56.8*	179.6	
	(1)	(1.6)	(1)	(3.1)	0.76
Dry matter	3.5**	-0.1	1.5**	2.91	
	(1)	(0)	(0.4)	(0.8)	0.91
Starch	5.4**	6.3**	1.4+	6.2	
	(1)	(1.2)	(0.3)	(1.2)	0.91
Sucrose	1.1**	2.5**	1.3**	2.7	
	(1)	(2.3)	(1.2)	(2.5)	0.76
β-carotene	2456.0**	755.3**	216.4+	2723.0	
	(1)	(0.3)	(0.1)	(1.1)	0.96
Iron	0.2	3.2**	1.6**	2.9	
	(1)	(16)	(8)	(14.5)	0.29
Zinc	0.14*	1.9**	0.3*	1.1	
	(1)	(13.6)	(2.1)	(7.9)	0.57
Calcium	21172.5**	37504.0**	45481.9**	83804.4	
	(1)	(1.8)	(2.2)	(4.0)	0.66
Magnesium	621.7	30815.4**	8512.1**	14322.1	
	(1)	(49.6)	(13.2)	(23.0)	0.24

The operational broad sense heritabilities (h^2) were high (> 0.7) for harvest index, DM, starch, β-carotene and sucrose content of storage roots, moderate (0.3 to 0.7) for storage root yield, Zn and calcium content of storage roots, and low (< 0.3) for Fe and magnesium content of storage roots.

The subdivision of GxE sums of squares (Table 2.6) into heterogeneity of regression and deviations from regressions for all traits that had ratios σ^2_{GxE} : σ^2_G larger than 2 (Table 2.5) showed that the variance components relative to regression for genotypes (Het. R.G) were significant on the p = 0.1 level for storage root yield and p = 0.01 level for storage root magnesium content. The heterogeneity of regression with respect to genotypes explained about 1/5 of the total GxE interaction for storage root yield and about 2/5 of the total GxE interaction for magnesium storage root content. The variance component relative to heterogeneity of regression with respect to environments (Het.R.E) was negative or close to zero for all traits, except calcium (366.6 ppm^2) and magnesium (884.3 ppm^2) – but also for these two traits the regression explained no significant part of the variance component due to genotype by environment interactions. However the deviations from regression lines with respect to genotypes (Dev.R.G) and environments (Dev.R.E) were significant for all the traits in the subdivision analysis of GxE. For storage root yield, all the accessions had slopes of regression lines larger than 0.55 (Table 2.7). High regression slopes (b

> 1) associated with low mean squares for deviations from regression (MS Dev. R) were observed for the accessions 'Resisto' and 'Kakamega' (Table 2.7), whereas lower values of b and MS deviations were observed for 'SPK004/6/6' and 'Naspot_5/50'.

Table 2.6. An ANOVA for genotype (G) by Environment (E) interaction (GxE) with subdivision (SUB) of GxE interaction using regression analysis for storage root yield, iron, zinc, calcium and magnesium contents of storage roots (Het. R. = heterogeneity due to regression, Dev. R. = deviation from regression lines.

Trait	Effect	df	MS	σ^2	Rel. σ^2
Root yield	E	7	1725.7	81.2**	1888
	G	9	168.2	4.3	100
	GxE	63	98.9	26.5**	616
	SUB Het. R.G	**9**	**163.2**	**4.7+**	**18**
	Dev. R.G	54	88.2	21.1**	80
	Het. R.E	**7**	**90.8**	**-0.4**	**-2**
	Dev. R.E	56	99.9	27.0**	12690
Iron	E	7	74.0	3.4**	1700
	G	9	8.7	0.2	100
	GxE	63	6.2	1.6**	800
	SUB Het. R.G	**9**	**4.9**	**-0.1**	**-6**
	Dev. R.G	54	6.4	1.8**	106
	Het. R.E	**7**	**6.6**	**0.02**	**3**
	Dev. R.E	56	6.2	1.6**	100
Zinc	E	7	41.1	1.9**	950
	G	9	4.0	0.1*	100
	GxE	63	1.7	0.3*	150
	SUB Het. R.G	**9**	**0.8**	**-0.1**	**-33**
	Dev. R.G	54	1.8	0.4*	133
	Het. R.E	**7**	**1.4**	**-0.02**	**-10**
	Dev. R.E	56	1.7	0.3*	100
Calcium	E	7	998000.7	37504.0**	177
	G	9	513529.3	21172.6**	100
	GxE	63	174768.2	45481.9**	215
	SUB Het. R.G	**9**	**179795.9**	**366.6**	**0.8**
	Dev. R.G	54	173930.2	45062.9**	99.1
	Het. R.E	**7**	**284778.1**	**6188.1**	**13.6**
	Dev. R.E	56	161016.9	38606.3**	85.7
Magnesium	E	7	640903.5	30815.4**	4956.6
	G	9	41294.1	621.7	100
	GxE	63	31346.3	8512.1**	1369.2
	SUB Het. R.G	**9**	**82102.3**	**3701.0****	**43.5**
	Dev. R.G	54	22886.9	4282.4**	60.3
	Het. R.E	**7**	**47066.3**	**884.3**	**10.4**
	Dev. R.E	56	29381.3	7529.6**	88.5

+ significant at the 0.1 level.
* significant at the 0.05 level.
** significant at the 0.01 level.

Table 2.7. Estimates obtained using the dynamic concept of genotype by environment interaction for storage root yield, iron (Fe), zinc (Zn), calcium (Ca) and magnesium (Mg) content of storage roots.

	Parameter	Storage root yield	Fe	Zn	Ca	Mg
Genotypes						
Resisto	b	1.366	1.355	1.307	1.133	0.785
	MS Dev. R.	16.62	0.68	1.13	37302.9	5297.2
Kakamega	b	1.397	1.051	1.022	-0.037	0.854
	MS Dev. R.	15.82	3.57	1.22	85220.6	11146.9
Ejumula	b	1.592	0.886	0.840	0.639	1.045
	MS Dev. R.	44.48	1.13	0.24	88829.0	15960.4
SPK004/6/6	b	0.753	0.809	1.069	1.180	0.737
	MS Dev. R.	14.20	4.58	1.14	104577.5	8591.4
Naspot_5/50	b	0.595	1.314	0.926	1.286	1.557
	MS Dev. R.	8.29	2.78	0.21	77864.9	15111.1
Zambezi	b	0.567	0.820	0.815	1.175	0.848
	MS Dev. R.	42.98	1.38	0.39	30655.1	3878.6
KMI61	b	0.834	0.767	1.080	0.658	0.537
	MS Dev. R.	27.33	6.46	0.86	29415.8	4848.4
Carrot_C	b	0.671	1.377	1.130	1.838	1.720
	MS Dev. R.	91.75	2.99	0.67	144282.8	16754.4
Abuket_1	b	1.133	1.183	1.059	1.310	1.427
	MS Dev. R.	68.86	2.45	1.41	49978.8	8032.3
SPK004/6	b	1.093	0.438	0.752	0.819	0.491
	MS Dev. R.	67.28	2.86	1.05	134558.5	13370.6
	LSD R. (0.05)	0.81	0.99	0.73	1.40	0.63
	B-test MS Dev.	+	Ns	Ns	Ns	Ns
Environments						
MBK1	b	0.949	1.472	1.562	1.115	0.928
	MS Dev. R.	69.71	4.00	0.85	104331.3	15597.1
MBK2	b	2.027	0.056	1.003	0.896	0.299
	MS Dev. R.	74.79	1.97	0.32	35601.9	5746.8
NM1	b	2.098	2.043	1.135	0.313	1.135
	MS Dev. R.	86.53	0.93	0.49	34672.7	7589.8
NM2	b	0.322	0.774	-0.112	0.102	0.496
	MS Dev. R.	25.09	2.75	0.26	48093.2	5244.0
SR1	b	0.697	1.724	1.504	2.101	1.232
	MS Dev. R.	40.04	2.70	0.71	60106.2	12584.7
SR2	b	0.842	-0.371	1.374	0.699	1.031
	MS Dev. R.	18.79	2.67	1.45	42777.7	14098.5
KA1	b	0.743	1.211	0.547	1.910	3.154
	MS Dev. R.	20.31	4.68	1.14	93960.7	21820.9
KA2	b	0.322	1.092	0.987	0.863	-0.275
	MS Dev. R.	14.95	1.83	0.88	144015.7	20152.7
	LSD R. (0.05)	2.04	2.28	1.85	1.54	1.96
	B-test MS Dev.	Ns	ns	Ns	Ns	Ns

KA1 Kachwekano season 1; KA2 Kachwekano season 2; MBK1 Mobuku season 1; MBK2 Mobuku season2; NM1 Namulonge season 1; NM2 Namulonge season 2; SR1 Serere season 1; and SR2 Serere season 2; MS Dev. R. Mean Square of Deviations from the regression

Only accessions with large or low values of b were significantly different for slopes of regression lines [i.e. 'Ejumula' (b = 1.592) or 'Kakamega' (b = 1.397) were significantly different compared with 'Naspot_5/50' (b = 0.595) or 'Zambezi' (b = 0.567)]. Although the slopes of regression lines were not significantly different (P =0.05), it is worth noting that steep b values of regression lines were observed for Namulonge and Mobuku in season 1 and 2, respectively (b > 2) – but for season 1 at Mobuku a medium slope (b = 0.949) and for season 2 at Namulonge a very low slope (b = 0.322) was observed. With respect to genotypes and nutritional traits (Table 2.7), no significant differences were observed among line slopes of regression for Fe and Zn. Calcium did differ for two accessions 'Kakamega' (b nearly zero) and 'Carrot_C' (b = 1.838). However, several significant differences of regression slopes were observed for magnesium, for example,

'Naspot_5/50' and 'Carrot_C' with steep regression slopes were significantly different from most accessions with b values smaller than 1. The MS deviations were not significantly different among genotypes and environments for all mineral traits. Although there are striking differences among genotypes and environments for the stability parameters, variance of genotype *j* across environments, variance of environment *k* across genotypes, and the ecovalence (Table 2.8), it appears that low values (high stability) were associated with low performance in yield or low levels in nutrients (correlations not presented).

Table 2.8. Estimates obtained using the static concept of genotype x environment interaction for storage root yield, iron (Fe), zinc (Zn), calcium (Ca) and magnesium (Mg) content of storage roots.

	Parameter	Storage root yield	Fe	Zn	Ca	Mg
Genotypes						
Resisto	σ_j^2	175.1	7.38	4.48	96058.4	24274.9
	Ecovalence	25.7	1.05	1.17	32859.9	6025.2
Kakamega	σ_j^2	181.7	7.15	3.20	73114.2	32916.9
	Ecovalence	27.1	3.07	1.05	126698.7	10239.0
Ejumula	σ_j^2	256	3.88	1.66	96490.5	48667.5
	Ecovalence	68.3	1.02	0.26	82655.8	13744.9
SPK004/6/6	σ_j^2	61.0	6.35	3.33	159110.0	24764.9
	Ecovalence	17.4	4.06	0.99	91253.3	9582.4
Naspot_5/50	σ_j^2	37.6	8.78	1.95	149248.4	90653.9
	Ecovalence	21.2	2.75	0.19	70819.1	22900.1
Zambezi	σ_j^2	64.5	3.67	1.70	95124.3	26353.4
	Ecovalence	53.0	1.30	0.40	27797.4	4067.6
KMI61	σ_j^2	83.4	7.71	3.14	46820.4	13399.6
	Ecovalence	25.7	5.74	0.75	31049.0	11022.6
Carrot_C	σ_j^2	117.5	9.57	3.20	292285.1	109188.5
	Ecovalence	87.9	3.08	0.61	158731.1	30983.7
Abuket_1	σ_j^2	169.7	7.28	3.51	128409.7	72114.0
	Ecovalence	60.5	2.22	1.22	47619.5	12720.0
SPK004/6	σ_j^2	160.6	3.16	2.06	148796.1	19176.3
	Ecovalence	58.4	3.62	1.02	116973.1	19772.8
Environments						
MBK1	σ_k^2	71.4	4.74	1.36	132657.2	16084.7
	Ecovalence	61.9	3.68	0.83	93165.0	13877.6
MBK2	σ_k^2	109.7	1.76	0.54	57427.2	5338.8
	Ecovalence	77.5	2.24	0.29	31991.6	6377.0
NM1	σ_k^2	123.2	3.10	0.76	33965.8	10073.0
	Ecovalence	89.5	1.42	0.44	45965.6	6793.8
NM2	σ_k^2	23.3	2.77	0.23	43086.6	5296.5
	Ecovalence	27.1	2.47	0.54	68603.5	5316.7
SR1	σ_k^2	40.7	4.02	1.19	195042.4	15106.5
	Ecovalence	36.5	2.68	0.69	92301.7	11325.8
SR2	σ_k^2	24.1	2.45	1.09	53701.41	15274.7
	Ecovalence	16.9	3.40	1.32	40934.7	12534.5
KA1	σ_k^2	23.8	4.96	1.76	200637.7	45075.5
	Ecovalence	18.7	4.19	1.07	110112.9	31374.5
KA2	σ_k^2	14.3	2.45	1.02	151934.9	18109.5
	Ecovalence	18.1	1.63	0.78	128613.6	22112.2

σ_j^2 variance of genotypes across environments; σ_k^2 variance of environments across genotypes; KA1 Kachwekano season 1; KA2 Kachwekano season 2; MBK1 Mobuku season 1; MBK2 Mobuku season2; NM1 Namulonge season 1; NM2 Namulonge season 2; SR1 Serere season 1; and SR2 Serere season 2

For storage root yield, the first (PC1) and second (PC2) principal components of the AMMI analysis explained 48.0% and 28.4% of GxE interaction, respectively. The AMMI biplot (Figure 2.2) displays a pattern of GxE interaction.

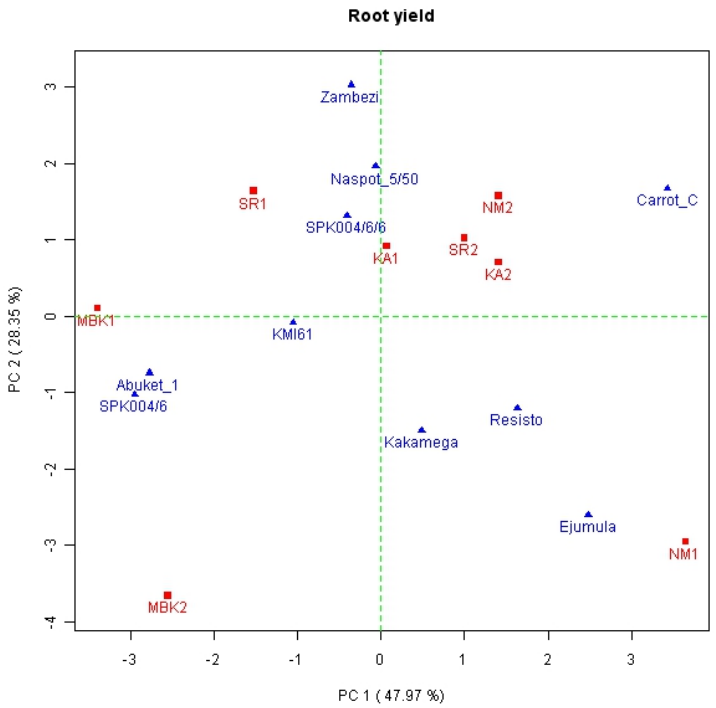

Figure 2.2. The AMMI biplot of 10 sweetpotato clones evaluated for storage root yield in 8 environments in Uganda. Means for genotypes: 'Naspot_5/50', 'KMI61', 'Zambezi', 'Carrot_C', 'Resisto', 'Kakamega', 'Abuket_1', 'SPK004/6', 'SPK004/6/6', and 'Ejumula' were 7.7, 12.6, 14.2, 14.9, 15.8, 16.3, 16.9, 17.7, 17.8, and 18.8 t.ha^{-1}, respectively. Means for environments: NM2, KA2, SR2, KA1, SR1, MBK1, MBK2, NM1 were 6.6, 8.4, 9.0, 10.5, 13.1, 17.6, 23.1, and 33.9 t.ha^{-1}, respectively.

Low-yielding environments exhibited positive PC1 and PC2 values, whereas high yielding environments exhibited positive PC1 and negative PC2 values (Namulonge Season 1) or negative PC1 and PC2 values (Mobuku Season 2). The seasons of each location were associated for Kachwekano, Serere, and tentatively at Mobuku, but the seasons at Namulonge were clearly not associated. Namulonge season 2 grouped among Kachwekano and Serere in season 2. High yielding accessions with small differences to the zero PC1 and PC2 values ('SPK004/6/6', 'Kakamega', and 'Resisto') were observed as well as large differences to the zero PC1 and PC2 values ('Abuket1' and 'SPK004/6'). Also low yielding accessions exhibited small differences to the zero PC1 and PC2 values ('Naspot_5/50', 'KMI61') as well as large differences to the zero PC1 and PC2 values. For storage root iron, PC1 and PC2 components of the AMMI analysis explained 36.7% and 30.0% of GxE interaction, respectively (Figure 2.3). The environments of Namulonge showed smaller

differences to the zero PC1 and PC2 values compared to the environments of Serere, and Mobuku. The Kachwekano environments are in between. Accessions with lower iron storage root contents across environments showed small differences to the zero PC1 and PC2 values ('Kakamega', 'Zambezi', 'Ejumula' and 'Resisto') or large differences to the zero PC1 and PC2 values (KMI61). Accessions with elevated iron contents across environments displayed larger differences to the zero PC1 and PC2 values ('Naspot 5/50', 'Abuket 1', 'Carrot_C', and 'SPK004/6/6'). For storage root zinc, the PC1 and PC2 components of the AMMI analysis explained 52.0% and 16.7% of GxE interaction, respectively (Figure 2.4). The seasons of each location were associated for Namulonge, Kachwekano, and Mobuku, but were less pronounced for Serere.

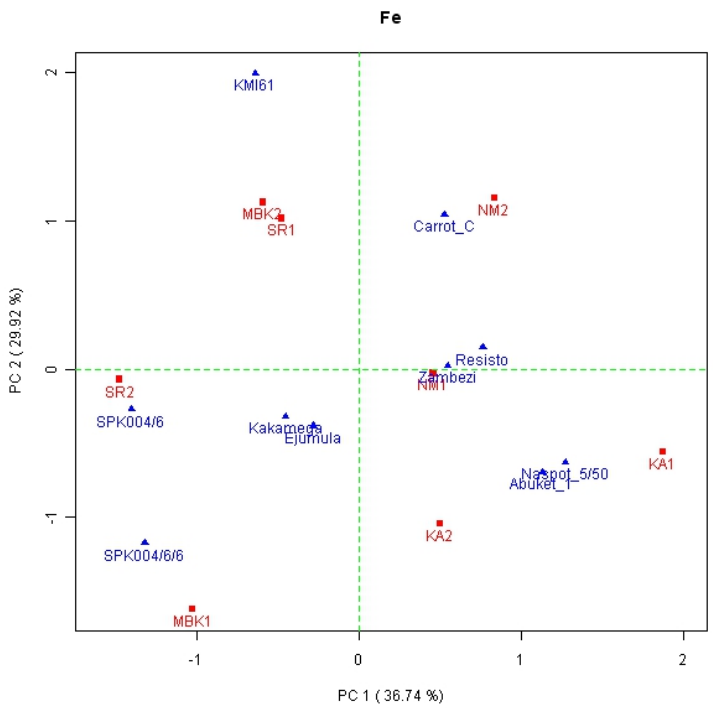

Figure 2.3. The AMMI biplot of 10 sweetpotato accessions evaluated for iron storage root content in 8 environments in Uganda. Means for genotypes: 'Kakamega', 'KMI61', 'Zambezi', 'Resisto', 'Ejumula', 'SPK004/6', 'Naspot_5/50', 'Abuket_1', 'Carrot_C', and 'SPK004/6/6' were 15.3, 16.3, 16.7, 16.7, 17.0, 17.1, 17.4, 17.7, 17.8, and 17.8 ppm, respectively. Means for environments: MBK2, MBK1, NM1 SR2, KA1, SR1, KA2, and NM2 were 13.6, 15.3, 16.1, 17.2, 18.0, 18.5, 18.9, and 19.0 ppm, respectively.

Again the environments of Namulonge, showed smaller differences to the zero PC1 and PC2 values compared to all environments except Mobuku season 2. No accessions with higher Zn contents in storage roots (>10 ppm) showed low differences to the zero PC1 and PC2 values, while others ('SPK004/6' and 'Abuket_1') showed large differences to the zero PC1 and PC2 values. For storage root calcium, PC1 and PC2 components of the AMMI analysis explained 44.4% and 30.8% of GxE interaction, respectively (Figure 2.5). The seasons of Namulonge and Mobuku were associated. Conversely, the seasons for Kachwekano and

Serere were not associated and large differences in PC2 values were observed. Again, the environments of Namulonge had small differences to the zero PC1 and PC2 values, but both environments were among environments with low calcium mean values across genotypes. Accessions with higher calcium contents in storage roots across environments (> 1850 ppm) showed low differences to the zero PC1 and PC2 values ('Zambezi', 'Abuket_1' and 'Resisto') as well as large differences to the zero PC1 and PC2 values ('SPK004/6/6' and 'Carrot_C'). For storage root magnesium, PC1 and PC2 components of the AMMI analysis explained 45.8% and 20.5%, respectively. The AMMI biplot (Figure 2.6) displays the pattern of the interactions. The seasons of Namulonge and Mobuku were associated. However this was not observed for Kachwekano and Serere. There were extreme differences in PC1 and PC2 values for Kachwekano season 1 and season 2. Among accessions with elevated magnesium levels across environments (> 500 pmm) clones with larger differences to the zero PC1 and PC2 values ('Ejumula', 'Carrot_C' and 'Abuket_1') were observed as well as one clone with smaller differences to the zero PC1 and PC2 values ('Zambezi').

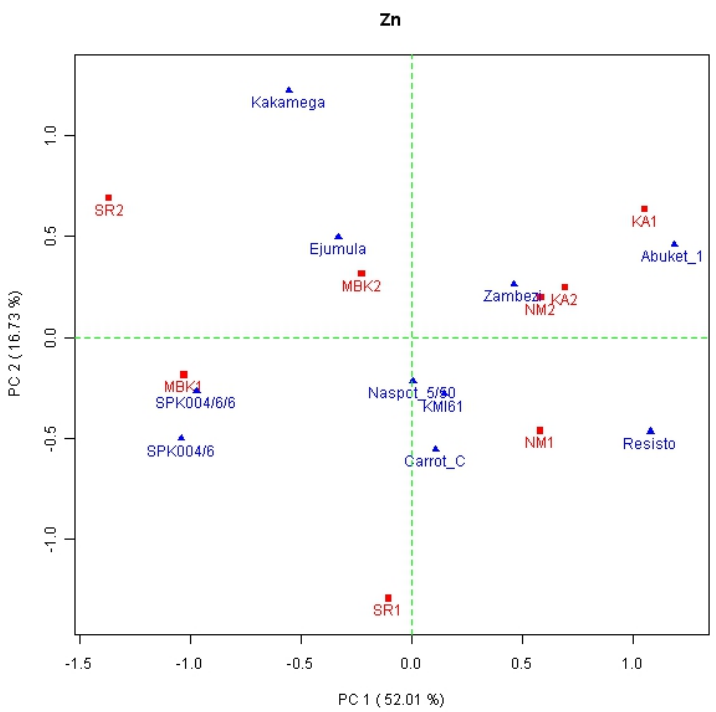

Figure 2.4. The AMMI biplot of 10 sweetpotato accessions evaluated for zinc storage root content in 8 environments in Uganda. Means for genotypes: 'Kakamega', 'Resisto', 'Ejumula', 'Naspot_5/50', 'KMI61', 'Zambezi', 'Carrot_C', 'Abuket_1', and 'SPK004/6/6' were 9.0, 9.2, 9.2, 9.3, 9.3, 9.3, 9.6, 9.7, 10.1, 10.2, and 10.5 ppm, respectively. Means for environments: MBK2, MBK1, NM1, KA1, SR2, SR1, KA2, and NM2 were 6.4, 9.1, 9.3, 10.3, 10.2, 10.5, 10.7 and 10.7 ppm, respectively.

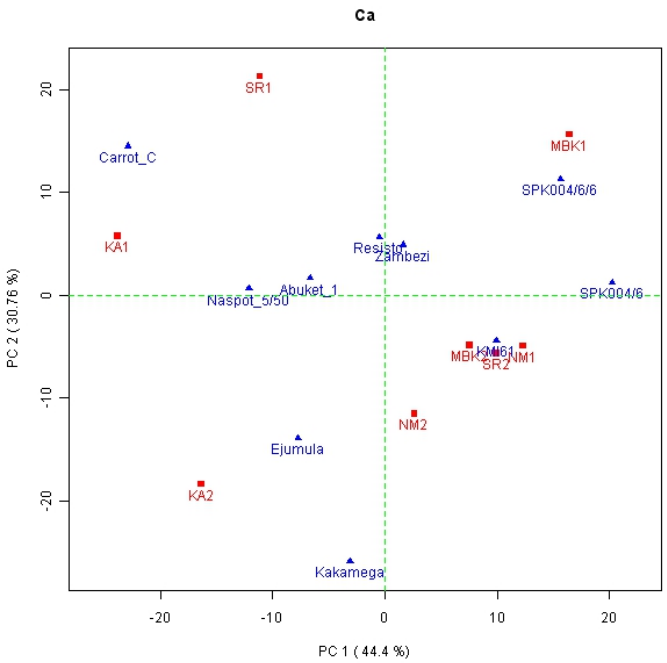

Figure 2.5. The AMMI biplot of 10 sweetpotato accessions evaluated for calcium storage root content in 8 environments in Uganda. Means for genotypes: 'KMI61', 'Kakamega', 'Naspot_5/50', 'SPK004/6', 'Resisto', 'Abuket_1', 'SPK004/6/6', 'Ejumula', 'Zambezi', and 'Carrot_C' were 1521.9, 1669.3, 1823.9, 1860.3, 1895.0, 1899.3, 1967.6, 1994.6, 2002.6, and 2153.6 ppm, respectively. Means for environments: NM2, MBK2, KA2, NM1, SR2, SR1, MBK1, and KA1 were 1627.2, 1636.9, 1737.9, 1844.9, 1894.7, 1899.2, 2139.3 and 2250.3 ppm, respectively.

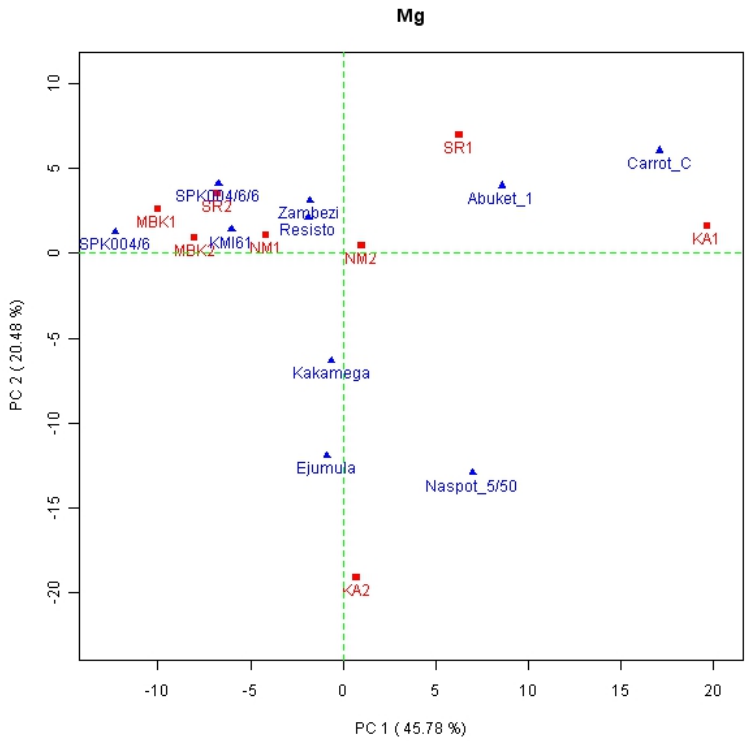

Figure 2.6. The AMMI biplot of 10 sweetpotato accessions evaluated for magnesium storage root content in 8 environments in Uganda. Means for genotypes: 'KMI61', 'SPK004/6/6', 'Kakamega', 'Naspot_5/50', 'Resisto', 'SPK004/6', 'Ejumula', 'Abuket_1', 'Zambezi', and 'Carrot_C' were 429.5, 461.8, 469.5, 489.5, 493.8, 498.8, 514.3, 532.3, 572.7, and 595.0 ppm, respectively. Means for environments: SR2, MBK2, MBK2, NM2, SR1, NM1, KA2, and KA1 were 305.1, 376.3, 452.2, 482.7, 504.0, 514.6, 587.9, and 903.1 ppm, respectively.

Moderate to high positive correlations (r = 0.6 to 0.9) were observed between trait pairs: storage root yield and harvest index, Fe and Zn, and calcium and magnesium on the basis of all clones used in the study (Table 2.9). On the other hand, high negative correlations (r = -0.762) were observed between starch and sucrose contents of the storage roots.

Moreover, a moderate negative correlation between starch and β-carotene (r = -0.477) and less pronounced negative correlation between DM and β-carotene (r = -0.2) were observed. However, a separate analysis without the check clone 'Resisto' (N=9 clones) revealed that the negative correlation between starch and β-carotene, and DM and β-carotene was negligible.

Table 2.9. Pearson correlation coefficients among observed traits.
Observed traits: YLD = Storage root yield, tha^{-1}; HI = harvest index, %; DM = dry matter content of storage roots, %; STA = starch content of storage roots, % DM; SUC = sucrose content of storage roots, % DM; BC = β-carotene content of storage roots, ppm DM; Fe = iron content of storage roots, ppm DM; Zn = zinc content of storage roots, ppm DM; Ca = calcium content of storage roots, ppm DM; Mg = magnesium content of storage roots, ppm DM.

	YLD	HI	DM	STA	SUC	BC	Fe	Zn	Ca
					Estimates based on all clones (N=10)				
HI	0.670								
DM	0.066	-0.057							
STA	-0.042	-0.162	0.342						
SUC	0.11	0.171	-0.207	-0.762					
BC	0.122	0.253	-0.2	-0.477	0.368				
Fe	-0.042	-0.091	0.018	-0.401	0.225	0.067			
Zn	-0.098	-0.039	0.004	-0.211	0.129	0.053	0.747		
Ca	0.101	0.175	0.140	-0.293	0.317	0.228	0.376	0.346	
Mg	0.064	0.086	0.082	-0.242	0.196	0.036	0.545	0.416	0.735
					Estimated based on all clones without check clone Resisto (N =9)				
HI	0.660								
DM	0.144	0.087							
STA	-0.048	-0.102	-0.061						
SUC	0.117	0.108	0.067	-0.741					
BC	0.164	0.219	0.217	-0.211	0.186				
Fe	-0.066	-0.106	0.052	-0.521	0.234	0.079			
Zn	-0.116	-0.052	-0.078	-0.375	0.160	0.113	0.759		
Ca	0.119	0.210	0.171	-0.405	0.392	0.249	0.390	0.358	
Mg	0.103	0.145	0.088	-0.338	0.274	0.095	0.563	0.452	0.764

Discussion

The significant (p>0.05) environment effects on yield and harvest index, the two yield parameters in the present study, are consistent with previous studies (Grüneberg *et al.*, 2005; Mwanga *et al.*, 2007; Eyzaguirre *et al.*, 2009). The best yielding environments NM1 and MBK2 are likely a result of favorable rain conditions characteristic of the environments. Unlike MBK1 where the crop grew on irrigation only, the crop at MBK2 benefited from both irrigation and natural rainfall. The low yields obtained at NM2 are probably due to poor rains at the beginning of the season. It is important to note that the environmental effects were significant for all the nutritional traits studied except dry matter (Table 2.3). However, this should not be misunderstood to mean significant GxE interactions (Tumwegamire *et al.*, 2011). The non-significant environmental effects on DM indicate selection and characterization in one environment can be extrapolated to other environments.

Genotypes were not significantly ($p > 0.05$) different for root yield, Fe and magnesium contents (Table 2.4). However, other studies have reported significant differences among genotypes for root yields (Collins *et al.*, 1987; Grüneberg *et al.*, 2005; Eyzaguirre *et al.* 2009), Fe, and magnesium (Grüneberg *et al.*, 2009b). This is likely due to the limited number of varieties and a more narrow set of clones used in the present study compared to previous studies. The high yields observed for accessions, 'Ejumula', 'SPK004/6', and 'SPK004/6/6' confirm previous results with the same varieties (Mwanga *et al.*, 2007; Mwanga *et al.*, 2009). The three varieties are released in Uganda, and represent the potential gains in breeding for OFSP clones with high root yields, dry matter and β-carotene (Mwanga *et al.*, 2009). These accessions of the category "OFSP dry and starchy" clearly have higher storage root dry matter and higher starch contents compared to the check clone 'Resisto', which belongs to the traditional OFSP category "OFSP moist and sweet". However, in this study we observed that the check, 'Resisto', had significantly higher β-carotene content (≈350 ppm on dry weight basis) compared to clones of the category "OFSP dry and starchy". This was not clearly observed in the previous study with 2 environments (Tumwegamire *et al.*, 2011). However, the present estimates are consistent with those reported elsewhere (Laurie, 2008; Grüneberg *et al.*, 2009b).

As expected, the σ^2_{GxE} component for β-carotene and starch were non-significant ($p > 0.05$), suggesting the possibility of improving the traits with high selection efficiency in the early stages of a sweetpotato breeding program. Our results are consistent with Grüneberg *et al.* (2005) on non-significant σ^2_{GxE} components for β-carotene and starch. In the present study, σ^2_{GxE} component for dry matter were highly significant ($p < 0.01$) but were fractional (0.4) compared to the corresponding σ^2_G component (1), again, consistent with the observation of Grüneberg *et al.* (2005). Furthermore, the proportion of σ^2_{GxE} compared

to the corresponding σ^2_G component was close to 1 for harvest index and sucrose content of storage roots. The observation for harvest index is similar to what Grüneberg *et al.* (2005) observed. These favorable variance component ratios for selection are reflected in heritability estimates of larger than 0.7 for harvest index, dry matter, starch, sucrose, and β-carotene; the later is very high at 0.96. On the basis of this observation as well as previous GxE studies (Grüneberg *et al.* 2005) there is negligible GxE interactions for β-carotene, and stability analysis reveals no information. However, significant environmental main effects on β-carotene – which are much less pronounced compared to genotypic main effects on β-carotene, were observed in this study as well as in previous studies (Grüneberg *et al.,* 2005). In this study the significant σ^2_E was about 3 times smaller than σ^2_G. It is nearly certain that the environment affects β-carotene levels in sweetpotato, but with no significant interactions with genotypes. Hence, we suggest that the trait complex harvest index, root DM, starch, sucrose, and β-carotene can be selected in early breeding stages with high selection efficiency. However, to prove this concept for selection in early breeding stages, variance component estimates in early breeding stages using thousands of clones should be done because it can be expected that σ^2_G is larger at these stages. This might not result in higher operational broad-sense heritabilites because breeding is operating with fewer environments (usually 1 or 2, rarely 3) in early breeding stages.

Traits with significant ($p<0.05$) or highly significant ($p<0.01$) σ^2_{GxE} components (Table 2.5) and ratios of σ^2_{GxE} / σ^2_G larger than 2 included storage root yields and all mineral contents of storage roots. Very high σ^2_{GxE} for root yields were also reported by Grüneberg *et al.* (2005). It is well known that breeding for yield is complex and requires more environments (Ngeve *et al.*, 1993; Collins *et al.*, 1987; Manrique and Harmann, 2002; Grüneberg *et al.*, 2005); however, harvest index, a major yield determining factor, might be very useful to select for yield and yield stability in sweetpotato (Grüneberg *et al.*, 2005). The significant GxE interactions for minerals in the present study deviate from preliminary findings reported by Grüneberg *et al.* (2009b) and suggest that breeding for storage root iron, zinc, calcium, and magnesium contents (low σ^2_G and relative high σ^2_{GxE}) is also complex in sweetpotato and requires information about the causes of these GxE interactions before the breeder can embark on enhancing these minerals. However, breeding for enhanced mineral contents in sweetpotato would be desirable in the frame of the biofortification program.

For storage root yield, this study demonstrated that the dynamic concept of using slope of regression lines is useful for selection among genotypes. However, only about 1/5 of the GxE interaction for storage root yield was explained by the heterogeneity of regression due to genotypes. This is consistent with Grüneberg *et al.* (2005). The reason that only 1/5 of the GxE interaction for storage root yield was explained by the heterogeneity of regression lines in both studies might be due to the fact that different agro-ecological zones were used as test environments. Within a single agro-ecological zone it is expected that the dynamic concept using slope of regression lines is more applicable versus multiple environments. For example, we observed in an extended GxE analysis for storage root yield by AMMI, that locations in different seasons

showed associated PC1 and PC2 values (Figure 2.2). Although the heterogeneity of regression lines with respect to environments was not significant, it was observed that Namulonge season 1 and Mobuku season 2 had steep slopes of regression lines indicating the usefulness of these environments to differentiate among accessions for storage root yield. Such environments are also useful for preliminary yield tests in early breeding stages.

However, unusual weather during crop growth can make these locations less useful for yield selection such as we experienced at Namulonge in season 2. The difference in the discriminatory capacity of Namulonge in season 1 and 2 was very clear in Figure 2.1. Namulonge changed in the slope of regression line from nearly 2 in season 1 to nearly 0.3 in season 2. To monitor the suitability of selection environments in early breeding stages, experienced breeders often include at least 5 check clones in trials (Eyzaguirre *et al.*, 2009). The AMMI analysis for storage root yield revealed a possibility to find as widely adapted varieties ('Kakamega' and 'SPK004/6/6') among high DM OFSP varieties as 'Resisto', a low DM OFSP check.

For Fe, Zn and Ca, regression analysis for either genotypes or environments did not result in a significant fit of the regression model and explained nearly zero percent of the total GxE interaction. However, for magnesium the variance component due to the heterogeneity of regression lines explained nearly 2/5 of GxE interactions. This suggests that genotypes in environments with elevated magnesium performance, measured on the basis of the average storage root magnesium contents across genotypes, have different uptake capacities in these environments. Since Namulonge demonstrated a slope of regression of b = 1.135 associated with relative low deviations from the regression line (7589.8) in season 1 it appears that this environment was suitable to differentiate among genotypes for magnesium storage root content. However, this suitability for selection can easily change in the event of unfavorable weather conditions (see Namulonge season 2 in Table 2.7).

On the basis of this study it appears that the dynamic concept of stability is unsuitable to select and improve selection strategies for iron, zinc, and calcium contents of storage roots. Also the static concept of stability appears unsuitable to select for iron, zinc, and calcium contents of storage roots (Table 2.8), because stability (low variance of accessions across environments and low ecovalence) is simply associated with undesired low Fe, Zn, and Ca contents of storage roots.

The trend that accessions with elevated Fe, Zn, and Ca contents (Table 2.8) show larger GxE interactions is clearly reflected by the AMMI analysis for Fe contents (Figure 3). The AMMI bi-plots clearly showed that all clones with elevated iron contents across environments ('Naspot_5/50', 'Abuket1', 'Carrot_C', and 'SPK004/6/6') displayed larger differences to the zero PC1 and PC2 values. Hence breeding for elevated Fe contents and stability of these Fe contents across environments appears to be very problematic. However, the AMMI analysis for storage root Zn content (Figure 2.4) showed that accessions exist with higher Zn contents (> 10 ppm) and low differences to the zero PC1 and PC2 values such as 'Carrot_C'. It appears that

at Namulonge, both seasons with elevated Zn mean values across genotypes, is an interesting selection environment to differentiate among genotypes because of its relatively small differences to the zero PC1 and PC2 values compared to other environments.

The same – elevated high mineral contents and low contribution to GxE interactions - was also observed for Ca in 'Zambezi' and 'Ejumula' (Figure 2.5) and for Mg in 'Zambezi' (Figure 2.6) indicating that simply associating desired high Fe, Zn, Ca, and Mg contents of storage roots generally with higher contribution to genotype by environment interactions is an insufficient cause and description of GxE interactions for mineral contents in sweetpotato storage roots. However, the number of accessions used in this study is not large enough to conclusively show that elevated mineral contents and low GxE exists in sweetpotato. This might merit further studies aiming at the heritability of elevated mineral contents combined with low contribution to GxE.

I think the study can not provide any recommendations for selection strategies to elevate storage root mineral contents. The study only demonstrates that improving mineral contents in sweetpotato is much more complicated and complex. However, it appears that it is possible to select and to design breeding strategies to enhance these traits in sweetpotato. Medium to high positive correlations among mineral traits (Table 2.9) are clearly in favor for selection aimed at elevated mineral contents in sweetpotato. Additional studies aimed at the heritability of elevated mineral contents combined with low contribution to GxE there is merit to investigate if selection can be made efficient through an index comprising mineral contents. It should be noted that an improvement of Mg content – also not a priority trait for bio-fortification – indirectly should affect positively Fe, Zn and Ca contents due to the correlation structure among these traits.

The positive correlation between root yield and harvest index has been previously reported by Grüneberg *et al.* (2005) and (2009b). The first study (Tumwegamire *et al.*, 2011) did not estimate this correlation. However, other positive correlations (Table 2.9) observed in this study for trait pairs Fe and Zn, Fe and Mg, Ca, and Mg are consistent with the previous work (Tumwegamire *et al.*, 2011) and similar to genetic correlations reported by Grüneberg *et al.* (2009a). This is also true for the negative correlation estimated observed in this study between root starch and sucrose content, as well as starch and β-carotene. Unlike in this study, the previous work (Tumwegamire *et al.*, 2011; Grüneberg *et al.,* 2009b) found moderate to high negative correlation between β-carotene and DM, but it appears that this negative correlation disappears or becomes negligible within the "OFSP dry and starchy" varieties. It is of interest to develop "OFSP dry and starchy" varieties on large scale for African farmers and consumers who prefer this type of sweetpotato. The less pronounced negative correlation between β-carotene and DM in breeding populations makes it easier for breeding for the two nutrients in sweetpotato. This also supports an argument to reduce crosses between "OFSP moist and sweet" and African high DM white-fleshed sweetpotatoes. However, it also

appears that within "OFSP dry and starchy" the positive correlations between β-carotene and minerals overall is less pronounced so that by means of selecting for more β-carotene – or intense color – there is an indirect selection for elevated mineral contents.

In conclusion, the environment affects β-carotene levels in sweetpotato, but without important interactions with genotypes. This is also true for starch and DM. It is nearly certain that for harvest index and sucrose, GxE interactions are noteable in sweetpotato, but the magnitude of these interactions is not large. I suggest that the trait complex harvest index, root DM, starch, sucrose, and β-carotene can be selected in early breeding stages with high selection efficiency. For minerals, significant GxE interactions must be expected and their magnitude appears to be in between the GxE interactions of the trait complex "harvest index, root DM, starch, sucrose, and β-carotene" and the GxE interactions of the storage root yield. The present work demonstrates that improving mineral contents in sweetpotato is complicated and complex and no recommendations on selection strategies to elevate storage root mineral contents can be proposed. To enhance mineral contents in sweetpotato, further studies are needed on the heritability of low contribution to GxE interactions among clones with elevated mineral contents. Medium to high positive correlations among mineral traits are clearly in favor for selection aiming at elevated mineral contents in sweetpotato.

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CHAPTER THREE 03

Genetic Diversity in White- and Orange-fleshed Sweetpotato Farmer Varieties from East Africa evaluated by Simple Sequence Repeat (SSR) Markers

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Abbreviations: *AMOVA, analysis of molecular variance; DM, drymatter; j, Jaccard's similarity coefficient; OFSP, orange-fleshed sweetpotato; PCR, polymerase chain reaction; SPVD, sweetpotato virus disease; SSR, simple sequence repeat; UPGMA, unweighted pair group method analysis; WFSP, white- or cream-fleshed sweetpotato.*

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Abstract

Sweetpotato [*Ipomoea batatas.* (L.) Lam] farmer varieties are still the backbone of production and breeding programs in Sub-Sahara Africa. Usually, farmer varieties in SSA are white, or cream-fleshed sweetpotato (WFSP), but recently orange-fleshed sweetpotato (OFSP) were found in East Africa (EA). The objective of the study was to characterize WFSP and OFSP germplasm from EA. Eighty five EA farmer varieties (29 OFSPs and 56 WFSPs) and seven varieties of non-African origin as check clones were analyzed for diversity using 26 simple sequence repeat (SSR) markers. A total 158 alleles were scored with an average of 6.1 alleles per SSR loci. The mean of Jaccard's similarity coefficients was 0.54. The unweighted pair group method analysis (UPGMA) revealed a main cluster for EA germplasm at a similarity coefficient of 0.52. At a similarity coefficient of about 0.55 sub clusters within the EA germplasm were observed, but these were neither country nor flesh color specific. Analysis of molecular variance (AMOVA) found a significant difference between EA and non-African germplasm, and a non significant difference between OFSP and WFSP germplasm. In conclusion, the EA germplasm appears to be distinct from non-African germplasm; and OFSP and WFSP farmer varieties from EA are clearly very closely related. OFSP farmer varieties from EA might show similar adaptation to Sub-Sahara African environments as WFSP and might have a big potential to alleviate vitamin A deficiency (VAD).

Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a hexaploid crop, usually clonally propagated by stem cuttings, but true seed production easily occurs by open pollination (Martin and Jones, 1986). It is of neotropical origin and crossed the Pacific via Polynesia before the discovery of the New World (Huaman *et al*., 1999; Zhang *et al*., 2000). In Africa it was introduced by explorers from Spain and Portugal during the 16th century (O'Brien, 1972; Zhang *et al*., 2000, 2004). To date sweetpotato has become a staple food crop in some countries of Eastern and Central Africa (Scott *et al*., 2000; Ewell, 2002), particularly in Uganda where daily per capita intake is about 240g (FAO, 2007). This reliance in Sub-Saharan African (SSA) and elsewhere underscores the importance of a crop as third in importance after potato (*Solanum tuberosum L*.) and cassava (*Manihot esculenta* Crantz) (FAO, 2007). In SSA, farmer varieties are still the backbone of sweetpotato production and breeding (Abidin, 2004; Grüneberg *et al*., 2009).

The awareness of sweetpotato as a healthy food crop is increasing, especially the orange-fleshed sweetpotato (OFSP) that are very rich in pro-vitamin A carotenoids (Woolfe, 1992). Vitamin A deficiency (VAD) presents severe public health problems in SSA and Asia (Pfeiffer and McClafferty, 2007) but can be alleviated by consuming OFSP (Low *et al*., 2007). However, the germplasm in SSA is nearly exclusively white-fleshed and characterized by high storage root dry mater (DM) contents (around 30%). Most of introduced OFSP germplasm from the Americas, which has low DM contents (approximately 22% to 26%), have collapsed (CIP unpublished) due to extreme high pressure of sweetpotato virus disease (SPVD) in SSA, especially in East Africa (Gibson *et al*., 1998). SPVD often causes yield losses of up to 90% in high virus pressure zones of SSA (Gibson *et al*., 1998; Karyeija *et al*., 2000). Recently, germplasm collection exercises have found about 25 and 10 OFSP farmer varieties in Uganda and Tanzania, respectively (CIP, 2005) with elevated DM contents (about 30% DM).

Molecular markers have been used for phylogenetics and germplasm evaluation to study the origin of sweetpotato and its dissemination into the Pacific and Asia (He *et al*., 1995, Hu *et al*., 2003, Prakash *et al*., 1996, and Zhang *et al*., 2004). African germplasm has been studied by Gichuki *et al.* (2003), on basis of RAPD markers and 74 accessions from different regions of the world (including 17 East African accessions), and Gichuru *et al.* (2006) on basis of four SSR primers and 57 African accessions. A large genetic diversity in African germplasm was observed and the possibility was suggested that sweetpotato has an additional secondary diversity center around the East Africa region. This is evidenced by a large number of farmer varieties adapted to East Africa, which meet environmental challenges and consumer preference in SSA much better than introduced germplasm (Mwanga *et al*., 2007, 2009). The main objectives of this study

were to characterize genetic relationships among and between East African OFSP and WFSP farmer varieties, and how these two phenotypic groups compare with non-African OFSP and WFSP accessions.

Materials and Methods

Plant Material

A total of 92 sweetpotato cultivars were used for the study (Table 3.1). Eighty five (85) cultivars were collections from East Africa. Seven cultivars were of non African origin, namely: 'Jewel' and 'Resisto' from the United States, 'Xushu 18' and 'Yanshu' from China, 'Naveto' from Papua New Guinea, and 'Zapallo' and 'Jonathan' from Peru. Fifty five accessions were collected from Uganda, 23 from Kenya, six from Tanzania, and one from Zambia. Twenty six of the accessions were African OFSP farmer varieties from Uganda (14), Kenya (7), Tanzania (4) and Zambia (1). Moreover, two modern varieties developed in Uganda were used in this study, namely SPK004/1 (Naspot 7) and SPK004/6 (Naspot 9). The accessions or clones, with a CIP ID Code or with a CIP ID Code in process (Table 3.1) are held in trust at CIP's gene bank as *in vitro* plantlets.

DNA extraction

Total DNA was isolated from 200 mg of fresh leaf tissue using a modified protocol by Dellaporta *et al.* (1983). The leaves were obtained from an individual plant for each accession or clone. The leaf tissue was ground in 600µl of Dellaporta buffer (containing ß-mercapto ethanol) using a mortor and a pestle. The contents were transferred to labeled tubes (1.5 ml) to which 42 µl of 20% sodium dodecyl sulfate (SDS) was added and mixed well.

Table 3.1. Description of clones used for the genetic diversity study in farmer varieties from East Africa and 7 non-African varieties as checks.

Clone	CT	Origin		Local ID Code	FC	SC	CIP ID Code	Collecting Institute
		Country	District					
MSK1025 Bitambi	FV	UG	Masaka	UG01	C	B	i.p.	NaCRRI
SRT40 Mary	FV	UG	Soroti	UG02	C	C	No	NaCRRI
APA365 Anam Anam	FV	UG	Apac	UG03	C	C	i.p.	NaCRRI
MBR539 Kitekamaju	FV	UG	Mbarara	UG04	W	C	i.p.	NaCRRI
Jayalo	FV	KE	Siaya	KE22	Y	PR	i.p.	KARI
KBL172 Magabali	FV	UG	Kabale	UG05	C	C	i.p.	NaCRRI
KMI61	FV	UG	Kumi	UG06	O	C	i.p.	NaCRRI
Sudan	FV	UG	Luwero	UG07	LO	C	No	NaCRRI
MLE165 Namafumbiro	FV	UG	Mbale	UG08	C	C	No	NaCRRI
SRT30 Nyara	FV	UG	Soroti	UG09	LO	C	No	NaCRRI
Nyandere	FV	KE	Siaya	KE01	PY	PR	i.p.	KARI
Obuogo_1	FV	KE	Siaya	KE02	C	C	i.p.	KARI
Kuny kubiongo	FV	KE	Siaya	KE03	C	PR	No	KARI
Marooko	FV	KE	Siaya	KE04	C	C	i.p.	KARI
Carrot Dar	FV	TZ	Ilara	TZ01	DO	C	i.p.	SRI Kibaha
KSR652 Mugumire	FV	UG	Kisoro	UG10	C	C	i.p.	NaCRRI
ARA 208 Ombivu	FV	UG	Arua	UG11	C	PR	i.p.	NaCRRI
ARA 214	FV	UG	Arua	UG12	C	C	i.p.	NaCRRI
MLE173 Kijovu	FV	UG	Mbale	UG13	C	PR	i.p.	NaCRRI
LIR 257 Otada	FV	UG	Lira	UG14	C	C	No	NaCRRI
MBR536 Karebe	FV	UG	Mbarara	UG15	C	C	i.p.	NaCRRI
KSR652 Kakoba	FV	UG	Kisoro	UG16	Y	PR	i.p.	NaCRRI
Bunduguza	FV	UG	na.	UG17	C	PR	i.p.	NaCRRI
KSR675 Nora II	FV	UG	Kisoro	UG18	C	C	i.p.	NaCRRI
KBL618 Kigabali	FV	UG	Kabale	UG19	C	C	i.p.	NaCRRI
MLE163 Kyebandula	FV	UG	Mbale	UG20	C	C	i.p.	NaCRRI
MLE184 Manafayareta	FV	UG	Mbale	UG21	W	PR	No	NaCRRI
Mayai	FV	TZ	Zanzibar	TZ02	DO	C	No	ARI Kizimbani
Carrot_C	FV	TZ	Ilara	TZ03	DO	C	i.p.	SRI Kibaha
ARA244 Shinyanga	FV	UG	Arua	UG22	LO	C	i.p.	NaCRRI
Tororo_3	FV	UG	Tororo	UG23	C	C	i.p.	NaCRRI
KBL632 Nyinakamanzi	FV	UG	Kabale	UG24	C	PR	No	NaCRRI
LIR296	FV	UG	Lira	UG25	LO	PR	i.p.	NaCRRI
SRT52	FV	UG	Soroti	UG26	O	C	No	NaCRRI
KMI83 Ikala2	FV	UG	Kumi	UG27	LO	C	i.p.	NaCRRI
SRT02 Araka white	FV	UG	Soroti	UG28	C	C	i.p.	NaCRRI
SRT01 Osapat	FV	UG	Soroti	UG29	Y	C	i.p.	NaCRRI
MBR521 Nkwasahansi	FV	UG	Mbarara	UG30	C	PR	i.p.	NaCRRI

Table 3.1. Continued.

Clone	CT	Origin		Local ID Code	FC	SC	CIP ID Code	Collecting Institute
		Country	District					
SRT34 Abuket 2	FV	UG	Soroti	UG31	LO	C	i.p.	NaCRRI
SRT39 Rwanda	FV	UG	Soroti	UG32	O	C	No	NaCRRI
HM A490 Kawogo	FV	UG	Hoima	UG33	C	B	No	NaCRRI
HM A493 Tanzania	FV	UG	Moima	UG34	LO	C	i.p.	NaCRRI
PAL161	FV	UG	Palisa	UG35	LO	C	i.p.	NaCRRI
KML883 Sikempya	FV	UG	Kamuli	UG36	W	C	No	NaCRRI
Zambezi	FV	ZB	na	ZBO1	DO	PR	i.p.	ZARI
KSR637 Kamabereikumi	FV	UG	Kisoro	UG37	C	C	i.p.	NaCRRI
SPK004/6	MV	UG	NaCRRI	UG38	O	PR	No	NaCRRI
SRT49 Sanyuzameza	FV	UG	Soroti	UG39	Y	PR	No	NaCRRI
Resisto	MV	USA	na	na	DO	B	440001	na
Kala	FV	UG	Soroti	UG40	LO	C	i.p.	NaCRRI
SRT33 Abuket 1	FV	UG	Soroti	UG41	O	P	i.p.	NaCRRI
KBL627 Mukazi	FV	UG	Kabale	UG42	C	C	i.p.	NaCRRI
Ejumula	FV	UG	Katakwi	UG43	DO	C	No	NaCRRI
Ukerewe	FV	TZ	Ukerewe	TZ04	Y	PR	i.p.	ARI Ukiruguru
KBL619 Kamamazi	FV	UG	Kabale	UG44	C	P	i.p.	NaCRRI
K-37	FV	KE	Siaya	KE06	LO	C	i.p.	KARI
APA352 Oketodede	FV	UG	Apac	UG45	C	C	i.p.	NaCRRI
SPK 004/1	MV	UG	NaCRRI	UG46	LO	PR	i.p.	NaCRRI
Wagabolige MBR600	FV	UG	Busonga	UG47	C	C	No	NaCRRI
Kisakyabikiramaria IGA963	FV	UG	Mbarara	UG48	C	C	No	NaCRRI
Nyongerabalenzi	FV	UG	Iganga	UG49	C	C	No	NaCRRI
Plot143	FV	KE	Kakamega	KE07	C	na.	i.p.	KARI
PAL153 Abukoki	FV	UG	Palisa	UG50	C	C	i.p.	NaCRRI
KMI56 Opira	FV	UG	Kumi	UG51	C	B	No	NaCRRI
Cheglina	FV	KE	Homabay	KE08	C	C	i.p.	KARI
K-118	FV	KE	Siaya	KE09	LO	C	i.p.	KARI
K-52	FV	KE	Kakamega	KE10	C	na.	No	KARI
Oguroiwe	FV	KE	Siaya	KE11	C	C	i.p.	KARI
Nyatonge	FV	KE	Siaya	KE12	C	C	i.p.	KARI
Polista	FV	KE	Mwanza	KE13	C	PR	i.p.	KARI
K-566632	MV	KE	KARI	KE14	O	PR	i.p.	KARI
KMI81 Ikala	FV	UG	Kumi	UG52	LO	C	i.p.	NaCRRI
KRE733 Kitambi	FV	UG	Kabalore	UG53	C	PR	i.p.	NaCRRI
Pipi	FV	TZ	Zanzibar	TZ05	LO	C	i.p.	ARI Kizimbani
Kemb10	FV	KE	KARI	KE15	C	C	i.p.	KARI
MSK1047 Bwanjure	FV	UG	Masaka	UG54	W	PR	i.p.	NaCRRI
K-135	FV	KE	Migori	KE16	O	C	i.p.	KARI
Wera	FV	KE	na	KE17	Y	C	i.p.	KARI
K-134	FV	KE	Migori	KE18	LO	PR	No	KARI

Table 3.1. Continued.

Clone	CT	Origin		Local ID Code	FC	SC	CIP ID Code	Collecting Institute
		Country	District					
SPK004	FV	KE	Kakamega	KE19	LO	P	441768	KARI
Nyaguta	FV	KE	Siaya	KE20	C	P	i.p.	KARI
Budagala	FV	KE	Mwanza	KE21	C	na.	No	KARI
MBR580 Nylon	FV	UG	Mbarara	UG55	C	C	No	NaCRRI
Jewel	MV	USA	na	na	DO	PR	440031	na
Xushu-18	MV	CH	na	na	C	PR	440025	na
Yanshu-1	MV	CH	na	na	C	PR	440024	na
Naveto	FV	PNG	na	na	C	P	440131	na
Tanzania	FV	TZ	na	TZ06	Y	C	440166	na
SPK004 (CIP)	FV	KE	na	na	LO	P	No	na
Zapallo	MV	PE	na	na	O	C	420027	na
Jonathan	FV	PE	na	na	O	C	420014	na

(CT = clone type, FV = farmer variety, MV = modern variety; UG = Uganda, TZ = Tanzania, KE =: Kenya, ZB = Zambia, PGN = Papua New Guinea, PE = Peru, CH = China; FC = flesh color: W = white, C = cream, PY = pale yellow, Y = yellow, LO = light orange, O = orange, DO = deep orange; SC = skin color, B = brown, C = cream, PR = purple red, P = pink; i.p. = designation of CIP code in process, No = no acquisition from CIP; na. = no available information).

The mixture was incubated at 65°C for 10 minutes before adding 160µl of 5M potassium acetate and mixed again. The new mixture was then incubated on ice for 10 min. The tubes were centrifuged at 15115 g (13000 rpm) for 10 minutes. About 650µl of the supernatant were transferred into new 1.5ml tubes. An equal amount of cold iso-propanol was added to the supernatant and centrifuged at 15115 g (13000) rpm for 10 minutes to precipitate the DNA as a pellet. Iso-propanol was discarded and DNA pellet was washed by adding 500 µl of 70% Ethanol and centrifuged at 15115 g (13000 rpm) for 5 minutes before discarding the ethanol. The DNA pellets were air-dried for 35 minutes and suspended in about 200µl of autoclaved TE buffer (pH 8). Finally 2 µl of DNase-free RNase A were added to the DNA and the test tubes incubated at 37oC for 30 minutes. The DNA was conserved at -20°C until it was used.

Simple Sequnce Repeat Amplification

DNA samples were quantified and a total of 3 ng of total genomic DNA from each of the samples was used for polymerase chain reactions (PCRs). Twenty six pairs of SSR primers (Table 3.2) confirmed for sweetpotato DNA amplification (Buteler *et al*., 1999; Diaz and Grüneberg, 2008) were used for the reactions.

Table 3.2. Description of SSR markers used to characterize sweetpotato genotypes by currently used names, motifs, forward and reverse primers, and annealing temperature.

Name	Forward Primers	Reverse Primers	Motif	Temp. °C	Reference
IB242	5-gcggaacggacgagaaaa-3	5-atggcagagtgaaaatggaaca-3	(ct)3ca(ct)11	58	Buteler et al 1999
IB297	gcaatttcacacacaaacacg	cccttcttccaccactttca	(ct)13	58	Buteler et al 1999
IB316	caaacgcacaacgctgtc	cgcgtcccgcttatttaac	(ct)3c(ct)8	58	Buteler et al 1999
IB324	tttggcatgggcctgtatt	gttcttctgcactgcctgattc	*	56	Tseng et al 2002
IBCIP-1	cccacccttcattccattact	gaacaacaacaaaaggtagagcag	(acc)7a	63	Yañez 2002
IB-R03	gtagagttgaagagcgagca	ccatagacccattgatgaag	(gcg)5	58	Benavides (unp.)†
IB-S07	gcttgcttgtggttcgat	caagtgaagtgatggcgttt	(tgtc)7	60	Benavides (unp.)†
IB-S10	ctacgatctctcggtgacg	cagcttctccactccctac	(ct)12	60	Benavides (unp.)†
IB-S11	ccctgcgaaatcgaaatct	ggacttcctctgccttgttg	(ttc)10	58	Benavides (unp.)†
IB-R12	gatcgaggagaagctccaca	gccggcaaattaagtccatc	(cag)5a	60	Benavides (unp.)†
IB-R13	gtaccgagccagacaggatg	cctttgggattggaacacac	(ttc)6	58	Benavides (unp.)†
IB-R16	gacttccttggtgtagttgc	agggttaagcgggagact	(gata)4	60	Benavides (unp.)†
IB-S17	cagaagagtacgttgctcag	gcacagttctccatcctt	(gga)4	58	Benavides (unp.)†
1B-S18	ctgaacccgacagcacaag	gggaagtgaccggacaaga	(tagc)4	58	Benavides (unp.)†
IB-R20	cttcactctgctcgccatta	gtacttggacgggaggatga	(ggc)5	54	Benavides (unp.)†
IB-R21	gacagtctccttctcccata	ctgaagctcgtcgtcaac	(gac)5	58	Benavides (unp.)†
IBC12	tctgagcttctcaaacatgaaa	tgagaattcctggcaaccat	(ttc)6	56	Solis et al (unp.) ‡
J175	atctatgaaatccatcactctcg	actcaattgtaagccaaccctc	(aatc)4	58	Solis et al (unp.) ‡
J10A	tcaaccactttcattcactcc	gtaattccaccttgcgaagc	(aag)6	58	Solis et al (unp.) ‡
J67	cacccatttgatcatctcaacc	ggctctgagcttccattgttag	(gaa)5	58	Solis et al (unp.) ‡
J116A	tcttttgcatcaaagaaatcca	cctcagcttctgggaaacag	(cct)6	58	Solis et al (unp.) ‡
JB1809	cttctcttgctcgcctgttc	gatagtcggaggcatctcca	(cct)6(ccg)6	60	Solis et al (unp.) ‡
IBJ522a	acccgcatagacactcacct	tgaccgaagtgtatctagtgg	(cac)6-7	57	Solis et al (unp.) ‡
IBC5	ccacaaaaatcccagtcaaca	agtggtcgtcgacgtaggtt	(aag)8	62	Solis et al (unp.) ‡
IBJ544b	agcagttgaggaaagcaagg	caggatttacagccccagaa	(tct)5	61-62	Solis et al (unp.) ‡
IB-S01	tcctccaccagctctgattc	ccattgcagagccatacttg	(aga)10	56	Benavides (unp.)†

† unp. = unpublished developed from 2002 to 2003 at CIP
‡ unp. = unpublished developed from 2005 to 2006 at CIP

A final volume of reaction mixture was 10 µl containing 25 mM MgCl2, 10X buffer, 10mM dNTPS, 1 uM M13 FW 700/800, 1 µM forward primer, 1 µM reverse primer, 5 U/µl Taq Pol, 10 ng/µl DNA, and ddH2O was used for the PCR. The amplification conditions were set up thus: 94°C for 4 minutes, denaturation at 94°C for 1 minute; annealing at between 56.0 and 62.0oC (depending on the annealing temperature of the primer as per Table 3.2); polymerization at 72°C for 1 minute; repeated step 2 for 30 times, and a final extension at 72°C for 7 minutes. Amplification products were analyzed and read on a computer automated Licor (4300) DNA Analyzer (Licor Biosciences Lincoln, NE) for 25 pairs of SSR primers.

Simple Sequnce Repeat data scoring and analysis

Genotypes were scored for the presence (1) or absence (0) of each fragment. Only those with medium or high intensity were taken into account. Fragments with the same mobility on the gel but with different intensities were not distinguished from each other when genotypes were being compared. Using NTSYS-pc version 1.8 computer software, similarity matrices were constructed from the binary data with Jacard's coefficients (Jaccard, 1908). Jaccard's similarity = Nab/Na+Nb, where Nab represents the number of fragments shared by accessions *a* and *b*, Na the amplified fragments in sample *a*, and *Nb* the amplified fragments in sample *b*. A dendogram was constructed from the genetic similarity matrix by weighted paired group method (UPGMA) (Sneath and Sokal, 1973). Analysis of Molecular Variance (AMOVA) was performed using Arlequin 3.1 version computer software (Excoffier *et al*., 2006) to quantify the genetic variation and relationship levels between and within East African and non-African germplasm on one hand, and OFSP and WFSP on the other. For the two levels of AMOVA, four populations namely East African OFSP germplasm; East African WFSP germplasm; Non African OFSP germplasm; and Non African WFSP germplasm were used. A matrix of genetic distances between different populations of germplasm was also generated by AMOVA.

Results

A total of 158 polymorphic bands were scored for the 25 SSR primers and used to differentiate 85 local plus seven introduced sweetpotato cultivars (Table 3.3). All markers were polymorphic, and the number of bands or alleles ranged from 2 to 11 per SSR marker loci, with an average of 6.1 alleles. The PCR products ranged between 110 bp and 395 bp in size.

The frequencies of pair-wise similarity coefficients for SSR analysis of the 92 sweetpotato accessions is shown in Figure 3.1. The SSR based Jaccard's similarity coefficients ranged between 0.30 and 1.00 with a mean of 0.54. Most similarity coefficients were observed between 0.5 and 0.59, accounting for 54.0% of the total frequency of pair-wise similarity coefficients. Additional 25% and 17.0% of the coefficients, respectively, ranged from 0.40 to 0.49 and from 0.60 to 0.69.

The genetic variability and relationships among the studied sweetpotato accessions are presented in a dendogram (Figure 3.2). A number of accessions with a similarity coefficient of 1.00 were identified. These include (i) UG15 and UG17, (ii) UG04 and UG23, and (iii) KE07 and KE01 among the WFSP farmer varieties; and (i) UG31, UG07 and UG12, and (ii) 'Zapallo' and UG32 among the OFSP farmer varieties. Our results also identified some accessions (mostly East African) that clustered closely at the early fusion steps of the cluster analysis.

Table 3.3: Number of polymorphic alleles and their bp range generated by SSR markers in 85 farmer varieties from East Africa and 7 introduced cultivars.

Name	No. alleles	pb range
IB S17	8	182 – 204
J116a	9	207 - 251
IB 242	6	136 - 155
IB-S11	9	254 - 305
IB-S01	7	233 - 268
IB-R13	9	225 - 298
IB-R12	5	356 - 395
IBCIP-1	4	155 - 167
IB-S07	4	193 - 211
IB-S10	11	307 - 337
J67	7	191 - 217
IB-S18	2	296 - 298
J10A	8	191 – 225
J175	5	133 – 149
IB316	5	151 – 167
IBC5	9	108 – 130
IBJ544b	7	191 – 214
IBJ522a	5	235 – 305
IB-R03	5	302 – 312
IB-R16	5	215 – 243
IB324	4	136 – 152
IB-R20	3	206 – 223
IB-R21	3	181 – 207
JB1809	5	144 – 155
IBC12	9	110 – 134
IB297	4	150 – 182
Mean 6.1 for polymorphic alleles per SSR loci (total 158)		

These include KE17 and KE09 (j = 0.98), KE15 and UG40 (j = 0.98), UG52 and UG27 (j = 0.97), KE12 and UG50 (j = 0.98), UG18 and UG02 (j = 0.97), UG48 and UG55 (j = 0.95), UG54 and SPK004 (CIP) (j = 0.98), UG05 and UG19 (j = 0.82), TZ04 and KE06 (j = 0.97), TZ02 and TZ03 (j = 0.97), and KE14 and Jewel (j = 0.96). Interesting with this result is that unlike the duplicate accessions, some of the closely clustered accessions differ in countries of origin (e.g. KE12 and UG50) and root flesh colour (e.g. TZ04 and KE06) which may suggest common ancestry.

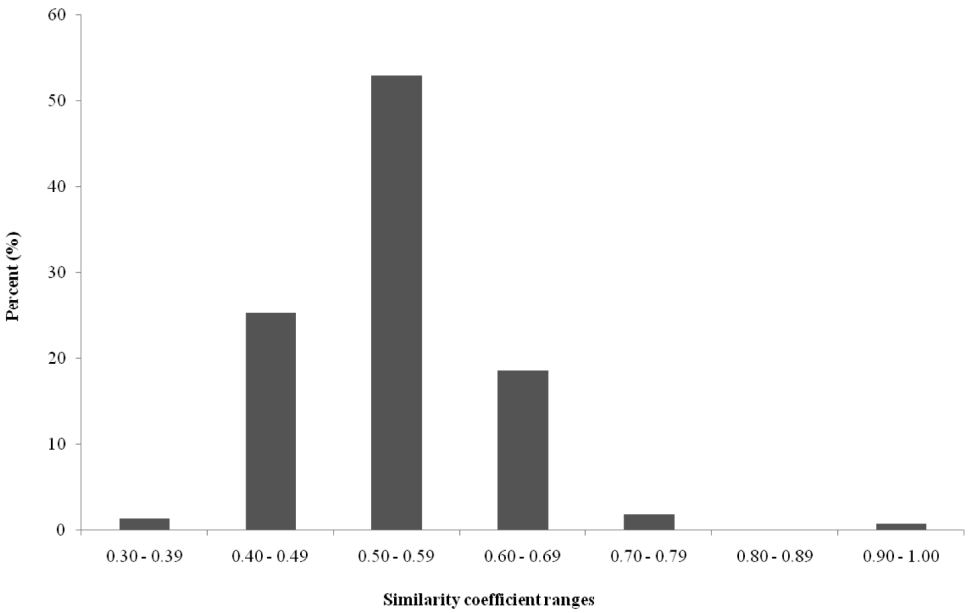

Figure 3.1. Frequency distribution of pairwise SSR similarity coefficients among 85 EA farmer varieties and 7 non-African varieties.

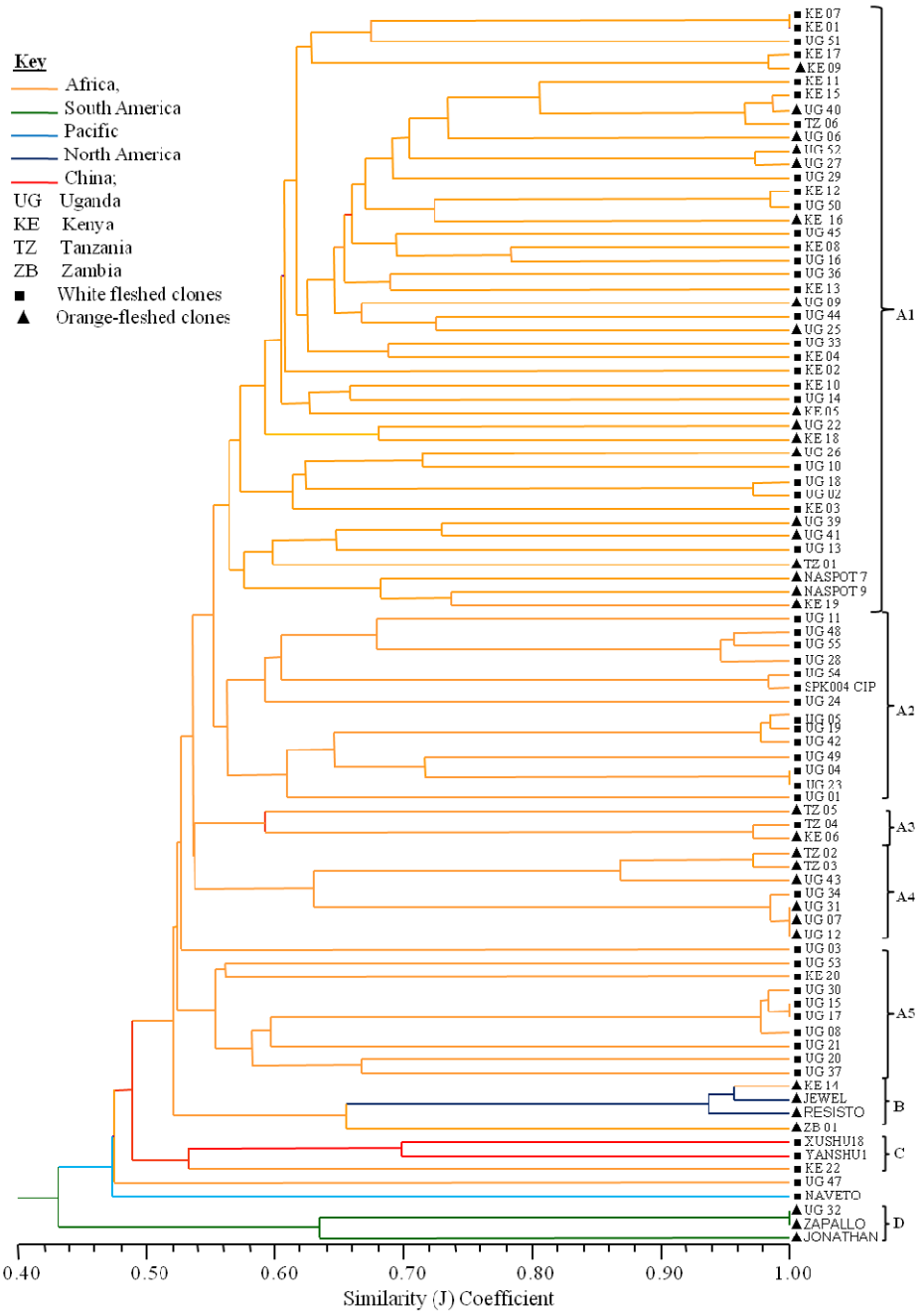

Figure 3.2. Dendrogam of the UPGMA cluster analysis on the basis of Jaccard's SSR based genetic similarities among 85 EA farmer varieties and 7 varieties of non-African origin used as check clones.

The majority of East African farmer varieties were clustered at final fusion steps with the non-African germplasm. At about 0.52 similarity coefficient, most East African farmer varieties, except UG47, ZB01, KE22 and KE14, formed a main cluster (A) which is clearly separate from other clusters B, C and D that comprise of mostly non-African accessions. The exceptional accessions namely ZB01 and KE14 closely clustered with OFSP varieties 'Jewel' and 'Resisto' from the USA, while KE22 closely clustered with the modern Chinese varieties 'Xushu 18' and 'Yanshu 1. UG47 neither closely clustered with East African nor non African accessions.

In spite of a distinct cluster (A) by East African sweetpotato farmer varieties, at about 0.55 similarity coefficient, clear sub-clusters A1 – A5 were identified. The sub-clusters A1 and A2 contained the well know farmer varieties TZ06 and KE19, respectively. However, none of the sub-clusters contained accessions originating from one country or with similar root flesh colour.

The AMOVA was used to distinguish between the East African sweetpotato germplasm and non-African germplasm (Table 3.4). A second analysis examined differences between OFSP germplasm and WFSP germplasm (Table 3.5). The difference between East African and non-African accessions was significant and accounted for 11.6% of the molecular variance. Contrastingly, the difference between OFSP and WFSP accessions was not significant and was explained by -14.16% of the molecular variance. In both scenarios, the variation due to individual accessions in different populations was significant ($p > 0.001$) and accounted for the majority, 82.9% and 92.25%, of the observed molecular variance, respectively.

Table 3.4. Analysis of Molecular Variance (AMOVA) of 92 sweetpotato accessions grouped into East African versus non-African germplasm

Source of variation	df	Sum of squares	Variance components	Percentage variation
Among groups†	1	60.34	2.60***	11.61
Among populations‡	2	85.44	1.22***	5.44
within groups				
Within populations	85	1551.31	18.56***	82.95
Total	88	1697.09	22.38	

†Groups are East African germplasm and Non-African germplasm.
‡Populations are East African OFSP cultivars, East African non-OFSP cultivars, Non-African OFSP cultivars, and Non-African non-OFSP cultivars.
*** Significant at the 0.001 level.

Table 3.5. Analysis of Molecular Variance (AMOVA) of 92 sweetpotato accessions grouped into OFSP versus WFSP germplasm.

Source of variation	df	Sum of squares	Variance components	Percentage variation
Among groups†	1	47.571	-2.85ns	-14.16
Among populations‡	2	79.724	4.41***	21.91
within groups				
Within populations	85	1551.31	18.56***	92.25
Total	88	1697.09	20.12	

†Groups are OFSP germplasm and WFSP germplasm;
‡Populations are East African OFSP cultivars, East African non-OFSP cultivars, Non-African OFSP cultivars, and Non-African non-OFSP cultivars;
ns = none significant, *** Significant at the 0.001 level.

The genetic distances matrix is presented in Table 3.6. A significantly short genetic distance (0.045) was observed between OFSP and WFSP East African farmer varieties. In contrast, a significantly ($p<0.05$) large genetic distance (0.289) was observed between OFSP and WFSP non-African accessions. Furthermore, both OFSP (0.195 and 0.231) and WFSP (0.212 and 0.193) East African farmer varieties showed significant ($p<0.01$) long genetic distances in comparison to OFSP and WFSP non African accessions, respectively.

Table 3.6. The average genetic distances among sweetpotato accessions

	East African OFSP germplasm	East African WFSP germplasm	Non African OFSP germplasm
African white fleshed germplasm	0.045***		
Non African OFSP germplasm	0.195***	0.212***	
Non African non OFSP germplasm	0.231***	0.193***	0.289*

*, and *** are significant at $p \leq 0.05$ and $p \leq 0.001$ levels, respectively.

Discussion

With a total of 158 polymorphic loci, ranging between 2 and 11 loci per primer, the present study showed high levels of polymorphism with the SSR markers. This result confirms the extraordinary discriminatory capacity of the SSR markers reported in previous studies (Gichuru *et al*., 2006). Buteler *et al*. (1999) also obtained high polymorphism, ranging between 3 and 10 alleles per SSR in sweetpotato. Yada *et al*. (2010) obtained two to six alleles per primer. However, Hwang *et al*. (2002) obtained a lower level of polymorphism, ranging between 1 and 4 alleles per SSR locus using mostly different SSR primers and annealing temperatures. Hwang *et al*. (2002) attributed high level of polymorphism to large genome size and heterozygosity of sweetpotato. It should be noted that genetic diversity due to heterozygosity in sweetpotato is driven by both the mating system (outcrossing in combination with self incompatibility) and the high ploidy level of sweetpotato (autohexaploid) (Zhang *et al*., 2000). This heterozygosity and the genetic diversity can be easily maintained by vegetative propagation (Grüneberg *et al*., 2009). The present study never estimated heterozygozity, hence, we possibly never fully detected variability within accessions assayed.

The mean genetic similarity coefficient of 0.54 obtained in our study is low, suggesting large diversity among the studied accessions. Some accessions had a similarity coefficient of 1.00. Comparably, Zhang *et al*. (2000) reported a low similarity coefficient (0.588) among sweetpotato accessions from South America. It should be noted that South America is known to be a centre of diversity and our observed similarity coefficient in predominately African material is only slightly lower. Higher mean similarity coefficient values of 0.64, 0.79, and 0.69 were reported by Hwang et al. (2002), Abdelhameed *et al*. (2007) and Tseng *et al*. (2002), respectively, and concluded a low diversity of the studied germplasm. In our study, an additional 25% of the similarity coefficients were observed between 0.40 and 0.49. This is likely accounted for by the presence of non-African accessions in the studied germplasm.

All cultivars with a similarity coefficient of 1.00 are considered duplicate cultivars by the present study. These include (i) UG15 and UG17, (ii) UG04 and UG23, and (iii) KE07 and KE01 among the WFSP farmer varieties; and (i) UG31, UG07 and UG12, and (ii) 'Zapallo' and UG32 among the OFSP farmer varieties. All duplicates were of either similar flesh colour or country of origin, which improves confidence in our results. The presence of duplicates among the studied accessions is possibly due to farmers' practice of adopting different variety names in different locations (Abidin, 2004). It should be noted that for the past two decades, repeated introductions of foreign germplasm into East Africa have been made as part of CIP's efforts to promote OFSP to combat VAD in the region. Although most of the introduced germplasm have

failed due to susceptibility to SPVD and lower acceptability a few of these might have been adopted on a small scale. The cultivar UG32 is identical in its genetic profile to 'Zapallo'. It is probable that 'Zapallo' was locally named 'Rwanda' by farmers in Soroti in Uganda and collected and named UG32 as a putative local African OFSP clone.

These results also identified some closely clustered accessions suggesting close relationship between the accessions. These include KE17 and KE09, KE15 and UG40, UG52 and UG27, KE12 and UG50, UG18 and UG02, UG48 and UG55, UG54 and SPK004 (CIP), UG05 and UG19, TZ04 and KE06, TZ02 and TZ03, and KE14 and 'Jewel'. The presence of closely related accessions originating from different East African countries is possibly due to free exchange of germplasm between the countries. Equally, the presence of closely related cultivars that differ in flesh colour (orange and non-orange) suggest a possibility that OFSP cultivars have evolved from sister WFSP accessions as opposed to only introduced OFSP accessions. However, one exception where KE14 and Jewel are closely related suggests a possibility that some of the OFSP cultivars are interbreeds with introduced germplasm. It should be mentioned that the recently established regional breeding programs are working nearly exclusively with polycross seed nurseries, often in a farmer participatory approach, and orange-fleshed storage root color is one of the breeding objectives. 'Jewel' and 'Resisto' have been heavily used as OFSP parents in EA breeding programs.

In this study, East African farmer varieties with an exception of UG47, KE14, KE22 and ZB01, cluster independently from non-African accessions at a similarity coefficient value of 0.52 (Figure 3.2), suggesting a clear distant relationship between the two germplasm pools. The genetic data reinforces our findings that UG32 is actually 'Zapallo' and KE14 is closely related to 'Jewel'. These were collected by error as farmer varieties in Uganda and Kenya, respectively. Gichuki *et al*. (2003) made similar observations while comparing white-fleshed varieties collected from East Africa with germplasm from other geographical regions. Nevertheless, the positions of UG47 and KE22 within the non-African germplasm are difficult to explain. Abdelhameed et al. (2007) using AFLP analysis found out that UG32 clustered with Tanzanian accessions. The most striking result of our study is that all East African OFSP farmer varieties, except ZB01 and KE14 neither clustered with accessions from other regions of the world nor independently from other East African accessions.

The sub-clusters A1 – A5 identified within the main East African A cluster suggested high genetic diversity within the population. Moreover it is interesting to observe that like the closely clustered accessions, the sub-clusters are neither country nor flesh colour specific. Whereas absence of non-country specific sub-clustering of East African sweetpotato cultivars has been reported before (Gichuru *et al*., 2006) our study is the first to report absence of non-flesh colour specific sub clusters within the East African sweetpotato germplasm. This result further enhances the suggestion that East Africa OFSP farmer varieties have evolved

from sister WFSP accessions as opposed to being introduced OFSP accessions. This might be important information for local breeding programs and merits the application of molecular markers to characterize local OFSPs before they are used in a breeding program. It has been noted (Gichuki *et al*., 2003) that East African farmer varieties are unique in several important characteristics like high dry matter content, high resistance to viruses and vigorous foliage growth, while low in β-carotene and earliness to harvest.

The AMOVA results (Table 3.4) showed that East African sweetpotato farmer varieties are distinct from non-African sweetpotato accessions. Previous studies have suggested this (Gichuki et al., 2003; Abdelhameed *et al*., 2007), but had few if any OFSP farmer varieties in their data set to demonstrate this distinction. Abdelhameed *et al*. (2007) only included Carrot C (coded TZ03 in this study) while Gichuki *et al*. (2003) and Gichuru *et al*. (2006) had none. Furthermore, our AMOVA results (Table 3.5) found no genetic difference between the OFSP and WFSP accessions. No previous work has made this comparison. As expected, between individual variations were most significant and accounted for the majority of the molecular variance. Similar findings have been reported by several previous studies on genetic diversity of sweetpotato germplasm (Zhang *et al*., 2000; Zhang et al., 2002; Gichuki *et al*., 2003; Gichuru *et al*., 2006; and Abdelhameed *et al*., 2007). Moreover, it is a clear indication that breeders can form in breeding programs different populations with significant levels of genetic difference, which is a prerequisite to exploit heterosis and improvement of populations.

The genetic distances (Table 3.6) are consistent with population differences identified by the AMOVA. The significant short genetic distance observed between East African OFSP and WFSP farmer varieties confirm their close genetic relatedness. Also the significant distances between either East African OFSP or East African WFSP and non-African OFSP or non-African WFSP accessions confirm their genetic distinctiveness. The larger and significant genetic distance between non-African OFSP accessions and non-African WFSP accessions is a likely a function of origin. OFSP are mostly from the Americas and WFSP mostly from Chinese. Despite the lower number of representative cultivars in either of the groups, our finding is consistent with previous studies (Gichuki *et al*., 2003; Abdelhameed *et al*., 2007).

In conclusion it is much clear from this study that East African farmer varieties, irrespective of flesh colour, are distinct from non-African germplasm. It is further clear that majority of the East African OFSP farmer varieties are closely related with their sister East African WFSP farmer varieties. However, there are a few exceptions of OFSP accessions that appeared to have non-African lineage and might be introduced accessions or improved clones related to the introduced accessions. Our results underscore the importance of including East African OFSP farmer varieties in OFSP breeding program targeting East Africa.

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