Breeding investigations for fresh root yield and nutritional quality traits for sweetpotato (*Ipomoea batatas* [L.] Lam.) germplasm

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Thesis Abstract

Sweetpotato (*Ipomoea batatas* (L.) Lam.) is an important crop for smallholder farmers in sub-Saharan Africa (SSA), providing food, income, and nutritional security. In Zimbabwe, white-fleshed sweetpotato (WFSP) varieties are favored for their high dry matter content, but they lack β-carotene, limiting their ability to combat vitamin A deficiency. Despite this, Zimbabwe lacks a systematic breeding programme targeting both yield and β-carotene enhancement in WFSP. This study aimed to establish a sweetpotato breeding programme with the following objectives: (1) assess genotypic variation in fresh storage root yield and micronutrient content (β-carotene, Fe, Zn); (2) identify high-yielding, nutrient-rich genotypes; (3) evaluate genotype × environment interactions (GEI) for target traits; (4) assess genetic diversity using single nucleotide polymorphism (SNP) markers; and (5) determine combining ability for yield and β-carotene improvement. A multi-location trial of 22 genotypes (including CIP-derived lines and Zimbabwean landraces) revealed significant differences ($p < 0.01$) in β-carotene, Fe, and Zn contents, root yield, and the number of commercial roots per plot. Genotype O-105 recorded the highest β-carotene content (12.5 mg/100 g), while Zn and Fe ranged from 12 to 20.5 ppm and 45.2 to 118.5 ppm, respectively. Genotype O-104 combined high yield with superior levels of all three nutrients. A strong positive correlation ($r = 0.80$; $p < 0.01$) between storage root yield and number of commercial roots suggests effective selection using conventional breeding methods. Genotype-by-environment interaction analysis across eight environments revealed significant genotypic differences ($p < 0.001$) for storage root yield and micronutrient content ($p < 0.001$). Commercial storage root yield ranged from 1.02 to 8.38 t/ha. Genotypes G3, G19, G16, G22, and G2 were identified as stable and high yielding. Genotypes G19, G12, and G16 had the highest β-carotene levels, while G12 and G18 excelled in Fe and Zn, respectively. Broad-sense heritability was high ($H^2 > 0.65$) for all traits, supporting genetic gains through selection. The 22 genotypes evaluated in the multi-location trials represent a carefully selected subset derived from the broader germplasm base of 327 accessions analysed for genetic diversity. The diversity study using 30 SNP markers on these 327 accessions provided insights into the overall genetic variability, population structure, and parental diversity within the sweetpotato germplasm. Genetic diversity analysis using 30 SNP markers on 327 accessions revealed moderate diversity (mean GD = 0.36). The mean polymorphism

information content (PIC) was 0.29, and the minor allele frequency (MAF) averaged 0.34. A high fixation index (FST = 0.68) and low heterozygosity (mean = 0.12) suggest limited parental diversity. Population structure analysis identified two subpopulations, indicating significant genetic differentiation among groups. These results are valuable for guiding germplasm conservation and improvement. Combining ability analysis using a North Carolina Design II with eight parents and 16 crosses, evaluated across three locations, revealed significant differences in number of commercial roots per plant and β-carotene content. Crosses Kau 4 × O-105, Magutse × O-105, and Dube × O-105 yielded up to 26.97 t/ha, while Dube × O-104 and Dube × O-105 showed high β-carotene levels (up to 11.49 mg/100 g). Most parents, particularly O-105 and Dube, had strong general combining ability (GCA). Broad-sense heritability was high for both traits (0.85–0.93), indicating both additive and non-additive gene effects, supporting the use of both recurrent selection and hybridization in breeding. Parental lines O-104, O-105, and P-201, and their top-performing crosses, are recommended for further breeding to enhance sweetpotato yield and nutritional quality in Zimbabwe.

Declaration 1: Plagiarism

I, Nomusa Chizhande, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original work.
2. The thesis has not been submitted for any degree or examination at any other university.
3. The thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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Signed [redacted] Date: July 2025

Nomusa Chizhande

As the candidate's supervisors, we agree to the submission of this dissertation for examination

Signed……[redacted]…… Professor Julia Sibiya (Main Supervisor)

Signed …… Professor Edmore Gasura (Co-supervisor)

Declaration 2: Publications & Manuscripts

Chapter 5 was published

Chizhande, N., Sibiya, J., Gasura E., Mutari, B., Chaingeni, D., Kutywayo, D., Musundire, L., Mathew, I., and Dossa, E. 2025. Genetic Diversity and Population Structure of Sweetpotato Accessions (*Ipomoea batatas* [L.] Lam.) Revealed by Single Nucleotide Polymorphism Markers. Plant Breeding; 0:1–10 https://doi.org/10.1111/pbr.70021

Chapter 4 of this thesis has been submitted for publication and details read as follows:

Chizhande, N., Sibiya, J., Gasura, E., Mutari, B., Mathew, I. and Chibvongodze, M. Adaptability and Stability Analyses of Root Yield and Micronutrient Concentrations in Sweetpotato (*Ipomoea batatas* [L.] Lam.) Genotypes. Plant-Environment Interactions. Manuscript ID: 3174430

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May Almighty God bless you All.

Dedication

This thesis is dedicated to God Almighty in the name of Jesus Christ, my family, including my spouse Collins and my three children, Farirai, Phoebe, and Collins Jnr. To my late father Eliam Mandhlazi and late mother, Diana.

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List of Abbreviations

AFLP	Amplified Fragment Length Polymorphism
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
BCC	Beta Carotene
CIP	International Potato Centre
F	Fixation Index
FAO	Food and Agricultural Organization
Fe	Iron
GD	Genetic Diversity
G x E	Genotype by Environment interaction
GVTC	Gwebi Variety Testing Centre
He	Expected Heterozygosity
HI	Harvest index
HRS	Harare Research Station
IBS	Identity by State
ISSRs	Inter-Simple Sequence Repeats
LSD	Least Significant Difference
MAF	Minor Allele Frequency
MANOVA	Multivariate Analysis of Variance
MCMC	Monte Carlo Markov Chain
MET	Multi-Environment Trials
MHRS	Marondera Horticulture Research Station
MPU	Makoholi Production Unit
NCD II	North Carolina Design II
OFSP	Orange Fleshed Sweetpotato
PIC	Polymorphic Information Content
RAPD	Random amplified polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
RY	Root Yield
SNP	Single Nucleotide Polymorphisms

SSA	Sub-Saharan Africa
UPGMA	Unweighted Pair-Group Method
VAD	Vitamin A Deficiency
WFSP	White Fleshed Sweetpotato
Zn	Zinc

Chapter One: Introduction to Thesis

1.0 Background

Sweetpotato (*Ipomoea batatas* (L.) Lam), is a significant crop in sub-Saharan Africa (SSA) contributing to both food security and revenue in many households (Lebot and Champagne, 2009; Sardos et al., 2014; Behl et al., 2015; Motsa et al., 2015; Dipsa et al., 2016). It is ideal for cultivation in marginal areas because of its low input requirements, flexibility in planting dates, and resistance to drought (Villordon et al., 2006). However, pests and diseases, low soil fertility, drought stress, and a lack of better cultivars still pose challenges to its production (Nakashima et al., 2009; Mwanga et al., 2011; Begna, 2022). In Zimbabwe, per capita intake ranges from 1 to 7 kg, making it an essential component of the diet (Zimbabwe National Vulnerability Assessment Committee, 2004). Because of its significance, the Zimbabwean government designated sweetpotato as one of the staple crops. According to Escobar-puentes et al. (2022), sweetpotato is among the starchy crops that are staple foods in some African nations while serving as supplemental or food security in others.

As a food security crop, sweetpotato is typically subjected to piece meal harvests and stored according to a flexible schedule (Escobar-puentes et al., 2022). Consequently, the sweetpotato storage roots are frequently left in the ground and only picked when necessary (Mwanga et al., 2011). This ensures a year-round food supply that does not require infrastructure for storage during the off-season (Dipsa et al., 2016). This is particularly important when the previous season's storage roots is depleted especially in the weeks immediately preceding major harvests, often lasting one to two months (Roncoli and Orlove, 2011). Thus, sweetpotato serves as a useful food reserve when the primary staple has been negatively impacted by drought and other biotic factors like pests and diseases (Qiu et al., 2020). To generate revenue, fresh storage roots are also sold in local markets.

In the tropical regions, fresh storage roots are commonly consumed after boiling, frying, or roasting. In certain regions of East Africa, roots are occasionally cut into chips and sun-dried before being milled into flour. Sweetpotato is crucial to rural food security in Northern Cameroon, where dried chips are kept for use during times of famine when supplies of staples like sorghum and millet run low. Most of the population in Zimbabwe consume boiled sweetpotato. In Africa, leaves are also eaten. The leaves, which can contain up to 27% protein (dry matter basis), have gained attention for their nutritional value.

Besides its importance as food, sweetpotato is also used in the industrial sector for starch production, natural colorants, and fermented goods. According to Fauza (2009) and Duvernay et al. (2013) the

fermented products include wine, ethanol, lactic acid, acetone, and butanol. Furthermore, cattle feed, is also made from all the plant components of sweetpotato, including their culls (Claessens et al., 2009). As animal feed, sweetpotato is extensively utilized throughout Asia, especially in Japan, Taiwan, and South Korea. A third of the sweetpotato produced in the USA are processed and dehydrated for use as animal feed.

Sweetpotato contains essential nutrients which include minerals, vitamins, proteins, and carbohydrates (Stathers et al., 2003). Of its dry weight, the storage roots contribute 25–30% carbohydrates and 2.5–7.5% proteins. Additionally, the dry matter constitutes 200–300 mg of potassium (K), 0.8 mg of iron (Fe), 11 mg of calcium (Ca), 20–30 mg of vitamin C, and copper, zinc, manganese, vitamin B2, B6, and E. (Sanusi and Babatunde, 2017). Provitamin A is found in the yellow and orange fleshed storage roots. Therefore, as a food, sweetpotato can be used to address malnutrition, which is prevalent in most countries on the continent, including in Zimbabwe.

Undernourishment accounts for more than one-third of child fatalities in Zimbabwe. Approximately 27% of children under five years of age in Zimbabwe are stunted, while about 10% are underweight (UNICEF, 2024). Numerous strategies, including dietary diversity, food fortification, and nutrient supplementation, have been proposed to lower the incidence of micronutrient malnutrition in groups that are vulnerable across the globe. In an effort to lower the prevalence of micronutrient malnutrition, the Zimbabwean government implemented the National Food Fortification Strategy in 2015 after realizing the country's high rate of malnutrition (World Health Organization, 2015).

However, there have been drawbacks to the effectiveness of food fortification, including the other integrated intervention options previously stated, with regards to sustainability, coverage, and cost-effectiveness (Bouis, 2003; White et al., 2009; Bouis and Welch, 2010; Kimani and Warsame, 2019). Therefore, one of the sustainable ways to raise the amounts of vitamins and minerals (Fe and Zn) in staple crops is to generate micronutrient-dense crops through traditional plant breeding and contemporary biotechnology (biofortification) (Harvest Plus, 2018). A food-based approach to address micronutrient deficiency in impoverished households can benefit from the use of crops with high iron and zinc content, as described by Pfeiffer and Mcclafferty (2007), Tryphone and Nchimbi-Msolla (2015), and Kimani and Warsame (2019). The main benefits of biofortification are as follows: i) it can reach a large number of rural poor households dispersed across isolated areas or living in remote areas without access to commercially marketed fortified food products; ii) it is an economical way to reach tens of millions of vulnerable communities on a long-term basis (shared germplasm); iii) it is based on the staple foods that impoverished households produce and consume; iv) it has low ongoing costs due to a one-time investment in cultivars that self-fortify; and v) it is environmentally friendly (Mayer et

al., 2008; Saltzman et al., 2013). To address vitamin A deficiency affecting the impoverished populations in many sub-Saharan African countries, including Zimbabwe, orange-fleshed sweetpotato offers a relatively inexpensive and readily accessible source of vitamin A. Orange-fleshed sweet potato (OFSP) is crucial in addressing vitamin A deficiency due to its high beta-carotene content, making it an important crop for fighting malnutrition in various areas and boosting food security.

Research has shown that to optimize both storage root yield and nutritional value in OFSP production, special attention should be paid to selecting suitable growing conditions as determined by the local soil, climate, and management practices. By considering findings from site-specific studies and multi-environment trials, breeders and farmers can choose OFSP varieties that are best suited to their unique conditions, enhancing productivity, resilience, and nutritional benefits across different regions. These localized insights help OFSP realize its potential for sustainable agriculture and better public health.

1.1 Constraints to sweetpotato production

Several factors affect the production of sweetpotato resulting in low storage root yield. These include both biotic and abiotic factors. Biotic limitations, including viral infections, insect pests such as weevils, and weeds have been reported to cause significant losses in sweetpotato productivity (Ndunguru et al., 2009). Amongst the viral infections, sweetpotato virus disease (SPVD) caused by the co-infection and mutually beneficial relationship of sweetpotato feathery mottle virus and sweetpotato chlorotic stunt virus (Gasura et al., 2008) is the most destructive disease that lowers root production, quality, and plant growth (Gibson, 2006; Osiru et al., 2009). Additionally, according to Tsakama et al. (2010), SPVD reduces the amount of time that roots can be left in the ground and shortens the amount of time that harvested crops are stored. About 50–100% yield reduction results from infection by SPVD (Gibson et al., 1998).

Another significant barrier to sweetpotato production is the presence of sweetpotato weevils, specifically *Cylas punctcollis* and *Cylas brunneus* (Stathers et al., 2003; Mkuki and Rwegasira, 2021). Weevils tunnel through vegetation and consume roots and vines, which lowers crop quality and commercial storage root yield (Stathers et al., 2003). Weevil infestations can result in yield losses of up to 100%, according to Stathers et al. (2003). Furthermore, because of the numerous fissures that arise when the soil dries, infestation levels are higher in dry environments (Mkuki and Rwegasira, 2021). Sweetpotato productivity is also impacted by other biotic factors such nematodes, Alternaria leaf spot, stem blight, black rot, Fusarium rot, bacterial rot, millipedes, and vertebrate pests like rats (Cattivelli et al., 2011). In East Africa, there have also been reports of wandering animals including goats and cattle destroying crops.

Furthermore, heavy rainfall early in the growth season, results in significant commercial storage root yield losses due to weed infestations (Cattivelli et al., 2011). According to Knezevic and Datta (2015), the timing of the weed invasion is crucial. The essential period for weed competition occurs between two- and six-weeks post-planting. In comparison to weeded sweetpotato plots, Wadl et al. (2018) and Cattivelli et al. (2011) observed a yield loss of almost 90% in weedy sweetpotato plots.

Low soil fertility and drought are two abiotic factors that have a major impact on sweetpotato production (Abrham, 2021). Sweetpotato commercial storage root yield is negatively affected by declining soil fertility since inorganic fertilizers are expensive and difficult to supply (Cattivelli et al., 2011). Furthermore, most smallholder farmers' soils are depleted and deteriorated, which reduces the effectiveness of applied fertilizers. According to Saleh and Zahor (2007), continuous cropping without the addition of organic and inorganic manures has resulted in loss of soil fertility and consequently, a reduction in productivity.

A major abiotic factor that restricts sweetpotato production is drought, which has an impact on both crop quantity and quality (Cattivelli et al., 2011; Abrham, 2021). Drought was cited by Oduro (2013) as one of the top obstacles to Ghana's production of sweetpotato in a participatory rural appraisal. While sweetpotato is known to withstand drought, prolonged and frequent dry periods along with irregular rains significantly reduce commercial storage root yield (Johanson and Ives, 2001). Lower storage root yields of sweetpotato were reported by An et al. (2003) during the hot, dry season as opposed to the cool, wet season; however, the response differed depending on the genotype. Drought impacts root yield, dry matter content and composition, insect and disease occurrences, as well as crop growth and development (Cattivelli et al., 2011; Semagn et al., 2005). The OFSP is not only susceptible to viral infections and has poor dry matter content, but it is also susceptible to drought, which results in low productivity (Cattivelli et al., 2011; Mwanga and Ssemakula, 2011). According to Mwanga et al. (2011), farmers rejected the less drought tolerant types, during participatory sweetpotato breeding and selection trials. Thus, the output and productivity of sweetpotato are greatly impacted and decreased by drought.

To initiate a breeding programme, the Crop Breeding Institute in Zimbabwe assembled a diverse set of sweetpotato genotypes. However, the potential of these genotypes for cultivation in diverse environments and use by the sweetpotato processing industry and consumers is not known. Hence there was a need to evaluate them for both their nutritional and agronomic performance under different environments and determine their breeding value. Consequently, to support the national efforts in improving economic, food, and nutrition security, as well as boosting the commercialization of

sweetpotato genotypes in Zimbabwe, this study was set up with the overall goal of identifying sweetpotato genotypes that combine high yield potential and nutritional quality.

1.2 Problem statement and justification

Sweetpotato yields in Sub-Saharan Africa (SSA) were previously estimated at 4.0 to 4.5 t /ha between 1987 and 2006, suggesting limited breeding progress. However, more recent data show an increase to 7.1 t/ha by 2024, with a 1.7% annual growth rate (IndexBox, 2024). In Zimbabwe, national yields average around 6 t/ha, though controlled trials using improved planting material have reached up to 25 t/ha (Makunde et al., 2023). Other countries with active breeding programmes such as Malawi, Mozambique, Uganda, Zambia, and South Africa report improved yields of 18 to 32 t/ha, while smallholder yields remain at 5 to 9 t/ha (International Potato Center [CIP], 2023). These findings highlight the need for targeted breeding in Zimbabwe, where significant yield gaps exist and investment in breeding has lagged. A structured breeding programme, supported by this research, is therefore essential for developing high-yielding, nutrient-rich varieties adapted to local conditions, thereby closing yield gaps, strengthening food security, and improving public health outcomes.

Vitamin A deficiency remains one of the most concerning health challenges on the African continent. In many developing countries, VAD is associated with blindness, stunted growth, and increased child mortality. Earlier estimates suggested that up to three million children under the age of five in sub-Saharan Africa (SSA) may have been partially or completely blind due to vitamin A deficiency (VAD) (Semagn et al., 2005; WHO, 2009; Tumwegamire et al., 2016). More recent evidence, however, indicates that approximately 48% of children in SSA remain at risk of VAD, though the number experiencing vision loss is likely lower, reflecting the expanded coverage of vitamin A supplementation programmes (UNICEF, 2024). In Zimbabwe, where this intervention will initially be implemented, an estimated 20% of children under five are currently affected by VAD (HarvestPlus, 2024), although nationally representative data on VAD-related blindness remain limited. Therefore, while VAD continues to pose a significant public health risk, particularly in early childhood, the burden of blindness in Zimbabwe is likely lower than earlier SSA-wide projections suggest.

Vitamin A deficiency primarily affects mothers who are pregnant or nursing as well as preschoolers. According to a 2009 WHO report on VAD estimates from 1995 to 2005, the prevalence of biochemical VAD and night blindness in preschool-aged children was found in 122 countries and 45 countries, respectively. In most Zimbabwean communities, VAD is a severe health issue amongst mothers and small children, where 18% of children aged 6-59 months had low serum retinol levels, which is

considered a marker of Vitamin A deficiency and over one-third of child deaths are due to undernutrition (UNICEF, 2024).

However, the white fleshed sweetpotato (WFSP) types with high root dry matter content, which are preferred by farmers in Zimbabwe have low levels of β-carotene, thus hindering the efforts to combat vitamin A deficiency (VAD). In addition, there is no breeding programme in Zimbabwe aimed at improving the sweetpotato production and β-carotene concentration of white-fleshed sweetpotato. Therefore, to increase the β-carotene levels of the WFSP in Zimbabwe, a well-designed breeding programme is essential, so that the different population groups that consume WFSP in the country can have access to vitamin A. Consequently, to create promising cultivars that consider end consumers' preferences, complementary parents with high amounts of β-carotene or other beneficial qualities must be chosen for hybridization in a breeding programme. Before a variety is released, pre-breeding analysis including combining ability tests, gene action and heritability of selected traits must be determined and subsequent selections subjected to multi-environmental trials for performance and stability analysis.

1.3 Aims & Objectives

1.3.1 Overall Objective

The overall aim of this study was to improve sweetpotato productivity and nutritional quality by developing cultivars with high nutritional content and yield.

1.3.2 Specific objectives

The specific objectives were:

1) To evaluate genotypic variation in fresh storage root yield, β-carotene, iron, and zinc concentrations.
2) To assess the impact of genotype by environment interaction (GEI) on micronutrient content (β-carotene, Fe, and Zn) and fresh storage root yield in promising sweetpotato genotypes.
3) To determine the genetic diversity and relationships among local and imported sweetpotato accessions using single nucleotide polymorphism markers (SNPs).
4) To evaluate the combining ability effects of selected parents and clones for the storage root number, fresh root yield, and β-carotene to inform future breeding and selection efforts.

1.4 Hypotheses

1) There is sufficient genetic variation among sweetpotato genotypes for key agronomic and nutritional traits.

2) Genotype-by-environment interactions significantly influence fresh storage root yield, β-carotene, Fe and Zn concentration in sweetpotato genotypes across multi-locations.
3) Local and imported sweetpotato genotypes exhibit significant genetic diversity.
4) Fresh storage root yield and β-carotene concentration are influenced by both additive and non-additive gene effects.

1.5 Outline of the thesis

Six separate chapters aligned to the study's objectives make up this thesis. The background, problem statement, and objectives of the study are provided in Chapter 1, which serves as the introduction to the thesis. The structure of each of the research chapters is that of a stand-alone, publishable research paper. Consequently, there are some unavoidable overlaps and repetitions of information and references throughout the chapters. American Psychological Association (APA) 7th edition was used as a referencing style.

The chapters are outlined as follows:

Chapter 1: Introduction to thesis

Chapter 2: A review of literature

Chapter 3: Assessment of genetic variability for agronomic and nutritional traits among sweetpotato genotypes grown in Zimbabwe

Chapter 4: Genotype x environment interaction and stability analyses of root yield and micronutrient concentrations in sweetpotato (*Ipomoea batatas* [L.] Lam) genotypes

Chapter 5: Genetic Diversity and population structure of sweetpotato accessions *(Ipomoea batatas* [L.] Lam) revealed by single nucleotide polymorphism markers

Chapter 6: Genetic analysis of β-carotene content, root yield and yield-attributing traits in sweetpotato (*Ipomoea batatas* [L.] Lam) genotypes

Chapter 7: Thesis Overview

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Chapter Two: A Review of Literature

2.1 Introduction

The purpose of this review is to highlight the status of research in breeding sweetpotato for high root yield and nutritional quality. Thus, the chapter evaluates literature on β-carotene, genetic diversity in root yield, sweetpotato as a key crop for food and nutrition security, and general relationships between yield and nutritional content for selection during breeding. A basic overview of the agronomic needs, breeding techniques, mating designs, and genotype by environment interaction for sweetpotato is also given in this chapter. This information provides the necessary background needed for the research.

2.2 The importance of sweetpotato

Sweetpotato *(Ipomoea batatas* (L.) Lam.), is a significant crop in sub-Saharan Africa (SSA) that is a vital for both food security and revenue (Lebot and Champagne, 2009; Behl et al., 2015; Dipsa et al., 2016; Gurmu, 2019). In marginal areas, it has numerous advantages over cereal crops because of its drought tolerance, low input requirements, flexibility in planting dates, and piece meal harvesting (Villordon et al., 2009). According to estimates, Zimbabwean households consume between 1 and 7 kg per capita annually of sweetpotato per person in urban areas and between 3 and 5 kg in rural regions (WHO, 2015). Vitamins and minerals present in sweetpotato help to supplement diets high in grains that are deficient in micronutrients. According to van Jaarsveld et al. (2006), orange-fleshed sweetpotato (OFSP) types are known to have high levels of β-carotene, a precursor to vitamin A, which helps prevent vitamin A deficiency (VAD). Vitamin A deficiency is believed to endanger 43 million African children under the age of five. As a result, OFSP consumption has been promoted as a solution to the malnutrition issue, particularly regarding young children.

Orange fleshed sweetpotato is an inexpensive and abundant source of vitamin A. It offers β-carotene, a precursor to vitamin A (Osiru et al., 2009; Tumwegamire et al., 2016). Sweetpotato's orange hue is indicative of its high β-carotene content. According to Tumwegamire et al. (2016), the majority of orange-fleshed sweetpotato genotypes have 3000–16000 µg 100 g^{-1} of β-carotene, which adds to 250–1300 µg 100 g^{-1} of retinol activity equivalent (RAE). Alpha-carotene and beta-cryptoxanthin are two additional important dietary provitamin A carotenoids (Ryu et al., 2018). Recommended daily allowances (RDA) for vitamins per day can be readily met by OFSPs in little doses, which can include 300–3000 µg RAE 100 g^{-1} fresh weight (Martin, 1993).

2.3 Sweetpotato utilisation

Sweetpotato is utilized as food for animals and humans as well as for biofuel. Due to their high carbohydrate content, fresh roots are frequently cooked, fried, or roasted before consumption. In addition, the tubers can be cut into chips, sun-dried, and then ground into flour. Both the roots and the leaves are eaten in Africa.

In other countries such as Japan, Taiwan, South Korea and the USA, sweetpotato leaves are used for livestock feeding. It is highly nutritious with starch being the main nutrient at 20-26%, while protein (2-3%), vitamins (vitamin A: approximately 28355 IU per 100 g, vitamin C: about 2.4 mg per 100g, vitamin B6: around 0.209 mg per 100 g, vitamin E: roughly 0.26 mg per 100g) and minerals such as potassium (542 mg/g), phosphorous (40-60 mg/g) and calcium (30 mg/g) are also available in the tuber (Nandutu, 2017). The OFSP are utilized in many different contexts, including as snacks, porridge, and for juice production in Tanzania, Ethiopia, Kenya, Uganda, and Rwanda, among other nations. It has been stated that OFSP can be turned into a variety of products, including cookies, fried chips, doughnuts, pancakes, and chapatti, which are consumed by both urban and rural populations. Value addition into diverse products has increased the consumption of OFSP (Nkhata et al., 2020).

2.4 Production challenges

Despite its importance, sweetpotato yields are low among resource limited farmers. In comparison to typical yields attained under commercial agriculture, where farmers have better access to irrigation and fertilizers, smallholder farmers' yields are quite low averaging 5 t/ha against a potential of 23-25 t/ha (Rosen et al., 2015). According to James (2015), the annual production of sweetpotato in African nations including Tanzania, Kenya, Rwanda, and Uganda, is 1.70, 1.00, 0.90 and 0.34 metric tonnes, respectively. From an estimated 3.80 million hectares, sub-Saharan Africa (SSA) generates a mean of 22.63 million tonnes of sweetpotato yearly (FAOSTAT, 2017). With a mean yield of 3.8 t/ha, the average harvested area over the previous ten years was 536 451 hectares (FAOSTAT, 2015). The low yields are mostly caused by a combination of biotic and abiotic stresses, a lack of improved varieties, and restricted access to disease-free planting materials (Gibson et al., 2009; Mwanga et al., 2011; Cattivelli et al., 2011; Maquia et al., 2013). Most farmers cultivate old landrace cultivars using repetitive propagation of vines obtained from virus-infected mother plants (Wolfgang et al., 2005).

2.4.1. The lack of improved cultivars

Low sweetpotato production in most African countries is due to unavailability of high yielding, disease-resistant planting materials (Stathers et al., 2003; Villordon et al., 2006; Ndunguru et al., 2009).

Most of the planting materials used are low-yielding as a result of persistent sweetpotato viral infections (Mwololo et al., 2007; Wokorach et al., 2020). Farmers acquire and grow these virally-infected, low-yielding planting materials through informal seed systems (Semagn et al., 2005; Haile, 2020). These low yielding sweetpotato cultivars often lack farmer preferred traits (Ngailo et al., 2016). Currently, local landraces are popularly used by most smallholder farmers. The landraces are late maturing and low-yielding, despite being suited to local agro-ecologies (Gibson et al., 1998; Semagn et al., 2005).

Sweetpotato remains one of the least exploited crops, with breeding efforts still in their early stages compared to major crops like maize, rice, and cassava (Kriegner et al., 2003; Gasura et al., 2010). Past attempts to boost productivity and manage pests and diseases by introducing exotic varieties into diverse agro-ecologies have largely been unsuccessful (Kapinga et al., 2009b; Gasura et al., 2010). These introduced varieties often underperform compared to locally adapted landraces (Abidin et al., 2005b; Gasura et al., 2010). For example, orange-fleshed sweetpotato varieties failed almost entirely in Uganda and were rejected in Tanzania due to poor root yields, low dry matter, and weak drought tolerance (Kulembeka et al., 2005; Mwanga et al., 2007; Mwanga and Ssemakula, 2011). While some studies report comparable performance between local and introduced varieties, these mixed results highlight the urgent need for continued sweetpotato research and development (Mbwaga et al., 2007).

2.4.2. Biotic constraints

Several biotic limitations, including viral infections, insect pests, and weeds, have an impact on sweetpotato productivity (Ndunguru et al., 2009). Sweetpotato viral infections and sweetpotato weevils are significant diseases and insects, respectively. According to Gasura et al. (2008) and Grandgirard et al. (2008), sweetpotato feathery mottle and sweetpotato chlorotic stunt viruses combine synergistically and induce dual infections, which result in the sweetpotato virus disease (SPVD). Over 15 distinct viruses have been identified as causes of SPVD in sub-Saharan Africa and Asia (Ndunguru et al., 2009; Qiu et al., 2020). This disease is extremely destructive, resulting in a 50–100% decrease in plant growth and root production (Gibson, 2006; Osiru et al., 2009). Additionally, the SPVD shortens the root tubers' underground shelf life (Tsakama et al., 2010).

Effective management of viral diseases in sweetpotato involves several strategies. One approach is the use of resistant or tolerant varieties, such as Kakamega and Tanzania, which have shown resistance to SPVD and other viral infections, helping reduce virus spread and yield losses (Legg et al., 2011). Another strategy is vector control, focusing on aphids, which transmit many sweetpotato viruses. Insecticides and non-chemical methods, like reflective mulches and natural predators, are used to

manage aphid populations. Additionally, using certified, virus-free planting material is crucial to prevent virus introduction and spread, with tissue culture techniques being a key method for producing clean planting material (Schut et al., 2014). Field sanitation practices, such as crop rotation, removal of infected plants, and weed control, also reduce viral load in the soil and prevent reinfection, as recommended in integrated pest management (IPM) strategies. Lastly, regular monitoring and early detection of symptoms are essential for controlling viral outbreaks by tracking viral incidence and aphid populations.

Detecting and identifying viruses in sweetpotatoes remains challenging, mainly due to the common occurrence of mixed infections and complex viral interactions, such as Sweetpotato Virus Disease (SPVD) (Gibson et al., 1998; Tairo, 2006). Although methods like serological tests and PCR have been developed to detect viruses, they are designed to test for only one virus at a time, which increases the cost, time, and labor involved (Gibbs and Padovan, 1993; Colinet et al., 1996; Alicai et al., 1999; Kreuze et al., 2000). A more efficient multiplex PCR method, capable of detecting multiple viruses in one test, is still not available. Controlling viral diseases in subsistence farming is also difficult, as targeting insect vectors is often not affordable, and there is a shortage of virus-free planting material in tropical Africa (Karyeija et al., 1998; CIP, 1999). In Uganda, the limited availability of certified virus-free planting material is a major obstacle to sweetpotato production. Producing virus-free planting material could improve seed quality and significantly boost sweetpotato yields in the region.

Another significant barrier to sweetpotato production is the presence of sweetpotato weevils, specifically *Cylas punctcollis* and *C. brunneus* (Stathers et al., 2003; Mkuki and Rwegasira, 2021). The crop's quality and output can be reduced by up to 100% because of the weevils' burrowing and feeding on vines and roots (Stathers et al., 2003). Sweetpotato weevils, including *Cylas puncticollis* Boheman and *C. brunneus* Fabricius, are the primary pests affecting the crop in Sub-Saharan Africa, while *C. formicarius* is the main pest issue in the Americas and Asia (Stathers et al., 2003; Mugisa et al., 2022). Adult *Cylas* species feed on the surface of storage roots, leaves, and vine epidermis, while the larvae, which cause the most damage, burrow into the storage roots and consume the inner tissue. Infested roots produce bitter toxins and terpenoids as a defense mechanism, which lowers the quality of the roots for both local consumption and market sales (Taylor et al., 2012). Weevil infestations tend to be more severe in dry conditions, as the pests become more active and access the storage roots through cracked soil (Qiu et al., 2020). Recommended control measures for weevils include early planting and harvesting, crop rotation, hilling, field sanitation, chemical treatments, and flooding (Stathers et al., 2003; Taylor et al., 2012; Mugisa et al., 2022).

Breeding for resistance to *Cylas* species (SPWs) remains a central goal in sweetpotato breeding programmes in Sub-Saharan Africa (SSA). The lack of known genetic sources of resistance to these weevils used to be a major barrier in breeding (Mwanga et al., 2009; Stevenson et al., 2009; Anyanga et al., 2013). However, in the last decade, researchers have discovered genotypes, including landraces, with stronger resistance to weevils, offering potential for their use in breeding programmes (Muyinza et al., 2012; Anyanga et al., 2013; Kagimbo et al., 2019). For example, the Ugandan landrace "New Kawogo" has shown moderate resistance to *C. puncticollis* and *C. brunneus*, likely due to its high concentration of hydroxycinnamic acid (HCA) esters on root surfaces (Muyinza et al., 2012; Anyanga et al., 2013). "New Kawogo" is being used as parental material for breeding SPW resistance in Uganda (Yada et al., 2015; Zhou, 2020) and to study resistance mechanisms to *Cylas* species (Anyanga et al., 2017).

However, one of the challenges in breeding for SPW resistance, especially at the molecular level, is the limited genomic resources available for sweetpotato. In previous studies, Yada et al. (2015) used 133 simple sequence repeat (SSR) markers to identify SPW resistance loci by analyzing a segregating population of 287 clones derived from a cross between "New Kawogo" and "Beauregard." They found twelve SSR markers linked to SPW resistance (Yada et al., 2017a). More recently

Oloka (2019) developed a genetic linkage map using single nucleotide polymorphisms (SNPs) and identified four quantitative trait loci (QTL) related to weevil resistance. Despite these findings, many of the markers and QTL identified have not been widely used in crop improvement due to their limited ability to explain phenotypic variation, making them less useful for marker-assisted selection. However, current efforts are focused on discovering more QTL for SPW resistance using SNPs to accelerate genomic breeding for weevil resistance.

There is still a need to find and develop genotypes with stronger resistance to SPWs, as the yield potential and root quality of "New Kawogo" are lower compared to newer varieties. Additionally, "New Kawogo" is white-fleshed and lacks β-carotene, which is found in orange-fleshed varieties that are important for addressing vitamin A deficiency in SSA (Yanggen and Nagujja, 2006). The shape of "New Kawogo" roots is also less desirable in the market, which calls for continued research to identify better genotypes with both improved resistance and marketable traits.

To effectively breed for SPW resistance, it is crucial to gain a deeper understanding of the genetics behind resistance and identify suitable parental genotypes. These genotypes, when combined, should produce progeny that exceed their parents in terms of resistance to SPWs, along with enhanced quality and agronomic traits, such as higher storage root yield and improved dry matter content.

Weeds represent a major biotic constraint in sweetpotato cultivation, as they aggressively compete with the crop for essential resources such as light, water, and nutrients, ultimately reducing both yield and quality. The crop is particularly vulnerable during its early growth phase due to its slow canopy development, which allows weeds to establish and proliferate if not properly managed (Niederwieser, 2004). Common and persistent weed species found in sweetpotato fields include *Euphorbia heterophylla* (wild poinsettia), *Imperata cylindrica* (spear grass), and *Cyperus rotundus* (purple nutsedge), all of which are difficult to control and highly competitive (Mwangi et al., 2005; Akobundu, 1987). Among these, *Cyperus rotundus* is particularly problematic due to its extensive underground tuber network and rapid regrowth, often leading to severe yield losses in root and tuber crops (Holm et al., 1991). The continued lack of efficient and sustainable weed control options poses a significant challenge, especially in low input sweetpotato farming systems, underscoring the need for integrated weed management approaches that consider the specific weed spectrum and local farming conditions.

2.4.3. Abiotic constraints

Drought and low soil fertility are two abiotic factors that have a major impact on sweetpotato output (Mwanga et al., 2011; Haile, 2020). Soil fertility is a major challenge for sweetpotato production, especially in SSA and Asia, where smallholder farmers often deal with degraded and nutrient-poor soils. Declining soil fertility is a serious concern in the production of sweetpotato mainly because most smallholder farmers apply fertilizer at suboptimal rates to recover lost minerals (Cattivelli et al., 2011). Soil fertility has decreased also because of continuous cropping without the addition of organic and inorganic manures, further decreasing productivity (Haile, 2020). Since sweetpotato is a nutrient-demanding crop, inadequate soil fertility results in lower yields and poor-quality storage roots. Several studies have focused on improving soil fertility using various agronomic and soil management techniques to optimize nutrient availability and soil structure, ultimately enhancing productivity (Palm et al., 1997).

Research on fertilizer application suggests that both inorganic and organic fertilizers, particularly nitrogen (N), phosphorus (P), and potassium (K), can significantly boost sweetpotato yields. Masarirambi et al. (2012) and Adekiya et al. (2019) found that using balanced NPK fertilizers, especially when combined with organic manure, improved both the quantity and quality of sweetpotato. However, excessive reliance on synthetic fertilizers can lead to environmental harm, which has sparked interest in integrated nutrient management (INM) practices. Tsegaye et al. (2006) demonstrated that INM, which combines organic matter with chemical fertilizers, enhances soil structure, water retention, and biological activity, providing long-term benefits for sweetpotato growth.

Organic fertilization, including compost and manure, has also been shown to improve soil fertility while promoting environmental sustainability. Organic manure increased sweetpotato yields and improved tuber nutrient content. Farmyard, chicken, and cow organic manures can promote impressive yield gains (up to +219%), increase biomass production (up to +40%), and improve sweet potato nutrient density (vitamin C, β-carotene, sugars, and phenols) (Low et al., 2020; Cordeiro et al., 2023). Better soil fertility, carbon sequestration, soil structure, and environmental health are all benefits of sustainability (Antonious, 2024). Biochar, a soil amendment made from organic material, has also been shown to improve soil fertility. Rosen et al. (2015) found that biochar increased sweetpotato yields by enhancing soil pH, nutrient retention, and microbial activity. Rosen et al. (2015) also observed that biochar improved soil water retention and nutrient cycling, particularly in low-fertility soils, benefiting sweetpotato growth.

Furthermore, agro ecological practices such as crop rotation and intercropping also address soil fertility issues. For example, incorporating green manures such as legume crops, which fix nitrogen, has been proven to enhance soil fertility (Kang, 2001). Kang (2001) reported a 30% increase in sweetpotato yield when intercropping with legumes like cowpea. Change et al. (2006) showed that rotating sweetpotato with nitrogen-fixing legumes like soybeans improved soil fertility and increased sweetpotato yields. Similarly, Kang (2001) found that intercropping sweetpotato with groundnut promoted better nutrient cycling and improved soil health.

Research on soil microbial communities reveals their important role in enhancing soil fertility. Bünemann et al. (2005) highlighted that organic fertilization boosts microbial activity, improving nutrient cycling. Wang et al. (2014) showed that organic inputs resulted in a more diverse soil microbiome, promoting better nutrient uptake and soil structure.

Finally, Integrated Soil Fertility Management (ISFM) combines these practices into a comprehensive approach. Mahanjana (2018) demonstrated that ISFM, which combines organic and inorganic fertilizers, crop rotation, and soil conservation techniques, significantly improved sweetpotato yields and soil fertility in East Africa. These strategies contribute to sustainable productivity by improving both soil health and crop performance.

Another key abiotic factor limiting sweetpotato productivity is drought, which has an impact on yield quantity and quality (Cattivelli et al., 2011). While sweetpotato is generally considered drought-tolerant, extended and frequent dry spells, along with unpredictable rainfall, can lead to significant yield reductions (Ives, 2001; Kangalawe and Liwenga, 2009; Schafleitner et al., 2010). Drought negatively impacts not only crop growth and development but also the yield, dry matter content,

composition, and susceptibility to pests and diseases (Semagn et al., 2005; Mcharo and La Bonte, 2007; Ekanayake et al., 2017). For example, Mwololo et al. (2007) found that drought increased the occurrence and severity of viral diseases in sweetpotato. Additionally, newly introduced orange-fleshed sweetpotato (OFSP) varieties, despite their potential, were unable to withstand drought, leading to reduced productivity and farmer rejection (Ssemakula, 2011). Varieties that are less tolerant to drought hinder farmers' efforts, resulting in their unpopularity and eventual rejection. Gibson (2006) noted that participatory breeding and selection trials were disrupted by drought, and farmers abandoned varieties that were less drought tolerant. Consequently, due to its greater susceptibility to drought, most of the orange fleshed sweetpotato (OFSP) have low production and have not been widely adopted by farmers (Ssemakula, 2011). Thus, drought, alongside other factors, significantly impairs sweetpotato production, resulting in lower yields.

Drought-resistant sweetpotato varieties can sustain relatively high yields even in water-scarce conditions by employing different resistance strategies, such as escape, tolerance, avoidance, or recovery from drought stress (Ekanayake et al., 2017). These mechanisms, either individually or in combination, help the crop withstand drought at various stages of growth. Drought is especially detrimental during the crop establishment and storage root filling stages, as it disrupts the production, movement, and distribution of photosynthetic products. (Ekanayake et al., 2017). Prolonged drought can lead to reduced yields, poor root quality, and, in severe cases, total crop loss. In particular, drought during the storage root initiation phase results in fewer and smaller roots, ultimately lowering sweetpotato yield (Low et al., 2020).

Sweetpotato's ability to withstand drought is closely linked to its root system, particularly its deep taproots, which allow the plant to access moisture from deeper soil layers. Studies on root traits such as root depth and lateral roots have shown that deep-rooted varieties are more drought-resistant, as they are better able to access water stored in the soil (Ochieng' et al., 2023; Nweke, 2016). Additionally, varieties with higher water use efficiency (WUE) are better suited to drought conditions, and breeding efforts are increasingly focused on enhancing WUE for improved yields under water-limited conditions (Chave et al., 2014).

Soil moisture management plays a key role in mitigating drought impacts on sweetpotato crops. Mulching with organic materials like crop residues can significantly improve soil moisture conservation and maintain higher yield potential during dry periods (Zaidi et al., 2016). Drip irrigation, particularly in water-scarce regions, has also been shown to increase sweetpotato yields by 20% to 30% compared to rain-fed systems, as it provides consistent moisture with minimal water waste (Karanja et

al., 2015). Additionally, water harvesting techniques, such as constructing small reservoirs and contour bunds, have proven effective in improving soil moisture availability and boosting yields in semi-arid regions (Fungo et al., 2017).

Farmers can also adopt agronomic practices like early planting to avoid exposure to water stress during critical growth stages (Tsegaye et al., 2009). Early planting helps sweetpotato utilize available soil moisture more effectively and reach maturity before prolonged dry periods (Mbayaki, 2021). Intercropping sweetpotato with drought-resistant crops like legumes can further improve moisture retention and soil fertility, enhancing overall resilience (Change et al., 2006).

In the face of climate change, climate-smart agriculture (CSA) practices have become crucial for improving drought resilience. CSA involves strategies such as integrating drought-tolerant varieties, improving soil water management, and utilizing early warning systems to enhance productivity and adaptability to climate variability (Kariuki et al., 2021). To varied degrees, some of these techniques have been tried and evaluated in sweetpotato systems. Research by Ndolo et al. (2019) and Low et al. (2017), for example, emphasizes the adoption and breeding of drought-tolerant sweetpotato cultivars, especially in sub-Saharan Africa, to maintain productivity in water-limited environments. Mulching, ridging, and organic amendments are examples of soil and water conservation techniques that have been suggested to enhance root development and soil moisture retention (Ewell, 2002; Woolfe, 1992). Even though seasonal forecasting tools and early warning systems are more frequently used at larger agricultural scales, their incorporation into sweetpotato cultivation is still restricted and mostly advised rather than widely used (Kariuki et al., 2021). While CSA concepts have been partially applied in the production of sweetpotato, specifically in the areas of breeding and soil management, their complete integration particularly regarding climatic services and digital tools remains an area that needs more study and application.

2.5 Sweetpotato genetic improvement

Numerous problems, such as self- and cross-incompatibility, the extremely heterozygous character of individual clones, and the enormous number of chromosomes (2n = 6x = 90), impede the genetic improvement of sweetpotato (Kriegner et al., 2003; Yang, 2017). Several meiotic and cytological defects further complicate sweetpotato genetic investigations (Tan et al., 2008). Since homozygosity for particular loci cause differences in predicted segregation patterns, inheritance studies frequently reveal these differences. In sweetpotato, most significant agronomic features are inherited quantitatively (Tan et al., 2008).

Due to the high level of self-incompatibility exhibited by all genotypes, self-fertilization in sweetpotato is rare. Cross-incompatibility can also make it challenging to get seeds from crosses between certain parents (Collins et al., 1987). Meiotic anomalies and cytological inconsistencies inside the pollen mother cell might result in incompatibility (Martin and Ortiz, 1967; Du Plooy, 1982; Oracion et al., 1990). Genetic recombination in breeding populations is restricted by incompatibility, which creates a barrier to the development of new types by traditional breeding methods.

2.5.1 The genetics of beta carotene, root yield, iron and zinc

Developing sweetpotato varieties that are both nutrient-rich and resilient to environmental stresses, such as drought and poor soil fertility, is essential for ensuring climate adaptation and sustainability (Afzal et al., 2021; Bünemann et al., 2005). Breeding efforts targeting enhanced beta-carotene, zinc, and iron content can help address widespread deficiencies, such as Vitamin A deficiency, iron deficiency anemia, and zinc deficiency (Bechoff et al., 2017). Genetic research on these traits is crucial for developing enhanced varieties that address nutrient deficiencies and boost productivity.

Sweetpotato's high beta-carotene content is vital for combating Vitamin A deficiency. Genetic research has shown that beta-carotene accumulation is controlled by multiple genes, with environmental factors influencing its expression (Cattivelli et al., 2011). Bünemann et al. (2005) conducted a genome-wide association study (GWAS) to identify genetic regions linked to beta-carotene levels, aiding in the selection of biofortified varieties. However, further research is required to fully grasp the genetic mechanisms and identify more markers for improving beta-carotene content.

Root yield is an essential trait in sweetpotato breeding. Research by Tan et al. (2008) has shown that root yield is influenced by multiple genes and environmental factors. Afzal et al. (2021) discovered that varieties with larger root systems and higher leaf biomass generally produce better yields. More studies are needed to identify the genetic factors controlling root yield and to improve its stability across varying environmental conditions.

Zinc and iron are crucial micronutrients in sweetpotato, which can help address deficiencies that lead to anemia and stunted growth. Mgonja et al. (2016) found significant genetic variation in zinc and iron content, indicating that these traits are heritable and can be selected for breeding. Bechoff et al. (2017) identified sweetpotato varieties with higher iron levels under specific conditions. Additional research is necessary to identify the genes responsible for micronutrient accumulation and to better understand how genetic and environmental factors interact to influence these traits.

While progress has been made in understanding the genetic basis of these important traits, further research is critical to developing high yielding, biofortified sweetpotato varieties that address both food security and malnutrition. These traits are polygenic and influenced by environmental factors, making it crucial to understand the genotype x environment interactions. Identifying specific genetic loci for these traits is necessary for effective breeding (Tan et al., 2008; Cattivelli et al., 2011; Taylor et al., 2012). Ongoing research is critical for developing biofortified, climate-resilient sweetpotato varieties that contribute to nutritional security and address the challenges of climate change.

2.5.2 Genetic diversity in sweetpotato

Genetic diversity studies in sweetpotato are crucial for understanding the extent and structure of variation within and between populations. Such studies provide the foundation for effective conservation and utilization of sweetpotato germplasm, which is important for breeding programmes and ensuring long-term crop improvement. These investigations have contributed to the classification and grouping of various sweetpotato genotypes through morphological and molecular markers, uncovering diversity patterns tied to geographical origins, farmer preferences, and ecological adaptations (Zhang et al., 2000; Gichuki et al., 2003). For instance, Gichuki et al. (2003) utilized SSR markers to evaluate genetic diversity among sweetpotato genotypes in East Africa, discovering significant variability that is beneficial for selecting parents in breeding programmes. Studies on diversity are also crucial for preserving and utilizing landraces, which frequently harbor unique alleles that risk being lost due to the increasing reliance on uniform commercial varieties. Research conducted in Latin America and Asia has demonstrated that traditional varieties often carry valuable adaptive traits that could be harnessed for future breeding efforts (Zhang et al., 2000).

In sweetpotato, like other crops such as rice and maize, comprehending genetic diversity has facilitated the creation of core collections that encapsulate the highest genetic variation with the fewest genotypes. These core collections assist breeders in choosing parents that enhance heterosis and generate genetically varied offspring (Huaman et al., 1999). Research on genetic diversity is essential to sweetpotato improvement, because it supplies the genetic variation necessary for effective trait-based breeding, adaptation, and conservation, rather than directly pinpointing individual traits.

2.6 Molecular markers for assessing genetic variation in sweetpotato

In genetic studies and selection, molecular markers including restriction fragment length polymorphism (RFLP), random amplification polymorphic DNA (RAPD), simple sequence repeat (SSR), and single nucleotide polymorphism (SNP) are frequently employed (Mundt et al., 2005; So et al., 2015; Verma et al., 2019). One of the earliest molecular markers to be used to characterize germplasm was the

restriction length polymorphisms technique (RFLPs) (Paull et al., 1998). This method makes use of variations in the cleavage sites of particular endonucleases to generate strands of DNA with varying lengths. Due to insertion or deletion mutations, the lengths, or "fragments," will vary; these can be seen and scored on an electrophoresed gel or Southern blot. According to Mueller and Wolfenbarger (1999), RFLP markers have the following benefits: they are consistent, can differentiate between multiple alleles of the same gene, and are not biased toward any one allele.

Restriction Fragment Length Polymorphisms (RFLPs) were among the earliest molecular tools used in sweetpotato genetic research and played a significant role in elucidating the genetic structure and diversity of the crop. RFLPs were widely applied in assessing genetic diversity, supporting marker-assisted breeding, and identifying genomic regions associated with key agronomic traits. One of the earliest applications of RFLP in sweetpotato was the analysis of genetic diversity among cultivated varieties and wild relatives of *Ipomoea batatas*, which provided valuable insights into genetic relationships and available breeding resources (Mukherjee et al., 2012). RFLP markers were also used to identify genomic regions linked to important traits such as disease resistance and root yield. Huang and Sun (2000) employed RFLP -based linkage analysis s to map genes associated with pest resistance and yield-related traits contributing to early molecular breeding efforts in sweetpotato. In addition, RFLPs were applied to the mapping of nutritional traits, including β-carotene content. Huang and Sun (2000) identified genetic regions associated with β-carotene accumulation, an important target for biofortification strategies aimed at alleviating vitamin A deficiency. Although RFLPs have largely been replaced by higher-throughput and more efficient marker systems such as RAPDs, SSRs, and SNPs, they provided a critical foundation for subsequent advances in sweetpotato molecular genetics.

Random Amplified Polymorphic DNA (RAPD) markers were widely used in early sweetpotato genetic studies, offering a simple and cost-effective method for molecular research. RAPD markers generate random DNA fragments using short, arbitrary primers, and although they are easy to apply, their low reproducibility and limited informativeness posed challenges. Despite these drawbacks, RAPD markers were crucial in the initial genetic investigations of sweetpotato. These markers were used to assess genetic diversity and relationships among sweetpotato cultivars and wild relatives. Nakao et al. (2002) employed RAPD markers to study the genetic relationships among sweetpotato accessions in Japan, helping identify distinct genetic groups and evaluate variability in the germplasm, which is valuable for breeding programmes focused on improving yield and disease resistance.

The RAPD markers also played a key role in mapping genes related to important traits, such as disease resistance and root yield. Afzal et al. (2021) used RAPD markers to identify genetic loci associated

with these traits, contributing to the development of molecular tools for marker-assisted selection (MAS) in breeding programmes. RAPD markers were also employed for cultivar identification and authentication. Moulin et al. (2012) applied RAPD markers to differentiate between sweetpotato cultivars, ensuring proper labeling in markets and facilitating the protection of local germplasm. RAPD markers were used in studies to map genetic loci associated with the nutritional content of sweetpotato, including beta-carotene levels. Mwanga et al. (2021) utilized RAPD markers, alongside other techniques, to explore genetic diversity related to carotenoid content, contributing to the identification of candidates for biofortification efforts to improve the vitamin A content of sweetpotato.

Overall, despite the limitations of RAPD markers, they were a valuable tool in early genetic studies of sweetpotato, especially in areas such as genetic diversity, trait mapping, variety identification, and biofortification. However, while RAPD markers played an important role in the early stages of sweetpotato genetic research, their low reproducibility and limited transferability have made them less popular in recent years. This has led to the increased use of more reliable molecular markers, such as Simple Sequence Repeats (SSRs) and Single Nucleotide Polymorphisms (SNPs).

The SSR markers have been integral in constructing genetic maps and identifying quantitative trait loci (QTLs) linked to key traits such as yield, disease resistance, and nutritional content, as well as in cultivar identification and genetic fingerprinting, which is essential for accurate authentication and quality control. In sweetpotato, SSR markers have been widely used to assess the genetic diversity and relationships among sweetpotato cultivars and wild relatives. Nair et al. (2017) used SSR markers to study genetic diversity in sweetpotato cultivars, revealing significant variation among them. This information is vital for germplasm conservation and can support breeding programmes aimed at improving yield and disease resistance. Wang et al. (2014) used SSR markers to develop a genetic map for sweetpotato and identify QTLs related to root yield, a critical trait for breeding programmes focused on productivity. This research demonstrated the effectiveness of SSR markers in marker-assisted selection (MAS). Wang et al. (2014) identified SSR markers for resistance to sweetpotato virus disease (SPVD), which have been used in breeding programmes to select resistant varieties, crucial for maintaining productivity in regions affected by viral diseases. SSR markers have also been used in marker-assisted selection in the improvement of the nutritional content of sweetpotato, including increasing beta-carotene levels. Tumwegamire (2017) used SSR markers to identify genetic loci linked to carotenoid content in sweetpotato, contributing to the development of bio fortified varieties that address vitamin A deficiency in developing countries. For cultivar identification and genetic fingerprinting, Sharma et al. (2015) used SSR markers to differentiate between sweetpotato varieties in India, assisting in the certification and commercialization of sweetpotato cultivars. In summary, SSR

markers have proven to be highly effective tools in sweetpotato genetic research, due to their higher reproducibility and transferability compared to RAPD markers.

Single Nucleotide Polymorphism (SNP) markers, on the other hand, have become increasingly popular in sweetpotato genetic studies due to their high throughput, precision, and the availability of high-density genotyping platforms. These markers are highly valuable for exploring genetic variation, mapping important traits, and conducting association studies in crops like sweetpotato. The SNP markers provide essential information for molecular breeding, particularly for enhancing yield, disease resistance, and nutritional content.

In sweetpotato, SNP markers have been employed to assess the genetic diversity and population structure in several germplasm collections. Rosen et al. (2015) used SNP markers to evaluate the genetic diversity of sweetpotato cultivars and landraces in China. The study demonstrated the ability of SNP markers to identify genetic relationships among cultivars, which can inform breeding and conservation strategies. In addition, SNP markers have been frequently used in genetic mapping and to identify quantitative trait loci (QTLs) for important sweetpotato traits. Zhang et al. (2016) developed a high-density SNP map for sweetpotato and conducted a genome-wide association study (GWAS) to identify QTLs related to root yield and storage root traits. This research provided valuable insights into the genetic factors influencing yield, supporting efforts to improve sweetpotato productivity through breeding.

The SNP markers have also been instrumental in identifying genetic loci linked to disease resistance. Id et al. (2020) used SNP markers to explore the genetic basis of SPVD resistance, identifying significant loci associated with resistance. This work is crucial for developing disease-resistant sweetpotato varieties, especially in regions heavily affected by viral diseases. Additionally, SNP markers have been applied in selections for enhanced nutritional content of sweetpotato, including increased beta-carotene levels. Ferrucci et al. (2008) conducted a GWAS using SNP markers to identify loci associated with beta-carotene content, highlighting their potential in marker-assisted selection (MAS) aimed at biofortifying sweetpotato to address Vitamin A deficiency. With advances in high-throughput genotyping technologies such as next-generation sequencing (NGS), SNP markers are increasingly used in large-scale breeding programmes. Tang et al. (2009) employed SNP markers derived from genotyping-by-sequencing (GBS) to conduct a genetic study on sweetpotato in China, demonstrating the utility of the markers for large-scale genotyping and high-density genetic mapping. This would facilitate identification of markers for marker-assisted breeding for various traits in sweetpotato. Overall, SNP markers have proven to be a powerful tool in sweetpotato genetic studies, thus a critical

component for advancing molecular breeding programmes and enhancing the productivity and nutritional value of sweetpotato.

2.7 Gene action

Quantitative genes with small gene effects govern the majority of agronomic traits in crops (Mitra, 2001). These quantitative traits are often not easy to select for as they are affected greatly by the environment. Therefore, understanding the gene action, which can be additive, dominant, or epistatic, can lead to the appropriate strategy for breeding and selection of these traits (Acquaah, 2009). According to Mugisa et al. (2022), additive gene effects regulate β-carotene inheritance. Inheritance of dry matter was also found to have additive gene effects (Chiona, 2009). When the number of roots per plant and size were analyzed, heterosis was discovered, suggesting intra-allelic interaction between alleles of the same gene or dominance gene activity (Gasura and Mukasa, 2011). These results suggest that quantitative genes in sweetpotato regulate root output, β-carotene, and maybe mineral content.

Most agronomic features in crops are controlled by quantitative genes with negligible effects (Mitra, 2001). Strong environmental impacts make it difficult to select for these quantitative features. Therefore, creating successful breeding techniques requires an understanding of gene function, whether it be additive, dominant, or epistatic (Acquaah, 2009). For example, it has been discovered that additive gene effects control dry matter content (Chiona, 2009) and β-carotene inheritance (Mugisa et al., 2022). Given that allele effects are cumulative and heritable, early-generation selection can effectively improve traits governed by additive gene action through recurrent selection or family-based selection (Acquaah, 2009).

On the other hand, characteristics like root size and number that show heterosis (hybrid vigor) point to the existence of intra-allelic interactions or dominance gene action (Gasura and Mukasa, 2011). Breeding techniques such as hybrid breeding or making use of heterotic groupings may be more successful for certain qualities, particularly when crossing genetically diverse parents to capture dominance effects and find high-performing genotypes. Clonal selection or recurrent selection in subsequent generations may be necessary to stabilize the intended gene combinations over time if epistatic interactions (gene-gene interactions), which are more intricate and unpredictable, are involved (Acquaah, 2009).

Genetic analysis of offspring produced by suitable mating designs can be used to infer the gene action governing a specific trait (Acquaah, 2009). Mating designs such as diallel crosses, North Carolina Designs (I, II, III), and generation mean analysis provide for an understanding of the relative

significance of additive and non-additive effects. This information is crucial for designing efficient breeding strategies that are suited to the genetic makeup of the traits under improvement (Falconer and Mackay, 1996; Hallauer et al., 2010).

Dissecting gene action is difficult but necessary for improving traits in the sweetpotato (*Ipomoea batatas*), an outcrossing, hexaploid crop with significant heterozygosity. Mating designs have been used in earlier research to better understand how important agronomic and nutritional features are inherited. For instance, general and specific combining abilities (GCA and SCA respectively) for characteristics including storage root production, dry matter content, and resistance to sweetpotato virus disease have been evaluated using diallel crosses (Gasura and Mukasa, 2011; Mwanga et al., 2011). These investigations demonstrated that the expression of traits is significantly influenced by both dominance and additive gene activities.

The North Carolina Design II (NC II), which is especially useful for evaluating additive and dominant genetic variations in cross-pollinated species like sweetpotato, was used in this investigation. By systematically crossing several males with several females, this design makes it possible to identify both additive and non-additive gene effects and to accurately estimate the genetic contributions of each parent (Acquaah, 2009). The necessity to assess complex traits such as β-carotene concentration, root number, zinc and iron and to find prospective parents and crosses for future development, led to the selection of this design. By understanding the gene action involved, we can implement more targeted selection approaches such as recurrent selection for additive traits or hybridization for traits influenced by dominance to accelerate genetic gains in sweetpotato breeding.

2.8 Combining ability effects and gene action

Combining ability is a measure of a parent's average performance across all its crossings with several other parents (Falconer et al., 2004). One of the most crucial techniques in plant breeding for determining the parents for hybridization is combining ability analysis. The general combining ability (GCA) measures how well a parent or genetic stock combines with a test subject or set of test subjects. According to Falconer et al. (2004), the value is represented as a departure from overall mean crosses, which is the mean of all F1s that share this parent. The performance expectation deviance based on GCA is known as the specific combining ability (SCA). The SCA is an interaction effect, while GCAs are major effects. Falconer et al. (2004) state that while SCA variance is caused by non-additive genetic variance, such as dominance and epistatic effects (additive x dominance, dominance x dominance interaction variance), GCA is due to additive variance and additive x additive interaction variance in the base population. The prevalence of additive or non-additive variation is indicated by the ratio of the

GCA variance to the SCA variance. Double the variation resulting from GCA is the amount of additive genetic variance. According to Baker (1978), the dominant gene action type in diallel crosses is shown by the relative relevance of GCA and SCA for yield and other attributes.

General combining ability is important in breeding programmes aiming to improve β-carotene content. Gibson (2006) used combining ability analysis to evaluate the potential of different sweetpotato genotypes for β-carotene breeding. Their findings suggested that genotypes with high GCA for β-carotene can be utilized in hybridization programmes to increase β-carotene content in offspring. The study also highlighted that parental lines with favorable GCA could be selected for creating new varieties that consistently produce high β-carotene content across different environments. While GCA is useful for selecting parents with desirable general traits, SCA identifies specific cross combinations that perform better than the average of their parents. Chen and Wang (2024) performed combining ability analysis for both root yield and nutrient content, including β-carotene, iron, and zinc. They observed that certain crosses exhibited significant SCA effects, resulting in progeny with superior root yield and micronutrient content compared to the parental lines. These findings highlight the potential for using SCA to identify crosses that have superior combinations of high yield and high nutritional content. In the context of iron and zinc content, Mgonja et al. (2016) utilized combining ability analysis to identify sweetpotato varieties with favorable genetic backgrounds for improving micronutrient content. The study found that some genotypes showed high GCA for iron and zinc content, making them excellent candidates for further breeding. Additionally, crosses with significant SCA effects were identified, indicating the potential for creating high-performing hybrid varieties with elevated micronutrient levels.

2.9 Correlation between traits and selection

In plant breeding, understanding the correlation among traits is essential, especially for quantitatively inherited traits, since it guides the effectiveness and direction of selection tactics (Falconer & Mackay, 1996; Acquaah, 2009). Genetic or phenotypic trait correlations show how closely connected traits are to one another and whether they can be improved at the same time. While negative correlations show a trade-off, where improving one feature may result in lowering another, positive correlations imply that selection for one trait may lead to a corresponding improvement in the other. Uncorrelated traits can be chosen on their own without causing problems (Acquaah, 2009).

Traits can exhibit variable genetic or phenotypic correlations, which can be exploited for simultaneous selection (Acquaah, 2009). When two attributes have a positive correlation, it implies that improving one will also improve the other. When two traits are negatively connected, choosing one results in a

reduction of the other trait. Traits that are not correlated can be improved independently (Acquaah, 2009). Selection of high β-carotene, iron and zinc contents in orange-flesh sweetpotato is challenged by negative genetic correlations of these traits with dry matter content (Grüneberg et al., 2005; Binu and Bala, 2012), making it difficult to select these traits simultaneously. Due to the fact that plastids produce both starch and β-carotene, there is increased competition for assimilates in the pathways, which is why there is a negative association between dry matter accumulation and β-carotene synthesis (Kriegner et al., 2003). Researchers have, therefore, explored various genetic, agronomic, and biotechnological strategies to overcome this trade-off and develop high-yielding, nutrient-rich sweetpotato varieties.

Laurie et al. (2013) focused on bio fortifying sweetpotato varieties with both high yield and β-carotene content, aiming to mitigate the trade-off between these traits. This challenge was addressed by selecting breeding parents that exhibited moderate to high levels of both traits, and by employing a stepwise selection approach that balanced yield and nutritional quality. By evaluating genotypes across multiple environments and selecting clones that maintained stable performance for both root yield and β-carotene, they were able to identify and advance lines that minimized the negative correlation between these traits. Stathers et al. (2003) emphasized the importance of selecting genotypes that maintain high β-carotene while improving yield stability across different conditions. It was achieved by conducting multi-environment trials to evaluate genotype-by-environment interactions, enabling the identification of stable, high-performing clones. Their strategy involved combining phenotypic selection with an understanding of environmental effects to breed sweetpotato varieties that consistently express both nutritional quality and yield across diverse agro ecological zones. Abidin et al. (2005) developed sweetpotato varieties with both high β-carotene and acceptable yield in East Africa, demonstrating the potential for concurrent improvement of both traits through proper selection. They accomplished this by using a systematic breeding approach that involved crossing high β-carotene lines with locally adapted, high-yielding varieties, followed by rigorous field evaluations across multiple environments to select progeny exhibiting both traits. Their work highlighted the effectiveness of combining trait-specific parental lines and multi-location testing to overcome negative correlations and develop well-adapted, nutrient-rich cultivars.

Employing a selection index approach, Chen and Wang (2024) successfully identified genotypes that balance both high dry matter and β-carotene content, thus providing a practical model for breeding efforts. On the other hand, Balázs et al. (2023) found that balanced fertilization, especially with nitrogen and phosphorus, enhanced both root yield and β-carotene content, mitigating the trade-off between these traits. In addition, controlled irrigation during critical stages improved both yield and β-

carotene synthesis, demonstrating that water management can reduce the negative impact of water stress on these traits (Balázs et al., 2023).

Semagn et al. (2005) explored genetic transformation to enhance the carotenoid biosynthesis pathway in sweetpotato, increasing β-carotene content without negatively affecting dry matter accumulation, offering a promising biotechnological solution for biofortification. Using these transgenic approaches, Qiu et al. (2020) developed transgenic sweetpotato by overexpressing genes involved in both carbohydrate and carotenoid biosynthesis, showing that genetic engineering can optimize the balance between these pathways and overcome the trade-off.

Despite advancements, the challenge of the negative association between dry matter and β-carotene synthesis remains. Continued research is essential in studies using advanced genomic tools (e.g., CRISPR-Cas9) and refined GWAS techniques can help identify loci and genes influencing both traits independently. Bai et al. (2014) conducted a GWAS to identify genetic loci related to β-carotene content, finding loci that independently affect β-carotene accumulation, offering potential targets for marker-assisted selection (MAS) to improve both traits. Multi-trait selection and advanced breeding methods should consider genetic and environmental interactions to develop varieties with both high yield and nutritional content. Further optimization of agronomic practices, such as nutrient management, irrigation, and soil health, is necessary to improve both yield and β-carotene content. Continued exploration of genetic engineering and biotechnological innovations is critical to overcoming the trade-off and producing bio fortified sweetpotato varieties. This comprehensive approach, integrating genetic, agronomic, and biotechnological strategies, is essential to developing sweetpotato varieties that address both food security and nutritional challenges effectively.

2.10 Genotype by environment (G×E) interaction and stability in sweetpotato

The term genotype by environment (G×E) interactions describes how different genotypes behave in various environmental settings (Acquaah, 2009). Because genotypes that do well in one environment might not do well in another, these interactions make selection more difficult. Sweetpotato are especially vulnerable to G×E impacts since they are cultivated in a variety of agro-ecological zones (Janssens, 1983; Collins et al., 1987; Manrique and Hermann, 2000; Grüneberg et al., 2005; Osiru et al.,2009). Numerous studies have demonstrated that G×E interactions have a major impact on important agronomic features in sweet potatoes, particularly those linked to yield. Manrique and Hermann (2001), for instance, discovered that yield varied significantly depending on the environment, although nutritional characteristics like β-carotene content were typically less impacted. Likewise,

according to Grüneberg et al. (2005), strong G×E interactions could alter genotype rankings across years and locations, complicating selection decisions.

2.10.1 Genotype x environment interaction of β-carotene and nutritional traits

It has also been demonstrated that environmental factors including temperature, light intensity, and soil fertility affect β-carotene, a crucial nutritional characteristic of orange-fleshed sweetpotato (OFSP). According to Cattivelli et al. (2011), breeding for nutritional stability is possible but necessitates targeted selection because certain genotypes maintained steady β-carotene levels across a variety of conditions, while others showed significant variability. This was further highlighted by Bünemann et al. (2005), who found environmentally responsive β-carotene-associated loci in a genome-wide association study (GWAS), indicating that both genetic and environmental factors need to be considered.

Genotype x environment interactions also affect micronutrient characteristics like iron and zinc concentration. Due to variables including soil fertility, Tumwegamire (2017) discovered that sweet potato genotypes differed in how they expressed micronutrients in various settings. This variability indicates a need for site-specific management and selection strategies to achieve consistent nutritional outcomes across locations.

2.10.2 Genotype x environment interaction of yield traits

One of the characteristics most impacted by G×E interactions is yield. Significant G×E effects on sweet potato root yield were discovered by Afzal et al. (2021). While some genotypes performed consistently across environments, others showed high sensitivity, especially in stressful situations like drought. Similarly, Gurmu et al. (2024) noted that during multi-location experiments, many OFSP clones in Ethiopia displayed inconsistent yield performance. To fully utilize the crop's genetic potential, they underlined the significance of selecting for both broad and specific adaptation. Breeding efforts for sweetpotato have historically been limited in Zimbabwe, and thorough information on G×E interactions and the stability of current varieties is lacking. This disparity makes it more difficult to design and suggest cultivars that are appropriate for a range of production settings.

2.10.3 Implications for breeding and stability analysis

The recommendation of varieties with consistent performance across environments is significantly hampered by the occurrence of substantial G×E interactions. According to Tumwegamire et al. (2016), it reduces the predictability of genotype performance, may delay genetic gain, and makes breeding programmes less effective. Breeders need to assess genotypes in representative contexts in order to find

those that exhibit either specific adaptation (better performance in specific environments) or wide adaptability (consistent performance across environments) (Abidin, 2004; Acquaah, 2009). Acquaah (2009) defines stability as a genotype's capacity to sustain performance under a variety of changing circumstances. The development, release, and targeting of sweetpotato cultivars to appropriate agro-ecological zones thus depend on an understanding of G×E interactions (Manrique and Hermann, 2000; Grüneberg et al., 2005). Breeders need reliable biometrical methods to measure genotype stability and G×E interactions to enable this. For this, tools like mixed models, GGE biplots, and AMMI (Additive Main Effects and Multiplicative Interaction) are frequently utilized (Caliskan et al., 2007; Pramanik et al., 2024). These analyses shed light on interaction patterns, genotype performance, and the selection of stable, productive clones under a range of environmental circumstances.

2.11. Analysis of stability and G x E interactions

The existence of significant G x E interaction effects makes it challenging to recommend varieties for broader adaptation. To address this, it is essential to select varieties that consistently perform well across various test environments. As a result, analyzing multi-location data is crucial, as it plays a key role in crop improvement (Yan and Rajcan, 2003). Stability analysis is necessary to identify superior varieties that maintain consistent performance across different environments or to recommend specific varieties suited for particular environments based on desired traits. Several methods have been developed to analyze G x E interactions, quantify their extent, and understand the nature of these effects. These techniques have been discussed by various researchers (Lin et al., 1986; Flores et al., 1998; Hussein et al., 2000). The same methods used to quantify G x E interactions are also applied to assess a variety's stability across multiple environments for various traits.

Both univariate and multivariate approaches are available for phenotypic stability estimation and G×E interaction analysis (Pramanik et al., 2024). Based on the variance of a genotype across environments, ecovalence and regression coefficients, deviation mean squares, or coefficient of determination, the variance of a genotype across environments (Finlay and Wilkinson, 1963; Purchase et al., 2000; Descalsota-empleo et al., 2019), or rank orders of genotypes using mean or variance ranks to identify stability (Pramanik et al., 2024) are the basis for univariate stability statistics. On the other hand, multivariate analysis of variance (MANOVA), cluster analysis, principal component analysis, additive main effects and multiplicative interactions (AMMI), GGE-biplot, geometrical methods, and stochastic dominance are some of the multivariate techniques used to identify G x E interactions (Leon and Becker, 1988; Gauch and Zobel, 1997; Purcahse et al., 2000; Yan, 2001).

The Additive Main Effects and Multiplicative Interaction (AMMI) (Gauch and Zobel, 1988) and the Genotype plus Genotype by Environment Interaction (GGE) biplot analysis (Yan et al., 2000; Yan, 2001; Yan and Rajcan, 2002) are widely used statistical methods for analyzing multi-environment data. According to Yan et al. (2002), Yan and Rajcan (2003), and Yan et al. (2007), both Genotype (G) and Genotype by Environment Interaction (G x E) are critical factors that need to be considered simultaneously, while Environment (E) is less significant. They recommended that the GGE biplot is particularly useful for identifying G x E interaction patterns, helping to determine which variety performs best in specific environments and assisting in the identification of mega-environments. Conversely, Gauch (2006) and Gauch et al. (2009) argued that the AMMI model is more effective for accurately estimating G x E interaction effects and variety stability across environments, as it combines ANOVA and Principal Component Analysis (PCA) in a single approach, breaking down the variation into G main effects, E main effects, and G x E interaction effects (Gauch, 1988; Gauch and Zobel, 1988; Zobel et al., 1988). Despite their different approaches, both the GGE and AMMI models provide equivalent accuracy. Therefore, researchers may choose either method or use both to quantify G x E interaction and conduct stability analysis.

2.12 Conclusion

The review of literature shows that sweetpotato is an essential crop for food security and nutrition, especially in regions like Africa, where it provides vital nutrients, including β-carotene, a precursor to Vitamin A. While progress has been made in improving both yield and nutritional content in sweetpotato, several research gaps remain in genotype by environment interaction and combining ability in sweetpotato breeding for nutritional traits. Although studies have examined GxE interactions for individual traits like yield or β-carotene content, few studies have focused on GxE interactions involving multiple traits (e.g., yield, β-carotene, zinc, and iron) simultaneously. More research is needed to identify genotypes that perform well across environments for all traits of interest. While combining ability analysis has been useful, integrating genomic tools to better understand the genetic basis of combining ability could improve the efficiency of breeding programmes. More studies are needed to identify the specific genetic regions responsible for combining ability for nutritional traits. Accurate phenotyping for traits like β-carotene, iron, and zinc is often challenging due to environmental variability and complex interactions with other traits. The development of high-throughput phenotyping tools could improve the accuracy of breeding for these traits. While multi-trait selection has shown promise, more advanced breeding techniques are required to integrate genetic and environmental factors for optimizing both yield and nutrition together. Additional research is needed to improve agronomic practices, particularly in nutrient management, irrigation, and soil health, to

enhance both yield and β-carotene content. Continued exploration of biotechnological strategies, especially genetic modification and transgenic technologies, is crucial for developing sweetpotato varieties with improved yield and nutritional profiles. This research builds on existing knowledge and emphasizes the need to address the trade-off between yield and nutritional content. Whereas significant advancements have been made, continued research in genetic mechanisms, breeding strategies, agronomic practices, and biotechnological innovations is vital for developing sweetpotato varieties that are both high-yielding and nutritionally enhanced, ultimately improving food security and health outcomes, particularly in developing regions.

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Chapter Three: Characterization of Sweetpotato Genotypes using Agronomic and Nutritional Quality Traits

Abstract

Characterization of plant genetic resources is essential as it aids in the efficient use of the germplasm collections and selection of parents for specific traits in a breeding programme. In this study, 22 sweetpotato genotypes were assessed at four different locations in Zimbabwe in a randomized complete block design with two replications, in 2020–2021 season. The aim was to: (i) ascertain the genotypic variation in fresh storage root yield, β-carotene, iron (Fe), and zinc (Zn); and (ii) evaluate the relationships between β-carotene, Fe, Zn, and root yield in various environments. Genotypes differed considerably ($p < 0.01$) in terms of β-carotene, Fe, Zn, and the number of commercial roots per plot as well as fresh storage root yield. The genotype Dube had the highest fresh storage root yield of 27.49 t/ha followed by O-104 with 19.68 t/ha. Red Jewel and Nyekete had the lowest number of commercial roots per plot of 5.25 and 5.13 respectively, while P-201 had the highest number of commercial roots per plot of. 65.62. The maximum concentration of β-carotene (12.5 mg/100g) was observed in genotype O-105. For Fe, genotype O-106 had the highest concentration of 118.5 ppm and O-103, the lowest (45.25 ppm). Beauregard had the greatest zinc level of 20.5 ppm compared to P-203 which had the lowest zinc (2.00 ppm). Overall, O-104 genotype had high levels of β-carotene, Fe, Zn, and fresh storage root yield (t/ha). The number of commercial roots per plot and fresh storage root yield showed strong positive associations ($r = 0.80$; $p < 0.01$), indicating that both traits might be selected simultaneously. The amount of β-carotene and iron did not significantly correlate with fresh storage root yield. The investigation showed the existence of genetic variation for fresh storage root yield and nutrients, which is useful for further improvement of sweetpotato.

Key words: β-carotene, Fe and Zn concentration, genotypes, sweetpotato breeding, nutrient deficiencies

3.1 Introduction

Sweetpotato is an essential food security crop in sub-Saharan African (SSA) countries and ranks seventh globally among food crops. The sweetpotato roots are consumed either roasted, baked, boiled or fried (Kaganz, 2005). Additionally, the root is used as an industrial raw material for the extraction of biofuel, starch, alcohol, and animal feed (Schafleitner et al., 2010**;** Mussoline and Wilkie, 2015). The crop's young, succulent leaves are utilized as both food and fodder. The orange fleshed sweetpotato (OFSP) cultivars, in particular, are high in carbohydrates and β-carotene, a precursor to vitamin 'A' (Ssemakula, 2011; Frano et al., 2022), hence they can be used to curb Vitamin A deficiency (VAD).

Sweetpotato is popular amongst smallholder farmers as it can grow in marginal soil and arid land conditions and still produce more per unit area than staple crops like wheat, rice, and cassava (Schafleitner et al., 2010). In addition, it can withstand drought caused by inadequate and erratic rainfall. Sub-Saharan Africa (SSA) generates a mean of 22.63 million tonnes of sweetpotato yearly from an estimated 3.80 million hectares (FAOSTAT, 2017). Production of sweetpotato in SSA is challenged mostly by a lack of high yielding, disease-resistant planting materials (Stathers et al., 2003;Villordon et al., 2009; Ndunguru et al., 2009; Ngailo et al., 2016a). In terms of diseases, sweetpotato viral infections are the most persistent and common contaminant of planting materials, and contribute to low yields (Mwololo et al., 2007; Wokorach et al., 2020) as these infected materials are distributed informally amongst farmers (Semagn et al., 2005; Haile, 2020). In addition, most farmers use local landraces that are late maturing and low yielding despite being adapted to local agro-ecologies (Gibson et al., 1998; Semagn et al., 2005). As the exchange of planting materials amongst farmers is unavoidable, it is, therefore, important to improve the yield and quality of the varieties that farmers use through breeding.

Smallholder farmers use different names for the sweetpotato varieties they grow. For example, in Tanzania's Maswa district, sweetpotato varieties are known by more than 100 local names, according to Kagimbo et al. (2018). Sometimes, several types may go by the same name, or the same variety may go by different names in different places. However, for the crop to be effectively bred, genotypes with high yields and high nutritional content must be carefully characterized and chosen. The crucial first step in crop improvement and sustainable agricultural production, is to identify appropriate genotypes with farmer and consumer preferred traits (Elameen et al., 2008; Placide et al., 2015). Understanding the genetic variability that exists through characterization of germplasm collections helps plant breeders in the choice of parents with desirable characteristics for cultivar improvement (Yoshida et al., 2015) and in efficient management and use of the genetic resources (Méndez et al., 2015). The outcome

of a breeding programme in terms of genetic gain depends on the level of genetic variability in the source population (Placide et al., 2015).

There are numerous methods that have been employed in determining genetic variability among agricultural genetic resources. According to Mohammadi and Prasanna (2003), these techniques are dependent on the availability of data pertaining to plant morphology, agronomic performance, pedigree, biochemical and molecular studies. One popular technique for identifying genetic variation within and between genotypes is field phenotyping (Yoshida et al., 2015). Huaman (1991) created standardized phenotypic descriptors for sweetpotato, which have been widely applied in numerous sweetpotato genetic studies (Ngeve, 1993; Elameen et al., 2008; Tairo et al., 2008; Placide et al., 2015). These investigations revealed a high degree of genetic variation in agronomic parameters such as dry matter and nutrient content, storage root yields, and leaf growth, as well as tolerance to biotic and abiotic challenges. Variation for root yield in sweetpotato has been investigated and is widely reported, but variation for β-carotene, Fe and Zn and their associations with yield are not widely reported. Therefore, prior to their use in breeding programmes, it was essential to characterise the germplasm collections used in this study by assessing genetic variation in yield and nutritional traits as a critical step toward sweetpotato improvement.

Sweetpotato in Zimbabwe includes introductions from the International Potato Center (CIP), many of which are not yet well characterised for adaptation to local conditions or for use in breeding programmes. The objectives were thus to i) assess genetic variation in root yield, β-carotene, iron (Fe), and zinc (Zn) in the sweetpotato germplasm collection in Zimbabwe and 2) determine the correlations among the traits and 3) assess performance of the genotypes to identify superior ones for possible improvement.

3.2 Materials and Methods

3.2.1 Study sites

The study was conducted during the 2020/21 cropping season at four locations (Figure 1) in Zimbabwe. The test locations included Harare Research Station (HRS), Gwebi Variety Testing Center (GVTC), Marondera Horticultural Research Station (MHRS), and Makoholi Production Unit (MPU). The description of the locations is given in Table 3.1.

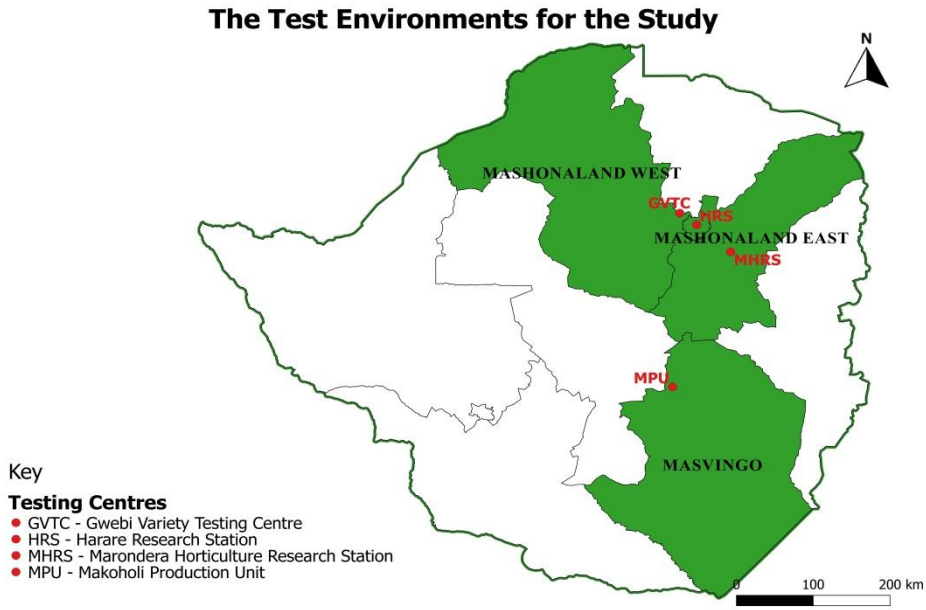

Figure 3.1: Geographic location of the four test environments used in the study, showing the testing centres across Mashonaland West, Mashonaland East, and Masvingo Provinces of Zimbabwe.

Table 3.1: Description of experimental sites

Location[c]	Soil type	Latitude	Longitude	Altitude (masl)[a]	Annual Rainfall (mm)
Harare	Clay	18.11S	31E	1506	831
Gwebi	*MG/SCL*	17.69S	30E	1449	850
Marondera	Sandy-loam	18.11S	31E	1630	873
Makoholi	Sandy-clay	19.50S	30E	1204	647

[a] *masl* meters above sea level, [b] *MG/SCL* magnesium sodium chloride,

3.2.2 Plant materials, experimental design and field establishment

The study comprised a total of 22 genotypes of sweetpotato established at four locations (Table 3.2). Nine were elite introductions obtained from CIP-Mozambique and while the thirteen landraces were all sourced from Zimbabwe. The experimental design at each site was a randomized complete block design with two replications. Sweetpotato vine cuttings were planted during the 2020/21 summer rainfall season, timed with the onset of sustained rains. At Harare and Gwebi, rainfall onset and soil moisture conditions supported field planting mid November 2020. At Marondera, planting similarly occurred during the mid November 2020 once field conditions stabilized with the rains. At Makoholi, where rainfall establishment was slightly delayed, planting took place between early December 2020. The plot sizes were four rows, 3 m long rows with 0.90 m inter-row spacing and 0.30 m intra-row spacing. In total there were 10 plants per row and 40 plants per plot. Weeding was done mechanically

as and when required. All the other agronomic practices for sweetpotato production were followed across all the study locations as recommended (Echodu et al., 2019).

Table 3.2: List of all Genotypes used in the Study for Characterisation for Agronomic and Nutritional Quality Traits during the 2020/21 Season

Code	Genotype	Origin[a]	Flesh colour	Skin colour	Type
G1	Red Jewel	Zimbabwe	Cream	Cream	Landrace
G2	Germany 2	Zimbabwe	White	Pink	Landrace
G3	Dube	Zimbabwe	Cream	Cream	Landrace
G4	Cordner	Zimbabwe	Orange	Cream	Landrace
G5	Chigondo	Zimbabwe	Cream	Cream	Landrace
G6	Harare	Zimbabwe	Cream	Cream	Landrace
G7	Fost	Zimbabwe	White	Pink	Landrace
G8	Shirikadzi	Zimbabwe	White	Pink	Landrace
G 9	Kau 4	Zimbabwe	Cream	Cream	Landrace
G10	Irene	Zimbabwe	Cream	Cream	Landrace
G11	Nyekete	Zimbabwe	Cream	Cream	Landrace
G12	Beauregard	Zimbabwe	Orange	Orange	Landrace
G13	O-101	CIP-Mozambique	Orange	Orange	Improved
G14	O-102	CIP-Mozambique	Orange	Orange	Improved
G15	O-103	CIP-Mozambique	Orange	Orange	Improved
G16	O-104	CIP-Mozambique	Orange	Orange	Improved
G17	O-105	CIP-Mozambique	Orange	Orange	Improved
G18	O-106	CIP-Mozambique	Orange	Pink	Improved
G19	P-201	CIP-Mozambique	Orange	Orange	Improved
G20	P-202	CIP-Mozambique	Orange	Cream	Improved
G21	P-203	CIP-Mozambique	purple white	Purple	Improved
G22	Chingovha	Zimbabwe	Cream	Cream	Landrace

[a]*CIP* International Potato Centre in Mozambique, [b]*Zim* Zimbabwe [c]CIP-International Potato Centre

3.2.3 Data Collection

The sweetpotato growth cycle ranges between 100 to 150 days from planting to harvesting (Rosero et al., 2020). When the sweetpotato attained physiological maturity, 135 days after planting, the roots were harvested. To determine the fresh weight and nutritional quality, roots were taken from the two central rows of each plot and weighed. A procedure created by Cole et al. (2014) was followed for the field sampling of commercial roots and these were taken for nutritional analysis in the laboratory. Storage root yield was measured by weighing all harvested commercial roots from each plot using a digital field scale, and the yield was expressed in tonnes per hectare (t/ha) by converting the total weight per plot to a per-hectare. The number of commercial storage roots was counted, and the amount of commercial storage root yield per plot was calculated. Commercial roots were described as having a minimum diameter of three centimetres and being free of rotting sections, insect damage, and fissures (Ekanayake et al., 2017).

Selected commercial storage roots were thoroughly washed with tap water and rinsed with distilled water to remove adhering soil and debris. The roots were gently peeled using a hand peeler and shredded. A 100 g composite sample of the shredded roots was weighed, placed in glass Petri dishes, and oven-dried at 70°C until sufficiently dry for grinding. The dried samples were ground using a stainless-steel cutting mill to pass through a 1 mm sieve and stored in airtight plastic containers until mineral composition analysis.

Vine yield was measured as the total fresh biomass of vines per plot. All the above-ground biomass from the two central rows of each plot was harvested at maturity. The harvested material was weighed using a digital field scale, and vine yield was expressed in tonnes per hectare (t ha^{-1}).

3.2.4 Mineral composition analysis

Using the Atomic Absorption Spectrophotometer, model Varians AA-1275 the Fe and Zn concentrations were measured in accordance with the protocol outlined by AOAC (2000.). For iron, 2483A wavelengths were utilized, and for zinc, 2133A wavelengths. The β-carotene content of the sweetpotato storage roots was estimated using a visual colour chart developed by HarvestPlus, which provides a rapid, field-based method for screening orange-fleshed sweetpotato (OFSP) genotypes based on flesh colour intensity. After harvesting, three storage roots of varying sizes were selected from each plot, washed, and cut transversely at the midsection to expose the internal flesh. The exposed surfaces were immediately compared under natural light to the standard colour chart, which assigns a numerical value (typically on a scale of 1 to 9) corresponding to increasing β-carotene concentration. This method allows for a semi-quantitative estimation of provitamin A content and has been validated as a practical tool for distinguishing low, medium, and high β-carotene genotypes (Low et al., 2017). Although less precise than laboratory-based spectrophotometric methods, the chart provides a cost-effective and non-destructive approach suitable for large-scale field trials.

3.2.5 Data analysis

Analysis of Variance

A combined analysis of variance (ANOVA) across environments was conducted using Genstat 18th edition (Payne et al., 2018).

The following statistical model was used for combined analysis of variance across environments:

$$Y_{ijkl} = \mu + G_i + E_j + GE_{ij} + R_{k(j)} + B_{l(k)} + \varepsilon_{ijkl}$$

Where: Y_{ijkl} is observed value of genotype in block l and replication k of environment j, μ is the grand mean, G_i is effect of genotype, E_j is environment or location effect, GE_{ij} is the interaction effect of genotype i with environment j, $R_{k(j)}$ is the effect iof replication k in environment j, $B_{l(k)}$ is the effect of block l in replication k, $\boldsymbol{\varepsilon}_{ijkl}$ is error (residual) effect of genotype *i* in block l and replication k of environment j.

Genetic Parameters

Broad sense heritability was calculated as follows: $H^2 = \sigma^2_g/\sigma^2_P \; x \; 100$; where σ^2_g is the genotypic variance and σ^2_P is the phenotypic variance then expressed in percentage. σ^2_P calculated as $\sigma^2_g + \sigma^2_e$; where σ^2_e is environmental variance.

The Genotypic Coefficient of Variation (GCV) and Phenotypic Coefficient of Variation (PCV) were estimated to quantify the amount of variability in a trait as follows:

$$GCV = (\sqrt{\sigma^2 g} / \bar{X}) * 100$$

$$PCV = (\sqrt{\sigma^2 p} / \bar{X}) * 100$$

where: $\sigma^2 g$ = genotypic variance (estimates the genetic component of variation), $\sigma^2 p$ = phenotypic variance (total variation observed) and $\bar{X}$ = general mean (average value) of the trait.

Pearson's correlations were calculated to assess the associations among root yield, root Fe, root Zn and root β-carotene. All the statistical analyses were performed using Genstat® Discovery 18th Edition VSN International, Hemel Hempstead, UK (VSN International, 2020).

3.3 Results

3.3.1. Analysis of variance

The ANOVA results summarized in Table 3.3 reveal that the environment had a statistically significant impact ($P < 0.01$) on all evaluated traits, including the number of commercial roots, root yield, vine yield, β-carotene, iron, and zinc content. Genotypic differences were also significant for several traits, with root yield showing significance at the 1% level ($P < 0.01$), while vine weight, β-carotene, and iron content exhibited highly significant variation among genotypes ($P < 0.001$), indicating strong genetic control over these traits. The interaction between genotype and environment was significant only for the NOCR ($P < 0.01$) and all other traits, except for commercial storage root yield.

Table 3.3: Analysis of variance showing mean squares and significance tests of number of commercial roots, root yield, vine weight, β-carotene, iron and zinc content of 22 genotypes evaluated across four locations in Zimbabwe during the 2020/21 summer season

		NOCR	Root yield	Vine yield	β-carotene(mg/100g)	Iron(ppm)	Zinc(ppm)
Source of variation	**Df**	**MS**	**MS**	**MS**	**MS**	**MS**	**MS**
Env	3	11207.8***	49780000***	3201.77***	11.93**	11072.2***	973.42***
Rep(Env)	4	2473.1***	1.36E+06	10.05	0	0	0
Block(Env*Rep)	8	104.4	5425000*	138.22*	145.631***	.7*	1.56
Gen	21	1118.2	26250000**	267.82***	117.877***	2604.4***	24.49*
Gen x Env	63	265.5**	2882913	133.3***	7.327***	1892***	36.51***
Residual	80	164.2	3681192	26.89	9.61E-05	5.91E-12	1.34E-13

[a]df =degrees of freedom, [b]* = Significant (P< 0.05); [c]** = significant (P< 0.01) [d]***highly significant at p < 0.001 probability level, [e]E = environment interaction, [f]Gen=Genotype, [g]NOCR=Number of commercial roots, [h]PPM=Parts per million

3.3.2. Mean performance of genotypes

The mean number of commercial storage roots per plot ranged from 5.13 to 65.62. Genotypes P-201, P-202, German 2, and Dube recorded substantially higher mean root numbers of 65.62, 32.20, 37.75, and 37.25, respectively (Table 3.4). Storage root yield varied widely, ranging from 1.32 to 27.49 t ha^{-1}. Genotype Dube exhibited the highest yield (27.49 t ha^{-1}), followed by P-201 (19.91 t ha^{-1}) and O-104 (19.68 t ha^{-1}). In contrast, markedly lower yields were observed for Red Jewel (1.32 t ha^{-1}), O-103 (4.07 t ha^{-1}), and Nyekete (4.27 t ha^{-1}).

Iron (Fe) concentration ranged from 45.0 to 118.5 ppm (Table 3.4). The highest Fe contents were recorded for genotypes O-106 (118.5 ppm), O-101 (99.5 ppm), and Dube (97.25 ppm), while P-203 exhibited the lowest Fe concentration. Mean zinc (Zn) concentration ranged from 12.0 to 20.5 mg 100 g^{-1}, with Beauregard (20.5 mg 100 g^{-1}) and P-202 (19.75 mg 100 g^{-1}) showing the highest Zn levels. In addition, genotypes O-105 and P-202 recorded relatively high β-carotene contents of 12.59 and 11.23 mg 100 g^{-1}, respectively.

Table 3.4: Mean performance of 22 sweetpotato genotypes across four environments in Zimbabwe for yield-related and nutritional traits.

Genotype	NOCR	Root Yield t/ha	Iron(ppm)	Zinc(ppm)	β-carotene mg/100g
Red Jewel	5.25[a]	1.32[a]	83.50[abc]	16.00[ab]	0[a]
Germany 2	37.75[fg]	16.92[fg]	59.75[ab]	14.25[ab]	0.03[a]
Dube	37.25[fg]	27.49[h]	97.25[a-c]	15.75[ab]	0.01[a]
Cordner	17.38[a-e]	9.28[a-f]	56.25[ab]	17.25[ab]	3.43[b]
Chigondo	23.25[b-f]	13.73[c-g]	57.25[ab]	17.25[ab]	0.01[a]
Harare	15.63[a-d]	7.67[a-d]	84.25[a-c]	16.50[ab]	0.03[a]
Fost	26.63[c-g]	16.34[c-g]	68.00[a-c]	18.25[ab]	0.01[a]
Shirikadzi	30.88[d-g]	14.40[d-g]	79.50[a-c]	18.50[ab]	0.01[a]
Kau 4	22.88[b-f]	9.90[b-f]	68.75[a-c]	16.50[ab]	0.06[a]
Irene	22.63[b-f]	9.64[a-f]	88.75[a-c]	17.00[ab]	0.03[a]
Nyekete	5.13[a]	4.27[ab]	57.25[ab]	15.50[ab]	0[a]
Beauregard	5.75[a]	5.79[a-c]	85.75[a-c]	20.50[b]	7.23[cd]
O-101	11.50[a-c]	4.88[ab]	99.50[bc]	16.50[ab]	0.12[a]
O-102	26.13[c-g]	6.80[a-d]	77.25[a-c]	17.75[ab]	10.52[ef]
O-103	9.13[ab]	4.08[ab]	50.00[ab]	12.00[a]	6.71[c]
O-104	28.38[d-g]	19.68[g]	68.75[a-c]	18.25[ab]	8.21[c-e]
O-105	32.25[efg]	10.58[b-f]	74.75[a-c]	17.50[ab]	12.59[f]
O-106	19.88[a-e]	8.48[a-e]	118.50[c]	16.75[ab]	7.39[cd]
P-201	65.62[h]	19.91[g]	54.50[ab]	16.75[ab]	9.86[d-f]
P-202	41.25[g]	14.15[c-g]	69.75[a-c]	19.75[b]	11.23[f]
P-203	9.50[ab]	4.48[ab]	45.25[a]	17.25[ab]	0[a]
Chingovha	18.75[a-e]	13.34[c-g]	84.50[a-c]	17.00[ab]	0.01[a]
Mean	23.30	11.05	74	16.94	3.52
LSD	13.67	1762.70	14.97	1.41	2.74
Se	4.84	623.7	15.48	2.09	0.968
CV	26.60	29.90	21.40	27.80	14.80
p – value	<0.001	<0.001	0.001	0.001	<0.001
Sig.	***	***	***	***	***

[a]CV= Coefficient of variation; [b]LSD= Least significant difference at $p<0.05$;
[c]*** = highly significant at $P< 0.001$, means followed by the same letter are not significantly different, [d]se=standard error, [e]NOCR=Number of commercial roots per plot

3.3.3. Genetic Parameters

Broad-sense heritability, along with genotypic and phenotypic coefficients of variation for the measured traits, are summarised in Table 3.5. Heritability estimates were high for commercial storage root yield and β-carotene content, moderate for number of commercial roots and vine yield, and low for iron concentration. Zinc concentration exhibited no detectable genetic variance under the conditions of this study. In all traits, phenotypic variation exceeded genotypic variation, indicating varying degrees of environmental influence.

Table 3.5: Genetic Parameters of some the traits measured across four sites

Trait	H^2	GCV (%)	PCV (%)
NOCR	76.7	20.31	34.89
Commercial storage root yield (t/ha)	87.9	28.3	41.01
Vine yield(t/ha)	55.6	19.66	43.03
β-carotene(mg/100g)	95.6	128.69	140.05
Fe (ppm)	26.7	12.61	43.6
Zn (ppm)	0	0	23.63

H^2 (%) broad sense heritability, PCV (%) phenotypic coefficient variation, GCV (%) genotypic coefficient variation

3.3.4. Correlation among traits

The number of commercial roots and storage root yield were significantly correlated (Table 3.6). There was a negative correlation between Fe and number of storage roots per plot. The storage root yield and iron are showing a non-significant correlation. Fe and β-carotene content were also negatively correlated.

Table 3.6: Correlation among the traits; number of commercial roots, root yield, Fe, zinc and β-carotene content

	NOCR	Storage Root Yield	Iron (Fe)	Zinc (Zn)	β-carotene
NOCR	1	0.8024 **	-0.1831^{ns}	Non	0.3967 ^{ns}
Storage Root Yield	0.8024 **	1	0.0296^{ns}	Non	0.0563 ^{ns}
Iron (Fe)	-0.1831^{ns}	0.0296^{ns}	1	Non	-0.0478 ^{ns}
Zinc (Zn)	Non	Non	Non	-1	Non
β-Content	0.3967^{ns}	0.0563 ^{ns}	-0.0478 ^{ns}	Non	1

** = significant at 0.01, ns = non-significant, Non=no correlation

3.4 Discussion

The first step in a plant breeding programme is to determine the availability of genetic variation within the population for the traits under improvement. In this study, the analysis of variance (ANOVA) showed highly significant differences among the genotypes for all the traits measured. Traits including the number of commercial roots per plot (NOCR), storage root yield per plot, vine yield per plot, β-carotene (mg/100g), iron(ppm) and zinc(ppm) content, were significantly affected by the environment ($p < 0.001$). This is in line with results from earlier research that showed sweetpotato performance was greatly affected by location-specific variables such soil fertility, temperature, and rainfall patterns (Tumwegamire et al., 2011). For most characteristics, such as root yield, vine fresh weight, β-carotene, iron, and zinc content, genotypic differences were highly significant ($p < 0.001$ or $p < 0.01$). This suggests a substantial

genetic variation within the 22 sweetpotato genotypes evaluated, which is a prerequisite for effective selection and improvement through breeding (Acquaah, 2012; Hallauer et al., 2010).

The sweetpotato genotypes evaluated in this study differed in their adaptation to the trial sites, reflecting their origin from diverse agro-ecological zones and resulting in substantial variation in storage root yield (Table 3.3). Different types of sweetpotato genotypes interact differently with their growth environment. Genetic variation among test entries may also account for the diversity in root yield among genotypes of sweetpotato that have been evaluated (Lebot and Champagne, 2009; Rukundo et al., 2013; Kagimbo et al., 2018). Differences in genetic background among sweetpotato genotypes influence dry matter accumulation and storage root development (Rukundo et al., 2013).

According to Lebot and Champagne (2009), storage root yield is a function of growth time. As a result, variations in the time to maturity among genotypes of sweetpotato may also have played a role in the variations observed in root yield. Previous research (Tairo et al., 2008; Ngailo et al., 2016b) has reported significant differences in root yield between genotypes of sweetpotato. Dube, P-201, and O-104, all classified as long-season genotypes, demonstrated significantly superior yield potential relative to the other genotypes assessed (Table 3.4). For mean performance on root yield, the range from 1.32 t/ha to 27.49 t/ha indicated the presence of adequate genetic variability for selection in sweetpotato improvement. Welch and Graham (2004) reported that high yielding and nutrient-enriched varieties will address the problem of malnutrition and ensure high sweetpotato production for farmers. In sweetpotato breeding efforts, these genotypes are promising parents that can be employed to improve yield and yield-related attributes.

Significant variation between genotypes for the dry matter content and number of roots per plot were noted by Gasura et al. (2008). Genotypic differences could be the cause of notable variation in the number of roots. For example, various genes among sweetpotato types affect the expression of storage root development and dry matter accumulation (Rukundo et al., 2013). The genotypes P-202, Germany 2, and Dube evaluated in this study had the greatest number of storage roots (Table 3.4). To increase the overall number of storage roots in existing genotypes through breeding, these genotypes are potential parents for hybridization.

The high level of Fe and Zn content observed in two of the genotypes (Berearugard and P-202) (Table 3.4) is notable. Both micronutrients were present in considerable amounts in the two cultivars. These genotypes are suitable parents for the biofortification breeding programme. The β-carotene levels were low in the white/cream fleshed. These findings are in agreement with Stathers et al. (2003) findings that indicated low β-carotene levels in white/cream genotypes. The results further support the idea that the relative levels of β-carotene in roots can be determined by their flesh color, with orange and cream indicating the highest and lowest levels, respectively. To effectively choose parents for the breeding of better varieties with higher amounts of β-carotene, it is necessary to isolate and identify genotypes with high levels of β-carotene (Binu and Bala, 2012; Naidoo et al., 2015; Kiarie, 2016). A dual breeding pipeline strategy can, thus be implemented, with one focusing on orange-fleshed and the other one on white-fleshed varieties, to address distinct consumer preferences.

The moderate to high broad-sense heritability observed in this study indicates that a significant portion of the phenotypic variation for certain traits is primarily due to genetic differences among genotypes, rather than environmental influences. This suggests that these traits are largely under genetic control, making them more predictable and responsive to selection through phenotypic evaluation. As a result, breeders can expect more consistent trait expression across varying environments, facilitating effective selection and leading to genetic gains over time (Acquaah, 2012; Bernardo, 2020).

Significant G x E interactions observed for traits such as number of commercial roots (NOCR), vine fresh weight, iron (Fe), zinc (Zn), and β-carotene content imply differential genotype performance across environments. These interactions indicate changes in ranking among genotypes depending on the location, complicating the prediction of performance in specific environments. As a result, more sophisticated breeding approaches—such as environment-specific selection or multi-environment trials—are required to identify and develop superior genotypes with both high performance and stability (Begna, 2022; Gasura et al., 2013; Yan & Kang, 2003). These findings align with earlier studies that emphasize the complexity introduced by G×E interactions in crop breeding and underscore the importance of considering environmental variation when evaluating genotypes (Gasura et al., 2013; Yan & Tinker, 2006).

Although not very strong, the GCV (20.31%) was lower than the PCV (34.89%) for number of commercial roots, indicating environmental effect. This suggests that, even in the presence of some ambient noise, phenotypic selection can be successful (Falconer & Mackay, 1996). Gains via selection may be achievable when moderate to high heritability and moderate GCV are present (Johnson et al., 1955).

The large GCV suggests that direct selection for commercial storage yield may be highly successful and that genotype-to-genotype genetic differences are substantial. This is consistent with findings by Sharma et al. (2018) and Kumar et al. (2020), who noted that yield is a good target for selection due to strong heritability and GCV in root and tuber crops. The accuracy of phenotypic selection may be limited by environmental variance overshadowing genetic variance, as indicated by the high PCV in comparison to GCV (Burton and DeVane, 1953). As a result, vine fresh weight selection could not be as accurate in the field and may need additional replications or controlled settings. Selection for increased beta-carotene concentration is highly successful, as these levels indicate very strong genetic control with little environmental influence (Ramesh et al., 2019). Sweetpotato and cassava have also been found to have high GCV and heritability in biofortification features like β-carotene (Gurmu et al., 2014). Rapid genetic increase and early-generation selection seem to be the best options for this characteristic. Poor heritability values in iron suggests that the environment has a significant impact, which makes choosing challenging and unreliable in the present. In micronutrient breeding, similar patterns have been documented, with characteristics such as Fe and Zn frequently exhibiting strong environmental interaction (Gregorio et al., 2000). To increase reliability when breeding for Fe content, multi-location trials or marker-assisted selection may be necessary.

Breeding food crops involves the primary task of simultaneously selecting for different traits associated with quality and production, as well as additional traits including resistance to biotic and abiotic challenges Luby and Shaw (2009). This is because a successful food crop variety has several attributes that both provide farmers with economic sustainability and are valued by consumers. Therefore, it would be advantageous to assist the selection process in the breeding programme if there are positive associations between two or more desirable traits, such as the concentration of Fe and Zn as reported in this study.

3.5 Conclusions and recommendations

Beauregard, O-102, O-103, O-104, O-105, O-106, P-201, and P202 contained above average amounts of root Fe and Zn and high concentrations of β-carotene. It is therefore recommended to employ these genotypes as parents in breeding programmes for biofortification or variety release provided that these genotypes align with consumer preferences in terms of taste, flesh color, and texture.

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Chapter Four: Adaptability and Stability Analyses of Storage Root Yield and Micronutrient Concentrations in Sweetpotato (*Ipomoea Batatas* [L.] Lam) Genotypes

Abstract

High yielding and micronutrient dense sweetpotato cultivars could contribute to alleviating food security and micronutrient deficiency, which is a prevalent problem in developing countries. Developing these improved cultivars involves selection across diverse environments, which requires an understanding of genotype x environment interaction (GEI). This study evaluated root yield (RY), β-carotene, iron (Fe), and zinc (Zn) concentrations in 22 sweetpotato genotypes across four different locations to identify superior genotypes for broad and specific adaptation. Trials were conducted at four different locations across two seasons in a randomized block design with two replications. The data were subjected to the genotype and genotype by environment (GGE) biplot analyses. Significant ($p<0.05$) genotype x environment interactions were reported for fresh storage root yield, β-carotene, Fe and Zn content. There was wide genotypic variation in RY, and micronutrient contents. The most desirable genotypes were G3, G19 and G16 with higher than 7.5 t/ha of RY and G19, G12 and G16 that had high β-carotene. These genotypes were selected for breeding for improved cultivars. Overall, seven genotypes G3, G19, G16, G22, G4, G5 and G2 with high and stable RY, and high micro-nutrient concentrations were selected for developing breeding populations. These genotypes are recommended for sweetpotato breeding programme in Zimbabwe and similar environments.

Keywords: AMMI, GGE, multi-environment, stability analysis, Fe, Zn, root tuber yield

4.1 Introduction

Sweetpotato **(***Ipomoea batatas* [L.] Lam**)** is widely grown for its storage root yield that are high in micronutrient content. It is highly nutritious with starch being the main nutrient at 20-26%, while protein (2-3%), vitamins (vitamin A: approximately 28355 IU per 100g, vitamin C: about 2.4 mg per 100g, vitamin B6: around 0.209 mg per 100g, vitamin E: roughly 0.26 mg per 100g) and minerals such as potassium (542 mg/g), phosphorous (40-60 mg/g) and calcium (30 mg/g) are also available in the storage root (Nandutu and Howell, 2009). Its high nutritional content could be harnessed to address dietary deficiencies in micronutrient such as iron (Fe) and zinc (Zn) prevalent in developing countries (Welch and Graham, 2004; Gregory et al., 2017; Kihara et al., 2020). However, there are very few sweetpotato varieties that combine high yield potential with high micronutrient contents. It is imperative to develop suitable varieties with high yield potential and high concentrations of micronutrients such as β-carotene, Fe and Zn.

Breeding for improved cultivars with desirable characteristics requires evaluation of genotypes across target population environments. However, genotype x environment interactions (GEI) affect agronomic performance, which confounds the selection process and reduces breeding efficiency (Begna, 2020; Laurie et al., 2013). Genotype by environment interaction (GEI) reduces the correlation between genotype and phenotypic expression, and ultimately reduces potential genetic gain (Van Oosterom et al., 1993). Differentials in genotype performance across environments have been attributed to GEI and can be used to determine whether a genotype exhibits wide or specific adaptation to the environments (Yan et al., 2001; Abidin et al., 2005). It is imperative to evaluate genotypes in multiple environments to identify superior and adapted genotypes for developing breeding populations and improved cultivars.

A wide range of techniques have been used to analyze the adaptability and stability of genotypes (Efroni et al., 2008; Metzger et al., 2009; Pereira et al., 2009). Genotype and genotype by environment (GGE) biplot (Yan, 2001), and additive main effects and multiplicative interaction (AMMI) analyses (Gauch and Zobel, 1997) are widely used in multi-environment trials (MET). These approaches combined provide robust methods for the breeder to identify and select superior genotypes while offering a method to predict untested genotypes or environments. The objectives of this study were to evaluate genotype performance in storage root yield and β-

carotene content, Fe and Zn contents across different environments and determine the genotype x environment interaction (GEI) effects affecting trait expression.

4.2 Materials and methods

4.2.1 Plant materials

The study investigated 22 sweetpotato genotypes that were sourced from the International Potato Centre (CIP), in Mozambique, and Crop Breeding Institute (CBI) in Zimbabwe (Table 4.1). The CIP materials were introductions to Zimbabwe with no adaptation, agronomic performance and nutritional content measured. Their inclusion contributed to the available genetic diversity for sweetpotato breeding in Zimbabwe. The genotypes from Zimbabwe were landraces that are commonly grown and adapted to local conditions. The landraces lacked nutritional value analysis.

Table 4. 1: Genotypes evaluated for adaptability and stability studies across four locations during the 2021/22 and 2022/23 season

Code	Genotype	Source	Flesh colour	Skin colour	Type
G1	Red Jewel	CBI-Zimbabwe	Cream	Cream	Landrace
G2	Germany 2	CBI-Zimbabwe	White	Pink	Landrace
G3	Dube	CBI-Zimbabwe	Cream	Cream	Landrace
G4	Cordner	CBI-Zimbabwe	Orange	Cream	Landrace
G5	Chigondo	CBI-Zimbabwe	Cream	Cream	Landrace
G6	Harare	CBI-Zimbabwe	Cream	Cream	Landrace
G7	Fost	CBI-Zimbabwe	White	Pink	Landrace
G8	Shirikadzi	CBI-Zimbabwe	White	Pink	Landrace
G 9	Kau 4	CBI-Zimbabwe	Cream	Cream	Landrace
G10	Irene	CBI-Zimbabwe	Cream	Cream	Landrace
G11	Nyekete	CBI-Zimbabwe	Cream	Cream	Landrace
G12	Beauregard	CBI-Zimbabwe	Orange	Orange	Released
G13	O-101	CIP-Mozambique	Orange	Orange	Clone
G14	O-102	CIP-Mozambique	Orange	Orange	Clone
G15	O-103	CIP-Mozambique	Orange	Orange	Clone
G16	O-104	CIP-Mozambique	Orange	Orange	Clone
G17	O-105	CIP-Mozambique	Orange	Orange	Clone
G18	O-106	CIP-Mozambique	Orange	Pink	Clone
G19	P-201	CIP-Mozambique	Orange	Orange	Clone
G20	P-202	CIP-Mozambique	Orange	Cream	Clone
G21	P-203	CIP-Mozambique	purple white	Purple	Clone
G22	Chingovha	CBI-Zimbabwe	Cream	Cream	Released

[a]*CIP* International Potato Centre in Mozambique, CBI=Crop Breeding Institute

4.2.2 Experimental sites

The experiments were established in four locations over two seasons (2021/22 and 2022/23) giving a total of eight environments (season by location). The locations included Makoholi Crop Production Unit which is in the drier region parts of Zimbabwe. The other three locations were the Harare Research Station, the Gwebi Variety Testing Center, and the Horticulture Research Center, all in Zimbabwe's highveld region and represented high agricultural potential environments. The climatic conditions, soil types, micronutrient profiles, and agro-ecological characteristics of the locations were diverse (Table 4.2).

Table 4. 2: Agro-environmental characteristics of the experimental locations used for adaptability and stability studies during the 2021/22 and 2022/23 cropping seasons.

Parameter	HRS	GVTC	HRC	MKHL
Latitude	18.11S	17.69S	18.11S	19.50S
Longitude	31E	30E	31E	30E
Altitude (m.a.s.l)	1506	1449	1630	1204
pH (Calcium Chloride)	5.4	6.1	5.4	5.7
OM (%)	2.1	2.0	0.7	2.3
N (ppm)	19	18	13	22
P (ppm)	73	67	70	77
Ca (mg/100 g)	9.0	10.7	8.5	9.1
Mg (mg/100 g)	5.6	6.3	6.7	6.0
K (mg/100 g)	0.24	0.38	0.28	0.35
Zn (ppm)	2.40	1.46	0.57	2.19
Fe (ppm)	13.13	10.27	6.11	7.05
Soil type	Clay	Clay loam	Sandy-loam	Sandy-clay
Rainfall (mm)	750	850	850	500
Temperature-Maxmum	27 °C	28 °C	27	35 °C
Temperature-Minimum	-8 °C	-10 °C	-5	-14 °C

HRS= Harare Research Station, GVTC = Gwebi Variety Testing Center, HRC = Horticulture Research Centre, MKHL = Makoholi Experiment Station OM = organic matter content, masl = meters above sea level, mm = millimetres, ppm = parts per million, mg/100 g = milligram equivalents per 100 g. Soil chemical properties were determined from composite soil samples collected at each site prior to planting.

4.2.3. Experimental design, field management

The trials were established under rain-fed conditions and laid out in a randomized block design with two replications at each of the locations. Each plot consisted of four, 6 m long rows, with inter-row and intra-row spacings of 0.90 m and 0.30 m, respectively. Weeding was carried out manually when required and standard agronomic practices for sweetpotato were applied.

4.2.4 Data collection

Planting occurred mid-December after the onset of rains and were harvested end of April. When the sweetpotato attained physiological maturity, 135 days after planting, the roots were

harvested. Both the number of commercial storage roots per plot were counted and the amount of commercial root yield per plot calculated. Commercial roots were described as having a minimum diameter of three centimeters and being free of rotting sections, insect damage, and fissures (Ekanayake et al., 2017). To determine the fresh weight and nutritional quality, roots were taken from the two central rows of each plot and weighed. A procedure created by Cole et al. (2014) was followed for the field sampling of commercial roots and these were taken for nutritional analysis in the laboratory. Vine yield was measured by harvesting all above-ground biomass from the two central rows of each plot at maturity and weighing it using a digital field scale; the yield was then expressed in tonnes per hectare (t/ha). Storage root yield was measured by weighing all harvested commercial roots from each plot using a digital field scale, and the yield was expressed in tonnes per hectare (t/ha) by converting the total weight per plot to a per-hectare.

To determine the nutritional content, three storage roots of varying sizes were selected per plot. The selected storage roots were properly cleaned with tap water and then rinsed with distilled water. Thereafter they were peeled and chopped into small pieces. The chopped tubers were then weighed to 100 g composite samples and placed in a glass petri dish. The samples were oven dried at 70°C before milling. The samples were then ground in a stainless cutting mill until they could pass a 1 mm sieve. They were then kept in plastic containers with tight-fitting covers until their mineral composition could be ascertained.

Micronutrient content analysis was carried out at the Department of Research and Specialist Services (DR&SS) in Harare, Zimbabwe, at the food laboratory of the Chemistry and Soils Research Institute. Using the atomic absorption spectrophotometer model, 50 g of milled dry sweetpotato root samples were evaluated for Fe and Zn contents following a protocol described in Elango et al. (2021). The wavelengths used were 2483A for the iron and 2133A for zinc. The β-carotene content of the sweetpotato storage roots was estimated using a visual colour chart developed by Harvest Plus, which provides a rapid, field-based method for screening orange-fleshed sweetpotato (OFSP) genotypes based on flesh colour intensity. After harvesting, three storage roots of varying sizes were selected from each plot, washed, and cut transversely at the midsection to expose the internal flesh. The exposed surfaces were immediately compared under natural light to the standard colour chart, which assigns a numerical value (typically on a scale of

1 to 9) corresponding to increasing β-carotene concentration. This method allows for a semi-quantitative estimation of provitamin A content and has been validated as a practical tool for distinguishing low, medium, and high β-carotene genotypes (Low et al., 2017). Although less precise than laboratory-based spectrophotometric methods, the chart provides a cost-effective and non-destructive approach suitable for large-scale field trials.

4.2.5 Data analysis

Analysis of Variance

A combined analysis of variance across environments was done using GenStat 18th edition (Payne et al., 2018) statistical package. The following statistical model was used:

$$\boldsymbol{Y_{ijklm} = \mu + G_i + L_j + R_{l(jk)} + B_{m(jkl)} + GL_{ij} + GY_{ik} + LY_{jk} + GLY_{ijk} + e_{ijklm}}$$

Where: Y_{ijklm} =response of the ith genotype in jth location and lth replication within year and mth block within location, μ =grand mean, G_i =random effect of the ith genotype, L_j =fixed effect of the $_j$th location, Y_k =fixed effect of the year k, $R_{l(jk)}$ =fixed effect of the replicate l nested within location j in year k, $B_{m(jkl)}$ =fixed effect of the block m nested within location j in year k and replicate l, GL_{ij} =random effect of the interaction between genotype i and location j, GY_{ik} = random effect of the interaction between genotype i and year k, LY_{jk} = random effect of the interaction between location j and year k, GLY_{ijk} = random effect of genotype by location by year interaction, and e_{ijlkm} = random error.

The AMMI stability value (ASV) was calculated to quantify and rank genotypes (Rezene et al., 2014). This was carried out using a formula provided by Purchase et al. (2000);

$$\text{AMMI Stability Value (ASV)} = \sqrt{\left[\left(\frac{SSIPCA1}{SSIPCA2}(IPCA1)\right)^2 + [IPCA2]^2\right]}$$

where, $\frac{SSIPCA1}{SSICPA2}$represents the weighted value assigned to the first interaction principal component score due to its high contributions in the GXE model, SSIPCA1 and SSIPCA2 are the sum of squares for IPCA1 and IPCA2, respectively, IPCA1 and IPCA2 are the first and second IPCA scores for 155 each genotype. The larger the ASV value the more specifically adapted the

genotype to a certain environment and the smaller ASV indicates a more stable genotype across environments (Purchase et al., 2000; Geravandi et al., 2011; Thiyagu et al., 2012).

The model for a GGE biplot (Yan, 2001; Yang et al., 2007) based on singular value decomposition (SVD) of t principal components is:

$$\bar{Y}_{ij} - \mu_i - \beta_j = \sum_{k=1}^{t} \lambda_k \alpha_{ik} \gamma_{jk} = \varepsilon_{ij}$$

Where $\bar{Y}_{ij}$ is the performance of genotype i in environment j, μ is the grand mean, β_j is the main effect of environment j, k is the number of principal components (PC); λ_k is singular value of the k^{th} PC; and α_{ik} and γ_{jk} are the scores of i^{th} genotype and j^{th} environment, respectively for PC_k; ε_{ij} is the residual associated with genotype i in environment j.

4.3. Results

4.3.1 Combined analysis of variance

The combined analysis of variance (ANOVA) for root yield, β-carotene, iron, and zinc content across 22 sweetpotato genotypes evaluated in eight environments is summarized in Table 4.3. Statistically significant differences ($p < 0.001$) were detected among genotypes for root yield, iron, and zinc, while differences in β-carotene content were significant at the $p < 0.05$ level. The effects of incomplete block structures within environments [Block(Env*Rep)] were also highly significant ($p < 0.001$), indicating substantial variation due to experimental design factors. Significant GEI effects ($p < 0.001$) were observed for β-carotene, iron, and zinc. These findings indicate that the expression of β-carotene, iron, and zinc in sweetpotato genotypes was significantly influenced by environmental conditions and their interaction with genotypic performance.

Table 4. 3: Combined analysis of variance for root yield, β-carotene, iron and zinc concentrations of 22 sweetpotato genotypes evaluated across eight environments in Zimbabwe.

		Root yield t/ha		β-carotene(mg/100g)		Iron(ppm)		Zinc(ppm)	
Source of variation	**Df**	**SS**	**MS**	**SS**	**MS**	**SS**	**MS**	**SS**	**MS**
Env	3	165482569	55160856***	17.895	5.965*	116237.7	38745.9***	4489.489	1496.496***
Rep(Env)	4	6804919	1701230	0.001	0	1360.8	340.2***	4.045	1.011
Block(Env*Rep)	8	58256777	7282097**	2089.015	261.127***	30047.1	3755.9***	106.449	13.306**
Gen	21	633907400	30186067***	5235.72	249.32***	67267.1	3203.2***	857.666	40.841***
Gen*Env	60	95982115	1599702	219.548	3.659***	98476.9	1641.3***	2867.215	47.787***
Residual	255	719197770	2820383	509.966	2	179146.2	702.5	1212.034	4.753

Env =environment, Rep(Env) =Replications nested in environments, Block(Env*Rep) =incomplete block within an environment, Gen =genotype, Gen*Env =genotype by environment interaction, df =degrees of freedom, SS =mean sum of squares, MS =mean square error, ppm =parts per million. *, **, ***indicate significance at P≤0.05, P≤0.01 and P≤0.001, respectively.

4.3.2 Genotype mean performance for root yield and nutrient content

The root yield, β-carotene, Fe and Zn mean performance of the 22 sweetpotato genotypes are presented in Table 4.4. The mean β-carotene content of the genotypes ranged between 0.0 and 13.47 mg/100 g. Genotype G17 expressed the highest β-carotene content of 13.47 mg/100 g, whilst eight genotypes, G5, G22, G3, G7, G2, G6, G10, G9, G11, G21, G1 and G8, had no β-carotene. Genotype G15 had the lowest Fe content of 50.12 ppm while the highest Fe content was recorded for genotype G18 with 108.06 ppm. Genotype G12 expressed the highest Zn content of 20.07 ppm and genotype G15 recorded the lowest Zn content. Mean root yield ranged from 1.02 t/ha (G1) to 8.38 t/ha (G3), with a grand mean RY of 6.18 t/ha, while 59% of the genotypes had mean root yield that was greater than the average. Although G3 and G19 were the highest yielding genotypes, these two were not among the top performers with respect to root β-carotene content, Fe and Zn concentrations (Table 4.4).

Table 4. 4: Mean performances for root yield, beta carotene, iron and zinc across eight environments and two growing seasons

Genotype	Yield	Rank	Genotype	Beta carotene	Rank	Genotype	Iron	Rank	Genotype	Zinc	rank
G3	8382$^{a.}$	1	G17	13.477^{a}	1	G18	108.06^{a}	1	G12	20.37^{a}	1
G19	7689^{ab}	2	G14	12.446^{b}	2	G13	96.44^{ab}	2	G20	19.69^{b}	2
G16	7458^{abc}	3	G20	11.811^{c}	3	G14	86.25^{bc}	3	G16	19.19^{c}	3
G22	7378^{a-d}	4	G19	7.661^{d}	4	G8	86.12^{bc}	4	G14	18.5^{d}	4
G2	7179^{b-e}	5	G12	7.23^{e}	5	G17	84.5^{bc}	5	G8	18.19^{d}	5
G12	6815^{b-e}	6	G16	6.41^{f}	6	G6	82.5^{cd}	6	G17	17.37^{e}	6
G4	6599^{b-e}	7	G18	6.001^{g}	7	G12	81.0^{cd}	7	G19	17.25^{ef}	7
G17	6421^{cde}	8	G15	5.66^{h}	8	G20	80.37^{cd}	8	G21	17.00^{efg}	8
G18	6385^{c-f}	9	G4	3.227^{i}	9	G22	77.87^{cd}	9	G4	16.81^{fgh}	9
G5	6383^{c-f}	10	G13	0.112^{j}	10	G16	77.19^{cd}	10	G7	16.81^{fgh}	10
G20	6361^{c-f}	11	G9	0.03^{k}	11	G3	74.5^{cde}	11	G10	16.5^{ghi}	11
G14	6212^{d-g}	12	G2	0.016^{l}	12	G10	70.0^{def}	12	G6	16.56^{ghi}	12
G11	6200^{d-g}	13	G6	0.015^{l}	13	G1	69.06^{def}	13	G22	16.44^{hi}	13
G7	6173^{d-h}	14	G10	0.015^{l}	14	G7	68.06^{def}	14	G1	16.37^{hi}	14
G15	6146^{d-h}	15	G5	0.009^{m}	15	G9	68.00^{def}	15	G18	16.31^{hi}	15
G9	6040^{e-h}	16	G7	0.005^{mn}	16	G2	62.69^{efg}	16	G13	16.19^{ij}	16
G8	6038^{e-h}	17	G22	0.004^{mn}	17	G21	58.75^{fg}	17	G5	15.75^{jk}	17
G10	5918^{e-h}	18	G8	0.004^{mn}	18	G19	58.06^{fg}	18	G3	15.44^{k}	18
G21	5153^{fgh}	19	G3	0.002^{n}	19	G5	55.81^{fg}	19	G11	15.31^{k}	19
G13	5066^{gh}	20	G11	0^{n}	20	G4	55.56^{fg}	20	G2	14.69^{l}	20
G6	4969^{h}	21	G21	0^{n}	21	G11	51.69^{g}	21	G9	14.62^{l}	21
G1	1017^{i}	22	G1	0^{n}	22	G15	50.12^{g}	22	G15	13.5^{m}	22
Grand Mean	**6181**			**3.37**			**72.85**			**16.767**	
Min	**969**			**0**			**50.12**			**13.5**	
Max	**8382**			**13.47**			**108.06**			**20.37**	
CV	**3.6**			**21.3**			**8.3**			**7.5**	
LSD	**132.65**			**0.04**			**6.47**			**3.44**	

4.3.3. Genotype x environment interaction for Fe, Zn and β-carotene using AMMI model

The combined AMMI analysis of variance revealed that G x E interaction effects were significant at ($p<0.001$) for Fe, Zn and β-carotene contents (Table 4.5). The environment effects accounted for the largest proportions of variation for Zn (38.2%) and β-carotene (47.2%). Both IPCA1 and IPCA 2 were significant ($p<0.01$) for Fe, Zn and β-carotene (Table 4.5).

Table 4. 5: AMMI analysis of variance of iron, zinc and βeta-carotene for sweetpotato genotypes evaluated across eight environments

Source of variation	Df	Iron (ppm)	Zinc (ppm)	BCC (mg/100g)	Total variation explained (%)		
		MS	MS	MS	Iron	Zinc	BCC
Genotype (G)	21	3576***	44.50***	348.01***	36.7	21.8	26.3
Environments (E)	7	15832***	505.88***	6.73***	19.3	38.2	47.2
Blocks	8	236ns	1.28***	0ns	9.4	9.4	5.4
Interactions (GxE)	147	1707***	33.9***	4.88***	12.6	14.2	6.6
IPCA1	27	3597***	77.04***	17.9***	-74.3	-71.1	-57
IPCA2	25	2574***	61.25***	5.89***	-13	-9.8	-27.5
Residuals (GxE)	95	942***	14.44***	0.91***	-5	-7.2	-11.2
Pooled error	168	320	0.39	0	-7.7	-11.9	-4.3

df =degrees of freedom, * = Significant (P< 0.05); ** = significant (P< 0.01) ***highly significant at p < 0.001 probability level, G x E = genotype by environment interaction. NOCR=Number of commercial roots, BCC= βeta-carotene content, ppm=Parts per million SS = sum of squares, MS = mean squares, IPCA = Interaction principal component axis

4.3.4. Stability analysis using yield stability index and AMMI stability value

The ASV of the genotypes across environments ranged from 1.36 for genotype G3 to 13.55 for genotype G1 (Table 4.7). Based on ASV, the most stable genotypes were G3, G19, G16, G22, G4, G5 and G2 that exhibited low ASV while genotypes such as G1, G6, G11, G10, G15, and G13 with high ASV were the least stable.

Table 4. 6: Ranking of the 22 Genotypes based on AMMI Stability Analysis Value (ASV)

Genotype	ASV	Rank
G3	1.364	1
G19	4.404	2
G16	4.581	3
G22	4.994	4
G4	5.207	5
G2	5.571	6
G5	5.884	7
G20	6.248	8
G17	6.42	9
G8	6.459	10
G7	7.179	11
G14	7.703	12
G18	7.752	13
G9	7.862	14
G12	8.762	15
G13	9.521	16
G11	9.604	17
G15	9.667	18
G10	9.698	19
G21	9.857	20
G6	9.972	21
G1	13.554	22

4.3.5 GGE biplot analysis for mega-environments and genotype response to specific and wider adaptation

Together, PC1 and PC2 explained 97.90% of the variation in the β-carotene concentration in sweetpotato (Figure 4.1). The GGE biplot analysis for β-carotene revealed two mega environments, one containing Gwebi 2021 and the other containing all the other seven environments (Figure 4.1). The seven environments did not have any vertex genotype. The genotypes G14, G17, although on the vertex did not coincide with any of the environments, while G20, although best performing in the seven environments, was not a vertex genotype.

For storage iron both PC1 and PC2 explained 66.30% of the total variation due to genotype and GxE interactions for sweetpotato storage root (Figure 4.2). The which-won-where view of GGE biplot for iron revealed four mega environments. The first mega environment consisted of Gwebi 2022 only. The second mega environment was made up of Gwebi 2021 and Makoholi 2021. The third mega

environment had Harare 2022 and Makoholi 2022, and the fourth mega environment was composed of Marondera 2022, Marondera 2021 and Harare 2021 (Figure 3). The vertex genotypes were G4 (for the first mega environment Gwebi 2022), G22 (for the mega environment Gwebi 2021 and Makoholi 2021), G12 (for the third mega environment Marondera 2021, Marondera 2022 and Harare 2021) and G14 and G2 (for the mega environment Makoholi 2022 and Harare 2022).

The PC1 and PC2 explained 76.82% of the total variation in zinc content in sweetpotato genotypes (Figure 4.3). The which-won-where view of GGE biplot for zinc revealed three mega environments: mega environment one with Harare 2021, Marondera 2021 and Harare 2022, and Marondera 2022, Makoholi 2021, Makoholi 2022, Gwebi 2021 (Figure.4). The vertex genotypes were G12 and G20 (Marondera 2022, Makoholi 2021, Makoholi 2022, Gwebi 2021), G 14 (Marondera 2021 and Harare 2022), G4 and G22 (Harare 2021).

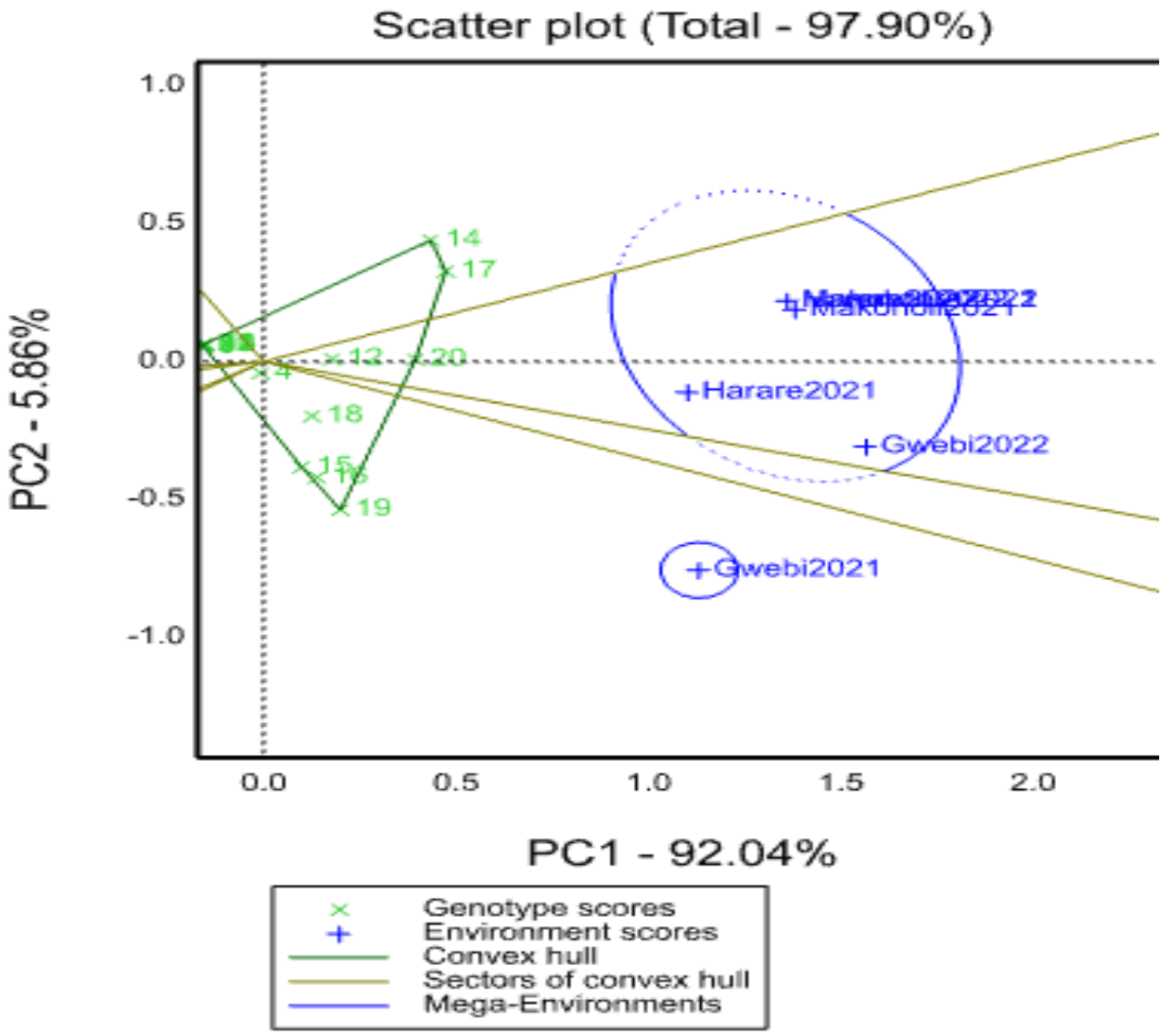

Figure 4.1: A GGE-Biplot view for β-carotene showing "which-won-where"and mega-environments.

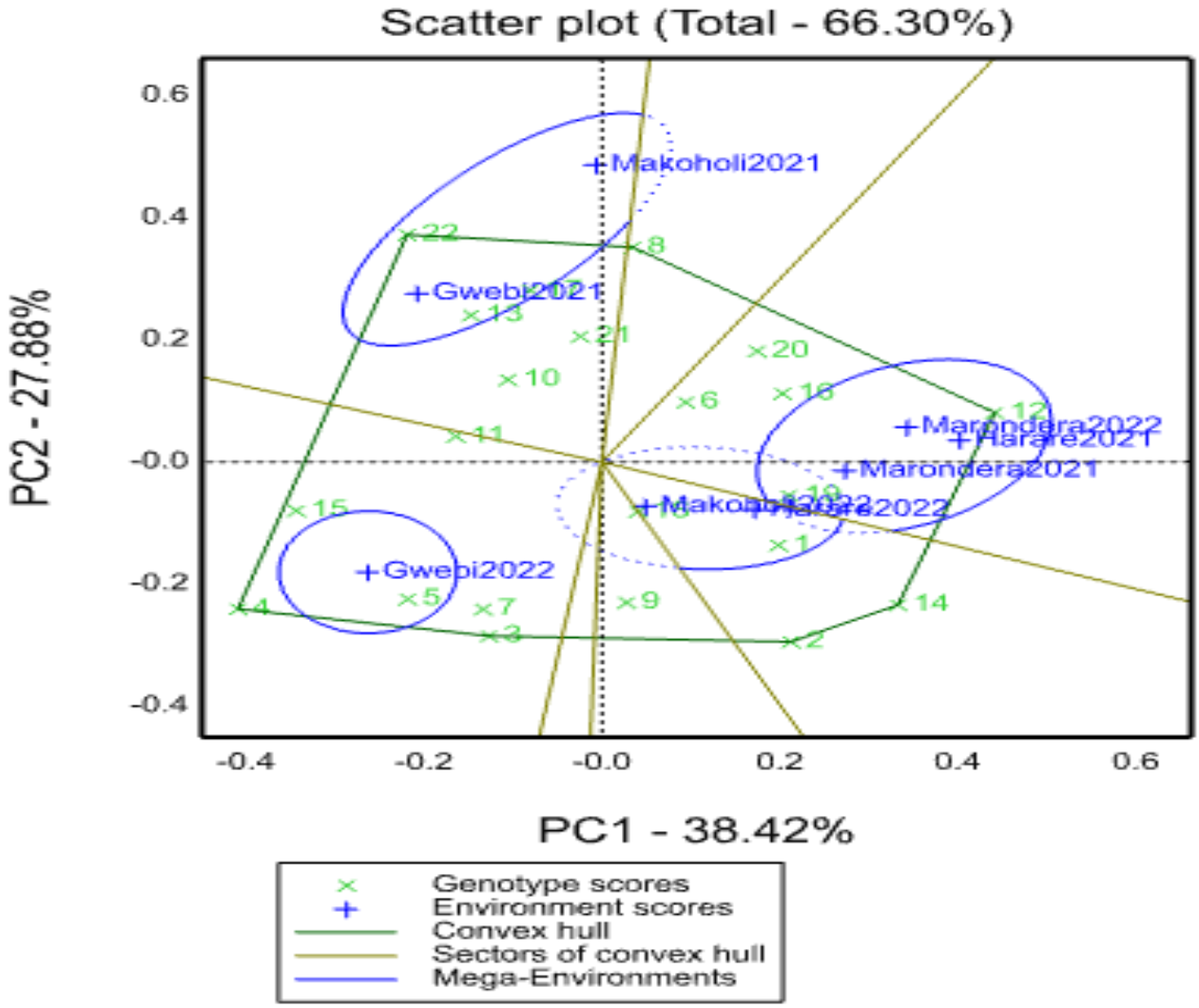

Figure 4.2: GGE-Biplot view for iron showing "which-won-where" and existence of mega-environments.

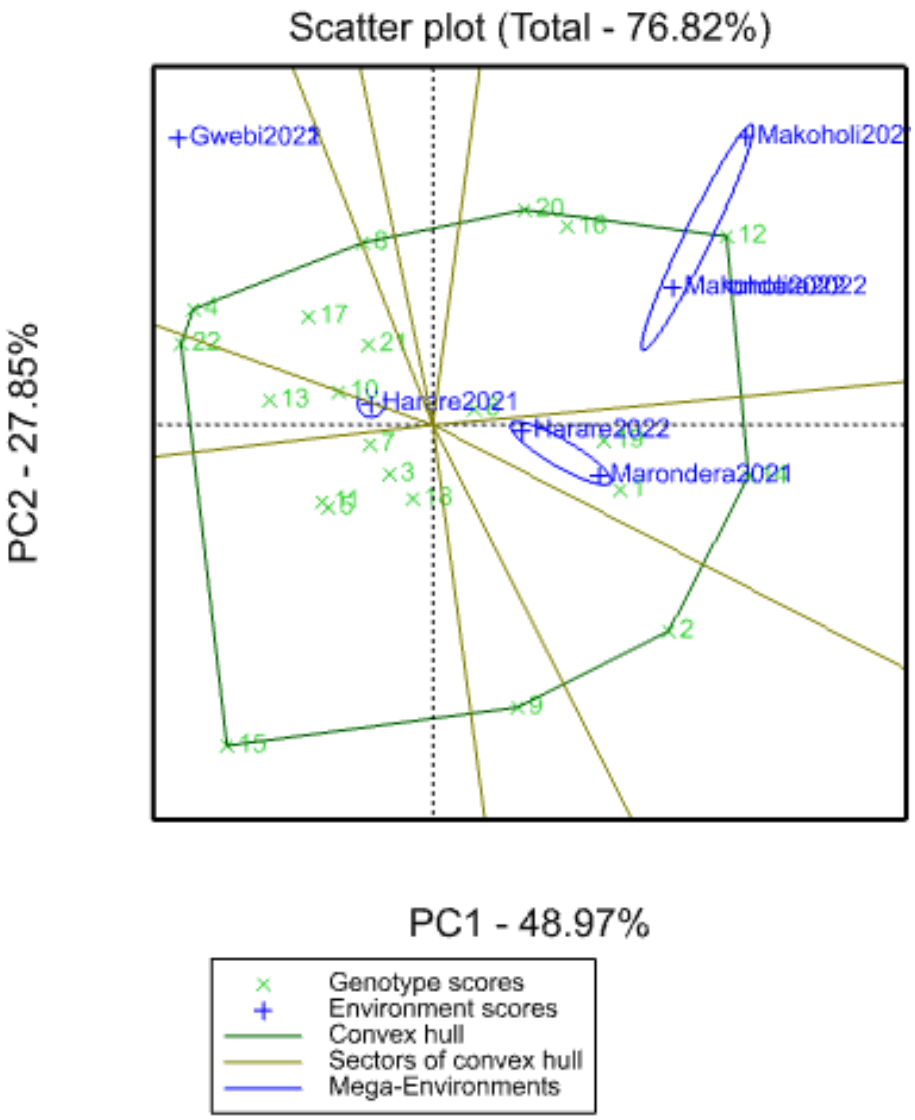

Figure 4.3: A GGE-Biplot view for Zinc showing “which-won-where” and existence of mega-environments.

4.4. Discussion`

4.4.1. Variability and genotype x environment interaction effects in root yield and micronutrient concentrations

The significant genotype variation found in this study for, β-carotene, Fe and Zn suggests that there is enough genetic variation for breeding and improving these traits. Crop improvement is hinged on availability of genetic variation for selection and population development (Wallace and Cowling, 2013). However, the significant genotype x environment interactions found could complicate the selection process. Selection should be conducted in individual locations, which increases breeding costs (Elliot et al., 2010). The interactions also offer opportunities for identifying widely adapted genotypes. Genotypes that are consistently ranked high in multiple environments are widely adapted and can be recommended for production across a wider network of environments.

In this study, the genotype-by-environment interaction (GEI) for root yield was minimal and not statistically significant, indicating that genotype rankings for root yield remained fairly consistent across different environments. As noted by Welch and Graham (2004) and Beebe (2020), such results suggest that the genetic traits influencing root yield are relatively stable across various testing conditions, leading to consistent performance of genotypes. These findings imply that reliable assessment of genotypes for root yield can be achieved using fewer testing locations, which could help reduce the overall cost of field trials.

4.4.2 Yield stability

As reported by Purchase et al. (2000), genotypes with lower AMMI Stability Values (ASV) are considered more stable across different environments. In this study, sweetpotato genotypes G3, G19, G16, G22, and G4 exhibited the lowest ASV scores for fresh root yield, indicating a high degree of yield stability across the evaluated environments. A genotype that exhibits wide adaptation has stable yield across multiple environments (Ssemakula, 2011; Brown et al., 2020). Conversely, a genotype with specific adaptation is particularly high yielding in a narrow range of environments (Brown et al., 2020).

4.4.3 GGE biplot analysis

According to Yan and Tinker (2006), the crossover genotype x environment interaction indicates that the target environments can be classified into several mega-environments, which are collections of sites that continuously share the optimal genotype set across time.

A site in a mega-environment serves as a proxy for the target environment and has the ability to distinguish across genotypes (Yan and Tinker, 2006). This is because fewer but better test conditions could yield as or more useful data on genotype performance (Yan and Holland, 2010). Compared to Gwebi, Makoholi is better at screening for drought tolerance. Consequently, under conditions of constrained financial and labor resources, this approach may considerably lower evaluation costs, improving the breeding programme's overall efficiency.

4.5. Conclusions and recommendations

The high yielding genotypes were G2, G19, G16, G22, and G3. The levels of β-carotene were high in G19, G12, and G16. For β-carotene concentration, G20 was identified as a broadly adapted genotype, showing high mean performance and stability across environments (low ASV), consistent with the GGE biplot which indicated it performed well across the seven-environment mega-environment. No genotype displayed specific adaptation for β-carotene, as vertex genotypes did not align with any environment. For storage root iron content, several genotypes G4 (Gwebi 2022), G22 (Gwebi and Makoholi 2021), G12 (Marondera and Harare 2021), G14 and G2 (Makoholi and Harare 2022) exhibited specific adaptation to distinct mega-environments in the GGE biplot, consistent with their AMMI-based stability rankings values. While these genotypes performed very well in particular environments, their stability across all environments was lower, compared to broadly adapted genotypes. Similarly, for zinc content, genotypes G12 and G20 (Marondera 2022, Makoholi and Gwebi 2021), G14 (Marondera 2021 and Harare 2022), G4 and G22 (Harare 2021) were specifically adapted to defined mega-environments. Their high performance in those environments corresponded with their AMMI rankings, highlighting strong G x E interactions that limit their broad adaptation. Different test sites had different ranks for the best genotypes in terms of iron, zinc, beta carotene. G19 and G16 are recommended for promotion in areas where both yield and nutritional quality (particularly β-carotene) are priorities, due to their consistent performance across traits. Further multi-location trials should be conducted to confirm the stability of nutrient accumulation (especially Fe and Zn) across diverse agro-ecologies. Incorporation of location-specific soil and agronomic data is recommended to guide targeted variety deployment and fertilizer recommendations. Where resources allow, farmers and extension services should adopt simple tools like color charts or mobile-based apps

for rapid assessment of root color and potential provitamin A content in the field. Breeding programmes should continue to focus on multi-trait selection, not only for yield, but also for micronutrient density while validating trait stability under different environmental conditions. Finally, on-farm participatory evaluations are recommended to assess acceptability, storage life, and cooking quality of the promising genotypes, ensuring their successful adoption by local communities.

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Chapter Five: Genetic Diversity and Population Structure of Sweetpotato Accessions (*Ipomoea Batatas* [L.] Lam.) Revealed by Single Nucleotide Polymorphism Markers

Abstract

Use of molecular markers has improved the analysis of genetic variation by eliminating environmental influences on genotype performance. The objective of this study was to assess the genetic diversity and population structure of 327 sweetpotato genotypes sourced from the major sweetpotato-growing regions of Zimbabwe and from the International Potato Centre (CIP) in Mozambique using low-density Diversity Array Technology (DArTseq) SNP chip covering the 90 chromosomes of sweetpotato. The genetic diversity (GD) varied from 0.12 to 0.50, with a mean of 0.36. The mean polymorphic information content (PIC) was 0.29. There was a good representation of minor alleles within the population, with an average minor allele frequency (MAF) of 0.34. The average observed heterozygosity of 0.12 was consistent with the cross-pollinating system in sweetpotato yet could perpetuate a narrow genetic base. There was limited interbreeding between the populations of sweetpotato, as indicated by a mean fixation index (F) of 0.68. The high F values indicated that most alleles per genotype were contributed by one parent, which is unusual in allogamous species such as sweetpotato. The sweetpotato genotypes in this study were clustered into two sub-populations with significant differences within the sub-populations. Genetic variation among genotypes is essential for the improvement of sweetpotato.

Keywords: Genetic diversity, genotyping, SNP markers, Sweetpotato, Polymorphic Information Content

5.1. Introduction

Sweetpotato (*Ipomoea batatas* [L.] Lam.) is an important root crop used for food, feed, and biofuel. The importance of sweetpotato has increased due to the rising prices of staple food crops such as maize (*Zea mays*), wheat (*Triticum aestivum L*), rice (*Oryza sativa*), and Irish potato (*Solanum tuberosum*) (Sapakhova et al., 2023). Although its high biomass on fresh weight basis and adaptability to diverse production environments make it ideal for production in marginal environments (Chiona 2009; Cole et al., 2014), nevertheless, several biotic (viruses and weevils) and abiotic (drought, low soil fertility) factors still challenge its production.

In addition, a lack of improved varieties for production has led to low average yields of 5 t/ha attained by farmers against a potential of 23-25 t/ha (van Vugt and Franke, 2018). Many smallholder farmers still cultivate landraces and varieties that have low yield potential (Eriksson et al., 2018). However, landraces can serve as valuable sources of genes for adaptation to certain biotic and abiotic stresses, although improved varieties may also possess stress-resilient traits through targeted breeding. Incorporating landraces in breeding programmes can broaden the gene pool for crop improvement but must be followed by effective and efficient selection for high yield and desirable agronomic performance (Lazaridi et al., 2024). Therefore, understanding the available genetic variation and population structure is imperative for devising suitable breeding strategies.

To evaluate genetic variation for significant traits and assess the population structure for conservation purposes, morphological and molecular markers have been employed (Emanuelli et al., 2013). Molecular markers are particularly useful for evaluating genetic diversity and relatedness among various genetic resources. To assess genetic variation in sweetpotato, several marker types have been used, such as simple sequence repeats (SSRs) or microsatellites (Butler et al., 2002; Gichuru et al., 2006; Koussao et al., 2014; Ngailo et al., 2016), inter-simple sequence repeats (ISSRs) (Huang and Sun, 2000), random amplified polymorphic DNA (RAPD) (Gasura and Mukasa, 2011; Maquia et al., 2013), amplified fragment length polymorphism (AFLP) (Zhang et al., 2000; Elameen et al., 2008), selective amplification of microsatellite polymorphic loci (SAMPL) (Yu-Tien Tseng et al., 2002) and single nucleotide polymorphisms (SNPs) (Arif et al., 2010). Single nucleotide polymorphisms (SNPs) markers, in particular, facilitate genetic studies because they are amenable to automation and are highly reproducible (Jehan and Lakhanpaul, 2006) compared to the other markers. However, most of these advanced marker systems have been more extensively applied in other crops, with relatively fewer studies conducted specifically on sweetpotato.

The Crop Breeding Institute (CBI) in Zimbabwe aims to improve sweetpotato varieties in nutritional and processing quality, and to meet market preference. The programme is new and sourcing different germplasm within and outside Zimbabwe warranting genetic diversity studies. Therefore, this study aimed to assess the population structure and genetic diversity of local and introduced sweetpotato genotypes in Zimbabwe using SNP markers. The study will contribute to baseline information required to inform breeding efforts for sweetpotato improvement in Zimbabwe and its germplasm exchange partners.

5.2. Materials and Methods

5.2.1 Plant material

A total of 327 sweetpotato genotypes were used in this study (S1 Table). The genotypes consisted of landraces collected from the major sweetpotato-growing regions of Zimbabwe (Fig.5.1) and 181 genotypes from the International Potato Centre (CIP) in Mozambique. From Zimbabwe, 89 landraces were collected from Mashonaland East, 27 from Manicaland, 16 from Masvingo, and 10 from Mashonaland Central provinces. The genotypes were grouped based on their geographic region for further analysis, with the other groups being composed of genotypes obtained from CIP-Mozambique as one group and the other group genotypes sourced in Zimbabwe. The group of genotypes from Zimbabwe was further subdivided into four sub-populations based on the province from which they were collected.

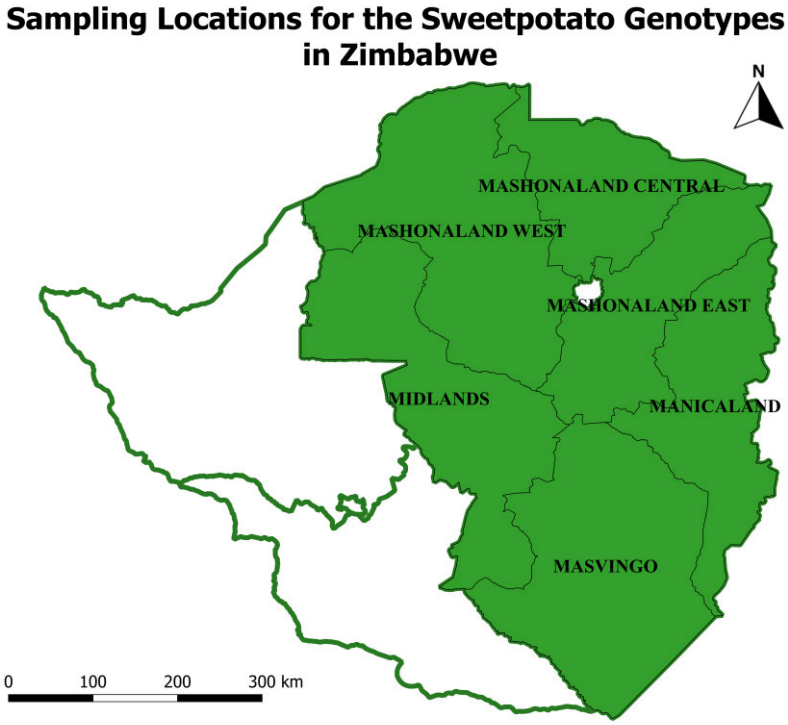

Figure 5.1: Provinces of Zimbabwe (shaded) representing regions from which sweetpotato genotypes were sampled.

5.2.2 Leaf sampling and shipment

Fresh leaf samples were collected from 3-week-old seedlings of each genotype for deoxyribonucleic acid **(**DNA) extraction. Supplementary information S3 provides the leaf sampling, drying, packaging, and shipment protocol used in this study as guided by Intertek laboratory in Sweden https://www.intertek.com/agriculture/testing/. Four leaf disks were punched out for each accession using a leaf-cutting punch. To avoid cross-contamination between accessions, 70% alcohol was used to sterilize the puncher. Sampled leaf discs were oven-dried at 35^{o}C for 24 hours, and the plates were immediately secured with lids after drying. The sampling plates were packaged and shipped to the Intertek laboratory in Sweden https://www.intertek.com/contact/ema/sweden/. The samples were genotyped on a low-density Diversity Array Technology (DArTseq) SNP chip covering the 90 chromosomes of sweetpotato. Diversity Arrays Technology Single Nucleotide Polymorphism (DArT SNP) markers were aligned to the reference genomes of wild sweetpotato *Ipomoea Trifida v.3.*

5.2.3 Data filtering and SNP calling

The snpReady software was used to filter the first 37 SNPs from the genotyping-by-sequencing (GBS) pipeline by eliminating SNPs with 20% missing data and less than 5% minor allele frequency (MAF) (Italo 2018). Individual genotypes with missing data, more than 20% were eliminated. SNPs with a

MAF of 0.05 and a call rate of 80% or above were kept. As a result, analysis was conducted using 327 genotypes and 30 SNPs and of the 30 twenty-seven were polymorphic (Table 5.3).

5.2.4 Data analysis

The Nei and Li (1979) technique was used to calculate the number of alleles per locus, the number of effective alleles per locus, Shannon's Information Index, and gene diversity. An analysis of molecular variance (AMOVA) was conducted to partition total genetic variation within and among the different groups of the genotypes using GenAlex version 6.5. and R studio version 4.3.0 (Peakall and Smouse 2012). Population structure analysis was performed using the Structure software version 2.3.4 (Pritchard et al., 2009).

The burn-in period and the Markov Chain Monte Carlo (MCMC) replications were set at 10,000. The Structure analysis was done for K ranging from 1 to 10 with 5 iterations at each K to determine the optimum number of clusters. The ideal K value was identified using the Evanno method, which relies on ΔK (Evanno et al., 2005).

Genetic diversity parameters such as expected heterozygosity (He), overall genetic diversity (GD), polymorphic information content (PIC), major allele frequency, and the inbreeding coefficient (Fis) were calculated. In addition, pairwise genetic distances and the kinship matrix among the 327 sweetpotato genotypes were assessed. These analyses were conducted using GenAlex version 6.5 and R Studio version 4.3.0. The principal coordinate and cluster analysis were carried out using the KDCompute platform. A dendrogram was then generated on the dissimilarity matrix using the Gower's Ward.D2 hierarchical clustering method.

5.4 Results

5.4.1 Analysis of molecular variance

The analysis of molecular variance (AMOVA) among the 327 sweetpotato genotypes showed that all the variance observed was due to genotypic differences within the two populations (Table 5.1). The expected heterozygosity of genes within populations was 0.09 for population I and 0.15 for population II (Table 5.2). The corresponding fixation indices (F_{ST}) for both populations I and II were 0.08. The estimated Wright's fixation index (PhiPT max) of 0.591 and 0.291 were obtained for sub-populations I and II, respectively.

Table 5.1: Analysis of molecular variance of sweetpotato populations based on 30 SNPs

Source	Df	SS	MS	Est. Var.	%
Among Pops	1	9.391	9.391	0.029	0%
Within Pops	324	1951.367	6.023	6.023	100%
Total	325	1960.758		6.052	100%

df = degree of freedom, SS = sum of squares, Est.Var = estimated variance, % = percentage variation

Table 5.2: Expected heterozygosity, fixation indices and membership of the two populations found among the 327 genotypes assessed with SNP markers

	FST		He	Mean Wright Fst	No of genotypes	Membership
I	-	0.08	0.09	0.59	250	0.75
II	0.08	-	0.15	0.29	77	0.25

FST= allele frequency divergence among subpopulations; He=expected heterozygosity

5.4.2 Genetic parameters of the markers and genotypes

The PIC for the markers ranged from 0.11 to 0.37, with an average of 0.29 for the 30 SNP markers (Table 5.3). The most informative markers were snpIB00001, snpIB000010, snpIB00012, snpIB00032, and snpIB00051, while snpIB00057 was the least informative. The minor allele frequency ranged between 0.3 and 0.5, averaging 0.26. The average expected heterozygosity (He) and observed heterozygosity (Ho) were 0.12 and 0.36, respectively. The marker snpIB00032 had the maximum heterozygosity of 0.69. The maximum Nei genetic diversity index was 0.5 and the minimum was 0.12, with an average of 0.36 (Table5.3).

Table 5.3: Genetic diversity parameters revealed by 30 SNP markers among the 327 sweetpotato accessions.

SNP_Name	Chr	Position (ref. *Ipomoea trifida v.3*)*	Allele	MAF	PIC	Allele No	Ho	He	Nei
snpIB00031	1	24315805	C/T	0.22	0.28	2	0.02	0.34	0.34
snpIB00032	1	31682527	C/T	0.49	0.37	2	0.69	0.5	0.5
snpIB00021	2	6247633	T/G	0.19	0.26	2	0.09	0.3	0.3
snpIB00027	2	13184152	G/T	0.24	0.3	2	0.02	0.37	0.37
snpIB00035	3	12595421	C/G	0.07	0.12	2	0.02	0.13	0.13
snpIB00026	3	24217089	A/T	0.29	0.33	1	0	0.41	0.41
snpIB00036	4	8685123	C/T	0.25	0.31	2	0.13	0.38	0.38
snpIB00037	4	29217872	A/G	0.14	0.21	2	0.01	0.24	0.24
snpIB00038	5	738566	C/T	0.1	0.16	2	0.02	0.17	0.17
snpIB00040	6	13312429	A/C	0.37	0.36	2	0.05	0.47	0.47
snpIB00030	6	19672316	G/C	0.09	0.16	2	0.08	0.17	0.17
snpIB00042	7	969986	A/T	0.39	0.36	1	0	0.48	0.48
snpIB00043	7	17963596	C/T	0.27	0.32	2	0.06	0.39	0.39
snpIB00029	7	23485155	T/G	0.2	0.27	2	0.1	0.32	0.32
snpIB00044	8	3253902	C/T	0.34	0.35	2	0.47	0.45	0.45
snpIB00045	8	3449546	C/T	0.19	0.26	2	0.05	0.31	0.31
snpIB00001	8	6218106	A/G	0.42	0.37	2	0.01	0.49	0.49
snpIB00046	9	437404	C/T	0.23	0.29	2	0.03	0.36	0.36
snpIB00010	10	4446069	G/A	0.5	0.37	2	0.03	0.5	0.5
snpIB00049	10	22810642	G/T	0.23	0.29	2	0.02	0.36	0.36
snpIB00050	11	1435859	A/G	0.11	0.18	1	0	0.2	0.2
snpIB00051	11	5905491	G/T	0.47	0.37	2	0.03	0.5	0.5
snpIB00012	12	1719732	C/A	0.47	0.37	2	0.61	0.5	0.5
snpIB00052	12	8660781	A/G	0.28	0.32	2	0.06	0.4	0.4
snpIB00053	12	23669355	A/T	0.25	0.3	2	0.01	0.37	0.37
snplB00054	13	221791	C/G	0.23	0.29	2	0.04	0.36	0.36
snpIB00056	14	16102914	C/T	0.3	0.33	2	0.53	0.42	0.42
snpIB00057	14	18292043	C/G	0.06	0.11	2	0.02	0.12	0.12
snpIB00058	15	619627	A/G	0.2	0.27	2	0.02	0.32	0.32
snpIB00060	15	7544880	C/T	0.34	0.35	2	0.25	0.45	0.45
Minimum				0.06	0.11	1	0.23	0.12	0.12
Maximum				0.5	0.37	2	0	0.5	0.5
Mean				0.26	0.29		0.12	0.36	0.36

MAF = Minor allele frequency, PIC = Polymorphic information content, Ho = Observed heterozygosity, He = Expected heterozygosity, Nei = Nei genetic distance

The genotypes' genetic diversity (GD) varied from 0.12 to 0.50, averaging 0.36 (Table 5.4). The polymorphic information content (PIC) showed a broad range from 0.11 to 0.37, with a mean of 0.29. The minor allele frequency (MAF) spanned from 0.06 to 0.50, averaging 0.34. Observed

heterozygosity ranged from 0.00 to 0.23, with a mean of 0.12. The Fixation index (F) had a mean of 0.68, ranging from 0.36 to 1.00 (Table 5.4).

Table 5.4: Genetic parameters of 327 sweetpotato genotypes measured with 30 SNP markers.

Statistics	GD	PIC	MAF	Ho	FST
Mean	0.36	0.29	0.26	0.12	0.68
Lower	0.12	0.11	0.06	0.00	0.36
Upper	0.50	0.37	0.50	0.23	1.00

MAF=minor allele frequency, GD=gene diversity, PIC=polymorphic information content, Ho=observed heterozygosity, FST=Fixation Index.

5.4.3 Population structure as revealed by SNP markers

The highest Evanno's ΔK value occurred at K=2 (Fig 5.2). The scree plot shows a significant drop in ΔK after K=2 and all the other values of K show no change in ΔK in the scree plot, confirming that K was optimal at 2. The two populations were divided into the largest group with 250 genotypes and the smaller group with 77 genotypes (Fig. 5.3). The distribution of the genotypes into clusters was based on kinship. Very few individual genotypes exhibited kinship to both groups. Different colours represent separate clusters, while the length of the coloured segment shows the estimated proportion of the membership of a genotype in a particular population.

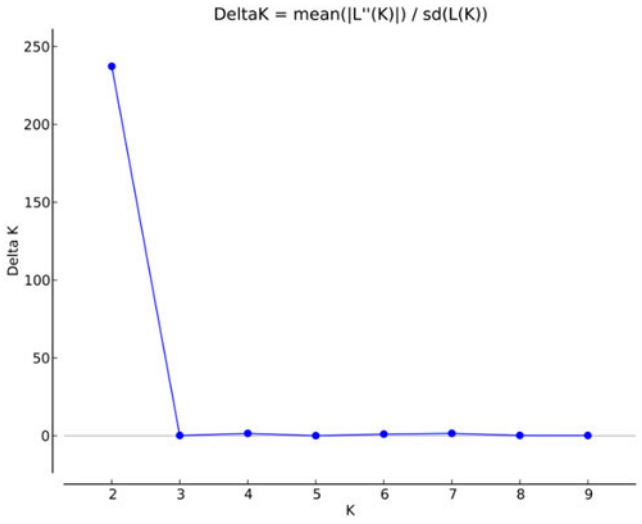

Figure 5.2: A scree plot showing the Delta K values for number of clusters determined among 327 sweetpotato genotypes measured using 30 SNP markers

Figure 5.3: Population structure of 327 sweetpotato genotypes based on 30 SNP marker

5.4.4 Cluster analysis of the genotypic data for the 327 genotypes

The neighbor-joining dendrogram clustered the 327 genotypes into five clusters: C1, C2, C3, C4, and C5 based on the SNP markers (Fig.5.4). The biggest cluster was Cluster 2, which comprised 52% of the genotypes. The next biggest cluster was Cluster 3, with 22%, and Cluster 1, with 13%. Clusters 4 and 5 were the smallest, with 10 and 3% membership, respectively. The names of individuals belonging to each cluster are provided in Supplementary Table S2.

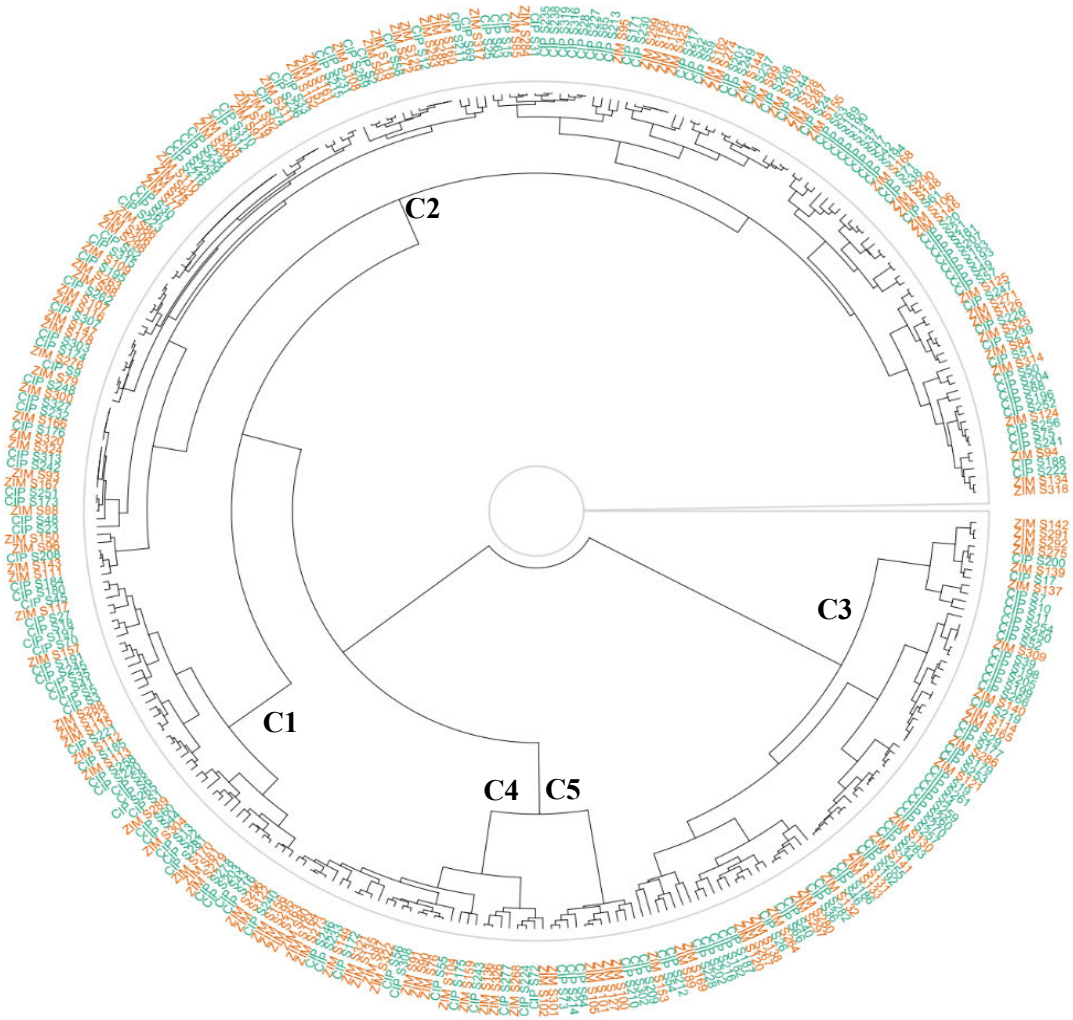

Figure 5.4: Neighbor-joining dendrogram showing the clustering of 327 accessions genotyped with SNP markers. C1-5=cluster 1 to 5

5.4.5 Principal coordinate clustering

The principal coordinate analysis (PCoA) showed variability among sweetpotato accessions based on the 30 SNP markers. The two PCs on the PCoA biplot accounted for 90% of the genotype variation (Fig 5.5). The genotypes from CIP-Mozambique were mostly clustered in the bottom two quadrants, while the genotypes from Zimbabwe were scattered in the top quadrants. The genotypes from Zimbabwe did not show further clustering by their source province.

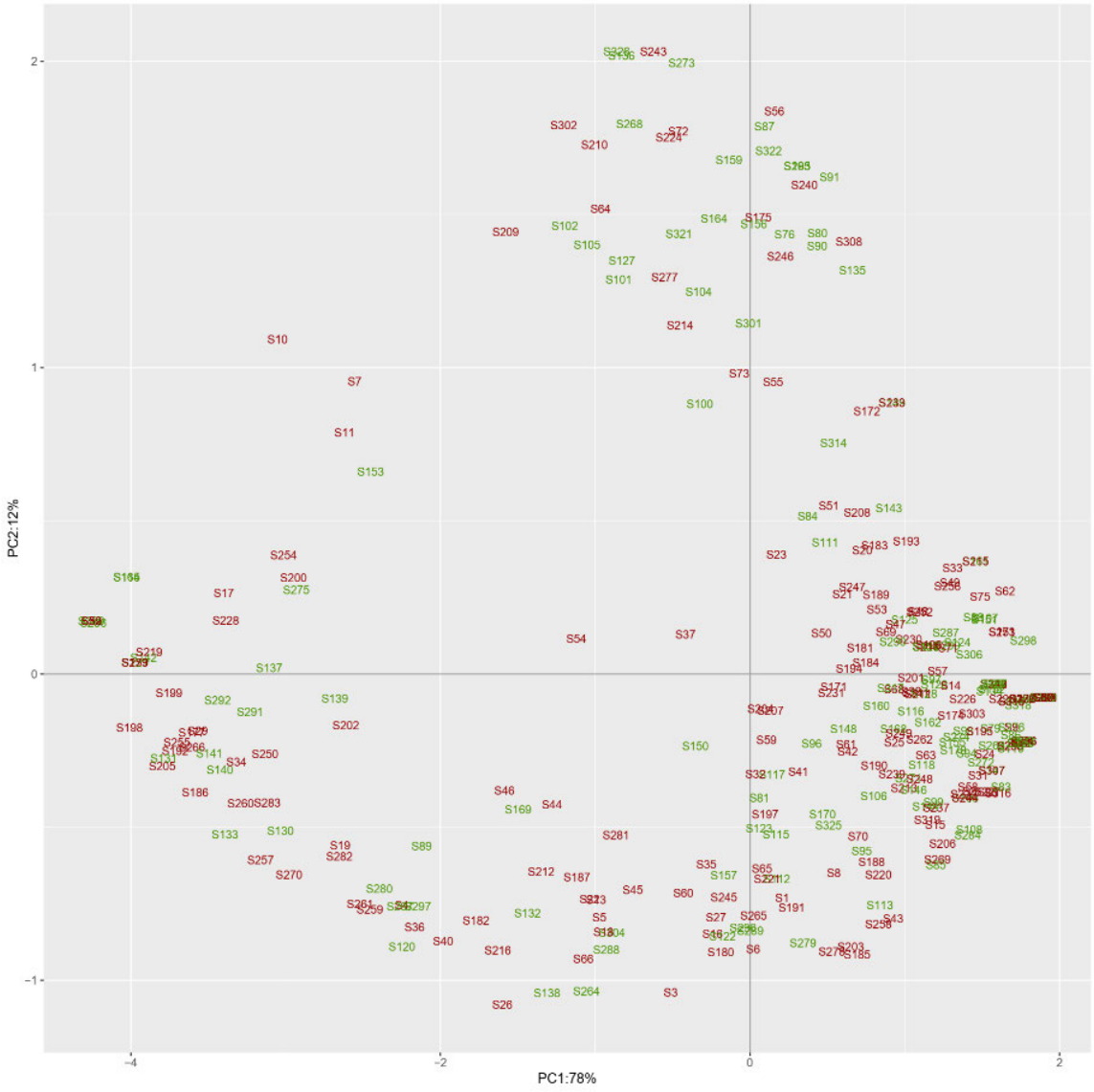

Figure 5.5: Principal coordinate analysis showing variability among sweet potato accessions from different regions in Zimbabwe based on 30 SNP markers.

5.5 Discussion

The average PIC value of 0.29 is regarded as moderate to high for SNP markers. Values above 0.25 are typically considered meaningful for genetic diversity research since biallelic SNPs have a maximum PIC of 0.50 (Botstein et al., 1980; Baloch et al., 2017). As a result, the SNP markers employed here showed adequate discriminatory power to evaluate genetic variation and successfully distinguish between the genotypes. Usually, bigger sets of markers may have higher resolution. Smaller sets of markers can offer some advantages by balancing accuracy and cost-effectiveness in

breeding programmes. Given that the markers are SNP, small and negligible errors can occur compared to a larger data set but it is more affordable and provides useful information for characterization and identifying variation. The 30 markers used in this study were selected for genome coverage, threshold on missing values, chromosome position, genetic distances, and validation in progeny. The markers used in this study were highly informative based on high PIC values and MAF. For the purposes of broad characterization, the markers were sufficient because the sweetpotato genotypes were diverse and being a hexaploid. Gemenet et al. (2020) used 30 SNP in a quality control study and found that the small number of markers was sufficient with only a 4% difference compared to using 300 markers. The PIC values and expected heterozygosity (He) are indicators of genetic diversity within breeding populations, evolutionary pressures, and mutation rates at specific gene locations (Botstein et al., 1980; Shete et al., 2000). PIC values are particularly helpful in linkage analysis, indicating how well markers track inheritance between parents and offspring (Zhang et al., 2016). Though SNPs have lower PIC values due to their bi-allelic nature compared to SSR markers, they offer higher resolutions for genetic differentiation among genotypes because they detect differences at specific loci (Helyar et al., 2011; Suvi et al., 2020). The three markers that showed higher polymorphisms can be used in the future genotyping of sweetpotato clones to identify distant parents for developing and deploying varieties. The markers with low PIC may still be linked to important traits or regions of interest. Low PIC of a marker does not discount its potential value in genetic studies (Gupta et al., 2001).

This study's heterozygosity (Ho) mean of 0.12 was very low, suggesting that the sweetpotato genotypes were highly homozygous. This is unusual for sweetpotato since it is allogamous. Sweetpotato is a hexaploidy with generally high heterozygosity for most loci (Monden and Tahara, 2017; Lindqvist-Kreuze et al., 2024). However, most sweetpotato genotypes in Zimbabwe produce sterile flowers due to unfavorable photoperiodicity and altitude. As such, sweetpotato is predominantly reproduced vegetatively and cloned, which could have caused the low level of heterozygosity (Gurmu et al., 2013). Low heterozygosity and high inbreeding coefficient (F) values are better understood as representing the distinct genetic makeup of the sampled germplasm, which was influenced by clonal propagation as opposed to intrinsic self-fertilization. Prior research has documented similar trends, attributing low genetic diversity in sweetpotato collections to vegetative propagation, rather than reproductive biology (Roullier et al., 2013; Mabaya et al., 2025). These results highlight the difficulty of interpreting diversity measurements in clonally generated polyploids, even though they would seem unusual for a self-incompatible, outcrossing species like sweetpotato. In contrast, other reports have shown high heterozygosity in sweetpotato (Monden and Tahara, 2017; Lindqvist et al., 2024).

Ultimately, the lack of heterozygosity in the study genotypes could pose a serious bottleneck for breeding and can threaten sweetpotato production should new biotic and abiotic stresses emerge. Low levels of heterozygosity are often associated with limited genetic variation for resistance to emerging biotic or abiotic stresses (Baafi et al., 2016). The study showed that the inbreeding coefficient (FIS) varied widely and had a high mean value, indicating that the genotypes in the population underwent significant inbreeding. The F value estimates the likelihood that two alleles at every locus within an organism are descendants of the same parent (Wright and Adams, 2012). High F values in the study indicated that one parent contributed the most alleles per genotype. This further emphasizes that most genotypes were clones or developed from self-pollination, where the same parent contributes all the chromosomes to the offspring. This is common in sweetpotato, which suffers from a lot of cross-incompatibility. Ultimately, there are high levels of inbreeding (Gurmu et al., 2013). Due to a lack of diversity within individual genotypes, inbreeding could lead to suppressed yield potential or unfavorable nutritional content.

Generally, with some exceptions, genotypes were randomly allocated to different groups and subgroups. Some closely related genotypes were grouped into the same cluster or sub-cluster (cluster 2), confirming the existence of a relationship between the pedigree and SNP marker groupings in this study. Some of these genotypes appeared to be clustered according to the pedigree group (DOF/31, DOF/34, DOF/52, DOF/53, DOF/56, DOF/61, DOF/63, DOF/64), but there were some inconsistencies. For instance, Chemugomo, Masvingo 8, Hwedza 2, DOF/37, and Murehwa clustered together in cluster 5 despite being unrelated by pedigree. Similar findings of genotypes clustering according to their pedigree grouping were earlier reported (Dhliwayo et al., 2009; Semagn et al., 2012; Yang et al., 2017).

Genotypes were not clustered based on geographical location, which could be due to the exchange of genetic material in geographical regions. Therefore, crossing more distant sweetpotato genotypes might create wider genetic variation and exploit heterosis during breeding for new varieties (Molin et al., 2013). The molecular variability indicated that genetic variation existed only between genotypes within populations, and no variation was observed between different populations.

This might be attributed to the limited number of markers that were used in this study. On the other hand, the exchange of genetic material among the sources means that there is potentially no differentiation based on the collection areas. Consequently, the observed relationships among genotypes within each sub-population could be exploited to design an effective sweetpotato breeding programme in Zimbabwe.

5.6 Conclusion and recommendations

The underlying genetic diversity and population structure in the sweetpotato introductions from CIP and local germplasm can potentially be exploited for improving sweetpotato cultivars in Zimbabwe and other countries with similar germplasm. The SNP markers used in this study were polymorphic and exhibited discriminating capability to diagnose allelic differences among the 327 genotypes. The sweetpotato genotypes were genetically divergent, providing adequate allelic diversity for recombination. Genotypes such as G40 and G9, G142 and G73, G114 and G73, I40 and G210, and G18 and G114 were distantly related and could be useful parents for recombination and developing breeding populations.

5.7 Supplementary Information

S1: List of Genotypes used in the study

S1 List of genotypes used in the study.xlsx

S2: List of genotypes in sub-clusters

S2 List of genotypes in clusteers.xlsx

S3: Intertek sampling, drying and shipment protocol

AGT401 Intertek General Leaf Samplinç

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Chapter Six: Genetic Analysis of B -Carotene Content, Root Yield and Yield-Related Traits in Sweetpotato (*Ipomoea Batatas* [L.] Lam)

Abstract

Information on the inheritance of traits in new sources of germplasm is important in devising breeding strategies for the development of superior genotypes in any breeding programme. The objective of this study was to determine the gene action and combining ability effects for storage root yield, yield-related traits, and β-carotene concentration in newly generated sweetpotato families. Sixteen sweetpotato families developed from a 4 x 4 North Carolina mating Design II and their 8 parents were evaluated in a 6 x 4 lattice design with two replications in three different locations in Zimbabwe. Highly significant differences were observed among families across the three test environments for the number of commercial roots ($p < 0.01$) and β-carotene content ($p < 0.001$). Crosses of Magutse x O-105, Kau 4 x O-105 and Kau 4 x O-103 had the best mean root yields of 26.97, 22.53 and 22.02 t ha^{-1}, respectively. The highest β-carotene content was recorded for the crosses Dube x O-104, Kau 4 x O-105 and Dube x O-105 with means of 11.49, 10.83 and 10.05 mg/100 g, respectively. The general combining ability (GCA) effects of parental genotypes O-103 and P 201 were high and positive for the number of commercial roots, storage root yield and harvest index. The parent with the best GCA effects for β-carotene content was O-104. The SCA effects of families were significantly different for all traits. The narrow-sense heritability ranged from 0.61 to 0.90. High broad-sense heritability values of 0.93 and 0.85 were obtained for β-carotene content and (total commercial root number), respectively. The findings indicate that both additive and non-additive gene effects are important for storage root yield and β-carotene content. This implies that recurrent selection would be effective as a breeding strategy in improving these traits. The parental genotypes O-104, O-105 and P-201 and the families, Red jewel x O-105 and Magutse x O-105 were selected for developing breeding populations for improving β-carotene content and storage root yield.

Keywords: Combining ability, heritability, orange fleshed sweetpotato, gene action, general combining ability, specific combining ability.

6.1 Introduction

Sweetpotato is the third most important root crop after cassava and yam (Muoneke and Ukpe, 2010). It is high in starch, micronutrients and relatively more drought tolerant than cereals, which makes it ideal for production under marginal environments. The high nutritional value serves as a source of energy, calcium, iron, vitamins and some minerals (Nkhata et al., 2020) and makes the crop essential in addressing micronutrient deficiencies for many people in developing countries. The orange-fleshed range-fleshed sweetpotato varieties with high β-carotene content are particularly important for supplementing vitamin A (Mashavakure et al., 2025) Therefore, developing varieties with enhanced nutritional content is important and requires genetic variation for nutrients and yield traits.

Genetic variation can be created through hybridization of diverse parents for the traits to be improved. In breeding programmes, initial evaluation of genotypes identifies superior genotypes with favorable traits that can be used as parents. However, superior genotypes do not always transfer their preferable traits to the progeny. Several factors including genetic, environmental and cross-compatibility affect the transfer of traits to offspring during reproduction. The phenomenon is known as combining ability and can be investigated to identify superior genotypes and their offspring (Falconer and Mackay, 1996; Acquaah, 2012). General combining ability (GCA) effect is the average performance of a genotype in a series of cross combinations, while specific combining ability (SCA) effect is the performance of a cross combination that deviates from that expected based on the general combining abilities of the parents involved in the cross (Begna, 2022). Non-additive gene action, such as dominance or epistasis, is responsible for the SCA effects, while additive gene action is responsible for the GCA effects (Acquaah, 2009).

Depending on how important GCA and SCA effects are for a given trait, gene action influencing the traits can be either additive or non-additive (Acquaah, 2009). Additive gene action is heritable in the following generation, as it correlates with narrow sense heritability and is the most significant component of genetic variance for selection. Combining ability and gene action can be determined using different mating schemes. North Carolina Design II (NCD II), polycross, and diallel are some of the popularly used mating designs (Chiona, 2009; Ngailo et al., 2016; Kagimbo et al., 2019). The reproductive system of the species under study and the goals of a breeding programme have an impact on the choice of mating design. In sweetpotato breeding, North Carolina mating design II is one of the designs that is most frequently utilized (Kagimbo et al., 2019). In this experimental design, the genotypes of two distinct groups of parents, one group consisting of male parents and the other of

female parents are crossed using a factorial mating scheme to systematically evaluate all possible combinations between the two groups.

The mean square values for males and females, respectively, can be used to estimate the GCA effects of the two parents in this design. Likewise, the SCA effects of families can be directly estimated from male x female interaction (Kagimbo et al., 2019). The magnitude of GCA and SCA effects for traits vary with mating design and germplasm. Chiona (2009) and Balcha (2015) found significant GCA and SCA effects for root yield and concluded that it was controlled by both additive and non-additive gene effects. For β-carotene content, additive gene effects were preponderant due to the high GCA effects observed (Oduro, 2013). Root yield was under additive gene control as reported by Balcha (2015).

While studies by other researchers provide useful guidelines in improving the traits, it is imperative that genetic analyses be conducted for every germplasm intended for breeding because combining ability varies with genotype and environmental factors and the breeding strategy employed. Therefore, the objectives of this study were to evaluate the combining ability effects of parents and families, and to determine the mode of gene action controlling β-carotene content, root yield and its components in sweetpotato germplasm maintained at the Crop Breeding Institute (CBI). The genotypes included introductions from the International Potato Center (CIP) that are being used to widen the gene pool in improving yield and nutritional content of sweetpotato.

6.2. Materials and methods

6.2.1 Plant materials

Eight parents (Table 6.1) selected based on high β-carotene content, flowering ability and high root yield were used to generate the crosses. These included four male parents (0-103, 0-104, 0-105, P-201), which were orange fleshed obtained from the International Potato Centre (CIP) and four female parents (Magutse, Red Jewel, Kau 4, Dube), which were white fleshed adapted to local growing conditions. Crosses were generated at the Harare agricultural research institute in a greenhouse during the 2022 season using a 4 x 4 North Carolina Design II mating design resulting in 16 families.

Table 6.1: Description of the selected eight sweetpotato parents used in the study

No.	Parent	Source	Root Flesh Color	Avg Root yield t/ha	Avg β-carotene content as µg/100 g
G1	O-103	CIP-Mozambique	OF	19.92	4.69
G2	O-104	CIP-Mozambique	OF	11.80	11.80
G3	O-105	CIP-Mozambique	OF	13.67	13.67
G4	P-201	CIP-Mozambique	OF	20.70	20.70
G5	Magutse	Local landrace	WF	11.38	0.00
G6	Red Jewel	Local landrace	WF	6.02	0.00
G7	Kau 4	Local landrace	WF	6.04	0.00
G8	Dube	Local Land race	WF	9.38	0.00

CIP = International Potato Center Avg=Average, OF=Orange flesh, WF=White flesh

6.2.2. Generating the F1 hybrids

A crossing block was established at the Harare agricultural research institute in January 2022. The eight parents were grown in 20-liter plastic pots. The plants received four weekly irrigations, and one month after planting, 233 kg/ha of fertilizer containing nitrogen, phosphorus, and potassium (23:10:5) was administered. Weeds were hand pulled

F_1 hybrid sweetpotato seeds were generated through controlled hand pollination. Flowers were manually pollinated in the early morning between 6:00 am and 10:00 am, when floral receptivity was highest, and subsequently tagged and labelled. Mature pollen was collected from dehiscing anthers of the designated male parent using a fine brush and immediately applied to the stigma of the emasculated female parent. Emasculation involved the careful removal of anthers from the female flower prior to pollen release to prevent self-pollination.

To ensure isolation and prevent unintended pollination, flower buds of both male and female parent plants were enclosed in fine-mesh pollination bags before anthesis, excluding insects and external pollen. The bags were temporarily removed during hand pollination and replaced immediately thereafter. Pollinated flowers were re-bagged and monitored until capsule maturity. Mature capsules were harvested, and the dried seeds were stored in labelled paper envelopes.

6.2.3. Preparation of seeds, growing seedlings and progeny evaluation

The F_1 seeds derived from controlled sweetpotato crosses were processed following the protocol described by Lebot (2010). Initially, seeds were scarified by soaking them in 98% concentrated

sulfuric acid for 40 minutes to break dormancy. They were then thoroughly rinsed with tap water for five minutes to remove any residual acid.

Viability assessment was conducted using a floatation method. Seeds were immersed in a 200 mL beaker filled with water; viable seeds sank to the bottom, while nonviable seeds floated and were discarded. From each cross, approximately 50 to 150 seeds were generated, although this number varied depending on the compatibility of the parent genotypes, environmental conditions, and pollination success. It is important to emphasize that each seed is genetically unique**,** despite being derived from the same mother and father. This genetic variation arises due to the highly heterozygous and hexaploid nature of sweetpotato (*Ipomoea batatas*), which results in considerable recombination during meiosis. On average, 1 to 4 seeds were produced per pollinated flower, although this number was also influenced by fertilization efficiency and flower viability.

A subsample of thirty viable seeds from each cross was selected for germination testing. Seeds were placed in petri dishes lined with moist filter paper and monitored for germination. Successfully germinated plantlets were transplanted into polystyrene seedling trays containing a standard nursery mix. After 30 days, the seedlings were transferred to 10-liter plastic pots containing a 3:1:1 mixture of topsoil, sand, and compost for further growth.

Once established, thirty vines ranging from 20 to 30 cm in length were cut from the potted F_1 plants and transplanted into field plots across three distinct sites for progeny evaluation. To facilitate comparative analysis, vines from the parental genotypes were also planted alongside the F_1 clonal families at each site.

6.2.4. Evaluation of parents and F1 hybrids

The parental genotypes and progenies were evaluated at Gwebi Varietal Testing Centre (GVTC), Horticultural Research Centre (HRC) and Harare Research Station (HRS). The geo-climatic descriptions of the experiment locations are presented in Table 6.2. In total, 16 clonal families each having 20 genotypes of the F1 hybrids and the 8 parents were established using a 6 x 4 lattice design with two replications per location. Each plot consisted of two ridges, 3 m long rows. The inter-row and intra-row spacing were 1.0 m and 0.30 m, respectively. Twenty plants were planted per plot. Weeding was done regularly as required at each site. The trials were irrigated three times a week and no fertilizer or pesticides were applied.

Table 6.2: Description of the study sites

Location[c]	Soil type	Latitude	Longitude	Altitude (masl)[a]	Annual Rainfall (mm)
HRS	Clay	18.11S	31E	1506	831
GVTC	Clay	17.69S	30E	1449	850
HRC	Sandy-loam	18.11S	31E	1630	873

[a] masl meters above sea level, HRC Horticultural Research Centre HRS Harare Research Station, GVTC Gwebi Variety Testing Centre

6.2.5. Data collection

Data on storage root yield, total number of commercial roots, β-carotene content and harvest index were collected for genetic analysis. Trials were harvested 135 days after planting. The number of surviving plants per plot was counted at harvest. The number of commercial roots and non-commercial roots per plot were counted and expressed as the percentage of the total number of roots per plot. Number of commercial storage roots were counted per plot at harvest. Root weight was measured as fresh storage root weight per plot at harvest. Commercial roots were counted as the number of roots that were bigger than 5 cm in diameter. Samples of storage roots were collected after harvest for β-carotene content analysis. The samples were analyzed at the Soils and Chemistry Institute, Department of Research and Specialist Services (DR&SS), Harare, Zimbabwe**,** using spectrophotometry protocol developed by Jaarsveld et al. (2006). The β-carotene results were expressed as µg per 100 g.

Data on storage root yield, total number of commercial roots, β-carotene content, and vine yield were collected for genetic analysis. Harvest index (HI) was determined to assess the efficiency of biomass partitioning into storage roots. To calculate HI, plants were carefully harvested at physiological maturity, and both the total fresh biomass (including vines, leaves, and roots) and the fresh weight of storage roots were recorded. The harvest index was then calculated using the formula:

$$\text{Harvest Index} = \frac{\text{Fresh weight of storage roots}}{\text{Total fresh Biomass(shoots +roots)}}$$

Biomass measurements were taken using a digital field scale immediately after harvest to ensure accuracy. All data were collected from the central plants within each plot to minimize border effects and environmental variability.

6.2.6. Data analyses

The data were submitted to an analysis of variance (ANOVA) using GenStat 20th edition Payne et al. (2018). At the 0.05 level of significance, the means were separated using the Fischer's test procedure. Using the linear model provided by Hallauer et al. (2010), combining ability analysis was performed in accordance with the NCDII mating design:

The following general linear model was used for the NCD II mating design:

$$Yijkl = \mu + l + rk + gi + gj + sij + gil + gjl + sijl + eijkl$$

Y*ijkl* = the observed value of the progeny of the *i*th male crossed with *j*th female in the *l*th location and *k*th replication, μ = the overall population mean, *l* =effect of lth location, rk =effect of kth replication nested under *l*th location, gi = GCA effect of ith male, gj = GCA effect of jth female, sij = SCA effect of ith male crossed with jth female, gil = interaction effect between *l* and gi, gjl = interaction effect between *l* and gj, sijl = interaction effect between *l* and sij and eijkl = random experimental error.

The GCA and SCA effects were calculated according to (Singh and Chaudhary, 1979) as follows:

$GCA_m = X_m - \mu$, and $GCA_f = X_f - \mu$

Where: X_F and X_M = Mean of male and female parents, respectively

GCA_M and GCA_F = General combining ability of male and female parents, respectively

μ = Overall mean of crosses in the trial

$SCAx = OV - EV$

$= OV - [GCAf + GCAm + \mu]$

Where: OV = Observed mean value of the cross

EV = Expected mean value of the cross based on the 2 GCAs of its parents

SCAx = Specific combining ability of the cross x

The GCA or SCA was significant at 0.05 probability level if it was greater than the the product of 't' value and root mean square error (Dabholkar, 1999).

The general predicted ratio (GPR) (Baker, 1978) was used to determine the relative importance of GCA and SCA in influencing the expression of the traits. The Baker's ratio was calculated from the GCA and SCA variance components following Falconer et al. (2004):

Baker's ratio $= \frac{\sigma^2 GCA_f + \sigma^2 GCA_m}{\sigma^2 GCA_f + \sigma^2 GCA_m + \sigma^2 SCA}$

where $\sigma^2 GCA_f$ is the GCA female variance, $\sigma^2 GCA_m$ is the GCA male variance, and $\sigma^2 SCA$ is the SCA variance. If the Baker's ratio is >0.5, it implies that GCA is more important than SCA in the inheritance of the character, and a ratio < 0.5 implies that SCA is more important than GCA in the inheritance of the character (Baker, 1978). Therefore, a Baker's ratio above 0.5 provides that additive gene effects conditioned that particular trait while values lower than 0.5 indicate that non-additive gene effects were preponderant.

From NCD II analysis, the broad and narrow sense heritability estimates were calculated following Dabholkar (1999). The broad-sense heritability was calculated as follows:

$$H^2 = \frac{4\sigma^2 GCA_F + 4\sigma^2 SCA}{\left(\frac{\sigma^2 e}{r}\right) + \sigma^2 SCA + \sigma^2 GCA_F}$$

The narrow sense heritability estimates were determined based on female additive variance as follows:

$$h^2 F = \frac{4\sigma^2 GCA_f}{\left(\frac{\sigma^2 e}{r}\right) + \sigma^2 SCA + \sigma^2 GCA_f}$$

Where: h^2_F = family narrow sense heritability, $\sigma^2 GCA_F$ = genetic variance for general combining ability based on female parents, $\sigma^2 SCA$ = genetic variance component for specific combining ability, $\sigma^2 e$ = error variance and r = number of replications.

6.3. Results

6.3.1. Analysis of Variance

The male GCA effects were highly significant for β-carotene content ($p < 0.001$) (Table 6.3). There were significant GCA_{male} x environment interaction effects that affected root yield and harvest index. The SCA effects were significant for the total number of productive roots ($p < 0.01$). For β-carotene, fresh root yield, total number of commercial roots and harvest index, the GCA to SCA variance ratios were 0.91, 0.61, and 0.71, respectively. With a Baker's ratio greater than 0.5, the GCA effects were larger for β-carotene, fresh root yield, total productive root number, and harvest index (Table 6.3).

In terms of β-carotene concentration, root production, and harvest index, the male variance was generally greater than the female variance (Table 6.3). Similarly, for β-carotene concentration and root

yield, genotypic variances were greater than environmental variances, while for total root number and harvest index, they were lower. For both the total number of roots and the β-carotene content root yield, additive variances were greater than dominant variances.

6.3.2 Heritability estimates and Baker's ratio

Estimates of narrow-sense heritability (h^2) and broad-sense heritability (H^2) for the traits evaluated are summarised in Table 6.3. Broad-sense heritability was generally higher than narrow-sense heritability across traits. Broad-sense heritability was high for β-carotene content and total root number, moderate for fresh root yield and low for harvest index (HI). Baker's ratio values were close to unit for harvest index and higher than 0.5 for the other traits (β-carotene content, root number and fresh root yield). All cases indicated a relatively greater contribution of additive genetic effects (Table 6.3).

Table 6.3: Mean squares and significant tests of combining ability effects for four traits measured in 16 sweetpotato families evaluated at three sites in Zimbabwe.

Source	D.F	β-carotene content	RY	TRN	HI
Site	2	16.38	308.28**	5830.7***	15675.4***
Rep(Site)	3	13.62	175.55	895.1	81.4
Block(RepxSite)	24	16.8	172.35**	1574.1**	312.7***
GCA_{female}	3	26.59	73.23	814.3	127.5
GCA_{male}	3	164.06***	64.78	1751.7	212.9
GCA_{female} x Site	8	25.13	107.08	923.9	90.6
GCA_{male} x Site	6	31.65	299.79***	1357.3	430.5***
GCA_{female} x GCA_{male}	9	22.99	109.45	1797.7**	191.7
GCA_{female} x GCA_{male} x Site	18	15.8	105.7	643.7	116.1
Error	42	15.8	83	744.8	120
Male variance		5.71	24.17	15.02	45.83
Female variance		0.72	8.45	29.94	2.72
Male x Female Variance		2.56	20.81	106.78	4.9
Genotypic variance		7.71	46.59	116.01	2.36
Additive variance(AV)		30.86	186.38	464.04	9.43
Dominance variance(DV)		10.25	83.25	427.15	19.64
Environmental variance(EV)		2.68	27.66	157.24	42.63
Baker's Ratio		0.714	0.61	0.611	0.908
(h^2)		0.704	0.601	0.442	0.51
(H^2)		0.938	0.847	0.85	0.31

* = significant at 0.05 probability level, ** = significant at 0.01 probability level, *** = significant at 0.001 probability level, DF = degrees of freedom, TRN = total productive root number, RY = fresh root yield t/ha, HI=harvest index GCA_F = general combining ability of female, GCA_M = general combining ability of male, SCA = specific combining ability, GCA_F*Loc = general combining ability of female x location, GCA_M*Loc = general combining ability of male x location, SCA*Loc = specific combining ability x location GPR = General predicted ratio, h^2 = narrow sense heritability H^2 = broad sense heritability

6.3.3 Means for the four Parents and 16 Families

Overall, the crosses outperformed the parents for most traits, particularly β-carotene content, root yield, and harvest index, indicating successful recombination and possible heterosis. Notably, O-105 and O-104 appeared to be strong donor parents for β-carotene**,** while crosses involving O-105 frequently combined high yield, high TRN, and improved harvest index for example Magutse × O-105 and Kau 4 × O-105 (Table 6.4).

Table 6.4: Means for the four traits of sweetpotato parents and 16 families evaluated across three test sites

	Genotypes	β-carotene content(mg/100g)	TRN	Root Yield(t/ha)	Harvest Index
Parents	O-103	4.69	76	19.92	37.72
	O-104	10.34	44	11.80	28.40
	O-105	4.21	48	13.67	25.41
	P-201	4.94	58	20.70	31.15
	Magutse	N/A	38	11.38	30.66
	Red Jewel	N/A	10	6.02	17.88
	Kau 4	N/A	38	6.04	21.94
	Dube	N/A	40	9.38	19.09
	Mean	**3.02**	**44**	**12.36**	**26.53**
Crosses	Magutse x O-103	1.92	43	19.03	33.14
	Magutse x O-104	5.12	38	13.65	26.82
	Magutse x O-105	7.73	103	26.97	47.04
	Magutse x O-P-201	2.52	56	17.28	35.40
	Red Jewel x O-103	4.06	69	16.23	27.37
	Red Jewel x O-104	4.06	52	14.45	41.98
	Red Jewel x O-105	8.84	62	17.48	46.50
	Red Jewel x P-201	1.81	63	19.35	38.12
	Kau 4 x O-103	4.86	34	22.02	28.11
	Kau 4 x O-104	3.88	32	12.93	35.62
	Kau 4 x O-105	10.83	59	22.53	40.28
	Kau 4 x P-201	7.15	54	19.97	37.63
	Dube x O-103	4.50	46	11.92	29.22
	Dube x O-104	11.49	56	14.80	33.01
	Dube x O-105	10.05	52	15.13	25.68
	Dube x P-201	2.49	60	17.33	33.89
	Mean	**5.71**	**54.71**	**17.57**	**34.99**
	Overal Mean	**6.04**	**56**	**16.52**	**30.67**
	CV(%)	**60.72**	**48**	**47.66**	**32.24**
	LSD	**4.12**	**30.90**	**9.79**	**12.92**

TRN= total productive root number, N/A=Not Applicable

6.3.4. General combining ability effects of parents

The general combining ability (GCA) effects of the parental genotypes for the four traits evaluated are presented in Table 6.5. Considerable variation in GCA effects was observed among the parents. Parent O-103 had higher positive GCA effects for total number of commercial roots (TRN), while P-201, O-103, Magutse and Dube exhibited positive GCA effects for storage root yield. In contrast, O-104 and O-105 displayed negative GCA effects for TRN, root yield, and harvest index. Red Jewel, Kau and Dube also had negative GCA effects for harvest index).

For β-carotene content, O-104 and P-201 showed a positive GCA effect, whereas O-103 and O-105, had negative effects.

Table 6.5: Estimates of the general combining ability of the exotic male lines and local female lines and per se mean performance of BCC, TRN, root yield and harvest index

	Genotype	BCC	CRN	Root yield	Harvest index
Exotic Males	O-103	-1.85*3	+19.50*3	+3.14**	+7.06**
	O-104	+3.79	-12.50*	-4.98**	-2.26**
	O-105	-2.34	-8.50*	-3.11**	-5.25**
	P-201	+0.40	+1.50*	+3.93**	+0.44**
Local Females	Magutse	0.0	+6.5**	+3.18**	+8.26**
	Red Jewel	0.0	-21.5**	-2.18**	-4.51**
	Kau 4	0.0	+6.5**	-2.16**	-0.45**
	Dube	0.0	+8.5**	+1.17**	-3.30**

BCC-β carotene, CRN-Total number of Commercial storage roots

6.3.5. Specific combining ability effects

The specific combining ability effects of the four qualities are shown for the families in Table 6.6. Estimates of specific combining ability (SCA) effects for the four traits across the 16 crosses are presented in Table 6.6. Substantial variation in SCA effects was observed among the families. The cross Magutse × O-105 exhibited the highest positive SCA effect for total root number. Positive SCA effects for storage root yield were recorded for several crosses, notably Magutse × O-105, Red Jewel × O-104, Red Jewel × O-105, Kau 4 × O-104, and Kau 4 × O-105.

For β-carotene content, the crosses Magutse × O-105, Red Jewel × O-105, Kau 4 × O-105, Dube × O-104, and Dube × O-105 showed positive SCA effects. Positive SCA effects for harvest index were observed in Magutse × O-105, Red Jewel × O-104, Red Jewel × O-105, Kau 4 × P-201, Dube × O-103, and Dube × P-201.

In contrast, several crosses exhibited negative SCA effects for root yield, including Magutse × O-104, Magutse × P-201, Red Jewel × O-103, Red Jewel × P-201, Kau 4 × O-103, Kau 4 × P-201, and Dube × P-201. Negative SCA effects for β-carotene content were observed in crosses involving O-103, O-104, and P-201 with several female parents (Table 6.6).

Table 6.6: Estimates of SCA effects for four traits measured on 16 sweetpotato crosses evaluated across three locations

No.	Crosses	TRN	Root Yield	β-carotene content	HI
1	Magutse x O-103	-37.94**	-4.61*	-0.83	+2.99ns
2	Magutse x O-104	-4.44	-2.85	-0.33	-8.46*
3	Magutse x O-105	+41.06**	3.87	+1.20	+6.96*
4	Magutse x P-201	-8.94	-1.41	-0.72	-1.49ns
5	Red Jewel x O-103	+15.06*	-2.41	-0.14	-9.10**
6	Red Jewel x O-104	+31.06**	4.29*	-0.42	+10.71***
7	Red Jewel x O-105	+23.06**	2.49	+1.56	+5.21*
8	Red Jewel x P-201	+27.06**	-1.25	-1.14	-6.838**
9	Kau 4 x O-103	-41.94**	-1.60	+0.12	-7.26**
10	Kau 4 x O-104	-16.44*	2.74	-0.47	+0.15ns
11	Kau 4 x O-105	-1.94	6.49**	+2.21*	+0.86ns
12	Kau 4 x P-201	-10.94*	-1.99	+0.77	+3.47*
13	Dube x O-103	-37.94**	-9.66**	0.00	+4.37*
14	Dube x O-104	+5.56	-0.80	+1.98*	-2.41ns
15	Dube x O-105	-0.44	-0.23	+1.96*	-13.04***
16	Dube x P-201	-4.94	-1.10	-0.80	+4.90*

TRN=total productive root number, HI=harvest index

6.4. Discussion

6.4.1 Variation among the test genotypes

The significant GxE interaction effects shown by the ANOVA in this study can be explained by the quantitative nature of the traits. Such traits are influenced by environmental and genotypic factors (Mbusa et al., 2018). GxE interactions provide opportunities and challenges for breeding. Among the challenges, GxE effects complicate selection and reduce response to selection and genetic gain during breeding. On the positive side, GxE help in identifying superior genotypes for specific or broad environments (Alam et al., 2024). Genotypic variation in root yield, β-carotene content, total number of roots has been reported in other multi-environment trials on sweetpotato (Alam et al., 2024), which allowed for selection of superior genotypes. The significant differences among the genotypes can be attributed to differences in genetic constitution. The genetic make-up of individuals is contributed by the parents involved in the combination leading to variation in characteristics and their response to environmental factors. Ultimately, it indicated that the test genotypes exhibited adequate diversity for selection and conducting gene action analysis.

6.4.2 Performance of newly developed families across sites

The range of yield found in this study were relatively higher than the range from 15 to 23 t/ha reported in Zimbabwe by Mutandwa (2008). Consideration may be given to further breeding families with root yields greater than 20 t/ha to increase yields. The families Magutse x O-104, Magutse x O-105, Red Jewel x O-105, Kau 4 x O-105, Kau 4 x P-201, Dube x O-104 and Dube x O-105 which had β-carotene content above 5 mg100 g^{-1} can be considered for further breeding. The parent that produced progenies with a high concentration of β-carotene was O-105. Most crosses had enhanced β-carotene concentration, as evidenced by mean scores that were higher across locations. Certain crosses including O-105, like Magutse x O-105, Red Jewel x O-105, Kau 4 x O-105, and Dube x O-105, showed increased mean β-carotene content across the three test locations, which was comparable to the β-carotene content of the best parent in the cross. These crosses were Magutse x P-201, Red Jewel x P-201, Kau 4 x P-201, and Dube x P-201. In cases where the performance of the crosses was higher than the expected mid-parent performance, there is potential dominance gene action (Kagimbo et al., 2019). The relatively high coefficients of variation across traits suggest substantial environmental influence, justifying multi-location evaluation. The results demonstrate the potential for selecting superior families combining high provitamin A content and desirable agronomic traits.

6.4.3 General combining ability

This study revealed that some female parents exhibited positive general combining ability (GCA) effects and were effective combiners. The only effective combiners for root yield showing a notably increased and positive GCA were Magutse and Dube. These parents can be utilized to create sweetpotato cultivars with high levels of β-carotene and root yield. These findings suggest that these genotypes possess favorable additive genes for root yield and can be exploited in the development of sweetpotato cultivars with improved productivity and high β-carotene content. Due to their positive GCA effects, the male parents O-103 and P-201 were chosen as good combiners for the qualities of number of commercial roots, storage root yield and harvest index. The positive GCA effects observed for these traits imply that these parents contribute favorable alleles that are consistently transmitted to their offspring. These results are in line with previous studies. For example, Tumwegamire et al. (2011) and Grüneberg et al. (2009) also reported significant GCA effects for root yield and dry matter content in sweetpotato, emphasizing the importance of additive gene action in the inheritance of these traits. Similarly, Gurmu et al. (2017) found that certain sweetpotato parents exhibited high GCA effects for β-carotene content, suggesting that improving nutritional traits through parent selection and hybridization is feasible. The consistency of these findings with previous research highlights the reliability of GCA estimates in identifying elite parents for key agronomic and nutritional traits. Furthermore, the identified good combiners in this study can be recommended for use in future hybridization programmes to develop varieties tailored to both yield improvement and nutritional enhancement. Male parent O-104 was a good general combiner for β-carotene content.

6.4.4 Specific combining ability effects of sweetpotato families

The family Magutse x O-105 was selected for total root number displaying positive SCA effect. Families Magutse x O-105, Red Jewel x O-104, Red Jewel x O-105, Kau 4 x O-104 and Kau 4 x O-105 were selected for root yield associated with their positive SCA effects. The families that showed higher and good SCA impacts for β-carotene content were Magutse x O-105, Red Jewel x O-105 Kau 4 x O-105, Dube x O-104, Dube x O-105. Similar findings to this one have been published by Kagimbo et al. (2019) and Mbusa et al. (2018) for the TRN and β-carotene content, respectively. Likewise, the families: Magutse x O-105, Red Jewel x O-104, Red Jewel x O-105, Kau 4 x P-201, Dube x O-103, Dube x P-201 were best specific combiners for harvest index. Sweetpotato varieties with increased yield and β-carotene content can be developed by utilizing the best selected families based on harvest index, total root number, root yield, and β-carotene. The families Magutse × O-105**,** Red Jewel × O-104**,** Red Jewel × O-105**,** Kau 4 × O-104**,** and Kau 4 × O-105 demonstrated strong

performance for root yield, exhibiting positive specific combining ability (SCA) effects. For enhanced β-carotene content, the families Magutse × O-105, Red Jewel × O-105, Kau 4 × O-105, Dube × O-104, and Dube × O-105 was identified as promising. In terms of harvest index, the top-performing families based on SCA included Magutse × O-105, Red Jewel × O-104, Red Jewel × O-105, Kau 4 × P-201, Dube × O-103, and Dube × P-201. These parents and crosses offer valuable genetic potential for developing sweetpotato varieties with improved root yield and elevated β-carotene levels. Therefore, continued selection within these families is recommended to develop orange-fleshed sweetpotato (OFSP) varieties with higher β-carotene content for future evaluation and dissemination.

6.4.5 Heritability estimates

The current findings are consistent with other research (Jones, 1986; Chiona, 2009) that found high levels of h^2 of more than 72%. The high H^2 of β-carotene content found in this study differs from the low H^2 of less than 40% seen in Chiona's (2009) results. Both HI and the amount of beta-carotene had greater estimates of wide sense heredity (0.31) and narrow sense heritability (0.71) than the other two. Non-additive gene action is less than additive gene action when estimations of wide sense heritability are near to those of narrow sense heredity. Heritability estimates, in general, are a useful tool for figuring out how a population will react to selection (Jones, 1986).

For the TRN, the narrow sense heritability (h2) was 0.24, and the broad sense heritability (H^2) was 0.58. The TRN narrow sense heritability value in this study is comparatively greater than the value of 0.1 reported by Ngailo et al. (2013). The current study determined that for RY, the narrow sense heritability and broad sense heritability values were, respectively, 0.61 and 0.85. In contrast to the current investigation, earlier estimates of the narrow sense heritability and BSH values for root yield were 34.9% and 96.9%, respectively (Chiona, 2009). RY had a narrow sense heritability of 0.22 and a BSH of 0.99, according to Ngailo et al. (2013).

Higher heritability values for total number of commercial storage roots and root yield were discovered in this study. The present study also reported storage root yield, yield-related characteristics, and additive and non-additive gene action to β-carotene in sweetpotato. The study's findings regarding the additive and non-additive gene activities for the traits showed that improving the trait in the current sweetpotato germplasm can be accomplished by focused selection as well as hybridization.

6.5. Conclusions and Recommendations

There was a notable difference between the parents and crosses in terms of harvest index, β-carotene content, root yield, and total number of roots. The results of the GCA and SCA variances were

noteworthy, indicating that the expression of total root number, root yield, β-carotene content, and harvest index was influenced by both additive and non-additive gene actions. For these qualities, additive gene action contributed more than non-additive gene action. With respect to total root number, root yield, and B carotene, the parents Kau 4 were the best female parents with favorable GCA effects. Among the male parents, O-105 was the best parents with positive GCA effects for all the traits measured.

Based on the findings, it is recommended that future sweetpotato breeding programmes prioritize parents with strong general combining ability (GCA), such as Kau 4 and O-105, for traits like total commercial number of storage roots, root yield, and β-carotene content. Since additive gene action played a more significant role in the expression of these traits, selection strategies should focus on accumulating favorable alleles through recurrent selection or pedigree breeding. Additionally, crosses involving Kau 4 and O-105 should be further evaluated in multi-location trials to confirm their performance and stability, particularly for improving nutritional quality and yield-related traits.

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7.1 Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam] is an important multi-purpose crop in sub-Saharan Africa (SSA). It is used for food, feed and industrial raw material. However, sweetpotato production and productivity is affected by a range of constraints including biotic, abiotic and socio-economic factors. Farmers in Zimbabwe prefer to grow the white fleshed sweetpotato (WFSP) varieties that have high root dry matter content. However, the WFSP varieties have no β-carotene, a precursor for Vitamin A. It is imperative to develop cultivars with high β-carotene content and high yield potential to improve food and nutrition security of SSA. Cultivar development depends on genetic variation for important traits and identification of superior genotypes for creating breeding populations. To achieve this, several studies were conducted to fulfill the following objectives:

The objectives of the study were as follows:

1. To develop high yielding sweetpotato genotypes with favorable nutritional content and to evaluate genotypic variation in fresh tuber yield, β-carotene, iron, and zinc concentrations.
2. To assess the impact of genotype by environment interaction (GEI) on micronutrient content (β-carotene, Fe, and Zn) and fresh root yield in promising sweetpotato genotypes.
3. To determine the genetic diversity and relationships among local and imported sweetpotato accessions using single nucleotide polymorphism markers (SNPs).
4. To evaluate the combining ability effects of selected parents and clones for the storage root number, fresh root yield, and β-carotene to inform future breeding and selection efforts.

7.2 Summary of the major research findings

The first study assessed genetic variability for agronomic and nutritional traits among sweetpotato genotypes grown in Zimbabwe. A total of 22 genotypes were evaluated across four locations in Zimbabwe using randomized complete block design with 2 replications. The study was conducted during the 2020/21 summer season as a preliminary screening step towards the documentation of both orange and white fleshed sweetpotato genotypes for breeding purposes. The main findings are listed below:

- Genotypes varied with respect to storage root yield, number of commercial roots per plot, β-carotene, Fe and Zn contents.
- Correlation analysis indicated that storage root yield had positive correlations with number of commercial roots per plot (r = 0.80) suggesting that both traits can be selected simultaneously in conventional breeding.
- The study showed that adequate variability for Fe and Zn concentration exists among the evaluated genotypes, which can be exploited for use in sweetpotato bio-fortification breeding programme in Zimbabwe.

The second study investigated genotype x environment interaction effects and determined stability of root yield and micronutrient concentrations in sweetpotato (*Ipomoea batatas* [L.] Lam) genotypes. Twenty-two genotypes were evaluated using a randomized complete block design across four locations over two seasons. The main findings of the study were:

- Genotypes G3, G19, G16, G22 and G2 were identified as high yielding with fresh root yield values of 8.38, 7.69, 7.46, 7.38 and 7.18 tons/ha, respectively.
- Seven genotypes G3, G19, G16, G22, G4, G5 and G2 with high root yield, and high micro-nutrient concentrations were selected for developing breeding populations.
- The environmental variance was high indicating that the β-carotene, iron and zinc are heavily influenced by environmental factors.

The third study determined the genetic diversity present among landraces collected from the major sweetpotato-growing regions of Zimbabwe and genotypes from the International Potato Centre (CIP) in Mozambique. A total of 327 sweetpotato genotypes were used in this study. These were genotyped using 27 informative single nucleotide polymorphism (SNP) markers. The main outcomes of the study were:

- The Analysis of Molecular Variance (AMOVA) results revealed significant genetic differences within the different groups in the germplasm.
- Cluster analysis allocated the test genotypes into five distinct genetic groups: I, II and III, IV and V. The biggest cluster was Cluster II which was comprised of 52% of the genotypes. The next biggest cluster was Cluster III with 22% and Cluster I with 13% of the genotypes. Cluster IV and V were the smallest with 3% membership, respectively
- Genotypes such as G40 and G9; G142 and G73; G114 and G73; I40 and G210; G18 and G114 were distantly related.

The fourth study determined the general combining ability (GCA) effects of parents, specific combining ability (SCA) effect of crosses, gene action and heritability estimates for β-carotene

content, yield and yield-related traits among newly developed sweetpotato crosses and their parents. Eight parents and their sixteen families generated from a 4 x 4 North Carolina Design II mating design were evaluated during the 2022/23 season across three locations using a 4 x 4 square lattice design with two replications. The main outcomes of the study were:

- The male GCA effects were highly significant for β-carotene content
- SCA effects were significant for total number of productive roots at ($p < 0.01$)
- Additive gene action was more influential for β-carotene content, total root number (TRN), root yield (RY) and harvest index (HI)
- The best parents for RY were Magutse and Kau 4, while Kau 4 was the best parent for improving β-carotene content. Male parents, O-104, O-105 and P-201 were selected as good combiners for β-, carotene root yield and harvest index expressing higher and positive GCA effects in a desirable direction.
- The best selected families for root yield were Magutse x O-103, Kau 4 x O-103. The following families: Red Jewel x P-201, Kau x O-105 and Dube x O-105 were the best specific combiners for β-carotene content. The families: Magutse x O-105, Red Jewel x O-104 and Kau 4 x P-201 were the best specific combiners for harvest index.
- The broad and narrow sense heritability estimates for β-carotene content RY, TRN and HI were moderate to high showing that these traits were heritable.
- The selected parents and families are useful genetic resources for development of sweetpotato varieties with enhanced β-carotene content, root yield and yield components.

7.3 Implications of the research findings

- The present study revealed significant variability in the concentrations of β-carotene, Fe and Zn, among 22 sweetpotato genotypes in Zimbabwe. Genotype Beauregard, O-102, O-103, O-104, O-105, O-106, P-201 and P202 were found to have high concentrations of β-carotene and above average contents of root Fe and Zn among the evaluated genotypes. The genotypes selected in this study are useful genetic resources for sweetpotato breeding.
- Superior and stable candidate clones, and suitable environments were identified using AMMI and GGE biplot methods. Accordingly, seven genotypes designated as G3, G19, G16, G22, G4, G5 and G2 were identified as high yielding for fresh root yields and micro-nutrient concentration.

- The genetically distinct groups of sweetpotato genotypes can be exploited in various crosses to develop new varieties with desired traits of economic importance. The presence of distantly related sweetpotato genotypes are valuable genetic resources for future crop breeding.
- The GCA/SCA ratios were closer to one for all the tested storage root parameters such as, β-carotene content, root yield, total root number and harvest index indicating that additive gene action was more important than non-additive gene action in the expression of these parameters. Additive genes play a major role in controlling characteristics like root yield and β-carotene concentration. In order to obtain cumulative genetic improvements, breeders should concentrate on selecting and recombining superior parents throughout generations.

In conclusion, the findings in this study will contribute to sweetpotato breeding for improved yield and nutritional content. The findings will further guide research and development support to help adapt to current and future environmental shifts. Future studies should focus on assessing the diversity associated with Beta carotene, iron and zinc content in the sweetpotato. On the other hand, the performance of best lines and crosses should be assessed under different agronomic practices given the variability in agricultural practices among farmers from different regions.