

**Breeding Dual-purpose Sweetpotato [*Ipomoea batatas* (L.) Lam.] Varieties
in Rwanda**

by

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Thesis Abstract

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a multi-purpose crop where the fresh roots are used for human food and aboveground biomass for animal feed. In Rwanda, sweetpotato plays a key role in the mixed crop-livestock farming systems providing economic opportunities from livestock and crop production enterprises. However, dual-purpose sweetpotato varieties (DPSVs) with farmer-preferred traits and enhanced yields are yet to be developed and deployed in sub-Saharan Africa including in Rwanda. Therefore, the objectives of this study were: (i) to assess the role of sweetpotato in the crop-livestock farming system practised in Rwanda, to identify farmer-preferred traits and to establish farmer-led priorities in breeding dual-purpose sweetpotato varieties, (ii) to assess the level of phenotypic diversity present among sweetpotato varieties grown in Rwanda, and to select suitable parents for breeding DPSVs, (iii) to characterize diverse sweetpotato germplasm using simple sequence (SSR) markers to identify potential parents for breeding DPSVs, and (iv) to determine gene action and heritability of storage root and aboveground biomass yields, and yield components, in sweetpotato varieties, and to undertake early clonal selections for future release of DPSVs.

In the first study, a participatory rural appraisal (PRA) was undertaken in the following three selected districts of Rwanda: Bugesera, Huye and Nyagatare. Data were collected through semi-structured interviews, focus group discussions and a transect walk. All respondents wanted to grow new sweetpotato varieties with improved storage root production combined with high aboveground biomass. About 87.7, 66.6 and 51.1% of the respondents indicated that root-related traits of the crop such as high dry matter content, red skin colour and yellow flesh colour were additional preferred traits, respectively.

Secondly, fifty one diverse sweetpotato genotypes were evaluated in field trials conducted at the Rubona and Karama experimental stations of the Rwanda Agriculture Board (RAB) using a 6 x 9 unbalanced alpha lattice design with three replications. The top two genotypes selected for their high yields of storage roots were RW11-4923 and RW11-2419, with yields of 20.91 t.ha⁻¹ and 20.18 t.ha⁻¹, respectively. The genotypes RW11-4923 and Wagambolige were the best performers for aboveground yields, producing 23.67 t.ha⁻¹ and 23.45 t.ha⁻¹ of vines, respectively. The genotype Ukerewe performed well for its dry root yield (7.09 t.ha⁻¹), while RW11-4923 had the highest mean dry vine yield (5.17 t.ha⁻¹). The genotypes RW11-2910 and 8-1038 had root-to-vine ratios of 2.0 and 1.5, respectively. Two main phenotypic groups with 10 sub-groups were detected through cluster analysis and 24 sweetpotato clones were selected for their combination of high storage root yields, heavy vine production and prolific flowering ability.

Thirdly, the above 24 selected sweetpotato genotypes were genotyped with nine highly polymorphic SSRs. Cluster analysis allocated the test genotypes into three distinct genetic groups: I, II and III, with 6, 5 and 13 genotypes, respectively. Eight genetically diverse clones were selected, namely SPK004 and K5132/61 (from Group I), 4-160, Ukerewe, RW11-2910 (Group II), RW11-1860, Wagabolige, 2005-179 (Group III), with key agronomic traits for breeding DPSVs.

Finally, a half-diallel mating design was used and crosses were performed involving eight parents selected for their complementary traits including storage root and aboveground biomass production, dry matter content and farmer-preferred traits. A total of 28 families and 8 parents were field evaluated at Rubona, Karama and Ngoma research stations of RAB. Families had highly significant ($P < 0.001$) differences for fresh root yield (FRY), root dry matter content (RDMC), dry root yield (DRY), fresh vine yield (FVY), vine dry matter content (VDMC), dry vine yield (DVY), total biomass on dry weight basis (TBDW), root-to-vine ratio (R:V) and harvest index (HI). The general combining ability (GCA) and specific combining ability (SCA) effects were significant for FRY, RDMC, DRY, R:V, HI and VDMC. The GCA/SCA ratios were 0.75, 0.81 and 0.88 for DRY, RDMC and FRY, respectively, suggesting that additive gene action was more important than non-additive gene action in the expression of these parameters. Conversely, the GCA/SCA ratio was relatively lower, ranging between 0.09 and 0.28 for vine and root-vine combined parameters, suggesting that the non-additive component of the genetic variance, either dominance or epistasis, was more influential in controlling the traits. This implies that parental performance cannot necessarily be the basis of progeny performance prediction for these traits. The broad-sense heritability (H^2) values were above 0.5 for all assessed traits, with FRY, HI and RDMC having higher estimates of 0.80, 0.81 and 0.92, in that order. RDMC had a high narrow-sense coefficient of genetic determination (NSCGD) of 0.80, while this parameter varied between 0.09 and 0.49 for the rest of the tested traits. The parent K5132/61 was the best combiner for FRY and HI, while the parents RW11-1860, RW11-2910, SPK004 and Ukerewe were best general combiners for RDMC. The parent Wagabolige was the best general combiner for FRY, DRY and R:V. Based on desirable SCA effects for FVY, DVY, TBDW, RDMC, R:V and FRY, the most promising families selected in this study were K5132/61 x Wagabolige, 4-160 x 2005-179, K5132/61 x RW11-1860 and RW11-2910 x 2005-179.

Overall, the study developed promising families with high storage root and aboveground biomass yields. From these families, novel progenies were selected and are recommended for advanced clonal selection across multiple sites to release DPSVs in Rwanda or similar agro-ecologies in SSA.

Declaration

I, **Damien Shumbusha**, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. The thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
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Signed:



Damien Shumbusha

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

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Prof. H Shimelis (Supervisor)

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Prof. MD Laing (Co-Supervisor)

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Dedication

To my wife, Denise,

To my children, Dino, Dylan and Dorian,

To my late parents, Laurent and Cansilde,

I dedicate this thesis.

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Introduction to Thesis

Background and justification

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a promising dual-purpose crop. Its storage roots are used for human food and its aboveground biomass are used for animal feed (Lestari and Hapsari, 2015; Mwanga et al., 2016; Mussoline and Wilkie, 2017). In Africa, above 22.6 million tonnes of storage root is annually produced on around 3.9 million hectares of agricultural lands (FAOSTAT, 2014). It has also the potential to continuously provide forage for livestock owing to its continued regeneration ability during the growing season before roots are matured and harvested (León-Velarde, 2000). The orange-fleshed sweetpotato varieties (OFSPs) are good sources of β -carotene, a precursor of vitamin A (Alvaro et al., 2017; Low et al., 2017), while purple-fleshed types are rich in antioxidants that are useful in preventing human diseases such as asthma and arthritis (Xu et al., 2015). It is expected that the crop will make significant contributions to agriculture in East African countries through generating farm income and contributing to food security (NISR, 2016).

In Rwanda, the usefulness of sweetpotato can be seen in terms of increased production and the role it plays in the mixed crop-livestock farming systems compared with other food security crops (Khalid et al., 2013; Mutimura et al., 2015). The crop ranks second after cassava in terms of total production (NISR, 2017). In the country, sweetpotato is one of the top 10 commodity crops with an annual production of 1,055,007 tonnes (NISR, 2017). Being rich in carbohydrates, sweetpotato provides 227 kcal/capita/day, a relatively higher quantity when compared with wheat (85 kcal/capita/day), sorghum (88 kcal/capita/day) and maize (145 kcal/capita/day) (FAOSTAT, 2014). Due to its dual-purpose attribute, sweetpotato is an alternative source of high quality forage production achievable from the same crop stand intended for storage root production for human consumption (Umunezero et al., 2016). In a study to evaluate the nutritional value of the 15 forage sources in Rwanda, sweetpotato vines ranked third after sorghum regrowth and maize stover, producing 494 g/kg DM of organic matter digestibility and 8 MJ/kg DM of metabolisable energy (Mutimura et al., 2015).

Umunezero et al. (2016) ranked land scarcity among the most important crop and forage production constraints in Rwanda. The high human population density (467 inhabitants/km²) (NISR, 2016) and subsequent land shortage affect negatively the livestock sector in the country. In addition, the Government of Rwanda has recently adopted the zero grazing policy in the framework of protecting environmental degradation (Kayigema and Rugege, 2014). Consequently, sweetpotato is an ideal crop for smallholder farmers providing livestock feed through a cut-and-carry fodder production strategy. Therefore, it is essential to

increase sweetpotato root and forage production and productivity per unit area. The use of multi-use crops such as sweetpotato could be a primary consideration in agricultural land scarce countries such as Rwanda.

Sweetpotato is a relatively drought tolerant crop providing a reasonable harvest under the low input farming systems of sub-Saharan African countries (Niyireba et al., 2013). Maize is an alternative forage crop being used in Rwanda but it is not widely cultivated (Mazimpaka et al., 2017). When maize forage is available, it should be supplemented with high protein feed sources such as sweetpotato vines in order to improve its nutritional value.

Sweetpotato yields are variable depending on genotype, use of production inputs and agro-ecological conditions (Etela and Anyanwu, 2011; Shumbusha et al., 2017). For example, dry root yields were reported to vary between 0.36-7.17 t/ha in the savannah zone and 0.55-5.67 t/ha in the humid forest zone of Nigeria (Larbi et al., 2007). On the other hand, dry vine yields varied from 1.09-2.43 t/ha and 0.93-4.97 t/ha in the savannah and forest zones, respectively. Thus targeted breeding is needed to explore the genetic variation to improve the productivity of the crop for food and fodder.

Sweetpotato breeding is challenged by a number of constraints such as poor flowering and fertility, self- and cross-incompatibility and its inherent hexaploidy and heterozygous genetic makeup (Jones et al., 1986; Buteler et al., 1997; Gurmu et al., 2013). Despite these challenges, marked breeding progress has been made in improving storage root yield and nutritional quality of the crop by the Consultative Group of International Agricultural Research (CGIAR) centres and national breeding programs. However, dual-purpose sweetpotato varieties (DPSPVs) are yet to be developed in Rwanda. Genetic improvement of dual-purpose sweetpotato germplasm collections can be enhanced due to the presence of maximum genetic variation for root and vine yield expression and ideal maturity periods of the crop (Niyireba et al., 2013; Lukuyu et al., 2014). Therefore, the present study focused on breeding sweetpotato both for improved root and aboveground yields to fully exploit the genetic potential of the crop.

Problem statement

In the past, extensive research has been conducted on breeding sweetpotato varieties with improved fresh root yields and β -carotene content (Ndirigwe et al., 2005; Shumbusha et al., 2014; Gurmu, 2015; Rukundo, 2015). However, limited research has been conducted on breeding dual-purpose varieties and yet the crop is potentially useful both for human food and animal feed (Umunezero et al., 2016). The crop may play an important role in the

cropping systems of Rwanda if both root and vines yields are combined in a single genetic background to develop dual-purpose clones (Niyireba et al., 2013). León-Velarde (2000) classified dual-purpose sweetpotato varieties according to the ratio of dry matter yields of roots to vines in order to discern the economic value of the crop for root production, forage production or dual-purpose. In Rwanda, there is need to develop dual-purpose sweetpotato varieties in order to fulfil the needs of smallholder farmers who depend on mixed crop-livestock farming system on a limited agricultural land.

Developing improved dual-purpose varieties requires detailed information on the needs and preferences of growers, the genetic potential of parental clones, the inheritance and gene action involved on storage root and aboveground yields and related agronomic traits. This information would be useful for designing breeding strategies for effective sweetpotato improvement (Tairo et al., 2008). Therefore, there is need to identify suitable genotypes that can serve as parental material for root and vine yield improvement.

DPSPVs have the potential for effective use of the current arable land which is dramatically dwindling due to population growth and urbanisation in Rwanda. There has been a significant increase in arable lands from 30% in 1996 to 50% in 2013 in Rwanda (FAOSTAT, 2014; NISR, 2016). As such, new farm lands are not available to cultivate food crops (de Graaff et al., 2011). It is projected that the current 10 million population of Rwanda is expected to double by 2030. The country is dependent on agricultural sector and farmers' income results from the sale of produce derived from food crops and livestock (NISR, 2016). To meet the food and feed demands, crop intensification is necessary by using improved genotypes and exploiting the genetic potential of crops with multiple uses such as sweetpotato. This will aid for sustainable sweetpotato production while reducing environmental degradation exerted on the limited agricultural lands. In the framework of reducing environmental degradation, a zero grazing policy is currently being applied in Rwanda. In contrast, there have also been Government initiatives to promote rapid livestock increase at farmer's level through: "one cow per family", "one cup of milk per child", or "send a cow". Therefore, there is need to secure forage for the livestock sector, while maintaining the balance of food crop production. Breeding dual-purpose sweetpotato varieties with high root and aboveground biomass yields on fresh- or dry-weight basis is one of the best approaches.

Objectives

The overall objective of this study was to contribute to increased food security through improvement of sweetpotato root and aboveground biomass yields for mixed crop-livestock

farmers and increased income of smallholder farmers in Rwanda. This was partly accomplished by breeding DPSVs using the following specific objectives.

The specific objectives of the study were;

1. To assess the role of sweetpotato in the crop-livestock farming system practised in Rwanda, to identify farmer-preferred traits and to establish farmer-led priorities in breeding DPSVs.
2. To assess the level of phenotypic diversity present among sweetpotato varieties grown in Rwanda, and to select suitable parents for breeding DPSVs.
3. To characterize diverse sweetpotato germplasm using simple sequence (SSR) markers to identify potential parents for breeding DPSVs.
4. To determine gene action and heritability of storage root and aboveground biomass yields, and yield components, in sweetpotato varieties, and to undertake early clonal selections for future release of DPSVs.

Research hypotheses

The hypotheses tested in the study were;

1. Sweetpotato plays an important role in mixed crop-livestock farming in Rwanda and dual-purpose traits are among farmer preferences in Rwanda.
2. There is a high level of genetic variability in storage root and aboveground biomass for sweetpotato germplasm in Rwanda assessed through phenotypic traits and SSR markers.
3. There is fixable gene action controlled by additive genes and the heritability of storage root and aboveground biomass yields is high to select DPSVs for release.

Thesis outline

The thesis consists of six chapters associated with activities of the above-mentioned objectives. Chapter one is a review of the literature, while chapters 2 to 5 are distinct research chapters. Consequently, there is some unavoidable repetition of references and introductory information between chapters. The format of references used in the chapters of this thesis is based on the journal of Crop Science system which is the most recommended thesis format adopted by the University of KwaZulu-Natal. Each of these chapters follows the format of a publishable paper. The contents of Chapter three have been published in the *Acta Agriculturae Scandinavica*, Section B – Soil & Plant Science.

The chapters are outlined as follows:

1. Introduction to Thesis
2. Chapter One: A review of the literature
3. Chapter Two: Assessment of the roles of sweetpotato and farmer-preferred traits in a crop-livestock farming system: implications for breeding dual-purpose varieties in Rwanda
4. Chapter Three: Phenotypic diversity analysis of sweetpotato for breeding dual-purpose varieties
5. Chapter Four: Characterization of dual-purpose sweetpotato germplasm using simple sequence repeat markers
6. Chapter Five: Gene action and heritability of storage root and aboveground biomass yields and yield components of dual-purpose sweetpotato clones
7. Chapter Six: Thesis Overview

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1. Chapter One: A review of the Literature

Abstract

Sweetpotato [*Ipomoea batatas* (L.) Lam] is an important, multi-purpose crop providing various livelihood opportunities to millions of smallholder farmers in sub-Saharan Africa (SSA). It is widely grown under the crop-livestock mixed farming systems in SSA, including Rwanda, providing food, feed and industrial raw materials. Despite the socio-economic significance of sweetpotato, and its economic potential, its productivity is relatively low in SSA due to an array of constraints. The objectives of this review were to highlight the primary constraints affecting sweetpotato productivity and to present the current opportunities for improved sweetpotato production, research and technology development. The review identifies the challenges of sweetpotato production and productivity, including a lack of access to improved cultivars, biotic and abiotic stresses, and socioeconomic constraints such as a shortage of healthy planting materials, and limited funding for research and technology development. Further, the review identifies various production and market opportunities for sweetpotato. These included the likelihood of the crop being adopted by farmers due to its low-input requirements, increasing demands to dual-purpose varieties, national policy support, increasing market demands for sweetpotato as food and processed products, gender equity issues that affect its production, and the availability of genetic and genomic resources for breeding. Finally, the review summarises crosscutting aspects in the improvement of the crop, such as genetic resources and diversity, trait association and gene action, which affect various traits of the crop during cultivar development. Overall, this review pointed out the underlying challenges and opportunities to sweetpotato production and improvement that could help to devise options to enhance sweetpotato productivity in SSA.

Keywords: crop improvement, dual-purpose varieties, *Ipomoea batatas*, production challenges

1.1. Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam] is one of the most widely grown root crops in sub-Saharan Africa (SSA) owing to its diverse economic value and the adaptation of the crop to growing under harsh environments. Approximately 13.4 million tonnes of sweetpotato storage root is annually produced on 3.2 million hectares of agricultural lands in SSA (Andrade et al., 2009). Sweetpotato is a rich source of carbohydrates, vitamins and micronutrients, making it a staple food for many rural households in SSA (Woolfe, 1992; Tumwegamire et al., 2011). The orange-fleshed sweetpotato varieties (OFSPs) are a good source of beta-carotene, a precursor of vitamin A (Low et al., 2017). Purple-fleshed types are high in antioxidants, which are useful in preventing some human diseases such as asthma, gout and arthritis (Bovell-Benjamin, 2007). The young leaves of some varieties of sweetpotato are cooked and consumed. The leaves have higher protein content than the storage roots (Antia et al., 2006; Bovell-Benjamin, 2007). Storage roots can be consumed boiled, pureed or baked (Jata et al., 2011). Sweetpotato puree and flour are widely used in some countries as a substitute for wheat flour to prepare different baked products. Rwanda imports substantial quantities of wheat flour for the production of bread and related products. The use of sweetpotato flour to prepare baked products allows for import substitution, and enhanced economic returns for both the processors and consumers, through reduced production costs (Sindi et al., 2013).

The above ground biomass of the crop is used in sweetpotato-based fodder systems, providing a rich source of protein for animals (Bashaasha et al., 1995; Bovell-Benjamin, 2007). In addition, green fodder constitutes a good source of vitamin A, which is important for animal health. Milk and meat production is dependent upon the quantity and quality of fodder that is available. Therefore, sweetpotato-based fodder production is an economic approach for fodder production under the smallholder mixed crop-livestock farming systems, given its relatively low costs of production (Peters, 2008). The value of a sweetpotato-based fodder system is important in countries such as Rwanda that has a high population density (467 inhabitants.km⁻²) (NISR, 2016), and no agricultural lands for grazing. Any surplus sweetpotato fodder can be processed into silage for scheduled cattle feeding. Consequently, dual-purpose sweetpotato varieties with high yields of storage roots and above ground biomass are important genetic resources for the crop-livestock sectors (Jata et al., 2011). Dual-purpose sweetpotato varieties can have a greater value per unit area than traditional varieties commonly grown for storage roots alone (Peters, 2008).

To date 30 sources of forage have been reported to have been used for animal feed in Rwanda. The large number of forage sources is related to the shortage of fodder for

livestock production in Rwanda, given the extreme demands for land for food production that exist. Above ground biomass of sweetpotato constitutes a major source of fodder for mixed crop-livestock farmers. In Rwanda, sweetpotato derived biomass is ranked third as a fodder, after roadside grass and banana peels (Mutimura et al., 2013). However, most of the varieties grown in the country have been selected for high root yields rather than for dual-purpose traits (Niyireba et al., 2013). Sweetpotato biomass contains relatively little dry matter content (DMC), (18.6% in the leaves and 17.9% in the stems) (Aregheore, 2004). Breeding efforts to increase the DMC would also increase the crude protein content and therefore the forage quality of the crop (Larbi et al., 2007).

Sweetpotato storage roots are also valuable as a source of industrial starch. The crop provides a high starch yield per unit area. Typically, sweetpotato starch is used in food processing as an ingredient in baked products and in preparing juices, ice cream and noodles. Woolfe (1992) reported other important sweetpotato starch based products include cyclodextrin, which is used in the pharmaceutical industry, and an oligosaccharide used as a reagent in blood tests. Sweetpotato storage roots are also used to preparing local and industrial beverages, e.g., sweetpotato beer, due to the high carbohydrate content (Afuape et al., 2014). Carotenoids and anthocyanins can be extracted from the OFSPs and purple-fleshed sweetpotato varieties, respectively, to be used as colorants in various food products (Arizio et al., 2014).

Despite the economic importance of sweetpotato in SSA, its productivity is relatively low due to an array of constraints. Therefore, the objectives of this review were to highlight the primary constraints affecting sweetpotato production and to present the current opportunities for sweetpotato production, research and technology development in SSA.

1.1.1. Trends in sweetpotato production and productivity

Sweetpotato is adapted to tropical or subtropical growing conditions. It requires hot conditions for adequate growth and productivity. Its production is highly concentrated in countries with lower per capita income such as in Africa, Asia and Latin America (Figure 1.1). The mean storage root yields of the crop in Africa and Latin America is less than 9 t. ha⁻¹, which is far below the attainable yields of above 22 t. ha⁻¹ reported in China (Grüneberg et al., 2015).

Sweetpotato Production Areas of Cultivation and Average Yields

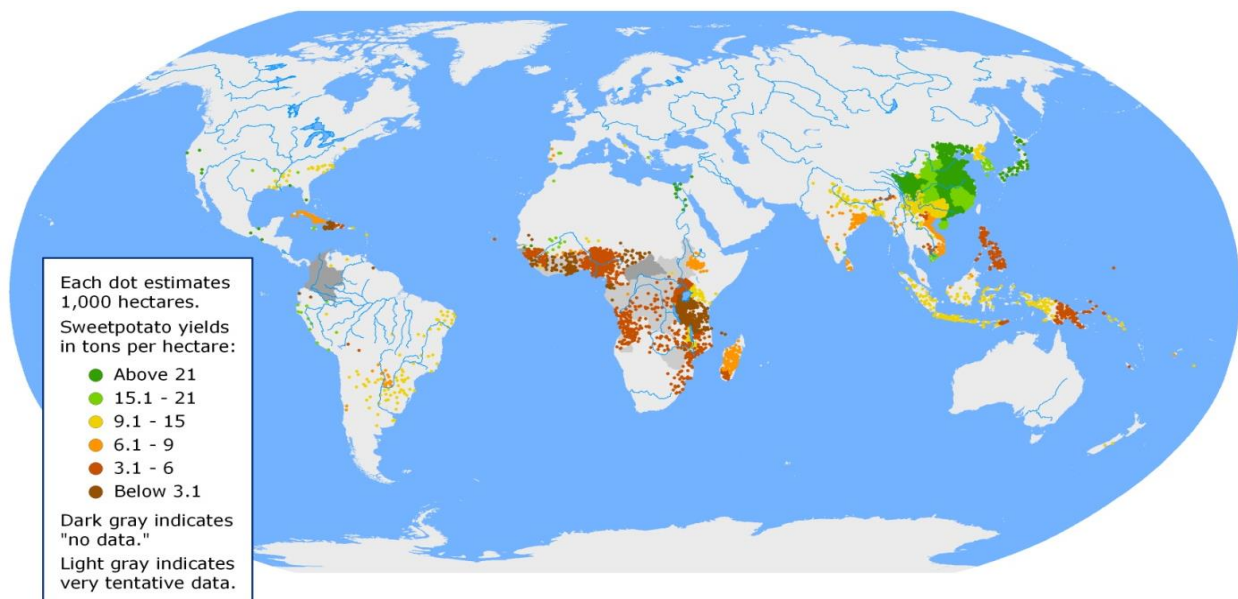


Figure 1.1: Sweetpotato production and productivity (CIP, 2008; Khoury et al., 2015)

1.2. Challenges to sweetpotato production and productivity

1.2.1. Lack of improved varieties

Sweetpotato genotypes with improved storage root and forage types are being developed by the International Potato Centre (CIP) and the International Livestock Research Institute (ILRI) and various national root crops breeding programs. Dual-purpose sweetpotato varieties are desirable for mixed crop-livestock farming systems, such as is practiced in Rwanda (Niyireba et al., 2013). However, sweetpotato varieties with strong dual-purpose attributes have not yet been released in SSA (Niyireba et al., 2013; Shumbusha et al., 2014). The Government of Rwanda adopted a zero grazing policy in a policy framework aimed at stopping environmental degradation (Peters, 2008; TechnoServe, 2008). Sweetpotato is potentially an ideal crop, suitable for smallholder mixed crop-livestock farmers, which can be used for forage production without negative environmental consequences.

1.2.2. Biotic stresses

Sweetpotato is vulnerable to several pests and diseases. Among pests, sweetpotato weevils (*Cylas spp.*) and sweetpotato butterfly (*Acraea acerata*) are reported to be serious insect pests damaging the crop in East Africa (Okonya et al., 2014). Sweetpotato production has also been mainly constrained by viruses due to clonal propagation of the crop through vine cuttings, and vector transmission of many viruses. In Rwanda, a co-infection has been

reported of sweetpotato chlorotic stunt virus (SPCSV) and sweetpotato feathery mottle virus (SPFMV). The two viruses act synergistically, causing a severe stunting disease, the sweetpotato virus disease (SPVD) (Mwanga et al., 2013). The use of clean planting material has boosted sweetpotato yields and market value and crop diversification (Nshimiyimana et al., 2016).

1.2.3. Abiotic stresses

Abiotic factors (drought and poor soil fertility) often limit sweetpotato production and productivity (Fuglie, 2007). Sweetpotato yield reduction due to drought can reach up to 60%, especially when it occurs during root initiation, the critical growing stage of the crop (Lebot, 2009). In Uganda, drought tolerance was ranked as the third most important selection trait by farmers after high yields and resistance to the SPVD (Gibson et al., 2008). The negative impact of pests and viruses is usually enhanced by drought (Fuglie, 2007).

1.2.4. Socio-economic constraints

1.2.4.1. Shortage of clean and adequate planting material

Sweetpotato is commonly propagated through vine cuttings. Enough soil moisture is required for maintenance and sustainable production of planting material during the main production season. In some countries such as in Rwanda, a limited number of farmers are able to conserve planting materials for the following cycle of production. These farmers keep parent plants alive in swamps or marshlands, or in irrigated agricultural lands. However, in Rwanda, most of the wetlands are dedicated to cereal production (rice and maize) due to the Government's priorities in the "Crop Intensification Programme". Most farmers in Rwanda therefore have limited access to reliable, year-round water sources for the maintenance of sweetpotato parent plants. This results in a severe shortage of sweetpotato planting material between June and September every year (Nshimiyimana et al., 2016).

There are no commercial nurseries involved in the production and delivery of sweetpotato planting material to supply to farmers. Instead, it is mostly distributed via the informal seed system. Only a few farmers are involved in the multiplication and distribution of planting materials under small-scale propagation schemes (Namanda et al., 2011).

1.2.4.2. Limited funding for sweetpotato research and technology development

In the SSA there has been a little progress in the breeding of sweetpotato, a situation that has been attributed to the limited investment in sweetpotato research and development in SSA countries (Chivenge et al., 2015). Most agricultural policies are in favour of grain crops

(MINAGRI, 2010). Sweetpotato is grown under smallholder farmer systems for food security, and as a means to earn modest cash income. Consequently it is often referred to as “a poor man’s crop”. Interestingly, most research and technology development and extension services of sweetpotato in SSA have been externally driven, primarily through the International Potato Centre (CIP) and the Alliance for a Green Revolution in Africa (AGRA). However, there is need for strong research and development driven by the national agricultural research systems (NARS), on the same scale as for cereals and pulses. This will allow for sustainable sweetpotato research and cultivar development in SSA that is geared towards the development of superior genotypes that incorporate farmers’ needs and preferences.

1.2.4.3. Lack of postharvest handling facilities

Sweetpotato storage root is highly perishable after harvest. This is often associated with loss of moisture and sugar content, leading to an undesirable texture and taste (Ray et al., 2010). Post-harvest damages of sweetpotato storage root are caused by various factors including physical, physiological and biological (Sudheer and Indira, 2007). Physiological deterioration is associated with increased respiration and sprouting of storage roots, while the biological agents include postharvest pests and diseases (Kasso and Bekele, 2016). Storage root requires controlled storage facilities for long-term storage. In SSA, there is a lack of proper postharvest handling techniques, resulting in losses to the quantity and quality of the crop (Samantaray et al., 2016). Gurmu (2015) reported that a lack of postharvest handling facilities during packaging and transport, a lack of well-designed storage facilities, a lack of knowledge on processing, a lack of processing equipment and a problem of transporting bulky products were among the major postharvest constraints to sweetpotato production in Ethiopia.

1.3. Opportunities for the improvement of sweetpotato production

1.3.1. Increased adoption rate of sweetpotato as low-input and value adding crop

Sweetpotato is a potentially important food security crop due to its relatively high yielding ability under harsh growing conditions and low production input requirements. It thrives under harsh growing conditions where major cereal crops would fail. Sweetpotato adapts to a wide range of rainfall patterns (Ewell, 2002), providing reliable forage and storage root yields. Additionally, farmers are able to practice ad hoc harvesting of the crop over a long period throughout the crop year, guaranteeing food security over time. The crop provides raw material for food industry where various processed products are produced, based on its starch, beta-carotene and anthocyanin contents (Nedunchezhiyan et al., 2012). Sweetpotato

derived starch, ethanol and citric acid are potential drivers for the increased adoption and production of the crop in SSA (Nedunchezhiyan et al., 2012).

1.3.2. Increased demand for dual-purpose sweetpotato varieties

There is an increased demand for sweetpotato products in regional and international markets. Dual-purpose sweetpotato varieties are in demand by farmers practicing mixed crop-livestock (Kamanzi and Mapiye, 2012). In Rwanda, the area of cultivated land increased from 30% in 1996 to 50% in 2013, due to population growth and the increased demand for food (FAOSTAT, 2013). The economy of the country is largely dependent on the agricultural sector. Farmers' income results from the sale of produce derived from food crops and livestock. To meet the food and feed demands of increasing population, crop intensification is needed by using improved genotypes of all crops, and by exploiting the genetic potential of crops with multiple uses, such as sweetpotato. The Rwandan Government has initiatives to promote livestock farming through a "one cow per family" and a "one cup of milk per child" program. Therefore, there is a need to secure adequate quantities of high quality forage for the growing national herd of livestock, but without compromising food crop production. Hence there is an increasing demand for dual-purpose sweetpotato varieties.

1.3.3. Favourable policy

Historically, sweetpotato has not featured as a priority crop in East Africa. However, most Eastern African countries have started to support research initiatives on the crop. Currently, the Rwanda Agriculture Board (RAB) is taking the lead in research and development of the crop in Rwanda. RAB is involved in strengthening sweetpotato breeding, multiplication and dissemination of planting materials to farmers (Ndagijimana et al., 2014). In addition, RAB has built infrastructures and sourced the necessary equipment for the production of healthy planting material using tissue culture techniques. The institution has also developed a greenhouse facility for the accelerated multiplication of planting material (Ndagijimana et al., 2014). The Government has been advocating the adoption of sweetpotato as an important crop in terms of its dual-purpose use and nutritional advantages (MINAGRI, 2010; MINAGRI, 2013). Local administrators have designated sweetpotato as a priority crop by providing land for planting material multiplication and dissemination (Nshimiyimana et al., 2016). In Rwanda, the OFSPs have been widely promoted for their health contributions (Ndirigwe et al., 2012).

1.3.4. Increased market demand for food and industrial processing

There is a strong demand for sweetpotato starch, which is increasingly used in the food industry to manufacture baked products, juices, ice cream and noodles. In addition, Woolfe (1992) reported the production of other important sweetpotato starch based products such as ascorbic acid and alcohol, which are useful in the pharmaceutical industry. Sweetpotato is regarded as a commodity crop serving for food and market in the country (Sindi et al., 2013). Currently, sweetpotato is processed into various products such as bread, biscuits, and cakes. These are value added products that have increased the market demand of the crop (Bocher et al., 2016).

1.3.5. Gender equity in sweetpotato production

Gender balance in sweetpotato production and economic gains is one of the important opportunities in sweetpotato production in Rwanda. One of the Millennium Development Goals (MDGs) is gender equality in all agriculture activities. This needs to include sweetpotato production in Rwanda (MINAGRI, 2010). This is to comply with the Economic Development and Poverty Reduction Strategy (EDPRS), which aims to increase economic growth and reduce poverty. Vision 2020 of Rwanda is based on these policies and strategies. Gender equity is emphasised in the current National Constitution (MINAGRI, 2010). Both males and females are involved in sweetpotato production in Rwanda. However, more women are involved in the production activities (Rukundo et al., 2015). Regarding decision making on which crop to grow, Shumbusha (unpublished data) found that the decision-making is shared among family members, mainly between the household head and his spouse. The same study showed that men were mainly involved in ploughing, transport of harvested sweetpotato roots and selling, while women were mainly involved in selection of planting material, planting, weeding and harvesting. Specifically for sweetpotato forage, family members across all gender are engaged in sweetpotato forage production and use, despite disparity in level of daily labour contribution (Njarui et al., 2016). According to Kamanzi and Mapiye (2012) women contribute highest labour to tasks that are performed daily such as cutting and carrying vines, and feeding cattle. The gender imbalance occurs at a financial level because men control the income earned from sales of sweetpotato products.

1.3.6. Demand for improved sweetpotato varieties with high yield, enhanced root dry matter content and quality fodder

Sweetpotato varieties that are currently grown in SSA have low yield levels (Gruneberg et al., 2015). These authors indicated that attained and potential storage root yields were estimated at 6t.ha⁻¹ and 40t.ha⁻¹, respectively. Various factors contribute to the gap between

the attainable and potential yields, but the unavailability of improved genotypes with high yield potential has been found to be leading major constraint (Rukundo et al., 2015). Further, high dry matter content (DMC) is the major farmer-preferred trait for sweetpotato varieties in SSA. High root DMC of sweetpotato varieties has been reported to be strongly linked with consumer preferences in East African countries (Shumbusha et al., 2014). Sweetpotato genotypes can have root DMC values ranging from 20 to 35% (Tumwegamire et al., 2016). The major components of DMC are carbohydrates, composed mainly of starch and sugars, and reduced cellulose, hemicellulose and pectins. Root DMC has direct positive influence on quality aspects such as texture, dryness, mouthfeel and taste of the storage roots (Woolfe, 1992). Furthermore, nutritional value is one of the criteria for quality forage. Earlier study showed that sweetpotato vines are among the forage sources with the highest metabolisable energy (ME) and organic matter digestibility (OMD) (Mutimura et al., 2015). The nutritional value of the ten popular feed sources including sweetpotato is shown in Table 1.1.

Table 1.1: Nutritional value of sweetpotato forage compared to other popular forage sources in Rwanda

Forage type	Scientific name	DMC (g/kg)	OMD (g/kg DM)	NDFd (g/kg DM)	ME (MJ/kg DM)
Banana pseudo-stem	<i>Musa sp.</i>	55	394	632	6
Calliandra	<i>Calliandra calothyrsus</i>	348	282	488	7
Ficus	<i>Ficus sp.</i>	357	365	452	7
Irish potato haulms	<i>Solanum tuberosum</i>	894	448	293	8
Leucaena	<i>Leucaena diversifolia</i>	334	365	520	8
Maize stover	<i>Zea mays</i>	935	500	388	8
Napier grass	<i>Pennisetum purpureum</i>	249	447	547	7
Sorghum regrowth	<i>Sorghum bicolor</i>	213	499	365	9
Sweetpotato vines	<i>Ipomoea batatas</i>	214	494	489	8
Wheat straw	<i>Triticum sp.</i>	884	388	575	6

DMC: dry matter content; OMD: organic matter digestibility; NDFd: neutral detergent fibre digestibility; ME: metabolisable energy (Mutimura et al., 2015).

1.3.7. Genomic and genetic resources for sweetpotato improvement

Use of complementary molecular breeding tools can speed up conventional sweetpotato breeding (Yencho and Khan, 2015). Currently, various molecular markers are used in sweetpotato genetic analysis and gene discovery such as Amplified Fragment Length Polymorphism (AFLP), Simple Sequence Repeats (SSR) and Random Amplified Polymorphic DNA (RAPD) (Maquia et al., 2013; Yada et al., 2017). The genetic effects of SPVD resistance, beta-carotene content, root knot nematode resistance, storage root dry matter content and yield have been elucidated using SSRs (Yada et al., 2017). Diverse crop genetic resources are essential for any breeding program. There are many sweetpotato

genotypes maintained in national germplasm repositories in SSA. The germplasm contains both locally-bred and introduced genotypes. The latter are mainly introduced from the neighbouring National Agricultural Research Institutes (NARIs) and the Consultative Group of International Agriculture Research centres (CGIAR) such as the International Potato Centre (CIP).

1.4. Genetic improvement of sweetpotato

1.4.1. Genetic variability

Sweetpotato has much genetic variability, and more than 8000 sweetpotato accessions and 26,000 closely-related species are maintained in 83 genebanks worldwide, including 4616 accessions available at CIP's genebank (Rao et al., 1994; Grüneberg et al., 2015). In eastern Africa, farmers grow and maintain genetically diverse sweetpotato landraces. This region is regarded as a secondary centre of diversity of sweetpotato (Gichuru et al., 2005). The Rwandan genebank contains around 170 sweetpotato genotypes. These genotypes have been characterised and maintained for various attributes (Shumbusha et al., 2017). Some unique varieties of the crop currently grown in Rwanda are presented in Table 1.2. Wild relative of sweetpotato have been reported to be useful in sweetpotato improvement programs, providing genes for disease resistance (Khoury et al., 2015).

Table 1.2: List of the most popular sweetpotato varieties currently grown in Rwanda

S/N	Variety name	Source	Specific attributes
1	Cacearpedo	RAB	High root yield, high beta-carotene content
2	Gihingumukungu	RAB	High root yield, high beta-carotene content
3	Kwezikumwe	RAB	Early maturity, high root yield
4	Mugande	RAB	Excellent taste, high dry matter content (DMC, >30%)
5	Naspot 9	NARO	High root yield, virus resistance, beta-carotene content
6	Naspot 10	NARO	High root yield, virus resistance, beta-carotene content
7	RW11-17	RAB	High root yield, high DMC, profuse vine production
8	RW11-1860	RAB	High root yield, high DMC, relatively profuse vine production
9	RW11-2419	RAB	High root yield, profuse vine production
10	RW11-2560	RAB	High root yield, beta-carotene content
11	RW11-2910	RAB	High root yield, profuse vine production
12	RW11-4923	RAB	High root yield, profuse vine production
13	SPK004	CIP	High root yield
14	Ukerewe	RAB	Excellent taste, high DMC, high root yield

RAB: Rwanda Agriculture Board; NARO: National Agriculture Research Organization/ Uganda; CIP: International Potato Centre; DMC: dry matter content.

1.4.2. Genetic diversity analysis

Characterization of available germplasm is useful for the purpose of identifying potential useful parents for a breeding programme (Laurie et al., 2013). Genetic diversity analyses can be carried out using phenotypic traits or molecular markers. Phenotypic characterization is useful for the detection of traits of interest and to identify suitable accessions for breeding or conservation (Manamela, 2009). Beah et al. (2014) reported significant contribution of a number of traits to the genetic variation among the genotypes studied in Sierra Leone. Morphological traits are routinely recorded using descriptors of sweetpotato developed by Huamán (1991). In SSA, several authors have used phenotypic traits to characterize sweetpotato accessions such as in Uganda (Yada et al., 2010), South Africa (Laurie et al., 2013) and in Mozambique (Maquia et al., 2013). In Rwanda, phenotypic characterization has been conducted to assess the level of diversity among the available germplasm (Shumbusha et al., 2017).

Molecular markers constitute an important and reliable tool in detecting relatedness between genotypes at the DNA level. In sweetpotato, various genomic resources have been used, including simple sequence repeats (SSRs) or microsatellites (Yada et al., 2017), inter-simple sequence repeats (ISSRs) (Hu et al., 2003), random amplified polymorphic DNA (RAPD) (Maquia et al., 2013), amplified fragment length polymorphisms (AFLP) (Cervantes-Flores,

2007), selective amplification of microsatellite polymorphic loci (SAMPL) (Tseng et al., 2002), DNA amplification fingerprinting (He et al., 1995) and single nucleotide polymorphisms (SNPs) (Arif et al., 2010).

Among the molecular markers, SSR markers have been used to detect the level of genetic diversity in sweetpotato (Yada et al., 2010). Simple sequence repeats are small tandem repeated base sequences ranging between 1-6 bp that are found in eukaryotic genomes (Powell et al., 1996). The SSRs are the most preferred useful markers due to their level of polymorphism and their distribution throughout the genome, and their high number of alleles per locus (Wende et al., 2013). Around 1600 sweetpotato gene based SSRs markers have been identified using Expressed Sequence Tags (EST) sequencing. There are currently more than 200 SSR primers useful for genetic analysis of sweetpotato (Grüneberg et al., 2015). In previous studies, 137 and 287 sweetpotato genotypes were genotyped using 23 and 250 SSRs markers in Brazil and Uganda, respectively (Rodriguez-Bonilla et al., 2014; Yada et al., 2017). The SSR markers can demarcate sweetpotato genotypes, based on their discriminatory power (Naidoo et al., 2016).

1.4.3. Breeding methods of sweetpotato

Sweetpotato is propagated vegetatively using vine cuttings. Thus, individuals derived from the same mother plant are genetically identical and represent clones. However, genetic recombination is an important step for successful breeding and selection of new varieties of all crops. Sweetpotato breeding aims to introduce genetic variation through designed crossing using a special mating design, or using polycrosses (Grüneberg et al., 2009). The objective of a mating design is to get information regarding parental values and families as well as to generate data regarding genetic parameters for breeding (Griffing, 1956). The diallel mating design has been used in determining combining ability in many crops. Diallel analysis depends on which combinations are relevant for assessing genetic parameters and may comprise parents, F1 progenies and reciprocals (Griffing, 1956).

1.4.4. Genetic analysis of qualitative and quantitative traits in sweetpotato

Sweetpotato is naturally hexaploid ($2n = 6x = 90$, $x = 15$) (Buteler et al., 1997). Each gene may therefore be represented by six alleles, which makes segregation patterns challenging to interpret. Inheritance of most economic traits in sweetpotato is quantitative (Cervantes-Flores, 2007). Due to the genetic and meiotic complexity of the crop, improved breeding tools are needed to enhance genetic gains of sweetpotato through breeding. Mapping of quantitative trait loci (QTL) associated with the important quantitative traits is one of the advanced breeding technologies to overcome sweetpotato breeding difficulties (Cervantes-

Flores, 2007; Yu et al., 2014). Also, a reference diploid with a highly homozygous genome has been generated from on two ancestors (*Ipomoea trifida* and *I. triloba*) of the cultivated sweetpotato (Yencho and Khan, 2015). Further problems for making crosses include sterility, self and cross incompatibilities between sweetpotato genotypes. In spite of breeding difficulties related to the nature of the crop, there has been marked progress in sweetpotato breeding through targeted crosses, followed by genetic analyses including combining ability tests, and the determination of gene action and the heritability of traits.

1.4.5. Combining ability analysis in sweetpotato

Combining ability analysis is used to determine and compare the performances of genotypes in hybrid combinations (Griffing, 1956). These procedures have been used as a basis to identify the best parents and their crosses. Two types of combining ability effects are distinguished, general combining ability (GCA) and specific combining ability (SCA). GCA is the average performance of a parent in a hybrid combination, while SCA is the expected performance of a cross based on the average performance of all crosses involved (Griffing, 1956). The relative importance of GCA and SCA is determined by the ratio, $2\sigma_g^2/(2\sigma_g^2 + \sigma_s^2)$, serving as the basis of predictability of the main type of gene action involved in controlling a trait (Baker, 1978).

1.4.6. Gene action and heritability

The nature of gene action is key as a selection guide in breeding programmes. Gene actions are mainly divided into two types: additive and non-additive gene actions. Non-additive gene action comprises of dominance, epistasis and overdominance (Bernardo, 2002). GCA is a measure of the additive gene action, while SCA is an estimate of deviation from the additivity, deviation which may be greater or lesser compared to the expected value (Olfati et al., 2012). When the ratio GCA to SCA approaches one, there is greater predictability of additive gene action. In earlier studies, various gene actions have been identified as controlling various traits in sweetpotato. Both additive and non-additive gene actions have been found to be important in controlling root yield, with additive gene action slightly more predominant (Shumbusha et al., 2014; Musembi et al., 2015). Given the nature of its vegetative reproduction system, 100% of the selected genetic effects are inherited by the progeny generation, providing the strongest possible selection response in sweetpotato.

The success of any genetic improvement program depends on the level of heritability of desired traits. Heritability indicates to what extent phenotypic values correspond to the breeding values (Falconer and Mackay, 1996). Where a gene governing a trait occurs at a high frequency in the progeny, this is an indication of its high heritability, and that genetic

gains can be achieved through conventional breeding (Bernardo, 2002). Heritability values are broadly classified into narrow- or broad-sense. Narrow-sense heritability is defined as the ratio of the additive genetic variance (σ^2_A) to the phenotypic variance (σ^2_P), while broad-sense heritability is the ratio of the total genetic variance (σ^2_G) to the phenotypic variance (σ^2_P) (Falconer and Mackay, 1996). High estimates of narrow sense heritability means that a strong response to selection, and strong genetic gains are more likely to be achieved by combining two parents with strong GCA effects (Freeman, 2009). However, progeny from crosses of parents with high levels of SCA may also produce superior hybrids (Freeman, 2009). In sweetpotato, broad-sense heritability estimates are also important. Broad sense heritability values have been reported for both fresh roots and vine yields with values of 0.68 and 0.50 (Rukundo et al., 2017), and 0.44 and 0.48 (Tumwegamire et al., 2016). In contrast, narrow-sense heritability values for storage root yield have been reported of 0.06 to 0.37 (Some et al., 2015).

1.4.7. Breeding sweetpotato for dual-purpose traits

Dual-purpose varieties have a comparative advantage over varieties developed only for their storage roots or aboveground biomass for farmers seeking to grow food and fodder, concurrently. Whilst SSA has a large genetic diversity in sweet potato, including dual-purpose varieties, most breeding programs have focused on breeding for enhanced storage root yields and dry matter content. León-Velarde (2000) reported a number of accessions having potential to be developed as dual-purpose varieties. Dual-purpose sweetpotato varieties are selected based on the ratio of root-to-vine production, and on a dry matter basis. Based on root to vine ratio, clones can be classified into five groups: forage, low-dual-purpose, high dual-purpose, low-root production and high root production clones (León-Velarde, 2000). In the past, production of roots was considered to be negatively correlated to that of aboveground biomass (Enyi, 1977). However, recent studies have shown that it is possible to obtain good performances for both traits by novel dual-purpose varieties (Lukuyu et al., 2014; Lestari and Hapsari, 2015).

1.5. Conclusions

Despite the great economic importance of the crop, there are many challenges affecting sweetpotato production and productivity in SSA such as a lack of growing material of improved cultivars, biotic and abiotic stresses, and socioeconomic constraints including shortage of clean and adequate planting materials and limited funding for research and technology development. The review described opportunities to sweetpotato production and improvement in SSA including increased adoption as a low-input crop, increased demand by

farmers, policy support, and availability of new genomic and genetic resources for breeding and gender equity in sweetpotato production.

The current review revealed a need to combine efforts from various stakeholders including farmers, breeders, socio-economists and policy makers in order to overcome the stated challenges and therefore to fully exploit the genetic potential of the crop for human-wellbeing. Understanding of the underlying challenges and opportunities to sweetpotato production and breeding help to devise options to enhance sweetpotato production and productivity in SSA.

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2. Chapter Two: Assessment of the roles of sweetpotato and farmer-preferred traits in a crop-livestock farming system: implications for breeding dual-purpose varieties in Rwanda

Abstract

Sweetpotato [*Ipomoea batatas* (L.) Lam] is a major food crop in the world. In Rwanda the crop is highly valued in a crop-livestock mixed farming system due to limited availability of agricultural lands. Sweetpotato provides human food and animal feed but has been under-researched especially in the breeding for dual-purpose varieties incorporating farmer-preferred traits. The objective of this study was, therefore, to assess the role of sweetpotato in the crop-livestock farming system, to identify farmer-preferred traits and to establish farmer-led priorities in breeding dual-purpose sweetpotato varieties in Rwanda. A participatory rural appraisal (PRA) study was conducted in three selected districts of Rwanda namely Bugesera, Huye and Nyagatare. Data on demographics, the uses of sweetpotato and farmers' trait preferences in sweetpotato varieties were collected and analysed. About 63% of the respondents were household heads and 56.7% were women. In the Nyagatare District most of farmers (76.7%) reported deriving a cash income from crop and livestock production. In the Huye and Bugesera Districts about 70% and 93.3% of interviewed farmers reported owning agricultural lands of less than 0.5 ha, respectively. The top five crops grown across the three districts were sweetpotato, beans, cassava, maize and sorghum. Sweetpotato was ranked the most valuable crop during focus group discussions. In Huye District, a high percent (56.7%) of respondents consumed sweetpotato every day, followed by Nyagatare with 53.3% consuming it at least twice a week. Over 70% of respondents believed that adoption of improved sweetpotato varieties could provide a greater increase in root and upper biomass yields than using improved crop management practices. All respondents wanted to grow new sweetpotato varieties with improved root production combined with high above ground biomass. About 87.7, 66.6 and 51.1% of the respondents indicated that root-related traits of the crop such as high dry matter content, red skin colour and yellow flesh colour were additional preferred traits, respectively. Therefore, farmer-preferred dual-purpose sweetpotato varieties with improved root and green fodder yields could be developed to enhance the sustainable production and adoption of sweetpotato in a mixed farming system in Rwanda. Findings from this study can also be the basis to formulate frameworks to develop farmer-preferred sweetpotato varieties.

Keywords: dual-purpose sweetpotato, farmer-preferred traits, farming system, focus group discussion, *Ipomoea batatas*, participatory rural appraisal

2.1. Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam] is an important crop in many regions of the world. Asia and Africa are the predominant sweetpotato producing continents, contributing to 76.4 and 19.2% of the world annual production, respectively. In Rwanda, sweetpotato is the fourth important crop after plantains, cassava and potato (FAOSTAT, 2013). The total annual production of the crop is 1,081,224 tonnes with an estimated area of 112,436 ha. Sweetpotato has multiple uses including food, animal feed and as an industrial raw material for the production of starch and colorants. It provides more edible energy per hectare than other food security crops such as maize, wheat and rice (Mukhopadhyay et al., 2011). The orange-fleshed sweetpotato varieties (OFSPs) are rich in beta-carotene content, the precursor of vitamin A, an essential nutrient (Ginting, 2013; Gruneberg et al., 2015). In developing countries, sweetpotato is mainly cultivated for its storage roots for human consumption and its above ground biomass for livestock feed, making it an ideal dual-purpose crop (León-Velarde, 2000; Ralevic et al., 2010; Valbuena et al., 2012). Sweetpotato is a relatively drought resilient crop, providing reasonable yields in marginal areas characterized by high production risks and limited production inputs (Almekinders and Elings, 2001).

The dual-purpose nature of sweetpotato is highly valued in crop-livestock mixed farming systems in sub-Saharan Africa, including that practiced in Rwanda where the availability of agricultural lands is severely limited (Kamanzi and Mapiye, 2012). Rwanda has a high population density estimated at 467 inhabitants.km² (FAOSTAT, 2013). Sweetpotato is grown across varied agro-ecological zones in smallholder farming systems. The most suitable agro-ecologies for cultivating the crop are the low and mid-altitudes including the semi-arid areas of Bugesera and Nyagatare, which are situated in the Eastern Province of Rwanda. The mean on-farm yield of sweetpotato in Rwanda is 9.53 t.ha⁻¹ which is below the attainable mean yield of 14.2 t.ha⁻¹ (FAOSTAT, 2013). The yield gap is attributed to biotic and abiotic stresses, and socio-economic constraints that vary across agro-ecologies in the country. Socioeconomic factors limiting sweetpotato production in Rwanda include: limited agricultural land; shortage of clean and adequate planting material; and poor agronomic management practices (Fuglie, 2007; Niyireba, 2013).

Farming in Rwanda is characterised by fragmented small plots of land measuring less than one hectare per household (MINAGRI, 2010). Each household involves in a number of interdependent farming enterprises, predominantly in crop and livestock production. The farming systems in the country are highly heterogeneous due to variable household resources (Dixon et al., 2001). Therefore, any strategy to develop these farming systems

should consider the prevailing farming practices, farmer's constraints and the overall socio-economic aspects (Bucagu et al., 2013). A research approach to document farmers' circumstances and constraints should involve farmers' participatory methods across the farming systems (Almekinders and Elings, 2001).

Participatory research techniques have been used successfully to identify farmers' perceived production constraints, preferred crop varieties and key traits for deployment of production packages and the development of suitable crop varieties (Ndolo et al., 2001; Ndirigwe et al., 2005; Tefera et al., 2013). Depending on the breeding goals and the environment, farmers can contribute significantly at different stages of crop cultivar design, development, release and adoption (Bhargav and Meena, 2014). Any crop improvement program should focus on the needs of smallholder farmers and their value chains to satisfy demands and to ensure a successful release and wide-adoption of newly bred cultivars for food security and improved livelihoods. Among participatory research techniques, the participatory rural appraisal (PRA) approach has been successfully used in identifying farmers' constraints, preferred traits and needs (Chiona, 2010; Muhinyuza et al., 2012; Kivuva et al., 2014). In Rwanda, sweetpotato is an important crop widely cultivated in the crop-livestock mixed farming systems due to limited agricultural lands. However, the crop has not been fully exploited with regards to breeding for dual-purpose varieties incorporating farmers-preferred traits. Therefore, the objectives of this study were to assess the role of sweetpotato in the crop-livestock farming system, to identify farmer-preferred traits, and to clarify the objectives in breeding dual-purpose varieties in Rwanda. Information from this study may be valuable in the breeding of dual-purpose sweetpotato varieties with improved root and green fodder yields for mixed farming systems across Africa.

2.2. Material and methods

2.2.1. Study sites

The study was conducted across three selected districts of Rwanda, namely Huye, Nyagatare and Bugesera (Figure 2.1). These districts are known for their sweetpotato production. Huye District (02° 29'S, 29° 46'E) is situated in the Southern Province with an altitude of 1,700 m above sea level [masl]. Huye has an average temperature of 18.7°C with a total annual rainfall of 1200 mm. Nyagatare and Bugesera Districts are situated in the Eastern Province and known for their mixed crop-livestock farming systems. Bugesera (02° 17' S; 30° 16' E) is located in the lowlands (< 1400 masl) with a total annual rainfall of 700-900 mm and a mean temperature of 20.8°C (Murayi et al., 1987). Bugesera is a hotspot area for sweetpotato virus diseases. Nyagatare District (1° 22' 51.6" S; 30° 17' 07" E) is

located in the East Savanna agro-ecological zone with an altitude of 1400 masl (Nabahungu and Visser, 2011). This district ranks first in livestock production in the country.

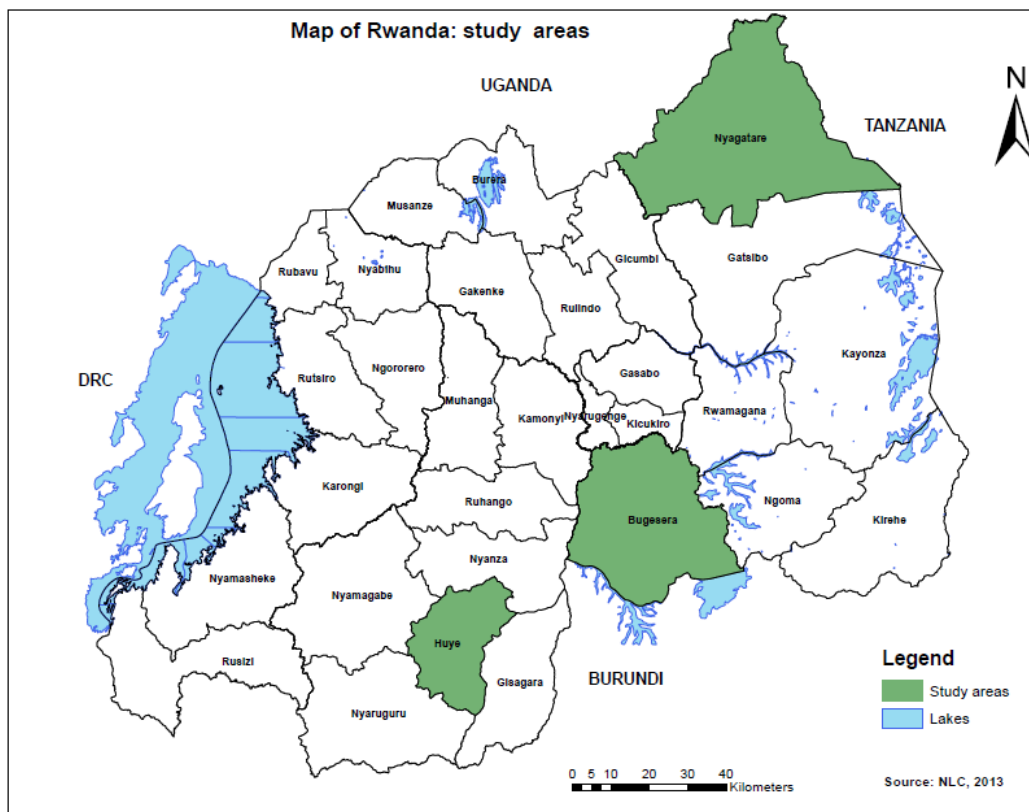


Figure 2.1: Map of Rwanda showing the study areas

2.2.2. Sampling procedure and data collection

A purposive sampling (Frankel and Devers, 2000) was used in order to increase the likelihood of including relevant sites and samples in the study. The following six administrative sectors were selected in the three districts: Mwogo, Ntarama and Rweru (Bugesera District), Huye (Huye District), and Katabagema and Tabagwe (Nyagatare District). In each sector, two administrative cells were sampled, resulting in a total of 12 cells. Two villages per cell were sampled, providing a total of 24 villages for the study. In each village three to eight farmers were sampled. This provided a total of 90 farmers sampled using semi-structured interviews. Focus group discussions (FGDs) were held involving nine focus groups comprising farmers, local leaders and key informants. Each focus group was composed of six to ten representative farmers who were sampled based on their experience in sweetpotato production. A total of 78 farmers participated in the FGDs across the three districts.

A multidisciplinary research team was constituted for the study. The team composed of a sweetpotato breeder, two research technicians, a socio-economist, an animal nutritionist and local key informants.

Data were collected through semi-structured interviews, focus group discussion and a transect walk. In addition, secondary data were collected from previous reports. Semi-structured questionnaires were used to collect data from individual farmers. Data collected through semi-structured interviews included the importance and uses of sweetpotato, constraints to sweetpotato production, farmers' interest in dual-purpose varieties and consumer preferences. Focus group discussions were held to gather information such as importance of the crop in food security, ranking of the currently grown sweetpotato varieties and their characteristics, and the role of gender in sweetpotato production. Focus group discussions also included pair-wise and matrix ranking of the crops grown. Gender balance was taken into consideration by involving both male and female farmers during the semi-structured interviews and focus groups. The gender groups were essential in order to collect data on role of males and females in sweetpotato production and post-harvest activities.

2.2.3. Data analysis

Data collected were analysed using Statistical Package for Social Sciences (SPSS) for windows Release version 21 (SPSS, 2012). The analyses involved descriptive statistics and cross-tabulations in order to calculate percentage of respondents for each question or focus group. Chi-square tests were computed in order to determine associations between collected parameters and the study districts, and therefore, to make statistical inferences.

2.3. Results

2.3.1. Demographic information

The roles of respondents among households were categorized as heads, spouses or children. In this study, all household heads were husbands. The majority of respondents composed of household heads in Bugesera (80%) and Nyagatare (66.7%), whereas a relatively equal percent of male and female heads were found in Huye (Table 2.1). There were significant ($X^2 = 10.263$; $P = 0.036$) differences between Sectors per District and between Districts on the roles of respondents. The age of respondents varied between 18 and 66 years old with a mean of 44.7 years. The numbers of women and men farmers sampled for the study were almost equal, with a slightly higher proportion of women respondents (54.4%). However, sampled male and female respondents varied significantly ($X^2 = 19.819$; $P = 0.0001$) among and between surveyed districts (Table 2.1). Interviewed

farmers had various level of education with 63.3% having passed primary school education, while 22.2% had no formal education.

Table 2.1: Roles in the households and gender of respondents during a formal PRA survey in three selected districts of Rwanda

Variable	Districts and Sectors ^a							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Roles in the household								
Head	12 (40)	7 (23.3)	5 (16.7)	24 (80)	13 (43.3)	4 (13.3)	16 (53.3)	20 (66.7)
Spouse	2 (6.7)	1 (3.3)	2 (6.7)	5 (16.7)	15 (50)	3 (10)	7 (23.3)	10 (33.3)
Children	1 (3.3)	0 (0.0)	0 (0.0)	1 (3.3)	2 (6.7)	0 (0.0)	0 (0.0)	0 (0.0)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 10.263; Df ^b = 4; P = 0.036							
Gender								
Male	11 (36.7)	6 (20)	4 (13.3)	21 (70)	4 (13.3)	3 (10)	11 (36.7)	14 (46.7)
Female	4 (13.3)	2 (6.7)	3 (10)	9 (30)	26 (86.7)	4 (13.3)	12 (40)	16 (53.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 19.819; Df = 2; P = 0.0001							

^a Values in parenthesis denote percentages

^b Df = degrees of freedom

2.3.2. Sources of incomes of households and forms of land ownership

Crop production activities were the main source of income for 60 and 73.3% of the respondents in the Bugesera and Huye Districts, respectively. A mixed crop-livestock system was the main source of income in the Nyagatare District, with 76.7% farmers pursuing their livelihood in this sector (Table 2.2). Sources of income varied significantly across districts ($X^2 = 16.121$, $P = 0.001$). About 70, 93.3 and 100% of the respondents owned farms in Huye, Bugesera and Nyagatare Districts, respectively. However, in the Huye District 26.7% of respondents rented farms (Table 2.2). Land tenure varied significantly ($X^2 = 14.096$; $P = 0.007$) between the study districts. Approximately 45% of the interviewees had farms of less than 0.5 ha. In the Nyagatare District 80% of the respondents had land holdings of 2 ha or more.

Table 2.2: Sources of incomes and land tenure among respondents in the three districts of Rwanda

Variable	Districts and Sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Source of income								
Crop production	8 (26.7)	4 (13.3)	6 (20)	18 (60)	22 (73.3)	2 (6.7)	5 (16.7)	7 (23.3)
Crop and livestock production	7 (23.3)	4 (13.3)	1 (3.3)	12 (40)	8 (26.7)	5 (16.7)	18 (60)	23 (76.7)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 16.121; Df = 2; P = 0.001							
Land tenure								
Owner	15 (50)	7 (23.3)	6 (20)	28 (93.3)	21 (70)	7 (23.3)	23 (76.7)	30 (100)
Rental	0 (0.0)	1 (3.30)	1 (3.3)	2 (6.7)	8 (26.7)	0 (0.0)	0 (0.0)	0 (0.0)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	29 (96.7) ^a	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square value = 14.096; Df = 2; P = 0.007							

^a: 1/30 of the interviewees in Huye District revealed that they borrowed land.

2.3.3. Crops grown by respondent farmers

Overall, 18 different crops were grown in the study areas (Table 2.3). The most widely grown crops were sweetpotato (21.4%), beans (20.8%), cassava (14.2%), maize (11.9%) and banana (9.2%).

Table 2.3: Crops grown by respondents farmers in the districts of Bugesera, Huye and Nyagatare in Rwanda during the 2015 season

No	Crops	Percent	Rank	No	Crops	Percent	Rank
1	Banana	9.2	6	10	Groundnut	2.2	8
2	Bean	20.8	2	11	Irish potato	0.6	14
3	Cassava	14.2	3	12	Amaranths	1.9	9
4	Maize	11.9	4	13	Carrot	0.3	16
5	Rice	1.4	10	14	Forage	0.3	17
6	Sorghum	10	5	15	Soybean	2.5	7
7	Sweetpotato	21.4	1	16	Cabbage	1.1	11
8	Tomato	0.6	13	17	Eggplant	1.1	12
9	Coffee	0.3	15	18	Onion	0.3	18

2.3.4. Decision making on which crop to grow

Table 2.4 shows how decision making is shared among family members. The decision of which crop to grow during a season was mostly made by household heads with 30, 36.7 and 37.9% in the Nyagatare, Huye and Bugesera Districts, respectively (Table 2.4). In Huye District 3.3% of the respondents mentioned that the responsibility was that of children due to the migration of their parents to urban areas in search of jobs in the commerce and manufacturing industries. About 40, 51.7 and 60% of respondents, respectively, in the Huye, Nyagatare and Bugesera Districts indicated that the Government provides directives regarding choice of crops to be grown especially in 'ring fenced' or 'dedicated' farming areas in terms of the national land consolidation policy. Non-significant differences were found between districts for the responsibility of respondents in decision making on what crop to grow.

Table 2.4: Responsibility for decision making on what crop to grow in the Bugesera, Huye and Nyagatare Districts of Rwanda, 2015

Variable	Districts and Sectors							Total
	Bugesera			Total	Huye	Nyagatare		
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Decision making in the household on what crop to grow								
Head	6 (20.7)	1 (3.4)	4 (13.8)	11 (37.9)	11 (36.7)	0 (0.0)	9 (30)	9 (30)
Spouse	1 (3.4)	1 (3.4)	1 (3.4)	3 (10.3)	6 (20)	0 (0.0)	3 (10)	3 (10)
Government	7 (24.1)	6 (20.7)	2 (6.9)	15 (51.7)	12 (40)	7 (23.3)	18 (60)	18 (60)
Total	14 (48.3)	8 (27.6)	7 (24.1)	29 (100) [†]	29 (96.7) [‡]	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 3.986; Df = 4; P = 0.5							

†: 1/30 interviewees in Bugesera District did not respond to the question

‡: 1/30 respondents attributed responsibility on which crop to grow to children.

2.3.5. Uses of sweetpotato in the farming systems

All the respondents pointed out that sweetpotato is commonly used for immediate consumption of roots (Table 2.5). Other most important uses include as a cash crop (60%) and for livestock feed (28.9%). Only 1.1% of the interviewees used storage roots for food processing.

About 80, 86.7 and 96.7% of the respondents used sweetpotato vines as a green fodder for livestock feed in the Huye, Bugesera and Nyagatare Districts, respectively (Table 2.6). A limited number of respondents (10.2%) mentioned the use of vines as planting material,

though a relatively high percentage (20%) was reported in the Huye District. Vine-based fodder was the commonest use in Nyagatare District, reported by nearly all the respondents (96.7%). There were non-significant differences for the use of sweetpotato vines across the three surveyed Districts.

Table 2.5: Different uses of sweetpotato roots by farmers in Bugesera, Huye and Nyagatare Districts of Rwanda

No	Uses	Number of respondents		Rank
		N	Percent	
1	Food	90	100	1
2	Processing	1	1.11	5
3	Cash crop	54	60	2
4	Feed	26	28.88	3
5	Planting material	3	3.33	4

N: denote number of farmers in a given option out of the total number of respondents.

Table 2.6: Uses of sweetpotato vines across the three districts of Rwanda

Variable	Districts and Sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Uses of sweetpotato vines				Respondents (%)				
Green fodder	12 (40)	7 (23.3)	7 (23.3)	26 (86.7)	24 (80)	7 (23.3)	22 (73.3)	29 (96.7)
Planting material	3 (10)	1 (3.3)	0 (0.0)	4 (13.3)	6 (20)	0 (0.0)	1 (4.3)	1 (3.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (30)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 3.936; Df = 2; P = 0.14							

2.3.6. Level of sweetpotato consumption and use of vines for livestock feed

In the Huye District most respondents (56.7%) consumed sweetpotato roots every day, followed by Nyagatare District where 53.3% interviewees consumed sweetpotato roots at least twice a week. On the other hand, 36.7% of the respondents consumed sweetpotato during a shortage of other main staple foods (Table 2.7). The frequency of eating sweetpotato roots per district is indicated in Table 2.7. Consumption frequency varied significantly ($X^2 = 27.950$; $P = 0.0001$) within and between districts. Overall, most farmers (52.2%) used sweetpotato vines for livestock feed, depending on its availability. In the Huye and Nyagatare Districts most respondents (60%) used vine-based fodder systems, followed

by those in Bugesera District with 36.7% (Table 2.7). The frequency of using sweetpotato vines as a green fodder varied significantly ($X^2 = 17.645$; $P = 0.007$) within and between study districts.

Table 2.7: Frequency of sweetpotato root consumption and use of vines for livestock feed reported by respondents in the Bugesera, Huye and Nyagatare Districts of Rwanda

Variable	Districts and sectors							
	Bugesera			Total	Huye	Nyagatare		Total
Mwogo	Ntarama	Rweru	Katagabema			Tabagwe		
Frequency of boiled root consumption				Respondents (%)				
Everyday	2 (6.7)	0 (0.0)	3 (10)	5 (16.7)	17 (56.7)	0 (0.0)	2 (6.7)	2 (6.7)
Once a week	3 (10)	3 (10)	0 (0.0)	6 (20)	0 (0.0)	1 (3.3)	3 (10)	4 (13.3)
Twice a week	4 (13.3)	3 (10)	1 (3.3)	8 (26.7)	6 (20)	4 (13.3)	12 (40)	16 (53.3)
When available	6 (20)	2 (6.7)	3 (10)	11 (36.7)	7 (23.3)	2 (6.7)	6 (20)	8 (26.7)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 27.950; Df = 6; P = 0.0001							
Frequency of using vines for livestock feed								
Everyday	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (13.3)	0 (0.0)	0 (0.0)	0 (0.0)
Once a week	6 (20)	3 (10)	0 (0.0)	9 (30)	1 (3.3)	2 (6.7)	2 (6.7)	4 (13.3)
Twice a week	2 (6.7)	3 (10)	5 (16.7)	10 (33.3)	7 (23.3)	2 (6.7)	6 (20)	8 (26.7)
Depending on availability	7 (23.3)	2 (6.7)	2 (6.7)	11 (36.7)	18 (60)	3 (10)	15 (50)	18 (60)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 17.645; Df = 6; P = 0.007							

2.3.7. Farmers strategies to increase sweetpotato productivity

Most respondents perceived that crop improvement would be the best strategy to increase sweetpotato root productivity. This was stated by more respondents (93.3%) in the Huye District than respondents in the Bugesera and Nyagatare Districts (76.7%) (Table 2.8). In Bugesera and Nyagatare Districts, a limited number of farmers (16.7%) believed that better crop management options could improve sweetpotato productivity (Table 2.8). Farmers' perceptions regarding strategies to increase root production were relatively similar across districts.

Among respondent farmers about 86.7% in Nyagatare and 90% in both Bugesera and Huye Districts believed that improved sweetpotato varieties could bring about high levels of fodder production, whereas only 10% of respondents in Bugesera and Nyagatare Districts proposed

better crop management options (Table 2.8). Perceived strategies to increase fodder production did not vary across districts.

Table 2.8: Farmers perceived strategies to increase sweetpotato production across three selected districts of Rwanda

Variable	Districts and sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Farmers perceived strategies to increase storage root production								
	Respondents (%)							
Improved variety	12 (40)	7 (23.3)	4 (13.3)	23 (76.7)	28 (93.3)	4 (13.3)	19 (63.3)	23 (76.7)
Crop management	3 (10)	1 (3.3)	1 (3.3)	5 (16.7)	2 (6.7)	2 (6.7)	3 (10)	5 (16.7)
Education on agricultural practices	0 (0.0)	0 (0.0)	2 (6.7)	2 (6.7)	0 (0.0)	1 (3.3)	1 (3.3)	2 (6.7)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 4.176; Df = 4; P = 0.383							
Perceived strategies to increase green fodder production from sweetpotato vines								
Crop improvement	13 (43.3)	7 (23.3)	7 (23.3)	27 (90)	27 (90)	7 (23.3)	19 (63.3)	26 (86.7)
Crop management	2 (6.7)	1 (3.3)	0 (0.0)	3 (10)	2 (6.7)	0 (0.0)	3 (10)	3 (10)
Access to more land	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (3.3)	0 (0.0)	1 (3.3)	1 (3.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 1.275; Df = 4; P = 0.866							

2.3.8. Use of sweetpotato vines for livestock feed and its relative value among various feed sources in Rwanda

Most respondents in all the surveyed districts used vines for cattle feed. The highest percentage (90%) of respondents fed their cattle using vines in the Nyagatare District. Huye and Bugesera Districts had relatively fewer farmers who used vines as green fodder with 56.7 and 66.7%, respectively (Table 2.9). The predominant system of cattle feeding using sweetpotato vines is based on cut-and-carry system. This system is in line with the zero freehold grazing policy of Rwanda devised to minimize land degradation. There were significant ($X^2 = 15.224$; $P = 0.004$) differences between districts and sectors in use of sweetpotato vines for feed.

The sweetpotato-based feed system ranked second among sources of forage by 43 and 47% of respondent farmers in the Bugesera and Nyagatare Districts, respectively (Table 2.9). In the Huye District, about 43% of the respondents ranked sweetpotato vines third, after Napier grass and *Calliandra* spp. In Rwanda, Napier grass (*Pennisetum purpureum*), *Calliandra* spp., maize and rice residues are important feed sources for livestock. Significant

differences ($X^2 = 17.189$; $P = 0.009$) were found between districts and sectors regarding the rank of sweetpotato vines as a fodder crop.

Table 2.9: The proportion of farmers (%) who used sweetpotato vines for feed and the rank among other feed sources in the Bugesera, Huye and Nyagatare Districts of Rwanda

Variable	Districts and Sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Proportion of farmers (%) who used sweetpotato vines for feed					Respondents (%)			
Cattle	9 (30)	7 (23.3)	4 (13.3)	20 (66.7)	17 (56.7)	5 (16.7)	22 (73.3)	27 (90)
Pigs	1 (3.3)	1 (3.3)	0 (0.0)	2 (6.7)	8 (26.7)	0 (0.0)	0 (0.0)	0 (0.0)
Goat	5 (16.7)	0 (0.0)	3 (10)	8 (26.7)	5 (16.7)	2 (6.7)	1 (3.3)	3 (10)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 15.224; Df = 4; P = 0.004							
Rank of sweetpotato vines for feed relative to other feed sources such as <i>Calliandra</i> spp., maize stalk, rice straw and Napier grass								
First	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (13.3)	0 (0.0)	0 (0.0)	0 (0.0)
Second	5 (16.7)	4 (13.3)	4 (13.3)	13 (43.3)	10 (33.3)	4 (13.3)	10 (33.3)	14 (46.7)
Third	5 (16.7)	3 (10)	3 (10)	11 (36.7)	13 (43.3)	1 (3.3)	4 (13.3)	5 (16.7)
Fourth	5 (16.7)	1 (3.3)	0 (0.0)	6 (20)	3 (10)	2 (6.7)	9 (30)	11 (36.7)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 17.189; Df = 6; P = 0.009							

2.3.9. Farmers-preferred sweetpotato varieties

Most respondent farmers expressed a desire for productive dual-purpose sweetpotato varieties in preference to specifically storage root or vine types. In the Huye District most farmers (96.7%) would prefer dual-purpose varieties, compared to Nyagatare and Bugesera Districts with 80 and 83.3% of farmers, respectively (Table 2.10). The proportions of respondents on the level of sweetpotato preferences were not significantly different across districts.

Table 2.10: Preferences of respondents (%) for sweetpotato varieties for root, fodder or dual-purpose production in three districts of Rwanda

Variable	Districts and sectors							Total
	Bugesera			Total	Huye	Nyagatare		
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Preferences of sweetpotato varieties				Respondents (%)				
Root production	2 (6.7)	2 (6.7)	0 (0.0)	4 (13.3)	1 (3.3)	0 (0.0)	4 (13.3)	4 (13.3)
Fodder production	1 (3.3)	0 (0.0)	0 (0.0)	1 (3.3)	0 (0.0)	1 (3.3)	1 (3.3)	2 (6.7)
Dual-purpose	12 (40)	6 (20)	7 (23.3)	25 (83.3)	29 (96.7)	6 (20)	18 (60)	24 (80)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 4.538; Df = 4; P = 0.338							

2.3.10. Constraints to sweetpotato production

Respondent farmers reported several constraints to sweetpotato production. Many respondents (43.3%) reported pests as the most important constraint in the Bugesera and Huye Districts, with 36.7% in Nyagatare (Table 2.11). Other constraints reported were diseases, shortage of planting material and drought. Non-significant differences were detected between districts and sectors for the reported constraints.

The top two main constraints to sweetpotato production identified through focused group discussion were sweetpotato virus disease (SPVD) and a lack of planting material. SPVD was described as a major constraint (Table 2.11) in all three surveyed districts. A lack of dual-purpose varieties and poor soil fertility were the overriding constraints specific to Huye District, whereas weevils and a lack of post-harvest facilities were reported as the main constraints in Nyagatare District.

Table 2.11: Major constraints to sweetpotato production in three selected districts of Rwanda

Variable	Districts and sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Major constraints to sweetpotato production based on farmer-researcher discussion								
Pests	5 (16.7)	3 (10)	5 (16.7)	13 (43.3)	13 (43.3)	3 (10)	8 (26.7)	11 (36.7)
Diseases	7 (23.3)	2 (6.7)	2 (6.7)	11 (36.7)	9 (30)	3 (10)	3 (10)	6 (20)
Soil degradation	1 (3.3)	1 (3.3)	0 (0.0)	2 (6.7)	1 (3.3)	0 (0.0)	0 (0.0)	0 (0.0)
Shortage of clean planting material	0 (0.0)	1 (3.3)	0 (0.0)	1 (3.3)	4 (13.3)	0 (0.0)	7 (23.3)	7 (23.3)
Lack of market	2 (6.7)	1 (3.3)	0 (0.0)	3 (10)	1 (3.3)	0 (0.0)	0 (0.0)	0 (0.0)
Lack of processing facility	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3 (10)	3 (10)
Drought	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2 (6.7)	1 (3.3)	2 (6.7)	3 (10)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 20.478; Df = 12; P = 0.059							

Major constraints based on focus group discussion

Constraint	Districts			Total scores	Overall ranking
	Bugesera Rank and scores	Huye Rank and scores	Nyagatare Rank and scores		
Lack of planting material	1 (6)	-	1 (7)	13	2
Virus disease	2 (5)	3 (4)	3 (5)	14	1
Drought	3 (4)	2 (5)	5 (2)	11	3
Insects	4 (3)	4 (3)	6 (1)	7	5
Lack of market	5 (2)	-	-	2	8
Weevils	-	5 (2)	2 (6)	8	4
Lack of post-harvest facilities	-	-	4 (4)	4	7
Lack of dual-purpose varieties	-	1 (6)	-	6	6
Poor soil fertility	-	6 (1)	-	1	9

-: Not ranked among the preference crops grown in the district and data did not allow to conduct significant tests.

2.3.11. Current level of production of dual-purpose sweetpotato varieties and use of production inputs

Most respondents in the study areas have not yet grown improved dual-purpose variety, especially in the Huye District (93.3%) (Table 2.12). About 60 and 66.7% of respondents in

Bugesera and Nyagatare Districts were not growing dual-purpose sweetpotato varieties, respectively. The distribution of farmers growing dual-purpose varieties was significantly different ($X^2 = 9.545$; $P = 0.008$) across districts and sectors. Over 80% of the respondents in Huye used fertilizers, whereas 60 and 90% of respondents in the Bugesera and Nyagatare Districts, did not use fertilisers, in that order (Table 2.12). Surprisingly, Nyagatare was the district with the most farmers not using fertilisers, although it is the most important district for livestock production. There were highly significant differences ($X^2 = 36.108$; $P = 0.0001$) between districts and sectors in the use of fertilisers.

Table 2.12: Proportion of respondents (%) growing dual-purpose sweetpotato varieties; and using fertilizers in three districts of Rwanda

Variable	Districts and sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Grow dual purpose sweetpotato varieties								
Yes	6 (20)	0 (0.0)	6 (20)	12 (40)	2 (6.7)	4 (13.3)	6 (20)	10 (33.3)
No	9 (30)	8 (26.7)	1 (3.3)	18 (60)	28 (93.3)	3 (10)	17 (56.7)	20 (66.7)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 9.545, Df = 2, P = 0.008							
Use of fertilizers								
Yes	2 (6.7)	5 (16.7)	5 (16.7)	12 (40)	26 (86.7)	0 (0.0)	3 (10)	3 (10)
No	13 (43.3)	3 (10)	2 (6.7)	18 (60)	4 (13.3)	7 (23.3)	20 (66.7)	27 (90)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 36.108; Df = 2, P = 0.0001							

2.3.12. Major characteristics of farmers-preferred sweetpotato varieties for storage root production

About 50 and 76.6% of farmers preferred marketable storage roots, in the Bugesera and Huye Districts, respectively, whereas in the Nyagatare District the farmers wanted medium sized roots (Table 2.13). Non-significant differences existed between districts and sectors in their choice of storage root size. Across districts, 50, 60 and 90% of respondents expressed their need for sweetpotato varieties with roots of red skin colour, respectively in the Nyagatare, Bugesera and Huye Districts. White-fleshed storage roots were preferred by 50% of respondents in Bugesera, and 63.3% in Nyagatare. Most farmers (73.3%) in Huye District preferred yellow-fleshed types. Districts and sectors differed significantly for flesh colour ($X^2 = 23.396$; $P = 0.001$) and skin colour ($X^2 = 12.15$; $P = 0.016$) preferences. High dry matter

content (DMC) was preferred by most respondents across all sites. Over 80% of respondents preferred high DMC in Bugesera and Huye, and 96.7% respondents in Nyagatare preferred this trait. Farmer preferences in terms of DMC were similar across districts.

Table 2.13: Farmer-preferred traits of sweetpotato roots in Bugesera, Huye and Nyagatare Districts of Rwanda

Trait and class	Districts and sectors							
	Bugesera			Total	Huye	Nyagatare		Total
	Mwogo	Ntarama	Rweru			Katabagema	Tabagwe	
Storage root size								
Small	0 (0.0)	0 (0.0)	1 (3.3)	1 (3.3)	3 (10)	0 (0.0)	0 (0.0)	0 (0.0)
Medium	8 (26.7)	2 (6.7)	3 (10)	13 (43.3)	4 (13.3)	2 (6.7)	14 (46.7)	16 (53.3)
Marketable	7 (23.3)	5 (16.7)	3 (10)	15 (50)	23 (76.6)	5 (16.7)	8 (26.7)	13 (43.4)
Either	0 (0.0)	1 (3.3)	0 (0.0)	1 (3.3)	0 (0.0)	0 (0.0)	1 (3.3)	1 (3.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 15.01; Df = 6; P = 0.059							
Skin colour								
White	6 (20)	3 (10)	0 (0.0)	9 (30)	3 (10)	1 (3.3)	11 (36.7)	12 (40)
Red	8 (26.7)	4 (13.3)	6 (20)	18 (60)	27 (90)	5 (16.7)	10 (33.3)	15 (50)
Either	1 (3.3)	1 (3.3)	1 (3.3)	3 (10)	0 (0.0)	1 (3.3)	2 (6.7)	3 (10)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 12.15; Df = 4; P = 0.016							
Flesh colour								
White	5 (16.7)	5 (16.7)	5 (16.7)	15 (50)	4 (13.3)	2 (6.7)	17 (56.7)	19 (63.3)
Yellow	10 (33.3)	2 (6.7)	2 (6.7)	14 (46.7)	22 (73.3)	5 (16.7)	5 (16.7)	10 (33.3)
Orange	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	4 (13.3)	0 (0.0)	0 (0.0)	0 (0.0)
Either	0 (0.0)	1 (3.3)	0 (0.0)	1 (3.3)	0 (0.0)	0 (0.0)	1 (3.3)	1 (3.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 23.396; Df = 6; P = 0.001							
Dry matter content								
High	12 (40)	6 (20)	7 (23.3)	25 (83.3)	25 (83.3)	7 (23.3)	22 (73.3)	29 (96.7)
Medium	3 (10)	2 (6.7)	0 (0.0)	5 (16.7)	5 (16.7)	0 (0.0)	1 (3.3)	1 (3.3)
Total	15 (50)	8 (26.7)	7 (23.3)	30 (100)	30 (100)	7 (23.3)	23 (76.7)	30 (100)
Significant test	Chi-square = 3.314; Df = 2; P = 0.191							

2.3.13. Importance of sweetpotato according to focus group discussions

During focus group discussions sweetpotato was ranked as the most important crop, with a total score of 16. The crop has been ranked first in both Bugesera and Huye Districts. A pair-wise ranking of the five crops is given in Table 2.14.

Table 2.14: Pair-wise ranks of five important crops widely grown and preferred by farmers among focus groups in three districts of Rwanda

Crop	Districts			Total scores	Overall ranking
	Bugesera; N=6	Huye; N=10	Nyagatare; N=10		
	Rank (scores)	Rank (scores)	Rank (scores)		
Sweetpotato	1 (6)	1 (8)	5 (2)	16	1
Dry bean	2 (4)	2 (6)	3 (5)	15	2
Sorghum	5 (1)	3 (4)	-	5	6
Cassava	4 (2)	4 (2)	4 (4)	8	4
Amaranth	-	5 (0)	-	0	7
Banana	3 (3)	-	1 (8)	11	3
Maize	-	-	2 (6)	6	5

:- The crop was not ranked among important crops grown in this district.

Among sweetpotato varieties widely grown in the study areas, the following were ranked in decreasing order of farmer-preferences: (1) Nsasagatebo, (2) Kwezikumwe, (3) Donata, (4) Kibandire and (5) Kigambo. The rank was attributed to the total score achieved by each variety. Variety Nsasagatebo was ranked first, followed by Kwezikumwe (locally known as Magereza) (Table 2.15).

Table 2.15: Matrix ranks of the five farmer-preferred sweetpotato varieties during focus group discussions in three districts of Rwanda

Variety	Districts			Total scores	Overall ranking
	Bugesera; N=6 Rank (scores)	Huye; N=10 Rank (scores)	Nyagatare; N=10 Rank (scores)		
Kwezikumwe	1 (60)	3(43)	-	103	2
Tura	3(48)	-	-	48	6
Donata	2(58)	-	-	58	3
Magande	4(42)	-	-	42	7
Magambo	5(36)	-	-	36	9
Kigambo	-	1(54)	-	54	5
Karebe	-	4(24)	-	24	12
Nsasagatebo	-	2(51)	1(58)	109	1
Kenya	-	-	5(33)	33	11
Gakoba	-	-	2(38)	38	8
Kibandire	-	-	3(57)	57	4
Mwamiryakimwe	-	-	4(34)	34	10

:- The crop was not ranked among the important crops grown in this district.

2.3.14. Gender balance in sweetpotato production and post-harvest activities through focus group discussion

The main crop management activities conducted during sweetpotato production are shared among family members; however, female farmers were more responsible than male farmers (Table 2.16). The men were involved in ploughing, transport of harvested sweetpotato roots and selling, while women were mainly involved in selection of planting material, planting, weeding and harvesting.

Table 2.16: Role of gender in sweetpotato production and post-harvest activities as stated by focus group discussants in three districts of Rwanda

No	Activity	Huye		Bugesera		Nyagatare	
		F	M	F	M	F	M
1	Selection of the variety to plant	✓		✓	✓	✓	
2	Ploughing	✓	✓	✓	✓		✓
3	Planting	✓		✓		✓	
4	Weeding	✓	✓	✓		✓	
5	Pest management	✓		✓	✓		
6	Harvesting	✓		✓		✓	
7	Conservation of vines	✓		✓		✓	
8	Transport of produce	✓	✓	✓	✓	✓	✓
9	Cooking	✓		✓		✓	
10	Selling	✓	✓	✓			✓

✓ = role; F = females; M = males

2.4. Discussion

This study investigated the varied role of sweetpotato in Rwanda as a food and fodder crop. It also determined key farmer-preferred traits of the crop as a guide to subsequent breeding of dual purpose varieties. The current findings confirmed the value of sweetpotato as a dual-purpose crop in Rwanda, given the limited agricultural land available for crop and livestock production in the country.

2.4.1. Household information

The roles of respondents among households included household heads, spouses and children. A relatively low percent of household heads in Huye District (Table 2.1) was due to the fact that most men worked in urban areas during the day, and that they were not available for the PRA study. The range in the ages of respondents was from 18 to 66 years, indicating a high proportion of economically active age-range in the country. The number of women respondents was slightly higher than that of men (Table 2.1) confirming that both men and women were involved in agriculture, with more involvement of females in sweetpotato production activities confirmed in the current study. These results on gender on sweetpotato production concur with those of Kivuva et al. (2014).

Crop production was the main source of income in the Bugesera and Huye Districts, whereas a mixed crop-livestock system characterized the farming system in the Nyagatare District (Table 2.2). This showed the overall importance of crop production in the country farming systems. The mixed crop-livestock farming in the Nyagatare District reflected the high level of livestock production in this district. Similar results on the important role of crop production in Rwanda were also reported by Muhinyuza et al. (2012). Land tenure varied significantly. Although access to land is a challenge in the country, plot size, land availability and accessibility were different across the surveyed districts.

2.4.2. Crops grown and decision making on which crop to grow

The top two crops were sweetpotato and dry bean, with scores of 21.4% and 20.8%, respectively (Table 2.3). This result indicates the importance of sweetpotato. The results, however, were different to those of Rukundo et al. (2015) and Nduwumuremyi et al. (2016) who found that sweetpotato only ranked third or above in various districts of Rwanda, including Bugesera District. In the districts of Bugesera and Nyagatare, household heads make the decision on which crops are to be grown during a season (Table 2.4). In contrast, in Huye District, the responsibility was that of children because of the migration of their parents to urban areas for other jobs in different industrial sectors. The relatively low proportion (30%) of household heads making decision in Nyagatare District could be

attributed to the dominant role of livestock production. Most farmers reported the involvement of the Government in making decision on which crop to grow. This is because of the Rwanda Ministry of Agriculture extension policy commonly known as the “Crop Intensification Program (CIP)”, in which selected crops are prioritized and cultivated in consolidated lands in pursuit of food security for the country.

2.4.3. Role of sweetpotato in the present farming systems

The current findings indicated that sweetpotato storage roots were commonly used for food (Table 2.5), whereas vines were used for feed across the study districts. This indicates the two primary roles of the crop in the mixed crop-livestock farming system. The roles of sweetpotato as food and forage were previously reported by others (Leon-Velarde et al., 1997; Niyireba et al., 2013; Gruneberg et al., 2015). Most respondents consumed sweetpotato every day in Huye District (Table 2.7), which may be due to the extensive production of the crop in that district, as reported by de Graaff et al. (2011). The district is characterised by a high population density and low soil fertility. As expected, a fodder system based on sweetpotato vines was commonly used in Nyagatare, a district with the most livestock production in Rwanda. Most farmers reported using sweetpotato vines as a fodder across all districts. This could explain the shortage of vines at different times of the year in the country. This reflects the need for sweetpotato varieties with strong dual-purpose attributes, and for different vine cutting regimes. Only a few number of farmers used roots for household food processing, indicating that the crop has not been fully exploited in local food processing.

2.4.4. Strategies to increase sweetpotato productivity

Farmers’ perceptions regarding strategies to increase root production were similar across districts (Table 2.8). Respondents perceived that cultivar improvement would be the best way to increase sweetpotato root productivity. This reflects the need to develop and disseminate new varieties with improved root yields. Similarly, most farmers expressed interest towards new varieties with greater fodder production potential (Table 2.8).

2.4.5. Use of sweetpotato fodder and its relative value among forages in Rwanda

Most farmers use sweetpotato fodder, especially in the Nyagatare District (Table 2.9). Farmers used a cut-and-carry system, which is in line with a zero grazing policy that is being applied in Rwanda, in the framework of minimizing land degradation. Despite the increase of feed prices caused by this policy, its importance was pointed out by Peters (2008) who noted that cattle were less likely to pick up diseases. In the present study, sweetpotato based-fodder was ranked second most important after Napier grass (Table 2.9). The two fodder

species were also reported to be useful by Klapwijk (2011) in a study conducted in Rwanda on the source and the availability of animal feed resources. The use of Napier grass combined with sweetpotato vines was previously reported by Claessens et al. (2008).

2.4.6. Preferences of dual-purpose sweetpotato varieties

Most respondents in all districts expressed their need for dual-purpose varieties, especially in Huye District (Table 2.10). Almost all the respondents (96.7%) in Huye chose to grow dual-purpose varieties instead of other types, which could be explained by the high population density characterising the area and limited agricultural lands. The high level of farmer preference for dual-purpose types was similar and consistent across the study districts, indicating that any effort to develop these varieties should meet the needs of all the districts.

2.4.7. Constraints to sweetpotato production

There were several constraints to sweetpotato production such as: pests, diseases, shortage of clean planting material, lack of dual-purpose varieties and drought (Table 2.11). Pests were reported by respondents as the most important constraints across districts; and diseases were specifically reported in Bugesera District. These results were in agreement with Rukundo et al. (2015) who reported that pests and diseases were among the top five constraints to sweetpotato production in Rwanda. The high frequency of diseases in Bugesera District, especially sweetpotato virus disease, may be attributed to the suitability of this agro-ecology, which is a semi-arid area with high temperatures favourable for disease development (Nduwumuremyi et al., 2016). Njeru et al. (2008) reported a high prevalence of SPVD in the area. Dual-purpose types are not yet widely grown in Huye District because farmers were not aware of these varieties.

2.4.8. Major characteristics of the preferred storage root

In Bugesera and Huye Districts, 50 and 76.6% of farmers preferred marketable root size of storage roots, respectively (Table 2.13). This reflects the commercial value of the crop, which is steadily increasing across districts. Relatively few farmers preferred marketable roots in Nyagatare District because of the commercial value of other crops such as maize and rice. Most farmers preferred red skin colour. Similarly, Ndirigwe et al. (2005) reported that red skin colour was consistently liked over time in Rwanda. In the Bugesera and Nyagatare Districts, white-fleshed sweetpotato varieties were preferred over cream, yellow and orange flesh colour (Table 2.13). The study of Hagenimana et al. (1998) indicated that orange flesh storage root colour strongly correlated with low dry matter content (DMC) in sweetpotato, and therefore, OFSPs were not popular with farmers. Several researchers

(Mwanga and Ssemakula, 2011; Low et al., 2013; Sindi et al., 2013) have reported the potential value of OFSPs because of their high total carotenoids content, a precursor of vitamin A. Most of the respondents across all study districts expressed a clear preference for sweetpotato varieties with high dry matter content, agreeing with the results of previous studies (Fuglie, 2007; Chiona, 2010; Laurie, 2010; Sseruwu, 2012). Breeding of sweetpotato in the study areas should take into consideration these farmers' preferred-traits.

2.5. Conclusions

The study revealed the importance of sweetpotato as a food security crop with dual purpose potential in Rwanda. All respondents expressed interest in growing sweetpotato varieties with improved root production combined with high above ground biomass. About 87.7, 66.6, 56.6 and 51.1% of the respondents indicated that root related traits of the crop such as high dry matter content, red skin colour, marketable root size and yellow flesh colour, were additional preferred traits, respectively.

From this study, farmers-preferred dual-purpose sweetpotato varieties with improved root and green fodder yields should be developed to enhance sustainable production and the adoption of sweetpotato in the mixed farming systems in Rwanda. These results can serve as a baseline to develop improved DPSVs with farmer-preferred traits.

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3. Chapter Three: Phenotypic diversity analysis of sweetpotato for breeding dual-purpose varieties

Abstract

Sweetpotato [*Ipomoea batatas* (L.) Lam] is an important crop with potential dual uses. Its storage roots are used for human food and its vines for livestock feed in a crop-livestock mixed farming systems in countries such as Rwanda. The genetic diversity of sweetpotato has not been explored to develop dual-purpose sweetpotato varieties (DPSVs). The objectives of this study were to assess the level of phenotypic diversity present among sweetpotato varieties grown in Rwanda, and to select suitable parents for breeding DPSVs. Fifty one diverse sweetpotato genotypes were evaluated in field trials conducted at the Rubona and Karama experimental stations of the Rwanda Agriculture Board (RAB) using a 6 x 9 unbalanced alpha lattice design with three replications. Genotypes and sites interacted significantly ($P < 0.05$), affecting fresh root yield, root dry matter content, dry root yield, marketable root number, marketable root weight, flowering ability and harvest index. The top two genotypes selected for their high yields of storage roots were RW11-4923 and RW11-2419, with yields of 20.91 t.ha⁻¹ and 20.18 t.ha⁻¹, respectively. The genotypes RW11-4923 and Wagambolige were the best performers for vine yields, producing 23.67 t.ha⁻¹ and 23.45 t.ha⁻¹ of vines, respectively. The genotype Ukerewe performed well for its dry root yield (7.09 t.ha⁻¹), while RW11-4923 had the highest mean dry vine yield (5.17 t.ha⁻¹). The genotypes RW11-2910 and 8-1038 had root-to-vine ratios of 2.0 and 1.5, respectively, which reflects their suitability as parents, from which to develop DPSVs. The following genotypes were also selected: 2005-179, RW11-2910, SPK004 for their exceptional flowering ability of 23.0, 20.5 and 19.83%, respectively. Two main phenotypic groups with ten sub-groups were detected through cluster analysis. Principal component analysis showed that the first four components accounted for 76.33% of the phenotypic variation present among the 51 genotypes. The sweetpotato clones were selected for their combination of high storage root yields, heavy vine production and prolific flowering ability, which are essential traits from which to develop DPSVs, concurrently incorporating farmer-preferred traits. Further, genomic analysis could be performed using diagnostic molecular markers to identify superior parents for breeding DPSVs.

Keywords: DPSV, genotype, *Ipomoea batatas*, storage root yield, vine yield

3.1. Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam; $2n = 6x = 90$] is an important root crop in most tropical and subtropical regions of the world. Its roots serve as a major source of human food especially in sub-Saharan Africa (SSA) (Woolfe, 1992), while the above ground biomass is potentially useful for livestock feed. Sweetpotato storage roots contain carbohydrates and essential micronutrients such as vitamins and minerals. The orange-fleshed sweetpotato varieties (OFSPs) are currently being promoted for their high beta-carotene content, a precursor of vitamin A, which is useful in combating malnutrition. Storage roots of the purple-fleshed sweetpotato varieties are rich in antioxidants and have been reported to prevent asthma, gout and arthritis in humans. Young and succulent leaves of some varieties of sweetpotato are consumed as cooked vegetables by rural communities in SSA. Succulent leaves were reported to be higher in protein content than storage roots (Antia et al., 2006). Sweetpotato storage roots can be consumed as boiled, pureed, fried or baked products (Jata et al., 2011). In Rwanda sweetpotato puree and flour are used as a substitute for wheat flour to prepare various baked products. The baking industry in Rwanda is heavily dependent on imported wheat flour. Use of sweetpotato flour to prepare baked products presents potential advantages for farmers, processors and consumers owing to the high yields of the crop per unit area, reduced cost of crop production and final product costs (Sindi et al., 2013). The above ground biomass of sweetpotato is widely used for livestock feed in a crop-livestock mixed farming systems in countries such as Rwanda where grazing lands are limited.

In the past the emphasis in sweetpotato breeding was to develop varieties with high storage root yields or improved pro-vitamin A content for human food. However, some varieties have shown the potential to produce high storage root yields and aboveground forage yields for livestock feed (Leon-Velarde et al., 1997). These types of sweetpotato are referred to as dual-purpose varieties (Leon-Velarde et al., 1997; León-Velarde, 2000; Lukuyu et al., 2014). Selection of varieties for dual uses is largely based on the relative proportion of root-to-forage dry matter production (León-Velarde, 2000). Dual-purpose sweetpotato varieties (DPSVs) have been developed for their storage roots for human food and vines for livestock feed. This has great economic significance in a crop-livestock mixed farming system such as in Rwanda where agricultural lands are limited. A good dual-purpose variety has the ability to regenerate quickly after sequential harvesting of a portion of the above ground biomass, ensuing continued forage production before the final storage root is harvested. Sweetpotato leaves and vines are nutritious with 11% crude protein content and over 62% of digestibility (Ruiz et al., 1980). Due to the high nutritional value of the aboveground biomass of the crop,

sweetpotato fodder based dairy production has been reported to increase mean milk yield by approximately 1.5 litres per day (Peters, 2008). Therefore, there is a need to develop farmer-preferred DPSVs to enhance storage root and above ground biomass yields in a crop-livestock mixed farming system.

In Rwanda, the availability of agricultural lands is steadily dwindling and yet the population is expected to double by 2030 (UNFPA, 2007; UN-DESA, 2015). To satisfy the needs for human food and livestock feed, more food and feed production are required by using improved genotypes and exploiting the genetic potential of crops with multiple uses. Growing dual purpose crop varieties would enable efficient uses of natural resources such as limited agricultural lands for sustainable crop production. Also farming systems which combine crop and livestock production are reported with improved livelihoods and resilience (Gibon et al., 2012).

Sweetpotato is an important crop in Rwanda and various breeding efforts of the crop have been reported (Ndirigwe et al., 2012; Rukundo et al., 2013; Shumbusha et al., 2014). The crop is widely grown by smallholder farmers using diverse genetic resources. The extent of genetic diversity of the crop grown by farmers and maintained in the Rwanda gene bank is not well explored. Using a set of 54 genotypes, Rukundo et al. (2015) reported the existence of considerable genetic variation in the crop. The gene bank of the sweetpotato research program of Rwanda Agriculture Board (RAB) maintains about 150 accessions which include landraces, locally bred clones and introductions. The country has acquired a considerable number of sweetpotato varieties, mostly from various national agricultural research institutes (NARIs) and Consultative Groups on International Agricultural Research (CGIAR) centres such as from the International Potato Center (CIP) and the International Institute for Tropical Agriculture (IITA). The genetic diversity of sweetpotato has not been explored to develop dual-purpose sweetpotato varieties (DPSVs) in Rwanda. A well-characterized germplasm is a pre-requisite in any crop improvement program.

Several methods are available to characterise germplasm and select complementary parents for breeding (Huaman, 1992). Agro-morphological characterisation has been widely and successfully used to determine the level of genetic diversity among sweetpotato genotypes (Tairo et al., 2008; Manamela, 2009; Yada et al., 2010). In sweetpotato improvement, understanding the level of genetic diversity is useful to limit genetic depression and to ensure genetic variation for selection. Therefore, the objectives of this study were to assess the level of phenotypic diversity present among sweetpotato varieties grown in

Rwanda, and to use this information in order to select suitable parents for breeding dual purpose varieties.

3.2. Material and methods

3.2.1. Germplasm

The study used 51 sweetpotato genotypes, of which 48 were sourced from the Rwanda sweetpotato germplasm collection and three accessions were introductions from the International Potato Centre (CIP). Fourteen genotypes were previously evaluated for root and vine yields on a dry weight basis. Among the fourteen, six new farmer-preferred sweetpotato varieties, namely RW11-17, RW11-1860, RW11-2419, RW11-2560, RW11-2910 and RW11-4923, were released in 2013 to be used for both food and fodder production in Rwanda (Shumbusha et al., 2014), in spite of their lack of strong dual-purpose attributes. Eight genotypes: Cacearpedo, SPK004, Kwezikumwe, Mugande, Wagabolige, 2002-154, 2002-155 and Naspot1 were included for their good root-to-vine ratio (Niyireba et al., 2013) (Table 3.1). The remaining 31 genotypes were selected based on their diverse geographical origin and variation in morphological traits, including root skin and flesh colour. Two genotypes, namely Kemb 10 and Kemb 37, were included in the study because they were previously reported to be high yielding in both root and vines in Kenya (Lukuyu et al., 2011). Six genotypes (Kyabafurika 538, Melesiyana, Naspot 8, Naspot 9, New kawogo and Seruruseke) were selected for their previously established drought tolerance (Rukundo, 2015).

Table 3.1: Description of the 51 sweetpotato genotypes used in this study

No.	Clone	Origin	Skin colour	Flesh colour
1	Mugande	RAB	Red	White
2	Kwezikumwe	RAB	Yellow	Yellow
3	SPK004	KALRO	Red	Light orange
4	Cacearpedo	RAB	Yellow	Orange
5	Naspot 1	NARO	Cream	Yellow
6	RW11-17	RAB	Red	Cream
7	RW11-1860	RAB	White	Pale yellow
8	2002-154	RAB	Red	White
9	2002-155	RAB	White	Cream
10	RW11-2419	RAB	White	White
11	RW11-2560	RAB	Cream	Deep orange
12	RW11-2910	RAB	Red	Light orange
13	RW11-4923	RAB	Purple red	Intermediate orange
14	Wagabolige	CIP	Cream	Intermediate orange
15	2000-024	RAB	Red	Yellow
16	6-468	RAB	Red	White
17	44-0164	CIP	Red	White
18	8-1038	RAB	Red	White
19	Carote	CIP	Red	Orange
20	2005-179	RAB	Red	White
21	NASPOT 10	NARO	Purple red	Deep orange

No.	Clone	Origin	Skin colour	Flesh colour
22	440165	CIP	Red	White
23	2005-110	RAB	White	Yellow
24	Giteke	Landrace	White	White
25	Kakamega 7	CIP	Red	Dark orange
26	Hakizakubyara	Landrace	Red	White
27	Mafutha	CIP	Cream	Intermediate orange
28	97-062	RAB	Red	Orange
29	OTADA 24	NARO	Red	White
30	Ukerewe	RAB	Red	Yellow
31	K5132/61	IITA	Red	White
32	4-160	RAB	White	White
33	5-214	RAB	White	White
34	UW	CIP	Cream	Intermediate orange
35	Imby	CIP	Red	White
36	NASPOT A	NARO	White	Cream
37	50	RAB	Red	Intermediate orange
38	2005-162	RAB	White	Yellow
39	NASPOT W6	NARO	Red	Orange
40	49	RAB	Dark purple	White
41	KEMB 37	CIP	Red	White
42	KEMB 10	CIP	White	Cream
43	2002-133	RAB	Purple red	Cream
44	9-466	RAB	White	White
45	NASPOT 13	NARO	Cream	Intermediate orange
46	Melesiyana	Landrace	Yellow	White
47	Seruruseke	Landrace	Red	Yellow
48	New Kawogo	NARO	Purple red	White
49	NASPOT 8	NARO	Purple red	Yellow
50	NASPOT 9	NARO	Red	Orange
51	Kyabafurika 538	NARO	Cream	White

Where, RAB: Rwanda Agriculture Board; CIP: International Potato Centre; NARO: National Agriculture Research Organization/Uganda; IITA: International Institute for Tropical Agriculture; KALRO: Kenya Agriculture and Livestock Research Organization.
n.a: not available

3.2.2. Study sites

The experiments were conducted at Rubona and Karama research stations of the Rwanda Agriculture Board (RAB) during March to July 2015. Both sites are characterized by clay and sandy soils (Rukundo et al., 2015). Rubona is located at a mid-altitude in Rwanda (1,700 meter above sea level [masl]); at 02° 29'S, 29° 46'E; with a mean temperature of 18.7°C, and a mean annual rainfall of 1200 mm. Karama (1400 m.a.s.l) is located in the lowlands of Rwanda (02° 17' S; 30° 16' E), with rainfall ranging between 700 to 900 mm, with a mean temperature of 20.8°C (Murayi et al., 1987). The Karama site is a known hot spot area for sweetpotato virus disease.

3.2.3. Experimental design and field management

Field experiments were conducted using a 6 x 9 unbalanced alpha lattice design with three replications at both of the sites. Each entry in a replication was represented by a three-row plot comprising 36 plants, 12 plants per a row. Spacing between plants within a row was 30

cm, with 80 cm between rows and 90 cm between plots. A sweetpotato variety Ukerewe was planted as guard rows in the trials. Weeding was done whenever necessary until the ground was fully covered by the plants. Organic manure was used, and no mineral fertilizer or pesticides were applied.

3.2.4. Data collection

Data were collected on both root and vine characteristics to select complementary clones. Root related traits included marketable root number (MRN), marketable root weight (MRW), fresh root yield (FRY), root dry matter content (RDMC) and dry root yield (DRY). Vine-based traits comprised of fresh vine yield (FVY), vine dry matter content (VDMC), dry vine yield (DVY), virus score (VS) and flowering frequency (FF). Combined root and vine parameters such as root-to-vine ratio (RV), total biomass on dry weight basis (TBDW) and harvest index (HI) were also recorded. Data on fresh root yield and root yield related traits such as marketable root number and marketable root weight were recorded from 10 middle plants of each clone, providing a plot mean data. A guard plant was left at either end of the row, giving a harvest plot of 2.4 m². Trials were harvested at maturity, 150 days after planting. With the exception of fresh vine yield that was measured at harvest, other foliar and vine characteristics such as virus score and flowering frequency were measured one month and three months after planting.

After harvest, root and vine yields (t.ha⁻¹) were determined on a dry weight basis, using the method described by Rodríguez (1999), Benesi et al. (2005) and Cervantes-Flores et al. (2011). A root or vine sample of 300 g from undamaged roots or vines was collected. To obtain the dry weight, samples were oven-dried at 65^oC for 72 hours to a constant weight. The dry matter content (DMC) was calculated as: $DMC (\%) = (\text{dry weight} / \text{fresh weight}) * 100$. Dry yields were expressed as: $[\text{Fresh yield} \times DMC] / 100$. The root-to-vine ratio (R:V) was calculated according to Leon-Velarde et al. (1997), and then classified into five groups: forage type (R:V of 0 to 1), low dual-purpose type (R:V >1.0-1.5), high dual-purpose type (R:V > 1.5-2.0), low root production type (R:V >2.0-3.0), and high root production type (R:V above 3.0).

3.2.5. Data analysis

Quantitative data analysis was performed using the General Linear Models (GLM) procedure of the SAS statistical program (SAS, 2008) to calculate analysis for variance (ANOVA). When significant treatment differences were detected by the ANOVA, then treatment means were separated using Fisher's Protected Least Significance Difference test (LSD) at the 5% significance level. Qualitative data were analysed using the Statistical Package for Social

Sciences (SPSS), 16th version. Multivariate analysis comprising cluster and principal component (PC) analyses were conducted. In order to determine the similarity and the level of genetic distance between genotypes, cluster analysis was performed using Euclidean distance, and a dendrogram was generated using the nearest neighbour method. Principal component analysis was performed to determine the number of influential components and to calculate explained variation. Communalities indicating the amount of variance in each variable were calculated. Eigenvalues were calculated as the amount of variance in the original variables accounted for by each component. Correlations between the first two principal components and traits were performed. Finally, a genotype and genotype by environment interaction (GGE) biplot analysis was used to determine the amount of variation explained by the genotypic and site effect.

3.3. Results

3.3.1. Analysis of variance (ANOVA) of root and vine parameters

The analysis of variance (ANOVA) for root, vine and root-vine combined parameters is summarised in Table 3.2. Genotypes and sites interacted significantly ($P < 0.01$) for MRN, MRW, FRY and DRY and at $P < 0.05$ for RDMC. Significant differences ($P < 0.01$) were detected between genotypes and sites affecting all root traits. There were non-significant interactions between genotypes and sites for the RV ratio and TBDW.

The ANOVA for vine and combined root-vine parameters is presented in Table 3.2. Sites had highly significant ($P < 0.01$) effects on all parameters, except vine dry matter content. Genotypes had high significant ($P < 0.01$) effects on all the vine parameters. Sites and genotypes interacted significantly only for the flowering frequency. Based on combined root-vine parameters, sites and genotypes varied significantly for RV, TBDW and HI. However, non-significant interaction effects were found between genotypes and sites for RV and TBDW.

Table 3.2: Analysis of variance (ANOVA) showing mean squares and significance tests of storage root and aboveground biomass parameters of 51 sweetpotato genotypes evaluated at Rubona and Karama sites of Rwanda during 2015

Source of variation	DF	Root parameters				
		MRN	MRW	FRY	RDMC	DRY
Sites	1	820.20**	127.03**	3983.80**	593.86**	581.29**
Replications	2	161.49**	6.15**	29.91	24.35	2.04
Incomplete blocks	25	20.09*	1.08*	50.61	8.1	5.07
Genotypes	50	50.45**	2.80**	95.23**	66.30**	10.86**
Sites x Genotypes	50	31.69**	1.48**	67.08**	18.06*	7.94**
Source of variation	DF	Vine parameters				
		FVY	VDMC	DVY	VS	FR
Sites	1	710.89**	22.79	23.43**	442.66**	215.31**
Replications	2	121.29	7.74	3.11	0.79	43.57
Incomplete blocks	25	133.82**	10.55	4.67**	1.76*	21.44
Genotypes	50	106.04**	22.73**	3.59**	2.77**	259.18**
Sites x Genotypes	50	61.18	7.56	2.38	1.07	64.20**
Source of variation	Df	Root and vine parameters				
		RV	TBDW	HI		
Sites	1	30.14**	838.12**	1.14**		
Replications	2	0.46	4.65	0.02		
Incomplete blocks	25	2.02*	13.62	0.03*		
Genotypes	50	3.50**	15.60*	0.06**		
Sites x Genotypes	50	1.31	13.31	0.02*		

* and ** stands for significant difference at 5 and 1% probability levels, respectively.

Df: degree of freedom; MRN: Marketable root number; MRW: Marketable root weight; FRY: Fresh root yield; RDMC: Root dry matter content; DRY: Dry root yield; FVY: Fresh vine yield; VDMC: Vine dry matter content; DVY: Dry vine yield; VS: Virus score; FR: Flowering frequency; RV: Root-to-vine ratio; TBDW: Total biomass on dry weight basis; HI: Harvest index.

3.3.2. Responses of genotypes for root and vine parameters

Means of root and vine-related traits on fresh- and dry-weight bases for the 51 genotypes are presented in Table 3.3. Fresh root yields (FRY) ranged between 3.69 and 20.91 t.ha⁻¹, while fresh vine yields (FVY) varied from 6.07 and 23.67 t.ha⁻¹. The best performing genotypes with high FRY were RW11-4923 (20.91 t.ha⁻¹), followed by RW11-2419 (20.18 t.ha⁻¹). The genotype RW11-4923 was the best performing for FVY (23.67 t.ha⁻¹), followed by Wagambolige (23.45 t.ha⁻¹). For the parameters RDMC and VDMC, the best performers were the genotypes Melesiyana and Kakamega-7, with 39.46% and 25.37%, respectively. The genotype Ukerewe had the highest dry root yield of 7.09 t.ha⁻¹ followed by RW11-4923 with 6.8 t.ha⁻¹. The top two performing genotypes for dry vine yield were RW11-4923 and NASPOT13, which produced 5.07 t.ha⁻¹ and 4.57 t.ha⁻¹, respectively. The top three genotypes with the highest flowering frequency were 2005-179, RW11-2910 and SPK004, with 23.0, 20.5 and 19.8%, respectively. Genotype Seruruseke had the highest root-to-vine ratio of 3.73, while Mafuta performed relatively well displaying the highest harvest index of 0.71.

Overall, test genotypes performed well at the Rubona than the Karama site. At Rubona site, higher mean values were recorded for fresh root yield, root dry matter content, dry root yield, fresh vine yield, dry vine yield, flowering frequency, root-to-vine ratio and harvest index. However, genotypes scored the lowest vine dry matter content at this site (21.69%) when compared to the Karama site (22.15%).

Table 3.3: Mean storage root and vine related traits on fresh- and dry weight bases for 51 sweetpotato genotypes evaluated at Rubona and Karama sites of Rwanda in 2015

Genotype	FRY (t.ha ⁻¹)	RDMC (%)	DRY (t.ha ⁻¹)	FVY (t.ha ⁻¹)	VDMC (%)	DVY (t.ha ⁻¹)	FF (%)	R:V	HI
Mugande	12.57 ^{e-o}	33.64 ^{e-m}	4.51 ^{f-p}	21.34 ^{e-l}	17.37 ^{ab}	1.80 ^{ab}	0.50 ^a	1.21 ^{a-g}	0.49 ^{c-k}
Kwezi	12.19 ^{c-o}	34.58 ^{f-p}	4.33 ^{d-o}	14.93 ^{a-i}	21.84 ^{e-o}	1.60 ^{ab}	12.50 ^{g-n}	1.74 ^{b-l}	0.60 ^{f-q}
SPK004	6.99 ^{a-g}	36.80 ^{l-s}	2.69 ^{a-h}	11.05 ^{a-d}	24.94 ^{k-o}	2.69 ^{ab}	19.83 ^{o-q}	0.96 ^{a-e}	0.43 ^{a-g}
Cacearpedo	15.21 ^{f-q}	35.13 ^{g-q}	5.42 ^{k-q}	13.46 ^{a-g}	25.10 ^{m-o}	3.43 ^{ab}	1.33 ^{ab}	2.13 ^{e-l}	0.58 ^{h-q}
Naspot 1	15.61 ^{f-q}	35.65 ^{n-s}	5.57 ^{k-q}	13.63 ^{a-h}	21.04 ^{b-j}	2.74 ^{ab}	9.83 ^{e-j}	2.04 ^{d-l}	0.63 ^{f-q}
RW11-17	7.71 ^{a-h}	34.31 ^{f-o}	2.62 ^{a-g}	16.76 ^{b-l}	21.81 ^{e-o}	3.17 ^{ab}	1.83 ^{a-c}	0.79 ^{a-d}	0.42 ^{a-f}
RW11-1860	13.17 ^{f-p}	35.62 ^{h-r}	4.67 ^{f-q}	9.96 ^{a-d}	22.41 ^{e-o}	2.22 ^{ab}	10.33 ^{f-l}	2.23 ^{f-l}	0.68 ^{p-q}
2002-154	17.87 ^{n-q}	29.33 ^{b-d}	5.26 ^{f-q}	22.28 ^{g-l}	19.06 ^{a-e}	4.26 ^{ab}	1.17 ^{ab}	1.40 ^{a-l}	0.55 ^{f-p}
2002-155	12.67 ^{e-o}	30.12 ^{b-e}	3.89 ^{b-m}	9.03 ^{ab}	23.86 ^{f-o}	2.00 ^{ab}	2.17 ^{a-c}	2.67 ^{j-m}	0.61 ^{f-q}
RW11-2419	20.18 ^{p-q}	31.30 ^{c-f}	6.60 ^{o-q}	12.86 ^{a-f}	22.30 ^{e-o}	2.80 ^{ab}	0.67 ^a	2.75 ^{k-m}	0.66 ^{n-q}
RW11-2560	16.76 ^{f-q}	24.87 ^a	4.30 ^{d-o}	18.71 ^{d-l}	22.49 ^{e-o}	4.23 ^{ab}	11.83 ^{g-m}	1.34 ^{a-h}	0.45 ^{b-h}
RW11-2910	11.61 ^{b-o}	37.30 ^{m-s}	4.45 ^{e-p}	10.37 ^{a-d}	23.50 ^{g-o}	2.28 ^{ab}	20.50 ^{p-q}	2.00 ^{d-l}	0.59 ^{n-q}
RW11-4923	20.91 ^q	33.99 ^{f-n}	6.80 ^{p-q}	23.67 ^l	22.76 ^{e-o}	5.07 ^b	13.00 ^{g-n}	1.43 ^{a-j}	0.58 ^{h-q}
Wagabolige	13.84 ^{g-q}	38.83 ^{q-s}	5.22 ^{f-q}	23.45 ^l	16.68 ^a	3.81 ^{ab}	0.67 ^a	1.46 ^{a-j}	0.58 ^{h-q}
2000-024	14.50 ^{n-q}	37.82 ^{o-s}	5.40 ^{k-q}	14.08 ^{a-h}	21.71 ^{d-o}	2.93 ^{ab}	13.67 ^{h-n}	2.07 ^{e-l}	0.64 ^{f-q}
6-468	5.17 ^{a-c}	32.90 ^{o-k}	1.83 ^{a-c}	12.46 ^{a-e}	20.83 ^{b-j}	2.58 ^{ab}	0.50 ^a	0.67 ^{a-c}	0.37 ^{a-c}
44-0164	11.67 ^{b-o}	33.37 ^{e-l}	3.79 ^{a-m}	16.64 ^{b-l}	22.61 ^{e-o}	3.54 ^{ab}	18.33 ^{n-q}	0.93 ^{a-e}	0.47 ^{b-l}
8-1038	17.63 ^{m-q}	30.17 ^{b-e}	5.19 ^{f-q}	16.18 ^{b-l}	19.73 ^{a-g}	3.02 ^{ab}	18.33 ^{n-q}	1.50 ^{a-k}	0.55 ^{f-p}
Carote	6.41 ^{a-f}	36.95 ^{l-s}	2.36 ^{a-f}	9.37 ^{ab}	25.02 ^{f-o}	2.20 ^{ab}	5.17 ^{a-f}	1.33 ^{a-h}	0.50 ^{c-l}
2005-179	10.38 ^{a-l}	32.32 ^{c-h}	3.31 ^{a-l}	16.05 ^{b-l}	22.78 ^{e-o}	3.16 ^{ab}	23.00 ^q	1.25 ^{a-g}	0.52 ^{e-n}
Naspot 10	16.94 ^{f-q}	32.60 ^{c-l}	5.71 ^{f-q}	12.8 ^{a-f}	23.07 ^{f-o}	2.90 ^{ab}	3.00 ^{a-d}	2.10 ^{e-l}	0.65 ^{m-q}
440165	10.95 ^{a-h}	35.87 ^{n-s}	4.14 ^{c-n}	20.53 ^{a-l}	21.25 ^{c-l}	4.38 ^{ab}	3.50 ^{a-d}	0.90 ^{a-e}	0.41 ^{a-f}
Kyabafurika 538	11.31 ^{a-o}	37.29 ^{m-s}	4.32 ^{d-o}	10.54 ^{a-d}	21.16 ^{b-k}	2.21 ^{ab}	1.00 ^a	2.33 ^{g-l}	0.64 ^{f-q}
Seruruseke	15.66 ^{f-q}	38.89 ^{q-s}	6.14 ^{m-q}	10.1 ^{a-d}	23.27 ^{f-o}	2.22 ^{ab}	13.83 ^{n-o}	3.73 ^m	0.68 ^{p-q}
New Kawogo	10.38 ^{a-l}	33.99 ^{f-n}	3.79 ^{a-m}	16.59 ^{b-l}	17.90 ^{a-d}	2.78 ^{ab}	10.17 ^{e-k}	1.56 ^{a-k}	0.53 ^{f-o}
Naspot 8	12.50 ^{d-o}	32.71 ^{c-g}	4.12 ^{c-n}	15.55 ^{b-l}	21.20 ^{c-k}	3.09 ^{ab}	12.83 ^{g-n}	1.36 ^{a-l}	0.55 ^{f-p}
2005-110	4.14 ^a	38.04 ^{o-s}	1.61 ^{ab}	13.23 ^{a-g}	22.14 ^{e-o}	3.02 ^{ab}	17.17 ^{m-q}	0.80 ^{a-d}	0.37 ^{a-d}
Naspot 9	16.55 ^{f-q}	32.81 ^{d-j}	5.61 ^{k-q}	10.81 ^{a-d}	21.31 ^{c-m}	2.28 ^{ab}	3.17 ^{a-d}	2.62 ^{f-m}	0.69 ^{p-q}
Giteke	10.29 ^{a-l}	36.42 ^{j-s}	3.84 ^{a-m}	18.93 ^{d-l}	19.54 ^{a-f}	3.61 ^{ab}	7.17 ^{b-g}	1.15 ^{a-g}	0.52 ^{d-m}
Melesiyana	8.00 ^{a-l}	39.46 ^s	3.23 ^{a-k}	18.60 ^{d-l}	21.77 ^{e-o}	4.12 ^{ab}	2.17 ^{a-c}	0.70 ^{a-c}	0.39 ^{a-e}
Kakamega 7	20.08 ^{p-q}	29.99 ^{b-e}	6.13 ^{m-q}	12.99 ^{a-f}	25.37 ^o	3.29 ^{ab}	4.17 ^{a-e}	2.23 ^{f-l}	0.63 ^{f-q}
Hakizakubura	5.34 ^{a-d}	36.98 ^{l-s}	1.98 ^{a-d}	14.96 ^{a-l}	21.81 ^{e-o}	3.26 ^{ab}	8.50 ^{d-l}	0.62 ^{ab}	0.37 ^{a-d}
Mafuta	10.95 ^{a-h}	37.51 ^{n-s}	4.09 ^{c-n}	6.07 ^a	25.15 ^{n-o}	1.34 ^a	2.50 ^{a-d}	3.69 ^m	0.71 ^q
97-062	14.03 ^{g-q}	26.97 ^{ab}	3.74 ^{a-m}	13.37 ^{a-g}	21.90 ^{e-o}	2.79 ^{ab}	16.17 ^{k-p}	1.56 ^{a-k}	0.59 ^{h-q}
OTADA 24	11.97 ^{c-o}	39.15 ^{rs}	4.68 ^{f-q}	21.19 ^{e-l}	23.44 ^{g-o}	4.56 ^{ab}	3.67 ^{a-d}	1.20 ^{a-g}	0.52 ^{d-m}
Ukerewe	18.25 ^{o-q}	37.57 ^{n-s}	7.09 ^q	16.17 ^{b-l}	20.08 ^{a-l}	3.24 ^{ab}	16.33 ^{l-p}	2.16 ^{e-l}	0.63 ^{k-q}

Genotype	FRY (t.ha ⁻¹)	RDMC (%)	DRY (t.ha ⁻¹)	FVY (t.ha ⁻¹)	VDMC (%)	DVY (t.ha ⁻¹)	FF (%)	R:V	HI
K5132/61	9.15 ^{a-k}	31.48 ^{c-g}	2.88 ^{a-j}	15.18 ^{a-i}	21.02 ^{b-j}	3.04 ^{ab}	16.33 ^{l-p}	0.90 ^{a-e}	0.42 ^{a-t}
4-160	10.59 ^{a-m}	34.70 ^{t-p}	3.74 ^{a-m}	18.90 ^{d-i}	19.81 ^{a-h}	3.61 ^{ab}	12.83 ^{g-n}	1.34 ^{a-h}	0.52 ^{e-n}
5-214	13.37 ^{t-p}	37.35 ^{m-s}	5.08 ^{h-q}	13.92 ^{a-h}	22.51 ^{e-o}	3.11 ^{ab}	7.83 ^{c-h}	1.66 ^{a-k}	0.60 ^{t-q}
UW	11.99 ^{c-o}	28.95 ^{bc}	3.43 ^{a-l}	10.03 ^{a-d}	22.46 ^{e-o}	2.09 ^{ab}	18.33 ^{n-q}	2.93 ^{lm}	0.67 ^{o-q}
Imby	11.68 ^{b-o}	33.53 ^{e-m}	4.03 ^{b-m}	13.78 ^{a-h}	21.60 ^{d-o}	2.93 ^{ab}	17.00 ^{m-q}	1.51 ^{a-k}	0.57 ^{g-q}
Naspot A	12.35 ^{c-o}	36.32 ^{t-s}	4.64 ^{t-p}	10.94 ^{a-d}	21.99 ^{e-o}	2.35 ^{ab}	15.33 ^{j-p}	1.91 ^{c-l}	0.61 ^{t-q}
50	5.81 ^{a-e}	34.94 ^{t-p}	2.03 ^{a-e}	18.93 ^{d-i}	22.01 ^{e-o}	3.97 ^{ab}	15.83 ^{j-p}	0.46 ^a	0.31 ^a
2005-062	9.96 ^{a-i}	37.94 ^{o-s}	3.80 ^{a-m}	15.99 ^{b-i}	23.54 ^{h-o}	3.58 ^{ab}	14.17 ^{i-o}	1.08 ^{a-g}	0.51 ^{d-m}
Naspot W6	4.53 ^{ab}	31.63 ^{c-g}	1.45 ^a	13.27 ^{a-g}	22.74 ^{e-o}	2.94 ^{ab}	18.33 ^{n-q}	0.53 ^{ab}	0.34 ^{ab}
49	13.35 ^{t-p}	36.64 ^{k-s}	4.65 ^{t-p}	9.43 ^{a-c}	25.30 ^o	2.20 ^{ab}	15.00 ^{j-p}	2.57 ^{h-m}	0.68 ^{p-q}
Kemb 37	8.52 ^{a-j}	31.24 ^{c-t}	2.76 ^{a-i}	8.39 ^{ab}	22.22 ^{e-o}	1.88 ^{ab}	0.50 ^a	1.60 ^{a-k}	0.61 ^{t-q}
Kemb 10	11.47 ^{b-o}	36.84 ^{t-s}	4.04 ^{b-m}	16.61 ^{b-i}	24.26 ^{l-o}	4.02 ^{ab}	5.33 ^{a-t}	1.15 ^{a-g}	0.52 ^{e-n}
2002-133	12.36 ^{d-o}	38.25 ^{p-s}	4.95 ^{g-q}	18.58 ^{c-i}	21.08 ^{b-j}	3.86 ^{ab}	7.17 ^{b-g}	1.19 ^{a-g}	0.52 ^{d-m}
9-466	15.16 ^{t-q}	27.36 ^{ab}	4.13 ^{c-n}	22.75 ^{h-i}	17.69 ^{a-c}	3.97 ^{ab}	1.50 ^{ab}	1.03 ^{a-t}	0.49 ^{c-j}
Naspot 13	16.08 ^{k-q}	36.98 ^{t-s}	6.50 ^{n-q}	21.65 ^{t-j}	21.46 ^{c-n}	4.57 ^{ab}	2.00 ^{a-c}	1.24 ^{a-g}	0.49 ^{c-k}
Mean: Rubona site	16.45	36.46	5.90	17.16	21.69	3.54	10.04	2.00	0.61
Mean: Karama site	8.12	32.37	2.59	12.91	22.15	2.74	8.71	1.23	0.47
Grand mean	12.29	34.42	4.25	15.04	21.92	3.14	9.37	1.60	0.54
CV (%)	7.50	9.70	5.50	13.20	15.30	9.90	10.90	4.80	2.60
LSD _{0.05}	10.17	5.40	3.44	12.97	5.38	2.51	8.60	1.79	0.20
SED	5.16	2.74	1.75	6.58	2.73	1.27	4.37	0.91	0.10

*FRY: Fresh root yield; RDMC: Root dry matter content; DRY: Dry root yield; FVY: Fresh vine yield; VDMC: Vine dry matter content; DVY: Dry vine yield; FF: Flowering frequency; RV: Root-to-vine ratio and HI: Harvest index.

**Means in a column with the same letter(s) are not significantly different at P < 0.05

3.3.3. Clustering of sweetpotato genotypes using root and vine related traits

The clustering of sweetpotato genotypes according to root and vine parameters is presented in Figure 3.1. The cluster analysis grouped the 51 test genotypes into two major groups (I and II), with 33 and 18 genotypes, in that order. The two clusters had a total of ten sub-clusters. Cluster I consisted of four sub-clusters: I-a, I-b, I-c and I-d with 19, 4, 2 and 8 genotypes, respectively. Cluster II had six sub-clusters: II-a, II-b, II-c, II-d, II-e and II-f with 3, 1, 6, 3, 4 and 1 genotype, in that order (Figure 3.1). Sub-clusters II-b and II-f may be considered as outliers since each composed of only one genotype, Wagambolige and Ukerewe, respectively. Except for the genotype Wagambolige, all other introduced genotypes such as Kemb 37 and Kemb 10 were clustered together (cluster I, sub-cluster I-a). With the exception of Naspot A and Naspot W6, all other Naspot series such as Naspot 1, Naspot 8, Naspot 9 and Naspot 10 were grouped in Cluster I. Apart from genotype Melesiyana which appeared in Cluster I, Sub-cluster I-b, other landraces such as

Seruruseke, Giteke and Hakizakubyara were grouped together in Sub-cluster I-d. The newly released varieties such as RW11-2419, RW11-17, RW11-2560, RW11-4923 and RW11-1860 were grouped together in Cluster I, with RW11-2560 and RW11-4923 forming their own sub-cluster, i.e., I-c. In Cluster II, genotypes of related serial number namely 2005-179, 2005-062 and 2005-110 were found, reflecting their genetic relatedness or breeding history.

The cluster analysis allowed grouping of genotypes sharing common root characteristics. Consequently, the genotypes RW11-2419, Kakamega-7 and 2002-154 were grouped in Cluster I-a, associated with their high performance in fresh root yield. The genotypes RW11-2910, 2000-024, Kyabafurika 538, Seruruseke, Melesiyana, Otada 24 and 2002-133 were grouped in Cluster I. These genotypes had high root dry matter content above 37%. The genotypes RW11-4923, RW11-2419, Seruruseke, Kakamega-7 and Naspot 13 appeared in Cluster I, which could be explained by their high dry root yield above 6 t.ha⁻¹.

Further the genotypes were conveniently grouped using vine yield and related traits. The genotypes 2002-154, RW11-4923 and 9-466 were identified in Cluster I. These genotypes had a relatively high fresh vine yield of above 22 t.ha⁻¹. The genotypes Cacearpedo, Carote, Kakamega-7, Mafuta and Kemb 10 were grouped in Cluster I, Sub-cluster I-a, observed for their relatively high vine dry matter content above 25%. The genotypes OTADA 24, Naspot 13, Kemb 10, 440165 and 2002-154 were identified in Cluster I, Sub-cluster I-a, which may have been due to their relatively high dry vine yield.

Combined root and vine parameters may have influenced genotype grouping. The genotypes Kwezi, 97-062, Imby and Naspot A were identified in Cluster II. These genotypes had a root-to-vine ratio ranging between 1.5 and 2.0, a typical characteristic of genotypes with dual-purpose ability. Genotypes RW11-1860, Seruruseke, Mafuta, RW11-2419 and Naspot 9 were identified in Cluster I, with the last two grouped in Sub-cluster I-a. These five genotypes had a relatively high harvest index above 68%. The genotypes 2005-110, Naspot W6, and genotype denoted "50" were grouped in Cluster II, with the last two identified in Sub-cluster II-c. These genotypes had harvest index below 50%, characteristic of genotypes with a high yield of above ground biomass. The genotypes Carote, Kemb 10, 2002-133, Giteke, OTADA 24 and 4-160 appeared in Cluster I. These genotypes had harvest index around 50%, characteristic of varieties with the ability to produce optimum yields of both roots and vines. The dissimilarity distance varied between 0 and 25% among the 51 genotypes evaluated in this study.

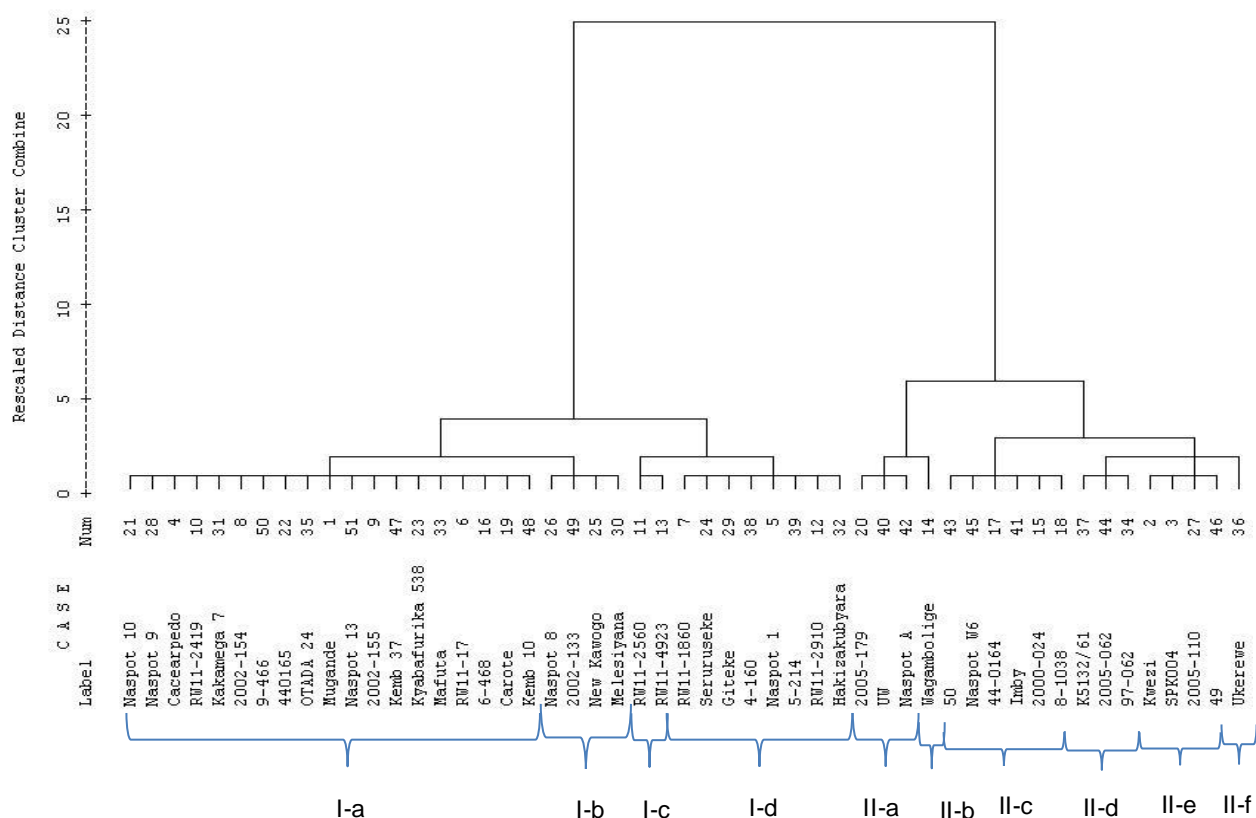


Figure 3.1: Dendrogram showing six main clusters of 51 sweetpotato genotypes evaluated using root, vine and related parameters across two sites in Rwanda

3.3.4. Principal component analysis

The principal component analysis (PCA) revealed four principal components (PCs) accounting for 76.33% of the variation in root, vine and related parameters of the 51 test genotypes (Table 3.4). Only 23.67% of the total variation was un-explained in the original variables. Estimates of extraction communalities varied from 0.32 to 0.97, indicating that the extracted components were representative for all the variables.

The first principal component was highly correlated (0.96) with root- related traits, such as fresh root yield and dry root yield. The second component was mainly correlated with vine-related traits such as fresh vine yield and dry vine yield, with correlation values of 0.98 and 0.93, respectively. This component was inversely correlated with root-to-vine ratio (-0.71). The third component was moderately correlated (0.89) with root dry matter content, while the fourth component was moderately correlated (0.74) with harvest index.

Table 3.4: Eigenvectors and eigenvalues of the first four principal components of the 13 storage root and vine related traits of 51 sweetpotato genotypes evaluated at the Rubona and Karama sites of Rwanda in 2015

No	Trait	Principal component			
		1	2	3	4
1	Marketable root number	0.82	-0.16	-0.18	-0.18
2	Marketable root weight	0.86	0.07	-0.25	-0.24
3	Fresh root yield	0.96	0.08	-0.16	-0.05
4	Root dry matter content	-0.12	-0.03	0.89	-0.05
5	Dry root yield	0.96	0.07	0.16	-0.06
6	Fresh vine yield	0.12	0.98	0.02	-0.02
7	Vine dry matter content	-0.04	-0.60	0.23	0.01
8	Dry vine yield	0.13	0.93	0.13	0.01
9	Virus score	0.03	0.06	-0.41	-0.38
10	Flowering frequency	-0.20	0.00	-0.22	0.67
11	Root-to-vine ratio	0.61	-0.71	0.04	-0.08
12	Total biomass on dry weight basis	0.83	0.49	0.19	-0.04
13	Harvest index	-0.08	0.03	0.19	0.74
Eigenvalues		4.65	2.91	1.34	1.09
Variance (%)		35.81	22.41	10.28	7.83
Cumulative variance (%)		35.81	58.22	68.50	76.33

Bold face font denote high correlations between the trait and principal component.

3.3.5. Genotype and genotype by environment interaction analysis

Genotype and genotype by environment interaction (GGE) biplots of fresh root yield are presented in Figure 2. The first principal component (PC1) representing genotypic effect had a relatively high contribution (66.74%) to the total variance of fresh root yield, while PC2 representing the test locations accounted for only 33.26% of the total variance. The genotypes RW11-4923, RW11-2419, Kakamega-7 and Ukerewe had relatively high PC1 values, with a high mean fresh root yields varying from 18.25 to 20.91 t.ha⁻¹. Conversely, , the genotypes 2005-110, 6-468, 50, Hakizakubyara, Kemb 10 and 49 had high negative PC1 values, with low fresh root yields. Genotypes having PC2 scores near zero such as Hakizakubyara, Imby and Kyabafurika were considered stable in terms of FRY.

Both test environments (Rubona and Karama sites) had positive PC1 scores, with Rubona having a relatively high PC1 score. Rubona had a PC2 near zero, and therefore it was more representative of an average environment. Genotype RW11-2560 performed well at the Rubona site, whereas genotype 8-1038 was the best performer at the Karama site (Figure 3.2).

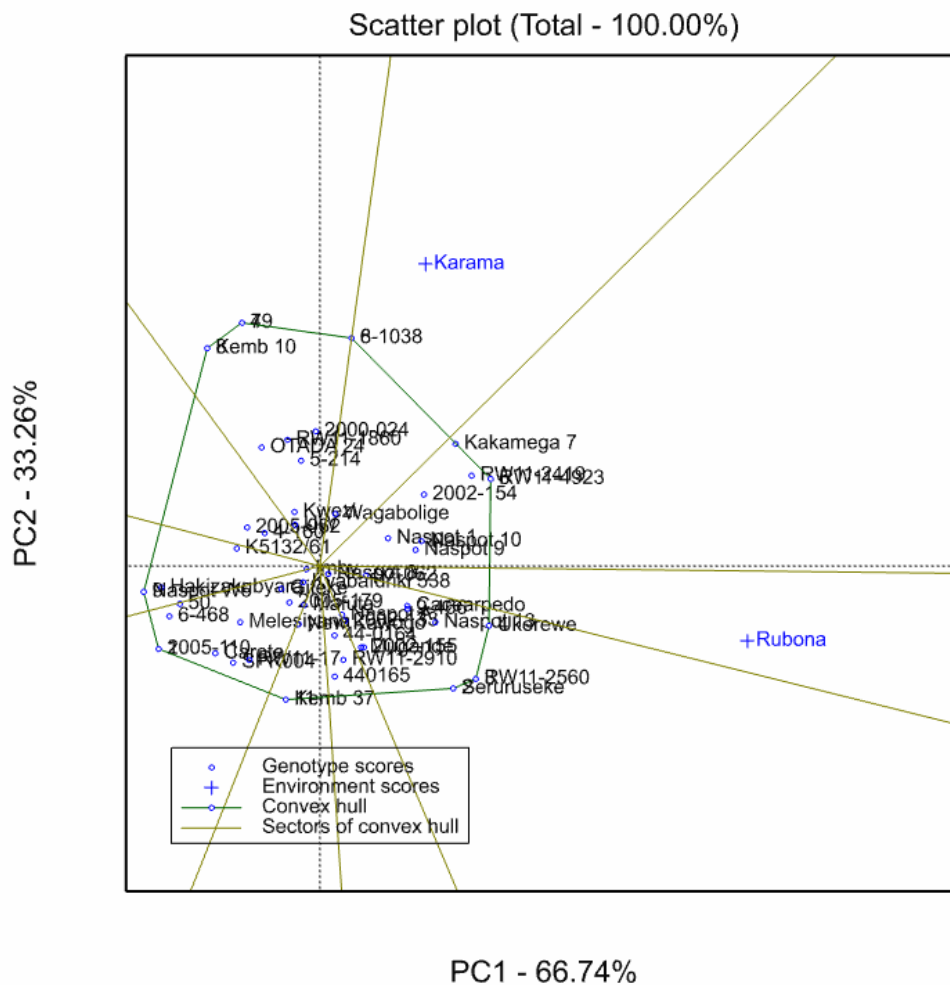


Figure 3.2: Genotype and genotype by environment interaction biplots for fresh root yield of 51 sweetpotato genotypes evaluated at the Karama and Rubona sites in 2016

The GGE biplots analysis of fresh vine yield is presented in Figure 3.3. The first principal component (PC1) representing genotypic effect showed a relatively high contribution (74.65%) to the total variance for fresh vine yield compared to PC2. The following genotypes: Wagambolige and RW11-4923 showed a relatively high PC1 values, with a high mean fresh vine yield of 23.45 and 23.67t.ha⁻¹, respectively. In contrast, genotypes Kemb 37 and Mafuta had high negative PC1 values, with low fresh vine yields of 8.39 and 6.07t.ha⁻¹,

in that order. The Rubona and Karama sites had positive PC1 scores. The Rubona site had a PC2 value relatively near zero, and was therefore more representative of an average environment. The genotype 9-466 was the best performer at Rubona, whereas genotype Kemb 10 performed best at the Karama site.

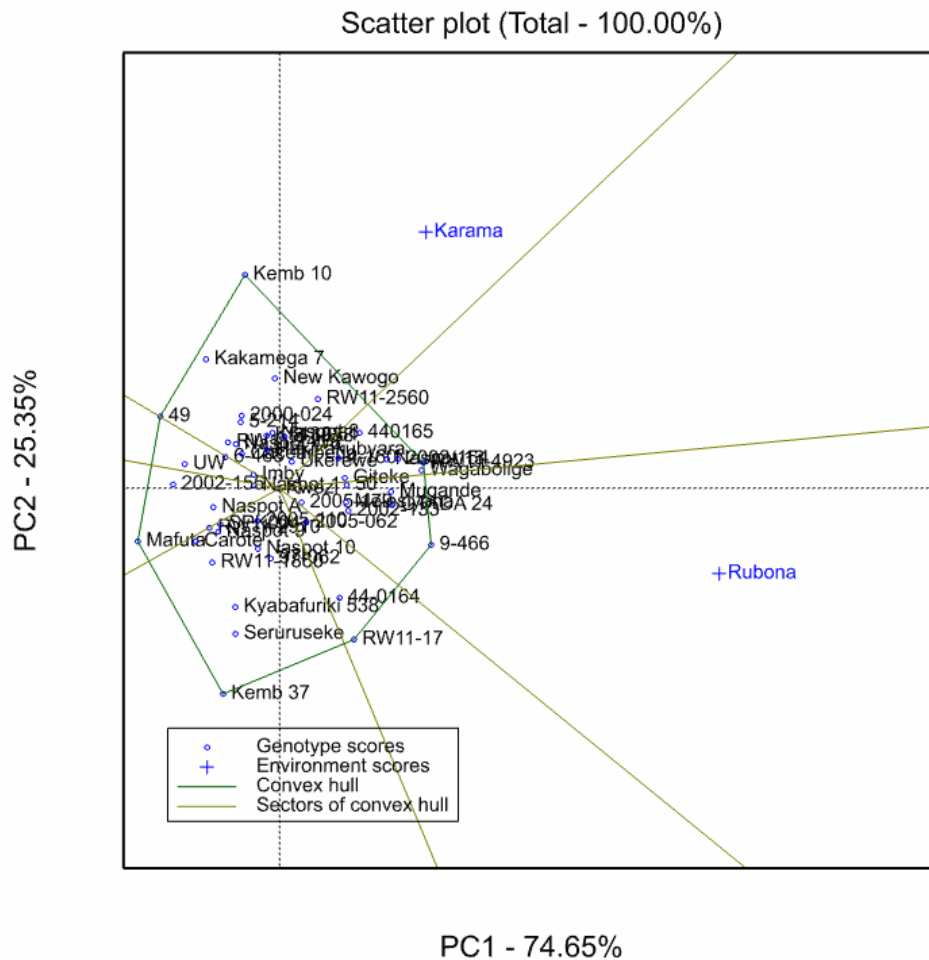


Figure 3.3: Genotype and genotype by environment interaction biplots for fresh vine yield of 51 sweetpotato genotypes evaluated at the Karama and Rubona sites in 2016

3.4. Discussion

3.4.1. Phenotypic diversity of sweetpotato genotypes for storage root yield and related traits

There were highly significant differences among 51 sweetpotato genotypes for storage root and vine related parameters across two testing sites. Various authors have noted the effect of test sites on storage root yields in sweetpotato (Grüneberg et al., 2005; Tumwegamire et al., 2011; Yada et al., 2011; Rukundo et al., 2015). These differences could be attributed to

variations in agro-ecological conditions characterising each site (Murayi et al., 1987; Rukundo et al., 2015). Genotypes and sites interacted significantly for marketable root number (MRN), marketable root weight (MRW), fresh root yield (FRY) and dry root yield (DRY) (Table 3.2). These results are consistent with previous studies (Adebola et al., 2013; Kivuva, 2013; Lukuyu et al., 2014; Shumbusha et al., 2014).

Marked differences were detected among genotypes for their mean root and vine performances (Table 3.3). Mean performances were highly influenced by sites. These findings were similar to those of Mwanga et al. (2011). The FRY varied from 3.69 and 20.91 t.ha⁻¹ falling within the range reported previously (Mwanga et al., 2011; Gruneberg et al., 2015). The wide range reflects the significant diversity of tested genotypes. Genotype RW11-4923 was the best performer for FRY (20.91 t.ha⁻¹) and the second in DRY (6.8 t.ha⁻¹) after Ukerewe (7.09 t.ha⁻¹). This was not surprising since the genotype RW11-4923 is among the newly released varieties with the ability to produce high biomass (Shumbusha et al., 2014). The genotypes Melesiyana and Seruruseke had the highest relative root dry matter content (RDMC) of 39.46% and 38.89%, respectively (Table 3.3). These genotypes are landraces, and they have considerable genetic value for a breeding programme because they would incorporate farmer-preferred traits such as RDMC. Dry root yield ranged between 1.45 t.ha⁻¹ and 7.09 t.ha⁻¹, which were higher values than those reported by Lukuyu et al. (2014). Although the genotype RW11-2560 had a higher FRY (16.76 t.ha⁻¹) than OTADA 24 (11.97 t.ha⁻¹), the later exhibited a higher DRY value (4.68 t.ha⁻¹) than the former (4.3 t.ha⁻¹). This indicates that genotypes with low or moderate FRY values may still perform well in terms of dry root yield.

The Rubona site had higher overall mean values for FRY, RDMC and DRY than the Karama site (Table 3.3). The mean FRY at the Rubona site was 16.45 t.ha⁻¹, the double that at Karama site (8.12 t.ha⁻¹). The Karama site is prone to severe drought events, and high levels of sweetpotato virus incidence, these two constraints combining to inhibit storage root development, resulting in low yields. Rukundo et al. (2015) reported similar findings except for DRY.

3.4.2. Phenotypic diversity of sweetpotato genotypes for above ground biomass and related traits

The test sites had a high significant effect ($P < 0.01$) on fresh vine yield (FVY), dry vine yield (DVY), virus score (VS) and flowering frequency (FF), except vine dry matter content (VDMC). These results partially disagree with Niyireba et al. (2013) who reported that VDMC varied between test locations. Genotypes differed significantly ($P < 0.01$) for FVY, DVY,

VDMC, VS and FF. Acquaaah (2007) described the influence of genetic make-up to trait expression in different environments. A highly significant difference between sites and between genotypes for vine-related traits was observed by previous authors (Larbi et al., 2007; Niyireba et al., 2013). Fresh vine yields ranged between 6.07 and 23.67 t.ha⁻¹, while DVY varied between 1.34 and 5.07 t.ha⁻¹. These ranges were similar to those reported by Andrade et al. (2010) and Lukuyu et al. (2011). The top two genotypes that performed high in FVY were RW11-4923 (23.67 t.ha⁻¹) and Wagambolige (23.45 t.ha⁻¹). The former is among the newly released varieties in Rwanda producing high quantity of both root and vines (Shumbusha et al., 2014), while the latter is reported ideal as a dual-purpose variety in Kenya (Lukuyu et al., 2011). The top three genotypes with the highest FF were 2005-179, RW11-2910 and SPK004, with 23.0, 20.5 and 19.83%, respectively. Across sites, the mean FVY and DVY were higher at the Rubona site at 17.16 and 3.54 t.ha⁻¹ than at the Karama site with 12.91 and 2.74 t.ha⁻¹, in that order. The current results on FVY were contrary to those of Rukundo et al. (2015) who reported different outcomes when evaluating another set of germplasm at the same sites.

3.4.3. Selection of sweetpotato genotypes with increased root-to-vine ratio

Highly significant differences ($P < 0.01$) were detected among genotypes for root-to-vine ratio (RV), total biomass on dry weight basis (TBDW) and harvest index (HI) (Table 3.2). A significant interaction effect ($P < 0.05$) was found between genotypes and sites for HI, which is a similar result to that of Gruneberg et al. (2015). The genotypes RW11-2910 and 8-1038 had RV values of 2.0 and 1.5, respectively, ratios that are within the range of genotypes with dual-purpose ability (León-Velarde, 2000). An increased HI was detected in the genotype Mafuta with 0.71, NASPOT9 at 0.69, and RW11-1860 and Seruruseke with HI values of 0.68. A high HI in sweetpotato indicates that storage roots constitute the main sink for photosynthesis (Bhagsari and Ashley, 1990). The HI values ranged between 0.31 and 0.71, which were within the range reported by Bhagsari and Ashley (1990). The site mean for HI was higher at Rubona at 0.61 than the mean HI achieved at Karama (0.47). Similarly, the mean RVs at Rubona and Karama were 2.0 and 1.23, respectively. These values were consistent with the findings of other authors (Niyireba et al., 2013; Shumbusha et al., 2014).

Genotypic diversity analysis classified the 51 genotypes into two major clusters of 33 and 18 genotypes, within which they were a further ten sub-clusters (Figure 3.1). The percentage dissimilarity varied from 0-25%, indicating a high level of phenotypic diversity between genotypes under study. Manamela (2009), Tairo et al. (2008) and Beah et al. (2014) reported a relatively low distance coefficient ranging from 0.57-1.87, 0.0-0.52 and 0.6-1.0,

respectively, indicating a low level of polymorphism in sweetpotato in their respective study environments.

In this study the first four principal components accounted for 76.33% of the total phenotypic variation (Table 3.4). The first principal component (PC1) resulted in an eigenvalue of 4.65, contributing 35.81% of the total variability, whereas PC2 with eigenvalue of 2.91 accounted for 22.41% of the total observed variability. In a previous study by Koussao et al. (2014), four PCs were detected explaining 67.22% of the variation measured, using 30 characters in sweetpotato. Afuape et al. (2011) reported three PCs explaining 76% of the variability when testing 21 sweetpotato genotypes using eight morphological characters, while Laurie et al. (2013) reported a variation of 58% explained by six PCs in a study of 57 accessions, using 29 traits. In the present study the first component was mainly correlated with FRY and DRY with a correlation of 0.96. This indicates that the two traits contributed much (35.81%) of the observed variability in PC1. The PC2 was correlated with FVY and DVY with correlations of 0.98 and 0.93, respectively, suggesting that these two traits accounted for most of the 22.41% variability in PC2. This implies that, for breeding purposes, selection of parents with traits associated with high storage root and vine yields in both fresh- and dry-weight bases would be important.

The results from the genotype and genotype by environment analysis (GGE) (Figure 3.2) revealed a large contribution of the PC1 to the total variance for FRY. Genotypes with relatively high positive PC1 values were RW11-4923, RW11-2419, Kakamega-7 and Ukerewe. Such genotypes were reported to be high yielders (Manrique and Hermann, 2000). Accordingly, genotypes RW11-4923 and Wagambolige had a high above average FVY in this study.

3.5. Conclusions

The current findings found considerable phenotypic diversity in the 51 genotypes when evaluated for dual-purpose traits. Marked phenotypic differences were observed for storage root yield and related traits, aboveground biomass, root-to-vine ratio (RV), total biomass on dry weight basis (TBDW) and harvest index (HI). Genotypes RW11-4923, RW11-2419, Kakamega-7 and Ukerewe were the best performers for fresh root yield, producing 20.91, 20.18, 20.08 and 18.25 t.ha⁻¹, respectively. Genotypes RW11-4923, Wagabolige, 9-466, 2002-154 and NASPOT 13 performed well for fresh vine yield, producing 23.67, 23.45, 22.75, 2002-154 and 21.65 t.ha⁻¹, in that order. The outstanding performers for dry root yield were Ukerewe, Naspot 13, Seruruseke and Kakamega-7, which produced 7.09, 6.5, 6.14 and 6.13 t.ha⁻¹, respectively. Genotypes RW11-2560, Melesiyana and Kemb10 had relatively

high dry vine yield of 4.23, 4.12 and 4.02 t.ha⁻¹, in that order. Genotypes RW11-2910, NASPOT1 and 8-1038 had good root-to-vine ratios for dual-purpose applications, whereas Mafuta, RW11-1860 and the genotype “49” had high harvest index values. Flowering ability varied between genotypes, and genotypes with a high flowering frequency were 2005-179, RW11-2910 and SPK004, with values of 23.0, 20.5 and 19.83%, respectively. Using PCA, two major clusters, and ten sub-clusters were detected through a genotypic diversity analysis of the tested germplasm. Out of the total phenotypic variation present among the 51 genotypes, principal component analysis showed that 76.33% was due to the first four components.

As a recommendation, genomic analysis needs to be performed with the selected set of genotypes using diagnostic molecular markers as a tool to identify superior parents for breeding DPSVs. The selected sweetpotato clones that consistently produced high yields of storage roots and vines may complement each other when used as parents, from which to develop DPSVs, while making sure to incorporate farmer preferred traits.

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4. Chapter four: Characterization of dual-purpose sweetpotato germplasm using simple sequence repeat markers

Abstract

Well-characterized sweetpotato [*Ipomoea batatas* (L.) Lam] germplasm is a pre-requisite for breeding dual-purpose varieties with improved storage root and above ground biomass production, and for systematic genetic conservation of the crop. The objective of this study was to characterize diverse sweetpotato germplasm using simple sequence (SSR) markers to identify potential parents for breeding dual-purpose sweetpotato varieties (DPSVs). Twenty-four sweetpotato genotypes selected for their promising storage root yields and related traits, and their biomass production, were genotyped with nine highly polymorphic SSR markers. Polymorphic information content (PIC) varied from 0.38 to 0.85 with a mean of 0.68. The SSR markers IB-R19 and SSR07 had the highest mean PIC value of 0.85. Genetic diversity within and among the tested genotypes showed marked variation, with a mean number of alleles of 10 and mean number of effective alleles of 6.86. Genetic distance estimates of white-, yellow- and orange-fleshed types were 1.24, 1.20 and 1.23, respectively, suggesting substantial genetic variation in the target population. The genetic differentiation (F_{ST}) values and genetic identity (GI) were higher in the yellow- and orange-fleshed types. Molecular variance analysis showed highly significant differences ($P < 0.001$) among and within individuals, with marked genetic variability among individuals contributing to 69% of the total genotypic variation. Cluster analysis allocated the test genotypes into three distinct genetic groups: I, II and III, with 6, 5 and 13 genotypes, respectively. Eight genetically diverse clones were selected, namely SPK004 and K5132/61 (from Group I), 4-160, Ukerewe, RW11-2910 (Group II), RW11-1860, Wagabolige, 2005-179 (Group III), with key agronomic traits for breeding dual-purpose sweetpotato varieties. This study characterized and selected genotypes that are useful genetic resources from which to design and develop dual-purpose varieties of sweetpotato.

Keywords: alleles, genetic diversity, genotype, simple sequence repeats, sweetpotato

4.1. Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam, $2n = 6x = 90$] is an important crop in the world. In Eastern Africa, it is among the top 10 commodity crops with 12,519,414 tonnes of production per annum (FAOSTAT, 2013). Its yield potential for both for food and forage for livestock makes its production attractive, especially in areas experiencing land scarcity (Jata et al., 2011). Young and succulent sweetpotato leaves and vines are eaten in some parts of sub-

Saharan Africa, constituting a good source of proteins for humans (Woolfe, 1992; Sun et al., 2014). Additional advantages of sweetpotato include its limited requirement of production inputs, that it stores well underground as a famine reserve crop, that it can tolerate extreme weather conditions, and that it can be harvested on continuously over a long period of time (Bashaasha et al., 1995). In Rwanda, sweetpotato ranks fourth after plantains, cassava and potatoes, with a total production of 1,081,224 tonnes per year (FAOSTAT, 2013). The potential of this crop as food and forage source has been recognised in Rwanda since the inception of the programme, “one cow per family”, by the Government of Rwanda, to enhance milk production by rural households. However, sweetpotato productivity in Rwanda is low, with estimated yield of 9.53 t.ha⁻¹ compared to the potential yield of 14.2 t.ha⁻¹ attainable using improved varieties and increased inputs (FAOSTAT, 2013).

Low productivity of sweetpotato is attributed to biotic, abiotic and socioeconomic constraints. The lack of improved sweetpotato varieties with high yields has been ranked second to drought among the main constraints limiting sweetpotato production in Rwanda (Rukundo et al., 2015). Other socioeconomic constraints include a high population density (430 inhabitants km⁻²), and therefore a shortage of agricultural land (Kayigema and Rugege, 2014). Notable biotic constraints affecting sweetpotato production include viruses and *Alternaria* stem blight (Gibson and Kreuze, 2015). Efficient use of the available sweetpotato germplasm will assist in the breeding of dual-purpose varieties with improved storage root yield and above ground biomass production, incorporating farmer-preferred traits.

Considerable genetic variation exists among sweetpotato germplasm collections globally. However, these genetic resources are not well characterised for breeding dual-purpose varieties with improved storage roots and above ground biomass production. Knowledge of the level of genetic diversity present among sweetpotato genetic resources is key in selecting genetically complementary parents for effective breeding or for conservation (Zhang et al., 2000; He et al., 2006). East Africa is believed to be one of the primary centres of genetic diversity of sweetpotato (Gichuki et al., 2003).

The Rwanda Agriculture Board (RAB) holds more than 170 accessions of sweetpotato acquired from various sources, including introductions from the Consultative Group for International Agriculture Research (CGIAR) centres, mainly the International Potato Centre (CIP). These accessions have been morphologically characterised for various attributes (Rukundo et al., 2015; Shumbusha et al., 2017). Morphological traits have been widely used to determine the genetic diversity of sweetpotato populations (Manamela, 2009; Yada et al., 2010; Elameen et al., 2011; Fongod et al., 2012). However, morphological characterisation of sweetpotato genotypes is subject to genotype x environment interactions, limiting the

selection efficiency of genetically diverse parents for breeding programs. Therefore, phenotypic trait evaluation and descriptions should be complemented with molecular characterisation to improve selection responses.

Molecular markers are effective tools for assessing genetic diversity and relatedness between diverse genetic resources. In sweetpotato, various genomic resources have been used, including simple sequence repeats (SSRs) or microsatellites (Jarret and Bowen, 1994; Gichuru et al., 2005; Koussao et al., 2014; Yada, 2014; Ngailo et al., 2016), inter-simple sequence repeats (ISSRs) (Huang and Sun, 2000; Hu et al., 2003), random amplified polymorphic DNA (RAPD) (Gasura et al., 2010; Maquia et al., 2013), amplified fragment length polymorphism (AFLP) (Zhang et al., 2000; Cervantes-Flores, 2007; Elameen et al., 2008), selective amplification of microsatellite polymorphic loci (SAMPL) (Tseng et al., 2002), DNA amplification fingerprinting (He et al., 1995) and single nucleotide polymorphism (SNPs) (Arif et al., 2010). Among the molecular markers, SSRs have been widely utilized as effective tool for genetic diversity assessment in various crops (Hu et al., 2004). SSRs have been reported to be highly polymorphic, informative and reproducible (Powell et al., 1996; Arizio et al., 2009; Zhao et al., 2013). Genetic classification using molecular markers will enhance the breeding efficiency of dual-purpose sweetpotato varieties, which is contingent upon the availability of polymorphic markers. There have been no prior studies on genetic clustering of dual-purpose sweetpotato collections using molecular data. In light of this, the objective of this study was to characterize diverse sweetpotato germplasm using selected polymorphic simple sequence (SSR) markers and to identify potential parents for breeding dual-purpose varieties.

4.2. Material and methods

4.2.1. Plant material and sampling

Twenty-four phenotypically distinct sweetpotato genotypes with suitable agronomic and horticultural qualities were selected out of 51 sweetpotato genotypes maintained at RAB (Table 4.1). These genotypes have been previously evaluated for phenotypic diversity of dual-purpose traits at the same Institute (Shumbusha et al., 2017). The 24 genotypes were selected mainly for their dual-purpose traits such as high storage root and vine yields, based on fresh- and dry-weight basis, better resulting in superior root to vine ratios and harvest indices.

Table 4.1: Description of the 24 sweetpotato genotypes used in this study

No.	Clone	Origin	Storage root skin colour	Storage root flesh colour
1	49	RAB	Dark purple	White
2	50	RAB	Red	Intermediate orange
3	2000-024	RAB	Red	Yellow
4	2005-179	RAB	Red	White
5	4-160	RAB	White	White
6	44-0164	CIP	Red	White
7	8-1038	RAB	Red	White
8	Giteke	Rwanda	White	White
9	K5132/61	IITA	Red	White
10	KEMB37	CIP	Red	White
11	Kwezikumwe	RAB	Yellow	Yellow
12	Mugande	RAB	Red	White
13	Naspot1	NARO	Cream	Yellow
14	NASPOT13	NARO	Cream	Intermediate orange
15	OTADA 24	NARO	Red	White
16	RW11-2910	RAB	Red	Light orange
17	RW11-17	RAB	Red	Yellow
18	RW11-1860	RAB	White	Pale yellow
19	RW11-2560	RAB	Cream	Deep orange
20	Seruruseke	Rwanda	Red	Yellow
21	SPK-004	KALRO	Red	Light orange
22	Ukerewe	RAB	Red	Yellow
23	UW	CIP	Cream	Intermediate orange
24	Wagabolige	CIP	Cream	Intermediate orange

Where, RAB: Rwanda Agriculture Board; CIP: International Potato Centre; NARO: National Agriculture Research Organization/ Uganda; IITA: International Institute for Tropical Agriculture and KALRO: Kenya Agriculture and Livestock Research Organization.

4.2.2. Genomic DNA extraction

Genomic DNA samples of sweetpotato genotypes were collected using FTA cards from five plants 45 days after planting. The sap was extracted from fresh tender leaves of five plants per genotype grown at RAB. DNA extraction was conducted using the protocol suggested by the International Potato Centre (Stewart Jr and Via, 1993).

4.2.3. SSR amplification and polymerase chain reaction (PCR)

Genotyping was conducted at SciCorp Laboratories in South Africa (SciCorp, SA (Pty), Ltd. South Africa). Bulk genomic DNA extracted from five plant samples were used in a bulked amplification. A single punch of each card per submission was considered and homogenised in the finnzymes dilution buffer (Kit). Two micro-litres of each bulked sample was used in the polymerase chain reaction (PCR). Eight polymorphic SSR markers were used for this study (Table 4.2). The markers were selected based on their high polymorphic information content (PIC) values that ranged from 0.52 to 0.81 and that they were developed for genetic analysis of sweetpotato (Karuri et al., 2009; Gwandu et al., 2012). The PCR amplification was conducted in a total reaction volume of 20 µl containing 2µl of genomic DNA. The PCR conditions were as follows: an initial denaturation at 94⁰C, followed by a denaturation period of 94⁰C for one minute (35 cycles), annealing at 61⁰C for one minute and a polymerization period at 72⁰C for one minute. The PCR products were fluorescently labelled and separated by capillary electrophoresis on an ABI 3130 automatic sequencer (Applied Biosystems, Johannesburg, South Africa) and analysed using a Gene Mapper 4.1.(Applied Biosystems, Johannesburg, South Africa).

Table 4.2: The eight SSR markers used to distinguish the 24 sweetpotato genotypes varying in storage root and aboveground biomass production

Name	Dye	Primer forward 5'-3'	Primer reverse 5'-3'
IB-R03	PET	GTAGAGTTGAAGAGCGAGCA	CCATAGACCCATTGATGAAG
1B-S07	FAM	GCTTGCTTGTGGTTCGAT	CAAGTGAAGTGATGGCGTTT
IB-R12	NED	GATCGAGGAGAAGCTCCACA	GCCGGCAAATTAAGTCCATC
IB-R16	VIC	GACTTCCTTGGTGTAGTTGC	AGGGTTAAGCGGGGAGACT
1B-R19	PET	GGCTAGTGGAGAAGGTCAA	AGAAGTAGAACTCCGTCACC
IB-CIP13	NED	CGTGCTTGAGGTCTGAGTAGAA	TCCCTAGAAGCTGCGTGAT
SSR 07	PET	TTTTCAACGACAAGCCTCTTGC	TCAAAGGTCCGCATGGAAATC
SSR 09		AAGTTAATCTAAGGTGGCGGGG	CGTCGATTCCAGTCTAATCCAATCC
690524	VIC	AAGGAAGGGCTAGTGGAGAAGGTC	CAAGGCAACAAATACACACACACG

4.2.4. Data analysis

Genotypic data were subjected to analyses with various measures of genetic diversity within and among genotypes using GenAlex software version 6.5 (Peakall and Smouse, 2006). The χ^2 test was performed to determine the differences in allele frequencies among the SSR markers. The analysis of genotypic data in this study was performed using two approaches. In the first approach, polymorphisms were treated as binary data (present or absent). In this

case, each amplified fragment was considered as one locus and evaluated as dominant markers. However, to determine the genetic structure within and among genotypes, a second approach based on the co-dominant nature of the marker was adopted.

Genetic diversity parameters such as number of alleles per locus (N_a), number of effective alleles (N_e), observed heterozygosity (H_o), unbiased expected heterozygosity (H_e), inbreeding coefficient (F_{IS}) and major allele frequency (A) were performed according to Nei and Li (1979), using GENALEX version 6.5 (Peakall and Smouse, 2006). Genetic diversity was assessed using Shannon's Index (Shenton et al., 1969). Other genetic parameters such as polymorphic information content (PIC) were estimated using GenAlex software. The PIC, which is a measure of allelic diversity, was calculated as $PIC = 1 - \sum(p_i^2)$, where p_i stands for the frequency of i^{th} allele found in all the individuals of the populations (Nei, 1973). The total genetic variation was partitioned within and among predetermined groups, defined by root flesh colour, as white, yellow and orange. The binary data were used to obtain a dissimilarity matrix using the Jaccard index. The cluster analysis was performed based on Neighbour-joining using the un-weighted pair group method using the arithmetic average (UPGMA) in DARwin 5.0 software (Perrier and Jacquemoud-Collet, 2006). A dendrogram was then generated using the dissimilarity matrix. To investigate the genetic relationships among accessions, genetic distances between all pairs of individual genotypes were estimated to draw a dendrogram. Bootstrap analysis was performed for node construction using 10,000 bootstrap values. To quantify the level of genetic diversity among the 24 genotypes, the total genetic variation was partitioned into within and among populations using an analysis of molecular variance (AMOVA), performed using GenAlex software.

4.3. Results

4.3.1. Genetic diversity within and among sweetpotato genotypes

Genetic diversity parameters within and among the 24 sweetpotato genotypes are presented in Table 4.3. The total number of polymorphic alleles per locus (N_a) ranged from 2 to 10, for IB-S07 and IB-R19, respectively. The number of effective alleles per locus (N_e) ranged between 1.60 and 6.86, with an overall mean of 4.05 alleles per locus. Both the highest total number of alleles and the number of effective alleles were detected in the locus IB-R19, with 10 and 6.86, respectively. Apart from Loci IB-R12 and SSR07 that had an observed heterozygosity value (H_o) of 1.0, other loci had H_o values of zero, suggesting that most of the loci are fixed. The overall mean of H_o was 0.22. The unbiased expected heterozygosity (H_e) value ranged between 0.38 (IB-S07) and 0.87 (IB-R19 and SSR07), with an overall mean of

0.69. Inbreeding coefficient (F_{IS}) represents the average deviation of the population's genotypic proportions from the Hardy-Weinberg equilibrium for a locus, with values ranged from 0 to 1.0. A negative F_{IS} value represents an excess of heterozygotes. For example, for Locus IB-R12, 70% of the genotypes were expected to be heterozygous at that locus under random mating conditions; however, 100% of the genotypes at this locus were heterozygotes. This may have been due to the high outcrossing nature of sweetpotato, or mutation at the specific locus. The results of the χ^2 test showed significant differences in allele frequencies at all loci for all sets of genotypes. The polymorphic information value ranged between 0.38 and 0.85, with a mean PIC of 0.68. Of the total SSR markers used in this study, 77.8% of the loci had a PIC value of more than 0.50. The highest PIC value was observed for the loci IB-R19 and SSR07, with a value of 0.85, and the lowest for Locus IB-S07 at 0.38.

Table 4.3: Genetic diversity within and among 24 sweetpotato genotypes based on selected microsatellites markers

SSR locus	Genetic parameter						
	N_a	N_e	H_o	H_e	F_{IS}	A	PIC
IB-R03	3	2.32	0.00	0.58	1.00	0.58	0.57
IB-S07	2	1.60	0.00	0.38	1.00	0.75	0.38
IB-R12	4	3.19	1.00	0.70	-0.46	0.44	0.69
IB-R16	3	1.77	0.00	0.44	1.00	0.71	0.43
IB-R19	10	6.86	0.00	0.87	1.00	0.29	0.85
IB-CIP13	8	5.54	0.00	0.84	1.00	0.33	0.82
SSR07	8	6.78	1.00	0.87	-0.17	0.21	0.85
SSR09	8	5.24	0.00	0.83	1.00	0.33	0.81
690524	5	3.16	0.00	0.70	1.00	0.46	0.68
Overall mean	5.7	4.05	0.22	0.69	0.71	0.23	0.68
SE	1.0	0.69	0.15	0.06	0.19	0.04	0.06

N_a : total number of alleles per locus; N_e : number of effective alleles per locus; H_o : observed heterozygosity; H_e : unbiased expected heterozygosity (gene diversity); F_{IS} : fixation index (inbreeding coefficient); A: maximum allele frequency per locus; PIC: polymorphic information content; SE: standard error.

4.3.2. Genetic diversity within and among the 24 sweetpotato genotypes classified by storage root flesh colour

Summary statistics of the genetic diversity present among the tested sweetpotato genotypes classified by storage root flesh colour are shown in Table 4.4. The genotypes were classified into three flesh colour-based populations as white, yellow and orange. The total number of alleles per locus was slightly higher for white types (4.56). In contrast, the number of effective alleles per locus was slightly higher in yellow-fleshed genotypes (3.76) followed by

orange types (3.42). Shannon's information index (I) ranged between 1.20 and 1.24, with an overall mean of 1.22. The diversity of the white-, yellow- and orange-fleshed genotypes was 1.24, 1.20 and 1.23, respectively. The observed gene diversity within genotypes (H_o) was the same across all flesh colour-based populations, with a value of 0.22. However, the highest mean gene diversity was found in orange-fleshed genotypes (0.71), with an estimated overall mean of 0.67 across genotypes. Polymorphism information content ranged between 0.58 (orange-fleshed genotypes) and 0.64 (white-fleshed genotypes), with an overall mean of 0.60. A high value of private allele per population was found for white-fleshed types (4.00).

Table 4.4: Genetic diversity within and among the 24 sweetpotato genotypes classified by storage root flesh colour

Populations	Genetic parameters							
	N	N_a	N_e	I	H_o	H_e	PIC	P_a
White	10.00	4.56	3.35	1.24	0.22	0.67	0.64	4.00
Yellow	7.00	4.33	3.76	1.20	0.22	0.64	0.60	3.00
Orange	7.00	4.00	3.42	1.23	0.22	0.71	0.58	3.00
Overall mean	8.00	4.30	3.51	1.22	0.22	0.67	0.60	-
SE	0.28	0.37	0.33	0.10	0.08	0.04	0.02	-

N: number of individuals within each population; N_a : total number of alleles per locus; N_e : number of effective alleles per locus; I: Shannon's information index; H_o : observed gene diversity within genotypes; H_e : average gene diversity within genotypes; F: fixation index; PIC: Polymorphism Information Content; P_a : private allele per population; SE: standard error.

4.3.3. Population differentiation

The gene flow (N_m) and genetic differentiation (F_{ST}) are shown in Table 4.5. The highest gene flow value (8.17) was found between white- and yellow-fleshed genotypes, while the lowest value (3.14) was between yellow- and orange-fleshed types. The genetic differentiation (F_{ST}) among the 24 sweetpotato genotypes ranged from 0.03 and 0.07, with yellow and orange types having higher values. The genetic identity was relatively high (1.00) between white- and yellow-fleshed types, while the lowest value (0.86) was between yellow- and orange-fleshed genotypes. The larger genetic distance (0.15) was between yellow- and orange-fleshed genotypes followed by the combination of white- and orange-fleshed genotypes.

Table 4.5: Pair-wise estimates of gene flow (N_m) (top diagonal, within the brackets), genetic differentiation (F_{st}) (top diagonal, without brackets); genetic identity (GI) (bottom diagonal, within the brackets) and genetic distance (GD) (bottom diagonal, without brackets)

Storage root flesh color	White	Yellow	Orange
White		0.03 (8.17)	0.05 (4.34)
Yellow	0.00 (1.00)		0.07 (3.14)
Orange	0.11 (0.89)	0.15 (0.86)	

N_m : gene flow = $0.25 (1 - F_{ST}) / F_{ST}$

4.3.4. Analysis of molecular variance (AMOVA)

AMOVA was performed to quantify the level of genetic variability among populations through partitioning the variability within and among populations (Table 4.6). There were highly significant differences ($P < 0.001$) of molecular variance among and within individuals. A large level of genetic variability was due to differences among individuals and therefore contributed 69% of the total variability. Non-significant differences were found among the three populations, suggesting their contribution to the total variability was minimal.

Table 4.6: Analysis of molecular variance among 24 sweetpotato genotypes of three populations evaluated with selected SSR markers

Source	DF	SS	MS	Estimated variance	Percent variation	F-statistics
Among Populations	2	9.471	4.735	0.000	0%	0.750
Among Individuals	21	112.550	5.360	2.180	69%	0.001
Within Individuals	24	24.000	1.000	1.000	31%	0.001
Total	47	146.021		3.180	100%	

DF: degree of freedom; SS: sum of squares; MS: mean squares

4.3.5. Cluster analysis using the neighbour-joining method

A dendrogram showing three distinct clusters reflecting genetic relationships among the 24 genotypes is presented in Figure 4.1. The analysis showed three major clusters denoted as I, II and III, with 6, 5 and 13 genotypes, respectively. Each of the three clusters had two sub-clusters, making a total of 6 sub-clusters. These sub-clusters were I-a and I-b (with 2 and 4 individuals, respectively), II-a and II-b (1 and 4) and III-a and III-b (5 and 8). The genotypes SPK004 and K5132/61 were identified in Cluster I (Figure 4.1). A higher flowering frequency is the common attribute of genotypes in Cluster I. The genotypes 4-160, Ukerewe and RW11-2910 were grouped in Cluster II. Ukerewe has higher dry root yield, RW11-2910 has high flowering rate and 4-160 is known for improved root dry matter content. The genotype 2005-179 was identified in Cluster III, Sub-cluster III-a, whereas the genotypes RW11-1860 and Wagabolige were identified in Cluster III, Sub-cluster III-b. The three genotypes are

grouped together probably because of their breeding history. The genotypes RW11-1860 and Wagabolige were previously selected for their high storage root and vines yields, whereas the genotype 2005-179 was identified with high storage root yielding ability and tolerance to sweetpotato virus disease (SPVD) and *Alternaria* stem blight disease. The above eight genotypes showed large genetic dissimilarity and possessed key agronomic and horticultural attributes, making them complementary and ideal candidates in a sweetpotato breeding programme.

Clustering of genotypes did not follow the geographic origin and collection history of the genotypes. For instance genotype Giteke, collected in Rwanda, was allocated to Cluster III, Sub-cluster III-b, together with the genotype Wagabolige, which was bred in Kenya and sourced from the International Potato Centre for this study (Figure 4.1). Similarly, the following three genotypes: SPK004, OTADA24 and K5132/61 were allocated in Cluster I, Sub-cluster I-b (Figure 4.1).

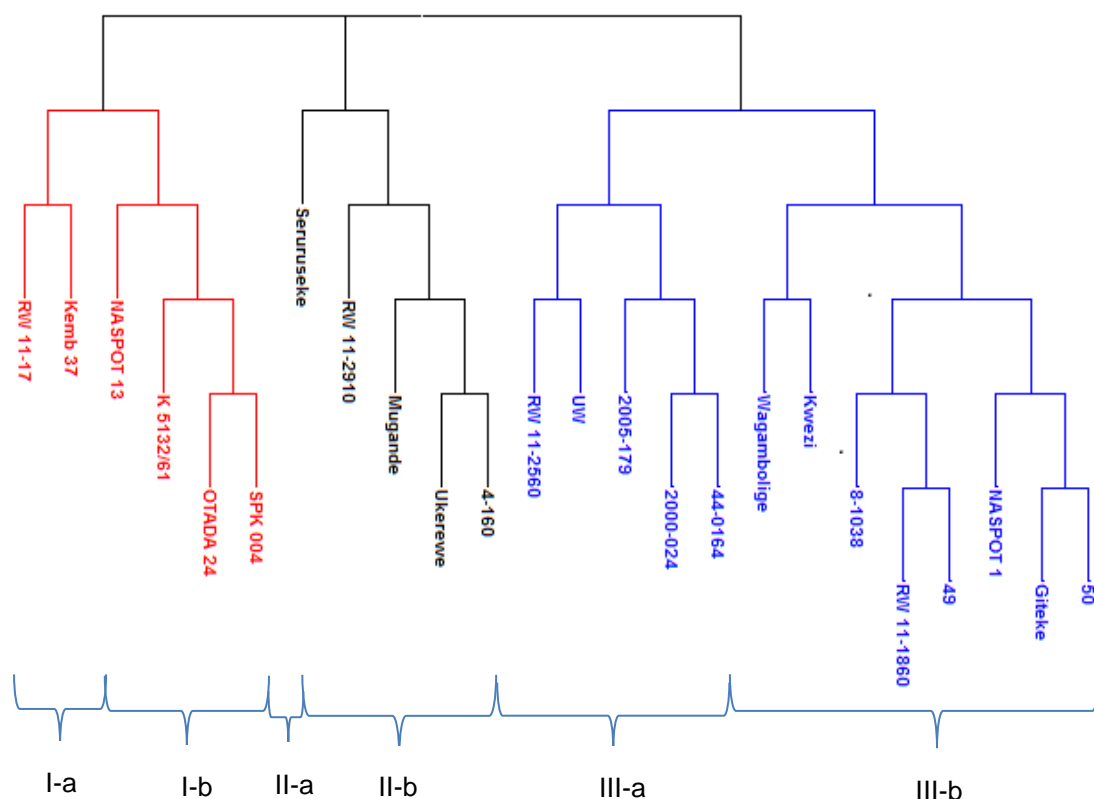


Figure 4.1: Dendrogram showing genetic variability among the 24 sweetpotato genotypes evaluated with selected SSR markers

The three genotypes were respectively sourced from the Kenyan Agricultural Research Institute (KARI), National Agricultural Research Organization (NARO) and International Institute for Tropical Agriculture (IITA). The clustering patterns were not in agreement with the predefined population structure using storage root flesh colour. Consequently, genotypes with corresponding storage root skin colour such as RW11-1860 (white), Wagabolige (cream), Kwezikumwe (yellow) and 8-1038 (red) were grouped in Cluster III, Sub-cluster III-b. Likewise, the genotypes 4-160, Ukerewe and RW11-2910 with white-, yellow- and orange-flesh colour, respectively, were allocated to Cluster II, Sub-cluster II-b.

4.4. Discussion

4.4.1. Genetic diversity within and among genotypes based on selected SSR markers

The current study assessed the level of genotypic diversity among and within the 24 sweetpotato genotypes selected for their dual-purpose traits in Rwanda. A χ^2 test showed significant differences in major allele frequencies at all loci for all sets of genotypes. The study showed that the number of polymorphic alleles per locus was different from the number of effective alleles per locus. This difference may have been attributed to the variability in the major alleles among the test genotypes. The mean number of alleles in this study was 5.7 (Table 4.3), which was higher than the values of 4.95 and 4.0 reported in the earlier studies by Mafu et al. (2014) and Yada et al. (2010), respectively. This may indicate a higher level of genetic variability among the presently studied sweetpotato population. This could be expected considering the outcrossing nature, high level of heterozygosity and the hexaploid nature of sweetpotato.

The overall mean of the unbiased expected heterozygosity (H_e) was higher (0.69) than the observed heterozygosity (H_o) (0.22) (Table 4.3). Previous studies in sweetpotato also found high H_e values. Ngailo et al. (2016) reported H_e value of 0.69 using Tanzania sweetpotato accessions. Likewise, Muhinyuza et al. (2015) reported higher value (0.75) of H_e when characterising 18 potato genotypes using 13 SSR markers in Rwanda. The relatively high H_e values suggest that the tested genotypes were predominantly heterozygous, which was expected.

The PIC is an estimate of the discriminatory power of each locus. In the current study, 66.7% of the loci had a PIC value above 0.60 (Table 4.3), reflecting a relatively high discriminating power of the markers used in this study. In a study by Karuri et al. (2009), 89 genotypes were successfully distinguished using 6 SSR markers, with an average PIC value of 0.40. The most polymorphic SSR loci were IB-R19 and SSR07 with PIC values of 0.85, followed

by IB-CIP13 with a PIC of 0.82 (Table 4.3). In earlier studies, Locus IB-R19 was reported to show a high PIC value of 0.80 (Karuri et al., 2009). The minimum and maximum PIC values found in this study were 0.38 and 0.85 (Table 4.3), respectively, which are higher than previous reports. Xu et al. (2004) and Mafu et al. (2014) reported PIC values ranging from 0.28 to 0.81 and 0.00 to 0.84, respectively. The three markers that exhibited higher polymorphism can be successfully used in future genotyping of sweetpotato clones to identify distantly related parents for variety development and deployment.

4.4.2. Genetic diversity based on storage root flesh colour

The total number of alleles per locus was higher for white-fleshed genotypes ($N=4.56$) than yellow- and orange-fleshed types which had 4.33 and 4.00, respectively. The overall mean number of alleles was 4.30 per locus (Table 4.4). In contrast, the number of effective alleles was larger for yellow-fleshed genotypes (3.76) compared to other types. The total and effective numbers of alleles reported in this study are within the range of those reported by Ngailo et al. (2016). A high number of alleles is an indication of a high level of genetic diversity of a set of test genotypes. The Shannon's information index (I) ranged from 1.20 and 1.24, with an overall mean of 1.22 (Table 4.4). This value was relatively large for white-fleshed types (1.24), followed by orange-fleshed types (1.23). Arizio et al. (2009) found a relatively high I mean value of 2.69. The overall mean value of the observed gene diversity (H_o) (0.22) was below the average gene diversity within genotypes (H_e) (0.67). All the populations (white, yellow and orange types) had similar H_o values of 0.22. The orange types had a slightly higher H_e (0.71) than white types (0.67) and yellow-fleshed types (0.64) (Table 4.4). This suggests that the likelihood of two alleles to be different is higher in orange- than white- and yellow-fleshed genotypes in the presently tested population. These results do not conform to the report of Arizio et al. (2009), who reported H_e values of 1.53 and 1.59 for orange-fleshed and white-fleshed genotypes, respectively. Getinet (2015) reported low values of 0.78 and 0.68 in a study to assess diversity of 18 potato clones in Ethiopia. The relatively high genetic diversity of sweetpotato reported in the present study is probably attributed to the inherent nature of self-incompatibility and cross-pollination of the crop (Gwandu et al., 2012). The PIC values ranged from 0.58 (for orange types) to 0.64 (for white-fleshed genotypes), with an overall mean value of 0.60 (Table 4.4). The mean polymorphism value found in the current study was similar to the report of Karuri et al. (2009). However, Yada (2010) reported a slightly higher PIC value of 0.62 when 10 SSR markers were used to characterise 192 sweetpotato accessions in Uganda.

4.4.3. Population differentiations

The pair-wise genetic differentiation analysis provided low (0.03) to moderate (0.05) values between white and yellow to white and orange populations, respectively (Table 4.5). According to standard guidelines for interpreting genetic differentiation (Wright, 1978), the range $0 < F_{st} < 0.05$ indicates little, $0.05 < F_{st} < 0.15$ indicates moderate, $0.15 < F_{st} < 0.25$ indicates large and $F_{st} > 0.25$ indicates a very large genetic differentiation.

In the present study, genetic identity values ranged between 0.86 and 1.00 (Table 4.5), with the largest values expressed by white- and yellow-fleshed genotypes. GI values were relatively higher in this study compared to previous reports. Ngailo et al. (2016) reported a GI ranging between 0.17 and 0.80, while the genetic distance (GD) ranged from 0.0 and 0.15, with the highest estimate being between yellow and orange types. The overall pair-wise estimate of genetic distance between genotypes reflected the moderate genetic diversity present in the current test genotypes. These results concur with those of Koussao et al. (2014) who reported moderate diversity among 112 sweetpotato genotypes. The present GD values were not in agreement to values reported by Muhinyuza et al. (2015) who found a relatively high genetic distance ranging between 0.44 and 0.93 in their diversity study involving 18 potato genotypes in Rwanda.

4.4.4. Analysis of molecular variance (AMOVA)

The total genetic variability partitioned into among and within genotypes revealed highly significant ($P < 0.001$) differences among and within genotypes (Table 4.6). However, non-significant differences were found among populations of white-, yellow- and orange-fleshed genotypes. A higher proportion of the genetic variability was contributed by the differences among individuals, which accounted for 69% of the total variability. Genotypes acquired from different sources could have related genetic make-up. These results concur with those of Ngailo et al. (2016) who reported a high contribution (87%) of among individuals in their study using 48 sweetpotato genotypes, while differing slightly with Rodriguez-Bonilla et al. (2014) who found a relatively large variation (75%) of within groups of sweetpotato genotypes in Puerto Rico.

4.4.5. Cluster analysis using the neighbour-joining method

Cluster analysis identified three major groups of genotypes (Figure 4.1). The genomic allocation of genotypes in the three groups was not related to their geographic origin. In this regard, genotypes collected from different locations were grouped together, whereas genotypes accessed from the same site did not always cluster together. Various authors

have accounted for genetic variability between different crop genotypes as the main source of genetic differentiation instead of geographic origin of collection (Yada et al., 2010; Gwandu et al., 2012; Laurie et al., 2013). For instance, in the present study Genotypes RW11-1860, 2005-179 and Wagabolige were placed in the same cluster despite their varied accession site and breeding history. Genetic similarities of sweetpotato collections from unrelated geographic zones were also observed by Ngailo et al. (2016). The genotypes RW11-1860 and Wagabolige, found in Cluster III and Sub-cluster III-b (Figure 4.1), were released for their high storage root yield and aboveground biomass production (Lukuyu et al., 2011). The genotypes 4-160, Ukerewe and RW11-2910 were grouped in Cluster II (Figure 4.1). Genotypes 4-160 and Ukerewe share a similar pedigree, and they have a common parentage and breeding history that would have resulted in the allocation of these entries to the same genetic group. Further, the storage root skin colour of genotypes Ukerewe and RW11-2910 is red partly attributing their common genetic backgrounds. The genotypes SPK004 and K5132/61 were grouped in Cluster III, reflecting common traits of high flowering frequency (data not shown) and their red skin colour, although the former was sourced from Kenya Agricultural Research Institute (KARI) and the later from the International Institute for Tropical Agriculture (IITA/Uganda).

The position of genotypes in the genetic tree was independent of the trait of storage root flesh colour. For instance, the genotypes RW11-2910, Ukerewe and 4-160 have orange-, yellow- and white flesh, respectively, but were grouped in Cluster II, Sub-cluster II-a (Figure 4.1). The genotypes Kwezikumwe and NASPOT1 were allocated to Cluster I. These genotypes are known for their high vine yields on dry matter basis and have their similar root-to-vine ratios (Niyireba et al., 2013). Therefore, this genetic relatedness information will assist in designing crosses using distantly related parental clones selected from unrelated clusters, in order to maintain a high level of heterozygosity, and therefore to eliminate inbreeding depression.

4.5. Conclusions

The nine SSR markers used in this study clearly distinguished the 24 sweetpotato genotypes. Marked genetic variation was reflected in a relatively large mean total number of alleles and mean number of effective alleles of 10 and 6.86, respectively. Considerable genetic variation was also shown by the genetic distance estimates of white-, yellow- and orange-fleshed genotypes, which were 1.24, 1.20 and 1.23, in that order. Yellow- and orange-fleshed genotypes showed a relatively high genetic differentiation (F_{ST}) value (0.07), while the highest genetic identity (GI) value (1.00) was between yellow- and white-fleshed types. AMOVA identified relatively large genetic variability among individuals that contributed

69% of the total variation. Cluster analysis showed that there were three distinct genetic groups: Clusters I, II and III, with 6, 5 and 13 genotypes, respectively.

In this study, eight genetically distant clones with key agronomic and dual-purpose traits were selected, namely SPK004 and K5132/61 from Cluster I, 4-160, Ukerewe, RW11-2910 from Cluster II, and RW11-1860, Wagabolige and 2005-179 from Cluster III. The selected genotypes constitute important genetic resources to be considered as parents in breeding DPSVs suitable for Rwanda.

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5. Chapter Five: Gene action and heritability of storage root and aboveground biomass yields, and yield components of dual-purpose sweetpotato clones

Abstract

In the past, extensive research and extension has been conducted on breeding and diffusion of sweetpotato [*Ipomoea batatas* (L.) Lam] varieties with enhanced storage root yield and β -carotene content for human food. However, limited research and development efforts have been carried out on breeding and popularisation of dual-purpose sweetpotato varieties with improved storage root and above ground biomass yields to serve for food and feed in the crop-livestock mixed farming systems prevalent in sub-Saharan Africa (SSA), including Rwanda. The objective of this study was to determine gene action and heritability of storage root and aboveground biomass yields and yield components in sweetpotato and to undertake early clonal selection for future release of dual-purpose varieties. Controlled crosses were performed involving eight parents selected for their complementary traits including storage root and vine production, dry matter content and farmer-preferred traits using a half-diallel mating design. The 36 families were field evaluated at Rubona, Karama and Ngoma research stations of the Rwanda Agriculture Board (RAB) from October 2016 to February 2017. Families had highly significant ($P < 0.001$) differences for assessed parameters. Further families and sites interacted significantly ($P < 0.001$) for fresh root yield (FRY), root dry matter content (RDMC), dry root yield (DRY), fresh vine yield (FVY), vine dry matter content (VDMC), total biomass on dry weight basis (TBDW) and root-to-vine ratio (R:V) and dry vine yield (DVY) except for harvest index (HI). The general combining ability (GCA) and specific combining ability (SCA) effects were significant for FRY, RDMC, DRY, R:V, HI and VDMC. GCA/SCA ratios were 0.75, 0.81 and 0.88 for DRY, RDMC and FRY, respectively, suggesting that additive gene action was more important than non-additive gene action in the expression of these parameters. Conversely, the ratio of GCA to SCA was relatively lower and ranged between 0.09 and 0.28 for vine and root-vine combined parameters, suggesting that the non-additive component of the genetic variance, either dominance or epistasis, was more influential in controlling the traits. This implies that parental performance cannot necessarily be the basis of progeny performance prediction for these traits. The broad-sense heritability (H^2) values were above 0.5 for all tested parameters, with FRY, HI and RDMC having higher estimates of 0.80, 0.81 and 0.92, in that order. RDMC had a high narrow-sense coefficient of genetic determination (NSCGD) of 0.80, while this parameter varied between 0.09 and 0.49 for the rest of the tested traits. The parent K5132/61 was the best combiner for FRY and HI, while the parents RW11-1860, RW11-2910, SPK004 and Ukerewe were best general combiners for RDMC. The parent Wagabolige was the best general combiner for FRY, DRY and R:V. Based on desirable SCA effects for FVY, DVY, TBDW, RDMC, R:V and FRY, the most promising families selected in this study were K5132/61 x Wagabolige, 4-160 x 2005-179, K5132/61 x RW11-1860 and RW11-2910 x 2005-179. From this study, promising dual-purpose progenies derived from the selected families are recommended for advanced clonal evaluation across multiple sites for releasing dual-purpose sweetpotato varieties in Rwanda or similar agro-ecologies in SSA.

Keywords: general combining ability, genetic variance, half-diallel, *Ipomoea batatas*, NSCGD, specific combining ability

5.1. Introduction

Sweetpotato [*Ipomoea batatas* (L.) Lam; $2n = 6x = 90$] is an important food, feed and cash crop in most tropical and subtropical countries. The storage roots of sweetpotato serve as a major source of human food especially in sub-Saharan Africa (SSA) (Low et al., 2017), while the aboveground biomass is widely used for feed in the crop-livestock mixed farming systems (León-Velarde, 2000). Projections indicate that sweetpotato will have significant advantages in East African countries through generating farm income and contributing to food security (Sindi et al., 2013; Kagimbo et al., 2017). In Rwanda where grazing and agricultural lands are limited, sweetpotato constitutes an important component of the crop-livestock farming system (Shumbusha et al., 2017). The importance of the crop in Rwanda is also reflected by the significantly higher quantity of annual production of fresh roots and percent contribution to the national crop production, each estimated at 1,000,000 tonnes and 13.3%, respectively (FAOSTAT, 2013; NISR, 2016).

In the past, international and national breeding programs focused on developing sweetpotato varieties primarily with improved fresh root yields. Limited emphasis was given on breeding dual-purpose sweetpotato varieties (DPSVs) that can simultaneously provide storage root and aboveground biomass for forage production. DPSVs can be successfully adopted in the mixed crop-livestock farming systems where agricultural lands are limited such as in Rwanda. Development of DPSVs requires selection of promising genotypes with greater storage root yield and aboveground biomass in a desirable genetic background.

A root-to-vine ratio has been successfully used to classify sweetpotato genotypes into five types, namely: (i) high root production, (ii) low root production, (iii) dual-purpose, (iv) low dual-purpose and (v) forage production (León-Velarde et al., 2009; Lukuyu et al., 2014; Lestari and Hapsari, 2015). Among the five types, dual-purpose and forage sweetpotato varieties are well-suited for forage production. However, DPSVs have a comparative advantage over forage types, since both root and forage can be produced by smallholder mixed crop-livestock farmers on the same land (Niyireba et al., 2013). Therefore, improving sweetpotato vine and storage root yields and yield-related traits through a well-designed breeding program enables release of DPSVs for integrated crop and livestock production.

The inherent hexaploid genetic makeup of sweetpotato provides varied segregation patterns after crosses (Buteler et al., 1997). Further, some genotypes show high level of heterozygosity, sterility, and self- or cross-incompatibilities (Martin and Jones, 1986). Despite these limitations marked breeding and genetic progress has been achieved through

characterization of germplasm pool, effective combination of parents through crosses, and unravelling the gene action and heritability of economic traits (Yada et al., 2017). Sweetpotato genetic resources of Rwanda were recently characterized (Shumbusha et al., 2017) and promising genotypes were selected with dual-purpose traits to develop DPSVs. There is need to understand the combining ability and heritability of the selected parents and their families for dual-purpose traits, for effective breeding and release of varieties in Rwanda.

Understanding the gene action and heritability of economic traits is essential in genetic analysis and plant breeding programs (Acquaah, 2012). To analyse gene action and heritability, a target population should be developed through systematic crosses of chosen parents using a well-designed mating scheme. A diallel mating design has been successfully used to determine the gene action in sweetpotato (Mwanga et al., 2002; Rukundo et al., 2017). Gene action may be estimated through components of genetic variance and combining ability analysis (Falconer and Mackay, 1996). General combining ability (GCA) is a measure of performance of the hybrid that the genotype produces with other genotypes, while specific combining ability is the deviation of a particular cross from the average of the GCA of the two crossed genotypes (Griffing, 1956). The relative magnitude of GCA and SCA can indicate the type of gene action involved and its suitable selection method leading to more genetic gains (Baker, 1978). Significant GCA effects indicate the importance of additive gene action, while the SCA reflects the non-additive gene action which consists of dominance and epistasis (Acquaah, 2012). Both additive and non-additive gene actions were detected to governing storage root yield, with additive gene action being more predominant (Mwije et al., 2014; Shumbusha et al., 2014).

Heritability is the proportion of the observed variation in a progeny that is inherited (Falconer and Mackay, 1996). Broad-sense heritability (H^2) was reported more useful in sweetpotato and that of vegetative propagated crops since both additive and non-additive gene action are fixed and transferred from parents to progenies (Acquaah, 2012). High estimates of narrow-sense heritability (h^2) indicate that cross combinations associated with high GCA effects are likely to lead to a high response to selection and genetic gains. High SCA effects are useful in producing superior progenies for subsequent selection (Freeman, 2009). Therefore, the objective of this study was to determine gene action and heritability of storage root and aboveground biomass yields and yield components in sweetpotato and to undertake early clonal selection for future release of dual-purpose varieties.

5.2. Material and methods

5.2.1. Study sites

A crossing block was established at the Southern Agriculture Zone Division (SAZD) of the Rwanda Agriculture Board (RAB), in Rubona Research Station. The progeny evaluation trials were conducted in the experimental fields of RAB at Karama, Ngoma and Rubona Research Stations from October 2016 to February 2017. Rubona is located at mid-altitude of Rwanda, while Karama and Ngoma are located in the lowlands of Rwanda (Murayi et al., 1987). The Karama site is situated in a drought-prone area due to its semi-arid agroecology. The detailed description of the study sites is summarised in Table 5.1.

Table 5.1: Description of the study sites

Parameter	Description	Karama	Ngoma	Rubona
GPS coordinates	Altitude (masl)	1400	1420	1700
	Latitude	02 ⁰ 17' S	02 ⁰ 16'S	02 ⁰ 29'S
	Longitude	30 ⁰ 16' E	30 ⁰ 55'E	29 ⁰ 46'E
Soil	Type	Clay and sandy	Clay	Clay and sandy
Mean temperature (°C)	Oct 2016 – Feb 2017	20.7	21.2	20.2
Rainfall (mm)	Oct 2016 – Feb 2017	301.8	428.8	510.2

masl: meter above sea level

5.2.2. Parental material

Eight genotypes were used for crosses. The genotypes were selected based on previous extensive germplasm characterization (Shumbusha et al., 2017). The eight parents were genetically distantly related for root and vine dry yields. Briefly, the genotypes were selected for their higher root production, higher forage production, high root and vine dry matter content, or other contrasting yield attributes (Table 5.2).

Table 5.2: Description of the eight sweetpotato parents used in crosses

No	Name/pedigree	Skin colour	Flesh colour	Attribute(s)	Origin
1	2005-179	White	White	Excellent flowering ability	NARO
2	4-160	White	White	Excellent flowering ability	RAB
3	K5132/61	Red	White	Excellent flowering ability	IITA
4	RW11-1860	White	Pale yellow	Higher root and aboveground biomass production	RAB
5	RW11-2910	Red	Light orange	Higher root and aboveground biomass production	RAB
6	SPK004	Red	Light orange	Higher root production	KALRO
7	Ukerewe	Red	Yellow	Locally adapted, higher dry matter content, farmer-preferred	RAB
8	Wagabolige	Cream	Orange	New introduction, dual-purpose type	CIP

Where, RAB: Rwanda Agriculture Board, CIP: International Potato Centre, NARO: National Agriculture Research Organization/ Uganda, KALRO: Kenya Agriculture and Livestock Research Organization, IITA: International Institute for Tropical Agriculture.

5.2.3. Crossing block, crosses and processing F1 seeds

Parents were planted in a well-prepared soil, supplemented with organic manure. The crossing block was initiated during the dry season under supplemental irrigation until the onset of rains in October 2015. Vines were tended to grow vertically using a plastic twine string tied on horizontal fixed wire (Figure 5.1-left). Weeding and pruning were carried out whenever necessary. Flowers ready to open were regularly emasculated and bagged using a piece of aluminium foil the day before hand-pollination to avoid any accidental self- and unwanted cross-pollination. The following day, emasculated flowers were hand-pollinated between 6:00-9:00 a.m. and labelled. Controlled crosses were performed using a half-diallel, Method 2, Model I as described by Griffing (1956). Matured botanical seeds were regularly harvested and each family was kept separately.

In early May 2016, botanical seeds of the families were scarified as follows: seeds were soaked in a concentrated (98%) sulfuric acid (H_2SO_4) for 30 minutes to break the mechanical dormancy imposed by the seedcoat followed by rinsing seeds using tap water for 5 minutes. A floating test was used to separate viable and nonviable seeds by putting seeds in a beaker half-full of water, where seeds that sink were considered viable. Viable seeds for each cross were then transferred in a Petri Dish lined with a moistened filter paper and kept in a laboratory at ambient temperatures. After two days, germinated seeds (Figure 5.1-right) were ready to be sown in seedling nursery beds.



Figure 5.1: Picture showing a crossing block of the study (left) and germinated sweetpotato seeds from crosses of parent 5 x parent 4 (right)

5.2.4. Seedling preparation and clonal evaluation

In August 2016, cuttings from mature seedlings (Figure 5.2-left) were planted under wet-land/swamp conditions to raise more vines (Figure 5.2-right) for progeny evaluation trials in three locations. At each site, the 36 families and parents (28 families and eight parents) were planted using a 9 x 4 lattice design with two replications. Twenty well-established plants from each family were chosen, and five cuttings per plant were planted to represent each entry in each replication. Spacing between plants in a row was 30 cm, with 80 cm between rows, giving a population of 41,666 plants. ha⁻¹. Evaluation trials were planted in October 2016 and harvested in February 2017. Harvesting was done at maturity, five months after planting, from the three middle plants of each entry and expressed as a plot mean. One plant at either end of the row was left as a border plant, giving a harvest area of 0.72 m² per sub-plot.



Figure 5.2: Seedling nursery beds (left) and vine bulking at Rubona site in Rwanda (right)

5.2.5. Data collected

Data collected included root, vine and combined root and vine parameters. The root yield data collected were fresh root yield (FRY), root dry matter content (RDMC) and dry root yield

(DRY). The data on aboveground biomass related parameters included fresh vine yield (FVY), vine dry matter content (VDMC) and dry vine yield (DVY).

Combined root and vine characteristics included root-to-vine ratio (RV), total biomass on dry weight basis (TBDW) and harvest index (HI). After harvest, root and vine yields (expressed in t.ha⁻¹) were determined on a dry weight basis, using the method described by Rodríguez (1999), Benesi et al. (2005) and Cervantes-Flores et al. (2011). A root or vine sample of 300 g from undamaged roots or vines was collected. To obtain the dry weight, samples were oven-dried at 65°C for 72 hours to a constant weight. The dry matter content (DMC) was calculated as: DMC (%) = (dry weight /fresh weight)*100. Dry yields were expressed as: [Fresh yield x DMC]/100. Classification of clones into dual-purpose genotypes was done according to Leon-Velarde et al. (1997), considering the ratio of total dry matter of roots to vines (R:V), where: (i) forage (R:V= 0-1), (2) low dual-purpose (R:V>1-1.5), high dual-purpose (R:V>1.5-2.0), low root production (R:V>2.0-3.0), high root production (R:V>3.0). Harvest index (HI) was calculated as total fresh storage root weight divided by total biomass (storage root + vines) weight. The TBDW was determined as the sum of dry matter yield of roots and vines.

5.2.6. Data analyses

5.2.6.1 Analysis of variance (ANOVA)

Data was subjected to the analysis of variance using the General Linear Models (GLM) procedure with the SAS statistical program (SAS, 2008). When significant treatment differences were detected following ANOVA, then treatment means were separated using Fisher's Protected Least Significance Difference test (LSD) at the 5% significance level.

5.2.6.1 Estimation of GCA and SCA effects and heritability

Data collected across locations were subjected to combined analysis of variance using the following model:

$$Y_{ijkl} = \mu + L_e + k(re)_k + g_i + g_j + s_{ij} + gL_{ie} + sL_{eij} + \varepsilon_{ijkl}$$

Where, Y_{ijkl} : the observed value of the cross between parent i and j in the k^{th} replication and l location ; μ : grand mean; L_e : location effect; $k(re)_k$: estimate of the k^{th} incomplete block within replications; $g_i + g_j$: GCA effects of i^{th} and j^{th} parents, respectively; s_{ij} : SCA effect; gL_{ie} : interaction effect between GCA and location; sL_{eij} : interaction effect between GCA and location; ε_{ijkl} : error term associated with the ij^{th} cross, in the k^{th} replication and l location.

Genetic information was determined on family mean basis. Genetic analysis was performed by using DIALLEL-SAS 05, in SAS version 9.3 (Zhang et al., 2005), and analysed according to Griffing Method 2 (one set of F1's and parents, but no reciprocals ($\frac{1}{2} p (p+1)$ combinations), Model 1 (all effects except the error are fixed) (Griffing, 1956). The relative importance of GCA and SCA was determined by first estimating these two variance components and then expressing them in the ratio, $2 \sigma^2_{GCA} / (2 \sigma^2_{GCA} + \sigma^2_{SCA})$ (Baker, 1978). In this formula, genetic components of the variation associated with GCA and SCA were estimated from their respective mean squares and the mean squares due to error (Singh and Chaudhary, 1979). Therefore, σ^2_{GCA} was obtained as: $[MS_{GCA} - (MS_e / r)] / (P+2)$, and $\sigma^2_{SCA} = MS_{SCA} - (MS_e / r)$, where: MS_{GCA} , MS_{SCA} and MS_e stand for mean squares for GCA, SCA and error, respectively; while P: number of parents; r: number of replications.

Broad-sense heritability (H^2) of root dry yield and vine dry yield was estimated using variance components as follows: $H^2 = Vg / Vp$, where, H^2 : Broad-sense heritability, Vg : Genetic variance and Vp : Phenotypic variance. The narrow-sense coefficient of genetic determination (NSCGD), which is a fixed parent equivalent of heritability in the narrow-sense (h^2) was estimated according to Fehr (1991), and later used by several researchers (Nsabiya et al., 2013; Mwijje et al., 2014). Therefore, $NSCGD = 2 \sigma^2_{GCA} / (2 \sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_e)$. Where, σ^2_{GCA} : variance component of GCA; σ^2_{SCA} : variance component of SCA; σ^2_e : error variance.

5.3. Results

5.3.1. Analysis of variance for root, vine and root-vine combined parameters

Analysis of variance of data collected at each site showed significant differences between test families for fresh root yield, root dry matter content, dry root yield, fresh vine yield, vine dry matter content, dry vine yield, total biomass on dry weight basis, root-to-vine ratio and harvest index (data not shown).

The combined ANOVA of all root, vine and root-vine parameters is presented in Table 5.3. There were highly significant ($P < 0.001$) differences among sites for all measured parameters. Families had highly significant ($P < 0.001$) differences for all parameters. Except HI, families and sites interacted significantly ($P < 0.001$) for FRY, RDMC, DRY, FVY, VDMC, TBDW and R:V, and $P < 0.01$ for DVY.

Table 5.3: Mean squares and significant tests for storage root and aboveground biomass traits of 36 families evaluated in three sites in Rwanda

Source of variation	DF	Mean squares and significant tests								
		Root parameter			Vine parameter			Root and vine parameter		
		FRY	RDMC	DRY	FVY	VDMC	DVY	TBDW	R:V	HI
Site (S)	2	14746.69***	6306.50***	1965.71***	31128.30***	11463.23***	300.73***	3312.72***	49.573***	4.35***
Rep (R) / S	3	202.72ns	210.24***	34.83**	4733.60***	655.27***	362.63***	617.80***	6.876**	0.07ns
Family (F)	35	548.32***	456.13***	29.30***	3655.80***	183.41***	132.51***	183.28***	4.623***	0.16***
F x S	70	163.14***	44.80***	14.44***	948.50***	65.65***	33.87**	69.40***	3.153***	0.04ns

, *: Significant at the 0.01 and 0.001 probability levels, respectively; ns: not significant; DF: degree of freedom; FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; R:V: root-to-vine ratio; HI: harvest index; H: broad-sense heritability.

5.3.2. Performance of 28 crosses and 8 parents for root, vine and combined root and vine parameters on fresh and dry weight basis across three sites

Mean performance of tested crosses and parents for all the nine parameters are presented in Table 5.4. FRYs ranged between 7.41 and 25.10 t. ha⁻¹, with a mean of 14.22 t. ha⁻¹. The top two performers for FRY were the parents Wagabolige (25.10 t. ha⁻¹) and Ukerewe (22.92 t. ha⁻¹) followed by the cross K5132/61 with 21.03 t. ha⁻¹. The parental genotype Ukerewe exhibited a high RDMC of 34.36%, followed by its progeny Ukerewe x SPK004 with 32.9%. The parent SPK004 and cross RW11-2910 x RW11-1860 were among the top four RDMC performers with 32.36% and 32.16%, respectively. Overall, 52.78% of the tested families performed well above the grand mean of 29.16%. DRY ranged between 2.46 and 7.34 t. ha⁻¹, with a mean of 4.19 t. ha⁻¹. The highest DRY value was recorded from parents Ukerewe and Wagabolige with 7.34 and 7.06 t. ha⁻¹, respectively, followed by the cross K5132/61 x Wagabolige, with 5.51 t. ha⁻¹. The cross RW11-2910 x 2005-179 ranked fourth for DRY with a mean of 4.96 t. ha⁻¹.

Vine parameters such as FVY, VDMC and DVY showed marked variation between families. FVYs varied between 18.58 and 51.63 t. ha⁻¹ with a mean of 36.85 t. ha⁻¹. The best performers for FVY were cross K5132/61 x Wagabolige, with 51.63 t. ha⁻¹, followed by a cross involving 2005-179 and RW11-1860 (48.59 t. ha⁻¹). The parents RW11-1860 and 4-160 ranked third and fourth in FVY, with mean values of 45.05 and 44.10 t. ha⁻¹, respectively. The VDMC ranged from 16.78 to 24.29% with a mean of 21.01%. The top two best performing crosses for VDMC shared the same parent Ukerewe, namely Ukerewe x 4-160 and Ukerewe x RW11-1860, with mean values of 24.29 and 22.91%, in that order. Among the parents, the highest mean VDMC value was recorded from parent RW11-1860 (23.02%), followed by 2005-179 (22.81%). The DVY values ranged from 4.12 and 10.23 t.

ha⁻¹, with a grand mean of 7.37 t. ha⁻¹. Parent RW11-1860 and cross K5132/61 x Wagabolige were the two best performers for DVY, with mean values of 10.23 and 10.17 t. ha⁻¹, in that order. A relatively higher DVY values were also recorded for the cross 2005-179 x RW11-1860 (10.03 t. ha⁻¹) and the parent Ukerewe (7.79 t. ha⁻¹).

Root-vine combined parameters such as TBDW, R:V and HI are presented in Table 5.4. TBDWs ranged from 9.01 to 15.81 t. ha⁻¹. The best yielders for this trait were parent RW11-1860 (15.81 t. ha⁻¹), followed by cross K5132/61 x Wagabolige (15.67%). Parent Ukerewe and a cross involving 2005-179 and RW11-1860 were among the top four, with mean TBDW of 15.13 t. ha⁻¹ and 13.8 t. ha⁻¹, respectively. The parameter R:V ranged between 0.58 and 2.72. High R:V values were recorded from the parents Wagabolige (2.72), Ukerewe (1.47), and crosses namely K5132/61 x RW11-1860 (1.60) and Ukerewe x Wagabolige (1.10). The highest HI values were recorded from the parent Wagabolige (0.58), followed by two parents Ukerewe and K5132/61, both with the same HI value of 0.55. The parents Ukerewe and K5132/61 contributed to a relatively high performance in their parentage such as in crosses Ukerewe x Wagabolige and Ukerewe x K5132/61, which had HI values of 0.46 and 0.44, respectively.

Table 5.4: Mean responses of sweetpotato parents and their progenies for nine parameters

Cross/Parent	FRY	RDMC	DRY	FVY	VDMC	DVY	TBDW	R:V	HI
Crosses									
2005-179 x RW11-1860	13.82	27.18	3.77	48.59	21.46	10.03	13.80	0.62	0.30
2005-179 x Wagabolige	15.14	25.69	4.08	46.44	20.39	8.57	12.65	0.60	0.33
4-160 x 2005-179	12.03	29.94	3.65	37.44	22.33	8.07	11.72	0.60	0.32
4-160 x RW11-1860	14.08	30.70	4.39	41.70	19.37	7.76	12.15	0.72	0.37
4-160 x RW11-2910	13.71	30.51	4.26	36.07	22.36	7.74	12.01	0.72	0.36
4-160 x Wagabolige	15.63	30.27	4.87	34.37	19.42	6.20	11.08	1.07	0.44
K5132/61 x 2005-179	12.56	23.47	3.00	30.21	20.59	6.19	9.19	0.81	0.37
K5132/61 x 4-160	18.10	24.53	4.54	29.73	20.37	5.78	10.32	0.86	0.43
K5132/61 x RW11-1860	19.05	25.89	4.95	42.88	18.92	7.50	12.45	1.60	0.40
K5132/61 x RW11-2910	14.79	28.34	4.29	36.08	18.75	6.75	11.04	1.05	0.38
K5132/61 x Wagabolige	21.03	24.97	5.51	51.63	20.30	10.17	15.67	0.67	0.35
RW11-1860 x Wagabolige	13.89	31.57	4.46	30.24	21.71	6.24	10.69	0.91	0.42
RW11-2910 x 2005-179	17.74	27.94	4.96	38.87	21.77	8.22	13.18	0.78	0.38
RW11-2910 x RW11-1860	11.57	32.16	3.76	34.53	22.03	6.99	10.74	0.89	0.37
RW11-2910 x Wagabolige	13.62	28.69	4.07	47.45	19.20	9.11	13.19	0.66	0.33
SPK004 x 2005-179	13.57	26.83	3.74	39.85	20.20	7.44	11.18	0.68	0.32
SPK004 x 4-160	14.09	29.35	4.11	36.13	21.63	7.33	11.44	0.72	0.37
SPK004 x K5132/61	13.69	28.36	4.11	40.65	21.16	8.24	12.15	0.63	0.34
SPK004 x RW11-1860	13.42	31.57	4.31	32.77	22.71	7.13	11.43	0.89	0.39
SPK004 x RW11-2910	10.44	31.74	3.37	28.71	21.18	5.84	9.22	0.79	0.37

Cross/Parent	FRY	RDMC	DRY	FVY	VDMC	DVY	TBDW	R:V	HI
Crosses									
SPK004 x Wagabolige	16.17	27.93	4.55	42.93	21.39	8.87	13.41	0.68	0.34
Ukerewe x 2005-179	14.66	29.90	4.35	37.94	22.62	7.81	12.16	0.73	0.36
Ukerewe x 4-160	11.94	30.34	3.73	30.21	24.29	7.24	10.97	0.61	0.32
Ukerewe x K5132/61	14.45	28.13	4.19	27.45	19.53	5.28	9.46	1.01	0.44
Ukerewe x RW11-1860	12.25	29.66	3.70	29.15	22.91	6.29	9.99	0.89	0.39
Ukerewe x RW11-2910	10.42	31.20	3.33	32.61	22.44	7.11	10.44	0.58	0.33
Ukerewe x SPK004	11.73	32.90	3.91	40.70	18.77	7.16	11.08	0.69	0.34
Ukerewe x Wagabolige	15.08	30.31	4.72	27.82	19.91	5.46	10.18	1.10	0.46
Parents									
2005-179	14.65	23.43	3.45	31.94	22.81	7.17	10.63	0.59	0.32
4-160	16.25	27.93	4.73	44.10	16.78	7.00	11.72	1.15	0.43
K5132/61	22.05	23.04	5.59	18.58	20.50	4.12	9.72	1.35	0.55
RW11-1860	17.33	31.60	5.57	45.05	23.02	10.23	15.81	0.84	0.41
RW11-2910	16.06	31.97	5.51	40.89	19.75	7.42	12.93	0.99	0.44
SPK004	7.41	32.36	2.46	40.02	18.14	6.57	9.03	1.11	0.41
Ukerewe	22.92	34.36	7.34	39.15	21.04	7.79	15.13	1.47	0.55
Wagabolige	25.10	28.66	7.06	29.17	17.80	4.91	11.97	2.72	0.58
Mean of crosses	14.24	28.93	4.17	36.9	20.99	7.38	11.54	0.81	0.37
Mean of parents	17.72	29.17	5.21	36.2	20.09	6.95	12.05	1.23	0.45
Grand mean	14.22	29.16	4.19	36.85	21.01	7.37	11.56	0.82	0.37
LSD (5%)	8.70	3.78	2.66	20.29	5.26	4.25	5.74	1.27	0.14
CV (%)	32.32	7.18	35.03	40.52	14.15	37.25	31.85	9.20	22.02

FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; R:V: root-to-vine ratio; HI: harvest index.

The 36 families performed differently across test sites for the nine tested parameters. The site mean for each parameter is presented in Table 5.5. The mean FVY at Karama site was the highest (41.8 t. ha⁻¹), followed by the Ngoma site, with a mean of 37.94 t. ha⁻¹. The families performed well at Ngoma site for FRY, DRY, DVY and TBDW, with mean values of 16.87, 5.02, 7.99 and 13.01 t. ha⁻¹, respectively. At the Rubona site higher mean values of 31.12 and 23.98% were recorded for RDMC and VDMC, in that order. The highest R:V and HI values were also recorded at the Rubona site, with 1.01 and 0.41, respectively.

Table 5.5: Mean performance of the 36 families for nine parameters evaluated at three sites in Rwanda

Site	Root parameter			Vine parameter			Root and vine parameter		
	FRY (t.ha ⁻¹)	RDMC (%)	DRY (t.ha ⁻¹)	FVY (t.ha ⁻¹)	VDMC (%)	DVY (t.ha ⁻¹)	TBDW (t.ha ⁻¹)	R:V	HI
Karama	9.83	26.34	2.57	41.80	17.33	6.95	9.52	0.57	0.29
Ngoma	16.87	30.03	5.02	37.94	21.71	7.99	13.01	0.87	0.40
Rubona	15.96	31.12	4.97	30.82	23.98	7.18	12.14	1.01	0.41
SED	4.44	1.93	1.36	10.34	2.68	2.17	2.92	0.65	0.07

FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; R:V: root-to-vine ratio; HI: harvest index; SED: standard error of the difference.

5.3.3. General and specific combining ability effects

A combined ANOVA for combining ability tests across sites is shown in Table 5.6. Results showed significant ($P < 0.05$) GCA effects for FRY, RDMC, HI, DRY, VDMC and R:V. Similarly, highly significant SCA ($P < 0.05$) effects were found for FRY, RDMC, R:V, HI, DRY and VDMC. Except for SCA by site interaction which had significant ($P < 0.5$) effects for RDMC, both GCA x S and SCA x S were not significant for the other parameters.

The estimates of GCA and SCA variance components are presented in Table 5.6. The GCA variance component (σ^2_{GCA}) with values above 1.00 were 1.28, 1.67, 7.66, 11.89 and 17.59, recorded for DRY, VDMC, FRY, FVY and RDMC, respectively. Combined root and vine parameters such as TBDW, R:V and HI had GCA variance components below 1.00. The highest SCA variance components (σ^2_{SCA}) were found for five parameters including DVY (7.58), RDMC (8.12), VDMC (10.37), TBDW (11.25) and FVY (216.40). The GCA/SCA ratio, also known as “Baker’s ratio” was greater than 0.5 for the root parameters DRY, RDMC and FRY, with 0.75, 0.81 and 0.88, respectively. The closer the ratio to unity, the greater the magnitude of additive genetic action. The ratios were less than unity for the parameters FVY (0.09), TBDW (0.07), DVY (0.14), R:V (0.17), VDMC (0.24) and HI (0.28). For the parameter FVY, GCA/SCA ratio showed the lowest ratio (0.09) due to the highest value of σ^2_{SCA} (216.40).

5.3.4. Heritability estimates

Both the broad-sense heritability (H^2) and the narrow-sense coefficient of genetic determination (NSCGD) are presented in Table 5.6. The H^2 estimates for family means across sites were above 50% for all test parameters, with three traits having relatively high estimates ≥ 0.8 such as FRY (0.80), HI (0.81) and RDMC (0.92). A relatively low H^2 value (0.59) was estimated for R:V. The NSCGD estimates ranged between 0.09 and 0.80. The

most prominent NSCGD estimate (0.80) was found for the parameter RDMC. The relatively high estimates of NSCGD were found on root parameters FRY, DRY and RDMC, with 0.44, 0.49 and 0.80, respectively. Among the tested parameters, RDMC had the highest estimates (≥ 0.8) for both H^2 and NSCGD.

Table 5.6: Mean square and significance tests of combining ability analysis for nine traits of eight sweetpotato parents and 28 crosses evaluated across three locations in Rwanda

Source of variation	DF	Root parameter			Vine parameter			Root and vine parameter		
		FRY (T/ha)	RDMC (%)	DRY (T/ha)	FVY (T/ha)	VDMC (%)	DVY (T/ha)	TBDW (T/ha)	RV	HI
GCA	7	129.42***	177.54***	6.87**	229.62 ^{ns}	21.05*	10.28 ^{ns}	11.49 ^{ns}	0.79*	0.03***
SCA	28	54.94***	10.32***	4.54**	327.13 ^{ns}	14.8*	11.35 ^{ns}	18.15 ^{ns}	0.84***	0.02***
GCA x Site (S)	14	32.59 ^{ns}	5.47 ^{ns}	2.82 ^{ns}	142.23 ^{ns}	6.17 ^{ns}	6.2 ^{ns}	13.6 ^{ns}	0.42 ^{ns}	0.01 ^{ns}
SCA x S	56	28.31 ^{ns}	6.36*	2.30 ^{ns}	201.98 ^{ns}	10.87 ^{ns}	7.55 ^{ns}	12.87 ^{ns}	0.45 ^{ns}	0.01 ^{ns}
Error	105	105.63	4.39	10.69	221.45	8.85	7.54	13.80	2.35	0.02
σ^2_{GCA}		7.66	17.53	1.28	11.89	1.67	0.65	0.46	0.04	0.002
σ^2_{SCA}		2.12	8.12	0.85	216.40	10.37	7.58	11.25	0.39	0.01
GCA / SCA		0.88	0.81	0.75	0.09	0.24	0.14	0.07	0.17	0.28
H^2		0.80	0.92	0.66	0.79	0.75	0.78	0.71	0.59	0.81
NSCGD		0.44	0.80	0.49	0.09	0.22	0.13	0.06	0.09	0.24

*, **, *** : significant at the 0.05, 0.01 and 0.001 probability levels, respectively; ^{ns}: not significant; DF: degree of freedom; FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; RV: root-to-vine ratio; HI: harvest index; GCA: general combining ability; SCA: specific combining ability; S: site.

5.3.5. General combining ability (GCA) effects

The GCA effects and their level of significance for the eight parents used in this study are presented in Table 5.7. The GCA effects were positive and significant ($P < 0.01$) for FRY in the parents K5132/61 (2.23) and Wagabolige (2.30), which is in a desirable direction for selection. Similarly, the parents RW11-1860, RW11-2910, SPK004 and Ukerewe exhibited high positive and significant GCA effects of 1.1, 1.35, 1.17 and 1.89, respectively, for RDMC. The newly introduced genotype Wagabolige had positive and significant ($P < 0.05$) GCA effects of 0.62 and 0.19 for DRY and R:V, in that order. GCA effects for other parents such as 2005-179 and K5132/61 were negative and significant ($P < 0.001$) for RDMC. The GCA effects for the parent 2005-179 were negative and significant ($P < 0.01$) for combined root-vine parameter HI and at $P < 0.05$ for R:V ratio.

Table 5.7: Estimates of the general combining ability effects of eight sweetpotato parents for nine traits evaluated in three locations in Rwanda

Parent	Root parameter			Vine parameter			Root and vine parameter		
	FRY (t.ha ⁻¹)	RDMC (%)	DRY (t.ha ⁻¹)	FVY (t.ha ⁻¹)	VDMC (%)	DVY (t.ha ⁻¹)	TBDW (t.ha ⁻¹)	RV	HI
2005-179	-0.38 ^{ns}	-2.17***	-0.42 ^{ns}	2.11 ^{ns}	0.66 ^{ns}	0.62 ^{ns}	0.21 ^{ns}	-0.18*	-0.04**
4-160	-0.18 ^{ns}	0.23 ^{ns}	-0.01 ^{ns}	-0.58 ^{ns}	-0.04 ^{ns}	-0.16 ^{ns}	-0.18 ^{ns}	-0.05 ^{ns}	0.00 ^{ns}
K5132/61	2.23**	-3.12***	0.2 ^{ns}	-2.15 ^{ns}	-0.85 ^{ns}	-0.60 ^{ns}	-0.36 ^{ns}	0.13 ^{ns}	0.03*
RW11-1860	-0.23 ^{ns}	1.11*	0.07 ^{ns}	1.31 ^{ns}	0.65 ^{ns}	0.47 ^{ns}	0.52 ^{ns}	0.05 ^{ns}	0.00 ^{ns}
RW11-2910	-1.19 ^{ns}	1.35**	-0.10 ^{ns}	0.10 ^{ns}	0.07 ^{ns}	0.10 ^{ns}	-0.02 ^{ns}	-0.06 ^{ns}	-0.01 ^{ns}
SPK004	-2.09*	1.17**	-0.50 ^{ns}	0.92 ^{ns}	-0.22 ^{ns}	-0.02 ^{ns}	-0.49 ^{ns}	-0.09 ^{ns}	-0.02 ^{ns}
Ukerewe	-0.47 ^{ns}	1.89***	0.12 ^{ns}	-3.67 ^{ns}	0.58 ^{ns}	-0.54 ^{ns}	-0.43 ^{ns}	0.02 ^{ns}	0.02 ^{ns}
Wagabolige	2.30**	-0.46 ^{ns}	0.62*	1.96 ^{ns}	-0.85 ^{ns}	0.14 ^{ns}	0.75 ^{ns}	0.19*	0.03 ^{ns}

*, **, *** : significant at the 0.05, 0.01 and 0.001 probability levels, respectively; ^{ns}: not significant; FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; RV: root-to-vine ratio; HI: harvest index.

5.3.6. Specific combining ability effects

SCA values and their level of significance are presented in Table 5.8. A cross of Ukerewe and Wagabolige resulted in significant ($P < 0.01$) negative SCA effects (-10.62) for FRY and -3.12 for DRY. In contrast, a cross involving 4-160 and 2005-179 parents had significant ($P < 0.05$) positive effects (2.91) for RDMC. The cross K5132/61 x Wagabolige exhibited significant ($P < 0.01$) positive effects (28.95) for FVY, 5.30 for DVY, and significant ($P < 0.05$) positive effects (4.85) for TBDW. The cross RW11-1860 x Wagabolige had significant ($P < 0.05$) negative effects (-5.34) for TBDW. The cross Ukerewe x Wagabolige had significant ($P < 0.05$) negative effects (-6.13) for TBDW. The cross K5132/61 x RW11-1860 had positive and significant ($P < 0.05$) SCA effect (0.55) for the parameter R:V. Significant SCA effects of -0.2 and -0.15 were recorded in the crosses K5132/61 x Wagabolige and RW11-2910 x Wagabolige, respectively, for HI. In the rest of crosses, the SCA values did not show significant effects for the recorded parameters.

Table 5.8: Estimates of specific combining ability effects for nine traits of 28 crosses of sweetpotato derived from eight parents evaluated across three locations in Rwanda

Cross	FRY (t.ha ⁻¹)	RDMC (%)	DRY (t.ha ⁻¹)	FVY (t.ha ⁻¹)	VDMC (%)	DVY (t.ha ⁻¹)	TBDW (t.ha ⁻¹)	RV	HI
2005-179 x RW11-1860	-0.23 ^{ns}	-0.73 ^{ns}	-0.18 ^{ns}	8.37 ^{ns}	-0.71 ^{ns}	1.64 ^{ns}	1.46 ^{ns}	-0.11 ^{ns}	-0.04 ^{ns}
2005-179 x Wagabolige	-2.20 ^{ns}	-2.20 ^{ns}	-0.41 ^{ns}	14.65 ^{ns}	-0.92 ^{ns}	1.88 ^{ns}	1.49 ^{ns}	-0.35 ^{ns}	-0.07 ^{ns}
4-160 x 2005-179	-2.06 ^{ns}	2.91*	-0.22 ^{ns}	-0.89 ^{ns}	0.85 ^{ns}	0.30 ^{ns}	0.09 ^{ns}	0.05 ^{ns}	-0.02 ^{ns}
4-160 x RW11-1860	-0.17 ^{ns}	0.40 ^{ns}	0.04 ^{ns}	4.16 ^{ns}	-2.10 ^{ns}	0.15 ^{ns}	0.20 ^{ns}	-0.15 ^{ns}	-0.02 ^{ns}
4-160 x RW11-2910	0.42 ^{ns}	-0.04 ^{ns}	0.07 ^{ns}	-0.25 ^{ns}	1.47 ^{ns}	0.51 ^{ns}	0.60 ^{ns}	-0.03 ^{ns}	-0.01 ^{ns}
4-160 x Wagabolige	-3.10 ^{ns}	-3.10 ^{ns}	-0.48 ^{ns}	-12.27 ^{ns}	3.44 ^{ns}	-1.10 ^{ns}	-1.58 ^{ns}	-0.31 ^{ns}	-0.02 ^{ns}
K5132/61 x 2005-179	-3.94 ^{ns}	-0.20 ^{ns}	-1.08 ^{ns}	-6.55 ^{ns}	-0.09 ^{ns}	-1.23 ^{ns}	-2.27 ^{ns}	-0.01 ^{ns}	0.01 ^{ns}
K5132/61 x 4-160	1.38 ^{ns}	-1.55 ^{ns}	0.05 ^{ns}	-4.34 ^{ns}	0.40 ^{ns}	-0.76 ^{ns}	-0.75 ^{ns}	-0.09 ^{ns}	0.02 ^{ns}
K5132/61 x RW11-1860	2.39 ^{ns}	-1.06 ^{ns}	0.38 ^{ns}	6.92 ^{ns}	-1.75 ^{ns}	0.33 ^{ns}	0.67 ^{ns}	0.55*	-0.01 ^{ns}
K5132/61 x RW11-2910	-1.53 ^{ns}	1.15 ^{ns}	-0.11 ^{ns}	1.33 ^{ns}	-1.34 ^{ns}	-0.05 ^{ns}	-0.20 ^{ns}	0.11 ^{ns}	-0.02 ^{ns}
K5132/61 x Wagabolige	-1.09 ^{ns}	-1.09 ^{ns}	-0.50 ^{ns}	28.95**	-0.20 ^{ns}	5.30**	4.85*	-0.74 ^{ns}	-0.20**
RW11-1860 x Wagabolige	-5.96 ^{ns}	-5.96 ^{ns}	-1.67 ^{ns}	-15.45 ^{ns}	0.18 ^{ns}	-3.67*	-5.34*	-0.06 ^{ns}	-0.02 ^{ns}
RW11-2910 x 2005-179	4.66*	-0.21 ^{ns}	1.18 ^{ns}	-0.14 ^{ns}	0.18 ^{ns}	0.20 ^{ns}	1.38 ^{ns}	0.15 ^{ns}	0.05 ^{ns}
RW11-2910 x RW11-1860	-1.67 ^{ns}	0.96 ^{ns}	-0.51 ^{ns}	-3.68 ^{ns}	0.45 ^{ns}	-0.88 ^{ns}	-1.37 ^{ns}	0.03 ^{ns}	0.00 ^{ns}
RW11-2910 x Wagabolige	-5.93 ^{ns}	-5.93 ^{ns}	-2.15 ^{ns}	4.71 ^{ns}	0.37 ^{ns}	1.64 ^{ns}	-0.51 ^{ns}	-0.57 ^{ns}	-0.15*
SPK004 x 2005-179	1.39 ^{ns}	-1.14 ^{ns}	0.36 ^{ns}	0.02 ^{ns}	-1.10 ^{ns}	-0.47 ^{ns}	-0.15 ^{ns}	0.08 ^{ns}	0.00 ^{ns}
SPK004 x 4-160	1.70 ^{ns}	-1.02 ^{ns}	0.32 ^{ns}	-1.00 ^{ns}	1.03 ^{ns}	0.21 ^{ns}	0.50 ^{ns}	0.00 ^{ns}	0.01 ^{ns}
SPK004 x RW11-1860	1.08 ^{ns}	0.34 ^{ns}	0.44 ^{ns}	-6.26 ^{ns}	1.41 ^{ns}	-0.62 ^{ns}	-0.21 ^{ns}	0.06 ^{ns}	0.03 ^{ns}
SPK004 x RW11-2910	-0.94 ^{ns}	0.26 ^{ns}	-0.33 ^{ns}	-9.11 ^{ns}	0.45 ^{ns}	-1.53 ^{ns}	-1.88 ^{ns}	0.08 ^{ns}	0.02 ^{ns}
SPK004 x Wagabolige	4.36 ^{ns}	4.36 ^{ns}	0.96 ^{ns}	1.88 ^{ns}	3.88 ^{ns}	2.14 ^{ns}	3.14 ^{ns}	-0.70 ^{ns}	-0.12 ^{ns}
SPK004x K5132/61	-1.10 ^{ns}	1.35 ^{ns}	-0.09 ^{ns}	5.08 ^{ns}	1.36 ^{ns}	1.24 ^{ns}	1.39 ^{ns}	-0.27 ^{ns}	-0.05 ^{ns}
Ukerewe x 2005-179	0.86 ^{ns}	1.21 ^{ns}	0.36 ^{ns}	2.70 ^{ns}	0.52 ^{ns}	0.42 ^{ns}	0.78 ^{ns}	0.03 ^{ns}	0.00 ^{ns}
Ukerewe x 4-160	-2.06 ^{ns}	-0.74 ^{ns}	-0.67 ^{ns}	-2.33 ^{ns}	2.89 ^{ns}	0.63 ^{ns}	-0.03 ^{ns}	-0.23 ^{ns}	-0.08 ^{ns}
Ukerewe x K5132/61	-1.97 ^{ns}	0.40 ^{ns}	-0.42 ^{ns}	-3.53 ^{ns}	-1.06 ^{ns}	-0.89 ^{ns}	-1.35 ^{ns}	-0.01 ^{ns}	0.01 ^{ns}
Ukerewe x RW11-1860	-1.71 ^{ns}	-2.30 ^{ns}	-0.78 ^{ns}	-5.30 ^{ns}	0.82 ^{ns}	-0.95 ^{ns}	-1.71 ^{ns}	-0.05 ^{ns}	-0.01 ^{ns}
Ukerewe x RW11-2910	-2.57 ^{ns}	-1.00 ^{ns}	-0.98 ^{ns}	-0.62 ^{ns}	0.93 ^{ns}	0.25 ^{ns}	-0.72 ^{ns}	-0.25 ^{ns}	-0.06 ^{ns}
Ukerewe x SPK004	-0.36 ^{ns}	0.88 ^{ns}	0.00 ^{ns}	6.65 ^{ns}	-2.45 ^{ns}	0.42 ^{ns}	0.39 ^{ns}	-0.10 ^{ns}	-0.03 ^{ns}
Ukerewe x Wagabolige	-10.62**	-10.62 ^{ns}	-3.12**	-16.96 ^{ns}	0.29 ^{ns}	-3.00 ^{ns}	-6.13*	-0.54 ^{ns}	-0.10 ^{ns}

*, **: significant at the 0.05 and 0.01 probability levels, respectively; ^{ns}: not significant; FRY: fresh root yield; RDMC: root dry matter content; DRY: dry root yield; FVY: fresh vine yield; VDMC: vine dry matter content; DVY: dry vine yield; TBDW: total biomass on dry weight basis; RV: root-to-vine ratio; HI: harvest index.

5.4. Discussion

5.4.1. Performance of tested parents and their progenies for root parameters across sites

The study found marked genotypic differences among tested genotypes across test sites. Variation between sites could have been due to the differences in microclimate and agroecological conditions (Table 5.1). Highly significant ($P < 0.001$) differences were recorded between sites for all root related parameters, namely FRY, RDMC and DRY (Table 5.3). The test sites were chosen to represent different agroecological zones that characterise the country. Highly significant differences ($P < 0.001$) were also found between families for root parameters. The family differences may be attributed to the unique genetic make-up of the tested genotypes in early selection stage, particularly because of strong and distinct genetic combinations resulted from the heterozygous and hexaploidy nature of the crop. Previous studies reported significant differences among sweetpotato families particularly during early breeding phases (Rukundo, 2015; Naidoo et al., 2016). Family and sites interacted significantly ($P < 0.001$) for the tested root parameters similar to previous studies (Grüneberg et al., 2005; Yada et al., 2011).

FRYs varied between 7.41 and 25.10 t.ha⁻¹ (Table 5.4), agreeing with values recently reported in Uganda by Tumwegamire et al. (2016). The highest FRY of 25.10 t.ha⁻¹ is quite similar to the yield performance of the varieties previously released in Rwanda (Shumbusha et al., 2014), but it is relatively low yield potential compared to the varieties NASPOT 12 O and NASPOT 13 O, recently released in Uganda (Mwanga et al., 2016). This would indicate that there is still the opportunity to reduce the gap between the actual and potential yield of FRY. The newly introduced genotype Wagabolige ranked first in having high FRY (25.10 t.ha⁻¹), followed by the locally adapted genotype Ukerewe (22.92 t.ha⁻¹), known for its high DMC. The parent Ukerewe exhibited a highest RDMC (34.36%), maintaining its rank of being among the top three high RDMC yielders. Likewise, the same parents Ukerewe and Wagabolige were the two best yielders of DRY, with 7.34 and 7.06 t.ha⁻¹, respectively. Overall, the 8 parents and 28 crosses performed differently in different test sites (Table 5.4). For root parameters, the highest mean FRY and DRY were observed at the Ngoma site, with 16.87 and 5.02 t. ha⁻¹ in that order.

5.4.2. Performance of the 36 tested families for vine parameters across three selected sites in Rwanda

In the present study, there were highly significant differences ($P < 0.001$) between sites and between families for FVY, VDMC and DVY. Families may have performed differently across

sites for FVY because of the inequitable distribution of rains that characterised the cropping period among the different agroecological zones of Rwanda. The interaction of family x sites were also highly significant for FVY and related parameters, a scenario previously noticed by (Tumwegamire et al., 2016). FVYs ranged between 18.58 and 51.63 t.ha⁻¹ and the best performer was the cross K5132/61 x Wagabolige (51.63 t.ha⁻¹), followed by 2005-179 x RW11-1860 (48.59 t.ha⁻¹) (Table 5.4). The mean FVY of 51.63 t.ha⁻¹ found in the current study is much higher to the highest mean (31.03 t.ha⁻¹) of the best performer among the genotypes selected during a later breeding stage in Mozambique (Andrade et al., 2017). The highest FVY mean (51.63 t.ha⁻¹) in the current study also was slightly higher compared to the highest mean recorded by (Mussoline and Wilkie, 2017). Expectedly, parents Wagabolige and RW11-1860 involved in each of these two FVY performing crosses were previously reported to have the ability to produce a large amount of vines (Lukuyu et al., 2011; Shumbusha et al., 2014). In terms of site performance, Karama site exhibited a highest FVY mean (41.80 t.ha⁻¹) compared to Rubona (30.82 t.ha⁻¹), unlike in the previous report by Shumbusha et al. (2017).

5.4.3. Response of the 36 tested families for combined root and vine parameters across threes selected sites in Rwanda

There were differential performances among parents and crosses for root and vine combined parameters (Table 5.4). The following genotypes: RW11-1860, K5132/61 x Wagabolige, Ukerewe and 2005-179 x RW11-1860 were the best yielders in TBDW, with 15.81, 15.67, 15.13 and 13.80 t.ha⁻¹, respectively. The clear contribution of parents RW11-1860 and Wagabolige to the TBDW was expected, mostly due to their performance in producing high root yields and a large amount of vines as reported in previous studies (Lukuyu et al., 2011; Shumbusha et al., 2014). The R:V ratios found in this study were within the range reported by earlier researchers (Niyireba et al., 2013). According to León-Velarde (2000), genotypes with the R:V ratio of 1.5-2.0 are classified into dual-purpose types. The family K5132/61 x RW11-1860 had a R:V ratio of 1.60, falling into the range for dual-purpose genotypes. The highest HI value of 0.58 was recorded on the parent Wagabolige, followed by two parents Ukerewe and K5132/61 with the same value of 0.55. Lestari and Hapsari (2015) recorded HI values of 0.74, relatively high values than reported in the current study. Overall, a highest mean TBDW was recorded at the Ngoma site (13.01 t.ha⁻¹), whereas Rubona had the highest mean of R:V (1.01) (Table 5.5). The mean HI value of the families was generally low in all the sites, suggesting a need to select genotypes with high HI, starting from earlier breeding stages.

5.4.4. General and specific combining ability effects

The highly significant GCA and SCA effects found in this study for FRY, RDMC and DRY could be an indication of both additive and non-additive gene action in governing the expression of these root parameters (Table 5.6). These findings concur with those of Todd et al. (2015). The highly significant GCA and SCA for root-vine combined parameters R:V and HI indicate the presence of both gene actions controlling the traits. There were non-significant GCA and SCA effects for vine related parameters such as FVY and DVY, suggesting that progeny performance cannot be predicted from parental performance. Except SCA x S which significantly affected RDMC, both GCA and SCA did not interacted significantly with sites for the rest of parameters. These results suggest the need to conduct multi-location trials, in order to ensure the stability of RDMC and then select the stable ones for a specific site. These findings are in agreement with those of Shumbusha et al. (2014) who reported a significant interaction of sites and seasons for RDMC.

The relative importance of GCA and SCA was closer to one for the root parameters such as DRY (0.75), RDMC (0.81) and FRY (0.88). This indicates that GCA was more important than SCA in family performance for the tested root parameters, suggesting that additive gene action was much more influential than non-additive gene action. These results confirm the earlier reports of Musembi et al. (2015) and Rukundo et al. (2017) who pointed out the large magnitude of additive variance for FRY and RDMC. In contract, GCA/SCA ratio was much lower than 1 for the vine and root-vine combined parameters, varying between 0.09 and 0.28, suggesting that the non-additive component of genetic variance, either dominance or epistasis or both, made a larger contribution to the total genetic variance for these traits. The results on FVY are in agreement with those of Rukundo (2015) who found a GCA:SCA below 0.5. This implies that progeny performance cannot be predicted from the parental performance.

Based on GCA values (Table 5.7), the newly introduced parent Wagabolige exhibited the highest positive and significant GCA effects (GCA = 2.30, $P < 0.01$) for FRY, followed by the parent K5132/61 (GCA = 2.23, $P < 0.01$). This implies that these parents were good combiners for FRY. Expectedly, the high DMC and farmer-preferred parent Ukerewe had the highest positive and significant GCA effects (GCA = 1.89, $P < 0.001$) for RDMC, confirming that this genotype should be included among parents in any breeding effort targeting RDMC improvement. Though, the parent K5132/61 was a good combiner for FRY in this study, it had the highest negative and significant GCA effects (GCA = -3.12, $P < 0.001$) for RDMC, suggesting the need to use a large number of parents in order to increase the chance of identifying combiners when dealing with several parameters. For root: vine parameter, the

parent Wagabolige produced the highest positive and significant GCA effects (GCA = 0.19, $P < 0.05$), supporting the earlier finding of Lukuyu et al. (2011).

Based on SCA effects and their significance (Table 5.8), the cross Ukerewe x Wagabolige produced high negative and significant ($P < 0.01$) SCA effects of -10.62 and -3.12 for FRY and DRY, respectively. However, the cross K5132/61 x Wagabolige had prominent positive and significant SCA effects (SCA = 28.95, $P < 0.01$) for the parameter FVY, indicating the presence of a large amount of non-additive gene action in controlling the trait. Interestingly, the same cross K5132/61 x Wagabolige appear with great frequency with significant and positive effects for several parameters such as DVY (SCA = 5.30, $P < 0.01$) and TBDW (SCA = 4.85, $P = 0.05$). Unexpectedly, the parents 4-160 and 2005-179 with the negative GCA effects in this study, produced a desired positive and significant SCA effects (SCA = 2.91, $P = 2.91$) for RDMC. Likewise, a cross of parents K5132/61 and Wagabolige with significant and positive GCA resulted in a cross with significant and negative SCA effects (SCA = -0.20, $P = 0.01$) for HI. This implies that the generated cross performed below the expectation based on GCA effects. The reason for this is not clear, though, since sweetpotato is hexaploid and highly heterozygous, desirable gene combinations may be broken down during meiosis, resulting in a progeny with no desirable trait. This is in agreement with the observations of Shumbusha et al. (2014) and Todd et al. (2015) who indicated that parents with high GCA effects did not necessarily produced progenies with high SCA.

5.4.5. Heritability estimates

Broad-sense heritability was reported more useful in sweetpotato and generally for vegetative propagated crops since both additive and non-additive gene action are fixed and transferred from parent to progenies (Acquaah, 2012). Also, estimates of h^2 remain necessary as they indicate at what extent by combining two parents with high GCA is likely to lead to a high response to selection and genetic gains (Freeman, 2009). However, Jones et al. (1986) clarified that since h^2 is a ratio of only additive over the total phenotypic variance, there is need for a greater precision in estimating it in order to reduce the phenotypic variance. In the present study, both broad-sense heritability (H^2) and narrow-sense coefficient of genetic determination (NSCGD), the fixed effect equivalent of h^2 for family means across sites were estimated. The H^2 estimates were above 0.5 for all tested parameters, where FRY, HI and RDMC had high estimates of 0.80, 0.81 and 0.92, respectively. The vine parameters VDMC, DVY and FVY had H^2 estimates of 0.75, 0.78 and 0.79, respectively. The lowest H^2 estimate of 0.59 was obtained for the parameter R:V. There are H^2 estimates from this study that concur with the earlier observations, while others

disagree. Martin and Jones (1986) reported H^2 estimates of 0.71 for fresh root weight using variance components. The H^2 estimates of 0.70 were reported for RDMC (Shumbusha et al., 2014), 0.50 for FVY (Rukundo et al., 2017) and 0.52 for HI (Gurmu, 2015).

Except for the parameter RDMC which had a high NSCGD of 0.80, the NSCGD estimates varied between 0.09 and 0.49 for the rest of parameters. Expectedly, all the NSCGD found in this study were lower than their corresponding H^2 value. The root parameters showed high NSCGD compared to vine and combined root-vine parameters. Among the tested parameters, RDMC had the highest estimates ≥ 0.8 for both H^2 and NSCGD, suggesting that the portion of additive variance to the total variance was much higher. Earlier researchers observed various NSCGD estimates in sweetpotato depending on the method used. The NSCGD estimates were 0.70 for FRY (Mwije et al., 2014), 0.82 for RDMC (Grüneberg et al., 2009). The low estimates of NSCGD found in this study for root-vine combined parameters may be attributed to the large interactions of sites and families.

5.5. Conclusions

The present study determined gene action and heritability of vine and root yield and related yield components in early generation sweetpotato clones. The GCA and SCA mean squares were significant for FRY, RDMC, DRY, R:V, HI and VDMC. All the combined root-vine parameters TBDW, R:V and HI had GCA variance components below 1.00, resulting in a low GCA to SCA ratio. The GCA/ SCA ratios were much greater than 0.5 for all the tested root parameters DRY, RDMC and FRY, with 0.75, 0.81 and 0.88, respectively, suggesting that additive gene action was more important than non-additive gene action in the expression of these parameters. In contrast, GCA/SCA was much lower than one for the vine and root-vine combined parameters, ranging between 0.09 and 0.28, suggesting that the non-additive component of genetic variance, either dominance or epistasis or both, was more influential in controlling the traits. This implies that parental performance cannot necessarily be the basis of progeny performance prediction.

The H^2 estimates were above 0.5 for all tested parameters, with FRY, HI and RDMC having high estimates of 0.80, 0.81 and 0.92, in that order. Except for the parameter RDMC which had a high NSCGD of 0.80, the NSCGD estimates varied between 0.09 and 0.49 for the rest of parameters. Expectedly, all the NSCGD estimates found in this study were lower than their corresponding H^2 values. RDMC had the highest estimates ≥ 0.8 for both H^2 and NSCGD, suggesting that the portion of additive variance to the total variance was much higher for this trait. This implies that good progeny can be predicted from the phenotype of the parents.

Based on GCA effects, the parent K5132/61 was the best combiner for FRY and HI. The parents RW11-1860, RW11-2910, SPK004 and Ukerewe were the best general combiner of RDMC, while the newly introduced parent Wagabolige was the best combiner for FRY, DRY and R:V. Based on the performance of crosses for root, vine and root-vine combined parameters, and their level of SCA significance, the promising families were K5132/61 x Wagabolige, 2005-179 x RW11-1860, 4-160 x 2005-179, K5132/61 x RW11-1860, RW11-2910 x 2005-179, Ukerewe x SPK004, Ukerewe x 4-160. Promising dual-purpose progenies derived from the selected families are recommended for advanced clonal evaluation across multiple sites for release in Rwanda or similar agro-ecologies in SSA.

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6. Chapter Six: Thesis Overview

6.1. Introduction

Sweetpotato is the fourth most important crop in Rwanda with a total annual production of 1,081,224 tonnes from an estimated area of 112,436 ha. The storage root is a major source of human food, while the aboveground biomass is used as a fodder for livestock. Due to its dual-purpose nature, sweetpotato is widely cultivated in the crop-livestock mixed farming systems in Rwanda, where agricultural and grazing lands are severely limited due to high population growth and urbanization. Farmers' derive cash income from the sale of various produce derived from food crops and livestock. To satisfy the needs for human food and livestock feed, more food and feed production is required. To contribute to both outputs, sweetpotato genotypes with improved root and vine yields can be developed through exploiting the genetic potential of dual-purpose types. To date, little effort has been made to breed for dual-purpose varieties incorporating farmer-preferred traits. In the past, emphasis in sweet potato breeding was given to developing sweetpotato varieties with high yields of storage roots or improved pro-vitamin A content for human food, without considering its potential dual-purpose traits. Breeding dual-purpose sweetpotato varieties is dependent on access to genetic diversity in the crop, and effective screening techniques that target the between root and shoot production. Therefore, breeding dual-purpose sweetpotato varieties is an overriding consideration in order to secure fodder for livestock, while maintaining a substantial source of food in Rwanda. This section presents the thesis overview and summarizes the research objectives and keys findings of the study.

The specific objectives of this study were as follows:

1. To assess the role of sweetpotato in the crop-livestock farming system practised in Rwanda, to identify farmer-preferred traits and to establish farmer-led priorities in breeding dual-purpose sweetpotato varieties (DPSVs).
2. To assess the level of phenotypic diversity present among sweetpotato varieties grown in Rwanda, and to select suitable parents for breeding DPSVs.
3. To characterize diverse sweetpotato germplasm using simple sequence (SSR) markers to identify potential parents for breeding DPSVs.
4. To determine gene action and heritability of storage root and aboveground biomass yields, and yield components, in sweetpotato varieties, and to undertake early clonal selections for future release of DPSVs.

6.2. Summary of the major findings

The first study involved a participatory rural appraisal (PRA) that was conducted in three selected districts namely Bugesera, Huye and Nyagatare. The study showed that:

- In the Nyagatare District most of farmers (76.7%) reported deriving a cash income from both crop and livestock production.
- In the Huye and Bugesera Districts about 70% and 93.3% of interviewed farmers reported owning agricultural lands of less than 0.5 ha, respectively.
- Sweetpotato was ranked the most valuable crop during focus group discussions.
- Over 70% of respondents believed that adoption of improved sweetpotato varieties could provide a greater increase in root and shoot biomass yields than using improved crop management practices.
- About 87.7, 66.6, 56.6 and 51.1% of the respondents indicated that root-related traits of the crop such as high dry matter content, red skin colour, marketable root size and yellow flesh colour were additional preferred traits, respectively.
- Farmers-preferred DPSVs with improved root and green fodder yields could be developed to enhance the sustainable production and adoption of DPSVs in mixed farming systems in Rwanda.

The second study assessed the phenotypic diversity present among sweetpotato genotypes grown in Rwanda. Fifty one diverse sweetpotato genotypes were evaluated in field trials conducted at the Rubona and Karama experimental stations of the Rwanda Agriculture Board (RAB), using a 6 x 9 unbalanced alpha lattice design with three replications. The key findings of this study were:

- Two top genotypes were selected for their high yields of storage roots, including RW11-4923 and RW11-2419, whereas genotypes RW11-4923 and Wagambolige were the best performers for vine yields.
- The genotype Ukerewe performed well for its dry root yield, while RW11-4923 had the highest mean dry vine yield.
- Genotypes RW11-2910 and 8-1038 had good root-to-vine ratios for dual-purpose attributes, whereas Mafuta, RW11-1860 had high harvest index values.
- Three genotypes were selected for their exceptional flowering rate of 23.0, 20.5 and 19.83%, respectively: 2005-179, RW11-2910 and SPK004.
- Two main phenotypic groups with ten sub-groups were detected through cluster analysis.

- The first component (PC1) was mainly correlated with FRY and DRY with a correlation of 0.96, while the second component (PC2) was correlated with FVY and DVY with correlations of 0.98 and 0.93, respectively. FRY and DRY contributed much of the variability (35.81%) in PC1, whereas FVY and DVY contributed 22.41% of the variability in PC2, suggesting that these two pairs of traits accounted for most of the variability in PC1 and PC2.
- Genomic analysis could be performed with the selected set of genotypes, using diagnostic molecular markers, to provide complementary data to identify superior parents for breeding DPSVs.

The third study characterized the selected sweetpotato genotypes using simple sequence (SSR) markers, to identify potential parents for breeding DPSVs. Twenty-four sweetpotato genotypes were selected for their promising storage root yields and related traits, and their biomass production. These were genotyped using nine highly polymorphic SSR markers. The study revealed that:

- Molecular variance analysis showed highly significant differences ($P < 0.001$) among and within individuals, with marked genetic variability among individuals contributing to 69% of the total genotypic variation.
- Cluster analysis allocated the test genotypes into three distinct genetic groups: I, II and III, with 6, 5 and 13 genotypes, respectively.
- Eight genetically diverse clones were selected, namely SPK004 and K5132/61 (from Group I), 4-160, Ukerewe, RW11-2910 (Group II), RW11-1860, Wagabolige, 2005-179 (Group III), with key agronomic traits for breeding DPSVs.

The fourth study determined the gene action and heritability of vine and root yield, and related yield components in sweetpotato. Eight parents selected for their contrasting attributes of root and vine production, dry matter content and farmer-preferred traits were crossed in a half-diallel, method 2. The 28 crosses and eight parents were field evaluated at Rubona, Karama and Ngoma research stations of the Rwanda Agriculture Board (RAB). The results of the study established that:

- The general combining ability (GCA) and specific combining ability (SCA) effects were significant for fresh root yield (FRY), root dry matter content (RDMC), dry root yield (DRY), root-to-vine ratio (R:V), harvest index (HI) and vine dry matter content (VDMC), suggesting that additive or non-additive gene action were present in controlling the traits.

- The relative importance of GCA and SCA (GCA/SCA) was greater than 0.5 for the root parameters DRY, RDMC and FRY, with 0.75, 0.81 and 0.88, respectively, suggesting that additive gene action was more important than non-additive gene action in the expression of these parameters.
- Conversely, GCA/SCA ratio was relatively low and ranged between 0.09 and 0.28 for vine and root-vine combined parameters, indicating that the non-additive component of genetic variance was more influential in controlling the traits.
- The broad-sense heritability (H^2) values were above 0.5 for all tested parameters, with FRY, HI and RDMC having higher estimates of 0.80, 0.81 and 0.92, in that order.
- RDMC had a high narrow-sense coefficient of genetic determination (NSCGD) of 0.80.
- The parent K5132/61 was the best combiner for FRY and HI; the parents RW11-1860, RW11-2910, SPK004 and Ukerewe were the best general combiners for RDMC; and Wagabolige was the best combiner for FRY, DRY and R:V.
- Based on desirable SCA effects for FVY, DVY, TBDW, RDMC, R:V and FRY, the most promising families selected in the current study were K5132/61 x Wagabolige, 4-160 x 2005-179, K5132/61 x RW11-1860 and RW11-2910 x 2005-179

6.3. Implications of the research findings

- The participatory rural appraisal (PRA) study pointed out the importance of sweetpotato as a food security crop with dual purpose potential in Rwanda, given the limited agricultural land available for crop and livestock production in the country, the population growth and urbanisation. Farmers indicated that root related traits of the crop such as high dry matter content, red skin colour, marketable root size and yellow flesh colour, were additional preferred traits. Therefore, farmers-preferred DPSVs with improved root and green fodder yields should be developed for sustainable production and adoption of sweetpotato in mixed farming systems in Rwanda.
- The present study indicated that the traits FRY and DRY contributed much (35.81%) of the observed variability associated with the first principle component (PC1), while FVY and DVY accounted for most (22.41%) of the variability and correlated in the second principle component (PC2). This implies that, for breeding purposes, selection of parents with traits associated with high storage root and vine yields in both fresh- and dry-weight bases would be important. The genotypes characterized and selected through this study are useful genetic resources from which to design and develop DPSVs suitable for Rwanda.

- The GCA/SCA ratios were closer to one for all the tested storage root parameters such as DRY, RDMC and FRY, with 0.75, 0.81 and 0.88, respectively, suggesting that additive gene action was more important than non-additive gene action in the expression of these parameters. In contrast, the GCA/SCA ratio was much lower than one for the aboveground biomass yield and root-vine combined parameters, ranging between 0.09 and 0.28, suggesting that the non-additive component of genetic variance, either dominance or epistasis or both, was more influential in controlling the traits. This implies that parental performance cannot necessarily be the basis of progeny performance prediction for these traits.
- RDMC had the highest broad-sense heritability (H^2) and narrow-sense coefficient of genetic determination (NSCGD) estimates, suggesting that the portion of additive variance to the total variance was much higher. This implies that good progeny can be predicted from the phenotype of the parents.
- Promising dual-purpose progenies derived from the selected families are recommended for advanced clonal evaluation across multiple sites for releasing DPSVs in Rwanda or similar agro-ecologies in SSA.