Breeding of sweetpotato (*Ipomoea batatas* (L.) Lam.) for drought tolerance and high dry matter content in Rwanda

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Thesis abstract

Sweetpotato is the third most important root crop next to cassava and potato in Rwanda. Drought stress remains the leading abiotic constraint to sweetpotato production in the Southern and Eastern Provinces of the country. Therefore, development and release of improved sweetpotato varieties incorporating end users' preferences such as high storage root yields and dry matter content under limited water conditions remains important for sustainable production. The specific objectives of this research were: (i) to assess farmers' perception, production constraints, preferences, and breeding priorities of sweetpotato in selected agro-ecologies of Rwanda, (ii) to characterise and identify breeding parents among 54 sweetpotato genotypes grown in Rwanda, East and Central Africa, (iii) to select drought tolerant sweetpotato genotypes under managed drought conditions using greenhouse and in-vitro screening techniques with early and late developmental traits, (iv) to determine general combining ability (GCA), specific combining ability (SCA) and maternal effects and heritability of drought tolerance and yield components of among newly developed sweetpotato clones and (v) to determine genotype x environment interaction and yield stability of sweetpotato breeding clones recently bred in Rwanda and to identify promising genotypes.

A participatory rural appraisal (PRA) study was carried out involving 495 farmers in eight representative districts to identify farmers' perception, production constraints, preferences, and breeding priorities of sweetpotato in the Eastern, Southern and Northern Provinces of Rwanda. Sweetpotato ranked among the five important food crops for food security and income generation. Drought stress, unavailability of improved cultivars and planting material, and pest and disease damage were perceived to be the five main constraints limiting sweetpotato production. The most important sweetpotato cultivar traits were high yield, early maturity, drought tolerance, disease and pest resistance, and good culinary taste. The characteristics of good storage roots identified by farmers included, high dry matter content, good culinary taste, good shape, root size, and sweetness. Each agro-ecological zone has its own specific sweetpotato production constraints and farmers' preferences, necessitating targeted breeding of different sweetpotato cultivars for each agro-ecological zone for enhanced productivity and successful adoption of cultivars.

Fifty four sweetpotato genotypes grown in Rwanda, East and Central Africa were field evaluated to identify breeding parents. Genotypes K513261, Kwezikumwe, 8-1038 and 2005-110 had the highest flowering rate of 44.97, 20.63, 19.05, and 14.82%, respectively. Suitable genotypes such as K513261, Purple 297, Kwezikumwe and New Kawogo were

identified with high storage root yields at 31.9, 28.6, 28.2 and 27.1 t ha^{-1}, respectively. Genotypes Ukerewe, 2005-103, Meresiyana and Mvugamo showed the highest mean dry matter content at 36.5, 35.5, 35.3 and 34.0%, respectively.

Greenhouse and in-vitro screening methods were compared for effective selection of drought tolerance using 54 diverse sweetpotato genotypes. Positive correlations were observed between vine yield and fresh weight gain; and between total biomass and fresh weight gain, during greenhouse and in-vitro studies, respectively. The genotypes 2005-146, 4-160, 8-1038, Karibunduki, Kwezikumwe, Purple 4419, NASPOT 9 O, Nsasagatebo, Karebe, IMBY 3102, Mwanakumi, 97-062 and Matembere were selected with comparatively high drought tolerance using the two screening procedures. The genotypes 2005-020, K513261, Kwezikumwe and Otada 24 were selected for high yield of storage roots, while 2005-034, 2005-110, SPK004 and Ukerewe were selected for high dry matter content, and 4-160, 8-1038, Nsasagatebo and Purple 4419 selected for high drought tolerance. The selected genotypes have a high flowering rate and are potential parents to breed for high yield and dry matter content of storage roots and drought tolerance.

Twelve genotypes selected for their high yield, dry matter content or drought tolerance were crossed using a full diallel mating design. Families were field evaluated at Masoro, Karama and Rubona Research Stations of Rwanda Agriculture Board to determine general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components. The GCA effects of parents and SCA effects of crosses were significant ($P<0.01$) for canopy temperature (CT), canopy wilting (CW), storage root, vine and biomass yields, and dry matter content of storage roots. The best general combiners for drought tolerance were the parents 8-1038, Otada 24 and 4-160 with the lowest CT and CW and relatively high yields. Best combiners for high storage roots yield were the parents Nsasagatebo, K513261 and Ukerewe, while Nsasagatebo, 2005-034 and Ukerewe were the best combiners for high dry matter content. Maternal effects were significant ($P<0.05$) among families for CT, CW, flesh color and dry matter content, vine yield and total biomass. Based on reduced CT and CW, the best families with significant SCA effects were 4-160 x Nsasagatebo, 4-160 x Ukerewe, Otada 24 x 4-160, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 , 513261 x 4-160, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020 and Nsasagatebo x Ukerewe, which were selected for breeding for drought tolerance. Across sites, the best five selected families with significant SCA effects for storage root yields were Nsasagatebo x Otada 24, Otada 24 x Ukerewe, 4-160 x Nsasagatebo, K513261 x 2005-034 and Ukerewe x K513261 with 11.0, 9.7, 9.3, 9.2, 8.6 t/ha, respectively. The best families with high dry matter content of 36.1, 35.1, 34.3,

34.0, and 33.9% were Ukerewe x 2005-034, 4-160 x Nsasagatebo, 2005-034 x Ukerewe, 2005-034 x K513261, 2005-020 x Ukerewe, in that order. The selected families are valuable genetic resources for sweetpotato breeding for drought tolerance, yield and yield components.

Genotype by environment interaction and yield stability of 45 selected sweetpotato breeding clones were evaluated across six environments in Rwanda. Candidate clones designated as clone 21 (4-160 x 2005-020), 137 (K513261 x 2005-034) and 22 (4-160 x 2005-020) had the highest storage root yields of 38.2, 23.4 and 20.8 t ha^{-1}, respectively. The highest dry matter content of storage roots of 40.6, 35.9 and 32.9% were recorded in clones 21, 137 and 259 (2005-034 x 8-1038), respectively. AMMI stability values (ASV) revealed the following most stable genotypes: Nsansagatebo, 210 (8-1038 x 4-160), 2005-110 and 456 (SPK004 x K513261), for storage root yields and clones 46 (Kwezikumwe x 2005-020), 509 (Ukerewe x Kwezikumwe), and 358 (Ukerewe x 8-1038) for dry matter content of storage roots. The study identified high yielding and stable candidate sweetpotato clones such as 21, 137 and 22 (4-160 x 2005-020) for their high yields and dry matter content of storage roots. These clones are recommended for direct production or sweetpotato breeding programmes in Rwanda and similar environments.

In general, the study generated valuable sweetpotato families with high combining ability for high drought tolerance, yields and dry matter content. The selected candidate sweetpotato clones are novel genetic resources that could be released as new cultivars after stability tests in Rwanda or similar environments.

Declaration

I, **Placide Rukundo**, 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:

    a) Their words have been re-written but the general information attributed to them has been referenced.

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5. This thesis does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the reference sections.

Signed:

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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May Almighty God bless you all.

Dedication

To the Almighty God,

To my wife (Agrippine) and children (Bruno and Armand),

To my late parents (François and Pascasie),

To my brothers and sisters,

To my uncle (Félicien) and to my aunt (Modeste), and

To my beloved and closest friends,

I dedicate this thesis.

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Chapter two

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Thesis introduction

Background

Sweetpotato (*Ipomoea batatas* [L.] Lam.) is an important crop grown in more than 119 countries on an estimated area of 8.3 million ha for food, feed and industrial raw material (Scott and Ewell 1993; FAOSTAT 2013). The annual global production of sweetpotato is estimated at 110.7 million tons of which 15% is from East and Central Africa (FAOSTAT 2013). In Rwanda, sweetpotato is the third most important root crop next to cassava and potato (FAOSTAT 2013). According to Ndirigwe (2006); Njeru et al. (2008) and NISR (2015), 98% of subsistence farmers in all Rwandan agro-ecological zones grow sweetpotato. This crop covers about 5.2% of the cultivated land and grown during both the main and off seasons. In Rwanda an area of 112436 ha was planted with sweetpotato with annual production of 1081224 tons (FAOSTA 2013). Sweetpotato productivity is very low in the country (9.62 tons ha^{-1}) than potentially achievable. Fresh root yields of 20 tons ha^{-1} are reported in China (Low et al. 2009).

Sweetpotato is an inexpensive source of β-carotene, anthocyanin, carbohydrate, vitamins and minerals. The orange-fleshed sweetpotato varieties are important sources of β-carotene which is the major precursor of vitamin A (Chassy et al. 2008), while the purple fleshed sweetpotato varieties are rich in anthocyanins and other polyphenolic components (Teow et al. 2007; Steed and Truong 2008). The level of β-carotene and anthocyanin in sweetpotato is as high as in carrot, pumpkin, *Vaccinium* species such as blueberry, cranberry, bilberry or red cabbage (Woolfe 1992; Steed and Truong 2008). The storage roots of sweetpotato are a major source of energy due to its high carbohydrate content which ranges between 80 to 90% of the dry weight. The carbohydrates consist mainly of starch, sugars and low quantity of pectin, hemicelluloses, and cellulose (Lebot 2009). Furthermore, sweetpotato is a source of vitamins C and B6, mineral salts and fibers (Woolfe 1992; Chassy et al. 2008).

Sweetpotato is grown mainly for food (Scott and Ewell 1993). Its consumption per capita per year is above 80 kg in Rwanda, Burundi and Uganda (FAOSTAT 2013). It is consumed in different forms varying within a country by regions and incomes of the population group. Storage roots, young leaves and tips of stems of sweetpotato serve for food. In rural areas sweetpotato storage roots are consumed boiled or baked, while people with more economic means tend to use it as fried chips or a snack (Woolfe 1992).

The storage roots, by-products of roots and vines of sweetpotato are commonly used as feed for cattle, pigs and other livestock (Woolfe 1992). In 2007, about half of all sweetpotato production in the world was used for animal feed (Lebot 2009). The crop is used as an important ingredient in the feed processing industries (Gupta et al. 2009). Studies have shown that sweetpotato could form a valuable component of forage crops. It contains nutrients that can support acceptable growth of livestock (Kariuki et al. 1998; Aregheore 2004; Gupta et al. 2009). Therefore, a mixture of sweetpotato forage with poor quality fodder sources can sustain the growth of livestock which may consequently increase availability of animal products for humans (Aregheore 2004). Despite the multiple uses of sweetpotato, its production and productivity are limited by various factors such as biotic, abiotic and socio-economic constraints.

Constraints to sweetpotato production

Drought is the leading abiotic stress limiting crop production globally. Recurrent drought is associated with global climate change (Blum 2002). Drought stress is especially important in countries practicing rain-fed agriculture such as in Rwanda. Limited water availability affects negatively crop yields through reduced vegetative growth, premature senescence of leaves, damages of plant tissues, poor flowering or sterility. These will severely reduce photosynthesis and crop yields (Taiz and Zeiger 2006; Blum 2011). In sweetpotato, water deficit causes a reduction of the development of vines limiting storage root formation and reduced root dry matter content (Woolfe 1992). Severe drought stress may lead to a complete crop loss. Under drought stress, the severity of biotic stresses such viral infection and pest attacks increase. Viral diseases are the most important biotic constraints to sweetpotato production (Fuglie 2007). According to Low et al. (2009), more than 20 different virus species are reported affecting sweetpotato production globally. The sweetpotato viral diseases (SPVD) are the result of co-infections amongst different viruses (Karyeija et al. 2000; Aritua et al. 2007). The SPVD can cause yield losses reaching up to 80% on susceptible varieties (Wambugu 2003). A number of fungal and bacterial diseases of sweetpotato have been reported leading to low yields in various regions (Low et al. 2009). Sweetpotato diseases affect stems, leaves and roots in various forms (Low et al. 2009). Fungal and bacterial pathogens cause low yield losses compared to viral diseases. Moreover, their distribution depends on environmental factors (Lebot 2009).

Key pests in sweetpotato include: wireworm, white grubs, the sweetpotato weevil, the sweetpotato flea beetle, the cucumber beetle, the white fringed beetle, the armyworm complex and the sugarcane beetle (Woolfe 1992;). Insect pests are often responsible for high yield losses and low quality of storage roots of sweetpotato. The magnitudes of pest infestation differ between regions within a country. However, the sweetpotato weevils are the most prevalent pests in East and Central Africa (Muyinza et al. 2007). Insect pests can cause yield losses of 60 to 97% associated with altered and poor quality of roots (Low et al. 2009). Two nematode species: the root knot nematode (*Meloidogyne* spp.) and reniform nematode (*Rotylenchulus reniformis*), have been reported to cause serious yield losses of sweetpotato in some areas (Muyinza et al. 2007; Lebot 2009). In the past years various researches have been conducted and successes are reported in controlling sweetpotato diseases and pests using various approaches (Wambugu 2003; Gibson et al. 2004; Aritua et al. 2007; Njeru et al. 2008; Alam et al. 2010). However, in Rwanda there are limited studies available on abiotic stress management such as breeding for drought tolerance.

Problem statement

Considerable proportions of rural communities in Rwanda have experienced periodic hunger during October to January every year, mainly due to severe drought stress and crop failures. In the country, there is a lack of drought tolerant varieties of major food crops including sweetpotato. According to MINIRENA (2014), rainfall in Rwanda has erratic distribution throughout the main cropping season. Thus, there is severe drought stress between June and September in the Southern and Eastern Provinces, which are the main sweetpotato production areas of the country. Consequently, development of drought tolerant sweetpotato varieties is essential for sustainable production and to ensure food security in Rwanda. This could be achieved through well-designed crosses and continuous selection of promising and complementary clones with drought tolerance.

The value of a new sweetpotato variety depends on whether it meets farmers' and end users' preferences and demands. Storage roots with high starch and low hexoses contents are attractive characteristics for processing purposes (Slafer and Savin 1994). A high starch and low reduced sugar content of sweetpotato storage roots reduce the cost of processing because of limited oxidation reactions (McKibbin et al. 2006). High dry matter content is the main preferred characteristic of sweetpotato for consumers and processing industries. Recent research initiatives are underway to promote new sweetpotato varieties in sub-Sahara Africa to tackle hunger and shortage of vitamin A through releasing orange-fleshed

sweetpotato varieties. However, these varieties are reportedly low in dry matter content compared to farmers' varieties (Cervantes-Flores et al. 2011; Mwanga et al. 2010). Therefore, breeding for drought tolerance and high dry matter content is important for sustainable sweetpotato production in Rwanda.

Objectives

The overall goal of this study was to contribute to improvement of food security in Rwanda through breeding of sweetpotato for drought tolerance and high dry matter content. To achieve this goal, the following studies were carried out encompassing five objectives.

The specific objectives of the study were:

1. To assess farmers' perception, production constraints, preferences, and breeding priorities of sweetpotato in selected agro-ecologies of Rwanda.
2. To characterise and identify breeding parents among 54 sweetpotato genotypes grown in Rwanda, East and Central Africa.
3. To select drought tolerant sweetpotato genotypes under managed drought conditions using greenhouse and in-vitro screening techniques with early and late developmental traits.
4. To determine general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components of among newly developed sweetpotato clones.
5. To determine genotype x environment interaction and yield stability of sweetpotato breeding clones recently bred in Rwanda and to identify promising genotypes

This study tested the following hypotheses:

1. Farmers' have different perceptions, production constraints and preferences of sweetpotato varieties in Rwanda.
2. There are variation in genetics, drought tolerance and dry matter content in Rwandan sweetpotato germplasm.
3. There are not maternal effects and specific combining ability on the inheritance of drought tolerance and dry matter content of sweetpotato.
4. Drought tolerance and dry matter content of sweetpotato are affected by additive gene action.

5. There is G x E interactions for dry matter content and drought tolerance of sweetpotato.

Thesis outline

This thesis consists of seven different chapters (Table 0.1) associated with activities of the above-mentioned objectives. Chapter 1 is a literature review, while Chapters 2 to 6 are distinct research chapters. Consequently, there is some inevitable 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 1 have been published in the Australian Journal of Crop Science and African Journal of Agriculture Research. Chapter 2 has been published in the journal of HortScience. Results of Chapter 3 have been published in the South African Journal of Plant and Soil and in the Journal of Tropical Agriculture (Trinidad). Chapter 4 is in press in the Journal of Research on Crops.

Table 0.1: Structure of the thesis

Chapter	Title
-	Thesis introduction
1	A review of the literature
2	Farmers' perceptions, production and productivity constraints, preferences, and breeding priorities of sweetpotato in Rwanda
3	Phenotypic characterisation of sweetpotato genotypes grown in Rwanda, East and Central Africa
4	Greenhouse and in-vitro screening of sweetpotato genotypes for drought tolerance
5	Combining ability, maternal effects and heritability of drought tolerance, yield and yield components among newly developed sweetpotato clones
6	Genotype by environment interaction and yield stability of sweetpotato clones in Rwanda
7	Overview of the study

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1. Chapter One: A review of the literature

Abstract

Sweetpotato is an important crop grown for food, feed and industrial raw material. In spite of the critical value of sweetpotato, its adoption and production in many tropical regions are limited by low dry matter content of storage root and drought stress, respectively. The sustainability of sweetpotato production will require the development and release of new sweetpotato varieties with high dry mater content of storage roots and drought tolerance. This review describes the aspects associated with development of sweetpotato cultivars with high dry matter storage root and drought tolerance. It highlights the effects of drought stress, mechanisms of adaptation of crops to drought stress, drought stress on sweetpotato, different mechanisms of development and synthesis of dry matter of sweetpotato storage root, methods to screen sweetpotato clones with drought tolerance and high dry matter content. Furthermore, the review summarizes breeding approaches, genotype x environment interaction and yield stability in sweetpotato. Information presented in this review may serve as important guideline in sweetpotato breeding towards high dry matter content of storage root and drought-tolerance.

Keywords: Breeding, genetics, drought tolerance, dry matter content, storage root, sweetpotato

1.1 Introduction

Sweetpotato (*Ipomoea batatas* [L.] Lam.) is an important crop worldwide grown in more than 119 countries on an estimated area of 8.3 million ha for food, feed and industrial raw materials (Scott and Ewell 1993; FAOSTAT 2013). The annual global production of sweetpotato is estimated at 106.5 million metric tons of which 15% is from East and Central Africa (FAOSTAT 2013). The sweetpotato storage roots are a major source of energy due to their high carbohydrate content which ranges between 80 to 90% of their dry weight. These carbohydrates consist mainly of starch, sugars and a low quantity of pectin, hemicelluloses, and cellulose (Lebot 2009). The orange-fleshed sweetpotato varieties are an important source of β-carotene which is the major provitamin A carotenoid (Chassy et al. 2008) while the purple-fleshed sweetpotato varieties are rich in anthocyanins and other polyphenolic components (Teow et al. 2007; Steed and Truong 2008). Sweetpotato is also a source of

vitamins C and B6, mineral salts and fibres (Woolfe 1992; Chassy et al. 2008). Due to its high nutritional value, sweetpotato has multiple uses.

The consumption of sweetpotato per capita per year was estimated to be 112 kg in Africa, 16 kg in Asia, 18 kg in Oceania, 2 kg in America, < 0.5 kg in Europe, 147 kg in Rwanda, 120 kg in Burundi and 88 kg in Uganda (Chassy et al. 2008). It is consumed in different forms. Consumption pattern varies within countries by regions and by income of the population group. Humans can consume sweetpotato roots, young leaves and the tips of stems as vegetables. Most rural poor consume boiled or baked sweetpotato roots, while people with more economic means tend to eat sweetpotato roots as fried chips or as a snack food (Woolfe 1992). In many rural areas, sweetpotato is mostly used as food and feed by small-scale farmers. The roots, by-product of roots and vines of sweetpotato are commonly used as feed for cattle, pigs, goat, sheep and rabbit (Woolfe 1992). In 2007, about half of all sweetpotato production in the world was used for animal feed (Lebot 2009). For this purpose, it is used as a raw material or ingredient in the feed processing industries (Gupta et al. 2009). Studies have shown that sweetpotato is a valuable forage containing nutrients that can support acceptable growth of livestock (Kariuki et al. 1998; Aregheore 2004; Gupta et al. 2009). Therefore, the mixture of sweetpotato forage with poor quality fodder has been suggested to sustain the growth of livestock and to increase the availability of animal products for human consumption (Aregheore 2004). Sweetpotato is an important source of raw material used to make different products such as soluble and refined starch and alcohol drinks (Woolfe 1992; Low et al. 2009). It is currently a target source of biofuel because of its ability to produce a high amount of starch biomass which can be fermented and converted into ethanol (Cervantes-Flores et al. 2011). However, the use of sweetpotato as a raw material for the biofuel and processing industries requires varieties with dry matter content that is above 35% of fresh weight (Gruneberg et al. 2009).

In spite of the critical value of sweetpotato, its adaption and production in many tropical regions are limited by storage root quality and drought stress, respectively (Lebot 2009). High dry matter content of storage roots is the main preference characteristic of sweetpotato consumers. In sub-Sahara Africa, farmers prefer sweetpotato varieties that have a high dry matter content (Mwanga et al. 2007; Cervantes-Flores et al. 2011). High dry matter content, low fibre, and good taste are the women farmers' preferred traits for an ideal sweetpotato variety (Gruneberg et al. 2009; Mwanga et al. 2010). Dry matter content that is above 25% is an important element for acceptability of a new sweetpotato variety by farmers (Shumbusha et al. 2010). Low dry matter content was a challenge towards promoting nutritionally

enriched orange-fleshed sweetpotato varieties developed to tackle blindness due to shortage of vitamin A in sub-Sahara Africa. Therefore, the increase of both β-carotene and dry matter is necessary to promote new orange-fleshed sweetpotato varieties (Cervantes-Flores et al. 2011; Mwanga et al. 2010). Storage roots with high starch and low hexos content are attractive characteristics for processing industries of sweetpotato (Slafer and Savin 1994). High starch and low soluble sugar content of sweetpotato root decrease the cost of processing because of the absence of oxidation reactions (McKibbin et al. 2006). These oxidation reactions are mainly favoured by high content of hexoses such as glucose and fructose and they are responsible for brown and dark colours and bitter taste of dried and fried food products from storage roots. This change of colour is a result of Maillard reaction (Dale and Bradshaw 2003). Li (2008) observed that the high dry matter content of the root significantly reduces the processing cost because of the low absorption of oil. Because the sustainability of sweetpotato production will depend on the consideration of end users' preferences, any breeding programme of the crop needs to incorporate valuable traits including high dry matter content before the release of elite clones.

The yield reduction due to drought stress was estimated at 60% (Van Heerden and Laurie 2008). In a field experiment, it was observed that drought stress for 20 days during the critical growing stage decreased yield by 15 to 39% of sweetpotato (Gong and Wang 1990). Moreover, insect pests and viral diseases were reported to be very severe in drought conditions (Fuglie 2007). Irrigation agriculture is an ideal and practical solution to overcome drought effect in crop production. However, farmers do not have access to irrigation water and infrastructures. Moreover, allocation of clean water for irrigation is a big challenge because of exponential increase of population and the current global climate change. Therefore, the sustainable solution to improve sweetpotato production is to develop and deploy drought tolerant varieties.

Breeding for drought tolerance requires knowledge on the physiological mechanisms involved in drought tolerance and the genetic control of yield and its components (Subbarao et al. 2005). Molecular breeding techniques may improve the response of selection to drought tolerance. However, their efficiency greatly depends on the availability of linked physiological and morphological traits (Subbarao et al. 2005). Further, it has been observed that the degree of expression of physiological and phenotypic traits varies depending on severity of drought stress and genotypes (Yang et al. 1991). The development of a new variety of sweetpotato with good quality such as high dry matter content and drought tolerance requires efficient methods of crossing, selection of potential clones and evaluation of the effects of genotype by environment interactions and yield stability. This permits the

release of end-users preferred varieties at the target production environment. Therefore, the following sections presented the physiological mechanisms of drought tolerance, root formation and dry matter synthesis and methods to screening for drought tolerance and high dry matter content in the sweetpotato.

1.2 Physiological mechanisms and conventional breeding of sweetpotato for drought-tolerance

1.2.1 Effects of drought stress

Drought is an extended period of dry weather characterized by a shortage of water supply to plants (Acquaah 2007). In drought conditions, water potential (Ψw) of soil becomes negative because of a concentration increase of soil solutes. The movement of cell water is determined by the water potential gradient (ΔΨw) that acts as a driving force for transport through a permeable cell membrane (Taiz and Zeiger 2006). A plant can continue to absorb water only if its Ψw is lower than of the soil. Drought stress requires changes in plant cells and tissues to adapt to drought stress conditions and continue to acquire the little available water of soil (Bartels and Sunkar 2005). Symptoms of drought stress start when a crop has used between 50 and 80% of extractable soil moisture (Acquaah 2007) and the failure of the plant to absorb the remaining soil water has severe consequence.

Water plays a crucial role in the life of the plant and its availability is a main factor that determines the plant population in the environment (Coley et al. 2009). Water is the main constituent of plant tissues but its quantity varies within plant tissues and plant species. The water content was estimated at 80 to 95% in masses of growing tissues, 85 to 95% in vegetative tissues, 35 to 75% in wood with dead cells, and at 5 to 15% in dried seeds (Taiz and Zeiger 2006). The distribution of plant species in the environment is associated with their tolerance to environmental stresses (Brenes et al. 2009). It was observed that the most widespread plant species are drought tolerant (Baltzer et al. 2008; Brenes et al. 2009). A low temperature was suspected to be the main limiting factor of life in the Antarctic environment. However, it was found that the water deficit is the major life threatening cause with a positive correlation observed between the soil moisture and the abundance of organisms in this environment (Kennedy 1993).

Drought is the primary abiotic stress that affects crop production and food availability globally. In many developing countries, agriculture depends on rainfall which in many cases

does not meet the crop need (Ober 2008). The limited occurrence, amount, and uneven distribution of rain affect growth and productivity of crops. Eventually this causes famines in many semi-arid countries (Acquaah 2007). Drought can cause the biggest loss in crop production compared to other isolated biotic or abiotic stress factors (Boyer 1982; Ober 2008). It affects crop production by reducing the genetic potential of a plant (Mitra 2001). Consequently, it is responsible of the difference between the mean yield and the yield potential of a crop and the cause of the yield instability in time (Sorrells et al. 2000).

Drought induces physiological, biochemical and molecular changes that have consequences on crop growth and productivity (Reddy et al. 2004). Drought induced osmotic stress causes the removal of water from the cytoplasm to the extracellular space and cell dehydration (Bartels and Sunkar 2005). Water deficit affects the photosynthesis ability of plants by changing the content and components of chlorophyll, reducing the net CO_2 uptake by leaves and by decreasing activities of enzymes in the Calvin cycle (Becana et al. 1998; Cornic 2000; Gong et al. 2005; Lawlor and Tezara 2009). The osmotic stress of water deficit inhibits strongly the growth of leaves and stems of plants. This has negative effects on the yield potential of the crop (Westgate and Boyer 1985). However, the degree of growth inhibition and yield reduction depends on the duration and intensity of drought stress and the genotypes of crop species (Monakhova and Chernyad'ev 2002; Bartels and Sunkar 2005).

The major cause of reduction in photosynthesis ability and growth under drought stress is the disequilibrium between the production of reactive oxygen species (ROS) and their scavenging systems (Becana et al. 1998; Noctor et al. 2014). Plants under abiotic stress generate ROS that cause oxidative reactions (Lin et al. 2006a). The main ROS are hydrogen peroxide (H_2O_2) and superoxide ($O_2^{\cdot -}$). These ROS are routinely produced in different cellular reactions catalysed by various enzymes such as lipoxygenase, peroxidase, NADPH oxidase and xanthine oxidase, but the main source of these molecules is the Fenton and Haber-Weiss reactions (Blokhina et al. 2003; Debarry et al. 2005; Lin et al. 2006b). The ROS damage lipids, carbohydrates and proteins of cell membrane and cell nucleic acids (Zhang and Kirkham 1996; Sairam et al. 1997; Fu and Huang 2001; Blokhina et al. 2003). When a plant is under a serious stress condition; there is an accumulation of ROS because scavenging and repairing mechanisms of ROS damages are surpassed (Lin et al. 2006b). Therefore, a crop genotype must have efficient mechanisms of defence against ROS to survive a severe drought osmotic stress and adapt to drought conditions.

1.2.2 Mechanisms of adaptation to drought stress in plant species

Crop genotypes can withhold the drought stress by dehydration tolerance, dehydration avoidance or drought escape (Ludlow 1989; Yue et al. 2006). It was observed that a genotype can use all or two of these strategies. However, a molecular study with 245 SSR markers has revealed that dehydration tolerance and dehydration avoidance have distinct genetic bases (Yue et al. 2006). Mechanisms involved in drought stress adaptation are outlined beliow:

1.2.2.1 Dehydration tolerance

Dehydration tolerance involves the desiccation tolerance, osmotic adjustment and antioxidant capacity. This strategy involves the resurrection and survival of genotypes after extended and extreme internal water deficit. These genotypes can be still alive when there is 95% of leaf water loss (Scott et al. 2000). Dehydration tolerance enables the plants to survive long and strong periods of water deficit and regrow when rain falls. It allows also plants to maintain metabolic activities for longer and to translocate more stored assimilates to the storage tissues (Fukai and Cooper 1995). Accumulation of compatible solutes is one of biochemical processes that results in the dehydration tolerance (McCue and Hanson 1990). It was reported that compatible solutes play an adaptive role by osmotic adjustment and protection of cellular compounds (Hare et al. 1998; Ain-Lhout et al. 2001). The compatible solutes are mainly nitrogen containing molecules such as amino acids and polyamines, and hydroxyl compounds. Types of these compatible solutes and levels of their accumulation vary with plant species (McCue and Hanson 1990). The compatible solutes work together with antioxidants which intervene to eliminate ROS and to repair damages of ROS.

Crop plants produce different antioxidants that have abilities to scavenge ROS. Antioxidants have small molecular mass such as ascorbic acid, glutathione, tocopherols, phenolic compounds, ROS-interacting enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX) and catalase (CAT) (Blokhina et al. 2003; Brosché et al. 2010). These molecules play an important role to control the equilibrium between the production and the elimination of free radicals. Moreover, they work in cohesive network reactions and use mainly redox reactions (Lin et al. 2006b). Crop varieties that are drought resistant or tolerant express high quantities of antioxidants than sensitive varieties (Herbinger et al. 2002; Lin et al. 2006b). Indeed, the quality and the quantity of these molecules are crop species dependent and their expression is affected by environmental conditions (Herbinger et al.

2002; Blokhina et al. 2003; Lin et al. 2006b). Therefore, understanding the expression and mechanisms of these molecules and their functional models can assist to identify and develop drought tolerant crop varieties.

1.2.2.2 Dehydration avoidance

Dehydration avoidance consists of minimizing the water loss and maximizing the water absorption under water deficit conditions. This model is mainly observed on succulent and C3 crop species (Yue et al. 2006). Water loss can be minimized by reducing the light absorbance through leaf rolling, stomata closing, dense trichome layer that increases the reflectance, steep leaf angles, decrease of leaf area and canopy through reduced growth or shedding of leaves (Ehleringer and Cooper 1992; Larcher 2000; Chaves et al. 2003). It was observed that perennial and deciduous crop plants reduce their foliage in drought seasons. Plants that are always green present sometimes thick leaves with solid cuticle, highly sclerophyllous and reduced size leaves (Lebreton et al. 1995; Sanguineti et al. 1999; Sorrells et al. 2000; Ain-Lhout et al. 2001; Taiz and Zeiger 2006). The water uptake is maximised by the increase of the capacity of the root system (Jackson et al. 2000). Root characteristics such as thickness, depth, length and density have been associated with drought avoidance in rice (Ekanayake et al. 1985). All these characteristics of roots and leaves observed in the strategy of dehydration avoidance have effects on the effective water use and control of evapotranspiration.

1.2.2.3 Drought escape

The strategy of drought escape is based on a short life cycle and developmental plasticity (Yue et al. 2006). Genotypes grow and reproduce before an appearance of a drought season (Passioura 1996; Richards 1996; Mitra 2001; Mckay et al. 2003). In the drought escape, it was suggested that a genotype must have a high metabolic activity and rapid growth to support the plant to complete its life cycle before the most intense period of drought. However, the selection based on phenology has revealed that the selection of both high photosynthetic activities and rapid growth can only be achieved under a well-watered environment (Sherrard and Maherali 2006). Therefore, the strong correlation of development duration and metabolic activities to promote the drought escape is not necessary under drought conditions.

1.2.3 Consequences of adaptation mechanisms to drought stress

Adaptation mechanisms to drought stress may incriminate crop growth and productivity (Larcher 2000). For instance, crop varieties of short life cycle can escape a drought period but they produce low yield (Acquaah 2007). Mechanisms of dehydration avoidance such as a stomatal closure and decrease of leaf area reduce assimilation of light and CO_2 necessary for photosynthesis and consequently lower biomass production (Cornic 2000; Larcher 2000; Lawlor and Tezara 2009). Dehydration tolerance with the accumulation of compatible solutes, the synthesis of antioxidants and the process of ROS scavenging depletes assimilates and energy. Consequently, these mechanisms reduce the ability of crop genotypes to synthesize organic end-products (Mitra 2001). Thus, the development of a drought tolerant sweetpotato variety needs to balance all drought tolerance mechanisms without sacrificing crop productivity (Passioura 1996; Richards 1996; Mitra 2001; Mckay et al. 2003).

1.2.4 Drought stress on sweetpotato

Sweetpotato has unique characteristics of drought tolerance compared to the widely grown crop species. The root system of sweetpotato has a big surface area that allows easy access to available soil water (Low et al. 2009). It is very rich in antioxidants such as vitamin C, carotenoids and polyphenolic substances (Blokhina et al. 2003; Lin et al. 2006b), which are powerful and scavenge hydroxyl and peroxyl radicals and to control oxidation of lipid and protein of cell membranes. These are also chelators of metals and inhibitors of Fenton and Haber-Weiss reactions, which are the principal sources of free radicals (Debarry et al. 2005). However, sweetpotato is negatively affected by drought stress.

In sweetpotato, it was observed that the water deficit reduces the number of leaves and tubers, size and composition of roots and vines, and gain of dry weight of shoot and roots (Bourke 1989; Pardales et al. 2000). In the greenhouse trial, sweetpotato genotypes revealed differences in vine length and diameter, leaf width and number of nodes per vine (Ricardo 2011). Drought stress reduced the yield of storage roots, total biomass, marketable fresh storage root and number of storage roots. However, it was observed that drought stress increased the dry matter content of storage root (Kivuva 2013). In a pot experiment to screen 15 sweetpotato varieties for drought tolerance, Sarawasti et al. (2004) observed that biomass and morphological traits such as main stem length, internode diameter and length, leaf area and number decreased in response to drought stress. Zhang el al. (2004) observed that soluble sugar and total amino acid increased as the loss of leaf water increased; but the

potassium content decreased significantly. Sweetpotato cells grown under an induced drought osmotic stress condition had reduced growth, an induction of plasmolysis, an increase of amino acid pool and sucrose and starch accumulation (Wang et al. 1999). It was suggested that the accumulation of starch and the plasmolysis process decrease significantly the cell cytoplasm. Consequently, a small quantity of compatible solutes is enough to adjust an osmotic pressure induced by a water deficit (Wang et al. 1999). The drought condition was found to reduce the ability of sweetpotato to eliminate ROS and this reduction varies from one variety to another (Herbinger et al. 2002; Blokhina et al. 2003; Lin et al. 2006b).

Germplasm collections from water limited regions showed distinctive leaf morphology compared to collections from environments with high rainfall. Moreover, the local landraces were found to be more drought tolerant than introduced varieties under limited water tropical regions (Carey et al. 1997). Indira and Kabeerathumma, (1988) observed that sweetpotato is sensitive to water shortage especially during establishment, vine development and storage root initiation. It was revealed that the shortage of water during critical periods of growth causes irreversible consequences on yield (Lin et al. 2006a). Anselmo et al., (1998) reported that drought is the main production constraint of sweetpotato in the region where agriculture is rainfall dependent. According to Ekanayake, (1990) a variety is drought tolerant when it produces an economic crop yield under limited water availability. Drought tolerance was associated with vine availability for planting after prolonged dry season (Gruneberg et al. 2009).

Drought stress causes physiological changes in sweetpotato. van Heerden and Laurie, (2008) reported that drought caused stomatal closure which reduces CO_2 uptake, photosynthesis and plant growth and yield. It was suggested that drought stress affect the metabolism of carbon and nitrogen (Haimeirong and Kubota 2003). The effects of osmotic stress induced by polyethylene glycol on sweetpotato seedlings were investigated by measuring changes in relative water content, malondialdehyde and proline contents and superoxide dismutase activity. A highly positive correlation between relative water content and drought resistance (r = 0. 783), a highly negative correlation between malondialdehyde contents and drought resistance (r= 0. 848), a highly positive correlation between superoxide dismutase activity and drought resistance (r = 0. 777) were observed. However, the proline contents in leaves did not reveal any relation with sweetpotato drought tolerance (Zhang et al. 2001). Under field trial, Niu et al. (1996) observed that leaf relative water content and catalase activity are best indicators of drought tolerance. Chowdhhury and Naskar (1993)

found the positive correlation between relative water content of leaves and yield of sweetpotato under water stress condition.

Soil water content is the main factor that determines the formation and growth of storage roots of sweetpotato (Bourke 1989). In field trials, it was observed that drought stress for 20 days in part of the growing period decreased storage root yields by 15 to 39% (Gong and Wang 1990). The constant soil humidity was proved to reduce adventitious roots (Pardales et al. 2000). In water logging conditions, plants do not develop effective roots because underground parts of plants do not have enough oxygen to carry out metabolic reactions. Consequently, storage roots rot. Inversely, prolonged drought conditions reduce the formation and growth of roots and dry matter accumulation (Bourke 1989; Pardales et al. 2000). Therefore, a balanced level of water availability is necessary for good production of sweetpotato.

1.3 Storage root formation, dry matter synthesis, accumulation and genetics in sweetpotato

The formation of sweetpotato storage roots is a complex process involving various phenomena such as stopping of root elongation, initiation of first and second vascular cambia, development of anomalous and interstitial cambia, increasing of radial growth, cell proliferation and expansion, and massive accumulation of starch and proteins (Desai 2008; Ravi et al. 2009). Typically, a storage root has to stop elongation growth but continues radial growth (Desai 2008). The initiation of storage root starts with the thickening of stellar structure of adventitious roots, followed by a formation of a circular primary vascular cambium and other several cambia in sub-apical regions of the thickening root (Ravi and Indira 1999). These cambia are meristematic tissues which undergo many mitotic cell divisions resulting into the formation of starch storing tissues, growth of storage root and suppression of stele lignification. All these processes are controlled by endogenous phytohormones which are expressed by different genes (Ravi et al. 2009).

Cytokinins are the main phytohormones involved in root formation. Zeatin riboside, trans-zeatin riboside and 9-glycosyl-N-62-isopentenyl adenosine were identified to be responsible for the initiation of cambia tissues (Tanaka et al. 2005; Wang et al. 2005). These cytokinins and others such as isopentenyladenine and dihydrozeatin riboside were proven to play a pivotal role in the initiation and proliferation of cambia tissues of storage root (Desai 2008).

Ku et al. (2008) observed that abscisic acid stimulates cell division of cambial meristematic tissues by interacting with other cytokinins and results in the growth of storage roots.

Storage root growth takes place at cellular level and involves the expansion in size by increasing the cell number, size and weight by accumulation of photosynthesis products (Desai 2008; Ravi et al. 2009). The accumulation of dry matter is associated with the ability of the root to attract photo-assimilated products from the leaves. The photosynthesized sucrose is moved from leaves through the stem, towards underground parts including storage roots (Li 2008). Sucrose is split into hexoses which are transformed to glucose-1 phosphate, which is then used to synthesise starch in the amyloplasts. Reactions of starch synthesis are mainly catalysed by ADP-glucose pyrophosphorylase and starch synthase (Nakatani and Komeichi 1992; Li 2008).

Studies of molecular mechanisms of synthesis and accumulation of dry matter revealed that products expressed by knotted-like homeobox (KNOXI), MADS-box and polyamine genes play an important role in the formation of sweetpotato storage roots (Chen et al. 2003; Ku et al. 2008; Tanaka et al. 2008). Products expressed by KNOXI genes were identified in initial and growing sweetpotato storage roots (Tanaka et al. 2008). It was observed that an up regulated of KNOXI genes expression is associated with the reduction of lateral root development (Scanlon et al. 2002) whereas the down regulation of these genes is linked to an increase of the number of lateral roots. Products of KNOXI genes were identified to regulate the cytokinin level in the storage roots of sweetpotato and a high expression of KNOXI genes was associated with a high synthesis of cytokinins (Chen et al. 2003; Tanaka et al. 2008). The concentration of trans-zeatin riboside content in the growing sweetpotato storage roots was identified to be correlated with the level of expression of KNOXI genes. This observation suggested an active involvement of products of KNOXI genes in the formation of storage roots of sweetpotato (Tanaka et al. 2008). Products of MADS-box genes were identified to stimulate the production of phytohormones such as jasmonic acid and cytokinins which participate in the initiation and development of sweetpotato storage roots (Ku et al. 2008). Spermidine and other products coded by polyamine genes were identified to play an important role of pathway signal transduction, protein kinase activation and transcription factors that increase genes expression during storage root formation and growth (Kasukabe et al. 2006). Indeed, many gene products were identified to be involved in dry matter synthesis. The expression of genes coding for these products was identified to be extremely highly influenced by genetic effects and not by factors such as water deficit (Ravi and Indira 1999; Ravi et al. 2009), soil and air temperature (Li 2008) and physiology and age

of seedling (Caldiz et al. 1996). However, there are many other aspects of storage root and dry matter synthesis that need to be further investigated and understood.

1.4 Breeding of sweetpotato

Sweetpotato breeding has been slower than that of several other staple crops because of the inherent nature of the crop including polyploidy, poor flowering and seed set, self- and cross-incompatibility, heterozygosity and large chromosome number. In other cases, flowering periods are different between sweetpotato genotypes and these periods are affected by environmental conditions (Jones et al. 1986). The hexaploidy status (Jones and Deonier 1965; Vimala and Hariprakash 2011) and the irregular meiotic division of sweetpotato (Ting and Kehr 1953; Jones and Deonier 1965; Maluf et al. 1983) have negatively affected the progress of breeding programmes. In addition, the pollen and fertilization incompatibility are a big challenge to sweetpotato breeders (Martin 1965). Thus, a successful breeding program has to overcome these challenges to achieve greater selection efficiency.

Application of induction techniques and control of environmental conditions have improved the flowering and seed production of sweetpotato (Jones, 1986). It was observed that the induction of physiological shocks, grafting, girdling and chemical treatment can improve the flowering of sweetpotato (Jones et al. 1986). Miller (1939) revealed that the fertilization of the ovule, and seed production are temperature, humidity and light dependent. When the temperature is very low, the fertilisation is poor because of inefficient germination of pollen and growth of pollen tube. Moreover, the tropical climate favours flowering and seed production than the temperate conditions. Jones et al. (1986) observed that seed production is reduced when sweetpotato vines present a high vegetative growth. The authors also pointed out that the circulation of air through the plant canopy improves the seed set of sweetpotato. All these findings have an important implication on sweetpotato breeding.

Sweetpotato breeding programmes often have a common overall objective but differ in specific objectives. The overall objective of sweetpotato breeding programme is usually to improve the quality and quantity of sweetpotato production though the selection and development of new varieties (Jones et al. 1986; Kapinga and Carey 2003). Specific objectives vary depending on needs. Many breeding programmes of sweetpotato focus on the development of new varieties with high nutrient content such as β-carotene, anthocyanin and iron, and high yield, dry matter and biomass production (Jones et al. 1986; Fuglie 2007;

Gruneberg et al. 2009; Mwanga et al. 2010). All breeding programmes usually lead to the development of cultivars with high yield, resistance to abiotic and biotic stresses, and other different characteristics that enhance acceptability by end users (Kapinga and Carey 2003) Therefore, it is necessary to define the objectives of a breeding programme because this guides the choice of potential parents and ensuing breeding method.

Each breeding programme requires a source of valuable genes. Therefore, characterisation of available germplasm and identification of potential parents is a starting point of breeding programmes (Mitra 2001; Shumbusha et al. 2010). There are recognized institutions such as Vegetable Breeding Laboratory of Charleston and Louisiana sweetpotato research center in USA, Asian Vegetable Research and Development Center (AVRDC) in Taiwan, Genetic Resources Unit of the International Institute for Tropical Agriculture (IITA) at Ibadan/Nigeria and the International Potato Centre (CIP) in Peru that keep genetic collections of sweetpotato (Villareal and Lo 1983; Iwanaga 1988; Tjintokohadi and Mok 2001). These institutions can provide potential parents for a sweetpotato breeding programme if local landraces do not have good sources of genes for characteristics of interest.

1.4.1 Breeding of sweetpotato for drought tolerance

Breeding of sweetpotato is carried out through random polycross and hand pollination (Gruneberg et al. 2009). In the polycross method, crossing blocks are installed and allowed to be naturally open pollinated by insects (Nyquist and Santini 2007). This method is very useful to generate a genetic diversity in a sweetpotato population but it is not efficient in genetic studies because of the source of pollen is unknown. Therefore, the hand pollination method was proposed to overcome this problem (Acquaah 2007). The hand pollination is carried out in four main steps of preventing insect pollination before doing hand pollination, hand pollination, preventing insect pollination after hand pollination and labelling (Jones and Deonier 1965; Jones et al. 1986). This method is commonly applied to ensure cross combinations of different characteristics in the hybrid seeds through a highly demanding practice (Jones et al. 1986; Wilson et al. 1989; Gruneberg et al. 2009). When using hand pollination the commonly used matting designs in the sweetpotato breeding are diallel and North Carolina (Mihovilovich et al. 2000; Mwanga et al. 2002; Chiona 2009; Gasura et al. 2010).

Breeding for drought tolerance is complicated because of a negative correlation between some stress adaptive traits and crop yield (Chapin et al. 1993). Zehui (1996) observed that the use of yield components as the unique indicators for drought tolerance is not sufficient.

Physiological, morphological and biochemical characters that may show the drought tolerance were proposed through greenhouse and laboratory studies (Blum 2002). However, some varieties selected under greenhouse and laboratory conditions did not show the drought tolerance under field conditions (Sorrells et al. 2000). This indicates that the expression of genes for drought tolerance is strongly affected by environmental conditions (Cheema and Sadaqat 2004).

Knowledge of environmental effects on the expression of genes leads to breeders to adopt new methods to develop drought tolerant varieties. Efforts of breeders are oriented on the development of varieties that can produce in an environment where the rainfall is irregular in the distribution and quantity. This is because crops must have a minimum level of water to sustain growth (Acquaah 2007). Zehui (1996) suggested that it is necessary to explore all morphological, biochemical and physiological characters associated with drought tolerance during the screening process. Also it was suggested that selection should be carried out in environments in which a new crop variety will be released and grown (Cheema and Sadaqat 2004; Abidin et al. 2005; Mwanga et al. 2007).

Sexual reproduction of sweetpotato generates genetic variability in which valuable clones are selected further. The mass selection method was first suggested because most important traits of sweetpotato are quantitative. Also the population improvement through recurrent selection method was adopted (Carey et al. 1992). Ekanayake, (1990) proposed two stages in the approach to screen sweetpotato for drought tolerance. Firstly, genotypes have to be evaluated in a screening nursery using yield and pulling resistance as selection criteria. Secondly, selected genotypes have to be evaluated under drought conditions in a field for physiological traits, water use efficiency and yield. Genotypes identified as drought tolerant could be used as progenitors for combining with other favourable traits.

Selection and breeding for varieties that perform very well under drought conditions is a key factor to improve the production of sweetpotato. Studying sweetpotato varieties for 70 days under drought conditions, Hou et al., (1999) observed a significant difference in a survival rate which was associated with drought tolerance. However, the authors did not find a correlation between drought tolerance and above ground growth. The evaluation of drought tolerance of 50 genotypes revealed a yield range from 0.76 to 73.85 g per plant and 17 genotypes were identified to be drought tolerant (Ding et al. 1997). Anselmo et al. (1998) investigated the drought tolerance of clones of high yielding cultivars and their progenies from open pollination in the Philippines for two years in the dry season. Based on yield, the authors found that some clones and open pollinated progenies were drought tolerant.

Identification and characterisation of genes have a positive effect on the genetic engineering for tolerance to drought stress (Acquaah 2007). Genetic engineers have tried to develop transgenic plants resistant to drought by using isolated genes. Genes coding for sperimidine synthase were used to improve environmental stress of sweetpotato. These transgenic plants have revealed tolerance to drought, salt, chilling and heat stresses (Kasukabe et al. 2006). Transgenic plants of sweetpotato containing the gene from *Spinacia oleracea* encoding the betaine aldehyde dehydrogenase revealed increased glycine betaine accumulation and betaine aldehyde dehydrogenase activity. These plants have shown tolerance to multiple environmental stresses with high ability of protection against cell damage, strong photosynthetic activity, reduced production of ROS and increased activity of free radical scavenging enzymes (Fan et al. 2012). Transgenic potato plants with the genes of Cu / Zn superoxide dismutase and ascorbate peroxidase were developed. These plants showed enhanced tolerance to multiple environmental stresses including high temperature compared to non-transgenic plants (Tang et al. 2006). Even though genetic engineering revealed promising results, its progress is limited by a shortage of successful screening methods and multidisciplinary approach and genotype by environment interactions (Mitra 2001).

1.4.1.1 Methods of screening for drought

Drought-tolerance studies can be carried out under field or controlled environmental conditions (Acquaah 2007). Field trials are carried out under natural conditions which are real environment of a plant but this environment presents some limitations of fluctuation of water availability caused by unpredictable rainfall. Moreover, environmental factors such as temperature, air humidity and light are variable. Therefore, field screening for drought tolerance is complicated by unpredictable environmental conditions (Lafitte et al. 2004). The rainout shelter and in vitro techniques were proposed to overcome the limitations of selection for drought tolerance under field conditions (Acquaah 2007). The rainout shelter is a mobile infrastructure that protects genotypes under experiment from rain. This method permits to control the uniformity of water supply to plants (Blum 2002). The in vitro approach consists on growing cells or tissues of plant or plantlets on a defined drought stressing culture media under an aseptic and controlled environment (Wang et al. 1999; Ahloowalia et al. 2004). The in vitro technique provides precise results but the working environment differs from the natural environment of crops. Therefore, the combination of in vitro screening with selection under the natural condition or under the rainout shelter could improve the quality of results.

Drought tolerance can be identified by quantifying phenological, morphological, physiological and biochemical characteristics and using molecular tools (Blum 2002). Phenological and morphological characteristics are the most used in breeding for drought tolerance. In these approaches data collection consists of measurement of plant growth (size of roots, stem and leaf area, accumulation of fresh and dry biomasses), growth stage (days to flowering and maturity), senescence, leaf rolling and yield loss (Spitters and Schaapendonk 1990; Cheema and Sadaqat 2004). The water content and water potential of the crops are indicators of drought tolerant varieties. A variety that maintains its internal water status under drought stress is considered drought tolerant (Acquaah 2007). Drought tolerance is also determined by quantifying plant biochemical products such as compatible solutes, chlorophyll, antioxidants and other proteins produced by plants as responses to drought stress (Wang et al. 1999; Reddy et al. 2004; Kasukabe et al. 2006). Diffusion porometry for leaf water conductance, root penetration, distribution and density in the field and infrared aerial photography for dehydration are used commonly in studies for drought tolerance (Mitra 2001).

Molecular tools to select for drought tolerance have been developed (Srisuwan et al. 2006; Acquaah 2007). The basis of this molecular approach is due to the progress of genomics, transcriptomics, metabolomics and proteomics. Among these tools, DNA molecular markers based on the hybridization, polymerase chain reaction and DNA sequence are the most commonly used (Tuberosa and Salvi 2006; Michael et al. 2008). Simple sequence repeats (SSRs) or microsatellites genetic markers are commonly used in sweetpotato studies. They have been used in genetic characterization of sweetpotato germplasm (Buteler et al. 1999; Veasey et al. 2008; Karuri et al. 2010) and analysis of paternity in polyploidy sweetpotato (Buteler et al. 2002). Other molecular markers such as Restriction Fragment Length Polymorphisms (RFLPs), Random Amplified Polymorphic DNAs (RAPDs), Sequence Tagged Sites (STS), Amplified Fragment Length Polymorphisms (AFLPs), Single Nucleotide Polymorphisms (SNPs) were also proposed in genetic and breeding studies (Acquaah 2007). However, the utilisation of molecular approach in a plant breeding requires a well-equipped laboratory and trained personnel (Srisuwan et al. 2006).

1.4.1.2 Inheritance of drought tolerance

Drought tolerance is reportedly a complex trait because of the heterogeneity of drought stress in time and space, and unpredictable characteristics of drought stress (Sorrells et al. 2000). Drought tolerance involves actions and interactions of various biochemical, morphological and physiological mechanisms that are controlled by products expressed by

different genes (Mitra 2001; Acquaah 2007). Moreover, it is difficult to study isolated single gene and to understand its role of drought tolerance in crop plants (Mitra 2001).

Both qualitative and quantitative inheritances were found in traits associated with drought tolerance. Ekanayake et al. (1985) observed that root characteristics are controlled by a qualitative inheritance under drought condition. Leaf rolling, osmotic adjustment and number of roots were identified to be qualitative traits (Mitra 2001). Study of water deficit mediator genes indicated that crop species vary in symptoms and reactions to water deficit (Sorrells et al. 2000). The genes responsible for earliness of stem reserves, leaf persistence and dwarfing were identified to be associated with drought tolerance (Foulkes et al. 2007). In rice and cowpea a drought resistance gene linked with genes for plant height and pigmentation was reportedly pleiotropic on a root system (Morgan 1995; Mitra 2001; Agbicodo et al. 2009). Other proposed candidate genes that are involved in drought tolerance are genes coding for dehidrin proteins that protect cellular components under dehydration conditions (Shinozaki and Yamaguchi-Shinozaki 2007), proteins controlling the equilibrium and damages of ROS (Foyer and Noctor 2005), proteins involving in the osmotic adjustment and plant morphology (Moinuddin et al. 2005; Ober 2008) and enzymes involved in the accumulation of compatible solutes (Mitra 2001). Indeed, drought tolerance involves many genes which code for products working in a highly coordinated network.

1.4.2 Breeding of sweetpotato for high dry matter content

High dry matter content is one of the main specific objectives of many sweetpotato breeding programmes. It was found that the dry matter content of sweetpotato varies depending on variety, location, climate, incidence of pests and diseases, cultural practices or soil types (Jones et al. 1986; Manrique and Hermann 2000; Shumbusha et al. 2010; Vimala and Hariprakash 2011). Narrow sense heritability ranging between 0.65 and 0.92 was identified for dry matter content. In addition, transgressive segregation for dry matter content has been observed in sweetpotato progenies (Cervantes-Flores et al. 2008). These findings and the existence of several enzymes involved in starch biosynthesis indicate that the dry matter content is a quantitative trait (Cervantes-Flores et al. 2008). Jones, (1986) reported that the value of a new sweetpotato variety depends on the combination of the desirable trait with other characteristics. Therefore, characteristics that meet farmers', consumers' and market preferences have to be considered in the selection process of new cultivars.

1.4.2.1 Approaches to screening for high dry matter content

1.4.2.1.1 Morphological markers

Screening for high dry matter content can be direct or indirect depending on the correlation between dry matter content and other traits (Acquaah 2007). In the direct approach the screening is mainly based on the weight of dry root mass (Ma et al. 2009; Vimala and Hariprakash 2011). To determine dry matter content, a precise quantity of fresh weight of root is excised and dried to constant weight. Then, the dry matter content is determined as a ratio of dry weight and initial fresh weight (Shumbusha et al. 2010). In the indirect approach, clones with a high dry matter can be selected by quantifying the starch continent of the root. This method is based on a high positive correlation between dry matter and starch content (Ma et al. 2009; Cervantes-Flores et al. 2011). Because of genotypic variance and genotype by environment interactions, it was suggested that dry matter and starch content may be improved with a high selection efficiency in the earlier stages (Grunerberg et al. 2005).

1.4.2.1.2 Molecular markers

Molecular markers are alternative tools that can be used in the screening for high dry matter content (Cervantes-Flores et al. 2011). These molecular markers have showed important potential to improve the efficiency and precision of conventional breeding techniques (Acquaah 2007). The large number of quantitative trait loci (QTLs) mapping studies for diverse crops species have provided an abundance of DNA marker-trait associations. The principle of molecular marker development consists of population development, QTL mapping, QTL validation, marker validation and marker-assisted selection (Collard and Mackill 2008). These molecular markers are useful for selection of traits with low heritability (Gupta et al. 1999; Collard and Mackill 2008).

1.5 Gene action and correlation between traits

Important traits in crops are controlled by quantitative genes which have different gene action (Mitra 2001). Gene effects are simply described by gene action which can be additive, dominant or epistatic (Acquaah 2007). The expression of a trait is dependent on genotype, environment and genotype by environment (G×E) interactions (Cheema and Sadaqat 2004). Therefore, the gene action needs a particular analysis in each case study involving various genotypes and environments through appropriate genetic designs (Acquaah 2007).

Various gene actions have been identified and described in different studies on sweetpotato. Miller, (1939) found that white skin, green stem and white flesh are dominant over red skin, red stem and yellow flesh of sweetpotato. Ma (2009) observed that the inheritance of β-carotene is controlled by additive gene effects. The additive gene effects were identified in the inheritance of dry matter and β-carotene content (Chiona 2009). Vimala and Hariprakash (2011) found the continuous and overlapping characters of vine, storage root, dry matter and cooking qualities of sweetpotato. More than five genes were suggested to be involved in the β-carotene synthesis and in combination with other genes to determine the flesh colour of storage roots of sweetpotato. Heterosis was observed for the size and number of roots per plant, indicating dominance gene action or intra-allelic interaction between alleles of the same gene (Gasura et al. 2010). These findings emphasise the quantitative nature of many sweetpotato traits and indicate that several plant characteristics associated with yield are controlled by more than two genes acting and interacting in a complex model. Therefore, the combination of two or more than two quantitative traits in one cultivar requires knowledge of the gene action and correlation between these traits to improve the selection response.

Traits can be positively or negatively correlated or not correlated (Acquaah 2007). The existence of positive correlation between traits implies that improvement of one trait results in the improvement of the other trait requiring simultaneous selection. While negative correlation between traits means that the improvement of one trait causes an obligatory decrease of the other trait. The absence of correlation indicates that each trait can be improved independently without affecting another (Acquaah 2007). However, the complete absence of correlation between one trait and others is a rare case in plant breeding. For example, the breeding for orange-flesh sweetpotato with a high β-carotene, iron and zinc contents is challenged by a strong negative genetic correlation with dry matter content (Gruneberg et al. 2009; Ma et al. 2009; Vimala and Hariprakash 2011). This negative association of dry matter and β-carotene content was attributed to a competition between starch and β-carotene because both are synthesised in plastids (Cervantes-Flores et al. 2008). Ma-Teresa et al. (1994) observed a negative correlation between root dry matter content and root yield. A negative correlation was also noted between dry matter and soluble sugar content of sweetpotato (Gruneberg et al. 2009). However, the correlation between dry matter and drought tolerance in sweetpotato is poorly documented.

1.6 Genotype by environment (G×E) interaction and yield stability

Plant growth and production are a result of interactions of its genetic potential and environment. Plants perform well in environments in which they are adapted (Acquaah 2007). The performance of genotypes is quantified in terms of wide and specific adaptability and yield stability (Abidin et al. 2005). Wide adaptability is generally attributed to genotypes performing well over large areas and presenting high mean yields across different environments. A variety has a specific adaptability when it ranks among the highest yielding genotypes at only some locations. The stability which can be static or dynamic is the ability of a genotype to perform consistently across a wide range of environments (Acquaah 2007). Knowledge of types of genotype by environment (G×E) interactions is very important before release to decide if a new variety has wide or specific adaptation (Manrique and Hermann 2000; Grunerberg et al. 2005).

G×E interactions are differential genotypic expressions across multiple environments (Acquaah 2007). They complicates the comparison of the performance of genotypes across environments when a high number of genotypes and locations are involved and quite often delay the selection process of a breeding programme (Caliskan et al. 2007). Prior to release of a new variety, genotypes of high yield potential are evaluated at different locations for several years to identify their G×E interactions and yield stability (Acquaah 2007). Therefore, breeders need robust biometrical methods to estimate phenotypic stability and to analyse G×E interactions (Bacusmo et al. 1988; Becker and Leon 1988).

1.6.1 Approaches to evaluate G×E interaction and yield stability

There are various methods to estimate the phenotypic stability and to analyse the G×E interactions (Bacusmo et al. 1988; Caliskan et al. 2007). These methods are classified into two main groups of univariate stability statistics and multivariate methods (Becker and Leon 1988). The univariate stability statistics can be parametric by using variance of a genotype across environments (Shukla 1972), ecovalence, regression coefficient (Finlay and Wilkinson 1963; Russell and Eberhart 1966; Shukla 1972), deviation mean squares, or coefficient of determination to identify the stability of genotypes (Becker and Leon 1988). It can also be nonparametric when it is based on rank orders of genotypes using mean or variance ranks (Becker and Leon 1988). Multivariate methods of analysis of G×E interactions consist of a wide range of methods including multivariate analysis of variance (MANOVA), cluster analysis, principal component analysis, additive main effects and

multiplicative interactions (AMMI), GGE-bioplot, geometrical methods and stochastic dominance (Becker and Leon 1988; Gauch and Zobel 1996; Purchase 1997; Yan 2001). Both univariate stability statistics and multivariate methods are based mainly on the analysis of variance, regression methods, or principal component analysis.

1.6.2 G×E interaction and yield stability of sweetpotato

Sweetpotato is very sensitive to environmental changes (Carpena et al. 1980; Bacusmo et al. 1988). Grunerberd et al. (2005) observed variations in the yield and stability in the multi-environmental trials of different genotypes of sweetpotato. A significant G×E interaction was found for the mean storage root weight and storage root yield. However, the contribution of genotype main effects to the total variability was bigger than the environment and G×E interaction effects (Caliskan et al. 2007). The analysis of combined and AMMI analysis of total storage root yield of sweetpotato genotypes revealed high significant effects of genotype, environment and G×E interactions. The genotype mean effects explained 67.9% of the total variation whereas environment and G×E interactions explained 21.0% and 10.4% respectively of total variation (Caliskan et al. 2007). Genotype, environment and G×E interaction effects for average storage roots were significant in combined and AMMI analysis. The genotype mean effects explained 49.5% of the total variation and G×E interactions explained 23.5% (Caliskan et al. 2007). Manrique and Hermann (2000) found that β-carotene content in roots increases with altitude. However, they did not find a high yielding variety with sufficient stability for total root yield. The G×E analysis with regression, AMMI and cluster analysis methods revealed that the G×E interactions for yield traits were larger than genetic variation. However, the G×E interactions for nutritional traits of sweetpotato were small (Grunerberg et al. 2005). Although the presence of significant G×E interactions for wide and specific yield stability and quality of sweetpotato has been reported (Ngeve 1993; Manrique and Hermann 2000; Caliskan et al. 2007), it has been observed that it is difficult to get a variety with wide stability together with high yield and good performance (Affleck et al. 2008).

Breeders and agronomists have to carry out multi-environmental trials to identify the stability and G×E interactions of a new cultivar before its release (Grunerberg et al. 2005). However, multienvironmental trials are very difficult to conduct because of cost of labor and lack of seed or planting materials. Vermeer (1990) and Affleck et al. (2008) suggested that identification of low number of best environments that have ability for differentiating genotypes can reduce the cost of the breeding programme. In this regard, the use of at least one favourable and one unfavourable environment in the early stage of selection of

sweetpotato was proposed to increase beneficial alleles in the breeding materials (Grunerberg et al. 2005). This also requires an appropriate method to quantify the stability across a range of environments.

The comparison of Russell's and Eberhart (1966), Tai's (1971) and biplot approaches in studies of G×E interactions and yield stability of root crops concluded that the biplot analysis presents advantages compared to other methods (Affleck et al. 2008). Caliskan et al., (2007) and Hermann (2005) suggested that the additive main effects and multiplicative interaction (AMMI) approach is the best to evaluate the G×E interactions and stability of sweetpotato genotypes in multilocational trials. In the investigation of G×E interactions and stability analysis of sweetpotato geneotypes, Caliskan et al. (2007) observed a significant correlation between at least one parameter of Russell's and Eberhart, Tai's, and Shukla's methods. The Russell's and Eberhart (1966) and Tai (1971) stability parameters gave similar ranking patterns of genotypes. However, these genotypes were not stable for total storage root yield. It was also found that ranking correlation based on the AMMI stability value (ASV) and coefficient of variation (CV) was similar for average storage root weight and total storage root (Caliskan et al. 2007). This indicates that the AMMI model provides similar information of genotype stability as Russell's and Eberhart, Tai's, and Shukla's methods. Highly significant ranking correlations were found among the deviations from regression, ASV, CV and stability variances (Adugna and Labuschagne 2002). This revealed a close similarity and effectiveness between univariate and multivariate methods to determine genotype stability and G×E interactions. Studies to determine the stability of sweetpotato genotypes in the multilocational trials have revealed that Russell’s and Eberhart (1966), Tai (1971), Shukla (1972) methods give the same results (Bacusmo et al. 1988). Ngeve (1993) using the regression method with Russell’s and Eberhart (1966) and Shukla (1972) approaches to analyse G×E interactions in sweetpotato found irregularity in identifying stable genotypes. Causes of this irregularity were attributed to the use of various regression parameters which interpret stability in different ways. Because of various methods to estimate the G×E interactions and yield stability, most breeders use more than one method to get accurate results (Bacusmo et al. 1988; Caliskan et al. 2007). However, the choice of a suitable method depends on the intended purpose and required outcome.

1.7 Conclusions

Drought stress is one of the yield limiting factors in sweetpotato production causing an annual yield loss estimated at 25%. It is associated with adverse changes at morphological,

physiological, biochemical and moleculear levels among genotypes. These changes are useful indicators in the selection and breeding of drought-tolerant genotypes in sweetpotato. The adoption of new varieties depends on the consideration of end-user's preferences during its development. High dry matter of storage root of sweetpotato is an important characteristic for consumers and processors. Dry matter content above 25% is an important factor for farmers to adopt a new variety of sweetpotato. For industrial use of sweetpotato varieties with a dry matter content that is above 30% of fresh root weight is required. These standards necessitate serious consideration of dry matter content in any breeding programme aiming to develop a new variety of sweetpotato. Further, breeding of sweetpotato for a specific trait requires understanding its genetic mechanism, presence of genetic diversity, efficient crossing and selection methods that lead to identification and development of potential clonal cultivars.

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2. Chapter Two: Farmers' perceptions, production and productivity constraints, preferences and breeding priorities of sweetpotato in Rwanda

Abstract

The role of farmers and their production constraints and preferences are important for sweetpotato breeding and adoption of cultivars and agronomic production packages. The objective of this study was to assess farmers' perception, production constraints, preferences and breeding priorities of sweetpotato in selected agro-ecologies of Rwanda. A total of 495 farmers were surveyed in 2013 in seven representative districts: Bugesera and Kayonza in the Eastern Province, Gakenke and Rulindo in the Northern Province, and Gisagara, Huye and Muhanga in the Southern Province. Data were collected through a participatory rural appraisal (PRA) methodology using a semi-structured questionnaire and focus group discussions. Pairwise comparison of 16 food crops allocated sweetpotato as one of the five important food crops for food security and income generation. Drought stress, unavailability of improved cultivars and planting material, pest and disease damage were perceived to be the five main constraints limiting sweetpotato production, contributing to 17.3, 15.0, 12.9, 11.7 and 11.5%, respectively. The most important sweetpotato cultivar traits were high yield, early maturity, drought tolerance, disease and pest tolerance and good culinary taste at 22.5, 18.5, 15.4, 12.7 and 10.1%, respectively. The characteristics of good storage roots identified by farmers included high dry matter content, good culinary taste, good shape, root size and sweetness representing 27.4, 18.8, 16.1, 11.6 and 9.4%, respectively. Each agro-ecological zone has its own specific sweetpotato production constraints and farmers' preferences, necessitating targeted breeding of different sweetpotato cultivars for each agro-ecological zone, for enhanced productivity and successful adoption of cultivars.

Keywords: Breeding priorities, farmers' preferences, production constraints, sweetpotato

2.1 Introduction

Globally the demand for quantity and quality food is fast increasing due to population growth, limited water and land and overexploitation of available resources (Tilman et al. 2001;

Godfray et al. 2010). Moreover, global climate change aggravates the biotic and abiotic stresses on food crops (Tester and Langridge 2010). These environmental changes will negatively affect crop production and food security. Therefore, novel mitigation strategies are required to boost crop productivity and ensure food security. Improved and resilient crop cultivars and their production technologies are among these strategies (Brown and Funk 2008).

Participatory plant breeding is usually conducted to ensure adoption of newly developed crop cultivars and their production packages by smallholder farmers of marginal agro-ecological and socio-economic groups (Ceccarelli et al. 2007). In the past, plant breeding focused on developing high yielding and improved crop cultivars in favourable environments and under controlled experimental situations (Bänziger and Cooper 2001). As such, conventional plant breeding did not consider farmers' preferences and attributes, locally available germplasm, and the real conditions of small-scale farmers, in pursuit of developing crop cultivars for broad adaptation (Witcombe et al. 1996; Ceccarelli et al. 2000). These failures to engage with the realities faced by local farmers have been identified as the primary causes for the consistently low adoption of newly developed “improved” crop cultivars and their production packages released by government and NGO scientists (Adesina and Baidu-Forson 1995).

There are varied preferences and needs by end users for crop cultivars. For instance, for industrial starch production, sweetpotato cultivars are required to have high dry matter content, while cultivars for human consumption should have other traits such as attractive skin and flesh colour, good cooking quality, and high β-carotene. Sweetpotato cultivars intended for animal feed should have high-protein content (Lebot 2009). Therefore, sweetpotato breeding should involve the needs of stakeholders in developing of new cultivars and new agricultural technologies to meet their diverse requirements (Atlin et al. 2001; Rees et al. 2003).

Agricultural technologies developed through participatory research have a greater chance of adoption and diffusion by farmers because they are developed in response to local constraints, and meet end users needs and preferences (Ashby and Lilja 2004). Various research approaches have been reported in participatory breeding of new crop cultivars, including, consultative approaches, collaborative approaches, collegial approaches and farmer experimentation (Ashby and Lilja 2004). Advantages of farmer participatory research include: 1) co-definition of breeding objectives, 2) participatory evaluation of germplasm, 3) identification of breeding priorities and 4) participatory selection of promising progenies

(Ceccarelli and Grando 2009). In one case, the incorporation of participatory approaches into conventional breeding programmes reduced the time taken for cultivar development from nine to six years (Lilja and Aw-Hasaan 2003).

In sweetpotato breeding, farmers' knowledge and experience during preliminary on-farm and on-station evaluations may enable quick identification of promising genotypes (Abidin et al. 2005). Song (1998) reported that the end-users participation in the improvement of seed systems led to the efficient utilisation of national genetic resources and promoted their production. In selection of high yielding genotypes, Ceccarelli et al. (2009) observed that farmers have the same selection ability as breeders. Therefore, close collaboration between farmers and breeders is necessary to speed up the breeding process and to respond to appropriate needs of stakeholders.

Application of participatory research requires integrated skills (Ceccarelli et al. 2009). A careful choice of research goals, target environments and selection of partners are critical steps of participatory research. It also demands a systematic understanding of different types of participatory research approaches to select the most appropriate tools (Ashby and Lilja 2004) such as participatory rural appraisal, focus group discussions, participatory selection in segregating populations and participatory cultivar testing and selection (Sperling 2001).

Sweetpotato is an important food and feed crop in sub-Sahara Africa and ranks fourth after maize, bananas and cassava (FAOSTAT 2013). It yields considerably well in poor soils and tolerates extreme weather conditions unsuitable for other food crops such as maize and banana (Woolfe 1992). Therefore, it has an important role in food security in many rural families of drought affected environments (Bashaasha et al. 1995). Rwanda is the third in sweetpotato production in East Africa and the first in per capita consumption of sweetpotato in Africa (Chassy et al. 2008). More than 95% of Rwandan farmers grow sweetpotato for household food security (Njeru et al. 2008). During the farming seasons many rural families rely on sweetpotato because of a shortage of other food security crops such as cassava, potato, banana and maize (Gibson et al. 2004; Njeru et al. 2008). Due to its high productivity per unit area and continuous availability, sweetpotato is an ideal food crop for Rwanda, the most densely populated (416 persons/km^2) country in Africa, with limited agricultural land (NISR 2012). The crop requires less production inputs such as fertilizers and pesticides than other major crops (Woolfe 1992). However, the average sweetpotato yield in Rwanda is low, 5.9 $t.ha^{-1}$ wet weight compared to yields of 22.8 and 21.7 5.9 $t.ha^{-1}$ reported in the USA and Japan, respectively (FAOSTAT 2013). This requires targeted participatory sweetpotato

breeding to develop improved and high yielding cultivars, and their production packages, according to the needs of the growers in the country. Therefore, the objective of this study was to assess farmers' perception, production and productivity constraints, preferences and breeding priorities of sweetpotato in selected agro-ecologies of Rwanda. Results of the study may assist in the breeding and sustainable production of sweetpotato in Rwanda and countries with similar agro-ecologies.

2.2 Materials and methods

2.2.1 Description of the study areas

The study was carried out in 2013 in Bugesera and Kayonza districts of Eastern Province, Gakenke and Rulindo districts of Northern Province, and Gisagara, Huye, and Muhanga districts of Southern Province of Rwanda (Figure 2.1). These districts were selected because of the importance of sweetpotato production in their food production (Ndamage et al. 1992). Agriculture is the main economic activity of the selected districts, employing more than 90% of the population. In these districts farmers grow many food crops including beans, sorghum, sweetpotato, bananas and maize (NISR 2010). The Rwanda Agricultural Board (RAB) has promoted cultivation of sweetpotato in these areas to produce raw materials for the Urwibutso Enterprise, which was established for the industrial production of sweetpotato biscuits, cakes, bread and juice (Rwakabuba 2012). In Gisagara, Huye, and Muhanga districts, a range food crops are grown, including sweetpotato which is the main food crop supplied to provincial cities (Kayitare 2006).

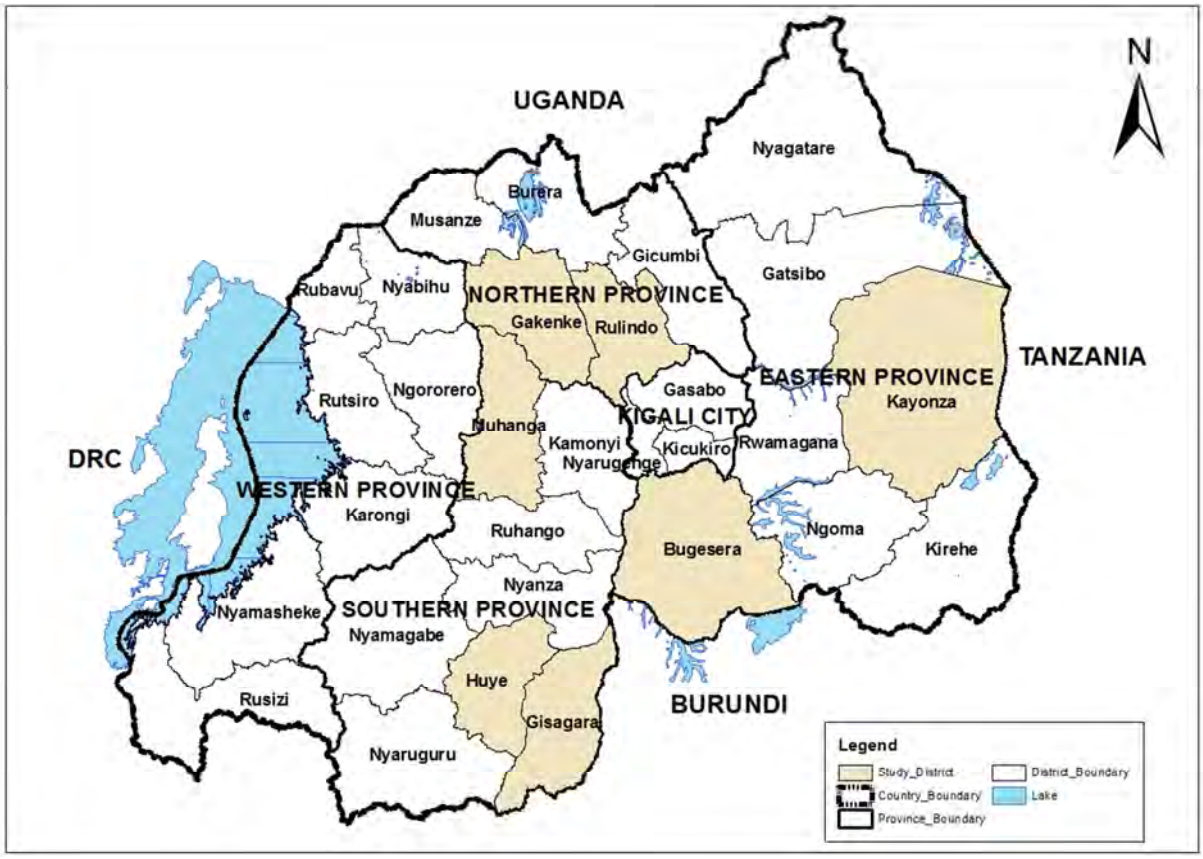

Figure 2.1: A map of Rwanda showing the districts where the survey was conducted.

2.2.2 Sampling method

A multistage sampling was used for the study. Two sectors in each district were sampled. In each sector two villages were sub-sampled and six to eight farmers were randomly selected in each village. This provided a total of 168 farmers for semi-structured interviews. A further 14 focus groups were established with 327 farmers for focus group discussions. Each focus group had between 20 and 26 farmers selected by local leaders and agronomists in each sector. Participants for group discussions were selected to represent the spectrum of individual farmers and farmers from various cooperative associations of the villages, taking into account gender balance.

2.2.3 Data collection

Data were collected using established participatory rural appraisal tools. A semi-structured questionnaire was used in the survey to collect information related to the importance of sweetpotato, constraints affecting sweetpotato production, characteristics of good cultivars, and good storage roots, farmers' agronomic practices, and sources of planting materials.

Different participatory rural appraisal (PRA) approaches were applied to identify periods of sweetpotato production, food availability across the year, the importance of sweetpotato in food security and income generation, farmer's preferences, the most serious constraints affecting sweetpotato and the role of gender in sweetpotato production. Seasonal calendar analyses were used to identify planting and harvesting periods of sweetpotato, the periods of limited availability and overproduction, and the fluctuation of sweetpotato prices on market. Pair-wise and ranking matrices were used to identify the importance of sweetpotato as a food security crop, and as an income generation crop. A matrix scoring method was used following Ceccarelli's (2012) to rank farmers' and consumers' preferences, constraints of sweetpotato production, characteristics of good storage roots and cultivars of sweetpotato, and the role of gender in sweetpotato production in Rwanda. Participants listed the best criteria and data were organised on flipcharts followed by ranking using a fixed number of votes. After votes were given by participants, percentage values of each parameter were calculated.

2.2.4 Data analysis

Data collected were analysed using SPSS (PASW statistics 18.0) computer package (SPSS 2006), Genstat 15th edition (Payne et al. 2011) and Microsoft Excel (Windows Office 2012). Variables were subjected to descriptive statistics, one-sample t-test and cross tabulation and chi-square analyses.

2.3 Results

2.3.1 Demographic description of the study areas

The most important variables and descriptions of farmers chosen for the study are presented in Table 2.1. The number of female respondents was higher than males. Females represented 58.4% while males were at 41.6%. The total number of interviewed farmers during the survey was 168 while 327 farmers were available for group discussions.

In this survey, 67.3% of the farmers had finished primary school, 4.2% had completed post-primary school, 1.4% had attended secondary school and 26.9% were illiterate (Table 2.1). Training in agricultural practices were limited, with only 28.5% of the interviewed farmers having been trained in some agricultural practices by various organizations such as World

Vision and Catholic Relief Services, the Food Agricultural Organisation of the United Nations, and national public agricultural institutions such as the Institut des Siences Agronomique du Rwanda (ISAR), the Rwanda Agricultural Development Authority (RADA) and the Rwanda Agricultural Board (RAB). Most farmers' training had focused on use of agricultural inputs, soil conservation and agronomic crop management.

Table 2.1: Description of sampled farmers from three provinces and seven districts of Rwanda in 2013

Variable	Eastern Province		Northern Province		Southern Province			Total	%	Variance	SD	SE	T-test statistic	CI (95%)	Probability*
	Bugesera	Kayonza	Gakenke	Rulindo	Gisagara	Huye	Muhanga								
Gender															
Female	37	31	49	56	39	36	41	289	58.4	72.2	8.5	3.2	12.9	(33.43, 49.15)	< 0.001
Male	26	19	36	34	38	26	27	206	41.6	46	6.8	2.6	11.5	(23.16, 35.70)	< 0.001
Age															
<25	13	6	7	12	10	0	0	47	9.5	28	5.3	2	3.4	(1.85, 11.65)	0.015
26-40	27	11	25	27	19	21	34	164	33.1	52.6	7.3	2.7	8.5	(16.68, 30.10)	< 0.001
>40	23	33	53	51	48	41	34	284	57.4	119.7	10.9	4.1	9.8	(30.45, 50.69)	< 0.001
Education level															
Illiterate	3	22	32	12	10	21	34	133	26.8	131.8	11.5	4.3	4.4	(8.45, 29.68)	0.005
Primary	56	2	50	78	67	28	26	333	67.3	434.7	20.9	7.9	6.1	(28.48, 67.04)	< 0.001
Post primary	3	0	4	0	0	7	7	21	4.2	9.9	3.1	1.2	2.6	(0.13, 5.94)	0.043
Secondary	0	0	0	0	0	7	0	7	1.4	6.8	2.6	1	1	(-1.42, 3.39)	0.356
Family size															
< 5	27	28	39	47	48	48	34	271	54.7	89.6	9.5	3.6	10.8	(29.90, 47.40)	< 0.001
6 to 10	36	22	46	43	29	14	34	224	45.2	130.1	11.4	4.3	7.4	(21.51, 42.61)	< 0.001
Belongs to association															
Yes	20	6	21	35	39	21	41	182	36.8	161.1	12.7	4.8	5.4	(14.25, 37.72)	0.002
No	43	44	64	55	39	41	27	313	63.2	137.2	11.7	4.4	10.1	(33.90, 55.56)	< 0.001
Trained on agricultural practices															
Yes	10	0	78	20	10	7	17	141	28.5	690.7	26.3	9.9	2	(-4.17, 44.44)	0.089
No	53	50	7	70	67	55	51	354	71.5	432.6	20.8	7.9	6.4	(31.34, 69.81)	< 0.001

(SD: Standard deviation; SE: Sstandard error; CI; Confidence interval; * Probability values based on one-sample t-test)

2.3.2 Farmers' perception and sweetpotato production

Importance of sweetpotato

The results from a pairwise comparison of the 16 food crops grown by farmers (banana, bean, cassava, cocoyam, fruit, Irish potato, maize, groundnut, dry peas, rice, sorghum, soybean, sunflower, sweetpotato, vegetables and yam), revealed that the positions of sweetpotato in terms of food security and income generation varied from one district to another (Tables 2.2 and 2.3). In Bugesera District, sweetpotato ranked fourth as a food security crop after banana, bean and cassava and ranked fifth in income generation. In Kayonza District, sweetpotato ranked fifth after bean, cassava, banana and rice for food security and ranked thirteenth in income generation. In Gakenke District, sweetpotato ranked fourth as a food security crop after banana, bean and cassava and third in income generation. In Rulindo District, it was the fourth food security crop and the fifth in income generation. In Gisagara District, sweetpotato was the third food security crop after banana and cassava and the fifth in income generation. In Huye District, it ranked third for food security after cassava and bean and the sixth in income generation. In Muhanga District, sweetpotato was the fourth after bean, cassava and banana as a food security crop and the sixth in income generation. In all districts of the study, cassava, banana and sweetpotato were among the first five food crops while banana was the only crop ranked among the first five crops in income generation.

Table 2.2: Score (%) of main food crops for food security following a pairwise comparison of farmers (N=327) of three provinces and seven districts of Rwanda

Crop	Province and District							Mean
	Eastern Province		Northern Province		Southern Province			
	Bugesera	Kayonza	Gakenke	Rulindo	Gisagara	Huye	Muhanga	
Bean	21.8	12.5	16.5	17.0	11.5	33.3	17.4	18.6
Cassava	16.4	11.7	15.6	18.4	12.7	26.7	16.1	16.7
Sweetpotato	11.7	9.2	15.2	17.0	12.2	20.0	12.7	14.1
Banana	13.7	10.8	17.4	15.3	13.8	0.0	13.2	12.0
Sorghum	10.9	8.3	3.3	13.3	8.3	13.3	8.8	9.5
Maize	10.9	5.8	2.1	5.5	11.4	6.7	10.1	7.5
Soybean	5.5	2.5	3.3	2.0	6.5	0.0	5.4	3.6
Cocoyam	0.0	5.8	10.3	3.1	1.5	0.0	3.1	3.4
Rice	0.0	10.0	0.0	0.0	8.7	0.0	4.1	3.3
Groundnuts	7.3	3.3	0.0	0.0	1.0	0.0	7.2	2.7
Dry peas	0.0	5.8	6.8	2.0	4.4	0.0	0.0	2.7
Irish potato	0.0	7.5	2.5	4.4	3.1	0.0	0.0	2.5
Yam	1.8	4.2	2.0	2.0	3.2	0.0	1.8	2.1
Vegetables	0.0	0.8	5.0	0.0	1.0	0.0	0.0	1.0
Sunflower	0.0	1.7	0.0	0.0	0.7	0.0	0.0	0.3
Fruits	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 2.3: Score (%) of main food crops for income generation after a pairwise comparison of farmers (N=327) of three provinces and seven districts of Rwanda

Crop	Province and District							Mean
	Eastern Province		Northern Province		Southern Province			
	Bugesera	Kayonza	Gakenke	Rulindo	Gisagara	Huye	Muhanga	
Banana	11.4	9.3	30.3	24.3	18.3	33.3	17.4	20.6
Cassava	22.7	7.6	27.7	12.6	16.6	20.7	16.0	17.7
Bean	29.6	12.7	2.0	13.7	10.7	0.0	15.7	12.1
Sorghum	18.2	6.8	2.0	3.3	4.8	20.0	15.1	10.0
Sweetpotato	6.8	2.5	15.7	10.2	6.5	6.7	9.8	8.3
Maize	2.3	4.2	6.1	10.3	13.2	6.7	5.3	6.9
Rice	0.0	11.9	0.0	0.0	14.7	6.0	6.5	5.6
Fruits	0.0	10.2	7.3	3.2	2.2	0.0	0.0	3.3
Groundnuts	4.6	11.0	0.0	1.5	1.5	0.0	4.5	3.3
Vegetables	0.0	5.9	4.0	5.9	3.0	0.0	3.2	3.2
Dry peas	0.0	5.9	5.0	8.9	1.2	0.0	0.0	3.0
Irish potato	0.0	5.9	0.0	0.0	3.5	6.7	0.0	2.3
Soybean	2.3	3.4	0.0	4.1	2.0	0.0	1.1	1.8
Cocoyam	0.0	1.7	0.0	1.7	1.7	0.0	5.4	1.5
Yam	2.3	0.9	0.0	0.2	0.0	0.0	0.0	0.5
Sunflower	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

2.3.3 Constraints of sweetpotato production

The main constraints of sweetpotato production and their relative importance as reported by farmers during group discussions are presented in Table 2.4. In Bugesera District, drought, shortage of planting materials (vines) and diseases were the three top constraints reported by farmers. Shortage of improved cultivars, drought and pests were the leading constraints of sweetpotato production in Kayonza District. In Gakenke District, drought, diseases and pests were considered the main three sweetpotato production constraints. In Rulindo District, drought, diseases and shortage of vines were regarded as the most important constraints of sweetpotato production. In Gisagara District, farmers reported that drought, pests and shortage of improved cultivars were the main production constraints. In Huye District, pests, drought, and shortage of vines were identified as the most important constraints of sweetpotato production. In Muhanga District, farmers prioritized drought, pest and shortage of vines as the three main constraints of sweetpotato production. Overall, in the surveyed districts, drought stress, shortage of improved cultivars and planting material,

pest and disease damage were the five main constraints of sweetpotato production reported by farmers. These constraints represented at 17.3, 15.0, 12.9, 11.7 and 11.5 %, respectively.

2.4: Constraints of sweetpotato production and their relative importance (%) of three provinces and seven districts of Rwanda

Constraint	Province and District							Mean
	Eastern Province		Northern Province		Southern Province			
	Bugesera	Kayonza	Gakenke	Rulindo	Gisagara	Huye	Muhanga	
Shortage of improved cultivar	11.0	19.8	10.1	6.0	14.6	10.0	10.1	11.7
Shortage of fertilizer	6.6	4.8	3.2	10.1	5.1	2.2	6.2	5.5
Shortage of land	3.0	11.5	10.8	3.0	12.1	9.8	13.3	9.1
Drought	15.7	19.1	17.2	15.7	16.3	17.2	20.1	17.3
Diseases	13.9	11.5	15.0	14.9	12.5	12.0	10.8	12.9
Pests	12.4	16.3	15.1	12.4	15.6	18.1	15.3	15.0
Heavy rain	0.0	0.0	5.0	4.0	2.1	2.0	0.0	1.9
Climate change	4.5	0.0	6.0	5.5	4.5	9.1	3.0	4.7
Training	9.0	2.0	5.3	8.5	5.4	5.3	2.0	5.4
Shortage of planting material	14.8	8.1	9.2	14.8	7.4	11.2	15.3	11.5
Low market demand	9.2	7.0	3.1	5.2	4.4	3.1	4.0	5.1

2.3.4 Farmers' preferences for sweetpotato cultivars and storage root traits

Various characteristics of a good sweetpotato cultivar and a good storage root were identified by respondent farmers (Table 2.5). The most farmers-preferred traits of a sweetpotato cultivar were high yield, early maturity, drought tolerance, disease and pest resistance, good culinary taste, big storage roots, broad adaptability, good appearance of the storage roots, and high vine yield (Table 2.5). These were reflected by the votes for high yield, early maturity, drought tolerance, disease and pest tolerance, and good culinary taste being 22.5, 18.3, 15.1, 12.3 and 10.1%, respectively.

Farmers reported various characteristics of good storage roots such as skin colour (white, cream, yellow, orange, brown, pink, red or purple), high dry matter content, low fibre content, good taste, big size, varied shapes (round elliptic, elliptic, ovate, obovate, oblong, long oblong, long elliptic or long irregular), and sweetness (Table 2.5). However, preferences varied between farmers. The main five characteristics of good storage roots identified by farmers were high dry matter content, good culinary taste, good shape, storage root size and storage root flesh colour with votes of 24.2, 18.4, 14.6, 12.9 and 9.5%, respectively. Farmers grow cultivars with various flesh colours (white, cream, orange, yellow). The value of orange

fleshed sweetpotato is known by farmers but cultivars with white flesh colour dominate other cultivars.

Table 2.5: Preferred characteristics of a good cultivar and storage root of sweetpotato and their relative score (%) by growers in Bugesera, Kayonza Gakenke, Rulindo Gisagara, Huye and Muhanga Districts of Rwanda

	Eastern Province		Northern Province		Southern Province			Score (%)
Cultivar	Bugesera	Kayonza	Gakenke	Rulindo	Gisagara	Huye	Muhanga	
Cultivar preferences								
High yield	19.8	24.8	25.3	19.4	23.3	22.6	22.3	22.5
Earlier maturity	17.7	16.7	17.5	18.7	21.2	17.2	19.4	18.3
Drought tolerance	16.0	15.1	16.8	13.0	13.6	15.5	15.6	15.1
Disease and pest resistance	13.2	13.0	12.4	11.2	11.1	12.0	13.1	12.3
Good culinary taste	9.3	12.5	12.0	10.3	9.2	9.3	8.2	10.1
Big storage root	9.2	11.2	1.6	10.2	9.7	8.9	9.9	8.7
Broad adaptation	3.8	1.8	4.5	4.8	3.8	4.1	3.8	3.8
Good appearance of storage root	3.1	3.1	1.8	4.1	2.5	3.5	3.1	3.0
High vine yield	3.2	1.2	4.1	4.2	3.1	3.6	2.7	3.2
All other traits	4.7	0.6	4.1	4.1	2.6	3.4	2.0	3.1
Storage root preferences								Votes (%)
High dry matter content	24.3	22.8	29.3	23.4	21.3	28.6	19.8	24.2
Good culinary taste	17.4	18.7	17.5	22.7	20.2	14.3	17.7	18.4
Good shape	16.6	15.1	14.7	13.0	13.6	13.5	16.0	14.6
Storage root size	12.1	13.0	12.4	11.2	16.1	11.9	13.2	12.9
Storage root fresh color	9.9	11.2	2.6	12.2	11.7	9.9	9.2	9.5
Sweetness	8.2	12.5	9.2	3.0	7.2	8.2	9.3	8.2
No sweet	3.8	1.8	4.4	2.0	3.8	2.1	3.8	3.1
Less fibers	3.1	3.1	4.6	4.8	3.5	4.5	3.1	3.8
Skin color	3.7	0.2	3.3	6.2	2.1	3.4	3.2	3.2
Others	1.0	1.6	2.0	1.5	0.6	3.6	4.7	2.1

2.3.5 Sweetpotato farming practices

Farmers grew sweetpotato on ridges (48.1%), flat ground (37.5%) or mound (14.4%). About 40.5% of farmers grew sweetpotato in an intercropping system with another crop. Sweetpotato is mainly intercropped with cassava, beans and maize. Farmers prepare cuttings for large scale planting from their own fields or collect vines from fields of neighbours. Production inputs such as fertilisers and pesticides are not commonly used by most of interviewed farmers for sweetpotato cultivation in Rwanda.

2.3.6 Seasonal calendar of sweetpotato production and market

The price of sweetpotato varied among districts and over months (Table 2.6). The price of one kilogram of sweetpotato reported by farmers ranged from 40-160 Rwandese francs (Rwf) (1USD=680 Rwf) at Bugesera, 50-180 at Kayonza, 60-170 at Gakenke, 70-180 at Rulindo, 70-200 at Gisagara, 70-200 at Huye and 70-200 at Muhanga. High market prices were reported in November, December and January when there was a slack while low prices were noted in the months of September, October, March and April during a glut.

Farmers indicated that the availability of sweetpotato is usually limited during the months of November, December, January and February. These periods correspond with the highest market prices for sweetpotato (Tables 2.6 and 2.7). Overproduction and a market glut of the crop occur from April to August (Table 2.7). Other food crops produced during the months of sweetpotato overproduction included bean, rice, sweetpotato, maize, Irish potato, cocoyam, pumpkin, banana, and sorghum.

Table 2.6: Market price variation of sweetpotato (Rwf/kg) in Bugesera, Kayonza Gakenke, Rulindo Gisagara, Huye and Muhanga Districts of Rwanda in 2013

District	Month											
	Jan	Feb	Mar	Apr	May	June	Jul	Aug	Sept	Oct	Nov	Dec
Bugesera	160	130	80	80	110	125	125	120	40	110	160	160
Kayonza	180	130	90	90	110	130	130	120	50	110	180	180
Gakenke	170	140	100	100	100	100	100	90	60	120	170	170
Rulindo	170	150	130	120	120	120	120	100	70	140	180	180
Gisagara	200	160	120	120	120	120	120	100	70	140	170	170
Huye	200	170	100	100	120	140	140	130	70	120	200	200
Muhanga	180	140	120	110	110	110	110	100	70	150	200	200
Average	180	145.7	105.7	102.9	112.9	120.7	120.7	108.6	90	127.1	180	180

Table 2.7: Availability and seasonal calendar of sweetpotato production in Rwanda

Period	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Limited supply	x	x									x	x
Overproduction				x	x	x	x	x				
Planting	x	x	x	x		x	x				x	x
Harvesting			x	x	x	x	x	x	X	x		

(Crosses (x) indicate time of year).

2.3.7 Gender and sweetpotato production

Activities of sweetpotato production are carried out by male and female farmers. However, female farmers contributed more than males in the overall sweetpotato production in Rwanda (Table 2.8). Farmers reported that the management of income derived from the sale of production depends on the market size. In case of big markets, for example during the sale of bulk quantity of sweetpotato such as to a school or factory, income is managed by males in 100% of cases. However, in cases of small markets, for example, selling few baskets of sweetpotato in a local market, the sales are managed by females in 70% of cases.

Table 2.8: Sweetpotato production activities and role of gender of three provinces and seven districts of Rwanda

Activity	Eastern Province		Northern Province		Southern Province	
	M	F	M	F	M	F
Land preparation	42.4	57.7	45.9	54.2	53.7	46.3
Fertilization	44.0	56.1	45.6	54.4	34.2	65.8
Preparation of planting material	5.1	95.0	27.3	72.8	23.0	77.0
Planting	0.0	100.0	10.3	89.7	15.1	84.9
Weeding	22.9	77.1	27.0	73.1	25.0	75.0
Harvesting	19.8	80.2	13.4	86.6	17.8	82.2
Sorting	5.5	94.6	10.9	89.2	9.8	90.2
Cleaning	7.5	92.5	4.1	95.9	5.6	94.4
Selling	16.9	83.2	17.9	82.1	16.8	83.2
Percentage (%)	18.2	81.8	22.5	77.6	22.3	77.7

2.4 Discussion

2.4.1 Use of sweetpotato for food security and income generation

Food insecurity is a major problem in many nations due to biotic and abiotic constraints. According to Tshuma (2012), food security is achieved at various levels such as individual, family, national, regional and global level. Food security encompasses physical and economic access to sufficient quality and quantity food for an active and healthy life. Sweetpotato has been reported to be an important crop in the food security and economy of poor households in the marginal agro-ecological zones (Bashaasha et al. 1995; Githunguri et al. 2006). Bashaasha et al. (1995) observed that farmers' sweetpotato plots contain many cultivars which have various attributes such as maturity periods. Variation in maturity periods contributes to the continuous supply of food over the year. In Rwanda, the contribution of sweetpotato to family food security and income generation varied from one district to another (Tables 2.2 and 2.3). However, in all the study areas sweetpotato was ranked among the top five major food crops.

2.4.2 Constraints to sweetpotato production

In the assessment of priorities for sweetpotato research in developing countries, Fuglie (2007) found common production constraints in almost all the major sweetpotato producing areas. Some constraints were specific to certain regions. Viral diseases, shortage of post-harvest processing technologies, lack of clean planting materials and improved cultivars with high and stable yield potential were the main constraints of sweetpotato production in almost the major sweetpotato producing regions. Sweetpotato weevils and butterflies were the main pests of sweetpotato while drought stress was the most important abiotic stress in Uganda (Bashaasha et al. 1995; Muyinza et al. 2007). Sseruwa (2012) observed that Kabare and Luwero districts of Uganda had similar production constraints. Production constraints of sweetpotato in three regions of Kenya were similar and farmers identified weevils as the major pest, while sweetpotato virus disease (SPVD) as the major disease. Drought was the third among major production constraints reported by farmers (Kivuva 2013). Kapinga and Carey (2003) reported that viral and Alternaria diseases, drought, shortage of planting materials and low soil fertility were the main production constraints of sweetpotato in Rwanda. Unlike previous finings the present study found types and intensity of sweetpotato production constraints differed across districts (Table 2.4). Drought stress, shortage of

improved cultivars and planting material, pest and disease damage were the five main constraints of sweetpotato production reported by farmers in Rwanda.

2.4.3 Attributes of good sweetpotato cultivars and storage roots

The selection of cultivars to be grown by farmers is tightly linked to farmers' preferences and cultivar characteristics. Different storage root characteristics such as storage root formation, root shape, surface defects, latex production, skin and fresh colour, dry matter content, sugar content and culinary taste are positive attributes for farmers' choices of cultivars in Uganda (Gibson et al. 2008). High dry matter content, good shape and culinary taste were the main characteristics of good storage roots in the present study. It was also observed that a good cultivar must have high yields, early maturity and drought tolerance (Table 2.5). In another study, Laurie and Magoro (2008) in South Africa found that the most important traits used by farmers to select good sweetpotato cultivars were sweet taste, dry texture and good yield. Desired traits of sweetpotato identified by Ugandan farmers were high yield, early maturity and high dry matter content of storage root (Sseruwu 2012). Githunguri et al. (2006) observed that yield is the most important selection criterion of a good cultivar of sweetpotato in Kenya. Low fiber and high dry matter content, and taste were the main characteristics influencing the choice of good storage root by Kenyan women farmers (Githunguri et al. 2006). In a participatory cultivar selection, characteristics such as high yield, early maturity and large storage root were the main attributes of a good cultivar (Gibson et al. 2008). High dry matter content is the main characteristic for sweetpotato processors and consumers, while skin colour and root shape are also important traits of preference for sweetpotato cultivars (Rees et al. 2003). These findings reveal that farmers and end-users preferences are diverse. Therefore there is a need for clear communication between breeders and stakeholders for the successful improvement of the crop, with high levels of farmer adoption of new cultivars.

High level of vitamin A deficiency (VAD) prevails in Rwanda especially among women. In the country, 7% of mothers showed some form of night blindness during their last pregnancy. A 5% VAD in a population is reported to be severe (Shaikh and Mahy 2003). To tackle VAD, the Government of Rwanda adopted a scheduled vitamin A supplements in the form of capsules to all children aged from 6 to 59 months. Also a single dose of vitamin A supplement is being given to mothers after two months of delivery. However, this practice is expensive and depends on positive perception by the population towards vitamin A supplementation. Contrastingly, Van Jaarsveld et al. (2005) found that daily consumption of

125 g of orange-fleshed sweetpotato improved the vitamin A need of children in South Africa. This suggests that sweetpotato could play a significant role in circumventing VAD in developing countries as a cheap, alternative and long-term food-based strategy. By virtue of its wide-area production and daily consumption by a large group of the population, promotion of the orange-fleshed sweetpotato cultivars could have substantial effect to combat VAD in Rwanda. Therefore, sweetpotato breeding programs in the country should consider β-carotene content as one of the important traits to develop high yielding and vitamin-A enriched cultivars.

2.4.4 Agronomic management of sweetpotato

In Uganda sweetpotato is cultivated on small plots, mainly in upland areas, during the rainy season and wetland during dry season for vine maintenance (Bashaasha et al. 1995). However, in Rwanda the wetlands are dedicated to cereal crop production, mainly rice and maize, with none of these lands used for sweetpotato production.

Sweetpotato is grown on ridges, mounds or flat ground in Rwanda. The size of ridges and mounds varies and the number of vines per mound and ridge depends on vine sizes. Bashaasha et al. (1995) reported that in highland areas, ridges are used to control soil erosion. In Rwanda, however, the effects of ridging, mounds or flat ground on yield of sweetpotato are not well-documented. Therefore, a detailed study is needed to develop recommendations for proper method of planting and land preparation for all soil conditions, and geographical aspects and gradients of lands.

This study showed that a high proportion (59.5%) of sweetpotato is grown under monoculture, but that it is sometimes intercropped with other crops, mainly cassava, beans and maize. The same observation was reported by Bashaasha et al. (1995). Intercropping is the practice of growing two or more crops together in one field (Khan et al. 2012). The main objective of intercropping is to maximize the land use, to control pests and diseases, to improve ecological protection and to maximize crop output from available land (Malézieux et al. 2009). Intercropping systems may have negative or positive effects on crop yield. Interspecific competition for light and nutrients has been reported in various intercropping systems (Hauggaard-Nielsen et al. 2001; Baumann et al. 2002). The comparison of monoculture and intercropping of cereals and legumes revealed that intercropping is more profitable than monoculture (Zhang et al. 2007). A field experiment to assess the productivity of three sweetpotato cultivars intercropped with three okra cultivars revealed that intercropping generally increased okra plants height, and the number of pods per okra plant.

It was also observed that both pod and storage root yields were not affected by intercropping (Njoku et al. 2007). Ndamage (1984) reported that the most beneficial effects were achieved with intercropping systems of sweetpotato and soybean, sweetpotato and bean, sweetpotato, bean and maize, and sweetpotato, soybean and maize. In intercropping systems, sweetpotato cultivars with few branches were preferred, while in a monoculture system, cultivars with spreading vines were preferable because of their ability to suppress the growth of weeds (Wilson et al. 1989). These attributes of sweetpotato in intercropping systems are profitable and sustainable for food security of small scale farmers.

Farmers use planting materials from their own fields or neighbours. This system may favour pest and disease epidemics. For example, the exchange of planting materials among farmers was reported to be the main cause of persistence and severity of sweetpotato viral diseases in East and Central Africa (Aritua et al. 2007). In sweetpotato production, farmers rarely used purchased inputs and this had negative effects on yields. Therefore, the combination of breeding and improvement of seed production systems and agricultural practices of sweetpotato are needed to enhance productivity.

2.4.5 Seasonal calendar of sweetpotato production

The price of sweetpotato varies through districts and months. In all surveyed districts, the high price was reported in November, December and January while low prices were reported in September, October, March and April (Table 2.6). Patterns of food prices are indicators of food availability (Godfray et al. 2010). In Rwanda, sweetpotato is planted and harvested throughout the year and the peak harvesting month is September. This peak period corresponds with the low price of sweetpotato on the market. During this period, many sweetpotato fields are cleared to plant other crops. Therefore large quantities of sweetpotato are marketed at the same time, leading to low demand and poor prices.

Unavailability of sweetpotato was reported in November, December and January (Table 2.7). This period is marked by food insecurity in many rural families. The main cause of this food shortage is that farmers do not grow crops during the dry spell of May to August. Therefore, during November to January limited crop harvests are available. Moreover, stocks of food crops harvested during September to January, and January to June, have been depleted or finished by then. The period of overproduction of sweetpotato was reported from April to August (Table 2.7). This period corresponds to a high level of food availability from several major crops for many rural families.

2.4.6 Gender and sweetpotato production

The present study showed that female farmers made greater contribution to sweetpotato production than male farmers (Table 2.8). This agreed with findings of Horenstein and Mundial (1989) who reported that sweetpotato is grown by rural households for food and cash, and women play a major role in its cultivation. Women have an important role to ensure household food security. Agriculture is the main activity of smallholders, and women famers who constitute the largest proportion of the smallholder farming system. According to FAO (2000) 96% of rural women work in fields and provide three-quarters of farm labour. As a rule of thumb in rural areas, women tend to focus on food crops and men on cash crops. This ties in with the finding that crop production by women contributed more to household food security than the income from cash crops usually managed by men (Quisumbing et al. 1995). Therefore, to improve food security and to satisfy the food needs of the current growing population, it is necessary to acknowledge the importance of women in food crop production systems and the need to involve women in development of new crop cultivars and agricultural technologies (Carney 1999).

Women participate in the market of agricultural products as suppliers and buyers. They sell different food and cash crops from their farms. However, their responsibility of managing income from agricultural products is limited (Horenstein and Mundial 1989). This study concurred with previous findings, showing that when there is a good market for sweetpotato, income from sales are managed by men, a social dynamic that may demotivate women from sweetpotato production for the cash economy.

2.5 Conclusions

Sweetpotato is among the main food crops of many rural poor households. In Rwanda its contribution in family food security and income generation varies from one district to another. To ensure food security for Rwanda's growing population, strategic sweetpotato production is imperative, gearing towards food security and income generation. Farmers identified the major production constraints of sweetpotato to include drought stress, shortage of improved cultivars, diseases and pests, and shortage of clean planting materials. Quality traits such as high dry matter content of storage roots and early maturity were important attributes for storage root and sweetpotato cultivars, respectively. Therefore, to sustain sweetpotato production, there is a need to breed and release drought tolerant cultivars with high dry

matter and β-carotene content. Further, sweetpotato breeding programme needs to consider all of the documented farmers' preferred traits such as disease and pest resistance, high yield and early maturity.

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3. Chapter Three: Phenotypic characterization of sweetpotato genotypes grown in Rwanda, East and Central Africa

Abstract

Identification of genetic variability and interrelationship among germplasm collections is fundamental in plant breeding programmes to select parents with complementary traits for breeding. The aim of this study was to characterize and identify breeding parents among 54 sweetpotato genotypes grown in Rwanda, East and Central Africa. Genotypes were field evaluated using 26 phenotypic traits under a 9 x 6 unbalanced alpha lattice experimental design with three replications at Karama and Rubona stations in Rwanda. There were significant ($P<0.01$) genotype by site interaction and genotype and site effects on flowering rate, yields of storage roots and vines, harvest index, weight of the largest root per plant and dry matter content. The principal component analysis (PCA) identified seven principal components (PC) that explained 77.8% of total variation present in the genotypes. Nineteen useful traits were identified as the main traits for effective phenotypic characterization of sweetpotato, showing high correlations with the seven PCs. Genotypic variance had the greatest contribution to the total sources of variation for flowering rate (65.3%), yield of storage root (52.4%), vine yields (62.8%), total biomass (56.3%), harvest index (61.1%), weight of biggest root (50.6%) and dry matter content (57.5%). Genotypes K513261, Kwezikumwe, 8-1038 and 2005-110 had the highest flowering rate of 45.0, 20.6, 19.1, and 14.8%, respectively. Suitable genotypes such as K513261, Purple 297, Kwezikumwe and New Kawogo were identified with high storage root yields at 31.9, 28.6, 28.2 and 27.1 $t.ha^{-1}$, respectively. Genotypes Ukerewe, 2005-103, Meresiyana and Mvugamo showed the highest mean dry matter content at 36.5, 35.5, 35.3 and 34.0%, respectively. Overall, genotypes K513261, Kwezikumwe, 2005-020, Otada 24, SPK004, Ukerewe, 2005-110 and 2005-034 were identified as potential breeding parents with superior storage root yield and dry matter content.

Keywords: Central and East Africa, genotype, phenotypic diversity, sweetpotato

3.1 Introduction

Sweetpotato (*Ipomoea babatas* [L.] Lam) is an important food security crop widely grown in the tropics (Woolfe 1992). In sub-Sahara Africa it remains the fourth important crop after cassava, banana and maize (FAOSTAT 2013). Sweetpotato adapts to many agro-ecological zones, with a growing period varying from three to five months, depending on genotype and environment (Afuape et al. 2011). This crop can grow in poor soils with relatively low levels of nutrients when compared to other root crops (Woolfe 1992).

Sweetpotato serves as human food, animal feed, industrial raw material and for biofuel production (Aregheore 2004; Low et al. 2009). In sub-Saharan Africa leaves of sweetpotato are also consumed as a vegetable which is rich in vitamins and minerals (Low et al. 2007; Ma et al. 2009). Sweetpotato has considerable potential to reduce malnutrition and improve food security in many developing countries owing to its comparatively high biomass production and adaptation to harsh growing environments (Hsiao-Feng et al. 2007; Courtney et al. 2008). Further, the crop may serve as a valuable source of income for small-scale farmers.

Identification of suitable genotypes with complementary economic traits is an important step for crop improvement and sustainable crop production (Tseng et al. 2002; Elameen et al. 2011). Understanding the genetic variability and genetic interrelationship present among germplasm collections is valuable to avoid redundancy, and allows plant breeders to select potential parents with desirable traits for cultivar development (Chaudhary and Singh 1982; Yoshida 2004). Afuape et al. (2011) reported that proper management and effective utilization of plant genetic resources depend on detailed understanding of their genetic variability. The failure to identify suitable and potential parents affects the outcome of the breeding programme, which is dependent on the degree of genetic variability present in the source population (Tseng et al. 2002).

Various methods are available to measure the genetic variation among crop genetic resources. These methods rely on the availability of data based on pedigree, plant morphology, agronomic performance, and biochemical and molecular analyses (Mohammadi and Prasanna 2003). Field phenotyping is a common method to determine genetic variation between and within genotypes (Yoshida 2004). Standardized phenotypic descriptors of sweetpotato have been developed (Huamán 1999) and widely used in various genetic studies of sweetpotato (Ngeve 1993; Tseng et al. 2002; Tairo et al. 2008; Elameen et al.

2011). These studies reported the presence of high level of genetic variation for tolerance to biotic and abiotic stresses, and agronomic traits such as foliage development, storage root yields, and dry matter and nutrient content.

Sweetpotato and beans (*Phaseolus vulgalis* L.) are the main staple food crops grown in Rwanda (Ndamage et al. 1992). Sweetpotato is grown by over 98% of the Rwandan farmers across all agro-ecological zones of the country (Ndirigwe 2006; Njeru et al. 2008). It occupies an estimated area of 10% of all the cultivated land in Rwanda grown in both the main and off-seasons (ISAR 2007). In terms of total production, sweetpotato is the third root crop after cassava and potato (FAOSTAT 2013).

Phenotypic markers reflect crop ideotypes, which are relatively cheap and easy to use, depending on prior knowledge of such traits and their expression (Elameen et al. 2011). However, phenotypic traits are highly affected by environmental factors (Elameen et al. 2011). When using phenotypic traits to characterize germplasm, it was recommended to test a set of genotypes across seasons and locations with sufficient replications for a meaningful comparison and selection (Jacoby et al. 2003). A combined use of morphological, biochemical and molecular (DNA) markers has been proposed for genetic diversity studies (Elameen et al. 2011).

Diverse genotypes of sweetpotatoes are being grown in Rwanda. One hundred and thirteen genotypes have been collected and maintained by the National Sweetpotato Research Programme of the Rwanda Agricultural Board (RAB). These collections include landraces, locally bred clones and introductions. However, this germplasm is not well characterized and the genetic diversity present in the collections is not known, which impacts breeding and strategic conservation of the crop. Therefore, the objectives of this study were to determine the phenotypic diversity among Rwandan grown sweetpotato germplasm and to identify superior parents for breeding purposes.

3.2 Materials and Methods

3.2.1 Plant materials

In this study 54 sweetpotato genotypes which are commonly grown in Rwanda were used. The details of the genotypes are presented in Table 3.1. These genotypes were selected from 113 genotypes maintained by the National Sweetpotato Research Programme of

Rwanda, based on their wide adoption by farmers, anecdotal yield potential, and farmers' preferences.

Table 3.1: Descriptions of 54 sweetpotato genotypes used in the study

No	Name	Origin	Skin color	Flesh color	Harvest Plus chart*
1	2000-031	ISAR	Red	Yellow	101U RHS ½
2	2002-153	ISAR	Red	White	-
3	2002-155	ISAR	White	White	-
4	2005-020	NARO	White	White	-
5	2005-034	NARO	Yellow	Orange	7507U RHS 9/3
6	2005-103	NARO	Red	Yellow	600U: RHS 1/3
7	2005-110	NARO	White	Yellow	600U: RHS 1/3
8	2005-133	NARO	Red	White	-
9	2005-146	NARO	White	White	-
10	4-160	ISAR	White	White	-
11	5-214	ISAR	White	White	-
12	8-1038	ISAR	Red	White	-
13	9-466	ISAR	White	White	-
14	97-062	ISAR	Pink	Orange	1355 U RHS 9/2
15	Cacearpedo	ISAR	Yellow	Orange	1355 U RHS 9/2
16	Caroline Lee	CIP	White	Yellow	7401/RHS 5/3
17	Carrote	CIP	Red	Orange	1355U RHS 9/2
18	Cyabafurika 538	NARO	White	Yellow	-
19	Ejumula	NARO - CIP	White	Orange	1355U RHS 9/2
20	Hakizakubyara	Landrace	Red	White	-
21	Imby 3102	CIP	Red	White	-
22	K513261	IITA	Red	White	-
23	Karebe	ISAR	Red	White	-
24	Karibunduki	Landrace	Red	White	-
25	Kawogo	CIP	Red	White	-
26	Kemb 37	CIP	Red	White	-
27	Kwezikumwe	ISAR	Yellow	Yellow	101U RHS ½
28	Magereza	Landrace	Red	White	-
29	Matembere	ARI-Ukiruguru	White	Orange	7507 RHS 9/3
30	Meresiyana	Landrace	Yellow	White	-
31	Mpakanjye	Landrace	White	Yellow	600U RHS 1/3
32	Mugande	ISAR	Red	White	-
33	Mvugamo	Landrace	White	White	-
34	Mwanakumi	ARI-Ukiruguru	Yellow	Yellow	600 U RHS 1/3
35	NASPOT 8	NARO - CIP	Cream	Yellow	-
36	NASPOT 9 O	NARO - CIP	Red	Orange	-
37	NASPOT A	NARO - CIP	White	Cream	-
38	NASPOTw6	NARO - CIP	Red	Orange	7507U RHS:9/3
39	Naveto	CIP	Red	White	-
40	New Kawogo	NAARI	Red	White	-
41	Nsasagatebo	Landrace	White	White	-
42	Nyirabusegenya	Landrace	Red	White	-
43	Nyiragatanga	Landrace	Red	White	-
44	Otada 148	NARO	Yellow	Orange	-
45	Otada 24	NARO	Red	White	-
46	Otada 48	NARO	Red	Orange	-
47	Otada 70	NARO	Red	White	-
48	Otada 96	NARO	Yellow	Cream	-
49	Purple 297	ISAR	Red	Purple	-
50	Purple 4419	ISAR	Red	Purple	-
51	Rukubinkondo	Landrace	Red	White	-
52	Seruruseke	Landrace	Red-purple	Yellow	-
53	SPK004	KARI	Red	Slight orange	1205 U:RHS: 3/3
54	Ukerewe	CIP	Red	Orange	7401U: RHS 5/3

(*Harvest Plus standardized color strips reflecting the total carotenoid content of sweeetpotato, CIP: International Potato Center, NARO: National Agriculture Research Organisation, NAARI: Namulonge Agricultural and Animal Production Research Institute, ISAR: Institut des Sciences Agronomiques du Rwanda, IITA: International Institute of Tropical Agriculture, ARI-Ukiruguru: Ukiruguru Agriculture Research Institute, KARI: Kenya Agriculture Research Institute, -: Data not available).

3.2.2 Study sites

Field trials were established at two locations, Karama and Rubona Research Stations of RAB. The study was conducted during November 2012 to May 2013. Soils were sampled from the study sites and analysed at the soil laboratory of RAB, Rubona station. Details of the study sites ([geographic coordinates and soil composition [pH, total nitrogen, potassium and available phosphorus]) are presented in Table 3.2. Both sites have sandy and clay soil types. During the study the minimum and maximum temperatures were 15.7 and 27 ^{o}C for Karama and 13.4 and 24.9 ^{o}C for Rubona, while the rainfall were 698.7 and 1339.4 mm for Karama and Rubona, respectively.

Table 3.2: Geographic location and soil characteristics of the study sites

Parameters		Description	Karama	Rubona
Geographic and altitude	coordinates	Latitude	S02^{O}16'46.5''	S02^{O}29'03.2''
		Longitude	E030^{O}16'06.2''	E029^{O}45'58.2''
		Altitude (m)	1330	1673
Soil		pH	5.60	5.00
		Total nitrogen (%)	0.48	0.19
		Potassium (meq 100 g^{-1})*	2.30	1.05
		Available phosphorus (meq 100 g^{-1})	0.82	1.77

* meq 100 g^{-1}: Milliequivalent per 100 g of soil.

3.2.3 Experimental design and trial establishment

Experiments were established using a 9 x 6 unbalanced alpha lattice design with three replications at both locations. Vine cuttings consisting of five nodes were prepared and planted on ridges. The distance between rows and plants were fixed at 80 cm and 40 cm, respectively. The size of each experimental plot was 3.84 m^{2}, each with three rows of 7 plants. A sweetpotato variety Kwezikumwe was planted as guard rows of experimental plots. Weeding was carried out two times, one month and three months after planting. No fertilizer and pesticide were applied. The trial at Rubona was established on 6th November 2012 and harvested on 29th April 2013 while at Karama on 16th November 2012 and on 9th May 2013, in that order.

3.2.4 Data collection

Data on flowering ability (flowering rate) were recorded at 30, 60, 90 and 120 days after planting as the percentage of plants which flowered in an experimental plot. Data on yield and yield components were recorded on seven sampled and tagged plants per experimental plot. These data included weight of storage roots, weight of vines, weight of the largest root, total biomass and harvest index, internode length, vine diameter, vine length and vine number. Qualitative data such as storage root formation, storage root shape, skin color of storage root, storage root surface defects, storage root flesh colour, latex production in storage roots and oxidation in storage roots, were recorded during harvest following the method developed by the International Potato Center (CIP) (Huamán 1999). General leaf shape, type of leaf lobes, shape of central lobe and number of lobes were also recorded using the CIP method (Huamán 1999). Dry matter content was determined after modifying the methods described by Carey and Reynoso (1996) and Tairo et al. (2008). Briefly, fresh root samples were collected from three healthy big roots per genotype. Approximately 50 to 55 g of the fresh weight were excised and kept in a paper bag prior to drying. Samples were dried in an oven at 70 ^{o}C for 72 hours. Dried samples were weighed with a sensitive balance and dry matter content determined using the formula: Dry matter content (DM) % = [(Dry weight/Fresh weight) x 100].

3.2.5 Data analysis

All collected quantitative data were subjected to the standard analysis of variance using the GLM procedure of the SAS 9.2 statistical programme (SAS 2004). When significant differences were detected, means were separated using the LSD test procedure at the 5% significance level (Cochran and Cox 1992). Qualitative data were analysed with a non-parametric method of Krusal-Wallis test procedure using SPSS (SPSS 2006). Cluster analysis of 26 phenotypic traits to determine genetic relationships and to identify unique genotypes. The phenotypic traits included in this analysis were yield and yield components (yields of roots and vines, total biomass, harvest index, largest root weight, root number per plant), storage root quality (skin color, storage root defect, fresh color, latex production and oxidation of storage root, dry matter content), vine (internode length, vine diameter, vine length, vine number), leaf (shape of central lobe, leaf general outline, lobe number, leaf lobe type) and inflorescence (flowering rate after first, second, third and fourth month of plating). A similarity matrix was determined using Euclidean distance and a dendogram generated using the nearest neighbor method (Mohammadi and Prasanna 2003). Genotype and

genotype by environment (GGE) interaction of storage root yield, dry matter content, vine yield and total biomass were determined with the GGE-biplot method using GenStat 14th edition (Payne et al. 2011).

3.3 Results

3.3.1 Flowering ability

Analysis of variance on flowering ability of the 54 sweetpotato genotypes is presented in Table 3.3. Genotype and site had significant interaction effects (P<0.01) on flowering rate for records of the first, third and fourth month, and at P<0.05 for the second month after planting. The effect of genotypes was significant (P<0.01) on flowering rate of the first, second, third and fourth months after planting. Also sites exerted significant effect on flowering rate. Genotypes K513261, Kwezikumwe, 8-1038 and 2005-110 showed the highest flowering rates at 45.0, 20.6, 19.1, 14.8%, respectively, while no flowering was observed on some genotypes, such as 2000-031, 2005-103, Otada 96, Otada 48 and NASPOT 9 O (Table 3.4).

Table 3.3: Analysis of variance of flowering rate among 54 sweetpotato genotypes evaluated at Rubona and Karama in Rwanda

		Month after planting			
Source of variation	DF	1st	2nd	3rd	4th
Sites	1	493.78**	459.15*	3115.93**	16.90**
Replications in sites	2	118.17	424.57	680.75	23.73**
Incomplete blocks	6	290.99	209.11	618.38	13.33
Genotypes	53	5271.18**	36776.01**	31301.80**	625.28**
Sites x Genotypes	53	5274.00**	6613.69*	19418.54**	144.67**

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

Table 3.4: Means of yield, yield components and dry matter content of 54 sweetpotato genotypes evaluated at Rubona and Karama in Rwanda

No	Name	Flowering rate (%)	Root yield (t ha^{-1})	Vine yield (t ha^{-1})	Biomass yield (t ha^{-1})	Dry matter content (%)
1	2000-031	0.0	5.8	55.7	61.4	32.8
2	2002-153	0.5	22.8	38.1	60.9	26.0
3	2002-155	0.3	24.3	37.8	62.1	23.9
4	2005-020	9.3	24.7	46.1	70.8	26.7
5	2005-034	2.7	15.4	47.3	62.8	31.8
6	2005-103	0.0	18.4	31.5	49.8	35.5
7	2005-110	14.8	13.5	54.1	67.6	33.2
8	2005-133	1.6	17.6	38.6	56.2	31.5
9	2005-146	0.0	20.1	57.9	78.0	33.1
10	4-160	4.0	17.3	39.9	57.2	31.0
11	5-214	4.2	16.0	34.0	50.0	32.5
12	8-1038	19.1	24.5	54.1	78.6	26.1
13	9-466	0.0	18.8	92.6	111.3	22.3
14	97-062	1.6	23.4	34.6	57.9	21.7
15	Cacearpedo	0.8	17.9	40.5	58.5	31.5
16	Caroline Lee	0.8	14.4	32.8	47.2	30.2
17	Carrote	0.8	14.4	42.6	57.0	29.7
18	Cyabafurika 538	0.5	13.0	26.1	39.1	31.4
19	Ejumula	0.8	17.8	25.7	43.5	29.8
20	Hakizakubyara	1.1	10.8	94.0	104.7	29.6
21	Imby 3102	13.8	19.5	40.0	59.5	31.7
22	K513261	45.0	31.9	42.3	74.2	24.6
23	Karebe	0.0	15.4	47.0	62.3	30.4
24	Karibunduki	0.0	26.6	33.8	60.4	28.2
25	Kawogo	0.8	6.8	52.8	59.6	30.2
26	Kemb 37	0.0	23.4	30.8	54.2	26.7
27	Kwezikumwe	20.6	28.2	37.8	66.0	30.8
28	Magereza	1.3	14.7	37.1	51.7	31.0
29	Matembere	5.8	9.2	29.6	38.7	29.7
30	Meresiyana	0.0	16.2	59.0	75.2	35.3
31	Mpakanjye	0.5	3.1	72.8	75.9	19.0
32	Mugande	1.9	25.2	50.4	75.5	30.0
33	Mvugamo	3.7	3.2	82.0	85.3	34.0
34	Mwanakumi	10.9	18.1	54.9	73.0	28.2
35	NASPOT 8	0.5	19.7	47.0	66.7	30.6
36	NASPOT 9 O	0.0	23.1	36.1	59.2	32.4
37	NASPOT A	3.4	14.6	31.9	46.4	30.0
38	NASPOTw6	14.0	9.9	83.6	93.5	26.5
39	Naveto	0.3	13.2	41.4	54.6	29.4
40	New Kawogo	0.0	27.1	45.9	73.0	29.1
41	Nsasagatebo	4.2	17.4	47.5	64.9	33.3
42	Nyirabusegenya	3.2	2.9	67.6	70.4	25.6
43	Nyiragatanga	0.5	15.3	38.6	53.9	28.4
44	Otada 148	0.3	16.3	38.3	54.6	33.9
45	Otada 24	1.6	23.5	53.9	77.4	32.1
46	Otada 48	0.0	21.1	37.1	58.2	33.9
47	Otada 70	0.8	21.6	85.8	107.4	30.7
48	Otada 96	0.0	13.1	44.2	57.3	30.0
49	Purple 297	0.3	28.6	62.4	91.0	27.3
50	Purple 4419	11.4	12.9	31.3	44.2	30.1
51	Rukubinkondo	0.3	11.9	67.3	79.2	32.8
52	Seruruseke	2.9	13.1	48.5	61.6	30.9
53	SPK004	5.3	10.7	48.8	59.6	33.2
54	Ukerewe	3.2	23.2	24.6	47.8	36.5
	Grand mean	4.6	17.2	47.7	64.9	29.6
	CV (%)	36.6	52.0	43.0	43.0	15.0
	LSD (5%)	8.0	14.4	33.0	33.0	7.1
	S.E.D.	4.1	7.3	16.8	16.8	3.6

3.3.2 Yield, yield components and dry matter content

A summarized analysis of variance on yield and yield components is presented in Table 3.5. The interaction effect of genotypes and sites was significant for storage root and vine yield, harvest index, weight of largest root per plant and dry matter content. Genotypes had significant effect on yields of storage roots and vines and total biomass, harvest index, weight of largest root, storage root number per plant and dry matter content. Significant differences were noted between the two sites on yield of storage roots and vines, harvest index, weight of largest storage root, root number per plant and dry matter content. However, there was a non-significant effect of sites on total biomass (Table 3.5).

Test genotypes expressed a range of variations in yields of storage root and vines, total biomass, and dry matter content (Table 3.4). Genotypes K513261, Purple 297, Kwezikumwe and New Kawogo produced the highest yields of storage roots varying between 27.1 and 31.9 $t.ha^{-1}$. The weight of storage root of genotypes Nyirabusegenya, Mpakanjye, Mvugamo and 2000-031 was minimal ($\leq$5.8 $t.ha^{-1}$). The highest vine yields ranging from 83.6 to 94.0 $t. ha^{-1}$ were observed in four genotypes: Hakizakubyara, 9-466, Otada 70 and NASPOTw6. The vine yields of genotypes Ukerewe, Ejumula, Cyabafurika 538 and Matembere was < 29.6 t ha^{-1}. Genotypes: 9-466, Otada 70, Hakizakubyara, and NASPOTw6 showed the highest total biomass that ranged between 93.5 to 111.3 t ha^{-1}. Genotypes: Matembere, Cyabafurika 538, Ejumula and Purple 4419 had the least total biomass of < 44.2 t ha^{-1}. The highest dry matter content of 34.0 to 36.5% was observed in genotypes Ukerewe, 2005-103, Meresiyana and Mvugamo, while DMC of < 22.3% was recorded in genotypes Nyirabusegenya, Mpakanjye, 97-062 and 9-466. Overall, genotypes at the Rubona site had the higher mean values of flowering rate, root yield and dry matter content while at Karama site they exhibited higher vine yields and total biomass (Table 3.6).

Table 3.5: Analysis of variance of yield and yield components among 54 sweetpotato genotypes evaluated at Rubona and Karama in Rwanda

Source of variation	DF	Storage root yield	Vine yield	Total biomass	Harvest index	Largest root weight	Root number per plant	Dry matter content
Sites	1	2454.76**	7264.91**	1273.66	0.72**	2218004.56**	115.92**	2497.83**
Replications in sites	2	397.52**	477.18	126.85	0.1	40238.06	2.38	109.07
Incomplete blocks	6	1932.83	3950.68	7535.61	0.20**	356604.9	5.01	115.67
Genotypes	53	12871.35**	85074.88**	71748.48**	3.48**	5452938.75**	113.76**	7152.49**
Sites x Genotypes	53	6886.73**	38791.47**	46841.45*	1.20**	2715942.88**	40.29	2565.25**

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

Table 3.6: Grand mean and standard deviation of yield and yield components of 54 sweetpotato genotypes when evaluated at Rubona and Karama in Rwanda

Sites	Flowering rate (%)	Root yield (t ha^{-1})	Vine yield (t ha^{-1})	Biomass yield (t ha^{-1})	Dry matter content (%)
Karama	3.01 ± 5.06	14.49 ± 7.98	52.43 ± 24.52	66.92 ± 23.98	26.79 ± 6.36
Rubona	5.1 ± 11.24	19.99 ± 8.63	42.96 ± 14.81	62.96 ± 15.78	32.34± 4.69

Values: mean ± standard deviation.

3.3.3 Genotypic relationship

The genetic clusters showing relationship among 54 sweetpotato genotypes using 26 phenotypic traits are presented in Figure 3.1. The cluster analysis revealed eight principal clusters designated from I to VIII among tested sweetpotato genotypes. The dissimilarity distance varied from 0 to 25% among test genotypes.

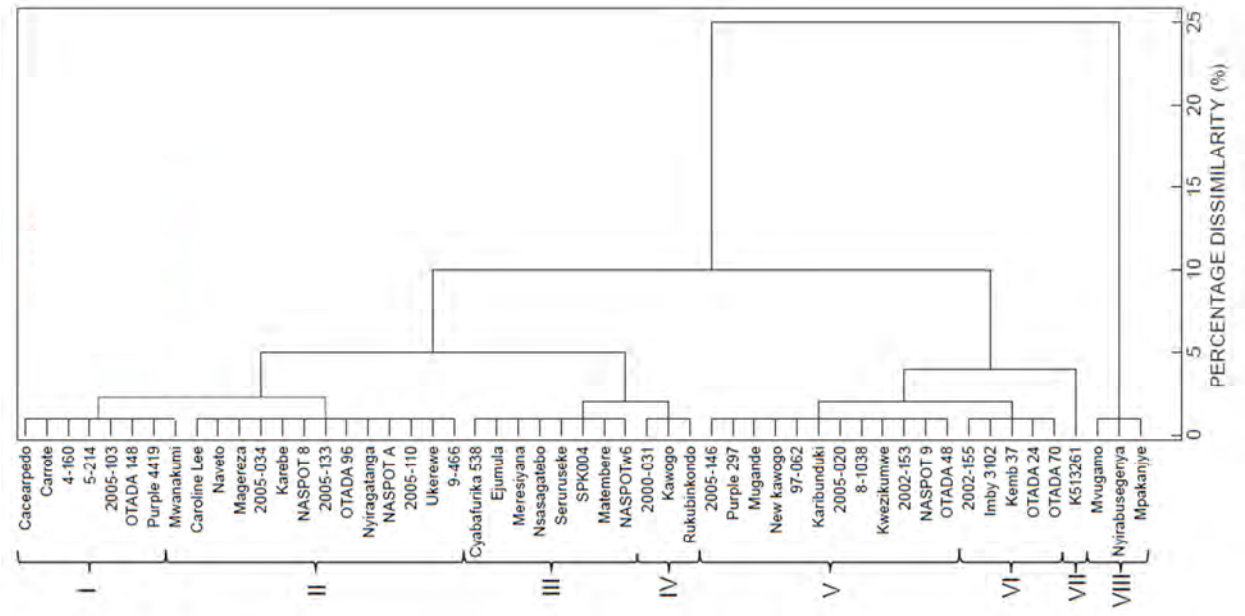

Figure 3.1: Dendrogram showing principal genetic clusters of 54 sweetpotato genotypes evaluated at Rubona and Karama in Rwanda using 26 phenotypic traits.

Genotype and genotype by environment (GGE) interaction biplots are presented in Figure 3.2 A, B, C and D on storage root yield, dry matter content, vine yield and total biomass. The first principal component (PC1) representing genotypic effect explained 65.07, 78.02, 80.17 and 73.40% of the total variation of storage root yield (A), dry matter content (B), vine yield

(C) and total biomass (D), respectively. Whereas, PC2, representing test sites had a relatively low contribution to the total variation than genotypic effect (Figure 3.2). The Karama site had the longest vector for dry matter content, vine yield and total biomass while the Rubona site had the longest vector for storage root yield. The length of an environment vector is proportional to the standard deviation of cultivar means in the environment, which is a measure of the discriminating power of the environment. Test environments with longer vectors have strong discriminating power of genotypes (Yan et al. 2007). Subsequently, Figure 3.2 shows that genotypes could be well-differentiated at Karama site based on dry matter content, vine yields and total biomass while at Rubona with storage root yields.

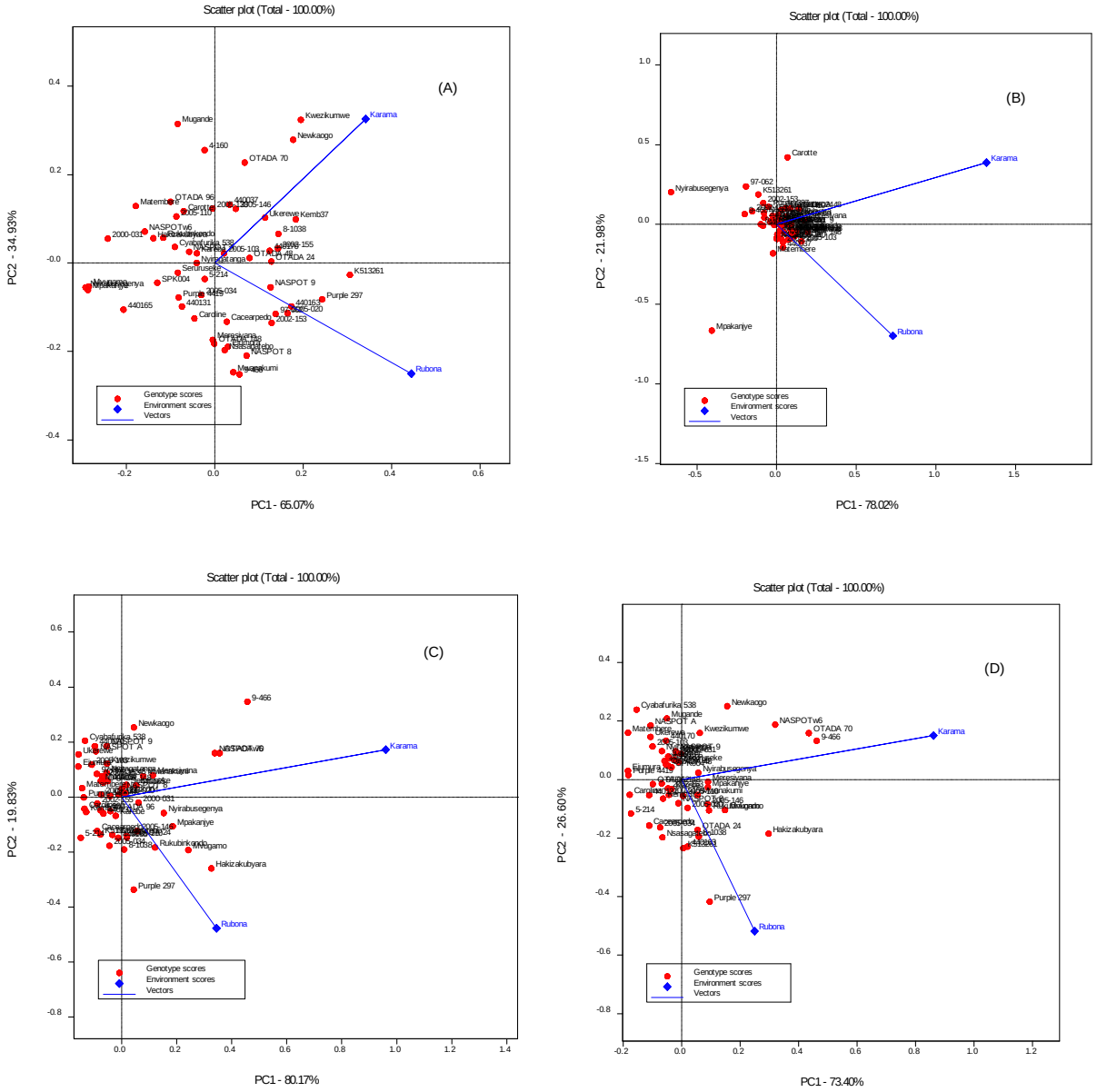

Figure 3.2: GGE biplot based on storage root yield (A), dry matter content (B), vine yield (C) and total biomass (D) of 54 sweetpotato genotypes tested at Karama and Rubona in Rwanda.

3.3.4 Principal component analysis

The PCA revealed seven main principal components representing 77.83 % of total variance among the 54 genotypes of sweetpotato (Table 3.7). The first four principal components explained 17.51, 15.92, 13.95, and 10.00 % of the total variance, respectively. These components represented 57.38 % of the total variance components (Table 3.7). Strong correlations were observed between PCs and phenotypic traits (Table 3.7). PC1 correlated better with leaf characteristics such as leaf general outline, leaf lobe type, lobe number and shape of central lobe while PC2 was well-correlated with flowering rate. PC3 has a strong relationship with storage root yield, weight of the biggest storage root and harvest index. PC4 correlated mainly with latex production and oxidation of storage root. Vine yield and total biomass had a stronger association with PC5. PC6 showed negative associations with vine and internode length. Finally PC7 showed positive correlations with skin color and storage root formation. Among the 26 phenotypic traits used in the current genetic diversity study, the PCA identified only 19 phenotypic traits with strong correlations with the seven principle components.

Table 3.7: Correlations between phenotypic traits of sweetpotato and main principal components generated using 26 traits and the rotation method of Varimax with Kaiser Normalization

Trait	Component						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Biggest root weight	-0.05	0.13	**0.91**	0.12	0.02	0.09	0.15
Dry matter content	0.13	-0.10	0.01	0.61	-0.09	-0.06	0.38
Flowering rate of first month	-0.01	**0.83**	0.10	-0.28	0.16	0.13	-0.01
Flowering rate of fourth month	0.10	**0.88**	-0.03	-0.08	-0.02	-0.11	0.02
Flowering rate of second month	0.05	**0.91**	0.21	-0.02	-0.06	0.13	-0.06
Flowering rate of third month	0.02	**0.89**	0.09	0.01	0.05	-0.13	0.06
Harvest index	-0.04	0.05	0.83	0.15	-0.40	0.23	0.10
Internode length	-0.15	0.04	-0.08	0.09	-0.04	**-0.88**	-0.19
Latex production	-0.15	-0.05	0.16	**0.91**	-0.01	0.11	-0.02
Leaf general outline	**0.94**	0.01	-0.04	-0.06	-0.02	0.02	-0.09
Leaf lobe number	**0.94**	0.11	-0.09	-0.01	0.07	0.09	-0.09
Leaf lobe type	**0.96**	0.07	-0.08	0.07	-0.03	0.09	-0.06
Oxidation	-0.09	-0.12	0.10	**0.93**	-0.03	0.04	0.02
Root number per plant	-0.07	0.01	0.11	0.03	-0.07	0.65	-0.20
Root shape	0.25	0.11	-0.51	0.29	-0.06	0.37	-0.20
Shape of leaf central lobe	**0.95**	0.00	-0.03	0.08	-0.04	0.02	-0.06
Skin color	-0.18	0.02	0.08	0.07	-0.05	-0.10	**0.86**
Storage root defect	-0.04	-0.42	0.23	-0.03	0.29	-0.04	-0.30
Storage root formation	-0.18	0.08	0.24	-0.02	-0.02	0.10	**0.79**
Storage root fresh color	0.20	-0.04	0.02	0.46	-0.16	-0.01	-0.05
Storage root yield	-0.08	0.16	0.92	0.16	-0.04	0.17	0.08
Total biomass	-0.01	0.08	0.04	-0.11	**0.94**	-0.06	-0.08
Vine diameter	-0.23	-0.14	-0.24	-0.14	0.52	0.32	0.29
Vine length	-0.14	-0.03	-0.11	-0.13	-0.01	**-0.88**	-0.10
Vine number	0.12	0.01	0.17	0.12	0.52	0.19	0.51
Vine yield	0.02	0.01	-0.32	-0.17	**0.89**	-0.12	-0.10
% of explained variance	17.51	15.92	13.95	10	7.48	6.75	6.21
Cumulative % of explained variance	17.51	33.43	47.38	57.38	64.87	71.62	77.83

(Bold faced scripts show component score coefficient matrix: The high value indicates a high correction between the trait and the PC).

3.4 Discussion

3.4.1 Phenotypic traits

In this study, the interaction effect of genotypes and sites were significant for flowering ability, yield of storage roots and vines, harvest index, weight of largest storage root, and dry matter content (Tables 3.3 and 3.5). Hafekamp (1988) reported that rainfall, temperature, light and soil nutrients are the main factors affecting plant growth and productivity. Environmental differences between Karama and Rubona (Table 3.2) and the inherent genetic variation present among test genotypes are principal causes of variability in yield responses. Crop genotypes have varied conversion efficiency given similar environmental resources (George et al. 2002). The variation in genetic constitution of crop genotypes influences the expression and level of heritable traits between and within environment (Acquaah 2007).

In the current study, sites had significant effects on yield and yield components. Tairo et al. (2008) observed that number of roots, weight of roots, fresh weight per plant and dry matter content of sweetpotatoes differed significantly among and within agro-ecological zones. This was also confirmed in the present study where sites differed significantly in affecting flowering rate, yields of storage roots and vines, harvest index, largest root weight, root number per plant and dry matter content (Tables 3.3 and 3.4). The significant differences of sites may be attributed to soil heterogeneity and environmental conditions (Table 3.2). A slight difference in soil nutrients was observed between Karama and Rubona sites (Table 3.2). Karama site was rich in total nitrogen and potassium. High soil fertility is reported to favour vegetative growth while decreasing formation of storage roots (Okpara et al. 2009). The high vine yields and total biomass recorded at the Karama site (Table 3.6) could be attributed to better soil fertility than the Rubona site.

Dry matter content of sweetpotato may increase with application of potassium fertilizer (George et al. 2002). This observation is different from the results of this study. The soil at Karama site contained a high potassium level (Table 3.2). However, in the present study the mean dry matter content of sweetpotato storage roots was low (26.8%) compared to the Rubona site (32.3%) (Table 3.6). Hartemink et al. (2000) contended that as rainfall increased the storage root yield of sweetpotato decreased. This observation is contrary to the result of this study. The rainfall of the Karama site during the experiment was 698.7 mm which was significantly less than the Rubona site (1339.4 mm). However, genotypes at the Rubona site

had remarkably high yields of storage roots (Table 3.6). Thus, it is important not to rule out the influence of multiple factors which may impact crop yields when tests are carried out under different environmental conditions.

Test genotypes showed broad variation in yields of storage root and vine, total biomass, dry matter content and flowering rate (Table 3.4). Genetic diversity analysis of sweetpotato using morphological and molecular markers revealed that all the characters evaluated were significantly different between genotypes (Karuri et al. 2010). Fongod et al. (2012) observed significant differences among sweetpotato accessions in agronomic and morphological characters. Using molecular, morphological and agronomic characterization methods, Maquia et al. (2013) observed a high level of genetic diversity in Mozambican sweetpotato germplasm. Gasura et al. (2010) observed that some of their test sweetpotato genotypes had strong or weak flowering ability while others failed to flower. Extreme phenotypic variations observed in his study confirm the presence of considerable genetic variations among sweetpotato genotypes in Rwanda. Sweetpotato shows broad phenotypic and genotypic diversity because of its inherent cross pollination owing to self- or cross-incompatibility, polyploidy and heterozygosity (Jones et al. 1986; Yoshida 2004). Lebot (2009) argued that the yield of sweetpotatoes could be determined by the length of the growing period. Across the present study sites growing periods were almost similar for all genotypes. Therefore, the broad variations observed among genotypes could be attributed to differences in genetic constitution.

The current study revealed that the effect of genotype and site were significantly different for flowering rate (Table 3.3). The within-plot variation for flowering rate indicates a high level of genetic variability among the test populations. Most sweetpotato genotypes flower naturally within the short day length of the tropics (Miller 1937; Jones et al. 1986). Sweetpotato flowers best during the cool season in tropical countries. The average daily temperature that favors seed set is between 20 and 25°C while maximum seed set occurred when the mean daily temperature was about 23.9◦C (Lebot 2009). Several techniques such as physiological shocks, grafting, girdling, chemical treatment and use of controlled environmental conditions help improve flowering in sweetpotatoes. Flower and seed production is enhanced under tropical than temperate climates (Jones et al. 1976). In general, flowering ability and seed set have important implications on sweetpotato breeding.

3.4.2 Genetic relationships among sweetpotato genotypes

Knowledge on genetic distance between potential parents is important for breeding (Acquaah 2007). Plant breeding programs require sufficient genetic diversity for designed crosses and creating new genetic recombinants. This enables selection of segeregants with better quantitative or qualitative responses such as yield or resistance to abiotic and biotic stresses (Korzun 2003).

Fongod et al. (2012) showed that cluster analysis of 19 sweetpotato genotypes using 26 characters revealed the existence of three major groups with a similarity index ranging from 0.42 to 1.00 before maturity and 0.34 to 1.00 at maturity based on the Euclidean distance. In cluster analysis of Tanzanian elite sweetpotato genotypes for resistance to sweetpotato virus disease and high dry matter content, Tairo et al. (2008) found two major groups with a low genetic similarity of 0.52. Also, significant differences between genotypes and genetic distance ranging from 0.26 to 0.80 were reported during morphological characterization of eight genotypes of *Solanum retroflexum* (Jacoby et al. 2003). A cluster analysis using morphological and SSR Markers separated some Kenyan sweetpotato genotypes into two major groups (Karuri et al. 2010). In this study, genotypes were assorted into eight main clusters (Figure 3.1) and a dissimilarity distance ranging from 0 to 0.25.

Preliminary evaluation of sweetpotato based on horticultural traits may assist in identification of unrelated parents for specific breeding programmes. These unrelated genotypes may contribute distinctive alleles from different loci (Dhillon and Isiki 1999). Based on high yields, dry matter content and flowering rate, the current study identified genotypes such as Ukerewe and 2005-034 (cluster II), SPK004 and 2005-110 (cluster III), Otada 24 (cluster IV), Kwezikumwe and 2005-020 (cluster V) and K513261(cluster VII) as potential parents for sweetpoato breeding towards high yield and dry matter content.

3.4.3 Principal component analysis

Principal component analysis (PCA) was applied as a statistical approach to identify the major variance components, their contributions and correlated traits (Heberger et al. 2003). This method assists in reducing the number of variables in the data collection in a breeding and selection process. Consequently, it saves time and resources and improves the selection responses in crop improvement programs (Johnson and Wichern 2007). Through this method, few variables explaining variations among individuals are identified among

various characters (Shimelis et al. 2013). Therefore, the PCA provides valuable information when there are several correlated traits, by reducing the costs of screening.

Principal component analysis assists in determining the relationships between traits, and the independent principal components that are effective on plant traits (Beheshtizadeh et al. 2013). In the evaluation of diversity among potato cultivars using agro-morphological and yield components, Ahmadizadeh and Felenji (2011), observed that three components explained 80.1% of the total variation among traits. The authors reported that the first PC was highly correlated with yield, tuber weight, dry matter content and harvest index. This PC was very important to select high yielding clones and parents for breeding programs. In the principal component analysis of 21 sweetpotato genotypes using 17 traits, Afuape et al. (2011) found three PCs explaining 76% of total variance. They also observed that the number of marketable and unmarketable roots, total number of roots, weight of marketable and unmarketable roots, total root weight, incidence and severity of root *Cylas* spp, length of biggest, medium and smallest marketable roots and number of branches are traits that are important to differentiate sweetpotato genotypes (Afuape et al. 2011).

In an agro-morphological characterization of different accessions of sweetpotato, Fongod et al. (2012) identified four main components before maturity and five main components at maturity, explaining 78.2 and 76.4%, respectively, of the total genetic variability. The PCA revealed seven main principal components representing 77.83 % of total variance among the 54 genotypes of sweetpotato (Table 3.7). The first four principal components explained 17.51, 15.92, 13.95, and 10.00% of the total variance, respectively. These components represented 57.38 % of the total variance components (Table 3.7). Strong correlations were observed between PCs and phenotypic traits (Table 3.7). PC1 is well-correlated with leaf characteristics, such as leaf general outline, leaf lobe type, lobe number and shape of central lobe while PC2 correlated with flowering rate. PC3 has a strong relationship with storage root yields, weight of the biggest storage root and harvest index. PC4 correlated fairly well mainly with latex production and oxidation of storage root. Vine yield and total biomass had a stronger association with PC5. PC6 showed negative associations with vine and internode length. Finally PC7 showed positive correlations with skin color and storage root formation. Among the 26 phenotypic traits used in the current study, the PCA identified only 19 phenotypic traits with strong correlations with the seven principle components.

3.5 Conclusions

The present study provided a preliminary analysis of the genetic diversity among 54 sweetpotato genotypes widely grown in the different agro-ecological zones of Rwanda using agro-morphological traits. Results showed a broad range of variation in root yield, weight of the largest root, number of roots per plant, dry matter content, vine yield and flowering rate among genotypes. Therefore, the studied genotypes represent a rich diversity that can serve as a basis for genetic improvement. Findings of this study need to be complemented through molecular characterization. Considering traits such as high yield, high dry matter content and flowering rate, this study identified sweetpotato genotypes K513261, Kwezikumwe, 2005-020, Otada 24, SPK004, Ukerewe, 2005-110 and 2005-034 as potential parents for genetic enhancement and breeding towards high yield and dry matter content.

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4. Chapter Four: Comparison of greenhouse and *in-vitro* screening of sweetpotato genotypes for drought tolerance

Abstract

Breeding sweetpotato (*Ipomoea babatas* [L.] Lam) for drought tolerance is hindered by unavailability of less expensive, reproducible and high throughput screening systems and the inherent quantitative inheritance of drought tolerance. Various methods are applied to screen for drought tolerance such as field, greenhouse or in-vitro techniques. The objective of this study was to compare greenhouse and in-vitro techniques for effective selection of drought tolerance in sweetpotatoes. Greenhouse and in-vitro experiments were established at Rubona research station of the Rwandan Agricultural Board using 54 sweetpotato genotypes. Genotypes were evaluated in the greenhouse using four levels of water regime [control, drought stress imposed by withholding water for one, two or three month(s)] while in-vitro tests were carried out using four treatment solutions [control or basic culture medium (0 M), control supplemented with 0.2, 0.4, or 0.6 M sorbitol]. In the greenhouse study, data collected included: soil water potential (Ψ_w), weights of storage root, biggest storage root and vines, dry matter content (DMC) of storage root and vine, and water content (WC) of vines. Whereas Ψ_w of culture media, fresh weight gain (FWG), DMC and WC were recorded during the in-vitro experiment. In the greenhouse test, Ψ_w of drought stressed treatments varied from -1.94 to -0.05 MPa and showed an increased trend with prolonged drought stress. The control treatment showed Ψ_w ranging between -0.02 to 0 MPa. During the in-vitro experiment, the mean Ψ_w values were - 0.07, - 0.81, -1.35 and -1.73 MPa for control, 0.2, 0.4, and 0.6 M sorbitol treatments, respectively. Under greenhouse conditions, genotypes by water regimes, genotype and water regime had significant effects ($P \leq 0.01$) on yield and yield related traits. Genotypes showed significant differences between the control and drought stress imposed for one month. Under in-vitro test, the control and 0.2 M sorbitol treatments were not significantly different in the FWG. However, the control treatment was significantly different from 0.4, and 0.6 M sorbitol concentrations. Positive correlations were observed between vine yield and FWG; and between total biomass and FWG, during greenhouse and in-vitro studies, respectively. Overall, genotypes 2005-146, 4-160, 8-1038, Karibunduki, Kwezikumwe, Purple 4419, NASPOT 9 O, Nsasagatebo, Karebe, IMBY 3102, Mwanakumi, 97-062 and Matembere were selected with comparatively high drought

tolerance using the two screening procedures. The selected genotypes are useful genetic resources to breed sweetpotatoes for drought tolerance.

Key words: Drought tolerance, greenhouse, in-vitro, sorbitol, sweetpotato

4.1 Introduction

Sweetpotato (*Ipomoea babatas* [L.] Lam) is an important crop widely grown in tropical and subtropical regions of the world (Woolfe 1992). It is estimated to be cultivated on an area of 2.1 million hectares with annual global production of 9.9 million tons (FAOSTAT 2013). Sweetpotato is grown for human food, animal feed and raw material for industries. In many tropical countries, sweetpotato is the second important root crop after cassava (FAOSTAT 2013). It is a highly productive crop per unit area and grows under variable climatic conditions making it an ideal crop in harsh environments (Haimeirong and Kubota 2003). Sweetpotato has a very important role to alleviate malnutrition and poverty (Woolfe 1992; Gasura et al. 2010). The aboveground part and by products of processed sweetpotato are commonly used as animal feed (Woolfe 1992). With the on-going initiative of biofuel production, sweetpotato is an alternative crop because of its high starch production per unit area (Lebot 2009).

Sweetpotato has a short growing period varying from 3 to 5 months depending on variety and location (Woolfe 1992). During this growth period, the crop faces water stress due to fluctuations of soil water content. For instance, in Rwanda, there is high yield loss of sweetpotato during the off season (April/May to September/October) production owing to severe drought occurrences during June to September. Yield loss and subsequent food insecurity in the major sweetpotatoes growing areas are primarily attributed to inadequate soil moisture and limited water availability (Sherrard and Maherali 2006). Low soil moisture content during the critical growth stages such as crop establishment and root initiation is responsible for poor crop growth and productivity (Pantuwan et al. 2002). The annual and global yield loss due to drought stress was estimated at 25% (Woolfe 1992). Under field experiment, Gong and Wang (1990) observed that drought stress for 20 days during root formation of sweetpotato caused yield reductions ranging from 15 to 39%.

The use of irrigation water is an alternative approach to manage drought stress under rain-fed crop production systems such as in Rwanda. This approach seems to be expensive, unsustainable and unaffordable by smallholder farmers. Moreover, the availability of clean

water for irrigation is critical because of exponential global population growth and climate change (Acquaah 2007). Other cultural practices such as mulching, fallowing and use of ground cover are commonly applied to preserve soil moisture (Acquaah 2007). Various international and national policies were adopted to counterattack the threat of drought stress such as promoting standard approaches to assess impact of drought stress, implementing effective systems of drought monitoring, early warning systems and emergency response and recovery (Gommes et al. 2010). Breeding for drought tolerance remains the most sustainable, feasible and economic approach to drought management. Therefore, to support the alternative management approaches, it is needed to develop and deploy new varieties with drought tolerance and high water use efficiency (Ober 2008).

Breeding for drought tolerance requires identification of suitable genetic resources, a controlled stress screening environment and high throughput selection methods to maximize selection gains (Subbarao et al. 2005). Owens (2001) reported that crop productivity has to increase by 60 and 20% in the developing and developed countries, respectively, to ensure food demand. The use of improved crop varieties with drought tolerance, and suitable agricultural practices are considered as appropriate approaches to crop production in arid and semi-arid areas (Ashraf and Harris 2005). Hence, breeding for drought tolerance is one of main objectives of plant breeding programs to improve food security.

Breeding of sweetpotato for drought tolerance is challenged by unavailability of inexpensive, reproducible and high throughput screening systems and the inherent quantitative inheritance of drought tolerance. Consequently, limited progress has been made in identifying genetic determinants of drought tolerance in sweetpotato. Drought tolerance has complex physio-biochemical processes at cellular level and its expression varies across different stages of plant development (Ekanayake and Wanda 2004; Andrade et al. 2009; Lebot 2009). Different screening approaches are suggested for drought tolerance such as field trials aiming at agronomic traits and laboratory experiments involving early traits for selection (Acquaah 2007; Gopal and Iwama 2007; He et al. 2009). Pot experiments to screen for drought tolerance in sweetpotato revealed that plant biomass, main stem length, internode diameter, internode length, leaf number and area, and root weight decreased in response to severe water stress (Saraswati et al. 2004). Greenhouse drought stress for 5 and 10 days after transplantation reduced the number of storage roots by 42% and 66%, respectively, compared with the control. Drought condition in the field resulted in a 49% reduction in storage root yield compared to irrigated conditions (Solis et al. 2014). Wang et al. (1999) found that the accumulation of amino acid levels such as alanine, glutamic acid and its derivatives, and starch were high in stressed cell compared to normal cells in

suspension cultures. In-vitro selection for identification of the salt tolerance of 276 sweetpotato clones, revealed 18 clones showing significantly higher in-vitro salt tolerance than control plants. When these salt tolerant clones were further tested under greenhouse conditions using solutions containing different concentrations of NaCl, only 3 clones showed salt tolerance with better growth and rooting ability than other clones and control plants (He et al. 2009). Therefore, combined use of different screening approaches targeting early and later growth stages of sweetpotato may assist in the selection of drought tolerant clones for breeding. Field selection for drought tolerance is often problematic because the balance of soil humidity is variable from season to season and year to year even at the same site. Selection under managed environments such as greenhouse and in-vitro are alternative approaches to improve selection gains. Therefore, the objective of this study was to compare greenhouse and in-vitro techniques for effective selection of drought tolerance in sweetpotatoes under managed condition and using early and late traits.

4.2 Materials and methods

4.2.1 Plant materials

The study used 54 sweetpotato genotypes described in Table 4.1. These genotypes were collected from the National Sweetpotato Research Program of the Rwandan Agricultural Board (RAB). A drought tolerant sweetpotato clone, Mugande, selected by the International Potato Center (CIP) based in Nairobi (Kenya) served as a control (Table 4.1, entry 32).

Table 4.1: Descriptions of sweetpotato genotypes used in the study

No	Name	Origin	Skin color	Flesh color	Harvest Plus chart*
1	2000-031	ISAR	Red	Yellow	101U RHS ½
2	2002-153	ISAR	Red	White	-
3	2002-155	ISAR	White	White	-
4	2005-020	NARO	White	White	-
5	2005-034	NARO	Yellow	Orange	7507U RHS 9/3
6	2005-103	NARO	Red	Yellow	600U: RHS 1/3
7	2005-110	NARO	White	Yellow	600U: RHS 1/3
8	2005-133	NARO	Red	White	-
9	2005-146	NARO	White	White	-
10	4-160	ISAR	White	White	-
11	5-214	ISAR	White	White	-
12	8-1038	ISAR	Red	White	-
13	9-466	ISAR	White	White	-
14	97-062	ISAR	Pink	Orange	1355 U RHS 9/2
15	Cacearpedo	ISAR	Yellow	Orange	1355 U RHS 9/2
16	Caroline Lee	CIP	White	Yellow	7401/RHS 5/3
17	Carrote	CIP	Red	Orange	1355U RHS 9/2
18	Cyabafurika 538	NARO	White	Yellow	-
19	Ejumula	NARO – CIP	White	Orange	1355U RHS 9/2
20	Hakizakubyara	Landrace	Red	White	-
21	IMBY 3102	CIP	Red	White	-
22	K513261	IITA	Red	White	-
23	Karebe	ISAR	Red	White	-
24	Karibunduki	CIP	Red	White	-
25	Kawogo	CIP	Red	White	-
26	KEMB 37	CIP	Red	White	-
27	Kwezikumwe	ISAR	Yellow	Yellow	101U RHS ½
28	Magereza	ISAR	Red	White	-
29	Matembere	ARI-Ukiruguru	White	Orange	7507 RHS 9/3
30	Meresiyana	Landrace	Yellow	White	-
31	Mpakanjye	Landrace	White	Yellow	600U RHS 1/3
32	Mugande	CIP	Red	White	-
33	Mvugamo	Landrace	White	White	-
34	Mwanakumi	ARI-Ukiruguru	Yellow	Yellow	600 U RHS 1/3
35	NASPOT 8	NARO – CIP	Cream	Yellow	-
36	NASPOT 9 O	NARO – CIP	Red	Orange	-
37	NASPOT A	NARO – CIP	White	Cream	-
38	NASPOTw6	NARO – CIP	Red	Orange	7507U RHS:9/3
39	Naveto	CIP	Red	White	-
40	New Kawogo	NARO - CIP	Red	White	-
41	Nsasagatebo	Landrace	White	White	-
42	Nyirabusegenya	Landrace	Red	White	-
43	Nyiragatanga	Landrace	Red	White	-
44	Otada 148	NARO	Yellow	Orange	-
45	Otada 24	NARO	Red	White	-
46	Otada 48	NARO	Red	Orange	-
47	Otada 70	NARO	Red	White	-
48	Otada 96	NARO	Yellow	Cream	-
49	Purple 297	ISAR	Red	Purple	-
50	Purple 4419	ISAR	Red	Purple	-
51	Rukubinkondo	Landrace	Red	White	-
52	Seruruseke	Landrace	Red-purple	Yellow	-
53	SPK004	KARI	Red	Slight orange	1205 U:RHS: 3/3
54	Ukerewe	CIP	Red	Orange	7401U: RHS 5/3

*HarvestPlus standardized colour strips for the estimation of the total carotenoid content of sweeetpotato, CIP: International Potato Center, NARO: National Agriculture Research Organisation, ISAR: Institut des Sciences Agronomiques du Rwanda, IITA: International Institute of Tropical Agriculture, ARI-Ukiruguru: Ukiruguru Agriculture Research Institute, KARI: Kenya Agriculture Research Institute, -: Data not available.

4.2.2 Greenhouse experiment

A greenhouse experiment was established at Rubona research station of RAB. The 54 genotypes were tested at four water regimes: control (T1, continually watered till maturity), drought stress imposed by withholding water for one (T2), two (T3) or three month(s) (T4). The various stress levels were meant to target vegetative growth, storage root initiation and storage root development for selection. Soil moisture was monitored using soil moisture sensor (Watermark meter, Irrometer, Riverside, CA 92516, Litho USA) to apply irrigation to the control treatment. The 54 genotypes x four water regimes yielded 216 treatment combinations and evaluated in a completely randomized design using three replications. Vine cuttings with three nodes and one leaf were raised in plastic trays under optimal humid conditions for two weeks to develop roots. The rooted vines were transplanted in polyethylene plastic pots filled with 15 kg of pot mix soil (100 kg sand, 100 kg manure). Prior to planting, each pot was watered to saturation level. All plants were grown for one month under irrigation for establishment. Then, the trial was conducted using the four water regimes described above.

4.2.3 *In-vitro* experiment

Drought tolerance of sweetpotato genotypes was investigated under in-vitro conditions following a modified method of Guo et al. (1999), Biswas et al. (2002) and He et al., (2009). Vine cuttings of three nodes were planted in a greenhouse for two weeks to develop roots. The rooted vine cuttings were washed with tap water to remove the soil, wiped with tissue paper, prior to determining their initial fresh weight using analytical balance, and planted in plastic trays containing oven sterilised sand. Ten plants of the same genotype were grown for each treatment. The planted trays were kept in a growth room (at 26 °C, photoperiod of 16 h light and 8 h darkness) for four weeks.

Four solutions were applied as a source of water and nutrients. The control solution (T_1) was prepared with 4.4 g/l Murashige and Skoog (MS) salts (Murashige and Skoog 1962) with vitamins, supplemented with 20 mg/l putrescine-HCl, 10 mg/l gibberillic acid, 0.2 g/l ascorbic acid, 0.1 g/l calcium nitrate, 2 mg/l calcium penthotenate and 0.1 g/l L-arginine. The drought stress conditions were mimicked by supplementing 0.2, 0.4, or 0.6 M sorbitol to the control solution and represented T_2, T_3, and T_4, respectively as applied by Rukundo el al (2012). Twenty ml of each solution was applied to each plant every week for three weeks.

4.2.4 Data collection

4.2.4.1 Greenhouse experiment

The soil water potential (Ψ_w) of each treatment was recorded weekly with a hand held soil moisture sensor. Weight of storage root, biggest storage root and vines of each plant were determined using analytical balance at harvest (120 days after planting). The dry matter content (DMC) of storage root and vine, and water content (WC) of vines were determined using a modified method described by Rodriguez (1999). Approximately 50 to 100 g of fresh weight were sampled from healthy and biggest root and vines of each plant and kept in a paper bag prior to drying. These samples were dried at 70^{O}C to a constant weight. The weight of dried samples was determined and the DMC was determined using the following formula: DM% = (dry weight/fresh weight) x100.

4.2.4.2 In-vitro experiment

The Ψ_w of each treatment was recorded with a water potential meter. Fresh weight gain (FWG), DMC and WC were determined as described above. The FWG was determined as the difference of final and initial fresh weights.

4.2.5 Data analysis

Data was analysed using the REML procedure (Cochran and Cox 1992) to calculate ANOVA and mean comparisons using GeneStat 14^{th} edition (Payne et al. 2011). The correlation between traits for greenhouse and in-vitro experiments was determined with 2-tailed test using SPSS (PASW Statistics 18.0) computer package (SPSS 2006).

4.3 Results

4.3.1 Greenhouse experiment

In a greenhouse trial, the Ψ_w of drought stress treatments decreased as the duration of drought stress increased. The mean Ψ_w varied from -0.66 to 0.0, -1.75 to 0.0 and -1.95 to -0.03 Mpa for T_2, T_3 and T_4, respectively (Table 4.2). In the control treatment, the mean Ψ_w ranged between -0.02 to 0.0 MPa (Table 4.2).

Table 4.2: Water potential readings (MPa) during the experiment

Treatment	Week*											
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Continuous irrigation (Control: T_1)	-0.01	0.00	-0.02	0.01	0.00	-0.02	0.00	-0.01	0.00	-0.01	-0.01	0.00
Drought stress of one month (T_2)	-0.01	0.00	-0.01	-0.01	0.00	0.00	0.00	0.00	-0.06	-0.25	-0.41	-0.66
Drought stress of two months (T_3)	0.00	0.00	-0.02	-0.01	-0.07	-0.14	-0.54	-0.91	-1.32	-1.57	-1.64	-1.75
Drought stress of three months (T_4)	-0.03	-0.47	-0.72	-1.70	-1.82	-1.93	-1.94	-1.95	-1.92	-1.94	-1.92	-1.94

* Values in table are means of three measurements.

Genotypes showed difference on growth rate between continuous irrigation and drought stress conditions (Table 4.3). As expected, plants grown on the continuous irrigation showed high vegetative growth and dense green leaves. Genotypes grown on drought stressed conditions shed excess leaves and reduced growth (Figure 4.1, Table 4.3). Some genotypes did not grow under the drought stress of three months (Figure 4.1).

Figure 4.1: Comparison of growth of sweetpotato plants of genotype Mvugamo under continuous irrigation (left) and drought stress of three months (right) under greenhouse conditions.

The control treatment induced the highest weight of biggest root, yields of storage root and vine, total biomass, root DMC, and vine WC (Table 4.3). The control and drought stress treatment of one month showed significant differences on the weight of biggest root, yields of storage root and vine and total biomass, storage root and vine DMC, and vine WC (Table 4.3). Drought stress of two and three months did not show significant differences on weight of biggest root, yields of storage root, root and vine DMC and vine WC (Table 4.3). The storage root DMC was inversely proportion to dry matter content of vines (Table 4.3). On the continuous irrigation the DMC were 23.4 and 13.9% for storage root and vine, respectively. Drought stress of three months provided DMC of 16.9 and 21.1% for storage root and vine, respectively (Table 4.3).

Table 4.3: Effects of four water stress levels on yield, yield components and vine water content of sweetpotato under greenhouse condition

Treatment	Biggest root weight (g)	Storage root yield (g)	Vine yield (g)	Total biomass (g)	Root DMC (%)	Vine DMC (%)	Vine WC (%)
Continuous irrigation	54.2[c]	124.9[c]	387.0[d]	512.0[d]	23.4[b]	13.9[a]	86.1[c]
Drought stress of one month	30.8[b]	64.7[b]	251.8[c]	316.5[c]	21.7[b]	16.2[b]	83.8[b]
Drought stress of two months	13.9[a]	30.4[a]	98.3[b]	128.7[b]	16.5[a]	19.8[c]	80.1[a]
Drought stress of three months	9.4[a]	22.1[a]	67.4[a]	89.5[a]	16.9[a]	21.1[c]	78.9[a]
Grand mean	28.7	62.2	204.4	266.7	20.2	17.3	82.7
CV (%)	49.4	58.6	28.8	28.3	43.4	22.0	4.6
LSD (5%)	22.8	58.5	94.4	121.0	14.0	6.1	6.1

DMC: dry matter content, WC: water content, * Means in a column followed by the same letter are not significantly different at P ≤ 0.05.

Genotype by water regime and the main effects of genotype and water regime had significant effects on root and vine yields, weight of biggest root, total biomass, root and vine DMC and vine WC (Table 4.4).

Table 4.4: Analysis of variance on yield and yield components of 54 sweetpotato genotypes evaluated under four water regimes in greenhouse

Source of variation	DF	Storage root yield	Biggest storage root weight	Vine yield	Total biomass	Storage root DMC	Vine DMC	Vine WC
Replications	2	12005	4511.5	28865	33218	348.52	329.96	329.96
Genotypes	53	781315*	138817.2*	1338664*	2435998*	15264.81*	1880.87*	1880.87*
Water regimes	3	1061919*	199635.9*	10621671*	18302213*	5685.02*	5377.51*	5377.51*
Genotypes x water regimes	159	733295*	192364*	2836371*	4614533*	43586.42*	5923.56*	5923.56*
Residual	430	570665	86707.4	1489168	2444132	32909.53	6221.09	6221.09
Total	647	3159199	622035.9	16314740	27830095	97794.3	19732.99	19732.99

DMC: dry matter content, WC: water content, * Significant difference (P ≤ 0.01); DF=degrees of freedom.

Under continued irrigation, genotypes: Caroline, Nsasagatebo, 2005-103, 8-1038, and Karibunduki had the highest yields of storage root (Table 4.5). During drought stress of three months, genotypes: IMBY 3102, KEMB 37, Karibunduki, 97-062 and 2002-155 revealed high storage root yields (Table 4.5). In terms of DMC, genotypes 2002-153, Magereza, 2000-031, NASPOT 9 O and 2005-020 were the best performers during continuous irrigation while genotypes Otada 148, 9-466, 2002-155, 2002-153 and Seruruseke were well-performed during drought stress of three months (Table 4.5). Genotypes Nsasagatebo, Kwezikumwe, Mugande, 2005-103 and 2005-146 had the highest vine yield during continuous irrigation.

Under drought stress of three months the best vine yields were observed in genotypes IMBY 3102, Mwanakumi, NASPOT 9 O, 2000-031 and Kawogo. The highest total biomass production were observed in genotypes Nsasagatebo, 2005-103, Mugande, Caroline and Kwezikumwe during continuous irrigation or genotypes IMBY 3102, 97-062, NASPOT 9 O, 2005-146 and 4-160 during drought stress condition of three months (Table 4.5).

Table 4.5: Mean storage root yield and dry matter content, vined yield, and total biomass production of 54 sweetpotato genotypes under continuous irrigation (T_1) and drought stress condition of three months (T_4)

Genotypes	Storage root yield (g)		Storage root DMC (%)		Vine yield (g)		Total biomass (g)	
	T_1	T_4	T_1	T_4	T_1	T_4	T_1	T_4
2000-031	85.8 a-f	11.9 a-h	30.5 g-i	23.9 f-j	429.9 j-t	105.0 m-o	515.7 g-m	116.9 k-r
2002-153	196.3 n-u	11.2 a-g	31.3 i	31.0 ij	279.4 a-e	73.0 d-m	475.7 e-m	84.2 c-n
2002-155	186.1 l-u	51.5 p-r	9.7 ab	31.7 j	213.7 ab	76.5 f-n	399.8 b-g	128.0 n-r
2005-020	97.8 c-k	30.1 i-o	29.9 g-i	18.6 c-i	382.9 d-p	58.5 a-j	480.7 e-m	88.6 d-p
2005-034	174.7 j-s	8.0 a-d	11.0 bc	12.2 a-f	390.9 e-q	97.2 k-o	565.6 h-o	105.2 i-r
2005-103	261.5 t-v	35.1 j-p	29.6 g-i	16.6 b-h	605.9 u-w	64.5 b-k	867.3 rs	99.7 g-q
2005-110	1.7.0 a	6.8 a-c	18.9 c-f	10.4 a-d	190.1 a	66.8 c-k	191.8 a	73.6 a-l
2005-133	118.8 e-o	25.5 d-k	29.7 g-i	19.4 c-j	465.8 p-t	81.5 h-o	584.6 k-o	107.1 i-r
2005-146	64.6 a-g	46.0 n-q	25.1 f-i	25.3 g-j	539.3 t-w	88.1 i-o	603.9 l-o	134.1 p-r
4-160	226.4 r-v	44.2 l-q	26.4 f-i	22.3 c-j	299.7 a-h	87.6 h-o	526.1 g-m	131.9 o-r
5-214	76 .0 a-h	37.0 j-p	23.0 e-i	23.7 e-j	213.9 ab	68.2 c-m	289.9 a-c	105.2 i-r
8-1038	255.8 s-v	7.6 a-d	26.8 f-i	23.7 e-j	444 l-t	71.5 d-m	699.8 n-q	79.1 b-m
9-466	75.6 a-h	34.2 j-p	25.3 f-i	44.9 k	339.8 c-m	52.3 a-i	415.4 b-h	86.5 c-o
97-062	150.1 h-r	62.3 q-s	26.1 f-i	25.6 g-j	285.6 a-f	86.8 h-o	435.7 c-k	149.1 r
Cacearpedo	180.7 k-t	27.6 g-m	27.2 f-i	12.1 a-f	378.5 d-p	74.6 e-n	559.2 h-o	102.2 h-q
Caroline	302.1 v	8.0 a-d	21.5 d-g	13.2 a-g	528 s-v	88.3 i-o	830.1 qr	96.3 f-p
Carotte	231.5 r-v	20.4 b-j	22.2 d-h	17.9 b-h	533.7 t-v	80.4 g-o	765.2 p-r	100.9 g-q
Cyabafurika 538	61.0 a-g	6.1 a-c	26.1 f-i	15.2 b-h	431.6 k-t	36.3 a-d	492.6 f-m	42.4 a-d
Ejumula	104.2 d-l	13.1 a-i	24.2 f-i	5.1 ab	313 b-i	72.0 d-m	417.2 b-i	85.1 c-n
Hakizakubyara	19.7 a-d	4.5 ab	22.9 e-i	24.4 f-j	448.3 m-t	66.7 c-k	468 e-l	71.2 a-k
IMBY 3102	116.4 e-n	113.6 t	28.1 g-i	24.3 f-j	349.1 c-o	180.4 p	465.4 e-l	294.0 s
K513261	125.6 f-p	22.6 c-j	1.6 a	26.4 h-j	331 c-l	39.5 a-e	456.6 d-l	62.1 a-i
Karebe	166.7 i-r	42.5 k-p	13.8 b-d	22.7 c-j	311 b-i	77.1 f-n	477.6 e-m	119.6 l-r
Karibunduki	232 r-v	68.9 rs	24.7 f-i	16.3 b-h	293.5 a-h	51.2 a-h	525.4 g-m	120.2 l-r
Kawogo	201.5 o-u	1.7 a	11.4 bc	23.3 d-j	509.7 r-u	103.8 l-o	711.2 o-q	105.5 i-r
KEMB 37	207.2 p-u	77.6 s	27.5 f-i	0.5 a	269.9 a-d	23.5 a	477.1 e-m	101.1 g-q
Kwezikumwe	133.3 f-q	11.9 a-h	23.6 e-i	0.5 a	649.4 wx	93.6 j-o	782.7 qr	105.6 i-r
Magereza	138.1 f-q	47.8 o-q	30.6 hi	11.4 a-f	417 i-s	67.8 c-l	555.1 h-n	115.6 k-r
Matembere	72.3 a-h	29.5 h-n	25.6 f-i	13.2 a-g	496.8 q-u	93.3 j-o	569.1 i-o	122.8 m-r
Meresiyana	180.7 k-t	6.8 a-c	25.1 f-i	0.5 a	257.6 a-c	55.1 a-i	438.3 c-k	61.9 a-i
Mpakanjye	141.1 g-q	26.3 e-l	28.0 g-i	11.7 a-f	454.4 n-t	69.0 c-m	595.5 l-o	95.3 f-p
Mugande	215.7 q-u	25.6 d-k	24.9 f-i	10.7 a-e	631.9 v-x	51.6 a-i	847.5 q-s	77.2 b-m
Mvugamo	53.6 a-f	5.3 a-c	27.0 f-i	25.6 g-j	346.9 c-o	60.2 a-j	400.5 b-g	65.5 a-j
Mwanakumi	58.9 a-g	1.7 a	28.4 g-i	20.6 c-j	292.2 a-g	117.1 o	351.1 b-f	118.8 l-r
NASPOT 8	57.2 a-g	8.7 a-e	28.2 g-i	19.2 c-j	440.6 l-t	67.8 c-l	497.8 f-m	76.5 b-m
NASPOT 9 O	122.5 e-p	35.0 j-p	30.1 g-i	0.5 a	406.7 h-r	111 no	529.2 g-m	146 qr
NASPOT A	97.2 c-k	1.7 a	11.8 bc	13.0 a-g	395.1 f-q	33 a-c	492.3 f-m	34.7 ab
NASPOTw6	63.2 a-g	20.3 b-j	12.0 bc	0.5 a	275.5 a-d	59.1 a-j	338.6 a-e	79.5 b-m
Naveto	40.5 a-e	20.9 b-j	26.7 f-i	21.8 c-j	258.4 a-c	72.0 d-m	298.9 a-c	92.9 e-p
New Kawogo	15.0 a-c	26.8 f-l	26.2 f-i	24.4 f-j	318.3 b-k	79 f-n	333.3 a-e	105.8 i-r
Nsasagatebo	267.5 uv	12.4 a-i	23.5 e-i	0.5 a	721.2 x	94.4 j-o	988.6 s	106.8 i-r
Nyirabusegenya	1.7 a	1.7 a	14.6 b-e	0.5 a	310.5 b-i	64.5 b-k	312.2 a-d	66.2 a-j
Nyiragatanga	109.8 e-m	14.1 a-i	26.8 f-i	20.4 c-j	399.7 g-r	81.6 h-o	509.5 g-m	95.7 f-p
Otada 148	150.8 h-r	9.0 a-f	28.5 g-i	29.7 k	316.1 b-j	32.3 a-c	466.9 e-l	41.3 a-c
Otada 24	55.4 a-f	5.4 a-c	25.7 f-i	26.8 h-j	342 c-n	34.6 a-c	397.4 b-g	40.1 a-c
Otada 48	85.5 a-i	2.9 ab	25.1 f-i	21.1 c-j	247.5 a-c	51.9 a-i	332.9 a-e	54.8 a-g
Otada 70	109.4 e-m	5.3 a-c	28.8 g-i	0.5 a	428.5 j-t	43.2 a-f	537.9 g-m	48.5 a-e
Otada 96	136.2 f-q	29.2 g-n	27.7 f-i	11.7 a-f	444.0 l-t	79.7 f-n	580.1 k-o	108.9 j-r
Purple 297	116.1 e-n	21.0 b-j	27.2 f-i	0.5 a	457.6 o-t	37.3 a-d	573.7 j-o	58.3 a-h
Purple 4419	193.7 m-u	45.3 m-q	25.6 f-i	27.2 h-j	431.5 k-t	73.1 d-m	625.2 m-p	118.4 l-r
Rukubinkondo	94.8 b-j	7.9 a-d	13.3 b-d	22.9 d-j	526.8 s-v	44.4 a-g	621.6 m-p	52.3 a-f
Seruruseke	105.2 e-l	15.0 a-i	27.5 f-i	27.8 h-j	429.3 j-t	68.6 c-m	534.5 g-m	83.7 c-n
SPK004	10.3 ab	1.7. a	26.8 f-i	9.7 a-c	271.4 a-d	28.1 ab	281.6 ab	29.8 a
Ukerewe	93.4 b-j	27.8 g-m	27.0 f-i	19.3 c-j	331.9 c-l	83.0 h-o	425.3 b-j	110.9 j-r
Grand mean	126.6	23.8	23.9	17.5	390.3	70.7	517.0	94.5
CV (%)	41.4	46.9	23.3	46.1	18.0	32.1	18.3	30.5
LSD (5%)	84.8	18.1	9.0	13.0	113.9	36.8	152.8	46.7

* Means in a column followed by the same letter are not significantly different at P ≤ 0.05.

4.3.2 *In-vitro* experiment

During in-vitro experiments, the mean Ψ_w were - 0.07, - 0.81, -1.35 and - 1.73 MPa for the control, 0.2, 0.4, and 0.6 M sorbitol treatments, respectively. Genotypes did not show significant differences for FWG when grown under the control (T_1) and 0.2 M (T_2) treatments. T_2 was significantly different from T_3 (0.4 M sorbitol) and T_4 (0.6 M sorbitol) in affecting FWG, DMC and WC (Table 4.6). The DMC and WC were inversely related (Table 4.6).

Table 4.6: Mean fresh weigh gain, dry matter content, and water content of 54 sweetpotato genotypes during in-vitro experiment using four sorbitol treatments

Treatment	FWG (g)	DMC (%)	WC (%)
T_1 (Control)	1.7^{c}	16.0^{a}	83.8^{d}
T_2 (0.2 M sorbitol)	1.8^{c}	18.0^{b}	82.0^{c}
T_3 (0.4 M sorbitol)	1.3^{b}	20.0^{c}	80.0^{b}
T_4 (0.6 M sorbitol)	0.8^{a}	23.0^{d}	77.0^{a}
Grand mean	1.3	19.3	80.7
CV (%)	28.3	19.7	4.7
LSD (5%)	0.6	6.1	6.1

DMC: dry matter content, WC: water content, FWG: fresh weight gain, * Means in a column followed by the same letter are not significantly different at $P \leq 0.05$.

During the in-vitro test, analysis of variance revealed significant differences among genotypes due to interaction effect of genotypes by stress treatments for FWG, DMC and WC (Table 4.7). The main effects of genotypes and treatments were also significant for FWG, DMC and WC (Table 4.7).

Table 4.7: Analysis of variance on fresh weigh gain, dry matter content, and water content of 54 sweetpotato genotypes during in-vitro experiment using four sorbitol treatments

Source of variation	DF	FWG	DMC	WC
Replications	2	0.83	7697.04	4922.17
Genotypes	53	60.90*	2687.69*	2133.80*
Treatments	3	457.55*	4760.92*	3764.55*
Genotypes x Treatments	159	115.36*	2884.88*	2275.20*
Residual	430	61.10	279.13	75.78
Total	647	695.75	18309.66	13171.50

DMC: dry matter content, WC: water content, FWG: fresh weight gain * Significant difference ($P \leq 0.01$), DF: Degrees of freedom.

The control treatment had the highest FWG at 4.9, 4.34, 4.2, 4.2 and 3.9 g displayed by genotypes Nsasagatebo, 2005-103, Mugande, Caroline and Kwezikumwe, respectively. At the 0.6 M sorbitol treatment, genotypes IMBY 3102, 97-062, NASPOT 9 O, 2005-146, 4-160 and 2002-155 revealed the highest FWG of 1.5, 0.8, 0.7, 0.7 and 0.7 g, respectively (Table 4.8). A high DMC of 21.2, 20.2, 18.4, 18.2 and 17.9% was observed in genotypes Naveto, K513261, Meresiyana, Otada 148 and Kwezikumwe, respectively. Under drought stress, the genotypes 2005-103, 9-466, Otada 70, New Kawogo and Kwezikumwe revealed the highest DMC of 39.4, 36.9, 32.3, 30.3 and 28.4 % (Table 4.8). The best genotypes that showed relatively high WC compared to the control were Caroline, 2005-110, Mvugamo, NASPOT A and 97-062 at 88.5, 87.7, 87.7, 87.6 and 87.4 %. Under 0.6 M sorbitol treatment, genotypes 8-1038, Nyiragatanga, IMBY 3102, SPK004 and Mvugamo expressed WC of 88.8, 83.5, 82.7, 81.9 and 81.9 % (Table 4.8).

Table 4.8: Mean fresh weigh gain, dry matter content and water content, of 54 sweetpotato genotypes grown in-vitro for four weeks in a basic culture medium (control: T1) and under supplementation of 0.6 M sorbitol (T4).

Genotypes	FWG (g)		DMC (%)		WC (%)	
	T1	T4	T1	T4	T1	T4
2000-031	2.6 g-m	0.6 k-r	16.4 h-m	19.7 b-f	83.6 c-h	80.3 g-k
2002-153	2.4 e-m	0.4 c-n	15.1 b-k	26.9 f-j	84.9 e-n	73.1 c-g
2002-155	2.0 b-g	0.6 n-r	15.5 d-m	20.3 b-g	84.5 c-l	79.7 f-k
2005-020	2.4 e-m	0.4 d-p	16.3 g-m	24.9 c-j	83.8 c-i	75.1 c-j
2005-034	2.8 h-o	0.5 i-r	14.5 b-h	25.0 c-j	85.5 h-n	75.0 c-j
2005-103	4.3 rs	0.5 g-q	16.5 h-m	39.4 l	83.5 c-h	60.6 a
2005-110	1.0 a	0.4 a-l	12.3 ab	23.6 b-i	87.7 no	76.4 d-k
2005-133	2.9 k-o	0.5 i-r	16.5 h-m	22.2 b-h	83.5 c-h	77.9 e-k
2005-146	3.0 l-o	0.7 p-r	14.8 b-i	23.1 b-i	85.2 g-n	77.0 d-k
4-160	2.6 g-m	0.7 o-r	13.8 a-h	21.5 b-h	86.2 h-o	78.5 e-k
5-214	1.5 a-c	0.5 i-r	14.0 a-h	20.2 b-g	86.0 h-o	79.8 f-k
8-1038	3.5 n-q	0.4 b-m	13.2 a-f	11.2 a	86.8 j-o	88.8 l
9-466	2.1 b-h	0.4 c-o	15.7 e-m	36.9 kl	84.3 c-k	63.1 ab
97-062	2.2 c-k	0.7 r	12.6 a-d	26.4 e-j	87.4 l-o	73.6 c-h
Cacearpedo	2.8 h-o	0.5 h-q	14.8 b-j	20.4 b-h	85.2 f-n	79.6 e-k
Caroline	4.2 qr	0.5 f-p	11.5 a	19.9 b-g	88.5 o	80.1 f-k
Carotte	3.8 p-r	0.5 g-q	14.3 a-h	18.4 a-e	85.7 h-o	81.6 h-l
Cyabafurika 538	2.5 f-m	0.2 a-d	15.8 e-m	22.6 b-i	84.2 c-k	77.4 d-k
Ejumula	2.1 b-i	0.4 c-n	15.1 b-k	28.0 g-j	84.9 e-n	72.1 c-f
Hakizakubyara	2.3 e-l	0.4 a-k	14.7 b-i	21.2 b-h	85.3 g-n	78.8 e-k
IMBY 3102	2.3 e-l	1.5 s	16.6 h-m	17.3 a-c	83.4 c-h	82.7 j-l
K513261	2.3 d-l	0.3 a-i	20.2 no	22.8 b-f	79.8 ab	77.2 d-k
Karebe	2.4 e-m	0.6 l-r	12.8 a-e	19.3 a-f	87.2 k-o	80.7 g-l
Karibunduki	2.6 g-m	0.6 l-r	15.3 c-l	22.1 b-h	84.7 d-m	77.9 e-k
Kawogo	3.6 o-q	0.5 i-r	16.4 g-m	22.4 b-i	83.6 c-i	77.6 d-k
KEMB 37	2.4 e-m	0.5 g-q	15.3 c-l	25.8 d-j	84.7 d-m	74.2 c-i
Kwezikumwe	3.9 qr	0.5 i-r	17.9 k-n	28.4 h-j	82.2 b-e	71.6 c-e
Magereza	2.8 h-n	0.6 k-r	13.4 a-g	21.6 b-h	86.6 i-o	78.4 e-k
Matembere	2.8 i-o	0.6 m-r	15.1 b-k	26.0 d-j	84.9 e-n	74.0 c-i
Meresiyana	2.2 c-k	0.3 a-i	18.4 m-o	25.0 c-j	81.6 a-c	75.0 c-j
Mpakanjye	3.0 l-o	0.5 f-p	15.4 c-l	26.2 d-j	84.6 d-m	73.8 c-i
Mugande	4.2 q-s	0.4 b-m	15.0 b-k	22.7 b-i	85.0 e-n	77.3 d-k
Mvugamo	2.0 b-g	0.3 a-j	12.3 ab	18.1 a-d	87.7 no	81.9 i-l
Mwanakumi	1.8 b-f	0.6 l-r	13.9 a-h	19.8 b-f	86.1 h-o	80.2 g-k
NASPOT 8	2.5 f-m	0.4 b-m	14.5 b-h	19.4 b-f	85.5 h-n	80.6 g-k
NASPOT 9 O	2.6 g-m	0.7 qr	16.2 g-m	22.9 b-i	83.8 c-i	77.2 d-k
NASPOT A	2.5 f-m	0.2 ab	12.4 a-c	18.1 a-d	87.6 m-o	81.9 i-l
NASPOTw6	1.7 a-e	0.4 b-m	16.2 g-m	26.1 d-j	83.8 c-i	73.9 c-i
Naveto	1.5 a-c	0.5 e-p	21.2 o	18.7 a-e	78.8 a	81.3 h-l
New Kawogo	1.7 a-e	0.5 i-r	17.7 i-n	30.3 i-k	82.3 b-g	69.7 b-d
Nsasagatebo	4.9 s	0.5 i-r	15.6 d-m	20.1 b-g	84.4 c-l	79.9 f-k
Nyirabusegenya	1.6 a-d	0.3 a-j	14.8 b-j	19.7 b-f	85.2 f-n	80.3 g-k
Nyiragatanga	2.5 g-m	0.5 f-p	14.3 a-h	16.6 ab	85.7 h-o	83.5 kl
Otada 148	2.3 e-l	0.2 a-c	18.2 l-o	19.9 b-g	81.8 a-d	80.1 f-k
Otada 24	2.0 b-g	0.2 a-c	16.1 f-m	21.9 b-h	83.9 c-j	78.1 e-k
Otada 48	1.7 a-e	0.3 a-g	14.8 b-j	20.6 b-h	85.2 f-n	79.4 e-k
Otada 70	2.7 g-m	0.2 a-e	14.8 b-i	32.3 j-l	85.3 g-n	67.7 a-c
Otada 96	2.9 k-o	0.5 j-r	17.8 j-n	23.9 b-i	82.2 b-f	76.1 d-k
Purple 297	2.9 j-o	0.3 a-h	15.4 c-l	21.5 b-h	84.6 d-m	78.5 e-k
Purple 4419	3.1 m-p	0.6 l-r	15.1 b-k	23.0 b-i	84.9 e-n	77.0 d-k
Rukubinkondo	3.1 m-p	0.3 a-f	15.7 e-m	19.0 a-f	84.3 c-k	81.0 g-l
Seruruseke	2.7 g-m	0.4 c-n	15.4 d-l	22.2 b-h	84.6 d-l	77.9 e-k
SPK004	1.4 ab	0.1 a	16.1 f-m	18.1 a-d	83.9 c-j	82.0 i-l
Ukerewe	2.1 b-j	0.6 j-r	16.1 g-m	18.3 a-e	83.9 c-i	81.7 h-l
Grand mean	2.6	0.5	15.4	22.6	84.6	77.4
CV (%)	18.3	30.5	12	22.2	2.2	6.5
LSD	0.8	0.2	3	8.1	3	8.1

DMC: dry matter content, WC: water content, FWG: fresh weight gain, DF: Degrees of freedom, Means in a column followed by the same letter are not significantly different at $P \leq 0.05$.

4.3.3 Relationship between drought tolerance parameters of greenhouse and in-vitro experiments

Positive correlations (P ≤ 0.01) were observed between vine yield measured during the greenhouse and fresh weight gain (FWG) of the *in-vitro* experiments, and between total biomass and FWG in that order (Table 4.9).

Table 4.9: Correlation coefficients showing pair-wise association of drought tolerance parameters of greenhouse and in-vitro experiments involving 54 sweetpotato genotypes.

	Experiments	Greenhouse					Laboratory	
	Parameters	Storage root yield	Vine yield	Total biomass	Storage root DMC	Vine DMC	DMC	FWG
Greenhouse	Storage root yield	1	0.15 ^{ns}	0.75 ^{s}	-0.01 ^{ns}	0.03 ^{ns}	0.00 ^{ns}	0.17 ^{ns}
	Vine yield		1	0.72 ^{s}	0.14 ^{ns}	-0.20 ^{ns}	-0.10 ^{ns}	0.28 ^{s}
	Total biomass			1	0.05 ^{ns}	-0.20 ^{ns}	-0.10 ^{ns}	0.28 ^{s}
	Storage root DMC				1	0.01 ^{ns}	0.08 ^{ns}	0.00 ^{ns}
	Vine DMC					1	0.19 ^{ns}	-0.20 ^{ns}
Laboratory	DMC						1	-0.48 ^{s}
	FWG							1

^{s}: significant difference at P≤0.01, ^{ns}: Non-significant. DMC: Dry matter content; WC: Water content, FWG; Fresh weight gain.

Overall, genotypes IMBY 3102, 2005-146, 2002-155, 97-062, Karebe, Kemb 37, Mwanakumi, NASPOT 9 O, Purple 4419, 4-160, and Matembere performed well under drought stress condition expressing high storage root yields, vine and total biomass (Table 4.5), and fresh weight gain (Table 4.8) during both experiments. These traits were correlated under the greenhouse and in-vitro tests (Table 4.9). Under the control treatment, genotypes Mugande, Kawogo, Caroline, Carotte, 2005-103, Nsasagatebo, 2005-146, Kwezikumwe and Rukubinkondo revealed the highest yields of storage root and vine and FWG (Tables 4.5 and 4.8).

4.4 Discussion

4.4.1 Intensity of drought stress under greenhouse and in-vitro experiments

In the present study, under continuous irrigation of greenhouse conditions the soil Ψ_w was almost constant and ranged between -0.02 and 0 MPa. The soil Ψ_w decreased as the duration of drought stress increased and varied from -1.95 to 0.0 MPa (Table 4.2). Similar

observations were reported by Rahimi et al. (2010) in their study of f leaf Ψ_w and relative WC under gradual drought stress in *Plantago ovata* and *P. psyllium.* Within five days after irrigation, the leaf Ψ_w was almost constant and varied between -0.7 and -1.0 MPa. However, there was a Ψ_w decline of -1.6 and -2.0 MPa after 8 days of irrigation and of -2.3 and -2.8 MPa after 10 days of irrigation for *P. psyllium* and *P. ovata*, respectively. The change of this Ψ_w was associated with the increase of solute concentration in the soil and resulted negative osmotic potential (Taiz and Zeiger 2006).

The control semi-solid MS medium with 30 g l^{-1} sucrose had a Ψ_w of -0.80 MPa. When this culture medium was supplemented with 0.4 M sorbitol and 0.012 M polyethylene glycol (PEG), the Ψ_w were -2.05 MPa and -1.30 MPa, respectively (Gopal and Iwama 2007). The dissolution of sugar in a solution of culture medium caused a Ψ_w decrease of the culture medium. In bananas, a culture medium supplemented with 0.09 M sucrose had a Ψ_w of -0.37 MPa. When this culture medium was supplemented with 0.1 M and 0.5 M sorbitol, the Ψ_w shifted to -0.63 Mpa and -1.72 Mpa, respectively (Rukundo et al. 2012). These findings agree with the observation of this study in which under the in-vitro condition, the Ψ_w decreased as the concentration of sorbitol increased at -0.07, -0.81, -1.35 and - 1.73 MPa for control (0.0 M), 0.2, 0.4, and 0.6 M sorbitol treatments, respectively. Both the greenhouse and in-vitro approaches showed the same trend; as the drought stress conditions increased, the Ψ_w decreased.

4.4.2 Effects of drought stress

4.4.2.1 Greenhouse experiments

Limited water availability at any crop growth stage causes unfavourable effects on growth. These effects vary depending on the intensity of stress and the crop growth stage (Deblonde and Ledent 2001; Farooq et al. 2012). The results from this study corroborate with the above observations. There was a significant difference between plants grown on continuous irrigation and drought stress conditions (Figure 4.3). Plants grown under continuous irrigation showed high vegetative growth and dense green leaves.

In sweetpotato production a yield loss of more 60%, due to drought stress was recorded in South Africa (van Heerden and Laurie 2008). This loss was associated with a decreased of the aboveground biomass accumulation. Therefore, it was suggested that the genetic improvement for drought tolerance of sweetpotato has to consider these characteristics which include well-developed aboveground plant parts or vines (van Heerden and Laurie

2008). Saraswati et al. (2004) reported that plant biomass, main stem length, internode diameter, internode length, leaf number and area, and root weight decreased in response to water stress. Previous findings agreed with the results of this study. Plants grown on drought stress conditions revealed a loss of leaves and reduced growth. Continued irrigation showed the highest yield of storage root, vine and total biomass, weight of biggest root, root DMC and vine WC (Table 4.3). The effects of continuous irrigation were significantly different from other treatments (Table 4.3).

Previous studies showed that water regimes of 100, 80, 60, 40 and 30% of field capacity had significant effect on shoot growth and weight. The strongest effects were observed in plants grown on the 30% treatment where shoot fresh weight, shoot dry weight, and shoot length was reduced by 79, 7 and 76.0%, respectively, at the time of harvest (Van Heerden and Laurie 2008). In this study, highest reduction of growth and yield was observed on drought stress of three months. However, the effects of drought stress of three months were not significantly different from drought stress of two months (Table 4.3). This indicates that drought tolerance in sweetpotato genotypes could be investigated by applying one month of continuous irrigation for establishment followed by two months of drought stress under greenhouse conditions.

4.4.2.2 *In-vitro* tests

Effects of drought stress induced by 0, 15 and 25 % PEG in laboratory experiments caused a reduction of shoot, root biomass and plant height (Bayoumi et al. 2010). The increase of osmotic inducer in basal culture medium caused a decrease of callus induction and plantlet growth (Biswas et al. 2002). These findings agreed with results of the present study. T_2 (control supplemented with 0.2 M sorbitol) were significantly different from T_3 (control supplemented with 0.4 M sorbitol) and T_4 (control supplemented with 0.6 M sorbitol) on FWG, DMC and WC (Table 4.6). The application of the same concentration of sorbitol (0.2 M) as an osmotic inducer on different varieties of banana plantlets showed that all varieties were negatively affected, but the degree of sensitivity varied significantly (Rukundo et al. 2012). The same observation was found in this study; the interaction between genotypes and treatment were significant for FWG, DMC and WC (Table 4.7). The control (T_1) and control complemented with 0.2 M sorbitol (T_2) did not show significant differences in fresh weight gain (Table 4.7). This indicates that the control supplemented with 0.4 M sorbitol could be the lowest concentration to be applied in screening for drought tolerance in sweetpotatoes under in-vitro condition suggesting more sorbitol concentrations in future studies.

4.4.3 Correlation between drought tolerance parameters during greenhouse and *in-vitro* experiments

Selection for drought tolerance is complicated by the lack of fast and reproducible screening approaches, and constant water stress conditions to efficiently evaluate a large number of genotypes (Ramirez-Vallejo and Kelly 1998; Talebi et al. 2009). Thus, drought indices which provide a measure of drought based on yield and yield related traits under drought conditions in comparison to the control have been used for screening drought-tolerant genotypes (Mitra 2001). These indices are either based on drought resistance or susceptibility of genotypes (Talebi et al. 2009). Selection of different genotypes under stress conditions is one of the main tasks of plant breeders to develop stress-tolerant cultivars (Clarke et al. 1984). This study revealed that in all evaluated parameters under greenhouse and in vitro experiments (Table 4.9); only three parameters with positive correlations (vine weight and fresh weight gain, and total biomass) could be considered as major selection criteria to identify drought tolerant sweetpotato genotypes under greenhouse and in-vitro tests.

4.5 Conclusions

This study indicates that the basal culture medium of sweetpotato supplemented with 0.4 M sorbitol could be the lowest concentration to be applied in screening for drought tolerance under in-vitro condition. In greenhouse trial, two months was enough to screen for drought tolerance in sweetpotatoes. Vine yields, total biomass and fresh weight gain are three important selection parameters to identify drought tolerant sweetpotato genotypes under greenhouse and in-vitro tests. In the absence of drought stress ideal genotypes are Mugande, Kawogo, Caroline, Carotte, 2005-103, Nsasagatebo, 2005-146, Kwezikumwe and Rukubinkondo for high storage root yields. Under drought stress conditions the best genotypes identified with the highest storage yields were IMBY 3102, 2005-146, 2002-155, 97-062, Karebe, Kemb 37, Mwanakumi, NASPOT 9 O, Purple 4419, 4-160, and Matembere.

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5. Chapter Five: Combining ability, maternal effects and heritability of drought tolerance, yield and yield components among newly developed sweetpotato clones

Abstract

Knowledge on gene action and traits expression are important for effective breeding. The objective of this study was to determine the general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components of candidate sweetpotato clones. Twelve genotypes selected for their high yield, dry matter content or drought tolerance were crossed using a full diallel mating design. Families were field evaluated at Masoro, Karama and Rubona Research Stations of Rwanda Agriculture Board. Success rate of crosses varied from 1.8 to 62.5% with a mean of 18.8%. Family by site interaction had significant effect ($P<0.01$) on storage root and vine yields, total biomass and dry matter content of storage root. The family effects were significant ($P< 0.01$) for all parameters measured. Broad sense heritability estimates were 0.95, 0.84, 0.68, 0.47, 0.74, 0.75, 0.50 and 0.58 for canopy temperature (CT), canopy wilting (CW), root yield, skin colour, flesh colour, dry matter content, vine yield and total biomass, respectively. The GCA effects of parents and SCA effects of crosses were significant ($P<0.01$) for CT, CW, storage root, vine and biomass yields, and dry matter content of storage root. The ratio of GCA/SCA effects for CT, CW, yield of storage roots and dry matter content of storage roots were higher than 50% suggesting the preponderance of additive over non-additive gene actions in the expression of these traits. The best general combiners for drought tolerance were the parents, 8-1038, Otada 24 and 4-160 with the lowest CT and CW and relatively high yields. Best combiners for high storage root yield were the parents, Nsasagatebo, K513261 and Ukerewe, while Nsasagatebo, 2005-034 and Ukerewe were the best combiners for high dry matter content. Maternal effects were significant ($P<0.05$) among families for CT, CW, flesh color and dry matter content, vine yield and total biomass. Based on reduced CT and CW, the best families with significant SCA effects were, 4-160 x Nsasagatebo, 4-160 x Ukerewe, Otada 24 x 4-160, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 , 513261 x 4-160, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020 and Nsasagatebo x Ukerewe, which were selected for breeding for drought tolerance. Across sites, the best five selected families with significant SCA effects for storage root yield were, Nsasagatebo x

Otada 24, Otada 24 x Ukerewe, 4-160 x Nsasagatebo, K513261 x 2005-034 and Ukerewe x K513261 with 11.0, 9.7, 9.3, 9.2, 8.6 t/ha, respectively. The best families with high dry matter content of 36.1, 35.1, 34.3, 34.0, and 33.9 % were Ukerewe x 2005-034, 4-160 x Nsasagatebo, 2005-034 x Ukerewe, 2005-034 x K513261, 2005-020 x Ukerewe, in that order. The selected families are valuable genetic resources for sweetpotato breeding for drought tolerance, yield and yield components in Rwanda or similar environments.

Key words: Canopy temperature, canopy wilting, drought tolerance, gene action, heritability, general combining ability, specific combining ability, storage root, sweetpotato.

5.1 Introduction

Sweetpotato *(Ipomoea batatas* [L.] Lam; 2n=6x=90) is an important root crop grown in more than 110 countries on an estimated area of $110x10^6$ ha with an annual production of 9 million tons (FAOSTAT 2013). In most sub-Saharan Africa countries, it is widely grown in smallholders farmesrs systems across various agro-ecological zones, with excellent tolerance to various abiotic and biotic stresses. Sweetpotato has become the main staple food for many families in Uganda, Rwanda, and Burundi in Eastern Africa, where annual per capita consumption fresh roots is above 80 kg (FAOSTAT 2013). The storage roots of sweetpotato are rich in carbohydrates and its leaves are rich in proteins. Orange fleshed sweetpotato varieties are rich in β-carotene, a precursor of vitamin A, while purple fleshed sweetpotato varieties contain anthocyanin, which is a powerful anti-antioxidant (Lebot 2009). Sweetpotato flour can be used as a partial substitute of wheat flour in bakeries and pasta products, allowing for import substitute for wheat flour (Tan et al. 2007). However, yield and yield components, and quality traits of sweetpotato genotypes vary due to differences in genetic constitution, the environment and genotype-by-environment interactions.

Quantitative characters including drought tolerance are influenced by genetic and non-genetic factors. The genetic components of quantitative traits are often controlled by many sets of genes with various gene action (Acquaah 2007). An ideotype is determined by genetic components explained by gene action such as additive, dominance, epistatic or overdominance effects, and the environment in which it is grown (Fasoula and Fasoula 2003). The magnitude and direction of genetic components are estimated through various parameters including combining ability, heritability and heterosis analyses. Knowledge of gene action and associated trait expression is important for effective breeding and selection (Grami et al. 1977; Ma-Teresa et al. 1994).

Combining ability analysis helps to identify superior parents to be used in breeding programs or to identify promising cross combinations for cultivar development (Acquaah 2007). General combining ability (GCA) is directly related to the breeding value of a parent and is associated with additive genetic effects, while specific combining ability (SCA) is the relative performance of a cross that is associated with non-additive gene action, predominantly contributed by dominance, epistasis, or genotype x environment interaction effects (Rojas and Sprague 1952; Falconer and Mackay 1996). Therefore, both GCA and SCA effects are important in the selection or development of breeding populations (Viana and Matta 2003).

Trait expression is influenced by both nuclear and cytoplasmic genes (Acquaah 2007). The cytoplasmic genes are known to have maternal inheritance, which is often determined through reciprocal crosses. The distribution of cytoplasmic genetic materials into gametes is unequal and unpredictable (Roach and Wulff 1987; Acquaah 2007). Grami and Stefansson (1977) reported that the maternal effects on protein and oil content in summer rape seed crop observed during the F1 generation change in the F2. This change was attributed to inadequate distribution of cytoplasmic components during gamete formation of female plants. Hence, it is difficult to maintain the maternal effects in sexually reproducing crops. Maternal genetic effects can be maintained in vegetatively propagated crops such as sweetpotato, owing to the inherently identical reproduction. Therefore, investigation and identification of maternal effects for desirable traits can be beneficial in breeding of sweetpotato, which may enhance responses to selection (Falconer and Mackay 1996).

Heritability is categorized into broad sense heritability (H^2) and narrow sense heritability (h^2) and is a measure of the proportion of the genetic variance out of the total phenotypic variance present in a population. It shows the degree to which offspring can be expected to resemble their parents for a specific trait (Ma-Teresa et al. 1994; Sleper and Poehlman 2006). When breeding clonally propagated species such as sweetpotato in which both additive and non-additive gene actions are fixed and transferred from parent to offspring, broad sense heritability is useful. However, in half sib families of sexually propagated crops, heritability in the narrow sense is important because alleles responsible for non-additive genetic variations are not fully recovered due to reshuffling of genes (Sleper and Poehlman 2006). Selection of traits with low heritability could be enhanced through the use of controlled screening methods or controlled environments, molecular markers or selection based on breeding values (Gasura et al. 2010). Ma-Teresa et al. (1994) reported that the heritability of dry matter content in sweetpotato was 75 -88% while Jones el al. (1986) and Lebot (2009) reported heritability levels for weight of storage roots of 61% for families and 59% for parentals (Jones et al. 1986; Lebot 2009).

Genetic studies in sweetpotato are limited due to self- and cross-incompatibility, high level of polyploidy and limited flowering ability and seed setting (Lin et al. 2007). Knowledge of the genetics of sweetpotato traits is helpful for efficient selection and breeding. Development of sweetpotato varieties with complementary traits to satisfy the food demand and changing end-users' preferences is dependent up on information on the genetic attributes of parents and progenies. This, in turn, depends on the magnitude and direction of genetic effects on traits of economic interest. Therefore, the objective of this study was to determine general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components of newly developed sweetpotato clones.

5.2 Material and methods

5.2.1 Plant materials

Twelve selected sweetpotato genotypes described in Table 5.1 were included in the study to generate new genetic combinations. The parents were selected based on field, *in-vitro* and greenhouse evaluations aiming at flowering ability, yield potential, dry matter content of storage root or drought tolerance (Rukundo et al. 2015).

Table 5.1: Description of sweetpotato parents used in crossing in the study

No	Genotype name	Agronomic traits	Skin color	Flesh color	Origin
1	2005-020	High yield	White	White	NARO
2	2005-034	High DMC	White	Orange	NARO
3	2005-110	High DMC	Yellow	Yellow	NARO
4	4-160	Drought tolerant	White	White	ISAR
5	8-1038	Drought tolerant	Red	White	ISAR
6	K513261	High yield	Red	White	IITA
7	Kwezikumwe	High yield	Yellow	Yellow	ISAR
8	Nsasagatebo	Drought tolerant	White	White	Landrace
9	Otada 24	High yield	Red	White	NARO
10	Purple 4419	Drought tolerant	Red	Orange	ISAR
11	SPK004	High DMC	Pink	Orange	KARI
12	Ukerewe	High DMC	Red	Orange	CIP

DMC: Dry matter content. ISAR: Institut des Sciences Agronomiques du Rwanda, IITA: International Institute of Tropical Agriculture, KARI: Kenya Agriculture Research Institute, NARO: National Agricultural Research Organisation/Uganda, CIP: International Potato Center.

5.2.2 Crosses and mating design

The 12 parents were crossed using a full diallel mating design. A crossing block was established between May 2013 and February 2014 at the Rubona Research Station of the Rwanda Agriculture Board (RAB). Plants were established in a well-prepared and mulched soil supplied with organic manure at planting. The crossing block was provided with supplemental irrigation twice a week. Vines were tended to grow on metallic trellises tied with plastic twine. Weeding and other agronomic practices were carried out when necessary. Flower buds that were near to open were closed with a piece of aluminium foil at about 4:00 pm. The next day each flower was hand pollinated between 6:00 and 9:00 am. Each pollinated flower was labelled and tagged (Figure 5.1). The dried capsules from successful crosses were regularly harvested, threshed and seed kept in a seed bag (Figure 5.2).

Figure 5.1: Immature capsules (left) and mature capsules (right) of sweetpotato resulted from hand crosses.

Figure 5.2: Germination of sweetpotato seeds after scarification (left) and seedling plants (right).

5.2.3 Field establishment for evaluation of clonal families

Seeds harvested after successful crosses were scarified using the method described by Wilson (1989) to induce germination. Briefly, seeds were soaked in concentrated sulphuric acid (98% H_2SO_4) using a vortex mixer for 40 minutes. The acid was discarded and seeds rinsed under running water for 10 minutes. Thereafter, seeds were placed in petri dishes lined with moistened filter paper and covered with cotton wool. The petri dishes were kept in the laboratory at ambient temperature. After three days germinated seeds were transplanted into a seedling nursery bed (Figure 5.2). Seedlings were used to provide vines for subsequent clonal evaluation trials.

Field trials were established in September 2014 at the Karama, Masoro and Rubona Research Stations of RAB. The climate and soil description of the sites are summarised in Table 5.2. Vine cuttings from 64 families (56 successful crosses and 8 parents) were planted in the field using an alpha lattice design with three replications. Cuttings with 4 to 5 nodes were planted with inter-row spacing of 80 cm and intra-row spacing of 50 cm. Experimental plots were bordered by growing two rows of a sweetpotato variety NASPOT 9 O. Weeding was carried out as required and no fertiliser and pesticide were applied. Harvesting was carried out 135 days after planting.

Table 5.2: Geographic location, soil characteristics and rainfall of the Karama, Masoro and Rubona Research Stations sites in Rwanda.

Parameters	Description	Karama	Masoro	Rubona
Geographic coordinates	Latitude	S02°16'46.5''	S01°55'40.0"	S02°29'03.2''
	Longitude	E030°16'06.2''	E030°10'04.0"	E029°45'58.2''
	Altitude (m)	1330	1482	1673
Soil	Types	Sandy and clay soils	Clay and kaolin soils	Clay and kaolin soils
Temperature (°C)	Minimum	17.2	15.7	13.4
	Maximum	28.4	27.1	26.9
Rain fall (mm)	Sept 2014- Feb 2015	567.9	722.4	804.3

5.2.4 Data collection

5.2.4.1 Success rate of crosses

The number of successful crosses carried out was recorded periodically and during harvesting. These data were used to determine success rate of crosses and compatibility between the selected parents. The mean number of viable seeds per capsule was recorded. The percentage of seed germination was determined after seed scarification.

5.2.4.2 Agronomic data

Drought tolerance among clonal families and parents were assessed using canopy temperature (CT) measured with an infrared thermometer (Major Tech, MT694) and canopy wilting (CW) data collected at the Karama site. CT and WT were recorded during sunny days between 12h00 and 15h00. CT was rated using a 1 to 5 scale where, score 1: no wilting, 2: few top leaves showed wilting, 3: half of the leaves showed wilting, 4: severe wilting, about 75 % of the leaves showed wilting and 5: severely wilted and plant death (Blum 2002). Fresh weight of storage root and vine yields, skin and flesh characteristics of storage root were

recorded using the standard descriptors developed by CIP (Huamán 1999). Furthermore, the dry matter content (DMC) was determined following the methods described by Carey and Reynoso (1996) and Tairo et al. (2008) with minor modifications. Briefly, two samples of 50 to 60 g were collected from the biggest, healthy storage roots of each clone and kept in a paper bag. These samples were dried in an oven at 70^{o}C for 72 hours. Dried samples were weighed with an analytical balance and the dry matter content was determined using the formula: Dry matter content (DM) % = [(Dry weight/Fresh weight) x 100].

5.2.5 Data analysis

5.2.5.1 Success rate of crosses, number of seeds per capsule and germination

The success rate (%) of crosses was determined as a ratio of number of harvested seed capsules per total number of crosses carried out. The number of seeds per capsule was determined and averaged for each family. The germination rate was determined as the ratio of germinated seed to total number of seed scarified and planted for each family.

5.2.5.2 Analysis of variance

Plot yield data of storage root, vine and total biomass were converted to t ha^{-1}. Data on yield, dry matter content of storage root and leaf temperatures were subjected to analysis of variance using the GLM procedure of the SAS 9.2 statistical program (SAS Institute, 2004). When significant differences were detected, means were separated using the LSD test procedure at the 5% significance level (Cochran and Cox 1992). The qualitative data of leaf wilting, skin colour and fresh colour were analysed using the non-parametric Krusal-Wallis test procedure of the SPSS computer package (PASW statistics 18.0) (SPSS 2006).

5.2.5.3 Estimation of general and specific combining ability effects and heritability

Analysis of variance was performed using the DIALLEL-SAS05 program (Zhang et al. 2005) to identify the significant level of general combining ability (GCA) of parents and specific combining ability (SCA) of crosses. The diallel analysis was performed using Griffing's (1956) Method 1 Model 2, with the genetic statistical model of:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + b_k + e_{ijkl}$$

Where: Y_{ij} = observed value of the cross between parent i and j; μ = overall mean; g_i = GCA effect of parent i; g_j = GCA effect of parent j; s_{ij} = SCA of the cross between parents i and j;

r_{ij}: reciprocal effect involving the reciprocal crosses between the i^{th} and j^{th} parents, b_k= effect of the k^{th} block; e_{ijkl} = experimental error associated with the $ijkl^{th}$ individual observation, I, j=1…, p: number of parents, k=1…,a : number of blocks, l=1…,c: number of replications.

The relative importance of GCA and SCA effects for each trait was determined following the general predicted ratio (GPR): GCA/SCA = 2MSGCA/(2MSGCA+MSSCA) (Baker 1978). The broad sense heritability (H^2) of the above traits was determined using the following formula:

$H^2 = Vg / V_p$

Where H^2: broad sense heritability, V_g: genetic variance and V_p: Phenotypic variance (Ma-Teresa et al. 1994; Acquaah 2007).

5.3 Results

5.3.1 Compatibility among twelve selected sweetpotato genotypes

Initially 12 parents were selected and included for full diallel crosses. However, complete incompatibility of both direct and reciprocal crosses was observed among the following pairs: 2005-110 x 2005-034, 4-160 x 2005-020, 4-160 x 2005-034, Kwezikumwe x 2005-034, Kwezikumwe x 4-160, SPK004 x 2005-034, SPK004 x 4-160. The proportion of compatible crosses chosen mong the remaining 8 parents are summarized in Table 5.3. Partial incompatibility was observed in crosses involving Otada 24 x 2005-034 and Ukerewe x Nsasagatebo (Table 5.3). The success rate of crosses varied from 1.8% (8-1038 x Ukerewe) to 62.5% (Ukerewe x K513261) with a mean of 18.8% (Table 5.3). The best cross combinations with success rates of > 45% were achieved in crosses between K513261 x 8-1038, 2005-034 x 8-1038 and 2005-034 x 8-1038. The number of seeds per capsule varied from about 1 (Otada 24 x 8-1038) to 3 (2005-034 x Ukerewe) with a mean of 1.6 (Table 5.3). About 3 seeds per capsule resulted from the following crosses: 2005-020 x Nsasagatebo, Ukerewe x 2005-020, 2005-034 x Ukerewe and Nsasagatebo x 8-1038. The germination rate varied from 0% (Ukerewe x 4-160, Nsasagatebo x 8-1038) to 85.1% (2005-020 x 2005-034) with a mean of 41.0% (Table 5.3).

Table 5.3: Compatibility and success rate of crosses with corresponding number of seeds per capsule, and germination rate of scarified seeds eight sweetpotato genotypes

No	Direct crosses	Compatibility	Success rate (%)	Seed/capsule	Germination *(%)*	No	Reciprocal crosses	Compatibility	Success rate (%)	Seed/capsule	Germination (%)
1	2005-034 x 2005-020	C	16.8	1.9	37.5	29	2005-020 x 2005-034	C	13.7	1.0	85.1
2	4-160 x 2005-020	C	15.4	1.5	38.5	30	2005-020 x 4-160	C	12.8	2.0	49.4
3	4-160 x 2005-034	I	0.0	0.0	0.0	31	2005-034 x 4-160	I	0.0	0.0	0.0
4	8-1038 x 2005-020	C	3.7	1.8	53.8	32	2005-020 x 8-1038	C	28.6	2.3	40.0
5	8-1038 x 2005-034	C	6.9	2.5	37.5	33	2005-034 x 8-1038	C	47.8	1.5	72.0
6	8-1038 x 4-160	C	27.0	1.8	30.0	34	4-160 x 8-1038	C	11.4	1.6	45.7
7	K513261 x 2005-020	C	41.2	0.9	53.1	35	2005-020 x K513261	C	28.5	1.0	25.7
8	K513261 x 2005-034	I	0.0	0.0	0.0	36	2005-034 x K513261	I	0.0	0.0	0.0
9	K513261 x 4-160	I	0.0	0.0	0.0	37	4-160 x K513261	I	0.0	0.0	0.0
10	K513261 x 8-1038	C	47.2	1.2	67.5	38	8-1038 x K513261	C	29.8	1.8	47.7
11	Nsasagatebo x 2005-020	C	15.2	1.1	20.8	39	2005-020 x Nsasagatebo	C	18.3	2.7	53.3
12	Nsasagatebo x 2005-034	C	10.5	1.7	10.0	40	2005-034 x Nsasagatebo	C	18.5	1.7	48.8
13	Nsasagatebo x 4-160	C	40.5	1.2	16.2	41	4-160 x Nsasagatebo	C	37.2	1.4	52.2
14	Nsasagatebo x 8-1038	C	8.3	3.0	0.0	42	8-1038 x Nsasagatebo	C	29.3	1.5	30.6
15	Nsasagatebo x K513261	C	19.0	1.7	72.4	43	K513261 x Nsasagatebo	C	44.6	1.5	14.6
16	Otada 24 x 2005-020	C	6.3	1.2	64.2	44	2005-020 x Otada 24	C	14.1	1.3	68.8
17	Otada 24 x 2005-034	I	0.0	0.0	0.0	45	2005-034 x Otada 24	C	20.9	1.5	67.7
18	Otada 24 x 4-160	C	10.3	2.7	47.4	46	4-160 x Otada 24	C	36.0	1.3	47.0
19	Otada 24 x 8-1038	C	11.4	0.9	59.5	47	8-1038 x Otada 24	C	13.2	1.8	14.3
20	Otada 24 x K513261	C	15.2	2.6	46.7	48	K513261 x Otada 24	C	11.8	1.5	20.0
21	Otada 24 x Nsasagatebo	C	38.6	1.7	67.6	49	Nsasagatebo x Otada 24	C	7.8	1.4	50.0
22	Ukerewe x 2005-020	C	30.2	2.8	66.7	50	2005-020 x Ukerewe	C	43.5	1.8	51.4
23	Ukerewe x 2005-034	C	18.6	1.5	50.0	51	2005-034 x Ukerewe	C	11.9	2.9	72.7
24	Ukerewe x 4-160	C	14.3	1.5	0.0	52	4-160 x Ukerewe	C	10.6	1.5	78.4
25	Ukerewe x 8-1038	C	27.5	2.5	82.9	53	8-1038 x Ukerewe	C	1.8	1.9	73.2
26	Ukerewe x K513261	C	62.5	2.5	48.4	54	K513261 x Ukerewe	C	13.4	1.4	47.1
27	Ukerewe x Nsasagatebo	I	0.0	0.0	0.0	55	Nsasagatebo x Ukerewe	C	4.8	1.0	66.7
28	Ukerewe x Otada 24	C	38.2	1.5	30.0	56	Otada 24 x Ukerewe	C	15.4	1.5	70.0
								Mean	**18.8**	**1.6**	**41.0**

C: Compatible, I: Incompatible

5.3.2 Analysis of variance

A separate analysis of variance of each site showed significant differences among tested families for all parameters measured (data not presented). The combined analysis of variance revealed significant interactions (P≤0.01) of family by site effects for storage root and vine yields, total biomass, and dry matter content of storage roots. A non-significant family by site interaction effect was detected for skin and flesh color of storage roots (Table 5.4). The family effects were significant (P≤ 0.01) for all parameters evaluated (Table 5.4). The effects of sites were significantly different at P≤0.05 for storage root and vine yields, total biomass, and dry matter content (Table 5.4). Overall, the family effects made a more significant contribution to the total variability than sites, and family by sites effects as shown by its having the highest sum of squares for all evaluated traits (Table 5.4). Broad sense heritability (H^2) values of 0.95, 0.84 0.68, 0.47, 0.74, 0.50, 0.58 and 0.75 were estimated for canopy temperature, canopy wilting, storage root yield, skin colour, flesh colour, yield of vine, total biomass and dry matter content, respectively (Table 5.4).

Table 5.4: Mean squares and significant tests summarized from a combined analysis of variance of canopy temperature, canopy wilting, yield of storage roots, skin and flesh color, yield of vines, total biomass and dry matter content of storage roots of 64 sweetpotato clones evaluated at three sites in Rwanda

Source of variation	DF	Traits and mean squares							
		CT	CW	Storage root	Skin color	Flesh color	Vine yield	Biomass	DMC
Site	2	64.68**	51.82**	606.98*	186.1 ns	2.08 ns	59597.94**	65617.55**	3214.97**
Rep (Site)	6	62.28ns	4.47 ns	577.78 ns	83.57 ns	1.01 ns	3160.25 ns	5428.14	545.08**
Family	63	31658.56**	982.45**	20534.25**	1456.59**	231.31**	174857.82**	286096.53**	76232.05**
Site x Family	126	1428.54 ns	129.61 ns	8274.97**	1267.96 ns	21.98 ns	114054.01**	134981.53**	22069.69**
H^2		0.95	0.84	0.68	0.47	0.74	0.50	0.58	0.75

DF: degree of freedom, CT: canopy temperature, CW: canopy wilting, H^2: broad sense heritability, DMC: Dry matter content, **: Significant at p<0.01, *: Significant at p<0.05, ^{ns}: not significant).

5.3.3 Field performance of families and parents

5.3.3.1 Canopy temperature and wilting

Experimental clones that showed the lowest CT (< 20^{o}C) were 4-160 x Ukerewe, 4-160 x Nsasagatebo, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020 and Nsasagatebo x Ukerewe. These clones had CT values of 18.9, 19.2, 19.3, 19.4, 19.7 and 19.8 ^{o}C, respectively (Table 5.5). The parental genotypes Nsasagatebo, 4-160 and 8-1038 selected for their known drought tolerance, ranked among the best ten with the lowest CT values measured at 17.8, 18.2 and 18.4 ^{o}C, in that order (Table 5.5). The lowest CW values of 0.9, 1.1, 1.2, 1.3, 1.4, and 1.50 were observed in the following crosses: 4-160 x Nsasagatebo, 4-160 x Ukerewe, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 and K513261 x 4-160, respectively (Table 5). Among the parents, Nsasagatebo showed the lowest CW (1.1), followed by 4-160 (1.5) and 8-1038 (1.6). High levels of CW of 4.0 to 4.3 were found in the families Otada 24 x 2005-020, 2005-034 x Nsasagatebo, Nsasagatebo x 2005-034 and 2005-020 x K513261 (Table 5.5).

5.3.3.2 Storage root yields

The highest overall mean storage root yield of 6.9 t ha^{-1} was observed at Rubona site followed by the Karama and Masoro sites with 6.5 and 4.5 t ha^{-1}, respectively (Table 5.5). At the Karama site, the five families showing the highest yields of storage roots were Nsasagatebo x Otada 24 (18.9 t ha^{-1}), K513261 x Nsasagatebo (16.8 t ha^{-1}), K513261 x 2005-034 (11.9 t ha^{-1}), Otada 24 x 4-160 (10.4 t ha^{-1}) and Ukerewe x 8-1038 (9.9 t ha^{-1}). The best yielding families at Masoro were 8-1038 x K513261 (13.3 t ha^{-1}), Ukerewe x K513261 (10.4 t ha^{-1}), Nsasagatebo x Otada 24 (9.8 t ha^{-1}), K513261 x Otada 24 (8.4 t ha^{-1}), and Ukerewe x Otada 24 (7.9 t ha^{-1}) (Table 5.5). At the Rubona site, the best five families for storage root yield were Otada 24 x Ukerewe (17.6 t ha^{-1}), 4-160 x Nsasagatebo (17.3 t ha^{-1}), Nsasagatebo x 8-1038 (16.8 t ha^{-1}), K513261 x 2005-034 (13.6 t ha^{-1}) and 2005-020 x Ukerewe (13.5 t ha^{-1}) (Table 5.5). Across the three sites, the best five families for storage root yield were Nsasagatebo x Otada 24, Otada 24 x Ukerewe, 4-160 x Nsasagatebo, K513261 x 2005-034 and Ukerewe x K513261 with yield of 11.0, 9.7, 9.3, 9.2 and 8.6 t ha^{-1}, respectively (Table 5.5). The parental genotypes used in these crosses exhibited mean storage root yields of 7.7 to 23.3 t ha^{-1}. The parents, 8-1038 and Ukerewe were the best yielders producing 23.3 and 21.5 t ha^{-1}, respectively (Table 5.5).

5.3.3.3 Dry matter content of storage root

Comparatively, the highest mean dry matter content of storage root (28.1%) was recorded at the Rubona site. At Masoro, the mean DMC was 26.0% while Karama had 22.4% (Table 5.5). At the Karama site, families such as Ukerewe x 2005-034, 4-160 x Nsasagatebo, Otada 24 x 4-160, K513261 x 2005-034, 8-1038 x 4-160 generated the highest DMC values of 35.8, 34.5, 34.4, 33.8 and 32.9 %, respectively (Table 5.5). The best DMC of 40.6, 39.8, 38.9, 38.4, 37.8 % were observed at the Masoro site in the families of 8-1038 x K513261, 2005-034 x Otada 24, Ukerewe x 2005-034, Ukerewe x Otada 24 and 4-160 x Nsasagatebo, respectively (Table 5.5). At Rubona site, the best five families were K513261 x Nsasagatebo (37.4%), Nsasagatebo x 8-1038 (37.2%), 8-1038 x K513261 (36.7%), Nsasagatebo x 2005-034 (35.5%) and Nsasagatebo x Ukerewe (35.3%) (Table 5.5). Across all the study sites, the five best performing families were 8-1038 x K513261, Nsasagatebo x 8-1038, Otada 24 x 4-160, Nsasagatebo x Ukerewe and 4-160 x Nsasagatebo with DMC values of 37.5, 37.2, 35.7, 35.3 and 35.1%, respectively (Table 5). Overall, the parental clones Ukerewe, 2005-034, Nsasagatebo, Otada 24, 4-160, K513261, 2005-020 and 8-1038 displayed high DMC values of 37.3, 35.8, 35.8, 35.1, 34.4, 34.0, 31.9 and 30.2%, respectively (Table 5.5).

Table 5.5: Mean canopy temperature (CT), canopy wilting (CW), yields of storage roots and vines, total biomass and dry matter content of storage roots of families and parents of sweetpotato clones evaluated across three sites in Rwanda

Clones	CT (oC)	CW	Storage root yield (t ha-1)			Mean (t/ha)	DMC (%)			Mean (%)
	Karama		Karama	Masoro	Rubona		Karama	Masoro	Rubona	
Direct crosses										
2005-020 x 2005-034	20.0	3.3	0.8	0.6	6.1	2.5	26.3	31.9	31.8	26.7
2005-020 x 4-160	21.0	3.8	1.7	2.8	3.4	2.6	32.8	35.2	33.6	33.9
2005-020 x 8-1038	20.7	3.4	0.0	0.9	1.5	1.2	0.0	32.8	34.2	33.5
2005-020 x K513261	22.0	4.3	4.0	5.5	4.4	4.6	28.6	36.0	31.7	32.1
2005-020 x Nsasagatebo	23.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2005-020 x Otada 24	20.8	3.5	1.6	1.4	8.1	3.7	28.7	34.7	33.4	29.0
2005-020 x Ukerewe	21.5	3.9	4.9	7.2	13.1	8.4	32.3	36.4	33.2	34.0
2005-034 x 4-160	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2005-034 x 8-1038	21.4	3.2	6.3	3.9	6.3	5.5	28.6	29.9	32.4	30.3
2005-034 x K513261	21.8	2.8	6.4	5.0	8.4	6.6	32.0	35.2	34.8	34.0
2005-034 x Nsasagatebo	23.1	4.1	0.4	3.5	5.3	3.0	26.2	0.0	32.2	29.2
2005-034 x Otada 24	0.0	0.0	0.0	1.9	2.3	2.1	0.0	39.8	28.0	33.0
2005-034 x Ukerewe	21.4	3.4	0.0	0.0	2.1	2.1	0	0.0	35.2	35.2
4-160 x 8-1038	19.3	3.7	6.4	3.1	6.7	5.4	29.8	33.7	35.1	32.9
4-160 x K513261	22.8	1.4	6.9	4.4	10.8	7.4	26.4	35.3	33.8	31.8
4-160 x Nsasagatebo	19.2	0.9	9.8	0.9	17.3	9.3	34.5	37.8	32.9	35.1
4-160 x Otada 24	21.7	3.1	2.1	0.0	1.9	2.0	27.2	0.0	33.7	30.0
4-160 x Ukerewe	18.9	1.1	1.1	4.9	3.2	3.0	29.1	35.3	24.2	26.2
8-1038 x K513261	23.1	2.8	0.0	13.3	6.3	6.5	0.0	40.6	36.8	37.5
8-1038 x Nsasagatebo	20.8	3.8	0.0	0.0	2.8	2.8	0.0	0.0	33.8	33.8
8-1038 x Otada 24	23.6	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8-1038 x Ukerewe	20.1	2.8	9.9	2.6	8.3	6.9	29.9	37.2	26.7	31.3
K513261 x Nsasagatebo	21.8	3.6	16.8	2.8	4.2	7.9	24.5	33.8	37.4	27.4
K513261 x Otada 24	21.2	2.8	4.8	8.4	9.9	7.7	28.4	32.1	33.7	31.4
K513261 x Ukerewe	20.8	2.7	0.0	3.5	12.3	5.3	0.0	26.1	34.3	30.2
Nsasagatebo x Otada 24	20.0	3.8	18.9	9.8	1.4	11.0	26.5	34.6	32.4	27.8
Nsasagatebo x Ukerewe	19.8	3.8	0.0	0.0	5.6	5.6	0.0	0.0	35.3	35.3
Otada 24 x Ukerewe	21.8	3.8	6.4	5.1	17.6	9.7	28.7	36.5	32.0	32.4
Reciprocal crosses										
2005-034 x 2005-020	21.0	2.3	5.0	7.2	6.9	6.4	29.2	32.2	30.7	30.7
4-160 x 2005-020	20.9	2.6	6.0	6.3	8.2	6.8	27.0	29.3	31.3	29.2
4-160 x 2005-034	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8-1038 x 2005-020	19.7	3.1	2.9	2.4	3.6	3.0	22.6	29.0	28.2	26.6
8-1038 x 2005-034	22.1	3.4	8.9	2.6	12.4	7.9	30.0	35.0	33.8	32.9
8-1038 x 4-160	19.4	1.7	7.9	5.1	5.4	6.1	32.9	35.5	32.6	33.6
K513261 x 2005-020	22.0	2.8	5.0	0.7	4.2	1.6	23.7	34.2	30.2	29.4
K513261 x 2005-034	22.4	3.2	11.9	2.0	13.6	9.2	33.8	36.4	31.4	33.9
K513261 x 4-160	21.7	1.5	6.0	0.8	4.5	3.8	27.6	33.3	33.6	31.5
K513261 x 8-1038	20.3	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nsasagatebo x 2005-020	21.5	1.2	3.0	4.0	3.2	3.4	23.9	33.6	31.7	29.7
Nsasagatebo x 2005-034	22.2	4.2	5.1	4.2	1.8	2.0	28.2	31.2	35.5	25.9
Nsasagatebo x 4-160	20.7	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nsasagatebo x 8-1038	21.2	3.3	0.0	0.0	16.8	5.6	0.0	0.0	37.2	37.2
Nsasagatebo x K513261	21.5	3.4	0.0	2.8	4.3	3.5	0.0	35.7	33.9	34.5
Otada 24 x 2005-020	22.8	4.0	1.6	3.4	6.0	3.7	29.9	31.1	31.8	30.9
Otada 24 x 2005-034	23.0	3.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Otada 24 x 4-160	0.0	0.0	10.4	3.4	8.8	7.5	34.4	31.5	31.2	35.7
Otada 24 x 8-1038	20.8	2.2	0.7	7.1	5.7	4.5	29.1	37.0	35.0	33.7
Otada 24 x K513261	20.8	1.9	7.1	6.8	7.4	7.1	28.1	31.9	34.5	31.5
Otada 24 x Nsasagatebo	20.0	1.3	0.0	0.0	2.8	2.8	0.0	0.0	34.0	34.0

Clones	CT (oC)	CW	Storage root yield (t ha-1)			Mean (t/ha)	DMC (%)			Mean (%)
	Karama		Karama	Masoro	Rubona		Karama	Masoro	Rubona	
Ukerewe x 2005-020	21.4	3.3	2.1	1.8	6.5	3.5	28.7	37.7	32.4	32.9
Ukerewe x 2005-034	22.0	3.1	4.6	5.6	7.0	5.7	35.8	38.9	33.8	31.5
Ukerewe x 4-160	21.9	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ukerewe x 8-1038	20.1	3.7	9.9	4.9	10.4	8.4	31.2	37.0	32.3	33.5
Ukerewe x K513261	22.2	3.2	5.2	10.4	10.3	8.6	26.3	36.0	32.9	31.8
Ukerewe x Nsasagatebo	21.9	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ukerewe x Otada 24	22.3	3.2	5.6	7.9	6.5	6.7	25.9	38.4	33.9	29.4
Parents										
2005-020	22.9	3.3	16.8	4.2	2.1	7.7	31.0	28.2	30.5	29.9
2005-034	20.3	4.0	18.9	9.8	9.8	12.8	32.8	40.5	34.3	35.8
4-160	18.2	1.5	19.6	12.6	9.1	13.8	36.0	42.5	32.7	37.1
8-1038	18.4	1.6	29.4	18.2	22.4	23.3	29.2	29.8	31.7	30.2
K513261	22.1	3.8	17.5	14.0	15.4	15.6	33.1	37.1	31.9	34.0
Nsasagatebo	17.9	1.1	8.4	4.2	14.7	9.1	35.0	39.5	33.0	35.8
Otada 24	22.2	3.6	14.7	12.6	11.9	13.1	35.1	40.1	30.3	35.1
Ukerewe	21.1	2.5	46.2	30.8	29.4	21.5	36.3	40.3	30.4	35.7
Average	17.0	2.7	6.5	4.5	6.9	5.7	22.4	26.0	28.1	25.5
LSD (5%)	4.1	1.4	19.7	5.5	10.5	13.2	14.6	2.2	3.1	8.7
CV (%)	1.3	2.2	11.0	6.2	28.8	16.0	8.4	0.1	3.1	3.3

CT: canopy temperature, CW: canopy wilting; DMC: dry matter content of storage roots

5.3.3.4 Combining ability and maternal effects

Parentals and families had highly significant (P≤0.01) general combining ability (GCA) and specific combining ability (SCA) effects, respectively, for CT, CW, yields of storage roots and vines, total biomass and dry matter content of storage root (Table 5.6). The ratios of GCA/SCA effect were >0.5 for CT, CW, yield of storage roots and dry matter content of storage roots, suggesting the predominance of additive over non-additive genetic effects. This ratio was <0.5 for yield of vines and total biomass, implying a significant role of non-additive genetic effect on these traits (Table 5.6).

The reciprocal crosses showing maternal effects were significant (P≤0.05) for CT, CW, flesh color and dry matter content, vine yields and total biomass (Table 5.6). The reciprocal crosses had significant (P≤0.05) differences for CT and WT, yields of storage roots and vines, flesh and skin color, total biomass and dry matter content of storage roots (Table 5.6). The GCA effects and sites had a highly significant interaction (P≤0.01) for vine yield (Table 5.6). Likewise, the SCA effects of crosses and sites had significant interactions for flesh color, yield of vines, total biomass, and dry matter content of storage roots (Table 5.6). Maternal effects and sites showed significant interaction in influencing flesh colour of storage roots, yields of vines and total biomass (Table 5.6).

Table 5.6: Summary mean squares and significant tests of combining abilities and maternal effects for canopy temperature, canopy wilting, yield of storage root, skin color, flesh color, vine yield, total biomass and dry matter content of storage roots of sweetpotato clones evaluated across three sites in Rwanda

Source of variation	DF	CT	CW	Storage root yield	Skin colour	Flesh colour	Vine yield	Total Biomass	DMC
GCA	7	4444.38**	131.99**	2318.59**	155.11**	30.41**	7444.48**	14929.05**	6221.73**
SCA	28	13937.89**	461.97**	14815.47**	941.52**	157.68**	129661.03**	218139.88**	36359.65**
REC	28	13276.30**	388.49**	3400.19**	359.96*	43.23**	37752.31**	53027.60**	33650.66**
MAT	7	2813.66**	95.65**	312.33 ns	50.59	4.67**	7168.89*	8215.46*	4113.67**
NMAT	21	10462.64**	292.84**	3087.86*	309.37*	38.56**	30583.43**	44812.14**	29537.00**
GCA x ENV	14	314.78	16.49	287.04^{ns}	169.03^{ns}	5.76^{ns}	13650.82**	12967.79^{ns}	2540.2^{ns}
SCA x ENV	56	377.05	57.29	4630.03^{ns}	530.24^{ns}	29.69**	60392.33**	72456.75**	9933.92**
REC x ENV	56	736.71	55.83	3357.9^{ns}	568.7^{ns}	26.53**	40010.87**	49556.99**	9595.56**
MAT x ENV	14	163.89	22.58	737.79^{ns}	148.5^{ns}	6.64*	14262.23**	17174.70**	2834.87^{ns}
NMAT x ENV	42	572.82	33.25	2620.11^{ns}	420.2^{ns}	19.89**	25748.64*	32382.29^{ns}	6760.70**
GCA/SCA		0.72	0.7	0.56	0.57	0.61	0.31	0.35	0.58

DF: degrees of freedom, CT: canopy temperature, CW: canopy wilting, DMC: dry matter content, GCA: general combining ability, SCA: specific combining ability, MAT: maternal effect, NMAT: non-maternal effect, **: Significant at p<0.01, *: Significant at p<0.05 (F-probability, ^{ns}: Not significant), REC: reciprocal crosses, ENV: environment, DMC: dry matter content.

5.3.3.5 General combining ability (GCA) effects

Negative GCA effects were estimated for the following parents: 8-1038 (-4.05), Otada 24 (-1.88) and 4-160 (-0.50) for canopy temperature and 8-1038 (-0.74), Otada 24 (-0.18), Ukerewe (-0.10) and 4-160 (-0.04) for canopy wilting, which are in a desirable direction for selection (Table 5.7). The highest GCA effects for yields of storage roots were 0.91, 0.81 and 0.48 for the parental genotypes Nsasagatebo, K513261 and Ukerewe, respectively (Table 5.7). The genotypes that revealed the highest GCA effects for dry matter content were Nsasagatebo (3.12), 2005-034 (2.90) and Ukerewe (0.67) (Table 5.7). The highest GCA effects of 2.86, 2.36 and 1.97 for vine yields were observed in the parents Nsasagatebo, 8-1038 and K513261, respectively. Likewise, the highest GCA effects of 3.71, 2.69 and 1.94 for total biomass were recorded for the genotypes Nsasagatebo, K513261 and Ukerewe, respectively (Table 5.7).

Table 5.7: Estimates of GCA effects for canopy temperature, canopy wilting, yield of storage roots, skin color, flesh color, vine yield, total biomass and dry matter content of eight sweetpotato parents

Genotype	CT	CW	Storage root yield	Skin color	Flesh color	Vine yield	Biomass	DMC
2005-020	0.22^{ns}	0.03^{ns}	-0.95*	-0.21^{ns}	0.01^{ns}	-1.52^{ns}	-2.50^{ns}	-0.19 ^{ns}
2005-034	0.89**	0.45**	-1.81*	0.10^{ns}	-0.07^{ns}	-4.25*	-6.13**	2.90**
4-160	-0.50*	-0.04^{ns}	-1.03^{ns}	-0.10^{ns}	0.07^{ns}	-1.30^{ns}	-2.33^{ns}	-1.16^{ns}
8-1038	-4.05**	-0.74**	-0.85^{ns}	-0.40^{ns}	0.18**	2.36^{ns}	1.53^{ns}	-1.68*
K513261	1.83**	0.25**	0.81^{ns}	-0.04^{ns}	-0.11*	1.97^{ns}	2.69^{ns}	0.40^{ns}
Nsasagatebo	2.38**	0.18*	0.91^{ns}	0.41^{ns}	0.02^{ns}	2.86^{ns}	3.71^{ns}	3.12**
Otada 24	-1.88**	-0.18*	-1.28*	-0.67**	-0.27*	-3.42^{ns}	-4.74*	-4.50**
Ukerewe	0.62**	-0.10^{ns}	0.48^{ns}	0.43^{ns}	-0.09^{ns}	1.60^{ns}	1.94*	0.67*

CT: canopy temperature, CW: canopy wilting, DMC: dry matter content, **: Significant at p<0.01, *: Significant at p<0.05, ^{ns}: Not significant).

5.3.3.6 Specific combining ability (SCA) and maternal effects

The SCA of direct crosses and reciprocals are presented in Table 5.8. The highest negative SCA effects of -13.26, -12.48, -11.61, -10.35 for canopy temperature were observed in the following crosses: Nsasagatebo x Otada 24, 2005-034 x 8-1038, 8-1038 x Nsasagatebo, Otada 24 x 4-160, respectively (Table 5.8). For canopy wilting, significantly negative SCA effects were recorded in Nsasagatebo x Otada 24 (-2.31), 8-1038 x Nsasagatebo (-2.06), 2005-034 x 8-1038 (-1.96), 4-160 x 2005-020 (-1.88) and Otada 24 x 4-160 (-1.54) (Table 5.8). Positive and high SCA effects of 15.75, 9.51, 8.92, 7.86, 6.15, 5.69 and 5.37 were observed for storage root yield in the crosses of 8-1038 x K513261, 4-160 x 8-1038, 2005-034 x 4-160, K513261 x Nsasagatebo, Otada 24 x Ukerewe, Nsasagatebo x Otada 24, 2005-020 x 2005-034, respectively (Table 5.8). The following crosses: Nsasagatebo x Otada 24, 8-1038 x K513261, 2005-034 x 4-160, 4-160 x 8-1038, expressed the highest positive SCA effects of 55.02, 48.44, 27.69 and 23.64, respectively, for vine yields. Similarly, the highest SCA effects for dry matter content were generated in the crosses of Nsasagatebo x Otada 24 (19.29), Otada 24 x 8-1038 (16.85), 4-160 x 8-1038 (14.92), Nsasagatebo x 2005-

020 (14.87), 2005-034 x 4-160 (12.68), Otada 24 x 4-160 (9.37) and 4-160 x K513261 (9.05) (Table 5.8).

The reciprocal crosses showing maternal effects were significant, affecting the success rate of crosses. The direct crosses involving Otada 24 x 2005-034 and Ukerewe x Nsasagatebo were incompatible, while the corresponding reciprocal crosses were compatible (Table 5.3). The maternal effects were significant on CT, CW, storage root yields, flesh colour, vine yields, total biomass and dry matter content of storage roots (Table 5.6). Several direct and reciprocal crosses revealed varied SCA effects (Table 5.8).

Table 5.8: Estimates of SCA and maternal effects for canopy temperature, canopy wilting, yield of storage roots, skin color, flesh color, vine yield, total biomass and dry matter content of sweetpotato genotypes derived from direct and reciprocal crosses of eight parents

Crosses	Traits									
	CT		CW		Storage root yield		Vine yield		DMC	
	Direct	Reciprocal	Direct	Reciprocal	Direct	Reciprocal	Direct	Reciprocal	Direct	Reciprocal
2005-020 x 2005-034	-1.93*	0.28 ns	-0.69*	-0.49*	5.37*	1.94 ns	7.46 ns	8.33 ns	-1.36 ns	1.99 ns
2005-020 x 4-160	2.32**	-9.48**	-0.38 ns	-1.88**	1.30 ns	2.09 ns	1.57 ns	-5.84 ns	1.45 ns	-2.34 ns
2005-020 x 8-1038	-4.39**	-1.06 ns	-0.57**	-0.13 ns	1.44 ns	1.08 ns	11.51*	5.16 ns	4.83**	-1.36 ns
2005-020 x K513261	-1.14 ns	0.52 ns	-0.20 ns	-0.75**	-3.07 ns	-1.48 ns	-11.29*	-8.37 ns	-0.82 ns	-1.38 ns
2005-020 x Nsasagatebo	0.18 ns	-1.19 ns	0.21 ns	-0.36 ns	-1.94 ns	1.69 ns	-9.95 ns	7.64 ns	-0.78 ns	14.87**
2005-020 x Otada 24	3.71**	-0.81 ns	0.69**	0.25 ns	-1.18 ns	-0.02 ns	-6.27 ns	-3.83 ns	-9.02**	0.98 ns
2005-020 x Ukerewe	-0.56 ns	-0.08 ns	0.70**	-0.27 ns	-0.95 ns	-2.47 ns	9.05 ns	0.81 ns	0.89 ns	-0.51 ns
2005-034 x 4-160	3.32**	0.00	0.94**	0.00	8.92**	0.00	27.69**	0.00	12.68**	0.00
2005-034 x 8-1038	-2.48**	0.35 ns	-1.96**	0.08 ns	-4.08*	1.21 ns	-22.64**	2.11 ns	-22.65**	1.30 ns
2005-034 x K513261	2.35**	0.31 ns	0.32 ns	0.23 ns	0.98 ns	1.28 ns	8.39 ns	14.63*	6.87**	-0.07 ns
2005-034 x Nsasagatebo	2.21**	-0.23 ns	0.13 ns	0.03 ns	2.03 ns	-0.53 ns	17.91**	-2.04 ns	6.49**	4.91*
2005-034 x Otada 24	6.32**	10.99**	1.62**	1.56**	-1.15 ns	-1.91 ns	-11.55*	-10.08 ns	1.21 ns	-16.49**
2005-034 x Ukerewe	-6.16**	-1.00 ns	-1.04**	-0.15ns	-3.50*	2.51 ns	-11.81*	4.84 ns	-8.5**	4.45*
4-160 x 8-1038	12.29**	-1.37**	1.85**	-1.04**	9.51**	0.38 ns	23.64**	5.66 ns	14.92**	0.38 ns
4-160 x K513261	5.44**	0.47 ns	0.45*	0.02 ns	-0.15 ns	-1.79 ns	-5.60 ns	-4.71 ns	9.05**	-0.17 ns
4-160 x Nsasagatebo	6.87**	9.86**	1.30**	1.53**	-0.45 ns	-4.67*	-2.42 ns	-18.08**	4.73**	-17.54**
4-160 x Otada 24	-1.24*	-10.35**	-0.29 ns	-1.54**	0.84 ns	2.67 ns	-2.44 ns	-5.07 ns	-1.78 ns	9.37**
4-160 x Ukerewe	-3.26**	10.46**	-0.36 ns	1.77**	-0.74 ns	-1.52 ns	3.38 ns	-18.68**	1.85 ns	-13.10**
8-1038 x K513261	0.70 ns	9.63**	0.95**	1.11**	15.75**	-3.27 ns	48.44**	-10.38 ns	3.94 ns	-15.99**
8-1038 x Nsasagatebo	-11.61**	0.18 ns	-2.06**	-0.26 ns	-4.41**	2.33 ns	-16.03**	-5.25 ns	-13.02**	1.48 ns
8-1038 x Otada 24	3.04**	-1.92**	0.78**	-0.44 ns	-2.23 ns	2.26 ns	-10.69*	11.20 ns	-2.58 ns	16.85**
8-1038 x Ukerewe	1.21*	0.01 ns	-0.30 ns	0.43 ns	-4.99**	0.74 ns	-13.96**	1.00 ns	-9.70**	1.11 ns
K513261 x Nsasagatebo	-0.64 ns	-0.11 ns	0.25 ns	-0.07 ns	7.86**	-2.78 ns	2.10 ns	-17.45**	2.30 ns	0.34 ns
K513261 x Otada 24	3.13**	-0.69 ns	0.78**	-0.48*	-0.44 ns	-0.30 ns	2.36 ns	-10.21 ns	3.64**	0.03 ns
K513261 x Ukerewe	-0.54 ns	0.69 ns	-0.46*	0.28 ns	0.05 ns	1.69 ns	10.08 ns	5.99 ns	2.19 ns	8.44**
Nsasagatebo x Otada 24	-13.26**	-0.03 ns	-2.31**	-1.22**	5.69*	-9.22**	55.02**	-2.92 ns	19.29**	-5.70**
Nsasagatebo x Ukerewe	3.73**	10.43**	0.09 ns	1.38**	4.99**	-0.93 ns	-9.38 ns	-1.28 ns	0.46 ns	-10.02**
Otada 24 x Ukerewe	2.91*	0.23 ns	0.66*	-0.29 ns	6.15**	-1.50 ns	15.11*	1.90 ns	8.31**	-1.51 ns

CT: canopy temperature, CW: canopy wilting, DMC: dry matter content, **: Significant at p<0.01, *: Significant at p<0.05, ns: Not significant.

5.4 Discussion

5.4.1 Success rate of crosses, seed set and germination

The self- and cross-incompatibility of sweetpotato remains a major impediment for sweetpotato breeding (Martin 1965; 1970; Kobayashi et al. 1993). Gasura et al. (2010) observed that some sweetpotato clones can be crossed easily. However, some female parents are difficult to cross with specific male parents. The same results were observed in this study. Complete incompatibility of both direct and reciprocal crosses was observed in seven pairs while eleven crosses showed partial incompatibility (Table 5.3). This result suggests that the success of genetic improvement of sweetpotato depends on an efficient selection of compatible parents.

The success rate of crosses varied from 3.7 to 66.7 % with a mean of 19.3% (Table 5.3). According to Lebot (2009) the success rates of crosses depend on various factors such as compatibility, vigour of parents and weather conditions. According to Jones and Deonier (1965) and Jones et al. (1986) each capsule of sweetpotato has a maximum of 4 seeds, often with 1 to 2 seeds. Reportedly hand pollinated flowers produced up to 2 and rarely 3 seeds per capsule while insect pollinated flowers produced 3 to 4 seeds per capsule (Gasura et al. 2010). Lebot (2009) reported that about 50% of hand pollinated flowers produce two seeds. Similar results were observed in this study in which the number of seeds per capsule varied from 1 to 3 with a mean of 2 (Table 5.3).

Sweetpotato seed germination is irregular because of the hard seed coat (Miller 1937). Chemical and mechanical scarification has been recommended to overcome this challenge (Wilson et al. 1989). In this study, variable seed germination was observed after scarification ranging from 10 and 85.1% with a mean of 43.8% (Table 5.3). Preliminary tests have shown that seeds that float in water germinate poorly. Most of the seed that sank was reportedly viable (Martin 1946).

5.4.2 Performance of newly developed families and parents

Previous reports pointed out highly significant ($P < 0.001$) effects of environment, genotype and genotype by environmental interactions on qualitative and quantitative traits of

sweetpotatoes (Mwololo et al. 2009; Adebola et al. 2013; Kathabwalika et al. 2013). In the present study significant interactions between family and site were observed affecting yields of storage roots and vines, total biomass and dry matter content of storage roots of sweetpotato. The family effects were significant for all parameters evaluated, while site effects were significant for yields of storage roots and vines, total biomass and dry matter content of storage roots (Table 5.4). Kathabwalika et al. (2013) reported that the effects of genotypes, environments and their interactions contributed to 43.4%, 34.8%, and 21.8%, of the variation in storage root yields, respectively. Likewise, the strong contribution of genotype has been observed in the performance of sweetpotato genotypes (Nedunchezhiyan et al. 2007; Chataika et al. 2010). The highest proportion of the sum of squares of families for all evaluated traits indicated the existence of considerable genetic variation among the newly developed clones (Table 5.4).

5.4.3 Drought tolerance

A positive and significant correlation between yield and canopy temperatures were observed under drought stress conditions (Royo et al. 2002; Guendouz et al. 2012). This suggested that canopy temperature can be regarded as a valuable parameter to identify drought tolerance of crop genotypes. The canopy temperatures of wheat genotypes grown under well-watered conditions and drought stressed conditions was significantly different (Guendouz et al. 2012). In this study, families showed variation in canopy temperatures ranging from 16.9 to 22.7 ^{o}C. These canopy temperatures found in this study were lower than the report of Guendouz et al. (2012) under irrigated conditions (23.8 to 28.0°C) and under water stressed conditions (27.0 to 30.7°C). Canavar (2013) reported that canopy temperature is lower and dependent on the ambient temperatures of the environment. Therefore, ambient temperatures of experimental sites are different and can provide variable canopy temperatures.

Genotypes with water stress tolerance express low canopy temperatures under water stressed conditions (Blum 2011; Pathan et al. 2014). This was also found in the present study in which some of the selected genotypes for drought tolerance (Nsasagatebo, 4-160 and 8-1038) had the lowest canopy temperatures (Table 5.5). The families that showed the lowest canopy temperature (< 20^{o}C) were, 4-160 x Ukerewe, 4-160 x Nsasagatebo, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020, Nsasagatebo x Ukerewe, with canopy

temperatures of 18.9, 19.2, 19.3, 19.4, 19.7, 19.8^{o}C, respectively (Table 5.5). Canopy temperatures measured using infrared thermometer provided useful data in determining drought tolerance of sweetpotato clones under water limited conditions. Therefore, this parameter can be considered as a rapid approach to assess drought tolerance in crop plants. However, other complementary techniques and parameters such as leaf water potential, canopy wilting, stomatal conductance, canopy senescence which are not plant destructive approaches and yield potential should be measured for efficient screening of crop genotypes for drought tolerance (Canavar 2013).

Canopy wilting is the first visible symptom of water stress (Carter et al. 2006; Pathan et al. 2014). A slow canopy wilting and minimal yield reduction under drought stress are important traits that should be evaluated to determine drought tolerance in crop genotypes (Pathan et al. 2014). For example, in soybean, slow canopy wilting and sustained nitrogen fixation under drought stress have resulted in yield increases in water-limited environments (Sinclair et al. 2007). In this study, the lowest mean canopy wilting scores of 0.86, 1.09, 1.19, 1.33, 1.33, 1.47, 1.50 were observed among the crosses of 4-160 x Nsasagatebo, 4-160 x Ukerewe, Otada 24 x 4-160, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 and K513261 x 4-160, respectively (Table 5.5). Among parents, Nsasagatebo developed the lowest level of canopy wilting (1.1), followed by 4-160 (1.5) and 8-1038 (1.6). Based on low canopy temperature and canopy wilting, the following families were ranked and selected: 4-160 x Nsasagatebo, 4-160 x Ukerewe, Otada 24 x 4-160, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 , 513261 x 4-160, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020 and Nsasagatebo x Ukerewe.

5.4.4 Yield of storage roots

Sites had significant effects on the yield of storage roots of sweetpotato clones. Previous reports showed that the average storage root yield was higher in the Nairobi region (16.8 t ha^{-1}) than in Western Kenya (15.2 t ha^{-1}) (Mwamburi and Ndolo 2013). Traits associated with storage root yields such as size of storage roots and number of storage roots per plant have been reported to be strongly affected by changes in environmental conditions (Nedunchezhiyan et al. 2007). In this study, sites caused variation in the storage root yields. The highest mean storage root yield of 6.9 t ha^{-1} was observed at Rubona, followed by Karama with 5.5 t ha^{-1} and Masoro with 4.5 t ha^{-1} (Table 5.5). In Uganda Gasura et al.

(2010) reported three classes; high yielding (18-30 t ha^{-1}), moderately yielding (11-17 t ha^{-1}) and low yielding (<11 t ha^{-1}) sweetpotato genotypes. Storage root yields ranging between 63.3 and 22.1 t ha^{-1} have been reported in South Africa (Adebola et al. 2013). The storage root yields found in this study were much lower than in these reports. The tested clones are in the early selection phase and their yield response could be affected by their genetic constitution and the environment. This requires continuous selection of genetically fixed, stable and high yielding clones across representative sites in Rwanda. Moreover, fertilizers, pesticides and irrigation were not applied in this study, whereas they were in the other trials such as reported by Adebola et al. (2013).

5.4.5 Dry matter content of storage roots

Dry matter content of sweetpotato storage roots is influenced by site and genotype effects (Shumbusha et al. 2010). Variable dry matter content has been reported in Kenya to range from 29.6 to 26.6%. Significant effects of site and genotype on dry matter content were observed in the present study. The highest dry matter content (28.3%) was observed at Rubona followed by Masoro (26.3 %) and Karama (22.6%) (Table 5.5).

In another study, dry matter contents of sweetpotato storage roots varied from 25.6 to 33.3 % among families, while these values were 25.3 to 45.4 % for individual clones (Courtney et al. 2008). In the present study, dry matter content among families varied from 25.9 to 37.5 % (Table 5.5). The best families in dry matter content across site were, 8-1038 x K513261, Nsasagatebo x 8-1038, Otada 24 x 4-160, Nsasagatebo x Ukerewe and 4-160 x Nsasagatebo. These families had dry matter content of 37.5, 37.2, 35.7, 35.3 and 35.1% in the storage roots, respectively (Table 5.5). These families are promising for future release, by showing DMC of >25%, an important attribute for farmer's adoption of new sweetpotato varieties in Rwanda. Therefore, further evaluations across representative growing environments are needed to identify their adaptability and stability.

5.4.6 Heritability

Genetic improvement of crop plants depends on the magnitude of heritability of economic traits (Maluf et al. 1983; Ma-Teresa et al. 1994). Previous results recorded heritability of 0.93 for dry matter content of sweetpotato storage roots among full-sibling families (Courtney et

al. 2008). Heritability of 0.11 to 0.75 was reported for root yield, 0.07 to 0.75 for root size, and 0.26 to 0.50 for dry matter (Ma-Teresa et al. 1994). Heritability of non-marketable roots was 0.6 (Maluf et al. 1983). The present study found heritability of 0.95, 0.84, 0.68, 0.47, 0.74 and 0.75, 0.50 and 0.58 for canopy temperature, canopy wilting, storage root yield, skin colour, flesh colour, dry matter content, yield of vines and total biomass, respectively (Table 5.4). Some of these estimates agree with previous findings. According to Courtney et al. (2008), heritability differs from one population to another, and with the test environment. Heritability for nutrient composition may vary due to soil nutrients such as the macro- and micro-elements. High heritability estimates indicate a higher frequency of genes controlling the traits (Ma-Teresa et al. 1994) and the potential to improve these traits with traditional breeding strategies (Courtney et al. 2008; Mwije et al. 2014). Accordingly, heritability observed for canopy temperature, canopy wilting, yield of storage roots and dry matter content of storage roots indicated that the genetic improvement of these traits can be achieved through conventional breeding.

5.4.7 General and specific combining ability effects

The GCA and SCA analysis revealed significant differences ($P<0.01$) among genotypes for canopy temperature, canopy wilting, yield of storage roots and vines, total biomass and dry matter content of storage roots (Table 5.6). Saad (1993) reported that effects of GCA and SCA were significant for yield, storage root number and mean root weight. GCA and SCA mean squares for flesh yield and root dry matter content were highly significant (Chiona 2009). Previous diallel analysis revealed significant GCA and SCA effects in the study of heritability of putative drought adaptation traits in sweetpotato (Mwije et al. 2014).

The GCA/SCA ratio was > 50% for canopy temperature, canopy wilting, storage root yields, skin colour, flesh colour and dry matter content of storage roots but nit for vines yield and total biomass (Table 5.6). These results agree with the findings of Chiona (2009) who reported that the ratio of GCA/SCA for storage root yield was 0.68. Baker (1978) indicated that high ratios of GCA/SCA mean that the additive gene action makes a stronger contribution to the expression of specific traits than non-additive gene action. This study revealed that the additive gene action had important effects in expression of canopy temperature, canopy wilting, storage root yield, skin colour, flesh colour and dry matter

content of storage roots, while the non-additive gene action had significant effects in the expression of vine yields and total biomass.

In the drought tolerance studies, genotypes that presented the highest negative general combining abilities for canopy temperature and canopy wilting were the most desirable. These genotypes were 8-1038 (-4.05), Otada 24 (-1.88) and 4-160 (-0.50) for canopy temperature and 8-1038 (-0.74), Otada 24 (-0.18), Ukerewe (-0.10) and 4-160 (-0.04) for canopy wilting (Table 5.7). The selection of parents based on their combining ability, and understanding the genetic control of key traits ensure the efficiency of a breeding programme (Nadarajan and Gunasekaran 2005; Sleper and Poehlman 2006). In the current study, good general combiners for drought tolerance were the parents, 8-1038, Otada 24 and 4-160. These genotypes revealed the lowest canopy temperature and wilting. Good combiners for high storage root yields were Nsasagatebo, K513261 and Ukerewe, while good combiners for high dry matter content were, Nsasagatebo, 2005-034 and Ukerewe (Table 5.7).

Specific combining ability effects are useful to identify specific crosses with desirable traits (Acquaah 2007). In this study, the best specific crosses for drought tolerance were Nsasagatebo x Otada 24, 2005-034 x 8-1038, 8-1038 x Nsasagatebo and Otada 24 x 4-160. These had the lowest canopy temperature and wilting level (Table 5.8). The crosses of 8-1038 x K513261, 4-160 x 8-1038, 2005-034 x 4-160, K513261 x Nsasagatebo, Otada 24 x Ukerewe, Nsasagatebo x Otada 24 and 2005-020 x 2005-034 were selected for their high storage root yields. The best crosses for high dry matter content were Nsasagatebo x Otada 24, Otada 24 x 8-1038, 4-160 x 8-1038, Nsasagatebo x 2005-020, 2005-034 x 4-160, Otada 24 x 4-160 and 4-160 x K51326 (Table 5.8).

5.4.8 Maternal effect

Maternal effects are common in sexually reproducing crops, and these can be detected by measuring the genetic differences of individuals arising from direct and reciprocal crosses (Grami and Stefansson 1977). A trait is controlled by nuclear genes when the direction of cross did not affect its quantity and quality of expression (Gedye 2005). Lin et al. (2007) reported maternal effects on yields of storage roots and vines in Clone I selections of sweetpotato. In the current study the maternal effects affected the compatibility between genotypes where partial compatibility was observed in the crosses of Otada 24 x 2005-034

and Ukerewe x Nsasagatebo (Table 5.3). The maternal effects were significant among families for canopy temperature, canopy wilting, flesh color, dry matter content, yield of vines and total biomass. This was confirmed by the significant effects of reciprocal crosses and their varied SCA effects (Table 5.6 and 5.8). The existence of maternal effects is important for sweetpotato breeders in considering the direction of crosses to be performed to improve a particular trait.

5.5 Conclusions

The present study examined combining abilities, maternal effects and heritability of drought tolerance, yield and yield components in newly developed sweetpotato clones. High levels of broad sense heritability (> 0.50) and significant GCA and SCA effects were detected for canopy temperature, canopy wilting, storage root yields and dry matter content of storage roots, indicating that these traits can be improved through conventional breeding. Both additive and non-additive gene actions were important in the expression of drought tolerance, storage root yields and storage root dry matter content of the tested sweetpotato crosses. The ratio of GCA/SCA >50% on canopy temperature, canopy wilting, yield of storage roots and dry matter content of storage roots revealed the predominance of additive gene action. The best general combiners were parents 8-1038, Otada 24 and 4-160 for drought tolerance; Nsasagatebo, K513261 and Ukerewe for high storage root yield; and Nsasagatebo, 2005-034 and Ukerewe for high dry matter content. Based on low canopy temperatures, low levels of canopy wilting and high storage root yields and dry matter content, the families selected for breeding or direct production were 2005-020 x 4-160, 2005-034 x 2005-020, 8-1038 x 4-160, 8-1038 x Ukerewe, Nsasagatebo x Otada 24, Otada 24 x 8-1038, Otada 24 x K513261, Ukerewe x 2005-034, and Ukerewe x 8-1038. The selected families are recommended for further evaluation to determine their yield potential and stability for release in Rwanda or similar environments.

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6. Chapter Six: Genotype by environment interaction and yield stability of sweetpotato clones in Rwanda

Abstract

Assessment of adaptability and yield stability of candidate genotypes is an important step in cultivar selection and recommendation for sustainable sweetpotato production. The objective of this study was to determine genotype by environment interaction and yield stability of 45 selected sweetpotao breeding clones. Field trials were conducted using an alpha lattice design with three replications across six environments in Rwanda. Data on fresh root yield and dry matter content were collected and subjected to the additive main effect and multiplicative interaction (AMMI) and genotype and genotype-environment (GGE) bi-plot analyses. Results showed significant interaction effects (p=0.001) of clone x site x season, clone x site and clone x season on yield and dry matter content of storage roots. Site x season interaction had significant effects on dry matter content of storage roots only. Candidate clones designated as clone 21 (4-160 x 2005-020), 137 (K513261 x 2005-034) and 22 (4-160 x 2005-020) had the highest storage root yield of 38.2, 23.4 and 20.8 t ha^{-1}, respectively. The highest dry matter content of storage roots of 40.6, 35.9 and 32.9% were recorded in clones 21, 137 and 259 (2005-034 x 8-1038), respectively. AMMI analysis showed that genotypes (G), environments (E) and G x E interaction effects contributed to 20.7%, 17.6% and 61.7% of the total variation of clones for fresh root yields, respectively. The contributions of G, E, and G x E effects, respectively, were 19.5%, 11.8% and 68.7% to the total variation in root dry matter content. AMMI stability values (ASV) revealed the following most stable genotypes: Nsansagatebo, 210 (8-1038 x 4-160), 2005-110 and 456 (SPK004 x K513261), for storage root yield and clones 46 (Kwezikumwe x 2005-020), 509 (Ukerewe x Kwezikumwe), Mugande, and 358 (Ukerewe x 8-1038) for dry matter content of storage roots. Overall, the present study identified high yielding and stable candidate sweetpotato clones such as 21, 137 and 22 (4-160 x 2005-020) for their high yields and dry matter content of storage roots. These clones are recommended for direct production or sweetpotato breeding programmes in Rwanda and similar environments.

Key words: AMMI, breeding clone, GGE-biplot, Rwanda, stability, sweetpotato.

6.1 Introduction

Sweetpotato (*Ipomoea batatus* L.) is an important food, feed and cash crop in many tropical and sub-tropical regions of the world (FAOSTAT 2013; Laurie and Magoro 2008). In sub-Sahara Africa, sweetpotato is grown across and estimated area of 2.1 million hectares, with an annual production of about 9.9 million tons (FAOSTAT 2013). In Rwanda, sweetpotato is an important component of the farming system. During the main crop growing season of Rwanda (season A) in 2015, sweetpotato occupied 5.2% of the total cultivated land accounting for 14.3% of the total crop production (NISR 2015). The use of sweetpotato as a food security crop and source of pro-Vitamin A for vulnerable people such as malnourished children, HIV patients and pregnant women has boosted its production in many areas of East Africa (Osiru et al. 2009).

Development of high and stable yielding and climate smart crop varieties such as sweetpotato is crucial for sustainable crop production and food security for the growing population of sub-Saharan Africa in the face of global climate change and varied preferences of end-users (Cochard et al. 2008). Assessment of adaptability and yield stability of candidate genotypes is an important step in cultivar selection and recommendation for sustainable sweetpotato production. Crop varieties perform well in environments in which they are adapted (Acquaah 2007). The performance of a genotype is the product of its genetic constitution, the environment and genotype by environment interaction (GxE) (Yan et al. 2001). The performance of a crop variety is quantified in terms of its wide or specific adaptability and yield stability (Abidin et al. 2005). A variety that performs well over large growing areas presenting a high mean yield has a wide adaptability (Acquaah 2007; Mwanga et al. 2007). A variety has a specific adaptability when it ranks among the highest yielder only at some locations (Acquaah 2007). Differential response of a genotype across a given set of environments is the results of GxE interactions (Nasayao and Saldaga 1988; Osiru et al. 2009; Russell and Eberhart 1966). Statistically, GxE interactions occur if the difference in performance between any two genotypes is inconsistent over the test environments (Acquaah 2007).

Genotype by environment interaction has direct relevance during cultivar selection and recommendation to growers (Caliskan et al. 2007; Nasayao and Saldaga 1988). Environmental effects often mask the genetic component which is the cause of poor genetic

gain during selection of quantitative traits such as yields and yield components (Fasoula and Fasoula 2003). This requires identification of promising genotypes adapted to the target growing areas after multi-environment trials involving target locations and growing seasons/years. This will aid to measure adaptability and yield stability of candidate varieties. Various statistical methods and parameters are available to measure GxE interaction and yield stability of genotypes (Bacusmo et al. 1988; Collins et al. 1987; Jones et al. 1986). The additive main effects and multiplicative interaction (AMMI) (Zobel et al. 1988) and genotype and genotype by environment (GGE) (Gabriel 1971) methods are the most widely used multivariate approaches to analyse data collected from multi-environment trials. The AMMI model combines analysis of variance for the genotype and environment main effects with principal component analysis of the G x E interactions (Gauch and Zobel 1996). The GGE integrates the genotypic main effect with the G x E interaction effect (Yan et al. 2000).

The storage root yield of sweetpotato is highly sensitive to environmental changes. Mwanga et al. (2007) reported that the GxE interactions have a great influence on the performance of sweetpotato. Gruneberg et al. (2005) reported that the G×E interaction component were larger than, or nearly equal to, the genetic variation of sweetpotato yields (Grunerberg et al. 2005). Manrique and Hermann (2000) and Tekalign (2007) observed lack of association between high yield and stable performance attributed to G×E interactions. GxE interaction was significant for yield and quality of sweetpotato storage root (Caliskan et al. 2007; Carpena et al. 1980; Manrique and Hermann 2000; Ngeve 1993). Grunerberg et al., (2005) observed a small GxE interaction for nutritional traits of sweetpotato in multi-environmental trials. This indicates that selection for high nutritional value could be conducted relatively in a few selected environments without compromising the efficiency of selection.

In an attempt to develop improved sweetpotato cultivars, candidate clones were crossed and suitable recombinants were selected under Rwandan conditions. Best performing and stable clones should be ranked and selected across representative test environments for direct production or for sweetpotato breeding programs. Therefore, the objectives of this study were to determine G x E interaction and yield stability of sweetpotato breeding clones recently bred in Rwanda and to identify promising genotypes.

6.2 Materials and Methods

6.2.1 Plant materials

A total of 45 clones were included in the present study. Thirty two were newly bred and candidate clones (Table 6.1). The candidate clones were selected based on their relatively high storage root yields and dry matter content of storage roots and drought tolerance. Twelve parental clones used in developing the new clones and a control variety ‘Mugange’ were included in the study. The description of the plant materials is given in Table 6.1.

Table 6.1: Description of sweetpotato clones and varieties used in this study based on previous study

ID	Pedigree/Name	Origin	Key traits	Skin color	Flesh color
21	4-160 x 2005-020	Newly bred	High yield and drought tolerance	Purple	Cream
22	4-160 x 2005-020	Newly bred	Drought tolerance	Cream	White
37	Kwezikumwe x 2005-020	Newly bred	Drought tolerant	Cream	Cream
42	Kwezikumwe x 2005-020	Newly bred	High DMC and drought tolerance	Pink	White
46	Kwezikumwe x 2005-020	Newly bred	High yield and drought tolerance	Cream	Yellow
62	Otada 24 x 2005-020	Newly bred	Drought tolerant	Purple	Yellow
81	Purple 4419 x 2005-020	Newly bred	High yield and DMC and drought tolerance	Cream	Cream
88	Purple 4419 x 2005-020	Newly bred	High yield and drought tolerance	Cream	Cream
103	SPK004 x 2005-020	Newly bred	Drought tolerant	Cream	Cream
137	K513261 x 2005-034	Newly bred	High yield and DMC and drought tolerance	Purple	White
210	8-1038 x 4-160	Newly bred	High yield and DMC and drought tolerance	Pink	White
249	2005-034 x 8-1038	Newly bred	High yield and DMC and drought tolerance	Cream	White
259	2005-034 x 8-1038	Newly bred	High yield and DMC and drought tolerance	Cream	Orange
321	SPK004 x 8-1038	Newly bred	High DMC	Purple	White
358	Ukerewe x 8-1038	Newly bred	High DMC and drought tolerance	Purple	White
381	2005-034 x K513261	Newly bred	High DMC and drought tolerance	White	Yellow
442	Purple 4419 x K513261	Newly bred	High DMC and drought tolerance	Pink	Orange
455	SPK004 x K513261	Newly bred	High DMC and drought tolerance	Pink	White
456	SPK004 x K513261	Newly bred	High DMC and drought tolerance	Purple	Yellow
460	Ukerewe x K513261	Newly bred	High DMC and drought tolerance	Purple	Cream
488	Nsasagatebo x Kwezikumwe	Newly bred	High DMC and drought tolerance	Cream	Yellow
509	Ukerewe x Kwezikumwe	Newly bred	High DMC	White	Cream
577	Nsasagatebo x Otada 24	Newly bred	High DMC and drought tolerance	Cream	Cream
613	Otada 24 x Purple 4419	Newly bred	High DMC and drought tolerance	White	White
639	K513261 x SPK004	Newlybred	High DMC and drought tolerance	Purple	Yellow
641	K513261 x SPK004	Newly bred	High DMC and drought tolerance	White	Orange
661	2005-020 x Ukerewe	Newly bred	High DMC and drought tolerance	Cream	Purple
700	8-1038 x Ukerewe	Newly bred	High DMC and drought tolerance	Pink	White
721	Otada 24 x Ukerewe	Newly bred	High DMC and drought tolerance	Pink	Yellow
733	Purple 4419 x Ukerewe	Newly bred	High DMC	Cream	Yellow
744	Purple 4419 x Ukerewe	Newly bred	High DMC	Purple	Yellow
746	Purple 4419 x Ukerewe	Newly bred	High yield	Cream	Yellow
P1	2005-020	NARO	High yield	White	White
P2	2005-034	NARO	High DMC	White	Orange
P3	2005-110	NARO	High DMC	Yellow	Yellow
P4	4-160	ISAR	Drought tolerant	White	White
P5	8-1038	ISAR	Drought tolerant	Red	White
P6	K513261	IITA	High yield	Red	White
P7	Kwezikumwe	ISAR	High yield	Yellow	Yellow
Control	Mugange	Local variety	Adopted and adapted	Red	White

ID	Pedigree/Name	Origin	Key traits	Skin color	Flesh color
P8	Nsasagatebo	Landrace	Drought tolerant	White	White
P9	Otada 24	NARO	High yield	Red	White
P10	Purple 4419	ISAR	Drought tolerant	Red	Orange
P11	SPK004	KARI	High DMC	Pink	Orange
P12	Ukerewe	CIP	High DMC	Red	Orange

ID: clone identification number, P1, P2 … P12 represent parents such as Parent 1 (P1), DMC: Dry matter content, ISAR: Institut des Sciences Agronomiques du Rwanda, KARI: Kenya Agriculture Research Institute, NARO: National Agricultural Research Organisation/Uganda, CIP: International Potato Center.

6.2.2 Description of the study sites

The study was conducted in two growing seasons (season A: September 2014 - February 2015 and season B: March - August 2015) each at Karama, Masoro and Rubona Research Stations of the Rwanda Agriculture Board (RAB), respectively, providing a total of six environments (Table 6.2). The study sites represent the major sweetpotato growing agro-ecology in Rwanda. Agro-climatic and geographic descriptions of the study sites are presented in Table 6.2. In general, soil, climatic, and biological conditions of the study sites vary considerably. Season A is the main growing season with extended and heavy rainfalls, while Season B is the short growing season with reduced rainfall.

Table 6.2: Description of Karama, Masoro and Rubona research sites of the Rwanda Agriculture Board where the present study was conducted

Environment code	Site	Season	Geographic position			Annual rainfall‡ (mm)	Temperature (°C)		Soil type
			Longitude	Latitude	Altitude †(m.a.s.l.)		Min.	Max.	
E1	Karama	A (September 2014 - February 2015)	E030°16'06.2''	S02°16'46.5''	1330	567.9	17.2	28.4	Sandy and clay soils
E2	Masoro		E030°10'04.0''	S01°55'40.0''	1482	722.4	15.7	27.1	Clay and kaolin soils
E3	Rubona		E029°45'58.2''	S02°29'03.2''	1673	804.3	13.4	26.9	Clay and kaolin soils
E4	Karama	B (March - August 2015)	_	_	_	351.8	22.1	32.2	_
E5	Masoro		_	_	_	407.3	19.5	31.4	_
E6	Rubona		_	_	_	461.7	17.6	28.5	_

† (m.a.s.l.): meters above sea level, ‡: Rainfall during growing season.

6.2.3 Experimental design and field establishment

Clones were established using a 5×9 alpha-lattice experimental design with three replications at each location. Vine cuttings of five nodes were prepared for field planting. Cuttings were planted on ridges with inter-row spacing of 80 cm and intra-row spacing of 50 cm. The experimental plot consists of three rows consisting of 30 plants. Experimental plots were bordered by growing two rows of a sweetpotato variety Ukerewe. Weeding was carried out as required and no fertilisers and pesticides were applied. Harvesting was carried out 135 days after planting.

6.2.4 Data collection

The following data were collected: weight of storage root, weight of vine and dry matter content of storage root. Data on yield and yield components were recorded on the inner row of experimental plots. Six plants were harvested and the weight of storage roots and vines were determined using a field balance. The recorded yields were converted to t ha^{-1}. The dry matter content was determined after modifying the methods described by Carey and Reynoso (1996). Fresh root samples were collected from five healthy, big roots from each plant within the harvested plot. About 100 g of fresh weight were excised on each root and a composite of 500 g were prepared in which 100g were sampled and kept in a paper bag prior to drying. Samples were dried in an oven at 70^{o}C for 72 hours. Dried samples were weighed with a sensitive balance and the dry matter content was determined using the formula: Dry matter content (DM) expressed in % = ((Dry weight/Fresh weight) x 100).

6.2.5 Data analysis

6.2.5.1 Analysis of variance

A combined analysis of variance across seasons and sites was carried out to identify the effects of genotypes, sites, seasons and their interactions on yield of storage root and vines, total biomass and dry matter content of storage root using GenStat 14th edition (Payne et al. 2011). The clones were treated as fixed factor, while environments (both spatial and temporal), replications within environments and blocks within replications were random factors. The additive main effects and multiplicative interaction (AMMI) and genotype and

genotype x environment (GGE) biplot models were computed sequentially to analyze G x E interaction and yield stability of genotypes. The AMMI model as formulated by Gauch and Zobel (1996) is:

$$Y_{ij=}\mu+\alpha_i+\beta_j+\sum_N \lambda_n \xi_{in} \eta_{jn}+\rho_{ij}+\varepsilon_{ij,}$$

Where Y_{ij}: the observed mean yield of genotype i in environment j, μ: the grand mean, α_i: the genotype main effect, β_j: the environment main effect, λ_n: the eigenvalues of the interaction principal component analysis (IPCA), ξ_{in} and η_{jn}: the genotype and environment scores for the IPCA axis, ρ_{ij}: the interaction residual, N: the number of IPCA retained in the model and ε_{ij}: the random error term. The ANOVA and ranking of best performing sweetpotato clones in each environment were performed with AMMI. Further, AMMI's stability value (ASV) was determined to rank tested sweetpotato clones based on their stability using the formulae of Purchase (1997):

$$ASV=\sqrt{\frac{SSIPC\ 1}{SSIPC\ 2}(IPCA\ 1)^2+(IPCA\ 2)^2}$$

Where, SS: sum of squares; IPCA1: interaction principal component analysis axis 1, IPCA2: interaction principal component analysis axis 2.

6.2.5.2 GGE biplot

The GGE biplot analysis allows to identify the relationship among sweetpotato clones and the environments. The variations caused by genotype and genotype x environment interactions were explored using GGE biplot based on the principal component analysis (PCA) of environment-centred data (Yan et al. 2000; Yan and Kang 2002). The GGE biplot was analysed using Genstat 14th edition (Payne et al. 2011). The basic model for a GGE biplot as described by Yan et al. (2001) is:

$$Y_{ij}= b_j + b_j\alpha_i +\lambda_l\zeta_{il}\eta_{jl}+\varepsilon_{ij},$$

Where Y_{ij}: Average yield of i genotype in the environment j, b_j: the average yield of all genotypes in environment j, α_i: the main effect of genotype i, λ_n: the singular value for principal component PC_n, ζ_{il} and η_{jl}: scores for genotype i and environment j on PC_n, respectively, and ε_{ij}: the residual associated with i genotype and j environment. The which-won-where polygon view pattern of GGE biplot was used to identify high yielding clones in a

specific environment and mega-environments in tested environments (Yan et al. 2000; Yan and Kang 2002). The GGE biplots based on average environment coordination (AEC) (Yan and Kang 2002) was used to determine the discriminating power of each test environment.

6.3 Results

6.3.1 Analysis of variance and performance of genotypes

The combined analysis of variance revealed significant effects (p=0.01) of the interactions of clone x site x season, clone x site and clone x season on storage root and vine yields, total biomass and dry matter content (Table 6.3). The site x season interaction had significant (p=0.001) effect on vine yields, total biomass and dry matter content only (Table 6.3). The main effects of clones, sites and seasons revealed significant effect (p<0.001) on the yields of storage root and vine, total biomass and dry matter content of test clones (Table 6.3).

Table 6.3: Combined ANOVA for yield and dry matter content of storage root, vine and total biomass of sweetpotato clones evaluated at three sites and two growing seasons in Rwanda

Source of variation	Df	Traits and sum of squares			
		Root weight	DMC	Vine weight	Total biomass
Replication	2	1037.2	527.9	1823.0***	3472
Clone	44	37187.0***	30442.2***	188243.0***	283427.0***
Site	2	7752.9***	7396.6***	96782.0***	144893.0***
Season	1	23783.8***	1765.3**	42771.0***	130345.0***
Clone x Site	88	45231.8***	39395.8***	328870.0***	489342.0***
Clone x .Season	44	24928.0**	26644.1***	153858.0***	247690.0***
Site x Season	2	36.5ns	9244.3***	122536.0***	124176.0***
Clone x Site x Season	88	40594.3**	41326.7***	288280.0***	408227.0***
Residual	538	174356.9	138874.3	851273	1418208
Total	809	354908.4	295617.2	2074437	3249780

Df: Degrees of freedom; *: Significant at P=0.05; **: Significant at P=0.01; ***: Significant at P=0.001; ns: Non-significant; DMC: dry matter content

The mean yield of storage root among the tested sweetpotato clones varied between 2.1 and 38.2 t ha^{-1} (Table 6.4). The clone 21 (4-160 x 2005-020) revealed the highest storage root yield of 38.2 t ha^{-1}. The clones that revealed the high yield of storage root (>20 t ha^{-1}) were 21, 137, 22, 577 and 259 with 38.23, 23.41, 20.79, 20.69 and 20.36 t ha^{-1}, respectively.

The mean yields of these clones did not show statistically significant difference with Mugande (23.6 t ha^{-1}) and Ukerewe (24.1 t ha^{-1}). The latter two genotypes are high yielding and well-adapted local varieties released by the Rwandan sweetpotato research programme (Table 6.4).

The mean vine yields varied from 13.7 to 94.3 t ha^{-1}. Some clones had the highest vine yields above >50 t ha^{-1} such as 81, 21, 259, 137 and 733, with 50.65, 51.34, 58.44, 72.96 and 94.3 t ha^{-1}, respectively (Table 6.4). Total biomass ranged from 21.4 to 104.9 t ha^{-1}. The highest biomass (>75 t ha^{-1}) was observed in clones 733, 137, 21 and 259 with 104.9, 96.4, 89.6 and 78.8 t ha^{-1} (Table 6.4).

Mean dry matter content (DMC) of storage root fresh weight of clones varied between 18.4 and 40.6 %. The highest storage root dry matter of 40.6, 35.9 and 32.9 % were recorded in the clones 21, 137 and 259, respectively. Clone 21 displayed the higher DMC (40.6 %) compared to locally known varieties Ukerewe (36.3 %) and Mugande (37.7 %) which are known for their high dry matter content of storage roots in Rwanda (Table 6.4).

Table 6.4: Mean storage root weight, vine weight, total biomass and dry matter content of 45 sweetpotato genotypes evaluated across three sites and two growing seasons in Rwanda[a]

ID	Pedigree/Name	Root weight (t ha^{-1})	Vine weight (t ha^{-1})	Total biomass (t ha^{-1})	DMC (%)
21	4-160 x 2005-020	38.23^{l}	51.34^{i-k}	89.57^{i-k}	40.58^{k}
22	4-160 x 2005-020	20.79^{i-j}	41.69^{d-j}	62.48^{d-i}	30.60^{d-i}
37	Kwezikumwe x 2005-020	7.22^{a-e}	45.80^{e-j}	53.03^{a-h}	29.61^{b-i}
42	Kwezikumwe x 2005-020	19.8^{g-k}	42.06^{d-j}	61.86^{c-i}	26.18^{a-g}
46	Kwezikumwe x 2005-020	18.22^{e-k}	45.77^{e-j}	63.99^{d-j}	31.66^{e-j}
62	Otada 24 x 2005-020	5.08^{a-d}	29.51^{a-i}	34.59^{a-e}	23.24^{a-e}
81	Purple 4419 x 2005-020	15.04^{b-k}	50.65^{h-k}	65.70^{e-j}	27.81^{a-j}
88	Purple 4419 x 2005-020	12.70^{a-k}	41.31^{d-j}	54.02^{a-h}	22.92^{a-e}
103	SPK004 x 2005-020	9.00^{a-i}	40.17^{b-j}	49.18^{a-h}	25.65^{a-f}
137	K513261 x 2005-034	23.41^{jk}	72.96^{kl}	96.37^{jk}	35.92^{h-j}
210	8-1038 x 4-160	9.35^{a-i}	36.21^{a-j}	45.55^{a-h}	29.58^{b-i}
249	2005-034 x 8-1038	7.37^{a-e}	39.91^{b-j}	47.28^{a-h}	27.52^{a-i}
259	2005-034 x 8-1038	20.36^{h-k}	58.44^{jk}	78.81^{h-k}	32.89^{e-j}
321	SPK004 x 8-1038	9.90^{a-i}	29.58^{a-i}	39.47^{a-g}	26.24^{a-g}
358	Ukerewe x 8-1038	16.54^{d-k}	38.58^{a-j}	55.12^{b-h}	32.24^{e-j}
381	2005-034 x K513261	11.20^{a-i}	39.20^{a-j}	50.40^{a-h}	18.40^{a}
442	Purple 4419 x K513261	7.70^{a-f}	15.01^{a-c}	22.71 ^{ab}	22.94 $^{a-e}$

ID	Pedigree/Name	Root weight (t ha^{-1})	Vine weight (t ha^{-1})	Total biomass (t ha^{-1})	DMC (%)
455	SPK004 x K513261	13.97^{b-k}	25.74^{a-i}	39.71 $^{a-g}$	29.67 $^{b-c}$
456	SPK004 x K513261	7.71^{a-f}	38.37^{a-j}	46.08^{a-h}	24.50^{a-f}
460	Ukerewe x K513261	15.98^{c-k}	31.15^{a-i}	47.13^{a-h}	30.21^{b-i}
488	Nsasagatebo x Kwezikumwe	19.19^{f-k}	20.26^{a-e}	39.45^{a-g}	31.75^{e-j}
509	Ukerewe x Kwezikumwe	12.59^{a-k}	25.01^{a-h}	37.6^{a-f}	32.41^{e-j}
577	Nsasagatebo x Otada 24	20.69^{i-k}	13.65^{a}	34.34^{a-e}	19.71^{ab}
613	Otada 24 x Purple 4419	10.75^{a-i}	21.76^{a-f}	32.5^{a-e}	19.84^{a-c}
639	K513261 x SPK004	18.57 $^{e-k}$	32.47^{a-j}	51.04^{a-h}	29.08^{b-i}
641	K513261 x SPK004	11.15^{a-i}	25.20^{a-h}	36.35^{a-e}	28.26^{b-i}
661	2005-020 x Ukerewe	11.55^{a-i}	20.32^{a-e}	31.87^{a-d}	22.97^{a-e}
700	8-1038 x Ukerewe	7.81^{a-f}	24.01^{a-g}	31.82^{a-d}	29.75^{b-i}
721	Otada 24 x Ukerewe	15.98^{c-k}	34.37^{a-j}	50.35^{a-h}	30.29^{c-i}
733	Purple 4419 x Ukerewe	10.54^{a-i}	94.33^{l}	104.86^{k}	31.50^{e-f}
744	Purple 4419 x Ukerewe	12.23^{a-j}	27.69^{a-i}	39.92^{a-g}	26.54^{a-h}
746	Purple 4419 x Ukerewe	8.38^{a-g}	25.34^{a-i}	33.72^{a-e}	24.05^{a-e}
P1	2005-020	3.74 ^{ab}	18.18^{a-d}	21.92^{ab}	25.26^{a-f}
P2	2005-034	4.44^{a-c}	24.30^{a-g}	28.75^{a-c}	27.37^{a-i}
P3	2005-110	13.50^{a-k}	38.92^{a-j}	52.41^{a-h}	34.82^{f-j}
P4	4-160	9.33^{a-i}	40.79^{c-j}	50.12^{a-h}	35.20^{g-j}
P5	8-138	13.80^{a-k}	43.08^{d-j}	56.88^{c-i}	30.60^{d-i}
P6	K513261	6.22 $^{a-d}$	28.77^{a-i}	34.98^{a-e}	23.81^{a-e}
P7	Kwezikumwe	14.54^{b-k}	45.06^{e-j}	59.60^{c-i}	28.85^{b-j}
Control	Mugande	23.59^{jk}	46.79^{f-j}	70.39^{f-j}	37.75^{j}
P8	Nsasagatebo	2.06^{a}	37.65^{a-j}	39.71^{a-g}	23.92^{a-e}
P9	Otada24	5.75^{a-d}	44.68^{e-j}	50.42^{a-h}	29.22^{b-i}
P10	Pulpe4419	8.71^{a-h}	14.51^{ab}	23.22^{ab}	20.59^{a-d}
P11	SPK 004	7.58^{a-f}	13.78^{a}	21.37^{a}	33.27^{e-j}
P12	Ukerewe	24.09^{k}	48.03^{g-k}	72.12^{g-k}	36.29^{ij}
Mean		13.03	36.10	49.10	20.88
CV (%)		10.60	5.10	5.20	4.70
LSD (5%)		11.79	26.50	33.63	10.52

[a] Means a column followed by by the same letter are not significant different at the 5% probability level, ID: clone identification number, DMC: dry matter contnet, CV: coefficient of variation, LSD: Least significant difference.

At the Karama site, the highest mean storage root yields were recorded, 21.2 and 10.8 t ha^{-1} during season A and B, respectively (Table 6.5). The Rubona site was the second in mean yields of storage root with 19.7 t ha^{-1} during season A and 8.94 t ha^{-1} in season B (Table 6.5). The Masoro site was the last yielding 14.5 and 3.1 t ha^{-1} during season A and B, in that order (Table 6.5). Rubona site was the leading in providing high mean dry matter content

(29.9 and 26.4 %) followed by the Masoro and Karama sites. Their dry matter contents were 28.6 and 25.1 and 23.6 and 21.7 % for Seasons A and B, respectively (Table 6.5). During Season A, vine yields of 71.4, 30.5 and 28.1 t ha^{-1} were recorded at the Rubona, Masoro and Karamam sites, respectively (Table 6.5). Karama site was the first in vine yields in Season B. Rubona site was the second and Masoro site was the last. The yields of the three sites were 44.3, 27.7 and 14.8 t ha^{-1}, in that order (Table 6.5).

6.5: Mean yields and dry matter content of storage root of 45 sweetpotato genotypes evaluated at three sites and two growing seasons in Rwanda

ID	Yield of storage roots (t ha^{-1})						Yield of vines (t ha^{-1})						Dry matter content of storage root (%)					
	Season A			Season B			Season A			Season B			Season A			Season B		
	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona
21	30.10	57.40	56.70	27.38	14.08	43.71	32.20	95.20	52.50	30.72	48.61	48.81	45.30	29.30	22.72	33.77	31.23	33.16
22	46.20	0.00	0.00	40.83	14.86	22.84	30.80	2.80	44.10	75.76	43.87	52.80	0.00	10.08	27.73	34.44	30.71	32.66
37	8.40	14.00	15.40	3.11	0.58	1.83	37.80	28.00	143.50	28.62	18.78	18.12	33.86	20.01	19.50	0.00	21.04	35.22
42	41.30	0.00	8.40	31.38	5.13	32.61	53.20	1.40	33.60	88.67	13.07	62.42	10.88	0.00	17.53	19.45	28.29	32.96
46	14.00	12.60	42.00	17.97	10.81	11.95	12.60	22.40	112.00	60.32	29.17	38.13	9.67	11.19	28.33	36.16	21.39	35.23
62	1.40	22.40	2.10	3.11	0.00	1.48	16.10	60.20	2.80	49.78	15.67	32.51	11.52	30.70	8.25	0.00	19.86	21.09
81	42.70	8.40	30.80	0.00	5.91	2.45	60.20	37.80	141.40	0.00	58.10	6.42	33.44	10.53	34.38	21.32	19.21	0.00
88	2.10	8.40	60.90	3.72	0.00	1.10	7.70	29.40	136.50	54.20	0.70	19.38	21.46	9.53	23.48	0.00	9.94	25.11
103	33.60	14.00	0.00	4.78	0.00	1.63	46.20	25.20	112.00	43.17	0.00	14.47	0.00	31.57	33.79	0.00	8.93	31.61
137	42.00	9.80	45.50	23.33	0.00	19.83	31.50	19.60	198.10	113.87	0.00	74.67	35.43	36.55	34.47	0.00	30.96	36.13
210	16.10	15.40	18.90	4.12	0.00	1.56	37.80	28.00	73.50	54.13	8.17	15.63	20.47	35.12	32.99	0.00	9.50	31.43
249	5.60	5.60	20.30	9.33	0.00	3.38	40.60	16.80	121.80	38.89	1.63	19.76	31.15	22.80	22.59	0.00	19.46	21.09
259	23.80	18.20	62.30	6.83	0.00	11.06	24.50	11.20	231.70	40.60	7.00	35.66	30.59	30.83	22.08	0.00	31.29	34.56
321	28.00	15.40	10.50	4.39	0.00	1.10	30.80	33.60	24.85	63.00	0.00	25.20	11.20	34.27	34.64	0.00	8.85	20.49
358	19.60	18.20	1.40	30.33	2.80	26.90	18.20	16.80	65.10	77.00	5.37	49.00	9.67	38.88	36.00	0.00	28.91	31.96
381	21.00	0.00	42.00	0.00	0.00	4.20	44.80	5.60	168.00	0.00	0.00	16.80	11.10	0.00	36.24	0.00	9.09	0.00
442	23.10	18.20	0.00	0.00	3.50	1.40	25.90	25.20	0.00	18.67	9.33	10.97	0.00	34.43	27.34	17.38	10.47	0.00
455	29.40	1.40	43.40	3.73	0.78	5.13	15.40	2.80	104.30	14.00	8.56	9.38	32.05	10.02	36.62	0.00	29.73	21.59
456	12.60	5.60	20.30	5.54	0.00	2.22	10.50	22.40	121.80	58.51	0.00	17.03	32.26	9.69	23.46	0.00	9.71	23.89
460	21.70	43.40	2.10	17.50	0.00	11.20	15.40	21.00	72.80	56.00	0.00	21.70	20.69	37.01	34.28	0.00	19.89	21.38

ID	Yield of storage roots (t ha^{-1})						Yield of vines (t ha^{-1})						Dry matter content of storage root (%)					
	Season A			Season B			Season A			Season B			Season A			Season B		
	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona
488	19.60	2.80	75.60	11.48	1.75	3.92	21.00	2.80	10.50	57.17	2.33	27.77	22.22	24.15	32.51	21.17	9.50	32.94
509	14.00	32.20	8.40	14.62	0.00	6.34	14.00	40.60	21.00	36.99	17.73	19.75	24.19	36.13	21.14	0.00	30.75	34.22
577	1.40	19.60	93.80	7.47	0.00	1.87	7.00	2.80	39.20	15.17	11.67	6.07	8.33	22.92	10.28	0.00	7.99	20.74
613	10.50	16.80	25.20	8.56	0.00	3.42	9.80	29.40	49.00	30.33	1.28	10.73	10.67	22.11	9.55	0.00	9.21	19.53
639	44.10	33.60	12.60	0.00	9.92	11.20	22.40	81.20	12.60	3.73	45.62	29.28	20.38	34.04	30.95	23.74	17.37	0.00
641	26.60	18.20	0.00	15.17	0.00	6.94	27.30	46.20	16.80	41.65	1.40	17.85	0.00	34.70	32.13	0.00	20.66	34.03
661	26.60	26.60	0.00	0.00	16.10	0.00	23.10	42.00	0.00	0.00	55.77	1.05	0.00	36.44	32.13	21.27	0.00	0.00
700	22.40	14.00	1.40	4.67	2.12	2.26	37.80	16.80	19.60	34.07	19.25	16.57	10.12	12.99	30.90	19.50	20.90	36.12
721	40.60	2.80	25.20	19.83	0.93	6.53	22.40	2.80	126.00	38.73	2.76	13.53	24.06	12.07	30.90	22.30	9.70	34.75
733	23.10	21.00	0.00	3.50	3.19	12.43	30.80	47.60	315.00	99.87	20.77	51.92	0.00	36.64	30.44	22.29	30.43	21.18
744	30.80	9.80	0.00	22.17	1.40	9.22	21.00	63.00	0.00	41.46	23.50	17.19	0.00	36.38	23.17	0.00	18.81	32.90
746	29.40	16.80	0.00	2.99	0.00	1.10	28.00	40.60	0.00	50.87	9.10	23.45	0.00	35.75	22.30	0.00	18.30	19.97
P1	6.30	1.40	0.00	13.88	0.93	11.96	8.40	14.00	0.00	52.97	7.35	26.37	0.00	18.83	10.00	18.88	26.73	29.13
P2	1.40	2.80	0.00	10.50	1.17	6.59	48.30	32.20	0.00	25.78	9.49	30.05	0.00	13.04	34.29	0.00	32.55	36.33
P3	9.80	4.20	0.00	5.15	0.00	7.51	9.10	100.80	50.41	26.60	19.28	27.30	22.57	36.06	20.64	29.63	30.24	21.80
P4	9.10	18.20	18.20	13.42	8.33	13.73	70.00	11.20	75.60	31.73	25.24	30.97	23.64	42.49	21.41	20.87	29.50	31.29
P5	3.50	12.60	21.00	7.31	4.20	7.37	33.60	39.20	149.10	7.93	10.50	18.14	31.62	29.80	31.71	22.55	19.93	0.00
P6	22.40	18.20	33.60	0.00	1.90	6.71	0.00	0.00	33.60	57.63	44.11	37.25	0.00	0.00	0.00	32.04	29.47	33.34
P7	0.00	0.00	0.00	11.32	14.70	11.29	19.60	39.20	8.40	130.98	16.10	56.08	0.00	12.29	23.73	24.55	31.12	33.43
Control	25.20	5.63	0.00	34.84	1.87	19.68	50.40	57.40	71.40	40.83	15.40	45.32	33.05	36.83	40.29	30.37	29.75	32.20
P8	29.40	32.20	42.00	15.93	3.19	18.84	14.70	54.60	116.20	21.08	6.53	12.77	13.23	39.45	0.00	20.36	22.48	0.00
P9	0.00	4.20	5.60	0.00	1.01	1.54	77.00	11.20	33.60	78.28	13.85	54.13	10.92	14.23	20.17	21.28	28.75	31.95
P10	43.40	1.40	0.00	0.00	3.03	4.43	27.30	8.40	0.00	28.00	2.80	20.53	0.00	0.00	36.13	15.09	16.06	8.26

ID	Yield of storage roots (t ha^{-1})						Yield of vines (t ha^{-1})						Dry matter content of storage root (%)					
	Season A			Season B			Season A			Season B			Season A			Season B		
	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona	Karama	Masoro	Rubona
P11	22.40	4.20	0.00	11.43	0.93	6.53	25.90	12.60	0.00	20.77	5.13	18.29	0.00	35.63	32.91	21.83	29.77	31.47
P12	29.40	43.40	39.90	15.59	2.92	13.33	23.10	68.60	105.00	53.04	8.87	29.55	19.72	40.29	30.44	21.24	30.29	33.78
Mean	21.20	14.47	19.68	10.83	3.07	8.94	28.10	30.50	71.40	44.30	14.75	27.70	23.61	28.57	29.88	21.70	25.08	26.42
CV (%)	32.20	8.40	32.80	0.40	3.90	31.20	22.20	19.30	18.00	9.10	8.60	58.60	10.40	6.50	16.60	8.60	21.90	12.00
LSD (5%)	28.56	18.66	59.65	5.66	6.55	10.90	34.32	38.18	136.00	41.19	17.31	31.75	19.08	19.76	47.88	15.93	18.94	20.37

ID: clone identification number, Season A: September 2014-February 2015, Season B: March-August 2015.

6.3.2 AMMI analysis

AMMI analysis of variance revealed significant (P≤0.001) effects of genotypes, environments and G x E interactions on yield of storage roots (Table 6.6). Genotypes, environments and G x E interactions contributed at 20.7 %, 17.6 % and 61.7 % respectively, to the total variation. IPCA 1 and IPCA 2 were significant (P ≤0.01) and explained 37.3 % and 11.3 % of the total treatment variation. Further, IPCA 1 and IPCA 2 contributed to 60.5 % and 18.3 % of variation in the G x E interactions, respectively.

Genotype, environment and the G x E interaction had significant effects (P≤0.01) on dry matter content of storage root (Table 6.6). The treatment (genotypes, environments and G x E interactions) represented 53.8 % of the total sum of squares. Genotypes, environments and G x E interactions contributed to 19.5 %, 11.8 % and 68.7 %, respectively to the treatment variation. The IPCA 1 and IPCA 2 had significant effect (P ≤0.01) explaining 26.4 % and 16.3 % of the total treatment variation and 38.4 % and 23.7% of the GxE interaction variance, respectively.

Table 6.6: AMMI analysis of variance for fresh root yield and root dry matter content of 45 sweetpoato clones tested across six environments in Rwanda

Source of variation	df	Fresh root yields				Root dry matter content			
		SS	% Total explained	% Treatment explained	% GxE explained	SS	% Total explained	% Treatment explained	% GxE explained
Total	809	354908				295617			
Treatments	269	179514**	53.84			156215**	53.84		
Genotypes	44	37187**		20.72		30442**		19.49	
Environments	5	31573**		17.59		18406**		11.78	
Block	12	8765^{ns}				3236^{ns}			
Interactions	220	110754**		61.7		107367**		68.73	
IPCA I	48	66960**		37.3	60.46	41173**		26.36	38.35
IPCA II	46	20267*		11.29	18.3	25451**		16.29	23.7
Residuals	126	23527^{ns}		13.11	21.24	40743		26.08	37.95
Error	528	166630	46.16			136166	46.16		

df: Degrees of freedom, *: Significant at P< 0.05, **: Significant at P < 0.01, ^{ns}: Non-significant, SS: sum of squares; GxE: genotype by environment interaction, IPCA: Interaction principal component analysis

The four best sweetpotato clones selected through AMMI for storage root yield across six environments is presented in Table 6.7. The clone 21 (4-160 x 2005-020) was selected as the first in three environments (E2, E5, E6), whilst clone 22 (4-160 x 2005-020) was selected across two environments (E1, E4) and clone 577 (Nsasagatebo x Otada 24) only in one environment (E3). Across all environments, the clones that appeared the best with high storage root yields were clone 21, 22 and 42 (selected 4 times), 137 (3 times), ukerewe (2 times) and clone 88, 259, 460, 488, 509, 577 and Kwezikumwe (once) (Table 6.7).

For dry matter content, the genotype Mugande (Control) was the first in three environments (E1, E4, E6) followed by the clones 21, 22 and 358 selected in E3, E5 and E2, respectively. The clones that were selected among the best four with high dry matter content across all environments were 100 with 4 times, clones 21, 22, 46 and 137 (three times), clone 358 (two times) and clones 81, 460, 641, P6 (K513261), P11 (SPK004) and P12 (Ukerewe) (Table 6.7).

Table 6.7: The best four clones of AMMI selections per environment based on fresh root yield and root dry matter content

Fresh root yield (t ha-1)						
Environment	Mean	PCA Scores	1	2	3	4
E1	21.2	3.464	22	42	137	P7
E2	14.47	0.919	21	460	P12	509
E3	19.68	-11.019	577	488	259	88
E4	10.83	2.715	22	42	21	137
E5	3.07	1.78	21	22	P12	42
E6	8.94	2.14	21	22	42	137
Storage root dry matter content (%)						
Environment	Mean	PCA Score	1	2	3	4
E1	25.88	1.878	Control	P12	137	358
E2	24.57	2.065	358	137	460	641
E3	16.61	-9.862	21	137	81	Control
E4	24.42	2.5	Control	22	P11	46
E5	12.7	1.634	22	46	P6	21
E6	21.08	1.784	Control	21	22	46

E1: Karama season A 2015, E2: Masoro season A 2015, E3: Rubona season A 2015, E4: Karama season B 2015, E5: Masoro season B 2015, E6: Rubona season B 2015, PCA: principal component analysis, P1...P12: parents used in crossing. See Tables 1 and 2, for codes of environments (E1-E6) and genotypes, respectively.

AMMI stability values (ASV) varied between 0.76 and 11.09 for storage root yield and 0.40 and 10.00 for dry matter content of storage roots (Table 6.8). The clones with the lowest ASV values for storage root yield were Nsansagatebo, 210, 2005-110, 456, 37, 321 and 249. Their ASVs were 0.76, 0.79, 0.99, 0.99, 1.03, 1.04 and 1.10, respectively (Table 6.8). Clones that had the lowest ASV values for dry matter content were 46, 509, Mugande, 358, Nsansagatebo, 613, 639, Ukerewe, 661, 321 and 641. Their ASVs were 0.40, 0.46, 0.52, 0.53, 0.64, 0.66, 0.68, 0.82, 0.89, 0.91 and 0.99, respectively (Table 6.8). The highest ASV values in undesirable direction were recorded for clones, 577 and 62 for storage root yield and dry matter content, respectively (Table 6.8).

Table 6.8: Mean yield and dry matter content of storage root, IPCA 1, IPCA 2 and AMMI stability values (ASV) of 45 sweetpotato clones evaluated in six environments in Rwanda

ID	Pedigree/Name	Storage root yield (t ha^{-1})				Dry matter content (%)			
		Mean	IPCA 1	IPCA 2	ASV	Mean	IPCA 1	IPCA 2	ASV
21	4-160 x 2005-020	38.23	-1.33	-1.33	3.42	17.65	1.44	1.57	2.41
22	4-160 x 2005-020	20.79	2.83	2.83	5.99	28.92	-1.01	1.52	1.99
37	Kwezikumwe x 2005-020	7.22	-0.26	-0.26	1.03	17.26	1.32	-1.35	2.15
42	Kwezikumwe x 2005-020	19.8	1.95	1.95	4.51	19.37	1.58	-0.4	2.05
46	Kwezikumwe x 2005-020	18.22	-1.56	-1.56	2.85	26.82	-0.06	-0.39	0.4
62	Otada 24 x 2005-020	5.08	0.6	0.6	2.52	44.58	-7.81	-1.17	10
81	Purple 4419 x 2005-020	15.04	-0.62	-0.62	1.97	21.58	-0.23	1.86	1.88
88	Purple 4419 x 2005-020	12.7	-3.8	-3.8	6.91	22.6	1.8	-2.79	3.61
103	SPK004 x 2005-020	9	1.48	1.48	2.71	19.52	-1.58	0.7	2.13
137	K513261 x 2005-034	23.41	-1.1	-1.1	3.06	24.89	-0.93	0.85	1.46
210	8-1038 x 4-160	9.35	-0.32	-0.32	0.79	18.24	0.32	2	2.04
249	2005-034 x 8-1038	7.37	-0.61	-0.61	1.1	24.24	1.1	1.8	2.28
259	2005-034 x 8-1038	20.36	-3.14	-3.14	5.72	21.61	-1.58	0.16	2.02
321	SPK004 x 8-1038	9.9	0.57	0.57	1.04	9.4	-0.68	-0.28	0.91
358	Ukerewe x 8-1038	16.54	1.94	1.94	3.54	28.2	0.04	0.53	0.53
381	2005-034 x K513261	11.2	-2.04	-2.04	3.97	18.18	0.3	-2.77	2.8
442	Purple 4419 x K513261	7.7	1.22	1.22	2.36	14.94	0.98	1.09	1.65
455	SPK004 x K513261	13.97	-1.85	-1.85	3.84	21.67	-1.49	-0.23	1.91
456	SPK004 x K513261	7.71	-0.53	-0.53	0.99	16.5	-1.98	-0.15	2.52
460	Ukerewe x K513261	15.98	1.6	1.6	3.97	23.66	0.95	-2.64	2.9
488	Nsasagatebo x Kwezikumwe	19.19	-4.31	-4.31	8.04	22.21	-0.25	1.99	2.02
509	Ukerewe x Kwezikumwe	12.59	0.77	0.77	2.52	23.75	-0.25	-0.33	0.46
577	Nsasagatebo x Otada 24	20.69	-6.09	-6.09	11.09	24.41	-0.33	1.25	1.32
613	Otada 24 x Purple 4419	10.75	-0.8	-0.8	1.64	11.71	-0.04	0.66	0.66
639	K513261 x SPK004	18.57	1.09	1.09	2.16	11.84	-0.27	0.59	0.68
641	K513261 x SPK004	11.15	1.61	1.61	2.94	15.24	-0.01	0.99	0.99
661	2005-020 x Ukerewe	11.55	1.48	1.48	3.06	21.08	-0.49	0.63	0.89
700	8-1038 x Ukerewe	7.81	1.15	1.15	2.12	20.26	1.7	1.51	2.63
721	Otada 24 x Ukerewe	15.98	0.07	0.07	2.43	14.97	0.99	1.3	1.81
733	Purple 4419 x Ukerewe	10.54	1.45	1.45	2.81	21.75	0.76	-1.42	1.72
744	Purple 4419 x Ukerewe	12.23	1.84	1.84	3.46	22.29	-0.59	-1.4	1.59
746	Purple 4419 x Ukerewe	8.38	1.36	1.36	2.49	23.5	1.89	0.27	2.42
769	2005-020	3.74	0.86	0.86	1.59	18.54	1.53	1.52	2.47
770	2005-034	4.44	0.96	0.96	1.75	16.05	1.22	1.68	2.29
771	2005-110	13.5	0.03	0.03	0.99	22.6	-1.48	0.36	1.92
772	4-160	9.33	-0.59	-0.59	1.39	19.81	-1.96	-0.98	2.68
773	8-138	13.8	-1.22	-1.22	2.24	14.92	-1.04	-0.21	1.34

ID	Pedigree/Name	Storage root yield (t ha^{-1})				Dry matter content (%)			
		Mean	IPCA 1	IPCA 2	ASV	Mean	IPCA 1	IPCA 2	ASV
774	K513261	6.22	1.05	1.05	1.92	15.81	1.14	-3.94	4.2
775	Kwezi	14.54	2.07	2.07	3.98	20.85	1.66	-2.1	2.98
776	Mugande	23.59	-1.11	-1.11	2.13	33.75	-0.39	-0.14	0.52
777	Nsasa	2.06	0.16	0.16	0.76	15.92	-0.26	0.55	0.64
778	Otada 24	5.75	1.1	1.1	2	21.22	0.6	-1.73	1.89
779	Pulpe4419	8.71	1.62	1.62	3.49	12.59	0.74	-1.51	1.78
780	SPK 004	7.58	1.37	1.37	2.59	25.27	2.12	0.11	2.69
781	Ukerewe	24.09	-0.98	-0.98	2.5	29.29	0.55	0.44	0.82

ID: clone identification number, IPCA: interaction principal component analysis, ASV: AMMI stability values.

6.3.3 GGE biplot analysis

The which-won-where polygon view of GGE biplot revealed differential response of genotypes across environments (Figure 6.1a). For storage root yield the principal component axis 1 (PC1) explained 54.22% of total variation while the principal component axis 2 (PC2) contributed to 21.01% of the variation. Both PC1 and PC2 explained 75.23% of the total variation due to genotype and GxE interactions for yield of sweetpotato storage root (Figure 6.1a). The six test environments were divided into two mega environments: mega environment one consisted of E1, E2, E4, E5, and E6 and mega environment two comprised of only E3. The clones 21, 259, P12, control (Mugande), and 137 were the highest yielding clones in mega environment 1, while C23, C21 and C8 were high yielders in mega environment 2 (Figure 6.1a).

The GGE biplot analysis for dry matter content revealed three mega environments. E1, E4, and E2 formed the first mega environment, while E3 and E6 were allocated in the second mega environment. E5 formed the third mega environment (Figure 6.1b). The best clones in dry matter content were 137, 21 and 46 in mega environment one, two and three, respectively (Figure 6.1b). The principal component axis one (PC1) explained 41.37% of total variation, while principal component two (PC2) explained 20.27%. Both PC1 and PC2 explained 61.64% of the total variation due to genotype and GxE interactions for dry matter content of sweetpotato storage root (Figure 6.1b).

The GGE biplots based on average environment coordination (AEC) for yield of sweetpotato storage root revealed that the environment E3 had the longest vector and

therefore it was the most discriminating environment (Figure 6.2a). This environment was followed by E1, E2 and E6, respectively (Figure 6.2a). The least discriminating environments for yield of storage root with the shortest vector were E4 and E5 (Figure 6.2a). The GGE biplot based on AEC classified the test environments in the following order: E3, E5, E2, E6, E1 and E4 as the most discriminating environment with regards to dry matter content of sweetpotato storage root (Figure 6.2b).

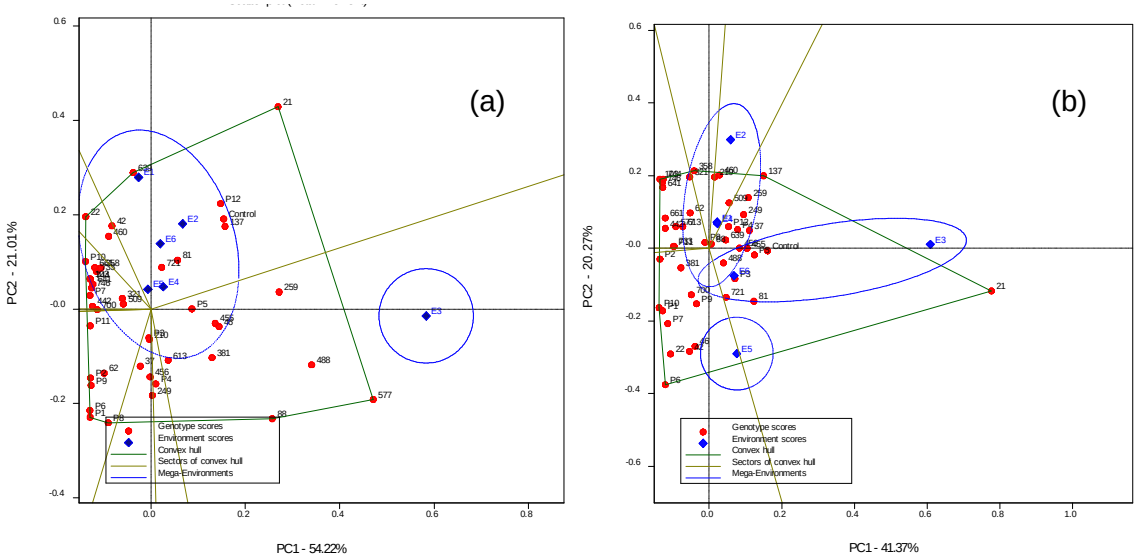

Figure 6.1: Which-won-where polygon view of GGE biplot and mega environments for storage root yield (a) and dry matter content of storage root (b) of sweetpotato. Numbers are genotypes, E1 to E6: environments, P1 to P8: Parents.

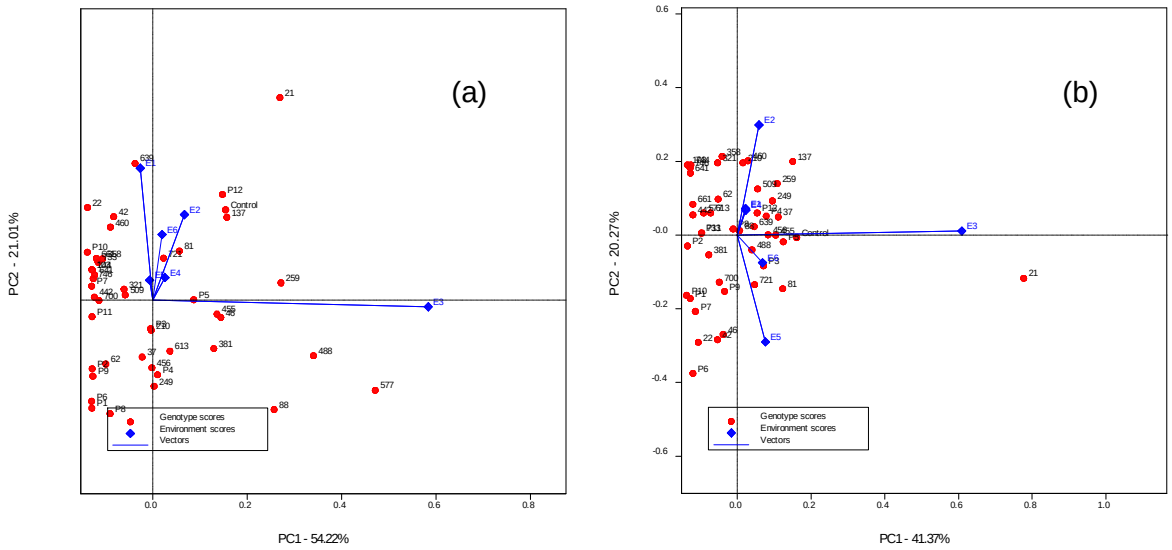

Figure 6.2: Discriminating power and representativeness of the test environments for root yield (a), dry matter content of storage root (b) of sweetpotato. Numbers are genotypes, E1 to E6: environments, P1 to P8: Parents.

6.4 Discussion

6.4.1 Analysis of variance response of sweetpoato genotypes

Under various growing environments, crop varieties exhibit rank differences in the expression of yield and yield components. The main causes of this variation are the genotype, environment, and genotype x environment interaction (Osiru et al. 2009; Russell and Eberhart 1966). Results of this study showed that the main effects of clones, sites and seasons and their interactions (clone x site x season, clone x site and clone x season) had significant effects ($P<0.01$) on yields of storage roots and vines, total biomass and dry matter content of storage roots of sweetpotatoes (Table 6.3). Previous studies showed that storage root yields of sweetpotato varied considerably when evaluated across selected test sites and growing seasons in Uganda (Osiru et al. 2009). Tan et al. (2007) reported the occurrence of significant effects of season x clone, site x clone and season x site x clone effects on the sweetpotato fresh storage root. The authors outlined non-significant interaction effects of season x clone and season x site x clone on dry matter content of storage roots suggesting the stability of this trait. A report by Nasayao and Saldaga (1988), Mwamburi and Ndolo (2013) and Adebola et al. (2013) showed significant effects of genotypes, sites and genotype by site interactions on yield and dry matter content of sweetpotato storage roots. Overall, the

above studies demonstrated the importance of multi-environmental trials (METS) of pre-released genotypes to identify promising clones and appropriate growing environments to enhance productivity.

During the present study the yield of storage root varied between 2.1 and 38.2 t ha^{-1} where the best clone (clone 21) yielded at 38.2 t ha^{-1} (Table 6.4). Mbwaga et al. (2007) observed a significant yield variation among sweetpotato genotypes producing between 23.0 and 26.0 t ha^{-1} of storage roots. A high yielding genotype with a yield potential of 20.7 t ha^{-1} across three different agro-ecological zones was reported elsewhere (Kathabwalika et al. 2013). Mean yields of 16.8 and 15.2 t ha^{-1} were reported in Nairobi and Western Kenya, respectively (Mwamburi and Ndolo 2013). The present study identified other promising clones such as 137, 22, 577 and 259 with mean storage yields of 23.4, 20.8, 20.7 and 20.4 t ha^{-1}, respectively (Table 6.4). These yield levels are comparable to previous findings. Interestingly, the mean yields of the presently selected and high yielding clones had not shown statistical significance difference to that of the locally popular varieties such as Mugande (23.6 t ha^{-1}) and Ukerewe (24.1 t ha^{-1}) (Table 6.4). Overall, clones 21, 137, 22, 577 and 259) are recommended as candidate varieties because of their high yield potential and genetic stability when compared to the control varieties widely grown in Rwanda.

In Rwanda high, vine yields of 83.6 to 93.9 t ha^{-1} and total biomass of 93.5 to 111.3 t ha^{-1} were reported (Rukundo et al. 2015) . In the current study, the highest vine yields and total biomass among sweetpotato clones were 94.3 t ha^{-1} and 104.9 t ha^{-1}, respectively across three sites and two growing seasons (Table 6.4). The study sites and growing seasons had marked differences in vine yields and total biomass (Table 6.5). These variations are due to genotype by environment interactions.

In the current study, dry matter content of storage roots varied from 18.4 and 40.9 %. Earlier studies reported a broad variation among genotypes in dry matter content of storage roots (Courtney et al. 2008). Cervantes-Flores et al. (2011) reported that dry matter content of storage roots showed a normal distribution with values of 15 to 35 % and a mean of 25 % when evaluating a mapping population. The current study recorded the highest dry matter content of storage roots of 40.6, 35.9, and 32.9 in the clones 21, 137, and 259, respectively. Clone 21 had a dry matter content of 40.6 % above Ukerewe (36.3 %) and Mugande (37.7 %) which are popular varieties in Rwanda for their high dry matter content (Table 6.4). In Rwanda, Shumbusha et al. (2010) indicated that high storage root dry matter content is an

important attribute for high adoption of sweetpotato varieties. In the country growers and end users prefer sweetpotato genotypes with dry matter content above 25 %. Therefore, the selected clones (21, 137 and 259) are ideal possessing high yielding potential and increased dry matter content for wide-area recommendation to farmers and end-users in the country.

Storage root yields of sweetpotato genotypes are reported to be variably expressed across test sites and growing seasons affecting cultivar ranks (Osiru et al. 2009). At the Karama site the highest mean yields were achieved at 21.2 and 10.8 t ha^{-1} during season A and B, respectively (Table 6.5). The yield levels were comparatively higher than the Rubona and Masoro sites across seasons. Conversely, the tested clones had the highest dry mater content at the Rubona site during both seasons (29.9 and 25.1 %) than the Masoro (28.6 and 25.1 %) and Karama (23.6 and 21.7 %) sites (Table 6.5). Variation in micro- and macro-climatic conditions and soil characteristics were reportedly the major factors causing differences in yields of sweetpotato across environments (Carey et al. 1997; Osiru et al. 2009).

6.4.2 AMMI analysis

Similar to the present study, AMMI analysis of variance for storage yields of sweetpotato was reported to show significant effects (p=0.01) of genotypes x locations, genotypes x seasons and locations x seasons interactions (Osiru et al. 2009). In a study conducted using AMMI analysis involving 28 sweetpotato breeding clones evaluated over two years and two locations, Adebola et al. (2013) found significant effects ($P < 0.01$) of environments, genotype and G x E interactions for yield of storage roots.

In the present study, environments and G x E interaction accounted for 53.8 % of the total sum of squares. The contribution of genotypes, environments and G x E interaction to the total variation, were 20.7 %, 17.6 % and 61.7% respectively (Table 6.6). In previous studies it was reported that environmental effects contributed significantly to the total variation (Bacusmo et al. 1988; Ngeve 1993), whereas other researchers reported genotypic main effects to be main contributors (Abidin et al. 2005; Caliskan et al. 2007; Grunerberg et al. 2005; Manrique and Hermann 2000). Gauch and Zobel (1996) pointed out that in multi-locational trials, the main effect of environments represented up to 80 % of the total variation, whereas genotype and GxE interactions each represented 10 %. Abidin et al. (2005) reported that the genotypic main effect was larger than the interaction effects, while

Adebola et al. (2013) described that environment showed the highest contribution to the total variance. Therefore, selection for specific adaptation was suggested to overcome the challenge of inconsistence ranking of test genotypes across environments.

The G x E interactions were partitioned into three interaction principle component axis (IPCA 1, IPCA 2, and IPCA 3) that were highly significant and explained 43.80%, 39.01% and 17.19%, respectively, of the total G x E interaction sums of squares (Adebola et al. 2013). In this study, the contribution of G x E interaction to treatment variation was 61.7%. The IPCA 1 and IPCA 2 were significant (P ≤0.01) and explained 37.3% and 11.29% of the total treatment variation and 60.49% and 18.3% of the GxE interactions, respectively (Table 6.6). In the current study the contribution of GxE interaction to total variation (61.7%) was high compared to the results of Adebola et al. (2013) who reported 18.71%. This variability could be attributed to differences in genetic constitution and growing environments.

The analysis of variance revealed that the interactions of location and year showed a significant effect on dry matter content of sweetpotato clones (Cervantes-Flores et al. 2011). Chiona (2009) reported that the effects of genotype and genotype x environment interaction were highly significant ($p<0.001$) for dry matter content. The IPCA1 and IPCA2 axes were highly significant ($p<0.01$) and explained 57.4% and 20.4% of the total G x E sum of squares, respectively. The results of this study revealed significant effects (P≤0.001) of the genotypes, environments and the G x E interaction on dry matter content of storage roots (Table 6.6). The treatment capturing genotypes, environments and G x E interactions represented 53.84 % of the total sum of squares (Table 6.6). The IPCA 1 and IPCA 1 were significant (P ≤0.01) and they explained 26.36% and 16.29% of the total treatment and 38.35% and 23.7% of the G x E interactions, respectively (Table 6.6).

The AMMI analysis revealed variations and variable ranking of four best sweetpotato clones with high yields and dry matter content of storage roots across six environments (Table 6.7). The clones that appeared among the best four AMMI model selected were 21, 22 and 42 (being selected 4 times), 137 (3 times), ukerewe (2 times) and clone 88, 259, 460, 488, 509, 577 and Kwezikumwe (once) for high storage root yields. The following genotypes were selected using the AMMI model for high dry matter content of storage roots: Mugande (4 times), clone 21, 22, 46 and 137 (three times), clone 358 (two times) and clone 81, 460, 641, K513261, SPK004 and Ukerewe (once) (Table 6.7). The observed variations in the ranks of

clones for yield and dry matter content of storage roots reaffirm the significant effects of GxE interaction in tested sweetpotato clones.

Genotypes with lower AMMI stability values (ASV) are considered more stable (Purchase 1997). The sweetpotato clones that revealed the lowest ASV for storage root yields were Nsansagatebo, 210, 2005-110, 456, 37, 321 and 249 with ASVs of 0.76, 0.79, 0.99, 0.99, 1.03, 1.04 and 1.10, respectively (Table 6.8). The lowest ASV of 0.40, 0.46, 0.52, 0.53, 0.64, 0.66, 0.68, 0.82, 0.89, 0.91 and 0.99 were observed in the clones 46, 509, Mugande, 358, Nsansagatebo, 613, 639, Ukerewe, 661, 321 and 641, respectively, for dry matter content (Table 6.8). These clones appeared to be stable for yield and dry matter content of storage roots in the tested environments.

6.4.3 GGE biplot analysis

The crossover genotype x environment interaction suggests that the target environments can be divided into different mega-environments which are groups of locations that consistently share the best set of genotypes across years (Yan and Rajcan 2002). In a mega-environment, a site represents the target environment and has a power to differentiate genotypes (Yan and Tinker 2006). The which-won-where view of GGE biplot for storage root yields revealed that the six tested environments were divided into two mega environments: mega environment one (E1, E2, E4, E5 and E6) and mega environment two (E3) (Figure 6.1a). The clones 21, 259, P12 (Ukerewe), control (Mugande) and 137 were the highest yielding clones in the mega environment one, while the clones 577, 488 and 88 were high yielders in mega environment two (Figure 6.1a). For dry matter content, E1, E4 and E2 constituted the first mega environment, while E3 and E6 formed the second mega environment. E5 formed the third mega environment (Figure 6.1b). Clones 137, 21 and 46 were best performers in mega environment one, two and three, respectively (Figure 6.1b). Similar findings were reported in the study of genotype x environment interaction for storage root yield in sweetpotato under managed drought stress conditions. The eight environments used to test sweetpotato were divided into three representative mega-environments (Kivuva et al. 2014). The results of this study showed that among the six test environments, two environments (for yield of storage roots) and three environments (for storage root dry matter content) are sufficient to classify sweetpotato clones.

Three test environments (test environments having a short vector, test environments presenting long vectors and small angles with the average environment coordination (AECO) abscissa and test environments having long vectors and large angles with AECO abscissa) were categorized by Yan el al. (2007). The first category of test environment does not provide enough information about genotypes. The second category of test environment is advised as ideal environments to identify superior genotypes while the third category of test environments is advised for culling unstable genotypes (Yan et al. 2007). Based on previous information, the environments E3 is the ideal environments for genotypes discrimination for storage root yields. The environments E1 and E2 were suitable for classification of unstable clones for storage root yields (Figure 6.2a). The environments E3 was also the ideal environment for genotypes discrimination for dry matter content, while environments E2 and E5 were the best environments to classify unstable genotypes for dry matter content (Figure 6.2b). This study showed that the environment E3 is the ideal environments for testing sweetpotato clones for their potential in yield and dry matter content of storage root.

6.5 Conclusions

Multi-environmental trials are useful when evaluating pre-released genotypes. It is useful to identify promising genotypes and appropriate growing environments. The following clones: 21, 137, 22, 577 and 259 had high yields and enough dry matter content of storage roots compared to local checks. These clones were relatively genetically stable. The ranks of best clones for yields and dry matter content of storage roots across test sites were variable. This showed the significant effects of GxE interactions and yield instability. The clones that seemed to be stable across all tested environments were Nsansagatebo, 210, 2005-110, 456, 37, 321 and 249 for storage root yields and clones 46, 509, Mugande, 358, Nsansagatebo, 613, 639, Ukerewe, 661, 321 and 641 for dry matter content of storage roots. Environment E3 (the Rubona site during Season A [September 2014 - February 2015]) was identified as the ideal environment that conveniently delineated genotypes based on fresh root yields and dry matter content of storage roots.

6.6 References

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7. Chapter Seven: Overview of the study

7.1 Introduction

Sweetpotato (*Ipomoea batatas* [L.] Lam.) is the third important root crop grown by 98% of subsistence farmers in all agro-ecological zones of Rwanda. Rwanda experiences severe drought spells during the off season (April/May to September/October) for crop production owing to the limited rainfall that falls from June to September. Most rural communities face periodic hunger during October to January every year in the country. The critical problem is that there is a limited number of drought tolerant varieties of major food crops, including sweetpotato. Consequently, drought tolerant sweetpotato varieties are required for sustainable sweetpotato production and to ensure food security in Rwanda. The value of a new sweetpotato variety depends on farmers' and end users' preferences. Sweetpotato storage roots with high dry matter content might be adopted by farmers and subsequently by consumers and processors. Therefore, breeding for drought tolerance and high dry matter content is an overriding consideration for enhancing sweetpotato production 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:

1. To assess farmers' perception, production constraints, preferences, and breeding priorities of sweetpotato in selected agro-ecologies of Rwanda.
2. To characterise and identify breeding parents among 54 sweetpotato genotypes grown in Rwanda, East and Central Africa.
3. To select drought tolerant sweetpotato genotypes under managed drought conditions using greenhouse and in-vitro screening techniques with early and late developmental traits.
4. To determine general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components of among newly developed sweetpotato clones.
5. To determine genotype x environment interaction and yield stability of sweetpotato breeding clones recently bred in Rwanda and to identify promising genotypes.

7.2 Summary of major findings

The first study focused on a survey involving 168 farmers and 14 focus group discussions across eight representative districts. The study identified key production and productivity constraints, preferences and breeding priorities of sweetpotato farmers in Rwanda. The specific outcome of this study showed that:

- Drought stress, unavailability of improved cultivars and planting material, and pest and disease damage are the five main constraints limiting sweetpotato production.
- High yield, early maturity, drought tolerance, disease and pest tolerance, and good culinary taste are the most important traits of a good sweetpotato cultivar.
- High dry matter content, good culinary taste, good shape, root size, and sweetness are main characteristics of good storage roots identified by farmers.
- Each agro-ecological zone had its own specific sweetpotato production constraints and farmers' preferences.

The second study characterized the phenotypic diversity of 54 sweetpotato genotypes grown in Rwanda, east and central Africa. Field trials were conducted using a 9 x 6 unbalanced alpha lattice design with three replications at the Karama and Rubona Research stations of Rwanda Agriculture Board. The main findings of this study were the following:

- Genotypes K513261, Kwezikumwe, 8-1038 and 2005-110 flowered the most.
- Genotypes K513261, Purple 297, Kwezikumwe and New Kawogo were identified as producing high storage root yields.
- Genotypes Ukerewe, 2005-103, Meresiyana and Mvugamo showed the highest mean dry matter content.
- Among 26 phenotypic traits used to characterize sweetpotato genotypes, only 19 traits were identified as the most influential characters for effective genetic diversity studies of sweetpotato.
- Overall, the following genotypes: K513261, Kwezikumwe, 2005-020, Otada 24, SPK004, Ukerewe, 2005-110 and 2005-034 were identified as potential breeding parents of sweetpotato for Rwanda with superior storage root yield and dry matter content.

The third study compared the use of greenhouse and in-vitro screening techniques of drought tolerance using 54 sweetpotato genotypes at the Rubona Research Station of the Rwandan Agricultural Board. The main findings of this study included:

- Positive correlations were observed between vine yield and fresh weight gain (FWG) and between total biomass and FWG, during greenhouse and *in-vitro* experiments, respectively.
- Genotypes such as 2005-146, 4-160, 8-1038, Karibunduki, Kwezikumwe, Purple 4419, NASPOT 9 O, Nsasagatebo, Karebe, IMBY 3102, Mwanakumi, 97-062 and Matembere were selected with comparatively high drought tolerance using two screening procedures.

The fourth study investigated the genetic basis and heritability of drought tolerance; yield and yield components. This was carried out using 12 genotypes selected for superior performance for the traits of storage root yield, dry matter content or drought tolerance. The clones were crossed using a full diallel mating design. Families were field evaluated at three sites to determine general combining ability (GCA), specific combining ability (SCA), maternal effects and heritability of drought tolerance, yield and yield components. The main outcomes of this study were:

- Broad sense heritability estimates were 0.95, 0.84, 0.68, 0.75, 0.50 and 0.58 for canopy temperature (CT), canopy wilting (CW), root yield, storage root dry matter content, vine yield and total biomass, respectively.
- The GCA effects of parents and SCA effects of crosses were significant ($P<0.01$) for CT, CW, storage root, vine and biomass yields, and dry matter content of storage roots.
- The ratio of GCA/SCA effects for CT, CW, yield of storage roots and dry matter content of storage roots were higher than 50%, suggesting the preponderance of additive over non-additive gene action in the expression of these traits. This indicates that the mating design should therefore be to enhance recurrent selection.
- The best general combiners for drought tolerance were the parents 8-1038, Otada 24 and 4-160 with the lowest CT and CW and relatively high yields.
- Best combiners for high storage root yields were the parents, Nsasagatebo, K513261 and Ukerewe, while Nsasagatebo, 2005-034 and Ukerewe were the best combiners for high dry matter content of storage roots.

- Maternal effects were significant (P<0.05) among families for CT, CW, flesh color and dry matter content, vine yield and total biomass.
- Based on reduced CT and CW, the best families with significant SCA effects were 4-160 x Nsasagatebo, 4-160 x Ukerewe, Otada 24 x 4-160, Nsasagatebo x 2005-020, Otada 24 x Nsasagatebo, 4-160 x K513261 , 513261 x 4-160, 8-1038 x 4-160, 4-160 x 8-1038, 8-1038 x 2005-020 and Nsasagatebo x Ukerewe, which were selected for breeding for drought tolerance.
- Across sites, the best five selected families with significant SCA effects for storage root yields were Nsasagatebo x Otada 24, Otada 24 x Ukerewe, 4-160 x Nsasagatebo, K513261 x 2005-034 and Ukerewe x K513261 with 11.0, 9.7, 9.3, 9.2, 8.6 t/ha, respectively.
- The best families with high dry matter content of storage roots were Ukerewe x 2005-034, 4-160 x Nsasagatebo, 2005-034 x Ukerewe, 2005-034 x K513261 and 2005-020 x Ukerewe.

The fifth study tested genotype x environment interaction and yield stability of 45 selected sweetpotato breeding clones using field trials established across six environments in Rwanda. The study revealed that:

- Interaction effects of clone x site x season, clone x site and clone x season on yields and dry matter content of storage roots were significant (p=0.001).
- Site x season interaction had significant effects on dry matter content of storage roots only.
- Candidate clones designated as clone 21 (4-160 x 2005-020), 137 (K513261 x 2005-034) and 22 (4-160 x 2005-020) had the highest storage root yields of 38.23, 23.41 and 20.79 t ha-1, respectively.
- The highest dry matter content of storage roots of 40.58, 35.92 and 32.89% were recorded in the following clones: 21, 137 and 259 (2005-034 x 8-1038), respectively.
- AMMI stability values (ASV) revealed that genotypes, Nsansagatebo and clones 210 (8-1038 x 4-160), 2005-110 and 456 (SPK004 x K513261) were the most stable for storage root yields and Clones 46 (Kwezikumwe x 2005-020), 509 (Ukerewe x Kwezikumwe), Mugande, and 358 (Ukerewe x 8-1038) were stable for dry matter content of storage roots.

- Candidate sweetpotato clones such as 21, 137 and 22 (4-160 x 2005-020) were selected for their high yields and dry matter content of storage roots. These clones are recommended for direct production or sweetpotato breeding programmes in Rwanda and similar environments.

7.3 Implications of the research findings

- Assessment of farmers' perceptions, production and productivity constraints, preferences and breeding priorities is is crucial to the success of any plant breeding programme, to ensure that any new varieties that are developed genuinely respond to the needs of end users. The Rwandan sweetpotato germplasm has considerable genetic variability for yield, yield components and drought tolerance. This variability is useful for genetic improvement of sweetpotato.
- Greenhouse and/or *in-vitro* screenings are alternative approachs to screening for drought tolerance in sweetpotato. High levels of broad sense heritability and significant effects of both additive and non-additive genetic effects on yield and dry matter content of storage roots, and drought tolerance suggest that these traits can be improved through conventional breeding.
- Maternal genetic effects were identified for some traits, highlighting the need for plant breeders to be cautious in their assignment of sweetpotato genotypes as maternal or paternal parents. Multi-environmental trials are useful when evaluating pre-released sweetpotato genotypes. Among the test environments, the environment designated as E3 (the Rubona Research Station, in Season A) provided the ideal environment for testing sweetpotato clones for yield and dry matter content of storage roots.
- Valuable sweetpotato families were developed with high combining ability for high drought tolerance, yield and dry matter content. The candidate sweetpotato clones could be released as new cultivars after stability testing in target and representative environments in Rwanda.