MAKERERE UNIVERSITY

GENETIC IMPROVEMENT OF YAM BEAN (*Pachyrhizus* species) FOR HIGH STORAGE ROOT YIELD, DRY MATTER CONTENT AND NUTRITIONAL QUALITY IN UGANDA

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DECLARATION

I, **Rolland Agaba,** declare that this thesis is original and has not been submitted for any other degree award or examination in any other university or institution of higher learning. Where information was synthesized from other sources, it's been clearly indicated and cited accordingly.

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DEDICATION

This thesis is dedicated to my parents Mr. Mbabazi Alex Runyasi and Mrs. Natukunda Mary Runyasi, to my exquisite and solicitous wife Mercy Nimusiima, and to our begotten children Noble Nimulungi Agaba and Noella Mulungi Agaba. My parents spared nothing to give me an education that formed a strong foundation for this achievement. My nuclear family endured extended absence and lived with less attention during my doctoral studies, may you live to test the sweet fruits of education. To my brothers and sisters your support and love contributed immensely to this success. To the two villages that natured my infancy, Nyamengo and Muhito, your foot paths opened wide the doors to education, may your offspring dare to walk this journey of actualization.

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LIST OF ABBREVIATIONS AND ACRONYMS

CIP	International potato center
FAO	Food and agricultural organization of the United Nations
FBY	Fresh biomass yield
Fe	Iron content of storage roots
G X E	Genotype by environment interaction
GCA	General combining ability
h^2_b	Broad sense heritability
h^2_n	Narrow sense heritability
HI	Harvest index
K	Potassium
NaCRRI	National Crops Resources Research Institute
NaSARRI	National Semi Arid Resources Research Institute
NIRS	Near infrared reflectance spectroscopy
P	Phosphorus content of storage roots
RDM	Storage root dry matter content
RDY	Storage root dry yield
RFY	Storage root fresh yield
RPO	Protein content of storage root
SCA	Specific combining ability
STA	Starch content of storage roots
VNY	Vine yields
Zn	Zinc content of storage roots
σ^2GCA_f	Female GCA variance
σ^2GCA_m	Male GCA variance
σ^2SCA	SCA variance

ABSTRACT

Yam bean (*Pachyrhizus* species) is a legume root crop newly introduced in East and Central Africa for food production. The crop has nutritious storage roots rich in protein, iron, zinc and vitamins in addition to wide eco-geographical adaptation and biological nitrogen fixation. However, the acceptance, adoption and utilization of yam bean is constrained by low storage root dry matter content (RDM) and yield yet high RDM is preferred for consumption and industrial applications among staple root crops in Africa. Thus genetic studies to improve RDM, yield and associated traits were needed as a basis for designing yam bean improvement programs. This study presents the first comprehensive results on genetic characterization, gene action, inheritance and response to selection for yield, RDM and nutritional quality traits in the yam beans. The objectives of this study were to: i) estimate genetic variability for RDM, yield and quality traits among the introduced yam bean germplasm in Uganda, ii) determine combining abilities and gene action for inheritance of RDM and associated traits in F_1 and F_2 yam bean populations and iii) assess response to selection for RDM and associated traits in selected F_3 yam bean populations.

Four trials were conducted for genetic characterization of RDM, yield and associated traits in 26 accessions of the three cultivated yam bean species at two locations over two seasons as a basis for parental selection. Then hybridisation was done by crossing three high RDM *P. tuberosus* – chuin cultivar and six low RDM accessions of *P. erosus* and *P. ahipa* using North Carolina II mating design (NCD II) and to generate F_1 populations. Field evaluations were done for parental lines, F_1 plants, F_2 segregating populations, and 83 F_3 families selected at 10% on the basis of high RDM. A randomised complete block design (RCBD) was used in all field experiments with spacing of 0.3m between plants and 1m between ridges. Data was collected on storage root fresh yield (RFY), storage root dry yield (RDY), vine yield (VNY), fresh biomass yield (FBY), harvest index (HI), protein (PRO), starch (STA), iron (Fe), zinc (Zn), potassium (K) and phosphorus (P) content of storage roots. The Near-infrared reflectance spectroscopy (NIRS) was used to determine the nutritional quality of storage root flour samples. Statistical and genetic analyses were done through analysis of variance, variance component analyses, combining ability and correlational analyses.

The results from genetic characterization of the 26 yam bean accessions revealed significant ($p<0.01$) genetic variation (σ^2_G) for RFY, RDM, RDY, VNY, FBY, STA, iron (Fe) and high broad sense heritabilities ranging from 58.4% to 83.6%. Similarly, the phenotypic coefficients of variation were high for RFY (66%), RDY (53.3%), VNY (60.5%), and FBY (59%), but medium for RDM (22.6%), STA (15.1%) and Fe (21.3%). Strong positive correlations were observed between RFY and both RDY ($r = 0.926$) and FBY ($r = 0.962$), besides RDY and FBY ($r = 0.899$) but low to moderate correlations amongst quality traits. Conversely, the results of study two on combining abilities and gene action revealed significant ($p<0.01$) mean squares of crosses for RDM, STA, RFY, RDY and FBY in F_1 and all traits in F_2. The GCA mean squares for females (GCA_f) and males (GCA_m) were also significant ($p<0.01$) for RFY, RDY, FBY, STA, PRO and RDM, RDY, STA respectively while SCA mean squares were only significant ($p<0.05$) for RDM, RFY and STA in F_1 generation. In F_2 generation, GCA_f were significant ($p<0.01$) for all traits except RDM and VNY but GCA_m were significant for RDM, RFY, RDY and FBY.

Likewise, the SCA mean squares were significant (P<0.01) for RDM, RFY, HI, FBY and STA suggesting both additive and non-additive gene action.

The narrow sense heritability and baker's ratios were moderately high (>0.5) for all the traits except VNY and PRO in F_1 and VNY in F_2 indicating the predominance of additive genetic effects and suggesting that performance of progenies could be reliably predicted from parents for most traits. The GCA effects were positive and significant (P<0.01) for RDM and STA among parents 209014 and 209018 in F_1 and F_2 respectively and for RDM, RFY, RDY and FBY of parent 209016 in F_2. While the SCA effects were positive and significant (p<0.01) for RDM in crosses; 209022 x 209014 and 209019 x 209013 in F_1 and 209016 x 209013 and 209031 x 209014 in F_2. These parents and crosses are promising for improvement of RDM RFY, RDY, FBY, and STA in yam beans. The results of study three from analysis of variance revealed significant genetic variation (p<0.001) among the 83 F_3 selected families for all the eight traits. Additive genetic variances (σ^2_A) were high and above unity for all the traits except VNY and PRO. Moderately high GCV values were observed for STA (10.28), RDM (13.42), RFY (18.8), RDY (23.71), FBY (19.91) and VNY (25.25). High narrow sense heritability (0.53 - 0.74%) and percentage response to selection (15.5 – 33.12%) were obtained for RDM, RFY, RDY, VNY, FBY and STA indicating high potential for genetic improvement of these traits in the yam bean germplasm in Uganda.

In conclusion, the three studies demonstrated that the yam bean germplasm in Uganda possesses considerable genetic variation that should allow genetic gains for RFY, RDM, RDY, FBY, STA and perhaps root Fe and PRO contents. The observed genetic variation ($\sigma^2_G = 9.3\%^2$) for RDM suggested that it is possible to breed for high dry matter yam beans by using low dry matter accessions without having access to high dry matter *P. tuberous*-chuins. The inheritance of RDM, RFY, RDY, FBY and STA was controlled by both additive and non-additive gene effects but with predominance of additive genetic effects. Lastly, the combination of high genetic variance, heritability and response to selection obtained in F_3 indicated potential to obtain high genetic gains for RDM, RFY, RDY, VNY, FBY, STA and Fe signifying that a systematic breeding program utilizing the available yam bean germplasm would develop well adapted, high yielding and high dry matter, protein and nutrient rich root crop for East and Central Africa.

THESIS STRUCTURE

This thesis is based on both published and yet to be published manuscripts presented in chapters 3, 4 and 5. Chapters 1, 2, 6 and 7 represent the introduction, literature review, general discussion, and conclusions and recommendations respectively. The thesis outline is as follows;

- Abstract: summary of the objectives, methods, key findings and conclusions from three studies.
- Chapter 1: General introduction, background to the study, statement of the research problem, objectives and hypotheses, and justification of the study.
- Chapter 2: Presents comprehensive review of literature on taxonomy, reproductive biology and breeding, agronomic, morphological and genetic diversity, inheritance and gene action and response to selection in yam beans.
- Chapter 3: Presents a study based on objective one covering the evaluation of genetic variability for yield, storage root dry matter and nutritional quality in yam beans which was published as "Agaba et al. (2016). Genetic variability for yield and nutritional quality in yam bean (*Pachyrhizus spp.*) *HortScience*, 51(9), 1079-1086. doi: 10.21273/HORTSCI10686-16"
- Chapter 4: Presents a study two from objective two on combing ability and inheritance of storage root dry matter and associated traits in F_1 and F_2 yam bean populations from which a paper has been published as "Agaba et al. (2017). Heritability, combining ability and inheritance of storage root dry matter in yam beans. *African Crop Science Journal* 25, no. 1 (2017): 83-95".
- Chapter 5: Presents the study on response to selection for storage root dry matter and associated traits among 83 F_3 yam bean families selected from F_2 population. A manuscript from this chapter was submitted to Australian Journal of Crop Science under the title "Agaba et al. (2018). Response to selection for storage root dry matter content and associated traits in yam beans (*Pachyrhizus* species)". In Press.
- Chapter 6: Presents the general discussion of the findings presented in chapters 3, 4 and 5.
- Chapter 7: Presents the thesis conclusions and recommendations.
- Then, a comprehensive list of references formatted according to American Psychological Association (APA) 6th edition for all cited literature sources is attached.

CHAPTER ONE
GENERAL INTRODUCTION

1.1. Background to the study

Tropical root crops are important for world food security as major sources of energy especially in developing countries (Lebot, 2009). These countries are faced with high rates of population growth and unsustainable subsistence farming methods practiced by resource poor farmers. In Africa, traditional root crops such as cassava (Gegios et al., 2010), sweet potatoes (Tumwegamire et al., 2011) and yams (Zanklan, 2003) constitute major food staples for millions of people making significant contribution to household incomes and acting as a major source of nutritional security for low income communities. However, wholesome dependence on conventional root crops especially in Sub-Saharan Africa is a risk factor for micronutrient deficiencies of vitamin A, iron and zinc (Gegios et al., 2010). Control strategies for micronutrient malnutrition have included supplementation with pharmaceuticals, fortification of foods, and dietary diversification. Enrichment of food staples with micronutrients such as iron, zinc and vitamin A through plant breeding has been adopted by agricultural research programs resulting in significant improvements in micronutrient deficiency rates (Pfeiffer & McClafferty, 2007; Tumwegamire et al., 2011).

Conversely, the management of micro nutrient deficiencies has involved introduction of high quality crops to supplement diets (Dini et al., 2013), for instance, the yam bean (*Pachyrhizus species*) was introduced into East and Central African countries of Uganda, Rwanda, Burundi, and D.R. Congo in 2010 by the International Potato Center (CIP) to bolster food security and sustainability of farming systems (Grüneberg, 2016; Heider et al., 2011) and to supplement iron (Fe) and protein content in diets of root crop dependent communities (Agaba et al., 2016). Investigations into the agronomic potential and adaptation of yam bean were initiated and so far, high storage root yields and yield stability have been reported across diverse agro-ecologies in Uganda (Andiku, 2013). Agaba et al. (2016) reported the presence of substantial genetic variation for yield and quality traits in the introduced yam bean germplasm and concluded that genetic improvement through selection would be worthwhile, signifying that the yam bean is adapted to the growing conditions and consumer needs in Uganda.

Elsewhere, such as in West Africa where yam beans were introduced nearly two decades ago (Zanklan et al., 2007), the crop was reported to be well adapted even to semi-arid field conditions with high storage root yields in Senegal (Annerose & Diouf, 1998), Benin (Zanklan et al., 2007) and Sierra Leaone (Belford et al., 2001). In Benin, yam bean storage roots have since been used to prepare "*Gari*" a food staple for millions of people often made from Cassava (Zanklan et al., 2007). Yam bean *Gari* has high content of protein and micronutrients compared to traditional forms made from Cassava (Padonou et al., 2013; Zanklan et al., 2007). The yam bean is hypothesized to contribute to restoration of depleted, marginal lands and to enhance sustainability of cropping systems due to biological nitrogen fixation, and to improve food and nutritional security especially iron and zinc in Sub-Saharan Africa (Adegbola et al., 2015; Agaba et al., 2016 ; Grüneberg, 2016). Nevertheless, the adoption of yam beans could be constrained by low dry matter content of the storage roots (Sørensen, 1996) because high dry matter trait is preferred among root crops in Africa for consumption and industrial applications (Tumwegamire et al., 2011). Therefore, genetic studies would be undertaken to improve storage root characteristics for accelerated adoption and integration of yam beans into farming systems in East and Central Africa as envisaged by Heider et al., 2011 and Zanklan et al., 2007.

1.2. Economic importance and eco-geographical distribution of yam beans

The yam bean is a leguminous root crop that originates from the neo-tropics of South and Central America (Sorensen, 1996). Yam beans are locally grown on a small scale in nearly all countries of Central and South America, South East Asia and West Africa. The exception is found in Mexico, the Philippines and Indonesia where commercial production of *Pachyrhizus erosus* (Mexican yam bean) is known on several hectares for domestic markets and export to the United States of America (Zanklan, 2003). The yam bean is variously known as *ahipa, ashipa, chuin, yushpe* in Peru; *jicama* in Mexico; *bunga* in the Philippines; *mishrikand, ram-kaseru, sankalu, sankeh alu, bangkoewang* in Indonesia; *ram-kaseru, sankalu, sankeh alu in India and dòushǔ or liáng shǔ* in China but has no local name in Africa because it is a recent introduction.

Whereas the Mexican yam bean (*P. erosus*) originates from the semiarid and humid tropics of Central America and Mexico, it is cultivated in the Caribbean, Guatemala, El Salvador and to a

limited extent in Honduras (Sørensen, 1996). In Mexico, *P. erosus* is widely grown, consumed and constitutes an important component of land use (Zaragoza Ramos-Castellanos et al., 2009). The *P. erosus* is the only species among the three cultivated yam beans which spread widely to different pantropical regions with notable success in Southeast Asian countries especially in Bangladesh (Noman et al., 2007). The wide distribution of *Pachyrhizus erosus* can be due to historical preference by the Spanish and Portuguese during the conquest of Latin America because of high yields that made the species more attractive for cultivation augmented policy of destroying the traditional Andean agricultural systems during the conquests (Ørting et al., 1996; Sørensen, 1996).

The two other cultivated species, *P. ahipa* (Wedd.) Parodi and *P. tuberosus* (Lam.) Spreng majorly have a South American distribution. *Pachyrhizus ahipa* also referred to as the Andean yam bean native to the south-western Amazon, in the Andean valleys of Bolivia and highlands of northern Argentina (Ørting et al., 1996). In the early years of domestication, *P. ahipa* was mainly cultivated by the Incan civilization but is presently in cultivation by local communities in the subtropical East Andean valleys of Bolivia and northern Argentina (Rodríguez-Navarro et al., 2009; Sørensen, 1996). However, production and use of *P. Ahipa* declined significantly over the years, coinciding with the collapse of the aboriginal cultures following the Conquest of America by the Spanish and the Portuguese and its cultivation remains relatively low globally (Doporto et al., 2011; Leidi et al., 2003). Oré Balbin et al. (2007) reported that the cultivation of Amazonian yam bean (*P. tuberosus*) was much reduced and that various landraces were in eminent danger of extinction mainly because of low commercial and scientific-agronomic interest in the species. The *P. tuberosus* is distributed throughout the Amazonian region of South America and the Caribbean (Santayana et al., 2014) and is mainly cultivated in lowland Ecuador, Bolivia, Peru, and Brazil (Grüneberg et al., 2003; Gupta et al., 2003; Ørting et al., 1996; Sørensen, 1996).

Currently, the three cultivated species of yam beans are reported in Brazil (Mélo, Krieger, & Montenegro, 1994), United States, Japan, German, China, India, Hawaii, Thailand, Malaysia and the Philipines (Ramos-de-la-Peña et al., 2013; Reddy, 2015), Nigeria, Senegal and Benin

(Adegbola et al., 2015; Padonou et al., 2013; Zanklan et al., 2007), and recently in Uganda, Rwanda, Burundi, and D.R. Congo (Agaba et al., 2016 ; Grüneberg, 2016; Heider et al., 2011). Due to its high yield potential, nitrogen fixing capacity, wide eco-geographical adaptation and low input requirements, the yam bean cultivation forms an integral part of sustainable land use that offer ecological and socio-economic benefits to farmers (Halafihi et al., 1994; Oré Balbin et al., 2007) making it important for low input farming systems in the developing world especially in the tropical and subtropical countries. Therefore, the yam beans might be practically adapted to the agro-ecological conditions and farmer needs in Uganda.

1.3. Agronomy and crop husbandry of yam beans

Among the neo-tropical legume genera with edible tuberous/storage roots, such as *Apios* Fabr., *Pachyrhizus* Rich. ex DC, *Pediomelum* Rydb. and *Vigna* Savi, *Pachyrhizus species* is the only one cultivated extensively both as a garden crop and mono-cropped on a commercial scale (Sørensen, 1996). Yam bean cultivation has a few agronomic and climatic requirements except for the labour intensive reproductive pruning (Sørensen, 1996) which involves removal of reproductive parts especially flowers and up to one third of vegetative parts especially in *P. erosus* and *P. ahipa* to enhance storage root formation and enhance storage root yields (Sørensen, 1996; Zanklan et al., 2007). In *P. tuberosus*, reproductive pruning is mainly practiced in *Ashipa* cultivar in Manabi province of Ecuador (Sørensen, 1996).

The propagation of yam beans by seed makes it easy to transport, disseminate and store germplasm as well as cultivate on a large scale as compared to conventional root crops such as sweetpotato and cassava that are vegetatively propagated. However, fields for planting yam beans should be ploughed to a depth of 0.25m and harrowed to a smooth seedbed to ensure optimal germination (Sørensen, 1996). The yam bean can be cultivated in a perennial system by vegetative regeneration where one or two of the laterally produced roots are picked when a harvestable storage root size is attained, leaving the root closest to the vegetative top which allows subsequent production of new storage roots for another 8 months in the field (Sørensen, 1996). Vegetative regeneration is mainly practiced in the Ashipa landraces of *P. tuberosus* by the Indians of the Amazon (Sørensen, 1996).

For better yields, the yam beans should be planted on ridges (Sørensen, 1996). The planting distances/crop density varies from 20 to 60 cm between rows and 6 to 25 cm between plants within rows giving approximately 8-35 plants/m^2 depending on the species and farming system (Sørensen, 1996). In West Africa, planting distances of 0.75 m between rows and 0.25 m within rows (between plants) have been adopted (Zanklan, 2003). Planting distances significantly influence number and storage roots fresh yield in yam beans (Mora et al., 2014). In yam bean cultivation, there is no need for nitrogen fertilizers as reported by Halafihi et al. (1994) that the addition of nitrogen fertilizer to yam bean fields resulted in significant reduction in storage root yields, due to inhibition of infection with nitrogen-fixing Rhizobium and Bradyrhizobium bacteria. This could be due to carbohydrate deprivation of the nodules associated with low assimilate partioning to the storage roots since excess nitrogen triggers protein synthesis which require considerable energy and organic synthases in the shoot. Therefore, the application of mineral nitrogen increases vegetative growth at the expense of storage root formation and leads to low nodulation in yam beans (Halafihi et al., 1994).

1.4. Consumption and utilization of yam bean

The yam bean is globally underutilized despite its wide adaption and high potential for production of human food and animal feed (Tapia & Sørensen, 2003). Utilization of yam bean is mainly limited by low dry matter content in storage roots of most accessions (Sørensen, 1996; Sørensen et al., 1997) and the presence of toxic compounds especially rotenone in seeds and vines that make these parts not suitable for human consumption (Grüneberg et al., 1999; Lautié et al., 2013).

The storage roots are usually consumed raw as a root fruit/vegetable or salad in native America and Asia (Gupta et al., 2003; Primiani, 2015; Ramos-de-la-Peña et al., 2012) because more than 85% of fresh weight is moisture content (Grüneberg et al., 1999; Santayana et al., 2014). However, a recently discovered chuin cultivar of *P. tuberosus* around the Ucayali River in Peru has low moisture content (about 70 %) and dry matter content of between 26 – 36 % which is considered high in the yam bean gene pool (Grüneberg et al., 2003; Zanklan et al., 2007). This

chuin cultivar compares favorably with most tropical root and tuber crops in terms of dry matter, and starch (Sorensen et al., 1997; Velasco and Grüneberg, 1999; Zanklan et al., 2003). The chuin has been used and processed like cassava (Sørensen et al., 1997, Grüneberg et al., 2003) and can be used to prepare protein rich "Gari", a food staple eaten daily by millions of people in West Africa (Zanklan et al., 2007).

Recent studies demonstrated potential for application of yam bean storage root extracts in the management of diabetes (Park & Han, 2015; Park et al., 2015). The extracts from *Pachyrhizus erosus* storage roots were found to significantly decrease postprandial blood glucose levels by inhibiting alpha-glucosidase and alpha-amylase treptozotocin (STZ)-induced diabetic mice which suggests potential application in the treatment of diabetes (Park & Han, 2015). Park et al. (2015) further reported that the Jicama (*Pachyrhizus erosus*) extract decreased the expression of glucose 6-phosphatase and phosphoenol pyruvate carboxykinase in the liver and increased insulin sensitivity in an animal model of type 2 diabetes. Other studies have shown the application of yam beans in the cosmetics industry for instance, a starch extract from yam bean roots is used in manufacturing of natural skin brightening / whitening and moisturizer cosmetics in Indonesia (Primiani, 2015; Rizky et al., 2013). Estrella-Parra et al. (2016) reported the use of powdered yam bean seeds in the management of mange, lice, and fleas in México indicating potential for utilizing rotenone in organic insecticides.

1.5. Opportunities and constraints for adoption of yam bean in Uganda

The yam bean offers a number of agronomic and adaptation advantages that might make the crop attractive to researchers and farmers in non-traditional areas like Uganda. Yam bean gives high storage root yields under low-input conditions, has short growth period, resistance against pests and diseases, and good adaptability to a wide range of climatic and edaphic conditions (Sørensen, 1996). Yam bean performs well in hot and humid climates and adapts well both in sub-tropical and under semi-arid conditions indicating potential for its cultivation in various agro-ecologies of Uganda (Agaba et al., 2016).

The cultivation of yam bean may improve soil fertility through biological nitrogen fixation and the crop can be grown without fertilizer application (Castellanos et al., 1997; Halafihi et al., 1994; Nielsen et al., 2000). The yam bean has the capability to increase soil fertility due to excellent *Rhizobium-Bradyrhizobium* relationship and potassium use efficiency unlike well-known tropical root crops like cassava (*Manihot esculenta Crantz*), sweet potato (*Ipomoea batatas* (L.) Lam.) or yams (Dioscorea spp.) (Badillo & Castellanos, 1996; Castellanos et al., 1997). The capacity to fix nitrogen makes the yam bean an important crop for low input farming systems. This makes yam bean a potentially important crop for restoration of impoverished soils especially in low input agricultural systems in the developing world particularly in Africa (Zanklan et al., 2007). Nitrogen is a major limiting factor in cropping systems across Africa, so biological nitrogen fixation which improves soil fertility makes the introduction of the yam beans attractive and may enhance their adoption in East and Central Africa (Grüneberg, 2016; Heider et al., 2011). In addition, yam beans storage roots are nutritionally richer compared to traditional root crops due to the high amounts of starch, proteins, vitamins and micronutrients (Fe, Zn) (Dini et al., 2013; Ratanadilok et al., 1996). This may explain why the crop has been identified as a field crop with high potential for integration into farming systems where micronutrient deficiencies are rampant especially in Africa (Agaba et al., 2016 ; Grüneberg, 2016; Heider et al., 2011; Zanklan et al., 2007).

Nonetheless, the adoption and sustainable integration of yam bean in Uganda as in other East and Central African countries could be constrained by the labour intensive agronomic practice of reproductive pruning known to enhance storage root yields. Reproductive pruning is not a common practice in existing farming systems in Uganda and may become a limiting factor in cultivation of the yam beans. The low dry matter of most yam bean germplasm available in Uganda may also limit its adoption and utilization given that high dry matter is preferred among root crops (Tumwegamire et al., 2011). This means that making yam bean an attractive food and industrial crop in East and Central Africa requires investment in research, to mainly improve storage root dry matter content (Grüneberg et al., 1999) and enhance yields without need for reproductive pruning. This is based on the suggestion by Zanklan, (2003) that an improved and broadly adapted high quality yam bean could provide alternative food sources in Sub-Saharan

Africa where root crops are major staples. Fortunately, it's possible to improve storage root dry matter content in yam beans through intraspecific and interspecific hybridisation especially with the chuin cultivar (Grüneberg et al., 2003).

1.6. Problem Statement

In Uganda as in many African countries, root and tuber crops form the second most important source of human nutrition after cereals (Tumwegamire et al., 2011). However, these food sources are generally deficient in vital nutrients such as proteins, zinc and iron which have resulted in severe micro nutrient deficiencies especially among weaning children, breast feeding mothers and the elderly (Gegios et al., 2010). The recently introduced yam bean has storage roots that are rich in proteins, micro nutrients (iron, zinc), lipids, sugars, fibers, ash, and vitamins (Noman et al., 2007). Grüneberg (2016) reported that yam bean could supplement staple food sources and offer alternative root crops for communities in East and Central Africa. Nevertheless, the yam bean is neglected and underutilized globally by researchers mainly because of low storage root dry matter content (Grüneberg et al., 2003; Rizky et al., 2013). Therefore, the adoption and utilization of the yam bean might become constrained in new areas such as Uganda where farmers and consumers of root crops prefer high dry matter varieties (Tumwegamire et al., 2011). Even though there is an opportunity to use chuin cultivar which has relatively high dry matter content of above 30% (Zanklan, 2003) to incorporate high dry matter in the remaining yam bean genepool through breeding (Grüneberg et al., 2003), genetic improvement of storage root dry matter content and yield traits in yam bean has remained unstudied and there are no breeding programs targeting high dry matter cultivar development. Also, there are no reported high dry matter yam bean varieties and information on genetic improvement of yam beans is limited. A few hybridisation studies have been conducted to assess compatibility and the possibility to incorporate high dry matter from the chuin into the remaining yam bean gene pool (Grüneberg et al., 2003; Sørensen, 1996). Despite these efforts, there is lack of information on the nature and magnitude of genetic parameters for yield, dry matter content and nutritional quality as well as combining ability, gene action and response to selection for dry matter content and associated traits for the yam bean germplasm in Uganda. Such information is vital to design

appropriate selection and breeding strategies for the improvement of the available yam bean germplasm.

1.7. Justification of the Study

To widen nutritional options of root crop dependent communities in Uganda, the introduction of high quality yam beans with high yields, nutritional quality and resistance to pests and diseases was essential. The yam bean has high biological nitrogen fixation and is widely adapted to diverse agro ecologies and climate vagaries. However, the adoption and subsequent cultivation of yam beans in Uganda and other East and Central African countries, requires extensive germplasm evaluation and genetic studies to acquire useful information for selecting suitable parents for inclusion in hybridisation and selection programs to breed high dry matter and high yielding varieties. The choice of effective selection and appropriate breeding strategy for yam beans in Uganda requires information on the nature and extent of genetic variability, heritability and variance components as well as inheritance and response to selection for dry matter, yield and nutritional quality traits of the available yam bean germplasm. Information on combining abilities is important for optimizing breeding and selection methods through identification of superior parents, crosses and progenies in yam bean populations.

The determined genetic parameters, inheritance mechanisms and response to selection for yield, dry matter content and nutritional quality traits in yam bean germplasm in Uganda would form a basis for initiating breeding programs. Such genetic studies are recommended as a foundation for improvement of storage root yields, dry matter and quality traits in yam beans (Silva & Ticona-Benavente, 2016). Improved yam beans with high dry matter and dry matter related traits are attractive and profitable to farmers for consumption and processing and would accelerate adoption of the crop into existing farming systems in Uganda (Agaba et al., 2016). The integration of improved yam bean varieties in food systems of root crop dependent communities would offer rich food and enhance the intake of protein, micro-nutrients like iron and zinc, and vitamins, and mitigate micro-nutrient deficiencies especially among infants, breast feeding mothers and the elderly.

1.8. The aim of the study

The goal of this study was to advance knowledge on the genetics of yam bean germplasm in Uganda for breeding high DM varieties with improved yields and nutritional quality

1.7.1 The specific objectives

The specific objectives of the study were as follows;

1. To determine genetic variation for storage root yield, dry matter and nutritional quality of yam bean germplasm in Uganda
2. To assess combining abilities and gene action controlling inheritance of storage root dry matter and associated traits in yam bean germplasm in Uganda
3. To determine response to selection for storage root dry matter and associated traits in yam bean populations

1.7.2 Hypotheses

1. There is substantial genetic variation for storage root yield components, dry matter and nutritional quality among yam bean germplasm in Uganda.
2. The inheritance of storage root dry matter and associated traits in yam bean are controlled by additive gene effects.
3. There is high response to selection for storage root dry matter and associated traits in yam bean populations.

CHAPTER TWO
LITERATURE REVIEW

2.1 Genetic variability for yield, dry matter and quality traits in yam beans

2.1.1 Taxonomy and genetic diversity of yam beans

The yam bean is taxonomically diverse and constituted of five species within the genus *Pachyrhizus*, which belongs in the legume family- *Fabaceae*, subfamily- *Faboidae*, tribus- *Phaseoleae* and subtribe -*Diocleinae* (Lackey, 1977; Sørensen, 1996). The five species are genetically distinct in their domestication, eco-geographical distribution and farmer selection. Three species are cultivated and distinguished following their eco-geographical origins into the Amazonian yam bean (*P. tuberosus*) from the Amazon, Mexican yam bean (*P. erosus*) from Mexico and the Andean yam bean (*P. ahipa*) from subtropical Andean valleys of Bolivia (Sørensen, 1996). Two species, *P. panamensis* and *P. ferrugineus* are still wild (Ørting et al., 1996; Silva & Ticona-Benavente, 2016).

Several studies have reported high genetic variability for agronomic and morphological characteristics among the cultivated yam beans (Agaba et al., 2016 ; Delêtre et al., 2013; Grüneberg, 2016; Santayana et al., 2014; Silva & Ticona-Benavente, 2016; Sørensen, 1996; Zanklan et al., 2007). Zanklan et al. (2007) conducted variance components analysis and revealed significant inter and intraspecific genetic variation among morphological and agronomic traits between and within the three cultivated species evaluated at two contrasting locations (Songhai and Niaouli) in Benin, West Africa. High genetic variation was recorded for storage root yields and associated traits among the three cultivated yam beans despite the presence of significant G x E interactions for most yield traits. The author argued that the significant G x E interaction effects were due to irrigation at Songhai as compared to water stress at Niaouli location (Zanklan et al., 2007). Zanklan et al. (2007) also reported large genetic variation for quality traits; starch, sucrose, fructose, and glucose and suggested that rapid genetic progress was possible for genetic improvement of yield and quality traits through interspecific hybridization and directional selection.

Santayana et al. (2014) found that the genetic diversity in *P. ahipa* and *P. tuberosus* was lower than in *P. erosus,* and that *P. ahipa* is the least diverse when characterized by simple sequence repeats markers. While Delêtre et al. (2013) reported *P. ahipa* as a species with the least genetic variability among the five yam bean species. Only two landraces of *P. ahipa* have been described (Santayana et al., 2014) as consisting of bushy erect plants and climbing herbaceous plants predominantly grown in southern and northern Bolivia respectively (Ørting et al., 1996). More recently, diversity analysis by Silva and Ticona-Benavente (2016) demonstrated the presence of wide diversity using 10 morpho-agronomic traits of 64 yam bean accessions *viz.,* plant height, number of secondary branches, shoot biomass, stem diameter, root biomass, length/diameter ratio (L/D), and shape. The genetic diversity was significant for all traits except stem diameter and visual assessment of root shape which indicated possibility for improvement through breeding for root yields and associated traits.

The Amazonian yam bean (*P. tuberosus*) is the most diverse and three distinct cultivar groups were identified from field studies in Bolivia, Ecuador and Peru, and classified into Ashipa, chuins and Jíquima based on differences in morphology, agricultural practices and storage root characteristics (Sørensen et al., 1997). Tapia and Sørensen (2003) observed large genetic variability between and within the three cultivar groups of the Amazonian yam bean based on ten qualitative and seven quantitative morphological characters with greater discriminating powers. High genetic variability was observed for morphological characters *viz.,* weight of seed per plant, thickness of the root cortex, shape and type of the lobe of the terminal leaflet, colour of the root pulp, growth habit (determinate vs. indeterminate), internode length and days to flowering while less genetic variability was recorded for length of the flower, width of the vexillum, length/width ratio of the terminal leaflet, length of seed and the days to physiological maturity (Tapia & Sørensen, 2003). Through principal component analysis, the petal and the length/width ratio were identified as the most morphologically varied (Tapia & Sørensen, 2003). According to Zanklan (2003), Ashipa and Jíquima cultivar groups have low dry matter content (below 20%) while the chuin cultivar group has high dry matter content (above 30%).

2.1.2 Morphological diversity in yam beans

The five *species* of yam beans are morphologically diverse to permit key trait improvements through breeding. Morphological variability is pronounced among the three (*P. ahipa, P. erosus* and *P. tuberosus*) cultivated species (Zanklan, 2003). Sørensen (1996) reported that yam bean plants range from robust climbing vines to determinate bushy-erect forms and their growth seasons vary from less than five months to more than a year. The species can be differentiated by growth characteristics into vines or semi-erect herbaceous and/ or lignified perennial plants with one or more tuberous roots, trifoliolate leaves with stipules or pinnately arranged leaflets with caducous stipels, and differences in inflorescence ranging from complex to simple raceme (Sørensen, 1988, 1996). The floral structure of *Pachyrhizus* is composed of an ovary with a basal crenate disc-formed nectarium, ventrally ciliated and recurving style, and the vertical surface of the stigma is subglobose. All the species are morphologically characterized by the presence of a "false beard" of short hairs along the dorsal (adaxial) side of the ovary, continuing almost to the base of the stigma along the incurved side of the style (Sørensen, 1996). The straight legume is septate between the seeds, which are a square, more or less flattened, or a rounded kidney, shape. Colors range from olive green and deep maroon to black, or from black and white to mottled cream (Sørensen, 1996).

According to Santayana et al. (2014), several landraces/cultivar groups exist within each species characterized by intrinsic morphological and physiological differences and their degree of domestication. Yam bean landraces vary from those with multiple laterally produced storage roots to quite advanced cultivars with single vertically produced storage roots (Sørensen, 1996). Døygaard and Sorensen (1998), conducted principal component analysis of the *genus Pachyrhizus* using morphological characters and reported that the three cultivated species are morphologically distinct. Several characterization studies revealed inherent morphological diversity among the four different cultivar groups locally known as chuin, Ashipa, Yushpe, and Jíquima the Amazonian yam bean (*Pachyrhizus tuberosus*) (Silva & Ticona-Benavente, 2016; Tapia & Sørensen, 2003). However, cultivar groupings such that the chuins and the Jíquimas have a uniform, vertical tap-root (Sørensen et al., 1997) but the chuins have high storage root dry matter content and lobed leaflets Length / Width (L/W) ratio.

The Jíquimas, Ashipas, and Yushpe have relatively low storage root dry matter and the leaflets are entire to deeply lobed heart-shaped with a low L/W ratio (Tapia & Sørensen, 2003).

2.1.3 Storage root yield and dry matter content in yam beans

The economic value of root crops to farmers, consumers and industries is determined by their storage root dry matter content which reflects true biological yield (Teye et al., 2011). Yam bean exhibits high yield potential and variability of edible storage roots ranging from 10 to 145t ha^{-1} per hectare (Silva & Ticona-Benavente, 2016; Zanklan et al., 2007). Karuniawan (2005) reported storage root yields of 10 to 36 t ha^{-1} in Eastern Indonesia while Annerose and Diouf (1998) estimated storage root yields of up to 145 t ha^{-1} in Mexico from low input fields with no fertilizer application. In the Philippines, storage root yields of between 80 and 90 t ha^{-1} were recorded (Ratanadilok and Thanisawanyangkura, 1998). While in West Africa, storage root yields of up to 44 t ha^{-1} and 23 t ha^{-1} were reported in reproductively pruned and non-pruned fields in Benin (Zanklan, 2003). In the Amazon region, where the crop is economically important, storage root yields of between 77.0 t ha^{-1} and 125.9 t ha^{-1} have been recorded (Nielsen et al., 2000 ; Tapia & Sørensen, 2003). The yield potential of yam bean compares favorably with yields of common root and tuber crops such as cassava and sweetpotato (Mtunda, 2009; Tumuhimbise et al., 2014; Tumwegamire et al., 2011), suggesting the yam bean could be attractive to farmers in new areas where root crops are major food staples.

The *Pachyrhizus* species show considerable variation in storage root dry matter with low dry matter genotypes (RDM < 20%) and high dry matter genotypes especially the chuins (25-36%) (Grüneberg et al., 2003; Sørensen et al., 1997). Zanklan (2003) reported presence of significant genetic variation for tuber dry matter content in *P. tuberosus* and *P. ahipa*. Dry matter content varied from 13.5% in *P. erosus* to 36% in *P. tuberosus* chuin has been reported (Zanklan et al., 2003; Forsyth et al., 2002). The chuin cultivar of *P. tuberosus* which is largely cultivated along the Ucayali Rivers and their tributaries in the Amazonian Peru has low moisture content of between 68 to 72 % of fresh tuber weight (Sørensen et al., 1997) and is ranked high in dry matter content (between 26 – 30%) (Grüneberg et al., 1998) and can be consumed like cassava after cooking (Sørensen et al., 1997).

This is because the dry matter content of chuins compares well with the average storage root dry matter content of Cassava that varies from between 20% and 40% (Teye et al., 2011). Most cultivated sweetpotato varieties in Uganda have an average dry matter content of about 30% (Tumwegamire et al., 2011). However, yam bean storage roots are generally characterized by high moisture content, usually more than 85% of the total weight (Sorensen, 1996; Velasco and Grüneberg, 1999) and the dry mater content is generally low (12 – 22%) so that their utilization is limited by this sole character (Grüneberg et al., 2003) which explains why yam bean has remained a minor crop (Jacobsen et al., 2015). However, Zanklan (2003) reported that the chuin cultivar offers an opportunity to develop widely adapted high dry matter, protein rich yam beans that can diversify food sources for African communities.

2.1.4 Characterization of quality traits in yam beans

A number of studies have been undertaken to determine and characterize quality traits in yam beans and considerable variability has been reported among the cultivated species by various researchers (Kale, 2006; Noman et al., 2007; Ratanadilok et al., 1998; Velasco & Grüneberg, 1999). The yam bean storage roots contains a balanced and nutritious composition of proteins, starch, lipids, sugars, fiber, ash, minerals (iron and zinc), and vitamins (Ratanadilok et al., 1996) and appreciable amounts of carbohydrates and crude fiber (Buckman et al., 2015; Noman et al., 2007). This carbohydrate mainly consists of good quality starch that is easily digestible (Bergthaller et al., 2001). The yam bean storage roots are therefore considered a good source of energy and are an easily digestible food which makes the crop of great nutritional and economic importance (Buckman et al., 2015).

Karuniawan (2004) reported that 100g of fresh yam bean comprises of 2.1 - 10.7 g starch and 1.0 - 2.2 g of protein. Yam bean storage roots dry weight contains 56% to 58% starch content of which 11.6 to 16.8% is amylase (Forsyth et al., 2002), 8-18% protein, 1.4 mg/100g zinc, and 160 mg/100g Magnesium (Wassens, 2011) and high iron concentrations (130 mg/kg) (Kale, 2006). This explains why yam beans are considered as an interesting new source of starch (Bergthaller et al., 2001) and protein (de Mélo et al., 1994). The above cited nutritional status makes the yam bean a valuable protein rich food (Velasco and Grüneberg, 1999).

This is because the protein content in yam bean is three to five times higher than in well-known tropical root crops such as cassava (*Manihot esculenta* Crantz), sweetpotato (*Ipomoea batatas*) and yams (*Dioscorea spp.*) (Velasco and Grüneberg, 1999; Zanklan 2003). Therefore, yam bean storage roots are a rich food source recommended for the elderly, breast feeding mothers and weaning infants (Sørensen et al., 1997).

2.1.5 Assessment of root quality by near infrared reflectance spectroscopy (NIRS)

Conventional wet chemistry based procedures for evaluation of root nutritional quality is rather complex, as each trait to be measured requires unique analytical methods, most of them tedious and time consuming (Grüneberg et al., 1999). Near-infrared reflectance spectroscopy (NIRS) has been adopted as an alternative technique that could be used to analyze many traits simultaneously. NIRS has proven an accurate, precise, and rapid alternative to wet chemistry procedures for determining concentrations of major classes of chemical compounds in organic materials (Tumwegamire et al., 2011; Zanklan, 2003). It is a non-destructive, reliable and rapid method to determine quality traits simultaneously provided that the corresponding calibration equations have previously been developed (Sánchez et al., 2014; Zanklan, 2003). The NIRS method utilizes reflectance signals resulting from bending and stretching vibrations in molecular bonds between carbon, nitrogen, hydrogen and oxygen. However, calibration is required to correlate the spectral response of each sample at individual wave lengths to known chemical concentrations from laboratory analyses.

The NIRS has been adopted to estimate quality traits in many tropical root crops (Grüneberg et al., 1999; Lebot, 2009; Tumwegamire et al., 2011) mainly due to its convenience and easy sampling techniques. The NIRS technique has been effectively used to achieve rapid screening of germplasm, assessing genetic control and heritability studies (Raymond, 2002) as well as prediction of disease/pest resistance for instance the soybean cyst nematode (SCN) resistance in soybean (Cao et al., 2002). In sweetpotato, NIRS has been used to screen micronutrients especially Fe, Zn and β-carotene concentrations (Tumwegamire et al., 2011). The NIRS has also been applied to the analysis of nitrogen concentration in oven-dried potato samples and to measure total reducing sugars in fresh potato slices (Peiris et al., 1999).

In yam beans, NIRS has been used to assess the genetic diversity within and between species of yam beans (Zanklan, 2003). NIRS has also been used to analyze change in physical and chemical composition of seeds of the three cultivated species of yam bean (Zanklan, 2003).

2.2 Gene action controlling inheritance of storage root yield, dry matter and quality traits in yam beans

2.2.1 Hybridisation and breeding in yam beans

Pachyrhizus species are diploid (2n = 2x = 22) (Santayana et al., 2014), predominately self-pollinating (Ørting et al., 1996; Sørensen, 1996) but permit successful hybridisation between the species (Grüneberg et al., 2003). The diploid nature of the yam bean species makes it easier to evaluate recombinant lines after crossing since recessive alleles would be expressed in few progenies than at high ploidy levels. The species have bisexual flowers which are mainly self-pollinating save for a 2 - 4% incidence of out crossing in *P. ahipa* which is influenced by the availability of pollinators (Sørensen, 1996). The self-fertilizing nature of the genus *Pachyhizus* gives inbred homozygous lines as inputs and or outputs of breeding, influencing choice of selection methods (Grum, 1994; Zanklan, 2003).

Hybridisation studies have demonstrated that all *Pachyrhizus* species are sexually compatible except for one of the wild species *P. ferrugineus* (Grüneberg et al., 2003; Sørensen, 1996). This compatibility has led to arguments that the three cultivated yam beans may belong to one primary genepool given that fertile and vigorous interspecific hybrids can be developed (Grüneberg et al., 2003). However, there are no naturally occurring hybrids in areas shared by the species because their flowering periods do not overlap under native natural conditions (Sørensen, 1996). Most breeding methods applicable to self-fertilizing crops are suitable for *Pachyrhizus* species except the bulk method (Grum, 1994; Zanklan, 2003). Breeding of yam bean is concerned above all with the development of types with high dry matter content, yields and quality traits such as protein, iron and zinc content (Grüneberg et al., 2003; Zanklan et al., 2007). Simultaneous selection for traits such as storage root yield and dry matter content may give economic results of simultaneous breeding goals in yam beans.

2.2.2 Combining ability

Combining ability studies are very rare in yam beans probably because the crop is marginalized in crop science and few resources have been invested in evaluating the genetic potential of such minor crops. There is only one study reported on combining ability for quantitative traits in yam beans moreover on one species (*Pachyrhizus erosus*) based on agronomic markers (Jha & Singh, 2014). The study assessed 66 crosses for days to flowering, vine length, number of primary branches per plant, number of leaves per plant, vine weight per plant, root length, root girth and root yield per plant. The results showed that general combining ability estimates were high for storage root yield and yield contributing traits, and specific combining ability was highly associated with performance of the crosses. Four female parents, ML-4, ML-13, ML-17 and ML-32 had positive and significant GCA effects and were good combiners for storage root yields and yield components (root length and root girth) (Jha & Singh, 2014).

The findings by Jha and Singh (2014) further revealed that parental lines exhibited high GCA effects for storage root yields and high GCA effects for yield associated traits. In addition, male testers were found good combiners for all traits except vine yield, which suggested that the evaluated males were good gene sources for improvement of characters of economic importance in yam beans especially yield traits. Jha and Singh (2014) further reported significant and positive SCA effects and high mean performances for several crosses (ML-8 x T-1, ML-5 x T-3, ML-32 x T-3, ML-17 x T-2 and ML-13 x T-3 for storage root yield and its main components, root girth and root length. It was observed that there is a close association between performance of parents and crosses with their combining ability effects and parents exhibiting high GCA effects contained more favorable dominant alleles for the traits of interest. However, these genetic parameters represent only one species and there are to date no relevant combining ability studies for storage root dry matter and associated traits in all cultivated yam beans, this gap forms the focus of current study reported in chapter four of this thesis.

2.2.3 Inheritance of yield traits in yam beans

Although very little progress has been achieved in understanding the inheritance mechanism of quantitative traits in yam beans such as storage root yield and dry matter content (Agaba et al.,

2016), few genetic studies conducted on yam beans suggests high genetic variation indicating possible polygenic additive gene effects (Agaba et al., 2016 ; Jha & Singh, 2014; Silva & Ticona-Benavente, 2016). Jha and Singh (2014) studied the inheritance of quantitative traits in yam beans using 22 female lines, three male testers and 66 crosses. They reported presence of both additive x additive and additive x dominance gene effects for storage root yields and yield contributing traits, root length and root girth which demonstrated the potential to exploit heterosis in yam beans. These results could be corroborated by the high genetic variation (σ^2_G) reported for yield traits among 26 accessions constituted of the three cultivated yam bean species in Uganda which strengthened the argument for high genetic improvement after a few cycles of selection and recombination (Agaba et al., 2016).

2.2.4 Heritability studies in yam beans

Heritability explains the proportion of phenotypic variance expressed among genotypes that can be attributed to genetic differences among them (Safavi et al., 2011) and the magnitude of heritability indicates the reliability with which the genotype will be recognized by its phenotypic expression (Chandrababu & Sharma, 1999). Therefore, a high heritability estimate of a trait provides a measure of the effectiveness of selection on phenotypic basis for that particular trait (Singh et al., 2003) and assists breeders to choose selection methods suitable for optimal trait improvement and higher genetic transfers from parents to offspring (Kiryowa et al., 2009). Heritability of dry matter content in root crops has been of great interest to researchers and breeding programs. In sweetpotatoes, several studies have reported high heritability estimates for root traits in different designs and environments (Ma-Teresa et al., 1994; Tumwegamire et al., 2011), while other studies reported moderate to high heritability estimates for dry matter content in cassava (*Manihot esculenta Crantz*) (Kawano, 2003; Ntawuruhunga & Dixon, 2010).

In yam beans however, heritability studies are still limited. Cesar and Sørensen (2003) reported relatively high heredity index values in yam bean for morphological traits such as the number of days to flowering, days to physiological maturity, length of the principal stem and the length to width ratio of the terminal leaflet. This suggests that the phenotypic expression of these characters is a good indication of its genetic value. The heredity index values for root traits such

as the width of the root and thickness of root cortex were very low which implies that improvement of these traits through selection would be slow. However, Agaba et al. (2016) observed high broad sense heritability estimates ranging from 58.4 to 83.6% for yield and related traits namely, storage root yield, dry yield, dry matter content, vine yield, fresh biomass yield, as well as for quality traits *viz.*, starch and iron content of storage roots in yam beans which suggested potential for improvement these characters.

2.3 Breeding and response to selection for high dry matter and associated traits in yam beans

2.3.1 Selection studies in yam beans

A few selection studies have been conducted to assess compatibility and the possibility to incorporate high dry matter from the chuin into the remaining yam bean gene pool (Grüneberg et al., 2003; Sørensen, 1996). Initial hybridisation experiments were carried out to investigate the compatibility of interspecific hybridisation of the three cultivated species (Grum, 1994; Sorensen et al., 1993). Subsequent studies have shown that yam bean species are compatible and give fertile, viable, and vigorous hybrid plants from all cross combinations (Grum, 1994; Grüneberg et al., 2003; Sørensen, 1996), including from reciprocal crosses. However, the seed from crosses between *P. ahipa* (female) x *P. tuberosus* (male) were reported un able to germinate (Sørensen, 1996). Sørensen (1996) further reported that the wild species, *P. panamensi* is fully compatible with the cultivated species while several crosses with the *P. ferrugineus* were unsuccessful except for seed set from *Pachyrhizus ferrugineus x Pachyrhizus erosus* combination.

Other hybridisation experiments with subsequent pedigree selection have included three way interspecific F_1 crosses involving *Pachyrhizus erosus x ahipa, P. erosus x tuberosus* and reciprocal crosses to breed new cultivars with desirable agronomic characters such as yield, tuber quality, earliness, nitrogen fixation, photo-thermal neutrality and reduced flower set (Sørensen, 1996). However, these studies fell short of addressing storage root dry matter content which is a major trait limiting the industrial viability of yam bean.

Rizky et al. (2013) reported genotypes with higher dry matter, protein and starch content from intraspecific and interspecific crosses between *P. erosus* and *P. ahipa*. The dry matter content of the hybrids was higher (26%) than the dry matter content (6.11 %) of both parents and interspecific hybrid genotype AC 216-139 d x EC 550 was identified with the highest value for dry matter content. Also, the starch content (6.73%) of hybrid genotypes was higher than that of parents (2. 66%) and the protein content hybrids was higher than that of parental genotypes. Nevertheless, the genetic improvement of dry matter content of storage roots through interspecies hybridisation has been widely recommended in literature (Grüneberg et al., 2003; Kisambira, 2014; Zanklan, 2003).

2.3.2 Response to selection in yam beans

Response to selection reflects the difference between the mean phenotypic values of the offspring of the selected parents and the parental generation before selection. Regardless of species, trait of interest and breeding methods, response to selection serves as a simple universal expression for expected genetic improvement (Falconer and Mackay, 1996). Holland et al. (2003) and Nyquist (1991) discussed relevance of selection, response units and their genetic relationships for accurate prediction of genetic gain. Selection units are the operational unit of selection and can be individuals or families while response units are individuals in the improved population following selection (Jines, 2007).

Plant species possess a vast diversity of modes of reproduction to derive selection and response units thus selection units are often families replicated within and across environments (Holland et al., 2003; Jines, 2007; Nyquist, 1991). Breeders are therefore often interested in predicting selection responses from recombining various selection units in numerous ways to determine the most desirable strategy when given a limited amount of resources (Jines, 2007). Predicting response to selection enables plant breeders to determine desirable breeding methods and develop appropriate selection strategies to enhance gains (Jines, 2007). Breeding programs requires selection of parents and progenies which depends on the extent of variability in the base population and the magnitude of variance components that control the phenotypic expression of the target traits (Gatti et al., 2005).

There are currently no studies on response to selection in yam beans. Nevertheless, Zanklan et al. (2007) suggested that selection could be used to improve starch, sucrose, fructose and glucose while Tapia and Sørensen (2003) concluded from morphological analysis of genetic variation that response to selection for tuber yield/weight, seed yield, and thickness of root cortex would be high. Recently, potential for genetic gains was identified for fresh storage root yield, root dry matter, dry matter yields, biomass yields, starch content and yield, and root Fe contents reported for the yam bean germplasm in Uganda (Agaba et al., 2016). Silva et al. (2016) argued that the presence of wide diversity among yam bean genotypes means that new varieties can be obtained by selection in a short time given the high potential for genetic gain. Chapter five of this thesis presents the first set of findings for response to selection for high storage root dry matter, yield and components in segregating yam bean populations.

2.4 Mating designs and partitioning of genetic variances

Mating designs are important in breeding programs to evaluate parental genotypes, develop recombinant F_1 crosses as the base population for selection, generate synthetic populations and provide information for estimation of gene action and genetic gains (Hallauer et al., 2010). Nduwumuremyi et al. (2013) reviewed the most used mating designs in plant breeding and genetics studies and the associated statistical approaches for successful plant breeding. The review identified key factors affecting choice of mating designs and for estimating genetic variances by plant breeders and geneticists as objectives of the study, time, space, cost and other biological limitations. Earlier studies by Acquaah (2012) had proposed the type of crossing to be used (artificial or natural), the type of pollination (self- or cross-pollinated), the type of pollen dissemination (wind or insect), the presence of a male-sterility system, the purpose of the project (for breeding or genetic studies) and the size of the population required as the factors influencing the choice of mating design. The commonly used mating designs as described and studied by different researchers (Acquaah, 2012; Hallauer et al., 2010; Kearsey & Pooni, 1996) namely, bi-parental progenies (BIP), polycross, topcross, North Carolina (I, III, III), Diallels (I, II, III, IV) and Line X tester design were extensively discussed by (Nduwumuremyi et al., 2013) and therefore the detailed application of North Carolina II mating design is described in section 2.4.1.

2.4.1 The North Carolina II mating design

The North Carolina II mating design (NCII) is one of the most used factorial mating designs for genetic analysis whose theoretical basis was described by Comstock and Robinson (1952). In NCII, every male is crossed with every female creating male and female half sib (HB) families in which sets of progenies have either the same father but different mothers or vice versa (Comstock & Robinson, 1952; Kearsey & Pooni, 1996). This is accomplished by a systematic crossing scheme in which males and females are mated in all possible combinations to give progeny families (Mtunda, 2009). The design is most adapted to plants that have multiple flowers so that each plant can be used repeatedly as both male and female during hybridisation (Nduwumuremyi et al., 2013). Blocking is used in NCII to allow the mating of a single group of males to a single group of females to be kept intact as a unit (Acquaah, 2007).

The NCII was particularly developed for estimation of the average degree of dominance without attempt to estimate the epistatic effects. The dominance effect is estimated by the interaction between the line effect and F_2 parent (Xu, 2003). North Carolina II mating design was adopted in this study because of wide application in inheritance studies that utilize combining abilities to estimate additive and non-additive gene effects (Acquaah, 2007; Amongi et al., 2015). NCII is suitable for estimation of variance components, combining abilities and inferring additive and dominance genetic effects but reliability of genetic estimates is influenced by sample size of parents (Comstock & Robinson, 1952; Kearsey & Pooni, 1996; Nduwumuremyi et al., 2013). The NCII design allows multivariate analysis to estimate variance components (Nduwumuremyi et al., 2013). Mtunda (2009) reported that in NCII, the expected values of different components of genetic variance i.e. additive and dominance are determined by equating with the observed values of components of genetic variation.

The NCII analysis is essentially a two-way ANOVA in which the variation may be partitioned into difference between males (m) and females (f) and their interaction (Nduwumuremyi et al., 2013). The mean squares for male and female parents give estimates of general combining ability (GCA) which estimates additive component of variation for females and males separately (Mtunda, 2009). While the mean squares for the interaction between the female and males are

equivalent to specific combining ability (SCA) variance (Acquaah, 2012), which estimates non-additive genetic effects particularly the dominance variance (Kearsey & Pooni, 1996). Maternal effects can also be determined from the variance ratio of mean squares of females to males (MS_F/MS_M) provided the number of males and female parents are equal. In addition, the NCII mating design provides a test of significance and allows estimation of additive and dominance variances in absence of epistasis leading to estimation of heritabilities (Kearsey & Pooni, 1996). However, reliability of NCII for estimation of variance components requires two assumptions namely, no epistasis and variance effects due to common environmental effects of families is negligible (Kiryowa et al., 2009).

CHAPTER THREE

GENETIC VARIABILITY FOR YIELD AND NUTRITIONAL QUALITY TRAITS AMONG YAM BEAN GERMPLASM IN UGANDA

3.1. Introduction

The yam bean is a storage root forming legume belonging to the genus *Pachyrhizus* Rich. ex DC, comprised of three cultivated species: *Pachyrhizus erosus* (L.) Urban (Mexican yam bean), *Pachyrhizus ahipa* (Wedd.) Parodi (Andean yam bean), and *Pachyrhizus tuberosus* (Lam.) Spreng (Amazonian yam bean) and two wild species, *P. panamensi* found in Venezuela and Panama and *P. ferrugineus* in Colombia (Ingham, 1990; Lackey, 1977; Sørensen, 1988). *Pachyrhizus species* are diploid and permit successful hybridisation between the species (Grüneberg et al., 2003) with no obstacle in self-pollination (Ørting et al., 1996; Santayana et al., 2014). The cultivated species have potential for high storage root yields and nutritional quality (Santayana et al., 2014). Storage root yields of more than 80 t ha^{-1} have been reported in Central America and Asia (Karuniawan, 2004; Silva & Ticona-Benavente, 2016; Sørensen, 1996). While in Africa, on-farm trials have recorded average yields of 24 t ha^{-1} from two *P. erosus* accessions (CIP-209018 and CIP-209019) in Benin (Adegbola et al., 2015; Grüneberg, 2016; Zanklan et al., 2007), 17 t ha^{-1} from 10 *P. erosus* accessions in Senegal (Annerose & Diouf, 1998) and 14 t ha^{-1} from 15 *P. erosus* accessions in Sierra Leone (Belford et al., 2001).

The yam bean storage roots contain 56-58% starch (Forsyth et al., 2002) and 8 to 18% protein on dry basis (Velasco and Grüneberg, 1999), vitamins such as niacin, riboflavin and thiamine, minerals (potassium, sodium, phosphorus, calcium and magnesium) and micronutrients especially iron and zinc (Dini et al., 2013; Noman et al., 2007; Sørensen, 1996). The yam bean was introduced in Uganda in 2010 to improve food security and nutritional status of root crop dependent communities (Grüneberg, 2016; Heider et al., 2011). However, the yam bean accessions remained largely uncharacterized before this study except for the composition, physicochemical and functional characteristics of seed flour (Kisambira et al., 2014; Kisambira et al., 2015) and agronomic performance showing wide adaptation across diverse agro-ecological environments in Uganda (Andiku, 2013).

Genetic diversity assessment in yam beans is vital for designing appropriate selection and effective breeding strategies for improvement of morphological and-agronomic traits (Silva & Ticona-Benavente, 2016). A few studies have attempted to characterize genetic variation in the yam bean gene pool using morphological (Tapia & Sørensen, 2003) and molecular markers (Delêtre et al., 2013; Santayana et al., 2014). However, there is still lack of comprehensive characterization of the yam bean species for agronomic traits especially yield, dry matter and nutritional quality. Recently Silva and Ticona-Benavente (2016) assessed the diversity of 64 yam bean genotypes in the Brazilian Amazon using 10 morphoagronomic traits; plant height, number of secondary branches, shoot biomass, stem diameter, root biomass, number, length, diameter, length/diameter ratio (L/D), and shape. Significant diversity was recorded for all characters except for stem diameter and root shape suggesting wide diversity and high potential for yield and yam bean breeding program in the Amazonian region (Silva & Ticona-Benavente, 2016).

Nonetheless, there is lack of information on genotypic variability, genotype by environment interactions and heritability estimates for yield components, dry matter content and nutritional quality for the yam bean germplasm in Uganda. Such information is vital to guide selection of suitable parents for breeding varieties that are high yielding, high dry mater, adapted and with high quality in terms of protein, iron and zinc contents for integration into farming systems in Uganda. Therefore, this study was conducted to estimate genetic variance components, broad sense heritability (h^2_b), genotypic coefficients of variation (GCV) and phenotypic coefficients of variation (PCV) and correlations for yield components [storage root fresh yield (RFY), root dry matter yield (RDY), vine yield (VNY), fresh biomass yield (FBY), harvest index (HI)] and nutritional quality traits such as storage root dry matter (RDM), starch (STA), protein (PRO), iron (Fe), zinc (Zn), potassium (K), and phosphorus (P) among 26 yam bean accessions in Uganda.

3.2. Materials and Methods

3.2.1. Experimental sites and germplasm

Field experiments were carried out in two agro-ecological locations in Uganda; National Crops Resources Research Institute (NaCRRI) at Namulonge (32°36'E and 0°31'N) and the National Semi Arid Resources Research Institute (NaSARRI) at Serere (1°29'39"N and 33°27'19"E). These sites represent the major evaluation areas for root crops in Uganda and possess diverse agro ecological conditions suitable for wide evaluation of root crop agronomic and morphological performance (Tumwegamire et al., 2011). Namulonge is located in the central region and is characterized by a bimodal rainfall, red ferralitic soils and low soil pH. Serere is located in the Eastern agro-ecological zone and is characterized by longer periods of drought, erratic rainfall patterns, and sandy loam soils with moderate soil pH (Table 3.1).

Table 3.1. Environmental characteristics of experimental sites used for field evaluations of yam bean accessions during 2012 and 2013 growing seasons

Location	Vegetation	Soil type	Altitude (m.a.s.l)	Rain fall (mm)	Temperature (^{0}C)	
					Mean	Range
Namulonge	Tropical rain Forest	Sandy clay (pH 4.9 to 5.0)	1150	1095-1320	22.2	15.5-28
Serere	Tall savanna grass	Sandy roam (pH 5.2-6.0)	1140	900 -1300	26	23.9–30

M.a.s.l = Meters above sea level

A total of 26 yam bean accessions representing the three cultivated *Pachyrhizus* species (10 of *P. ahipa*, 11 of *P. erosus* and 5 of *P. tuberosus*) from the gene bank of International Potato Center (CIP) in Lima, Peru, were used in this study (Table 3.2). These accessions were introduced in 2010 in four East and Central African countries of Uganda, Rwanda, Burundi, and D.R. Congo under the framework of the AHIPA project (Grüneberg, 2016; Heider et al., 2011).

Table 3. 2. Characteristics of yam bean accessions used in the yield components and nutritional quality study

Accession No.	[z]CIP Code	Species	Plant type	Origin
1	209004	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
2	209006	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
3	209007	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
4	209016	*Pachyrhizus erosus*	Climbing	Guatemala
5	209017	*Pachyrhizus erosus*	Climbing	Brazil
6	209018	*Pachyrhizus erosus*	Climbing	China
7	209019	*Pachyrhizus erosus*	Climbing	Mexico
8	209023	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
9	209025	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
10	209027	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
11	209028	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
12	209031	*Pachyrhizus ahipa*	Bushy-erect	Bolivia
13	209033	Pachyrhizus ahipa	Bushy-erect	Bolivia
14	209034	*Pachyrhizus ahipa*	Bushy-erect	Argentina
15	209046	*Pachyrhizus erosus*	Climbing	Costa Rica
16	209047	*Pachyrhizus erosus*	Climbing	Mexico
17	209048	*Pachyrhizus erosus*	Climbing	Costa Rica
18	209049	*Pachyrhizus erosus*	Climbing	Mexico
19	209050	*Pachyrhizus erosus*	Climbing	Mexico
20	209051	*Pachyrhizus erosus*	Climbing	Mexico
21	209052	*Pachyrhizus erosus*	Climbing	Tonga
22	209055	*Pachyrhizus tuberosus*	Climbing	Brazil
23	209057	*Pachyrhizus tuberosus*	Climbing	Brazil
24	209058	*Pachyrhizus tuberosus*	Climbing	Brazil
25	209060	*Pachyrhizus tuberosus*	Climbing	Tonga
26	209061	*Pachyrhizus tuberosus*	Climbing	Tonga

[z] International potato center, Source: CIP gene bank, Lima, Peru.

3.2.2. Experimental design and agronomic practices

The experiments started with the screening and seed multiplication of the introduced yam bean germplasm in the screen house followed by field trials (Fig. 2). The objective of the screening experiment was to select genotypes for characterisastion and seed multiplication for field trials. Field trials were established in a randomized complete block design (RCBD) with two plot replications during two growing seasons in April 2012 and 2013 at each location. Each plot comprised two 3 m long ridges, 1 m a part. On each ridge, 10 seeds of each yam bean accession were planted at a spacing of 30 cm apart to achieve a target population of 33,333 plants ha^{-1}.

The major agronomic practice was reproductive pruning in which all flower buds were continuously removed beginning at the first flower bud formation to reduce flower-root sink competition for nutrients and photosynthates (Rizky et al., 2013). The practice of reproductive pruning was adopted because it encourages storage root formation (Forsyth & Shewry, 2002), and enhances storage root yields by 70% to 100% (Leidi et al., 2004; Matos et al., 1998; Rizky et al., 2013; Zanklan et al., 2007). The complete removal of the flowers was practiced compared to the traditional practice in the Americas and Asia where one pod on each plant or selected few plants are left for seed production (Delêtre et al., 2013; Zanklan et al., 2007). The experiments were kept weed-free through regular hand and hoe weeding, and neither fertilizers nor pesticides were applied during the growing period.



Figure 1. Yam bean trials from seed multiplication to harvesting.

Legend: A and B = yam bean seed multiplication at Namulonge before field trials; C = one month old yam bean trial at Namulonge; D = four months old yam bean trial at Namulonge; E = two months old yam bean trial at Serere; F = *P. erosus* storage root depicting good yield at Serere 6 months after planting.

3.2.3. Data collection

Yam bean plants were harvested individually at maturity, 6 months after planting. Data recorded on the numbers of plants harvested (NPH) per plot, weight of fresh storage roots (WFR) and above ground foliage (Vine weight, WVN). This data were used to estimate storage root fresh yield (RFY = WFR/NPH), vine yield (VNY = WVN/NPH), fresh biomass yield (FBY = RFY + VNY) in t ha^{-1}, and harvest index (HI = RFY/FBY) as percentage. Storage roots were detached using a field knife, collected into a pile per plot and from each pile, 3-5 fresh storage roots were randomly collected and processed in the quality laboratory at NaCRRI. The samples were washed with flowing tap water and rinsed with deionized water, peeled, and cut longitudinally into four sections using a stainless steel knife. Two opposite sections of each storage root slices were used to prepare a compound sample of 100 g fresh weight. Each sample was packaged in transparent polythene bags and vacuum-freeze dried at -31^{0}C for 72 hours using a vacuum-freeze drier (YK-I 18-50, True Ten Industries –Korea) to obtain dry weight and freeze dried samples for further quality determination.

Storage root dry matter content (RDM) was calculated as the average difference between fresh and dry weight estimates of root samples following the formula; RDM = (Dry weight/Fresh weight) *100 (Wilken et al., 2008).The RDM was used to estimate storage root dry yield (RDY = RDM * RFY / 100) in t ha^{-1}. Each freeze dry sample was milled into flour using a stainless steel mill (Dayton split phase motor-3383-L70, Thomas Scientific-USA) fitted with a 0.425 mm sieve (Fig. 3). The flour samples were stored in Kraft paper bags in deep freezers at -20^{0}C until analysis. Freeze dried samples were analyzed by near infrared reflectance spectroscopy (NIRS system 5000-M, FOSS scientific 2000) at the Nutritional Quality Laboratory at NaCRRI, Naulonge Central Uganda to determine root protein (PRO), starch (STA), iron (Fe), zinc (Zn), potassium (K) and phosphorus (P) as described by Velasco and Grüneberg (1999) who used fresh yam bean tuber slices to determine dry matter and protein contents. In this study, flour samples milled from freeze dried yam bean storage roots were used as described by Tumwegamire et al. (2011) for sweet potato. PRO and STA were recorded as percentage, Fe and Zn as $mgkg^{-1}$, and K and P as mg $100g^{-1}$ on a dry weight basis.

The NIRS calibrations for yam bean freeze dried storage root samples were available at the quality laboratory at NaCRRI in Uganda and each flour sample was scanned three times by NIRS to obtain replicates of near-infrared spectra output within the range of 400 to 2500 nm (Ozaki et al., 2006) (Fig. 2)



Figure 2. Sample processing in the NIRS laboratory at Namulonge.

A = Dayton split phase motor-3383-L70 used to grind samples; B = Grinding of dry yam bean samples; C = Packaged flour of yam bean samples before NIRS analysis; D = Measuring weight of samples; E = NIRS cubes with sample flour; F = NIRS analysis showing spectra readings of yam bean sample

3.2.4. Data analysis

Statistical data analysis was carried out in four steps: (1) Descriptive statistics to determine environmental performance and least significance differences between means, (2) analysis of variance (ANOVA) estimating variance components and therefore considering all factors as random, (3) estimating phenotypic coefficients of variation (PCV%) and genotypic coefficients of variation (GCV%) and broad sense heritabilities (h^2_b), and (4) determination of correlation coefficients among traits. Data analysis was carried out by PLABSTAT (Utz, 1997) and GenStat 14th edition (VSN International Ltd, Hemel Hempstead, UK) (Payne et al., 2011) .

In the first analysis step, performance of locations and seasons for each trait x_i (i.e. RFY, RDY, VNY, FBY, HI, RDM, PRO, STA, Fe, Zn, K, and P) were analyzed and descriptive LSD values for means determined. This analysis was conducted in PLABSTAT following the model statement x_i = S + L + SL + G + GS + GL + GSL + R: SL + RGSL, which corresponds to the following statistical model,

$$Y_{ijkln} = \mu_i + s_{ij} + l_{ik} + sl_{ijk} + g_{il} + gs_{ilj} + gl_{ilk} + gsl_{iljk} + bl(sl)_{in(jk)} + \varepsilon_{iljkn}$$

where Y_{ijkln} is the plot value of the ith trait of the j th season, for the k location, for the lth genotype and nth block; μ_i is the trial mean of the ith trait while factors s_{ij}, l_{ik}, g_{il}, sl_{ijk}, gs_{ilj} , gl_{ilk}, and gsl_{iljk} represent the effects of seasons, locations, genotypes, season-location interactions, genotype-season interactions, genotype-location interactions, and genotype-season-location interactions respectively; $bl(sl)_{in(jk)}$ is the effect of blocks and ε_{iljkn} is the plot error.

In the second analysis step, significance tests and variance component were estimated. Each trait x_i was analysed with the above given statistical model, considering two forms of treating the effects as fixed or random. At first the effects l_{ik}, g_{il}, *and* gl_{ilk} were treated as fixed, and all remaining effects as random to determine mean square values and F-test for each effect. This was associated with the calculation of means of genotypes across seasons and locations, and LSD values for the main effects (g_{il}).

In the second run, all effects were considered to be random, and variance components due to genotypes (σ_G^2), genotype by season (σ_{GxS}^2), genotype by location (σ_{GxL}^2), genotype by season by location (σ_{GxSxL}^2), and the error term (σ_ε^2) were calculated.

In a third analysis step, GCV%, PCV%, were calculated as suggested by Burton and Devane (1953) and Singh and Chaudhary (1985), while h_b^2 was according to Falconer and Mackay (1996);

$$GCV(\%) = \frac{\sqrt{\sigma_G^2}}{\bar{x}_{i...}} * 100,$$

$$PCV(\%) = \frac{\sqrt{\sigma_P^2}}{\bar{x}_{i...}} * 100,$$

$$h_b^2 = \frac{\sigma_G^2}{\sigma_P^2} * 100 = \frac{\sigma_G^2}{\left(\sigma_G^2 + \frac{\sigma_{GxS}^2}{s} + \frac{\sigma_{GxL}^2}{l} + \frac{\sigma_{GxSxL}^2}{s*l} + \frac{\sigma_\varepsilon^2}{s*l*r}\right)} * 100$$

Where $\bar{x}_i$ ... is the overall trait mean; s, l and r are the number of seasons, locations, and replications respectively; GCV and PCV are coefficients of variation.

In the final analysis, Pearson's phenotypic correlation coefficients among traits were calculated. The correlations were calculated for each season, location and replication separately, followed by calculating the average correlation between each trait pair across seasons, locations and replications). These phenotypic correlations can be considered as a good approximation of genotypic correlation estimates (Hill et al., 1998).

3.3. Results

The analysis of variance revealed significant ($p<0.05$) genotypic differences for all yield traits and two quality traits, STA and Fe (Table 3.3). The differences in morpho-agronomic characteristics were observed among accessions evaluated under field conditions at Namulonge and Serere in 2012 and 2013 (Fig. 3). Similarly, seasons were significantly different for all yield and quality traits except HI, RDM, STA and Potassium.

Table 3. 3 Mean squares from the analysis of variance for yield components and quality traits of 26 yam bean accessions evaluated at Namulonge and Serere, 2012 and 2013 first cropping seasons

		Mean squares for yield components					
[z]Source of Variation	Df[y]	Storage root fresh yield	Storage root dry yield	Vine yield	Fresh biomass yield	Harvest index	Storage root dry matter
Season	1	3979.5*	67.8*	210.3*	6209.8**	1769.9	2.0
Location	1	2737.7	18.1	44.7	2222.3	2145.8	850.0
L x S	1	390.6	2.5	5.3	555.8	375.8	0.2
R (L x S)	4	219.5*	3.4*	16.3*	282.1*	778.6**	10.4
Genotype	25	571.2**	6.6*	29.9*	720.5**	812.4**	95.0**
G x S	25	130.2**	2.6*	11.7**	151.3*	600.9**	7.4*
G x L	25	139.4	2.0	13.7	136.3	1200.1*	17.9**
G x L x S	25	120.1*	1.8	20.1**	169.3**	545.2**	4.7
Error		64.8	1.3	5.0	81.3	219.3	4.4
		Mean squares for root quality traits [x]					
		Protein	Starch	Iron	Zinc	Potassium	Phosphorous
Season	1	94.0**	0.13	2518.8**	150.4*	402578	79740**
Location	1	211.6	46.4	2076.7	583.1	284448	201122
S x L	1	0.8	44.7	131.2*	0.2	60270	1898
R(LxS)	4	3.0	281.1*	14.8	12.2	68930	3553
Genotype	25	3.9	480.1*	190.9*	15.5	491369	4597
G x S	25	4.0*	195.4*	73.7	11.0**	291803**	5220*
G x L	25	2.7	127.5	73.6	8.2	216025	5871
G x S x L	25	2.3	164.4	90.0	6.1	252090**	3231
Error		2.4	111.4	126.2	5.2	122158	2828

* Significance at the 0.05 level, ** Significance at the 0.01 level.

[z]G x L= genotype by location interaction; G x S = genotype by season interaction; L x S = location by season interaction; G x L x S= genotype by location by season interaction.

[y] df, degrees of freedom, [x] dry weight basis.



Figure 3. Morpho-agronomic characteristics of three cultivated yam bean species under field trials at Namulonge and Serere in Uganda.

A = *P. ahipa*, B = *P. erosus*, C = *P. tuberosus*

Genotype by season (G x S) interaction effects were significant for all yield and quality traits except for root iron while genotype by location interaction effects (G x L) were only significant for HI and RDM. The three way genotype by season by location (G x S x L) interaction were significant ($p< 0.05$) for all yield traits except RDM and RDY while the three way interaction was only significant ($P<0.01$) for K. Environmental means were clearly higher at Namulonge compared to Serere in all traits except RDM and VNY that recorded better performance at the later research site. Significant differences ($LSD_{0.05}$) were observed between seasons 2012 and 2013 for RFY, FBY, RDY, VNY, PRO, Fe, P and Zn at Namulonge and for all yield and quality traits at Serere except HI, RDM and STA content (Table 3.4). Namulonge season 2012 was the best performing environment for yield traits recording highest values for RFY (22.1 t ha^{-1}), RDY (2.7 t ha^{-1}), FBY (26.4 t ha^{-1}) and HI (84.6%), while Namulonge season 2013 gave the highest estimates for quality traits; protein (11.2%), starch (52.3%), iron (28.7 mg kg^{-1}), zinc (15 mg kg^{-1}), and phosphorus (268 mg $100g^{-1}$) content. The poorest performing environment was Serere 2013 with the lowest values for RFY (6.2 t ha^{-1}), RDY (0.9 t ha^{-1}), FBY (9 t ha^{-1}), HI (72.4 %), starch (50.4 %), and potassium (815 mg 100g-1) (Table 3.4).

Table 3. 4 Environmental means for yield and quality traits of yam beans accessions across four environments (2 locations x 2 seasons).

	Yield traits					Root quality traits						
Environment /Season	RFY (t ha^{-1})	RDY (t ha^{-1})	VNY (t ha^{-1})	FBY (t ha^{-1})	HI (%)	RDM (%)	PRO (%)	STA (%)	Fe (mg kg^{-1})	Zn (mg kg^{-1})	K (mg $100g^{-1}$)	P (mg $100g^{-1}$)
Namulonge 2012	22.1	2.7	3.9	26.4	84.6	13.4	10.0	51.3	23.3	13.2	1138	235
Namulonge 2013	10.7	1.3	1.5	12.2	76.1	13.1	11.2	52.3	28.7	15.0	1084	268
Mean ($\bar{x}$)	16.4	2.0	2.7	19.3	80.4	13.2	10.6	51.8	26.0	14.1	1111	251
Serere 2012	12.2	1.8	4.5	16.6	75.5	17.3	7.9	51.3	15.4	9.9	937	167
Serere 2013	6.2	0.9	2.8	9.0	72.4	17.2	9.4	50.4	24.0	11.6	815	212
Mean ($\bar{x}$)	9.2	1.4	3.6	12.8	74.0	17.3	8.6	50.8	19.7	10.7	878	191
Grand mean	12.8	1.7	3.2	16.1	77.2	15.3	9.6	51.3	22.9	12.4	993	221
LSD[x](0.05)	5.7	0.7	1.6	6.5	10.7	1.2	0.7	6.5	1.5	1.3	101	23

RFY = storage root fresh yield; RDY = storage root dry yield; VNY = vine yields; FBY = fresh biomass yield; HI = harvest index; [y] Fresh weight basis; [x] RDM = storage root dry matter content; PRO = protein content of storage roots; STA = starch content; Fe = iron content (mg kg^{-1}); Zn = zinc content (mg kg^{-1}); K = potassium content; P = phosphorus content;

[x]LSD, least significant difference at 0.05 alpha level with all factors considered as fixed except replication.

The mean performance of the 26 yam bean accessions across environments (Table 3.5) revealed large and significant variations for all traits among accessions. For several accessions, high RFYs were observed such as 209017 with 31.8 t ha^{-1}. Accessions 209055 and 209060 combined high values for RFY, PRO, Fe, and Zn while accession 209006 had the lowest combinations of RFY (2.2 t ha^{-1}), RDY (0.4 t ha^{-1}) and FBY (2.5 t ha^{-1}) making it the worst performing genotype. The mean RDM content was 15.3 % ranging from 9.9 % in 209050 to of 20.5 % in 209061, which is low compared to other root crops in Africa such as cassava (*Manihot esculenta Crantz*) (Akinwale et al., 2010; Tumuhimbise et al., 2014).

In contrast, other root quality values were high in most accessions and varied widely ranging from 8.1 % to 10.8 % PRO, 36.5 % to 63.1 % STA, 13.6 to 31.8 mg kg^{-1} Fe, 10.3 to 16.7 mg kg^{-1} Zn, 558 to 1430 mg $100g^{-1}$ K, and 160 to 260 mg $100g^{-1}$ P. The highest PRO, STA, Fe, Zn, K and P content were observed in accessions, 209051, 209061, 209049, 209047 and 209049 respectively (Table 3.5). The least performing accession with respect to several root quality traits was 209031 [i.e PRO (8.1 %), Fe (13.6 mg kg^{-1}), Zn (10.3 mg kg^{-1}) and P (160 mg $100g^{-1}$)]. In general, the mean values for root quality traits such as PRO, Fe and Zn at 9.6 %, 22.8 mg $kg^{-1}$and 12.4 mg kg^{-1}respectively are remarkable for a root crop (Table 3.5).

Table 3. 5 Mean performance of yam bean genotypes for observed traits across seasons and locations

	Yield components [z, y]					Root quality traits [x, w]						
Genotype	RFY (t ha^{-1})	RDY (t ha^{-1})	VNY (t ha^{-1})	FBY (t ha^{-1})	HI (%)	RDM (%)	Pro (%)	Sta (%)	Fe (mgkg^{-1})	Zn (mgkg^{-1})	K (mg100g^{-1})	P (mg100g^{-1})
209004	3.2	0.6	2.6	5.8	73.7	18.4	10.0	60.3	23.2	13.5	987	235
209006	2.2	0.4	0.3	2.5	82.8	16.1	9.5	55.8	23.3	11.6	828	205
209007	6.3	1.1	1.1	7.4	67.1	20.0	10.4	51.0	25.5	13.1	1024	234
209016	25.6	2.9	3.8	29.4	79.5	11.4	9.8	43.2	31.1	11.0	1176	230
209017	31.8	3.4	3.9	35.7	87.2	11.5	9.4	40.5	22.0	11.2	1339	225
209018	18.7	1.9	4.7	23.4	71.4	14.7	9.5	43.5	16.5	11.4	1263	217
209019	17.5	2.0	1.8	19.3	91.2	11.4	8.8	47.1	20.9	10.9	1114	196
209023	6.4	1.1	1.8	8.2	83.1	16.9	9.9	57.7	17.8	12.4	652	224
209025	3.8	0.7	0.4	4.2	84.2	18.3	8.2	55.1	15.9	10.9	617	170
209027	2.9	0.5	0.2	3.1	86.0	17.2	8.9	58.3	21.5	12.6	715	201
209028	3.9	0.6	2.0	5.9	75.4	15.5	9.7	52.3	19.5	11.4	790	219
209031	5.4	1.1	2.0	7.4	71.5	19.2	8.1	59.3	13.6	10.3	763	160
209033	3.7	0.8	0.9	4.6	74.0	19.7	10.5	57.6	23.4	13.6	880	217
209034	8.3	1.5	5.8	13.9	70.8	19.7	9.3	61.4	13.9	13.1	558	179
209046	15.0	1.6	4.2	19.3	77.1	12.5	10.0	47.3	29.7	12.9	1467	253
209047	27.1	3.3	3.3	31.1	82.6	12.0	9.6	47.4	26.6	12.0	1124	223
209048	18.3	2.4	3.1	21.4	86.2	12.8	9.4	52.0	25.0	12.4	837	236
209049	15.0	1.6	1.7	16.7	89.3	11.5	10.2	41.0	31.8	12.6	1269	260
209050	17.9	1.8	5.0	22.9	75.7	10.7	9.9	36.5	23.2	11.3	1163	229
209051	22.4	2.4	4.8	27.2	80.2	11.0	10.8	39.2	26.0	13.2	1430	254
209052	14.7	1.5	2.6	17.3	83.0	9.9	9.7	43.1	27.5	11.2	1081	242
209055	20.9	3.5	4.6	25.5	82.8	16.8	10.3	59.3	24.3	14.4	989	236
209057	9.0	1.4	6.6	18.0	54.3	15.1	8.7	49.6	20.2	12.1	755	231
209058	10.1	2.0	2.7	12.8	76.5	18.8	9.9	54.1	21.9	14.1	971	213
209060	16.1	2.5	5.2	21.4	74.4	15.1	9.2	57.7	21.3	13.3	1076	212
209061	6.8	1.3	6.9	13.7	46.5	20.5	10.8	63.1	28.7	16.7	952	234
Mean	12.8	1.7	3.2	16.1	77.2	15.3	9.6	51.3	22.9	12.4	993	220
LSD[v]	11.8	1.7	3.5	12.7	25.2	2.8	2.1	14.4	8.8	3.4	556	74

[z] RFY = storage root fresh yield; RDY = storage root dry yield; VNY = vine yields; FBY = fresh biomass yield; HI = harvest index; [y] Fresh weight basis; [x] RDM = storage root dry matter content; PRO = protein content of storage roots; STA = starch content; Fe = iron content (mg kg^{-1}); Zn = zinc content (mg kg^{-1}); K = potassium content; P = phosphorus content; [w] dry weight basis; [v] LSD, least significant difference at the 0.05 alpha level with all factors considered as fixed except replication

The variance ratios, σ^2_G / σ^2_{GxS} / σ^2_{GxL} / σ^2_{GxSxL} / σ^2_ε were 1/0.05/0.09/0.53/1.23, 1/-0.06/-0.11/0.58/1.08, 1/0.38/0.10/0.52/2.73, and 1/-0.71/-0.52/2.42/1.61 for RFY, FBY, RDY, and VNY respectively (Table 3.6). Similarly, the ratios of variance components for STA, RDM, and iron were 1:0.19:-0.23:0.66:0.28, 1:0.06:0.36:0.02:0.47, and 1:-0.25:-0.25:-1.08:0:7.55 respectively. The ratios of variance components are only given for traits with significant σ^2_G. For RFY and FBY a combination of large σ^2_G and relatively low σ^2_{GxS}, σ^2_{GxL}, and σ^2_{GxSxL} were observed (σ^2_{GxS}, σ^2_{GxL}, and σ^2_{GxSxL} smaller than σ^2_G). For the quality traits; STA, RDM and iron had medium to large σ^2_G combined with relatively low σ^2_{GxS}, σ^2_{GxL}, and σ^2_{GxSxL}. A high error (σ^2_ε / σ^2_G = 7.56) was observed in the estimation of variance components for iron content while all other traits with significant σ^2_G, the σ^2_ε were low (σ^2_ε / σ^2_G < 3).

Table 3. 6. Variance components, genotypic coefficient of variation (GCV %), phenotypic coefficient of variation (PCV %) and broad sense heritability (h^2_b) for 12 traits in yam beans.

Traits	Variance components [x]					[y] GCV (%)	[z] PCV (%)	[v] h^2_b
	σ^2_G	σ^2_{GxS}	σ^2_{GxL}	σ^2_{GxSxL}	σ^2_ε			
RFY, t^2 ha^{-2}	52.7**	2.5	4.8	27.7*	64.8	56.7	66.0	73.8
RDM, $\%^2$	9.3**	0.7	3.3**	0.2	4.4	20.0	22.6	78.4
RDY, t^2 ha^{-2}	0.48*	0.18	0.05	0.25	1.31	40.8	53.3	58.4
HI, $\%^2$	55.4	13.9	163.7*	163.0**	219.3	9.64	17.9	28.9
VNY, t^2 ha^{-2}	3.1**	-2.1	-1.6	7.5**	5.0	55.0	60.5	82.7
FBY, t^2 ha^{-2}	75.3**	-4.5	-8.2	44.0**	81.3	53.9	59.0	83.6
PRO, $\%^2$ [w]	0.06	0.42	0.08	0	2.4	2.6	8.1	9.8
STA, $\%^2$	40.2*	7.7	-9.2	26.5	111.4	12.4	15.1	67.0
Fe, mg^2 kg^{-2}	16.7*	-4.1	-4.1	-18.1	126.2	17.8	21.3	70.0
Zn, mg^2kg^{-2}	0.29	1.24	0.52	0.44	5.19	4.3	11.2	15.0
K, mg^2kg^{-2}	29453	9928	-9016	64966**	122158	17.3	25.0	48.0
P, mg^2kg^{-2}	403	886*	459	-50	3052	9.1	17.2	27.9

* Significance at the 0.05 level, ** Significance at the 0.01 level; [x] σ^2_G= Genotypic component of variance; σ^2_{GxS} = genotype by season variance; σ^2_{GxL} - genotype by location variance; σ^2_{GxSxL} - genotype by season by location variance; [y] Genotypic coefficient of variation (%); [z] Phenotypic coefficient of variation (%); [v] Broad sense heritability (%); [z] RFY = storage root fresh yield; RDY = storage root dry yield; VNY = vine yields; FBY = fresh biomass yield; HI = harvest index; [y] Fresh weight basis; [x] RDM = storage root dry matter content; PRO = protein content of storage roots; STA = starch content; Fe = iron content (mg kg^{-1}); Zn = zinc content (mg kg^{-1}); K = potassium content; P = phosphorus content; [w] dry weight basis;

The results of coefficients of variation are presented in Table 3.6. High estimates of genotypic coefficient of variation (GCV) were observed for SFRY (56.7%), VNY (55%), FBY (53.9%), and RDY (40.8%), while medium GCV values were recorded for STA (12.4%), RDM (20%) and Fe (17.8%). Similarly, the phenotypic coefficients of variation (PCV) were high for RFY (66%), VNY (60%), FBY (59%), RDY (53.3%) and low for STA (15.1%), RDM (22.6%), and Fe (21.3%). In addition, broad sense heritability (h^2_b) estimates for yield traits were high (larger than 50%) for RFY, RDY, VNY, FBY, and only low (smaller than 30%) for HI. But for quality traits, high h^2_b were observed for RDM (78.4%) Fe (70%) and STA (67%), medium for P content (48%) and low for the remaining quality traits (smaller than 30%) (Table 3.6).

Phenotypic correlation coefficients for yield components and nutritional quality traits are presented in Table 3.7. The coefficients show strong and significant ($p<0.001$) positive correlations between RFY and both RDY ($r = 0.926$) and FBY ($r = 0.962$), as well between RDY and FBY($r = 0.899$). Correlations between FBY and VNY were moderate ($r = 0.552$). RFY showed weak but significant negative correlations with RDM ($r = - 0.423$) and STA ($r = -0.314$). For PRO, significant moderate to strong correlations with iron ($r = 0.499$), phosphorus ($r = 0.700$) and zinc ($r = 0.756$) content of storage roots were observed. Moreover, root iron content was observed to be strongly associated with root zinc ($r = 0.754$) and root phosphorus content ($r = 0.648$).

potentials across various agro ecologies in Uganda. Nonetheless, the three species *viz.*, the Mexcian yam bean (*P. erosus*), the Andean yam bean (*P. ahipa*), and the Amazonian yam bean (*P. tuberosus*) have been reported as closely related (Santayana et al., 2014; Sørensen, 1996; Zanklan et al., 2007). Infact, Grüneberg et al. (2003), argued that the three cultivated yam beans might belong to one primary genepool since fertile and vigorous interspecifc and intraspecific hybirds could be developed amongst them. Its was therefore prudent to conduct multi-locational trials of yam bean accessions to evaluate the genetic disimilarity of the current germplasm in Ugabda.

The high genetic variation for storage root yield observed in this study was consistent with the findings from contrasting locations in Benin, West Africa (Zanklan et al., 2007) while the mean values were similar or slightly lower than values reported in Sierra Leone by Belford et al. (2001). The RDM values observed in this study for Serere (17.1% and 17.3% in season 1 and 2, respectively) (Table 3. 4) corresponds to observations by Zanklan et al. (2007) in *P. erosus* grown under water stressed conditions at Niaouli in Benin.

The yield recorded in yam beans was close to values reported for traditional root crops such as cassava whose average yield in Uganda is 16.8 t ha^{-1}(Tumuhimbise et al., 2014). Yet growing yam bean is advantageous because it has potential to be grown twice a year at many locations in Uganda, given the five month gestation period compared to cassava for instance which is planted once a year. The findings confirmed yam bean as a starchy root crop with a germplasm mean of 51.3% STA on dry weight basis and up 63% in *P. tuberosus* accession 209061 (Table 3.5). This corresponds to starch content in other root crops such as sweetpotato (Tumwegamire et al., 2011) and cassava (Tumuhimbise et al., 2014). However, as a legume the yam bean contains high protein content and remarkable iron content in the storage roots (Table 3.4). The mean iron content of 22.9 mg kg^{-1} in yam bean accessions are similar to the findings reported by several authors (Dini et al., 2013; Doporto et al., 2011; Grüneberg et al., 2003; Heider et al., 2011; Santayana et al., 2014). However, the iron content found in this study was low compared to values of up to 130 mg. kg^{-1} reported by Kale (2006).

selection for high PRO content would be effective in improving Fe, Zn, K and P content of yam bean storage roots. The moderately strong positive correlation (r = 0.563) between RDM and STA suggested that STA constituted a large proportion of dry weight in the evaluated yam beans. However, selection for high RFY was associated with reduction in RDM (r = -0.423) and STA (r = -0.314), suggesting that yam bean accessions with higher yields tended to have lower RDM and STA content. This revealed that Dry matter and starch content would be compromised as RFY increases, a characteristic that can be explained by the high moisture content of yam bean storage roots as observed by Rizky et al. (2013).

3.5.Conclusion

The yam bean germplasm evaluated in this study possesses considerable genetic variation that offers opportunities for trait improvement of RFY, RDY, RDM, and VNY, FBY, HI, starch, iron and potassium through selection and may permit a worthwhile yam bean breeding program in Uganda. Also, high dry matter yam beans that are high yielding can be developed from low dry matter yam beans given the high genotypic variances (σ_G^2) for these important traits. The results further revealed that the yam bean is well adapted to the growing conditions of Uganda with potential for high storage root yields.

CHAPTER FOUR

COMBINING ABILITY AND INHERITANCE OF STORAGE ROOT DRY MATTER AND ASSOCIATED TRAITS IN F_1 AND F_2 YAM BEAN POPULATIONS

4.1. Introduction

The yam bean (*Pachyrhizus species*) is widely grown for its nutritious storage roots in many countries of tropical America and Asia (Sørensen, 1996). Yam bean is traditionally a minor and underutilized crop (Jacobsen et al., 2015; Sørensen, 1996) mainly because of low storage root dry matter content (RDM) that limits its food and industrial applications. Nonetheless, the crop has attracted scientific and nutritional interest because its storage roots are rich in vitamins (A, C, E, K Niacin, Riboflavin and Thiamine) (Noman et al., 2007) and micronutrients such as iron up to 130 mg /kg (Kale 2006) and zinc (1.4 mg/100g) (Dini et al., 2013), 56 to 58% starch (Forsyth et al., 2002) and 8 to 18% proteins (Velasco and Grüneberg 1999, Zanklan et al., 2007) on dry weight basis. The improvement of RDM has been identified as a major breeding goal for yam beans to diversify utilization options (Grüneberg et al., 2003; Zanklan et al., 2007). Fortunately, improvement of RDM and associated traits in the yam bean gene pool is possible through hybridization among the low dry matter germplasm (Agaba et al., 2016) and much faster with the inclusion of high RDM (26 to 36%) cultivar of *Pachyrhizus tuberosus* known as chuin in the crosses (Grüneberg et al., 2003; Ørting et al., 1996; Zanklan et al., 2007). All *Pachyrhizus* species are propagated by true seed, self-compatible and permit successful interspecific hybridisation (Sorensen, 1990) producing fertile and vigorous hybrids (Grüneberg et al., 2003).

Most studies have only evaluated morphological and genetic variability in yam bean gene pool (Agaba et al., 2016; Ørting et al., 1996; Santayana et al., 2014; Silva & Ticona-Benavente, 2016; Zanklan et al., 2007). There is limited information on combining ability and gene action for yield traits and the crop is an orphan in breeding programs (Jha & Singh, 2014), and remain undeveloped and genetically under exploited. There is general lack of genetic studies that involve all the cultivated yam bean species resulting in scanty information on genetic parameters, combining abilities and mode of inheritance for dry matter and associated traits. The only

available estimates of combining abilities and gene action in yam beans were reported by Jha and Singh (2014) indicating positive and significant GCA and SCA effects for quantitative traits such as root yield, root length and root girth in *Pachyrzus* erosus. These results have not been corroborated across different yam bean species as a basis for selecting good parents and promising crosses for improvement of dry matter and associated traits.

Combining ability analysis provides tools for evaluation of additive and non-additive variances (Amongi et al., 2015), for identification of parents and crosses with good general combining ability (GCA) and specific combining ability (SCA) respectively based on performance of their progenies. Combining ability analysis in North Carolina II mating design provides tools to determine genetic architecture and inheritance of traits in a breeding population (Kearsey & Pooni, 1996; Nduwumuremyi et al., 2013). GCA and SCA effects are vital for crop improvement by aiding selection of crosses with superior genotypes and designing efficient breeding programs. The objective of this study was to determine variance components, combining abilities, heritability estimates and mode of inheritance of RDM and related traits; storage fresh root yield (RFY), storage root dry yield (RDY), harvest index (HI), Vine yields (VNY), fresh biomass yield (FBY), starch content (STA) and protein content (PRO) as a basis for breeding high dry matter yam beans. The knowledge of combining ability and inheritance of RDM and associated traits is essential to develop appropriate procedure for selecting suitable parents and designing efficient breeding strategy for improvement of the yam bean gene pool.

4.2. Materials and Methods

4.2.1. Study Area and Experimental Sites

Field experiments were carried out at the National Crops Resources Research Institute (NaCRRI) located at Namulonge (0°32'N, 32° 36'E), Wakiso District, 28 km North of Kampala in Central Uganda. The site has an elevation of 1,150 meters above sea level and a mean annual temperature of 22.2°C with annual minimum and maximum temperatures of 16 and 28°C respectively. Namulonge is characterized by red ferralitic soils with low pH 4.9-5.0 and receives a bimodal rainfall with annual mean of 1,270 mm (Tumwegamire et al., 2011)

4.2.2. Generation of Breeding Population

Crosses were made between three high dry matter chuin cultivars (209013, 209014, 209015) belonging to *P. tuberosus* and six low dry matter female parents consisting of three *P. ahipa* (209004, 209022, 209031) and *P. erosus* (209016, 209018, 209019) using the North Carolina II (NC II) mating design Comstock and Robinson (1952) to develop 16 populations (Table 4.1). The low female parents were selected from study one on the basis of good yield, low dry matter content and high genetic variability while the male parents (chuin cultivars) were imported from the CIP gene bank in Peru for hybridisation as sources of high dry matter content. The NCII mating design was adopted because it has wide application in inheritance studies and is suitable for estimation of variance components, combining abilities and inference of additive and non-additive gene effects (Amongi et al., 2015; Kearsey & Pooni, 1996; Nduwumuremyi et al., 2013). All the male *P. tubersus*-chuin and the *P. erosus* female parents had spreading growth habit while the *P. ahipa* female parents had determinate / erect growth habit.

Table 4.1 Yam bean populations and their parents evaluated in F_1 and F_2 generations under field conditions at NaCRRI, Namulonge during the first cropping seasons, April of 2013 and 2014 respectively

No.	Population	Female (Low RDM)	Male (High RDM)
1	209076	209004	209013
2	209077	209004	209014
3	209078	209004	209015
4	209079	209022	209013
5	209080	209022	209014
6	209082	209031	209013
7	209083	209031	209014
8	209085	209016	209013
9	209086	209016	209014
10	209087	209016	209015
11	209088	209018	209013
12	209089	209018	209014
13	209090	209018	209015
14	209091	209019	209013
15	209092	209019	209014
16	209093	209019	209015

RDM = storage root dry matter content, Low RDM < 25% while High RDM > 25%

Crosses were obtained between three high dry matter chuin cultivars belonging to *P. tuberosus* and six low dry matter female parents consisting of three *P. ahipa* and *P. erosus* species. The hybridisation was done following North Carolina II (NC II) mating design with no reciprocals in accordance with Comstock and Robinson (1952). The NCII mating design has wide application in inheritance studies and is suitable for estimation of variance components, combining abilities and inference of additive and non-additive gene effects (Amongi et al., 2015; Kearsey & Pooni, 1996; Nduwumuremyi et al., 2013).

4.2.3. Field evaluations of F_1, F_2 and parents

The F_1 and F_2 progenies and their parents were evaluated under field conditions at the National Crops Resources Research Institute (NaCRRI), Namulonge during the first rains of April 2013 and 2014 respectively. The trails were planted in a randomized complete block design (RCBD) with two plots replications. The plots consisted of two ridges measuring three meters long, and spaced one meter apart Seeds were sown at a spacing of 0.3 meters on each ridge. The plots were kept weed free and no reproductive pruning of flowers was done nor were fertilizers or pesticides applied during the crop growth cycle. The F_2 seed harvested from F_1 plants were planted in April, 2014 following similar experimental and agronomic practices as in F_1.

4.2.4. Data collection

The trials were harvested six months after planting and data recorded for number and weight of roots, weight of above ground foliage for determination of storage root fresh yield (RFY), vine yields(VNY), fresh biomass yield (FBY= RFY+VNY) and harvest index (HI= 100x RFY/FBY). Storage roots from each plant were taken to the NaCRRI nutrition quality laboratory for determination of storage root dry matter content (RDM), starch (STA) and protein contents (PRO).

The sampled roots were washed thoroughly using flowing tap water to minimize soil contamination and then washed in deionized water to minimize non plant source iron, peeled and sectioned into longitudinal slices. A sample of 100g fresh weight was packed in polythene bags

and vacuum-freeze dried at -31^{0}C for 72 hours (using a vacuum freeze drier, YK-118-50, True-Ten Industries, Korea, 1995). The freeze dried samples were weighed immediately after leaving the freeze drier and dry weight recorded. RDM was calculated as the percentage of dry weight relative to fresh weigh Wilken et al. (2008). STA and PRO were obtained as estimates from the near-infrared reflectance spectroscopy (NIRS) following same procedures as described in section 3.2.3.

4.2.5. Statistical and Genetic Analyses

Mean performance of the crosses and parents were obtained for storage root dry matter and associated traits based on the general analysis of variance model in GenStat 14th edition (VSN International Ltd, Hemel Hempstead, UK) (Payne et al., 2011). The means of crosses were further processed using the general combining ability model in which male and female parents were fited as fixed factors and the residual taken as an estimate of SCA effects (female x male interaction). GCA effects were estimated from the parameter estimates for parents from the ANOVA of North Carolina II design (NCII) while the SCA effects were calculated as the difference between the observed and predicted means of RDM, RFY, RDY, VNY, FBY, STA and PRO among 16 crosses. The significance of GCA and SCA effects were tested using a standard two-tailed t-test.

The estimates of narrow sense heritability (h^2_n), broad sense heritability (h^2_b) and Baker's ratio were calculated from the GCA and SCA variance components following Falconer et al. (1996);

Narrow sense heritability (h^2_n),

$h^2_n = [\sigma^2_{GCA(Female)} + \sigma^2_{GCA(Male)}] / [\sigma^2_{GCA(Female)} + \sigma^2_{GCA(Male)} + \sigma^2_{SCA} + \sigma^2_e]$,

Where; σ^2 = Sample variance, $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)}]$ = Additive gene effect, $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA(Male)} + \sigma^2_{SCA} + \sigma^2_e]$ = Phenotypic effect and σ^2_e = Sample error variance

Broad sense heritability (h^2_b) which estimates the proportion of phenotypic variation due to total genetic effects:

$h^2_b = [\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA}] / [\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA} + \sigma^2_e]$,

Where; $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA}]$ = Total genetic effect, and $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA} + \sigma^2_e]$ = Phenotypic effect.

Then Baker's ratio (BR) was calculated as:

$BR = [\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)}] / [\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA}]$

Where; $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)}]$ = Additive gene effect and $[\sigma^2_{GCA\ (Female)} + \sigma^2_{GCA\ (Male)} + \sigma^2_{SCA}]$ = Total genetic effect

The gene action controlling inheritance of dry matter content in yam bean was then inferred from the relative magnitudes of GCA and SCA. Baker's ratio was used to estimate the relative significance of additive and non-additive gene effects (Baker 1978). In the estimation of genetic parameters using NCII ANOVA, absence of maternal effects and epistasis was assumed (Kearsey and Pooni, 1998) for the inheritance of RDM and associated triats.

4.3.Results

4.3.1. Analysis of variance for RDM and related traits in F_1 and F_2 generations

Mean squares for combining abilities for RDM and associated traits in F_1 and F_2 yam bean populations are presented in Table 4.2. Analysis of variance revealed significant differences between the mean squares of crosses ($P<0.01$) for RDM, STA RFY, RDY and FBY in F_1 generation and all the traits in F_2 except VNY. The mean squares for female general combining ability (GCA_f) were highly significant ($p<0.01$) for RDY, FBY, STA and RFY in F_1 while all the traits were highly significant in F_2 except RDM and VNY. The mean squares for male general combining ability (GCA_m) were significant for RFY and HI ($p<0.05$), and highly significant for RDY ($p<0.01$), RDM and STA ($p<0.001$) in F_1 as well as for RDM and RDY ($p<0.01$) and RFY and FBY ($p<0.001$) in the F_2 generation. However, the GCA_m mean squares were not significant for HI and STA content of the F_2 yam bean generation. The interaction mean squares between male and female parents (SCA effects) were significant (0.05) for RFY and highly significant

(P<0.001) for RDM and STA in F_1 but significant (0.05) for STA, highly significant (p<0.01) for HI, as well as for RDM, RFY and FBY (p<0.001) in the F_2 (Table 4.2).

Table 4. 2 Mean squares for combining abilities of storage root dry matter and associated traits in F_1 and F_2 yam bean populations

Source of Variation	df	Mean Squares							
		RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
F_1 Generation									
Crosses	15	22.23***	22.03**	1.21**	29.32	0.3239	32.54**	112.45***	0.7213
GCA-Female	5	0.91	36.75***	1.69**	54.31	0.2395	59.36**	75.26**	0.96*
GCA-Male	2	72.25***	22.07*	2.36**	0.88*	0.5156	19	338.74***	0.8606
SCA (Male x Female)	8	23.05***	12.82*	0.62	20.81	0.3287	19.17	79.12***	0.5382
Residual Error	23	1.745	0.245	0.043	1.394	0.046	0.420	0.645	0.370
CV%		29.497	14.031	13.825	13.071	14.362	16.842	10.191	18.737
F_2 Generation									
Crosses	15	22.79***	7.28***	0.56**	10.64***	0.2028	9.35***	194.13***	0.76**
GCA-Female	5	39.37	11.75***	5.06***	24.75***	0.3406	15.27***	414.99***	1.42***
GCA-Male	2	10.54**	5.87***	1.96**	0.447	0.0534	6.60***	8.65	0.163
SCA(Male x Female)	8	14.44***	4.49***	1.40	3.47**	0.1471	5.91***	89.37*	0.456
Residual Error	23	1.38	0.21	0.20	0.975	0.021	0.260	1.948	0.258
CV%		27.884	14.569	33.133	11.276	9.412	14.662	18.492	16.734

df = degrees of freedom, CV% = coefficient of variation; *, ** and *** represents significant at P<0.05, 0.01 and 0.001 respectively; ns = not significant; GCA = general combining ability; SCA = specific combining ability; RDM = root dry matter content; RFY = fresh root yield; RDY = root dry yield; HI = harvest index; VNY = Vine yields; FBY = fresh biomass yield; STA = root starch content; PRO = root protein content

4.3.2. Estimates of variance components, heritability, predictability and Bakars' ratio

The variance components for combining abilities, heritability estimates, predictability ratios ($\sigma^2GCA_f/\sigma^2SCA$) and Bakers' ratio for RDM and associated traits among F_1 and F_2 yam bean populations are presented in Table 4.3. The magnitude of GCA_f variance were higher than SCA variance for RFY, RDY HI, FBY and PRO in F_1 and all the traits in F_2 resulting in a predictability ratio of higher than unity in F_1 and F_2 respectively. The estimates for σ^2GCA_m were higher than the σ^2SCA for only RDM in F_1 suggesting that the current male parents (chuins) are good combiners for high dry matter content in yam beans.

Baker's ratio values were moderate to high with the minimum of 0.38 for VNY to maximum of 0.76 for RDM in F_1 and ranged from 0.52 to 0.82 in F_2 (Table 4.3). The narrow sense heritability estimates were moderate (> 0.3 <0.4) for VNY and PRO, high (h^2_n = 0.5) for STA, FBY, HI, RFY, RDY and RDM in F_1 and all traits in F_2 except for VNY (h^2_n = 0.48). Similarly, the broad

sense heritability estimates were high for all traits ranging from 0.51 to 0.99 across F_1 and F_2 generations.

Table 4. 3 Combining ability variances, heritability estimates, predictability and Bakers ratios for storage root dry matter and associated traits in F_1 and F_2 yam bean populations

Parameter (σ^2)	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
F_1 population								
σ^2GCA_f	0.52	14.60	0.66	21.17	0.08	23.58	29.85	0.24
σ^2GCA_m	41.40	4.36	0.46	10.58	0.09	3.72	67.62	0.10
σ^2SCA	13.21	12.57	0.57	19.42	0.28	18.75	78.48	0.17
$\sigma^2GCA_f/\sigma^2SCA$	0.04	1.16	1.15	1.09	0.27	1.26	0.38	1.40
$\sigma^2GCA_m/\sigma^2SCA$	3.13	0.35	0.81	0.55	0.33	0.20	0.86	0.58
Bakers' ratio	0.76	0.60	0.66	0.62	0.38	0.59	0.55	0.67
h^2_n	0.74	0.60	0.65	0.60	0.34	0.59	0.55	0.38
h^2_b	0.97	0.99	0.98	0.97	0.91	0.99	1.00	0.58
F_2 population								
σ^2GCA_f	28.53	4.62	0.33	9.51	0.13	6.00	165.22	0.47
σ^2GCA_m	7.64	1.13	0.04	-0.11	0.01	1.27	1.34	-0.02
σ^2SCA	10.46	4.28	0.08	2.50	0.13	5.65	87.42	0.20
$\sigma^2GCA_f/\sigma^2SCA$	2.73	1.08	4.03	3.81	1.02	1.06	1.89	2.36
$\sigma^2GCA_m/\sigma^2SCA$	0.73	0.26	0.47	-0.04	0.05	0.22	0.02	-0.10
Bakers' ratio	0.78	0.57	0.82	0.79	0.52	0.56	0.65	0.69
h^2_n	0.75	0.56	0.56	0.73	0.48	0.55	0.65	0.50
h^2_b	0.97	0.98	0.69	0.92	0.92	0.98	0.99	0.71

σ^2GCA_f = General combining ability variance for females; σ^2GCA_m = General combining ability variance for males; h^2_n = narrow sense heritability; h^2_b = broad sense heritability; RDM = root dry matter content; RFY = fresh root yield; RDY = root dry yield; HI = harvest index; VNY = Vine yields; FBY = fresh biomass yield; STA = root starch content; PRO = root protein content

4.3.3. General combining ability (GCA effects) for RDM and associated traits in the F_1 and F_2 generations

The GCA effects for the eight storage root dry matter and associated traits in F_1 and F_2 yam beans populations are presented in Table 4.4. The GCA effects for RDM were positive and significant ($p<0.001$) for parent 209014 in both F_1 and F_2 while parents 209016 and 209018 showed significant positive contribution to RDM in F_2. However, negative significant GCA effects for RDM were observed in parent 209013 across F_1 and F_2, as well as in parent 209022 in the F_2 generation. Parents 209014, 209016 and 209018 had high GCA effects which made them good combiners for high dry matter in yam beans. The parents with negative GCA effects, namely, 209013, and 209022 were less desirable in the development of high dry matter population.

On the other hand, negative but significant (<0.05) GCA effects for RFY were recorded for parents 209004 and 209022 in F_1 while parent 209016 had positive significant GCA effects only in F_2 generation. In terms of RDY, parent 209016 had positive significant (P<0.01) GCA affects while 209022 had negative but significant GCA effects in F_2 generation. Parent 209016 had positive and significant (p<0.01) GCA effects for RDY in F_2 generation. The only significant GCA effects for FBY were observed in parent 209018 in F_1 and 209016 in F_2. GCA effects for STA were significant and positive for parents 209014 (p<0.001) in F_1 and 209016(p<0.05) plus 209018(p<0.001) in F_2 generation but negative for 209013 in F_1 and 209022 across F_1 (p<0.05) and F_2 (p<0.001) generations.

Table 4. 4 Estimates of general combining ability (GCA effects) for storage root dry matter and associated traits for 9 parents of yam bean evaluated in F_1 and F_2 trials

Parent†	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
F_1 Population								
209013	-3.701***	-1.564	-0.6	0.426	-0.284	-0.966	-8.105***	0.427
209014	3.169***	2.126	0.65	-0.184	0.300625	2.004	6.675***	-0.211
209015	0.799	-0.844	-0.074	-0.364	-0.024	-1.556	2.145	-0.325
209004	0.376	-4.393*	-1.036*	-6.839	-0.042	-4.914	-3.148	0.115
209016	-0.924	1.997	0.323	5.281	-0.296	1.346	0.843	0.312
209018	0.116	3.307	0.731	2.681	0.168	6.136*	3.473	0.848
209019	-0.124	-0.413	-0.126	-2.129	0.148	-1.054	2.803	-0.488
209022	1.056	-4.863*	-0.818	-0.739	-0.423	-6.194	-10.458*	-1.041
209031	-0.224	4.117	0.98	2.251	0.457	3.926	4.503	-0.136
SE_f	0.763	0.286	0.119	0.682	0.124	0.374	0.464	0.351
SE_m	0.539	0.202	0.084	0.482	0.088	0.265	0.328	0.248
F_2 Population								
209013	-1.137***	-0.809	-0.292	0.283	-0.109	-0.921	-1.322	0.018
209014	1.683***	-0.229	0.126	-0.317	0.084	-0.141	1.268	-0.185
209015	-0.397	1.501	0.281	-0.027	0.058	1.559	0.398	0.206
209004	0.373	-0.924	-0.355	-1.502	-0.344	-1.268	-2.727	0.198
209016	3.323***	3.316*	0.905**	1.128	0.603	3.912**	7.783*	0.384
209018	3.163***	0.236	0.264	0.218	0.051	0.282ns	14.303***	0.655
209019	-0.887	-1.064	-0.266	-1.532	0.021	-1.038	-1.067	0.519
209022	-10.307***	-3.424	-1.013**	-7.302	-0.039	-3.458	-34.127***	-1.056
209031	-0.817	0.146	-0.043	5.338	-0.312	-0.158	-1.227	-1.229
SE_f	0.678	0.262	0.258	0.570	0.084	0.294	0.806	0.293
SE_m	0.480	0.185	0.183	0.403	0.060	0.208	0.570	0.207

'Bold genotypes are high RDM male parents (chuin cultivar); SE_f = standard error for female parents; SE_m = standard error for male parents; *, **, *** = P< 0.05, 0.01 and 0.001 respectively; RDM = root dry matter content; RFY = fresh root yield; RDY = root dry yield; HI = harvest index; VNY = Vine yields; FBY = fresh biomass yield; STA = root starch content; PRO = root protein content.

4.3.4. Specific combining ability (SCA effects) for RDM and associated traits in the F_1 and F_2 generations

Both positive and negative SCA effects were recorded for the eight traits of yam bean crosses evaluated in F_1 and F_2 trials (Table 4.5). Positive and highly significant ($p<0.001$) SCA effects for RDM were recorded for crosses, 209022 x 209014 in F_1, as well as 209016 x 209013 and 209031 x 209014 in F_2 implying that these crosses are suitable for improvement of RDM in yam beans. Likewise, positive and significant ($p<0.05$) SCA effects were recorded for RDM in 209019 x 209013 in the F_1 generation. However, the cross 209022 x 209014 did not flower in the F_1 generation and was therefore not evaluated in the F_2 trial indicating that such a cross is not reliable for improvement of RDM in yam beans. In contrast, significant and negative specific combining ability for RDM were observed among crosses 209018 x 209014, 209022 x 209013 in F_1 as well as 209016 x 209015, 209018 x 209014, and 209031 x 209013 in the F_2 generation.

Significant and positive SCA effects for RFY were observed in 209031 x 209014 while the same female parent 209031 gave negative but significant SCA effects in the cross 209022 x 209013. The SCA effects for RFY were not significant in the F_2 generation. The estimates of the SCA effects for STA in the F_1 generation were significant but negative for crosses 209018 x 209014($p<0.05$), 209004 x 209013 and 209022 x 209013($p<0.01$). The cross 209022 x 209014 had positive and significant SCA effects for STA in the F_1 but was lost due to in ability for produce F_2 seed. On the other hand, positive and significant (0.05) SCA effects were observed for STA in cross 209016 x 209013 while significant (0.05) negative SCA effects were recorded for 209016 x 209015 in the F_2 generation. The SCA effects for the cross 209022 x 2209013 were zero in the F_1 generation for all the eight traits assessed suggesting limited influence of non-additive gene effects.

Table 4. 5 Estimates of specific combining ability (SCA effects) for storage root dry matter and associated traits in F_1 and F_2 yam bean populations evaluated at NaCRRI, Namulonge in April 2013 and 2014 respectively.

Crosses	RDM (%)	RFY (t ha-1)	RDY (t ha-1)	HI (%)	VNY (t ha-1)	FBY (t ha-1)	STA (%)	PRO (%)
F_1 population								
209004 x 209013	0.09	2.56	0.55	5.11	0.39	1.74	-9.97**	0.29
209004 x 209014	0.46	-2.98	-0.64	-6.53	-0.19	-2.70	3.65	-0.74
209004 x 209015	-0.55	0.42	0.09	1.43	-0.20	0.96	6.33	0.45
209016 x 209013	1.42	1.44	0.29	1.00	0.10	0.58	3.44	-0.17
209016 x 209014	-2.13	-3.61	-0.84	2.00	-0.66	-3.92	-0.38	0.73
209016 x 209015	0.71	2.16	0.55	-3.00	0.56	3.34	-3.05	-0.57
209018 x 209013	2.22	-0.84	-0.08	1.18	-0.42	3.80	7.35	0.24
209018 x 209014	-2.63*	2.98	0.53	-3.09	0.83	1.15	-7.89*	-0.42
209018 x 209015	0.41	-2.14	-0.45	1.90	-0.41	-4.95	0.54	0.18
209019 x 209013	3.09*	1.37	0.51	-1.57	0.14	-0.34	7.50	-0.69
209019 x 209014	-2.52	-0.92	-0.32	1.90	-0.18	-0.31	-3.69	0.75
209019 x 209015	-0.57	-0.45	-0.19	-0.33	0.04	0.65	-3.81	-0.07
209022 x 209013	-8.46***	0.45	-0.26	-5.52	0.26	0.31	-11.03**	0.71
209022 x 209014	8.46***	-0.45	0.26	5.52	-0.26	-0.31	11.03**	-0.71
209031 x 209013	1.64	-4.98*	-1.02	-0.20	-0.46	-6.09	2.71	-0.38
209031 x 209014	-1.64	4.98*	1.02	0.20	0.46	6.09	-2.71	0.38
s.e	1.32	0.50	0.21	1.18	0.22	0.65	0.80	0.61
F_2 population								
209004 x 209013	-1.31	-0.07	-0.18	1.85	0.19	0.12	-8.28	-0.07
209004 x 209014	0.02	-3.20	-0.55	-2.27	-0.47	-3.67	2.30	-0.72
209004 x 209015	1.28	3.27	0.72	0.43	0.28	3.55	5.98	0.79
209016 x 209013	3.98***	-0.87	0.09	-0.07	-0.28	-1.14	10.15*	-0.45
209016 x 209014	0.06	2.21	0.50	-0.04	0.63	2.83	1.26	0.38
209016 x 209015	-4.05***	-1.34	-0.60	0.12	-0.35	-1.69	-11.41*	0.06
209018 x 209013	1.59	0.59	0.25	-2.75	0.11	0.70	5.73	0.90
209018 x 209014	-2.99**	0.31	-0.25	2.55	-0.08	0.24	-8.39	-0.20
209018 x 209015	1.40	-0.90	0.00	0.21	-0.03	-0.94	2.66	-0.70
209019 x 209013	0.54	0.62	0.23	0.43	0.09	0.71	1.00	-0.32
209019 x 209014	-1.91	0.40	-0.10	0.32	-0.20	0.21	-3.77	0.46
209019 x 209015	1.36	-1.03	-0.13	-0.75	0.11	-0.92	2.77	-0.15
209022 x 209013	0.00	0.00	0.00	0. 00	0.00	0.00	0.00	0.00
209031 x 209013	-4.81***	-0.28	-0.40	0.55	-0.11	-0.39	-8.60	-0.08
209031 x 209014	4.81***	0.28	0.40	-0.55	0.11	0.39	8.60	0.08
s.e	1.17	0.45	0.45	0.99	0.15	0.51	1.40	0.51

s.e = standard error; *, **, *** = significant at $p<0.05, 0.01, 0.001$ respectively; RDM = storage root dry matter content; RFY = fresh root yield; RDY = storage root dry yield; HI = harvest index; VNY = vine yields; FBY = fresh biomass yield; STA = storage starch content; PRO = storage protein content.

4.3.5. Mean performance of parents in F_1 and F_2 generations

The mean performance of parents and their F_1 and F_2 hybrids for the eight RDM and related parameters are presented in Table 4.6. The parents were classified into two groups, namely high dry matter genotypes (209013, 209014 and 209015) with a range of 29.32% to 33.21% and the low dry matter group (209004, 209016, 209018, 209019, 209022 and 209031) with RDM of 7.83 to 15.72% across F_1 and F_2 trials. The highest dry matter parent was consistently 209015 across F_1 and F_2 generations. The RFY estimates among parents varied from 1.73 - 39.63 t ha^{-1} in F_1 and 4.09 - 18.44 t ha^{-1} in F_2 with a mean 15.83 t ha^{-1} and 10.89 t ha^{-1} respectively. As regards RDY, parent 20916 produced the highest yield (4.38 t ha^{-1}) in the F_1 while 209015 had the highest RDY (4.23) in the F_2 generation.

In case of HI, high values were recorded for all the parents in F_1 and F_2 with the highest value of 94.93% in 209016 under F_1 as well as 88.68% in parent 209014 in F_2. The NVY varied from the lowest values (0.9 t ha^{-1}) in 209031 and 5.8 t ha^{-1} in 209022 under F_1 to the highest of 7.32 t ha^{-1} in 209019 and 4.99 t ha^{-1} in 209013 in F_2. In terms of STA, parent 209018 consistently performed poorly in with 34.46 % and 25.96% while parent 209013 had the highest performance of 75.54%, and 75.78% in F_1 and F_2 generations respectively. The PRO was high and varied from 8.21 - 11.4% in F_1 and 7.89 - 11.18% in the F_2 generation. The parents 209016 and 209004 had the highest PRO in F_1 and F_2 respectively. The FBY varied from 2.62 - 33.07 t ha^{-1} in F_1 and 5.31 - 17.53 t ha^{-1}.

Table 4. 6 Mean performance of yam bean parents for storage root dry matter and associated traits evaluated along F_1 and F_2 trials at NaCRRI, Namulonge during the rains of April 2013 and 2014

Parents	RDM (%)	RFY (t ha-1)	RDY (t ha-1)	HI (%)	VNY (t ha-1)	FBY (t ha-1)	STA (%)	PRO (%)
F_1 population								
209013	29.33	12.54	3.64	68.43	5.83	18.37	75.54	9.77
209014	30.76	13.26	4.11	86.99	2.03	15.29	73.95	10.05
209015	32.66	11.74	3.97	81.64	3.00	14.74	76.2	8.21
209004	14.31	3.97	0.64	52.94	5.00	8.97	61.04	11.04
209016	10.00	39.63	4.38	94.93	2.57	42.2	39.6	11.40
209018	9.15	30.55	2.47	91.84	2.53	33.07	34.46	10.67
209019	11.50	23.39	2.63	77.79	7.32	30.71	51.7	10.34
209022	14.71	5.63	0.51	58.83	1.33	4.97	52.64	10.78
209031	15.73	1.73	0.27	67.39	0.90	2.62	46.12	10.00
Mean	**18.68**	**15.83**	**2.51**	**75.64**	**3.39**	**18.99**	**56.8**	**10.25**
CV%	**8.90**	**28.2**	**42.00**	**12.3**	**59.9**	**21.2**	**14.5**	**8.80**
SEM	**1.667**	**4.46**	**1.06**	**9.27**	**2.03**	**4.03**	**8.23**	**0.90**
LSD(0.05)	**3.845**	**10.29**	**2.44**	**21.37**	**4.68**	**9.29**	**18.98**	**2.08**
F_2 population								
209013	29.6	12.52	3.67	72.71	4.99	17.53	75.78	9.93
209014	30.8	13.74	4.21	88.68	1.72	15.46	75.57	9.1
209015	33.21	12.28	4.23	78.76	4.14	16.42	77.66	7.89
209004	13.17	4.09	0.59	57.33	4.48	8.45	61.68	11.18
209016	7.83	13.16	1.23	79.72	1.97	15.13	28.31	10.11
209018	9.01	14.08	1.28	79.9	2.06	16.15	25.96	10.06
209019	9.53	18.44	1.91	79.27	4.77	23.21	36.74	9.36
209022	11.76	5.26	0.57	78.08	0.97	5.80	46.98	11.04
209031	15.02	4.39	0.57	71.78	0.93	5.31	42.96	8.81
Mean	**17.77**	**10.89**	**2.03**	**76.25**	**2.89**	**13.72**	**52.4**	**9.72**
CV%	**9.10**	**47.3**	**47.7**	**15.00**	**67.7**	**44.1**	**11.00**	**12.20**
s.e.m	**1.617**	**5.16**	**0.97**	**11.47**	**1.96**	**6.06**	**5.76**	**1.18**
LSD(0.05)	**2.80**	**8.93**	**1.68**	**19.85**	**3.39**	**10.48**	**9.96**	**2.04**

C.V. = coefficient of variation, s.e.m = standard error of the mean, LSD = least significant difference

4.3.6. Performance of crosses in F_1 and F_2 generations

The RDM values for crosses in F_1 generation varied from 10.32% in 209022 x 209013 to 34.11% in 209022 x 209014. However, the best performing cross (209022 x 209014) in F_1 generation did

not produce seed and was eliminated from further analysis (Table 4.7). The cross 209004 x 209014 with RDM of 25.43% was the next best and consistently performed better than the other crosses in F_1 and F_2 populations. Whereas crosses 209016 x 209013 and 209016 x 209014 had less RDM than the population mean of 21.43% in F_1 generation, the same crosses had better RDM values in F_2 generation than the mean (17.73%). The cross 209022 x 209013 had the lowest RDM of 10.32 and 5.89% across F_1 and F_2 generations respectively. Crosses, 209004 x 209015, 209018 x 209014, 209018 x 209015 and 209031 x 209014 had higher dry matter values than their respective generation means across F_1 and F_2 populations which were associated with male parents (209014 and 209015) that were good combiners for RDM. These parents constitute vital sources of high RDM genes for initiating a breeding program to improve the remaining yam bean germplasm.

The mean RDM of the crosses (21.43%) was higher than for the parents 18.68% and varied from 10.32% in cross 209022 x 209013 to 34.11% in 209022 x 209014. The mean RFY of the crosses was lower than for the parents depicting the reverse relationship between dry matter and yield in yam bean. The lowest HI (81.67%) was found in cross 209022 x 209013 and the highest of 94.59% in 209016 x 209014 in F_1 and 74.88% in 209019 x 209015 to 83.35% in209031 x 209013 in F_2 trial. The mean performance of STA for crosses was high, and varied from 56.8-67.31% in F_1 and 52.4% to 61.51% in F_2 populations.

Table 4. 7 Mean performance of crosses for storage root dry matter and associated traits in F_1 and F_2 generations evaluated at NaCRRI, in April 2013 and 2014

Progenies	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
F_1 population								
209004 x 209013	18.19	5.69	0.88	86.19	1.17	6.49	46.09	11.68
209004 x 209014	25.43	3.83	0.94	73.94	1.18	5.02	74.49	10.01
209004 x 209015	22.06	4.27	0.95	81.72	0.85	5.12	72.64	11.09
209016 x 209013	18.23	10.96	1.98	94.21	0.62	11.59	63.49	11.42
209016 x 209014	21.54	9.60	2.10	94.59	0.45	10.06	74.45	11.68
209016 x 209015	22.02	12.40	2.77	89.42	1.35	13.76	67.25	10.27
209018 x 209013	20.06	9.99	2.02	91.79	0.57	19.60	70.03	12.36
209018 x 209014	22.08	17.50	3.88	86.90	2.41	19.92	69.57	11.07
209018 x 209015	22.75	9.41	2.17	91.72	0.84	10.26	73.47	11.55
209019 x 209013	20.69	8.48	1.76	84.22	1.11	8.27	69.51	10.10
209019 x 209014	21.95	9.87	2.17	87.08	1.38	11.27	73.10	10.90
209019 x 209015	21.53	7.38	1.57	84.67	1.27	8.66	68.45	9.97
209022 x 209013	10.32	3.11	0.29	81.67	0.66	3.78	37.72	10.94
209022 x 209014	34.11	5.90	2.06	92.09	0.73	6.14	74.56	8.89
209031 x 209013	19.15	6.66	1.33	89.97	0.82	7.50	66.42	10.76
209031 x 209014	22.73	20.31	4.62	89.76	2.32	22.65	75.79	10.88
Mean	**21.43**	**9.09**	**1.97**	**87.50**	**1.11**	**10.63**	**67.31**	**10.85**
CV%	**9.10**	**30.69**	**32.62**	**6.02**	**42.61**	**43.00**	**4.94**	**6.16**
s.e.m	**1.91**	**2.82**	**0.64**	**5.27**	**0.48**	**4.63**	**3.32**	**0.67**
LSD(0.05)	**4.22**	**6.23**	**1.42**	**11.63**	**1.05**	**10.24**	**7.32**	**1.49**
F_2 population								
209004 x 209013	15.26	6.66	0.76	77.81	1.63	8.28	47.95	8.76
209004 x 209014	19.41	4.10	0.81	73.09	1.17	5.27	61.12	7.90
209004 x 209015	18.59	12.31	2.23	76.08	1.88	14.19	63.93	9.79
209016 x 209013	23.50	10.10	2.29	78.52	2.11	12.20	76.89	8.56
209016 x 209014	22.40	13.75	3.11	77.95	3.21	16.95	70.59	9.19
209016 x 209015	16.21	11.93	2.17	78.40	2.20	14.13	57.05	9.26
209018 x 209013	20.95	8.48	1.80	74.93	1.94	10.41	78.99	10.18
209018 x 209014	19.19	8.78	1.72	79.63	1.95	10.73	67.46	8.87
209018 x 209015	21.50	9.29	2.13	77.58	1.97	11.26	77.64	8.76
209019 x 209013	15.85	7.21	1.26	76.36	1.89	9.10	58.89	8.83
209019 x 209014	16.22	7.57	1.34	75.65	1.79	9.37	56.72	9.40
209019 x 209015	17.41	7.87	1.47	74.88	2.08	9.95	62.38	9.18
209022 x 209013	5.89	4.23	0.28	70.16	1.74	5.97	24.78	7.57
209022 x 209014	nsd	nsd	Nsd	nsd	nsd	nsd	nsd	nsd
209031 x 209013	10.57	7.51	0.85	83.35	1.36	8.88	49.13	7.32
209031 x 209014	23.01	8.65	2.06	81.66	1.78	10.43	68.93	7.27
Mean	**17.73**	**8.56**	**1.62**	**77.09**	**1.91**	**10.47**	**61.51**	**8.73**
CV%	**12.43**	**33.61**	**40.85**	**7.44**	**19.60**	**28.54**	**18.43**	**16.17**
s.e.m	**2.23**	**2.89**	**0.67**	**5.72**	**0.38**	**3.00**	**11.39**	**1.42**
LSD(0.05)	**3.79**	**4.91**	**1.14**	**9.75**	**0.64**	**5.11**	**19.40**	**2.41**

C.V. = coefficient of variation; s.e.m = standard error of the mean; LSD= least significant difference; nsd = no seed set- no data

4.3.7. Pearson's correlation coefficients among RDM and related parameters in F_1 and F_2 yam bean populations

Pearson's correlation coefficients for the eight RDM and associated parameters are presented in Table 4.8. In the F_1 generation, significant ($p<0.01$) positive correlation ($r = 0.74$) was observed between RDM and STA. Similarly, RFY had significant and positive correlations with VNY ($p<0.01$), RDY and FBY ($p<0.001$). On the other hand, moderate but significant ($p<0.05$) negative correlation ($r = -0.568$) was observed between RDM and PRO. A moderate to high positive and significant correlations were observed between RDY and STA ($p<0.05$), VNY ($p<0.01$) and FBY ($p<0.001$). Moreover, FBY had positive moderate ($r = 0.595$) and significant ($p<0.05$) correlation with VNY.

Table 4. 8 Phenotypic correlation coefficients (F_1 below diagonal, F_2 above diagonal) for storage root dry matter and associated traits among yam bean progenies evaluated at Namulonge in April 2013 and 2014

Parameter	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
RDM (%)	-	-0.525*	0.774***	0.299	0.397	0.522*	0.938***	0.337
RFY (t ha^{-1})	0.104	-	0.921***	0.427	0.771**	0.54***	0.541*	0.509
RDY (t ha^{-1})	0.328	0.968***	-	0.368	0.783***	0.928***	0.759**	0.456
HI (%)	0.126	0.452	0.449	-	0.075	0.389	0.34	-0.23
VNY (t ha^{-1})	0.132	0.719**	0.719**	-0.19	-	0.827***	0.364	0.457
FBY (t ha^{-1})	0.058	0.924***	0.881***	0.442	0.595*	-	0.53	0.516
STA (%)	0.74**	0.376	0.517*	0.198	0.195	0.358	-	-0.44
PRO (%)	(-0.568)*	0.196	0.024	0.32	-0.153	0.357	-0.212	-

*, **, *** = significant at $p<0.05$, 0.01, 0.001 respectively; RDM = storage root dry matter content; RFY = storage fresh root yield; RDY = storage root dry yield; HI = harvest index; VNY = Vine yields; FBY = fresh biomass yield; STA = storage starch content; PRO = storage protein content

In the F_2 generation, RDM had moderate to high positive and significant correlation with FBY ($p<0.05$), RDY ($p<0.001$) and STA ($p<0.001$) but a moderate and significant negative correlation ($r = -0.525$) with RFY. In contrast to the F_1 generation, RFY recorded a significant ($p<0.05$) correlation with STA in addition to similar positive and significant correlations with VNY (($p<0.01$), RDY ($p<0.001$) and FBY ($p<0.001$). The correlations between RDY, VNY FBY and STA were consistently positive and significant in the F_2 generation. It was also observed that the correlation between VNY and FBY was positive and highly significant ($p<0.001$) in the F_2 generation as compared to the F_1 generation.

4.4. Discussion

In this study, parental lines, F_1 and F_2 progenies were evaluated to determine combining abilities and gene action controlling inheritance of RDM and associated traits; RFY, RDY, VNY, BFY, STA and PRO to obtain vital information for selecting appropriate parents and breeding strategies for future yam bean breeding programs. The current results identified suitable parents to improve storage root dry matter content (RDM) and associated traits in yam bean. The results showed that inheritance of RDM and associated traits especially RFY, RDY, FBY and STA was mainly under additive gene effects and that genetic variability among parents was sufficient to permit improvement of these traits through selection. Significant GCA means squares were observed for males and females showing that the nine yam bean parents evaluated in this study possessed good combining ability for improvement of RDM and associated traits except HI. Significant variation observed between crosses offered an opportunity for selection of high dry matter lines with good storage root yields and starch content. However, significant SCA mean squares for RDM, RFY, HI, FBY and STA in F_1 and F_2 suggested that non-additive gene action partly influence the inheritance of these traits in yam beans. But average GCA mean squares estimates for most traits were larger than SCA indicating that additive gene action was more important than non-additive gene action (Table 4.2).

The high variance (σ^2) estimates recorded for combining abilities reveal the presence of substantial genetic variation in the parent genotypes and the progenies indicating excellent prospects for yam bean improvement program. Baker's ratio of above 0.5 indicated that inheritance in all the traits except VNY were controlled by additive gene effects across F_1 and F_2 generations suggesting that selecting superior genotypes in the early generations would be effective for these traits (Amongi et al., 2015; Habarurema et al., 2012). High baker's ratio revealed the relative importance of GCA to SCA effects in the genetic determination of RDM and associated traits and enhanced the argument for predominance of additive genes in the inheritance of the trait. Similarly the large predictability ratio ($\sigma^2GCA_f/\sigma^2SCA$) of three times above unity in F_1 and close to unity in F_2 confirmed the prevalence of additive gene effects in the inheritance of RDM in yam bean progenies. According to Bi et al. (2015), a large ratio of GCA to SCA effects reveals preponderance of additive gene effects while a small value signifies the

presence of dominant and or epistatic gene effects. Therefore from the predictability ratios for RDY, HI, STA and PRO in F_1 and RDM in F_2 of above 0.5 indicated that additive gene effects were more influential than non-additive gene effects in the inheritance of these traits, suggesting a good prospect for yam bean improvement using current parents. The presence of additive gene affects indicates a high chance for predicting the performance of progenies based on phenotypic scores of the parents (Owolade et al., 2009). The action of additive gene effects in the inheritance of RDM and related traits was supported by the suggestions of Grüneberg et al. (2003) that improvement of root dry matter content in the yam beans was possible through inter and intra specific hybridisation.

The high narrow sense heritability estimates observed for RDM, RFY, RDY, HI, FBY and STA in F_1 and all traits in F_2 except VNY (Table 4.3) suggested the presence of sufficient genetic potential among the parents to pass on the traits to subsequent generations. High heritability estimates suggested that the performance of the progeny could be succinctly predicted from parents and that the current germplasm had high potential for significant response to selection in early generations. According to Majidi et al. (2009), such heritability estimates provide an indication of the expected response to selection in segregating populations, and are useful in designing an effective breeding program for improvement of quantitative traits. However, the current heritability estimates might have been overestimated because combining ability studies from one location tend to have high genetic effects and capture less environmental variance. Such results cannot be generalized beyond the particular test environment. Therefore, increasing sample size, replication and testing of progenies across multi-locations might improve the accuracy of heritability estimates obtained in this study.

Positive and significant GCA effects (Table 4.4) are desirable in breeding programs for improvement of RDM, RFY, RDY, and STA in yam beans. Significant GCA effects suggested the presence of additive gene effects and implied that improvement of these traits was possible using the current parents. Similar results were reported by Jha and Singh (2014) showing significant and positive GCA effects for root yield, root length and root girth among 22 yam bean female lines, three male testers and 66 crosses.

In this study, the male parent 209014 was found a good combiner for STA in F_1, and RDM in both F_1 and F_2 generations while female 209016 was identified as a good combiner for RDM, RFY, RDY, VNY and STA in the F_2 generation (Table 4.4). Similarly, female parent 209018 had significant ($P<0.001$) GCA effects for RDM and STA in F_2. Positive and significant GCA effects among low RDM female parents suggested that these traits could be improved through intraspecific hybridisation without using the high RDM chuin cultivars of *P. tuberosus* which is in agreement with the findings reported by Agaba et al. (2016). Negative but significant ($P<0.001$) GCA effects were recorded for RDM in parent 209013 across F_1 and F_2, as well as in 209022 for RDM, RDY and STA in F_2, which implied that such parents might be poor combiners for trait improvement. This result is in agreement with the negative but significant GCA effects previously reported for primary branches per plant and vine weight in yam beans (Jha and Singh, 2014). The GCA effect of a given trait is of inherent value to a given parent and identifies the ability of the parent to produce superior progenies when crossed with other parents (Won & Yoshida, 2000).

SCA analysis identified crosses, 209022 x 209014 as suitable for improvement of RDM and STA in F_1 as well as 209019 x 209013 for RDM. Also, the cross 209016 x 209013 constituted valuable breeding material for RDM and STA while 209031 x 209014 represented promising families for high inheritance of RDM in F_2 segregating yam bean population. It was observed that crosses with positive and significant SCA effects also gave high mean values of RDM compared to the population means in F_1 and F_2 generations. Such associations between SCA effects and mean performance of the crosses have been reported in yam beans (Jha and Singh 2014), and sweetpotato (Singh and Naskar 1991). Significant GCA and SCA effects and predominance of additive genes for inheritance of root traits such as root length, girth yield and earliness were recently reported in yam beans by Jha and Singh (2014). Kearsey and Pooni (1996) argued that the magnitudes of GCA and SCA estimates showed the importance of additive and non-additive gene effects in the inheritance of quantitative traits and offer vital genetic information about potential genetic progress in breeding programs.

The mean performance for the parents and progenies showed wide variation for all the traits across F_1 and F_2 (Table 4.6). The mean values were higher in the progeny than in the parents for the RDM, HI, STA and PRO in the F_1 and in HI and STA under the F_2 generation. The mean RDM and associated trait values for yam bean parents and progenies in this study falls within or below the ranges reported elsewhere (Grüneberg et al., 2003, Sørensen 1996, Zanklan et al., 2007). The yam bean parents used in this study were categorized into the low RDM and the high RDM groups. The high RDM genotypes (209013, 209014 and 209015) belong to *the* chuin cultivar of *P. tuberosus* described as a good source of high dry matter trait for yam bean breeding (Grüneberg et al., 2003; Sørensen, 1996; Zanklan et al., 2007) while the *P. erosus* accessions could be a good source of genes for yield traits while the *P. ahipa* might be a source of early maturity and semi erect growth habit. Recent molecular based characterization of the yam beans showed clear separation between chuin and Ashipa cultivar groups of the *P. tuberosus* (Santayana et al., 2014). The chuin is the only high dry matter cultivar among the four different cultivars of *P. tuberosus* known as Ashipa, Yushpe, and Jíquima cultivars (Sørensen 1996). The significant positive correlations coefficients (Table 4.8) suggested that simultaneous selection for RDM and RDY, FBY and STA as well as for RFY and RDY, FBY and VNY was possible.

4.5.Conclusions

These results revealed that both additive and non-additive gene effects contributed to the inheritance of RDM, RFY, RDY, FBY and STA in yam beans, however, additive gene action was predominant with high GCA effects and narrow-sense heritability estimates indicating potential for high genetic gain from selection. Therefore, the yam bean accessions in Uganda constituted suitable germplasm for improvement of RDM and associated traits.

CHAPTER FIVE

RESPONSE TO SELECTION FOR STORAGE ROOT DRY MATTER CONTENT AND ASSOCIATED TRAITS IN YAM BEANS

5.1. Introduction

The success of plant breeding programs depends on the ability to select superior individuals or families with considerable genetic variation and predicting response to selection for the traits of interest. The selection of elite plants from segregating yam bean populations should influence the level of expected response to selection and foster trait improvements in a breeding program. Tapia and Sørensen (2003), recommended studies to determine response to selection in yam beans based on the high levels of variation observed from morphological characterization of *Pachyrhizus tuberosus*. The yam bean possesses considerable variation for most agronomic traits across species (Agaba et al., 2016 ; Silva & Ticona-Benavente, 2016; Zanklan et al., 2007) which offers opportunities for genetic improvement through hybridisation and selection.

Several studies have reported on genetic parameters and potential for selection in yam bean breeding populations (Grüneberg et al., 2003; Santayana et al., 2014; Silva & Ticona-Benavente, 2016; Sørensen, 1996; Zanklan et al., 2007). Intensive selection studies of local yam bean landraces in Mexico have resulted in high yielding *P. erosus* cultivars and field selections for cultivars have been conducted based on storage root shape, size, growth habit, pest resistance, and seed yield as the selection criteria (Sørensen, 1996). Similarly, hybridisation experiments have been conducted to examine interspecific compatibility of the three cultivated species, *P. erosus*, *P. ahipa* and *P. tuberosus* resulting in fertile and vigorous hybrids (Grum, 1994; Grüneberg et al., 2003; Sørensen, 1988, 1996). However, these experiments did not investigate response to selection or the use of high dry matter chuin cultivar of *P. tuberosus* as a parent for improvement of storage root dry matter and associated traits in segregating yam bean populations. The possibility of breeding high dry matter varieties remains the most important target for yam bean improvement programs (Hosein, 2001; Zanklan et al., 2007).

The success of genetic improvement largely depends on the magnitude of genetic variability present in the base population. The estimation of genetic parameters such as genotypic coefficients of variation (GCV), phenotypic coefficients of variation (PCV) and heritability gives a better indication of genetic variation and potential response to selection for the trait of interest. It is important to estimate heritability but the influence of environmental factors mean that heritability alone is not sufficient. Therefore, genetic coefficients of variation and response to selection are important in designing suitable selection procedures and efficient breeding programs (Jamoza et al., 2014). The extent of PCV and GCV indicates the relative amount of variation exhibited by different traits which acts as a basis for selection and breeding. Traits exhibiting relatively high GCV estimates may respond favorably to selection.

Stringent early generation selection can be effective in identifying superior breeding lines that are capable of high response in advanced non-segregating generations (Yang, 2009). The current study utilizes early generation selection to evaluate F_3 yam bean progenies for variance components, phenotypic coefficients of variation (PCV) and genotypic coefficients of variation (GCV), heritability and response to selection for storage root dry matter content (RDM) and associated traits *viz.*, root fresh yield (RFY), root dry yield (RDY), harvest index (HI), fresh biomass yield (FBY), vine yield (VNY), protein (PRO) and starch (STA) in yam bean. Knowledge of genetic variation and heritability estimates for desirable traits is a prerequisite for success of crop improvement programs (Roychowdhury et al., 2012) especially in yam beans where genetic studies are limited. These estimates could inform the choice of selection and breeding procedures as a requirement for yam bean improvement program in Uganda. The objective of the present study was to determine response to selection for RDM and associated traits in F_3 segregating yam bean populations developed from crosses between the high dry matter chuin cultivar of *P. tuberosus* and low dry matter *P. ahipa,* and *P. erosus* accessions.

5.2. Material and methods

5.2.1. Experimental site and germplasm

The experiment was carried out under field conditions at National Crops Resources Research Institute (NaCRRI), Namulonge, Wakiso District, Central Uganda. Namulonge is located at

32°36"E and 0°31"N, at 1150 m above sea level, and has a bimodal rainfall pattern with a mean of 1,270 mm and two distinct rainy and dry seasons of nearly equal length. The site experiences a mean annual temperature of 22.2°C ranging from 15.9 to 28.9°C (Tumuhimbise et al., 2014; Tumwegamire et al., 2011).

A hybrid population of 16 crosses was generated according to North Carolina II mating design using nine yam bean accessions categorized into high and low storage root dry matter (RDM) parents (Table 5.1). During hybridisation, every male was crossed with every female creating female and male half sib groups as described by Kearsey and Pooni (1996). The crosses were made between three high RDM *P. tuberosus*-chuin cultivars and six low RDM (three *P. ahipa* and three *P. erosus*) parents targeting high dry matter cultivar development. The crosses involved no reciprocals on the assumption that there was no maternal and epistatic effects for inheritance of the target traits as stated in Comstock and Robinson (1952). The F_2 generation was produced by self-pollinating F_1 plants grown under field conditions at NaCRRI, Namulonge. The F_2 seed was subjected to 10% selection intensity on the basis of highest dry matter content to obtain 83 selected progenies constituting the study population.

Table 5. 1 Characteristics of the nine parental genotypes used to generate crosses used in the study

Parent name [z]	Species	[x] RDM Category	Parent Type
209004	*P. ahipa*	Low RDM	Female Parent
209013	*P. Tuberosus - chuin Cultivar*	High RDM	Male Parent
209014	*P. Tuberosus - chuin Cultivar*	High RDM	Male Parent
209015	*P. Tuberosus - chuin Cultivar*	High RDM	Male Parent
209016	*P. Erosus*	Low RDM	Female Parent
209018	*P. Erosus*	Low RDM	Female Parent
209018	*P. Erosus*	Low RDM	Female Parent
209022	*P. ahipa*	Low RDM	Female Parent
209031	*P. ahipa*	Low RDM	Female Parent

[z]Name codes given by the International Potato Center gene bank, Peru.
[x]RDM = storage root dry matter content (Low RDM < 20 %, High RDM > 20 %)

5.2.2. Experimental design and progeny evaluation

The F_3 progenies constituting of 83 families were planted and evaluated in the field during the first rainy season in April 2015. The 83 families were selected form the F_2 population of 830 segregants at 10% selection intensity on the basis of high dry matter yields. Each family was sown using five seeds per plot at a spacing of 0.3 meters between plants. Plots consisted of ridges measuring 1.5m long and 1 meter apart. The plots were arranged in a randomized complete block design (RCBD) with three replications. The experimental field was kept weed free and no reproductive pruning of flowers or fertilizers or agrochemicals were applied during the crop growth cycle.

5.2.3. Data collection

Yam bean plants were harvested individually at maturity, 6 months after planting and data recorded on weight of fresh storage roots (WFR) and above ground foliage (Vine weight, WVN). These traits were used to estimate storage root fresh yield (RFY t ha^{-1}), vine yield (VNY t ha^{-1}), fresh biomass yield (FBY = RFY + VNY) t ha^{-1}, and harvest index (HI = RFY/FBY) recorded as percentage.

From each plant, a fresh storage root sample was collected and taken to the nutritional quality laboratory at NaCRRI for determination of RDM, starch and protein content. The samples were separately washed, peeled, and sliced to prepare compound samples of 100 g fresh weight. Next, each sample was packaged in transparent polythene bag and freeze dried at -31^{0}C for 72 hours (using a vacuum freeze drier, YK-118-50, True-Ten Industries, Korea, 1995) to obtain dry weight. Storage root dry matter (RDM) content was obtained from the ratio of dry weight to fresh weight and expressed as the percentage (RDM = 100*Dry weight/Fresh weight) according to Wilken et al. (2008). The RDM was used to estimate storage root dry yield (RDY = RFY* RDM/ 100), which was recorded as t ha^{-1}. Next, each freeze dried sample was ground into flour using a stainless steel mill (Dayton split phase motor-3383-L70, Thomas Scientific-USA) fitted with a 0.425 mm sieve. The flour samples were stored in Kraft paper bags in deep freezers at -20^{0}C until Near-Infrared Reflectance Spectroscopy (NIRS) analysis was conducted.

The NIRS system 5000-M, FOSS scientific 2000 was used to determine starch (STA), and protein content (PRO) as described by Velasco and Grüneberg (1999) for yam bean with modifications to use flour samples instead of fresh storage roots, following procedure for sweetpotato as described by Tumwegamire et al. (2011). The estimates of STA and PRO were obtained as predicted outputs from NIRS (Ozaki et al., 2007) and recorded as percentages on dry weight basis. Each flour sample was scanned on NIRS three times to obtain replicates of near-infrared spectra for each sample within the range of 400 to 2500 nm to minimize prediction error. The NIRS calibrations for yam bean freeze dried storage root samples are available at the nutritional quality laboratory, NaCRRI in Uganda and were bench marked at plant and nutrition quality laboratory at CIP in Peru (Agaba et al., 2016).

5.2.4. Data analysis

The data was subjected to analysis of variance to estimate genetic parameters and test the significance of trait variability across the 83 F_3 yam bean families. Genotypic and phenotypic coefficients of variation and heritability (h^2) estimates were calculated from variance components according to Kearsey and Pooni (1996) and Singh and Chaudhary (1985) following the formulas;

$$GCV\,\% = \frac{\sqrt{\sigma_g^2}}{\dot{x}} * 100;$$

$$PCV\,\% = \frac{\sqrt{\sigma_p^2}}{\dot{x}} * 100$$

Then Narrow sense heritability (h^2_b) was determined following Kearsey and Pooni (1996) as follows;

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{e/r}^2} * 100$$

Where;

GCV% = genotypic coefficient of variation; σ^2g = genotypic variance; PCV % = phenotypic coefficient of variation; σ^2p = phenotypic variance; σ^2e = environmental variance and $\dot{x}$ = grand mean of the trait. These components in the above formulae were obtained from the ANOVA (Table 5.2) as follows;

$$\text{Genotypic variance } (\sigma^2_g) = \frac{\text{Genotypic mean square (GMS)- Error means squares (EMS)}}{\text{Number of replications (r)}}$$

$$\text{Phenotypic variance } (\sigma^2_p) = \sigma^2_g + \sigma^2_e / r$$

$$\text{Environmental variance } (\sigma 2e) = MSe-(\sigma^2_g)/2$$

The response to selection (R) was calculated as $R = ih^2\sigma_p$ and percentage response to selection (R %) = (R/x̄)* 100) as reported by Acquaah (2007).

Where;

i = selection intensity,

h^2 = narrow sense heritability,

σ_p = phenotypic standard deviation of the parental population (selection differential i.e the mean phenotypic value of the individuals selected as parents expressed as a deviation from the population mean)

$$= \sqrt{(\sigma^2_p)} = \sqrt{\sigma^2_g + \frac{\sigma^2_e}{r}}$$

The selection intensity (i) of 1.755 is obtained from statistical tables corresponding to 10% of the F_2 population was used (Acquaah, 2007). The selection at 10% is moderately stringent and suitable for early generation selections such as in F_2 when segregation is highest. Stringent selection intensity guarantees that the selected population is likely to contain genotypes with the desired gene combinations.

Table 5. 2 Skelton ANOVA showing procedure for estimation of variance components for the F_3 families as proposed by Kearsey and Pooni (1996)

Source of variation	df	Mean squares	F denominator	Expectation
Replication	R-1	MS_R	MS_W	
Between families	n-1	MS_B	MS_W	$\sigma^2_w + r\sigma^2_B$
Within families	n(r-1)	MS_W		σ^2_w

df = degrees of freedom; R = number of replications; n = number of families; r = size of each family in the F_3 population

Genotypic variance $(\sigma^2_g) = (MS_B - MSw)/r$; Environmental variance $(\sigma^2 e) = MSw - (\sigma^2 g)/2$; Phenotypic variance $(\sigma^2_p) = \sigma^2 g + MSw/r$; Phenotypic standard deviation $(\sigma_p) = \sqrt{(\sigma^2 g + MSw/r)}$

5.3.Results

5.3.1. Analysis of variance

The mean squares from combined analysis of variance for the eight RDM and associated traits among the selected 83 F_3 yam bean families are presented in Table 5.3. There was significant ($p<0.001$) genetic variation among the 83 yam bean families for all the eight traits, RDM, FRY, RDY, HI, VNY, FBY, STA and PRO. The within family variation was non-significant across traits indicating that the performance of given families in one environment could be extrapolated to other environments.

Table 5. 3 Analysis of variance for storage root dry matter and associated traits in F_3 yam bean population evaluated at NaCRRI- Namulonge during rainy season of April 2015.

		Mean Squares							
Source of Variation	df	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
Replication	2	42.71	32.1	4.53	585.6	2.51	118.41	310.5	26.52
Between families	82	195.4***	53.5***	3.7***	355.7***	12.8***	100.0***	911.8***	13.6***
Within families	1162	59.86	23	1.41	170.89	6.18	38.07	254.97	6.03
Coefficient of variation (CV)		1.63	1.74	0.92	1.51	1.53	1.93	1.99	0.71

Significance levels, *** at 0.001, RDM = root dry matter content (%); RFY = fresh root yield (t ha-1); RDY = root dry yield (t ha-1); VY = Vine yields (t ha-1); BY = fresh biomass yield (t ha-1); HI = harvest index; PRO = protein content of roots (%); STA = starch content of roots (%)

5.3.2. Mean performance, phenotypic and genotypic variance components

The results revealed remarkable phenotypic and genotypic variation for the eight RDM and associated traits (Table 5.4). There were wide variations for RDM, RFY, HI, FBY and STA as shown by the high estimates of genotypic variances (σ^2_g). STA was the most varied with a phenotypic and genotypic variation of 59.33 and 43.79 respectively. The mean RDM ranged from 12.43 to 31.83 % with a population average of 22.4 % while the mean STA content on dry weight basis was 64.38%. These values were higher than the corresponding estimates in the respective parent populations (Agaba et al., 2016). The storage root yields varied from 2.6 to 19 t ha^{-1} with a mean of 7.58 t ha^{-1}, and moderate phenotypic and genotypic variances at 3.5 and 2.03 respectively.

Table 5.4 Mean performance, phenotypic and genotypic variance components for storage root dry matter and associated traits in F_3 yam bean population evaluated at NaCRRI, Namulonge during rainy season of April, 2015

Trait	Range		Mean	s.e.m	Variance component	
	Min	Max	($\bar{x}$)		σ^2_p	σ^2_g
RDM, %	12.43	31.83	22.40	0.44	12.72	9.03
RFY, t ha^{-1}	2.60	19.00	7.58	0.28	3.50	2.03
RDY, t ha^{-1}	0.47	3.76	1.65	0.06	0.24	0.15
HI, %	54.74	86.70	75.28	0.63	23.30	12.32
VNY, t ha^{-1}	0.79	7.66	2.64	0.13	0.84	0.44
FBY, t ha^{-1}	3.37	28.35	10.21	0.39	6.53	4.13
STA, % DM	35.80	81.55	64.38	0.96	59.33	43.79
PRO, % DM^w	9.89	15.07	12.10	0.12	0.89	0.50

RDM = root dry matter content, RFY = fresh root yield, RDY = root dry yield, VY = Vine yields, BY = fresh biomass yield, HI = harvest index, PRO = protein content of roots, STA = starch content of roots, DM = dry matter basis, s.e.m = standard error of the mean, σ^2p = phenotypic variation, σ^2g = genotypic variation

5.3.3. Additive and environmental variances, and coefficients of variation

The estimates of additive and environmental variances, phenotypic standard deviation, genotypic coefficient of variability (GCV), phenotypic coefficient of variability (PCV), narrow sense heritability (h^2) and response to selection (R) for eight traits of F_3 yam bean population are presented in Table 5.5. The additive genetic variances were high and above unity for RDM, RFY, RDY, HI, FBY and STA. However, the environmental variance was also relatively high across all traits indicating presence of environmental effect on these traits. The phenotypic coefficients of variation (PCV) and genotypic coefficients of variation (GCV) were low to moderately high ranging from 6.41 and 4.66 in HI to 34.77 and 25.25 for VNY.

The estimates of GCV were moderate for STA (10.28), RDM (13.42), RFY (18.8), RDY (23.71), FBY (19.91) and VNY (25.25). The PCV values were higher than all GCV values across the traits indicating the importance of environmental variance in the expression of these traits.

Table 5. 5 Estimates of additive and environmental variances, coefficients of variation, heritability and response to selection for storage root dry matter and associated traits among 83 F_3 yam bean families

Parameter	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)	PRO (%)
Additive variance (σ^2_A)	9.03	2.03	1.33	12.32	0.44	4.13	43.79	0.50
Environmental Variance (σ^2_E)	55.34	21.98	1.33	164.73	5.96	36.00	233.08	5.78
Phenotypic standard deviation (σ_p)	3.57	1.87	0.49	4.83	0.92	2.56	7.70	0.94
Phenotypic coefficient of variation (PCV %)	15.93	24.66	29.78	6.41	34.77	25.04	11.96	7.78
Genetic coefficient of variation (GCV %)	13.42	18.80	23.71	4.66	25.25	19.91	10.28	5.86
Narrow sense heritability (h^2)	0.71	0.58	0.63	0.53	0.53	0.63	0.74	0.57
Response to selection (R)	4.45	1.91	0.55	4.48	0.85	2.84	9.98	0.94
R as %age of mean (R %)	19.85	25.14	33.12	5.95	32.18	27.79	15.50	7.73

Response to selection was calculated at selection intensity of 1.755; RDM = root dry matter content, RFY = fresh root yield, RDY = root dry yield, VY = Vine yields, BY = fresh biomass yield, HI = harvest index, PRO = protein content of roots, STA = starch content of roots

5.3.4. Estimates of heritability and response to selection

The estimates of narrow sense heritability, response to selection (*R*) and *R* expressed as percentage of trait mean for the eight evaluated traits are also presented in Table 5.5. The narrow sense heritability and response to selection are important genetic parameters for selecting the best promising parents and performing progenies. In the current study, narrow sense heritability was moderately high (0.53 to 0.74) and associated with high estimates of R indicating that all the traits were highly heritable with potential for improvement. High estimates of percentage response to selection (R%) was observed for RDM, RFY, RDY, VNY, FBY and STA ranging from 15.5 - 33.12%. Despite the high narrow sense heritability estimates for HI (0.53) and PRO (0.57), their percentage response to selection were low at 5.95% and 7.73% respectively suggesting that improvement of HI and PRO would require several cycles of selection.

5.3.5. Genotypic correlations among eight RDM and associated traits

The genotypic correlation coefficients for the eight RDM and associated traits among the 83 F_3 yam bean families are presented in Table 5.6. There was a significant ($p<0.001$) positive correlation between RDM and RDY, STA but significantly ($p<0.01$) negative correlation with PRO. The RFY had significant ($p<0.001$) correlations with RDY, VNY and FBY. The strong

positive and significant correlation between RDY and RDM, RFY could be due to RDY being a product of the latter traits. It was also observed that the correlations between RDY and VNY, FBY and STA were significant ($p<0.001$) while VNY had a strong ($r = 0.786$) and significant ($P<0.001$) correlation with FBY. The RPO had negative and significant ($P<0.05$) correlations with RFY, RDY, FBY and STA which revealed difficulty for simultaneous improvement of these traits in yam beans (Table 5.6).

Table 5. 6. Estimates of genetic correlation coefficients among root dry matter and associated traits in F3 yam bean selected populations evaluated at NaCRRI, Namulonge during rainy season of April 2015

	RDM (%)	RFY (t ha^{-1})	RDY (t ha^{-1})	HI (%)	VNY (t ha^{-1})	FBY (t ha^{-1})	STA (%)
RDM (%)	1						
RFY (t ha^{-1})	(-0.123)	1					
RDY (t ha^{-1})	0.408***	0.809***	1				
HI (%)	0.01	0.146	0.166	1			
VNY (t ha^{-1})	(-0.091)	0.612***	0.488***	(-0.493***)	1		
FBY (t ha^{-1})	-0.117	0.963***	0.771***	(-0.083	0.786***	1	
STA (%)	0.699***	0.046	0.422***	0.268*	(-0.128)	-0.007	1
PRO (%)	(-0.320**)	(-0.217*)	(-0.334**)	0.045	(-0.201)	(0.231*)	(-0.295*)

*, **, *** = significant at 0.05, 0.01, and 0.001 respectively; RDM = dry matter content (%); RFY = fresh root yield (t ha^{-1}); RDY = root dry yield (t ha^{-1}); HI = harvest index (%); VNY = Vine yields (t ha^{-1}); FBY = fresh biomass yield (t ha^{-1}); STA = starch content (%); PRO = protein content (%)

5.4. Discussion

The results from the ANOVA showed that the 83 F_3 yam bean families were genetically divergent for all the eight quantitative traits (RDM, RFY, RDY, HI, VNY, STA and PRO), given that the mean squares for between families (genotypic variation) were higher than for within family variation (environmental variation) for all the traits. This indicated presence of high genetic variability among the 83 families, suggesting that the parental germplasm had a broad genetic base and inherent potential for genetic improvement through hybridisation and selection. Similar results were reported by Tapia and Sørensen (2003) indicating high genetic variation for morphological traits which suggested potential for genetic improvement of yam beans. Nevertheless, the current findings showed that the magnitude of phenotypic coefficient of variation (PCV) were larger than genotypic coefficient of variation (GCV) for all traits which

icated that environmental effects contributed to the phenotypic expression of these attributes. e difference between GCV and PCV estimates was small in most traits except HI and PRO nent, implying environmental influence in the expression of these characters was minimal ich confirmed the good prospects for genetic improvement of the traits.

wide range of variation was observed for RDM, STA, RFY, FBY, RDY and VNY with the gh GCV and PCV estimates revealing potential for improvement of these characters by ingent selection. The least variation observed in protein content as shown by very low GCV d PCV estimates revealed that selection would be ineffective in early generations and should e delayed till later generations (F5- F6) to achieve worthwhile genetic gain (Nalugo et al., 016). GCV is a measure of relative genetic variation of a trait in a population and traits with gh GCV estimates may respond favorably to selection (Jamoza et al., 2014).

imilarly, the heritability estimates were high (0.53 to 0.74) for all traits showing that a large oportion of the total variance could be passed on to progenies and selection for these traits ould be effective. Heritable variation shows the reliability of phenotypic values in predicting he breeding value of quantitative traits in a random mating population (Falconer & Mackay, 1996). The current heritability estimates for dry matter content (0.71) was higher than the reported values (0.66) in Tapia and Sørensen (2003), a finding that suggested that the use of P. *tuberosus*-chuin cultivar in hybridisation improved the genotypic variation for dry matter content and associated traits.

In view of the high GCV and heritability estimates observed for most traits in this study, these genetic parameters provides opportunities for improvement of dry matter and associated traits in yam beans. These results agree with the findings by Zanklan et al. (2007) who reported large genetic variation within and between the three cultivated yam bean species for traits such as root dry matter content, root fresh yield, root dry yield, biomass yield, harvest index, protein and starch contents. Similarly, a recent diversity study involving 64 Amazonian yam bean accessions reported significant genetic variability in the crop and concluded that yam beans could be effectively improvement for storage root yields (Silva & Ticona-Benavente, 2016).

effectiveness of selection for desired genotypes in breeding programs depends not only on genetic variation and heritability estimates but is measured by the magnitude of response to lection (*R*) for the desirable traits in a selection cycle. The results indicated that in a single cle of selection, high percentage response to selection (*R* %) ranging from 5.95% to 33.12% achievable on the mean basis. The estimates of response to selection were also high at 85, 25.14, 27.79 and 15.5% observed for RDM, RFY, FBY and STA respectively which gested high potential for genetic improvement of the evaluated germplasm through recurrent lection. This finding was supported by literature showing importance of response to selection in breeding programs (Hamdi et al., 2003; Mishra et al., 2015). On the contrary, traits with values of response to selection *viz.*, 5.95% (HI) and 7.73% (PRO), also had low heritability imates, HI (0.53) and PRO (0.57) and low GCVs which indicated that a large portion of their riation was due to environmental factors. The high heritability estimates obtained in this study upled with moderately high R% for most traits suggested presence of additive genetic effects most yield and associated traits in yam beans.

gh and strong genetic correlations were observed for RDM and STA; RFY and VNY, FBY; DY and FBY; and between VNY and FBY followed by moderate significant correlation tween RDM and RDY; and RDY with STA and VNY as well as between RDM and RDY. ese correlations reflect genetic association and possible correlated response suggesting that lecting simultaneously for multiple traits is possible. Acquaah (2007) argued that the fectiveness of indirect selection depends on the magnitude of genetic correlation and the itability of the secondary traits being selected. Given that the heritability of these traits was or high, then it is safe to mention that selection for the high RDM and related traits in yam ans would give indirect correlated response.

5. Conclusion

e findings of this study showed that early generation selection based on phenotypic rformance of yam bean genotypes could effectively be utilized for improvement of RDM, Y, RDY, VNY, FBY and starch content. These findings further demonstrated that worthwhile

ɛtic progress is achievable through stringent selection for high storage root dry matter and ɔciated traits in early generations of yam bean breeding.

CHAPTER SIX

GENERAL DISCUSSION

Genetic variability for yield, dry matter and quality traits in yam beans

study determined genetic variability for storage root yield, dry matter and nutritional ent among 26 accessions of three cultivated low dry matter yam bean species. The results ved high genetic variability and agronomic performance among the three cultivated yam species for yield traits *viz.*, root fresh yield (RFY), root dry matter (RDM), root dry yield Y), vine yield (VNY), fresh biomass yield (FBY), harvest index(HI), and nutritional quality s: storage root starch (STA), protein (PRO), iron (Fe), zinc (Zn), potassium (K) and sphorus (P) (Chapter 3). The high genetic variability was supported by highly significant n squares (Table 3.3), heritability estimates and coefficients of variation (Table 3.6). This onstrates that the yam bean species have potential for genetic improvement regarding these s. Recent studies also reported wide diversity for agronomic traits especially storage root d, number of secondary branches, shoot biomass, plant height, root length and root diameter ng 64 yam bean genotypes in the Brazilian Amazon (Silva & Ticona-Benavente, 2016), and rage root dry matter, number of roots per plant, total biomass and harvest index among 34 essions in West Africa (Zanklan et al., 2007).

e yield results demonstrated that the yam bean is well adapted to the two main root crop wing agro ecologies of Uganda namely, Namulonge and Serere. The mean yields (12.8 t ha^{-1}) d RDM (9.9 to 20.5%) recorded for the evaluated yam bean accessions compares closely well h conventional root crops such as cassava whose average yield in Uganda is estimated about 0 t.ha^{-1} to 16.8 t.ha^{-1} (Tumuhimbise et al., 2014). However, the average RDM of 15.3% in m beans was low compared to values in cassava but the mean values for Fe, Zn, K, and P were ber at 22.9 mg kg^{-1}, 12.4 mg kg^{-1}, 993 mg.100 g^{-1}, and 220 mg.100 g^{-1} respectively. Such Fe ntent in yam beans was higher compared to sweetpotato that contains 21.6 mg kg^{-1} of iron mwegamire et al., 2011).

yam bean yields achieved in this study are low compared to West Africa where on-farm have recorded average yields of 24 t ha^{-1} from two *P. erosus* accessions (CIP-209018 and 209019) in Benin (Adegbola et al., 2015; Grüneberg, 2016; Zanklan et al., 2007), 17 t ha^{-1} 10 *P. erosus* accessions in Senegal (Annerose & Diouf, 1998) and 14 t ha^{-1} from 15 *P.* accessions in Sierra Leone (Belford et al., 2001). Nevertheless, it should be noted that the African resuts are from one species, *Pachyrhizus. Erosus* whose yield compares favorably stance at 18.7 and 17.5 t ha^{-1} (Agaba et al., 2016).

eral authors have reported Fe contents similar or marginally higher than observed in this y in yam beans (Dini et al., 2013; Doporto et al., 2011; Grüneberg et al., 2003; Heider et al., . Santayana et al., 2014). However the Fe content with a maximum of 31.8 mg kg^{-1} in ssion 209049 (Table 3.5) was low considering that Kale (2006) reported Fe content of up to mg kg^{-1} in yam bean storage roots. Nevertheless, confirmation of high Fe levels in yam bean ge roots and Fe bioavailability merits further research considering the potential nutritional ct given the high levels of Fe deficiency in the world food supply (Pfeiffer and McClafferty, 7)). It was also observed that yam beans can be grown at diverse locations in Uganda, twice a compared to staple root crops especially cassava that allows only one crop per year.

etic variance (σ^2_G) was remarkably large with high heritability estimates for most traits pt HI, K and P implying that genetic improvement was possible with rapid response to tion in early progeny generations. The results showed that the current yam bean genotypes potential for improvement of RDM ($\sigma^2_G = 9.3\%^2$) without using the high dry matter chuin nts. This finding permits a new hypothesis that the high moisture content in a large portion yam bean germplasm could be a result of farm based recurrent selection during the estication and adoption of the crop in the native countries. Significant genetic variance for ($\sigma^2_G = 40.2\%^2$) was associated with high germplasm mean of 51.3% indicating that the yam can be used as a source of industrial starch. These results are in agreement with the findings Forsyth et al. (2002) who reported that the starch content of 56 - 58% in yam beans was ble for food applications that require low amylose content. It should be noted that the rved significant σ^2_G for Fe with a magnitude of 16.7 $mg^2\ kg^{-2}$, high heritability, and small

nces between GCV and PCV (Table 3.5), indicated that it was possible to obtain genetic for root Fe in yam bean. Conversely, genetic variance components for PRO, Zn, K and P not significant which indicated that there was limited room for genetic improvement of traits using the current yam bean germplasm.

Combining ability and gene action for root dry matter and associated traits in yam beans

study assessed F_1 and F_2 populations of yam beans to identify parents with good combining ies, estimate variance components and infer gene action controlling storage root dry matter ssociated traits as a basis for establishment of yam bean breeding programs in Uganda. The ts showed significant genotypic variability among the yam bean parents and progenies (both nd F_2) which suggested that the evaluated germplasm was suitable for improvement of yield related traits (RDM, RFY, RDY, and STA) through selection of elite progenies in early rations. The crosses were significantly different for all traits except VNY while general bining ability effects (GCA) and specific combining ability effects (SCA) were also ificant ($p<0.05$) for RDM, RFY, RDY HI, FBY, and STA and PRO indicating that booth A. and SCA effects were important in determination of progeny performance and that both itive and non-additive effects controlled inheritance of these traits. Significant SCA mean ares for RDM, RFY, HI, FBY and STA in F_2 suggested non-allelic interaction between the ents indicating that non-additive gene effects partly influenced the inheritance of these traits yam beans. However, the GCA means squares, variance estimates and GCA effects were ger than corresponding SCA estimates signifying preponderance of additive gene action. ers ratio further differentiated GCA as high for RDM, RFY, RDY, HI, FBY, STA and PRO F_1 and all the traits in F_2 confirming the predominance of additive gene action over non-itive gene effects which suggests that crosses involving high dry matter chuin cultivars would e elite progeny whose RDM values are close to or higher than the mid parent value. This gests that applying NCII mating design and subsequent selections among progenies would e worthwhile genetic gain for dry matter and related traits in early as well as in advanced erations of yam beans.

ults further showed significant and strong correlations ($r > 0.6$) between RDM and STA; nd RDY, VN, FBY; RDY and VNY, FBY, STA across F_1 and F_2 suggesting possibility of neous improvement of these traits. Strong positive correlation between RFY and VNY in F_2 was surprising given that there are reports of competition between the two agronomic a yam beans such that reproductive punning is recommended to enhance storage root yield et al., 2004; Rizky et al., 2013; Zanklan et al., 2007). These findings suggest that yam could be successfully grown minus the need for the labour intensive reproductive pruning ithout affecting the desired high root yields.

esponse to selection for RDM and associated traits in F_3 populations

enetic potential for response to selection of RDM and associated traits was investigated g the selected 83 F_3 yam bean families using the variance components analysis based on the Carolina II mating design (Table 5.2). The results showed highly significant ($p<0.001$) on between family groups (Table 5.3) associated with small differences between PCV and high additive variance and heritability estimates as well as percentage response to ion (R%) for all the traits except HI and PRO (Table 5.5). These results show that cation of hybridisation followed by selections among populations would improve these s and that there is potential for high genetic gains for RDM in yam bean breeding.

study presents the first set of results on response to selection and percentage response to ion in the yam bean gene pool. Response to selection (R) refers to the improvement of acters in genotypic value for the new population compared with the base population under cycle of selection at a given selection intensity (Wolie et al., 2013). The high percentage nse to selection (R%) observed in this study in a single cycle of selection in early erations of yam bean segregating populations suggested potential for implementation of a ding program based on the evaluated germplasm. The results clearly showed that to improve M and associated traits especially RDM, STA, RFY, FBY and RDY, effective selection could based on progeny performance in early segregating generations.

m by plant breeders often results in changes, not only in the trait for which selection is racticed, but in other traits through correlated response. The results of correlation analysis d highly significant correlations between RDM and RDY as well as STA but negative FY and PRO indicating that early generation selection for high dry matter content would elly affect storage root yields and protein content but significantly improve storage root ld and starch content of yam bean. However the significant association of RFY with VNY and FBY suggested that selection of progenies with high vine yields would ly improve RFY as well as RDY and that above ground biomass has considerable e effect on the storage root yields in yam bean.

ositive and significant correlations are essential for selection of superior genotypes that combine several desirable quantitative traits. The magnitude of correlation coefficients e: a measure of genetic association among quantitative traits which informs choice of ng strategy that would maximize genetic gains and quicken crop improvement. According lconer and Mackay (1996), the extent of correlated response is a function of the bilities of the correlated traits, as well as the genetic correlation between the traits. This that estimates of correlations between traits are reliable indicators of genetic potential for aneous improvement of traits. The current correlation coefficients showed strong and large n of common variation between traits indicating possibility for combined improvement might inform future selection procedures and breeding plans in yam beans.

CHAPTER SEVEN
CONCLUSIONS AND RECOMMENDATIONS

7.1. Conclusions

The results from this study established the presence of substantial and exploitable genetic variation that should permit genetic improvement for yield and quality traits among the yam bean germplasm in Uganda. The yam bean germplasm available in Uganda possess potential for breeding high dry matter yam beans by using low dry matter accessions due to the observed genetic variation among low dry matter yam beans without having access to the high dry matter *chuin* material. The high estimates of heritability, GCV and small differences between GCV and PCV values observed for yield traits indicated presence of high genetic variation and revealed high genetic determination of observed phenotypic variation. This study confirmed yam bean as a starchy root crop with elevated protein content and well adapted at the locations in Uganda where it was tested. Correlational analysis indicated the possibility of simultaneous selection and improvement of RFY, RDY, and FBY; RDM and STA; and RDY and FBY in yam beans.

The results from combining ability and inheritance studies revealed that both additive and non-additive gene effects contributed to the inheritance of RDM, RFY, RDY, STA, and FBY in F_1 and F_2 yam bean populations. The significant mean squares for crosses and GCA effects across F_1 and F_2 indicated these traits are mainly under additive gene effects and that genetic variability among parents was sufficient to permit improvement of these traits through selection. The Baker's ratio was above 0.5 for all traits except VNY which confirms the role of additive gene effects in the inheritance of these traits. The predominance of GCA over SCA variance suggested that stringent early generation selection would be effective to improve RDM and associated traits in the current yam bean germplasm. The predominance of additive gene effects in the inheritance of RDM, RFY, RDY, FBY and STA was associated with high variance estimates and narrow-sense heritability in F_1 and F_2 generations indicating substantial variation in the parent genotypes. GCA effects identified parent 209014 as the best combiner for improvement of both RDM and STA across F_1 and F_2 generations. While 209016 was a good combiner for RDM, RFY, RDY, FBY and STA in the F_2.

3. Future evaluations of the yam bean germplasm in Uganda should be done across several agro ecological locations, using a large number of accessions and replications as compared to the two locations used in this study.

4. Participatory evaluations of yam beans should be conducted with farmers, consumers and traders to determine adoption potential and possible constraints for the successful integration into farming systems in Uganda.

5. Whereas this study demonstrated wide genetic variation and additive genetic effects for storage root iron with potential for genetic gains in early breeding generations, more information is required on the bioavailability of root iron, and in root products to ascertain whether the yam bean consumers can nutritionally benefit by including it in their diets.

REFERENCES

Acquaah, G. (2007). *Principles of plant genetics and breeding* (1st ed.). Malden, MA, USA: Blackwell Publishing Ltd.

Acquaah, G. (2012). *Principles of plant genetics and breeding* (2nd ed.). Oxford: Wiley-Blackwell.

Adegbola, P. Y., Nestor, A. A., Houessionon, P., Alokpai, N., Hell, K., Thiele, G., . . . Mensah, G. A. (2015, August 9-14). *Socio-economic analysis of Pachyrhizus erosus cultivation in Benin: Profitability and cost function analysis.* Paper presented at the 29th International Conference of Agricultural Economists. Milan, Italy.

Agaba, R., Tukamuhabwa, P., Rubaihayo, P., Tumwegamire, S., Mwanga, R. O. M., Ssenyonjo, A., . . . Grüneberg, W. J. (2016). Genetic Variability for Yield and Nutritional Quality in Yam bean (*Pachyrhizus spp.*). *HortScience, 51*(9), 1079-1086. doi:10.21273/HORTSCI10686-16

Akinwale, M., Akinyele, B., Dixon, A., & Odiyi, A. (2010). Genetic variability among forty-three cassava genotypes in three agro-ecological zones of Nigeria. *Journal of Plant Breeding and Crop Science, 2*(5), 104-109.

Amongi, W., Nkalubo, S. T., Gibson, P., Edema, R., & Ochwo-Ssemakula, M. (2015). Genetics of drought tolerance in common bean genotypes adapted to Ugandan conditions. *Journal of Plant Breeding and Crop Science, 7*(1), 18-27.

Andiku, C. (2013). *Evaluation of yam bean (Pachyrhizus spp.) accessions for root yield and nutritional quality under different agro ecologies in Uganda* (Msc Diss), Makerere University, Kampala, Uganda.

Annerose, D., & Diouf, O. (1998). *Recherches sur l'adaptation de la culture de Pachyrhizus DC. en zones semi-arides. Pachyrhizus.* Paper presented at the 2. International Symposium on Tuberous Legumes. Celaya (Mexico). 5-8 Aug 1996.

Badillo, V., & Castellanos, J. (1996). *Fijación simbiotica de nitrógeno bajo condiciones de campo en Jícama (Pachyrhizus ahipa (Wedd.) Parodi y P. erosus (L.) Urban).* Paper presented at the Proceedings of 2nd International Symposium on Tuberous Legumes, Celaya, Mexico.

Belford, E. J., Karim, A. B., & Schröder, P. (2001). Exploration of the tuber production potential of yam bean (*Pachyrhizus erosus* (L.) Urban) under field conditions in Sierra Leone. *Journal of applied botany, 75*(1-2), 31-38.

Bergthaller, W., Kersting, H. J., Velasco, L., & Grüneberg, W. J. (2001, 8-12 July). *Andean yam bean (Pachyrhizus ahipa) tubers, a new source of legume starch.* Paper presented at the Proceedings of the 4th European Conference on Grain Legumes, Cracow, Poland.

Buckman, E. S., Plahar, W. A., Oduro, I. N., & Carey, E. E. (2015). Effects of sodium metabisulphite and blanching pretreatments on the quality characteristics of yam bean (*Pachyrhizus erosus*) flour.

Burton, G. W., & Devane, E. (1953). Estimating heritability in tall fescue (Festuca arundinacea) from replicated clonal material. *Agronomy Journal, 45*(10), 478-481.

Cao, M., Sleper, D., Arelli, P., Roberts, C., & Shyu, C. (2002). Classifier development of NIR (near infrared spectroscopy) derived data to predict SCN resistance. *Crop Science*, 207.

Castellanos, J., Zapata, F., Badillo, V., Peña-Cabriales, J., Jensen, E., & Heredia-García, E. (1997). Symbiotic nitrogen fixation and yield of *Pachyrhizus erosus* (L) urban cultivars and Pachyrhizus ahipa (WEDD) parodi landraces as affected by flower pruning. *Soil Biology and Biochemistry, 29*(5), 973-981.

Chandrababu, R. J., & Sharma, R. K. (1999). Heritability estimates in almond [Prunus dulcis (Miller) D.A. Webb]. Scientia. Horticulture, 79: 237-243. *Scientia Horticulture, 79*(3), 237-243.

Comstock, R., & Robinson, H. (1952). *Estimation of average dominance of genes*. Paper presented at the Heterosis, Ames, Iowa.

Comstock, R., & Robinson, H. (1952). *Genetic parameters, their estimation and significance.* Paper presented at the Proc. Sixth Int. Grosslands Conf.

de Mélo, E. A., Krieger, N., & Montenegro-Stamford, T. L. (1994). Physicochemical properties of Jacatupe (*Pachyrhizus erosus* L. Urban) starch. *Starch/Starke, 46*, 245-247.

Delêtre, M., Soengas, B., Utge, J., Lambourdière, J., & Sørensen, M. (2013). Microsatellite Markers for the Yam Bean Pachyrhizus (Fabaceae). *Applications in Plant Sciences, 1*(7).

Dini, C., Doporto, M. C., García, M. A., & Viña, S. Z. (2013). Nutritional profile and anti-nutrient analyses of Pachyrhizus ahipa roots from different accessions. *Food Research International, 54*(1), 255-261.

Doporto, M. C., Mugridge, A., García, M. A., & Viña, S. Z. (2011). Pachyrhizus ahipa (Wedd.) Parodi roots and flour: Biochemical and functional characteristics. *Food Chemistry, 126*(4), 1670-1678.

Døygaard, S., & Sorensen, M. (1998). *Principal component analysis of morphological characters in the genus Pachyrhizus DC.* Paper presented at the Proceedings of 2nd International Symposium on tuberous legumes: Celaya, Guanajuato, Mexico.

Estrella-Parra, E. A., Gómez-Verjan, J. C., Céspedes, C. L., Alarcón, J., Cano-Santana, Z., Reyes-García, A., . . . Reyes-Chilpa, R. (2016). Volatile organic compounds from Pachyrhizus ferrugineus and *Pachyrhizus erosus* (Fabaceae) leaves. *Boletín Latinoamericano y del Caribe de Plantas Medicinales y Aromáticas, 15*(3).

Falconer, D., & Mackay, T. (1996). Introduction to quantitative genetics., 4th edn (Longman Group Ltd: Essex, UK).

Forsyth, J. L., & Shewry, P. R. (2002). Characterization of the Major Proteins of Tubers of Yam Bean (Pachyrhizus ahipa). *Journal of agricultural and food chemistry, 50*(7), 1939-1944. doi:10.1021/jf011017j

Gatti, I., Lopez Anido, F., Cravero, V., Asprelli, P., & Cointry, E. (2005). Heritability and expected selection response for yield traits in blanched asparagus. *Genetics and Molecular Research, 4*(1), 67-73.

Gegios, A., Amthor, R., Maziya-Dixon, B., Egesi, C., Mallowa, S., Nungo, R., . . . Manary, M. J. (2010). Children Consuming Cassava as a Staple Food are at Risk for Inadequate Zinc, Iron, and Vitamin A Intake. *Plant Foods for Human Nutrition (Dordrecht, Netherlands), 65*(1), 64-70. doi:10.1007/s11130-010-0157-5

Grum, M. (1994). *Breeding of new yam bean (Pachyrhizus Rich. ex DC.). Cultivars in Tonga involving interspecific hybrids.* Paper presented at the First International Symposium on Tuber Legumes. 21-24 April 1992, Jordbrugsforlaget, Copenhagen, Denmark.

Grüneberg, W. J. (2016). *Enhancing the nutrient-rich yam bean (Pachyrhizus spp.) storage roots to improve food quality and availability and sustainability of farming systems in Central*

and West Africa. (International Potato Center Report No. 978-92-9060-474-7). Retrieved from https://goo.gl/ovVCNL on 2016-12-02

Grüneberg, W. J., Freynhagen-Leopold, P., & Delgado-Váquez, O. (2003). A new yam bean (Pachyrhizus spp.) interspecific hybrid. *Genetic resources and crop evolution, 50*(7), 757-766.

Grüneberg, W. J., Goffman, F. D., & Velasco, L. (1999). Characterization of yam bean (Pachyrhizus spp.) seeds as potential sources of high palmitic acid oil. *JAOCS, Journal of the American Oil Chemists' Society, 76*(11), 1309-1312.

Gupta, K., Talwar, G., Jain, V., Dhawan, K., & Jain, S. (2003). Salad crops root, bulb, and tuber crops. *Encyclopaedia of Food Science*, 5060-5073.

Habarurema, I., Asea, G., Lamo, J., Gibson, P., Edema, R., Séré, Y., & Onasanya, R. O. (2012). Genetic analysis of resistance to rice bacterial blight in Uganda *African Crop Science Journal, 20*(Supplement s1), 105-112.

Halafihi, M., Grum, M., Stölen, O., & Sørensen, M. (1994, April 21- 24). *Biological nitrogen fixation in Pachyrhizus Rich. ex DC.* Paper presented at the First International Symposium on Tuberous Legumes, Jordbrugsforlaget, Copenhagen, Denmark.

Hallauer, A. R., Carena, M. J., & Filho, J. B. M. (2010). Quantitative genetics in maize breeding. *Handbook of plant breeding, 6*, 81-167. doi:10.1007/978-1- 4419-0766-0

Hamdi, A., El-Ghareib, A., Shafey, S., & Ibrahim, M. (2003). Genetic variability, heritability and expected genetic advance for earliness and seed yield from selection in lentil. *EGYPTIAN JOURNAL OF AGRICULTURAL RESEARCH, 81*, 125-138.

Heider, B., Tumwegamire, S., Tukamuhabwa, P., Ndirigwe, J., Bouwe, G., Bararyenya, A., . . . Wassens, R. (2011). Nutritional improvement of yam bean and sustainability of farming systems in Central and West Africa. *Afr Crop Sci, 10*, 93-95.

Hill, J., Becker, H. C., & Tigerstedt, P. M. A. (1998). *Quantitative and Ecological Aspects of Plant Breeding*: Chapman and Hall.

Holland, J. B., Nyquist, W. E., & Cervantes-Martinez, C. T. (2003). Estimating and Interpreting Heritability for Plant Breeding. *Plant Breeding Reviews, 22*, 9-112.

Hosein, F. (2001). Isolation of high quality RNA from seeds and tubers of the Mexican yam bean (*Pachyrhizus erosus*). *Plant Molecular Biology Reporter, 19*(1), 65-65.

Ingham, J. L. (1990). Systematic aspects of phytoalexin formation within tribe Phaseoleae of the Leguminosae (subfamily Papilionoideae). *Biochemical Systematics and Ecology, 18*(5), 329-343.

Jacobsen, S.-E., Sørensen, M., Pedersen, S. M., & Weiner, J. (2015). Using our agrobiodiversity: plant-based solutions to feed the world. *Agronomy for Sustainable Development, 35*(4), 1217-1235.

Jamoza, J. E., Owuoche, J., Kiplagat, O., & Opile, W. (2014). Broad-sense heritability estimation and correlation among sugarcane (Saccharum spp . hybrids) yield and some agronomic traits in western Kenya. *International Journal of Agricultural Policy and Research, 2*(January), 16-25.

Jha, V., & Singh, B. (2014). Combining ability analysis for quantitative traits in yam bean [Pachyrhizuserosus (L.) Urb.]. *Annals of Agri Bio Research, 19*(2), 243-246.

Jines, M. P. (2007). *Enhancing genetic gain in maize with tropical germplasm, QTL mapping, and spatial methodologies*. (PhD), North Carolina State University Raleigh, NC. Retrieved from https://goo.gl/vEpdgF

Kale, P. R. (2006). *Studies on nutritional and processing properties of storage roots of different yam bean (Pachyrhizus spp.) and wild mung bean (Vigna vexillata) species*. (Ph.D Diss), Universitat Gottingen, CuvillierVerlag, Gottingen, Germany Klacek.

Karuniawan, A. (2004). *Cultivation Status and Genetic Diversity of Yam Bean (Pachyrhizus Erosus (L.) Urban) in Indonesia*: Cuvillier Verlag.

Karuniawan, A. (2005). Multivariate Analysis of Morphological Traits in yam bean (*Pachyrhizus erosus*). *Zuriat, 16*(1), 44-51.

Kawano, K. (2003). Thirty years of cassava breeding for productivity: biological and social factors for success. *Crop Science, 43*, 1325-1335.

Kearsey, M. J., & Pooni, H. S. (1996). *The genetical analysis of quantitative traits*. United Kingdom: Stanley Thornes (Publishers) Ltd.

Kiryowa, M., Tukamuhabwa, P., & Adipala, E. (2009). Genetic analysis of resistance to soybean rust disease *African Crop Science Journal, 16*(3), 211-217.

Kisambira, A. (2014). *Physicochemical characteristics of yam bean (Pachyrhizus spp) seed flour*. (Msc. Thesis), Makerere University, http://hdl.handle.net/10570/3254

Lackey, J. (1977). A revised classification of the tribe Phaseoleae (*Leguminosae: Papilionoideae*), and its relation to canavanine distribution. *Botanical Journal of the Linnean Society, 74*(2), 163-178.

Lebot, V. (2009). *Tropical Root and Tuber Crops: Cassava, Sweet Potato, Yams and Aroids* (Vol. 17). UK: CABI Publishing.

Leidi, E. O., Fernández, M., Sarmiento, R., Semedo, J., Marques, N., Matos, A. A., . . . Matos, M. C. (2004). Factors affecting root and seed yield in ahipa (*Pachyrhizus ahipa* (Wedd.) Parodi), a multipurpose legume crop. *European journal of agronomy, 20*(4), 395-403.

Leidi, E. O., Rodríguez-Navarro, D., Fernández, M., Sarmiento, R., Semedo, J., Marques, N., & Sørensen, M. (2004). Factors affecting root and seed yield in ahipa (*Pachyrhizus ahipa* (Wedd.) Parodi), a multipurpose legume crop. *European journal of agronomy, 20*(4), 395-403.

Leidi, E. O., Sarmiento, R., & Rodríguez-Navarro, D. N. (2003). Ahipa (*Pachyrhizus ahipa* [Wedd.] Parodi): an alternative legume crop for sustainable production of starch, oil and protein. *Industrial Crops and Products, 17*(1), 27-37. doi:http://dx.doi.org/10.1016/S0926-6690(02)00056-0

Ma-Teresa, L., Gerpcio-Sta, C., & Enrique, C. (1994). Heritability estimates of some root characters in sweetpotato. *Philipp Journal of Crop Science, 19*, 27-32.

Majidi, M. M., Mirlohi, A., & Amini, F. (2009). Genetic variation, heritability and correlations of agro-morphological traits in tall fescue (*Festuca arundinacea* Schreb.). *Euphytica, 167*(3), 323-331.

Matos, M. C., Matos, A. A., & Vieira da Silva, J. B. (1998). *Effect of manual and chemical pruning on tuber production of Pachyrhizus ahipa (Wedd.) Parodi).* Paper presented at the Second International Symposium on Tuberous Legumes, Mexico.

Mishra, P. K., Ram, R. B., & Kumar, N. (2015). Genetic variability, heritability, and genetic advance in strawberry (*Fragaria* × *Ananassa* Duch.). *Turkish Journal of Agriculture and Forestry, 39*(3), 451-458.

Mora, A., Morera, J., & Sorensen, M. (2014). Yield performance of Yam Bean (*Pachyrhizus erosus* (L.) Urban) as a result of different planting distances.

Mtunda, K. J. (2009). *Breeding , Evaluation and Selection of Cassava for High Starch Content and Yield in Tanzania.* (PhD PhD), University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Nalugo, R., Wambi, W., Sebbuliba, J., Okello, D., & Puppala, N. (2016). Gene effects for resistance to groundnut rossette disease in exotic Valencia groundnuts. *African Crop Science Journal, 24*(1), 89-95.

Nduwumuremyi, A., Tongoona, P., Habimana, S., & Husbandry, A. (2013). Mating designs: Helpful tool for quantitative plant breeding analysis. *Journal of Plant Breeding and Genetics, 01*(03), 117-129.

Nielsen, P. E., Sørensen, M., & Halafihi, M. (2000). Yield potential of Yam Bean [*Pachyrhizus erosus* (L.) Urban] accessions in the Kingdom of Tonga, South Pacific. *Tropical agriculture, 77*(3), 174-179.

Noman, A., Hoque, M., Haque, M., Pervin, F., & Karim, M. (2007). Nutritional and anti-nutritional components in *Pachyrhizus erosus* L. tuber. *Food Chemistry, 102*(4), 1112-1118.

Ntawuruhunga, P., & Dixon, A. G. O. (2010). Quantitative variation and interrelationship between factors influencing cassava yield. *Journal of Applied Biosciences, 26*, 1594 - 1602.

Nyquist, W. E. (1991). Estimation of heritability and prediction of selec- tion response in plant populations. *Critical Reviews in Plant Sciences, 10*, 235–322.

Oré Balbin, I., Sørensen, M., Kvist, L. P., & Delgado Vasquez, O. (2007). Review of the Pachyrhizus tuberosus (Lam.) Spreng. cultivar groups in Peru. *Plant Genetic Resouces Newsletter, 151*(3), 2-13.

Ørting, B., Grüneberg, W. J., & Sørensen, M. (1996). Ahipa (*Pachyrhizus ahipa* (Wedd.) Parodi) in Bolivia. *Genetic resources and crop evolution, 43*(5), 435-446.

Ozaki, Y., McClure, W. F., & Christy, A. A. (2007). *Near-infrared spectroscopy in food science and technology*: John Wiley & Sons.

Padonou, S., Hounyèvou, A., Ahounou, J., Houssou, A., Fandohan, P., Aïhou, K., . . . Koudande, D. (2013). Yam bean (*Pachyrhizus erosus*) tuber processing in Benin: production and evaluation of the quality of yam bean-gari and yam bean-fortified gari. *International*

Journal of Biological and Chemical Sciences, 7(1), 247-259. doi:http://dx.doi.org/10.4314/ijbcs.v7i1i.21

Park, C. J., & Han, J.-S. (2015). Hypoglycemic Effect of Jicama (*Pachyrhizus erosus*) Extract on Streptozotocin-Induced Diabetic Mice. *Preventive Nutrition and Food Science, 20*(2), 88-93. doi:10.3746/pnf.2015.20.2.88

Park, C. J., Lee, H.-A., & Han, J.-S. (2015). Jicama (*Pachyrhizus erosus*) extract increases insulin sensitivity and regulates hepatic glucose in C57BL/Ksj-db/db mice. *Journal of Clinical Biochemistry and Nutrition, 58*(1), 56.

Payne, R. W., Harding, S. A., Murray, D. A., Soutar, D. M., Baird, D. B., & Glaser, A. I. (2011). *The guide to Genstat release 14, Part 2: Statistics*. Hemel Hempstead, Hertfordshire HP1 1ES, UK: VSN International.

Peiris, K. H. S., Dull, G. G., Leffler, R. G., & Kays, S. J. (1999). Spatial variability of soluble solids or dry-matter content within individual fruits, bulbs, or tubers: Implications for the development and use of NIR spectrometric techniques. *HortScience, 34*(1), 114-118.

Pfeiffer, W. H., & McClafferty, B. (2007). Biofortification: breeding micronutrient-dense crops. In M. Kang & P. Priyadarshan (Eds.), *Breeding major food staples* (pp. 61-91). Ames: Blackwell Publishing.

Primiani, C. N. (2015). The Phytoestrogenic Potential of Yam Bean (*Pachyrhizus erosus*) on Ovarian and Uterine Tissue Structure of Premenopausal Mice. *Biology, Medicine, & Natural Product Chemistry, 4*(1).

Ramos-de-la-Peña, A. M., Renard, C. M., Wicker, L., & Contreras-Esquivel, J. C. (2013). Advances and perspectives of *Pachyrhizus spp.* in food science and biotechnology. *Trends in Food Science & Technology, 29*(1), 44-54.

Ramos-de-la-Peña, A. M., Renard, C. M., Wicker, L., Montañez, J., de la Luz Reyes-Vega, M., & Contreras-Esquivel, J. C. (2012). Optimization of the liquefaction and saccharification of structural polysaccharides of jicama (*Pachyrhizus erosus* L.) tissue by enzymatic pulping. *LWT-Food Science and Technology, 46*(1), 232-238.

Ratanadilok, M., Suriyawan, K., & Thanaisawanrayangkura, S. (1996). *Yam Bean (Pachyrhizus erosus (L.) Urban) and its economic potential* Paper presented at the Second International Symposium on Tuberous Legume, Celaya-Mexico

Ratanadilok, N., Suriyawan, K., & Thanaisawanrayangkura, S. (1998). *Yam bean (Pachyrhizus erosus (L.) Urban) and its economic potential.* Paper presented at the 2. International Symposium on Tuberous Legumes, Celaya (Mexico), 5-8 Aug 1996.

Raymond, C. A. (2002). Genetics of Eucalyptus wood properties. *Annals of Forestry Sciences, 59*, 525-531.

Reddy, P. P. (2015). Yam Bean, *Pachyrhizus erosus Plant Protection in Tropical Root and Tuber Crops* (pp. 267-279): Springer.

Rizky, W. H., Hasani, S., & Karuniawan, A. (2013). Tuber yield and quality of nine genotypes Yam Bean (Pachyrhizus spp.) due to sink-reproductive pruning. *Horticulture, 62*, 445-448.

Rodríguez-Navarro, D. N., Camacho, M., Temprano, F., Santamaria, C., & Leidi, E. O. (2009). Assessment of nitrogen fixation potential in ahipa (Pachyrhizus ahipa) and its effect on root and seed yield. *Experimental Agriculture, 45*(02), 177-188.

Roychowdhury, R., Datta, S., Gupta, P., & Jagatpati, T. (2012). Analysis of genetic parameters on mutant populations of mungbean (Vigna radiata L.) after ethyl methane sulphonate treatment. *Notulae Scientia Biologicae, 4*(1), 137.

Sánchez, T., Ceballos, H., Dufour, D., Ortiz, D., Morante, N., Calle, F., . . . Davrieux, F. (2014). Prediction of carotenoids, cyanide and dry matter contents in fresh cassava root using NIRS and Hunter color techniques. *Food Chemistry, 151*, 444–451.

Santayana, M., Rossel, G., Núñez, J., Sørensen, M., Delêtre, M., Robles, R., . . . Heider, B. (2014). Molecular characterization of cultivated species of the genus Pachyrhizus Rich. ex DC. by AFLP markers: calling for more data. *Tropical Plant Biology, 7*(3-4), 121-132.

Silva, E. S. d., & Ticona-Benavente, C. A. (2016). Diversity of yam bean (Pachyrhizus spp. Fabaceae) based on morphoagronomic traits in the Brazilian Amazon. *Acta Amazonica, 46*(3), 233-240.

Silva, I. d. C., Cuchiara, C., Winhelmann, M., Bianchi, V., Braga, E., Dutra, L., & Peters, J. (2016). In vitro multiplication of pear tree cultivar Cascatense. *Semina: Ciências Agrárias (Londrina), 37*(2), 581-593.

Singh, R., & Chaudhary, B. (1985). *Biometrical Methods in Quantitative Genetic Analysis*. New Delhi: Kalayani Publishers.

Sorensen, M. (1990). *Observations on distribution, ecology and cultivation of the tuber-bearing legume genus Pachyrhizus Rich. ex DC (Fabaceae: Phaseoleae).* (Vol. 90). Agric Univ Wageningen Pap 90–3:1–38.

Sørensen, M. (1988). A taxonomic revision of the genus Pachyrhizus (Fabaceae-Phaseoleae). *Nordic Journal of Botany, 8*(2), 167-192.

Sørensen, M. (1996). *Yam Bean: Pachyrhizus DC.-Promoting the conservation and use of underutilized and neglected crops. 2* (Vol. 2): Bioversity International.

Sorensen, M., Døygaard, S., Estrella, J. E., Kvist, L. P., & Nielsen, P. E. (1997). Status of the South American tuberous legume Pachyrhizus tuberosus (Lam.) Spreng. . *Biodiversity & Conservation, 6*(12), 1581-1625.

Sorensen, M., Grum, M., Paull, R., Vaillant, V., Venthou-Dumaine, A., & Zinsou, C. (1993). Yam bean (Pachyrhizus species): London: Chapman & Hall.

Tapia, C., & Sørensen, M. (2003). Morphological characterization of the genetic variation existing in a Neotropical collection of yam bean, Pachyrhizus tuberosus (Lam.) Spreng. *Genetic resources and crop evolution, 50*(7), 681-692.

Tapia, C., & Sørensen, M. (2003). *Morphological characterization of the genetic variation existing in a Neotropical collection of yam bean, Pachyrhizus tuberosus (Lam.) Spreng.*

Teye, E., Asare, A., Amoah, R., & Tetteh, J. (2011). Determination of the dry matter content of cassava (Manihot esculenta, Crantz) tubers using specific gravity method. *Journal of Agricultural and Biological Science, 6*(4), 23-28.

Tumuhimbise, R., Melis, R., Shanahan, P., & Kawuki, R. (2014). Genotype ×environment interaction effects on early fresh storage root yield and related traits in cassava. *The Crop Journal, 2*(5), 329-337.

Tumwegamire, S., Kapinga, R., Rubaihayo, P. R., LaBonte, D. R., Grüneberg, W. J., Burgos, G., . . . Mwanga, R. O. (2011). Evaluation of Dry Matter, Protein, Starch, Sucrose, β-carotene, Iron, Zinc, Calcium, and Magnesium in East African Sweetpotato [Ipomoea batatas (L.) Lam] Germplasm. *HortScience, 46*(3), 348-357.

Tumwegamire, S., Rubaihayo, P., LaBonte, D., Diaz, F., Kapinga, R., Mwanga, R., & Grüneberg, W. (2011). Genetic diversity in white-and orange-fleshed sweetpotato farmer

varieties from East Africa evaluated by simple sequence repeat markers. *Crop Science, 51*(3), 1132-1142.

Utz, H. (1997). PLABSTAT: a computer program for the computation of variances and covariances. *Universität Hohenheim, Germany.*

Velasco, L., & Grüneberg, W. J. (1999). Analysis of dry matter and protein contents in fresh yam bean tubers by near-infrared reflectance spectroscopy. *Communications in Soil Science & Plant Analysis, 30*(13-14), 1797-1805.

Wassens, R. (2011). *Assessment of the suitability of yam bean for the production of gari.* Wageningen University, The Netherlands, M.Sc. Thesis, The Netherlands.

Wilken, M. F., Erickson, G. E., Benton, J. R., Buckner, C. D., Klopfenstein, T. J., Karges, K., & Gibson, M. (2008). Evaluation of Methods for Dry Matter Determination of Ethanol Byproducts. *Nebraska Beef Cattle Reports*, 49.

Wolie, A., Dessalegn, T., & Belete, K. (2013). Heritability, variance components and genetic advance of some yield and yield related traits in Ethiopian collections of finger millet (Eleusine coracana (L.) Gaertn.) genotypes. *African Journal of Biotechnology, 12*(36), 5529.

Won, J. G., & Yoshida, T. (2000). Combining abilty in the rice lines selected for direct seeding in flooded paddy field. *Plant Production Science, 4*, 366-371.

Xu, S. (2003). Advanced statistical methods for estimating genetic variances in plants. *Plant Breeding Reviews, 22*, 113-163.

Yang, R. C. (2009). When Is Early Generation Selection Effective in Self-Pollinated Crops? *Crop Science, 49*(6), 2065-2070.

Zanklan, A. S. (2003). *Agronomic performance and genetic diversity of the root crop yam bean (Pachyrhizus spp.) under West African conditions.* Georg-August University Göttingen Germany.

Zanklan, A. S., Ahouangonou, S., Becker, H. C., Pawelzik, E., & Grüneberg, W. J. (2007). Evaluation of the Storage Root-Forming Legume Yam Bean (spp.) under West African Conditions. *Crop Science, 47*(5), 1934-1946.

Zaragoza Ramos-Castellanos, J., Acosta-Gallegos, J. A., Rodriguez Orozco, N., & Muñoz Ramos, J. J. (2009). Biological nitrogen fixation and tuber yield of yam bean in central Mexico. *Agricultura Técnica en México, 35*(3), 277-283.