Breeding and evaluation of cassava for high storage root yield and early bulking in Uganda

By

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Thesis abstract

Cassava (*Manihot esculenta* Crantz), is the world's most widely grown starch storage root crop. It is a principal food staple in sub-Saharan Africa where it accounts for approximately one-third of the total production of staple food crops. It plays a key role as a food security and an income-generating crop for millions of smallholder farmers. In Uganda, cassava ranks second to bananas (*Musa* spp.) in terms of area occupied, total production and per capita consumption; however, nearly 5% of the total population experiences hunger with the prevalence of food energy deficiency at the country level standing at 48%. Cassava is a crop with high potential to alleviate food shortages and energy deficiencies, owing to its unique advantages of producing acceptable yields and starch on infertile soils amidst erratic rainfall, when most other crops would fail. Hoewever, its yield potential has not been fully realised since most of the cassava cultivars grown are susceptible to pests and diseases, low yielding and late bulking. The main objective of the research was to develop high yielding, early bulking cassava genotypes that combine resistance to cassava brown streak disease (CBSD) and cassava mosaic disease (CMD) with farmer preferred traits for cultivation in Uganda. The specific objectives were to: (i) evaluate farmers' attitudes to and/or perceptions of cassava early bulking, production constraints and cultivar preferences; (ii) determine the extent of genetic variability in storage root bulking and other important traits of selected cassava genotypes; (iii) assess the effects of genotype x environment interaction on early bulking and related traits of selected cassava genotypes; (iv) develop and evaluate cassava F_1 families for early bulking in terms of the attainment of early, high fresh storage root yield (FSRY) and resistance to CBSD and CMD; and (v) determine the combining ability and gene action controlling early bulking and yield-related traits, as well as resistance to CBSD and CMD. Through the farmer participatory survey, a number of cassava production constraints were identified, key of which were: diseases, especially CBSD and CMD; lack of early bulking cultivars; rodents and insect pests. Farmers rated early bulking as the second most important preferred trait after FSRY, but suggested that early bulking should be complemented with high dry mass content (DMC), sweetness, high FSRY and resistance to pests and diseases. The analysis of variance of 12 cassava genotypes selected for evaluation in three diverse locations and at five different harvest times indicated significant variation among genotypes, harvest times, locations and their interactions for FSRY and most of the other traits evaluated. Fresh storage root yield and the other traits evaluated were predominantly under the control of genetic variation, indicating that genetic advance would be achieved through

hybridisation of the test genotypes. Additive main effects and multiplicative interaction (AMMI) analysis of the data collected at nine months after planting (MAP) indicated a non-significant GEI for early FSRY, but significant GEI for other traits assessed. Eight of the 12 genotypes analysed had relatively low interaction with locations for early FSRY, signifying that these genotypes were relatively stable for early FSRY. Thirty-six F_1 families were generated from a 9 x 9 diallel and exhibited a high degree of variation between and within families for all the traits assessed at the seedling evaluation stage. Diallel analysis at the seedling evaluation stage at 10 MAP indicated that additive gene effects were predominant in the expression of early FSRY and most of the other traits analysed. At the clonal evaluation stage, the 36 families were assessed for early FSRY at 8 MAP and this trait together with most of the other traits assessed were found to be predominantly under the control of non-additive gene effects. High mid- and better-parent heterosis for early FSRY was recorded in most families at the clonal evaluation stage with NASE3 x Nyara, Nyara x B11 and NASE3 x B11 recording the highest. Selection from the 36 families at the clonal evaluation stage based on farmers' top two preferred traits, viz. early bulking for FSRY and DMC, plus resistance to CBSD and CMD identified 50 genotypes that had early FSRY of ≥25 t ha^{-1} at 8 MAP compared to the best parent, CT1 that had 15.9 t ha^{-1} at 8 MAP. The selected genotypes also had high DMC and dual resistance to CMD and CBSD. Advancement of the selected genotypes should go a long way towards increasing cassava yield per unit time, reducing food shortages and increasing the income of smallholder farmers in Uganda.

Declaration

I, ROBOONI TUMUHIMBISE declare that:

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

Robooni Tumuhimbise (Candidate)

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

Signed

…….. Date……

Prof. Rob Melis (Principal supervisor)

Signed

…….. Date……

Dr. Paul Shanahan (Co-supervisor)

Dedication

To the Almighty God who has seen me through this training and to my late dad Mr. Semu Rwandekyezi, my mamma Mrs Constance Rwandekyezi and other family members who have always stood by me all through my academic journey!

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May God Bless You Splendidly!

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Introduction to the thesis

1 Cassava production and importance worldwide

Cassava (*Manihot esculenta* Crantz), a native to South America (Allem, 2002), is an important storage root crop worldwide (Ceballos et al., 2004; El-Sharkawy, 2012). It is a key component of the diet of over 800 million people across several continents (El-Sharkawy, 2012). The crop is a high starch producer with levels of up to 90% of its total storage root dry mass (Jansson et al., 2009), and about 70 million people derive more than 500 kcal day^{-1} from consuming cassava storage roots (Kawano, 2003; Burns et al., 2011). It is currently the world's fourth most important staple and carbohydrate rich food crop (El-Sharkawy, 2012), with a worldwide production estimated at 257 million tonnes (MT), of which about 146 MT come from Africa (FAO, 2012).

Cassava has numerous agronomic traits that confer comparative advantages in adverse environments where farmers often lack the resources to improve the income-generating capacity of their land through purchased inputs. It is a hardy crop as it tolerates infertile soils, periodic and extended droughts, and biotic stresses (Calle et al., 2005; El-Sharkawy, 2007). The crop is highly suited to intercropping with many types of crops and its time of harvest is flexible. It has a wide variety of food, feed and industrial uses (Westby, 2002; Tonukari, 2004; Jansson et al., 2009). These attributes make cassava a significant crop in food production and income generation, in particular benefitting the poor in the tropical regions of the world (Henry and Hershey, 2002). Due to its tolerance to poor soils and harsh climatic conditions, cassava is generally cultivated by smallholder farmers as a subsistence crop in a diverse range of agricultural and food systems (Alves, 2002). It is often classified as a classical food security crop as its storage roots may be harvested as and when needed (DeVries and Toenniessen, 2001).

Every part of a cassava plant can be utilised, but its starchy storage roots are by far the most commonly used part (Ceballos et al., 2004; Ojulong et al., 2007). The storage roots are a rich source of carbohydrates (Westby, 2002; Baguma, 2004; Jansson et al., 2009; El-Sharkawy, 2012) mostly present as starch (31% of fresh mass), with smaller amounts of free sugars (less than 1% of fresh mass). Storage roots also have a high content of dietary fibre, magnesium, sodium, riboflavin, thiamine, nicotinic acid and citrate (Bradbury and Holloway, 1988). They are low in protein (0.53%), although levels as high as 1.5% have been reported

(Westby, 2002). Cassava leaves are often used as a vegetable in Africa and are a cheap source of proteins, vitamins A, B and C, and other minerals (Fregene et al., 2000; IITA, 2001 Benesi, 2005).

2 Cassava production in Uganda

Cassava was introduced to the people living around Lake Victoria in Uganda by Arab traders in 1862 (Langlands, 1972). By the 1920s the crop had spread rapidly to most parts of the country (Langlands, 1966; 1972). This rapid spread was seemingly due to cassava's ability to grow and produce high yields where most other crops would fail and its flexibility in the cropping and food systems, as well as in harvesting dates (Jameson, 1964).

Although cassava was originally introduced as a mere food security crop, it is currently a key staple food crop in Uganda, ranking second to bananas in terms of area occupied, total production and per capita consumption (Ssemakula et al., 2004; UBOS, 2008; FAO, 2012). Current production of cassava in the country is estimated at 4.9 MT, which accounts for about 3.4% of Africa's total cassava production and 1.9% of total cassava production worldwide (FAO, 2012).

It plays a significant role in the diet of Ugandans and contributes a substantial proportion of the calorie requirements of the population (COSCA, 1996; Balyejusa-Kizito, 2006) accounting for approximately 11% of the total national calorie intake with its per capita consumption estimated at 132 kg person^{-1} year^{-1} (FAO, 2009). About 75% of farmers grow cassava for home consumption and about 25% grow it for cash and other uses. Local beer, animal feed, and the use of brewing waste as a cementing agent in local building are other uses of cassava (Otim-Nape and Zziwa, 1990).

Cassava is responsible for increased food security in most parts of Uganda. In the millet-cotton farming areas covering west Nile, north, east and north-eastern Uganda, cassava is used on its own or as an additive to either millet or sorghum flour to make local bread. In the banana-coffee farming areas covering south and south-western Uganda, cassava is mainly cultivated for fresh storage root consumption (MAAIF, 2007).

3 Production trends for cassava in Uganda from 2000 - 2012

There has generally been a steady increase in the area under cassava production in Uganda over the 2000 - 2012 period (Figure 1). However, total production and yield per unit area of cassava has generally shown a slight decline (FAO, 2012). Over these 12 years, yield and

production peaked in 2005 and declined thereafter largely due to the emergence of cassava brown streak disease (CBSD) in 2004 (Alicai et al., 2007; Ntawuruhunga and Legg, 2007). Due to the increasing demand for cassava as a basic food crop and source of income for smallholder farmers, as well as for its future potential as an industrial crop, research interventions involving farmers are urgently needed to improve cassava cultivars so as to reverse this declining trend in the country.

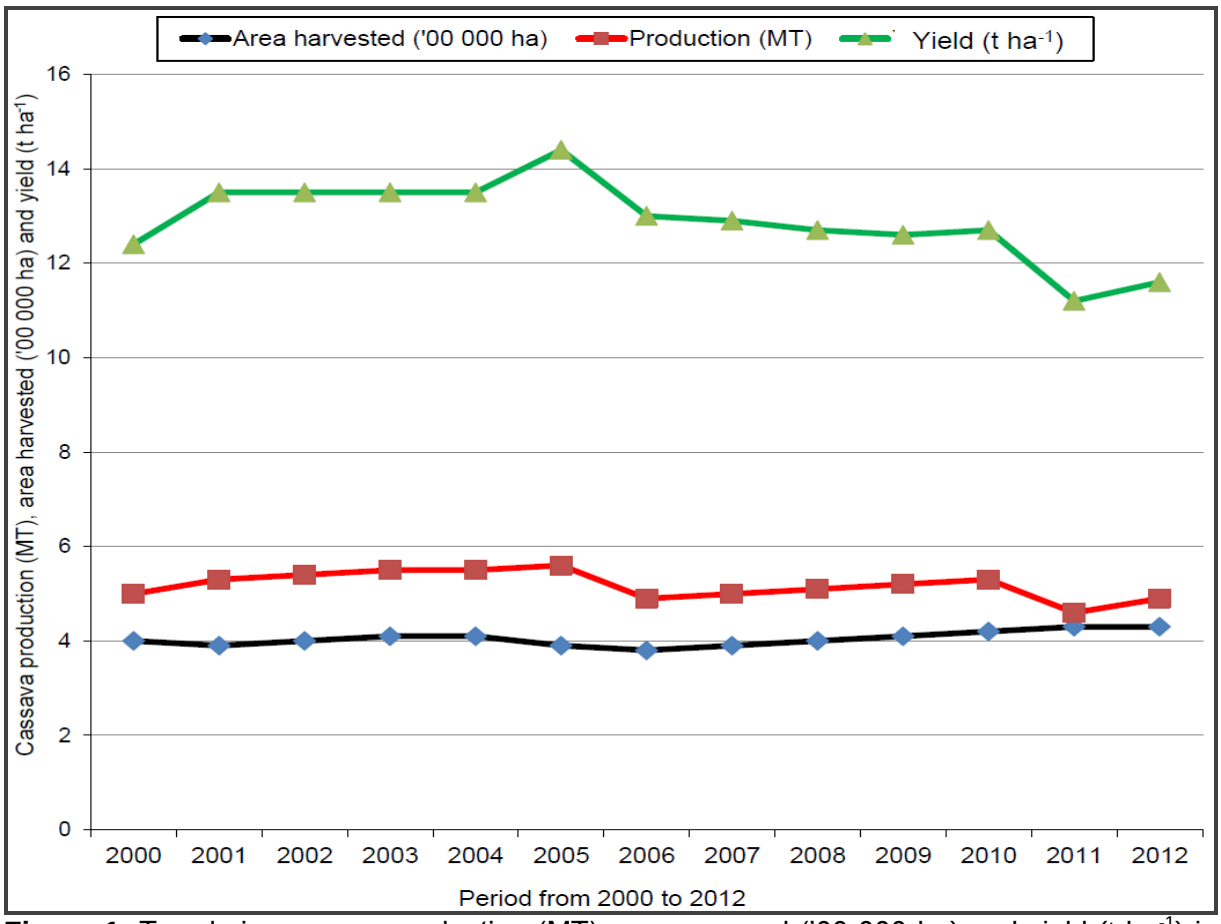

Figure 1: Trends in cassava production (MT), area covered ('00 000 ha) and yield (t ha^{-1}) in Uganda from 2000 to 2012 (FAO, 2012).

4 Cassava production constraints in Uganda

Despite the growing importance of cassava as a food security and income generating crop for smallholder farmers in Uganda, as well as for its potential to contribute to national economic development, its production is retarded by a wide range of factors. These include: the use of inferior and low yielding cultivars, lack of improved early bulking cultivars (Ntawuruhunga et al., 2006), declining soil fertility, erratic droughts, lack of credit facilities and farm inputs, postharvest physiological deterioration, and pests and diseases (Ssemakula et al., 2004; Alicai et al., 2007; Legg et al., 2011).

5 Cassava breeding and research in Uganda

Plant breeding has one of the highest rates of return among the investments in agricultural research (Ceballos et al., 2004). Cassava production in Uganda has to some extent benefited from technological inputs through breeding (Jameson, 1964; Kawuki et al., 2011). Cassava breeding and research in Uganda dates back to the 1930s, when cassava mosaic disease (CMD) broke out in eastern Uganda (Jameson, 1964; Langlands, 1972). In response, cassava germplasm was introduced from Amani Research Station in Tanzania into Uganda. The germplasm was evaluated and proved resistant, and subsequently several selections were made and released, known as the Bukalasa series of which Bukalasa8 and Bukalasa11 were the best (Ocitti p'Obwoya and Otim-Nape, 1986; Otim-Nape, 1988).

In the early 1980s, CMD again became a serious problem in most parts of Uganda, particularly in the eastern region, which led to the introduction of additional CMD resistant cultivars from Amani (Otim-Nape, 1993). Germplasm of the Tropical *Manihot* Series (TMS), from the International Institute of Tropical Agricultural (IITA) Nigeria, were introduced into Uganda in 1989 (Otim-Nape, 1993). In 1994, the best genotypes from the series, TMS60142, TMS 30337, TMS30572, were released officially to the farmers under the names of NASE1, NASE2 and NASE3, respectively (Otim-Nape et al., 2001; Abele et al., 2007). Thereafter, several other cultivars have been released to farmers.

6 Need for high yielding, early bulking cassava cultivars in Uganda

Despite the scientific success stories of the Green Revolution that took place in the 20th century, millions of people in Uganda still go to bed hungry and little has changed in the lives of subsistence farmers (WFP, 2013). Uganda, which is 236 040 km^2 in extent, is among the most overpopulated countries in Africa, with an estimated population of 34 million people (UBOS, 2012). Nearly 5% of the total population experiences hunger with the prevalence of food energy deficiency at the country level standing at 48% (WFP, 2013). Cassava is a crop with high potential to alleviate food shortages, owing to its unique advantages of producing acceptable yields and starch on infertile soils amidst erratic rainfall, when most other crops would fail. However, most of the cassava cultivars currently grown in Uganda are low yielding and late bulking, with the majority of them being harvested 12 to 14 MAP (Abele et al., 2007; Tumuhimbise et al., 2012). Late bulking cultivars occupy land for extended periods of time and consequently the land cannot be effectively utilised for the sequential cultivation of other crops. Moreover, studies have revealed that late bulking is the single most important factor responsible for the rejection and abandonment of cassava cultivars in African countries

(Okechukwu and Dixon, 2009; Kamau, et al., 2011) with Uganda being no exception. In addition, one of the key strategies to improve the efficiency of cassava production in terms of storage root yield per unit time is by shortening its growth period through breeding and identification of early bulking cultivars (Wholey and Cock, 1974).

Early bulking is currently considered a key requirement in order for cassava to make the transition from being a traditional crop to an industrial one (Okogbenin and Fregene, 2002). It is also important in situations where there is mounting pressure on agricultural land forcing farmers to intensify production, and in semi-arid regions where early bulking cultivars can be harvested after only one cycle of rain. More important is that earliness enables escape from late season droughts, pests and diseases, and is especially perceived as a key control strategy for CBSD, which is currently epidemic in east, central and southern Africa (Legg et al., 2011). Therefore, to better harness the potential of cassava in the face of changing climatic conditions, there is a need to develop, evaluate and select early bulking cultivars that can be harvested at 7 - 9 MAP. This should go a long way towards increasing cassava yield per unit time, reducing food shortages, increasing the income of smallholder farmers in Uganda, and also relieving the Ugandan economy from the burden of importing relief food. Moreover, with the demands of an expanding market for cassava as a source of food, income and industrial raw material, there is a need for cultivars that are early bulking and have desirable storage root qualities. Until now this remains a challenge in Uganda.

7 Research objectives

The main objective of the research was to develop high yielding, early bulking cassava genotypes that combine resistance to CBSD and CMD with farmer preferred traits for cultivation in Uganda.

The specific objectives of the research were to:

1. Evaluate farmers' attitudes to and/or perceptions of cassava early bulking;
2. Identify cassava production constraints and cultivar preferences of the farmers;
3. Determine the extent of genetic variability in storage root bulking and other important traits of selected cassava genotypes in Uganda;
4. Assess the effects of genotype x environment interaction on early bulking and related traits of selected cassava genotypes in Uganda;
5. Develop and evaluate cassava F_1 families for high storage yield, early bulking and resistance to CBSD and CMD; and

6. Determine the combining ability and gene action controlling early bulking and yield-related traits, as well as resistance to CMD and CBSD.

8 Thesis structure

The thesis has seven chapters arranged chronologically from one to seven.

Chapter 1: Literature review.

Chapter 2: An appraisal of farmers' attitudes to and/or perceptions of cassava early bulking, production constraints and cultivar preferences in Uganda.

Chapter 3: Genetic variability in storage root bulking and other important traits of selected cassava genotypes in Uganda.

Chapter 4: Genotype x environment interaction effects on early bulking and related of selected cassava genotypes in Uganda.

Chapter 5: Diallel analysis for early storage root yield and related traits at the F_1 seedling evaluation stage.

Chapter 6: Diallel analysis for early storage root yield and related traits at the F_1 clonal evaluation stage.

Chapter 7: General overview

Chapters 2 to 6 are written as discrete publication-ready papers and consequently there will be some overlap of content and references[1].

[1] Referencing format in this thesis is for American Crop Science Journal (with some modifications)

References

Abele, S., E. Twine, P. Ntawuruhunga, Y. Baguma, C. Kanobe, and A. Bua. 2007. Development and dissemination of improved cassava varieties in Uganda: Analysis of adoption rates, variety attributes and speed of adoption. In: Proceedings of Second International Conference of African Association of Agricultural Economists, Accra, Ghana. August 2007. p. 479-482.

Alicai, T., C.A. Omongo, M.N. Maruthi, R.J. Hillocks, Y. Baguma, R. Kawuki, A. Bua, G.W. Otim-Nape, and J. Colvin. 2007. Re-emergence of cassava brown streak disease in Uganda. Plant Diseases 91:24-29.

Allem, A.C. 2002.The origins and taxonomy of cassava. In: R.J. Hillocks, et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p.1-16.

Alves, A.A.C. 2002. Cassava botany and physiology. In: R.J. Hillocks et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 67-89.

Baguma, Y. 2004. Regulation of starch synthesis in cassava. PhD thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Balyejusa-Kizito, E. 2006. Genetic and root growth studies in cassava (*Manihot esculenta* Crantz): Implications for breeding. PhD. thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Benesi, I.R.M. 2005. Characterization of Malawian cassava germplasm for diversity, starch extraction and its native and modified properties. PhD thesis, University of the Free State, Bloemfontein, South Africa.

Bradbury, J.H., and W.D. Holloway. 1988. Chemistry of tropical root crops: significance for nutrition and agriculture in the pacific. ACIAR Monograph No. 6, Australian Centre for International Agricultural Research, Canberra.

Burns, A., R. Gleadow, J. Cliff, A. Zacarias, and T. Cavagnaro. 2011. Cassava, the drought, war and famine crop in a changing world. Sustainability 2:3572-3607.

Calle, F., J.C. Perez, W. Gait´an, N. Morante, H. Ceballos, G. Llano, and E. Alvarez. 2005. Diallel inheritance of relevant traits in cassava (*Manihot esculenta* Crantz) adapted to acid-soil savannahs. Euphytica 144:177-186.

Ceballos, H., C.A. Iglesias, J.C. Pérez, and A.G.O. Dixon. 2004. Cassava breeding: opportunities and challenges. Plant Molecular Biology 56:503-516.

Collaborative study of cassava in Africa (COSCA), Uganda. 1996. Production prospects for cassava in Uganda. COSCA working paper No. 17.

DeVries, J., and G. Toenniessen. 2001. Securing the harvest: biotechnology, breeding and seed systems for African crops. Chapter 13: Cassava. CABI Publishing, Oxon, UK and New York, USA. p. 147-156.

El-Sharkawy, M.A. 2007. Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semi-arid environments. Brazilian Journal of Plant Physiology 19:257-286.

El-Sharkawy, M.A. 2012. Stress-tolerant cassava: the role of integrative ecophysiology-breeding research in crop improvement. Open Journal of Soil Science 2:162-186.

Food and Agriculture Organisation (FAO). 2009. FAO food balance sheet. FAO, Rome. http://www.faostat.fao.org/ (Accessed 25 July 2012).

Food and Agriculture Organization (FAO). 2012. Food and Agriculture Organisation statistical database for agriculture. Crops and products domain. http://faostat.fao.org/ (Accessed 19, August 2013).

Fregene, M., A. Bernal, M. Doque, A. Dixon, and J. Tohme. 2000. AFLP analysis of African cassava (*Manihot esculenta* Crantz) germplasm resistant to cassava mosaic disease (CMD). Theoretical and Applied Genetics 100:678-685.

Henry, G., and C. Hershey. 2002. Cassava in South America and the Caribbean. In: R.J. Hillocks et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p.17-40.

IITA, 2001: Cassava. IITA/Crops. http://www.iita.org/. (Accessed 19 August 2012).

Jameson, J.D. 1964. Cassava mosaic disease in Uganda. East African Agricultural and Forestry Journal 29:208-213.

Jansson, C., A. Westerbergh, J. Zhang, X. Hu, and C. Sun. 2009. Cassava, a potential biofuel crop in (the) People's Republic of China. Applied Energy 86:95-99.

Kamau, J., R. Melis, M. Laing, J. Derera, P. Shanahan, C. Eliud, and K. Ngugi. 2011. Farmers' participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. Journal of Plant Breeding and Crop Science 3:44-52.

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

Kawuki R. S., A. Pariyo, T. Amuge, E. Nuwamanya., G. Ssemakula, S.Tumwesigye, A. Bua Y. Baguma, C. Omongo, T. Alicai, and J. Orone. 2011. A breeding scheme for local adoption of cassava (*Manihot esculenta* Crantz).Journal of Plant Breeding and Crop Science 3:120-30.

Langlands, J. 1966. Cassava in Uganda 1886-1920. Uganda Journal 2:211-216.

Langlands, J. 1972. Cassava in Uganda. Uganda Journal 10:273-286.

Legg, J.P., S.C. Jeremiah, H.M. Obiero, M.N. Maruthi, I. Ndyetabula, G.Okao-Okuja, H. Bouwmeester, S. Bigirimana, W. Tata- Hangy, G. Gashaka, G. Mkamilo, T. Alicai, and L.P. Kumar. 2011. Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa. Virus Research 159:161-170.

Ministry of Agriculture, Animal Industry and Fisheries (MAAIF). 2007. The national cassava policy: The Republic of Uganda. p. 1-18.

Ntawuruhunga, P., and J. Legg. 2007. New spread of cassava brown streak virus disease and its implications for the movement of cassava germplasm in the east and central African region. Crop crisis control project, IITA, Uganda. Report p.1-6.

Ntawuruhunga, P., G. Ssemakula, H. Ojulong, A. Bua, P. Ragama, C. Kanobe, and J. White. 2006. Evaluation of advanced genotypes in Uganda. African Crop Science Journal 14:17-25.

Ocitti p'Obwoya, C.N., and G.W. Otim-Nape. 1986. On-farm survey of root crops-based farming system in Soroti, Kumi and Tororo Districts, eastern Uganda. Uganda National Root Crops Improvement Programme, Serere research station, Soroti. Report p.1-30.

Ojulong, H., M.T. Labuschagne, and M. Fregene. 2007. A cassava clonal evaluation trial based on a new cassava breeding scheme. Euphytica 160:119-129.

Okechukwu, R.U., and A.G.O. Dixon. 2009. Performance of improved cassava genotypes for early bulking, disease resistance, and culinary qualities in an inland valley ecosystem. Agronomy Journal 101:1258-1265.

Okogbenin, E., and M. Fregene. 2002. Genetic and QTL mapping of early root bulking in an F_1 mapping population of non-inbred parents in cassava (*Manihot esculenta* Crantz). Theoretical and Applied Genetics 106:58-66.

Otim-Nape G.W. 1988. Cassava situation in Luwero District. A mission report by the Uganda Root Crops Programme, Namulonge Research Station, Kampala. Report p.1- 8.

Otim-Nape, G.W. 1993. Epidemiology of the African cassava mosaic geminivirus disease in Uganda. PhD thesis, University of Reading, Reading, UK.

Otim-Nape, G.W., and S. Zziwa. 1990. Cassava as a major staple food crop in Uganda. Phase I of collaborative study of cassava in Africa. Namulonge research station, Kampala. Report p. 1-48.

Otim-Nape, G.W., T. Alicai, and M. Thresh. 2001. Changes in the incidence and severity of cassava mosaic virus disease, varietal diversity and cassava production in Uganda. Annals of Applied Biology 138:313-327.

Ssemakula, G.N., W.S. Sserubombwe, A. Bua, J. Jagwe, R.S.B. Ferris, and J.B.A. Whyte. 2004. Constraints and potential for cassava commercialisation in Uganda. In: Proceedings of regional workshop on improving the cassava subsector, Nairobi, Kenya. April 2002. p. 57-60.

Tonukari, N.J. 2004. Cassava and the future of starch. Electronic Journal of Biotechnology7.http://www.ejbiotechnology.info/content/vol7/issue1/ISSN: (Accessed 03 March 2012).

Tumuhimbise, R., R. Melis, P. Shanahan, and R. Kawuki. 2012: Farmers' perceptions on early storage root bulking in cassava (*Manihot esculenta* Crantz) in east and central Uganda and their implication for cassava breeding. World Journal of Agricultural Sciences 8:403-408.

Uganda Bureau of Statistics (UBOS). 2008. Agricultural production in Uganda http://www.ubos.org/ (accessed 31 July 2010).

Uganda Bureau of Statistics (UBOS). 2012. The 2012 Uganda population and housing census. Bulletin p. 1-6.

Westby, A. 2002: Cassava utilization, storage and small-scale processing. In: R.J. Hillocks et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 281-300.

Wholey, D.W., and J.H. Cock. 1974. Onset and rate of root bulking in cassava. Experimental Agriculture 10:193-198.

World Food Programme (WFP). 2013. Comprehensive food security and vulnerability analysis, Uganda. Report p. 1-4.

CHAPTER 1

Literature review

1.1 Introduction

The literature review in this chapter covers topics relevant to the research focus of this thesis in order to provide theoretical base for the study. It covers the origin of cassava, its cytology and taxonomy, as well as its genetic diversity and it provides insight into cassava breeding for improved storage root yield and early bulking. Environmental conditions for cassava growth and development, storage root initiation and bulking process, flowering characteristics, hybridisation, breeding objectives and methods, and also the selection processes are also covered. Other cassava aspects covered include: combining ability effects, their influence and implications on cassava breeding, variability and genotype x environment interaction effects. Finally, the key cassava pests and diseases in Uganda, as well as postharvest physiological deterioration are discussed.

1.2 Agricultural origin of cassava

Cassava is an ancient starchy root crop species (Allem, 2002). It has been evolving as a food crop ever since it became important in the second and third millennium BC (Lathrap, 1973; Allem, 2002). The crop is believed to have been domesticated before 4000 BC and its centre of origin is hypothesised to be South America (Allem, 2002; Nassar and Ortiz, 2008). Its domestication process involved selection for root size, growth habit, stem number and ability of clonal propagation through stem cuttings (Jennings, 1976).

1.3 Cytology and taxonomy of cassava

Cassava is placed in the *Fruticosae* section of the genus *Manihot*, which is a member of the Euphorbiaceae (Jennings and Iglesias, 2002). The *Fruticosae* section contains low-growing shrubs adapted to savannah, grassland or desert and is considered less primitive than *Arboreae* section of Euphorbiaceae, which contains tree species (Jennings and Iglesias, 2002). All the species of *Manihot* have $4x = 2n = 36$ chromosomes and are regarded as polyploids with $n = 18$. However, although cassava is normally considered as a polyploid species (Westwood, 1990; El-Sharkawy, 2003), analyses conducted during diakinesis and metaphase I consistently indicated the presence of 18 small and similar pairs of associated homologous chromosomes, or bivalents (Jennings and Iglesias, 2002; Wang et al., 2011).

Cassava is therefore, a functional diploid (Jennings, 1976; De Carvalho and Guerra, 2002; Nassar and Ortiz, 2008).

Cassava is also classified based on its morphological characters such as leaf shape and size, plant height, stem colour, petiole length and colour, inflorescence and flower colour, storage root shape and colour, earliness, and content of cyanogenic glycosides (Nassar and Ortiz, 2006). Based on cyanogenic glycoside, cassava cultivars are classified as bitter and sweet (Nassar and Ortiz, 2006). Onwueme (1982), however, stated that some caution should be exercised in using the level of glycosides as a distinguishing characteristic for cassava cultivars since the exact level of glycosides in a particular cultivar will vary according to the environmental conditions under which the plant is grown. The glycoside content of a cultivar may be high under some conditions and low in others. Sweet cultivars are reported to have a short growing season with their storage roots maturing early (Nassar and Ortiz, 2006; Amenorpe et al., 2007).

1.4 Genetic diversity in cassava

Genetic diversity in plants is explained by various evolutionary processes, which include hybridisation, mutations, migration and polyploidy (Colombo et al., 2000). In cassava, it is believed that the wide range of genetic diversity was generated through centuries of farmer selection (Jennings and Iglesias, 2002). Nassar (2004), however, indicates that the wide genetic diversity in cassava is as a result of natural hybridisation between the wild *Manihot* spp*.* and cultivated cassava, and controlled interspecific hybrids between *M. esculenta* and several wild *Manihot* spp*.* or through apomixis. Jennings (1963) suggested that a high genetic diversity of cassava genotypes resulted from introduction of cassava genotypes by immigrants, followed by natural hybridisation in the fields. Fregene et al. (2000) explained that the genetic diversity for example in East African cassava is structured according to the adaptation to biotic and abiotic stresses, agronomic practices, and post-harvest use. Asante and Offei (2003) on the other hand stated that as much as the genetic diversity in *Manihot* spp*.* is high, diversity within a given geographical region may be low, and is associated with the exchange of planting materials between farmers and selection for desired traits.

1.5 Environmental conditions for cassava growth

Cassava is grown in tropical and subtropical areas of the world between latitude 30^{o}N and 30^{o}S of the equator under various ecological and agronomical conditions (Onwueme, 1978; IITA, 2001; El-Sharkawy, 2012). It is grown from sea level to elevations of 2000 metres above

sea level under annual precipitation ranging from 500 to >2000 mm. The crop requires a warm moist climate with mean temperature of 24 to 30^{o}C. The ideal soils for cassava are light sandy loam with medium fertility (IITA, 1990). Cassava can also tolerate drought and can grow in low nutrient soils, but does not tolerate a pH above 8, excess soil moisture, and temperatures of ≤10^{o}C (Onwueme, 1978; IITA, 2001). Physiologically, low availability of moisture in the soil causes the growth of cassava plant to cease, and it then sheds some of its older leaves, thereby reducing its total transpiration surface. When moisture is again available, the plant quickly resumes growth and produces new leaves.

1.6 Growth and development of cassava

Cassava is a perennial crop which can continue to grow for a number of years if it is not uprooted (Alves, 2002; El-Sharkawy, 2003, 2007). Its stems may grow to a height of 1 to 4 m and its morphological characteristics are highly variable, indicating a high degree of interspecific hybridisation (Alves, 2002; Chavarriaga and Halsey, 2005). The crop is generally established using stem cuttings, although in breeding programmes its propagation in the first cycle is by sexual seeds (Fukuda, et al., 2002; Alves, 2002). When cuttings are used as propagation materials, roots grow first and the buds that later grow into stems appear (Alves, 2002; Fukuda, et al., 2002; El-Sharkawy, 2003).

Cassava grown from botanical seeds usually develops a primary tap root system, which is characteristic of dicotyledonous species (Alves, 2002; Ceballos et al., 2004). The taproot from which adventitious roots originate grows vertically downward into soil (Alves, 2002). The taproot and some adventitious roots subsequently become storage roots. Cassava grown from stem cuttings develops adventitious roots, which arise from the basal-cut surface of the cutting and occasionally from the bud under the soil (Izumi et al., 1999; El-Sharkawy, 2003). Those roots develop to make a fibrous root system and only a few of them start to bulk and become storage roots (Izumi et al., 1999; Alves, 2002). Ceballos et al. (2004), however, reported that when seeds are germinated in seedling containers and later transplanted, the tap root often does not develop, and the seedling-derived plants may be more similar to subsequent stake-derived plants in terms of root growth and development.

1.7 Storage root development and bulking

The formation and growth of storage roots that show secondary thickening is termed root bulking (Izumi et al., 1999). Root bulking results from the increase in number of cells due to cell division and proliferation and their accumulation of starch. Increase in root size occurs

through increase in cell number and cell size while the storage root weight increases through accumulation of photosynthates (Alves, 2002; El-Sharkawy, 2003; Ravi et al., 2009). Therefore, storage root bulking depends on the sink strength, the potential of leaves to export photosynthates and on the photosynthetic efficiency of leaves (Keutgen et al., 2001).

1.7.1 Storage root bulking process

Storage root bulking involves secondary growth by genesis of a circular primary vascular cambium as well as several anomalous circular cambia (Figure 1.1) in the sub-apical region of roots (Doku, 1969; Indira and Sinha, 1970; Hunt et al., 1977; Izumi et al., 1999; Alves, 2002; El-Sharkawy, 2003). At the onset of secondary thickening, primary vascular cambium initials are first laid down within the parenchymatous zone between the protoxylem and protophloem and are connected to form a continuous and irregular cylinder through division of the single layered pericycle (Hunt et al., 1977; Ravi et al., 2009). This is accompanied by the formation of a cork cambium in the outer layers of the pericycle. Subsequent vascular cambial activity leads to centripetal production of thin walled storage parenchyma, secondary vascular tissues and a regular cylinder of vascular cambium. Differentiation of vascular cambium is accompanied by the origin of anomalous circular cambia in the central pith around central metaxylem cells as well as around each of the discrete protoxylem elements.

Anomalous circular secondary cambia also originate around secondary xylem elements derived from the vascular cambium (Izumi et al., 1999; Ravi et al., 2009). Interstitial cambial strips unassociated with vascular tissues also develop within the secondary parenchyma and contribute to storage roots growth. Active cell division in these cambia results in the formation of thin walled, starch storing parenchyma cells causing thickening of storage roots and lignifications. The xylem parenchyma cells store the bulk of starch grains (Doku, 1969; Hunt et al., 1977). Starch deposition in the first produced parenchyma cells occurs 25 days after planting (Indira and Sinha, 1970; Hunt et al., 1977). The time of onset of both the secondary thickening and of starch deposition can either be delayed by excising buds, or accelerated by applying sucrose or glucose (Indira and Sinha, 1970), implying that the sugar alone can initiate storage root differentiation (Yang et al., 2011).

A number of studies have differed on the time when thickened roots appear in cassava during its growth and development (Doku, 1969; Wholey and Cock, 1974; Izumi et al., 1999; Okogbenin and Fregene, 2002). For instance, Izumi et al. (1999) showed that root bulking begins about 3 months after planting (MAP) but maintained that rapid starch deposition does

not occur before 6 MAP. Based on sequential harvesting experiments in various Ghanaian cassava cultivars, Doku (1969) reported that root bulking of most genotypes began during the second month and produced reasonable fresh storage root yields by 6 MAP. Wholey and Cock (1974), however, in their trials designed to investigate differences in onset of root bulking and rate of bulking found that thickened roots were present after 2 MAP, and that root bulking increased with time but, the rate of bulking differed between cultivars. They also found that after three months, the number of thickened roots per plant remained fairly constant for all cultivars except for one in which the thickened root number increased with time. Based on fresh storage root mass (FSRM) accumulated by different genotypes at different times, Wholey and Cock (1974) concluded that earliness was related to early onset of bulking, rapid bulking, or a combination of both factors. Similar findings on accumulation of different amounts of FSRM at different harvest times by different cultivars have been reported elsewhere indicating existence of early bulking genotypes (Chang-Ho et al., 2005, Kamau, 2006; Amenorpe et al., 2007; Mtunda, 2009; Okogbenin et al., 2013).

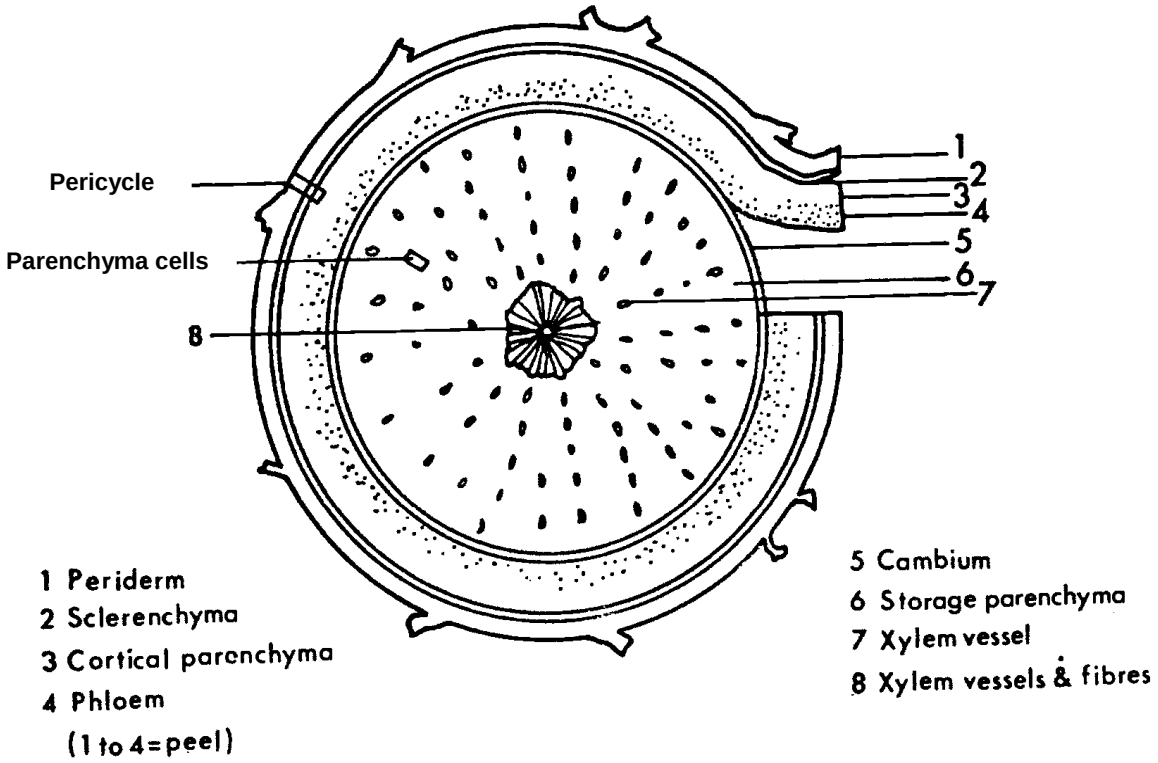

Figure 1.1: Transverse section of a young storage root (Hunt et al., 1977)

1.7.2 Dynamics of storage root bulking

The rate of cassava storage root bulking fluctuates over a long period due to changes in the agro-climatic conditions (Ekanayake et al., 1998). Unlike in cereal grains, the cassava

storage root can undergo periods of arrested growth during unfavorable conditions and then continue growing once conditions improve. High yielding cultivars have a high bulking rate over a long period, whereas cultivars with intermediate and low storage root yield have a low bulking rate for short duration or low bulking rate for longer duration (Hershey, 2011, Okogbenin et al., 2013). Bitai and Lian (1978) found that early maturing, short duration sweet potato cultivars exhibit fast initiation growth of storage roots whereby their yields reach a maximum within a short growing period. They indicated that the bulking rate of tubers of early maturing cultivars declines or even pauses in the early period of growth, whereas for the late maturing cultivars, the bulking rate increases at the middle and later growth period. Suja et al. (2009) indicated that high and low yielding cassava cultivars differ in their bulking rate and the period at which they exhibit the maximum bulking rate. They revealed that short duration cultivars exhibit maximum bulking rate during their early growing stage.

1.7.3 Storage root number

Ekanayake et al. (1997) found that the storage root number (SRN) in cassava is determined during the first 3 MAP. Wholey and Cock (1974) also indicated that SRN is generally determined early in the growth cycle although some cultivars appear to continue producing new storage roots up to 7 MAP. The number of thickened roots ranges from five to 20 per plant. Fewer storage roots are formed in drier environments. The number of fibrous roots which form storage roots depends on several factors such as: genotype, assimilate supply, shading, photoperiod and temperature (Ekanayake et al., 1997). Enyi (1972) showed that the number of shoots per plant may affect the SRN, plants with more than one shoot producing more roots than plants with only one.

1.7.4 Storage root yield

Yield in plants refers to the mass of produce harvested from a single plant or the quantity of produce harvested per unit of land area. In cassava, it is often defined in terms of marketable storage root yield, although leaves, stems or even seeds could potentially be additional economic products (Hershey, 2012).

Several attempts have been made to describe the ideal cassava plant type for maximum yields and, according to Cock (1975), the highest yielding cassava plants would have a single erect stem, late branching, short thick internodes, and long leaf retention capacity. However, he recognised environmental limitations of this ideal plant and suggested that in fertile soils harvest index (HI) was important, and that under low soil fertility HI is irrelevant. Hunt et al.

(1977) on the other hand suggested that the most prominent trait associated with yield is leaf longevity. Several others indicators of high yielding cassava were suggested including late branching (Cock et al., 1979); large individual leaves or profuse branching (Cock et al., 1979); narrow-lobed, vertical positioned leaves (Ramanujam, 1985); optimal leaf area index, large and numerous leaves and high HI (Byrne, 1984). Lahai and Ekanayake (2009) suggested that dry mass production and partitioning are important determinants of storage root yield in cassava and that they could be important selection criteria in breeding for enhanced yield. Byrne (1984) indicated that in selection for high yielding cassava, the obvious approach would be to select for the ideal plant type and that this should be based on late branching, large leaf size, and the number of roots on a mass-screening scale, but not for long leaf life.

1.8 Flowering in cassava

Cassava bears separate male and female flowers on the same plant, and is thus referred to as a monoecious crop (Kawano, 1980). The time interval between planting to flowering depends on the specific genotype and environmental conditions, and may vary from one to more than 24 months (Jennings and Iglesias, 2002). Male and female flowers are borne on the same branched panicle, with female flowers at the base and male flowers toward the tip. Male flowers are more numerous than female flowers (Fukuda et al., 2002). Flowers often begin to open around midday, remaining open for about one day. Female and male flowers in an inflorescence open at different times. Female flowers open first and the male flowers follow from one to a few weeks later, a condition called protogyny. By the time male flowers open, the female flowers on the same branch will have been fertilised or have aborted. However, since flowering on a single plant may last for more than two months, pollen from one flower may fertilise other flowers on the same plant (Kawano, 1980; Wang et al., 2011). Thus, both self-pollination and cross-pollination occur naturally. Cassava is an outcrossing and highly heterozygous species due to the protogynous nature of the flower anthesis (Fukuda et al., 2002). However, there is no genetic or physiological barrier that prevents self-pollination (Kawano et al., 1982). A number of factors influence flowering in cassava and they include: genotype, soil moisture, soil fertility, photoperiod and temperatures (Kawano et al., 1978; Irikura et al., 1979; Kawano, 1980).

1.8.1 Cassava pollen grains

Cassava pollen grains are relatively large in size and sticky, and therefore wind-pollination appears to be of little consequence (Kawano, 1980). Several species of honeybees and

wasps are main pollinators of cassava flowers. Pollen grains show size differences within the same genotype. The larger grains are about 130 to 150 µm in diameter, whereas the smaller grains range from 90 to 110 µm (Kawano, 1980). In some genotypes, the larger grains are more abundant, whereas in others the smaller grains are more common. The larger pollen grains have been observed to have better in vitro germination (60% after 2 h at 40°C) than the smaller ones, which may have less than 20% germination (Chavarriaga-Aguirre and Halsey, 2005). Cassava pollen rapidly loses viability after it is shed. Ninety seven per cent of seed set occurs when the pollen is used immediately after its collection, 56% when pollen is stored for 24 h at 25°C, and 0.9% after keeping pollen for 48 h. In practice, however, cassava breeders take care to perform pollinations within one 1 h after collection of pollen to ensure successful fertilisation (Kawano, 1980; Chavarriaga-Aguirre and Halsey, 2005).

1.8.2 Fruits and seed formation

After pollination, the flower ovary develops into a fruit within 70 to 90 days. The fertility of genotypes is variable and may be very low. An average of one seed per fruit is commonly achieved through controlled pollination from a potential three seeds from a tri-locular ovary (Osiru et al., 1996; Jennings and Iglesias, 2002). The genotype of the female parent is more important in determining success of fertility than that of the pollen parent (Jennings, 1963). According to Osiru et al. (1996), a mature fruit is a globular capsule, 1.0 to 1.5 cm in diameter with six narrow longitudinal wings along which it naturally splits explosively to release the seed. Fruit maturation generally occurs 75 to 90 days after pollination. The newly harvested seeds are dormant and require three to six months storage at ambient temperatures before germination. Seeds take about 16 d to germinate. Germination can be hastened by carefully filing the sides of seed coats at the radicle end and by temperature management. Ellis et al. (1982) found that few seeds germinated unless the temperature exceeded 24^0C, and that the best rates occurred at 30 to 35^oC.

1.8.3 Factors that affect hybridisation and seed production

Cassava hybridisation process is affected by the flowering ability and/or low rate of flower production by some genotypes, lack of synchrony in the flowering period of the genotypes and male sterility (Kawano et al., 1978; Ceballos et al., 2012). Different levels of male sterility have been reported in cassava genotypes (Bai, 1985). Cours (1951) studied the morphological variation of many cassava varieties and reported that 20% of the varieties presented deformed anthers and were sterile males. When Magoon et al. (1968) assessed a number of cassava genotypes they identified different levels of male sterility. Male sterility in

cassava is attributed to several factors, including the non-disjunction of the microspore; abnormal tapetum behaviour; cytological abnormalities and functional male sterility (Jennings, 1963; Magoon et al., 1968; Jos and Nair, 1984) which is reflected by absence of anther dehiscence.

1.9 Mating designs in breeding

The importance of mating designs in plant breeding is two-fold: 1- to generate information for the breeder to understand the genetic control of the trait of interest; and 2- to generate a breeding population that can be used as a basis for the selection and development of potential varieties (Acquaah, 2009). The information generated helps breeders to determine an appropriate breeding strategy, as well as to assess the progress that can be expected for a given selection intensity.

The diallel mating designs are the most popular designs used by cassava breeders to obtain information on the value of the hybrids and parents, and to assess the gene action involved in the various traits (Calle et al., 2005; Jaramillo et al., 2005; Perez et al., 2005; Cach et al., 2006; Zacarias and Labuschagne, 2010; Kulembeka et al., 2012). This helps to develop appropriate selection procedures and understand heterotic patterns of progeny at an early stage of hybridisation programmes. Diallel mating designs permit the estimation of the magnitude of additive and non-additive components of the heritable variance (Griffing 1956). Data obtained from such cross combination is useful and can be analysed in several ways, but the most commonly used are those proposed by Hayman (1954) and Griffing (1956). Diallel mating designs are also important in estimating the general and specific combining ability of the parents and crosses, respectively (Griffing, 1956; Ortiz et al., 2001; Sleper and Poehlman, 2006).

1.9.1 General and specific combining ability

General combining ability (GCA) of a parental line is the average contribution a parental line makes to the hybrid performance in a series of hybrid combinations in comparison to the contribution of other parental lines to hybrid performance in the same series of hybrid combinations (Sleper and Poehlman, 2006). It evaluates the additive portion of the genetic effects (Falconer and Mackay 1996; Sleper and Poehlman, 2006). Parents with good GCA for specific characters may be useful in a hybridisation programme for improvement of those traits (Parkes et al., 2013). Specific combining ability (SCA) on the other hand is the contribution of a parental line to hybrid performance in a cross with another parental line, in

relation to its contributions in crosses with an array of specified parental lines (Sleper and Poehlman, 2006). It evaluates non-additive gene action and is utilised to identify the cross combinations with superior performance (Falconer and Mackay, 1996; Sleper and Poehlman, 2006). Determination of inheritance of agronomic traits in cassava using combining ability has steadily gained prominence, with most of this work done by CIAT and by the national research institutes of countries where cassava is a staple crop (Perez et al., 2005; Jaramillo et al., 2005; Calle et al., 2005; Cach et al., 2006; Kamau, 2006; Munga, 2008; Owolade et al., 2009; Mtunda, 2009; Zacarias and Labuschagne, 2010; Kulembeka et al., 2012; Parkes et al., 2013).

1.9.2 Gene action

Gene action and gene effects have been extensively studied in many crop species (Sleper and Poehlman, 2006; Acquaah, 2009; Brown and Caligari, 2009). Gene action is important in determining cultivar type (hybrid, pure line, synthetic), breeding methodology used to develop cultivars, and in the interpretation of quantitative genetic experiments. The study of gene action is approached in two ways, viz. GCA and SCA effects (Griffing, 1956; Sprague, 1966; Falconer and Mackay, 1996; Brown and Caligari, 2009). The GCA and SCA effects represent the additive vs. dominant gene effects in populations. Four types of gene action are recognised; additive, dominance, epistatic, and over-dominance (Sleper and Poehlman, 2006; Acquaah, 2009). Because gene effects do not always fall into clear-cut categories, and quantitative traits are governed by genes with small individual effects, they are often described by their gene action rather than by the number of genes by which they are encoded. Gene action is conceptually the same for major genes as well as minor genes, the essential difference being that the action of minor gene is small and significantly influenced by the environment (Acquaah, 2009).

1.10 Variation of traits

The success of genetic improvement of any trait depends on the nature of variability present for that trait (Falconer and Mackay, 1996). Therefore, an understanding of the nature and magnitude of variability present in the gene pool for the traits of interest is of greatest importance. Phenotypic variation of any trait is a combination of mainly three components, viz. genetic variation, environmental variation and variation due to the interaction between the genetic and the environmental factors (Falconer and Mackay, 1996; Sleper and Poehlman, 2006; Acquaah, 2009; Brown and Caligari, 2009).

1.10.1 Genetic variation

Acquaah (2009) defines genetic or heritable variation as the variation that can be attributed to genes that encode specific traits, and can be transmitted from one generation to the next. Since genes are expressed in an environment, the degree of expression of a heritable trait is impacted by its environment, some more so than others.

A phenotype (P), defined as the characteristic that is observed, is as a result of a combination of its genetic constitution, called the genotype (G), and the environment (E) and a component attributed to the interaction between the genetic and environmental components (GxE). This is usually expressed as:

Phenotype = Genotype + Environment + G x E (Falconer and Mackay, 1996; Sleper and Poehlman, 2006; Brown and Caligari, 2009). From this equation for phenotypic expression, it follows that any variation seen in the phenotype is due to variation in the factors resulting in the phenotype. The relationship can then be presented as:

$$V_P = V_G + V_E + V_{GxE.}$$

Where:

V_P = Phenotypic variation

V_G = Genotypic variation

V_E = Variation as a result of the environment

V_{GxE} = variation due to genotype x environment interaction effects

Genotypic variation is generally divided into two components, which are additive and non-additive components (Falconer and Mackay, 1996; Sleper and Poehlman, 2006; Brown and Caligari, 2009). Additive variation is due to the cumulative effect of alleles on all gene loci influencing a trait, and is usually of most value in a crop improvement programme (Falconer and Mackay, 1996). Non-additive variation is divided into dominance variation, caused by the interaction of specific alleles at a gene locus, and epistatic variation, caused by the interaction among gene loci (Falconer and Mackay, 1996). The non-additive variation is normally given little attention since only the additive component of genetic variation is heritable (Falconer and Mackay, 1996; Sleper and Poehlman, 2006; Brown and Caligari, 2009). Genetic or heritable variation in nature originates from gene recombination, modifications in chromosome number, and mutations (Falconer and Mackay, 1996). Rather than wait for them to occur naturally, plant breeders use a variety of techniques and methods

to manipulate these three phenomena more and more extensively, as they generate genetic variation for their breeding programmes (Acquaah, 2009).

1.10.2 Environmental variation

Environmental variation is usually associated with environmental conditions prevailing on the site where the crops are grown (Ceccarelli and Grando, 1991; Annicchiarico and Perenzin, 1994). Some of these conditions, such as plant to plant competition and population density can be controlled by use of agronomical practices, where others, such as rainfall, wind are uncontrollable. Environmental variation is normally difficult to control because it is non-heritable. For example, when an individual from a clonal population (identical genotype) are grown in the field, the plants will exhibit differences in the expression of some traits because of non-uniform environments. The field is often heterogeneous with respect to plant growth factors such as nutrients, moisture, light, and temperature (Ceccarelli and Grando, 1991)

1.10.3 Genotype by environment interaction

Genotype x environment interaction (GEI) occurs when different genotypes respond differentially to any changes in the environments (Eberhart and Russell, 1966; Ssemakula and Dixon, 2007). Genotype x environment interaction varies with the genotypes tested and the sites chosen for testing (Buerno, 1986; Lebot, 2009). Especially complexly inherited quantitative traits are influenced by environmental effects. A significant GEI for a quantitative trait such as yield can reduce the usefulness of subsequent analyses, restrict the significance of inferences that would otherwise be valid, and seriously limit the feasibility of selecting superior genotypes (Flores et al., 1998). Differences between genotypic values may increase or decrease from one environment to another which might cause genotypes to rank differently between environments. Genotypes are normally tested over a wide range of diverse environments and agricultural experiments to determine the extent and nature of GEI may involve a large number of genotypes (Egesi et al., 2007; Aina et al., 2009).

Cassava is subject to considerable GEI (Kvitschal et al., 2006; Ssemakula and Dixon, 2007; Lebot, 2009). Studies with different cassava genotypes tested in contrasting environments have shown that FSRY is subject to strong GEI (Ssemakula and Dixon, 2007; Aina et al., 2009). Tan and Mak (1995) detected that GEI effects were significant for FSRY, commercial storage root number, HI, starch and cyanide content. Although significant, their effects were smaller than the genotype effects, except for commercial storage root number and FSRY. They found only cyanide content exhibited a linear GXE relationship with the environment.

Buerno (1986) reported important genotype x location and genotype x location x year interaction for FSRY when testing a number of genotypes in the humid tropics of Brazil. Huhn (1996) reported that the dry matter content of cassava storage roots had high cultivar-by-year interaction and cultivar-temperature interaction.

1.11 Cassava breeding

Plant breeding has the highest rates of return among the investments in agricultural research of which cassava has also benefited (Kawano, 2003; Ceballos et al., 2004; Ceballos et al., 2012). Plant breeding objectives differ from programme to programme because the environmental conditions that affect production and the adversities that limit yield differ from one production area to another (Sleper and Poehlman, 2006). They also depend on crop species involved and their ultimate uses (Ceballos et al., 2004; 2012). Ceballos et al. (2012) indicated that in cassava, high and stable production of fresh storage roots is the key breeding objective in most cassava breeding projects. They further indicated that productivity plays a major role in industrial uses of cassava, whether for starch, animal feed or bio-ethanol, whereas stability of production is fundamental in the regions where cassava is the main subsistence crop.

Conventional cassava breeding involves selection of best parental genotypes for the traits of interest, hybridising them and conducting multi-stage offspring selections (Kawano et al., 1998; Jennings and Iglesias, 2002; Ceballos et al., 2004; 2012). This is often aimed at the accumulation of beneficial alleles and elimination of detrimental ones. High frequencies of genes for specific desirable characteristics, including yield components, storage root quality, resistance to pests and diseases, tolerance to soil and climatic stresses, and stability of production across environments are progressively accumulated through recurrent selection (Hahn et al., 1980a; CIAT, 2002; Ojulong et al., 2008). Recurrent selection combined with a broad genetic base has been reported to be the most efficient procedure for improving cassava base populations (Hahn, 1978; Bryne, 1984; CIAT, 2002; Fregene et al., 2007). Progenies resulting from each recombination cycle are evaluated and selections recombined again to form a new population. A conservative time-frame for developing an improved cultivar can be between 8 - 10 years (Dixon et al., 2008).

1.11.1 Cassava selection cycle

The cassava selection cycle takes about five to six years from the time the botanical seed is germinated until selection cycle reaches the last regional trial stage when several locations

can be included (Jennings and Iglesias, 2002; Ceballos et al., 2004). Table 1.1 adopted from (Ceballos et al., 2012) illustrates the selection scheme currently used at CIAT. Ceballos et al. (2012) indicated that the scheme represents the way most cassava-breeding projects operate, beginning with the crossing of elite genotypes, including multiple rounds of selection, and ending with a few genotypes reaching the stage of regional trials across several locations. They, however, report that variations among cassava-breeding programmes regarding the numbers of genotypes and plants representing them through the different stages exist. Selection starts with nurseries planted with seedlings derived from botanical seeds. Considering the low correlation between the performance at seedling and clonal propagation stages, Jennings and Iglesias (2002) and Ceballos et al. (2004; 2012) suggested that early selections should be based on highly heritable traits only, such as plant type, branching habit and, particularly, reaction to diseases as indicated by Hahn et al. (1980b) and Morante et al. (2005). The second stage of selection, called clonal evaluation trial (CET) uses the few surviving genotypes from the seedling stage that can produce 6 to 10 vegetative cuttings required for CET. The capacity to produce this number of cuttings is another selection criterion utilised at the F_1 stage Ceballos et al. (2004; 2012). The selection at CET depends largely on HI (Kawano 2003; Morante et al. 2005), plant type (Kawano et al., 1978), dry mass content and cyanogenic glycosides (Iglesias and Hershey, 1994). The first three evaluation stages are carried out at one location (Table 1.1). Subsequent selections, advanced yield trial, regional trial - I and regional trial - II are conducted at more locations (Jennings and Iglesias, 2002; Ceballos et al., 2004; 2012). The common characteristic with all cassava breeding programmes is that from the early stages to the later stages of breeding, the number of genotypes evaluated is reduced, whereas the number of test locations increases.

Table 1.1: Description of evaluation and selection stages utilised in the International Center for Tropical Agriculture cassava breeding programme (Ceballos et al., 2012)

Time (months)	Stage	Plants per plot (number)	Repetitions	Locations	Genotypes evaluated
18	Crossing blocks	-.-	-.-	-.-	
19 - 30	F_1	1	1	1	2500
31 - 42	Clonal evaluation trial (CET)	6 - 8	1	1	1500-3000
43- 54	Preliminary yield trial (PYT)	10	3	1	100-300
55 - 56	Advanced yield trial (AYT)	20	3	1 - 2	75-150
67 - 78	Regional trial (RT) - I	25	3	2 - 6	20-40
79 - 90	Regional trial (RT) - II	25	3	5 - 10	20-40

Source: Ceballos et al. (2012)

1.11.2 Breeding methods

Breeding methods in cassava are essentially defined by the mode of its reproduction, genetic variability available and breeding objectives (Fukuda et al., 2002). Cassava presents sufficient segregation in the first generation after hybridisation because it is a highly heterozygous species (El-Sharkawy, 2012; Ceballos et al., 2012). Once a superior cassava hybrid has been identified in the first generation, its genotype is fixed by vegetative propagation, which is an advantage in breeding cassava (Fukuda et al., 2002; Grüneberg et al., 2009). The main disadvantages are the need to work with large populations, the difficulty in getting a precise estimation of the performance of the genotypes generated, and the low rate of vegetative propagation (Ceballos et al., 2004; 2012). Fukuda et al. (2002) indicated that there are no classic breeding methods developed for the vegetatively propagated crops and that normally the methods developed for self-pollinating crops are the ones applied to cassava, with some modifications because of cassava's specific characteristics. The main breeding methods used in cassava cultivation are cultivar introduction and selection, intra- and inter- specific hybridisations and breeding of polyploids.

A. Cultivar introduction and selection

Cultivar introduction and selection are one of the key breeding methods used by most national cassava breeding programmes in Africa. The process involves recruiting genotypes from established cassava breeding programmes, like the International Center for Tropical Agriculture (CIAT) and International Institute for Tropical Agriculture (IITA), followed by field evaluation (Fukuda et al., 2002). Fukuda et al. (2002) indicated that this method is not only simplest and least expensive method, but also has greatest chance of success because of the wide genetic diversity exploited. Assessment and selection of the cultivars introduced involve formation of a study collection, followed by yield, pest and diseases evaluations and finally trials with producer participation in various localities and years (Fukuda et al., 2002).

B. Intraspecific hybridisation

Crossing among cassava parental genotypes of the same species, followed by selection among the progeny is the most common method used in cassava breeding (Fukuda et al., 2002; Jennings and Iglesias, 2002; Ceballos et al., 2012). The success of this method depends basically on correct parent choice and an efficient selection of genotypes within the progeny resulting from each cross. Parent selection is based on the phenotypic assessment of the genotypes and/or their general and specific combining abilities, estimated by the performance of the respective progeny. A large population should be used to obtain the

desirable recombinants. Since cassava genotypes are highly heterozygous for most of the gene loci, segregation occurs in the first generation. The F_1 hybrids are first selected from within the segregating families (progeny). Then each selected individual is propagated vegetatively and the new genotypes assessed by yield trials (Fukuda et al., 2002; Jennings and Iglesias, 2002; Ceballos et al., 2004; Lebot, 2009).

C. Interspecific hybridisation

Successful crosses between cultivated cassava and its related wild species have been reported (Nichols, 1947; Jennings, 1957). Ceballos et al. (2012) reported that several traits of commercial importance have been found in wild relatives of cassava and that they could be introgressed into the cassava gene pool. They further found that among the most relevant traits are the tolerance to postharvest physiological deterioration (PPD) in *M. walkerae*, increased protein content in *M. tristis* and *M. peruviana*, resistance to the cassava green mite in *M. esculenta* sub spp. *flavellifolia*, and amylose-free starch in *M. crassisepala* and *M. chlorosticta*. Blair et al. (2007) suspected that the resistance to cassava mosaic disease and the hornworm originated from in segregating progenies from crosses involving *M. glaziovii* as one of the progenitors. Nassar and Ortiz (2008) reported improved nutritional quality in wild relatives of cassava. However, Fukuda et al. (2002) recommended that although interspecific hybridisation in cassava has potential, it should only be done after completely understanding its merits and demerits and whenever the modifications of some characteristics of *M. esculenta* are very necessary/desired.

D. Breeding of polyploids

This breeding method is based on the premise that polyploidy is associated with certain unique characteristics of the plant such as canopy vigour, including larger and thicker leaves and good leaf retention (Fukuda et al., 2002; Lebot, 2009). Leaves of polyploids are distinctly large even at the seedling stage. Their leaf stomata are generally larger and fewer per unit of the area of lamina. Also, their pollen grains are large (Lebot, 2009). Triploidy, as an effective tool in cassava improvement, especially for the production of high starch varieties for industrial use, was first realised in Kerala, India (Lebot, 2009). The triploids produced in India have been reported to be more vigorous than tetraploids, have stout stems, high leaf retention capacity, high percentage dry mass content (above 45%), and high starch content (Sreekumari et al., 2000) and high early bulking capacity (Suja et al., 2009). However, the method has been not been commonly used (Fukuda et al., 2002).

1.12 Breeding and selection for early bulking

There is an increasing trend towards developing early bulking cassava in response to increasing demand for early bulking cultivars by farmers (Kamau, 2006; Mtunda, 2009; Chikoti 2011; Tumuhimbise et al., 2012; Bassey and Gamaliel, 2013). The comparative maturity of crop cultivars are expressed in various ways, some of the common ones being days to heading in small grains and days to silking in maize or days to ripening (Sleper and Poehlman, 2006). In cotton, earliness may be measured by days to first flower, duration of ball-forming, or percentage of lint at first harvest (Shah, 2004). However, there is not a common understanding about the concept as it applies to cassava (Hershey, 2012). Physiologists have not recognised distinct stages of development in cassava, as are commonly defined for crops where seeds are the common product. Throughout most of the plant's life, foliage and storage roots develop simultaneously. Thus, there are no clear shoot traits to show when cassava plants start accumulating starch in the roots, except by harvesting the storage roots (CIAT, 1972; Kawano, 1987), which makes it difficult for breeding programmes to identify early bulking cultivars.

In the absence of direct plant shoot traits to follow in selection of early bulking cassava, indirect methods have been forwarded, for example Kawano (1987) recommended the use of FSRY as the criterion for assessing early bulking. Hershey (2012) reported that research on early bulking done at CIAT suggests that genotypes with the highest FSRY at an early harvest time tend also to be highest yielding genotypes at later stages and that therefore, high yield is co-selected for with early bulking. This was confirmed by Okogbenin et al. (2013) who indicated that productivity at 12 MAP can be used as a criterion to screen for early bulking because early fresh storage root yielders are the high yielders at later stages of FSRY evaluation.

In a study conducted by Okogbenin and Fregene (2002) to investigate traits associated with early bulking, they found that starch initiation time, storage root diameter, plant height, harvest index, dry foliage mass, number of storage roots and plant vigour were all significantly correlated with dry storage root yield. Thus, they suggested that those factors were components triggering early yield as a complex trait. Regression analysis of their experimental data showed that storage root diameter, dry foliage mass and harvest index were the most important factors for storage root bulking, suggesting that both the source and sink capacities were important in determining early bulking. Storage root diameter appeared to be the most important factor at the initial phase of root bulking, whereas harvest index and

foliage emerged as the most influential factors at the late phase of storage root development during the evaluation period. They concluded that one should select for high HI, dry foliage mass or both when breeding for early bulking.

Hershey (2012) suggested that storage root quality may be a primary indicator of maturity for farmers, because some genotypes appear to reach a certain starch content or quality earlier than others. He further suggested that late cultivars may maintain high quality levels for a longer period, irrespective of yield. He also indicated that another definition of maturity relates to storage root shape, whereby genotypes with short storage roots will generally produce storage roots of commercially useful diameter, earlier than those with long storage roots.

Studies conducted at CIAT by Kawano (1990) and Ojulong et al. (2010) showed that HI determined for the seedling and first clonal generations remained constant in subsequent clonal generations in a wide range of environmental conditions, indicating that HI is a better trait to select for than storage root yield when breeding for early bulking. Generally, there is not adequate information on the various factors that may define cassava early bulking. In the current study, selection for early bulking will be based on FSRY.

1.13 Breeding and selection for high storage root yield

High fresh storage root yield is achieved first by selecting plants that have both a genetic structure and a plant structure which maximises performance, and then by bringing together resistances or tolerances to the factors which limit yield (Jennings and Iglesias, 2002). The genetic base may be enlarged by making interspecific crosses with some of the many shrub species of the *Fruticocosae* section of *Manihot*. For instance, Ojulong (2006) reported that crossing of one of the elite CIAT cultivars MTAI 8 to the wild relative *M. tristis* increased the percentage dry mass content above the normal average of about 35%, with percentage dry mass content ranging from 34.4 to 42.7%. Some detrimental effects, however, did accompany the crosses, most noticeably being the reduction in HI. He thus recommended that when selecting for percentage dry mass content, caution should be exercised and HI and fresh storage root yield should be monitored.

Dry mass production and partitioning are important determinants of FSRY in cassava and could be important selection criteria in breeding programmes for improved FSRY (Lahai and Ekanayake, 2009). Cassava genotypes that produce high storage root dry mass also produce high leaf area index and FSRY (Lahai and Ekanayake, 2009). The distribution of dry mass is particularly important in cassava because the crop has simultaneous development of leaves,

stems and storage roots and the supply of assimilate is partitioned between these parts (Osiru and Hahn, 1998). This results in a delicate balance between shoot and storage root growth for maximum FSRY (Ramanujam, 1985). Generally, genotypes that allocate higher proportion of dry mass to storage roots than the stems and leaves give higher FSRY (Osiru and Hahn, 1998).

Fresh storage root yield in cassava is positively correlated with several plant traits that include: canopy mass (Ntawuruhunga and Dixon, 2010); number of storage roots per plant (Ojulong, 2008; Aina et al., 2009); plant height (Ntawuruhunga and Dixon, 2010) and HI (Ojulong, 2008; Aina et al., 2009; Ntawuruhunga and Dixon, 2010). The positive correlations for these traits confirm that they can be considered good criteria for selection for yield. Kawano et al. (1978) suggested that harvest index should be used with caution in the selection process because plants with high harvest indices and little canopy yield, even when they present high fresh storage root yield, are undesirable because they produce little propagation material.

1.14 Cassava pests and diseases in Uganda

Cassava production in Uganda is constrained by a number of pests and diseases (Ssemakula et al., 2004; Sseruwagi et al., 2004; Alicai et al., 2007). The most important diseases are cassava mosaic disease (CMD) and cassava brown streak (Hillocks and Thresh, 2000; Alicai et al., 2007; Legg et al., 2011; Ogwok et al., 2012). Cassava mosaic disease is caused by a whitefly (*Bemisia tabaci*) transmitted begomoviruses (family Geminiviridae) that occurs inside cassava leaves and stems (Otim-Nape et al., 1997; Sseruwagi et al., 2004; Ogbe et al., 2006). The leaves of diseased cassava plants are discoloured, with patches of normal green colour mixed with light green, yellow, and white areas. This discolouration is known as chlorosis, and it makes the formation of photosynthate by the leaves very hard. When cassava mosaic infection is severe, the leaves are very small and distorted, and the plants are stunted (Hillocks and Thresh, 2000).

Cassava brown streak disease is also caused by whitefly transmitted viruses of the family Potyviridae (Alicai et al., 2007; Ogwok et al., 2012). The disease represents a serious threat to food security in Uganda. It reduces cassava yields and also renders storage roots useless for human consumption due to the necrosis it causes to the starch storage tissues (Hillocks and Jennings, 2003). The CBSD used to be the second most important disease threatening cassava production after CMD, but now it ranks as the most devastating disease (Legg et al.,

2011; Ogwok et al., 2012). It is spread by infected cuttings, and by whitefly as the insect vector. Unlike CMD symptoms, the foliar symptoms of CBSD are less conspicuous and farmers are often unaware of the problem until the storage roots are harvested and the corky, yellow-brown necrotic rot becomes evident (Hillocks and Thresh, 2000).

Prior to 2004, high incidence of CBSD had never been recorded in Uganda, and was primarily known as a disease of the lowland cassava growing areas (Ntawuruhunga and Legg, 2007). However, from late 2004 onwards it became apparent that CBSD was becoming more and more widespread in parts of south-central Uganda. An important feature of CBSD in the country, is that its incidence is highest, and severity greatest in CMD-resistant cultivars that are being promoted for the management of the CMD pandemic. It is most prominent in cultivars such as TME 14, TME 204 and many other cultivars that are popular with farmers as supposedly being more resistant, and therefore the disease has spread very rapidly within and between farming communities.

Breeding and cultivation of cassava cultivars with resistance to CMD and CBSD is the most recommended method for managing these diseases (Hillocks and Jennings, 2003; Munga, 2008; Kulembeka et al., 2012; Parkes et al., 2013). The method works best, especially in areas where the disease pressure is high (Hillocks and Thresh, 2000).

Cassava insect pests include white flies, mealy bug (*Phenacoccus manihoti*) and the green spider mite (*Mononychellus tanajoa*) (Ojo et al., 1989). Among these pests, the green mite and white flies are the most important pests of cassava in Uganda (Sseruwagi et al., 2004; Ssemakula et al., 2004). Cassava green mite was inadvertently introduced into Uganda, where it was first reported in 1971 (Ojo et al., 1989). The amount of crop damage by cassava green mite depends on the fertility of the soil, cultivars, and the rainfall patterns. Heavy infestation of susceptible cultivars, especially during the dry season in poor soils can cause total leaf defoliation resulting in yield reduction of up to 46% (Ojo et al., 1989).

1.15 Postharvest physiological deterioration

Cassava storage roots have the shortest postharvest shelf life if compared to any of the key root crops (Salcedo and Siritunga, 2011). Storage roots are highly perishable and deteriorate within 24 h after harvest due to a rapid PPD process (Wheatley and Schwabe, 1985; Plumbley and Richard, 1991; Buschmann et al., 2000). Postharvest physiological deterioration is the main cause of the reduction in storage root acceptability after harvest and continues to be a huge challenge in the commercialisation of cassava (Beeching et al., 1999;

Buschmann et al., 2000). It involves vascular streaking due to the development of dark bluish or brownish radial veins or streaks near xylem vessels of the root pith tissue after harvest. It is visually observed as blue fluorescent tissue under ultraviolet light and blue-black streaking of the vascular tissues (Beeching et al., 1999). In addition, coloured occlusions and tyloses from the adjacent parenchyma are seen to block vessels (Richard, 1981). It is usually apparent within 48 h after harvest as rings of a dry, brown to black discolouration.

A number of factors enhance PPD, and the most critical is mechanical damage, which takes place during harvesting (Buschmann et al., 2000; Salcedo and Siritunga, 2011). The first symptoms of PPD appear in areas where the storage root peel has been damaged or removed or in the proximal and distal ends of the storage root, which are the most susceptible zones to physical damage. Additional factors include: storage root shape, root length, presence of peduncles (which minimises the exposure of storage root tissues to oxygen and thus storage roots with peduncles suffer less PPD); peel adherence and texture, soil compaction, and harvesting method (Salcedo and Siritunga, 2011).

Postharvest physiological deterioration response is under the influence of genetic factors, as well as the environment as confirmed by comparative evaluation studies by Buschmann et al. (2000). They indicated a considerable variation in degree of development and severity of PPD among different cassava cultivars and within the same cultivars. During an evaluation of eight cassava cultivars at three different locations in Colombia, Kawano and Rojanaridpiched (1983) found a highly significant interaction between location and season, suggesting that PPD was under the influence of environmental conditions.

Breeding has great potential to improve resistance to cassava PPD, however, little progress has been made for this trait (Morante et al., 2010). Efforts to improve resistance to cassava PPD has been complicated by a number of factors including: lack of proper assessment of the reaction to PPD due to the requirement of a relatively large number of large size storage roots (Morante et al., 2010), lack of genetic variability for resistance to PPD (Kawano and Rojanaridpiched, 1983; Ceballos et al., 2004) and positive correlation between PPD and storage root dry mass content (van Oirschot et al., 2000; Ceballos et al., 2004), suggesting that increasing storage root dry mass content indirectly increases PPD. This is frustrating to cassava breeders since high storage root dry mass content, a trait of major importance in most cassava breeding programmes is positively linked to high PPD.

1.16 Literature summary

Cassava, a native to South America, is an important storage root crop worldwide. It is a hardy crop with unique advantages of producing acceptable yields on infertile soils amidst erratic rainfall when most other crops would fail. In spite of cassava's hardiness, its yield potential is seldom realised because of numerous limiting factors including: soil infertility, droughts, pests, diseases, use of inferior and low yielding cultivars, and lack of improved early bulking cultivars. Nonetheless, there are a number of opportunities for genetic improvement of cassava, especially in terms of resistance to pests and diseases, storage root yield and early bulking. Improvement of these traits, particularly early bulking, stands to greatly benefit the many subsistence farmers and their families who rely on cassava and its products. Early bulking cultivars are crucial in production areas where there is growing pressure on agricultural land forcing farmers to intensify production, and in drier areas where early bulking cultivars can be harvested after only one cycle of rain. Conventional cassava breeding through hybridisation is, however, affected by a number of cassava intrinsic factors, including high levels of genetic heterozygosity, variable flowering patterns, low seed set and germination. Overall, the literature discussed in this chapter provides an understanding of the challenges, opportunities, and progress in cassava breeding.

References

Acquaah, G. 2009. Principles of plant genetics and breeding. Second edition. Blackwell publishing, Oxford, UK.

Aina, O.O., A.G.O. Dixon, I. Paul, and E.A. Akinrinde. 2009. GxE interaction effects on yield and yield components of cassava (landraces and improved) genotypes in the savannah regions of Nigeria. African Journal of Biotechnology 8:4933-4945.

Alicai, T., C.A. Omongo, M.N. Maruthi, R.J.Hillocks, Y. Baguma, R. Kawuki, A. Bua, G.W. Otim-Nape and J. Colvin. 2007. Re-emergence of cassava brown streak disease in Uganda. Plant Diseases 91:24-29.

Allem, A.C. 2002. The origins and taxonomy of cassava. In: R.J. Hillocks, et al. (eds.), Cassava: Biology, production and utilisation. CABI, Wallingford, UK. p. 1- 6.

Alves, A.A.C. 2002. Cassava botany and physiology. In: R.J. Hillocks, et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 67-89.

Amenorpe, G., H.M. A. Amoatey, A. Darkwa, G.K. Banini, and V.W. Elloh. 2007. Peak root and starch weights of ten early bulking cultivars of cassava (*Manihot esculenta* Crantz) in Ghana. Journal of Ghana Science Association 9:54-60.

Annicchiarico, P., and M. Perenzin. 1994. Adaptation patterns and definition of macro environments for selection and recommendation of common wheat genotypes in Italy. Plant Breeding 113:197-205.

Asante, I.K., and S.K. Offei. 2003. RAPD-based genetic diversity study of fifty cassava (*Manihot esculenta* Crantz) genotypes. Euphytica 131:113-119.

Bai, K. V. 1985. Recent advances in cassava genetics and cytogenetics. In: Cassava breeding: A multidisciplinary review. In: Proceedings of a Workshop held in the Philippines, June 1985. p. 36-49.

Bassey, E.E., and I.H. Gamaliel. 2013. Screening cassava (*Manihot esculenta* Crantz) genotypes for tuber bulking, early maturity and optimum harvesting time in Uyo, South Eastern Nigeria. Peak Journal of Agricultural Sciences 1:83-88.

Beeching, J.R., H. Buschmann, R. Gómez-Vásquez, Y. Han, C. Iglesias, H. Li, K. Reilly, and M.X. Rodriguez. 1999. An abiotic stress response in cassava: postharvest physiological deterioration. In: M.F. Smallwood et al. (eds.), Plant responses to environmental stress. Oxford: BIOS p. 205-210.

Bitai, Z., and N. P. Lian. 1978. Parents selection and its combination for early maturing high starch and high yielding sweet potato breeding. Jiangsu Journal of Agricultural Science 4:22-27

Blair, M.W., M.A. Fregene, S.E. Beebe, and H. Ceballos. 2007. Marker assisted selection in common beans and cassava. In: E.P. Guimaraes et al. (eds.), Marker-assisted selection (MAS) in crops, livestock, forestry and fish: current status and the way forward. FAO Publishing, Rome, Italy. p. 81-115.

Brown, J., and P. D.S. Caligari. 2009. An introduction to plant breeding. Second edition. Blackwell Publishing Ltd, Oxford, UK.

Buerno, A. 1986. Evaluation of cassava cultivars to select parents for cross breeding. Revista Brasileira de Mandioca 5:23-54.

Buschmann, H., M.X. Rodriguez, J. Tohme, and J.R. Beeching. 2000. Accumulation of hydroxycoumarins during post-harvest deterioration of tuberous roots of cassava (*Manihot esculenta* Crantz). Annals of Botany 86:1153-1160.

Byrne, D. 1984. Breeding cassava. Plant Breeding Reviews 2:73-133.

Cach, N.T., J.I. Lenis, J.C. Perez, N. Morante, F. Calle, and H. Ceballos. 2006. Inheritance of useful traits in cassava grown in sub-humid conditions. Plant Breeding 125:177-182.

Calle, F., J.C. Perez, W. Gaitan, N. Morante, H. Ceballos, G. Llano, and E. Alvarez. 2005. Diallel inheritance of traits in cassava (*Manihot esculenta* Crantz) adapted to acid soil savannas. Euphytica 144:177-186.

Ceballos, H., C.A. Iglesias, J.C. Pérez, and A.G.O. Dixon. 2004. Cassava breeding: opportunities and challenges. Plant Molecular Biology 56:503-515

Ceballos, H., P. Kulakow, and C. Hershey. 2012. Cassava breeding: Current status, bottlenecks and the potential of biotechnology tools. Tropical Plant Biology 5:73-87.

Ceccarelli, S., and S. Grando. 1991. Selection environments and environmental sensitivity in barley. Euphytica 57:157-167.

Chang-Ho, P., K. Kim, H. Aswidinnoor, and F. Rumawas. 2005. Varietal differences of drymatter accumulation and related characters in cassava (*Manihot esculenta* Crantz). Korean Journal of Crop Science 50: 45-54.

Chavarriaga-Aguirre, P., and M. Halsey. 2005. Cassava (*Manihot esculenta* Crantz): Reproductive biology and practices for confinement of experimental field trials. Report prepared for the programme for biosafety systems, Washington, USA. p. 1-20.

Chikoti, P. C. 2011. Development of cassava (*Manihot esculenta* Crantz) cultivars for resistance to cassava mosaic disease in Zambia. PhD thesis, University of KwaZulu-Natal, South Africa.

CIAT. 1972. Centro Internacional de Agricultura Tropical. Annual report for 1971.

CIAT. 2002. Improved cassava for the developing world. Annual report for 2001.

Cock, J.H. 1975. Characteristics of high yielding cassava varieties. Experimental Agriculture 12:135-143.

Cock, J.H., D. Franklin, G. Sandoval, and P. Juri.1979. The ideal cassava plant for maximum yield. Crop Science 19:271-279.

Colombo, C., G. Second, and A. Charrier. 2000. Diversity within American cassava germplasm based on RAPD markers. Genetics and Molecular Biology 31:189-199.

Cours, G. 1951. Le manioc â Madagascar. Mémories de l'Institut Scientifique de Madagascar. Serie B3. 2:203-400.

De Carvalho, R.D., and M. Guerra. 2002. Cytogenetics of *Manihot esculenta* Crantz (cassava) and eight related species. Hereditas 136:159-168.

Dixon, A.G.O., M.O. Akoroda, R.U. Okechukwu, F. Ogbe, P. Ilona, L.O. Sanni, C. Ezedinma, J. Lemchi, G. Ssemakula, M.O. Yomeni, E. Okoro, and G. Tarawali. 2008. Fast track participatory approach to release of elite cassava genotypes for various uses in Nigeria's cassava economy. Euphytica 160:1-13.

Doku, E.V. 1969. Cassava in Ghana. Accra, Ghana Universities Press. p. 44.

Eberhart, S.A., and W.A. Russell. 1996. Stability parameters for comparing varieties. Crop Science 6:36-40.

Egesi, C.N., P. Ilona, F.O. Ogbe, M. Akoroda, and A. Dixon. 2007. Genetic variation and genotype x environment interaction for yield and other agronomic traits in cassava in Nigeria. Agronomy Journal 99:1137-1142.

Ekanayake I.J., D.S.O. Osiru, and M.C.M. Porto. 1998. Physiology of cassava. IITA Research guide no. 55. Third edition. IITA, Ibadan, Nigeria. p. 32.

Ekanayake, I.J., D.S.O. Osiru, and M.C.M. Marcio. 1997. Morphology of cassava. IITA Research Guide 61.

Ellis, R.H., T.D. Hong, and E.H. Roberts. 1982. An investigation of the influence of constant and alternating temperature on the germination of cassava seed using a two-dimensional temperature gradient plate. Annals of Botany 49:241-246.

El-Sharkawy, M.A. 2003. Cassava biology and physiology. Plant Molecular Biology 56:481-501.

El-Sharkawy, M.A. 2007. Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments. Brazilian Journal of Plant Physiology 19:257-286.

El-Sharkawy, M.A. 2012. Stress-tolerant cassava: the role of integrative ecophysiology-breeding research in crop improvement. Open Journal of Soil Science 2:162-186.

Enyi, B.A.C. 1972. Effect of shoot number and time of planting on growth, development and yield of cassava (*Manihot esculenta* Crantz). Journal of Horticultural Science 47:457-466.

Falconer, D.S and T.F.C. Mackay, 1996. Introduction to quantitative genetics. Fourth edition. Longman Scientific and technical Co., Exssex, England.

Flores, F., M.T. Moreno, and J.I. Cubero. 1998. A comparison of univariate and multivariate methods to analyse GxE interaction. Field Crops Research 56:271-286.

Fregene, M., A. Bernal, M. Durque, A. Dixon, and J. Tohme. 2000. AFLP analysis of African cassava (*Manihot esculenta* Crantz) germplasm resistant to the cassava mosaic disease (CMD). Theoretical and Applied Genetics 100:678-685.

Fregene, M.A., M.W. Blair, S.E. Beebe, and H. Ceballos. 2007. Marker-assisted selection in common beans and cassava. In: marker-assisted selection (MAS) in crops, livestock, forestry and fish: current status and the way forward. FAO Publishing, Rome, Italy. p.471.

Fukuda, W.M. G., S. de Oliveira, Silva, and C. Iglesias. 2002. Cassava breeding. Crop Breeding and Applied Biotechnology 2:617-638.

Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing system. Australian Journal of Biological Sciences 9:463-93.

Grüneberg, W., R. Mwanga, M. Andrade, and J. Espinoza. 2009. Selection methods Part 5: Breeding clonally propagated crops. In: S. Ceccarelli et al. (eds.), Plant breeding and farmer participation. Food and Agriculture Organization, Rome, Italy. p. 275-322.

Hahn, S.K., A.K. Howland, and E.R. Terry. 1980a. Correlated resistance of cassava to mosaic and bacterial blight diseases. Euphytica 29:305-311.

Hahn, S.K., E.R. Terry and K. Leuschner, 1980b. Breeding cassava for resistance to cassava mosaic disease. Euphytica 29:673-683.

Hayman, B.I. 1954.The theory and analysis of diallel crosses. Genetics 39:789-809.

Hershey, C., 2012: Cassava genetic improvement: theory and practice. FAO Publishing, Rome, Italy. In press.

Hillocks, R.J., and D.L. Jennings. 2003. Cassava brown streak disease: A review of present knowledge and research needs. International Journal of Pest Management 49:225-234.

Hillocks, R.J., and J.M. Thresh. 2000. Cassava mosaic and cassava brown streak virus diseases in Africa. Roots 7:1-12.

Huhn, M. 1996. Non-parametric analysis of genotype x environment interactions by ranks. In: genotype by environment interaction. Kang, M.S., and Gauch HG. (eds.), CRC Press, Boca Raton, New York. p. 213-228.

Hunt, L.A., D.W. Wholey, and J.H. Cock. 1977. Growth physiology of cassava. Field Crops Abstract 30:77-91

Iglesias, C.A. and C. Hershey, 1994. Cassava breeding at CIAT: Heritability estimates and genetic progress in the 1980s. In: Ofori, F. and S.K. Hahn (eds.), Tropical root crops in a developing economy. ISTC/ISHS, Wageningen, Netherlands. p. 149-163.

IITA, 1990. Cassava in Tropical Africa. A reference manual. Balding and Mansell International, Wesbech, UK. p.176.

IITA, 2001: International Institute of Tropical Agriculture: Cassava subsector analysis report Uganda. p.1-68.

Indira, P., and S.K. Sinha. 1970. Studies on the initiation and development of tubers in *Manihot esculenta* Crantz. Indian Journal of Plant Physiology 13:24-39.

Irikura, Y., J.H. Cock, and K. Kawano. 1979. The physiological basis of genotype-temperature interactions in cassava. Field Crops Research 2:227-239.

Izumi, Y., E. Yuliadi, Sunyoto, and M. Iijima. 1999. Root system development including root branching in cuttings of cassava with reference to shoot growth and tuber bulking. Plant Production Science 2:267-272.

Jaramillo, G., N. Morante, J.C. Perez, F. Calle, H. Ceballos, B. Arias, and A.C. Bellotti. 2005. Diallel analysis of cassava adapted to the mid-altitude valleys environment. Crop Science 45:1058-1063.

Jennings, D. L. 1957. Further studies in breeding cassava for virus resistance. East Africa Agriculture Journal 22:213-229.

Jennings, D.L. 1963. Variation in pollen and ovule fertility in varieties of cassava, and the effect of interspecific crossing on fertility. Euphytica 12:69-76.

Jennings, D.L. 1976. Cassava, *Manihot esculenta* (Euphorbiaceae). In: Simmonds, N. (ed.), Evolution of crop plants. Longman, London. p. 81-51.

Jennings, D.L., and C. Iglesias. 2002. Breeding for crop improvement. In: R.J. Hillocks et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 149-166.

Jos, J.S., and R.B. Nair. 1984. Genetics of male sterility in a genotype of cassava. Current Science 53:494-496.

Kamau, J. W. 2006. Participatory based development of early bulking cassava varieties for the semi-arid areas of Eastern Kenya. PhD thesis, University of KwaZulu-Natal, South Africa.

Kawano, K. 1980. Cassava. In: Hybridisation of crop plants. America Society of Agronomy and Crop Science Society of America, Madison, Wisc, USA. p. 225-233.

Kawano, K. 1987. Inherent and environmental factors related to cassava varietal selection In: Hershey, C. (ed.), Cassava breeding: a multidisciplinary review. CIAT, Cali, Colombia. p. 207-226.

Kawano, K. 1990. Harvest index and evolution of major food drop cultivars in the tropics. Euphytica 46:195-202.

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

Kawano, K., A. Amaya, and M. Rios. 1978. Factors affecting efficiency of hybridization and selection in cassava. Crop Science 17:373-376.

Kawano, K., and C. Rojanaridpiched. 1983. Genetic study on postharvest root deterioration in cassava. The Kasetsart Journal 17:14-26.

Kawano, K., K. Narintaraporn, P. Narintaraporn, S. Sarakarn, A. Limsila, J. Limsila, D. Suparhan, V. Sarawat, and W. Watananonta. 1998. Yield improvement in a multistage breeding program for cassava. Crop Science 38:325-332.

Kawano, K., K. Narintaraporn, P. Narintaraporn, S. Sarakarn, A. Limsila, J. Limsila, Keating, B.A., J.P. Emenson, and S. Fukai. 1982. Enviromental effects on growth and development of cassava (*Manihot esculenta* Crantz), I, crop development. Field Crops Research 5:271-281.

Keutgen, M., F. Kubota, and K. Saitou. 2001. Effects of exogenous injection of sucrose solution to plant on the carbon distribution to tuberous root and tuberous root production in sweet potato (*Ipomoea batatas* Lam.). Japan Journal of Crop Science 70:575-579.

Kulembeka, H.P., M. Ferguson, L. Herselman, E. Kanju, G. Mkamilo, E. Masumba, M. Fregene, and M.T. Labuschagne. 2012: Diallel analysis of field resistance to brown streak disease in cassava (*Manihot esculenta* Crantz) landraces from Tanzania. Euphytica 187: 277-288.

Kvitschal, M.V., P.S.V. Filho, C.A. Scapim, M.C. Gonçalves-Vidigal, M.G. Pequeno, E. Sagrilo and F. Rimoldi, 2006: Evaluation of phenotypic stability of cassava clones by AMMI analysis in northwestern Paraná state. Crop Breeding and Applied Biotechnology 6:236-241.

Lahai, M.T., and I.J. Ekanayake. 2009. Accumulation and distribution of dry matter in relation to root yield of cassava under a fluctuating water table in inland valley ecology. African Journal of Biotechnology 8:4895-4905

Lathrap, D.W. 1973. The antiquity and importance of long-distance trade relationships in the moist tropics of Pre-Columbian South America. World Archaeology 5:170-186.

Lebot, V. 2009. Tropical Root and Tuber Crops Cassava, sweet potato, yams and aroids. Crop Production Science in Horticulture Series,17. MPG Books Group, Reading, UK.

Legg, J.P., S.C. Jeremiah, H.M. Obiero, M.N. Maruthi, I. Ndyetabula, G. Okao-Okuja, H. Bouwmeester, S. Bigirimana, W. Tata-Hangy, G. Gashaka, G. Mkamilo, T. Alicai, and L.P. Kumar. 2011. Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa. Virus Research 159:161-170.

Magoon, M.L., J.S. Jos, and K.M. Vasudevan. 1968. Male sterily cassava. Nucleus 11:1-6.

Morante, N., T. Sánchez, H. Ceballos, F. Calle, J.C Pérez, C. Egesi, C.E. Cuambe, A.F. Escobar, D. Ortiz, A.L. Chávez, and M. Fregene. 2010. Tolerance to postharvest physiological deterioration in cassava roots. Crop Science 50:1333-1338.

Morante, N., X. Moreno, J.C. Perez, F. Calle, J.I. Lenis, E. Ortega, G. Jaramillo, and H. Ceballos. 2005. Precision of selection in early stages of cassava genetic improvement. Journal of Root Crops 31:81-92.

Mtunda, K.J. 2009. Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.

Munga, T.L. 2008. Breeding for cassava brown streak resistance in coastal Kenya. PhD Thesis, University of KwaZulu-Natal, South Africa.

Nassar, N.M A., and R. Ortiz. 2006. Cassava improvement: challenges and impacts. Journal of Agricultural Science 145:163-171.

Nassar, N.M.A. 2004. Cassava: Some ecological and physiological aspects related to plant breeding. Gene Conserve 3: 229-245.

Nassar, N.M.A., and R. Ortiz. 2008. Cassava genetic resources: manipulation for crop improvement. Plant Breeding Reviews 31:247–275.

Nichols, R.F.W. 1947. Breeding cassava for virus resistance. East Africa Agriculture and Forestry Journal 12:184-194.

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

Ntawuruhunga, P., and J. Legg. 2007. New spread of cassava brown streak virus disease and its implications for the movement of cassava germplasm in the east and central African region. Crop crisis control project, IITA, Uganda. Report p.1- 6.

Ogbe, F.O., A.G.O. Dixon, J.A. Hughes, O.J. Alabi, and R. Okechukwu. 2006. Status of cassava begomoviruses and their new natural hosts in Nigeria. Plant Diseases 90:548-553.

Ogwok, E., J. Odipio,M. Hasley, E. Gaitan-Solis, A. Bua, N.J. Taylor, C.M. Fauquet, and T. Alicai. 2012. Transgenic RNA interference (RNAi)-derived field resistance to cassava brown streak disease. Molecular Plant Pathology 13:1019-1031.

Ojo, J.B., G.J. de Moraes, and R.H. Markham. 1989. Handbook on the cassava green mite (*monoychellus tanajoa* Bondar) in Africa. IITA, Ibadan, Nigeria p. 210.

Ojulong, H., M.T. Labuschangne, M. Fregene, and L. Herselman. 2008. Introgression of genes for dry matter content from wild cassava species. Euphytica 164:163-172.

OJulong, H.F. 2006. Quantitative and molecular analyses of agronomic traits in cassava (*Manihot esculenta* Crantz). Doctoral Thesis, University of the Free State, Bloemfontein, South Africa.

Ojulong, H.F., M.T. Labuschagne, L. Herselman, and M. Fregene. 2010. Yield traits as selection indices in seedling populations of cassava. Crop Breeding and Applied Biotechnology 10:191-196.

Ojulong, H.F., M.T. Labuschagne, M. Fregene, and L. Herselman. 2008. A cassava clonal evaluation trial based on a new cassava breeding scheme. Euphytica 160:119-129.

Okogbenin, E., and M. Fregene. 2002. Genetic and QTL mapping of early root bulking in an F_1 mapping population of non-inbred parents in cassava (*Manihot esculenta* Crantz). Theoretical and Applied Genetics 106:58-66.

Okogbenin, E., T.L. Setter, M. Ferguson, R. Mutegi, H. Ceballos, B. Olasanmi, and M. Fregene. 2013. Phenotypic approaches to drought in cassava: review. Frontiers in Physiology 4:1-15.

Onwueme, I .C. 1982. The Tropical Tuber Crops. John Willey and sons. Chichester.

Onwueme, I.C. 1978. The tropical tuber crops: yams, cassava, sweet potato, and cocoyam's. Wiley, New York, USA.

Ortiz, R., S. Madsen, W.W. Wagoire, J. Hill, S. Chandra, and O. Stolen. 2001. Additive main effect and multiplicative interaction model for diallel-cross analysis. Theoretical and Applied Genetics 102:1103-1106.

Osiru, D.S.O., and S.K. Hahn. 1998. Dry matter production and partitioning in cassava (*Manihot esculenta*) intercropped with maize or groundnuts. In: Akoroda, M.O. and I.J. Ekanayake (eds.), Root crops and poverty alleviation, Proceedings of Sixth Symposium of ISTRC-AB held at Lilongwe, Malawi, Ibadan: IITA/ International Society for Tropical Root Crops. p. 76.

Otim-Nape, G.W., A. Bua, J.M. Thresh, Y. Baguma, and S. Ogwal. 1997. Cassava mosaic virus disease in Uganda: the current pandemic and approaches to control. Natural Resource Institute, Chatham, UK.

Owolade, O.F, A.G.O. Dixon, and A.Y.A. Adeoti. 2006: Diallel analysis of cassava genotypes to anthracnose disease. World Journal of Agricultural Science 2:98-104.

Parkes, E. Y., M. Fregene, A. Dixon, B. Boakye-Peprah, and M.T. Labuschagne. 2013. Combining ability of cassava genotypes for cassava mosaic disease and cassava bacterial blight, yield and its related components in two ecological zones in Ghana. Euphytica 194:13-24.

Perez, J.C., H. Ceballos, F. Celle, N. Morante, W. Gaitan, G. Llano, and E. Alvarez. 2005. Within family genetic variation and epistasis in cassava (*Manihot esculenta* Crantz) adapted to the acid-soil environment. Euphytica 145:77-85.

Plumbley, R.A., and J.E. Richard. 1991. Post-harvest deterioration of cassava. Tropical Science 31:295-303.

Ramanujam, T. 1985. Leaf density profile and efficiency in partitioning dry matter among high and low yielding cultivars of cassava (*Manihot esculenta* Crantz). Field Crops Research 10: 291-303.

Ravi, V., S.K. Naskar, T. Makeshkumar, B. Babu, and B. S. Prakash-Krishnan. 2009. Molecular physiology of storage root formation and development in sweet potato (*Ipomoea batatas* (L.) Lam.). Journal of Root Crops 35:1-27.

Richard, J.E. 1981. Biochemical changes involved in the post-harvest deterioration of cassava roots. Tropical Science, 23:3-9.

Salcedo, A., and D. Siritunga. 2011. Insights into the physiological, biochemical and molecular basis of postharvest deterioration in cassava (*Manihot esculenta*) roots. American Journal of Experimental Agriculture 1:414-431.

Shah, M.K.N. 2004. Genetics of early crop maturity in upland cotton (*Gossypium hirsutum* (L.). Doctoral Thesis, Bahauddi Zakariya University, Mutan, Pakistan.

Sleper, D.A., and J.M. Poehlman. 2006. Breeding field crops. Fifth edition. Blackwell Publishing. Iowa, USA.

Sprague, G. F. 1966. Quantitative genetics in plant improvement. In: K. J. Frey (ed.), Plant breeding, Iowa State University Press, Ames. p. 315-343.

Sreekumari, M.T., K. Abraham, and S.G. Nair. 2000. Triploidy Breeding in cassava. CTCRI, Technical Bulletin Series 30, Trivandrum, India.

Ssemakula, G., and A. Dixon. 2007. Genotype x environment interaction, stability and agronomic performance of carotenoid-rich cassava clones. Scientific Research and Essay 2:390-399.

Ssemakula, G.N., W.S. Sserubombwe, A. Bua, J. Jagwe, R.S.B. Ferris, and J.B.A. Whyte. 2004. Constraints and potential for cassava commercialisation in Uganda. In: Proceedings of regional Workshop on improving the cassava sub-sector, Nairobi, April 2002. p. 57-60.

Sseruwagi, P., W.S. Sserubombwe, J.P. Legg, J. Ndunguru, and J.M. Thresh. 2004. Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review. Virus Research 100:129-142.

Suja, G., K.S. John, J. Sreekumari, and T. Srinivas. 2009. Short-duration cassava genotypes for crop diversification in the humid tropics: growth dynamics, biomass, yield and quality. Journal of Science and Food Agriculture 90:188-198.

Tan, S.L., and C. Mak, 1995. Genotype x Environment influence on cassava performance. Field Crop Research 42:111-123.

Tumuhimbise, R. R. Melis, P. Shanahan, and R. Kawuki. 2012. Farmers' perceptions on early storage root bulking in cassava (*Manihot esculenta* Crantz) in east and central Uganda and their implication for cassava breeding. World Journal of Agricultural Sciences 8:403-408.

Van Oirschot, Q.E.A., G.M. O'Brien, D.D. Dufour, M.A. El-Sharkawy, and E. Mesa. 2000. The effect of pre-harvest pruning of cassava upon root deterioration and quality characteristics. Journal of Science and Food Agriculture 80:1866-1873.

Wang, C., Z. Lentini, E. Tabares, M. Quintero, H. Ceballos, B. Dedicova, C. Sautter, C. Olaya, and Z. Peng. 2011. Microsporogenesis and pollen formation in cassava (*Manihot esculenta* Crantz). Biologia Plantarum 55:469-478.

Westwood, N.N. 1990. Maintenance and storage: clonal germplasm. Plant Breeding Reviews 7:111–128.

Wheatley, C., and W. Schwabe. 1985. Scopoletin involvement in postharvest deterioration of cassava roots (*Manihot esculenta* Crantz). Journal of Experimental Botany 36:783-791.

Wholey, D.W., and J.H. Cock. 1974. Onset and rate of root bulking in cassava. Experimental Agriculture 10:193-198.

Yang, J., A. Dong, and Z. Peng. 2011. Expression profiling of cassava storage roots reveals an active proess of glycolysis/glyconeogenesis. Journal of Intergrative Plant Biology 53:193-211.

Zacarias, A.M., and M.T. Labuschagne, 2010. Diallel analysis of cassava brown streak disease, yield and yield related characteristics in Mozambique. Euphytica 176:309-320.

CHAPTER 2

Farmers' attitudes and/or perceptions on cassava early bulking, production constraints and cultivar preferences in Uganda[2]

Abstract

Development of early bulking cassava has become important in the national cassava breeding programmes in Africa as a result of increasing demand for such cultivars by farmers. However, in Uganda insufficient information is available regarding farmers' preferred cultivar traits, including early bulking, as well as production constraints. The objective of this study was to assess farmers' production constraints, awareness of early bulking and preferred traits in cassava. For this purpose, a participatory rural appraisal involving 120 cassava farmers was conducted in three major cassava growing districts in Uganda: Jinja; Busia and Mukono, using a multistage sampling technique. A number of cassava production constraints were identified, key of which were: diseases, especially cassava brown streak and mosaic diseases and lack of early bulking cultivars. Seventy five percent of the farmers had knowledge of early bulking cassava cultivars, of which some were identified in the farmers' fields. Farmers indicated that early bulking cultivars are more valued, especially in provision of quick food and income, allowing for sequential cropping systems within a short period, as well as in escaping late season droughts, pests and diseases. Farmers also rated early bulking as the second most important preferred trait after high fresh storage root yield. They, however, suggested that early bulking should be complemented with high dry mass content, sweetness, high fresh storage root yield and resistance to pests and diseases. Since farmers select cultivars based on multiple criteria, development of suitable high yielding early bulking cassava cultivars, combining farmer preferred traits, requires that participatory plant breeding approaches must be an integral part of cassava breeding in Uganda.

[2] Some results of this study were published: Tumuhimbise, R. R. Melis, P. Shanahan, and R. Kawuki. 2012. Farmers' perceptions on early storage root bulking in cassava (*Manihot esculenta* Crantz) in east and central Uganda and their implication for cassava breeding. World Journal of Agricultural Sciences 8:403-408.

2.1 Introduction

Cassava (*Manihot esculenta* Crantz) is an important starchy storage root crop grown worldwide. Its production has increased from about 176 million tonnes (MT) in 2000 to about 257 MT in 2012 (FAO, 2012), and is expected to grow further due to the higher demand for food, as well as for cassava's potential as a source of raw material for industrial products. It is a principal staple food in sub-Saharan Africa, where it accounts for approximately one-third of the total production of staple food crops (FAO, 2012). It plays a key role as food security and an income-generating crop for most smallholder farmers in developing countries. Cassava has the ability to produce a high amount of starch per unit area (Tonukari, 2004), flexibility in harvesting dates and is tolerant to marginal soils where most other crops would fail (Egesi et al., 2007; El-Sharkawy, 2012). These traits have made cassava a popular crop among smallholder farmers in sub-Saharan Africa.

In Uganda, cassava is grown throughout the country, primarily by smallholder farmers, with the main production system being intercropping (IITA, 2001). Several cultivars are grown in the country of which some are known to farmers to be early bulking. According to these farmers early bulking cultivars are those cultivars that produce enlarged storage roots of not less than 10 cm girth at ≤12 months after planting (MAP) and are acceptable to the market. They also believe that such cultivars should produce reasonable storage root yields of about 10 t ha^{-1} when harvested at ≤12 MAP. Such cultivars have become more important in situations where there is mounting pressure on land and farmers need to intensify production, and in drier areas where early cultivars are harvested after only one cycle of rain (El-Sharkawy, 2007; Suja et al., 2009; Kamau et al., 2011). Indeed, according to Okogbenin and Fregene (2002), early bulking is a key requirement for the transition of cassava from a traditional to an industrial crop.

Farmers in Africa perceive sweet cassava cultivars to be early bulking and bitter cultivars as late bulking (Amenorpe et al., 2007). Nweke et al. (1994) found that late bulking is the single most important factor for rejection of a cassava cultivar in most African countries, and Uganda is no exception. Late bulking cultivars occupy land for a long period of time and consequently the land occupied cannot be effectively utilised for the cultivation of other crops (Suja et al., 2009). In addition, Wholey and Cock (1974) stressed that one way of improving the efficiency of cassava production in terms of fresh storage root yield per unit time is by shortening its growth period through the identification and selection of early bulking cultivars. In breeding for early bulking, key storage root quality traits such as high dry mass content,

cyanogenic potential, sweetness and other organoleptic-associated traits, should not be ignored.

A considerable number of plant breeding programmes in developing countries have failed due to lack of involvement of farmers, leading to low adoption rates of released varieties (Efisue et al., 2008; Kamau, et al., 2011; Were et al., 2012). Duguma et al. (2010) stressed that in a breeding programme, the target production system has to be well understood and characterised in the context of farming and non-farm activities. The authors further stressed that the description of the production environment should be detailed and clear decisions made for the target groups within the area. Farmers usually have indigenous knowledge of their respective local environments that could be of value to the cassava improvement process (Ceccarelli and Grando, 2007; Efisue et al., 2008; Were et al., 2012); moreover they are also aware of the key agronomic traits appropriate for their localities and quality traits such as taste, size and colour of the harvested product. Therefore, it is imperative that breeding programmes provide forums for input from the farmers.

Approaches that involve the active participation of target clientele in breeding can quickly identify key traits needed in parental genotypes (Witcombe, 2009). Unfortunately, this is an aspect that is largely ignored, a phenomenon which in part explains why many farmers at times continue to grow landraces, which have farmer-preferred attributes as opposed to the new officially released varieties (Witcombe, 2009). During the early 1990s, breeders tended to focus on high crop yields and resistance to pests and diseases, without considering farmers' views and trait preferences (Sumberg and Reece, 2004; Ceccarelli and Grando, 2007). Moreover, they would often work in isolation from farmers and at times unaware of the importance of preferences beyond yield, and resistance to pests and diseases. Taste, cooking qualities and earliness are just a few of the dozens of crop traits of interest to smallholder farmers. However, in the past 12 years participatory plant breeding approaches such as surveys and focus group discussions have been deemed necessary to elicit such vital information on what is needed by farmers (Ceccarelli and Grando, 2007; Efisue et al., 2008; Kamau et al., 2011; Parkes, 2011; Were at al., 2012). In the public sector, such surveys are often referred to as participatory rural appraisals and are comparable to the market research approach of the private sector (Sumberg and Reece, 2004).

Based on this background information, this study was conducted with the following objectives:

1. To identify constraints encountered by farmers in cassava production;
2. To assess farmers' awareness of cassava early bulking;
3. To understand farmers' cassava cultivar selection criteria; and
4. To identify farmer-preferred traits.

2.2 Materials and methods

2.2.1 Study sites

This study was conducted in three major cassava growing districts in Uganda; Jinja and Busia both located in eastern Uganda, and Mukono located in central Uganda (Figure 2.1). Jinja district lies at 00°30′N 33°12′E; Busia, 00°23′N 34°00′E; and Mukono, 00°20′N 32°45′E. Cassava in these districts is consumed in different forms. In Busia it is consumed mainly in the form of a local bread; in Mukono in boiled form; and in Jinja in both forms (bread and boiled). In addition, the production of cassava in these areas is largely concentrated among smallholder farmers whose farming conditions are diverse. The farmers are resource-poor and encounter several production constraints.

2.2.2 Data collection and sampling method

Data on cassava-based cropping systems practiced by farmers, their production constraints, awareness of early bulking and preferred traits, as well as cultivar selection criteria were collected using questionnaire-led interviews (Appendix 2.1) and field observations. A district was used as the basis for sampling. From each district, 40 cassava farmers were sampled. A multistage sampling method was used in selection of farmers to participate in interviews. The first stage involved purposive selection of three districts, which was based on relative importance in cassava production in those districts. They are all key cassava growing areas in Uganda. The second stage involved random sampling of four sub-counties per district, giving a total of 12 sub-counties. The last stage involved random sampling of 10 cassava growing households per sub-county, making a total of 120 household respondents. The identification of farmer-households was facilitated by the government agricultural extension workers at the sub-county headquarters and also by the local council officials. Subsequently, a team of researchers comprised of four agricultural extension workers and a breeder administered questionnaire-led interviews to the farmers. Each of the research team members interviewed one individual farmer at a time, and also made field evaluations to identify cassava cultivars grown.

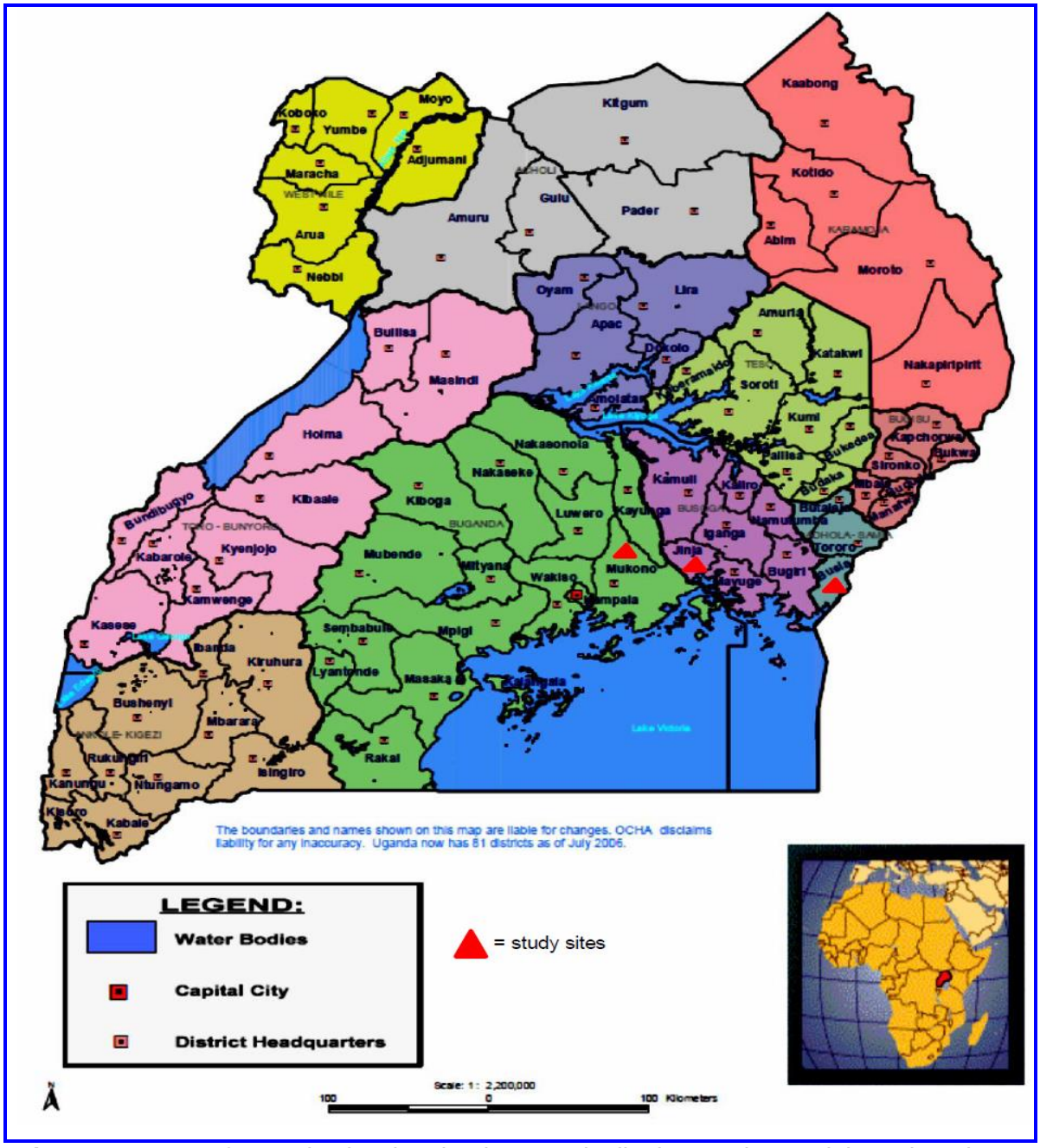

Figure 2.1: Map of Uganda showing the three study districts: Mukono, Jinja and Busia

2.2.3 Data analysis

The data collected were coded and analysed using a Statistical Package for Social Scientists (SPSS), 16th version (Carver and Nash, 2009). A combination of analyses that included percentages, means, and cross tabulations was performed. Histograms were constructed for some data to show the relationships between variables.

2.3 Results

2.3.1 Cassava production constraints

A number of cassava production constraints were identified in the districts (Table 2.1). The incidence of diseases was the most common problem in all districts, indicated by 100% of the farmers in Busia, 92.5% in Jinja and 100% in Mukono. The key diseases identified were cassava brown streak disease (CBSD) and cassava mosaic disease (CMD) (Figure 2.2). Lack of early bulking cassava cultivars was the second most important problem reported by 77.5% of the farmers in Busia, 50.0% in Jinja and 67.5% in Mukono. Rodents, especially mole rats (*Cryptomys hottentotus*), squirrels (*Sciurus carolinensis*) and porcupines (*Hystrix africaeaustralis*), were the third most important problem. The problem was most common in Jinja, where it was indicated by 70.0% of the farmers and least in Mukono where it was indicated by 17.5% of the farmers. Insect pests, especially green spider mites (*Mononychellus tanajoa*), white flies (*Bemisia tabaci*) and termites (*Cryptotermes* spp.) were the next major constraint in these districts, indicated by 47.5% of the farmers in Busia, 50.0% in Jinja and 22.5% in Mukono. Other key cassava production constraints in their order of importance were: unavailability of high yielding cultivars, weeds, theft and lack of cassava markets, which was mostly reported in Jinja by 32.5% of the farmers. The lack of agricultural credit facilities, farm implements and inputs, as well as poor underground storability of storage roots by some cultivars were identified as minor constraints to cassava production. The problem of underground storability was reported in only two districts, Busia and Mukono. The problem of cassava storage root bitterness was also reported in only two districts, Busia and Jinja.

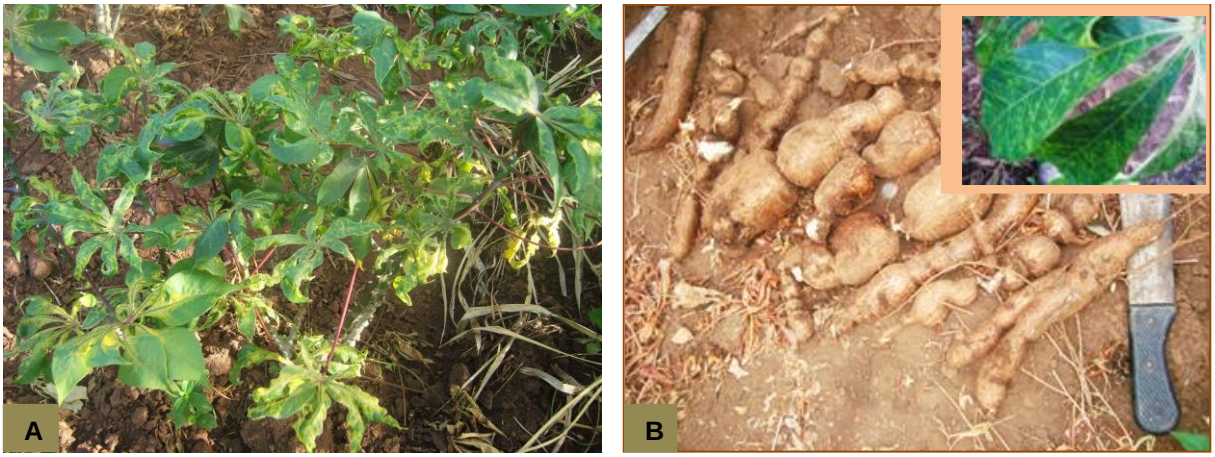

Figure 2.2: Key cassava diseases observed during the survey conducted in 2010. **A:** stunted cassava plant with severely distorted leaves due cassava mosaic disease; **B:** storage root constrictions and leaf chlorosis due to cassava brown streak disease.

Table 2.1: Cassava production constraints as identified by farmers in Busia, Jinja and Mukono districts in Uganda

Production constraints	Survey districts*			Mean (%)
	Busia (%)	Jinja (%)	Mukono (%)	
Diseases, especially CBSD and CMD	100.0	92.5	100.0	97.5
Lack of early maturing cultivars	77.5	50.0	67.5	65.0
Rodents (mole rats, squirrels, porcupines)	50.0	70.0	17.5	45.8
Insect pests (green mites, white flies termites)	47.5	50.0	22.5	40.0
Inaccessibility of high yielding cultivars	17.5	47.5	25.0	30.0
Weeds	37.5	22.5	10.0	23.3
Poor underground storability	10.0	-	7.5	5.8
Bitterness of storage roots	17.5	32.5	-	16.7
Declining soil infertility	30.0	20.0	12.5	20.8
Erratic droughts	10.0	25.0	12.5	15.8
Scarcity of labour	25.0	2.5	10.0	12.5
Theft	32.5	25.0	10.0	22.5
Lack of farm implements and inputs	10.0	7.5	2.5	6.7
Land shortage	2.5	27.5	15.0	15.0
Lack of agricultural credit facilities	7.5	5.0	2.5	5.0
Lack of markets	25.0	32.5	10.0	22.5
Lack of extension services	7.5	10.0	32.5	16.7

*Number of respondents per district = 40; CBSD = cassava brown streak disease; CMD = cassava mosaic disease

2.3.2 Crops grown other than cassava

Several other food crops were grown by the cassava farmers in Busia, Jinja and Mukono districts (Table 2.2). Among these crops, maize (*Zea mays*) was the most commonly grown crop, indicated by 92.5% of the farmers in Busia, 87.5% in Jinja and 90.0% in Mukono. This was followed by dry bean (*Phaseolus vulgaris*), indicated by 42.5% of the farmers in Busia, 65.0% in Jinja and 75.0% in Mukono. Sweet potato (*Ipomea batatas*) was another important food crop, indicated by 47.5% of the farmers in Busia, 65.0% in Jinja and 55.0% in Mukono. Cooking banana (*Musa spp.*) was grown by 5.0% of the farmers in Busia, 50.0% in Jinja and 57.5% in Mukono. Other root and tuber crops that were identified in the survey districts were Irish potato (*Solanum tuberosum*) and cocoyam (*Xanthosoma sagittifolium)*.

Table 2.2: Percentages of farmers that were growing different food crops in Busia, Jinja and Mukono in Uganda, other than cassava

Crops grown other than cassava	Survey districts*			Mean (%)
	Busia (%)	Jinja (%)	Mukono (%)	
Maize	92.5	87.5	90.0	90.0
Sorghum	55.0	-	5.0	20.0
Sweet potato	47.5	65.0	55.0	55.8
Dry bean	42.5	65.0	75.0	60.8
Soybean	17.5	5.0	10.0	10.8
Cooking banana	5.0	50.0	57.5	37.5
Ground nuts	32.5	22.5	22.5	25.8
Finger millet	12.5	5.0	-	5.8
Cocoyam	2.5	10.0	22.5	11.7
Irish potato	7.5	7.5	15.0	10.0
Rice	5.0	2.5	2.5	3.3
Egg plant	2.5	2.5	5.0	3.3
Irish potato	7.5	7.5	15.0	10.0
Tomato	7.5	2.5	-	3.3
Simsim	6.0	-	-	2.0

*Number of respondents per district = 40

2.3.3 Cassava based cropping systems practiced by farmers

Across the survey districts cassava was predominantly (93.0%) grown as an intercrop, most commonly with maize, and/or dry bean (Figure 2.3). Seventy five per cent of the farmers intercropped cassava with maize, 73.0% with dry bean, 52.0% with dry bean and maize, 32.0% with sorghum, 15.0% with sweet potato, and 10.0% with finger millet. Intercropping cassava with one other crop was most common, but in some cases, cassava was intercropped with two other crops.

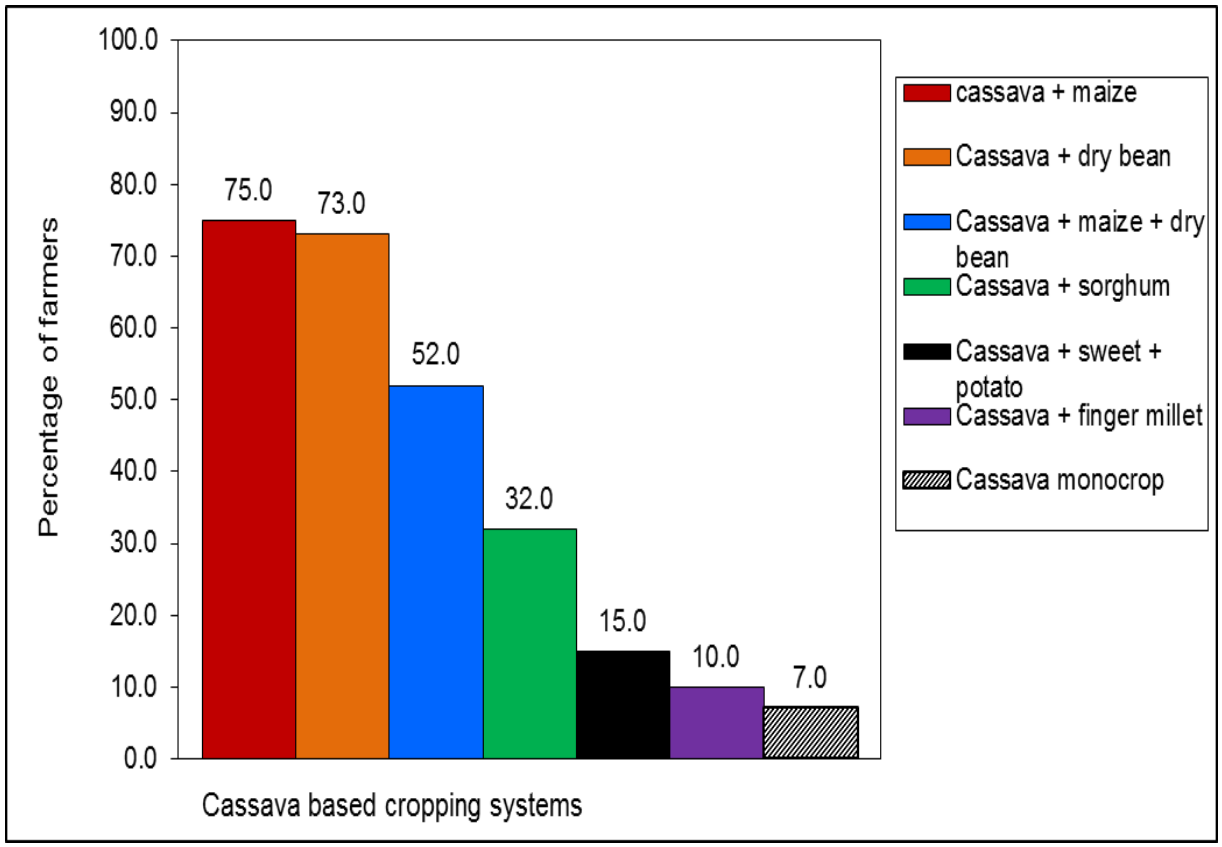

Figure 2.3: Percentages of farmers who were practicing different cassava based cropping systems across the three survey districts in Uganda

2.3.4 Cassava cultivars grown by farmers

A wide range of cassava cultivars was grown by farmers, and in each of the survey districts more than 10 cassava cultivars were identified (Table 2.3). In Busia district, Magana was the most common cultivar, grown by 92.5% of the farmers and the least common were Namukono and NASE14, each grown by 5.0% of the farmers. In Jinja, NASE3 was the most commonly (42.5%) grown cultivar while the least common were Ofwono and NASE4, each grown by 2.5% of the farmers. In Mukono, TME14 was the most commonly (82.5%) grown cultivar while NASE3, Mufumbacayi and Ebwanatereka were the least common. Most of the cassava cultivars grown were generally late bulking, with Akena and Ofwono being the latest bulking cultivars, indicated to be harvested ≥16 MAP. The cultivars identified by farmers as early bulking were harvested at approximately 12 MAP and they were: Taso, NASE3, NASE2 NASE4, Mercury, Mufumbacayi, Ebwanatereka, Bufulubi, Selefu, MH97/2961, Mwezigumu and TME14.

Table 2.3: Common cassava cultivars grown in Busia, Jinja and Mukono districts of Uganda

Cassava cultivars	Survey districts*			Harvest time (MAP)	Remark on bulking
	Busia (%)	Jinja (%)	Mukono (%)		
Magana	92.5	10.0	-	14	medium bulking
Taso	32.5	-	-	12	early bulking
NASE3	77.5	42.5	2.5	12	early bulking
Akena	7.5	20.0	35.0	≥16	late bulking
NASE2	12.5	-	10.0	12	early bulking
NASE4	32.5	2.5	5.0	12	early bulking
Mercury	55.0	-	-	12	early bulking
Namukono	5.0	-	-	16	late bulking
Mufumbacayi	5.0	27.5	2.5	12	early bulking
Luderudu	7.5	-	5.0	15	late bulking
Ebwanatereka	-	20.0	2.5	12	early bulking
Bufulubi	-	37.5	-	12	early bulking
Selefu	-	37.5	-	12	early bulking
Njule	-	7.5	7.5	14	medium bulking
Bunduguza	-	12.5	-	16	late bulking
MH97/2961	-	5.0	27.5	12	early bulking
Mwezigumu	-	5.0	-	12	early bulking
TME204	-	-	10.0	14	late bulking
TME14	22.5	17.5	82.5	12	early bulking
Bwanjule	-	-	22.5	14	medium bulking
TME3	-	-	22.5	15	late bulking
Ofwono	-	2.5	12.5	≥16	late bulking
NASE14	5.0	5.0	15.0	15	late bulking

*Number of respondents per district = 40; MAP = Months after planting

2.3.5 Farmers' awareness of early storage root bulking in cassava

The largest percentage (75.0%) of the farmers had knowledge of early bulking cassava cultivars and only 5.0% was not sure of this trait (Figure 2.4). Farmers with knowledge about early bulking cultivars indicated that such cultivars develop bigger storage roots with girth ≥10 cm and/ or produce storage root yield of about 10 t ha^{-1} at ≤12 MAP.

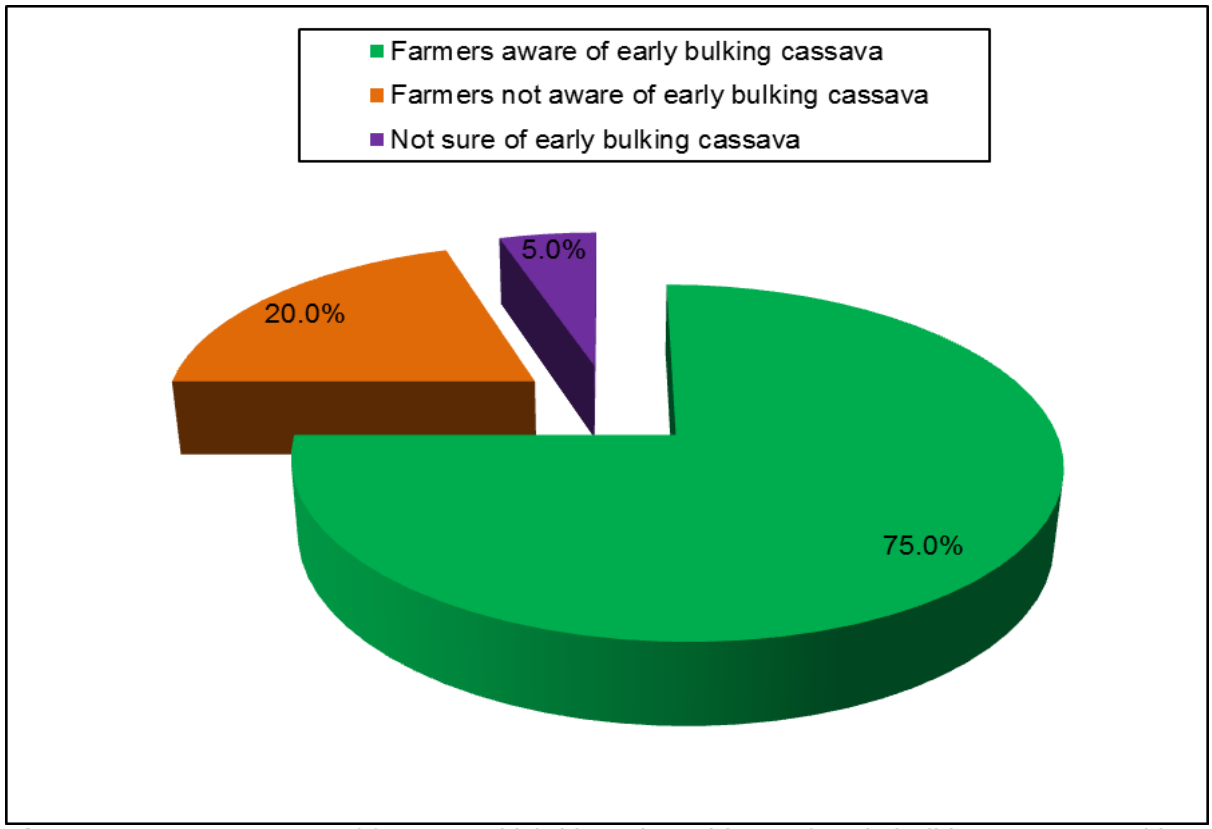

Figure 2.4: Percentages of farmers with/without knowldege of early bulking cassava cultivars in the three study districts in Uganda

2.3.6 Indicative signs of early storage root bulking cassava cultivars

Farmers suggested a number of putative indicators that differentiate early bulking cassava cultivars from late bulking cultivars (Figure 2.5). A majority of these farmers (47.5%) revealed that early bulking cultivars are associated with cracking of soil when the cassava crop is still young (3 - 4 MAP). A few farmers reported that the leaves of early bulking cultivars turn brown and begin to fall off at an early stage of plant growth. Farmers also indicated that early bulking cultivars are in most cases characterised by early flowering (37.5%), early canopy development (21.7%), early branching (20.8%) and short thick light-brown stems (6.7%).

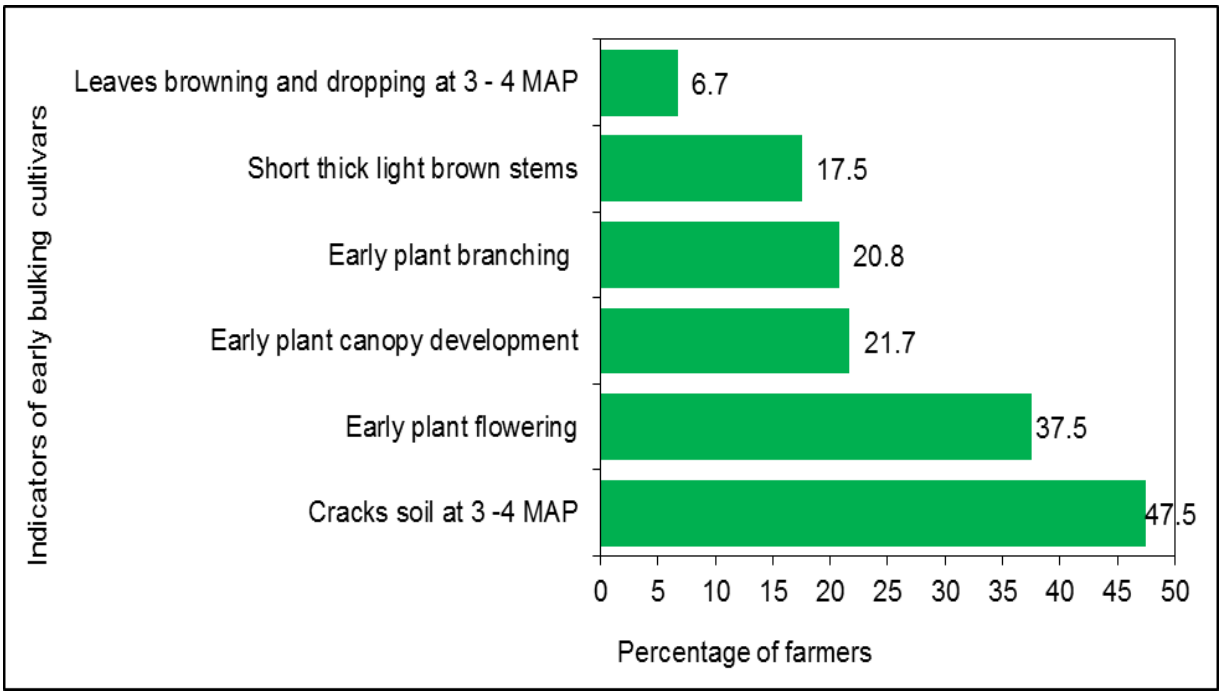

Figure 2.5: Percentages of farmers across the three study districts in Uganda who suggested indicators of early bulking cassava cultivars

2.3.7 Perceived importance of early storage root bulking cassava

Farmers pointed out a number of benefits associated with growing early bulking cassava cultivars (Figure 2.6). Among the benefits indicated, provision of quick and constant food was most common among farmers (91.7%). This was followed by provision of quick income through cassava sales, which was indicated by 60.0% of the farmers. Other benefits associated with the growing of early bulking cultivars were that they escape droughts, late season pests and diseases.

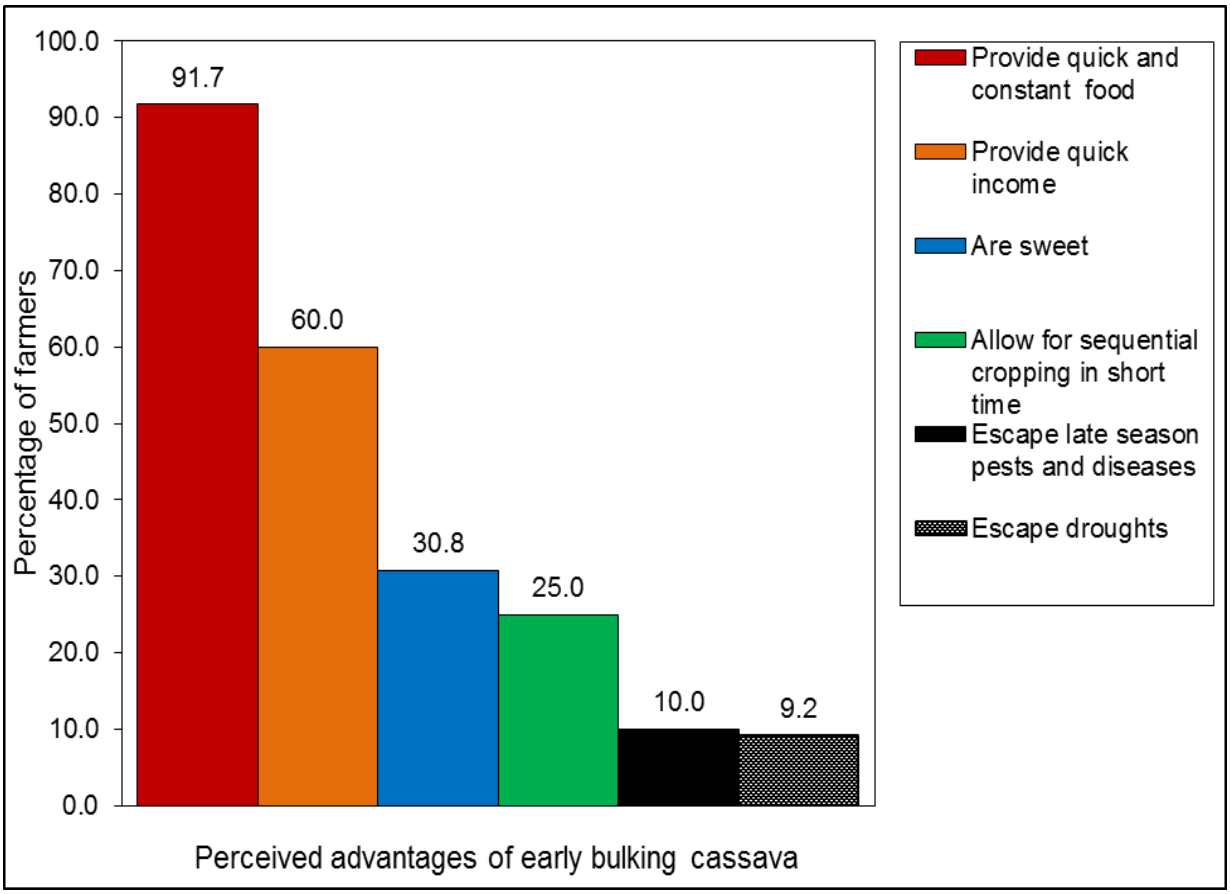

Figure 2.6: Importance of early bulking cassava cultivars as mentioned by farmers across the three survey districts in Uganda

2.3.8 Cassava cultivar selection criteria by farmers

Cassava cultivars were selected by farmers using certain known criteria that were common across the survey districts (Table 2.4). On average across these districts, cultivar selection by farmers largely depended on high fresh storage root yield (80.0%), early bulking (71.6%), resistance to pests and diseases (63.3%), and sweetness (50.8%). Selection based on tolerance to drought was the least common among farmers.

Table 2.4: Cassava cultivar selection criteria as indicated by farmers in Busia, Jinja and Mukono districts of Uganda

Cassava cultivar selection criteria	Survey districts*			Mean (%)
	Busia (%)	Jinja (%)	Mukono (%)	
High fresh storage root yield	85.0	77.5	77.5	80.0
Early bulking	77.5	65.0	72.5	71.6
Resistance to pests and diseases	75.0	55.0	60.0	63.3
Sweetness of storage roots	45.0	57.5	50.0	50.8
High storage root dry matter content	25.0	30.0	25.0	26.7
Medium branching height	20.0	30.0	15.0	21.7
Easy cooking ability of storage roots	20.0	25.0	17.5	20.8
Underground storability of storage roots	17.5	10.0	15.0	14.2
Availability of planting material	12.5	15.0	12.5	13.3
Late storage root bulking	15.0	10.0	10.0	11.7
Non-fibrous storage roots	15.0	10.0	17.5	14.2
Bigger storage roots	12.5	7.5	20.0	13.3
Drought tolerance	-	-	2.5	0.8

*Number of respondents per district = 40

2.3.9 Traits suggested to be incorporated into early bulking cassava

Farmers suggested a number of traits they would like to see incorporated into early bulking cassava cultivars (Table 2.5). Their suggestions did not vary much across the three study districts. The majority of the farmers (58.3%) suggested high dry mass content, followed by sweetness (53.3%) and high fresh storage root yield (41.7%). High dry mass content of the storage roots was prioritised by 67.0, 55.0 and 52.5%, cassava sweetness by 62.5%, 47.5% and 50.0%, high fresh storage root yield by 55.0, 45.0 and 25.0% of the farmers in Busia, Jinja and Mukono districts, respectively.

Table 2.5: Traits desired by farmers in the new early storage root bulking cassava cultivars in Busia, Jinja and Mukono districts of Uganda

Traits to be incorporated into early bulking cassava	Survey districts*			Mean (%)
	Busia (%)	Jinja (%)	Mukono (%)	
High dry matter content	67.5	55.0	52.5	58.3
Sweetness	62.5	47.5	50.0	53.3
High fresh storage root yield	55.0	45.0	25.0	41.7
Resistance to pests and diseases	22.5	30.0	32.5	28.3
Drought tolerance	5.0	12.5	0.0	5.0
Easy cooking ability	22.5	30.0	37.5	30.0
Long underground storage root storability	27.5	25.0	32.5	28.3
Medium branching height	0.0	2.5	17.5	6.7
Large storage roots	17.5	12.5	0.0	10.0
Long oval storage roots	7.5	7.5	2.5	5.8
Non-fibrous storage roots	10.0	15.0	30.0	18.3
Firm storage roots after cooking	10.0	17.5	27.5	18.3

*Number of respondents per district = 40

2.4 Discussion and conclusions

The findings of this study revealed that the majority of the farmers were aware of early bulking cassava cultivars and understood the constraints affecting cassava production in their localities. Farmers with knowledge about early bulking cultivars indicated that such cultivars produce enlarged storage roots (girth ≥10 cm) that are acceptable to the market and/ or produce storage root yield of about 10 t ha^{-1} at ≤12 MAP.

Cassava production in all the three surveyed districts was associated with numerous constraints, most importantly CBSD and CMD. These two virus diseases have indeed caused a substantial reduction in productivity for most cassava cultivars, not only in Uganda, but also in the whole of the east African region (Legg et al., 2011). Lack of early bulking cultivars was the second most important constraint after diseases. This problem is not specific for Uganda, but has also been reported in other countries where farmers' needs assessments have been carried out, for example Kenya (Kamau, 2006), Tanzania (Mtunda, 2009), Ghana (Amenorpe et al., 2007), Zambia (Chikoti 2011; Chalwe, 2012) and Nigeria (Bassey and Gamaliel, 2013).

The local economies of the surveyed districts were largely driven by agricultural activities. A number of other food crops, including maize, dry bean, sweet potato and cooking banana were grown by cassava farmers. It is a common practice by most smallholder farmers in Uganda to have a range of food crops grown on their small plots of land for self-sufficiency in terms of household food demands.

Cassava was predominantly grown as an intercrop, most often with maize and/or dry beans. The popularity of intercropping cassava was attributed to the attempts by farmers to alleviate the problems caused by cassava pests and diseases, obtain high aggregate output from small pieces of land, as well as to increase soil fertility. The practice was also viewed as an insurance against failure of one of the crops in the event of adversity. These findings agree with research of IITA (2001) and Agwu and Anyaeche (2007), which showed that cassava is largely grown as an intercrop in Africa.

Several cassava cultivars were grown by farmers, with more than 10 cultivars identified in each of the surveyed districts. Each cultivar was selected for its special attributes preferred by farmers. For example, Magana was most common among Busia farmers because farmers preferred it for its high fresh storage root yield (FSRY), intermediate early storage root bulking, tolerance to the prevalent pests and diseases, especially CMD and CBSD, and for its sweetness. In Jinja, NASE3 was the most common cultivar because it was believed to be

early bulking, resistant to CMD and tolerant to CBSD. Cultivars NASE3 and TME14 were most common in Jinja and Mukono, respectively due to their preference for high FSRY, early bulking and tolerance to pests and diseases. Although NASE4, Mufumbacayi and Ebwanatereka were appreciated for their early bulking, they were unpopular among farmers in Jinja and Mukono due to their susceptibility to diseases, particularly CBSD. This suggested that farmers select cultivars that combine a series of desired traits to constitute their selection index.

Although in formal cassava breeding it has been difficult to identify the aboveground cassava traits associated with early bulking cultivars, farmers have indigenous knowledge on how to identify them. Early bulking cultivars were reported to be associated with cracking of soil early in their development, early flowering, early canopy development, early branching, short thick light brown stems, and browning of leaves that drop 3 - 4 MAP. Wholey and Cock (1974) and Kawano (1987) found that there are no clear aboveground cassava traits that show when cassava storage roots have developed, necessitating the uprooting of plants. Harvest index was recommended as a method for assessing early bulking cassava by CIAT (1972). Most of the plant descriptions of early bulking cassava cultivars by farmers are not quantified and therefore selection needs to be complemented by formal breeding methods.

Farmers selected preferred cassava cultivars on the basis of certain known criteria that were common across the three surveyed districts. Farmers' selection for cultivars largely focused on high FSRY, early bulking, resistance to pests and diseases, and sweetness. These selection criteria reflected the degree of importance attached to farmers' multiple needs and priorities, as well as their context of production environments and farming systems. Early bulking was selected for because farmers believed that early bulking cultivars escape late season pests, diseases and droughts, allow for sequential multiple cropping within a short time, and are sweet. Above all, farmers believed that early bulking cultivars provide quick food and income. In addition, in the context of the current CBSD epidemic in the east African region (Legg et al., 2011; Kulembeka et al., 2012), where reasonable levels of resistance have not yet been attained, early bulking is considered a key CBSD control strategy. A few farmers, however, preferred late bulking cultivars as a way of ensuring food security for their households. One of the attributes of late bulking local cultivars was long underground storability which allows the farmers to harvest when convenient.

Farmers expressed a strong need for improved early bulking cultivars, but stressed that they should, in the order of importance, combine high dry mass content, sweetness, high yielding ability, and resistant to the prevalent pests and diseases in Uganda especially CMD and CBSD.

In final conclusion, this study revealed that research geared towards breeding high yielding early bulking cassava requires a multidisciplinary approach that considers cultural, socio-economic and environmental factors. Several factors limiting cassava production in the surveyed districts were identified, key of which were diseases, especially CMD and CBSD, and lack of high yielding early bulking cultivars. Similarly, farmer preferred traits that characterise early bulking cultivars were identified. The identified production constraints and cultivar preferences, such as high yielding and early bulking, need to be prioritised in the cassava breeding process. It is anticipated that the involvement of farmers in the subsequent cassava evaluations and selections will ensure rapid and successful adoption of the improved high yielding, early bulking cultivars with farmer preferred traits. Successful adoption of high yielding, early bulking cultivars in the existing cassava based farming systems is in turn expected to lead to improved livelihoods of smallholder farmers in Uganda.

References

Agwu, A.E., and C.L. Anyaeche. 2007. Adoption of improved cassava varieties in six rural communities in Anambra State, Nigeria. African Journal of Biotechnology 6:89-98.

Amenorpe, G., H.M. Amoatey, A. Darkwa, G.K. Banini, and V.W. Elloh. 2007. Peak root and starch weights of ten early bulking cultivars of cassava (*Manihot esculenta* Crantz) in Ghana. Journal of Ghana Science Association 9:54-60.

Bassey, E.E., and I.H. Gamaliel. 2013. Screening cassava (*Manihot esculenta* Crantz) genotypes for tuber bulking, early maturity and optimum harvesting time in Uyo, South Eastern Nigeria. Peak Journal of Agricultural Sciences 1:83-88.

Carver, R.H., and J.G. Nash. 2009. Doing data analysis with SPSS Version 16. Cengage Learning Publishing, Canada, USA.

Ceccarelli, S., and S. Grando. 2007. Decentralized-participatory plant breeding: an example of demand driven research. Euphytica 155:349-360.

Chalwe, A. 2012. Manipulating morphological traits of cassava to enhance host plant resistance and biological control of cassava green mite in Zambia. PhD thesis, University of KwaZulu-Natal, South Africa.

Chikoti, P. C. 2011. Development of cassava (*Manihot esculenta* Crantz) cultivars for resistance to cassava mosaic disease in Zambia. PhD thesis, University of KwaZulu-Natal, South Africa.

CIAT. 1972. Annual report. Centre for Tropical Agriculture. Cali Colombia.

Duguma, G.,T. Mirkena, A. Haile, L. Iñiguez, A.M. Okeyo, M. Tibbo, B. Rischkowsky, J. Sölkner, and M.Wurzinger. 2010. Participatory approaches to investigate breeding objectives of livestock keepers. Livestock Research for Rural Development. Volume http://www.lrrd.org. (Accessed 27th April 2012).

Efisue, A., P. Tongoona, J. Derera, A. Langyintuo, M. Laing, and B. Ubi. 2008. Farmers' perceptions on rice varieties in Sikasso Region of Mali and their implications for rice breeding. Journal of Agronomy and Crop Science 194:393-400.

Egesi, C.N., P. Ilona, F.O. Ogbe, M. Akoroda, and A. Dixon. 2007. Genetic variation and genotype x environment interaction for yield and other agronomic traits in cassava in Nigeria. Agronomy Journal 99:1137-1142.

El-Sharkawy, M.A. 2007. Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments. Brazilian Journal of Plant Physiology 19:257-286.

El-Sharkawy, M.A. 2012. Stress-tolerant cassava: the role of integrative ecophysiology-breeding research in crop improvement. Open Journal of Soil Science 2:162-186.

Food and Agriculture Organisation (FAO). 2012. Food and Agriculture Organisation statistical database for agriculture. Crops and products domain. http://faostat.fao.org. (Accessed 19 June 2013). FAO, Rome, Italy.

International Institute of Tropical Agriculture (IITA). 2001. IITA: Cassava subsector analysis report Uganda. p. 1-68.

Kamau, J. W. 2006. Participatory based development of early bulking cassava varieties for the semi-arid areas of Eastern Kenya. PhD thesis, University of KwaZulu Natal, South Africa.

Kamau, J., R. Melis, M. Laing, J. Derera, P. Shanahan, C. Eliud, and K. Ngugi. 2011. Farmers' participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. Journal of Plant Breeding and Crop Science 3:44-52.

Kawano, K. 1987. Inherent and environmental factors related to cassava varietal selection In: Hershey, C. (ed.), Cassava breeding: a multidisciplinary review. CIAT, Cali, Colombia. p. 207-226.

Kulembeka, H.P., M. Ferguson, L. Herselman, E. Kanju, G. Mkamilo, E. Masumba, M. Fregene, and M.T. Labuschagne. 2012. Diallel analysis of field resistance to brown streak disease in cassava (*Manihot esculenta* Crantz) landraces from Tanzania. Euphytica 187:277-288.

Legg, J.P., S.C. Jeremiah, H.M. Obiero, M.N. Maruthi, I. Ndyetabula, G. Okao-Okuja, H. Bouwmeester, S. Bigirimana, W. Tata- Hangy, G. Gashaka, G. Mkamilo, T. Alicai, and L.P.Kumar. 2011. Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa. Virus Research 159:161-170.

Mtunda, K.J. 2009: Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.

Nweke, F.I., A. Dixon, R. Asiedu, and S.A. Folayan. 1994. Cassava varietal needs of farmers and potential for production growth in Africa. COSCA working paper 10.

Okogbenin, E., and M. Fregene. 2002. Genetic and QTL mapping of early root bulking in an F_1 mapping population of non-inbred parents in cassava (*Manihot esculenta* Crantz). Theoretical and Applied Genetics 106:58-66.

Parkes. E.Y. 2011. Assessment of genetic diversity, combining ability, stability and farmer preference of cassava germplasm in Ghana. PhD thesis, University of the Free State, Bloemfontein, South Africa.

Suja, G., K.S. John, J. Sreekumar, and T. Srinivas. 2009. Short-duration cassava genotypes for crop diversification in the humid tropics: growth dynamics, biomass, yield and quality. Journal of Science and Food Agriculture 90:188-198.

Sumberg, J., and D. Reece. 2004. Agricultural research as new product development. Experimental Agriculture 40: 295-331.

Tonukari, N.J. 2004. Cassava and the future of starch. Electronic Journal of Biotechnology7.http://www.ejbiotechnology.info/content/vol7/issue1/ISSN: (Accessed 03 March 2012).

Were, W.V., P. Shanahan, R. Melis, and O.O. Omari. 2012. Gene action controlling farmer preferred traits in cassava varieties adapted to mid-altitude tropical climatic conditions of western Kenya. Field Crops Research 133:113-118.

Wholey, D.W., and J.H. Cock. 1974. Onset and rate of root bulking in cassava. Experimental Agriculture 10:193-198.

Witcombe, J.R. 2009. Methodologies for generating variability Part 3: The development of base populations and their improvement by recurrent. In: Ceccarelli, et al. (eds.), Plant breeding and farmer participation. FAO, Rome, Italy. p. 139-157.

Yang, J., A. Dong, and Z. Peng. 2011. Expression profiling of cassava storage roots reveals an active process of glycolysis/glyconeogenesis. Journal of Intergrative Plant Biology 53:193-211.

Appendix 2.1: Participatory rural appraisal questionnaire used during the survey

SECTION A: General identification information

a) Date……Name of farmer……..…..
b) District…….. Sub-county……Village …….…….
c) Farm size……
d) GPS of homestead: Coordinates …… Altitude…….

SECTION B: Cropping systems

1. What crops do you grow other than cassava?

Crop	Acreage
a- …….	a- …….
b- …….	b- …….
c- …….	c- …….
d- …….	d- …….
e- …….	e- …….

2. How much of your land is grown to cassava?.....
3. Do you plant cassava as a pure crop or intercrop? ……
   Pure stand ☐ Intercrop ☐
4. If intercrop, when is the intercrop introduced?
   a- After cassava …… b- Before cassava ..... c- Together with cassava…….
5. When cassava is intercropped, what is your major crop? Cassava or the intercrop?
   ……
6. Why do you intercrop cassava?
   ……
   ……..
7. Why do you grow cassava?
   .....
   .....
8. Which cassava cultivars do you grow on your farm?
   ……
   ……
   ……..
9. Which of these cultivars do you like most and why?
   ……
   ……
   ……
10. Where do you get planting material/seed?
    a. Fellow farmers;
    b. Ministry of Agriculture;
    c. NARO;
    d. NGOs
    e. Others …….

11. What factors do you consider when selecting planting materials?

……
……

12. Would you like planting improved cassava cultivars? Yes/No

- What improved qualities would you like in such cultivars?
  ……
  ……
  ……

13. What challenge do you encounter in cassava production?
……
……
……

SECTION C: Farmers' perception of early bulking and preferred traits

14. After how many months from planting do you harvest your cassava?
……
15. Do you have early bulking/maturing cassava varieties on your farm? Yes/No
If yes, what are they and how long do they take to be harvested?

……
……
……
16. What are the characteristics of early bulking cultivars?
……
……
……
17. What are the advantages/disadvantages of early bulking cassava?
a- Advantages
……
……
……
b- Disadvantages……
……
……
……
18. What attributes would you want incorporated in early bulking cultivars?
……
……
……
……

CHAPTER 3

Evaluation of genetic variability among cassava genotypes for storage root bulking and related traits in Uganda

Abstract

Genetic variability is important in selecting suitable genotypes for crop improvement. The objective of this study was to assess the extent of variation among selected genotypes for the rate of storage root bulking based on fresh storage root yield (FSRY). Twelve genotypes sourced from farmers' fields and the National Cassava Breeding Programme in Uganda were evaluated in a randomised complete block design at three contrasting locations: Jinja, Nakasongola and Namulonge. Assessments were done from 5 to 13 months after planting (MAP) at two monthly intervals. Genotype, harvest time, location and their interactions were significant ($P<0.001$) for FSRY and most of the other traits assessed. Time to attain peak FSRY and the other traits differed among genotypes and locations. Genotype CT2 was identified as the overall best performer for FSRY. Genotypes: Nyara, B11, CT5, NASE4, TME14 and NASE3 attained first peak FSRY at ≤ 9 MAP and could therefore be selected as early bulking genotypes. Estimates of variance components revealed that a large portion of the phenotypic variance was accounted for by the genotypic component for all traits assessed, indicative of substantial genetic variability among the genotypes that was unaffected by non-additive interaction with the environment. From principal components analysis, the greater percentage, at 51.1% of the total variation in the genotypes was accounted for by PC1, which was largely contributed to by harvest index (HI), dry storage root yield (DSRY), FSRY and storage root girth (SRG). The PC2 accounted for 19.6% of the total variation which was largely contributed to by dry mass content and storage root number (SRN). The six traits that mainly contributed to PC1 and PC2 are of major interest to cassava breeders. Fresh storage root yield was positively and significantly correlated with DSRY ($r = 0.98$), SRG ($r = 0.76$), HI ($r = 0.69$) and SRN ($r = 0.36$), but negatively correlated with cassava mosaic disease severity ($r = -0.08$). The information generated in this study will inform future breeding initiatives to develop high yielding, early bulking cassava genotypes with farmer and consumer preferred traits in Uganda.

3.1 Introduction

Cassava (*Manihot esculenta* Crantz) is an important storage root crop grown world-wide. It is the fourth most important food crop and an essential component of the diet of millions of people in many parts of the world (Cach et al., 2005). Cassava is cultivated mainly for its starchy storage roots (Kawano, 2003; Salcedo and Siritunga, 2011) and as such is one of the energy bases in the nutrition of smallholder farmers that grow it (Gleadow et al., 2009; Burns et al., 2011),

Cassava is traditionally considered a long-duration crop, yet a number of studies have demonstrated the existence of early bulking genotypes (Wholey and Cock, 1973; Suja et al., 2009; Mtunda, 2009; Ntawuruhunga and Dixon, 2010; Kamau et al., 2011; Bassey and Gamaliel, 2013; Okogbenin et al., 2013). As early bulking in cassava depends on genetic and environmental factors (Mtunda, 2009; Ntawuruhunga and Dixon, 2010) a deeper understanding of the relationship between these factors is essential in order to successfully breed early bulking cassava genotypes.

Early bulking has increasingly become an important trait in cassava as it is believed that earliness will transform cassava from a traditional to an industrial crop. It is also considered to be important in situations where mounting pressure on land for urban and industrial development compels farmers to intensify production, and in semi-arid regions, where early bulking genotypes can be harvested after only one cycle of rain (Amenorpe et al., 2007; El-Sharkawy, 2007; Suja et al., 2009; Okechukwu and Dixon, 2009; Kamau et al., 2011).

Storage roots are the key harvestable plant part for most cassava farmers and in most cases their yield reflects the productivity of the entire cassava plant (Aina et al., 2007; Yang et al., 2011). Storage root yield is the central trait in all cassava breeding programmes, and has been reported to be genetically associated with number of storage roots, harvest index, storage root size and canopy size (Cock et al., 1979; Ntawuruhunga and Dixon, 2010). Its improvement can be achieved through exploiting the genetic variability within cassava germplasm (Aina et al., 2007). Certainly, high levels of genetic variability are required amongst parental germplasm to facilitate an effective long term plant breeding programme and also to justify the need for selection. Moreover, selection progress has been reported to be directly related to the magnitude of genetic variance within a population (Hallauer, 1992; Kawuki et al., 2011; Kawuki et al., 2013).

Extensive research has been directed towards identifying the optimum harvest time for cassava based on peak storage root yield (Indira and Sinha, 1970; Kamau, 2006; Amenorpe et al., 2007; Suja et al., 2009; Mtunda, 2009; Bassey and Gamaliel, 2013); however, different harvest dates are reported for different genotypes and regions. Therefore optimum harvest time is dependent on genotype, growing conditions; rate of storage root bulking and economic aspects. Storage root bulking, which determines storage root yield, is as a result of the formation and growth of storage roots that undergo secondary thickening (Izumi et al., 1999). The growth of storage roots results from an increase in root size and mass and depends on the sink strength, photosynthetic efficiency of leaves and the potential of leaves to export photosynthates (Alves, 2002; Lahai and Ekanayake, 2009).

The fact that cassava genotypes vary in their rate and pattern of assimilate partitioning and consequently their earliness, partly explains differences in harvest dates (Alves, 2002; El-Sharkawy, 2003; Aina et al., 2009). Nevertheless, given that cassava is grown for various uses such as production of starch for industrial applications, direct consumption or sold for economic returns, which might influence the time of harvest, studies are needed to establish the optimal harvest times for the genotypes cultivated in each region. Moreover, such information can be utilised in breeding for high yielding, early bulking cassava genotypes, as well as in identifying research gaps in the quantification and understanding of the existing variation in cassava. Accordingly, this research was conducted with the following objectives:

1. To assess the extent of variation in the rate of storage root bulking in selected cassava genotypes; and
2. To examine the effect of harvest time and location on storage root bulking and related traits.

3.2 Materials and methods

3.2.1 Experimental sites

Trials were conducted from April 2011 to June 2012 at Namulonge and Jinja National Agricultural Research Institutes and also at Nakasongola on private farmland. Namulonge is located in central Uganda at 32°36'E and 0°31'N, 1134 meters above sea level (masl). During the trial period, mean rainfall was 1264 mm and temperature range was 15.8 to 27.8°C. Jinja is located in eastern Uganda at 33°11'E and 0°27'N, 1173 masl. During the experimental period, mean rainfall was 1324 mm and temperature range was 16.3 to 28.1°C. Nakasongola is a drought-prone area located in central Uganda at 32°27'E and 1°18'N, 1091 masl. During

the experimental period, mean rainfall was 790 mm and temperature range was 18.6 to 30.4°C.

3.2.2 Experimental germplasm

Twelve genotypes (Table 3.1) were selected from farmers' fields and from the National Cassava Breeding Programme (NCBP) at the National Crops Resources Research Institute (NaCRRI), Namulonge. Genotypes from farmers' fields were landraces, while genotypes from the NCBP were introductions from the International Institute of Tropical Agriculture (IITA) and genotypes developed by crossing cassava lines from the International Centre for Tropical Agriculture (CIAT) with lines from Uganda. Selection of the genotypes was based on their performance for storage root yield and quality traits, early bulking and relative degrees of field resistance to two diseases prevalent in Uganda: cassava brown streak disease (CBSD) and cassava mosaic disease (CMD).

Table 3.1: Cassava genotypes evaluated at three locations and harvested at five harvest dates in Uganda, 2011/12

Genotype No.	Genotype	Entry code	Type of genotype
1	Bukalasa11	B11	landrace
2	Nyaraboke	Nyara	landrace
3	TME14	TME14	improved[a]
4	TMS30572	NASE3	improved[a]
5	MM96/4271	NASE14	improved [a]
6	SS4	NASE4	improved [a]
7	TMS192/0067	Akena	improved [a]
8	FS37- 4	CT1	new genotype[b]
9	FS25 - 5	CT2	new genotype[b]
10	FS7-18	CT3	new genotype[b]
11	FS27-15	CT4	new genotype[b]
12	FS1- 4	CT5	new genotype[b]

[a]International Institute of Tropical Agriculture introductions; [b]Genotypes developed by hybridising lines from the International Centre for Tropical Agriculture with lines from Uganda.

3.2.3 Experimental design

The trial at each location was laid out in a randomised complete block design with three replications. Healthy stem cuttings, each 25 cm in length were horizontally planted in a flat seedbed at a spacing of 1 x 1 m giving a population density of 10 000 plants ha^{-1}. Each plot measured 5 x 12 m comprising six rows of 12 plants each. The first and last rows and the first and last plant within each row of each plot were considered as border plants. The plots and blocks were separated by 2 m and 2.5 m alleys, to reduce inter-plot and inter-block plant competition, respectively. The trials were conducted without supplemental irrigation and weeded regularly.

3.2.4 Data collection

Sequential harvesting was conducted from five months after planting (MAP) to 13 MAP at two monthly intervals. On each harvest date, data on the following traits were collected from a net plot of four randomly selected and hand uprooted plants of each genotype: storage root girth (SRG); storage root number (SRN); storage root mass (SRM); shoot mass (STM); harvest index (HI); dry mass content (DMC); fresh storage root yield (FSRY); dry storage root yield (DSRY); cassava brown streak disease root necrosis (CBSD-RN) and postharvest physiological deterioration (PPD). Cassava mosaic disease severity (CMD-S) was assessed once during the crop growth at 6 MAP on a scale of 1-5, where: 1 = no symptoms; and 5 = severe mosaic symptoms (Banito et al., 2007). The SRG of the four biggest storage roots plant^{-1} of each genotype was determined as the circumference (cm) at the widest point of the mid-section of a storage root. Storage roots of the four plants were bulked, counted and weighed to obtain SRN and SRM (kg), respectively. The FSRY (t ha^{-1}) per genotype was then estimated from the SRM of the four-plant bulk of storage roots as:

$$FSRY = \frac{SRM \times 10\,000}{4 \times 1000}$$

The STM (kg) was obtained by weighing the aboveground plant parts (stems and foliage).

Harvest index was calculated as the ratio of SRM to total biomass (TBM: mass of storage roots, stems and foliage):

$$HI = \frac{SRM}{TBM}$$

The DMC expressed as a percentage was determined by selecting three representative storage roots from each four-plant bulk of storage roots, which were washed, peeled and sliced using knives. Randomly selected slices were weighed to obtain a 0.1 kg fresh mass sample per genotype before being dried for 48 h in a forced-draught oven at 80°C. The dried samples were then reweighed to obtain the dry mass and DMC was calculated as:

$$DMC\ (\%) = \frac{Dry\ mass}{Fresh\ mass} \text{ x } 100$$

Dry storage root yield (DSRY) (t ha^{-1}) was calculated as:

$$DSRY = \frac{DMC\ \%}{100} \text{ x } FSRY$$

Because the main damage caused by CBSD is to the storage roots, the storage root necrosis due to CBSD (CBSD-RN) was scored on a scale of 1 to 5 where: 1 = no visible necrosis, and 5 = severe necrosis (Hillocks et al., 1996).

Postharvest physiological deterioration was determined following the procedures by Wheatley et al. (1985) and Ch´avez et al. (2005) with some modifications. Four physically undamaged large storage roots (girth ≥10.0 cm) were randomly chosen from each genotype and their proximal and distal ends cut off. The exposed distal ends of the storage roots were covered with polyethylene sheets (Figure 3.1) and the storage roots were then stored under room temperature for seven days. After seven days, 10 transverse slices, 2 cm thick were cut along each storage root, starting from the proximal end. A score of 1 – 10 was assigned to each slice, corresponding to the percentage of the cut surface showing discolouration (1 = 10%, 2 = 20%, …. 9 = 90%, 10 = 100%). The mean score for PPD of each storage root was calculated by averaging the score across the 10 slices.

Figure 3.1: Cassava storage roots prepared for postharvest physiological deterioration evaluation

3.2.5 Data analysis

All data were analysed using Genstat, version 14 (Payne et al., 2011). The data collected from each location were first subjected to analysis of variance (ANOVA) and then the error variances for the locations were tested for homogeneity using Hartley's Fmax test (Hartley, 1950). The differences were not significant ($P<0.05$) thus an unweighted, combined ANOVA across the three locations was conducted. Means were separated using least

significance differences (LSD) at 5% significance level. The following mixed model, with genotype declared as fixed effects and locations and harvest time as random effects was used:

$$P_{ijk} = \mu + G_i + T_j + L_k + GT_{ij} + TL_{jk} + GL_{ik} + GTL_{ijk} + e_{ijk}$$

Where:

P_{ijk} = phenotypic value of genotype i harvested at time j and tested at location k;

μ = population mean;

G_i = effect of the i^{th} genotype;

T_j = effect of the j^{th} harvest time;

L_k = effect of the k^{th} location;

GT_{ij} = effect of the interaction between the i^{th} genotype and the j^{th} harvest time;

TL_{jk} = effect of the interaction between the j^{th} harvest time and the k^{th} location

GL_{ik} = effect of the interaction between the i^{th} genotype and the k^{th} location;

GTL_{ijk} = effect of the interaction between i^{th} genotype, j^{th} harvest time and k^{th} location

e_{ijk} = random error term associated with genotype i at harvest time j in location k

In order to estimate the variance components for the genotype, environment and genotype x environment for each trait at each harvest time separately, the genotype and environment effects were considered random in the statistical model for each harvest time (Payne et al., 2011). The phenotypic variance component for each trait was obtained as the sum of the variance components for genotype, environment and genotype x environment interaction according to the following equation (Hallauer and Miranda, 1981; Hallauer, 1992):

$$\delta^2_P = \delta^2_G + \delta^2_E + \delta^2_{G\times E}$$

Where:

δ^2_P = Phenotypic variance component;

δ^2_G = Genotypic variance component;

δ^2_E = Environmental variance component; and

δ^2_{GxE} = Genotype x environment variance component.

Broad sense heritability of each trait at each harvest time was calculated as the proportion of the phenotypic component of variance accounted for by the genotypic component of variance:

$$H_b = \left(\frac{\delta^2 G}{\delta^2 G + \delta^2 E + \delta^2 GxE}\right) \times 100$$

The phenotypic coefficient of variation (PCV%) and genotypic coefficient of variation (GCV%) were calculated according to Burton and De Vane (1953) as:

$$PCV(\%) = \left(\sqrt{\delta^2 P} / \bar{x}\right) x\,100$$

$$GCV(\%) = \left(\sqrt{\delta^2 G} / \bar{x}\right) x\,100$$

Where: $\bar{x}$ = mean of the trait.

Pearson's phenotypic correlations between traits were performed for the genotypes averaged across five harvest times and three locations (Payne et al., 2011). Principal components analysis (PCA) was performed to identify the traits that contributed to the total variation of genotypes. For the PCA the data for the genotypes was averaged across the five harvest times and three locations. The PCA removes the intercorrelation that may exist between variables by transforming the original variables into smaller hypothetical components (Suzan et al., 1975).

3.3 Results

3.3.1 Combined analysis of variance across harvest time and location

The genotype and harvest time mean squares (MS) in the combined ANOVA were highly significant (P<0.001) for all traits (Table 3.2). Location MS were highly significant (P<0.001) for all traits except CBSD-RN that was non-significant. Genotype x harvest time MS were highly significant (P<0.001) for all traits, except SRN (P<0.05). Harvest time x location MS were highly significant (P<0.001) for FSRY, HI, DMC, DSRY, SRG and PPD and very significant (P<0.01) for SRN. Genotype x location MS were highly significant (P<0.001) for HI, DSRY, SRN, SRG and CBSD-RN, and very significant (P<0.01) for FSRY and DMC. Genotype x harvest time x location MS were non-significant for all traits and were therefore, not discussed further. Coefficients of variation ranged from 11.1% for DMC to 38.1% for FSRY.

Table 3.2: Combined analysis of variance for eight traits of 12 cultivars evaluated in three locations at five harvest times in Uganda, 2011/12

		Mean squares							
Source of variation	**DF**	**FSRY**	**HI**	**DMC**	**DSRY**	**SRN**	**SRG**	**PPD**	**CBSD-RN**
Genotype (G)	11	1250.3***	0.172***	348.4***	151.8***	79.3***	262.5***	5246.9***	22.77***
Harvest Time (T)	4	6004.1***	0.567***	1872.0***	723.5***	61.6***	1455.6***	3635.2***	18.43***
Location (L)	2	2352.3***	0.210***	165.5***	265.3***	52.5***	296.8***	1874.7***	0.99
G x T	44	186.2***	0.013***	41.2***	23.6***	7.3*	16.05***	694.2***	1.54***
T x L	8	667.4***	0.029***	214.1***	24.9***	14.6**	48.2***	739.2***	0.98
G x L	22	209.9**	0.020***	23.5**	28.2***	21.8***	13.3***	145.3	1.17***
G x T x L	88	87.6	0.005	19.1	10.3	4.5	4.7	266.5	0.64
Residual	358	99.1	0.006	12.7	11.9	4.6	6.6	166.5	0.51
CV (%)		38.1	25.7	11.1	39.1	22.6	21.0	25.7	31.40

DF = degrees of freedom; FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); PPD = postharvest physiological deterioration (%); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; L = location; G = genotype; T = harvest time; CV = coefficient of variation (%); * = P<0.05; ** = P<0.01; *** = P<0.001.

Genotype by harvest time interaction effects

Averaged across harvest times, FSRY ranged from 7.9 t ha^{-1} in NASE3 to 25.0 t ha^{-1} in CT2, with an overall mean of 16.8 t ha^{-1} (Table 3.3). Averaged across genotypes, FSRY was highest (26.1 t ha^{-1}) at 13 MAP and lowest (6.7 t ha^{-1}) at 5 MAP. Lowest mean FSRY of 2.8 t ha^{-1} was recorded by NASE3 at 5 MAP while highest of 41.0 t ha^{-1} was recorded by CT1 at 13 MAP. Nyara had peak mean FSRY at two harvest dates, 7 and 11 MAP; B11 at 7 and 13 MAP; CT5, NASE4, TME14 and NASE3 at 9 and 13 MAP (Figure 3.2). Akena had peak mean FSRY at 11 MAP while NASE14, CT1, CT2, CT3 and CT4 consistently recorded the highest mean FSRY at 13 MAP.

Averaged across harvest times, HI was highest (0.41) for genotypes CT2 and NASE4 and lowest (0.23) for NASE3 (Table 3.3). Averaged across genotypes, the trait was highest (0.39) at both 11 and 13 MAP. Lowest mean HI (0.12) was recorded by Akena at 5 MAP and highest (0.51) by CT2 at 11 MAP. Most genotypes, viz. CT1, CT2, CT3, CT4, Nyara and TME14 attained highest mean HI at 11 MAP. NASE4 attained its highest mean HI at both 11 and 13 MAP and NASE3 at 9 MAP. The rest of the genotypes viz. Akena, B11, NASE14 and CT5 attained their highest mean HI at 13 MAP.

Table 3.3: Effect of genotype x harvest time on fresh storage root yield and harvest index averaged across three locations in Uganda, 2011/12

	FSRY						HI					
	Harvest time (Months)						Harvest time (Months)					
Genotype	5	7	9	11	13	Mean	5	7	9	11	13	Mean
NASE14	4.7	8.6	12.7	26.9	33.9	17.4	0.15	0.22	0.24	0.33	0.34	0.26
Akena	2.3	12.6	23.7	32.3	29.6	20.1	0.12	0.28	0.37	0.45	0.46	0.33
B11	11.8	15.2	13.2	16.1	23.0	15.9	0.31	0.29	0.34	0.39	0.42	0.35
CT1	7.4	18.8	19.1	33.3	41.0	23.9	0.23	0.31	0.33	0.43	0.41	0.34
CT2	12.3	18.3	24.8	32.9	36.5	25.0	0.34	0.35	0.42	0.51	0.44	0.41
CT3	6.8	16.1	20.5	25.9	30.7	20.0	0.24	0.33	0.39	0.47	0.45	0.37
CT4	5.1	8.9	13.3	18.8	20.0	13.2	0.15	0.19	0.27	0.33	0.30	0.25
CT5	7.4	13.7	14.6	11.2	21.4	13.7	0.26	0.36	0.35	0.36	0.39	0.34
NASE3	2.8	5.0	11.2	7.3	13.1	7.9	0.15	0.18	0.30	0.22	0.29	0.23
NASE4	6.5	15.0	22.9	21.2	30.4	19.2	0.27	0.33	0.46	0.50	0.50	0.41
Nyara	4.0	10.9	8.0	12.0	10.9	9.2	0.20	0.27	0.27	0.33	0.31	0.28
TME14	8.7	14.5	19.8	17.7	22.3	16.6	0.22	0.25	0.31	0.33	0.32	0.29
Mean	6.7	13.2	17.0	21.3	26.1	16.8	0.22	0.28	0.34	0.39	0.39	0.32
$LSD_{0.05}$	Genotype mean					4.1						0.06
$LSD_{0.05}$	Harvest time mean					2.7						0.02
$LSD_{0.05}$	Genotype x harvest time mean					9.2						0.13

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; $LSD_{0.05}$ = least significant difference at 5%.

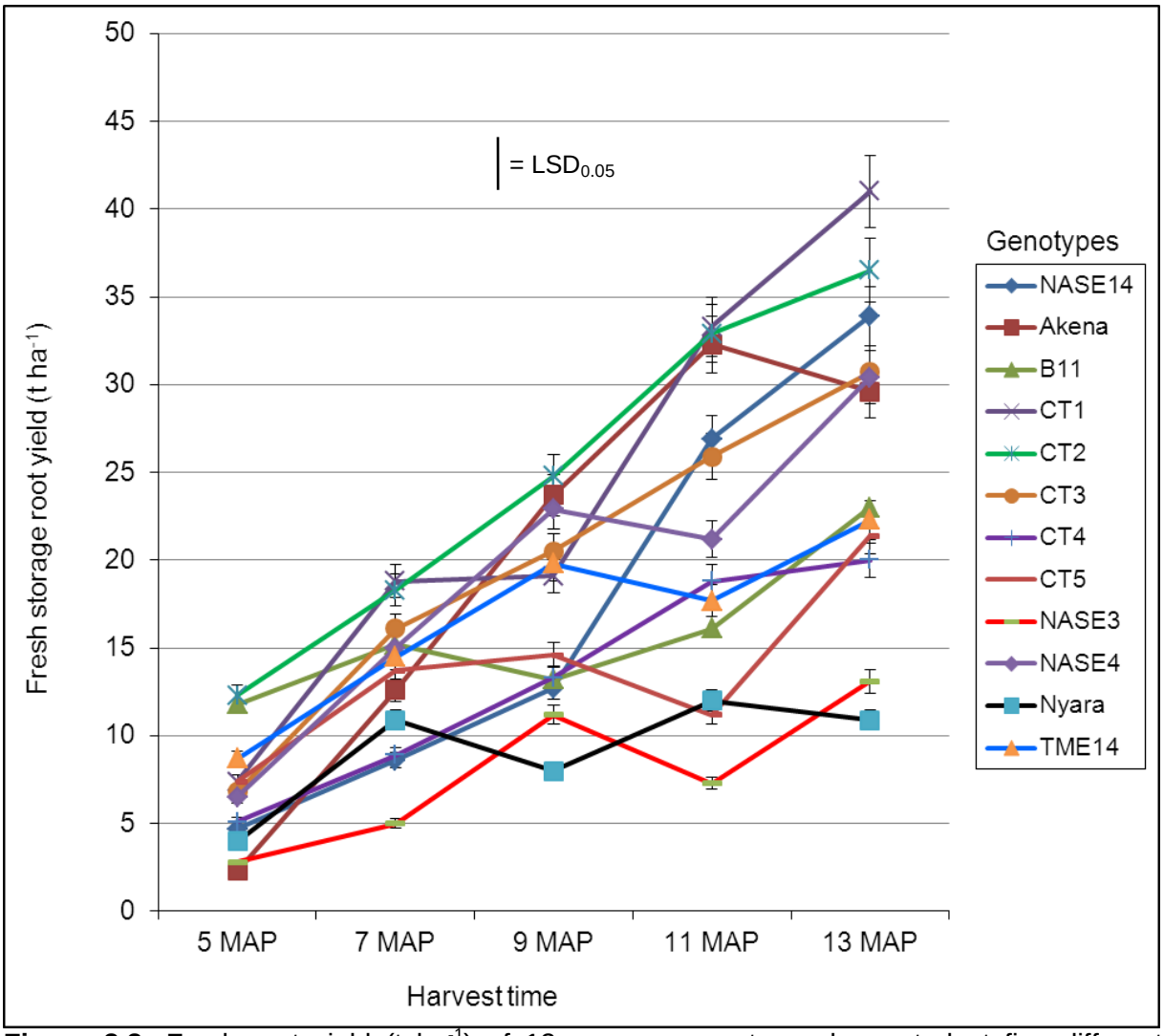

Figure 3.2: Fresh root yield (t ha^{-1}) of 12 cassava genotypes harvested at five different months after planting (MAP) averaged across three locations in Uganda, 2011/12

Averaged across harvest times, the highest DMC of 36.9% was recorded by genotype B11 and the lowest of 26.8% by NASE3 (Table 3.4). Averaged across genotypes, the highest DMC of 36.1% was recorded when plants were harvested at 9 MAP and the lowest of 25.4% was recorded at 5 MAP. Lowest mean DMC (20.1%) was recorded by NASE3 at 5 MAP whereas highest DMC (39.9%) was recorded by B11 at 9 MAP. Most genotypes recorded highest mean DMC before or at 9 MAP. For example, CT2 recorded highest mean DMC at 7 MAP; and NASE14, B11, CT1, CT4, CT5, NASE3, NASE4, Nyara and TME14 at 9 MAP. For most genotypes the differences between mean DMC at 7 and 9 MAP were non-significant.

Averaged across harvest times, the highest DSRY of 8.2 t ha^{-1} was recorded by CT1 and the lowest of 2.5 t ha^{-1} by NASE3 (Table 3.4). Averaged across genotypes, the highest DSRY of 8.2 t ha^{-1} was recorded at 13 MAP and the lowest of 1.8 t ha^{-1} at 5 MAP. Overall DSRY ranged from 0.5 t ha^{-1} for Akena at 5 MAP to 13.3 t ha^{-1} for CT1 at 13 MAP. Genotype TME14 recorded its highest mean DSRY at 9 MAP while genotypes Akena, CT2, CT4 and Nyara recorded their highest mean DSRY at 11 MAP. The rest of the genotypes recorded highest DSRY at 13 MAP.

Table 3.4: Effect of genotype x harvest time on dry mass content and dry storage root yield averaged across three locations in Uganda, 2011/12

	DMC						DSRY					
	Harvest time (Months)						Harvest time (Months)					
Genotype	5	7	9	11	13	Mean	5	7	9	11	13	Mean
NASE14	23.4	29.2	35.2	34.9	33.1	31.2	1.2	2.6	4.7	10.0	11.2	5.9
Akena	21.0	28.5	34.5	35.7	30.7	30.1	0.5	3.7	8.2	11.5	9.1	6.6
B11	34.2	39.3	39.9	38.4	32.9	36.9	4.0	5.8	5.2	6.3	7.1	5.7
CT1	24.1	34.7	37.8	36.1	32.5	33.0	1.9	6.5	7.2	12.1	13.3	8.2
CT2	24.6	36.8	34.4	33.3	28.4	31.5	3.0	6.8	8.8	10.9	10.7	8.0
CT3	28.0	35.6	38.6	39.1	35.3	35.3	2.0	5.8	8.0	10.1	10.7	7.3
CT4	25.2	32.7	36.3	33.9	30.1	31.6	1.3	3.0	4.9	6.3	6.2	4.3
CT5	27.1	35.2	36.1	29.1	26.9	30.9	2.0	4.9	5.4	3.3	5.8	4.3
NASE3	20.1	25.3	30.4	28.0	30.3	26.8	0.6	1.3	3.8	2.5	4.4	2.5
NASE4	23.2	30.6	35.8	35.4	30.6	31.1	1.6	4.6	8.1	7.6	9.1	6.2
Nyara	24.5	29.3	34.2	33.1	29.1	30.0	1.1	3.5	2.7	4.1	3.3	2.9
TME14	28.9	36.3	40.1	38.4	32.9	35.3	2.6	5.3	7.9	6.8	7.2	6.0
Mean	25.4	32.8	36.1	34.6	31.1	32.0	1.8	4.5	6.2	7.6	8.2	5.7
$LSD_{0.05}$	Genotype mean					1.5						1.4
$LSD_{0.05}$	Harvest time mean					1.0						0.9
$LSD_{0.05}$	Genotype x harvest time mean					3.3						3.2

DMC = dry mass content (%); DSRY = fresh storage root yield (t ha^{-1}); $LSD_{0.05}$ = least significant difference at 5%.

Averaged across harvest times, the highest SRN of 8.5 was recorded by CT1 and lowest of 4.3 by Nyara (Table 3.5). Averaged across genotypes, highest SRN of 7.6 was recorded at 7 MAP and the lowest of 5.9 at 9 MAP. Highest mean SRN of 10.3 was recorded by NASE14 at 5 MAP and lowest of 3.3 by NASE3 at 13 MAP.

Averaged across harvest times, SRG was highest in genotype CT2 at 16.1 cm and lowest in NASE3 at 7.3 cm (Table 3.5). Averaged across genotypes, highest SRG of 17.0 cm was recorded at 13 MAP whereas the lowest SRG of 7.3 cm was recorded at 5 MAP. Highest mean SRG was consistently recorded by CT2 at all harvest times. Lowest mean SRG also at all harvest times was recorded by NASE3.

Table 3.5: Effect of genotype x harvest time on storage root number and storage root girth averaged across three locations in Uganda, 2011/12

	SRN						SRG					
	Harvest time (Months)						Harvest time (Months)					
Genotype	5	7	9	11	13	Mean	5	7	9	11	13	Mean
NASE14	10.3	5.9	5.3	6.0	6.9	6.9	5.3	6.5	8.5	11.8	15.6	9.5
AKENA	5.9	6.8	5.1	5.8	5.4	5.8	5.0	10.2	13.9	15.7	19.2	12.8
B11	9.1	7.6	4.6	5.0	4.8	6.2	10.4	11.8	11.4	13.8	15.3	12.6
CT1	8.6	9.6	6.7	8.4	9.4	8.5	7.8	11.3	12.9	15.3	17.4	12.9
CT2	8.7	9.4	8.0	7.4	7.8	8.3	10.4	13.9	15.7	19.2	21.3	16.1
CT3	5.3	7.2	5.5	6.2	6.1	6.1	8.4	12.2	14.9	17.3	19.0	14.4
CT4	6.7	7.9	6.4	7.7	6.3	7.0	6.4	9.5	10.0	14.7	16.5	11.4
CT5	7.3	7.9	6.3	5.5	6.7	6.7	8.6	11.7	12.4	12.1	15.7	12.1
NASE3	5.9	5.7	4.2	4.3	3.3	4.7	3.6	5.8	7.5	7.3	12.5	7.3
NASE4	7.5	9.3	8.5	7.6	8.0	8.2	8.4	12.1	14.3	18.2	19.3	14.5
Nyara	4.7	5.6	3.6	3.5	3.9	4.3	5.6	8.5	10.1	11.5	14.3	10.0
TME14	7.2	8.1	6.4	5.8	6.7	6.9	8.1	12.3	14.8	14.8	17.7	13.5
Mean	7.3	7.6	5.9	6.1	6.3	6.6	7.3	10.5	12.2	14.3	17.0	12.3
$LSD_{0.05}$	Genotype mean					0.9						1.1
$LSD_{0.05}$	Harvest time mean					0.6						0.7
$LSD_{0.05}$	Genotype x harvest time mean					2.0						2.4

SRN = storage root number plant^{-1}; SRG = storage root girth (cm); $LSD_{0.05}$ = least significant difference at 5%.

Averaged across harvest times, PPD was highest at 62.1% in genotype B11 and lowest in NASE3 at 25.2% (Table 3.6). Averaged across genotypes, PPD was highest at 9 MAP at 47.1% and lowest at 30.8% at 5 MAP. The highest mean PPD corresponded with the harvest time at which genotypes had the highest mean DMC and also with genotypes having highest mean DMC (Table 3.4). Mean PPD was highest for B11 at 5 - 9 MAP, Akena at 11 MAP and TME14 at 13 MAP. On the other hand, mean PPD was lowest in NASE4 at 5 MAP, NASE3 at 7 and 9 MAP, and CT2 at 11 and 12 MAP.

Averaged across harvest times, the highest CBSD-RN score of 3.9 was recorded by Akena and the lowest of 1.5 by NASE4 and Nyara (Table 3.6). Averaged across genotypes, the highest CBSD-RN score of 2.8 was recorded at 13 MAP and the lowest of 1.7 at 5 MAP. Genotype Akena consistently recorded highest CBSD-RN mean score at all harvest times. On the other hand, Nyara recorded lowest CBSD-RN mean score at 5, 11 and 13 MAP; CT1 and NASE4 at 7 and 9 MAP, respectively.

Table 3.6: Effect of genotype x harvest time on postharvest physiological deterioration and cassava brown steak disease necrosis averaged across three locations in Uganda, 2011/12

	PPD						CBSD-RN					
	Harvest time (Months)						Harvest time (Months)					
Genotype	5	7	9	11	13	Mean	5	7	9	11	13	Mean
NASE14	33.2	34.7	44.0	37.9	51.2	40.2	2.3	3.4	3.1	2.6	3.2	2.9
AKENA	30.5	31.1	70.6	60.6	44.6	47.5	2.8	3.6	4.9	3.8	4.4	3.9
B11	63.7	70.5	82.5	42.7	51.2	62.1	1.2	1.9	1.8	1.7	3.1	1.9
CT1	28.3	33.9	44.4	51.4	35.0	38.6	1.5	1.0	2.3	1.8	1.8	1.7
CT2	21.0	28.2	35.8	27.0	29.0	28.2	1.7	2.2	4.1	3.0	3.3	2.9
CT3	42.2	61.6	58.8	46.9	47.8	51.4	1.4	2.7	2.6	2.9	2.7	2.4
CT4	27.0	40.2	49.5	40.9	29.5	37.4	1.4	1.8	2.4	2.2	2.4	2.1
CT5	30.8	43.6	41.9	29.7	30.1	35.2	2.2	2.2	2.8	2.8	3.8	2.8
NASE3	22.7	18.2	23.7	31.1	30.2	25.2	1.3	1.9	1.7	2.4	2.1	1.9
NASE4	14.4	24.1	32.7	30.3	41.8	28.7	1.3	1.7	1.1	1.6	2.0	1.5
Nyara	31.2	23.4	27.8	28.6	40.4	30.3	1.0	1.7	1.7	1.2	1.7	1.5
TME14	25.0	47.0	53.2	35.3	52.2	42.5	1.8	2.3	1.9	2.3	2.7	2.2
Mean	30.8	38.0	47.1	38.5	40.3	39.0	1.7	2.2	2.5	2.4	2.8	2.3
$LSD_{0.05}$	Genotype mean					4.2						0.3
$LSD_{0.05}$	Harvest time mean					2.7						0.2
$LSD_{0.05}$	Genotype x harvest time mean					9.3						6.7

PPD = postharvest physiological deterioration (%); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%.

Location by harvest time interaction effects

The highest mean FSRY was recorded at Jinja (20.0 t ha^{-1}) and when harvesting was done at 13 MAP (26.1 t ha^{-1}) (Table 3.7). Lowest mean FSRY was recorded at Namulonge (12.9 t ha^{-1}) and for harvest time at 5 MAP (5.0 t ha^{-1}). Highest mean FSRY at 5 MAP was recorded by Namulonge; at 7 and 9 MAP by Nakasongola; and at 11 and 13 by Jinja. Lowest mean FSRY at 5 MAP was recorded at Jinja and from 7 - 13 MAP at Namulonge. The mean FSRY from 5 - 11 MAP at Jinja and Namulonge were not statistically different to each other (Figure 3.3). Significant difference between the two sites in mean FSRY was observed at only 13 MAP. Both the lowest mean FSRY of 5.5 t ha^{-1} at 5 MAP and the highest of 35.3 t ha^{-1} at 13 MAP were recorded at Jinja.

Mean HI was highest when plants were harvested at both 11 and 13 MAP (0.39) and at both Jinja and Nakasongola (0.34) (Table 3.7). Lowest mean HI for harvest time was recorded at 5 MAP (0.22) and for location at Namulonge (0.28). Jinja recorded highest HI at 5, 7 and 13 MAP whereas Nakasongola recorded highest HI at 9 and 11 MAP. From 7 to 13 MAP lowest HI was consistently recorded at Namulonge. Lowest and highest mean HI of 0.20 at 5 MAP and 0.44 at 11 MAP, respectively were both recorded at Nakasongola.

Averaged across locations highest DMC of 36.1% was recorded at 9 MAP and lowest of 25.4% at 5 MAP (Table 3.7). Averaged across harvest times highest DMC of 32.8% was recorded at Nakasongola and lowest of 30.9% at Jinja. Highest mean DMC at 5, 9 and 11 MAP was recorded by Nakasongola; at 7 MAP by Namulonge; and at 13 MAP by Jinja. Lowest mean DMC from 5 - 9 MAP was recorded by Jinja; at 11 MAP by Namulonge; and at 13 MAP by Nakasongola.

Mean DSRY for harvest time was highest at 13 MAP (8.2 t ha^{-1}) and lowest at 5 MAP (1.8 t ha^{-1}) and for location it was highest at Jinja (6.7 t ha^{-1}) and lowest at Namulonge (4.3 t ha^{-1}) (Table 3.7). Highest DSRY at 5 MAP was recorded at Namulonge; at 7 and 9 MAP at Nakasongola; and at 11 and 13 MAP at Jinja. Lowest DSRY at 5 MAP was recorded at Jinja; at 7, 9 and 11 MAP at Namulonge; and at 13 MAP at Nakasongola. Lowest and highest mean DSRY of 1.4 t ha^{-1} at 5 MAP and 11.5 t ha^{-1} at 11 MAP, respectively were both recorded at Jinja.

Table 3.7: Location x harvest time interaction effects on mean fresh storage root yield, harvest index, dry mass content and dry storage root yield across five harvest times in Uganda during 2011/12

	FSRY				**HI**			
	Location				**Location**			
Harvest time (Months)	JN	NK	NM	Mean	JN	NK	NM	Mean
5	5.5	5.6	8.9	6.7	0.25	0.20	0.22	0.22
7	14.2	15.8	9.5	13.2	0.30	0.29	0.25	0.28
9	19.1	20.4	11.5	17.0	0.35	0.37	0.28	0.34
11	25.9	23.5	14.5	21.3	0.39	0.44	0.34	0.39
13	35.3	22.8	20.1	26.1	0.43	0.40	0.33	0.39
Mean	20.0	17.6	12.9	16.8	0.34	0.34	0.28	0.32
$LSD_{0.05}$	Harvest time			2.7				0.02
$LSD_{0.05}$	Location			2.1				0.02
$LSD_{0.05}$	Harvest time x location			4.6				0.04
	DMC				**DSRY**			
	Location				**Location**			
Harvest time (Months)	JN	NK	NM	Mean	JN	NK	NM	Mean
5	23.5	28.0	24.6	25.4	1.4	1.6	2.4	1.8
7	28.7	34.7	35.0	32.8	4.4	5.7	3.4	4.5
9	35.1	37.7	35.5	36.1	6.9	7.7	4.2	6.2
11	34.6	35.6	33.7	34.6	9.3	8.4	5.1	7.6
13	32.8	28.0	32.4	31.1	11.5	6.4	6.6	8.2
Mean	30.9	32.8	32.2	32.0	6.7	6.0	4.3	5.7
$LSD_{0.05}$	Harvest time mean			1.0				0.9
$LSD_{0.05}$	Location mean			0.7				0.7
$LSD_{0.05}$	Harvest time x location mean			1.7				1.6

JN = Jinja; NK = Nakasongola; NM = Namulonge; FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content (%); DSRY = dry storage root yield; $LSD_{0.05}$ = least significant difference at 5%.

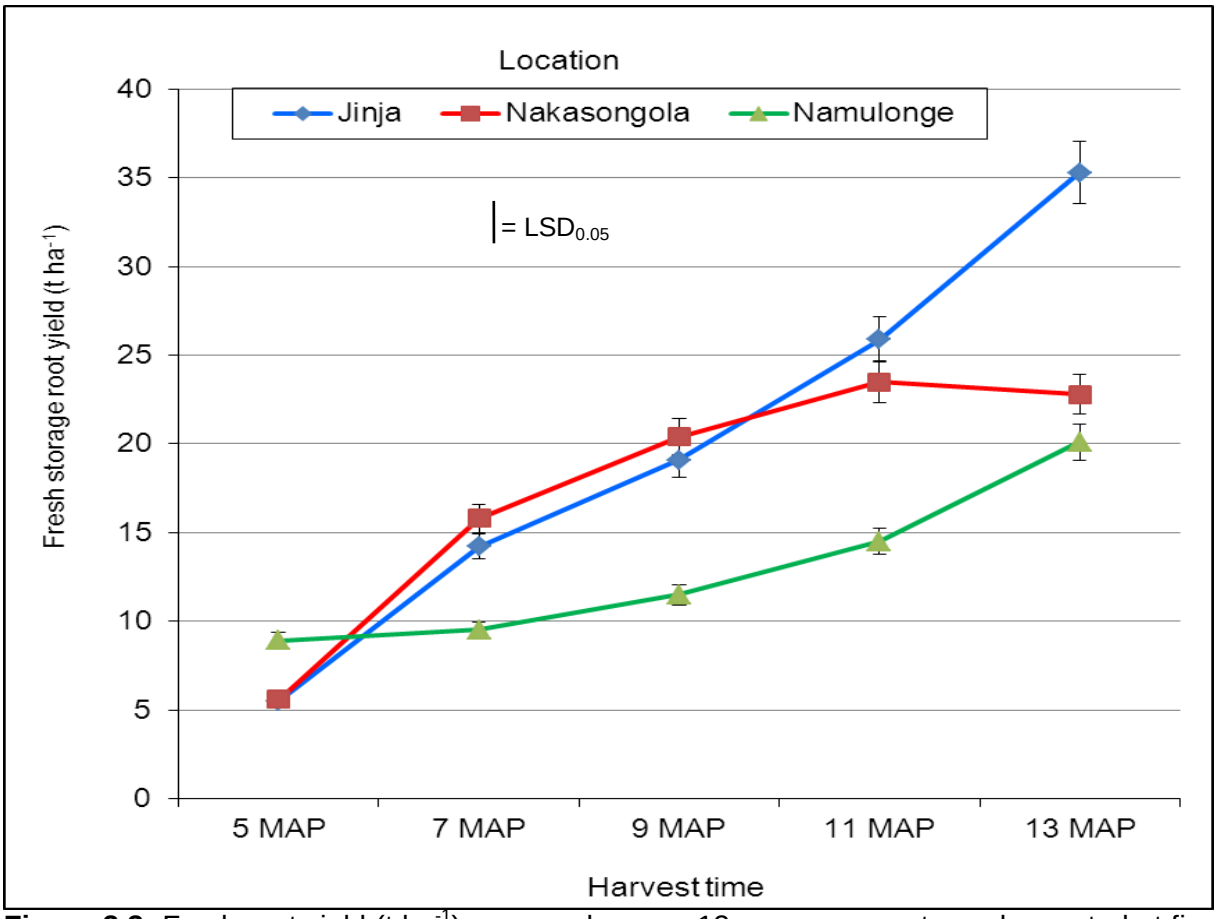

Figure 3.3: Fresh root yield (t ha^{-1}) averaged across 12 cassava genotypes harvested at five different months after planting (MAP) at three locations in Uganda, 2011/12

Mean SRN for harvest time was highest at 7 MAP (7.6) and lowest at 9 MAP (5.9) and for location it was highest at Nakasongola (7.2) and lowest at both Jinja and Namulonge (6.3) (Table 3.8). The highest SRN was recorded at Nakasongola at all harvest times except at 11 MAP where it was highest at Namulonge. Lowest SRN: at 5 and 7 MAP was recorded at Jinja; at 11 MAP at Nakasongola; and at 9 and 13 MAP at Namulonge. Mean SRN ranged from 4.8 at 9 MAP at Namulonge to 8.5 at 9 MAP at Nakasongola.

Mean SRG for location was highest at Jinja (13.4 cm) and lowest at Namulonge (10.9 cm) (Table 3.8). Mean SRG for harvest time was highest at 13 MAP (17.0 cm) and lowest at 5 MAP (7.3 cm). Highest mean SRG at 5 and 7 MAP was recorded at Nakasongola; and from 9 - 13 MAP at Jinja. Namulonge recorded the lowest mean SRG at all harvest times except at 5 MAP where it was recorded at Jinja. The lowest and highest mean SRG of 6.6 cm at 5 MAP and 19.5 cm at 13 MAP, respectively were both recorded at Jinja.

Mean PPD for harvest time was highest at 9 MAP (47.1%) and lowest at 5 MAP (30.8%) and for location it was highest at Namulonge (42.3%) and lowest at Nakasongola (35.8%) (Table 3.8). Namulonge recorded highest mean PPD at all harvest times except at 7 MAP where it was recorded at Nakasongola. On the other hand, lowest mean PPD at 5, 11 and 13 MAP was recorded at Nakasongola and at 7 and 9 MAP at Jinja. Mean PPD ranged from 28.1% at 5 MAP at Nakasongola to 51.0% at 9 MAP at Namulonge.

Mean CBSD-RN score for harvest time was highest at 13 MAP (2.8) and lowest at 5 MAP (1.7) and for location it was highest for Namulonge (2.4) and lowest for Jinja (2.2) (Table 3.8). Namulonge recorded highest CBSD-RN mean score at all harvest times except at 7 MAP where it was recorded at Nakasongola. The lowest CBSD-RN mean score at 5 MAP was recorded at Nakasongola; at 7 MAP at Namulonge; and from 9 – 13 MAP at Jinja. Mean CBSD-RN ranged from 1.5 at 5 MAP at Nakasongola to 2.9 at 13 MAP at Namulonge.

Table 3.8: Effect of location x harvest time on mean storage root number, storage root girth, postharvest physiological deterioration and cassava brown streak disease root necrosis averaged across twelve genotypes evaluated in Uganda, 2011/12

	SRN				**SRG**			
	Location				**Location**			
Harvest time (Months)	JN	NK	NM	Mean	JN	NK	NM	Mean
5	6.1	8.5	7.2	7.3	6.6	8.7	6.7	7.3
7	7.3	8.0	7.5	7.6	11.0	11.1	9.3	10.5
9	5.8	7.0	4.8	5.9	13.8	12.5	10.3	12.2
11	6.1	5.9	6.3	6.1	15.8	14.7	12.4	14.3
13	6.3	6.8	5.8	6.3	19.5	15.9	15.6	17.0
Mean	6.3	7.2	6.3	6.6	13.4	12.6	10.9	12.3
$LSD_{0.05}$	Harvest time			0.6				0.7
$LSD_{0.05}$	Location			0.4				0.5
$LSD_{0.05}$	Harvest time x location mean			1.0				1.2
	PPD				**CBSD-RN**			
	Location				**Location**			
Harvest time (Months)	JN	NK	NM	Mean	JN	NK	NM	Mean
5	30.6	28.1	33.9	30.8	1.7	1.5	1.8	1.7
7	35.6	41.3	37.3	38.0	2.3	2.2	2.0	2.2
9	43.1	47.1	51.0	47.1	2.3	2.6	2.7	2.5
11	40.3	31.7	43.5	38.5	2.1	2.4	2.4	2.4
13	44.0	31.0	45.7	40.3	2.7	2.8	2.9	2.8
Mean	38.7	35.8	42.3	39.0	2.2	2.3	2.4	2.3
$LSD_{0.05}$	Harvest time mean			2.7				0.2
$LSD_{0.05}$	Location mean			2.1				0.1
$LSD_{0.05}$	Harvest time x location mean			4.6				0.3

JN = Jinja; NK = Nakasongola; NM = Namulonge; SRN = storage root number plant^{-1}; storage root girth (cm); PPD = postharvest physiological deterioration (%); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%.

Location by genotype interaction effects

Mean FSRY for genotype ranged from 4.6 t ha^{-1} for Nyara at Namulonge to 31.8 t ha^{-1} for CT1 at Jinja (Table 3.9). The best two genotypes for FSRY at: Jinja were CT1 and CT2; Nakasongola were CT2 and NASE4; and Namulonge were CT1 and CT2 (Figure 3.4). The worst two genotypes for the trait at: Jinja were NASE3 and Nyara; Nakasongola were B11, NASE3 and CT4; and Namulonge were Nyara and NASE3.

Mean HI ranged from 0.18 for both NASE3 and NASE14 at Namulonge to 0.44 for both B11 and CT2 at Jinja (Table 3.9). Two genotypes with highest HI at: Jinja were B11 and CT2; Nakasongola were NASE4 and CT2; and Namulonge were NASE4 and CT2. Two genotypes with lowest HI at: Jinja were CT4 and NASE3; Nakasongola were CT4 and Nyara; and Namulonge were NASE3 and NASE14.

Table 3.9: Effect of location x genotype interaction on fresh storage root yield and harvest index averaged across five harvest times in Uganda, 2011/12

	FSRY				HI			
	Location				Location			
Genotype	JN	NK	NM	Mean	JN	NK	NM	Mean
NASE14	25.3	19.8	6.9	17.4	0.27	0.32	0.18	0.26
AKENA	25.1	20.7	14.5	20.1	0.35	0.34	0.30	0.33
B11	22.8	9.7	15.0	15.9	0.44	0.27	0.35	0.35
CT1	31.8	22.8	17.1	23.9	0.37	0.34	0.32	0.34
CT2	30.9	24.1	20.0	25.0	0.44	0.42	0.37	0.41
CT3	22.4	20.6	17.0	20.0	0.39	0.41	0.32	0.37
CT4	14.8	11.9	13.0	13.2	0.24	0.27	0.23	0.25
CT5	14.8	15.2	11.0	13.7	0.38	0.36	0.30	0.34
NASE3	7.0	11.9	4.7	7.9	0.20	0.31	0.18	0.23
NASE4	17.7	23.3	16.6	19.2	0.42	0.42	0.40	0.41
Nyara	9.6	13.2	4.6	9.2	0.31	0.31	0.21	0.28
TME14	17.6	18.2	14.0	16.6	0.31	0.32	0.23	0.29
Mean	20.0	17.6	12.9	16.8	0.34	0.34	0.28	0.32
$LSD_{0.05}$	Genotype mean			4.1				0.03
$LSD_{0.05}$	Location mean			7.2				0.02
$LSD_{0.05}$	Genotype x location mean			7.3				0.06

JN = Jinja; NK = Nakasongola; NM = Namulonge; FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; $LSD_{0.05}$ = least significant difference at 5%.

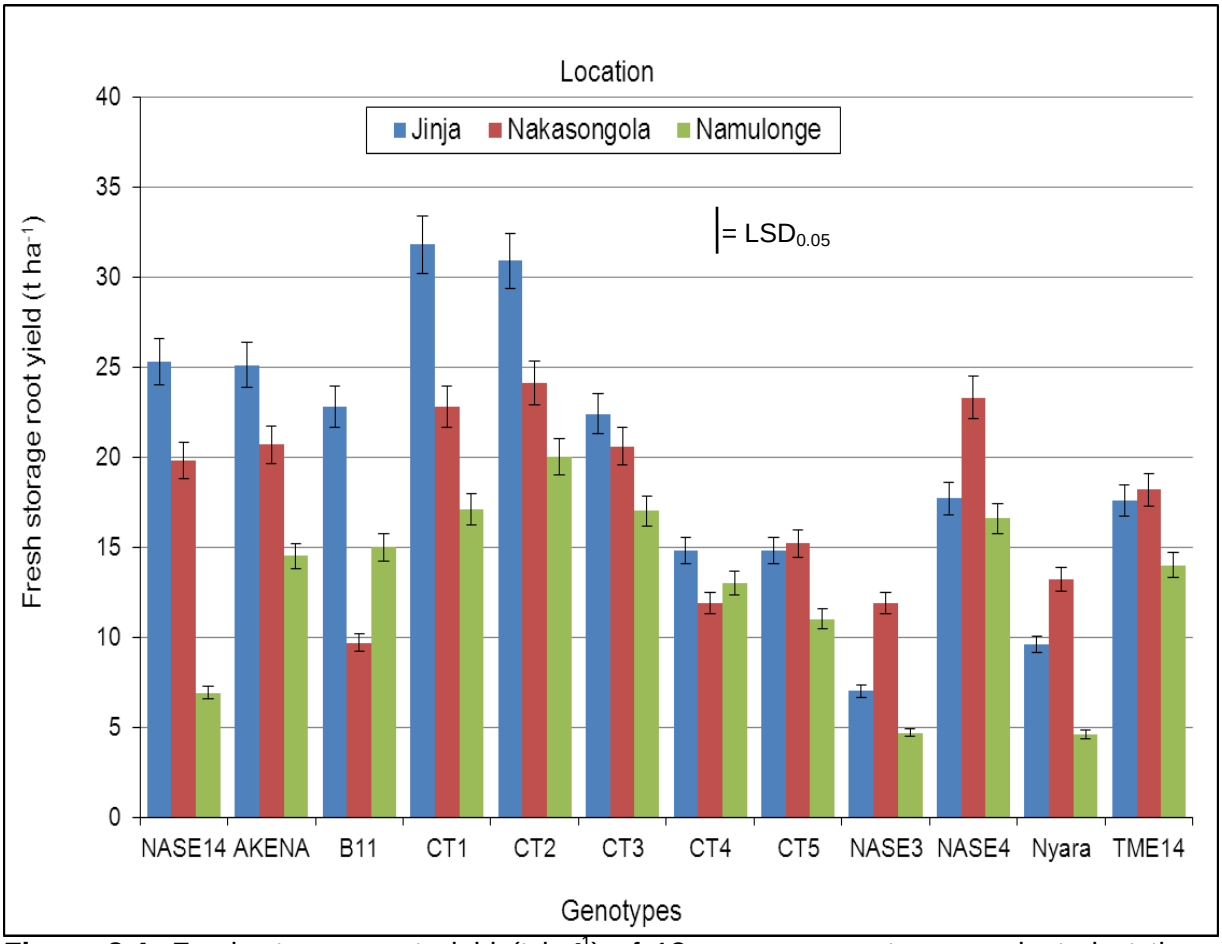

Figure 3.4: Fresh storage root yield (t ha^{-1}) of 12 cassava genotypes evaluated at three locations averaged across five harvest times in Uganda, 2011/12

Mean DMC ranged from 25.0% for NASE3 at Jinja to 37.2% for B11 at Namulonge (Table 3.10). The best two genotypes for DMC at: Jinja and Nakasongola were B11 and TME14; and Namulonge were B11 and CT3. The worst two genotypes for the trait at: Jinja and Nakasongola were Akena and NASE3; and Namulonge were NASE3 and CT5.

Mean DSRY ranged from 1.5 t ha^{-1} for both Nyara and NASE3 at Namulonge to 11.2 t ha^{-1} for genotype CT1 at Jinja (Table 3.10). The best two genotypes for DSRY at: Jinja were CT1 and CT2; Nakasongola were CT2 and CT3; and Namulonge were also CT2 and CT3. The worst two genotypes for the trait at: Jinja were NASE3 and Nyara; Nakasongola were B11 and CT4; and Namulonge were Nyara and NASE3.

Table 3.10: Effect of location x genotype interaction on dry mass content and dry storage root yield averaged across five harvest times in Uganda, 2011/12

	DMC				DSRY			
	Location				Location			
Genotype	JN	NK	NM	Mean	JN	NK	NM	Mean
NASE14	30.6	31.5	31.4	31.2	8.7	6.8	2.4	5.9
AKENA	28.0	30.0	31.3	30.1	7.8	7.0	4.9	6.6
B11	36.7	36.9	37.2	36.9	8.6	3.5	5.0	5.7
CT1	32.7	31.9	34.5	33.0	11.2	7.4	5.9	8.2
CT2	30.9	32.5	31.1	31.5	10.0	7.9	6.2	8.0
CT3	33.9	36.0	36.0	35.3	8.0	7.6	6.4	7.3
CT4	30.3	32.0	32.6	31.6	4.8	3.9	4.3	4.3
CT5	31.3	33.0	28.4	30.9	4.7	5.0	3.1	4.3
NASE3	25.0	29.8	25.6	26.8	1.9	4.1	1.5	2.5
NASE4	29.4	32.0	32.8	31.1	5.6	7.4	5.7	6.2
Nyara	28.3	31.7	30.1	30.0	3.1	4.3	1.5	2.9
TME14	34.0	36.1	35.9	35.3	6.1	6.7	5.1	6.0
Mean	30.9	32.8	32.2	32.0	6.7	6.0	4.3	5.7
$LSD_{0.05}$	Genotype mean			1.5				1.4
$LSD_{0.05}$	Location mean			0.7				0.7
$LSD_{0.05}$	Genotype x location mean			1.3				2.5

JN = Jinja; NK = Nakasongola; NM = Namulonge; DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); $LSD_{0.05}$ = least significant difference at 5%.

Mean SRN ranged from 2.7 for Nyara at Namulonge to 9.8 for NASE4 at Nakasongola (Table 3.11). The best two genotypes for mean SRN at: Jinja were CT1 and NASE14; Nakasongola were CT1 and NASE4; and Namulonge were CT2 and TME14. The worst two genotypes for the trait at: Jinja were NASE3 and Nyara; Nakasongola were B11 and CT3; and Namulonge were Nyara and NASE3.

Mean SRG ranged from 5.3 cm for NASE3 at Namulonge to 17.3 cm for CT2 in Jinja (Table 3.11). The best two genotypes for SRG at: Jinja were B11 and CT2; Nakasongola were CT2 and NASE4; and Namulonge were CT2 and CT3. The worst two genotypes for the trait at all three locations were NASE3 and NASE14.

Table 3.11: Effect of location x genotype interaction on storage root number and storage root girth averaged across five harvest times in Uganda, 2011/12

	SRN				SRG			
	Location				Location			
Genotype	JN	NK	NM	Mean	JN	NK	NM	Mean
NASE14	7.8	8.3	4.6	6.9	10.7	10.9	7.0	9.5
Akena	6.6	5.9	4.9	5.8	13.9	12.2	12.3	12.8
B11	5.7	5.4	7.6	6.2	16.4	11.1	10.2	12.6
CT1	9.0	9.4	7.2	8.5	13.8	12.6	12.5	12.9
CT2	7.4	8.9	8.5	8.3	17.3	16.3	14.7	16.1
CT3	5.6	5.8	6.8	6.1	14.8	14.3	14.0	14.4
CT4	5.9	7.9	7.2	7.0	11.9	11.1	11.2	11.4
CT5	5.9	6.8	7.6	6.7	13.1	12.9	10.3	12.1
NASE3	4.4	6.7	3.0	4.7	8.0	8.7	5.3	7.3
NASE4	7.1	9.8	7.6	8.2	14.7	15.2	13.5	14.5
Nyara	4.1	5.9	2.7	4.3	11.1	11.5	7.3	10.0
TME14	6.2	6.3	8.1	6.9	14.6	14.1	11.9	13.5
Mean	6.3	7.2	6.3	6.6	13.4	12.6	10.9	12.3
$LSD_{0.05}$	Genotype			0.9				1.1
$LSD_{0.05}$	Location			0.4				0.5
$LSD_{0.05}$	Genotype x location			1.5				1.9

JN = Jinja; NK = Nakasongola; NM = Namulonge; SRN = storage root number plant^{-1}; SRG = storage root girth (cm); $LSD_{0.05}$ = least significant difference at 5%.

Lowest and highest mean PPD of 21.4% for NASE3 and 69.1% for B11, respectively were both recorded at Jinja (Table 3.12). The best two genotypes with the lowest mean PPD at: Jinja and Nakasongola were NASE3 and NASE4; and Namulonge were NASE3 and Nyara. The worst two genotypes with the highest PPD at all three locations were B11 and CT3. These two genotypes also had highest DMC (Table 3.12).

Mean CBSD-RN score ranged from a low of 1.3 for Nyara at Namulonge to a high of 3.9 for Akena at all locations (Table 3.12). The two best genotypes with the lowest CBSD-RN mean score at all locations were NASE4 and Nyara. The worst two genotypes with the highest CBSD-RN mean score at: Jinja were Akena and NASE14; Nakasongola were Akena and CT5; and Namulonge were Akena and CT2.

Table 3.12: Effect of location x genotype interaction on postharvest physiological deterioration and cassava brown streak disease root necrosis averaged across five harvest times in Uganda, 2011/12

	PPD				CBSD-RN			
	Location				Location			
Genotype	JN	NK	NM	Mean	JN	NK	NM	Mean
NASE14	37.5	35.2	47.9	40.2	3.0	2.4	3.3	3.0
AKENA	47.0	41.2	54.2	47.5	3.9	3.9	3.9	3.9
B11	69.1	56.5	60.8	62.1	2.3	1.9	1.7	2.3
CT1	39.2	36.3	40.3	38.6	1.5	1.7	1.9	1.5
CT2	27.9	25.3	31.5	28.2	2.6	2.7	3.3	2.6
CT3	50.2	48.6	55.6	51.4	2.3	2.2	2.6	2.3
CT4	39.1	34.4	38.8	37.4	2.1	2.3	1.8	2.1
CT5	35.0	34.1	36.6	35.2	2.4	3.1	2.7	2.4
NASE3	21.4	23.0	31.1	25.2	1.7	1.7	2.2	1.7
NASE4	27.0	24.8	34.2	28.7	1.5	1.5	1.5	1.5
Nyara	31.7	29.2	29.9	30.3	1.4	1.6	1.3	1.4
TME14	39.7	41.5	46.4	42.5	1.9	2.5	2.2	1.9
Mean	38.7	35.8	42.3	39.0	2.2	2.3	2.4	2.3
$LSD_{0.05}$	Genotype mean			4.2				0.3
$LSD_{0.05}$	Location mean			2.1				0.1
$LSD_{0.05}$	Genotype x location mean			7.2				0.5

JN = Jinja; NK = Nakasongola; NM = Namulonge; PPD = postharvest physiological deterioration; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%.

Cassava mosaic disease severity

The data for CMD-S were analysed separately to those for the other traits as the trials were scored for CMD-S on one date only at 6 MAP. In the ANOVA for CMD-S (Table 3.13), the genotype MS were highly significant (P<0.001), the location MS were significant (P<0.05), and genotype x location MS were very significant (P<0.01).

Table 3.13: Analysis of variance for cassava mosaic disease severity scores at six months after planting for 12 cultivars evaluated in three locations in Uganda, 2011

Source of variation	DF	Mean squares
Genotype	11	18.48***
Location	2	1.95*
Genotype x location	22	0.62**
Residual	46	0.31
CV (%)		44.5

DF = degrees of freedom; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CV = coefficient of variation (%); * = P<0.05; ** = P<0.01; *** = P<0.001.

Averaged across locations, the highest mean CMD-S score of 3.6 was recorded by B11 and Nyara while the lowest of 1.0 was recorded by NASE14, Akena, CT1, CT2, CT3, CT4, CT5 and TME14 (Table 3.14). Averaged across genotypes, the highest score of 1.7 was recorded at Namulonge and lowest of 1.3 at Jinja. The highest mean CMD-S score of 3.2 and 4.0 at Jinja and Nakasongola, respectively were recorded by B11. The highest CMD-S of 4.3 in

Namulonge was recorded by Nyara. Genotypes Akena, NASE14, CT1, CT2, CT3, CT4, CT5 and TME14 had a score of 1.0 at all locations

Table 3.14: Mean cassava mosaic disease severity scores for 12 cassava genotypes assessed at six months after planting in three locations in Uganda, 2011

	Location			
Genotypes	JN	NK	NM	Mean
NASE14	1.0	1.0	1.0	1.0
AKENA	1.0	1.0	1.0	1.0
B11	3.2	4.0	3.7	3.6
CT1	1.0	1.0	1.0	1.0
CT2	1.0	1.0	1.0	1.0
CT3	1.0	1.0	1.0	1.0
CT4	1.0	1.0	1.0	1.0
CT5	1.0	1.0	1.0	1.0
NASE3	1.0	1.7	1.7	1.4
NASE4	1.0	1.0	1.7	1.2
Nyara	3.0	3.7	4.3	3.6
TME14	1.0	1.0	1.0	1.0
Mean	1.3	1.4	1.7	1.5
$LSD_{0.05}$ Genotype mean				0.4
$LSD_{0.05}$ Location mean				0.2
$LSD_{0.05}$ Genotype x location				0.3

JN = Jinja; NK = Nakasongola; NM = Namulonge; LSD = $LSD_{0.05}$ = least significant difference at 5%.

3.3.2 Estimates of phenotypic, genotypic and environmental variance components

Variance components for genotype, environment and genotype x environment interaction were determined for each harvest date separately. The variance component for genotypes at all five harvest times was higher for all traits than that for environment and genotype x environment interaction (Table 3.15). Similarly, for all traits, a large proportion of the phenotypic component of variance was accounted for by the genotypic component of variance as reflected by H_b being >50.0% for all traits at all harvest times, except for SRN at 5 MAP. Apart from CMD-S that was evaluated only at 6 MAP, H_b estimates for all traits at all harvests times were relatively high. Lowest H_b estimates at: 5, 9 and 11 MAP were recorded by SRN; 7 MAP by FSRY; and 13 MAP by DMC. Highest H_b estimates at: 5 and 11 MAP were recorded by SRG; 7 and 9 MAP by PPD; and 13 MAP by CBSD-RN. Highest GCV and PCV at: 5 and 11 MAP were recorded by DSRY; at 7 and 9 MAP by PPD; 13 MAP by CBSD-RN and by FSRY, respectively. Dry mass content recorded the lowest GCV and PCV at all harvest times.

Table 3.15: Estimates of variance components and broad sense heritability for nine traits for 12 cassava genotypes evaluated at three locations on five separate harvest times in Uganda, 2011/12

	Variance components							
Traits	δ^2_P	δ^2_G	δ^2_E	δ^2_{GxE}	H_b	$\bar{x}$	**GCV (%)**	**PCV (%)**
5MAP								
FSRY	10.1567	6.4000	3.8367	-0.08000	63.0	6.7	37.8	47.6
DSRY	1.0372	0.9060	0.1712	-0.04000	87.3	1.8	52.9	56.6
DMC	15.3344	12.6300	1.6844	1.02000	82.4	25.4	14.0	15.4
HI	0.0050	0.0045	0.00055	0.00001	88.9	0.22	30.5	32.1
PPD	208.256	174.800	25.4222	8.03333	83.9	30.8	42.9	46.9
SRN	2.8302	1.1210	0.5129	1.19633	39.6	7.3	14.5	23.0
SRG	4.6562	4.2780	0.3459	0.03233	91.9	7.3	28.3	29.6
CBSD-RN	0.4647	0.2382	0.0082	0.21833	51.3	1.7	28.7	40.0
CMD-S	1.0360	0.9700	0.0510	0.01500	93.6	1.6	61.3	63.8
7MAP								
FSRY	18.0522	11.0600	4.4389	2.5533	61.3	13.2	25.2	32.2
DSRY	2.9390	1.9790	0.5950	0.3650	67.3	4.5	31.3	38.1
DMC	23.6122	21.7900	2.2789	-0.4567	92.3	32.8	14.2	14.8
HI	0.0038	0.0030	0.0004	0.0004	78.0	0.28	19.6	22.0
PPD	299.8444	283.3000	16.3778	0.1667	94.5	38.0	44.3	45.6
SRN	2.2304	1.5910	0.7371	-0.0977	71.3	7.6	16.6	19.7
SRG	6.8297	6.0960	0.4920	0.2417	89.3	10.5	23.5	24.9
CBSD-RN	0.6038	0.5581	0.0512	-0.0055	92.4	2.2	34.0	35.3
9 MAP								
FSRY	30.0778	22.6000	6.9311	0.5467	75.1	17.0	28.0	32.3
DSRY	4.0982	2.9610	0.9839	0.1533	72.3	6.2	22.8	32.7
DMC	7.5166	5.5380	0.8379	1.1407	73.7	36.1	6.5	7.6
HI	0.0043	0.0029	0.0008	0.0006	69.0	0.34	15.8	19.3
PPD	370.1333	326.9000	22.0000	21.2333	88.3	47.1	38.4	40.8
SRN	2.0920	1.2680	0.2783	0.5457	60.6	5.9	19.1	24.5
SRG	7.2753	6.2780	0.8530	0.1443	86.3	12.2	20.5	22.1
CBSD-RN	0.8285	0.6759	0.0692	0.0834	81.6	2.5	32.9	36.4
11 MAP								
FSRY	61.4556	48.5000	19.2889	-6.3333	78.9	21.3	32.7	36.8
DSRY	10.9689	9.0500	2.5822	-0.6633	82.5	7.6	39.6	43.6
DMC	15.9689	12.1300	2.3789	1.4600	76.0	34.6	10.1	11.5
HI	0.0081	0.0070	0.0010	0.0001	86.8	0.39	21.5	23.1
PPD	138.1778	111.7000	12.6111	13.8667	80.8	38.5	27.5	30.5
SRN	2.5584	1.6670	0.3128	0.5787	65.2	6.1	21.2	26.2
SRG	11.7289	10.5900	1.3056	-0.1667	90.3	14.3	22.8	23.9
CBSD-RN	0.3801	0.3308	0.0832	-0.0339	87.0	2.4	24.0	25.7
13 MAP								
FSRY	90.1444	68.3000	27.3111	-5.4667	75.8	26.1	31.7	36.4
DSRY	9.5656	7.1300	2.7189	-0.2833	74.5	8.2	32.6	37.8
DMC	24.1433	11.8700	5.6433	6.6300	49.2	31.1	11.1	15.8
HI	0.0086	0.0068	0.0014	0.0004	79.6	0.39	21.1	23.8
PPD	100.5333	65.1000	15.0000	20.4333	64.8	40.3	20.0	24.8
SRN	3.2907	2.4800	0.6517	0.1590	75.4	6.3	25.0	28.8
SRG	14.3411	12.2000	1.4978	0.6433	85.1	17.0	20.1	22.3
CBSD-RN	1.0288	0.9077	0.0633	0.0577	88.2	2.8	34.0	36.2

MAP = months after planting; FSRY = fresh storage root yield (t ha^{-1}); DSRY = dry storage root yield (t ha^{-1}); DMC = dry mass content (%); HI = harvest index; PPD = postharvest physiological deterioration (%); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); CBSD-RN = cassava brown streak root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity sored on scale of 1-5 at 6 MAP; GCV = genotypic coefficient of variation (%); PCV = phenotypic coefficient of variation (%); H_b = broad sense heritability (%); G = genotype; E = environment; P = phenotype; δ^2 = variance component. $\bar{x}$ = mean of the trait.

3.3.3 Contribution of the traits to genotype variation

Principal components analysis indicated that the first two principal components explained 70.6% of the total variation and had eigenvalues greater than one (Table 3.16). The PC1 alone accounted for 51.1% of the total variation, mostly contributed to by storage root related traits. All traits contributing to this PC were positively correlated, and based on the value of the PC coefficients for these traits at least four traits namely HI, DSRY, FSRY and SRG made the major contribution to PC1. The PC2 accounted for a smaller fraction of total variance (19.6%) and again this was largely determined by storage root related traits, viz. DMC, SRN and PPD. The PC3 accounted for 12.7 % of total variation with an eigenvalue of less than one and was largely contributed to by SRN and HI.

Table 3.16: Principal component (PC) scores, eigenvalues and proportions of total and cumulative variances for first three PCs for seven cassava traits of 12 cassava genotype averaged across five harvest times and three locations in Uganda, 2011/12

	Principal components		
Traits	**PC1**	**PC2**	**PC3**
HI	0.41691	0.05546	0.40904
DMC	0.26062	- 0.54718	- 0.28595
DSRY	0.50125	0.09454	- 0.04360
FSRY	0.48894	0.19923	0.01679
SRG	0.45605	0.02891	0.21925
SRN	0.16783	0.46717	- 0.78873
PPD	0.17831	- 0.65559	- 0.28030
Eigenvalue	3.57	1.37	0.89
Percentage variation	51.1	19.6	12.7
Cumulative percentage variation	51.1	70.6	83.4

HI = harvest index; DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); FSRY = fresh storage root yield (t ha^{-1}); SRG = storage root girth (cm); SRN = storage root number; PPD = postharvest physiological deterioration; PC = principal component.

3.3.4 Phenotypic correlations of agronomic and disease resistance traits

Most of the agronomic traits were significantly correlated with one another, whereas resistance to CMD and CBSD traits were not (Table 3.17). Fresh storage root yield was highly significantly (P<0.001), positively correlated with DSRY, SRN, HI, DMC, PPD and SRG; and very significantly (P<0.01), positively correlated with CBSD-RN. Of these significant correlations with FSRY, DSRY had the highest correlation (r = 0.98), followed by SRG (r = 0.76). Similarly, DSRY was highly significantly (P<0.001), positively correlated with FSRY, SRN, HI, DMC, PPD and SRG and very significantly (P<0.01), positively correlated with CBSD-RN. The CBSD-RN was highly significantly (P<0.001), negatively correlated with CMD-S and positively correlated with PPD; very significantly (P<0.01), positively correlated with FSRY, DSRY and SRG; and significantly (P<0.05), negatively correlated with SRN. The CMD-S had a significant (P<0.05), negative correlation with SRN and also a negative, but

non-significant correlation with FSRY, DSRY, HI and SRG. Harvest index had a highly significant (P<0.001), positive correlation with FSRY, DSRY, SRG and a very significant (P<0.01), positive correlation with SRN and PPD. Postharvest physiological deterioration was highly significantly (P<0.001), positively correlated with FSRY, DSRY, DMC, SRG, CMD-S and CBSD-RN; very significantly (P<0.01), positively correlated with HI; and significantly (P<0.05), negatively correlated with SRN. Of the correlated traits with PPD, DMC had the highest correlation (r = 0.48).

Table 3.17 Phenotypic correlations between eight traits of 12 cassava genotypes averaged across harvest times and locations in Uganda, 2011/12

Traits	FSRY	SRN	HI	DSRY	SRG	DMC	PPD	CMD-S	CBSD-RN
FSRY	1.00								
SRN	0.38***	1.00							
HI	0.69***	0.13**	1.00						
DSRY	0.98***	0.35***	0.69***	1.00					
SRG	0.76***	0.24***	0.72***	0.76***	1.00				
DMC	0.31***	0.07^{ns}	0.38***	0.45***	0.44***	1.00			
PPD	0.17***	- 0.10*	0.12**	0.24***	0.21***	0.48***	1.00		
CMD-S	$- 0.08^{ns}$	- 0.15*	$- 0.02^{ns}$	$- 0.06^{ns}$	$- 0.02^{ns}$	0.10^{ns}	0.26***	1.00	
CBSD-RN	0.13**	- 0.11*	0.06^{ns}	0.12**	0.14**	0.05^{ns}	0.22***	- 0.23***	1.00

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DSRY = dry storage root yield (t ha^{-1}); SRG = storage root girth (cm); DMC = dry mass content (%); PPD = postharvest physiological deterioration; CMD-S = cassava mosaic disease root necrosis scored on scale of 1-5; CMD-S = cassava brown streak disease root necrosis scored on scale of 1-5; ns = non-significant; * = P<0.05; ** = P<0.01; *** = P<0.001.

3.4 Discussion and conclusions

This research was aimed at assessing the extent of variation among selected cassava genotypes for rate of cassava storage root bulking and other traits. It was envisaged that the information generated would help inform future improvement programmes for high yielding, early bulking cassava cultivars in association with other important traits, as well as in identifying research gaps in the quantification and understanding of the existing variation in cassava genotypes in Uganda.

The traits evaluated to meet the stated objectives of this study were FSRY, SRM, STM, TBM, HI, DMC, DSRY, SRN, SRG, PPD, CBSD-RN and CMD-S. For most of these traits in the combined ANOVA across harvest times and locations, the main effects (location, genotype and harvest time) and the two-way interaction effects were significant. Genotype MS were significant for all traits, indicating that the genotypes evaluated were different, and that by hybridising among them, genetic advance would be achieved for all the traits. Similarly, the significant MS for location for all traits, except for CBSD-RN, indicated that the locations were different to each other and consequently had significant influence on the performance of the

genotypes for the various traits. This in part establishes the need for a decentralised breeding scheme for cassava in Uganda. Significant differences between harvest times for all the traits evaluated were a clear indication of significant differences in the growth and development of the test genotypes over time. Similar results were reported by Suja et al. (2009) when evaluating short-duration cassava genotypes for growth dynamics, biomass, yield and quality. Likewise, a study by Ngeve (2003) to determine the effect of harvest time and test environments on cassava storage root yields and culinary qualities, found significant differences among genotypes and locations for FSRY and SRN.

The significant genotype x location interaction effects for the traits assessed indicated that some of the genotypes had specific adaptation to one or more of the locations (Egesi et al., 2007; Aina et al., 2009), while the significant genotype by harvest time interaction effects was indicative of differences between genotypes in bulking rates and patterns as previously reported by Okechukwu and Dixon (2009), Suja et al. (2009), Kamau et al. (2011) and Okogbenin et al. (2013). In addition, significant harvest time x location interaction effects indicated that the performance patterns for each trait across the harvest times differed between the locations and therefore the optimal time of expression for each trait (in months after planting) was location specific.

Genotype CT2 was identified as the overall highest performer for FSRY, HI (together with NASE4) and SRG, while genotype B11 was identified as the highest performer for DMC, but the worst with respect to PPD. The DMC and PPD were found to be positively and highly correlated in line with other studies (Van Oirschot et al., 2000; Ch´avez et al., 2005). The top two genotypes, CT1 and CT2 in terms of FSRY, SRN and DSRY were genotypes developed by hybridising CIAT with Ugandan genotypes.

With respect to the locations, Jinja registered the best performance for HI, FSRY, DSRY, SRG, CBSD-RN and CMD-S averaged across genotypes and harvest times. Nakasongola recorded the best performance for DMC, SRN and PPD. Namulonge, on the other hand, recorded the lowest performance for all the traits evaluated. This was possibly due to the highest severity for CMD and CBSD and also high white fly (*Bemisia tabaci*) incidence being recorded at this location compared to the other two which undoubtedly contributed to the reduced performance of the genotypes for the evaluated traits. The good performance of the genotypes for the traits mentioned at Jinja could be due to the high rainfall (1324 mm) it received during the experimental period. Even though Nakasongola received the lowest

amount of rainfall (790 mm) during the experimental period, it performed better than Namulonge for all the traits, and better than Jinja for DMC, SRN and PPD possibly due to having more fertile soils and less viral diseases.

As expected, performance for the majority of the traits, including FSRY, was lowest when plants were harvested at 5 MAP and generally higher at each subsequent harvest time, a trend that in part reflects the dynamics in cassava growth and development (Cock et al., 1979; Ekanayake et al., 1998; Lahai et al., 1999; Alves, 2002), and dry mass accumulation in the roots as affected by source-sink relations (Alves, 2002; Lahai and Ekanayake, 2009). Cassava established from stem cuttings grows through phases: the vegetative phase characterised by rapid growth of stems and foliage; the root bulking phase characterised by rapid growth of storage roots; and the senescence phase (Cock et al., 1979; Ekanayake et al., 1998). At every phase of cassava's growth and development, dry mass production and partitioning between plant organs occurs, although the rate differs during the growth stages of the plant and is also cultivar dependent. Partitioning of dry mass is particularly important in cassava because the crop has simultaneous development of leaves, stems and storage roots and thus the available assimilate is partitioned between these plant parts (Cock, 1984; Ekanayake, 1993; Alves, 2002). The distribution pattern of photo-assimilates among different organs of the cassava plant changes markedly during the growth cycle, with shoots dominating in the first 3 to 5 MAP, while the storage roots become the major sink for assimilates during the rest of the growth cycle (El-Sharkawy, 2003). Root bulking in this study was gradual in the first 7 months, with most of the bulking in terms of FSRY for the majority of the cultivars having taken place by 9 MAP, irrespective of locations.

Genotypes showed significant differences in time taken to attain peak FSRY. By way of example, genotypes Nyara attained peak FSRY at two harvest dates (7 and 11 MAP); B11 at 7 and 13 MAP; CT5, NASE4, TME14 and NASE3 at 9 and 13 MAP. The two peaks for FSRY exhibited by most genotypes indicated that the first and second phases of storage root bulking usually occur from 3 to 9 MAP and from 13 to 19 MAP, respectively (Ekanayake et al., 1998). The first storage root bulking phase is when storage roots begin to enlarge while the leaf area reaches a maximum, whereas the second storage root bulking phase is when storage roots are the dominant sink (Cock, 1979; Ekanayake et al., 1998). Since the performance for each genotype was different at each location and at each harvest time, the clear implication for selection is that the optimal harvest times for early storage root bulking are location dependent.

Estimates of variance components revealed that a large portion of the phenotypic variance was accounted for by the genotypic component for all traits, indicative of the existence of considerable genetic variation variation among the 12 genotypes that was unaffected by the environment. The implication thereof is that with conventional hybridisation among these genotypes, substantial genetic advance would be achieved for all the traits. The PCV estimates for all traits were higher than the GCV estimates (also reported by Akinwale et al., 2010; Ntawuruhunga and Dixon, 2010; Manu-Aduening et al., 2013) signifying that the overall variation for the traits was not only genetically determined, but was also due to environmental effects, which is a summation of genotype x environment and error variances. Appropriate experimental designs coupled with precise phenotyping are critical interventions and/or investments for breeding programmes that target increasing genetic gain through increasing the trait heritabilities. Nevertheless, the difference between PCV and GCV for all traits in this study was relatively low, indicative of low environmental influence (Akinwale et al., 2010).

All traits at almost all harvest times had high H_b estimates, implying that broad-sense genetic gains would be obtained based on phenotypic selection at each of the harvest times for these traits. Similarly, the high H_b estimates observed for all traits at almost all harvest times suggested that the heritable portion of variation was large for these traits at each harvest time which should be readily exploited by plant breeders. The implication of high H_b is that rapid progress in selection should be achievable, even with using simple selection procedures. The low to medium H_b estimate recorded for FSRY and SRN indicates that the expression of these traits was strongly influenced by the environment, suggesting that direct phenotypic-based selection for these traits might be ineffective.

The PCA revealed that the greater proportion, 51.1% of the total variation in the genotypes evaluated, was accounted for by PC1, which was largely contributed to by the storage root yield related traits, viz. HI, DSRY, FSRY and SRG. The PC2 accounted for 19.6% of the total variation in the genotypes and was largely contributed to by DMC, SRN and PPD. With the exception of PPD, the rest of the traits that were major contributors to PC1 and PC2 are key traits in cassava breeding and are normally used in selection for high FSRY (Kawano et al., 1998; Ojulong, 2006).

Phenotypic correlation analysis revealed that the other agronomic traits were positively and highly correlated with FSRY, indicative of their interdependence and importance in influencing FSRY. The high positive correlations between FSRY and HI, SRG, DSRY and

SRN agree with those reported by Suja et al. (2009), Okechukwu and Dixon (2009) and Parkes et al. (2013). Similarly, as previously reported by Van Oirschot et al. (2000) and Ch´avez et al. (2005), PPD was found to be positively and highly correlated ($r = 0.471$; $P<0.001$) with DMC. The positive correlation between DMC is undesirable since an improvement in DMC indirectly accelerates PPD and PPD renders storage roots unattractive for commercialisation or consumption (Ch´avez et al., 2005). Cassava mosaic disease severity had a negative correlation with all the yield-related traits, demonstrating the devastating effects of CMD on cassava productivity.

In conclusion, there was high genetic variability among genotypes for FSRY and all other traits evaluated, indicating that significant progress would be achieved in the selection for these traits, even with simple phenotypic selection procedures. Similarly, with conventional hybridisation among these genotypes, substantial genetic advance would be achieved for all the traits. Time to attain peak FSRY and the other traits differed from genotype to genotype and from location to location, with CT1 recording the highest mean FSRY of 41.0 t ha^{-1} at 13 MAP across locations. Genotypes: Nyara, B11, CT5, NASE4, TME14 and NASE3 attained first peak FSRY at ≤ 9 MAP and could therefore be selected as early bulking genotypes. Averaged over genotypes, there was no significant difference in FSRY from 9 - 13 MAP at Nakasongola, suggesting that there was no further yield to be gained from leaving the storage roots underground for any additional months beyond 9 MAP. Further studies are required to more accurately determine the optimum time for harvesting the test genotypes and also to confirm their earliness in other diverse environments.

References

Aina, O.O., A.G.O. Dixon, and A.E. Akinrinde. 2007. Genetic variability in cassava as it influences storage root yield in Nigeria. Journal of biological sciences 7:765-770.

Aina, O.O., A.G.O. Dixon, I. Paul, and E.A. Akinrinde. 2009. GxE interaction effects on yield and yield components of cassava (landraces and improved) genotypes in the savannah regions of Nigeria. African Journal of Biotechnology 8:4933-4945.

Akinwale, M. G., B. O. Akinyele, A. G. O. Dixon, and A. C. Odiyi. 2010. Genetic variability among forty-three cassava genotypes in three agro-ecological zones of Nigeria. Journal of Plant Breeding and Crop Science 2:104-109.

Alves, A.A.C. 2002. Cassava botany and physiology. In: R.J. Hillocks et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 67-89.

Amenorpe, G., H.M. Amoatey, A. Darkwa, G.K. Banini, and V.W. Elloh. 2007. Peak root and starch weights of ten early bulking cultivars of cassava (*Manihot esculenta* Crantz) in Ghana. Journal of Ghana Science Association 9:54-60.

Banito, A.J., V. Verdier, K.E. Kpemoua, and K. Wydra. 2007. Assessment of major cassava diseases in Togo in relation to agronomic and environmental characteristics in a systems approach. African Journal of Agricultural Research 2:418-428.

Bassey, E.E., and I.H. Gamaliel. 2013. Screening cassava (*Manihot esculenta* Crantz) genotypes for tuber bulking, early maturity and optimum harvesting time in Uyo, South Eastern Nigeria. Peak Journal of Agricultural Sciences 1:83-88.

Burns, A., R. Gleadow, J. Cliff, A. Zacarias, and T. Cavagnaro. 2011. Cassava, the drought, war and famine crop in a changing world. Sustainability 2:3572-3607.

Burton, G.W., and E.H. DeVane. 1953. Estimating heritability in tall fescus (*Festuca arundinacea*) from replicated clonal material. Agronomy Journal 45:478-481.

Cach, N. T., J. C. Perez, J. I. Lenis, F. Calle, N. Morante, and H. Ceballos. 2005. Epistasis in the expression of relevant traits in cassava (*Manihot esculenta* Crantz) for sub humid conditions. Journal of Heredity 96:586-592.

Ch´avez, A.L., T. S´anchez, G. Jaramillo, J.M. Bedoya, J. Echeverry, E.A. Bola˜nos, H. Ceballos, and C.A. Iglesias. 2005. Variation of quality traits in cassava roots evaluated in landraces and improved clones. Euphytica 143:125-133.

Cock, J.H. 1984. Cassava In: Goldsworthy, P.R., and N.M. Fisher (eds.), The physiology of tropical field crops, John Wiley and Sons, New York, USA. p. 529-549.

Cock, J.H. D. Franklin, G. Sandoval, and P. Juri. 1979. The ideal cassava plant for maximum yield. Crop Science 19:271-279.

Egesi, C. N., P. Ilona, F. O. Ogbe, M. Akoroda, and A. Dixon. 2007. Genetic variation and genotype x environment interaction for yield and other agronomic traits in Cassava in Nigeria. Agronomy Journal 99:1137-1142.

Ekanayake I.J., D.S.O. Osiru, and M.C.M. Porto. 1998. Physiology of cassava. IITA Research guide no. 55. Third edition, IITA, Ibadan, Nigeria. p. 32.

Ekanayake, I.J. 1993. Growth and development of cassava a simplified phasic approach. Tropical Root and Tuber Crops Bulletin 7:4-5.

El-Sharkawy, M.A. 2003. Cassava biology and physiology. Plant Molecular Biology 56:481-501.

El-Sharkawy, M.A. 2007: Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments. Brazilian Journal of Plant Physiology 19:257-286.

Gleadow, R.M., J.R. Evans, S. McCaffery, T.R. Cavagnaro. 2009. Growth and nutritive value of cassava (*Manihot esculenta* Crantz) are reduced when grown in elevated CO_2. Plant Biology 11:76-82.

Hallauer, A.R. 1992. Use of genetic variation for breeding populations in cross pollinated species. In: Stalker, H.T., and J.P Murphy (eds.), Plant breeding in the 1990s. Proceedings of the symposium on plant breeding in the 1990s held at North Carolina State University, Raleigh, NC. CABI International, Wallington, UK. p. 37-67.

Hallauer, A.R., and J.B. Miranda.1981. Quantitative genetics in maize breeding. Iowa State University. Press, Ames, USA.

Hartley, H.O. 1950. The use of range in analysis of variance. Biometrika 37:271-280.

Hillocks, R.J., M. Raya, and M.J. Thresh. 1996. The association between root necrosis and aboveground symptoms of brown streak virus infection in cassava in southern Tanzania. International Journal of Pest Management 42:285-289.

Indira, P. and S.K. Sinha.1970. Studies on the initiation and development of tubers in *Manihot esculenta* Crantz. Indian Journal of Plant Physiology 13:24-39.

Izumi, Y., E.Yuliadi, M. Sunyoto, and M. Iijima. 1999. Root system development including root branching in cuttings of cassava with reference to shoot growth and tuber bulking. Plant Production Science 2:267-272.

Kamau, J. W. 2006. Participatory based development of early bulking cassava varieties for the semi-arid areas of Eastern Kenya. PhD thesis, University of KwaZulu-Natal, South Africa.

Kamau, J., R. Melis, M. Laing, J. Derera, P. Shanahan, C. Eliud, and K. Ngugi. 2011. Farmers' participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. Journal of Plant Breeding and Crop Science 3:44-52.

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

Kawano, K., K. Narintaraporn, P. Narintaraporn, S. Sarakarn, A. Limsila, J. Limsila, D. Suparhan, V. Sarawat, and W. Watananonta. 1998. Yield improvement in a multistage breeding program for cassava. Crop Science38:325-332.

Kawuki, R. S., L. Herselman, M. T. Labuschagne, I. Nzuki, I. Ralimanana, M. Bidiaka, M. C. Kanyange, G. Gashaka, E. Masumba, G. Mkamilo, J. Gethi, B. Wanjala, A. Zacarias, F. Madabula, and M. E. Ferguson. 2013. Genetic diversity of cassava (*Manihot esculenta* Crantz) landraces and cultivars from southern, eastern and central Africa. Plant Genetic Resources: Characterization and Utilization 11:170-181

Kawuki, R.S., M. Ferguson, M.T. Labuschagne, L. Herselman, J. Orone, I. Ralimanana, M. Bidiaka, S. Lukombo, M.C. Kanyange, G. Gashaka, G. Mkamilo, J. Gethi, H. Obiero. 2011. Variation in qualitative and quantitative traits of cassava germplasm from selected national breeding programmes in sub-Saharan Africa. Field Crops Research 122:151-156.

Lahai, M.T., and I.J. Ekanayake. 2009. Accumulation and distribution of dry matter in relation to root yield of cassava under a fluctuating water table in inland valley ecology. African Journal of Biotechnology 8:4895-4905.

Lahai, M.T., J.B. George, and I.J. Ekanayake. 1999. Cassava (*Manihot esculenta* Crantz) growth indices, root yield and its components in upland and inland valley ecologies of Sierra Leone. Journal of Agronomy and Crop Science 182:239-247.

Manu-Aduening, J.A, B.B. Peprah, and A. Agyeman. 2013. Genetic variability of cassava progenies developed through introgression of cassava mosaic disease resistance into Ghanaian landraces. Journal of crop Science and Biotechnology 16:23-28.

Mtunda, K.J. 2009. Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.

Ngeve, J.M. 2003. Cassava root yields and culinary qualities as affected by harvest age and test environment. Journal of the Science of Food and Agriculture 83:249-257.

Ntawuruhunga P., and A.G.O. Dixon. 2010. Quantitative variation and interrelatiohip between factors influencing cassava yield. Journal of Applied Biosciences 26:1594-1602.

Ojulong, H. F. 2006: Quantitative and molecular analyses of agronomic traits in cassava (*Manihot esculenta* Crantz). PhD thesis, University of The Free State Bloemfontein, South Africa.

Okechukwu, R.U., and A.G.O. Dixon. 2009. Performance of improved cassava genotypes for early bulking, disease resistance, and culinary qualities in an inland valley ecosystem. Agronomy Journal 101:1258-1265.

Okogbenin, E., T.L. Setter, M. Ferguson, R. Mutegi, H. Ceballos, B. Olasanmi, and M. Fregene. 2013. Phenotypic approaches to drought incassava: review. Frontiers in Physiology 4:1-15.

Parkes, E. Y., M. Fregene, A. Dixon, B. Boakye-Peprah, and M.T. Labuschagne. 2013. Combining ability of cassava genotypes for cassava mosaic disease and cassava bacterial blight, yield and its related components in two ecological zones in Ghana. Euphytica 194:13-24.

Payne, R.W., S.A. Harding, D.A Murray, D.M. Soutar, D.B. Baird, A.I. Glaser, S.J. Welham, A.R. Gilmour, R. Thompson, and R. Webster. 2011. The guide to genstat release 14, part 2: statistics. VSN International, Hemel Hempstead, UK.

Salcedo, A. and D.Siritunga. 2011. Insights into the physiological, biochemical and molecular basis of postharvest deterioration in cassava (*Manihot esculenta*) roots. American Journal of Experimental Agriculture 1:414-431.

Suja, G., K.S. John, J. Sreekumar, and T. Srinivas. 2009. Short-duration cassava genotypes for crop diversification in the humid tropics: growth dynamics, biomass, yield and quality. Journal of Science and Food Agriculture 90:188-198.

Suzan, J.D., R. Gnanadesikan, and J.R. Kettenring. 1975. Robust estimation and outlier detection with correlation coefficients. Biometrika 62:531-545.

Van Oirschot, Q.E.A., G.M. O'Brien, D.D. Dufour, M.A. El-Sharkawy, and E. Mesa. 2000. The effect of pre-harvest pruning of cassava upon root deterioration and quality characteristics. Journal of Science and Food Agriculture 80:1866-1873.

Wheatley, C., C. Lozano, and G. Gomez. 1985. Post-harvest deterioration of cassava roots. In: J.H. Cock, and J.A. Reyes (eds.), Cassava: Research, production and utilization.UNDP-CIAT, Cali. p. 655-671.

Wholey, D.W., and J.H. Cock. 1974. Onset and rate of root bulking in cassava. Experimental Agriculture 10:193-198.

CHAPTER 4

Genotype x environment interaction effects on early fresh storage root yield and related traits in selected cassava genotypes in Uganda

Abstract

Cassava exhibits substantial differential genotypic responses to varying environmental conditions, a phenomenon termed genotype by environment interaction (GEI). A significant GEI presents challenges in the selection of superior genotypes. The objective of this study was to assess the effect of genotype, environment and GEI on early fresh storage root yield (FSRY) and other key traits in cassava viz. dry mass content, harvest index, storage root number (SRN), cassava brown streak disease root necrosis (CBSD-RN) and cassava mosaic disease severity (CMD-S). Consequently, 12 cassava genotypes were evaluated in a randomised complete block design at three contrasting locations (Jinja, Nakasongola and Namulonge) in Uganda. The trials were harvested at nine months after planting and the data collected were analysed using the additive main effects and multiplicative interaction (AMMI) model. The AMMI1 biplots and associated IPCA1 scores were used to compare the interactions of genotypes and locations. The AMMI analysis of variance showed significant variation among genotypes for early FSRY and all other traits assessed. Locations were significantly different for all traits except, CBSD-RN. The GEI effects were non-significant for early FSRY, but significant for all other traits. For early FSRY, 48.5% of the treatment sum of squares (SS) was attributed to genotypes, 27.3% to environments and 24.1% to GEI indicating predominance of genotypic variation for early FSRY. Predominance of genotypic variation was also indicated in all the other five traits assessed. Similarly, for early FSRY, genotypes interacted less strongly with Namulonge than Nakasongola and Jinja, but their average performance was less at Namulonge than at both Jinja and Nakasongola. Akena, CT2, CT4 and NASE14 were the most stable genotypes for early FSRY while B11, NASE14, NASE3 and CT1 were the least stable genotypes. The majority of the genotypes (67%) had low interaction with locations for early FSRY, suggesting that most genotypes were stable for the trait. The ranking of genotypes based on genotype selection index identified Akena and CT2 as the overall best genotypes combining high early FSRY and stability. Significant negative correlation was observed between CMD-S and early FSRY, as well as SRN, indicative of the significant negative effects of cassava mosaic disease on early FSRY and stability in cassava.

4.1 Introduction

Cassava (*Manihot esculenta* Crantz) is one of the most important food crops in sub- Saharan Africa. It is grown by most smallholder farmers partly because of its flexibility in harvesting time and ability to perform well in drought-prone and marginal areas under poor management, where other crops would fail (Alves, 2002; Egesi et al., 2007). In spite of this, cassava presents substantial differential genotypic responses under varying environmental conditions, a phenomenon termed as genotype x environment interaction (GEI) (Egesi et al., 2007; Ssemakula and Dixon, 2007). Genotype x environment interactions is a routine occurrence in plant breeding programmes (Kang, 1998; Ssemakula and Dixon, 2007). Consequently, GEI and yield-stability analyses have increasingly become important in measuring varietal stability and suitability for cultivation across seasons and ecological zones (Gauch and Zobel, 1990; Adesola and Omolayo, 2011). An understanding of GEI can be helpful in identifying ideal test conditions and in formulating recommendations for areas of optional genotype adaptation. Multi-environment trials have been found to be essential in plant breeding for studying varietal stability and predicting yield performance of varieties across environments (Osiru et al., 2009; Das et al., 2010).

The expression of a phenotype of an individual is determined by both the genotype and the environment effects (Falconer and Mackay, 1996). These two effects are not always additive because of GEI. A significant GEI results from changes in the magnitude of differences between genotypes in different environments or from changes in the relative ranking of the genotypes (Eberhart and Russell, 1966; Lin et al., 1986; Ebdon and Gauch, 2002; Ssemakula and Dixon, 2007). It presents limitations in the selection of superior genotypes, and thus, reduces the usefulness of the subsequent analysis of means and the inferences that would otherwise be valid (Shaffi and Price, 1998). To account for GEI effects, breeders evaluate genotypes in several environments in order to identify those with high and stable performance. Genotypes with insignificant GEI are considered to be stable (Eberhart and Russell, 1966; Adugna and Labuschagne, 2002; Ssemakula and Dixon, 2007).

Stability analysis methods are divided into two main groups; univariate and multivariate (Lin et al., 1986). Among multivariate methods, the additive main effects and multiplicative interaction analysis (AMMI) is widely used for GEI assessment. This method has been shown to be effective because it captures a large portion of the GEI sum of squares (Ebdon and Gauch, 2002). It clearly separates main and interaction effects that depending on their statistical significance, present plant breeders with different kinds of selection opportunities,

and the model often provides meaningful interpretation of agronomic data (Gauch and Zobel, 1997; Ebdon and Gauch, 2002). The AMMI analysis is useful in informing important decisions in breeding programmes such as which genotypes exhibit specific adaptation and the selection of testing environments (Gauch and Zobel, 1997). This is particularly important for new breeding programmes that have not yet optimized their respective cultivar testing networks. The results of an AMMI analysis are often presented in a biplot which displays both the genotype and environment values and their relationships using the singular vector technique (Gauch and Zobel, 1997; Ebdon and Gauch, 2002).

The identification of yield-contributing traits and knowledge of GEI and associated yield stability are important considerations in breeding new cultivars with improved adaptation to the environmental constraints that prevail in target environments (Gauch and Zobel, 1997). It was established in a previous study (Chapter 3) that the first peak in fresh storage root yield (FSRY) in cassava genotypes occurs around nine months after planting (MAP) and so for the purposes of this study the performance and stability of the genotypes were evaluated for FSRY, defined as early FSRY, and related traits at 9 MAP. In that context, this research was conducted with two specific objectives:

1. To study the influence of genotype, environment and GEI on early FSRY and related traits; and
2. To identify stable genotypes for early FSRY and related traits.

4.2 Materials and methods

4.2.1 Experimental sites

Trials were conducted from April 2011 to January 2012 at Namulonge and Jinja National Agricultural Research Institutes and also at Nakasongola on private farmland. Namulonge is located in central Uganda at 32°36'E and 0°31'47N, 1134 meters above sea level (masl); Jinja is in eastern Uganda at 33°11'E and 0°27'N, 1173 masl; and Nakasongola is in central Uganda at 32°27'E and 1°18'N, 1091 masl. From planting to harvesting, mean rainfall and temperature range, respectively at: Namulonge were 1121 mm and 16.7 to 28.7^{o}C; Jinja were 1095 mm and 17.3 to 29.2^{o}C; and Nakasongola were 424 mm and 18.5 to 29.4^{o}C.

4.2.2 Experimental germplasm

The experimental germplasm used in this study is as described previously (Chapter 3, section 3.2.2).

4.2.3 Data collection

All the data used for this study, except cassava mosaic disease severity (CMD-S), which was assessed at six months after planting (MAP), were collected at 9 MAP as described previously (Chapter 3, section 3.2.4). Traits considered for this study in addition to early FSRY and CMD-S were: dry mass content (DMC), harvest index (HI), storage root number (SRN) and cassava brown streak disease root necrosis (CBSD-RN). The selection of these traits for AMMI analysis was based on their strong association with FSRY and the fact that their GEI effects were significant (P≤0.05) at 9 MAP. That is, traits evaluated in chapter 3 whose GEI effects were non-significant at 9 MAP, except FSRY, were not included in the AMMI analysis.

4.2.4 Data analysis

The data for each location were first analysed independently and then the error variances for the environments tested for homogeneity using Hartley's Fmax test (Hartley, 1950). The differences were non-significant (P<0.05), consequently an unweighted combined AMMI analysis of variance was conducted across the locations. Correlation of the various plant parameters was done using Pearson correlation coefficients (Payne et al., 2011). The AMMI analysis of variance (ANOVA) was performed using the following model:

$$Y_{ij} = \mu + g_i + e_j + \sum_{n=1}^{N} \lambda_n \alpha_{in} \gamma_{jn} + \rho_{ge} + \varepsilon_{ij}$$

Where: Y_{ij} = observed yield of genotypes; μ = grand mean; g_i = genotypic main effect; e_j = environmental main effect; N = number of PCA axes considered; λ_n = singular value of the n^{th} PCA axis; α_{in} = scores for the i^{th} genotype on the n^{th} axis; and γ_{jn} = scores for the j^{th} environment on the n^{th} axis; ρ_{ge} = residual for IPCAs not fitted; ε_{ij} = error term.

Since the Interaction Principal Component Axis two (IPCA2) mean squares (MS) was non-significant in the AMMI analysis for all traits, the AMMI1 model was adopted and biplots of the IPCA1 scores versus the genotype and environment means were presented for each trait (Purchase et al., 2000; Mulema et al., 2008). The biplots were used to assess the performance and interaction patterns of the genotypes and environments. Based on the biplots, genotypes with broad or specific adaptation to target agro-ecologies or environments for the traits evaluated were identified.

Stability of performance across locations is not the only factor for selection, as the most stable genotypes would not necessarily give the best performance for the traits of interest. Farshadfar (2008) developed the genotype selection index (GSI) which simultaneously selects for performance and stability. The GSI for each genotype is calculated as the sum of the corresponding rankings for mean performance and the AMMI stability value (ASV). The ASV is a measure of the stability of a genotype (the lower the value the greater the stability) based on weighted IPCA1 and IPCA2 scores (Purchase et al., 2000). However, since the IPCA2 axis was non-significant for all the traits in this study the GSI was modified, with ranking based on ASV replaced by ranking based on IPCA1 scores only as follows:

$$GSI_i = RIPCA1_i + RY_i$$

Where:

GSI_i = genotype stability index for the i^{th} genotype across locations for each trait;

$RIPCA1_i$ = rank of the i^{th} genotype across environments based on IPCA1; and

RY_i = rank of the i^{th} genotype based on mean performance across locations.

A genotype with the lowest GSI for a particular trait was considered the best for combined performance and stability (Farshadfar, 2008; Farshadfar et al., 2012).

4.3 Results

4.3.1 Variation in traits in response to genotypes and locations

In the combined AMMI ANOVA, the genotype MS were highly significant (P<0.001) for all the traits evaluated (Table 4.1). The MS for locations were highly significant (P<0.001) for HI and SRN; very significant (P<0.01) for early FSRY; and significant (P<0.05) for DMC and CMD-S. Genotype x environment MS were highly significant (P<0.001) for SRN; very significant (P<0.01) for DMC, CBSD-RN and CMD-S; and significant (P<0.05) for HI.

The IPCA1 MS were highly significant (P<0.001) for SRN; very significant (P<0.01) for HI; and significant (P<0.05) for DMC, CBSD-RN and CMD-S. Early FSRY had non-significant IPCA1 MS (in association with a non-significant GEI) while the IPCA2 MS were non-significant for all traits. It was evident from the AMMI analysis that the % treatment SS attributed to genotypes was higher than that attributed to environments and GEI for all the traits evaluated (Table 4.1). For example, for early FSRY, 48.5% of the treatment sum of squares (SS) was attributed to genotypes, 27.3% to environments and 24.1% to GEI, and 0.1% to IPCA residual. Although the GEI was non-significant for the trait, it is interesting to

note that the IPCA1 and IPCA2 captured 72.4 and 27.6 % of the GEI SS, respectively. Unlike in early FSRY, the % treatment SS attributed to GEI was higher than that to environments in DMC, HI, SRN, CBSD-RN and CMD-S. In FSRY, HI, CBSD-RN and CMD-S, the % GEI SS attributed to IPCA1 was more than twice that attributed to IPCA2.

Table 4.1: AMMI analysis of 12 cassava genotypes evaluated at nine months after planting across three locations in Uganda for early fresh storage root yield and related traits

		Mean squares					
Source of variation	**DF**	**FSRY**	**DMC**	**HI**	**SRN**	**CBSD-RN**	**CMD-S**
Treatment	35	175.3***	36.4***	0.024***	13.1***	2.88***	3.39***
Genotype (G)	11	270.7***	67.6***	0.038***	18.8***	6.30***	9.32***
Location (E)	2	838.5**	68.2*	0.085***	43.2***	0.51	1.59*
G x E Interaction	22	67.3	17.8**	0.012*	7.4***	1.38**	0.62**
IPCA1	12	89.3	17.7*	0.019**	9.0***	1.98*	0.84*
IPCA2	10	40.9	17.9	0.004	5.5	0.66	0.30
Error	66	53.7	7.4	0.007	2.6	0.63	0.42
		Sum of squares					
Source of variation	**DF**	**FSRY**	**DMC**	**HI**	**SRN**	**CBSD-RN**	**CMD-S**
Treatment	35	6135.0	1272.2	0.85	456.7	100.7	118.8
Genotype (G)	11	2977.0	744.1	0.42	207.2	69.3	102.6
Location (E)	2	1677.0	136.4	0.17	86.4	1.0	3.2
G x E Interaction	22	1480.0	391.7	0.26	163.2	30.3	13.0
IPCA1	12	1071.0	212.5	0.22	107.9	23.7	10.1
IPCA2	10	409.0	179.2	0.04	55.2	6.6	3.0
Error	66	3544.0	490.4	0.45	168.6	40.5	28.0
% Treatment SS due to G	11	48.5	58.5	49.4	45.4	68.9	86.4
% Treatment SS due to E	2	27.3	10.7	19.9	18.9	1.0	2.7
% Treatment SS due to GEI	22	24.1	30.8	30.7	35.7	30.1	10.9
% GEI due to IPCA1	12	72.4	54.3	85.0	66.1	78.2	77.7
% GEI SS due to IPCA2	10	27.6	45.7	15.0	33.9	21.8	22.3

DF = degrees of freedom; FSRY = fresh storage root yield (t ha^{-1}); DMC = dry mass content (%); HI = harvest index; SRN = storage root number $plant^{-1}$; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; IPCA1 & 2 = interaction principal component axes one and two; SS = sum of squares; significance level * = P<0.05; ** = P<0.01; *** = P<0.001.

4.3.2 Performance and genotype x location interaction effects for early fresh storage root yield and related traits across locations

As the IPCA2 for all six traits was non-significant, the AMMI1 model was adopted and for each trait, the genotype and location IPCA1 scores were plotted against the mean performances of the genotypes and locations. A genotype or location with high IPCA1 scores (negative or positive) indicated high interaction and was considered to be unstable across the respective locations or genotypes, while a genotype or location with low IPCA1 scores near zero indicated low interaction and was considered to be stable.

Early fresh storage root yield

Although the GEI and associated IPCA1 were non-significant for early FSRY, the apparent performance and interaction patterns were presented in an AMMI1 biplot (Figure 4.1). For early FSRY, Akena, CT2, CT4 and NASE14 had low IPCA1 scores and were consequently the most stable genotypes (Figure 4.1). Genotypes B11, NASE4, NASE3 and CT1 were the least stable considering their large IPCA1 scores. Grouping of genotypes according to their average early FSRY indicated that CT2 had the highest early FSRY followed by Akena, NASE4 and CT3, while Nyara followed by NASE3, NASE14 and B11, had the least early FSRY. Ranking of genotypes based on GSI which incorporates both the IPCA1 and mean performance rankings, identified Akena and CT2 as the best genotypes combining high early FSRY and stability, and these were followed by CT3 and CT4 (Table 4.2). Based on IPCA1 scores alone, 67% of the genotypes had IPCA1 scores less than a unit, implying that a majority of the genotypes were stable for early FSRY. Namulonge had no interaction effects for this trait with genotypes, indicated by negligible IPCA1 scores. Nakasongola and Jinja on the other hand had high contrasting interaction effects for early FSRY with genotypes, indicated by high contrasting IPCA1 scores. Nakasongola though unstable, was the best location for early FSRY, followed by Jinja.

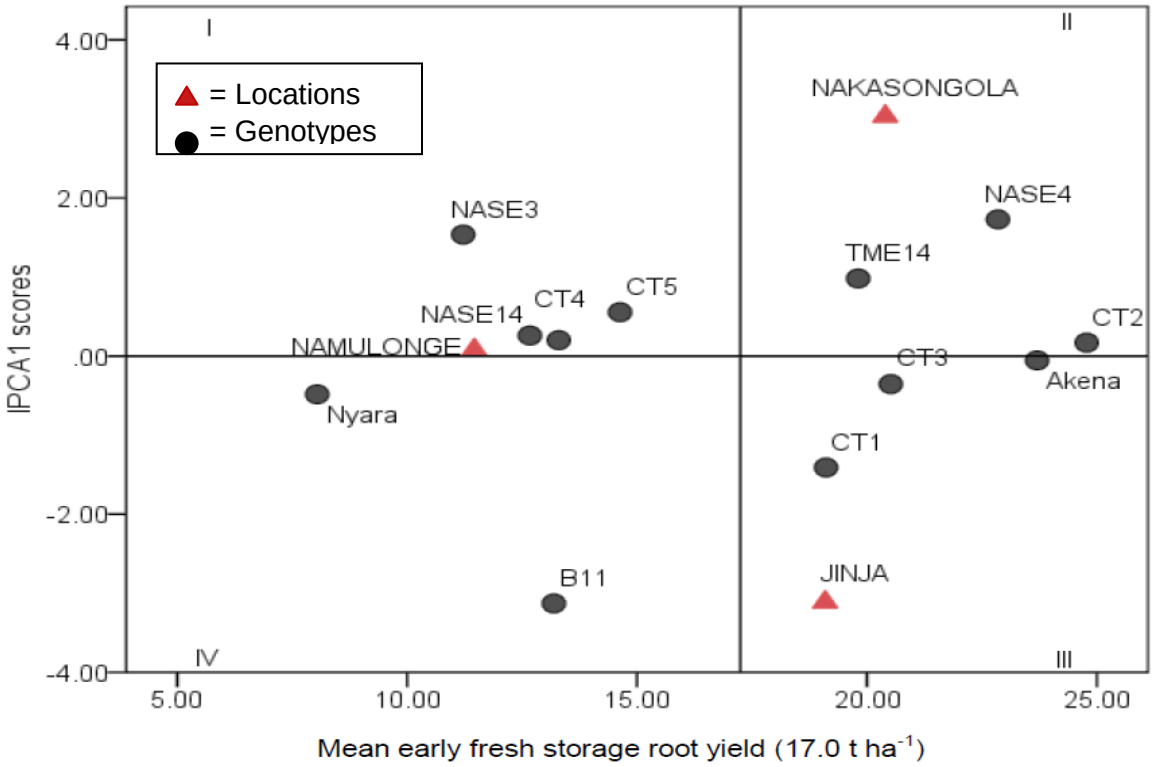

Figure 4.1: Biplot of mean early fresh storage root yield and IPCA1 scores for 12 cassava genotypes evaluated nine months after planting at three locations in Uganda.

Table 4.2: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index for fresh storage root yield evaluated nine months after planting across three locations in Uganda

.	Fresh storage root yield (t ha^{-1})					
Genotypes	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	23.7	2	-0.0550	1	3	1
B11	13.2	9	-3.1293	12	21	11
CT1	19.1	6	-1.4087	9	15	9
CT2	24.8	1	0.1697	2	3	1
CT3	20.5	4	-0.3534	5	9	3
CT4	13.3	8	0.2006	3	11	4
CT5	14.6	7	0.5550	7	14	6
NASE14	12.7	10	0.2594	4	14	6
NASE3	11.2	11	1.5370	10	21	11
NASE4	22.9	3	1.7282	11	14	6
Nyara	8.0	12	-0.4845	6	18	10
TME14	19.8	5	0.9813	8	13	5

GSI = genotype selection index; IPCA1 = interaction principal component axis one

The non-significantly different response patterns of the genotypes across the locations were investigated for apparent crossover type GEI by plotting the mean performance of each genotype at each location (Figure 4.2). The performance patterns of the genotypes across the locations indicated that there was an apparent change in rank order of the genotypes at each location for early FSRY. For example, CT1 was one of the top three genotypes at Jinja but was only seventh best at both Namulonge and Nakasongola. B11 was the fourth best genotype at Jinja, but was eighth and twelfth best at Namulonge and Nakasongola, respectively. Also, NASE3 was the eighth best early yielding genotype in Nakasongola but was last and second last at Jinja and Namulonge, respectively.

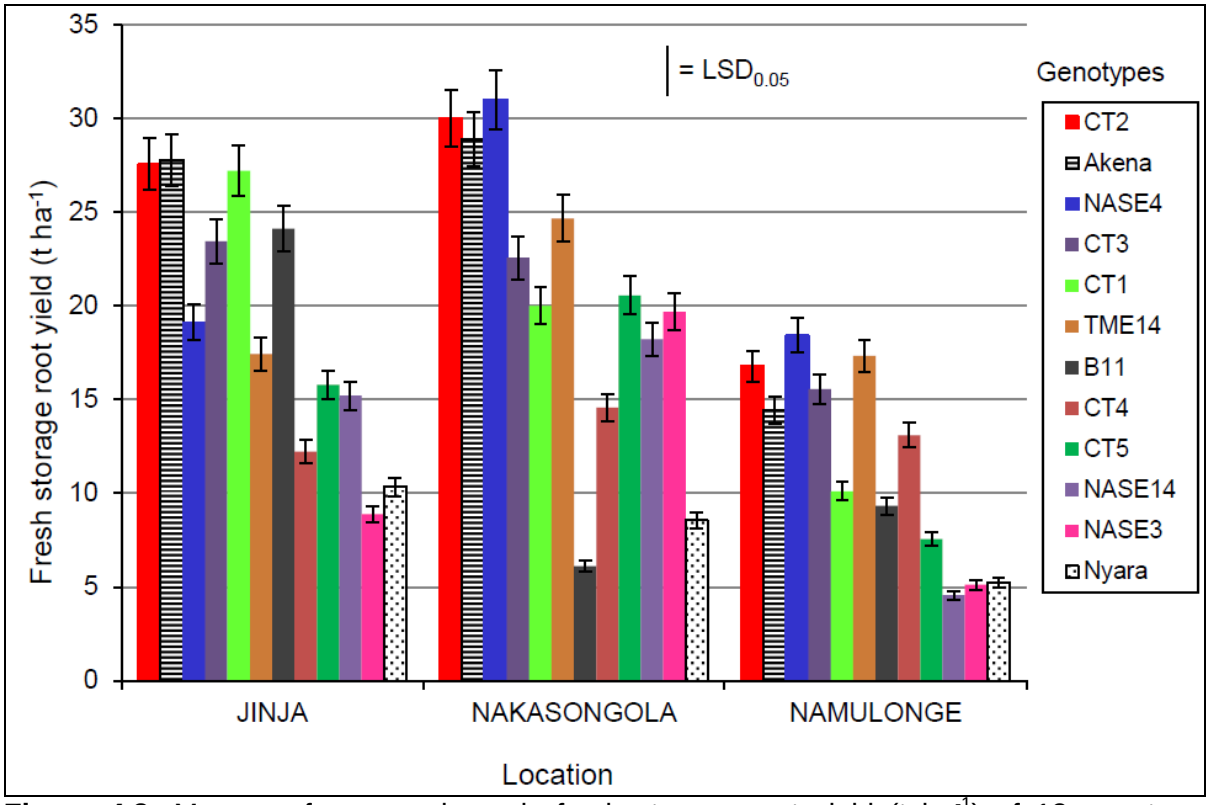

Figure 4.2: Mean performance in early fresh storage root yield (t ha^{-1}) of 12 genotypes evaluated nine months after planting at three locations in Uganda.

Dry mass content

Most of the genotypes had low IPCA1 scores for DMC, with Akena, CT4, CT5 and CT2 the most stable genotypes for this trait, while the least stable genotypes were NASE3, NASE4, B11 and CT1 (Figure 4.3). TME14 had the highest DMC followed by B11, CT3 and CT1, while Nyara followed by NASE3, CT2 and Akena had the lowest mean DMC. Based on GSI ranking, CT4 was the overall best genotype combining high DMC and stability, followed by CT3, CT5 and TME14 all ranked second best (Table 4.3). Nakasongola and Namulonge had high contrasting interactions for this trait with genotypes, while Jinja had relatively low interaction with the genotypes and was therefore the most stable location for DMC.

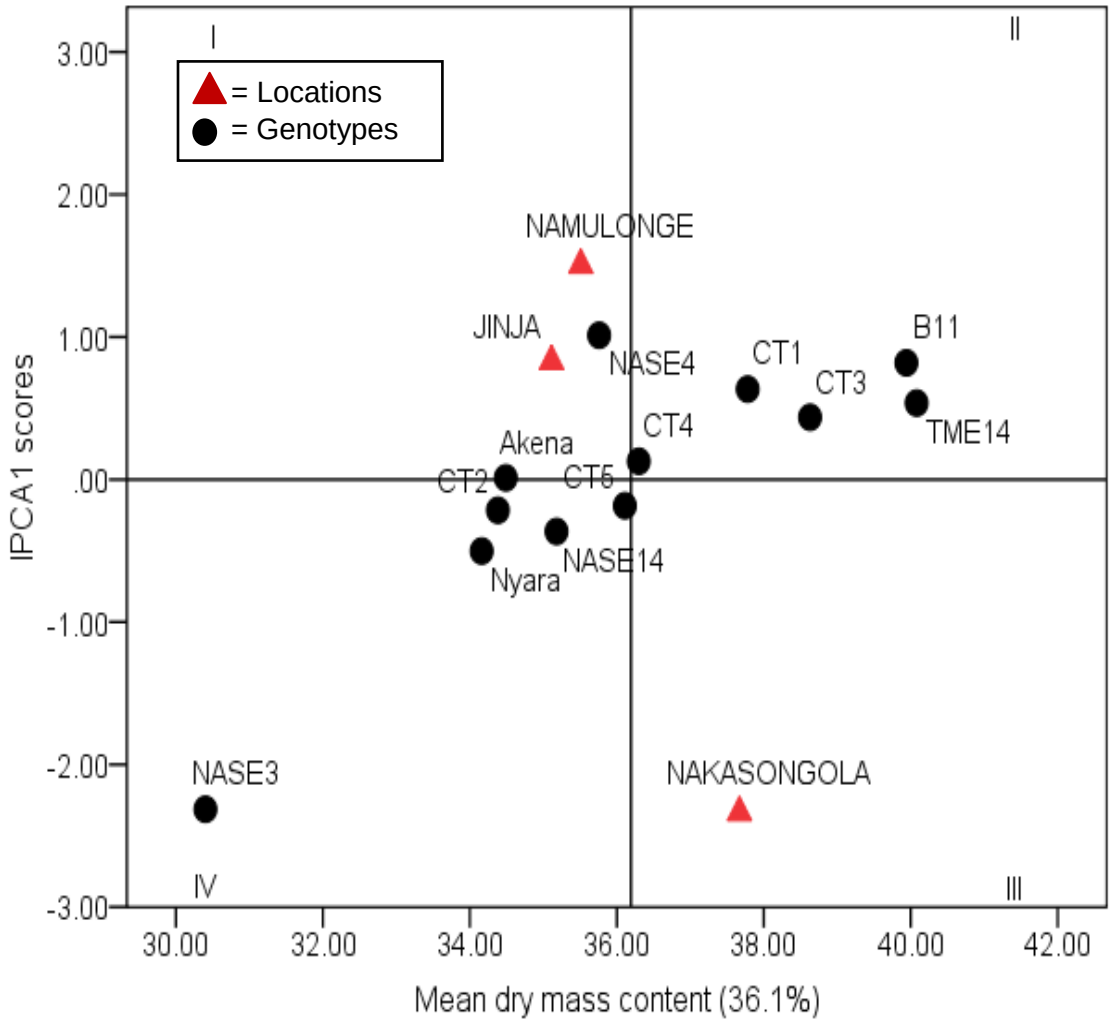

Figure 4.3: Biplot of mean dry mass content and IPCA1 scores for 12 cassava genotypes evaluated nine months after planting at three locations in Uganda.

Table 4.3: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index for dry mass content yield evaluated nine months after planting across three locations in Uganda

	Dry mass content (%)					
Genotype	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	34.5	9	0.0125	1	10	5
B11	39.9	2	0.8196	10	12	6
CT1	37.8	4	0.6337	9	13	7
CT2	34.4	10	-0.2153	4	14	9
CT3	38.6	3	0.4367	6	9	2
CT4	36.3	5	0.1276	2	7	1
CT5	36.1	6	-0.1845	3	9	2
NASE14	35.2	8	-0.3642	5	13	7
NASE3	30.4	11	-2.3143	12	23	12
NASE4	35.8	7	1.0129	11	18	10
Nyaraboke	34.2	12	-0.5022	7	19	11
TME14	40.1	1	0.5375	8	9	2

GSI = genotype selection index; IPCA1 = interaction principal component axis one

Harvest index

The most stable genotypes for HI were NASE4, CT1, CT5 and TME14, while the least stable were B11, NASE3, Nyara and CT2 (Figure 4.4.). NASE4 had the highest HI, followed by CT2, CT3 and Akena while NASE14, CT4, Nyara and NASE3 had the lowest HI. NASE4 was the overall best genotype with the highest GSI ranking combining high HI and stability, followed by CT5, CT1 and Akena, respectively (Table 4.4). Namulonge had minimal interaction with genotypes for this trait while Nakasongola and Jinja had high interactions with the genotypes for the trait. Although Jinja and Nakasongola strongly interacted with the genotypes for HI, their location means were higher than for Namulonge.

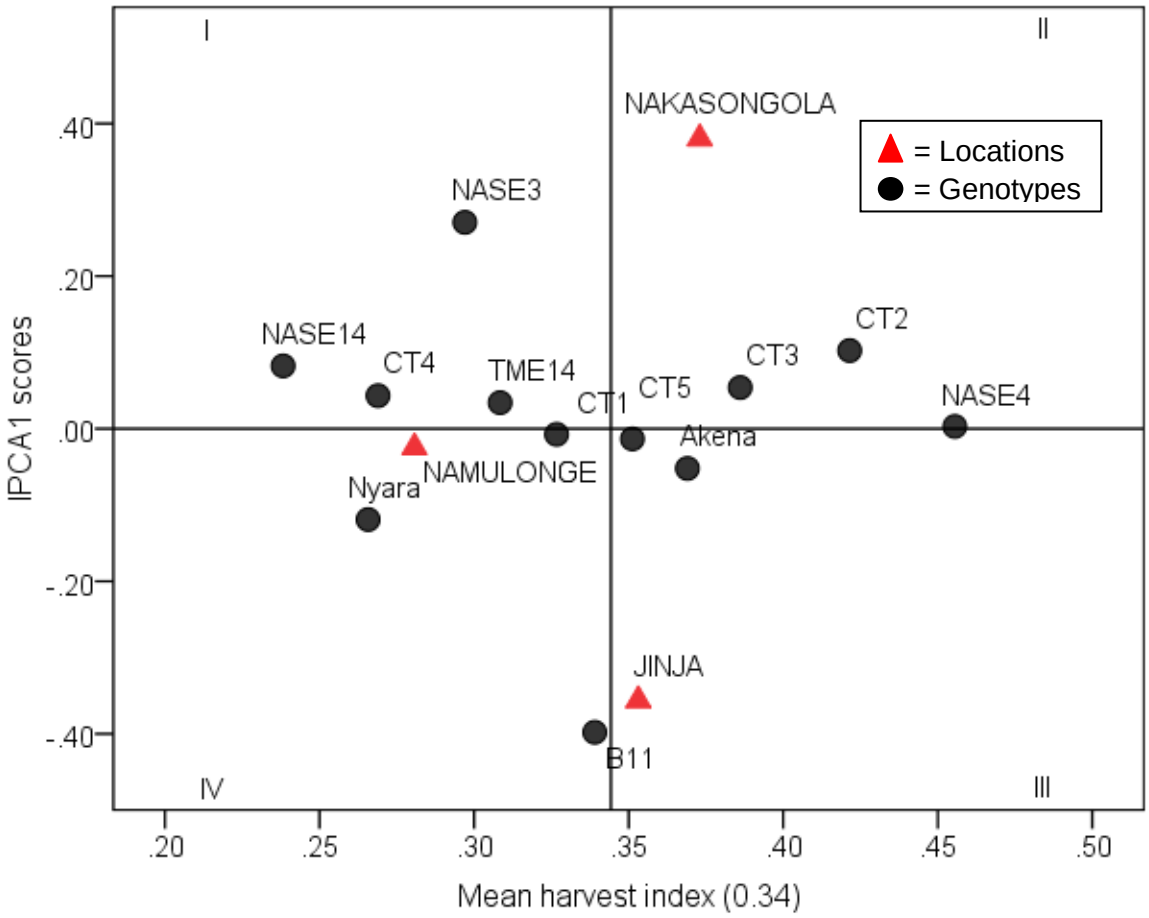

Figure 4.4: Biplot of mean harvest index and IPCA1 scores for 12 cassava genotypes evaluated nine months after planting at three locations in Uganda.

Table 4.4: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index for harvest index evaluated nine months after planting across three locations in Uganda

	Harvest index					
Genotypes	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	0.37	4	-0.0519	6	10	4
B11	0.34	6	-0.3981	12	18	8
CT1	0.33	7	-0.0073	2	9	3
CT2	0.42	2	0.1025	9	11	6
CT3	0.39	3	0.0541	7	10	4
CT4	0.27	10	0.0434	5	15	7
CT5	0.35	5	-0.0133	3	8	2
NASE14	0.24	12	0.0824	8	20	9
NASE3	0.30	9	0.2705	11	20	9
NASE4	0.46	1	0.0029	1	2	1
Nyara	0.27	10	-0.1192	10	20	9
TME14	0.31	8	0.0342	4	12	6

GSI = genotype selection index; IPCA1 = interaction principal component axis one

Storage root number

For SRN, CT5, Akena, Nyara and CT4 had low IPCA1 scores and were the most stable genotypes whereas B11, TME14, NASE4 and CT3 were the least stable considering their large IPCA1 scores (Figure 4.5). NASE4 had the highest SRN followed by CT2, CT1 and TME14. Nyara, followed by NASE3, B11 and Akena had the lowest SRN. With the lowest GSI ranking, CT5 was the overall best genotype combining high SRN and stability, followed by CT4, CT1 and CT2 (Table 4.5). Jinja effectively had no interaction with genotypes as indicated by its negligible IPCA1 score and was considered the most stable location across the genotypes for the trait. As evidenced by their high IPCA1 scores of opposite sign Namulonge and Jinja had high contrasting interactions with the genotypes.

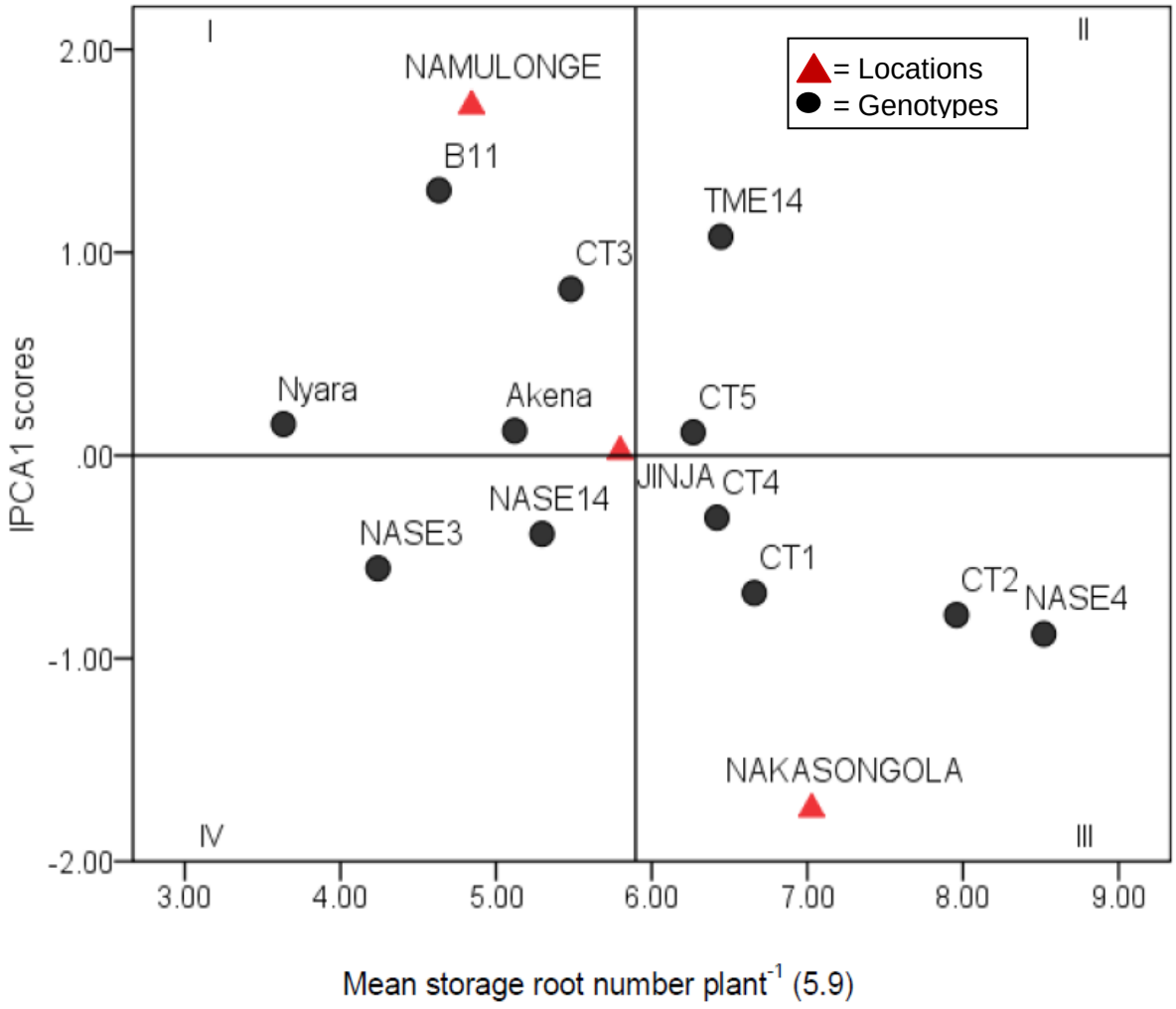

Figure 4.5: Biplot of mean storage root number and IPCA1 scores for 12 cassava genotypes evaluated nine months after planting at three locations in Uganda.

Table 4.5: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index for storage root number evaluated nine months after planting across three locations in Uganda

	Storage root number plant^{-1}					
Genotypes	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	5.1	9	0.1213	2	11	5
B11	4.6	10	1.3062	12	22	12
CT1	6.7	3	-0.6781	7	10	3
CT2	8.0	2	-0.7858	8	10	3
CT3	5.5	7	0.8199	9	16	10
CT4	6.4	5	-0.3072	4	9	2
CT5	6.3	6	0.1142	1	7	1
NASE14	5.3	8	-0.3870	5	13	7
NASE3	4.2	11	-0.5559	6	17	11
NASE4	8.5	1	-0.8804	10	11	5
Nyara	3.6	12	0.1546	3	15	8
TME14	6.4	4	1.0783	11	15	8

GSI = genotype selection index; IPCA1 = interaction principal component axis one

Cassava brown streak disease root necrosis

For CBSD-RN, Jinja had relatively low interaction effects with genotypes, while Namulonge and Nakasongola had relatively high contrasting interaction effects (Figure 4.6). Jinja was therefore relatively stable for this trait. The most stable genotype for CBSD-RN was TME14, which was followed by NASE14, CT4 and Akena in this order. The least stable genotypes were: CT5, CT2, NASE3 and CT1. In terms of the mean CBSD-RN scores the best genotypes were: NASE4, NASE3, Nyara and B11 while the worst genotypes were: Akena, CT2, NASE14 and CT5. The GSI ranked TME14 and NASE4 as best genotype combining least CBSD-RN and high stability, followed by B11 and Nyara with the same rank of 3 (Table 4.5).

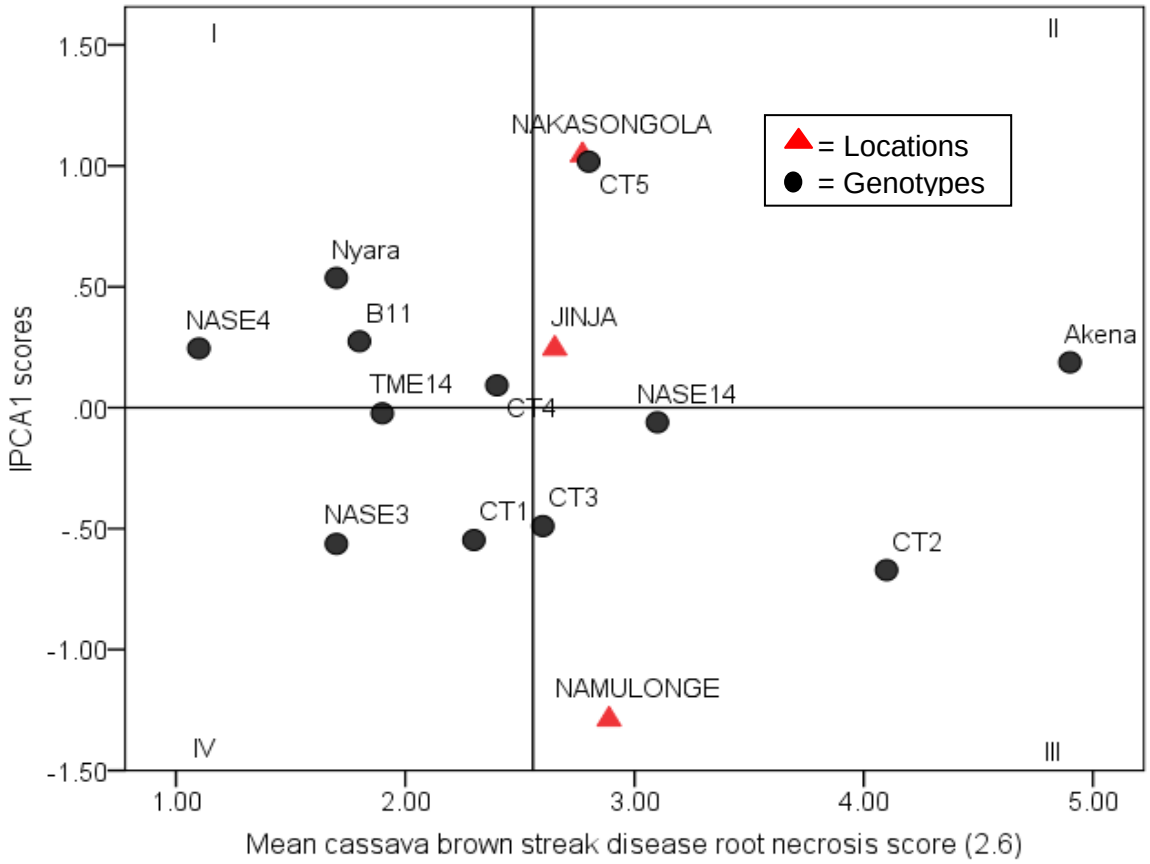

Figure 4.6: Biplot of mean cassava brown streak disease root necrosis scores (scale of 1-5) and IPCA1 scores for 12 cassava genotypes evaluated nine months after planting at three locations in Uganda.

Table 4.6: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index cassava brown streak root necrosis evaluated nine months after planting across three locations in Uganda

	Cassava brown streak disease root necrosis scores					
Genotypes	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	4.9	12	0.1876	4	16	10
B11	1.8	4	0.2745	6	10	3
CT1	2.3	6	-0.5473	9	15	8
CT2	4.1	11	-0.6711	11	22	12
CT3	2.6	8	-0.4894	7	15	8
CT4	2.4	7	0.0928	3	10	3
CT5	2.8	9	1.0173	12	21	11
NASE14	3.1	10	-0.0600	2	11	6
NASE3	1.7	2	-0.5631	10	12	7
NASE4	1.1	1	0.2455	5	6	1
Nyara	1.7	2	0.5364	8	10	3
TME14	1.9	5	-0.0232	1	6	1

GSI = genotype selection index; IPCA1 = interaction principal component axis one

Cassava mosaic disease severity

The majority of the genotypes were relatively stable for CMD-S, except for B11 and Nyara that were highly unstable (Figure 4.7). The most stable genotypes for this trait were Akena, CT3, NASE14, CT1 and NASE4. Nakasongola was the most stable location for CMD-S considering its low IPCA1 score. With high IPCA1 scores of opposite sign, Namulonge and Jinja had very high contrasting interactions with the genotypes. With GSI rankings of 1 the overall best genotypes combining low CMD-S and high stability were NASE14, TME14 and CT3, followed by Akena with a rank of 4 (Table 4.7).

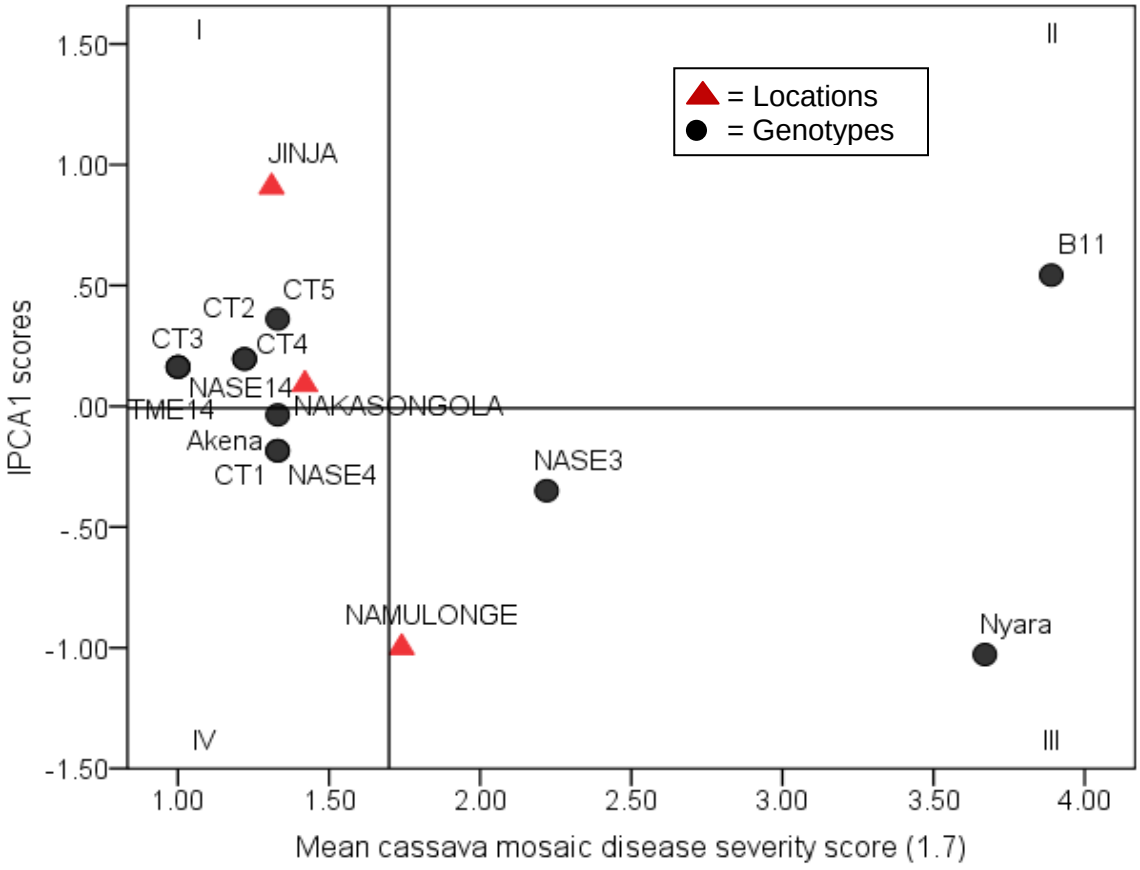

Figure 4.7: Biplot of mean cassava mosaic severity scores (scale of 1-5) and IPCA1 scores for 12 cassava genotypes evaluated six months after planting at three locations in Uganda

Table 4.7: Ranking of 12 cassava genotypes by mean performance, IPCA1 scores and genotype selection index for cassava mosaic disease severity evaluated six months after planting across three locations in Uganda

	Cassava mosaic disease severity scores					
Genotypes	**Mean**	**Rank**	**IPCA1 scores**	**Rank**	**GSI**	**Rank**
Akena	1.3	6	-0.0358	1	7	4
B11	3.9	12	0.5430	11	23	11
CT1	1.3	6	-0.1847	5	11	5
CT2	1.2	4	0.1957	7	11	5
CT3	1.0	1	0.1626	2	3	1
CT4	1.2	4	0.1957	7	11	5
CT5	1.3	6	0.3611	10	16	9
NASE14	1.0	1	0.1626	2	3	1
NASE3	2.2	10	-0.3500	9	19	10
NASE4	1.3	6	-0.1847	5	11	5
Nyara	3.7	11	-1.0281	12	23	11
TME14	1.0	1	0.1626	2	3	1

GSI = genotype selection index; IPCA1 = interaction principal component axis one

4.4 Phenotypic correlations among agronomic and disease traits

Fresh storage root yield was positively correlated with HI (P<0.001), SRN (P<0.001) and DMC (P<0.01); and negatively correlated with CMD-S (P<0.001) and CBSD-RN (Table 4.1). The highest correlation with FSRY was recorded by HI (r = 0.67), followed by SRN (r = 0.64). Although CMD-S had negative correlations with all the traits only three were significant, viz. FSRY (P<0.001), SRN (P<0.001) and HI (P<0.05). The CBSD-RN had negative but non-significant correlations with FSRY, DMC, SRN and CMD-S. Storage root number had highly significant (P<0.001) positive correlations with FSRY, HI and DMC and negative correlation with CMD-S.

Table 4.1 Phenotypic correlations between eight traits for six cassava genotypes evaluated at nine months after planting across three locations in Uganda

Traits	**FSRY**	**HI**	**DMC**	**SRN**	**CBSD-RN**	**CMD-S**
FSRY	1.00					
HI	0.67***	1.00				
DMC	0.26**	0.35***	1.00			
SRN	0.64***	0.50***	0.28***	1.00		
CBSD-RN	-0.07^{ns}	- 0.02^{ns}	- 0.01^{ns}	- 0.04ns	1.00	
CMD-S	-0.35***	- 0.19*	- 0.05^{ns}	- 0.38***	- 0.10^{ns}	1.00

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content (%); CMD-S = cassava mosaic severity on a scale 1-5; CBSD-RN = cassava mosaic disease severity on a scale 1-5; significance level; * = P<0.05; ** = P<0.01; *** = P<0.001; ns = non-significant.

4.5 Discussion and conclusions

Significant genotype x environment interaction is a common phenomenon in multi-location trials. It reduces association between phenotypic and genotypic values, and may cause genotype selections from one environment to perform poorly in another (Falconer and Mackay, 1996). In particular, the absence or presence of statistically significant crossover type of GEI indicates whether test genotypes maintain a consistent rank order across the locations or there is a change in rank order across the genotypes. In the latter case, different genotypes will be recommended as the top performers for each target location (Gauch, 2006; Egesi et al., 2007).

Genotype effects were significant in the AMMI ANOVA for early FSRY and all other traits, indicating significant variation in the performance of the genotypes for early FSRY and the other traits evaluated. This, in turn, indicated that the genotypes used in this study constituted a pool of germplasm with sufficient genetic variation and that by selecting and hybridising among the constituent genotypes, good progress in the improvement of cassava for early FSRY and related traits should be achieved. The location effects were also significantly different for all traits except CBSD-RN, indicating that the overall mean performances of the genotypes attained in each location were significantly different for most traits. This underlines the need to conduct multi-locational trials in order to identify both the generally and specifically adapted genotypes with good performance for these traits. Significant location effects for FSRY, DMC and CMD-S were similarly reported by Ssemakula and Dixon (2007), Aina et al. (2009) and Akinwale et al. (2011). The significant genotype x location interaction effects for SRN, HI, DMC, CBSD-RN and CMD-S again necessitates testing genotypes in multi-location trials in order to identify the generally or specifically adapted genotypes

The genotype and environment effects were highly significant for FSRY while the GEI interaction was non-significant. This indicated that the response patterns of the genotypes to change in location were non-significantly different and therefore the genotypes could be evaluated in terms of their significantly different performances for FSRY at 9 MAP averaged across the three locations. Although the GEI was non-significant, it was interesting that in the AMMI ANOVA for FSRY, 48.5% of the treatment SS was attributed to genotypes, 27.3% to environment, 24.1% to GEI. For all the other traits, genotypes also contributed the greater percentage of the treatment SS, signifying the predominance of genetic variation among the genotypes over variation among the locations and variation due to the interaction between the genotypes and locations for all the traits studied. Again, the relatively high variation in the

genotypes means that prospects are good for developing cassava genotypes with improved performance for these traits with the caveat that the genotypes will present differential responses to production environments that are similar to those evaluated in this study.

In the AMMI ANOVA, IPCA1 accounted for over 50.0% of the GEI %SS in all the traits studied and was also significant for all traits except early FSRY. Subsequently fitted IPCAs contributed less than 50.0% of the GEI SS and were non-significant, indicating that they captured largely random noise. In agreement with this finding, Gauch (2006) reported that significant IPCA1 and subsequent axes in AMMI capture interaction exclusively in a monotonic sequence that decreases from the first and largest component to the last and smallest component. Therefore, the significant IPCA1 scores sufficed in enabling visual assessment of the genotype and location performances and their interactions in the AMMI1 biplots (Mulema et al., 2008; Osiru et al., 2009).

Based on AMMI biplots and associated IPCA1 scores, the IITA introductions (Akena; NASE3, NASE4, NASE14 and TME14) and the genotypes developed by hybridising the CIAT and Ugandan germplasm (CT1, CT2, CT3, CT4 and CT5) were the most responsive to the locations effect. They represented either the best or the poorest performers in most locations having been displaced nearer or farthest from the IPCA1 origin. Nevertheless, different genotypes emerged as the best in different locations. For example, the most stable genotypes for early FSRY were Akena, CT2, CT4 and NASE14; for DMC, Akena, CT4, CT5 and CT2; for HI, NASE4, CT1, CT5 and TME14; for SRN, Akena, Nyara, CT4 and NASE14; for CBSD-RN, CT5, CT2, NASE3 and CT1; and for CMD-S, Akena, CT3, NASE14, CT1 and NASE4.

As would be expected, there was an inverse relationship between early FSRY and both CMD-S and CBSD-RN as indicated by the negative correlations between them. Namulonge had the lowest early FSRY compared to Nakasongola and Jinja, which could be attributed to the high scores for CMD-S and CBSD-RN recorded at Namulonge. Namulonge is in fact well known as a hot spot for both the CMD and CBSD causal viruses, as well as for white flies (*Bemisia tabaci*), which are vectors of both diseases (Otim-Nape, 2001; Sseruawagi et al., 2004; Alicai et al., 2007).

Overall, there was a high degree of genetic variation among the genotypes compared to the variation due to environment differences and GEI for all traits. The GEI was non-significant for early FSRY, which indicated that the genotypes had non-significantly different patterns of

response to change in location and could be evaluated in terms of their mean response over the locations. However, although for FSRY the genotypes did not significantly interact with the locations there were apparent changes in rank order of the genotypes at each location. The results of this study suggest that it is possible to make progress in breeding and selection for early yielding cassava genotypes with resistance to CBSD and CMD, as well as for the other economically important traits assessed in this study. However, the presence of significant GEI for all of the traits evaluated except FSRY will complicate selection for early yielding genotypes in combination with the other traits evaluated in this study.

References

Adesola, L. N., and J.A. Omolayo. 2011. Genotype x environment interaction and yield stability analyses of rice grown in tropical inland swamp. Notulae Botanicae Horti Agrobotanici Cluj-Napoca 39:220-225.

Adugna, W., and M.T. Labuschagne. 2002. Genotype x environment interactions and phenotypic stability analyses of linseed in Ethiopia. Plant Breeding 121:66-71.

Aina, O.O., A.G.O. Dixon, I. Paul, and E.A. Akinrinde. 2009. GxE interaction effects on yield and yield components of cassava (landraces and improved) genotypes in the savannah regions of Nigeria. African Journal of Biotechnology 8:4933-4945.

Akinwale, M. G., B.O. Akinyele, A. C. Odiyi, and A.G.O. Dixon, 2011: Genotype x environment interaction and yield performance of 43 improved cassava (*Manihot esculenta* Crantz) genotypes at three agro-climatic zones in Nigeria. British Biotechnology Journal 1:68-84.

Alicai, T., C.A. Omongo, M.N. Maruthi, R.J.Hillocks, Y. Baguma, R. Kawuki, A. Bua,G.W. Otim-Nape, and J. Colvin. 2007. Re-emergence of cassava brown streak disease in Uganda. Plant Diseases 91:24-29.

Alves, A.A.C. 2002. Cassava botany and physiology. In: R.J. Hillocks, et al. (eds.), Cassava: Biology, production and utilization. CABI, Wallingford, UK. p. 67-89.

Das, S., R.C. Misra, M.C. Patnaik, and S.R. Das. 2010. GxE interaction, adaptability and yield stability of mid-early rice genotypes. Indian Journal of Agricultural Research 44:104-111.

Ebdon, J.S., and H.G. Gauch. 2002. Additive main effects and multiplicative interaction analysis of national turfgrass performance trials. Crop Science 42:497-506.

Eberhart, S.A., and W.A. Russell. 1996. Stability parameters for comparing varieties. Crop Science 6:36-40.

Egesi, C.N., P. Ilona, F.O. Ogbe, M. Akoroda, and A. Dixon. 2007. Genetic variation and genotype x environment interaction for yield and other agronomic traits in cassava in Nigeria. Agronomy Journal 99:1137-1142.

Falconer, D.S., and T.F.C. Mackay.1996: Introduction to Quantitative Genetics. Fourth edition, Longman, New York. p.132-133.

Farshadfar, E. 2008. Incorporation of AMMI stability value and grain yield in a single non parametric index (GSI) in bread wheat. Pakistan Journal of Biological Sciences 11:1791-1796.

Farshadfar, E., N. Mahamodi, and A. Yaghotipoor. 2012. AMMI stability value and simultaneous estimation of yield and yield stability in bread wheat (*Triticum aestivum* L.). Australian Journal of Crop Science 5:1837-1844.

Gauch, H.G. 2006. Statistical analysis of yield trials by AMMI and GGE. Crop Science 46:1488-1500.

Gauch, H.G., and R.W. Zobel. 1990. AMMI analysis of yield trials - Additive main effects and multiplicative interaction analysis of two international maize cultivar trials. Crop Science 30:493-500.

Gauch, H.G., and R.W. Zobel. 1997. Identifying mega-environments and targeting genotypes. Crop Science 37:311-326.

Hartley, H.O. 1950. The use of range in analysis of variance. Biometrika 37:271-280.

Kang, M.S. 1998. Using genotype-by-environment interaction for crop cultivar development. Advanced Agronomy 62:199-252.

Lin, C. S., M. R. Binns, and L. P. Lefkovitch.1986. Stability analysis: Where do we stand? Crop Science 26:894-900.

Mulema, J. M. K., E. Adipala, O. M. Olanya, and W. Wagoire. 2008. Yield stability analysis of late blight resistant potato selections. Experimental Agriculture 44:145-155.

Osiru, M.O., O.M. Olanya, E. Adipala, R. Kapinga, and B. Lemaga. 2009. Yield stability analysis of *Ipomoea batatas* L. cultivars in diverse environments. Australian Journal of Crop Science 3:213-220.

Otim-Nape, G.W., T. Alicai, and M. Thresh. 2001. Changes in the incidence and severity of cassava mosaic virus disease, varietal diversity and cassava production in Uganda. Annals of Applied Biology 138:313-327.

Payne, R.W., S.A. Harding, D.A Murray, D.M. Soutar, D.B. Baird, A.I. Glaser, S.J. Welham, A.R. Gilmour, R. Thompson, and R. Webster. 2011. The guide to genstat release 14, part 2: statistics. VSN International, Hemel Hempstead, UK.

Purchase, J.L., H. Hatting, and S.C. Van Deventer. 2000. Genotype x environment interaction of winter wheat (*Triticum aestivum* L.) in South Africa: II. Stability analysis of yield performance. South African Journal of Plant and Soil 17:101-107.

Shafii, B., and W. J. Price. 1998. Analysis of genotype-by-environment interaction using the additive main effects and multiplicative interaction model and stability estimates. Journal of Agricultural, Biological, and Environmental Statistics 3:335-345.

Ssemakula, G., and A. Dixon. 2007. Genotype x environment interaction, stability and agronomic performance of carotenoid-rich cassava clones. Scientific Research and Essay 2:390-399.

Sseruwagi, P., W.S. Sserubombwe, J.P. Legg, J. Ndunguru, and J.M. Thresh. 2004. Methods of surveying the incidence and severity of cassava mosaic disease and whitefly vector populations on cassava in Africa: a review. Virus Research 100:129-142.

CHAPTER 5

Diallel analysis of early storage root yield and related traits in cassava at the F_1 seedling evaluation stage

Abstract

In cassava breeding schemes, selection at the seedling stage has largely been based on high heritability traits. Moreover, combining ability and family data at this stage are seldom analysed, leading to a loss of potential genetic information and material. To assess the general combining ability (GCA) of the parents and their specific combining ability (SCA), as well as the possibility of selecting for early fresh storage root yield (FSRY) and related traits, 36 F_1 cassava families were developed from a 9 x 9 half-diallel and evaluated in a 6 x 6 triple lattice design at the National Crops Resources Research Institute in Uganda. The families mean squares (MS) were significant for all traits, suggesting significant differences among families for all traits. The GCA MS were significant for all traits, whereas SCA MS were only significant for dry mass content (DMC) and storage root number (SRN), indicating the predominance of additive gene effects in controlling expression of most traits. This was confirmed by the percentage of the families sum of squares (SS) due to GCA being over 50.0% in eight of the 10 traits evaluated. Percentage families SS due to SCA effects accounted for over 50.0% of the variability in only two of the 10 traits (DMC and SRN), indicating predominance of non-additive gene action in the expression of these two traits. Among the parents, CT4 was the best general combiner for FSRY, SRN, dry storage root yield, storage root girth, storage root length, resistance to cassava mosaic and brown streak diseases; CT2 for harvest index; CT5 for plant height; and TME14 for DMC. Among the families, NASE3 x CT2, CT5 x CT3 and CT1 x B11 had the best SCA effects for FSRY while CT4 x B11, CT4 x Nyara and CT4 x CT1 were the best families for mean FSRY. Principal components and correlation analyses indicated the possibility of carrying out selection for yield traits at the early seedling generational stage of cassava breeding. The information generated can be utilised as a model for reducing loss of potential useful genetic data and material, and subsequently improve the cassava breeding cycle.

5.1 Introduction

Cassava (*Manihot esculenta* Crantz) is the world's most widely grown starch storage root crop and is the principal food staple in sub-Saharan Africa where it accounts for approximately one-third of the total production of staple food crops (FAO, 2012). It is a cross-pollinating, heterogeneous crop species with 2n = 4x = 36 chromosomes (Nassar, 2000; Ceballos et al., 2012), and behaves as a diploid (Wang et al., 2011). The primary propagation method of cassava is by stem cuttings but in breeding programmes, its propagation in the first stage following sexual recombination is by botanical seeds (Alves, 2002). Its breeding is characterised by one fundamental principle, which is breaking the normal clonal propagation of highly heterozygous genotypes by introducing a crossing step that culminates in sexual seed production and increased genetic variation (Grüneberg et al., 2009). Each plant grown from botanical seed can be considered a potentially new cultivar, creating the basis for selection (Kawano, 2003; Grüneberg et al., 2009).

During the 1960s, cassava breeding was primarily done by establishing extensive open-pollinated crossing blocks called polycross nurseries, where half-sib progeny were developed; however, in recent years there has been a move towards full-sib crossing schemes (Ceballos et al., 2004). The full-sib crossing schemes employ controlled pollinations, where selected mating designs are used to generate full-sib families for genetic studies (Griffing, 1956; Brown and Caligari, 2009). One of the mating designs that has been widely used by cassava breeders to generate full-sib progeny for genetic studies is the diallel (Calle et al., 2005; Perez et al., 2005; Owolade et al., 2009; Zacarias and Labuschagne, 2010; Kulembeka et al., 2012), the analysis of which facilitates the identification of parents that are good general combiners, and parents in specific combinations that produce superior progeny. It also provides genetic information on the mode of inheritance of selected traits for a set of genotypes and the environments in which they were evaluated. The genetic information generated assists breeders to employ effective breeding methodologies for crop improvement (Jaramillo et al., 2005; Zacarias and Labuschagne, 2010). The statistical analysis of diallels is usually performed according to the models developed by Griffing (1956), and Eberhart and Gardner (1966), which partition the total variation into general combining ability (GCA) of the parents and specific combining ability (SCA) of the crosses.

One of the key breeding strategies in a successful breeding programme is the identification of appropriate parental lines. Parental line selection in most cassava breeding programmes is usually based on the parents' *per se* performance, with little use of GCA as a criterion for

parental selection (Ceballos et al., 2004). In crop improvement, GCA estimates can also be used to predict genetic gains (Bhullar et al., 1979; Falconer and Mackay, 1996).

Existing cassava breeding schemes extend the cassava breeding cycle, as selection at the F_1 seedling stage is primarily based on high heritability traits such as plant type, branching habits and reaction to certain diseases (Iglesias et al., 1994; Ceballos et al., 2004), excluding certain traits such as fresh storage root yield, harvest index, and dry mass content (Ojulong et al., 2010). Moreover, parental and family data are seldom recorded at the seedling stage and used in seedling selection; hence the breeding process is effectively mass phenotypic recurrent selection. As combining ability data collection in most cassava breeding programmes, is traditionally done on the clonal generations, there is potential loss of valuable genetic material and information at the F_1 seedling evaluation stage.

Against this background, the objectives of this study were to: 1- generate the F_1 population segregating for fresh storage root yield (FSRY) and related traits; 2- estimate the general combining ability (GCA) of nine cassava parental lines and their specific combining ability (SCA) through their progeny for FSRY and related traits; and 3- determine the gene action controlling FSRY and related traits.

5.2 Materials and methods

5.2.1 Experimental site

The trial was established at the National Crops Resources Research Institute (NaCRRI) in Namulonge, Uganda. Namulonge is located at 32°36'E and 0°31'N, at 1134 m above sea level, and has sandy clay loam soils. It has a bimodal rainfall pattern, with two distinct rainy seasons and dry seasons of nearly equal length. The peak rainfall occurs between March to May and September to November. During the experimental period, Namulonge recorded mean rainfall of 980 mm and temperatures ranging from 15.9 to 28.9^{o}C.

5.2.2 Parental selection and hybridisation

Nine genetically diverse parents (Table 5.1) were selected from farmers' fields and the National Cassava Breeding Programme (NCBP) at NaCRRI. Parents from farmers' fields were landraces, while parents from the NCBP were composed of introductions from the International Institute of Tropical Agriculture (IITA) and genotypes generated by crossing lines from the International Centre for Tropical Agriculture (CIAT) with those of Uganda. The selection of parents was based on their *per se* performance for early bulking, FSRY, dry mass content, flowering ability and relative degrees of field resistance to cassava mosaic

disease (CMD) and cassava brown streak disease (CBSD). Parents were planted in a crossing block in Kasese district under irrigation in paired rows to facilitate generating the 36 families of F_1 progeny of a 9 x 9 half-diallel design. Controlled pollinations were performed following the standard procedures described by Kawano (1980) with some modifications. Three months after pollination, botanical seeds were harvested and stored in labelled paper bags for three months to break seed dormancy. Afterwards, 100 seeds from each family were germinated in a greenhouse in plastic bags filled with soil (Figure 5.1).

Table 5.1: Nine parents crossed in a 9 x 9 half-diallel during 2010/11

Parent	Entry code	Type	Special positive attributes	Special negative attributes
Bukalasa11	B11	landrace	high DMC, early bulking, sweet	very S to CMD
Nyaraboke	Nyara	landrace	high DMC, sweet, medium bulking	very S to CMD
TME14	TME14	improved[a]	R to CMD, T to CBSD, high DMC	medium bulking
TMS30572	NASE3	improved[a]	R to CMD, T to CBSD, sweet	late bulking
FS37-4	CT1	new genotype[b]	R to CMD, T to CBSD, high yield	medium bulking
FS25-5	CT2	new genotype[b]	R to CMD, high yield, early bulking	very S to CBSD
FS7-18	CT3	new genotype[b]	R to CMD, early bulking, high DMC	S to CBSD
FS27-15	CT4	new genotype[b]	R to CMD, T to CBSD, high shoot yield	Low yield
FS1-4	CT5	new genotype[b]	R to CMD, early bulking, sweet	S to CBSD

DMC = dry mass content; CMD = cassava mosaic disease; CBSD = cassava brown streak disease; [a]IITA introductions; [b]genotypes developed between CIAT and Uganda lines, R = resistant; T = tolerant; S = susceptible

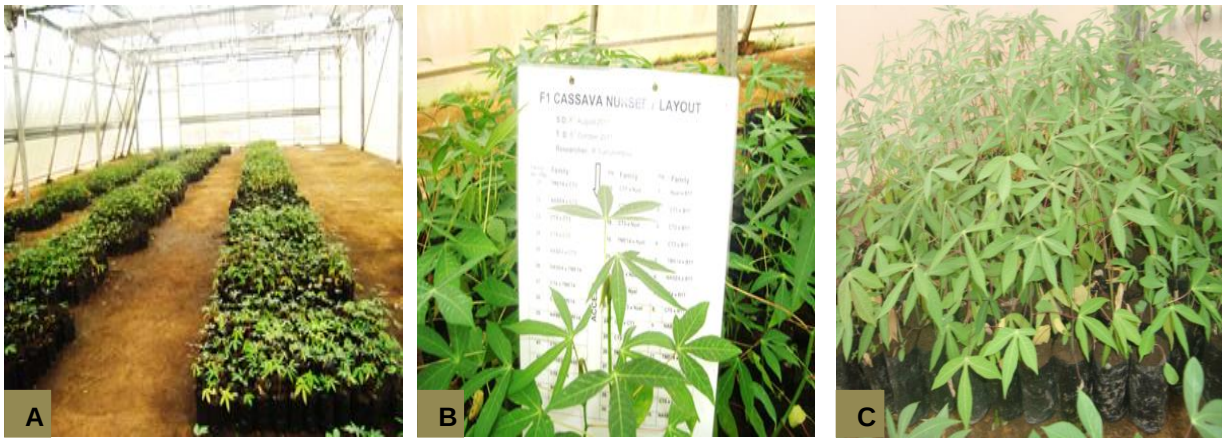

Figure 5.1: Cassava botanical seed germination. **A:** seedlings grouped and raised in plastic black bags; **B:** a list of 36 half-diallel families in the greenhouse; and **C:** fast growing seedlings at 40 days after planting.

5.2.3 Trial design

The seedling stage trial was planted in October 2011 and was laid out as a 6 x 6 triple lattice design with three replicates. Sixty vigorous seedlings from each full-sib seedling stage family were selected and randomly divided into three groups of 20 seedlings, and the groups were

randomly allocated to replications. Planting was done at spacing of 1 x 1 m providing a population density of 10 000 plants ha^{-1}. The trials were conducted without supplemental irrigation and weeded regularly.

5.2.4 Data collection

Plants were scored only once for CMD severity (CMD-S) at six months after planting (MAP) using a scale of 1-5, where: 1 = no symptoms; and 5 = very severe mosaic symptoms (Banito et al., 2007). At harvest time (10 MAP), 11 plants were randomly selected from each family per replication, and were measured for height (PHT) (cm) using a metre ruler as the distance from the ground to the shoot tip. The plants were then uprooted individually. Storage roots $plant^{-1}$ were counted and weighed to obtain storage root number (SRN) and mass (SRM) (kg $plant^{-1}$), respectively. Early fresh storage root yield (FSRY) (t ha^{-1}) was estimated from SRM $plant^{-1}$ as:

$$\text{FSRY} = \text{SRM} \times \frac{10\,000}{1000}$$

Storage root length (SRL) was measured as the length (cm) between the ends of a storage root, and the storage root girth (SRG) as the circumference (cm) at the widest point of the mid-section of storage root. Harvest index (HI) was calculated as the ratio of storage root mass to total biomass (TBM) (kg $plant^{-1}$):

$$\text{HI} = \frac{\text{SRM}}{\text{TBM}}$$

Dry mass content expressed as a percentage was determined by selecting at least two storage roots from a bulk of storage roots of each plant, which were washed, peeled and sliced. The sliced fresh samples were weighed to obtain 0.1 kg before being dried for 48 h in a forced-drought oven at 80°C. The dried samples were then reweighed to obtain the dry mass and the DMC was calculated as:

$$\text{DMC}\,(\%) = \frac{\text{DRM}}{\text{FRM}} \times 100$$

Where: DMC = dry mass content expressed as a percentage; DRM = dry root mass (kg) and FRM = fresh root mass (kg).

Dry storage root yield (DSRY) (t ha^{-1}) was computed as the product of FSRY (t ha^{-1}) and DMC as:

$$\text{DSRY} = \frac{\text{DMC}\ \%}{100} \times \text{FSRY}$$

Because the main damage caused by CBSD is to the storage roots, the storage root necrosis due to CBSD (CBSD-RN) was scored on a scale of 1 to 5 where: 1= no visible necrosis, and 5 = severe necrosis (Hillocks et al., 1996).

5.2.5 Data analysis

Data for each of the 36 families were averaged for statistical analyses. The analysis of variance (ANOVA) for the traits was done using Genstat 14th edition (Payne et al., 2011). The relative contributions of the traits to the total variability of the 36 families were analysed according to Jollife (2002), using principal component analysis (PCA) in Genstat (Payne et al., 2011). Pearson's phenotypic correlations between the 36 family means for each trait were also performed using Genstat 14 (Payne et al., 2011). The diallel analysis was conducted using SAS-05 diallel programme (Zhang et al., 2005) in SAS 8th edition. Griffing's (1956) diallel method 4, model 1 for a fixed model was fitted to estimate the GCA and SCA effects as:

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

Where:

Y_{ij} = observed value of the cross between parent i and j;

μ = overall mean;

g_i = GCA effect of parent i;

g_j = GCA effect of parent j;

s_{ij} = SCA of the cross between parents i and j;

b_k= effect of the kth block;

e_{ijkl} = experimental error.

The relative importance of GCA and SCA effects for each trait was determined from the percentage of the families sum of squares (SS) due to GCA and SCA (Kulembeka et al., 2012; Were et al., 2012).

5.3 Results

5.3.1 Performance of the individual genotypes within families

The botanical seed-derived F_1 genotypes were evaluated for 10 traits (Table 5.2). Among the 10 traits evaluated, SRN, SRL, FSRY, DSRY, CBSD-RN and CMD-S were positively skewed and the rest, negatively skewed. Fresh storage root yield ranged from 1.0 to 94.0 t ha^{-1} with a mean of 19.3 t ha^{-1}. There was a complete range of scores from 1 to 5 recorded for CMD-S and CBSD-RN with means of 2.1 and 1.9, respectively. A high range of 1.0 - 23.0 $plant^{-1}$ and a mean of 5.6 $plant^{-1}$ for SRN were recorded. Harvest index ranged from as low as 0.1 to as high as 0.9 with a mean of 0.4. Dry mass content ranged from 14.3 to 47.8% with a mean of 35.5% while DSRY ranged from 0.3 to 36.9 t ha^{-1} with a mean of 7.1. The SRL and SRG ranged from 1.5 to 65.0 cm and 1.0 to 29.3 cm, respectively. Plant height ranged from 120.0 to 320.0 cm with a mean of 184.6 cm. In addition, the seedling plants developed multiple stems and branches ranging from 1 to 3 and 2 to >10, respectively (Figure 5.2).

Table 5.2: Summary statistics of 10 traits measured in 1188 F_1 cassava seedlings evaluated at 10 months after planting at Namulonge, 2011/12

	Statistics				
Traits	**Minimum**	**Maximum**	**Mean**	**SD**	**Skewness**
SRN	1.0	23.0	5.6	3.5	0.8
SRG	1.0	29.3	14.6	6.3	- 0.2
SRL	1.5	65.0	22.3	10.7	0.2
DMC	14.3	47.8	35.5	4.4	- 0.6
HI	0.1	0.9	0.4	0.2	- 0.2
FSRY	1.0	94.0	19.3	16.5	1.5
DSRY	0.3	36.9	7.1	6.1	1.5
PHT	120.0	320.0	184.6	40.7	- 0.4
CBSD-RN	1.0	5.0	1.9	1.2	1.2
CMD-S	1.0	5.0	2.1	0.7	0.7

SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); DMC = dry mass content (%); HI = harvest index; FSRY = fresh storage root yield (t ha^{-1}); DSRY = dry storage root yield (t ha^{-1}); PHT = plant height (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; SD = standard deviation

Figure 5.2: Seedling stage plants of the 36 F_1 families generated from a 9 x 9 half-diallel before harvest and at harvest 10 months after planting in 2012 at Namulonge, Uganda. **A**: seedling plants with multiple stems originating from the base of plants; **B**: multiple stem plants segregating for cassava mosaic disease severity; **C**: seedling plants with one stem from the base but branched at about 1 m height; **D**: seedling plants with well-developed taproot and side storage roots; **E**: an uprooted seedling plant with over 10 well-developed medium size storage roots; and **F**: an uprooted seedling plant with well-developed large storage roots.

5.3.2 Mean performances of the 36 F_1 families

The highest mean performance for FSRY of 28.3 t ha^{-1} was recorded by family CT4 x B11 and the least of 11.7 t ha^{-1} by Nyara x B11 (Table 5.3). The mean performance for HI ranged from 0.31 (CT4 x CT3) to 0.54 (CT2 x Nyara). The mean performance for SRN ranged from 3.8 (NASE3 x TME14) to 7.9 (CT4 x Nyara) and the mean performance for DMC from 31.3% (CT5 x CT2) to 38.5% (TME14 x Nyara). The highest mean performance for DSRY of 10.6 t ha^{-1} was produced by family CT4 x Nyara and the least of 4.3 t ha^{-1} by family NASE3 x Nyara. Family CT5 x B11 recorded the highest mean performance for PHT (219.6 cm) and NASE3 x CT3 the lowest (152.7 cm). The highest mean performance for SRG was observed in family CT4 x CT1 and the lowest in NASE3 x CT3. The highest mean performance for SRL was observed in family CT1 x Nyara and the least in CT3 x Nyara. Families CT4 x TME14, CT5 x CT2 and CT5 x TME14 recorded the lowest mean score of 1.3

for CMD-S and the highest of 3.8 was recorded in Nyara x B11 (family of a cross between parents very susceptible to CMD). The least mean score of 1.4 for CBSD-RN was recorded by CT4 x CT1 (family of parents tolerant to CBSD) and the highest of 2.7 by CT5 x CT2 (family of a cross between parents susceptible to CBSD).

Table 5.3: Family means for the 10 traits evaluated in F_1 cassava at the seedling evaluation stage at Namulonge, 2011/12

	Trait means									
Families	**FSRY**	**HI**	**SRN**	**DMC**	**DSRY**	**PHT**	**SRG**	**SRL**	**CMD-S**	**CBSD-RN**
CT1 x B11	24.3	0.41	7.0	36.2	8.8	212.2	14.8	28.1	2.8	1.8
CT1 x Nyara	20.1	0.40	6.6	35.7	7.2	203.8	14.3	30.0	2.2	1.7
CT2 x B11	19.0	0.50	5.4	34.9	6.7	184.3	16.2	20.3	2.8	2.3
CT2 x CT1	20.4	0.51	5.4	35.5	7.2	176.3	14.7	20.7	1.5	1.9
CT2 x Nyara	19.1	0.54	4.2	33.7	6.5	179.5	15.2	19.2	2.7	2.3
CT3 x B11	17.1	0.44	5.3	38.4	6.8	188.8	14.6	21.2	2.0	1.9
CT3 x CT1	17.8	0.45	5.5	38.3	6.7	168.8	13.1	22.4	1.7	2.0
CT3 x CT2	18.8	0.53	4.8	38.2	7.2	162.7	15.0	21.1	1.7	2.4
CT3 x Nyara	14.2	0.46	4.0	34.5	5.2	167.6	12.1	14.3	2.3	2.6
CT4 x B11	28.3	0.38	6.8	34.6	9.9	189.6	17.0	25.0	2.3	1.8
CT4 x CT1	27.7	0.36	7.5	35.4	9.9	186.3	17.8	27.4	1.7	1.4
CT4 x CT2	25.9	0.41	5.9	35.0	9.1	183.9	15.3	24.1	1.8	1.8
CT4 x CT3	16.5	0.31	4.7	32.1	5.6	169.2	14.2	22.8	1.3	1.6
CT4 x Nyara	28.2	0.37	7.9	35.8	10.6	198.2	16.4	26.3	1.8	1.8
CT4 x TME14	25.0	0.42	7.5	36.2	9.1	180.6	16.0	28.3	1.3	1.6
CT5 x B11	16.9	0.48	6.6	34.6	5.9	219.6	14.7	26.2	2.5	2.4
CT5 x CT1	19.6	0.42	5.0	34.8	7.1	195.5	13.1	19.1	1.9	1.9
CT5 x CT2	20.2	0.48	5.3	31.3	6.4	205.8	15.5	21.3	1.3	2.7
CT5 x CT3	20.2	0.45	6.8	34.9	7.2	212.0	16.0	26.2	2.2	2.3
CT5 x CT4	24.9	0.46	5.8	34.3	8.5	203.6	13.8	22.8	1.5	1.5
CT5 x Nyara	15.4	0.52	4.5	33.1	5.2	184.6	13.9	20.2	3.2	2.2
CT5 x TME14	15.9	0.48	5.4	37.8	6.1	194.7	13.9	22.7	1.3	2.1
NASE3 x B11	13.6	0.47	5.0	35.8	4.9	172.8	13.7	19.7	3.0	1.8
NASE3 x CT1	18.2	0.40	5.4	34.9	6.7	183.4	12.5	20.2	1.8	1.8
NASE3 x CT2	27.1	0.47	6.1	35.0	9.7	165.4	14.0	17.7	1.8	1.6
NASE3 x CT3	12.0	0.41	3.9	36.1	4.5	152.7	10.9	15.7	2.0	2.4
NASE3 x CT4	26.4	0.37	6.4	36.2	10.4	185.6	15.7	25.5	1.7	1.6
NASE3 x CT5	14.9	0.39	4.3	34.6	5.3	175.0	12.3	19.1	1.7	1.9
NASE3 x Nyara	12.1	0.47	4.0	35.3	4.3	154.4	12.1	17.1	2.3	2.1
NASE3 x TME14	14.5	0.43	3.8	35.0	5.2	160.3	11.1	16.0	2.0	2.5
Nyara x B11	11.7	0.47	4.0	34.4	4.0	205.5	14.3	20.0	3.8	1.6
TME14 x B11	14.8	0.41	6.4	37.0	5.5	177.2	14.6	20.9	3.2	1.6
TME14 x CT1	19.1	0.48	4.2	38.0	7.4	172.6	14.6	20.3	1.7	1.9
TME14 x CT2	19.6	0.49	6.0	36.1	7.1	174.2	15.8	21.5	2.0	2.0
TME14 x CT3	15.9	0.45	5.2	37.1	6.0	154.6	14.4	22.1	2.5	1.8
TME14 x Nyara	19.5	0.44	5.2	38.5	7.5	190.1	15.4	24.3	2.2	1.9
MEAN	19.3	0.44	5.5	35.5	7.0	183.1	14.4	21.9	2.1	2.0
SED	4.9	0.04	1.0	1.7	1.9	13.0	1.5	2.8	0.4	0.4
$LSD_{0.05}$	9.7	0.08	2.0	3.3	3.8	26.0	3.0	5.49	0.8	0.7

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; SRN = storage root number $plant^{-1}$; DMC =dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); PHT = plant height (cm); SRG = storage root girth (cm); SRL= storage root length (cm); CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error.

5.3.3 Diallel analysis of variance for traits

In the ANOVA, the mean squares (MS) for families were: highly significantly (P<0.001) different for HI, PHT, SRN, SRL and CMD-S; very significantly (P<0.01) different for FSRY and DMC; and significantly (P<0.05) different for DSRY, SRG and CBSD-RN (Table 5.4). The GCA MS were highly significantly (P<0.001) different for FSRY, HI, DSRY, PHT, SRG, SRL and CMD-S and very significantly (P<0.01) different for the rest of the traits (DMC, SRN and CBSD-RN). The SCA MS were very significantly (P<0.01) different for SRL and significant (P<0.05) different for SRN.

The families sum of squares (SS) were partitioned into the SS due to parents (GCA effects) and the interaction between parents (SCA effects). The percentage of the families SS due to GCA and SCA effects provides an estimate of the relative importance of additive and non-additive gene effects in the expression of the traits assessed. The GCA effects accounted for over 50.0% of variability expressed by families in FSRY, HI, DSRY, PHT, SRG, SRL, CBSD-RN and CMD-S while SCA effects accounted for over 50.0% of the family variability for only DMC and SRN. The experimental errors for the traits were relatively low, with coefficients of variation ranging from 5.8% for DMC to 33.6% for DSRY.

Table 5.4: ANOVA of a 9 x 9 half-diallel for 10 traits of cassava F_1 seedling stage families evaluated during crop growth and at 10 months after planting at Namulonge in 2011/12

		Mean squares				
Source of variance	**DF**	**FSRY**	**HI**	**DSRY**	**DMC**	**PHT**
Families	35	74.3**	0.008***	9.6*	8.3**	895.5***
GCA	8	218.9***	0.023***	25.2***	16.7**	2759.0***
SCA	27	31.4	0.003	5.0	5.9	343.5
Error	70	35.6	0.003	5.5	4.2	254.5
CV%		30.8	11.600	33.6	5.8	8.7
% families SS due to GCA		67.3	66.600	60.2	45.5	70.4
% families SS due to SCA		32.7	33.400	39.8	55.5	29.6
		Mean squares				
Source of variance	**DF**	**SRN**	**SRG**	**SRL**	**CBSD-RN**	**CMD-S**
Families	35	3.8***	7.3*	41.6***	0.32*	1.1***
GCA	8	7.5**	20.5***	91.9***	0.72**	3.5***
SCA	27	2.7*	3.4	26.6**	0.19	0.4
Error	70	1.4	3.5	11.3	0.20	0.2
CV%		21.9	12.9	15.3	22.90	23.4
% families SS due to GCA		45.6	63.9	50.5	51.90	73.3
% families SS due to SCA		54.4	36.1	49.5	48.10	26.7

DF = degrees of freedom; FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DSRY = dry storage root yield (t ha^{-1}); DMC = dry mass content (%); PHT = plant height (m); SRN = storage root number; SRG = storage root girth (cm); SRL = storage root length (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; GCA = general combining ability; SCA = specific combining ability; MS = mean squares; SS = sum of squares; * = P<0.05; ** = P<0.01; *** = P<0.001.

5.3.4 General combining ability

Combining ability analysis (Table 5.5) revealed that parent CT4 had highly significant ($P<0.001$) and positive GCA effects for FSRY, DSRY, SRN and SRG, and the lowest negative GCA effects for CMD-S and CBSD-RN, signifying that it was the best general combiner for these respective traits. CT2 had a highly significant ($P<0.001$), positive GCA effect for HI; a significant ($P<0.05$), positive GCA effect for SRG, and a significant ($P<0.05$) negative GCA effect for CBSD-RN. CT1 had significant ($P<0.05$), negative GCA effects for CBSD-RN and CMD-S. For CT5, a highly significant ($P<0.001$), positive GCA effect was recorded for PHT and a significant ($P<0.05$), positive GCA effect for HI. As expected, the two landrace parents, B11 and Nyara commonly known to be very susceptible to CMD (Otim-Nape et al., 1994), both had highly significant ($P<0.001$), positive GCA effects for CMD-S. B11 also had a highly significant ($P<0.001$) and positive GCA effect for PHT. TME14 had a very significant ($P<0.01$), positive GCA effect for DMC and negative GCA effect for PHT. Parent CT3 had a highly significant ($P<0.001$), negative GCA effect for PHT and significant ($P<0.05$), negative GCA effects for FSRY and DSRY. NASE3 had highly significant ($P<0.001$), negative GCA effects for PHT, SRG and SRL, as well as a significant ($P<0.05$), negative GCA effect for SRN.

Table 5.5: General combining ability effects for 10 traits of nine cassava parents from the half-diallel analysis of 36 F_1 seedling stage families evaluated 10 months after planting at Namulonge, 2011/12

	General combining ability effects				
Parents	**FSRY**	**HI**	**DSRY**	**DMC**	**PHT**
B11	-1.32	0.003	-0.476	0.230	12.18***
Nyara	-2.09	0.019	-0.758	-0.459	2.70
CT1	1.74	-0.016	0.728	0.658	4.89
CT2	2.17	0.056***	0.590	-0.656	- 4.67
CT3	-3.20*	-0.006	-0.963*	0.761	-12.63***
TME14	-1.52	0.008	-0.294	1.597**	- 8.64**
CT4	7.21***	-0.064***	2.469***	-0.662	4.61
CT5	-1.01	0.019*	-0.585	-1.275**	18.00***
NASE3	-1.98	-0.019	-0.709	-0.194	-16.40***
$LSD_{0.05}$	2.45	0.021	0.955	0.843	6.50
SE	1.22	0.010	0.479	0.439	3.30
	General combining ability effects				
Parents	**SRN**	**SRG**	**SRL**	**CBSD-RN**	**CMD-S**
B11	0.364	0.640	0.826	-0.050	0.819***
Nyara	-0.517	-0.228	-0.593	0.069	0.533***
CT1	0.376	-0.056	1.816*	-0.188*	-0.224*
CT2	-0.118	0.906*	-1.355	0.188*	-0.167
CT3	-0.544	-0.723	-1.398	0.184	-0.158
TME14	-0.002	0.087	0.078	-0.040	-0.086
CT4	1.217***	1.543***	3.821***	-0.354***	-0.467***
CT5	-0.041	-0.304	0.297	0.193*	-0.177
NASE3	-0.734*	-1.875***	-3.493***	-0.002	-0.071
$LSD_{0.05}$	0.494	0.766	1.381	0.184	0.202
SE	0.275	0.576	1.038	0.092	0.151

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DSRY = dry storage root yield (t ha^{-1}); DMC = dry mass content (%); PHT = plant height (m); SRN = storage root number; SRG = storage root girth (cm); SRL= storage root length (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S= cassava mosaic disease severity scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

5.3.5 Specific combining ability

Family NASE3 x CT2 recorded a significant (P<0.05) and highly positive SCA effect for FSRY (Table 5.6). CT5 x CT4 recorded a very significant (P<0.01) and highest positive SCA effect for HI. All the significant SCA effects for DMC were negative and were observed in families; CT3 x CT2 (P<0.05), CT5 x CT2 (P<0.05) and CT4 x CT3 (P<0.01). Only one family; NASE3 x CT2 had a significant (P<0.05) and positive SCA effect for DRY. Very significant (P<0.01) and high positive SCA effects for SRN were observed in families: CT5 x CT3, CT4 x Nyara and NASE3 x CT2, with CT5 x CT3 recording the highest SCA effect of +1.88. Family CT1 x Nyara recorded a highly significant (P<0.001), positive SCA effect for SRL, followed by CT5 x CT3 with a very significant (P<0.01), positive SCA effect for the trait. Family CT5 x CT3 recorded a very significant (P<0.01), and positive SCA effect for SRG. CT5 x CT3 recorded a significant (P<0.05) and positive SCA effect for PHT. Negative and significant SCA effects for CMD-S were observed in CT3 x B11 (P<0.01) and CT5 x TME14 (P<0.05).

Negative and significant (P<0.05) SCA effects for CBSD-RN were observed in families NASE3 x CT2 and Nyara x B11, with NASE3 x CT2 recording the lowest SCA effect of -0.55.

Table 5.6: Specific combining ability effects for 10 traits from the half-diallel analysis of 36 F_1 cassava seedling stage families evaluated 10 months after planting at Namulonge, 2011/12

	Specific combining ability effects									
Families	**FSRY**	**HI**	**DMC**	**DSRY**	**SRN**	**SRG**	**SRL**	**PHT**	**CMD-S**	**CBSD-RN**
Nyara x B11	-4.25	0.001	-0.94	-1.78	- 1.40*	- 0.57	-2.21	7.49	0.39	-0.38*
CT1 x B11	4.54	-0.015	-0.19	1.53	0.80	- 0.18	3.52*	12.07	0.14	0.08
CT2 x B11	-1.23	-0.004	-0.17	-0.41	- 0.30	0.20	-1.11	- 6.32	0.09	0.20
CT3 x B11	2.29	0.000	1.85	1.25	0.01	0.29	-0.17	6.13	-0.76**	- 0.13
TME14 x B11	-1.74	-0.041	-0.41	-0.70	0.57	- 0.52	-1.94	- 9.39	0.34	- 0.24
CT4 x B11	3.05	0.004	-0.50	0.96	- 0.31	0.36	-1.59	- 10.27	-0.11	0.28
CT5 x B11	-0.15	0.011	0.14	0.01	0.78	- 0.09	3.07	6.29	-0.24	0.26
CT1 x Nyara	1.04	-0.043	-0.02	0.26	1.25	0.20	6.90***	13.15	-0.24	- 0.11
CT2 x Nyara	-0.31	0.021	-0.70	-0.30	- 0.65	0.07	-0.83	- 1.62	0.20	0.05
CT3 x Nyara	0.10	0.006	-1.31	-0.03	- 0.47	- 1.33	-5.65***	- 5.52	-0.14	0.42
TME14 x Nyara	3.78	-0.029	1.82	1.55	0.26	1.16	2.84	12.91	-0.38	- 0.09
CT4 x Nyara	3.73	-0.022	1.40	1.90	1.64**	0.70	1.10	7.82	-0.33	0.09
CT5 x Nyara	-0.90	0.043	-0.65	-0.42	- 0.40	0.02	-1.41	- 19.23*	0.71**	- 0.06
CT2 x CT1	-2.83	0.028	-0.05	-1.08	- 0.35	- 0.57	-1.67	- 6.97	-0.20	- 0.06
CT3 x CT1	-0.12	0.030	1.39	-0.07	0.13	- 0.57	0.04	- 6.57	-0.05	- 0.02
TME14 x CT1	-0.51	0.041	0.19	-0.01	- 1.64*	0.15	-3.60*	- 6.76	-0.12	0.13
CT4 x CT1	-0.60	-0.004	-0.10	-0.28	0.35	1.86	-0.14	- 6.32	0.26	0.02
CT5 x CT1	-0.54	-0.029	-0.16	0.00	-0.83	- 0.92	-4.99**	- 10.44	0.17	- 0.03
CT3 x CT2	0.43	0.039	2.59*	0.60	-0.04	0.37	1.91	- 3.12	-0.10	0.03
TME14 x CT2	-0.41	-0.015	-0.41	-0.20	0.66	0.43	0.84	4.42	0.16	- 0.08
CT4 x CT2	-2.85	-0.020	0.76	-0.89	-0.66	- 1.53	-0.27	0.83	0.37	0.01
CT5 x CT2	-0.33	-0.042	-2.35*	-0.54	-0.07	0.55	0.48	9.34	-0.42	0.39
TME14 x CT3	1.27	0.006	-0.84	0.23	0.27	0.65	1.51	- 7.21	0.65**	- 0.34
CT4 x CT3	-6.84*	-0.066*	-3.56**	-2.93	-1.48*	-1.07	-1.60	- 5.86	-0.14	- 0.19
CT5 x CT3	5.07	-0.004	-0.15	1.81	1.88**	2.61**	5.29**	23.50*	0.40	0.01
CT4 x TME14	-0.04	0.034	-0.28	-0.04	0.85	- 0.05	2.46	1.50	-0.21	0.07
CT5 x TME14	-0.93	0.008	1.90	-0.01	-0.06	- 0.33	0.38	2.24	-0.50*	- 0.05
CT5 x CT4	-0.68	0.062**	0.74	-0.41	-0.84	- 1.89*	-3.19	- 2.07	0.05	-0.27
NASE3 x B11	-2.50	0.044	0.21	-0.87	-0.15	0.51	0.43	- 6.00	0.16	-0.08
NASE3 x Nyara	-3.20	0.024	0.40	-1.19	-0.23	- 0.25	-0.75	- 14.99	-0.22	0.07
NASE3 x CT1	-0.95	-0.008	-1.06	-0.35	0.27	0.02	-0.06	11.85	0.03	0.00
NASE3 x CT2	7.55*	-0.007	0.32	2.83*	1.40**	0.49	0.64	3.44	-0.09	-0.55*
NASE3xCT3	-2.22	-0.011	0.03	-0.85	-0.32	- 0.95	-1.35	- 1.32	0.13	0.23
NASE3 x TME14	-1.40	-0.005	-1.97	-0.82	-0.92	- 1.49	-2.49	2.28	0.06	0.58*
NASE3 x CT4	4.24	0.012	1.54	1.69	0.43	1.62	3.23	14.36	0.11	0.00
NASE3 x CT5	-1.50	-0.050	0.53	-0.43	-0.48	0.06	0.36	- 9.62	-0.18	-0.25
$LSD_{0.05}$	5.94	0.051	2.05	2.33	1.20	1.86	3.35	15.91	0.49	0.45
SE	2.96	0.026	1.06	1.17	0.60	0.93	1.68	7.98	0.25	0.22

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); PHT = plant height (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; $LSD_{0.05}$ = least significant difference at 5%; SE= standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

5.3.6 Traits contribution to the families variability

Principal component (PC) analysis revealed that the first two PCs were most important and explained 68.1% of the total variation among the 36 families (Table 5.7). The PC1, PC2, and PC3 accounted for 53.0, 15.1 and 11.3%, respectively of the total variability. All the traits in PC1 were positively correlated, with DSRY, FSRY, SRG, SRL and SRN having a relatively higher correlation with PC1. All the highly correlated traits with PC1 were storage root related traits, and therefore, PCI was largely controlled by storage root traits. The PC2 and PC3 were highly correlated with HI and DMC, indicating that they were key traits contributing to the variability of these two PCs. Dry matter content and HI contributed to two PCs (PC2 and PC3), while DSRY, FSRY, SRG, SRL and SRN contributed to only one PC (PC1).

Table 5.7: Principal component loadings, eigenvalues and percentage variation of eight traits evaluated in 36 F_1 cassava seedling stage families at 10 months after planting at Namulonge, 2011/12

	Principal components		
Traits	**PC1**	**PC2**	**PC3**
DMC	0.149	0.529	- 0.710
DSRY	0.431	0.221	0.038
FSRY	0.424	0.150	0.170
HI	0.080	0.706	0.555
PHT	0.288	- 0.335	0.280
SRG	0.401	0.059	0.219
SRL	0.418	- 0.159	- 0.113
SRN	0.433	- 0.097	- 0.137
Eigenvalue	4.24	1.21	0.90
Percentage variation	53.0	15.1	11.3
Cumulative percentage variation	53.0	68.1	79.4

DMC = dry mass content (%); DSRY= dry storage root yield (t ha^{-1}); FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; PHT = plant height (cm); SRG = storage root girth (cm); SRL = storage root length (cm); SRN = storage root number $plant^{-1}$

5.3.7 Phenotypic correlations

Fresh storage root yield was highly significantly (P<0.001) and positively correlated with all agronomic traits studied except HI and DMC (Table 5.8). Although there were significant correlations between FSRY and CMD-S (P<0.01), and CBSD-RN (P<0.05) they were negative. Among all the traits significantly correlated with FSRY, DSRY had the highest correlation (r = 0.98). Harvest index had very significant (P<0.01), negative correlations with SRN and SRL (P<0.05). The CMD-S was negatively and very significantly (P<0.01) correlated with FSRY, DSRY and DMC. Cassava brown streak disease root necrosis was negatively and very significantly (P<0.01) correlated with SRN and significantly (P<0.05) correlated with FSRY and SRL. Storage root girth and SRL were positively and highly significantly (P<0.001) correlated with one another and also with PHT, SRN, FSRY and DSRY.

Table 5.8: Phenotypic correlation coefficients for agronomic and disease traits for 36 families evaluated at the seedling stage at Namulonge, 2011/12

Traits	FSRY	SRN	SRG	SRL	DMC	HI	PHT	DSRY	CMD-S	CBSD-RN
FSRY	1.00									
SRN	0.69***	1.00								
SRG	0.65***	0.69***	1.00							
SRL	0.61***	0.79***	0.63***	1.00						
DMC	0.15^{ns}	0.24**	0.13^{ns}	0.23**	1.00					
HI	- 0.03^{ns}	-0.25**	0.01^{ns}	-0.24**	0.11^{ns}	1.00				
PHT	0.36***	0.46***	0.42***	0.57***	-0.03	-0.13	1.00			
DSRY	0.98***	0.70***	0.64***	0.62***	0.30***	-0.02^{ns}	0.35***	1.00		
CMD-S	- 0.28**	-0.15^{ns}	-0.11^{ns}	-0.01^{ns}	-0.25**	-0.11^{ns}	0.04^{ns}	-0.19**	1.00	
CBSD-RN	- 0.08*	-0.26**	-0.22*	-0.18*	-0.01^{ns}	-0.03^{ns}	-0.01^{ns}	-0.01^{ns}	0.01^{ns}	1.00

PHT = plant height (cm); SRN = storage root number (cm) plant^{-1}; SRG = storage root girth (cm); SRL = storage root length (cm); DMC = dry mass content (%); HI = harvest index; FSRY = fresh root yield (t ha-1); DSRY = dry storage root yield (t ha^{-1}); CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; ns = correlation not significant at 0.05; * = significant at P<0.05; ** = at P<0.01 ; *** = at P<0.001.

5.4 Discussion and conclusions

The objective of this study was to generate a segregating cassava population for early FSRY, estimate the GCA of nine cassava parental lines and their SCA through their progeny for early FSRY, and determine the gene action controlling early FSRY and related traits.

A segregating cassava population comprising of 36 families from a 9 x 9 half-diallel exhibited a high degree of variation between individual genotypes and families for all the traits evaluated. Fresh storage root yield of the individual genotypes varied from 1.0 t ha^{-1} to 94.0 t ha^{-1} and SRN from 1.0 to 23.0. A complete range of scores from 1 to 5 was recorded for CMD-S and CBSD-RN. For families, the mean performance for FSRY varied from 11.7 t ha^{-1} (Nyara x B11) to 28.3 t ha^{-1} (CT4 x B11), and for SRN, mean performance varied from 3.8 (NASE3 x TME14) to 7.9 plant^{-1} (CT4 x Nyara). Mean scores for CMD-S among families varied from 1.3 (CT4 xTME14, CT5 x CT2 and CT5 x TME14) to 3.8 (Nyara x B11). The mean FSRY and SRN at the seedling evaluation stage in this study are comparable with those reported by Ojulong et al. (2010) and Mtunda (2009), although they were slightly higher. The higher values for these two traits in this study are attributed to the technique that was used for germinating botanical seeds. Botanical seeds were germinated in plastic bags and the resulting seedlings with undamaged roots were transplanted to the field. Ceballos et al. (2004) indicated that cassava seeds germinated in seedling containers and later transplanted as seedlings to the field often develop normal adventitious storage roots and that the mature plants that develop from such seedlings are similar in terms of the storage root formation to the plants derived from stem-cuttings. The positive skewness that was observed in SRN, SRL,

FSRY, DSRY, CBSD-RN and CMD-S indicated that these traits could be improved by conventional breeding through hybridisation.

The MS for families were significant for all traits, indicating significant differences among the 36 families for all traits. In terms of GCA effects and associated transmission of desirable additive gene action from parents to progeny, CT4 had the highest positive and significant GCA effects for FSRY, DSRY, SRN and SRG, and lowest negative GCA effects for CMD-S and CBSD-RN, indicating that it was the best general combiner and best parent to utilise for the improvement of these traits. Since lower disease scores indicate higher disease resistance, negative GCA effects are desirable for disease resistance breeding (Kulembeka et al., 2012; Parkes et al., 2013). CT4 was the best parent to utilise in the improvement of FSRY and SRN because of its high positive and significant GCA effects for these traits. CT2 was the best parent for developing progeny with improved HI; TME14 for improved DMC; CT5 for increased height; and NASE3 and CT3 for reduced height. The GCA effect is considered as the intrinsic genetic value of a parent for a trait which is due to additive gene action and it is fixable (Simmonds, 1979).

The performance of a single cross progeny could be adequately predicted on the basis of GCA if the SCA mean squares are not significant and the best performing progeny may be produced by crossing the two parents having the highest GCA effects (Griffing, 1956). Analysis of SCA showed that families developed from contrasting parents in terms of GCA effects for particular traits, had correspondingly high and significant SCA effects, suggesting that specific combinations of alleles may be important in controlling traits or that there could be some inter-locus gene interaction. By way of example, for FSRY, crossing NASE3, which had a negative GCA effect (-1.98), with CT2 that had a positive GCA effect (+2.17), resulted in family NASE3 x CT2 expressing a significant and high positive SCA effect (+7.55) for FSRY. For CMD-S, crossing CT3 that had a negative GCA effect (-0.158) with B11 that had the highest positive GCA effect (+0.819), resulted in family CT3 x B11 expressing a very significant and the lowest negative SCA effect (-0.76) for CMD-S.

In addition, in relation to GCA and SCA effects, all families that were identified as being best in mean performance for particular traits involved a parent with correspondingly high GCA effects for the respective traits in their families. By way of example, the first three best performing families for mean FSRY, namely: CT4 x B11 (28.3 t ha^{-1}), CT4 x Nyara (28.2 t ha^{-1}) and CT4 x CT1 (27.7 t ha^{-1}) all had CT4 as the common parent which had the highest GCA

effect for this trait. Similarly, for CMD-S, the first three best families with low mean score of 1.3, namely CT4 x CT3, CT5 x CT2 and CT5 x TME14 all had parents with the lowest negative GCA effects for CMD-S. This indicates the importance of conducting combining ability analysis in selecting the best parents for a successful breeding programme as previously indicated by Ceballos et al. (2004) and Zacarias and Labuschagne (2010).

The percentage of the families SS accounted for by families GCA and SCA provides an estimation of the relative importance of additive and non-additive gene effects in the expression of traits (Calle et al., 2005; Kulembeka et al., 2012; Were et al., 2012). In this study, GCA effects accounted for over 50.0% of the variability expressed by families for FSRY, HI, DSRY, PHT, SRG, SRL, CBSD-RN and CMD-S indicative of the predominance of additive gene action in the expression of these eight traits. Specific combining ability effects accounted for over 50.0% of the families SS for only DMC and SRN, suggesting predominance of non-additive gene action in the expression of these two traits. Therefore, additive effects played a more fundamental role in controlling most of the traits than non-additive effects. The relative importance of GCA effects for FSRY observed in this study was in agreement with Chikoti (2011), Zacarias and Labuschagne (2010) (first season results), and Kulembeka et al. (2012), but in disagreement with Jaramillo et al. (2005), Were et al. (2012) and Parkes et al. (2013). The relative importance of GCA effects for CBSD resistance was in agreement with Munga (2008), Mtunda (2009) and Kulembeka et al. (2012). For CMD resistance, the relative importance of GCA effects was in agreement with Lokko et al. (2006) and Parkes et al. (2013).

The assessment of the contribution of the traits to the overall variability of the 36 families using PCA indicated that the first two PCs explained 68.1% of the total variation and were therefore, most important. The PC1 accounted for 53.0% of the total variability and was correlated with storage root related traits: FSRY, DSRY, SRG, SRL and SRN, indicating that they were key contributing traits to the total variation. The PC2 and PC3 accounted for 15.1% and 11.3% of the total variation, respectively with HI and DMC the next set of traits contributing to the total variability. In agreement with these results, Ojulong et al. (2010) indicated that FSRY and SRN are key selection criteria usually used by breeders at the seedling evaluation stage. The main contributing traits to PC2 and PC3, HI and DMC are also usually used as selection criteria in seedling and advanced trial selections. Kawano et al. (1998) indicated that HI and DMC are usually used during the early stages of selection programmes because of their relatively high stability. Nevertheless, selection based on the

key traits contributing to PC1, PC2 and PC3 of this study would save a lot of time and resources in a breeding programme.

Phenotypic correlations indicated that FSRY was highly correlated with all the traits studied except HI and DMC. Its correlation with CMD-S and CBSD-RN was negative. The negative correlation between FSRY and CMD-S is in agreement with that reported by Aina et al. (2009) and Parkes et al. (2013). Similarly, negative correlation between FSRY and CBSD-RN is in agreement with that reported by Munga (2008). Hahn et al. (1980) also indicated that diseases and pests generally reduce FSRY in cassava. The low correlation (r = -0.03) between FSRY and HI is in agreement with that reported by Kawano et al. (1998) at the early stages of selection, compared to the high correlation they observed at the advanced stages of selection. Non-significant correlation between FSRY and DMC suggests that either of the traits can be selected independently without affecting the other. This is important since the selection for FSRY at the seedling stage cannot affect DMC results at a later stage of selection. Furthermore, considering the low and non-significant correlation between FSRY and DMC and the fact that the genetic control of these two traits is fixed through vegetative propagation at the early stages of a cassava breeding programme, it is possible to select simultaneously for yield and DMC at the seedling stage.

In conclusion, there was a high degree of variation between individual genotypes and families for all traits studied, indicating potential for selection and improvement. The GCA effects accounted for over 50.0% of variability expressed by families in eight of the 10 traits evaluated while the SCA effects accounted for over 50.0% of the variability in only two of the 10 traits (DMC and SRN), indicating that the additive gene effects played a more important role in controlling the expression of most traits. Among the parents evaluated, CT4 was the best general combiner for FSRY, SRN, DSRY, SRG, SRL and resistance to CMD and CBSD; CT2 for HI; CT5 for PHT; and TME14 for DMC. Most of the families that had CT4 as one of the parents, had exceptionally good performance for early FSRY and most of the other traits assessed. The findings of this study clearly demonstrate that it is possible to conduct combining ability analysis for storage root related traits at the seedling stage of cassava breeding. Combining ability analysis for storage root related traits at this early stage was possible because of the high SRN produced by the seedling plants ranging from 1 - 23 storage roots plant^{-1}. This high SRN was attributed to the method that was used in raising seedlings (using seedling containers) combined with good growing conditions in Uganda. Combining ability analysis at the seedling stage cannot be undertaken in areas where

storage root development by seedlings is poor and also in fields where variability is high. Results of this study also demonstrated that it is possible to simultaneously select for yield and quality traits such as DMC at the seedling stage using simple statistical methods such as phenotypic correlation and principal components analysis. This study could be utilised as a model for reducing the potential loss of useful genetic data and breeding material and subsequently improve the effectiveness and efficiency of the standard cassava breeding cycle, which takes nearly 8 – 10 years.

References

Alves, A.A.C. 2002. Cassava botany and physiology. In: R.J. Hillocks et al. (eds.), Cassava: biology, production and utilization. CABI, Wallingford, UK. p. 67-89.

Banito, A.J., V. Verdier, K.E. Kpemoua, and K. Wydra. 2007. Assessment of major cassava diseases in Togo in relation to agronomic and environmental characteristics in a systems approach. African Journal of Agricultural Research 2:418-428.

Bhullar, G.S., K.S. Gill, and A.S. Khehra.1979. Combining ability analysis in diallel and fractional diallel crosses in linseed. Theories of Applied Genetics 55:77-80.

Brown, J., and P. Caligari. 2009. An introduction to plant breeding, Second edition. Blackwell publishing, Oxford, UK.

Calle, F., J.C. Perez, W. Gait´an, N. Morante, H. Ceballos, G. Llano, and E. Alvarez. 2005. Diallel inheritance of relevant traits in cassava (*Manihot esculenta* Crantz) adapted to acid-soil savannas. Euphytica 144:177-186.

Ceballos, H., C.A. Iglesias, J.C. Pérez, and A.G.O. Dixon. 2004. Cassava breeding: Opportunities and challenges. Plant Molecular Biology 56:503-516.

Ceballos, H., P. Kulakow, and C. Hershey. 2012. Cassava breeding: Current status, bottlenecks and the potential of biotechnology tools. Tropical Plant Biology 5:73-87.

Chikoti, P. C. 2011. Development of cassava (*Manihot esculenta* Crantz) cultivars for resistance to cassava mosaic disease in Zambia. PhD thesis, University of KwaZulu-Natal, South Africa.

Eberhart, S.A., and C.O. Gardner. 1966. A general model for genetic effects. Biometrics 2:864-881.

Falconer D.S, and T.F.C. Mackay. 1996. Introduction to quantitative genetics. Fourth edition. Prentice Hall. Peterson Education Limited, England.

Food and Agriculture Organisation (FAO). 2012. FAO: Crops and products domain. http://faostat.fao.org. (Accessed 19, August 2013).

Griffing, B.1956. Concept of general and specific combining ability in relation to diallel crossing system. Australian Journal of Biological Sciences 9:463-93.

Grüneberg, W., R. Mwanga, M. Andrade, and J. Espinoza. 2009. Selection methods Part 5: Breeding clonally propagated crops. In: Ceccarelli, et al. (eds.), Plant breeding and farmer participation. Food and Agriculture Organisation, Rome. p. 275-322.

Hahn, S.K., A.K. Howland, and E.R. Terry. 1980. Correlated resistance of cassava to mosaic and bacterial blight diseases. Euphytica 29:305-311.

Hillocks, R.J., M. Raya, and M.J. Thresh. 1996. The association between root necrosis and aboveground symptoms of brown streak virus infection in cassava in southern Tanzania. International Journal of Pest Management 42:285-289.

Iglesias, C.A., C. Hershey, F. Calle, and A. Bolanos. 1994: Propagating cassava (*Manihot esculenta* Crantz) by sexual seed. Experimental Agriculture 30:283-290.

Jaramillo, G., N. Morante, J.C. Perez, F. Calle, H. Ceballos, B. Arias, and A.C. Bellotti. 2005. Diallel analysis in cassava adapted to the mid-altitude valleys environment. Crop Science 45:1058 -1063.

Jollife, I.T. 2002. Principal component analysis. Second edition. Springer-Verlag New York, Inc. USA.

Kawano, K. 1980. Cassava. In: W.R. Fehr and H.H. Hadley (eds.), Hybridisation of crop plants. America Society of Agronomy and Crop Science Society of America, Madison, Wisc, USA. p. 225-233.

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

Kawano, K., K. Narintaraporn, P. Narintaraporn, S. Sarakarn, A. Limsila, J. Limsila, D. Suparhan, V. Sarawat, and W. Watananonta. 1998. Yield improvement in a multistage breeding program for cassava. Crop Science, 38:325-332.

Kulembeka, H.P., M. Ferguson, L. Herselman, E. Kanju, G. Mkamilo, E. Masumba, M. Fregene and M.T. Labuschagne. 2012. Diallel analysis of field resistance to brown streak disease in cassava (*Manihot esculenta* Crantz) landraces from Tanzania. Euphytica 187:277–288.

Lokko, Y., A.G.O. Dixon, S.K. Offei, and E.Y. Danquah. 2006. Combining ability analysis of resistance to mosaic virus disease in cassava. African Crop Science Journal 14:221- 230.

Mtunda, K.J. 2009. Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.

Munga, T.L. 2008. Breeding for cassava brown streak resistance in coastal Kenya. PhD Thesis, University of KwaZulu-Natal, South Africa.

Nassar, N. M.A. 2000. Wild cassava, *Manihot* spp.: Biology and potentialities for genetic improvement. Genetics and Molecular Biology 23:201-212.

Ojulong, H.F., M.T. Labuschagne, L. Herselman, and M. Fregene. 2010. Yield traits as selection indices in seedling populations of cassava. Crop Breeding and Applied Biotechnology 10:191-196.

Otim-Nape, G.W., A. Bua, and Y. Baguma.1994. Accelerating the transfer of improved production technologies: Controlling African cassava mosaic virus disease epidemics in Uganda. African Crop Science Journal 2: 479-495.

Owolade, O.F, A.G.O. Dixon, and A.Y.A. Adeoti. 2006. Diallel analysis of cassava genotypes to anthracnose disease. World Journal of Agricultural Science 2:98-104.

Parkes, E. Y., M. Fregene, A. Dixon, B. Boakye-Peprah, and M.T. Labuschagne. 2013. Combining ability of cassava genotypes for cassava mosaic disease and cassava bacterial blight, yield and its related components in two ecological zones in Ghana. Euphytica 194:13-24.

Payne, R.W., S.A. Harding, D.A. Murray, D.M. Soutar, D.B. Baird, A.I. Glaser, S.J. Welham, A.R. Gilmour, R. Thompson, and R. Webster. 2011. The guide to genstat release 14, part 2: Statistics. VSN International, Hemel Hempstead, UK.

Perez, J.C., H. Ceballos, F. Calle, N. Morante, W. Gait´an, G. Llano, and E. Alvarez. 2005. Within family genetic variation and epistasis in cassava (*Manihot esculenta* Crantz) adapted to the acid-soils environment. Euphytica 145:77-85.

Simmonds, N. W. 1979. Principles of crop improvement. First edition. Longman Group Ltd, London. UK.

Wang, C., Z. Lentini, E. Tabares, M. Quintero, H. Ceballos, B. Dedicova, C. Sautter, C. Olaya, and Z. Peng. 2011. Microsporogenesis and pollen formation in cassava (*Manihot esculenta* Crantz). Biologia Plantarum 55:469-478.

Were, W.V., P. Shanahan, R. Melis, and O.O. Omari. 2012. Gene action controlling farmer preferred traits in cassava varieties adapted to mid-altitude tropical climatic conditions of western Kenya. Field Crops Research 133:113-118.

Zacarias, A.M., and M.T. Labuschagne. 2010. Diallel analysis of cassava brown streak disease, yield and yield related characteristics in Mozambique. Euphytica 176:309-320.

Zhang, Y., M.S. Kang, and K. R. Lamkey. 2005. Diallel-SAS05: A comparative programme for Griffing's and Gardner-Eberhart analyses. Agronomy Journal 97:1097-1106.

CHAPTER 6

Diallel analysis of early storage root yield and related traits in cassava at the F_1 clonal evaluation stage

Abstract

Cassava is a principal food crop in the crop production systems and food cultures of most people in Uganda, yet relatively little progress has been made in determining the combining ability and gene action for yield and other key traits in the Ugandan germplasm. Such information is fundamental in the selection of parents and breeding strategies for an effective breeding programme. This study was therefore aimed at estimating the general combining ability (GCA) of the parents and their specific combining ability (SCA) for earliness and other key traits, as well as determining the gene action controlling the selected traits. Thirty-six full-sib families generated from a 9 x 9 half-diallel mating design of nine cassava genotypes selected from the National Cassava Breeding Programme and farmers' fields, were evaluated in two distinct environments for eight months using a 3 x 12 row by column design with three replications. Family, GCA and SCA effects and their interactions with environments were significant for most traits evaluated, indicating, respectively significant differences in the mean performances of the families, additive and non-additive gene action in the expression of the traits, and the non-additive influence of the environments. Significance of the interaction of family, GCA and SCA effects with environments suggests that selection of superior genotypes and parents should be based on multi-location evaluation. The relative importance of additive over non-additive gene action varied between traits indicating the need for specific breeding strategies for each of these traits. Among the parents, CT5 and CT1 were the best general combiners for early fresh storage root yield and most of the other traits. The best four families with high SCA effects for early fresh storage root yield in the order of importance were: CT1 x Nyara, CT1 x B11; CT5 x TME14 and NASE3 x B11, while the best four families for mean early fresh storage root yield were: CT3 x Nyara, CT1 x Nyara, CT5 x CT4 and TME14 x CT2 . Cassava parental lines and families with good combining ability for early FSRY and farmer preferred traits will be utilised in the development of early bulking cassava with farmer preferred traits in Uganda.

6.1 Introduction

Cassava is the second most important food crop of Uganda, providing food and income for the majority of smallholder farmers (MAAIF, 2007). Among the key traits farmers look for when selecting cassava cultivars are high storage root yield, earliness, resistance to pests and diseases, and dry mass content (Tumuhimbise et al., 2012). Earliness, in particular, is currently a key farmer preferred trait due to its perceived importance in providing quick food and income to farmers, as well as in escaping late season droughts, pests and diseases (Kamau, 2006; Suja et al., 2009; Tumuhimbise et al., 2012). The National Cassava Breeding Programme (NCBP) has responded to farmers' preferences by developing and/or introducing improved cultivars from the International Institute of Tropical Agriculture (IITA) and International Centre for Tropical Agriculture (CIAT) (Abele et al., 2007; Kawuki et al., 2011). Nonetheless, some farmers have continued to grow landraces that are important as potential genetic resources for cassava breeding programmes. However, little progress has been made in determining the combining ability and inheritance of agronomic and disease traits of the genotypes grown in Uganda and/or used in the NCBP. As a result, there is insufficient information on the combining ability and inheritance of yield and other important traits in cassava in Uganda, a situation that frustrates efforts to improve cassava through breeding.

Traits such as yield are quantitatively inherited and the knowledge about their mode of inheritance helps breeders to employ suitable breeding strategies for their improvement (Calle et al., 2005; Kiani et al., 2007). A number of mating designs including: polycross (Amini et al., 2011); North Carolina (Comstock and Robinson, 1948); line x tester (Basbag et al., 2007) and diallel (Griffing, 1956) have been developed to serve this purpose. Of these designs, the diallel mating design has been widely used by cassava breeders to generate full-sib progeny for genetic studies (Calle et al., 2005; Perez et al., 2005; Cach et al., 2006; Owolade et al., 2009; Mtunda, 2009; Zacarias and Labuschagne, 2010; Kulembeka et al., 2012).

Diallel analysis provides information on heterosis and the effects due to reciprocal, maternal, general combing ability (GCA) and the specific combining ability (SCA) of parents in crosses (Glover et al., 2005). Several analysis methods have been devised for the diallel mating design (Jinks and Hayman, 1953; Hayman, 1954; Griffing, 1956; Gardner and Eberhart, 1966).

Knowledge of the gene action controlling plant traits is critical in deciding on the type of breeding methods that would successfully improve the performance of the traits of interest (Dudley and Moll, 1969). Griffing's (1956) diallel analysis method has also been widely used to estimate the GCA of parents and SCA of families in a breeding programme. Estimating GCA of parents helps in developing superior genotypes, while estimating SCA effects, helps in determining the performance of hybrids (Falconer and Mackay, 1996; Rauf et al., 2005; Méndez-Natera et al., 2012). Therefore, an analysis based on a large number of progenies from diverse parents is important in formulating an efficient strategy for varietal improvement.

The objectives of this study were to:

1. Determine the combining ability of nine cassava parental genotypes and heterosis of 36 half-diallel families for early storage root yield and related traits; and
2. Develop and select cassava genotypes with early storage root yield combined with resistance to cassava mosaic disease and cassava brown streak disease and high dry mass content.

6.2 Materials and methods

6.2.1 Experimental locations

Experiments were conducted at Namulonge and Bulindi Agricultural Research Institutes in Uganda during 2012/13. Namulonge is located at 32°36'E and 0°31'N, at 1134 m above sea level (masl) and has sandy clay loam soils. During the experimental period, it recorded a mean annual rainfall of 1206 mm and temperatures ranging from 15.1 to 28.5^{o}C. Bulindi is located at 31°28'E and 01°28'N, at 1230 masl, and has sandy loam soils. During the experimental period, it recorded mean rainfall of 760 mm and temperatures ranging from 16.9 to 29.8°C. The two sites experience a bimodal rainfall pattern, with two distinct rainy seasons and dry seasons of nearly equal length. Peak rainfall occurs between March to May and September to November.

6.2.2 Plant germplasm

Nine parents (described in Chapter 5, Table 5.1,) were crossed in a 9 x 9 half-diallel mating design, generating 36 full-sib families. The resulting seedlings were planted in a seedling evaluation trial (SET) that was laid out as a 6 x 6 triple lattice design with three replications. After harvesting the SET, 30 genotypes per family that produced at least 12 cuttings were planted in a clonal evaluation trial (CET) at Namulonge and Bulindi. A total of 1080 genotypes were selected from the SET and were advanced to the CET.

6.2.3 Experimental design

The CETs comprising of 1080 F_1 genotypes were planted at Namulonge and Bulindi in a 3 x 12 row by column design with three replications. Two 25 cm long cuttings of each selected genotype were planted contiguously within the rows of the respective family plots of each replication. Parental genotypes were planted alongside the CET in a randomised complete block design with three replications. The trials were planted in the first week of September 2012 at a spacing of 1.0 x 1.0 m between and within rows, providing a population density of 10 000 plants ha^{-1}. The trials were conducted without supplemental irrigation and weeded regularly.

6.2.4 Data collection

Based on results described previously (Chapter 3, section 3.3.1), where the majority of the genotypes attained a relatively high early fresh storage root yield at nine months after planting (MAP), and also on harvest dates reported in the literature for early yielding cassava genotypes (Nweke et al., 1994; Amenorpe et al., 2007; Kamau, 2011; Okogbenin et al., 2013), the trial was harvested 8 MAP. However, the plants were scored for CMD severity (CMD-S) at 6 MAP using a scale of 1-5, where: 1 = no symptoms; and 5 = very severe mosaic symptoms (Banito et al., 2007). At harvest, plants were individually measured for height (PHT) (cm) and then uprooted. The storage roots of two plants per genotype in a plot were counted and weighed to obtain storage root number (SRN) and mass (SRM) (kg), respectively. Shoot mass (STM) (kg $plant^{-1}$) of each genotype was obtained by weighing the total shoot (kg). Fresh storage root yield (FSRY) (t ha^{-1}) was estimated from SRM (kg $plant^{-1}$) as:

$$FSRY = SRM \times \frac{10\ 000}{1000}$$

Storage root length (SRL) was measured as the length (cm) from end to end of a storage root, and storage root girth (SRG) as the circumference (cm) at the widest point of the mid-section of a storage root. Harvest index (HI) was calculated as the ratio SRM to total plant biomass (TBM) on a fresh mass basis (kg) as:

$$HI = \frac{SRM}{TBM}$$

Percentage dry mass content (DMC) was determined by selecting at least two storage roots from a bulk of storage roots per genotype, which were washed, peeled and sliced using a knife. The sliced samples were weighed to obtain 0.1 kg before being dried for 48 h in a

forced-drought oven at 80°C. The dried samples were weighed to obtain the dry mass and DMC% was calculated as:

$$\text{DMC } (\%) = \frac{\text{DRM}}{\text{FRM}} \times 100$$

Where: DRM = dry storage root mass (kg); FRM = fresh storage root mass (kg).

Dry storage root yield (DSRY) was computed as the product of DMC and FSRY as:

$$\text{DSRY } (\text{t ha}^{-1}) = \frac{\text{DMC } \%}{100} \times \text{FSRY}$$

Because the main damage caused by CBSD is to the storage roots, the storage root necrosis due to CBSD (CBSD-RN) was scored on a scale of 1 to 5 where: 1 = no visible necrosis, and 5 = severe necrosis (Hillocks et al., 1996).

6.2.5 Data analysis

The data collected for each site were first analysed individually and then the error variances for the environments tested for homogeneity using Hartley's Fmax test (Hartley, 1950). As the differences were not significant, an unweighted combined analysis of variance of the data for the two locations was conducted. Data for the respective nine parents and 36 families were independently averaged for statistical analysis. The analysis of variance (ANOVA) for the traits were done using Genstat 14th edition (Payne et al., 2011). The relative contributions of the various traits to the total variation between families based on family means across locations were determined using principal components (PCA) according to Jollife's (2002) methodology in Genstat (Payne et al., 2011). Pearson's phenotypic correlations between traits based on family means were also performed using Genstat 14 (Payne et al., 2011). The diallel analysis was conducted using the SAS-05 diallel programme (Zhang et al., 2005) in the SAS 8th edition. Griffing's (1956) diallel method 4, model 1 for a fixed model was fitted to estimate the GCA and SCA:

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

Where:

Y_{ij} = observed value of the cross between parent i and j;

μ = overall mean; g_i = GCA of the parent i;

g_j = GCA of the parent j;

s_{ij} = SCA of the cross between parents i and j;

b_k = effect of the kth block; and

e_{ijkl} = experimental error.

The relative importance of GCA and SCA effects for each trait under study was determined from their percentages of the family sum of squares (SS) due to GCA and SCA (Calle et al., 2005; Kulembeka et al., 2012; Were et al., 2012).

Mid-parent heterosis (MPH) and better-parent heterosis (BPH) of the F_1 progeny were determined for some traits, according to Falconer and Mackay (1996) as:

$$MPH\ (\%) = \frac{F_1 - MP}{MP} \times 100$$

$$BPH\ (\%) = \frac{F_1 - BP}{BP} \times 100$$

Where:

F_1 = F_1 hybrid performance;

$MP = \frac{P_1 + P_2}{2}$ with P_1 and P_2 the performances of the parents; and

BP = mean of the better parent in the cross.

To identify and select high yielding, early bulking F_1 cassava genotypes with resistance to CBSD and CMD and combining high DMC, a four-step selection process was performed on the data averaged across the two sites as follows:

1: Four hundred and twenty F_1 genotypes with yields greater than or equal to 25 t ha^{-1}, were identified from the population of 1080 F_1 progeny to constitute the first subset.

2: F_1 genotypes with CBSD-RN score of one were selected from the first subset to constitute the second subset.

3: F_1 genotypes with CMD-S score of one were selected from the second subset to constitute the third subset.

4: F_1 genotypes with DMC greater than 38.5% were selected to constitute the final set of the top 50 genotypes for advancement.

6.3 Results

6.3.1 Performance of individual F_1 genotypes

Ten traits were evaluated in this study, eight of which were positively skewed and two negatively skewed (Table 6.1). The traits had wide ranges, for example: FSRY ranged from 0.0 - 90.0 t ha^{-1} with a mean of 12.2 t ha^{-1} while DSRY ranged from 0.0 - 33.6 t ha^{-1} with a mean of 4.3 t ha^{-1}. There was a complete range of scores from 1 - 5 recorded for CMD-S and CBSD-RN with means of 1.7 and 2.7, respectively. Harvest index ranged from as low as 0.1 to as high as 0.9 with a mean of 0.3. Plant height varied from 102.5 - 330.0 cm with a mean of 151.8 cm. Storage root number $plant^{-1}$ ranged from 0.0 - 28.0. Storage root girth and length ranged from 5.0 - 92.0 cm and 4.5 - 34.2 cm, respectively.

Figure 6.1: Cassava F_1 clonal trial in Namulonge, 2012/13. **A**: Some of the two-plant plots free of cassava mosaic and brown streak disease symptoms; **B**: a plot with some genotypes showing severe cassava mosaic symptoms; **C**: a cassava genotype that scored 5.0 for cassava brown streak disease root necrosis at harvest; **D**: a cassava genotype that scored 1.0 for cassava brown streak disease root necrosis at harvest; **E**: genotype showing more than eight big storage roots at harvest; **F**: a genotype with long stems and fully bulked storage roots at harvest.

Table 6.1: Summary statistics of 10 traits measured in clonal stage F_1 cassava genotypes at eight months after planting across two sites in Uganda, 2012/13

	Statistics					
TRAIT	**Minimum**	**Maximum**	**Mean**	**SEM**	**SD**	**Skew**
FSRY	0.0	90.0	12.2	0.23	11.9	1.79
HI	0.10	0.9	0.3	0.03	0.14	0.35
DMC	21.5	54.7	34.8	0.10	5.29	- 0.70
DSRY	0.0	33.6	4.3	0.09	4.89	1.86
SRN	0.0	28.0	6.0	0.07	3.86	1.48
SRG	4.5	34.2	12.5	0.07	3.85	1.68
SRL	5.0	92.0	23.5	0.15	8.02	0.88
PHT	102.5	330.0	151.8	0.93	51.43	- 0.13
CMD-S	1.0	5.0	1.7	0.02	1.23	0.25
CBSD-RN	1.0	5.0	2.7	0.03	1.52	0.23

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content; DSRY = dry storage root yield (t ha^{-1}); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); PHT = plant height (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; SEM = standard error of mean; SD = standard deviation.

6.3.2 Diallel analysis of variance for traits

In the ANOVA, the environment means squares (MS) were: highly significant (P<0.001) for FSRY, DSRY, DMC, SRG, and CMD-S; very significant (P<0.01) for PHT and SRN; and significant (P<0.05) for CBSD-RN (Table 6.2). Families MS were: highly significant (P<0.001) for HI, DMC, SRG, SRL, CBSD-RN and CMD-S; very significant (P<0.01) for PHT, FSRY and SRN; and significant (P<0.05) for DSRY. Families SS were partitioned into that due to parents (GCA effects) and the interaction between parents (SCA effects). General combining ability (GCA) MS were: highly significant (P<0.001) for HI, FSRY, DMC, SRN, SRG, SRL, CBSD-RN and CMD-S; very significant (P<0.01) for PHT; and significant (P<0.05) for DSRY. Specific combining ability (SCA) MS were: highly significant (P<0.001) for DMC, CBSD-RN and CMD-S; very significant (P<0.01) for HI and SRG; and significant (P<0.05) for FSRY and SRL. Environment x family MS were highly significant (P<0.001) for DMC and very significant (P<0.01) for PHT. Environment x GCA MS were highly significant (P<0.001) for FSRY and very significant (P<0.01) for DSRY and DMC, while the environment x SCA MS were very significant (P<0.01) for DMC and significant (P<0.05) for CMD-S.

The proportion of the families SS due to GCA and SCA effects expressed as a percentage provides an indication of the relative importance of additive and non-additive gene effects in the expression of the trait evaluated. The GCA effects accounted for over 50.0% of the variability expressed by the families in DMC, SRG, CBSD-RN and CMD-S, while SCA effects accounted for over 50% of the variability in the families for the rest of the traits evaluated (Table 6.2).

Table 6.2: Analysis of variance of a 9 x 9 half-diallel for 10 traits of 36 cassava F_1 clonal stage families evaluated at eight months after planting across two sites in Uganda, 2012/13

		Mean squares				
Sources of variation	**DF**	**FSRY**	**HI**	**DMC**	**DSRY**	**SRN**
Environment (E)	1	1361.7***	0.008ns	239.78***	212.83***	22.43**
Families	35	27.8**	0.007***	13.62***	3.24*	3.54**
GCA	8	51.0***	0.015***	32.25***	4.58*	7.51***
SCA	27	21.0*	0.005**	8.10***	2.84	2.37
E x Families	35	20.5	0.003	8.74***	2.80	2.38
E x GCA	8	3.5***	0.003	10.93**	6.83**	2.67
E x SCA	27	0.8	0.003	8.10**	1.61	2.30
% families SS due to GCA		41.9	49.5	54.1	32.3	48.4
% families SS due to SCA		58.1	50.5	45.9	67.7	51.6
Error	140	14.2	0.002	3.16	1.87	1.83
CV (%)		31.0	14.200	5.10	32.10	22.8

		Mean squares				
Sources of variation	**DF**	**SRG**	**SRL**	**CBSD-RN**	**CMD-S**	**PHT**
Environment (E)	1	316.00***	6.31ns	1.14*	2.96***	8581.9**
Families	35	4.58***	23.81***	1.92***	0.71***	2371.0**
GCA	8	10.30***	48.80***	5.06***	1.62***	4455.4**
SCA	27	2.88**	16.40*	0.98***	0.43***	1753.4
E x Families	35	2.15	10.50	0.16	0.15	2371.0**
E x GCA	8	2.84	12.71	0.13	0.11	1357.4
E x SCA	27	1.94	9.84	0.16	0.17*	785.9
% families SS due to GCA		51.5	46.8	60.3	52.3	42.3
% families SS due to SCA		48.5	53.2	39.7	47.7	57.7
Error	140	1.43	9.74	0.27	0.10	1220.9
CV (%)		9.50	13.31	19.10	19.20	23.0

DF = degrees of freedom; PHT = plant height (cm); HI = harvest index; FSRY = fresh storage root yield (t ha^{-1}); DSRY = dry storage root yield (t ha^{-1}); DMC = dry mass content (%); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; GCA = general combining ability; SCA = specific combining ability; SS = sum of squares; CV = coefficient of variation; * = P<0.05; ** = P<0.01; *** = P<0.001.

6.3.3 Mean performance and general combining ability effects

The mean performance and GCA effects of the parents for the various traits averaged across the two sites were considered for discussion. All five parents of CIAT ancestry had positive GCA effects for FSRY, which were significant (P<0.05) for CT1 and CT5 (Table 6.3). In addition, CT5 had positive and highly significant (P<0.001) GCA effects for HI and SRN, very significant (P<0.01) GCA effects for PHT and SRL and a negative, very significant (P<0.01) GCA effect for CMD-S. It, however, recorded an undesirable highly significant (P<0.001), negative GCA effect for DMC as well as a positive, but non-significant GCA effect for CBSD-RN. CT1 also had positive and significant (P<0.05) GCA effects for DSRY and SRL, as well as a desirable negative, significant (P<0.05) GCA effect for CBSD-RN. With the exception of Nyara, B11 and NASE3, the other parents had desirable negative GCA effects for CMD-S, which was expected given the low mean scores for CMD-S of these parents. TME14 recorded the lowest negative and highly significant (P<0.001) GCA effect of -0.17 for CMD-S followed by CT2 with a very significant (P<0.01) GCA effect of -0.15. Similarly,

negative and highly significant (P<0.001) GCA effects for CBSD-RN were recorded in CT4 and NASE3; significant (P<0.05) for CT1 and non-significant for Nyara, with CT4 recording the lowest negative GCA effect of -0.58 for the trait. B11 had the best positive, highly significant (P<0.001) GCA effect for DMC and CT5 the best positive, very significant (P<0.01) GCA effect for PHT. CT2 had the best mean performance and very significant (P<0.01) GCA effect for SRG. Overall, CT5 was the best general combiner for most of the traits evaluated.

Table 6.3: Means and general combining ability effects for 12 traits of nine cassava parents used in 9 x 9 half-diallel analysis of 36 F_1 clonal stage families evaluated eight months after planting averaged across two sites in Uganda, 2012/13

	FSRY		HI		DMC		DSRY		PHT	
Parents	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**
B11	2.5	- 0.58	0.32	0.011	40.5	1.25***	1.0	- 0.05	154.7	14.37***
CT1	15.9	1.60*	0.43	0.001	39.3	0.27	6.2	0.60*	163.4	- 0.25
CT2	13.8	0.06	0.38	0.015*	31.3	- 0.78*	4.3	- 0.07	141.6	- 8.61
CT3	12.7	0.13	0.42	- 0.010	41.4	0.27	5.4	0.08	148.0	- 9.84
CT4	10.1	0.05	0.24	- 0.036***	33.7	- 0.51	3.7	- 0.01	125.6	3.34
CT5	9.0	1.67*	0.32	0.030***	34.6	- 1.53***	3.2	0.37	193.6	16.40**
NASE3	3.1	- 0.95	0.22	- 0.011	35.4	0.03	1.1	- 0.31	112.3	- 9.99
Nyara	2.9	- 0.24	0.28	0.005	34.7	- 0.09	1.0	- 0.10	108.7	3.48
TME14	9.1	- 1.74**	0.35	- 0.007	39.7	1.09**	3.7	- 0.50	153.4	- 8.89
MEAN	8.8		0.33		36.7		3.3		144.6	
$LSD_{0.05}$	4.4	2.36	0.10	0.017	2.2	1.11	1.7	0.88	26.7	12.36
SE	2.2	0.73	0.01	0.008	1.7	0.34	0.8	0.27	44.0	5.06

	SRN		SRG		SRL		CBSD-RN		CMD-S	
Parents	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**	**Mean**	**GCA**
B11	1.5	- 0.32	10.7	0.31	18.0	0.60	2.5	0.06	3.8	0.07
CT1	5.0	- 0.01	13.8	0.20	44.7	0.99*	2.7	- 0.18*	1.0	- 0.03
CT2	4.9	- 0.33	15.5	0.70**	30.7	- 1.20*	4.7	0.65***	1.0	- 0.15**
CT3	3.6	- 0.17	14.0	0.04	29.9	0.64	4.0	0.21**	1.0	- 0.04
CT4	3.6	0.59**	12.1	- 0.25	27.7	0.53	2.5	- 0.58***	1.0	- 0.14**
CT5	4.4	0.79***	13.0	0.48	31.9	1.31**	3.8	0.11	1.0	- 0.13**
NASE3	3.0	0.08	10.9	- 0.90**	25.6	- 1.77***	3.2	- 0.28***	1.0	0.43***
Nyara	1.6	- 0.35	11.3	- 0.10	22.2	- 0.97*	1.8	- 0.12	3.3	0.16**
TME14	4.1	- 0.29	13.0	- 0.46	35.0	- 0.13	2.2	0.13	1.0	- 0.17***
MEAN	3.5		12.7		29.5		3.0		1.6	
SE	1.0	0.22	2.4	0.27	3.7	0.47	0.4	0.07	0.2	0.05
$LSD_{0.05}$	1.9	0.55	2.3	0.57	6.7	1.20	0.8	0.12	0.2	0.11

FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); PHT = plant height (cm); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; GCA = general combining ability; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

6.3.4 Mean performance and specific combining ability

The mean performance and SCA effects of the 36 F_1 families for the various traits averaged across the two sites were considered for discussion. The best mean performance for FSRY (17.0 t ha^{-1}) and DSRY (6.2 t ha^{-1}) were recorded by family CT3 x Nyara, whereas the best significant (P<0.05), positive SCA effects of 3.50 and 1.43 for the respective traits were recorded by family CT1 x Nyara (Table 6.4). Family TME14 x Nyara had the best mean performance for DMC (38.2%) and very significant (P<0.01), positive SCA effect of 2.40. For the SRN, the highest mean performance of 7.6 was recorded in family CT5 x CT4, while the best positive but non-significant SCA effect of 0.96 was recorded in family NASE3 x B11 followed by family CT4 x Nyara with a SCA effect of 9.0.

Family CT2 x B11 recorded the highest mean performance for SRG of 15.4 cm and positive significant (P<0.05) SCA effect of 1.92. For SRL, the best mean performance of 27.6 cm was observed in CT5 x CT1, while the best positive but non-significant SCA effect of 2.10 for the trait was observed in CT2 x B11 (Table 6.5). All the significant SCA effects for SRL were negative and were recorded by Nyara x B11 (P<0.05), NASE3 x Nyara (P<0.05) and TME14 x CT1 (P<0.001). The lowest mean score for CBSD-RN of 1.8 was recorded by CT4 x Nyara while the lowest and highly significant (P<0.001), negative SCA effect of 0.82 was recorded by TME14 x CT3. Families, CT5 x B11 and TME14 x Nyara recorded the lowest mean score of 1.2 for CMD-S, with TME14 x Nyara also recording the lowest and highly significant (P<0.001), negative SCA effect for the trait.

The highest mean of 199.6 cm and significant (P<0.05), positive SCA effect of 29.44 for PHT were observed in CT4 x CT3 (Table 6.6). For HI, CT5 x TME14 had the highest mean performance of 0.42 and a very significant (P<0.01), positive SCA effect of 0.05, followed by CT5 x Nyara with a mean performance of 0.41 and a significant (P<0.05), positive SCA effect of 0.04.

Table 6.4: Mean performance and specific combining ability effects for fresh storage root yield, dry storage root yield, dry mass content and storage root number of nine cassava parents used in a 9 x 9 half-diallel analysis of cassava F_1 clonal stage families evaluated eight months after planting averaged across two sites in Uganda, 2012/13

	FSRY		DSRY		DMC		SRN	
Families	**Mean**	**SCA**	**Mean**	**SCA**	**Mean**	**SCA**	**Mean**	**SCA**
Nyara x B11	10.6	- 2.28	3.8	- 0.79	36.6	0.57	4.5	- 0.78
CT1 x B11	9.5	3.07	3.3	0.96	35.2	- 1.14	6.1	0.51
CT2 x B11	13.4	1.75	4.8	0.62	35.5	0.12	6.4	0.33
CT3 x B11	9.3	0.51	3.2	0.26	37.1	0.79	5.3	- 0.13
TME14 x B11	15.0	0.14	5.2	- 0.08	36.6	- 0.62	5.3	- 0.01
CT4 x B11	10.3	- 2.36	3.3	- 0.96	34.0	- 1.67	5.6	- 0.61
CT5 x B11	14.0	- 2.69	4.9	- 0.77	35.4	0.75	6.1	- 0.27
NASE3 x B11	10.4	1.87	3.8	0.77	37.4	1.20	6.6	0.96
CT1 x Nyara	16.2	3.50*	5.8	1.43*	36.1	1.11	6.3	0.79
CT2 x Nyara	10.0	- 1.68	3.6	- 0.74	32.4	- 1.62	4.9	- 0.30
CT3 x Nyara	17.0	0.40	6.2	0.02	33.9	- 0.99	5.9	0.47
TME14 x Nyara	12.1	0.74	4.0	0.51	38.2	2.40**	5.1	- 0.15
CT4 x Nyara	14.3	1.18	4.7	0.38	34.2	- 0.07	7.1	0.90
CT5 x Nyara	12.3	0.76	4.5	0.12	31.8	- 1.47	5.6	- 0.81
NASE3 x Nyara	12.2	- 2.61	4.2	- 0.94	34.9	0.08	5.5	- 0.11
CT2 x CT1	12.2	0.15	4.6	0.12	34.9	0.61	5.8	0.18
CT3 x CT1	10.6	- 1.90	3.8	- 0.81	34.9	- 0.35	6.2	- 0.09
TME14 x CT1	9.5	- 2.96	3.2	- 1.01	36.7	0.63	4.6	- 1.02
CT4 x CT1	12.4	- 1.32	4.3	- 0.46	34.0	- 0.55	5.9	- 0.65
CT5 x CT1	12.0	- 0.10	4.1	- 0.23	32.4	- 1.18	7.1	0.40
NASE3 x CT1	11.5	- 0.46	4.0	- 0.00	35.9	0.84	5.9	- 0.12
CT3 x CT2	12.5	0.65	4.7	0.28	34.6	0.29	5.6	0.15
TME14 x CT2	14.9	- 0.06	5.0	0.08	36.0	0.83	5.5	0.18
CT4 x CT2	10.9	- 0.74	4.2	- 0.19	34.2	0.54	5.6	- 0.55
CT5 x CT2	9.1	0.56	3.3	0.21	32.9	0.28	7.2	0.84
NASE3 x CT2	14.4	- 0.63	4.8	- 0.38	33.1	- 1.05	4.8	- 0.84
TME14 x CT3	14.4	- 0.97	4.3	- 0.35	35.2	- 0.84	5.7	0.28
CT4 x CT3	13.1	1.29	4.5	0.42	34.4	- 0.16	6.8	0.46
CT5 x CT3	12.5	- 1.77	4.4	- 0.48	34.7	1.23	7.2	- 0.38
NASE3 x CT3	10.6	1.79	3.5	0.67	35.0	0.00	5.1	- 0.76
CT4 x TME14	8.3	0.17	2.9	0.03	35.1	- 0.32	5.8	- 0.90
CT5 x TME14	13.0	2.91	4.6	1.06	34.6	0.27	6.8	- 0.38
NASE3 x TME14	13.1	0.02	4.7	- 0.23	33.5	- 2.35**	6.4	0.37
CT5 x CT4	15.3	1.02	5.0	0.38	33.4	0.53	7.6	0.26
NASE3 x CT4	9.6	0.74	3.5	0.40	36.1	1.70*	7.2	0.56
NASE3 x CT5	13.6	- 0.72	4.8	- 0.28	32.9	- 0.41	6.4	- 0.42
MEAN	12.2	-	4.3	-	34.8	-	6.0	-
SE	2.3	1.78	0.8	0.66	1.8	0.84	1.4	0.54
$LSD_{0.05}$	4.5	2.51	1.6	0.92	2.0	2.06	1.6	1.09

FSRY = fresh storage root yield (t ha^{-1}); DRY = dry storage root yield (t ha^{-1}); DMC = dry mas content (%); SRN = storage root number $plant^{-1}$; SCA = Specific combining ability; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

Table 6.5: Mean performance and specific combining ability effects for storage root girth, storage root length, cassava brown streak disease root necrosis and cassava mosaic disease severity of nine cassava parents used in a 9 x 9 half-diallel analysis of cassava F_1 clonal stage families evaluated eight months after planting averaged across two sites in Uganda, 2012/13

	SRG		SRL		CBSD-RN		CMD-S	
Families	**Mean**	**SCA**	**Mean**	**SCA**	**Mean**	**SCA**	**Mean**	**SCA**
Nyara x B11	12.0	- 0.71	20.6	- 2.46*	2.2	- 0.50**	2.7	0.73***
CT1 x B11	13.5	0.55	26.8	1.74	2.1	- 0.56**	1.8	0.03
CT2 x B11	15.4	1.92*	24.9	2.10	3.9	0.401*	1.8	0.14
CT3 x B11	12.8	0.01	26.0	1.32	3.5	0.49**	1.5	- 0.20
TME14 x B11	12.2	- 0.17	24.1	0.14	3.0	0.07	1.5	- 0.08
CT4 x B11	11.7	- 0.85	22.7	- 1.88	2.4	0.15	1.6	- 0.01
CT5 x B11	12.3	- 0.97	24.2	- 1.14	3.2	0.29	1.2	- 0.44***
NASE3 x B11	12.1	0.24	22.5	0.19	2.2	- 0.34	2.0	- 0.15
CT1 x Nyara	12.9	0.35	25.2	1.72	2.6	0.19	1.9	0.12
CT2 x Nyara	13.1	- 0.02	19.6	- 1.66	3.3	0.03	1.3	- 0.37
CT3 x Nyara	12.8	0.40	23.5	0.41	2.9	0.08	1.9	0.09**
TME14 x Nyara	12.2	0.25	24.4	2.00	3.1	0.38*	1.2	- 0.46***
CT4 x Nyara	12.4	0.32	24.0	0.99	1.8	- 0.25	1.5	- 0.17
CT5 x Nyara	13.1	0.22	25.2	1.37	2.7	0.01	1.5	- 0.23
NASE3 x Nyara	10.7	- 0.80	18.3	- 2.36*	2.4	0.06	2.6	0.29*
CT2 x CT1	12.8	- 0.56	22.3	- 0.89	3.5	0.28	1.3	- 0.25*
CT3 x CT1	12.5	- 0.20	25.7	0.64	3.7	0.95***	1.5	- 0.11
TME14 x CT1	11.7	- 0.48	20.9	- 3.43**	2.5	- 0.20	1.7	0.21
CT4 x CT1	12.7	0.31	23.6	- 1.40	2.0	- 0.01	1.5	- 0.04
CT5 x CT1	12.9	- 0.27	27.6	1.86	2.2	- 0.53**	1.8	0.25*
NASE3 x CT1	12.1	0.30	22.4	- 0.25	2.2	- 0.13	1.9	- 0.20
CT3 x CT2	13.6	0.39	22.1	0.46	3.2	- 0.38*	1.5	- 0.05
TME14 x CT2	12.5	- 0.24	22.8	0.69	3.7	0.17	1.5	0.17
CT4 x CT2	11.5	- 1.45*	22.5	- 0.73	2.6	- 0.18	1.5	0.09
CT5 x CT2	13.2	- 0.42	22.4	- 1.18	3.6	0.06	1.3	- 0.10
NASE3 x CT2	12.7	0.39	21.7	1.21	2.7	- 0.39*	2.3	0.37**
TME14 x CT3	11.9	- 0.15	22.6	- 2.02	2.3	- 0.82***	1.6	0.16
CT4 x CT3	12.6	0.35	25.6	0.98	2.2	- 0.19	1.4	- 0.02
CT5 x CT3	12.8	- 0.23	23.7	- 1.74	3.1	0.05	1.7	0.14
NASE3 x CT3	11.0	- 0.58	22.3	- 0.05	2.5	- 0.18	2.1	- 0.02
CT4 x TME14	11.8	0.03	24.4	0.53	2.2	- 0.13	1.4	0.07
CT5 x TME14	13.2	0.75	25.9	1.27	3.1	0.12	1.6	0.23
NASE3 x TME14	11.1	0.02	22.4	0.82	3.0	0.42*	1.6	- 0.31*
CT5 x CT4	13.6	0.88	26.4	0.32	2.3	0.02	1.5	0.10
NASE3 x CT4	11.7	0.41	23.4	1.18	2.5	0.59**	2.0	- 0.02
NASE3 x CT5	12.1	0.05	22.2	- 0.75	2.5	- 0.03	2.0	0.04
MEAN	12.5	-	23.5	-	2.7	-	1.7	-
SE	1.2	0.65	3.6	1.14	0.5	0.18	0.3	0.13
$LSD_{0.05}$	1.4	1.01	3.2	2.27	0.6	0.29	0.4	0.30

SRG = storage root girth (cm); SRL = storage root length (cm); CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; SCA = specific combining ability; LSD0.05 = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

Table 6.6: Mean performance and specific combining ability effects for plant height and harvest index of nine cassava parents used in a 9 x 9 half-diallel analysis of cassava F_1 clonal stage families evaluated eight months after planting averaged across two sites in Uganda, 2012/13

	PHT		HI	
Families	**Mean**	**SCA**	**Mean**	**SCA**
Nyara x B11	165.3	- 4.41	0.33	- 0.021
CT1 x B11	171.1	5.15	0.37	0.005
CT2 x B11	182.3	24.70*	0.38	0.014
CT3 x B11	134.4	- 21.96	0.36	0.005
TME14 x B11	163.3	6.00	0.34	- 0.006
CT4 x B11	134.1	- 35.39**	0.30	- 0.011
CT5 x B11	199.6	17.00	0.36	- 0.023
NASE3 x B11	165.1	8.90	0.37	0.035*
CT1 x Nyara	175.6	20.57	0.36	0.010
CT2 x Nyara	132.4	- 14.33	0.34	- 0.014
CT3 x Nyara	153.5	8.06	0.35	- 0.000
TME14 x Nyara	154.5	8.06	0.35	0.016
CT4 x Nyara	174.4	15.74	0.28	- 0.032
CT5 x Nyara	145.5	- 26.20*	0.41	0.040*
NASE3 x Nyara	137.8	- 7.50	0.33	0.002
CT2 x CT1	150.1	7.13	0.36	- 0.007
CT3 x CT1	126.4	- 15.30	0.39	0.033
TME14 x CT1	124.9	- 17.75	0.33	- 0.011
CT4 x CT1	159.9	4.97	0.33	0.011
CT5 x CT1	175.1	7.17	0.33	- 0.053**
NASE3 x CT1	129.6	- 11.96	0.35	0.014
CT3 x CT2	132.1	- 1.27	0.37	0.015
TME14 x CT2	114.4	- 19.89	0.35	- 0.001
CT4 x CT2	147.0	0.43	0.33	0.013
CT5 x CT2	156.4	- 3.20	0.37	- 0.0111
NASE3 x CT2	139.7	6.43	0.33	- 0.009
TME14 x CT3	129.0	- 4.11	0.36	0.036*
CT4 x CT3	174.8	29.44*	0.29	- 0.014
CT5 x CT3	170.6	12.21	0.34	- 0.030
NASE3 x CT3	124.9	- 7.07	0.30	- 0.031
CT4 x TME14	138.1	- 8.21	0.27	- 0.029
CT5 x TME14	175.0	15.63	0.42	0.048**
NASE3 x TME14	153.2	20.27	0.28	- 0.043*
CT5 x CT4	161.3	- 10.27	0.36	0.030
NASE3 x CT4	148.5	3.28	0.32	0.033
NASE3 x CT5	145.9	- 12.35	0.35	- 0.003
MEAN	151.8	-	0.34	-
SE	34.8	12.30	0.03	0.018
LSD (0.05)	39.8	20.33	0.06	0.037

PHT = plant height (cm); HI = harvest index; SCA = specific combining ability; $LSD_{0.05}$ = least significant difference at 5%; SE= standard error; * =P<0.05;** = P<0.01; *** = P<0.001.

6.3.5 Estimates of mid- and better-parent heterosis of the families

For brevity, ony six traits (FSRY, SRN, HI, DMC, CBSD-RN and CMD-S) were considered for heterosis analysis. The best three families with desirable high positive MPH and BPH for FSRY were NASE3 x Nyara, Nyara x B11 and NASE3 x B11 (Table 6.7). Mid-parent heterosis for FSRY ranged from -24.0% (TME14 x CT1) to 306.7% (NASE3 x Nyara), while BPH ranged from -40.3% (CT1 x B11 and TME14 x CT1) to 293.5% (NASE3 x Nyara). The majority of the families with high positive MPH and BPH for FSRY were from crossing at least an improved parent with a landrace. For SRN, the best three families with positive MPH and BPH were NASE3 x B11, Nyara x B11 and CT4 x Nyara. Mid-parent heterosis for this trait ranged from 1.1% (TME14 x CT1) to 193.3% (NASE3 x B11), while BPH ranged from -8.0% (TME14 x CT1) to 181.2% (Nyara x B11). The best three families with positive MPH and BPH for HI were NASE3 x CT4, NASE3 x B11 and CT5 x Nyara. Mid-parent heterosis for this trait ranged from -12.0% (CT5 x CT1) to 39.1% (NASE3 x CT4), while BPH ranged from -28.6% (NASE3 x CT3) to 181.2% (NASE3 x CT4).

For DMC, both the MPH and BPH were low (Table 6.8). Only four families (TME x Nyara, TME14 x CT2, CT4 x CT2 and NASE3 x CT4) had positive MPH, while only two families (CT4 x CT2 and NASE3 x CT4) had positive BPH. Mid-parent heterosis for this trait ranged from -13.4% (CT3 x CT1) to 5.2% (CT4 x CT2), while BPH ranged from -18.1% (CT3 x Nyara) to 2.0% (NASE3 x CT4). The best three families with desirable low negative MPH for CBSD-RN were: CT2 xCT1, CT5 x CT1 and CT4 x CT3, while the best three families with desirable low negative BPH for this trait were: NASE3 x CT5, NASE3 x CT3 and CT4 x CT1. Mid-parent heterosis for CBSD-RN ranged from -35.1% (CT2 x CT1) to 55.0% (TME14 x Nyara) while BPH ranged from -21.9% (NASE3 x CT5 and NASE3 x CT3) to 83.3% (CT2 x Nyara). For CMD-S, the best families with desirable low negative MPH were: TME14 x Nyara, CT2 x Nyara (-39.5%), CT3 x B11 (37.5%), TME14 x B11 (37.5%) and CT5 x B11 (37.5%). Only one family (Nyara x B11) had a negative BPH for CMD-S.

Table 6.7: Mean performance, mid-parent and better-parent heterosis for fresh storage root yield, storage root number and harvest index evaluated at the clonal evaluation stage at eight months after planting, averaged across two sites in Uganda, 2012/13

	FSRY			SRN			HI		
Parents	**Mean**	**MPH**	**BPH**	**Mean**	**MPH**	**BPH**	**Mean**	**MPH**	**BPH**
B11	2.5			1.5			0.32		
CT1	15.9			5.0			0.43		
CT2	13.8			4.9			0.38		
CT3	12.7			3.6			0.42		
CT4	10.1			3.6			0.24		
CT5	9.0			4.4			0.32		
NASE3	3.1			3.0			0.22		
Nyara	2.9			1.6			0.28		
TME14	9.1			4.1			0.35		
Families									
Nyara x B11	10.6	292.6	265.5	4.5	190.3	181.2	0.33	10.0	3.1
CT1 x B11	9.5	3.3	- 40.3	6.1	87.7	22.0	0.37	- 1.3	- 4.0
CT2 x B11	13.4	64.4	- 2.9	6.4	100.0	30.6	0.38	8.6	0.0
CT3 x B11	9.3	22.4	2.2	5.3	107.8	47.2	0.36	- 2.7	- 4.3
TME14 x B11	15.0	158.6	64.8	5.3	89.3	29.3	0.34	1.5	- 2.9
CT4 x B11	10.3	63.5	2.0	5.6	119.6	55.6	0.30	7.1	- 6.3
CT5 x B11	14.0	143.5	55.6	6.1	106.8	38.6	0.36	12.5	12.5
NASE3 x B11	10.4	271.4	235.5	6.6	193.3	120.0	0.37	37.0	15.6
CT1 x Nyara	16.2	72.3	1.9	6.3	90.9	26.0	0.36	1.4	- 16.3
CT2 x Nyara	10.0	19.8	- 7.5	4.9	50.8	0.0	0.34	3.0	- 10.5
CT3 x Nyara	17.0	117.9	35.0	5.9	126.9	63.9	0.35	0.0	- 16.7
TME14 x Nyara	12.1	96.7	33.0	5.1	78.9	24.4	0.35	11.1	0.0
CT4 x Nyara	14.3	120.0	41.6	7.1	173.1	92.2	0.28	7.7	0.0
CT5 x Nyara	12.3	106.7	36.7	5.6	86.7	27.3	0.41	36.7	28.1
NASE3 x Nyara	12.2	306.7	293.5	5.5	139.1	83.3	0.33	32.0	17.9
CT2 x CT1	12.2	- 17.2	- 23.3	5.8	17.2	18.4	0.36	- 11.1	- 16.3
CT3 x CT1	10.6	25.9	- 33.3	6.2	44.2	24.0	0.39	- 8.2	- 9.3
TME14 x CT1	9.5	- 24.0	- 40.3	4.6	1.1	- 8.0	0.33	- 5.4	- 23.3
CT4 x CT1	12.4	- 4.6	- 22.0	5.9	37.2	18.0	0.33	- 1.5	- 23.3
CT5 x CT1	12.0	- 3.6	- 24.5	7.1	51.1	42.0	0.33	- 12.0	23.3
NASE3 x CT1	11.5	25.1	- 27.7	5.9	47.5	18.0	0.35	7.7	- 18.6
CT3 x CT2	12.5	-5.7	- 9.4	5.6	31.8	14.3	0.37	- 7.5	- 11.9
TME14 x CT2	14.9	30.1	8.0	5.5	22.2	12.2	0.35	- 9.1	- 7.9
CT4 x CT2	10.9	- 8.8	- 21.0	5.6	31.8	14.3	0.33	6.5	- 13.2
CT5 x CT2	9.1	- 20.2	- 34.1	7.2	54.8	46.9	0.37	5.7	- 2.6
NASE3 x CT2	14.4	70.4	4.3	4.8	21.5	- 2.0	0.33	10.0	- 13.2
TME14 x CT3	14.4	32.1	13.4	5.7	48.1	39.0	0.36	- 6.5	- 14.3
CT4 x CT3	13.1	14.9	3.1	6.8	88.7	88.9	0.29	3.0	- 31.0
CT5 x CT3	12.5	15.2	- 1.6	7.2	80.0	63.6	0.34	- 8.1	- 19.0
NASE3 x CT3	10.6	34.2	- 16.5	5.1	54.5	41.7	0.30	- 6.3	- 28.6
CT4 x TME14	8.3	- 13.5	- 8.8	5.8	50.6	41.5	0.27	- 8.5	- 22.9
CT5 x TME14	13.0	43.6	42.9	6.8	60.0	65.9	0.42	25.4	20.0
NASE3 x TME14	13.1	114.8	44.1	6.4	80.7	56.1	0.28	- 1.8	- 20.0
CT5 x CT4	15.3	60.2	51.5	7.6	90.0	72.7	0.36	28.6	12.5
NASE3 x CT4	9.6	45.5	51.5	7.2	118.2	63.6	0.32	39.1	33.3
NASE3 x CT5	13.6	124.8	51.1	6.4	73.0	45.5	0.35	29.6	9.40

FSRY = fresh storage root yield (t ha^{-1}); SRN = storage root number $plant^{-1}$; HI = harvest index; DMC = dry mass content (%); MPH = mid-parent heterosis, BPH = better parent heterosis

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Table 6.8: Mean performance and mid-parent heterosis for cassava mosaic diseases severity evaluation stage at six months after planting and dry mass content and cassava brown steak disease root necrosis evaluated at eight months after planting at the clonal evaluation stage averaged across two sites in Uganda, 2012/13

	DMC			CBSD-RN			CMD-S		
Parents	**Mean**	**MPH**	**BPH**	**Mean**	**MPH**	**BPH**	**Mean**	**MPH**	**BPH**
B11	40.5			2.5			3.8		
CT1	39.3			2.7			1.0		
CT2	31.3			4.7			1.0		
CT3	41.4			4.0			1.0		
CT4	33.7			2.5			1.0		
CT5	34.6			3.8			1.0		
NASE3	35.4			3.2			1.0		
Nyara	34.7			1.8			3.3		
TME14	39.7			2.2			1.0		
Families									
Nyara x B11	36.6	- 2.7	- 9.6	2.2	2.3	22.2	2.7	- 23.9	- 18.2
CT1 x B11	35.2	-11.8	- 13.1	2.1	-19.2	- 16.0	1.8	- 25.0	80.0
CT2 x B11	35.5	- 1.1	- 12.3	3.9	8.3	52.0	1.8	- 25.0	80.0
CT3 x B11	37.1	- 9.4	- 8.4	3.5	7.7	40.0	1.5	- 37.5	50.0
TME14 x B11	36.6	- 8.7	- 9.6	3.0	27.7	36.4	1.5	- 37.5	50.0
CT4 x B11	34.0	- 8.4	- 16.0	2.4	-4.0	- 4.0	1.6	- 33.3	60.0
CT5 x B11	35.4	- 5.7	- 12.6	3.2	1.6	28.0	1.5	- 37.5	50.0
NASE3 x B11	37.4	- 1.4	- 7.7	2.2	-22.8	- 12.0	2.0	- 16.7	100.0
CT1 x Nyara	36.1	- 2.4	- 8.1	2.6	15.6	44.4	1.9	- 11.6	90.0
CT2 x Nyara	32.4	- 1.8	- 6.6	3.3	1.5	83.3	1.3	- 39.5	30.0
CT3 x Nyara	33.9	-10.9	- 18.1	2.9	0.0	61.1	1.9	- 11.6	90.0
TME14 x Nyara	38.2	2.7	- 3.8	3.1	55.0	72.2	1.2	- 44.2	20.0
CT4 x Nyara	34.2	0.0	- 1.4	1.8	-16.3	0.0	1.5	- 30.2	50.0
CT5 x Nyara	31.8	- 8.2	- 8.4	2.7	-3.6	50.0	1.5	- 30.2	50.0
NASE3 x Nyara	34.9	- 0.4	- 1.4	2.4	-4.0	33.3	2.6	20.9	160.0
CT2 x CT1	34.9	- 1.1	- 11.2	2.4	-35.1	- 11.1	1.3	30.0	30.0
CT3 x CT1	34.9	-13.4	- 15.7	3.7	10.4	37.0	1.5	50.0	50.0
TME14 x CT1	36.7	- 7.1	- 6.6	2.5	2.0	13.6	1.7	70.0	70.0
CT4 x CT1	34.0	- 7.4	- 13.5	2.0	-23.1	- 20.0	1.5	50.0	50.0
CT5 x CT1	32.4	-12.3	- 17.6	2.2	-32.3	- 18.5	1.8	80.0	80.0
NASE3 x CT1	35.9	- 3.9	- 8.7	2.2	-25.4	- 18.5	1.9	90.0	90.0
CT3 x CT2	34.6	- 4.8	- 16.4	3.2	-26.4	- 20.0	1.5	50.0	50.0
TME14 x CT2	36.0	1.4	- 9.3	3.7	7.2	68.2	1.5	50.0	50.0
CT4 x CT2	34.2	5.2	1.5	2.6	27.8	4.0	1.5	50.0	50.0
CT5 x CT2	32.9	- 0.2	- 4.9	3.6	-15.3	-5.3	1.3	30.0	30.0
NASE3 x CT2	33.1	0.2	- 6.5	2.7	-31.6	- 15.6	2.3	130.0	130.0
CT4 x CT3	35.2	-13.2	- 15.0	2.2	-32.3	-8.3	1.5	50.0	50.0
TME14 x CT3	34.4	- 8.4	- 16.9	2.3	-25.8	4.5	1.6	60.0	60.0
CT5 x CT3	34.7	- 8.7	- 16.2	3.1	-20.5	- 18.4	1.7	70.0	70.0
NASE3 x CT3	35.0	- 8.9	- 15.5	2.5	-30.6	- 21.9	2.1	110.0	110.0
CT4 x TME14	35.1	- 4.4	- 11.6	2.2	-6.4	0.0	1.4	40.0	40.0
CT5 x TME14	34.6	- 6.9	- 12.8	3.1	14.8	40.9	1.6	60.0	60.0
NASE3 x TME14	33.5	-10.8	- 15.6	3.0	11.1	36.4	1.6	60.0	60.0
CT5 x CT4	33.4	- 2.2	- 3.5	2.3	-27.0	-8.0	1.5	50.0	50.0
NASE3 x CT4	36.1	4.5	2.0	2.5	-12.3	0.0	2.0	100	100.0
NASE3 x CT5	32.9	- 6.0	- 7.1	2.5	-28.6	- 21.9	2.0	100.0	100.0

PHT = plant height (cm); CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; MPH = mid-parent heterosis; BPH = better parent heterosis.

6.3.6 Phenotypic correlations between traits

Most of the traits were positively and significantly correlated with one another, except CMD-S and CBSD-RN (Table 6.9). With the exception of CBSD-RN and CMD-S, there were highly significant (P<0.001), and positive correlations between FSRY and all the other traits assessed. Of the traits significantly correlated with FSRY, DSRY had the highest correlation. Similarly, DSRY had highly significant (P<0.001), positive correlations with all the traits assessed, except CMD-S and CBSD-RN. The CBSD-RN had a highly significant (P<0.001), negative correlation with CMD-S and a very significant (P<0.01), positive correlation with SRG. The CMD-S on the other hand had negative but non-significant correlations with: FSRY, HI, SRN and SRL. For HI, highly significant (P<0.001) positive correlations were recorded with FSRY, SRG, SRL, and DSRY; and also very significant (P<0.01), positive correlation with DMC.

Table 6.9: Phenotypic correlation coefficients for agronomic and disease traits of 36 cassava F_1 families harvested at eight months after planting and averaged across two sites in Uganda, 2012/13

Traits	FSRY	SRN	SRG	SRL	DMC	HI	PHT	DSRY	CMD-S	CBSD-RN
FSRY	1.00									
SRN	0.51***	1.00								
SRG	0.70***	0.13*	1.00							
SRL	0.48***	0.40***	0.33***	1.00						
DMC	0.20***	-0.13*	0.24***	0.11*	1.00					
HI	0.33***	0.11^{ns}	0.29***	0.31***	0.19**	1.00				
PHT	0.28***	0.22***	0.22***	0.12*	0.09^{ns}	- 0.04	1.00			
DSRY	0.98***	0.46***	0.71***	0.47***	0.36***	0.33***	0.28***	1.00		
CMD-S	0.10^{ns}	-0.03^{ns}	0.05^{ns}	-0.07^{ns}	-0.12*	$- 0.04^{ns}$	0.02^{ns}	0.12^{ns}	1.00	
CBSD-RN	-0.01^{ns}	-0.15*	0.20**	0.03^{ns}	0.01^{ns}	0.14^{ns}	-0.14^{ns}	-0.01^{ns}	-0.23***	1.00

FSRY = fresh storage root yield (t ha^{-1}); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SRL = storage root length (cm); DMC = dry mass content (%); HI = harvest index; PHT = plant height (cm); DSRY = dry storage root yield (t ha^{-1}); CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; ns = correlation not significant at 0.05 * = significant at P<0.05; ** = at P<0.01 ; *** = at P<0.001 level.

6.3.7 Traits contribution to the families variability

The PCA indicated that the first three PCs explained 75.7% of the total variation and had eigenvalues greater than one (Table 6.10). The PC1, PC2 and PC3 accounted for 50.4, 14.1 and 11.2%, respectively of the total variability. All the variables in PC1 were positively correlated with PC1, with five of them: DSRY, FSRY, SRM, SRG and STM being highly correlated with PC1 indicating that they contributed most to this PC1. The PC2 was highly correlated with four traits: DMC, HI, SRN and STM, indicating that they most contributed to this PC. The PC3 was highly correlated with DMC, HI, SRN, and SRL and, therefore, these four traits largely contributed to PC3. The PC4 was largely

contributed to by PHT and SRL. Dry mass content, HI and SRN were important in two of the four principal components, while DSRY, FSRY, PHT, SRG, SRM and STM were important in one of the four PCs, indicating their relative importance in the general performance of the genotypes.

Table 6.10: Principal component (PC) scores, eigenvalues and proportions of total and cumulative variance for the first four PCs for 12 traits of 36 F_1 clonal stage cassava families averaged across sites in Uganda, 2012/13

	Principal components			
Traits	**PC1**	**PC2**	**PC3**	**PC4**
DMC	0.1264	0.4568	0.5309	0.1076
DSRY	0.4334	0.0723	0.0845	- 0.0902
FSRY	0.4345	0.0018	- 0.0053	- 0.1130
HI	0.1413	0.6456	- 0.3653	0.2470
PHT	0.1617	- 0.2744	0.2803	0.8819
SRN	0.2482	- 0.3147	- 0.4910	0.1505
SRM	0.4345	0.0018	- 0.0053	- 0.1130
SRG	0.3463	0.1523	0.2081	- 0.1366
SRL	0.2527	0.1173	- 0.4262	0.1495
STM	0.3566	- 0.3975	0.1815	- 0.2289
Eigenvalues	5.04	1.41	1.12	0.83
Percentage variation	50.4	14.1	11.2	8.3
Cumulative percentage variation	50.4	64.5	75.7	84.0

DMC = dry mass content (%); DSRY = dry storage root yield (t ha^{-1}); FSRY = fresh storage root yield (t ha^{-1}); HI = harvest index; PHT = plant height (cm); SRN = storage root number $plant^{-1}$; SRM = storage root mass (kg $plant^{-1}$); SRG = storage root girth (cm); SRL = storage root length (cm); STM = shoot mass (kg $plant^{-1}$) PC = principal component.

6.3.8 Selection of F_1 genotypes for advancement

The genotypes selected from the 36 families were coded as per the following examples: genotype one selected from family one was coded FM1-1; genotype 11 from family two as FM2-11, and so on. Selection of the top F_1 genotypes for advancement was performed using a four step process. The selection criteria was based on farmers' top two preferred traits namely, early storage root yield/bulking and DMC, plus the resistance to the two most prevalent diseases of cassava in Uganda (CBSD and CMD). These criteria were based on the results from the participatory rural appraisal (PRA) presented in Chapter 2, Table 2.4. A total of 50 F_1 genotypes were selected (Table 6.11). All 50 selections were early bulking, high yielding genotypes with high DMC and dual resistance to CBSD and CMD. All the 50 genotypes selected had a higher FSRY than the best parent (CT1). The best F_1 genotype (FM29-8) for FSRY was recorded by family (CT5 x CT1) which was generated from parents with high positive and significant GCA effects for FSRY (Table 6.3). Seventeen of the 50 genotypes selected had DMC above 41.4% recorded by the best parent (CT3). Similarly, 24 genotypes of the 50 selected genotypes had a harvest index higher than that of the best parent (CT1). For SRN, 94% of the selected genotypes were better than the best parent (CT1) which had 5.0 storage roots $plant^{-1}$.

Table 6.11: Overall mean performances of the 50 best F_1 genotypes selected in a four-step process based on high fresh storage root yield, resistance to cassava brown streak disease root necrosis and cassava mosaic disease severity, and high dry mass content.

			Traits						
S/N	**Genotype**	**Family**	**FSRY**	**SRN**	**SRG**	**DMC**	**HI**	**CBSD-RN**	**CMD-S**
1.	FM29-8	CT5 x CT1	75.0	9.5	17.0	42.4	0. 57	1.0	1.0
2.	FM7-11	CT5 x B11	60.0	6.0	12.2	44.3	0.56	1.0	1.0
3.	FM22-18	CT4 x CT2	56.0	22.0	13.4	39.3	0.32	1.0	1.0
4.	FM22-27	CT4 x CT2	54.0	9.0	12.3	40.3	0.50	1.0	1.0
5.	FM10-8	CT4 x CT3	51.0	9.5	16.0	49.8	0.30	1.0	1.0
6.	FM10-3	CT4 x CT3	51.0	15.0	19.4	43.4	0.36	1.0	1.0
7.	FM32-23	CT5 x TME14	50.0	12.0	16.4	41.8	0.50	1.0	1.0
8.	FM16-41	TME14 x Nyara	47.0	10.0	18.2	44.9	0.44	1.0	1.0
9.	FM8-27	NASE3 x B11	47.0	8.0	19.2	42.8	0.48	1.0	1.0
10.	CR30-8	NASE3 x CT1	45.0	9.0	17.8	39.8	0.33	1.0	1.0
11.	FM10-1	CT4 x CT3	41.0	14.0	18.2	39.7	0.26	1.0	1.0
12.	FM4-9	CT3 x B11	40.0	8.0	17.0	42.0	0.47	1.0	1.0
13.	FM20-11	CT3 x CT2	39.0	9.0	19.2	39.1	0.55	1.0	1.0
14.	FM23-28	CT5 x CT2	39.0	12.5	19.7	39.1	0.29	1.0	1.0
15.	FM8-33	NASE3 x B11	38.5	11.0	13.7	42.4	0.46	1.0	1.0
16.	FM23-29	CT5 x CT2	37.0	11.5	16.4	42.5	0.47	1.0	1.0
17.	FM35-21	NASE3 x CT4	37.0	15.0	19.0	39.2	0.42	1.0	1.0
18.	FM19-9	NASE3 x Nyara	35.0	12.5	15.6	43.5	0.39	1.0	1.0
19.	FM35-25	NASE3 x CT4	35.0	10.0	17.6	43.1	0.42	1.0	1.0
20.	FM22-2	CT4 x CT2	35.0	11.0	19.8	39.5	0.39	1.0	1.0
21.	FM28-28	CT4 x CT1	35.0	8.0	15.4	39.4	0.49	1.0	1.0
22.	FM35-12	NASE3 x CT4	33.0	15.0	13.0	40.3	0.39	1.0	1.0
23.	FM20-32	CT3 x CT2	32.5	6.0	18.5	39.8	0.55	1.0	1.0
24.	FM2-16	CT1 x B11	32.0	12.0	17.0	39.2	0.35	1.0	1.0
25.	FM17-44	CT4 x Nyara	31.0	10.5	18.9	39.8	0.31	1.0	1.0
26.	FM8-26	NASE3 x B11	31.0	9.0	18.0	39.6	0.46	1.0	1.0
27.	FM2-26	CT1 x B11	30.0	5.5	16.6	42.3	0.65	1.0	1.0
28.	FM2-20	CT1 x B11	30.0	4.0	19.7	40.8	0.40	1.0	1.0
29.	FM12-24	NASE3 x CT3	30.0	10.0	19.8	40.5	0.41	1.0	1.0
30.	FM30-29	NASE3 x CT1	30.0	4.0	16.0	39.9	0.67	1.0	1.0
31.	FM10-4	CT4 x CT3	30.0	10.0	18.6	39.5	0.26	1.0	1.0
32.	FM13-14	CT1 x Nyara	29.0	13.0	15.2	42.2	0.40	1.0	1.0
33.	FM21-15	TME14 x CT2	29.0	11.0	15.2	41.3	0.43	1.0	1.0
34.	FM1-31	Nyara x B11	29.0	10.0	15.0	39.7	0.54	1.0	1.0
35.	FM6-27	CT4 x B11	29.0	8.5	20.0	38.6	0.28	1.0	1.0
36.	FM35-25	NASE3 x CT4	28.5	10.0	17.2	50.0	0.42	1.0	1.0
37.	FM28-6	CT4 x CT1	27.5	8.0	16.2	41.3	0.44	1.0	1.0
38.	FM17-44	CT4 x Nyara	27.5	16.5	14.6	39.8	0.30	1.0	1.0
39.	FM6-2	CT4 x B11	26.5	9.0	18.2	38.6	0.31	1.0	1.0
40.	FM13-24	CT1 x Nyara	26.0	5.5	17.1	47.5	0.43	1.0	1.0
41.	FM35-28	NASE3 x CT4	26.0	7.0	17.2	41.5	0.24	1.0	1.0
42.	FM28-30	CT4 x CT1	26.0	6.0	18.8	39.3	0.52	1.0	1.0
43.	FM6-35	CT4 x B11	26.0	8.0	18.0	38.9	0.52	1.0	1.0
44.	FM24-7	NASE3 x CT2	26.0	8.0	18.4	38.9	0.46	1.0	1.0
45.	FM11-32	CT5 x CT3	26.0	12.0	13.0	38.7	0.45	1.0	1.0
46.	FM4-24	CT3 x B11	25.0	7.5	15.7	43.5	0.45	1.0	1.0
47.	FM8-34	NASE3 x B11	25.0	13.0	13.4	40.7	0.49	1.0	1.0
48.	FM2-39	CT1 x B11	25.0	6.5	17.2	39.8	0.53	1.0	1.0
49.	FM2-8	CT1 x B11	25.0	6.0	15.0	39.8	0.38	1.0	1.0
50.	FM2-29	CT1 x B11	25.0	5.0	18.2	39.7	0.38	1.0	1.0
	Parents								
1.	CT1		15.9	5.0	13.8	39.3	0.43	2.7	1.0
2.	CT2		13.8	4.9	15.5	31.3	0.38	4.7	1.0
3.	CT3		12.7	3.6	14.0	41.4	0.42	4.0	1.0
4	CT4		10.1	3.6	12.1	33.7	0.24	2.5	1.0
5.	TME14		9.1	4.1	13.0	39.7	0.35	2.2	1.0
6.	CT5		9.0	4.4	13.0	34.6	0.32	3.8	1.0
7.	NASE3		3.1	3.0	10.9	35.4	0.22	3.2	1.0
8.	Nyara		2.9	1.6	11.3	34.7	0.28	1.8	3.3
9.	B11		2.5	1.5	10.7	40.5	0.32	2.5	3.8
	Maximum		75.0	26	20.0	50.0	0.67	4.7	3.8
	Minimum		25.0	1.5	10.7	31.3	0.22	1.0	1.0
	Mean		31.2	8.9	16.2	40.5	0.42	1.3	1.1
	SE		1.8	0.6	0.3	0.4	0.01	0.1	0.1
	CV (%)		44.8	48.0	15.7	7.8	26.2	42.6	43.1

FSRY = fresh storage root yield (t ha^{-1}); SRN = storage root number; SRG = storage root girth; HI = harvest index; DMC = dry mass content (%); CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; CV = coefficient of variation (%); SE = standard error of mean.

Seventy five percent of the selected genotypes had SRG higher than that of the best parent (CT2), which had a SRG of 15.5 cm. All the selected genotypes had a score of 1.0

for both CMD-S and CBSD-RN and were therefore resistant for CMD and CBSD, respectively (Table 6.11).

6.4 Discussion and conclusions

The F_1 clonal trial was harvested at eight months after planting in order to identify high yielding, early bulking progeny with increased resistance to CMD and CBSD. Families and individual genotypes had a high level of variation for 10 traits evaluated, namely DSRY, HI, DMC, SRN, SRG, SRL, PHT, CBSD-RN and CMD-S and FSRY. For example, FSRY in the individual genotypes ranged from a low of 0.0 t ha^{-1} to a high of 90.0 t ha^{-1} with a mean of 12.2 t ha^{-1} while HI ranged from a low of 0.1 to a high of 0.9 with a mean of 0.3. A complete range of scores from 1 to 5 was recorded for CMD-S and CBSD-RN with means of 1.6 and 2.7, respectively. The best genotype for high FSRY and early bulking in combination with high DMC and dual resistance to CMD and CBSD was FM29-8 from family CT5 x CT1. Genotype FM22-18 from family CT4 x CT2 recorded the highest SRN of 22.0. The mean performance for FSRY, HI and CMD-S reported are comparable to those recorded by Munga (2008), Mtunda (2010), Chikoti (2011) and Were et al. (2012), while the CBSD-RN scores reported are comparable to those of Munga (2008), Mtunda (2010) and Kulembeka et al. (2012).

The main effects for environment (site) were significant for most of the traits evaluated, indicative of significant differences in the mean performances of the sites. Namulonge and Bulindi have distinctly different climatic conditions (NARO, 2001) and experience different pressures for CMD and CBSD. Namulonge, situated in central Uganda, experiences higher levels of CMD and CBSD due to its high white fly (*Bemisia tabaci*) populations compared to Bulindi, situated in north-western Uganda. In addition, the soil sample analyses conducted for the two sites before establishment of trials revealed significant differences, with Namulonge recording more fertile soils (Appendix 6.1). Also, the rainfall and temperatures recorded at these two sites during the experimental period confirmed the differences between them (Appendix 6.1). Bulindi recorded higher temperatures, while Namulonge recorded higher rainfall. Aina et al. (2009) demonstrated that rainfall is the critical climatic factor that discriminates different agro-ecological zones for cassava.

Significant differences between family MS for all traits indicated significant genotypic differences between the families. Although significant genotype x environment interaction effects have been recorded for most agronomic and morphological traits in cassava (Jaramillo et al., 2005; Calle et al., 2005; Cach et al., 2006; Egesi et al., 2007; Were et al., 2012), in this study significant interaction between environment and family MS were only

recorded for DMC and PHT (Table 6.2). This implies that families in this study recorded stable performance across the two test environmemets for all traits except DMC and PHT, and that selection for all the family traits assessed except DMC and PHT could be done at either site. Significant interaction between environment and GCA MS for FSRY, DSRY and DMC as well as significant interaction between environment and SCA MS for DMC and for CMD-S implies that evaluation and selection of suitable genotypes for commercial or as parents should be based on multilocation testing. Those that show high GCA and SCA effects across environments are the best genotypes. However, due to low multiplication rate of cassava planting materials (Ceballos et al., 2004), it is a tradition by most cassava breeding programmes that the first clonal evaluation trials are established at one location and to some extent not replicated (Ceballos et al., 2004). Therefore, there is a need to develop technologies that can improve the multiplication rate of cassava such as tissue culture or the cut-back method reported by Were el al. (2012) to conduct replicated mulitlocation trials.

General combining ability and SCA MS were significant for most traits indicating the significance of additive and non-additive gene action in controlling the traits, respectively. The expression of all traits studied except PHT, DRY and SRN was significantly under the control of both additive and non-additive genes. The presence of family, GCA and SCA × environment interaction effects for FSRY, DSRY, DMC and CMD-S implied that the gene action determining the expression of these traits, whether additive or non-additive or a combination of both, was site specific and was therefore not stably expressed across environments (Were et al., 2012).

General combining ability measures the average performance of a parent in its crosses while SCA refers to performance of a cross greater or less than what would be expected on the basis of the average performance of the parents involved (Griffing, 1956). The proportion of the SS for families due to GCA and SCA effects provides an indication of the relative importance of additive and non-additive gene effects in the expression of traits (Calle et al., 2005, Kulembeka, 2012). In this study, the GCA effects accounted for over 50.0% of the families SS for DMC, SRG, CBSD-RN and CMD-S, indicating the predominance of additive gene action in controlling these traits. In contrast, the SCA effects for FSRY and the remaining traits accounted for over 50.0% of the families SS indicating that they were predominantly under non-additive gene control. Based on % families SS accounted for by SCA effects, Jaramillo et al. (2005), Were et al. (2012) and Kulembeka et al. (2012) also reported that FSRY was under the control of

non-additive gene action. The relative importance of GCA effects for CBSD-RN observed in this study were in agreement with the observations of Munga (2008), Mtunda (2009) and Kulembeka (2012), but were in disagreement with Zacarias and Labuschagne (2010). Cassava mosaic disease resistance was also found to be predominantly controlled by additive gene effects as previously reported by Lokko et al. (2006) and Parkes et al. (2013).

In terms of general combining ability and associated transmission of desirable additive gene action from parents to progeny, parents CT1 and CT5 had the highest significant positive GCA effects for FSRY and they were, therefore, the best parents to use when breeding for high FSRY. In addition, CT5 had the highest significant positive GCA effects for PHT, HI, SRN and SRL. For DSRY, the parent with highest significant positive GCA effect was CT1 and it was therefore the best general combiner for DSRY. The parents with the highest significant positive GCA effects for DMC were B11 and TME14. For CBSD-RN, CT1, CT4 and NASE3 had significant negative GCA effects, suggesting that they were best parents to use in breeding cultivars with resistance to CBSD. Parents CT2, CT4, CT5 and TME14 had very low mean scores, as well as significant negative GCA effect for CMD-S.

The desirable SCA effects for FSRY and DSRY were recorded in family CT1 x Nyara, while the desirable SCA effect for DMC was recorded in TME14 x Nyara. The best SCA effect for SRN was observed in NASE3 x B11 followed by CT4 x Nyara. Family CT2 x B11 recorded the best SCA effect for SRG whereas family CT2 x B11 recorded the best SCA effect for SRL. The best SCA effect for CBSD-RN was recorded in TME14 x CT3 and the best SCA effects for CMD-S in TME14 x Nyara.

With the exception of DMC and HI, high MPH and BPH were recorded for the traits in most of the families. The high MPH and BPH for most of the traits in most of the families is certainly attributable to the diverse parents that were used in study. The parental lines were selected from a genetically diverse pool of lines from farmers' fields (landraces) and the NCBP available as introductions. Low MPH for HI was also reported in Zacarias and Labuschagne's (2010) study.

Most of the yield and yield related traits were significantly positively correlated with one another demonstrating the interdependence of these traits. Fresh storage root yield was positively and significantly correlated with PHT, SRN, SRL, DMC, HI and DSRY, with

DSRY recording the highest correlation. Harvest index and SRN recorded positive correlations with FSRY which confirms these traits as good indicators of FSRY (Ntawuruhunga, et al., 2001; Ojulong, 2006; Aina et al., 2009). Cassava mosaic disease was negatively, but non-significantly correlated with FSRY, HI, SRN and SRL. This is in agreement with the findings that diseases and pests reduce storage root yield in cassava (Hahn et al., 1980; Parkes et al., 2013).

Principal components analysis revealed that the first three PCs explained 75.1% of the total variation, with DMC, DSRY, FSRY, HI, SRM, STM and PHT contributing the most to overall variation of the 36 families. These are the key traits farmers and breeders desire to have in a cassava cultivar and are selected for during cassava breeding.

In final conclusion: significant advances were made in terms of developing high yielding, early bulking cassava progeny with high DMC and resistance to CMD and CBSD using local and introduced cultivars as parents. Parents and families with good combining ability for early FSRY and farmer preferred traits were identified and will be exploited in future cassava breeding programmes for early bulking and other relevant traits in Uganda. Both additive and non-additive gene actions were involved in the expression of the traits. However, non-additive gene effects were more important than additive gene effects in the expression of most traits including early FSRY. For traits: DMC, SRG, CBSD-RN and CMD-S where additive genetic effects were predominant, a hybridisation scheme followed by phenotypic recurrent mass selection may be effective in identifying desirable recombinants. On the other hand, for traits: FSRY, DSRY, SRN, HI, SRL and PHT, where there was predominance of non-additive genetic effects in their expression, a different approach might be used. For instance, cassava genotypes could be grouped into heterotic pools and specific hybrid combinations made in order to exploit non-additive gene action, which will be fixed through vegetative propagation of the subsequent generations or a reciprocal recurrent selection approach could be pursued.

References

Abele, S., E. Twine, P. Ntawuruhunga, Y. Baguma, C. Kanobe, and A. Bua. 2007. Development and dissemination of improved cassava varieties in Uganda: Analysis of adoption rates, variety attributes and speed of adoption. In: Proceedings of Second International Conference of African Association of Agricultural Economists, Accra, Ghana. August 2007. p. 479-482.

Aina, O.O., A.G.O. Dixon, I. Paul, and E.A. Akinrinde. 2009. GxE interaction effects on yield and yield components of cassava (landraces and improved) genotypes in the savannah regions of Nigeria. African Journal of Biotechnology 8:4933-4945.

Amenorpe, G., H.M. A. Amoatey, A. Darkwa, G.K. Banini, and V.W. Elloh. 2007. Peak root and starch weights of ten early bulking cultivars of cassava (*Manihot esculenta* Crantz) in Ghana. Journal of Ghana Science Association 9:54-60.

Amini, F., A. Mirlohi, M., M. Majidi, S.F Shojaie, and R. Kölliker. 2011. Improved polycross breeding of tall fescue through marker-based parental selection. Plant Breeding 130:701-707.

Banito, A.J., V. Verdier, K.E. Kpemoua, and K. Wydra. 2007. Assessment of major cassava diseases in Togo in relation to agronomic and environmental characteristics in a systems approach. African Journal of Agricultural Research 2:418-428.

Basbag, S.,R. Ekinci, and O. Gencer. 2007. Combining ability and heterosis for earliness characters in line x tester population of *Gossypium hirsutum* L. Hereditas 144:185-190.

Cach, N.T., J.L. Lenis, J.C. Perez, N. Morante, F. Calle, and H. Ceballos. 2006. Inheritance of useful traits in cassava in sub humid conditions. Plant breeding 125:177-182.

Calle, F., J.C. Perez, W. Gaitan, N. Morante, H. Ceballos, G. Llano, and E. Alvarez. 2005. Diallel inheritance of relevant traits in cassava (*Manihot esculenta* Crantz) adapted to acid soil savannas. Euphytica 144:177-186.

Chikoti, P. C. 2011. Development of cassava (*Manihot esculenta* Crantz) cultivars for resistance to cassava mosaic disease in Zambia. PhD thesis, University of KwaZulu Natal, South Africa.

Comstock, R.E., and H.F. Robinson. 1948. The components of genetic variance in populations of bi-parental progenies and their use in estimating the average degree of dominance. Biometrics 4:254-266.

Dudley, J.W., and R.H. Moll. 1969. Interpretation and use of estimates of heritability and genetic variance in plant breeding. Crop Science 9:257-262.

Egesi, C. N., P. Ilona, F. O. Ogbe, M. Akoroda, and A. Dixon. 2007. Genetic variation and genotype x environment interaction for yield and other agronomic traits in cassava in Nigeria. Agronomy Journal 99:1137-1142.

Falconer D.S, and T.F.C. Mackay. 1996. Introduction to quantitative genetics. Fourth edition. Prentice Hall. Peterson Education Limited, England.

Gardner, C.O., and S.A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439-452.

Glover, M.A., D.B. Willmot, L.L. Darrah, E.H. Bruce, and X. Zhu. 2005. Diallel analyses of agronomic traits using Chinese and US maize germplasm. Crop Science 45:1096-1102.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Australian Journal of Biological Science 9:463-493.

Hahn, S.K., A.K. Howland, and E.R. Terry. 1980. Correlated resistance of cassava to mosaic and bacterial blight diseases. Euphytica 29:305-311.

Hartley, H.O. 1950.The use of range in analysis of variance. Biometrika 37:271-280.

Hayman, B.I. 1954. The theory and analysis of diallel crosses. Genetics 39: 789-809.

Hillocks, R.J., M. Raya, and M.J. Thresh. 1996. The association between root necrosis and aboveground symptoms of brown streak virus infection in cassava in southern Tanzania. International Journal of Pest Management 42:285-289.

Jaramillo, G., N. Morante, J.C. Perez, F. Calle, H. Ceballos, B. Arias, and A.C. Bellotti. 2005. Diallel analysis in cassava adapted to the mid-altitude valleys environment. Crop Science 45:1058-1063.

Jinks, J.I., and B.I. Hayman.1953. The analysis of diallel crosses. Maize Genetics News Letter 27:48-54.

Jollife, I.T. 2002. Principal component analysis. Second edition, Springer-Verlag New York, Inc. USA.

Kamau, J. W. 2006. Participatory based development of early bulking cassava varieties for the semi-arid areas of Eastern Kenya. PhD thesis, University of KwaZulu-Natal, South Africa.

Kamau, J., R. Melis, M. Laing, J. Derera, P. Shanahan, C. Eliud, and K. Ngugi. 2011. Farmers' participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. Journal of Plant Breeding and Crop Science 3:44-52.

Kawuki R. S., A. Pariyo, T. Amuge, E. Nuwamanya., G. Ssemakula, S.Tumwesigye, A. Bua Y. Baguma, C. Omongo, T. Alicai, and J. Orone. 2011. A breeding scheme for local adoption of cassava (*Manihot esculenta* Crantz). Journal of Plant Breeding and Crop Science 3:120-130.

Kiani, G., G.A. Nematzadeh, S.K. Kazemitabar, and O. Alishah. 2007. Combining ability in cotton cultivars for agronomic traits. International Journal of Agriculture and Biology 3:521-522.

Kulembeka, H.P., M. Ferguson, L. Herselman, E. Kanju, G. Mkamilo, E. Masumba, M. Fregene and M.T. Labuschagne. 2012. Diallel analysis of field resistance to brown streak disease in cassava (*Manihot esculenta* Crantz) landraces from Tanzania. Euphytica187:277-288.

Lokko, Y., A.G.O. Dixon, S.K. Offei, and E.Y. Danquah. 2006. Combining ability analysis of resistance to mosaic virus disease in cassava. African Crop Science Journal 14:221-230.

Méndez-Natera, J.R., A. Rondón, J. Hernández, and J. Fernando Merazo-Pinto. 2012. Genetic studies in upland cotton (*Gossypium hirsutum* L.) II, general and specific combining ability. Journal of Agricultural Science and Technology 14:617-627.

Ministry of Agriculture, Animal Industry and Fisheries (MAAIF). 2007. The national cassava policy (Draft): The Republic of Uganda p.1-18.

Mtunda, K.J. 2009. Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.

Munga, T.L. 2008. Breeding for cassava brown streak resistance in coastal Kenya. PhD thesis, University of KwaZulu-Natal, South Africa.

NARO. 2001. Mid-term plan 2001-2005. Responding to research challenges for modernization of Agriculture. National Agricultural Research Organisation (NARO), Ministry of Agriculture, Animal Industry and Fisheries, Entebbe, Uganda.

Ntawuruhunga, P., PR, Rubaihaho, J.B.A .Whyte, A.G.O. Dixon, D.S.O. and Osiru. 2001. Interrelationships among traits and path analysis for yield components of cassava: a search for storage root yield indicators. African Crop Science Journal 9: 599-606.

Nweke, F.I., A. Dixon, R. Asiedu, and S.A. Folayan. 1994. Cassava varietal needs of farmers and potential for production growth in Africa. COSCA working paper 10.

Ojulong, H. F. 2006. Quantitative and molecular analyses of agronomic traits in cassava (*Manihot esculenta* Crantz). PhD thesis, University of the Free State Bloemfontein, South Africa.

Okogbenin, E., T.L. Setter, M. Ferguson, R. Mutegi, H. Ceballos, B. Olasanmi, and M. Fregene, 2013. Phenotypic approaches to drought incassava: review. Frontiers in Physiology 4:1-15.

Owolade, O.F, A.G.O. Dixon, and A.Y.A. Adeoti. 2006. Diallel analysis of cassava genotypes to anthracnose disease. World Journal of Agricultural Science 2:98-104.

Parkes, E. Y., M. Fregene, A. Dixon, B. Boakye-Peprah, and M.T. Labuschagne. 2013. Combining ability of cassava genotypes for cassava mosaic disease and cassava bacterial blight, yield and its related components in two ecological zones in Ghana. Euphytica 194:13-24.

Payne, R.W., S.A. Harding, D.A Murray, D.M. Soutar, D.B. Baird, A.I. Glaser, S.J. Welham, A.R. Gilmour, R. Thompson, and R. Webster. 2011. The guide to genstat release 14, part 2: statistics. VSN International, Hemel Hempstead, UK.

Perez, J.C., H. Ceballos, F. Calle, N. Morante, W. Gait´an, G. Llano, and E. Alvarez. 2005. Within family genetic variation and epistasis in cassava (*Manihot esculenta* Crantz) adapted to the acid-soils environment. Euphytica 145:77-85.

Rauf, S., T. M. Khan, and S. Nazir. 2005. Combining ability and heterosis in *Gossypium hirsutum* L. International Journal of Agriculture and biology 7:109-113.

Suja, G., K.S. John, J. Sreekumari, and T. Srinivas. 2009. Short-duration cassava genotypes for crop diversification in the humid tropics: growth dynamics, biomass, yield and quality. Journal of Science and Food Agriculture 90:188-198.

Tumuhimbise, R., R. Melis, P. Shanahan, and R. Kawuki. 2012. Farmers' perceptions on early storage root bulking in cassava (*Manihot esculenta* Crantz) in east and central Uganda and their implication for cassava breeding. World Journal of Agricultural Sciences. 8:403-408.

Were, W.V., P. Shanahan, R. Melis, and O.O. Omari. 2012. Gene action controlling farmer preferred traits in cassava varieties adapted to mid-altitude tropical climatic conditions of western Kenya. Field Crops Research 133:113-118.

Zacarias, A.M., and M.T. Labuschagne. 2010. Diallel analysis of cassava brown streak disease, yield and yield related characteristics in Mozambique. Euphytica 176:309-320.

Zhang, Y., M.S. Kang, and K. R. Lamkey. 2005. Diallel-SAS05: A comparative programme for Griffing's and Gardner-Eberhart analyses. Agronomy Journal 97:1097-1106.

Appendix 6.1: Climatic data and soil nutrient analysis for Namulonge and Bulindi Agricultural Research Institutes in Uganda, 2012/13

	Climatic data			Soil chemical elements						
	Rainfall (mm)	Temp (^{o}C)	pH	OC	OM	N	P	Ca	Mg	K
Location	Oct-May	Min-Max		%			(ppm)			
Namulonge	1206	15.1 - 28.5	6.1	4.2	7.3	0.33	0.7	1276.0	762.1	435.7
Bulindi	760	16.9 - 29.8	6.0	2.6	4.5	0.23	3.2	971.0	334.4	476.4

CHAPTER 7

Overview of the research findings and implications for cassava breeding in Uganda

7.1 Introduction

Improvement of cassava for high storage root yield and early bulking in Uganda, where cassava is a key food and cash crop, can contribute to increased food security and economic development. One way of improving the efficiency of cassava production in terms of fresh storage root yield (FSRY) per unit time is by developing early bulking genotypes with shortened growth periods. Early bulking cassava genotypes are crucial for Uganda given the mounting pressure on land and the practice of multiple sequential cropping within a short period. Early bulking cultivars will also be advantageous in drier areas as they can be harvested after only one cycle of rain.

The main objective of this research was to develop high yielding, early bulking cassava genotypes that combine resistance to cassava brown streak disease (CBSD) and cassava mosaic disease (CMD) with farmer preferred traits. This was achieved through the following research activities:

1. Evaluation of farmers' attitudes to and/or perceptions of cassava early bulking, production constraints and cultivar preferences in Uganda;
2. Determination of the extent of genetic variability in storage root bulking and other important traits of selected cassava genotypes in Uganda;
3. Examination of genotype x environment interaction (GEI) effects on early FSRY and related traits of selected cassava genotypes in Uganda;
4. Development and evaluation of cassava F_1 families for high FSRY, early bulking and resistance to CBSD and CMD; and
5. Assessment of combining ability and gene action controlling early bulking and yield-related traits, as well as resistance to CMD and CBSD.

7.2 Summary of the research findings

7.2.1 Farmers' attitudes to and/or perceptions of cassava early bulking, production constraints and cultivar preferences in Uganda

- Several cassava production constraints were identified, key of which were diseases, especially CMD and CBSD, and a lack of improved early bulking cultivars.
- A number of different cassava cultivars were grown by farmers, with more than 10 cultivars identified in each district.

- Early bulking was the second most important farmer-preferred trait after high FSRY.
- Farmers suggested a number of attributes to be incorporated into early bulking cassava genotypes, the most important of which were: high dry mass content (DMC), sweetness and high FSRY.

Farmer participation in this research helped to identify the key factors that limit cassava production in Uganda. For example, CMD and CBSD are diseases of great economic importance not only in Uganda, but also in the whole of the east African region (Legg et al., 2011). Lack of early bulking cultivars is another limiting factor to cassava production in Uganda, which has also been identified in other east African countries (Mtunda, 2009; Kamau et al., 2011). Initially, information on the existing and potential impact of early bulking cassava cultivars in Uganda was rather limited, but the data collected from the PRA will form the basis for further research on the development of adapted early bulking cultivars.

More than 10 cassava cultivars were identified in each of the surveyed districts. Each cultivar had special attributes attached to it by the farmers, indicating that they select cultivars on the basis of a series of preferred traits effectively constituting an informal selection index. Early bulking was the second most important farmer-preferred trait. Farmers indicated that early bulking cultivars escape late season pests, diseases and droughts, they allow for multiple sequential cropping, and they are sweet. Above all, it was believed that early bulking cultivars generate food and income quicker. Farmers suggested a number of other attributes that they want incorporated into early bulking cultivars. Their key suggestions in order of importance were: high DMC, sweetness, high FSRY and resistance to pests and diseases. It was evident that to design a successful breeding programme to meet smallholder production system requirements, the farmers' trait preferences and production constraints must be clearly understood and taken into consideration. Accordingly, the farmers' trait preferences, production constraints and general suggestions were considered in the cultivar evaluations and selections conducted in this research and breeding programme.

7.2.2 Variation between selected cassava genotypes for storage root bulking and other important traits

- High variability for FSRY and all the other traits assessed was observed among the genotypes.

- Relatively high broad sense heritability estimates were observed for all the traits evaluated.

The genotype mean squares for FSRY, harvest index (HI), dry storage root yield, storage root number, storage root girth, postharvest physiological deterioration, cassava brown streak disease root necrosis (CBSD-RN), cassava mosaic disease severity and DMC were significant for the selected cassava genotypes evaluated as potential parents for a breeding programme. The high variability between genotypes for the traits evaluated implied that the genotypes could serve as parents for the improvement of all the traits evaluated. The relatively high broad-sense heritability estimates for each of the traits indicated that a large proportion of the phenotypic component of variance for all the traits was accounted for by the genotypic variance component relative to the environmental and genotype x environment variance components. In turn, this indicated considerable genetic variation among the genotypes in the expression of the traits that were unaffected by the environment. This genetic variability is important in a hybridisation and/or selection programme because it means that significant genetic gain through phenotypic selection is practically feasible for all the traits under study.

7.2.3 Genotype x environment interaction effects on early fresh storage root yield and other important traits

- Genotype effects were significantly different for early FSRY and other traits.
- Location effects were significantly different for all traits except CBSD-RN
- The GEI effects were non-significant for early FSRY, but significant for all other traits.

Significant genotype effects for early FSRY and all other traits indicated significant variation in the mean performance of the genotypes across locations for these traits. Significant location effects for all traits except CBSD-RN meant that the overall means of the genotypes at each location i.e. the location means were significantly different for most traits. The variation between genotypes and locations underlines the need to conduct multi-locational trials in order to identify both the generally and specifically adapted genotypes with good performance for the traits under consideration. Non-significant GEI effects for early FSRY, but significant GEI for all other traits indicated stable performance of the genotypes across the three locations for early FSRY, but unstable performance for other traits. Indeed, the greater percentage (67%) of the genotypes viz., Akena, CT2, CT4, NASE14, CT3, Nyara, CT5 and TME14 was stable for early FSRY.

7.2.4 Diallel analysis for early fresh storage root yield and related traits at the F_1 seedling and clonal evaluation stages

- A number of similarities and differences were observed regarding the diallel analyses conducted at the F_1 seedling and clonal evaluation stages, but the most crucial included the following:

Similarities:

- A high degree of variation among individual genotypes and families was observed for all traits assessed at both stages.
- Both additive and non-additive gene action were involved in the expression of the traits at the seedling and clonal stages.
- Parent genotypes that had been developed by hybridising CIAT and Ugandan germplasm had good combining ability for most of the traits at both stages.

Differences:

- Parent CT4 was the best general combiner for early FSRY and most other traits at the seedling stage while CT5 was the best general combiner for FSRY and most other traits at the clonal stage.
- The first three families with the best SCA effects for early FSRY at the seedling stage were: NASE3 x CT2, CT5 x CT3 and CT1 x B11 while the first three families at the clonal stage with the best SCA effects: CT1 x Nyara, CT1 x B11 and CT5 x TME14.

The high degree of variation between individual genotypes and families observed for all traits at both the seedling and clonal stages indicated high potential for selection of all traits assessed. High variation between individual genotypes and families for all traits at the seedling and clonal stages was also reported by Mtunda (2009) and Chikoti (2011).

At both the seedling and clonal stages, both the additive and non-additive gene actions were involved in the expression of the traits. Traits with predominant additive genetic effects could be further improved through cycles of recurrent selection. For traits where there was a predominance of non-additive gene effects in their expression, specific hybrid combinations could be made of parents drawn from different heterotic groups to maximise the expression of non-additive gene action. Following hybridisation of the selected parents, the non-additive gene effects that predominate in some traits could be “captured” or fixed in subsequent generations by exploiting the vegetatively propagatable nature of cassava. A reciprocal recurrent selection breeding strategy should be employed when breeding for traits under both additive and non-additive gene action. The challenge

remains to combine maximal expression of additively and non-additively determined traits within single new genotypes.

Combining ability analysis at the seedling stage was conducted to investigate the genetic control of storage root related traits given the high number of storage roots, from 1 - 23 plant^{-1}, which was produced by the seedling plants in this study. This high number of storage roots at the seedling evaluation stage was attributed to a combination of the technique that was used for germinating the botanical seeds and the good growing conditions (rainfall and temperatures) in Uganda. Seeds were germinated in plastic bags and the resulting seedlings with undamaged roots transplanted to the field. Ceballos et al. (2004) indicated that cassava seeds germinated in seedling containers and later transplanted as seedlings to the field often develop adventitious storage roots and that the mature plants that develop from such seedlings are similar in terms of the storage root formation to the plants derived from stem-cuttings. Usually, diallel analysis for storage root traits cannot be undertaken in areas where storage root development of transplanted seedlings is affected by high in-field variability. The diallel analysis conducted at the seedling stage in this study reduces the potential loss of useful background genetic data and breeding material when advancing to the clonal selection stages, and could be replicated wherever conditions permit to improve the effectiveness of cassava breeding programmes. Overall, parents and families with good combining ability for early FSRY and other pertinent traits at both the seedling and clonal evaluation stages were identified and will be exploited in the future cassava breeding programmes for early bulking and relevant traits in Uganda.

7.3 Progress in breeding for high yielding, early bulking cassava in Uganda

Significant advances were made in terms of breeding high yielding, early bulking cassava progeny with high DMC and resistance to CMD and CBSD using local and introduced cultivars as parents. For example, the best 50 F_1 genotypes selected based on farmers' most preferred traits namely, early bulking for FSRY and DMC, plus resistance to CBSD and CMD, were significantly better than their parents. All 50 selected genotypes had a higher early FSRY (≥25 t ha^{-1}) than the best parent's early FSRY (15.9 t ha^{-1}) (Chapter 6, Table 6.9). The best F_1 genotype (FM29-8), with an early FSRY of 75.0 t ha^{-1}, was obtained from CT5 x CT1, a family that was generated from parents with high positive and significant GCA effects for FSRY (Table 6.3). In addition, 17 out of 50 genotypes selected had DMC above the 41.4% recorded by the best parent (CT3). Similarly, 24 out of the 50 selected genotypes had a HI higher than 0.43 recorded by the best parent (CT1). All 50

selected genotypes had a score of 1.0 for both CMD-S and CBSD-RN and were therefore resistant to both CMD and CBSD. High mid- and better-parent heterosis were recorded for early FSRY in most of the families, a result that is certainly attributable to the genetically diverse parents that were used in the hybridisation programme.

7.4 Implications of the findings of this study for future cassava breeding

In this study high yielding, early bulking F_1 genotypes with high DMC and resistance to CMD and CBSD were identified. The next step is to generate sufficient planting materials of the genotypes to conduct preliminary yield trials and subsequent advanced yield trials. These trials will place emphasis on selecting high yielding and early bulking genotypes that have resistance to the pandemic diseases of cassava in Uganda, CBSD and CMD. Farmer participation at every stage of the evaluation trials will be a priority to ensure that high yielding, early bulking cultivars with farmer preferred traits are eventually released for cultivation. Participation of farmers at all stages of clonal evaluation will also ensure the rapid and successful adoption of the released cultivars. Should this strategy result in the improved high yielding, early bulking cassava cultivars with resistance to CMD and CBSD being rapidly adopted and integrated into the existing cassava based cropping systems as anticipated, the improved livelihoods of smallholder farmers and associated economic development will be self-evident in Uganda.

References

Chikoti, P. C. 2011. Development of cassava (*Manihot esculenta* Crantz) cultivars for resistance to cassava mosaic disease in Zambia. PhD thesis, University of KwaZulu Natal, South Africa.

Kamau, J., R. Melis, M. Laing, J. Derera, P. Shanahan, C. Eliud, and K. Ngugi. 2011. Farmers' participatory selection for early bulking cassava genotypes in semi-arid Eastern Kenya. Journal of Plant Breeding and Crop Science 3:44-52.

Legg, J.P., S.C. Jeremiah, H.M. Obiero, M.N. Maruthi, I. Ndyetabula, G. Okao-Okuja, H. Bouwmeester, S. Bigirimana, W. Tata-Hangy, G. Gashaka, G. Mkamilo, T. Alicai, and L.P. Kumar. 2011. Comparing the regional epidemiology of the cassava mosaic and cassava brown streak virus pandemics in Africa. Virus Research 159:161-170.

Mtunda, K.J. 2009. Breeding, evaluation and selection of cassava for high starch content and yield in Tanzania. PhD thesis, University of KwaZulu-Natal, South Africa.