Identification and development of cassava brown streak disease resistant and early storage root bulking varieties in Malawi

by

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Thesis abstract

Cassava (*Manihot esculenta* Crantz) production in Malawi, like in most of the East African countries, has suffered from cassava brown streak disease (CBSD), a disease that affects both the quality and yield of storage roots. The incidence of CBSD in Malawi has increased in recent years causing yield loss of up to 25%. Currently there is no information that indicates the availability of resistant cassava varieties in Malawi. In addition, most cassava varieties grown in Malawi are late bulking (12-18 months), and this contributes to high CBSD incidences, which increase with plant age. Therefore, there is need to develop CBSD resistant and early storage root bulking varieties, which can be harvested before the disease (storage root necrosis) becomes severe. Early storage root bulking, CBSD resistant varieties will not only provide good storage root quality and productivity per unit area of land, but will also facilitate the release of land for other farming activities. The main objective of the study was to develop cassava varieties that are resistant to CBSD and early storage root bulking, in order to improve the yield and quality of cassava in Malawi. The specific objectives of the study were (1) to assess farmers' knowledge of CBSD and its management, (2) to identify early storage root bulking cassava genotypes as well as traits associated with early storage root bulking, (3) to assess the effect of harvest time on cassava genotype performance, stability and adaptability, (4) to evaluate cassava genotypes for resistance to CBSD and its associated yield losses and (5) to determine the mode of gene action and the importance of combining ability effects in the inheritance of CBSD resistance and early storage root bulking traits.

Assessment of farmers' knowledge of CBSD indicated that the majority of the farmers did not know the disease through foliar symptoms and only 10.1% of the farmers were able to identify CBSD. The study established that CBSD is a continuing threat to the cassava industry, where high incidence levels were observed. On average, 75.0% and 71.7% of the farms had plants with leaf and storage root symptoms, respectively. The average CBSD leaf incidence per farm was 31.2% with levels up to 86.7% on some farms. At harvest, 88.3% of the farmers' cassava fields exhibited storage root necrosis. Most farmers were found to lack a source of clean planting material and the lack of new improved varieties was reported as the most important constraint of cassava production, apart from CBSD. Therefore, the results suggest that education of farmers on the efficient management of this viral disease through selection of clean planting material should be provided.

Early storage root bulking and agronomic traits associated with early bulking in cassava, was studied at two sites over two seasons with 16 genotypes. High yields of up to 9.5 t ha^{-1} at 6 months after planting (MAP) and 17.8 t ha^{-1} at 9 MAP were obtained and four varieties were

identified as early-bulking (Mulola, Phoso, Mbundumali and Maunjili). The study further identified harvest index and shoot mass as the major selection criteria in improving fresh storage yield and dry storage root yield. The results indicated that both source and sink capacities were important for determining early yield. Therefore, these two traits are the key determinants of early storage root bulking and should be used when selecting early bulking varieties.

On the effect of harvest time, the study revealed that genotype, environment and genotype x environment interaction have a significant influence on the performance of varieties, regardless of the harvest time. Most of the cassava varieties exhibited specific adaptation to certain environments. The study identified five varieties (Mulola, Phoso, Maunjili, Beatrice and Unknown) that exhibited consistent performance, stability and adaptability across the three harvest periods (6, 9 and 12, MAP). The results, therefore, showed that multi-location studies in cassava, regardless of the time of harvest, could help discriminate genotypes with superior performance, stability and general adaptation. In terms of resistance to CBSD, high significant differences in CBSD incidence and severity values were observed (some varieties reached as high as 94.9% and severity of up to 3.8). The CBSD storage root severity increased with the prolonged stay of the crop in the field. The study established that yield loss due to CBSD was significantly associated with storage root severity at different harvest times and a maximum yield loss of 43.1% was recorded at 12 MAP on Kalawe, while at 9 and 6 MAP, maximum yield loss was 24.8% and 10.9%, respectively. The study identified five varieties to be resistant/or tolerant to CBSD (Phoso, Maunjili, Mpale, Sauti and TMS4(2)1425). The results, in general, suggest that an integrated approach should be used by farmers in order to effectively manage CBSD, which among others include using varieties that are early bulking and resistant/tolerant to CBSD, selecting planting material free from CBSD, sanitation and roguing infected plants from the field, especially shortly after sprouting.

Four parental genotypes (Silira, Mulola, Phoso and Mkondezi) were identified as the best general combiners for the CBSD resistance and early storage root bulking. Thirteen progenies exhibiting CBSD resistance and early storage root bulking traits were identified and selected for advancement. The study established that resistance in cassava for CBSD, as well as for early storage root bulking is controlled by both additive and non-additive gene action. However, additive gene action is more important than non-additive type of gene action in the inheritance of CBSD resistance and early storage root bulking. The implication is that mass phenotypic recurrent selection after hybridisation of elite clones could, therefore, be effective for the development of varieties resistant to CBSD as well as addressing challenges related to late storage root bulking.

Declaration

I, Michael Malandula Chipeta 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.
4. This thesis does not contain any other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
    a. Their words have been rewritten, but the general information attributed to them has been referenced;
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Signed
…….. Date……
Michael Malandula Chipeta (Candidate)

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

Signed
…….. Date……
Prof. Rob Melis (Principal supervisor)

Signed
…….. Date……
Dr Julia Sibiya (Co-supervisor)

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Dedication

This dissertation is dedicated to Eugene Chipeta and Juliana Kachama. You are the reason I work very hard.

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1 Thesis introduction

1.1 General importance of cassava

Cassava *(Manihot esculenta* Crantz*)* is regarded as the major staple food crop for more than 800 million people in the world (Lebot, 2009). It is an essential energy source for many resource-constrained people facing problems of food availability, especially in the developing countries (Axtell and Adams, 1993). Cassava produces a higher amount of food calories per hectare than do most other tropical crops (Onwueme, 1978), and it is estimated that about one-third of the sub-Sahara African population obtains more than half of their calories from foods made from cassava storage roots (IITA, 1990). The amount of energy obtained from cassava products is likely to increase due to an increased production of cassava in this region. Cassava's importance is mainly derived from its multifaceted use, in which leaves provide a significant proportion of protein, iron and other nutrients when used as vegetables; storage roots contain about 25 to 35% starch which is used in food industries as sweetened products, thickeners and the textile and paper industries (FAO, 1993; Hahn, 1988; Moyo et al., 1999; Nweke et al., 2002).

1.2 Importance of cassava in the Malawian farming systems

Despite the fact that maize (*Zea mays*) is by far the most important staple food crop in Malawi accounting for over half (54%) of the caloric intake of households (Minot, 2010), cassava is second to maize and is a staple food crop for almost 30-40% of the population. This is especially the case in the lakeshore areas of Karonga, Rumphi, Nkhata Bay, Nkhotakota, Salima and Mangochi districts (Chiwona-Karltun and Mkumbira, 2000; Moyo et al., 1999; Shaba et al., 2003), where it contributes more than 7% of total caloric intake (Kambewa, 2010). In some districts such as Mzimba, Kasungu, Lilongwe, Dedza, Dowa, Machinga and Mulanje, cassava is becoming a major cash crop and therefore it forms an important part of the farming systems throughout the country (MoAFS, 2004).

It is expected that cassava will continue to play a pivotal role in the farming systems as a major food crop as well as an income provider. This is due to its comparative advantages over other crops, such as drought tolerance, low requirements for inputs such as fertilizers and chemicals, flexibility in planting and harvesting, convenience in ground storability, adaptation to a wide range of agro-ecological conditions, efficiency in utilization of mineral reserves of marginal soils,

diverse modes of utilization and high dry matter yield per hectare (MoAFS, 2007; Westby, 2002).

1.3 Cassava production trends

Brazil was the leading world producer up to the early 1960s (FAO and IFAD, 2005). However, a significant increase in production has been registered in Africa in recent years. Africa presently contributes more than half of the total world production (FAO and IFAD, 2005; Hillocks et al., 2002). Currently, Nigeria is the leading world producer (FAO and IFAD, 2005; FAOSTAT, 2016; Hillocks et al., 2002; Phillips et al., 2004), contributing about 19% and 35% to total world and African production, respectively. Other notable cassava producers in Africa include the Democratic Republic of Congo (19% of African production), Ghana (8%), Tanzania (7%) and Mozambique (6%) (Hillocks et al., 2002). The increase in cassava production in Africa has mainly been attributed to the increase in area under cultivation, tolerance of the crop to pests and diseases, and in response to hunger as a cheap source of calories (FAO and IFAD, 2005; Hillocks et al., 2002).

In the last decade, Malawi has registered a significant increase in cassava production (Figure 1.1), due to the increased area under cassava cultivation, better institutional support such as research in development of high yielding varieties, increased dependence on cassava for food security, an alternative source of income, and the improved management practices (IITA/SARRNET, 2007). It is anticipated that production will continue to grow due to increased support to cassava production by different stakeholders, and also because more farmers are becoming aware of the importance of crop diversification as a means to sustained crop production and food security.

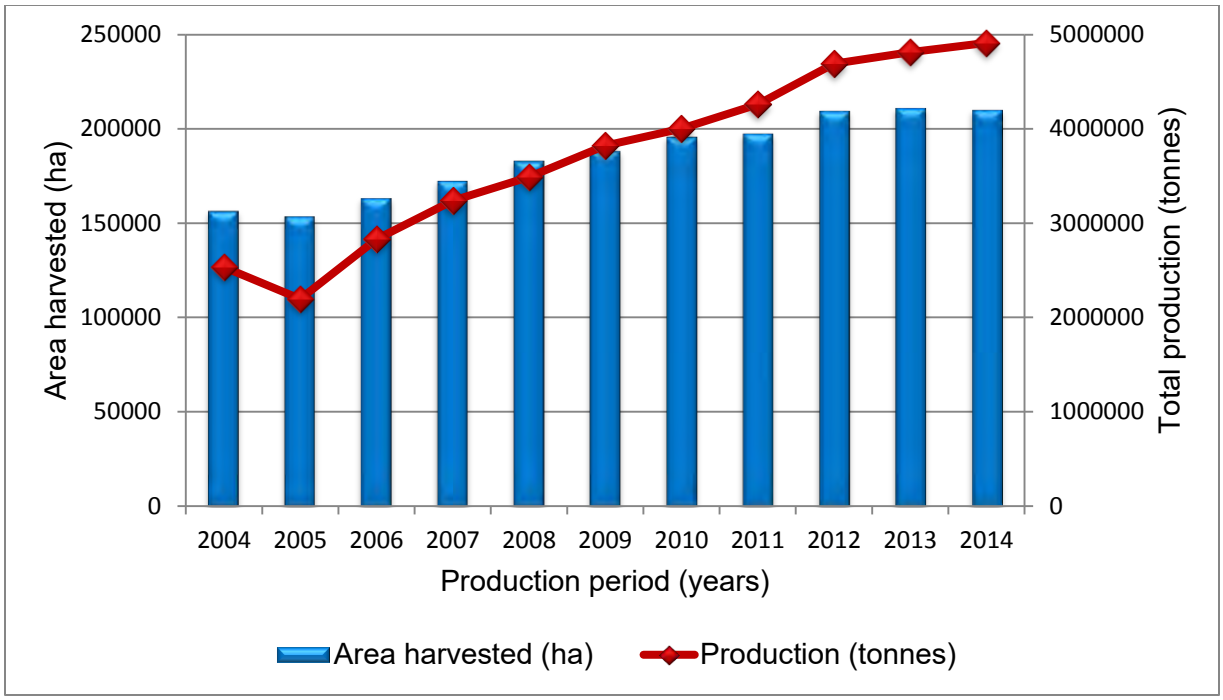

Figure 1.1. Total cassava production (tonnes) and area harvested (ha) from 2004-2014

Source FAOSTAT (2016)

1.4 Constraints to cassava production

There are various hurdles to sustained cassava productivity in terms of yield and quality globally, and more particularly in Africa. The main biotic constraints are pests and diseases (FAO and IFAD, 2005) and these are prominent in both traditional and new areas of production (Dixon and Ssemakula, 2008). Pests affect production by causing damage to cassava foliage, thereby reducing the photosynthetic area and inhibiting nutrient transport by damaging the stems (IITA, 1990). Diseases affect plant establishment and vigour, inhibit photosynthetic efficiency and cause pre- or post-harvest deterioration by damaging the storage roots, stems and foliage (Dixon et al., 2003; IITA, 1990; Mahungu et al., 1994). The major pests and diseases in Africa are cassava mealy bug (CMB) (*Phenacoccus manihoti*), cassava green mite (CGM) (*Mononychellus tanajoa*), whitefly (*Bemesia* species), cassava mosaic disease (CMD), cassava bacterial blight (CBB) and cassava brown streak disease (CBSD) (Dixon et al., 2003; Legg and Thresh, 2003).

Due to the clonal propagation of cassava, the crop is vulnerable to the effects of virus diseases, which are a major threat to sustained cassava production, affecting the livelihoods of millions of

Africans (Legg and Thresh, 2003). Recently, CBSD has become of great concern in the East African region, where it diminishes consumption and market qualities of the storage roots (Abaca et al., 2012; Alvarez et al., 2012; Mbanzibwa et al., 2011; Winter et al., 2010). The disease has not spared Malawi, where most farmers, especially along the lakeshore, have been affected (Benesi et al., 2010; Gondwe et al., 2003; Shaba et al., 2003).

Cassava production is also affected by other constraints such as low yield potential, long growth period/late bulking, early postharvest deterioration, infertile soils, planting of unimproved varieties, and shortage of labour, land and capital for cassava production (Dahniya, 1994; IITA, 1990). In Malawi, the most pressing abiotic constraint is the use of late storage root bulking local varieties (Gondwe et al., 2003). The combination of late storage root bulking and CBSD infections makes the farmer more vulnerable to food insecurity, as by the end of the season s/he realises very little from the long awaited harvest.

1.5 Generation of genetic variability among parental genotypes

Morphological (phenotypic) and agronomic characterisation enables plant breeders to gain a better understanding of the nature of the diversity among genotypes (Cowen and Frey, 1987; Schut et al., 1997). This facilitates the selection of parents from large sets of genotypes and the prediction of performance of the progenies from such crosses (Schut et al., 1997). The use of diverse parental combinations in breeding may provide a large supply of allelic variation that can be used to create favourable gene combinations with increased levels of genetic variation, increased heterosis and with a marked increase in transgressive segregants (Lokko et al., 2006). Therefore, characterisation of genetic variability based on phenotypic data (reaction to CBSD and maturity) among cassava genotypes can help in the selection of parental genotypes for genetic recombination.

1.6 Problem statement

The incidence of CBSD in Malawi has increased in recent years causing yield loss of up to 25% (Gondwe et al., 2003). This is mainly due to the use of the clonal propagation, which encourages the build-up of the viral load, thereby rendering agronomic practices ineffective in curbing the disease spread. In addition, the use of susceptible, late storage root bulking varieties has contributed to CBSD alarming spread in farmers' fields. Currently there is no information that indicates the availability of resistant cassava varieties (Theu and Mazuma,

2008), despite the large number of varieties being grown (IITA/SARRNET and Malawi Government, 2004). Since the disease was reported in Malawi, only limited research work on resistance breeding has been initiated (Shaba et al., 2003). In this regard, there is a need to evaluate/screen cassava varieties in order to identify sources of CBSD resistance and to develop resistant varieties through breeding. In addition, most cassava varieties grown in Malawi are late bulking (12-18 months), and this contributes to high CBSD incidences, which increase with plant age (Alvarez et al., 2012; Hillocks et al., 2002). Therefore, there is need to develop early storage root bulking varieties which can be harvested before the disease (storage root necrosis) becomes severe. This in turn will effectively reduce the production period, resulting in a faster rate of return to investment. Early storage root bulking and CBSD resistant varieties will not only provide good storage root quality and productivity per unit area of land, but will also facilitate the release of land for other farming activities.

1.7 Research goal

The overall aim of the study was to assess the farmers' perception to cassava brown streak disease, develop early storage root bulking varieties and resistant to CBSD in order to improve the yield and quality of cassava and subsequently contribute to food security, and improved income among smallholder farmers in Malawi.

1.7.1 Research objectives

The specific objectives of the research were the following;

1. To assess farmers' knowledge of cassava brown streak disease and its management in Malawi
2. To identify early storage root bulking cassava genotypes as well as traits associated with early storage root bulking
3. To assess the effect of harvest time on cassava genotypes performance, stability and adaptability
4. To evaluate cassava genotypes for resistance to cassava brown streak disease and its associated yield losses
5. To determine gene action and the importance of combining ability effects in the inheritance of CBSD resistance and early storage root bulking traits

1.8 Thesis organisation

The thesis has been organised according to the specific objectives. Each chapter is independent and chapters 2 to 6 have been prepared in accordance with journal publication formats. Therefore, there might be overlap of content and references[1].

1. Thesis introduction
2. Chapter 1: Literature review
3. Chapter 2: Assessment of farmers' knowledge of cassava brown streak disease and its management in Malawi
4. Chapter 3: Early storage root bulking index and agronomic traits associated with early bulking in cassava
5. Chapter 4: Effect of harvest time on cassava genotypes performance, stability and adaptability
6. Chapter 5: Evaluation of cassava genotypes for resistance to cassava brown streak disease and its associated yield loss
7. Chapter 6: Combining ability and mode of gene action for resistance to cassava brown streak disease and early storage root bulking
8. Chapter 7: Thesis overview

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[1] Referencing format in this thesis is for American Crop Science Journal

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Chapter 1

1 Literature review

1.1 Introduction

This review summarises the key research findings pertaining to cassava brown streak disease (CBSD) and early storage root bulking in cassava (*Manihot esculenta* Crantz) and identifies some of the research gaps that require immediate to long term interventions. This review focuses on, but is not limited to, the origin of cassava, causal organism of CBSD and the symptoms associated with the disease, its economic impact, control strategies, mechanism of resistance, genetic variability and inheritance pattern, gene action, early maturity, traits associated with early maturity, genetic variability, association between CBSD and plant age, and farmers' preferences for various cassava traits.

1.2 Cassava the crop, origin and spread

Cassava (*Manihot esculenta* Crantz) is a perennial root crop cultivated worldwide, mainly in the lowland tropics (Grüneberg et al., 2009). It is a monoecious, highly heterozygous plant which contains 36 chromosomes and shows regular bivalent pairing during meiosis. Pachytene studies indicate that *Manihot* species are probably segmental allotetraploids derived from crossing between two taxa whose haploid complements had six chromosomes in common, but differed in the other three (Grüneberg et al., 2009; Jennings and Iglesias, 2002).

Cassava is believed to have originated from the Amazon region of South America (Grüneberg et al., 2009; Henry and Hershey, 2002). Phylogeographical studies further suggest that cassava was domesticated from wild *Manihot* species populations along the southern border of the Amazon basin (Olsen and Schaal, 1999, 2001). This is supported by the fact that the largest density of diversity and wild species are found in West-Central Brazil. Around the sixteenth century, cassava spread from the region to the rest of the world by the Portuguese navigators, first to West Africa and later to Eastern Africa, Madagascar and Southern India (Grüneberg et al., 2009; Hillocks, 2002). In Malawi, cassava mainly came from Tanzania and Mozambique between the 17th and the 19th centuries through the traders and people migrating between the two countries (Chipeta and Bokosi, 2013; Terry et al., 1981). Since its introduction in Malawi, cassava has gained in importance both as a food security crop and a source of income for many

smallholder farmers and the less affluent farmers. However, recently, cassava production in Malawi has experienced the huge set back due to viral infections such as CBSD and CMD (Gondwe et al., 2003; Shaba et al., 2003).

1.3 Cassava brown streak disease

The CBSD is currently the most devastating disease of cassava alongside cassava mosaic disease (CMD). The disease is endemic mainly in the coastal areas of East Africa (Alvarez et al., 2012; Mbanzibwa et al., 2011; Ntawuruhunga and Legg, 2007; Winter et al., 2010), from Kenya in the north to Mozambique to the south. For decades it has also been prevalent in Malawi (Nichols, 1950). It has also been reported from some locations in Uganda and Zambia (Hillocks et al., 1996). The prevalence of CBSD in Malawi was confirmed by Benesi et al. (2010), who reported that CBSD was only prevalent along the rift valley in the north and south of Malawi, while earlier studies (Gondwe et al., 2003; Shaba et al., 2003) showed that CBSD was prevalent in the whole lakeshore strip, that is, from Karonga in the north to Mangochi in the south.

1.3.1 Disease causing agent

Cassava brown streak disease is caused by the cassava brown streak virus (CBSV) (Monger et al., 2001a) and the Ugandan cassava brown streak virus (UCBSV) of the genus *Ipomovirus* and family *potyviridae* (Mbanzibwa et al., 2011; Monger et al., 2001b). A detailed identification of the causal agent involved several molecular tools in which a partial sequence of 1114 nucleotides of a virus from cassava brown streak diseased (CBSD) material, collected from Tanzania, was obtained. The detected sequence from the reverse transcription (RT)-PCR procedure was subsequently compared with known closely related viruses (*Potyviridae*). The closest sequence identity was with the coat protein of sweet potato mild mottle virus (genus *Ipomovirus).* This provided evidence that CBSV is an *Ipomovirus* and because it is consistently associated with CBSD, can be considered to be the causal agent (Monger et al., 2001a).

1.3.2 Disease spread and transmission

Storey (1936) in Tanzania demonstrated that the CBSV was spread through vegetative propagation and through grafting, which was confirmed by Munga (2008) and Mohammed et al. (2012), who reported a transmission efficiency of 92% and 100%, respectively, using grafting.

Other studies (Lister, 1959) showed that CBSV was also transmissible through sap, which has been confirmed in more recent studies (Mohammed et al., 2012; Munga, 2008). Munga (2008) reported some transmission when injecting plants with CBSV-infected sap or rubbing the sap on the leaves with carborundum powder, while Mohammed et al. (2012) were not successful when they used the methods. Other reported successful inoculation techniques are soaking cuttings in infected sap, and topping and spraying (Munga, 2008). In Kenya (Mware et al., 2009) it was shown that whiteflies (*Bemisia tabaci)* contributed considerably to the spread of CBSD as there was a significant and positive correlation between *B. tabaci* populations and CBSD incidence. The question of whether CBSV was transmitted by two species of whitefly (*B. tabaci* or *B. afer*) (Bock, 1994) was put to rest in 2005 (Maruthi et al., 2005), when it was finally resolved that *B. tabaci* was the vector, with a transmission efficiency of approximately 25% (Legg et al., 2011; Mware et al., 2009).

1.3.3 Symptoms associated with cassava brown streak disease

Cassava brown streak disease symptoms are manifested in various organs, namely, leaves fruits, stems and storage roots (Alvarez et al., 2012; Calvert and Thresh, 2002; Hillocks et al., 2001). These symptoms vary in expression and severity, and depend on the plant genotype, the stage of plant growth and the weather conditions (Alvarez et al., 2012; Calvert and Thresh, 2002; Hillocks and Jennings, 2003; Hillocks and Thresh, 2000).

Leaf symptoms

Leaf symptoms are mainly manifested as chlorosis around the secondary veins (Alvarez et al., 2012; Hillocks et al., 1996), which may extend to the tertiary veins. The most common leaf symptoms are manifested as yellow blotches, which are not closely associated with the leaf veins, but are more or less evenly distributed over the whole leaf surface. These symptoms are mainly expressed on mature or nearly mature leaves which shed in dry weather or during the cool season (Nichols, 1950). In susceptible varieties, symptoms are characterized by brown to black streaks on the young stem, which elongate and coalesce, forming blotchy patches which are subsequently followed by the formation of necrotic or black lesions in the leaf scars. Later they increase in size, killing the dormant buds (Nichols, 1950).

Storage root symptoms

In the storage roots, CBSD is quite damaging and is manifested both internally and externally (Alvarez et al., 2012). Internal symptoms are characterized by yellow to brown corky patches in

the root pulp or blue to black streaks under the root cortex, while on external symptoms storage roots appear necrotic which also develop characteristic constrictions (Alvarez et al., 2012; Bull et al., 2011; Calvert and Thresh, 2002; Hillocks and Thresh, 2000).

Relationship between above and below ground symptoms

It is not very clear whether there is positive correlation between leaf symptoms and storage root necrosis. It has been shown, for instance, that some varieties with clear leaf symptoms may fail to express storage root symptoms, while others not showing leaf symptoms may exhibit storage root symptoms (Legg and Thresh, 2003). Molecular studies conducted by Moreno et al. (2011), showed a high correlation between the CBSV load in the aboveground plant organs with the CBSV load in the cassava storage roots. In Tanzania (Hillocks et al., 1996), studies revealed that most varieties with leaf symptoms also had storage root necrosis. In Mozambique, Hillocks et al. (2002) reported that in mature plants, storage root necrosis occurred together with foliar symptoms. In contrast, Hillocks et al. (2001) reported that the presence of foliar symptoms was clearly not an indication that a variety will show storage root necrosis but generally, storage root necrosis develops after foliar symptoms (Hillocks and Thresh, 2000). These variations in leaf and storage root symptom expression are therefore a manifestation of varietal differences. That varieties differ in the expression of foliar symptoms, and the degree to which they exhibit stem and storage root symptoms, has also been reported by other workers (Hillocks and Jennings, 2003; Nichols, 1950). The contrasting reports on CBSD symptoms indicate that there is an information gap regarding the relationship between the above and the below ground symptoms, thereby giving room for further research on the subject.

1.3.4 Control strategies for cassava brown streak disease

As cassava is vegetatively propagated, it is prone to viral infections as planting material are being carried from one field to the other and from one growing cycle to the next (Legg and Thresh, 2003). This practice promotes the build-up of viral diseases including CBSD. The disease, therefore, can be managed by selecting planting material free from CBSD and roguing of any infected plants from the field, especially shortly after sprouting (Hillocks and Jennings, 2003; Hillocks and Thresh, 2000; IITA/SARRNET and Malawi Government, 2004; Legg et al., 2011).

A viable option, in which the disease can effectively be controlled, is planting varieties that are resistant to the disease (Hillocks and Thresh, 2000; IITA/SARRNET and Malawi Government,

2004; Shaba et al., 2003). There is a general consensus that genotypes react differently to CBSD infection depending on the environment/location. Thus, a resistant variety developed elsewhere may be rendered susceptible if introduced into a contrasting environment or location. Winter et al. (2010) found that varieties, which were susceptible to CBSD isolates from Mozambique and Tanzania, were resistant to infections with isolates from Malawi, Kenya and Uganda. Therefore, the control of CBSD in a particular location or country should take place by developing resistant varieties in the area and with locally preferred traits.

Early harvesting is used by some farmers in order to avoid yield losses due to CBSD (Hillocks, 2003; Hillocks et al., 2001). However, this method in itself reduces yield, unless it is being practised on early bulking varieties. Therefore, efforts should be driven towards the simultaneous development of early storage root bulking and CBSD resistant varieties.

1.3.5 Mechanisms of cassava brown streak disease resistance

Resistance has been defined as the hereditary capability of the host to reduce the development of a pathogen after its infection so that severity of the disease is minimized (Chahal and Gosal, 2002). Different types of resistance in cassava in relation to CBSD have been described by Hillocks (2004). Firstly, there is the type 1 resistance, where the plant readily becomes infected with the virus and shows distinctive leaf symptoms, but storage root necrosis is less severe, or its onset is delayed until after the main period of storage root-bulking. This type of resistance is called tolerance. When the plant readily becomes infected with the virus, but only mild symptoms are expressed in leaves and storage roots, the resistance is called type 2 and is also known as tolerance. In some cases plants show leaf symptoms when inoculum pressure is high, but fewer plants become infected compared to fully susceptible controls. But once infected, severe storage root necrosis may develop. This type of resistance to infection is known as type 3. When the plant shows no symptoms under high inoculum pressure, and the virus cannot be detected in any part of the plant, the reaction is called hypersensitivity or immunity and is referred to as type 4. This reaction is attributed to either the failure of the vector to transmit the virus to the varieties or the virus is transmitted, but does not multiply beyond the site of infection.

1.3.6 The economic impact of cassava brown streak disease

The impact of CBSD on cassava is two-fold, namely, a low yield and a poor storage root quality (Gondwe et al., 2003; Hillocks et al., 2001). There are contrasting findings on the impact of CBSD on the yield of cassava. Nichols (1950) and Bock (1994) reported small differences

between the yield of healthy and infected plants. Hillocks et al. (2001), on the other hand, reported yield losses of up to 70% with susceptible varieties in studies conducted in Tanzania. These substantial losses are not surprising given that CBSD leads to the production of fewer and smaller storage roots, and distorted storage roots due to pitting and constrictions. In addition, low storage root yield is also attributed to the retarded storage root fill in more susceptible varieties, which tends to increase with the physiological age of the crop (Hillocks, 2003). In Malawi, yield losses in the range of 20-25% have been reported (Gondwe et al., 2003) and at present, the average yield losses are likely to be higher, as the disease continues to spread and the severity increases. It would, therefore, be important to quantify yield loss among smallholder farmers in Malawi due to CBSD as this would give the current overall status of the disease's impact.

It has been reported that the impact of CBSD is vividly manifested through the quality of diseased storage roots especially where the infection results in storage root necrosis (Bock, 1994; Gondwe et al., 2003; Hillocks et al., 2001; Nichols, 1950), making the storage roots unmarketable and sometimes unfit for human consumption. In addition, CBSD affects the viability of the cuttings (Hillocks and Jennings, 2003) and the subsequent growth, resulting in a low plant population, which in turn may lead to low yields.

1.3.7 Diagnosis of cassava brown streak disease

Good management strategies for viral diseases can effectively only be implemented when there are robust virus detection and identification methods (Naidu and Hughes, 2001). The methods used to detect virus infections are those based on visual symptoms (interaction of the host and the pathogen) and protein or nucleic acid properties of the virus (Lima et al., 2012; Naidu and Hughes, 2001).

The symptoms of CBSD are usually inconspicuous in young developing leaves (4-5 months of growth), while in mature plants it becomes difficult to differentiate them from the effects of the onset of winter and dry season, and also from the symptoms of other biotic stresses such as CMD and CGM (Hillocks, 2004; Hillocks et al., 1996). Additionally, viral symptoms depend on the virus strain involved, plant genotype and climatic conditions which sometimes make it impossible to visually diagnose the virus infections (Calvert and Thresh, 2002; Hillocks and Thresh, 2000; Lima et al., 2012). This means that more robust virus indexing methods need be

used. The commonly used methods are those that depend on the serological (protein) and molecular (RNA) properties of the virus.

Protein based detection methods depend on antigen-antibody interactions, where polyclonal or monoclonal antibodies produced against the proteins of interest are used as probes to detect the target proteins by techniques known as enzyme-linked immunosorbent assay (ELISA) (Kumar, 2012; Lima et al., 2012; López et al., 2009; Naidu and Hughes, 2001). This technique is widely used in virus indexing because of its low cost, adaptability and high sensitivity, so that even low viral particle concentrations can be detected with ease and can accommodate large samples within a specified short period of time (Lima et al., 2012; Naidu and Hughes, 2001).

Nucleic acid detection methods mainly use polymerase chain reaction (PCR) in which the target RNA is converted to a complementary DNA (cDNA) copy by reverse-transcription, which is used for amplification, a process called reverse transcription-polymerase chain reaction (RT-PCR) (Naidu and Hughes, 2001). This method has been developed for the detection of cassava brown streak virus by Monger et al (2001a) and is currently in use. In addition to the advantages of ELISA, the PCR method can utilise any region of the viral genome for detection, whereas ELISA can make use of about 10% of the viral genome (Gould and Symons, 1983).

1.4 Genetics of cassava-pathogen interaction and inheritance pattern

An interaction between a pathogen and the host plant is a prerequisite for the development of disease infections. The genetic material (DNA) governs the properties of each of the two organisms (Fehr, 1991). The degree of susceptibility or resistance (reaction of the host) to various pathogens is an inherited characteristic, and it is this understanding that has effectively led to breeding and distributing varieties resistant to pathogens causing particular diseases (Agrios, 2005).

The scientific basis of plant breeding for resistance to diseases was established by Biffen and his co-workers from Cambridge University in the early 1900s, in which it was demonstrated that the disease resistance in plants could be inherited in the Mendelian fashion and that disease control might be achieved by incorporation of one or a few genes conferring resistance (Acquaah, 2012; Carlile, 1995). Resistance conferred by the incorporation of one or a few genes into a crop plant is known as monogenic (Acquaah, 2012; Fehr, 1991). Authors, who initially proposed the concept, considered that for each gene capable of conferring specific resistance on a host plant, a corresponding complementary gene exists or will arise in the pathogen

populations capable of overcoming this specific resistance (Agrios, 2005; Fehr, 1991). Where single gene resistance is in operation, dominance gene action is reportedly to be more common than monogenic recessive resistance (Acquaah, 2012).

However, it is now widely recognised that resistance may be controlled by any number of genes and that many varieties possess resistance that is effective against all races of a particular pathogen (Agrios, 2005). When the resistance is contributed by many genes, each with a minor effect, it is commonly referred to as a polygenic or horizontal resistance (Acquaah, 2012; Agrios, 2005; Fehr, 1991).

In cassava, resistance is predominantly of the horizontal type which is governed by many genes (polygenic) (Bellotti and Kawano, 1980). For pests such as cassava mealy bug and cassava green mite, there is partial resistance (Le Ru and Calatayud, 1994). Cassava mosaic disease resistance is also controlled by quantitative genes and appears to be recessive in nature (Hershey, 1987; Jennings and Iglesias, 2002).

Cassava brown streak disease has been the least studied viral disease of cassava, but attempts have been made to understand the genetics of CBSD resistance which, amongst others, led to breeding studies in Tanzania involving interspecific hybridisation between *M. glaziovii* and *M. melanobasis.* Later, resistance to CBSD was identified to be polygenic and recessive in nature (Jennings and Iglesias, 2002; Munga, 2008).

1.5 Genetic variability in cassava for resistance to cassava brown streak disease

The genetic variation in plants is an important resource for plant breeders, as it guides the direction of improvement to be pursued. In cassava, there is a wide array of variation for various traits such as yield, storage root number, dry mass content, starch content, harvest index, early storage root bulking, abiotic stress tolerance, pest and disease resistance etc. (Abaca et al., 2012; Akinwale et al., 2010; Chipeta et al., 2015; Chipeta et al., 2013; Hillocks et al., 2001; Jennings and Iglesias, 2002; Kamau et al., 2010; Kulembeka et al., 2012; Mtunda, 2009; Munga, 2008; Nichols, 1950; Okechukwu and Dixon, 2009; Parkes, 2011; Suja et al., 2010; Theu and Mazuma, 2008; Were et al., 2004; Zacarias and Labuschagne, 2010).

Since the first reports of CBSD, a series of studies have been conducted to understand and identify the various sources of resistance from both the cultivated and wild species of cassava (Abaca et al., 2012; Bock, 1994; Hillocks et al., 2001; Hillocks et al., 2002; Jennings, 1960;

Jennings and Iglesias, 2002; Nichols, 1950; Storey, 1936; Thresh, 2003). These and many more studies have indicated the potential existence of variability in cassava germplasm, which needs be fully exploited (Ceballos et al., 2004), and this has greatly renewed the thrust of many scientists working on cassava, both in academia and research institutions.

1.6 Gene action and importance of combining abilities

Economically important traits are governed by many genes with minor effects on the expressed traits. The mode in which these genes are expressed in a population is referred to as gene action, and they are classified into four types, namely, additive, dominance, epistasis and over-dominance (Acquaah, 2012; Sleper and Poehlman, 2006). In general, these gene actions are grouped into two, additive and non-additive (Sleper and Poehlman, 2006). Additive gene action represents the heritable portion of variation that is passed from parents to offspring and thus plant breeders place much emphasis on this as it dictates what the progeny will be like (Acquaah, 2012). With cassava being a highly heterozygous crop, it has been argued that non-additive (dominance) gene action plays an important role in the genetic expression of traits, thereby proposing exploitation of this gene action as any genetic gain would be carried forward through vegetative propagation (Ceballos et al., 2004). Knowledge of gene action is useful to plant breeders in aiding the selection of parents for use in the hybridization programmes and also in the choice of appropriate breeding procedures for the genetic improvement of various quantitative traits.

The nature of gene action in quantitative traits is studied with the use of mating designs and associated biometrical analysis, such as diallel cross (methods 1,2,3, 4, partial), North Carolina designs (I, II, III), line x tester, bi-parental and polycross (Acquaah, 2012; Chahal and Gosal, 2002; Hinkelmann, 2012).

General combining ability refers to the average performance of a line or genotype in all its crosses and it is a measure of the breeding value of a given genotype due to additive gene effects (Ceballos et al., 2004; Falconer and Mackay, 1996). On the other hand, specific combining ability refers to the combinations (crosses) that do relatively better or worse than would be expected on the basis of the average performance of the genotypes involved in a cross which result from specific allelic combinations or dominance effects (Ceballos et al., 2004; Falconer and Mackay, 1996; Griffing, 1956).

Different studies report divergent findings on the type of gene action influencing various traits in cassava. It is not clear whether these differences are due to the materials (reference population) used, study sites (environment), mating designs deployed, type of analysis employed or evaluation stage (seedling or clonal). Zacarias and Labuschagne (2010), using a diallel mating design in Mozambique, reported higher SCA variance than GCA variance for CBSD resistance, demonstrating that resistance is largely under the influence of non-additive gene action, while Munga (2008) in Kenya and Kulembeka et al. (2012) in Tanzania, using the same design, found that additive gene action was more predominant. These results, however, are based on a single location (with the exception of Kulembeka, 2012, who used two locations), fixed reference population and different analysis methods.

For storage root mass, a preponderance of non-additive gene effects has been reported (Kamau et al., 2010; Parkes, 2011; Zacarias and Labuschagne, 2010), while for storage root number, both additive (Chipeta et al., 2013; Kamau et al., 2010; Mtunda, 2009) and non-additive (Chipeta et al., 2013) gene effects have been reported. Cassava mosaic disease resistance is said to be predominantly additive in nature (Dixon, 2004), but some studies have reported predominance of non-additive gene effects (Kamau et al., 2010; Parkes, 2011).

The contradictory reports on the nature of gene action determining important traits, present a confusing picture for any cassava breeder on which to base breeding strategies. However, as premised by Ceballos et al. (2004), since non-additive gene effects are likely to play a significant role in cassava breeding due to the heterozygotic nature of the crop, it would be worthwhile for cassava breeders to exploit the dominance effects, which are ultimately due to non-additive effects.

1.7 Earliness in cassava

Various studies on earliness in cassava have reported varying yields. Fresh storage root yields of 25 to 28 t ha^{-1} at six months after planting (MAP) have been reported in two studies (Nair and Unnikrishnan, 2007; Okechukwu and Dixon, 2009), while another study (Asante, 2010) reported 15.5 t ha^{-1} at 6 MAP. Okogbenin and Fregene (2002) also reported dry storage root yield of about 14.5 t ha^{-1} at 7 MAP. These reported yields indicate that variability exists in cassava, which needs to be exploited in order to breed for early bulking cassava varieties. Earliness in cassava is due to a genotype's ability to quickly accumulate assimilate reserves in its storage roots and to produce a high and increasing number of storage roots during the growth cycle (Segnou, 2000).

1.8 Relationship between cassava brown streak disease and cassava maturity period

There is no linearity in the time taken between the appearance of foliar symptoms of CBSD and the development of storage root necrosis, but it varies from variety to variety (Hillocks and Jennings, 2003; Hillocks et al., 2001; Hillocks and Thresh, 2000). Above ground symptoms are clearly expressed in the early stages of plant growth, while storage root symptoms are mainly exhibited at an advanced stage of plant growth predominantly from seven MAP (Benesi et al., 2010; Hillocks et al., 2001; Hillocks et al., 2002), but may start as early as five MAP (Alvarez et al., 2012; Hillocks et al., 2002). Hillocks et al. (2001) reported storage root necrosis at six MAP in Tanzania for the Mreteta and Albert varieties with severe storage root symptoms observed at 8 MAP. Surveys (Gondwe et al., 2003; Hillocks et al., 2002; Rwegasira and Rey, 2012) and an experimental study ((Hillocks et al., 2001) showed that CBSD severity was associated with plant age in which plants older than seven or eight months were severely affected. In some instances, it has been shown that famers tend to harvest their crop prematurely as a means of avoiding the devastating effects of CBSD (Hillocks and Jennings, 2003; Hillocks et al., 2001; Hillocks et al., 2002). This means that the crop is harvested before reaching its full potential thereby lowering yields. The yield loss can be minimised by planting varieties that bulk early and reach their full yield potentials before CBSD has a debilitating impact on storage root mass. Such early bulking varieties may also escape storage root necrosis if they are harvested within 7 – 8 months of planting (Hillocks and Jennings, 2003). This implies that farmers cannot keep plants in the field for a long period of time, thereby negating the role of cassava as being a primary food security crop.

Most of the findings reported on the relationship between plant age and CBSD infection have been based on surveys, while very few have been based on sound empirical evidence. It would be more valuable to substantiate the survey findings with empirical studies, particularly in Malawi where there has been hardly any scientifically sound research conducted on this issue.

Two key questions to be addressed as per Hillocks et al. (2001) report: (1) are all farmers aware of the occurrence of the CBSD in all cassava growing areas, specifically in Malawi, and (2) is early harvesting in the absence of early storage root bulking varieties a potential solution to reducing the impact of the disease, and if so, will it require the development of early storage root bulking varieties?

1.9 Farmers' preference of cassava varieties

Several studies conducted in Africa (Agwu and Anyaeche, 2007; Dahniya, 1994; Munga, 2008; Okechukwu and Dixon, 2009; Tumuhimbise et al., 2012) and Malawi, in particular (Benesi et al., 2010), have explicitly shown that most farmers prefer early bulking varieties that exhibit resistance to common diseases prevailing in a particular locality, in addition to being high yielding. A study by Munga (2008) showed that about 26% of the famers in Kenya abandoned some varieties due to late bulking. Efforts should therefore be driven towards development of early bulking varieties which can easily be adopted by farmers.

1.10 Participatory variety selection

Conventional plant breeding has been in existence for decades and several strides have been made in the development and release of crop varieties. One key characteristic of the conventional plant breeding is that decisions to breed and release a variety originate from the breeder and not necessarily from the farmer who is the end user of the technology developed. The end result has at times been a poor adoption and utilisation of the new varieties by the farmers. As such, there has been a shift in approach, where conventional plant breeding includes participatory plant breeding (PPB) (Morris and Bellon, 2004), where farmers are involved in the research in ways that are meaningful and useful to them so that they are no longer just viewed as the passive recipients of technologies (Vernooy et al., 2009). Witcombe et al. (1996) categorised farmer participatory approaches into participatory varietal selection (PVS) and PPB, the former being a more rapid and cost-effective way of identifying farmer-preferred varieties than PPB. Participatory plant breeding has been applied in various crops (Bänziger and Cooper, 2001; Desclaux, 2005; Smith et al., 2001; Sthapit et al., 1996). There have been few reports of PPB application in cassava (Manu-Aduening et al., 2006; Were, 2011).

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Chapter 2

2 Assessment of farmers' knowledge of cassava brown streak disease and its management in Malawi[1]

Abstract

There is little information available on farmers' knowledge about cassava brown streak disease (CBSD), despite extensive studies on incidences and severities. The objective of this study was to assess farmers' knowledge of CBSD symptoms and management. In addition, the study established whether the varieties that farmers grow were perceived to be early, medium or late bulking. The study was conducted in three districts of Malawi, namely, NkhataBay, Nkhotakota and Salima by administering semi-structured interviews in combination with the disease incidence and severity survey. Farmers' knowledge of disease symptoms and management was associated with CBSD incidence and severity. However, majority of the farmers did not know the disease through foliar symptoms and only 10.1% of the farmers were able to identify CBSD. On the average, 75.0% and 71.7% of the farms had leaf and storage root symptoms, respectively. Furthermore, 66.6% of the farms had co-infection of CBSD and cassava mosaic disease (CMD), while 80.0% of the farms had CMD infection. The average CBSD leaf incidence per farm was 31.2% with some farms with levels up to 86.7%. At harvest, 88.3% of the farmers' fields exhibited storage root necrosis. Cassava brown streak disease leaf and storage root severities differed significantly ($P<0.001$) from one district to the other and between varieties. The study also showed that CBSD was aggravated by the continued usage of late bulking varieties, which implies that early harvesting of these varieties could lead to a significant yield loss. Therefore, there is need to increase the efforts in the development of early bulking varieties. Most farmers were found to lack a source of clean planting material. A need for improved extension services to improve cassava cultivation methods and pest management was identified. The lack of new improved varieties was reported as the most important constraint of cassava production, apart from CBSD. Education of farmers on the efficient management of this viral disease through the selection of clean planting material should be provided. The development of early root bulking varieties as a long-term solution in minimising CBSD impact should be supported.

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2.1 Introduction

Cassava (*Manihot esculenta* Crantz) brown streak disease (CBSD) is currently the most devastating disease of cassava alongside cassava mosaic disease (CMD), mainly in the coastal areas of East Africa, from Kenya in the north to Mozambique in the south (Alvarez et al., 2012; Mbanzibwa et al., 2011; Nichols, 1950; Winter et al., 2010). It has also been reported in some locations in Burundi, Uganda and Zambia (Bigirimana et al., 2011; Hillocks et al., 1996). For decades the disease has been prevalent in Malawi (Nichols, 1950). The existence of CBSD in Malawi was confirmed by Benesi et al. (2010) who revealed that CBSD was present along the rift valley in the north and south of Malawi, while earlier studies (Gondwe et al., 2003; Shaba et al., 2003) showed that CBSD was present in the whole lakeshore strip, that is, from Karonga in the north to Mangochi in the south.

Due to the clonal nature of propagation in cassava, the crop is vulnerable to the effects of viral diseases which are a major threat to cassava production, while at the same time they pose a risk to the livelihoods of millions of Africans (Legg and Thresh, 2003; Patil et al., 2015). The CBSD has become of great concern in the East African region because it reduces yield and diminishes consumption and market qualities of the storage roots (Abaca et al., 2012; Alvarez et al., 2012; Mbanzibwa et al., 2011; Winter et al., 2010). There have been several surveys on CBSD in the African region and in Malawi in particular, which concentrated on assessing disease incidence and severity (Alicai et al., 2007; Gondwe et al., 2003; Hillocks et al., 1999; Hillocks et al., 2002; Mbewe et al., 2015; Rwegasira and Rey, 2012) based on field observations, without assessing farmers' knowledge in terms of capacity to identify this viral disease of cassava.

For cassava production, most farmers obtain planting materials from their own fields and neighbouring farms. In most cases, cuttings are generated without correctly checking the foliage for disease symptoms and this in turn perpetuates the viral infections. Farmers can avoid planting diseased material if they can effectively and correctly diagnose leaf or stem symptoms on the plants prior to the planting season.

There are reports (Hillocks and Jennings, 2003; Hillocks et al., 2001; Hillocks et al., 2002) that farmers tend to harvest their crop early as a means of reducing the CBSD impact on the yield and quality of cassava, which implies that some farmers are aware of the disease. The foregoing raises two pertinent questions to be addressed: (1) whether farmers are aware of the occurrence of the CBSD on their farms in the cassava growing areas of Malawi (i.e., whether

they can explicitly identify the leaf symptoms of the disease) and (2) whether early harvesting in the absence of early storage root bulking varieties is a potential solution for reducing the impact of the disease. These problems could be addressed through direct involvement of the farmers in the form of properly designed surveys. Farmers' surveys are always helpful in setting the research agenda and designing the extension strategies as well as evaluating the effectiveness of projects and development interventions (Khan and Damalas, 2015). The objective of this study was, therefore, to determine the extent of CBSD incidence and severity in cassava fields and to assess farmers' knowledge of CBSD symptoms and management. Furthermore, it hoped to determine whether the varieties farmers grow are perceived to be early, medium or late bulking.

2.2 Materials and methods

2.2.1 Study area

The study was conducted in three districts of Malawi, namely, NkhataBay, Nkhotakota and Salima (Figure 2.1). NkhataBay district has a warm tropical climate and lies at 450-550 m above sea level with an average annual maximum temperature over 32^{o}C, an average minimum temperature of 20^{o}C along the lake, and an annual rainfall well over 2000 mm. Typically, the rainy season occurs between November and March (GoM, 2006a). Nkhotakota elevation ranges from 493 to 1638 m above sea level. It has a tropical climate and consists of two main seasons. These are the wet season from November to April and the dry season from May to October. On the average, the district receives an annual rainfall of about 1400 mm, which might be as low as 860 mm and as high as 1600 mm. Nkhotakota district experiences an average annual maximum temperature of 28.7^{o}C and an average minimum temperature of 20^{o}C (GoM, 2010). Salima district experiences a warm tropical climate with a mean annual temperature of 22^{o}C and maximum of 33^{o}C. It has an altitude ranging from 200 to 1000 m above the sea level (GoM, 2006b).

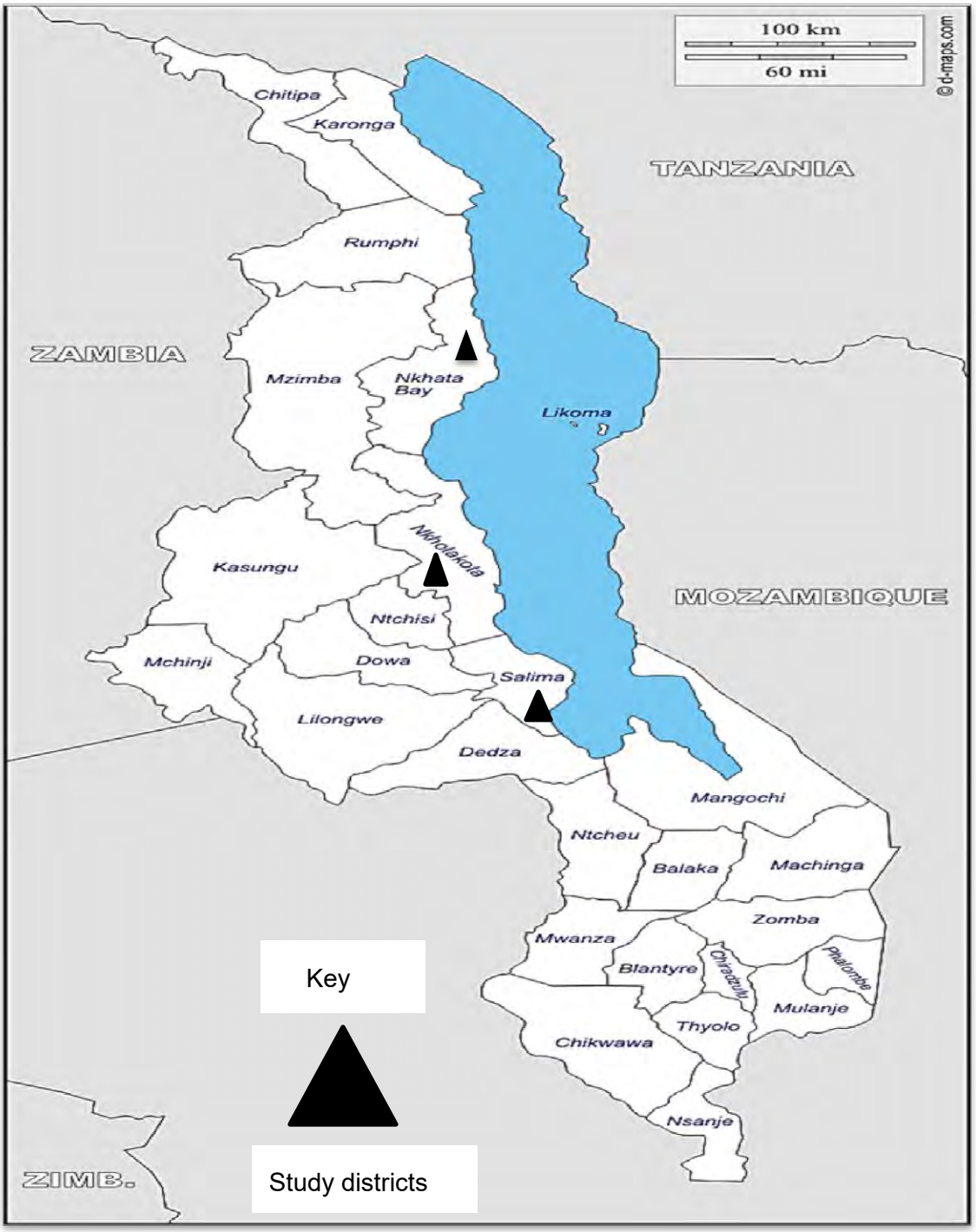

Figure 2.1. Map of Malawi showing three study districts: NkhataBay, Nkhotakota and Salima

2.2.2 Study design

Selection of the sample

The three districts (along the lakeshore) were purposively chosen for the study as they represent the major cassava growing areas, in addition to being hot spots for CBSD. Initially, 120 farmers and farms were enlisted for the study (40 per district) according to information provided by district-level key informants. Due to a limitation in resources, only 60 cassava farmers and farms (20 per district) were systematically sampled at 15 km interval along the length and width along the major roads. At each sampling interval, the selection of the farmers was based on their willingness to participate. Each farm sampled was regarded as a representative of the surrounding farms. The research team comprised of the principal investigator and two research assistants conversant with the local languages and with experience in cassava research in order to identify the local varieties and the CBSD symptoms. The study was conducted in July 2014. The study had two components: a semi-structured interview of farmers, and a disease incidence and severity survey.

Semi-structured interviews

A semi-structured questionnaire was administered to cassava farmers to assess their knowledge of CBSD in terms of symptoms, impact of CBSD on cassava growth and productivity, processing methods of infected storage roots, causes and control strategies, and availability of extension services. The semi-structured interviews were administered to farmers while they were in the field to achieve a better understanding of the questions. The questionnaire was pre-tested on a small group of farmers before the survey and adjustments were made to ensure that the right information was obtained during the actual interviews.

Disease incidence and severity surveys

Disease incidence surveys were based on both the foliar and storage root necrosis symptoms and they were conducted to determine the extent and distribution of CBSD and to identify the most severely affected varieties. In the incidence survey, 30 plants on a diagonal line across the field were scored for the presence or absence of symptoms of CBSD, CMD, cassava green mite (CGM) and cassava mealy bug (CMB), while in the severity survey, the same plants were scored for CBSD using a scale from 1 to 5 (1 = no apparent symptoms, 2 = slight foliar chlorotic leaf mottle, no stem lesions, 3 = foliar chlorotic leaf mottle and blotches with mild stem lesions,

no dieback, 4 = foliar chlorotic leaf mottle and blotches with pronounced stem lesions, no dieback and 5 = defoliation with stem lesions and pronounced dieback (IITA, 1990). For storage root necrosis severity, three plants showing CBSD symptoms were uprooted and scored for storage root necrosis severity, while storage root necrosis incidence was based on the presence or absence of storage root necrotic symptoms on a farm. Where no plants showed CBSD foliar symptoms, three plants were randomly uprooted to check for necrosis in the storage roots. Additional information was recorded on number of storage root plant^{-1}, storage root length (cm), storage root mass (kg plant^{-1}) and above ground mass (kg plant^{-1}).

2.2.3 Data analysis

Both quantitative and qualitative data collected were analysed using the Statistical Package for Social Sciences (SPSS), version 16, to generate means, standard deviations and frequencies.

2.3 Results

2.3.1 Cassava based farming systems

The total farm size ranged from 0.49 to 20.00 ha with a mean land holding size of 3.01 ha per farmer (Table 2.1). The lowest land holding size was recorded in NkhataBay with a mean of 1.65 ha, while Salima had the largest land holding size per farmer with an average land holding size of 4.06 ha. Of all the crops that farmers grow, except sugarcane in Nkhotakota, cassava had the largest area of land in all the three districts with an overall mean of 0.90 ha, and with a minimum of 0.12 and maximum of 3.43 ha.

Apart from cassava, the farmers in the districts also grow a variety of crops, either as a monocrop or in a mixed cropping system with cassava. Overall, 63.3% of the farmers practice mixed cropping with cassava and the main intercrop is maize (94.7% of the farmers), followed by sweet potatoes (26.3%) (Table 2.2). Most farmers in Salima grow cassava to generate income (40.0%) (Table 2.3) and it has the lowest number of farmers (35.0%) practising mixed cropping.

Table 2.1. Mean land area (ha) allocated to cassava and other crops grown by farmers in the sampled districts.

	District											
	NkhataBay			Nkhotakota			Salima			Total		
Crop	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Cassava	0.12	3.00	0.88±0.14	0.49	3.00	0.99±0.13	0.25	3.43	0.84±0.17	0.12	3.43	0.90±0.09
Maize	0.12	2.00	0.42±0.10	0.06	0.98	0.56±0.07	0.12	1.96	0.57±0.10	0.06	2.00	0.52±0.05
Rice	0.10	0.12	0.11±0.01	0.01	4.00	0.48±0.26	0.01	0.98	0.49±0.49	0.01	4.00	0.42±0.20
Tobacco	-	-	-	-	-	-	0.49	0.49	0.49	0.49	0.49	0.49
Ground nuts	0.12	0.15	0.13±0.01	0.01	0.49	0.27±0.10	0.12	0.37	0.49±0.03	0.01	0.49	0.23±0.03
Cotton	-	-	-	-	-	-	0.25	0.49	0.49±0.05	0.25	0.49	0.44±0.05
Cowpeas	-	-	-	0.10	0.25	0.16±0.05	0.12	0.25	0.49±0.07	0.10	0.25	0.17±0.03
Beans	-	-	-	0.49	0.49	0.49	-	-	-	0.49	0.49	0.49
Soybeans	-	-	-	0.12	0.49	0.31±0.19	0.04	0.37	0.20±0.07	0.04	0.49	0.23±0.07
Bambara nuts	0.12	0.15	0.13±0.01	-	-	-	0.12	0.12	0.12	0.12	0.15	0.13±0.01
Sugarcane	0.01	0.15	0.08±0.07	3.43	3.43	3.43	-	-	-	0.01	3.43	1.20±1.12
Sweet potato	0.00	0.49	0.13±0.03	0.01	0.49	0.19±0.08	0.25	0.25	0.25±0.00	0.00	0.49	0.16±0.03
Banana	0.01	0.30	0.15±0.08	-	-	-	-	-	-	0.01	0.30	0.15±0.08
Vegetables	0.11	0.11	0.11	-	-	-	-	-	-	0.11	0.11	0.11
Total farm size (ha)	0.74	5.00	1.65±0.21	0.74	12	3.31±0.81	0.49	20	4.06±1.02	0.49	20	3.01±0.45

Table 2.2. Percentage of farmers practising mixed cropping with cassava and the main cassava intercrops

Intercrop	District			Overall
	NkhataBay	Nkhotakota	Salima	
Maize	92.9	100.0	85.7	94.7
Beans	0.0	5.9	0.0	2.6
Groundnuts	14.3	11.8	0.0	10.5
Cowpeas	0.0	17.7	28.6	13.2
Sweet potato	28.6	35.3	0.0	26.3
Soybeans	0.0	17.6	14.3	10.5
Bambara nuts	7.1	0.0	0.0	2.6
Mixed cropping*	70.0	85.0	35.0	63.3

*Proportion of farmers practicing mixed cropping.

Table 2.3. Percentage of farmers indicating the purpose for which they grow cassava

Purpose	District			Overall
	NkhataBay	Nkhotakota	Salima	
Source of food	35.0	65.0	0.0	33.3
Source of income	0.0	0.0	40.0	13.3
Both food and income	65.0	35.0	60.0	53.3

2.3.2 Sources of planting material, farmers' knowledge of maturity period and features of the cassava varieties grown

Farmers obtained planting material from multiple sources (Figure 2.2). The major sources of planting material were farmers' own fields (83.3%) followed by neighbouring farms (55.0%). However, research institutions were the least source of cassava planting material (3.3%). There was, generally a mix of varieties within each farm (except in Salima where farmers grow only one type of cassava known as *Mbundumali*) and farmers were able to distinguish one variety from the other. The commonly grown varieties included *Mbundumali, Gomani, Masoyabazungu, Beatrice* and *Ng'wenyani.* These varieties were at various growth stages during the visits, but the majority of the plants were seven to nine months old (61.7%). Overall, 75% of the varieties

were harvested before 12 MAP with only 5% harvested between 18 to 24 MAP. In NkhataBay and Nkhotakota districts, late storage root bulking varieties (12-24 months) were common, while in Salima district, cassava was commonly harvested six to seven (40%) MAP (Table 2.4).

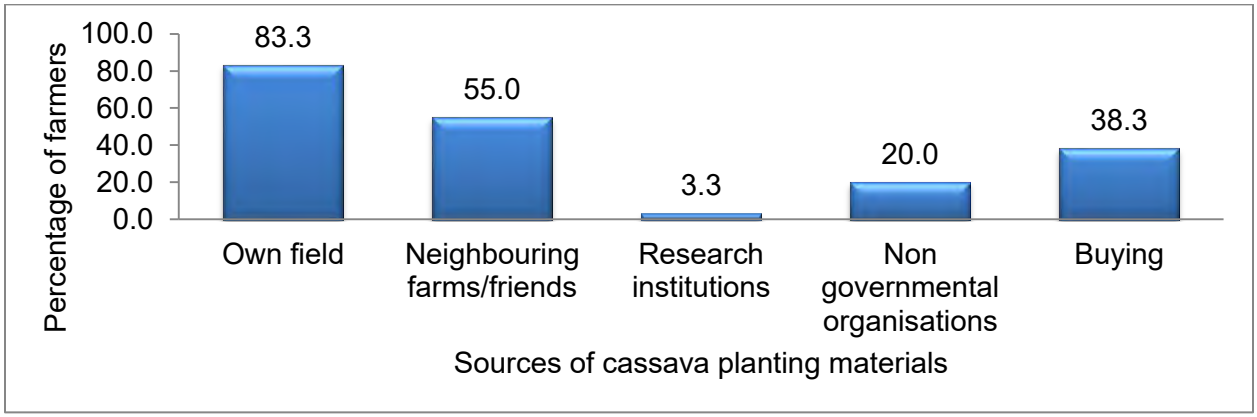

Figure 2.2. Percentage of farmers that obtain cassava planting materials from different sources

(Some farmers obtained planting material from more than one source)

Table 2.4. Percentage of farmers indicating the harvest time of the varieties they grow

Duration (Months)*	District			
	NkhataBay	Nkhotakota	Salima	Overall
6	5.0	10.0	50.0	21.7
7	0.0	10.0	40.0	16.7
8	5.0	15.0	20.0	13.3
9	10.0	15.0	5.0	10.0
10	15.0	40.0	10.0	21.7
12	95.0	100.0	30.0	75.0
18	15.0	0.0	0.0	5.0
24	15.0	0.0	0.0	5.0

*= most farmers indicated many harvest times in a season.

Table 2.5 lists the most important traits that farmers prefer in cassava varieties. Most farmers regarded high yield as the most important trait (61.7% of the farmers). In addition to high yield,

sweetness was also highly preferred (53.3%). The least important attribute of the varieties was fibreless storage roots. The study showed that at least 73.3% of the farmers had abandoned some varieties at some stage for reasons of low yield (54.5%), fibrous storage roots (15.9%), pests and diseases (13.6%), scarcity of planting material (13.6%), late storage root bulking (6.8%), watery storage roots (2.3%), and due to the introduction of new varieties (2.3%).

Table 2.5. Preferred characteristics of cassava varieties (% of farmers)

Characteristic	District			Overall	Rank
	NkhataBay	Nkhotakota	Salima		
High number of storage roots	90 (2)	70 (2)	70 (1)	76.7	1
Big storage roots	95 (1)	90 (1)	35 (3)	73.3	2
Sweetness	50 (3)	65 (3)	45 (2)	53.3	3
Early storage root bulking	35 (4)	10 (4)	15 (4)	20.0	4
Pest and disease resistance	35 (4)	5 (5)	5 (5)	15.0	5
Fibreless storage roots	30 (5)	10 (4)	0 (6)	13.3	6

Values in brackets are rankings of traits by farmers in terms of importance (1 = most important, 6 = least important).

2.3.3 Status of cassava brown streak disease severity and incidence

Cassava brown streak disease leaf and storage root severity

Cassava brown streak disease severity on the foliage differed significantly ($P<0.001$) from one district to the other (Table 2.6), with an overall severity mean of 2.70. The highest disease severity score on the foliage was recorded in Salima (3.35) and the lowest in Nkhotakota (1.65). There was also a highly significant difference ($P<0.001$) in terms of CBSD storage root severity from one district to the other with the overall mean severity of 1.84. NkhataBay (2.50) recorded the highest storage roots severity. Disease severity by variety also revealed highly significant differences ($P<0.001$) for both leaf and storage root necrosis (Table 2.7). The most susceptible variety was *Chipule* with a mean leaf severity of 4.67 and a storage root necrosis score of 3.33. Other varieties that were highly affected included *Masoyabazungu, Mbundumali, Chakuwawa, Kanononо, Mpuma* and *Thupula* with a mean leaf severity score of 3 or higher (Table 2.7). The results also revealed significant differences ($p<0.05$) in terms of storage root mass (kg plant^{-1}) in the three districts; the lowest storage root mass was recorded in NkhataBay (0.46 kg plant^{-1}) and the highest was recorded in Nkhotakota (0.66 kg plant^{-1}) (Table 2.6).

Table 2.6. Cassava brown streak leaf and storage root severity and other agronomic traits measured

Trait	District									Total			
	NkhataBay			Nkhotakota			Salima						
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	F-Prob
CBSDL	1.00	4.00	3.02±0.10	1.00	4.00	1.65±0.14	1.00	5.00	3.35±0.19	1.00	5.00	2.70±0.10	0.000
CBSDR	1.00	4.00	2.50±0.13	1.00	3.00	1.27±0.08	1.00	4.00	1.69±0.11	1.00	4.00	1.84±0.08	0.000
SRN	1.00	14.00	4.56±0.42	1.00	15.00	5.02±0.43	1.00	24.00	5.78±0.54	1.00	24.00	5.11±0.27	0.166
SRM	0.01	1.38	0.46±0.04	0.03	2.03	0.66±0.06	0.11	2.27	0.64±0.07	0.01	2.27	0.58±0.03	0.021
SRL	11.50	61.50	26.10±1.37	9.83	60.00	30.62±1.51	9.33	47.00	22.7±1.00	9.33	61.50	26.38±0.79	0.000
AGM	0.12	1.40	0.55±0.04	0.12	1.73	0.58±0.05	0.17	1.84	0.63±0.05	0.12	1.84	0.59±0.03	0.455

CBSDL = cassava brown streak disease leaf severity (based on a 1-5 rating scale), CBSDR = cassava brown streak disease storage root severity (based on a 1-5 rating scale), SRN = storage root number plant^{-1}, SRM = storage root mass (kg plant^{-1}), SRL = storage root length (cm), AGM = above ground mass (kg plant^{-1}).

Table 2.7. Cassava brown streak disease severity on the most affected varieties

Variety	Trait					
	CBSD leaf severity	CBSD storage root severity	Storage roots number plant^{-1}	Storage root mass (kg plant^{-1})	Storage root length (cm)	Above ground mass (kg plant^{-1})
Beatrice	1.17±0.17	1.08±0.08	5.00±1.17	0.63±0.12	33.87±3.59	0.47±0.06
Bloodfool	1.00±0.00	1.00±0.00	3.50±0.50	0.69±0.23	37.17±4.17	0.56±0.45
Chakuwawa	3.00±0.00	1.67±0.33	3.33±0.88	0.38±0.08	22.05±3.67	0.40±0.11
Chipule	4.67±0.33	3.33±0.33	3.00±0.58	0.41±0.05	17.14±3.91	0.60±0.03
Gomani	2.13±0.29	1.93±0.27	3.93±0.61	0.54±0.13	31.50±2.66	0.63±0.10
Guguza	1.83±0.54	1.00±0.00	4.33±1.38	0.85±0.24	36.64±2.98	0.88±0.23
Kadamphuno	2.00±1.00	1.50±0.50	6.50±0.50	0.55±0.16	30.59±6.42	0.59±0.02
Kanonono	3.00±0.00	2.00±0.00	2.00±0.58	0.23±0.03	16.67±0.44	0.48±0.05
Masoyabazungu	3.06±0.19	2.56±0.27	6.63±0.76	0.51±0.09	25.59±2.14	0.56±0.07
Mbawala	2.43±0.37	1.71±0.29	5.14±1.16	0.55±0.15	27.52±1.04	0.46±0.12
Mbundumali	3.18±0.20	1.56±0.10	6.06±0.55	0.65±0.07	23.22±1.02	0.64±0.05
Mpuma	3.17±0.17	2.67±0.19	4.75±1.02	0.46±0.08	22.52±1.81	0.57±0.09
Ng'wenyani	2.33±0.44	2.33±0.44	3.89±0.59	0.73±0.05	33.74±4.99	0.56±0.05
Thupula	3.00±0.00	1.00±0.00	7.00±1.00	0.95±0.21	21.50±2.00	0.88±0.14
Unknown	2.50±0.50	1.50±0.29	3.25±0.75	0.41±0.11	22.46±4.26	0.47±0.05
F-Prob.	0.000	0.000	0.316	0.617	0.000	0.789

Cassava brown streak disease leaf and storage root necrosis incidence

Cassava brown streak disease incidence varied from one farm to the other and from one district to the other. On average, 75.0% and 71.7% of the farms had foliar and storage root incidence, respectively. The highest number of farms with CBSD incidence was recorded in NkhataBay, where 95.0% of the farms had foliar CBSD and 90% had storage root necrosis (Figure 2.3). Moreover, 66.6% of the farms had co-infection of CBSD and CMD, while 80.0% of the farms had CMD infection. All farms in NkhataBay and Salima had CMD, while in Nkhotakota only 40.0% of the farms had CMD. The average CBSD leaf incidence per farm was 31.2% with some farms showing incidence up to 86.7%. Salima recorded the highest mean incidence of 39.3%

(Table 2.8). Average CMD incidence was 42.1% with a maximum of 100%. The CBSD storage root necrosis evaluation showed that the incidence was highest in NkhataBay (83.3%) and lowest in Nkhotakota (22.9%) with an overall incidence of 54.3%.

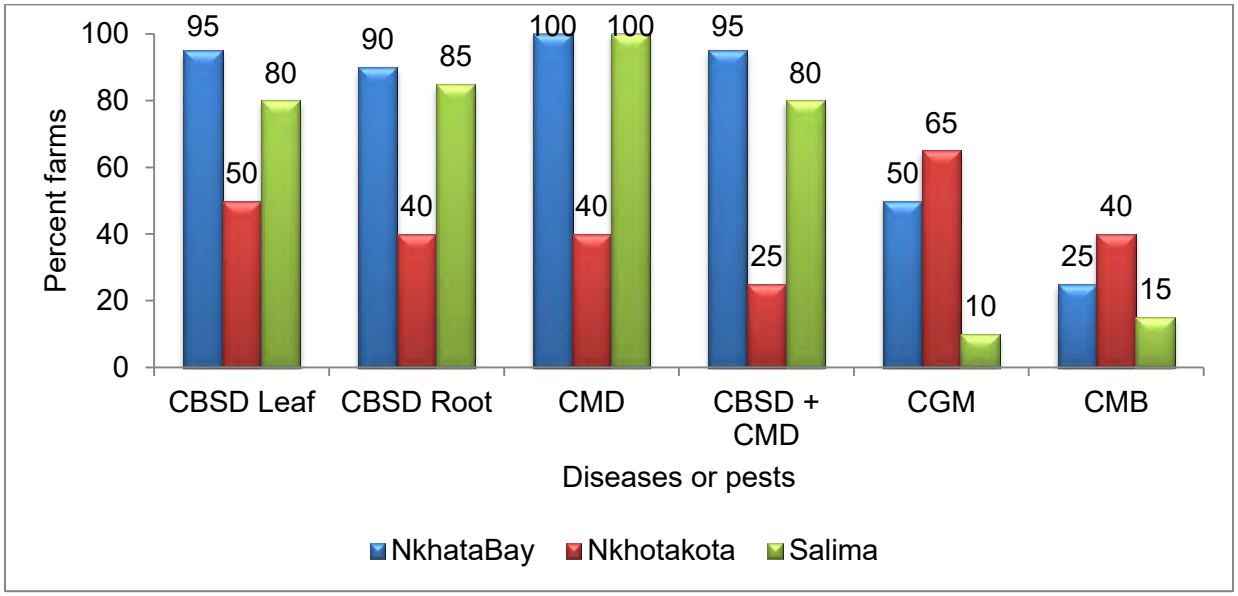

Figure 2.3. Percentage of farms with cassava brown streak disease (CBSD), cassava mosaic disease (CMD), cassava green mite (CGM) and cassava mealy bug (CMB)

Table 2.8. Leaf and storage root CBSD incidence (%) and other diseases and pests

Disease/Pest	District			
	NkhataBay	Nkhotakota	Salima	Overall
CBSDRI	83.3	22.9	52.9	54.2
CBSDLI	35.7	18.7	39.3	31.2
CMDI	35.6	4.2	84.5	42.1
CBSDI+CMDI	8.3	0.2	29.0	12.7
CGMI	4.4	8.4	1.9	4.8
CMBI	0.7	2.5	2.4	1.8

CBSDLI = cassava brown streak disease leaf incidence, CBSDRI = cassava brown streak disease storage root incidence, CMDI = cassava mosaic disease incidence, CGMI = cassava green mite incidence, CMBI = cassava mealy bug incidence.

2.3.4 Farmers' knowledge of cassava brown streak disease

Assessment of farmers' knowledge of CBSD indicated that the majority of the farmers did not know the disease through foliar symptoms, as only 10.1% were able to do so. Surprisingly 88.3% of the farmers' fields exhibited storage root necrosis at harvest. The highest number of farms (95%) experiencing CBSD storage root symptoms was recorded in NkhataBay (Figure 2.4). None of the farmers in Nkhotakota district knew CBSD through foliar symptoms, while Salima had the highest number of farmers (25%) who were able to identify CBSD through foliar symptoms.

On causes of CBSD, farmers mentioned several reasons, such as low soil fertility (17.0%), diseased planting material (13.2%), other diseases (13.2%), late storage root bulking (7.5%), flooding (7.5 %), parasitic weeds (3.8%) and rituals (3.8%). As for the impact of CBSD on cassava crop, the majority of the farmers (41.5%) stated that CBSD lowers yield (Table 2.9) as most of the infected tissues are discarded or sliced off to obtain clean tissues. On the other hand, 34.0% of the farmers said that CBSD lowers both yield and quality. They stated that food prepared from CBSD infected storage roots is tasteless, smells bad, the colour changes from whitish to greyish, and is difficult to cook. Furthermore, farmers across the three districts stated that the storage roots with CBSD infections have low market value as most buyers shun storage roots with necrotic patches.

In terms of control strategies, most farmers (26.4%) indicated that planting varieties that are resistant to CBSD would be the most feasible control strategy (Table 2.10). Another measure that farmers thought could help in reducing CBSD would be uprooting all infected plants (17%). Crop rotation, spraying with chemicals and early harvesting were other control strategies mentioned by the farmers.

2.3.5 Constraints to cassava production highlighted by the farmers

Apart from CBSD, the most pressing problem reported by the farmers across the three districts is lack of new improved varieties (42.7%), followed by CMD (33.3%) (Table 2.11). Other challenges included low soil fertility, lack of organised cassava markets, weeds, damage by animals, shortage of land and flooding. The CMD was a very serious problem in Salima, where an incidence of 84.7% was recorded and 50.0% of the farmers reported that CMD causes serious damage to their crop (Table 2.11). The farmers complained that low yields were obtained, characterised by lower numbers of storage roots plant^{-1}. The farmers stated that there

has been a declining trend in yield realised ha^{-1}, particularly when they obtain planting material from the same field in successive years.

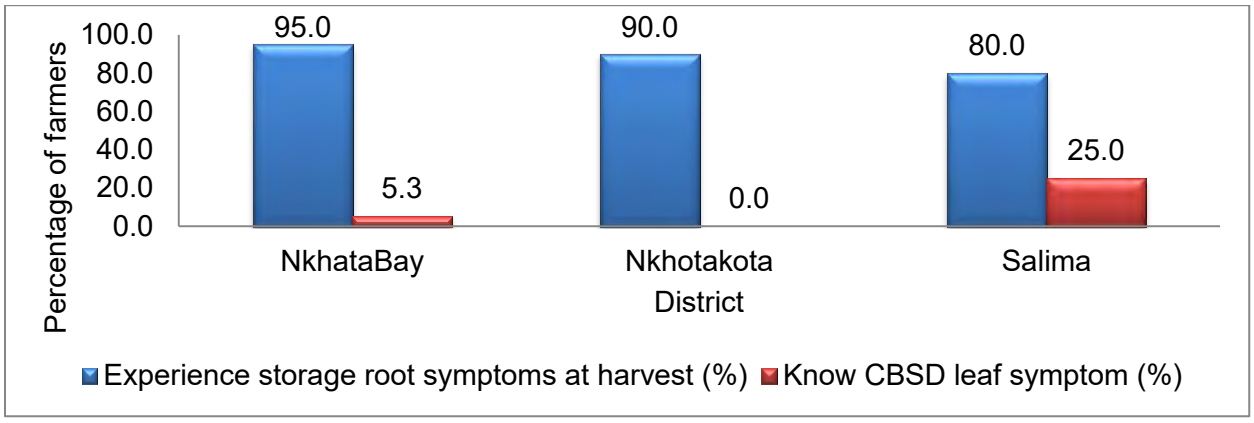

Figure 2.4. Percentage of farmers' fields showing CBSD storage root necrosis during harvest and those who can identify leaf symptoms of the disease

Table 2.9. Percentage of farmers indicating the impact of CBSD on cassava

Impact	District			Overall
	NkhataBay	Nkhotakota	Salima	
Low yield	41.0	66.7	12.5	41.5
Both low yield and poor quality	47.4	11.1	43.8	34.0
Poor quality	5.3	16.7	37.5	18.9
None	5.3	5.6	6.3	5.7

Table 2.10. Some control measures for CBSD suggested by farmers (%)

Control measure	District			Overall
	NkhataBay	Nkhotakota	Salima	
Planting resistant varieties	21.1	22.2	37.5	26.4
Uprooting infected plants	21.1	5.6	25.0	17.0
Crop rotation	15.8	16.7	12.5	15.1
Spraying with chemicals	10.5	0.0	6.3	5.7
Early harvesting	0.0	11.1	0.0	3.8

Table 2.11. Constraints to cassava production as identified by farmers (%) apart from CBSD

Constraint	District				
	NkhataBay	Nkhotakota	Salima	Overall	Rank
Lack of new improved varieties*	45.0	55.0	30.0	42.7	1
Diseases (CMD)	20.0	35.0	50.0	33.3	2
Pests (CGM, CMB)	15.0	15.0	20.0	16.7	3
Animals (wild and domesticated)	20.0	10.0	15.0	15.0	4
Weeds	35.0	0.0	0.0	13.3	5
Lack of organised cassava markets	0.0	0.0	5.0	1.7	6
Shortage of land	0.0	0.0	5.0	1.7	6
Flooding	5.0	0.0	0.0	1.7	6
Low soil fertility	5.0	0.0	0.0	1.1	7

*Lack of improved varieties in terms of yield, disease resistance, germination/sprouting and stunted plant growth.

2.3.6 Extension services on cassava production and disease management

An average of 18.3% of the cassava farmers had ever received extension services for cassava production. Only Salima recorded a high number of farmers (40%) receiving extension services (Figure 2.5), which were entirely provided by non-governmental organisations (ADRA and Land-O-Lakes) and focused on plant spacing and pest and disease control. When farmers were asked to mention the most critical areas that extension services should concentrate on, the majority of the farmers mentioned cultivation methods (71.7%), and pests and disease control measures (45.0%) as areas which needed immediate attention (Table 2.12). Some farmers (23.3%) also wished to know where and how to obtain improved cassava varieties.

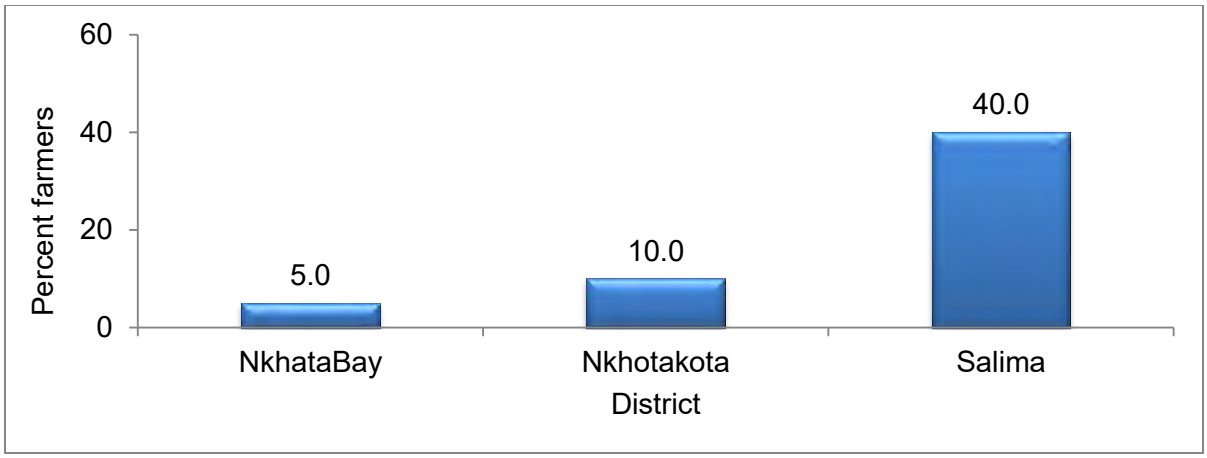

Figure 2.5. Percentage of farmers that receive extension services on cassava production

Table 2.12. Extension services for cassava needed by farmers (%)

Production practice	District			Overall
	NkhataBay	Nkhotakota	Salima	
Cultivation methods	80.0	80.0	55.0	71.7
Pest and disease control	40.0	40.0	55.0	45.0
Marketing of cassava	0.0	5.0	5.0	3.30
Where and how to obtain improved varieties	5.0	50.0	15.0	23.3
Storage methods	0.0	0.0	15.0	5.0

2.4 Discussion

2.4.1 Cassava based farming systems

The study revealed that more land was allocated to cassava production than any other crop. This means that farmers largely depend on cassava as a source of food and income. It has been reported that more than 40% of the Malawi population, more especially in the lakeshore districts (including study areas), depend on cassava as a source of food and income (Moyo et al., 1999). Increased land allocation to cassava production has been reported to be a major contributing factor to the increased total cassava production in Malawi (Chipeta and Bokosi,

2013; IITA/SARRNET, 2007) and also in Africa in general (FAO and IFAD, 2005; Hillocks, 2002).

Most farmers practice mixed cropping with other food crops. This means that during periods when cassava is not ready they use these crops for food security. Most farmers who grow cassava for food practice mixed cropping as opposed to those growing it as a source of income. For example, most farmers in Salima grow cassava to generate income and it has the lowest number of farmers practising mixed cropping. The results indicate that cassava is not only a food security crop in these districts but also a cash crop. This is in contrast with what Chiwona-Karltun and Mkumbira (2000), Moyo et al. (1999) and Shaba et al. (2003) reported, namely that cassava serves only as a food crop in the lakeshore areas. During the study, middle men could be seen buying and transporting fresh cassava storage roots to the nearest markets and the research team found several cassava fields that had been uprooted to cater for the fresh markets.

2.4.2 Sources of planting material, farmers' knowledge of maturity period and features of the varieties grown

Research institutions were the least preferred source of cassava planting material. Farmers often use planting material from their own fields as they do not have an alternative source, although farmers in Salima tended to buy some of their planting material. Their local varieties are often unimproved, low yielding, susceptible to major pests and diseases, and fibrous. A similar pattern was observed in several African countries (Chikoti, 2011; Mtunda, 2009; Munga, 2008) where the majority of the farmers obtained planting material from their own fields, despite the availability of breeding programs where improved varieties could be sourced.

Farmers' fields are a reservoir of genetic diversity as they contain different plant varieties, including both landraces and improved varieties. There was a mix of varieties on most farms (except in Salima where farmers grow only *Mbundumali*) and farmers were able to distinguish one variety from the other. Planting different varieties helps to conserve germplasm that could be a good source of various traits, such as high yielding, pest and disease resistance, delayed postharvest deterioration, carotenoid content and other traits required by plant breeders.

Most of the varieties grown by the farmers were late bulking. Where cassava is mainly grown for food (Such as NkhataBay and Nkhotakota districts), late storage root bulking varieties, which were harvested between 12 and 24 months after planting, were common. However, in Salima

district, where the prime reason for cassava production is to generate income, cassava was harvested six to seven MAP. Considering that some farmers prefer to harvest early, efforts should focus on the development of early storage root bulking varieties with pest and disease resistance.

According to the farmers, yield is determined by storage root size and number of storage roots. Most farmers regarded high yield as the most important trait. In NkhataBay and Nkhotakota districts most farmers preferred big storage roots to a high number of storage roots. Where cassava is mainly grown to generate income (Salima district), high number of storage roots was preferred to big storage root size, mainly because sales are based on the number of storage roots. In addition to high yield, sweetness was also highly preferred. Other traits like pest and disease resistance, early storage root bulking, and fibreless storage roots were ranked lower, but will need to be given attention in future breeding strategies. These traits tend to be highly prioritised by farmers and have been reported by several other researchers (Agwu and Anyaeche, 2007; Benesi et al., 2010; Chikoti, 2011; Dahniya, 1994; Kamau et al., 2011; Mtunda, 2009; Munga, 2008; Okechukwu and Dixon, 2009; Tumuhimbise et al., 2012; Were, 2011).

2.4.3 Status of cassava brown streak disease severity and incidence

Cassava brown streak disease leaf and storage root severity

Although disease severity on the foliage was higher in Salima, the disease severity on the storage roots was highest in NkhataBay. The differences in disease severity in storage roots and leaves may be attributed to differential response of the varieties to CBSD, age of the plants at the time of the study as well as weather conditions in the districts as has been previously reported (Alvarez et al., 2012; Hillocks and Jennings, 2003; Hillocks and Thresh, 2000). During the study, most of the plants in NkhataBay were much older (up to 24 months) than those in Salima (up to 9 months) and Nkhotakota (9 months). This could explain why CBSD severity on storage roots was higher in NkhataBay. Similar findings were also reported by Hillocks et al. (2001) and other researchers (Gondwe et al., 2003; Hillocks et al., 2002; Rwegasira and Rey, 2012), who found that CBSD storage root severity was associated with plant age.

The lowest yields were recorded where CBSD was more severe, whereas the highest yields were recorded where CBSD was less intense. Though there have been contrasting reports on the association of CBSD and yield (Bock, 1994; Nichols, 1950), this study agrees with Gondwe

et al. (2003) and Hillocks et al. (2001) that CBSD lowers plant yield, especially when plants stay in the field for an extended period.

Cassava brown streak disease leaf and storage root necrosis incidence

CBSD storage root necrosis assessments showed that the incidence was highest in NkhataBay and lowest in Nkhotakota. Although Salima recorded the highest leaf incidence, a similar trend was not exhibited in the storage roots and this might be due to the fact that most plants in NkhataBay were much older than those in Salima. This is consistent with the view that CBSD storage root necrosis increases with plant age (Gondwe et al., 2003; Hillocks et al., 2001; Hillocks et al., 2002; Rwegasira and Rey, 2012). Furthermore, there was a strong relationship between leaf and storage root symptoms, where most plants with leaf symptoms also showed necrotic storage roots

A comparison of this study with previous reports suggests that CBSD has continued to spread and increase in both incidence and severity, thereby impacting negatively cassava production, productivity, and utilisation.

2.4.4 Farmers' knowledge of cassava brown streak disease

Assessment of farmers' knowledge of CBSD indicated that the majority of the farmers did not know the disease through foliar symptoms, despite the presence of storage root necrosis. Salima had the highest number of farmers who were able to identify CBSD through foliar symptoms and this was most likely due to the activities of a non-governmental organisation (Land-O-Lakes) in the area that organises farmers into groups/clubs and informs them on CBSD disease identification. Salima was the area with the highest disease incidence. One reason could be that most farmers in Salima generally do not keep their own planting material, but they buy from other farmers, while not checking adequately for disease symptoms during planting. The study showed that 10% of the cassava farmers knew CBSD by foliar symptoms, and Gondwe et al. (2003) reported that none of the cassava farmers knew about CBSD several years ago. This means that there has been not enough effort in bringing awareness of the disease in more than a decade period when the prevalence of CBSD in Malawi was extensively reported (Gondwe et al., 2003; Hillocks and Jennings, 2003; Shaba et al., 2003).

Farmers use different management techniques to prevent, avoid or control pests and diseases, depending on the levels of knowledge and experience in farming. There were several methods that farmers used to counteract CBSD. Most farmers indicated that planting varieties that are

resistant to CBSD would be the most feasible control strategy. This was expounded by the fact that some of the varieties that they grew did not succumb much to CBSD. Another measure that farmers thought that could help in reducing CBSD would be uprooting all infected plants, though the majority of the farmers expressed reservations with this method, since many farmers struggle to find planting material at the beginning of the planting season. Although early harvesting has been reported to be one way in which farmers reduce or avoid the CBSD impact (Gondwe et al., 2003; Hillocks and Jennings, 2003; Hillocks et al., 2001; Hillocks et al., 2002), the present study showed that only 3.8% of the farmers practiced this method. A possible explanation of why only few farmers used this method is that most of the varieties that they grew were late bulking or harvesting was done in piece-meal as family food security strategy, which means that early harvesting would lead to low yield. Therefore, efforts should be made to develop early bulking varieties.

2.4.5 Constraints to cassava production highlighted by the farmers

Apart from CBSD, cassava farmers experience several other challenges. The most pressing problem reported by the farmers was lack of new improved varieties, followed by CMD. The CMD is a very serious problem in Salima where farmers complained that during harvest, low yields were obtained characterised by fewer numbers of storage roots per plant. The farmers stated that there has been a declining trend in yield, particularly when they obtain planting material from the same field in successive years. It appears that the combined effect of CMD and CBSD weakens the efforts of cassava commercialisation in Malawi due to low yields and poor quality of the crop produced. In view of these challenges, farmers expressed the need for extension services to equip them with techniques to manage efficiently the pests and diseases in this crop.

2.5 Conclusions

The CBSD is a continuing threat to cassava production and productivity in Malawi as manifested by high levels of incidence and severity. Furthermore, there is a big gap between the extent of CBSD in the fields and the knowledge that farmers have regarding CBSD, as only 10.1% of the farmers knew the presence of CBSD in their fields against a recorded incidence of 88.3%. In the absence of early storage root bulking varieties, farmers lose a significant part of their potential yield when they resort to early harvesting as a way of reducing CBSD impact. In addition, farmers lack a source of clean planting material and receive little extension service for cassava

production. Based on field observations, it can be stated that cassava will continue to be under threat in Malawi if, 1) no breeding interventions are introduced to address the problem, and 2) no extension education is provided to farmers on how to diagnose and prevent the disease through selection of clean planting material. In view of the impact and extent of the disease and the late maturity period associated with cassava, concerted efforts towards the development of early storage root bulking varieties as a long term solution in avoiding CBSD impact should be made.

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Chapter 3

3 Early storage root bulking index and agronomic traits associated with early bulking in cassava[1]

Abstract

One of the attempts by farmers in counteracting the devastating effects of cassava brown streak disease (CBSD) on yield and quality of cassava is early harvesting. However, most varieties grown by farmers in Malawi are late bulking , which increases the disease severity, while on the other hand, early harvesting results in significant yield losses. Farmers, therefore, need early storage root bulking cassava varieties in order to reduce the time to harvest, while at the same time minimising devastating effects of CBSD on yield and quality of cassava. The study was, therefore, conducted to identify high yielding and early storage root bulking cassava genotypes and the traits associated with early storage root bulking and estimate the yield loss due to early harvesting. Trials were conducted using a triple square lattice design at two locations for two growing seasons with three harvest intervals (6, 9 and 12 months after planting, MAP). High yields up to 9.5 t ha^{-1} at 6 MAP and 17.8 t ha^{-1} at 9 MAP were obtained. Furthermore, the study revealed that yields obtained at 9 MAP were higher than those obtained at 12 MAP for some genotypes, which suggests that such genotypes would be considered as early storage root bulking type. Simple correlation analysis identified harvest index, storage root number, storage root diameter and storage root length as the selection criteria to achieve high fresh storage root yield (t ha^{-1}) and dry storage root yield (t ha^{-1}). The path coefficient analysis allocated harvest index and shoot mass as the major selection criteria in improving fresh and dry storage root yield. The study suggests that both source and sink capacities were important for determining early yield. Therefore, these two traits are the key determinants of early storage root bulking and should be used when selecting early bulking varieties, and should be coupled with indirect selection for storage root number, storage root diameter and storage root length.

[1] Published: Field Crops Research Vol. 198 (2016): 171–178

3.1 Introduction

Cassava (*Manihot esculenta* Crantz) plays an important role in the traditional tropical cropping systems, more particularly on small farms in the subsistence farming sector. It is often grown in mixed stands with other food or cash crops. Cassava's importance is mainly derived from its wide range of adaptation, its tolerance to low soil fertility, drought, pests and diseases, a high dry matter yield ha^{-1}, flexibility in planting and harvesting and a diverse range of utilization (Ceballos et al., 2004; FAO, 2013; Leihner, 2002; MoAFS, 2007; Onwueme, 1978; Westby, 2002).

Cassava production is affected by numerous constraints that include pests and diseases, in particular cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), low yield potential, long growth period/late storage root bulking, early postharvest deterioration, use of low yielding varieties, and shortage of labour, land and capital for cassava production (Dahniya, 1994; IITA, 1990). The combination of late storage root bulking and CBSD infection makes the farmer vulnerable to food insecurity, as by the end of the season she/he realises yields that are well below the potential of the crop.

Cassava has no defined maturity period, which means that it can be harvested whenever economic yields can be obtained. Maximum dry matter (DM) accumulation in storage roots generally occurs between 300-360 days after planting (DAP), and is mainly influenced by changes in temperature (Alves, 2002). This is the period when most of the cassava is harvested (that is, 12 months after planting, MAP). However, the highest rates of DM accumulation in storage roots occur within 180-300 DAP (6-10 MAP), and varies according to genotype and environment. This infers that cassava harvesting can start as early as 6 MAP. According to FAO (2013), in cases where the storage root is used as food, the best time to harvest is between 8 to 10 MAP. Studies have reported high dry matter storage root yield (9.0 to 14.5 t ha^{-1}) at 7 MAP (Mtunda, 2009; Okogbenin and Fregene, 2002) and high fresh storage root yields (15.5 to 28.0 t ha^{-1}) at 6 and 7 MAP (Asante, 2010; Mtunda, 2009; Nair and Unnikrishnan, 2006; Okechukwu and Dixon, 2009; Tumuhimbise, 2013). A good measure of DM distribution in storage roots is its harvest index (HI, the ratio of storage root mass to the total plant mass), which represents the efficiency of storage roots production. Significant differences in HI have been reported among varieties, indicating that it can be used as a selection criterion for higher yield potential in cassava (Alves, 2002; Kawano, 2003). Harvest index values of 0.49–0.77 have been reported at 10–12 MAP (Alves, 2002), which means that varieties exhibiting a HI within this range at 6-9

MAP could be early storage root bulking. Since early bulking is partly due to a genotype's ability to quickly accumulate assimilate reserves in its storage roots (Alves, 2002; Segnou, 2000), there is a need to exploit this variability in order to breed for early storage root bulking cassava varieties.

Development of early storage root bulking varieties has received much attention across the globe (Kamau et al., 2011; Nair and Unnikrishnan, 2006; Okechukwu and Dixon, 2009; Okogbenin and Fregene, 2002; Okogbenin et al., 2008; Olasanmi et al., 2014; Suja et al., 2010; Tumuhimbise, 2013; Wholey and Cock, 1974), and more particularly in the wake of the CBSD epidemic which is threatening the cassava industry in east and southern Africa. Late harvesting of cassava contributes to a high CBSD incidence, which increases with plant age (Alvarez et al., 2012; Gondwe et al., 2003; Hillocks et al., 2001; Hillocks et al., 2002; Rwegasira and Rey, 2012). It is clearly documented that most famers prefer early bulking varieties that can also withstand pest and disease damage (Agwu and Anyaeche, 2007; Benesi et al., 2010; Chipeta et al., 2016; Dahniya, 1994; Munga, 2008; Okechukwu and Dixon, 2009; Tumuhimbise et al., 2012). A greater commitment, therefore, has to be made to develop early bulking varieties so that they reach full bulking before the CBSD (storage root necrosis) becomes severe. This in turn would effectively reduce the production period, resulting in a faster rate of return to investment. In Malawi, due to scarcity of livestock feed during later months of the year (dry periods), most livestock fend for themselves, which means that keeping cassava in the field for longer time exposes the crop to the animals. This in turn increases the cost of production as farmers resort to guarding their fields and if not, crop losses occur due to animal feeding. Therefore, highly productive early storage root bulking varieties would not only provide good storage root quality and productivity per unit area of land, but with early harvesting would also facilitate the release of land for other farming activities (for example, early land preparations for the following season, production of other short duration crops such as vegetables more especially in wetlands or areas close to water sources), and reduce the exposure to biotic and abiotic stresses, thereby increasing productivity. The objectives of this study were to: (1) identify high yielding and early storage root bulking cassava genotypes, (2) determine agronomic traits influencing early storage root bulking through path coefficient analysis, (3) estimate yield loss due to early harvesting.

3.2 Materials and methods

3.2.1 Plant material

Planting material was sourced from national agricultural research stations and farmers' fields. A total of 16 genotypes were evaluated (Table 3.1) and their selection was based on their popularity with farmers, availability of clones for replicated trials and their response to various diseases prevalent in Malawi.

Table 3.1. Cassava genotypes evaluated during studies

Code	Genotype	Source	Code	Genotype	Source
G1	Maunjili	Introduction from IITA	G9	Phoso	Locally bred/improved
G2	Mulola	Introduction from IITA	G10	Mbundumali	Local genotype
G3	Mpale	Introduction from IITA	G11	Yizaso	Locally bred/improved
G4	TMS4(2)1425	Introduction from IITA	G12	Beatrice	Local genotype
G5	01/1316	Locally bred/Improved	G13	Unknown	Local genotype
G6	01/1569	Locally bred/Improved	G14	Kalawe	Locally bred/improved
G7	Chamandanda	Locally bred/Improved	G15	96/1708	Locally bred
G8	Sauti	Locally bred/improved	G16	MK05/0297	Locally bred

3.2.2 Experimental sites

The experiments were conducted in Malawi at two different sites i.e. Chitala Agricultural Research Station, Salima District (Central Malawi) and Kasinthula Agricultural Research Station, Chikwawa District (Southern Malawi) over two growing seasons (2014 and 2015). Chitala Agricultural Research Station lies on latitude 13°40' South and on longitude 34°15' East. It is at an altitude of 606 m above sea level. The station receives rains for three months, normally between December and March, and has mean annual temperatures of 28°C maximum and 16°C minimum. The soils are sandy clay to sandy clay loam with the pH range of 4.4 to 6.7. Kasinthula Agricultural Research Station is located on 16°0'S latitude, 34°5'E longitude and at 70 m above sea level. The yearly average maximum and minimum temperatures of the site are

35.6°C and 18.6°C, respectively, and the annual average rainfall is 520 mm. Table 3.2 details soil characteristics of the two sites and Figure 3.1 summarises rainfall and temperature pattern during the evaluation periods.

Table 3.2. Soil status of the two sites in 2014 and 2015

	Chitala		Kasinthula	
Characteristics	2014	2015	2014	2015
Soil texture	SC - SCL	SL -SC	SL -SCL	SC - C
Soil pH	4.4 - 6.7	5.9 - 6.3	5.8 - 6.1	4.2 - 4.8
Phosphorus (ppm)	1.4 - 2.2	61.6 - 97.2	58.4 - 93.1	1.4 - 4.2
Organic carbon (%)	0.8 - 1.3	0.4 - 0.5	0.5 - 0.7	0.7 - 0.9
Estimated nitrogen (%)	0.09 - 0.13	0.04 - 0.05	0.05 - 0.07	0.07 - 0.09
Potassium (meq/100g)	0.2 - 0.3	0.6 - 0.8	0.5 - 0.6	0.3 - 0.4

SC = sandy clay, SCL = sandy clay loam, SL = sandy loam, C = clay.

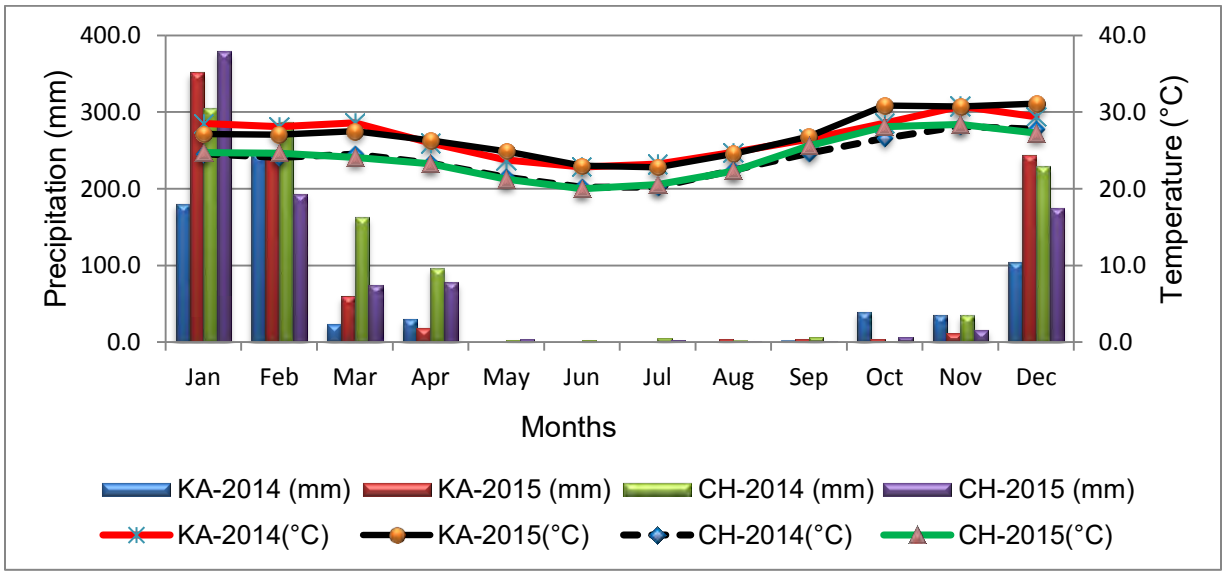

Figure 3.1. Total monthly rainfall (mm) and average monthly temperature (°C) for Chitala and Kasinthula in 2014 and 2015

KA = Kasinthula Research Station, CH = Chitala Research Station.

3.2.3 Experimental design

The experiments were laid out using a square lattice design constituting the 16 genotypes. Three replications per site were used and each replication had four blocks and each block had four plots (4x4). A gross plot consisted of five ridges and the inner three ridges were considered as the net plot, excluding the plants at the end of each row (each ridge consisted of six plants which gave 12 net plants and 30 gross plants). Plants were spaced at 1 m × 1 m and 2 m between replications. The trials were planted in January in 2014 and repeated in 2015 under rain-fed conditions and neither fertilizers nor pesticides were applied. Manual weeding was done when necessary.

3.2.4 Data collection

Data for individual genotype were collected at 6, 9 and 12 MAP for the following traits: fresh storage root yield (t ha^{-1}), dry storage root yield (t ha^{-1}), shoot mass (t ha^{-1}), number of storage roots $plant^{-1}$, storage root length (cm), plant height (cm), plant height at first branching (cm), harvest index, dry storage root mass content (%), starch content (%) using the specific gravity method, storage root diameter (cm) and levels of branching. At each harvest interval, data were collected on three plants per plot. The percentage dry mass (DM), starch content and harvest index (HI) were determined as described by Fukuda et al. (2010):

1. Dry mass (DM) % = 158.3 x SG – 142.
2. Starch content (%) = 112.1 x SG – 106.4; Where SG = specific gravity = $\frac{Wa}{(Wa - Ww)}$. Where Wa = mass in air of storage roots (kg) and Ww= mass in water of storage roots (kg).
3. Dry storage root yield (t ha^{-1}) = $\frac{\text{Fresh storage root yield}}{100} \times \text{DM\%}$
4. Harvest index (HI) = $\frac{\text{Mass of storage roots}}{\text{Mass of storage roots + aboveground mass}}$

In order to estimate yield loss due to early harvesting, an early bulking index (EBI) was developed by taking the ratio of fresh or dry storage root yield at sampling periods 6 and 9 MAP to fresh or dry storage root yield at 12 MAP and converted to a percentage.

Early bulking index (EBI) = $\frac{\text{Storage root mass at 6 or 9 MAP}}{\text{Storage root mass at 12 MAP}} \times 100$

A genotype with high EBI is considered as early bulking with a non-significant yield loss attributable to early harvesting.

3.2.5 Data analysis

Variance components were analysed using the restricted maximum likelihood (REML) procedure as described by O'Neill (2010) and Payne et al. (2014a) using GenStat, 17th edition for each environment separately. Genotypes, harvest time and environments were considered as fixed effects while replications, blocks within replications and error were considered random effects in the model. A combined analysis of variance was done for the mean data from each environment. Bartlett (1947) test was used to calculate the homogeneity of variances between environments in order to determine the validity of the combined analysis of variance on the data. The combined statistical mixed model was fitted as follows*:*

$$Y_{ijklm} = \mu + R_i + \beta_j + G_k + E_l + H_m + (GE)_{kl} + (GH)_{km} + (EH)_{lm} + (GEH)_{klm} + e_{ijklm}$$

Where Y_{ijklm} = an observation in the j^{th} block within i^{th} replication, μ = the overall mean, R_j = the effect of i^{th} replication (i = 1, 2, 3), β_j = the effect of j^{th} block within the replication (j = 1, 2, 3, 4), G_k = the main effect of k^{th} genotype (k = 1, 2….16), E_l = main effect of l^{th} environment (l = 1,2,3,4), H_m = the main effect of m^{th} harvesting time (m = 1, 2, 3), $(GE)_{kl}$ = the interaction effect of k^{th} genotype and l^{th} environment, $(GH)_{km}$ = the interaction effect of k^{th} genotype and m^{th} harvesting time, $(EH)_{lm}$ = the interaction effect of l^{th} environment and m^{th} harvesting time, $(GEH)_{klm}$ = the interaction effect of k^{th} genotype, l^{th} environment and m^{th} harvest time, e_{ijklm} = experimental error associated with the observation in the j^{th} block within the i^{th} replication.

Simple phenotypic correlations were done to assess the associations between the traits using GenStat statistical package 17th edition (Payne et al., 2014b). To determine traits that directly or indirectly contribute to early storage root bulking (fresh and dry mass), a path coefficient analysis was done for the data collected at 6 and 9 MAP, using Microsoft excel 2010 as described by Akintunde (2012).

3.3 Results

3.3.1 Variation due to genotype, harvest time, environment (location/season) and their interactions

Table 3.3 shows different sources of variation and their influence on the traits measured. Genotype had a highly significant (P<0.001) effect on all the traits except for storage root diameter (cm), plant height (cm) and plant height at first branch (cm). Harvest time impacted highly significantly (P<0.001) on all the traits except storage root number plant^{-1}, storage root diameter (cm) and plant height (cm). Environment (location/season) had a highly significant (P<0.001) influence on a number of traits except storage root diameter (cm), plant height (cm) and plant height at first branch (cm). Genotype x harvest time interaction was significant (P<0.05) for fresh storage root yield, dry storage root yield, harvest index, storage root length and levels of branching.

There was a highly significant (P<0.001) genotype x environment (location/season) interaction effect on all the traits except for dry mass content, starch content, storage root diameter, plant height and plant height at first branch. On the other hand, harvest time x environment (location/season) interaction was highly significant (P<0.001) for most of the traits. Genotype x harvest time x environment (location/season) interaction was only significant (P<0.05) for dry storage root yield, shoot mass and levels of branching.

Table 3.3. Levels of significance for genotype, harvest time, environment (locations and seasons) and their interactions

Source of variance	DF	FSRY	DSRY	HI	DMC	SC	SM	SRN	SRL	LB	PHT1B	PHT	SRD
Genotype (G)	15	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.462	0.187	0.268
Harvest time (H)	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.575	<0.001	<0.001	0.038	0.078	0.103
Environment (E)	3	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.011	<0.001	<0.001	0.397	0.565	0.496
G x H	30	0.007	0.003	<0.001	0.287	0.309	0.088	0.465	0.016	<0.001	0.482	0.418	0.418
G x E	45	<0.001	<0.001	0.002	0.087	0.101	<0.001	<0.001	<0.001	<0.001	0.382	0.487	0.531
H x E	6	<0.001	<0.001	0.017	<0.001	<0.001	<0.001	0.410	<0.001	0.197	0.533	0.491	0.460
G x H x E	90	0.058	0.017	0.151	0.147	0.147	<0.001	0.487	0.977	0.016	0.481	0.45	0.473

DF = degrees of freedom, FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), HI = harvest index, DMC = dry mass content (%), SC = starch content (%), SM = shoot mass (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm), LB = levels of branching (on a scale of 1 to 5), PHT = plant height (cm), PHT1B = plant height at first branch (cm), SRD = storage root diameter (cm), F-Prob > 0.05 = not significant.

3.3.2 Mean performance of genotypes for storage root yield and harvest index

Performance of the genotypes in terms of fresh storage root yield at the two locations and two seasons (Table 3.4) revealed that Phoso was the highest yielding genotype at 6 MAP (9.5 t ha^{-1}) followed by Mulola (9.3 t ha^{-1}) and 01/1316 was the lowest yielding (3.5 t ha^{-1}). At 9 MAP, Phoso (17.8 t ha^{-1}) and Mulola (15.0 t ha^{-1}) also had the highest yields. A similar trend was observed at 12 MAP where the two genotypes Mulola (27.9 t ha^{-1}) and Phoso (24.2 t ha^{-1}) were the highest yielding genotypes, while TMS4(2)1425 (7.1 t ha^{-1}) and 01/1316 (12.1 t ha^{-1}) recorded lowest yields at 9 and 12 MAP, respectively. With respect to harvesting time across the environments (location/season), the highest yields were obtained at 12 MAP (19.2 t ha^{-1}) and the lowest was at 6 MAP (7.2 t ha^{-1}) and a significant increase in yield was observed from one harvest time to the other (Figure 3.2). Averaged across environments and harvest times, best performers were Mulola (17.4 t ha^{-1}) and Phoso (17.2 t ha^{-1}) and the lowest yielding genotype was 01/1316 (7.9 t ha^{-1}). At 12 MAP, five genotypes (Mbundumali, 01/1316, Sauti, Chamandanda, and Mpale) yielded lower than Phoso at 9 MAP.

Genotype Phoso consistently yielded higher than any other genotype at all harvest times (Table 3.4). Genotype 01/1316 was the lowest-yielding genotype at 6 MAP (1.4 t ha^{-1}) and 12 MAP (4.9 t ha^{-1}) while TMS4(1)1425 was the lowest-yielding genotype at 9 MAP (2.5 t ha^{-1}). Highest dry storage root yield was obtained at 12 MAP (6.9 t ha^{-1}) and lowest yield was recorded at 6 MAP (2.6 t ha^{-1}). At 9 MAP, most of the genotypes gave storage root yield that were above the average in terms of dry storage root yield (4.3 t ha^{-1}) unlike at 6 and 12 MAP which showed that 9 MAP would be most ideal to obtain high dry storage root yield.

At 6 MAP, the HI ranged from 0.39 to 0.69, while at 9 MAP it ranged from 0.48 to 0.74 and at 12 MAP, the lowest HI was 0.54 and the highest 0.78 (Table 3.5). Mulola recorded the highest HI at all harvest times (0.69 at 6 MAP, 0.74 at 9 MAP and 0.78 at 12 MAP) across locations and seasons. Other genotypes that recorded high HI at the three harvest times were Phoso, Maunjili and 01/1569. On the other hand, the lowest HI was exhibited by Yizaso at 6 MAP, TMS4(2)1425 at 9 MAP and 01/1316 at 12 MAP.

Table 3.4. Effect of genotype, harvesting time and genotype by harvesting time interaction across environments (locations and seasons) on fresh and dry storage root yield

Genotype	Fresh storage root yield (t ha^{-1})				Dry storage root yield (t ha^{-1})			
	6MAP	9MAP	12MAP	Mean	6MAP	9MAP	12MAP	Mean
01/1316	3.5	8.1	12.1	7.9	1.4	3.3	4.9	3.2
01/1569	8.3	13.4	22.3	14.7	2.7	4.5	7.4	4.9
96/1708	8.1	13.0	20.8	14.0	2.7	4.5	6.5	4.6
Beatrice	6.5	13.9	18.7	13.0	2.4	4.9	7.9	5.0
Chamandanda	6.5	10.5	16.1	11.0	2.5	4.2	5.9	4.2
Kalawe	7.8	12.4	18.7	12.9	3.2	4.7	7.4	5.1
Maunjili	8.6	13.7	23.7	15.3	3.1	4.8	8.6	5.5
Mbundumali	6.5	10.2	15.1	10.6	2.7	4.1	5.4	4.1
MK05/0297	5.4	11.8	18.0	11.7	1.8	4.0	6.2	4.0
Mpale	7.5	11.5	17.5	12.1	2.7	4.2	6.5	4.5
Mulola	9.3	15.0	27.9	17.4	3.2	4.8	8.6	5.6
Phoso	9.5	17.8	24.2	17.2	3.3	5.8	10.2	6.4
Unknown	7.8	13.3	19.3	13.5	2.7	4.7	7.1	4.8
Sauti	6.6	10.2	15.2	10.6	2.0	3.3	6.0	3.8
TMS4(2)1425	4.2	7.1	20.7	10.6	1.5	2.5	6.0	3.3
Yizaso	8.6	12.0	17.8	12.8	3.0	4.3	5.9	4.4
Mean	7.2	12.1	19.2	**12.8**	2.6	4.3	6.9	**4.6**
F-Prob. : G = < 0.001; H = < 0.001; G x H = < 0.007;					G = < 0.001; H = < 0.001; G x H = < 0.003			
SE± : G =1.0 ; H = 0.7 ; G x H = 1.5;					G = 0.3; H = 0.2 ; G x H = 0.5			

MAP = months after planting, G = genotype, H = harvest time.

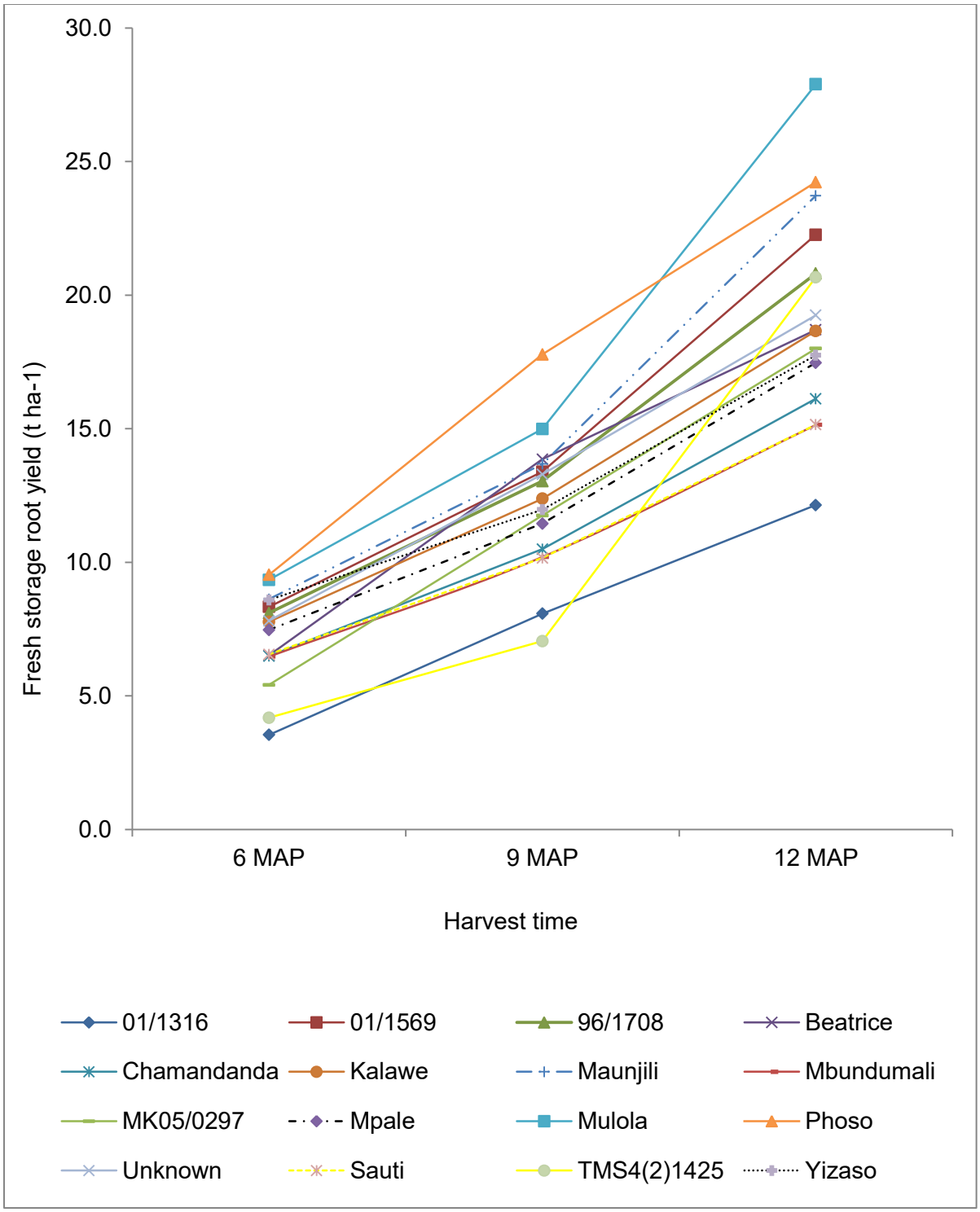

Figure 3.2. Fresh storage root yield for 16 genotypes harvested at 6, 9 and 12 months after planting (MAP) across locations and seasons

Table 3.5. Effect of genotype, harvesting time and genotype by harvesting time interaction on harvest index across environments (locations and seasons)

Genotype	Harvest time			Mean
	6 MAP	9 MAP	12 MAP	
01/1316	0.42	0.53	0.54	0.50
01/1569	0.56	0.65	0.74	0.65
96/1708	0.57	0.64	0.68	0.63
Beatrice	0.44	0.58	0.61	0.54
Chamandanda	0.55	0.56	0.69	0.60
Kalawe	0.52	0.56	0.62	0.57
Maunjili	0.60	0.64	0.74	0.66
Mbundumali	0.48	0.53	0.57	0.53
MK05/0297	0.40	0.50	0.54	0.48
Mpale	0.53	0.59	0.64	0.59
Mulola	0.69	0.74	0.78	0.74
Phoso	0.55	0.63	0.74	0.64
Unknown	0.55	0.61	0.68	0.61
Sauti	0.44	0.55	0.56	0.52
TMS4(2)1425	0.46	0.48	0.58	0.51
Yizaso	0.39	0.52	0.62	0.51
Mean	0.51	0.58	0.65	**0.58**
F. Prob. : G = <0.001; H = <0.001; G x H = <0.001				
SE± : G = 0.01; H = 0.007; G x H = 0.02				

MAP = months after planting, G = genotype, H = harvest time

3.3.3 Early storage root bulking genotypes

At 6 MAP, all genotypes were below 50% of their 12 MAP fresh storage root yield (Table 3.6). The highest early-bulking index (EBI) at 6 MAP was achieved by genotype Yizaso (48.3%) followed by Sauti (43.4%). Though Phoso and Mulola did not achieve a high EBI, they were the highest yielding genotypes at 6 MAP (9.5 t ha^{-1} for Phoso and 9.3 t ha^{-1} for Mulola). At 9 MAP, Phoso and Beatrice had attained over 70% of their 12 MAP yield. Phoso was the highest yielding genotype at 9 MAP (17.8 t ha^{-1}), followed by Mulola (15.0 t ha^{-1}). TMS4(2)1425 recorded the lowest EBI at both 6 (20.3%) and 9 (34.3%) MAP.

Based on dry storage root yield (Table 3.7), Mbundumali and Yizaso gave over 50% of their 12 MAP yield at 6 MAP. The highest yielders at 6 MAP were Phoso, Mulola, Kalawe, Yizaso and Maunjili with over 3 t ha^{-1} which was higher than the best early storage root bulkers. At 9 MAP, the fastest storage root bulking genotype was also Mbundumali which attained well over 75% of its 12 MAP yield. Furthermore, Yizaso and Chamandanda attained above 70% of their 12 MAP

yield at 9 MAP. Though Phoso and Beatrice had lower EBI than the best early bulkers at 9 MAP, they registered the highest yields.

3.3.4 Path analysis

Harvest index, storage root number, storage root diameter and storage root length showed strong positive correlation with fresh storage root yield and dry storage root yield, while shoot mass and plant height at first branch were negatively and weakly associated with fresh storage root yield and dry storage root yield at 6 MAP (Table 3.8) and (Table 3.9). At 9 MAP, the harvest index, storage root number and storage root diameter exhibited strong positive correlations with both fresh storage root yield and dry storage root yield. Other traits were weakly associated with the yield traits. The path coefficient analysis revealed that at 6 MAP the harvest index exerted the highest direct positive effect on both the fresh storage root yield (0.93) and the dry storage root yield (1.00), followed by the shoot mass (0.32 for fresh storage root yield and 0.61 for dry storage root yield). The storage root number and the storage root diameter exhibited the highest total indirect effects for both the fresh storage root yield and the dry storage root yield. At 9 MAP, a similar trend as observed at 6 MAP was found, where the harvest index predicted more strongly, in a direct way, both the fresh storage root yield (0.97) and the dry storage root yield (0.88) and this was followed by the shoot mass (0.59 for fresh storage root yield and 0.69 for dry storage root yield). On the other hand, the storage root number and the storage root diameter strongly predicted the fresh storage root yield and the dry storage root yield in an indirect way.

Table 3.6. Early bulking index and mean fresh storage root yield across environments (locations and seasons)

Genotype	6 MAP		9 MAP		12 MAP FSRY (t ha^{-1})
	EBI (%)	FSRY (t ha^{-1})	EBI (%)	FSRY(t ha^{-1})	
01/1316	28.9	3.5	66.9	8.1	12.1
01/1569	37.2	8.3	60.1	13.4	22.3
96/1708	38.9	8.1	62.5	13.0	20.8
Beatrice	34.8	6.5	74.3	13.9	18.7
Chamandanda	40.4	6.5	65.2	10.5	16.1
Kalawe	41.7	7.8	66.3	12.4	18.7
Maunjili	36.3	8.6	57.8	13.7	23.7
Mbundumali	43.0	6.5	67.5	10.2	15.1
MK05/0297	30.0	5.4	65.6	11.8	18.0
Mpale	42.9	7.5	65.7	11.5	17.5
Mulola	33.3	9.3	53.8	15.0	27.9
Phoso	39.3	9.5	73.6	17.8	24.2
Unknown	40.4	7.8	68.9	13.3	19.3
Sauti	43.4	6.6	67.1	10.2	15.2
TMS4(2)1425	20.3	4.2	34.3	7.1	20.7
Yizaso	48.3	8.6	67.4	12.0	17.8
Mean	37.4	7.2	63.6	12.1	19.2
F-Prob	0.041	< 0.001	< 0.001	< 0.001	< 0.001
SE±	1.8	0.4	0.7	0.5	1.2

MAP = months after planting, FSRY = fresh storage root yield, EBI = early bulking index.

Table 3.7. Early bulking index and mean dry storage root yield across environments (locations and seasons)

Genotype	6 MAP		9 MAP		12 MAP DSRY (t ha^{-1})
	EBI (%)	DSRY (t ha^{-1})	EBI (%)	DSRY (t ha^{-1})	
01/1316	28.6	1.4	67.3	3.3	4.9
01/1569	36.5	2.7	60.8	4.5	7.3
96/1708	41.5	2.7	69.2	4.5	6.5
Beatrice	30.4	2.4	62.0	4.9	7.8
Chamandanda	42.4	2.5	71.2	4.2	5.9
Kalawe	43.2	3.2	63.5	4.7	7.5
Maunjili	36.0	3.1	55.8	4.8	8.7
Mbundumali	50.0	2.7	75.9	4.1	5.3
MK05/0297	29.0	1.8	64.5	4.0	6.2
Mpale	41.5	2.7	64.6	4.2	6.5
Mulola	37.2	3.2	55.8	4.8	8.9
Phoso	32.4	3.3	56.9	5.8	10.2
Unknown	38.0	2.7	66.2	4.7	7.0
Sauti	33.3	2.0	55.0	3.3	5.9
TMS4(2)1425	25.0	1.5	41.7	2.5	6.0
Yizaso	50.8	3.0	72.9	4.3	5.9
Mean	37.2	2.6	62.7	4.3	6.9
F-Prob	0.032	< 0.001	0.01	0.025	0.009
SE±	1.2	0.1	5.8	0.2	0.3

MAP = months after planting, DSRY = dry storage root yield, EBI = early bulking index.

Table 3.8. Direct (boldfaced main diagonals), alternate/indirect path coefficient values and correlation coefficients of fresh and dry storage root yield against agronomic characters at six months after planting

Fresh storage root yield												
Traits	HI	SM	LR	LB	SRN	PHT1B	PHT	SRD	SRL	SC	FSRY (rP)	Total indirect effects
HI	**0.93**	-0.17	-0.01	-0.06	0.06	-0.03	-0.17	0.16	0.08	0.00	**0.79**	**-0.14**
SM	-0.50	**0.32**	0.01	-0.02	0.00	0.02	0.21	-0.06	0.03	0.00	**0.02**	**-0.30**
LR	-0.11	0.05	**0.06**	0.08	-0.02	0.00	-0.04	0.09	0.06	-0.02	**0.15**	**0.09**
LB	-0.40	-0.04	0.03	**0.15**	-0.05	0.02	-0.06	0.00	-0.08	-0.01	**-0.44**	**-0.59**
SRN	0.67	0.00	-0.01	-0.09	**0.08**	-0.02	-0.04	0.11	0.10	0.00	**0.80**	**0.72**
PHT1B	-0.69	0.13	0.00	0.06	-0.04	**0.04**	0.16	-0.13	-0.02	0.01	**-0.48**	**-0.52**
PHT	-0.59	0.25	-0.01	-0.03	-0.01	0.03	**0.26**	-0.13	0.00	0.01	**-0.23**	**-0.49**
SRD	0.68	-0.08	0.02	0.00	0.04	-0.03	-0.16	**0.22**	0.07	0.00	**0.77**	**0.55**
SRL	0.35	0.06	0.02	-0.06	0.04	0.00	-0.01	0.08	**0.20**	-0.01	**0.67**	**0.47**
SC	0.02	0.03	-0.02	-0.03	0.01	0.01	0.07	-0.01	-0.03	**0.05**	**0.09**	**0.04**
Dry storage root yield												
Traits	HI	SM	LR	LB	SRN	PHT1B	PHT	SRD	SRL	SC	DSRY (rP)	Total indirect effects
HI	**1.00**	-0.33	-0.03	0.03	0.08	-0.13	0.06	0.03	-0.02	0.01	**0.70**	**-0.30**
SM	-0.54	**0.61**	0.04	0.01	0.00	0.07	-0.07	-0.01	-0.01	0.03	**0.13**	**-0.48**
LR	-0.12	0.10	**0.26**	-0.04	-0.03	0.01	0.02	0.02	-0.02	-0.14	**0.06**	**-0.20**
LB	-0.43	-0.07	0.14	**-0.06**	-0.07	0.07	0.02	0.00	0.02	-0.07	**-0.45**	**-0.39**
SRN	0.72	0.00	-0.06	0.04	**0.11**	-0.08	0.01	0.02	-0.03	0.03	**0.77**	**0.66**
PHT1B	-0.75	0.24	0.01	-0.03	-0.05	**0.17**	-0.06	-0.03	0.01	0.08	**-0.40**	**-0.57**
PHT	-0.64	0.48	-0.04	0.01	-0.02	0.10	**-0.09**	-0.03	0.00	0.09	**-0.12**	**-0.03**
SRD	0.73	-0.15	0.10	0.00	0.05	-0.10	0.06	**0.04**	-0.02	-0.02	**0.70**	**0.65**
SRL	0.37	0.11	0.08	0.02	0.05	-0.02	0.00	0.02	**-0.06**	-0.06	**0.52**	**0.58**
SC	0.03	0.06	-0.11	0.01	0.01	0.04	-0.02	0.00	0.01	**0.34**	**0.37**	**0.03**

HI = harvest index, SM = shoot mass, LB = levels of branching, SRN = storage root number per plant, PHT1B = plant height at first branching, PHT = plant height, SRD = storage root diameter, SRL = storage root length, SC = starch content, FSRY = fresh storage root yield, DSRY = dry storage root yield, rP = phenotypic correlation coefficient.

Table 3.9. Direct (boldfaced main diagonals), alternate/indirect path coefficient values and correlation coefficients of fresh and dry storage root yield against agronomic characters at nine months after planting

Fresh storage root yield											
Traits	HI	SM	LB	SRN	PHT1B	PHT	SRD	SRL	SC	FSRY (rP)	Total indirect effects
HI	**0.97**	-0.39	0.00	0.05	0.16	-0.06	0.11	0.00	-0.02	**0.83**	**-0.14**
SM	-0.64	**0.59**	0.03	0.03	-0.26	0.10	-0.06	0.01	0.00	**-0.21**	**-0.80**
LB	0.02	0.10	**0.17**	-0.02	-0.01	0.00	0.03	-0.05	0.02	**0.25**	**0.08**
SRN	0.34	0.10	-0.02	**0.15**	-0.09	0.05	0.01	0.03	-0.01	**0.56**	**0.41**
PHT1B	-0.45	0.46	0.01	0.04	**-0.34**	0.11	-0.03	0.06	0.00	**-0.15**	**0.19**
PHT	-0.45	0.47	0.00	0.06	-0.29	**0.12**	-0.05	0.07	0.01	**-0.07**	**-0.19**
SRD	0.70	-0.24	0.03	0.01	0.06	-0.04	**0.16**	-0.01	-0.02	**0.64**	**0.48**
SRL	0.00	0.02	-0.04	0.02	-0.10	0.04	-0.01	**0.20**	0.02	**0.15**	**-0.05**
SC	-0.27	0.05	0.05	-0.03	-0.01	0.01	-0.06	0.28	**0.06**	**-0.14**	**0.02**
Dry storage root yield											
Traits	HI	SM	LB	SRN	PHT1B	PHT	SRD	SRL	SC	DSRY (rP)	Total indirect effects
HI	**0.88**	0.67	-0.12	0.00	-0.18	-0.09	-0.12	0.13	0.00	**0.69**	**-0.19**
SM	0.86	**0.69**	0.11	0.01	-0.05	0.09	0.12	-0.04	0.01	**-0.16**	**-0.85**
LB	-0.64	0.41	**0.19**	0.02	0.01	0.00	0.00	0.01	-0.02	**0.39**	**0.20**
SRN	0.01	0.07	0.03	**0.09**	-0.08	0.01	0.02	0.00	0.01	**0.41**	**0.32**
PHT1B	0.30	0.07	0.00	0.01	**-0.53**	-0.07	-0.08	0.01	-0.04	**-0.19**	**0.34**
PHT	-0.40	0.32	0.00	0.00	0.18	**0.20**	0.03	-0.01	0.02	**-0.06**	**-0.26**
SRD	-0.40	0.33	0.00	0.01	0.15	0.02	**0.26**	0.03	0.00	**0.52**	**0.26**
SRL	0.61	-0.16	0.01	0.00	-0.03	-0.01	0.04	**0.18**	0.07	**0.17**	**-0.01**
SC	0.00	0.01	-0.01	0.00	0.05	0.00	0.00	0.04	**0.37**	**0.18**	**-0.23**

HI = harvest index, SM = shoot mass, LB = levels of branching, SRN = storage root number per plant, PHT1B = plant height at first branching, PHT = plant height, SRD = storage root diameter, SRL = storage root length, SC = starch content, FSRY = fresh storage root yield, DSRY = dry storage root yield, rP = phenotypic correlation coefficient.

3.4 Discussion

Malawi, like most of the east and southern African countries has been greatly affected by CBSD, a disease that increases with plant age. One of the attempts to reduce the CBSD impact on yield and quality of cassava is early harvesting. However, most varieties in Malawi are late bulking (12-24 months), which means that early harvesting of such varieties would lead to a significant yield sacrifice among smallholder farmers. This study was therefore aimed at assessing the degree of variation in the rate of cassava storage root bulking among selected cassava genotypes, in order to generate information that would guide future improvement programmes for high yielding and early bulking cassava varieties in Malawi and other countries facing similar challenges.

3.4.1 Genotypic effects on early storage root yield and harvest index

Since yield is a complex trait, several variables were assessed in order to identify traits with a direct bearing on early storage root yield (fresh mass and dry mass). The traits included harvest index, storage root number, storage root diameter, storage root length, plant height, starch content, leaf retention and plant height at first branch. Significance of genotypic variance for most of the traits, including early storage root yield, indicated that there is a genetic potential for developing early storage root bulking varieties that could be used to counteract the devastating effects of CBSD in Malawi. Harvest time was identified as a critical factor in identifying genotypes that would best perform in a particular environment, as was clearly exhibited by the levels of significance.

Dry matter distribution to the storage roots increased with the age of the plants and this may reflect an increase in source activity as the plant develops and in the sink action as the storage roots enlarge. Alves (2002) reported that maximum dry matter (DM) accumulation in the storage roots occurs between 10-12 MAP, which is not different from what this study established where the highest yields were obtained at 12 MAP. However, this study revealed that yields obtained at 9 MAP were higher than those obtained at 12 MAP for some genotypes, which suggests that these genotypes would be early storage root bulking. The high yields obtained in this study (up to 9.5 t ha^{-1} at 6 MAP and 17.8 t ha^{-1} at 9 MAP) are not far from global trends where yields of up to 14.5 t ha^{-1} at 7 MAP (Okogbenin and Fregene, 2002) and 15.5 to 28 t ha^{-1} at 6 MAP (Asante, 2010; Nair and Unnikrishnan, 2006; Okechukwu and Dixon, 2009) have been reported. This means that there is a high genetic potential in cassava to breed for early bulking varieties.

The literature indicates that the highest values of HI at 10-12 MAP may range from 0.49–0.77 (Alves, 2002) which suggests that genotypes exhibiting similar values at 6 and 9 MAP could be regarded as early bulking. In this study, at 9 MAP, HI values ranged from 0.48 to 0.74 indicating that at 9 MAP the HI can be used as a selection criterion for high yield potential in cassava.

3.4.2 Early bulking index and yield loss due to early harvesting

Early bulking index is a measure of how quickly a genotype reaches its yield potential. The EBI on both the fresh and dry storage root yield basis revealed that the local varieties (Mbundumali, Yizaso and Beatrice) were the earliest bulking genotypes at both 6 and 9 MAP. However, these genotypes were not the highest yielding. Genotypes such as Phoso, Mulola and Maunjili gave highest yields at 6 and 9 MAP in spite of their lower EBI values. It appears that the advantage of the local varieties is in rapidly reaching their yield potential, while the actual yield potential is rather low. Early harvesting of genotypes with a high EBI suggests that there would be about 25% yield loss attributable to early harvesting. For example, a genotype with an EBI of 74% at 9 MAP would mean that the farmer would lose only 26% of the yield if it is harvested at 9 MAP instead of 12 MAP. The study found that the yield loss due to early harvesting of early-bulking varieties is much lower than what would be lost due to CBSD, which can be up to 43.1% (chapter 5). Others (Hillocks et al., 2001) have reported a yield loss of up to 70% due to CBSD on late bulking varieties. The EBI identified Mbundumali, Beatrice, Kalawe, Phoso and Yizaso as the early storage root bulking genotypes.

Since EBI gives the proportion of the potential yield only, there is a need to integrate the index with the actual yield realized at a particular harvest time. However, as observed by Kawano (2003), the yield per se is not an efficient selection criterion for early-bulking, but rather the HI. Therefore, based on yield, HI and EBI, the genotypes Phoso, Mbundumali, Mulola, and Maunjili were identified as the most productive early storage root bulking genotypes at both 6 and 9 MAP. The highest yields for these genotypes would be obtained at 9 MAP. Therefore, this study proposes that early harvesting in Malawi be 9 MAP. Mbundumali is a very popular sweet variety in Malawi but it is susceptible to CBSD and CMD, and the results showed that it could be harvested at any time between 6 and 9 MAP as it exhibited minimal yield increase from one harvest time to the other. This would help minimize yield losses due to CBSD, which becomes catastrophic on plants that are left in the field beyond 9 months.

There are various strategies of managing CBSD in the field. These include, using varieties tolerant to CBSD, selecting planting material free from CBSD, sanitation and roguing of any infected plants from the field, especially shortly after sprouting (Hillocks and Jennings, 2003; Hillocks and Thresh, 2000; IITA/SARRNET and Malawi Government, 2004; Legg et al., 2011). The present results have clearly demonstrated the benefits of early harvesting, more especially for early-bulking cassava genotypes in light of the CBSD impact. Early harvesting is used by some farmers in order to avoid yield losses due to the CBSD (Hillocks, 2003; Hillocks et al., 2001). However, this method in itself reduces yield unless it is practised on early bulking varieties. The heavy yield loss due to early harvesting has been addressed in this study through the identification of early storage root bulking genotypes.

3.4.3 Traits associated with early storage root bulking

Simple correlation analysis identified the harvest index, storage root number, storage root diameter and storage root length as the selection criteria to achieve early high fresh storage root yield and dry storage root yield. The path coefficient analysis allocated harvest index and shoot mass as the major selection criteria in improving early fresh storage root yield and dry storage root yield.

The path analysis revealed that indirect effects of storage root number, storage root diameter and storage root length were larger than their direct effects, even though the observed correlation between these traits and fresh and dry storage root yield were significant. Therefore, the path coefficient interpretation suggests that the correlations arise because storage root number, storage root diameter and storage root length are correlated with other variables that have direct effects on the storage root yield, and not because they themselves directly predict early storage root yield.

Since harvest index and shoot mass explained the highest variation in early storage root yields, this study suggests that both source and sink capacities were important for determining early yield. Therefore, these two traits are the key determinants of early storage root bulking and should be used when selecting early bulking varieties. Past studies (Kawano, 1990; Kawano, 2003; Kawano, 1987; Okogbenin and Fregene, 2002) also reported HI and shoot mass as the most important traits associated with storage root yield.

3.5 Conclusions

The study identified several varieties as early-bulking. Productive early storage root bulking varieties would not only provide good storage root quality and high productivity per unit land area and time, but could also reduce the exposure to biotic (in particular CBSD) and abiotic

stresses. The early bulking varieties enable the release of the land to other farming activities, thereby increasing overall cropping productivity. The harvest index and shoot mass were identified to be the key determinants of early storage root bulking and should be used when selecting early-bulking varieties.

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Chapter 4

4 Genotype x environment interaction and stability analysis of cassava genotypes[1]

Abstract

Cassava (*Manihot esculenta* Crantz) responds to the effect of genotype by environment interaction (GEI), which makes identifying superior genotypes in terms of performance, stability and adaptability challenging. Currently there is limited information about the GEI effect of cassava genotypes at different times of harvesting (TOH). Due to the increasing demand for early storage root bulking varieties, and confounding effects of site, crop age, and season during selection, there is a need for the objective characterization of genotypes in terms of adaptability and stability with respect to TOH. The study was, therefore, conducted to identify high yielding, stable and adaptable cassava genotypes harvested at different times (6, 9 and 12 months after planting, MAP). The study was conducted in four environments using sixteen genotypes in a triple square lattice design. Variance components for individual environment were analysed using the restricted maximum likelihood (REML), while the combined analysis was performed using the additive main effects and multiplicative interaction (AMMI) model. The AMMI analysis of variance at three TOH revealed that variances due to genotypes, environments, and GEI were significant for most of the traits. However, at 6 MAP, the GEI was not significant for most of the traits. The significance of the main effects indicated stability of some genotypes across environments, while GEI significance indicated that some genotypes were specifically adapted to certain environments. The non-significance of GEI at 6 MAP for almost all traits means that genotypes can be reliably evaluated in any single environment. The study identified five genotypes (Mulola, Phoso, Maunjili, Beatrice and Unknown) that exhibited consistent performance, stability and adaptability across the three harvest periods.

4.1 Introduction

Cassava (*Manihot esculenta* Crantz) is a popular food and income generating crop among resource constrained farmers due to its comparative advantages over other crops. These advantages include, drought tolerance, low requirements for inputs like fertilizers and chemicals, flexibility in planting and harvesting times, adaptation to a wide range of agro-

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ecological conditions, diverse modes of utilization and high dry matter yield ha^{-1} (FAO, 2013; MoAFS, 2007; Westby, 2002).

Though cassava is widely adapted to a variety of environmental conditions, it is reported that the adaptability of most varieties is narrow, and many traits show large genotype by environment interaction (GEI) effects (Akinwale et al., 2011; Benesi et al., 2004; Dixon and Nukenine, 1997; Noerwijatia et al., 2014 ; Ssemakula and Dixon, 2007; Tumuhimbise et al., 2014). The GEI may be defined as the differential genotypic expression across environments, and one of its major effects is that it reduces the association between the phenotypic and genotypic values (Romagosa and Fox, 1993). The presence of significant GEI makes identifying superior genotypes difficult as the rank order for genotypes will vary between environments (Bowman, 1972; Ceccarelli, 2012). The assessment of GEI is important in designing the best breeding strategy for the development of genotypes with adequate adaptation to target environments. Genotypic adaptation across environments can effectively be assessed through statistical analysis of the stability of individual genotypes. A stable genotype is one that is consistently well ranked over a wide range of environments, and such genotype is deemed to have a good general or wide adaptation, while in the case of stability that is confined to a limited range, the genotype is considered to have a specific or narrow adaptation (Fox et al., 1997). Therefore, the level of GEI is a major element in determining many key aspects of a breeding programme, including whether to aim for wide or specific adaptation, and will affect the choice of locations for selection (Fox et al., 1997; Romagosa and Fox, 1993).

Cassava has no defined maturity time, and there has been increasing demand by farmers for early storage root bulking varieties (Agwu and Anyaeche, 2007; Benesi et al., 2010; Dahniya, 1994; Munga, 2008; Okechukwu and Dixon, 2009). This has necessitated the development of early storage root bulking varieties that could be harvested between 6 and 10 months after planting (Kamau et al., 2011; Nair and Unnikrishnan, 2006; Okechukwu and Dixon, 2009; Okogbenin and Fregene, 2002; Okogbenin et al., 2008; Olasanmi et al., 2014; Suja et al., 2010; Tumuhimbise, 2013; Wholey and Cock, 1974). However, there is limited information about the stability and adaptability of cassava genotypes at different times of harvesting (TOH). Due to confounding effects of site, crop age, and season during the selection at different TOH, there is a need for the objective characterization of genotypes in terms of adaptability and stability with respect to TOH. Various statistical tools can be applied to data obtained from multi-environment trials. Two frequently used statistical analyses are the additive main effects and multiplicative interaction (AMMI) model and the genotype main effects and genotype x environment interaction effects (GGE) model (Crossa et al., 1991; Gauch, 2006; Gauch and Zobel, 1988; Yan et al., 2007). The present study

uses AMMI to partition the overall variation into genotype main effects, environment main effects, and genotype x environment interactions (Crossa et al., 1991; Gauch, 2006; Gauch and Zobel, 1988). The objectives of this study were to: 1) identify high yielding, stable and adaptable cassava genotypes at different times of harvesting through the application of multivariate analyses techniques, 2) to explain the magnitude of interaction of each genotype and environment at different times of harvesting.

4.2 Materials and methods

4.2.1 Plant material

Planting material with a diverse background was sourced from the National Agricultural Research Stations and famers' fields. A total of 16 genotypes were evaluated (Chapter 3) and their selection was based on their popularity with farmers and their response to various diseases prevalent in Malawi.

4.2.2 Experimental sites

The trials were conducted in Malawi at two sites, Chitala Agricultural Research Station in Salima district (Central Malawi) and Kasinthula Agricultural Research Station in Chikwawa district (Southern Malawi) over two growing seasons (2014 and 2015). Chapter 3 details soil characteristics of the two sites and the rainfall and temperature patterns. In this study, a combination of location (L = 2) and year/season (Y = 2) constitutes a single environment. This gives a total of four test environments, that is, Chitala 2014 = E1, Chitala 2015 = E2, Kasinthula 2014 = E3 and Kasinthula 2015 = E4.

4.2.3 Experimental design

The trials were laid out as described in chapter 3, section 3.2.3.

4.2.4 Data collection

Data for individual genotypes were collected at 6, 9 and 12 MAP for the following traits: fresh storage root yield (t ha^{-1}), dry storage root yield (t ha^{-1}), shoot mass (t ha^{-1}), number of storage roots $plant^{-1}$, storage root length (cm), plant height (cm), plant height at first branching (cm), harvest index, dry storage root mass content (%), starch content (%), root

diameter (cm) and levels of branching. At each harvest interval, the unit of measurement was three plants per plot.

The percentage dry mass (DM), starch content and harvest index (HI) were determined as described by Fukuda et al. (2010):

1. Dry mass (DM) % = 158.3 x SG – 142.
2. Starch content (%) = 112.1 x SG – 106.4; Where SG = specific gravity = $\frac{Wa}{(Wa - Ww)}$.
   Where Wa = mass in air of storage roots (kg) and Ww = mass in water of storage roots (kg)
3. Dry storage root yield (t ha^{-1}) = $\frac{\text{Fresh storage root yield}}{100} \times \text{DM\%}$
4. Harvest index (HI) = $\frac{\text{Mass of storage roots}}{\text{Mass of storage roots + aboveground mass}}$

4.2.5 Data analysis

Variance components were analysed using the restricted maximum likelihood (REML) procedure (O'Neill, 2010; Payne et al., 2014), using GenStat, 17th edition, for each environment separately. Genotypes and environments were fitted as fixed effects, while replications, blocks within replications and error were considered random effects in the model. A combined analysis of variance was done from the mean data from each environment. The Bartlett (1947) test was used to determine the homogeneity of variances between environments to determine the validity of the combined analysis of variance on the data. The AMMI analysis was performed on the combined data to partition the variation due to genotype (G), environment (E) and genotype by environment interaction (GEI) using GenStat, 17th edition. The following AMMI model was adopted (Gauch, 1988);

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge} + \varepsilon_{ger}$$

where Y_{ge} = the trait of genotype g in environment e, μ = the grand mean, α_g = the genotypes deviation from grand mean, β_e = the environment deviation, λ_n = is the eigenvalue of PCA axis n, γ_{gn} and δ_{en} = are the genotype and environment PCA scores for PCA axis n, ρ_{ge} is the residual of AMMI model and ε_{ger} = the random error.

AMMI stability value (ASV)

Since the AMMI model does not make provision for a quantitative stability measure, the AMMI stability value (ASV) as described by Purchase et al. (2000) was used to quantify and rank the genotypes according to their yield stability. The ASV was calculated as follows:

$$\text{AMMI Stability Value (ASV)} = \sqrt{\left[\frac{\text{IPCA1 Sum of Squares}}{\text{IPCA2 Sum of Squares}}(\text{IPCA1 score})\right]^2 + [\text{IPCA2 score}]^2}$$

Where IPCA = interaction principal component axis.

However, in selecting preferred varieties, stability *per se* is not the only parameter considered since the most stable varieties are not necessarily the best performers for the trait of interest. Therefore, the genotype stability index (GSI) was developed to cater for both stability and performance (Farshadfar, 2008).

Genotype stability index (GSI)

The GSI was calculated by the following formula: GSI = RASV + RY (Farshadfar, 2008)

Where the RASV is the rank of the AMMI stability value and RY is the rank of genotype's mean across environments. The GSI incorporates both the genotype mean and stability in a single criterion. A low value of this parameter shows desirable genotypes with a high genotype mean and stability. The larger the IPCA score, either negative or positive, the more specifically adapted a genotype is to certain environments. Smaller ASV scores indicate a more stable genotype across environments.

Biplots construction

To understand interaction patterns of genotypes with environments as well as identifying genotypes with specific adaptation, biplots of IPCA1 scores against IPCA2 were constructed using GenStat, 17th edition.

4.3 Results

4.3.1 Mean square values and percentage sum of squares contribution to total variation for various traits

The AMMI analysis of variance at three TOH revealed that variances due to genotypes, environments, and G x E interactions were significant for most of the traits (Table 4.1 and Table 4.2). However, at 6 MAP, the GEI was not significant for most of the traits except for shoot mass, leaf retention, levels of branching, storage root number and plant height. At 9 MAP, only GEI for fresh storage root yield was not significant. At 12 MAP, the variance due

to GEI was not significant for the dry mass content, harvest index and starch content. Since most of the traits were not significant at 6 MAP for GEI, their results have not been included in this section, except where explicitly stated. Also traits whose GEI proved to be non-significant (except fresh storage root yield) at the respective harvest intervals have neither been presented nor discussed.

4.3.2 Fresh storage root yield, dry storage root yield, shoot mass and dry mass content

The main effects of G and E accounted for 20.1% and 20.0% variation, respectively, and GEI effects represented 19.0% of the total variation for fresh storage root yield harvested at 9 MAP, while harvesting at 12 MAP, the G, E and GEI accounted for 15.4%, 21.3% and 29.7% of the total variation, respectively. For dry storage root yield, the G, E and GEI explained 18.7%, 30.7% and 18.9% of the variation, respectively, at 9 MAP, while at 12 MAP, the G, E and GEI contributed 7.7%, 54.4% and 17.7% to the total variation, respectively. At 9 MAP, the G, E and GEI contributed 11.0%, 27.3% and 23.8%, respectively to the total variation for dry mass content while at 12 MAP, 4.8%, 47.3% and 13.2% were contributed by the G, E and GEI, respectively. The G, E and GEI contributed about 11.3%, 32.5%, and 21.7% to the shoot mass variation, respectively, at 9 MAP, and 11.2%, 23.3% and 27.3% respectively, at 12 MAP. The E accounted for the largest amount of variation for shoot mass, dry storage root yield and dry mass content, except for the fresh storage root yield and shoot mass at 12 MAP, which showed that GEI was the greatest contributor (Table 4.1).

4.3.3 Harvest index, starch content, storage root length and storage root number

The harvest index contribution to total variation at 9 MAP was 43.7%, 20.0% and 14.4% for the G, E and GEI, respectively: while at 12 MAP the G, E and GEI accounted for 34.6%, 11.8% and 13.8%, respectively, of the total variation. Both at 9 and 12 MAP, the G was the least contributor to variation for the starch content, and the highest contributor was E (27.3% at 9 MAP and 47.0 at 12 MAP). For the storage root length, E contributed the most to the total variation at 9 MAP (37.8%), while at 12 MAP, G accounted for most of the variation (28.9%). The GEI explained most of the variation for storage root number at both 9 (28.8%) and 12 (33.4%) MAP, while E was the least contributor, at 9 MAP (2.5%) and at 12 MAP (0.3%) (Table 4.2).

4.3.4 Percentage variance contribution of principal component axes to genotype by environment interaction

The interactive principal component axis 1 (IPCA1) was significant (P<0.05) for all the traits, while IPCA2 was only significant for the dry mass content, harvest index and starch content at 9 MAP. At 12 MAP, the IPCA1 was highly significant (P<0.001) for the fresh storage root yield, shoot mass, dry storage root yield, storage root length and storage root number. On the other hand, IPCA2 was significant for fresh storage root yield, shoot mass and dry storage root yield (Table 4.1 and Table 4.2).

Of the GE interaction, IPCA1 and IPCA2 explained 54.4% and 31.4% at 9 MAP and 63.6% and 26.5% at 12 MAP, respectively, for the fresh storage root yield (Figure 4.1). For the dry storage root yield at 9 MAP, 91.6% of the GEI was explained by IPCA1 and IPCA2, while at 12 MAP, IPCA1 and IPCA2 accounted for 89.6% of the GEI (Figure 4.2). In terms of the shoot mass, at 9 MAP IPCA1 explained about 87.6% and IPCA2 7.8% of the GEI, while at 12 MAP, 51.2% and 37.9% were explained by IPCA1 and IPCA2, respectively (Figure 4.3). For the storage root number, IPCA1 and IPCA2 at 12 MAP explained a greater proportion (92.7%) of the GEI than at 9 MAP (78.61%) (Figure 4.4). The IPCA1 accounted for 99.5% of the GEI for the storage root length at 9 MAP, while IPCA2 explained only 0.3%. At 12 MAP, the IPCA1 explained 55.5% and IPCA2 explained about 25.6% of the GEI for the storage root length (Figure 4.5).

Table 4.1. Mean square values and % sum of squares for storage root yield, shoot mass, dry storage root yield, dry mass content

Source of variation	DF	Fresh storage root yield (t ha^{-1})		Shoot mass (t ha^{-1})		Dry storage root yield (t ha^{-1})		Dry mass content (%)	
		9MAP	12MAP	9MAP	12MAP	9MAP	12MAP	9MAP	12MAP
Total	191	45.0	101.4	27.45	63.5	9.22	13.88	93.4	175.6
Treatments	63	80.6***	203.8***	54.53***	119.1***	19.09***	33.58***	175.9***	347.7***
Genotypes (G)	15	115.2***	198.1***	39.45***	90.9***	21.96***	13.59***	130.8**	107.9^{ns}
Environments (E)	3	574.4***	1374.4***	568.83***	942.2***	180.28***	480.79***	1621.5***	5286.8***
Block	8	50.8	141.6	42.95	97.9	7.84	7.70	76.2	87.6^{ns}
Interactions (GEI)	45	36.2^{ns}	127.7***	25.27***	73.6***	7.39**	10.44***	94.5**	98.3^{ns}
IPCA 1	17	52.1*	215.1***	58.59***	99.7***	12.24***	18.13***	133.4***	154.1^{ns}
IPCA 2	15	34.1^{ns}	101.7***	5.90^{ns}	83.8***	6.42^{ns}	7.51*	88.8*	63.6^{ns}
Residuals	13	17.9	43.4	4.06	27.8	2.16	3.75	50.1	65.5
Error	120	25.9	44.9	12.20	32.0	4.13	3.95	51.3	91.1
% SS due to Treatments		59.1	66.3	65.5	61.9	68.3	79.8	62.1	65.3
% SS due to Genotype		20.1	15.4	11.3	11.2	18.7	7.7	11.0	4.8
% SS due to Environment		20.0	21.3	32.5	23.3	30.7	54.4	27.3	47.3
% SS due to GEI		19.0	29.7	21.7	27.3	18.9	17.7	23.8	13.2

*; **, *** = significant at the 5%, 1% and 0.1% probability levels, respectively, ns = not significant, DF = degrees of freedom, MAP = months after planting, GEI = genotype by environment interaction, IPCA = interaction principal component axis, SS = sum of squares.

Table 4.2. Mean square values and % sum of squares for harvest index, starch content, storage root length and storage root number

		Harvest index		Starch content (%)		Storage root length (cm)		Storage root number plant^{-1}	
Source of variation	DF	9MAP	12MAP	9MAP	12MAP	9MAP	12MAP	9MAP	12MAP
Total	191	0.017	0.016	46.8	87.6	93.5	102.2	4.05	7.61
Treatments	63	0.041***	0.029***	88.2***	173***	190.3***	197.1***	5.29**	10.04*
Genotypes (G)	15	0.095***	0.069***	65.6**	54.1^{ns}	152.1***	376.6***	6.07*	9.58^{ns}
Environments (E)	3	0.218***	0.118***	813.2***	2623.5***	2249***	754.5***	6.45^{ns}	1.20^{ns}
Block	8	0.009	0.011	38.2	43.9	67.0	99.2	10.983	8.00
Interactions (GEI)	45	0.011**	0.009^{ns}	47.4**	49.3^{ns}	65.8*	100.1**	4.952*	10.79*
IPCA 1	17	0.017***	0.009^{ns}	66.9**	77.3^{ns}	95.1**	147.1***	5.92*	21.70***
IPCA 2	15	0.009*	0.009^{ns}	44.5*	31.9^{ns}	59.4^{ns}	76.7^{ns}	4.97^{ns}	5.42^{ns}
Residuals	13	0.003	0.009	25.1	32.9	35.0	65.5	3.67	2.71
Error	120	0.005	0.009	25.7	45.7	44.4	52.7	2.94	6.31
% SS due to Treatments		78.0	60.3	62.1	65.1	67.2	63.6	43.1	43.5
% SS due to Genotype		43.7	34.6	11.0	4.9	12.8	28.9	11.8	9.9
% SS due to Environment		20.0	11.8	27.3	47.0	37.8	11.6	2.5	0.3
% SS due to GEI		14.4	13.8	23.8	13.3	16.6	23.1	28.8	33.4

*; **, *** = significant at the 5%, 1% and 0.1% probability levels, respectively, ns = not significant, DF = degrees of freedom, MAP = months after planting, GEI = genotype by environment interaction, IPCA = interaction principal component axis, SS = sum of squares.

4.3.5 High yielding, stable and adaptable cassava genotypes at different times of harvesting

To identify the best performing and stable genotypes across the environments, a GSI was used which selects based on both the mean performance and ASV. A low GSI value shows desirable genotypes with high genotype mean and stability. Genotypes with general or specific adaptability were identified using a biplot of IPCA1 scores against IPCA2. According to the AMMI 2 model, the genotypes scattered around the origin (0,0) indicate stability and general adaptability, while distances from the origin (0,0) are indicative of the amount of interaction that was exhibited by either genotypes over environments or environments over genotypes. Genotypes and environments that fall into the same sector interact positively, and the interaction is negative if they fall into opposite sectors. A genotype showing a high positive interaction with an environment clearly has the ability to exploit the agro-ecological conditions of the specific environment (specific adaptation).

Fresh storage root yield and dry storage root yield

For fresh storage root yield, genotypes Phoso and Mulola were the best yielding genotypes at both 9 and 12 MAP. For example, Phoso produced 19.7 t ha^{-1} at 9 MAP and 22.1 t ha^{-1} at 12 MAP, while 15.5 t ha^{-1} and 27.6 t ha^{-1} were realised from Mulola at 9 and 12 MAP, respectively. TMS4(2)1425 was the lowest yielding genotype at 9 MAP (5.7 t ha^{-1}), while 01/1316 was the lowest yielder at 12 MAP (10.7 t ha^{-1}). For the dry storage root yield, genotype Phoso yielded the best (8.8 t ha^{-1}) at 9 MAP followed by Beatrice (5.4 t ha^{-1}), while Mulola (8.2 t ha^{-1}) out yielded all other genotypes at 12 MAP, closely followed by Maunjiri (7.2 t ha^{-1}). The most stable genotypes based on GSI were Maunjiri and Beatrice at 9 MAP, and Phoso and Unknown at 12 MAP for fresh storage root yield. The GSI selected genotypes Mbundumali at 9 MAP, and Kalawe and Chamandanda at 12 MAP, as the most unstable genotypes for fresh storage root yield. For dry storage root yield, genotypes Maunjiri, 01/1516, Beatrice and Chamandanda were identified as the most stable genotypes at 9 MAP, while Mulola and Unknown were the most stable genotypes at 12 MAP. The least stable genotype for storage root yield was Sauti at 9 MAP and 01/1316 at 12 MAP (Table 4.3).

At 9 MAP, genotypes TMS4(2)1425, 01/1316, Chamandanda and Mbundumali exhibited specific adaptability for fresh storage root yield for environment E3, while genotypes Yizaso and

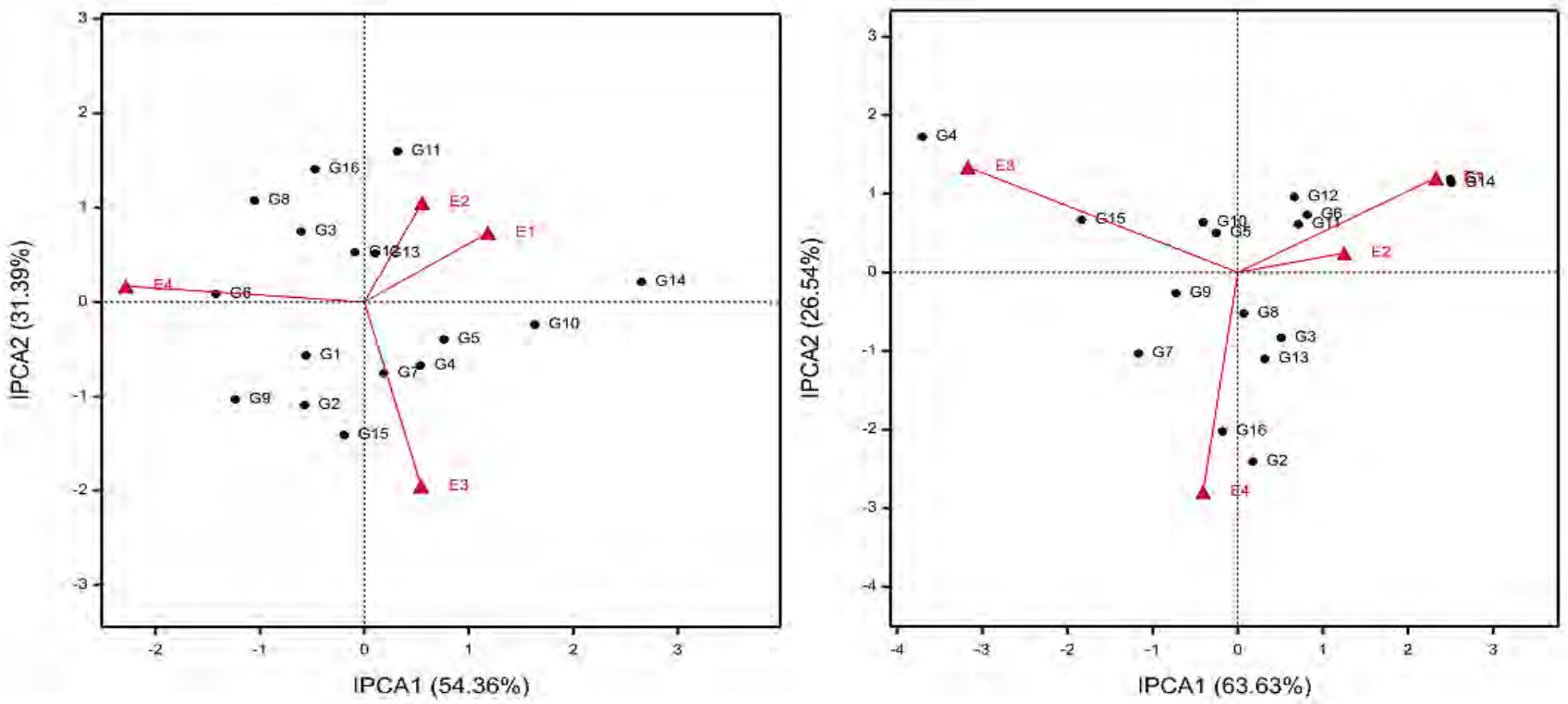
Kalawe showed positive interaction and specific adaptation for E1 and E2 (Figure 4.1). Genotypes Mpale, 01/1569, Sauti and MK05/0297 were specifically adapted to environment E4. On the other hand, genotypes Maunjili, Mulola, Phoso, Beatrice and Unknown were not sensitive to environmental interaction and therefore showed general adaptation. At 12 MAP, genotypes TMS4(2)1425 and 96/1708 revealed specific adaptation for environment E3, MK05/0297 for E4, while Maunjili and Kalawe were specifically adapted to E1.

For dry storage root yield (Figure 4.2), at 9 MAP, genotypes Maunjili, 01/1569, Chamandanda, Beatrice and Unknown showed good general adaptation. Genotypes Mpale and Sauti had a positive interaction with environment E4, while Phoso negatively interacted with E1 and E2. Genotype Yizaso was specifically adapted to environments E1 and E2, while Kalawe and 96/1708 were more sensitive to E3. At 12 MAP, environments E1 and E3 had more interactive forces, and genotypes Beatrice, Kalawe and Maunjiri were specifically adapted to E1, while TMS4(2)1425 was specifically adapted to E3. The environment E4 was specifically suitable for Sauti and MK05/0297.

Table 4.3. Ranks of 16 genotypes in four environments using mean performance, AMMI stability value and genotype selection index for fresh and dry storage root yield

	Fresh storage root yield (t ha^{-1})								Dry storage root yield (t ha^{-1})							
	9 months after planting				12 months after planting				9 months after planting				12 months after planting			
Genotype	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank
Maunjili	15.1	1.14	7	1	21.6	6.21	17	6	5.3	0.65	8	1	7.2	4.88	17	6
Mbundumali	9.9	2.88	29	13	13.9	1.18	17	6	4.2	0.93	19	8	4.9	1.12	20	8
Yizaso	13.3	1.72	19	8	15.0	1.84	19	8	4.6	1.57	20	9	4.9	0.17	14	5
Beatrice	14.0	0.56	7	1	16.8	1.89	19	8	5.4	0.82	9	2	6.8	2.65	17	6
Unknown	13.4	0.56	8	2	17.9	1.36	11	2	5.2	0.68	10	3	6.0	0.66	9	2
Kalawe	13.5	4.67	22	10	17.2	6.22	25	10	5.3	1.49	13	4	6.5	4.79	19	7
96/1708	13.2	1.47	17	6	19.9	4.53	18	7	5.0	2.07	22	10	5.9	2.15	20	8
MK05/0297	11.3	1.65	23	11	17.6	2.10	17	6	4.2	1.99	26	11	5.9	0.93	12	3
Mulola	15.5	1.49	11	3	27.6	2.48	12	3	5.1	1.38	14	5	8.2	0.95	6	1
Mpale	11.5	1.31	16	5	17.3	1.50	14	4	4.4	1.85	22	10	5.8	0.78	13	4
TMS4(2)1425	5.7	1.17	21	9	20.0	9.20	20	9	2.2	0.50	18	7	5.8	2.62	22	10
01/1316	9.1	1.40	22	10	10.7	0.80	18	7	3.8	0.57	17	6	4.0	1.48	23	11
01/1569	14.3	2.49	18	7	19.6	2.12	16	5	5.0	0.47	8	1	6.2	1.41	13	4
Chamandanda	11.4	0.84	14	4	14.7	3.03	25	10	4.7	0.12	9	2	5.2	1.94	21	9
Sauti	11.3	2.15	24	12	13.1	0.56	16	5	3.7	1.91	27	12	4.9	1.48	20	8
Phoso	19.7	2.41	14	4	22.1	1.79	8	1	8.8	4.40	17	6	7.1	1.53	12	3

ASV = AMMI stability value, GSI = genotype selection index.

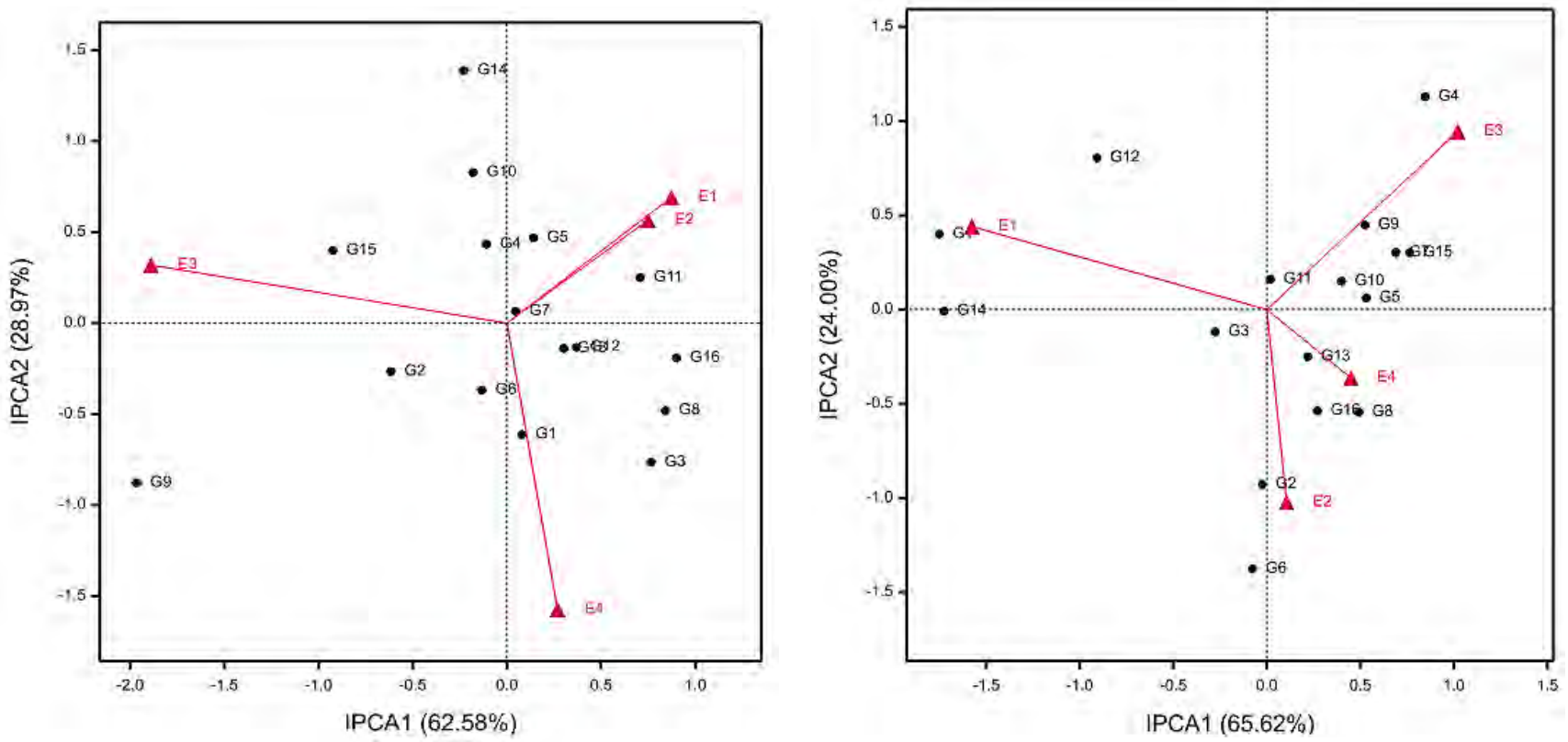


9 months after planting

12 months after planting

Figure 4.1. Biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2) for fresh storage root yield at 9 and 12 months after planting

(G1 = Maunjili, G2 = Mulola, G3 = Mpale, G4 = TMS4(2)1425, G5 = 01/1316, G6 = 01/1569, G7 = Chamandanda, G8 = Sauti, G9 = Phoso, G10 = Mbundumali, G11 = Yizaso, G12 = Beatrice, G13 = Unknown, G14 = Kalawe, G15 = 96/1708, G16 = MK05/0297, E1 = Chitala 2014, E2 = Chitala 2015, E3 = Kasinthula 2014, E4 = Kasinthula 2015).



9 months after planting

12 months after planting

Figure 4.2. Biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2) for dry storage root yield at 9 and 12 months after planting

(G1 = Maunjili, G2 = Mulola, G3 = Mpale, G4 = TMS4(2)1425, G5 = 01/1316, G6 = 01/1569, G7 = Chamandanda, G8 = Sauti, G9 = Phoso, G10 = Mbundumali, G11 = Yizaso, G12 = Beatrice, G13 = Unknown, G14 = Kalawe, G15 = 96/1708, G16 = MK05/0297, E1 = Chitala 2014, E2 = Chitala 2015, E3 = Kasinthula 2014, E4 = Kasinthula 2015).

Shoot mass, storage root number and storage root length

At 9 MAP, genotypes MK05/0297 (11.1 t ha^{-1}) and Sauti (9.4 t ha^{-1}) and at 12 MAP, genotypes Yizaso (22.6 t ha^{-1}) and Beatrice (19.2 t ha^{-1}), gave the highest shoot mass. In terms of storage root number $plant^{-1}$, genotypes Beatrice (5.8) and Mulola (5.7) had the highest number at 9 MAP, while Sauti (6.9) and Mulola (6.4) had the highest number of storage roots at 12 MAP (Table 4.4). Genotypes Phoso (37.7 cm) and 01/1569 (36.6 cm) outperformed all genotypes for storage root length at 9 MAP, and 01/1569 (47.0 cm) and TMS4(2)1425 (41.0 cm) at 12 MAP (Table 4.5).

Based on the GSI (Table 4.4), genotypes Beatrice and Phoso were the most stable genotypes at both 9 and 12 MAP for shoot mass. For storage root number, genotypes Mulola (both at 9 and 12 MAP), Beatrice (9 at MAP) and Phoso (at 12 MAP) were found to be the best performing and most stable genotypes. For storage root length (cm), the GSI selected genotypes MK05/0297 (at 9 and 12 MAP), Phoso (at 9 MAP) and Yizaso (at 12 MAP) as the most stable (Table 4.5).

The ranking of all genotypes using the GSI for the five traits (fresh storage root yield, dry storage root yield, shoot mass, storage root number and storage root length), which exhibited significant GEI at both 9 and 12 MAP, revealed that the best five genotypes in terms of mean performance and stability were Mulola, Phoso, Maunjili, Beatrice and Unknown. The least stable genotypes based on the five traits were TMS4(2)1425, 01/1316 and Sauti (Table 4.6).

AMMI 2 biplots showed that genotypes 01/1316 and Maunjili exhibited specific adaptation to environment E1, Kalawe and Chamandanda to E3, Mbundumali and Unknown to E2, MK05/0197, TMS4(2)1425 and Mpale to E4 for shoot mass at 9 MAP. The environment that fitted the least was E4 as it showed the highest interactive forces. Genotypes 96/1708, Phoso and Beatrice were stable and showed good performance regardless of the environment. At 12 MAP, environment E2 was the least responsive environment, while genotypes Phoso, Beatrice, MK05/0297 and Unknown showed wide adaptation. Environment E1 was more suitable for genotypes Maunjili and Kalawe. Genotypes 01/1316, Yizaso and TMS4(2)1425 were adapted to environment E3 and 96/1708 and Chamandanda interacted positively with E4 (Figure 4.3).

Genotypes Mbundumali and Kalawe interacted negatively for storage root number with environment E4, while 01/1569 had a positive interaction with E4. Genotypes TMS4(2)1425, MK05/0297, 01/1316 and Phoso were more adapted to environments E1 and E3. Genotypes that were more resilient to environmental variations were Maunjili, Mulola, Mpale,

Chamandanda, Yizaso, Beatrice and Unknown. At 12 MAP, general adaptation was exhibited by genotypes Mulola, Phoso, Unknown and MK05/0297. Environment E2 was suitable for genotypes Sauti, Mbundumali and 01/1316 exploited E1, while Yizaso and Beatrice interacted positively with E3. Environment E4 was suitable for genotypes TMS4(2)1425, Chamandanda and 96/1708. At both 9 and 12 MAP, environments E2 and E4 contributed the most to GEI as revealed by long projections from the origin (0, 0).

For storage root length at 9 MAP, environment E4 and genotype Kalawe interacted positively and this environment was the sole contributor to GEI. Environments E1, E2 and E3 showed similar interactive forces. All genotypes except Kalawe had a similar interaction pattern with environments E1, E2 and E3. At 12 MAP, genotypes Mbundumali, Yizaso and MK05/0297 were generally well adapted to all the environments. Genotype Mulola was specifically adapted to environment E2, TMS4(2)1425 and 96/1708 adapted specifically to E3, and Beatrice and Kalawe showed general adaptation with E4. The greatest contributors to GEI for this trait were environments E3 and E4 (Figure 4.5).

Table 4.4. Ranks of 16 genotypes in four environments using mean performance, AMMI stability value and genotype selection index for shoot mass and storage root number

Genotype	Shoot mass (t ha^{-1})								Storage root number plant^{-1}							
	9 months after planting				12 months after planting				9 months after planting				12 months after planting			
	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank
Maunjili	5. 6	6.71	17	5	15.4	4.74	24	10	4.3	0.06	13	5	3.7	0.53	19	10
Mbundumali	7.1	10.99	22	9	13.3	0.63	16	5	4.6	1.24	23	10	4.8	1.43	12	4
Yizaso	9.1	14.81	17	5	22.6	2.24	13	4	4.5	0.52	18	7	4.7	2.00	18	9
Beatrice	9.0	5.38	6	1	19.2	0.94	7	2	5.8	0.54	9	2	4.6	2.36	22	11
Unknown	6.0	10.24	21	8	14.3	0.45	13	4	4.9	0.28	11	3	4.7	0.44	10	3
Kalawe	7.4	17.55	20	7	14.4	1.26	18	6	5.0	2.14	21	9	5.2	1.81	13	5
96/1708	7.4	8.83	13	3	16.0	2.42	19	7	4.2	0.47	20	8	4.6	1.15	15	7
MK05/0297	11.1	25.95	17	5	17.5	0.81	8	3	5.2	0.57	13	5	4.2	0.33	13	5
Mulola	4.4	6.75	21	8	12.5	0.96	21	8	5.7	0.31	6	1	6.4	1.26	9	2
Mpale	7.2	9.59	18	6	15.7	1.49	16	5	4.9	0.44	12	4	4.8	1.73	13	5
TMS4(2)1425	7.2	14.79	22	9	14.0	2.70	27	11	2.9	0.86	28	11	3.7	2.68	28	14
01/1316	7.3	10.59	18	6	15.0	2.42	23	9	4.2	0.57	23	10	4.4	2.05	24	12
01/1569	4.9	5.83	18	6	15.5	1.80	18	6	5.0	1.75	20	8	4.6	0.51	14	6
Chamandanda	5.0	8.88	21	8	11.1	1.46	24	10	4.0	0.25	17	6	3.6	1.85	26	13
Sauti	9.4	11.10	14	4	16.8	2.07	16	5	5.2	1.79	18	7	6.9	14.04	17	8
Phoso	7.4	2.12	7	2	17.9	0.81	6	1	4.9	0.74	20	8	4.7	0.42	7	1

ASV = AMMI stability value, GSI = genotype selection index.

Table 4.5. Ranks of 16 genotypes in four environments using mean performance, AMMI stability value and genotype selection index for storage root length

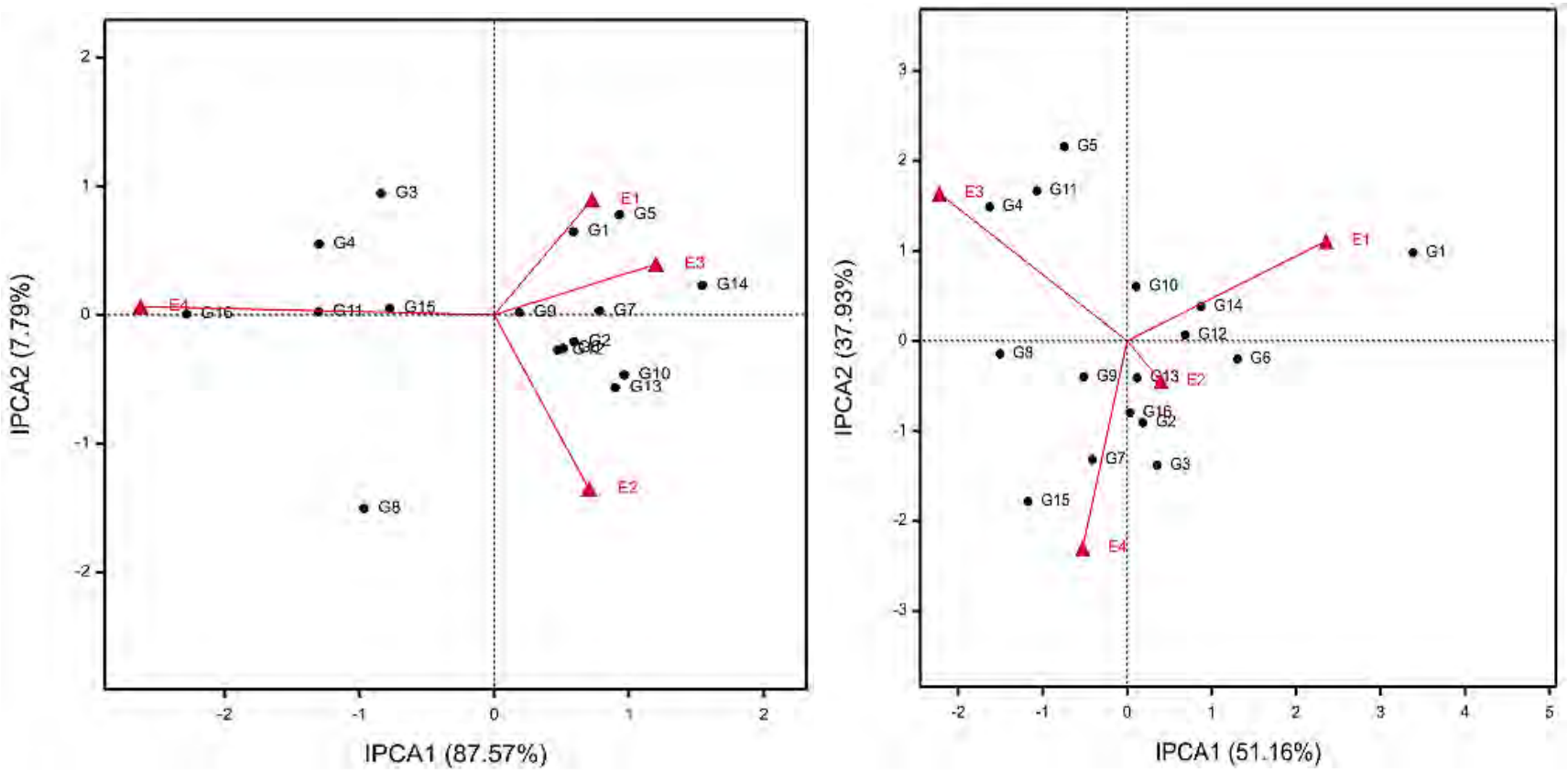
Genotype	Storage root length (cm)							
	9 months after planting				12 months after planting			
	Mean	ASV	GSI	Rank	Mean	ASV	GSI	Rank
Maunjili	27.8	1.38	18	8	27.2	1.56	22	10
Mbundumali	30.8	0.70	9	2	32.6	0.20	13	4
Yizaso	33.6	4.67	20	9	37.5	0.24	9	1
Beatrice	33.0	1.85	13	4	39.1	3.86	18	7
Unknown	29.4	2.18	21	10	33.0	2.70	21	9
Kalawe	32.5	2.12	16	6	35.8	3.64	22	10
96/1708	36.4	2.54	15	5	40.2	4.95	18	7
MK05/0297	31.8	1.09	9	2	38.5	0.64	10	2
Mulola	30.3	1.17	12	3	39.0	3.37	17	6
Mpale	28.6	3.25	24	12	35.8	1.63	18	7
TMS4(2)1425	27.5	3.58	29	13	41.0	7.96	18	7
01/1316	28.6	1.44	17	7	28.1	1.77	23	11
01/1569	36.6	3.61	17	7	47.0	3.04	12	3
Chamandanda	27.8	2.11	22	11	27.0	0.62	19	8
Sauti	26.1	1.56	22	11	29.8	1.02	18	7
Phoso	37.7	1.58	8	1	37.1	1.24	14	5

ASV = AMMI stability value, GSI = genotype selection index.

Table 4.6. Overall ranking of genotypes based on GSI for five traits evaluated at 9 and 12 MAP

Genotype	9 Months after planting						12 Months after planting						
	FSRY	DSRYY	SM	SRN	SRL	Mean rank	FSRY	DSRY	SM	SRN	SRL	Mean rank	Overall rank
Maunjili	1	1	5	5	8	2	6	6	1	10	10	7	3
Mbundumali	13	8	9	10	2	13	6	8	2	4	4	4	8
Yizaso	8	9	5	7	9	11	8	5	3	9	1	5	7
Beatrice	1	2	1	2	4	1	8	6	4	11	7	9	4
Unknown	2	3	8	3	10	4	2	2	4	3	9	2	2
Kalawe	10	4	7	9	6	9	10	7	5	5	10	10	9
96/1708	6	10	3	8	5	7	7	8	5	7	7	8	6
MK05/0297	11	11	5	5	2	8	6	3	5	5	2	3	5
Mulola	3	5	8	1	3	2	3	1	6	2	6	1	1
Mpale	5	10	6	4	12	10	4	4	6	5	7	5	6
TMS4(2)1425	9	7	9	11	13	15	9	10	7	14	7	12	12
01/1316	10	6	6	10	7	12	7	11	8	12	11	13	11
01/1569	7	1	6	8	7	5	5	4	9	6	3	6	5
Chamandanda	4	2	8	6	11	6	10	9	10	13	8	14	10
Sauti	12	12	4	7	11	14	5	8	10	8	7	11	11
Phoso	4	6	2	8	1	3	1	3	11	1	5	3	2

FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SM = shoot mass (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm)

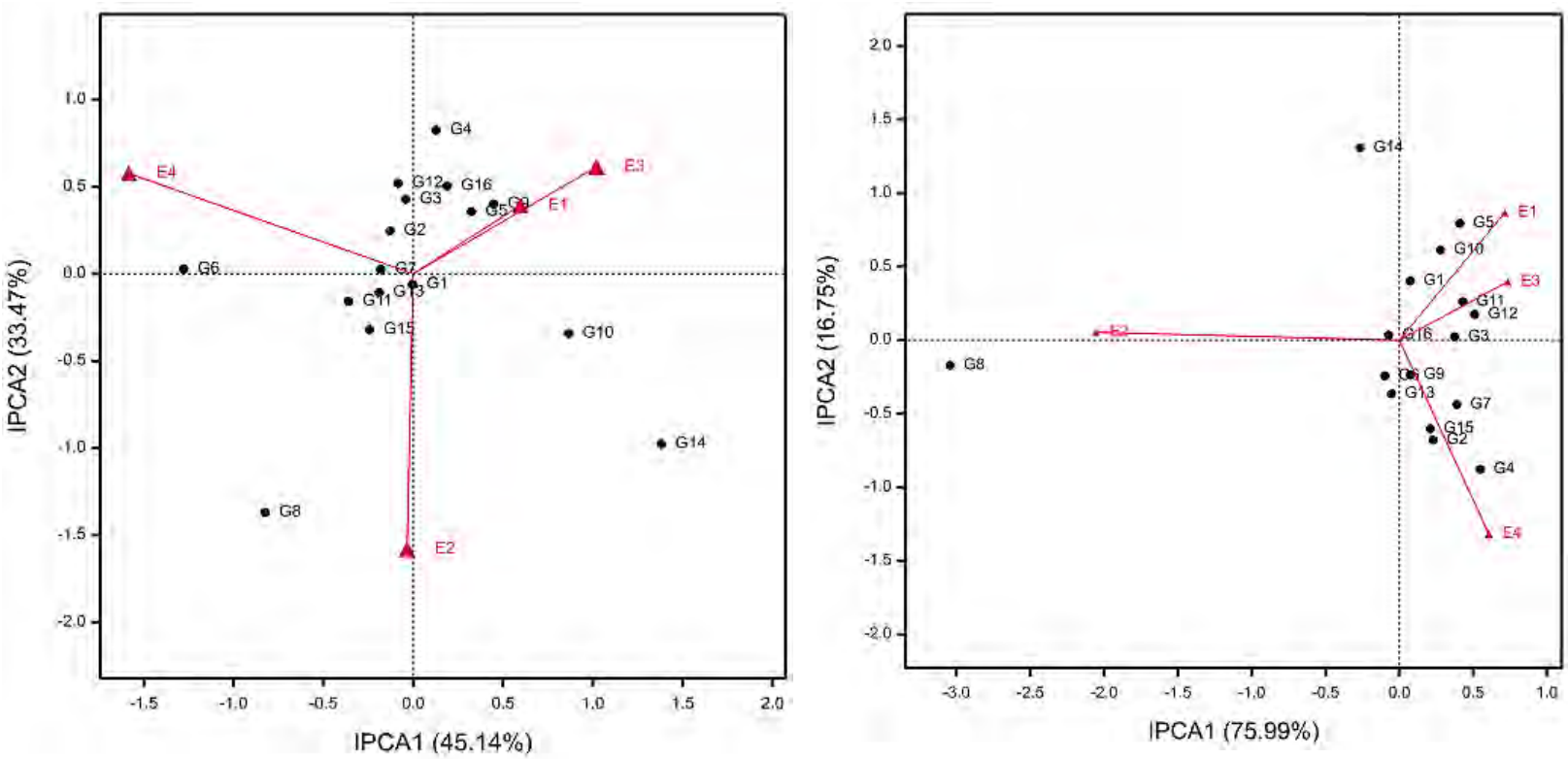


9 months after planting

12 months after planting

Figure 4.3. Biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2) for shoot mass

(G1 = Maunjili, G2 = Mulola, G3 = Mpale, G4 = TMS4(2)1425, G5 = 01/1316, G6 = 01/1569, G7 = Chamandanda, G8 = Sauti, G9 = Phoso, G10 = Mbundumali, G11 = Yizaso, G12 = Beatrice, G13 = Unknown, G14 = Kalawe, G15 = 96/1708, G16 = MK05/0297, E1 = Chitala 2014, E2 = Chitala 2015, E3 = Kasinthula 2014, E4 = Kasinthula 2015).

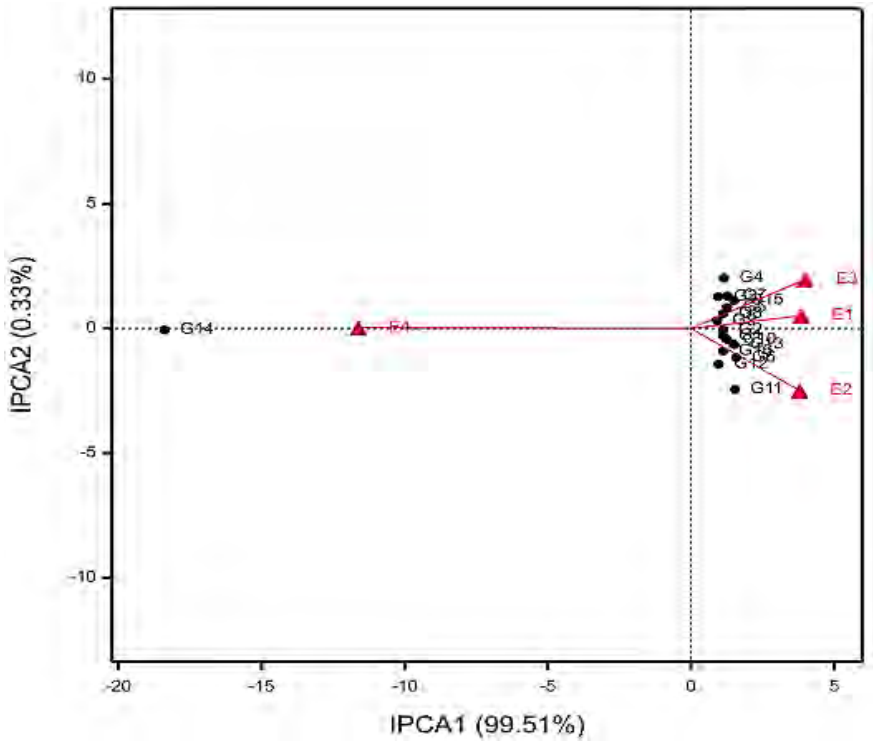


9 months after planting

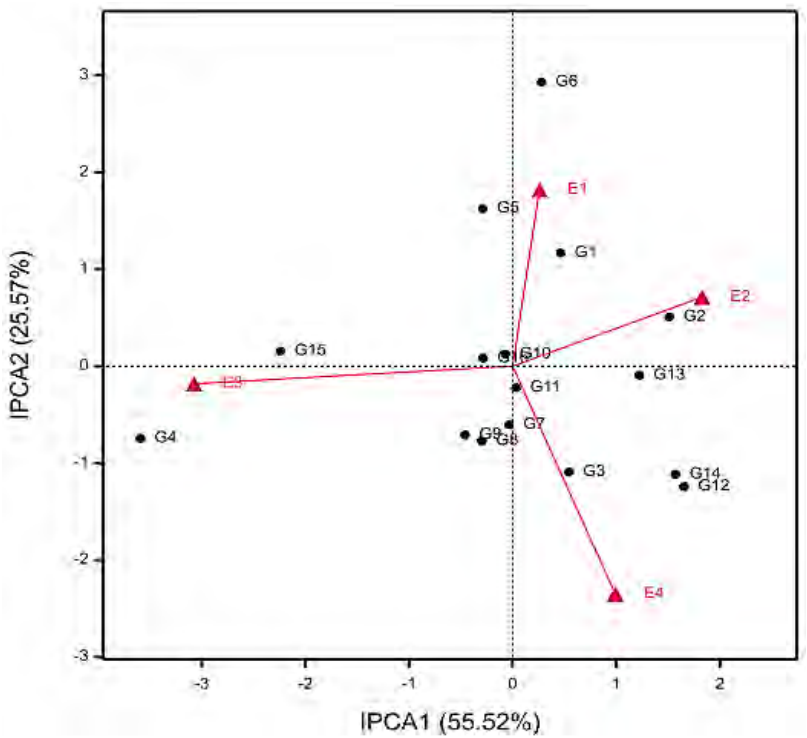
12 months after planting

Figure 4.4. Biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2) for storage root number plant^{-1} at 9 and 12 months after planting

(G1 = Maunjili, G2 = Mulola, G3 = Mpale, G4 = TMS4(2)1425, G5 = 01/1316, G6 = 01/1569, G7 = Chamandanda, G8 = Sauti, G9 = Phoso, G10 = Mbundumali, G11 = Yizaso, G12 = Beatrice, G13 = Unknown, G14 = Kalawe, G15 = 96/1708, G16 = MK05/0297, E1 = Chitala 2014, E2 = Chitala 2015, E3 = Kasinthula 2014, E4 = Kasinthula 2015).



9 months after planting



12 months after planting

Figure 4.5. Biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2) for storage root length at 9 and 12 months after planting

(G1 = Maunjili, G2 = Mulola, G3 = Mpale, G4 = TMS4(2)1425, G5 = 01/1316, G6 = 01/1569, G7 = Chamandanda, G8 = Sauti, G9 = Phoso, G10 = Mbundumali, G11 = Yizaso, G12 = Beatrice, G13 = Unknown, G14 = Kalawe, G15 = 96/1708, G16 = MK05/0297, E1 = Chitala 2014, E2 = Chitala 2015, E3 = Kasinthula 2014, E4 = Kasinthula 2015).

4.4 Discussion

The significance of the main effects of genotypes and environments indicated the stability of some genotypes across environments, while the significance of GEI indicated that some genotypes were specifically adapted to certain environments. The significance of the genotypic variances at the three harvesting periods (6, 9 and 12 MAP) for fresh storage root yield and most other traits indicated the presence of high variability between genotypes. This suggests that judicious selection among these genotypes may result in more significant genetic gains in a breeding program aimed at improving the targeted traits. The fresh storage root yield variation due to genotype was higher than the environmental influence at 6 MAP, had an equal contribution at 9 MAP and was lower at 12 MAP, which suggests that yield is a complex polygenic trait influenced by both genotype and environment. This means that superior and better performing genotypes are those having good genetic background managed under ideal growing conditions (environment). The harvest index and storage root number were largely controlled by genotypic effects, regardless of the time of harvest. This agrees with Kawano (2003) who reported that harvest index is largely under genetic control. This trait has been widely used to indirectly select for storage root yield (Alves, 2002). Alves (2002) indicated that the storage root number plant^{-1} is determined at an early stage of cassava growth and is a strong indicator of the potential of a variety for high yield. Others (Akinwale et al., 2010; Alves, 2002; Chipeta et al., 2013; DaSilva, 2008; Kamau et al., 2010) have found a strong positive correlation between harvest index and storage root yield. This means that potential yield of a genotype can be determined at an early stage. Some farmers use the storage root number as a measure of the potential yield for a particular variety (chapter 2).

The large and significant environmental variances for most traits, in particular the shoot mass, dry storage root yield, dry mass content and starch content, at all harvest periods, indicate the large environmental effect on these traits. A significant GEI revealed the differential performance of genotypes in different environments (specific adaptation), and also reveals changes in the average performance of cassava genotypes due to the environment. A significant GEI rationalizes the need for a more definitive analysis to increase selection efficiency and give varietal recommendations. This differential performance (GEI) can be reduced by selecting genotypes that are stable within a wide range of environments. The non-significant GEI at 6 MAP for almost all traits means that genotypes can be reliably evaluated in any single environment. These results, therefore, imply that early storage root bulking varieties

(harvested at 6 MAP) may not necessarily be subjected to multi-location trials for their stability performance. However, the GEI in cassava is a common occurrence as shown at 9 and 12 MAP of this study and which is confirmed by several other studies (Agyeman et al., 2015; Aina et al., 2009; Akinwale et al., 2011; Alves, 2002; Benesi et al., 2004; Dixon and Nukenine, 1997; Kundy et al., 2014; Kvitschal et al., 2006, 2009; Mtunda, 2009; Noerwijatia et al., 2014 ; Ssemakula and Dixon, 2007; Tumuhimbise et al., 2014) and confirms the need for multi-location trials (Fox et al., 1997; Romagosa and Fox, 1993).

The IPCAs indicated a significant contribution to the GEI. However, IPCA1 had the greatest contribution to the GEI, as it explained more of the GEI variation. Only two IPCAs were selected which accounted for most of the variation, which ranged from 78.6% to 99.8% for all traits. This agreed with the findings of Gauch and Zobel (1996), who recommended that the most accurate model for AMMI can be predicted using the first two IPCAs. The two IPCAs scores of this study were used to calculate the ASV as proposed by Purchase et al. (2000).

The selection of 1) high yielding genotypes based on mean performance, 2) stable genotypes based on GSI (mean performance and ASV) and 3) adaptability of genotypes based on biplots of the first interaction principal component axis (IPCA1) versus the second interaction principal component axis (IPCA2), identified five genotypes (Mulola, Phoso, Maunjili, Beatrice and Unknown) that exhibited a consistent performance, stability and adaptability across the three harvest periods. In addition, these genotypes could be regarded as early storage root bulking genotypes, because regardless of the harvesting period (6, 9 and 12 MAP) they gave very high yields, despite being produced under very minimal inputs (no chemical fertilizers, no pesticides application and no supplementary irrigation).

Most studies on stability and adaptability in cassava have been based on a single harvest generally at 12 MAP (Agyeman et al., 2015; Aina et al., 2009; Akinwale et al., 2011; Benesi et al., 2004; Ssemakula and Dixon, 2007), at 10 MAP (Noerwijatia et al., 2014) and at 9 MAP (Tumuhimbise, 2013). The present study is, therefore, the first attempt to report on performance, stability and adaptability across different harvest periods using AMMI.

4.5 Conclusions

A high variability existed among cassava genotypes for fresh storage root yield and related traits. The study revealed that large and significant environmental variances for most traits, at all harvest times, caused significant differences between the environments, which was responsible

for most of the variation between the cassava genotypes. Most of the cassava genotypes exhibited specific adaptation to certain environments, except for Mulola, Phoso, Maunjili, Beatrice and Unknown, which were high yielding, stable and adaptable to a wide range of environments at 6, 9 and 12 MAP. It was also shown that multi-location studies in cassava, regardless of the time of harvest will help to discriminate genotypes with superior performance, stability and general adaptation.

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Chapter 5

5 Evaluation of cassava genotypes for resistance to cassava brown streak disease and its associated yield loss

Abstract

Cassava brown streak disease (CBSD) affects cassava storage roots by causing necrotic patches and constriction, which make storage roots unmarketable and unfit for human consumption. Storage root necrosis progresses with prolonged stay of the crop in the field, resulting in yield and quality losses. Therefore, a study was conducted to assess yield loss due to CBSD at three harvest times (6, 9 and 12 MAP) and identify varieties resistant/tolerant to the disease. Sixteen genotypes were evaluated using a square lattice design with three replications at two locations for two growing seasons. Genotypes varied highly significantly ($P<0.001$) in their reaction to CBSD, which was characterized by highly significant incidence and severity means. The CBSD incidence for some genotypes reached as high as 94.9% and severity of up to 3.8. Highly significant ($P<0.001$) genotypic variations for storage root yield (t ha^{-1}), yield loss due to CBSD infection (%) and CBSD storage root severity were also observed. Furthermore, yield loss due to CBSD at different harvest times was significantly associated with storage root severity, and a maximum yield loss of 43.1% was recorded at 12 MAP on Kalawe, while at 9 and 6 MAP the maximum yield loss was 24.8% and 10.9%, respectively. This implies that productive early storage root bulking (harvested at 6 and 9 MAP) and CBSD resistant cassava varieties could provide good storage root quality and high productivity per unit area of land, while reducing exposure to biotic (in particular CBSD) and abiotic stresses. The results suggest that an integrated approach should be used by farmers in order to effectively manage CBSD, which among others includes using varieties that are early bulking and resistant/tolerant to CBSD, selecting planting material free from CBSD, sanitation and roguing infected plants from the field especially shortly after sprouting.

5.1 Introduction

Cassava (*Manihot esculenta* Crantz) has gained in importance both as a food security crop and a source of income for many smallholder farmers. However, recently, cassava in East Africa

and Malawi in particular, has experienced a setback due to cassava brown streak disease (CBSD) and cassava mosaic disease (CMD) (Benesi et al., 2010; Gondwe et al., 2003; Legg and Raya, 1998; Shaba et al., 2003). The CBSD is a viral disease that attacks every part of the plant, namely, leaves, fruits, stems and storage roots (Calvert and Thresh, 2002; Hillocks et al., 2001). Above ground symptoms are clearly expressed in the early stages of plant growth, while storage root symptoms are mainly exhibited at an advanced stage, predominantly from seven months after planting (MAP) (Benesi et al., 2010; Hillocks et al., 2001; Hillocks et al., 2002), but may start as early as five MAP (Hillocks et al., 2002). Studies have shown that CBSD severity is associated with plant age, whereby plants older than seven or eight months tend to be severely affected (Gondwe et al., 2003; Hillocks et al., 2001; Hillocks et al., 2002; Rwegasira and Rey, 2012). In some instances, it has been shown that famers tend to harvest their crop prematurely as a means of avoiding the devastating effects of CBSD (Hillocks and Jennings, 2003; Hillocks et al., 2001; Hillocks et al., 2002).

The CBSD affects cassava by lowering the storage root quality and yield. The impact of CBSD is vividly manifested through the quality of diseased storage roots, especially where the infection results in storage root necrosis (Bock, 1994; Gondwe et al., 2003; Hillocks et al., 2001; Nichols, 1950), making the storage roots unmarketable and sometimes unfit for human consumption. In addition, CBSD affects the viability of the cuttings (Hillocks and Jennings, 2003) and the subsequent growth, resulting in low plant population which in turn may lead to low yields.

Most of the yield losses are attributed to the production of fewer storage roots, smaller and distorted storage roots due to pitting and constrictions and retarded storage root growth, which tends to become more severe with the physiological age of the crop. The effects on yield are not clearly manifested, as some studies have reported small differences between healthy and secondary infected plants (Bock, 1994; Nichols, 1950). An attempt was made by Hillocks et al. (2001) in Tanzania to quantify yield loss due to CBSD by removing storage roots with a severity score of ≥ 3. They reported yield losses of up to 70% in susceptible varieties. However, this method has been criticised as it tends to overestimate yield losses, since a common practice among smallholder farmers is to remove necrotic patches on the storage roots. In Malawi, Gondwe et al. (2003) made a similar attempt to assess economic losses experienced by smallholder farmers. They used the number and the size of storage roots obtained from healthy and symptomatic plants, and further assessed the percentage necrosis on all the storage roots on each plant and they reported a yield loss in the range of 20-25%. This method is also not effective as it only measures the loss in useable storage roots. In addition, the large variation

that occurs in storage root yield between adjacent cassava plants (healthy and symptomatic) may surpass any variation due to CBSD (Hillocks, 2004). Therefore, an accurate assessment of yield loss (mass basis) would be to remove and weigh necrotic patches, which should be subtracted from the total mass. In this study, therefore, an attempt has been made to quantify yield loss due to CBSD by removing necrotic areas on storage roots. The objectives of this study were to: (1) evaluate and identify cassava genotypes resistant/tolerant to CBSD and (2) assess yield loss due to CBSD at different harvesting periods.

5.2 Materials and methods

5.2.1 Plant material

Planting material was sourced from national agricultural research stations and farmers' fields. A total of 16 genotypes were evaluated (Chapter 3) and their selection was based on their popularity with farmers and their response to various diseases prevalent in Malawi.

5.2.2 Experimental sites

The trials were conducted in Malawi at two sites, Chitala Agricultural Research Station, Salima district (Central Malawi) and Kasinthula Agricultural Research Station, Chikwawa district (Southern Malawi) over two growing seasons (2014 and 2015). Chitala Agricultural Research Station lies on latitude 13^{o}40' South and on longitude 34^{o}15' East. It is at an altitude of 606 m above sea level. The station receives rain for three months, normally between December and March and has the mean annual temperatures of 28^{o}C maximum and 16^{o}C minimum. The soils are sandy clay to sandy clay loam with the pH range of 4.4 to 6.7. Kasinthula Agricultural Research Station is located on 16°0'S latitude, 34°5'E longitude and 70 m above sea level. The yearly average maximum and minimum temperatures of the site are 35.6°C and 18.6°C, respectively, and annual rainfall is 520 mm on average. Detailed description of soil characteristics of the two sites and meteorological conditions have been described in Chapter 3.

5.2.3 Experimental design

The experiments were laid out using a square lattice design constituting 16 genotypes as described in chapter 3 section 3.2.3. Each plot was separated by a CBSD infected spreader row. Plants used in the spreader rows were obtained in fields that had a CBSD incidence of

100% and a mean severity of 4 or 5. The selection was done to ensure that the infector row had a high viral load to effectively augment the CBSD pressure. The trials were planted in January in 2014 and repeated in 2015 under rain-fed conditions and neither fertilizers nor pesticides were applied. Manual weeding was done when necessary.

5.2.4 Data collection

Symptoms on the shoots (leaves and stems) were recorded on each plant every month up to 12 months after planting (MAP) at Chitala, while at Kasinthula scoring was done at 1, 3, 6, 9 and 12 MAP (due to low disease pressure observed). A severity score of 1–5 (IITA, 1990) was used where 1 = no apparent symptoms, 2 = slight foliar chlorotic leaf mottle, no stem lesions, 3 = foliar chlorotic leaf mottle and blotches with mild stem lesions, no dieback, 4 = foliar chlorotic leaf mottle and blotches and pronounced stem lesions with no dieback and 5 = defoliation with stem lesions and pronounced dieback. Disease incidence was measured as a proportion of plants showing symptoms to the total number of plants sampled. At harvest (6, 9, 12 MAP), each storage root was cut into slices and the maximum severity score taken for each storage root where 1 = no necrosis, 2 = mild necrotic lesions (1-10%), 3 = pronounced necrotic lesions (11-25%), 4 = severe necrotic lesions (26-50%) and 5 = very severe necrotic lesions (>50%). A storage root disease severity mean value was calculated on a per plant basis, and then averaged over plants to give a mean value for each genotype. In addition to CBSD, data were collected on storage root mass (kg $plot^{-1}$) and converted to storage root yield (t ha^{-1}). At each harvest interval, the unit of measurement was three plants.

5.2.5 Data analysis

A preliminary analysis indicated that the maximum CBSD incidence (%) and CBSD shoot severity scores were observed at 6 and 9 MAP, respectively. The mean disease incidence and shoot severity score were calculated per genotype based on all individual plant scores per genotype at 6 and 9 MAP, respectively. Storage root yield loss (%) was computed as a ratio of the mass of removed necrotic patches to total storage root mass. Necrotic patches were removed from all storage roots with a severity score of ≥3.

$$\text{Yield/tissue loss \%} = \frac{\text{Mass of removed necrotic patches}}{\text{Total storage root mass}} \times 100$$

The area under disease progress curves (AUDPC) values were calculated for CBSD severity scores and incidence as suggested by Shaner and Finney (1977) as follows:

$$\text{AUDPC} = \sum_{i=1}^{n} \left[(X_{i+1}+X_i)][t_{i+1} - t_i \right] /2$$

Where, X_i = the disease score or incidence at i^{th} day, t_i = the time in days after appearance of the disease at i^{th} day, n = the total number of observations/scores.

Data from individual locations, but combined across seasons were analysed using PROC mixed procedure performed in SAS® 9.3 software (SAS Institute, 2011). Genotypes were considered fixed effects while year, replications and blocks within replications and error were considered random effects in the model. The following combined statistical mixed model was fitted;

$Y_{ijkl} = \mu + R_i + \beta_j + S_k + G_l + (SG)_{kl} + + e_{ijkl}$

Where Y_{ijkl} = an observation in the j^{th} block within i^{th} replication, μ = the overall mean, R_i = the effect of i^{th} replication (I = 1- 3), β_j = the effect of j^{th} block within the replication (j = 1- 4), S_k = the main effect of k^{th} season/year (l= 1, 2), G_l = the main effect of l^{th} genotype (l=1-16), $(SG)_{kl}$ = the interaction effect of k^{th} season and l^{th} genotype, e_{ijkl} = random error.

5.3 Results

5.3.1 Incidence and severity of cassava brown streak disease

Symptoms of CBSD were first observed in the spreader rows approximately 1 MAP and thereafter on test genotypes (96/1708 and Unknown). Typical above and below ground CBSD symptoms were observed, such as leaf chlorosis and blotches, stem lesions and die back, leaf chlorosis without root necrosis, or leaf chlorosis with root necrosis. Other symptoms were root necrosis without leaf chlorosis or blotches, leaf chlorosis and blotches and stem lesions without root necrosis, root constrictions without necrosis, or root necrosis with constrictions.

Genotypes varied significantly in their reaction to CBSD as exhibited by the highly significant ($P<0.001$) incidence and severity mean square values, both at Chitala and Kasinthula in the two growing seasons (Table 5.1). The results also showed that season/year of evaluation had a significant ($P<0.05$) influence on the incidence and severity of CBSD (at Chitala). Very significant variations ($P<0.01$) were also observed in the genotype by year interaction, except for CBSD severity at Kasinthula.

Mean CBSD incidence at Chitala across two seasons ranged from 0.0% (for Phoso, Mpale) to 94.9% (Unknown) (Table 5.2), while at Kasinthula (Table 5.3), it ranged from 0.0% (01/1316, 01/1569, Beatrice, Chamandanda, Phoso, Sauti) to 52.2% (Unknown). The CBSD leaf severity ranged from 1.0 (Phoso) to 3.8 (Mbundumali) at Chitala, while at Kasinthula, it ranged from 1.0 to 3.0 (Unknown). The CBSD incidence at Chitala averaged 9.0% in 2014 and 26.7% in 2015, while the Kasinthula site recorded 11.3% and 6.4% in 2014 and 2015, respectively. Of the two sites, Chitala had a higher average CBSD incidence (17.9%) and severity (2.1) than Kasinthula (8.8% incidence, 1.4 severity score).

Table 5.1. Mean square values for cassava brown streak disease and cassava mosaic disease for two seasons and locations

Source of variation	DF	Chitala		Kasinthula	
		CBSDI	CBSDS	CBSDI	CBSDS
Year (Y)	1	7475.3***	9.4**	569.8ns	0.3ns
Rep/year	2	214.4	6.7	105.4	0.8
Block/rep	3	63.4	0.5	48.1	0.0
Genotype (G)	15	3153.7***	4.4***	1403.4***	1.9***
G X Y	15	566.6**	2.3**	462.3*	0.7ns
Error	59	228.2	1.0	229.3	0.5
Corrected Total	95				

DF = degrees of freedom, CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity (1-5), *, **, *** = significant at 5%, 1% and 0.1%, respectively, ns = not significant.

Table 5.2. Mean cassava brown streak disease incidence and severity score for two growing seasons at Chitala

Genotype	CBSDI			CBSDS		
	2014	2015	Mean	2014	2015	Mean
01/1316	7.0	4.0	5.5	3.3	3.0	3.2
01/1569	0.0	2.4	1.2	1.0	2.3	1.7
96/1708	2.8	18.2	10.5	2.3	1.3	1.8
Beatrice	5.8	37.6	21.7	1.0	4.3	2.7
Chamandanda	1.2	0.0	0.6	1.0	2.0	1.5
Kalawe	3.3	69.7	36.5	3.0	3.3	3.2
MK05/0297	0.0	25.9	13.0	1.0	1.7	1.3
Maunjili	0.0	41.9	21.0	1.0	1.7	1.3
Mbundumali	11.4	32.5	21.9	3.3	4.3	3.8
Mpale	0.0	0.0	0.0	1.3	1.0	1.2
Mulola	15.9	10.6	13.2	2.0	3.3	2.7
Phoso	0.0	0.0	0.0	1.0	1.0	1.0
Sauti	0.0	21.4	10.7	1.0	2.3	1.7
TMS4(2)1425	2.2	50.0	26.1	1.3	1.7	1.5
Unknown	93.3	96.5	94.9	4.0	2.0	3.0
Yizaso	1.6	16.2	8.9	1.0	3.3	2.2
Mean	9.0	26.7	17.9	1.8	2.4	2.1
F. Prob.	<0.001			<0.001		
CV%	84.6			47.8		
LSD (0.05)	17.5			1.2		

CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity score (1-5)

Table 5.3. Mean cassava brown streak disease incidence and severity score for two growing seasons at Kasinthula

Genotype	CBSDI			CBSDS		
	2014	2015	Mean	2014	2015	Mean
01/1316	0.0	0.0	0.0	1.0	1.0	1.0
01/1569	0.0	0.0	0.0	1.0	1.0	1.0
96/1708	40.0	32.2	36.1	2.3	3.0	2.7
Beatrice	0.0	0.0	0.0	1.0	1.0	1.0
Chamandanda	0.0	0.0	0.0	1.0	1.0	1.0
Kalawe	0.0	4.2	2.1	1.0	1.3	1.2
MK05/0297	1.8	0.0	0.9	1.3	1.0	1.2
Maunjili	0.0	3.7	1.9	1.0	1.3	1.2
Mbundumali	0.0	4.2	2.1	1.0	2.0	1.5
Mpale	3.3	0.0	1.7	1.3	1.0	1.2
Mulola	71.2	0.0	35.6	3.0	1.0	2.0
Phoso	0.0	0.0	0.0	1.0	1.0	1.0
Sauti	0.0	0.0	0.0	1.0	1.0	1.0
TMS4(2)1425	7.0	0.0	3.5	2.0	1.0	1.5
Unknown	49.3	55.1	52.2	3.0	3.0	3.0
Yizaso	7.4	2.8	5.1	1.3	1.0	1.2
Mean	11.3	6.4	8.8	1.5	1.4	1.4
F. Prob.	<0.001			<0.001		
CV%	171.7			50.9		
LSD (0.5)	17.5			0.8		

CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity score (1-5),

5.3.2 Disease progress for cassava brown streak disease severity

The CBSD severity on test genotypes was first observed at two MAP for MK05/0297, Mulola and Unknown (Figure 5.1). By 5 MAP, 50% of the genotypes had a severity score of ≥ 2.0 and a highest score (4.0) was observed on Unknown genotype, followed by Mbundumali. For 50% of the genotypes, the CBSD leaf severity remained relatively low (≤2) during the entire 12 months growth period.

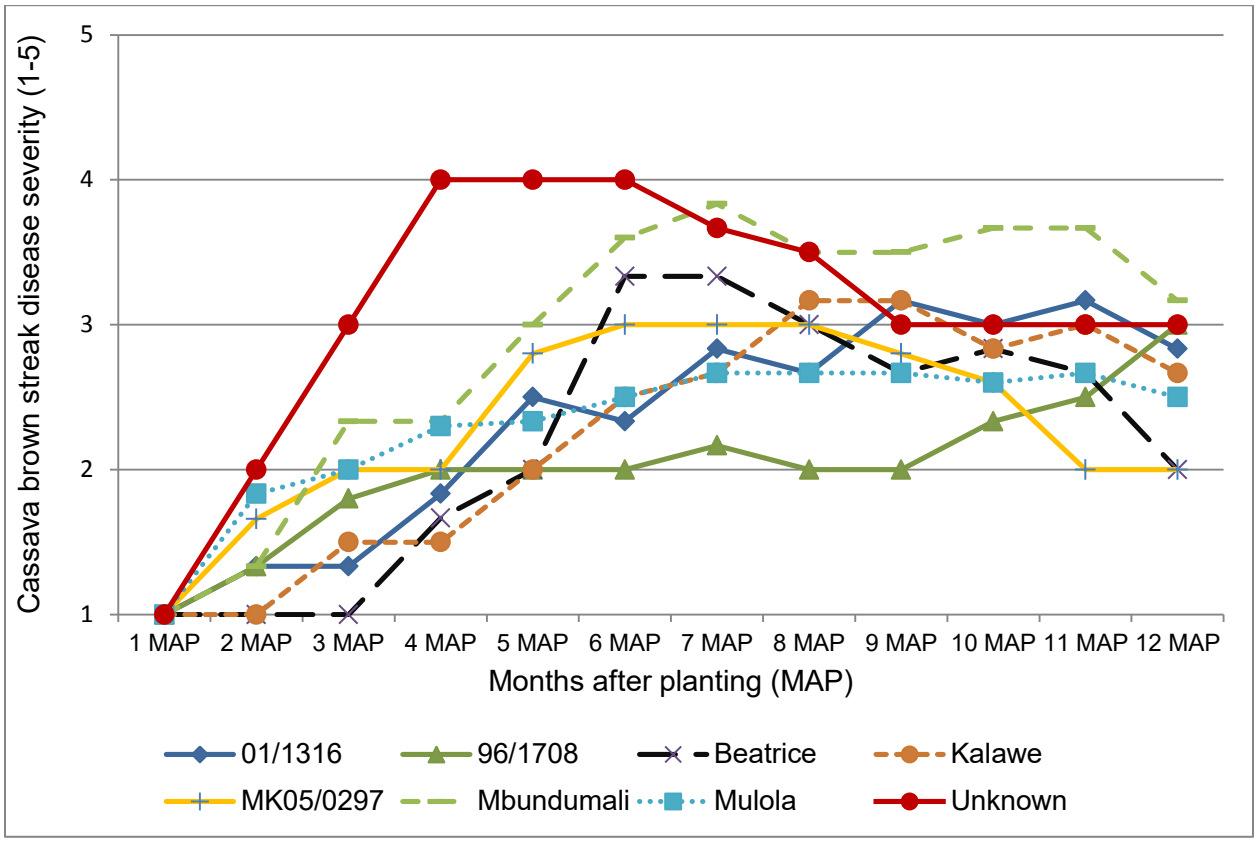

Figure 5.1. Cassava brown streak disease severity progress for eight genotypes with score of 2 or above across seasons and locations

5.3.3 Area under disease progress curves for cassava brown streak disease

Highly significant differences (P<0.001) were observed among the 16 genotypes in AUDPC for CBSD incidence and severity across the years at both Chitala and Kasinthula (Table 5.4). The year of evaluation had a significant influence (P<0.05) on AUDPC for CBSD incidence at both sites and AUDPC for CBSD severity at Chitala. Interaction effects of genotypes and year of

evaluation were significant (P<0.05) for AUDPC for CBSD incidence at both sites and AUDPC for CBSD severity at Chitala only.

The mean CBSD incidence AUDPC value at Chitala for 2014 was 2256 and was highly significantly (P<0.001) less than the mean 2015 AUDPC value of 5972. The AUDPC for CBSD incidence across the two years at Chitala ranged from 292 for Phoso to 23880 for Unknown (Table 5.5). At Kasinthula, the mean CBSD incidence AUDPC for 2014 was 1066, which was highly significantly (P<0.001) lower than the mean 2015 AUDPC value of 2088. Averaged across the years, AUDPC for CBSD incidence at Kasinthula ranged from 0 for Sauti to 13624 for Unknown. The AUDPC for CBSD severity was variable at Chitala across the two years, and ranged from 400 for Phoso to 1165 for Unknown. The 2014 season recorded lower AUDPC severity value of 586 (ranging from 360 for Sauti to 1210 for Unknown) than 2015 with an AUDPC value of 763 (ranging from 400 for Phoso to 1170 for Mbundumali). At Kasinthula, the AUDPC for CBSD severity across two years ranged from 360 for Sauti to 836 for Unknown, with the 2015 season recording a higher value (476) than 2014 (422).

Table 5.4. Mean square values for area under disease progress curve for cassava brown streak disease

Source of variance	DF	Chitala		Kasinthula	
		AUDPC-CBSDI	AUDPC-CBSDS	AUDPC-CBSDI	AUDPC-CBSDS
Year (Y)	1	331479920***	745538***	25084842*	67990^{ns}
Rep/year	2	31479722	180488	1210288	6322
Block/rep	3	2952994	40334	435989	9745
Genotype (G)	15	189990175***	277299***	72007250***	116992***
G X Y	15	12719517*	55831*	25044973***	30475^{ns}
Error	59	6515669	30505	5340859	22556
Corrected Total	95				

DF = degrees of freedom, AUDPC = area under disease progress curve, CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity, *, **, *** = significant at 5%, 1% and 0.1%, respectively, ns = not significant.

Table 5.5. Area under disease progress curve for cassava brown streak disease at Chitala and Kasinthula

Genotype	Chitala						Kasinthula					
	AUDPC CBSDI			AUDPC CBSDS			AUDPC CBSDI			AUDPC CBSDS		
	2014	2015	Mean	2014	2015	Mean	2014	2015	Mean	2014	2015	Mean
01/1316	2435	6742	4589	740	960	850	0	130	65	360	420	390
01/1569	354	2408	1381	410	680	545	667	0	333	420	360	390
96/1708	1644	2947	2295	740	620	680	3679	9469	6574	565	960	763
Beatrice	584	8657	4621	490	1030	760	45	0	23	370	360	365
Chamandanda	334	803	569	530	520	525	83	0	42	370	360	365
Kalawe	1029	10673	5851	660	960	810	74	375	225	370	390	380
MK05/0297	1179	3255	2217	460	730	595	53	214	133	370	450	410
Maunjili	63	2834	1448	380	530	455	0	333	167	360	390	375
Mbundumali	2119	11488	6803	880	1170	1025	167	597	382	390	540	465
Mpale	420	617	518	480	450	465	100	0	50	370	360	365
Mulola	3582	8092	5837	740	950	845	4485	679	2582	600	560	580
Phoso	126	458	292	400	400	400	125	0	63	361	360	361
Sauti	0	3451	1725	360	720	540	0	0	0	360	360	360
TMS4(2)1425	662	3382	2022	490	550	520	1256	0	628	440	360	400
Unknown	21396	26365	23880	1210	1120	1165	5887	21361	13624	652	1020	836
Yizaso	167	3383	1775	410	810	610	431	250	340	400	360	380
Mean	2256	5972	4114	586	763	674	1066	2088	1577	422	476	449
F-Prob.	<0.001			<0.001			<0.001			<0.001		
CV%	62.1			25.9			146.6			33.4		
LSD (0.05)	2948.9			201.8			266.9			173.5		

AUDPC = area under disease progress curve, CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity.

5.3.4 Storage root yield and yield loss due to cassava brown streak disease

Highly significant genotypic variations (P<0.001) for storage root yield, yield loss due to CBSD infection and CBSD storage root severity score were observed across seasons and locations, except yield loss at Kasinthula (Table 5.6). The harvest time effect was very significant (P<0.01) for storage root yield at both sites, yield loss at Chitala and CBSD storage root severity score at both sites. There were highly significant differences (P<0.001) between years for storage root yield at both sites and yield loss at Chitala. The interaction effects of genotype by year and genotype by harvest time were significant (P<0.05) for storage root yield, yield loss and CBSD storage root severity score at Chitala and storage root yield at Kasinthula.

Table 5.6. Mean square values for storage root yield, yield loss due to cassava brown streak disease and cassava brown streak disease storage root severity score

Source of variation	DF	Chitala			Kasinthula		
		Yield (t ha^{-1})	Yield loss (%)	CBSDR score	Yield (t ha^{-1})	Yield loss (%)	CBSDR score
Year (Y)	1	739.0^{***}	5015.7^{***}	1.4^{ns}	815.6^{***}	79.3^{ns}	0.5^{ns}
Rep/year	2	23.7	346.8	0.4	310.9	9.0	1.5
Block/rep	3	25.7	171.4	0.6	87.7	149.4	1.4
Genotype (G)	15	157.8^{***}	944.1^{***}	4.0^{***}	188.6^{***}	206.4^{ns}	2.1^{**}
Harvest time (T)	2	2063.8^{***}	2114.5^{***}	9.5^{***}	2560.2^{***}	118.9^{ns}	4.4^{**}
G x Y	15	39.3^{**}	800.7^{***}	1.6^{*}	100.0^{**}	226.2^{ns}	0.9^{ns}
G x T	30	41.7^{***}	466.6^{*}	1.4^{*}	76.9^{*}	141.6^{ns}	0.5^{ns}
Error	219	19.4	307.7	0.9	46.5	146.7	0.8
Corrected Total	287						

DF = degrees of freedom, CBSDR = cassava brown streak disease storage root severity score (1-5), *, **, *** = significant at 5%, 1% and 0.1%, respectively, ns = not significant.

The highest mean storage root yields were obtained at 12 MAP at both Chitala (16.0 t ha^{-1}) and Kasinthula (22.5 t ha^{-1}). At Chitala at 6 MAP, the mean storage root yield ranged from 1.6 t ha^{-1} (TMS4(2)1425) to 10.0 t ha^{-1} (Yizaso); at 9 MAP, storage root yield ranged from 2.6 t ha^{-1} (TMS4(2)1425) to 14.5 t ha^{-1} (Kalawe); and at 12 MAP, storage root yield ranged from 9.2 t ha^{-1}

(Chamandanda) to 25.5 t ha^{-1} (Maunjili) (Table 5.7). Storage root yield obtained at Kasinthula were generally higher than those obtained at Chitala. At 6 MAP, the storage root yield ranged from 4.3 t ha^{-1} (01/1316) to 12.8 t ha^{-1} (Phoso). At 9 MAP the storage root yield ranged from 10.2 t ha^{-1} (Kalawe) to 22.8 t ha^{-1} (Phoso), while at 12 MAP the storage root yield ranged from 14.5 t ha^{-1} (Kalawe) to 33.3 t ha^{-1} for Mulola (Table 5.8).

The highest yield loss due to CBSD at Chitala was recorded at 12 MAP, which ranged from 0% to 43.1%, with highest loss on genotype Kalawe. The lowest yield loss due to CBSD was recorded at 6 MAP by 96/1708, and it ranged from 0% to 10.9%. At 9 MAP, highest yield loss (24.8%) was observed for genotype Yizaso (Table 5.7). At Kasinthula (Table 5.8), the storage root yield loss due to CBSD ranged from 0% to 12.5% at 6 MAP, 0% to 16.7% at 9 MAP and 0% to 23.3% at 12 MAP. Highest losses were recorded on Mulola at 12 MAP (23.3%), 01/1316 and TMS4(2)1425 at 9 MAP (16.7%) and on 96/1708 at 6 MAP (12.5%).

5.3.5 Correlation coefficients between area under disease progress curves values, cassava brown streak disease storage root and leaf severity scores and yield loss

The CBSD incidence (AUDPC) was highly significantly correlated (at $P<0.001$) with the CBSD storage root severity score at all harvest times (Pearson, r = 0.26 at 6 MAP, 0.42 at 9 MAP, 0.35 at 12 MAP), CBSD leaf severity score (Pearson, r = 0.65 at 3 MAP, 0.66 at 6 MAP, 0.60 at 9 MAP, 0. 56 at 12 MAP) and yield loss due to CBSD (Pearson, r = 0.17 at 6 MAP, 0.37 at 9 MAP, 0. 30 at 12 MAP) (Table 5.9). The CBSD severity score (AUDPC) was highly significantly ($P<0.001$) correlated with the CBSD storage root severity score (Pearson, r = 0.31 at 6 MAP, 0.46 at 9 MAP, 0.30 at 12 MAP), CBSD leaf severity score (Pearson, r = 0.61 at 3 MAP, 0.81 at 6 MAP, 0.83 at 9 MAP, 0.77 at 12 MAP) and yield loss due to CBSD (Pearson, r = 0.21 at 6 MAP, 0.45 at 9 MAP, 0.31 at 12 MAP).

Table 5.7. Mean storage root yield, storage root yield loss due to cassava brown streak disease and cassava brown streak disease storage root severity score at three harvest times at Chitala across seasons

Genotype	Storage root yield (t ha^{-1})			Yield loss (%) due to CBSD			CBSD storage root score (1-5)		
	6 MAP	9 MAP	12 MAP	6 MAP	9 MAP	12 MAP	6 MAP	9 MAP	12 MAP
01/1316	2.8	5.9	9.7	1.7	0.0	0.0	1.3	1.3	1.5
01/1569	6.1	11.0	21.4	0.3	14.6	0.0	1.3	1.7	1.8
96/1708	5.7	8.4	14.2	10.9	2.2	0.0	1.7	1.8	2.2
Beatrice	6.0	11.8	17.1	1.3	20.1	13.6	1.8	2.0	3.0
Chamandanda	4.3	6.7	9.2	4.4	5.9	0.0	1.2	1.8	2.0
Kalawe	8.1	14.5	22.9	0.0	12.9	43.1	1.3	2.3	2.8
MK05/0297	5.3	10.1	13.0	3.8	0.0	0.0	1.5	1.2	1.3
Maunjili	6.7	11.5	25.5	0.0	0.0	4.0	1.2	1.2	1.8
Mbundumali	5.4	8.3	12.6	8.5	17.4	16.7	2.0	2.3	2.0
Mpale	4.6	9.2	14.7	0.0	0.1	0.0	1.0	1.3	1.5
Mulola	6.4	11.2	22.5	0.0	17.1	34.7	1.0	2.7	3.2
Phoso	6.2	12.8	18.1	0.0	0.8	8.7	1.0	1.7	1.8
Sauti	5.1	8.3	11.7	3.0	0.0	2.2	1.5	1.5	2.0
TMS4(2)1425	1.6	2.6	9.4	0.0	0.0	4.3	1.0	1.3	1.5
Unknown	6.0	11.1	16.6	0.0	23.9	18.6	1.7	3.3	3.0
Yizaso	10.0	12.7	16.9	0.0	24.8	33.4	1.5	2.7	3.7
Mean	5.6	9.7	16.0	2.1	8.7	11.2	1.4	1.9	2.2
F-Prob.	0.001			0.049			0.038		
CV%	42.1			238.6			52.7		
LSD (0.05)	1.3			5.0			0.3		

CBSD = cassava brown streak disease, MAP = months after planting.

Table 5.8. Mean storage root yield, storage root yield loss due to cassava brown streak disease and cassava brown streak disease storage root severity score at three harvesting times at Kasinthula across seasons

Genotype	Storage root yield (t ha^{-1})			Yield loss (%) due to CBSD			CBSD storage root score (1-5)		
	6 MAP	9 MAP	12 MAP	6 MAP	9 MAP	12 MAP	6 MAP	9 MAP	12 MAP
01/1316	4.3	10.3	14.6	0.0	16.7	0.0	1.5	2.0	1.5
01/1569	10.6	15.8	23.1	1.4	0.0	0.1	1.5	1.3	1.8
96/1708	10.5	17.7	27.5	12.5	7.5	6.9	2.2	1.8	2.2
Beatrice	7.0	16.0	20.3	0.4	0.0	1.6	1.3	1.2	1.5
Chamandanda	8.7	14.3	23.0	0.0	1.2	4.6	1.8	2.0	2.0
Kalawe	7.5	10.2	14.5	0.0	1.4	0.0	1.0	1.5	1.2
MK05/0297	5.5	13.4	23.0	0.7	2.2	2.4	1.0	1.5	1.7
Maunjili	10.6	15.9	21.9	0.0	1.7	2.3	1.2	2.0	1.8
Mbundumali	7.5	12.1	17.7	0.0	0.0	0.0	1.2	1.3	1.3
Mpale	10.4	13.7	20.2	0.0	0.9	0.0	1.0	1.7	1.3
Mulola	12.3	18.8	33.3	0.0	2.6	23.3	1.5	1.8	2.8
Phoso	12.8	22.8	30.3	0.0	0.5	0.0	1.2	1.3	1.3
Sauti	8.0	12.1	18.6	0.1	0.0	1.1	1.2	1.3	1.7
TMS4(2)1425	6.7	11.5	32.0	10.1	16.7	0.3	1.7	2.0	1.7
Unknown	9.7	15.5	22.0	0.0	3.6	8.7	1.8	2.3	3.0
Yizaso	7.2	11.3	18.6	0.0	0.0	6.0	1.2	1.0	2.2
Mean	8.7	14.5	22.5	1.6	3.4	3.6	1.4	1.6	1.8
F-Prob.	0.02			0.52			0.93		
CV%	44.8			423.1			56.2		
LSD (0.05)	1.9			3.5			0.3		

CBSD = cassava brown streak disease, MAP = months after planting.

Table 5.9. Pearson correlation coefficients among area under disease progress curve values, cassava brown streak disease storage root and leaf severity scores and yield loss due to cassava brown streak disease

Parameter	AUDPC CBSDI	AUDPC CBSDS	CBSDR score 12MAP	CBSDR score 6MAP	CBSDR score 9MAP	CBSDL score 12MAP	CBSDL score 3MAP	CBSDL score 6MAP	CBSDL score 9MAP	Yield loss 12MAP	Yield loss 6MAP	Yield loss 9MAP
AUDPC CBSDI	1.00											
AUDPC CBSDS	0.81***	1.00										
CBSDR score 12MAP	0.35***	0.30***	1.00									
CBSDR score 6MAP	0.26***	0.31***	0.11ns	1.00								
CBSDR score 9MAP	0.42***	0.46***	0.30***	0.22**	1.00							
CBSDL score 12MAP	0.56***	0.77***	0.20**	0.24***	0.29***	1.00						
CBSDL score 3MAP	0.65***	0.61***	0.21**	0.19**	0.32***	0.29***	1.00					
CBSDL score 6MAP	0.66***	0.81***	0.28***	0.22**	0.40***	0.47***	0.46***	1.00				
CBSDL score 9MAP	0.60***	0.83***	0.32***	0.32***	0.40***	0.67***	0.36***	0.57***	1.00			
Yield loss 12MAP	0.30***	0.31***	0.70***	0.10ns	0.33***	0.22**	0.14ns	0.30***	0.34***	1.00		
Yield loss 6MAP	0.17*	0.21**	0.08ns	0.69***	0.23**	0.13ns	0.20**	0.16*	0.15*	0.09ns	1.00	
Yield loss 9MAP	0.37***	0.45***	0.25***	0.24***	0.78***	0.37***	0.22**	0.36***	0.41***	0.35***	0.18*	1.00

AUDPC = area under disease progress curve, CBSDI = cassava brown streak disease incidence, CBSDS = cassava brown streak disease severity, CBSDR = cassava brown streak disease storage root severity, CBSDL = cassava brown streak disease leaf severity, MAP = months after planting, *, **, *** = significant at 5%, 1% and 0.1%, respectively, ns = not significant.

5.4 Discussion

Host plant resistance is one of the viable options for cassava farmers to reduce the devastating effects of CBSD. Breeding for disease resistance begins with identification of germplasm with desirable attributes and to concentrate the trait of interest (CBSD resistance). This study aimed at identifying cassava varieties that are resistant/tolerant to CBSD, by assessing incidences, severities and yield loss attributed to CBSD storage root severity. Yield losses were determined by using a common practice among farmers in which storage root necrotic patches are cut out so that only clean storage roots form part of the yield obtained. This method was preferred to the other methods used by Gondwe et al. (2003) and Hillocks et al. (2001), which tend to overestimate yield loss due to CBSD.

The genotypes showed variable CBSD symptoms, both in the shoot and storage roots. These included leaf chlorosis and blotches, stem lesions and die back, leaf chlorosis without storage root necrosis, or leaf chlorosis with storage root necrosis. Other symptoms were storage root necrosis without leaf chlorosis or blotches, leaf chlorosis and blotches and stem lesions without storage root necrosis, storage root constrictions without necrosis, or storage root necrosis with constrictions. These symptoms are typical of CBSD (Hillocks and Jennings, 2003; Hillocks et al., 1996; Hillocks and Thresh, 2000; Mohammed et al., 2012; Nichols, 1950).

The CBSD development varied from season to season and from location to location. This resulted into different levels of incidence and severity, suggesting that there was a substantial effect of the environment on the development and expression of CBSD. Reports suggest that environment plays a big role in the CBSD symptom expression (Hillocks and Jennings, 2003; Hillocks et al., 1996; Hillocks and Thresh, 2000).

The results from this study indicated significant genotypic variations for CBSD severity (shoot and storage roots) and incidence, which suggested a differential response of the varieties to CBSD infection. This implies that there is significant genetic variation in the germplasm which could be exploited by plant breeders to develop varieties that are resistant to CBSD. A differential response of cassava genotypes to CBSD has been reported by many researchers (Abaca et al., 2012; Hillocks and Jennings, 2003; Hillocks et al., 2001; Kaweesi et al., 2014; Munga, 2008; Nichols, 1950; Rwegasira and Rey, 2012).

The observations showed that after 9 MAP, the CBSD leaf incidences and severity scores declined, most likely due to leaf fall and regrowth which obscures foliar CBSD scores. However,

the CBSD severity in the storage roots advanced with a prolonged stay of the crop in the field. This is consistent with previous reports, that above ground symptoms are clearly expressed in the early stages of plant growth, while storage roots symptoms are mainly exhibited at an advanced stage of plant growth (Benesi et al., 2010; Chipeta et al., 2016a; Gondwe et al., 2003; Hillocks et al., 2001; Hillocks et al., 2002; Rwegasira and Rey, 2012).

The AUDPC estimates gave an estimate of the total disease pressure over the 12 month period. Correlation coefficients between AUDPC values for CBSD severity with CBSD severity scores (at 6, 9 and 12 MAP) were highly significant and positive. This showed that ranking of genotypes by AUDPC and CBSD severity (6, 9 and 12 MAP) was generally similar. These results suggest that that CBSD data can be collected at 6 or 9 MAP, without loss of information.

A significant association between CBSD on leaves and storage roots was found. Similar trends have also been reported by several others (Abaca et al., 2012; Hillocks et al., 1996; Hillocks et al., 2001; Hillocks and Thresh, 2000; Hillocks et al., 2002; Moreno et al., 2011). This implies that foliar symptoms are a good indication of the resistance. However, this should be done with caution bearing in mind that foliar symptoms tend to be inconspicuous after leaf fall and regrowth.

The highest yield losses were recorded at 12 MAP. Maximum yield loss for the most susceptible varieties at the respective harvest times were 43.1%, 24.8% and 10.9% at 12, 9 and 6 MAP. The differential yield losses at three harvest times, means that delayed harvesting has negative implications on the yield of cassava where CBSD is prevalent. Conversely, early harvesting can help salvage significant yields, more especially for the early bulking varieties as reported by Chipeta et al. (2016b). The results, therefore, demonstrate that yield loss due to CBSD is higher than what would be lost due to early harvesting. Early storage root bulking cassava varieties could provide good storage root quality and high productivity per unit land area and time.

A comparison of these results with other studies shows that yield loss due to CBSD (up to 43.1%) is lower than the losses of 60-70% reported by other scientists (Hillocks et al., 2001; Shaba et al., 2003). However, yield losses are significantly higher than the 20-25% reported by Gondwe et al. (2003). The difference could be due to estimation methods, where in this study, actual yield loss was estimated by removing necrotic patches (a common practice among smallholder farmers) and weighing only usable portions (Hillocks, 2004); and could also be due to genotypic differential in resistance/tolerance to CBSD.

Based on the lower yield losses due to CBSD, low AUDPC values, low foliar CBSD symptoms and low storage root CBSD severity scores, five genotypes (Phoso, Maunjili, Mpale, Sauti and TMS4(2)1425) were identified as resistant/or tolerant to CBSD. Genotypes Phoso and Maunjili were among the top three high yielding genotypes and these genotypes have been reported (Chipeta et al., 2016b) to be early storage root bulking. Therefore, these varieties could be promoted for use by farmers in Malawi, and could be utilised in breeding programs in order to address CBSD problem.

5.5 Conclusions

The study showed that there is a significant association between CBSD on leaves and storage roots, which suggested that a genotype expressing foliar symptoms could very likely exhibit storage root symptoms. The CBSD storage root severity increased with a prolonged stay of the crop in the field and yield loss of up to 43% can be incurred due to CBSD when susceptible cassava is harvested at 12 MAP. The study identified five genotypes as resistant/or tolerant to CBSD (Phoso, Maunjili, Mpale, Sauti and TMS4(2)1425). Therefore, these genotypes can directly be used by farmers, as some of these are early bulking and high yielding (Phoso, Maunjili). They can also be used in hybridization programs to develop new varieties. In order to effectively manage CBSD, farmers need to integrate various strategies such as using varieties that are early bulking and resistant/tolerant to CBSD, selecting planting material free from CBSD, sanitation and roguing of any infected plants from the field, especially shortly after sprouting.

5.6 References

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Chapter 6

6 Combining ability and mode of gene action for resistance to cassava brown streak disease and early storage root bulking

Abstract

Cassava (*Manihot esculenta* Crantz) brown streak disease (CBSD) is currently one of the major constraints to sustained cassava production in Malawi. Its economic impact is mainly manifested in the storage roots, where it causes pitting, necrosis and constriction. The CBSD can effectively be managed by using resistant varieties as well as through early harvesting, especially if the varieties are early bulking. However, the development of resistant and early storage root bulking varieties requires an understanding of gene action controlling the inheritance of the two traits. Currently, there is very little information in Malawi regarding the inheritance pattern and relative importance of general combining ability (GCA) and specific combining ability (SCA) of the two traits. Therefore, a study was conducted to determine the mode of gene action and the relative contribution (importance) of GCA and SCA effects in the inheritance of CBSD resistance and early storage root bulking traits. The information generated is essential in the selection of parents and in the design of breeding strategies for an effective breeding programme. Thirty six families were generated using a 6 x 6 North Carolina Design II and the progenies were evaluated for CBSD resistance and early bulking at two locations, using a triple square lattice design. The GCAs due to female (GCA_f) and male (GCA_m) were very significant ($P<0.01$) for CBSD and early storage root bulking and other traits recorded. Significant ($P<0.05$) female x male interaction effects (SCA) were also observed for CBSD. The results suggested that both additive and non-additive gene effects were involved in the genetic control of CBSD resistance, but there was predominance of additive gene action. For early storage root bulking, the results implied that additive gene effects were important. Four parents (Silira, Mulola, Phoso, and Mkondezi) were identified as the best general combiners for the CBSD, early storage root bulking and other traits. Thirteen progenies, exhibiting CBSD resistance and early storage root bulking, were identified and selected for advancement.

6.1 Introduction

Cassava (*Manihot esculenta* Crantz) is one of the major food crops in Malawi providing food and income to up to 40% of the population (Moyo et al., 1999). Cassava brown streak disease (CBSD) has become one of the major constraints towards sustainable cassava production in eastern and southern Africa in general (Alvarez et al., 2012; Nichols, 1950; Ntawuruhunga and Legg, 2007; Winter et al., 2010) and Malawi in particular (Benesi et al., 2010; Chipeta et al., 2016a; Gondwe et al., 2003). It is mainly characterised by necrotic symptoms on the storage roots which tend to increase with plant age (Alvarez et al., 2012; Bull et al., 2011; Calvert and Thresh, 2002; Hillocks and Jennings, 2003). Its major impacts are manifested through the reduction of yield and market quality of the storage roots (Gondwe et al., 2003; Hillocks et al., 2001). In the long run it affects and reduces the viability of planting material (Hillocks and Jennings, 2003) as disease pressure tends to build up over time. This leads ultimately to a scarcity of clean planting material, further confounding the existing challenges regarding the low multiplication rate of cassava planting material (Ceballos et al., 2012). The reported estimated yield loss due to CBSD vary considerably from as high as 70% (Hillocks et al., 2001) to as low as 20% (Gondwe et al., 2003).

A viable and sustainable control strategy is the use of resistant varieties, which is highly effective, even in high disease pressure areas. Development of resistant varieties requires, among others, an understanding of the mode of gene action governing resistance, so that appropriate breeding material (parental genotypes) and strategies are selected.

The mode of gene action is studied through the use of appropriate mating designs and associated biometrical analysis, such as North Carolina design II (Acquaah, 2012; Chahal and Gosal, 2002; Hinkelmann, 2012). The North Carolina design II and other designs help to estimate the breeding value (due to additive genes) of a given genotype used in the cross known as general combining ability (GCA), which refers to the average performance of genotype when crossed with other genotypes (Ceballos et al., 2004; Falconer and Mackay, 1996; Griffing, 1956a). It also measures the specific combining ability (SCA), which refers to the crosses that do relatively better or worse than would be expected on the basis of the average performance of the genotypes involved in a cross, which result from specific allelic combinations or dominance effects (Acquaah, 2012; Griffing, 1956b).

A considerable number of reports suggest that CBSD is mainly controlled by additive gene action (Ceballos et al., 2015; Kulembeka et al., 2012; Munga, 2008; Tumuhimbise, 2013; Were,

2011), except Zacarias and Labuschagne (2010) who reported the predominance of non-additive gene action. Another viral disease of importance is cassava mosaic disease (CMD) of which the resistance is said to be predominantly influenced by additive gene effects (Ceballos et al., 2015; Chikoti, 2011; Lokko et al., 2006; Parkes, 2011; Tumuhimbise, 2013), although Kamau et al. (2010) reported predominance of non-additive gene effects. Fresh storage root yield is largely influenced by non-additive gene effects (Calle et al., 2005; Ceballos et al., 2015; Kamau et al., 2010; Parkes, 2011; Tumuhimbise, 2013; Zacarias and Labuschagne, 2010), but other findings suggest preponderance of additive gene action (Ceballos et al., 2004; Chikoti, 2011; Munga, 2008). The contradictory reports on the nature of gene action determining important traits from different authors present a confusing picture for any cassava breeder. It is a considered view that differences arise due to the differences in the reference population used, the study sites, the mating designs and type of analysis employed, and the evaluation stage (seedling or clonal). A genotype x environment effect (G x E interaction) and statistical analysis techniques used seem to be the major contributing elements to the differences observed. Significant GCA x E and SCA x E have been widely reported (Lokko et al., 2006; Ojulong, 2006; Tumuhimbise, 2013; Were, 2011). This implies that gene action estimates cannot be consistent across the studies done in different environments. This suggests that localised genetic studies could provide a clear insight in the nature of gene action on which breeders can base their cassava improvement programs.

The main objective of this study was to develop and identify F1 genotypes (progenies) that are resistant to CBSD and early storage root bulking and specifically, to determine the gene action and the relative contribution (importance) of GCA and SCA effects in the inheritance of CBSD resistance and early storage root bulking traits.

6.2 Materials and methods

6.2.1 Breeding material and development of progenies

The breeding material consisted of 12 cassava genotypes, out of which six were used as female and the other six were designated as male genotypes. These genotypes were sourced from National Agricultural Research Stations and farmers' fields (Table 6.1) and their selection was based on their popularity with farmers, flowering ability to produce reasonable

amount of seeds for each of the required F1 crosses, and their response to various diseases prevalent in Malawi.

A crossing block constituting the 12 genotypes was established at Bunda College of Agriculture in Lilongwe, in December in 2013/2014 season. Female and male genotypes were planted in separate blocks (4 blocks for female and 4 for male) and each block comprised 12 ridges (10m long each) and each genotype occupied two ridges in each block. Controlled pollinations were done following the standard procedures described by Kawano (1980). The parents were crossed in a North Carolina Mating Design II (NCDII) (Comstock and Robinson, 1952) to produce 36 F1 crosses. On average, 108 seeds were generated from each cross. The seeds were germinated and grown in a screen-house in plastic bags. They were watered twice a day to ensure good germination and development.

Table 6.1. Genotypes used as female and male parents in North Carolina Design II

Female Genotype	Original Source	Male Genotype	Original Source
01/1316	Local	Beatrice	Local
01/1569	Local	Kachamba	Local
Chamandanda	Local	Masoyabazungu	Local
Depwete	Introduction from IITA	Mbundumali	Local
Mulola	Introduction from IITA	Mkondezi	Local
Silira	Introduction from IITA	Phoso	Local

IITA = International Institute for Tropical Agriculture

6.2.2 Field experiments

Seedling trial

Sixty five days after planting (DAP), the seedlings were transplanted (3 January, 2015) to the experimental field at Bunda College Student Research Farm during the rainy season as a seedling nursery. A total of 1152 (32 genotypes per cross) seedlings were planted in a simple 6 x 6 square lattice design at 0.5 m and 1 m spacing within and between rows, respectively. No irrigation and fertilizers were applied at this stage but all recommended cultural practices were followed. The overall goal of a seedling trial was to produce enough stem cuttings for the clonal study. At harvest time, 12 months after planting (MAP), 360 genotypes (10 genotypes per

cross/family) were selected to proceed with clonal trial. The genotypes selected were those which were free from disease (CBSD, CMD) and pest (cassava green mite-CGM and cassava mealy bag- CMB) damage, and had the capacity to produce six good quality vegetative cuttings to proceed with the trial.

Clonal evaluation trial

The trials were conducted at two locations, Chitala Agricultural Research Station in Salima district and Bunda Research Farm in Lilongwe in the 2015/2016 season. Table 6.2 details soil characteristics of the two sites and Figure 6.1 summarizes the mean annual rainfall and temperatures. The trials were laid out using a square lattice design constituting the 36 families. Three replications per site were used and each replication had six blocks and each block had six plots (6x6). Each replication contained the 48 entries (12 parents and 36 families), planted together in the respective plots of each replication. A plot consisted of three ridges and the first two ridges consisted of families and a third ridge contained a parental genotype. The plant spacing was 1 m x 1 m between and within rows, giving a plant population of 10 000 plants ha^{-1}. Each plot was separated by a CBSD infected spreader row. Plants used in the spreader rows were obtained in fields that had a CBSD incidence of 100% and a severity of 4 or 5. The trials were planted in January in 2016 under rain-fed conditions and neither fertilizers nor pesticides were applied, but all other cultural practices were followed.

Table 6.2. Soil status of the two sites in 2016

Characteristics	Bunda	Chitala
Soil texture	SC - SCL	SCL - SL
Soil PH	4.05 - 4.64	4.68 - 5.07
Phosphorus (ppm)	87.93 - 119.90	1.29 - 4.25
Organic carbon (%)	0.50 - 0.70	0.87 - 1.15
Estimated nitrogen (%)	0.05 - 0.07	0.09 - 0.12
Potassium (meq /100g)	0.32 - 0.57	0.40 - 0.84

SC = sandy clay, SCL = sandy clay loam, SL = sandy loam

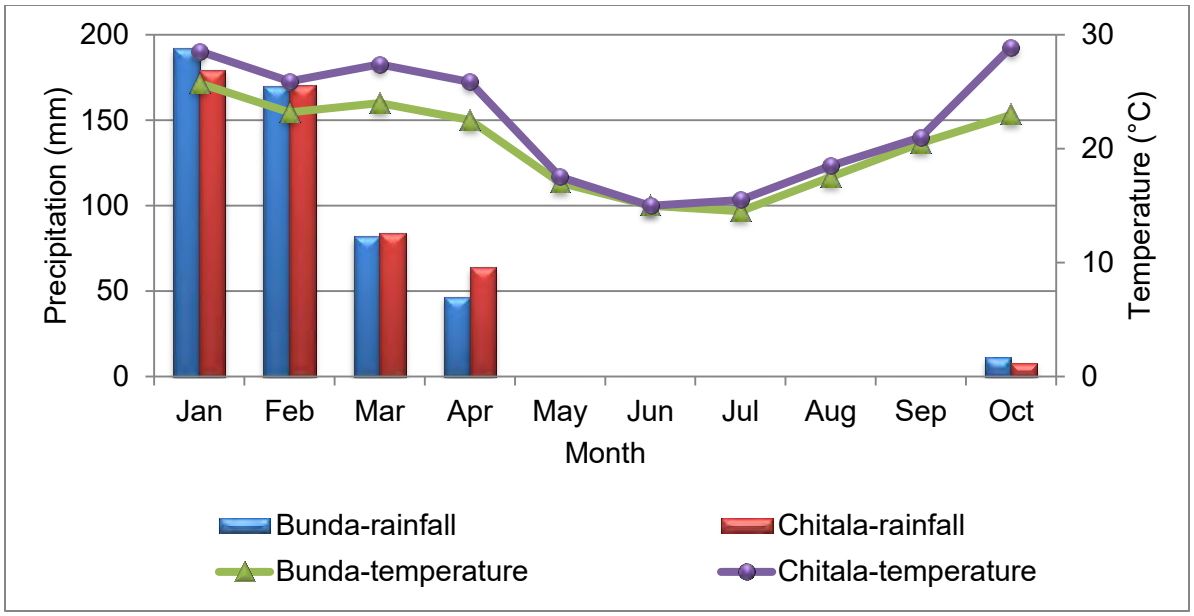

Figure 6.1. Total monthly rainfall (mm) and average monthly temperature (°C) for Bunda and Chitala in 2016

6.2.3 Data collection

Disease and pest data

Cassava brown streak disease severity symptoms on shoots (CBSDS) were recorded on each plant every month up to 9 MAP. A severity score of 1–5 (IITA, 1990) was used where 1 = no apparent symptoms, 2 = slight foliar chlorotic leaf mottle, no stem lesions, 3 = foliar chlorotic leaf mottle and blotches with mild stem lesions, no dieback, 4 = foliar chlorotic leaf mottle and blotches and pronounced stem lesions with no dieback and 5 = defoliation with stem lesions and pronounced dieback. The CBSD incidence (CBSDI) was measured as a proportion of plants showing symptoms to the total number of plants sampled. At harvest (9 MAP), each storage root was cut into slices and the maximum severity score taken for each storage root (CBSDRS), where 1 = no necrosis, 2 = mild necrotic lesions (1-10%), 3 = pronounced necrotic lesions (11-25%), 4 = severe necrotic lesions (26-50%) and 5 = very severe necrotic lesions (>50%). The CBSDRS mean value was calculated on a per plant basis, and then averaged to give a mean value for each family. Assessments were also made for CMD severity (CMDS) monthly using a scale of 1-5 (IITA, 1990), where 1 = No symptoms observed, 2 = Mild chlorotic pattern over entire leaflets, 3 = Strong mosaic patterns all over leaf, narrowing and distortion of lower one third of leaflets, 4 = Severe mosaic pattern, severe distortion of 2/3 leaflets and

general reduction of leaf size, 5 = Severe mosaic, severe distortion of 4/5 or more leaflets, twisted and misshapen leaves and severe reduction of leaf size.

Yield and yield components data

Data for individual genotype were collected at harvest (9 MAP), for the following traits: fresh storage root mass (kg plant^{-1}) and converted to fresh storage root yield (FSRY) (t ha^{-1}), shoot mass (kg plant^{-1}) converted to biomass yield (BMY), storage root number plant^{-1} (SRN) , storage root length (SRL) (cm), storage root diameter (SRD) (cm) and plant height (PHT) (cm). Additional variables such as harvest index (HI), dry storage root mass content (DMC) (%), starch content (SC) (%) and dry storage root yield (t ha^{-1}) were computed as follows:

The percentage dry mass (DM), starch content and harvest index (HI) were determined as described by Fukuda et al. (2010):

1. Dry mass (DM) % = 158.3 x SG – 142.
2. Starch content (%) = 112.1 x SG – 106.4; Where SG = specific gravity = $\frac{Wa}{(Wa - Ww)}$. Where Wa = mass in air of storage roots (kg) and Ww = mass in water of storage roots (kg).
3. Dry storage root yield (t ha^{-1}) = $\frac{\text{fresh storage root yield}}{100} \times \text{DM\%}$
4. Harvest index (HI) = $\frac{\text{mass of storage roots}}{\text{mass of storage roots + aboveground mass}}$

6.2.4 Data analysis

Data were analysed at two levels. 1) at genotype level where all F1 individuals were subjected to an analysis of variance using the restricted maximum likelihood (REML) procedure (O'Neill, 2010; Payne et al., 2014) using GenStat, 17th ed. and 2) on family basis where genotypes within a family were averaged to determine the family's performance.

A preliminary analysis indicated that maximum CBSDS and CBSDI were observed at 6 and 7 MAP, respectively. The mean shoot severity score and disease incidence were calculated per family, based on all individual plant scores per family at 6 and 7 MAP, respectively.

Analysis of variance for female × male analysis

The combined data were analysed using PROC Mixed procedure performed in SAS® 9.3 software (SAS Institute, 2011). A five step analysis of variance was performed as follows: step 1: analysis of all genotypes comprising parents and crosses pooled over sites, step 2: analysis of parents across sites, step 3: analysis of parents versus crosses (estimate of average heterosis), step 4: analysis of crosses across sites and step 5: female x male analysis (partitioning of the crosses).

Since there was a large number of progenies from each parent, progeny from a given parent was taken to represent a random population and its mean performance was used to estimate the parents' breeding value. Therefore, genotypes were fitted as random factors, which in turn enabled estimation of variance components. The following combined statistical mixed model was fitted to estimate variance components (Gallais, 2003):

$Y_{ijk} = \mu + r_k + f_i + m_j + (fm)_{ij} + e_{ijkl}$

Where Y_{ijk} is the observed value of the progeny of the i^{th} female crossed with j^{th} male in the k^{th} replication, μ is the overall population mean, f_i is the GCA of the i^{th} female with variance σ^2_f, m_j is the GCA of the j^{th} male with variance σ^2_m, $(fm)_{ij}$ is the SCA of the cross between i^{th} female and j^{th} male with variance σ^2_{fm}, r_k is the replication effect and e_{ijk} is the residual effect (environmental and genetic) at the level of the plant within a plot, of variance σ^2_e.

Combining ability effects

Estimates of GCA of females and males and SCA of the hybrids were computed as described by Singh and Chaudhary (1985). Significance of the combining ability effects were determined by using the t- test at 0.05 and 0. 01 levels of probability. t (calculated) for GCA effect = $\frac{GCA}{S.E}$, and t (calculated) for female x male interaction (SCA) effects = $\frac{SCA}{S.E}$. Standard error (S.E) was adapted from the female x male analysis (partitioning of the crosses) of variance output. The distribution of crosses in relation to GCA and SCA effects was determined by denoting significant positive combining ability effects as high, non-significant as average and significant negative as low for FSRY and other agronomic traits. For CBSD and CMD, significant positive combining ability effects were considered as low, non-significant as average and significant negative as high (Chipeta, 2012; Saleem, 2008). The GCA and SCA values with negative

effects show contribution towards resistance, and positive values show contribution towards susceptibility for CBSD and CMD (Chipeta, 2012).

Estimates of heterosis

Heterosis is the performance of hybrid individuals compared with their parents (Fehr, 1991). The performance can be compared with the mean performance of the two parents involved in the cross known as mid-parent heterosis or it could be compared with the performance of a better parent known as high-parent heterosis (heterobeltiosis). In this study, only heterobeltiosis is used. High-parent heterosis (heterobeltiosis) (HPH) (%) = $\frac{(F_1\text{-HP})}{HP} \times 100$;

Where, F_1 = F_1 hybrid performance, HP = performance of better parent in the cross.

Genetic components

The relative contribution of genetic components was determined to obtain estimates of GCA variance (δ^2GCA_f and δ^2GCA_m) and SCA variance (δ^2SCA_{fm}) for each character studied. δ^2GCA_f, δ^2GCA_m and δ^2SCA_{fm} were estimated from the female, male and female x male expected mean square values, respectively. Additive (δ^2A) and dominance (δ^2D) variances were estimated from respective GCA and SCA variances as follows:

$\delta^2A = 4\,\frac{(\delta^2GCA_f + \delta^2GCA_m)}{2}$ and $\delta^2D = 4\,\delta^2SCA_{fm}$.

Phenotypic (δ^2p) and genotypic (δ^2g) variances were estimated as $\delta^2g = \delta^2A + \delta^2D$, and $\delta^2p = \delta^2A + \delta^2D + \delta^2e$. Where δ^2e = error mean square (variation within full sibs)

Broad (H^2) and narrow (h^2) sense heritability was calculated from the estimated components of variance as: $H^2 = \frac{\delta^2g}{\delta^2p}$ and $h^2 = \frac{\delta^2A}{\delta^2p}$, respectively.

Genetic ratio (GR) = $\frac{\delta^2A}{(\delta^2A + \delta^2D}$ (Falconer and Mackay, 1996) was used in determining progeny performance. The closer this ratio is to one, the greater the chances of predicting progeny performance based on GCA, that is, value less than 1, was taken as predominance of non-additive type of gene action, and greater than 1 as additive gene action.

Proportional contribution of females, males and female × male interaction to variation

Contribution of females, males and their interaction to the total variance were calculated as described by Singh and Chaudhary (1985)

Contribution of females = $\frac{\text{SS Females}}{\text{SS Crosses}}$ x100%; Contribution of males = $\frac{\text{SS Males}}{\text{SS Crosses}}$ x100%

Contribution of (female × male) = $\frac{\text{SS Female x Male}}{\text{SS Crosses}}$ x100%; Where *SS* = the sum of squares.

6.2.5 Identification and selection of cassava brown streak disease resistant and early storage root bulking genotypes

The genotypes selected from the seedling trial were coded based on the place where and the year when the crosses were generated, while keeping track of the pedigree of each cross. For example: the crosses were generated at Bunda College (BC) Research Farm in 2014 (14). The first genotype selected from family one was coded BC14/001, the second genotype BC14/002 and so on up to BC14/360. After the clonal trial, the best genotypes were selected based on resistance to CBSD and early storage root bulking, using FSRY as an indicator. In addition to CBSD, CMD resistance was incorporated as a selection criterion due to the magnitude and significance of the disease in Malawi. The CBSD selection was based on both above ground severity and storage root severity. A genotype with a score of 1 or 2 on above and below ground CBSD symptoms was rated as resistant. The initial selection involved the identification of families with desirable significant mean values for CBSD, CMD and FSRY. The second step involved selection of families exhibiting significant SCA effects. Within those families, progenies with CBSD and CMD severity scores of ≤ 2 were selected. Finally, genotypes with high FSRY of ≥ 10 t ha^{-1} were selected to constitute material for further evaluation.

6.3 Results

6.3.1 Genetic variation and mean performance of individual genotypes

The analysis of variance for individual genotypes (n=360) across locations revealed very significant (P< 0.01) differences for CBSDS and CBSDRS, CMDS, and FSRY (data not shown). The CBSDS ranged from 1 (62 genotypes) to 5 (4 genotypes). The CBSDRS also ranged from 1 (37 genotypes) to 5 (62 genotypes). The CMDS scores ranged from 1 (98 genotypes) to 4.7 (2 genotypes). The FSRY ranged from 0.45 t ha^{-1} to 39.2 t ha^{-1}.

6.3.2 Genetic variation and mode of gene action for resistance to cassava brown streak disease and cassava mosaic disease

Parents, as well as the crosses, exhibited very significant (P<0.01) differences in their reaction to CBSDS, CBSDRS and CBSDI (Table 6.3). Pooled analysis across two locations showed very significant (P< 0.01) variance among GCA due to females (GCA_f), GCA due to males (GCA_m), and SCA for both CBSDS and CBSDI. These females (GCA_f), males (GCA_m) and female x male interaction (SCA) effects accounted for 19.8%, 33.4% and 46.7% of the sum of squares for CBSDS, respectively. The GCA_m effects were 1.6 times larger than GCA_f effects and the GCA_m sum of squares contributed more than the GCA_f sum of squares to total variance for CBSDS CBSDI. There were also very significant (P< 0.01) location main effects, GCA_f x location, GCA_m x location and SCA x location interaction effects for both CBSDS and CBSDI.

Very significant (P<0.01) variations were observed among parents and crosses for the reaction to CMD across the two locations (Table 6.3). The GCAs (both due to females and males) and SCA effects were also very significant (P< 0.01) for CMDS and CMDI with GCA_m predominantly higher than the GCA_f and SCA. The GCA_m sum of squares contributed more than GCA_f and SCA to the total variance for CMDS and CMDI. The location main effects, GCA_f x location, GCA_m x location and SCA x location interaction effects, exhibited significant (P< 0.01) variation.

Table 6.3. Mean squares for cassava brown streak disease and cassava mosaic disease across two locations

Source	DF	CBSDS	CBSDRS	CMDS	CBSDI	CMDI
Location	1	161.44**	193.55**	141.88**	236785.61**	245949.02**
Rep(Location)	4	3.42	0.52	0.25	1747.08	175.42**
Genotypes	47	0.75**	0.69*	1.01**	755.6**	1278.42**
Parents	11	1.49**	1.04	1.60**	1199.36**	2302.74**
Parents vs crosses	1	0.66	1.35	0.09	1783.61*	23.39
Crosses	35	0.52**	0.57**	0.82**	585.41**	991.48**
GCA_f	5	0.73**	0.74*	0.76**	788.93**	727.17**
GCA_m	5	1.22**	1.38**	3.49**	802.47**	3743.11**
SCA	25	0.34*	0.37	0.30**	501.3**	494.02**
GCA_f x location	5	0.69**	0.31	0.76**	723.94**	762.55**
GCA_m x location	5	0.92**	1.15**	3.49**	645.69**	3607.92**
SCA x location	25	0.35*	0.40	0.30**	539.10**	488.22**
Error	187	0.21	0.42	0.06	261.80	102.29
%SS GCA_f		19.84	18.70	13.22	19.25	10.48
%SS GCA_m		33.44	34.70	60.46	19.58	53.93
%SS SCA		46.71	46.50	26.32	61.17	35.59
GCA/SCA		5.74	5.73	14.17	3.17	9.05

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CBSDI = cassava brown streak disease incidence, CMDS = cassava mosaic disease severity, CMDI = cassava mosaic disease incidence, DF = degrees of freedom, GCA_f = general combining ability for female, GCA_m = general combining ability for male, SCA = specific combining ability, SS = sum of squares, *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

6.3.3 Performance of cassava genotypes for resistance to cassava brown streak disease and cassava mosaic disease

On average, CBSDS symptoms started appearing at 3 MAP across the two locations and progressed with time (Figure 6.2). Maximum severity was observed at 6 MAP followed by a decline in severity. A similar trend was also observed for CBSDI, with the maximum at 7 MAP (Figure 6.3). The mean CBSDS among parents ranged from 2.0 (Phoso) to 3.0 (Beatrice) (Table 6.4. For CBSDRS, the best rated parents were Kachamba (2.6), Silira (2.7) and Depwete (2.7). Among the families, CBSDS ranged from 1.4 (Silira x Mkondezi) to 3.5 (Mulola x Mbundumali) and 10 families recorded a score of ≤ 2 (Table 6.5). The CBSDRS ranged from 2.0 (Depwete x

Beatrice) to 3.9 (01/1569 x Mbundumali and 01/1569 x Phoso). The CBSDI ranged from 17.9% (Silira x Phoso) to 95.2% (Chamandanda x Mbundumali), while the CBSDRI ranged from 50.9% (Silira x Masoyabazungu) to 95.2% (01/1569 x Mbundumali).

The CMDS symptoms appeared at 1 MAP and the maximum scores were observed at 4 MAP (Figure 6.2). Similarly, maximum CMDI was recorded at 4 MAP (Figure 6.3). Mean CMDS among parents ranged from 1.8 for Phoso to 3.4 for Kachamba (Table 6.4). The lowest CMDI values were recorded on Phoso (36.3%). Among families, CMDS ranged from 1.2 (Chamandanda x Phoso and 01/1316 x Phoso) to 3.9 (Depwete x Kachamba). In terms of CMDI, values ranged from 11.4% (01/1316 x Phoso) to 100% (Depwete x Kachamba) (Table 6.5).

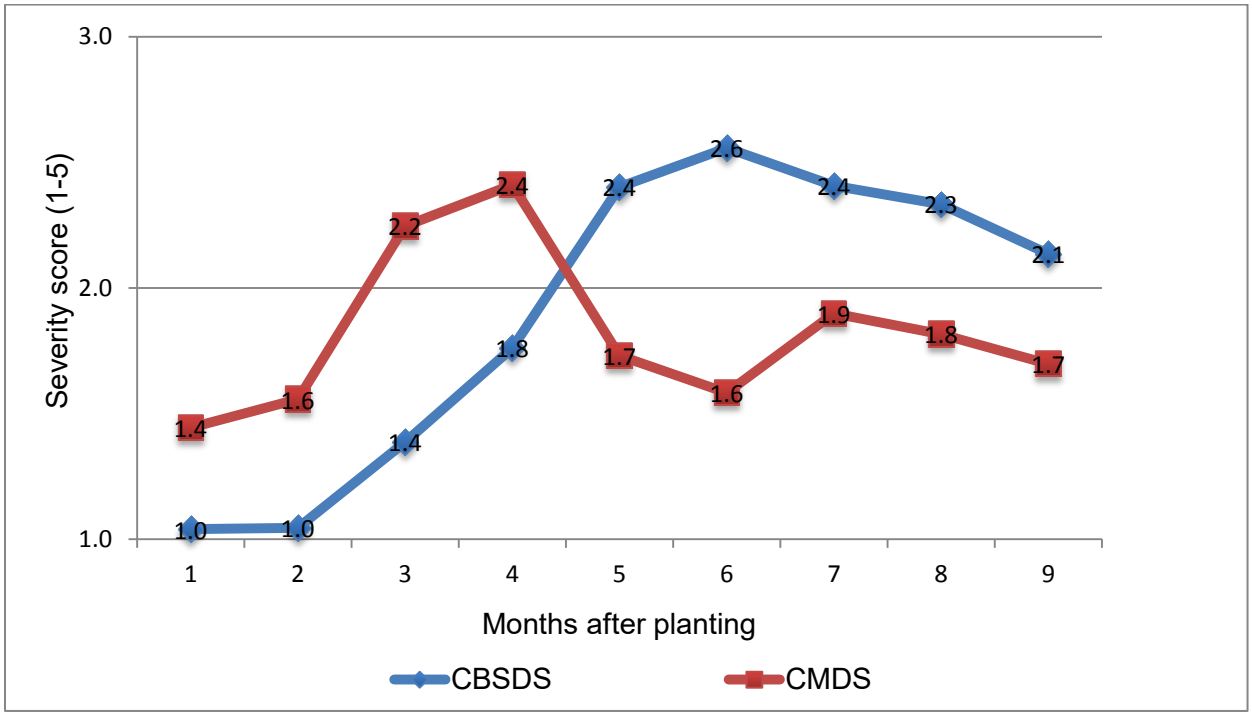

Figure 6.2. Progress for cassava brown streak disease severity (CBSDS) and cassava mosaic disease severity (CMDS)

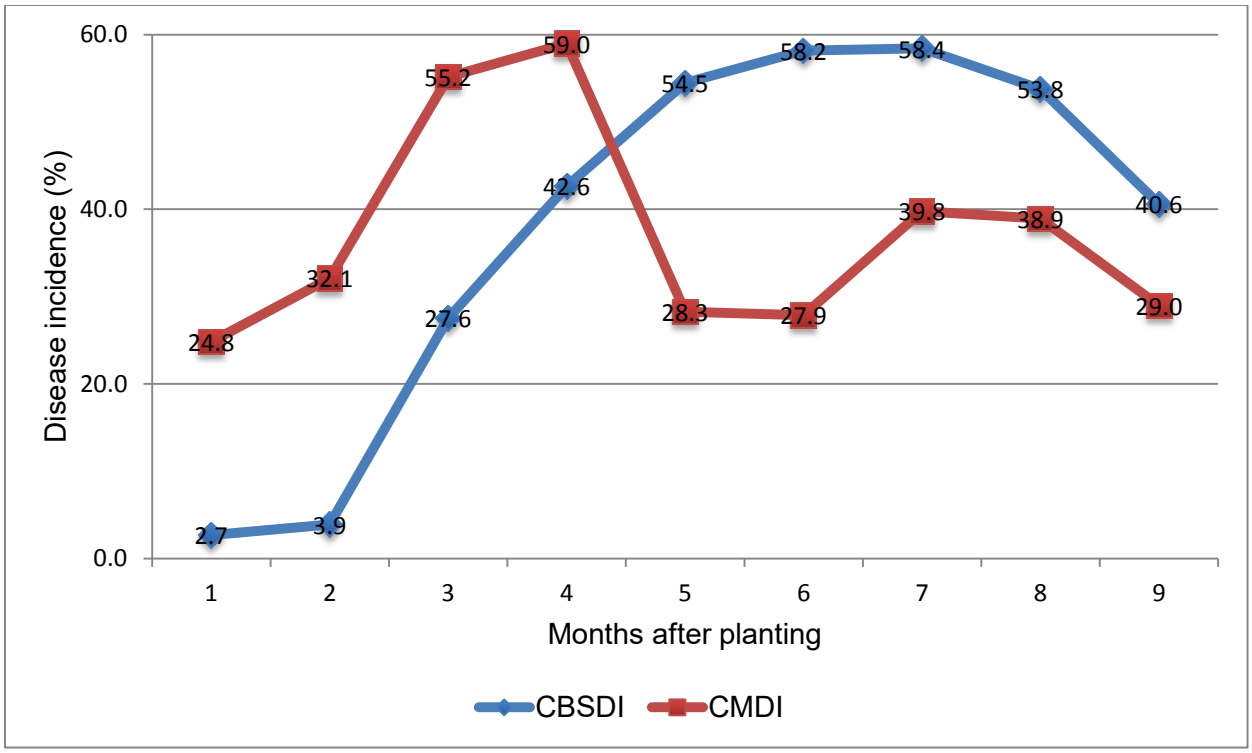

Figure 6.3. Progress for cassava brown streak disease incidence (CBSDI) and cassava mosaic disease incidence (CMDI)

Table 6.4. Mean performance of parents for cassava brown streak disease and cassava mosaic disease across two locations

Genotypes	CBSDS	CBSDRS	CMDS	CBSDI	CBSDRI	CMDI
Female						
01/1316	2.8	2.9	2.0	66.3	76.8	45.2
01/1569	2.5	3.0	2.5	55.8	74.1	64.4
Chamandanda	2.6	3.2	2.2	61.5	74.7	51.0
Depwete	2.3	2.7	2.9	55.4	62.1	69.6
Mulola	2.9	3.2	2.5	68.1	74.4	61.5
Silira	2.2	2.7	2.5	43.3	63.9	62.2
Mean	2.6	2.9	2.4	58.4	71.0	59.0
F-Prob.	0.004	0.13	<.0001	0.004	0.06	<.0001
Male						
Beatrice	3.0	2.8	2.9	63.7	74.1	73.4
Kachamba	2.7	2.6	3.4	62.2	58.3	89.4
Masoyabazungu	2.5	2.8	2.5	63.7	62.8	64.0
Mbundumali	2.7	3.5	2.1	65.0	82.3	44.6
Mkondezi	2.4	2.9	2.0	53.7	75.3	46.2
Phoso	2.0	3.1	1.8	42.3	73.2	36.3
Mean	2.6	2.9	2.4	58.4	71.0	59.0
F-Prob.	0.0002	0.005	<.0001	0.005	0.002	<.0001
CV%	23.2	24.3	13.7	33.6	25.1	21.5
SE±	0.1	0.2	0.1	4.6	4.2	2.9

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CBSDI = cassava brown streak disease incidence, CMDS = cassava mosaic disease severity, CMDI = cassava mosaic disease incidence.

Table 6.5. Mean performance of families for cassava brown streak disease and cassava mosaic disease across two locations

Family	CBSDS	CBSDRS	CMDS	CBSDI	CBSDRI	CMDI
01/1316 x Beatrice	3.0	2.2	2.3	48.7	75.7	57.9
01/1316 x Kachamba	2.7	2.4	3.1	55.2	56.0	80.0
01/1316 x Masoyabazungu	2.5	3.7	2.0	70.8	77.8	51.0
01/1316 x Mbundumali	3.2	3.2	2.0	88.4	81.2	37.4
01/1316 x Mkondezi	3.1	3.0	1.6	71.4	83.8	33.3
01/1316 x Phoso	2.4	2.7	1.2	63.3	86.1	11.4
01/1569 x Beatrice	2.9	3.0	3.3	85.2	76.7	83.0
01/1569 x Kachamba	2.8	2.5	2.9	57.0	52.3	75.5
01/1569 X Masoyabazungu	3.0	2.3	3.0	84.9	63.3	91.7
01/1569 x Mbundumali	2.4	3.9	1.4	34.2	95.2	19.4
01/1569 x Mkondezi	2.0	2.1	2.1	33.3	77.8	46.2
01/1569 x Phoso	2.0	3.9	2.4	40.5	79.4	70.8
Chamandanda x Beatrice	2.6	3.3	2.2	42.1	78.3	52.2
Chamandanda x Kachamba	3.1	2.2	3.4	70.8	54.0	88.0
Chamandanda x Masoyabazungu	2.4	3.0	2.4	63.3	59.6	64.5
Chamandanda x Mbundumali	3.2	3.4	2.2	95.2	81.9	48.6
Chamandanda x Mkondezi	1.9	3.6	1.5	43.4	83.6	33.3
Chamandanda x Phoso	2.3	3.4	1.2	54.2	90.5	19.6
Depwete x Beatrice	2.7	2.0	3.3	72.6	56.9	86.7
Depwete x Kachamba	2.0	2.3	3.9	66.7	58.5	100.0
Depwete x Masoyabazungu	2.0	2.7	2.7	54.2	61.9	64.1
Depwete x Mbundumali	2.3	3.6	2.7	50.3	73.0	68.3
Depwete x Mkondezi	3.2	3.0	2.9	66.7	70.4	79.2
Depwete x Phoso	1.7	2.5	1.5	22.2	51.9	19.4
Mulola x Beatrice	3.1	3.4	2.8	55.6	80.1	70.5
Mulola x Kachamba	3.3	3.1	3.6	70.7	69.4	96.3
Mulola x Masoyabazungu	3.0	3.0	2.8	80.0	63.2	76.7
Mulola x Mbundumali	3.5	3.6	1.8	64.3	86.3	32.4
Mulola x Mkondezi	2.6	3.0	2.4	82.2	77.1	61.1
Mulola x Phoso	1.8	3.0	1.7	55.6	70.2	31.7
Silira x Beatrice	3.4	2.6	3.5	77.8	76.9	90.0
Silira x Kachamba	2.5	2.7	3.4	52.8	59.7	96.7
Silira x Masoyabazungu	2.1	2.1	1.8	29.0	50.9	36.1
Silira x Mbundumali	1.8	3.2	2.3	57.5	75.9	61.6
Silira x Mkondezi	1.4	2.5	1.4	25.0	59.1	24.1
Silira x Phoso	1.9	3.0	2.5	17.9	61.1	64.8
Mean	2.6	2.9	2.4	58.4	71.0	59.0
F-Prob.	<0.001	0.21	<.0001	0.001	0.92	<.0001
CV	23.2	24.3	13.7	33.6	25.1	21.5
SE	0.3	0.41	0.19	11.34	10.28	7.32

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CBSDI = cassava brown streak disease incidence, CMDS = cassava mosaic disease severity, CMDI = cassava mosaic disease incidence.

6.3.4 Genetic variation and mode of gene action for early storage root bulking and agronomic traits associated with early bulking

In Chapter 3, early storage root bulking genotypes were identified and defined as those that are high yielding, have high HI as well as high early bulking index (EBI). Based on those results, early harvesting in Malawi was proposed at 9 MAP and traits directly associated with early storage root bulking were HI and biomass yield (Chipeta et al., 2016b).

Parents and families showed very significant (P<0.01) differences for FSRY, SRN, SRL, HI, SC, PHT and BMY. Significant (P<0.05) differences were observed for DSRY and DMC (Table 6.6). Pooled across two locations, the GCA_f was very significant (P<0.01) for FSRY, SRN, SRL, HI, BMY and significant (P<0.05) for DSRY, DMC, SC and PHT. The GCA_m was very significant (P<0.01) for FSRY, SRN, SRD, HI, DMC, SC, PHT and significant (P<0.05) for DSRY. The SCA effects showed significant (P<0.05) differences for SRN, SRL, HI and PHT. There were also very significant (P< 0.01) location main effects for FSRY and all other agronomic traits except for SRN and SRL. The GCA_f x location were very significant (P<0.01) for SRN, SRD, DMC, SC, PHT and BMY. The GCA_m x location effects were not significant for all the traits. The SCA x location interaction effects significantly affected SRN and SRL. The GCA (GCA_f +GCA_m) effects sum of squares accounted for more variance of the total variance than the female x male interaction (SCA) effects, except for DSRY and SRL where SCA contributed most. The GCA_m effects were larger than the GCA_f effects for all the traits, except for SRN, SRL and BMY (Table 6.6).

6.3.5 Mean performance of cassava genotypes for early storage root bulking and other agronomic traits associated with early bulking

Table 6.7 shows mean values for FSRY and other traits associated with FSRY for parents. The highest yielding parents were Mulola (11.1 t ha^{-1}) and Mbundumali (10.6 t ha^{-1}). The same genotypes that produced high FSRY, gave the highest DSRY, highest SRN and highest HI values. The mean performance of the families for FSRY ranged from 4.5 t ha^{-1} (Silira x Beatrice) to 13.5 t ha^{-1} (01/1569 x Mbundumali) (Table 6.8). The DSRY was also variable ranging from 2.3 t ha^{-1} for Silira x Beatrice to 5.5 t ha^{-1} for 01/1569 x Mkondezi. The highest SRN $plant^{-1}$ of 8.5 was obtained on 01/1569 x Mbundumali. In terms of HI, the highest value was exhibited by Silira x Mkondezi (0.61). The BMY varied from 5.9 t ha^{-1} (Silira x Kachamba) to 13.8 t ha^{-1} (01/1569 x Mbundumali).

Table 6.6. Mean squares for storage root yield and other agronomic traits across two locations

Source	DF	FSRY	DSRY	SRN	SRL	SRD	HI	SC	DMC	PHT	BMY
Location	1	269.89**	162.30**	8.41	3.21	10.85**	0.72**	1393.04**	2780.72**	24989.16**	71.3**
Rep(location)	4	110.16	27.52	22.68	110.19	0.86	0.02	146.79	293.39	1093.03	64.76
Genotypes	47	33.04**	5.52**	8.97**	57.33**	0.89**	0.02**	109.45**	218.05**	1171.82**	16.60**
Parents (P)	11	36.68**	3.07*	8.56**	51.23*	1.26**	0.04**	122.37**	243.32**	1762.63**	11.21*
P vs C	1	67.11	80.91**	41.08**	1150.01**	14.81**	0.01	1944.00**	3874.77**	12156.75**	138.48**
Crosses (C)	35	30.92**	4.13*	8.19**	28.02**	0.37*	0.02**	52.98**	105.63*	672.28**	14.80**
GCA_f	5	58.92**	6.78*	18.69**	75.79**	0.45	0.03**	92.05*	183.89*	648.21*	30.38**
GCA_m	5	72.74**	7.32*	16.43**	20.35	0.91**	0.05**	144.43**	288.76**	1843.35**	27.87**
SCA	25	16.96	2.96	4.44*	20.01*	0.25	0.01*	26.88	53.35	442.88*	9.07
GCA_f x location	5	29.75	3.47	15.28**	48.75**	0.65**	0.01	122.08**	242.37**	1543.63**	43.10**
GCA_m x location	5	19.98	4.04	4.23	5.19	0.12	0.003	49.21	97.67	458.8	5.57
SCA x location	25	13.79	2.62	5.12**	23.36*	0.25	0.01	31.25	62.41	130.52	7.47
Error	140	15.15	2.51	2.5	14.4	0.23	0.01	33.53	66.87	229.48	6.18
%SS GCA_f		27.2	23.4	32.6	38.6	17.5	24.1	24.8	24.9	13.8	29.3
%SS GCA_m		33.6	25.3	28.7	10.4	35.0	34.9	38.9	39.1	39.2	26.9
%SS SCA		39.2	51.3	38.7	51.0	47.5	40.9	36.2	36.1	47.1	43.8
GCA/SCA		7.8	4.8	7.9	4.8	5.44	8.0	8.8	8.9	5.6	6.4

FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = Storage root number $plant^{-1}$, SRL = storage root length (cm), SRD = storage root diameter (cm), HI = harvest index, SC = starch content (%), DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}), DF = degrees of freedom, GCA_f = general combining ability for female, GCA_m = general combining ability for male, SCA = specific combining ability, SS = sum of squares, *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

Table 6.7. Mean performance of parental genotypes (females and males) for storage root yield and other agronomic traits across two locations

Genotype	FSRY	DSRY	SRN	SRL	SRD	HI	SC	DMC	PHT	BM
Female										
01/1316	9.0	4.1	6.2	23.6	3.0	0.47	26.5	45.7	117.5	7.9
01/1569	9.9	4.2	6.7	25.2	3.1	0.48	25.8	44.7	123.2	9.8
Chamandanda	8.1	3.8	5.1	22.2	3.1	0.44	28.1	48.0	124.3	8.7
Depwete	7.5	3.4	6.2	21.5	2.9	0.45	28.7	48.8	112.5	8.2
Mulola	11.1	4.7	7.3	24.4	3.2	0.52	24.3	42.5	118.8	8.8
Silira	8.5	3.9	6.3	22.2	3.0	0.51	26.9	46.3	118.8	7.0
Mean	9.0	4.0	6.3	23.2	3.0	0.48	26.7	46.0	119.2	8.4
F-Prob.	0.003	0.03	<.0001	<.0001	0.06	0.0002	0.017	0.017	0.025	0.002
Male										
Beatrice	7.0	3.3	5.2	22.0	2.8	0.41	29.1	49.3	121.5	8.0
Kachamba	7.6	3.7	6.1	22.9	2.9	0.47	29.1	49.3	111.3	7.2
Masoyabazungu	9.1	4.0	6.4	23.0	3.0	0.49	26.9	46.3	115.4	8.5
Mbundumali	10.6	4.5	7.0	24.2	3.1	0.48	25.6	44.4	131.5	9.9
Mkondezi	10.1	4.4	6.3	23.1	3.2	0.52	25.4	44.1	114.7	8.2
Phoso	9.8	4.1	6.9	23.7	3.2	0.51	24.3	42.6	120.7	8.6
Mean	9.0	4.0	6.3	23.2	3.0	0.48	26.7	46.0	119.2	8.4
F-Prob.	0.001	0.024	<.0001	0.118	0.001	<.0001	0.001	0.001	<.0001	0.004
CV	43.3	41.2	25.4	14.5	15.1	17.3	21.2	17.3	13.1	33.0
SE	0.7	0.3	0.3	0.6	0.1	0.01	0.9	1.3	2.6	0.5

FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm), SRD = storage root diameter (cm), HI = harvest index, SC = starch content (%), DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}).

Table 6.8. Mean performance of families for storage root yield and other agronomic traits across two locations

Crosses	FSRY	DSRY	SRN	SRL	SRD	HI	SC	DMC	PHT	BMY
1x7	8.8	4.2	5.0	24.5	2.9	0.43	29.1	49.4	131.2	8.8
1x8	10.0	4.8	6.7	23.3	3.1	0.51	27.0	46.3	118.7	7.5
1x9	8.5	3.4	6.0	22.8	2.8	0.47	25.9	44.9	98.1	7.2
1x10	9.2	4.2	6.5	23.9	3.1	0.48	26.5	45.7	124.0	8.3
1x11	7.9	3.7	5.1	22.6	3.1	0.43	27.4	46.9	117.7	7.3
1x12	9.8	4.1	8.2	24.2	3.2	0.51	23.2	41.1	115.4	8.4
2x7	6.9	3.3	5.1	24.0	3.0	0.45	30.6	51.5	121.6	7.1
2x8	6.6	3.3	5.9	22.3	2.9	0.43	30.6	51.4	106.4	8.2
2x9	9.9	4.1	6.4	23.5	3.1	0.49	23.8	41.8	116.3	10.2
2x10	13.5	5.3	8.5	29.7	3.4	0.48	23.0	40.7	143.9	13.8
2x11	11.4	5.5	6.4	23.9	3.0	0.52	26.7	46.0	123.9	9.7
2x12	11.0	4.0	8.1	27.9	3.0	0.54	20.3	36.9	127.3	9.7
3x7	7.0	3.4	4.5	22.9	2.9	0.41	29.4	49.8	121.2	8.1
3x8	7.5	3.9	5.4	22.8	3.1	0.49	30.9	51.8	114.6	6.5
3x9	7.2	3.5	5.9	20.5	2.9	0.41	30.6	51.5	118.2	8.7
3x10	7.9	3.4	4.9	22.0	2.9	0.43	27.0	46.4	137.3	8.8
3x11	10.2	4.6	4.8	23.2	3.4	0.49	26.1	45.2	115.1	8.9
3x12	9.0	3.7	5.3	21.8	3.3	0.42	24.8	43.3	139.2	11.0
4x7	5.6	2.5	4.7	20.5	2.6	0.37	30.4	51.2	113.2	8.4
4x8	5.2	2.8	6.4	20.3	2.4	0.36	31.8	53.2	105.5	7.2
4x9	6.7	3.1	5.5	20.2	2.9	0.47	28.6	48.6	102.3	7.0
4x10	8.2	3.6	7.9	21.7	3.0	0.44	26.8	46.1	130.2	10.1
4x11	7.6	3.5	6.0	22.1	2.8	0.53	26.6	45.8	114.6	7.1
4x12	11.9	5.1	7.0	24.1	3.5	0.56	28.0	47.9	109.1	9.2
5x7	9.3	4.0	6.7	21.1	2.8	0.45	25.9	44.8	120.7	8.3
5x8	9.2	4.2	5.9	25.4	3.2	0.50	27.0	46.4	114.6	7.8
5x9	12.9	5.2	8.2	26.9	3.4	0.54	22.2	39.6	127.1	10.0
5x10	12.9	5.2	7.1	24.9	3.3	0.55	22.0	39.2	125.4	9.6
5x11	13.2	5.3	8.5	25.6	3.5	0.54	23.1	40.8	115.4	10.1
5x12	9.0	4.2	7.6	22.6	3.0	0.53	25.6	44.4	109.8	6.7
6x7	4.5	2.3	5.1	19.2	2.7	0.38	29.2	49.5	121.2	7.4
6x8	7.3	3.5	6.1	23.5	2.8	0.52	27.3	46.7	108.2	5.9
6x9	9.4	4.7	6.7	24.2	3.1	0.56	30.5	51.3	130.2	7.7
6x10	11.6	5.4	7.4	23.2	3.0	0.52	28.3	48.2	128.1	8.5
6x11	10.5	3.9	7.2	21.4	3.2	0.61	22.5	40.0	101.3	6.0
6x12	7.9	3.5	5.4	21.9	3.1	0.50	24.0	42.1	123.5	6.9
Mean	9.0	4.0	6.3	23.2	3.0	0.48	26.7	46.0	119.2	8.4
F-Prob.	0.34	0.36	0.03	0.02	0.28	0.02	0.69	0.69	0.02	0.27
CV	43.3	41.2	25.4	14.5	15.1	17.3	21.2	17.3	13.09	33.0
SE	1.59	0.67	0.66	1.37	0.19	0.03	2.31	3.26	6.37	1.13

1 = 01/1316, 2 = 01/1569, 3 = Chamandanda, 4 = Depwete, 5 = Mulola, 6 = Silira, 7 = Beatrice, 8 = Kachamba, 9 = Masoyabazungu, 10 = Mbundumali, 11 = Mkondezi, 12 = Phoso, FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm), SRD = storage root diameter (cm), HI = harvest index, SC = starch content (%), DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}).

6.3.6 General combining ability effects for resistance to cassava brown streak disease and cassava mosaic disease

The GCA effects were computed to show both the magnitude and direction of the genetic effects. GCA effects for CBSDS showed that six parents (3 females and 3 males) had desirable negative values (Table 6.9). The two best general combiners were Phoso (-0.53) and Silira (-0.38) which exhibited significant negative values. In terms of CBSDRS, three females and four males displayed desirable GCA effects. Kachamba was the best general combiner which had a significant negative value (-0.37) followed by Silira (-0.25), Depwete (-0.24), Beatrice (-0.17), Masoyabazungu (-0.13), 01/1316 (-0.05) and Mkondezi (-0.04). For CBSDI, Phoso (-16.13) and Silira (-15.09) were the most desirable general combiners with significant negative values. The CBSDRI revealed that four parents had desirable negative GCA effects but only three parents exhibited significant negative GCA effects. These were Kachamba (-12.67), Depwete (-8.89) and Masoyabazungu.

Five parents namely, 01/1316, Chamandanda, Mkondezi, Mbundumali and Phoso exhibited significant negative GCA effects for CMDS (Table 6.9). The overall best general combiner which contributed the most to resistance was Phoso (-0.67) followed by Mkondezi (-0.43). In terms of CMDI, the same genotypes that showed desirable GCA effects for CMDS showed significant desirable negative values and the best combiner was Phoso (-22.69).

6.3.7 Specific combining ability effects for resistance to cassava brown streak disease and cassava mosaic disease

The CBSDS displayed various degrees of SCA effects (Table 6.10). Twenty one families had non-significant but desirable SCA effects and the best two families were Silira x Mkondezi (-0.60) and Silira x Mbundumali (-0.56). The CBSDRS SCA effects were variable from significant to non-significant, and positive to negative (Table 6.10). Nineteen families exhibited negative SCA effects while all were non-significant but the most desirable families were 01/1569 x Mkondezi (-0.78), Chamandanda x Kachamba (-0.59) and 01/1569 x Masoyabazungu (-0.55). The highest significantly negative and desirable SCA effects for CBSDI were recorded for 01/1569 x Mbundumali (-28.24), Chamandanda x Beatrice (-24.64) and 0/1316 x Masoyabazungu (-22.87), but overall, 18 crosses displayed desirable SCA effects (Table 6.10). For CBSDRI, 52.8% of the families (19 families) had desirable non-significant SCA effects and Depwete x Phoso was singled out to be the most desirable combination (-12.43).

Seven families exhibited significant and desirable SCA effects for CMDS, and the best three combinations were 0/1569 x Mbundumali (-0.75), Silira x Masoyabazungu (-0.68) and Silira x Mkondezi (-0.66). Overall, 16 families displayed desirable SCA effects. In terms of CMDS, families that displayed desirable SCA effects for CMDS were also found to be the most desirable ones for CMDI with significant negative SCA effects and these included Silira x Masoyabazungu (-31.13), 01/1569 x Mbundumali (-30.65) and Depwete x Phoso (-27.49) (Table 6.10).

Table 6.9. General combining ability effects for cassava brown streak disease and cassava mosaic disease across two locations

Genotype	CBSDS	CBSDRS	CMDS	CBSDI	CBSDRI	CMDI
Female						
01/1316	0.27*	-0.05	-0.39**	7.91	5.76	-13.82**
01/1569	-0.03	0.03	0.09	-2.57	3.13	5.45
Chamandanda	0.03	0.23	-0.27**	3.11	3.66	-7.96**
Depwete	-0.22	-0.24	0.42**	-2.98	-8.89*	10.63**
Mulola	0.33*	0.27	0.08	9.63*	3.40	2.47
Silira	-0.38**	-0.25	0.06	-15.09**	-7.05	3.23
Male						
Beatrice	0.41**	-0.17	0.49**	5.25	3.11	14.38**
Kachamba	0.18	-0.37*	0.97**	3.78	-12.67**	30.42**
Masoyabazungu	-0.05	-0.13	0.02	5.28	-8.21*	5.02
Mbundumali	0.19	0.55**	-0.37**	6.56	11.26**	-14.34**
Mkondezi	-0.20	-0.04	-0.43**	-4.74	4.32	-12.79**
Phoso	-0.53**	0.16	-0.67**	-16.13**	2.20	-22.69**
SE± $_{(GCA)}$	**0.14**	**0.17**	**0.08**	**4.63**	**4.20**	**12.67**

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CBSDI = cassava brown streak disease incidence on foliage, CBSDRI = cassava brown streak disease storage roots incidence, CMDS = cassava mosaic disease severity, CMDI = cassava mosaic disease incidence, *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

Table 6.10. Specific combining ability effects for cassava brown streak disease and cassava mosaic disease across two locations

Family	CBSDS	CBSDRS	CMDS	CBSDI	CBSDRI	CMDI
01/1316 x Beatrice	-0.20	-0.50	-0.26	-22.87*	-4.19	-1.68
01/1316 x Kachamba	-0.27	-0.07	0.09	-14.91	-8.11	4.42
01/1316 x Masoyabazungu	-0.27	0.96*	-0.06	-0.77	9.23	0.78
01/1316 x Mbundumali	0.19	-0.26	0.30	15.55	-6.81	6.58
01/1316 x Mkondezi	0.45	0.20	0.03	9.85	2.73	0.96
01/1316 x Phoso	0.11	-0.33	-0.13	13.14	7.15	-11.04
01/1569 x Beatrice	-0.06	0.21	0.29	24.10*	-0.50	4.16
01/1569 x Kachamba	0.07	-0.09	-0.62**	-2.63	-9.16	-19.38**
01/1569 X Masoyabazungu	0.57	-0.55	0.43*	23.78*	-2.58	22.22**
01/1569 x Mbundumali	-0.27	0.43	-0.75**	-28.24*	9.85	-30.65**
01/1569 x Mkondezi	-0.28	-0.78	0.05	-17.77	-0.65	-5.44
01/1569 x Phoso	-0.02	0.78	0.59**	0.75	3.04	29.10**
Chamandanda x Beatrice	-0.39	0.35	-0.41*	-24.64*	0.58	-13.17
Chamandanda x Kachamba	0.33	-0.59	0.31	5.53	-8.01	6.52
Chamandanda x Masoyabazungu	-0.13	-0.02	0.22	-3.47	-6.81	8.42
Chamandanda x Mbundumali	0.46	-0.31	0.41*	27.15*	-4.01	11.92
Chamandanda x Mkondezi	-0.52	0.48	-0.19	-13.41	4.63	-4.93
Chamandanda x Phoso	0.25	0.08	-0.32	8.84	13.62	-8.77
Depwete x Beatrice	-0.04	-0.48	0.00	11.92	-8.31	2.67
Depwete x Kachamba	-0.51	0.02	0.12	7.45	9.10	-0.03
Depwete x Masoyabazungu	-0.24	0.12	-0.17	-6.55	8.01	-10.54
Depwete x Mbundumali	-0.22	0.33	0.22	-11.73	-0.40	13.06
Depwete x Mkondezi	1.07**	0.36	0.48**	15.98	3.98	22.34**
Depwete x Phoso	-0.06	-0.34	-0.64**	-17.07	-12.43	-27.49**
Mulola x Beatrice	-0.16	0.37	-0.17	-17.73	2.60	-5.36
Mulola x Kachamba	0.24	0.31	0.12	-1.13	7.71	4.43
Mulola x Masoyabazungu	0.14	-0.06	0.27	6.64	-3.02	10.26
Mulola x Mbundumali	0.40	-0.11	-0.37*	-10.34	0.65	-14.68*
Mulola x Mkondezi	-0.11	-0.12	0.29	18.93	-1.58	12.44
Mulola x Phoso	-0.52	-0.39	-0.14	13.01	-6.36	-7.09
Silira x Beatrice	0.82*	0.06	0.49**	29.22**	9.82	13.41
Silira x Kachamba	0.15	0.39	-0.03	5.69	8.46	4.04
Silira x Masoyabazungu	-0.05	-0.44	-0.68**	-19.64	-4.83	-31.33**
Silira x Mbundumali	-0.56	-0.06	0.21	7.61	0.73	13.76
Silira x Mkondezi	-0.60	-0.14	-0.66**	-13.58	-9.13	-25.35**
Silira x Phoso	0.26	0.20	0.65**	-9.33	-5.04	25.28**
SE±	**0.34**	**0.41**	**0.19**	**11.33**	**10.28**	**7.32**

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CBSDI = cassava brown streak disease incidence on foliage, CBSDRI = cassava brown streak disease storage roots incidence, CMDS = cassava mosaic disease severity, CMDI = cassava mosaic disease incidence, *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

6.3.8 General combining ability effects for early storage root bulking and agronomic traits associated with early bulking

Table 6.11 shows GCA values for FSRY and other agronomic traits. High FSRY was mainly influenced by two female and four male parents. The overall best combiner with significant positive GCA effect was Mulola (2.04), followed by Mbundumali (1.53). In terms of DSRY, Mulola (0.69) was rated as the overall best combiner as it displayed a significant positive effect. Other good combiners, though not significant, were Mbundumali (0.51), 01/1569 (0.22) and 01/1316 (0.05). Mulola (1.01), Mbundumali (0.73) and Phoso (0.63) significantly contributed to SRN. Five parents (3 females and 2 males) revealed positive GCA values for SRL but the best general combiners with significant positive effects were 01/1569 (2.02) and Mulola (1.23).

Equal numbers of female (3) and male (3) parents were desirable good parents for SRD. However, three parents Phoso (0.16), Mulola (0.16) and Mkondezi (0.15) gave significant GCA values. In terms of HI, seven parents (3 female and 4 males) showed desirable GCA effects. Significant values were observed on parents Mulola (0.04) and Silira (0.03), Mkondezi (0.04) and Phoso (0.03). Desirable SC GCA effects were generated by three female parents (Depwete = 1.97, Chamandanda = 1.41 and Silira = 0.21) and three male parents (Beatrice = 2.36, Kachamba = 2.35 and Masoyabazungu = 0.19). Six parents exhibited desirable GCA effects for DMC, One female (Depwete = 2.79) and two males (Beatrice = 3.34 and Kachamba = 3.32) registered significant positive effects. In terms of PHT, seven genotypes contributed towards short plants and five towards tall plants. Most significant positive contributors to short plants were parents Depwete (-6.69) and Kachamba (-7.87). On the other hand, tall PHT was significantly contributed by parents Chamandanda (5.09) and Mbundumali (12.30). High BMY was significantly contributed by parents 01/1569 (1.39) and Mbundumali (1.46). Other desirable GCAs were recorded on parents Mulola (0.37), Chamandanda (0.28), Phoso (0.26) and Masoyabazungu (0.08).

6.3.9 Specific combining ability effects for early storage root bulking and agronomic traits associated with early bulking

The SCA effects for these traits have been presented in Table 6.12. For FSRY, 20 families exhibited desirable SCA effects, but was only significant for one family (Depwete x Phoso = 3.65) and this was followed by 01/1316 x Kachamba (2.37). Twelve families had a desirable positive effect for DSRY but only one was significant (Depwete x Phoso = 1.55). Significant and

positive SCA effects were recorded for two families for SRN. These were 01/1316 x Phoso (1.32) and Silira x Mkondezi (1.78). However, a total of 18 families had a positive SCA effects for SRN. In terms of SRL, 15 families had a positive SCA effect, but only two were significant (Mulola x Masoyabazungu = 2.66 and 01/1569 x Mbundumali = 3.45) and one cross generated significant negative SCA effects (01/1569 x Kachamba = -2.66).

One family (Depwete x Phoso) exhibited a significant positive SCA effect (0.50) for SRD. Twenty two families had a positive SCA effect for the HI, but only one cross (Depwete x Phoso) gave significant SCA value (0.08) for HI. No family had a significant SCA effect for SC. Among those with a positive directional effect, Mulola x Phoso (3.74) was the most desirable combination. None of the families had a significant SCA for the DMC. However, family Mulola x Phoso (5.27) registered the best SCA effect. Four families registered a significant SCA effect for PHT (2 positive and 2 negative). Family Silira x Masoyabazungu (15.26) was the most desirable combination for plant height followed by Chamandanda x Phoso (13.43). Eighteen families had desirable SCA effects for BMY, but only one SCA effect was significant (01/1569 x Mbundumali = 2.52).

Table 6.11. General combining ability effects for storage root yield and other agronomic traits across two locations

Genotype	FSRY	DSRY	SRN	SRL	SRD	HI	SC	DMC	PHT	BMY
Female										
01/1316	-0.01	0.05	-0.07	0.38	-0.01	-0.01	-0.21	-0.31	-1.67	-0.47
01/1569	0.86	0.22	0.43	2.02**	0.02	0.00	-0.92	-1.30	4.04	1.39**
Chamandanda	-0.90	-0.25	-1.17**	-0.97	0.06	-0.04**	1.41	1.98	5.09*	0.28
Depwete	-1.48*	-0.57*	-0.06	-1.71**	-0.18*	-0.03	1.97**	2.79*	-6.69**	-0.22
Mulola	2.04**	0.69**	1.01**	1.23*	0.16*	0.04**	-2.45**	-3.46**	-0.35	0.37
Silira	-0.50	-0.14	0.00	-0.95	-0.04	0.03*	0.21	0.29	-0.42	-1.34**
Male										
Beatrice	-2.01**	-0.73**	-1.13**	-1.15*	-0.23**	-0.07**	2.36**	3.34**	2.35	-0.37
Kachamba	-1.41*	-0.26	-0.25	-0.24	-0.14	-0.01	2.35**	3.32**	-7.87**	-1.22**
Masoyabazungu	0.08	0.00	0.14	-0.17	-0.02	0.01	0.19	0.28	-3.81	0.08
Mbundumali	1.53*	0.51	0.73**	1.05	0.08	0.00	-1.14	-1.63	12.30**	1.46**
Mkondezi	1.07	0.39	0.02	-0.05	0.15*	0.04**	-1.35	-1.90	-4.51	-0.21
Phoso	0.74	0.08	0.63*	0.56	0.16*	0.03*	-2.41**	-3.41**	1.55	0.26
SE± $_{(GCA)}$	**0.65**	**0.26**	**0.27**	**0.56**	**0.08**	**0.01**	**0.94**	**1.33**	**2.60**	**0.46**

FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = storage root number plant^{-1}, SRL = storage root length (cm), SRD = storage root diameter (cm), HI = harvest index, SC = starch content (%), DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}), *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

Table 6.12. Specific combining ability effects for storage root yield and other agronomic traits across two locations

Crosses	FSRY	DSRY	SRN	SRL	SRD	HI	SC	DMC	PHT	BMY
1x7	1.76	0.83	-0.12	2.04	0.09	0.02	0.25	0.35	11.35	1.24
1x8	2.37	0.98	0.65	-0.02	0.17	0.05	-1.90	-2.68	9.05	0.77
1x9	-0.58	-0.62	-0.41	-0.56	-0.23	-0.01	-0.80	-1.13	-15.58*	-0.76
1x10	-1.33	-0.39	-0.50	-0.67	0.04	0.01	1.14	1.60	-5.86	-1.11
1x11	-2.24	-0.74	-1.22	-0.89	-0.07	-0.08*	2.19	3.06	4.68	-0.37
1x12	0.01	-0.05	1.32*	0.11	0.00	0.01	-0.88	-1.20	-3.64	0.23
2x7	-0.97	-0.25	-0.54	-0.08	0.13	0.03	2.44	3.41	-3.96	-2.29*
2x8	-1.85	-0.66	-0.59	-2.66*	-0.03	-0.04	2.42	3.41	-8.96	-0.33
2x9	-0.04	-0.18	-0.46	-1.54	0.05	0.00	-2.24	-3.15	-3.13	0.34
2x10	2.04	0.55	0.98	3.45**	0.24	0.00	-1.72	-2.41	8.37	2.52*
2x11	0.41	0.87	-0.39	-1.30	-0.17	-0.01	2.22	3.15	5.19	0.08
2x12	0.41	-0.33	0.74	2.12	-0.23	0.02	-3.12	-4.41	2.49	-0.32
3x7	0.91	0.41	0.51	1.85	0.06	0.03	-1.10	-1.55	-5.46	-0.19
3x8	0.74	0.44	0.50	0.83	0.12	0.06	0.38	0.54	-1.81	-1.00
3x9	-1.03	-0.22	0.58	-1.53	-0.18	-0.04	2.28	3.21	-2.23	-0.01
3x10	-1.77	-0.91	-0.95	-1.26	-0.23	-0.01	0.03	0.05	0.76	-1.31
3x11	0.96	0.41	-0.39	1.07	0.18	0.01	-0.66	-0.93	-4.68	0.46
3x12	0.15	-0.13	-0.53	-0.96	0.07	-0.04	-0.93	-1.32	13.43*	2.05
4x7	0.11	-0.18	-0.46	0.20	-0.07	-0.02	-0.67	-0.93	-1.61	0.56
4x8	-0.94	-0.43	0.39	-0.89	-0.33	-0.08*	0.75	1.06	0.84	0.27
4x9	-0.93	-0.30	-0.88	-1.12	0.07	0.00	-0.35	-0.49	-6.37	-1.26
4x10	-0.87	-0.31	0.89	-0.86	0.02	-0.02	-0.73	-1.05	5.42	0.49
4x11	-1.03	-0.33	-0.26	0.64	-0.18	0.04	-0.76	-1.06	6.65	-0.82
4x12	3.65*	1.55*	0.06	2.04	0.50**	0.08*	1.74	2.48	-4.91	0.78
5x7	0.20	0.06	0.46	-2.17	-0.13	0.00	-0.80	-1.11	-0.45	-0.05
5x8	-0.50	-1.57*	-1.22	1.20	0.13	0.00	0.38	0.56	3.61	0.28
5x9	1.78	-0.85	0.69	2.66*	0.18	0.01	-2.28	-3.21	12.06	1.17
5x10	0.33	-1.34*	-1.00	-0.59	-0.02	0.03	-1.19	-1.68	-5.71	-0.62
5x11	1.02	-1.14	1.16	1.28	0.16	-0.02	0.14	0.18	1.09	1.51
5x12	-2.82	0.28	-0.36	-2.37	-0.32	-0.02	3.74	5.27	-10.60	-2.29*
6x7	-2.02	-0.87	0.83	-1.84	-0.08	-0.07*	-0.12	-0.16	0.14	0.73
6x8	0.16	-0.11	0.95	1.55	-0.05	0.02	-2.04	-2.89	-2.73	0.02
6x9	0.80	0.82	1.16	2.09	0.12	0.04	3.38	4.76	15.26*	0.52
6x10	1.59	1.06	1.25	-0.09	-0.05	0.00	2.47	3.50	-2.98	0.02
6x11	0.88	-0.41	1.78**	-0.79	0.08	0.06	-3.13	-4.40	-12.92*	-0.85
6x12	-1.41	-0.48	-0.56	-0.92	-0.02	-0.05	-0.56	-0.81	3.24	-0.44
SE± (SCA)	**1.59**	**0.67**	**0.66**	**1.37**	**0.19**	**0.03**	**2.31**	**3.26**	**6.37**	**1.13**

1 = 01/1316, 2 = 01/1569, 3 = Chamandanda, 4 = Depwete, 5 = Mulola, 6 = Silira, 7 = Beatrice, 8 = Kachamba, 9 = Masoyabazungu, 10 = Mbundumali, 11 = Mkondezi, 12 = Phoso, FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm), SRD = storage root diameter (cm), HI = harvest index, SC = starch content (%), DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}), *, ** = significant at 0.05 and 0.01 levels of probability, respectively.

6.3.10 Genetic components for cassava brown streak disease and cassava mosaic disease resistance

The within family (δ^2w) variation was larger than the between (δ^2b) family variation for CBSDS, CBSDRS and CMDS (Table 6.13). The GCA variance (δ^2GCA) for CBSDS was larger than the SCA variance (δ^2SCA). For CMDS, δ^2GCA was greater than δ^2SCA. In terms of additive (δ^2A) and dominance (δ^2D) variance, CBSDS generated higher δ^2A value than δ^2D value. The CMDS δ^2A values were larger than the δ^2D values. The ratio of additive (δ^2A) variance to the total genetic variance ($\delta^2A + \delta^2D$), known as the genetic ratio (GR), was less than 1 for both CBSDS and CMDS. Heritability values both narrow (h^2) and broad (H^2) sense were generally high for both CBSDS and CMDS.

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Table 6.13. Genetic components heritability values for cassava brown streak disease and cassava mosaic disease across two locations

Genetic component	CBSDS	CBSDRS	CMDS
δ^2G_b family	0.25	0.11	0.50
δ^2G_w family	0.35	0.52	1.07
δ^2GCA	0.09	0.04	0.20
δ^2SCA	0.04	0.05	0.08
δ^2A	0.28	0.16	0.80
δ^2D	0.17	0.19	0.33
δ^2e	0.21	0.51	0.06
GR	0.62	0.46	0.71
h^2	54.00	31.00	70.00
H^2	86.00	75.00	98.00

CBSDS = cassava brown streak disease severity on foliage, CBSDRS = cassava brown streak disease storage roots severity, CMDS = cassava mosaic disease severity, δ^2G_b = genetic variation between families, δ^2G_w = genetic variation within families, δ^2GCA = General combining ability variance, δ^2SCA = specific combining ability variance, δ^2A = additive variance, δ^2D = dominance variance, δ^2e = error variance, GR = genetic ratio, h^2 = narrow sense heritability (%), H^2 = broad sense heritability (%).

6.3.11 Genetic components for early storage root bulking and agronomic traits associated with early bulking

In terms of FSRY and all other agronomic traits, the analysis revealed a larger within family (δ^2w) variation than the between family variation (δ^2b), except for DSRY which exhibited a larger between family variation than the within family variation (Table 6.14). The δ^2GCA for FSRY and all other traits, except SRL and PHT, were generally higher than the δ^2SCA. The additive (δ^2A) and dominance (δ^2D) variance are direct derivatives of δ^2GCA and δ^2SCA, respectively, and δ^2A was, therefore, greater than δ^2D for all the traits where δ^2GCA was greater than δ^2SCA. The ratio of additive (δ^2A) variance to the total genetic variance ($\delta^2A + \delta^2D$) was less than 1 for all the traits except DMC. The narrow sense heritability (h^2) values ranged from 29% (SRL) to 60% (FSRY) and the broad sense heritability (H^2) values ranged from 57% (DSRY) to 86% (HI and SRN).

Table 6.14. Genetic components and heritability values for storage root yield and other agronomic traits across two locations

Genetic components	FSRY	DSRY	SRN	SRL	SRD	DMC	HI	PHT	BMY
δ^2G_b family	3.89	0.40	0.71	2.37	0.04	7.50	0.003	80.00	1.25
δ^2G_w family	5.88	0.33	1.64	4.26	0.07	9.50	0.005	247.00	2.85
δ^2GCA	2.71	0.23	0.73	1.56	0.02	10.16	0.002	44.61	1.11
δ^2SCA	0.58	0.08	0.62	2.89	0.01	0.00	0.002	66.45	0.46
δ^2A	10.86	0.91	2.92	6.24	0.10	40.66	0.007	178.42	4.46
δ^2D	2.30	0.32	2.46	11.57	0.05	0.00	0.007	265.80	1.85
δ^2e	15.23	2.72	2.59	11.33	0.21	63.87	0.007	243.53	7.68
GR	0.83	0.74	0.54	0.35	0.67	1.00	0.50	0.40	0.71
h^2	60.00	42.00	47.00	29.00	45.00	66.00	43.00	34.00	50.00
H^2	72.00	57.00	86.00	82.00	67.00	66.00	86.00	85.00	71.00

FSRY = fresh storage root yield (t ha^{-1}), DSRY = dry storage root yield (t ha^{-1}), SRN = storage root number $plant^{-1}$, SRL = storage root length (cm), SRD = storage root diameter (cm), HI=Harvest index, DMC = dry mass content (%), PHT = plant height (cm), BMY = biomass yield (t ha^{-1}), δ^2G_b = genetic variation between families, δ^2G_w = genetic variation within families, δ^2GCA = general combining ability variance, δ^2SCA = specific combining ability variance, δ^2A = additive variance, δ^2D = dominance variance, δ^2e = error variance, GR= genetic ratio, h^2 = narrow sense heritability (%), H^2 = broad sense heritability (%).

6.3.12 F1 genotypes selected for further evaluation

The twelve best families were identified on the basis of significant mean values and significant SCA effects. Only five of these families produced desirable progenies (10) with low mean values for CBSDS, CBSDRS and CMDS (≤ 2) and a high FSRY (≥ 10 t ha^{-1}). A total of 13 progenies (Table 6.15) were selected and the additional three progenies were derived from families that were not necessarily the best for the traits of interest. All the selected progenies (except two for CBSDS) exhibited a high parent heterosis for CBSDS, CBSDRS, CMDS and FSRY.

Table 6.15. Selected genotypes with their mean values for cassava brown streak disease, cassava mosaic disease and fresh storage root yield

Genotype	Family	CBSDS		CBSDRS		CMDS		FSRY	
		Mean	HPH	Mean	HPH	Mean	HPH	Mean	HPH
BC14/030	1 x 11	1.0	-60.0	1.5	-42.3	1.0	-16.7	12.0	79.1
BC14/132	5 x 12	1.0	-33.3	1.0	-66.7	1.0	-47.4	10.8	-0.9
BC14/139	5 x 12	1.7	11.1	2.0	-33.3	1.3	-29.8	12.9	18.7
BC14/176	5 x 7	1.7	-42.5	2.0	-25.9	1.0	-61.5	17.7	61.9
BC14/206	2 x 11	2.0	-20.0	1.5	-42.3	1.0	0.0	11.6	31.3
BC14/266	6 x 11	1.0	-52.4	2.0	-9.1	1.0	-33.3	13.1	59.8
BC14/270	6 x 11	1.0	-52.4	2.0	-9.1	1.0	-33.3	15.6	89.6
BC14/271	6 x 9	1.7	-20.6	1.3	-39.4	1.7	-1.9	15.3	32.2
BC14/273	6 x 9	1.0	-52.4	1.3	-39.4	1.0	-41.2	13.5	16.4
BC14/277	6 x 9	2.0	-4.8	1.0	-54.5	1.0	-41.2	25.4	119.0
BC14/305	4 x 10	1.0	-61.5	1.0	-69.7	1.3	-57.0	14.4	45.5
BC14/314	4 x 12	2.0	33.3	1.0	-66.7	1.0	-47.4	29.6	199.0
BC14/319	4 x 12	1.0	-33.3	1.0	-66.7	2.0	5.3	28.0	182.8

1 = 01/1316, 2 = 01/1569, 4 = Depwete, 5 = Mulola, 6= Silira, 7 = Beatrice, 9 = Masoyabazungu, 10 = Mbundumali, 11 = Mkondezi, 12 = Phoso, CBSDS = cassava brown streak disease shoot severity, CBSDRS = cassava brown streak disease storage root severity, CMDS = cassava mosaic disease severity, FSRY = fresh storage root yield (t ha^{-1}), HPH = high parent heterosis (%).

6.4 Discussion

6.4.1 Genetic variation and mode of gene action for resistance to cassava brown streak disease and cassava mosaic disease

One of the most essential steps in any crop improvement program is the selection of parents to produce a new generation of segregating progenies. This can only be done if there is substantial variation in the breeding material to initiate a breeding program.

Significant location main effects, GCA_f x location, GCA_m x location and SCA x location interaction effects for both CBSD and CMD, indicated the importance of the environment and the genotype x environment interaction (GEI) effects for these traits. These significant interactions, suggested that the expression of both additive and non-additive genes for the control of CBSD and CMD resistance were not stable across the two locations. The GEI in cassava is very common (Chipeta et al., 2016b; Lokko et al., 2006; Ojulong, 2006; Tumuhimbise, 2013; Were, 2011). The GEI, which necessitates multi-location trials in cassava, has implications on the speed of variety development.

The significance of mean square values for GCA_f for CBSD and CMD indicated that there were significant genetic differences among the female parents, while the GCA_m significance suggested that there were significant genetic differences among the male parents. Female x male interaction (SCA) mean squares were also found to be significant for CBSD and CMD expression. This suggests that the behaviour of different males was not consistent over different females and likewise, performance of females was not consistent over different males. The significance of GCA mean squares for the two diseases indicated the significance of the additive component of genotypic variance and the significance of SCA mean squares suggested the significance of dominance variance. The results, therefore, suggest that both additive and non-additive gene action controlled CBSD and CMD resistance. The importance of both additive and non-additive genes in the expression of CBSD has previously been reported (Kulembeka et al., 2012; Munga, 2008; Tumuhimbise, 2013; Zacarias and Labuschagne, 2010) and CMD (Chikoti, 2011; Lokko et al., 2006).

A comparison of GCA (sum of female and male) and SCA effects' contribution to the total variation of the families showed that for both CBSD and CMD sum of squares (SS) for GCA

were substantially greater than SCA SS, suggesting that the observed variation in reaction to these diseases was mainly due to additive gene action. Although both GCA and SCA mean squares for severity were significant, for both two diseases, the relative importance of the respective gene actions showed that CBSD and CMD were predominantly controlled by additive gene effects, as the ratio of GCA/SCA was significantly greater than 1. The preponderance of additive gene action in controlling CBSD (Ceballos et al., 2015; Kulembeka et al., 2012; Mtunda, 2009; Munga, 2008; Tumuhimbise, 2013; Were, 2011) and CMD resistance (Ceballos et al., 2015; Chikoti, 2011; Lokko et al., 2006; Parkes, 2011; Tumuhimbise, 2013) has been widely reported in the literature.

6.4.2 Genetic variation and mode of gene action for early storage root bulking and agronomic traits associated with early bulking

Significant to highly significant variations were observed among parents and families for FSRY, SRN, SRL, HI, SC, PHT, BMY, DSRY and DMC. This variation showed that genotypic effects were important in this set of crosses. The assessment of environmental effects showed that environment also affected the performance of the families. The results suggest that genotype, environment and genotype x environment constituted the final performance of the families in relation to storage root yield and the yield components.

The genetic effects of females and males for FSRY, SRN, SRL, HI, BMY, DSRY, DMC, SC and PHT were revealed by the significance of GCA_f and GCA_m. The non-significance of female x male interaction (SCA) for FSRY and other agronomic traits except SRN, SRL, HI and PHT, suggested that the behaviour of different males was consistent over different females and similarly, performance of females was consistent over different males. The GCA mean squares were significant for FSRY and all other agronomic traits, which meant that the additive component of genotypic variance was significant too. Except for SRN, SRL, HI and PHT, the results suggested that the dominance variance was not significant for FSRY and other agronomic traits. However, for SRN, SRL, HI and PHT both the additive and non-additive gene actions played a role.

The non-significance of GCA_f x location and GCA_m x location for FSRY, HI and DSRY suggested that the performance of both females and males were consistent across the two locations, that is, the expression of additive genes was not dependent on location. It, therefore, appears that GEI effects would not cause any difficulty in selection of genotypes for high FSRY, HI and

DSRY among the progenies. This contrasts other findings (Calle et al., 2005; Lokko et al., 2006; Tumuhimbise, 2013; Tumuhimbise et al., 2014; Were, 2011), who reported significant GCA x location interaction effects.

GCA (GCA_f +GCA_m) effects sum of squares accounted for more variance of the total variance than the female x male interaction (SCA) effects, except for DSRY and SRL where SCA contributed the most. The relative importance of GCA and SCA in predicting progeny performance for FSRY and other agronomic traits was determined through their ratios, which indicated that more variance was due to GCA than SCA for FSRY and all other traits. This indicated that additive gene action was more important for the control of these traits. Predominance of additive gene effects for FSRY have also been reported (Cach et al., 2006; Ceballos et al., 2004; Chikoti, 2011; Munga, 2008), but others (Calle et al., 2005; Ceballos et al., 2015; Tumuhimbise, 2013) have indicated that FSRY is mainly governed by non-additive gene action. The differences observed could emanate from estimation methods of additive and non-additive effects. Some prefer using % sum of squares and others use variance estimates corresponding to the expected mean squares.

6.4.3 Performance of cassava genotypes for resistance to cassava brown streak disease and cassava mosaic disease

Families or progenies with CBSD and CMD score of ≤2 were considered to be resistant. Most of the families and progenies registered scores greater than 2 and hence were susceptible and undesirable. Performance of the families in relation to the parents for CBSDS and CBSDRS revealed that the best performers (resistant-R) were derived from combinations where both parents were best performers (R x R, Silira x Phoso) or where one of the parents showed resistance and the other susceptibility (R x S or S x R). The most resistant families were derived from a combination of S x R. For example, of the 10 best families for CBSDS resistance, three were derived from S x R, two from R x S, one from R x R and five from parents which displayed moderate resistance. Similarly, best single progenies were generally derived from best families. For example, of the 62 progenies with a score of 1, 15 were derived from S x R, nine from R x S, eight from R x R and the rest from families which displayed moderate resistance.

Lowest CMDS and CMDI scores were observed on parents Phoso (1.8) and 01/1316 (2.0). Of the 12 most resistant families (score ≤2), one was derived from R x R, three from R x S, three from S x R and five from moderately resistant parents. A similar observation was made for the

performance of progenies in relation to their families, where the best ranking single progenies were derived from better ranked families.

6.4.4 General and specific combining ability effects for resistance to cassava brown streak disease and cassava mosaic disease

The GCA estimates for CBSD showed that best general combiners were those parents that had lowest mean CBSDS and CBSDI scores. Based on both lower mean scores and high GCA values, four parents (Silira, Depwete, Phoso and Mkondezi) were identified to be resistant as well as being the overall general combiners. These four parents can be desirable parents for inclusion in breeding program aimed at developing varieties resistant to CBSD as they have exhibited the capacity to transmit desirable CBSD resistant traits. The SCA results revealed that desirable families (9) for CBSD resistance emerged from parents with varying levels of GCA effects, such as, low × high (Mulola × Phoso and 01/1316 × Kachamba), low × average (Mulola × Mkondezi and Chamandanda × Masoyabazungu), average × average (01/1569 × Mkondezi), average x high (Depwete x Phoso), high x average (Silira x Masoyabazungu and Silira x Mkondezi), low × low (01/1316 × Beatrice), implying that families performance was not solely dependent on parents GCA effects. Five families (Mulola × Phoso, 01/1569 × Mkondezi, Depwete x Phoso, Silira x Masoyabazungu and Silira x Mkondezi), showed that they are the promising families that could be advanced for further improvement.

The GCA analysis identified five parents (01/1316, Chamandanda, Mkondezi, Mbundumali and Phoso) as best parents to transmit CMD resistance to the progenies when crossed with other parents. Based on significant negative SCA effects, six families were identified as having best combinations for CMD. The distribution of these families showed that best progenies were mainly derived from parents with desirable GCA effects. Based on significantly low mean values and significant negative SCA effects, the best families for CMD resistance identified were, 01/1569 x Mbundumali, Depwete x Phoso, Mulola x Mbundumali, Silira x Masoyabazungu and Silira x Mkondezi.

6.4.5 Mean performance of cassava genotypes for early storage root bulking and agronomic traits associated with early bulking

Best performing parents for FSRY also produced highest DSRY, SRN and HI. The FSRY for the parents ranged from 7.01 t ha^{-1} to 11.1 t ha^{-1}, for families ranged from 4.5 t ha^{-1} to 13.5 t ha^{-1}, and from 0.45 t ha^{-1} to 39.2 t ha^{-1} for single progenies. The large differences exhibited in the material shows that most of the genetic variation is concentrated in the within families (progenies). The performance of the families in relation to the parents for FSRY, DSRY, SRN, SRL, SRD, HI, PHT and BMY revealed that the best performers were mainly derived from families where one or both parents were best performers. Similarly, best progenies were generally derived from high yielding families.

6.4.6 General and specific combining ability effects for early storage root bulking and agronomic traits associated with early bulking

The GCA estimates for FSRY, DSRY, SRN, SRL, SRD, HI, SC, DMC, PHT and BMY showed that the best general combiners were those parents that also had best mean scores. These desirable parents can be included in breeding programs aimed at developing high yielding varieties. The results for the SCA revealed that desirable families (9) for FSRY emerged from parents with varying levels of GCA effects, such as, low × high (Silira× Mbundumali), low × average (Depwete × Phoso), average × average (01/1569 × Mkondezi and 01/1569 x Phoso), average x high (01/1569 x Mbundumali), high x average (Mulola x Masoyabazungu and Mulola x Mkondezi). This implied that families' performance was not exclusively dependent on parents' GCA effects. Based on the high mean performance of the families and the high SCA effects, seven families (Silira× Mbundumali, Depwete × Phoso, 01/1569 × Mkondezi, 01/1569 x Phoso, 01/1569 x Mbundumali, Mulola x Masoyabazungu and Mulola x Mkondezi) proved promising families from which superior progenies could be selected for further evaluation.

Overall, the performance of the families and progenies for CBSD and CMD resistance, FSRY and other agronomic traits, revealed that the best progenies were derived from parents with varying ranges of GCA effects and not necessarily from best general combiners only. The study revealed that it was difficult to find best general combiners for all traits (CBSD, CMD, FSRY, DSRY, SRN, HI, SRL, SRD, DMC, PHT, SC, BMY), except for those traits that are interdependent such as FSRY, SRN, DSRY, HI, SRL, SRD and BMY. Parents Phoso and Mkondezi were identified to be the best general combiners for all traits. Parents Silira and

Depwete were good general combiners for CBSD, parents 01/1316 and Chamandanda for CMD, and parents Mulola and 01/1569 for FSRY. This information is important for any future breeding program aimed at addressing any of these challenges.

It was also difficult to identify best families for all the mentioned combined traits, except for CBSD and CMD which had three families in common (Depwete x Phoso, Silira x Mkondezi and Silira x Masoyabazungu). One family (Depwete x Phoso) was common to all the traits. Put together, 12 families were identified to be outstanding for these traits based on mean performance and SCA effects. Of the 12 best families, only 5 families gave desirable outstanding progenies (10 progenies). A total of 13 progenies were selected based on lower mean values for CBSD and CMD (≤ 2) and higher mean values for FSRY (≥ 10 t ha^{-1}). The additional 3 progenies were derived from families that exhibited undesirable mean performance, GCA and SCA effects.

6.4.7 Genetic components and heritability values for cassava brown streak disease, cassava mosaic disease and early storage root bulking across two locations

It was established that there was a larger within family (δ^2w) than between family variance (δ^2b) for reaction to CBSD and CMD, FSRY and all other agronomic traits, except for DSRY. This was also observed from the mean values, where extreme ranges were exhibited in the within families compared to between families. Cassava is regarded as a special crop as it allows the estimation of within family variation due to the vegetative nature of its propagation. Ceballos et al. (2015) made a similar observation where the within-family genetic variances for FSRY, HI, DMC and plant type score was larger than the between family variations. In most cases, cassava breeders select genotypes for the next generation based on individual genotype performance not as a family.

The GCA variances (δ^2GCA) were greater than the SCA (δ^2SCA) variances for all the traits studied, except for SRL and PHT and almost equal for HI. Larger δ^2GCA than δ^2SCA implied that the traits were mainly influenced by additive genes. To determine the relative importance of GCA and SCA in the genetic control of the different traits, as well as the expected amount of improvement based on the GCAs and SCAs, the proportions of additive variance to the total genetic variances were calculated (i.e. $GR= \delta^2A/(\delta^2A + \delta^2D)$. The GR for CBSDS was 0.62, 0.46 for CBSDRS and 0.71 for CMDS. For the agronomic traits the GRs were: FSRY = 0.83, DSRY =

0.74, SRN = 0.54, SRL = 0.35, SRD = 0.67, DMC = 1, HI = 0.50, PHT = 0.40, BMY = 0.71. These values indicate by far that the largest contribution to the improvement for these traits comes from GCA and ultimately from additive gene action. However, the ratio was less than 1 for all the traits (except DMC), which means that both additive and non-additive gene effects are involved the expression of the studied traits. Ceballos et al. (2004) and Hershey (1987) suggested that any breeding method in cassava should maintain heterozygosity and take into account both additive and non-additive genetic variance because it is not only additive effects that are important in determining the performance of derived progenies, as there is also a large component of dominance effects that translates into significant heterosis for traits such as FSRY. Therefore, both GCA and SCA need be exploited in order to come up with an efficient breeding program.

Other findings on the preponderance of additive gene effects for CBSD resistance (Ceballos et al., 2015; Kulembeka et al., 2012; Mtunda, 2009; Munga, 2008; Tumuhimbise, 2013; Were, 2011), CMD resistance (Ceballos et al., 2015; Chikoti, 2011; Lokko et al., 2006; Parkes, 2011; Tumuhimbise, 2013) and FSRY (Ceballos et al., 2004; Chikoti, 2011; Munga, 2008) support these results. The preponderance of non-additive gene action for CBSD resistance (Zacarias and Labuschagne, 2010), CMD resistance (Kamau et al., 2010) and FSRY (Ceballos et al., 2015; Kamau et al., 2010; Parkes, 2011; Tumuhimbise, 2013; Zacarias and Labuschagne, 2010) contradicts the present findings.

The effectiveness of selection for a trait depends on the relative importance of genetic and non-genetic factors in the expression of phenotypic differences among genotypes (Fehr, 1991). Therefore, heritability of a character has a major impact on the methods chosen for population improvement and selection. Narrow sense heritability (h^2) for CBSDS was 54%, 31% for CBSDRS, 70% for CMDS and 60% for FSRY. The broad sense heritability (H^2) was 86% for CBSDS, 75% for CBSDRS, 98% for CMDS and 72% for FSRY. The heritability values were generally high for most of the traits. The high broad sense heritability indicated that all the characters had high genetic variance, that is, additive and non-additive variance. The high H^2 values reported here are consistent with other reports (Akinwale et al., 2010; Kawano et al., 1998; Mahungu et al., 1994; Parkes, 2011; Zacarias and Labuschagne, 2010). Narrow sense heritability is said to be more important, as it measures the relative importance of the additive portion of the genetic variance that can be transmitted to the next generation of the offspring (Fehr, 1991). The narrow sense heritability values were high for CBSDS, CMDS and FSRY. According to Falconer and Mackay (1996), high h^2 is caused by high additive effects and low

dominant gene action. In this study, additive gene action was more pronounced as evidenced from high GCA variances than SCA variances and relatively high genetic ratio values. Since heritability values were high, breeding methods that use selection based on phenotype would be effective for these traits.

6.5 Conclusions

The study established that resistance in cassava for CBSD and CMD, as well as early storage root bulking is controlled by both additive and non-additive gene action. However, additive gene action is more important than non-additive type of gene action in the inheritance of resistance for these two diseases and early storage root bulking. Mass phenotypic recurrent selection after hybridisation of elite clones would, therefore, be effective for the development of varieties resistant to the two diseases, as well as addressing challenges related to late storage root bulking. Four parents with good combining ability for CBSD and CMD resistance have been identified in addition to early storage root bulking. Thirteen new genotypes with CBSD and CMD resistance, as well as early storage root bulking traits, have been identified. These genotypes will need to be widely tested before superior varieties can be identified for release in Malawi.

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Chapter 7

7 Thesis overview

7.1 Introduction

Cassava brown streak disease (CBSD) and late storage root bulking are among the major constraints to sustained cassava production in Malawi. The CBSD affects cassava by diminishing the market quality of storage roots and reducing storage root yield (Gondwe et al., 2003; Hillocks et al., 2001). The CBSD severity and incidence increase with the prolonged stay of the crop in the field (Hillocks and Jennings, 2003). Two major approaches for CBSD management are use of resistant varieties and early harvesting. However, in Malawi, no major strides have been made to develop CBSD resistant varieties. On another hand, early harvesting leads to significant yield sacrifices unless the varieties themselves are early bulking, which is not the case at present. Therefore, effective and sustainable control measures for the CBSD will be the integration of resistant and early storage root bulking varieties.

To respond to these two challenges, a study was done to develop and identify cassava varieties that are resistant to the CBSD, and are early storage root bulking, in order to improve the yield and quality of cassava and subsequently contribute to food security and improved income among smallholder farmers in Malawi. Five research objectives were formulated to achieve the desired outcomes and these were: (1) an assessment of farmers' knowledge of cassava brown streak disease and its management in Malawi, (2) identification of early storage root bulking cassava genotypes as well as traits associated with early storage root bulking, (3) assessment of the effect of harvest time on cassava genotypes performance, stability and adaptability, (4) an evaluation of cassava genotypes for resistance to cassava brown streak disease and its associated yield losses and (5) determination of gene action and the importance of combining ability effects in the inheritance of the CBSD resistance and early storage root bulking traits.

The major findings and their implication in the development of CBSD resistant and early storage root bulking varieties are summarised as follows;

7.2 Major findings

7.2.1 Farmers' knowledge of cassava brown streak disease and its management in Malawi

The majority of the farmers did not know the disease through foliar symptoms and only 10.1% of the farmers were able to identify CBSD. The study established that CBSD is a continuing threat to the cassava industry, where high incidence levels were observed. On average, 75.0% and 71.7% of the farms had cassava plants with leaf and storage root symptoms, respectively. The average CBSD leaf incidence per farm was 31.2%, with some farms with levels up to 86.7%. At harvest, 88.3% of the farmers' fields exhibited storage root necrosis. Most farmers were found to lack a source of clean planting material. A need for improved extension services to improve the cassava cultivation methods and pest management was identified. The lack of new improved varieties was reported as the most important constraint of cassava production, apart from the CBSD.

7.2.2 Early storage root bulking index and agronomic traits associated with early bulking

The study identified four varieties as early-bulking (Mulola, Phoso, Mbundumali and Maunjili). High fresh storage root yields were obtained of up to 9.5 t ha^{-1} at 6 MAP and 17.8 t ha^{-1} at 9 MAP. The study revealed that yields obtained at 9 MAP were higher than those obtained at 12 MAP for some genotypes. The study identified harvest index and shoot mass as the most important traits that could be used for selecting early storage root bulking varieties.

7.2.3 Effect of harvest time on cassava genotypes performance, stability and adaptability

The study revealed that genotype, environment and genotype x environment interaction have a significant influence on the performance of varieties regardless of the harvest time. Most of the cassava varieties exhibited specific adaptation to certain environments. The study identified five varieties (Mulola, Phoso, Maunjili, Beatrice and Unknown) that exhibited consistent performance, stability and adaptability across the three harvest periods.

7.2.4 Evaluation of cassava genotypes for resistance to cassava brown streak disease and its associated yield losses

High significant CBSD incidence and severity values were observed (some varieties reached an incidence as high as 94.9% and severity of up to 3.8). The CBSD storage root severity increased with prolonged stay of the crop in the field. The study established that the yield loss due to CBSD was significantly associated with CBSD storage root severity at different harvest times. Maximum yield loss of 43.1% was recorded at 12 MAP on Kalawe, while at 9 and 6 MAP, maximum yield loss was 24.8% and 10.9%, respectively. The study identified five varieties to be resistant/or tolerant to CBSD (Phoso, Maunjili, Mpale, Sauti and TMS4(2)1425).

7.2.5 Gene action and the importance of combining ability effects in the inheritance of cassava brown streak disease resistance and early storage root bulking traits.

The study revealed that both male GCA_m and female GCA_f have an influence on transmission of CBSD resistance and early storage root bulking traits. Four parents (Silira, Mulola, Phoso, and Mkondezi) were identified as the best general combiners for the CBSD and early storage root bulking. Thirteen progenies exhibiting CBSD resistance and early storage root bulking traits were identified and selected for advancement. The study established that resistance in cassava for CBSD as well as early storage root bulking is controlled by both additive and non-additive gene action. However, additive gene action is more important than non-additive type of gene action in the inheritance of CBSD resistance and early storage root bulking.

7.3 Implications of the findings in relation to the development of cassava brown streak disease resistant and early storage root bulking varieties

The results, in general, suggest that farmers need to be educated on the efficient management of this viral disease. In order to effectively manage CBSD, farmers need to integrate various strategies, such as using varieties that are early bulking, resistant/tolerant to CBSD, selecting planting material free from CBSD, sanitation and roguing of any infected plants from the field especially shortly after sprouting. The development of CBSD resistant and early storage root bulking varieties as a long-term solution in avoiding CBSD impact should be supported. The study has generated new material with desirable attributes (CBSD resistance and early bulking) that need further screening for CBSD and early storage root bulking. The release of varieties

which address these challenges might translate to significant gain in terms of food security and improved livelihoods of farmers.

7.4 References

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