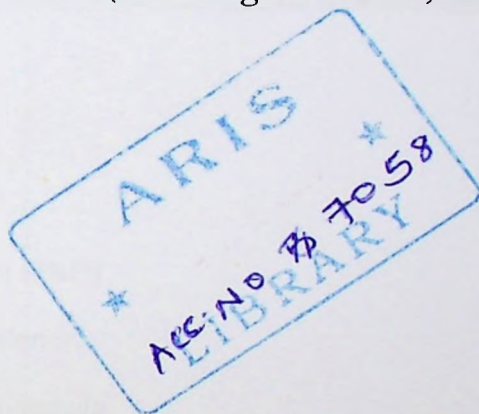


**PHYSIOLOGICAL AND MORPHOLOGICAL RESPONSES OF
FARMER PREFERRED CASSAVA (*Manihot esculenta* Crantz)
CULTIVARS TO DROUGHT STRESS IN UGANDA**

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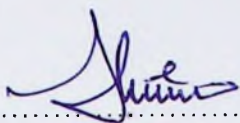


**THESIS SUBMITTED TO SCHOOL OF GRADUATE STUDIES IN
PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE
AWARD OF A DEGREE OF MASTER OF SCIENCE IN CROP
SCIENCE OF MAKERERE UNIVERSITY.**

2013

DECLARATION

I declare that the work in this thesis is my own and has not been submitted for the award of a degree to any other university.

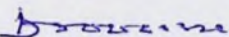


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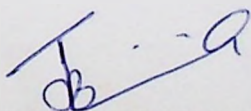
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DEDICATION

I dedicate this work to my parents Mr. Towet John and Mrs. Judith Towet for their support in my career development and to my beloved wife Ms. Kwaga Godia, my daughter Vanessa and my sons David and Jonan in gratitude for their love and fervent prayers.

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ABSTRACT

Cassava is the most important staple food crop in the tropics feeding over 800 million people, mainly resource poor small scale-farmers. In Uganda, cassava ranks 2nd to bananas in terms of total production and per capita consumption but ranks 2nd to maize in production area, (UCA, 2010) and it is the leading food security crop. Cassava is commonly cultivated in areas considered marginal for most other crops, with low-fertility soils and annual rainfall of less than 600 mm in semi-arid environments thus making it vulnerable to drought stress. Drought tolerance mechanisms in cassava and strategies for its management developed elsewhere, but no such information was available in Uganda. The main objective of this study was to assess the physiological and morphological responses of cassava cultivars in Uganda to drought.

A total of 56 cassava cultivars were collected from 17 districts in Uganda covering the major agro-ecological zones of the country. One check MM96/0686 known to be drought tolerant was acquired from International Institute for Tropical Agriculture (IITA) and included in the collections. The 56 cultivars were evaluated in the field in a randomized complete block design (RCBD) with two replicates in two drought prone areas of Nakasogola and Bullisa and one location with normal rainfall regime at Makerere University Agricultural Research Institute Kabanyolo (MUARIK). Based on their performance 5 month after planting (MAP), 15 cultivars were identified for rain-out shade study at MUARIK. Cultivars contrasting in their response to drought stress were selected based on number of surviving plants after three month of constant drought stress for detailed studies. In the rain-out shade, plants were established in a RCBD with 2 replicates in large polythene bags of 80 cm deep and 60 cm diameter. All experiments received adequate water supply by adding 5L of water once every two days for 1 MAP and

thereafter adjusted to two watering regimes 1) stressed treatment (5L of water once every three weeks) and 2) non-stressed treatment (5L of water twice every week). Data was collected on crop establishment, plant height, leaf area and leaf retention, number of fibrous roots, fibrous root length, number of storage roots, fresh storage root weight, stomatal conductance, xylem pressure potential, shoot weight and harvest index. These assessments were done on five plants per cultivar per treatment starting one MAP at a month interval except for root data, shoot weight and harvest index that were collected at harvest.

Results from field experiments indicated significant differences among cultivars as evaluated across locations for the number of plants that survived and degree of wilting. Genotype by environment (GxE) interaction was highly significant for number of surviving plants and leaf wilting. The cultivars which had the highest number of plants surviving in Bullisa and Nakasongola until end of the experiment (5 MAP) were considered drought tolerant, while those which had no surviving plant were considered most susceptible to drought stress.

In the rain-out shade, cultivars showed significant reductions in morphological traits. Considerable reductions were in plant height (3-35%), shoot biomass (3-60%), leaf longevity (66-84%) and leaf area (38-56%), while significant increases were in fibrous root density (2-56%) and length (4-59%). Drought stress caused a general increase in xylem pressure potential (27-79%) of all the cultivars evaluated, while reducing stomatal conductance (57-86%) of these cultivars. Yield responses to soil moisture deficit also showed significant difference for all parameters measured. Analysis of variance of yield parameters of cultivars across the two water regimes indicated considerable significant differences for storage root number, storage root length, fresh storage root weight and harvest index (HI), while there was no significant difference for storage root

circumference. There were also considerable variations in performances of cultivars across the two water regimes for all the yield parameters. Correlation analysis showed a significantly positive relationship of shoot weight with both storage root length ($r=0.64^*$) and circumference ($r=0.63^*$). In addition, leaf longevity had a positive significant relationship with harvest index ($r=0.64^*$). In addition, there was positive significant correlation between leaf area and storage root length ($r=0.66^*$) and storage root weight ($r=0.76^*$) while there was negative significant correlation of leaf wilting with storage root circumference ($r=-0.68^*$). Furthermore, there was also negative significant correlation between fine root number with harvest index (HI) ($r=-0.68^*$) and drought response index (DRI) ($r=-0.80^{**}$).

Basing on the generated data, the major conclusion of this study is that although cassava is known to be drought tolerant, severe moisture stress has significant devastating effects on both vegetative growth and yield of cassava. In addition, it is also concluded that cultivars respond differently to drought stress with some being tolerant (MM96/0686, MM96/4271, omongole) while others were very susceptible to drought stress (Bamunanika, Bao and Nase 12). It can also be concluded that cassava tolerates drought stress by closing stomata, shading leaves, reducing plant growth, increasing fibrous root density and length, but unfortunately all these tolerance mechanisms are at the expense of yield. The existence of significant variations among cultivars in the mechanisms of tolerating drought offers opportunities for genetic improvement for these important traits. Breeders should therefore accumulate genes for drought tolerance in breeding materials to develop cultivars with high yield potential for dry ecologies.

CHAPTER ONE

INTRODUCTION

1.1 Background

Cassava (*manihot esculenta*, Crantz) is a perennial starchy root crop widely grown throughout the lowland tropics (Allem, 2002; Hillocks, 2002). Fresh storage roots contain 30-40% dry matter composed of about 85% starch (El-Sharkawy, 2012). It is the most important staple food crop in the tropics feeding over 800 million people, mainly resource poor small scale farmers and it ranks 4th as a source of energy after rice, sugarcane and maize (Burns *et al.*, 2010). It's the cheapest source of calories for both human and animal feed providing more than 50% calorific requirements (Alves, 2002; Balagopalan, 2002). In Uganda, cassava ranks 2nd to bananas in terms of total production and per capita consumption while ranking 2nd to maize in production area (UCA, 2010) and it is the leading food security crop.

Native to the American tropics, cassava was introduced to Africa by Europeans in the slave ships returning from Brazil in 1550's (Allem, 2002; Hillocks, 2002). The Portuguese used it as a food source for enslaved Africans awaiting transport to slave markets (Nassar, 2006). Due to its ease of cultivation and ability to do well in poor soils, resist drought and insect damage, the Portuguese began cultivating cassava at their stations along the coast of West Africa. Soon afterwards, cassava diffused to all parts of west and central Africa (Nassar, 2002, 2006). The Portuguese were also responsible for introducing cassava to East Africa, Madagascar, India, Ceylon, Malaysia, and Indonesia by the 1700s (Nassar *et al.*, 2002; Nassar, 2003; Onwueme, 2002). Cassava was introduced to Uganda from Tanzania by Arab traders between 1862 and

1875 (Hillocks, 2002). Its cultivation greatly increased between 1931 and 1933 and subsequently became a cheap source of food presently grown throughout the country. A total of 3.5 million MT of the crop were produced from 450,000 ha of land grown until 1980's when mosaic epidemic devastated the crop (NARO, 2005). However, with the release of disease resistant varieties, production rose to 5.2 million MT in 2009 but reduced to 4.8 million MT in 2011 (FAOSTAT, 2011) properly due to break down of disease resistance and effects of climate change and variability on the improved cultivars currently under production.

Currently, cassava is being grown for its starchy storage roots (Hillocks 2002, Onwueme, 2002) although in many Africa countries like Democratic Republic of Congo and Sierra Leone boiled cassava leaves are eaten as vegetables due to their high protein, vitamins and minerals (Yeoh and Chew, 1976; Onwueme and Winston, 1994; Lebot, 2009; Ceballos *et al.*, 2010). The roots are principally used as human food, either fresh (boiled, baked, fried or pounded) or in numerous processed forms (Onwuene, 2002). Cassava is also increasingly becoming an important animal feed and raw material for producing starch, starch-based products and or starch-derivatives which are important raw materials for many industrial uses such as food processing, paper, textile and adhesive manufacturing, alcohol production and in the oil drilling industry (Balagopalan, 2002; Kawano, 2003; Onwuene, 2002). Cassava starch is also a raw material for producing many derived sugar products such as glucose, fructose, maltodextrins and mannitol, each of which has specific properties and uses in food, chemical or pharmaceutical industries (Onwuene, 2002).

Total world cassava production increased from 70 million tons in 1960 to 252.203 million MT in 2011. Of this total, 51% is produced in Africa, 31% in Asia and 18% in Latin America (FAO, 2011). Nigeria contributes 33% of the 51% ranking first in Africa in terms of cassava production while Uganda contributes 5% ranking sixth in Africa (FAO, 2011). Cassava yields vary with cultivars, season of planting, soil type and fertility. However, with improved varieties and good management practices, cassava has a potential of up to 40-50 t/ha of root dry weight in Africa, however, yields are very low between 3-4 t/ha. Attaining optimal yields is mainly constrained by a number of abiotic and biotic factors, which include; the use of inferior low yielding varieties, lack of good quality planting material, pests and diseases, and worst of all drought stress due to global climatic changes (NARO, 2005).

Throughout the world and particularly in the developing countries, agricultural production is steadily moving into semi-arid areas as a result of increasing population pressure and global climatic changes and variability. Cassava has long been recognized as a crop that usually has ability to withstand drought stress and produces reasonable yields under conditions of moisture deficit (Osiru *et al.*, 1994). It can survive dry periods of up to 4-6 months and it's commonly cultivated in areas considered marginal for most other crops, with low-fertility soils and annual rainfall less than 600 mm in semi-arid environments. It is therefore considered a leading contributor to food-security against famine, requiring minimal inputs, and an important crop for drought prone areas (El-Sharkawy, 1993; Agilli and Pardales, 1999; Aina *et al.*, 2007). However, extreme water deficit affects the growth, development and productivity of cassava. The extent to which productivity is affected largely depends on the stage of growth and the varieties response to drought stress. The critical period of water deficit effect in cassava is from 1-5 months after

planting (MAP) at the stage of root initiation and tuberization. This is because this stage of development largely determines the later growth of cassava and their subsequent yields (Alves, 2002; Pardales and Yamauchi, 2003).

Despite the fact that cassava has been recognized for decades as a drought tolerant crop and that considerable proportion of the crop is grown in areas where annual rainfall rarely exceeds 600 mm, no studies have been carried out in Uganda to understand the traits associated with drought tolerance mechanisms in the local and newly introduced farmer-preferred cassava cultivars in Uganda, and how the different cassava cultivars respond to drought stress. It is important to understand traits associated with drought tolerance mechanisms in cassava in order to undertake systematic genetic improvement in cassava breeding programs. This study assessed; 1) morphological and physiological basis for drought tolerance in cassava that enable it to adapt to water stress and maintain growth, development and productivity during stress periods and, 2) how different local and newly introduced cassava genotypes respond to drought stress.

1.2 Justification of the study

Cassava is a very important crop in Uganda owing to the extensive use of its various products and or by-products. The consumption of cassava cuts across all parts of the country and its adaptability to different climatic and soil conditions even in marginal soils has endeared cassava to most people that have to do continuous cultivation on limited available land. It stands out as a leading food security crop in Uganda, especially among resource poor farmers particularly in marginal agricultural areas. It has a number of attributes that have made it an attractive crop for small-holder farmers with limited resources. Cassava is an efficient carbohydrate-producing

crop, with tolerance to low soil fertility and drought, and the roots can be left in the ground for long periods as a food reserve and thus provide an insurance against famine. In addition, it is well adapted to traditional mixed cropping agricultural systems and subsistence cultivation in which farmers seek to minimize risks of total crop failure.

Cassava cultivation is steadily moving into semi-arid areas as a result of increasing population pressure in better watered agricultural lands and continuous effects of climate change and variability, thus food security in such areas is of great concern. To ensure sustainable production of cassava in these areas, there is need to identify cassava cultivars that will not only survive extreme environments but also give good yields in Uganda. Very little is known about the physiological and morphological responses of the local and newly introduced farmer grown cassava cultivars in Uganda to drought stress, therefore the main goal of this study was to determine the physiological and morphological mechanisms and or traits associated with drought tolerance and to assess how different farmer-preferred cassava cultivars in Ugandan respond to drought stress. Cultivars found to be drought tolerant will be recommended for drought prone areas, while at the same time used as candidate parental lines for breeding for drought resistance.

1.3 Objectives

1.3.1 General objective

The overall objective of this study was to assess how different cassava cultivars in Uganda respond to drought stress and determine the physiological and morphological mechanisms associated with drought tolerance

1.3.2 Specific objectives

1. To identify morphological traits that enable cassava to withstand drought stress
2. To determine physiological traits associated with drought tolerance mechanisms in cassava
3. To determine cultivar differences with regard to their response to drought stress

1.4 Hypotheses

1. Farmer grown cassava cultivars show different physiological reactions to drought stress
2. Different cassava cultivars differ in their morphological response to drought stress
3. Drought tolerance mechanisms do not vary from one cultivar to another among farmer grown cassava cultivars

CHAPTER TWO

LITERATURE REVIEW

2.1 Cassava

Cassava is a perennial and or an annual/biennial crop popularly grown for its storage starchy roots. It is regarded as annual or biannual because the edible roots are usually harvested within the first or second year (Hahn *et al.*, 1990). The storage roots can be harvested from 6-24 months after planting depending on cultivar and growing conditions (Ngendahayo and Dixon, 2001; Alves, 2002). The crop is widely grown as an annual staple food and animal feed by resource-poor smallholders. Cassava is used directly for human consumption in form of fresh storage roots and leaves. The leaves constitute an excellent source of protein supplement (Yeoh and Chew, 1976; Onwueme and Winston, 1994; Lebot, 2009; Ceballos *et al.*, 2010). A significant portion of storage roots is used worldwide for industry uses such as starch extraction, glucose manufacturing, alcohol, and recently for biofuel (El-Shakawy, 2012). However, attainment of these important uses of cassava is curtained largely by drought stress which adversely reduces cassava yields as a result of its effects on plant phasic development, growth, assimilate partitioning and root development (Osiru *et al.*, 1994; Aina *et al.*, 2007)).

2.2 Drought tolerance

It is a known fact that plants require resources to produce optimally and lack and or excess of these resources would have implications on their productivity. Water is one of the most important inputs essential for the production of crops constituting about 80% of the growing tissues. Water influences photosynthesis, respiration, absorption, translocation and utilization of

mineral nutrients all of which are vital for normal plant growth and development. Soil moisture deficit affects the growth and development of a plant directly and consequently, its yield and quality (Olanrewaju *et al.*, 2009; Omonona and Akinpelu, 2010).

Drought stress is the most serious yield-reducing constraint in agriculture. It limits agricultural production by preventing crops from expressing their full genetic potential (Clifford *et al.*, 1998; Liang *et al.*, 2002). Plants respond to water deficit at many different levels: morphologically, physiologically, cellular and metabolically. The responses are dependent upon the duration and severity of stress, the genotype of the stressed plant, the stage of development and the organ and cell type in question (Bray, 1994).

The importance of water in cassava production cannot be over emphasized. Water is needed in cassava production though not in quantities that will cause rot to the tubers. Cassava is a drought resistant crop that does well where other crops fail. The physiological mechanisms underlying tolerance to water stress in cassava are related to the cassava extensive fine root system that can penetrate below 2m soil depth, thus enabling the crop to exploit deep water if available (Osiru, 1994; Clifford, 1998; Aina *et al.*, 2007), and the remarkable sensitivity of cassava stomata to both atmospheric and soil water stress (El-Sharkawy, 2003, 2004). Plant responses to drought stress are complex, varied, and involve interactions between different molecular, biochemical, morphological and physiological processes (Alves, 2002; Liang *et al.*, 2002). Breeding for drought tolerance in many major crop species has produced important advances in varietal development (Blum, 1998; 2005).

Drought tolerance is generally defined as the ability of a given cultivar to show a relatively small yield reduction upon exposure to drought. This implies that breeding for stress adaptation is at the expense of yield potential. Whole plants respond to drought through morphological, physiological, cellular and metabolic modifications occurring in all plant organs (El-Sharkawy and Cadavid, 2002). At the cellular level, plant responses to water deficit may result from cell damage, whereas other responses may correspond to adaptive processes (Liang *et al.*, 2002). The responses are dependent upon the duration and severity of stress, the genotype of the stressed plant, the stage of development, and the organ and cell type in question (Bray, 1994). Multiple responses allow the plant to tolerate water stress (Trejo *et al.*, 1995; Griffiths *et al.*, 1997; Liang *et al.*, 2002).

2.3 Stomatal conductance and water deficit

Water losses in form of vapour through the stomata opening is referred to as transpiration. In most plants water loss during periods of drought causes a reduction in leaf water potential (a measure of the amount of water in the leaf), thus causing the stomata to close. The stomata respond rapidly so that little water is lost from the leaves (CIAT, 1986; El-Sharkawy, 2007). Studies on cassava have shown that the physiological mechanisms underlying cassava tolerance to water stress are related to the remarkable sensitivity of cassava stomata to both atmospheric and soil water stress (Alves and Setter, 2000; El-Sharkawy, 2003; Omonona and Akinpelu, 2010). When water is available, cassava maintains a high stomatal conductance and can keep internal CO₂ concentration high, but when water becomes limiting, the plant closes its stomata in response to even small decreases in soil water potential (Tardieu and Simonneau, 1998; Alves and Setter, 2000; El-Sharkawy, 2003). The rapid closure of cassava stomata and the resulting

decline in transpiration lessens the decrease in leaf water potential and soil water depletion, thus protecting leaf tissues from turgor loss and desiccation (El-Sharkawy & Cock, 1984; Cock *et al.*, 1985; Alves and Setter, 2000; El-Sharkawy, 2003).

In addition, leaf area growth is decreased in response to water stress and is rapidly reversed following the release from stress (Alves and Setter, 2000; Liang *et al.*, 2002; Vysotskaya *et al.*, 2007). This limits the production of transpirational surface during stress, and conserves carbohydrates until rewatering thus keeping sink demand well balanced with plant assimilatory capacity. Cassava appears to cope with water deficit using mechanisms of dehydration avoidance by changing stomatal behavior and leaf expansion rate in direct response to soil drying before the occurrence of any detectable decrease in shoot water potential (Itani *et al.*, 1992; Serraj and Sinclair, 2002). Although the combined effect of reducing leaf surface area and stomatal closure can improve crop water use efficiency, it also leads to reductions in potential photosynthesis and in turn total biomass and root yield (Liang *et al.*, 2002). Considerable varietal differences in stomatal conductance have been observed and this parameter seems to be useful to pre-select germplasm conferring adaptation to prolonged dry periods (Alves and Setter, 2000; El-Sharkawy, 2003). Stomatal conductance is reported to be predominantly controlled by abscisic acid (ABA) in the xylem sap and potassium availability in the guard cells (Hartung *et al.*, 2002; Vysotskaya *et al.*, 2007).

Cassava leaf stomata are also very sensitive to air humidity, irrespective of soil water content, they close rapidly in dry air when evaporation is high under field conditions, which may be translated into high leaf water potential. This mechanism enables cassava to maximize its water

use efficiency (WUE) during periods of prolonged drought. When air humidity is high (e.g. early in the morning and during rainy periods), the stomata remain open. Thus, in a humid atmosphere and in the presence of soil water deficits, cassava leaves remain photosynthetically active and the crop can produce well (El-Sharkawy, 2007). When soil water is not a problem, stomata sensitivity to humidity could also be disadvantageous because stomata closure followed by reduced transpiration and photosynthesis could limit growth. Therefore there is need for scientists to develop cassava varieties that have less stomatal sensitivity. Thus in this study variation in stomatal sensitivity under drought stress is investigated.

2.3 Leaf growth and water deficit

In cassava, leaf size increases to a peak at about four month after planting and thereafter it decreases rapidly. Leaf area expansion decreases upon imposition of water deficit, such that expansion and development of the transpiration surface is drastically decreased (Alves and Setter, 2000). It is thought that such arrested growth, with limited investment in osmolyte production, assists plants in attaining high productivity in environments with cycles of intermittent drought, followed by re-watering (Serraj and Sinclair, 2002; Alves and Setter, 2000). By minimizing investment of resources in osmolyte accumulation and leaf growth during a drought episode, more resources are available for recovery of growth and metabolic activities after renewed rainfall, when the bulk of growth occurs (Alves and Setter, 2004b). It is generally observed that cassava growth resumes after a mild, short-term stress; however, growing cells may not expand fully to the size of controls, and water stress may reduce the number of cells produced per leaf (Lecoeur *et al.*, 1995; Schuppler *et al.*, 1998; Granier and Tardieu, 1999; Tardieu *et al.*, 2000). The decreased cell production, may be because leaf meristems produce

fewer cells under stress, so that fewer cells are available for expansion in the post-treatment phase (Granier *et al.*, 2000). In addition, the rate of new leaf initiation by apical meristems can limit future growth.

Leaf expansion is among the most sensitive of the processes that are affected by water deficit. When cassava is water stressed, it reduces its Leaf Area Index (LAI) by decreasing the size of its leaves and slowing the rate of formation of new branches (El-Sharkawy, 2007). A smaller LAI causes the plant to capture less sunlight and so the overall growth of the plant is reduced.

Studies have indicated that this sensitivity is expressed in terms of smaller cells and reductions in the numbers of cells produced by leaf meristems (Lecoeur *et al.*, 1995; Schuppler *et al.*, 1998; Granier and Tardieu, 1999; Tardieu *et al.*, 2000). Studies on cassava indicated that inhibition of both cell expansion and the production of cells contributed to losses in leaf area, depending on the developmental stage at which a leaf was stressed. In leaves that were no longer engaged in cell division, diminished cell expansion affected leaf area by reducing mature cell size whereas, in younger leaves, inhibition of cell division resulted in fewer cells per leaf. Therefore reduction in leaf area is an important adaptive mechanism for plants suffering water shortage.

It has also been noted that another mechanism of tolerance to drought in cassava is its ability to compensate partly for previous losses in dry matter production due to water stress by an increase in leaf canopy area and by higher photosynthetic rates in the newly developed leaves after recovery, as compared to the unstressed plants (El-Sharkawy, 2006; El-Sharkawy 2007). These higher photosynthetic rates in new leaves of previously stressed cassava were associated with

higher leaf conductances, higher nutrient contents, as well as with stronger sinks for carbohydrate in storage roots (Cayón *et al.*, 1997; El-Sharkawy 2007).

2.4 Leaf retention under moisture deficit stress

Leaf longevity is one of the main traits associated with high yields in cassava (El-Sharkawy *et al.* 1992; El-Sharkawy, 2003; Cock *et al.*, 2005). Indeed clones with the leaf retention trait have been observed to produce more total fresh biomass and higher root dry matter than plants without the trait (Lenis *et al.* 2006). Thus, this trait presents an additional opportunity to increase cassava yields. Furthermore, leaf retention during water deficit is positively correlated with high drought tolerance, productivity, and root quality. During hours of greatest sunlight, cassava droops its leaves to reduce the influence of the sun and the heat. Drought stress normally leads to shading of leaves in cassava as a means of minimizing loss of water by transpiration. This invariably reduces photosynthetic surface and activities of cassava thus affecting storage root development significantly which eventually translates to low and poor yield of the crop (Alves, 2002).

Delayed leaf retention after drought treatment has been achieved in transgenic cassava plants, developed at Eidgenössische Technische Hochschule (ETH) Zurich, via auto regulatory senescence inhibition through the expression of the isopentenyl transferase (*ipt*) gene encoding cytokinin production under the control of the senescence-regulated *SAG12* promoter from *Arabidopsis* (Zhang and Gruissem, 2004). From this study, it was evident that two transgenic lines showed significant “stay-green” and repressed chlorophyll degradation after darkness-induced senescence treatment of mature leaves from both *in vitro* and greenhouse-grown plants.

In addition, 40% more leaves were harvested from transgenic lines compared to wild type. The transgenic plants also had early root bulking under greenhouse conditions.

2.5 Cassava roots and moisture deficit stress

Roots are the main starch storage organs in cassava. Initially they develop as a fibrous root system and only a few (between three and ten) start to bulk and become storage roots as the other fibrous roots remain thin and continue to be active in water and nutrient absorption (Alves, 2002). Once a fibrous root becomes a storage root, its ability to absorb water and nutrients decrease considerably (Alves, 2002).

Alves (2002) reported that cassava is commonly grown in areas receiving < 800mm rainfall per year with a dry season of 4-7 months, where tolerance of water deficit is an attribute. The critical period of water deficit effect in cassava is from 1-5 MAP, which coincides with the stages of root initiation and tuberization. Water deficit during at least 2 months of this period can reduce storage in root yield from 32-60% (Pardales and Esquibel, 1996). The reduction in storage root yield depends on the duration of the water deficit and is determined by the sensitivity of a particular growth stage of water stress (Pardales and Yamauchi, 2003; Omonona and Akinpelu, 2010).

Studies by Algerico *et al.*, (2005) observed that the storage roots of the plants under the drought conditions were smaller and woody. This is explained as a mechanism where root function shifts from storage of assimilates to serving as a main channel of water and nutrients to the shoots as a response to water shortage. Genotypes that tolerate drought have longer and more adventitious

roots as ways to adapt to water shortage. Root depth and extension into deep soil is crucial for crop performance under limited water supply if there is moisture available at deep soil level (Osiru *et al.*, 1994). During water stress, cassava fibrous roots extend for more than 2 m into deeper, wetter soil from where cassava can extract between 20% and 40% of its total water uptake (El- Sharkawy, 2006). This is of paramount importance in areas with bimodal rainfall patterns and those with one short-wet annual period where excess water percolates deeper in soil profile and, hence, it could be extracted during long dry periods. Root-derived ABA has been reported to be important in long-distance signaling in drought treated plants (Hartung *et al.*, 2002; Davies *et al.*, 2005; Vysotskaya *et al.*, 2007).

Another characteristic that has been implicated in cassava tolerance to prolonged water stress is the obligate association with vesicular arbuscular mycorrhizal fungi (VAM) (Sieverding and Howeler, 1985). It was found out that among 20 cassava cultivars growing in large pots outdoors, the percent infected root length under stress varied from ~50 to ~90%, and these values were highly correlated with total plant root length across cultivars (Sieverding *et al.*, 1985). Compared to cereal crops, cassava has a sparse fine root system and the extensive fungal hyphae-network in the soil may increase water absorption capacity of infected roots. The same has been reported in barley by using a new split-root hyphae system in plants under well-watered and water-stressed conditions in growth chamber. Khalvati *et al.*, (2005) found that water was transported from the fungi hyphae to barley root compartment under water stress, as compared to nonhyphae treatment. In that study, VAM-infected plants suffered less (relative to non-infected plants) from water stress in terms of leaf elongation rate, leaf turgor pressure, stomatal conductance and photosynthetic rate.

2.6 Plant vigor and moisture deficit stress

Several studies have shown that compared with the control (normal watering), the final root yields of the stressed crop were increased in vegetative vigorous varieties while reduced in less vigorous types and slightly reduced or remained unchanged in varieties with intermediate vigor. These responses were closely related to leaf area characteristics (i.e. peak LAI and leaf area duration over the growing cycle), and to patterns of photo-assimilate partitioning between top growth (stems and leaves) and storage roots. The vigorous types responded positively to stress because top growth was reduced and the harvest index was increased, whereas the less vigorous types responded negatively because leaf area was drastically reduced to levels below optimal LAI for root yield (Richards, 2000; Hall, 2004; DaMatta and Ramalho, 2006; El-Sharkawy 2007).

The stability of root yields in intermediate types under both favorable and stressful environments stemmed from the ability to maintain leaf area near optimum during critical stages of the growing cycle. It suffices to note that, the relationship between leaf area and storage root yield is also important when cassava is subjected to a cold period coupled with water shortages in the subtropics where leaf area is reduced (Richards, 2000; Hall, 2004; DaMatta and Ramalho, 2006). Iglesias and Brekelbaum, (1996) noted that information on plant vigour and leaf area in responses to water shortages is fundamental in selecting germplasms for different environment.

2.6 Osmotic adjustment (OA)

The accumulation of solutes in response to water deficit (osmotic adjustment, OA) is another way of increasing drought tolerance in higher plants. With osmotic adjustment, tissues can

maintain positive turgor at lower water potentials and diminish stress-related damage to membrane and organelle systems, particularly if certain compatible solutes are accumulated (Alves and Setter, 2004). Although major differences in the extent of osmotic adjustment are found in cultivars of some crop species, implying genetic variation, the potential value of this trait in crops may be limited to enhancing root growth to access water at greater depth (Serraj & Sinclair, 2002; El-Sharkawy and Cadavid, 2002; El-Sharkawy, 2003), or permitting tissue survival under severe desiccation episodes. In cassava, studies have found that the extent of osmotic adjustment (OA) is small in response to short-term water deficit during the rapid growth stage, consistent with the observation that leaf water potential remains relatively unchanged during water deficit episodes (El-Sharkawy *et al.* 1992; Alves and Setter, 2004). By limiting its resource investment in osmolyte accumulation and limiting water loss, some cassava cultivars may have a drought response that confers high productivity in environments with brief cycles of intermittent drought, followed by recovery of water status, when the bulk of growth occurs (Itani *et al.*, 1992; Serraj and Sinclair, 2002).

2.7 Dry matter partitioning and source/sink relationship

During cassava growth the carbohydrates from photosynthesis have to be distributed to assure good development of the source (active leafs) and provide dry matter (DM) to the sink (storage root, stems, and growing leaves). Cassava DM is translocated mainly to the stems and storage roots, and DM accumulation in the leaves decrease during the crops cycle. Cassava accumulates DM more in the leaves than in the stems and storage roots until 60-75 days after planting (DAP), then the roots increase rapidly reaching 50-60 % of the total DM around 120 DAP (Alves, 2002). After four month, more DM accumulates in the roots than in the rest of the plant. At harvest (12

months) DM is present mainly in roots, followed by stems and leaves (Alves, 2002; El-Sharkawy, 2003). The distribution of DM to the economically useful plant parts is measured by harvest index (HI) and in cassava HI represents the efficiency of storage root production and is usually determined by the ratio of storage root weight to the total plant biomass weight (Alves, 2002; El-Sharkawy, 2003). The number of storage roots and their mean weight are yield components that determine sink capacity.

2.8 Absciscic acid and water deficit

A regulatory system that contributes to cassava's sensitivity to water deficit is the one involving the stress hormone Absciscic acid (ABA). In addition to closing stomates, ABA promotes characteristic developmental changes that can help plants cope with water deficit, including restriction of shoot growth and leaf area expansion (Creelman *et al.*, 1990; Lecoecur *et al.*, 1995; Alves and Setter, 2000, 2004), and stimulation of root extension (Sharp *et al.*, 1994). Studies have also indicated that for certain plant responses, sensitivity to water deficit is correlated with changes in ABA concentrations and genotypic responsiveness to ABA (Blum and Sinmena, 1995; Trejo *et al.*, 1995; Cellier *et al.*, 1998; Alves and Setter, 2000). Cassava leaves were found to accumulate substantial quantities of ABA in response to water deficit, and the highest ABA accumulation was in young leaves engaged in cell division and expansion (Alves and Setter, 2000). This is because water stress stimulates the rates of both biosynthesis and degradation of ABA and there is evidence that ABA catabolism into biological inactive products increase with age (Cornish and Radin, 1990; Alves and Setter, 2000; Alves and Setter, 2004). So, the difference between expanding and mature leaves may be a consequence of the lower capacity of expanding leaves to catabolize ABA and secondly the difference between expanding and mature

leaves might be due to difference in ABA transport. ABA rapidly decreases to control levels upon rewatering (Alves and Setter, 2000; Alves and Setter 2004) thus Confirming that ABA has a role in stomatal closure and leaf area growth reduction.

2.9 Breeding for drought tolerance

Under stressful environments with extended drought of several months, where major cereal and legume crops might fail, cassava produces reasonably well. This inherent capacity to tolerate complex stresses is supported by several morphological, physiological and biochemical mechanisms and traits, such as long leaf life, tight stomatal control over gas exchange, high photosynthetic potential and extensive fine root systems (El-Sharkawy, 2012). Core germplasm has been characterized and several clones tolerant to water stress and low-fertility soils have been identified to breed for drier areas in Africa and Latin America (El-Sharkawy, 1993). Several plant traits that may be of value in crop breeding and improvement have been identified, such as an extensive fine root system, long leaf life, strong root sink and high leaf photosynthesis (El-Sharkawy, 2004). Selection of parental materials for tolerance to drought and infertile soils under representative field conditions have resulted in developing improved cultivars that have high yields in favorable environments while producing reasonable and stable yields under stress (El-Sharkawy, 2004). This has led breeders in drought-prone regions to develop dedicated selection programs towards the development of drought adapted cultivars, using programmed stress environments and other selection tools (Blum 1988).

Heritability for yield under stress largely depends on 2 key factors; 1) the existence of genes for drought resistance in the population, which are effective in the stress environments under which

selection is performed (Blum *et al.* 2001), and 2) the degree of control over the homogeneity and general stress conditions in the selection nursery. Selection in stress-managed environments that do not suffer from additional problems (weeds, diseases, soil variability, etc.) will provide better heritability estimates for yield under stress than in unmanaged environments. Therefore, with the appropriate genetic materials and minimization of the error variance, heritability for yield under stress can be high and selection effective. Drought resistance can be recombined with high yield potential if selection is designed to recombine a high yield potential genotype with relevant dehydration-avoidance factors that are not associated with lower yield potential (Blum, 2005).

2.10 Summary of Literature

Cassava is known to adapt to conditions of both atmospheric and soil water shortage through various mechanisms, such as shedding leaves, closing stomata, osmotic adjustment, increasing root length, decreasing the leaf area and rapid wilting of leaves to lower light interception (El-Sharkawy, 1993, 2003; Aina *et al.*, 2007). However, no studies have been carried out in Uganda to understand how farmer preferred cassava cultivars respond to drought stress with regard to the above mentioned traits. This study will therefore bridge the knowledge gap on the physiological and morphological traits associated with drought tolerance in farm grown cultivars under Ugandan conditions.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Experimental sites

Field based studies were conducted in three locations, two drought prone areas of Nakasongola and Bullisa districts and one location with normal rainfall regime at Makerere University Agricultural Research Institute Kabanyolo (MUARIK). The rain-out shade experiment was conducted at MUARIK. MUARIK is located in central Uganda $0^{\circ} 28'N$, $32^{\circ} 37'E$ and 1,150m above sea level. It has deep red tropical soils (ferralsols) with a pH of 5.2 – 6.0 (Tenywa *et al.*, 2000) and a bimodal mean annual rainfall of 1300 mm characteristic of the Lake Victoria Crescent area (Arnold, 1993). Nakasongola District is located in the north-western part of central region of Uganda $01^{\circ} 18'32"N$ $32^{\circ} 27'23"E$ at an altitude of 1130 above sea level. It's one of Uganda's driest districts with annual rainfall ranging between 600 mm and 1000 mm and a five-month long dry season (Nakasongola District Environment Policy, 2009), making it suitable for the drought tolerance experiments. Bullisa District is located in the northern part of western region of Uganda at $02^{\circ} 10'30"N$ $31^{\circ} 24' 00"E$ and 600 m above sea level. The soil is characterized by deep nitosols and andosols enriched with shiny ped surface at the lower horizon. Bullisa is also characterized by high day average temperatures of $33.2^{\circ}C$ and very low average night temperatures of $17.5^{\circ}C$. It has a bimodal type of rainfall with its peak in October and long dry spell of November to April, with January being the driest month.

The locations for the study were selected after collecting and analyzing Uganda's metrological data for the last 10 years and coming up with districts with drought conditions (Figure 1).

Kotido was outstandingly dry but because of the insecurity in the area and for the safety of experiments from animals a decision was made to conduct trials in safer areas rather than Kotido thus, the districts of Bullisa and Nakasongola were selected for drought prone areas and MUARIK for normal rainfall conditions.

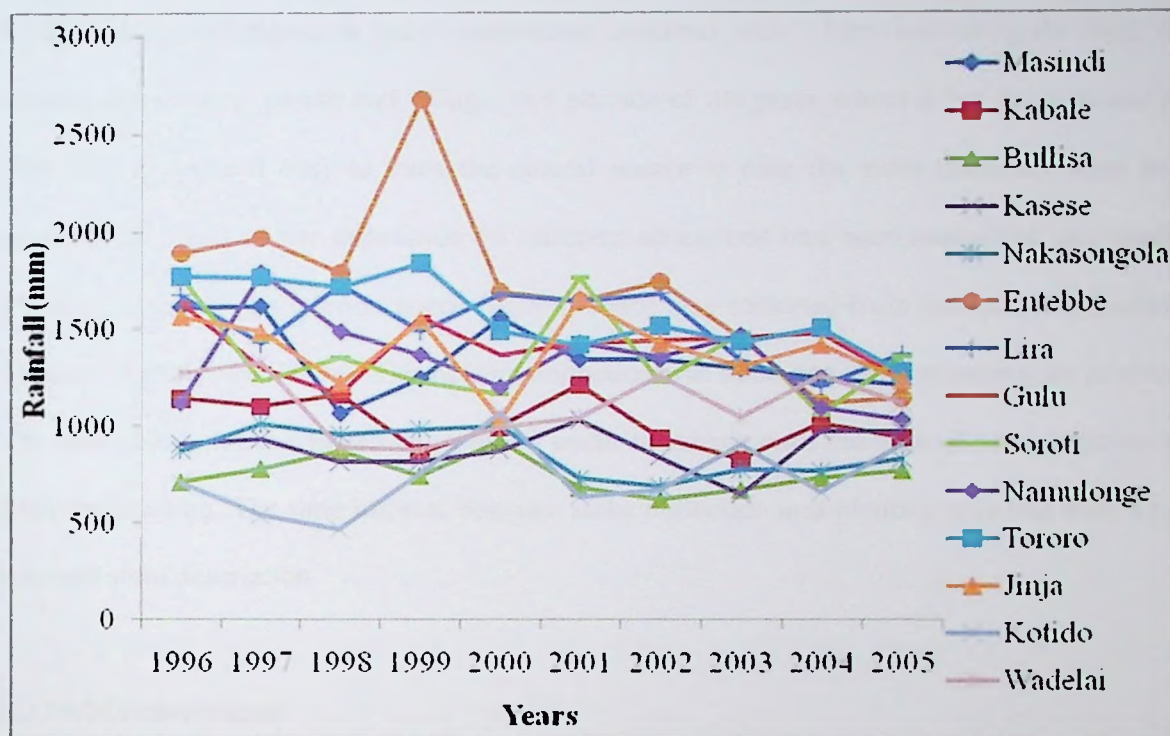


Figure 1 Average annual rainfall of 14 selected districts in Uganda for 10 years

3.2 Selection and collection of cassava cultivars

A diverse set of germplasm which included 44 landraces and 12 improved varieties (Annex 2) were collected from 17 districts of Uganda (Mukono, Jinja, Iganga, Bugiri, Busia, Tororo, Mbale, Pallisa, Kumi, Kaberamaido, Dokolo, Lira, Masindi, Buliisa, Hoima, Kibale and Mityana) (Annex 1) and assembled for initial field screening. The districts are some of the major cassava producing areas in central, northern, eastern and western parts of the country. In

partnership with staff of the national cassava programme of National Agricultural Research Organisation (NARO), germplasm were identified after discussions with the farmers on preferred traits of the cultivar, and collections made based on the farmers' knowledge and crop performance in the field. Three stems of selected cultivars were cut, chopped into small pieces of 25cm long and placed in the transportation container with a label indicating the local name, district, sub-county, parish and village, and altitude of the place where it has been picked from. This was to make it easy to trace the natural source in case the same materials were needed again. By the end of the expedition 56 different accessions had been assembled and ready for planting. One drought tolerant check (MM96/0686) was collected from International Institute of Tropical Agriculture (IITA). Germplasm collection was done one week prior to start of planting. The assembled planting materials were left under the shade until the time of transportation to the field for planting. The time interval between stake collection and planting was less than 4 weeks to avoid stem deterioration

3.3 Field experiments

The field trials were planted between 27th-30th October 2008 in Bullisa, Nakasongola and Kabanyolo with the aim of ensuring the long December – April drought coincides with the critical growth stage of cassava. The experiments were carried out in fields previously occupied by maize. The land was ploughed and disc harrowed. The experiments consisting of the 56 different cultivars were laid out in a randomized complete block design (RCBD) with two replicates, ten plants/cultivar per replicate spaced at 1m x 1m. Two replicates were used due to shortage of planting materials. After field screening, 15 cultivars contrasting in response to drought stress were selected on the basis of number of surviving plants after the three month of

moisture deficit stress. Six cultivars exhibiting tolerance to drought, four moderately tolerant and five most susceptible cultivars were selected and advanced for detailed physiological and morphological analysis under controlled moisture conditions (Annex 4).

3.4 Potted experiments

These experiments were set up at MUARIK in a rain-out shade using 15 cassava cultivars selected from the field experiments for detailed analysis. The rain-out shade was a shelter constructed with wooden poles and covered with transparent polythene sheet on top to prevent rain water from reaching the experimental units. Plants were established in large polythene bags of 80 cm deep and 60 cm diameter. The bags were filled with 150 kg of soil each collected from a nearby field that had been under fallow for the last two years. The soil was collected from a depth of 0-15 cm, air dried and thoroughly mixed before sieving through a 10 mm screen to remove uneven particles. 10 holes of 1 mm were drilled evenly into the base of each pot to ensure good drainage. Two days prior to planting the pots were sufficiently watered to saturation and allowed to drain. Planting was done on 20th May 2010. The trial was laid out in a RCBD with 10 potted plants per cultivar in every treatment and replicated twice. The experiments were blocked because the sides of the rain-out shade were open and variation in amount of light received by the cultivars and air humidity were expected. Two healthy cuttings of uniform size (25 cm long) were planted in each pot and later thinned to one plant 30 days after planting (DAP). All the pots received adequate water supply by adding five litres of water once every two days to maintain it at optimal levels for the first one month after planting and thereafter adjusted to two watering regimes (i.e. limited and adequate watering regimes). Limited watering regime (stressed) involved adding five litres of water once every three weeks, while adequate

watering (non-stressed) received five litres twice every week following the procedures of Igram and Anderson (1993). Five weeks after planting five cultivars were highly affected by cassava mosaic disease making all the leaves shrivelled and deformed to the extent that could not be used for drought physiological and morphological data. The five cultivars were dropped leaving only 10 cultivars for detailed physiological studies. The experiments were harvested on 4th Feb 2011.

3.5 Experimental measurements

Field data collection on crop establishment (sprouting) was carryout one month after planting (MAP) while data on number of surviving plants, plant vigour and leaf wilting was collected monthly starting 1 MAP and ended five MAP. This is because by four MAP most of the plants in Bullisa and Nakasongola had dried because of severe drought. In the rain-out shade experiments data on establishment was collected 1 MAP while other physiological and morphological data collection was collected monthly starting 2 MAP. This is because in the rain-out shade there was control on the amount of water the plants were receiving, while in the field we were relying on rain-fed conditions. Five plants/cultivar per treatment in each replicate were randomly selected for data collection on physiological, morphological and yield parameters.

3.5.1 Physiological parameters

1). *Stomatal conductance*; was recorded every week using a steady state porometer, and measurements recorded in millimoles (Mmols). Measurements of stomatal conductance were taken on the youngest fully expanded exposed leaves (3/plant) between 10:00hrs and 13:00hrs. This is because at this time of the day the stomata are still open and active because of high radiation. This was done by placing the leaf in the middle of the porometer sensor until the

readings become consistent and stable then the machine was set to calculate average readings on each leaf which were recorded and entered in field books.

2). *Xylem pressure potential*; was measured using pressure chamber apparatus (soil moisture equipment corporation, Santa Barbara, USA) using leaf petioles. Five plants were selected from each cultivar in each treatment and measurements were done on three youngest fully expanded leaves. To minimize errors the leaf was detached from the plant and immediately sealed in the steel chamber with only the cut end (petiole) protruding out. Pressure was applied to the chamber from a pressure source of compressed nitrogen gas. When the sap meniscus just appeared at the xylem surface the pressure was recorded in bars. Measurements were done between 10:00 and 13:00 hours.

3). a). *Plant wilting*; was visually scored using a scale of 0-5; where 0 = dry/dead plant, 1 = extreme stress with virtually all leaves wilted and fallen (total wilting), 2 = more than average wilting, 3 = average leaf wilting, 4 = better than average and 5 = Normal vigorous growth. This was done by just looking at the general appearance of the 10 plants of each cultivar in each treatment and wilting scores recorded.

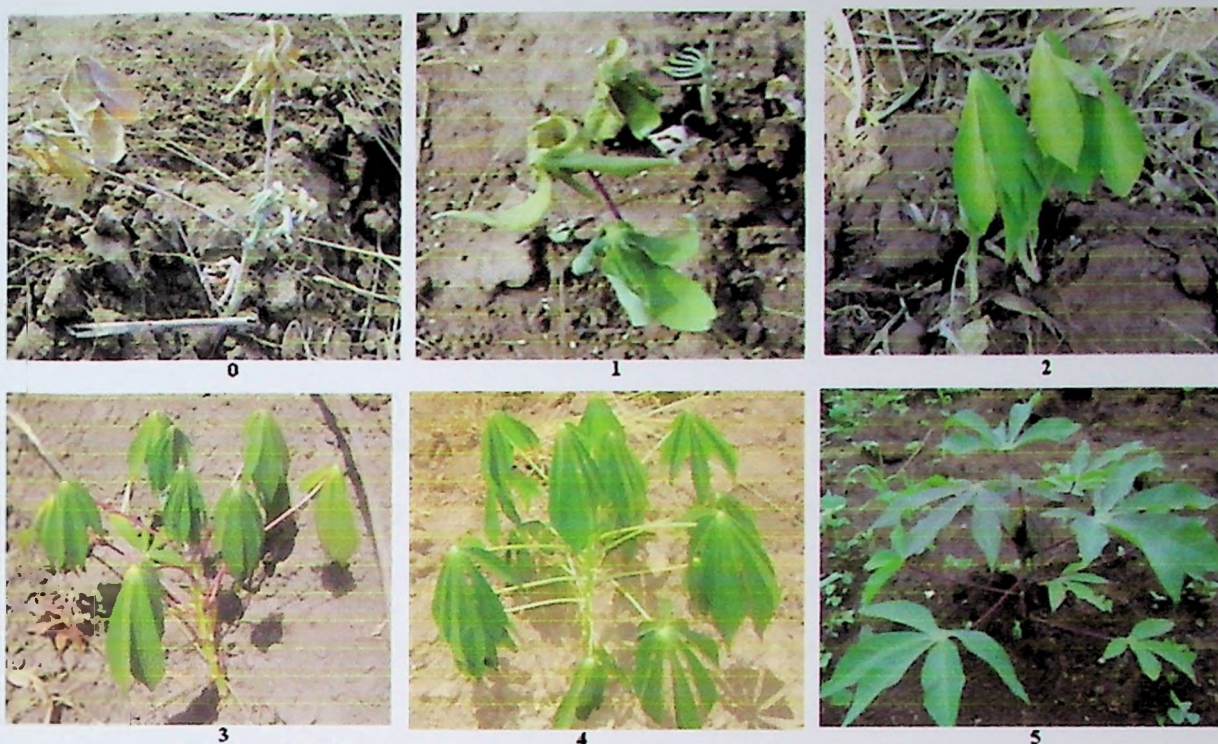
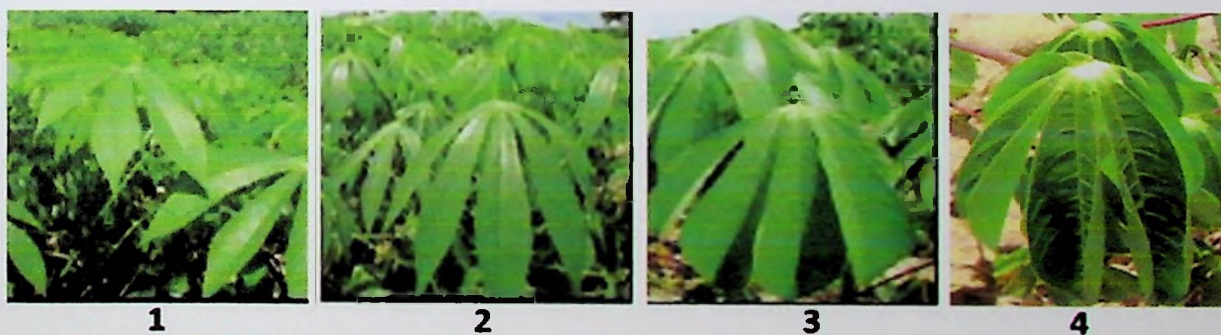


Figure 2 Scales for scoring plant wilting in response to drought stress in the field

b). leaf rolling/wilting; Leaf wilting/rolling was used for rain-out shade experiments. It was estimated visually on a scale of 1-5. Where 1 represented little stress with most leaves retained and 5 represented extreme stress with virtually all leaves wilted and fallen (Osiru *et al.*, 1994).



3.5.2 Morphological parameters

Plant height; was determined by measuring the length of primary stem of the cassava plant using a meter ruler and recorded in centimeters to one decimal. This measurement was taken from the soil level to the highest point of the plant. Measurements on plant height were taken every month starting three MAP.

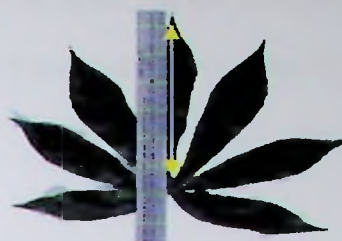
Leaf retention (amount of leaves retained per plant); was determined by calculating the percentage of leaves remaining on the plant after a period of water deficit stress. Data was collected monthly starting 3 MAP on five plants per cultivar in each treatment by measuring the total plant height and height of the plant portion still having leaves and percentage leaf retention calculated using the formula;

$$\text{Percentage leaf retention} = \frac{\text{height of plant portion with leaves}}{\text{Total plant height}} \times 100$$

Leaf area; Three leaves per plant on five plants per cultivar per treatment were selected for assessment of leaf area. Measurements were taken at one month interval for six month starting two MAP. Leaf area was determined by measuring the middle lobe length (MLL) and maximum middle lobe width (MLW) of young fully expanded leaf using a meter rule following procedures described by Alves and Setter (2000). The MLL/ MLW ratios were computed to determine leaf shapes of different genotypes using the scales; 9-13 = Linear, 6-8 = hastate, 5-6 = lanceolate, 4 = oblong and 3 = obovate (Alves and Setter, 2000). Using the equation, $A=aL^b$ (A = leaf area, L = central lobe length (cm) and a & b coefficients of the central lobe shapes) developed by Alves and Setter, (2000), most cultivars had obovate shapes and so the most suitable equation used to determine leaf areas was $1.6507L^{1.7806}$.



a= maximum width of central lobe



b= length of central lobe

Figure 3 Showing procedures of measuring leaf area using central leaf lobe

Fibrous root system; five plants/cultivar per treatment were sampled at harvest (9 MAP) and adventitious roots arising from the cut end and the lower portion of the node of the cassava stem cuttings were carefully removed from surrounding soil with a gentle stream of water. To determine the effect of soil moisture deficit stress on cassava root system, fibrous root length were measured in centimetres and recorded to one decimal following the root intersect method proposed by Tenant (1975). This involved scattering roots on a grid and counting the number of root gridline interaction points and the number of points were then multiplied by the conversion factor 2.3571 appropriate for the 3 cm by 3 cm grid used.

3.5.3 Yield parameters

Nine months after planting, five plants/cultivar/treatment were harvested. The harvested plants were separated into storage roots, fibrous roots, stems and leaves (including petioles). The above-ground and below-ground biomass was weighed separately. Harvest index (HI) calculated following procedures described by Fukuda *et al.*, (2010) as given below;

$$HI = \frac{\text{weight of roots}}{\text{weight of roots} + \text{weight of above ground biomass.}}$$

Crop yield was determined by counting the number of fresh storage roots on each of the five plants harvested and fresh storage root weight was determined by weighing all the fresh storage roots obtained from each of the sampled plants.

3.6 Statistical Analysis

In both field and rain out shade experiments, data were recorded on plot basis and analysis across-sites and treatments for all the traits were done. GENSTAT 12th edition (VSN International Ltd. www.vsni.co.uk) was used for the analysis of variance (ANOVA) and correlation analysis. While the Linear Mixed Model selection in the Restricted Maximum Likelihood (ReML) was used for ANOVA for GxE following the procedure in GENSTAT. Since the study, quantified effects of each of the treatments (stressed and non-stressed conditions), generalized linear mixed model selection provided a more flexible approach for analyzing the nonnormal data when random effects were present. GxE data was analyzed as a generalized linear mixed model, treating effects of the different locations as a random effect. Means were compared using Fishers Protected Least Significant Difference (LSD) test at $P \leq 0.05$.

CHAPTER FOUR

RESULTS

4.1 Field evaluation of cassava cultivars across locations

56 farmer preferred cassava cultivars were evaluated in three locations, two of which were drought prone (Nakasongola and Bullisa), while the other, Makerere University Agricultural Research Institute Kabanyolo (MUARIK) had a normal rainfall regime (1400mm annual rainfall). The aim of the evaluation was to assess the responses of farmer grown cassava cultivars to moisture deficit stress and estimate the genotype by environment (G x E) interaction. Sprouting was up to 100% in the 3 sites however, due to the early drought that set in during cassava establishment, most of the plants in Bullisa and Nakasongola dried. Results on average number of plants surviving, plant vigor and leaf wilting are presented in Annex 3. Data on these parameters was taken on monthly basis for four month starting one month after planting. Data collection in this experiment stopped four months after establishment since most of the plants in Bullisa and Nakasongola sites dried up within three months (Figure 4). Mean squares from the analysis of variance indicated significant differences ($P \leq 0.001$) among cultivars as evaluated across locations for the number of plants that survived and the degree of wilting after drought stress. G x E was also significant ($P \leq 0.001$) for both traits (Table 1). These reflect genotypic differences towards adaptation to different environments and tolerance to moisture stress conditions. Kabanyolo was included in analysis of GxE because it was expected that cultivars that perform well in drought areas should perform equally well in areas with normal rainfall. It was also to give a good comparison of reduction in performance of cultivars due to drought stress.

Table 1 Analysis of variance for selected traits measured in the field

Variable	d.f.	Mean squares		
		No. of plants	Vigor (1-5) ^b	Wilting (0-5) ^a
Site	2	1614.67	89.60	56.05
Replication/Site	3	55.50	2.53	1.85
Variety	55	18.71***	0.72	0.92**
GxE	110	8.15***	0.52	0.46***
Error	160	4.20	0.45	0.25
F (variety)		2.15	1.30	1.89
F-prob (variety)		P≤ 0.001	0.125	0.003
F (GxE)		1.94	1.16	1.81
F-prob(GxE)		P≤ 0.001	0.203	P≤ 0.001

^a 0-5 (0 = dry/dead plant, 1 = extreme stress with virtually all leaves wilted and fallen (total wilting), 2 = more than average wilting, 3 = average leaf wilting, 4 = better than average, 5 = normal vigorous growth).

^b (1-5) 1= poor plant vigour, 5 = very vigorous/healthy plant

***Significant at $p \leq 0.001$, **Significant at $p \leq 0.01$, *Significant at $p \leq 0.05$

Rainfall being the critical factor distinguishing the three different growing environments, MAURIK (1400mm) Nakasongola (600mm) and Buliisa (500mm) signified a high level of soil moisture stress in the two locations. Results indicate that moisture stress had significantly ($P \leq 0.0001$) devastating effects on both number of surviving plants and degree of wilting (Table 1). The overall performance of cultivars across locations indicates that Buliisa had the most severe effects of drought followed by Nakasongola, while Kabanyolo experienced less effect since it received normal rainfall regime (1400mm) for cassava growth. There were significant reductions in the number of surviving plants after drought stress with an average of 2, 4 and 10 surviving plants/cultivar in Billisa, Nakasongola and Kabanyolo, respectively (Figure 5).



^a Healthy cassava plant in Kahanvolo



^b Cassava plant wilting to death in Buliisa

Figure 4 shows contrast of normal plants in Kabanyolo and drying plants in Bullisa sites

The different cassava cultivars evaluated in the 3 sites responded differently to moisture deficit stress. Cultivars MH97/2961, Gwalanda, Kwatamumpare, and TME 14 performed well under low soil moisture conditions with above 40% surviving plants on average and an average plant vigour greater than 1.5 score, while Nase 3, Bamunanika, Mulyandongo performed poorly with less than 20% of plants surviving (Fig 6 and 7). The rest of the cultivars evaluated had intermediate performances (Annex 3). On average, cultivars in Buliisa and Nakasongola had plant vigour scores of less than one indicating that they either dried up or were drying

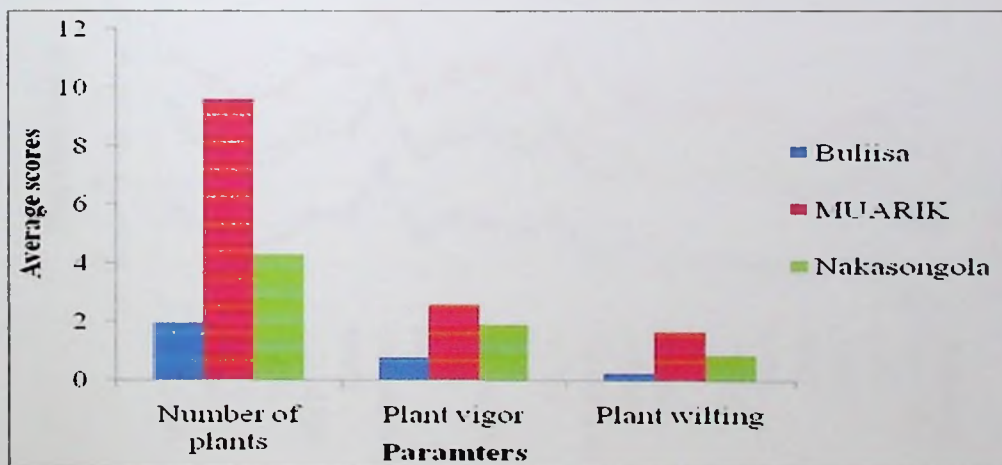


Figure 5 Performance of cassava cultivars across three locations

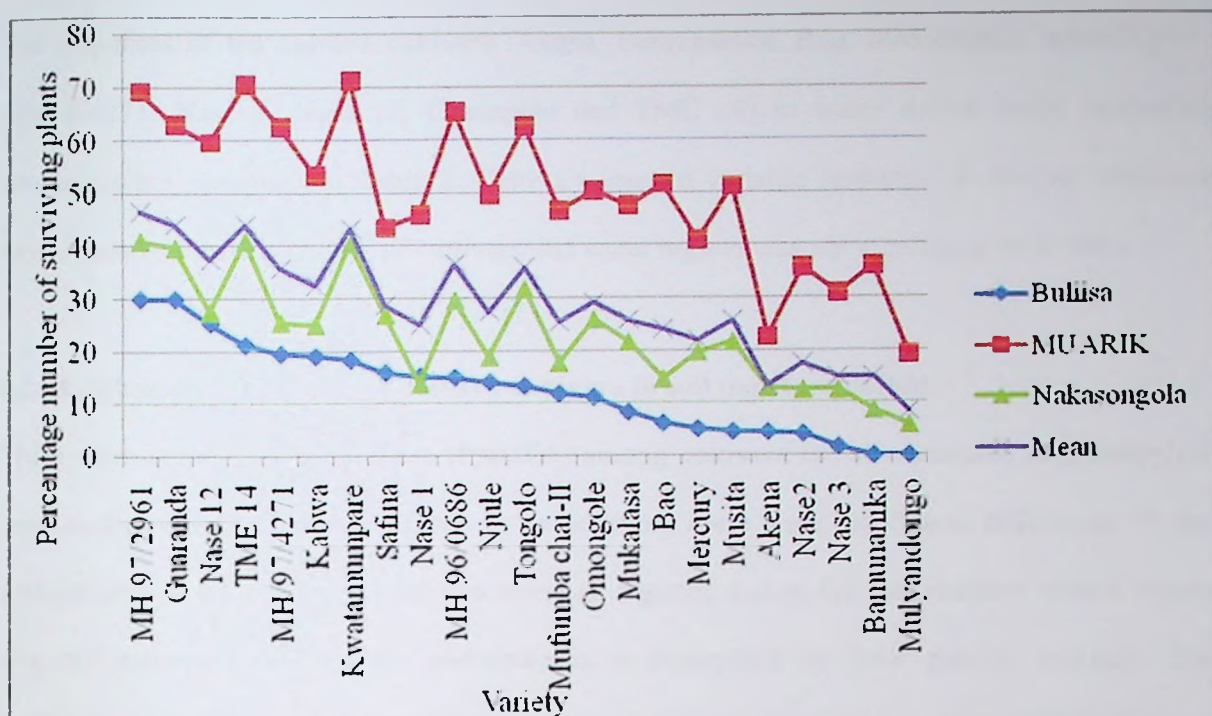


Figure 6 percentage of surviving plants under moisture deficit stress

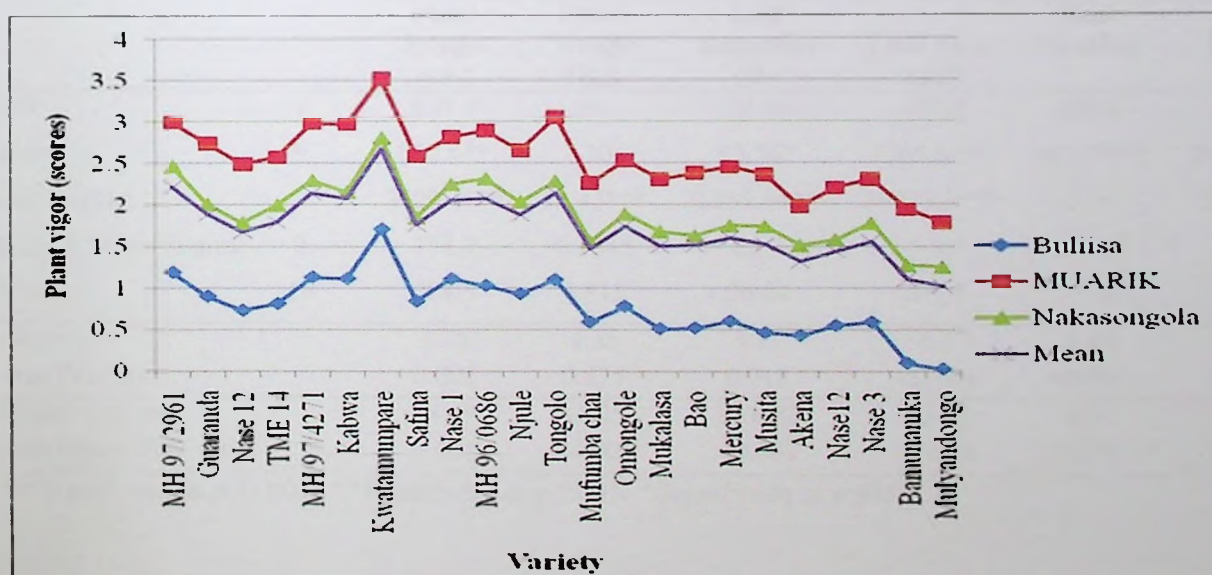


Figure 7 Plant vigour in response to drought stress

4.1 Rain-out shade experiment

The responses of ten cassava cultivars (Akena, Bamunanika, Bao, MM96/0686, MM97/2961, MM96/4271, Nase 3, Nase 12, Omongole and TME 14) to water deficit under controlled conditions are presented in Table 2. Cultivars showed variable responses in the six measured traits; however, the interaction of cultivars and water regime was not significant ($P \leq 0.001$).

4.2 Morphological response of cassava cultivars to soil moisture deficit

There were significant differences ($P \leq 0.001$) among cultivars for all measured morphological traits except for shoot weight (Table 2). In addition, there were significant differences in the performance of all cultivars in the two watering regimes except for root number, which means that the variations in cultivars performances is controlled by their genetic makeup. The performance of different cassava cultivars in the two watering regimes is presented in Table 3.

Table 2 Analysis of variances for selected morphological traits under two watering regimes

Source of variation	d.f	Mean squares					
		Plant Height (cm)	Shoot Weight (Kg)	Leaf Retention (%)	Leaf Area (cm ²)	Root Number	Root Length (cm)
Block	1	815.1	0.1	53.74	37.4	43.06	179.92
Variety	9	962.6**	1.104	83.36*	1965.6***	187.37***	280.32***
Water Regime	1	2920.4***	12.43***	26355.94***	39913.3***	0.16	270.14**
Variety x Water Regime	9	171.2	0.7346	55.7	316	19.15	21.33
Residual	19	201.5	0.815	26.84	299.4	27.21	23.19
F (Variety)		4.78	1.35	3.11	6.57	6.89	12.09
F-Prob (Variety)		0.002	0.275	0.018	<0.001	<0.001	<0.001
F (Water Regime)		14.49	15.25	981.92	133.32	0.01	11.65
F-Prob (Water Regime)		0.001	<0.001	<0.001	<0.001	0.94	0.003

***Significant at $p \leq 0.001$, **Significant at $p \leq 0.01$, *Significant at $p \leq 0.05$

Plant height

Low soil moisture generally reduced plant heights of all the cultivars evaluated with the highest reduction of above 22% observed in Bamunanika, Bao and Akena. Cultivars MH97/2961 and MM96/0686 were more tolerant to moisture deficit with less than 6% reduction in plant height under drought conditions (Table 3). No significant differences were observed for plant height for the non-stressed plots. This is because moisture deficit stress influences respiration, photosynthesis, absorption, translocation and utilization of mineral nutrients, and cell division thus causing stunted growth.

Leaf area

Under non-stressed treatment, variety Akena, produced the highest leaf area of 213.4cm^2 per plant and Nase 12 had the lowest leaf area of 109cm^2 . On the other hand, Omongole had the least leaf area of 59cm^2 per plant under drought stress conditions (Table 3). No significant differences were observed in leaf area under the stressed treatment. None the less, drought stress considerably reduced the leaf area per plant in all the cultivars evaluated. The highest decline in leaf area of 56%, 48% and 47% was observed in Omongole, Akena and Bamunanika respectively. Nase 3, TME 14 and Bao exhibited some level of tolerance to moisture deficit compared to other cultivars. This is indicated by the low percentage reduction in leaf area of 38% in these cultivars.

Leaf Retention

Drought stress had severe effects on leaf retention in all cultivars with the highest reductions of >80% observed in TME 14, Bao and MM96/4271 (Table 3). MM96/O686 and Bamunanika

retained more leaves than the rest of the cultivars with leaf retention declines of 65.97% and 68.8% respectively under drought conditions.



a Healthy cassava with all the leaves under normal watering



b Cassava which has lost almost all the leaves due to moisture stress

Figure 8 MM96/4271 under normal watering and under drought stress

Fibrous root number and length

Drought stress resulted into increased number of fibrous roots per plant in five cassava cultivars (Bamunanika, MM96/4271, MM96/0686, Nase 12 and Omongole. Considerable increases were registered in Nase 12 which increased from 18 roots per plant under non-stressed conditions to 29 roots per plant under drought conditions (Table 3). This is illustrated by the highest negative percentage reduction (-56%) in number of roots per plant. Other cultivars that registered slight increase in root numbers include; Bamunanika, MM96/4271, MM96/0686 and Omongole whose fibrous root numbers increased by 5%, 5%, 1.5% and 2% respectively. In addition, drought stress generally caused an increase in fibrous root length of most cultivars with remarkable increases registered in cultivars Akena and TME 14 whose fibrous root length increased by 59% and 36% respectively (Table 3). The increase in number and length of cassava roots under drought stress is most likely a coping mechanism to increase the surface area for water and or mineral absorption.

Shoot/Above ground biomass

No significant differences in shoot weight were observed for both within the stressed and the non-stressed plots (treatments). Nonetheless, there were pronounced effects on shoot biomass due to drought stress. Drought stress severely reduced the shoot biomass of Akena, Bamunanika, Nase 3 and MH97/2961 by >50% (Table 3). Cultivars which had the least percentage reductions in shoot biomass were TME 14 (7%) and MM96/0686 (3%). The reduction in shoot biomass after imposition of drought stress could be due to the lost of leaves, stunted stem growth and reduced leaf area.

Table 3 Response of selected cassava cultivars under two watering regimes

Variety	Plant height (cm)			Shoot weight (Kg)			% Leaf retention			Leaf area (cm ²)			Root No.			Root Length(cm)		
	NS	ST	%Red	NS	ST	%Red	NS	ST	%Red	NS	ST	%Red	NS	ST	%Red	NS	ST	%Red
Akena	124.20	80.40	35.27	4.15	1.83	55.90	68.10	16.27	76.11	213.40	111.40	47.80	18.75	12.88	31.31	20.99	33.33	-58.79
Bamunika	129.40	100.10	22.64	3.33	1.53	54.05	61.67	19.24	68.80	162.50	86.70	46.65	28.00	29.50	-5.36	40.29	39.25	2.58
Bao	92.60	70.20	24.19	2.62	1.45	44.66	70.57	12.58	82.17	157.80	97.50	38.21	31.75	30.62	3.56	50.19	52.33	-4.26
MH97/2961	87.60	85.00	2.97	3.95	1.58	60.00	62.87	17.40	72.32	137.00	79.00	42.34	38.88	36.00	7.41	37.08	38.50	-3.83
MM96/4271	80.10	68.10	14.98	1.93	1.48	23.32	80.23	14.28	82.20	112.30	63.90	43.10	29.00	30.38	-4.76	43.83	49.67	-13.32
Nase 12	84.10	70.40	16.29	1.55	0.85	45.16	63.19	14.15	77.61	109.10	67.50	38.13	18.38	28.75	-56.42	28.58	37.42	-30.93
Nase 3	104.50	82.80	20.77	2.98	1.45	51.34	75.31	15.78	79.05	137.60	85.40	37.94	22.12	18.62	15.82	26.67	30.67	-15.00
MM96/O686	70.00	66.30	5.29	2.48	2.40	3.23	70.47	23.98	65.97	155.10	86.00	44.55	24.50	24.88	-1.55	27.21	35.29	-29.69
Omongole	70.70	58.80	16.83	2.08	1.50	27.88	59.15	12.67	78.58	133.60	59.00	55.84	24.62	25.12	-2.03	26.10	26.04	0.23
TME 14	96.60	81.50	15.63	2.28	2.12	7.02	57.64	9.45	83.61	131.40	81.60	37.90	37.75	35.75	5.30	28.58	39.01	-36.49
LSD	ns	16.8		ns	ns		9.478	ns		41.42	ns		ns	9.01		9.16	12.9	
CV (%)	18.3	9.7		38.2	46.7		6.3	34.3		12.6	20.9		22.4	14.6		12.3	14.9	

ST : Stressed experiment (watered once every 21 days after 2MAP)
NS : None stressed experiments (watered twice a week)
ns : non significant
% Red: Percentage reduction
- %Red: an increase in that measured parameter under moisture deficit stress
LSD : Least significant difference; CV (%): coefficient of variation

3 Physiological responses of cassava cultivars to soil moisture deficit

Physiological parameters measured include; xylem pressure potential, stomatal conductance and leaf rolling/wilting. Xylem pressure potential indicates the demand for water within the plant due to evapotranspiration. High xylem pressure potential causes many physiological processes such as slowing/stopping cell elongation and photosynthesis, and may eventually result in death of the plant. Xylem pressure potential is used to evaluate the plants' need for water or how well it is adapted to its environment. Stomata conductance is the closing and opening of the stomata in the plant. The plant regulates water by opening and closing of its stomata. In case of low soil moisture the plant closes its stomata to minimize water loss by evapotranspiration. The closing of the stomata reduces the amount of carbon dioxide taken in and thus the amount of assimilates produced by the plant.

Table 4 Analysis of variances for physiological traits under two watering regimes

Source of variation	d.f	Mean Squares		
		Stomatal conductance (Mmols)	Leaf wilting (1-5) ^a	Xylem Press. Pot. (Bars) ^b
Block	1	846	0.625	1.60
Variety	9	1859	0.1717	1.34
Water Regime	1	169509***	35.156***	66.74***
Variety x Water Regime	9	1073	0.1858	1.88
Residual	19	1316	0.1711	1.81
<i>F</i> (Variety)		1.41	1.00	0.74
<i>F</i> Prob. (Variety)		0.251	0.47	0.67
<i>F</i> (Water Regime)		128.77	205.53	36.89
<i>F</i> Prob. (Water Regime)		<0.001	<0.001	<0.001

***Significant at $p \leq 0.001$, **Significant at $p \leq 0.01$, *Significant at $p \leq 0.05$

Stomatal conductance

Results on stomatal conductance showed no significant variations amongst cultivars but there were significant difference ($P \leq 0.001$) across watering regimes (Table 4). Mid-day stomatal conductance was relatively lower in all cultivars under moisture stress conditions with percentage stomatal conductance reduction ranging between 57% in Nase 3 to 86% in Nase 12. Relative to normal watering, moisture deficit reduced stomatal conductance of Nase 12 and MM96/4271 by 86% and 84% respectively making them the most responsive to drought (Table 5). MM96/4271 had relatively higher stomatal conductance of 232Mmols and MM96/0686 had the lowest stomatal conductance of 118Mmols under non-stressed conditions. Overall, there were considerable reductions in stomatal conductance in all cultivars due to drought stress (Table 5).

Xylem pressure potential

Xylem pressure potential varied significantly across watering regimes with drought stress causing a general increase in xylem pressure potential of all the cassava cultivars evaluated (Table 4 and 5). Results however, indicated no significant variation among cultivars in both stressed and non-stressed plots (Table 5). The highest pressure potential of 8 bars was observed in TME 14 and the lowest of 3.6 bars was observed in omongole. The xylem pressure potential of TME 14 rose from 1.5 bars under non-stressed conditions to 8 bars under drought stress making it to have the highest increase in xylem pressure. Furthermore, cultivars omongole, Bao, MH97/2961 and Akena had their xylem pressure potentials at around 3.8 bars indicating better adaptation to water deficit conditions (Table 5).

Leaf wilting

Leaf wilting was recorded using a score scale of 1-5; 1 being normal and 5 severe wilting and results indicated that drought stress caused significant leaf wilting in all cultivars. The highest wilting of 72.41% and 70.70% was in Nase 12 and Bamunanika (Table 5). Nase 12 showed more severe wilting (3.6) under drought stress conditions. MH96/0689, MH97/2961, MH97/4271 and Akena were relatively stable with wilting score of about 2.5 (Figure 10). These results indicate that MM96/0686, MH97/2961, MM96/4271 and Akena are fairly tolerant to drought stress.

Table 5 Physiological traits as affected by two watering regimes

Variety	Leaf wilting (1-5)			Stomatal conductance (Mmol)			Xylem pressure potential(Bars)		
	ST	NS	% Incr.	NS	ST	% Red.	ST	NS	% Incr.
Akena	2.81	1.13	59.99	215.90	61.10	71.70	3.83	2.00	47.78
Bamunanika	3.63	1.06	70.70	189.70	53.40	71.85	5.33	2.17	59.29
Bao	2.88	1.13	60.87	168.20	41.20	75.51	3.75	2.00	46.67
MH97/2961	2.44	1.00	58.98	171.90	38.70	77.49	3.83	1.50	60.84
MH97/4271	2.81	1.00	64.44	232.90	37.40	83.94	4.00	1.92	52.00
Nase 12	3.63	1.00	72.41	163.90	22.90	86.03	4.00	1.42	64.50
Nase 3	2.81	1.00	64.44	136.60	58.60	57.10	5.08	1.67	67.13
MH96/O689	2.44	1.13	53.86	118.00	24.00	79.66	3.75	2.00	46.67
Omongole	3.19	1.13	64.71	173.00	37.50	78.32	3.67	2.67	27.25
TME 14	2.81	1.13	59.99	135.30	28.50	78.94	7.50	1.58	78.93
LSD	ns	ns		ns	ns		ns	ns	
CV(%)	19.4	7.80		25	58.8		41.40	29.90	

ST : Stressed experiment (watered once every 21 days).

NS : None stressed (watered twice a week)

% Incr. : Percentage increase $(ST-NS)/ST*100$

% Red. : Percentage reduction $(NS-ST)/NS*100$

LSD : Least significant difference

CV (%): coefficient of variability

4.4 Variation in cassava yield components under drought stress

Analysis of variance of yield parameters of cassava cultivars across the two watering regimes is given in Table 6. Significant differences ($P<0.05$) were observed among cultivars and watering regimes for most of the measured yield components. There were highly significant differences ($P<0.001$) in cultivar performance in the two watering regimes implying that the expression of these traits is influenced by drought (Table 6). There was no significant interaction between variety and water regimes (Table 6). Results also showed that low soil moisture reduced cassava yields in all the cultivars (Table 7).

Table 6 Analysis of variances for yield components as affected by two watering regimes

Source of variation	d.f.	Mean Squares				
		Stor root Number	Stor root length (cm)	Stor root Circumf. (cm)	Stor root weight (Kg)	Harvest index
Block	1	0.13	0.00	3.08	0.32	0.004
Variety	9	9.78***	20.7*	4.22	1.62**	0.022**
Water Regime	1	27.64***	39.68*	211.27***	31.24***	0.331***
Variety x Water Regime	9	0.38	15.78	2.08	0.72	0.006
Residual	19	0.85	8.29	3.99	0.43	0.007
F (Variety)		11.55	2.50	1.06	3.78	3.20
F-Prob. (Variety)		<0.001	0.044	0.435	0.007	0.016
F (Water Regime)		32.63	4.7	52.93	73.02	49.10
F-Prob. (Water Regime)		<0.001	0.041	<0.001	<0.001	<0.001

*, Value significant at $P\leq 0.05$; **, Value significant at $P\leq 0.01$; ***, Value significant at $P\leq 0.001$

Stor, storage

Number of storage roots

Significant differences ($P\leq 0.001$) were observed among cultivars and watering regimes for number of storage roots in cassava (Table 6). Relative to the number of storage roots per plant in non-stress conditions, low soil moisture resulted in an overall reduction of storage root number between 25% in Bamunanika to 47% in MH97/2961 (Table 7). Drought had the least effect on storage root number in Bamunanika 25% and Akena 27.8% reduction as compared to other

varieties which recorded >33% reduction in root number. The highest reduction in tuber number due to low soil moisture was in Bao and Omongole 38% each and 47% in MH97/2961 (Table 7).

Storage root length and circumference

There were significant differences ($P \leq 0.05$) in storage root length among cultivars and across watering regimes (Table 6). In addition, there were also significant variations ($P \leq 0.001$) in storage root circumference across the two watering regimes. Drought stress caused an increase in storage root length particularly for cultivars MM96/O686 (11.6%), TME 14 (14.6%) and Akena (27.9%) while significantly reducing storage root circumferences of the same cultivars with percentage reductions of 31.4% for Akena, 40.4% for TME 14 and 23.6% for MM96/0686 (Table 7). This could be due to shift in function of cassava storage roots from bulking to water absorption. Low soil moisture also caused a high reduction in storage root length of MH/97/2961 (41.3%), Nase 12 (33.9%), Bao (33.0%).

Fresh storage root weight

There were significant variations ($P \leq 0.01$) in fresh storage root weight among cassava cultivars evaluated and across watering regimes (Table 6). Drought generally reduced fresh storage root weight in all the cultivars causing average reductions of between 30% in MM96/0686 and 85% in Nase 12. The least drought effects were in cultivar MM96/0686 (30.2%). All other cultivars had >50% reduction in storage root weight resulting from drought stress (Table 7).

Harvest Index (HI)

Results showed significant difference ($P \leq 0.01$) for harvest index among cultivars and across watering regimes (Table 6). There were significant difference ($P \leq 0.01$) for harvest index among cultivars in non-stressed plots and no significant difference among cultivars in stressed treatments (Table 7). Low soil moisture caused an average reduction of HI between 10-57% among cultivars. Cultivars Akena (9.6%), MM96/O686 (13.0%) and MM96/4271 (29.3%) showed minimal reductions in harvest index in response to drought stress, while Bao (52.1%) and Nase 12 with (57.4%) had over 50% reduction in HI under low soil moisture (Table 7).

Drought Response Index (DRI)

Drought response index (DRI) calculated as the ratio of yield under drought stress to the yield under non-stress conditions is used to estimate the yield response of a cultivar under moisture deficit conditions. The higher the DRI of a particular cultivar under drought stress, the better that cultivar. Results indicated that cultivars MM96/4271 with DRI of 0.41, omongole (0.47) and MM96/O686 (0.7) performed better than the rest of the cultivars under low soil moisture conditions. Cultivars Nase 12, Bao and Bamunanika with DRI of 0.15, 0.18 and 0.19 respectively, were highly affected by drought stress (Table 7).

Table 7 Variations in cassava yield components under two watering regimes

Variety	Stor root number			Stor root length (cm)			Stor root circumference (cm)			Stor root weight(kg)			Harvest Index		DRI ^a
	NS	ST	% Red.	NS	ST	% Red.	NS	ST	% Red.	NS	ST	% Red.	NS	ST	% Red.
Akena	4.50	3.25	27.78	16.15	20.65	-27.86	14.77	10.14	31.35	4.55	1.60	64.84	0.52	0.47	9.62
Bamunanika	5.00	3.75	25.00	19.48	13.67	29.83	13.24	7.45	43.73	3.47	0.67	80.69	0.51	0.29	43.14
Bao	4.00	2.50	37.50	15.56	10.42	33.03	11.48	9.50	17.25	2.37	0.42	82.28	0.48	0.23	52.08
MH/97/2961	3.75	2.00	46.67	16.46	9.67	41.25	13.67	8.34	38.99	1.77	0.50	71.75	0.33	0.20	39.39
MM96/4271	5.75	3.75	34.78	15.38	16.60	-7.93	13.00	9.10	30.00	2.62	1.07	59.16	0.58	0.41	29.31
Nase 12	4.00	2.62	34.50	13.67	9.03	33.94	11.97	7.75	35.25	1.77	0.27	84.75	0.54	0.23	57.41
Nase 3	9.75	6.50	33.33	16.25	12.83	21.05	15.17	8.27	45.48	3.65	0.75	79.45	0.55	0.34	38.18
MM96/O686	4.25	2.75	35.29	15.85	17.69	-11.61	14.59	11.15	23.58	2.22	1.55	30.18	0.46	0.40	13.04
Omongole	4.25	2.63	38.12	13.96	10.31	26.15	11.94	8.17	31.57	1.50	0.70	53.33	0.43	0.24	44.19
TME 14	3.38	2.25	33.43	13.44	15.40	-14.58	14.88	8.87	40.39	2.05	0.77	62.44	0.47	0.24	48.94
LSD	1.32	ns		2.94	6.83		ns	ns		1.48	ns		0.12	ns	
CV (%)	12	36.8		8.3	22.1		11.3	27.8		25.2	68		10.5	35.1	

LSD, Least significant difference

CV (%), coefficient of variation

ns, Non significant

^a DRI, Drought response index calculated as the ratio of total yield under drought stress to the total yield under non-stress conditions.

Stor, storage

4.5 Correlation of yield components with physiological and morphological traits

Data for correlations between yield parameters and other measured traits is presented in Table 8. Storage root number did not show any significant relationship with other morphological and physiological parameters. However, storage root length had significant positive correlations with Shoot weight ($r=0.64^*$) and leaf area ($r=0.66^*$). Storage root circumference showed a significant positive correlation with shoot weight ($r=0.63^*$) and a significant negative correlation with leaf wilting ($r=-0.68^*$). Storage root weight had a significant positive relationship with leaf area alone ($r=0.76^*$). Harvest index and leaf retention were positively correlated ($r=0.64^*$) while harvest index and non-storage root number were negatively correlated ($r=-0.68^*$). Drought response index (DRI) had a strong negative correlation with non-storage root number ($R=-0.80^{**}$) and non-storage root length ($R=-0.65^*$).

Table 8 Correlation coefficients among measured morphological and physiological traits

	Stor root number	Stor root length	Stor root circumf.	Stor root weight	Harvest index	DRI ^a
Plant height	0.27	0.47	0.09	0.58	0.17	0.44
Shoot weight	-0.01	0.64*	0.63*	0.60	0.02	0.27
Leaf Area	-0.01	0.66*	0.52	0.76*	0.29	0.53
Leaf Retention	0.53	0.50	0.42	0.49	0.64*	0.07
Leaf Wilting	-0.06	-0.24	-0.68*	-0.13	0.02	0.21
Xylem Press. Pot.	0.07	0.15	0.13	0.05	-0.05	0.25
Stomatal cond.	0.15	0.38	-0.19	0.49	0.42	0.23
Root Number	-0.47	-0.34	-0.23	-0.62	-0.68*	-0.80**
Root Length	-0.17	-0.08	-0.32	-0.22	-0.09	-0.65*

^a DRI, Drought Response Index, measured as ratio of yield under stress to yield under non-stressed conditions

*, **, Value significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

Circumf. – Circumference

Stor, Economic roots (storage roots of economic value)

CHAPTER FIVE

DISCUSSION

5.0 Introduction

Fifty six (56) farmer preferred cassava cultivars were evaluated in the field and based on their performance 15 cultivars were identified for rain out shade study. Results from field screening of 56 cassava cultivars indicated significant differences among cultivars across locations. Cultivars showed significant variations in the way they responded to drought stress suggesting that drought tolerance is influenced by genetic variability of the cultivar which is consistent with observations by El-Sharkawy, (2007), who reported considerable variability among cassava cultivars in response to water deficit stress with some being drought tolerant, while others being very susceptible. Genotype by environment (GxE) effects showed highly significant ($P \leq 0.001$) variations for all the parameters evaluated in the field in Bullisa, Nakasongola and Kabanyolo, reflecting genotypic differences in adaptation to different environments and tolerance to water deficit stress. The significant difference of genotype by environment effects suggests that cultivars/genotypes can be selected for adaptation to drought prone environments. Cultivars MH97/2961, Gwalanda, TME 14, Kwatamumpare and MM96/0686, would therefore be recommended for cultivation in drought prone environments of Uganda since they had the highest number of surviving plants for more than 3 months of moisture deficit after establishment. The early death of cassava plants due to drought stress in Bullisa and Nakasongola suggests that effects of drought are more severe at the early stages of the crops development which is similar to observations by Pardales and Esquibel, (1996) who reported that effects of drought stress in cassava were more severe during early stages of establishment than in later stages of development.

5.1 Morphological response of cassava cultivars to soil moisture deficit

Results showed that moisture stress had significant devastating effect on both vegetative and root growth of cassava. There were significant ($P \leq 0.001$) reductions for plant height, leaf area, leaf retention and shoot bio-mass while on the other hand there were significant increases in root number and root length in all the cultivars.

Although cassava is considered to be drought tolerant and can survive for over 4-5 months of soil moisture deficit where other crops cannot survive, results from this study showed that moisture deficit stress reduced plant heights of all the cultivars by a range of 15-35% (Table 3). This is similar to observations made by Aina *et al.* (2007) who report total plant height reduction of 35-47%, but below 62.1% reported by Bergantin *et al.*, (2004). The reduction in plant height can be attributed to the reduction in leaf area and the number of leaves retained by the plant which ranged between 38-55% and 66-84% respectively which explains the average reduction in shoot biomass of 37.3%. These led to reduction on the photosynthetic area and consequently the amount of assimilates required for stem elongation and plant growth.

Studies conducted by Bergantin *et al.* (2004) indicated that drought causes stunting in cassava plant heights and leaf production leading to a 62% reduction in plant height. In addition, earlier studies by Pardales and Esquibel (1996) reported that shoot development in cassava is highly suppressed when young plants are exposed to prolonged conditions of limited soil water. In this study, cultivars MM96/4271 and MM96/0686, which had the least reductions in plant height of 3-5% are considered drought tolerant and could be recommended for production in drought prone environments of Uganda. The small reduction in plant height in MM96/4271 and

MM96/0686 respectively can be attributed to their extensive root systems in search for water in deep soil horizons and the bigger photosynthetic leaf area they maintained under moisture stress (Table 3). These variations will therefore be useful in selecting drought tolerant cultivars for drought prone areas.

The reduction in the total above ground biomass under drought condition was also variable depending on the cultivar. Compared with the control (adequate watering), soil water deficit stress across all cultivars caused an average reduction in total above ground biomass of 37.3%, which is similar to observations made by Okogbenin *et al.* (2003) who reported a decline of 37% in shoot biomass due to moisture stress. The highest reduction in above ground biomass was in Akena 56% followed by MH97/2961 with 60% reduction while the least reduction was in MM96/0686 with 3% and TME 14 with an average reduction of 7%. Basing on these results, cultivars MM96/0686 and TME 14, with least reductions in above ground biomass are considered drought tolerant, since they maintain a high photosynthetic area. Reduction of above ground biomass could be attributed to reduction in leaf retention primarily due to leaf abscission caused by drought stress (Bergantin *et al.*, 2004)

Compared to the control, moisture stress significantly ($P \leq 0.001$) reduced leaf area in all cultivars by 36-58% (Table 3). This data demonstrates cassava's ability to tolerate prolonged moisture deficit by reducing transpirational surface area and hence reducing the amount of water lost during drought conditions. The reduction in leaf area is attributed to reduction in cell expansion and fewer cells produced by leaf meristems (Tardieu *et al.* 2000; Alves and Setter, 2000; 2004b). Studies by Lecoecur *et al.* (1995) and Alves and Setter (2000) have reported that abscisic acid

(ABA) is responsible for reduced leaf area as it's in shoot growth by inhibiting meristematic cell division and elongation.

Increased longevity of leaves or improved leaf retention has been suggested as a possible means to increase productivity of cassava under drought conditions. Cultivars with higher leaf retention (stay green) produce more root dry matter than plants with poor leaf retention (Lenis *et al.* 2005). This is because continued availability of photosynthetic surfaces leads to high production of assimilates (Okogbenin *et al.* 2003). However, in this study all the cultivars responded to soil moisture deficit by shading leaves as a means of reducing the plant evapotranspiration surface. There were notable cultivar differences in response to drought stress with cultivars reducing the number of their leaves by 65-85%. This is similar to observations by Okogbenin *et al.* (2003), who reported that cassava responded to water shortage by reducing its leaf canopy by over 40% to reduce water use indicating that leaf shedding is an effective adaptation mechanism to moisture stress. However, these compromises assimilate production and hence yield. This explains the low storage root yields observed in drought stressed experiments compared to non-stressed plants (Table 7). Studies by Lenis *et al.* (2006) indicated that cassava with greater leaf longevity produced higher root dry matter of 33% compared to drought susceptible accessions making leaf retention a desirable trait in achieving high crop yields. Thus, it's important to select for longer leaf retention when developing cultivars for dry areas since cultivars that retain more leaves with high photosynthesis during drought stress are desirable. Based on this, cultivars MM96/0686, Bamunanika and MH97/2961 with high leaf retention are good candidates for drought breeding.

Almost all the cultivars in this study responded to low soil moisture by increasing their fibrous root number and root length. There was a general increase in fibrous root length of between 4% in MH97/2961 to 59% in Akena (Table 3). This has been shown to be an important mechanism employed by cassava to exploit a greater soil volume for soil moisture during the dry season and it probably explains why MM96/0686 retained more leaves and had less reduction in plant height and shoots biomass (Table 3). Drought stress significantly increased the fibrous root length in Akena by over 59% suggesting that Akena diverts relatively high proportions of dry matter for the growth of an extensive fibrous root system at the expense of other vegetative growth. This can be explained by high percent reduction in plant height, shoot biomass, leaf area and number of leaves retained per plant (Table 3). Promotion of continued root growth at low soil moisture is also due to osmotic adjustment in the growing region of the root (dehydration avoidance). This allows roots to penetrate deeper into the soil and take up more water. This is important characteristic in areas with bimodal rainfall or those with short wet periods where excess water percolates into deeper soil profile and hence could not be extracted. Similar observations have been reported by Verslues *et al.*, (2006) and El-Sharkawy (2007). Alves and Setter (2000) also reported that the increase in fibrous root length was due to stimulation by ABA which increased root meristematic cell division and elongation. However, for the plant to increase the root length, there is always a shift of resources into root growth at the expense of photosynthetic and reproductive tissues which explains the low yields obtained in these cultivars during dry periods (Table 7). This therefore implies that there is need to strike a balance between root length and vegetative growth when selecting varieties for drought prone areas.

5.2 Physiological response of cassava cultivars to soil moisture deficit

There was a considerable reduction in stomatal conductance in response to low soil moisture stress in nearly all the cultivars. This ranged from 55-87% (Table 5), which is higher than observations made by El-Sharkawy (2007) who reported an average of 43% reduction in stomatal conductance. The variations in the findings of this study and what was reported by El-Sharkawy (2007) could be attributed to environmental conditions since this experiment was in a rain out shade, while El-Sharkawy (2007) conducted his experiments in an open space and only imposed drought conditions by covering the soil with a polythene sheet. Thus, the rain-out shade could have modified the micro-environment under which this experiment was conducted causing an increasing in stomatal conductance. In addition to the conditions of study, the observed differences in stomatal conductance were probably partly due to differences in stomatal densities and leaf area of the test cultivars. Studies by Alves and Setter (2000) and Osiru *et al.* (1994) reported that cassava partially closed their stomata when subjected to moisture stress. Studies have also indicated that when water is available, cassava maintains a high stomatal conductance and can keep internal CO₂ concentration high, but according to El-Sharkawy (2002) when water becomes limiting, cassava closes stomata in response to even small decreases in soil water potential. This is an important physiological mechanism that allows cassava to survive moisture stress conditions giving it a comparative advantage over other crops with poor stomatal control. The higher value of stomatal conductance rates for Akena during the moisture stress (Table 5) may be attributed to better root system which can explore greater volumes of soil for moisture.

The rapid closure of cassava stomata and the resulting decline in transpiration lessens the decrease in leaf water potential and soil water depletion, thus protecting leaf tissues from turgor

stress and desiccation (Alves and Setter, 2000). In addition to beneficial effects of stomatal conductance by preventing severe leaf dehydration, and consequently preventing impairment to photosynthetic capacity of the leaf, the partial closure of stomata reduces water loss through transpiration thereby maximizing water use efficiency. This ensures a comparative advantage of cassava in dry areas over other crops with poor stomatal conductance.

Drought tolerance in the test cultivars may be explained by the relation between xylem pressure potential and stomatal conductance (Table 5). In the dry season, xylem pressure potential slightly increased by (4-8 bars) which is below the 10 bars required to disrupt physiological process or to kill the plant. The xylem pressure potential was relatively stable around 3 bars on average though it was high for some varieties like Bamunika (5 bars), Nase 3 (5 bars) and TME 14 (8 bars). These can be explained by their extensive root systems and high stomatal conductance in moisture deficit conditions

3.3 Yield components

Cassava is highly productive under favourable environments and from this study water stress severely reduced the mean final yield by about 67%. The mean performance of cultivars under different watering regimes showed that cultivars MM96/0686, Omongole and MM96/4271 had low reductions in storage root yield of 40% on average but other cultivars including Bamunika, Bao and Nase 12 had huge reductions in storage root weight of over 80% when subjected to drought stress (Table 7), which is in line with studies by Connor and Palta (1981) who reported a reduction in storage root yield by 32-60% when subjected to moisture stress from 1-5 months after planting. However, the findings from this study are considerably higher than the

Observations made by Okogbenin *et al.* (2003) who reported a 22% reduction in tuber yield. The results from this study also indicate that the cumulative effect of moisture deficit stress had greater impact on yield attributes of cassava. The number of storage roots harvested declined by 35% and 47% in Bamunanika and MM96/4271 respectively, which are comparative to those reports by Aina *et al.* (2007) of 38-95% decline in storage root number under moisture deficit. This can be explained by low xylem pressure potentials and the pronounced increment in fibrous root length of the cultivars evaluated in this study (Tables 5 and 7). Besides, a different panel of cultivars was evaluated in each study.

The effects of moisture stress on yield parameters indicates that the mechanisms by which cassava tolerates drought stress leads to a halt in the partitioning of assimilates for root bulking hence adversely affecting economic yield. This is explained by the reduction in storage root circumference of up to 45% and storage root length increase of 30% on average as seen in all the cultivars under evaluation (Table 7). Significant increases in storage root length due to water stress were observed in some cultivars ranging i.e. Akena, MM96/0686, and TME 14. This is attributed to the fact that there is a shift in function of storage roots from storage of assimilates to water uptake (Alves, 2002). Water stress reduced the number of storage roots initiated and even where few storage roots were formed, the stress apparently reduced bulking of underground storage organs possibly due to reduced bulking rate. These results are similar to observations by Okogbenin *et al.* (2003) who reported a decline of 22% in root yield due to moisture stress. Connor and Palta (1981) reported that water stress after 1-5 MAP led to reduction in storage root yield by 32-60%. The leaf area which is also reduced during the drought stress further limited the growth of storage organs. Based on these results it can be concluded that the reduction in

Cassava yield during stress is caused by the reduction in total biomass production. This is in line with observations made by Okogbenin *et al.* (2003).

Root Index (HI) is closely related to root yield and is critical in determining yield. This is because HI reflects the partitioning efficiency of assimilates towards economic root production. In this study the existence of significant variation ($P \leq 0.001$) in HI among cultivars and in different watering regimes implies that cultivars yield differently and their yields vary across environments meaning the balance between the formation of leaves and the filling of roots is controlled by both genetics and environmental factors (HI, is a key quantitative trait). This suggests that poor growth conditions like water deficit conditions cause poor assimilate partitioning and thus affect root bulking (Okogbenin *et al.*, 2003). Cassava therefore can survive conditions of moisture stress where other crops cannot, but with adverse effects on economic yield and yet root yield stability which is of more significance to the farmers, implying that they require cultivars that can also produce well under prolonged stress (Okogbenin *et al.*, 2003). Kumar *et al.* (2003) reported similar observations of reduced economic yield in sorghum when subjected to drought stress.

Correlations of yield components with other morphological and physiological traits

A non significant ($P \leq 0.001$) relationship of storage root number with other traits could suggest that storage root number is majorly determined by the genetic nature of the cultivar and less affected by the impact of the environment on other morphological and physiological traits. The positive significant ($P \leq 0.001$) correlation of shoot weight with both storage root length and storage root circumference implies that an increase in shoot biomass leads to an increase in

storage root size (Table 7). This is because the increase in shoot biomass increases production of assimilates which are directed to the filling of the storage organs (Okogbenin *et al.*, 2003). The larger the leaf area, the higher the photosynthetic rate and the higher the amount of assimilates produced. Thus leaf area has a direct bearing on yield as already demonstrated by previous studies (Alves and Setter 2004b; Aina *et al.*, 2007). In addition to this, leaf longevity measured as leaf retention had a positive significant ($P \leq 0.001$) relationship with harvest index (Table 8). High leaf longevity (stay green) ensures production of assimilates over a longer period, hence leads to higher yields (Okogbenin *et al.*, 2003), thereby explaining the relatively higher storage root weight in MM96/0686 (Tables 3 and 8). This implies that while breeding for drought tolerance, it is important to select for high leaf retention. Furthermore, the negative significant ($P \leq 0.001$) correlation of leaf wilting with storage root circumference implied that less wilting leads to an increase in storage root circumference. Wilting leads to drooping of leaves which changes their orientation towards sunlight. It also leads to shriveling of leaves which, together with drooping greatly reduces the plant's photosynthetic area and closure of stomata.

A highly significant ($P \leq 0.001$) negative correlation between root number and length with harvest index and DRI implies that there was low yield in cultivars which had high fibrous root density. This could be because these cultivars invested more resources in fibrous root production and elongation at the expense of storage root development. Verslues *et al.* (2006) also reported reduced yields in cultivars with high fibrous root densities.

CHAPTER SIX

GENERAL CONCLUSIONS AND RECOMMENDATIONS

General conclusions

study was undertaken with the aim of assessing the response of farmer preferred cassava cultivars to water deficit and also to determine whether there are cultivar differences in their response to drought stress. Tolerance to drought stress was found to be variable among cultivars with some cultivars (MM96/0689, Omongole and MM96/4271) being tolerant, while Bamunanika, Bao and TME 12 were very susceptible to drought much as they were high yielding under adequate moisture. Genotype by environment (GxE) effects were highly significant for all the parameters evaluated in the field thereby reflecting genotypic differences in adaptation to different environments and tolerance to water deficit. It is therefore concluded that the significant variation in genotype by environment (GxE) effects suggests that cultivars can be selected for adaptation to specific drought environments.

The study revealed that all the cultivars were affected by drought stress though the extent to which each responded to stress differed. In general all cultivars responded to drought stress by closing stomata, shading of leaves, reducing plant growth, increasing fibrous root density and reduction of storage root circumferences. Cultivars MM96/0686, Bamunanika, MM96/2961 and NASE 12 retained more leaves, while cultivars Akena, MM96/0686, NASE 12, MM96/2961 and MM96/4971 increased the number and lengths of fibrous roots in response to drought stress. Further more Akena, MM96/0686, MM96/4271, Omongole, Nase 12 and TME 14 had the least reductions in fresh storage root yields and harvest index. It is therefore concluded

Cultivars MM96/0686, MH97/2961 and NASE 12 performed better across water regimes for drought tolerance traits (harvest index, leaf retention and fresh storage root yield). The study also revealed that these response mechanisms are affected by both the cultivar and the environment.

Observations made on morphological, physiological and yield parameters showed that although a cultivar is considered to be drought tolerant, severe stress results in severe effects on overall growth and yield. Cultivars responded to drought stress by reducing overall plant height and leaf area, shedding leaves, closing stomata, and producing numerous and long fibrous roots. They also responded by reducing the number and size of the storage roots while increasing their density. It is therefore concluded that cassava employs both morphological and physiological mechanisms to tolerate drought stress which offers opportunities for genetic improvement. The findings from this study has considerable significance for breeding for drought tolerance.

Recommendations

One of the first empirical studies that assessed the effect of drought in cassava under local conditions. Considering the severe effects of drought stress in cassava and the variable environmental conditions, breeding for drought tolerance remains the most effective way to ensure successful cultivation of cassava in drought prone areas. Due to the ever-changing climatic conditions, it is necessary to develop cultivars that show tolerance to a wide range of environmental conditions since a consistently tolerant cultivar reduces the risk of yield loss when weather conditions change drastically. Although drought tolerance is a complex trait, it is recommended that screening strategies/efforts should put more emphasis on high leaf area, high leaf retention (stay green), stomatal sensitivity to moisture deficit, increased fibrous

root length and yield under drought conditions as key selection traits in target environments. It is also recommended that breeding work aim at accumulating drought tolerance genes in breeding materials so as to increase the number of cultivars adapted to dry environments with high yield potential. To fast track the process of developing drought tolerant cassava, regional and international collaboration is highly recommended. It is also strongly recommended that the national breeding programme incorporates materials proved to be drought tolerant elsewhere into the local gene pool.

Furthermore, studies to understand the inheritance pattern of drought associated traits will significantly enhance the rate of genetic gain for drought tolerance. More research work on cassava is needed to identify the most effective combination of physiological mechanisms that may suit a particular climatic-hydrological-edaphic environment. Optimization field experimentation, automation of data collection and use of precise selection index would be critical. For production purposes, cultivars MM96/0686, Omongole and MM96/4271 are recommended for production in drought prone areas, while Bamunanika, Bao and Nase 12 are recommended for areas with adequate soil moisture.

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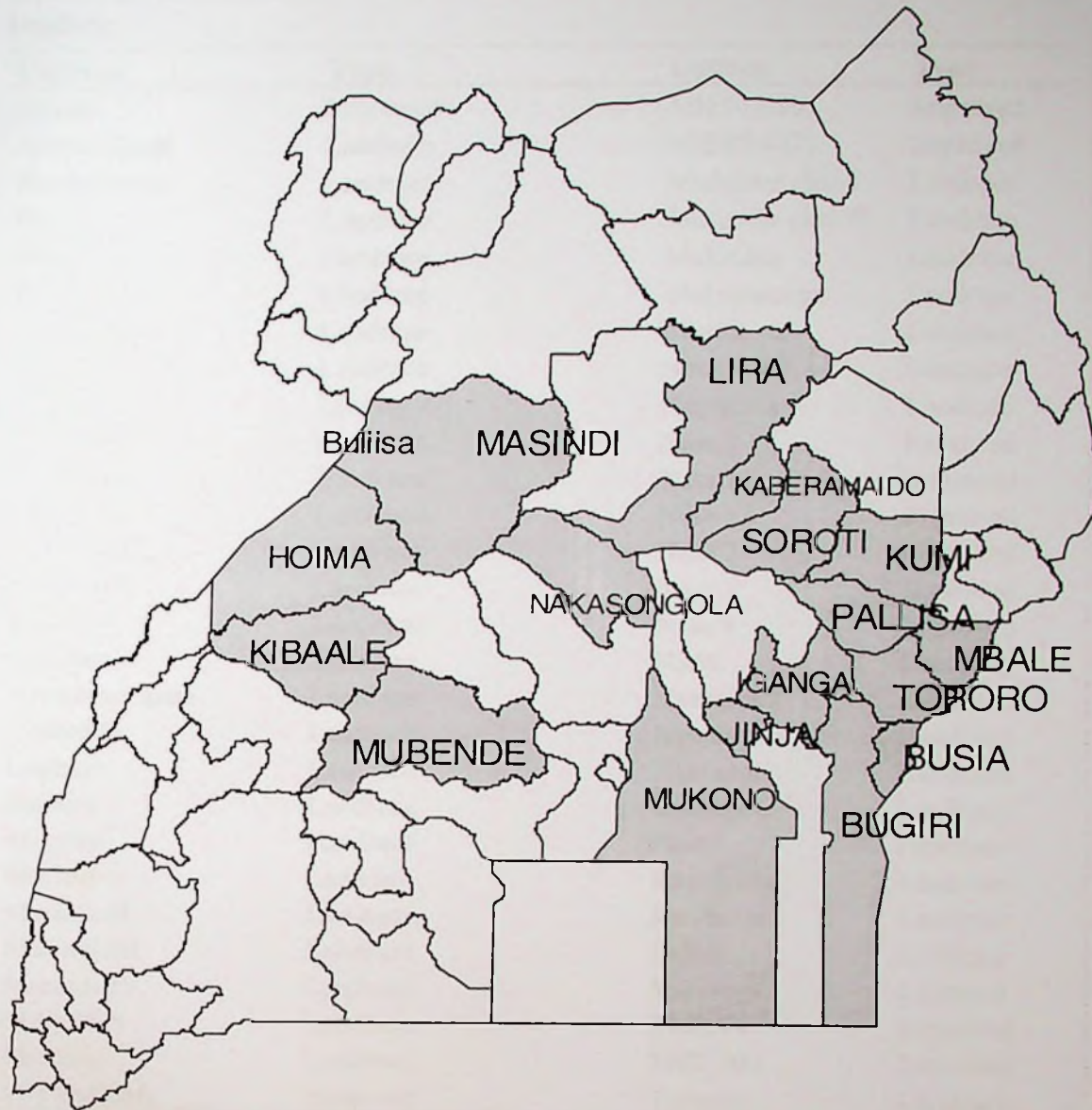
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Annex 1: Map of Uganda showing districts where different cassava cultivars were collected



Annex 2: Cassava cultivars collected from across the country for drought studies

Cultivar	Type	Cultivar	Type
Akena	Improved	MH 97/2961	Improved
Alado-Alado	Landrace	MH/97/4271	Improved
Bamunanika	Landrace	Mufumba chai-I	Landrace
Bao	Landrace	Mufumba chai-II	Landrace
Bukalasa	Landrace	Mukalasa	Landrace
Buliisa-I	Landrace	Mulyandongo	Landrace
Derodero	Landrace	Musita	Landrace
Ecilecil	Landrace	Namukoni	Landrace
Egabu	Landrace	Namulalu	Landrace
Guaranda	Landrace	Nase 1	Improved
Hoima-I	Landrace	Nase 11	Improved
Hoima-II	Landrace	Nase 12	Improved
Hoima-III	Landrace	Nase 2	Improved
Hoima-IV	Landrace	Nase 3	Improved
Kabwa	Landrace	Nase 9	Improved
Kakofira	Landrace	Njule	Landrace
Kwatamumpare	Landrace	Nyakakwa	Landrace
Luderudu	Landrace	Nyamutukura	Landrace
Lugbara	Landrace	Nyaranda	Landrace
Maburu	Landrace	Omongole	Landrace
Magana	Landrace	Palao	Landrace
Masindi-I	Landrace	Rugogoma	Landrace
Masindi-II	Landrace	Rwaburaru	Landrace
Masindi-III	Landrace	Safina	Landrace
Masindi-IV	Landrace	Sogasoga	Landrace
Masindi-V	Landrace	TME 14	Improved
Mercury	Landrace	TME 204	Improved
MH 96/0686	Improved	Tongolo	Landrace

Annex 3: Performance of varieties within and across locations

Variety	Number of plants				Plant vigor				Plant wilting			
	Bul.	Kab.	Nak.	Mean	Bul.	Kab.	Nak.	Mean	Bul.	Kab.	Nak.	Mean
MH 97/2961	6.00	13.82	8.18	9.33	1.19	2.99	2.47	2.22	0.91	2.45	2.11	1.82
Guaranda	6.00	12.58	7.93	8.83	0.90	2.74	2.01	1.89	0.68	2.13	1.41	1.41
TME 204	5.40	9.26	6.84	7.17	0.70	2.43	1.69	1.61	0.61	1.73	1.00	1.11
Nase 12	5.08	11.91	5.52	7.50	0.73	2.49	1.79	1.67	0.53	1.85	0.87	1.08
TME 14	4.26	14.07	8.17	8.83	0.81	2.57	2.00	1.79	0.57	2.16	1.67	1.46
MH/97/4271	3.92	12.48	5.10	7.17	1.13	2.98	2.30	2.14	0.50	2.28	1.08	1.29
Hoima-IV	3.84	12.40	6.26	7.50	1.18	3.11	2.31	2.20	0.61	2.59	1.38	1.53
Kabwa	3.83	10.66	5.01	6.50	1.11	2.97	2.16	2.08	0.54	2.05	0.92	1.17
Kwatamumpare	3.68	14.23	8.09	8.67	1.71	3.52	2.81	2.68	0.84	3.05	2.08	1.99
Hoima-III	3.42	12.48	4.11	6.67	0.95	2.81	1.99	1.92	0.46	2.34	0.83	1.21
Safina	3.20	8.68	5.38	5.76	0.84	2.58	1.85	1.76	0.39	1.45	0.96	0.93
Nase 1	3.07	9.16	2.77	5.00	1.11	2.81	2.25	2.06	0.32	1.44	0.57	0.78
MH 96/0686	3.01	13.06	5.93	7.33	1.03	2.89	2.32	2.08	0.52	2.32	1.50	1.45
Buliisa-I	2.92	12.23	4.85	6.67	1.00	3.01	2.15	2.05	0.56	2.67	1.19	1.47
Njule	2.83	9.91	3.77	5.50	0.93	2.65	2.04	1.88	0.27	1.54	0.70	0.84
Bukalasa	2.81	9.57	5.48	5.95	0.95	2.75	2.03	1.91	0.32	1.67	1.00	1.00
Masindi-III	2.75	11.57	4.68	6.33	0.53	2.28	1.61	1.48	0.31	1.72	0.74	0.92
Tongolo	2.68	12.48	6.34	7.17	1.10	3.05	2.29	2.15	0.49	2.56	1.43	1.50
Nyakakwa	2.50	8.83	4.67	5.33	0.96	2.77	2.09	1.94	0.26	1.59	0.94	0.93
Mufumba chai-II	2.37	9.31	3.55	5.08	0.59	2.26	1.56	1.47	0.19	1.35	0.69	0.74
Masindi-I	2.26	12.07	6.17	6.83	1.03	2.93	2.09	2.02	0.45	2.42	1.18	1.35
Omongole	2.25	10.07	5.17	5.83	0.78	2.53	1.89	1.74	0.18	1.48	0.92	0.86
Magana	2.15	8.69	4.58	5.14	1.04	2.79	2.19	2.01	0.29	1.51	1.08	0.96
Nyamutukura	1.84	11.40	4.76	6.00	1.34	3.16	2.40	2.30	0.37	2.29	1.12	1.26
Rwaburaru	1.84	11.89	4.27	6.00	0.87	2.86	2.02	1.92	0.34	2.44	0.92	1.23
Hoima-I	1.76	11.57	5.67	6.33	0.95	2.92	2.17	2.01	0.38	2.36	1.31	1.35
Hoima-II	1.76	11.81	3.93	5.83	0.75	2.56	1.91	1.74	0.14	1.82	0.73	0.90
Rugogoma	1.67	10.49	4.84	5.67	0.98	2.87	2.15	2.00	0.31	2.04	1.08	1.14
Mukalasa	1.67	9.49	4.34	5.17	0.51	2.30	1.68	1.50	0.10	1.39	0.76	0.75
Masindi-II	1.59	12.64	3.77	6.00	0.83	2.80	1.99	1.87	0.32	2.53	0.90	1.25
Masindi-IV	1.42	9.74	4.34	5.17	0.68	2.52	1.77	1.66	0.11	1.68	0.72	0.84
Palao	1.28	8.19	3.70	4.39	0.68	2.42	1.91	1.67	0.09	1.20	0.79	0.69
Bao	1.25	10.31	2.93	4.83	0.52	2.38	1.63	1.51	0.08	1.68	0.50	0.76
Kakofira	1.18	7.30	4.10	4.19	1.36	3.10	2.38	2.28	0.19	1.37	0.93	0.83
Mercury	1.03	8.19	3.95	4.39	0.60	2.45	1.75	1.60	0.08	1.43	0.77	0.76
Maburu	1.00	9.07	4.42	4.83	1.09	3.04	2.39	2.17	0.24	1.84	1.22	1.10
Musita	0.92	10.23	4.34	5.17	0.46	2.36	1.74	1.52	0.09	1.65	0.85	0.86

Variety	Number of plants				Plant vigor				Plant wilting			
	Bul.	Kab.	Nak.	Mean	Bul.	Kab.	Nak.	Mean	Bul.	Kab.	Nak.	Mean
Akena	0.90	4.51	2.59	2.67	0.43	1.98	1.51	1.31	0.00	0.74	0.48	0.40
Namukoni	0.87	9.30	3.55	4.58	0.56	2.41	1.69	1.55	0.06	1.59	0.63	0.76
Nyaranda	0.87	8.31	3.05	4.08	0.84	2.76	1.92	1.84	0.10	1.72	0.66	0.83
Egabu	0.83	8.41	2.76	4.00	0.41	2.17	1.55	1.38	0.00	1.25	0.44	0.56
Sogasoga	0.83	8.16	3.01	4.00	0.69	2.39	1.69	1.59	0.00	1.20	0.44	0.55
Nase 2	0.83	7.16	2.51	3.50	0.55	2.20	1.58	1.44	0.00	0.97	0.41	0.46
Nase 11	0.75	6.83	3.92	3.83	0.21	2.01	1.30	1.17	0.00	1.01	0.47	0.49
Ecilecil	0.74	6.58	2.67	3.33	1.12	3.19	2.20	2.17	0.00	1.35	0.50	0.62
Lugbara	0.69	9.06	4.36	4.70	0.49	2.42	1.77	1.56	0.11	1.65	0.95	0.91
Luderudu	0.66	7.00	3.34	3.67	0.78	2.61	2.06	1.82	0.06	1.24	0.86	0.72
Nase 9	0.62	8.53	3.04	4.06	0.57	2.40	1.75	1.57	0.00	1.34	0.56	0.63
Mufumba chai-I	0.34	7.66	4.00	4.00	0.13	1.87	1.41	1.14	0.00	0.98	0.80	0.59
Alado-Alado	0.33	6.66	2.01	3.00	0.41	2.09	1.53	1.34	0.00	0.89	0.32	0.40
Nase 3	0.33	6.17	2.51	3.00	0.59	2.30	1.78	1.56	0.00	0.84	0.40	0.41
Masindi-V	0.08	7.91	2.51	3.50	0.19	2.08	1.37	1.21	0.00	1.22	0.42	0.55
Derodero	0.04	7.72	2.46	3.41	0.48	2.38	1.77	1.54	0.00	1.43	0.61	0.68
Bamunanika	0.00	7.22	1.72	2.98	0.10	1.94	1.27	1.10	0.00	1.24	0.34	0.53
Mulyandongo	0.00	3.83	1.17	1.67	0.03	1.78	1.25	1.02	0.00	0.63	0.22	0.29
Namulalu	0.00	4.92	1.51	2.14	0.93	2.89	2.14	1.99	0.00	0.97	0.34	0.44
Mean	1.97	9.60	4.30	5.29	0.78	2.60	1.92	1.76	0.25	1.68	0.87	0.93

Bul – Bullisa, Kab – Kabanyolo, Nak - Nakasongola

Annex 4: Cassava cultivars selected for rain-out shade studies

Variety	Number of surviving plants after drought stress		
	Bullisa	Nakasongola	Average
MH 97/2961	6	8	7
Guaranda	6	8	7
TME 14	4	8	6
Nase 12	5	6	5
MM96/4271	4	5	5
MM96/0686	3	6	5
Kabwa	4	5	4
Bukalasa	3	5	4
Omongole	2	5	4
Magana	2	5	3
Bao	1	3	2
Akena	1	3	2
Nase 3	0	3	1
Bamunanika	0	2	1
Mulyandongo	0	1	1