INHERITANCE OF TOLERANCE TO DROUGHT FROM SELECTED POTATO (*Solanum tuberosum)* CULTIVARS IN UGANDA

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DECLARATION

This thesis is my original work and has never been submitted for a degree in any other university

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This thesis has been submitted for examination with our approval as university supervisors

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DEDICATION

To my dear husband Fred Tumwebaze and to our beloved son Ahimbisibwe Jessy.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

ABSTRACT

Potato is one of the important staple foods and source of income in the highlands of Uganda. However, its production is being affected by fluctuation in precipitations in both timing and amount, resulting into drought and reduced potato productivity. Many regions in the world that previously had stable and reliable rainfall patterns, particularly in tropical highlands currently suffer from intermittent droughts. This is primarily attributed to global warming. Also, in Uganda the area of substantial potato production is expanding into locations at lower altitudes, where drought is more common. Therefore, drought stress mitigation measures and coping mechanisms need to be devised to face future challenges of climate change particularly in developing countries. This study therefore, aimed at describing the mechanisms of inheritance of drought tolerance in Ugandan potato varieties that will help develop breeding materials that are tolerant to drought and potential to provide acceptable yield in both quantity and tuber quality.

A green house experiment was conducted twice at Kachwekano Zonal Agricultural Research and Development Institute (KAZARDI) from October, 2011 to February, 2012 and April 2012 to July 2012 to evaluate and characterize eight potato genotypes; five of which were obtained from CIP (international potato center) breeding collection for drought tolerance, and three local varieties in Uganda with unknown reaction to drought. The experimental materials were tested for drought tolerance at three levels of simulated moisture deficit. The moisture deficit treatments were to maintain the moisture level at full field capacity, 50% field capacity and 25% field capacity. The moisture deficit levels constituted the main plot while the clones comprised the subplot. The treatment combinations were repeated four times.

Data was collected on leaf chlorophyll content, relative leaf water content, number of days to 50 percent flowering, percent ground cover, leaf area, plant height, number of stems per plant, stem diameter, stress score, increment in plant height after imposing stress, dry matter content and yield components. Analysis of variance for effect of watering regime against eight potato genotypes indicated that potato genotypes performed significantly different ($P \leq 0.05$) for all the traits evaluated, in both repeats. Results from both growth, physiological and yield parameters revealed that the new potato clones bred for drought tolerance were less affected by drought

stress compared to adapted varieties. Kachpot1 gave the least stress score (1, 2.4 and 3.9) followed by Clone 395017.242 (1, 2.4 and 3.9) in the plots watered to field capacity, half and quarter field capacity respectively. The overall mean yield reduced from 21 tons per hectare in well watered plots to 12.5 in 50% moisture stressed plots and 10 tons per hectare in 25% moisture stressed plots. The highest yield under 25% moisture stress was obtained from clone 394034.7(12.6 tons per hectare), followed by 391533.1 (11.1) and 393077.159 (10.9). Percent yield reduction from normal watering to severe stress was least in clone 391533.1 (38.5%), followed by 394034.7 (39%), and 395017.242 (49.6).

Four best performing clones under moisture stress were crossed with three susceptible varieties in North Carolina 2 design generating 12 progeny families in order to determine the combining ability. Analysis revealed that parents 391533.1 and 395017.242 were the best combiners for most of the traits implying that they can be used to breed and select for cross combinations with tolerance to drought. Relative importance of GCA to SCA was high based on baker's ratio for % dry matter content (0.8), leaf area (0.7), plant height (0.6), relative leaf water content (0.5), stem diameter (0.6), groundcover (0.5) and total number of tubers (0.6), implying that the relative contribution of additive gene action for these traits is high compared to the non additive gene action. This suggests that these traits are highly heritable and selection can be done in early generations to develop varieties tolerant to drought. Also broad sense heritability was high for most traits than the narrow sense heritability implying low environmental effects in the overall phenotypic expression of the observed traits.

CHAPTER ONE

1.1. Background

Potato (*Solanum tuberosum* L.) belongs to the Solanaceae or nightshade family and to a large and diversified genus *Solanum*. The Solanaceous family also includes plants such as tomato, eggplant, tobacco, and chili peppers (Schafleitner, 2008). It occupies a wide eco-geographical range and is unique among the major world food crops in producing stolons (underground stems) which under suitable environmental conditions swell to form tubers (Hijmans, 2001). The genus *Solanum* contains approximately 2000 species, including over 150 tuber-bearing species which form a polyploidy series ranging from diploids to hexaploids, with 75% of them being diploid (Poehlman, 1995).

Potato is native to the Andes Mountains in Chile, Peru and Bolivia in South America and has been cultivated for about 2400 years (Weisser, 2010). It was later introduced into Europe by the Spanish conquisquadores in the mid-16thcentury, becoming such an important food source that a failure in the crop caused by blight in Ireland triggered a famine (Schafleitner, 2008). It later spread throughout the world including to the warm tropics (Theisein, 2007). In Africa, the crop was introduced by colonialists (Hakiza *et al.,* 2000). It was introduced in Uganda towards the beginning of the 1900's as a back garden vegetable (Hakiza *et al.,* 2000). In Kenya, it was introduced by government officials and individual travellers. By 1940, the potato was already being grown in the highlands of Kigezi, Toro and on the slopes of Mt. Elgon in Bugisu and Sebei (Hakiza *et al.,* 2000).

1.2. Importance of potato

Worldwide, more than 320 million tons of potatoes are currently produced from 20 million hectares. This ranks potato as the fourth most important staple crop in the world after maize, rice and wheat (FAO and CFC, 2010). It has high yield potential, excellent nutritional characteristics and it is important both as human food and in the starch industry (Griffin & Leslie, 2007**)**. The tubers are a source of starch, protein, antioxidants and vitamins (Burlingame, Mouille & Charrondie, 2009). Potato represents about 43 percent of the global output of root and tuber crops, followed by cassava with 30 percent, and sweet potato 17 percent (FAO, 2008). Potato constitutes part of the diet of half a billion consumers in the developing countries (Mondal, 2003). Over the past two decades, both the area planted to potato and its production has

increased faster than has for any other crops in the developing countries, including sub-Saharan Africa (PRAPACE, 1998; FAO, 2008). This is due to the crop's comparatively short vegetative period that allows farmers over a wide range of differing climatic conditions to find an appropriate season for its cultivation. Potatoes grow even in unfavorable conditions and at high altitudes, and it is ideal for small farmers and highly important for many farming families in the world's mountainous regions. Production in Africa has continually increased, rising from 2 million tons in 1960 to a record of 16.7 million tons in 2007 (FAO, 2008). This is attributed to improvements in crop varieties and cultivation methods, accompanied by a shift in eating habits in many countries towards more industrially processed potato based products. The world's highest ever potato yield (50.2 t/ha) was recorded in New Zealand (FAOSTAT, 2007).

1.3. Potato production in Uganda

Potato in Uganda is produced by approximately 200,000-300,000 smallholder farmers. Most of these are poor with farm holdings of 1-2 ha, living mainly in the highland areas of the country (IITA-FOODNET *et al*., 2001) with almost 50% being produced in Kabale district in the southwestern part of the country. With the introduction of genotypes adapted to warmer temperatures, some mid-elevation areas like Mubende, Mityana, Rakai, Bushenyi, Sironko and Masaka also took up potato growing (Wagoire *et al.*, 2001). In Uganda potatoes are essentially a food security crop with steadily growing urban domestic markets. Uganda is the ninth largest producer in Africa with an annual production of 650,000 tonnes and a yield of 7.0 t/ha (FAOSTAT, 2008). There is however still a high potential for improving potato yields. According to PRAPACE, 1996), up to 25mt/ha can be achieved in Uganda under good management and when suitable varieties are deployed.

1.4. Potato production constraints in Uganda

The low potato yields obtained in Uganda are attributed to a number of biotic, abiotic and edaphic constraints, as well as poor agronomic practices, and poorly adapted varieties (FAO 2001). Among the biotic constraints, late blight (*Phytophthora infestans*) and bacterial wilt (BW) (*Ralstonia solanacearum*) diseases are the most important and widespread (Hakiza *et al*., 2000). The main abiotic potato production constraint in Uganda is the unpredictable weather that results in moisture stress as a result of frequent droughts.

1.5 Problem Statement

Although less emphasized, water deficit stress is currently the major abiotic stress limiting agricultural production (Reddy, Chaitanya & Vivekanandan. 2004). It prevents crops from realizing their full genetic potential (Boyler, 1982; Rodriguez, Canales & Borras. 2005). Water deficit affects potato production, leading to reduced yield and tuber quality (Hassanpanah, Gurbanov, Gadimov & Shahriari. 2008). Drought stress severely limits plant production and performance in addition to impairing growth and development more than any other environmental factor (Shao, *et al*, 2009). Most of the potato varieties in Uganda were released on the strength of their high yields or resistance to diseases, especially to late blight. However, all these strengths are rendered void if the crop receives less than average soil moisture in a season. The current global warming, which causes fluctuations in precipitation distribution, increases the risk of plants being exposed repeatedly to drought (Miyashita, Tanakamaru, Maitani, Kimura & 2005**),** and potato losses are likely to increase. Therefore, there is need to develop genotypes that are able to withstand drought stress. Unfortunately, there is no sufficient information on the inheritance of drought tolerance in potato. This study therefore aimed at establishing the mechanisms of inheritance of drought tolerance in Ugandan potato varieties.

1.6 Rationale of the study

The combination of population growth and climate change present one of the greatest challenges of the 21st century to productively grow nutritious crops in water-scarce environments (Pimentel *et al*., 2004). Every **y**ear up to 82% of annual crop yields are lost to abiotic stresses and the amount of productive arable land is continuously decreasing, forcing agricultural production to move to areas where the potential effects of abiotic stresses is even greater (Skinner, 2005). Climate change will further exacerbate the water crisis by causing a decline in water run-off in many regions, especially in environments in the developing world where rainfall is highly variable and soils are degraded (Schafleitner, 2008).

The majority of the world potato production areas are found in developing countries which produce about 30% of the world's potato. Unfortunately, they are vulnerable to extreme droughts, resulting into great harvest losses (Schafleitner, 2009). Many regions in the world that previously had stable and reliable rainfall patterns, particularly in tropical highlands currently suffer from intermittent droughts. Northern, Eastern and Southern Africa are reportedly among

the most water-vulnerable regions of the world (Rijsberman, 2006). This is primarily attributed to global warming and such stresses are expected to continue and predicted to be more severe by 2025 (Rijsberman, 2006).

In south western Uganda, rainfall intensity has become very unpredictable with huge seasonal and annual fluctuations every other year. The amount of rainfall has decreased between 1961and 2001, and temperature changes have been more pronounced at the higher altitudes than in the lowlands. The temperature in Kabale district has shot up by 2ºC (3.6°F) in the last three decades **(**Wandiga, 2004). This implies that fluctuations in rainfall pattern will continue due to global warming. Also, in Uganda substantial potato production is expanding into locations at lower altitudes, where drought is more common. Therefore drought stress mitigation measures and coping mechanisms need to be devised to face future challenges of climate change. This study therefore aimed at developing breeding materials that are tolerant to drought and have potential to provide acceptable yield in both quantity and tuber quality. The breeding materials will in turn be used to produce varieties that are tolerant to drought hence maintain or even increase potato production despite the unforeseen but expected vagaries of weather changes.

1.7. Objectives

1.7.1. General Objective:

- To contribute to the sustenance and or increase in potato production in Uganda through developing drought tolerant varieties.

1.7.2. Specific objectives

- To characterize selected potato genotypes for drought tolerance.
- To determine the combining ability of drought tolerant genotypes with some of the adapted drought sensitive varieties.
- To determine the effect of water stress on potato tuber quality and total tuber yield.

1.8 Research Questions

1. Are there potato cultivars in Uganda with sufficient levels of tolerance to drought?

2. Do selected potato cultivars have a good combining ability with some of the locally adapted varieties?

3. Does water stress affect potato tuber quality in drought tolerant genotypes?

CHAPTER TWO

2.0. Literature review

2.1. Potato botany

Potato plants are herbaceous perennials that grow about 60 cm high, depending on the variety (Tony, 2006). A potato plant is a cluster of true main stems, a true main stem may develop stolons botanically called rhizomes, below-ground branches from below-ground buds, and above-ground branches from aerial buds (Struik & Ewing, 1995). Potato growth can be divided into four distinct stages, the early vegetative growth, tuberization, tuber bulking, and maturity. The early vegetative growth (Stage I) includes early plant development from planting to initiation of tubers. This stage varies from 30 to 60 days, depending on the potato cultivar and environmental conditions. Tuberization (Stage 2) is the period during which the stolon tips swell to form visible tubers. It generally takes about 2 to 4 weeks (Usman, 2004). Tuber bulking (Stage 3) includes the stage of linear tuber dry matter accumulation to near maturity, and this stage takes about 60 days. At this stage, flowers appear on the main and secondary stems. Leaf area index **(**LAI**)** reaches its maximum 3.5-6.0 during stage 3**.**The maturation stage (Stage 4), represents the final 10-24 days of growth, and is characterized by senescence of the shoot, along with the decline in leaf, shoot, and root dry weight. Drought stress conditions can change the time required to complete each stage of development. Usman, 2004; Kleinkopf, 1983). From the study done by (Fernie & Willmitzer, 2001), physiologically mature potato tubers contain approximately 80% water, between 15% and 25% of starch, and nearly 2% of protein. Potato plants bear white, pink, red, blue or purple flowers with yellow stamens. Generally white flowered potatoes tend to have white skinned tubers while those with coloured flowers tend to have pinkish tuber skins (Winch, 2006). The potato flower is 3 to 4 cm in diameter, and contains five sepals and petals, and a bi-lobed ovary and a single style. The stamens are attached to the corolla tube and bear erect anthers which form a close column around the style. The anthers are bright yellow, except for those produced on male sterile plants, which are either light-yellow or yellow-green coloured (Tony, 2006).

The potato mostly requires long day lengths (around sixteen hours), abundant rainfall, and cool temperatures for optimum growth. Potatoes are cross-pollinated, mainly by insects, including bumblebees, but a substantial amount of self-fertilization occurs (Amador *et al.,* 2001).

2.2. Abiotic stress and water scarcity as a major worldwide problem

Environmental stresses, such as drought, salinity, extreme temperatures and radiation represent the most limiting factors for the growth of plants and agricultural production. These abiotic stresses cause huge crop losses worldwide (Rodriguez *et al*., 2005). Water stress is one of these factors. Its severity is influenced by different factors, such as the moisture-storing capacity of soils, evaporative demands, and quantity and distribution of rainfall (Wery *et al*., 1994). Potato has a sparse and shallow root system, which makes it very sensitive to water deficiency (Jefferies, 1993). As a result, tuber yield in potato may be considerably reduced by soil moisture deficits unless it is mitigated (Porter *et al.*, 1999). Although irrigation would counteract the effects of soil moisture deficits, most potato producing areas in the tropics have limited access to irrigation water sources (Fabeiro *et al*., 2001).

2.2. Drought effects on plants

The effect of water stress on potato and other plants range from morphological to biochemical and physiological, and are evident at all phenological stages of plant growth. Water deficit is responsible for reduced number of leaves, low plant water potentials, reduced leaf area, plant dwarfing, limited ground cover, limited stem extension and tuber yield reduction (Hassanpanah, 2010), Lahlou *et al.* 2003, Schafleitner *et al.*, 2007, Jose & Tad-Awan, 2008). The sustained soil moisture deficit produces small or cucumber-shaped tubers, while intermittent water stress produces knobby tubers or tubers with secondary growth (Nolte *et al*., 2003). Water stress also makes the plants more susceptible to pest and diseases, such as potato early death caused by *Verticillium dahliae*, early blight caused by *Alternaria solani*, black dot caused by *Colletotrichum coccodes*, common scab caused by *Streptomyces scabies* and powdery mildew (Nolte *et al*., 2003). Water dificiency also increases the content of reducing sugar in the stem, and promotes tuber cracking and malformation, surface abrasions, hollow heart, brown centre, internal brown spot, vascular discoloration or bruising, degradation of starch in the tuber stem end and concentration of total glycoalkaloids (Papathanasiou *et al*., 1999).

Photosynthesis is one of the major metabolic processes that are directly affected by drought. A reduction in photosynthesis results in decrease in leaf expansion, stomata closure, impaired photosynthetic machinery, enhanced formation of reactive oxygen species, premature leaf senescence, decreased translocation of assimilates and associated reduction in crop yield (Farooq

et al., 2009b). There is a linear relationship between the reduction in tuber yield and amount of soil moisture when the available soil moisture is less than that lost daily by evapo-transpiration (Susnoschi & Shimshi, 1985). However, this apparently simple relationship disguises a complex set of responses at all stages of growth. Water stress delays tuber initiation and bulking (Walworth and Carling, 2002), and it reduces photosynthetic efficiency (Burton, 1981; Van loon, 1981), but drought during the period of tuber initiation and bulking has the most drastic effect on yield. Tuber initiation is blocked during the interval of water stress (Mackerron & Jefferies, 1988), as is the initiation of stolons (Harverkort *et al*., 1990). Thus, drought reduces the number of tuber initiation events in a manner proportional to the duration of the stress. Further bulking of tubers initiated prior to the onset of stress is dramatically decreased during drought periods, affecting loss in dry matter that is proportional to both the severity and duration of the stress (Van Loon, 1981, Mackerron and Jefferies, 1988). Longterm drought (1–2 weeks or longer) reduces leaf area index and canopy longevity (Deblonde & Ledent, 2001).

Even relief of drought stress can have adverse effects. When tuber growth is inhibited for periods of several days, the tubers' basal portion ceases to grow (Iritan, 1981). When adequate soil watering is resumed, the apical end of the tuber resumes growing, yielding malformed pear-shaped, dumb-bell-shaped or knobby tubers that reduce the marketable potential of the crop. Prolonged periods of water stress during tuber development cause depletion of starch in the basal end, leading to translucent sugar or jelly ends, low in starch and high in reducing sugars, which cause browning during cooking (Iritani and Weller,1973; Sowokinos *et al*., 1985).

2.3.0. Plant responses to water deficits

Plants respond to drought by inducting several morphological, physiological and molecular mechanisms that enable them to withstand the stress. Drought resistance mechanisms can be grouped into three categories, i.e. drought escape, drought avoidance and drought stress tolerance (Weisser, 2010).

2.3.1. Drought escape

In drought escape, plants adapt by spurring rapid growth and early maturation, flowering/fruiting and senescence, thus, permitting them to reproduce before the environment becomes dry. The plants combine short life cycles with high rates of growth and gas exchange, using maximum

available resources while moisture in the soil lasts (Mooney *et al*., 1987). This keeps tissues from being excessively exposed to dehydration (Price *et al*., 2002).

2.3.1. Drought stress avoidance

Drought stress avoidance consists of mechanisms that reduce water loss from plants and improve water uptake. Reduction of water loss is effected by reducing epidermal (stomatal and lenticular) conductance and thickening of the cuticle (cutin and cuticular waxes) and epicuticular waxes, so that absorption of radiation is decreased by leaf rolling or folding and thus reduce the evaporative surfaces (leaf area) (Chaves *et al.,* 2003). Water uptake is improved by maintenance of turgor through an extensive and efficient (deep and thick) root system with large active surface area and an increase in hydraulic conductance. Increasing investment in the root, reallocation of nutrients stored in older leaves and higher rates of photosynthesis are some of the mechanisms through which plants manage drought effects (Chaves *et al*., 2003). Plants under drought conditions survive by managing a balancing act between maintenance of turgor and reduction of water loss (Mitra, 2001).

2.3.2. Drought tolerance

Drought tolerance is defined as the ability to grow, flower and display economic yield under sub-optimal water supply (Farooq *et al*., 2009a). Plants are tolerant to desiccation to some extent, and that moderate short term disturbances of plant water balance do not immediately affect yield (Schafleitner, 2009). The mechanism of the plant to tolerate drought stress consists of maintenance of cellular stability and turgidity through osmotic adjustment, compatible solutes, antioxidation and a scavenging defence system (Madhava *et al*., 2006).

2.4 Physiological mechanisms

Physiological mechanisms such as osmotic adjustment (OA), reduced water loss through the cuticle, avoidance of xylem cavitation and altered root-to-shoot ratio and water use efficiency are important in providing some yield in 'resource-poor' cropping systems (Blum 2005). Among these mechanisms water use efficiency and osmotic adjustments are the most important. Water use efficiency is defined as the ratio between total dry matter (DM) produced (or yield harvested) and water used (or applied) (Jones, 1993). Osmotic adjustment (OA) is the net increase in intercellular solutes in response to water stress (Morgan, 1984), which allows turgor maintenance at lower water potential. Osmotic adjustment has been considered as one of the crucial processes

in plant adaptation to drought, because it sustains the tissues' metabolic activity and enables regrowth upon wetting (Tangpremsri *et al*., 1995). Over expression of these transcription factors lead to improved dehydration tolerance sometimes without apparent deleterious growth effects on the plant. However, adverse effects of these transcription factors have been expressed in other species, mainly through stunted growth (Kang *et al*., 2002).

2.5. Gene regulation during plant response to drought stress

Many genes respond to drought at the transcriptional level, and their products are thought to function in drought tolerance and response (Shinozaki & Yamaguchi-Shinozaki, 2000). Although hundreds of genes have been found to be involved in abiotic stress responses, few of them have been well characterized (Shinozaki & Yamaguchii, 2000, 2007), the functions of the majority of the genes remain unknown and probably more genes are yet to be discovered.

Up-regulated genes include; transcription factors and genes related to cell signaling such as kinases and phosphatases, which regulate numerous functions, including metabolic changes and cell defense functions (Schafleitner, 2008). Solute concentrations are increased, lowering osmotic potential, to induce uptake of water from drying soils. Increased expression of lipid transfer genes and fatty-acid and wax synthase genes suggest the reinforcement of cell membranes and cuticles (Schafleitner, 2008). Numerous studies have shown that ABA accumulation is a key factor in controlling downstream responses that are essential for adaptation to stress. However, molecular and genomic analyses have suggested that both ABA-dependent and ABA-independent regulatory systems are involved in stress-responsive gene expression (Shinozaki and Yamaguchi-Shinozaki, 2000).

2.6.0 Genetic studies in potato

Genetic variability is the foundation in all breeding programs. The entire genetic variability is partitioned into two components, that is general combining ability (GCA) and specific combining ability (SCA) (Sprague, 1966). General combining ability designates the average performance of a line in a hybrid combination while specific combining ability designates those cases in which certain combinations perform better or worse than expected when compared to the parents (Sprague & Tatum, 1942). GCA estimates the effect of all crosses that include a common parent for the trait in question while SCA refers to the effect of each pair of parents for

a specific combination for the trait in question. GCA effects are due to additive type of gene action and SCA effects to non-additive (dominant and epistatic) gene action (Falconer, 1981). The GCA of a parental clone provides an assessment of its breeding value, as judged by the mean performance of its progenies from crosses with other clones. Combining ability studies for parents is important because those with high means may not be able to transmit them to the hybrids. Combining ability analysis not only provides an assessment of the parents' gametic input, but also helps to interpret the genetic basis of quantitative traits such as dry matter, yield and yield associated traits (Mendoza and Hynes,1974). Evaluation of parents based on GCA and means can result in selection of those with a high reservoir of genes that are superior as well as determine the nature of gene action (Vanaja, 2003; Malini *et al*. 2006).

2.6.1. Combining ability in potato

Potato is a highly heterozygous crop in which non-additive gene action is important for expression of most characters. Heterosis and combining ability are powerful tools in identifying the best combiner to use in crossing, either to exploit heterosis or to accumulate fixable genes (Mondal & Hossain, 2006). Crossing in potato is advantageous in that once a hybrid with desirable traits is identified; it can be multiplied vegetatively for a longtime without risks of segregation (Mondal & Hossain, 2006). Hayder *et al*., (2009), in their study on combining ability and genetic variability in potato found out that both GCA and SCA variances were significant for plant height and tuber weight/plant, meaning that these characters were controlled by both additive and non additive gene action in their expression. In the same study, it was found that GCA variances were lower in magnitude that the corresponding SCA variances indicating predominance of non additive gene action. Geleta *et al.*, (2006) got similar results in tomato. According to a study by Mandal & Hossen, (2009), the crosses with positive SCA for yield in general, involved either only the good combining parent or at least one good combiner and an average or poor combiner.While studying the role of combining ability effects in identifying superior parents in potato breeding programs, Bradshaw & Mackay (1994) concluded that both GCA and SCA effects contribute to the genetic variation observed in a population. Plaisted *et al*., (1989) stated that larger estimates of SCA variance than the corresponding GCA may be a characteristic of tetraploid potatoes.

2.6.2 . Breeding for drought tolerance in potato

Conventional breeding and marker-assisted selection have been important mechanisms for achieving yield improvements under drought-prone environments for most crops (Bennett 2003). Breeding strategies in potato include introgression from wild species, and breeding at both diploid and tetraploid levels (Caligari, 1992). Variation in complex traits is the basis for crop breeding especially when traits are introgressed from wild relatives into domesticated varieties (Gur & Zamir 2004). In breeding programs, wild species have been used as donors of some specific traits that are not available in the standard *tuberosum* varieties. In addition, unadapted species have also been used as a source of added genetic variability for all traits. The identification of such variation can lead to the statistical association of the trait with particular polymorphic region(s) of the plant's genome. Such regions are termed quantitative trait loci (QTL) Salvi & Tuberosa 2005; Mitchell-Olds & Schmitt 2006) and are identified by observing the frequency of co-segregation of particular DNA sequence polymorphisms or markers (detected by various means) and the trait of interest (Quarrie 1996). These techniques have been used to isolate the genes responsible for QTL. Marker-assisted selection (MAS) improves the efficiency of breeding programmes especially where complex traits are involved (Quarrie 1996). As a consequence, MAS is well established in many breeding programmes, including those selecting for improved drought resistance (Schneider *et al*., 1997; Foolad *et al.,* 2003; Serraj *et al.,* 2005).

2.6.3. Methods used to screen for drought

Both field and green house experiments have been used. In the field, assessing the variation in yield due to stress has been done conventionally to evaluate the sensitivity of potato to drought. One method reported as a rapid technique for screening potato for tolerance to drought is the use of growth reduction of leaf discs floated on a polyethylene glycol (PEG) 6000 solution of y-0.4m.pa compared to floated discs over distilled water (Bansal *et al.,* 1991). Results showed that PEG treatments mimicked the effect of water stress in all approaches employed. This technique is simple, non-destructive and has been proven to be reliable, giving results that are in general agreement with what is known about the drought tolerance of genotypes. Demagante et al., 1995 used the degree of reduction in plant growth rate of ten genotypes to study whether apical cutting is a reliable technique for screening drought tolerance. Conventional breeding approaches to improve water scarcity in potato have had limiting results, reported by Weiser (2010), and thus

gene transfer technology (genetic engineering), seems to be the option for developing drought tolerance in potato varieties. Fluorescence measurement, allows the rapid assessment of quantum yield of electron flow through photosystem (PS) II, a method that has been used widely for detecting water stress in plants (Reddy *et al.,* 2004).

Imaging thermography technique (IRT) has been used to study stomatal responses to drought stress (Jones, 2004) and can be used in a simple way to look for differences in leaf temperature, and thereby infer differences in transpiration and stomatal behavior. It has been used to screen for and identify mutants with altered stomatal function (Merlot *et al.,* 2002). Relative leaf water content was reported by Curtois *et al*., (2000) as a more reliable indicator of the plants' water stress, though less heritable. Relative leaf water content can be defined as the water content of a given amount of leaf relative to its fully hydrated or fully turgid state. (Rana&Prometheus, 2010). It is the most appropriate measure of the plant's water status in terms of the physiological consequences of cellular water deficit (Barrs & Weatherly, 1962, Boyer *et al*., 2008). Unstressed leaves have a RWC of 90-95 % depending on humidity and light. Stressed and wilted leaves may drop to as low as 50 %. Few leaves can recover from a RWC of 40 %. In the dark, the RWC will be about 99 %. Chlorophyll stability during drought was also reported to be a promising criterion for selecting for drought resistance (Arunyanark *et al*., 2008), as water stress results in significant decrease in chlorophyll content.

Sectional conclusion

Since water deficiency is responsible for; reduced leaf area, plant dwarfing, limited ground coverage, limited stem extension and tuber yield reduction, and measurements of these parameters are simple and non-destructive, in this study data was collected on these mentioned parameters to identify genotypes that would be less affected by drought stress. Furthermore seeing that drought reduces the number and size of tubers, leads to production of malformed tuber shapes and reduced skin quality, the harvested potato tubers per genotype and watering regime were graded, counted, and weighed.

Tuber shapes and skin quality were also described to identify genotypes that would still produce marketable tubers in drought stressed conditions. Relative leaf water content was measured to indicate the physiological consequence of the cellular water deficit especially as it was easy and

simple to measure. Chlorophyll content of the leaves was also measured in this study to determine the genotype that would maintain stable chlorophyll amounts under drought conditions.

CHAPTER THREE

EVALUATION AND CHARACTERIZATION OF SELECTED POTATO GENOTYPES FOR TOLERANCE TO DROUGHT

3.1. Introduction

Potato is both a staple food and major source of house hold income in the highlands of Uganda. Despite its importance, farm yields are often below 10t ha^{-1}(mainly 7t ha^{-1}) in comparison to 25t ha^{-1} or more in good growth conditions (PRAPACE, 1996, 2000), IITA-FOODNET *et al.*, 2001). The low productivity is due to a number of constraints including late blight (LB) and bacterial wilt (BW) diseases, but also viruses namely potato leaf roll virus (PLRV), potato virus Y (PVY), Potato virus X (PVX), potato virus S (PVS), potato virus A (PVA) and potato virus M (PVM) affect potato yields. Variability in climatic pattern resulting into drought presents another serious threat to potato production in Uganda. This is aggravated by Uganda's dependence on rainfall for agriculture due to less available water for irrigation and unaffordable associated costs. Drought is responsible for reduced number of leaves, reduced leaf area, plant dwarfing, limited groundcover and yield reduction (Hassanpanah, 2010). Sustained soil moisture deficit produces small or cucumber shaped tubers while intermittent water stress produces knobby tubers or tubers with secondary growth (Nolte *et al*., 2003). This study therefore, aimed at characterizing new potato clones for tolerance to drought under Uganda's conditions.

3.2. Materials and Methods

The study was conducted in a greenhouse at Kachwekano Zonal Agricultural Research and Development Institute (KAZARDI), Kabale district in south western Uganda. The institute is situated at 029^0 57'E 01^0 16'S at 2200 m above sea level (masl). The area receives a bimodal rainfall regime with March-May as the first rainy season and September –December as the 2^{nd} season. This study was carried out twice in the second and first season (2011B and 2012A respectively). Eight genotypes were used; five of which were clones obtained from International Potato Center CIP's breeding collection for drought tolerance and three were local varieties in Uganda with unknown reaction to drought.

Table 1.clones and varieties that were used in the study

Genotype	Origin	Response to drought
Uganda 11	KAZARDI	Unknown
Victoria	KAZARDI	Unknown
Kachpot1	KAZARDI	Unknown
394034.7	CIP	Tolerant
395017.242	CIP	Tolerant
393315.1	CIP	Tolerant
391591.96	CIP	Tolerant
393077.159	CIP	Tolerant

CIP- International potato center; **KAZARDI**- Kachwekano Zonal Agricultural Research and Development Institute

3.2.1. Experimental procedure and design

The experimental materials were tested for drought tolerance at three levels of simulated moisture deficit in a split plot design. The moisture deficit treatments were taken as moisture level at full field capacity, 50% field capacity and 25% field capacity). The moisture deficit levels constituted the main plot while the potato genotypes comprised of the sub plot. Wooden boxes, 3.0 m long and 1.1 m wide were used for as main plot treatments. The boxes were sub-divided into eight partitions each 0.75 m long by 0.55m wide and each partition accommodated one potato genotype. The box partitions were lined with a polythene sheet before adding soil, to prevent rotting of wood when it comes in contact with wet soil and wood absorbing some of the moisture. In each partition 67kg of steam sterilized soil were added to a depth of 18cm. Fertilizer (NPK 17:17:17) was applied to experimental plots at a rate of 100 kg ha^{-1} uniformly across the experimental plots. In each of the eight box partitions, four tubers representing a genotype were planted. Each treatment combinations were repeated four times.

Field capacity of soil was determined by oven drying soil samples at 105^{o}C to constant mass after saturating one cubic metre of soil with water until it drained freely. The amount of water to give the plants was calculated basing on the amount of water in the soil at field capacity, thus the well watered plots received four liters of water, 50% stressed plots, two litres and 25% stressed plots, one liter every Tuesday of the week.

3.2.2. Management of experimental plants before application of treatments

Experimental potato plants after germination were sprayed with Agrozeb 80 WP(a coordination product of Zinc ion and Manganese ethylene bisdithiocarbamate) at 2.5g l^{-1} and Agro-thoate 40EC (Dimethoate 400gl^{-1}) at 2.0ml l^{-1} of the commercial products to protect them from late

blight and insect pest attack respectively. Hand weeding was done every time weeds appeared. After the first weeding 22kg of steam sterilized soil were added to cover the open stolons and enable them form tubers. Plants were well watered to field capacity up to tuber initiation.

3.2.3. Application of moisture deficit treatments

The plants were watered to field capacity up tuber initiation and then subjected to three watering regimes where one set was watered optimally (four liters), another given half the optimum amount (two liters) and the third set a quarter (one liter).Watering was done by uniformly spreading the measured amount of water over the soil in each plot by hand.

3.2.4. Data collection

The planted boxes were monitored every four days until the first tubers germinated. From the 14^{th} day after planting, monitoring of germination was continued at weekly interval up to full emergence. Leaf area was calculated after measuring the entire leaf width and length using a meter rule from the leaf stalk to the leaf tip of the 7^{th} leaf of two adjacent plants. This is because the 7^{th} leaf was the most open and thus easy to measure. It was tagged for identification as growth continued. Plant height was measured using a meter rule from the soil level in the box to the tip of the tallest branch. Water used was calculated based on the amount of water added (irrigated) and soil moisture measurements. Percentage ground cover was visually estimated on a 0-100% scale where 100% refers to plots where soil couldn't be seen from the top of the box.

Soil moisture content was measured daily using a moisture probe (soil P^H and Moisture meter 16", Sunflower supplies) and oven drying at weekly interval. Amount of water in the soil was obtained by sampling soil from three soil depths namely (top (5cm), middle (15cm) and bottom (25cm) using a soil auger. The samples were then bulked together into crucibles whose empty weight had been measured. The weight of the crucible plus fresh soil was measured and crucibles put in the oven. The soil samples were dried at 105^oC for 48 hours until there was no change in weight. The amount of water in the soil was then calculated from the difference between weight of the crucible plus fresh soil and weight of the crucible and dry soil. The number of days to wilting was recorded after one week (every stress period).

The chlorophyll content of experimental potato plant leaves was measured using a chlorophyll meter (CCM-200-Opti-sciences, Inc, Hudson, New Hampshire) from two leaves per plant making eight in a sub-plot and an average obtained. The diameter of the largest Potato stem from two adjacent plants per sub-plot was measured using a vanier caliper. Number of stems on each plant per sub-plot was counted and recorded. Moisture stress was scored following the CIP scale where;

1= plots where all the plants and leaves were green and turgid

2=plots where only 30% of the plants or leaves had wilted

3 = 50% of the plants or leaves wilted

7 = 80% of the plants or leaves wilted

9 = 100% of the plants and leaves wilted or complete death of the plant (, 2007).

The relative leaf water content (RLWC) was determined by sampling three leaves from one plant in each plot. Three square centimeter leaf discs were cut from each leaflet and immediately placed in Petri dishes containing distilled water and stored at 4^{o}c overnight. The leaf disc were then removed from Petri dishes and each blotted to surface-dryness with a paper towel before weighing again to determine the weight of the leaf discs at full turgor. The discs were then dried in an oven overnight at 90^{o}C and weighed the next day to determine the dry weight. Subsequently, the relative water content (RLWC) of the leaves was determined from equation 1

RLWC%= FW-DW/TW-DW)*100……...……. (1)

Where FW means fresh weight DW is the dry weight and TW is turgid weight (Boyer *et al*., 2008)

Effect of simulated drought stress on fresh tuber yield and tuber quality

Upon harvesting, the number and weight of tubers per sub-plot was determined. Tuber shape, tuber skin color and quality (surface abrasions, cracked surface, with scabies, peeling off) fresh colour and vascular bundle quality were assessed and recorded. Sample tubers from each treatment combination were collected and used to determine dry matter content. Dry matter content was determined by slicing two 30 – 40 mm diameter mature tubers from each sub-plot, into small pieces to increase the surface area of drying. The tuber slices were weighed, dried in an oven at 80^{o} C for 48 hours and re-weighed to measure dry weight. The dry matter content was expressed as percentage of dry weight over fresh weight (g) (Ekanayake, 1990; Jones, 1993).

3.2.5. Data analysis

Quantitative data were analyzed using analysis of variance in Genstat 14th edition statistical software. Means for significant treatments were compared by Fisher's protected least significant differences (LSD) at 5% ($P<0.05$). The expected Skelton ANOVA tables for single and combined analysis are shown in table 2 and 3 below.

Table 2.Treatments: 4 reps, 3 watering regimes and 8 genotypes

Source of variation	DF	Type of effect	Expected mean squares	F-test denominator
Total	95			
Replications	3	Random	δ^2e +24 δ^2reps	Main plot error
Watering regimes	2	Fixed	δ^2e +32 δ^2W	Main plot error
Main plot error	6		δ^2e (main plot error)	Sub-plot error
genotypes	7	Fixed	δ^2e +4 δ^2 W x G +12 δ^2G	Sub-plot error
Watering regime X genotype	14	fixed	δ^2e +4 δ^2 W x G	Sub-plot error
Sub-plot error	63		δ^2e (sub-plot error)	

Table 3.Treatments: 2 Experiments, 4 reps, 3 watering regimes and 8 Genotypes

Source	d.f	Type of effect	Variance components	F-test denominator
Experiment	1	Random	σ^2 e + 96 σ^2 Expt	Rep within experiment
Rep/ Expt	6	Random	σ^2 rep/expt	Main plot error
Watering regime	2	Fixed	σ^2 e + 64 σ^2 WR + 32 σ2 WR*Expt	watering regime*expt
Expt. Watering regime.	2	Random	σ^2 e + 32 σ^2 WR*Expt	Main-plot error
Error (main plot error	12		σ^2 e	Sub-plot error
Genotype	7	Fixed	σ^2 e + 24 σ^2 genotype +12 σ^2 G*Expt +4 σ^2 Expt*genotype	Genotype *expt
Expt. genotype	7	Random	σ^2 e +12 σ^2 G*Expt	Sub-plot error
Watering regime. Genotype	14	Fixed	σ^2 e + 2 σ^2 G * W.R + 4 σ^2 Expt*WR *genotype	Expt * WR *genotype
Expt. Watering regime. Genotype.	14	Random	σ^2 e + 4 σ^2 Expt*wr *genotype	sub-plot error
Error (sub-plot error)	126		σ^2 e	

3.3. Results

3.3.1 Genotype response to moisture deficit

Analysis of variance for effect of watering regime against eight potato genotypes indicated that potato genotypes performed significantly different ($P \leq 0.05$) for all the traits evaluated, in both repeats (tables 4a&b & 5a&b). These were chlorophyll content, Relative leaf water content, number of days to 50 percent flowering, percent ground cover, leaf area, plant height, number of stems per plant, stem diameter, stress score, increment in plant height after imposing stress and dry matter content.

In the first experiment of testing, significant differences across the three watering regimes were obtained for groundcover, stress score, dry matter content and increment in plant height. The interaction between watering regimes and genotype was significant ($P \leq 0.05$) for stress score and increment in plant height after imposing stress (Table 4a&b). In the second trial, watering regimes were significant for leaf area, stem diameter, stress score and dry matter content while the interaction between watering regimes and genotypes was significant only for groundcover and stress score (Table 5a&b).

Results from combined analysis of the experimental repeat, revealed that the two repeats were significantly different from each other for most of the growth and physiological parameters tested, apart from plant height, stem diameter and stress score. Experiment by watering regime showed significant results for all the growth and physiological parameters tested while experiment by genotype was significant for all the parameters tested apart from relative leaf water content (Table 6).

Table 4a . ANOVA of tested indicators of drought stress in the first trial of characterizing potato genotypes for tolerance to drought. (2011B).

Source	d.f	MEAN SQUARES							
		Leaf Area	No. of stems	Plant height	Ground cover	Stem diameter	Increment in plant height	Stress score	Dry matter content
Rep	3	7161	0.20	2197.60	195.20	0.04	88.50	3.99	24.60
W-R	2	555	0.10	405.00	1632.2***	0.07	3822.7***	125.6***	205.6*
MP Error	6	46090	0.20	536.80	47.20	0.03	108.40	2.09	18.40
G	7	162725***	5.9***	5517.4***	1483.0***	0.68***	615.9***	20.3***	140.0***
W-R-G	14	17426	0.60	80.70	50.90	0.02	140.2**	6.9***	7.10
SP Error	63	11443	0.40	83.10	51.50	0.02	55.90	0.60	9.30

W-R, watering regime, G, genotype, W-R-G, watering regime by genotype. *, **, ***Significant at P≤0.05, 0.01, and 0.001, respectively. Those without stars were not significant. Error (mp) = main plot error, Error (sp) = sub-plot error

Table 4b . ANOVA of tested indicators of drought stress in the first trial of characterizing potato genotypes for tolerance to drought. (2011B)

Source	d.f	MEAN SQUARES		
		50%flowering	chlorophyl content	relative leaf water content
Rep	3	24.0	47.28	19.23
W-R	2	729.4	14.97	1700.08*
Residual	6	229.3	49.14***	75.08
G	7	1394.7***	866.2***	80.21
W-R-G	14	179.5***	24.1*	19.38
Residual	18-59	38.3	9.8	50.4

Table 5a. ANOVA of tested indicators of drought tolerance in the second trial. (2012A)

Source	**d.f.**	**Leaf Area**	**No.of stems**	**Plant height**	**Ground cover**	**Stem diameter**	**Increment in plant height**	**Stress score**	**Dry matter content**
Rep	3	17823	1.84	518.60	117.10	0.04	96.21	1.86	36.90
W-R	2	33095*	2.91	1120.40	665 .50***	0.15*	413.30	172.2***	21.6*
Error	6	5845	7.91	1080.20	132.60	0.02	278.03	5.99	2.80
G	7	304904***	13.17**	2525.2***	222.5***	0.93***	271.3*	16.1***	43.6***
W-R-G	14	19002	4.34	147.40	64.2**	0.61	144.31	6.3*	5.70
Error	63	23095	3.89	205.10	20.00	0.06	93.64	3.07	3.70

Table 5b. ANOVA of tested indicators of drought tolerance in the second trial. (2012A)

Source	d.f	MEAN SQUARES		
		50%flowering	chlorophyl content	relative leaf water content
Rep	3	4.49	16.26	2.8
W-R	2	7.41	78.35	589.6
Residual	6	39.85	37.42	40.2
G	7	195.18***	70.19*	115.5
W-R-G	14	9.97	22.29	43.4
Residual	18-59	26.63	30.03	106.2

Table 6. A combined ANOVA of the tested indicators of drought tolerance among selected genotypes in the two repeats of testing (2011 B and 2012 A)

Source of variation	**Mean squares**						
	d.f	**LA**	**NS**	**PH**	**SD**	**GC**	**IPH**
Experiment	1	167608**	101.598**	5285.4	0.02	1050.01*	2534.61**
Experiment. Rep	6	6603	1.29	1358.1	0.03	156.18	92.34
Watering-regime	2	10356	2.099	208	0.14	123.82	863.35
Expt. watering-regime	2	15951	1.959	1317.4	0.08	2173.91**	3372.66**
Residual (main- plot)	12	26128	3.239	808.5	0.03	89.89*	193.21
Genotype	7	130438	5.192	2277.5	0.73	665.4	422.16
Expt. genotype	7	337190***	12.786**	5765.2***	0.88***	1040.02***	465.11**
Watering-regime. genotype	14	22222	2.65	123.6	0.02	52.42	120.43
Expt. watering-regime. genotype	14	37835	2.088	104.5	0.04	62.7	164.11
Residual(sub-plot)	126	15025	1.942	144.1	0.04	35.75	74.76

Table 6. Continued.

Source of variation		Mean squares				
	d.f	CHLPL	50%A	RLWC	SS	DMC
Experiment	1	20728.08**	1592.15**	795.66***	9.377	1579.325**
Experiment. Rep	6	20.13	25.86	2.29	2.93	30.784
Watering-regime	2	642.1	13.52	326.23	2.344	55.717
Expt. watering-regime	2	165.16	14.41	1945.86**	295.262***	171.067**
Residual (main-plot)	12	133.35**	44.49**	55.68	4.039*	10.598
Genotype	7	919.09	404.87	75.97	10.927	28.812
Expt. genotype	7	546.05***	683.68***	92.32	25.438***	154.782***
Watering regime. genotype	14	98.85	15.7	49.3	5.04	5.675
Expt. Watering-regime. genotype	13-14	102.68	18.8	13.49	8.099	7.112
Residual (sub-plot)	117-126	34	18.84	80.2	1.903	6.512

LA, leaf area, NS, number of stems, PH, plant height, GC, groundcover, SD, stem diameter, IPH, increment in plant height, SS, stress score

3.3.1. Comparison of yield performance under stress, of the eight genotypes within and across the two trials

Results from analysis of variance revealed significant differences among genotypes for tuber yield, total weight of tubers, average weight of tubers, and average number of tubers. In the first experiment, significant differences were obtained for all the yield components across the watering regimes, while the interaction between genotype and watering regime gave significant differences for only average weight of tubers, total number of tubers and average number of tubers (table 7). In the second experiment, watering regimes and their interaction with genotypes were significant for yield in tons per hectare, total weight of tubers and average weight of tubers (table 8). Combined analysis of yield from the two trials showed that the two experiments were not different from each other. Experiment by watering regime and experiment by genotype showed significant differences for all the traits tested (Table 9). Genotypes showed significant differences for yield in tons per hectare, watering regime by genotype was significant for total number of tubers while the interaction between experiment, watering regime and genotype was significant for average weight of tubers.

Table 7. ANOVA of yield and its components in the first trial (2011 B).

Source of variation	d.f.	YT/ha	Total no.tubers	Av. no. of tubers	Total weight of tubers	Av. weight of tubers
Rep_	3	74.01ns	22.57ns	2.284	125929ns	335.82
Watering_regime	2	1849.97***	1153.78*	62.66*	314783***	2321.82***
Main plot error	6	48.11	111.64	9.047	81866	85.51
Genotype	7	94.45***	644.71***	42.34***	160711***	872.88***
Watering.regime. Genotype	14	14.51	194.04**	13.97***	24684ns	160.62*
Sub-plot error	63	12.99	67.13	4.464	22109	68.6

Table 8. ANOVA of yield and its components evaluated in the second trial 2012A

Source of variation	d.f.	Y/ha	Total. no. of tubers	Total weight. of tubers	Av.weight of tubers
Rep	3	31.821	84.76	54145	165.9
Watering_regime	2	504.88***	23.09	859076***	2007.56**
Residual	6	18.025	114.26	30671	112.51
Genotype	7	42.86***	236.26***	72930***	424.91***
Watering_regime.genotype	14	13.05*	53.94	22198*	108.24*
Residual	63	6.819	38.88	11603	53.37

Table 9. A combined ANOVA of yield components from the first and second trials (2011 B and 2012 A).

Source of variation		Mean squares			
	df	YT_ha	Total weight of tubers	Average weight of tubers	Total number of tubers
Experiment	1	3.638	6190	975.33	854.3
Experiment.Rep	6	52.914	90037	250.86	53.66
Watering regime	2	220.687	375512	34.04	682.94
Expt.watering regime	2	2134.158**	3631403**	4295.34***	493.94*
Residual(main-plot)	12	33.069**	50819	99.01	112.95
Genotype	7	107.443**	56268	804.77	369.34
Expt.genotype	7	29.866**	182822***	493.02***	511.62***
Watering regime.genotype	14	11.096	28002	95.84	167.1*
Expt.watering regime.genotype	14	16.457	18880	173.02*	80.88
Residual(sub-plot)	126	9.906	16856	60.99	53

3.3.2. Effect of moisture stress on the performance of genotypes under the three watering regimes

Genotypes performed differently across the three watering regimes within both the first and second experiments. Combined analysis from the two repeats revealed reduction of means by drought stress on most of the parameters.

Ground cover. The overall mean percentage ground cover from the two repeats was reduced from 64% to 57.6% by half field capacity moisture stress and to 52.3% by a quarter field capacity moisture stress. Ground cover under severe stress was highest in variety Kachpot1 with 60%, followed by Uganda 11, 56.9% and clone 395017.242, 55.6%. It was lowest in clone 394034.7 (41%), 391691.96 (49.9%) and variety Victoria (50.5%) (Table 10). The highest percentage ground cover reduction under severe stress was recorded in clone 393077.159 (24.8%), followed by varieties Uganda 11 and Victoria with 22.8 and 22.5 percentages respectively. It was least in clone 391533.1 (5.7%), 391691.96 (10.3%) and variety Kachpot1 (16.5%) (Table 10).

Table 10. Effect of induced moisture stress on genotype ground cover (%)

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	53.3	55.5	49.5	56.3	52.5	53.8	54.8	54.0	51.6
391691.96	60.5	56.3	53.5	50.8	48.8	46.3	55.6	52.5	49.9
393077.159	76.3	67.0	58.8	65.0	53.8	47.5	70.6	60.4	53.1
394034.7	49.0	37.8	28.3	52.5	57.0	53.8	50.8	47.4	41.0
395017.242	70.0	59.5	51.3	68.8	60.0	60.0	69.4	59.8	55.6
Kachpot1	77.5	68.8	66.3	66.3	57.5	53.8	71.9	63.1	60.0
Uganda 11	78.5	72.5	65.0	68.8	55.0	48.8	73.6	63.8	56.9
Victoria	74.0	66.5	52.3	56.3	53.8	48.8	65.1	60.1	50.5
Mean	**67.4**	**60.5**	**53.1**	**60.6**	**54.8**	**51.6**	**64.0**	**57.6**	**52.3**
LSD	**10.1**			**8.5**			**8.4**		
%CV	**11.9**			**8**			**10.3**		

FC = field capacity, 50%FC = 50 percent field capacity; 25%FC = 25 percent field capacity; LSD = Least significant difference of means (Gomez and Gomez, 1983); CV = Coefficient of variation (Gomez and Gomez, 1983).

Plant height

Results from the combined analysis from the two experiments showed that the overall mean plant height was reduced from 86.9cm with plots watered at field capacity, to 79.7cm in half well watered plots and 78.5cm in quarter of the well watered plots. Plant height was mostly reduced in clone 393077.159 (19.5%) under severe stress, followed by variety Victoria (17.7%), and clone 395017.242 (12.4%). There was less reduction in clone 391533.1(0.1%), followed by 391691.96 (3.3%) and variety Uganda 11 (5.3%).(Table.11).

Table 11. Effect of water stress on maximum plant height

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	68.9	68.2	71.8	107.2	97.3	104.1	88.0	82.8	87.9
391691.96	121.4	110.8	113.1	99.0	104.4	100.0	110.2	107.6	106.5
393077.159	92.6	88.9	82.4	98.6	81.1	71.4	95.6	85.0	76.9
394034.7	40.5	38.4	42.6	77.2	63.9	66.6	58.9	51.1	54.6
395017.242	65.3	53.9	66.9	101.2	96.7	79.0	83.3	75.3	72.9
Kachpot1	92.9	77.0	80.2	100.3	92.4	92.2	96.6	84.7	86.2
Uganda 11	80.6	72.5	76.1	63.6	63.4	60.5	72.1	68.0	68.3
Victoria	81.3	79.0	69.3	99.5	87.4	79.4	90.4	83.2	74.4
Mean	**80.4**	**73.6**	**75.3**	**93.3**	**85.8**	**81.7**	**86.9**	**79.7**	**78.5**
LSD	**12.9**			**20.2**			**10.8**		
%CV	**11.9**			**16.5**			**14.7**		

Increment in plant height from the imposition of moisture stress to end of stressing period

Increment in plant height from no stress to the end of the stressing period was reduced by severe stress from 21.6cm under field capacity to 11.3cm under half field capacity and to 7.6cm under a quarter field capacity. The highest effect on increase in plant height after stress under severe stress was recorded in clone 394034.7(93.8%), followed by 395017.242 (71%) and Uganda 11 (69.3%). It was low in 391533.1 (46%), 391691.96 (53.7%) and 393077.159(65.6) (table 12)

Table 12. Effect of moisture stress on increment in plant height after imposing stress

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	33.8	20.4	12.5	8.5	7.2	10.4	21.1	13.8	11.4
391691.96	46.9	19.5	15.9	21.7	8.7	15.8	34.3	14.1	15.9
393077.159	25.0	10.1	6.6	6.8	4.8	4.3	15.9	7.4	5.5
394034.7	12.2	15.0	2.2	20.7	8.0	-0.2	16.5	11.5	1.0
395017.242	18.2	9.0	2.8	15.5	21.1	7.0	16.8	15.1	4.9
Kachpot1	38.4	13.9	9.3	26.6	5.1	12.5	32.5	9.5	10.9
Uganda 11	44.0	14.7	12.1	4.2	0.2	2.7	24.1	7.3	7.4
Victoria	15.7	9.3	3.5	7.6	13.9	4.1	11.6	11.6	3.8
Mean	**29.3**	**14.0**	**8.1**	**13.9**	**8.6**	**7.1**	**21.6**	**11.3**	**7.6**
LSD	**10.6**			**9.7**			**11.6**		
%CV	**43.7**			**59.8**			**64.1**		

Leaf relative water content

The overall mean percentage relative leaf water content reduced from 79 under field capacity to 74 under half field capacity and 64 in a quarter moisture stressed plots. The least reduction was in clone 394034.7 (11.9%) followed by 393077.159, Kachpot1 and Uganda 11 both with 18%. Variety Victoria had the highest reduction with 24 %.(table 13). Percent relative leaf water content under quarter field capacity moisture stress was highest in clone 393034.7 (71.25%), 393077.159(64.34%) and 395017.242 (63.32%). It was least in Variety Victoria with 57.95% (Table 13).

Table 13. Effect of moisture stress on relative leaf water content

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	82.8	66.4	62.1	80.4	86.6	65.8	81.61	76.5	63.95
391691.96	72.4	66	52.8	80.8	75.7	66.8	76.61	70.85	59.8
393077.159	80.5	72.6	57.8	77.1	82.5	70.9	78.8	77.57	64.34
394034.7	82.9	71.5	66.9	78.9	84.2	75.6	80.87	77.89	71.25
395017.242	84.8	74	60.4	71.9	66	66.3	78.38	69.98	63.32
Kachpot1	73	66	57.3	81.2	76.2	67.6	77.07	71.1	62.46
Uganda 11	82.4	70.8	55.8	83.7	83	79	83.05	76.87	67.4
Victoria	77.9	61	58.8	76.4	81.4	57.1	77.18	71.24	57.95
Mean	**79.6**	**68.5**	**59**	**78.8**	**79.5**	**68.6**	**79.2**	**74**	**63.81**
LSD	**13.18**			**9.65**			**4.58**		
%CV	**10.3**			**13.6**			**12.4**		

Stress score. Stress effect reflected by wilting of plants increased from normal watering, to medium stress and then severe stress. The highest increase in wilting was recorded in variety Victoria from 1 in well watered plots to 7 in half well watered plots and 8.5 in a quarter well watered plots. This was followed by clone 393077.159 (1, 3.5 and 6.5) respectively and 394034.7 (1, 3 and 4.8). Stress score was least in clone 395017.242 (1, 2.4 and 3.9), followed by variety Kachpot1 (1, 2.3 and 3.5) and clone 391533.1(1, 2 and 4) (Table 14).

Table 14. Stress score of plants due to moisture stress indicated by wilting of plants

WR / Genotype	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	1	2.3	5.5	1	3.8	7	1.0	2	4.0
391691.96	1	2	2.5	1	5	7	1.0	3	4.8
393077.159	1	3	5.5	1	2.8	7.5	1.0	3.5	6.5
394034.7	1	2	6.2	1	2.8	2.8	1.0	2.9	4.7
395017.242	1	3	5.5	1	1.8	2.3	1.0	2.4	3.9
Kachpot1	1	1.8	2.5	1	2.8	4.5	1.0	2.3	3.5
Uganda 11	1	2.3	3	1	3.8	6	1.0	3	4.5
Victoria	1	7.5	9	1	6.5	8	1.0	7	8.5
Mean	**1**	**3**	**5**	**1**	**3.6**	**5.6**	**1.0**	**3.4**	**5.01**
LSD		**1.1**			**2.5**			**3.0**	
%CV		**26.7**			**37**			**35.1**	

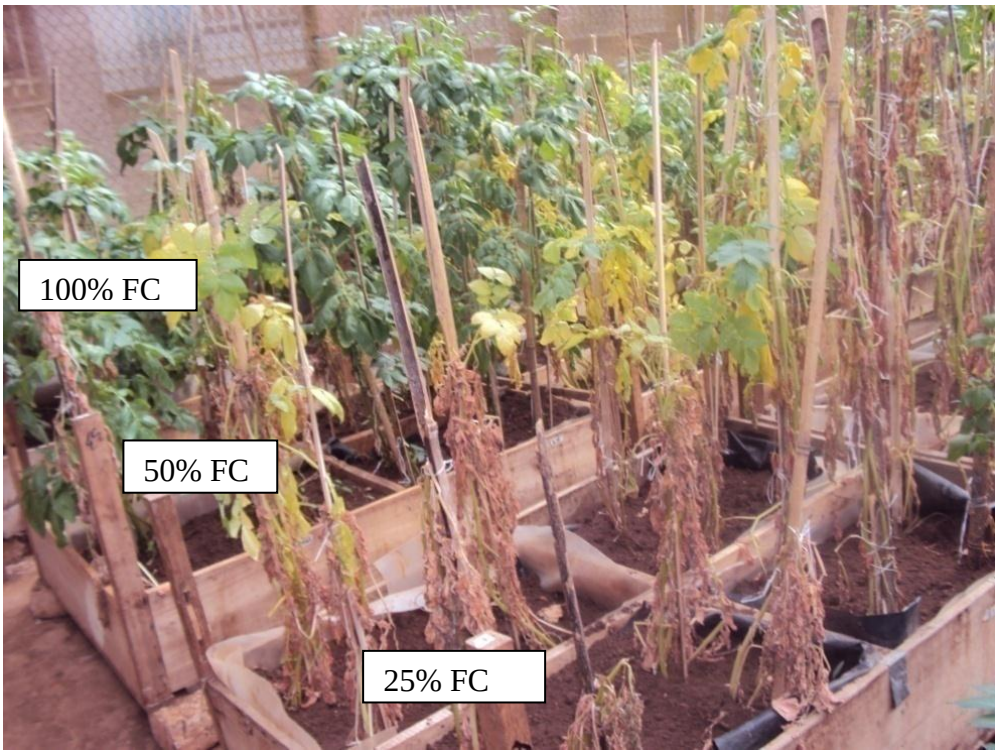

Figure 1. Appearance of plants across the water regimes prior to dehalming
50%FC=fifty percent field capacity, 25%FC=twenty five percent field capacity and FC=full field capacity.
The front box shows the plots that were given quarter of the field capacity, middle half of the field capacity and those at the extreme end watered to field capacity.

50% flowering

Numbers of days to 50% flowering across the watering regimes were not significantly different, however they increased with increase in moisture stress. Plots watered at field capacity attained 50% flowering at 58

days while those in both 50% and 25% moisture stress attained flowering at 59 days. Clones 395017.242, 394034.7 and 391533.1 flowered earlier under severe stressed plots at 47 and both at 56 days respectively. (Table 15)

Table 15. Effect of moisture stress on number of days to 50% flowering

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	61.0	59.8	58.5	54.3	54.3	54.3	57.6	57.0	56.4
391691.96	70.0	70.0	69.8	54.3	54.3	54.3	62.1	62.1	62.0
393077.159	62.0	66.0	66.0	54.0	57.8	56.0	58.0	61.9	61.0
394034.7	52.2	47.9	57.7	52.3	56.0	54.3	50.9	52.0	56.0
395017.242	46.5	51.5	46.5	56.0	54.3	50.8	51.3	52.9	48.6
Kachpot1	68.8	68.0	70.0	50.8	50.8	52.5	59.8	59.4	61.3
Uganda 11	71.8	69.8	71.8	63.0	66.5	64.8	67.4	68.1	68.3
Victoria	56.8	56.8	58.5	57.8	56.0	57.8	57.3	56.4	58.1
Mean	**61.1**	**61.2**	**62.3**	**55.3**	**56.2**	**55.6**	**58.0**	**58.7**	**59.0**
LSD	4.4			7.3			4.6		
%CV	5.1			9.3			7.4		

Leaf chlorophyll content

Leaf chlorophyll content increased with increase in moisture stress from an average of 22.5 in plots watered at field capacity, to 24.8 in those watered at 50% field capacity and 25.6 in 25% stressed plots. Clone 391691.96(30.8) had the highest chlorophyll content in severe stressed plots, followed by 394034.7 and Kachpot1 both with 28.8. (Table 16)

Table 16. Effect of moisture stress on leaf chlorophyll content

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	22.6	28.7	28.5	14.7	17.6	14.1	18.7	23.1	21.3
391691.96	38.4	52.6	48.7	17.9	12.4	12.8	28.2	32.5	30.8
393077.159	27.8	33.2	40.0	14.1	10.0	9.5	20.9	21.6	24.8
394034.7	16.6	18.2	45.5	14.3	13.2	12.2	15.4	15.7	28.8
395017.242	15.9	18.2	20.8	17.6	19.8	19.5	16.7	19.0	20.2
Kachpot1	39.4	41.2	47.0	17.7	11.3	10.5	28.6	26.3	28.8
Uganda 11	49.8	51.3	46.7	16.3	13.2	7.6	33.0	32.2	27.1
Victoria	24.7	44.7	32.1	12.3	11.2	14.0	18.5	27.9	23.0
Mean	**29.4**	**36.0**	**38.7**	**15.6**	**13.6**	**12.5**	**22.5**	**24.8**	**25.6**
LSD	8.6			7.7			10.8		
%CV	17.8			39.5			24.0		

Leaf area

Moisture stress decreased leaf area by 5.1% under the severe stressed plots. However 50% moisture stress did not affect leaf area, it instead increased by 2.9cm from that under well watered plots The highest leaf area reduction under severe stress was recorded in variety Uganda 11 with 23%, followed by clone 393077.159, 13.8%, 394034.7 with 13.3% and variety Victoria 12.3%. Moisture stress did not affect leaf area in clone 395017.242; it was instead higher in stressed plots than that attained under field capacity. The least leaf area reduction was in clone 391691.96 with 6.3% and 391533.1 with 6.5% (Table 17).

Table 17. Effect of moisture stress on potato leaf area

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	335.0	352.0	412.0	652.0	568.0	511.0	493.5	460.0	461.6
391691.96	543.0	584.0	521.0	438.0	389.0	399.0	490.8	486.5	459.9
393077.159	477.0	483.0	381.0	547.0	406.0	501.0	511.9	444.8	441.2
394034.7	279.0	256.0	278.0	479.0	335.0	379.0	379.2	295.9	328.7
395017.242	467.0	632.0	709.0	654.0	1096.	817.0	560.5	864.0	762.6
Kachpot1	638.0	529.0	516.0	605.0	734.0	644.0	621.9	631.7	579.6
Uganda 11	633.0	522.0	548.0	514.0	386.0	347.0	573.4	454.3	447.4
Victoria	404.0	463.0	392.0	498.0	474.0	399.0	451.1	468.7	395.4
Mean	**472.0**	**478.0**	**470.0**	**548.0**	**549.0**	**499.0**	**510.3**	**513.2**	**484.5**
LSD	151.2			184.3			206.3		
%CV	22.6			25.6			24.4		

Number of stems per plant

Number of stems per plant were not affected by moisture stress, instead 50% moisture stressed plots got the highest number of stems (3.2) while both plots watered to field capacity and those at 25% moisture stress got the same number (2.9) .the highest number of stems plant^{1} under severe stress was attained by variety Victoria and clone 393077.159 both with 4 stems (Table 18).

Table 18.Number of stems under the three watering regimes

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	1.5	3.1	2.2	3.8	3.5	3.3	2.6	3.3	2.7
391691.96	2.3	1.9	1.8	4.3	5.3	4.3	3.3	3.6	3.0
393077.159	2.8	2.5	2.6	4.0	6.3	4.5	3.4	4.4	3.6
394034.7	1.6	1.4	1.3	1.8	4.0	1.8	1.7	2.7	1.6
395017.242	2.3	2.0	2.8	4.3	1.5	1.0	3.3	1.8	1.9
Kachpot1	2.4	2.3	3.0	2.8	4.0	3.8	2.6	3.2	3.4
Uganda 11	1.4	1.5	1.4	3.3	4.8	3.8	2.3	3.1	2.6
Victoria	3.5	3.7	3.5	5.3	3.8	5.3	4.4	3.7	4.4
Mean	2.2	2.3	2.3	3.7	4.1	3.4	2.9	3.2	2.9
LSD	0.9			3.1			1.5		
%CV	28.1			49.8			46.3		

Stem diameter

Stem diameter decreased with increase in moisture stress, however plots watered at 50% field capacity got lower values compared to those at 25% moisture stress (Table 19). Clone 391533.1 and 395017.242 were not affected by stress, they instead got higher values in the severe stressed plots. Also clone 391691.96, 393077.159 and Kachpot1 got lower percentage reductions with 1.2, 3.5 and 3.9% respectively. Clone 393077.159 got the highest percentage reduction in stem diameter with 9.5% followed by varieties Victoria and Uganda 11 with 9.1 and 8.3% respectively (Table 19).

Table 19. Effect of moisture stress on potato stem diameter

WR / Genotype	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	1.16	1.10	1.13	1.11	0.98	1.18	1.13	1.04	1.15
391691.96	1.49	1.33	1.28	0.78	0.72	0.97	1.14	1.03	1.12
393077.159	1.53	1.58	1.35	1.36	1.30	1.44	1.45	1.44	1.40
394034.7	1.04	1.09	0.96	1.23	1.18	1.09	1.13	1.13	1.03
395017.242	1.11	1.08	1.13	1.61	1.52	1.91	1.36	1.30	1.52
Kachpot1	1.58	1.43	1.48	1.51	1.29	1.49	1.54	1.36	1.48
Uganda 11	1.77	1.76	1.68	1.49	1.33	1.31	1.63	1.54	1.49
Victoria	1.34	1.38	1.26	1.68	1.58	1.49	1.51	1.48	1.37
Mean	**1.38**	**1.35**	**1.28**	**1.35**	**1.24**	**1.36**	**1.36**	**1.29**	**1.32**
LSD	0.22			0.34		0.21			
%CV	11.7			18.4		15.4			

3.3.3. Effect of moisture stress on Yield

Combined mean yield in tons per hectare from two repeats reduced with increase in moisture stress among all the genotypes (table 14). The overall mean yield in tons per hectare reduced from 21 tons per hectare in well watered plots to 12.5 in 50% moisture stressed plots and 10 tons per hectare in 25% moisture stressed plots. The highest yield under 25% moisture stress was obtained from clone 394034.7 (12.6 tons per hectare), followed by 391533.1 (11.1) and 393077.159 (10.9). It was least in variety Victoria (8.2), Kachpot1 and Uganda 11 with 8.7 and 9.1 tons per hectare respectively. Percent yield reduction from normal watering to severe stress was least in clone 391533.1 (38.5%), followed by 394034.7 (39%), and 395017.242 (49.6). The highest yield reduction was in variety Victoria (68.8%) followed by Uganda 11 (58.3%) and Kachpot1 (56.7%). (Table 20)

Table 20. Effect of induced moisture stress on potato total fresh yield in tons per hectare

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	20.0	12.1	10.9	16.0	10.2	11.3	18.0	11.2	11.1
391691.96	18.2	9.7	6.7	22.4	13.6	11.7	20.3	11.6	9.2
393077.159	26.7	13.9	9.4	19.6	16.4	12.5	23.1	15.2	10.9
394034.7	26.7	13.9	13.3	14.8	12.4	12.0	20.7	13.2	12.6
395017.242	24.9	13.9	10.9	15.4	11.3	9.4	20.1	12.6	10.2
Kachpot1	19.4	6.1	4.9	20.9	15.0	12.6	20.1	10.5	8.7
Uganda 11	20.6	10.3	6.1	22.9	15.8	12.1	21.8	13.0	9.1
Victoria	27.9	10.9	7.9	20.1	15.1	8.6	24.0	13.0	8.2
Mean	23.0	11.4	8.8	19.0	13.7	11.3	21.0	12.5	10.0
LSD	5.1			3.7			2.2		
%CV	25.1			17.8			21.7		

Total weight of tubers

The highest weight of tubers under severe stress was recorded in clone 394034.7 (521.6g), followed by 391533.1 (457g) and 393077.159 (450.1g). It was lowest in variety Victoria (339.1), Kachpot1 and Uganda 11 with 359.9g and 373.9g respectively. Percent weight reduction from normal watering to severe stress was least in clone 391533.1 (38.5%), followed by 394034.7 (39%), and 395017.242 (49.6). The highest yield reduction was in variety Victoria (68.8%) followed by Uganda 11 (58.3%) and Kachpot1 (56.7%) (Table 21).

Table 21. Effect of moisture stress on total weight of tubers from four plants (in grams) across the water regimes

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	825	500	450	661	422	464	743.2	460.8	457
391691.96	750	400	275	923	559	482	836.4	479.7	378.6
393077.159	1100	575	388	807	675	513	953.6	625	450.5
394034.7	1100	575	550	611	512	493	855.3	543.5	521.6
395017.242	1025	575	450	637	465	388	830.8	520	418.9
Kachpot1	800	250	200	862	617	520	831.2	433.5	359.9
Uganda 11	850	425	250	944	649	498	897.1	537.3	373.9
Victoria	1150	450	325	831	623	353	990.4	536.6	339.1
Mean	**950**	**469**	**361**	**784**	**565**	**464**	**867.2**	**517**	**412.4**
LSD	**210.1**			**152.2**			**90.8**		
%CV	**25.1**			**18.8**			**21.7**		

Dry matter content

Across genotypes and experimental repeats, tuber dry matter content increased with increase in moisture stress .The lowest dry matter content (19.7%) was recorded in the well watered plots, and the highest (22.8%) in the severe (quarter stressed plots).The highest dry matter content across the watering regimes was recorded in variety Kachpot1 (25.3%), Uganda 11 (24.5%), CIP 391691.96 (23.7). (Table 22)

Table 22. Effect of moisture stress on % tuber dry matter content

	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
WR / Genotype	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	19.5	24.16	20.76	19.37	17.39	20.14	19.44	20.78	21.71
391691.96	24.61	27.91	31.73	16.35	19.42	22.17	20.48	23.67	26.95
393077.159	20.76	25.55	23.49	16.62	17.32	19.33	18.69	21.43	21.41
394034.7	18.84	20.25	21.6	16.48	16.59	17.23	17.66	18.42	19.42
395017.242	20.84	23.04	22.99	15.93	17.14	16.98	18.38	20.09	19.98
Kachpot1	26.26	31.85	31.79	20.08	21.08	21.01	23.17	26.46	26.4
Uganda 11	22.61	28.92	29.43	22.19	22.77	21.15	22.4	25.85	25.29
Victoria	19	25.41	23.58	16.39	18.04	18.55	17.7	21.73	21.06
Mean	**21.55**	**25.89**	**25.99**	**17.93**	**18.72**	**19.57**	**19.74**	**22.3**	**22.78**
LSD	**4.6**			**2.6**			**2.8**		
%CV	**12.5**			**10.2**			**11.8**		

3.3.4. Effect of moisture stress on graded tuber number and quality

Tubers obtained from the characterization experiment for each genotype by irrigation treatment combination were graded, counted and weighed. The overall mean from the two experiments showed decreased tuber number with increase in moisture stress as shown in table 23 below. Total number of tubers was high in the well watered plots but was the same in both the 50% and 25% moisture stressed plots.

Table 23. Effect of moisture stress on total tuber number

WR / Genotype	Expt 1 (2011B)			Expt 2 (2012A)			Pooled		
	FC	50%FC	25%FC	FC	50%FC	25%FC	FC	50%FC	25%FC
391533.1	30	31	29	37	30	36	33	31	31
391691.96	62	44	29	28	24	21	45	34	37
393077.159	35	23	23	27	28	23	31	25	27
394034.7	24	20	22	22	23	26	23	21	22
395017.242	22	23	25	15	21	28	18	22	22
Kachpot1	45	26	16	23	19	25	34	23	25
Uganda 11	38	27	21	19	19	23	28	23	24
Victoria	24	27	20	22	24	20	23	26	22
Mean	**35**	**28**	**23**	**24**	**24**	**25**	**29**	**26**	**26**
LSD	**11.5**			**4.4**			**5.1**		
%CV	**28.8**			**25.7**			**27.7**		

Tuber shape, skin colour, and skin quality, were described (Appendix 1). Variety Uganda 11 and Kachpot 1 produced tubers with soft skins in stressed plots. Also CIP 391691.96 and 393077.159 produced tubers with scabies in some plots while Uganda 11, CIP 391691.96 and Kachpot1 produced tubers with secondary growth as shown in the figure below.

Figure 2. Secondary growth and scabies due to moisture stress

Five genotypes maintained their tuber shape and reasonable size across the three watering regimes, however, Kachpot1, 391691.96 and Uganda 11 formed different shapes of tubers in the stressed plots including; bottle neck shaped tubers, knobby and cucumber shaped tubers (figure 3)

Figure 3. Different malformed potato tuber shapes due to moisture stress

3.4.5. Correlation amongst yield and growth traits tested in the characterization experiment.

There were positive correlations between yield and stem diameter, relative leaf water content, plant height and increment in plant height after imposing stress. Out of these only the correlation with stem diameter was significant at $p \leq 0.5$. Other positive significant correlations were obtained between number of stems and stress score, plant height and increment in plant height, chlorophyll content and dry matter content, 50% flowering and dry matter content and then 50% flowering and chlorophyll content. (Table 24)

Table 24.Correlations of tuber yield and other tested drought tolerance trait means averaged from two trials of the characterization experiment

Yield	1	-			
LA	2	-0.17	-		
SS	3	-0.29	-0.20	-	
SD	4	0.78*	0.41	0.33	-

RLWC	5	0.09	-0.56	-0.45	-0.19	-						
PH	6	0.35	0.27	0.31	-0.12	-0.56	-					
NS	7	-0.12	-0.13	0.86**	0.32	-0.53	0.59	-				
IPH	8	0.37	0.27	-0.25	-0.34	-0.06	0.72*	-0.05	-			
DMC	9	-0.22	0.25	-0.03	0.35	0.13	0.47	0.16	0.69	-		
CHLPL	10	-0.23	-0.04	0.11	0.24	0.24	0.44	0.23	0.61	0.91**	-	
50%A	11	-0.17	-0.17	0.22	0.37	0.37	0.30	0.33	0.34	0.80*	0.89**	-
		1	2	3	4	5	6	7	8	9	10	11

*, ** represent significance at 0.05 and 0.001 probability levels respectively. Correlations without stars were not significant at P<0.05.
LA=leaf area, SS=stress score, SD=stem diameter, RLWC=relative leaf water content, PH=plant height, NS=number of stems, IPH=increment in plant height, DMC=dry matter content, CHLPL=chlorophyll content and 50%A = 50% anthesis.

3.4. Discussion of results

The experiments for characterizing potato genotypes for tolerance to drought were identically managed in the two repeats of testing. The two experiments produced significantly different values for several growth and physiological parameters apart from plant height, stem diameter and stress score. Results from these two repeats were different because the second trial was attacked by aphids at the vegetative stage, and the aphids failed to respond to insect's spray forcing the experiment to be terminated earlier. The crop was dehaulmed earlier (at 3.5 months compared to the first experiment which was dehaulmed at four months, thus tuber dry matter was affected because tubers never had enough time to fill up. However, yield was not affected indicating uniformity of experimental conditions in the screen house (Table 5 and 10).

In both trials the effect of water moisture deficit varied among genotypes, for both growth parameters and yield components which demonstrate the variability in the level of drought tolerance that exists among the eight potato genotypes. The mean ground cover reduced from 64% in field capacity watered plots, to 57.6% in half field capacity and 52.3% in plots at quarter field capacity. The highest percentage ground cover reduction under severe stress was recorded in clone CIP 393077.159 (24.8%), followed by varieties Uganda 11 (22.8) and Victoria (22.5%). It was lowest in clone 391533.1 (5.7%), 391691.96 (10.3%) and variety Kachpot1 (16.5%). The overall mean plant height was reduced from 86.9cm under well watered plots, to 79.7cm in half well watered plots and 78.5cm in quarter of the well watered plots. Plant height was mostly reduced in clone 393077.159 (19.5%) under severe stress, followed by variety Victoria (17.7%), and clone 395017.242 (12.4%). There was less reduction in plant height in clone 391533.1(0.1%), followed by 391691.96 (3.3%) and variety Uganda 11 (5.3%). The reduction in plant height can be probably due to poor cell enlargement due to water stress, Water stress suppresses cell expansion and cell growth due to low

turgour pressure (Neera *et al*., 2011, Kumar *et al*., 2007, Shao *et al*., 2009 and Schafleitner *et al,* 2007) also reported that water stress is responsible for plant dwarfing and reduction in ground coverage. Leaf area was also reduced by moisture stress. There was 5.1% leaf area reduction in severe stressed plots. Uganda 11 had the highest leaf area reduction (23%) while clone 391691.96 had the least reduction (6.3%). Reduction in leaf area is attributed to suppression of leaf expansion through reduced photosynthesis (Shakeel *et al*., 2011).

Leaf chlorophyll content increased with increase in moisture stress (22.5,24.8 and 25.6), in the plots watered to field capacity,50% field capacity and 25% field capacity respectively. Arunyanark, (2009), reported a similar finding in peanut. Dry matter content also increased with increase in moisture stress; Field capacity **(**19.7%), half field capacity (22.3%) and quarter field capacity (22.8%) (Sharma *et al.,* 2011; Tad-Awan, 2008 and Kumar *et al*., 2007) reported similar findings. The highest tuber dry matter content was in adopted varieties Kachpot1 (25.3%) and Uganda 11, (24.5%), which were released basing on their high yields, resistance to late blight disease and good processing qualities.

The highest yield under 25% moisture stress was obtained from clone 394034.7 (12.6 tons per hectare), followed by 391533.1 (11.1), 393077.159 (10.9), 395017.242 (10.2), 391691.96 (9.2). It was least in variety Victoria (8.2), Kachpot1 and Uganda 11 with 8.7 and 9.1 tons per hectare respectively. Percent yield reduction from normal watering to severe stress was least in clone 391533.1 (38.5%), followed by 394034.7 (39%), and 395017.242 (49.6). The highest yield reduction was in variety Victoria (68.8%) followed by Uganda 11 (58.3%) and Kachpot1 (56.7%). Neera *et al*., (2011), reported yield reduction in potato under stress. Results from this study show that clones from CIP were less affected by moisture stress. They could hence be possessing drought tolerant genes. Clones that reached 50% flowering early; 395017.242(51 days), 394034.7(53 days) and 391533.1 (57 days) maintained high yields in the stressed plots. Tuber yields from these plots were: 394034.7(12.6 tons per hectare), followed by 391533.1 (11.1) and 395017.242 (10.2). These clones could be early maturing, suggesting that they formed tubers early before the imposition of stress and thus escaped it (Price *et al*., 2002).

Stress score is a visual indicator of drought stress and is used to identify genotypes that are tolerant to drought. In this study, stress scores were least in clone 395017.242 (1, 2.4 and 3.5), followed by variety Kachpot1 (1, 2.3 and 3.9), 391533.1 (1, 2 and 4) and 391691.96 (1, 3 and 4.5). It was highest in variety Victoria with (1, 7 and 8.5) in the well watered, 50% stressed and 25% stressed plots respectively. Genotypes that exhibited lower stress scores compared to others was most likely due to higher turgor pressure in the

stems and leaves that maintained the moisture content of leaf tissues, (Price *et al*., 2002a) and the drying of leaves in susceptible genotypes was most likely due to extreme loss of water because of heat from rising temperatures and inadequate transpiration cooling (Fischer &Fukai, 2003).

There was a high positive significant correlation between leaf wilting and number of stems per plant (0.85) meaning that the higher the number of stems the higher the wilt score. Variety Victoria and clone 393077.159 which had the highest number of stems (4) in the severe stressed plots had the highest wilt score (1, 7 and 8.5) and (1, 3.4 and 6.5) respectively despite the good yield obtained by clone 393977.159 under severe stress. This could be attributed to many stems competing for the little available water. Namazzi S (2011) reported a similar finding in rice. In her study, genotypes with high tiller numbers also had high leaf rolling scores. Variety Kachpot1 and Uganda 11 did not show severe signs of leaf stress but yielded poorly in the stressed plots. This suggests that most of the moisture was used in maintaining the vegetative parts. They also resulted in the highest percentage ground cover (60% for Kachpot1 and 56.0% for Uganda 11) in the severely stressed plots (Table 9).

Relative leaf water content is the most appropriate measure of plant water status in terms of the physiological consequence of cellular water deficit (Barrs & Weatherly, 1962). In this study, relative leaf water content was least affected under quarter moisture stress in clone, 394034.7,which had the highest percent relative leaf water content (71%), followed by 393077.159 (64%) and then 391750.242 (63%). It was mostly affected in Victoria with 58%.

Conclusion

Potato clones 391533.1,394034 .7, 393077.159 and 395017.242 were characterized as drought tolerant and 3916 moderately tolerant basing on less drought effect on yield , physiological and growth parameters , while varieties; Uganda 11 and Kachpot1 were susceptible

Recommendation

It is possible that there are potato clones with drought tolerance traits. It is therefore recommended to evaluate these genotypes more under different environmental conditions. The study also revealed that no single genotype possessed all the drought tolerance traits, thus wide selection involving many genotypes is recommended.

CHAPTER FOUR

DETERMINING THE COMBINING ABILITY OF DROUGHT TOLERANT GENOTYPES WITH SOME ADAPTED DROUGHT SENSITIVE VARIETIES

4.1. Introduction

Potato varieties currently grown in Uganda were released basing on high yields, resistance to diseases especially late blight and good processing qualities. However, the reaction of these varieties to water stress is not known and the above good attributes are rendered void if the crop receives less than average moisture in a season. Many regions in the world that previously had stable and reliable rainfall patterns, particularly in tropical highlands currently suffer from intermittent droughts which are expected to continue (Rijsberman, 2006). This is primarily attributed to global warming. Chapter three of this study characterized released adapted varieties as drought susceptible and new clones from CIP as drought tolerant, hence need to study the combining ability in order to introgress the drought tolerant genes from tolerant clones into the drought susceptible varieties.

Combining ability studies for parents is important because those with high means may not be able to transmit them to the hybrids. Combining ability analysis does not only provide an assessment of parents' gametic input, but also helps to interpret the genetic basis of quantitative traits such as dry matter, yield and yield associated traits (Mendoza & Hynes, 1974). Evaluation of parents based on general combining ability (GCA) and means can result in selection of those with a high reservoir of genes that are superior as well as determine the nature of gene action (Vanaja, 2003; Malini *et al*., 2006). GCA of a parental clone provides an assessment of its breeding value, as judged by the mean performance of its progenies from crosses with other clones. Crossing in potato is advantageous in that once a hybrid with desirable traits is identified; it can be multiplied vegetatively for a longtime without risks of segregation (Mondal & Hossain, 2006). Therefore four drought tolerant genotypes were crossed with three susceptible genotypes to determine their combining ability.

4.2. Materials and methods

4.2.1. Crossing and F1 seed generation

Four clones selected from drought tolerance characterization experiment were crossed with three local varieties. The selected clones used were CIP 391691.96, CIP 393077.159, CIP 395017.242 and CIP 391533.1 while the local varieties were Uganda 11 (CIP 720097), Nakpot 5 CIP 381471.18, and Victoria

(CIP 381381, 20). The new clones were males while the adapted varieties were the females. CIP clone 394034.7 was not used in the hybridization experiment despite its good performance under moisture stress because only two plants flowered and did not produce enough pollen for fertilization. Likewise Variety Kachpot1 was not used because of failure to get successful crosses with it. It was instead replaced with Nakpot5, a released high yielding variety whose reaction to drought stress was also not known. The experiment was conducted at Kachwekano Zonal Agricultural Research and Development Institute (KAZARDI), Kabale district in south western Uganda. The institute is situated at 029^0 57'E 01^0 16'S at 2200 m above sea level (masl).

Fifteen tubers per genotype were planted in a crossing block at 75 cm between rows and 30 cm between plants. In order to increase the number of berries, NPK fertilizer at 100kgs ha^{-1} was added. The plants were protected against late blight attack using agro-laxyl at 2.5g l^{-1} and insect pest damage with Agro-thoate at 2.0ml l^{-1}. At flowering stage, approximately 50-60 days after planting, flowers of the selected female parents were manually emasculated by carefully removing the anthers, using a pair of forceps taking care not to damage the stigma. This was done to prevent self pollination. Pollen was collected from mature flowers of the selected male parents by shaking the anthers into Appendorf tubes. The emasculated flowers were pollinated by rubbing the stigma onto the collected pollen powder in the open lid of the Appendorf tube. Pollination was done in the morning between 8:00 and 11:00. A label showing female and male parent, and date of pollination, was attached on the pollinated flower with a water resistant thread. Successful fertilization was identified by berry formation after one week. At maturity, approximately 40 days after pollination, berries of the same cross were harvested and bulked together in labeled polythen bags and kept at room temperature for 3-4 weeks to ripen. After ripening and adequate softening, seeds were manually extracted by pressing the berries in a cloth bag. Extracted seeds were washed thoroughly with soapy water to dissolve the mucilage. The clean seeds were dried and packed in plastic petri dishes for storage until sown for raising F1 progeny seedlings.

4.2.2. Evaluation of F1 progenies for drought tolerance.

Dried true potato seeds from the crosses were sown in seedling boxes containing steam sterilized soil on 20th March, 2012. After germination, the seedlings were treated with Agrozeb 80WP fungicide in powder form to protect them from late blight attack. Four Seedlings from an F1 family were transplanted at 5-leaf stage on 2nd May, 2012 into each plot. Like the parents, a wooden box (4.5 x 1.1 m) was used as the main plot and

twelve families as the sub-plot treatment. The box was divided into twelve partitions (0.75 x 0.55) to accommodate all the twelve F1 families. Two replications were used. In each partition, two litres of water were added after every three days for two weeks to provide enough water for the establishment of the seedlings.

The seedlings were sprayed with agro-thoate and agro-laxyl to prevent insect and late blight attack, respectively. A label showing the progenitors was put on each partition. For each F1 progeny cross, 24 seedlings were transplanted. After seedling establishment, a compound NPK 17:17:17 fertilizer was applied at a 100 kg per hectare. Seedlings took two weeks to be well established as growing plants, after this irrigation followed moisture measurements as earlier described in chapter three, thus the four plants in each partition received four litres of water per week to keep the soil moist to field capacity. This was continued up to two months, after which the plants were subjected to three watering regimes as the parents.

The control (those watered to field capacity received four litres of water, the other set was given 2 liters (half field capacity) and the third set given 1 liter (quarter field capacity) every week. Similar data like for the parents was collected apart from number of days to 50% flowering and number of stems per plant. Data were subjected to analysis of variance using Genstat statistical package 14th edition.

Table 25. F1 Potato families that were transplanted for drought tolerance studies

Family code	Male parent	Female parent	No. of plants transplanted
V x .1	393315.1	Victoria	24
V x .159	393077.159	Victoria	24
V x .96	391691.96	Victoria	24
V x .242	395017.242	Victoria	24
R x .1	393315.1	Uganda 11	24
R x .159	393077.159	Uganda 11	24
R x .96	391691.96	Uganda 11	24
R x .242	395017.242	Uganda 11	24
N x .1	393315.1	Nakpot5	24
N x .159	393077.159	Nakpot5	24
N x .96	391691.96	Nakpot5	24
N x .242	395017.242	Nakpot5	24


Figure 4. Experimental layout for F1 progenies

Table 26: Skelton ANOVA for F1 analysis

Source	df	Type of effect	Expected MS	F-test denominator
Rep	1	Random	δ^2e +36 δ^2rep	Error
Watering regime	2	Fixed	δ^2e +24 δ^2W+12 δ^2Rep *W	Rep*Watering
Rep * Watering regime	2	Random	δ^2e+12 δ^2reps *W	Error
GCA grp1	2	Fixed	δ^2e +24 δ^2 GCA grp1	Error
GCA grp2	3	Fixed	δ^2e +18 δ^2 GCA grp2	Error
GCAgrp1*GCAgp2	6	Fixed	δ^2e+6 δ^2 GCA grp1 * GCA grp2	Error
Watering regime * GCAgrp1	4	Fixed	δ^2e +8 δ^2 W* GCA grp1	Error
Watering regime * GCAgrp2	6	Fixed	δ^2e +6 δ^2 W* GCA grp2	Error
Watering regime * GCAgrp1*GCAgrp2	12	Fixed	δ^2e+2 δ^2 W* GCA grp1 x GCA grp2	Error
Residual (error)	33		δ^2e	
Total	71			

Results

4.3 Analysis of combining ability

Analysis of variance of the F1 generation revealed significant GCA and SCA (specific combining ability) in a few parameters among those that were tested. Significant GCA differences were obtained for leaf area at ($p<0.01$) from the susceptible parent (table 27) and at ($P<0.001$) from the tolerant parent. Stem diameter gave significant GCA results at ($p<0.5$) from both the susceptible and tolerant parents (table 28). Ground cover was significant at ($p<0.01$) from the tolerant parent. Increment in plant height was significant at ($p<0.01$)

from the tolerant parent. Watering regimes were significant for relative leaf water content and leaf area at ($p<0.5$), while stress score and groundcover were significant at ($P<0.001$). The interaction between watering regime and GCA from the susceptible parent was significant for ground cover ($p<0.5$) and increment in plant height at ($p<0.01$) and significant at ($p<0.5$) for increment in plant height from the tolerant parent. The interaction between SCA and watering regimes were significant at ($p<0.5$) for leaf area and groundcover (table 29).

Table 27. Analysis of variance for combining ability of indicators of drought tolerance in potato

		Mean squares			
Source	d.f	Dry matter content	leaf area	Plant height	Relative leaf water content
rep	1	0.93	224583***	5378.4***	69.28
WR	2	37.1	59079	460.9	306.79
rep.WR	2	10.3	71802	26.4	374.04
GP1	2	19.66	111397**	179.1	16.3
GP2	3	26.43	148629***	405.2	135.7
GP1.GP2	6	8.43	33437	195.1	53.08
GP1.WR	4	16.75	31866	157.4	12.46
GP2.WR	6	12.43	30619	424	48.9
GP1.GP2.WR	12	21.91	32367*	412.6	62.28
Residual	33	12.6	14653	305.3	75.72

Where GCA =General combining ability, WR=watering regime, grp1=susceptible parents, grp2=tolerant parents and Grp1.grp2=SCA

Table 28. Analysis of variance of combining ability for drought tolerance indicators continued

Source of variation	**df**	**Stem diameter**	**Stress score**	**ground cover**	**Increment in plant height**
rep	1	0.09	64.22**	23.35	0.18
WR	2	0.16	147.68	416.54	45.3
rep.WR	2	0.2907	23.097	400.85	208.71
GP1	2	0.20052*	5.264	131.37	59.55
GP2	3	0.24357*	2.685	277.46**	210.68**
GP1.GP2	6	0.11	1.394	32.29	38.58
GP1.WR	4	0.02	3.576	151.04*	164.62**
GP2.WR	6	0.08	1.699	109.93	101.94*
GP1.GP2.WR	12	0.09	2.512	101.68*	82.78
Residual	33	0.06	5.23	47.62	42.08

Table 29.Analysis of variance for combining ability of tuber yield and its component characters in potato

Source	Mean squares				
	Total no. of tubers	Number of tubers per plant	Total weight of tubers(g)	Weight of tubers per plant(g)	Yield in tons per hectare
Rep	4.5	9.09	64992	138	27.673
Watering regime	750.4	8.01	325037	97.92	196.248
Rep.Watering regime	501.2	6.03	88955	77.76	49.56
GCA.grp1	98.3	14.8	26180	0.83	16.299
GCA.grp2	482.2*	36.36	18472	74.81	10.878
GCA grp1.GCA grp2	146.1	17.88	749	20.04	4.119
WR.GCA grp1	136	39.22	19395	40.33	11.982
WR.GCA grp2	121.2	41.5	20300	47.66	11.326
WR.GCA grp1.Gca grp2	223.4	46.33	16746	65.83	9.8
Residual	144.9	37.29	15576	61.38	7.283

Significant GCA differences were obtained from the tolerant parents at ($p \leq 0.5$) for total number of tubers. Watering regimes were significant at ($p \leq 0.5$) for total number of tubers and for total weight of tubers at ($p \leq 0.001$) (table 29).

4.3.1 General combining ability (GCA) effects

Parent 391533.1 had positive significant GCA effects for stem diameter. Uganda 11 had significant GCA effects for number and weight of tubers per plant. Victoria had negative significant GCA effects for weight of tubers per plant. Nakpot5 had negative significant GCA effects for average weight of tubers and positive significant GCA effects for total number of tubers and so was 393077.159. Clone 391533.1 had negative significant GCA effects for total weight of tubers and 393077.159 positive significant effects for yield in tons per hectare (table 30 and 31).

Table 30. Estimates of GCA effects of parents for different characters in potato

Parent	Dry matter content	Leaf area	Plant height	Relative leaf water content	Leaf chlorophyll content
Nakpot5	-0.78	6	-3.2	0	1.18
Uganda 11	-0.22	-71	1.6	0.8	-0.5
Victoria	0.99	65	1.6	-0.8	-0.69
391533.1	-0.82	12	4.4	-1.7	-0.54
391692.96	-0.55	-86	-3.4	3.4	-0.48
393077.159	1.8	-48	3.8	0.9	0.33
395017.242	-0.43	122	-4.7	-2.7	0.69
SE GCA	0.7,0.8	24.7,28.5	3.6,4.1	1.8,2.1	0.8,0.9

Table 30. Continued

Parent	Stem diameter	Stress score	Groundcover	Increment in plant height
Nakpot5	0.029	-0.11	0.96	-0.37
Uganda 11	-0.102	0.51	-2.67	1.73
Victoria	0.073	-0.4	1.71	-1.36
391533.1	0.006*	0.19	4.07	-4.02
391692.96	-0.101	0.36	-4.04	3.05
393077.159	-0.066	-0.53	-2.6	2.63
395017.242	0.161	-0.03*	2.57	-1.66
SED	0.05, 0.06	0.5, 0.5	1.4, 1.6	1.3, 1.5

The first standard error is for the first three susceptible varieties and the second for the last four tolerant clones.

Table 31. GCA effects of yield components

Source	Total no. of tubers	Number of tubers per plant	Total weight of tubers (grams)	weight of tubers per plant (grams)	yield in tons per hectare
Nakpot5	0.67	-0.1	0.4	23*	0.59
Uganda 11	0.19*	0.21*	-2.2	-38*	-0.94
Victoria	-0.86	-0.12	1.8	15	0.35
391533.1	-2.08*	3	-4.1	-1*	0.05*
391692.96	0.73	-0.5	-2.9	-40	-1
393077.159	0.3*	-1	-0.4	2*	0.04*
395017.242	1.05	-1.5	7.4	38	0.9
SED	1.3,1.5	1.6,1.8	2.5,2.8	25.5,29.4	0.6,0.6

4.3.2. Specific combining ability (SCA) effects

Hybrids had both significant positive and negative as well as non-significant SCA effects. Nakpot5 x 393077.159 had significant positive SCA effects and Victoria x 391533.1 negative significant effects for dry matter content (Table 26). A cross between Uganda 11 and 391533.1 had positive significant SCA for plant height. Nakpot5 x 393077.159 had positive significant SCA for leaf chlorophyll content. Nakpot5 x 395017.242 had negative significant SCA for yield in tons per hectare. Hybrids Nakpot5 x 393077.159 and Victoria x391692.96 had positive significant SCA for ground cover while Victoria x 395017.242 and Victoria x391692.96 had negative significant effects for the same trait. Victoria x 391692.96 had positive SCA effects for increment in plant height, Uganda 11 x 391533.1 and Uganda 11 by 391692.96 positive significant SCA effects for average number of tubers, Nakpot5 x 3977.159, negative significant SCA effects for average weight of tubers and Nakpot5 x 395017.242 negative significance SCA effects for total weight of tubers(Table 32 and 33).

Table 32. SCA effects for the tested characters

Susceptible parent	Tolerant parent	Dry matter content	Leaf area	Plant height	Relative leaf water content
Nakpot5	391533.1	0.72	-6	6.8	0.4
	391692.96	1.05	67	-3.3	-0.4
	393077.159	0.12*	-74	1.9	-2
	395017.242	-1.89	13	-5.4	2
Uganda 11	391533.1	-0.63	-67	0.2*	-3.2
	391692.96	-0.4	-51	2.4	3.2
	393077.159	0.32	75	-4.9	0
	395017.242	0.71	43	2.2	0
Victoria	391533.1	-0.09*	73	-7.1	2.8
	391692.96	-0.65	-17	0.9	-2.8
	393077.159	-0.45	-1*	2.9	2
	395017.242	1.19	-55	3.2	-2
	SED	1.5	49.4	7.1	2.1

Table 32. continued

Drought susceptible parent	Drought tolerant parent	Stem diameter	Stress score	Chlorophyll content	Ground cover	Increment in plant height
Nakpot5	391533.1	-0.15	0.39	1.29	-1.57	1.10
	391692.96	0.17	-0.28	0.71	5.71	-4.75
	393077.159	0.04	0.28	0.13*	0.10*	-0.53
	395017.242	-0.07	-0.39	-2.13	-4.24	4.18
Uganda 11	391533.1	0.02	-0.24	-0.70	2.06	-2.70
	391692.96	-0.10	0.60	-1.24	-5.67	5.46
	393077.159	0.06	-0.51	-0.49	-0.78	1.42
	395017.242	0.02	0.15	2.43	4.39	-4.18
Victoria	391533.1	0.13	-0.15	-0.59	-0.49	1.60
	391692.96	-0.07	-0.32	0.53	-0.04**	-0.71
	393077.159	-0.10	0.24	0.36	0.68	-0.89
	395017.242	0.05	0.24	-0.30	-0.15*	0.01**
	SED	0.10	0.90	1.60	2.80	2.70

Table 33. SCA effects for yield and its components

Cross	Total no. of tubers	Number of tubers per plant	Total weight of tubers(grams)	Weight of tubers per plant(grams)	yield in tons per hectare
Nakpot5*391533.1	-1.9	-1.37	-25	-0.59	-0.47
Nakpot5*391692.96	3.6	0.97	42	-0.43	0.96
Nakpot5*393077.159	-1.1	0.86	-16	-0.11*	-0.44
Nakpot5*395017.242	-0.6	-0.47	-1*	1.13	-0.06
Uganda 11*391533.1	0.6	0.11*	-24	0.43	-0.64
Uganda 11*391692.96	-2.7	0.06*	-9	-1.11	-0.21
Uganda 11*393077.159	-4.2	-2.08	26	2.41	0.65
Uganda 11*395017.242	6.3	1.9	8	-1.73	0.2
Victoria*391533.1	1.3	1.25	49	0.16*	1.11
Victoria*391692.96	-0.9	-1.03	-32	1.54	-0.75
Victoria*393077.159	5.3	1.22	-10	-2.3	-0.21
Victoria*395017.242	-5.7	-1.43	-7	0.6	-0.15

4.3.3. Baker's ratio, narrow and broad sense coefficients of genetic determination

Variance components, Baker's ratio, the broad sense coefficient of genetic determination (BSCGD) and narrow sense coefficient of genetic determination (NSCGD) for the different traits were calculated (Table 34). Dry matter content, leaf area, plant height, stem diameter, relative leaf water content and groundcover had high baker's ratio (0.83,0.70,0.68,0.59,0.64,0.56 respectively) (Table.34). The narrow sense coefficient of genetic determination was high for leaf area (0.5,) dry matter content and yield in tons ha^{-1} (0.76). Broad sense co-efficient of genetic determination was high for leaf area (0.7), stem diameter (0.5), groundcover (0.58) and increment in plant height after the imposition of stress (0.55). The total number of tubers had a high baker's ratio (0.66), Baker's ratio was also high for Total weight of tubers (1) and so was yield in tons ha^{-1}(0.99). Yield in tons ha^{-1} gave both a high narrow and broad sense coefficient of genetic determination (0.76).

Table 34. Variance components, Baker's ratio, Broad and Narrow sense coefficient of genetic determination obtained for the different traits.

Parameter	δ2e	δ^2GCA1	δ^2GCA2	δ^2SCA	δ^2g	δ2p	BR	NSCGD	BSCGD
Dry matter content	6.30	0.56	1.12	0.36	2.03	8.33	0.83	0.20	0.24
Leaf area	732.65	4336.27	7850.14	4351.75	15638.26	23864.70	0.74	0.51	0.69
Plant height	152.65	1.10	14.03	7.06	22.20	174.86	0.68	0.09	0.13
Relative leaf water content	37.86	0.00	5.44	2.54	7.07	44.93	0.64	0.10	0.16
Stem diameter	0.03	0.01	0.01	0.01	0.03	0.06	0.59	0.30	0.51
Chlorophyll	7.68	0.74	0.00	1.33	2.02	9.70	0.34	0.07	0.21
Ground cover	23.81	4.48	14.09	14.35	32.93	56.74	0.56	0.33	0.58
Increment in plant height	21.04	1.60	10.54	13.38	25.60	46.66	0.47	0.26	0.55
Total no .of tubers	72.45	1.07	22.76	12.28	36.12	108.57	0.66	0.22	0.33
Number of tubers plant^{-1}	18.65	0.00	0.98	0.00	0.70	19.34	1.18	0.04	0.04
Total weight of tubers	7788.00	766.30	593.60	0.00	1311.06	9099.07	1.00	0.15	0.14
Weight of tubers plant^{1}	3.69	0.00	2.45	0.00	0.00	30.12	2.12	0.04	-0.02
Yield in tones per hactare	3.64	1.00	10.70	0.08	11.78	15.42	0.99	0.75	0.76

4.3.4 Discussion of results

Clone 395017.242 had negative significant GCA effects for stress score. Significant GCA effects for stress score are not desirable since high scores indicate drought susceptibility. Among the tolerant parents, this clone had the least stress score (Table14), and the mean stress score of the crosses involving this parent were the least, implying it transferred this trait to the off springs. Among the susceptible parents Uganda 11 had the highest yield in tons per hectare (7.2) under 25% moisture stress and the tolerant parents clone 395017.242 had the highest with 6.88), and across between Uganda 11 and 395017.242 gave a low yield (5.08) (appendix 4), indicating deviation in the performance predicted on the basis of GCA of the parents. This is Specific combining ability which refers to those cases in which certain combinations perform better or worse than expected compared to the parents (Sprague Tatum, 1942). Yield was least reduced from no stress to severe stress in across between Uganda 11 and 391533.1(18.1%), followed by Nakpot5 x391691.96(32.9%) and Nakpot5 x391533.1(48.7%).Generally crosses that involved parent 391533.1 had least yield reductions by stress, followed by those that involved 395017.242(appendix 5).

Parent 391533.1 had positive significant GCA effects for yield in tons per hactare and in the characterization experiment; its yield was the least reduced by stress and gave the second highest yield under stress. Also generally crosses that involved clone 391533.1 had lower percentage leaf area reductions; Uganda 11 and 391533.1(18.3%), Nakpot5 x 391533.1(34.2%), Victoria x 391533.1 (38.2%). Clone 391533.1 was among parents whose leaf area was least affected by drought and it also had positive GCA effects foe leaf area. This suggests that this clone is a good combiner for these traits and transferred them to its offsprings. Thus in order to get good cross combinations, GCA of the parents is very important (Hydar *et al.,* 2009). Leaf area was not affected by stress in the characterization experiment, across involving this cross gave the highest area under stress and a cross between Uganda 11 and 395017.242 had its area least affected by drought (Appendix 8). Clone 395017.242 had positive GCA effects for leaf area meaning it transferred this trait to its progenies.

Parents Nakpot5, 391692.96 and 395017.242 had negative GCA effects for plant height, thus contributed negatively towards the height of the progenies in which they are involved while 391533.1, 393077.159, Uganda 11 and Victoria contributed positively to plant height. Short statured plants are important in hybrid development as they utilize fertilizers better without lodging and minimize additional costs for staking (Namazzi, 2011). A cross between Nakpot5 and clone 393077.159 gave positive significant SCA effects for percent dry matter content, wilt positive but non-significant SCA effects for weight of tubers per plant. Selection can be done to get progenies with good traits involving these parents.

Relative importance of GCA to SCA was high based on baker's ratio for %dry matter content (0.8), leaf area (0.7), plant height (0.6), relative leaf water content (0.5), stem diameter (0.6), groundcover (0.5) and total number of tubers (0.6) implying that the relative contribution of additive gene action for these traits is high compared to the non additive gene action. This suggests that these traits are highly heritable and selection for these traits can be done in early generations to develop varieties with tolerance to drought stress. Also broad sense heritability was higher for most of the traits than the narrow sense heritability (Table 34), implying low environmental effects in the overall phenotypic expression of the observed traits.

Data on number of days to 50% flowering and number of stems per plant was not used to evaluate F1s because plants from the same family flowered at different intervals and others never flowered

at all, thus it was difficult to estimate 50% flowering. True potato seed develops into one stem, therefore all experimental plants had one stem.

Conclusion

Parents 395017.242 and 393315.1 were found to be good donors for genes responsible for less wilting of the vegetative parts, increased leaf area, and high yield under stress. Both additive and non-additive gene action were important; however additive gene action was more important for most traits basing on Baker's ratio, implying that the performance of the offsprings is expected to be reasonably predicted from the parents. Heritability in the broad sense was high for most traits suggesting low environmental effect in the overall phenotypic expression of the observed traits.

Recommendation

Parents 395017.242 and 393315.1 can be utilized to produce hybrids that yield well under stress.

CHAPTER FIVE

CONCLUSIONS AND RECOMMENDATIONS

5.1. Conclusions

The study characterized potato genotypes for tolerance to drought stress; determined the combining ability between the tolerant genotypes with the susceptible ones. The study also determined the effect of drought stress on potato tuber quality. Potato clones 391533.1,394034 .7, 393077.159 and 395017.242 were characterized as drought tolerant and 391692.96 as moderately tolerant basing on less drought effect on yield , physiological and growth parameters , while varieties; Victoria, Uganda 11 and Kachpot1 were susceptible.

Parent 391533.1 had positive significant GCA effects for yield in tons per hectare, and a cross between this parent and variety Victoria gave the highest yield in tons per hectare, followed by two that involved parent 395017.242 (appendix 2). Victoria was released by the potato program at KAZARDI as a high yielding variety in addition to other good traits but this study characterized it as the most susceptible parent and clone 391533.1 among those least affected by drought though low yielding, this suggests that clone 391533.1 transferred drought tolerance traits to Victoria. Generally crosses that involved parent 391533.1 gave high yields on average under severe stress with less percentage reductions compared to yield in non-stressed plots, also followed by those that involved parent 395017.242 (appendix 5). Again the progenies involving these parents had the highest and least area reduction under stress as well as groundcover and less stress scores. This suggests that these parents transferred the ability to produce these good attributes under stress to their progenies.

Results revealed that both additive and non-additive gene effects were involved in determining drought tolerance in potato. However, basing on Baker's ratio, additive gene effects were more important.

5.2. Recommendations.

From the above conclusion, it is possible that there are potato clones with drought tolerance traits and which can be transferred to susceptible genotypes. All the CIP clones used in hybridization gave promising results with at least each of them combining with one adopted variety to produce a reasonable high yield under severe stress (appendix 5). Therefore I recommend wide testing of these hybrids in order to release varieties that are tolerant to drought.

The study revealed that parents that performed well in the characterization experiment transferred the good traits to the progenies. Knowledge about performance of parents should always be obtained in order to use parents for inheritance studies.

Parent 391533.1and 395017.242 were found to be good combiners for increased leaf area, ground coverage, less stress effect on the vegetative parts and increased yield, thus can be utilized in breeding to develop genotypes with tolerance to drought.

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APPENDICES

Appendix 1 .Effect of moisture stress on potato tuber shape, skin colour and quality

		Skin colour	Skin quality	Tuber shape
Victoria	1	pink	normal	round
	2	pink	normal	round
	3	pink	normal	round
Uganda 11	1	pink with red eyes	normal	round
	2	red	normal	round with secondary growth
	3	pink with red eyes	normal	cucumber shaped with secondary growth
Kachpot1	1	red	normal	round
	2	red	normal	Cucumber-shaped. bottle –naked, knobby
	3	red	normal	Cucumber- shaped
391692.96	1	purple	normal	oval
	2	purple	with scabies	Cucumber-shaped and bottle naked
	3	purple	normal	Cucumber-shaped, bottle-naked
	1	white with red eyes	normal	round
393077.159	2	white with red eyes	normal	round
	3	white with red eyes	normal	round
395017.242	1	white	normal	round
	2	white	normal	round
	3	white	normal	round
391533.1	1	white	normal	oval
	2	white	normal	oval
	3	white	normal	oval
394034.7	1	red	normal	oval
	2	red	normal	oval
	3	red	normal	oval

1=Field capacity,2=50% field capacity and 3= 25%field capacity

Appendix 2.Yield performance of parents used in the crossing experiment

PARENT	yha[1]	TNT	TWT	AWT
Nakpot5	9.09	29	372	13.34
Uganda 11	7.56	26.5	312	13.65
Victoria	8.85	30.5	365	13.31
391533.1	8.56	24.6	349	16.43
391692.96	7.51	25.7	310	12.94
393077.159	8.54	28.2	352	12.43
395017.242	9.41	36.1	388	11.94
Mean	8.5	28.6	350	13.4

Appendix 3. Yield parameters of F1 crosses

CROSS	TNT	TWT(g)	AWT(g)	Yt/ha
Nakpot5*391533.1	23	347	15.75	8.68
Nakpot5*391692.96	29.7	374	12.42	9.06
Nakpot5*393077.159	27.5	359	12.22	8.7
Nakpot5*395017.242	35.8	410	12.97	9.94
Uganda 11*391533.1	23	288	17.08	6.97
Uganda 11*391692.96	20.8	262	12.04	6.36
Uganda 11*393077.159	21.8	340	15.05	8.24
Uganda 11*395017.242	40.2	358	10.42	8.67
Victoria*391533.1	27.7	413	16.47	10.01
Victoria*391692.96	26.7	293	14.36	7.1
Victoria*393077.159	35.3	358	10.02	8.68
Victoria*395017.242	32.2	396	12.42	9.61

Appendix 4. Tuber fresh yield of the F1 across the three watering regimes

Parent	watering regimes		
GP1	1	2	3
Nakpot5	13.16	7.51	6.62
Rutuku	9.76	5.73	7.2
Victoria	12.46	8.05	6.04
391533.1	10.78	8.27	6.62
391692.96	9.85	6.03	6.64
393077.159	13.74	5.54	6.33
395017.242	12.79	8.54	6.88

Appendix 5. Tuber fresh yield of the F1 across the three watering regimes

GP1	WR1	WR2	WR3	% REDUCTION
Rutuku*393077.159	11.5	9.4	3.8	66.9
Victoria*395017.242	13.3	9	6.3	51.1
Nakpot5*391692.96	11.3	8.6	7.3	32.7
Rutuku*391533.1	7.7	6.9	6.3	18.1
Rutuku*391692.96	8.4	6.6	4	52.3
Nakpot5*395017.242	13	10.3	6.5	50
Victoria*391533.1	13.8	10.1	6.2	55
Nakpot5*391533.1	11.7	8.4	6	48.7
Nakpot5*393077.159	16.7	5.4	4	76
Rutuku*395017.242	12.1	8.8	5.1	57.8
Victoria*391692.96	9.8	6.7	4.7	52
Victoria*393077.159	13	8.8	4.2	67.6

WR1=Field capacity, WR1=50% field capacity and WR3= 25%field capacity

Appendix 6.Effect of drought on F1hybrid Groundcover.

	WR	1	2	3	%Reduction
GP1	GP2				
Nakpot5	391533.1	45.0	40.0	40.0	11.1
	391692.96	45.0	40.0	37.5	16.7
	393077.159	45.0	40.0	25.0	44.4
	395017.242	45.0	40.0	27.5	38.9
Uganda 11	391533.1	45.0	42.5	37.5	16.7
	391692.96	40.0	25.0	12.5	68.8
	393077.159	39.0	20.0	37.5	3.8
	395017.242	45.0	42.5	40.0	11.1
Victoria	391533.1	48.0	42.5	40.0	16.7
	391692.96	45.0	40.0	22.5	50.0
	393077.159	45.0	53.0	34.0	24.4
	395017.242	50.0	39.0	38.0	24.0
	Mean	44.8	38.7	32.7	
	LSD	**4.1**			

Appendix 7.Stress score of the F1 hybrids under the three watering regimes

	WR	1	2	3
GP1	GP2			
Nakpot5	391533.1	1	5	6
	391692.96	1	3.5	6
	393077.159	1	2.5	6
	395017.242	1	5	3
Uganda 11	391533.1	1	5.5	5.5
	391692.96	1	5	9
	393077.159	1	2.5	5.5
	395017.242	1	4.5	7
Victoria	391533.1	1	2.5	6
	391692.96	1	2.5	6
	393077.159	1	3	4.5
	395017.242	1	2	7
	Mean	**1**	**3.5**	**5.7**
	LSD		**1.3**	

Appendix 8. Effect of drought on F1 hybrid leaf area

	WR	1	2	3	% Reduction
GP1	GP2				
Nakpot5	391533.1	468	345	308	34.2
	391692.96	424	402	221	47.9
	393077.159	379	227	132	65.2
	395017.242	697	428	382	45.2
Uganda 11	391533.1	257	242	210	18.3
	391692.96	202	176	84	58.4
	393077.159	465	352	139	70.1
	395017.242	499	457	413	17.2
Victoria	391533.1	621	532	384	38.2
	391692.96	430	415	129	70
	393077.159	522	451	162	69
	395017.242	678	442	362	46.6
	Mean	**470.2**	**372.4**	**243.8**	
	LSD	71.1			

Appendix 9.Effect of drought on F1 hybrid relative leaf water content.

CROSS	WR1	WR2	WR3	% REDUCTION
	1	2	3	
Rutuku*393077.159	87	80.2	71.2	18.2
Victoria*395017.242	92.7	82.1	76.9	17.0
Nakpot5*391692.96	80.1	79.5	79.5	0.7
Rutuku*391533.1	84.2	77.5	78.9	6.3
Rutuku*391692.96	80.4	73.6	76.4	5.0
Nakpot5*395017.242	89.9	89.1	85.8	4.6
Victoria*391533.1	86.3	87.1	74.4	13.8
Nakpot5*391533.1	87.3	77.3	72.3	17.2
Nakpot5*393077.159	88.7	79.8	75	15.4
Rutuku*395017.242	86	80	75.8	11.9
Victoria*391692.96	83.2	83.3	82.7	0.6
Victoria*393077.159	82.7	78.4	64.9	21.5
Mean	**85.71**	**80.66**	**76.15**	