MAKERERE UNIVERSITY

INHERITANCE AND STABILITY OF EARLINESS IN POTATO

(*Solanum tuberosum* L.)

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BSc. Agric. (Hon.) MUK

REG No: 2010/HD02/3427U

A THESIS SUBMITTED TO THE DIRECTORATE OF RESEARCH AND GRADUATE TRAINING IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE AWARD OF THE DEGREE OF MASTER OF SCIENCE IN PLANT BREEDING AND SEED SYSTEMS OF MAKERERE UNIVERSITY

APRIL, 2014

DECLARATION

I PAULA IRAGABA, declare that the work presented in this thesis is my own research and has not been submitted for the award of the degree in any other University.

Signed……. Date…….

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This thesis has been submitted with our approval as the university supervisors.

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DEDICATION

This work is dedicated to my parents Mr. and Mrs. Manirakiza, who have foregone some pleasures of this world to see me through education and to my nephews and nieces so that they may find inspiration to excel in academia.

ACKNOWLEDGEMENT

I am particularly grateful to the Alliance for a Green Revolution in Africa (AGRA) for funding my post graduate education. I am also greatly indebted to my supervisors Dr. Geoffrey Tusiime and Dr. Rogers Kakuhenzire for their devotion and guidance throughout my research project. In the same spirit, I specially thank Prof. Paul Gibson who has always been there in times of need and for mentoring me, Madam Pauline Gibson, thank you for the moral support. I extend my gratitude to Dr. Richard Edema, the coordinator of the AGRA/PASS plant breeding program, Makerere University for the smooth running of the project and his commitment to student welfare. My fellow graduate students thank you for sharing and the encouragement. My thanks also go to the academic staff of the School of Agricultural Sciences of Makerere University for equipping me with the basic scientific knowledge and skills.

I thank the Directors of Research of Kachwekano Zonal Agricultural Research and Development Institute (ZARDI) and Mbarara ZARDI for allowing me to use both field and laboratory facilities for my work at no extra cost. Kachwekano ZARDI is further acknowledged for providing the potato germplasm for my research work. I wish to recognize the support from Namugga Prossy; Ag. head of Potato section at Kachwekano ZARDI, staff at this research institute, staff of Kalengyere field station and Madam Peace Kankwasta; head of crop production section at Mbarara ZARDI for their invaluable support. My field assistants in all the three sites, you did a recommendable job and may God bless you.

I specially thank my parents Mr. and Mrs. Manirakiza, sisters, brothers and friends for the prayers, guidance and encouragement rendered to me at a time when I needed your support most. Last but not the least; I thank the Almighty God for bringing me this far. Glory and honor to his name now and forever.

Amen.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF APPENDICES

ABSTRACT

Potato is an important food and cash crop in Uganda. Recent climate change characterized by erratic rainfall and elevated temperature have been recognized as major threat to potato production and productivity. Thus, breeding for adaptation to these conditions will be imperative to sustain potato production. This will require developing high yielding, short growth-cycle genotypes for both high and low elevations. Breeding strategies to guide development of such genotypes require understanding the mode of inheritance of earliness and its impact on potato tuber yield and quality. In order to address this, a study was designed with the aim of developing early maturing and high yielding potato cultivars adaptable to agro-ecologically diverse farming systems. Specifically, the objectives were to determine the mode of inheritance of earliness in potato and to determine the magnitude of genotype (G) by environment (E) interactions for earliness and fresh tuber yield in selected potato clones with horizontal resistance to late blight.

To address the first objective, five late maturing potato clones with partial resistance to late blight were crossed with five early maturing but low yielding lines using a North Carolina 2 (NC2) design. The F_1 progeny were evaluated and the combining abilities of parents showed that both additive and non additive gene effects controlled earliness though additive gene effects were more dominant. Parent 396038.107 portrayed good general combining ability for both earliness and high yield thus it can be used to improve potato genotypes for earliness and fresh tuber yield.

To determine the magnitude of G x E interaction, nine advanced potato clones were evaluated across three sites located at different altitudes ranging from 1400 m to 2450 m above sea level for two seasons to estimate the magnitude of genotype by environment interaction and stability for earliness and fresh tuber yield. Genotype 396026.103 and 391046.14 were found to be the most stable for earliness and high fresh tuber yield across all the environments.

CHAPTER ONE
GENERAL INTRODUCTION

1.0 Back ground

1.1 Origin and distribution of potato

The potato (*Solanum tuberosum* Lin.) is a starchy, tuberous crop from the Solanaceae family. Its centre of origin and diversity is the Andean highlands of South America particularly southern Peru and northern Bolivia (Woolfe, 1987; Hawkes, 1994). Following the Spanish conquest of the Inca empire, the conquerors introduced the crop in Europe about the second half of the 16th century (Schafleitner, 2008). The crop was subsequently disseminated to territories beyond Europe by European sailors, explorers and Christian missionaries between the 17th and 19th century (Hawkes, 1994).

Potato was introduced in Uganda around 1900 by European Christian missionaries as a backyard crop primarily consisting of European varieties (Hakiza *et al.*, 2001). Since then, the crop has gradually gained importance as a food and cash income crop especially in highlands. Previously, best adapted to altitudes higher than 1700 m above sea level, few varieties adapted to low altitude zones, below 1600 m above sea level, have been developed resulting in growth in importance of the crop in warmer lowlands in Uganda (Nakitandwe, 2003). Lowland potato production is very crucial as the demand of potato increases and also due to the need for food crop diversification in lowland farming systems after the outbreak of banana and cassava diseases that affected production of these basic staples in these agro-eco-systems in Uganda (Nakitandwe, 2003). However, there are currently few potato cultivars that are well adapted to low and mid-altitudes with good culinary characteristics that can offer fair fresh tuber yields (Nakitandwe, 2003). Thus potato variety diversity in mid-altitudes and lowlands is imperative to improve yield quantity and quality of ware potato produced in these areas where potato is not traditionally and commonly grown.

1.1.1 Importance of potato

Potato is the world's fourth-widely grown food crop, after rice, wheat and maize (Muthoni & Nyamongo, 2009; CIP, 2011). The global land area used for potato production is steadily

growing due to the rising demand for fresh potato and its processed products (Griffin & Leslie, 2007). The crop is an important food resource and it contributes significantly to the quality of peoples' diets because of its high energy, vitamin C and protein content (Kooman & Rabbinge, 1996; Griffin & Leslie, 2007). It is also a source of income and employment in developing countries particularly in densely populated tropical highlands (FAO, 2008; CIP, 2011). The high energy content of potato and its ease of production have made it an appropriate component of urban agriculture providing food security to at least 800 million people globally (Hoffler & Ochieng, 2008. This is due to its fast growth, adaptability to different agro-ecologies, high yields and responsiveness to agro- input use (Ferris *et al.*, 2001). Thus, potato is a high potential crop for solving the food needs of low-income earners in both urban and rural areas.

Potato is ideal for places where land is limited and labour is abundant, conditions that characterize much of the tropical highlands (FAO, 2008). It also has considerable, untapped potential for further increases in yield and productivity, especially in some marginal farming areas where other crops have extremely low yield potential (FAO, 2008). In light of global climate change and reduced rainfall reliability, potato offers great opportunities to farmers than most other root and tuber crops as it can easily fit in the prevailing short rainfall, high temperature regimes (Majaliwa *et al*., 2010).

1.1.3 Major potato production constraints

Potato production like other crops is affected by both biotic and abiotic stresses. Biotic factors affecting potato production and productivity include; insect pests, bacteria, fungi and viruses. The main disease affecting potato production in Uganda especially in highlands is late blight. It accounts for up to 70% in yield loss on some occasions (Ojiambo *et al*., 2001; Kakuhenzire, 2009). The abiotic agents limiting potato production include low soil fertility, inadequate moisture supply, stress due high temperatures and drought, erratic and sometimes violent rainfall (Ferris *et al.*, 2001). Some of these factors are aggravated by the low income of potato farmers in most developing countries limiting use of productivity enhancement inputs (FAO, 2008). Potato produced in highlands in most developing countries, Uganda inclusive, is not sufficient to satisfy increasing demand of ware and processing potato because of shortage of land in the primary agro-ecology where the crop is mainly produced. Spreading potato production to mid-altitude

and low-land areas that possess ample land would partly alleviate this problem. However, mid and low altitude agro-ecologies are characterized by short rainfall patterns, high temperature regimes with heat levels above the optimum for ideal potato growth, tuber formation and bulking with the current varieties in Uganda. It is therefore, imperative that short growth cycle potato varieties that are tolerant to high temperature and with low water requirement but would offer optimal yields are developed and promoted. Such cultivars would need to be early maturing considering a short rainfall regime in mid-altitude and lowland agro-ecologies, candidate potato production areas for the future if local supply of fresh ware potato is to be sustained with growing demand.

1.2 Statement of the problem

Most available potato varieties in Uganda attain their physiological maturity late, exceeding 100 days from planting to obtain their full yield potential (>15t ha^{-1}). Additionally, most of the potato varieties are better adapted and yield best in highlands (> 2000 m above sea level). It is in highlands too where potato with good culinary characteristics are obtained. This is because of cooler environment and higher total annual rainfall than in mid-elevations and lowlands. However, because of recent climatic changes characterized by erratic rainfall pattern and elevated environmental temperature (Miyashita *et al.,* 2005, Majaliwa *et al*., 2010) performance of these varieties in the traditional highland areas is likely to deteriorate. In the mid-altitudes and lowlands (<1700 m above sea level) potato yield may completely fail unless varieties resilient to climate change are developed. These scenarios call for developing varieties that mature early, are able to maximize growth in short rainfall regimes in elevated temperatures and obtain high yields at the same time. More so, there are potato clones with good agronomic traits and multiple disease resistance that have been developed by the potato research system in Uganda in collaboration with the International Potato Centre (CIP) but whose yield and maturity period stability across diverse environments has not been determined and documented. This has delayed their release and deployment as future varieties in Uganda. This study is an attempt to determine adaptation and stability of the selected advanced potato clones in diverse environments from 2500 to 1400 m above sea level and use the selected genotypes with earliness and/or late blight resistance to develop a new segregating population for screening and selection for earliness and high yields for locally developed progenies in Uganda.

1.3 Justification of the study

Most commercially grown potato varieties in Uganda are best adapted to highlands. Attempts to grow them in mid-altitudes and low lands result in sub-optimal yield to attract any farmer's interest for commercial production besides loss in tuber cooking qualities. Mid-altitudes and lowlands hold the future for increasing potato production to satisfy the growing demand because of low population pressure and availability of arable land. Potato productivity in highlands in Uganda is also declining due changes in climate with reduced rainfall accompanied with temperature elevation. Sustained supply of fresh potato will therefore not be realized unless early maturing cultivars with high temperature tolerance and low moisture requirement that are likely to characterize the highlands in future are developed and promoted. This will additionally improve potato production in lower altitude by developing varieties that are more resilient to harsh conditions in non-traditional potato growing areas where potato cultivation is expanding. Early maturing cultivars would also free land quickly in highlands making it readily available for other crops thus enhancing general agricultural productivity. In lowlands, early maturing varieties will make the crop more attractive to farmers as it generates high yield quickly in an economical sense. With recent climatic changes, breeding for cultivars that mature early in a shorter cropping season can facilitate drought escape (Banziger *et al.,* 2000) or water use efficiency where irrigation is done. However, the genetic control of earliness in potato for tropical highlands needs to be understood and determined qualitatively or quantitatively. Additionally, stability of earliness in potato needs to be determined. This knowledge would enable development of a breeding strategy for earliness in potato for the future in Uganda and elsewhere.

1.4 Objectives of the study

1.4.1 Overall objective

The overall objective of this study is to contribute to improvement of potato production through developing early maturing and high yielding cultivars adaptable to agro-ecologically diverse farming systems in Uganda.

1.4.2 Specific objectives

The specific objectives of the study are;

1. To determine the mode of inheritance of earliness in potato as a guide in developing future varieties for wide adaptation.
2. To determine the magnitude of genotype by environment (G x E) interactions for earliness and tuber yield in selected potato clones with horizontal resistance to late blight.

1.5 Research Questions

1. Is the mode of inheritance of earliness in potato qualitative or quantitative?
2. Is there significant genotype by environment interactions for earliness and tuber yield in selected potato clones with horizontal resistance to late blight?

1.6 Scope of the Research

The research work reported herein involved studying inheritance and stability of earliness in *Solanum* potato in the tropics. This was achieved through two experiments conducted in south western Uganda at different altitudes. The first experiment focused on inheritance of earliness and generation of new segregating population combining three traits; earliness, late blight resistance and high fresh tuber yield. In this experiment, five varieties with good agronomic traits but with long maturation period were crossed with five early maturing varieties using the North Carolina 2 design. The second experiment involved determining the magnitude of genotype by environment interaction for earliness and total fresh tuber yield. In this experiment, nine potato genotypes with multiple disease resistance were studied over two seasons in three diverse locations due to their differences in altitudes, rainfall patterns and temperature regimes.

1.7 Expected outputs

- The gene action and inheritance based on combining abilities to breeding for earliness in potato is understood.
- Breeding populations of families combining earliness and high yields in potato for future screening and evaluation for new variety developed.
- Potato clones with wide adaption and able to grow in diverse environments identified and recommended.

CHAPTER TWO
LITERATURE REVIEW

2.1 Potato Botany

Potato is an annual plant belonging to a genus *Solanum* in the family Solanaceae (Acquaah, 2007). The family also contains other important crops such as tomato, eggplant, tobacco, pepper and tree tomato among commonly grown foods. The cultivated potato, *Solanum tuberosum,* an autotetraploid with 48 chromosomes, is a herbaceous, freely branching dicotyledonous perennial, usually 30 to 100 cm tall in normal growing conditions (Acquaah, 2007). It has alternate compound pinnate leaves, made up of three or four pairs of oval leaflets and a terminal leaflet. Potato can flower with cymose inflorescences which arise opposite the leaves (not axillary) near the ends of branches. The floral petals are gamopetalous with 5-lobed corollas, which maybe white, yellow, purple, blue or striped or multi-coloured, and about 3 cm in diameter (Sleper & Poehlman, 2006; Acquaah, 2007). The stamens are attached to the corolla tube and bear erect anthers which form a closed column or cone around the style. The anthers are bright yellow except those produced in male sterile plants which have light yellow or light green anthers. Flowers in cultivated potato mostly open early in the morning although a few may continue to develop throughout the day (Sleper & Poehlman, 2006). The fruit formed on potato is a spherical berry about 1.5-2 cm in diameter, green or purplish, containing 100 small seeds on average. The roots are numerous, fine, fibrous and adventitious. Potato requires long day lengths (12-16 hours), abundant rainfall, and cool temperatures to flower (Sleper & Poehlman, 2006). Largely, potatoes are cross-pollinated by insects although self-fertilization may occur (Virginia *et al.*, 2001). When the aerial part of the plant dies back following the normal growth cycle or adverse weather conditions the tubers remain in the ground and sprout to form new plants when the dormancy of the tuber breaks and conditions favor growth.

2.1.1 Growth stages of potato

The development of a potato plant is normally divided into five distinct growth stages (Randall, 1993). The first stage is sprout development; this starts as sprout initiation at the eyes of potatoes and ends when the sprouts emerge from the soil. Meanwhile, the roots begin to develop at the base of the emerging sprout. During this stage, the seed piece is the sole source of energy for the

developing plant. The second stage is vegetative phase whereby as leaves, branches, roots and stolons form and elongate. This starts at emergence and stops at tuber initiation. Photosynthesis begins during this stage. Stage one and two lasts 30-70 days and this period depends on the environmental factors, physiological age of tubers and the kind of cultivar. The next stage is tuber initiation/ tuber set characterized by change of the stolons tips but not yet enlarging. The plant may initially produce 20 to 30 small tubers but only 5 to 15 tubers typically reach maturity. Tuber initiation stage takes about two weeks. The fourth stage is tuber bulking. Tuber cells expand with the accumulation of water, nutrients and starch. Tubers become the dominant site for deposition of carbohydrates and mobile inorganic substrates. The duration of this stage is affected by cultivar and environmental factors. The last stage of potato development is maturation. Vines turn yellow and lose leaves, photosynthesis gradually decreases, tuber growth rate slows down, and tuber skin becomes firm and eventually the vines die. It is in this stage that maximum tuber dry matter is attained (Randall, 1993).

2.2 Potato production in Uganda

Potato in Uganda is mainly grown as a food security crop with the bulk of the crop being grown in the highlands of South Western Uganda with Kabale and Kisoro accounting for more than 60% of the total potato that is produced in the country (Ferris *et al.,* 2001). Other potato producing areas include; Mbarara (6.2%), Mubende (2.3%), Kapchorwa (2.2%), Mbale (1.0%), Nebbi (0.6%), Bushenyi (0.5%), Sironko (0.4%) and Masaka (0.1%) (Ferris *et al.,* 2001). Between, 200,000 to 300,000 households in Uganda are involved in potato production either as a food or cash crop or both (Ferris *et al.,* 2001). Uganda ranks the ninth in potato production in Africa. However, Uganda's mean yield estimated at 7.0 t ha^{-1} (Aliguma *et al.,* 2007) is one of the lowest in the Africa and by world standards. Recently, due to the increased demand of fresh potato particularly in the urban areas, potato cultivation is steadily spreading to non-traditional production zones particularly low altitudes in order to meet increasing demands.

2.3 Potato crop maturity period

Plant maturity period is a complex physiological trait usually evaluated by plant breeders because of its agronomic, economic and breeding implications (Haga *et al.,* 2012). The maturity period of any crop is considered an agronomic trait. Therefore, manipulating cultural practices such as use of clean seed, physiological seed maturity, early planting, fertilizers, management of pest and disease would contribute to the crop realizing its maximum genetic potential (Stoller, 2004; Cook, 2008). Potato maturity is typically estimated by monitoring the vine characteristics (Haga *et al.,* 2012). The change of potato plant's leaves is an indicator that the crop has reached maturity (FAO, 2008). Potato cultivars are classified into maturity types based on the lengths of the season required to produce a harvestable product (Ruzukas *et al.,* 2009; Haga *et al.,* 2012). Variability among cultivars for number of days from planting to crop physiological maturity has led to designating of the potato cultivars into very early, early, medium, late and very late maturity classes (CIP, 2007; Ruzukas *et al.,* 2009). Breeders normally evaluate maturity period while developing new cultivars because it's a critical aspect in commercial potato production. Standard maturity measure in potato is lacking because tubers are produced under ground and monitoring their development presents many challenges. Potato breeders commonly assess potato maturity class based on physiological changes in the potato vine. Tuber production is associated with changes in the whole plant such as reduction in leaf development, flowering and fruit set (Haga *et al.,* 2012).

2.4 Breeding for earliness in potato

Conventional potato breeding involves initial crossing of parents possessing complementary traits based on the phenotype followed by selection in subsequent clonal generations (Sleper & Poehlman, 2006). The selection is based on phenotypes over with the aim of identifying clones with as many desirable traits as possible for release as new varieties (Lynch & Walsh, 1998; Bradshaw & Bonierbale, 2010). Since the choice of parents is largely dependent on their performance, it is hard to predict the segregation pattern of the F_1 progeny because potato is a highly heterozygous crop (Wolfgang *et al*., 2009). Successful breeding is achieved through combining the desired alleles into a single genotype and testing their stability and adaptation (Acquuah, 2007). Potatoes are highly heterozygous hence dominance and epistatic effects contribute to clone performance. However, the value of the cross should not be assumed unless

the progeny has been tested (Muthoni *et al.,* 2012). Potato breeding has been used to improve cultivars for resistance to biotic and abiotic factors, earliness and high yield (Razukas & Jundalas, 2006; Azhar *et al.,* 2007). Among these traits, earliness in potato is important especially in areas with land scarcity, multiple cropping systems or short rainy seasons. Such cultivars would be good for highlands in Uganda and elsewhere where cultivars would need to mature quickly making land readily available for other crops for the subsequent cropping season thus enhancing general agricultural productivity. Earliness in shorter rainy seasons facilitates drought escape, an attribute that is crucial in climate change situations of reduced or erratic rainfall patterns (Banziger *et al*., 2000). Breeding for earliness in potato has also been considered beneficial since it leads to escape from some diseases that appear late in the season such as late blight (Razukas & Jundalas, 2006). However, breeding for earliness in potato has not been purposely pursued in Uganda for reasons of generating versatile varieties capable of adaptation to diverse environments. Achieving this requires understanding the mode of inheritance conditioning this trait (El-Bramawy & Shaban, 2007). It will be important to determine if the gene action for earliness is due to additive, non-additive, dominant or epistatic effects and their interaction with the environment.

2.5 Combining ability in potato breeding

Combining ability estimates the combination and expression of the parental traits amongst each other during the processes of hybridization so that favourable genes or characters are transmitted to their progenies (Fehr, 1987). It is the magnitude of additive and non-additive gene action as defined by Shattuck *et al.,* (1993). Combining ability is used in plant breeding to compare the performance of a given parent in hybrid combinations (Griffing, 1956; Hayder *et al*., 2009). It comprises general combining ability (GCA) and specific combining ability (SCA). GCA designates the average performance of a parental line in a hybrid combination. SCA is the contribution of an inbred line to hybrid performance in a cross with a specified in bred line in relation to its contributions in crosses with a range of specified inbred lines (Sleper & Poehlman, 2006; Panhwar *et al.,* 2008). SCA allocates situations where certain crosses do better or worse than expected based on the performance of the parents involved (Panhwar *et al.,* 2008). GCA is mainly attributed to additive gene action while SCA is due to non-additive gene effects (Shattuck *et al.,* 1993). In potato breeding, both GCA and SCA are vital in conditioning traits and they are

both fixed in the F_1 generation because there is no further segregation with clonal breeding stock. GCA seems to be significantly larger than SCA for tuber yield and quality traits in crosses between non- related parents whereas SCA appears to be more important among related parents (Ortiz & Golmizaie, 2004). In regard to crop maturity, GCA effects tend to be more important than SCA effects (Johansen *et al.*, 1967). Additionally, additive and non additive effects operate to influence maturity and total tuber yields (Buso *et al.*, 2008).

2.6 Genotype by environment interaction

Cultivars of a crop are often grown in a wide range of conditions which are influenced by differences in soil types, soil fertility levels, temperatures, rainfall, heat and cultural practices (Fehr, 1987). The knowledge of the association between crop performance and environment is vital in plant breeding, genetic studies and determines cultivar stability. Crop performance is a function of the genotype (G), the environment (E) and the interaction between the genotype and environment (G x E). This becomes important when certain genotypes significantly change ranks in different environments (Weikai & Manjit, 2002; Bernardo, 2010). The genotype main effects which constitute differences in mean yield between genotypes provide the only relevant information when genotype (G) by environment (E) interaction (G x E) effects are absent or ignored. However, differences between genotypes may vary widely among environments in the presence of high G x E interaction (Rodriguez *et al.*, 2007). The magnitude and potential of G x E interaction is important in crop improvement because its effects can be used in raising yields for target regions by identifying the most adapted cultivars. It also helps to identify genotypes that exhibit stable performance across diverse environments (Bernardo, 2010). This consequently helps to deploy limited resources to targets in breeding with knowledge of G x E interactions and maintaining different genotypes for diverse target regions (Weikai & Manjit, 2002).

Different approaches have been adapted to cope with G x E interactions. One of the approaches used is to ignore the interaction especially where differences between genotypes remains constant or does not cause change of ranks across different environments. In this case, breeders are encouraged to expand the testing environments and recommend cultivars to be grown based on the overall mean performance. The second approach used is reducing the magnitude of G x E interaction by separating the test environments into homogeneous sub-groups. Cultivars can thus

be recommended to be grown in a given sub-group of environment. The third approach is exploiting the presence of G x E interactions in cases where the effects are positive.

Stability analysis of cultivars using multiplicative models is done to identify cultivars best suited to specific environments (Fehr, 1987; Bernardo, 2010). Additive main effects and multiplicative interaction (AMMI) is a commonly used method to identify whether genotypes are stable or un-stable (Bernardo, 2010). The AMMI bi-plots are very helpful in visualizing and interpreting the performance of different genotypes across diverse environments based on the interactive principal component scores and the means of genotype (Gauch, 2006; Bernardo, 2010). The genotypes and environments with high means are plotted to the right hand side of the bi-plot.

Genotype by environment interaction study done in Uganda by Abalo *et al.,* (2001) indicated significant differences in the performance of twelve elite potato genotypes across cropping seasons and locations. Similar findings were reported by Ntawurunga *et al.,* (2001) on adaptation of cassava cultivars in Uganda. These results reveal that Uganda is agro ecologically diverse thus selecting for broad adaptability may be limited by presence of highly significant G x E interactions.

2.7 Effect of different environmental components on potato maturity and fresh tuber yield

The yield of a crop in any environment can be explained by available resources to support optimal plant growth and yield (Bidinger *et al.,* 1996). Crops respond differently to a host of environmental factors that is all variables encountered in producing a crop (Fehr, 1987; Weikai & Manjit, 2002). Genetic and environmental factors and their interactions affect the number of seeds produced by each genotype and the proportion of the seed that reaches maturity. To survive a certain stress, the plant may produce reduced number of viable seed (Weikai & Manjit, 2002). Environmental stresses experienced during a growing season may affect potato production by reducing photosynthetic efficiency, inhibition of stolon and tuber initiation and altered partioning of the limited photosynthate (Bradshaw & Mackay, 1994; Bishop & Long, 2012).

The potato crop realizes greatest yield under optimal growing conditions with adequate light, water and cool temperatures. The potato is very sensitive to moisture stress where early and mid

season moisture stress significantly reduce tuber yield (Bradshaw & Mackay, 1994; Lynch *et al.*, 1995). Potato requires adequate soil moisture at all stages of its development in order to realize its full yield potential.

Temperatures significantly affect the duration of vegetative period in potato and consequently the fresh tuber yield (Muzurczyk *et al.,* 2003). Photosynthesis, respiration, organ initiation and relative growth, dry matter production and distribution is all dependant on temperature (Muzurczyk *et al.,* 2003). Potatoes are normally classified into different maturity classes basing on the days from planting to onset of senescence or leaf ripening. This is directly related to bulking rate (Muzurczyk *et al.,* 2003). Additionally, long drought and high temperatures limit potato bulking (Abalo *et al.,* 2003). Tuber development declines as soil temperature rises and the process completely stops above 30 ^{0}C. Considering the recent variability in climate and environment, there is need to develop cultivars that are resilient to low water requirement in a short growth cycle. These will be able to withstand the changes in weather and therefore ensure sustainability of potato production.

CHAPTER THREE

MODE OF INHERITANCE OF EARLINESS IN POTATO, *Solanum tuberosum* (Lin.)

3.1 Introduction

Potato is an important cash and food security crop in the highlands of East and Central Africa in agro-ecological altitudes exceeding 1800 metres above sea level (asl). In Uganda, the crop is a major source of food and cash income mainly in Kabale and Kisoro districts (Ferris *et al.*, 2001). However, recent climate variability threatens its production due to reduced rainfall reliability and elevated environmental temperature (Majaliwa *et al*., 2010). This will particularly result into food and income insecurity of many resource-poor farmers in highlands. This can be partly solved by developing and promoting early maturing potato genotypes that maximize the shorter growing period in order to realize high yields. One of the methods of developing new genotypes involves combining the desired traits from the local germplasm into the target parents to generate new hybrid progenies (Bernardo, 2010). Selection and improvement of these traits would require the knowledge of genetic variance present in these cultivars thus the need to determine their combining abilities (Falconer & Mackay, 2009; Bernardo, 2010). Partitioning the variances into genetic components will facilitate plant breeding procedures to elucidate the nature of gene action controlling inheritance of such traits (Nadarajan & Gunasekaran, 2005; Falconer & Mackay, 2009). Consequently, a study comprising ten parents with contrasting maturity period, yield and with other farmer preferred traits were selected and tested to determine the mode of genetic inheritance governing earliness in potato.

3.2 Materials and methods

3.2.1 Experimental site

A field experiment was conducted at Kalengyere Research Station, 1^0 13’14.92’’S, 29^0 47’46.49E in South Western Uganda at an altitude of 2,450 m above sea level (a.s.l.) (Kakuhenzire, *et al*, 2009) during the second rainy (September - December) season of 2011. This area has a bi-modal rainfall separated by a dry spell ranging from 30-60 days. The site has volcanic (Andosols) soils with a p^H ranging between 4.75 and 6.5 (Kanzikwera *et al*., 2001).

3.2.2 Selection and establishment of parental lines

The parental lines were selected from germplasm maintained at Kachwekano ZARDI. Five farmer preferred, high yielding, late blight resistant but late maturing potato clones were used as females while five early maturing lines but less preferred by farmers due to low yields were used as males. The parents were selected based on the literature regarding their performance (Table 1). Fifteen tubers of each parental genotype were planted in single rows. In each row, seed tubers were planted at 50 cm from each other and the rows were 100 cm apart. Compound N.P.K. (17:17:17) fertilizer was applied at a rate of 100 kg ha^{-1} of each of its elemental constituents in two splits to enhance flowering, berry set and true seed production. Half the required quantity of fertilizer per plot (190 g) was added at the time of planting in furrows as a side dressing and thoroughly mixed with the soil in the rows before planting the seed tubers. The second half was added at the time of first weeding (approximately 40 days after planting) as a top-dressing to enhance vegetative growth and flowering. Insect pests, particularly aphids and leaf miners were controlled with Agrothoate 40 EC (Dimethoate 400g l^{-1}) applied at a rate of 3 ml $litre^{-1}$ of water with a hand operated knap sac sprayer. Late blight was controlled using Agro-zeb 80 WP (a combination product of zinc ion and manganese ethylene bisdithiocarbamate) and Ridomil 68 WG Gold (Metalaxyl-M; 40g kg^{-1} + mancozeb 640g kg^{-1}) fungicides. Weeding and earthing up was done two times; at 40 and 55 days after planting respectively. The crop was dehaulmed at 110 days after planting and was harvested 10 days later.

Table 1: Characteristics of the parents used in the inheritance study for earliness

Clone /variety	Parent	Maturity period (days)	Reaction to late blight
Uganda 11 (720097)	Female	120-130	Resistant
Nakpot 5 (381471.18)	Female	120-130	Resistant
Cruza (720108)	Female	120-130	Resistant
393280.82	Female	110-120	Resistant
396038.107	Female	110-120	Resistant
Mbumbamagara	Male	70-80	Not known
Kimuri	Male	70-80	Not known
Victoria (381381.20)	Male	80-90	Moderately resistant
Nakpot 1 (382171.4)	Male	75-85	Resistant
391046.14	Male	75-85	Moderately resistant

Source: Kachwekano ZARDI, 2011.

3.2.3 Crossing of parents

The female and male parents were crossed using North Carolina 2 (NC2) design that is one group of parents (males) was crossed with another group of parents (females) with contrasting traits. This is done in order to determine the relative magnitude of general and specific combining ability variance to be able to estimate Baker's ratio and heritability (Singh & Chaudhary, 2007). Baker's ratio indicates the relative importance of additive and non-additive effects (Ahangar *et al.,* 2008; Hasanuzzaman *et al.,* 2012). Female parent flowers about to open were monitored to ensure timely crossing. One day before flower opening, receptive female flowers were emasculated using a pair of forceps to avoid selfing (Plate 1). Pollen was collected from mature flowers of the selected male parents by shaking the anthers in an Eppendorf tube to release the pollen. The pollen would be used on the very day it was collected. The stigma of the emasculated female flowers was rubbed on the pollen powder in the open lid of the Eppendorf tube (Plate 1).

Plate 1: Emasculated flowers (a) before being pollinated and being pollinated (b)

Plate 2: Three of the successful crosses with berries about to reach maturity

Each cross was tagged with a label indicating the parents and the date when that cross was done (Plate 2). The success of the cross was identified by formation of a berry about 7 days later. Mature berries were harvested at full maturity after colour change from deep green to pale yellow. Berries of the same cross were harvested and bulked together in labeled plastic envelopes and kept at room temperature for two weeks to ripen. True seeds were hand extracted by crushing the ripe berries in a clean piece of cloth with little household detergent solution. Extracted seeds were then washed thoroughly in a soapy solution of the detergent. The cleaned seeds were sun-dried on filter papers and packed in paper envelopes, labeled and later stored at room temperature until they were sown to produce F_1 progenies.

3.2.4 Establishing of F_1 generation and clone numbering

The true potato seed obtained from successful crosses was sown in nursery beds on 20th March 2012 for germination to obtain F_1 progeny seedlings for evaluation during the first rains of 2012. After germination, the seedlings were sprayed with Agro-zeb 80 WP fungicide to protect them from early attack by *Phytophthora infestans*. When the seedlings attained 3-5 leaves stage, they were transplanted in an open field in an alpha lattice experimental design. In this design, each block is not planted with all treatments so that reasonably small-sized blocks can be maintained with large numbers of treatments. Small blocks enhance homogeneity of experimental units and

increase the precision of the experiment. In this study, a partially balanced alpha lattice design was used with six blocks each containing six progeny crosses or tuber families in three replications. Clone numbering was done at the time of transplanting. The clone name would start with a letter P followed by a four digit number representing the year in which the cross was done, then 2 digits representing tuber family, followed by a dot and then one or two digits representing the clone number. Each plot consisted of two rows with five plants each. The seedlings in each plot were transplanted at 80 cm between rows and 40 cm between seedlings. A wider spacing than the recommended was used to prevent tuber mixing from different clones. Insect pests, particularly aphids and leaf miners were controlled with Agrothoate 40 EC applied at 3 ml $litre^{-1}$ of water using a hand operated knap sac sprayer. Late blight was controlled using Agro-zeb 80 WP and Ridomil 68 WG Gold fungicides. Weeding and earthing up was done twice; at 40 and 55 days after planting, respectively. The crop was dehaulmed at 110 days after planting and harvested 10 days later.

3.2.5 Variables measured to determinate the mode of inheritance of earliness

Data were collected for days from seedling transplanting to flower bud initiation, tuber initiation, duration of anthesis and onset of leaf ripening or senescence from both parents and F_1 progenies. Yield parameters collected included number of tubers per plant, average tuber weight for each plant since they were independent genotype and consequently fresh tuber yield (tha^{-1}) per genotype (plant).

3.2.6 Data analysis

Data were analyzed using ANOVA in GenStat statistical software (14^{th} Edition). Where genotype means were significant, means were compared using Fisher's protected least significant difference (LSD) test at 5 % probability level. GCA and SCA values and the respective variance components were obtained from the ANOVA. The variance components were calculated using expected mean squares using formulae indicated in the skeleton ANOVA (Appendix 1). The variance components were used to determine Baker's ratio in order to estimate the relative importance of additive and non-additive gene effects. The variance components were also used to estimate narrow and broad sense coefficient of genetic determination which are analogous to

narrow and broad sense heritability respectively. Summary statistics was used to generate frequency distribution histograms to show the pattern of segregation.

3.3 Results

3.3.1 Analysis of variance for tuber initiation, senescence, number of tubers per plant and fresh tuber yield

The analysis of variance revealed highly significant (P<0.001) effects of the genotype for days from transplanting to tuber initiation and onset of leaf ripening or senescence of the F_1 progeny (Table 2). Similar genotype effects were also found for the number of tubers per plant and fresh tuber yield among the F_1 progeny (Table 2).

Table 2: Mean squares for different vegetative growth and fresh tuber yield parameters of the F_1 progenies evaluated at Kalengyere Research Station from May to September, 2012

Source of variation	Df	Tuber initiation (Days)	Senescence (Days)	Number of tubers plant^{-1}	Yield (t ha^{-1})
Total df		1034.0	980.0	901.0	582.0
Rep	2	928.7	95.2	878.5	434.4
Blocks/Rep	15	126.7		81.4	74.1
Genotype	35	364.4***	1902.3***	213.7***	13.1*
Genotype*Rep (plot error)	55	112.6		84.9	43.4
RCB error	70		139.5		
LEE		115.3		85.8	6.5
LEE ddf		57.5		51.8	37.6
Plants within plots (Residual)		18.6	26.7	50.1	26.6
Residual df		927.0	873.0	795.3	509.0
CV% (per plot basis)		9.4	4.4	23.9	9.8

*, **, and *** represent significance level at P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001 respectively. LEE is lattice effective error, df is degrees of freedom, ddf is denominator degrees of freedom and CV is coefficient of variation.

3.3.2 Performance in days from planting to tuber initiation, senescence, number of tubers per plant and fresh tuber yield for parents

The performance of parents which were propagated from tubers behaved differently from the F_1 progenies which were propagated from seedlings. The earliest genotype to form tubers was Nakpot 1 whereas genotype 391046.14 was the last to start tuber formation (Table 3). However,

Nakpot 1, Kimuri and Mbumbamagara reached onset of senescence early at about 63 days after planting while Cruza began to show signs of senescence at 89 days after planting (Table 3). Amongst the parents, cultivar Mbumbamagara had the highest number of tubers per plant while Nakpot 1 had the lowest (Table 3). Parents, 393280.82 had the highest total fresh tuber yield while Kimuri and Mbumbamagara had the lowest, respectively (Table 3).

Table 3: Tuber initiation, plant senescence and fresh tuber yield of parents evaluated at Kalengyere Research Station from May to September, 2012

Parents	Type	Tuber initiation (days)	Senescence (days)	Number of tubers plant^{-1}	Yield tha^{-1}
Nakpot 1	Male	32.7	62.8	4.7	15.0
Kimuri	Male	36.5	62.9	11.2	5.7
Mbumbamagara	Male	42.0	63.1	16.1	9.1
Victoria	Male	41.2	72.7	8.6	18.9
391046.14	Male	46.4	84.3	7.3	15.9
Nakpot 5	Female	37.7	83.0	8.3	30.6
393280.82	Female	42.2	85.0	11.0	32.7
396038.107	Female	40.5	80.1	11.2	31.5
Cruza	Female	42.8	89.1	13.0	20.5
Uganda 11	Female	41.4	82.9	8.1	26.0
Mean		40.4	76.6	10.0	20.6
SEM		1.2	3.3	1.0	1.5

3.3.3 Measurement of F_1 progeny for number of days from planting to tuber initiation, days from planting to senescence, number of tubers per plant and fresh tuber yield

Crosses that involved female parent 396038.107 formed tubers earlier than other progeny crosses, at approximately 32 days after transplanting (Table 4). These were followed by crosses involving male parent Nakpot 1 in which tubers were initiated at about 36 days after transplanting. Crosses involving Uganda 11 delayed to form tubers after transplanting (Table 4). Based on the overall mean, crosses with Mbumbamagara and Victoria initiated tubers early (Table 4). Crosses involving 396038.107 matured earlier than any other progeny cross while crosses involving Uganda 11 matured last. Crosses with 396038.107 matured significantly earlier than the rest. Crosses with Kimuri and 391046.14 also reached on set of senescence below the overall mean (in days after planting) (Table 4).

Crosses involving 391046.14 had the highest mean number of tubers per plant while crosses with 398280.82 had the lowest number of tubers per plant. Crosses involving 396038.107, Nakpot 1, Cruza and Uganda 11 were above the overall average number of tubers per plant (Table 4).

Amongst the F_1 progenies, crosses involving 396038.107 had the highest fresh tuber yield per hectare (8.9 t ha^{-1}) while crosses with Nakpot 5 had the lowest total fresh tuber yield (Table 4). The mean yield of progeny crosses with Nakpot 1, 393280.82 and Mbumbamagara was better i.e., above the overall mean yield (Table 4).

Table 4: Vegetative growth and yield parameters of F_1 progenies at Kalengyere Research Station from May to September, 2012

Crosses	Type	Tuber initiation (days)	Senescence (days)	Number of tubers $plant^{-1}$	Yield (tha^{-1})
396038.107	Female	32.1	82.9	14.6	8.9
Nakpot 1	Male	36.0	88.7	14.3	8.0
Mbumbamagara	Male	37.0	88.4	13.2	6.9
Victoria	Male	37.0	88.9	12.1	6.2
391046.14	Male	37.4	87.5	15.0	6.4
393280.82	Female	37.9	89.7	11.3	8.0
Cruza	Female	38.0	88.7	14.4	5.7
Kimuri	Male	38.5	87.6	12.3	6.4
Nakpot 5	Female	38.9	88.2	12.4	4.8
Uganda 11	Female	39.0	91.5	14.2	6.4
Mean		37.2	88.2	13.4	6.8
$LSD_{(0.05)}$		2.7	3.1	2.4	4.2

3.3.4 Estimates of combining ability and variance components

Analysis of variance showed high significant ($P<0.001$) in GCA amongst female parents for days from transplanting to tuber initiation, senescence and fresh tuber yield (tha^{-1}). The number of tubers per plant was significant at probability level of 0.05 in GCA of female parents (Table 5). The GCA of male parents and SCA effects were not significant ($P<0.05$) for days from transplanting to tuber initiation, senescence and number of tubers per plant while those of fresh tuber yield (tha^{-1}) were significantly ($P<0.001$) different (Table 5).

Table 5: Mean squares and variance components for days from transplanting to tuber initiation, crop senescence, number of tubers per plant and fresh tuber yield for general and specific combining abilities for parents of F_1 progenies respectively evaluated at Kalengyere between May and September, 2012

Source of variation	d.f.	Tuber initiation		Senescence		Number of tuber per plant		Yield (tha^{-1})	
		MS	VC	MS	VC	MS	VC	MS	VC
Total/Cross	24	9.3^{**}	5.22	10.12^{**}	9.14	6.13^{*}	2.68	5.13^{***}	4.84
GCAfemale	4	42.5^{***}	7.70	51.12^{***}	10.03	10.62^{*}	1.44	14.01^{***}	2.74
GCAmale	4	4.2^{ns}	0.03	1.95^{ns}	0.19	8.20^{+}	0.95	2.60^{***}	0.46
SCA	16	2.2^{ns}	-1.82	1.91^{ns}	0.94	4.48^{ns}	1.04	3.54^{***}	3.25
Error term	38-70	4.0	4.03	5.12	5.12	3.44	3.44	0.29	0.29

*, **, and *** represent significance level at $P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively, ns is non significant, MS is mean square and VC is variance component, error term is on entry mean basis

3.3.5 Estimation of Baker's ratio, narrow and broad sense coefficient of genetic determination

Baker's ratio estimated from variance components was 1.0 for tuber initiation (Table 6). The narrow sense coefficient of genetic determination (NCGD) which is similar to narrow sense heritability and broad sense coefficient of genetic determination (BCGD) analogous to broad sense heritability were estimated from variance components; both were 0.66 (Table 6). The Baker's ratio for onset of senescence estimated from transplanting date was 1.00. Narrow sense heritability and broad sense heritability were 0.64 and 0.64, respectively (Table 6). Baker's ratio for average number of tubers per plant was 0.70. Narrow sense heritability and broad sense heritability were 0.35 and 0.50, respectively (Table 6). The Baker's ratio for fresh tuber yield was 0.50. Narrow sense heritability for fresh tuber yield was 0.48 was obtained. Broad sense heritability for fresh tuber yield was 0.96 (Table 6).

Table 6: Estimation of Baker's ratio, narrow and broad sense coefficient of genetic determination

	Tuber initiation	Senescence	Number of tuber	Yield (tha^{-1})
[1]Baker's ratio ($[\partial^2$ GCAf$+\partial^2$ GCAm$]$ / $[\partial^2$ GCAf$+\partial^2$ GCAm$+\partial^2$SCA$]$)	1.00	1.00	0.70	0.50
[2]NS-CGD ($[\partial^2$ GCAf$+\partial^2$ GCAm$]$ / $[\partial^2$ GCAf$+\partial^2$ GCAm$+\partial^2$SCA$+\partial^2$ e$]$)	0.66	0.64	0.35	0.48
[3]BS-CGD ($[\partial^2$ GCAf$+\partial^2$ GCAm$+\partial^2$SCA$+\partial^2$ e$]$ / $[\partial^2$ GCAf$+\partial^2$ GCAm$+\partial^2$SCA$+\partial^2$ e$]$)	0.66	0.64	0.50	0.96

[1]Relative importance of GCA and SCA according to Baker (1978); [2]Narrow sense coefficient of genetic determination for a fixed model (analogous to h^2); [3]Broad sense coefficient of genetic determination for a fixed model (analogous to H^2). ∂^2e is the error component.

3.3.6 Estimates of general combining ability effects for parents

Parent 396038.107 had a negative significant (P<0.001) GCA effect on days from transplanting to tuber initiation while GCA effects of other parents were not significant (P<0.05) (Table 7). Parent 396038.107 also had negative significant (P<0.001) GCA effect on days from transplanting to senescence (P< 0.001) while parents 393280.82 and Uganda 11 had positive significant (P< 0.001) GCA effects (Table 7).

Analysis further revealed that, cultivar 391046.14 had the highest GCA for average number of tubers per plant while cultivar 393280.82 had negative significant (P<0.05) GCA effect for the same variable (Table 7). Parents with positive significant GCA effects were 396038.107, 393280.82 and Nakpot 1 (P< 0.001). Parents Cruza, Nakpot 5 (P< 0.001), Victoria (P<0.01), 391046.14 while Kimuri (P<0.05) had negative significant GCA for fresh tuber yield (Table 7).

Table 7: General Combining Ability (GCA) values of parents in days from transplanting to tuber initiation, on set of senescence and yield parameters of the F_1 progenies evaluated at Kalengyere Research Station from May to September, 2012

Parent	Tuber Initiation (days)	Senescence (days)	Number of tubers plant^{-1}	Yield t ha^{-1}
396038.107	-5.1***	-5.3***	1.2	2.2***
393280.82	0.7	1.5***	-2.1*	1.2***
Cruza	1.8	0.5	1.1	-1.1***
Nakpot 5	1.7	-0.02	-1.0	-2.0***
Uganda 11	0.8	3.3***	0.8	-0.3
391046.14	0.2	-0.7	1.6	-0.4*
Kimuri	1.4	-0.6	-1.1	-0.4*
Mbumbamagara	-0.2	0.2	-0.1	0.1
Nakpot 1	-1.2	0.5	0.9	1.2***
Victoria	-0.2	0.6	-1.3	-0.6**
SE(GCA)	0.9	0.4	0.8	0.2

SE refers to standard error, *, **and *** refer to significant GCA effects at P<0.05, P<0.01 and P<0.001 respectively. GCA effects without stars were non-significant at P<0.05.

3.3.7 Estimates of specific combining ability effects

The specific combining ability (SCA) for tuber initiation were not significant (P<0.05) for all the parental crosses. The most negative SCA value was obtained from the cross between Nakpot 5 and Victoria (Table 8) although Nakpot 5 had a high GCA. There was significant (P<0.05) SCA

effect for the crosses between Uganda 11 and Mbumbamagara (-2.4), 393280.82 and Mbumbamagara (2.5) while the rest of the crosses had non-significant SCA effects for senescence (Table 8). The SCA values for average number of tubers per plant were significant ($P<0.05$) among crosses of Uganda 11 and Nakpot 1 which had the highest SCA of 4.1 while the cross between of Uganda 11 and Mbumbamagara which had the lowest SCA of -4.3 (Table 8). The fresh tuber yield had significant positive SCA effects between Cruza x Mbumbamagara, 396038.107 x 391046.14, 393280.82 x Nakpot 1 ($P<0.001$), 393280.82 x Kimuri ($P<0.01$) and 396038.107 x Mbumbamagara ($P<0.05$). Negative highly significant ($P<0.001$) SCA effects were obtained in crosses involving 393280.82 x Mbumbamagara, Cruza x Nakpot 1, 396038.107 x Kimuri, 393280.82 x 391046.14. The crosses between Uganda 11 x Mbumbamagara and 396038.107 x Nakpot 1 also had significant ($P<0.05$) negative SCA effects (Table 8).

Table 8: Specific Combining Ability (SCA) values of parents for different growth (in days from transplanting) and yield parameters of the F_1 progeny evaluated at Kalengyere Research Station from May to September, 2012

Female	Male	Tuber Initiation	Senescence	Number of tubers plant^{-1}	Yield (t ha^{-1})
396038.107	Nakpot 1	-0.3	-1.4	-2.4	-1.1*
396038.107	Mbumbamagara	-1.1	0.5	3.0	1.1*
396038.107	Victoria	1.0	-0.8	-0.5	-0.1
396038.107	Kimuri	-0.4	0.6	-0.7	-2.0***
396038.107	391046.14	0.9	1.1	0.5	2.1***
393280.82	Nakpot 1	-1.1	-0.4	-0.4	2.8***
393280.82	Mbumbamagara	-1.9	2.5*	-0.7	-2.8***
393280.82	Victoria	2.2	0.2	0.5	0.7
393280.82	Kimuri	1.3	-0.5	1.5	1.6**
393280.82	391046.14	-0.4	-1.8	-0.8	-2.3***
Uganda 11	Nakpot 1	1.0	1.1	4.1*	0.5
Uganda 11	Mbumbamagara	1.1	-2.4*	-4.3*	-1.6**
Uganda 11	Victoria	-0.3	1.4	1.7	-0.5
Uganda 11	Kimuri	-0.1	-0.4	0.3	0.8
Uganda 11	391046.14	-1.7	0.4	-1.7	0.8
Nakpot 5	Nakpot 1	1.5	0.9	0.4	0.5
Nakpot 5	Mbumbamagara	1.9	0.3	1.4	0.2
Nakpot 5	Victoria	-2.6	-1.1	-1.6	-0.3
Nakpot 5	Kimuri	-0.9	-1.0	-0.4	-0.6
Nakpot 5	391046.14	0.1	0.9	0.2	0.1
Cruza	Nakpot 1	-1.0	-0.2	-1.7	-2.7***
Cruza	Mbumbamagara	-0.9	-0.8	0.7	3.0***
Cruza	Victoria	-0.4	0.3	-0.1	0.2
Cruza	Kimuri	0.2	1.3	-0.6	0.2
Cruza	391046.14	1.2	-0.6	1.7	-0.7
SE(SCA)		2.0	1.0	1.9	0.5

SE represents standard error, *, **and *** refer to significant SCA effects at P<0.05, P<0.01 and P<0.001 respectively. SCA effects without stars were not significant at P<0.05.

3.3.8 Frequency distribution for days from transplanting to onset of senescence of F_1 progenies

Graphic representation of days from transplanting to onset of senescence of the F_1 progeny showed that histograms for most crosses were right skewed. Out of the 25 crosses made, only

two crosses had left skewed histograms while three of the crosses showed histograms tending to normal distribution (Figure 1).

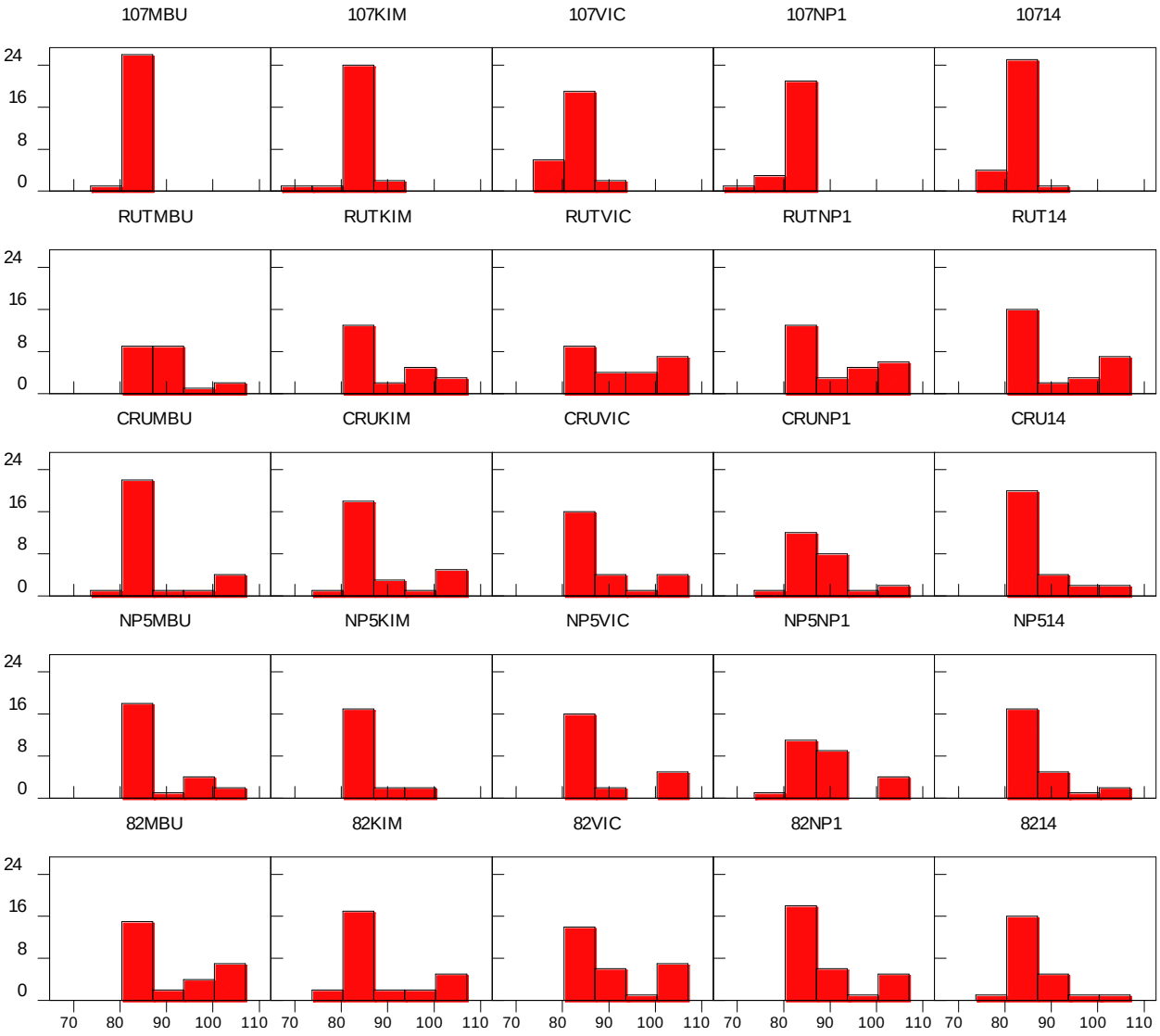

Figure 1: Frequency distribution of F_1 segregating population for days from transplanting to senescence

3.4 Discussion

Analysis of variance showed significant ($P<0.05$) clone effect for both growth and yield parameters implying that there is genetic variability amongst the materials that were used in the study. This is important since it justifies the basis for making improvements in any breeding program. Selection for the traits of interest can be done based on the mean performance of the clones. Thus, it was useful to study the combining ability of the parents for these traits in order to

provide information on their gene action for earliness for use now and in future *Solanum* potato variety improvement in Uganda. Desirable parents would be those with significant GCA effects in the right direction (desirable effect) for the trait of interest (Singh & Chaundary, 2004). The right direction for earliness is negative gene action while the yield parameter, positive gene action is the right direction. For all the studied traits, the parents exhibited significant and non significant positive and negative GCA effects implying both desirable and non desirable GCA effects were transferred by parents to the progeny. Parents with negative GCA effects for days from transplanting to tuber initiation and onset of senescence were desirable in bringing about earliness whereas those with positive GCA effects were responsible for late maturity. Some crosses between a parent with negative GCA and one with a positive GCA gave an early maturing hybrid. This could probably be due to a combination of genes governing earliness. Parents with positive GCA effects for yield for example 396038.107, 393280.82 and Nakpot 1 were desirable for bringing about improved yield in their off springs.

Among the parents used in the study, only 396038.107 exhibited negative GCA effects for growth parameters and positive GCA effects for yield parameters which are desirable attributes for obtaining progenies combining earliness and high yields. Other parents had desirable GCA effects for some traits and un desirable GCA effects for some other traits. Nakpot 1 had desirable GCA effects for tuber initiation and the yield and un desirable GCA effect for senescence thus it could be used to improve traits where it has desirable combining ability.

In this study, some parents with undesirable GCA effects combined to produce crosses with significant SCA effects indicating a deviation in the performance predicted on the basis of GCA of its parents. SCA refers to cases in which certain parental combinations do relatively better or worse than expected on the basis of average performance of the parents involved. For example, a cross between Uganda 11 and Mbumbamagara which had undesirable GCA effects on senescence, progenies that resulted in significant SCA effect (-2.4) for senescence. This can therefore, be used to exploit heterosis since SCA effects measure the usefulness of a particular cross combination in obtaining heterosis. Thus crosses which had the desirable SCA effects are considered the best and can be exploited through heterotic breeding to generate better hybrids through transgressive segregation (Chowdhary *et al.*, 2007).

The high GCA effects observed for number of tubers per plant could be helpful in identifying outstanding parents with favourable alleles for contributing to high fresh tuber yield (Hayder *et al*., 2009). The estimation of GCA effects revealed that it is the most desirable parent which contributed significant positive effects for number of tubers per plant. The high performance of such a parent for that trait may be mainly due to quantitative genes providing a basis for predicting the performance of the progenies.

Although parent 396038.107 is a long maturing genotype, it had a high GCA (-5.1) for early tuber initiation possibly due to gene complementation. This implies that in crosses where it was used, progenies formed tubers 5 days earlier than the overall mean of all parental crosses. This clone therefore, can be suitable in breeding for early tuber formation which is an important character in breeding for earliness in potato.

In variables where the analysis of variance showed significant GCA effects and non significant SCA effects for example tuber initiation, it implies additive gene action was more predominant than the non-additive gene effects. It also signifies that this trait is highly heritable and hence less influenced by the environment. In other cases where both GCA and SCA effects were significant it implied that both additive and non-additive gene effects governed phenotype expression. The relative importance of these effects was determined using Baker's ratio. For instance, Baker's ratio for tuber initiation was 1.0 implying that additive gene effects were more important than non additive gene effects. Thus, it would be easy to select for this trait phenotypically. Baker's ratio is an indication of how well the hybrid performance can be predicted from the GCA values of the parents. If the ratio is high, then crosses will usually produce populations that perform near the mid-parent value, and one can make crosses between parents based on the parent's GCA values, which are usually in line with the parental performance itself if inbreeding depression is not major. Since the result is predictable, fewer crosses can be made. A high Baker's ratio suggests primarily addiditve inheritance in crosses among a group of parents

The high narrow sense heritability values obtained 0.66 and 0.64 for tuber initiation and onset of senescence implied that earliness was mainly governed by additive gene action. This was revealed by a high Baker's ratio obtained for these traits. The days from transplanting to tuber initiation and onset of senescence also had high broad sense heritability values implying that

their inheritance was largely controlled by genotypic effects and less affected by environmental factors. Thus rapid improvement for earliness could be achieved using standard selection procedures such as mass selection based on the parental phenotypes (Sharma *et al.,* 2010). The narrow sense heritability values for number of tubers per plant and fresh tuber yield were low implying non-additive effects affected the expression of these traits. Broad sense heritability value for the number of tubers per plant was low indicating the effects of environmental factors while fresh tuber yield had a high value for broad sense heritability suggesting little effect of environment on phenotype expression.

The frequency distribution among progenies for days from planting to onset of senescence further revealed that additive gene action controlled potato maturity period since most of them were skewed to the right. Frequency distributions that were left skewed implied that dominant gene action controlled inheritance of earliness in the materials used in the study (Roy, 2000).

3.5 Sectional conclusion and recommendation

This chapter mainly addressed the mode of inheritance of earliness in potato. This was achieved by crossing five late maturing and high yielding potato clones with five early maturing but low yielding potato genotypes. North Carolina II (NC2) crossing design was used. Results revealed that both additive and non-additive gene effects were involved in determining earliness in potato. However, basing on Baker's ratio, additive gene effects were found to be more important. Clone 396038.107 was found to have desirable general combining ability for early tuber initiation and onset of senescence and total fresh tuber yield thus could be used to improve these traits in potato cultivars where earliness is required.

Flowering data were not analyzed because most seedlings did not flower at all. In a few where flower buds were initiated, these did not open. Out of the 750 seedlings transplanted, flower buds opened in only 110. This indicates that flowering is not a good measure for earliness; days from transplanting to tuber initiation and senescence would be better parameters. The clones obtained from F_1 progenies should be tested further in on-station trials to select the best performers.

CHAPTER FOUR

MAGNITUDE AND PATTERN OF GENOTYPE BY ENVIRONMENT INTERACTIONS FOR EARLINESS AND TUBER YIELD AMONG SELECTED POTATO CLONES IN UGANDA

4.1 Introduction

Multi-location trials (MLT) are generally conducted to confirm cultivar performance for important traits and to evaluate the stability or general adaptation of cultivars that are found promising in on-station trials. Multi-location trials through Additive Main Effects and Multiplicative Interaction (AMMI) analyses (Varela *et al*., 2006) provide information about the overall performance of the genotypes, environments and the genotype by environment (G x E) interactions over a range of locations. The magnitude of G x E interactions affects the breeding progress and it helps in evaluation and selection of superior genotypes. Interactions help to identify factors responsible for genotype adaptation. In this study, G x E interactions were investigated among 11 advanced potato clones in six environments constituted by three locations during two rainy seasons.

4.2 Materials and methods

4.2.1 Experimental sites

Field experiments were conducted at Kalengyere Research Station located at 1^0 13'14.92''S, 29^0 47'46.49, 2,450metres above sea level (a.s.l), Kachwekano Zonal Agricultural Research and Development Institute (ZARDI) situated at 1^0 15'07.04''S $29^0$56'25.06'', 2,204m a.s.l and Mbarara ZARDI situated $0^0$36'20.16''S $30^0$37'14.91, 1430m a.s.l. The experiments were conducted during the second (September - December) rainy season of 2011 and first (March-June) rainy season of 2012 to test 11 advanced clones for earliness and adaptability. The three sites receive bi-modal rainfall, however, at different times, intensities and quantities. The two rainy seasons at the three sites are separated by a short dry spell lasting 30-60 days depending on the location. The sites are also located at different elevations which affect the temperature regimes and thus constituting different environments. At all the trial sites, monthly rainfall, daily temperatures and relative humidity data were recorded during the study period (Figures 2 and 3; Appendices 7 and 8)

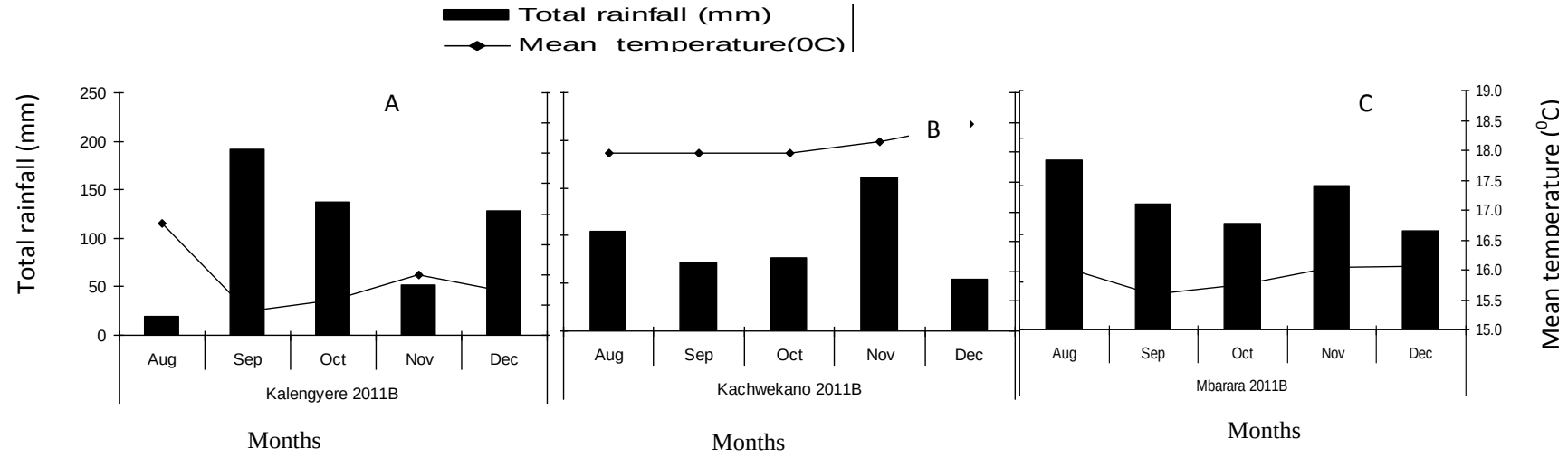

Figure 2: Total monthly rainfall (mm) and mean temperatures (^{0}C) at Kalengyere (A), Kachwekano (B) and Mbarara (C) from August to December, 2012.

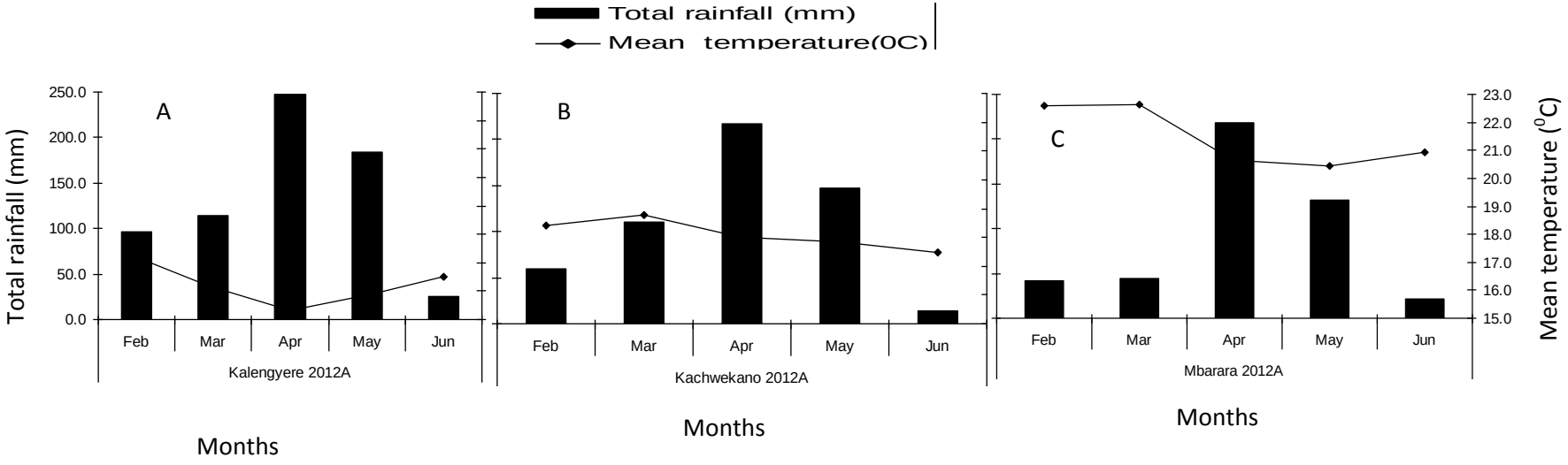

Figure 3: Total monthly rainfall (mm) and mean temperatures (^{0}C) at Kalengyere (A), Kachwekano (B) and Mbarara (C) from February to June, 2012.

4.2.2 Experimental treatments and design

Nine (9) genotypes which had maturity periods ranging from early to mid early in preliminary trials carried out at Kalengyere research station by the Kachwekano ZARDI potato program were evaluated (Table 9). Two cultivars Victoria and Nakpot 1 which are early maturing were included as standard local checks. The study was conducted for two seasons using a randomized complete block design (RCBD) at each site. Two replications per site were used during second rainy season of 2011 due to seed tubers shortage while three replications were used in the first rains of 2012. Each cultivar was grown in a ridge by furrow planting constituting two rows plot, 6.4 m^2 in size. Each plot was planted with 20 tubers at 0.8m spacing between rows and 0.4 m between seed tubers in a row.

Table 9: Potato genotypes used to determine the magnitude of G x E for earliness and tuber yield during 2011B (September- December, 2011) and 2012A (March-June, 2012) at Kalengyere, Kachwekano and Mbarara

Genotype	Tuber shape	Skin colour	Flesh colour	Depth of eyes	Maturity
395112.19	Round	Pink-red	Yellow	Shallow	Mid-early
396029.250	Round	White-cream	Pale yellow	Shallow	Early
395011.2	Oval	White-cream	Pale yellow	Shallow	Early
396026.103	Oblong	Red	Yellow	Shallow	Early
396241.4	Oval	White-cream	Cream	Deep	Early
396031.119	Round	Pink-red	Yellow	Shallow	Mid-early
396244.12	Oval	White-cream	Pale yellow	Shallow	Mid-early
391046.14	Oval	White-cream	Yellow	Shallow	Early
393280.82	Round	Red	Yellow	Deep	Mid-early
Nakpot 1	Round	White-cream	Cream	Shallow	Early
Victoria	Round	Red	Cream	Deep	Early

Source: KAZARDI

A compound N.P.K. (17:17:17) fertilizer was applied uniformly at 100 $Kgha^{-1}$ of each of its elemental constituents in two equal splits. Half of this quantity of fertilizer per plot (190 g) was added at the time of planting in furrows as a side dressing before placing the seed tubers and thoroughly mixed with the soil in the rows. The second half was added at the time of first weeding as a top-dressing to enhance vegetative growth. Weeding and earthing up of the experiment was done twice at 40 and 55 days after planting. Insect pests, particularly aphids and leaf miners were controlled with Agrothoate 40 EC (Dimethoate $400gl^{-1}$) applied at 3 ml per litre of water with a hand operated knap sac sprayer. Late blight was controlled using Agro-zeb 80

WP (a coordination product of zinc ion and manganese ethylene bisdithiocarbamate). The crop was later dehaulmed when all genotypes had reached their senescence or leaf ripening and harvested 14 days later.

4.2.3 Variables for determining G x E effects on earliness and tuber yield

Data were collected on days from planting to flower bud initiation (BI), tuber initiation (TI), days from planting to 50% flowering, duration of flowering in days and days from planting to senescence and yield parameters. At harvesting time the number of plants that reached maturity were counted and recorded. Harvested tubers from each plot were graded into three grade categories based on tuber diameter as small (< 30 mm), medium (30-45 mm) and large (> 45mm) an example is shown in pictures taken in June, 2012 at Kachwekano and Kalengyere respectively (Plate 3).

The graded tubers per plot were counted, weighed and data recorded. These data were used to derive, average number of tubers per plant, average tuber weight and total fresh tuber yield ($t\ ha^{-1}$) per genotype. Three medium-sized tubers per plot were randomly sampled and their fresh tuber weight recorded for use in determining tuber dry matter content.

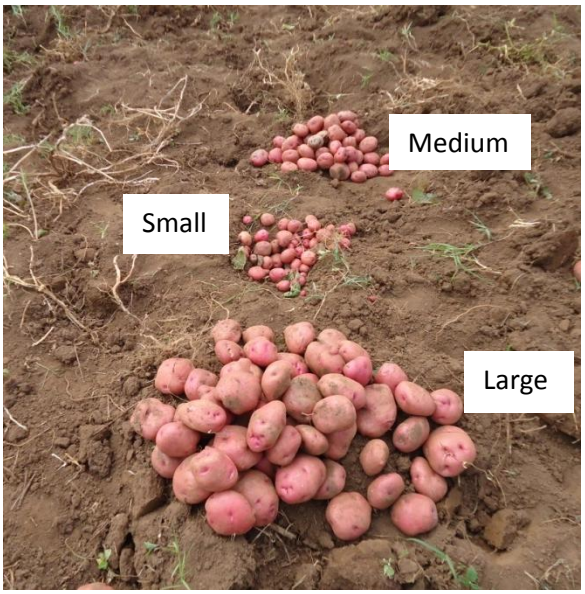

Plate 3: Three tuber grades of 396026.103

Plate 4: Weighing the graded tubers

Plate 5: Tubers of some of the most promising genotypes (a) 391046.14 and (b) 396026.103

Tuber samples for dry matter determination were taken to the laboratory and cut into small pieces to facilitate faster drying. The cut tuber pieces were weighed and weight recorded. Cut pieces were dried in oven at 105 ^{0}C until constant weight was obtained. Dry matter content (%) was computed as; dry weight/fresh weight * 100.

4.2.4 Data processing and analysis

The data were edited in MS Excel computer package (Microsoft Office, 2007) and analyzed in GenStat computer package (14th edition, VSN International Ltd, 2011) with relevant statistical procedures. The significance of treatments was tested using analysis of variance (ANOVA). Where treatment effects were significant, differences among treatment levels were compared using Fisher's Protected Least Significant Differences (LSD) test at 5% probability (Gomez and Gomez, 1984). Genotypic stability for earliness and total fresh tuber yield across environments was analyzed using Additive Main Effects and Multiplicative Interaction (AMMI). The stability of the genotypes in different environments was shown by use of bi-plots whereby genotype and environment means were plotted against IPCA (Interactive Principal Component Analysis) 2 scores which explains component of interaction.

4.3 Results

4.3.1 Magnitude of genotype (G) by environment(E) interaction for days from planting to flower bud initiation, tuber initiation and on set of senescence

Analysis of variance showed that the number of days from planting to flower bud initiation, tuber initiation and senescence traits was significantly ($P< 0.05$) affected by the potato genotype (Table 10). Locations, seasons and interaction between genotype and season, and between genotype and location were not significant ($P<0.05$) all variables except genotype by season for flower bud initiation. However, interaction between location (L) and season (S), G x E and third level interaction among genotype (G), location and season were highly significant ($P<0.001$) (Table 10).

Table 10: Mean squares for senescence, flower bud and tuber initiation (in days from planting) of selected potato genotypes at Kalengyere, Kachwekano and Mbarara during September-December, 2011 and March-June; 2012

Source of variation	D.f	Effect	F-test denominator	Flower Bud initiation	Tuber initiation	Senescence
Location	2	Fixed	L x S	539.7^{ns}	9.9^{ns}	1213.9^{ns}
Season	1	Fixed	L x S	969.3^{ns}	641.8^{ns}	130.0^{ns}
L x S	2	Random	Rep/Env't	153.7^{***}	122.2^{***}	337.1^{***}
[1]Rep/Env't	9	Random	Error	0.5	5.8	11.1
[2]Genotype	9	Fixed	G x E	121.9^{**}	119.8^{*}	866.3^{***}
G x E	45	Random	Error	42.0^{***}	49.8^{***}	99.8^{***}
G x L	18	Fixed	G x L x S	36.1^{ns}	32.6^{ns}	106.9^{ns}
G x S	9	Fixed	G x L x S	100.1^{*}	81.6^{ns}	142.1^{ns}
G x L x S	18	Random	Error	18.7^{***}	51.1^{***}	71.5^{***}
Pooled error	81	Random		1.6	7.6	13.1

*, **, and *** represent significance level at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively, ns= non-significant, L is location, S is season, G is genotype, E is environment, df is degrees of freedom

[1]Two reps were used in season 1 due to limited seed while three reps were used in season two across all locations.

[2]One of the eleven genotypes was removed from the analysis of variance because it was highly infected with potato bacterial wilt; *Ralstonia solanacearum* during the second season. Unbalanced ANOVA was used.

4.3.1.1 Flower bud initiation

Assessment of genotype, location and cropping season showed that potato genotypes started flowering earlier during the second rainy season of 2011 (September-December 2011) than the first rainy season of 2012 (March-June; 2012) (Table 11). Across locations and seasons, genotype 396029.250 was the earliest to initiate flower buds. The last genotype to initiate flower

buds was 395011.2. Overall, genotypes formed flower buds earlier in Mbarara, Kachwekano and Kalengyere respectively (Table 11). Genotype 396029.250 consistently started flowering earlier than any other clone across location and seasons. Genotype 396026.103 showed similar trend except in the second Kalengyere rainy season of 2011. Genotype 391046.14 was late to initiate flowers both at Kalengyere and Kachwekano during both seasons while its behavior at Mbarara was erratic; flowering early in second rainy season of 2011 but was late during the first rainy season of 2012 (Table 11).

4.3.1.2 Number of days from planting to tuber initiation

Potato genotypes started forming tubers earlier during the second season of 2011 than in 2012A (March-June; 2012). In all, genotype 396241.4 started tuberization earlier than any other clone while 395011.2 started forming tubers last (Table 11). Across locations, the test genotypes started tuber formation earlier in Mbarara than Kachwekano and Kalengyere where tuber initiation started almost at the same time (Table 11). Genotype 391046.14 initiated tuber formation early during both seasons at all the sites except during first rainy season of 2012 at Kalengyere. Genotype 396026.103 initiated tubers early at Kalengyere and Mbarara during 2011B and late in 2012A. At Kachwekano, it was early in both seasons (Table 11).

4.3.1.3 Days from planting to onset of senescence

The test genotypes reached maturity earlier in March-June; 2012 than in September-December, 2011. The cultivars matured earliest in Mbarara and latest in Kachwekano. Overall, the earliest maturing genotype across locations and seasons was 396241.4 while 396031.119 matured last (Table 11). Within locations, genotype 396244.12 matured early during both seasons at any given location. Genotype 391046.14 depicted similar trend except during the first rainy season of 2012 at Kalengyere. Genotype 396026.103 was earlier at Mbarara during both seasons than at Kalengyere and Kachwekano (Table 11).

Table 11: Performance of the selected genotypes in terms of days from planting to flower bud initiation, days to tuber initiation and days to onset of senescence at Kalengyere, Kachwekano and Mbarara during the second rainy season of 2011 and first rainy season of 2012

	Flower bud initiation						Tuber initiation						Senescence					
	Kalengyere		Kachwekano		Mbarara		Kalengyere		Kachwekano		Mbarara		Kalengyere		Kachwekano		Mbarara	
Genotype	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A
391046.14	40.0	43.0	38.0	46.3	30.5	37.7	40.0	48.0	37.5	45.7	39.0	39.0	74.0	85.0	79.5	78.7	67.0	73.7
393280.82	40.0	45.3	36.0	36.3	36.0	38.3	40.0	44.0	40.0	42.0	46.0	42.7	90.0	87.3	103.0	92.7	87.0	79.3
395011.2	37.0	56.0	31.0	47.3	34.0	40.0	40.0	59.7	39.0	54.0	45.0	49.0	71.0	93.7	91.0	74.7	82.0	76.3
395112.19	40.0	30.7	35.5	34.7	36.0	37.0	43.0	39.3	47.5	45.3	38.5	44.3	93.0	85.7	105.0	81.7	87.0	77.0
396026.103	41.5	39.0	34.5	37.0	30.0	31.7	43.0	40.3	45.0	47.0	40.0	50.7	88.0	85.3	91.0	82.7	73.0	73.7
396029.250	36.5	33.7	32.5	36.0	33.0	27.3	43.0	41.0	37.5	39.0	47.0	36.3	84.0	84.3	102.0	86.7	83.0	76.7
396031.119	40.0	49.0	35.0	45.7	34.0	34.3	43.0	51.0	33.0	51.7	46.0	36.0	93.0	101.7	96.0	94.0	87.0	81.3
396241.4	43.0	43.0	37.0	48.5	34.0	36.0	37.0	41.0	37.5	46.0	37.0	38.0	67.0	63.3	74.0	66.7	71.0	68.3
396244.12	37.0	45.7	35.0	50.0	30.0	36.3	38.5	39.3	34.0	46.7	40.0	40.3	71.0	66.7	80.5	94.7	73.0	68.3
Nakpot 1	37.0	41.0	32.0	38.0	34.0	38.0	40.0	43.3	32.0	46.7	37.0	43.3	71.0	87.3	74.0	81.0	67.0	77.0
Victoria	38.0	42.7	36.0	45.0	33.5	41.0	37.0	43.3	33.0	44.0	37.0	49.3	69.0	81.3	74.0	72.0	67.0	73.7
Mean	39.3	42.8	34.8	42.7	33.2	36.0	40.5	44.7	38.4	46.8	41.6	42.6	80.0	83.4	89.6	82.4	76.8	74.8
$LSD_{genotype}$	1.5	2.3	0.9	1.8	1.2	3.3	1.5	4.4	2.1	10.3	1.5	5.9	1.4	10.1	1.3	7.0	1.5	4.6

4.3.2 Magnitude of genotype (G) by environment (E) interaction G x E for number of tubers per plant, average tuber weight (g) and yield (t ha^{-1})

The analysis of variance showed that the number of tubers per plant, average tuber weight (g) and yield (t ha^{-1}) were significantly (P<0.05) influenced by potato genotypes (Table 12). The locations, seasons and interactions between genotype by season and genotype by location were not significant (P<0.05). The above variables were significantly (P<0.001) affected by interaction between location by season and genotype by location by season (Table 12).

Table 12: Mean squares for number of tubers per plant, average tuber weight (g) and yield (t ha^{-1})of selected potato genotypes evaluated across three locations over two seasons (September-December, 2011 and March-June; 2012)

Source of variation	d.f	Effect	F-test denominator	No. tubers per plant	Mean tuber weight (g)	Yield tha^{-1}
Location	2	Fixed	L x S	74.8^{ns}	12896^{ns}	513.6^{ns}
Season	1	Fixed	L x S	44.1^{ns}	1290^{ns}	516.8^{ns}
L x S	2	Random	Rep/Env't	35.2***	3277***	1190.9***
[1]Rep/Env't	9	Random	Error	2.4	219	19.7
[2]Genotype	9	Fixed	G x E	21.0*	3075***	657.3***
G x E	45	Random	Error	8.4***	781***	60.6***
G x L	18	Fixed	G x L x S	7.0^{ns}	799^{ns}	55.4^{ns}
G x S	9	Fixed	G x L x S	9.4^{ns}	705^{ns}	76.6^{ns}
G x L x S	18	Random	Error	9.3***	801***	57.7***
Pooled error	81	Random		2.5	221	19.2

*, **, and *** represent significance level at P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001 respectively, ns= non-significant. Unbalanced ANOVA was used.
[1]Two reps were used in season 1 due to limited seed while three reps were used in season two across all locations.
[2]One of the eleven genotypes was removed from the analysis of variance because it was highly infected with potato bacterial wilt; *Ralstonia solanacearum* during the second season.

4.3.2.1 Number of tubers per plant

The number of tubers per plant of the test genotypes was higher in September-December, 2011 than in March-June 2012 rainy season. The highest number of tubers per plant was obtained at Mbarara while the lowest number was obtained at Kachwekano (Table 13). Among the experimental genotypes, Clone 396026.103 had the highest number of tubers per plant while Nakpot 1 had the lowest (Table 13). Clone 396026.103 had a high number of tubers per plant across locations and seasons (Table 13). Clone 391046.14 had the higher number of tubers per

plant at Kalengyere in 2011B than in 2012A. Kachwekano and Mbarara had high number of tubers per plant during both seasons (Table 13).

4.3.2.2 Average tuber weight

The average tuber weight for the genotypes was generally higher during the March-June; 2012 than in September-December, 2011 rainy season. The test genotypes had the highest average tuber weight at Kalengyere and the lowest at Mbarara. Generally, Nakpot 1 and 396026.103 respectively had the heaviest tubers while the genotype 395011.2 had the lowest average tuber weight (Table 13). Genotype 396026.103 had a consistent high mean tuber weight across location and season. 391046.14 had similar trends except in 2012A at Mbarara where it had a low mean tuber weight. Genotype 396029.250 had a low average tuber weight at Kalengyere during both seasons and at Kachwekano during season 2011B. High average tuber weight was obtained in 2012A at Kachwekano and at Mbarara (Table 13).

4.3.2.3 Fresh tuber yield (t ha^{-1})

Genotypes yielded highest in September-December, 2011 than in March-June; 2012 rainy season. The test genotypes had the highest fresh tuber yield (t ha^{-1}) at Kalengyere and lowest at Kachwekano. The highest yielding genotype was clone 396026.103 while 396244.12 was the least across locations and seasons (Table 13). Clone 391046.14 had high yield at Kalengyere and Mbarara across seasons while at Kachwekano, its yield was low in 2011B. Kalengyere had the highest yield in first rainy season of 2012. The performance of clone 396029.250 was erratic yielding below the overall average at Kalengyere during 2011B and at Kachwekano during both seasons while at Kalengyere during 2012A and at Mbarara during both seasons the yield was above average (Table 13).

Table 13: Performance of the selected genotypes in terms of number of tuber per plant, average tuber weight in grams and fresh tuber yield in tons per hectare at Kalengyere, Kachwekano and Mbarara during the second rainy season of 2011 and first rainy season of 2012

	Number of tubers per plant						Average tuber weight (g)						Yield tha^{-1}					
	Kalengyere		Kachwekano		Mbarara		Kalengyere		Kachwekano		Mbarara		Kalengyere		Kachwekano		Mbarara	
Genotype	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A	2011B	2012A
391046.14	7.0	9.0	8.0	9.0	14.0	11.0	114.9	113.1	82.3	112.4	82.4	61.5	25.9	32.2	19.5	28.8	34.9	20.4
393280.82	13.0	6.0	12.0	8.0	12.0	8.0	73.0	139.7	103.4	94.4	86.8	57.6	28.4	25.2	29.4	22.6	31.3	11.9
395011.2	9.0	7.0	5.0	6.0	10.0	6.0	63.6	89.5	58.1	83.7	54.4	47.9	17.3	16.6	9.5	14.8	15.3	9.3
395112.19	7.0	13.0	9.0	7.0	10.0	8.0	123.4	81.4	104.9	112.9	92.2	73.0	25.6	32.3	28.8	24.8	28.0	16.0
396026.103	9.0	10.0	7.0	10.0	14.0	10.0	130.1	135.4	129.5	130.9	87.4	70.6	34.8	40.6	26.9	34.1	38.4	17.5
396029.250	9.0	12.0	7.0	8.0	12.0	8.0	72.6	108.2	84.9	107.3	109.2	91.7	21.2	37.7	19.8	21.7	36.5	19.7
396031.119	7.0	8.0	7.0	7.0	12.0	7.0	157.8	116.1	114.1	137.5	80.6	68.4	30.5	25.2	24.8	23.5	29.6	14.2
396241.4	8.0	7.0	5.0	4.0	11.0	8.0	88.7	105.3	75.2	76.6	91.3	84.2	22.2	20.8	11.2	5.8	30.4	5.7
396244.12	8.0	5.0	7.0	7.0	7.0	10.0	59.2	104.5	82.4	73.5	56.3	73.2	14.0	11.9	18.1	15.0	11.6	11.2
Nakpot 1	6.5	5.0	5.5	1.0	11.0	3.0	178.6	243.1	169.3	219.3	125.0	130.9	34.0	30.6	30.3	4.9	41.2	6.2
Victoria	11.0	9.0	8.0	7.0	15.0	9.0	80.0	131.3	82.8	137.7	97.0	78.8	27.5	37.9	19.1	28.4	42.3	20.7
Mean	9.0	9.0	7.0	7.0	12.0	9.0	96.3	112.4	91.8	106.7	85.1	70.7	24.7	28.0	21.4	21.9	29.8	14.7
$LSD_{genotype}$	4.2	2.7	2.5	3.1	3.7	2.8	38.5	23.4	22.0	21.3	28.1	34.8	8.5	8.4	5.3	7.7	8.7	8.5

2011B and 2012A refers to the second rainy season of 2011 and first rainy season of 2012 respectively. LSD is least significant difference at probability level of 0.05.

4.3.3 Genotype and location effects on dry matter content (%)

Tuber dry matter content (%) was evaluated during the first rainy season of 2012 (March-June) across the three locations. Analysis of variance revealed that percentage dry matter content was significantly (P<0.001) affected by potato genotype (Table 14). The genotype by location interactions was not significant (0.05).

Table 14: Analysis of variance for tuber dry matter content (%) of selected potato genotypes evaluated at Kalengyere, Kachwekano and Mbarara during March-June; 2012

Source of variation	d.f.	Sums of squares	Mean square	v.r.	F pr.
Rep stratum	2	26.1	13.0	1.4	
Location	2	40.6	20.3	2.2	0.227
Residual 1	4	36.9	9.2	1.4	
Genotype	10	474.2	47.4***	7.3	<.001
Location x Genotype	20	169.7	8.5	1.3	0.217
Residual 2	60	392.4	6.5		

*** represent significance at 0.001 probability level, ns refers to non significance at P<0.05.

The genotype 39029.250 had the highest dry matter content in Kachwekano, 396244.12 had the highest dry matter content in Mbarara, 395112.19 was the highest at Kalengyere. 396031.119 had the lowest value for dry matter across the locations (Figure 4). Clones 391046.14 and 396026.103 were stable across locations.

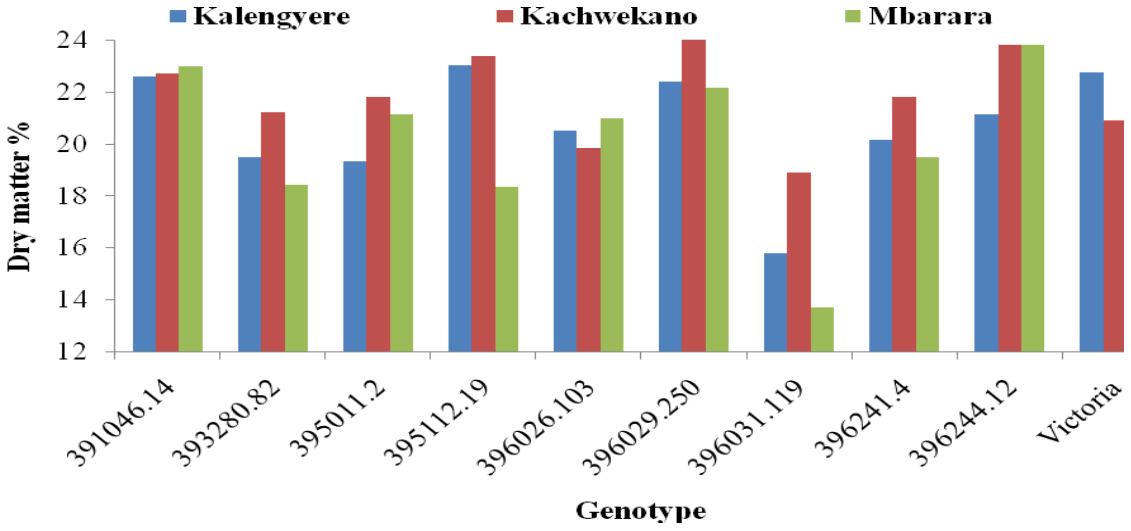

Figure 4: Dry matter content (%) of selected potato genotypes evaluated at three locations during March to June, 2012 rainy season

4.3.4 Stability of selected potato genotypes for important variables for measuring earliness

The stability analysis based on Additive Main and Multiplicative Interaction (AMMI) revealed that genotypes, environments and G x E interactions were highly significant (P< 0.001) for days from planting to flower bud initiation, tuber initiation and phenotypic senescence (Table 15).

Table 15: AMMI mean squares for days from planting to flower bud initiation, tuber initiation and senescence of selected potato genotypes grown at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

Source	Df	Flower bud initiation	Tuber initiation	Senescence
Total	119	34.48	32.4	119.0
Treatments	59	68.22***	62.0***	233.9***
Genotypes	9	71.31***	92.0***	783.5***
Environments	5	386.41***	151.5***	572.4***
Rep/environment	6	0.59ns	6.6ns	2.9ns
G x E	45	32.25***	46.1***	86.4***
IPCA 1	13	70.53***	76.5***	133.1***
IPCA 2	11	25.95***	65.8***	101.7***
IPCA residuals	21	11.86***	16.9***	49.5***
Error	54	1.41	2.9	6.3

*** represent significance at 0.001 probability, ns refers to lack of significance at 0.05 probability level.

The AMMI ANOVA showed that the number of tubers, mean tuber weight and fresh tuber yield were highly significantly (P<0.01) affected by genotype, environment, G x E interactions and the IPCA scores (Table 16).

For all the variables studied, the sums of squares for G x E interactions were always higher than the genotype effects.

Table 16: AMMI mean squares for number of tubers per plant, mean tuber weight and fresh tuber yield of selected potato genotypes grown at at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

Source	df	Yield t ha^{-1}	Number of tubers $plant^{-1}$	Mean tuber weight g^{-1}
Total	119	89.0	7.3	746
Treatments	59	161.4^{***}	12.0^{***}	1333^{***}
Genotypes	9	497.0^{***}	16.6^{***}	2783^{***}
Environments	5	559.7^{***}	49.4^{***}	4283^{***}
Rep/environment	6	21.3^{ns}	3.1^{ns}	178^{ns}
G x E	45	50.0^{***}	7.0^{***}	716^{***}
IPCA 1	13	92.4^{***}	11.7^{***}	1328^{***}
IPCA 2	11	54.0^{**}	7.0^{**}	814^{***}
IPCA residuals	21	21.7^{ns}	4.0^{ns}	286^{ns}
Error	54	17.4	2.5	166

, * represent significance at 0.01 and 0.001 probability levels, ns is non- significance at 0.05 probability level

The bi-plot for flower bud initiation (Figure 5) shows that IPCA scores 396029.250 and 396031.119 were approximately equal to zero. 396026.103, 395112.19 and Victoria also did not vary significantly from one environment to another (Figure 5).

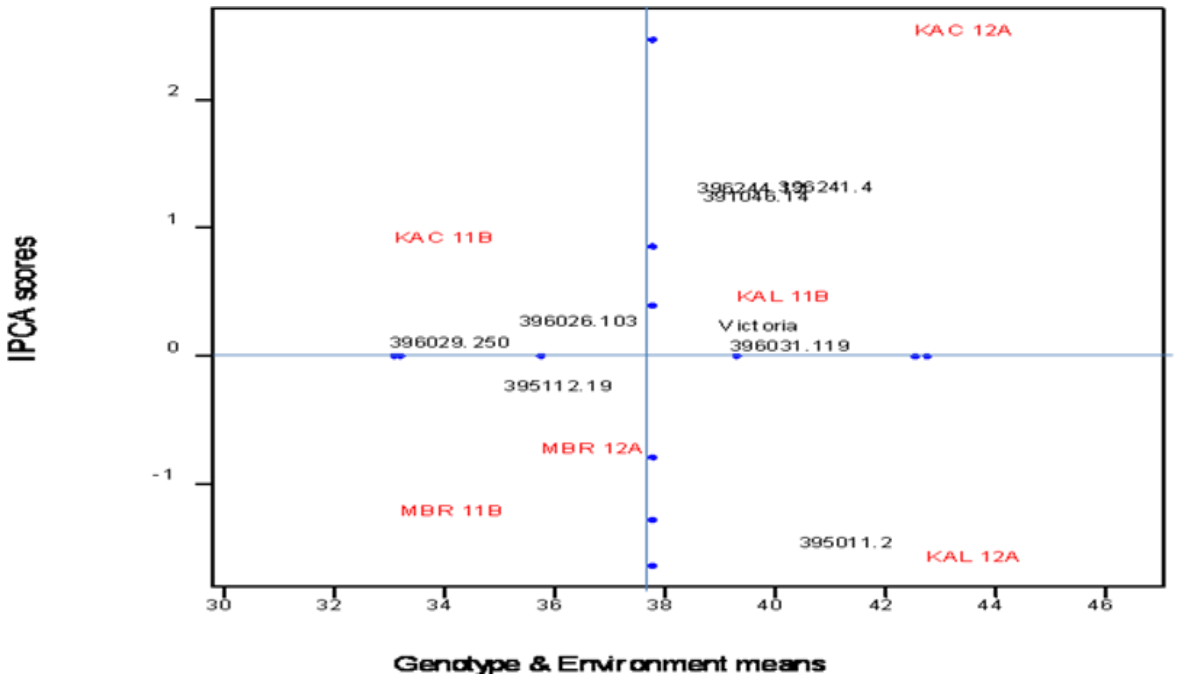

Figure 5: Bi-plot of genotypes and environment IPCA 1 scores against means for flower bud initiation in days after planting of selected potato genotypes evaluated at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

With reference to onset of senescence or leaf ripening, its only 396241.4 that had an IPCA score close to zero Victoria, 391046.14, 396244.12 and 395011.2 were relatively earlier than other genotypes but they were specifically adapted to one environment (MBR 12A) (Figure 6).

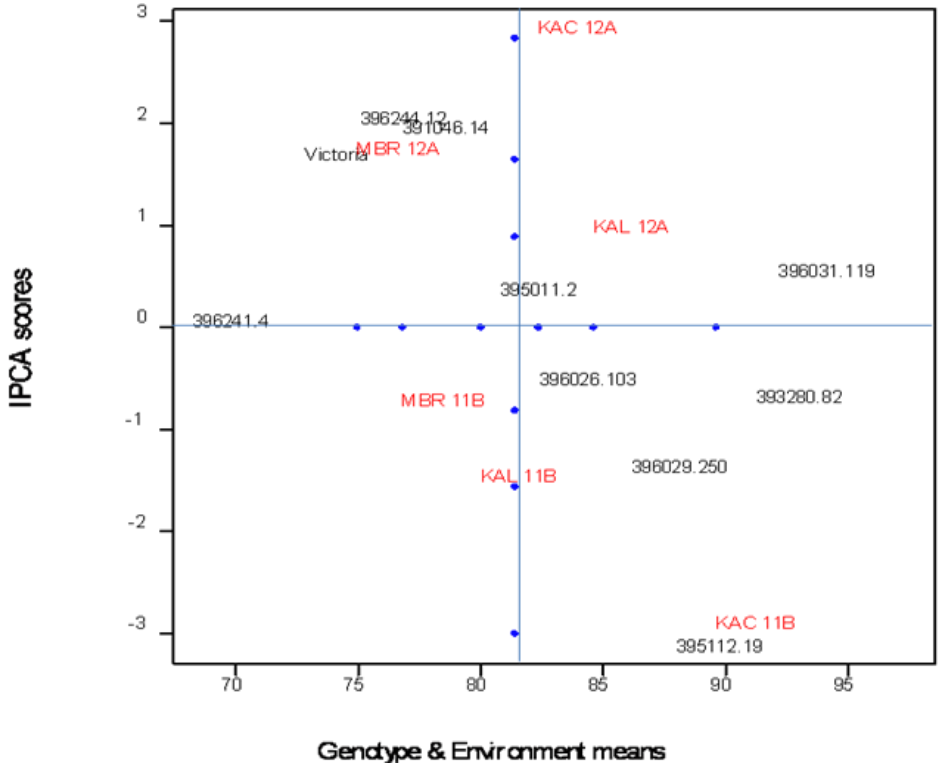

Figure 6: A Bi-plot of genotypes and environment IPCA 1 scores against means for senescence in days after planting of selected potato genotypes evaluated at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

Most genotypes had IPCA scores ranging from +1 to -1 regarding the number of tubers per plant. However, 391046.14, 396026.103, 396029.250 and 393280.82 are the only ones that appeared in the quadrants with higher number of tubers per plant (Figure 7).

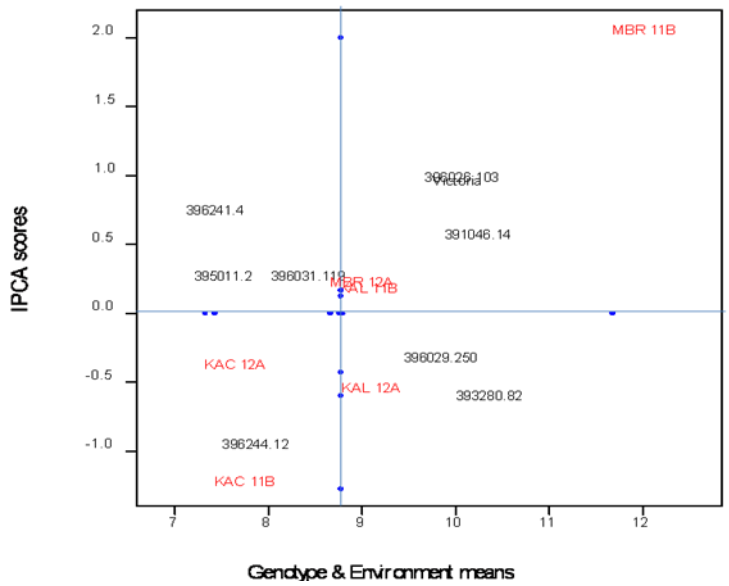

Figure 7: A Bi-plot of genotypes and environment IPCA 1 scores against means for average tuber weight (g) selected potato genotypes evaluated at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

Clone 396029.250 had the lowest IPCA score approximating to zero for fresh tuber yield (Figure 8). Clone 396031.119, 395112.19, Victoria and 396026.103 also had fairly low IPCA scores above the average fresh tuber yields (Figure 8).

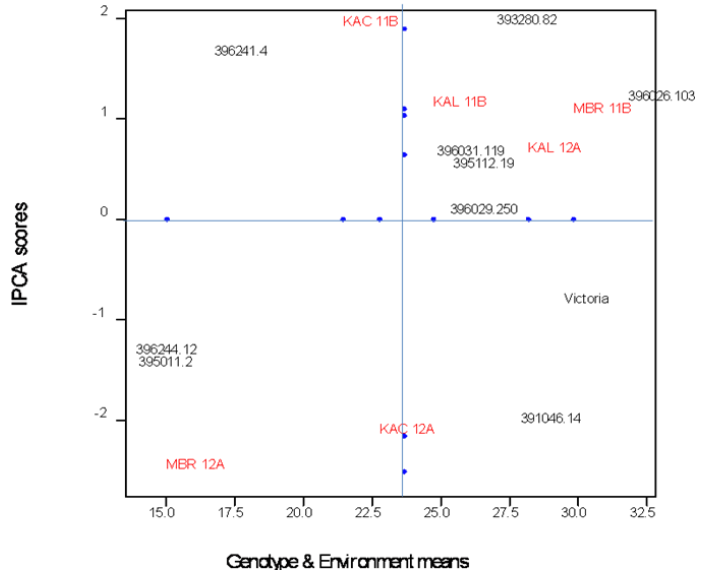

Figure 8: A Bi-plot of genotypes and environment IPCA 2 scores against means of fresh tuber yield in tons per hectare of selected potato genotypes evaluated at Kalengyere (KAL), Kachwekano (KAC) and Mbarara (MBR) during September-December, 2011 (11B) and March-June; 2012 (12A)

4.3.5 Correlation amongst growth and yield traits of selected potato genotypes grown at Kalengyere, Kachwekano and Mbarara during March-June; 2012

The total fresh tuber yield (t ha^{-1}) was positively correlated with number of days from planting to tuber initiation, onset of senescence, duration of bulking, number of tubers per plant and average tuber weight (g) (Table 17). Yield was negatively correlated with days from planting to flower bud initiation and dry matter content (%) (Table 17). There were high and significant ($P< 0.001$) correlations between yield and senescence; yield and duration of bulking; and that of senescence and duration of bulking (Table 17). Total fresh tuber yield had a perfect positive relationship with duration of bulking and a very strong positive relationship with days from planting to onset of senescence. Dry matter content (%) was negatively correlated with number of days from planting to beginning of flower bud initiation, tuber initiation, senescence, duration of bulking, average tuber weight and total fresh tuber yield. However, it had a positive relationship with the number of tubers per plant. The number of days from planting to beginning of tuber initiation was positively correlated with senescence (Table 17). Senescence had a strong positive relationship with duration of bulking which in turn was positively correlated with total fresh tuber yield. Results also showed that number of days from planting to flower bud initiation and total tuber yield had a moderate negative correlation. The dry matter content (%) and average tuber weight had a significant ($P< 0.05$) negative correlation (Table 17).

Table 17: Correlation between various traits of 11 selected potato genotypes averaged across three locations over two seasons (September-December, 2011 and March-June; 2012)

		1	2	3	4	5	6	7	8
1	Days to flower bud initiation	-							
2	Tuber initiation(days)	0.17	-						
3	Senescence (days)	-0.35	0.49	-					
4	Duration of bulking (days)	-0.45	0.19	0.95***	-				
5	Number of tubers per plant	-0.25	0.10	0.32	0.32	-			
6	Average tuber weight (g)	-0.36	-0.26	-0.01	0.08	-0.36	-		
7	Dry matter content (%)	-0.18	-0.17	-0.28	-0.26	0.46	-0.64*	-	
8	Yield (t ha^{-1})	-0.45	0.19	0.95***	1.00***	0.32	0.08	-0.26	-

*, *** represent significance at 0.05 and 0.001 probability levels respectively. Correlations without stars were not significant at $P<0.05$.

4.4 Discussion

The potato genotypes used in the study responded differently in the various environments. Potato genotypes for example started flowering earliest in Mbarara, 1400m a.s.l probably due to warm climate associated with low elevations and latest at Kalengyere located at 2450m a.s.l due to the cool climate associated with highlands. Abalo *et al.,* (2003) reported similar results about yield stability studies with potato genotypes for late blight resistance. The differences in performance of genotypes among the studied traits across locations and seasons are an indication of presence of genotype by environment interaction (Abalo *et al.,* 2001).

Potato yields largely varied between the second rainy season of 2011 and first season of 2012 at Mbarara. This could be attributed to the large differences that prevailed between the two seasons at this site. The second cropping season of 2011at Mbarara received more rainfall than first season of 2012. Similarly, the mean temperature was relatively low in 2011B unlike during the first season of 2012 which experienced an extended period of moisture stress. This finding is in agreement with the findings of Abalo *et al.,* (2003) who reported that long drought and high temperatures limit potato bulking.

Supplementary studies about stability of earliness and fresh tuber yield were undertaken using additive multiplicative main interactions (AMMI) model described by Gauch & Zobel, (1996). Highly significant differences ($P< 0.001$) were obtained for genotypes, environments and genotype by environment interaction. This implied that genotypes varied in their performance for all traits from across locations. Thus selection across environments should be done based on overall means. More so, genotypes could be selected based on a specific environment (Zhao & Shizhong, 2012). The differences noted could probably be attributed to the differences in the conditions in given environments. Nakitandwe *et al.,* (2003) reported similar findings.

The IPCA scores of the genotypes in the AMMI analysis were an indication of stability or adaptation over environments. The greater the magnitude of IPCA scores either in the positive or negative direction for a given genotype, the more it is specifically adapted to certain environments. Genotypes which had IPCA scores approximating to zero were more stable over all the environments in the study e.g**.** considering early flower bud initiation, its only396029.250,

396026.103 and 395112.19 that could be recommended to be grown in all the environments in which they were tested in since their IPCA scores were close to zero.

The positive correlation between days from planting to tuber initiation, duration of bulking, senescence, number of tubers per plant and average tuber weight with total fresh tuber yield indicate that they positively affect yield. The strong correlation between onset of senescence and duration of bulking with yield implied that a factor that affects either onset of senescence or duration of bulking would increase or decrease the yield by the same number of units thus yield could be predicted based on these two parameters. Dry matter content (%) had a negative correlation with average tuber weight which implied that the higher the average tuber weight the lower the dry matter content and vice versa. This finding contradicts the findings of Nakitandwe, (2003). The difference could probably be attributed to different environments and genetic materials that were used with regard to partitioning of assimilate between the sink (tubers) and the source (shoot). The results further revealed that maturity period or onset of senescence of a given genotype was not correlated with average tuber weight implying these two parameters were not dependant on each other. Most importantly albeit weakly, total fresh tuber yield was negatively correlated with days from planting to flower bud initiation implying that yield was higher in genotypes where flower buds appeared earlier. The advantage is that vegetative growth is stopped early in the crop development cycle and the plants channel photosynthetic biomass in tuber bulking than among genotypes where flower development starts later.

4.5 Sectional conclusion and recommendation

The G x E effects on earliness and fresh tuber yield was studied for nine selected potato genotypes. The study was done over two seasons in three different locations. Significant differences were observed among the genotypes and among genotype by environment interactions. Among the genotypes in an environment, the within genotype variances were also significantly different ($P<0.05$). The performance of genotypes 396026.103 and 391046.14 did not vary significantly. Thus, indicating stability for both earliness and high yield across environments. These should be subjected to on-farm trials for further testing and be considered candidate cultivars for release in the environments in which they were tested. Genotypes 395112.19 and 393280.82 were specifically adapted to Kachwekano; genotype 396029.250 was

specifically adapted to Kalengyere and Mbarara. The performance of these genotypes could be tested further and in the environments in which they are specifically adapted and be considered for release in the given environments.

CHAPTER FIVE

GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

5.1 General discussion

Most of the past potato variety improvement efforts in Uganda concentrated on developing cultivars adaptable to cool highland environments with particular emphasis on late blight and high yields. Attempts to grow these cultivars in lowland areas usually results in low yields due to high temperature and a short rainfall cycle (Poehlman & Sleper, 1995). Improving potato productivity across varied environments requires developing cultivars with wide adaptability or specifically for low altitude adaptation. Such clones would have characteristics for early tuber formation and bulking. Although high fresh tuber yield and favoured culinary characteristics remain the primary goals of potato breeding, early maturing cultivars are necessary in areas where conditions favouring potato growth and high yields are not optimal particularly in the lowland and mid-altitude areas with short rainfall regimes and high temperature. This study was conducted with an ultimate goal of contributing to the improvement of potato production in Uganda through developing early maturing, high yielding and stable cultivars adaptable to diverse agro ecologies with emphasis to low and mid-altitude areas.

The first experiment of the study was aimed at determining the mode of inheritance of earliness in potato. The results revealed that both additive and non additive gene action govern maturity in potato. However, basing on results of Baker's ratio, additive gene action was found more influential in determining maturity in potato than non-additive effects. The frequency distribution among the F_1 progenies further revealed that additive gene action controlled potato maturity period since most of them were skewed to the right.

The second experiment was conducted to determine the magnitude of genotype by environment interactions, in the newly developed clones for to earliness and high stable yields. These clones were characterized as having horizontal resistance to late blight, but with maturity period ranging from early to mid early. Results revealed significant G x E interactions indicating that selection needs to be done for genotypes that are relatively stable across the environments. This should avail farmers with genotypes that are high yielding and stable over time and space.

The total fresh tuber yield across the environments ranged from 13.6 to 32.1 tons per hectare. These values are far above the Ugandan national average yield of 6.8tha^{-1} (FAOSTAT, 2010). Thus the genotypes are worth being promoted in order to improve the productivity of the potato sector. Based on the results from analysis of variance and AMMI, the most stable genotypes for earliness with relatively high yields were 396026.103 and 391046.14.

5.2 Conclusion

This study revealed that;

Parents with negative GCA and SCA effects were desirable for earliness characters such as tuber initiation and days to onset of senescence. The positive GCA and SCA were desirable for yield parameters such as number of tubers per plant, average tuber yield and total fresh tuber yield. The breeding implication is that parents with desirable GCA and SCA effects should be used according to the specific trait. The genetic studies revealed that inheritance of maturity and yield in potato is controlled by additive and non- additive gene actions though the former is more important than the latter.

The significant interactions between location by season (L x S) and genotypes by location by season (G x L x S) justify the rationale for having undertaken the study. The analysis for stability for genotypes using AMMI helped to identify some genotypes that were consistently early maturing with relatively stable high yields. Among the genotypes evaluated, 396026.103 and 391046.14 were the most stable regarding earliness and high fresh tuber yields.

Some of the new genotypes tested performed much better than the local checks in terms of earliness and yield such as 396026.103 and 391046.14, thus they should be considered as candidate cultivars for future release across the three environments in which they were tested.

5.3 Recommendations

The clones obtained from F_1 progenies should be multiplied to increase the seed while their performance is tested against their parents in on-station trials, later on the promising genotypes should be subjected to multi-location trials in order to study the stability of their performance and to also enrich findings about their gene action.

Parent 396038.107 exhibited desirable general combining effects for both earliness and high yield thus it should be used in potato breeding for further improvement.

Potato maturity period of F_1 progeny should not be based on days from transplanting to flowering because this trait is not consistent in all genotypes because some or most F_1 potato plants may not flower. Days from transplanting to tuber initiation and senescence are better phenotypic measures for maturity of F_1s.

The promising stable varieties identified should be subjected to on-farm trials for evaluation by farmers. This will facilitate farmers to appreciate the distinguishing qualities of these genotypes including the desired culinary characteristics that were not addressed in this study. This will enhance the acceptability and adoption of these new genotypes.

The genotypes that were early and had high yields in specific environments but lacked stability across environments should be considered for restricted release to those specific environments where they are best adapted.

The potential disadvantages of early maturing potato varieties should be explored in further studies.

References

Abalo, G., Hakiza, J.J., El-Bedewy, R and Adipala, E., 2003. Genotype x environment interaction studies on yields of selected potato genotypes in Uganda. *African Crop Science Journal* 11:9-15.

Abalo, G., Hakiza, J.J., Kakuhenzire, M.R., El-Bedewy, R and Adipala, E., 2001. Agronomic performance of the twelve elite potato genotypes in south western Uganda. *African Crop Science Journal* 9:17-23.

Acquaah, G., 2007. Potato Breeding. In *Principles of Plant Genetics and Breeding*. Blackwell Publishing Ltd, Malden MA, USA. pp: 537-545.

Ahangar, L., Ranjbar, G.A. and Nouroozi, M., 2008. Estimation of combining ability for yield and yield components in rice (Oryza sativa L.) cultivars using diallel cross. *Pakistan Journal of Biological Sciences* 11:1278-1281.

Aliguma, L., Magala, D. and Lwasa, S., 2007. *Uganda; Connecting small scale producers to markets. The case of Nyabyumba united farmers group in Kabale district, Uganda.* Re-governing markets innovative practice series. pp: 5-20.

Azhar, F.M., Hussain, A. and Shakeel, A., 2007. Combining ability of plant characters related to earliness in *Gossypium hirsutum* L. *Journal of Agriculture and Social sciences* 2: 63-66.

Banziger, M., G.O. Edmeades, D.Beck, and M. Bellon, 2000. Breeding for drought and nitrogen stress tolerance in maize. From Theory to Practice. Mexico, D.F, CIMMYT. pp: 16-17.

Bernardo, R., 2010. *Breeding for Quantitative Traits in Plants*. Second edition, Stemma press USA.

Bidinger, F.R., Hammer, G.L. and Muchow R.C., 1996. The Physiological Basis of Genotype x Environment Interactions in Crop Adaptation. Plant Adaptation and Crop Improvement. Cooper, M. and Hammer, G.L. (eds). CAB international 450pp.

Bishop, B. and Long, C., 2012. http://msue.anr.msu.edu/news/new_potato_maturity_and stress_graphic _tool_available_on_enviro-weather.

Bradshaw, J.E. and Mackay, G.R., 1994. *Potato Genetics.* University press, Cambridge, UK.

Bradshaw, J.E. and Bonierbale, M., 2010. Potatoes, pp: 1-52. In Bradshaw, J.E., edition. Root and tuber crops. Hand book of plant breeding 7. Springer science + Business media, New York.

Buso, G.S.C., Paiva, M.R., Torres, A.C., Resende, F.V., Ferreira, M.A., Buso, J.A. and Dusi, A.N., 2008. Genetic diversity studies of Brazilian garlic cultivars and quality control of garlic clover production. *Journal of Genetics and Molecular Research* 7: 534-541

Chowdhary, A. M., Sajad, M. and Ashraf, I. M. 2007. Analysis on combining ability of metric traits in bread wheat, *Triticum aestivum. J. Agric. Res.,* 2007, 45: 1-8.

CIP, 2011. Understanding the profitability of the seed potato value chain in Kenya. *Final financial report, September*, 2011.

Cook, E. David, 2008. Genetic and environmental parameters affecting Nalto soybean.

El-Bramawy, M. A. S. and Shaban, W. I. 2007. Nature of gene action for yield, yield components and major disease resistance in Sesame (*Sesamum indicum* L.). *Res. J. Agri and Bio Sci.*, 3:821-826.

Falconer, D.S. and Mackay, T.F.C., 2009. *Introduction to Quantitative Genetics*. 4th Ed. Dorling Kindersley PVT Ltd. New Delhi India.

FAO, 2008. International year of potato, 2008. http://www.potato2008.org/

FAOSTAT, 2010. http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor, Retrieved on 22/11/2012.

Fehr, W.R., 1987. *Principles of Cultivar Development. Volume 1. Theory and Technique*, Iowa state university. Macmillan publishing company. New York.

Ferris, G. Okoboi, C. Crissman, P. Ewell and B. Lemaga, 2001. Uganda's Irish Potato Sector. pp: 6-37.

Griffin, D. and Leslie J.D., 2007. *Breeding new potato varieties. True Crops*, Volume 2: Number 1. Spring, 2007.

Griffings, B., 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*. 9:463-493

Gomez, K. A. and Gomez. A. A. 1984. *Statistical Procedures for Agricultural Research.* John Wiley and Sons, New York.

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

Gauch, H.G and Zobel, R.W., 1996. AMMI analysis of yield trials. In genotype by environment interactions. CPS Press USA. pp: 85-122

Haga, E., Weber, B. and Jansky, S., 2012. Examination of potential measures of vine maturity in potato. *American Journal of Plant Sciences.* 3: 495-505

Hakiza, J.J., Turyamureeba, G., Kakuhenzire, R., Odongo, B., Mwanga, R.M., Kanzikwera, R. and Adipala, E., 2000. Potato and Sweet potato improvement in Uganda: A historical perspective. *African Potato Association Conference Proceedings.* 5: 47-58.

Hasanuzzaman, M., Hakim, M.A., Jannatul, F., Islam, M.M. and Rahman, L., 2012. Combining ability and heritability analysis for yield and yield contributing characters in chilli (*Capsicum annum)* landraces. *Plant Omics Journal* 5: 337-344.

Haydar, A., Alam, M.K., Khokan, E.H., Ara, T., and Khalequzzaman, K.M., 2009. Combining ability and genetic variability studies in potato. *J. Soil. Nature* 3 (2): 1-3.

Hawkes, J.G. 1994. Origin of cultivated potato and species relationships. pp: 3-42.

Hoffler, H. and Ochienge, B.O, 2008. High commodity prices- Who gets the money? *Preliminary findings for World Food Day* 2008. Heirich Boll Foundation.

Johansen, R.H., Miller, J.C., Newsom, D.W. and Fontenot, J.F., 1967. The influence of environment on the specific gravity, plant maturity and vigour of potato progenies. *American Potato Journal*. 14:107-122.

Kachwekano ZARDI, 2011. Technical report. Evaluation of potato clones of population B3C2 for field resistance to late blight (*Phytophthora infestans*), high yields and consumer acceptable qualities in Uganda.

Kakuhenzire, R., Adipala, E. and Olanya, O.M., 2009. Development of decision support tools for integrated management of potato late blight in the highlands of Uganda. PhD. Thesis. Faculty of Agriculture, Makerere University, 175pp.

Kanzikwera, C.R., Tenywa, J.S., Osiru, D.S.O., Adipala, E. and Bhagsari, A.S., 2001. Interactive effect of Nitrogen and Potassium on flowering and berry set in true potato seed mother plants. *African Crop Science Journal,* 9:109-125.

Kooman, P.L. and Rabbinge, R., 1996. An analysis of the relation between dry matter allocation to the tuber and earliness of a potato crop. *Annals of Botany* 77: 235-242

Lynch, D.R., Foroud, N., Kozub, G.C. and Farries, B.C., 1995. The effect of moisture stress at three growth stages on the yield, components of yield and processing quality of eight potato varieties. *American Potato Journal.* 72: 375-388.

Lynch, M. and Walsh, B., 1998. *Genetics and Analysis of Quantitative Traits.* Sinauer Associates Incorporated, Sanderland USA 874pp

Majaliwa, J.G.M., Mukwaya, P. and Isubikalu, P., 2010. Climate change adaptation strategies in the semi-arid region of Uganda. 2nd *Ruforum Biennial meeting* 20th- 24th September. 2010, Entebbe, Uganda. pp: 88-90

Miyashita, K., Tonakamaru, S., Maitani, T. and Kimura, K., 2005. Recoverly responses of photosynthesis, transpiration and stomatal conductance in kidney bean following drought stress. *Journal of Environmental and Experimental Botany* 53: 205-214

Muthoni, J. and Nyamongo, D.O., 2009. A review of constraints to ware Irish potato production in Kenya. *Journal of Horticulture and Forestry* l: 98-102

Muthoni, J., Shimelis, H., Melis, R. and Kabira, J., 2012. Reproduction biology and early generation's selection in conventional potato breeding. *Australian Journal of Crop Science* 6: 488-497.

Muzurczyk, W., Lutomirska, B. and Wierzbicka, A., 2003. Relation between air temperature and length of vegetation period of potato crops. *Agricultural and Forest Meteorology Journal.* 118: 169-172.

Nadarajan, N. and Gunasekaran, M., 2005. *Quantitative Genetics and Biometrical Techniques in Plant Breeding.* Kalyani Publishers, New Delhi India.

Nakitandwe J., 2003. Resistance to late blight and yield stability of sift and population B_3 potato selections in Uganda. Msc. Thesis, Makerere University, Kampala. Nakitandwe J., Adipala, E., El-Bedewy, R., Wagoire, W. and Lemaga, B., 2005. Adaptability of SIFT potato genotypes in different agro ecologies of Uganda. *African Crop Science Journal.* 13: pp: 107-116.

Ntawuruhunga, P.H., Rubaihayo, P.R, Whyte, J.B.A., Dixon, A.G.O. and Osiru, D.S.O., 2001. Additive main effects and multiplicative interaction analysis for storage root yield of cassava genotypes evaluated in Uganda. *African Crop Science Journal*. 9: 591-598.

Ojiambo, P.S., Namanda, S., Olanya, O.M., El-Bedewy, R., Hakiza, J.J., Adipala, E. and Forbes, G., 2001. Impact of Fungicide application and late blight development on potato growth parameters and yield in the tropical highlands of Kenya and Uganda. *African Crop Science Journal*, 9: 225-233.

Ortiz, R. and Golmirzaie, A.M., 2004. Combining ability analysis and correlation between breeding values in true potato seed. *Plant Breeding Journal* 123: 564-567

Panhwar, S.A., Baloch, M.J., Jatoi, W.A., Veesar, N.F. and Majeedano, M.S., 2008. Combining ablity estimates from line x tester mating design in upland cotton. *Proc. Pakistan Acad. Sci.* 45: 69-74.

Poehlman, J.M. and Sleper, D.A., 1995. *Breeding Field Crops.* Forth Edition. pp: 419-433.

Randall, C.R., 1993. *Potato Health Management.* St. Paul, Minn: APS Press. USA.

Rodriguez, M., Rau, D., Papa, R. and Attene, G., 2007. Genotype by environment interactions in barley (*Hordeum vulgare* L.) different responses of landraces, recombinant inbred lines and varieties to Mediterranean environment. pp: 1-17.

Roy, 2000. *Plant Breeding. Analysis and Expectation of Variation*. Narosa Publishing House, New Delhi. pp: 300-304

Ruzukas, A. and Jundulas, J., 2006. Potato breeding for nematode and disease resistance pp: 26-29.

Ruzukas, A., Jankauskiene, Z., Jundulas, J. and Asakaviciute, R., 2009. Research of technical crops (potato and flax) genetic resources in Lithuania. *Agronomy Research* 7: 59-72.

Schafleitner, R., 2008. Hunting for drought tolerance genes in ancient Andean landraces. *Public release on 28th.June.2008. American Society of Plant Biologists.*

Sharma, V.K., Semwal, C.S. and Uniyal, S.P., 2010. Genetic variability and character association analysis in bell pepper (*Capsicum annum* L.). *J. Hort. For.*, 2: 58-65.

Shattuck, V.I., Christie, B. and Corso, C., 1993. Principles of Griffing's combining ability analysis. *Genetica* 90: 73-77.

Singh, R.K. and Chaudhary, B.D., 2007. *Biometrical Methods in Quantitative Genetic Analysis*. Kalyani publishers, New Delhi, India.

Sleper, D.A. and Poehlman, J.M., 2006. *Breeding Field Crops,* 5th edition. Blackwell publishing professional, 2121 state avenue, Ames, Iowa.

Stoller, J., 2004. Crop Health Guide, Maximizing plant genetic expression. pp: 3-16

Varela, M., J. Crossa, J. Rane, A. Kumar Joshi and R. Trethowan, 2006. Analysis of a three-way interaction including multi-attributes. *Australian Journal of Agricultural Research* 56:1 185-1193.

Virginia, A., Jordi B., J. Martínez-García, E. Monte, M. Rodríguez-Falcon, E. Russo and S. Prat, 2001. Regulation of potato tuberization by day length and gibberellins. *International Journal of Developmental Biology,* 45: 37–38.

Weikai , Y. and Manjit S. K., 2002. *GGE bi-plot Analysis. A Graphical Tool for Breeders, Genetists and Agronomists.* CRS press New York, USA.

Wolfgang, J., Mwanga, R., Andrade, M. and Espinoza, J., 2009. Selection methods. Breeding clonally propagated crops. Pp 275-322. In Ceccarelli, S., Guimaraes, E.P. and Weltzien, E. (edition). Plant breeding and farmer participation, FAO, Rome.

Woolfe, J.A., 1987. The potato in the human diet. Cambridge University Press, New York. pp: 231.

Zhao, F. and Shizhong, X., 2012. Genotype by environment interaction of quantitative traits: A case study in barley. *G3 Journal.* 2: 779-788.

Appendix

Appendix 1: Skeletal ANOVA for combining abilities

Source of variation	Df	Ss	Ms	f-cal	f-	Exp.ms	Variance component
Total							
Crosses	24					∂^2e + ∂^2c	
GCAf	4					∂^2e + 5∂^2GCAf	
GCAm	4					∂^2 e + 5GCAm	
SCA	16					∂^2 e + ∂^2SCA	
Error	24					∂^2 e	

Appendix 2: Analysis of variance of growth parameters for one season across 3 environments each with 2 replications evaluated during the second season of 2011

Source of variation	d.f	MS Bud initiation	MS Tuber initiation	MS 50%Anthesis	MS Anthesis duration	MS Senescence
Environment	2	269.15	66.92	1019.84	2152.55	888.5
R/ENV	3	0.24	0.52	0.02	1.98	0.5
GENOTYPE	10	11.61^{ns}	45.57^{ns}	25.81^{ns}	3247.89^{***}	593.5^{***}
G X E	20	8.12	23.52	14.45	670.00	32.7
Pooled error	30	0.14	0.58	0.02	0.68	0.1
Total	65					

*, **, and *** represent significance level at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively, ns= non-significant

Appendix 3: Analysis of variance of yield parameters for one season across 3 environments each with 2 replications evaluated during the second season of 2011

Source of variation	df	MS Average tuber weight/g	MS Number of tubers per plant	MS Yield /tha^{-1}
Environment	2	1545.9	109.5	414.9
R/ENV	3	437.5	2.0	2.5
GENOTYPE	10	4435.9***	12.5^{ns}	296.1***
G x E	20	739.1	5.9	58.1
Pooled error	30	166.6	2.6	17.0
Total	65			

*, **, and *** represent significance level at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively, ns= non-significant

Appendix 4: Skeleton ANOVA for 2 seasons across 3 environments each with 2 replications

Source of variation	Df	Ms	f-cal	Exp. Ms	Var. components
Env.	5	Msenv.	MsE/MsR/E	∂^2e + 11∂^2R/E + 22∂^2 E	
Location	2	MsL	MsL/ msLS	∂^2e + 22∂^2LxS + 44∂^2 L	
Season	1	MsS	MsL/ msLS	∂^2e + 22∂^2LxS + 66∂^2 S	
L x S	2	msLS	msLS/ mse	∂^2e + 11∂^2R/E + 22∂^2 E	
Rep/env	6	MsR/E	ms(R/E)/ mse	∂^2e + 11∂^2R/E	
Variety	10	msG	MsG/ msGE	∂^2 e + 2∂^2GxE + 12∂^2G	
G x E	50	msGxE	MsGE/ mse	∂^2 e + 2∂^2GxE	
G x L	20	MsGxL	msGL/msGLS	∂^2 e + 2∂^2GLS + 4∂^2GL	
G x S	10	MsGxS	msGS/msGLS	∂^2 e + 2∂^2GLS + 6∂^2GS	
G x L x S	20	MsGxLxS	MsGLS/ mse	∂^2 e + 2∂^2GLS	
Error	60	MSErr.		∂^2 e	
Total	131				

Appendix 5: Mean squares for percentage tuber dry matter for selected potato genotypes evaluated for one season across 3 environments each with 3 replications during the first season of 2012

Source of variation	d.f.	Kalengyere m.s.	Kachwekano m.s.	Mbarara m.s.
Rep	2	29.8	0.71	1.0
Genotype	10	20.2**	10.9+	33.2**
Residual	20	5.0	5.46	9.2
Total	32			

*, and ** represent significance level at $P \leq 0.05$, $P \leq 0.01$

Appendix 6: Analysis of variance for across locations for tuber dry matter content for selected potato genotypes evaluated for one season across 3 locations each with 3 replications during the first season of 2012

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Location	2	41	20.3	1.9	0.15
Location/Rep	6	63	10.5	1.6	0.16
Genotype	10	474	47.4***	5.6	<.001
G X E	20	170	8.5ns	1.3	0.21
Residual	60	392	6.5		
Total	98	1140			

*, **, and *** represent significance level at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$ respectively, ns= non-significant

Appendix 7: Weather characteristics at Kalengyere, Kachwekano and Mbarara during the second rainy season of 2011; September-December, 2011

	KALENGYERE 2011B					KACHWEKANO 2011B					MBARARA 2011B				
	Aug	**Sep**	**Oct**	**Nov**	**Dec**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
RF (mm)	19.7	192.1	137.3	52.4	127.9	103.9	71.6	77.3	161.3	54.7	177.7	131	110.5	151	103.8
Max(^{0}C)	21.8	20.0	20.4	20.9	21.0	24.7	23.7	24.0	23.5	23.8	27.1	26.2	26.4	25.9	26.2
Min(^{0}C)	11.8	10.7	10.8	11.1	10.5	11.3	12.2	12.0	12.8	13.2	16.0	15.6	15.7	16.0	16.1
Avg(^{0}C)	16.8	15.4	15.6	16.0	15.7	18.0	18.0	18.0	18.2	18.5	21.6	20.9	21.1	21.0	21.1
RH (%)	86.9	87.4	87.7	84.3	84.2	88.3	77.5	84.2	89.8	90.1	70.1	74.7	74.4	70.5	69.2

RF represents total rainfall, Max is mean maximum temperature, Min is mean minimum temperature, Avg is average temperature and RH is relative humidity.

Source: Kalengyere meteorology station and Ministry of water and environment, department of meteorology, Kampala.

Appendix 8: Weather characteristics at Kalengyere, Kachwekano and Mbarara during the first rainy season of 2012; March-June, 2012

	KALENGYERE 2012A					KACHWEKANO 2012A					MBARARA 2012A				
	Feb	**Mar**	**Apr**	**May**	**Jun**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Feb**	**Mar**	**Apr**	**May**	**Jun**
RF (mm)	95.9	114.1	247.6	184.6	25.1	59.9	110.6	217.0	147.0	14.4	42.4	44.6	217.7	132.2	21.7
Max(^{0}C)	22.9	21.1	20.1	20.7	21.9	10.6	11.6	13.4	12.9	11.7	15.5	16.1	15.4	15.1	15.0
Min(^{0}C)	11.5	11.1	10.6	11.0	11.2	26.3	26.0	22.7	22.7	23.2	29.7	29.1	25.9	25.8	26.8
Avg(^{0}C)	17.2	16.1	15.3	15.8	16.5	18.4	18.8	18.0	17.8	17.5	22.6	22.6	20.6	20.5	20.9
RH (%)	84.9	83.4	84.2	83.4	85.4	75.3	79.9	81.5	78.6	74.0	69.4	70.0	74.0	72.2	58.8

RF represents total rainfall, Max is mean maximum temperature, Min is mean minimum temperature, Avg is average temperature and RH is relative humidity.

Source: Kalengyere meteorology station and Ministry of water and environment, department of meteorology, Kampala