Development of high yielding and early maturing potato (*Solanum tuberosum* L.) genotypes with resistance to *Phytophthora infestans* in Uganda

by

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THESIS SUMMARY

Late blight, caused by *Phytophthora infestans,* is a major disease limiting potato yield and productivity in Uganda, especially in the highlands, and accounts for up to 70% of the yield losses and sometimes-even results in a total crop destruction. Breeding for host plant resistance is a sustainable approach to late blight control and management in Uganda, as other measures are expensive, ineffective or not easy to deploy. Additionally, the development of early maturing varieties is imperative to address the changing weather patterns and crop adaptation in different agro-ecologies. The overall goal of this study was to contribute to food security in Uganda through developing high yielding and early maturing potato genotypes that are resistant to the late blight disease. The specific objectives of the study were to: (1) document farmers' knowledge of preferred traits in potential new varieties and their perspectives on late blight prevalence and severity, (2) phenotypically characterize potato genotypes in Uganda, (3) assess the genetic diversity among potato genotypes using SSR markers, (4) determine the yield response of potato genotypes to late blight disease in the tropical highlands of Uganda, (5) determine the combining ability effects for yield, yield related traits, resistance to *Phytophthora infestans* and early maturity in potato genotypes.

A participatory rural appraisal (PRA) involving 577 individual farmers showed that farmers' practices in potato production and disease management varied greatly. Most of the respondents used farm saved seed, while only 2% from Eastern and South-western Uganda obtained seed from research stations. The major pests were aphids and cutworms, while late blight and bacterial wilt were the prominent diseases. Commonly grown varieties were Rwangume and Victoria. The most preferred attributes in new varieties were high yield, resistance to late blight, early maturity and marketability, in that order. Late blight has been experienced by 98% of the farmers and 96% of these reported to have used fungicides to manage the disease.

Phenotypic characterization of 48 potato genotypes in Kachwekano and Karengyere research stations showed significant sites differences ($P < 0.01$) among the genotype performances for all measured parameters. The cluster analysis using 15 phenotypic traits grouped genotypes into three major clusters and the similarity distance ranged from 0.5 to 1.0. The mean tuber yield for the two sites was 29.8 t ha^{-1} and tuber yield was higher in Kachwekano than Karengyere. The best yielding genotypes were 396038.105 (54.5 t ha^{-1}) and NAKPOT5 (50.9 t ha^{-1}). Fifty two percent of the genotypes were high yielding (30 t ha^{-1} and above) and the most stable genotypes in terms of tuber yield were Rutuku, 395112.32, 395017.14 and 393220.54.

Forty-eight genotypes, including advanced clones from population B3C2 of the International Potato Centre, commercial and farmers' varieties, were evaluated under two environments for two seasons to determine their reaction to late blight in an 8 x 6 alpha lattice design with three replications. Genotypes showed significant differences in yield and resistance to blight. The most resistant genotypes were 395077.12 and 392657.8 with disease severity of 12% and 14%, respectively. The mean tuber yield under late blight infection was 19.8 t ha^{-1} and the best yielding genotype across sites was 395112.32 (35.6 t ha^{-1}). The following genotypes; 395112.32, 391919.3, 393220.54. 393077.54, 396038.107. 392657.8, Kinigi, 395014.17, NKRN59.58, NKRK19.17 and 395011.2 had high yield and high to medium resistance to *Phytophthora infestans* and thus were identified as promising parents for subsequent crosses.

In addition, 20 selected tetraploid potato genotypes were characterized using 16 SSR markers to determine the pattern and level of genetic diversity amongst them to identify suitable parents for breeding purposes. The microsatellites showed considerable variation among genotypes and the 16 primer pairs amplified 64 alleles. The number of polymorphic alleles per locus ranged from 2 to 8, polymorphic information content (PIC) values from 0.0948 to 0.7832, while heterozygosity values ranged from 0.0997 to 0.805. A dendrogram was constructed using UPGMA clustering algorithm based on SSR data matrices, and this grouped the potato clones into three major clusters with a genetic distance of 1.0 to 5.7.

Combining ability effects for resistance to late blight, yield and yield related traits were determined using 12 potato genotypes were crossed in a North Carolina mating design II (NCD II) in two sets of six parents each to generate 18 families. Both additive and non-additive gene action controlled yield and late blight resistance in potato. However, additive gene action was predominant over non-additive for total tuber weight and late blight resistance. Broad-sense heritability estimates were 0.78 for total tuber weight and 0.68 for relative area under disease progress curve (rAUDPC). Parents Kinigi, 392657.8, 396034.103, 396038.107, 395011.2, NKRK19.17, NKRN59.58 and 395017.14 had good general combining ability (GCA) effects for both late blight disease resistance and yield related traits. Crosses 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest specific combining ability (SCA) effects for all the yield related traits, while families Kinigi x NKRK19.17and 392657.8 x NKRN59.41 had the lowest SCA effects for rAUDPC. This study showed some evidence of maternal effects for rAUDPC (1.45) and ATW (1.56), although these were not significant at $P \leq 0.05$. The selected parents and families were the best candidates to develop improved potato varieties that combined both high yield and resistance to late blight. These will be subjected to further clonal evaluation before possible release.

Combining ability effects for yield and yield related traits and earliness were also determined in a different set of 12 genotypes divided into two sets of six parents each and crossed in a North Carolina

mating design II (NCD II) mating scheme to generate 18 families. Additive gene action predominantly controlled days to flowering, total number of tubers, total tuber weight and average tuber weight. Broad-sense heritability estimates were 0.70 for total tuber weight and 0.78 for days to flowering. Mean total tuber yield was 9.3 t ha^{-1}, while the average number of days to flowering was 54. Parents Rwangume, 396038.107, 395011.2 and NKRK19.17 had desirable GCA effects for the number of days to flowering. For yield and related traits, parents 396038.107, 393077.54, Rwangume, NKRK19.17, Kimuri, and 392657.8 had desirable GCA effects. The selected parents had desirable attributes for high yield and early maturity and families will be subjected to further clonal evaluation and selection.

Overall, this study documented the potato production constraints, farmers' perceptions on late blight management and varietal attributes. It also identified potato genotypes with desirable combining ability for tuber yield, late blight resistance and early maturity. The nature of gene action controlling yield, late blight disease resistance and early maturity was also determined. The predominant control of additive genetic effects on most of the tested traits implies that advances in breeding can be made through population improvement methods and selection. Nevertheless, for traits with significant non-additive genetic effects, a hybridization breeding strategy could be employed to develop hybrids. In general, clones with these traits can be selected and evaluated further for eventual release as varieties in Uganda.

DECLARATION

I, Namugga Prossy, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original work.

2. This thesis has not been submitted for any degree or examination at any other university.

3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a. Their words have been re-written but the general information attributed to them has been referenced.

b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.

5. This thesis does not contain text, graphics or tables copied and pasted from the internet, unless specifically acknowledged, and the source being detailed in the thesis and in the reference section.

Signed……  ……

Namugga Prossy

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

……  ……

Dr. Julia Sibiya (Supervisor)

…….

Prof. Rob Melis (Supervisor)

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DEDICATION

This thesis is dedicated

To my Heavenly Father from whom all good things come

To Jesus Christ and to the Holy Spirit for teaching me all things

To my mother for giving all and siblings for their enduring love

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Introduction to Thesis

Importance of Potato

On a world scale, potato (*Solanum tuberosum L.*) is the fourth most important staple crop after maize, rice and wheat with more than 320 million tons being produced from 20 million hectares (International Potato Center (CIP), 2016). In addition, it represents about 43% of the global output of root and tuber crops, followed by cassava with 30% and sweet potato with 17% (Food and Agricultural Organisation (FAO), 2008). It is important both for human consumption and in the starch industry. In addition to its importance as a food crop, potato is an essential source of income and employment in developing countries, particularly in the densely populated tropical highlands (CIP, 2011). The potato crop matures in a relatively short time depending on the variety, it is adaptable to different agro-ecologies, gives high yields, and responds highly to agro-input use (Ferris et al., 2001). Thus, a high potential crop can solve the food needs of low-income people in both urban and rural areas.

Potato production in Uganda

Uganda is the ninth largest producer of potato in Africa with an annual production of 774 600 tons harvested from about 106 000 hectares (FAO Statistics (FAOSTAT), 2016). The crop is grown by about 300 000 smallholder households in Uganda (Uganda Bureau of Statistics (UBOS), 2016). The major production areas are the highlands of South-western Uganda, comprising of Kabale, Kanungu and Kisoro districts, which account for 60% of total national production. The other potato production areas are Kapchorwa, Sironko, Bulambuli and Bududa districts on the slopes of Mt Elgon in eastern Uganda and Nebbi district in north-western Uganda. Its cultivation has spread to non-traditional areas in central Uganda, especially Mubende, Rakai and Masaka districts (Figure 0-1). In all these districts, potato is both a staple food and a major source of household income, with more women and children involved in the field production activities. There is also a steadily growing urban domestic market for potato varieties with processing qualities (Ferris et al., 2001). Currently, the most widely grown varieties for food and processing are Victoria, Kinigi, Rutuku, Rwangume and Kachpot 1.

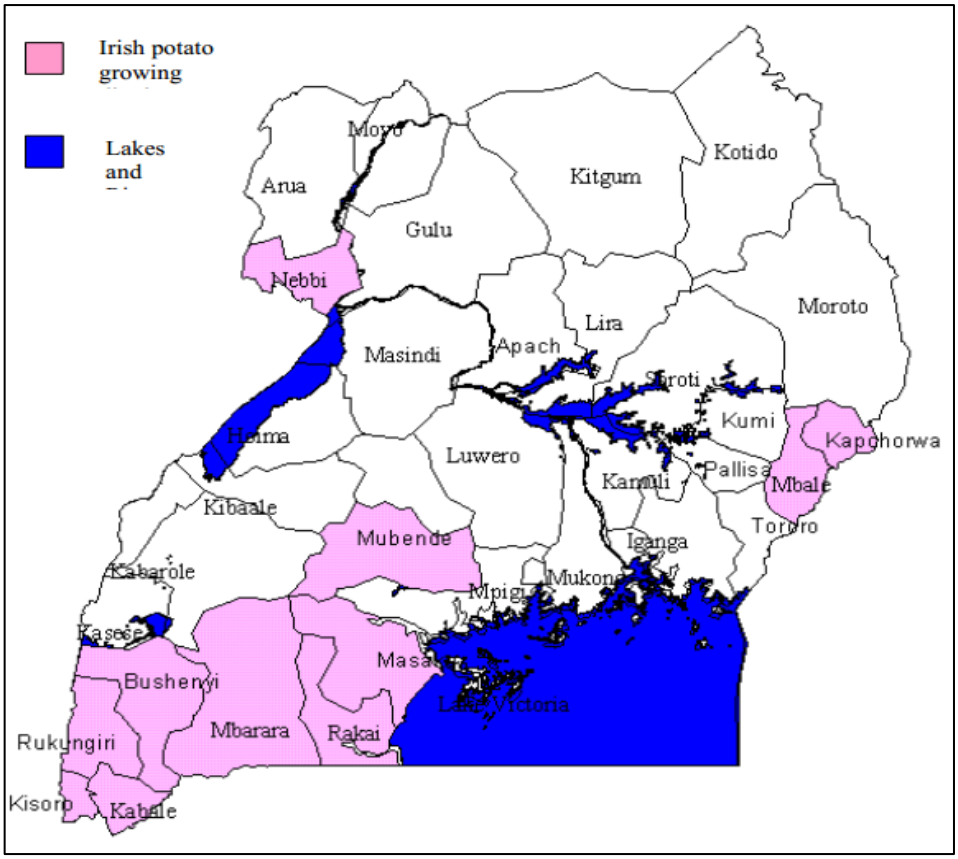

Figure 0-1: Major potato growing areas in Uganda

Source: Ferris et al. (2001)

Potato production constraints

Potato yields in Uganda have remained as low as 4.8 t ha^{-1} (FAOSTAT, 2016) against a potential of about 25 t ha^{-1} which can be achieved under good management and when suitable varieties are deployed. These low yields have been attributed to a number of confounding factors such as socio-economic constraints, poorly adapted and adopted varieties, abiotic and biotic stresses. Some of these factors are aggravated by the low income of farmers, which limits them from using productivity enhancement inputs (FAO, 2008). The abiotic agents limiting potato production include low soil fertility, inadequate moisture supply, stress due to high temperatures and drought, and erratic and sometimes violent rainfall (Gildemacher et al., 2009). Diseases are the major limiting factor and these include; late blight caused by *Phytophthora infestans* (Mont.) de Bary, bacterial wilt (BW) (*Ralstonia solanacearum*) (Yabuuchi et al., 1995) and viruses (Muhinyuza et al., 2012).

Socio-economic constraints

Several socio-economic constraints affect potato production in Uganda. These include seasonality in production, which has a major effect on the supply and demand, resulting in rapid and significant fluctuations of the price on the market. Most farmers produce potatoes twice a year due to the bimodal

rainfall patterns in most potato growing areas of Uganda. However, off-season production is limited to areas where irrigation is possible and in Uganda, this is practiced in wetlands (Gildemacher et al., 2009). There is also an inadequate supply of clean seed tubers and as a result, farmers almost solely depend on informal seed tuber sources (Kaguongo et al., 2008). Furthermore, the high cost of inputs, especially seed tubers, fungicides and fertilizers, greatly limits potato production (Aheisibwe et al., 2015). Poor marketing channels also affect potato production. As a result, most farmers sell potatoes directly from the field without storing, which leads to low prices and exploitation by traders and brokers (Common Fund for Commodity (CFC), 2011). Establishing a formal seed potato system is crucial in addressing some of the above constraints.

Abiotic constraints

The major abiotic stress limiting potato production is moisture stress (Reddy et al., 2004). It prevents the crop from realizing its full genetic potential (Rodríguez et al., 2005) and results in reduced yield and tuber quality in potato (Hassanpanah et al., 2008). Drought stress severely limits plant production and performance, in addition to impairing growth and development more than any other environmental factor (Shao et al., 2009). Drought is becoming a big threat in the face of the changing climate. Characterization of potato genotypes for drought tolerance in Uganda showed a yield reduction rate ranging from 50 -70% among three commercial varieties (Victoria, Uganda 11 and Kachpot 1) (Kesiime, 2013). Declining soil fertility is another major constraint in most potato growing areas and is aggravated by the continuous cultivation without adequate replenishment of the mined nutrients (Muthoni and Nyamongo, 2009). In Uganda, this is complicated by small land sizes, where farmers continuously plant crops on the same land, and soil erosion in the hilly areas. The cost of fertilizers is often prohibitive to most farmers.

Biotic constraints

Important diseases are bacterial wilt, viral and late blight. Bacterial wilt is an important yield-reducing biotic factor worldwide after late blight (Mwangi et al., 2008). The pathogen persists in the soil for several years and has no established chemical control. The disease is increasingly threatening potato production with occasional losses of 100% in the event of its appearance in the early stages of crop growth (Lemaga, 1999). Bacterial wilt infestation has been reported at both low and high altitudes with more damage in warmer potato growing areas. The spread of BW is accelerated by the unavailability of quality disease –free seed tubers as most farmers recycle their own seed tubers (Kinyua et al., 2001). Problems associated with BW are expected to increase because of the absence or shortening of rotations. The disease survives in the soil for several seasons, and an essential component of bacterial wilt management is denying the bacteria a host by not growing potatoes or any other host crop for several seasons, combined with a strict removal of volunteer potato plants (Gildemacher et

al., 2009). Management of BW in Uganda is through the use of clean planting materials, recommended crop rotations with non-host plants and removal of volunteer plants of host species (Kakuhenzire et al., 2013) However, most farmers use home saved seed tubers and currently most potato varieties grown are only tolerant to BW; there is no registered resistant variety at present.

In addition, several viral diseases occur in potato and among them the potato virus S (PVS), X (PVX), Y (PVY), A (PVA), M (PVM) and the leaf roll virus (PLRV) are economically important (Palukaitis, 2012). Yield losses vary greatly from 10-80% depending on the virus (Naik and Karihaloo, 2007). Viruses reduce crop yields through seed tuber degeneration and affect the quality of potato (Wasswa, 2013). Three potato viruses, namely PVS, PLRV and PVS, have been reported to occur in Uganda (Kakuhenzire et al., 2000). The incidence of potato viruses in Uganda has been amplified by the informal seed system, whereby seed tubers are reused for generations without renewal (Wagoire et al., 2005).

Late blight, on the other hand, is the major disease limiting potato yield and productivity especially in the highlands. The disease accounts for up to 70% yield losses in most growing regions (Sedláková et al., 2011). It causes both foliar and tuber decay (Acquaah, 2012). Tubers can become infected when the disease moves down the lower stem, below ground, and through the stolon. Potato tubers can also become infected when late blight spores from infected leaves and stems are washed into the soil via cracks or crevices in the hill and come in contact with tubers. Late blight is the major reason for the use of fungicides on potatoes in Uganda (Low, 1997). As much as the disease management can be through the use of fungicides, most small-scale farmers cannot afford these because both contact and systemic fungicides are expensive. Additionally, fungicide application is by hand and farmers rarely use protective clothing, thus posing health risks and diverse environmental hazards (Kromann et al., 2009; Forbes, 2012). Therefore, breeding for host resistance is a sustainable approach to late blight control and management in Uganda.

Varieties currently grown by farmers

In Uganda, the National Potato Research Program has released many potato varieties with resistance to *Phytophthora infestans* over the years. However, most of these varieties have not been adopted by farmers who continue to plant their own varieties which they have maintained for a long time (over 30 years) and have farmer preferred attributes (Witcombe, 2009). Most of these potato varieties are late maturing with physiological maturity attainable after 100 days from planting and a yield potential of >15 t ha^{-1}. Late maturing varieties occupy the limited land for a longer time of a season and are associated with long dormancy periods. These varieties were selected for the highlands (>2000 meters above sea level (masl)), and are therefore well adapted and produce good yields of tubers with an excellent culinary qualities. Attempts to grow these varieties at low and mid-altitudes (<1700

masl) have resulted in a loss of tuber quality and low yields (Hassanpanah et al., 2008). Early maturing varieties with wide adaptation would thus allow all year round cultivation of potato with favourable rotation periods and improved yields in the face of climate change. This is especially advantageous for smallholder farmers in areas with land shortage who depend entirely on potato for both food and income security. Additionally, these varieties could be grown in low-lying areas given that in Uganda the substantial area of potato production is expanding to the lower altitudes areas where the rainfall season is short lived.

Research rationale

Presently, there is little or no information available on the performance and variability of potato germplasm in Uganda with regard to late blight resistance and early maturity. Such information and knowledge is vital for a successful breeding program and will aid in developing varieties that are customized to meet the demands of different end users. Detailed information on the available potato germplasm is needed and genetic variation present could be exploited in the crop improvement program.

Since most of the varieties currently grown by farmers are late maturing, earliness would be a key factor in potato production and productivity, especially in the face of a changing climate. This is supported by the fact that rainfall patterns are changing and temperatures are gradually increasing. Consequently, varietal performance in the traditional highlands is likely to decline with eventual failure in mid- and low-altitudes (Majaliwa et al., 2010). Early maturing varieties would also release land for other farming activities and/or crops, especially in the highlands were land fragmentation and shortage is a threat to agricultural production and farm income. As a result, it is imperative to breed and develop potato varieties with wide adaptability, which are able to mature within short rainfall cycles, and give high yields even at elevated temperatures. This will promote a sustainable potato production to meet the growing demand. However, earliness in potato has not received sufficient attention in Uganda and elsewhere, as there seems to be scanty information regarding the subject. It is against this background, that this study was conducted to obtain information on the inheritance of earliness.

High levels of resistance to potato late blight were found in wild species *Solanum demissum* (Wastie 1991). This resistance, denoted as qualitative, race-specific or R gene was conferred by single genes and hence was easy to incorporate into new varieties. However, due to the changing pathogen population this resistance has often been rendered ineffective in currently grown varieties. The failure of the *S. demissum* resistance to provide protection in farmers' fields warrants breeding for resistance which is referred to as called horizontal, field, or quantitative resistance (Bradshaw et al. 1995; Forbes 2012). Horizontal resistance, which is based on minor genes, would be more durable and effective against various pathogenic strains of *Phytophthora infestans* (Landeo et al., 1999; Kumar et al., 2007).

There is also a need to improve varieties for resistance, while maintaining the desired attributes of economic importance, such as early bulking, high tuber yield and dry matter content (Fry and Goodwin, 1997; Landeo et al., 1999). Continuous cultivation of susceptible varieties will increase the disease inoculum making potato growing practically impossible, especially for small-scale farmers who cannot afford the use for fungicides (Forbes, 2012; Byarugaba et al., 2013). As a result, potato varieties with horizontal resistance to *Phytophthora infestans* are required to counteract the effects of the highly evolving pathogen population. Additionally, it is crucial to investigate the nature of gene action controlling resistance to *Phytophthora infestans* and earliness in potato in the germplasm used for the current study. In order to select suitable parents, germplasm characterisation was done. Since variety adoption is accelerated by developing varieties with farmer preferred attributes, a participatory rural appraisal (PRA) was conducted to establish knowledge of farmers' preferred traits in potential potato varieties and farmers' perspectives on late blight prevalence and severity.

Overall goal

The overall goal of the study was to develop early maturing potato genotypes that are resistant to late blight disease, and with wide adaptability and desirable farmer and consumer traits.

Specific objectives

The specific objectives of the study were:

1) To document farmers' knowledge of preferred traits in potential new varieties and farmers' perspectives on late blight prevalence and severity.

2) To phenotypically characterize and assess the genetic diversity among potato genotypes using SSR markers potato genotypes in Uganda.

3) To determine the yield response of potato genotypes to late blight disease in the tropical highlands of Uganda.

4) To determine the combining ability effects for yield, yield related traits and resistance to late blight disease of potato genotypes.

5) To determine the combining ability effects for yield, yield related traits and early maturity among potato genotypes in Uganda.

Research hypotheses

The following research hypotheses were tested:

1) Farmers are aware of major constraints to potato production and have special attributes in potato varieties developed.

2) Genetic variation exists among the available potato germplasm that can be improved by selection for yield, earliness and late blight disease resistance.

3) Changes in the environment considerably affect resistance to late blight disease and yield in potato.

4) Late blight disease resistance, tuber yield and related traits in potato is largely controlled by additive gene action.
5) Earliness, tuber yield and related traits is controlled by additive gene action and can be improved by selection among progenies.

Thesis outline

This thesis consists of seven distinct chapters in accordance with the number of activities related to the above mentioned objectives. Chapters 2-7 are written as discrete research papers, each following the format of a stand-alone research paper (whether or not the chapter has already been published). This is the dominant thesis format adopted by the University of KwaZulu-Natal. As such, there is some unavoidable repetition of references and some introductory information between chapters. The referencing system used in the chapters of this thesis is based on the Crop Science Journal. Chapter 2 has been published in the Australian Journal of Crop Science; Chapter 3 has been published in the South African Journal of Plant and Soil, Chapter 4 has been published in the American Journal of Potato Research while Chapter 5 has been published in the Journal of Agricultural Science. The structure of the thesis is as indicated below:

Chapter	Title
	Thesis introduction
1	Literature Review
2	Participatory assessment of potato farming systems, production constraints and cultivar preferences in Uganda
3	Phenotypic characterisation of potato genotypes in Uganda
4	Response of potato genotypes to late blight in the tropical highlands of Uganda
5	Assessment of genetic diversity among potato genotypes in Uganda using SSR markers
6	Combining ability analysis of tuber yield and related traits and late blight disease resistance in potato
7	Combining ability analysis of tuber yield and related traits and earliness in potato
8	An overview of research findings

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Chapter 1: Literature Review

1.1 Introduction

The literature review covers the most critical aspects relevant to this research with emphasis on breeding for resistance to late blight, earliness and improved yield. It provides current knowledge on potato breeding, the origin, distribution and genetics of the crop, plus information on the use of wild relatives in the production of new varieties. This is followed by a summary of the literature on participatory research approach in cultivar development and breeding for earliness in potato in the face of climate change. Recent information on breeding for resistance to late blight, describing the pathogen, disease distribution and management, is reviewed. Early breeding efforts, both conventional and by the use of molecular markers are elaborated in this chapter, in addition to the search for resistance to late blight. Breeding for improved yield as a major breeding objective is highlighted, with parental selection being key, based on the combining abilities and analysis of genetic diversity.

1.1.1 Origin and distribution of potato

Potato (*Solanum tuberosum* L.) belongs to the Solanaceae or nightshade family and to the large and diversified genus *Solanum*. The Solanaceous family also includes plants such as tomato, eggplant, tobacco, and chili peppers (Ashkenazi et al., 2001; Hyps and Schafleitner, 2008). The genus *Solanum* contains approximately 2000 species, including over 150 tuber-bearing species, which form a polyploidy series ranging from diploids to hexaploids, with 75% of them being diploid (Poehlman and Sleper, 1995). Potato occupies a wide eco-geographical range and is unique among the major world food crops in producing stolons (underground stems), which under suitable environmental conditions swell to form tubers (Hijmans, 2001). It is native to the Andes Mountains in Chile, Peru and Bolivia in South America, and has been cultivated for about 2400 years (Weisser, 2010). It was later introduced into Europe in the mid-16thcentury, becoming such an important food source that a failure in the crop caused by blight in Ireland triggered a famine (Hyps and Schafleitner, 2008). Potato later spread throughout the world including to the warm tropics. In Africa, the crop was introduced by colonialists (Hakiza et al., 2000). It was introduced in Uganda towards the beginning of the 1900s as a back garden vegetable. By 1940, the potato was already being grown in the highlands of Kigezi, Toro and on the slopes of Mt. Elgon in Bugisu and Sebei (Hakiza et al., 2000).

1.1.2 Genetics of potato

Potato is an autotetraploid (2*n*=4*x*=48, endosperm balance number (4EBN)) and there can be four different alleles at a locus (Acquaah, 2012). The tetraploid nature of cultivated potato makes heterozygosity and epistasis vital in the selection of breeding procedures. This can be exploited to

improve desirable characteristics (Sleper and Poehlman, 2006). Intralocus and epistatic gene interactions occur and can be exploited by employing appropriate breeding methods (Acquaah, 2012). Asexually propagated species such as potatoes have evolved taking advantage of non-additive gene action. In addition, increased heterozygosity leads to increased heterosis. The level of heterozygosity is influenced by how different the four alleles are within a locus. The more diverse the alleles are within a locus, the higher the heterozygosity and the greater the number of increased interlocus interactions.

1.2 Participatory research approach

According to Bänziger and Cooper (2001), both poor acceptance of improved varieties by farmers, and lack of breeding progress in the performance of adopted varieties under low input conditions, are the probable causes of low productivity gains in low input target locations. It was observed that participatory variety selection (PVS) may improve the adoption of varieties and boost productivity (Joshi and Witcombe, 1996). To accelerate variety adoption, farmer preferred qualities must be taken into consideration (Muthoni et al., 2013). In participatory plant breeding (PPB), the preferences of the end-users and production environments are identified through a participatory rural appraisal (PRA) (Witcombe et al., 2005). Understanding both farmers' needs and the target environment, creates a favourable atmosphere where both groups can exchange ideas and work towards a common goal (Muthoni et al., 2013).

Participatory methods of cultivar development consider the value of farmers' indigenous knowledge, innovations and preferences. This was demonstrated during the farmer field school at the International Potato Centre (CIP) in Peru (Ortiz et al., 2008). Substantial differences in field selections of breeding lines between breeders and farmers were established in the studies by several authors (Ceccarelli et al., 2001; Sperling et al., 2001; Ceccarelli and Grando, 2007). The importance and efficiency of decentralized participatory selection in identifying promising and high yielding entries at the target production environments has been demonstrated (Muhinyuza et al., 2012). Thus, under a participatory approach, farmers provide information on plant types, varietal preferences and or desired attributes (Sperling et al., 2001). This, therefore, assists in the adoption of the new improved varieties by the farmers.

1.3 Assessment of genetic diversity

Knowledge of genetic relationships and crop diversity enables logical organization of variable germplasm in gene banks and aids in the selection of parents in a breeding program (Muthoni et al., 2014) and paves a way to genetic gains (Sun et al., 2003). Additionally, genetic characterization is essential for cultivar identification and protection as well as to guarantee intellectual property rights and trademark (Coombs et al., 2004). In potato, information on genetic diversity is used in co-ancestry or pedigree studies to avoid closely related parents and hence inbreeding depression (Muthoni et al., 2014). To achieve this, molecular markers have been used in genetic studies because of their high

resolution and reliability in the identification of varieties and genetic characterization of potato (Rocha et al., 2010).

1.3.1 Assessment of genetic diversity using phenotypic traits

Morphological characterization is the first step in description and classification of genetic resources (Arslanoglu et al., 2011). Phenotypic characterisation in potato involves the assessment of variations in flower, leaf and tuber characteristics. It has been used for several purposes including identification of duplicates, genetic diversity pattern and correlation with characteristics of agronomic importance (Fekadu and Zelleke, 2013). Field phenotyping is usually used to determine genetic variation among genotypes (Yoshida 2004). Phenotypic markers reveal crop ideotypes, which are comparatively cheap and easy to use, depending on prior knowledge of such traits and their expression (Elameen et al. 2011). However, phenotypic traits are highly affected by environmental factors or the developmental stage of the plant (Elameen et al. 2011). Potato is a clonally propagated crop that exhibits a high degree of incompatibility and in breeding depression (Muthoni et al., 2012). This makes parental selection vital if breeding progress is to be made (Hirut, 2015). It is also imperative that genotypes that are superior in terms of genetic diversity and agronomical properties are selected for crop improvement studies (Pandey et al., 2005; Sandhu and Gopal, 2006).

1.3.2 Assessment of genetic diversity using molecular markers

Breeders commonly complement phenotypic information with a genotypic assessment of diversity using molecular markers to capture allelic diversity in a smaller core set of parents. They can also use genetic distance based on molecular markers to complement co-ancestry/pedigree analysis to avoid closely related parents and hence inbreeding depression and to ensure genetic variation for continued progress. Molecular markers have been used in potato for construction of genetic linkage maps (Bonierbale et al., 1994), trait tagging (Bryan et al., 2002), fingerprinting analysis (Milbourne et al., 1997; Norero et al., 2004), phylogeny studies (Debener et al., 1990; Raker and Spooner, 2002), and characterization of accessions from germplasm banks (Gebhardt et al., 2004; Ghislain etal., 2006). Molecular markers have been identified for resistance against late blight (Colton et al., 2006), nematodes (Zhang et al., 2007) and viruses (Gebhardt et al., 2006) in potatoes.

Among other markers, random amplified polymorphic DNA (RAPDs) markers have been used to detect polymorphism. Simple sequence repeats (SSR) markers or microsatellites have also been used for high reproducibility and provide more genetic information. Both markers have been used in the molecular characterization of potato varieties (Rocha et al., 2010). Marker studies have resulted in the development of a new potato genetic identity (PGI) kit based on 24 SSR markers with two markers for each of the 12 linkage groups of potato and separated by at least 10 cM. The kit provides high locus-specific polymorphic information content and high quality of amplicons as determined by clarity and reproducibility (Ghislain et al., 2009). The SSRs have been employed extensively in potato

for studies of diversity, genetic structure, classification, finger printing, genetic linkage mapping, tracing germplasm migrations (Provan et al., 1996; Feingold et al., 2005); establishment of core collections (Ghislain et al., 2006) and investigations of duplicate collections across gene banks. Genetic fingerprinting using SSRs has been used to differentiate tetraploid potato clones (Ashkenazi et al., 2001). As a result, this current study was undertaken to determine the genetic relationships among potato clones and identify parents for the breeding program. To achieve this, microsatellites were used because they are highly polymorphic, abundant, simple to use, they can function with low–quality DNA, provide high genetic information and are highly reproducible (Muthoni et al., 2014). In addition, they are co-dominant markers and can be used to detect heterozygosity.

1.4 Breeding for earliness in potato

Earliness is a quantitative trait, affected by genetic and physiological factors of a plant and the environmental conditions (Basbag et al., 2007). Earliness in potato has been reported to contribute to disease escape, especially of those that appear late in the season, such as late blight. Earliness is also beneficial in areas with multiple cropping systems and limited land, and with a short growing season. Early maturing varieties are more economical in their use of irrigation waters, tend to escape insect infestations such as aphids and may escape frost injury or disease infestation (Sleper and Poehlman, 2006). In areas with short rains, early varieties facilitate drought escape, a feature essential in view of climate change (Bänziger et al., 2000).

Earliness in potato has not received sufficient attention in Uganda and elsewhere, as there seems to be scanty information regarding the subject. However, some findings suggest that additive and non–additive genetic effects control earliness in potato, though additive genetic effects were found to be more important (Iragaba, 2013). Despite this finding, detailed information regarding the inheritance of this trait and the combining ability of parents from different maturity groups is required, in order to breed and develop varieties that are early maturing.

1.4.1 Potato maturity

Crop maturity is an agronomic trait. Crops undergo progressive growth stages from emergence to senescence, characterized by their reproductive capacity and phenology (Khan et al., 2013). In most annual crops, evolution from the vegetative to the reproductive phase is marked by the beginning of flowering and seed production (Bond, 2000). However, in the case of potato, most genotypes maintain the capacity to develop new leaves and continue to grow throughout the major part of their life cycle. This makes the assessment of progress to maturity complex. Crop development is comprised of a series of phenological events such as completion of canopy growth, termination of sympodial growth, the onset of tuber formation, or the onset of the rapid increase in harvest index, sagging of plants and senescence of leaves (Struik, 2010; Khan et al., 2013). The successive stages of growth, and

determining the duration of phenological phases of potato genotypes, could therefore be used to understand and define the concept of maturity type and to classify genotypes.

Potato maturity is normally assessed by monitoring vine characteristics, and change of potato plant's leaves is an indicator that the crop has reached maturity (Haga et al., 2012; Iragaba, 2013). Potato varieties are classified into maturity types based on the lengths of the season required to produce a harvestable product (Haga et al., 2012; Khan et al., 2013). Variability among varieties for number of days from planting to maturity has led to designation of the potato varieties as early, medium, late and very late maturity classes (Ruzukas et al., 2009). Breeders normally evaluate maturity period while developing new varieties, because it is a critical aspect in commercial potato production. Standard maturity measurements in potatoes are lacking because tubers are produced underground and monitoring their development presents many challenges. As a result, breeders commonly assess potato maturity classes based on physiological changes in the potato vine. Tuber production is associated with changes at the whole plant level such as reduction in leaf development, flowering and fruit set (Haga et al., 2012). For the purpose of this study, the number of days to 50% flowering and the onset of leaf senescence, and the tuber yield were used to evaluate the earliness of different genotypes.

1.5 Breeding for late blight resistance in potato

1.5.1 Causal organism

Late blight (LB) caused by *Phytophthora infestans* (Mont.) de bary, is the most devastating disease of potato leading to yield losses of up to 70% (Sedláková et al., 2011). *Phytophthora infestans* is a coenocytic (multinucleate) oomycete with diploid nuclei and produces short lived motile biflagellate zoospores (Fry et al., 1993). The pathogen reproduces both sexually and asexually. Asexual reproduction is associated with production of lemon shaped spores called sporangia. Sporangia are produced on the branch tips of the alternately branched sporangiophores that grow from infected tissue (Fry, 2008; Kaila, 2015). Infections of foliage or tubers are initiated by sporangia either directly with a germ tube, or indirectly by liberating zoospores (Fry et al., 1993). On entering the tissue, the pathogen forms a specified hyphal structure, called an infection vessel which extends and colonizes intercellular plant tissues to absorb nutrients. After some time, sporangiophores grow out of stomatal openings (Guest and Brown, 1997).

Phytophthora infestans is essentially an obligate parasite , which exists as an asexual organism and therefore requires a living host to survive (Chycoski, 1995). The pathogen is a heterothallic fungus that reproduces sexually by means of two mating types, labelled A1 and A2 (Daggett et al., 1993; Goodwin et al., 1998). In tropical Africa, isolates of the A1 mating type with divergent sexuality, along with augmented fungicide resistance, were noticed in the potato growing regions of Uganda. Spores

produced by sexual mating are called oospores and both mating types must infect the same plant for oospores to be produced. Oospores have thickened walls and can survive in the soil for a long period, even without a living host (Fry, 2008). The recent spreading of the A2 mating type has had a major impact on late blight severity and incidence. Sexual reproduction has also led to a more diverse population of *P. infestans* with increased adaptability to host and environment (Cooke et al., 2011; Wiik, 2014).

1.5.2 Disease distribution

The existence of late blight disease has been reported in all major potato growing areas of the world (Hijmans et al., 2000) and is favoured by moderately low temperatures and extended times of leaf dampness. It is particularly detrimental in the highland tropics where potatoes are grown throughout the year coupled with poor ability of farmers to understand and manage the disease (Garrett et al., 2001). Late blight regularly reduces potato productivity leading to huge differences between actual and realised yields. Attempts to develop late blight resistant varieties, therefore, call for superior attention to disease management.

The development of potato late blight essentially depends on the source of inoculum, the environment; and the genetics of the host and pathogen (Kaila, 2015). Seed tubers are pivotal in dispersing *P. infestans* from one place to another. Tubers become infected through lenticels when spores are eroded into the soil by rain from diseased leaves (Fry et al., 1993). For the disease development, temperature and humidity are of major importance. The optimum temperatures for late blight disease development are near 20^0C. Thus, conducive environment in most tropical highlands of Uganda, the limited use of resistant varieties where available, and the variability in the strains of *P. infestans* complicate the control of the disease (Mulema et al., 2004). Because of recent changes in the population structure of the late blight fungus, potato varieties are threatened by the recurrence of the disease (Kumar et al., 2007).

1.5.3 Management of potato late blight disease

At the farm level, late blight can effectively be managed by using both systemic and contact fungicides. However, these are responsible for several health and environmental risks (Kromann et al., 2011; Forbes, 2012), especially in developing countries where farmers rarely use protective clothing during fungicide application. In areas of high disease pressure such as the highlands, regular spraying is required for susceptible varieties, and disease management is complicated without the use of costly systemic fungicides (Kromann et al., 2009). Poor disease management is due to several factors and these include partial access to fungicides, high disease pressure and inadequate farmer knowledge of disease dynamics (Forbes, 2012). However, the present resistance is not enough to exclude the use of fungicides. Additionally, vast areas of potato production in Uganda are planted with highly susceptible varieties for particular reasons such as market demand. For example Cruza, a resistant

variety obtained from Rwanda has been replaced by varieties with more uniform tuber size and shape, preferred skin color (red or pink) and cream flesh. Market demand is a major factor influencing cultivar adoption as markets are becoming more specialized towards certain variety traits. In addition, the development and adoption of late blight resistant potato varieties is hindered by the low multiplication rate, bulkiness and perishability of the tubers (Forbes, 2012). Despite this, host resistance remains the most sustainable option in late blight management.

1.5.4 Breeding efforts for late blight resistance

Early efforts to breed for resistance against late blight focused on qualitative resistance controlled by major R genes. Even though R genes are greatly effective when compatible races are present, race-specific resistance controlled by major resistance (R) gene is not considered resilient due to interminable changes in the pathogen. As a result, the focus currently is on quantitative, race non-specific resistance (horizontal resistance) due to minor genes, which is more durable and effective against various pathogenic strains of *Phytophthora infestans* (Landeo et al., 1999; Kumar et al., 2007). Some researchers have also found that the defeated R genes are associated with partial resistance (Stewart et al., 2003; Forbes, 2012). To breed potato varieties with durable resistance, there is need to breed for quantitative resistance against *Phytophthora infestans* (Landeo et al., 1999; Landeo et al., 2000; Forbes, 2012).

Quantitative resistance has been reported in *S. tuberosum*, several wild *solanum* species and in potato clones derived from population B of the International Potato Centre (CIP) breeding program (Landeo et al., 2000; Wulff et al., 2007). As much as quantitative resistance is considered more durable, its expression is affected by varying environmental conditions that poses a threat to its stability across the production zones. This demands for the study of phenotypic stability in crop performance in terms of late blight resistance and an analysis of genotype and environment interactions (Wulff et al., 2007).

1.5.5 Conventional breeding for resistance to Phytophthora infestans

Conventional breeding methods are generally slow (10–15 years) as they are fundamentally based on several generations of back crossing, field evaluation and phenotypic selection. However, this is complicated by the polyploidy nature of potato (2n = 4x = 48), tetrasomic inheritance and chromatid segregation, and as a result breeding efforts largely rely on the typical reproductive features of potato (Gopal, 2006). The genus *Solanum* offers a greatly varied gene pool, which can be utilized for late blight resistance breeding in potato (Tiwari et al., 2013). Formerly, a few wild potato species were exploited extensively in conventional breeding to introgress race-specific resistance into the cultivated gene pool. These were obtained from the late blight-resistant hexaploid Mexican *Solanum* species demissum.

Predominantly, potato breeding focused on the introgression of 11 R genes through conventional methods. As a result, most existing potato varieties have resistance genes from *S. demissum* (Bradshaw and Ramsay, 2005).

Utilization of wild *Solanum* gene pools at tetraploid (4EBN) (endosperm balance number) and diploid (2EBN/1EBN) levels requires designing specific crossing schemes. The major gene pool consists of the cultivated potato (4EBN) without any barrier to gene flow. The secondary gene pool consists of most of the 2EBN or less common 4EBN wild species, while the tertiary gene pool includes 1EBN wild species that are distantly related to the cultivated crop. These can be exploited through somatic hybridization (Tiwari et al., 2013). For instance, five major R genes, were cloned from potato including the *S. demissum* and *S. bulbocastanum* derived late blight resistance R1 and RB respectively (Van Der Vossen et al., 2003; Carputo et al., 2011).

1.5.6 Search for resistance

Two novel R genes imparting resistance to *Phytophthora infestans* were detected in tetraploid potato accessions and it was demonstrated that even when broken down, the residual effects bring about significant tolerance to late blight in the field (Trognitz et al., 2008). Molecular markers can be used in the selection for R genes to complement phenotypic selection (Wulff et al., 2007). Recent molecular research has shown R genes to be involved in every facet of resistance, including genetic features leading to pathogen recognition, signalling and response. The authors stress that appropriate means should be identified to allow sustainable use of R genes in modern potato varieties (Trognitz et al., 2008). Therefore, it is appropriate to continue research on all elements required for plant resistance, including the R genes, and to identify appropriate means of their sustainable use in the breeding of modern potato varieties (Trognitz et al., 2008).

1.6 Breeding for improved yield

Identification of parents with excellent yield and desirable attributes is the basis of the breeding program. Increased tuber yield is the primary objective of potato breeding. New potato varieties are needed to address the need of a rapidly growing population. These must give more yield of marketable product at less cost of production, with inbuilt resistance to pests and diseases (Acquaah, 2012). In addition, there is also need for potato varieties that are early bulking to avoid drought, especially in the face of changing climate and spread of potato growing to non-traditional areas (Bradshaw and Bonierbale, 2010). However, the greatest need is to raise fresh weight yields from a world average of 17 t ha^{-1} to over 40 t ha^{-1} obtained in Europe and North America (Acquaah, 2012). Tuber yield and shape are influenced by photoperiod and response to photoperiod and is quantitatively inherited (Acquaah, 2012).

When breeding for high tuber yields, interlocus and intralocus interactions were shown to be important, therefore procedures that maximize the frequency of tetra allelic loci should be considered in breeding potato for increased yields (Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006; Muthoni et al., 2012). Consequently, the segregation of heterotic seedlings in a population is likely to be greatest when three conditions are fulfilled: 1) the parents possess as low a coefficient of inbreeding as possible, 2) as many loci as possible have different alleles and, 3) the parents belong to different gene pools which improves the chances of allelic diversity (Muthoni et al., 2012).

1.7 Parental selection

The main pathway to breeding new potato varieties traditionally, involves crossing of two parents with complementary traits. This will result in genetic variation on which phenotypic selection is practiced over a number of generations for clones with required attributes for release as new varieties (Bradshaw and Ramsay, 2005; Acquaah, 2012). The value of a cross combination is determined with mid-parent values and progeny test (Bradshaw et al., 2003; Acquaah, 2012). Tubers harvested from each superior F^1 family are grown in rows for evaluation, and then the amount of seed tubers increased for subsequent selection generations. Each row represents a clone from a single F^1 plant (Bradshaw and Mackay, 1994). Selected clones are tested in multi-location trials for evaluation in relation to wide or specific adaptation and yield stability (Sleper and Poehlman, 2006).

1.7.1 Molecular marker-assisted selection (MAS)

Molecular marker-assisted selection (MAS) is one of the most efficient applications of biotechnology to plant breeding as it involves the analysis of DNA in its natural state. The use of MAS includes the introgression of genes from one genotype to another through a backcross breeding scheme (Barone, 2004). Molecular markers that are closely linked to the gene controlling the trait to be transferred, allow accurate screening to be performed directly on DNA extracted from young leaves (positive selection) without waiting for the specific developmental stage at which the trait is expressed. This results in the reduction of selection time and space in a breeding programme.

In potato breeding, molecular markers have been used for cultivar identification, analysis of recombination between genomes, identification of genes controlling traits, phylogenetic studies, and assisted selection (Williams et al., 1993; Gebhardt, 1994). Presently, the potato genetic map is one of the most highly saturated maps with diverse molecular markers. This, therefore, provides wide opportunities for optimal use of DNA analysis for MAS. Two potato genetic maps were constructed initially, compared with each other later and also aligned with the tomato RFLP genetic map (Bonierbale et al., 1988; Tanksley et al., 1992). Through development of new molecular markers, the potato genetic map was improved and currently it has more than 350 markers, which cover approximately 90% of the potato genome. This makes it a valuable tool for localizing genes that control the expression of useful traits (Barone, 2004).

1.7.2 Selection for resistance to late blight disease

Resistance to *Phytophthora infestans* alone does not offer enough advantage for a clone to become a successful cultivar (Umaerus et al., 1983).This implies that selection for late blight disease resistance needs to be combined with other traits of economic importance such as tuber yield, tuber quality and acceptable maturity (Bisognin and Douches, 2002). In order to combine different traits, a selection criteria capable of recognizing suitable clones at early generation stage is needed. Additionally, an efficient selection strategy should reduce the number of selected clones significantly and keep superior ones for later generations of selection (Tai & Young, 1984). Tagging of resistance loci with molecular markers permits marker assisted selection for early selection and somewhat augments the time-consuming and environmentally sensitive trials (Tiwari et al., 2013).

1 7.3 Selection for yield

In potato, tuber yield is a complex trait associated with many interrelated traits and progress of breeding for its improvement is mainly conditioned by nature of variability present in the population and number of association of the various component traits (Luthra et al., 2001; Pradhan et al., 2011). Tuber quality is one of the market-limiting trait and should be evaluated and selected for early in a potato breeding program (Love et al., 1998).

1.7.4 Selection in early generations for agronomic traits

Maximum genetic variation is exposed and available for selection in the early generations, that is, seedling and first clonal generations. Thus, any increase in the selection efficiency in these stages is likely to result in great improvements in the quality of materials being advanced (Bradshaw and Mackay, 1994). However, intensive visual selection of individual clones in the early generation was found to be ineffective (Caligari, 1992; Bradshaw et al., 1998). Several studies have demonstrated that the repeatability of the performance of clones selected in early generations is low to very low in subsequent generations. Population means for major characters of economic importance, such as. tuber yield (g/plant),average tuber weight (g), and tuber shape, improved as the generations advanced from seedling to second clonal generation (Gopal 1997). This denotes that these traits cannot be efficiently selected for in seedling generation. Additionally, plant vigour was higher in the clonal generations than in the seedling generation. In addition, vigorous growth was obtained in clonal generations than in seedling generation. Correlation coefficients between seedling and clonal I generations and between clonal I and II generations for progeny means were low to moderate for most traits. This implies that high selection pressure in these early generations would be unfavourable (Gopal, 1997). For tuber yield, correlation coefficients between seedling generation and clonal II were low ($r = 0.34$), whereas those between seedling and clonal I generation and between clonal I and clonal II were moderate ($r = 0.56$ and 0.50, respectively). For plant vigour and tuber shape, all correlation coefficients were modest ($r = 50$ to $r = 69$). Tuber colour and uniformity in seedling generation were found to be highly correlated with those in clonal I ($r = 0.81$, and $r = 0.92$) respectively

(Gopal, 1997). Similarly, Kumar and Gopal (2006) established that all inter-generation correlation coefficients (from seedling to third clonal generation) were high ($r > 0.70$) for tuber shape, size, uniformity in tuber shape, uniformity in tuber size, and uniformity in tuber colour. On the contrary, most of the inter-generation correlation coefficients for tuber yield, plant vigour, tuber number and average tuber weight were of low magnitude except between second and third clonal generations where these were high for tuber yield and its components (Kumar and Gopal, 2006).

Clonal evaluations in early breeding stages should be based on traits with high heritability such as. quality traits (skin and tuber colour, and possibly eye depth and tuber shape) and for tolerance and resistance to pathogens; while the evaluation at later stages should be conducted in many target environments and based on traits with lower heritability (quantitative traits such as yield and yield components, dormancy, dry matter and starch content, tuberization) (Bradshaw, 2007). Conversely, selection for yield and yield components appears to be more effective in the second clonal generation (Caligari et al., 1986).

1.8 Combining abilities and gene action in potato breeding

Combining ability is commonly used in plant breeding to compare the performance of a particular parent in hybrid combinations (Haydar et al., 2009). It is the aptitude of parents to combine amongst each other during the processes of hybridization, so that favourable genes or characters are transmitted to their progenies (Muthoni et al., 2012). General combining ability (GCA) is the average performance of a parental line in a hybrid combination and is due to additive gene action. Specific combining ability (SCA) is the contribution of an inbred line to hybrid performance in a cross with a specified inbred line and is due to non-additive gene effects (Shattuck et al., 1993; Acquaah, 2012). Because traits are fixed in the F^1generation, both genetic effects are of great importance in potato breeding (Muthoni et al., 2012). However, information regarding the relative importance of GCA and SCA in potato seems to be variable. For instance, Ortiz and Golmirzaie (2004) found GCA to be significantly larger than SCA for tuber yield and quality traits in crosses between non-related parents, whereas SCA was more important among related parents. The predominance of SCA effects in closely related materials was explained to be caused by the limited number of different alleles. As a result, variation in additive gene action is limited, while non-additive gene action like epistasis increases, making SCA more evident in the resulting progenies (Ruiz de Galarreta et al., 2006; Neele et al., 1991). Narrowing of the genetic base through selection has been speculated to be a probable cause for obtaining greater estimates of SCA variance for various characters, in addition to directional selection in a population resulting into a large degree of dominance and epistasis (Muthoni et al., 2012).

General combining ability was only slightly more important than SCA for average tuber weight in the first two clonal generations, while for tuber yield per plant and number of tubers per plant SCA was much more important in both seedling and clonal generations (Ruiz de Galarreta et al., 2006). Gopal

(1998) also found that GCA for various traits varied from one generation to another and correlation coefficients between generations for GCA ranged from r = 0.5 to r = 0.8. On the other hand, some researchers found SCA to be more important in the inheritance of tuber yields (Gopal, 1998; Ruiz de Galarreta et al., 2006). Buso et al. (2000) reported both additive and non-additive effects to influence maturity and total tuber yields. In other studies, GCA was discovered to be more important in determining the inheritance of number of stems, stolon length, plant appearance, skin colour, tuber shape, tuber yield, eye depth, number of tubers per plant, average tuber weight, harvest index, foliage weight, and total biomass (Neele et al., 1991). In another study, the GCA effect was significant for total tuber yield and number of tubers per plant (Muthoni et al., 2012), while both SCA and GCA effect were significant for average tuber weight.

Knowledge of combining ability of parents for quantitative resistance to *Phytophthora infestans* is valuable in breeding late blight resistant varieties (Kumar et al., 2007). The GCA was found to be more influential in late blight resistance and foliage maturity type in potato (Visker et al., 2004). In addition, estimates of genetic variance due to GCA were found to be of a higher magnitude than SCA in the proportions of 0.59 and 0.63 for two consecutive years (Kumar et al., 2007). Other authors (Stewart et al., 1992; Wastie et al., 1993; Kaushik et al., 2000) reported significant differences between parents for their GCA for quantitative resistance to late blight. Both additive and non-additive genetic effects have been reported for early blight resistance in potato (Christ and Haynes, 2001). This means that where characters are largely influenced by GCA and additive genetic action, improvement can be made by selection and resistance transferred to the respective progenies. However, because the findings are seemingly differing and dependent upon the population, this study was undertaken to determine the nature of gene action for maturity, tuber traits and resistance to *Phytophthora infestans* among selected potato genotypes.

1.9 Conclusions

The cultivated potato is tetraploid in nature making heterozygosity and epistasis key factors in selecting breeding procedures. The crop has a higher yield potential relative to other crops and is growing in economic importance in the tropical highlands. The review highlighted the importance participatory methods of cultivar development to enhance variety adoption and key constraints to potato production. Potato yields have remained low in Uganda due to a number of factors. Late blight is the major disease hampering production and use of fungicides is the only management option, however, these are costly and pose several environmental and health risks. Consequently, this leaves host resistance as the most sustainable approach to potato late blight control. Information on the existence, use of early maturing varieties and nature of gene action controlling early maturity in potato is limited. Therefore, this study was done to identify early maturing potato clones and elucidate further on the inheritance of earliness in potato.

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Chapter 2 : Participatory assessment of potato farming systems, production constraints and cultivar preferences in Uganda

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Abstract

Potato (*Solanum tuberosum* L.) is a major food and cash crop, mainly grown by small-scale farmers in the highland regions of Uganda. Farmer practices and constraints in potato production and management differ from one area to another and so are desired attributes. A survey was conducted in eight major potato producing districts of Uganda. The study districts were from Central, Eastern and South-western regions of the country. The survey was carried out from May to August 2015. A semi-structured questionnaire was administered to 577 individual farmers. The results showed that potato is produced for both food and cash benefits in all the districts. Only 2% of the respondents from Eastern and South-western Uganda obtained seed from research stations, while all respondents from Central Uganda used farm saved seed. The major production challenges were pests and diseases. The major pests were aphids and cutworms while late blight and bacterial wilt were the prominent diseases. Across the three regions, Rwangume and Victoria were the commonly grown varieties, while Cruza and Marierahinda were the most rejected varieties. The latter were rejected on account of being white skinned with low marketability and Cruza becomes marshy on cooking. High yield, resistance to late blight, early maturity and marketability were the most preferred attributes in new varieties. Late blight had been experienced by 98% of the farmers and 96% of these reported to have used fungicides to manage the disease. From this study, breeding for late blight resistance is key in late blight management and to reduce the undesirable effects of fungicide usage.

Keywords: Attributes, variety, farmer practices, diseases, late blight, management

2.1 Introduction

Potato (*Solanum tuberosum* L.) is a major food and cash crop, mainly grown by small-scale farmers in the highland regions of many African countries. Uganda is the ninth largest producer of potato in Africa with an annual production of 188 000 tons harvested from about 39 000 ha per year (FAOSTAT, 2014). The major production areas are the highlands of South-western Uganda, comprising of Kabale, Kanungu and Kisoro districts which account for 60% of total national production. The other potato producing areas are Kapchorwa, Sironko, Bulambuli and Bududa districts on the slopes of Mt Elgon in Eastern Uganda and Nebbi district in north-western Uganda. Potato cultivation has spread to non-traditional producing areas in Central Uganda, especially Mubende, Rakai and Masaka districts.

Potato yields in Uganda have remained low about 4.8 t ha^{-1} (FAOSTAT, 2014) against a potential of about 25 t ha^{-1} which can be achieved under good management and when suitable varieties are deployed. These low yields have been attributed to a number of confounding factors which are biotic, abiotic, and socio-economic constraints, as well as poorly adapted and adopted varieties. Diseases are the major limiting factor and these include; - late blight caused by *Phytophthora infestans* (Mont.) de Bary, bacterial wilt (BW) (*Ralstonia solanacearum* Yabuuchi et al., 1995), and viruses (Muhinyuza et al., 2012).

Late blight is the most devastating disease of potato leading to yield losses of up to 70% (Sedláková et al., 2011). The disease is present in all main potato growing areas (Hijmans, 2001). It is favoured by moderately low temperatures and extended times of leaf dampness. It is particularly detrimental in the highland tropics where potatoes are grown throughout the year, coupled with poor ability of farmers to understand and manage the disease (Garrett et al., 2001). Late blight regularly reduces potato productivity, leading to large differences between actual and realised yields. Attempts to develop late blight resistant varieties, therefore, call for superior attention to disease management.

Most of the available potato varieties in Uganda are late maturing with physiological maturity attainable after 100 days from planting if they are to reach the full yield potential of more than 15 t ha^{-1}. These varieties were selected for the highlands (>2000 meters above seas level (masl)), and thus are well adapted and produce good yields with excellent culinary qualities in the highlands. Attempts to grow these varieties at low and mid-altitudes (<1700 masl) have resulted in a loss of tuber quality and low yields (Hassanpanah et al., 2008). Early maturing varieties would allow all year round cultivation of potato with favorable rotation periods and improved yields in the face of climate change. This is especially advantageous for smallholder farmers who depend

entirely on potato for both food and income security in areas with land shortage. Additionally, these varieties would be grown in low altitude areas of Uganda with short-lived rainfall seasons, where potato production is currently expanding. Short rainy seasons are often erratic; early maturing varieties stand a higher chance of carrying the crop to full maturity.

The National Agricultural Research Organisation (NARO) in collaboration with the International Potato Center (CIP) have released many potato varieties. However, farmers have not adopted some of these varieties. Farmers prefer their own varieties that they have kept for a long time because of some special attributes (Witcombe, 2009). It was reported that participatory variety selection (PVS) may improve the adoption of varieties and boost productivity (Joshi and Witcombe, 1996). To accelerate variety adoption, farmer preferred qualities must be considered in the process of cultivar development. In participatory plant breeding (PPB), the preferences of the end-users and the production environments are identified through a participatory rural appraisal (PRA) (Witcombe et al., 2005). It is against this background, therefore, that a participatory rural appraisal was carried out to identify key potato production constraints, varieties grown, and farmers' knowledge of potato diseases.

2.2 Materials and methods

2.2.1 Study sites

A survey was carried out in three major potato growing regions in Uganda, namely, Central, Eastern Highlands (Mount Elgon) and South-western highlands (Kigezi region), from May to September 2015. All regions are suitable for potato production with a bimodal rainfall pattern of short rains (from March to May) and long rains (from August to December). However, in the South-western highlands; potato growing is almost done throughout the year (Low, 1997; Ferris et al., 2001) at altitudes ranging from 1200-2500 masl. The traditional production zones of Kigezi and Mount Elgon are favourable for potato production due to their deep volcanic soils, high altitudes with mild temperatures (10 – 30^{o} C) and abundant rainfall (900 – 1400 mm).

Sampling was done at different administrative levels from district, sub–county to villages. In each of these regions major potato producing districts were chosen as follows: Rakai and Lwengo in Central Uganda; Kween, Kapchorwa and Mbale in Eastern Uganda; and Kabale, Kanungu and Kisoro from South-western Uganda. Sub-counties where potato is the main crop were identified with the help of the district production staff and sub-county chiefs. Individual farmers were approached with the guidance of village chairpersons. In all these areas, potato is a major food and cash crop.

2.2.2 Data collection and analysis

Primary data were collected using a semi-structured questionnaire that was administered to individual farmers. The questionnaire constituted open ended questions to allow full expression so as to obtain as much information from farmers as possible. A pretesting was done on fifteen farmers in Eastern Uganda, changes were effected and the formal survey started. The survey team consisted of a breeder, research assistant, an agriculture extension officer and three enumerators from each district. Only households with potato fields were sampled and interviews were carried out in the field to ascertain the varieties grown, incidence of late blight and management practices. The interviews were conducted in local languages and in some areas such as Eastern Uganda, interpreters were used.

Data were collected on farm characteristics and location using a global positioning system (GPS-Garmin Inc. Kansas, USA), where latitudes, longitudes and altitudes were recorded. Farmers listed the major crops on their farms, potato varieties currently grown and those abandoned. Additionally, data were collected on source of seed; production constraints, desired attributes, and knowledge of late blight symptoms and management options. The data were analysed using SPSS software (SPSS, 2010) and Microsoft excel. Data analysis was descriptive (percentages and means).

2.3 Results

2.3.1 Household and farm characteristics

A total of 577 farmers were interviewed from three major potato growing regions in eight districts, 31 sub-counties and 165 villages. Sixty percent of the interviewed farmers were from South-western Uganda. An equal number of males and females were surveyed in Kanungu (50%), more females in Kabale, Kisoro, Kween and Kapchorwa, while more males (were surveyed in Central Uganda. The farms are located between1256 and 2480 masl. Most of the respondents (30% and above) were aged between 21 and 55 years in all the surveyed districts. Rakai district had more young people of less than 21 years of age (6%) involved in potato growing while Kisoro had 23% of the people aged above 55 years (Table 2.1).

Table 2.1: Description of household characteristics in surveyed districts of Uganda in the year 2015.

Variable	District								
	Lwengo	Rakai	Kapchorwa	Kween	Mbale	Kabale	Kisoro	Kanungu	
Altitude (masl)	1338	1256	2061	2442	1709	2480	2106	1959	
Number of farmers interviewed	68	63	42	30	28	164	112	70	**Total /577**
Gender									
% Males	62	54	48	47	71	47	48	50	
% Females	38	46	52	53	29	53	52	50	
Age of respondents (%)									
Less than 21	0	6	0	0	0	3	2	0	
Between 21-35	37	46	38	57	32	42	37	49	
Between 36-55	50	37	50	30	61	37	38	37	
More than 55	13	11	12	13	7	18	23	14	
Size of family land under potato (ha)	2.0	1.0	3.1	1.6	0.9	0.7	1.1	0.9	
Average years of potato production	6.1	9.7	10.4	13.5	11.3	14.1	14	11.1	

Masl =meters above sea level

2.3.2 Potato cropping system in Uganda

Five commonly grown crops were mentioned in order of importance in the study districts. In all the districts, farmers ranked potato as their number one crop followed by either beans or maize. Sorghum, peas and sweet potatoes were typically grown in the Kigezi region; banana and coffee in Rakai, Lwengo and Mbale, while barley and wheat were common in Kween and Kapchorwa (Table 2.2). These crops are planted on small-scale farms for food and income as well as to guard against the risk of crop failure and for rotational purposes.

Table 2.2: Five commonly grown crops in each district as mentioned by farmers.

District	Crops in order of importance				
Kabale	Potato	Beans	Sorghum	Sweet potato	Peas
Kisoro	Potato	Beans	Maize	Sorghum	Sweet potato
Kanungu	Potato	Beans	Sorghum	Sweet potato	Maize
Rakai	Potato	Beans	Maize	Banana	Coffee
Lwengo	Potato	Maize	Beans	Banana	Coffee
Kween	Potato	Maize	Barley	Cabbage	Wheat
Kapchorwa	Potato	Maize	Onions	Wheat	Beans
Mbale	Potato	Beans	Onions	Banana	Coffee

The most common source of planting materials used in the three regions and the respective districts was farm saved seed. This is either from the previous harvest or from other farmers. Additional seed was obtained from the markets and local traders in Eastern Uganda, while in Central Uganda there was exclusive use of farm saved seed. To some extent, farmers used seed from research stations, especially farmers in South-western Uganda (Table 2.3).

Table 2.3: Seed source in the three potato growing regions (% of respondents)

	Seed source				
Region	Farm saved	Other farmers	Research station	Market	Local traders
Central	59.2	40.0	0.0	0.8	0.0
Eastern	33.0	34.0	3.0	20.0	10.0
South Western	43.0	17.4	15.4	14.2	10.0
Mean	**45.1**	**30.5**	**6.1**	**11.7**	**10.0**

Rwangume was the most popular potato variety followed by Victoria across all the districts. However, in Kisoro the variety Kinigi was preferred to Rwangume. Rwashaki and Rutuku were generally found in the South-western region, with Sutama typically in Kisoro, and Kabera and Kasumali in the Central region. Kachpot 1 and Wanale were found in Eastern Uganda (Table 2.4). Farmers tended to give varieties names of the person and places from where they had obtained these varieties. For example, the potato variety Rwangume was called by different names in the three regions: Deodeo in the Central, and Kabale and/or Rwangyema in Eastern Uganda. The name is assumed to be the farmer or the area from where the seed was obtained. However, some farmers were not aware of the varieties they were growing.

Farmers in each district mentioned potato varieties abandoned over the past ten years. Cruza was the most commonly abandoned variety in Uganda and Mbale district. Mbubamagara, Rutuku, Marierahinda, and Kimuri were abandoned in South-western Uganda, while Kabale, Marierahinda, Kabera, Singo and Kawanda were abandoned in the Central region. In addition, Cruza, and Meru were rejected in Eastern Uganda. Farmers gave a range of reasons as to why they abandoned these varieties. Reduced yield was the most common reason given across all the regions. This was followed by reduced market, susceptibility to blight, and introduction of new and high yielding varieties (Table 2.5). The long maturity period was typically cited in Eastern Uganda. General susceptibility to pests and diseases, and unavailability of seed were also mentioned.

Table 2.4: Common potato varieties across the surveyed districts (% of respondents)

	District							
Cultivar	Kabale	Kisoro	Kanungu	Rakai	Lwengo	Kween	Kapchorwa	Mbale
Rwangume	52.3	23.0	48.0	78.4	95.6	43.4	44.3	62.1
Victoria	20.0	6.0	10.9	14.3	4.4	36.3	53.5	30.8
Kinigi	18.7	47.0	34.0	0.0	0.0	0.0	0.0	0.0
Rutuku	1.8	0.0	5.7	0.0	0.0	0.0	0.0	0.0
Rwashaki	7.2	14.0	1.4	0.0	0.0	0.0	0.0	0.0
Wanale	0.0	0.0	0.0	0.0	0.0	20.3	2.2	7.1
Kasumali	0.0	0.0	0.0	7.3	0.0	0.0	0.0	0.0
Sutama	0.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0

2.3.3 Potato production constraints

In general, diseases were the main constraint limiting potato production across all the regions. Other challenges were pests, high cost of agro-inputs, limited land for potato production, reducing yields and unfavorable weather conditions (Table 2.6). Major diseases were bacterial wilt in the lowland and late blight in the highland areas. Cutworms and aphids were the most predominant pests across all the regions. The potato tuber moth was mainly cited in the highland regions, while leaf miner was mentioned in the districts of Kabale, Kisoro and Kanungu.

Table 2.5: Abandoned potato varieties and reasons for abandonment over the past ten years (% of respondent farmers) in the surveyed districts

Abandoned varieties/District	Kabale	Kisoro	Kanungu	Rakai	Lwengo	Kween	Kapchorwa	Mbale
Cruza	35.0	33.3	51.8	0.0	0.0	26.7	47.1	48.0
Mbumbamagara	20.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0
Kimuri	18.6	0.0	33.1	0.0	0.0	0.0	0.0	0.0
Rutuku	16.0	10.4	7.1	0.0	0.0	0.0	0.0	0.0
Singo	0.0	0.0	0.0	22.8	34.9	0.0	0.0	0.0
Sutama	0.0	29.1	0.0	0.0	0.0	0.0	0.0	0.0
Sangema	0.0	23.0	0.0	0.0	0.0	0.0	30.8	37.9
Marierahinda	10.4	4.2	0.0	28.5	15.4	0.0	0.0	0.0
Kabale	0.0	0.0	0.0	40.8	1.5	23.3	0.0	14.1
Kabera	0.0	0.0	0.0	7.9	48.2	0.0	0.0	0.0
Meru	0.0	0.0	0.0	0.0	0.0	50.0	22.1	0.0
Reason for rejection								
Reduced or no market	30.1	40.0	22.6	27.3	17.6	19.3	19.4	9.8
Susceptible to blight	7.7	0.0	0.0	16.7	20.5	4.6	0.0	0.0
Low/reduced yields	36.3	43.8	38.4	44.9	38.2	40.0	32.1	25.6
New and high yielding varieties	14.7	5.3	10.4	0.0	0.4	11.2	0.0	3.7
Long maturity period	0.0	0.0	0.0	0.0	0.0	8.3	12.4	7.3
Unavailability of seed	0.0	8.2	8.2	0.0	0.0	0.0	11.1	19.5
Susceptible to pests and diseases	3.5	2.4	6.5	0.0	0.0	0.0	6.0	0.0
Others	7.7	0.3	13.9	11.1	23.3	16.6	19.0	34.1

*0.0 variety not abandoned/ absent in that district

Table 2.6: Potato production constraints as cited by farmers (% of respondents)

Constraint/District	Kabale	Kisoro	Kanungu	Rakai	Lwengo	Kween	Kapchorwa	Mbale
Diseases	42.5	54.9	26.6	34.0	23.5	42.9	38.9	38.6
Pests	5.7	16.7	8.9	36.2	25.7	30.4	19.4	28.1
Limited capital to buy inputs	0.0	0.0	7.8	2.8	7.5	0.0	0.0	0.0
Low yields	6.9	3.1	16.1	0.0	0.0	1.8	1.4	0.0
High cost of agro-inputs	2.0	3.1	0.0	7.1	12.7	3.6	0.0	3.5
Unfavorable weather conditions	0.0	3.7	6.4	0.0	5.6	0.0	2.4	0.0
Limited land for potato production	3.7	0.0	6.2	2.1	6.2	1.8	0.0	0.0
Low market prices at harvest	0.0	0.0	0.0	7.1	4.4	10.7	9.7	7.0
Declining soil fertility	4.5	3.7	0.0	2.8	0.0	0.0	0.0	3.1
Others	34.7	14.8	28.0	7.9	14.4	8.8	28.2	19.7
Major diseases								
Bacterial wilt	47.5	36.2	42.4	47.2	39.6	48.3	47.6	44.3
Late blight	47.5	38.6	42.4	49.6	56.8	50.0	48.8	45.9
Viral diseases	4.4	24.1	14.5	2.4	0.0	1.7	1.2	9.8
Others	0.6	1.1	0.7	0.8	3.6	0.0	2.4	0.0
Major pests								
Cutworms	15.5	8.8	19.8	24.5	31.5	77.8	46.3	35.0
Aphids	35.7	41.7	49.5	6.0	15.4	5.6	12.4	55.0
Leaf miners	9.4	32.4	4.5	11.0	0.0	0.0	0.0	0.0
Potato tuber moth	15.5	5.9	1.8	10.0	18.0	5.6	2.4	0.0
Others	23.9	11.2	24.4	48.5	35.1	11.0	38.9	10.0

2.3.4 Farmers' knowledge of late blight and management of the disease

Most of the respondents had experienced late blight on their farms. It is a common disease devastating potato in both the highland and lowland areas. Farmers have to spend a lot of money in controlling late blight, which increases the costs of production. Farmers recognize late blight in different ways; spotted and burnt like leaves, leaves dry out, in severe cases both leaves and stems rot (Table 2.7). On the other hand, some farmers had no idea of the symptoms, while others confused nutrient deficiency and maturity with late blight. Over 50% of the respondents in the districts of Kabale, Kisoro and Kanungu, mentioned that the disease is common in season B (October –December), while in Central Uganda farmers experienced late blight during both seasons. In Eastern Uganda the disease was found to be more severe in season A and heavy rain was the main condition enhancing the disease in all the districts (Table 2.7). Most of the respondents did not know how late blight is spread, although a few farmers mentioned that the disease is spread through the air by wind and rain.

2.3.5 Varietal attributes

These were scored independently and high yield was identified as the most preferred attribute across the three potato growing regions followed by marketability, resistance to blight and early maturity. (

Table 2.8). General resistance to pests and diseases was important for farmers in the Kanungu, Rakai and Kapchorwa districts. Farmers from all regions considered a good cooking quality important, while resistance to bacterial wilt was a major attribute mentioned by farmers in Eastern Uganda. A red tuber skin is preferred by farmers in Kabale, Kisoro and Mbale districts, while yellow flesh is preferred by farmers in Lwengo district (10.3%).

Table 2.7: Farmers ability to recognize late blight (% of respondents in each district)

Symptoms/District	Kabale	Kisoro	Kanungu	Rakai	Lwengo	Kween	Kapchorwa	Mbale
Burnt leaves	16.7	22.3	10.3	34.5	23.5	40.0	42.5	55.7
Spotted leaves	44.2	49.8	43.9	48.5	54.8	43.3	19.8	33.7
Rotting of leaves and stems	8.0	0.0	12.2	0.0	2.9	0.0	7.1	0.0
Leaves dry and rot	19.6	27.0	12.2	0.0	1.5	0.0	14.3	0.0
Premature falling of leaves	6.7	0.9	8.4	1.6	2.6	6.7	2.0	0.0
Yellowing of leaves and stem	4.8	0.0	13.0	15.4	14.7	10.0	14.3	10.6
Season when late blight is severe								
A	1.2	17.0	5.7	44.9	27.7	78.0	90.3	85.7
B	92.7	71.4	57.1	25.9	52.5	5.3	7.3	3.6
Both A and B	5.5	10.7	37.1	28.8	19.5	16.7	2.4	7.4
Enhancing conditions								
Heavy rains	97.6	95.5	100.0	76.2	80.9	93.3	95.2	85.7
Not sure	1.8	2.7	0.0	15.8	8.8	3.3	0.0	10.7
Others	0.6	1.8	0.0	8.0	10.3	3.4	4.8	3.6
Method of spread								
Rain	9.1	0.9	0.0	1.6	14.7	13.3	9.5	7.1
None	86.0	97.3	100.0	85.7	72.1	80.0	78.6	85.7
Others	4.9	1.8	0.0	12.7	13.2	6.7	11.9	7.2

*season A (short rains of March –May) and season B (long rains of August-December)

Table 2.8: Desired attributes in new potato varieties (% of respondents in each district)

Attributes	District								
	Kabale	Kisoro	Kanungu	Rakai	Lwengo	Kween	Kapchorwa	Mbale	Mean across districts
High yielding	44.8	28.5	33.7	25.0	23.7	23.5	20.6	29.3	28.6
Marketable	23.1	18.4	15.7	15.1	16.7	13.3	14.8	0.0	14.6
Resistant to late blight	10.1	16.1	22.6	20.8	20.9	17.7	11.0	22.1	17.7
Early maturing	7.5	19.6	2.9	17.6	18.1	20.0	22.1	15.6	15.4
Good cooking quality	3.9	4.5	0.0	6.4	0.0	15.5	0.0	3.6	4.2
Resistant to pests and diseases	0.0	0.0	13.7	15.1	0.0	0.0	10.5	0.0	4.9
Resistant to bacterial wilt	0.0	8.4	11.4	0.0	10.3	10.0	21.0	21.4	10.3
Red skin	10.6	4.5	0.0	0.0	0.0	0.0	0.0	8.0	2.9
Yellow flesh	0.0	0.0	0.0	0.0	10.3	0.0	0.0	0.0	1.3

2.4 Discussion

This study focused on obtaining information about potato production in Uganda, the major production constraints, current potato varieties and preferences, and farmers' knowledge about late blight disease and management. Individual farmers were interviewed to obtain the necessary information.

The results of this study have shown that potato is an important crop for both food and income security in Uganda. In addition to potato, farmers grow other crops for both food and household income. The major crops grown across all regions are beans and maize. Potato is generally grown in pure stands and occasionally mixed with other crops. Intercropping of potato with crops like maize, beans, banana and cassava is common in Central and Eastern regions, primarily as a measure to guard against crop failure. A variety mix is common in most fields in Eastern Uganda. This could be attributed to poor harvesting techniques whereby not all potatoes are harvested, resulting in a large number of volunteers. In addition, the improper storage facilities could be a reason, as small space is used for several varieties which can result in the mixing of the varieties. However, it could also be a way of minimizing the risk of crop failure (Sperling and Loevinsohn, 1993; Muthoni et al., 2013).

The overriding use of farm saved seed in Central Uganda can be attributed to the absence of research stations and a lack of training on the value of quality seed (indexed for seed borne diseases). On the other hand, the use of quality seed potato in the other regions can be ascribed to their proximity to the research stations and non-governmental organisations (NGOs) focusing on potato. However, the percentage of farmers using quality seed potatoes (2%) is still low, which can be explained by the high cost of seed, the bulkiness of potato seed and insufficient quantities produced by these research stations and NGOs (Aheisibwe et al., 2015). In addition, farmers can keep their seed for two to three seasons without replacement (Muthoni et al., 2013). However, a continual use of potato seed from the informal sources promotes the spread of seed borne diseases, especially bacterial wilt (Kinyua et al., 2001) and viruses (Kakuhenzire et al., 2000).

A range of potato varieties are grown across the three regions, but the dominant varieties are Rwangume and Victoria. The wide adaptability of Victoria was mentioned by Ferris et al. (2001). The variety matures early although it is very susceptible to late blight. The popularity of Rwangume in several parts of the country may be due to its red skin color, good cooking quality, a large number of tubers and the relative tolerance to late blight. In addition, Rwangume generally

has a high market demand. The absence of new and improved varieties in Central Uganda may be explained by the fact that most varieties are developed for the highlands, require cool temperatures and have a long maturity period. As a result, their productivity cannot be achieved in areas with short rainfall cycles and higher temperatures. The focus of potato research and farmer training have so far been centered on the highland areas. Therefore, breeding efforts should be geared towards early maturing varieties with wide adaptability.

In general, there has been a high turnover of varieties in South-western Uganda compared to other regions. This could be explained by the fact that potato breeding and evaluation of new candidate varieties takes place in this region. As a result, farmers in South-western Uganda have easy access to the new varieties and can obtain them from the on- farm trials. The variety Cruza has almost been abandoned in both Western and Eastern Uganda, while several varieties were rejected in the different districts. The abandonment of Cruza by most farmers could be attributed to its high tendency to crumble when overcooked and because of its white skin. This finding on Cruza is in agreement another study (Low, 1997) which found that it was the most likely variety to be abandoned by commercial farmers in Bukinda (57%), Karengyere (44%) and Kabale district. The results of this present study indicate that white skin varieties are more easily abandoned than the red skin varieties, as the white skin varieties fetch lower market prices. As a result, the white skin varieties are mainly grown for food security, for example in Kabera and Singo in Central Uganda.

Some farmers abandoned Victoria because of its high susceptibility to diseases, mainly late blight. Most varieties were abandoned on account of the low yields and poor marketability, as was also found in some areas of Kenya (Muthoni et al., 2013).The introduction of new, high yielding varieties will also influence the rejection of some varieties. Low (1997), working on threats to sustainable potato production in South-western Uganda reported that in addition to ease of selling, four important reasons for the varietal adoption were; high yield, good tuber size, late blight resistance and interest to try the new variety plus early maturity. There is therefore a need to develop high yielding varieties with end-user traits. Early maturity is a key trait in variety development, especially in the face of changing climate and shift of potato cultivation from the traditional highlands to mid- and low altitude area in Uganda.

Diseases were the most important production constraint. Over 35% of the farmers mentioned both bacterial wilt and late blight as major diseases affecting potato production, followed by viruses. This result in confirmed by several other researchers in Eastern Africa (Kaguongo et al., 2010; Muhinyuza et al., 2012; Muthoni et al., 2013), who found diseases to be the most limiting factor

in potato production. Farmers in the present study rated bacterial wilt as a more important disease than late blight. Ortiz et al. (1997), found out the same in a study to understand farmers' responses to late blight. This may be because bacterial wilt (BW) is both seed and soil borne, with no efficient chemical control available, and its effect is escalated by the use of seed from informal sources (Kinyua et al., 2001). As much as late blight is a devastating disease of potato, in most surveyed districts, farmers say it can be managed by fungicides. However, this has a big bearing on the cost of production (Forbes, 2012). Therefore, the use of resistant varieties is paramount if potato production is to be sustainable. Conversely, farmers in this study never mentioned the use of resistant varieties to control late blight. This may be due to the fact that such varieties are not presently available.

Declining soil fertility was typically mentioned in the highland areas and may be attributed to the high rate of soil erosion, the poor soil fertility management practices and over cultivation due to small land holdings, coupled with a high population density (Low, 1997; Lemaga et al., 2001; Muthoni et al., 2013). The low market prices at the harvest time was particularly mentioned by farmers in Central and Eastern Uganda. This may be due to limited or absence of storage facilities, resulting in the selling of potatoes soon after harvest at the prevailing market prices.

The failure of farmers to recognize late blight, its symptoms and understand the spread of the disease was also observed by Ortiz et al. (1997) in a study on farmers' responses to late blight. This lack of knowledge emphasizes the need for farmer education and training on potato production and disease management. Over 20% of the respondents in the districts of Kanungu and Rakai said the disease is severe in both seasons. Heavy rainfall was especially mentioned as the most enhancing condition for the spread of late blight in all the districts, which is in agreement with the findings of Ortiz et al. (1997).

The results of this study identified high yield (over 70% respondents) as the most preferred attribute across the three potato growing regions. These findings are similar to those from previous studies by Low (1997) and Muhinyuza et al. (2012), who found high yield, good marketability, resistance to diseases and early maturity as the most desirable attributes in new varieties their adoption.

2.5 Conclusion

This PRA study has resulted in understanding of potato production in Uganda. Potato is grown for both food and income, and largely by small-scale farmers. In addition to potato, farmers grow other crops for household income and food security. Farmers grow different potato varieties and

seed used for subsequent seasons is mainly farm saved. Varieties grown differ from one area to another and so are those that have been abandoned by farmers for various reasons. Potato growing is constrained by many factors, but according to the farmers diseases are the most limiting and late blight is the most devastating disease followed by bacterial wilt especially in the low lands. Farmers manage late blight by using fungicides. Bacterial wilt was also a big threat However, this is not sustainable for the environment and the cost is not affordable by the majority of the small scale farmers. Therefore, there is a need to develop potato varieties with resistance to the main disease and with farmers' preferred traits.

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Chapter 3 : Phenotypic characterisation of potato (*Solanum tuberosum L.*) genotypes in Uganda

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Abstract

Identification of genetic variation and interrelationships among germplasm collections is essential for parental selection and trait identification among parents for use in breeding programs. The aim of this study was to characterise 48 potato genotypes to identify suitable parents for crop improvement purposes. Genotypes were evaluated in the field using 8 x 6 alpha lattice design with three replications at Kachwekano and Karengyere stations in Uganda. Sites had significant effects on genotype performance for all measured parameters. Genotypic effects were significant ($P < 0.01$) for total tuber yield, main stem number and plant height. The mean tuber yield for the two sites was 29.8 t ha^{-1} and tuber yield was higher in Kachwekano than Karengyere. The best yielding genotype in Kachwekano was 396038.105 (54.5 t ha^{-1}) and in Karengyere NAKPOT5 (50.9 t ha^{-1}). Significant positive correlations ($p \leq 0.001$) were observed between tuber yield and plant height; duration of flowering, and days to flowering and plant height. The most stable genotypes in terms of tuber yield were Rutuku, 395112.32, 395017.14 and 393220.54. The cluster analysis revealed three principal clusters with nine sub-clusters. Variation for the different traits exhibited by genotypes in this study should be exploited in crop improvement programs.

Keywords: Agro-morphological, genetic diversity, potato, genotype, phenotypic traits

3.1 Introduction

Globally, potato (*Solanum tuberosum* L.) is the fourth most important crop after maize, rice and wheat with more than 320 million tons of potatoes being produced from 20 million hectares (CIP, 2016). Potato is a major food and cash crop in the highland regions of many African countries, and is mainly grown by small-scale farmers. Uganda is the ninth largest producer of potato in Africa with an annual production of 188000 tons harvested from about 39000 ha per year (FAOSTAT, 2016).

The identification of suitable genotypes with complementary traits is key in crop improvement (Tseng et al., 2002; Elameen et al., 2011). Knowledge of genetic interrelationship among pools of germplasm enables plant breeders to select possible parents with desired traits for cultivar development (Yoshida, 2004). Proper management and utilisation of plant genetic resources entirely depends on the extensive understanding of their genetic variability (Rukundo et al., 2015). Genetic variability is the basis of plant breeding and it is a prerequisite before the beginning of breeding work (Simmonds, 1962).

Several methods have been used to measure genetic variation among plant genetic resources. These include data based on plant morphology, agronomical performance, and biochemical and molecular markers (Mohammadi and Prasanna, 2003). Morphological characterization is the first step in description and classification of genetic resources (Arslanoglu et al., 2011). Phenotyping is usually done to determine the genetic variation among genotypes (Yoshida, 2004). Phenotypic markers are comparatively cheap and easy to use (Elameen et al., 2011). Potato is a clonally propagated crop that exhibits a high degree of incompatibility and inbreeding depression (Muthoni et al., 2012). This makes parental selection vital if breeding progress is to be made (Hirut, 2015). It is also imperative that genotypes with superior agronomical properties are selected for crop improvement studies (Pandey et al., 2005; Sandhu and Gopal, 2006). It is against this background that this study was undertaken to determine the phenotypic diversity among 48 potato genotypes and to identify superior parents for breeding purposes.

3.2 Materials and methods

3.2.1 Genetic material

The germplasm used in this study consisted of 48 potato genotypes, which included advanced clones from the International Potato Centre (CIP), and commercial and farmers' varieties. The details of the genotypes are presented in Table 3.1

Table 3.1: Source of the 48 potato genotypes used in the study.

No	Genotype	Source	No.	Genotype	Source	No.	Genotype	Source
1	395017.14	CIP	17	396031.108	CIP	33	Rutuku	NARO
2	391919.3	CIP	18	391046.14	CIP	34	NKRK19.10	NARO
3	395109.34	CIP	19	396038.105	CIP	35	NKRN59.124	NARO
4	394905.8	CIP	20	395011.2	CIP	36	396026.103	NARO
5	395077.12	CIP	21	393220.54	CIP	37	NKR159.41	NARO
6	391580.3	CIP	22	392633.64	CIP	38	NAKPOT1	NARO
7	395096.2	CIP	23	394895.7	CIP	39	Cruza	NARO
8	392657.8	CIP	24	396034.268	CIP	40	NKRN59.48	NARO
9	393077.54	CIP	25	Kimuri	Farmer	41	Victoria	NARO
10	392661.18	CIP	26	Petero	Farmer	42	NKRN59.61	NARO
11	391002.6	CIP	27	Mabondo	Farmer	43	Rwashaki	NARO
12	395438.1	CIP	28	NKRN59.11	NARO	44	Rwangume	NARO
13	396038.101	CIP	29	NKRN59.58	NARO	45	NKRN59.29	NARO
14	395015.6	CIP	30	396034.103	NARO	46	Kinigi	NARO
15	392797.22	CIP	31	396038.107	NARO	47	Kachpot1	NARO
16	395112.32	CIP	32	NKRK19.17	NARO	48	NAKPOT5	NARO

CIP = International Potato Center, NARO = National Agriculture Research Organisation

3.2.2 Planting sites

The field trials were established at the Kachwekano and Karengyere research stations of the National Agricultural Research Organisation (NARO). Kachwekano is located in South-western Uganda, 01º 16'S 29º 57'E at 2200 meters above sea level (masl). The soil type at this location is isomeric typic palehumult (Kakuhenzire et al., 2013). Karegyere research station is located at 01º 13.2'S, 29º 47.8'E in South-western Uganda at an altitude of 2450 masl. Both sites have a bi-modal rainfall pattern separated by a dry spell ranging from 30 to 60 days.

3.2.3 Experimental design and trial establishment

Experiments were established during the season of 2015 (September to December) using an 8 x 6 alpha lattice design with three replications at both locations. The Karengyere trial was planted on 15th September 2015 and harvested on 8th January 2016. The trial in Kachwekano was planted on 18th September 2015 and harvested on 14th January 2016. The plot size was 4.5 m long by 3.0 m wide. Four rows of 15 tubers each were spaced at 75 cm between rows and 30 cm between

plants. Planting was done by hand. At the time of planting N:P:K: 17:17:17% fertilizer was applied at a rate of 100 kg ha^{-1}. Chemical pest and disease control was done and late blight was controlled using recommended fungicides. Hand weeding and ridging were carried out as recommended.

3.2.4 Data collection

Data were recorded on different agro-morphological characters. Qualitative traits recorded were, flower color, tuber shape, skin texture, skin color, flesh color, eye color and depth as described by Arslanoglu et al. (2013) (Table 3.2). Quantitative data collected included plant height, main stem number, days to flowering and duration of flowering. Measurements for plant height and main stem number were done on ten randomly selected plants in each plot and replication. The plant height (cm) was measured as the distance between the top point of the plant and the ground surface after flowering; the main stem number which is the number of mains stem per plant, was counted at 50% flowering and days to flowering was recorded as the number of days from planting to 50% flowering of the plants in a plot. The duration of flowering was recorded as the difference between the number of days from 50% flowering of the plants in a plot to 50% flower senescence. At harvest, data was recorded for the number of plants in the two middle rows, the number of tubers and total tuber weight. Genotypes with yields above 30 t ha^{-1} were classified as high yielding (HY); moderate yielding (MY) when the yields ranged between 15 to 30 t ha^{-1}, and low yielding (LY) yielding at yields below 15 t ha^{-1}.

Table 3.2: Description of qualitative traits of potato genotypes used in the study.

Character	Description
Flower color	(1) White, (2) Violet, (3) Blue, (4) Pink
Eye color	(1) White, (2) Red, (3) Pink, (4) Purple
Skin color	(1) White, (2) White with pink points, (3) Red, (4) Purple, (5) Pink, (6) Cream
Flesh color	(1) White, (2) Cream, (3) Light yellow, (4) Yellow, (5) Dark yellow)
Eye depth	(1) Very deep, (3) Deep, (5) Medium, (7) Shallow, (9) Very shallow
Skin texture	(1) Very rough, (3) Rough, (5) Intermediate, (7) Smooth, (9) Very smooth
Tuber shape	(1) Globe, (2) Short-oval, (3) Oval, (4) Long-oval, (5) Long, (6) Very long
Flower frequency	(1) Very high, (2) High, (3) Moderate, (4) Rare
Pollen Production	(1) Present, (2) Absent

3.2.5 Data analysis

Data were analysed using the Genstat 14th edition (Payne et al., 2011) software package. When significant differences were detected, means were separated using the least significant difference (LSD) test procedure at the 5% significance level, using the Fisher's protected LSD. Correlations between quantitative and qualitative traits were determined using Spearman's rank correlation. (SPSS, 2010). A cluster analysis was carried out using 15 morphological traits to determine genetic relationships among genotypes.

3.3 Results

3.3.1 Flower and tuber characteristics

Qualitative characteristics of the 48 tested genotypes are presented in Table 3.3. There were marked differences in the flowering ability of genotypes ranging from rare to very high. With regard to pollen production, 85% of the genotypes had pollen. Genotypes had different flower colors ranging from pink (14 genotypes), purple (12 genotypes), white (10 genotypes), violet (10 genotypes) to blue (2 genotypes). The majority of the genotypes had globe shaped tubers (27 genotypes), while otther ranged from oval (12 genotypes), short –oval (6 genotypes) to long-oval (3 genotypes). The skin color of the tubers varied from white (16 genotypes) to pink (12 genotypes), red (11 genotypes), white with pink points (4 genotypes), purple (3 genotypes) and cream (2 genotypes). The skin texture of the tubers was predominantly smooth, while a few had an intermediate (11 genotypes) or rough texture (8 genotypes). The majority of the genotypes had a cream tuber flesh (32 genotypes), while others had white fleshed tubers with a purple ring (2 genotypes), namely Cruza and Petero and the remainder had white fleshed tubers. The eye color of the tubers was largely white (22 genotypes) and red (17 genotypes). With regards to eye depth of the tubers, most genotypes (33 genotypes) had shallow eyes, six genotypes medium and the remaining genotypes had deep eyes.

3.3.2 Analysis of variance

The analysis of variance for tuber yield, main stem number, plant height, days to flowering and duration of flowering are presented in Table 3.4. Sites had significant effects on all measured parameters ($P < 0.01$) except days to flowering. Genotype effects were significant ($P < 0.01$) for yield, main stem number and plant height. Genotype and site interactions were only significant for the main stem number ($P < 0.01$).

3.3.3 Genotype means

Genotype means for tuber yield, main stem number, plant height, days to flowering and duration of flowering are presented in Table 3.5. The mean tuber yield across the two locations was 29.8 t ha^{-1}. The average yield was better at Kackwekano (31.9 t ha^{-1}) than at Karengyere (27.7 t ha^{-1}). Genotypes were assigned yield classes, where genotypes with yields above 30 t ha^{-1} were classified as high yielding (HY); moderate yielding (MY) when the yields ranged between 15 to 30 t ha^{-1}, and low yielding (LY) yielded below 15 t ha^{-1}. On the basis of yield classes, 52% of the genotypes were high yielding (30 t ha^{-1} and above), 8% were low yielding, while the rest were moderate yielding (between 15 and 30 t ha^{-1}). The highest yielding genotype across sites was 397038.105 with 46.0 t ha^{-1}, while the genotype 392633.64 had the the lowest yield (12.9 t ha^{-1}). On average, the genotypes at Kachwekano produced more stems and took more days to flower. At Karengyere, genotypes were taller and had a longer flowering duration. The tallest genotype was NAKPOT5 (68.4 cm), while genotype Kimuri was the shortest (33.4 cm).

Table 3.3: Qualitative characteristics of the 48 potato genotypes used in the study.

	Characteristics								
Genotype	**Flower color**	**Flower frequency**	**Tuber shape**	**Skin color**	**Skin texture**	**Flesh color**	**Eye color**	**Eye depth**	**Pollen production**
395017.14	Pink	Very high	Oval	White	Smooth	White	White	Shallow	Present
391919.3	Violet	Very high	Long-oval	Purple	Smooth	Cream	Purple	Medium	Absent
395109.34	Pink	Moderate	Short-oval	White, pink points	Smooth	Cream	Pink	Medium	Present
NKR159.41	Pink	Moderate	Oval	White	Smooth	Cream	White	Shallow	Present
395077.12	Violet	Moderate	Globe	White, pink points	Smooth	Cream	Pink	Shallow	Present
NAKPOT1	Blue	Rare	Globe	White	Smooth	White	White	Shallow	Present
Kimuri	White	Rare	Globe	White	Rough	White	White	Shallow	Present
Cruza	Violet	Very high	Short-oval	White	Smooth	White, purple	Purple	Shallow	Absent
391580.3	White	Very high	Globe	White	Intermediate	Cream	White	Shallow	Present
Petero	Pink	High	Globe	Red	Smooth	White, purple	Purple	Deep	Present
Rwashaki	Purple	Very high	Globe	Pink	Smooth	Cream	Pink	Deep	Present
395438.1	Pink	Moderate	Short-oval	Red	Smooth	Cream	Red	Shallow	Present
Rwangume	Purple	Moderate	Globe	Red	Smooth	Cream	Red	Medium	Present
NKRN59.29	Violet	Very high	Globe	Pink	Intermediate	Cream	Pink	Shallow	Present
392797.22	Violet	Moderate	Long-oval	Purple	Intermediate	White	White	Deep	Absent
Kinigi	Blue	Rare	Globe	Purple	Intermediate	Cream	Purple	Deep	Present
396038.105	Purple	Very high	Short-oval	Pink	Intermediate	White	Red	Shallow	Present
395011.2	Purple	High	Oval	White	Intermediate	Cream	White	Deep	Present
Kachpot1	Violet	Very high	Globe	Red	Rough	Cream	Red	Medium	Absent
392633.64	White	Moderate	Globe	White	Smooth	Cream	White	Shallow	Present

	Characteristics								
Genotype	**Flower color**	**Flower frequency**	**Tuber shape**	**Skin color**	**Skin texture**	**Flesh color**	**Eye color**	**Eye depth**	**Pollen production**
394895.7	Violet	Moderate	Long-oval	White	Rough	White	White	Shallow	Present
395096.2	Pink	Rare	Globe	White, pink points	Smooth	White	Red	Medium	Present
NKRN59.48	Pink	Moderate	Oval	Pink	Smooth	Cream	Red	Shallow	Present
Victoria	Pink	Rare	Globe	Red	Smooth	White	Red	Shallow	Present
NKRN59.61	White	Rare	Globe	Red	Rough	Cream	Red	Shallow	Present
396038.101	Violet	Moderate	Globe	Red	Rough	White	Red	Shallow	Present
Mabondo	Purple	High	Globe	White	Smooth	White	Red	Shallow	Absent
395015.6	White	Moderate	Oval	Red	Smooth	Cream	White	Shallow	Present
NKRN59.11	Purple	Moderate	Short-oval	Pink	Smooth	Cream	Red	Medium	Absent
NKRN59.58	White	Very high	Oval	Pink	Intermediate	Cream	White	Shallow	Present
396031.108	White	Moderate	Globe	White	Rough	Cream	White	Shallow	Present
396026.103	Purple	Moderate	Globe	Red	Rough	Cream	Red	Shallow	Present
396034.103	Purple	Very high	Globe	Red	Rough	Cream	Red	Medium	Present
396038.107	Purple	Very high	Globe	Pink	Intermediate	Cream	Red	Medium	Present
392661.18	Pink	Very high	Oval	White	Smooth	White	White	Shallow	Present
391002.6	White	Very high	Globe	White	Smooth	White	White	Shallow	Present
395112.32	Pink	High	Globe	Pink	Smooth	Cream	White	Shallow	Present
393220.54	Violet	High	Globe	White, pink points	Smooth	Cream	Red	Shallow	Present
396034.268	Pink	High	Globe	Red	Intermediate	Cream	Red	Shallow	Present
NAKPOT5	Violet	Moderate	Oval	White	Smooth	White	White	Shallow	Present
391046.14	White	Very high	Oval	Cream	Smooth	Cream	White	Shallow	Present

	Characteristics								
Genotype	**Flower color**	**Flower frequency**	**Tuber shape**	**Skin color**	**Skin texture**	**Flesh color**	**Eye color**	**Eye depth**	**Pollen production**
NKRK19.17	Purple	High	Short-oval	Pink	Smooth	Cream	Red	Deep	Present
392657.8	Purple	Very high	Oval	Pink	Smooth	Cream	Pink	Shallow	Present
393077.54	Pink	High	Globe	White	Intermediate	Cream	White	Medium	Present
Rutuku	Purple	Moderate	Oval	Red	Smooth	Cream	Red	Shallow	Present
NKRK19.10	Pink	Moderate	Globe	Pink	Smooth	Cream	White	Shallow	Absent
NKRN59.124	White	Moderate	Oval	Cream	Smooth	Cream	White	Shallow	Present
394905.8	White	High	Globe	White	Intermediate	White	White	Shallow	Present

Table 3.4: Analysis of variance showing mean squares and significance tests of tuber yield, main stem number, plant height, days to flowering and duration of flowering of 48 potato genotypes evaluated at Kachwekano and Karengyere sites in 2015**.**

		Mean squares				
Source of variation	DF	**Tuber yield**	**MSN**	**PH**	**DAF**	**DOF**
Block	7	245.97***	4.91***	216.89**	30.07	56.38
Replication	2	732.68***	4.50**	156.24	270.52***	1900.63***
Block/replicate	18	408.14***	2.25**	158.96**	20.18	5.14
Genotype	47	457.99***	6.25***	281.63***	21.79	28.40
Site	1	1341.60***	274.37***	1655.79***	5.84	1725.78**
Genotype*site	47	75.55	2.77***	90.61	29.92	27.85
Residual	163	58.13	1.21	73.62	35.00	49.36
Total	287	163.48	3.45	126.40	32.46	58.59

DF = degrees of freedom, MSN = main stem number, PH = plant height, DAF = days to flowering, DOF = duration of flowering,

*, **, *** significant at P≤0.05, P ≤0.01 and P≤0.001 respectively

Table 3.5: Tuber yield, main stem number, plant height, days to flowering and duration of flowering for 48 genotypes evaluated at Kachwekano and Karengyere research stations in Uganda

Genotype	Kachwekano	Karengyere	Mean yield across sites (t ha^{-1})	Class	MSN	PH (cm)	DAF	DOF
395017.14	13.1 a	12.6 abc	12.9	LY	1.9	46.1	48.8	33.3
391919.3	14.7 ab	11.3 ab	13.0	LY	2.7	62.0	44.0	38.8
395109.34	15.8 abc	10.9 a	13.4	LY	1.4	65.5	50.0	29.8
NKR159.41	16.5 abc	12.6 abc	14.6	LY	1.0	46.8	44.5	27.0
395077.12	18.6 a-d	20.1 a-h	19.4	MY	2.6	51.3	44.5	35.3
NAKPOT1	18.9 a-d	18.9 a-g	19.0	MY	3.2	50.7	51.5	34.0
Kimuri	19.3 a-d	14.9 a-d	17.1	MY	3.2	53.1	52.5	35.8
Cruza	20.3 a-e	20.3 a-h	20.3	MY	1.3	52.2	51.0	33.5
391580.3	20.3 a-e	20.3 a-h	20.3	MY	2.5	52.4	50.3	27.3
Petero	20.4 a-e	17.8 a-g	19.1	MY	2.6	33.4	41.0	29.0
Rwashaki	20.5 a-e	17.3 a-f	18.9	MY	3.4	39.5	46.3	28.0
395438.1	20.7 a-f	15.4 a-e	18.1	MY	1.0	50.4	43.5	17.8
Rwangume	21.2 a-g	21.2 a-i	21.2	MY	2.7	48.3	50.3	31.5
NKRN59.29	22.6 a-h	24.9 c-l	23.8	MY	2.8	44.3	41.5	32.0
392797.22	22.7 a-h	22.7 a-i	22.7	MY	2.0	52.9	47.0	35.5
Kinigi	24.0 a-i	24.0 a-j	24.0	MY	2.5	51.8	46.3	34.3
396038.105	24.5 a-j	24.5 b-k	24.5	MY	2.3	58.6	47.5	32.5
395011.2	25.5 a-k	25.5 c-l	25.5	MY	2.8	53.3	47.0	31.3
Kachpot1	28.8 b-l	22.1 a-i	25.4	MY	3.2	57.4	39.5	39.0
392633.64	28.9 b-l	24.6 b-k	26.8	MY	4.0	52.8	41.5	30.5

Genotype	Kachwekano	Karengyere	Mean yield across sites (t ha^{-1})	Class	MSN	PH (cm)	DAF	DOF
394895.7	30.3 c-l	25.7 c-l	28.0	MY	3.6	59.3	43.3	23.0
395096.2	32.1 d-m	50.9 o	41.5	HY	3.3	68.4	45.3	36.0
NKRN59.48	32.3 d-n	27.7 d-n	30.0	MY	4.0	51.2	41.8	31.0
Victoria	32.7 d-n	21.3 a-i	27.0	MY	2.7	55.3	42.0	35.0
NKRN59.61	34.2 e-n	30.4 f-n	32.2	HY	1.5	40.7	47.5	35.8
396038.101	35.3 f-n	27.4 d-m	31.3	HY	4.4	50.9	48.3	30.5
Mabondo	35.7 g-n	28.2 d-n	31.9	HY	1.6	48.4	46.3	32.5
395015.6	35.9 h-n	37.7 k-o	36.8	HY	4.6	62.7	46.8	29.8
NKRN59.11	35.9 h-n	27.5 d-n	31.7	HY	4.8	59.2	43.0	30.3
NKRN59.58	36.0 h-n	24.1 a-j	30.0	HY	3.7	48.9	42.8	32.0
396031.108	36.0 h-n	23.8 a-i	29.9	MY	3.8	54.0	45.0	33.5
396026.103	36.6 h-n	29.6 f-n	33.1	HY	4.3	62.0	44.0	34.0
396034.103	36.8 h-n	34.1 i-n	35.4	HY	3.0	56.6	40.8	33.3
396038.107	37.8 i-n	47.7 o	42.8	HY	4.7	66.9	45.0	30.5
392661.18	38.6 j-o	37.7 k-o	38.1	HY	5.1	64.8	42.0	28.0
391002.6	39.4 k-p	40.7 mno	40.3	HY	3.9	58.8	47.8	32.8
395112.32	40.0 k-q	31.0 g-n	35.5	HY	4.4	58.2	45.0	34.8
393220.54	40.3 l-q	40.3 mno	40.3	HY	3.0	54.3	44.0	40.8
396034.268	40.8 l-q	28.4 d-n	34.6	HY	4.5	61.0	47.3	39.3
NAKPOT5	41.7 l-q	28.6 d-n	35.1	HY	3.0	64.8	42.3	34.8
391046.14	42.5 l-q	50.1 o	46.3	HY	1.6	49.9	48.8	36.8
NKRK19.17	45.2 m-q	28.8 e-n	37.0	HY	4.1	64.8	46.3	35.5

Genotype	Kachwekano	Karengyere	Mean yield across sites (t ha^{-1})	Class	MSN	PH (cm)	DAF	DOF
392657.8	46.4 m-q	41.1 no	43.7	HY	2.2	53.5	45.5	33.3
393077.54	46.5 m-q	39.9 mno	43.2	HY	3.4	62.3	48.0	35.3
Rutuku	46.7 n-q	32.7 h-n	39.7	HY	4.5	65.2	45.8	34.3
NKRK19.10	52.9 opq	38.5 l-o	45.7	HY	3.5	63.4	47.3	34.0
NKRN59.124	54.1 pq	34.0 i-n	44.1	HY	3.5	53.9	41.8	36.0
394905.8	54.5q	37.6 j-o	46.0	HY	2.1	55.4	40.3	31.8
Mean	32	27.7	29.8	MKach	4.0	52.6	47.4	28.9
SED	7.3	6.8	5.0	MKar	2.0	57.4	43.4	36.5
LSD	14.6	13.6	9.9	GM	4.0	55.0	45.4	32.7
CV (%)	28.1	30	29.1	SED	0.9	7.1	4.1	5.8
				LSD	1.8	13.9	8.1	11.6
				CV (%)	36.9	15.7	12.6	25.3

HY = high yield; MY = medium yield; LY = low yield, **means in a column followed by the same letters are not significantly different at P=0.05, PH = plant height, MSN = main stem number, DAF = days to flowering, DOF = duration of flowering, MKach = mean Kachwekano, MKar = mean Karengyere, GM = grand mean, SED = standard error of difference, LSD = least significant difference, CV = coefficient of variation

3.3.4 Correlations between qualitative and quantitative traits

Correlations between morphological traits are presented in Table 3.6. For qualitative traits the following correlations were positive and significant; eye color with flesh color and skin color ($p \leq 0.001$), flower color with flower frequency ($p \leq 0.01$) and foliage cover ($p \leq 0.05$) and flower frequency with foliage cover ($p \leq 0.05$). Also tuber shape and eye depth were positively correlated. Eye depth was negatively correlated with eye color ($p \leq 0.001$), flesh color ($p \leq 0.01$), flower color ($p \leq 0.05$) and skin color ($p \leq 0.05$). Additionally, a significant negative correlation was observed between growth habit and skin texture ($p \leq 0.05$). Correlations between duration of flowering, and days to flowering and plant height were positive and significant ($p \leq 0.001$). On the other hand, a significant ($p \leq 0.01$) negative correlation was observed between days to flowering and main stem number. Significant positive corelations were also observed between duration of flowering and tuber yield ($p \leq 0.01$). The correlation between plant height and main stem number was negative and significant ($p \leq 0.05$). A significant positive correlation ($p \leq 0.001$) was observed between tuber yield and plant height.

.

Table 3.6: Spearman correlation coefficients between qualitative traits and pair-wise correlations between quantitative traits of 48 potato genotypes tested at Kachwekano and Karengyere research stations

Qualitative traits	Eye color	Eye depth	Flesh color	Flower color	Flower frequency	Foliage cover	Growth habit	Skin color	Skin texture	Tuber shape
Eye color	-									
Eye depth	0.54***	-								
Flesh color	0.49***	-0.34**	-							
Flower color	0.26	-0.33*	0.08	-						
Flower frequency	0.15	-0.21	0.25	0.34**	-					
Foliage cover	0.11	-0.09	0.14	0.28*	0.33*	-				
Growth habit	-0.12	-0.05	-0.05	-0.17	-0.01	-0.13	-			
Skin color	0.52***	-0.30*	0.25	0.18	-0.13	0.08	0.03	-		
Skin texture	0.15	-0.09	0.12	0.23	-0.02	0.14	-0.32*	-0.09	-	
Tuber shape	-0.16	0.31*	-0.09	-0.05	0.01	0.05	-0.13	-0.06	0.21	-

Quantitative traits	Days to flowering	Duration of flowering	MSN	Plant height
Days to flowering	-			
Duration of flowering	0.69***	-		
MSN	-0.41**	-0.09	-	
Plant height	0.76***	0.66***	-0.31*	-
Total tuber yield	0.25	0.41**	0.09	0.52***

MSN = main stem number; *, **, *** significant at P≤0.05, P ≤0.01 and P≤0.001 respectively

3.3.5 Level of genotypic diversity between genotypes

The level of genotypic diversity between the 48 genotypes is shown in Figure 3-1. The cluster analysis grouped genotypes into three major clusters, with 33, 8 and 7 genotypes. At the second level, major cluster 1 had 5 sub-clusters, major clusters 2 and 3, had 2 and 3 sub-clusters respectively. Among these 9 sub- clusters, genotypes were randomly grouped. Sub- cluster 1b had only one genotype (Rwashaki) and all genotypes from sub-clusters 8 and 9 were obtained from the international potato centre. From major cluster 1, 15 genotypes were identified to be used as parents. These were 395017.14, NAKPOT5, NAKPOT1, NKRN59.41, 391046.14, NKRN59.58, 393077.54, 396026.103, 396034.103, 391919.3, NKRK 19.17, 396038.107, Rwangume, Rutuku, NKRN59.48 and 392657.8. Three genotypes (393220.54, Kinigi and Kimuli) were selected from major cluster 2, while no genotype was identified from major cluster 3. All the selected genotypes possessed different desirable traits necessary for crop improvement. These ranged from high yields to early maturity and resistance to diseases, mainly late blight among others. The similarity distance varied from 0.5 to 1.0.

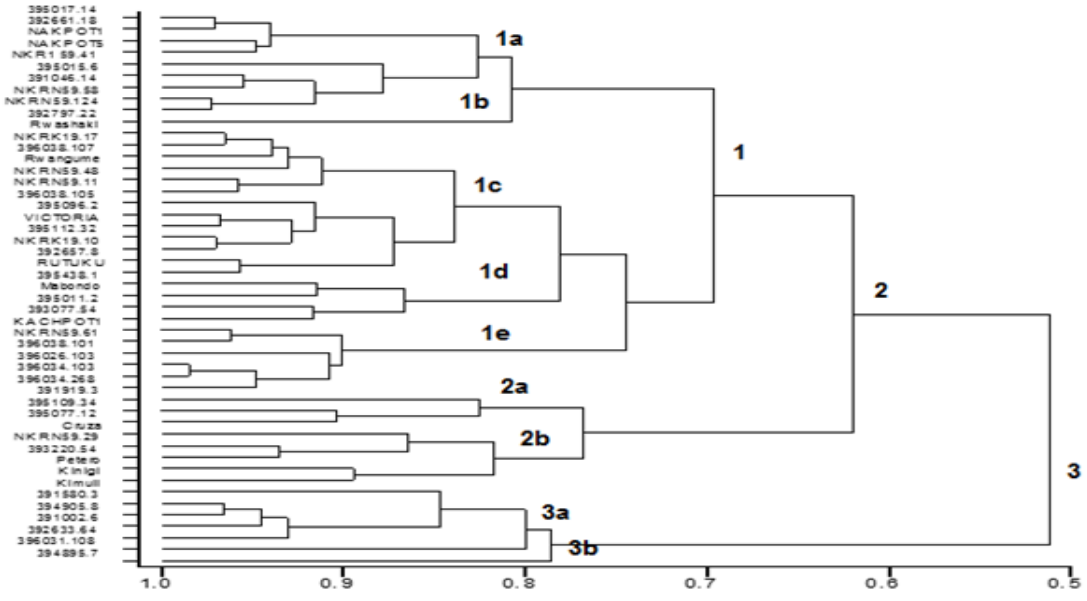

Figure 3-1: Dendogram showing principal genetic clusters of 48 potato genotypes using 15 phenotypic traits

3.4 Discussion

Genotypes with a good foliage cover had a higher flower frequency hence positive relationship. Genotypes with a high to very high flower frequency and pollen were chosen to be used as

parents. Genotypes with pink, purple and blue flowers had a good foliage cover compared to those with white flowers. This possibly explains the positive correlation between flower color and foliage cover. A high percentage of the studied genotypes had cream flesh color (67%) and the desired tuber shape of globe to oval (81%). The eye depth also influenced tuber shape.

Tuber characteristics in potato are subject to environment and genotype interactions (Abebe et al., 2013). Varietal preferences by farmers are high yields, disease resistance, early maturity, good marketability and good cooking quality (Low, 1997; Kaguongo et al., 2008; Muthoni et al., 2012). The most preferred tuber characteristics are high dry matter, smooth red or pink skin, shallow eyes and a cream flesh color (Tesfaye et al., 2010). In Uganda, skin color is a very important trait and greatly influences market demands and adoption (Forbes, 2012). For example, varieties like NAKPOT1 and NAKPOT5 have had low acceptance and marketability because of their white skin, despite their high yields. The variety Cruza, with resistance to *Phytophthora infestans* and bacterial wilt is not preferred by farmers because of purple coloration of the vascular rings when fried and because it becomes marshy on cooking (Low, 1997; Kaguongo et al., 2008). On the other hand Victoria, a variety that despite its susceptibility to late blight has had wide acceptance in the country because of its red skin, early maturity and high yields. Tuber shape is also increasingly becoming a trait of economic importance for processing (Muhinyuza et al., 2015). The preferred tuber shape is oblong and oval. In view of this, the selected parents for crosses possessed most of these traits. Tuber characteristics that may influence the choice by consumers include tuber shape, eye depth, and skin and flesh color as well as skin texture.

The quantitative flowering characteristics that were measured included the number of days to flowering and the flowering duration. The number of days to flowering and flowering duration are important in designing a crossing program to ensure synchronization in flowering and achieving hybridization (Acquaah, 2007). Duration of flowering ranged from 17 to 40 days. A long flowering duration range of 1 to 8 weeks was found among Indian and exotic potato varieties (Manivel et al., 2005). Genotypes with a longer duration of flowering were mainly selected to be used as females for breeding purposes, while those with sufficient pollen production were mainly used as males.

The evaluated genotypes varied significantly in tuber yield and other morphological characters. Environmental differences between Kachwekano and Karengyere, plus the inherent genetic variation among the test genotypes, were the primary causes of the variation in tuber yield. Muhinyuza et al. (2015) reported that the total tuber yield is affected by both by the genotype and

environment. According to Acquaah (2007), the genetic composition of a genotype influences the expression of heritable traits between and within environments.

The significant positive correlation between tuber yield and duration of flowering (r=0.41) implies that those genotypes with more flowering days produced higher yields compared to others. This may be explained by the longer vegetative growth stage, which supports the conversion of more photosythates to yield. The long flowering duration at Karengyere can be explained by the higher altitude conditions that could have favoured flowering over a longer period. The significant positive correlation between tuber yield and plant height observed in the present study is supported by other studies (Luthra, 2001; Mostafa and Felenji, 2011; Datta et al., 2014). The negative correlation between the number of stems and plant height may be explained by the fact that genotypes with more stems have to partition the photosythates to more sinks, leading to shorter stems (Datta et al., 2014).

Knowledge of genetic distance between possible parents is essential for breeding (Acquaah, 2007). Sufficient genetic diversity is required in designing a crossing program to generate new genetic recombinants. This allows selection of segregants with improved quantitative or qualitative traits such as yield (Korzun, 2003). Jacoby et al. (2003) reported significant differences between genotypes and genetic distance, ranging from 0.26 to 0.80 in a morphological characterization study of eight genotypes. In the present study, genotypes were assembled into three major clusters and nine sub- clusters with genetic distance ranging from 0.5 to 1.0. The grouping of potato genotypes obtained from CIP in one cluster points to a common ancestry as some of the genotypes could be selections from a single cross (Muthoni et al. 2014).

Potato is a clonally propagated crop that exhibits a high degree of incompatibility and inbreeding depression (Muthoni et al., 2012). Kaushik et al. (2007) reported that the use of suitable parents is the most efficient way of increasing yield and controlling diseases. In this study genotypes were selected on the basis of tuber yield and other agro- morphological characteristics. The following genotypes were selected from the different clusters for possible use as parents; 396034.103, 392657.8, NKRN59.58, NKRN19.17, Kinigi, Rutuku, NAKPOT5,396026.103, 393077.54, NKRN59.48, NKRN59.41, 396038.107, 393220.54, Rwangume, 391046.14 and 391919.3. These will be used in the development of potato varieties that are high yielding, early maturing and resistant to late blight.

3.5 Conclusions

The present study provided an analysis of the diversity among 48 potato genotypes evaluated at two locations in Uganda. Tuber yield, number of days to flowering, duration of flowering, pollen production, tuber shape, eye depth, and flower frequency were used to select the possible parents for further breeding purposes. The results of this study indicated that tuber shape is a very important trait in potato and is related to eye depth. Flesh and skin color can be simultaneously improved given their relation with eye color. Plant height and duration of flowering can be used to improve yield. Traits that were found to be negatively correlated with yield should be independently selected for. Variation for the different traits exhibited by the genotypes in this study should be exploited in breeding to obtain potato varieties with desirable qualities. Additional studies on these genotypes should focus on other yield related parameters such as the number of tubers per plant, average weight per tuber and number of secondary stems per plant. Furthermore, the processing aspects of these genotypes for quality product development should be considered.

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Chapter 4 : Yield response of potato genotypes to late blight disease caused by *Phytophthora Infestans* in Uganda

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Abstract

Potato (*Solanum tuberosum L*.) is a major food and cash crop, mainly grown by small-scale farmers in the highland regions of Uganda. Potato late blight is one of the major diseases limiting production with potential yield losses over 70%, making host resistance a strong element in integrated disease management. Many previously resistant potato varieties released in Uganda have become susceptible, demanding novel sources of resistance. The study was carried out to screen and select high yielding potato genotypes with resistance to *Phytophthora infestans* in Uganda. Forty eight genotypes, including advanced clones from the population B3C2 of the International Potato Centre, commercial and farmers' varieties, were evaluated under two environments for two seasons. Trials were laid out in an 8 x 6 alpha lattice design with three replications. Data were collected on the number of tubers per genotype, marketable tuber weight, total tuber yield, and late blight severity based on the relative area under the disease progress curve (rAUDPC). Genotypes showed significant differences in yield and resistance to blight. A higher disease severity was observed in Karengyere (56%). The average rAUDPC (= 100 max) across locations indicated that genotypes 395077.12 and 392657.8, with disease severity of 12% and 14%, respectively, were the most resistant, while Victoria (53%) and NKRN59.124 (48%) were the most susceptible. Mean tuber yield under late blight infection was 19.8 t ha^{-1}. The best yielding genotype across sites was 395112.32 (35.6 t ha^{-1}), while 394905.8 (10.3 t ha^{-1}) yielded the lowest. The mean marketable tuber yield was 15.0 t ha^{-1} with genotypes 395112.32 and 395109.34 having the highest yield of 33.6 t $ha^{-1}$and 24.5 t ha^{-1} respectively. Strong positive correlations were observed between yield and yield related parameters ($p \leq 0.001$), while those between rAUDPC and yield traits were negative. The following genotypes, 395112.32, 391919.3, 393220.54. 393077.54, 396038.107. 392657.8, Kinigi, 395014.17, NKRN59.58, NKRK19.17 and 395011.2, were identified as promising parents. These exhibited high to medium resistance to

Phytophthora infestans and high yields and will be used in the development of potato clones resistant to late blight.

Keywords: *Solanum tuberosum*, disease resistance, relative area under disease progress curve, tuber number, marketable weight

4.1 Introduction

Potato (*Solanum tuberosum L*) is the fourth most important staple crop after maize, rice and wheat worldwide (CIP, 2016). It is an important food and cash crop with uses in the starch industry. Uganda is the ninth largest producer of potato in Africa with an annual production of 774 600 tons harvested from about 106 000 hectares per year (FAOSTAT, 2016). The crop is grown by about 300 000 small-holder households in Uganda (UBOS 2016). However, potato yields have remained low, about 4.8 t ha^{-1} (FAOSTAT, 2016), against a potential of 25 t ha^{-1}, which can be achieved under good management and when suitable varieties are deployed. These low yields have been attributed to a number of confounding factors, which are biotic, abiotic, and socio-economic constraints, as well as poorly adapted and adopted varieties (Gildemacher et al., 2009). Diseases are the major limiting factor and these include - late blight caused by *Phytophthora infestans* (Mont.) de Bary, bacterial wilt (BW) ((*Ralstonia solanacearum* Yabuuchi et al., 1995), and viruses (Muhinyuza et al., 2012).

Late blight is the most devastating disease of potato, leading to yield losses of up to 70% (Sedláková et al., 2011). The disease occurs in all main potato growing areas (Hijmans et al., 2000), being favoured by moderately low temperatures and extended periods of leaf dampness. It is particularly detrimental in the highland tropics where potatoes are grown throughout the year, coupled with a poor ability of farmers to understand and manage the disease (Garrett et al., 2001). Late blight regularly reduces potato productivity leading to huge differences between realised yields.

Late blight causes both foliar and tuber decay (Acquaah, 2012). Tubers can become infected when the disease moves down the lower stem, below ground, and through the stolon. Potato tubers can also become infected when late blight spores from infected leaves and stems are washed into the soil via cracks and come into contact with tubers. Late blight is the major reason for the use of fungicides on potatoes in Uganda (Low, 1997). As much as disease management can be through the use of fungicides, most small-scale farmers cannot afford these because fungicides are expensive. In addition, fungicide application is by hand and farmers rarely use

protective clothing, thus posing health risks and diverse environmental hazards (Kromann et al., 2009; Forbes, 2012). Therefore, breeding for host resistance is a sustainable approach to manage and control late blight in Uganda. In view of this, advanced resistant breeding populations and candidate clones developed by the International Potato Centre (CIP) were obtained. These are suitable for a variety of agro-ecological zones including tropical highlands (CIP, 2012). The clones belong to 'population B recombination cycle 3 (Pop B3)', which lacks any known major or R genes against *P. infestans*. This population is the latest advanced source released by CIP for durable resistance to *Phytophthora infestans* (Landeo et al., 2001; Yao et al., 2011).

Developing potato varieties with durable resistance necessitates breeding for quantitative resistance against *Phytophthora infestans* (Landeo et al., 1999; Landeo et al., 2000; Forbes, 2012). This is because the R genes quickly break down due to the rapidly changing pathogen population. The aim of this study was to determine the yield response of different potato genotypes under late blight infection and identify parents with durable resistance for breeding purposes.

4.2 Materials and methods

4.2.1 Genetic materials

Plant materials in this study was made up of 48 potato genotypes which included advanced clones from CIP, commercial varieties and landraces commonly grown by farmers. The CIP clones are reported to have horizontal resistance to late blight. The details of the genotypes are presented in Table 4.1.

Table 4.1: Description of the 48 potato genotypes used in the study

No.	Genotype	Source	Year of release	No.	Genotype	Source	Year of release
1	391006.2	CIP	Not yet released	25	396580.3	CIP	Not yet released
2	391046.14	CIP	Not yet released	26	Cruza	NARO	1992
3	391919.3	CIP	Not yet released	27	Kachpot1	NARO	2006
4	392633.64	CIP	Not yet released	28	Kimuli	Farmer	Not available
5	392657.8	CIP	Not yet released	29	Kinigi	Farmer	1992
6	392661.18	CIP	Not yet released	30	Mabondo	Farmer	1989
7	392797.22	CIP	Not yet released	31	NAKPOT1	NARO	1996
8	393077.54	CIP	Not yet released	32	NAKPOT5	NARO	1996
9	393220.54	CIP	Not yet released	33	NAROPOT1	NARO	2015
10	394895.7	CIP	Not yet released	34	NAROPOT3	NARO	2015
11	394905.8	CIP	Not yet released	35	NKRK19.10	NARO	Not yet released
12	395011.2	CIP	Not yet released	36	NKRK19.17	NARO	Not yet released
13	395015.6	CIP	Not yet released	37	NKRN59.11	NARO	Not yet released

No.	Genotype	Source	Year of release	No.	Genotype	Source	Year of release
14	395017.14	CIP	Not yet released	38	NKRN59.124	NARO	Not yet released
15	395017.229	CIP	Not yet released	39	NKRN59.29	NARO	Not yet released
16	395077.12	CIP	Not yet released	40	NKRN59.41	NARO	Not yet released
17	395096.2	CIP	Not yet released	41	NKRN59.48	NARO	Not yet released
18	395109.34	CIP	Not yet released	42	NKRN59.58	NARO	Not yet released
19	395112.32	CIP	Not yet released	43	NKRN59.61	NARO	Not yet released
20	395438.1	CIP	Not yet released	44	Petero	Farmer	Not available
21	396026.103	CIP	Not yet released	45	Rutuku	NARO	1962
22	396038.101	CIP	Not yet released	46	Rwangume	NARO	2016
23	396038.105	CIP	Not yet released	47	Rwashaki	Farmer	Not released
24	396077.159	CIP	Not yet released	48	Victoria	NARO	1992

CIP = International Potato Centre, NARO = National Agriculture Research Organisation

4.2.2 Study sites

Field trials were established at the Kachwekano and Karengyere research stations of the National Agricultural Research Organisation (NARO). The study was conducted for two seasons in 2016 B (September to December) and 2017A (March to June). Kachwekano is located in South-western Uganda, 01º 16'S 29º 57'E at 2200 meters above sea level (masl). The soil type is isomeric typic palehumult (Kakuhenzire et al., 2013). Karegyere research station is located at 01º 13.2'S, 29º 47.8'E in South-western Uganda at an altitude of 2450 masl. Both sites have a bi-modal rainfall pattern separated by a dry spell ranging from 30 to 60 days. In both study sites, late blight occurs in epidemic proportions due to disease build-up as a result of continued potato farming.

4.2.3 Seed preparation and experimental design

The materials from CIP were received as *in vitro* plantlets, and were sub-cultured at the Kachwekano research station to raise 100 plantlets each. These were planted out in the screen house to generate minitubers in 2015 A. The generated mini-tubers were planted out in the season of 2015 B (September to December) to increase their numbers and size for evaluation in the subsequent seasons.

Evaluation trials were conducted for two seasons in 2016 (Season A: March to June and Season B: September to December). Genotypes were planted in an 8 x 6 alpha lattice design with three replications for two seasons. The plot size was two rows of 15 plants each at a spacing of 35 x 75 cm. Genotypes were exposed to natural infestation of late blight using spreader rows of a susceptible cultivar (Victoria) planted next to each plot. Variety Cruza was included as a resistant check. At the time of planting fertilizer N P K (17:17:17 %) was applied at a rate of 100 kg ha^{-1}.

Pest and disease control were done except for late blight. All recommended agronomic practices were followed.

4.2.4 Data collection

4.2.4.1 Disease evaluation and analysis

With the first appearance of the symptoms, plants in each plot were visually rated at 7-day interval for percentage leaf and stem area with late blight lesions. This was done by comparing the green and non-green leaf portions affected by the disease. Evaluations continued until susceptible clones reached 100% leaf blight. The area under the disease progress curve AUDPC was calculated within a single experiment for all plots and assessment dates (Campbell and Madden, 1990; Yuen and Forbes, 2009).

$$AUDPC = \sum_{i=1}^{n-1} [(T_{i+1} - T_i)(D_{i+1} + D_i)/2] \quad \text{(Equation 1)}$$

$$RAUDPC = \frac{\sum (T_{i+1} - T_i) * \left(\frac{D_{i+1} + D_i}{2} \right)}{T_{Total} * 100} \quad \text{(Equation 2)}$$

Where T_i is the ith day when an estimation of percentage foliar late blight is made and D_i is the estimated percentage of area with blighted foliage at T_i. T_{total} is the number of days at which the final assessment was recorded.

4.2.4.2 Yield and yield related traits

Yield for each plot was measured at harvest. The total number of tubers from each plot were counted and converted in tonnes per hectare (t ha^{-1}). To determine the marketable tuber weight (MTW), harvested tubers from each plot were separated into marketable (>30 mm) and unmarketable (<30 mm) types based on size. These were counted, weighed and marketable tuber yield expressed in t ha^{-1}.

4.2.5 Data analysis

Data were analysed using Genstat 14th edition (Payne et al., 2011) software package. Where significant differences were detected, means were separated using Fisher's protected least significant difference (LSD) test at 5% significance level. Combined analysis of variance was conducted with genotypes as the main effect.

4.3 Results

4.3.1 Weather data

Weather conditions were conducive for development of late blight in the trials. There was regular rainfall, and temperatures varied between 15 ºC and 18 ºC (Table 4.2) for the two sites and seasons. The relative humidity was high throughout the growing period, encouraging late blight epidemic in the study. In general, more rainfall was received in Karengyere, while Kachwekano recorded the highest temperatures.

Table 4.2: Rainfall, mean temperatures and relative humidity at Kachwekano and Karengyere research stations during the experimental period

Site	**2016B**			**2017A**			
Karengyere	**RF (mm)**	**AT (°C)**	**RH (%)**		**RF (mm)**	**AT(°C)**	**RH (%)**
September	162.4	16.8	88.2	March	114.1	16.1	83.4
October	174.1	16.1	86.5	April	247.6	15.3	84.2
November	272.6	13.4	88.4	May	184.6	15.8	83.4
December	65.8	17.2	82.8	June	25.1	16.5	85.4
Kachwekano							
September	80.3	17.2	86.3	March	110.6	18.0	79.9
October	184.3	16.3	86.8	April	217.0	17.1	81.5
November	201.5	15.2	86.3	May	147.0	18.2	78.6
December	95.8	16.8	82.1	June	14.4	18.9	74.0

RF =Total rainfall, AT = Average air temperature, RH=Relative humidity

4.3.2 Analysis of variance

The analysis of variance for the relative area under the disease progress curve (rAUDPC), marketable tuber yield (MTY), total number of tubers (TTN) and total tuber yield (TTY) among tested genotypes is presented in Table 4.3. Highly significant ($p<0.001$) differences were observed for all the measured parameters at both locations. Significant genotype x environment interactions were observed for both seasons and locations.

4.3.3 Late blight disease severity

Reaction of potato genotypes to late blight disease was expressed in terms of the relative area under disease progress curve (rAUDPC). Highly significant differences were observed among genotypes for their susceptibility to potato late blight ($P\leq0.001$) within locations and seasons (Table 4.4). The mean rAUDPC for both locations and seasons was 0.32. Late blight was more severe in Karengyere for both seasons and the highest mean score observed was 0.56 in 2016B. The most resistant genotypes were 395077.12 (0.12), 392657.8 (0.14) and 391919.3 (0.15), while genotypes Victoria (0.53), NKRN59.29 (0.48) and 391006.2 (0.47) were the most susceptible. Cruza, the resistant standard check, had a rAUDPC value of 0.24, while the susceptible check Victoria had a rAUDPC of 0.53. However, some clones were highly variable in their rAUDPC values across the two locations and seasons.

Table 4.3: Combined analysis of variance for rAUDPC and yield related traits of potato genotypes tested for two seasons at two locations in Uganda.

		rAUDPC	**TTY**	**MTW**	**TTN**
Source of variation	DF	MS	MS	MS	MS
Block	7	0.02	117.26**	26.27***	3646*
Replication	2	0.15**	682.32***	148.35***	2103***
Block/replicate	14	0.06**	275.08***	18.67***	5038***
Genotype	47	0.02	302.45***	27.70***	9730***
Location	1	1.09***	104.83	85.61***	24047***
Season	1	4.73***	24955.74***	2925.49***	236042***
Genotype*location	47	0.02	110.02***	14.29***	3416***
Genotype*season	47	0.02	74.16**	18.90***	6210***
Location*season	1	3.65***	124.35*	0.137	109
Genotype*location*season	47	0.02	71.32***	10.001	2922***
Residual	362	0.02	44.73	6.103	1589
Total	576	0.05	127.84	16.137	3508

*significant at P≤0.05; ** significant at P≤0.01; *** significant at P≤0.001; DF= degrees of freedom; MS = means squares; F pr = F probability; rAUDPC = relative area under the disease progress curve, TTN = Total number of tubers, TTY = total tuber yield; MTW = marketable tuber weight.

Table 4.4: Relative area under disease progress curve of 48 potato genotypes evaluated for two seasons at two locations in Uganda

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	0.29	0.42	0.36	0.77	0.41	0.59	0.47
391046.14	0.28	0.25	0.27	0.60	0.35	0.48	0.37
391919.3	0.04	0.12	0.08	0.40	0.04	0.22	0.15
392633.64	0.28	0.46	0.11	0.69	0.39	0.54	0.45
392657.8	0.13	0.08	0.11	0.29	0.06	0.17	0.14
392661.18	0.25	0.30	0.27	0.68	0.32	0.50	0.39
392797.22	0.36	0.31	0.33	0.61	0.37	0.49	0.41
393077.54	0.19	0.27	0.23	0.58	0.37	0.47	0.35
393220.54	0.04	0.13	0.08	0.36	0.11	0.24	0.16
394895.7	0.15	0.22	0.18	0.58	0.37	0.48	0.33
394905.8	0.30	0.51	0.40	0.52	0.44	0.48	0.44
395011.2	0.10	0.14	0.12	0.53	0.15	0.34	0.23
395015.6	0.15	0.23	0.19	0.62	0.20	0.41	0.30
395017.14	0.11	0.21	0.16	0.58	0.18	0.38	0.27
395017.229	0.06	0.21	0.14	0.43	0.29	0.36	0.25
395077.12	0.02	0.08	0.05	0.28	0.10	0.19	0.12
395096.2	0.12	0.11	0.11	0.41	0.10	0.26	0.19
395109.34	0.15	0.08	0.11	0.42	0.06	0.24	0.18

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
395112.32	0.13	0.21	0.17	0.38	0.17	0.27	0.22
395438.1	0.11	0.18	0.15	0.40	0.23	0.32	0.23
396026.103	0.40	0.31	0.36	0.64	0.33	0.48	0.42
396038.101	0.29	0.30	0.30	0.73	0.35	0.43	0.42
396038.105	0.23	0.20	0.22	0.62	0.39	0.50	0.36
396077.159	0.14	0.26	0.20	0.63	0.27	0.45	0.33
396580.3	0.26	0.40	0.33	0.75	0.18	0.46	0.40
CRUZA	0.10	0.22	0.16	0.39	0.28	0.33	0.24
KACHPOT1	0.36	0.35	0.35	0.66	0.23	0.44	0.40
KIMULI	0.31	0.25	0.28	0.65	0.29	0.47	0.38
KINIGI	0.24	0.30	0.27	0.45	0.33	0.39	0.33
MABONDO	0.14	0.29	0.21	0.36	0.30	0.33	0.27
NAKPOT1	0.23	0.13	0.18	0.65	0.25	0.45	0.32
NAKPOT5	0.14	0.21	0.18	0.67	0.35	0.51	0.34
NAROPOT1	0.24	0.27	0.26	0.62	0.33	0.47	0.37
NAROPOT3	0.21	0.18	0.20	0.71	0.31	0.51	0.35
NKRK19.10	0.13	0.21	0.17	0.61	0.23	0.42	0.29
NKRK19.17	0.18	0.26	0.22	0.51	0.41	0.46	0.34
NKRN59.11	0.29	0.33	0.31	0.63	0.30	0.47	0.39
NKRN59.124	0.28	0.15	0.21	0.56	0.20	0.38	0.30

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
NKRN59.29	0.24	0.38	0.31	0.77	0.54	0.66	0.48
NKRN59.41	0.11	0.13	0.12	0.55	0.13	0.34	0.23
NKRN59.48	0.20	0.27	0.23	0.66	0.35	0.51	0.37
NKRN59.58	0.13	0.26	0.19	0.40	0.32	0.36	0.28
NKRN59.61	0.11	0.25	0.18	0.59	0.46	0.53	0.35
PETERO	0.24	0.41	0.32	0.58	0.37	0.48	0.40
RUTUKU	0.17	0.23	0.20	0.66	0.31	0.48	0.34
RWANGUME	0.22	0.20	0.21	0.45	0.32	0.38	0.30
RWASHAKI	0.14	0.21	0.17	0.51	0.41	0.46	0.32
VICTORIA	0.39	0.50	0.44	0.74	0.51	0.63	0.53
Mean	**0.19**	**0.25**		**0.56**	**0.29**		**0.32**
LSD (0.05)	**0.15**	**0.11**		**0.21**	**0.18**		**0.16**
CV (%)	**48.1**	**27.4**		**23.0**	**38.3**		**30.6**
P-value	**0.001**	**0.001**		**0.001**	**0.001**		**0.001**

LSD = Least significant difference, CV = Coefficient of variation, RAUDPC = relative area under disease progress curve

4.3.4 Total tuber yield

The mean total tuber yield of 48 potato genotypes is presented in Table 4.5. Genotypes showed highly significant differences (P≤0.001) for total tuber yield (TTY) within locations and across seasons under late blight infection. The mean TTY was 19.8 t ha^{-1}. The TTY was higher in Kachwekano than at Karengyere in the 2016B season, while both sites had the same yield in 2017A. The highest overall yield recorded was 27.3 t ha^{-1} in 2016B at Kachwekano. In general, genotypes 395112.32 (35.6 t ha^{-1}), 395109.34 (31 t ha^{-1}) and 395096.2 (30.3 t ha^{-1}) were the best yielders, while 394905.8 (10.3 t ha^{-1}), 392633.64 (10.9 t ha^{-1}) and NKRN 59.124 (11.3 t ha^{-1}) were the lowest yielders across sites and seasons. The lowest yielders were below the standard susceptible check Victoria (14.1 t ha^{-1}), whereas the best yielders were above the resistant check Cruza (28.2 t ha^{-1}). At Kachwekano, the highest yielders were 395112.32 (40 t ha^{-1}) and 393220.54 (30.7 t ha^{-1}), while the lowest were NKRN 59.29 (9.2 t ha^{-1}) and NKRN 59.41 (9.6 t ha^{-1}). Genotypes 392657.8 (35.3 t ha^{-1}) and 395096.2 (32.4 t ha^{-1}) yielded best in Karengyere, whereas 394905.8 (6.4 t ha^{-1}) and NKRN 59.124 (9.8 t ha^{-1}) were the lowest yielders.

Table 4.5: Total tuber yield in t ha^{-1} of 48 potato genotypes evaluated at two locations for two seasons in Uganda

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	23.0	9.3	16.2	24.7	15.8	20.2	18.2
391046.14	21.7	12.1	16.9.	23.2	6.1	14.7	15.8
391919.3*	34.2	17.3	25.8	32.7	25.4	29.0	27.4
392633.64	16.3	7.3	11.8	10.2	10.0	10.1	10.9
392657.8	24.3	9.8	17.0	47.1	23.5	35.3	26.2
392661.18	28.2	13.8	21.0	29.1	12.8	20.9	21.0
392797.22	20.0	12.0	16.0	24.5	15.3	19.9	18.0
393077.54	33.2	10.5	21.9	36.4	13.2	24.8	23.4
393220.54*	41.3	20.1	30.7	18.4	16.6	17.5	24.1
394895.7	18.8	17.0	17.9	12.1	8.6	10.3	14.1
394905.8	23.6	4.8	14.2	10.3	2.5	6.4	10.3
395011.2	21.6	11.3	16.5	21.6	20.1	20.9	18.7
395015.6	25.9	17.9	21.9	30.9	22.2	26.5	24.2
395017.14	45.7	12.8	29.2	25.3	12.7	19.0	24.1
395017.229	35.5	15.5	25.5	6.9	9.6	8.2	16.9
395077.12	31.1	19.6	25.4	39.6	14.7	27.2	26.3
395096.2	36.9	19.4	28.1	41.5	23.3	32.4	30.3
395109.34*	38.8	22.5	30.6	33.5	29.2	31.4	31.0
395112.32*	56.3	23.8	40.0	41.0	21.4	31.2	35.6

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
395438.1	21.6	9.6	15.6	13.3	9.3	11.3	13.5
396026.103	23.3	11.2	17.2	17.7	13.5	15.6	16.4
396038.101	27.3	11.8	19.5	17.9	6.9	12.4	16.0
396038.105	35.7	17.9	26.8	29.3	19.0	24.2	25.5
396077.159	27.0	9.4	18.2	25.1	13.2	19.1	18.7
396580.3	29.0	14.2	21.6	19.4	19.0	19.2	20.4
CRUZA	35.1	18.7	26.9	41.5	17.6	29.6	28.2
KACHPOT1	23.7	14.2	18.9	25.7	12.5	19.1	19.0
KIMULI	28.5	13.6	21.0	17.6	12.6	15.1	18.1
KINIGI	27.5	12.2	19.9	38.4	13.8	26.1	23.0
MABONDO	33.9	16.7	25.3	23.4	12.7	18.1	21.7
NAKPOT1	24.7	16.6	20.7	19.7	5.1	12.4	16.5
NAKPOT5	21.5	7.5	14.5	33.9	8.4	21.2	17.8
NAROPOT1	19.3	11.8	15.5	23.1	11.0	17.0	16.3
NAROPOT2	26.1	16.3	21.2	26.2	12.1	19.2	20.2
NKRK19.10	27.3	10.2	18.8	31.5	3.9	17.7	18.2
NKRK19.17	24.9	12.2	18.5	21.4	9.5	15.4	17.0
NKRN59.11	19.6	13.8	16.7	26.6	7.2	16.9	16.8
NKRN59.124	20.0	5.8	12.9	14.4	5.1	9.8	11.3
NKRN59.29	12.0	6.5	9.2	25.4	5.0	15.2	12.2

Site	Kachwekano			Karengyere			
	Season						
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
NKRN59.41	13.6	5.6	9.6	20.7	6.8	13.8	11.7
NKRN59.48	26.0	8.3	17.2	16.0	15.7	15.8	16.5
NKRN59.58	27.5	9.7	18.6	15.8	11.1	13.4	16.0
NKRN59.61	22.8	5.4	14.1	23.8	12.4	18.1	16.1
PETERO	25.3	13.1	19.2	33.7	15.2	24.5	21.8
RUTUKU	33.9	17.2	25.6	28.8	14.2	21.5	23.5
RWANGUME	26.3	24.1	25.2	34.8	18.1	26.5	25.8
RWASHAKI	26.3	15.2	20.7	26.0	14.3	20.1	20.4
VICTORIA	22.1	5.4	13.8	21.9	6.8	14.3	14.1
Mean	**21.9**	**9.5**		**21.2**	**7.4**		**15.0**
LSD (0.05)	**12.7**	**5.9**		**5.9**	**9.3**		**10.8**
CV (%)	**28.8**	**27.7**		**36.6**	**43.5**		**34.1**

LSD = Least significant difference, CV = Coefficient of variation.

4.3.5 Marketable tuber yield

The marketable tuber yield (MTY) in tons per hectare for the 48 potato genotypes is presented in Table 4.6. There was a highly significant (P≤0.001) genotype effect for marketable tuber weight across locations. The mean marketable tuber yield was 15.0 t ha^{-1}, highest being 15.8 t ha^{-1} at Kachwekano. More marketable yield was obtained from Kachwekano for both season compared to Karengyere. Across sites and seasons, genotypes 395112.32 and 395109.34 had the highest marketable weight of 33.6 t $ha^{-1}$and 24.5 t ha^{-1} respectively, while the lowest was recorded for genotypes NKRN59.29 (8.6 t ha^{-1}) and NKRN59.41 (8.4 t ha^{-1}).

Table 4.6: Marketable tuber yield in t ha^{-1} of 48 potato genotypes evaluated at two locations for two seasons in Uganda

Site	Kachwekano			Karengyere			
			Season				
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	27.45	6.22	16.84	29.88	10.83	20.36	18.60
391046.14	12.57	5.58	9.08	14.33	4.85	9.59	9.33
391919.3	21.49	9.84	15.67	25.51	13.60	19.56	17.61
392633.64	12.45	4.90	8.68	8.23	6.56	7.40	8.04
392657.8	21.81	7.38	14.60	43.63	16.53	30.08	22.34
392661.18	19.93	11.60	15.77	23.01	7.99	15.50	15.63
392797.22	16.59	9.65	13.12	21.51	7.55	14.53	13.83
393077.54	28.16	7.78	17.97	31.38	8.70	20.04	19.01
393220.54	36.44	15.93	26.19	16.53	10.17	13.35	19.77
394895.7	14.62	14.36	14.49	7.46	4.61	6.04	10.26
394905.8	17.32	1.92	9.62	7.00	0.94	3.97	6.80
395011.2	16.12	6.87	11.50	18.21	14.92	16.57	14.03
395015.6	18.27	12.92	15.60	24.59	11.21	17.90	16.75
395017.14	37.25	9.07	23.16	18.68	7.13	12.91	18.03
395017.229	29.83	12.83	21.33	4.13	4.06	4.10	12.71
395077.12	23.00	15.56	19.28	35.44	8.72	22.08	20.68
395096.2	26.68	15.01	20.85	31.95	15.16	23.56	22.20
395109.34	33.46	15.32	24.39	29.02	20.22	24.62	24.51
395112.32	58.60	19.50	39.05	41.34	14.95	28.15	33.60

Site	Kachwekano			Karengyere			
			Season				
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
395438.1	18.52	7.72	13.12	8.82	2.86	5.84	9.48
396026.103	19.07	7.33	13.20	12.98	7.44	10.21	11.71
396038.101	23.06	12.90	17.98	20.72	5.46	13.09	15.54
396038.105	24.30	7.93	16.12	27.63	3.06	15.35	15.73
396077.159	32.52	14.97	23.75	23.22	10.65	16.94	20.34
396580.3	17.34	9.54	13.44	20.73	5.48	13.11	13.27
CRUZA	23.49	5.35	14.42	16.99	6.86	11.93	13.17
KACHPOT1	18.36	11.41	14.89	16.99	12.35	14.67	14.78
KIMULI	25.46	12.10	18.78	28.41	8.45	18.43	18.61
KINIGI	19.48	11.59	15.54	21.81	7.31	14.56	15.05
MABONDO	20.33	8.20	14.27	12.37	5.73	9.05	11.66
NAKPOT1	23.52	8.88	16.20	35.14	7.84	21.49	18.85
NAKPOT5	19.80	8.75	14.28	13.05	3.18	8.12	11.20
NAROPOT1	21.92	14.26	18.09	16.13	2.80	9.47	13.78
NAROPOT3	19.35	5.43	12.39	31.15	3.34	17.25	14.82
NKRK19.10	22.30	7.09	14.70	22.31	2.03	12.17	13.43
NKRK19.17	20.04	9.23	14.64	17.78	5.53	11.66	13.15
NKRN59.11	15.49	8.81	12.15	23.30	3.35	13.33	12.74
NKRN59.124	14.69	3.86	9.28	12.40	2.11	7.26	8.27
NKRN59.29	5.16	3.94	4.55	23.28	2.16	12.72	8.64

Site	Kachwekano			Karengyere			
			Season				
Genotype	2016B	2017A	Across seasons	2016B	2017A	Across seasons	Across seasons and sites
NKRN59.41	10.27	4.17	7.22	16.30	2.98	9.64	8.43
NKRN59.48	20.91	5.91	13.41	11.23	8.49	9.86	11.64
NKRN59.58	23.30	7.11	15.21	12.94	3.23	8.09	11.65
NKRN59.61	16.26	2.47	9.37	20.33	7.11	13.72	11.54
PETERO	20.27	9.21	14.74	29.12	6.01	17.57	16.15
RUTUKU	30.01	14.54	22.28	24.63	9.87	17.25	19.76
RWANGUME	19.42	18.60	19.01	28.86	9.08	18.97	18.99
RWASHAKI	22.25	12.87	17.56	21.38	6.91	14.15	15.85
VICTORIA	15.94	1.59	8.77	14.91	2.73	8.82	8.79
Mean	**13.0**	**5.6**	**9.3**	**11.8**	**4.3**	**8.1**	**8.9**
LSD (0.05)	**4.8**	**1.8**		**2.8**	**2.2**		**3.9**
CV (%)	**15.6**	**13.9**		**17.1**	**24.5**		**17.1**

LSD = Least significant difference, CV = Coefficient of variation

4.3.7 Relationships between late blight disease and yield parameters

Phenotypic correlations between four traits are presented in Table 4.8. Correlations between MTW, total tuber number and total tuber yield were positive and highly significant (p≤0.001) across sites and seasons. For all sites and seasons, a highly significant positive correlation (p≤0.001) was observed between the total number of tubers and total tuber yield. Correlations between RAUDPC and other traits were negative and significant for both sites (p≤0.01). However, for across sites and seasons, correlations between RAUDPC and other traits were non-significant except for total number of tubers.

Table 4.7: Phenotypic correlation between traits of 48 potato genotypes tested for two seasons at two locations in Uganda

Traits	MTW	TTN	TTY	RAUDPC
Kachwekano				
MTW	1.00			
TTN	0.63***	1.00		
TTY	0.87***	0.59***	1.00	
RAUDPC	-0.34***	-0.24***	-0.39***	1.00
Karengyere				
MTW	1.00			
TTN	0.66***	1.00		
TTY	0.87***	0.67***	1.00	
RAUDPC	-0.23**	-0.12*	-0.21**	1.00
Across seasons and sites				
MTW	1.00			
TTN	0.65***	1.00		
TTY	0.87***	0.63***	1.00	
RAUDPC	-0.02	-0.07*	-0.02	1.00

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; RAUDPC = relative area under the disease progress curve; TTY = total tuber yield; MTW = marketable tuber weight; TTN = total number of tubers

4.4 Discussion

The present study evaluated the response of 48 potato genotypes for late blight disease, yield and related traits for two seasons from two major potato growing locations in the highland regions of Uganda. The evaluated genotypes varied significantly in resistance to *Phytophthora infestans*

disease, marketable tuber weight and total tuber yield across seasons as well as sites. The highly significant differences observed among genotypes at both sites and seasons indicate variability in the genetic makeup of the different potato clones. The significant interaction shows that the clones did not respond equally in all environments, pointing to specific adaptation. The study environments also distinguished genotype performance suggesting the existence of environmental variation. Significant interaction of genotypes with environment in relation to late blight disease development and yield parameters have been observed in other studies (Muhinyuza et al., 2015; Hirut, 2015).

In general, a high total tuber yield is influenced by a combined genotype and environment effect. This is true for all growth and yield related parameters (Muhinyuza et al., 2014). Genotypes with the highest number of total tubers were not necessary the highest yielders implying that total tuber yield is predominantly influenced by tuber weight. However, Mehdi et al. (2008) found that the total tuber yield is mainly attributed to a higher number of tubers per plant and tuber size. This may explain the positive correlation between total tuber yield and marketable tuber weight. The higher total tuber yield and marketable tuber weight from both sites in 2016B could be explained by the late onset of the late blight. The disease appeared several days after flowering and barely affected yield. The similar yield obtained from both locations in 2017A could be attributed to the same level of disease pressure at both locations.

The severity of late blight and the resulting yield reduction in the present study seems to be correlated with the amount of precipitation received during the growing season. The prevailing weather conditions at Karengyere offered a favourable environment for disease development leading to high RAUDPC values and the subsequent reduction in all yield parameters. This is because temperature and humidity are the principal factors in late blight disease development (Hannukkala et al., 2007; Sedkalova et al., 2011; Forbes, 2012).

Disease development varied across locations and resulted in differential responses of genotypes for late blight severity. Genotypes with lower RAUDPC values did not necessarily have higher total tuber yield nor other yield parameters. For example, genotype 395077.12 had the lowest mean RAUDPC across sites and seasons, but was not the best yielder, while the highest yielder 395112.32 had a relatively high RAUDPC of 0.22. However, some consistency was observed for the lowest yielding and susceptible genotypes like 394905.8, NKRN 59.41 and NKRN59.124. The poor yield performance of some genotypes with low RAUDPC values could be explained by the fact that most of the resources are channelled to fighting the pathogens. The differential

performance of clones with moderately resistance to *Phyphthora infestans* across seasons and environments has been reported in other studies (Mulema et al., 2004; Forbes et al., 2005). These inconsistencies in reaction to late blight disease can be attributed to isolate variability and environmental variation or a synergy of all (Flier et al., 2003; Forbes et al., 2005).

The commercial varieties that were previously resistant and farmer varieties had high RAUDPC values, an implication that their resistance has broken down. This could be supported by the fact that most of the varieties were bred on the concept of qualitative resistance with single R genes, which is easily broken down by the changing pathogen population (Landeo et al., 1999; Landeo et al., 2000; Kumar et al., 2007). This justifies the need to breed for horizontal resistance.

The positive and highly significant correlations between marketable tuber weight, total tuber number and total tuber yield observed in this study were reported elsewhere (Muhinyuza et al., 2015; Hirut, 2015). The negative correlation between RAUDPC and total tuber yield, plus other yield related traits, has been reported in other studies (Dowley et al., 2008; Mantecón, 2009). These results suggest that late blight affects tuber yield through the destruction of the foliage and the resultant reduction of the photosynthetic area.

Overall, genotypes with good levels of resistance to potato diseases had high tuber yields and would be promising candidate parents in a disease breeding program. Kaushik et al. (2007) stated that the use of breeding materials with high yield and good resistance levels to potato late blight are one of the most effective strategies to control the disease and improve yield.

4.5 Conclusion

Genotypes in the current study showed significant differences in the level of resistance to *Phytophthora infestans*, yield and yield related traits. Genotype 395112.32 was the best performer in all seasons and sites for all yield related aspects, except for total number of tubers. The following clones: 395112.32, 395109.34, 393220.54, 395011.2, 391919.3, 395077.12, 393077.54 395096.2, 395017.14, 392657.8 and Rwangume had a high to moderate resistance to late blight disease across the study sites and seasons. The use of host plant resistance is the most effective disease management strategy to control late blight and increase yield without causing harm to the environment from overuse of fungicides. The study largely selected eleven high yielding potato genotypes with sufficient level of late blight resistance that can be commended for the use in a breeding program or for direct introduction following yield stability tests and official release.

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Chapter 5 : Genetic characterization and diversity assessment of potato genotypes using SSR markers

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Abstract

Information on the diversity of genetic materials is vital for choosing parents in a breeding program. The objective of the study was to determine the pattern and level of genetic diversity among 20 selected tetraploid potato genotypes using 16 SSR markers to identify suitable parents for breeding purposes. The microsatellites showed considerable variation among genotypes and 64 alleles were amplified by the 16 primer pairs. The number of polymorphic alleles per locus ranged from 2 to 8, with an average of 3.9. The highest number of null alleles was observed was six for genotype Nakpot1. The overall size of the amplified product varied from 48 bp (marker STI0023) to 309 bp (marker STM5121). The PIC values ranged from 0.0948 to 0.7832, with an average of 0.4307 per locus. Heterozygosity values ranged from 0.0997 to 0.805, with an average of 0.466919. Significant positive linear correlations were observed between PIC values and number of alleles (r=0.905), and between heterozygosity values and the number of alleles (r=0.8659) at $p < 0.001$. The cluster analysis separated the genotypes into three different groups. The genetic distance between clones ranged from 1 to 5.7. The variety Cruza had the highest genetic distance, while the shortest genetic distance was observed between 396026.103 and 396034.104. The microsatellites used in this study provided useful information regarding the variability of the tested genotypes and their selection for breeding purposes.

Key words: Genetic variation, polymorphism, clustering, heterozygosity, microsatellites

5.1 Introduction

The cultivated potato, *Solanum tuberosum* L., is a highly heterozygous autotetraploid species (2n = 4x = 48), with a genome size of 844 Mb (Muthoni et al., 2014). Pollination of the species is primarily through outcrossing and it experiences severe inbreeding depression (Park et al., 2009). The crop displays tetrasomic inheritance, which results in an increased number of progeny classes and allelic dosage (Hirut, 2015).

Selection of parental materials and understanding of appropriate parents to be used for a particular mating design are key in breeding (Acquaah, 2007). To select the best parents and cross-combinations, breeders have use a number of approaches. These include; -combining ability effects, use of mid-parent values, progeny tests, estimated breeding values, and genetic diversity (Gopal, 2015). However, to obtain reliable results with the intricacies of potato genetics and inheritance pattern, various methods should be combined to aid in the selection of parents (Sharma and Nandineni, 2014). While a narrow genetic base would result into inbreeding depression as a consequence of accumulation of deleterious alleles in a population (Gopal, 2014), a high level of genetic diversity among potato genotypes, possessing different desirable traits, is important for crop improvement. This is because the selection of parents based on genetic diversity will maximize heterozygosity, broaden the genetic base and produce heterotic progenies (Sun et al., 2003).

Diversity assessment can be achieved through the use of phenotypic information, pedigree, biochemical and molecular markers (Govindaraj et al., 2015). The use of molecular markers is the most reliable method of assessing genetic diversity because they are stable and independent of the environment. They are also not affected by the developmental stage of the plant, pleiotropic and or epistatic effects. Different molecular markers have been used to estimate the genetic diversity in plants and animals. These comprise of random amplified polymorphic DNAs (RAPDs), restriction fragment length polymorphism (RFLPs), amplified fragment length polymorphism (AFLP), microsatellites or simple sequence repeats (SSRs), and single nucleotide polymorphisms (SNPs), among others. With RAPDs, the primers are commercially available and do not require prior information of the target DNA sequence. However, this type of marker does not easily demonstrate Mendelian inheritance of the loci and is unable to differentiate between homozygotes and heterozygote. The key strength of RFLP markers is that they are codominant markers and relatively easy to score because of the large size difference. The major shortcoming of these markers is that they either require sequence information or probes. This makes it difficult and time-consuming to develop markers for species lacking known molecular information (Liu and

Cordes, 2004). AFLPs are reliable but expensive, labour intensive with long assays (Tiwari et al., 2013).

Microsatellites are therefore the most commonly used markers due to their strong molecular approach to genetic diversity studies. Microsatellites are highly polymorphic, abundant, co-dominant and can be used to detect heterozygosity. They are simple to use, provide high genetic information and are highly reproducible (Muthoni et al., 2014). Additionally, the SSRs have the capacity to reflect ploidy status with the high heterozygosity of the tetraploid potatoes. It is against this back ground that SSR markers were used in this study to determine the genetic relationships among 20 potato clones with variable resistance to late blight.

5.2 Materials and method

5.2.1 Plant materials

The test materials comprised of 20 potato genotypes. These were 11 commercial varieties from the National Potato Program, six farmer varieties, three CIP clones of which two were released as varieties in Uganda and two crosses from the national potato research centre with variable resistance to *Phytophthora infestans* (Table 5.1).

Table 5.1: List of the twenty potato genotypes and their sources

Entry	Clones	Source	Entry	Clones	Source
1	Cruza	NARO	11	NKRI59.41	NARO
2	Kabera	Farmer	12	Petero	Farmer
3	Kachpot1	NARO	13	Rwangume	NARO
4	Kimuri	Farmer	14	Rwashaki	NARO
5	Kinigi	Rwanda	15	Rutuku	NARO
6	Mabondo	Farmer	16	Shutama	Farmer
7	Mbubamagara	Farmer	17	Victoria	NARO
8	Nakpot1	NARO	18	396026.103	CIP
9	Nakpot5	NARO	19	396034.103	CIP
10	NKRK19.10	NARO	20	396038.107	CIP

Notes: CIP=International Potato Centre, NARO=National Agricultural Research Organisation

5.2.2 DNA extraction and SSR amplification

Fresh young leaves were picked from one month old plants in the field for DNA extraction. The DNA was obtained using fast technology for analysis of nucleic acids (Whatman FTA cards),

following modified protocols of FTA paper technology (Mbogori et al., 2006). One FTA classic card measures 750 x 130 mm and each was labelled prior to the day of sampling. Ten plants were sampled from each clone and one leaf per plant. Each sampled leaf was immediately placed on the FTA card and pressed using a pair of pliers until both sides of the FTA paper were covered with the sap. Ethanol 70% was used to clean the pliers between samples to prevent cross contamination. The FTA card was then dried at room temperature for 2–5 hours, after which they were packed and sent to INCOTEC South Africa (PTY) Ltd. for laboratory analysis. The DNA was extracted from FTA cards and 16 microsatellite markers were used. These were; - STM2013, STM1104, STM1049, STM0037, STI0012, STI0023, STI0030, STI0036, STI0032, STWAX-2, STI046, STI031, STM0030, STM1031, STM5121, STM0019a and STPoA58.

5.2.3 Data analysis

The PCR products were fluorescently labelled and separated by capillary electrophoresis on an ABI 313oxl automatic sequencer (Applied Biosystems, Johannesburg, South Africa). The analysis was performed using GeneMapper 4.1. The SSR marker alleles were scored for the presence or absence of the band for all the 20 potato genotypes. Each amplified fragment was considered as one locus. The GGT 2.0 program (Berloo, 2008) was used to calculate the Euclidian distances between bulked samples and the matrix of the genetic distances was used to create a UPGMA dendogram. The genetic similarity matrix of potato genotypes was calculated using the Jaccard‟s coefficient (Anderberg, 1973). Genetic diversity parameters, such as the total number of alleles per locus, expected heterozygosity and polymorphic information content (PIC) were determined. The PIC, which is a measure of allelic diversity, was calculated, based on the equation: PIC = 1 – Σ (pi^2), where pi is the frequency of i^{th} allele in the accessions. The Pearson's correlation coefficients showing pair-wise association between PIC, heterozygosity value and the number of alleles were calculated using Genstat statistical package, 14th edition (Payne et al., 2011).

5.3 Results

5.3.1 Allelic information

The 16 SSR markers (Table 5.2) uniquely differentiated the 20 potato genotypes used in this study. The markers differed significantly in their ability to establish variability amongst the clones. Particular markers generated several alleles, while others produced a few. The 16 SSR primers identified a total of 64 alleles among the test clones. The number of polymorphic alleles scored across the SSR loci ranged from 2 to 8 with an average of 3.9. The number of polymorphic alleles above average was obtained from only 50% of the markers. Null alleles were observed for some

markers and the genotype with the highest frequency recorded was NAKPOT1. With this genotype 38% (6) of the markers failed to yield detectable amplification. This was followed by genotype Mbubamagara with 31% of null alleles. The overall size of the amplified product varied from 48 bp (marker STI0023) to 309 bp (marker STM5121).

The heterozygosity values, the measure of allelic diversity at a locus ranged from 0.0997 to 0.805 with an average of 0.466919. The level of polymorphism among the potato clones was evaluated by calculating polymorphic information content (PIC) values for each of the 16 SSR loci which differed significantly from locus to another. These ranged from 0.0948 for markers STI002 to 0.7832 for STI031, with an average value of 0.4307 per locus (Table 5.2). However, markers STI0023, STM1049, STM0037 and STM5121 had a very limited ability to detect differences among the potato genotypes as shown by their low PIC values. The marker with the highest PIC value (0.805) was STI031. There was significant positive linear correlations between the PIC values and the number of alleles, and between heterozygosity values and the number of alleles at the SSR locus ($r = 0.905$ and $r = 0.8659$; $p < 0.001$) respectively (Table 5.3).

Table 5.2: SSR, chromosome location, repeat types and primer sequences, allelic information, heterozygosity and PIC values of 16 SSR loci used for genotyping

Marker name	Chromosome	Repeat	Primer sequences(5'-3') Forward-Reverse	Allele size (range bp)	No of alleles	He	PIC	PGI Kit
STM2013	7	(TCTA)6	TTCGGAATTACCCTCTGCC AAAAAAAGAACGCGCACG	164-166	2	0.420	0.338	No
STM1104	8	(TCT)5	TGATTCTCTTGCCTACTGTAATCG CAAAGTGGTGTGAAGCTGTGA	185-189	4	0.565	0.509	Yes
STM1049	1	(ATA)6	CTACCAGTTTGTTGATTGTGGTG AGGGACTTTAATTTGTTGGACG	201-210	3	0.277	0.257	No
STM0037	11	(TC)5(AC)6AA(AC)7(AT)4	AATTTAACTTAGAAGATTAGTCTC ATTTGGTTGGGTATGATA	89-96	3	0.265	0.247	Yes
STI0012	4	(ATT)n	GAAGCGACTTCCAAAATCAGA AAAGGGAGGAATAGAAACCAAAA	185-191	3	0.602	0.531	Yes
STI0023	10	(CAG)n	GCGAATGACAGGACAAGAGG TGCCACTGCTACCATAACCA	48-49	2	0.099	0.095	No
STI0030	12	(ATT)n	TTGACCCTCCAACTATAGATTCTTC TGACAACTTTAAAGCATATGTCAGC	53-54	2	0.388	0.313	Yes
STI0036	2	(AC)n(TC)imp	GGACTGGCTGACCATGAACT TTACAGGAAATGCAAACTTCG	134-147	4	0.582	0.544	No
STI0032	5	(GGA)n	TGGGAAGAATCCTGAAATGG TGCTCTACCAATTAACGGCA	128-144	6	0.760	0.723	Yes
STWAX-2	8	(ACTC)n	CCCATAATACTGTCGATGAGCA GAATGTAGGGAAACATGCATGA	239-243	4	0.427	0.393	No
STI046	2	(GAT)n	CAGAGGATGCTGATGGACCT GGAGCAGTTGAGGGCTTCTT	200-218	7	0.776	0.746	No
STI031	1	(TCA)n	CAGAGGATGCTGATGGACCT GGAGCAGTTGAGGGCTTCTT	140-156	8	0.805	0.783	No
STM0030	12	Compound(GT/GC)(GT)8	AGAGATCGATGTAAAACACGT GTGGCATTTTGATGGATT	153-178	5	0.549	0.506	No
STM5121	1	(TGT)n	CACCGGAATAAGCGGATCT TCTTCCCTTCCATTTGTCA	306-309	2	0.124	0.117	Yes
STM0019a	6	(AT)7(GT)10(AT)4 (GT)5(GC)4(GT)4	AATAGGTGTACTGACTCTCAATG TTGAAGTAAAAGTCCTAGTATGTG	210-225	5	0.504	0.478	Yes
STPoA58	5	(TA)13	TTGATGAAAGGAATGCAGCTTGTG ACGTTAAAGAAGTGAGAGTACGAC	246-250	3	0.328	0.313	Yes

He = heterozygosity value, PIC = polymorphic information content, PGI Kit = Potato genetic identity kit, Yes = Marker belongs to the kit, No = Marker does not belong to the kit

Table 5.3: Correlation coefficients showing the relationship between polymorphic information content, heterozygosity value and number of alleles

	He	Number of alleles
He	-	
Number of alleles	0.844****	-
PIC	0.9943***	0.8905***

******* = significant at P≤0.001, He = heterozygosity value, PIC = polymorphic information content

5.3.2 Cluster analysis of potato clones

A dendrogram was constructed using UPGMA clustering algorithm based on SSR data matrices, and grouped the potato clones into three major clusters (Figure 5.1). The first cluster consisted of ten clones, seven of which are commonly grown varieties bred by the International Potato Center (CIP) and released in Uganda. The two lines in this cluster (NKRK19.10 and NKRN59.41) are crosses with a common ancestry from the same female parent (Rutuku x Kackpot1 and Rutuku x NakPot5), respectively. The second cluster consisted of seven clones, four of which (Kabera, Shutama, Mbumbamagara and Kimuli) are farmers' varieties, while the rest were from population B3C2 obtained from CIP. The third cluster consisted of Kachpot1, Mabondo and NakPot1. Shutama was the least genetically related to other clones (1.9) followed by Kabera, Kachpot1 and Mbumbamagara. The most closely related varieties were 396026.103 and 396034.104. Varieties Shutama and Mbumbamagara, were considered by farmers to be the same but given different names in the potato growing districts of Kisoro and Kabale, respectively. However, the results of this study revealed a genetic difference between the two with genetic distances of 1.9 and 1.6, respectively, albeit the two belonged to the same cluster. There was a close relationship between the genetic clustering and the phenotypic characteristics of the studied genotypes. For example, 57% of the susceptible genotypes belonged to cluster two and all these take between 70-90 days to maturity. Additionally, 86% of the moderately late blight resistant and high yielding genotypes were in cluster one. The genetic distance between the clones ranged from 1.0 to 5.7 (Table 5.4). The highest range was found for Cruza, indicating that it is less related to the other clones in this study. The shortest genetic distance between 396026.103 and 396034.104 (1.0) could be due to the fact that both are from population B2C3 and are possibly selections from a single cross.

Table 5.4: Jaccard's similarity matrix for 20 potato genotypes analysed using 17 SSR markers

	CR	KB	K1	KL	KG	MD	MB	N1	N5	19.1	9.41	PT	RG	RS	RT	SH	VC	6.1	4.1	8.1
Cruza																				
Kabera	4.7																			
Kachpot1	5.5	4.8																		
Kimuli	4.3	3.6	3.9																	
Kinigi	2.8	5.1	4.7	4.0																
Mabondo	5.7	5.4	2.9	4.6	5.0															
Mbumbamagara	4.5	4.2	3.7	3.0	4.4	4.1														
Nakpot1	4.5	4.8	3.4	4.1	4.2	2.7	3.6													
Nakpot5	3.7	3.5	4.5	3.5	3.9	4.9	3.7	4.4												
NKRK19.10	4.5	3.6	4.7	4.1	4.4	5.1	4.6	4.9	2.6											
NKRI59.41	3.1	4.2	5.3	4.8	3.6	5.1	4.6	4.0	2.9	3.6										
Petero	3.1	4.0	4.0	3.5	3.2	4.4	4.0	4.3	3.5	3.8	3.9									
Rwangume	3.8	4.3	5.2	4.4	4.2	5.1	4.1	4.6	3.4	3.6	3.5	3.6								
Rwashaki	3.2	4.1	3.8	3.8	3.6	3.9	3.5	3.8	3.3	3.4	3.2	1.9	2.5							
Rutuku	3.8	3.8	4.3	3.1	3.5	5.0	4.1	4.4	2.5	3.2	3.9	3.2	2.6	3.1						
Shutama	4.2	3.6	4.6	3.9	4.0	5.3	3.8	4.7	3.5	4.3	4.0	4.4	5.3	4.7	4.4					
Victoria	3.0	3.8	5.2	4.2	2.7	5.2	4.2	4.3	3.3	3.9	2.3	3.5	3.9	3.6	4.0	3.0				
396026.103	5.1	3.3	5.1	4.0	4.8	5.2	4.8	5.2	3.3	3.1	4.1	4.1	3.8	4.0	3.5	4.3	3.8			
396034.103	5.3	3.3	5.2	4.2	5.1	5.3	4.7	5.3	3.5	3.6	4.2	4.2	3.9	4.1	3.7	4.2	4.0	1.0		
396038.107	4.4	3.2	4.4	1.9	4.5	4.8	3.6	4.4	2.9	3.4	4.1	3.8	4.6	3.8	3.5	3.8	3.9	3.8	3.9	

Notes: CR=Cruza; KB=Kabera; K1=Kachpot1; KL=Kimuli; KG=Kinigi; MD=Mabondo; MB=Mbumbamagara; N1=Nakpot1; N5=Nakpot5; 19.1=NKRK19.10; 9.41=NKRI59.41; PT=Petero; RG=Rwangume; RS=Rwashaki; RT=Rutuku; SH=Shutama; VC=Victoria, 6.1=396026.103, 4.1=396034.103, 8.1=396038.107

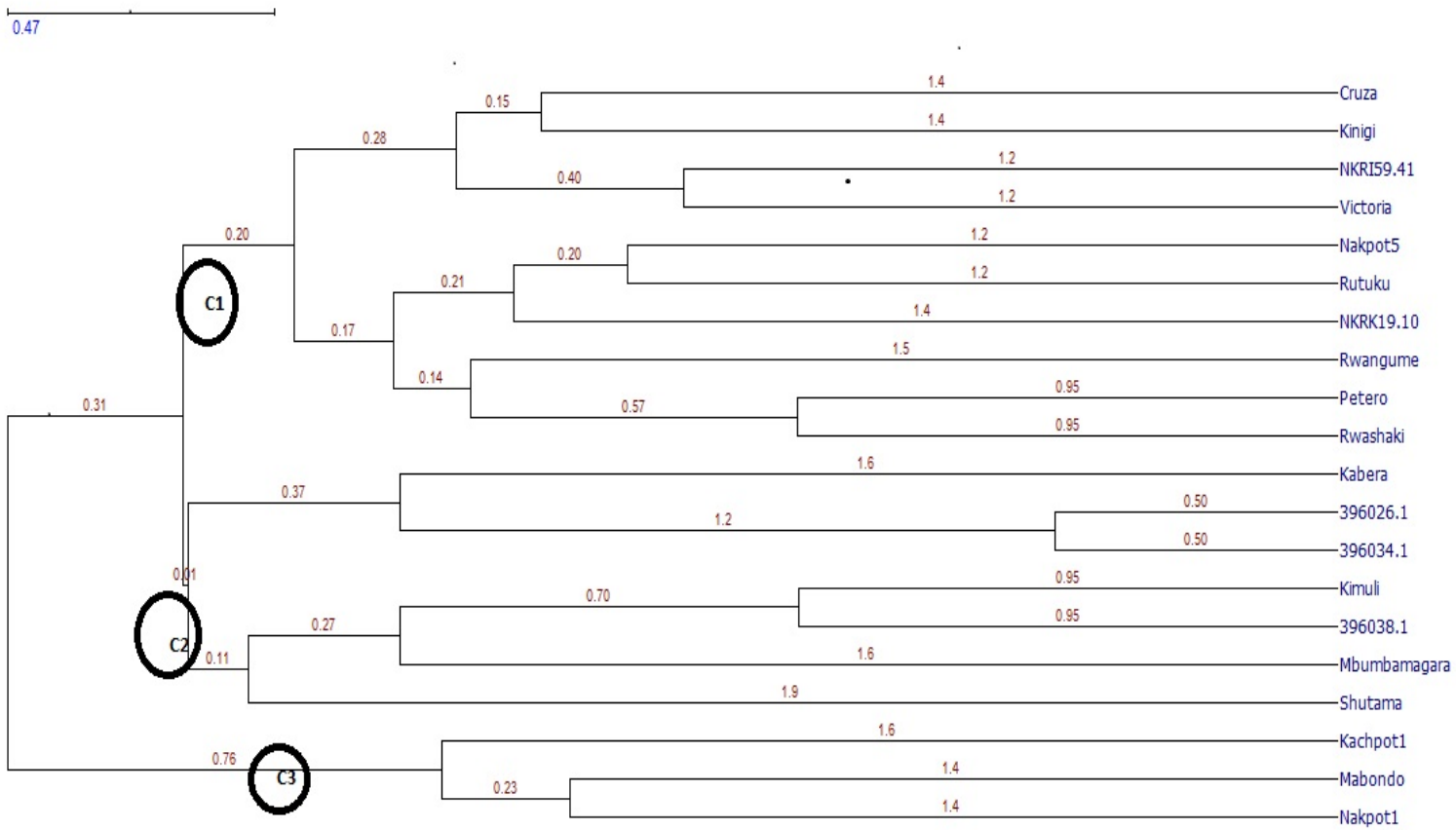

Figure 5.1: Dendogram showing genetic relationship among 20 potato clones obtained using 16 SSR markers generated by UPGMA.

5.4 Discussion

The 64 alleles revealed by microsatellites in this study and the number of alleles per locus (range 2 to 8) was low compared to earlier studies. For instance, Sharma and Nandineni (2014) obtained 139 alleles, while alleles per locus ranged from 6 to 11 in a study of 44 potato genotypes using 17 SSR markers. Ghislain et al. (2009) detected 137 alleles using 24 SSR markers on 742 potato genotypes with the range of 3 to 9 alleles per locus. In both studies more potato genotypes were used with almost the same primers. However, Muthoni et al. (2014) identified 160 alleles and the SSR loci ranged from 2 to 14 with 20 potato clones using 24 SSR markers. In this study more alleles were identified with almost the same number of markers and genotypes. On the other hand, Solano et al. (2103) recorded 64 alleles using seven SSRs and 40 potato clones, while Muhinyuza et al. (2015) observed 84 alleles with 13 SSR markers and 18 genotypes. It can thus be observed that other than the number of markers and genotypes used, other factors contribute to the total number of alleles detected. The lower total number of alleles in this study can be attributed to the high percentage of null alleles in some genotypes where several markers failed to produce detectable variation.

However, several markers performed differently in the current study compared to the earlier studies. For instance in ST1046 (0.776), a relatively higher PIC values were observed by Rocha (2010), Muthoni et al. (2014) and Muhinyuza et al. (2015), with values of 0.97, 0.836 and 0.842, respectively. Some markers used in this study had extremely low PIC values compared with those from the previous studies, with the following results: ST10023 had 0.795 and 0.813; STM5121 had 0.374; STM1049 had 0.784, while STM0037 had 0.683 PIC values (Muthoni et al., 2014; Ghislain et al., 2009). In other studies, STI0030 had a PIC value of 0.76 (Hirut, 2015), while STI0036 had a PIC value of 0.839 (Muthoni et al., 2014). The low PIC values in this study could be explained by the fact that most of the genotypes used were not closely related, yet microsatellites are particularly useful for closely related genetic materials. Furthermore, the differences in the laboratory procedures could have resulted into the observed variations in PIC values.

The significant variation of genetic distance among genotypes showed the presence of genetic diversity. The genotypes from CIP tended to be clustered together, suggesting a common ancestry. Farmer's varieties can be used as parents in the breeding program given they are less related, while clones 396026.103 and 396034.103 may not be crossed as this may result in reduced genetic variation and inbreeding depression in their progenies. Cruza is an old variety with the highest genetic distance; and thus can be used as a parent in the breeding program.

5.5 Conclusion

The study determined the pattern and level of genetic diversity among the selected 20 tetraploid potato genotypes using 16 SSR markers to identify suitable parents for breeding purposes. The microsatellites were useful and revealed considerable genetic variation among genotypes that can be exploited for possible crop improvement. Three major clusters were obtained and the following genotypes were selected for use in the crop improvement program: Kinigi, Rwangume and NKRI59.41 from cluster one; 396034.103, 396038.107 and Kimuri from cluster two; and Nakpot1 from cluster three. These will be used in the development of potato varieties that are high yielding, early maturing and resistant to late blight.

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Chapter 6 : Combining ability analysis of yield and resistance to late blight disease caused by *Phytophthora infestans* in Uganda

Abstract

Breeding for resistance to late blight disease caused by *Phytophthora infestans* (Mont.) de Bary in potato is the most economic, effective and ecologically sustainable method to control the disease and to boost productivity. Therefore, in an effort to develop potato varieties with improved tuber yield and late blight resistance, 10 potato genotypes were selected from available germplasm in Uganda and used in crosses. The objectives of the study were to estimate combining ability effects for yield, yield related traits and late blight resistance; gene action controlling resistance to *Phytophthora infestans* as well as identify promising potato genotypes for potential release to farmers. Eighteen F^1 families generated from two sets of 12 parents, using a North Carolina Design II were evaluated for relative area under disease progress curve (rAUDPC) for late blight disease, yield and yield related traits in two late blight hotspot locations. Results revealed that both additive and non-additive genetic effects were important in controlling yield and late blight resistance in potato. However, additive gene action was predominant over non-additive. The GCA/SCA ratio for total tuber weight and late blight resistance was 0.53 and 0.62, respectively. Broad-sense heritability estimates were 0.78 for total tuber weight and 0.68 for rAUDPC. This study showed some evidence of maternal effects for rAUDPC (1.45) and ATW (1.56), although these were not significant at $P \leq 0.05$. Parents Kinigi, 392657.8, 396034.103, 396038.107, 395011.2, NKRK19.17, NKRN59.58 and 395017.14 had good general combining ability (GCA) effects for both late blight resistance and yield related traits. Crosses of 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest SCA effects for yield related traits, while families Kinigi x NKRK19.17and 392657.8 x NKRN59.41 had the lowest SCA effects for rAUDPC. The relatively high heritability estimates and predominant additive genetic effects imply that genetic advances in resistance to *Phytophthora infestans* and tuber yield among these genotypes can be realized by selecting superior clones. The best parents, based on GCA values and families based on SCA values were selected for development of improved potato varieties that combined both high yield and resistance to *Phytophthora infestans* resistance. The best clones will be subjected to further evaluation and release.

Key words: Heritability**,** *Solanum tuberosum,* gene action, rAUDPC, *Phytophthora infestans* resistance

6.1 Introduction

Late blight of potato caused by *Phytophthora infestans* (Mont.) de Bary is the most devastating disease in the tropical highlands of Uganda. The disease causes estimated yield losses ranging between 30 and 100% in different parts of the country (Byarugaba et al., 2013). Late blight is the major reason for the use of fungicides on potatoes in Uganda (Low, 1997). As much as the disease management can be through the use of fungicides, most small-scale farmers cannot afford this method because both contact and systemic fungicides are expensive. Additionally, fungicide application is by hand and farmers rarely use protective clothing, thus posing health risks and diverse environmental hazards (Kromann et al., 2009; Forbes, 2012). Poor disease management is due to several reasons and these include partial access to fungicides, high disease pressure and inadequate farmer knowledge of disease dynamics (Forbes, 2012). Therefore, breeding for host resistance is a sustainable approach to late blight control and management in Uganda. Though breeding for resistance to *Phytophthora infestans* has been a priority of the potato breeding program in Uganda over the past years, previously released resistant varieties have quickly succumbed to virulent races of the pathogen (Mulema et al., 2004: Byarugaba et al., 2013).

Early efforts to breed for resistance against late blight focused on qualitative resistance controlled by major R genes. Even though R genes are greatly effective when compatible races are present, race-specific resistance controlled by major resistance (R) genes is not considered resilient due to interminable changes in the pathogen. As a result, the focus nowadays is on quantitative, race non-specific resistance (horizontal resistance) through minor resistance genes, as this resistance is more durable and effective against various pathogenic strains of *Phytophthora infestans* (Landeo et al., 1999; Kumar et al., 2007). Based on this concept, the International Potato Centre (CIP) developed, by recurrent selection, a population group B3 with quantitative resistance to *Phytophthora infestans* with no known major (R) genes. Late blight resistance in this population was improved after several cycle of recombination (B3C0, B3C1 and B3C2) (Landeo et al., 2001; Kaila, 2015). In addition, population B3 genotypes have a wider genetic background for various economic traits. This germplasm is available to many developing countries for breeding purposes, Uganda included (Landeo et al., 2001; Yao et al., 2011). As a result, the National Potato Program of Uganda obtained some of these clones for evaluation together with the existing and adapted varieties. The clones which proved high yielding in the target environments, and with resistance

to late blight, were identified (Namugga et al., 2017). These clones were used as parents to generate new progenies with variable resistance to late blight.

In potato, both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in determining economic traits, as all genetic effects are fixed at the F^1 stage and there is no further segregation. A combining ability analysis is the basis for identification of the best parents and their crosses (Mondal and Hossain, 2006). The objectives of this study were to estimate combining ability effects and gene action for yield, yield related traits and late blight resistance. The selected best performing genotypes will be used for clonal evaluation and eventual release in Uganda.

6.2 Materials and methods

6.2.1 Study sites

Crosses to generate potato seed and the seedling generation were conducted at the Kachwekano research station. This site is located in South-western Uganda at an altitude of 2200 m above sea level (masl) on a latitude of 01° 16'S and longitude of 29° 57'E. The clonal evaluation to determine combining abilities for late blight and tuber yield and its components was conducted at two sites of Kachwekano and Karengyere in South-western Uganda. Karengyere is located at an altitude of 2450 masl, 01°13.2′ S, 29° 47.8 'E. These two sites have volcanic (Andosols) soils with a bi-modal rainfall pattern separated by a dry spell ranging from 30-60 days.

6.2.2 Parental materials and crosses

Twelve genetically diverse clones were selected and used as parents. Seven clones were obtained from the National Potato Program of Uganda and five were from the International Potato Centre (CIP) belonging to population B3C2 with variable resistance to late blight. These parents were selected based on their flowering abilities, high to medium yields and acceptable level of resistance to *Phytophthora infestans* (Namugga et al., 2017). The parents were grouped into two sets of six parents each based on their flowering abilities, yield and resistance to late blight. Both males and females were high yielding, resistant to late blight and good flowering abilities. Crosses were made using a North Carolina Design II (NCD II) to generate 18 families (Table 6.1). In the first set three female clones (Kinigi, 396034.103 and 392657.8) were crossed with three males (395017.14, NKR59.41 and NKRK19.17), whereas in the second set three female parents (396026.103, 393220.54 and 396038.107 (NAROPOT1) were crossed with three males (NKRN59.48, NKRN59.58 and 395011.2). In total, 18 families were developed (2 sets x 9 family each). At flowering, following emasculation, controlled hand pollination was performed (Acquaah,

2007). At maturity, berries of the same cross were harvested and bulked together. These were labelled and kept at room temperature to ripen. After softening, seeds were manually extracted and washed thoroughly with water. These were air dried and stored in petri dishes up to planting time. Crosses were done for two seasons.

Table 6.1: Description of parents used in the study

Set	Male/Female	Parents	Source	Yield (t ha^{-1})		Reaction to late blight
				Mean	Class	rAUDPC (%)
1	Female	Kinigi	CIP	32.0	HY	32.9
1	Female	396034.103	Uganda	35.4	HY	27.5
1	Female	392657.8	CIP	43.7	HY	14.1
1	Male	395017.14	Uganda	18.9	MY	27.1
1	Male	NKR59.41	Uganda	24.1	MY	22.9
1	Male	NKRK19.17	Uganda	37.8	HY	34.1
2	Female	396026.103	CIP	33.1	HY	42.0
2	Female	393220.54	CIP	40.3	HY	15.9
2	Female	396038.107	Uganda	37.7	HY	36.5
2	Male	NKRN59.48	Uganda	30.0	HY	26.1
2	Male	NKRN59.58	Uganda	30.0	HY	27.7
2	Male	395011.2	CIP	25.5	MY	22.9

Source: Namugga et al. (2017). CIP = International Potato Centre, HY = high yield, MY = medium yield

6.2.3 Seedling generation

At planting, a minimum of 100 F^1 seeds per cross was sown in seedling trays filled with fine sterilized soil. Planting was done on 22nd of February 2017. After 30 to 40 days, the seedlings were transplanted into boxes in the screen house for further growth and to generate mini-tubers. Each box contained 40 plants at a spacing of 20 cm x 20 cm. Sixty to one hundred seedlings were planted for each cross depending on the numbers. N: P: K (17:17:17 %) fertilizer was applied in the boxes at a rate of 100 kg ha^{-1}. Fungicides (both mancozeb and agrolaxyl) and agrothoate as pesticide were used when required. True potato seedlings from 18 crosses were harvested separately 90-120 days after transplanting. Tubers were harvested from each plant. One tuber from each plant was taken to produce tuber families. Seed increase was carried out in the season of 2016B at Kachwekano research station. Two sets of tuber families were selected and saved for planting in two environments.

6.2.4 Trial establishment and experimental design

Eighteen families, each having 60 progenies, and their parents were planted at the two locations in South-western Uganda (Karengyere and Kachwekano research stations) during the main cropping season of 2017A (March-June). Planting was done on the 14th and 16th of March 2017 at Karengyere and Kachwekano, respectively. These locations are known to experience severe late blight disease pressure during the rainy season. Consequently, clones were evaluated under natural disease infestation. To increase the disease inoculum, a susceptible variety, 'Victoria' was planted adjacent to each row and around each replication as spreader rows. No control measure was taken against late blight. Trials were established using an alpha lattice design (6 x 5) with two replications. Each entry was represented by an experimental unit consisting of 40 plants assigned in a plot size of two rows of 4.5 m long at a spacing of 0.75 m x 0.3 m. All the necessary agronomic practices were carried out as recommended.

6.2.5 Data collection

Data collected included reaction to late blight infection, the total number of tubers per plant, total tuber weight, marketable tuber weight and average tuber weight. Late blight assessment started with the first appearance of the symptoms. Plants were visually rated at seven day intervals for percentage leaf and stem area with late blight lesions. This was done visually by comparing the green and non-green leaf portions affected by the disease using a 1 to 9 scale designed by the International Potato Centre, that is, 1=0%, 2=2.5%, 3=10%, 4=25%, 5=50%, 6=75%, 7=90%, 8=97.5% and 9=100% leaf area showing disease symptoms (Henfling, 1987). The mean percentage blighted foliar area per plot was calculated. Evaluations continued until the susceptible genotype reached 90-100% of leaf blight assessments and the area under the disease progress curve (AUDPC) (Campbell and Madden, 1990) was calculated (Bradshaw, 2007). The relative area under the disease progress curve (rAUDPC) was used in the analysis of variance. The rAUDPC was calculated using the following formula:

$$AUDPC = \sum_{i=1}^{n-1} [(T_{i+1} - T_i)(D_{i+1} + D_i)/2] \quad \text{(Equation 1)}$$

$$RAUDPC = \frac{\sum (T_{i+1} - T_i) * \left(\frac{D_{i+1} + D_i}{2} \right)}{T_{Total} * 100} \quad \text{(Equation 2)}$$

In equation 1, Ti = is the ith day when an estimation of percentage foliar late blight is made and Di = is the estimated percentage of area with blighted foliage at Ti. The total is the number of days at which the final assessment was recorded.

Total tuber weight (TTW) was measured and expressed in t ha^{-1}. This was calculated as the total weight of all the tubers harvested in a plot and converted to t ha^{-1}. Total tuber number (TTN) was the total number of tubers harvested per plant. Average tuber weight (ATW) was calculated as the total tuber weight per plant divided by the total tuber number of tubers per plant.

6.2.6 Data analyses

6.2.6.1 Analysis of variance

Data for the different traits over the two sets and across environments were subjected to the standard analysis of variance using the GLM procedure of SAS 9.3 (SAS Institute Inc, 2011) statistical program. Analyses of variance of NCD II pooled over sets and across environments (Hallauer and Miranda 1988) were conducted for rAUDPC and yield data. Main effects due to female and male effects within sets are independent estimates of GCA, while male x female interaction effects represent SCA variance within sets. Spearman correlation coefficients were calculated for the studied traits to determine their association.

6.2.6.2 Estimation of general and specific combining ability effects

Data were analysed over sets and across environment. Parents were considered as fixed effects in the test of significance. The GCA and SCA values for each trait were calculated following the NCD II mating design across sites using the following linear model (Hallauer et al., 1988):

$$Y_{ijkpq} = \mu + S_p + g_i(S_p) + g_j(S_p) + h_{ij}(S_p) + E_q + r_k(SE)_{pq} + (ES)_{pq} + (Eg)_{iq}(S_p) + (Eg)_{jp}(S_p) + (Eh)_{ijq}(S_p) + (Eh)_{ijq}(S_p) + e_{ijkpq}$$

Where: $i = 1, 2, 3$; $j = 1, 2, 3$; $k = 1, 2$; $p = 1, 2$; $q = 1, 2$; the terms for the model are defined as follows: Y_{ijkpq} denotes the value of a family from the mating between the ith female parent, the jth male parent, in the kth block, within set p and in the qth environment; μ = grand mean; S_p = the average effect of the pth set; $g_i(S_p)$ = the GCA effect common to all F^1 families of the ith female parent nested within pth set; $g_j(S_p)$ = the GCA effect common to all F^1 families of the jth male parent nested within pth set; $h_{ij}(S_p)$ = the SCA effect specific to F^1 families of the ith female and jth male parent nested within pth set; E_q= average effect of qth environment; $r_k(SE)_{pq}$ = the effect of the kth replication nested within the pth set and qth environment; $(ES)_{pq}$= the interaction between site and set effects; $(Eg)_{iq}(S_p)$ and $(Eg)_{jp}(S_p)$ = the interaction between site and GCA

of the ith female and *j*th male parent, respectively nested within sets; (E*h*)*ijq*(S*p*) = the interaction between site and SCA, nested within sets; and e*ijkpq* = the random experimental error.
General and specific combining abilities (GCA and SCA respectively) for the parents and crosses were determined according to the following formulae (Singh and Chaudhary, 2007).

The GCA for each of the male and female parents was calculated using the following formula:

$GCA_m = X_m - \mu$,
$GCA_f = X_f - \mu$.

The SCAs of the crosses were computed from the formula:
$SCA_X = X_X - E(X_X) = X_X - [GCA_m + GCA_f + \mu]$
Where: GCA_m = general combining ability of male parent; X_m = mean of the male parent; μ = overall mean of all crosses; GCA_f = general combining ability of the female parent, X_f = mean of the female; SCA_X = specific combining ability of the two parents in the cross; X_X = observed mean value of the cross; $E(X_X)$ = expected values of the cross basing on the GCAs of the two parents

The significance of GCA and SCA effects was determined as indicated below
GCA standard error = Square root of MSE/r x f x m x sites
** (f = m)
SCA standard error = Square root of MSE/r x sites
Where
MSE = error mean square
r= replications*
f = number of female parents
m = number of male parents* number of sites
GCA or SCA were significant at P≤0.05 and P≤0.01 when estimates were greater than SE *1.96 and SE*2.576 respectively.

The relative importance of GCA and SCA in influencing the performance of the crosses were estimated using the general predicted ratio (GPR) for all the traits (Baker, 1978), as indicated below:

$$\frac{\text{GCA}}{\text{SCA}} = \frac{\text{MSQGCA pooled}}{\text{MSQGCA (pooled)} + \text{MSQ SCA}}$$

MSQGCA (pooled) $= (\text{MSQGCAmale} + \text{MSQGCA female})/(\text{number of replications})$

Where; MSQGCA and MSQSCA are the mean squares for GCA and SCA, respectively. When the ratio is >0.5, GCA is more important than SCA in the inheritance of the character concerned, while the reverse is true when the ratio is <0.5, SCA is more important (Baker, 1978).

Throughout the text, variation due to males within sets, females within sets, and males x females within sets will be referred to as GCAm, GCAf and SCA variation, respectively. For rAUDPC negative estimates of GCA and SCA effects were taken as high in the desirable direction, and for TTN, TTW, MTW, and ATW positive estimates of GCA and SCA effects were taken as high to identify high genotypes.

6.2.6.3 Estimating heritability and maternal effects

Heritability estimates were calculated using the female additive variance as follows:

Narrow sense heritability based on female additive variance:

$h_f^2 = 4\sigma^2_f / (\sigma^2_e / r + 4\sigma^2_{mf} + 4\sigma^2_f) = V_{Af} / V_P$

Where

r = number of replication

σ^2_e = environmental variance = MS_e

σ^2_f = variance of female parents = GCA_f variance = MS_f

σ^2_{fm} = variance due to interaction between females and males = SCA variance = MS_{mf}

V_{Af} = additive genetic variance due to female parents

V_P = phenotypic variance

Broad sense heritability as follows:

$h_f^2 = 4\sigma^2_{f+} 4\sigma^2_{mf} / (\sigma^2_e / r + 4\sigma^2_{mf} + 4\sigma^2_f) = V_{Gf} / V_P$

Where V_{Gf} = total genetic variance

The other terms are as described above in narrow sense heritability.

Test for maternal effects: The ratio of MS_f: MS_m estimates the levels of maternal effects provided f = m in the design.

$F = MS_f / MS_m$, $F_{m,\ f}$ degrees of freedom at $P<0.05$. If the ratio is greater than 1 there is ample evidence to suggest presence of maternal effects.

6.3 Results

6.3.1 Analysis of variance for crosses across sites

The combined analysis of variance and ratio of GCA/SCA for the relative area under the disease progress curve (rAUDPC), total tuber number (TTN), total tuber weight (TTW), marketable tuber

weight (MTW), and average tuber weight (ATW) among the families are summarized in Table 6.2. There were significant differences among crosses for all the traits. The environmental (site) effect was significant (P≤ 0.01) for TTW, MTW and ATW. The GCA mean square for females (GCA_f) were significant for all traits and GCA mean square for males (GCA_m) were significant for all traits except ATW. The SCA effects were significant for all the tested traits. The GCA_m x environment interaction was significant for the total number of tubers and average tuber weight. No significant interactions were observed between environment and sets for all the traits assessed. The GCA_f effects were higher than the GCA_m effects for rAUDPC and ATW, while additive GCA_m effects were dominant for TTN, TTW and MTW. For ATW, SCA effects were higher than the additive main effects of either male or female parents. However, the GCA was more important than the SCA in the expression of all the traits. The ratio of additive/ non-additive genetic effects ranged from 0.38 (ATW) to 0.62 (rAUDPC).

Table 6.2: Combined analysis of variance of potato genotypes for late blight resistance, tuber yield and related traits tested at two locations in South -Western Uganda.

		Means squares				
Source of variation	**DF**	**rAUDPC**	**TTN**	**TTW**	**MTW**	**ATW**
Set[1]	1	3.24	20674.58**	5.31	0.61	0.27
Site	1	16.22	21.87	49.37**	26.42**	1.03**
Replication (Site)	2	86.34*	2772.87	68.94***	51.93***	1.55***
Female (Set)	10	63.12**	4978.03***	20.22**	11.78***	0.40**
Male (Set)	10	43.60*	6887.63***	32.11***	15.78***	0.26
Female*Male (Set)	20	40.95*	6328.15***	29.12**	14.28***	0.68***
Site*Set	2	11.8	970.93	7.40	9.37	0.17
Site*Female (Set)	10	12.81	1406.67	4.11	5.53	0.25
Site*Male (Set)	10	10.01	2517.81*	8.89	2.67	0.40**
Site*Female*Male (Set)	20	4.03	425.78	3.30	4.76	0.10
Error	62	20.16	1133.55	6.15	3.36	0.14
R-Square		0.60	0.78	0.74	0.75	0.72
		0.62	0.54	0.53	0.55	0.38

[1]Set within an environment, DF = Degrees of freedom; *= significant at P≤0.05; **= significant at P≤0.01; ***= significant at P≤0.001; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; TTW = total tuber weight; MTW = marketable tuber weight; ATW = average tuber weight; GCA/SCA ratio calculated according to Baker (1978).

6.3.2 Heritability estimates and maternal effects

The estimates of broad and narrow -sense heritability (H^2 and h^2) and test for maternal effects for rAUDPC and yield related traits across locations are presented in (Table 6.3). The broad sense heritability values ranged from 0.68 to 0.82 and were highest for TTN. The narrow-sense heritability values ranged from 0.27 to 0.43, whereby rAUDPC had the highest value. In general, this study showed some evidence of maternal effects for some traits (rAUDPC, F = 1.45 and ATW, F = 1.56), although these were not significant at $P \leq 0.05$.

Table 6.3: Broad and narrow -sense heritability (H^2 and h^2) and test for maternal effects for rAUDPC and yield related traits across two locations in South-western Uganda

Heritability/Traits	rAUDPC	TTN	TTW	MTW	ATW
H^2	0.68	0.82	0.78	0.77	0.77
h^2	0.43	0.36	0.31	0.34	0.27
MS_F/MS_M	1.45	0.72	0.63	0.75	1.56

GCA/SCA ratio calculated according to Baker (1978); H^2 = broad sense heritability; h^2 = narrow sense heritability; MS_F = mean square of the female parent; MS_M = mean square of the male parent; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; TTW = total tuber weight; MTW = marketable tuber weight; ATW = average tuber weight

6.3.3 General combining ability effects of parents

The GCA effects of the potato parents at Kachwekano and Karengyere are presented in Table 6.4. Significant GCA effects were observed among all the parents for ATW. Parents Kinigi, 392657.8, and NKRN59.41 had significant GCA effects for MTW, while Kinigi, 392657.8, 396026.103, 395017.14, NKRN59.41and 395011.2 had significant GCA effects for TTW. Significant GCA effects for rAUDPC were found for Kinigi, 392657.8, 395017.14, NKRK19.17, 396026.103, 396038.107, NKRN59.48 and 395011.2. Among the female parents, 396038.107 had the lowest GCA effect for rAUDPC (-1.18) followed by 392657.8 (-0.82), while for the male parents, the lowest GCA effect was for NKRN59.48 (-1.9) followed by NKRK19.17 (-1.09). For yield and related traits, 392657.8 had the highest GCA effects for TTW (0.32) and MTW (0.48) followed by 396026.103 TTW (0.27) and MTW (0.22). For ATW, 396034.103 had the highest GCA of 0.06 followed by 396026.103 (0.03). Kinigi had the lowest GCA effect for all the yield related traits. Parent 395017.14 had the highest GCA effect for TTW (1.60) and MTW (1.03). NKRN59.41 had the lowest GCA effects for TTW (-0.54) and MTW (-0.29).

Table 6.4: Estimates of general combining ability effects for rAUDPC, TTN, MTW and ATW of 12 potato parents evaluated in two locations in South-western Uganda.

Parents and set	TTN	TTW	MTW	ATW	rAUDPC
			Set1		
Female					
Kinigi	-4.549	-0.502**	-0.355**	-0.073**	1.201**
396034.103	2.535	0.177	-0.121	0.065**	-0.385
392657.8	2.014	0.324*	0.475**	0.008**	-0.816*
Male					
395017.14	3.806	0.315*	0.248	-0.019**	1.473**
NKRN59.41	-6.986	-0.538**	-0.294*	-0.017**	-0.387
NKRK19.17	3.181	0.233	0.046	0.037**	-1.086**
SE	27.840	0.120	0.170	0.010	0.420
			Set2		
Female					
396026.103	3.632	0.271*	0.224	0.032**	0.833*
393220.54	-2.910	-0.213	-0.179	-0.021**	0.345
396038.107	-0.722	-0.058	-0.045	-0.011**	-1.177**
Male					
NKRN59.48	0.444	-0.150	-0.165	-0.016**	-1.960**
NKRN59.58	-6.826	-0.242	-0.095	-0.023**	0.255
395011.2	6.382	0.392**	0.260	0.039**	1.704**
SE	48.670	0.260	0.090	0.003	0.430

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; MTW = marketable tuber weight.

6.3.4 Specific combining ability effects of families

The SCA effects of 18 potato F^1 families evaluated at Kachwekano and Karengyere are presented in Table 6.5. All crosses showed significant SCA effects for ATW, except Kinigi x 395017.14 and 396026.103 x 395011.2. For MTW, the SCA effects were significant for the crosses 392657.8 x 395017.14, 393220.54 x NKRN59.58 and 393220.54 x NKRN59.48. Furthermore, the SCA effects for TTW were significant for the crosses of 396034.103 x 395017.14 and 393220.54 x

NKRN59.58. The crosses, 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest SCA effects for all the yield related traits (TTW, MTW and ATW). For rAUDPC, significant SCA effects were observed for the crosses of 392657.8 x NKRK19.17 only. The lowest SCA effects for rAUDPC were (-2.29) and (-1.92) for the crosses Kinigi x NKRK19.17and 392657.8 x NKRN59.41, respectively.

Table 6.5: Estimates of specific combining ability (SCA) effects for rAUDPC, TTN, MTW and ATW of 18 F^1 potato families evaluated in two locations in South-western Uganda.

Crosses and sets	TTN	TTW	MTW	ATW	rAUDPC
Set1					
Kinigi x 395017.14	2.340	0.053	-0.127	-0.003	1.185
Kinigi x NKRN59.41	-2.681	-0.069	-0.128	-0.017*	1.101
Kinigi x NKRK19.17	0.340	0.016	0.255	0.020*	-2.287
396034.103 x 395017.14	-3.181	-0.690*	-0.380	-0.122**	-0.627
396034.103 x NKRN59.41	0.986	0.386	0.364	0.059**	0.822
396034.103 x NKRK19.17	2.194	0.303	0.016	0.063**	-0.194
392657.8 x 395017.14	0.840	0.636	0.507*	0.125**	-0.558
392657.8 x NKRN59.41	1.694	-0.317	-0.236	-0.042**	-1.923
392657.8 x NKRK19.17	-2.535	-0.319	-0.271	-0.083**	2.481*
SE	83.510	0.660	-0.127	0.020	1.260
Set2					
396026.103 x NKRN59.48	-12.028	-0.418	-0.368	0.026**	-0.498
396026.103 x NKRN59.58	7.806	0.255	0.100	-0.015*	-0.556
396026.103 x 395011.2	4.222	0.163	0.268	-0.010	1.054
393220.54 x NKRN59.48	17.264	0.711	0.513*	0.031**	0.653
393220.54 x NKRN59.58	-12.590	-0.915*	-0.521*	-0.101**	-0.858
393220.54 x 395011.2	-4.674	0.204	0.008	0.070**	0.205
396038.107 x NKRN59.48	-5.236	-0.294	-0.145	-0.057**	-0.155
396038.107 x NKRN59.58	4.785	0.661	0.421*	0.117**	1.414
396038.107 x 395011.2	0.451	-0.367	-0.276	-0.060**	-1.259
SE	146.010	0.780	0.290	0.010	1.260

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; MTW = marketable tuber weight.

6.3.5 Family means across locations

Means and ranking of rAUDPC, TTN, TTW and ATW within and across locations are presented in Table 6.6. The mean rAUDPC (= 100 max) across locations indicated that families 393220.54 x NKRN59.58 and Kinigi x NKRN59.41 with disease severity of 2.5% and 4.2%, respectively, were the most resistant, whereas families 392657.8 x 395017.14 (14.8%), 396034.103 x NKRK19.17 and 396026.103 x 395011.2 (12.3%) were the most susceptible to late blight. The highest mean total number of tubers were obtained from the families Kinigi x NKRK19.17 (42.4) and 396034.103xNKRK19.17 (36.7), while the lowest were from the families 392657.8 x NKRK19.17 (9.5) and 393220.54 x NKRN59.58 (16.3). Families 392657.8 x 395017.14 and 396034.103 x NKRK19.17 were the best yielders with a TTW of 13.3 t ha^{-1} and 11.1 t ha^{-1}, respectively, while families Kinigi x NKRN59.41 (3.8) and 393220.54xNKRN59.58 (2.3) were the lowest in TTW across locations. In addition, families with the highest MTW were 396026.103 x NKRN59.48 (9.7) and 396026.103 x 395011.2 (5.8) whereas Kinigi x NKRK19.17 (1.7) and 396038.107 x NKRN59.48 (2.4) had the lowest MTW. The families 392657.8 x 395017.14 (96.9) and 396026.103 x 395011.2 (75.8) had the highest ATW, whereas families 393220.54 x NKRN59.58 (23.8) and Kinigi x NKRN59.41 (24) had the lowest ATW. A ranking of the families revealed that families 393220.54 xNKRN59.58, Kinigi x NKRN59.41, 396038.107 x NKRN59.48, 392657.8 x NKRN59.41 and 396026.103xNKRN59.48 were the most resistant to late blight. The highest yielding families were 392657.8 x 395017.14, 396034.103 x NKRK19.17, 396026.103 x 395011.2, 393220.54 x 395011.2 and 392657.8 x NKRK19.17.

6.3.6 Correlation between traits.

Correlation between the five traits are presented in Table 6.7. Significant ($P < 0.001$) and positive correlation was found between TTW and ATW. Correlation between rAUDPC and all yield related traits were negative and only significant ($P < 0.001$) for TTW and ATW.

Table 6.6: Family and parent means of tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight of 28 potato families evaluated at two locations in Uganda

	rAUDPC		TTN		TTW (t ha^{-1})		MTW (t ha^{-1})		ATW (g)	
Families	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
Kinigi x 395017.14	8.5	18	36.1	6	7.7	14	5.6	7	40.0	18
Kinigi x NKRN59.41	4.2	2	24.3	25	3.8	31	3.8	20	16.6	31
Kinigi x NKRK19.17	8.0	15	42.4	1	7.2	18	1.7	31	45.6	14
396034.103 x 395017.14	8.2	17	34.2	11	7.4	16	4.6	14	37.6	21
396034.103 x NKRN59.41	9.3	20	33.3	13	8.4	13	4.9	12	45.7	13
396034.103 x NKRK19.17	12.3	30	36.7	4	11.1	2	3.8	21	45.4	16
392657.8 x 395017.14	14.8	32	26.7	24	13.3	1	4.6	13	96.9	1
392657.8 x NKRN59.41	6.8	9	19.0	29	6.1	24	4.5	16	45.5	15
392657.8 x NKRK19.17	10.2	23	9.5	31	9.2	8	2.8	27	57.7	5
396026.103 x NKRN59.48	7.3	13	26.9	23	6.6	20	9.7	1	33.4	25
396026.103 x NKRN59.58	9.9	21	34.4	10	8.9	12	4.6	15	54.9	8
396026.103 x 395011.2	12.3	31	27.9	20	11.1	3	5.8	5	75.8	2
393220.54 x NKRN59.48	10.2	24	27.5	21	9.2	9	5.4	9	52.4	10
393220.54 x NKRN59.58	2.5	1	16.3	10	2.3	32	2.4	29	13.9	32
393220.54 x 395011.2	10.3	26	23.8	27	9.3	7	2.7	28	49.3	11
396038.107 x NKRN59.48	6.4	7	27.3	22	5.8	26	2.4	30	31.5	26
396038.107 x NKRN59.58	10.2	25	36.3	5	9.2	10	3.3	25	56.9	6
396038.107 x 395011.2	8.5	19	31.0	18	7.6	15	5.5	8	43.3	17
Parents										
Kinigi	10.1	22	35.2	7	9.1	11	7.6	2	55.7	7

396034.103	8.1	16	24.0	26	7.3	17	6.7	3	48.7	12
392657.8	5.3	5	34.2	12	4.8	27	5.2	10	27.8	27
395017.14	11.0	27	31.9	15	9.9	6	1.4	32	53.7	9
NKRN59.41	4.4	3	29.6	19	3.9	30	4.9	11	24.0	29
NKRK19.17	5.3	6	31.1	17	4.8	28	4.0	19	27.0	28
396026.103	4.6	4	38.1	3	4.1	29	3.1	26	23.8	30
393220.54	11.4	28	5.1	32	10.3	5	5.7	6	67.4	3
396038.107	7.7	14	34.8	8	6.9	19	4.3	17	39.6	20
NKRN59.48	7.0	11	31.6	16	6.3	22	4.0	18	39.8	19
NKRN59.58	7.2	12	34.5	9	6.5	21	3.7	23	36.7	23
395011.2	6.9	10	19.4	28	6.2	23	3.7	22	37.5	22
Mean	**8.4**		**29.3**		**7.5**		**4.4**		**44.0**	
CV (%)	**30.3**		**24.0**		**26.5**		**31**		**27.0**	

rAUDPC = relative area under the disease progress curve; TTN = total tuber number; TTW = total tuber weight; MTW = marketable tuber weight; ATW = average tuber weight.

Table 6.7: Pair-wise correlation coefficients of late blight disease and yield related parameters in 18 F^1 potato families tested at two locations in Uganda

Trait	ATW	MTW	TTN	TTW	rAUDPC
Average tuber weight	-				
Marketable tuber weight	0.13	-			
Total number of tubers	-0.18	-0.13	-		
Total tuber weight	0.86***	0.08	-0.12	-	
rAUDPC	-0.86***	0.08	-0.12	-0.99***	-

*= significant at P≤0.05; **= significant at P≤0.01; ***= significant at P≤0.001; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; MTW = marketable tuber weight.

6.4 Discussion

This study aimed at determining the combining abilities for late blight resistance as well as tuber yield and related traits in selected potato genotypes and advanced clones from the International Potato Center. Information on combining ability and genetic mechanisms controlling late blight disease, yield and yield related traits in potato is essential in parental selection and designing a breeding program.

There was differential performance of parents and their families for the different traits between sites. The significant mean squares for families on rAUDPC and yield related traits at the two sites indicated the presence of genetic variation among parents and their crosses. This suggests that clones that are high yielding and resistant to late blight may be selected. Both additive and non-additive gene action were significant in inheritance of the traits measured. However, GCA effects were more important than SCA for all the traits except ATW. This implies that inheritance of these traits, except ATW, is due to additive genetic effects, hence further genetic gains can be realized by selecting superior clones.

The GCA to SCA ratios, based on the Bakers ratio, for the total number of tubers, total tuber yield and marketable tuber yield were 0.54, 0.53, and 0.55 respectively, indicating the preponderance of additive genetic effects. Predominance of additive genetic effects observed for these traits has also been reported in previous studies (Killick, 1997; Gopal, 1998; Hirut 2015; Muhinyuza et al. 2016). However, other studies reported both GCA and SCA to be significant for potato yield, with GCA being less important in magnitude than SCA (Bradshaw and Mackay, 1994; Ortiz and Golmirzaie, 2004; Ruiz de Galarreta et al., 2006; Haydar et al., 2009). On the other hand, some studies only reported significant SCA effects for yield were reported (Gopal, 1998; Ruiz de Galarreta et al. 2006; Muthoni et al. 2015). Tai (1976) reported that differences between progenies for tuber yields and number of tubers per plant were dominated by SCA effects, while for average tuber weight and specific gravity the GCA effect was more important. The differences in the importance of GCA and SCA effects observed in many studies could be attributed to differences in genetic material used. For example Neele et al. (1991) and Ortiz and Golmirzaie (2004) reported GCA to be significantly greater than SCA for tuber yields and yield related traits while Muthoni et al. (2015) reported SCA effects to be greater than GCA.

The GCA/SCA ratio for rAUDPC was 0.62. This gives an indication that the additive effect was important in the expression of late blight resistance among the potato clones used. This agrees with previous reports on the relative importance of GCA and SCA for potato late blight resistance (Bradshaw and Mackay, 1994; Kumar et al. 2007; Hirut, 2015; Muhinyuza et al. 2016). Landeo et

al. (2001) reported large additive genetic variance for late blight resistance in a random sample of the B3C1 population, using three different mating designs. In other studies, the SCA variances were greater than the GCA variances for late blight resistance (Killick and Malcolmson, 1973; Kaushik et al., 2000), while Landeo et al. (2000) found both additive and non-additive genetic effects to be equally important for horizontal resistance. The dominance of additive genetic effects for late blight resistance in this study confirms the absence of major (R) genes among the parents and showed that minor genes were responsible for the resistance.

All traits were highly heritable as revealed by heritability estimates. The broad sense heritability value for rAUDPC (0.68) was similar to that reported in other studies (Christ and Hynes, 2001; Visker et al., 2004). Conversely, both broad and narrow sense (0.43) heritability value were lower compared to the 0.79 and 0.78 respectively, obtained by Hynes and Christ, (1999) in a diploid hybrid potato population. Broad sense heritably values for total tuber weight (0.78), average (0.77) and marketable tuber weight (0.77) were high, suggesting that genetic advances in resistance to *Phytophthora infestans* and tuber yield among these genotypes can be realized. Also with such large heritability estimates, it could be suggested that relatively few genes are involved. The narrow sense heritability estimates obtained differed from other findings, for example, Ortiz et al. (1997) obtained 0.54 and 0.27 for average tuber weight and marketable tuber weight, respectively. The presence of maternal effects for rAUDPC (1.45) and ATW (1.56) points to cytoplasmic inheritance, where DNA in the chloroplasts is not subject to Mendelian inheritance (Acquaah, 2012).

The highly significant negative correlation between rAUDPC, and average tuber weight and total tuber weight observed in this study, shows the negative effect late blight imposes on tuber yield through the reduction of photosynthetic capacity of the foliage destruction. Several authors (Dowley et al. 2008; Mantecón, 2009; Muhinyuza et al. 2015; Hirut, 2015) have reported comparable results. For yield related traits, the total tuber weight was significantly and positively correlated with average tuber weight (0.86). Hirut (2015) found a slightly higher correlation coefficient between total tuber weight and average tuber weight of 0.88 in combining ability studies of potato clones in Ethiopia. Mehdi (2008) found total tuber yield to be largely influenced by higher number of tubers per plant and tuber size. This implies that total tuber weight can be selected for indirectly using average tuber weight. The total number of tubers was negatively correlated with average and marketable tuber weight, which was confirmed by Ruiz de Galarreta et al. (2006) and Muhinyuza et al. (2016).

6.5 Conclusion

This study found additive gene action to be more important than non- additive genetic effects in the inheritance of yield, related traits and resistance to late blight disease in potato. The following families were selected based on high yields and resistance to late blight: 393220.54 x NKRN59.48, 396038.107 x NKRN59.58, 392657.8 x 395017.14, Kinigi x NKRK19.17 and 392657.8 x NKRN59.41. These will be subjected to further testing and possible eventual release as varieties. The best general combiners were 393220.54, Kinigi, 395011.2, 392657.8, 396026.103, NKRN59.48, NKRN59.58. These parents were selected for future crop improvement purposes.

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Chapter 7 : Combining ability analysis of earliness and yield of potato genotypes in Uganda

Abstract

Potato (*Solanum tuberosum L*.) is a major food and cash crop mainly grown by small-scale farmers in the highland regions of Uganda. Changing global weather patterns require varieties which are able to grow within the short rainfall cycles and yield optimally under the prevailing conditions. In an effort to develop early maturing varieties with improved tuber yield, potato genotypes were selected from available germplasm in Uganda. The objectives of this study were to estimate combining ability effects for early maturity, yield and yield related traits; gene action controlling earliness in potato, as well as to identify promising potato genotypes for further evaluation. Eighteen F^1 families generated from two sets of 12 parents using a North Carolina Design II were evaluated for days to 50% flowering, leaf senescence, yield and yield related traits in two different locations. Both additive and non-additive genetic effects influenced the traits expression. However, additive genetic effects were predominant over the non-additive for most of the traits. The GCA/SCA ratios were 0.68, 0.55, 0.58 and 0.78 for days to flowering, total number of tubers, total tuber weight and average tuber weight, respectively. Broad sense heritability estimates were 0.7 for total tuber weight and 0.78 for days to flowering. Mean total tuber yield was 9.3 t ha^{-1}, while the average number of days to flowering was 54. The predominance of additive genetic effects imply that, genetic gains can be achieved through different selection methods and traits transferred to the respective progenies. Parents Rwangume, 396038.107, 395011.2 and NKRK19.17 had desirable GCA effects for the number of days to flowering. For yield and related traits, parents 396038.107, 393077.54, Rwangume, NKRK19.17, Kimuri, and 392657.8 had desirable GCA effects. The selected parents had desirable attributes for high yield and early maturity and families will be subjected to further clonal evaluation and selection.

Key words: Earliness, *Solanum tuberosum*, heritability, gene action, maturity, combining ability

7.1 Introduction

Earliness is a quantitative trait and it is affected by genetic and physiological factors of a plant plus environmental conditions (Basbag et al., 2007). Earliness in potato has been reported to contribute to disease escape especially of those that appear late in the season like late blight. It is also beneficial in areas with multiple cropping systems and limited land and short favourable growing seasons. Early maturing varieties are more economical in their use of irrigation water, tend to escape insect infestations by for example aphids and may escape frost injury or disease infestation (Sleper and Poehlman, 2006). In areas with short rains, early varieties facilitate drought escape, a feature essential in view of climate change (Bänziger, 2000).

Crop maturity is an agronomic trait and crops undergo progressive growth stages from emergence to senescence, characterized by their reproductive capacity and phenology (Khan et al., 2013). Potato maturity is normally assessed by monitoring vine characteristics and change of the potato plant's leaves is an indicator that the crop has reached maturity (Haga et al., 2012; Iragaba, 2013). Potato varieties are classified into maturity types based on the lengths of the season required to produce a harvestable product (Haga et al., 2012; Khan et al., 2013). Variability among varieties for the number of days from planting to maturity has led to designation of the potato varieties as early, medium, late and very late maturity classes (Ruzukas et al., 2009). Breeders normally evaluate maturity period while developing new varieties because it is a critical aspect in commercial potato production. Standard maturity measurements in potatoes are lacking because tubers are produced underground and monitoring their development presents many challenges. As a result, breeders commonly assess potato maturity classes based on physiological changes and to some extent phenological and morphological changes in the potato vine. Tuber production is associated with changes at the whole plant level, such as reduction in leaf development, flowering and fruit set (Haga et al., 2012).

In potato, both the general combining ability (GCA) effects of parents and specific combining ability (SCA) effects of their crosses are important in determining economic traits. This is due to the fact all genetic effects are fixed at the F^1 through the development of clones and there is no further segregation (Muthoni et al., 2012). Earliness in potato has not received sufficient attention in Uganda and elsewhere as there seems to be scanty information regarding the subject. However, some findings suggest that both additive and non–additive genetic effects control earliness in potato, though additive genetic effects were found to be more important (Iragaba, 2013). Despite this finding, detailed information regarding inheritance of this trait and combining ability of parents is limited. It is against this background that this study was undertaken to

determine the genetic control of earliness in potato in order to develop varieties which are early maturing with high yields.

7.2 Materials and methods

7.2.1 Parental materials and crosses

Twelve genetically diverse clones were selected and used as parents. Six clones were obtained from the National Potato Program of Uganda and four were advanced clones from the International Potato Centre (CIP) belonging to population B3C2 with variable resistance to late blight. These were selected based on their flowering abilities, number of days to flowering, flowering duration and high to medium yields (Namugga et al., 2017). Parents were assembled into two sets of six parents each based on their flowering abilities, yield and resistance to late blight. Crosses were made using a North Carolina Design II (NCD II) to generate 18 families. (Table 7.1). In the first set three female clones (Rwangume, 396026.103 and 396038.107) were crossed with three males (Kimuri, 391046.14 and NKRK19.17) and in the second set, three female parents; 392657.8, 393220.54 and 396038.107 were crossed with three males; NKRN59.48, Rwangume and 395011.2. Parents Rwangume and 396038.107 were used in both sets. In total, 18 families were generated (two sets of nine families each). Controlled hand pollination was performed at flowering following emasculation (Acquaah, 2007). At maturity, berries of the same cross were harvested and bulked together. These berries were labelled and kept at room temperature to ripen. After softening of the berries, the seeds were manually extracted and washed thoroughly with water. These seeds were air dried and stored in petri dishes up to planting time.

Table 7.1: Description of parents used in the crossing block

Set	Male/Female	Parents	Source	Yield (t ha-^{1})	Days to flowering
1	Female	Rwangume		25.2	59
1	Female	396026.103		33.1	54
1	Female	396038.107		42.8	61
1	Male	Kimuri		17.1	52
1	Male	391046.14		34.6	52
1	Male	NKRK19.17		37.0	61
2	Female	392657.8		43.7	55
2	Female	393077.54		43.2	59
2	Female	396038.107		42.8	61
2	Male	Rwangume		25.2	59
2	Male	395011.2		25.5	54
2	Male	NKRN59.48		30.0	61

Source: Namugga et al. (2017)

7.2.2 Planting sites

The field trials were established at Kachwekano research station and on a farm in Nyabumba. Both sites are located in South-western Uganda. Kachwekano is located in, 01º 16'S 29º 57'E at 2200 meters above sea level (masl) while Nyabumba at 1400 masl. These different elevations affect the temperature regimes, hence creating different environments. Both sites have a bi-modal rainfall pattern separated by a dry spell ranging from 30 to 60 days. Planting was done in March and harvesting in July 2017.

7.2.3 Experimental design and trial establishment

Experiments were established during the planting season between March and June 2017 using a 7 x 4 alpha lattice design with two replications at both locations. Parents Rwangume and 396038.107 were used in both sets. The 18 F^{1} families were planted in two row plots of 20 tubers each at 75 cm between rows and 30 cm between plants. Planting was by hand and N: P: K: 17:17:17% fertilizer was applied at a rate of 100 kg ha^{-1}. Pest and disease control was done using recommended insecticides and fungicides. Hand weeding and ridging were carried out as recommended.

7.2.4 Data collection

Data were collected on days to flowering and leaf senescence. Days to flowering were recorded as number of days from planting to when 50% of the plants in a plot flowered. Leaf senescence was measured as the number of days from flowering to 100% of the leaves dying off. At harvest, yield related data was taken on the total number of tubers (TTN) harvested per plant, total weight of all the tubers harvested in a plot (TTW) and expressed in t ha^{-1}. Average tuber weight (ATW) was calculated as the total tuber weight divided by the total tuber number of tubers per plant.

7.2.5 Data analyses

7.2.5.1 Analysis of variance

Data for the different traits over two sets and across environments were subjected to the standard analysis of variance using the GLM procedure of SAS 9.3 (SAS, 2011) statistical program. Analyses of variance of NCD II pooled over sets and across environments (Hallauer and Miranda 1988) were conducted for all the traits. Main effects due to female and male effects within sets are independent estimates of GCA while male x female interaction effects represent SCA variance within sets. Spearman correlation coefficients were calculated for the studied traits to determine their association.

7.2.5.2 Estimation of general and specific combining ability effects

Data were analysed over sets and across environment. Parents were considered as fixed effects in the test of significance. The GCA and SCA values for each trait were calculated following the NCII mating design across sites using the following linear model (Hallauer et al., 1988):

$$Y_{ijkpq} = \mu + S_p + g_i(S_p) + g_j(S_p) + h_{ij}(S_p) + E_q + r_k(SE)_{pq} + (ES)_{pq} + (Eg)_{iq}(S_p) + (Eg)_{jp}(S_p) + (Eh)_{ijq}(S_p) + (Eh)_{ijq}(S_p) + e_{ijkpq}$$

Where: i = 1, 2, 3; j = 1, 2, 3; k = 1, 2; p = 1, 2; q = 1, 2; the terms for the model are defined as follows: Y_{ijkpq} denotes the value of a family from the mating between the ith female parent, the jth male parent, in the kth block, within set p and in the qth environment; μ = Grand mean; S_p = the average effect of the pth set; $g_i(S_p)$ = the GCA effect common to all F^1 families of the ith female parent nested within pth set; $g_j(S_p)$ = the GCA effect common to all F^1 families of the jth male parent nested within pth set; $h_{ij}(S_p)$ = the SCA effect specific to F^1 families of the ith female and jth male parent nested within pth set; E_q= average effect of qth environment; $r_k(SE)_{pq}$ = the effect of the kth replication nested within the pth set and qth environment; $(ES)_{pq}$= the interaction between site and set effects; $(Eg)_{iq}(S_p)$ and $(Eg)_{jp}(S_p)$ = the interaction between site and GCA

of the ith female and *j*th male parent, respectively nested within sets; (E*h*)*ijq*(S*p*) = the interaction between site and SCA, nested within sets; and e*ijkpq* = the random experimental error.

General and specific combining abilities (GCA and SCA respectively) for the parents and crosses were determined according to the following formulae:

The GCA for each of the male and female parents was calculated using the following formula (Singh and Chaudhary, 2007):

$GCA_m = X_m - \mu$,

$GCA_f = X_f - \mu$.

The SCAs of the crosses were computed from the formula:

$SCA_X = X_X - E(X_X) = X_X - [GCA_m + GCA_f + \mu]$

Where: GCA_m = general combining ability of male parent; X_m = mean of the male parent; μ = overall mean of all crosses; GCA_f = general combining ability of the female parent, X_f = mean of the female; SCA_X = specific combining ability of the two parents in the cross; X_X = observed mean value of the cross; $E(X_X)$ = expected values of the cross basing on the GCAs of the two parents

The significance of GCA and SCA effects was determined as indicated below

GCA standard error = Square root of MSE/r x f x m x sites

** (f = m)

SCA standard error = Square root of MSE/r x sites

Where

MSE = error mean square

r.= replications*

f = number of female parents

m = number of male parents* number of sites

GCA or SCA were significant at P≤0.05 and P≤0.01 when estimates were greater than SE *1.96 and SE*2.576 respectively.

The relative importance of GCA and SCA in influencing the performance of the crosses were estimated using the general predicted ratio (GPR) for all the traits (Baker, 1978), as indicated below:

$$\frac{\text{GCA}}{\text{SCA}} = \frac{\text{MSQGCA pooled}}{\text{MSQGCA (pooled)} + \text{MSQ SCA}}$$

MSQGCA (pooled) $= (\text{MSQGCAmale} + \text{MSQGCA female})/(\text{number of replications})$

Where; MSQGCA and MSQSCA are the mean squares for GCA and SCA, respectively. When the ratio is >0.5, GCA is more important than SCA in the inheritance of the character concerned, while the reverse is true when the ratio is <0.5 (Baker, 1978).

Throughout the text, variation due to males within sets, females within sets, and males x females within sets will be referred to as GCAm, GCAf and SCA variation, respectively. For TTN, TTW, MTW, and ATW positive estimate of GCA and SCA effects were taken as high to identify high genotypes.

7.2.5.3 Estimating heritability

Heritability estimates were calculated using the female additive variance as follows:

Narrow sense heritability based on female additive variance:

$h_f^2 = 4\sigma^2_f / (\sigma^2_e /r + 4\sigma^2_{mf} + 4\ \sigma^2_f) = V_{Af} / V_P$

Where

r = number of replication

σ^2_e = environmental variance = MS_e

σ^2_f = variance of female parents = GCA_f variance = MS_f

σ^2_{fm} = variance due to interaction between females and males = SCA variance = MS_{mf}

V_{Af} = additive genetic variance due to female parents

V_P = phenotypic variance

Broad sense heritability as follows:

$h_f^2 = 4\sigma^2_{f+} 4\sigma^2_{mf} / (\sigma^2_e /r + 4\sigma^2_{mf} + 4\ \sigma^2_f) = V_{Gf} / V_P$

Where V_{Gf} = total genetic variance

The other terms are as described above in narrow sense heritability.

7.3 Results

7.3.1 Analysis of variance for crosses across sites

The combined analysis of variance and ratio of GCA/SCA for days to flowering (DAF), leaf senescence (LS), and total tuber number (TTN), total tuber weight (TTW) and average tuber weight (ATW) among the families is presented in Table 7.2. There were significant differences within sets observed for TTN P≤0.01) and ATW (P≤0.05). The environmental effect was significant (P≤ 0.001) for all the traits except for number of days to flowering. The GCA mean squares for females (GCA_f) were significantly different for DAF, TTN and TTW at P≤0.001, P≤0.01 and P≤0.05, respectively. The GCA mean square for males (GCA_m) were significantly different for DAF (P≤0.001), TTN, and TTW (P≤0.05). The SCA effects for the crosses were significant for all

the tested traits except ATW. The environmental interactions with families were only significant for TTW. The GCA_f effects were higher than male GCA effects for LS, TTN, TTW and ATW, while the additive male effects were slightly more for DAF. Overall, the GCA was more important than the SCA in the expression of all the traits. The additive/ non-additive genetic effects using Baker's ratio was highest for ATW (0.78) and lowest for LS (0.41).

Table 7.2: Combined analysis of variance for days to flowering, leaf senescence, and tuber yield and related traits at in Uganda

		Mean Square				
Source of variation	**Df**	**DAF**	**LS**	**TTN**	**TTW**	**ATW**
Set[1]	1	29.73	13.91	8048.27**	6.63	0.12*
Site	1	39.15	1702.85***	26336.87***	1387.66***	1.64***
Replication (Site)	2	71.49*	76.15	580.28	28.96*	0.00
Female (Set)	10	81.68***	40.4	4284.60**	22.26*	0.05
Male (Set)	10	87.31***	21.93	3030.40*	20.60*	0.02
Female*Male (Set)	20	79.45***	89.75*	6085.46***	31.46**	0.02
Site*Set	1	57.18	25.54	211.27	7.27	0.08
Site*Female (Set)	10	11.63	18.82	895.97	8.66	0.04
Site*Male (Set)	10	20.16	59.23	1523.32	11.26	0.03
Site*Female*Male (Set)	20	18.69	52.85	1019.75	19.42*	0.02
Error		20.09	29.03	1266.45	9.65	0.03
R-Square		0.84	0.78	0.85	0.92	0.82
GCA/SCA ratio		0.68	0.41	0.55	0.58	0.78

[1]Set – set within an environment, DF= degrees of freedom *= significant at P≤0.05; **= significant at P≤0.01; ***= significant at P≤0.001; DAF = days to 50% flowering; LS = days to leaf senescence; TTN = total tuber number; TTW = total tuber weight; ATW= average tuber weight; GCA/SCA ratio calculated according to Baker (1978).

7.3.2 Heritability estimates

Estimates of broad and narrow sense heritability (H^2 and h^2) and test for maternal effects for the studied traits are presented in Table 7.3. The broad sense heritability values were highest for DAF and TTN (0.78) and lowest for ATW (0.39). The narrow sense heritability estimates were highest for DAF (0.40) and the lowest for LS (0.09).

Table 7.3: Broad and narrow -sense heritability (H^2 and h^2) for DAF, LS and yield related traits and yield related traits across two locations in South -western Uganda

Heritability/Traits	DAF	LS	TTN	TTW	ATW
H^2	0.78	0.45	0.78	0.70	0.39
h^2	0.40	0.09	0.31	0.28	0.34

H^2 = broad sense heritability; h^2 = narrow sense heritability; DAF = days to 50% flowering; LS = days to leaf senescence; TTN = total tuber number; TTW = total tuber weight; ATW = average tuber weight

7.3.3 General combining ability effects of parents

The GCA effects of potato parents at are presented in Table 7.4. Significant GCA effects were observed among all the parents for ATW. Female parents 392657.8 and 396038.107 had significant GCA effects for DAF, while male parents Rwangume and NKRN59.48 had GCA effects significant for TTW. Among the female parents, 396038.107 had the lowest GCA effects for DAF (-1.44) followed by Rwangume (-0.42), while 392657.8 had the highest (1.14). Male parents 395011.2 and NKK 19.17 had the lowest GCA effects for DAF (-0.59 and -0.38, respectively). For yield and related traits, Rwangume had the highest GCA effects for TTW (0.41) followed by NKRK19.17 (0.28), while the lowest GCA effect was for NKRN59.48 (-0.20). Additionally, the GCA effects for ATW were highest for 393077.54 (0.02).

Table 7.4: Estimates of general combining ability (GCA) effects for DAF, LS, TTN, TTW and ATW of 12 potato parents evaluated in two locations in Uganda.

	Traits				
	DAF	**LS**	**TTN**	**TTW**	**ATW**
			Set1		
Females					
Rwangume	-0.421	-0.403	-1.800	-0.238	-0.002**
396026.103	0.319	-0.045	3.358	0.188	0.002**
396038.107	0.102	0.448	-1.558	0.049	0.000
Males					
Kimuri	0.298	-0.602	5.381	-0.031	0.003**
391046.14	0.078	0.239	-3.808	-0.253	-0.012**
NKRK19.17	-0.376	0.362	-1.573	0.284	0.009**
SE	0.900	1.680	37.080	0.270	0.001
			Set2		
Females					
392657.8	1.144**	-0.124	8.402	0.025	-0.004**
393077.54	0.299	-0.382	-4.743	-0.008	0.018**
396038.107	-1.443**	0.506	-3.659	-0.016	-0.014**
Males					
Rwangume	0.561	0.209	5.402	0.411*	0.002
395011.2	-0.589	0.277	1.029	-0.207	-0.01
NKRN59.48	0.028	-0.486	-6.431	-0.200**	0.008
SE	0.800	2.710	55.310	0.460	0.002

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; DAF = days to flowering; LS = days to leaf senescence; TTN = total tuber number; TTW = total tuber weight; ATW= average tuber weight

7.3.4 Specific combining ability effects of families

The SCA effects of 18 potato F^1 families are presented in Table 7.5. Crosses largely showed significant SCA effects for ATW while no significant SCA effects were observed for other traits. The highest SCA effects for TTW were among the crosses of Rwangume x NKRK19.17 (0.36) followed by 393077.54 x 395011.2 (0.25). Crosses of 396038.107 x Rwangume had highest SCA

effects for ATW (0.021). For number of days to 50% flowering, families of Rwangume x NKRK19.17 (-1.38) and 396038.107 x 395011.2 (-0.75) had the lowest SCA effects.

Table 7.5: Estimates of specific combining ability (SCA) effects for DAF, LS, TTN, TTW and ATW of 18 F^1 potato families evaluated in two locations in South-western Uganda.

Traits	**DAF**	**LS**	**TTN**	**TTW**	**ATW**
		Set1			
Rwangume x Kimuri	0.296	0.215	5.216	-0.040	-0.003
Rwangume x 391046.14	1.079	0.249	-10.157	-0.318	0.007**
Rwangume x NKRK19.17	-1.375	-0.465	4.941	0.359	-0.004*
396026.103 x Kimuri	-0.507	0.295	-1.128	0.190	0.002
396026.103x 391046.14	-0.635	-1.211	6.182	0.298	-0.007**
396026.103 x NKRK19.17	1.142	0.916	-5.054	-0.488	0.004*
396038.107 x Kimuri	0.210	-0.510	-4.088	-0.150	0.001
396038.107 x 391046.14	-0.444	0.961	3.976	0.020	0.000
396038.107 x NKRK19.17	0.234	-0.451	0.113	0.130	0.000
SE	2.670	5.030	111.240	0.800	0.002
		Set2			
392657.8 x Rwangume	-0.790	1.060	2.805	0.063	-0.002
392657.8 x 395011.2	1.240	-1.260	0.303	-0.136	-0.006**
392657.8 x NKRN59.48	-0.450	0.210	-3.108	0.073	0.008**
393077.54 x Rwangume	-0.480	0.420	2.760	0.185	-0.019
393077.54 x 395011.2	-0.490	0.450	-0.550	0.254	0.017**
393077.54 x NKRN59.48	0.970	-0.870	-2.220	-0.439	0.001
396038.107 x Rwangume	1.260	-1.470	-5.569	-0.249	0.021**
396038.107 x 395011.2	-0.750	0.810	0.244	-0.118	-0.011**
396038.107 x NKRN59.48	-0.520	0.660	5.326	0.366	-0.009**
SE	2.410	8.140	165.940	0.060	0.007

SE = standard error; *, ** significantly different from zero at ≥ 1.96SE and 2.56SE respectively *= significant at P≤0.05; **= significant at P≤0.01; DAF = days to flowering; LS = days to leaf senescence; TTN = total tuber number; TTW = total tuber weight; ATW= average tuber weight

7.3.5 Family means across locations

The mean performance of parents and their families varied greatly across the test environments. Means of DAF, LS, TTN, TTW and ATW within locations are presented in Table 7.6. The mean number of days to flowering was 54, while total tuber weight was 9.3 t ha^{-1}. Average tuber weight was 0.5. The number of days to flowering ranged from 44.1 to 62 days. Families with less days to flowering were 396038.107 x 395011.2 (44.1) and 396038.107 x NKRN59.48 (47.5). The average number of days to 100% leaf senescence were 30.6 and mean total number of tubers was (134.1). Families Rwangume x Kimuri (204) and 392657.8 x Rwangume (202.5) had more tubers than others, while 393077.54 x NKRN59.48 (82.5) had the lowest number of tubers. The average total tuber weight was 9.3 t ha^{-1} and families 393077.54 x Rwangume (14.7 t ha^{-1}) and (Rwangume x NKRK19.17 (13.0 t ha^{-1}) were the best yielders. The average tuber weight ranged from 0.3 to 0.6.

Table 7.6: Family and parent means of days to flowering, leaf senescence, total number of tubers, tuber weight and average tuber weight of 18 potato families evaluated at two locations in Uganda

	Trait and mean performance across sites				
Crosses	**DAF (days)**	**LS (%)**	**TTN**	**TTW (t ha^{-1})**	**ATW (kg)**
Rwangume x Kimuri	56.3	28.5	204.8	11.8	0.4
Rwangume x 391046.14	58.5	32.0	106.5	9.8	0.4
Rwangume x NKRK19.17	46.9	29.6	175.8	14.6	0.5
396026.103 x Kimuri	56.0	30.3	168.5	14.4	0.5
396026.103 x 391046.14	54.6	32.4	200.0	14.0	0.4
396026.103 x NKRK19.17	59.9	36.6	156.5	13.0	0.5
396038.107 x Kimuri	58.0	29.0	147.5	12.5	0.5
396038.107 x 391046.14	54.5	38.3	164.0	12.3	0.4
396038.107 x NKRK19.17	55.4	33.9	195.0	14.9	0.5
392657.8 x Rwangume	58.9	35.1	202.5	14.4	0.5
392657.8 x 395011.2	62.4	26.1	175.0	11.1	0.4
392657.8 x NKRN59.48	58.1	28.9	131.5	12.0	0.5
393077.54 x Rwangume	56.8	31.5	149.8	14.7	0.5
393077.54 x 395011.2	52.1	31.9	119.0	12.5	0.6
393077.54 x NKRN59.48	60.4	23.6	82.5	9.8	0.6
396038.107 x Rwangume	56.8	27.5	120.8	13.0	0.5
396038.107 x 395011.2	44.1	36.9	126.5	11.0	0.3

396038.107 x NKRN59.48	47.5	33.3	117.0	8.7	0.4
Parents					
Rwangume	55.0	34.8	142.3	16.1	0.6
396026.103	45.3	24.5	110.3	7.9	0.3
396038.107	56.4	31.6	68.5	7.1	0.5
Kimuri	53.5	37.3	85.5	7.3	0.3
391046.14	57.5	32.0	73.8	6.1	0.5
NKRK19.17	45.8	25.3	107.8	6.1	0.4
392657.8	46.5	20.3	114.0	9.4	0.5
393077.54	54.0	30.0	120.5	12.8	0.6
395011.2	56.8	20.5	186.5	14.4	0.8
NKRN59.48	58.3	35.3	82.8	8.5	0.5
Mean	54.0	30.6	134.1	9.3	0.5
CV (%)	8.0	23.0	25.6	33.4	32.3

DAF = days to 50% flowering; LS = days to leaf senescence; TTN = total tuber number; TTW = total tuber weight; ATW= average tuber weight

7.3.6 Correlation between traits

The correlations between the five traits are presented in (Table 7.7). The correlations were significant and positive at Kachwekano between TTW and TTN ($p \leq 0.001$), TTW and ATW ($p \leq 0.01$), and DAF and ATW ($p \leq 0.05$). At Nyabumba, significant, positive correlations were observed between TTW, and TTN and ATW ($p \leq 0.001$), while that the correlations between LS and DAF was positive and significant at ($p \leq 0.05$). Across locations, correlations were positive and significant between LS and TTW ($p \leq 0.001$); LS and ATW ($p \leq 0.01$); TWW, and TTN and ATW ($p \leq 0.001$); and TTN and ATW (($p \leq 0.01$).

Table 7.7: Phenotypic correlation between four traits of 18 potato families

Trait	LS	TTW	TTN	DAF	ATW
Kachwekano					
Leaf senescence	-				
Total tuber weight	0.059	-			
Total number of tubers	0.007	0.649***	-		
Days to flowering	-0.054	0.214	0.004	-	
Average tuber weight	0.024	0.376**	0.036	0.259*	-
Nyabumba					
Leaf senescence	-				
Total tuber weight	-0.161	-			
Total number of tubers	-0.107	0.680***	-		
Days to flowering	0.277*	-0.109	0.119	-	
Average tuber weight	-0.132	0.515***	0.153	-0.239	-
Across locations					
Leaf senescence	-				
Total tuber weight	0.343***	-			
Total number of tubers	0.156	0.688***	-		
Days to flowering	0.139	0.131	0.071	-	
Average tuber weight	0.278**	0.639***	0.269**	0.122	
	1	2	3	4	

*= Significant at P≤0.05; **= Significant at P≤0.01; ***= Significant at P≤0.001; DAF = days to flowering; LS = days to leaf senescence; TTN = total number of tubers; TTW = total tuber weight; ATW= average tuber weight

7.4 Discussion

The significant mean squares of families for days to flowering and total tuber weight indicated the presence of genetic variation among parents and their crosses. This suggests that genotypes that are early maturing with high yields can be selected for. The significant GCA and SCA mean squares of the traits observed shows that both additive and non-additive gene action were involved in the expression of the traits.

The Baker's ratio for number of days to 50% flowering was 0.68, while the ratio was 0.41 for leaf senescence. These results signify the predominance of additive genetic effects in the control of

days to flowering and non- additive effects for leaf senescence. These findings differ from what has been reported in other studies. For instance, Iragaba (2013) found both additive and non–additive gene action controlling earliness in potato, though additive genetic effects were more important. Buso et al. (2000) reported both additive and non-additive effects to influence maturity and total tuber yields. However, because traits are fixed in the F^1 generation when clones are developed, both genetic effects are of great importance in potato breeding (Muthoni et al., 2012). According to Singh and Chaundary (2004), parents with significant GCA and SCA effects in the right direction would be the desired for the trait of interest. For early maturity, the desirable gene action is negative, while for yield, is positive. In this study, both desirable and non-desirable GCA effects were passed on to the respective progenies. Parents Rwangume (-0.42), 396038.107 (-1.44) and NKRK 19.17 (-0.38) had desirable GCA effects for days to flowering and passed these on to their progenies. Crosses of female parent 393077.54 displayed significant and negative SCA effects for days to flowering and leaf senescence. The best combiners were 396037.108, 393077.54, Rwangume and NKRK19.17.

The current study found that the GCA effects for tuber yield related traits (TTN, TTW and ATW), were more important than SCA effects. For example, the Baker's ratio for total number of tubers was 0.55, total tuber weight was 0.58 and average tuber weight was (0.78). This implies that additive genes largely influenced the expression of these traits. The predominance of additive genetic effects observed for these traits has been reported in previous studies (Killick, 1977; Gopal, 1998; Hirut 2015; Muhinyuza et al. 2016). These studies reported GCA to be more important in magnitude than SCA in affecting potato yield. However, some authors found both GCA and SCA to be significant for potato yield with GCA being less important in magnitude than SCA (Bradshaw and Mackay, 1994; Ortiz and Golmirzaie, 2004; Ruiz de Galarreta et al., 2006; Haydar et al., 2009). In other studies, significant SCA effects for yield have been reported (Gopal, 1998; Ruiz de Galarreta et al., 2006; Muthoni et al., 2015). Differences between progenies for tuber yields and number of tubers per plant were found to be dominated by SCA effects, while for average tuber weight and specific gravity the GCA effect was more important (Tai, 1976). The variations in the significance of GCA and SCA observed in several studies might be due to differences in genetic material used (Neele et al., 1991; Ortiz and Golmirzaie, 2004; Muthoni et al., 2015). The broad sense heritability estimates revealed number of days to 50% flowering (0.78), total number of tubers (0.78) and total tuber weight (0.70) to be highly heritable traits. The narrow sense heritability estimates obtained in this study were varying and relatively low. Several authors (Ortiz et al., 1997; Bradshaw et al., 2000; Iragaba, 2013) found comparatively higher

values for leaf senescence, days to flowering, total tuber yield, marketable and average tuber yield among different populations.

The positive and highly significant correlations between yield and tuber related traits (TTW and TTN =0.688, TTW and ATW = 0.639, ATW and TTN= 0.269) have been reported in other studies (Muhinyuza et al. 2015; Hirut, 2015). Likewise, Mehdi (2008) found total the tuber yield to be largely influenced by higher number of tubers per plant and tuber size. This denotes that improving one trait would subsequently improve the other. The significant positive association observed between leaf senescence and days to flowering, total tuber weight and average tuber weight obtained in this study may be attributed to the fact that crop maturity is an agronomic trait where a plant undergoes progressive growth stages from emergence to senescence, characterized by their reproductive capacity and phenology (Struik, 2010; Khan et al., 2013). This could also be due to the differences in environmental conditions as plant senescence takes place faster at higher temperatures (Kooman and Haverkort, 1995).

7.5 Conclusion

The significant differences observed among GCA_f, GCA_m and SCA effects for the genotypes points to the presence of sufficient genetic variation, which can be exploited for crop improvement. Both additive genetic effects were important in inheritance of the traits measured. For traits where additive genetic effects were predominant, improvement can be made by selection and traits transferred to the respective progenies. Where characters were largely influenced by SCA and non- additive genetic action, further genetic gains can be achieved through hybridization of the desirable parents. Overall, parents Rwangume, 393077.54, 396038.107, 395011.2 and NKRK 19.17 had desirable GCA effects for days to flowering, total and average tuber weight, indicating that they had desirable attributes for high yield and early maturity.

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Chapter 8 : Overview of the study

8.1 Introduction and research objectives

Potato *(Solanum tuberosum* L.*)* is an important source of food globally. In Uganda it is both a food and cash crop, mainly grown by small scale farmers in the highlands, which account for 60% of total national production. However, the production is hampered by several biotic, abiotic, and socio-economic factors as well as poorly adapted and adopted varieties. Among the biotic constraints, late blight caused by *Phytophthora infestans* (Mont.) de Bary is the major disease preventing the full genetic expression of the crop, especially in the tropical highland regions. Low yields and lack of early maturing varieties is another limitation in potato production. In order to improve productivity, genotypes that are high yielding, resistant to late blight and early maturing, should be developed to address the challenges of food security and the changing weather patterns. This chapter summarizes the research objectives and major research findings of the study.

The objectives of the study were:

1) To document farmers' knowledge preferred traits in potential new varieties and their perspectives on late blight prevalence and severity.

2) To phenotypically characterize potato genotypes in Uganda.

3) To assess the genetic diversity among potato genotypes using SSR markers.

4) To determine yield response of potato genotypes to late blight disease in the tropical highlands of Uganda.

5) To determine the combining ability effects for yield, yield related traits and resistance to late blight disease of potato genotypes.

6) To establish the mode of inheritance for early maturity and tuber yield among potato genotypes of different maturity groups.

8.2 Research summary

To document farmer practices, key production constraints, cultivar preferences, perspectives on late blight prevalence, severity and management in major potato growing areas, a participatory rural appraisal (PRA) was conducted in three major potato growing regions involving 577 individual farmers. The major findings were as follows:

- Most of the respondents used farm saved seed, while only 2% of the farmers from Eastern and South-western Uganda obtain seed from research stations.
- The major production challenges were pests and diseases. The major pests were aphids and cutworms, while late blight and bacterial wilt were the prominent diseases.
- Across the three regions, Rwangume and Victoria were the commonly grown varieties, while Cruza and Marierahinda were the most rejected varieties. The latter were rejected on account of being white skinned and their low marketability
- High yield, resistance to late blight, early maturity and marketability were the most preferred attributes in new varieties.
- Late blight had been experienced by 98% of the farmers and 96% of these reported to have used fungicides to manage the disease.

To phenotypically characterize 48 potato genotypes, in order to identify suitable parents for crop improvement purposes, genotypes were evaluated using an alpha lattice design with three replications at Kachwekano and Karengyere stations in Uganda. The main outcomes were:

- The environment had significant effects on the genotype performance for all measured parameters.
- The mean tuber yield for the two sites was 29.8 t ha^{-1} and tuber yield was higher in Kachwekano than Karengyere. The best yielding genotype in Kachwekano was 396038.105 (54.5 t ha^{-1}) and in Karengyere NAKPOT5 (50.9 t ha^{-1}).
- Fifty two % of the genotypes were high yielding (30 t ha^{-1} and above) and the most stable genotypes in terms of tuber yield were Rutuku, 395112.32, 395017.14 and 393220.54
- Significant positive correlations ($p \leq 0.001$) were observed between tuber yield and plant height; duration of flowering, and days to flowering and plant height.

To determine yield response of potato genotypes to late blight disease in the tropical highlands of Uganda, 48 genotypes were evaluated for two seasons in two environments. The trials were laid out in a 8 x 6 alpha lattice design with three replications. The major outcomes were as follows:

- Genotypes showed significant differences in yield and resistance to blight.
- Disease severity was higher in Karengyere (56%) than Kachwekano and the most resistant genotypes were 395077.12 and 392657.8, with disease severity of 12% and 14% respectively.
- The mean tuber yield under late blight infection was19.8 t ha^{-1} and the best yielding genotype across sites was 395112.32 (35.6 t ha^{-1}).

- The following genotypes; 395112.32, 391919.3, 393220.54. 393077.54, 396038.107. 392657.8, Kinigi, 395014.17, NKRN59.58, NKRK19.17 and 395011.2, were identified as promising parents for subsequent crosses. These genotypes exhibited high to medium resistance to Phytophthora infestans and high yields.

To determine the pattern and level of genetic diversity among potato genotypes, in order to to identify suitable parents for breeding purposes, 20 selected potato genotypes were studied using 16 SSR markers. The main outcomes were as follows:

- The microsatellites showed considerable variation among genotypes and 64 alleles were amplified by the 16 primer pairs. The number of polymorphic alleles per locus ranged from 2 to 8, polymorphic information content PIC) values from 0.0948 to 0.7832, while heterozygosity values ranged from 0.0997 to 0.805.
- Linear correlations between PIC values, and the number of alleles and heterozygosity were positive and significant at $p < 0.001$.
- The cluster analysis separated the genotypes into three different groups. The genetic distance between clones ranged from 1 to 5.7. Cruza had the highest genetic distance, while the shortest genetic distance was observed between 396026.103 and 396034.104.
- The microsatellites used in this study provided useful information regarding the variability of the tested genotypes and their selection for breeding purposes.

To determine the combining ability effects for yield and yield related traits and late blight resistance of selected potato clones and their crosses, 12 potato genotypes were identified as promising parents. These were crossed in a North Carolina mating design II in two sets of six parents each to generate 18 families for determining their combining ability. Key findings were as follows:

- Results revealed both additive and non-additive genetic effects controlling yield and late blight resistance in potato. However, additive gene action was predominant over non-additive for total tuber weight (GCA/SCA = 0.53) and late blight resistance (GCA/SCA = 0.62).
- Broad-sense heritability estimates were 0.78 for total tuber weight and 0.68 for rAUDPC.
- This study showed some evidence of maternal effects for some traits (rAUDPC, F = 1.45 and ATW, F = 1.56).

- Parents Kinigi, 392657.8, 396034.103, 396038.107, 395011.2, NKRK19.17, NKRN59.58 and 395017.14 had good general combining ability (GCA) effects for both late blight disease resistance and yield related traits.
- Families 392657.8 x 395017.14 and 396038.107 x NKRN59.58 had the highest SCA effects for all the yield related traits, while families Kinigi x NKRK19.17and 392657.8 x NKRN59.41 had the lowest SCA effects for rAUDPC.
- The selected parents and families were the best candidates to develop improved potato varieties that combined both high yield and resistance to *Phytophthora infestans*.

To determine the combining ability effects for yield and yield related traits and earliness of selected potato clones and their crosses, 12 potato genotypes were identified as promising parents. These were crossed in a North Carolina mating design II in two sets of six parents each to generate 18 families for determining their combining ability. Results showed that:

- Additive gene effects predominantly controlled number of days to flowering (GCA/SCA = 0.68), total number of tubers (GCA/SCA = 0.55), total tuber weight (GCA/SCA = 0.58) and average tuber weight (GCA/SCA = 0.78).
- Broad sense heritability estimates were 0.7 for total tuber weight and 0.78 for days to flowering.
- Mean total tuber yield was 9.3 t ha^{-1} while the average number of days to flowering was 54.
- Parents Rwangume, 396038.107, 395011.2 and NKRK19.17 had desirable GCA effects for the number of days to flowering. For yield and related traits, parents 396038.107, 393077.54, Rwangume, NKRK19.17, Kimuri, and 392657.8 had desirable GCA effects.
- The selected parents had desirable attributes for high yield and early maturity and families and will thus be subjected to further clonal evaluation and selection.

8.3 Implications of the research findings to breeding potato for higher yields, resistance to *Phytophthora infestans* and early maturing

In general, this study identified potato clones that are resistant to late blight and early maturing with high yields. However, these require further evaluation and selection to obtain clones for possible release as varieties in Uganda. The following implications were noted for crop improvement purposes:

The involvement of farmers in identification of breeding priorities in early stages of cultivar development and selection is pivotal in accelerating variety adoption. Their ideas need to be considered for future potato breeding programs in Uganda.

The different yield classes, plus the cluster analyses obtained, will be utilized in designing targeted crosses and help in maintaining diversity among the genotypes.

There is substantial genetic variation for potato tuber yield, late blight resistance and early maturity among the potato genotypes in Uganda.

This study showed some evidence of maternal effects for rAUDPC and ATW. Although these were not significant at $P \leq 0.05$, their presence would influence the choice parents in a crossing scheme. Parents for improvement of these traits would be used as females.

The significance of both additive and non-additive effects in controlling tuber yield, yield related traits, resistance to *Phytophthora infestans* and early maturity implies that:- For traits were non-additive genetic effects were significant, the traits are controlled largely by dominance genetic effects and therefore a hybridization breeding strategy can be employed to develop hybrids. For traits were additive genetic effects were predominant, advances in breeding can be made through population improvement methods and selection.