Breeding potato (*Solanum tuberosum* L.) for high yield and resistance to late blight in Rwanda

By

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THESIS ABSTRACT

Potato (*Solanum tuberosum* L.) is one of the most important food crops in the world, and in developing countries its production has increased over the last decade. Potato has a high content of carbohydrates as a source of energy, significant amounts of quality protein, and substantial amounts of vitamins, especially vitamin C. In Rwanda, it is grown throughout the country and its importance is expanding considerably. Despite the increase of both cultivated area and production, potato productivity remains low in Rwanda with a national mean yield of 13.6 t ha^{-1}. Late blight disease caused by *Phytophtora infestans* (Mont.) Anton de Bary is one of the most important limiting factors to potato productivity in the country. The overall goal of this study was therefore to develop high yielding and late blight resistant potato cultivars in Rwanda. The specific objectives were; (i) to identify and analyse farmers' key constraints in potato production, and establish farmers' preferred traits to be included in cultivar development and variety selection in Rwanda, (ii) to determine yield response and late blight reaction of potato genotypes in Rwanda in order to identify suitable parents for breeding, (iii) to assess the genetic relationship and divergence among potato genotypes grown in Rwanda using SSR markers so as to identify suitable parents for crosses, (iv) to estimate combining ability effects for late blight resistance, yield and yield related traits and to estimate heterosis for yield in potato, and (v) to select the best potato clones for further evaluation and release.

A participatory rural appraisal (PRA) study was conducted through a structured survey involving 144 households and 22 focus groups selected from Musanze, Gicumbi and Nyamagabe districts of Rwanda. The structured survey used a questionnaire administered to farmers to collect information on the importance of potatoes and other main crops. Focus group discussions used matrix scoring of key production constraints and pair-wise ranking of traits. The most important potato production constraints were lack of access to credit, lack of high yielding cultivars, insufficient clean seeds and late blight disease. High yield, disease resistance and high dry matter content were the most important attributes preferred by farmers.

A total of 44 potato genotypes were evaluated under three environments (Kinigi, Rwerere and Nyamagabe) in Rwanda to select high yielding and late blight resistant parents. Experiments were laid out in an 11 x 4 alpha lattice design with two replications. Data were collected on late blight severity (%) based on the relative area under the disease progress curve (rAUDPC: 100% max), total tuber yield, marketable tuber weight and dry matter content. Genotypes had significant differences for blight resistance and yield levels among test locations. Eighteen genotypes (CIP 393371.58, CIP 393637.171, CIP 396033.102, CIP 395112.36, CIP 393280.57, CIP 393385.39, CIP 396026.103, CIP 393280.82, CIP 396036.201, CIP 393077.54, CIP 391047.34, CIP 39111.19, CIP 381381.13, Ngunda, Kigega, Kirundo, Nderera and Gikungu) were selected showing positive combinations of quantitative and qualitative traits such as late blight resistance, high tuber yield, dry matter content and productive flowers.

Evaluation of genetic relationship and divergence of the 18 selected genotypes were conducted using 13 simple sequence repeat (SSR) markers for an efficient choice of parents for breeding. The 13 SSR primers identified 84 alleles across all genotypes. The number of alleles per locus ranged from 3 to 10 and the average was 6.5. The polymorphic information content (PIC) of loci ranged from 0.51 to 0.85 with an average of 0.71. Heterozygosity (He) varied from 0.59 to 0.86 with an average of 0.75. Significant positive correlations were detected between PIC and He (r= 0.99), PIC and number of alleles (r=0.76) and, He and number of alleles (r=0.80). The genetic distance between clones ranged from 0.44 to 0.93 and the average was 0.75. The SSR analysis provided five different genetic clusters of the potato clones useful for breeding. Cluster I consisted of clone CIP 393357.58 standing alone. Cluster II composed of six genotypes: CIP 393637.171, CIP 393385.39, CIP 396026.103 and CIP 395112.36, Nderera, and Gikungu. Cluster III allocated five clones: CIP 396033.102, CIP 393280.82, CIP 391047.34, CIP 396036.201 and CIP 393077.54. Cluster IV included three genotypes; 39111.19, 381381.13 and Kirundo, while cluster V consisted of two varieties Ngunda and Kigega. The genetic distance between clones ranged from 0.44 to 0.93. The shortest genetic distance (0.44) was found between Ngunda and Kigega whereas the highest distance at (0.93) was identified between clone CIP 393357.58 and Ngunda. Among the 18 genotypes, clone CIP 393357.58 was the least genetically related to the other genotypes. Overall, results showed that the thirteen microsatellite markers clearly distinguished all the eighteen potato genotypes. Nine genotypes CIP 393357.58, CIP 391047.34, CIP 393385.39, CIP 393280.82, CIP 396036.201, Gikungu, Ngunda, Kigega and Nderera were therefore identified as promising parents for subsequent crosses.

The selected potato parents were crossed using a 10 x 10 half diallel mating design to generate 45 F_1s. Only 28 families with sufficient individuals and the eight parents were evaluated in experiments laid out in a 6 × 6 lattice design with two replications across two sites (Kinigi and Nyamagabe) in Rwanda. Late blight resistance was estimated using the relative area under the disease progress curve (rAUDPC: 100 % max). Furthermore, data on total tuber yield, total tuber number, and average tuber weight were collected and subjected to analyses. Results showed that across sites additive and non-additive gene action were present affecting yield and late blight resistance in potato. Additive was predominant over non-additive gene action for both traits. All the families and their F_1 progenies selected for further evaluation had improved levels of late blight resistance, high yields and heterosis. The study identified ten top families (Gikungu x CIP 391047.34, Giukungu x CIP 393036.201, Kigega x CIP 393036.201, Kigega x CIP 393280.82, Gikungu x CIP 393385.39, CIP 393280.82 x CIP 391047.34, Nderera x CIP 393036.201, Ngunda x CIP 393280.82, Ngunda x CIP 391047.34, Gikungu x Ngunda) expressing high tuber yield and resistance to late blight. Moreover 58 and 46 promising clones were identified at Kinigi and Nyamagabe respectively for further clonal evaluation and variety release in Rwanda. Overall, the current study selected valuable potato genotypes with high combining ability for late blight resistance and tuber yield.

DECLARATION

I, Jean Baptiste Muhinyuza, declare that

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

Signed

Jean Baptiste Muhinyuza

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

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Prof. Shimelis Hussein (Supervisor)

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Prof. Rob Melis (Co-Supervisor)

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Dr. Julia Sibiya (Co-Supervisor)

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DEDICATION

To my beloved and closest people, my wife (Anatolie), children (Fleury, Delitha, Salomon, Rhania-Salomé), my parents (Bruno and Winifride) and to my late brother (Andrew Mukiza),

I dedicate this thesis.

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INTRODUCTION TO THESIS

Importance of potato

Potato *(Solanum tuberosum* L.; 2n=4x=48*)* is one of the major food crops grown worldwide (Hawkes, 1994). It is the third most important food security crop in the world after rice (*Oryza sativa* L.) and wheat (*Triticum* (Haverkort et al., 2009). Among root and tuber crops, potato is first in total production, followed by cassava (*Manihot esculenta* Crantz), sweet potato (*Ipomoea batatas* L.), and yam (*Dioscorea batatas* Deene) (CIP, 2008). The total estimated area under potato production in the world is 19 463 041 hectares with a total production of 368 096 362 tons (FAOSTAT, 2013). Asia is the largest potato producer, with around 180 460 442 tons annually, followed by Europe, Africa, North America and Latin America (Table 0.1). Over the last decade, potato production increased, especially in developing countries (Table 0.2). In these countries, potato's production rate is the highest among other main food crops such as wheat, maize, and rice (CIP, 2008; FAO, 2013). In Africa, Egypt is the leading potato producer, followed by Malawi and Algeria while Rwanda is the sixth largest producer (Table 0.3).

Table 0.1 Potato production by region

Region	Harvested area (ha)	Quantity (t)	Yield (t ha^{-1})
Africa	2 005 331	30 198 747	15.1
Asia	10 058 568	180 460 442	17.9
Europe	5 725 707	112 980 347	19.7
Latin America	959 404	15 621 180	16.3
North America	567 875	24 465 019	43.1
World	**19 463 041**	**368 096 362**	**18.9**

Source: (FAOSTAT, 2013)

Table 0.2 Developed and developing world potato production (1990-2010)

Countries	Year								
	Production (10^6 t)								
	1990	**1992**	**1994**	**1996**	**1998**	**2000**	**2002**	**2006**	**2010**
Developed	195.22	184.64	168.69	193.59	162.25	182.04	163.58	155.25	143.88
Developing	84.09	93.44	102.33	117.71	131.41	146.51	152.41	159.12	180.53
World	**279.32**	**278.09**	**271.07**	**311.31**	**300.67**	**328.55**	**315.95**	**314.27**	**324.42**

Source: (FAO, 2011)

Table 0.3 Eleven highest potato producing countries in Africa

Country	Harvested area (ha)	Quantity (t)	Yield (t ha^{-1})
Egypt	178 000	4 800 000	26.9
Malawi	258 585	4 535 955	17.5
Algeria	140 000	4 400 000	31.4
Kenya	135 000	2 500 000	18.5
South Africa	66 000	2 252 391	34.1
Rwanda	164 691	2 240 715	13.6
Morocco	60 000	1 450 000	24.2
Nigeria	270 000	843 000	3.1
Ethiopia	69 999	775 503	7.2
Uganda	106 000	774 600	7.3
Angola	105 862	670 136	6.3

Source: (FAO, 2013)

Potato is a rich source of various nutrients and can provide enhanced nutrition to the growing population of the world (Secor, 1999). It has a high content of carbohydrates that produce much energy with significant amounts of quality protein, substantial amounts of vitamins, especially vitamin C, and minerals including phosphorous, calcium, zinc, potassium, and iron (FAO, 2008). Such important nutritional value makes potato an efficient crop in combating malnutrition (FAO, 2008). Based on its overall economic importance, the volume of potatoes produced and consumed worldwide has increased substantially (CIP, 2008; FAO, 2013).

Potato production in Rwanda

In Rwanda, potato is the second major food crop after cassava (Table 0.4) and plays an important role in the economy as a cash crop (FAOSTAT, 2013). Although potatoes are grown throughout Rwanda, the production is concentrated in the zone of high altitude (Munyemana and Von Oppen, 1999). This zone includes the highlands of volcanic soils, the highlands of Buberuka and the highlands of Congo/Nile Divide located in Southwest and North of the country (Munyemana and Von Oppen, 199). The region accounts for more than 80% of the national potato production, while the rest is produced on marginal plantations throughout the country (Munyemana and Von Oppen, 199). In this highland region, potato is the staple food with more than 60% of the production being used directly for home consumption (Crissman, 2002). The per capita consumption of potatoes in Rwanda is among the highest in the world and is approximately 125 kg per person per annum (FAO, 2010).

Table 0.4 Production of five major crops in Rwanda

Commodity	Quantity (t)	Rank
Cassava	2 731 421	1
Potatoes	2 237 706	2
Sweet potatoes	1 005 305	3
Maize	573 038	4
Dry beans	432 587	5

Source: (FAOST, 2013)

Since 1960, both area coverage and production have considerably increased in the country. This increased importance of potato is expressed by the continued growing of the cultivated area, the rapid production growth, and the relative increase of its consumption and market (FSRP, 2000). The average production growth rate during the period 1966-1992 was estimated at 5.2% per year, which was almost twice the population growth rate in Rwanda (FSRP, 2000). Between 1992 and 1999, a war, which led to genocide, occurred in Rwanda and many farmers fled the country, lost their seed stocks, resulting in a decline in potato production and area covered. After the war, the area planted expanded again very quickly and new evidence of high potato production has been observed (FSRP, 2000).

In 2000, the area under potatoes was estimated at 92 000 ha with a total production of 730 000 tons and an average yield of 7.93 t ha^{-1} (MINAGRI, 2000). In 2013, the potato area harvested was approximately 164 691 ha with a total production of 2 240 715 tons and an average yield of 13.6 t ha^{-1} (FAO, 2013). In addition, potato marketing increased considerably from an estimated 35% of the production in 1988 (Dürr, 1983; Scott, 1988) to 50% in 2002 (Goossens, 2002). Potato became a staple food and since then, the Rwandan Ministry of Agriculture has classified potato as a priority crop for development (MINAGRI, 2000).

Potato production constraints in Rwanda

The mean yield of potatoes in Rwanda is 13.6 t ha^{-1} compared to 40-60 t ha^{-1} achievable yields of the crop (FAO, 2013). The low yields of potato are a result of different factors, the major ones being farmers still growing unimproved and disease susceptible varieties, abiotic stresses (high temperature, drought, acidic soil) and biotic stresses (diseases, insects, weeds). Potato diseases alone account for the yield loss of 70% (Kirk et al., 2004). There is thus a need for more research on potato improvement for yield potential, better yield stability and improved disease resistance. To increase yield globally, breeders at CIP and national research programs are focusing on developing potatoes with higher yielding capacity and disease resistance.

Diseases and pests are the major constraints to potato production and productivity worldwide (Fry, 1977). The most serious diseases that affect potatoes are late blight caused by *Phytophthora infestans* (Mont.) de Bary, bacterial wilt (*Ralstonia solanacearum* Yabuuchi et al.), and viruses (Hide and Lapwood, 1992). Potato late blight is the most serious disease causing yield losses ranging from 50 to 100% wherever potatoes are grown (Hide and Lapwood; Fry, 1977b). Unchecked, potato late blight spreads very quickly given the polycyclic production of secondary inoculum and this can result in great yield losses (Zwankhuizen et al., 1998). In Rwanda, potato late blight disease causes severe yield losses. Disease severity in some fields results in reduced photosynthesis with subsequent yield loss reaching up to 70% (Kirk et al., 2004). Resource poor farmers do not control the disease using fungicides due to unaffordability. Furthermore, there are limited late blight resistant varieties available in the country. As a result, substantial crop and yield losses occur each year. The most sustainable and cost effective means for managing the disease would be through exploiting host plant resistance among other integrated disease management strategies (Kirk et al., 2001; Kirk et al., 2005, Nærstad et al., 2007; Muhinyuza et al., 2008). Bacterial wilt and viruses are diseases that may seriously affect potato production. There is no chemical control for bacterial wilt and viral diseases; they can severely affect potato yield when disseminated into seed tubers (Hide and Lapwood, 1992). Serious pests include potato tuber moth caused by *Phtholimaea operculella* (Zeller), a very damaging insect on potatoes both in the field and during storage, leaf miner fly (*Liriomyza huidobrensis* Blanchard) and nematodes (Evans and Trudgill, 1992; Raman and Radcliffe, 1992; CIP, 2008).

Potato diseases and pests management

The potato crop needs to be protected against pests and diseases in order to reduce or avoid serious epidemics and subsequent yield losses. The aim of controlling plant diseases is to reduce yield losses and at the same time improve quality (Agrios, 2005). Current strategies to protect potatoes against major diseases such as late blight, bacterial wilt and viruses include the use of disease free seed, growing resistant varieties, inoculum-suppressing cultural practices including crop rotation and sanitation, and chemical control (Secor, 1999). Control strategies, which have been developed, have failed to eliminate potato late blight completely. No single measure used alone can successfully control late blight in potatoes (Schumann, 1991). Integrated strategies such as utilization of resistant and/or tolerant varieties; certified late blight free-seed, limitation and avoidance of conducive environments, climatic monitoring and disease prediction are some agronomic practices that can be utilized for control of potato late blight (Hide and Lapwood, 1992). The use of

resistant or tolerant varieties combined with additional control strategies such as cultural practices and well-applied fungicides can together limit crop and yield losses and maintain potato late blight at acceptable economic threshold levels (Fry et al., 1979). Following the occurrence of new and more virulent strains of *P. infestans* Fry (1997a; b) observed that the use of protective fungicides could complement cultivar resistance to reduce foliar potato late blight. Kirk et al. (2001; 2005) and Muhinyuza et al. (2008) stated that reduced application rates and frequencies of a protectant residual fungicide could be successfully incorporated into a control programme using host resistance. *Phytophthora infestans* is a genetically versatile organism which has overcome vertical resistance in *S. tuberosum*. Current research for late blight management is directed towards developing cultivars with durable resistance and this would therefore limit the reliance on intensive fungicide applications. Although there are no chemicals to protect against bacterial wilt and viral diseases, epidemics can be minimized by regular monitoring and spraying when necessary against aphids, the vectors of viruses. Major pests such as insects and nematodes can cause destruction of the potato crop. Their control measures include regular monitoring and use of natural enemies against insects while sanitation, crop rotations and resistant varieties may prevent nematode spread (Raman and Radcliffe, 1992).

Rationale and problem statement

Control of potato late blight relies mainly on intensive use of fungicides (Schumann, 1991). However, their access to farmers is limited because they are expensive and their application costs are very high (CIP, 1999), making them unaffordable to most Rwandan growers with limited financial means. Furthermore, there is an increasing global concern about the intensive use of pesticides on the environment and human health. Research on integrated management of late blight has been attempted in Rwanda to integrate host plant resistance with low levels and calendar-based application of fungicides (Muhinyuza et al., 2008). In addition, potato varieties with relatively high yields and high levels of tolerance to late blight have been produced by CIP over the past few years and made available to developing countries (CIP, 1999; ISAR, 2008). However, for effective breeding for high yield and late blight resistance, these CIP materials and locally adapted genotypes need to be evaluated and screened under target growing environments.

In addition, in the past major emphasis has been placed on seed production with little attention to all other factors that could contribute to improved potato productivity in Rwanda (ISAR, 2008). There is therefore a need to screen existing varieties and develop new cultivars for high yield and resistance to late blight. It is hence imperative to develop cultivars for yield improvement by combining existing late blight resistant materials with the best

agronomic characteristics for high yields. In order to develop high yielding and late blight disease resistant genotypes, an understanding of the genetic variability and inheritance of the resistance to *P. infestans* and the genetic diversity of the available genotypes is important for effective breeding. The evaluation of potato parents and their progenies to estimate combining ability and heterosis for late blight resistance and yield is critical in order to select the best clones. It is also essential to assess farmers' knowledge on the impact of late blight, investigate their production constraints, potato variety preferences, and production systems in order to subsequently enhance the potential for adoption of newly developed varieties.

Research objectives

The main objective of this study was to develop high yielding and late blight resistant potato cultivars in Rwanda. The specific objectives were:

(i) To identify and analyse farmers' key constraints in potato production, and establish farmers' preferred traits to be included in cultivar development and variety selection process in Rwanda

(ii) To determine yield response and late blight reaction of potato genotypes in Rwanda in order to identify suitable parents for breeding

(iii) To assess genetic relationship among potato genotypes grown in Rwanda using SSR markers

(iv) To estimate combining ability and heterosis for potato late blight resistance and yield

(v) To select the best potato clones for further evaluations and release

Outline of the thesis

This thesis consists of six different chapters in accordance with a number of activities related to the above objectives (see outline below). Chapters 1-5 are written in the form of research chapters whether or not the chapter has already been published. Chapter 6 gives general discussion of the results of respective chapters and conclusion, and identify future directions for research. The referencing system used in the chapters of this thesis is based on the Journal of Crop Science. 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. Chapters 2 and 3 have been published in the "International Journal of Development and Sustainability" and the "American Journal of Potato Research", respectively. Chapter 4 is accepted in Australian Journal of Crop Science.

Chapter	Title
-	Introduction to thesis
1	Review of the literature
2	Participatory assessment of potato production constraints and trait preferences in potato cultivar development in Rwanda
3	Yield response and late blight reaction of potato genotypes in Rwanda
4	Assessment of genetic relationship among potato genotypes grown in Rwanda using SSR markers
5	Combining ability analysis of yield and late blight resistance of potato in Rwanda
6	Overview

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CHAPTER I: A REVIEW OF THE LITERATURE

1.1 Introduction

This literature review is intended to go over current knowledge in breeding potato for high yield and resistance to late blight to provide theoretical foundation for the research to be undertaken. It critically reviews all the most important research topics in potato breeding relevant to this research. This literature review is divided into five sections. The first section covers topics related to taxonomy, origin and domestication. The importance of potatoes and production trends is reviewed in the second section. The third section covers information on farmers' trait preferences in potato breeding. The fourth section focuses on the general significance of genetic diversity in plant breeding, detailed information on potato genetic improvement and breeding for high yield, genetics of late blight, and breeding for resistance to late blight in potato. Finally in the fifth section, gene action, combining ability of potato yield and late blight resistance are discussed. The literature may serve as a general frame work and important background information for potato breeders, pathologists, agronomists or producers.

1.2 Potato taxonomy, origin and domestication

The taxonomy of cultivated potatoes has been controversial with anywhere from one to 20 species recognized (Huaman and Spooner, 2002). The word "potato" commonly refers to plants belonging to the species *Solanum tuberosum* L. and other cultivated tuber-bearing species found in South America. These plants belong to the family *Solanaceae*, genus *Solanum*, section *Petota*. Most species in section *Petota* possess underground stolons bearing potato tubers at their tips, but some species lack these characteristic structures. Therefore, section *Petota* was divided into two subsections; subsection *Potatoe* containing both cultivated and wild tuber-bearing species, and subsection *Estolonifera* that contains non-tuber-bearing series (Hawkes, 1992). The tuber is the edible part of the potato, which is a part of the stem that stores food and plays a role in propagation. The tuber is also regarded as an enlarged stolon. Stolons are formed from lateral buds at the bottom of the stem (Beukema and Van der Zaag, 1990).

Spooner et al. (2005) reported that all landraces of cultivated potato form a common gene pool and have a monophyletic origin from Andean and Chilean landrace complex. Using simple sequence repeat (SSR) DNA markers in combination with morphological analysis,

Spooner et al. (2007) suggested classifying the cultivated potatoes into four species; *S. tuberosum*, *S. ajanhuiri*, *S. juzepczukii*, and *S. curtilobum*. According to Huaman and Spooner (2002), all landrace populations of cultivated potatoes are a single species, *S. tuberosum*, with eight cultivar groups. The landrace potato cultivars are highly diverse, containing diploids (2*n* = 2*x* = 24), triploids (2*n* = 3*x* = 36), tetraploids (2*n* = 4*x* = 48), and pentaploids (2*n* = 5*x* = 60). The tetraploids are the highest yielding and they are the sole cytotype of modern cultivars (Ames and Spooner, 2008).

Cultivated potato (*Solanum tuberosum L.*) originated in the Andes of Peru and Bolivia in South America. This species was first domesticated in Bolivia more than 8,000 years ago (Hawkes, 1994). It, thereafter, expanded to Mexico and Central America (Hawkes, 1994). Spanish explorers took it into Europe from where it reached North America, Asia and Africa (Beukema and Van der Zaag, 1990). In Rwanda, potato was introduced by the German missionaries at the end of 19th century (Monares, 1984). At that time, Rwandans did not appreciate this crop product and refused to grow and use it. However, potato cultivation became important when a serious famine occurred in Rwanda during the 1940s (Munyemana and Von Oppen, 1999). Subsequently, potato was adopted as one of the subsistence crop especially in the highland region, which is favourable for its successful production. Potato became a commodity crop and remained very popular so that in 1979, a national program was established geared towards potato improvement [Programme National pour l'amélioration de la pomme de terre (P.N.A.P.)] within the Institut des Sciences Agronomiques du Rwanda (ISAR), to encourage and strengthen its production (Kidane-Mariam, 1987). Because of its significance as a staple food the Government of Rwanda considers it as a food security crop and an important source of income to the growers and traders (Monares, 1984).

1.3 Importance of potatoes and production trends

Potatoes are among the most widely-grown crop plants in the world, giving good yield under various soil and weather conditions (Lisinska and Leszcynski, 1989). Potato is the third most important food security crop in the world after rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) (Haverkort et al., 2009). Its production growth rate is the highest among other main food crops such as wheat, maize, and rice, due to its high yield potential and excellent nutritional characteristics. In addition, potato food quantity produced on one hectare is two to four fold higher than the food grain crops produced on the same unit area (FAO, 2008). In terms of water uptake, potato produces more food per unit water than any other major crop and is seven times more efficient than cereals (CIP, 2008).

According to Lachman et al. (2001) annual world-wide production of potatoes is approximately 350 million tons and more than one billion people worldwide eat potato (CIP, 2008). The world average per capita consumption in 2005 was estimated at 33.7 kg (FAO, 2008), while the Rwandan per capita consumption of potatoes is approximately 125 kg per person per annum; among the highest in the world (FAO, 2008). The highest potato consumption is in Europe with a per capita consumption of about 96 kg, followed by North America at 63 kg. The per capita consumption is low in Latin America (24 kg), Asia (12 kg) and Africa (8 kg) (FAO, 2008). However, in developing countries the per capita consumption and production is increasing and its production growth is more than any other food crops (FAO, 2013). The high consumption rate of potatoes is attributed to both their palatability and high nutritive value (Rytel et al., 2005). Potatoes serve as a major food source, as well as an inexpensive source of energy and good quality protein (Lachman et al., 2001).

Potato is very rich in nutrients and can provide nutrition to the growing global population (Secor, 1999). It is a very low fat food with high content of carbohydrates that produce much energy. Also it has significant amounts of quality protein such as lysine, substantial amounts of vitamins, especially vitamin C, B and A (Kolasa et al., 1993; Lachman et al., 2000; Dale et al., 2003). Such important nutritional value makes potato an efficient crop in combating malnutrition (FAO, 2008).

Kant and Block (1990) stated that potatoes are the third largest source of vitamin B_6 for adults (19-74 years of age). They also reported that potatoes are the second most important contributor of vitamin B_6 for the elderly, who are especially at risk of chronic disease. Vitamin B_6 is involved in amino acid, nucleic acid, glycogen, and lipid metabolism. It influences hormone modulation, erythrocyte production, and immune and nervous system functions. It is also proposed to play a major role in the etiology and/or treatment of various chronic diseases such as sickle cell anemia, asthma, and cancer (Kolasa, 1993). Potato tubers are also important sources of minerals including phosphorous, calcium, zinc, potassium, and iron and their value in the human diet is often understated or ignored, particularly as a source of ascorbic acid (Dale et al., 2003., Yilmaz et al., 2005; Andre et al., 2007). Overall, based on its absolute nutrient values; the volume of potatoes consumed worldwide is the highest. Also potato production has shown a steady growth rate in recent years in developing countries (CIP, 2008). Potato has an important role in the food security, nutrition and combating hunger (FAO, 2013).

1.4 Farmers' potato trait preferences and participatory research in potato breeding

Muhinyuza et al. (2008) reported that late blight negatively impacts on potato yield. Previous studies (Luthra et al., 2005) confirmed that genotypes with good levels of resistance to potato diseases had high tuber yields and are promising candidate parents in a disease breeding programme. Moreover, these genotypes should exhibit desirable tuber characteristics and productive flowers for sexual recombination for breeding. According to Kaushik et al. (2007) the use of accessions with high yield and resistance to potato late blight as parents in late blight breeding programme is one of the most effective strategies to control the disease and increase yield. High yield, disease tolerance and high dry matter content are the most important attributes preferred by farmers in Rwanda. Mehdi et al. (2008) found that total tuber yield is mainly attributed to higher number of tubers per plant and increased tuber size.

According to Rhodes and Booth (1982) a participatory rural appraisal research approach should involve both farmers and scientists when developing new technologies. Technologies should be adapted to local conditions with active farmer participation for successful research and development. However, the link between research and farmers is very weak or absent in developing countries (Ortiz et al., 2008). This results in a failure to adopt new technologies. In many cases where farmers were actively involved in plant breeding at various levels of the breeding process, the new varieties were successfully adopted (Graham et al., 2001). Participatory methods consider the value of farmers' knowledge, their preferences, ability and innovation, and their active exchange of information and technologies as it was demonstrated during farmer field school approach at CIP (Ortiz et al., 2008). For example, in Indonesia, farmers' guided research on cultivation practices were linked with integrated pest management (IPM) capacity building through farmer field school enabling farmers to learn, interact and implement new technologies with researchers. In Peru, participatory research was successful in the combined use of varieties and fungicides within farmer field school. In Bolivia, farmers were involved in making crosses and selection in potato (Graham et al., 2001). In Kenya, farmers were involved in evaluating sweet potato varieties and selected four based on their high yield and wide adaptation, which coincided with the breeders' selection (Ndolo et al., 2001). In Rwanda, farmers participated in screening potato breeding lines distributed by CIP during on-farm trials and successfully released improved varieties with late blight resistance (Devaux and Tegera, 1981).

It is essential, therefore, to consider farmers' knowledge and preferred traits to be included in cultivar development and variety selection process, which would enhance the potential for adoption of new varieties.

1.5 Genetic diversity and breeding for high yield and late blight resistance

1.5.1 Genetic diversity analysis

Genetic diversity analysis in potatoes is required to identify complementary and unrelated parents to limit genetic depression and to ensure genetic variation for sustained potato improvement (Tarn et al., 1992; Spooner et al., 2007). Microsatellites or simple sequence repeats (SSR) DNA markers have been used in determining potato genetic diversity, genetic structure, and classification (Spooner et al., 2007). Simple sequence repeats are tandem repeats of short sequence motifs that occur ubiquitously in eukaryotic genomes and can function with low-quality DNA (Morgnate and Olivieri, 1993). Moreover, they are appropriate, cost-effective and simple tools for laboratories in developing countries with financial constraints. Genetic distance estimates using molecular markers are helpful to identify the best parents for new pedigrees (Acquaah, 2007). The SSR markers are currently the most powerful tools to study genetic relationships because of their high genetic information content, high reproducibility, and simplicity to use (Powell et al., 1996; Jones et al., 1997).

1.5.2 Breeding potato for high yield

Identification of superior parents with high yield and desirable traits is the basis of the breeding programme. Developing late blight resistant varieties will continue to be a major goal for potato research as long as *Phytophtora infestans* continues to be a production problem. However, since cultivated potato is tetraploid and highly heterozygous, crosses are made between parents with complementary features as selection of parents is based on phenotype rather than genotype (Bradshaw and Mackay, 1994). Conventional breeding uses hybridization, followed by clonal selection to improve potato for the desired character (Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). The selection procedure starts with identification of desirable parents among commercial cultivars, which are heterozygous, followed by crossing selected superior genotypes for the traits under consideration.

The value of a cross combination is determined with mid-parent values and progeny test (Acquaah, 2007). Genetic variation is achieved in the F_1 generation after designed hybridization (Bradshaw and Mackay, 1994; Acquaah, 2007). Selected superior F_1 individuals are clonally propagated and maintained in their original genetic state (Bradshaw and Mackay, 1994; Acquaah, 2007). Tubers harvested from each superior F_1 plant are

grown in rows for evaluation. Each row represents a clone from a single F_1 plant (Bradshaw, 1994). Selected and advanced clones are tested in multi-location trials for evaluation in relation to wide or specific adaptation and yield stability (Sleper and Poehlman, 2006).

1.5.3 Potato genetics

Solanum tuberosum is tetrasomic with four different alleles at one locus (Bradshaw and Mackay, 1994; Carputo and Barone, 2005). The autotetraploid nature of potato makes the four sets of chromosomes entirely homologous. Pairing is thus completely random within each group of four homologous chromosomes at meiosis and this results in tetrasomic inheritance (Sleper and Poehlman, 2006). Therefore, dominance or intra-locus interaction and inter-locus interaction (epistasis) occur, and are all important in potato breeding programmes. The level of heterozygosity is influenced by the four different alleles within a locus; the more diverse the alleles are within a locus, the higher the heterozygosity (Acquaah, 2007). Five tetrasomic conditions are possible at an individual locus in an autotetraploid (Acquaah, 2007) (Table 1.1).

Table 1.1 Multi-allelelism in an autotetraploid potato: the number of first, second and third order possible interactions for the five different tetrasomic conditions

Tetrasomic condition	1st	2nd	3rd	Total
$a_1a_2a_3a_4$	6	4	1	11
$a_1a_1a_2a_3$	3	1	0	4
$a_1a_1a_2a_2$	1	0	0	1
$a_1a_1a_1a_2$	1	0	0	1
$a_1a_1a_1a_1$	0	0	0	0

$a_1a_1a_1a_1$: mono-allelic locus; all alleles are identical; balanced
$a_1a_1a_1a_2$: di-allelic locus; two different alleles in unequal frequency; unbalanced

$a_1a_1a_2a_2$: di-allelic locus; two different alleles occur with equal frequency; balanced

$a_1a_1a_2a_3$: tri-allelic locus; three different alleles

$a_1a_2a_3a_4$: tetra-allelic locus; four different alleles

Eleven different interactions are possible for the tetra-allelic condition whereas the mono-allelic has none. The tetra-allelic condition gives the maximum heterosis due to inter-locus interactions of the tetrasomic potato (Sleper and Poehlman, 2006). The highest level of heterosis will occur as the frequency of tetra-allelic loci increase. Similarly the number of

inter-locus interactions will also occur as the frequency of tetra-allelic loci increases. In potato breeding inter and intra-locus interactions are therefore all important (Sleper and Poehlman, 2006)

1.5.4 Potato late blight disease and resistance breeding

1.5.4.1 The pathogen

Potato late blight caused by the oomycete fungus *Phytophthora infestans*, is the most important potato disease worldwide (Fry, 1997b). The pathogen *P. infestans* attacks potatoes both in the field and during storage (Agrios, 2005). *P. infestans* is thought to have originated in South America (Abad and Abad, 1997) and its worldwide spread is enhanced by global trade (Andrivon, 1996). Late blight is also an important disease of tomato (*Lycopersicon esculentum* Mill.) and is also found on wild plant species, mainly solanaceous hosts (Erwin and Ribereiro, 1996).

Potato late blight is best known historically as the cause of the great Irish potato famine during the 1840s (Schumann, 1991). At that time, microorganisms were believed to be the result rather than the cause of diseases. The role of fungi as the causative agents of plant diseases was not fully understood. Following the Irish potato famine, the oomycete *P. infestans* was confirmed as the primary cause of the disease, potato late blight (Schumann, 1991; Peterson, 1995).

Despite many efforts to control the disease, potato late blight is still a major challenge in potato production. This is thought to be due to the appearance of new and virulent pathotypes of *P. infestans* that overcome resistance Fry (1997a; b). The appearance of virulent pathotypes is thought to have occurred during the 1970s through the import of potatoes from Mexico (Fry and Goodwin, 1997) to Europe and during the early 1990s to North America (Deahl et al., 1991). But in Eastern African region, *P. infestans* that attacks potato has not been reported to change and it still belong to the US-1 clonal lineage (Vega-Sanchez et al., 2001).

The pathogen aggressiveness has increased over the years and resistance to commonly used fungicides has been reported (Hohl and Iselin, 1984; Mukalazi et al., 2000). Moreover, RW-1 and RW-2 genotypes were identified within one of the fields in Rwanda (Pule et al., 2013). They had a limited distribution suggesting that they were not more aggressive than the US-1 lineage in Rwanda (Pule et al., 2013).

1.5.4.2 Potato late blight disease cycle

The causal organism of potato late blight is a biotrophic pathogen and survives as mycelium in potato tubers in storage to be used for seed, tubers that are inadvertently not harvested and left in fields, and in discarded piles of culled potatoes (Drenth et al., 1995). It can also survive in soil as a sexually originated oospore (Drenth et al., 1995). The thick walled oospore is a sexual spore resulting from conjugation of two mating types typically designated as A_1 and A_2 (Strömberg, 2001; Agrios, 2005). Mycelia within potato tubers, and possibly but rarely, oospores serve as the primary inoculum for seasonal epidemics of potato late blight. Both asexual and sexual stages produce sporangia. Sporangia produced on infected leaves are carried away by wind or splashed by water to the foliage of new plants, which germinate and initiate an epidemic (Agrios, 2005). The pathogen can enter into the tubers via lenticels, eyes, growth cracks and wounds or via stolons depending on varieties (Świeżyński and Zimnoch-Guzowska., 2001).

Potato late blight is a sporadic disease that occurs only when microclimate conditions within the canopy are favourable and inoculum is present (Lacy and Hammerschmidt, 1995). Conducive environmental conditions include air temperatures between 7 and 27°C and relatively long periods (10 hours or more) of leaf wetness. Favourable conditions for infection and development coincide with periods of high relative humidity (RH>90%) and moderate temperatures (15-25°C) (Harrison and Lowe, 1989; Lacy and Hammerschmidt, 1995). Under these conditions, sporangia can cause new infections and lead to a polycyclic epidemic due to the rapid production of asexual generations of secondary inoculum of the pathogen (Zwankhuizen et al., 1998). Crop loss occurs through destruction of foliage and consequent reduction of photosynthetic capacity and tuber infection by spores that are washed down from leaves into the soil to enter tubers through wounds, lenticels and directly through the periderm of the tuber (Howard, 1997; Agrios, 2005).

1.5.4.3 Breeding for late blight resistance

When race-specific resistance in the wild potato *S. demissum* was detected, major R-genes were transferred into the domesticated potato (*S. tuberosum*) (Umaerus et al., 1983; Landeo et al., 1995). Since then, breeding for vertical resistance was practiced and this resulted in a rapid selection and production of varieties resistant to potato late blight (Landeo et al., 1995) until the late 1960s when *P. infestans* overcame vertical resistance (Umaerus et al., 1983). These varieties were no longer resistant and vertical resistance proved unreliable. Currently, the emphasis by breeders is on horizontal resistance, which is more general, and non-race specific.

Breeding for horizontal resistance has already resulted in the development of cultivars with intermediate resistance, known as partial resistance. Horizontal resistance to late blight is often observed in late maturing cultivars rather than in early maturing cultivars (Umaerus and Umaerus, 1994). Horizontal resistance is under polygenic control and expression of resistance is quantitative resulting from an additive contribution of several genes.

It has been reported that screening germplasm under field conditions is the most effective and reliable method for disease evaluation; genotypes are exposed to natural infestation or inoculated in the test plots under field conditions (Guzmàn, 1964; Wulff et al., 2007). In the field, under natural infestation, screening can be done in different locations with high disease pressure by planting together susceptible and resistant cultivars to be tested (Forbes et al., 1993; Gopal and Singh, 2004). Screening potato germplasm for late blight resistance can also be achieved in controlled environment using laboratory methods that utilize leaf disks, detached leaflets or detached leaves (Dorrance and Inglis, 1997). Although field screening is the most reliable method, the experiments must be conducted either in a well known disease pressure site where genotypes are to be exposed to natural infestation or field inoculations must be performed.

1.6 Gene action controlling potato yield and late blight resistance

A large base of germplasm with genetic variability can be used to develop high yielding and potato late blight resistant cultivars through selection and breeding (Bradshaw and Mackay, 1994). Crossing between two unrelated parents will generate genetic variation from which to practice phenotypic selection (Bradshaw and Mackay, 1994). Segregating progeny from which to select superior clones contains genetic material transferred from its parents. The general combining ability (GCA) gives an indication on the average performance of a parent into its progeny; it provides an estimation of the parental gametic contribution to its offspring by the mean performance of the progeny (Bradshaw and Mackay, 1994; Falconer and Mackay, 1996). Specific combining ability (SCA) is the deviation from the progeny mean from the expected on the basis of GCA (Bradshaw and Mackay, 1994). In this case, the performance of the progeny is either superior or inferior to the parents (Falconer and Mackay, 1996). Several workers agree on the relative importance of the general combining ability (GCA) of parents and the specific combining ability (SCA) of crosses for potato late blight resistance. The GCA is under the control of additive gene action while the SCA is controlled by dominant genes, and both have been reported to be significant for late blight resistance (Bradshaw and Mackay, 1994). This imply that both additive and non-additive gene action are important for resistance to late blight in potato (Bradshaw and Mackay, 1994). Landeo et al. (2000) found both additive and non-additive gene action equally

important for horizontal resistance, while several reports confirmed the predominance of additive gene action over the non-additive gene action in inheritance of quantitative resistance to late blight (Stewart et al., 1992; Wastie et al., 1993; Kumar et al., 2007).

Yield and disease resistance are characters quantitatively inherited (Falconer and Mackay, 1996). Many genes are involved, with each gene contributing a small effect to the phenotypic expression of the character. Additive gene action would thus be more important than non-additive gene action (Falconer and Mackay, 1996). It has been reported that both GCA and SCA are 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, Gopal et al., 2008; Haydar et al., 2009). This implies that both additive and non-additive gene action are important for potato tuber yield with non-additive gene action more predominant. However, for potato late blight resistance in general, both GCA and SCA have been reported to be significant with GCA more important in magnitude than SCA (Bradshaw and Mackay, 1994; Mondal and Hossain, 2006; Ruiz de Galarreta et al., 2006; Gopal et al., 2008; Haynes et al., 2008). This indicates that additive gene action is more important than non-additive gene action for resistance to late blight in potato (Bradshaw and Mackay, 1994).

Factorial and diallel mating designs are among the most widely used genetic designs appropriate to estimate the magnitude of additive and non-additive components of heritable variance for late blight resistance and potato yield (Neele et al., 1991). In a factorial design referred to as North Carolina Design II, a set of clones is crossed with another set which complements it for a desirable character while the diallel mating design uses a set of crosses among clones in all combinations for the trait under consideration (Bradshaw and Mackay, 1994).

1.7 Conclusions

This chapter reviewed important aspects of potato breeding and management options of late blight disease of potato. The review highlighted participatory research approach to enhance the potential for adoption of new developed varieties. The SSR markers are currently the most powerful tools to study genetic relationships because of their high genetic information content, high reproducibility, and simplicity to use. Reviews on gene action, combining ability of potato yield and late blight resistance showed that additive and non-additive gene actions are important for tuber yield and resistance to late blight. Non-additive gene action is reported to be more predominant for yield whereas additive gene action is more dominant for resistance to late blight.

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2 CHAPTER II: PARTICIPATORY ASSESSMENT OF POTATO PRODUCTION CONSTRAINTS AND TRAIT PREFERENCES IN POTATO CULTIVAR DEVELOPMENT IN RWANDA

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Abstract

Potato (*Solanum tuberosum* L.) is the major food and cash crop in the highland regions of Rwanda. Understanding the present socio-economic conditions of potato producing farmers will have a paramount importance in designing possible improvement strategies based on their priorities. The objectives of this research were to identify farmers' key potato production constraints and establish preferred traits in potato cultivar development in Rwanda. A participatory rural appraisal (PRA) study was conducted through structured survey involving 144 households and 22 focus groups with 258 participants in Musanze, Gicumbi and Nyamagabe districts. The structured survey used a questionnaire administered to farmers to collect information on importance of potatoes and other main crops. While focus groups discussions used matrix scoring of key production constraints and pair-wise ranking of traits. Potato is the most important food and cash crop, followed by maize, beans and wheat. The dominant potato varieties are Kirundo, Cruza, Mabondo and Victoria. The most important potato production constraints are lack of access to credit, lack of high yielding cultivars, insufficient clean seeds and late blight disease. Variety Mabondo is the most tolerant to late blight, followed by Cruza, Kirundo, Kinigi and Rutuku in all the districts. High yield, disease tolerance and high dry matter content are the most important attributes preferred by farmers.

Keywords: Farmers' preferred traits, participatory rural appraisal, potato, Rwanda

2.1 Introduction

In Africa the area under potato (*Solanum tuberosum* L.) production is 2 005 331 ha with an average yield of 15.1 t ha^{-1} (FAOSTAT, 2013). In Rwanda there are approximately 164 691 ha under potato production with an average yield of 13.6 t ha^{-1} (FAOSTAT, 2013). Potato serves as a food and income security source and provides important nutrients. Potato has a high content of carbohydrates, significant amounts of quality protein, and substantial amounts of vitamins, especially vitamin C (FAO, 2008).

In Rwanda, potato is the second major food crop after cassava (FAOSTAT, 2013) and its importance is expanding (ISAR, 2008). The highland regions located in southwest and north of the country have the most favourable climatic conditions for potato production (MINAGRI, 2000). These highland regions account for more than 80% of the national potato production, and the remainder is produced in marginal agro-ecologies all over the country (Munyemana and Von Oppen, 1999). However, information on presently grown varieties, farmers' key production constraints and desired traits in potato cultivar development is inadequate and not well documented in Rwanda. Devaux and Tegera (1981) attempted participatory approach in Rwanda to involve farmers into potato variety evaluation, but farmers were not fully integrated into the whole breeding process in achieving client-oriented breeding.

Many studies (Sperling et al., 2001; Ceccarelli and Grando, 2007) on participatory breeding indicated that conventional breeding has not been as beneficial for poor farmers, especially those in marginal areas, because plant breeders did not consider the specific preferences of the farmers. As a consequence, despite many available improved varieties, few are adopted. Farmers for instance still grow unimproved local varieties because officially recommended and released varieties lack the traits of their preference (Witcombe, 2009).

Several scientists have emphasized the need for active farmer participation in plant breeding as critical for successful adoption of improved varieties and their production packages (Witcombe et al., 2005; Gyawali et al., 2007). However, the link between research and farmers is still very weak or absent in most developing countries (Ortiz et al., 2008).

A participatory approach through researcher-farmer interaction and collaboration may increase potato productivity in target environments. Farmers may provide information on varietal preferences, plant types or desired traits to be maintained or introduced (Sperling et al., 2001). Moreira (2006) conducted a case study on participatory maize breeding in Portugal considering parameters defined by small-scale farmers. The author observed increased yield in poly-cropping systems while maintaining the quality traits under a

sustainable agricultural system. Previous studies (Ceccarelli et al., 2001; Sperling et al., 2001) demonstrated the importance and efficiency of decentralized participatory selection in identifying promising and high yielding entries at target production environments. These studies established the existence of considerable differences in field selections of lines between breeders and farmers.

Participatory methods consider the value of farmers' knowledge, their preferences, ability and innovation, and their active exchange of information and technologies, as it was demonstrated during farmer field school approach at the international potato research centre (Ortiz et al., 2008). In the last decade the participatory research approach in potatoes at CIP has provided a fruitful interaction between farmers and researchers and promoted learning and innovation (Graham et al., 2001). For example, in Indonesia, farmers guided research on potato cultivation practices linked with integrated pest management (IPM) capacity building through farmer field school, where they were able to learn, interact and implement new technologies together with researchers (Graham et al., 2001). In Peru, farmers managed research on interactions between potato varieties and fungicides within farmer field school. In Bolivia farmers were involved in making crosses and selection in potato (Graham et al., 2001).

Ndolo et al. (2001), reported farmers' involvement at various levels of breeding process in Kenya, where they were involved in evaluating sweet potato varieties and several were selected due to their high yield and wide adaptation, which coincided with the breeders' selection.

According to Gyawali et al., 2007, plant breeding should actively involve clients in the selection and breeding stages especially during the selection within segregating populations (Gyawali et al., 2007).

Therefore, the assessment of farmers' knowledge and preferences in cultivar development was undertaken in the course of this study through farmer participatory approaches. The objectives of this study were to identify and analyse farmer's key constraints in potato production, and establish farmers' preferred traits to be included in cultivar development and variety selection in Rwanda.

2.2 Material and methods

2.2.1 Description of the study areas

The research focused on the highland regions of Rwanda located in north and southwest of the country and covered three main potato growing districts which are Musanze in the highland of volcanic soils, Gicumbi in the Buberuka area, and Nyamagabe within Congo-Nile divide. These regions are the most fertile and productive, and their climatic conditions are well-suited for potato production in Rwanda (Munyemana and Von Oppen, 1999). The study areas are located at an altitude between 1800 and 2500 meters above sea level (ISAR, 2008) with a bimodal rainfall pattern with the short and long rains during October to mid-December and March to June, respectively. However, rain is almost always present in these regions and potatoes are planted throughout the year. In these areas, average annual temperature and rainfall are at 16ºC and 1500mm, respectively (ISAR, 2008). Table 2.1 summarizes details of the study areas including altitude, the global positioning system (GPS) coordinates, and the annual rainfall. Major crops cultivated in the regions are potatoes, maize, beans, wheat, peas, vegetables and sorghum (ISAR, 2008).

2.2.2 Sampling procedures and data collection

2.2.2.1 Structured survey

A questionnaire was developed and administered to farmers to collect information on farm size, land allocated to potatoes and other main crops, and source of potato seeds. Different administrative levels were considered which included district and village (Table 2.1). Three major potato districts and twelve villages were involved. Four potato growers as respondents were selected at random per village. This resulted in a total of three districts, 36 villages, and 144 respondents. Data were gathered using a structured survey questionnaire to get characteristics of the farms and production systems in the districts. Secondary data were collected from previous surveys and reports of national agricultural research institution.

Table 2.1 Physical data of the surveyed area

District	Village	Altitude (m)	Geographical coordinates	Average annual rainfall for the district (mm)
Musanze	Butakanyundo	2192	01° 52′251″S and 029° 55′ 296″E	1650
	Karurambi	2311	01° 54′ 562″S and 029° 53′ 715″E	
	Manjari	2230	01° 54′ 829″S and 029° 54′501″E	
	Nyejoro	2232	01° 44′ 450″S and 029° 58′ 219″E	
	Kabeza	2456	01° 43′ 803″S and 029° 54′ 050″E	
	Rwebeya	2019	01° 27′ 918″S and029° 37′ 022″E	
	Nengo	2155	01° 54′ 135″S and 029° 56′ 398″E	
Gicumbi	Gahanga	2176	01° 55′ 727″S and 029° 55′ 349″E	1200
	Kabaya	2164	01° 56′ 219″S and 029° 55′ 174″E	
	Mugunzamao	1846	01° 27′ 952″S and 029°39′720″E	
	Kirimbi	2419	02° 24′ 255″S and 029° 23′ 718″E	
	Mugote	1851	01° 45′ 739″S and 030° 00′ 231″E	
	Kirenge	2150	01° 61′ 759″S and 030° 01261″E	
	Ryarubuguza	2245	01°61′545″S and 030° 02′ 571″E	
Nyamagabe	Akanyirandoli	2187	02° 50′ 756″S and 029° 94′ 893″E	1600
	Bivumu	2186	02° 50′ 850″S and 029° 48′ 883″E	
	Cyimicanga	2168	02° 50′ 200″S and 029° 49′ 391″E	
	Mujuga	2288	02° 53 ′110″S and 029° 45′ 553″E	
	Bususuruke	2342	02° 51′ 677″S and 029° 43′ 318″E	
	Gashaka	2486	02° 22′ 512″S and 029° 22′ 915″E	
	Uwisuri	2420	02° 24′ 255″S and 029° 23′ 720″E	
	Rwamakara	2442	02° 23′425″S and 029° 23′ 358″E	

Source: District agricultural offices (2010)

2.2.2.2 Participatory rural appraisal

A purposive sampling procedure was used to identify three districts chosen for their importance in potato production in highland regions (Munyemana and von Oppen, 1999). In each district six to nine major potato villages were selected. This provided a total of three districts and 22 villages. Subsequently 22 focus groups were constituted across the study areas to collect data through focus group discussions. Per village, with the help of the village leaders and extension workers, a focus group was established composed 10 to 15 representative farmers who had adequate knowledge about the villages, the farms, crops and local conditions and problems in the district. A total of 258 farmers participated in the 22 focus groups in the study areas.

Using matrix scores and pair-wise ranking, farmers listed and ranked crops grown, advantages of the potato crop in the area, constraints to potato production, potato varieties grown and farmers' preferences, prominent traits to be considered for future improvement and availability of late blight resistant varieties.

During data collection, participatory rural appraisal allowed farmers to express their opinions through group discussions. A checklist was prepared in advance to guide the discussion. Farmers identified preferred traits to be included in selection of potato varieties and expressed their choices and priorities. Pair-wise ranking compared traits of interest pair by pair and groups were asked to choose the preferred one among the two. In matrix scoring, the criteria were placed in rows in a matrix and farmers were asked to give a score from 1 to 10 for each characteristic to complete the matrix; where 1= not a constraint, 2= negligible, 3= small, 4= minor , 5: fairly important , 6: important , 7: very important , 8: high important , 9: Highly important , and 10: First-rate. The total score was the sum of all the scores given by all the farmers that participated to evaluate the same trait across the row in a matrix. Thus, relatively high scores imply the most important constraints.

2.2.3 Data analysis

Data were analyzed using SPSS (Release15.0) computer package (SPSS Inc., 2006) to obtain descriptive statistics.

2.3 Results

2.3.1 Socio economic benefits of growing potato in the study areas

Farmers indicated various reasons they were growing potatoes. Potato is used as both a food and cash crop. It is also a short season crop and it can be grown throughout the year. The number of years that potatoes have been grown in the study areas and the number of times they were grown per year are presented in Table 2.2. It appeared that potato was grown at least twice a year by most farmers. Musanze in the highland regions was the first district where potatoes were grown.

Table 2.2 Prevalence of potato production by district (formal survey)

District	Number of years potato grown	Number of times potato grown per year	Size of the largest plot grown with potato (ha)
	Mean	Mean	Mean
Musanze	16.7	2.7	1.9
Gicumbi	10.5	1.8	1.7
Nyamagabe	12.3	2.2	1.6

2.3.2 Gender composition and decision making in potato production and utilization

An almost equal number of males and females took part in the formal surveys and the focus group discussions (Table 2.3). Gender involvement in decision making on potato production and utilization is presented in Table 2.4. Both husband and wife were involved in the main potato production activities. They were equally involved in decisions related to planting time, variety to plant, planting materials, routine crop husbandry, harvesting, transporting and marketing across the study areas. However, some activities such as weeding, cooking, and storage protection were exclusively done by women while predominantly men were totally concerned with pest management.

Table 2.3 The number of farmers interviewed and gender composition (formal survey and focus group discussions)

District	**Male**	**Female**	**Total**
Formal survey			
Musanze	25 (52%)	23 (48 %)	48 (33.3%)
Gicumbi	24 (50%)	24 (50%)	48 (33.3%)
Nyamagabe	24 (50%)	24 (50%)	48 (33.3%
Total	**73 (50.7%)**	**71 (49.3%)**	**144 (100%)**
Focus group discussions			
Musanze	57 (52.8%)	51 (47.2%)	108 (41.9%)
Gicumbi	28 (50%)	28 (50%)	56 (21.7%)
Nyamagabe	46 (48.9%)	48 (51.1%)	94 (36.4%)
Total	**131 (50.8%)**	**127 (49.2%)**	**258 (100%)**

Table 2.4 Decision maker on potato production and utilization (focus group discussions) across the regions

Frequency					
Task	**Husband**	**Wife**	**Both (Husband and Wife)**	**Total**	**Decision maker**
Planting time	1	2	**19**	22	Both
Planting materials	9	-	13	22	Both
Variety to plant	3	3	16	22	Both
Weeding	-	11	11	22	Wife
Pest management	12	-	10	22	Husband
Routine crop care	9	8	5	22	Both
Harvesting	-	-	22	22	Both
Transporting	2	-	20	22	Both
Storage protection	1	18	3	22	Wife
Cooking	-	22	-	22	Wife
Marketing	4	-	18	22	Both

2.3.3 Economic importance

Focus groups were used to collect general information through discussion. Farmers listed the main food crops they grew in each district and ranked them. Pair-wise ranking was used where farmers were asked to compare food crops. They identified by ranking major crops grown according to their greatest importance as the main food. Major food crops grown by farmers in Musanze, Gicumbi and Nyamagabe districts are presented in Table 2.5. Potatoes, dry beans and maize were important in all the three districts. Sweet potato was very important in Gicumbi district, important in Nyamagabe district and absent in Musanze district. The main food crops mentioned that were grown across the highland regions were used for home consumption and as important sources of income. Major cash crops were ranked according to their greatest importance in three districts (Table 2.6).

Table 2.5 Pair-wise ranking of major food crops grown in Musanze, Gicumbi and Nyamagabe districts (focus group discussions)

	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
Crop	Mean	Rank	Mean	Rank	Mean	Rank
Sweet potato	-	-	5.2	2	4.0	5
Potato	3.3	1	4.2	3	6.7	1
Dry beans	2.6	2	5.8	1	5.0	3
Maize	1.5	3	1.8	6	5.1	2
Wheat	0.2	5	0.0	10	4.6	4
Peas	0.0	8	1.6	7	3.5	6
Sorghum	0.2	6	3.0	4	1.4	7
Banana	0.4	4	0.6	8	0.4	9
Vegetables	1.0	7	2.2	5	1.4	8
Fruits	0.0	9	0.2	9	0.2	10
Cassava	-	-	-	-	0.2	11
Soya	-	-			0.2	12
Mean	**1.0**		**2.4**		**2.7**	

[a] N= number of villages per district that participated in group discussions

Table 2.6 Pair-wise ranking of major cash crops grown in Musanze, Gicumbi and Nyamagabe districts (focus group discussions)

	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
Crop	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
Sweet potato	-	-	2.0	4	1.5	7
Potato	3.0	1	5.4	1	5.7	1
Dry beans	1.5	2	4.6	2	0.5	9
Vegetables	1.2	3	2.4	3	0.8	8
Wheat	0.4	4	1.0	6	4.2	2
Maize	0.4	5	1.4	5	2.1	4
Tea	-		0.4	9	2.0	5
Fruits	0.1	6	-		0.1	11
Peas	0.0	8	0.6	8	2.7	3
Banana	0.1	7	1.0	7	0.4	10
Sorghum	0.0	9	0.0	10	1.8	6
Pyrethrum	0.0	10	-		-	
Tobacco	0.0	11	-		-	
Mean	**0.6**		**1.9**		**2.0**	

[a] N= number of villages per district that participated in group discussions

2.3.4 Farming systems

2.3.4.1 Land allocation

The mean land area in hectares allocated to potatoes was higher than other food crops grown in the study areas. Average land size per household across the highland regions was 1 ha and 0.8 ha of this land area representing about 90% of the total household land was used for cultivation (Table 2.7). Within the land used for cultivation, 20 to 22.7% were allocated to potato production and the rest to other crops (Table 2.8).

Table 2.7 Household farm size and cultivated land in the study areas (formal survey)

District	Total farm size (ha)	Total cultivated land (ha)
	Mean	Mean
Musanze	0.8	0.8
Gicumbi	0.9	0.8
Nyamagabe	1.3	0.9
Average	**1.0**	**0.8**

Table 2.8 Importance of crops grown per household in the study areas (formal survey)

Crop	Income generation		Family food use	
	Percentage	Mean area (ha)	Percentage	Mean area (ha)
Potato	22.7	0.5	20	0.5
Maize	9.1	0.2	8	0.2
Vegetables	4.5	0.1	16	0.4
Peas	13.6	0.3	8	0.2
Beans	9.1	0.2	8	0.2
Wheat	13.6	0.3	12	0.3
Sweet potato	4.5	0.1	8	0.2
Bananas	13.6	0.3	12	0.3
Sorghum	9.1	0.2	8	0.2
Total	**100**	**2.2**	**100**	**2.5**

2.3.4.2 Seed source and use of production inputs

The source of seed potatoes in the study areas is presented in Table 2.9. In the highland regions, most of the farmers acquired potato seeds from traders (41.7%) and open market (38.9%). Research institutions and private companies played a minor role as seed providers and represented only 10.4% and 4.8%, respectively. Few farmers (4.2%) kept their own seeds from their own harvests.

Table 2.9 Source of potato seeds (formal survey)

Seed source	Number of farmers	Percentage
Own field	6	4.2
Trader	60	41.7
Open market	56	38.9
Private company	7	4.8
Research institution	15	10.4
Total	**144**	**100**

2.3.5 Major production constraints

Matrix scoring identified the most important potato production constraints in three districts (Table 2.10). Inaccessibility to credit was number one constraint followed by late blight and unclean seeds in Musanze district. Low yield was the major constraint, late blight the second and unclean seed the third in Nyamagabe district (Table 2.10). In Gicumbi district, lack of access to credit was the major production constraint. The second most important constraint in that district was unclean seeds followed by poor storage facilities and low yield, whereas late blight was among the least important constraints. Other less important constraints identified by farmers were dormancy period, low market price, soil degradation, inaccessibility to fertilizers and fungicides (Table 2.10).

Table 2.10 Matrix scoring of potato production constraints in the study areas (focus group discussions)

	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
Constraint	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
Late Blight	98.8	3	55.4	5	98.6	3
Unclean seeds	93.1	4	100.4	2	87.0	4
Poor storage facilities	53.6	7	73.6	3	62.5	6
Dormancy period	66.0	6	32.6	8	56.7	7
Low yield	110.4	2	72.4	4	103.0	1
Low price	75.4	5	55.2	6	66.6	5
Lack of fertilizers	21.5	9	20.6	9	26.0	9
Lack of pesticides	17.2	10	17.4	10	25.2	10
inaccessibility to credit	112.6	1	104.0	1	100.8	2
Soil degradation	26.8	8	39.0	7	49.4	8
Mean	**67.6**		**57.1**		**67.6**	

[a] N= number of villages per district that participated in group discussions

2.3.6 Importance of diseases and insects

The major potato diseases in the highland regions are presented in Table 2.11. With the aid of pictures of disease symptoms, farmers recognised the most important diseases occurring on the potato crop. Guided by the moderator, farmers grouped biotic stresses into four categories such as fungal diseases (late blight mainly), bacterial wilt, viral diseases and insect pests. In Musanze district late blight was the major biotic problem, followed by bacterial wilt, viral diseases and insect pests, while in Gicumbi district bacterial wilt was the main disease affecting potato crop. In Nyamagabe district, bacterial wilt was the least important disease (Table 2.11). Farmers reported that important crop damage (25-50%) caused by late blight, bacterial wilt and viruses' infections at 28.7, 25.5 and 27.7%, of the crops respectively (Table 2.12). Serious crop damage (more than 50%) occurred due to bacterial wilt (32%) and late blight (19.2%) while viruses were considered to cause less damage (Table 2.12).

Table 2.11 Pair-wise ranking of major potato diseases and pests in the study area (focus group discussions)

Disease/pest	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
	Mean	Rank	Mean	Rank	Mean	Rank
Late blight	3.0	1	2.0	2	3.0	1
Bacterial wilt	2.0	2	3.0	1	0	4
Viral diseases	1.0	3	1.0	3	2.0	2
Insect pests	0.0	4	0.0	4	1.0	3
Overall Mean	**1.5**		**1.5**		**1.5**	

[a] N= number of villages per district that participated in group discussions

Table 2.12 Crop damage reported by farmers due to potato diseases (formal survey)

Type of damage	Late blight (%)	Bacterial wilt (%)	Viruses (%)
Complete crop loss	9.2	5.7	5.8
Serious damage(50%+)	19.2	32.0	14.6
Important damage (25-50%)	28.7	25.5	27.7
Non-important damage (<25%)	30.7	25.2	37.4
No damage at all	12.3	11.7	14.6
Total	**100.0**	**100.0**	**100.0**

2.3.7 Farmers-preferred varieties and traits

2.3.7.1 Potato varieties grown in the study areas

Potato varieties grown in the study areas are presented in Table 2.13. Varieties Kirundo, Cruza, Mabondo, Victoria, Gikungu and Sagema were grown in all the three districts. In Musanze district the most important varieties grown by farmers were Kinigi (mean = 4.2), Petero (4.0), Kirundo (3.4), Mabondo (2.8) and Kigega (1.8). In Gicumbi district, most important varieties included Rutuku (mean = 4.8), Kirundo (3.6), Mabondo (2.4) and Cruza (1.4). Rutuku was a given name to any of the red skin varieties. It should be probably Kinigi, Victoria or Gikungu which were the most important red varieties available in the region. In Nyamagabe district, Cruza (mean = 3.4) was significantly different from the others. It was followed by local (mean= 1.4), Kirundo (1.1) and Victoria (1.1).

Table 2.13 Pair-wise ranking of potato varieties grown in Musanze, Gicumbi and Nyamagabe districts (focus group discussions)

	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
Variety	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
Cruza	1.5	7	1.4	4	3.4	1
Mabondo	2.8	4	2.4	3	0.4	7
Makoroni	1.2	9	1.2	6	-	-
Kirundo	3.4	3	3.6	2	1.1	3
Victoria	1.0	10	1.2	5	1.1	4
Gikungu	0.6	14	1.2	7	0.4	8
Sangema	0.0	15	0.4	10	0.8	5
Petero	4.0	2	-	-	-	-
Kinigi	4.2	1	-	-	-	-
Nyirakabondo	0.8	12	-	-	-	-
Nyabizi	1.6	6	-	-	-	-
Bineza	1.0	11	-	-	-	-
IPP	0.7	13	-	-	-	-
Kigega	1.8	5	-	-	0.2	9
Rwishaki	1.2	8	-	-	-	-
Rutuku	-	-	4.8	1	-	-
Mbumbe	-	-	0.2	12	-	-
Nderera	-	-	0.4	11	-	-
Mizero	-	-	0.8	8	-	-
Makerere	-	-	0.6	9	-	-
Gasore	-	-	-	-	0.1	10
Nyirangeli	-	-	-	-	0.0	11
Local	-	-	-	-	1.4	2
Mugogo	-	-	-	-	0.5	6
Kenya	-	-	-	-	0.0	12
Mean	**1.6**		**0.7**		**0.4**	

[a] N= number of villages per district that participated in group discussions

2.3.7.2 Late blight tolerant varieties in the highland regions

Pair-wise ranking of varieties according to reaction to late blight is presented in Table 2.14. Kinigi was the most tolerant variety in Musanze district and Rutuku was the most tolerant in Gicumbi while Cruza was the best in late blight tolerance in Nyamagabe district. In Musanze district the three most tolerant cultivars were ranked as follows: Kinigi (mean score = 5.8), Mabondo (3.6) and Makoroni (2.8). In Gicumbi district, Rutuku (4.6) was the most tolerant variety followed by Cruza (4.2) and Mabondo (2.8). In Nyamagabe district the ranking was as follows: Cruza (2.1), local (1.6), and Mabondo (1.5).

Table 2.14 Pair-wise ranking of late blight tolerant varieties in the study area (focus group discussions)

	District[a]					
Musanze (N=9)			**Gicumbi (N=5)**		**Nyamagabe (N=8)**	
Variety	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
Mabondo	3.6	2	2.8	3	1.5	3
Cruza	1.9	6	4.2	2	2.1	1
Kirundo	2.6	4	2.0	4	0.6	8
Victoria	1.0	10	0.0	10	0.7	6
Sangema	0.0	15	0.2	9	0.8	4
Gikungu	0.6	12	1.0	6	0.6	9
Kigega	1.1	9	-	-	0.2	10
Makoroni	2.8	3	1.8	5	-	-
Kinigi	5.8	1	-	-	-	-
Petero	2.1	5	-	-	-	-
Nyirakabondo	0.9	11	-	-	-	-
Bineza	1.9	7	-	-	-	-
Nyabizi	0.2	14	-	-	-	-
IPP	0.3	13	-	-		
Rwishaki	1.1	8	-	-	-	-
Rutuku	-	-	4.6	1	-	-
Makerere	-	-	0.0	11	-	-
Nderera	-	-	0.8	7	-	-
Mizero	-	-	0.6	8	-	-
Gasore	-	-			0.7	7
Mugogo	-	-	-	-	0.0	13
Nyirangeli	-	-	-	-	0.1	11
Local	-	-	-	-	1.6	2
Kenya	-	-	-	-	0.1	12
Mean	**1.1**		**0.7**		**0.4**	

[a] N= number of villages per district that participated in group discussions

2.3.7.3 Farmers-preferred potato traits in the study areas

Pair-wise ranking identified high yield, disease tolerance and high dry matter content as the most important attributes preferred by farmers across the regions (Table 2.15). Marketability, tolerance to poor soil, big tuber size with round shape (Table 2.16) were additional important attributes considered by famers in the study areas.

Table 2.15 Pair-wise ranking of farmers-preferred potato characteristics across the study areas

	District[a]					
	Musanze (N=9)		Gicumbi (N=5)		Nyamagabe (N=8)	
Characteristics	**Mean**	**Rank**	**Mean**	**Rank**	**Mean**	**Rank**
High yield	4.0	1	4.6	1	4.1	1
Disease resistance	3.4	1	3.4	1	3.7	2
Good taste	0.4	4	0.8	2	0.5	6
Short dormancy	1.1	3	0.8	2	1.6	4
Early maturity	2.1	2	2.0	2	2.0	5
High dry matter content	3.7	1	3.8	1	2.6	3
Mean	**2.5**		**2.6**		**2.4**	

[a] N= number of villages per district that participated in group discussions

Table 2.16 Advantages and disadvantages of the most grown varieties as presented by key informants

District	Varieties	Advantages	Disadvantages
Musanze, Gicumbi and Nyamagabe	Kinigi, Kirundo, Rutuku and Mabondo	- High yielding - High dry matter content - Marketability - Tolerance to late blight - Big tuber size and good shape (Round)	- Susceptible to bacterial wilt
Musanze	Petero	- High yielding - High dry matter content	- Susceptible to diseases
Musanze, Gicumbi and Nyamagabe	Cruza	- High yielding - High tolerance to diseases - Tolerance to poor soil (acidic)	- Low dry matter content - small-to medium tuber size - Late maturity
Nyamagabe	Local	- Resistance to diseases	- Late maturity - Small tuber size - Low yield
Musanze, Gicumbi and Nyamagabe	Victoria	- High yielding - Big tuber size and good shape (Round) - Early maturity	- Susceptible to diseases - Low dry matter content

2.4 Discussion and conclusions

The study revealed that both women and men are equally involved in decision making in the main activities of potato production and utilization. The PRA established that potato is the most important food crop and an important source of income in the study areas. Other major crops cultivated in the regions are, maize, beans, wheat, peas, vegetables and sorghum.

Landholdings are very small as Rwanda is one of the most densely populated countries in the world with 430.6 persons km^{-2} of land area (World Bank, 2011). The average land size is 1.0 ha per farmer with more than 50% of that land allocated to potato production. Potato is the principal crop in the study areas and inoculum of *Phytophthora. infestans*, the causal agent of late blight, is always present due to continuous cropping and conducive conditions for late blight occurrence and spread in the highland regions (Muhinyuza et al. 2008).The survey showed that the sources of potato planting materials are mainly traders and open market, whereas research institutions and private companies play a minor role as seed providers. It is clear that farmers do not have access to clean seeds, which may lead to high incidence and severity of important diseases in the regions. Utilization of infected planting materials is a common way of disease spread of the crop. Selection and use of clean planting materials could reduce incidence and severity of important diseases.

Major potato production constraints include lack of access to credit, lack of high yielding cultivars, insufficient clean planting materials, late blight, dormancy period, low market price, soil degradation, inaccessibility to fertilizers and fungicides. Serious crop damage occurs due to late blight, bacterial wilt and viruses while insect pests are considered to cause less damage in the study areas. However, late blight is the most important disease in the potato areas of Rwanda as it was stated previously by different authors (Kirk et al., 2004; ISAR, 2008; Muhinyuza et al., 2008).

Pair-wise ranking established that the most important potato varieties grown in the three districts covered by the study are Kirundo, Cruza, Mabondo, Victoria, Gikungu and Sagema. However, 24 different potato varieties were recorded in the study areas. Although some of these varieties are susceptible to late blight, high levels of genetic variability exist within the different varieties. Using pair-wise ranking, farmers established late blight tolerant varieties across the study areas. Mabondo is considered the most tolerant variety across the districts, followed by Cruza and Kirundo. However, Kinigi is considered the most tolerant variety in Musanze district and Rutuku the most tolerant in Gicumbi while Cruza is considered the most late blight tolerance in Nyamagabe district. Moreover, Nyirakabondo, Victoria, Makere

are considered the least tolerant varieties in Musanze, Nyamagabe and Gicumbi respectively. These results were consistent with previous reports that Cruza, Kinigi and Mabondo are the most late blight tolerant varieties while Victoria is the least tolerant following many years of testing in ISAR (ISAR, 2008).

Pair-wise ranking indicated that high yield, disease tolerance and high dry matter content are the most important attributes preferred by farmers across the regions. Moreover, early maturity and short dormancy period, marketability, tolerance to poor soil, big tuber size with round shape are also important attributes considered by famers across the study areas.

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3 CHAPTER III: YIELD RESPONSE AND LATE BLIGHT REACTION OF POTATO GENOTYPES IN RWANDA

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Abstract

Potato (*Solanum tuberosum* L.) genotypes with relatively high yield level and resistance to the late blight disease are being developed by the International Potato Centre (CIP) and made available to developing countries. However, for effective breeding for high yield and late blight resistance, these CIP and locally adapted genotypes need to be evaluated and screened under target growing environmental conditions. The objectives of the study were to determine yield response and late blight resistance of potato genotypes grown in Rwanda and candidate clones obtained from CIP and to identify suitable parents for breeding. A total of 44 potato genotypes, 30 acquired from CIP and 14 local varieties were evaluated under three environments (Kinigi, Rwerere and Nyamagabe). Experiments were laid out in an 11 x 4 alpha lattice design with two replications. Data were collected on late blight severity (%) based on the relative area under the disease progress curve (rAUDPC: 100% max), total tuber yield, marketable tuber weight and dry matter content. Genotypes had significant differences in blight resistance and yield levels. Eight genotypes (CIP 391047.34, CIP 393385.39, CIP 393280.82, CIP 396036.201, Gikungu, Ngunda, Kigega and Nderera) were identified as promising parents for subsequent crosses. The selected genotypes display farmers-preferred traits, productive flowers, high to medium late blight resistance and high yields.

Keywords: Disease resistance, genotypes, late blight, potato, Rwanda

3.1 Introduction

Potato (*Solanum tuberosum* L., 2n=4x=48) is an important food security crop in Eastern and Central Africa (ECA) (Kaguongo et al. 2013). In the ECA region, the area under the crop has considerably increased in recent years, but yields on small-scale farms are low. The average potato productivity is less than 10 t ha^{-1} compared to the potential yield of 40 to 60 t ha^{-1} attainable by a progressive farmer in developing countries (FAO 2008). Although most production is concentrated in the highlands (1600-2800 m above sea level), potato is grown throughout Rwanda and its importance is expanding considerably as a food and cash crop (ISAR 2008). Potato is the second major food crop after cassava (FAOSTAT 2013) and its production is growing and it is becoming a source of income security for many Rwandans, especially small-scale farmers who depend on the crop for their livelihoods (Chapter 2). The per capita potato consumption in Rwanda is approximately 125 kg per person per annum (FAO 2008). Potato is grown twice a year following the bimodal rainfall patterns in Rwanda.

Both the cultivated area and production of potato has progressively expanded in Rwanda. However, potato productivity is still amongst the lowest in the world, averaging 9.0 t ha^{-1} compared to a world average of 16.4 t ha^{-1} (FAO 2008). The major limiting factors to potato productivity in Rwanda include lack of high yielding varieties, diseases, post harvest losses due to poor handling and storage facilities, insufficient clean seed potatoes, poor seed distribution system, and inadequate production technologies (FAO 2008). Among these, diseases are the main potato production constraints in Rwanda. The major diseases of potato include late blight caused by *Phytophthora infestans (Mont.) de Bary*, early blight (*Alternaria solani* Sorauer), rhizoctonia stem canker (*Rhizoctonia solani* Kuhn), bacterial wilt (*Ralstonia solanacearum* Smith.), tuber soft rot *Pectobacterium carotovora*, and viruses (ISAR, 2008). Of the potato diseases, late blight is the most serious in the major production zones of Rwanda (Kirk et al. 2004). Potato late blight epidemics in Rwanda are associated with unavailability of resistant varieties. The disease causes serious crop and yield losses (Kirk et al. 2004). Fungicides are costly and not widely used by small-scale farmers in Rwanda (Chapter 2). The most sustainable and cost effective means for managing late blight disease in potatoes would be through host plant resistance in combinations with other integrated disease management strategies (Kirk et al. 2001; Kirk et al. 2005; Nærstad 2007). Therefore, breeding potato for late blight resistance and high yield would enhance productivity.

Potato genotypes with relatively high yield and a high level of resistance to late blight have been developed by the International Potato Centre (CIP) in the past few years (Landeo et al. 1997). These genotypes are continuously introduced to Rwanda to strengthen the existing

potato genetic resources against potato late blight disease. The latest introductions from CIP are population B3 genotypes, which carry only quantitative resistance to late blight (Landeo et al. 1997). These new introductions as well as available local potato genotypes need to be evaluated and screened for late blight resistance and yield levels to identify the best genotypes to be used as parents in subsequent crosses and selection. The objectives of the study were to determine yield response and late blight resistance of potato genotypes grown by farmers in Rwanda and candidate clones obtained from CIP and to identify suitable parents for breeding to be done by Rwandan potato breeders.

3.2 Materials and methods

3.2.1 Plant material

The study used 44 potato genotypes; 30 were acquired from CIP and 14 are local varieties widely grown in Rwanda. The details of the germplasm are described in Table 3.1. Seed potatoes for planting were supplied by the Potato Seed Propagation facility of the Northern zone of Rwanda Agriculture Board (RAB).

Table 3.1 List of 44 potato genotypes used in the study

Number	Genotypes	Source	Population	Year of release
1	CIP 391047.34	CIP	B3C1	Not yet released
2	CIP 393077.54	CIP	B3C1	Not yet released
3	CIP 393371.58	CIP	B3C1	Not yet released
4	CIP 393637.171	CIP	-	Not yet released
5	CIP 396033.102	CIP	B2C2	Not yet released
6	CIP 395111.19	CIP	-	Not yet released
7	CIP 395112.36	CIP	B3C2	Not yet released
8	CIP 393280.57	CIP	B3C1	Not yet released
9	CIP 393382.44	CIP	B3C1	Not yet released
10	CIP 391058.175	CIP	B3C1	Not yet released
11	CIP 395015.6	CIP	B3C2	Not yet released
12	CIP 395096.2	CIP	B3C2	Not yet released
13	CIP 393385.39	CIP	-	Not yet released
14	CIP 396004.225	CIP	B3C2	Not yet released
15	CIP 396034.103	CIP	B3C2	Not yet released
16	CIP 396026.103	CIP	B3C2	Not yet released
17	CIP 393280.82	CIP	B3C2	Not yet released
18	CIP 396027.205	CIP	B3C2	Not yet released
19	CIP 391014.14	CIP	-	Not yet released
20	CIP 396036.201	CIP	-	Not yet released
21	CIP 396043.226	CIP	B3C2	Not yet released
22	CIP 395111.13	CIP	B3C2	Not yet released
23	CIP 396038.107	CIP	B3C2	Not yet released
24	CIP 391046.46	CIP	-	Not yet released
25	CIP 395112.19	CIP	B3C2	Not yet released
26	CIP 381381.13	CIP	-	Not yet released
27	C62	CIP		Not available
28	C200	CIP		Not available
29	C281	CIP		Not available
30	C80	CIP		Not available
31	Bineza	Rwanda		Not available
32	Cruza	Rwanda		1985
33	Gikungu	Rwanda		1992
34	Kigega	Rwanda		1992
35	Kinigi	Rwanda		1983
36	Kirundo	Rwanda		1983
37	Kivu	Rwanda		Not available
38	Mabondo	Rwanda		1989
39	Mizero	Rwanda		1992
40	Nderera	Rwanda		1992
41	Ngunda	Rwanda		1992
42	Nyirakabondo	Rwanda		Not available
43	Sangema	Rwanda		1980
44	Victoria	Rwanda	-	1989

CIP = Centro Internacional de la Papa

3.2.2 Study sites

The trials were conducted across three selected locations in Rwanda: Kinigi, Rwerere and Nyamagabe. The locations are the major research sites of the RAB and known for their potato production and late blight epidemics. Kinigi represents the highlands of volcanic soils. It is located at an altitude of 2200 meters above sea level (masl), on longitude of 29º 38'

East and latitude 1º 30'South (ISAR 1987). Annual temperature and rainfall averages at 16ºC and 148 cm, respectively. Rwerere is located at an altitudal zone of 2060-2312 masl on longitude of 29º 19' East and latitude of 1º 36' South with an annual rainfall and temperature of 120 cm and 20ºC, respectively. It represents the highlands of Buberuka. Nyamagabe is located at an altitude of 1600-2800 masl on longitude of 29º 33' East and latitude of 1º 33' South with respective annual rainfall and temperature of 160 cm and 19 ºC. It represents the highlands of Congo/Nile Divide (ISAR 1987). In warm regions such as the tropical highlands of Rwanda, inoculum is almost continuously present due to continuous cropping and favourable conditions for late blight occurrence and spread. In most potato growing areas in Rwanda, average annual precipitation ranges from 120 cm to over 160 cm. In general, rainfall is bimodal with a minor peak occurring in October and a major peak in March/April. High elevations and low latitudes combine to form an isothermal temperature regime with an average annual temperature of about 16ºC (Durr 1983; ISAR 1983).

3.2.3 Experimental design

Trials were conducted using an 11 x 4 alpha lattice design with 11 blocks of 4 plots each with two replications. All genotypes were established in two row plots of 10 tubers per row giving a total of 20 plants per plot with inter-row spacing of 0.9 m and intra-row spacing of 0.3 m. In each trial, the two local varieties, Cruza and Victoria, were used as resistant and susceptible checks, respectively. Experiments were established under rain-fed conditions. At all the borders of the experimental plots, the susceptible cultivar Victoria was planted as spreader rows to serve a source of inoculum (Porter et al. 2004). In the study sites, late blight occurs in epidemic proportions due to disease build-up as a result of continued potato mono-cropping on the same field over time. Genotypes were planted and harvested in October 2011 and February 2012, respectively. Fertilizer was applied in the form of N_{17}-P_{17}-K_{17} at a rate of 250 kg ha^{-1} as split applications at planting and hilling. Neither pesticides nor fungicides were applied. Weeds were controlled by using hoeing and hand cultivation.

3.2.4 Data collection

Data collected included late blight disease reaction, total tuber weight, marketable tuber weight, dry matter content and qualitative traits. Starting with the first appearance of the symptoms, plants within each plot were visually rated at 7 day intervals for percent 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 the 1 to 9 scale devised 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 susceptible genotypes reached 90-100% of leaf blight assessments. For all plots and assessment dates, the area under the disease progress curve AUDPC (Campbell and Madden, 1990) was calculated within a single experiment (Bradshaw 2007). The rAUDPC (%) was used in the analysis of variance. The rAUDPC was calculated using the following formula:

$$rAUDPC = \frac{\sum (T_{i+1} - T_i) * \left(\frac{D_{i+1} + D_i}{2} \right)}{T_{Total} * 100} \qquad (1)$$

In equation 1, T_i is the i^{th} day when an estimation of percent 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.

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}. After data analysis, genotypes with yields above 30 t ha^{-1} were classified as high yielders (HY) or moderate yielders (MY) when yields ranged between 15 to 30 t ha^{-1}, and low yielders (LY) when yielded below 15 t ha^{-1}.

To determine marketable tuber weight (MTW), the tubers harvested in a plot were separated into marketable and unmarketable types based on size, disease defect and general appearance for the market. The MTW (%) was calculated as the total weight of all the marketable tubers harvested in a plot divided by the total weight of all the tubers harvested in that plot multiplied by a hundred.

Dry matter content was evaluated following the CIP protocol (Bonierbale et al. 2006). Dry matter content was measured within 24 hours after harvest to avoid post-harvest changes due to shrinkage loss. Tubers samples for dry matter content analyses were undamaged and free of disease. Three to five tubers per plot were chopped into sizes of 1-2 cm cubes, mixed thoroughly to sample all parts of the tuber because dry matter content is not uniform throughout the tuber. Two sub-samples of about 200-250 g each were weighted to determine their fresh weight. Each sub-sample was placed in a paper bag and oven dried at 80°c until constant dry weight is reached. This weight was immediately recorded for each sub-sample as dry weight. Dry matter content was calculated using the following formula: dry matter = (dry weight / fresh weight) x 100. (2)

The mean dry matter content of the two-sub-samples was calculated to get the dry matter content of each sampled plot (equation 2). Genotypes with dry matter content more than 23% were classified high dry matter (H); medium (M) if dry matter content ranged between 20 to 23% or low (L) when dry matter content was below or equal to 20% (Chujoy 2010). Qualitative data collected were flower colour, pollen production, tuber shape, tuber flesh and tuber skin colour, and eye depth.

3.2.5 Data analysis

Data collected were subjected to analysis of variance (ANOVA) using the GLM procedure of SAS (SAS Institute 2004). Mean separation was performed using the least significant difference (LSD) procedure at a 5% probability level. Pearson correlation coefficients were calculated using PROC CORR of SAS (SAS Institute 2004) to determine trait associations. Separate ANOVA were conducted per location with genotypes as the main effect and later combined ANOVA were calculated across locations.

3.3 Results

3.3.1 Weather data

Weather conditions were conducive during the trials, promoting development of late blight. There was regular rainfall, and temperatures were around 18 ºC (Table 3.2) throughout the growing period promoting late blight epidemic in the study.

Table 3.2 Rainfall and mean temperatures of Kinigi, Nyamagabe and Rwerere during the experimental period

Year	2011			2012	
Month	**October**	**November**	**December**	**January**	**February**
			Kinigi		
Rainfall (mm)	149	162	121	100	132
Mean temperature (ºC)	15.7	15.6	15.5	16.0	16.1
			Nyamagabe		
Rainfall (mm)	129	110	124	147	152
Mean temperature (ºC)	19.2	18.5	18.6	18.9	19.0
			Rwerere		
Rainfall (mm)	139	146	110	102	106
Mean temperature (ºC)	19.9	19.6	19.6	19.9	20.1

3.3.2 Analysis of variance

Table 3.3 summarizes the analysis of variance for the relative area under the disease progress curve (rAUDPC), total tuber weight (TTW), marketable tuber weight (MTW) and dry matter content (DM) among tested genotypes. There were significant differences among genotypes for rAUDPC, TTW, MTW and DM within and across locations.

Table 3.3 Analysis of variance on selected agronomic traits of potato genotypes tested at three locations in Rwanda

Source of variation	DF	rAUDPC		TTW		MTW		DM	
		MS	F pr	MS	F pr	MS	F pr	MS	F pr
Kinigi									
Replication	1	767	<0.001***	79.2	0.2330	1172.4	0.0429*	35.0	0.01**
Block	10	509.3	<0.001***	179.8	0068*	303.1	0.397	6.8	0.1915
Genotype	43	141.1	<0.001***	279.8	<0.001***	611.9	0.0128*	10.5	0.0145*
Rep*block	10	26.1	0.5376	59	0.3910	879.2	0.0065**	2.6	0.8064
Residual	23	28.6		52.9		256.4		4.5	
Total	87								
Nyamagabe									
Replication	1	440.1	0.0174*	4.6	0.6062	542.5	0.0430*	0.25	0.8354
Block	10	177.8	0.0252*	194.1	<0.001***	654.3	0.0003**	5.1	0.5449
Genotype	43	308.8	<0.001***	128.4	<0.001***	402.4	0.0011**	12.7	0.0192*
Rep*block	10	29.9	0.9094	36.1	0.0610	173.1	0.2160	9.6	0.1424
Residual	23	67.4		16.8		118.8		5.7	
Total	87								
Rwerere									
Replication	1	372.7	0.0062**	63.6	0.0521**	37.1	0.6327	26.9	0.0061**
Block	10	229.8	0.00031**	136.3	<0.001***	281.9	0.1217	3.1	0.4342
Genotype	43	246.3	<0.001***	154.6	<0.001***	368.2	0.0155*	6.9	0.0145*
Rep*block	10	21.3	0.8624	40.6	0.0238*	238.6	0.2001	2.9	0.4892
Residual	23	34		15.2		159.2		2.9	
Total	**87**								

* = 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, TTW = total tuber weight; MTW = marketable tuber weight; DM = dry matter content

3.3.3 Late blight disease reaction

Susceptibility to late blight disease was expressed in terms of relative area under the disease progress curve [rAUDPC (%)].There were highly significant differences (P≤0.001) among genotypes for their susceptibility to potato late blight (Table 3.4) within locations. The mean rAUDPC (= 100 max) across locations indicated that genotype CIP 393280.57 with disease severity of 9.3% and genotype Gikungu (11.1%) were the most resistant, whereas genotypes C281 (47.6%) and C62 (45.7%) were the most susceptible. Nyamagabe had the highest disease severity (33.2 %), followed by Rwerere (30.9%) and Kinigi (20.8%) (Table 3.4).

Table 3.4 Relative area under the disease progress curve (%) of 44 potato genotypes evaluated at three locations in Rwanda

	Location				
	Kinigi	Nyamagabe	Rwerere	Across locations	
Genotype	rAUDPC	rAUDPC	rAUDPC	rAUDPC	Rank
CIP 393280.57 *	7.7 no	10.0 o	10.3 p	9.3	1
Gikungu *	2.3 w	18.0 l-o	12.9 n-p	11.1	2
CIP 395111.13 *	11.8 m-o	12.1 no	12.1 o-p	12.0	3
Kinigi *	8.4 r-w	13.7 m-o	14.2 m-p	12.1	4
CIP 393280.82 *	14.1 k-o	11.6 no	11.8 op	12.5	5
CIP 395111.19 *	10.5 m-o	16.1 m-o	16.2 m-p	14.3	6
CIP 396043.226 *	18.3 h-o	14.9 m-o	15.1 m-p	16.1	7
Mizero *	3.9 v-w	27.5 h-n	21.2 l-p	17.5	8
Kigega *	6.7 t-w	28.2 h-m	21.5 k-p	18.8	9
Ngunda *	2.8 v-w	29.3 e-m	25.5 i-n	19.4	10
CIP 393371.58 *	20.2 h-n	22.8 j-o	21.9 k-p	21.6	11
CIP 396027.205 *	22.6 e-l	22.6 j-o	21.1 j-m	22.1	12
Sangema *	13.3 n-w	29.4 e-m	24.8 i-o	22.5	13
CIP 396004.225 *	26.3 c-j	21.2 k-o	20.6 l-p	22.7	14
CIP 391058.175 *	22.8 e-m	22.7 j-o	23.2 j-p	22.9	15
Mabondo *	20.4 g-q	22.7 j-o	25.9 i-n	23.0	16
Bineza *	21.6 f-o	24.0 j-o	25.4 i-n	23.7	17
CIP 391047.34 *	21.2 f-n	25.5 h-o	25.5 i-n	24.1	18
Nderera *	19.9 h-q	30.6 d-m	25.7 i-n	25.4	19
Cruza	11.9 m-o	33.6 c-l	32.2 f-l	25.9	20
CIP 396034.103 *	32.7 a-e	24.5 i-o	24.6 i-o	27.3	21
Kirundo *	9.5 r-w	45.6 a-e	27.3 h-m	27.6	22
CIP 395112.19 *	31.1 a-g	26.4 h-o	27.0 i-m	28.2	23
CIP 393077.54 *	13.5 l-o	38.4 a-j	36.8 b-i	29.6	24
CIP 381381.13	19.0 h-n	51.5 ab	19.0 h-n	29.8	25
CIP 393385.39 *	19.7 h-m	35.7 b-k	34.7 e-k	30.1	26
Nyirakabondo *	15.3 l-t	53.5 a	31.2 g-l	33.4	27
CIP 396036.201 *	27.6 b-i	36.8 a-k	35.9 c-i	33.5	28
CIP 396038.107 *	16.6 j-o	43.4 a-g	41.3 a-g	33.7	29
CIP 396026.103 *	25.5 d-j	38.4 b-f	37.8 b-i	33.9	30
Kivu *	26.7 b-k	41.0 a-i	35.6 d-j	34.4	31
CIP 395112.36 *	31.8 a-f	36.0 b-k	35.7 c-j	34.5	32
CIP 395015.6 *	34.7 a-d	36.3 b-k	35.8 c-j	35.6	33
C200 *	23.1 e-l	42.5 a-g	41.6 a-g	35.7	34
Victoria	28.0 b-f	43.5 a-g	40.5 a-g	37.3	35
CIP 393637.171	18.4 h-o	48.4 a-d	46.0 a-e	37.6	36
CIP 396033.102	30.8 a-g	41.8 a-h	41.9 a-g	38.2	37
CIP 3910141.14	16.7 j-o	50.7 a-b	48.6 a-d	38.7	38
CIP 393382.44	24.9 d-k	50.3 a-c	47.7 a-e	41.0	39
CIP 391046.46	36.8 a-c	43 a-g	44.1 a-g	41.3	40
C80	32.9 a-e	46.4 a-e	45.0 a-f	41.4	41
CIP 395096.2	41.3a	45.5 a-e	45.3 a-f	44.0	42
C62	35.1 ab	52.2 ab	49.8 ab	45.7	43
C281	37.5 ab	53.3 a	51.9 a	47.6	44
Mean	**20.8**	**33.2**	**30.9**	**30.6**	
LSD (0.05)	**11.0**	**16.9**	**13.3**		
CV	**25.7**	**24.7**	**20.8**		
P-value	**0.001**	**0.001**	**0.001**		

rAUDPC = relative area under the disease progress curve; [a] means in a column followed by the same letters are not significantly different at P=0.05, * = Selected as potential parents for crosses

3.3.4 Total tuber weight

Mean total tuber yield is presented in Table 3.5. Genotypes showed significant differences (P≤0.001) for total tuber yield within locations. Genotypes CIP 393371.58 and CIP 391047.34 with TTW of 50.9 t ha^{-1} and 37.3 t ha^{-1}, respectively, were the best yielders, whereas C80 at 7.3 t ha^{-1} and Mabondo (10.1 t ha^{-1}) were the lowest in TTW across locations. At Rwerere, the highest yielder was genotype Kigega, while the lowest was Mabondo (7.8 t ha^{-1}). Genotype Bineza (2.2 t ha^{-1}) and genotype Kinigi (1.6 t ha^{-1}) were the lowest yielders at Kinigi and Nyamagabe respectively. The overall mean for total yield across locations was 24.7 t ha^{-1}. Rwerere with 30.4 t ha^{-1} had the highest total yield, followed by Kinigi (28.9 t ha^{-1}) and Nyamagabe (14.9 t ha^{-1}).

Table 3.5 Total tuber yield in t ha^{-1} of 44 potato genotypes evaluated at three locations in Rwanda

Genotype	Location				
	Kinigi	Nyamagabe	Rwerere	Across locations	
	Mean	Mean	Mean	Mean	class
C80	7.8 l-n	5.5 l-p	8.5 n	7.3	LY
Mabondo	19.2 i-m	3.5 op	7.8 n	10.1	LY
Bineza	2.2 n	10.9 g-o	21.1lm	11.4	LY
C281	14.4 k-n	4.8 m-p	22.6 k-m	13.9	LY
CIP 395096.2*	15.9 k-m	14.4 f-j	18.5 m	16.3	MY
Gikungu *	16.3 i-n	3.3 op	31.8 e-i	17.1	MY
Nyirakabondo *	20.2 i-m	3.9 n-p	27.7 h-k	17.3	MY
Mizero *	6.3 nm	13.9 f-l	35.2 c-h	18.5	MY
CIP 396027.205*	24.1f-k	9.6 i-p	24.0 i-m	19.2	MY
CIP 3910141.14*	29.6 e-j	10.3 h-o	18.5 m	19.5	MY
CIP 393637.171*	17.0 i-n	7.7 i-p	34.4 d-h	19.8	MY
CIP 396004.225*	14.4 k-n	20.0 c-f	29.2 h-k	21.2	MY
Kivu *	36.7 e-k	12.0 f-n	24.8 i-m	21.2	MY
CIP 396034.103*	24.0 f-k	14.8 e-j	25.2 i-m	21.3	MY
CIP 395015.6*	28.5 e-k	10.4 h-o	25.5 i-m	21.5	MY
Nderera *	20.7 hm	3.9 n-p	40.0 cd	21.5	MY
CIP 393382.44*	31.1 e-i	11.0 g-o	23.7 j-m	21.9	MY
Kinigi *	28.1 e-k	1.6 p	37.4 c-f	22.4	MY
Sangema *	23.9 f-k	14.1 f-k	29.6 f-k	22.6	MY
CIP 391046.46*	17.04 i-m	15.9 e-i	36.6 c-g	23.2	MY
C200 *	27.0 e-k	7.0 j-p	36.3 c-g	23.5	MY
CIP 393280.57*	22.2 g-l	20.3 c-f	28.1 g-k	23.6	MY
C62 *	35.5 d-g	5.5 l-p	30.0 f-k	23.7	MY
CIP 396043.226*	26.3 e-k	18.9 c-g	27.7 h-k	24.3	MY
CIP 395112.19*	22.6 g-l	19.6 c-f	31.8 e-i	24.7	MY
CIP 395112.36*	38.8 b-f	14.0 f-k	22.6 k-m	25.2	MY
CIP 395111.13*	20.7 h-m	15.5 e-i	39.2 c-e	25.2	MY
CIP 391058.175*	26.6 e-k	25.9 b-d	25.9 i-m	26.1	MY
CIP 396026.103*	38.1 b-f	19.2 c-g	23.3 k-m	26.9	MY
CIP 393385.39*	35.5 d-g	20.0 c-f	25.9 i-m	27.2	MY
CIP 396033.102*	26.3 e-k	14.4 f-j	41.1 bc	27.3	MY
CIP 396038.107*	41.1 a-e	20.3 c-f	22.2 k-m	27.9	MY
Kirundo *	39.6 b-e	5.9 l-p	40.4 cd	28.6	MY
CIP 396036.201*	36.3 c-g	14.8 e-j	39.3 c-e	30.1	HY
Cruza	48.5 a-d	22.9 c-e	26.3 i-m	32.6	HY
Ngunda *	51.1 a-c	12.4 f-m	35.5 c-h	33	HY
CIP 381381.13*	47.4 a-d	15.5 e-i	40.3 cd	33.4	HY
CIP 393077.54*	36.6 b-g	27.0 bc	37.0 c-g	33.5	HY
Victoria	51.5 ab	15.5 d-h	31.4 d-h	33.8	HY
Kigega *	38.5 b-f	13.1 f-m	50.0 a	33.9	HY
CIP 393280.82*	37.8 b-f	33.3 b	31.5 e-j	34.2	HY
CIP 395111.19*	47.4 ab	18.9 c-g	42.6 a-c	34.4	HY
CIP 391047.34*	41.1 a-c	33.3 b	37.4 c-f	37.3	HY
CIP 393371.58*	55.9 a	48.1 a	48.5 ab	50.9	HY
Mean	**28.9**	**14.9**	**30.4**	**24.7**	
LSD (0.05)	**11**	**8.5**	**12.8**		
CV	**25.1**	**27.4**	**8.0**		
P-value	**0.001**	**0.001**	**0.001**		

HY = high yield; MY = medium yield; LY = low yield, * = selected as potential parents for crosses

[a] means in a column followed by the same letters are not significantly different at P=0.05

3.3.5 Marketable tuber weight

Marketable tuber yield is presented in Table 3.6. There was a significant (P≤0.05) genotype effect for marketable tuber weight across locations. Genotypes CIP 395111.13 and CIP 393371.58 with MTW of 84.7% and 84.3% were the highest in marketable yield, while genotypes Kivu (46.8%) and Bineza (27%) were the lowest across locations. At Kinigi, genotypes 396038.107 (94.3%) and Bineza (0.0%) were the highest and lowest in MTW respectively. At Nyamagabe the highest genotype in MTW was CIP 396038.107 (94.7%) and genotype CIP 3910141.4 (28.7%) being the lowest; whereas at Rwerere the highest and lowest in MTW were Ngunda (92.5%) and Bineza (35.6%), respectively. The overall mean for marketable yield across locations was 65.6%. Rwerere with MTW of 71.3 % had the highest marketable yield, followed by Kinigi (69.9%) and Nyamagabe (55.6%).

Table 3.6 Marketable tuber weight (%) of 44 potato genotypes evaluated at three locations in Rwanda

Genotype	Location			Across locations	
	Kinigi	Nyamagabe	Rwerere		
	Mean	Mean	Mean	Mean	Rank
Bineza	0.0 h	45.3 i-n	35.6 i	27.0	44
CIP 395096.2	38.9 fg	29.1 n	66.6 a-h	44.8	43
Kivu	7.6 a-f	30.4 n	38.4 i	46.8	42
CIP 396036.201	33.0 gh	47.5 h-n	69.9 a-h	50.1	41
Nyirakabondo	43.2 e-g	66.1 b-j	49.8 g-i	53.0	40
C62	45.5 d-g	35.2 mn	85.6 a-d	55.5	39
CIP 393385.39	69.6 a-f	49.1 f-n	51.0 g-i	56.6	38
Victoria	62.1 a-g	46.0 i-n	67.4 b-h	57.6	37
C80	45.5 d-g	70.0 a-g	59.8 d-i	58.4	36
CIP 395015.6	75.3 a-e	35.4 l-n	65.7 b-h	58.8	35
CIP 395112.36	59.7 b-g	60.4 b-k	56.7 f-i	58.9	34
Sangema	84.0 ab	48.0 g-n	46.2 hi	59.4	33
CIP 381381.13	75.9 a-e	43.7 j-n	59.3 e-i	59.6	32
CIP 391046.46	48.1 c-g	61.3 b-k	71.7 a-h	60.4	31
Gikungu	60.3 b-g	56.6 c-l	64.6 b-h	60.5	30
Cruza	64.5 a-g	51.1 f-n	66.6 a-h	60.7	29
Kigega	78.8 a-c	31.6 mn	74.0 a-g	61.5	28
C200	75.6 a-e	42.2 k-n	68.3 a-h	62.1	27
CIP 3910141.14	80.0 a-c	28.7 n	78.0 a-f	62.2	26
Mabondo	58.3 b-g	54.4 d-l	75.7 a-g	62.8	25
CIP 396033.102	77.5 a-d	35.8 l-n	83.8 a-e	65.7	24
CIP 393637.171	70.8 a-f	47.2 h-n	82.0 a-f	66.7	23
C281	76.9 a-d	46.4 i-n	77.5 a-f	66.9	22
CIP 393077.54	86.5 ab	46.7 i-n	68.0 a-h	67.1	21
CIP 396004.225	81.9 ab	30.9 mn	88.5 ab	67.1	20
Kirundo	86.30 ab	67.7 a-i	47.5 hi	67.2	19
CIP 393382.44	75.9 a-e	53.3 e-m	74.5 a-g	67.9	18
CIP 395112.19	82.0 ab	55.5 c-l	66.8 a-h	68.1	17
CIP 393280.57	72.8 a-e	58.5 c-k	75 a-g	68.8	16
CIP 395111.19	76.3 a-d	74.4 a-d	60.8 c-i	70.5	15
Kinigi	73.7 a-e	63.7 b-j	78.2 a-f	71.9	14
CIP 396027.205	76.9 a-d	62.2 b-k	78.1 a-f	72.4	13
CIP 396034.103	75.5 a-e	65.0 b-j	80.8 a-f	73.8	12
CIP 393280.82	76.1 a-g	69.2 a-h	80.1 a-f	75.1	11
Nderera	77.5 a-d	70.4 a-g	79.2 a-f	75.7	10
CIP 396043.226	75.4 a-e	70.5 a-g	84.3 a-e	76.1	9
CIP 396038.107	94.3 a	58.7 b-k	78.3 a-f	77.1	8
CIP 396026.103	81.7 ab	71.2 a-f	79.5 a-f	77.5	7
Mizero	70.7 a-f	77.8 a-c	88.2 a	78.9	6
Ngunda	86.0 ab	63.2 b-k	92.5 a	80.6	5
CIP 391058.175	81.4 ab	80.0 ab	85.8 a-c	82.4	4
CIP 391047.34	87.6 ab	76.5 a-d	86.2 a-c	83.5	3
CIP 393371.58	81.4 ab	89.2 a	82.2 a-f	84.3	2
CIP 395111.13	83.9 ab	80.7 ab	89.6 ab	84.7	1
Mean	**69.9**	**55.6**	**71.3**	**65.6**	
LSD (0.05)	**33.0**	**22.5**	**26.0**		
CV (%)	**22.9**	**19.6**	**17.7**		
P-value	**0.01**	**0.0007**	**0.02**		

[a] means in a column followed by the same letters are not significantly different at P=0.05

3.3.6 Dry matter content

The mean dry matter content of genotypes is summarized in Table 3.7. Genotypes had significant differences (P≤0.05) for dry matter content within locations. Genotypes 396036.201 with dry matter content of 23.3% and C62/Bineza (17.5%) were the highest and lowest in DM across locations, respectively. At Kinigi, genotype Ngunda (20.9%) was the highest in DM and Bineza (7.7%) the lowest. At Nyamagabe the highest in DM was CIP 39112.19 (25.8%) and the lowest was CIP 393637.171 (11.7%). At Rwerere, genotypes 396036.201 (25.1%) and Nderera (16 %) were the highest and lowest in DM, respectively. The average DM was 20.5% across locations. At Nyamagabe genotypes displayed the highest DM of 22.5% among the three locations followed by Rwerere (21.4%) and Kinigi (17.7%).

Table 3.7 Dry matter content (%) of 44 potato genotypes evaluated at three locations in Rwanda

Geneotype	Location				
	Kinigi	Nyamagabe	Rwerere	Across locations	
	DM	DM	DM	DM	Class
Bineza	7.7 f	21.1 a-g	23.6 a-d	17.5	L
C62	15.7 c-e	19.3 f-g	17.5 hi	17.5	L
CIP 393637.17	19.3 a-d	11.7 h	21.7 a-f	17.6	L
Nderera	15.9 b-e	21.2 a-g	16.0 i	17.7	L
CIP 395096.2	15.3 de	18.9 g	19.2 f-i	17.8	L
Mizero	14.9 e	20.4 d-g	20.3 d-h	18.5	L
CIP 395112.36	14.9 e	21.4 a-g	20.1 d-h	18.8	L
CIP 396004.23	15.5 e-g	20.0 b-d	21.7 a-f	19.0	L
CIP 391046.46	16.6 a-e	21.0 a-g	19.9 e-h	19.2	L
CIP 396033.1	15.7 c-e	20.7 c-g	22.3 a-f	19.6	L
Cruza	17.7 a-e	23.5 a-g	18.0 g-i	19.6	L
CIP 393385.39	17.8 a-e	20.9 a-g	20.5 c-h	19.7	L
CIP 393280.82	15.5 c-e	23.4 a-g	20.6 c-h	19.8	L
C281	16.0 b-e	22.3 a-g	21.5 c-g	19.8	L
Kivu	16.8 a-e	22.7 a-g	20.6 c-h	20.0	L
CIP 391014.14 *	19.1 a-e	22.2 a-g	19.4 f-i	20.2	M
Kigega *	17.1 a-e	21.7 a-g	21.6 a-f	20.2	M
CIP 393280.57 *	18.2 a-e	21.8 a-d	21.5 b-g	20.5	M
C200 *	18.0 a-e	22.7 a-g	20.8 c-h	20.5	M
CIP 396038.11 *	18.5 a-e	20.8 b-g	22.5 a-f	20.6	M
CIP 391047.34 *	18.2 a-e	22.7 a-g	21.0 c-h	20.6	M
Kirundo *	18.2 a-c	21.4 a-g	22.6 a-f	20.7	M
Victoria	62.1 a-g	21.5 a-g	21.7 a-f	20.7	M
CIP 395111.13 *	17.1 a-e	24.7 a-e	20.7 c-h	20.8	M
CIP 396043.23 *	17.6 a-e	23.5 a-g	21.7 a-f	20.9	M
Sangema *	19.7 a-c	20.2 d-g	23.3 a-e	21.1	M
CIP 395111.19 *	19.0 a-e	24.6 a-e	19.8 e-h	21.2	M
Gikungu *	18.8 a-c	21.7 a-g	23.1 a-e	21.2	M
CIP 396027.21 *	17.0 a-e	25.1 a-d	21.6 a-f	21.3	M
Kinigi *	18.5 a-c	24.0 a-f	21.2 c-g	21.3	M
C80 *	16.6 a-e	23.6 a-g	24.0 a-c	21.4	M
CIP 395015.6 *	19 a-e	25.1 a-d	20.2 d-h	21.4	M
CIP 396034.1 *	18.0 a-e	24.5 a-e	21.8 a-f	21.5	M
CIP 393371.58 *	18.1 a-e	22.5 a-g	24 a-c	21.6	M
CIP 396026.1 *	19.8 a-c	25.5 a-c	19.9 e-h	21.7	M
Mabondo *	18.5 a-c	24.6 a-e	21.9 a-f	21.7	M
CIP 393382.44 *	19.2 a-e	23.9 a-f	22.3 a-f	21.8	M
CIP 393077.54 *	19.6 a-d	25.5 a-c	21.2 a-g	22.1	M
Nyirakabondo *	20.5 a	21.0 a-g	25.0 ab	22.2	M
CIP 395112.19 *	18.4 a-e	25.8 a	22.7 a-f	22.3	M
CIP 381381.13 *	17.2 a-e	25.1 a-d	24.8 ab	22.4	M
Ngunda *	20.9 a	23.9 a-f	23.0 a-e	22.6	M
CIP 391058.18 *	20.4 a	25.7 ab	23.3 a-e	23.2	H
CIP 396036.2 *	18.9 a-e	24.8 a-e	25.1 a	23.3	H
Mean	**17.7**	**22.5**	**21.4**	**20.5**	
LSD (0.05)	**4.4**	**4.9**	**3.5**		
CV (%)	**11.9**	**10.6**	**8.0**		
P-value	**0.03**	**0.0414**	**0.0289**		

DM = dry matter content; H = High dry matter content; M = medium dry matter content; L = low dry matter content; * = selected as potential parents for crosses; [a] means in a column followed by the same letters are not significantly different at P=0.05

3.3.7 Tuber and flower characteristics

Morphological and horticultural characteristics of the 44 tested genotypes are presented in Table 3.8. There were marked differences on tuber shape among potato genotypes. The tuber shape varied from oblong (24 genotypes); round (8 genotypes), compressed (6 genotypes); long-oblong (genotypes CIP 393077.54 and CIP 395096.2); ovoid (Sangema and Mabondo); irregular (C200) and oval (Bineza). With regards to skin colour, 18 genotypes had red skin; five pink skin (CIP 396033.102, CIP 396034.103, CIP 395112.19 and Victoria) and white skin (21 genotypes). The tuber flesh of the genotypes was predominantly white except 20 genotypes which had yellow fleshed tubers. Nine genotypes (CIP 39111.19, CIP 393280.57, CIP 393385.39, Sangema, Kinigi, Kirundo, Mabondo and Nderera) had deep tuber eyes while the remaining genotypes had shallow eyes. Twenty five genotypes had purple flowers; one genotype (Sangema) had no flower; whereas the 18 remaining genotypes had white flowers. Overall, 22 genotypes produced pollen while the other 22 had either no flower or flowers with sterile stamens.

Table 3.8 Tuber and flower characteristics of 44 potato genotypes evaluated across three locations in Rwanda

Genotype	Characteristics					
	Flower color	Eye depth	Tuber fresh color	Skin color	Tuber shape	Pollen production
CIP 391047.34*	White	Shallow	Yellow	White	Round	Present
CIP 393077.54*	Purple	Shallow	White	White	Long-oblong	Present
CIP 393371.58*	White	Shallow	White	White	Oblong	Present
CIP 393637.171*	White	Shallow	Yellow	White	Oblong	Present
CIP 396033.102*	Purple	Shallow	Yellow	Pink	Oblong	Present
CIP 395111.19*	White	Deep	White	Red	Compressed	Present
CIP 395112.36*	Purple	Shallow	Yellow	Red	Oblong	Present
CIP 393280.57*	Purple	Deep	Yellow	Red	Oblong	Present
CIP 393382.44	White	Shallow	Yellow	Red	Oblong	Absent
CIP 391058.175	White	Shallow	Yellow	White	Oblong	Absent
CIP 395015.6	White	Shallow	White	Red	Oblong	Absent
CIP 395096.2	Purple	Shallow	Yellow	White	Long-oblong	Absent
CIP 393385.39*	Purple	Deep	White	Red	Oblong	Present
CIP 396004.225	Purple	Shallow	White	Red	Oblong	Absent
CIP 396034.103	Purple	Shallow	Yellow	Pink	Oblong	Absent
CIP 396026.103*	White	Shallow	White	Red	Oblong	Present
CIP 393280.82*	Purple	Shallow	Yellow	Red	Oblong	Present
CIP 396027.205	Purple	Shallow	Yellow	Red	Oblong	Absent
CIP 3910141.14	White	Shallow	White	Red	Round	Absent
CIP 396036.201*	Purple	Shallow	Yellow	Red	Oblong	Present
CIP 396043.226	Purple	Shallow	White	Red	Oblong	Absent
CIP 395111.13	White	Shallow	White	Red	Oblong	Absent
CIP 396038.107	Purple	Shallow	White	Pink	Oblong	Absent
CIP 391046.46	Purple	Shallow	White	White	Oblong	Absent
CIP 395112.19	Purple	Shallow	White	Pink	Round	Absent
CIP 381381.13*	White	Shallow	White	White	Oblong	Present
C62*	White	Shallow	Yellow	White	Oblong	Present
C200	Purple	Shallow	White	White	Irregular	Absent
C281*	Purple	Deep	Yellow	White	Flattened	Present
C80	Purple	Shallow	Yellow	Red	Flattened	Absent
Bineza*	White	Shallow	Yellow	White	Oval	Present
Cruza	White	Shallow	White	White	Round	Absent
Gikungu*	Purple	Shallow	Yellow	Red	Oblong	Present
Kigega*	Purple	Shallow	White	White	Round	Present
Kinigi	Purple	Deep	White	Red	Round	Absent
Kirundo*	White	Deep	White	Red	Round	Present
Kivu	White	Shallow	Yellow	White	Round	Absent
Mabondo	Purple	Deep	Yellow	White	Ovoid	Absent
Mizero	Purple	Shallow	White	White	Compressed	Absent
Nderera*	White	Deep	White	White	Compressed	Present
Ngunda*	White	Shallow	White	White	Oblong	Present
Nyirakabondo	Purple	Shallow	White	White	Oblong	Absent
Sangema	No flower	Deep	Yellow	White	Ovoid	Absent
Victoria*	Purple	Shallow	White	Pink	Compressed	Present

*= Selected as potential parents for crosses

3.3.8 Correlation between traits

Correlations between the four traits are presented in Table 3.9. Correlation between TTW and rAUDPC was highly significant (p≤0.001) and negative (-0.27) across locations; whereas TTW and MTW had a very significant (p≤0.01) positive correlation at Nyamagabe and across locations, highly significant (p≤0.001) positive correlation at Kinigi, and significant (0.05) at Rwerere. Correlation between rAUDPC and DM was significant and negative at Kinigi and Nyamagabe; whereas correlations between TTW and DM (0.26), MTW and DM (0.38) were significant and positive at Kinigi.

Table 3.9 Phenotypic correlation between traits of 44 potato genotypes tested across three locations in Rwanda

Trait	rAUDPC	TTW	MTW	DM
Kinigi				
rAUDPC	1			
TTW	- 0.11ns	1		
MTW	-0.34**	0.35***	1	
DM	-0.33**	0.26*	0.38***	1
Nyamagabe				
rAUDPC	1			
TTW	- 0.26*	1		
MTW	-0.32**	0.28**	1	
DM	-0.26*	0.18 ns	0.19 ns	1
Rwerere				
rAUDPC	1			
TTW	- 0.26*	1		
MTW	-0.15ns	0.20*	1	
DM	-0.03ns	0.04	-0.08 ns	1
Across locations				
rAUDPC	1			
TTW	- 0.27***	1		
MTW	-0.31***	0.42 **	1	
DM	-0.07 ns	-0.07 ns	0.02 s	1

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; MTW = marketable tuber weight; DM = dry matter content.

3.4 Discussion

The present study evaluated 30 candidate clones from CIP and 14 locally grown potato genotypes across three agro-ecologies in Rwanda to identify suitable parents for breeding. The current potato yield in the country is low (9 t ha^{-1}) and farmers require improved high yielding and late blight resistant potato varieties (Chapter 2). Moreover, other important agronomic, phenotypic and horticultural attributes as well as desirable consumer traits are important considerations in generating a new breeding population. Evaluated genotypes varied significantly in tuber yield, late blight resistance, marketable tuber yield and dry matter content within locations. According to Kaushik et al. (2007) the use of accessions with high yield and resistance to potato late blight as parents in late blight breeding program will be one of the most effective strategies to control the disease and increase yield. Therefore, genotypes identified as potential parents were selected showing high to medium responses for late blight resistance and high yields. Moreover, these genotypes exhibited desirable tuber characteristics and productive flowers for crosses. Mehdi (2008) found that total tuber yield is mainly attributed to higher number of tubers per plant and tuber size, which may explain the positive correlation between TTW and MTW. In general, higher total tuber yield is influenced by a combined genotype and location effect and all other growth and yield attributes (Luthra 2005). In addition, the negative correlation between TTW and rAUDPC indicated that late blight impacts negatively on tuber yield through destruction of foliage and consequent reduction of photosynthetic capacity. Similar results were reported (Dowley et al. 2008; Mantecón 2009) and indicated that late blight negatively impacts on potato yield. Previous studies (Brazil et al. 2002; Kaushik et al. 2007; Muthoni et al. 2013) confirmed that genotypes with good levels of resistance to potato diseases had high tuber yields and are promising candidate parents in a disease breeding program. It is clear that no single approach to a universal control method for late blight will be successful, but the use of host plant resistance is the most effective disease management strategy to control late blight and increase yield without harm to the environment due to overuse of fungicides (Kirk et al. 2005; Tähtjärv et al. 2013). Tuber characteristics included depth of eyes, skin and flesh color and tuber shape which may influence consumer choice. These traits are genetic and the selected parents had shallow eyes and oblong to round shape, which are preferred by consumers in Rwanda (Kabira and Lemaga 2006).

Overall, eighteen genotypes (CIP 393371.58, CIP 393637.171, CIP 396033.102, CIP 395112.36, CIP 393280.57, CIP 393385.39, CIP 396026.103, CIP 393280.82, CIP 396036.201, CIP 393077.54, CIP 391047.34, CIP 39111.19, CIP 381381.13, Ngunda, Kigega, Kirundo, Nderera and Gikungu) were selected showing positive combinations of

quantitative and qualitative traits such as late blight resistance, high tuber yield, marketable tuber yield, dry matter content, fertility and desirable tuber characteristic such as shallow eyes and oblong to round shape. This implies that breeding efforts in Rwanda should use the above selected parents. However, the best eight selected genotypes as promising parents for subsequent crosses and selection toward the development and release of new varieties for Rwanda were, CIP 391047.34, CIP 393385.39, CIP 393280.82, CIP 396036.201, Gikungu, Ngunda, Kigega and Nderera. Further studies to determine quality characteristics such as postharvest storage and processing aspects are also required. These quality characteristics are important for the marketing and processing industries and are essential criteria for quality product developments and to meet consumer requirements.

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4 CHAPTER IV: ASSESSMENT OF GENETIC RELATIONSHIP AMONG POTATO GENOTYPES GROWN IN RWANDA USING SSR MARKERS

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Abstract

Evaluation of genetic relationship and divergence is important for an efficient choice of parents for breeding and strategic conservation. The objective of this study was to determine genetic relationship among Rwandan potato genotypes using thirteen selected polymorphic simple sequence repeat (SSR) markers to identify suitable parents for breeding. The thirteen SSR primers identified 84 alleles across all genotypes. The number of alleles per locus ranged from 3 to 10 with an average was 6.5. The polymorphic information content (PIC) of loci ranged from 0.51 to 0.85 with an average of 0.71. Heterozygosity (He) varied from 0.59 to 0.86 with an average of 0.75. Significant positive correlations were detected between PIC and He (r= 0.99), PIC and number of alleles (r=0.76) and, He and number of alleles (r=0.80). The genetic distance between clones ranged from 0.44 to 0.93 and the average was 0.75. Overall the SSR analysis provided five different genetic clusters of the potato clones useful for breeding.

Keywords: Polymorphic information content, potato, Rwanda, SSR markers

4.1 Introduction

Potato (*Solanum tuberosum* L., 2n=4x=48) is a food security crop globally and ranks third after wheat and rice (Haverkort et al., 2009). In Rwanda, potato is the second major food crop after cassava (FAOSTAT, 2013) and its importance is expanding (ISAR, 2008). Lack of high yielding and late blight disease resistant varieties are among the major limiting factors to potato productivity in Rwanda (FAO, 2008; ISAR, 2008).

Genetic analysis using phenotypic or molecular makers helps to determine the variations present among genetic resources for breeding and strategic conservation. Genetic diversity analysis in potatoes is therefore required to identify complementary and unrelated parents to limit genetic depression and to ensure genetic variation for sustained potato improvement (Tarn et al., 1992, Spooner et al., 2007). Potato is a highly heterozygous crop and commercially grown through vegetative reproduction or tubers (Bradshaw, 2007). Microsatellites or simple sequence repeats (SSR) DNA markers have been used in determining potato genetic diversity, genetic structure, and classification (Spooner et al., 2007); tracing germplasm migrations (Rios et al., 2007); fingerprinting (Provan et al., 1996; Schneider and Douches, 1997; Moisan-Thiery et al., 2005); genetic linkage mapping (Feingold et al., 2005); establishment of core collections (Ghislain et al., 2006) and investigations of duplicate collections across gene banks (Del Rio et al., 2006). The SSR markers are currently the most powerful tools to study genetic relationships because they are easy to handle, inherited in a co-domimant fashion, multiallelic and highly polymorphic even among closely related cultivars, due to mutations causing variations in the number of repeating units (Spooner et al., 2005).

Potato breeders use various methods to select the best parents for making crosses and to select progenies from recombined parents such as the use of pedigree information, phenotypic performance for specific traits, adaptability and yield stability, and designed crosses using various mating designs. Further, genetic distance estimates using molecular markers are helpful to identify the best parents for new pedigrees (Acquaah, 2007). Chapter 3 identified suitable clones with high yield and disease resistance using local and introduced genetic resources from the international potato centre (CIP). Consequently, eighteen potato clones were recently selected showing genetic complementarities for yield and late bight resistance useful in the development of farmers-preferred potato varieties in the country. These clones were systematically characterized using phenotypic traits indicating their suitability and genetic differences for breeding (Chapter 3). In light of this, the objective of this study was to determine the genetic relationship among the eighteen selected Rwandese potato clones to identify parents for a breeding programme.

4.2 Materials and methods

4.2.1 Plant materials

The study used eighteen potato genotypes showing high to medium responses for late blight resistance and high yields; thirteen advanced clones were acquired from CIP and five were local varieties widely grown in Rwanda (Muhinyuza et al., 2014). The details of the germplasm are described in Table 4.1.

Table 4.1 List and sources of potato genotypes used in the study

No	Genotypes	Source	Population	Year of release	Yield (t ha^{-1})	rAUDPC (%)
1	CIP 391047.34	CIP	B3C1	Not yet released	37.4	24.1
2	CIP 393077.54	CIP	B3C1	Not yet released	33.5	29.6
3	CIP 393371.58	CIP	B3C1	Not yet released	50.9	21.6
4	CIP 393637.171	CIP	-	Not yet released	19.8	37.6
5	CIP 396033.102	CIP	B2C2	Not yet released	27.3	38.2
6	CIP 395111.19	CIP	-	Not yet released	34.4	14.3
7	CIP 395112.36	CIP	B3C2	Not yet released	25.2	34.5
8	CIP 393280.57	CIP	B3C1	Not yet released	23.6	9.3
9	CIP 393385.39	CIP	-	Not yet released	27.2	30.1
10	CIP 396026.103	CIP	B3C2	Not yet released	26.9	33.9
11	CIP 393280.82	CIP	B3C2	Not yet released	34.2	12.5
12	CIP 396036.201	CIP	-	Not yet released	30.1	33.5
13	CIP 381381.13	CIP	-	Not yet released	33.4	29.8
14	Gikungu	Rwanda		1992	17.1	11.1
15	Kigega	Rwanda		1992	33.9	18.8
16	Kirundo	Rwanda		1983	28.6	27.6
17	Nderera	Rwanda		1992	21.5	25.4
18	Ngunda	Rwanda		1992	33	19.4

CIP=International potato center; rAUDPC = relative area under the disease progress curve

4.2.2 DNA extraction and genotyping

4.2.2.1 DNA sampling

DNA samples were collected from four week old plants, using Whatman FTA cards. Samples were collected from fresh young leaves of ten plants per genotype. Each sampled leaf per plant was immediately placed on the FTA card and pressed using a pair of pliers until both sides of the FTA paper were soaked with the sap (Ndunguru et al., 2005). Ethanol (70%) was used to clean the pliers between sampling to prevent cross contamination. The FTA cards were dried at room temperature.

4.2.2.2 SSR analysis

Samples on the FTA cards from the 18 genotypes were analyzed at the INCOTEC-PROTEIOS laboratory in South Africa (Incotec, SA Pty. Ltd. South Africa). All the samples from each genotype were used in bulked amplification, using DNA extracted from the 10 bulked punches from each FTA card per genotype. Thirteen SSR markers selected from the linkage group of potato and using their high polymorphic information content (PIC) (Ghislain et al., 2004; Feingold et al., 2005; Ghislain et al., 2009; Rocha, 2010) were used in this study. Seven of them belong to the latest potato genetic identity (PGI) kit (Ghislain et al., 2009) while the others were identified from other studies and selected based on high PIC (Ghislain et al., 2004; Feingold et al., 2005; Ghislain et al., 2009; Rocha, 2010). The PCR products were fluorescently labeled and separated by capillary electrophoresis on an ABI 3130 automatic sequencer (Applied Biosystems, Johannesburg, South Africa). The SSR marker alleles were scored for presence or absence of the band for all the 18 potato genotypes. Each amplified fragment was considered as one locus. The genetic similarity matrix of the 18 potato genotypes was calculated using the Jaccard's coefficient (Anderberg, 1973).

4.2.3 Data analysis

Microsatellite data analysis was performed using GeneMapper 4.1 for genotyping. The program GGT 2.0 (Van Berloo, 2007) was used to calculate the Euclidian distances between bulked samples, the matrix of the genetic distances were used to create an unweighted pair group method with arithmetic mean (UPGMA) dendrogram of the results. The polymorphic information content (PIC), is a measure of allelic diversity and was calculated as $PIC = 1 - \Sigma(pi^2)$, where pi is the frequency of i^{th} allele detected in all individuals of the populations (Nei, 1973; Rafalski et al., 1996). Pearson's correlation coefficients showing pair-wise association between PIC, He and number of alleles were calculated using Genstat statistical package,

14th edition (Payne et al., 2011). Further a dendrogram was constructed by UPGMA method using phenotypic data on yield and late blight resistance responses of genotypes (Muhinyuza et al., 2014) using Genstat statistical package 14th edition (Payne et al., 2011).

4.3 Results

The thirteen SSR primers identified 84 alleles across all the eighteen potato genotypes clones. The average number of alleles per locus ranged from 3 to 10 and the average was 6.5 (Table 4.2). The PIC estimated for all loci ranged from 0.85 (STM 0037) to 0.51 (STM1049) with an average of 0.71. These results indicate that the selected microsatellites are very informative in genetically distinguishing the test genotypes. Heterozygosity (He) is a measure of allelic diversity at a locus. The expected heterozygosity values varied from 0.59 to 0.86 with an average of 0.75 (Table 4.2). Significant and positive correlations were found between PIC and He ($r=0.99$, $P<0.001$), PIC and number of alleles ($r=0.86$, $P<0.001$) and, He and number of alleles ($r=0.88$, $P<0.001$) (Table 4.3). The dendrogram constructed using the UPGMA clustering algorithm based on SSR data matrices grouped the potato genotypes into five major clusters (Figure 4.1). Cluster I consisted of clone CIP 393357.58 standing alone. Cluster II composed of six genotypes: four CIP clones (CIP 393637.171, CIP 393385.39, CIP 396026.103 and CIP 395112.36) and two local varieties (Nderera, and Gikungu). Cluster III allocated five CIP clones (CIP 396033.102, CIP 393280.82, CIP 391047.34, CIP 396036.201 and CIP 393077.54) representing 38.5% the CIP clones. This shows the genetic similarity among potato clones sourced from CIP. Cluster IV included three genotypes: two CIP clones (CIP 39111.19 and CIP 381381.13) and one local variety (Kirundo). Cluster V consisted of two local varieties (Ngunda and Kigega) (Fig. 4.1). The genetic distance between clones ranged from 0.44 to 0.93 (Table 4.4). The shortest genetic distance (0.44) was found between Ngunda and Kigega whereas the highest distance at (0.93) was identified between clone CIP 393357.58 and Ngunda. Among the 18 genotypes, clone CIP 393357.58 was the least genetically related to the other genotypes, followed by CIP 395112.36 and CIP 381381.13 (Fig. 4.1). Overall, results showed that the thirteen microsatellite markers clearly distinguished all the eighteen potato genotypes.

Table 4.2 SSR fragment size standard for each SSR marker, allelic information, PIC and He values of the 13 SSR loci used to 18 genotypes

NO	Marker name	Repeat	Primer sequences (5'-3') Forward-Reverse	No of alleles	Allele Size (bp)	PIC	He	PGI Kit
1	STM0030	Compound(GT/GC)(GT)n	AGAGATCGATGTAAAACACGT GTGGCATTTTGATGGATT	8	140-185	0.7977	0.8218	Yes
2	STM1104	(TCT)n	TGATTCTCTTGCCTACTGTAATCG CAAAGTGGTGTGAAGCTGTGA	6	177-201	0.6713	0.7161	Yes
3	STI0023	(CAG)n	GCGAATGACAGGACAAGAGG TGCCACTGCTACCATAACCA	6	160-220	0.6780	0.7279	No
4	STI0036	(AC)n(TC)imp	GGACTGGCTGACCATGAACT TTACAGGAAATGCAAACTTCG	10	127-157	0.8461	0.8615	No
5	STM5127	(TCT)n	TTCAAGAATAGGCAAAACCA CTTTTTCTGACTGAGTTGCCTC	9	253-298	0.7724	0.8004	Yes
6	STM1052	(AT)nGT(AT)n(GT)n	CAATTTCGTTTTTTCATGTGACAC ATGGCGTAATTTGATTTAATACGTAA	5	220-240	0.5792	0.6154	Yes
7	STM2013	(TCTA)n	TTCGGAATTACCCTCTGCC AAAAAAAGAACGCGCACG	5	155-190	0.7466	0.7822	No
8	STI046	(GAT)n	CAGAGGATGCTGATGGACCT GGAGCAGTTGAGGGCTTCTT	9	195-229	0.8420	0.8582	No
9	STM1049	(ATA)n	CTACCAGTTTGTTGATTGTGGTG AGGGACTTTAATTTGTTGGACG	4	195-215	0.5101	0.5944	No
10	STM0037	(TC)n(AC)nAA(AC)n(AT)n	AATTTAACTTAGAAGATTAGTCTC ATTTGGTTGGGTATGATA	10	80-110	0.847	0.8619	Yes
11	STM1106	(ATT)n	TCCAGCTGATTGGTTAGGTTG ATGCGAATCTACTCGTCATGG	3	170-180	0.5707	0.6465	Yes
12	STI0012	(ATT)n	GAAGCGACTTCCAAAATCAGA AAAGGGAGGAATAGAAACCAAAA	6	182-215	0.7864	0.8120	Yes
13	ST WAX-2	(ACTC)n	CCCATAATACTGTCGATGAGCA GAATGTAGGGAAACATGCATGA	3	235-265	0.5848	0.6593	No
		Mean		**6.5**		**0.71**	**0.75**	

PIC= polymorphic information content**,** He: Heterozygosity, bp: base pairs

Table 4.3 Correlation coefficients showing pair-wise association between polymorphic information content (PIC), heterozygosity (He) and number of alleles

	PIC	He
PIC	-	
He	0.99***	-
Number of alleles	0.86***	0.88***

******* = significant at P≤0.001, PIC = polymorphic information content (PIC), He: heterozygosity.

Table 4.4 Jaccard's similarity matrix of 18 potato genotypes analyzed using 13 SSR markers

Genotypes*	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	Ngunda	Kigega	Kirundo	Nderera	Gikungu
C1																		
C2	0.83																	
C3	0.71	0.86																
C4	0.79	0.86	0.69															
C5	0.83	0.83	0.79	0.92														
C6	0.77	0.54	0.77	0.64	0.82													
C7	0.75	0.75	0.69	0.69	0.73	0.55												
C8	0.85	0.77	0.62	0.75	0.91	0.60	0.70											
C9	0.85	0.77	0.69	0.75	0.92	0.75	0.56	0.64										
C10	0.77	0.77	0.71	0.83	0.64	0.73	0.75	0.75	0.58									
C11	0.85	0.77	0.62	0.75	0.64	0.64	0.64	0.55	0.73	0.55								
C12	0.86	0.86	0.77	0.82	0.67	0.82	0.91	0.73	0.90	0.83	0.55							
C13	0.85	0.83	0.77	0.92	0.73	0.70	0.67	0.78	0.90	0.75	0.73	0.70						
Ngunda	**0.93**	**0.93**	0.85	0.91	0.67	0.90	0.80	0.90	0.90	0.82	0.73	0.78	0.67					
Kigega	0.85	0.92	0.69	0.83	0.45	0.82	0.56	0.80	0.78	0.82	0.70	0.70	0.67	**0.44**				
Kirundo	0.85	0.85	0.86	0.73	0.64	0.64	0.83	0.82	0.92	0.83	0.75	0.60	0.64	0.82	0.83			
Nderera	0.85	0.69	0.86	0.75	0.64	0.55	0.55	0.82	0.82	0.83	0.75	0.70	0.70	0.73	0.64	0.60		
Gikungu	0.85	0.85	0.79	0.67	0.82	0.60	0.64	0.60	0.83	0.82	0.83	0.83	0.70	0.80	0.73	0.64	0.55	

* C1: CIP 391047.34; C2: CIP 393077.54; C3: CIP 39371.58; C4: CIP 3937.171; C5: CIP 3960.102; C6: CIP 395111.19; C7: CIP 395112.36; C8: CIP 39280.57; C9: CIP 393385.39; C10: CIP 396026.103; C11: CIP 39280.82; C12: CIP 396036.201; C13: CIP 381381.13

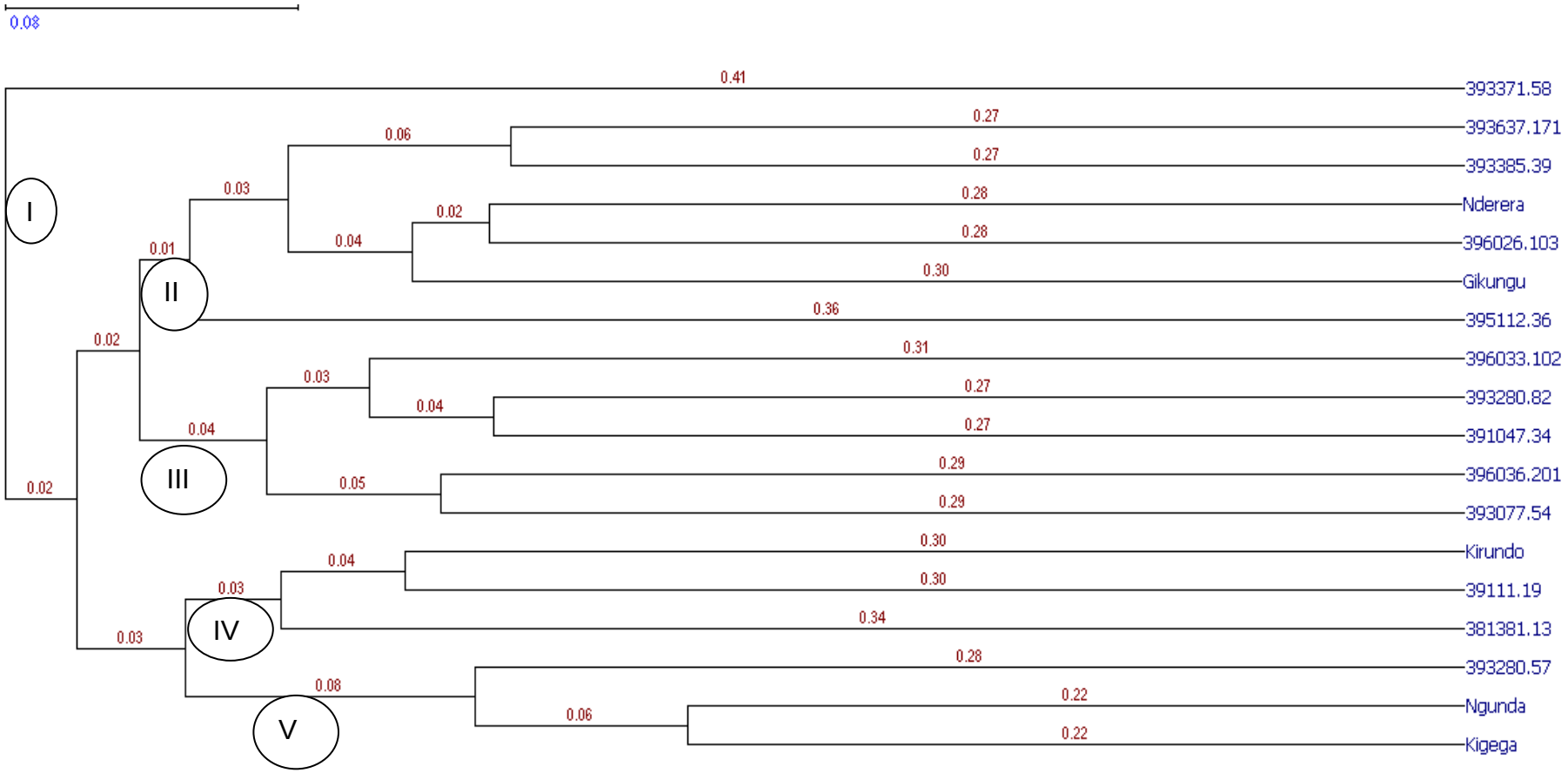

Figure 4.1 Dendrogram showing genetic relationship among 18 potato genotypes using 13 SSR markers generated by UPGMA. The four clusters among the genotypes are denoted from I to V.

4.4 Discussion

Precise identification of genetic relationship and divergence of genetic resources is a useful tool for an efficient choice of parents for breeding and genetic conservation strategies. Further, genetic diversity analysis is useful to estimate genetic distance of germplasm pool. This will assist in minimizing the use of closely related parents in breeding which would otherwise lead to genetic depression and reduced genetic variation. The current study was therefore carried out to establish genetic relationship among the selected eighteen potato clones to identify appropriate parents for hybridization. In this study microsatellite markers were used for potato genetic identification because of their high genetic information content, high reproducibility, and simplicity to use (Powell et al., 1996; Jones et al., 1997). Moreover, they are appropriate, cost-effective and simple tools for laboratories in developing countries with financial constraints. The results revealed high polymorphism levels among 18 potato genotypes. According to Coombs et al. (2004) and Ghislain et al. (2006), polymorphism level is usually high for potato cultivars because potato is inherently heterozygous and essentially tretrapoid. Significant variation of genetic distance among genotypes indicated the presence of genetic variability among the selected potato genotypes. The dendrogram generated from the genotypic data grouped clone CIP 393371.58 in a single cluster, making it the least genetically related genotype. They also elucidated the presence of genetic similarity among CIP clones. Two local varieties Ngunda and Kigega showed also genetic similarity among them due probably to closely related parents in breeding. Their crosses would otherwise lead to genetic depression and reduced genetic variation in their progenies.

4.5 Conclusion

The DNA-based genotyping using simple sequence repeats have been shown to discriminate between tetraploid potato genotypes. There is considerable genetic variability among selected potato genotypes which is useful for potato breeding in Rwanda. The SSR genetic markers were useful and provided five distinct genetic groups enabling breeders to design targeted crosses for hybrid development to exploit heterosis, and maintain genetic diversity.

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5 CHAPTER V: COMBINING ABILITY ANALYSIS OF YIELD AND LATE BLIGHT RESISTANCE OF POTATO IN RWANDA

Abstract

In an attempt to develop potato cultivars with improved tuber yield and late blight resistance ten potato genotypes were selected from available germplasm in Rwanda. The objectives of this study were to estimate combining ability effects for yield, yield related traits and late blight resistance and to estimate heterosis for these triats in potato. Crosses were performed using a 10 x 10 half- diallel mating design to generate 45 F_1s. Only 28 families with sufficient individuals and the eight parents were evaluated in experiments laid out in a 6 × 6 lattice design with two replications across two sites (Kinigi and Nyamagabe) in Rwanda. Late blight resistance was estimated using the relative area under the disease progress curve (rAUDPC: 100 % max). Furthermore, data on total tuber yield, total tuber number, and average tuber weight were collected and subjected to analyses. Results showed that additive and non-additive gene actions were present affecting yield and late blight resistance in potato. Additive was predominant over non-additive gene action for both traits. All the families and their F_1s progenies selected for further evaluation had high levels of late blight resistance and high yields. The study identified ten top families with high tuber yield and resistance to late blight across two sites for further clonal evaluation and release.

Keywords: Combining ability, gene action, late blight, potato, Rwanda

5.1 Introduction

Potato (*Solanum tuberosum* L.) is a staple food crop grown in 149 countries across the world (Hijmans, 2001). It is one of the four most important food crops along with rice (*Oryza sativa*), wheat (*Triticum aestivum* L.), and maize (*Zea mays* L.) (Lang, 2001).

Potato breeding towards the development of new cultivars involves sexual recombination to generate genetic variation and select novel recombinants for agro-morphological traits (Acquaah, 2007). Segregating F_1 progeny from which to select superior clones contains suitable genetic constitution from its parents. It is important to understand the mode of gene action involved in the expression of important traits. Understanding gene action will help in selecting suitable parents and segregates in a breeding programme (Falconer and Mackay, 1996).

Combining ability and heterosis analyses are the bases for identification of the best parents and their crosses (Mondal and Hossain, 2006). The general combining ability (GCA) gives an indication on the average contribution of a parent to its progeny; it provides an estimation of the parental gametic contribution to its offspring by the mean performance of the progeny (Bradshaw and Mackay, 1994; Falconer and Mackay, 1996). The specific combining ability (SCA) is the deviation from the progeny mean from the expected on the basis of GCA (Bradshaw and Mackay, 1994). In this case, the performance of the progeny is either superior or inferior to the parents. Yield and disease resistance are quantitatively inherited (Falconer and Mackay, 1996). In quantitative inheritance many genes are involved, each contributing a small effect to the phenotypic expression of the character concerned. In the literature, it has been reported that both GCA and SCA effects are significant for potato yield and late blight resistance with slight differences in magnitude across experiments (Bradshaw and Mackay, 1994; Gopal et al., 2008).

Potato genotypes with relatively high yield level and resistance to the late blight disease are being developed by the International Potato Centre (CIP) (Landeo et al., 1997). These genotypes are frequently introduced to developing countries including Rwanda to strengthen the existing potato genetic resources to boost productivity and control potato late blight disease. Subsequently, the national potato programme of the Rwanda Agriculture Board (RAB) is continuously evaluating and screening the CIP genetic stocks and locally adapted genotypes under target growing environmental conditions to identify clones with high yield and late blight resistance. Consequently, a number of best genotypes were identified to be used as parents in subsequent crosses and selection (Chapters 3 and 4) The objectives of this study were to estimate combining ability effects for yield and yield related traits and late

blight resistance and to estimate heterosis in potato. The selected best parental genotypes or families will be used for further breeding or clonal evaluation and release in Rwanda.

5.2 Materials and methods

5.2.1 Study sites

The study was conducted at two sites: Kinigi and Nyamagabe in Rwanda. Crosses to generate potato seeds and the seedling crop were conducted at Kinigi is located in the highlands of volcanic soils at an altitude of 2200 meters above sea level (masl), on longitude of 29º 38' East and latitude 1º 30' South (ISAR, 1987). Annual temperature and rainfall averages at 16ºC and 1480 mm, respectively. Clonal evaluation to determine combining abilities for late blight and tuber yield and its components was conducted at Kinigi and Nyamagabe. Nyamagabe is located in the highlands of Congo/Nile divide in the Southern Agricultural zone at an altitude of 2300 masl on longitude of 29º 33' East and latitude of 1º 33' South (ISAR, 1987) with respective annual rainfall and temperature of 1600 mm and 19 ºC.

5.2.2 Parental materials and crosses

Ten genetically diverse parents were selected and crossed in a 10 x 10 half diallel mating design. Parents were selected based on their good flowering abilities, high to medium yields and acceptable level of resistance to late blight. These parents were CIP 393371.58, CIP 391047.34, CIP 393385.39, CIP 393280.82, CIP 393036.201, Gikungu, Kigega, Nderera, Ngunda and Kirundo (Table 5.1). A booster dose of fertilizer was applied in the form of N_{17}-P_{17}-K_{17} at a rate of 250 kg ha^{-1} at planting. Weeds were controlled by hand as required and no fungicides or pesticide was applied. Controlled hand pollination was performed following emasculation (Aquaah, 2007). At maturity, approximately 40 days after pollination, berries of the same cross were identified, harvested and bulked together, labelled and kept at room temperature for approximately two weeks to ripen. After softening, seeds were manually removed by pressing the berries in a cloth bag. Extracted seeds were washed thoroughly with water and soap, dried and packed in paper envelops for storage until planting time.

Table 5.1 Description of parents used in the crossing block

Genotypes	Source	Yield (t ha^{-1})		Reaction to late blight	Flowering ability and pollen production
		Mean	Class	RAUDPC (%)	
CIP 391047.34	CIP	37.4	HY	24.1	Excellent
CIP 393371.58	CIP	50.9	HY	21.6	Good
CIP 393385.39	CIP	27.2	MY	30.1	Excellent
CIP 393280.82	CIP	34.2	HY	12.5	Excellent
CIP 393036.201	CIP	30.1	HY	33.5	Excellent
Gikungu	Rwanda	17.1	MY	11.1	Excellent
Kigega	Rwanda	33.9	MY	18.8	Excellent
Nderera	Rwanda	21.5	HY	25.4	Excellent
Ngunda	Rwanda	33	HY	19.3	Excellent
Kirundo	Rwanda	28.6	MY	27.6	Good

CIP=International Potato Center; HY = High yield; MY = Medium Yield; rAUDPC = relative area under the disease progress curve.

5.2.3 F1 seedling evaluation trial

A total of 45 crosses were expected from a 10 x 10 half diallel. However, cross combinations involving two parents: Kirundo or clone CIP 393371.58 produced insufficient seeds (<50 seeds per cross) or dropped flowers after fertilization. This was below the required number of seeds of 100 to 250 per family to account for potential germination and transplanting losses and expected genetic assessment. Therefore 17 families were left out and only 28 families included, constituting an 8 x 8 half diallel. A minimum of 100 F_1 seeds per cross was sown on a mixture of compost and sand on raised seed bed. All the seeds collected from each cross constituted F_1 seeds and the individual plants grown from these seeds are F_1 seedling plants. Sixty seedlings randomly selected from each cross were grown separately in the field to produce F_1 tubers. The selected seedlings were grown separately in the field, without replications (Hahn et al., 1979; Ceballos et al., 2004).

5.2.4 Clonal I evaluation trial

Each of the selected seedling plant represented a clone. The 28 F_1 populations were grown along with parents in a 6 x 6 lattice design with two replications. During the long rainy season between February and June 2013, a total of 40 plants per plot per family were planted in two rows of 20 plants each. The spacing was (0.9 x 0.3) m between and within rows, respectively, providing a population density of 38 000 plants ha^{-1}. The plot area was 5.4 m^2. For each evaluation, spreader rows of a susceptible cultivar 'Victoria' were included in each plot and around each replication.

5.2.5 Pathogen preparation and inoculation

Potato leaflets with young late blight lesions were collected from infested plants and transferred to the laboratory for isolation of *Phytophthora infestans*. Newly infected leaflets were collected in a plastic envelope and immediately transferred in the laboratory and washed with distilled water. Each leaflet was washed in distilled water and placed in a sterile glass petri-dish with sterile filter paper moistened with distilled water. The petri-dishes were incubated at 20°C for 24 hours to allow the fungus on the leaflet to sporulate.

Sporulation media were made of modified rye B agar (Caten et al., 1968) consisting of the filtrate of pre-rinsed rye (*Secale cereale* L.) seeds (100 g. ℓ^{-1}) boiled for 1 hour, de-ionized (di) H_20 added to a final volume of 1.0 ℓ, glucose (7.5 g ℓ^{-1}) , β-sitosterol (0.05 g ℓ^{-1}) and agar (15.0 g ℓ^{-1}). The mycelial/sporangial mat was rinsed in cold (4°C) sterile, distilled water and scraped from the agar plate surface with a rubber policeman. Sporangia were counted with a haemocytometer and the final concentration was adjusted to $1x10^4$ sporangia $m\ell^{-1}$. Sporangial cultures were incubated for 2-3 hours at 4°C to stimulate zoospore release. Plants and soil were thoroughly watered prior to inoculation.

In all experiments, plots were inoculated late in the evening at 6.00 pm using a hand-held sprayer until run off. After inoculation, the trial was watered in the mornings and evenings with approximately eight litres of water per square meter each day using a watering-can in order to improve potato moisture and field humidity to promote sporulation and infection.

5.2.6 Data collection

Data collected included late blight disease reaction, total tuber weight, average tuber weight and number of tubers per plant. Late blight assessment started with the first appearance of the symptoms. Plants were visually rated at 7 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 the 1 to 9 scale devised 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 rAUDPC (%) was used in the analysis of variance. The rAUDPC was calculated using the following formula:

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

In equation 1, T_i is the i^{th} day when an estimation of percent 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.

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.

5.2.7 Data analysis

The analysis of variance (ANOVA) for the traits was done using the GLM procedure of SAS (SAS Institute, 2004). Mean separation was performed using the least significant difference (LSD) procedure at a 5% probability level. Pearson's phenotypic correlation coefficients between the 28 families for each trait were calculated using PROC CORR of SAS (SAS Institute, 2004) to determine trait associations. Separate ANOVA were conducted per location with genotypes as the main effect and later combined ANOVA were calculated across locations after homogeneity of variance test. The diallel analysis was conducted using SAS-05 diallel programme (Zhang et al., 2005) in SAS 8th edition. Griffing's (1956) diallel method 2, model 1 for a fixed model was fitted to estimate the GCA and SCA effects as: $Y_{ij} = \mu + g_i + g_j + b_k + s_{ij} + e_{ijkl}$ where: Y_{ij} = observed value of the cross between parent i and j; μ = overall mean; g_i = GCA effect of parent i; g_j = GCA effect of parent j; s_{ij} = SCA of the cross between parents i and j; b_k= effect of the k^{th} block; e_{ijkl} = experimental error. The relative importance of GCA and SCA effects for each trait was determined according to the

general predicted ratio (GPR) as follows: GCA/SCA = $2MS_{GCA}/(2MS_{GCA}+MS_{SCA})$ (Baker 1978). When the GCA/SCA ratio is greater than 0.5, additive effects are more important than non-additive effects in the inheritance of the concerned trait, whereas if the ratio is smaller than 0.5, dominance effects are more important in the inheritance of the concerned character (Baker, 1978). Heterosis estimates were calculated based on mid-parent (MPH) and better parent (BPH) heterosis (Falconer and Mackay, 1996) according to the following equations: MPH (%) = $100*(F_1-MP)/MP$ where F_1 = mean of the F_1 hybrid performance, and MP = mean of the two parents making the cross. Better parent heterosis (BPH) was calculated as follows: BPH (%) = $100*(F_1-BP)/BP$; Where: BP is better parent = P_1 or P_2 involved in the particular F_1 the cross.

5.3 Results

5.3.1 Analysis of variance

Table 5.2 summarizes the combined analysis of variance for the relative area under the disease progress curve (rAUDPC), total tuber weight (TTW), total tuber number (TTN) and average tuber weight (ATW) among the families. There were very significant differences (P≤0.01) among families for rAUDPC, TTW and ATW. The environmental (site) effect was highly significant (P≤ 0.001) for TTW and TTN, and very significant (P≤0.01) for ATW. The interaction between Families x sites had highly significant (P≤ 0.001) effects on rAUDPC and TTW.

Table 5.2 Combined analysis of variance of potato for late blight resistance, tuber yield and related traits at Kinigi and Nyamagabe in Rwanda

		Mean squares			
Source of variation	**DF**	**rAUDPC**	**TTW**	**TTN**	**ATW**
Families	35	246.8***	61.9***	2.9 NS	133.3**
Sites	1	26 NS	313.9***	46.7***	735.8**
Rep (sites)	2	8.2 NS	5.1 NS	5 NS	9.9 NS
Families x sites	35	87.3***	32.9***	1.9 NS	82.8 NS
Error	70	27.9	9.6	2	53.9
Total	**143**				

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; NS: non-significant p>0.05; DF: degrees of freedom; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight.

5.3.2 Family means within and across locations

Means and ranking of rAUDPC, TTW, TTN and ATW within and across locations are presented in Table 5.3. The mean rAUDPC (= 100 max) across locations indicated that families Gikungu x CIP 391047.34 with disease severity of 8.1% and Kigega x CIP 393036.201 (9.5%) were the most resistant, whereas families Kigega x Ngunda (41%) and Nderera x CIP 393280.82 (34.4%) were the most susceptible. Families Gikungu x CIP 391047.34 and CIP 393280.82 x CIP 391047.34 with TTW of 34.9 t ha^{-1} and 30.4 t ha^{-1}, respectively, were the best yielders, whereas family Gikungu x Nderera at 16.5 t ha^{-1} and Nderera x Ngunda (20.0 t ha^{-1}) were the lowest in TTW across locations. Families Gikungu x CIP 391047.34 with an average of 7.3 in TTN and Gikungu x Nderera (3.8) were the highest and lowest in TTN across locations, respectively. Families Kigega x Gikungu and Ngunda x CIP 393280.82 with ATW of 79.7 g and 77.9 g respectively were the highest in ATW, while families CIP 393036.201 x CIP 393385.39 (53.9) and Gikungu x CIP 393280.82 (55.7 g) were the lowest across locations in ATW. The ranking showed that the 10 most resistant potato families were Gikungu x CIP 391047.34 (rAUDPC of 8.1%), Kigega x CIP 393036.201 (9.5%), Kigega x CIP 393036.82 (10.3%), Gikungu x Ngunda (11.2%), Gikungu x CIP 393385.39 (13.9%), Gikungu x Nderera (14.2%), CIP 393036.201 x CIP 393385.39 (14.7%), CIP 393280.82 x CIP 391047.34 (16.4%), Nderera x CIP 393036.201 (20.4%), Ngunda x CIP 393280.82 (21.1%); while the 10 highest yielding potato families were Gikungu x CIP 391047.34 (34.9 t ha^{-1}), CIP 393280.82 x CIP 391047.34 (30.4 t ha^{-1}), Kigega x CIP 393280.82 (30 t ha^{-1}), Gikungu x Ngunda (29.2 t ha^{-1}), Ngunda x CIP 393280.82 (29.1 t ha^{-1}), Kigega x Gikungu (28.4 t ha^{-1}), Ngunda x CIP 391047.34 (28.4 t ha^{-1}), Kigega x CIP 393036.201 (26.8 t ha^{-1}) and Kigega x Ngunda (26.7 t ha^{-1}). The most resistant potato families were almost the highest yielding ones.

5.3.3 General and specific combining ability variances of potato tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight at Kinigi

General and specific combining ability variances for the four traits at Kinigi are presented in Table 5.4. There were highly significant differences ($P \leq 0.001$) among families for rAUDPC and TTW. GCA was highly significantly ($P<0.001$) different for TTW and significant ($P<0.05$) for ATW. The SCA was highly significantly ($P<0.001$) different for rAUPC and TTW. The ratio GCA/SCA provided an estimate of the relative importance of additive and non-additive gene effects in the expression of the traits assessed. GCA was more important than SCA in the expression of TTW and ATW, whereas the opposite was true for rAUDPC and TTN at Kinigi.

Table 5.3 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 when evaluated at two locations in Rwanda

Families	Traits															
	rAUDPC				TTW (t ha^{-1})				TTN				ATW (g)			
	Kinigi	Nyamagabe	Across locations		Kinigi	Nyamagabe	Across locations		Kinigi	Nyamagabe	Across locations		Kinigi	Nyamagabe	Across locations	
	Mean	Mean	Mean	Rank	Mean	Mean	Mean	Rank	Mean	Mean	Mean	Rank	Mean	Mean	Mean	Rank
Kigega x Gikungu	16.7	28.2	22.5	19	30.3	26.5	28.4	**9**	5	5	5.0	25	83.7	75.6	79.7	**1**
Kigega x Ngunda	39.8	42.1	41.0	36	34.7	18.7	26.7	14	7.5	4.5	6.0	11	63.6	63.9	63.8	27
Kigega x Nderera	18.7	43.2	31.0	**31**	40.2	16.6	28.4	**10**	5.5	3	4.3	32	72.8	67	69.9	9
Kigega x CIP 393036.201	10.1	8.8	9.5	**2**	25.1	28.5	26.8	13	5.5	5	5.3	19	65.3	63.4	64.4	25
Kigega x CIP 393280.82	11.7	8.8	10.3	**3**	33.4	26.5	30.0	**4**	7.5	5	6.3	**6**	73.9	66.6	70.3	7
Kigega x CIP 3910147.34	23.6	19.2	21.4	16	26	17.9	22.0	28	5	3.5	4.3	33	70.6	65.3	68.0	13
Kigega x CIP 393385.39	26.9	29.0	28.0	30	33.7	15.9	24.8	**22**	6	6	6.0	12	73.2	72.4	72.8	**5**
Gikungu x Ngunda	9.2	13.2	11.2	**4**	32.8	25.6	29.2	**6**	5	5	5.0	26	63.5	73.4	68.5	11
Gikungu x Nderera	12.3	16.1	14.2	8	16.9	16	16.5	36	4	3.5	3.8	36	63.3	66.3	64.8	22
Gikungu x CIP 393036.201	32.2	30.2	31.2	32	22.8	17.8	20.3	34	7.5	3.5	5.5	17	60.5	62.7	61.6	31
Gikungu x CIP 393280.82	39.4	15.1	27.3	27	21.7	20.9	21.3	31	5	5.5	5.3	**20**	52.4	58.9	55.7	35
Gikungu x CIP 3910147.34	7.7	8.4	8.1	**1**	35.3	34.4	34.9	**1**	7.5	7	7.3	**1**	60	64.4	62.2	30
Gikungu x CIP 393385.39	13.1	14.6	13.9	**6**	25.6	24.2	24.9	**21**	7	5.5	6.3	**7**	55.7	73.5	64.6	**24**
Ngunda x Nderera	30.7	14.4	22.6	20	27	21.9	24.5	24	7	3.5	5.3	21	60.4	79.9	70.2	**8**
Ngunda x CIP 393036.201	16.7	26.2	21.5	**17**	26.5	24.2	25.4	19	8	5	6.5	**3**	67.1	67.2	67.2	16
Ngunda x CIP 393280.82	12.8	29.3	21.1	15	30.3	27.8	29.1	**7**	5	4.5	4.8	**29**	78.1	77.6	77.9	**3**
Ngunda x CIP 3910147.34	24.6	22.8	23.7	**23**	29.9	26.9	28.4	11	8.5	5	6.8	**2**	53.5	74.4	64.0	26
Ngunda x CIP 393385.39	20.8	32.9	26.9	26	21.3	21.6	21.5	30	6.5	4	5.3	**22**	60.6	73.7	67.2	17
Nderera x CIP 393036.201	18.1	22.7	20.4	14	24.8	28.4	26.6	15	7.5	5	6.3	8	57.2	61.4	59.3	**33**
Nderera x CIP 393280.82	39.3	29.4	34.4	**35**	25.5	26.5	26.0	17	6.5	5	5.8	**13**	57.9	73.1	65.5	**21**
Nderera x CIP 3910147.34	35.2	32.6	33.9	34	20.1	19.8	20.0	**35**	5	4	4.5	31	62	64.5	63.3	29
Nderera x CIP 393385.39	19.9	30.6	25.3	**24**	21.6	20	20.8	32	4	4	4.0	35	77.3	65.7	71.5	**6**
CIP 393036.201 x CIP 393280.82	29.4	17.8	23.6	22	26.0	26	26.0	**18**	7	5.5	6.3	9	62.5	65.1	63.8	28
CIP 393036.201 x CIP 391047.34	27.1	24.2	25.7	25	20.8	20.8	20.8	33	6.5	4	5.3	23	65.7	71.9	68.8	10
CIP 393036.201 x CIP 393385.39	14.5	14.8	14.7	9	26.5	26.5	26.5	16	6	6.5	6.3	10	51.4	56.4	53.9	36
CIP 393032.82 x CIP 391047.34	21.9	10.9	16.4	11	30.4	30.4	30.4	**2**	6	5.5	5.8	14	56.9	72.5	64.7	23
CIP 393032.80 x CIP 393385.39	27.6	36.8	32.2	33	20.4	23.9	22.2	**27**	4	4.5	4.3	34	65.6	70	67.8	**15**
CIP 391047.34 x CIP 393385.39	22.1	21.7	21.9	18	21.9	21.9	21.9	29	6	4	5.0	**27**	58.5	77.3	67.9	14
Parents																
Kigega	17.0	13.4	15.2	10	30.4	30.4	30.4	**3**	6.5	6.5	6.5	4	63.6	73.1	68.4	12
Gikungu	13.9	11.0	12.5	5	27	21.9	24.5	**25**	6	5.5	5.8	**15**	57.5	75.3	66.4	18
Ngunda	19.1	17.6	18.4	13	31.9	26.8	29.4	**5**	6	4.5	5.3	24	72.4	76.9	74.7	4
Nderera	26.2	28.5	27.4	28	28.6	28.6	28.6	8	7	6	6.5	5	63	69	66.0	19
CIP 393036.201	19.0	16.8	17.9	12	24.6	24.6	24.6	23	5.5	5.5	5.5	18	57	64.3	60.7	32
CIP 393280.82	21.2	25.5	23.4	21	29.4	26.1	27.8	12	5	4.5	4.8	30	78.1	79.3	78.7	2
CIP 390147.34	15.8	12.1	14.0	7	25	25	25.0	20	4.5	7	5.8	16	67.4	48.4	57.9	34
CIP 393385.39	19.7	35.7	27.7	29	24.9	22.2	23.6	26	5.5	4.5	5.0	28	63.6	68.3	66.0	20
Mean	**21.5**	**22.4**	**21.9**		**27.2**	**24.2**	**25.7**		**6**	**4.9**	**5.5**		**64.3**	**68.9**	**66.6**	
CV (%)	**28.1**	**19.6**	**24.1**		**10.3**	**13.9**	**12.1**		**30.3**	**18**	**26.3**		**14**	**7.3**	**11**	
S.E.D.	**5.7**	**3.9**	**5.2**		**2.9**	**2.7**	**3.1**		**2**	**0.8**	**1.4**		**10**	**5.4**	**7.3**	

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

Table 5.4 General and specific combining ability variances of potato tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight based on an 8x8 half diallel mating design at Kinigi

Source of variance	Traits				
	DF	rAUDPC	TTW	TTN	ATW
Families	35	148.6***	52.7***	2.8 NS	122.9 NS
GCA	7	29.3 NS	38.8***	0.6 NS	103.4*
SCA	28	85.5***	23.2***	1.7NS	50.9 NS
Error	35	18.4	3.9	1.7	41.0
CV%		28.1	10.3	30.2	14.0
GCA/SCA		0.41	0.77	0.41	0.80

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; NS = non-significant p>0.05; DF: degrees of freedom; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight.

5.3.4 General combining ability effects of potato parents at Kinigi

General combining ability effects of parents at Kinigi are presented in Table 5.5. Parent Kigega had the highest GCA effects for TTW (4.2) and ATW (7.15) followed by parent CIP 391047.34 with TTW (1.1) and ATW (1.42) while parents Nderera with TTW (-2.09) and Gikungu with ATW (-3.27) had the lowest GCA effects for TTW and ATW respectively. Kigega had the lowest GCA effects for rAUDPC (-1.99) followed by parent CIP 393385.39 (-1.93). Gikungu had the highest GCA effects for TTN (0.31) while parent CIP393385.39 (-0.34) had the lowest.

Table 5.5 General combining ability effects of potato parents at Kinigi

Parents	General combining ability effects			
	rAUDPC	TTW	TTN	ATW
Kigega	-1.99*	4.20**	-0.23	7.15**
Gikungu	1.06	-1.70	0.31	-3.27*
Ngunda	2.11**	0.06	0.26	0.18
Nderera	1.32	-2.09*	-0.18	-1.69
CIP 396036.201	-1.57	-0.36	0.06	-1.12
CIP 393280.82	-0.63	-0.84	0.21	-0.65
CIP 391047.34	1.63	1.1	-0.09	1.42
CIP 393385.39	-1.93*	-0.37	-0.34	-2.02

TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; * and ** denote significant differences at p=0.05 and p=0.01, respectively.

5.3.5 Specific combining ability effects of potato families at Kinigi

Table 5.6 summarises specific combining ability effects of potato families at Kinigi. The best and positive SCA effects of 10.22 and 8.75 for TTW traits were recorded in families Gikungu x CIP 393036.201 and Kigega x Ngunda respectively. The lowest SCA effects of -13.32 and -10.70 for rAUDPC were observed in families Gikungu x CIP 393036.201 and Kigega x Nderera respectively.

Table 5.6 Specific combining ability effects of 28 potato families at Kinigi

Families	Specific combining ability effects			
	rAUDPC	TTW	TTN	ATW
Kigega x Gikungu	19.26**	5.01*	1.38*	-4.63
Kigega x Ngunda	-2.89	8.75**	-0.56	1.12
Kigega x Nderera	-10.70**	-4.19*	-0.11	-4.47
Kigega x CIP 393036.201	-6.21*	2.41	1.63	3.52
Kigega x CIP 393280.82	4.70	-4.49*	-0.01	-0.25
Kigega x CIP 3910147.34	5.79*	1.20	0.28	0.33
Kigega x CIP 393385.39	-8.40*	1.78	-0.46	-5.83
Gikungu x Ngunda	7.50*	-2.74*	0.88	-0.72
Gikungu x Nderera	15.49**	-1.63	-1.16	-7.01
Gikungu x CIP 393036.201	-13.32**	10.22**	1.08	0.04
Gikungu x CIP 393280.82	-8.86*	0.96	0.43	-4.74
Gikungu x CIP 3910147.34	6.53*	0.46	0.73	-2.05
Gikungu x CIP 393385.39	-3.91	1.38	1.98*	8.04*
Ngunda x Nderera	-0.35	4.75*	2.38**	-9.36*
Ngunda x CIP 393036.201	-1.22	-5.59**	0.13	-2.76
Ngunda x CIP 393280.82	-4.90	-1.55	0.98	-6.64
Ngunda x CIP 3910147.34	14.09**	-2.80*	0.28	-8.00*
Ngunda x CIP 393385.39	13.54**	-6.78**	-0.96	-0.51
Nderera x CIP 393036.201	8.17*	1.26	1.08	0.95
Nderera x CIP 393280.82	4.89	-3.44*	0.43	3.67
Nderera x CIP 3910147.34	-9.97**	0.30	0.23	-12.64**
Nderera x CIP 393385.39	0.98	5.73**	0.48	-3.75
CIP 393036.201 x CIP 393280.82	2.77	-4.04*	-0.31	-4.08
CIP 393036.201 x CIP 391047.34	-7.69*	2.51*	0.48	-1.05
CIP 393036.201 x CIP 393385.39	-1.03	5.28**	0.23	-3.71
CIP 393032.82 x CIP 391047.34	3.68	1.15	0.83	-2.12
CIP 393032.80 x CIP 393385.39	0.03	-1.37	-0.41	-4.63
CIP 391047.34 x CIP 393385.39	-5.38	-2.92	-1.11	3.70

TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; * and ** denote significant differences at p=0.05 and p=0.01, respectively.

5.3.6 General and specific combining ability variances of potato tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight at Nyamagabe

General and specific combining ability variances of potato tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight at Nyamagabe are presented in Table 5.7. There were highly significant differences (P≤0.001) among families for all the selected traits. GCA was highly significantly different (P<0.001) for rAUDPC, very significant (P<0.01) for TTW and TTN, significant (P<0.05) for ATW. SCA was highly significantly different (P<0.001) for rAUDPC, TTW and ATW, and very significant (P<0.01) for TTN. The GCA/SCA ratio provided an estimate of the relative importance of additive and non-additive gene effects in the expression of the traits assessed. GCA was more important than SCA in the expression of all traits at Nyamagabe.

Table 5.7 General and specific combining ability variances of potato tuber weight, relative area under the disease progress curve, total tuber number and average tuber weight based on an 8x8 half diallel mating design at Nyamagabe

Source of variance	Traits				
	DF	rAUDPC	TTW	TTN	ATW
Families	35	185.5***	42***	2.1***	93.2 ***
GCA	7	101.2***	20.9**	1.2**	29.5*
SCA	28	90.6***	21***	1.0**	50.9 ***
Error	35	9.6	5.7	0.4	12.9
CV%		19.6	13.9	18	7.4
GCA/SCA		0.69	0.66	0.70	0.54

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight.

5.3.7 General combining ability effects of potato parents at Nyamagabe

General combining ability effects of potato parents at Nyamagabe are presented in Table 5.8. Parent CIP 396036.201 had the highest GCA effect (2.25) for TTW followed by parent CIP 391047.34 (0.91) while parent Gikungu (-2.36) had the lowest GCA effects for the same trait. Nderera had the lowest GCA effects for rAUDPC (-2.55) followed by parents CIP 393385.82 (-1.81) and Gikungu (1.79). Parent CIP 391047.34 had the highest GCA effects for TTN while parents Kigega (-0.21) and Gikungu (-0.21) had the lowest. Parents CIP 393280.82 (1.69) and CIP 396036.201 (1.59) had the highest GCA effects for ATW.

Table 5.8 General combining ability effects of potato parents at Nyamagabe

Parents	General combining ability effects			
	rAUDPC	TTW	TTN	ATW
Kigega	1.94*	-1.52*	-0.21	0.35
Gikungu	-1.79*	-2.36*	-0.21	-1.66*
Ngunda	7.13**	-0.47	-0.56*	1.23
Nderera	-2.55*	0.20	0.09	-2.56*
CIP 396036.201	-1.36	2.25*	0.29*	1.59*
CIP 393280.82	-1.81*	0.22	-0.16	1.69*
CIP 391047.34	-1.09	0.91	0.53*	1.11
CIP 393385.39	-0.46	0.77	0.23	-1.75*

TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; * and ** denote significant differences at p=0.05 and p=0.01, respectively.

5.3.8 Specific combining ability effects of 28 potato families at Nyamagabe

Specific combining ability effects of 28 potato families at Nyamagabe are summarised in Table 5.9. The families Gikungu x CIP 393036.201 (10.32) and Kigega x Nderera (5.58) had the best and positive SCA effects for the trait TTW while the families Kigega x CIP 393036.201 (-14.16), Kigega x Nderera (-12.92) and Gikungu x CIP 393036.201(-10.82) had the lowest and negative SCA effects for rAUDPC. Ten potato families with reduced SCA effects of rAUDPC were Kigega x CIP 393036.201 (-14.16), Kigega x Nderera, (-12.92) Gikungu x CIP 393036.201(-10.82), Kigega x CIP 393385.39 (-10.66), CIP 393036.201 x CIP 391047.34 (-8.92), CIP 391047.34 x CIP 393385.39 (-8.67), Nderera x CIP 393385.39 (-8.47), CIP 393036.201 x CIP 393385.39 (7.15), Gikungu x CIP 391047.34 (-5.03) and Ngunda x CIP 393280.82 (-4.94), which is in a desirable direction for resistance breeding.

Table 5.9 Specific combining ability effects of 28 potato families at Nyamagabe

Families	Specific combining ability effects			
	rAUDPC	**TTW**	**TTN**	**ATW**
Kigega x Gikungu	19.58**	-1.60	0.02	-3.67
Kigega x Ngunda	11.75**	-5.59*	-1.12*	-3.41
Kigega x Nderera	-12.92**	5.58*	0.22	-3.22
Kigega x CIP 393036.201	-14.16**	1.53	0.02	-4.17
Kigega x CIP 393280.82	-3.26*	-4.98*	-1.02*	-5.57*
Kigega x CIP 3910147.34	5.78*	-7.67**	0.77	2.06
Kigega x CIP 393385.39	-10.66**	2.11	0.07	5.93*
Gikungu x Ngunda	2.49	-3.55*	-0.62	-5.75*
Gikungu x Nderera	-2.88	-1.12	0.72	-5.71*
Gikungu x CIP 393036.201	-10.82**	10.32**	2.52*	-4.41
Gikungu x CIP 393280.82	-4.12*	2.15	0.97*	4.59*
Gikungu x CIP 3910147.34	-5.03*	-0.83	-1.72*	11.57**
Gikungu x CIP 393385.39	6.13*	1.55	0.07	1.79
Ngunda x Nderera	-4.11*	2.97	0.57	6.91*
Ngunda x CIP 393036.201	4.76*	-4.41*	-0.62	2.01
Ngunda x CIP 393280.82	-4.94*	4.46*	0.82*	-10.35**
Ngunda x CIP 3910147.34	1.04	1.87	0.12	1.88
Ngunda x CIP 393385.39	3.56*	-4.73*	-0.57	-3.85
Nderera x CIP 393036.201	-0.62	-0.68	0.22	-2.80
Nderera x CIP 393280.82	6.18*	-3.85*	-0.82*	3.90
Nderera x CIP 3910147.34	-3.93*	1.15	0.97*	-11.03**
Nderera x CIP 393385.39	-8.47**	5.24*	0.27	7.95*
CIP 393036.201 x CIP 393280.82	2.50	-4.75*	-1.02*	5.20*
CIP 393036.201 x CIP 391047.34	-8.92**	3.05	0.77	1.57
CIP 393036.201 x CIP 393385.39	-7.15**	4.49*	0.07	6.60*
CIP 393032.82 x CIP 391047.34	9.08**	3.23*	0.72	-2.64*
CIP 393032.80 x CIP 393385.39	-3.25	-0.62	0.52	-4.51*
CIP 391047.34 x CIP 393385.39	-8.67**	-0.91	1.32*	-19.79**

TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight; * and ** denote significant differences at p=0.05 and p=0.01, respectively.

5.3.9 Correlation between traits

Correlations between the four traits are presented in Table 5.10. Correlation between TTW and rAUDPC was significant (p≤0.05) and negative (r =-0.39) across locations, and very significant (p≤0.01) and negative (r =-0.52) at Nyamagabe; whereas TTW and TTN had a highly significant (p≤0.001) positive (r =0.66; 0.59) correlation at Nyamagabe and across locations. Correlation between TTN and ATW was significant (p≤0.05) and negative (r =-0.37) at Kinigi; whereas correlation between rAUDPC and TTN was very significant (p≤0.01) and negative (r =-0.47) at Nyamagbe.

Table 5.10 Phenotypic correlation between four traits of 28 potato families tested across two locations in Rwanda

Trait	rAUDPC	TTW	TTN	ATW
Kinigi				
rAUDPC	1			
TTW	- 0.23ns	1		
TTN	0.08ns	0.32ns	1	
ATW	-0.25ns	0.28ns	-0.37*	1
Nyamagabe				
rAUDPC	1			
TTW	- 0.52**	1		
TTN	-0.47**	0.66***	1	
ATW	0.08ns	-0.22 ns	-0.22 ns	1
Across locations				
rAUDPC	1			
TTW	- 0.39*	1		
TTN	-0.25ns	0.59 ***	1	
ATW	0.04 ns	0.12 ns	-0.37*	1

Significance levels: *p≤0.05; ** p≤0.01; ***p≤0.001; NS: Not significant; TTW = total tuber weight; rAUDPC = relative area under the disease progress curve; TTN = total tuber number; ATW= average tuber weight.

5.3.10 Heterosis

The families were ranked based on their mean performance for total tuber yields and resistance to late blight, and on the F_1 heterosis. Ten top families with the highest means on yield and lowest rating for late blight resistance were selected for high tuber yield and resistance to late blight. The F_1 progenies of the selected 10 families were ranked based on the yield performance at Kinigi and Nyamagabe. Total tuber weight (TTW) per clone was measured and expressed in t ha^{-1}. This was calculated as the total weight of all the tubers harvested per clone per plot and converted to t ha^{-1}. After data analysis, clones with yields above 16 t ha^{-1} were selected per site for further evaluations. A total of 58 and 46 top clones were identified at Kinigi and Nyamagabe respectively and their heterosis calculated. Clones MK-79, MK-78 and MK-80 from family Gikungu x CIP 393036.201, exhibited the highest mid-parent heterosis of 36.05, 28.68, and 28.68% and highest best-parent heterosis of 34.44, 27.41, and 27.41%, respectively for total tuber yield at Kinigi. Parents Gikungu and Kigega were part of 20 and 19 progenies respectively out of the 58 clonal progenies while parents CIP 393036.201 and CIP 391047.34 were part of 27 and 12 progenies respectively of the 58 clonal progenies at Kinigi. Families Gikungu x CIP 393036.201, Kigega x Nderera, Kigega x CIP 393036.201, Nderera x CIP 393036.201 and CIP 393280.82 x CIP 391047.34 had 13, 9, 7, 7 and 7 progenies respectively out of 58 clonal progenies at Kinigi (Table 5.11).

Table 5.11 Heterosis for the best 58 F_1 recombinants identified on total tuber yield performance at Kingi

Families	Total tuber yield					
	Clone name	Clone ID	Mean (t ha^{-1})	Rank	MPH%	BPH%
Gikungu x CIP 393036.201	MK-79	4	35.1	1	36.1	34.4
Gikungu x CIP 393036.201	MK-78	3	33.2	2	28.7	27.4
Gikungu x CIP 393036.201	MK-80	7	33.2	3	28.7	27.4
Kigega x Nderera	MK-11	3	32.3	4	9.5	9.2
Gikungu x CIP 393036.201	MK-77	2	30.4	5	17.8	17.0
Kigega x CIP 393036.201	MK-56	4	29.4	6	6.9	6.2
Gikungu x CIP 393036.201	MK-82	10	29.4	7	13.9	13.3
CIP 393280.82 x CIP 391047.34	MK-22	6	28.5	8	4.8	4.4
Kigega x CIP 393036.201	MK-57	5	27.5	9	0.0	0.0
Gikungu x CIP 391047.34	MK-71	1	27.5	10	5.7	5.5
Gikungu x CIP 391047.34	MK-73	4	27.5	11	5.7	5.5
Ngunda x CIP 393280.82	MK-1	3	26.6	12	-13.2	-12.7
Kigega x Nderera	MK-16	12	26.6	13	-9.8	-9.5
Gikungu x CIP 393036.201	MK-84	12	26.6	14	3.1	2.9
Kigega x Nderera	MK-18	17	25.6	15	-13.2	-12.8
CIP 393280.82 x CIP 391047.34	MK-29	18	24.7	16	-9.2	-8.5
Nderera x CIP 393036.201	MK-37	7	24.7	17	-7.1	-6.6
Kigega x CIP 393385.39	MK-49	9	24.7	18	-10.6	-9.7
Gikungu x CIP 393036.201	MK-85	13	24.7	19	-4.2	-4.1
Gikungu x CIP 393036.201	MK-88	16	23.7	20	-8.1	-7.8
Gikungu x CIP 393036.201	MK-89	17	23.7	21	-8.1	-7.8
Gikungu x CIP 393036.201	MK-83	11	22.8	22	-11.6	-11.1
Kigega x Nderera	MK-13	7	22.8	23	-22.7	-22.0
Kigega x CIP 393036.201	MK-64	14	22.8	24	-17.1	-15.4
Ngunda x CIP 393280.82	MK-2	4	21.8	25	-28.8	-27.7
Ngunda x CIP 393280.82	MK-4	8	21.8	26	-28.8	-27.7
CIP 393280.82 x CIP 391047.34	MK-20	2	21.8	27	-19.8	-18.4
Gikungu x CIP 393036.201	MK-76	1	21.8	28	-15.5	-14.8
Gikungu x Ngunda	MK-43	9	20.9	29	-29.0	-26.8
Kigega x CIP 393385.39	MK-48	8	20.9	30	-24.4	-22.2
Kigega x CIP 393036.201	MK-58	6	20.9	31	-24.0	-21.7
Kigega x Nderera	MK-12	4	19.5	32	-33.9	-32.9
Kigega x Nderera	MK-14	8	19.5	33	-33.9	-32.9
Nderera x CIP 393036.201	MK-34	4	19.5	34	-26.7	-24.8
Nderera x CIP 393036.201	MK-41	20	19.5	35	-26.7	-24.8
Gikungu x CIP 393036.201	MK-87	15	19.5	36	-24.4	-23.3
Kigega x Nderera	MK-10	2	19	37	-35.6	-34.5
CIP 393280.82 x CIP 391047.34	MK-21	5	19	38	-30.1	-27.9
CIP 393280.82 x CIP 391047.34	MK-25	11	19	39	-30.1	-27.9
Nderera x CIP 393036.201	MK-31	1	19	40	-28.5	-26.5
Nderera x CIP 393036.201	MK-36	6	19	41	-28.5	-26.5
Kigega x CIP 393036.201	MK-59	7	19	42	-30.9	-27.9
Ngunda x CIP 393280.82	MK-9	19	18	43	-41.3	-39.6
Kigega x Nderera	MK-15	9	18	44	-38.9	-37.8
Nderera x CIP 393036.201	MK-32	2	18	45	-32.3	-30.1
Gikungu x CIP 391047.34	MK-74	5	18	46	-30.7	-29.6
Gikungu x CIP 391047.34	MK-75	10	18	47	-30.7	-29.6
Kigega x Nderera	MK-19	20	17.1	48	-42.0	-40.9
CIP 393280.82 x CIP 391047.34	MK-30	20	17.1	49	-37.1	-34.3
Gikungu x Ngunda	MK-45	13	17.1	50	-41.9	-38.7
Kigega x CIP 393036.201	MK-54	2	17.1	51	-37.8	-34.2
Gikungu x CIP 391047.34	MK-72	2	17.1	52	-34.2	-32.9
Gikungu x CIP 393036.201	MK-81	8	17.1	53	-33.7	-32.2
Ngunda x CIP 393280.82	MK-5	2	16.1	54	-47.5	-45.6
CIP 393280.82 x CIP 391047.34	MK-28	16	16.1	55	-40.8	-37.7
Nderera x CIP 393036.201	MK-35	5	16.1	56	-39.5	-36.7
Kigega x CIP 393036.201	MK-55	3	16.1	57	-41.4	-37.5
Kigega x CIP 393280.82	MK-67	7	16.1	58	-46.1	-45.4

MPH: mid-parent heterosis, BPH: best-parent heterosis

Clones MN-21, MN-31 and MN-41 from the families Kigega x CIP 393385.39, Gikungu x CIP 391047.34 and Gikungu x CIP 393036.201, exhibited the highest mid-parent (160.08, 73.99 and 63.44%) and highest best-parent (125.00, 63.20, and 54.47%) heterosis for total tuber yield respectively at Nyamagabe. Parents Gikungu and Kigega contributed 22 and 14 progenies respectively out of the 46 clonal progenies while parents CIP 393036.201 and CIP 391047.34 contributed 17 and 13 progenies respectively of the 46 clonal progenies at Nyamabage. Families Gikungu x CIP 393036.201 and Gikungu x CIP 391047.34 contributed 11 and, 9 progenies respectively out of 46 clonal progenies at Nyamagabe (Table 5.12).

Table 5.12 Heterosis for the best 46 F_1 recombinants identified based on total tuber yield performance at Nyamagabe

Families	Total tuber yield					
	Clone Name	Clone ID	Mean (t ha^{-1})	Rank	MPH%	BPH%
Kigega x CIP 393385.39	MN-21	17	68.4	1	160.08	125.00
Gikungu x CIP 391047.34	MN-31	7	40.8	2	73.99	63.20
Gikungu x CIP 393036.201	MN-41	4	38	3	63.44	54.47
Gikungu x CIP 391047.34	MN-29	3	32.3	4	37.74	29.20
Gikungu x CIP 393036.201	MN-38	1	31.3	5	34.62	27.24
Gikungu x CIP 393036.201	MN-46	13	31.3	6	34.62	27.24
Gikungu x CIP 391047.34	MN-32	8	28.5	7	21.54	14.00
Gikungu x CIP 391047.34	MN-28	2	27.5	8	17.27	10.00
Kigega x CIP 393385.39	MN-18	1	26.6	9	1.14	-12.50
Gikungu x CIP 391047.34	MN-33	9	25.6	10	9.17	2.40
Gikungu x CIP 391047.34	MN-35	13	24.7	11	5.33	-1.20
Gikungu x CIP 393036.201	MN-44	11	24.7	12	6.24	0.41
Ngunda x CIP 393280.82	MN-1	3	22.8	13	-13.80	-14.93
Ngunda x CIP 393280.82	MN-2	7	22.8	14	-13.80	-14.93
Kigega x Nderera	MN-6	4	22.8	15	-22.71	-25.00
CIP 393280.82 x CIP 391047.34	MN-9	5	22.8	16	-10.76	-12.64
Gikungu x CIP 391047.34	MN-36	18	22.8	17	-2.77	-8.80
Gikungu x Ngunda	MN-16	12	21.8	18	-10.47	-18.66
Gikungu x CIP 391047.34	MN-34	10	21.8	19	-7.04	-12.80
Gikungu x CIP 393036.201	MN-48	16	21.8	20	-6.24	-11.38
Kigega x Nderera	MN-8	17	20.9	21	-29.15	-31.25
Nderera x CIP 393036.201	MN-14	2	20.9	22	-21.43	-26.92
Kigega x CIP 393036.201	MN-23	5	20.9	23	-24.00	-31.25
Gikungu x CIP 391047.34	MN-30	4	20.9	24	-10.87	-16.40
Gikungu x CIP 393036.201	MN-45	12	20.9	25	-10.11	-15.04
CIP 393280.82 x CIP 391047.34	MN-11	7	19.5	26	-23.68	-25.29
Kigega x CIP 393036.201	MN-24	13	19.5	27	-29.09	-35.86
Gikungu x CIP 391047.34	MN-37	20	19.5	28	-16.84	-22.00
Gikungu x CIP 393036.201	MN-39	2	19.5	29	-16.13	-20.73
Gikungu x CIP 393036.201	MN-47	14	19.5	30	-16.13	-20.73
Kigega x CIP 393385.39	MN-19	8	19	31	-27.76	-37.50
Kigega x CIP 393036.201	MN-25	14	19	32	-30.91	-37.50
Kigega x Nderera	MN-4	1	18	33	-38.98	-40.79
CIP 393280.82 x CIP 391047.34	MN-10	6	18	34	-29.55	-31.03
CIP 393280.82 x CIP 391047.34	MN-12	16	18	35	-29.55	-31.03
Kigega x CIP 393280.82	MN-27	17	18	36	-36.28	-40.79
Gikungu x CIP 393036.201	MN-40	3	18	37	-22.58	-15.85
Kigega x Nderera	MN-5	3	17.1	38	-42.03	-43.75
Kigega x Nderera	MN-7	10	17.1	39	-42.03	-43.75
Nderera x CIP 393036.201	MN-15	9	17.1	40	-33.46	-36.19
Kigega x CIP 393385.39	MN-20	10	17.1	41	-34.98	-43.75
Gikungu x CIP 393036.201	MN-42	7	17.1	42	-26.45	-30.49
Gikungu x CIP 393036.201	MN-43	8	17.1	43	-26.45	-30.49
Ngunda x CIP 393280.82	MN-3	18	16.1	44	-39.13	-39.93
CIP 393280.82 x CIP 391047.34	MN-13	19	16.1	45	-36.99	-38.31
Kigega x CIP 393036.201	MN-26	18	16.1	46	-41.45	-47.04

MPH: mid-parent heterosis, BPH: best-parent heterosis

5.4 Discussion

The significant mean squares for families on rAUDPC and TTW indicated the presence of genetic variation among the parents and their crosses. This suggests that genotype resistance to potato late blight and high yield can be selected for. In addition, the significant environment (site) by family effect on the traits observed justifies multi-locational testing of varieties prior to their recommendation and release. 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 GCA to SCA ratios ranged from 0.41-0.80 and 0.54-0.70, respectively at Kinigi and Nyamagabe for tuber yield and yield related traits, indicating that additive gene action was predominant. Contradictory results were reported in the literature. 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; Gopal et al., 2008; Haydar et al., 2009); whereas other authors (Plaisted et al., 1962; Tai, 1976; Killick, 1997; Gopal, 1998) reported GCA to be more important in magnitude than SCA in affecting potato yield. Some authors reported GCA to be significantly greater than SCA for tuber yields and yield related traits in crosses between non-related parents (Neele et al., 1991; Ortiz and Golmirzaie, 2004). This is in agreement with findings in this study. Chapters 3 and 4 identified different and non-related parents used for crosses in the course of this study. The GCA/SCA ratios were 0.41 and 0.69 for rAUDPC at Kinigi and Nyamagabe respectively; indicating that both GCA and SCA are more or less equally important in the expression of late blight resistance in potatoes. This agrees with previous reports on the relative importance of GCA and SCA for potato late blight resistance: both GCA and SCA have been reported to be significant (Bradshaw and Mackay, 1994). This implies both additive and non-additive gene action are important in conditioning resistance to late blight in potato (Bradshaw and Mackay, 1994). Landeo et al. (2000) found additive and non-additive gene action equally important for horizontal resistance. In general, many reports supported the present findings with slight predominance of additive over the non-additive gene action in inheritance of quantitative resistance to late blight (Stewart et al., 1992; Wastie et al., 1993; Kumar et al., 2007).

Studies on family means and the positive correlation between TTW and MTN indicated that TTN had a significant influence on tuber yield in this study. Mehdi (2008) also found similar results where total tuber yield was mainly attributed to higher number of tubers per plant and tuber size. There was a negative correlation between TTN and ATW in this research. Ruiz de Galarreta et al. (2006) found similar results in the first clonal generation. In addition, the negative correlation between TTW and rAUDPC observed in this study indicates that late

blight impacts negatively on tuber yield through destruction of foliage and consequent reduction of photosynthetic capacity. Similar results were reported by others (Dowley et al. 2008; Mantecón 2009) and indicated that late blight negatively impacts on potato yield. The present study corroborated previous studies (Brazil et al. 2002; Kaushik et al. 2007; Muthoni et al. 2013) that genotypes with good levels of resistance to potato diseases have high tuber yields. The families selected for further evaluation had high levels of late blight resistance and high yields.

The best cross combinations were achieved when parents Gikungu, Kigega, CIP 393036.201 and CIP 391047.34 were involved. The first three clones, which exhibited the highest mid- and best-parent heterosis, were progenies from famiy Gikungu x CIP 393036.201 at Kingi and families Kigega x CIP 393385.39, Gikungu x CIP 391047.34 and Gikungu x CIP 393036.201 at Nyamagabe. These families included Gikungu, Kigega, CIP 393036.201 and CIP 391047.34 in their parentage indicating that these parents are the best and were therefore selected for future breeding and evaluation.

5.5 Conclusion

This study found both additive and non-additive gene action being important for high yield and resistance to late blight in potato, with predominance of additive over the non-additive gene action for both traits. Almost all the families and progenies selected for further test had high levels of late blight resistance, high yields and high F_1 heterosis. Overall, ten top families were selected including Gikungu x CIP 391047.34, Giukungu x CIP 393036.201, Kigega x CIP 393036.201, Kigega x CIP 393280.82, Gikungu x CIP 393385.39, CIP 393280.82 x CIP 391047.34, Nderera x CIP 393036.201, Ngunda x CIP 393280.82, Ngunda x CIP 391047.34, Gikungu x Ngunda expressing high tuber yield and resistance to late blight. Also 58 and 46 top clones were identified at Kinigi and Nyamagabe respectively for further evaluation and variety release in Rwanda.

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6 CHAPTER VI: OVERVIEW OF THE STUDY

6.1 Introduction

Potato *(Solanum tuberosum* L.*)* is an important source of food globally. In Rwanda, potato is the second major food crop after cassava and it is also an important cash crop for growers and traders. Potato grows well throughout Rwanda but the major production is localised in the high altitude zones. The productivity of the crop is low due to various biotic, abiotic and socio-economic constraints. Among the abiotic constraints, late blight disease caused by *Phytophthora infestans* (Mont.) de Bary is considered to be the major challenge preventing the full genetic expression of the crop. High yielding, late blight resistant and farmers-preferred potato varieties and their production technologies should be developed and made available to growers to enhance production and to achieve food security in Rwanda. This study focused therefore on pre-breeding experiments to identify high yielding and late blight potato resistant varieties with farmers' preferred traits that could increase potato production in Rwanda. The current chapter is intended to summarise the research objectives and highlights the core findings of the study and their implications for potato breeding for high yields and resistance to late blight.

The objectives of the study were as follows:

The main objective of this study was to evaluate new and existing potato genotypes based on their yield and resistance to late blight, select genotypes with good performance for the two traits that can be used as parents to develop high yielding potato clones in Rwanda. The specific objectives were:

(i) To identify and analyse farmer's key constraints in potato production, and establish farmers' preferred traits to be included in cultivar development in Rwanda.
(ii) To determine yield response and late blight reaction of potato genotypes in Rwanda to identify suitable parents for breeding.
(iii) To assess genetic relationship among potato genotypes grown in Rwanda using SSR markers.
(iv) To estimate combining ability and heterosis for potato late blight resistance and yield.
(v) To select the best potato clones for further evaluation and release.

6.2 Summary of major findings

6.2.1 Participatory assessment of potato production constraints and trait preferences in potato cultivar development in Rwanda

A participatory rural appraisal (PRA) study was conducted through structured survey involving 144 households and 22 focus groups with 258 participants in three major potato growing districts of Rwanda. The results of this study were the following:

- Potato was identified as the most important food and cash crop in the study areas.
- The most important biotic potato production constraint was late blight disease caused by *Phytopthtora infestans* Mont A. de Barrry.
- Unavailability of high yielding potato cultivars, insufficient clean seeds and lack of production inputs were also among the major potato production constraints in the concerned agriculture zones covered by the study.
- High yield, late blight resistance were the most important attributes to potato varieties preferred by farmers.

6.2.2 Yield response and late blight reaction of potato genotypes in Rwanda

A total of 44 potato genotypes were evaluated in the field using an 11 x 4 alpha lattice design with two replications under three environments of Rwanda. The outcomes were as follows:

- Potato genotypes had significant differences on late blight resistance and yield levels among test locations.
- Potato genotypes showed different late blight reactions
- Different yield levels were also observed and potato genotypes were grouped into high yielders, moderate yielders and low yielders.
- Eighteen genotypes: CIP 393371.58, CIP 393637.171, CIP 396033.102, CIP 395112.36, CIP 393280.57, CIP 393385.39, CIP 396026.103, CIP 393280.82, CIP 396036.201, CIP 393077.54, CIP 391047.34, CIP 39111.19, CIP 381381.13, Ngunda, Kigega, Kirundo, Nderera and Gikungu were selected showing positive combinations of late blight resistance, high tuber yield and productive flowers.
- This implies that breeding efforts in Rwanda should use the above selected parents

6.2.3 Assessment of genetic relationship among promising potato clones in Rwanda using SSR markers

A study on genetic relationship and divergence among 18 potato genotypes was conducted using 13 simple sequence repeat (SSR) markers for an efficient choice of parents for breeding and conservation. The study revealed that:

- The thirteen SSR primers identified 84 alleles across all genotypes and the number of alleles per locus ranged from 3 to 10 with an average of 6.5.
- The SSR analysis provided five different genetic clusters with clone CIP 393357.58 being a singleton, which was the least genetically related to the other genotypes.
- The genetic distance between clones ranged from 0.44 to 0.93 and the highest distance was observed between clone CIP 393357.58 and Ngunda.
- Ten different genotypes: CIP 393357.58, CIP 391047.34, CIP 393385.39, CIP 393280.82, and CIP 393036.201, Gikungu, Kigega, Nderera, Ngunda and Kirundo were identified as parents for further crosses.

6.2.4 Combining ability analysis of yield and late blight resistance of potato in Rwanda

Crosses were performed using a 10 x 10 half diallel mating design to generate 45 F_1s. Only 28 families with sufficient tubers and the eight parents were evaluated in experiments laid out in a 6 × 6 lattice design with two replications across two sites (Kinigi and Nyamagabe) in Rwanda. The outcomes were the following:

- Five parents: Gikungu, Kigega, CIP 393036.201, CIP 391047.34 and Nderera were identified as the best combiners for high yield and resistance to potato late blight. These parents were selected for future crosses.
- Moreover, ten families expressing high tuber yield and resistance to late blight were Gikungu x CIP 391047.34, Giukungu x CIP 393036.201, Kigega x CIP 393036.201, Kigega x CIP 393280.82, Gikungu x CIP 393385.39, CIP 393280.82 x CIP 391047.34, Nderera x CIP 393036.201, Ngunda x CIP 393280.82, Ngunda x CIP 391047.34 and Gikungu x Ngunda.
- These families were selected for further evaluation.
- In addition 58 and 46 promising clones were identified at Kinigi and Nyamagabe respectively for further clonal evaluation and variety release in Rwanda.

6.3 Breeding implications and the way forward

- Farmers' participation in potato varietal selection and identification of breeding priorities is critical for better dissemination and adoption of improved varieties. Their inputs will be integrated in the potato breeding programme in Rwanda.
- There is considerable genetic variability for potato tuber yield and late blight resistance among selected potato genotypes useful for potato breeding in Rwanda.
- The SSR genetic markers were useful and provided five distinct genetic groups enabling breeders to design targeted crosses for hybrid development to exploit heterosis, and maintain genetic diversity.
- The importance of both additive and non-additive effects in controlling potato tuber yield, late blight resistance and other agronomic traits suggested that breeding gain can be achieved through hybridization and selection in Rwanda potato breeding programme.
- Overall, the current study identified valuable potato genotypes with high combining ability for late blight resistance and tuber yield from which new high yielding and late blight resistance clones can be selected for future release as cultivars in Rwanda. These can be evaluated in similar agro-ecologies in sub-Saharan Africa.