Genetic Variability in Potato (*Solanum tuberosum* L.) Genotypes for Late blight [*Phytophthora infestans* (Mont.) de Bary] Resistance and Yield at Haramaya, Eastern Ethiopia

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Abstract: Late blight (*Phytophthora infestans* de Bary) is the most important and destructive disease of potato (*Solanum tuberosum* L). The pathogen has the ability to rapidly evolve and overcome resistance genes, leading commercial potato varieties to succumb to it too soon. As a result, evaluation of commercial potato varieties for resistance should not be a one-time task, but a routine breeding activity. This study was, therefore, conducted to determine the genetic variability of potato varieties in terms of resistance to the late blight disease and yield potential during the 2013/14 cropping season under natural epiphytotic conditions. A total of 21 potato genotypes (Alemaya 624, Araarsaa, Belete, Bubu, Bulle, Chala, Chiro, CIP-384321/3A, CIP-384321/3B, Gabbisa, Gera, Gorebela, Guasa, Gudanie, Jalanie, Jarso, Mara Charre, Moti, and Zemen) were evaluated using a randomized complete block design (RCBD) with three replications. The genotypes showed highly significant ($P < 0.01$) differences in reaction to the disease (disease intensity, severity, score and AUDPC) and yield potential. Only three varieties (Bubu, Belete and Bulle) were found to be resistant to the disease, with other three varieties (Gera, Araarsaa, and Mara Charre) being moderately resistant. The remaining 15 varieties (Al-624, Badhasa, Batte, Chala, Chiro, CIP-384321/3A, CIP-384321/3B, Gabbisa, Gorebela, Guasa, Gudanie, Jalenie, Jarso, Moti, and Zemen) were found to be susceptible to the disease. The highest marketable tuber yields ranging from 32.89 to 35.85 t ha^{-1} were recorded for Bubu, CIP-384321/3A, CIP-384321/3B, and Gudanie whilst the lowest marketable tuber yields ranging from 5.04 to 11.85 t ha^{-1} were recorded for Batte, Guasa, Jarso, Moti and Zemen. The marketable tuber yields of the other varietis lay variably in the intermediate ranges. High broad sense heritability (H^2) (47.78 to 91.02%) and genetic advance in percent mean (GAM) (58.87 to 96.31%) were computed for both disease and yield parameters. High genotypic and phenotypic variances were recorded with low magnitude of differences for all parameters, and the environmental variance was much lower than the two other variances. Strong and positive genotypic and phenotypic correlations were observed among the disease score parameters and unmarketable tuber yield while strong and negative correlations were observed between disease score and the two yield parameters (total and marketable tuber yields). This indicated that the traits are highly heritable with the involvement of more additive gene action and are amenable for selection. The dendrogram of the 21 potato genotypes using Unweighted Pair-group Method with Arithmetic means (UPGMA) analysis and Euclidean distances separated the genotypes into three clusters and four sub-groups where resistant and moderately resistant varieties with high yield potential were grouped into Cluster I (Belete, Bubu, Gera, Mara Charre, and Bulle) while Gudanie, CIP-384321/3-A, and CIP-384321/3-B were grouped into Cluster II. All susceptible and low yielding genotypes were grouped into Cluster III. The resistant varieties were found to be the most distant from many of the genotypes but were closer to each other. However, genetic similarities were observed among the susceptible genotypes. In conclusion, the results of the study have revealed that the potato varieties markedly varied in resistance to the late blight disease as well as in yield potential. The genetic variability and the high heritability, coupled with high genetic gain of the traits, indicate the potential of improving the crop for disease resistance and yield through selection. The results have also demonstrated that farmers could profitably cultivate the resistant and moderately resistant high-yielding potato varieties under rain-fed conditions with limited integrated management efforts against the disease.

Keywords: AUDPC (Area under Disease Progress Curve); Broad sense heritability; Euclidean distance; Genetic distance; Genetic variability; Varieties

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1. Introduction

Potato (*Solanum tuberosum* L.) is one of the most widely grown food crops after the three cereals viz., maize, rice and wheat (Vleeshouwers *et al*., 2011). In Eastern Africa, potato is the best crop for food and nutrition security where food security is a key priority for the over 200 million people whose number is predicted to double by 2030 (Kyamanywa *et al.,* 2011). Under such increasing pressure on the fixed land, increasingly degraded environment, and uncertainties resulting from climate change, producing crops like potato with high plasticity to environmental regimes and higher yield per unit area is indispensable. However, existing climate change may also increase the risk of epidemic disease development for potato production particularly of late blight of potato which may result in yield reductions (Baker *et al*., 2005; Hijmans, 2003).

Late blight [*Phytophthora infestans* (Mont.) de Bary] affects all parts of the crop and can destroy a potato field within a few days (Razukas *et al*., 2008). Late blight is not only the most serious fungal disease, but it also occurs almost everywhere where potatoes are grown and is especially important in the traditional potato growing areas. If not controlled, losses may reach 100 percent (Rubio-Covarrubias *et al*., 2005) and even lower infection levels may make the crop unfit for storage (Henfling, 1987). In the highlands of Ethiopia, late blight and bacteria wilt (*Ralstonia solanacearum*) are the most important potato diseases that cause an estimated yield loss of up to 70% (Mekonen *et al*., 2011).

Host resistance is the best control measure as compared to fungicidal sprays since the latter is expensive while the former is more economical and environmentally sustainable. Potato breeding for resistance to late blight has been going on worldwide for several decades. Despite this effort, the majority of commercially grown potato varieties succumb to late blight too soon. In the early 1900s, potato breeders successfully introgressed resistance from wild species (*Solanum demissum* Lindl.) into the cultivated potato. However, this major gene resistance was quickly overcome by *P. infestans* (Wastie, 1991). Subsequently, a total of 11 major dominant resistance genes (*R* genes) were identified, but these genes have been defeated by *P. infestans*. Even so, there is some evidence that they may be useful when combined with other sources of resistance (Stewart *et al.,* 2003).

In Ethiopia, 30 potato varieties have been released by the research system since 1987; however, a considerable number of the varieties have become susceptible to late blight and, hence, gone out of production (Gebremedhin, 2013).

However, no attempt has yet been made to assess the variability of potato varieties released in the country for resistance to late blight. The varieties are merely described as resistant or moderately resistant in the variety registry books (issued by the Ministry of Agriculture) as observed at the time of the release. This is because i) the varieties were tested for late blight resistance and released by different research centers at different times for different agroecological areas of the country; ii) the varieties may not show differential resistance for they carry different R-genes which confer resistance in the absence of virulent races of the pathogen and environment favourable to the pathogen; iii) each center maintains a portion of the released varieties for its geographic area; iv) centers are located at different agro-ecologies which may not equally favor all races at the same cropping season or v) there may be a race change, i.e., the presence of A2 type of the pathogen because this race is dispersed worldwide and not restricted to the temperate region (Drenth *et al*., 1995, Goodwin *et al*., 1995).

Researchers in Ethiopia obtained the germplasm for selection in the form of advanced clones, tuber families, and true potato seed. The variations were generated by crossing different genotypes and selfing the heterozygotes at International Potato Center (CIP) in Peru. (Gebremedhin *et al*., 2008). Most of the potato varieties that have been released before 2008 possess genes for either vertical resistance or horizontal resistance to late blight in the presence of unknown resistance major R genes (Gebremedhin, 2013). Earlier genetic analyses demonstrated that 11 known R genes introgressed from *Solanum demissum* (Black *et al*., 1953). The clustering of functional genes for qualitative and quantitative resistance to various pathogens suggests their evolution from common ancestors by local gene duplication, followed by functional diversification (Gebhardt and Valkonen, 2001; Oberhagemann *et al*., 1999; Leister *et al*., 1996; Leonards-Schippers *et al*., 1994).

Therefore, varieties released in Ethiopia for different agroecologies at different periods, carrying different genes for resistance and tested at different environments, are expected to have wide genetic variations. However, genetic variability study has not yet been conducted to estimate the extent of the variations and genetic distance among the released potato varieties in the country.

In addition, the late blight disease of potato has mutable features so that it can overpass any resistance. When limited potato cultivars are used for resistance, the disease can violate large potato cultivar groups in different years. As a result, potato cultivars described as resistant to *Phytophtora infestans* today might no longer be resistant to the disease in subsequent season (Song *et al*., 2003). Therefore, analyzing the late blight resistance helps not only to determine differences in disease development among various susceptible potato cultivars, but also to find differences in the same potato cultivar every separate research year (Razukas *et al*., 2008). A group of scientists have opinioned that it is necessary to apply a few methods for potato cultivars evaluation for susceptibility to the late blight such as testing of all cultivars in areas where the environment favors the pathogen (Lee *et al*., 2001). Therefore, it is believed that potatoes meant for breeding programs have to be tested not only under field conditions with the natural late blight infection, but also in the

laboratory by making artificial infection settings (Asakaviciute *et al.,* 2006; Razukas and Jundulas, 2005). This is because, in the case of selection for stress conditions, the genotype x environment interaction is of basic importance and the breeder is greatly challenged. Therefore, for stress conditions, direct selection is more effective in the same environment than selection for the mean of both favorable and unfavorable environments (Kirigwi *et al*., 2004; Cecarelli *et al*., 1998; Calhoun *et al*., 1994). Specifically, it is better to conduct studies on genetic variability of potatoes for late blight resistance in one environment where conditions favor the pathogen. Potato late blight occurs when meteorological conditions are suitable (Hansen *et al*., 2005). Therefore, this study was conducted to determine the degree of resistance to late blight by potato varieties released in Ethiopia and to elucidate their genetic variability in terms of resistance to the disease and yield potential.

2. Materials and Methods

2.1. Description of the Study Site

A field experiment was conducted under rain-fed condition during the 2013/14 main cropping season at the research field of Haramaya University on the main campus. The research site is located at 9 °26' N latitude, 42 °3' E longitude and at an altitude of 2022 meters above sea level. The mean annual rainfall is 760 mm (Belay *et al*., 1998). The mean maximum and minimum annual temperatures are 23.4°C and 8.5°C, respectively (Tekalign Tsegaw, 2011). The mean relative humidity is 50%, varying from 20 to 81%. The soil of the experimental site is a well-drained deep alluvial soil with a sub-soil stratified with loam and sandy loam (Tamire Hawando, 1973). The soil has pH of 8.0, organic carbon, total nitrogen, available phosphorus, and exchangeable potassium contents of 1.15%, 0.11%, 18.2 mg kg $soil^{-1}$, 0.65 $cmol_c$ kg $soil^{-1}$, respectively (Simret Burga, 2010).

2.2. Experimental Materials and Design

A total of 21 potato genotypes i.e. seven potato varieties, which were released by Haramaya University at different times for eastern Ethiopia, 10 potato varieties, which were released by different Research Centers for different agroecologies of the country, two farmers' local cultivars susceptible to late blight and two genotypes which are under yield trial, were used for the experiment (Table 1). The two farmers' local cultivars (Jarso and Batte), which are susceptible to late blight, were used as control plants. The oldest or the first released variety (Al-624) in the country and recently released variety (Moti) were considered as having one and more than one resistant genes (R-genes), respectively, which were used to compare other varieties with the oldest and most recently released ones. Other varieties are under cultivation throughout the country and they were evaluated as resistant and moderately resistant to late blight at the time of their release in different years.

The experiment was laid out as a Randomized Complete Block Design (RCBD) where each genotype was replicated three times. Each plot was 3.60 m x 4.50 m (16.2 m^2) consisting of six rows, that contained a total of 12 plants per row and 72 plants per plot. The spacing between plots and adjacent replications were 1.0 and 1.5 m, respectively.

Medium-sized and well sprouted potato tubers were planted at the spacing of 75 cm between rows and 30 cm between plants. All agronomic practices were applied as per the recommendation made by the Haramaya University for the region.

Table 1. Name, accession code, year of release, and yield potential under researchers' and farmers' management practices, maintainer center of potato varieties and recommended growing altitude.

No.	Variety or genotype	Accession code	Year of release	Yield (t/ha)		Breeding Center	Recommended Altitude (meters above sea level)
1	Moti	KP-90147-41	2012	4.27-7.98	3.35-6.496	Sinnana Research Center	2350-3350
2	Bubu	CIP-384321-3	2011	39-42	35-39	Haramaya University	1700-2000
3	Belete	CIP-393371.58	2009	47.2	28-33.8	Holeta Research Center	1600-2800
4	Araarsaa	CIP-90138.12	2006	20-42	37-50	Sinnana Research Center	2400-3350
5	Gudanie	CIP-386423.13	2006	29.0	21	Holeta Research Center	1600-2800
6	Mara Charre	CIP-389701-3	2005	33.3	28.4	Hwassa Research Center	1700-2700
7	Gabbisa	CIP-3870-96-11	2005	40.0	31	Haramaya University	1700-2000
8	Bulle	CIP-387224-25	2005	39.3	38.3	Haramaya University	1700-2000
9	Chala	CIP-387412-2	2005	42.0	35	Haramaya University	1700-2000
10	Gera	KP-90134.2	2003	25.9	-----	Sheno Research Center	2700-3200
11	Jalanie	CIP-37792-5	2002	40.3	29.10	Holeta Research Center	1600-2800
12	Guasa	CIP-384321.9	2002	24.4-33.0	22-25	Adet Research Center	2000-2800
13	Gorebela	CIP-382173.12	2002	30-52	26-30	Sheno Research Center	1700-2400
14	Badhasa	AL-114	2001	40.6	-----	Haramaya University	2400-3350
15	Zemen	AL-105	2001	37.2	-----	Haramaya University	1700-2000
16	Chiro	AL-111	1998	32-40	25-35	Haramaya University	2700-3200
17	Alemaya 624	Al-624	1987	-----	-----	Haramaya University	1700-2400
18	Batte	Local cultivar	-----	-----	-----	East Hararghe	
19	Jarso	Local cultivar	-----	-----	-----	East Hararghe	
20	CIP-384321/3A		-----	-----	-----	Under yield trial	
21	CIP-384321/3B		-----	-----	-----	Under yield trial	

Source: MoA, 2013 and 2012. Varieties with initial AL are the old potato genotypes (before 1987) maintained by Haramaya University; varieties with initial CIP are materials introduced from International Center for Potato, Peru after the first release of potato varieties in the country (1987) and varieties with KP initial are introductions other than from CIP.

Table 2. Assessment of late blight severity under field conditions (%) (Henfling, 1987).

Phytophthora infestans (%)		
Average	Boundaries	Symptoms
0	0	*P. infestans* not observed
2.5	Trace < 5	*P. infestans* present. Maximum 10 injuries per plant
10	5 < 15	Plants seem to be healthy, but injuries can be easily observed. There are no more than 20 affected leaves
25	15< 35	*P. infestans* is easily observed on the plants. About 25% of the leaf area is affected.
50	35< 65	Plants look green, but each one is affected by the pathogen, lower leaves are necrotic. About 50% of the leaf area is destroyed.
75	65< 85	Plants look green with brown spots. About 75% of the leaf area is affected. Leaves in the middle of the plant are destroyed
90	85< 95	Only upper leaves are green. Most of leaves are affected and many stems have external injuries
97.5	95< 100	Plants look brown, a few upper leaves are green and most of the stems are affected or dead
100		Leaves and stems are destroyed

2.3. Data Collection and Analysis

2.3.1. Disease Assessment and Yield Data Collection

Disease assessment began on 30 August 2013, i.e., 46 days after planting as soon as disease symptoms appeared on susceptible genotypes and then was carried out every 20 days until the majority of the genotypes attained physiological maturity. Disease incidence and intensity were assessed following CIP (2006) guideline and other established procedures described below. Area under the Disease Progress Curve (AUDPC) was also calculated from disease intensity recorded at different fixed date intervals. Disease assessment was done by the same three evaluators without knowing the value given at the previous reading.

The total tuber yield of each genotype was taken from plants in the four middle rows. Tubers were carefully collected after the hills were dug by hand. The collected total tubers in each plot were weighted and converted to tons per hectare. Tubers which were free from diseases, insect pests, and greater than or equal to 20 g in weight were sorted, and weighed for each plot and considered marketable. The remaining tubers (diseased, insect-attacked, and small-sized, i.e. < 20 g) were considered unmarketable.

Assessment of the severity of late blight under field conditions in percent was recorded on a plot basis taking into account the number of plants developing disease symptoms in a leaf and/or many leaves and plants free from disease following the procedures of Henfling (1987).

Disease intensity (percent severity index) was recorded on the basis of the percentage of leaf area affected by late blight and calculated for each disease assessment as follows.

$$\text{Late blight intensity \%} = \frac{\text{Summation of numerical rating}}{\text{No. plants examined} \times \text{Maximum disease score}} \times 100$$

The intensity of foliar blight that was expressed in percent of the infected leaf area was used for the disease rating scale as suggested by Mohan and Thind (1999). Depending on the final record of disease intensity (%), the genotypes were classified as resistant, moderately resistant, and susceptible as per the scale (Anonymous, 1997) (Table 3).

The area under disease progress curve value (AUDPC) was calculated using the following formula (Campbell and Madden, 1990) and it was interpreted directly without transformation as the higher the AUDPC, the more susceptible is the genotype (CIP, 2006).

$$\text{AUDPC} = \sum_{i=1}^{n-1}\left(\frac{y_i + y_i + 1}{2}\right)\left(t_{i+1} - t_i\right)$$

Where "t" is the time of each reading, "y" is the percent of affected foliage at each reading and "n" is the number of readings. The variable "t" can represent Julian days, days after planting.

Table 3. Disease score and description, intensity (%), and resistance category.

Disease Score	Score description in terms of foliage infected (%)	Disease intensity (%)	Category
0	No visible symptoms	Up to 5	Highly Resistant
1	1-10	5-20	Resistant
2	11-25	21-40	Moderately Resistant
3	26-50	Above 40	Susceptible
4	51-75		
5	>75		

2.3.2. Data Analysis

Data forAUDPC, disease score, severity, and intensity and yield parameters were subjected to analysis of variance (ANOVA). Least significant difference (LSD) test at 5% probability was used to compare means. The phenotypic and genotypic variance and coefficients of variation were estimated according to the methods suggested by Burton and Devane (1953). Heritability (H^2) in broad sense was computed using the formula adopted by Allard (1960) and Falconer and Mackay (1996) as: $H^2 = [\sigma^2g/ \sigma^2p] \times 100$, where, σ^2g=genotypic variance, σ^2p= phenotypic varianceand σ^2e= error variance. Genetic advance (GA) for each trait was computed using the formula adopted by Johnson *et al*., (1955) and Allard (1960) as:

$GA = (k)(\sigma^2p) * (H^2)$, and GA (as % of the mean) $= \left[\frac{(GA)}{X}\right] x100$

Where, k= selection differential (k=2.06 and 1.76 at 5% and 10%, respectively, selection intensity),σ^2p= phenotypicstandard deviation, H^2= heritability in broad sense andx=grand mean. Phenotypic and genotypic correlations between tuber yield and genotype resistance traits were estimated using the method described by Miller *et al.* (1958).

Genetic distance of genotypes was estimated using Euclidean distance (ED) calculated from the seven disease score and yield traits of the 21 potato genotypes after standardization (subtracting the mean value and dividing it by the standard deviation) as established by Sneath and Sokal (1973) as follows:

$$EDjk = \sqrt{\sum_{i=1}^{n}\left(Xij - Xik\right)^{2}}^{2}$$

Where, EDjk = distance between clones j and k; xij and xik= disease score and yield traits mean values of the ith character for genotypes j and k, respectively; and n= number of traits used to calculate the distance. The distance matrix from disease score and yield traits was used to construct dendrograms based on the Unweighted Pair-group Method with Arithmetic means (UPGMA). The results of the cluster analysis were presented in the form of dendrogram. In addition, mean average distance (ED) was calculated for each genotype by averaging the distance of a particular potato genotype over the other 20 genotypes. The calculated average distance was used to estimate which potato genotype is closest or distant to the others.

3. Results

3.1. Analysis of Variance and Mean Performance of Genotypes

Analysis of variance computed for seven late blight disease score and tuber yield parameters of the 21 potato genotypes is presented in Table 4. The analysis of variance indicated highly significant (P<0.01) variation among genotypes for all traits. The disease severity computed for each evaluation day and the last evaluation ranged from 14 to 100% (Table 6). The two farmers' cultivars (Batte and Jarso) and the two released varieties; Chiro and Zemen (old varieties, released in 1998 and 2001 next to the first released variety) were evaluated as the most susceptible genotypes with 100% disease severity. The lowest disease severity (14%) was recorded for three varieties, namely, Bubu, Belete, and Bulle of which the former two were released as recently as in 2011 and 2009 while the third variety was released in 2005. Disease severity for the other three varieties, namely, Gera, Mara Charre and Araarsaa was calculated as 29% (Table 6).

Table 4. Mean squares from analysis of variance (ANOVA) for yield and late blight as evaluated in 2013/14 cropping seasons at Haramaya.

Traits	Replication (2)	Genotype (20)	Error (40)	SE	CV (%)
Disease severity (%)	213.27	2145.98**	68.32	8.27	16.4
Disease intensity (%)	169.44	2142.90**	73.61	7.01	16.1
Disease score	0.4286	3.83**	0.312	0.56	16.8
AUDPC	135887	2148278**	73263	270.70	20.5
TTY t ha^{-1}	69.99	212.50**	23.05	4.80	20.3
MTY t ha^{-1}	68.06	269.72**	20.06	4.48	22.5
UNMTY t ha^{-1}	0.464	9.629**	1.571	1.60	23.2

*** =Significant at P<0.01; numbers in parenthesis indicates degrees of freedom; SE= standard error; CV (%)= coefficient of variation in percent;AUDPC= area under the disease progress curve; TTY t ha^{-1} = total tuber yield tons per hectare; MTY t ha^{-1} = marketable tuber yield tons per hectare; UNMTY t ha^{-1} = unmarketable tuber yield tons per hectare.*

Table 5. Mean disease severity, score, AUDPC and tuber yield (t ha^{-1}) of 21 potato genotypes as evaluated in 2013/14 cropping season at Haramaya.

Genotype	Disease severity (%)	Disease score	AUDPC	TTY t ha^{-1}	MTY t ha^{-1}	UNMTY t ha^{-1}
Moti	51cd	3bc	1788de	9.48i	5.04k	4.44bcde
Bubu	13hi	2c	225j	35.56ab	33.48ab	2.07ef
Belete	13hi	2c	225j	28.74bcd	27.26bc	1.48f
Araarsaa	27fgh	3bc	507ij	24.3def	22.81cde	1.48f
Gudanie	40def	3bc	704ghi	38.52a	35.85a	2.67def
Mara Charre	30efg	2c	736ghi	25.18de	20.15cdefg	5.04abcd
Gabbisa	50cd	3bc	1146fg	21.93defg	14.81fghij	7.11a
Bulle	10i	1cd	125j	25.78de	21.63cdef	4.15bcde
Chala	70b	4b	1955cd	26.07de	22.52cde	3.56def
Gera	25gh	2c	544hij	28.44bcd	24.59cd	3.85cdef
Jalanie	62bc	4b	1535def	16.59fghi	13.33ghij	3.26def
Guasa	67b	4b	1546def	15.41ghi	9.19jk	6.22abc
Gorebela	48cd	3bc	1133fg	19.26efgh	17.78defgh	1.48f
Badhasa	69b	4b	1445ef	23.11defg	16.59efghi	6.52ab
Zemen	87a	5a	2341bc	16.89fghi	11.85hijk	5.04abcd
Chiro	95a	5a	2761ab	17.19fghi	13.93ghij	3.26def
Alemaya 624	50cd	3bc	957gh	27.26cd	24.59cd	2.67def
Batte	87a	5a	2553ab	11.26i	5.04k	6.22abc
Jarso	95a	5a	2994a	13.93hi	10.07ijk	3.85cdef
CIP-384321/3A	30efg	3bc	993g	34.37abc	32.89ab	1.48f
CIP-384321/3B	42de	3bc	1498ef	37.33a	35.26a	2.07ef
LSD (5%)	13.64	0.9216	446.7	7.922	7.392	2.646

Means followed by the same letter with in a column are not significantly different at 5% level of significance; AUDPC= area under the disease progress curve; TTY t ha^{-1} = total tuber yield tons per hectare; MTY t ha^{-1} = marketable tuber yield tons per hectare; UNMTY t ha^{-1} = unmarketable tuber yield tons per hectare.

The varieties were grouped according to their year of release and their disease severity, which was compared with the mean disease severity of the two farmers' cultivars and the variety released for the first time in the county (AL-624 in 1987. All genotypes except Chiro and Zemen had reduced disease severity varying from 10 to 86% as compared to the two farmers' cultivars. When the genotypes were compared to the oldest variety, only eight genotypes had lower disease severity. Among the varieties released from 2003 onwards, only Chala and Moti had higher disease severity than the oldest variety (Table 6).

Based on the calculated AUDPC, the five varieties, namely, Bulle, Bubu, Belete, Araarsaa and Gera had the lowest AUDPC ranging from 125 to 544 while the others had the highest range, i.e., 704 to 2994. None of the genotypes had a disease score 1 except Bulle. Only four varieties (Bubu, Belete, Araarsaa and Gera) had a disease score of 2 and the remaining ones had a score of 3 and above (Table 5).

The mean marketable tuber yield ranged from 5.04 to 35.85 t ha^{-1} (Table 5). The highest marketable tuber yields were recorded for Gudanie (35.85 t ha^{-1}), CIP-384321/3B (35.26 t ha^{-1}), Bubu (33.48 t ha^{-1}), and CIP-384321/3A (32.89 t ha^{-1}) while the lowest marketable tuber yields were recorded for Batte (5.04 t ha^{-1}), Moti (5.04 t ha^{-1}), Guasa (9.19 t ha^{-1}), Jarso (10.07 t ha^{-1}), and Zemen (11.85 t ha^{-1}).

The varieties which scored lower disease severity and AUDPC had also higher marketable tuber yields. The lowest unmarketable tuber yields were registered for Belete, Gorebela, Araarsaa and CIP-384321/3-A while the highest was recorded for Gabbisa (7.11 t ha^{-1}) followed by Jarso (6.52 t ha^{-1}), Badhasa (6.52 t ha^{-1}), Batte (6.22 t ha^{-1}), and Guasa (6.22 t ha^{-1}).

Table 6. Disease intensity (%) in four different disease assessments and disease resistant category of potato genotypes.

		Days after planting				Decrease/increase intensity (%) over		
Genotype		46	62	77	92	Farmers	First released	Disease resistance category
Batte		14	38	90	100a			Susceptible
Jarso		17	38	100	100a			Susceptible
Mean farmers'		16	38	95	100			
AL-624	1987	3	11	33	56c	-44		Susceptible
Chiro	1998	14	33	100	100a	0	44	Susceptible
Zemen	2001	4	29	100	100a	0	44	Susceptible
Badhasa	2001	0	14	38	67b	-33	44	Susceptible
Mean (2001)		2	21.5	69	84	-16	44	
Gorebela	2002	4	11	38	56c	-44	0	Susceptible
Guasa	2002	1	14	56	90a	-10	34	Susceptible
Jalenie	2002	4	14	56	61b	-39	5	Susceptible
Mean (2002)		3	13	50	69	-31	13	
Gera	2003	0	4	17	29e	-71	-27	Moderately resistant
Chala	2004	4	33	61	67b	-33	11	Susceptible
Bulle	2005	0	0	1	14f	-86	-42	Resistant
Gabbisa	2005	4	11	38	56c	-44	0	Susceptible
Mara Charre	2005	1	3	29	29e	-71	-27	Moderately resistant
Mean (2005)		2	5	23	33	-67	-23	
Gudanie	2006	0	4	17	38d	-62	-18	Susceptible
Araarsaa	2006	0	4	14	29e	-71	-27	Moderately resistant
Mean (2006)		0	4	15	34	-66	-22	
Belete	2009	0	0	4	14f	-86	-42	Resistant
Bubu	2011	0	0	4	14f	-86	-42	Resistant
Mean (2010)		0	0	4	14	-86	-42	
Moti	2012	4	21	76	90a	-10	34	Susceptible
CIP-384321/3 A	1	11	38	42	42cd	-58	-14	Susceptible
CIP-384321/3 B	4	14	56	90	90a	-10	34	Susceptible
LSD (5%)					14.16			

3.2. Genetic Variability Components

Genetic variability estimates including genotypic and phenotypic variances, phenotypic (PCV) and genotypic (GCV) coefficients of variation, heritability, and genetic advance as percent mean were computed for disease score and yield parameters (Table 7). The results of the study revealed the presence of considerable variations among the genotypes for the seven parameters considered. The phenotypic variances were higher than the genotypic variances for all the traits studied. Although the phenotypic coefficients of variation were higher than the genotypic coefficients of variation, the differences were low in magnitude.

Table 7. Variability components for late blight resistance and tuber yield parameters in 21 potato genotypes as evaluated in 2013/14 cropping season at Haramaya.

Traits	Mean	GV	PV	EV	GVC (%)	PCV (%)	ECV (%)	H^2 (%)	GAM (5%)
Disease severity (%)	60.4	692.55	760.87	68.32	43.57	45.67	13.68	91.02	85.63
Disease intensity (%)	53.4	689.76	763.37	73.61	49.18	51.74	16.07	90.36	96.31
Disease score	3	1.17	1.48	0.312	36.10	40.62	18.62	78.99	66.09
AUDPC	1980	691671	764934	73263	42.00	44.17	13.67	90.42	82.28
TTY t ha^{-1}	23.65	63.15	86.20	23.05	33.60	39.26	20.30	73.26	59.25
MTY t ha^{-1}	19.94	83.22	103.28	20.06	45.75	50.97	22.46	80.58	84.60
UNMTY t ha^{-1}	3.71	2.35	4.92	2.571	41.34	59.81	43.22	47.78	58.87

GV= genetic variance; PV=phenotypic variance; EV=environmental variance; GCV=genotypic coefficient of variation; PCV= phenotypic coefficient of variation; ECV= environmental coefficient of variation; H^2= heritability in broad sense in percent; GAM (5%)= genetic advance in percent mean at 5% selection intensity; AUDPC= area under the disease progress curve;TTY t ha^{-1} = total tuber yield tons per hectare; MTY t ha^{-1} = marketable tuber yield tons per hectare; UNMTY t ha^{-1} = unmarketable tuber yield tons per hectare.

High heritability in broad sense was computed for disease severity (91.02%), AUDPC (90.42%), disease intensity (90.36%), while relatively low heritability was estimated for unmarketable tuber yield (47.78%) and total tuber yield (73.26%). Similarly, the highest genetic advances as a percent mean (96.31%) was recorded for disease intensity while the lowest was recorde for unmarketable tuber yield (58.87). Among the yield parameters, marketable tuber yield exhibited higher heritability (80.58%) and genetic advance as a percent mean (84.6%).

3.3. Phenotypic and Genotypic Correlations

According to the procedures for standard evaluation trials of advanced potato clones (CIP, 2006), correlation between yield and genotype resistance can be calculated if yield has been evaluated in addition to the AUDPC. In this study, genotypic correlation coefficients were computed in addition to phenotypic correlation coefficients to obtain better estimates of the associations between tuber yield and disease resistance (Table 8).

Positive and highly significant (rg=0.96) genetic correlation was observed between late blight intensity and AUDPC, whereas the two disease scores had negative and highly significant (rg=-0.97) correlations with marketable tuber yield. The AUDPC exhibited significant but negative correlations with total tuber yield (rg=-0.66) and marketable tuber yield (rg=-0.58), but positive and significant correlation with unmarketable tuber yield (rg=0.62). In general, total and marketable tuber yield were negatively and highly significantly correlated with disease parameters, while unmarketable tuber yield was positively correlated. The two yield parameters also exhibited negative genotypic correlation with unmarketable tuber yield.

Disease intensity showed positive and highly significantly phenotypic correlation with other disease parameters but highest with AUDPC (rp=0.96). Unmarketable tuber yield showed positive and significant phenotypic correlation with disease intensity while total and marketable tuber yield showed negative correlations. AUDPC also showed negative and highly significantly phenotypic correlation with total and marketable tuber yield (rp=-0.63).

Table 8. Genotypic and phenotypic correlation coefficients above and below diagonal, respectively, for late blight and yield parameters in 21 potato genotypes as evaluated in 2013/14 cropping season at Haramaya.

	Disease intensity	Disease Incidence	Disease Score	AUDPC	TTY t ha^{-1}	MTY t ha^{-1}	UNMTY t ha^{-1}
Disease intensity		0.29*	0.43**	0.96**	-0.64**	-0.97**	0.58**
Disease severity	0.32*		0.31*	0.96**	-0.56**	-0.55**	0.58**
Disease Score	0.34*	0.32		0.38*	-0.54**	-0.57**	0.34**
AUDPC	0.96**	0.96**	0.35*		-0.66**	-0.58**	0.62**
TTY t ha^{-1}	-0.32*	-0.66**	-0.58**	-0.65**		0.89**	-0.43**
MTY t ha^{-1}	-0.54**	-0.67**	-0.57*	-0.65**	0.91**		-0.66**
UNMTY t ha^{-1}	0.59**	0.61**	0.48**	0.63**	-0.53**	-0.81**	

** & ** =significant at P<0.05 and P<0.01, respectively. AUDPC= area under the disease progress curve, TTY t ha^{-1} = total tuber yield tons per hectare, MTY t ha^{-1} = marketable tuber yield tons per hectare, UNMTY t ha^{-1} = unmarketable tuber yield tons per hectare.*

3.4. Genetic Distance and Clustering of Potato Genotypes

Genetic distances among the 21 potato genotypes were estimated using Euclidean distance (Table 9). Euclidean distance ranged from 0.71 (between Chiro and Jarso) to 7.23 (between Bubu and Batte) with a mean and a standard deviation of 3.43 and 1.47, respectively. Bubu and Belete were most distant from Zemen, Chiro, Batte and Jarso with Euclidean distance >6.07. Bulle was also most distant from Batte (6.6), Jarso (6.69), Chiro (6.44) and Zemen (6.1). On the other hand, Belete was close to Bubu, Gera, Bulle, Araarsaa and CIP-384321/3 A and Bubu exhibited closeness to Gudanie, Gera and CIP-384321/3 A with Euclidean distance of <2. Based on average Euclidean distance value, AL-624 (2.67) followed by Jalenie (2.86), Chala (2.87) and Gorebela (2.91) were closest to others while Batte (4.32) and Jarso (4.16) followed by Bubu (3.97), Bulle (3.92), and Chiro (3.92) were the most distant genotypes to others.

The dendrograms from UPGMA cluster analysis based on ED matrixes are presented in Figure 1. When the dendrograms cut at 2, which is above the standard deviation of the genotypic distance, the tested potato genotypes were separated into three clusters (Cluster I, II and II). Cluster I, included five released varieties with sub-group I (Belete and Bubu) and sub-group II (Gera, Mara Charre and Bulle) while Cluster II comprised one released variety (Gudanie) and the two genotypes (CIP-384321/3-A and CIP-384321/3-B) which are under yield trial. All the other genotypes were grouped in Cluster III with two big sub-groups viz., sub-group III and sub-group IV which consist of 5 and 8 genotypes, respectively. The four out of six old varieties (released by Haramaya University) were grouped in Cluster III sub-group IV with the two farmers' cultivars. The most recently released variety (Moti) also fell in this sub-group. Sub-group III consisted of the first potato variety released in the country and varieties released starting from 2002 to 2006. The first Cluster only included relatively recently released varieties (2005 to 2011) except one variety (Gera) which was released in 2003.

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Figure 1. Dendrogram generated based on UPGMA clustering method depicting genetic relationships among 21 potato genotypes based on seven late blight and yield evaluation parameters

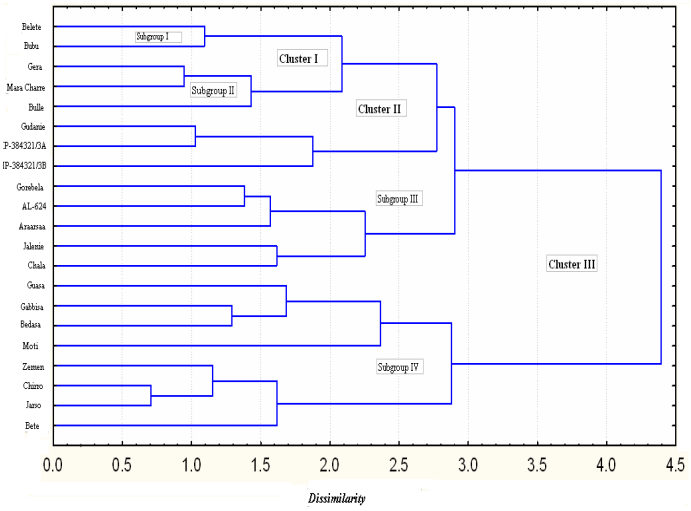

Table 9. Euclidean distance of 21 potato genotypic clones measured from seven late blight and tuber yield evaluation parameters and means Euclidean distance obtained by averaging each genotype distance to other 20 clones.

Genotype	Bubu	Gorebela	Gudanie	Guasa	Gera	Jalenie	Chala	Zemen	Chiro	Bulle	Moti	Batte	Gabbisa	Araarsaa	Mara	Badhasa	Jarso	AL-624	CIP-A	CIP-B (3.68)
Belete (3.7)	1.09	2.78	2.30	5.35	1.55	4.03	4.04	6.07	6.13	1.87	5.06	6.82	4.24	1.37	2.39	4.69	6.53	2.40	1.90	3.47
Bubu (3.97)		3.47	1.73	5.76	1.78	4.59	4.23	6.42	6.50	2.25	5.70	7.23	4.48	2.13	2.69	4.89	6.94	2.68	1.71	3.20
Gorebela (2.91)			3.16	3.28	2.49	1.61	2.18	3.69	3.61	3.36	2.78	4.44	3.18	1.60	2.59	3.13	3.97	1.38	2.54	3.09
Gudanie (3.54)				4.99	2.11	3.93	3.08	5.35	5.38	3.25	5.30	6.31	3.96	2.36	2.83	3.96	5.91	1.94	1.03	1.96
Guasa (3.38)					4.19	1.96	2.57	1.69	2.65	4.97	1.69	1.81	1.94	4.30	3.58	1.43	2.58	3.38	4.88	4.62
Gera (3.09)						3.29	3.20	5.10	5.37	1.33	4.14	5.76	2.80	1.67	0.95	3.42	5.70	1.75	2.06	3.11
Jalenie (2.86)							1.61	2.26	2.44	4.22	1.95	2.92	2.50	2.80	2.99	2.04	2.67	2.14	3.56	3.75
Chala (2.87)								2.37	2.37	4.42	3.06	3.39	2.68	3.02	3.09	1.90	2.84	1.77	2.90	2.64
Zemen (3.69)									1.17	6.10	2.60	1.21	3.27	4.90	4.68	2.22	1.13	3.83	5.17	4.66
Chiro (3.92)										6.44	3.05	2.06	4.05	4.93	5.09	3.02	0.71	3.90	5.09	4.52
Bulle(3.92)											4.70	6.60	3.46	2.48	1.53	4.37	6.69	2.97	3.18	4.29
Moti (3.59)												2.60	2.69	4.04	3.59	2.72	2.92	3.44	4.90	4.80
Batte (4.32)													3.55	5.66	5.18	2.75	1.58	4.72	6.13	5.71
Gabbisa (3.24)														3.57	2.03	1.29	4.13	2.77	4.06	4.17
Araarsaa (3.13)															2.21	3.78	5.33	1.54	1.75	3.13
Mara (3.1)																2.87	5.33	2.04	2.82	3.61
Badhasa (3.12)																	3.17	2.70	4.06	3.90
Jarso (4.16)																		4.35	5.60	5.09
AL-624 (2.67)																			1.64	2.12
CIP-A (3.34)																				1.80

Numbers in parenthesis indicates mean ED of potato genotypes, CIP-A= CIP-384321/3 A, CIP-B= CIP-384321/3 B and Mara= Mara Charre.

4. Discussion

Genetic variability was evident in potato genotypes (the released varieties, farmers' cultivars, and the genotypes under yield trial). Highly significant differences among the genotypes for late blight resistance and yield were revealed by the analysis of variance. This could be attributed to the fact that the released varieties carry varying numbers of R-genes, but were all considered as resistant in the absence of the races or where the environment did not favor the pathogen (Beukema and Van Der Zaag, 1979). This suggestion may be strengthened by the superiority of recently released varieties over the old ones in terms of resistance to late blight and tuber yield potential. In the early 1900s, potato breeders successfully introgressed resistance into cultivated potatoes from wild species (*Solanum demissum* Lindl.). A total of 11 major dominant resistance genes (*R* genes) were identified although they were later overcome by the disease. However, these genes are still useful when combined with other sources of resistance (Stewart *et al.,* 2003; Wastie, 1991). Most of the potato genotypes that have been released in Ethiopia before 2008 were either with major genes for vertical resistance or were developed for horizontal resistance against the disease in the presence of unknown resistance major R genes (Gebremedhin, 2013), which were named population A clones (Landeo *et al*.,1997). However, such resistance was short-lived because of the ability for the causal organism to overcome it (Landeo *et al*., 2000a, 2000b). But, breeding efforts on population A was stopped at CIP (starting from 1990s), and the emphasis shifted to the formation of a new population where horizontal resistance is improved in the absence of major resistance (R) genes. The new population was named as population B. The main feature of this population is that testing and selection were mainly done for horizontal resistance to late blight (unlike those applied for population A), which are simplified significantly in the absence of major (R) genes. Because of the elimination of the interference effect of major R genes, breeding material can be exposed readily to any local isolates in favorable environments and allow effective screening and selection for horizontal resistance (Landeo *et al*., 1997). Therefore, the potato varieties recently released in Ethiopia may carry either many R-genes as compared to the old varieties or were improved with horizontal resistance in the absence of major resistance (R) genes.

Many of the released genotypes have, however, become susceptible to the disease over time and are known either as resistant or moderately resistant. This may be because: i) the mycelia of different types of the fungus (mating types A1 and A2) grow together, one of them may form male cells (antheridia) and the other female cell (oogonia). The fertilized oogonium can resist unfavorable conditions such as drought and low temperatures (Henfling, 1987). This will happen because the distribution of *P. infestans* type A2 is worldwide not restricted to the temperate region (Fry and Goodwin, 1997; Drenth *et al*., 1995, Goodwin *et al*., 1995), ii) *Phytophtora infestans* have mutable features so that it can overpass any resistance and potato cultivars which were described as resistant to the disease may hardly resist the new late blight race (Song *et al*., 2003).

As suggested by Sivasubramanina and Madhavamenon (1973), genotypic and phenotypic coefficients of variations can be categorized as low (<10%), medium (10-20%) and high (>20%). In this study, high genotypic and phenotypic coefficients of variations were calculated for both late blight resistance and yield parameters. The estimated phenotypic coefficient of variation was relatively greater than the genotypic coefficient of variation for all the traits; however, the differences were low for most of the traits. This showed that the expressions of the traits were mainly the function of genetic factors with less sensitivity to environmental factors. This in turn indicates the presence of substantial genetic variability among the released potato varieties in the country.

Selection for a particular trait depends largely upon the genetic and non-genetic factors that affect the expression of phenotypic differences among genotypes. Therefore, heritability is an important estimate for the selection of traits in improving crops. Heritability estimates would be reliable if accompanied by a high estimate genetic advance (Singh and Chaudhry, 1985). As demonstrated by Robinson *et al.* (1949), heritability can be categorized as low (0-30%), moderate (30-60%) and high (60% and above) and as Johnson *et al*., (1955) suggested genetic advance as percent mean can be categorized as low (0-10%), moderate (10-20%) and high (20% and above). In the present study, high heritability (78.99 to 91.02%) and genetic advance as percent of mean (GAM) (66.09 to 96.31%) were computed for disease resistance parameters as compared to yield parameters (H^2, 47.78 to 80.58% and GAM, 58.87 to 84.6%). However, for both parameters a combination of high heritability with high genetic advance was observed, which signifies more additive gene action (Panse, 1957), and suggesting that these traits are amenable for selection.

Positive and highly significant correlations were observed among late blight parameters both at genotypic and phenotypic levels. Late blight intensity and AUDPC exhibited negative and highly significant correlations with total and marketable tuber yields, but positive and highly significant correlations with unmarketable tuber yield. These results suggest that high intensity of the disease reduced marketable yield but favored production of unmarketable tuber yield. If yield has been evaluated in addition to the AUDPC, the correlation between yield and genotypic resistance can be calculated as a value close to unity, indicating a very high linear association between tuber yield and resistance to the disease (CIP, 2006).

The dendrogram efficiently separated the more resistant, higher yielding and recent varieties (Cluster I, sub-group I) than the susceptible and the low yielding genotypes (Cluster III, sub-group IV). This research results are in line with the history of potato improvement in Ethiopia and in the world at large. Researchers in Ethiopia obtained the germplasm for selection in the form of advanced clones, tuber families, and true potato seed from International Potato Center (CIP) in Peru (Gebremedhin *et al*., 2008). The clones introduced at different times carry varied numbers of different resistance genes, which were developed either for vertical or horizontal resistance. The measured genetic

distance also enabled to grouping the old introduction (population A) into separate clusters, which differ from the recently introduced clones. Potato genotypes that have been developed and released before 2008 were from population type A (Gebremedhin, 2013). Other researchers also suggested that the clustering of functional genes for the resistance to various pathogens indicates they were from common ancestors (Gebhardt and Valkonen, 2001; Oberhagemann *et al*., 1999; Leister *et al*., 1996; Leonards-Schippers *et al*., 1994). Most of the varieties released before 2008 lost their resistance and exhibited genetic divergence from the recently released varieties. This might be due to the fact that the old varieties carry the race-specifc genes for resistance but this might not be true for the recently released varieties. The R genes conferring race-specific resistance provide only transient resistance to late blight, as new races rapidly overcome the R gene-mediated resistance (Fry and Goodwin, 1997; Wastie, 1991).

Consistent with the results of this study, Abou-Taleb *et al*., (2010) found that potatao cultivars with high, moderate, and low late blight resistance were grouped in different categories as estimated from RAPD marker. According to these authors, the lowest genetic similarity was obtained with the susceptible cultivars. However, Pattanayak *et al*. (2002) studied the genetic diversity among resistant and susceptible potato cultivars to late blight using RAPD markers and found no clear groupings based on late blight resistance and susceptibility. But, the authors found that susceptible and resistant potato cultivars showed narrow and wider genetic variations, respectively.

5. Conclusion

The presence of genetic viability was evident in potato genotypes from the analyses of both variance and genetic distance. The recently released varieties (Bubu and Belete) were more resistant to late blight than the others. They were grouped together and found to be most distant from many of the other genotypes, but are close to each other. The identified late blight resistant potato varieties, namely, Bubu, Belete and Bulle could be used for potato production during the rainy season as a management option to control late blight in Ethiopia. High yielding and moderately resistant varieties (Gera, Araarsaa and Mara Charre) may be considered for production during the rainy season with less frequent chemical spray before the disease symptoms are observed. The high yielding variety (Jalenie) and the two genotypes (CIP-384321/3A and CIP-384321/3B) but susceptible to late blight may be recommend for dry season production under irrigation or during the off or "belg" season, when environmental conditions are not favourable for the disease to occur. However, it is hardly possible to make recommendation for the use of resistant varieties alone as the best option due to the ability of the pathogen to rapidly evolve to overcome resistance genes.. Therefore, it is better to apply integrated disease control methods i.e. reduction of primary sources of inoculum and less frequent applications of fungicides to extend prolong resistance. The application of fungicides must depend on the characteristics of chemicals, disease pressure and growth stage of the potato crop. Integrated management of the disease would also increase the efficacy of control, reduces costs, and environmental side effects.

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