Genetic Gain of Tuber Yield and Late Blight [*Phytophthora infestans* (Mont.) de Bary] Resistance in Potato (*Solanum tuberosum* L.) Varieties in Ethiopia

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Abstract: Potato variety development for tuber yield and disease resistance has been conducted in Ethiopia uninterrupted since the first variety was released in 1987. However, there is an information gap about the genetic progress made over time which needs a periodic evaluation of the varieties. This study was conducted to determine the rate and magnitude of progress in tuber yield and resistance to late blight of 16 potato varieties released between 1987 and 2011 and two farmers' varieties. The varieties were planted in randomized complete block design with three replications at Haramaya, Hirna and Arberkete in eastern Ethiopia. The analysis of variance for each location revealed the presence of significant differences among the varieties in tuber yield and resistance to late blight. The mean total and marketable tuber yields increased over locations at the rate of 0.14 and 0.18 t ha^{-1}, respectively, and late blight severity score reduced at the rate of 0.31% per year over the 25 years of variety development in the country. However, the increased tuber yield varied across the locations. Late blight severity score explained total tuber yield variations between 31.39 to 80.1% across the locations. It could be concluded that most of the varieties became susceptible to late blight in favourable environments for the pathogen at Haramaya and only a few varieties (Bulle, Bubu, Belete and Gera) performed better for tuber yield and late blight resistance across all locations. What is more, the varieties released recently by different centres showed higher disease severity scores than the older varieties.

Keywords: Genetic progress; Late blight severity; Location; Resistant varieties.

1. Introduction

Potato was introduced to Ethiopia in 1858 by the German botanist Schimper (Pankhurst, 1964). Since its introduction, the crop has become a strategic crop aimed at enhancing food security and economic benefits to the country. Ethiopia is one of the principal potato producing countries in Africa. The area planted with potato increased from 30,000 to about 164,146 hectares between 2002 and 2007. The average yield of the crop has progressed from 7 to 11 t ha^{-1} (Baye and Gebremedhin, 2013). In 2013/14, potato was produced on 179,159 hectares of land with the total production of 1,612,006 tonnes (CSA, 2014) and in 2015/16 cropping season, the total land cultivated was increased to 0.3 million hectares and the yield also increased to 3.66 million tonnes with average national yield of 12.67 t ha^{-1} (CSA, 2016). Though the land under cultivation and yield of potato increased year after year, the average tuber yield obtained by smallholder farmers has remained low compared to the yields obtained at research stations, which amount to 26 to 47 t ha^{-1} (MoA, 2012 and 2013). The low yields are attributable to many factors, the most important of which are lack of high quality seed potatoes, proper management of the crop, high yielding and disease resistant varieties (Gildemacher *et al.*, 2009; Endale *et al.*, 2008). Late blight disease caused by *Phytophthora infestans* (Mont.) de Bary] and bacterial wilt (*Ralstonia solanacearum*) diseases are the two major problems that cause an estimated potato tuber yield loss of up to 70% in the country (Mekonen *et al.*, 2011).

In Ethiopia, strategic research for potato variety development and other agronomic managements began in 1975 (Gebremedhin, 2013). Starting the release of the first potato variety (Alemaya 624) in 1987, more than 27 potato varieties were developed and registered by the government research institutions (Baye and Gebremedhin, 2013; MoA, 2013 & 2012). The major focus was developing varieties for high yield and resistance to late blight for different agro-ecologies of the country by separate efforts of different research centres and Haramaya University. However, a considerable number of released varieties, which were resistant to the late blight disease at the time of release, have now become susceptible to the pathogen due to its ability to rapidly evolve to overcome resistant major genes (Stewart *et al.,* 2003; Wastie, 1991).

The major task of the breeder is to develop high yielding varieties, resistant or tolerant to stress and varieties that match the existing end use of the crop (Carter *et al.*, 2015). Breeders have often been unable to forecast future cropping scenarios and the economics of production. The varieties developed would be grown under management situations for which the breeders did not develop and showed lack of adaptation (Pfeiffer *et al.*, 2000). Genetic gain estimates in breeding programs are important to analyse and plan new actions and strategies since the increase in yield of the varieties developed through time may be due to yield

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potential of varieties, varieties resistance/tolerance to biotic and abiotic stresses, improved agronomic management or the combination of these factors.

Information on genetic progress achieved over time from a breeding program is essential to develop effective and efficient breeding strategies (Slater *et al*., 2016). The main challenge of estimating genetic gain for clonally propagated crops is lack of models suitable for features of this category of crop (Ru *et al*., 2015; Kleinwechter *et al*., 2014). However, genetic gain studies were developed for wheat in many countries (Austin *et al*., 1989; Waddington *et al*., 1987; Deckerd *et al*., 1985), for maize (Tollenaar, 1991), soybean (Gay *et al*., 1980), and barley (Wych and Rasmusson, 1983) that can be applied also to other crops.

Genetic gain can be estimated from breeding trials of institutions through time (Flavio *et al*., 1998) by comparing yields of the oldest varieties with others (Graybosch and Peterson, 2009). The other method is growing varieties released over a given period of time in the same environment under uniform cultural practices (Cox *et al*., 1998). The former method has a limitation in which inconsistency in cultural practices and varying levels of resistance among genotypes and disease pressure among environments confound true genetic differences. Selection of clones for high yield and resistance to late blight are the two major objectives of potato breeding at all research centres in Ethiopia. Selection of clones and developing and releasing them as varieties by different research centres in their domain agro-ecologies/regions may lead to differences in released varieties in contributing to progresses made to enhance yields in the country. However, the genetic progress made through releasing potato varieties in the country for a quarter of a century has not been evaluated either by each centre or the national potato research programme. Therefore, periodic evaluation of potato varieties for yield and resistance to the late blight disease is necessary by growing varieties released at different times in the same environment with uniform cultural practices. This may help in assessing the similarity of progress made over time by varieties developed by each centre and evaluate the efficiency of the existing breeding approach. To the knowledge of the researcher, genetic gain research in potato varieties has not been attempted in the country for the last 25 years. Therefore, this study was conducted; i) to determine the rate and magnitude of progress in increasing tuber yields of potato varieties developed in the country; ii) to evaluate the degree of resistance of the varieties to late blight and progresses made in selecting varieties resistant to the disease; and iii) to determine the share of late blight in causing variations in tuber yields among the varieties.

2. Materials and Methods

2.1. Description of the Study Sites

The field experiment was carried out at three locations namely; Haramaya, Hirna and Arbarakkate which are considered as the representative mid and highland potato growing areas of eastern and western Hararghe Zones in the country. The experiment was conducted for one cropping season in 2013.

Haramaya University, Rare research farm is located at 2002 metres above sea level, 9°42'32"N latitude and 42°03"85'E longitude. The area has a bimodal rainfall distribution and is representative of a sub-humid mid-altitude agro-climatic zone. The mean annual rainfall is 760 mm. The short rainy season extends from March to April and constitutes about 25% of the annual rainfall whereas the long rainy season extends from June to October and accounts for about 45% of the total rainfall (Belay *et al*., 1998). The mean maximum temperature is 23.4^{0}C while the mean minimum annual temperature is 8.25^{0}C (Tekalign, 2011).

The soil of the experimental site is a well-drained deep alluvial with a sub-soil stratified with loam and sandy loam. Previous work showed that it has organic carbon content of 1.15%, total nitrogen content of 0.11%, available phosphorus content of 18.2 mg kg soil^{-1}, exchangeable potassium content of 0.65 cmolc kg soil^{-1} (255 mg K kg soil^{-1}) and pH of 8.0 (Simret, 2010), and the soil of the experimental site is a well-drained deep alluvial with a sub-soil stratified with loam and sandy loam (Tekalign, 2011).

Hirna research sub-station of Haramaya University is located at 9 ^{o}12' North latitude, 41 ^{o} 4' East longitude, and at an altitude of 1870 metres above sea level. The area receives mean annual rainfall ranging between 990 to 1010 mm (HURC, 1996). The mean maximum and minimum annual temperatures are 21.8°C and 8.6°C, respectively (Tekalign, 2011). The soil of Hirna is *Vertisol* with a silty clay texture and pH of 7.09, and contains 1.75% organic, 0.18% total nitrogen 32 mg kg soil^{-1} available phosphorus, and 68 cmol$_c$ kg soil^{-1} exchangeable potassium (Nebret, 2011).

The third site is Arberekete on farmer's field, which is situated at a distance of about 171 km to the west of Haramaya and 339 km to the east of Addis Abeba. The site is located at 9 ^{o}14' North latitude, 41 ^{o}2' East longitude, and at an altitude of 2280 meters above sea level.

2.2. Experimental Materials, Design and Procedures

Eighteen (18) potato varieties were evaluated, of which 16 were improved varieties released by five research centres and Haramaya University from 1987 to 2011 and two farmers' varieties. The description of the varieties including the recommended growing altitudes and tuber yields as registered during the time of release are given in Table 1.

Table 1. Name, accession code, year of release, breeding/maintainer centre of potato varieties.

No	Variety	Accession code	Year of release	Average TY t ha^{-1}at RC	Breeding center	Recommended Altitude (m a.s.l.)
1	Alemaya 624	Al-624	1987	---	Haramaya University	1700 - 2400
2	Chiro	AL-111	1998	37.2	Haramaya University	2700 - 3200
3	Zemen	AL-105	2001	28.7	Haramaya University	1700 - 2000
4	Badhasa	AL-114	2001	40.6	Haramaya University	2400 - 3350
5	Gorebela	CIP-382173.12	2002	41	Sheno Research Centre	1700 - 2400
6	Guasa	CIP-384321.9	2002	36	Adet Research Centre	2000 - 2800
7	Jalenie	CIP-37792-5	2002	40.3	Holeta Research centre	1600 - 2800
8	Gera	KP-90134.2	2003	47.2	Sheno Research centre	2700 - 3200
9	Chala	CIP-387412-2	2005	42	Haramaya University	1700 - 2000
10	Bulle	CIP-387224-25	2005	39.3	Hwassa Research centre	1700 - 2700
11	Gabbisa	CIP-3870-96-11	2005	40	Haramaya University	1700 - 2000
12	Mara Charre	CIP-389701-3	2005	33.3	Hwassa Research centre	1700 - 2700
13	Gudanie	CIP-386423.13	2006	29	Holeta Research centre	1600 - 2800
14	Araarsaa	CIP-90138.12	2006	31	Sinnana Research centre	2400 - 3350
15	Belete	CIP-393371.58	2009	47.2	Holeta Research Centre	1600 - 2800
16	Bubu	CIP-384321-3	2011	40.5	Haramaya University	1700 - 2000
17	Batte	Farmers' variety				
18	Jarso	Farmers' variety				

Source: Ministry of Agriculture (MoA), 2013 and 2012. Average TY t ha^{-1} at RC = average tuber yield tonnes per hectare at research farms registered during the release of the varieties; m a.s.l = Metres above sea level.

The experiment was laid out as a Randomized Complete Block Design (RCBD) with three replications in each environment. Each potato variety was assigned to one plot in each replication and six rows with 12 plants. The gross plot size was 16.2 m^2 with spacing of 75 cm between rows and 30 cm between plants, respectively. The spacing of 1.5 m and 1 m was maintained between plots and blocks, respectively.

The experimental fields except at Arberekete were cultivated by a tractor to the depth of 25-30 cm and levelled. Then ridges were made by hand. Medium sized (39-75 g) and well sprouted seed tubers were planted at the sides of the ridges. Tubers were planted at the end of June at Haramaya and first week of July at Hirna and Arberekete during the main growing season after the rain commenced and when the soil was moist enough to support emergence and growth. The planting depth was maintained at about 5 to 10 cm.

Fertilizer was appliedat the rate of 75 kg N and 92 kg P_2O_5 ha^{-1}. The sources of nitrogen and phosphors were Urea (46% N) and DAP (18% N, 46% P_2O_5), respectively. The entire DAP fertilizer was applied at the depth of 10 cm below the seed tuber at planting, while urea was applied 7-10 cm away from the plant as two side dressings for in split application (50% + 50% 30 and 50 days after planting). Other agronomic managements (earthing up/cultivation, weeding) were applied as per the recommendation made for the crop.

The haulm was mowed two weeks before harvesting to thicken tuber periderm. This was done when yellowing or senescence was observed on the lower leaves. For yield estimation, tubers were harvested from forty plants from the four middle rows, leaving the plants growing in the two border rows as well as those growing at both ends of each row to avoid edge effects.

2.3. Data Collection

Total tuber yield of each variety was estimated from plants counted at harvest 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 tonnes per hectare. Tubers less than 20g were categorized as unmarketable (Lung'aho *et al.,* 2007). Tubers which were free from diseases, insect pests and those weighing 20 g or more were sorted, weighted for each plot and recorded as marketable yield (t ha^{-1}).

Disease assessment was conducted starting from 30 August 2013 after 46 days of planting as soon as disease symptoms appeared in susceptible varieties and then after every 20 days until the majority of the varieties attained physiological maturity. Disease incidence and severity were assessed following CIP (2006) guideline and other established procedures. Assessment of severity of late blight disease under field conditions in percent was recorded on a plot basis taking into account the number of plants developing disease symptoms on a leaf and/or many leaves and plants free from disease as described in Table 2 (Henfing, 1987). Disease assessment was done by the same three evaluators without knowing the value given in the previous reading (CIP, 2006).

Table 2. Assessment of severity of late blight under field conditions.

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 by injuries.
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, few upper leaves are green and most of the stems are hardly affected or dead
100		Leaves and stems are destroyed

Source: Henfing, 1987

2.4. Data Analysis

Data were subjected to analysis of variance (ANOVA) for each location and combined over environments following the standard procedure for RCBD given by Gomez and Gomez (1984) using the General Linear Model (GLM) of the SAS procedure of version 9.1 (SAS, 2007). Heterogeneity was observed from homogeneity test of error variances using Bartlett's test for both yield and disease severity parameters and mean comparison of varieties was conducted for each environment.

Regression analysis was used to calculate the genetic gain of yield potential and disease resistance (disease severity reduction). The average annual rate of genetic gain for each trait was estimated by regressing of the mean value of each trait against the corresponding year of release of each variety (Singh and Chaudhary, 2007). Regression analysis was also used to estimate disease severity as cause of genetic gain in tuber yield. In this regression analysis tuber yield was considered as dependent variable while disease severity was considered as independent variable. Correlation of year of release and mean value of each variety for each trait was also calculated to understand the association of year of release and the mean performance of varieties. The annual rate of genetic gain achieved over the last 25 years of potato improvement was determined as the ratio of genetic gain to the corresponding mean value of the oldest variety and expressed as a percentage.

Annual rate of gain = Cov (X, Y)/Var (X), where, X is the year of variety release, Y is the mean value of each trait for each variety; Cov is the covariance of X and Y and Var is variance of X (year of variety release). Percent genetic gain per year for each variety was calculated as Percent Genetic Gain Year^{-1} = {[(XG-XAL-624)/XAL-624]/YG-YAL-624*100}, where, X is the mean value of observations for a given trait and Y is the year of release of each variety (G). The increment over farmers' cultivars for each trait was calculated as Percent Increment of Variety (%) = XG – XFC/XFC*100, where, XG is the mean value of each variety for each trait and XFC is the mean value of the two farmers' varieties (Jarso and Batte) in eastern Ethiopia. In this experiment, Alemaya 624 was considered as the oldest variety since it was the first potato variety released in the country in 1987.

3. Results

3.1. Analysis of Variance and Mean Performance of Varieties

The analysis of variance for total and marketable tuber yield as well as late blight severity score in each environment/location revealed significant ($P<0.01$) differences among the varieties. The results of analysis of variance for all traits are presented in Tables 3, 4 and 5. Absence of homogeneity of error variances for these traits led to a procedure of conducting the mean comparison of varieties separately for each location.

Table 3. Mean square from the analysis of variance for tuber yields and late blight severity score of potato varieties at Haramaya in 2013.

Source of variation	Degree of freedom	Total tuber yield t ha^{-1}	Marketable tuber yield t ha^{-1}	Late blight severity (%)
Replication	2	40.35	27.12	267.13
Variety	17	295.48**	236.63**	2430.94**
Error	34	8.82	7.61	62.23

*Note: ** = significant at P<0.01.*

Table 4. Mean square from the analysis of variance for tuber yields and late blight severity score of potato varieties at Hirna in 2013

Source of variation	Degree of freedom	Total tuber yield t ha^{-1}	Marketable tuber yield t ha^{-1}	Late blight severity (%)
Replication	2	4.95	6.43	15.7
Variety	17	269.38**	254.36**	1889.3**
Error	34	7.58	7.43	252

*Note: ** = significant at P<0.01.*

Table 5. Mean square from the analysis of variance for tuber yields and late blight severity score of potato varieties at Arberkete in 2013.

Source of variation	Degree of freedom	Total tuber yield t ha^{-1}	Marketable tuber yield t ha^{-1}	Late blight severity (%)
Replication	2	4.06	3.02	162.02
Variety	17	134.95**	112.86**	1298.1**
Error	34	2.59	2.39	83.65

*Note: ** = significant at P<0.01.*

At Haramaya, all varieties except five (Mara Charre, Gudanie, Bubu, Belete and Gera) produced lower total and marketable tuber yields than the oldest variety (Alemaya 624) (Table 6 and 7). At Arberekete, five varieties including Belete (released in 2009) had lower total and marketable tuber yield (t ha^{-1}) than the oldest variety. On the other hand, all varieties except Gorebela (released in 2002) produced total tuber yields that were higher than the old and farmers' varieties at Hirna. All improved varieties except two at Haramaya and Arberekete exceeded the mean tuber yield of farmers' varieties. Considering the performance of varieties across the environments, most varieties except four exceeded the performance of the oldest variety in terms of tuber yield. Particularly, Mara Charre, Bubu, Gudanie and Gera exceeded the oldest variety in tuber yield by about 6.67 to 18.73 t ha^{-1} (Table 6 and 7).

Table 6. Percent genetic gain of total tuber yield year^{-1} over oldest variety and mean of the two farmers' varieties

		Haramaya			Hirna			Arberkete			Average
Variety	Year of release	Mean TTY	PGGY AL-624	PIMFC	Mean TTY	PGGY AL-624	PIMFC	Mean TTY	PGGY AL-624	PIMFC	PGGY AL-624
Alemaya 624	1987	27.26^{cd}		62.55	33.53^{hi}		14.09	33.6d		19.66	
Chiro	1998	17.19^{hij}	-3.36	2.50	44.64^{de}	3.01	51.89	41.96ab	2.26	49.43	0.91
Zemen	2001	16.89^{ij}	-2.72	0.72	45.21^{de}	2.49	53.83	34.8d	0.26	23.93	0.19
Badhasa	2001	23.12^{deg}	-1.08	37.87	38.52^{fg}	1.06	31.06	27.08f	-1.39	-3.56	-0.43
Gorebela	2002	19.27^{ghi}	-1.95	14.91	21.15^{k}	-2.46	-28.04	18.36h	-3.02	-34.62	-2.52
Guasa	2002	15.44^{ij}	-2.89	-7.93	50.45^{c}	3.36	71.66	40.15bc	1.30	42.98	0.82
Jalenie	2002	16.59^{ij}	-2.61	-1.07	42.93^{ef}	1.87	46.07	34.18d	0.12	21.72	-0.05
Gera	2003	28.47^{c}	0.28	69.77	55.27^{ab}	4.05	88.06	30.67e	-0.55	9.22	1.33
Chala	2005	26.07^{cde}	-0.24	55.46	51.49^{bc}	2.98	75.20	34.8d	0.20	23.93	1.06
Bulle	2005	25.78^{cde}	-0.30	53.73	35.13^{gh}	0.27	19.53	22.73g	-1.80	-19.05	-0.63
Gabbisa	2005	21.93^{e-h}	-1.09	30.77	47.64^{cd}	2.34	62.10	37.75c	0.69	34.44	0.76
Mara Charre	2005	54.31^{a}	5.51	223.85	56.52^{a}	3.81	92.31	39.79bc	1.02	41.70	3.31
Gudanie	2006	38.58^{b}	2.19	130.05	43.95^{de}	1.64	49.54	34.09d	0.08	21.40	1.24
Araarsaa	2006	24.3^{c-f}	-0.57	44.90	43.63^{de}	1.59	48.45	37.5c	0.61	33.55	0.62
Belete	2009	28.76^{c}	0.25	71.50	45.54^{de}	1.63	54.95	30.25e	-0.45	7.73	0.49
Bubu	2011	35.56^{b}	1.27	112.05	46.94^{cde}	1.67	59.71	43.2a	1.19	53.85	1.38
Jarso		13.94^{j}			30.52^{il}			25.32fg			
Batte		19.59^{f-i}			28.26^{j}			30.83e			
Mean released varieties		26.22	-0.49	56.35	43.91	1.95	49.40	33.81	0.03	20.39	0.56
Mean farmers' varieties		16.77			29.39			28.08			
LSD (5%)		4.93			4.57			2.67			
CV (%)		11.8			6.5			4.8			

Note: Means with the same letters are not significantly different at $P<0.05$. LSD = least significant difference, TTY = total tuber yield tons per hectare, PGGY AL-624 = percent genetic gain year^{-1} over AL-624, PIMFC = percent increment over mean of farmers' varieties, CV = coefficient of variation in percent, Average PGGY AL-624 = average percent genetic gain year^{-1} over AL-624 over three locations.

Table 7. Percent genetic gain of marketable tuber yield year^{-1} over oldest variety and mean of the two farmers' varieties.

		Haramaya			Hirna			Arberkete			
Variety	Year of release	Mean MTY	PGGY AL-624	PIMFC	Mean MTY	PGGY AL-624	PIMFC	Mean MTY	PGGY AL-624	PIMFC	Average PGGY AL-624
Alemaya 624	1987	24.59cd		68.89	28.69hi		12.33	29.89gh		22.65	
Chirro	1998	15.94fgh	-3.43	9.48	41.45de	4.04	62.29	37.84ab	2.42	55.27	1.32
Zemen	2001	15.85fgh	-2.72	8.86	43.59cd	3.71	70.67	31.71efg	0.43	30.12	0.69
Badhasa	2001	21.33de	-1.19	46.50	35.12fg	1.60	37.51	24.6j	-1.26	0.94	-0.18
Gorebela	2002	17.78efg	-2.03	22.12	18.44j	-2.38	-27.80	16.82l	-2.92	-30.98	-2.41
Guasa	2002	13.92gh	-3.04	-4.40	46.73bc	4.19	82.97	36.33bc	1.44	49.08	1.11
Jalenie	2002	15.66fgh	-2.59	7.55	38.43ef	2.26	50.47	31.02g	0.25	27.29	0.16
Gera	2003	26.59c	0.24	82.62	51.38a	4.94	101.17	27.98hi	-0.40	14.81	1.71
Chala	2005	24.52cd	-0.23	68.41	47.07abc	3.56	84.30	32.28efg	0.44	32.46	1.38
Bulle	2005	23.63cd	-0.43	62.29	32.22gh	0.68	26.16	20.41k	-1.76	-16.25	-0.46
Gabbisa	2005	20.14def	-1.18	38.32	43.21cd	2.81	69.19	34.06cde	0.78	39.76	0.95
Mara Charre	2005	47.48a	4.75	226.10	50.11ab	4.15	96.20	35.07cd	0.96	43.91	3.31
Gudanie	2006	35.85b	2.11	146.22	41.41de	2.33	62.14	31.23fg	0.24	28.15	1.60
Araarsaa	2006	22.81cd	-0.57	56.66	41.25de	2.30	61.51	33.64def	0.66	38.04	0.92
Belete	2009	27.26c	0.30	87.23	41.82de	2.08	63.74	28.16hi	-0.26	15.55	0.77
Bubu	2011	33.48b	1.28	129.95	43.91cd	2.21	71.93	39.54a	1.35	62.25	1.69
Jarso		12.07h			26.41i			21.62k			
Batte		17.04efg			24.67i			27.11ij			
Mean released varieties		24.18	-0.58	66.05	40.30	2.57	57.80	30.66	0.16	25.82	0.84
Mean farmers varieties		14.56			25.54			24.37			
LSD (5%)		11.9			4.52			2.57			
CV (%)		4.58			7.1			5.2			

Note: Means with the same letters are not significantly different at $P < 0.05$. LSD = least significant difference, MTY = marketable tuber yield tons per hectare, PGGY AL-624 = percent genetic gain year^{-1} over AL-624, PIMFC = percent increment over mean of farmers' varieties, CV = coefficient of variation in percent, Average PGGY AL-624 = average percent genetic gain year^{-1} over AL-624 over three locations.

Eight out of 16 varieties scored lower late blight severity than the oldest variety at Haramaya. All varieties except one (Chiro) had lower scores of late blight severity than the mean of two farmers' cultivars. At Haramaya, only 4 out of 11 varieties released between 1998 and 2005 had lower scores of late blight severity than the oldest variety (Alemaya 624). At Hirna, all varieties except Gorebela, and at Arberkete all varieties except Badhasa and Gorebela had lower scores of late blight severity than the oldest variety (Alemaya 624). At Arberkete all varieties except Badhasa and Gorebela had lower scores of late blight severity than mean late blight severity scores of the two farmers' varieties. The two recently released varieties (Bubu and Belete) had consistently the lowest late blight severity scores ($\leq$15%) in all three environments. Furthermore, other four varieties, namely, Gera, Bulle, Mara Charre and Araarsaa had late blight severity scores of not more than 30% in all the environments (Table 8).

3.2. Estimates of Gain for Tuber Yield

The highest estimates for annual percent genetic gain of total tuber yield was noted at Hirna (Gera = 4.05%) and the lowest was -3.02% at Arberkete for Gorebela (released in 2002). Mara Charre and Bubu which were released in 2005 and 2011, respectively, had the highest percent genetic gain over the oldest variety (Alemaya 624) for total tuber yield across the three locations (Table 6), while Gorebela scored consistently lower genetic gain (-2.03, -2.38 and -2.92% at Haramaya, Hirna and Arberkete, respectively) for marketable tuber yield (t ha^{-1}). Chiro at Haramaya had the lowest (-3.43%) and Gera at Hirna had highest percent genetic gain (4.94%) for marketable tuber yield relative to the oldest variety (t ha^{-1}) (Table 7).

The annual rate of gain over the oldest variety (Alemaya 624) in percent ranged between -1.62 (Haramaya) and 2.44% (Hirna) for total tuber yield while it was in the range between -1.77 and 2.68% for marketable tuber yield. The average annual rate of gain over the oldest variety in percent was 1.79 and 1.86% for total and marketable tuber yield, respectively (Table 9). Total tuber yield and year of release of the varieties had a positive but a weak (r = 0.09) association at Arberkete while having a relatively high (r = 0.39) for total and marketable tuber yields at Hirna. The coefficient of determination (R^2) was as low as 0.079 for total tuber yield at Arberkete and high (R^2 = 0.1523) for marketable tuber yield at Hirna (Figures 1 and 2). The absolute reduction and increase in tuber yields t ha^{-1} $year^{-1}$ were calculated as absolute reduction and increase in the mean tuber yield of the 15 varieties over the mean tuber yield of the oldest variety (Alemaya 624) divided by 25 years (starting 1987 the first variety release year) to 2011 (the year of recently released variety, Bubu in the experiment). The results are presented in Table 8. Reductions of 0.04 and 0.02 t ha^{-1} $year^{-1}$ of total and marketable tuber yields, respectively, was observed at Haramaya, whereas as increases of 0.46 and 0.58 t ha^{-1} $year^{-1}$ of total and marketable tuber yields, respectively, were recorded at Hirna.

The lowest absolute increase in total tuber yield (0.06 t ha^{-1} $year^{-1}$) over the mean of two farmers' cultivars was calculated at Haramaya while the highest absolute increase (0.38 t ha^{-1} $year^{-1}$) was calculated at Hirna. The lowest (0.11 t ha^{-1} $year^{-1}$) and highest (0.59 t ha^{-1} $year^{-1}$) absolute increase in marketable tuber yield over the mean of two farmers' cultivars was calculated for the same locations over the last 25 years (Table 9).

3.3. Estimates of Gain for Late Blight Resistance

All varities realeased up to 2006, except Bulle, Gera, Araarsaa, Mara Charre, Gudanie and Gorebela, hade late blight severity scores higher than that of the oldest variety (Alemaya 624) at Haramaya while all varieties except Gorebela both at Hirna and Arberkete and Badhasa at Arberkete had lower percent late blight severity scores. Percent genetic gain relative to Alemaya 624 ranged from the increase of 10.72% (Gorebela) at Arberkete to the reduction of 5.68% late blight severity $year^{-1}$ (Chiro) at Hirna. The two farmers' varieties had the highest percent late blight severity in all locations except Chiro at Haramaya, Badhasa at Arberkete and Gorebela at Hirna and Arberkete. Percent reduction of late blight severity ranged from 4.4% (Zemen) at Haramaya to 93.55% (Bubu) at Hirna as compared to the mean late blight severity score of the farmers' varieties (Table 8).

The absolute reduction in late blight severity was as high as 0.74% at Hirna and as low as 0.07% $year^{-1}$ at Arberkete over Alemaya 624 with average annual absolute reduction of 5.74%. Improved varieties absolute reduction of late blight severity for the last 25 years was highest (1.88% $year^{-1}$) at Hirna and lowest (0.60% $year^{-1}$) at Arberkete as compared to the mean of two farmers' varieties. Annual rate of gain reduction of late blight severity due to the improved and released varieties for the last 25 years was highest (10.4%) at Haramaya but it was lowest (1.0%) at Hirna with average annual rate of reduction of 5.74% (Table 9).

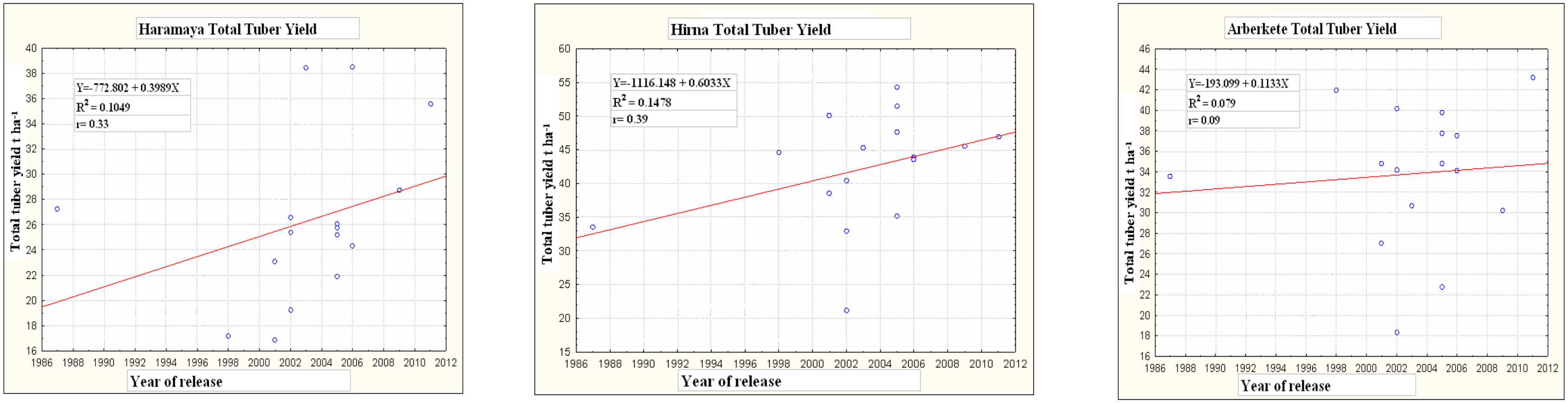

Figure 1. Regression equation of potato total tuber yield on year of variety release for three locations

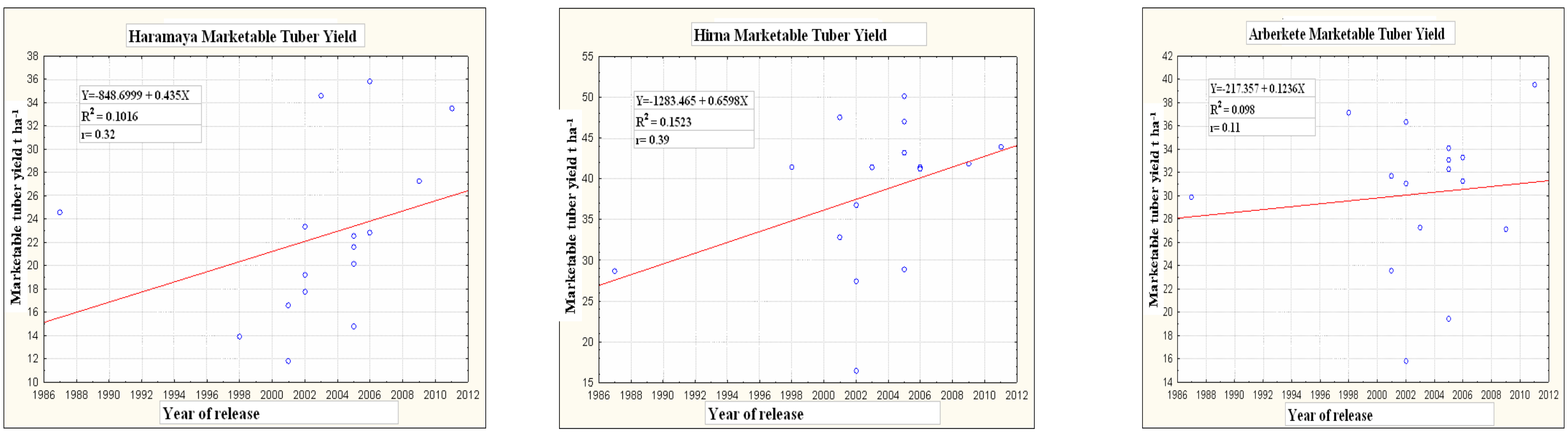

Figure 2. Regression equation of potato marketable tuber yield on year of variety release for three locations

The late blight severity score for varieties showed negative association with release year of varieties and had strong negative association at Arberkete (r = -0.52) and Haramaya (r = -0.51) and weak association at Hirna (r = -0.086). The R^2 was as high as 0.2694 and as low as 0.0074 at Arberkete and at Hirna, respectively (Figure 4). Late blight severity scores explained the observed total tuber yield variations by about 31.39, 80.1 and 67.89% at Haramaya, Hirna and Arberkete, respectively (Figure 5). Mean total tuber yield variation over locations was also explained by about 43.71% due to late blight severity (Figure 3). Late blight severity score and tuber yield had negative association that ranged from r = -0.024 (Haramaya) to r = -0.895 (Hirna) (Figure 5).

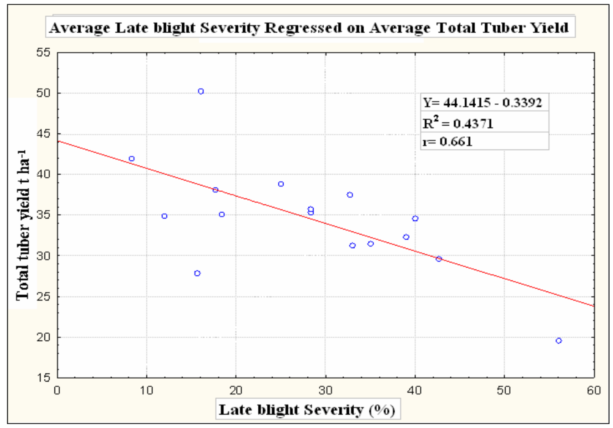

Figure 3. Regression equation of average late blight severity on average total tuber yield of varieties over three locations.

Table 9. Estimates of coefficient of determination, average rate of gain, annual absolute and relative genetic gain for tuber yield and late blight severity.

Trait	CD (R^2)	AAGG- AL-624	RAGG AL-624(%)	AGIFC	RGIFC (%)	Annual rate of gain (b) (%)
HU TTY t ha^{-1}	0.1049	-0.04	-0.16	0.06	0.24	-1.62
Hirna TTY t ha^{-1}	0.1478	0.46	1.38	0.38	2.25	2.44
Arber TTY t ha^{-1}	0.079	0.01	0.03	0.23	0.68	0.34
Average TTY t ha^{-1}	0.1186	0.14	0.45	0.23	1.06	1.79
HU MTY t ha^{-1}	0.1016	-0.02	-0.07	0.11	0.50	-1.77
Hirna MTY t ha^{-1}	0.1523	0.58	2.11	0.59	2.31	2.68
Arber MTY t ha^{-1}	0.098	0.03	0.11	0.25	0.82	0.38
Average MTY t ha^{-1}	0.1577	0.18	0.64	0.32	1.21	1.86
HULB Severity	0.2524	-0.13	-0.25	-1.76	-1.93	-10.40
Hirna LB Severity	0.074	-0.74	-2.31	-1.88	-3.03	-1.00
Arberkete LB Severity	0.2694	-0.07	-0.30	-0.60	-2.86	-8.30
Average LB Severity	0.3221	-0.31	-0.89	-1.39	-2.22	-5.74

Note: CD (R^2) = Coefficient of determination, AAGG-AL-624 = absolute annual average genetic gain over Alemaya 624 (oldest variety), RAGG-AL-624 (%) = relative annual average genetic gain over Alemaya 624 (oldest variety), AGIFC = absolute annual average increment over mean of farmers' varieties, and RGIFC (%) = relative annual average increment over mean of farmers' varieties.

Table 8. Trends of genetic gain of late blight severity year^{-1} over oldest variety and mean of the two farmers' varieties.

Variety	Year of release	Haramaya Mean Severity	Haramaya PGGY AL-624	Haramaya PIMFC	Hirna Mean Severity	Hirna PGGY AL-624	Hirna PIMFC	Arberkete Mean Severity	Arberkete PGGY AL-624	Arberkete PIMFC	Average PGGY AL-624
Alemaya 624	1987	50cd		-45.05	32b		-48.39	23d		-36.11	
Chiro	1998	95a	8.18	4.40	12cd	-5.68	-80.65	13def	-3.95	-63.89	1.30
Zemen	2001	87a	5.29	-4.40	12cd	-4.46	-80.65	18def	-1.55	-50.00	0.82
Badhasa	2001	68b	2.57	-25.27	23bc	-2.01	-62.90	37bc	4.35	2.78	1.56
Gorebela	2002	48d	-0.27	-47.25	60a	5.83	-3.23	60a	10.72	66.67	4.00
Guasa	2002	67b	2.27	-26.37	8cd	-5.00	-87.10	10ef	-3.77	-72.22	-1.27
Jalenie	2002	62bc	1.60	-31.87	17bcd	-3.13	-72.58	20def	-0.87	-44.44	-0.38
Gera	2003	25fg	-3.13	-72.53	5d	-5.27	-91.94	23d	0.00	-36.11	-3.10
Chala	2005	70b	2.22	-23.08	8cd	-4.17	-87.10	20def	-0.72	-44.44	-0.37
Bulle	2005	10h	-4.44	-89.01	15cd	-2.95	-75.81	22de	-0.24	-38.89	-3.07
Gabbisa	2005	50cd	0.00	-45.05	15cd	-2.95	-75.81	20def	-0.72	-44.44	-1.06
Mara Charre	2005	30ef	-2.22	-67.03	5d	-4.69	-91.94	13def	-2.42	-63.89	-3.02
Gudanie	2006	40de	-1.05	-56.04	12cd	-3.29	-80.65	23d	0.00	-36.11	-1.50
Araarsaa	2006	27f	-2.42	-70.33	10cd	-3.62	-83.87	18def	-1.14	-50.00	-2.51
Belete	2009	13gh	-3.36	-85.71	8cd	-3.41	-87.10	15def	-1.58	-58.33	-2.99
Bubu	2011	13gh	-3.08	-85.71	4d	-3.65	-93.55	8f	-2.72	-77.78	-3.17
Jarso		95a			60a			47b			
Batte		86.67a			63a			25cd			
Mean released varieties		47	0.14	-48.15	15	-3.23	-75.20	21	-0.31	-40.45	-0.98
Mean farmers varieties		91			62			36			
LSD (5%)		13.09			15.47			12.46			
CV (%)		15.2			45.4			32.4			

Note: Means with the same letters are not significantly different at P<0.05. LSD = least significant difference, Mean severity = severity of late blight in percent, PGGY AL-624 = percent genetic gain year^{-1} over AL-624, PIMFC = percent increment over mean of farmers varieties, CV = coefficient of variation in percent, Average PGGY AL-624 = average percent genetic gain year^{-1} over AL-624 over three locations.

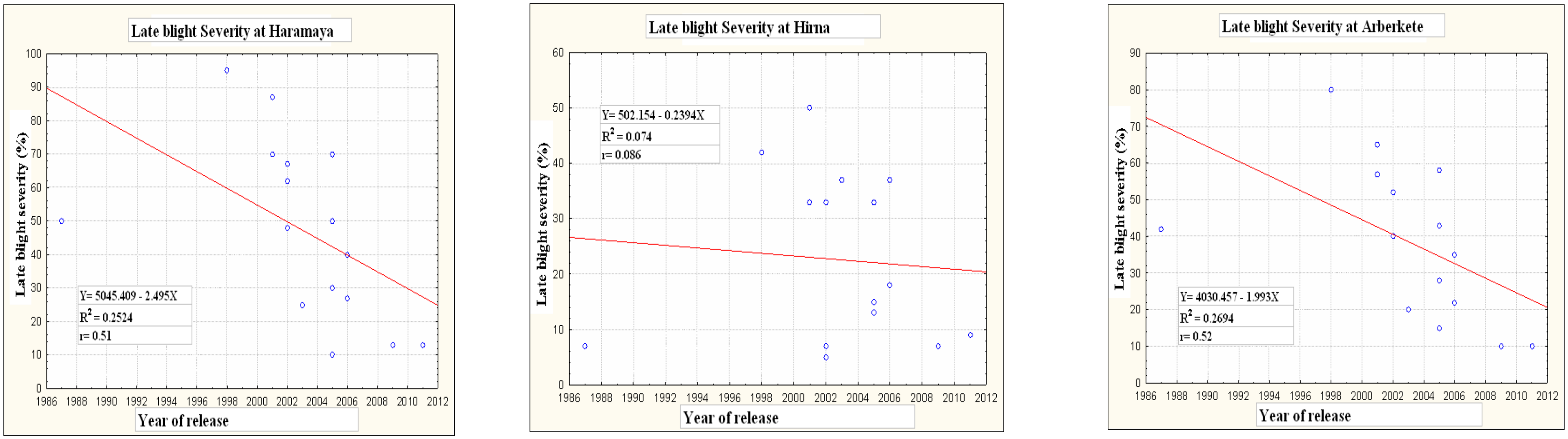

Figure 4. Regression equation of potato late blight severity on year of variety release at three locations

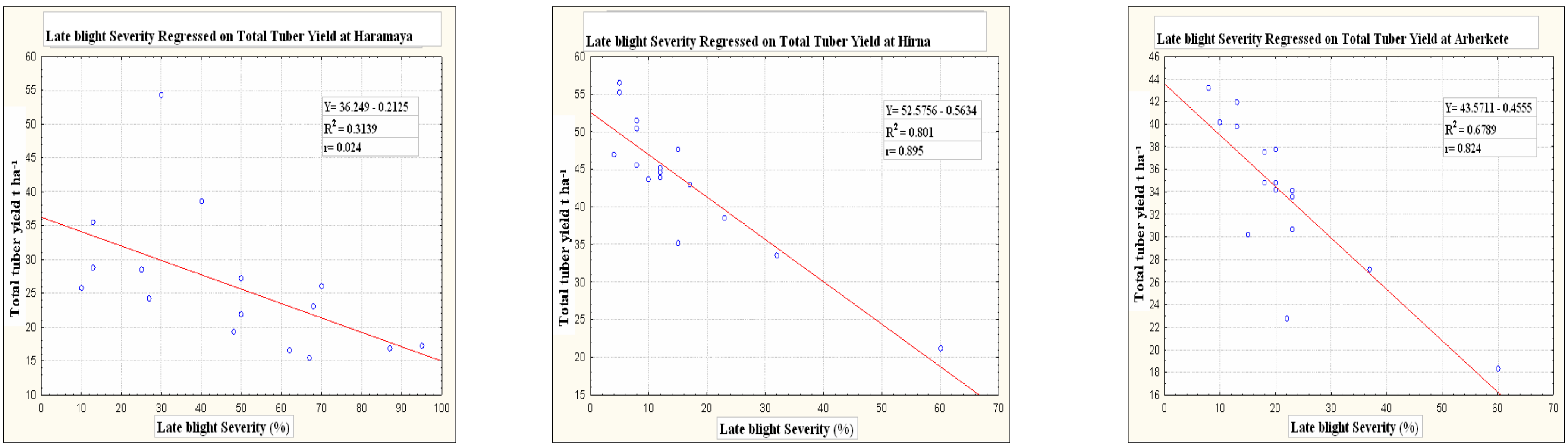

Figure 5. Regression equation of average late blight severity on total tuber yield of varieties at three locations

4. Discussion

Potato varieties developed for different agro-ecologies of the country by separate efforts of breeders at different research centres exhibited significant differences in tuber yields and severity to late blight. In general, 1.79 and 1.86% average annual rates of gain for total and marketable tuber yields, respectivly, were observed. This suggests that the varieties had differences in genetic makeup and potential for yield and resistance to late blight that may lead to differences in genetic gain across agro-ecologies. The varieties changed in the rank of performance from one environment to another due to genotype and environment interaction (GEI) that also affects breeding progress since it complicates the selection of superior varieties in all environments (Ebdon and Gauch, 2002; Falconer and Mackay, 1996). Yield depends on many factors which is controlled by many genes and subject to considerable modification by differences in environment (Beukema and Vander Zaag, 1990; Briggs and Knowles, 1985). Consistent with the results of this study, significant variations in tuber yields of potato varieties due to environment and variety x environment interactions were reported by other researchers (Flis *et al*., 2014; Mulugeta, and Dessalegn, 2013; Elfinesh, 2008; Mulema *et al*., 2008; Mateo *et al*., 2007).

Potato improvement for late blight resistance seems successful in Ethiopia since -5.74% of the annual rate of gain was computed for late blight severity score for when the successively released varieties were compared to the oldest variety. This shows that the general trend of potato improvement in the last 25 years in the country was developing more resistant varieties. In the early 1900s, potato breeders tried to develop potato varieties with varied numbers of major dominant resistance genes (*R* genes) and horizontal resistance against the disease in the presence of unknown resistance major R genes (population A) although they were later overcome by the disease. The potato varieties that had been released before 2008 were from this population (Gebremedhin, 2013). Starting from 1990s, CIP shifted to the formation of new populations (population B) where horizontal resistance is improved in the absence of major resistance (R) genes (Landeo *et al*., 1997). Therefore, the released varieties used in this study may carry either many R-genes as compared to the old varieties or were improved with horizontal resistance in the presence or absence of major resistance (R) genes. However, most of the varieties were more susceptible to late blight as compared to the oldest variety in hot spot areas, for example at Haramaya. This suggests the advantage of evaluating varieties for late blight resistance in areas where the environment favours the pathogen as suggested by a group of scientists (Lee *et al*., 2001). Because, for stress conditions, direct selection is more effective in the same environment than selection for the mean of both favourable and unfavourable environments (Kirigwi *et al*., 2004; Cecarelli *et al*., 1998; Calhoun *et al*., 1994).

Late blight severity score explained the tuber yield variations by about 66.1% on average. This is very high for the single factor contribution to tuber yield and it suggests the impossibility of attaining notable progress in tuber yield without incorporating resistance to late blight in potato varieties. Late blight is the most serious fungal disease that occurs almost everywhere in the world, and if not controlled, losses may reach as much as 100 percent (Henfling, 1987). In highland areas of Ethiopia, late blight disease causes up to 70% tuber yield loss (Mekonen *et al*., 2011). This fact was also observed in this study by the inverse relation of tuber yield and late blight severity score in percent.

The general trend of potato improvement as evaluated from average annual rate of gain in percent for tuber yield and late blight resistance could be considered high in the country for a quarter of a century. On the other hand, highly significant differences were observed among the varieties for tuber yield and late blight resistance due to location and genotype x location interaction. The annual gain rates of varieties and percent annual genetic gain across locations varied for tuber yield and late blight resistance. Only a few varieties specifically those developed by three centres consistently performed better for both traits. The majority of varieties (10 out of 16 varieties) had disease scores of >40% which can be considered as susceptible in disease hot spot areas (Haramaya). If genotypes perform differentially at different locations/environments, it is possible to increase genetic gains in yield from narrowing the environment(s) favourable for the varieties and thus maximizing yield in particular areas by exploiting genotype x environment interaction (Teferi, 2009; Dixon *et al.,* 1991).

The current typical potato breeding approach in Ethiopia is developing varieties by several research centres independently for different agro-ecologies for which the centres are responsible and/or located. This might not be considered as a good approach. Because the susceptibility of the majority of the varieties for late blight at environment favourable for the pathogen shows possible appearance of new races of the pathogen (A2 type) as it is not restricted to one region (Drenth *et al*., 1995; Goodwin and Sujkowski, 1995) and can be dispersed anywhere in the country. On the other hand, varieties might have lost resistance due to the ability of *P. infestans* to rapidly evolve to overcome resistant major genes (Stewart *et al.,* 2003; Wastie, 1991) and the new aggressive race of the pathogen can be distributed throughout the country. Varieties might also carry varying number of R-genes (major gene for vertical resistance), but they were all considered as resistant in the absence of the races or where the environment was not favourable for the pathogen (Beukema and Van Der Zaag, 1979).

5. Conclusion

The research revealed progressive improvement in potato varieties over a quarter of a century in the country for tuber yield and reduction of late blight severity. Raising the rate of genetic gain from 1% to more than 2% annually for the quarter of a century is considered as a key component of agricultural transformation. Therefore, potato improvement that achieved on average >1.7% in Ethiopia could be considered as a high annual rate of gain. The change in tuber yield was associated with changes in lower late blight severity score with changing of scores across locations in different varieties. Susceptibility of most of the varieties for late blight at Haramaya which was favourable for the pathogen was notable. It is also notable that three varieties, namely, Bubu, Belete and Gera performed better for tuber yield and late blight resistance across all locations. This suggests the need to change the existing potato breeding approach that depends on separate efforts of breeders to develop varieties for specific agro-ecologies. This implies developing potato varieties with high tuber yields and resistance to the late blight disease with wide agro-ecological adaptability with joint and nationally coordinated efforts of researchers and research centres across in the country.

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