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Yield, Yield-related Traits and Response of Potato Clones to Late Blight Disease, in North-Western Highlands of Ethiopia

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Abstract

Late blight disease of potato caused by *Phytophthora infestans* poses a significant threat to potato production in Ethiopia. The development of new high yielding genotypes with adequate late blight disease resistance will provide a strong component of an integrated management strategy for farmers. The objective of this study was to determine late blight resistance and yield of potato clones under field condition in north-western Ethiopia. Twenty-four clones (17 from the International Potato Centre B3C2 population and seven widely grown cultivars) were evaluated at three locations. The experiment was laid in a randomized complete block design with two replications. Late blight resistance and yield-related traits were determined. Results showed that clones differ significantly for all traits across locations. The following five clones combine high to moderate resistance to late blight with high yields: 396029.250, 395017.229, 396004.263, 396034.103 and 395077.12. These clones are useful genetic resources for resistance breeding against late blight disease and for enhanced yields.

Introduction

Ethiopia is among the ten leading sub-Saharan Africa countries in terms of area of potato production (FAOSTAT 2015). Potatoes are a source of both food and cash income in the densely populated highlands of the country, where 90% of the population resides (Gildemacher et al. 2009; Chindi et al. 2013). This makes potato a high-potential contributor to national food security (FAO 2009; Gildemacher et al. 2009). However, the national average yield of the crop is <11 t/ha, which is far below the attainable yield of 45 t/ha (Berihun and Woldegiorgis 2013; Chindi et al. 2013). Of the disease constraints that widen the gap between actual and attainable yield, late blight is the most serious (Fuglie 2007; Gildemacher et al. 2009; Forbes 2012; Sparks et al. 2014).

Potato late blight disease, caused by the heterothallic oomycete pathogen *Phytophthora infestans* (Mont.) de Bary, is a major threat that can cause complete crop failure (Trognitz et al. 2001; Fry 2008). Yield losses of 30 to 100% have been reported in Ethiopia (Kassa and Beyene 2001; Berihun and Woldegiorgis 2013). The disease damages leaves, stems and tubers and is found throughout the major potato producing areas of the country (CIP 2004; Villamon et al. 2005; Forbes 2012; Woldegiorgis 2013). The population of *P. infestans* in Ethiopia has the A1 clonal lineage mating type, which reproduces asexually with host specificity (Schiessendoppler and Molnar 2002).

Effective control of late blight disease requires integrated disease management (Mundt et al. 2002). The disease can be controlled by the application of fungicides, cultural practices such as early planting, eliminating the source of inoculum and/or using resistant cultivars (Garrett et al. 2001). However, deployment of these methods individually does not provide sufficient control of the disease. Fungicides can provide good control, but they are often unaffordable for small-scale farmers, who account for over 90% of

potato crop production in Ethiopia (Mizubuti and Forbes 2002; Schulte-Geldermann 2013). Also, fungicides can be harmful to human health and the environment. In some parts of Ethiopia, farmers plant potatoes early in the dry season to escape heavy late blight pressure, although yield levels are compromised due to insufficient soil moisture (Forbes et al. 2003). Additional factors that contribute to high levels of late blight infection are lack of certified clean seed, monocropping practiced by most farmers and the fact that tubers are left in the soil for an extended period (Chindi et al. 2013). Optimal management of potato late blight can best be achieved by incorporating durable resistance genes against virulent races of the fungus (Colon et al. 1995; Trognitz et al. 2001; Forbes 2012; Woldegiorgis 2013). This approach can be suitably integrated with other measures that fail to provide full control in isolation.

Durability of host resistance is the main concern in late blight resistance breeding (Umaerus and Umaerus 1994). Late blight resistance can be conditioned by race-specific and race non-specific or field resistance genes. It is well known that race-specific or vertical resistance is controlled by major genes. Several major genes have been identified in differential potato cultivars (Sleper and Poehlman 2006). However, the emergence of virulent pathotypes of the pathogen can rapidly overcome the resistance conferred by one or a few major genes. Consequently, the use of major genes in breeding for resistance to late blight is not recommended (Haynes et al. 2008; Forbes et al. 2014). Conversely, race non-specific or field resistance is conditioned by minor genes (Trognitz et al. 2001; Andrivon et al. 2006). Race non-specific resistance might not confer absolute protection, but is considered to be more durable than race-specific resistance, and is attributed to polygenically controlled quantitative resistance. Hence, this form of resistance is effective against a broad range of pathotypes of *P. infestans* (Bradshaw and Bonierbale 2010).

In Ethiopia, several new potato cultivars with resistance to late blight have been released to potato growers. However, a number of these cultivars have lost their resistance over time as virulent pathotypes emerged (Schulte-Geldermann 2013). Advanced resistant breeding populations and candidate clones have been developed by the International Potato Centre (CIP) for a variety of agro-ecological zones including tropical highlands (CIP 2012). This germplasm can serve as a valuable source of genetic variation in breeding programmes. Among these clones, 'population B recombination cycle 3 (Pop B3)', which lacks any known major or R genes (R1 to R11) against *P. infestans*, is the latest advanced source released by the CIP for durable late blight resistance (Landeo et al. 2001; Yao et al. 2011). Some of the clones derived from this population have shown promising performance in Ethiopia and of these CIP-393371.58 was released under the name 'Belete' in 2009 (CIP 2012).

Potato breeding in Ethiopia has generally focused on evaluating advanced clones developed by CIP for productivity and late blight resistance. However, little work has been done to identify locally adapted late blight resistant clones that could be used as parents by Ethiopian breeders (CIP 2012; Woldegiorgis 2013). Therefore, the objectives of this study were to (i) determine late blight resistance and (ii) yield of potato clones under field conditions in north-western Ethiopia, to identify those most suitable as parents for local breeding.

Material and Methods

Plant materials

The study used 24 potato genotypes. Seventeen clones were obtained from CIP, and seven were cultivars widely adapted to the mid- and high-altitude environments (>1500 metre above sea level) of Ethiopia (Table 1). The clones sourced from CIP are from population B group three, cycle two (B3C2) and have quantitative resistance to late blight. 'Guassa', a widely grown, high yielding (Woldegiorgis 2013; Shibabaw et al. 2014) but moderately susceptible cultivar, was used as a comparative control.

Study sites

The study was carried out at three selected locations in north-western Ethiopia: Injibara, Adet and Debark during the main cropping season (June to October 2014). These sites represent the main potato production areas in north-western Ethiopia. All three sites experience high late blight pressure during the rainy season. Injibara (10°57′N, 36°56′E) is located at an altitude of 2568 m above sea level (masl). The mean annual temperature and rainfall are 15°C and 1700 mm, respectively. The soils at this site are predominantly Nitosol (Shibabaw et al. 2014). Adet (11°17′N, 37°47′E) is situated at an altitude of 2240 masl and receives a mean total annual rainfall of 1238 mm with mean annual temperature of 17°C, with mainly red brown Nitosol soils (Zegeye et al. 2010). Debark (13°14′N, 37°89′E) is situated at an altitude of 2836 masl and receives a mean total annual rainfall of 974 mm with a mean annual temperature

Table 1 List of potato genotypes used in the study

No[a]	Genotype	Pedigree	Reported late blight reaction[b]	Population
1	392633.64	387132.2 × 387334.5	Resistant	B3C2
2	393220.54	381400.22 × 387170.9	Resistant	B3C2
3	395011.2	393085.5 × 392639.8	Resistant	B3C2
4	395015.6	393083.2 × 391679.12	Moderately resistant	B3C2
5	395017.14	393085.13 × 392639.8	Moderately resistant	B3C2
6	395017.229	393085.13 × 392639.8	Resistant	B3C2
7	395077.12	391586.109 × 393053.6	Resistant	B3C2
8	395096.2	393085.5 × 393053.6	Moderately resistant	B3C2
9	395109.34	391589.26 × 393079.4	Resistant	B3C2
10	395112.32	391686.15 × 393079.4	Moderately resistant	B3C2
11	396004.26	391002.6 × 393382.64	Moderately resistant	B3C2
12	396029.250	392633.54 × 393382.64	Resistant	B3C2
13	396031.108	392633.64 × 393382.64	Resistant	B3C2
14	396034.103	393042.5 × 393280.64	Resistant	B3C2
15	396038.101	393077.54 × 393280.64	Moderately resistant	B3C2
16	396038.105	393077.54 × 393280.64	Moderately resistant	B3C2
17	396038.107	393077.54 × 393280.64	Moderately resistant	B3C2
18	Belete	387170.16 × 389746.2	Resistant	B3C2
19	Gorebella	380088.4 × MEX BULK	–	Pop A[c]
20	Guassa	380479.15 × 3 BULK	Moderately susceptible	Pop A
21	Jalene	380479.15 × 3 BULK	–	Pop A
22	Shenkola	382132.14 × XY.13	Moderately susceptible	Pop A
23	Gudene	–	Moderately resistant	Pop A
24	Aba Adamu	Farmer's cultivar	–	–

[a]Genotypes 1 to 17 were acquired from the International Potato Centre, while 18 to 23 are Ethiopian cultivars selected from CIP germplasm, and 24 is an Ethiopian cultivar of unknown origin.
[b]The information for B3C2 clones was obtained from the CIP's website (http://www.cipotato.org).
[c]Population A contains major (R) gene for late blight resistance.

of 12.4°C. It has predominantly Luvic Andosols soils (Assen and Tegene 2008). All three locations have a monomodal rainy season that occurs between May and October, except for Injibara with rainy months extending from March to the end of November (Shibabaw et al. 2014).

Seed potato preparation and experimental set up

Disease-tested plantlets of 17 clones from a B3C2 population developed by CIP for non-specific resistance to late blight (Landeo et al. 1995) along with one local cultivar of unknown origin (Aba Adamu) and six Ethiopian cultivars (that had been developed jointly with CIP) were acquired from CIP and the tissue culture laboratory of the Amhara Regional Agricultural Research Institute (ARARI-TCL). Initial multiplication of plantlets was conducted by ARARI-TCL. Plantlets were then transplanted to a screen house and harvested in June 2013. Harvested tubers were kept in diffused light storage (DLS) system for 4 months to break dormancy. Tubers were planted for further multiplication in a field (at Injibara) in November 2013 under virus-free conditions (cold highland and using insecticides to control virus vectors). Tubers were then harvested and kept for 4 months prior to planting for the field tests.

A total of 24 entries were planted in the field during the rainy season. Two spray regimes (sprayed and unsprayed) were used at Injibara and Adet for comparative study. The two treatments were arranged in separate experiments. The distance between the experiments was 3 m. The trials were established using a randomized complete block design with two replications per each spray regime and in each location in June, 2014. In the unsprayed treatment, genotypes were exposed to natural infection using spreader rows of a susceptible local cultivar 'Enatbeguaro' to keep continuous infection pressure during the period of disease assessment. No pesticides or fungicides were applied in the unsprayed regime except in Adet where late blight occurred early (2 weeks after planting). In Adet, a contact fungicide (Mancozeb) was applied once in the second week after planting to maintain the genotypes. In the control or sprayed treatment, Ridomil MZ 72 (8% a.i.

metalaxyl + 64% a.i. mancozeb), Bravo (82.5% WP Chlorothalonil), Tanos (250 g/kg cymoxanil, 250 g/kg famoxadone) and Mancozeb (80% WP) were sprayed alternatively at weekly intervals per the recommendation of the manufacturer. Spraying started 2 weeks after planting and continued until the end of the season. At Debark, however, genotypes were evaluated only under unsprayed condition because there was not enough seed to plant control plots.

Each genotype was represented by an experimental unit consisting of 40 plants established in a plot of 9 m^2 (each plot had four rows, each row was 3 m long, with 0.75 m inter- and 0.3 m intrarow spacing). All necessary agronomic practices such as weeding and ridging were carried out by using hoe and hand cultivation. Phosphorus fertilizer in the form of diammonium phosphate was applied at the rate of 69 kg/ha and nitrogen at 81 kg/ha in the form of urea. The entire dose of phosphorus and half the dose of nitrogen were applied at planting; the other half of nitrogen was added 45 days after planting.

Data collection

Data collected included percentage of leaf area affected by late blight, from which area under disease progress curve (AUDPC) and days to 5% disease severity threshold determined, relative yield loss (RYL %) percentage, total tuber weight, marketable tuber weight, total tuber number per plant and marketable tuber number per plant.

Area under disease progress curve

Late blight disease severity was recorded visually as percentage of foliage affected at weekly intervals starting with the first appearance of the symptoms until the susceptible control had reached 100% infection. The percentage of late blight affected leaf area per plot was estimated using a scale comprising nine classes, corresponding to 0.01, 0.1, 1, 5, 25, 50, 75, 95 and 100% of diseased leaf tissue (Fry 1978; Niks et al. 2011). For all plots and assessment dates, the area under the disease progress curve AUDPC (Campell and Madden 1990) was calculated using the following formula:

$$\mathrm{AUDPC} = \sum_{i=1}^{n-1} \frac{[(t_{i+1} - t_i)(y_{i+1} + y_i)]}{2}$$

where 't' is the time of each reading, 'y' is the percentage of affected foliage at each reading, and n is the number of readings.

Area under disease progress curves were standardized to give relative area under the disease progress curve (rAUDPC) by dividing the AUDPC by the maximum potential AUDPC (Fry 1978) to allow for comparison between different locations. The maximum potential AUDPC is calculated by multiplying the total number of days between the first and last readings by 100 as shown in the formula below.

$$\mathrm{rAUDPC} = \frac{\mathrm{AUDPC}}{(\text{Last reading day} - \text{First reading day}) \times 100}$$

An interval susceptibility scale (0–9) was calculated as described by Yuen and Forbes (2009) using the rAUDPC value resulting in low values for resistance and high values for susceptible ones. In order to use this scale, the cultivar Guassa was assigned a susceptibility value of 6 based on its moderate susceptibility.

Days to 5% disease severity threshold (DT_5)

The number of days after planting for the plants to reach the 5% disease level for each plot was also estimated and assigned as days to 5% disease severity threshold (DT_5) as proposed by Dorrance et al. (2001). The measurement of DT_5, could include the major components of partial resistance such as infection efficiency, latent period and lesion growth rate (Dorrance et al. 2001; Pariaud et al. 2009). This makes DT_5 an important parameter especially under natural epidemics under field condition, where it is a difficult task to quantify inoculum dosage or control timing of inoculation (Dorrance et al. 2001).

Yield and yield-related traits

At harvest, yield was measured for each plot. Total tuber yield was calculated by converting the total weight of all the tubers harvested in a plot in t/ha. Total tuber yield from sprayed plots was compared with those from the unsprayed plots to obtain relative yield loss. Percentage relative yield loss (RYL%) was calculated as the ratio of the difference between the yield obtained from sprayed control and the unsprayed plots to the yield of the sprayed control as shown in the formula below:

$$\mathrm{RYL}\% = \frac{(\text{Tuber yield of the sprayed plot} - \text{Yield of unsprayed plot})}{\text{Yield of sprayed plot}} \times 100$$

Tubers of each plot were graded into three categories: >30 mm (marketable), <30 mm (unmarketable), and rotten and diseased (discarded) and were counted and weighted in kg. From the above grading, marketable tuber yield was expressed in t/ha, and the number of total tubers per plant and number of marketable tubers per plant were calculated. The relative reduction of marketable tuber yield, total tuber number and marketable tuber numbers was also calculated as RR = (sprayed – unsprayed)/sprayed and expressed as a percentage.

Data analysis

Data were subjected to analysis of variance (ANOVA) using GenStat for Windows 17th edition (Payne et al. 2014). Mean separation was performed using the least significant difference (LSD) procedure at a 5% probability level. Spearman correlation coefficient values were calculated to determine trait associations. Separate ANOVA was initially conducted per location with genotypes as the main effect. Homogeneity of variance was tested using Bartlett's test (Snedecor and Cochran 1989). Later combined ANOVA was calculated across locations.

Results

Weather conditions

Mean monthly temperatures and rainfall were recorded at each site (Table 2). Adet experienced lower rainfall and higher temperatures than the other two locations. Highest rainfall was encountered at Injibara, whereas the lowest temperature was recorded at Debark. This indicates that the fungal pathogen was exposed to a wide range of environments during the cropping season.

Analyses of variance

Analyses of variance for the traits measured are presented in Table 3. Highly significant ($P < 0.001$) differences were detected among genotypes for all the traits examined in each location. The sites also exhibited significant differences. Heterogeneity of error variances was observed from Bartlett's test for all the traits except for days to 5% disease severity threshold (DT_5). However, Dagnelie (as cited in Annicchiarico 2002) explained that when the regression slope (b) of experimental error mean square on environmental mean of a trait approaches zero, transformation of data is not required. Hence, combined analysis was performed with no transformation, since $b \approx 0$ for all traits that exhibited heterogeneous error variances.

The combined analysis of variance showed highly significant ($P < 0.001$) interactions of genotype × environment, genotype × treatment, treatment × environment and genotype × treatment × environment for all the parameters measured except for the treatment × environment interaction for total and marketable tuber numbers per plant.

Late blight disease severity

Late blight developed in the unsprayed plots across all three test environments. Late blight developed uniformly on the susceptible spreader row until the vines were 100% blighted. No disease was detected in the fungicide-treated plots both at Adet and Injibara. In general, Adet had lower rAUDPC (0.18) followed by Debark (0.24), while Injibara had the highest rAUDPC (0.31) (Table 4). The lower rAUDPC value at Adet could be associated with the relatively dry weather experienced during the study period (Table 2). The rAUDPC values for individual genotypes at the three environments varied from 0.01 (most resistant) to 0.63 (most susceptible). A comparison of rAUDPC values within locations and averaged across locations had the following ranges for the genotypes with the lowest scores: 396004.263 (0.04–0.13), 396038.105 (0.01–0.20), 396029.250 (0.02–0.17), 393220.54 (0.04–0.25) and 395011.2 (0.05–0.24). In contrast, rAUDPC was greatest on local and newly released cultivars, including Shenkola (0.31–0.53), Jalene (0.30–0.48), Guassa (0.25–0.45), Aba Adamu (0.27–0.52) as well as B3C2 clones such as 395015.6 (0.26–0.54) and

Table 2 Total monthly rainfall and temperatures of the sites during the study (Ethiopian Meteorology Agency)

	Total monthly rainfall (mm)						Mean monthly air temperature (C)					
Sites	June	July	August	September	October	Total	June	July	August	September	October	Mean
Injibara	265.8	427.5	405.9	399.3	114.6	1613.1	17.5[a]	16.8	16.2	15.9	17.2	16.5
Adet	130.6	204.9	194.1	151.8	108.5	789.9	19.6	18.7	17.6	17.8	18.3	18.4
Debark	108.5	231.5	290.5	201.0	44.1	875.6	15.0	14.2	13.6	13.8	13.8	14.1

[a]Temperature data at Injibara obtained from personal data logger (Watchdog Data Logger, Spectrum Technologies, Plainfield, IL, USA).

Table 3 Analysis of variance involving 24 clones at three locations during 2014 growing season

Location		Traits and mean squares						
Source of variation	Df	rAUDPC	DT_5	TTW	MTW	TTN	MTN	RYL%
Injibara								
Rep	1	0.036	252	2.55	2.26	0.215	0.239	371.7
Gen	23	0.032***	132***	11.70***	11.70***	3.387***	2.596***	568.3***
Residual	23	0.003	25	1.15	1.14	0.399	0.513	128.6
CV (%)		16.4	8.0	16.4	18.3	13.1	21.8	20
Adet								
Rep	1	0.0001	3	48.23	57.65	0.267	0.519	0.73
Gen	23	0.0206***	98***	56.69***	51.41***	18.58***	11.041***	406.3***
Residual	23	0.0014	19.4	12.62	10.1	3.16	1.299	37.88
CV (%)		20.4	6.0	9.2	8.9	16.5	13.2	26.0
Debark								
Rep	1	0.0004	6.75	57.72	51.007	0.012	6.822	
Gen	23	0.0661***	154**	70.236***	63.495***	14.35***	8.865***	
Residual	23	0.0044	42.6	4.461	4.414	2.932	1.344	
CV (%)		27.7	9.4	8.8	9.6	15.3	13.2	
Combined analysis of genotype and environment in experiments under late blight pressure								
Rep (Env)	1	0.0086	75.1	0.294	1.274	0.252	0.656	
Gen	23	0.0742***	266***	51.771***	53.716***	16.24***	9.916***	
Env	2	0.2076***	1356***	12477***	10829***	611.7***	470.06***	
Gen.Env	46	0.0222***	59**	43.425***	36.445***	10.04***	6.293***	
Residual	71	0.0031	30.9	7.428	6.616	2.106	1.12	
CV (%)		22.8	11.8	12.1	16.2	15.3	22.8	
Combined analysis of genotype, treatment and environment (Adet and Injibara)								
Rep (Env)	1			108232	131055	2.498	0.013	
Gen	23			99739***	99260***	35.17***	20.984***	
Env	1			29831368***	25885381***	1816.24***	1392.052***	
Trt	1			3707693***	3458444***	336.28***	278.348***	
Gen.Env	23			96228***	95304***	22.75***	16.616***	
Gen.Trt	23			50764***	45331***	6.68***	5.247***	
Env.Trt	1			193855***	167242***	1.641 ns	0.181 ns	
Gen.Trt.Env	23			42785***	40923***	8.19***	5.152***	
Residual	95			3908	4115	1.73	0.879	
CV (%)				9.6	10.6	14.4	13.1	

ns, non-significant; Df, degrees of freedom; AUDPC, area under the disease progress curve; rAUDPC, relative area under disease progress curve; DT_5, days to 5% disease severity threshold; TTY, total tubers yield; MTY, marketable tubers yield; TTN, total tuber numbers; MTN, marketable tuber numbers; RYL%, relative yield loss percentage; Rep, replication; Gen, genotype; Env, environment; Trt, treatment.
Significance levels: **Significant at $P \leq 0.01$; ***Significant at $P \leq 0.001$.

395112.32 (0.25–0.63). All of the local and newly released cultivars were in the higher half of the interval susceptibility scale among the 24 clones tested, except Gudene. Some clones were highly variable in their rAUDPC values across the three locations. For example, Belete had higher rAUDPC value of 0.42 at Adet than at Injibara (0.21) and Debark (0.07), with susceptibility scale scores ranging from 1 (Debark) to 9 (Adet).

Days to 5% disease severity threshold (DT_5)

Days to 5% disease severity threshold (DT_5) was shorter at Injibara (62.5) due to the early onset of late blight followed by Debark (69.4) and Adet (73.0) (Table 5). The first late blight lesions at Injibara were observed approximately 6 week after planting. In contrast, at Adet the first lesions were not observed until many of the genotypes had begun to flower. Most genotypes with low rAUDPC such as clones 396004.263, 396029.250, 396038.105, 395017.229 and 395011.2, reached their 5% disease severity late, whereas Guassa, Jalene, Gorebella, Shenkola, 396038.107, 395015.6, and 395112.32 developed late blight lesions early.

Yield loss

A reduction in tuber yield was observed for all genotypes in diseased plots compared to sprayed plots

Table 4 Relative area under the disease progress curve (rAUDPC) and susceptibility scale of 24 potato genotypes evaluated at three environments under late blight disease pressure

		Injibara		Adet		Debark		Mean	
	Genotype	rAUDPC[a]	Scale[b]	rAUDPC	Scale	rAUDPC	Scale	rAUDPC	Scale
1	396004.263	0.13 k	2	0.04 j,k	1	0.05 g,h	1	0.07	1
2	396029.250	0.17 k	2	0.04 k	1	0.02 i	0	0.08	1
3	396038.105	0.20 i–k	3	0.01 l	0	0.04 h,i	1	0.08	1
4	393220.54	0.25 d–h	3	0.14 g–j	3	0.04 h,i	1	0.14	2
5	395011.2	0.24 f–j	3	0.17 c–h	4	0.05 g,h	1	0.15	2
6	Gudene	0.13 k	2	0.17 c–f	4	0.18 e,f	3	0.16	3
7	395096.2	0.30 c–g	4	0.14 f–i	3	0.05 h	1	0.16	3
8	395109.34	0.19 j,k	3	0.08 g–j	2	0.20 d,e	3	0.16	3
9	395017.229	0.34 a–e	5	0.10 c–g	4	0.06 e–g	1	0.19	3
10	396034.103	0.22 e–i	3	0.21 c–f	5	0.15 e–g	2	0.19	3
11	396031.108	0.22 g–j	3	0.15 f–i	4	0.24 b–e	4	0.21	3
12	395077.12	0.31 c–g	4	0.10 g–j	2	0.22 c–e	3	0.21	3
13	Gorebella	0.36 a–e	5	0.08 j,k	2	0.24 c–e	3	0.23	4
14	Belete	0.21 h–k	3	0.42 a	9	0.07 f–h	1	0.23	4
15	395017.14	0.53 a,b	7	0.14 f–i	3	0.20 e,f	3	0.29	5
16	396038.101	0.32 b–f	4	0.16 c–i	4	0.41 a–c	6	0.29	5
17	392633.64	0.32 a–f	4	0.22 c–f	5	0.48 a–c	7	0.34	6
18	395015.6	0.54 a	7	0.26 c–f	6	0.28 a–e	4	0.36	6
19	Guassa	0.45 a–d	6	0.25 b–e	6	0.40 a–c	6	0.37	6
20	Aba Adamu	0.27 d–h	4	0.32 a,b	8	0.52 a,b	8	0.37	6
21	396038.107	0.43 a–d	6	0.20 c–f	5	0.52 a,b	8	0.38	6
22	Jalene	0.48 a–c	6	0.30 a–c	7	0.37 a–d	6	0.39	6
23	Shenkola	0.53 a	7	0.34 a,b	8	0.31 a–d	5	0.39	6
24	395112.32	0.41 a–e	5	0.25 a–d	6	0.63 a	9	0.43	7
	Mean	0.31		0.18		0.24		0.24	
	CV (%)	16.4		20.4		27.7			

rAUDPC, relative area under disease progress curve.

[a]means in a column followed by the same letter(s) are not significantly different at $P < 0.05$.

[b]Susceptibility scale, values were rounded to the nearest whole number.

(Table 5). However, there was wide variation in the RYL among environments and genotypes. Yield loss ranged from 16 to 88% at Injibara and from 6 to 46% at Adet. At Injibara, the lowest yield reduction occurred with Gudene (16%), 396029.250 (22%) and 395109.34 (43%), while the highest loss was recorded with 395017.14 (88%), 395015.6 (82%) and Jalene (77%). At Adet, the clones with low yield loss were 395011.2 (6%), Shenkola (7%) and 396004.263 (8%). The genotypes Guassa, Jalene and Gorebella had the highest yield losses recorded at 46, 45 and 40%, respectively. Average relative yield loss percentage for two locations revealed that clones 396029.250, Gudene, 392633.64, 395011.2, 396004.263 and 396034.103 were among the most tolerant/resistant genotypes with the lowest yield loss when compared to the rest of the clones. The cultivars Guassa and Jalene were heavily infected, with yield losses estimated at 61%. Most of the genotypes that had lower rAUDPC and DT_5 showed lower yield reduction. However, there are some genotypes that had lower yield levels than expected. For example, clone 396038.105 exhibited a low rAUDPC value. However, it showed yield loss of >40% indicating the high sensitivity of the genotype to late blight disease. Conversely, genotypes 392633.64, Aba Adamu, Shenkola and 395112.32 had high rAUDPC values, were >5 on the susceptibility scale and exhibited short DT_5, yet yield loss (<40%) was not as severe. This could be attributed to their tolerance to late blight infection.

Total tuber yield

There was significant variation in total tuber yield among the tested clones under late blight infection across the three locations (Table 6). Overall, the highest yield was recorded at Adet (38.8 t/ha) followed by Debark (23.9 t/ha) and Injibara (6.54 t/ha). At Injibara, the clones 396034.103, Belete and 396029.250

Table 5 Days to 5% disease severity threshold and relative yield loss of 24 potato clones when evaluated across three environments

Genotype	Days to 5% disease severity (DT_5)				Relative yield loss%		
	Injibara	Adet[a]	Debark	Mean	Injibara	Adet	Mean
396029.250	72.0 a,b	83.0 a,b	90.5 a	81.8	22 g,h	34 a–d	28
396004.263	75.0 a	83.0 a,b	79.0 a	79.0	58 a–f	8 i	33
395011.2	67.5 a–c	78.0 a–c	82.5 a	76.0	53 c–f	6 i	30
396038.105	67.0 a–c	88.0 a	71.0 a,b	75.3	47 d–g	39 a,b	43
395017.229	68.5 a,b	78.0 a–c	79.0 a	75.2	62 a–f	12 h,i	37
393220.54	67.0 a–c	78.0 a–c	79.0 a	74.7	50 c–f	23 c–h	37
Belete	72.0 a,b	66.0 d,e	85.0 a	74.3	53 c–f	33 a–d	43
395096.2	67.5 a–c	78.0 a–c	71.0 a,b	72.2	53 c–f	21 d–i	37
395077.12	65.0 a–d	83.0 a,b	67.5 a–c	71.8	62 a–f	27 b–g	45
Gudene	65.0 a–d	78.0 a–c	67.5 a–c	70.2	16 h	15 g–i	15
396034.103	60.5 b–f	73.5 b–d	71.0 a,b	68.3	54 b–f	13 f–i	33
396031.108	67.0 a–c	69.0 c–e	67.5 a–c	67.8	51 c–f	30 b–f	40
395109.34	67.5 a–c	69.0 c–e	64.0 a–d	66.8	43 e–g	33 a–d	38
Aba Adamu	69.5 a,b	67.5 c–e	60.0 d,e	65.7	53 c–f	16 e–i	34
392633.64	62.5 b–e	72.0 c,d	60.0 b–e	64.8	51 c–f	8 i	30
395017.14	56.0 c–g	73.5 b–d	64.0 a–d	64.5	88 a	28 b–e	58
396038.101	62.5 b–e	67.5 c–e	62.0 b–e	64.0	43 f,g	37 a–c	40
395112.32	65.0 a–d	67.5 c–e	58.0 e	63.5	62 a–f	16 e–i	39
Shenkola	53.5 d–g	66.0 d,e	67.5 a,b	62.3	71 a–e	7 i	39
395015.6	51.0 e–g	66.0 d,e	67.5 a–c	61.5	81 a,b	13 f–i	47
Gorebella	49.0 f,g	69.0 c–e	64.0 a–d	60.7	62 c–f	40 a,b	51
Jalene	48.5 g	67.5 c–e	65.5 a–c	60.5	77 a–c	45 a	61
Guassa	47.5 g	69.0 c–e	62.0 b–e	59.5	76 a–c	46 a	61
396038.107	53.5 d–g	61.0 e	60.0 c–e	58.2	75 a–d	23 c–h	49
Mean	62.5	73	69.4	68.3	57	24	40.4
CV (%)	8	6	9.4		20	26	

[a]Means in a column followed by the same letter(s) are not significantly different at $P = 0.05$.

with mean yields of 12.3, 10.4 and 10.0 t/ha, respectively, were the best yielding and these clones are not significantly different in terms of total yield. At Adet, the highest yielding clones under late blight epidemics were 396038.107 (48.8 t/ha), 396038.105 (47.0 t/ha) and 395017.229 (46.6 t/ha). At Debark, the clones 396038.105 (38.2 t/ha), Belete (32.4 t/ha) and Guassa (31.5 t/ha) had the highest yields. The best yielding cultivars in each location were resistant genotypes that showed scores of 4 or less on the interval susceptibility scale except for 396038.107 (Adet) and Guassa (Injibara). This suggests high yield potential for these two clones, although both had high (>50%) average yield loss.

Marketable tuber yield

Locations ranked the same for marketable tuber yield (MTY) and total tuber yield. The highest MTY was recorded at Adet (35.9 t/ha) followed by Debark (21.9 t/ha) and Injibara (5.8 t/ha). The loss in marketable yield, however, was relatively higher than the total tuber yield. At Injibara, marketable yield was reduced by 62% due to late blight. At Adet, the yield loss was 27% (Table 7).

Total tuber numbers

Under late blight infection, the highest total tuber numbers per plant was recorded at Debark (11.2) followed by Adet (10.8) and Injibara (4.8) (Data not shown). At Injibara, the genotypes 396034.103 (with 8.2 tubers per plant), 395077.12 (7.2) and Gudene (7.0) had the highest number of tubers per plant. At Injibara, the total tuber number showed 33% average reduction in unsprayed plots. At Adet, the clones with highest tuber number under late blight endemics were 395077.12 (16.8), Jalene (16.3) and Guassa (15.4). Tuber number had 19% average reduction due to late blight. At Debark, clones with the highest total number were Belete (17.5), 396031.108 (15.8) and Guassa (14.6).

Marketable tuber numbers

Marketable tuber numbers for each genotype in each location under natural late blight infestation ranked

Table 6 Total tuber yield of 24 potato genotypes under late blight pressure when evaluated at three environments in north-western Ethiopia

Genotypes	Sites and total tuber yield (t/ha)			
	Injibara[a]	Adet	Debark	Mean
396038.105	8.3 b–d	47.0 a,b	38.2 a	31.2
395017.229	6.8 c–g	46.6 a,b	28.0 b–e	27.1
395077.12	7.5 c–e	41.6 a–e	29.0 b–d	26.0
396034.103	12.3 a	36.6 d–h	27.2 c–e	25.3
Guassa	4.8 f–j	39.5 b–g	31.5 b,c	25.3
396029.250	10.0 a,b	36.0 d–h	29.7 b–d	25.2
Belete	10.4 a,b	30.9 h	32.4 b	24.6
396004.263	5.0 e–j	40.4 a–f	28.0 b–e	24.5
396038.101	7.1 c–f	42.6 a–d	21.9 f–h	23.8
396038.107	4.5 g–k	48.8 a	17.7 h,i	23.7
395112.32	5.9 d–j	46.2 a–c	18.8 g–i	23.6
393220.54	6.8 c–g	36.2 d–h	25.8 d–f	22.9
395109.34	9.0 b,c	30.3 h	29.2 b–d	22.8
392633.64	5.6 e–j	41.5 a–e	20.0 g,h	22.4
Gorebella	7.3 c–f	35.7 d–h	23.6 e–g	22.2
395011.2	4.1 h–k	41.8 a–e	19.9 g,h	22.0
Shenkola	3.8 i–k	37.7 c–h	23.5 e–g	21.6
395017.14	2.2 k	41.4 a–e	20.9 g,h	21.5
Jalene	4.1 h–k	40.9 a–e	18.7 g–i	21.2
395096.2	6.5 d–h	37.2 d–h	19.1 g–i	20.9
Gudene	8.3 b–d	31.9 f–h	20.9 g,h	20.4
396031.108	7.4 c–e	31.6 g,h	18.6 g–i	19.2
Aba Adamu	6.0 d–i	34.0 d–h	14.3 i	18.1
395015.6	3.4 j,k	33.7 e–h	17.0 h,i	18.0
Mean	6.5	38.8	23.9	23.1
CV (%)	16.4	9.2	8.8	

[a]Means in a column followed by the same letter(s) are not significantly different at P = 0.05.

similarly to total tuber numbers (Data not shown). The highest number of marketable tubers was recorded at Debark (8.8) followed by Adet (8.6) and Injibara (3.3). At Injibara, the genotypes 396034.103 (6.3), Belete (5.2) and 395077.12 (5.1) had the highest number of marketable tubers. At Adet, the clones with highest tuber numbers under late blight epidemics were 395077.12 (14.2), Jalene (12.9) and 395017.229 (11.7). At Debark, the genotypes Belete (14.7), 395077.12 (12.2) and Guassa (11.8) had highest total tuber numbers.

Marketable tuber numbers were reduced by 41 and 20% at Injibara and Adet, respectively. In general, the results revealed that late blight disease affected all the measured yield parameters at both Injibara and Adet although disease severity differed among genotypes. The disease had a significant effect on marketable and total yield leading to average reductions of 44 and 40%, respectively. Late blight had a significant, but lesser effect on total and marketable tuber numbers, with average reductions of 26 and 31%, in that order.

Relationships between yield and disease resistance parameters

Spearman's rank correlation coefficients were calculated among the AUDPC, DT_5, RYL%, TTY, MTY, TTN and MTN to determine associations between the parameters assessed (Table 8). Due to the presence of clone × location interactions, the correlation analysis is presented for each location separately. Significant negative correlations were detected between AUDPC and DT_5 across the three environments ($P < 0.001$). AUDPC had a negative correlation with TTY and MTY at Injibara and Debark ($P < 0.001$), and with TTN and MTN at Injibara ($P < 0.01$) and Debark ($P < 0.05$). Conversely, non-significant correlation was observed between AUDPC and yield and yield-related traits at Adet. DT_5 had a significant and positive correlation ($P < 0.01$) with TTY and MTY at Debark and Injibara and a significant correlation ($P < 0.05$) at Adet. Similarly, DT_5 had significant ($P < 0.05$) and positive correlation with MTN and TTN at Debark, highly significant ($P < 0.01$) and significant ($P < 0.05$) correlation with MTN at Injibara and Adet, respectively. However, only a weak association was detected between DT_5 and TTN at both Injibara and Adet. Total tuber yield had highly significant ($P \leq 0.01$) and positive correlation with MTY, TTN and MTN in all the environments. A positive correlation was found between relative yield loss and AUDPC at both Injibara ($P < 0.001$) and Adet ($P < 0.01$). At Injibara, relative yield loss had a highly significant ($P < 0.01$) and negative correlation with DT_5, TTY, MTY, TTN and MTN. Significant and negative correlation was found between relative yield loss and TTN ($P < 0.01$) and MTN ($P < 0.05$) at Adet.

Discussion

The present study evaluated the disease and yield responses of 24 selected potato clones to late blight at three major potato growing locations in the highlands of north-western Ethiopia. The study included 17 clones from a B3C2 population developed by CIP for non-specific resistance to late blight (Landeo et al. 1995), as well as one widely grown local cultivar and six newly released cultivars. Disease development varied across locations resulting in differential responses of genotypes for late blight severity and yield reduction. AUDPC values were the highest, DT_5 was shorter, relative yield loss was greater, and total and

Table 7 Marketable tuber yield of 24 potato genotypes when evaluated at three late blight affected environments with and without chemical control

	Unsprayed				Sprayed		
Genotypes	Injibara[a]	Adet	Debark	Mean	Injibara	Adet	Mean
396038.105	7.7 b–e	46.4 a	35.9 a	30.0	15.4 d–i	72.2 a	43.8
395077.12	6.6 d–g	40.0 a–d	28.3 b	25.0	19.0 b–d	56.2 b	37.6
396029.250	9.2 a–c	35.1 b–g	28.5 b	24.3	12.5 i–m	52.7 b–e	32.6
396034.103	11.2 a	35.7 b–g	25.7 b–d	24.2	25.9 a	41.7 g,h	33.8
395017.229	5.6 e–j	41.7 a,b	23.4 c–e	23.6	17.1 c–g	51.8 b–f	34.4
Guassa	4.0 h–k	38.4 b–e	28.4 b	23.6	19.6 b,c	72.9 a	46.2
Belete	9.9 a,b	28.9 g–i	30.3 b	23.0	20.7 b	42.7 f–h	31.7
396038.101	6.6 d–g	39.4 a–e	20.9 d–g	22.3	11.6 k–m	68.1 a	39.9
396004.263	4.1 g–k	37.1 b–f	23.5 c–e	21.6	11.1 k–m	41.5 g,h	26.3
395011.2	3.7 i–l	40.5 a–c	19.0 e–h	21.1	7.6 n	43.1 e–h	25.4
392633.64	5.2 e–j	38.2 b–f	19.3 e–h	20.9	10.9 l–n	44.1 d–h	27.5
395017.14	1.5 l	40.0 a–d	20.5 e–g	20.7	17.9 b–f	54.4 b,c	36.1
395096.2	6.0 e–i	36.7 b–f	18.1 f–h	20.3	13.1 h–l	45.6 c–h	29.4
393220.54	6.3 d–h	31.8 e–h	22.1 c–f	20.1	13.2 h–l	43.4 e–h	28.3
Jalene	3.6 i–l	39.4 a–e	17.4 f–i	20.1	17.0 c–g	68.5 a	42.8
395112.32	5.5 e–j	37.9 b–f	16.7 g–i	20.0	14.6 f–k	50.7 b–g	32.7
395109.34	8.8 b–d	23.9 i	26.8 b,c	19.9	15.3 e–j	31.8 i	23.6
396038.107	4.0 h–k	38.3 b–f	17.0 g–i	19.8	16.6 c–h	42.8 f–h	29.7
Gorebella	6.7 d–g	32.1 e–h	19.0 e–h	19.3	18.4 b–e	53.3 b–d	35.9
Gudene	7.2 c–f	30.6 f–i	17.9 f–h	18.6	9.5 m,n	35.9 h,i	22.7
Aba Adamu	5.1 f–j	33.4 c–h	12.8 i	17.1	11.8 j–m	38.8 h,i	25.3
396031.108	6.4 d–h	27.4 h,i	16.7 g–i	16.9	14.2 g–l	44.8 c–h	29.5
395015.6	2.0 k,l	32.4 d–h	14.7 h,i	16.4	16.9 c–g	37.5 h,i	27.2
Shenkola	3.2 j–l	34.9 b–h	23.1 c–e	20.4	12.9 i–m	39.1 h,i	26.0
Mean	5.8	35.9	21.9	21.2	15.1	48.9	32
CV (%)	18.3	8.9	9.6		10	8.4	

[a]Means in a column followed by the same letter(s) are not significantly different at P = 0.05.

marketable yields were the lowest at Injibara followed by Debark and Adet. The severity of late blight and associated yield reduction seems to be correlated with the amount of precipitation received during the growing season (Table 2). Umaerus and Umaerus (1994) and Hannukkala et al. (2007) also explained that environment plays a considerable role in the development of late blight. Temperature and humidity are the principal factors that affect disease development. Generally, moderate temperatures (10–25°C) and wet conditions (100% relative humidity) are required for sporulation (Harrison 1992). The present study found that Injibara, which had the most favourable environment for late blight disease development, had the highest disease severity, providing the best discrimination among the tested clones. The lower coefficient of variation recorded for AUDPC and relative yield loss percentage also confirms more uniform disease development at Injibara than the other sites.

Significant genotype × location interaction was observed for late blight resistance, yield and yield-related traits. The tested clones exhibited interval susceptibility scale differences <4 across the three locations, except for cultivar Belete (Fig. 1). Interestingly, Belete displayed the highest late blight susceptibility at Adet despite the relatively low disease pressure there. However, this clone was among the most resistant genotypes at both Injibara and Debark. The present findings differ from the observation of Haynes et al. (1998) who reported that highly resistant and susceptible genotypes were the most stable but that some of the intermediate clones were less stable. Observation of partially resistant clones behaving differently to *Phyphthora* infection in different locations has also been reported by Parker et al. (1992), Mulema et al. (2004) and Forbes et al. (2005). The discrepancies in late blight severity shown in some genotypes across locations could be associated with isolate variability, adaptation of the pathogen to quantitative resistance, environmental difference and/or a combination of all (Flier et al. 2003; Forbes et al. 2005). The population of the potato late blight pathogen in Ethiopia is A1 mating type, US-1 clonal lineage plus mtDNA haplotype Ia (Schiessendoppler and Molnar 2002). Thus, the interaction effect could be associated with the presence of an unknown

Table 8 Pairwise correlation coefficients showing association of late blight disease and yield-related parameters of 24 potato clones tested at three sites in north-western Ethiopia

Traits	AUDPC	DT_5	TTY	MTY	TTN	MTN
Injibara						
AUDPC	1.00					
DT_5	−0.78***	1.00				
TTY	−0.64***	0.39**	1.00			
MTY	−0.62***	0.39**	0.99***	1.00		
TTN	−0.34**	0.14 ns	0.57***	0.52***	1.00	
MTN	−0.49***	0.30**	0.72***	0.71***	0.66***	1.00
RYL%	0.78***	−0.56***	−0.73***	−0.72***	−0.36**	−0.50***
Adet						
AUDPC	1.00					
DT_5	−0.77***	1.00				
TTY	−0.11 ns	0.19*	1.00			
MTY	−0.12 ns	0.31**	0.91***	1.00		
TTN	−0.04 ns	0.18 ns	0.46***	0.63***	1.00	
MTN	−0.05 ns	0.25*	0.39**	0.60***	0.85***	1.00
RYL%	−0.31**	0.15 ns	−0.12 ns	−0.18 ns	−0.36**	−0.29*
Debark						
AUDPC	1.00					
DT_5	−0.91***	1.00				
TTY	−0.58***	0.48***	1.00			
MTY	−0.54***	0.45***	0.95***	1.00		
TTN	−0.21*	0.30**	0.37**	0.34**	1.00	
MTN	−0.24*	0.31**	0.55***	0.56***	0.84***	1.00

ns, non-significant; AUDPC, area under the disease progress curve; DT_5, days to 5% disease severity threshold; TTY, total tuber yield; MTY, marketable tuber yield; TTN, total tuber numbers; MTN, marketable tuber numbers; RYL%, relative yield loss percentage.
Significance levels: *Significant at $P \leq 0.05$; **Significant at $P \leq 0.01$; ***Significant at $P \leq 0.001$.

environmentally dependent R gene in Belete or a change in the pathogen genotype at Adet. More detailed research would be required to test diversity of pathogen genotypes among the locations.

Some clones showed ranking changes for yield and yield-related traits, which could also be associated with genotype × location interaction for the disease resistance. Significantly negative correlation of resistance parameters with yield and related traits was shown in the present study. In addition, variation in environmental factors such as daily temperature, rainfall and soil type is critical in affecting tuber yield (Fry 2008). Thus, the differences in tuber yield and yield-related parameters among the clones could be explained not only by differences in the level of disease severity but also by inherent difference in yield potential. This can be illustrated by genotype 395109.34, which had the highest yield at Injibara but the lowest at Adet, despite its stable susceptibility score (2–3).

Marked variability was detected in late blight resistance, tuber yield, marketable tuber yield, total tuber numbers and marketable tuber numbers within and across locations. AUDPC was highly correlated with

Fig. 1 Cultivar Belete (CIP-393371.58) at Adet on the 17th of September 2014.

DT_5 in all three study locations, suggesting that susceptible cultivars succumb to the disease early, resulting in higher AUDPC values. Similar findings have been reported by Dorrance et al. (2001) who noted that specific components of resistance such as infection efficiency, latent period and lesion growth rate,

which are included in the measurement of DT_5, would likely contribute to partial resistance. They also suggested that DT_5 is the most efficient method to measure components of resistance under field condition. Significant correlation was found between RYL % and AUDPC in both test locations confirming the great potential of AUDPC in detecting differences in disease development between cultivars.

A negative correlation was found between AUDPC and yield and yield-related traits, that is TTW, MTW, TTN and MTN under unsprayed conditions at Injibara and Debark. At Adet, only a weak correlation was observed between AUDPC and yield and yield-related traits, as well as between RYL and DT_5, TTY and MTY. This may have resulted from lower severity and late appearance of the disease at Adet. Mean rAUDPC values were approximately twofold higher at Injibara than in Adet. Estimation of low levels of disease severity often leads to high standard errors because of irregular distribution of disease within the crop (Danielsen and Munk 2004). In the presence of high disease severity at Injibara, RYL% was highly and negatively correlated with DT_5, yield and yield-related parameters as expected. The strong correlation between RYL % and DT_5 indicates that the early appearance of the disease has greatest potential to cause serious yield reductions.

Significant variation was observed among clones with regard to late blight infection under unsprayed regimes. The eight genotypes with the highest late blight resistance (i.e. those with interval susceptibility scores of ≤3, longer DT_5 and ≤37% yield loss) in all three locations were 396004.263, 396029.250, 393220.54, 395011.2, Gudene, 395096.2, 395017.229 and 396034.103. Clones 395109.34, 396031.108 and 395077.12 had moderate resistance (interval susceptibility score of 3 and yield loss ranging from 37 to 50%). These eleven clones are thus potential parents for late blight resistance breeding. Among these, five clones (396029.250, 395017.229, 396004.263, 396034.103 and 395077.12) were relatively high yielding (≥25 t/ha), had flowers and produced pollen (first author's personal observation). Clones exhibiting adequate levels of late blight resistance combined with high yields can be valuable genetic resources for breeding programmes and/or for large-scale production (after yield stability testing). The most susceptible genotypes across the study sites (>4 on the interval susceptibility scale and >50% yield loss) were 396038.107, Guassa, 395015.6, 396038.101, 395017.14 and Gorebella. The present study found that late blight resistance levels of the B3C2 clones were more variable under the present environments than their 'resistant to moderately resistant' reaction reported by CIP (Table 1). This could be attributed to differences in pathotypes and environments. The same result has also been reported by Yao et al. (2011).

Conclusions

Results from the current study revealed significant differences in the level of resistance to late blight disease and the effect of late blight on yield and related traits among the tested potato clones. The following clones had resistant to moderately resistant reaction to late blight disease across the study locations: 396004.263, 396029.250, 393220.54, 395011.2, Gudene, 395096.2, 395017.229, 396034.103, 395109.34, 396031.108 and 395077.12. All the local and newly released cultivars except Gudene were susceptible to late blight, suggesting the need for strategic resistance breeding using the novel parents. Correlations between AUDPC, DT_5 and RYL were significantly positive indicating that early appearance of the disease could result in higher AUDPC values and yield loss. Strong and significant correlation existed between AUDPC and DT_5 across the study sites, suggesting that DT_5 was the most important parameter in identifying resistant clones. Overall, the study identified high yielding clones with adequate levels of late blight resistance that are recommended for breeding or direct production after yield stability tests.

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References

Andrivon D, Pellé R, Ellissèche D. (2006) Assessing resistance types and levels to epidemic diseases from the analysis of disease progress curves: principles and application to potato late blight. Am J Potato Res 83:455–461.

Annicchiarico P. (2002) Genotype × Environment Interactions: challenges and opportunities for plant breeding and cultivar recommendations. FAO plant production and protection paper 174. Rome, Italy, FAO.

Assen M, Tegene B. (2008) Characterisation and classification of the soils of the platau of simen mountains national park (SMNP), Ethiopia. Ethiopian J Sci 31:89–102.

Berihun B, Woldegiorgis G. (2013) Potato research and development in Ethiopia: achievements and trends. In: Woldegiorgis G, Schulz S, Berihun B. (eds) Proceedings of the National Workshop on Seed Potato Tuber Production and Dissemination Experiences, Challenges and Prospects, 12–14 March 2012. Bahir Dar, Ethiopia, EIAR and ARARI, pp 35–44.

Bradshaw JE, Bonierbale M. (2010) Potatoes. In: Bradshaw JE. (ed) Root and Tuber Crops. New York, Springer, pp 1–52.

Campell CL, Madden L. (1990) Introduction to Plant Disease Epidemiology. New York, USA, John Wiley and Sons.

Chindi A, Woldegiorgis G, Solomon A, Tesema L, Negash K, Lemaga B, Schulz S. (2013) Enhancing potato seed production using rapid multiplication techniques. In: Woldegiorgis G, Schulz S, Berihun B. (eds) Proceedings of the National Workshop on Seed Potato Tuber Production and Dissemination: Experiences, Challenges and Prospects, 12–14 March 2012. Bahir Dar, Ethiopia, EIAR and ARARI, pp 91–100.

CIP (2004) Ethiopia: potato production areas and average yields. International Potato Centre. Internet Resource: http://gilb.cip.cgiar.org/countryprofiles/africa/ethiopia/. (verified Jun 12, 2015).

CIP (2012) International Potato Centre regional program for sub-Saharan Africa: about sub-Saharan Africa. CIP. Internet Resource: http://cipotato.org. (verified Oct 13, 2015).

Colon LT, Turkensteen LJ, Prummel W, Budding DJ, Hoogendoorn J. (1995) Durable resistance to late blight (*Phytophthora infestans*) in old potato cultivars. Eur J Plant Pathol 101:387–397.

Danielsen S, Munk L. (2004) Evaluation of disease assessment methods in quinoa for their ability to predict yield loss caused by downy mildew. Crop Prot 23:219–228.

Dorrance A, Inglis D, Helgeson J, Brown C. (2001) Partial resistance to *Phytophthora infestans* in four *Solanum* crosses. Am J Potato Res 78:9–17.

FAO. (2009) International Year of Potato 2008: New Light on a Hidden Treasure. Rome, Italy, Food and Agricultural Organisation.

FAOSTAT. (2015) Data base of agricultural production. Food and Agriculture Organization. Internet Resource: http://faostat3.fao.org/home/E. (verified Oct 11, 2015).

Flier W, Van den Bosch G, Turkensteen L. (2003) Stability of partial resistance in potato cultivars exposed to aggressive strains of *Phytophthora infestans*. Plant Pathol 52:326–337.

Forbes GA. (2012) Using host resistance to manage potato late blight with particular reference to developing countries. Potato Res 55:205–216.

Forbes G, Grunwald N, Mizubuti E, Andrade-Piedra G, Garrett K. (2003) Potato Late Blight in Developing Countries. USA, Food and Agriculture Organization.

Forbes GA, Chacón MG, Kirk HG et al. (2005) Stability of resistance to *Phytophthora infestans* in potato: an international evaluation. Plant Pathol 54:364–372.

Forbes G, Pérez W, Andrade-Piedra J. (2014) Field Assessment of Resistance in Potato to *Phytophthora infestans*. Lima, Peru, International Potato Center (CIP).

Fry WE. (1978) Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. Phytopathology 68:1650–1655.

Fry W. (2008) *Phytophthora infestans*: the plant (and R gene) destroyer. Mol Plant Pathol 9:385–402.

Fuglie K. (2007) Priorities for potato research in developing countries: results of a survey. Am J Potato Res 84:353–365.

Garrett K, Nelson R, Mundt C, Chacon G, Jaramillo R, Forbes G. (2001) The effects of host diversity and other management components on epidemics of potato late blight in the humid highland tropics. Phytopathology 91:993–1000.

Gildemacher P, Kaguongo W, Ortiz O et al. (2009) Improving potato production in Kenya, Uganda and Ethiopia: a system diagnosis. Potato Res 52:173–205.

Hannukkala A, Kaukoranta T, Lehtinen A, Rahkonen A. (2007) Late-blight epidemics on potato in Finland, 1933–2002; increased and earlier occurrence of epidemics associated with climate change and lack of rotation. Plant Pathol 56:167–176.

Harrison JG. (1992) Effects of the aerial environment on late blight of potato foliage: a review. Plant Pathol 41:384–416.

Haynes G, Lambert DH, Christ BJ, Weingartner DP, Douches DS, Backhmd JE, Secor G, Fry W, Stevenson W. (1998) Phenotypic stability of resistance to late blight in potato clones evaluated at eight sites in the United States. Am J Potato Res 75:211–217.

Haynes K, Christ B, Vinyard B. (2008) Determining the importance of combining ability for late blight resistance in early generations of potato breeding when susceptible clones are discarded. Am J Potato Res 85:445–454.

Kassa B, Beyene H. (2001) Efficacy and economics of fungicide spray in the control of late blight of potato in Ethiopia. Afr Crop Sci J 9:245–250.

Landeo J, Gastelo M, Pinedo H, Flores F. (1995) Breeding for horizontal resistance to late blight in potato free of R genes. In: Dowley LJ, Bannon E, Cooke LR, Keane T, O'Sullivan E. (eds) *Phytophthora Infestans*, Vol. 150, Dublin, Boole Press Ltd, pp 268–274.

Landeo JA, Gastelo M, Beltran G, Diaz L. (2001) Quantifying genetic variance for horizontal resistance to late blight in potato breeding population B3C1. In: Scientist and Farmer: Partners in Research for the 21st Century. Program Report, 1999–2000. Lima, Peru, CIP, pp 63–68.

Mizubuti ES, Forbes G. (2002) Potato late blight IPM in the developing countries. In: Liazarraga C. (ed) Late Blight: Managing the Global Threat. Proceedings of the

Global Initiative on Late Blight Conference, 11–13 July 2002. Hamburg, Germany, CIP, pp 93–97.
Mulema JMK, Olanya OM, Adipala E, Wagoire W. (2004) Stability of late blight resistance in population B potato clones. Potato Res 47:11–24.
Mundt CC, Cowger C, Garrett KA. (2002) Relevance of integrated disease management to resistance durability. Euphytica 124:245–252.
Niks RE, Parlevliet JE, Lindhout P, Bai Y. (2011) Breeding Crops with Resistance to Diseases and Pests. the Netherlands, Wageningen Acadamic Publishers.
Pariaud B, Ravigné V, Halkett F, Goyeau H, Carlier J, Lannou C. (2009) Aggressiveness and its role in the adaptation of plant pathogens. Plant Pathol 58:409–424.
Parker JM, Thurston HD, Villareal-Gonzalez MJ, Fry WE. (1992) Stability of disease expression in the potato late blight pathosystem: a preliminary field study. Am Potato J 69:35–44.
Payne RW, Murray DA, Harding SA, Baird DB, Soutar DM. (2014) GenStat for Windows, 17th edn. Hemel Hempstead, UK, VSN International.
Schiessendoppler E, Molnar O. (2002) Characterization of *Phytophthora infestans* populations in sub-Saharan Africa as a basis for simulation modeling and integrated disease management. In: Lizarraga C. (ed) Late Blight: Managing the Global Threat, Proceedings of the Global Initiative on Late Blight Conference, 11–13 July 2002. Hamburg, Germany, International Potato Center, pp 140.
Schulte-Geldermann E. (2013) Tackling low potato yields in eastern Africa: an overview of constraints and potential strategies. In: Woldegiorgis G, Schulz S, Berihun B. (eds) Proceedings of the National Workshop on Seed Potato Tuber Production and Dissemination Experiences, Challenges and Prospects, 12–14 March 2012. Bahir Dar, Ethiopia, EIAR and ARARI, pp 72–80.
Shibabaw A, Desalegn Y, Adgo E, Tewodros Y, Germer J, Asch F, Merene Y, Freyer B. (2014) Exploratory survey on climate change effects, value chain processes and supportive services: case study from potato based farming system of Awi-Zone, Ethiopia. IJAIR 2:2319–1473.
Sleper DA, Poehlman JM. (2006) Breeding Field Crops, 5th edn. IA, USA, Blackwell.
Snedecor GW, Cochran WG. (1989) Statistical Methods, 8th edn. Ames, IA, Iowa State University Press.
Sparks AH, Forbes GA, Hijmans RJ, Garrett KA. (2014) Climate change may have limited effect on global risk of potato late blight. Glob Change Biol 20:3621–3631.
Trognitz B, Bonierbale M, Landeo J, Forbes G, Bradshaw J, Mackay G, Waugh R, Huarte M, Colon L. (2001) Improving potato resistance to disease under the global initiative on late blight. In: Cooper HD, Spillane C, Hodgkin T. (eds) Broadening the Genetic Base of Crop Production. Wallingford, UK, CABI Publishing, pp 385–398.
Umaerus V, Umaerus M. (1994) Inheritance of resistance to late blight. In: Bradshaw JE, Mackay GR. (eds) Potato Genetics. Cambridge, UK, CAB International, pp 339–364.
Villamon FG, Spooner DM, Orrillo M, Mihovilovich E, Pérez W, Bonierbale M. (2005) Late blight resistance linkages in a novel cross of the wild potato species *Solanum paucissectum* (series *Piurana*). Theor Appl Genet 111:1201–1214.
Woldegiorgis G. (2013) Potato variety development strategies and methodologies in Ethiopia. In: Woldegiorgis G, Schulz S, Berihun B. (eds) Proceedings of the National Workshop on Seed Potato Tuber Production and Dissemination: Experiences, Challenges and Prospects, 12–14 March 2012. Bahir Dar, Ethiopia, EIAR and ARARI, pp 45–59.
Yao C-G, Song B-T, Jun L, Wu C-J, Cheng Q, Li D-C, Xie C-H. (2011) Population improvement of resistance to late blight in tetraploid potato: a case study in combination with AFLP marker assisted background selection. Agric Sci China 10:1177–1187.
Yuen JE, Forbes GA. (2009) Estimating the level of susceptibility to *Phytophthora infestans* in potato genotypes. Phytopathology 99:782–786.
Zegeye AD, Steenhuis TS, Blake RW, Kidnau S, Collick AS, Dadgari F. (2010) Assessment of soil erosion processes and farmer perception of land conservation in Debre Mewi watershed near Lake Tana, Ethiopia. Ecohydrol Hydrobiol 10:297–306.