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RESEARCH ARTICLE

Effects of Early and Late Harvest on Agronomic Performance and Stability of Late Blight Resistant (R-gene Free) Potato Genotypes

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Abstract

Late blight is an important constraint to potato production and genotype resistance is an effective disease control mesure. Ten late blight resistant potato genotypes (R-gene free) were assessed for yield performance and stability at early (90 days) and late harvest (120 days) at two locations in Kenya during two years. Significant differences ($P < 0.05$) in area under disease progress curves (AUDPC) were detected among potato genotypes. Resistant genotypes free of R-genes had significantly ($P < 0.05$) higher yield at late than early harvest, perhaps due to increased tuber bulking period. The rank of genotypes for AUDPC, late blight resistance, and tuber yield varied across seasons and locations (environment). Additive main effects and multiplicative interaction (AMMI) analysis of tuber yield and late blight resistance resulted in significant ($P < 0.05$) effects of genotypes (G) and environments (E). The proportion of genotypic variance was larger than the environmental variance and the G × E interactions. For tuber yield, the G, E, and G × E interactions accounted for 42.9, 39.6 and 17.5%; and 53.4, 29.7, and 16.9% at early and late harvests, respectively. For AUDPC, G, E, and G × E accounted for 80.2, 5.0, and 14.8%; as well as 82.3, 4.6, and 13% for early and late harvests, respectively. The resistance of potato genotypes without R-genes varied. Selective deployment of resistant genotypes can improve potato tuber yield.

Key words: AMMI analysis, harvest dates, *Phytophthora infestans*, R-gene free genotypes, *Solanum tuberosum*, yield

Introduction

Late blight disease, caused by *Phytophthora infestans* (Mont. De Bary) is a significant constraint in potato production (Turkeensteen and Zimnoch-Gucowska 2002). The disease is a major threat to potato cultivation in the tropical highlands, and yield losses vary from 35 to 75%, depending on cultivar susceptibility and environmental conditions (Ojiambo et al. 2001, Olanya et al. 2001). Although late blight can be controlled by fungicide applications, costs are prohibitive to most of the small-scale farmers and the detrimental effects of inappropriate fungicide applications are of tremendous concern. Similarly, fungicide effectiveness is often constrained by lack of sufficient knowledge of disease management practices by small-scale potato growers (Nyankanga et al. 2004).

The use of host plant resistance is the most effective and economically viable late blight management options especially for the resource-constrained potato farmers (Landeo 2002). Potato genotypes without major resistant (R) genes have partial resistance to late blight and are often stable and durable (Landeo et al. 1995). In general, genotypes with early maturity have been shown to be more susceptible to late blight than genotypes with late potato maturity (Visker et

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al. 2004). Several studies have documented late blight resistance, disease, and yield stability of potato cultivars under tropical and sub-tropical environments (Mulema et al. 2004, 2008; Olanya et al. 2006).

In the highland tropics, potatoes are grown twice a year and farmers often prefer early maturing genotypes or cultivars since there is substantial risk for tuber yield reduction by unfavourable climatic conditions and infection by pests and pathogens. In addition, early harvests of potato are preferred due to the short-term demand for food and fluctuations in market prices during critical periods of food shortages during the year. The maturity duration as a genotypic trait in potato has been defined based on either the occurrence of tuber formation or leaf senescence (Turkeensteen and Zimnoch-Gucowska 2002). The extent to which maturity duration and late blight resistance may impact tuber yield in specific production locations has not been ascertained. It has been documented that tuber formation in potato plants occurs at similar stages of plant growth, and that this process is independent of the maturity duration (Kawakami et al. 2005). Assessment of the relationships between potato maturity duration and late blight resistance in tropical environments would be beneficial for improved tuber yield.

The selection and breeding of potato cultivars for early bulking and late blight resistance may lead to improved potato production. Similarly, an assessment of disease and yield stability of resistant potato genotypes may contribute to increased potato yield. Disease and yield stability of potato clones have been previously examined in some highland tropical environments (Mulema et al. 2004, 2008). In this study, the extent to which late blight disease development can be minimized and yield stability maximized in potato genotypes free of R-genes when cultivated under early and late harvest scenarios at different locations were investigated. This research presents unique results on the agronomic performance and late blight resistance as well as disease stability that have not been previously documented. In previous studies, the cultivars utilized were either derived or developed from clones with vertical or high levels of resistance or had cultivars with quantitative resistance but with few major resistant genes. Due to the severe yield constraints imposed on cultivar performance in tropical highland environments, this research documents and characterizes disease and yield stability on new genotypes that could result in significant yield increases in the resource-constrained environments. The yield performance and disease reaction of these new potato genotypes and clones have not been previously investigated under environments in which late blight pressure is abundant all year around. Moreover, in many of the previous experiments, cultivar resistance and fungicides were utilized as synergistic or complementary management options for potato late blight. Due to the changing nature of pathogen populations (*P. infestans*) in various geographical regions, it is imperative to assess new potato genotypes and characterize resistance and tuber yield attributes so as to enhance potato productivity. Therefore, the objectives of this research were to: (1) evaluate early and late harvests in relation to potato yield and (2) quantify the stability of advanced R-gene free clones in the tropical climate environment of Kenya.

Materials and Methods

Potato genotypes and field experiments

The experiments were established at two locations: at the National Potato Research Center, Tigoni (Limuru) at 2,300 meters above sea level (masl) and Marimba (Meru) at 1,844 masl during the 2005 and 2006 cropping seasons. The average annual rainfall and mean temperatures for Tigoni are 800 mm and 18ºC, and 1,299 mm and 18.5ºC for Marimba, Meru. Major soil type for the two sites is humic nitisols (Jaetzold and Schmidt 1983).

Ten advanced late blight resistant potato clones from breeding population B3 developed by International Potato Center (CIP) breeding program and introduced to Kenya by CIP's Sub-Saharan Africa Regional Office in 2002 were utilized. They consisted of: 385524.9, 389746.2, 391696.96, 392617.54, 392637.10, 392657.8, 393280.57, 393371.58, 393385.39, and 393385.47 and two local check cultivars: Tigoni (moderately resistant to late blight) and Kerr's Pink (highly susceptible to late blight) which were evaluated in this study. Population B consists of genotypes with quantitative resistance to late blight, which is effective against a broad range of pathogen races or isolates. They were developed from a four-way hybrid cross between *Solanum acaule*, *Solanum bulbocastanum*, *Solanum phureja*, and *S. tuberosum*, genotypes with horizontal resistance free of R genes (Landeo et al. 1995, 1997). The absence of race-specific R genes in population B has been tested and confirmed (Landeo et al. 2001).

The 12 genotypes were planted in furrows in a randomized complete block design with three replicates. Each experimental plot consisted of four rows containing 10 plant shill^{-1} in each row with plant spacing of 30 $\times$ 75 cm within and between rows, respectively. In all the experimental plots, normal agronomic practices for potato production were followed. At planting, 500 kg ha^{-1} of compound fertilizer N : P : K (17:17:17) was applied for field plots. No fungicides were applied to the experimental plots. When necessary, aphids and other insects were controlled with metasystox (i.e. Oxydementonmethyl) insecticide. Weeds were controlled by hoe weeding. During both years, no artificial inoculations were made, and late blight disease was initiated from natural infections.

Assessment for late blight disease

Plants in experimental plots were assessed for late blight severity and disease development by visual rating of foliage for percent leaf area blighted when 5% leaf area was infected by the pathogen, and was observed on the most susceptible cultivar. Subsequent assessments of disease severity were recorded

every week visually on a scale 0% to 100%; where 0% = no disease and 100% = total leaf area affected by blight (Henfling 1987). Late blight on foliage was assessed until disease severity on the most susceptible cultivar approached 100%.

Potato tuber yield

Potato tubers were harvested from the experimental plots at 90 days (early harvest) and 120 days (late harvest) after plant emergence (DAE). Tubers from the four rows were harvested in each experimental plot. Potato tubers were sized and classified into marketable size (tuber diameter > 25 mm) and unmarketable size (with tuber diameter < 25 mm) and weighed. The weights of marketable and unmarketable tubers in each plot were used to compute the total tuber weight per area (hectare) for comparison of yield (kg plot^{-1}) among the genotypes.

Statistical analysis

The disease severity data were used to calculate AUDPC for each genotype following the midpoint rule as follows (Campbell and Madden 1990; Shaner and Finney 1977):

$$AUDPC = \Sigma \{[(y_i + y_{i+1})/2] (t_{i+1} - t_i)\}$$

Where y_i= percentage of foliage blighted at the ith assessment (observation); t = time in days after planting at the i th assessment (observation); and n = the number of disease assessments conducted. The AUDPC was standardized across seasons by dividing with the number of days disease assessment was conducted for each cropping season and location.

The yield stability of potato genotypes was computed by using the additive main effects and multiplicative interaction (AMMI) model[5,7] (Crossa et al. 1991; Fox et al. 1997) as described in the equation:

$$Y_{ger} = \mu + \alpha_g + \beta_e + \Sigma_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{en} + \varepsilon_{ger}$$

where: Y_{ger} is the yield of genotype g in the environment e for replications r; μ is the grand mean; α_g is the deviation of the mean of the genotype g; β_e is the deviation of the mean of the environment e; $\Sigma_n \lambda_n \gamma_{gn} \delta_{en}$ is the multiplicative fraction, with multiplicative parameters λ_n, the characteristic value of IPCA axis n; γ_{gn} is the genotype eigenvector for axis n; δ_{en} is the environment eigenvector for axis n; ρ_{en} is the residue of the interaction; ε_{ger} is the error associated with Y_{ger}. Biplots were used to visually illustrate yield stability across environments and the effects on yield and AUDPC. In the biplots, displacement along the x-axis reflects differences in main effects while the displacement along the y-axis shows differences in interaction effects. Genotypes or environments on the same parallel line relative to the y-axis have similar means and genotypes or environments on the right side of the midpoint of the axis reflect greater tuber yield than those on the left side of the midpoint vertical to the y-axis.

Analyses were performed using Genstat (LAWES Agricultural Trust, Rothamsted Experimental Station, Version 9, 2006). Comparisons of tuber yield across environments and seasons were based on the analysis of variance in which potato genotypes were designated fixed effects, and locations, seasons, and replications were considered random effects. Fisher's Least Significant Difference (LSD) was used to separate mean differences among the genotypes.

Results

Late blight severity

Disease levels (AUDPC) differed significantly ($P \leq 0.05$) among potato genotypes during the two years of the experiment at both locations for early and late harvests (Tables 1 and 2). The final AUDPC values were significantly ($P < 0.05$) greater for the cultivar Kerr's Pink than the other genotypes from population B3 irrespective of the location and the year (Table 2). As expected, late blight severity was significantly ($P < 0.05$) greater on the cultivar Kerr's Pink than the resistant check cultivar Tigoni, and the other genotypes. Variation in late blight progress was recorded among genotypes at both locations. With the exception of the susceptible check cultivar, Kerr's Pink, comparatively higher late blight levels were recorded at Marimba compared to the Tigoni location.

Potato tuber yield

Significant differences ($P \leq 0.05$) in tuber yield were observed among the genotypes and the interactions of genotype by locations, genotypes by years and genotypes by locations and years at early and late harvests (Tables 1 and 2). All

Table 1. Analysis of variance on the effects of genotypes, locations, and seasons on AUDPC and tuber yield of potato from field experiments conducted at Marimba and Tigoni locations

Source of variation	df	M.S. (90 DAE)	M.S. (120 DAE)	F-value (90 DAE)	F-value (120 DAE)
AUDPC[1]					
Rep	2	2.95	0.45	1.47^{ns}	0.22^{ns}
Genotype (G)	11	45.21	53.99	4.11**	4.91**
Location (L)	1	4.52	5.00	4.52*	5.00*
Years (S)	1	22.40	26.87	22.40**	26.87**
G*L	11	7.34	7.73	0.66**	0.70**
G*S	11	10.23	11.01	0.93**	1.00**
G*Rep	22	0.08	0.03	0.004**	0.001**
G*L*S	11	6.64	6.29	0.60**	0.57**
Tuber Yield[2]					
Rep	2	0.98	0.01	0.49^{ns}	0.24^{ns}
Genotype (G)	11	16.93	19.05	1.54**	1.73**
Location (L)	1	138.73	61.95	138.7**	61.9**
Years (S)	1	0.21	10.15	0.21^{ns}	10.2*
G*L	11	14.62	12.48	1.33**	1.13**
G*S	11	9.24	11.55	0.84**	1.05**
G*Rep	22	0.08	0.09^{ns}	0.004^{ns}	0.004^{ns}
G*L*S	11	8.80	9.23	0.08**	0.84**

[1]AUDPC refers to Area under disease progress curves (% disease-days).
[2]Tuber yield = potato yield at harvest.
* and ** = significant effects at 5% and 1% levels, ns = non-significant

Table 2. Mean Area under Disease Progress Curve (AUDPC) and tuber yield (kg plot^{-1}) for 12 potato genotypes harvested at 90 and 120 days after emergence (DAE) at Tigoni (Limuru) and Marimba (Meru) during Seasons 1 (2005) and 2 (2006)

Genotypes	Tigoni (Limuru)				Marimba (Meru)			
	AUDPC[1]		Tuber Yield[2] (kg plot^{-1})		AUDPC[1]		Tuber Yield[2] (kg plot^{-1})	
	90 DAE	120 DAE	90 DAE	120 DAE	90 DAE	120 DAE	90 DAE	120 DAE
Season 1								
392617.54	58	117	21	24	210	274	17	22
393385.39	87	82	22	24	18	134	19	25
392637.10	122	88	13	13	169	204	10	15
393280.57	122	58	25	31	35	88	15	26
392657.8	128	140	12	16	99	70	10	15
393385.47	187	53	8	14	88	193	10	17
393371.58	327	111	10	15	274	262	12	18
385524.9	449	589	26	26	292	344	16	31
389746.2	519	490	24	26	397	332	16	27
391696.96	811	630	16	22	175	233	11	14
K. Pink[3]	3,803	3,599	5	5	214	2,257	4	6
Tigoni[4]	402	560	29	29	257	163	12	18
Means	585	543	17	21	357	380	13	19
LSD (0.05)	249.9	265	2	3	80	189	3	4
Season 2								
392617.54	367	263	31	31	940	880	12	13
393385.39	671	624	26	27	640	693	13	18
392637.10	531	496	12	13	453	500	3	6
393280.57	636	554	24	25	353	253	10	12
392657.8	1,003	718	25	26	613	493	10	11
393385.47	204	158	20	22	600	353	8	11
393371.58	157	566	11	13	360	213	6	10
385524.9	385	478	36	36	700	707	9	13
389746.2	939	928	26	26	667	820	12	17
391696.96	1,108	1,295	29	33	633	620	9	11
K. Pink[3]	2,176	2,158	6	8	2,333	2,267	1	2
Tigoni[4]	677	811	20	21	460	500	12	13
Means	738	754	22	23	729	692	9	11
LSD (0.05)	313	267	5	4	492	382	3	4

[1]AUDPC refers to area under disease progress curves (% disease-days) of late blight incited by *Phytophthora infestans*,
[2]Tuber yield is potato yield at harvest,
[3]Kerr's Pink is susceptible and [4]Tigoni is resistant check cultivars.

genotypes had significantly greater tuber yield than Kerr's Pink, the susceptible cultivar. Some of the population B3 genotypes had significantly lower yield than Tigoni, the resistant check cultivar, while other potato genotypes had numerically similar tuber yield to the cultivar Tigoni, the resistant check. Some genotypes such as 385524.9, 389746.2, 392617.54, 393371.58, 393385.39, and 393385.47 had numerically greater tuber yield compared to cultivar Tigoni at both harvests at Marimba (Table 2). There was greater tuber yield at late harvest than during early harvest (Table 2). Tuber yield was also comparatively greater at Tigoni (Limuru) during the 2006 cropping season than during the 2005 planting season. At Marimba (Meru) tuber yield was greater in the 2005 than the 2006 cropping year.

Stability of potato genotypes to late blight

The main effects of genotypes (G), environment (E) were significantly ($P \leq 0.05$) different for AUDPC during early and late harvest (Table 3). The genotypes, environment, and the interactions accounted for 80.2, 4.97, and 14.8% and 82.3, 4.56, and 13.1% of the treatment sums of squares (variation) at 90 and 120 DAE, respectively (Table 3). The principal components 1 (IPCA 1) and 2 (IPCA 2) were also significantly ($P \leq 0.05$) different (Table 3). Based on AMMI model, potato genotypes 392637.10, 393280.57, 393371.58, and 393385.47 at Marimba (Meru) and 392617.54, 393385.47, 392637.10, and 393385.39 at Tigoni (Limuru) had ranking of higher levels of resistance to late blight at the two harvest dates (Table 4). Generally, genotypes 385524.9, 389746.2, and 391696.96 had moderate levels of resistance based on AMMI ranking for early and late harvest (Table 4).

Stability of potato genotypes to tuber yield

Based on AMMI analysis of tuber yield, genotypes and environment differed significantly ($P \leq 0.05$) and accounted for 43.0, 39.55, and 17.46% of the treatment sums of squares at 90 days of harvest. The treatment sums of squares for genotypes, environment, and interactions were 53.37, 29.75, and 16.87% for late harvest (Table 5). The principal components axes (IPCA) 1 and 2 were also significantly ($P \leq 0.05$) different (Table 5). The sum of squares for G, E and IPCA 1

Table 3. AMMI analysis of AUDPC for 12 potato genotypes harvested at 90 and 120 days after emergence (DAE). The potato genotypes were grown at two locations in Kenya during the 2005 (Season 1) and 2006 (Season 2) cropping seasons

Source of variation	df	S.S.	F-value	Explained
90 DAE				
Total	143	2954172	-	
Treatments[1]	47	68710489	41.01**	
Genotypes[2]	11	55127112	140.59**	80.23
Environments[3]	3	3416155	8.23*	4.97
Interactions[4]	33	10167222	8.64^{ns}	14.80
IPCA 1	13	7633222	16.47	
IPCA 2	11	2139079	5.46	
Error	88	3136804	-	
MSE			188.79	
120 DAE				
Total	143	69138267	-	
Treatments[1]	47	66094858	49.91**	
Genotypes[2]	11	54408615	175.55**	82.32
Environments[3]	3	3011675	14.24^{ns}	4.56
Interactions[4]	33	8674568	9.33^{ns}	13.12
IPCA 1	13	5996856	16.37	
IPCA 2	11	2175939	7.02	
Error	88	2479525	-	
MSE			167.86	

[1]Treatments consist of genotypes, environments and interactions.
[2]Genotypes refer to 12 potato cultivars including Tigoni (resistant check) and Kerr's Pink (susceptible check).
[3]Four environments were used in this study (Tigoni 2005 and 2006, and Marimba 2005 and 2006).
[4]Genotype x environment interactions.
* and ** = significant effects at 5% and 1% levels, ns = non-significant.

Table 4. The ranking of 12 potato genotypes based on estimates of AUDPC by AMMI. Potatoes were grown in four environments (2 locations by two cropping seasons) and harvested at different dates

Genotypes[1]	Tigoni (Limuru)				Marimba (Meru)			
	Season1[2]		Season2[2]		Season1[2]		Season2[2]	
	90 DAE[3]	120 DAE[3]	90 DAE	120 DAE	90 DAE	120 DAE	90 DAE	120 DAE
385524.9	448.0 (4)[4]	581.6 (3)	384.8 (9)	478.3 (10)	299.3 (4)	378.5 (3)	693.8 (4)	680.0 (4)
389746.2	528.3 (3)	471.9 (5)	940.3 (4)	927.3 (3)	339.4 (3)	414.5 (2)	713.7 (3)	756.3 (3)
391696.96	797.2 (2)	615.2 (2)	1,106.6 (2)	1,294.9 (2)	261.2 (5)	300.5 (5)	562.5 (7)	567.8 (6)
392617.54	36.9 (12)	95.7 (9)	364.8 (10)	262.3 (11)	344.9 (2)	369.0 (4)	829.2 (2)	806.3 (3)
392637.10	133.3 (8)	97.5 (8)	532.2 (8)	495.9 (9)	100.9 (11)	159.1 (8)	509.4 (10)	535.1 (7)
392657.8	119.4 (10)	131.7 (7)	1,002.2 (3)	717.4 (5)	155.4 (8)	110.2 (9)	567.2 (6)	462.1 (9)
393280.57	128.3 (9)	79.2 (10)	636.6 (7)	554.4 (8)	-1.5 (12)	-6.8 (12)	383.3 (12)	326.7 (12)
393371.58	352.1 (6)	157.6 (6)	160.7 (12)	566.3 (7)	113.7 (10)	50.5 (11)	491.8 (11)	378.1 (11)
393385.39	83.2 (11)	62.3 (12)	670.3 (6)	624.0 (6)	184.6 (6)	221.7 (6)	617.7 (5)	625.3 (5)
393385.47	178.3 (7)	77.3 (11)	203.1 (11)	157.7 (12)	140.2 (9)	80.4 (10)	556.7 (8)	440.5 (10)
Kerr's Pink	3,796.0 (1)	3,596.0 (1)	2,174.9 (1)	2,158.3 (1)	2,181.5 (1)	2,271.9 (1)	2,295.1 (1)	2,255.5 (1)
Tigoni	416.6 (5)	550.5 (4)	678.4 (5)	810.7 (4)	206.7 (7)	206.4 (7)	532.9 (9)	466.5 (8)

[1]Genotypes refer to 12 potato cultivars including Tigoni (resistant check) and Kerr's Pink (susceptible check).
[2]Four environments were Tigoni Seasons 1 (2005) and 2 (2006); and Marimba Seasons 1 (2005) and 2 (2006).
[3]Harvest days after potato emergence were 90 (early harvest) and 120 (late harvest).
[4]The number in parenthesis refer to ranking of genotypes based on their susceptibility to late blight. The genotype with highest susceptibility (AUDPC) had a ranking of 1, and the most resistant had a ranking of 12.

and 2 accounted for 98 and 96% of variation at 90 and 120 DAE, respectively.

Tuber yield accounted for 82.5 and 81.2% of the sum of squares at 90 and 120 DAE, respectively. All population B3 genotypes had high yield with the exception of clones 391696.96, 392657.8, and 393280.57 which had lower yield. The relative ranking of the genotypes for tuber yield based on AMMI model varied across seasons and locations. Generally genotypes 385524.9, 389746.2, 392617.54, 393371.58, 393385.39, and 393385.47 had higher rank of tuber yield, while Kerr's Pink had the lowest ranking for tuber yield when compared to other population B3 genotypes (Table 6).

Table 5. AMMI analysis of tuber yield for 12 potato genotypes harvested at 90 and 120 DAE. The potato genotypes were grown at two locations in Kenya during the 2005 - 2006 cropping seasons

Source of variation	df	S.S.	F-value	Explained
90 DAE				
Total	143	9,742	-	
Treatments[1]	47	9,276	42.43*	
Genotypes[2]	11	3,987	77.91*	42.98
Environments[3]	3	3,669	173.95[ns]	39.55
Interactions[4]	33	1,620	10.55*	17.46
IPCA 1	13	872	14.42	
IPCA 2	11	635	12.41	
Error	88	409	-	
MSE			2.17	
120 DAE				
Total	143	10,020	-	
Treatments[1]	47	9,604	45.85	
Genotypes[2]	11	5,126	104.57*	53.37
Environments[3]	3	2,857	310.07[ns]	29.75
Interactions[4]	33	1,620	11.02*	16.87
IPCA 1	13	873	15.08	
IPCA 2	11	440	8.98	
Error	88	392	-	
MSE			2.12	

[1]Treatments consist of genotypes, environments and interactions.
[2]Genotypes refer to 12 potato cultivars including Tigoni (resistant check) and Kerr's Pink (susceptible check).
[3]Four environments were used in this study (Tigoni 2005 and 2006, and Marimba 2005 and 2006).
[4]Genotypes by environments interactions.
* and ** = significant effects at 5% and 1% levels, ns = non-significant.

Discussion

Late blight and potato tuber yield

The potato genotypes from population B3 such as 392617.54, 393385.39, and 393371.58 had generally low AUDPC values and the disease levels in relation to the susceptible check cultivar, Kerr's Pink. This indicates that the inherent resistance of the B3 genotypes under tropical conditions may be contributing to the low levels of disease observed in this study. Therefore, these genotypes can be good sources of late blight resistance for further improvement of resistance to potato late blight. There were differential rankings in resistance of the genotypes with respect to late blight levels from location to location and from year to year. For example, the genotypes 392617.54 and 393383.39 had the lowest disease level at Tigoni location in season 1, while in season 2, genotypes 393385.47 and 392617.54 had the lowest disease level at 90 DAE. While at Marimba location, genotypes 393280.57 and 392657.8 had the lowest record of disease level. The variation in disease levels among genotypes between locations and seasons may be attributed to the differences in environmental conditions and the G × E interactions. Differences in climatic and environmental conditions and variable inoculum levels especially during the 2006 year in which heavy rainfall and cool temperatures were recorded can account for the variation in disease levels

Table 6. Ranking of 12 potato genotypes based on estimates of tuber yield (kg plot^{-1}) by AMMI. Potatoes were grown in four environments (2 locations by two cropping seasons) and harvested at different dates

Genotypes[1]	Tigoni (Limuru)				Marimba (Meru)			
	Season1[2]		Season2[2]		Season1[2]		Season2[2]	
	90 DAE[3]	120 DAE[3]	90 DAE	120 DAE	90 DAE	120 DAE	90 DAE	120 DAE
385524.9	20.65 (6)[4]	24.44 (5)	30.56 (2)	30.65 (3)	16.38 (2)	21.70 (6)	12.22 (2)	13.11 (4)
389746.2	21.87 (5)	24.33 (6)	26.39 (4)	27.01 (4)	18.00 (1)	25.02 (3)	14.08 (1)	17.73 (1)
391696.96	13.15 (8)	13.48 (11)	12.45 (10)	12.94 (10)	8.31 (11)	13.84 (11)	4.43 (11)	5.91 (11)
392617.54	24.64 (3)	31.42 (1)	23.61 (7)	24.61 (7)	14.71 (5)	24.94 (4)	10.14 (5)	12.47 (5)
392637.10	12.06 (9)	15.38 (8)	24.41 (6)	25.61 (6)	11.70 (8)	16.37 (9)	7.99 (7)	10.35 (9)
392657.8	7.85 (11)	13.77 (10)	20.07 (9)	21.73 (8)	10.78 (9)	16.29 (10)	7.53 (9)	10.75 (6)
393280.57	10.04 (10)	14.77 (9)	11.20 (11)	12.44 (11)	10.40 (10)	17.39 (7)	7.16 (10)	10.40 (8)
393371.58	25.97 (2)	28.68 (2)	36.46 (1)	35.67 (1)	15.59 (4)	25.07 (2)	10.58 (4)	16.15 (3)
393385.39	24.04 (4)	25.93 (4)	25.69 (5)	26.07 (5)	16.04 (3)	25.76 (1)	11.65 (3)	17.64 (2)
393385.47	15.37 (7)	20.21 (7)	29.03 (3)	33.30 (2)	12.04 (7)	16.69 (8)	7.89 (8)	8.70 (10)
Kerr's Pink	4.86 (12)	4.32 (12)	5.66 (12)	7.62 (12)	4.40 (12)	6.90 (12)	1.07 (12)	0.70 (12)
Tigoni	28.35 (1)	27.18 (3)	20.29 (8)	20.88 (9)	14.24 (6)	22.23 (5)	9.35 (6)	10.64 (7)

[1]Genotypes refer to 12 potato cultivars including Tigoni (resistant check) and Kerr's Pink (susceptible check).
[2]Four environments were Tigoni Seasons 1 (2005) and 2 (2006); and Marimba Seasons 1 (2005) and 2 (2006).
[3]Harvest days after potato emergence were 90 (early harvest) and 120 (late harvest).
[4]Number in parenthesis refer to ranking of genotypes based on their resistance to late blight. The genotypes with the greatest resistance had a ranking of 1, and the most resistant had a ranking of 12.

and explain the rapid late blight severity and disease levels recorded in this study.

Differences in genotype reaction in response to late blight pressure at various seasons and locations have been previously documented (El-Bedewy et al. 2001). It is evident that genotypes derived from population B3 devoid of major resistant genes and utilized in this study appear to have greater late blight resistance compared to the resistant check cultivar, Tigoni which is derived from population B clone (horizontal resistance). Therefore, theoretically, we may expect better disease resistance from B3 potato genotypes in the tropical highland environments. In general, severe epidemics of late blight have been documented and shown to be favoured by periods of high rainfall, high relative humidity, and temperatures below 20°C as well as prolonged leaf wetness durations such as those encountered in the tropics (Olanya et al. 2006). Based on cumulative results, the AUDPC values among genotypes did not appear to vary significantly ($P > 0.05$) at 90 and 120 DAE, implying that late blight levels at early and late harvest may be similar.

Tuber yield in potatoes have been reported to increase with prolonged periods of tuber bulking prior to harvest (Pandey et al. 2005). It has also been documented that delaying the desiccation date of potato vines increased tuber yield in potatoes (Visker et al. 2004). In our research, we noted consistent differences in tuber yield between 90 and 120 DAE such as between genotypes 393280.57 and 385524.9 at Marimba location during the potato cropping season 1. Although the increases in tuber yield varied with potato genotypes, locations, and seasons, such differences were not totally unexpected since the longevity of potato plants / leaves and their capacity to photosynthesize during tuber bulking have also been shown to contribute to yield. Lower tuber yield was recorded in Marimba compared to Tigoni location during the 2006 year. This may be due to the higher levels of late blight disease that subsequently reduced the foliage of potato cultivars in that particular cropping year. The comparative yield levels of potato genotypes between the two maturity periods may also imply that harvested tuber may be available for consumption by subsistence potato farmers within a relatively short duration of time to alleviate any shortages during the year. Similarly, for large-scale growers, they may utilize the harvest from 90 DAE for sale at markets. In previous research, it was shown that potato cultivars of different maturity classes and levels of resistance require the protection of the foliage from *P. infestans* for optimal performance of potatoes (Van Oijen 1991).

The significant negative correlation between the AUDPC and tuber yield (data not shown) recorded on many genotypes indicates that higher late blight epidemics can significantly impact tuber yield. Late blight has been found to reduce tuber yield by decreasing the cumulative light interception by potato leaves (Van Oijen 1991). This is because population B3 genotypes were developed for quantitative resistance to late blight with a large area of foliage able to withstand high late blight disease pressure. At Tigoni location in season 2, some potato genotypes such as 392657.8 (AUDPC of 1003 and 718 at 90 and 120 DAE), 389746.2 (AUDPC of 939 and 928 at 90 and 120 DAE, respectively) and 391696.96 (AUDPC of 1108 and 1295 at 90 and 120 DAE, respectively), had tuber yield values at 24.5, 25.7, and 29.0 kg plot^{-1} for 90 DAE, and 25.5, 26.2, and 33.0 kg plot^{-1} for 120 DAE, respectively. This implies that these genotypes have resistance responses in which pathogen infection occurs, but with relatively minor effect on tuber yield. These tuber yield values were even better than that of the resistant check cultivar (Tigoni), indicating that they have adequate resistance to late blight and good tuber yield.

Disease and yield stability

The difference in the performance of potato genotypes across locations and years is an indication of genotype × environment interactions (Abalo et al. 2003). Large additive genetic variances associated with horizontal resistance to late blight have been noted in population B3 clones in sub-tropical potato growing environment of Peru (Landeo et al. 2001). In this research, the proportion of the variation of treatment sum of squares attributed to genotypes was much larger than the proportion of treatment sum of squares apportioned to environment, and G × E interaction thus contributed more to the total variability in late blight resistance and tuber yield in the highland tropics. This finding is similar to other studies previously conducted on G × E interactions for tuber yield and late blight resistance (Lung'aho et al. 1998). However, our results are not in agreement with earlier G × E studies previously conducted (Abalo et al. 2003), in which the proportion of sum of squares accounted for by G × E interaction variation in tuber yield was usually larger than genotypic main effects. In general, there is no precise reason to expect similarity in the proportions of G, E, and G × E interactions in yield stability experiments since wide variation can be expected among the different experiments, crops, and environments as well as the differences in genotypic effects.

The stability of late blight resistance in tropical environments has been documented for other population B clones in which the rankings for late blight resistance differed across environments and the late blight resistance ranged from moderately resistant to resistant (El-Bedewy et al. 2001; Lung'aho et al. 1998). In a previous study, population B3 genotypes were similarly found to have disease resistance in the range of moderately resistant to resistant. This was expected as those genotypes were developed for horizontal resistance to late blight (Landeo et al. 1995). The results corroborate similar studies previously reported for population B genotypes evaluated in other tropical environments (Mulema et al. 2004; 2008).

Five genotypes (385524.9, 389746.2, 391696.96, 393385.39, and 393385.47) were shown to have stable tuber yield during early harvest and all the population B3 genotypes except 392617.54 and 392657.8 during late harvest were identified as being stable across many environments. Based on the stability analysis and graphical documentation of tuber yield versus environments (data not shown), some genotypes or environments were positioned on the same horizontal line (yield) perpendicular to the y-axis (environments), indicating that they have similar yield stability in those environments. Some potato genotypes had IPCA1 scores close to zero indicating that they have small interaction effects for late blight resistance and yield across environments. The G × E and stability analysis for evaluation of cultivar performance have been previously utilized in diverse crops (Cooper et al. 1996; Crossa et al. 1991; Fox et al. 1997). In our experiments, the ranking of potato genotypes for late blight reaction and yield, as well as for their disease and yield stability can be utilized for assessment of yield performance of cultivars and adaptation to diverse cropping environments. Therefore, selective deployment of potato genotypes for seasons 1 or 2; for maturity dates of 90 and 120; as well as between locations can be effectively utilized to maximize tuber yield in environments where late blight is a constant constraint.

Conclusions

The potato genotypes of Population B3 showed a reaction of moderately resistant to resistant to late blight. Six potato genotypes (385524.9, 389746.2, 392617.54, 393371.58, 393385.39, and 393385.47 were identified and classified as better yield performers than the other potato genotypes. Stability of genotypes with regard to disease and yield was demonstrated based on the small interaction effects of genotypes × environments and the low IPCA1 scores recorded in the experiments. Deployment of these genotypes will greatly improve tuber yield in diverse environments

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