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Yield Response of Potato (*Solanum tuberosum L.*) Genotypes to Late Blight Caused by *Phytophthora infestans* in Uganda

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Abstract

Potato (*Solanum tuberosum L.*) is a major food and cash crop, mainly grown by small-scale farmers in the highland regions of Uganda. Potato late blight is one of the major diseases limiting production with potential yield losses over 70%, making host resistance a strong element in integrated disease management. This study was carried out to screen and select high yielding potato genotypes with resistance to late blight in Uganda. Forty-eight genotypes, including advanced clones from the population B3C2 of the International Potato Centre, commercial and farmers' varieties, were evaluated under two environments for two seasons. Trials were laid out in an 8 × 6 alpha lattice design with three replications. Genotypes showed significant differences in yield and resistance to blight. A higher disease severity was observed in Karengyere (56%). The average RAUDPC (= 100 max) across locations indicated that genotypes 395,077.12 and 392,657.8, with disease severity of 12% and 14%, respectively, were the most resistant. Genotypes Victoria (53%) and NKRN59.124 (48%) were the most susceptible. Mean tuber yield under late blight infection was19.8 t ha^{-1}. The best yielding genotype across sites was 395,112.32 (35.6 t ha^{-1}) while 394,905.8 (10.3 t ha^{-1}), yielded the lowest. The mean marketable tuber weight was 8.9 kg with genotypes 395,112.32 and 395,109.34 having the highest marketable weight of 16.5 kg and 15.6 kg respectively. Correlations between yield and yield related parameters were positive ($p \leq 0.001$), while those between RAUDPC were negative. The following genotypes, 395,112.32, 391,919.3, 393,220.54. 393,077.54, 396,038.107. 392,657.8, Kinigi, 395,014.17, NKRN59.58, NKRK19.17 and 395,011.2, were identified as promising parents for a late blight resistance breeding program. These exhibited high to medium resistance to late blight disease and high yields.

Resumen

La papa (*Solanum tuberosum* L.) es un alimento importante y un cultivo redituable, cultivado principalmente por agricultores a pequeña escala en los altiplanos de Uganda. El tizón tardío de la papa es una de las principales enfermedades que limitan la producción con pérdidas potenciales de rendimiento sobre el 70%, haciendo de la resistencia del hospedante un elemento fuerte en el manejo integrado de la enfermedad. Este estudio se llevó a cabo para probar y seleccionar genotipos de papa de alto rendimiento con resistencia al tizón tardío en Uganda. Se evaluaron 48 genotipos, incluyendo clones avanzados de la población B3C2 del Centro Internacional de la Papa, variedades comerciales y de los productores, bajo dos ambientes por dos ciclos. Los ensayos se establecieron en un diseño de latice alfa 8 × 6 con tres repeticiones. Los genotipos mostraron diferencias significativas en rendimiento y resistencia al tizón. Se observó una mayor severidad de la enfermedad en Karengyere (56%). El promedio de RAUDPC (=100 max) entre las localidades indicaron que los genotipos 395,077.12 y 392,657.8, con una severidad de la enfermedad de 12% y 14%, respectivamente, fueron los más resistentes. Los genotipos Victoria (53%) y NKRN59.124 (48%) fueron los más susceptibles. La

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media del rendimiento de tubérculo bajo infección del tizón tardío fue de 19.8 t ha-1. El mejor genotipo para rendimiento entre los sitios fue 395,112.32 (35.6 t ha-1), mientras que 394,905.8 fue el de más bajo rendimiento (10.3 t ha-1). La media de peso de tubérculo comercial fue de 8.9 kg con los genotipos 395,112.32 y 395,109.34, teniendo el mayor peso comercial de 16.5 kg y 15.6 kg, respectivamente. Las correlaciones entre rendimiento y parámetros relacionados con él fueron positivas ($p \leq 0.001$), mientras que con RAUDPC fueron negativas. Los genotipos 395,112.32, 391,919.3, 393,220.54. 393,077.54, 396,038.107. 392,657.8, Kinigi, 395,014.17, NKRN59.58, NKRK19.17 y 395,011.2 se identificaron como progenitores prometedores para un programa de mejoramiento de resistencia al tizón tardío. Exhibieron resistencia de alta a media al tizón y altos rendimientos.

Keywords *Solanum tuberosum* · Disease resistance · Relative area under disease progress curve · Tuber yield · Marketable weight

Introduction

Potato (*Solanum tuberosum*) is the fourth most important staple crop worldwide after maize, rice and wheat (CIP 2016). Uganda is the ninth largest producer of potato in Africa with an annual production of 774,600 tons harvested from about 106,000 ha per year (FAOSTAT 2016). The crop is grown by about 300,000 smallholder households in Uganda (UBOS 2016). Potato yields have remained low, about 4.8 t ha^{-1} (FAOSTAT 2016). These low yields have been attributed to a number of confounding factors, which are biotic, abiotic, and socio-economic constraints, as well as poorly adapted and adopted varieties (Gildemacher et al. 2009). Potato is considered as disease harbor mostly include: - late blight caused by *Phytophthora infestans* (Mont.) de Bary, bacterial wilt (BW) (*Ralstonia solanacearum*) (Muthoni et al. 2013) and viruses (Muhinyuza et al. 2012).

Late blight (LB) is the most devastating disease of potato, leading to yield losses up to 70% (Sedláková et al. 2011). The disease occurs in all main potato growing areas (Hijmans et al. 2000), being favored by moderately low temperatures and extended times of leaf dampness. It is particularly detrimental in the highland tropics where potatoes are grown throughout the year, combined with poor ability of farmers to understand and manage the disease (Garrett et al. 2001). Late blight commonly reduces potato productivity leading to huge differences between yields obtained.

Late blight causes both foliar and tuber decay (Acquaah 2012). Tubers can become infected when the disease moves down the lower stem, below ground, and through the stolon. Potato tubers can also become infected when late blight spores from infected leaves and stems are washed into the soil via cracks or crevices in the hill and come into contact with tubers. Late blight is the major reason for the use of fungicides on potatoes in Uganda (Low 1997). As much as disease management can be done through to the use of fungicides, these are expensive for many small scale farmers. Additionally, fungicide application is by hand and farmers rarely use protective clothing, thus posing health risks and diverse environmental hazards (Kromann et al. 2009; Forbes 2012). Therefore, breeding for host resistance is a sustainable approach to manage and control late blight in Uganda. In view of this, advanced resistant breeding populations and candidate clones developed by the International Potato Centre (CIP) were obtained. These are suitable for a wide range of agro-ecological zones including tropical highlands (CIP 2012). The clones belong to 'population B recombination cycle 3 (Pop B3)', which lacks any known major or *R* genes against *P. infestans*. This population is the latest advanced source released by CIP for durable resistance to late blight (Landeo et al. 2001; Yao et al. 2011).

Obtaining potato cultivars with durable resistance requires breeding for quantitative resistance against *Phytophthora infestans* (Landeo et al. 1999; Forbes 2012). This is because the *R* genes quickly break down due to the rapidly changing pathogen population. The aim of this study was to determine the yield response of different potato genotypes under late blight infection and identify parents with durable resistance for breeding purposes.

Materials and Methods

Genetic Materials

Forty eight potato genotypes were used in this study which included advanced clones from CIP, reported to have horizontal resistance to late blight with varied adaptability, commercial varieties and landraces commonly grown by farmers. The details of the genotypes are presented in Table 1.

Study Sites

Field trials were located at the Kachwekano and Karengyere research stations of the National Agricultural Research Organisation (NARO). The study was conducted in the following two seasons of 2016 B (September to December) and 2017 A (March to June). Kachwekano is located in South Western Uganda, 01° 16'S 29° 57'E at 2200 m above sea level (masl). The soil type is isomeric typic palehumult (Kakuhenzire et al. 2013). Karegyere

Table 1 Description of the 48 potato genotypes used in the study

No.	Genotype	Source	Population	Year of release	No.	Genotype	Source	Population	Year of release
1	391006.2	CIP	B3C!	Not yet released	25	396580.3	CIP	–	Not yet released
2	391046.14	CIP	–	Not yet released	26	Cruza	NARO	–	1992
3	391919.3	CIP	LTVR	Not yet released	27	Kachpot1	NARO	–	2006
4	392633.64	CIP	–	Not yet released	28	Kimuli	Farmer	–	Not available
5	392657.8	CIP	B3C1	Not yet released	29	Kinigi	Farmer	–	1992
6	392661.18	CIP	–	Not yet released	30	Mabondo	Farmer	–	1989
7	392797.22	CIP	LTVR	Not yet released	31	NAKPOT1	NARO	–	1996
8	393077.54	CIP	B3C1	Not yet released	32	NAKPOT5	NARO	–	1996
9	393220.54	CIP	B3C1	Not yet released	33	NAROPOT1	NARO	B3C2	2015
10	394895.7	CIP	LTVR	Not yet released	34	NAROPOT3	NARO	B3C2	2015
11	394905.8	CIP	LTVR	Not yet released	35	NKRK19.10	NARO	–	Not yet released
12	395011.2	CIP	B3C2	Not yet released	36	NKRK19.17	NARO	–	Not yet released
13	395015.6	CIP	B3C2	Not yet released	37	NKRN59.11	NARO	–	Not yet released
No	Genotype	Source	Population	Year of release	No.	Genotype	Source	Population	Year of release
14	395017.14	CIP	B3C2	Not yet released	38	NKRN59.124	NARO	–	Not yet released
15	395017.229	CIP	B3C2	Not yet released	39	NKRN59.29	NARO	–	Not yet released
16	395077.12	CIP	B3C2	Not yet released	40	NKRN59.41	NARO	–	Not yet released
17	395096.2	CIP	B3C2	Not yet released	41	NKRN59.48	NARO	–	Not yet released
18	395109.34	CIP	B3C2	Not yet released	42	NKRN59.58	NARO	–	Not yet released
19	395112.32	CIP	B3C2	Not yet released	43	NKRN59.61	NARO	–	Not yet released
20	395438.1	CIP	LTVR	Not yet released	44	Petero	Farmer	–	Not available
21	396026.103	CIP	B3C2	Not yet released	45	Rutuku	NARO	–	1962
22	396038.101	CIP	B3C2	Not yet released	46	Rwangume	NARO	–	2016
23	396038.105	CIP	B3C2	Not yet released	47	Rwashaki	Farmer	–	Not released
24	396077.159	CIP	–	Not yet released	48	Victoria	NARO	–	1992

CIP International Potato Center; *NARO* National Agriculture Research Organisation

research station is located at 01° 13.2'S, 29° 47.8′E in South Western Uganda at an altitude of 2450 masl. Both sites have a bi-modal rainfall pattern separated by a dry spell ranging from 30 to 60 days. In both study sites, late blight occurs in epidemic proportions due to disease pressure as a result of continuous potato farming.

Seed Preparation and Experimental Set up

The plant materials from CIP were received as in vitro plantlets, and were subculture at Kachwekano research station to raise 100 plantlets each. These were planted out in a netted screen house to generate minitubers in 2015 A. The produced minitubers were planted out in the season of 2015 B (September to December) to increase the number and size of the minitubers for evaluation in the following seasons.

Field trials were conducted for two seasons in 2016 B (September to December) and 2017 A (March to June). Genotypes were planted in an alpha lattice design of a 8 × 6 with three replications for two seasons. The plot size was two rows of 15 plants each at a spacing of 35 × 75 cm. Genotypes were exposed to natural infestation of late blight using spreader rows of a susceptible cultivar 'Victoria' planted next to each plot. Variety 'Cruza' was included as a resistant check. At the time of planting fertilizer N P K 17:17:17 (%) was applied at a rate of 100 kg ha^{-1}. Pest and disease control were done except for late blight. All recommended agronomic practices were followed.

Data Collection

Disease Evaluation and Analysis

With the first appearance of the symptoms, plants in each plot were visually rated at 7-days interval for percentage leaf and stem area covered with late blight lesions. This was done by comparing the green and non-green leaf portions affected by the disease. Evaluations continued until susceptible clones reached 100% leaf blight. For all plots and assessment dates, the area under the disease progress curve AUDPC (Campbell and Madden 1990) was calculated within a single experiment

Table 2 Rainfall, mean temperatures and relative humidity at Kachwekano and Karengyere research stations during the experimental period

Site	2016B			2017A			
Karengyere	RF (mm)	AT (°C)	RH (%)		RF (mm)	AT(°C)	RH (%)
September	162.4	16.8	88.2	March	114.1	16.1	83.4
October	174.1	16.1	86.5	April	247.6	15.3	84.2
November	272.6	13.4	88.4	May	184.6	15.8	83.4
December	65.8	17.2	82.8	June	25.1	16.5	85.4
Kachwekano							
September	80.3	17.2	86.3	March	110.6	18.0	79.9
October	184.3	16.3	86.8	April	217.0	17.1	81.5
November	201.5	15.2	86.3	May	147.0	18.2	78.6
December	95.8	16.8	82.1	June	14.4	18.9	74.0

RF Total rainfall; *AT* Average air temperature; *RH* Relative humidity

(Bradshaw 2007). The RAUDPC was calculated using the following formula:

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

Where T_i is the ith day when an estimation of percent foliar late blight is made and D_i is the estimated percentage of area with blighted foliage at T_i. T_{total} is the number of days at which the final assessment was recorded.

Yield and Yield Related Traits

The number of plants in each plot were counted and yield recorded at harvest. The total number of tubers from each plot and genotype was counted. Total tuber yield was calculated as a function of number of plants, total weight of all the tubers per plot and converted to tons per hectare (t ha^{-1}). To determine the marketable tuber weight (MTW), harvested tubers from each plot were separated into marketable (>30 mm), and unmarketable (<30 mm).types.

Data Analysis

Data were analyzed using Genstat 14th edition (Payne et al. 2014) software package. Where significant differences were detected, means were separated using the least significant difference (LSD) test procedure at the 5% significance level, using the Fisher's protected LSD. Separate ANOVA were conducted per location with genotypes as the main effect. Means of combined seasons across sites were obtained for the measured traits.

Table 3 Analysis of variance for RAUDPC and yield related traits of potato genotypes tested for two seasons at two locations in Uganda

Source of variation	d.f	RAUDPC MS	TTY MS	MTW MS	TNT MS
Kachwekano					
Rep	2	0.03***	412.08***	65.30**	10243**
Genotype	47	0.05***	215.28***	28.60***	12325***
Season	1	0.20***	14315.13***	1447.30***	132698***
Genotype. Season	47	0.01	56.138**	7.78*	2161***
Residual	198	0.01	37.42	5.08	1073
Total	287				
Karengyere					
Rep	2	0.15**	155.62***	92.49***	14480***
Genotype	47	0.07***	221.14***	34.99***	9120***
Season	1	5.31***	10897.53***	1478.32***	112417***
Genotype. Season	47	0.02**	106.61***	11.803***	2928***
Residual	190	0.01	48.84	5.75	1254
Total	287				

*significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; *** significant at $P \leq 0.001$; *DF* degrees of freedom; *MS* means squares; *RAUDPC* relative area under the disease progress curve, *TNT* Total number of tubers; *TTY* total tuber yield; *MTW* marketable tuber weight;

Table 4 Relative area under disease progress curve of 48 potato genotypes evaluated for two seasons at two locations in Uganda

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	0.29	0.42	0.36 h-k	0.77	0.41	0.59 g-i	0.47
391046.14	0.28	0.25	0.27 b-k	0.60	0.35	0.48 b-i	0.37
391919.3	0.04	0.12	0.08 ab	0.40	0.04	0.22 a-c	0.15
392633.64	0.28	0.46	0.11 a-c	0.69	0.39	0.54 f-i	0.45
392657.8	0.13	0.08	0.11 a-c	0.29	0.06	0.17 a	0.14
392661.18	0.25	0.30	0.27 b-k	0.68	0.32	0.50 c-i	0.39
392797.22	0.36	0.31	0.33 f-k	0.61	0.37	0.49 c-i	0.41
393077.54	0.19	0.27	0.23 a-j	0.58	0.37	0.47 b-i	0.35
393220.54	0.04	0.13	0.08 ab	0.36	0.11	0.24 a-d	0.16
394895.7	0.15	0.22	0.18 a-i	0.58	0.37	0.48 b-i	0.33
394905.8	0.30	0.51	0.40 jk	0.52	0.44	0.48 c-i	0.44
395011.2	0.10	0.14	0.12 a-e	0.53	0.15	0.34 a-h	0.23
395015.6	0.15	0.23	0.19 a-i	0.62	0.20	0.41 a-i	0.30
395017.14	0.11	0.21	0.16a-h	0.58	0.18	0.38 a-i	0.27
395017.229	0.06	0.21	0.14 a-f	0.43	0.29	0.36 a-h	0.25
395077.12	0.02	0.08	0.05 a	0.28	0.10	0.19 ab	0.12
395096.2	0.12	0.11	0.11 a-d	0.41	0.10	0.26 a-f	0.19
395109.34	0.15	0.08	0.11 a-d	0.42	0.06	0.24 a-e	0.18
395112.32	0.13	0.21	0.17 a-h	0.38	0.17	0.27 a-f	0.22
395438.1	0.11	0.18	0.15 a-f	0.40	0.23	0.32 a-g	0.23
396026.103	0.40	0.31	0.36 h-k	0.64	0.33	0.48 c-i	0.42
396038.101	0.29	0.30	0.30 c-k	0.73	0.35	0.43 a-i	0.42
396038.105	0.23	0.20	0.22 a-j	0.62	0.39	0.50 c-i	0.36
396077.159	0.14	0.26	0.20 a-i	0.63	0.27	0.45 a-i	0.33
396580.3	0.26	0.40	0.33 f-k	0.75	0.18	0.46 b-i	0.40
CRUZA	0.10	0.22	0.16 a-g	0.39	0.28	0.33 a-g	0.24
KACHPOT1	0.36	0.35	0.35 g-k	0.66	0.23	0.44 a-i	0.40
KIMULI	0.31	0.25	0.28 c-k	0.65	0.29	0.47 b-i	0.38
KINIGI	0.24	0.30	0.27 b-k	0.45	0.33	0.39 a-i	0.33
MABONDO	0.14	0.29	0.21 a-j	0.36	0.30	0.33 a-g	0.27
NAKPOT1	0.23	0.13	0.18 a-i	0.65	0.25	0.45 a-i	0.32
NAKPOT5	0.14	0.21	0.18 a-i	0.67	0.35	0.51 c-i	0.34
NAROPOT1	0.24	0.27	0.26 b-k	0.62	0.33	0.47 b-i	0.37
NAROPOT3	0.21	0.18	0.20 a-i	0.71	0.31	0.51 d-i	0.35
NKRK19.10	0.13	0.21	0.17 a-h	0.61	0.23	0.42 a-i	0.29
NKRK19.17	0.18	0.26	0.22 a-j	0.51	0.41	0.46 b-i	0.34
NKRN59.11	0.29	0.33	0.31 e-k	0.63	0.30	0.47 b-i	0.39
NKRN59.124	0.28	0.15	0.21a-j	0.56	0.20	0.38 a-i	0.30
NKRN59.29	0.24	0.38	0.31 d-k	0.77	0.54	0.66 i	0.48
NKRN59.41	0.11	0.13	0.12 a-e	0.55	0.13	0.34 a-h	0.23
NKRN59.48	0.20	0.27	0.23 a-j	0.66	0.35	0.51c-i	0.37
NKRN59.58	0.13	0.26	0.19 a-i	0.40	0.32	0.36 a-h	0.28
NKRN59.61	0.11	0.25	0.18 a-i	0.59	0.46	0.53e-i	0.35
PETERO	0.24	0.41	0.32 f-k	0.58	0.37	0.48 b-i	0.40
RUTUKU	0.17	0.23	0.20 a-i	0.66	0.31	0.48 c-i	0.34

Table 4 (continued)

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
RWANGUME	0.22	0.20	0.21 a-j	0.45	0.32	0.38 a-i	0.30
RWASHAKI	0.14	0.21	0.17 a-i	0.51	0.41	0.46 a-i	0.32
VICTORIA	0.39	0.50	0.44 k	0.74	0.51	0.63 hi	0.53
Mean	0.19	0.25		0.56	0.29		0.32
LSD (0.05)	0.15	0.11		0.21	0.18		0.16
CV (%)	48.1	27.4		23.0	38.3		30.6

LSD Least significant difference; *CV* Coefficient of variation; *RAUDPC* relative area under disease progress curve, means in a column followed by the same letters are not significantly different at P=0.05

Results

Weather Data

Weather conditions were favorable for development of late blight in the trials. There was regular rainfall, and temperatures varied between 15 °C and 18 °C (Table 2) for the two sites and seasons. The relative humidity was high throughout the growing period, enhancing late blight epidemic in the study. In general, more rainfall was recorded in Karengyere and the highest temperatures were observed in Kachwekano area.

Analysis of Variance

The analysis of variance for the relative area under the disease progress curve (RAUDPC), marketable tuber weight (MTW), total number of tubers (TNT) and total tuber yield (TTY) among tested genotypes is presented in Table 3. Highly significant ($p < 0.001$) differences were observed for all the measured parameters at both locations. Significant genotype x environment interactions were observed in both seasons and locations with more differential performance in Karengyere.

Late Blight Disease Severity

Reaction of potato genotypes to late blight disease was expressed in terms of relative area under disease progress curve (RAUDPC). Highly significant differences were observed among genotypes for their susceptibility to potato late blight ($P \leq 0.001$) within locations and seasons (Table 4). The mean RAUDPC (=100 max) for both locations and seasons was 0.32 (32%). Late blight was more severe in Karengyere for both seasons and the highest mean score observed was 0.56 in 2016B. The most resistant genotypes across locations were 395,077.12 (0.12), 392,657.8 (0.14) and 391,919.3 (0.15), while genotypes Victoria (0.53), NKRN59.29 (0.48) and 391,006.2 (0.47) were the most susceptible. Cruza, the resistant standard check, had a RAUDPC value of 0.24, while the susceptible check Victoria had a RAUDPC of 0.53. However, some clones were highly variable in their RAUDPC values across the two locations and seasons.

Total Tuber Yield

Mean total tuber yield of 48 potato genotypes is presented in Table 5. Genotypes showed highly significant differences ($P \leq 0.001$) for total tuber yield (TTY) within locations and across seasons under late blight infection. The mean TTY was 19.8 t ha^{-1}. The TTY was higher in Kachwekano than at Karengyere in the 2016B season, while both sites had the same yield in 2017A. The highest overall yield recorded was 27.3 t ha^{-1} in 2016B at Kachwekano. In general, genotypes 395,112.32 (35.6 t ha^{-1}), 395,109.34 (31 t ha^{-1}) and 395,096.2 (30.3 t ha^{-1}) were the best yielders, while 394,905.8 (10.3 t ha^{-1}), 392,633.64 (10.9 t ha^{-1}) and NKRN 59.124 (11.3 t ha^{-1}) were the lowest yielders across sites and seasons. The lowest yielders came below the standard susceptible check Victoria (14.1 t ha^{-1}), whereas the best yielders were above the resistant check Cruza (28.2 t ha^{-1}). At Kachwekano, the highest yielders were 395,112.32 (40 t ha^{-1}) and 393,220.54 (30.7 t ha^{-1}) while the lowest were NKRN 59.29 (9.2 t ha^{-1}) and NKRN 59.41 (9.6 t ha^{-1}). Genotypes 392,657.8 (35.3 t ha^{-1}) and 395,096.2 (32.4 t ha^{-1}) yielded best in Karengyere whereas 394,905.8 (6.4 t ha^{-1}) and NKRN 59.124 (9.8 t ha^{-1}) were the lowest yielders.

Marketable Tuber Yield

The marketable tuber weight (MTW) per hectare for the 48 potato genotypes is presented in Table 6. There was a highly significant ($P \leq 0.001$) genotype effect for marketable tuber weight across locations. The mean marketable tuber weight across locations was 8.9 kg and the highest being 9.3 kg at Kachwekano. More MTW was obtained from Kachwekano

Table 5 Total tuber yield in t ha^{-1} of 48 potato genotypes evaluated at two locations for two seasons in Uganda

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	23.0	9.3	16.2 a-h	24.7	15.8	20.2 f-o	18.2
391046.14	21.7	12.1	16.9 c-h	23.2	6.1	14.7 a-g	15.8
391919.3*	34.2	17.3	25.8 k-o	32.7	25.4	29.0 o-r	27.4
392633.64	16.3	7.3	11.8 a-c	10.2	10.0	10.1 a-c	10.9
392657.8	24.3	9.8	17.0 c-h	47.1	23.5	35.3 r	26.2
392661.18	28.2	13.8	21.0 f-m	29.1	12.8	20.9 f-p	21.0
392797.22	20.0	12.0	16.0 a-h	24.5	15.3	19.9 e-n	18.0
393077.54	33.2	10.5	21.9 h-n	36.4	13.2	24.8 j-q	23.4
393220.54*	41.3	20.1	30.7 o*	18.4	16.6	17.5 c-k	24.1
394895.7	18.8	17.0	17.9 c-h	12.1	8.6	10.3 a-d	14.1
394905.8	23.6	4.8	14.2 a-g	10.3	2.5	6.4 a	10.3
395011.2	21.6	11.3	16.5 b-h	21.6	20.1	20.9 f-p	18.7
395015.6	25.9	17.9	21.9 h-n	30.9	22.2	26.5 m-r	24.2
395017.14	45.7	12.8	29.2 o	25.3	12.7	19.0 d-n	24.1
395017.229	35.5	15.5	25.5 i-o	6.9	9.6	8.2 ab	16.9
395077.12	31.1	19.6	25.4 i-o	39.6	14.7	27.2 n-r	26.3
395096.2	36.9	19.4	28.1 no	41.5	23.3	32.4 qr	30.3
395109.34*	38.8	22.5	30.6 o	33.5	29.2	31.4 qr	31.0
395112.32*	56.3	23.8	40.0 p*	41.0	21.4	31.2 qr	35.6
395438.1	21.6	9.6	15.6 a-h	13.3	9.3	11.3 a-e	13.5
396026.103	23.3	11.2	17.2 c-h	17.7	13.5	15.6 b-h	16.4
396038.101	27.3	11.8	19.5 d-k	17.9	6.9	12.4 a-f	16.0
396038.105	35.7	17.9	26.8 l-o	29.3	19.0	24.2 h-q	25.5
396077.159	27.0	9.4	18.2 c-h	25.1	13.2	19.1 e-n	18.7
396580.3	29.0	14.2	21.6 h-n	19.4	19.0	19.2 e-n	20.4
CRUZA	35.1	18.7	26.9 m-o	41.5	17.6	29.6 p-r	28.2
KACHPOT1	23.7	14.2	18.9 d-k	25.7	12.5	19.1 d-n	19.0
KIMULI	28.5	13.6	21.0 f-m	17.6	12.6	15.1 a-g	18.1
KINIGI	27.5	12.2	19.9 e-l	38.4	13.8	26.1 k-q	23.0
MABONDO	33.9	16.7	25.3 i-o	23.4	12.7	18.1 c-m	21.7
NAKPOT1	24.7	16.6	20.7 e-m	19.7	5.1	12.4 a-f	16.5
NAKPOT5	21.5	7.5	14.5 a-g	33.9	8.4	21.2 f-p	17.8
NAROPOT1	19.3	11.8	15.5 a-h	23.1	11.0	17.0 b-j	16.3
NAROPOT2	26.1	16.3	21.2 g-m	26.2	12.1	19.2 e-n	20.2
NKRK19.10	27.3	10.2	18.8 d-j	31.5	3.9	17.7 c-l	18.2
NKRK19.17	24.9	12.2	18.5 c-i	21.4	9.5	15.4 b-h	17.0
NKRN59.11	19.6	13.8	16.7 c-h	26.6	7.2	16.9 b-j	16.8
NKRN59.124	20.0	5.8	12.9 a-d	14.4	5.1	9.8 a-c	11.3
NKRN59.29	12.0	6.5	9.2 a	25.4	5.0	15.2 a-g	12.2
NKRN59.41	13.6	5.6	9.6 ab	20.7	6.8	13.8 a-g	11.7
NKRN59.48	26.0	8.3	17.2 c-h	16.0	15.7	15.8 b-i	16.5
NKRN59.58	27.5	9.7	18.6 c-i	15.8	11.1	13.4 a-g	16.0
NKRN59.61	22.8	5.4	14.1 a-f	23.8	12.4	18.1 c-m	16.1
PETERO	25.3	13.1	19.2 d-k	33.7	15.2	24.5 i-q	21.8
RUTUKU	33.9	17.2	25.6 j-o	28.8	14.2	21.5 g-p	23.5

Table 5 (continued)

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
RWANGUME	26.3	24.1	25.2 i-o	34.8	18.1	26.5 l-q	25.8
RWASHAKI	26.3	15.2	20.7 e-m	26.0	14.3	20.1 e-n	20.4
VICTORIA	22.1	5.4	13.8 a-e	21.9	6.8	14.3 a-g	14.1
Mean	27.3	13.2		25.5	13.2		19.8
LSD (0.05)	12.7	5.9		5.9	9.3		10.8
CV (%)	28.8	27.7		36.6	43.5		34.1

LSD Least significant difference; *CV* Coefficient of variation, means in a column followed by the same letters are not significantly different at P=0.05

for both season compared to Karengyere. Across sites and seasons, genotypes 395,112.32 and 395,109.34 had the highest, marketable weight of 16.47 kg and 15.40 kg respectively, while the lowest MTW was recorded for genotypes NKRN59.29 (2.7 kg) and NKRN59.41 (3.3 kg). At Kachwekano the highest marketable weight observed was 16.4 kg for genotypes 396,038.105 and 395,112.32, while the lowest was 2.7 kg and 3.4 kg for genotypes NKRN59.29 and NKRN 59.41 respectively. Genotypes 359,112.32 and 395,109.34 had the highest MTW of 16.5 kg and 15.6 kg respectively at Karengyere. The lowest MTW at Karengyere was for genotypes 394,505.8 (1.7 kg) and 395,017.229 (2.2 kg).

Relationships between Late Blight Disease and Yield Parameters

Phenotypic correlations between four traits are presented in Table 7. Correlations between MTW and total tuber yield were positive and highly significant ($p \leq 0.001$) across sites and seasons. For all sites and seasons, a highly significant positive correlation ($p \leq 0.001$) was observed between total the number of tubers and total tuber yield. Correlations between RAUDPC and other traits were negative and significant for both sites ($p \leq 0.01$).

Discussion

The present study evaluated the response of 48 potato genotypes for late blight disease, yield and related traits for two seasons from two major potato growing locations in the highland regions of Uganda. The evaluated genotypes varied significantly in resistance to late blight disease, marketable tuber weight and total tuber yield across seasons as well as sites. The highly significant differences observed among genotypes for both sites and seasons indicate variability in the genetic makeup of the different potato clones. The significant interaction shows that the clones did not respond equally in all environments indicating to specific adaptation. The study environments also distinguished genotype performance suggesting the existence of environmental variation. Significant interaction of genotypes with environment in relation to late blight disease development and yield parameters have been observed in other studies (Muhinyuza et al. 2014; Hirut 2015). However, the differential performance of genotypes in this study may not be attributed to be genotypic variations between pathogen populations at each site. According to (Njoroge et al. 2016), US-1 clonal lineage was predominantly found from isolates in western Uganda.

In general, higher total tuber yield is influenced by a combined genotype and environment effect. This is true for all growth and yield related parameters (Muhinyuza et al. 2014). Genotypes with the highest number of total tubers were not necessary the highest yielders implying that total tuber yield is predominantly influenced by tuber weight. However, Mehdi et al. (2008) found that total tuber yield is mainly attributed to higher number of tubers per plant and tuber size. This may explain the positive correlation between total tuber yield and marketable tuber weight. The higher total tuber yield and marketable tuber weight from both sites in 2016B could be explained by the late onset of the late blight. The disease appeared several days after flowering and barely affected yield. The similar yield obtained from both locations in 2017A could be suggested to the same level of disease pressure at both locations.

The severity of late blight and the resulting yield reduction in the present study seems to be correlated with the amount of precipitation received during the growing season. The prevailing weather conditions at Karengyere offered a favorable environment for disease development leading to high RAUDPC values and the subsequent reduction in all yield parameters. This is due to the fact that temperature and humidity are the principal factors in late

Table 6 Marketable tuber weight in kilograms per hectare of 48 potato genotypes evaluated at two locations for two seasons in Uganda

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
391006.2	11.75	3.58	7.67 c-j	12.50	6.00	9.25 g-l	8.47
391046.14	7.87	3.52	5.69 a-e	8.00	2.00	5.00 a-g	5.35
391919.3	14.72	6.62	10.67 h-m	15.67	7.17	11.42 k-n	11.05
392633.64	7.22	1.62	4.42 a-c	4.17	2.88	3.53 a-d	3.98
392657.8	11.17	3.60	7.38 b-i	28.05	11.08	19.57 p	13.48
392661.18	12.55	7.83	10.19 f-m	13.62	4.80	9.21 f-l	9.70
392797.22	9.62	5.38	7.50 b-i	10.62	4.78	7.70 b-k	7.60
393077.54	17.05	5.22	11.13 i-n	17.63	6.22	11.93 k-n	11.53
393220.54	26.33	10.75	18.54 p	9.55	6.12	7.83 c-k	13.18
394895.7	6.17	8.62	7.39 b-i	2.50	2.33	2.42 a	4.90
394905.8	12.05	1.05	6.55 a-h	3.17	0.18	1.68 a	4.12
395011.2	7.95	4.52	6.23 a-g	9.33	7.83	8.58 e-l	7.40
395015.6	9.17	7.13	8.15 c-j	14.72	7.95	11.33 k-n	9.75
395017.14	21.80	5.98	13.89 m-o	11.62	4.25	7.93 d-k	10.92
395017.229	15.30	6.62	10.96 i-n	2.12	2.22	2.17 a	6.57
395077.12	18.47	11.67	15.07 n-p	24.67	4.28	14.48 m-o	14.77
395096.2	17.22	8.45	12.83 k-o	18.78	10.17	14.48 m-o	13.65
395109.34	23.05	7.23	15.14 n-p	20.00	11.28	15.64 n-p	15.40
395112.32	20.55	12.22	16.38 op	23.45	9.62	16.53 op	16.47
395438.1	11.22	3.78	7.50 b-i	4.47	1.37	2.92 a	5.22
396026.103	12.22	3.45	7.83 c-j	8.12	2.95	5.53 a-i	6.68
396038.101	17.17	4.60	10.88 i-n	16.83	1.67	9.25 g-l	10.07
396038.105	22.45	10.33	16.39 op	12.83	7.37	10.10 j-m	13.25
396077.159	14.38	3.15	8.77 d-k	11.50	3.88	7.69 b-k	8.23
396580.3	14.45	6.65	10.55 h-m	8.17	8.33	8.25 e-k	9.40
CRUZA	13.08	8.45	10.77 h-m	14.55	4.75	9.65 h-l	10.22
KACHPOT1	13.05	7.02	10.03 f-m	11.67	5.12	8.39 e-k	9.22
KIMULI	11.95	4.72	8.33 c-j	7.80	3.28	5.54 a-i	6.93
KINIGI	16.72	5.83	11.28 i-n	21.22	4.83	13.03 l-o	12.15
MABONDO	10.62	6.17	8.39 c-j	7.38	2.00	4.69 a-f	6.55
NAKPOT1	13.42	7.22	10.32 g-m	9.12	1.45	5.28 a-h	7.80
NAKPOT5	10.05	3.00	6.53 a-h	16.95	1.45	9.20 f-l	7.87
NAROPOT1	10.38	5.63	8.01 c-j	12.62	3.50	8.06 d-k	8.03
NAROPOT3	15.28	7.12	11.20 i-n	14.00	3.50	8.75 f-l	9.97
NKRK19.10	15.00	3.63	9.32 e-l	11.45	0.80	6.13 a-j	7.72
NKRK19.17	9.00	3.05	6.03 a-f	8.88	2.50	5.69 a-j	5.87
NKRN59.11	8.33	3.72	6.03 a-f	10.62	1.63	6.13 a-j	6.08
NKRN59.124	7.47	1.70	4.58 a-d	7.05	1.33	4.19 a-e	4.38
NKRN59.29	3.00	2.47	2.73 a	4.22	1.17	2.69 a	2.72
NKRN59.41	5.38	1.37	3.38 ab	5.38	1.12	3.25 ab	3.32
NKRN59.48	9.17	2.22	5.69 a-e	6.38	4.28	5.33	5.52
NKRN59.58	12.83	2.90	7.87 c-j	5.38	1.33	3.36	5.62
NKRN59.61	8.03	0.95	4.49 a-c	7.50	4.00	5.75	5.12
PETERO	14.83	6.13	10.48 g-m	15.95	4.13	10.04	10.27
RUTUKU	19.33	9.05	14.19 m-o	18.17	6.13	12.15	13.17

Table 6 (continued)

Site	Kachwekano		Karengyere				
Genotype	2016B	2017A	Season				
			Across seasons	2016B	2017A	Across seasons	Across seasons and sites
RWANGUME	13.50	13.12	13.31 l-o	15.17	4.72	9.94	11.63
RWASHAKI	15.37	8.22	11.79 j-n	13.95	3.50	8.73	10.25
VICTORIA	9.17	0.93	5.05 a-e	9.42	1.13	5.28	5.17
Mean	13.00	5.60	9.30	11.83	4.33	8.08	8.86
LSD (0.05)	4.8	1.8		2.8	2.2		3.9
CV (%)	15.6	13.9		17.1	24.5		17.1

LSD Least significant difference, *CV* Coefficient of variation, means in a column followed by the same letters are not significantly different at P=0.05

blight disease development (Hannukkala et al. 2007; Sedláková et al. 2011 and Forbes 2012).

Disease development varied across locations and resulted in differential responses of genotypes for late blight severity. Significant genotype x location interaction was observed for RAUDPC and yield and yield related traits. Genotypes with lower RAUDPC values did not necessarily have higher total tuber yield nor other yield parameters. For example genotype 395,077.12 had the lowest mean RAUDPC across sites and seasons, but was not the best yielder, while the highest yielder 395,112.32 had a relatively high RAUDPC of 0.22. However, some consistency was observed for the lowest yielding and susceptible genotypes like 394,905.8, NKRN 59.41 and NKRN59.124. These findings are in agreement with the observations of Haynes et al. (1998) who reported that highly resistant and susceptible genotypes were the most stable. The poor yield performance of some genotypes with low RAUDPC values could be explained by the fact that most of the resources are used in fighting the pathogens. The differential performance of clones moderately resistant to *Phyphthora infestans* across seasons and environments has been reported in other studies (Mulema et al. 2004; Forbes et al. 2005). These variations in reaction to late blight disease can be attributed to adaptation to horizontal resistance, isolate variability and environmental variation or a synergy of all (Flier et al. 2003; Forbes et al. 2005).

Table 7 Phenotypic correlation between traits of 48 potato genotypes tested for two seasons at two locations in Uganda

Traits	MTW	RAUDPC	TTY
Kachwekano			
MTW	1.00		
RAUDPC	−0.34***	1.00	
TTY	0.87***	−0.39 ***	1.00
Karengyere			
MTW	1.00		
RAUDPC	0.87***	1.00	
TTY	−0.23**	−0.21**	1.00

Significance levels: *p ≤ 0.05; ** p ≤ 0.01; ***p ≤ 0.001; *RAUDPC* relative area under the disease progress curve; *TTY* total tuber yield; *MTW* marketable tuber weight; *TNT* total number of tubers

The commercial cultivars and farmer varieties had high RAUDPC values, an implication that their resistance has broken down. This could be supported by the fact that most of the varieties were breed on the concept of qualitative resistance with single *R* genes, which is easily broken down by the changing of pathogen population (Landeo et al. 1999; Landeo et al. 2000; Kumar et al. 2007). This justifies the need to breed for horizontal resistance.

The positive and highly significant correlations between marketable tuber weight, total tuber number and total tuber yield observed in this study were reported elsewhere (Muhinyuza et al. 2014; Hirut 2015). The negative correlation between RAUDPC and total tuber yield plus other yield related traits has been reported in other studies (Dowley et al. 2008; Mantecón 2009). These results suggest that late blight affects tuber yield through destruction of foliage and the resultant reduction of the photosynthetic area.

Overall, genotypes with high levels of resistance to potato diseases had high tuber yields and would be promising candidate parents in a disease resistance breeding program. Kaushik et al. (2007) stated that the use of breeding materials with high yield and resistance levels to potato late blight are one of the most effective strategies to control the disease and improve yield.

Conclusion

Genotypes in the current study showed significant differences in the level of resistance to late blight disease, yield and yield related traits. Genotype 395,112.32 was the best performer in

all seasons and sites in all yield related aspects, except for total number of tubers. The following clones: 395112.32, 395,109.34, 393,220.54, 395,011.2, 391,919.3, 395,077.12, 393,077.54 395,096.2, 395,017.14, 392,657.8, and Rwangume had a high to moderate level of resistance to late blight disease across the study sites and seasons. There is no single approach to a universal control method for late blight. Use of host plant resistance is the most effective disease management strategy to control late blight and increase yield without causing harm to the environment from overuse of fungicides. The study largely selected eleven high yielding potato genotypes with sufficient level of late blight resistance which can be commended for breeding or direct introduction following yield stability tests and official release.

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Compliance with Ethical Standards

Conflict of Interest The authors declared that they have no conflict of interest.

References

Acquaah, G. 2012. Principles of plant genetics and breeding. 2nd edition. Wiley-Black Well publishing, UK.

Bradshaw, J.E. 2007. Breeding potato as major staple crop. Breeding strategies for clonally propagated potatoes. In *Breeding major food staples*, ed. S.K. Manjit and P.M. Priyadarshan, 277–328. Iowa: Blackwell publishing.

Campbell, C.L., and L.V. Madden. 1990. *Introduction to plant disease epidemiology*. New York: Wiley.

CIP. 2012. International Potato Centre regional program for sub-Saharan Africa: about sub-Saharan Africa [online]. Available at http://cipotato.org. CIP, La Molina, Peru.

CIP. 2016. Potato facts and figures [Online]. Available at http://cipotato.org/potato/facts/. Accessed 9–15 July 2016. Centro Internacional de la Papa, Lima, Peru.

Dowley, L.J., J. Grant, and D. Griffin. 2008. Yield losses caused by late blight (*Phytophthora infestans* (Mont.) de Bary) in potato crops in Ireland. *Irish Journal of Agricultural and Food Research* 47: 69–78.

FAOSTAT. 2016. Production statistics. Available at http://faostat.fao.org. Accessed 11 July 2016.

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

Forbes, G.A. 2012. Using host resistance to manage potato late blight with particular reference to developing countries. *Potato Research* 55: 205–216.

Forbes, G.A., M.G. Chacón, H.G. Kirk, M.A. Huarte, M. Van Damme, S. Distel, G.R. Mackay, H.E. Stewart, R. Lowe, J.M. Duncan, H.S. Mayton, W.E. Fry, D. Andrivon, D. Ellissèche, R. Pellé, H.W. Platt, G. MacKenzie, T.R. Tarn, L.T. Colon, D.J. Budding, H. Lozoya-Saldaña, A. Hernandez-Vilchis, and S. Capezio. 2005. Stability of resistance to *Phytophthora infestans* in potato: An international evaluation. *Plant Pathology* 54 (3): 364–372.

Garrett, K., R. Nelson, C. Mundt, G. Chacon, R. Jaramillo, and G. Forbes. 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.R., W. Kaguongo, O. Ortiz, A. Tesfaye, G. Woldegiorgis, and W.W. Wagoire. 2009. Improving potato production in Kenya, Uganda and Ethiopia: A system diagnosis. *Potato Research* 52: 173–205.

Hannukkala, A., T. Kaukoranta, A. Lehtinen, and A. Rahkonen. 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 Pathology* 56: 167–176.

Hijmans, R., G. Forbes, and T. Walker. 2000. Estimating the global severity of potato late blight with GIS linked disease forecast models. *Plant Pathology* 49: 697–705.

Hirut, G.B. 2015. Genetic analyses of drought tolerance and resistance to late blight among potato genotypes. PhD Thesis. University of KwaZulu-Natal, South Africa.

Kakuhenzire, R., B. Lemaga, I.N. Kashaija, O. Ortiz, and B. Mateeka. 2013. Effect of *Crotalaria falcata* in crop rotation and fallowing on potato bacterial wilt incidence, disease severity and latent infection in tubers and field soil. *Biopesticide International* 6: 182–194.

Kaushik, S.K., V. Bhardwaj, P.H. Singh, and B.P. Singh. 2007. Evaluation of potato germplasm for adaptability and resistance to late blight. *Potato Journal* 34 (1–2): 43–44.

Kromann, P., A. Taipe, W.G. Perez, and G.A. Forbes. 2009. Rainfall thresholds as support for timing fungicide applications in the control of potato late blight in Ecuador and Peru. *Plant Disease* 93: 142–148.

Kumar, R., G. Kang, and S. Pandey. 2007. Inheritance of resistance to late blight (*Phytophthora infestans*) in potato. *Euphytica* 155: 183–191.

Landeo, J., M. Gastelo, G. Beltran, and L. Díaz. 1999. Quantifying genetic variance for horizontal resistance to late blight in potato breeding population B3C1. CIP program report 2000: 63–68.

Landeo, J.A., M. Gastelo, G. Beltran, and L. Diaz. 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, CIP, Lima, Peru. 63–68

Low, J. 1997. Potato in southwest Uganda: Threats to sustainable production. *African Crop Science Journal* 5: 395–412.

Mantecón, J.D. 2009. Importance of potato late blight in Argentina, and the effect of fungicide treatments on yield increments over 20 years. *Cieniae Investigación Agraria* 36: 115–122.

Mehdi, M., T. Saleem, H.K. Rai, M.S. Mir, and G. Rai. 2008. Effect of nitrogen and FYM interaction on yield and yield traits of potato genotypes under Ladakh condition. *Potato Journal* 35: 126–129.

Muhinyuza, J.B., H. Shimelis, R. Melis, J. Sibiya, and M.N. Nzaramba. 2012. Participatory assessment of potato production constraints and trait preferences in potato cultivar development in Rwanda. *International Journal of Development and Sustainability* 1: 358–380.

Muhinyuza, J.B., H. Shimelis, R. Melis, J. Sibiya, D. Gahakwa, and M.N. Nzaramba. 2014. Yield response and late blight reaction of potato genotypes in Rwanda. *American Journal of Potato Research* 92: 10–22.

Mulema, J.M.K., O.M. Olanya, E. Adipala, and W. Wagoire. 2004. Stability of late blight resistance in population B potato clones. *Potato Research* 47: 11–24.

Muthoni, J., H. Shimelis, R. Melis, and Z.M. Kinyua. 2013. Response of potato genotypes to bacterial wilt caused by *Ralstonia solanacearum* (Smith) (Yabuuchi et al.) in the tropical highlands. *American Journal of Potato Research* 90: 301–402.

Njoroge, A.W., G. Tusiime, G.A. Forbes, and J.E. Yuen. 2016. Displacement of US-1 clonal lineage by a new lineage of

Phytophthora infestans on potato in Kenya and Uganda. *Plant Pathology* 65: 587–592.

Payne, R.W., D.A. Murray, S.A. Harding, D.B. Baird, and D.M. Soutar. 2014. GenStat for windows, 17th edn. VSN International, Hemel Hempstead, UK.

Sedláková, V., J. Dejmalová, E. Hausvater, P. Sedlák, P. Doležal, and J. Mazáková. 2011. Effect of *Phytophthora infestans* on potato yield in dependence on variety characteristics and fungicide control. *Plant, Soil and Environment* 57: 486–491.

UBOS. 2016. Statistical abstract. Uganda Bureau of statistics.

Yao, C.-G., B.-T. Song, L. Jun, C.-J. Wu, Q. Cheng, D.-C. Li, and C.-H. Xie. 2011. Population improvement of resistance to late blight in tetraploid potato: A case study in combination with AFLP marker assisted background selection. *Agricultural Sciences in China* 10: 1177–1187.