Field screening of advanced potato clones for foliar resistance to late blight (*Phytophthora infestans*) in two agro-climatic regions

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Late blight caused by the pathogen *Phytophthora infestans* is regarded as the most important oomycete disease responsible for causing economic loss to potato production in Mauritius. This study was carried out to evaluate the field resistance of 18 advanced potato clones to late blight in two agro-climatic regions representative of the super-humid and humid zones of the island. Control susceptible cultivars were Spunta and Safari while varieties Vigora and Belle Isle were used as resistant controls. Disease severity, area under disease progress curve (AUDPC), relative area under disease progress curve (rAUDPC), tuber yield and relative yield loss were assessed to identify clones with foliar resistance to late blight under natural conditions. Significantly lower percentage disease severity was recorded in the breeding series 142/161, 29/5 and 161/142 compared to the susceptible controls which reached 100% leaf defoliation. Clones of the 29/5 and 142/161 series recorded the lowest final disease severity of 20% across both locations. Thirteen clones were identified as highly resistant to late blight with AUDPC and rAUDPC values ranging from 0.3 to 119.4 and 0.002 to 0.048 respectively. Among them, three clones (142/161/2, 29/5/3 and 29/5/14) recorded the highest marketable tuber yields of 23.6 t/ha, 22.4 t/ha and 21.3 t/ha respectively. The relative yield loss in the susceptible controls over the highly resistant clones averaged 274%. This suggests that the highly resistant clones were less affected in their yield by late blight and are potential candidates for cultivation under conditions where *P. infestans* is a recurring problem.

Keywords: *Phytophthora infestans*, disease progress curve, disease severity, late blight, marketable tuber yield

Late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is the main biotic constraint to potato production worldwide (Wulff et al. 2007; Forbes et al. 2014). In Mauritius, it is the most important oomycete disease causing severe crop damage and economic loss to potato production (Felix and Ricaud 1975). Symptoms on the leaves first appear as water-soaked pale green areas which rapidly enlarge into dark brown necrotic lesions. Under high humidity, a white mildew consisting of sporangia and spores of the pathogen can be seen on the lower surface of infected leaves, especially around the edges of the necrotic lesions. Symptoms are equally present on the stems and tubers. Light to dark brown lesions encircle the stems which become weak and collapse. Under cool and wet conditions the pathogen can destroy the potato foliage in 10 to 15 days and potential yield can be reduced up to 80% (Drenth and Guest 2004), while economic loss is estimated to be 10 billion euros per year in both crop loss and fungicide use (Haverkort et al. 2009).

Late blight infection is very difficult to control due to the genetic diversity of *P. infestans* populations (Fry 2008). The search for genetic resistance to late blight is a practical and economic way of controlling the disease. Initially the search concentrated on specific resistance also known as race-specific, monogenic, qualitative or complete resistance and is characterised by a hypersensitive response in the form of small necrotic lesions (Flier et al. 2003; Forbes et al. 2005). It is based on the recognition of avirulence genes of the pathogen by major plant resistance genes (R-genes) (Flor 1971). However, this type of resistance is not durable and is quickly overcome by new populations (Flier et al. 1998;

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Flier et al. 2003). More recently, the emphasis has been switched to non-specific resistance which is considered to be more stable over time and space (Goodwin et al. 1995; Parlevliet 2002; Forbes et al. 2005). This type of resistance is described as horizontal, quantitative or field resistance. It is governed by a large number of minor genes, with small and additive effects and does not involve gene-by-gene interaction and therefore is assumed to be race non-specific. Its stability is attributed to its capacity to maintain a balance between all the races of *P. infestans* present in a given location. Horizontal resistance acts in different ways, either through the production of toxic exudates on the leaf surface, confinement of the fungal structures to the cell walls, low colonisation of the mesophyll, slow collapse of the petioles or reduction of the pathogen reproductive range. In other words, it raises physiological or chemical barriers in the tissues of the host (Colon et al. 1995).

P. infestans populations exist in both the asexual and sexual forms (A1 and A2 mating types). In regions where sexual reproduction occurs, the resulting oospore can survive for months or years in the absence of living hosts, leading to more aggressive genotypes (Bashi et al. 1982; Drenth et al. 1995). In Mauritius, in addition to the existing US-1 genotype, resistance of new strains of *P. infestans* to metalaxyl-containing fungicides has been observed (Ganoo and Saumtally 2001). The main commercial varieties have shown susceptibility to the disease in both the super-humid regions where late blight pressure is highest and in the humid regions where it is present at lower intensity (Saumtally 2004) necessitating regular fungicide applications to prevent crop losses due to the disease. Consequently, they represent the second major cost component (16%) next to seed (45%) and contribute to the high cost of production of both ware and seed potato (FAREI 2017). Recently, genotypic characterisation of *P. infestans* from Mauritius using random amplified polymorphic DNA (RAPD), mitochondrial haplotyping and mating type analysis revealed that the isolates of *P. infestans* collected from distinct geographical regions were shown to belong to mitochondrial type II and mating type A2 and no A1 mating type was detected (Ibrahim and Taleb-Hossenkhan 2017).

With the introduction of the sexual form of *P. infestans* in many countries and the development of resistant strains, as well as concerns about their environmental effects of heavy fungicide applications, breeding efforts worldwide were focused on the development of late blight resistant cultivars (Wastie 1991; Forbes and Jarvis 1994; Jansky 2000; Rojas et al. 2014). Quantitative resistance is thought to result in a more durable resistance under field conditions (Fry 2008; Solomon-Blackburn et al. 2007). Among varieties delivering durable late blight resistance 'Sarpo Mira' was one of the few potato cultivars that have been reported to retain resistance in the field for several years (Kim et al. 2012; White and Shaw 2010). Similarly, breeding studies with resistant Solanum germplasm have shown that a wealth of R genes is present in the highly resistant Mexican *Solanum demissum* (Vleeshouwers et al. 2011).

This study was a search for further resistant cultivars and examined the extent advanced potato genotypes selected for their yield characteristics could as well present other desirable biotic traits such as late blight resistance in the context of sustainable potato production. The specific objectives were to (i) to assess the level of resistance of advanced potato clones to late blight and identify clones with high foliar resistance to *P. infestans* and (ii) to compare the yield performance of late blight resistant clones with that of commercial varieties known to be susceptible, under natural disease inoculum.

Materials and Methods

Potato clones

In this study eighteen advanced potato clones with marketable tuber yield above the national average yield (Cadersa et al. 2019) were evaluated for their foliar resistance to late blight at the Food and Agricultural Research and Extension Institute (FAREI) research stations in Mauritius. The potato clones were of the breeding series 142/161, 161/142, 21/5 and 29/5. They were derived from a series of four crosses between five parental breeding lines namely 02-14/2, 01-16/1, 05-3-10-1, 05-8-3A and 05-15-1 (Table 1) which had their origin from true potato seeds introduced from the International Potato Centre (CIP) in the 1980s. To date, no information is available on either their late blight resistance genes or whether resistance is qualitative or quantitative. Susceptible control varieties were Spunta and Safari which are the commercially grown varieties in the first and second seasons while Belle Isle and Vigora were the resistant known genotypes (MSIRI 2005; FAREI 2018).

Table 1: General description of 18 advanced potato clones evaluated for their resistance to *P. infestans* under natural occurrence in 2019

Potato clones	Parental cross	Recorded marketable yield (t/ha)
142/161/1	02 – 14/2 x 01 – 16/1	41.1 ± 7.4
142/161/2		41.4 ± 11.9
142/161/4		37.9 ± 12.3
142/161/5		36.8 ± 12.9
142/161/8		36.5 ± 11.4
142/161/9		51.7 ± 4.9
142/161/15		39.5 ± 6.0
161/142/16	01 – 16/1 x 02 – 14/2	31.4 ± 4.1
21/5/3	05-3-10-1 x 05-8-3A	31.3 ± 10.3
21/5/10		28.8 ± 7.7
29/5/2	05-15-1 x 05-8-3A	27.7 ± 6.4
29/5/3		34.5 ± 11.0
29/5/7		35.6 ± 8.1
29/5/10		38.0 ± 9.8
29/5/11		33.4±9.8
29/5/14		25.2 ± 5.6
29/5/16		29.9 ± 14.9
29/5/17		41.4 ± 7.3

Source: Cadersa et al. (2019)

Site description

Two trials were set up at Wooton and Réduit research stations on 9 May and 17 June 2019 respectively. Wooton is characterised by a Humic Ferruginous Latosol soil type in the super humid region at an elevation of 450 m above sea level with an annual precipitation of 2000 – 2500 mm. Réduit is situated in the humid region at an altitude of 213 m above sea level with an annual rainfall of 1800 – 2000 mm and Low Humic Latosol family soil type (Parish and Feillafé 1965).

Inoculum

Plants were exposed to the natural inoculum of *P. infestans.* The screening sites were purposely chosen because of the late blight disease pressure prevailing during the first potato season from mid-April to the end of June. Cool, wet weather with ambient relative humidity above 90% and mean minimum temperatures of 16 – 21°C favour late blight development (Harrison 1992).

Therefore, natural epidemics of *P. infestans* in the field can be used advantageously to screen large populations of potato genotypes for resistance to late blight (Gopal and Singh 2003). At these two sites, potato usually becomes severely infected by *P. infestans* throughout the potato growing season such that artificial inoculation was not necessary.

Experimental design and crop management

Both trials were laid out in a randomised block design with four replications. Plot sizes of 2.4 m^2 consisted of single row 3 m long and an inter row spacing of 0.8 m. Ten tubers were planted per row with a total of 40 tubers per variety per site. Spunta and Safari were used as "spreader rows" to ensure a uniform source of disease inoculum and each spreader variety was planted after each three rows such that all rows of the 18 clones received an equal amount of inoculum. Cultural practices viz fertiliser application, planting, earthing up, irrigation and pest control were as recommended for commercial plantations (MSIRI 2010). One application of the fungicide Ortiva 250 SC at 1ml/L was necessary 50 days post-planting as a preventive measure against early blight (*Alternaria solani*) to ensure that the latter do not mask the late blight symptoms during the disease assessment period. During the growing cycle, the crop was exposed to natural infection by *P. infestans* without any fungicide application for the control of the disease. Susceptible control varieties were harvested when they reached complete leaf defoliation while harvest for moderately to resistant clones was done at 90% crop senescence.

Data collection and measurement

The potato accessions were assessed for their reaction to late blight in terms of percentage of foliage destruction during the growing cycle. The presence of *P. infestans* was confirmed in the field as well as in infected plants by the appearance of light green to dark brown water soaked spots surrounded by a yellow chlorotic halo on the lower leaves and a white mildew area on the underside of the leaves (Mohan et al. 1996). Data was collected on the following parameters:

(i) Days to onset of the disease (DDA)

This was recorded by counting days from planting to the first appearance of late blight symptoms in each plot (genotype).

(ii) Late blight disease severity (%) on foliage

Late blight disease severity was scored at 5-day intervals starting when the first symptoms of the disease were observed and ending when the susceptible varieties reached 100% disease severity on a scale of 1– 9 as developed by James (1971) and Henfling (1987) (Table 2).

Table 2: Disease severity rating scale for potato late blight

Scale	Description	Blight infection (%)
1	No disease observed	**0**
2	Plants blighted, no more than 1 or 2 lesions per plant	**1**
3	Up to 10 lesions per plant, or general light infections	**5**
4	About 50 lesions per plant, up to 1 in 10 leaflets infected	**15**
5	Nearly every leaflet infected, but plants retain normal form, plants appear green	**30**
6	Every plant affected and about 50% of the leaf area is destroyed, plants appear green but flecked with brown	**50**
7	About 75% of the leaf area is destroyed, plants appear light brown	**75**
8	Plants nearly defoliated, stems are green	**90**
9	All leaves dead, stems dead or dying.	**100**

Subsequently, the area under disease progress curve (AUDPC), relative area under disease progress curve (rAUDPC) and resistance (susceptibility) scale values were calculated:

(iii) Area under disease progress curve (AUDPC)

The area under disease progress curve (AUDPC) represents the estimated percentages of leaf area affected which is recorded at different times during the epidemic (Fry 1978). It is calculated using the midpoint formula (Campbell and Madden 1990):

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

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

(iv) Relative area under disease progress curve (rAUDPC)

The relative area under disease progress curve (rAUDPC) value was obtained by dividing the AUDPC by the total number of days elapsed between the first and last evaluation of the foliage destruction:

$$rAUDPC = \frac{AUDPC / 100}{\text{(Time in days between the last evaluation and the first evaluation)}}$$

Evaluations with 100% disease infection have a value of 1. All the rAUDPC values are expressed as a proportion of this value. Hence, low rAUDPC values indicate low levels of infection during the evaluation period, corresponding to the more resistant genotypes (Pérez and Forbes 2008).

(v) Resistance (susceptibility) scale values

The resistance (susceptibility) scale values are used to measure the degree of resistance of the potato clones to *P. infestans* and help in classifying the clones as resistant or susceptible. The resistance scale values are calculated using the following equation:

$$S_x = S_y \, {}^{Dx}/_{Dy}$$

where S_y and D_y represent, respectively, the assigned susceptibility scale value and observed disease measure (rAUDPC) for the standard genotype, and S_x and D_x represent, respectively, the calculated susceptibility scale value and observed disease measurement for the genotype in question. The assigned susceptibility value of the control is divided by the resistance measure of the control (rAUDPC) to get a constant. This constant is multiplied by the resistance measure of each target cultivar to get the susceptibility value of that genotype.

(vi) Classification of resistance of potato genotypes

Resistance to late blight was classified on a 1–9 scale based on the computed resistance scale value developed by Malcolmson (1976); Darsow (1989); Yuen and Forbes (2009) where increasing number represents increasing susceptibility (Table 3).

Table 3: Category scale for resistance to potato late blight disease

Category of resistance	Resistance scale value (1–9 point scale)
Highly resistant	1
Resistant	1–2
Moderately resistant	3–4
Moderately susceptible	5–6
Susceptible	7–8
Highly susceptible	8–9

(vii) Tuber yield

At harvest, tubers in each plot were graded into marketable (≥ 30 mm) and unmarketable (≤ 30mm) grades, weighed separately in kilograms and converted to tonnes/ha. Total tuber yield was computed from the sum of marketable and unmarketable yield.

(viii) Percentage relative yield loss

The percentage relative yield loss (%RYL) for susceptible genotypes was calculated as the ratio of the difference between the mean yield obtained from the resistant genotypes (Ya) and the susceptible genotypes (Y) to the mean yield of the resistant genotypes (Rabbinge 1993).

$\%RYL = 100 \times [(Ya - Y) / Ya]$.

Data analysis

Data were subjected to analysis of variance (ANOVA) using the statistical software IBM SPSS version 21.0. Mean separation was performed using the Duncan Multiple Range Test procedure at the 5% probability level. Spearman correlation coefficient values were calculated to determine trait associations. Separate ANOVAs were initially conducted per trial site with genotypes as the main effect followed by the combined ANOVA across locations. Homogeneity of variance was verified using Bartlett's test (Snedecor and Cochran 1989).

Results

Climatic data

The total rainfall amounts recorded at Wooton and Réduit were 668.0 mm and 164.5 mm respectively with the highest level of precipitation occurring in the month of June. Mean minimum temperature was at par at both sites while mean maximum temperature was slightly higher at Wooton during May (Table 4).

Disease severity and progress of potato late blight

The disease progress curves for the control varieties and breeding clones showed similar trends at both Wooton and Réduit. The onset of late blight occurred on the susceptible control varieties Spunta and Safari at the same time. The onset at Wooton was at 58 days after planting (DAP) and earlier at Réduit at 38 DAP (Figure 1). Thereafter, the disease progressed rapidly to reach 100% leaf damage at 93 and 74 DAP at Wooton and Réduit respectively.

On the other hand, compared to Spunta and Safari, the percentage leaf disease severity was significantly lower in the breeding series 29/5, 142/161 and 161/142 as well as the resistant control varieties. At both locations, final disease severity was the lowest (< 20%) in breeding series 29/5 and 142/161 while accessions of the 21/5 series presented significantly higher levels of foliage destruction of 76.90 % and 51.25% at Wooton and Réduit respectively.

Table 4**:** Monthly rainfall (mm) and mean temperature (°C) at Wooton and Réduit during the growing season of 2019

			Temperature (°C)	
Trial sites	**Month**	**Rainfall (mm)**	**Mean minimum**	**Mean maximum**
Wooton	May	151.0	17.3	25.0
	June	287.0	16.6	23.0
	July	230.0	16.1	22.9
Total rainfall/mean temperature		668.0	16.7	23.6
Réduit	June	76.8	17.3	23.0
	July	48.4	16.6	23.1
	August	39.3	16.6	23.0
Total rainfall/mean temperature		164.5	16.8	23.0

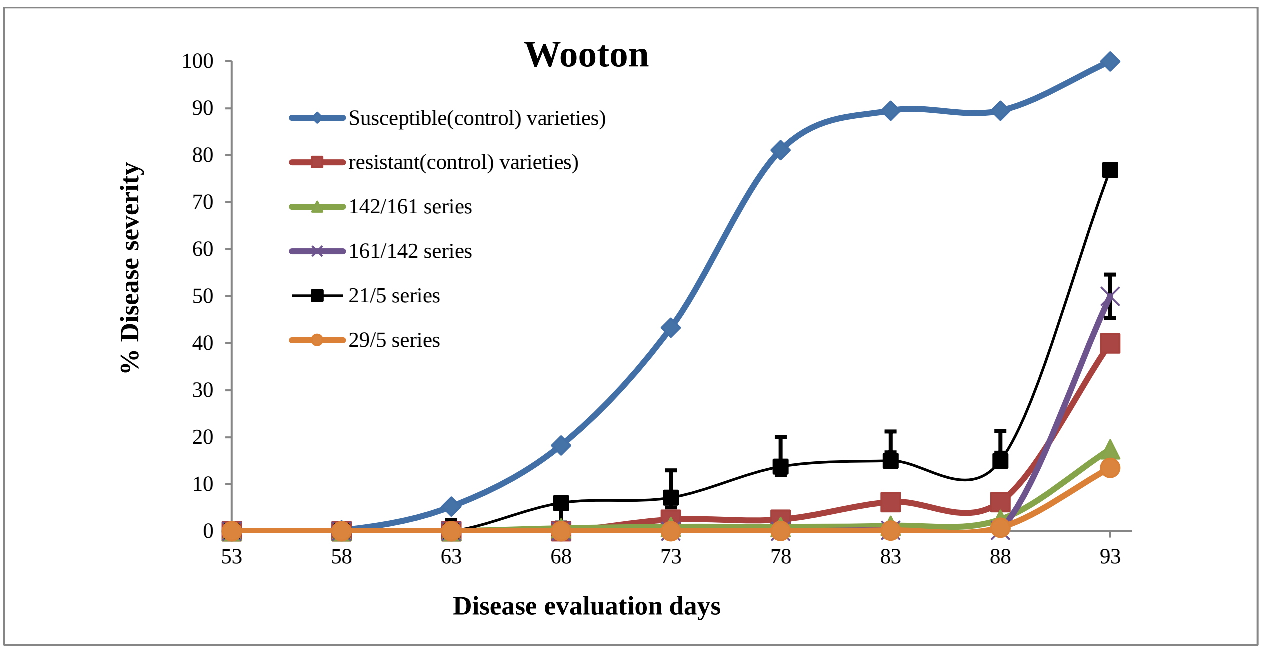


Figure 1**:** Disease progress curve for susceptible and resistant (control) varieties, breeding series 142/161, 161/142, 21/5 and 29/5 at Wooton and Réduit in 2019. Data points are mean % disease severity values. The vertical bars represent LSD value at each evaluation date at the 5% level of significance.

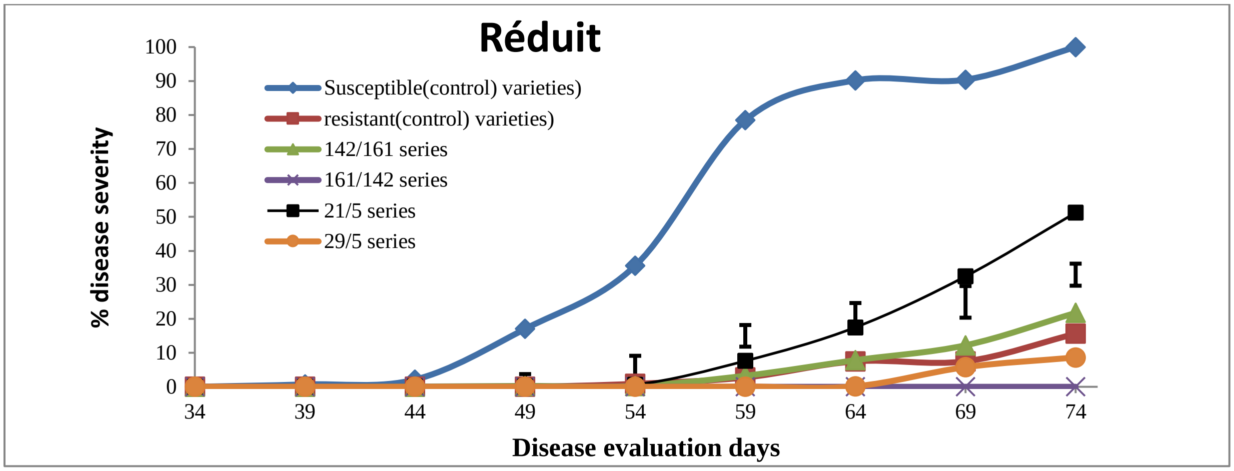


Figure 2 below highlights the field reaction of susceptible control varieties and resistant clones in the trials against late blight in the super humid region at Wooton and the humid region at Réduit.

Figure 2. Incidence of potato late blight in susceptible controls and local clones:
(A): Wooton at 66 DAP (left and right rows - resistant clones; middle row - susceptible variety Spunta) (A1): Dark brown necrotic lesions on Spunta leaves with powdery whitish areas.
(B): Réduit at 45 DAP (left - susceptible control Safari; right - resistant clone). (B1): Dark brown necrotic lessions on Safari leaves which are deformed and curled.

At both Wooton and Réduit, the susceptible cultivars are almost completely blighted whereas the resistant clones are not harmed by the disease.

Screening of potato clones to late blight infection

The analysis of variance table showed that at each location, there were significant differences among potato accessions (P ≤ 0.05) in AUDPC, rAUDPC, marketable yield (t/ha), percentage unmarketable yield and total tuber yield (t/ha) (Table 5). The combined analysis of variance indicated highly significant (P ≤ 0.005) interactions of genotype x environment for AUDPC and rAUDPC and significant (P ≤ 0.05) interaction of genotype x environment for marketable and total tuber yield. The effect of interaction was however not significant for percentage unmarketable yield. The magnitude of the mean square values of genotype for AUDPC and marketable tuber yield at each location was very high while across locations, the magnitude of the mean square value of environment for marketable tuber yield was the highest.

Table 5**:** Separate ANOVA and combined ANOVA for AUDPC, rAUDPC and tuber yield in 22 potato accessions at Wooton and Réduit CRS in the growing season of 2019.

		Mean squares values for the studied traits				
Location/ Source of variation	**DF**	**AUDPC**	**rAUDPC**	**MTY**	**UMTY**	**TTY**
Wooton						
Replication	3	10382.1	0.001	3.27	321.47	26.61
Genotype	21	1150787.1**	0.072**	96.16**	440.15*	134.89**
Residual	63	14000.7	0.001	10.99	133.26	18.66
Réduit						
Replication	3	62953.3	0.005	90.32	284.64	193.15
Genotype	21	1155604.8*	0.094**	182.46**	402.97**	292.81**
Residual	63	7825.8	0.001	21.42	140.57	55.18
Combined analysis of genotype and environment						
Genotype	21	2263268.3**	0.162**	238.51**	702.39**	326.66**
Environment	1	27403.5	0.006*	518.34**	1671.01**	212.58
Gen. x env.	21	41186.7**	0.014**	40.50*	126.79	101.71*
Residual	131	12166.6	0.001	17.58	145.48	40.42

DF: degrees of freedom; AUDPC: area under the disease progress curve; rAUDPC: relative area under disease progress curve; MTY: marketable tuber yield; UMTY: % unmarketable tuber yield, TTY: total tuber yield; Gen. x env.: genotype x environment. Significance levels: *significant at P ≤ 0.05; ** highly significant at P ≤ 0.005

Area under disease progress curve (AUDPC)

Significant differences (P ≤ 0.05) were observed among potato accessions in AUDPC values at each location and across locations (Table 6). At Réduit and Wooton equally, the highest AUDPC values were recorded in Safari and Spunta. Across locations, mean AUDPC values were significantly lower in all the 18 advanced clones as well as the resistant control varieties Vigora and Belle Isle compared to the susceptible control varieties, Safari (1914.3) and Spunta (1806.1). Among the advanced potato clones, the lowest AUDPC levels were reached in 13 accessions namely: (all seven accessions of the 29/5 series, five accessions of the 142/161 series and the accession 161/142/16) with values ranging from 0.3 to

119.4. However, AUDPC values of both accessions of the 21/5 series were significantly higher than the 13 clones but significantly lower than the susceptible controls Spunta and Safari.

Tuber yield of potato accessions

Significant differences (P ≤ 0.05) were also observed among potato accessions in marketable and unmarketable tuber yield. Varieties Safari and Spunta which presented the highest AUDPC levels; produced significantly lower marketable tuber yields at both Réduit and Wooton as well as across locations with means of 4.3 and 7.1 t/ha respectively (Table 6). Likewise, tuber yield decreased drastically in 21/5/3 (6.1 t/ha) and Vigora (8.3 t/ha) although they recorded relatively lower AUDPC values of 630.9 and 255.3 respectively. Across locations, 14 advanced clones gave significantly higher marketable tuber yield (12.2 - 23.6 t/ha) than Safari and Spunta. Clones 142/161/2, 29/5/3 and 29/5/14 recorded the highest marketable tuber yields of 23.6, 22.4 and 21.3 t/ha respectively.

Marketable tuber yield also differed between locations with relatively lower yield recorded at Wooton (2.7 - 19.6 t/ha) compared to Réduit (5.6 - 27.5 t/ha). Mean % unmarketable yield across locations ranged from 8.1% to 41.0%. Four clones (29/5/10, 29/5/14, 29/5/6 and 142/161/2) produced significantly lower % unmarketable yield of 8.1% to 14.7%.

Table 6**:** Performance of advanced potato clones in terms of their yield and area under disease progress curve (AUDPC) compared to late blight susceptible and resistant control varieties in two growing environments in 2019

	AUDPC			**Marketable tuber yield (t/ha)**			**Unmarketable tuber yield (%)**		
Potato accessions	**Réduit**	**Wooton**	**Mean**	**Réduit**	**Wooton**	**Mean**	**Réduit**	**Wooton**	**Mean**
142/161/1	41.9^{de}	46.9^{e}	44.4^{g}	23.8^{ab}	15.2^{abc}	19.5^{a-d}	15.4^{b-e}	18.6^{c-f}	17.0^{d-i}
142/161/2	188.1^{d}	50.6^{e}	119.4^{efg}	27.5^{a}	19.6^{a}	23.6^{a}	13.8^{b-e}	15.6^{d-f}	14.7^{ghi}
142/161/4	399.4^{c}	374.4^{cd}	386.9^{c}	17.5^{b-e}	9.3^{def}	13.4^{f-i}	23.1^{a-d}	31.1^{a-f}	27.1^{a-g}
142/161/5	0.0^{e}	20.0^{e}	10.0^{g}	11.5^{e-h}	12.9^{bcd}	12.2^{f-j}	29.6^{ab}	36.6^{abc}	33.1^{abc}
142/161/6	0.0^{e}	0.6^{e}	0.3^{g}	15.0^{def}	10.0^{caf}	12.5^{f-j}	39.5^{a}	42.5^{ab}	41.0^{a}
142/161/8	18.8^{e}	49.4^{e}	34.1^{g}	7.5^{fgh}	11.2^{cde}	9.4^{i-l}	25.8^{abc}	33.3^{a-e}	29.6^{a-e}
142/161/9	394.4^{c}	58.8^{e}	226.6^{de}	12.5^{e-h}	10.9^{cde}	11.7^{f-k}	24.4^{a-d}	33.6^{a-d}	29.0^{a-f}
142/161/15	380.0^{c}	48.1^{e}	214.1^{def}	22.5^{a-d}	8.8^{def}	15.6^{d-g}	26.5^{ab}	44.4^{ab}	35.5^{ab}
161/142/16	2.50^{e}	130.0^{e}	66.3^{g}	17.0^{b-e}	15.2^{abc}	16.1^{c-f}	15.3^{b-e}	26.0^{b-f}	20.64^{c-i}
21/5/3	755.6^{b}	506.3^{c}	630.9^{b}	5.6^{h}	6.5^{efg}	6.1^{lm}	17.9^{b-e}	30.1^{a-f}	24.0^{b-g}
21/5/10	123.1^{de}	428.1^{cd}	275.6^{d}	15.7^{c-f}	6.2^{efg}	10.9^{g-k}	5.0^{de}	25.5^{b-f}	15.2^{f-i}
29/5/2	1.9^{e}	26.3^{e}	14.1^{g}	11.1^{e-h}	9.5^{def}	10.3^{h-l}	19.5^{a-e}	13.0^{f}	16.3^{eai}
29/5/3	0.0^{e}	28.8^{e}	14.4^{g}	24.7^{ab}	20.1^{a}	22.4^{ab}	17.8^{b-e}	21.9^{c-f}	19.8^{c-i}
29/5/10	86.9^{de}	51.3^{e}	69.1^{g}	15.9^{cde}	13.7^{bcd}	14.8^{e-h}	5.6^{cde}	13.8^{ef}	9.7^{hi}
29/5/11	85.0^{de}	111.3^{e}	98.1^{fg}	14.0^{efg}	7.0^{efg}	10.5^{h-l}	17.9^{b-e}	44.0^{ab}	30.9^{a-d}
29/5/14	0.0^{e}	5.0^{e}	2.5^{g}	24.5^{ab}	18.1^{ab}	21.3^{ab}	12.1^{b-e}	14.5^{def}	13.3^{ghi}
29/5/16	140.6^{de}	65.6^{e}	103.1^{fg}	23.6^{abc}	13.8^{bcd}	18.7^{b-e}	1.0^{e}	15.1^{def}	8.1^{i}
29/5/17	0.0^{e}	16.3^{e}	33.1^{g}	12.6^{e-h}	14.9^{abc}	13.7^{f-i}	4.2^{de}	25.1^{baf}	14.6^{ghi}
Spunta	1839.8^{a}	1772.5^{b}	1806.1^{a}	9.3^{e-h}	4.9^{fg}	7.1^{klm}	32.3^{ab}	29.3^{a-f}	30.8^{a-d}
Safari	1858.5^{a}	1970.0^{a}	1914.3^{a}	5.9^{gh}	2.7^{g}	4.3^{m}	31.1^{ab}	46.4^{a}	38.7^{a}
Vigora	197.5^{d}	313.1^{d}	255.3^{d}	11.7^{e-h}	5.1^{fg}	8.3^{j-m}	28.1^{ab}	30.8^{a-f}	29.4^{a-e}
Belle Isle	0.0^{e}	18.8^{e}	9.4^{g}	25.7^{a}	15.4^{abc}	20.6^{abc}	21.4^{a-e}	25.0^{b-f}	23.2^{b-h}
SE±	**62.55**	**83.67**	**77.99**	**3.27**	**2.34**	**2.96**	**8.38**	**8.16**	**8.53**

Means in a column followed by the same letter are not significantly different P > 0.05.

Relationship between yield and disease resistance parameters

Spearman's rank correlation coefficients were calculated to determine the nature and strength of association between AUDPC and yield parameters for "all cultivars" and the "group of advanced clones" (Table 7). At Réduit, a non-significant correlation was obtained between AUDPC and yield parameters equally for all cultivars and advanced clones. Similarly, at Wooton, the same relationship was observed for both groups with AUDPC significantly and negatively correlated with marketable and total tuber yield. On the other hand, when sites were combined, non-significant correlations were detected between AUDPC and yield parameters for the group of advanced clones, while AUDPC was negatively and significantly correlated with yield parameters for the group comprising of all cultivars (Table 7).

Table 7: Spearman rank correlation coefficients showing association of AUDPC with yield parameters at Réduit, Wooton and across locations in 2019 for all cultivars and group of advanced clones

Yield parameters	Réduit		Wooton		Across locations	
	All cultivars[a]	Group of advanced clones[b]	All cultivars	Group of advanced clones	All cultivars	Group of advanced clones
MTY	-0.207	0.065	-0.518**	-0.285*	-0.356*	-0.115
UMTY	0.153	0.020	0.118	0.011	-0.162*	0.037
TTY	-0.119	0.069	-0.572**	-0.367**	-0.302**	-0.105

AUDPC: area under the disease progress curve; MTY: marketable tuber yield; UMTY: % unmarketable tuber yield, TTY: total tuber yield. Significance levels: *significant at P ≤ 0.05; ** significant at P ≤ 0.01

[a] clones and control varieties

[b] clones only with no control varieties

Comparative resistance of potato accessions to late blight

Significant differences (P≤0.05) were observed among potato accessions in rAUDPC at Réduit, Wooton and across locations with the highest values recorded in Safari, Spunta followed by the clone 21/5/3 (Table 8). Mean rAUDPC values were significantly lower in thirteen clones which ranged from 0.002 to 0.048 including all 29/5 series, five 142/161 series and the accession 161/142/16. rAUDPC value of Belle Isle (0.002) was at par with those of the 13 clones.

On a 1 to 9 numerical resistance scale, where ascending values correspond to increasing disease susceptibility, highly susceptible varieties were Safari (9.000) and Spunta (8.403), moderately resistant was 21/5/3 (2.902), resistant clones comprised of 142/161/4 (1.814), the control Vigora (1.358), 21/5/10 (1.277), 142/161/9 (1.078) and 142/161/15 (1.003). Thirteen clones (including all 29/5 accessions) and the control Belle Isle were identified as highly resistant with resistance scale values below 1.000 ranging from 0.001 to 0.606.

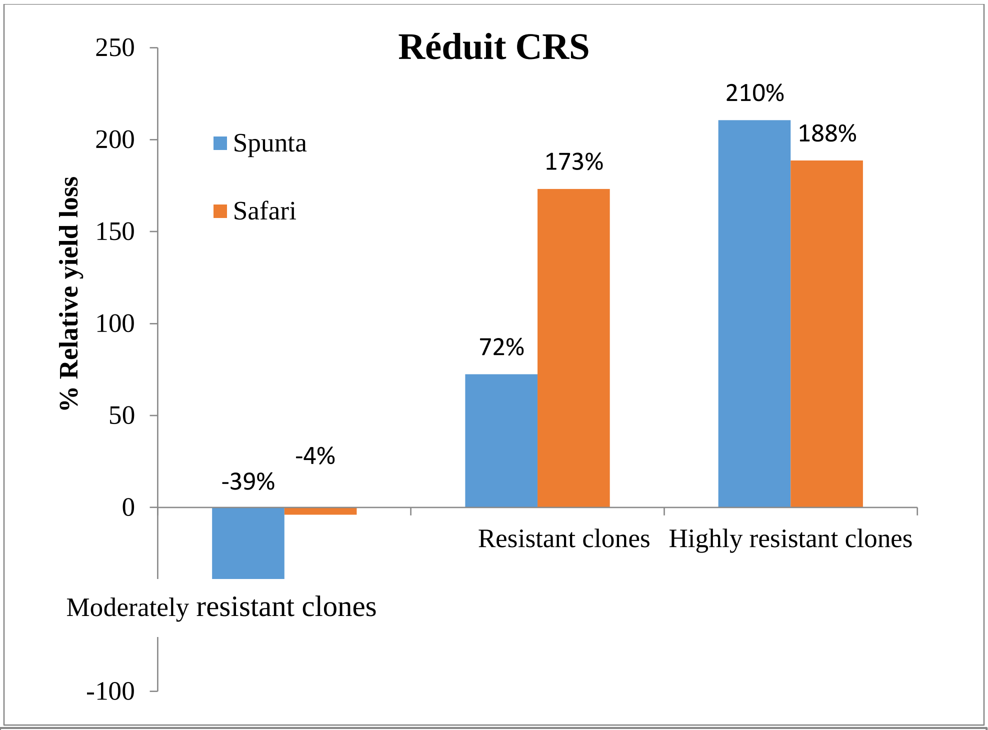
Table 8: Relative area under disease progress curve (rAUDPC), resistance scale values and category of resistance of 22 potato accessions in 2 environments during the growing season of 2019. Safari being the most susceptible variety at Réduit and Wooton respectively was assigned a susceptibility value of 9

	rAUDPC			**Resistance scale value**			**Category of resistance**
Potato accessions	**Réduit**	**Wooton**	**Mean**	**Réduit**	**Wooton**	**Mean**	
142/161/1	0.012^{e}	0.011^{e}	0.012^{f}	0.225	0.214	0.220	Highly resistant
142/161/2	0.054^{d}	0.013^{e}	0.033^{ef}	0.896	0.231	0.564	Highly resistant
142/161/4	0.110^{c}	0.938^{cd}	0.104^{e}	1.917	1.710	1.814	Resistant
142/161/5	0.000^{e}	0.005^{e}	0.003^{f}	0.000	0.091	0.046	Highly resistant
142/161/6	0.000^{e}	0.003^{e}	0.002^{f}	0.000	0.003	0.001	Highly resistant
142/161/8	0.005^{e}	0.012^{e}	0.009^{f}	0.046	0.226	0.136	Highly resistant
142/161/9	0.110^{c}	0.014^{e}	0.063^{de}	1.887	0.268	1.078	Resistant
142/161/15	0.110^{c}	0.118^{e}	0.060^{de}	1.787	0.220	1.003	Resistant
161/142/16	0.0007^{e}	0.323^{e}	0.016^{f}	0.000	0.594	0.297	Highly resistant
21/5/3	0.220^{b}	0.127^{c}	0.171^{b}	3.491	2.313	2.902	Moderately resistant
21/5/10	0.035^{de}	0.109^{cd}	0.071^{d}	0.599	1.956	1.277	Resistant
29/5/2	0.0005^{e}	0.006^{e}	0.003^{f}	0.009	0.120	0.064	Highly resistant
29/5/3	0.000^{e}	0.007^{e}	0.003^{f}	0.000	0.131	0.066	Highly resistant
29/5/10	0.025^{de}	0.013^{e}	0.019^{f}	0.422	0.234	0.328	Highly resistant
29/5/11	0.024^{de}	0.028^{e}	0.026^{f}	0.413	0.508	0.461	Highly resistant
29/5/14	0.000^{e}	0.002^{e}	0.007^{f}	0.000	0.023	0.011	Highly resistant
29/5/16	0.040^{de}	0.017^{e}	0.048^{f}	0.912	0.300	0.606	Highly resistant
29/5/17	0.000^{e}	0.017^{e}	0.008^{f}	0.000	0.303	0.151	Highly resistant
Spunta	0.530^{a}	0.443^{b}	0.480^{a}	8.709	8.098	8.403	Highly susceptible
Safari	0.530^{a}	0.493^{a}	0.512^{a}	9.000	9.000	9.000	Highly susceptible
Vigora	0.056^{d}	0.078^{d}	0.067^{d}	1.285	1.431	1.358	Resistant
Belle Isle	0.000	0.005^{e}	0.002^{f}	0.000	0.086	0.043	Highly resistant
SE±	**0.02**	**0.02**	**0.02**				

Means in a column followed by the same letter are not significantly different P > 0.05

Percentage relative yield loss (%RYL)

The percentage relative yield loss (% RYL) due to late blight disease was calculated for the highly susceptible varieties Safari and Spunta compared to the moderately resistant, resistant and highly resistant clones (Figure 3). At Wooton, marketable tuber yield in Safari decreased by 142%, 200% and 425% compared to the mean yield of the moderately resistant, resistant and highly resistant clones respectively. In Spunta, relative yield loss was 33%, 65% and 274% respectively. A similar trend was observed at Réduit where yield in Safari decreased by 173% and 188% compared to the mean yield of the resistant and highly resistant clones, while relative yield loss in Spunta was 72% and 210%. Across locations, the relative yield loss due to late blight in the susceptible controls averaged 274% over the highly resistant clones.



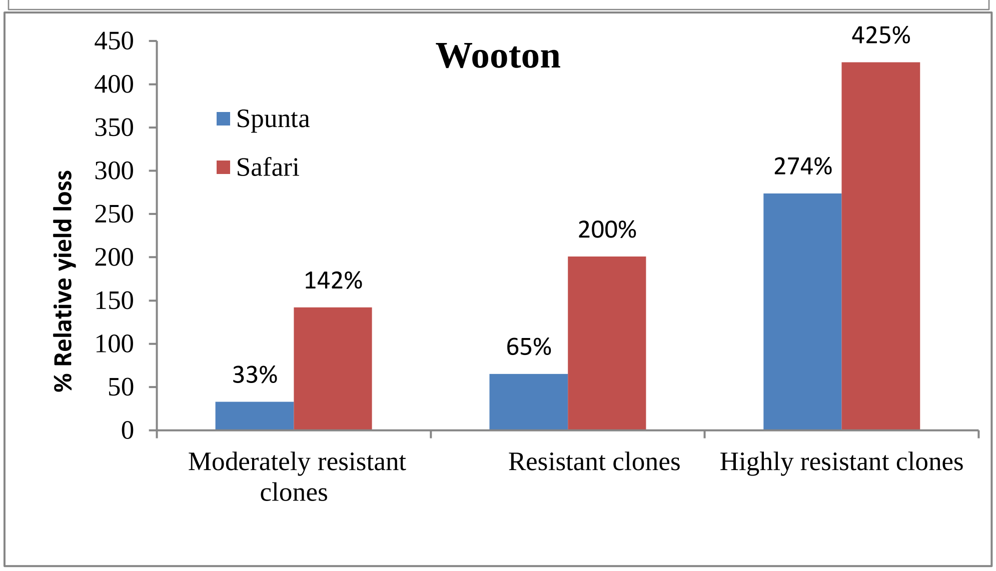


Figure 3: Percentage relative yield loss due to late blight disease in the highly susceptible varieties Safari and Spunta compared to the moderately resistant, resistant and highly resistant clones

Discussion

Resistance to foliar late blight in the potato clones evaluated in this study was generally expressed as lower percentage of disease severity, low AUDPC and rAUDPC values as well as high marketable tuber yield. The occurrence of late blight is determined by the plant disease triangle which is represented by a susceptible host, a virulent pathogen and a conducive environment (Francl 2001). Disease predictive models based on recognition of weather conditions identified temperature, relative humidity, rainfall, wind speed and leaf wetness as the most significant factors in the development of late blight (Fry et al. 1983; Andrade-Piedra et al. 2005; Henshall et al. 2006). Reports from Ahmed et al. (2015)

indicated that mean temperature in the range of 16 – 20°C and monthly rainfall of 45 – 112 mm are favourable to late blight, corroborate with the results of this study that the onset of late blight and its rapid progress during the month of July was attributed to the low mean temperature (16 – 23°C) and high precipitation (48 – 230 mm). These results also confirm that the super-humid region at Wooton and the humid region at Réduit were appropriate for late blight assessment and that no artificial inoculation of the pathogen *(P. infestans)* was necessary.

AUDPC and rAUDPC are standard procedures used to estimate the amount of disease across a given season and the higher the value, the higher is the disease infection (Forbes et al. 2014). The high AUDPC and rAUDPC values recorded in Spunta are in conformity with the findings of Mutty and Taleb-Hossenkhan (2008) on the susceptibility of the variety under inoculated conditions. However, a resistance scale value of 8.403 across the two locations classified Spunta as highly susceptible when exposed to natural infection of late blight. Similarly, Safari which is a new variety exploited on a commercial scale has also showed to be highly susceptible to late blight under the given set of conditions tested. The application of fungicides is currently the most important strategy in the control of late blight by farmers in Mauritius. Consequently, with the concerns about the negative effects of fungicides on the environment and on human health (Haverkort et al. 2008), the chances for both these commercial varieties to thrive in the context of climate smart agriculture is rather remote.

Genotype x environment interactions provided evidence that late blight epidemics was less severe in in the humid region at Réduit as shown by the lower AUDPC values of the resistant and highly resistant clones than in the super humid region at Wooton. This result also explains the relatively lower marketable yield recorded in the majority of the accessions at Wooton. Genotype was found to be consistently the most important source of variation accounting for the disparity in disease severity levels between the resistant/ highly resistant clones and the susceptible varieties/moderately resistant clones. Since there were no previous reports which could quantify the resistance level of the resistant controls, the results on the rAUDPC level and resistance scale values lend evidence that Vigora is resistant and Belle Isle highly resistant to late blight respectively.

Possible explanations for the high resistance to late blight of the 13 advanced clones of the 29/5, 142/161 and 161/142/16 series might be explained by their inherent nature of resistance to infection by *P. infestans* as reported by Landeo and Turkensteen (1989) and Ojiambo et al. (2000). Low AUDPC values (0.31 to 119.37) correlated with the findings of Olanya et al. (2005) and Solano et al. (2014) of the presence of R genes with qualitative resistance in Kenyan potato genotypes and Chilean potato landraces respectively. From recent literature (Ibrahim and Taleb-Hossenkhan 2017), since the local isolates of *P. infestans* were found to belong to mitochondrial type II and mating type A2 with high aggressivity on Spunta and that no resistance breakdown was observed on Belle Isle, it can be inferred that the highly resistant clones could have differential expression of quantitative resistance. This result is in accordance with previous studies that the ability of host cultivars to limit development of late blight is an important criterion in reducing disease infection rate or quantitative resistance (Landeo et al. 1997; Umaerus and Umaerus 1994).

The high relative yield loss of the susceptible varieties compared to the resistant and highly resistant clones was attributed to the shorter bulking period which declined with increasing disease severity (Nyankanga et al. 2004; Rakotonindraina et al. 2012). Despite the huge economic losses associated with late blight in terms of fungicide costs as well as revenue loss due to yield and quality reduction

(Guenthner et al. 2001; Haverkort et al. 2009), potato varieties susceptible to potato late blight (PLB) are still widely grown as farmers prefer the marginal cost of fungicides to the perceived risk of using a resistant cultivar (Cooke et al. 2011). This is because firstly, market demand for desirable tuber characteristics has been recognised as a major factor influencing and frequently limiting cultivar turnover as markets become specialised for certain varieties and secondly, disease resistance has not been stable; many varieties released as PLB resistant have rapidly become susceptible as the pathogen population evolves (Forbes 2012). However, in this study, the question of market preferences and high tuber yield has been addressed prior to evaluating the local clones for their late blight resistance. Consistent and high marketable yields achieved by clones 142/161/2, 29/5/3, 29/5/14 and the control Belle Isle (19.5 – 23.6 t/ha) under blighted field conditions suggests their ability to tolerate disease with little effect on tuber yield. The significant and negative correlation between AUDPC and tuber yield observed for the 22 potato accessions indicates that high late-blight epidemics can significantly affect tuber yield especially in the susceptible controls as well as in the moderately resistant clones (El-Bedewy et al. 2001; Hirut et al. 2016). On the other hand, the non-significant correlation coefficient between AUDPC and tuber yield for the group of advanced clones provides good evidence that they are less influenced in their yield by late blight and can therefore be grown in late blight prone environments.

Conclusions

The results of this study demonstrate the field resistance of advanced potato clones to late blight compared to the commercially grown varieties; 13 accessions were identified as highly resistant to *Phythothora infestans* among which four clones had very low disease severity as well as high marketable tuber yield. The resistant materials identified present good potential for cultivation in late blight-prone regions to replace the highly susceptible commercial varieties. The trial will be repeated in the next season to confirm the late blight resistance of the advanced clones to the current strains of *P. infestans* which have evolved from the mating type A1 to the mating type A2.

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Author statement

All authors read, reviewed, agreed and approved the final manuscript.

Conflict of interest:

None declared.

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