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Impact of Different US Genotypes of *Phytophthora infestans* on Potato Seed Tuber Rot and Plant Emergence in a Range of Cultivars and Advanced Breeding Lines

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Abstract Seed pieces of different potato cultivars and advanced breeding lines (ABLs) from north central US breeding programmes were inoculated with different genotypes of *Phytophthora infestans* (US-1, US-1.7, US-8, US-11 and US-14). The effect of these genotypes of *P. infestans* on seed piece rot severity after re-storage was assessed using an image analysis technique. *P. infestans* genotypes demonstrated variable ability to cause seed piece rot and to reduce plant emergence measured as final plant stand (%) and the relative area under the plant emergence curve (RAUEPC). The US-8 genotype of *P. infestans* was the most aggressive genotype, as indicated by tuber rot severity across all cultivars/ABLs tested, followed by US-14 in both years. The US-1, US-1.7 and US-11 genotypes were the least aggressive, causing only moderate seed piece rotting across cultivars/ABLs tested. Similar trends were observed in two field experiments, where the US-8 and US-14 genotypes delayed or reduced emergence. Values of final plant stand (%) and RAUEPC demonstrated that the cultivars/ABLs Atlantic, MSJ453-4Y and Torridon were the least susceptible across all *P. infestans* genotypes. In both experiments cv. Pike was the most susceptible. Other cultivars/ABLs demonstrated variable

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responses to different genotypes of *P. infestans*. No symptoms of *P. infestans* were observed on emerged plants up to 60 days after planting. The variability of susceptibility of tubers to different genotypes of *P. infestans* has implications for plant breeding efforts in that the major emphasis in the past has been to breed for foliar resistance, with limited emphasis on the reaction of the tuber. Results from this study suggest that highly aggressive genotypes of *P. infestans* such as US-8 may lead to severe tuber rotting and deterioration of tubers before emergence, but despite this observation the US-8 genotype is still predominant in North America.

Keywords Image analysis · Plant stand · Potato breeding · Potato late blight · RAUEPC · Transmission · Varieties

Abbreviations

ABL	Advanced breeding line
ARI	Average reflective intensity
AUEPC	Area under the emergence progress curve
DAI	Days after inoculation
DAP	Days after planting
RARI (%)	Relative average reflective intensity
RAUEPC	Relative area under the emergence progress curve

Introduction

Late blight of potato is the most important and most destructive disease of potato worldwide. The disease caused by the oomycete *Phytophthora infestans* (Mont.) de Bary is still the greatest threat to the potato crop, accounting for significant annual losses in North America (Guenther et al. 1999, 2001) and worldwide (Hijmans et al. 2000a, b). Foliar late blight results in destruction of the foliage of susceptible cultivars under favourable environmental conditions (Beaumont 1947; Cook 1949; Wallin 1953; Lapwood 1961; Harrison 1992; Stevenson et al. 2007). Tuber late blight results in tuber rotting both in the field and later in storage in tubers intended for either seed or consumption (Melhus 1915; Murphy and McKay 1924, 1925; Bonde and Schultz 1943, 1945; Lambert et al. 1998; Kirk et al. 1999). Seed tubers infected with *P. infestans* will either rot in storage, after planting in the field, or survive and initiate new epidemics of potato late blight (Doster et al. 1989; Dowley and O'Sullivan 1991; Stevenson et al. 2007). The foliar phase of the disease is correlated with infection in the tuber phase and vice versa (Bain et al. 1997). Tubers are usually infected by inoculum produced on the plant foliage that is subsequently washed down to the soil by water movement resulting from rainfall and irrigation (Andrivon 1995; Bain et al. 1997; Porter et al. 2005; Stevenson et al. 2007). Tubers can become blighted shortly after the disease has been established on the foliage. *P. infestans* survives in tubers, where it acts as a primary source of inoculum for infection in the following growing season (Bonde and Schultz 1943; Zwankhuizen et al. 1998). Transmission of potato late blight from infected seed tubers into developing sprouts and consequently to the foliage was first suggested by Berkeley (1846) and was demonstrated using molecular techniques by Appel et al. (2001).

The pathway by which *P. infestans* progresses from infected tubers to the newly formed plant is not fully understood. Several studies have investigated the relationship between foliar late blight severity and tuber blight severity (Hirst and Stedman 1962; Lacey 1965; Boyd 1980) likely done on the US-1 genotype of *P. infestans*. In spite of the frequent strong correlation between foliar blight severity and tuber blight, some of these studies demonstrated cases of high incidence of tuber blight in the absence of foliar symptoms. Also some studies (Hirst et al. 1965), again on the US-1 genotype, demonstrated low incidence of tuber blight after a severe foliar blight epidemic. It has been suggested that potato cultivars with high levels of foliar resistance tend to slow down the epidemics of the disease and may provide higher risk of tuber infection. In these resistant cultivars vegetative growth of *P. infestans* (mycelium and sporangia) is usually produced over longer periods of time, therefore giving sporangia and zoospores more time and chance to be washed down with rainfall to the soil and hence to tubers (Toxopeus 1958; Bain et al. 1997). Potato late blight in tubers is therefore of significant importance in (1) commercial production such as stored and freshly harvested table-stock (ware) and processing crops because of direct losses due to diseased tubers and (2) in seed production because these tubers may (a) initiate epidemics by transmission from infected tubers to sprouts, stems and foliage and (b) also directly reduce plant stand and delay plant emergence, resulting in further problems which affect yield and tuber size distribution (Bussan et al. 2007) and *Potato virus Y* transmission (Radcliffe and Ragsdale 2002).

The impact of potato late blight increased greatly during the 1990s following the migration of more genetically diverse and more aggressive genotypes of *P. infestans* from Mexico (Goodwin et al. 1994a). Recent work has indicated that the new immigrant *P. infestans* clones, especially the US-8 genotype, are more aggressive in tubers and sprouts (Lambert and Currier 1997; Kirk et al. 2001a). The new genotypes of late blight are 10 times more likely to produce infected sprouts than their predecessor, US-1 (Marshall and Stevenson 1996). Historically, studies of the transmission of the late blight pathogen from seed tubers to foliage were conducted when *P. infestans* populations were dominated by US-1, a clonal lineage (Goodwin et al. 1994b). Today, populations of *P. infestans* have changed and transmission studies need to continue because the US-8 genotype is now predominant and there is a gap in our understanding of these more aggressive genotypes. For example, under realistic agronomic conditions and practices such as currently used planting rates, seed cutting and potato late blight tolerances for seed tubers (<0.1%), prediction of the likelihood of successful transmission of the disease from seed tuber to the growing plant would require experimental units of several hectares. Such constraints necessitate adaptation of experimental designs and developing realistic expectations of outcomes whilst testing effects such as the impact of the genotype of *P. infestans* over a range of cultivars of *Solanum tuberosum*. Adaptations, including using smaller experimental units with 100% tuber-inoculation rates, are worth exploring.

The dynamics of potato blight development in tubers are largely influenced by temperature (Kirk et al. 2001c) and can result in non-emergence of plants owing to seed and sprout rot. After planting therefore, the most likely outcome of experiments utilizing 100% inoculated seed pieces would be to provide an indication of the interaction between genotypes of *P. infestans* and potato cultivars in terms of plant

establishment. The objectives of this study were to evaluate the potential of different genotypes of the potato late blight pathogen (*P. infestans*) to impact plant establishment in potato cultivars and advanced breeding lines (ABLs) differing in general resistance to late blight in terms of seed tuber rot severity and plant emergence.

Materials and Methods

Potato Germplasm

Potato breeding efforts at Michigan State University and other potato breeding programmes in the USA have resulted in potato cultivars that are largely resistant to foliar late blight (Douches et al. 2004; Kirk et al. 2001a, c) but not significantly less susceptible than other cultivars in terms of tuber blight resistance (Kirk et al. 2001b). Potato late blight resistance estimates for the cultivars/ABLs used in this study were breeders' estimates and are given below as foliar and tuber ratings, respectively. US cultivars are exclusively rated against the US-8 genotype of *P. infestans* and were Atlantic (S,S), Jacqueline-Lee (R,S), Pike (I,S), FL1879 (S,S), MSI152-A (I,S), MSJ317-1 (R,S), MSJ319-7 (I,S), MSJ316-A (I,S), MSJ453-4Y (I,S), MSJ456-2Y (I,S), MSJ461-1 (R,I), FL1833 (S,S), FL1867 (S,S), MN98642 (S,S), MN15620 (S, S), ND2443 (S,S), ND5822C-7 (S,S), Snowden (S,S) and Megachip (S,S), where S, R and I represent susceptible, resistant and intermediate, respectively. The UK cv. Torridon has a National Institute of Agricultural Biology late blight resistance rating of 8 (foliage), 7 (tuber), equivalent to R,R in the US scheme. All cultivars were classified as late maturing. Tubers for this study were obtained from the potato breeding programmes at Michigan State University, the University of Wisconsin, the University of Minnesota and North Dakota State University. Potato tubers from cultivars/ABLs harvested during the previous growing seasons (Tables 1, 2 and 3) were stored at 3 °C in the dark at 90% relative humidity until they were used. Tubers for the experiments were within the size grade range 50–150 mm diameter (any plane). Visual examination of a random sample of tubers from each entry for disease symptoms indicated that tubers were free from late blight. The sample was further tested with the ELISA immunodiagnostic Alert multiwell kit (Alert multiwell kit–*Phytophthora* sp., Neogen, Lansing, MI, USA). *P. infestans* was not detected in any of the tubers. Prior to inoculation, all tubers were washed with water to remove soil. The tubers were then surface-sterilized by soaking them in 2% sodium hypochlorite (Clorox) solution for 30 min. Tubers were dried in a controlled environment with continuous airflow at 15 °C in dry air (30% relative humidity) for 4 h prior to inoculation.

Culturing of *Phytophthora infestans* and Tuber Inoculations

Cultures of *P. infestans*–isolates *Pi*95-3 (US-1), *Pi*96-2 [US-1.7 (restriction fragment length polymorphism genotype; Young et al. 2009)], *Pi*02-007 (US-8), *Pi*96-1 (US-11) and *Pi*98-1 (US-14) were selected as the most aggressive isolates from the collection of Kirk (Michigan State University) and grown on rye agar Petri plates for

Table 1 Susceptibility of tubers of potato cultivars and advanced breeding lines to different genotypes of *Phytophthora infestans*; susceptibility is expressed in terms of relative average reflective intensity [RARI (%)]

Year	RARI (%)[a]					
Cultivar/ABL[c]	Genotypes of *Phytophthora infestans*[b]					
	Combined[d]	US-1	US-1.7	US-8	US-11	US-14
2003						
Pike	32.7 a[e]	39.8 a	11.9 a	36.4 ab	35.5 a	40.0 a
MSI152-A	29.6 ab	40.2 a	12.0 a	34.6 ab	23.4 b	37.7 a
MSJ317-1	28.0 a–c	28.6 b	12.6 a	35.8 ab	24.9 b	38.0 a
MSJ319-A	26.3 a–c	4.5 de	14.2 a	36.9 ab	25.5 b	40.2 a
Jacqueline Lee	26.0 a–c	38.9 a	12.0 a	34.4 ab	8.6 c	35.9 a–c
MSJ 461-1	21.6 b–d	38.6 a	2.3 a	21.6 bc	8.8 c	36.6 ab
Torridon	20.1 b–e	3.9 de	4.2 a	41.7 a	12.0 c	38.4 a
MSJ319-7	19.0 c–e	14.5 c	14.9 a	37.9 ab	1.0 d	36.9 ab
FL1879	15.7 d–f	13.2 cd	4.3 a	36.0 ab	0.1 d	25.0 c
MSJ453-4Y	13.8 d–f	13.6 cd	3.2 a	26.1 ab	0.4 d	25.7 bc
Atlantic	10.7 ef	1.4 e	4.2 a	37.4 ab	0.1 d	10.2 d
MSJ456-2Y	8.9 f	13.2 cd	0.9 a	9.4 c	9.7 c	11.4 d
$HSD_{0.05}$	9.73	9.95	15.12	16.63	7.30	11.30
2004						
MN98642	9.4 a	8.0 a	1.2 cd	21.4 a–c	7.8 a	8.7 b
Snowden	8.3 ab	3.9 b–f	5.8 b	19.0 b–d	7.1 a	5.7 b–d
MSJ461-1	7.6 a–c	1.3 ef	2.5 cd	28.3 a	3.4 ab	2.7 d–f
Pike	7.6 a–c	6.2 a–c	0.6 d	12.8 d–f	4.5 ab	14.1 a
MN15620	7.1 a–d	7.7 ab	1.0 cd	11.1 d–g	6.9 a	8.7 bc
MSI152-A	6.8 a–e	5.9 a–d	10.8 a	4.3 gh	7.4 a	5.8 b–d
FL1879	6.3 a–e	0.9 ef	1.5 cd	24.0 ab	4.2 ab	0.7 f
FL1833	6.2 a–f	1.8 ef	0.0 d	23.4 ab	5.4 a	0.3 f
Megachip	5.0 b–f	2.6 c–f	1.2 cd	11.8 d–g	4.7 ab	4.9 c–e
Torridon	4.6 c–f	2.0 d–f	1.1 cd	13.7 c–f	6.1 a	0.4 f
ND2443	4.5 c–f	3.3 c–f	0.2 d	17.3 b–e	0.7 b	0.9 f
Jacqueline Lee	4.1 d–f	4.7 a–e	0.8 cd	9.1 e–h	4.5 ab	1.7 ef
MSJ317-1	4.1 d–g	3.9 b–f	3.9 bc	9.6 e–h	0.2 b	2.8 d–f
ND5822C-7	3.6 e–g	2.4 c–f	1.4 cd	12.6 d–g	0.6 b	1.0 f
FL1867	2.8 fg	2.4 c–f	1.3 cd	7.1 fgh	0.3 b	2.9 d–f
Atlantic	0.7 g	0.0 f	0.6 d	2.5 h	0.4 b	0.2 f
$HSD_{0.05}$	3.37	4.07	3.15	8.41	4.63	3.81

[a] Normalized tuber tissue darkening score expressed % RARI=[1- Mean $ARI_{treatment}$ / Mean $ARI_{control}$] *100; % RARI has a minimum value of zero (no darkening) and maximum value of 100 (cut tuber surface is completely blackened). The numbers are derived from the mean average reflective intensity of three surfaces cut latitudinally 25, 50 and 75% from the cut inoculated surface of n=32 seed pieces

[b] Genotype classification according to Goodwin et al. (1995)

[c] Advanced breeding line

[d] Combined analyses of % RARI for all genotypes of *P. infestans*

[e] Values followed by the same letter are not significantly different at $P=0.05$ for comparisons of mean RARI values of cultivars/ABLs within different *P. infestans* genotypes (Tukey Multiple Comparison)

14 days in the dark at 18 °C. These isolates were acquired from field infections from 1995 to 2002 on foliage and tubers of potatoes commonly grown in Michigan, USA. Pathogenicity was determined on foliage and tubers in tuber and detached leaf tests. Single isolates representative of the range of genotypes were selected for this study because only individual isolates of US-1, US-1.7

Table 2 Final relative mean plant stand (expressed relative to final plant stand in the non-inoculated control) of potato cultivars and advanced breeding lines inoculated with different genotypes of *Phytophthora infestans* in 2003 and 2004

Year	Relative mean plant stand (%)[a]						Mean plant stand Control (%)
Cultivar/ABL[c]	*Phytophthora infestans* genotypes[b]						
	Combined[d]	US-1	US-1.7	US-8	US-11	US-14	
2003							
Atlantic	67.5 a[e]	100.0 a	100.0 a	4.2 a	100.0 a	33.3 ab	100.0 a
Torridon	61.8 ab	100.0 a	100.0 a	8.3 a	58.3 ab	4.2 ab	100.0 a
MSJ453-4Y	58.3 ab	70.8 a–c	91.7 a	4.2 a	91.7 ab	33.3 ab	100.0 a
MSJ319-7	55.0 ab	83.3 ab	62.5 a	33.3 a	91.7 ab	4.2 ab	100.0 a
MSJ456-2Y	48.3 ab	58.3 a–d	83.3 a	0.0 a	58.3 ab	41.7 a	100.0 a
FL1879	47.5 ab	41.7 b–e	91.7 a	0.0 a	87.5 ab	16.7 ab	100.0 a
MSJ317-1	38.3 ab	25.0 c–e	87.5 a	37.5 a	41.7 ab	0.0 b	100.0 a
MSJ461-1	36.7 ab	12.5 de	79.2 a	0.0 a	75.0 ab	16.7 ab	100.0 a
MSJ319-A	35.8 ab	83.3 ab	62.5 a	0.0 a	33.3 ab	0.0 b	100.0 a
Jacqueline Lee	31.7 ab	12.5 de	95.8 a	0.0 a	45.8 ab	4.2 ab	100.0 a
MSI152-A	25.0 ab	12.5 de	83.3 a	0.0 a	29.2 ab	0.0 b	100.0 a
Pike	17.5 b	0.0 e	79.2 a	0.0 a	8.3 b	0.0 b	100.0 a
$HSD_{0.05}$	48.56	54.86	69.93	69.30	84.99	0.68	
2004							
Torridon	86.9 a	96.6 a	106.9 a–c	24.1 a	103.4 a	103.4 a	90.6 a
MN98642	77.6 a	108.0 a	124.0 a	0.0 b	108.0 a	48.0 c–e	78.1 a
MSJ461-1	74.4 a	100.0 a	87.5 c	0.0 b	90.6 a	93.8 ab	100.0 a
Atlantic	73.8 a	87.5 a	96.9 a–c	0.0 b	96.9 a	87.5 a–c	100.0 a
FL1833	73.1 a	119.2 a	111.5 a–c	0.0 b	65.4 ab	69.2 a–e	81.3 a
Jacqueline Lee	72.3 a	90.3 a	90.3 bc	3.2 b	90.3 a	87.1 a–c	96.9 a
ND2443	71.3 a	93.3 a	86.7 c	3.3 b	80.0 a	93.3 ab	93.8 a
FL1879	71.0 a	103.2 a	100.0 a–c	0.0 b	77.4 a	74.2 a–d	96.9 a
MN15620	70.4 a	92.6 a	92.6 bc	0.0 b	88.9 a	77.8 a–d	84.4 a
ND5822C-7	70.0 a	89.3 a	96.4 a–c	0.0 b	82.1 a	82.1 a–c	87.5 a
FL1867	67.2 a	104.0 a	120.0 ab	4.0 b	80.0 a	28.0 ef	78.1 a
MSI157-A	67.1 a	92.9 a	103.6 a–c	7.1 ab	78.6 a	53.6 b–e	87.5 a
Megachip	62.1 a	107.1 a	103.6 –c	0.0 b	75.0 ab	25.0 ef	87.5 a
MS317-1	56.0 a	96.7 a	93.3 a–c	0.0 b	56.7 ab	33.3 d–f	93.8 a
Pike	47.5 a	95.8 a	116.7 a–c	0.0 b	25.0 b	0.0 f	75.0 a
Snowden	47.3 a	100.0 a	30.0 d	0.0 b	60.0 ab	46.7 c–e	93.8 a
$HSD_{0.05}$	45.70	37.06	30.96	17.76	51.99	44.83	31.43

[a] Final plant stand (%) 60 days after planting relative to stand in control plots
[b] Genotype classification according to Goodwin et al. (1995)
[c] Advanced breeding line
[d] Combined analyses of plant stand for all genotypes of *P. infestans* excluding data from non-inoculated control
[e] Values followed by the same letter are not significantly different at $P=0.05$ for comparisons of plant stand for different cultivar/ABL combinations within *P. infestans* genotypes (Tukey Multiple Comparison)

and US-11 were available (in the USA these isolates are rare) and using multiple isolates would have unbalanced the experimental design. A homogenized mixture of mycelium and sporangia of *P. infestans* was prepared from 200 plate cultures (9 cm diameter × 15 mm depth Petri plates) from each isolate. Each plate produced between 10^5 and 10^6 spores/ml from 50 ml of wash water. An estimate of the amount of mycelium from each plate was not attempted. Each seed

Table 3 Relative area under the percent plant emergence progress curve (expressed as a percentage relative to the non-inoculated control) of potato cultivars and advanced breeding lines inoculated with different genotypes of *Phytophthora infestans* in 2003 and 2004

Year	Mean RAUEPC (%)[a]						AUEPC Control
Cultivar/ABL[c]	*Phytophthora infestans* genotypes[b]						
	Combined[d]	US-1	US-1.7	US-8	US-11	US-14	
2003							
Atlantic	47.6 a[e]	68.3 a	76.7 a	3.3 a	51.7 a	25.4 ab	72.1 a
Torridon	41.0 ab	68.8 a	70.4 ab	1.7 a	41.0 ab	2.1 b	63.3 a
MSJ453-4Y	38.6 a–c	44.2 a–c	64.6 ab	2.1 a	43.6 ab	19.2 ab	68.8 a
MSJ319-7	38.4 a–c	60.8 ab	39.2 ab	21.7 a	43.1 ab	3.3 b	66.7 a
FL1879	37.6 a–c	37.1 a–d	70.4 ab	0.0 a	42.8 ab	13.3 ab	69.2 a
MSJ456-2Y	30.8 a–c	30.4 b–e	58.3 ab	0.0 a	35.1 ab	30.8 a	57.1 a
MSJ461-1	21.9 a–c	7.5 de	50.4 ab	0.0 a	28.1 ab	9.6 ab	59.2 a
MSJ319-A	19.6 a–c	48.8 ab	30.0 b	0.0 a	25.3 ab	0.0 b	54.2 a
MSJ317-1	18.7 a–c	12.5 c–e	41.3 ab	17.5 a	23.7 ab	0.0 b	48.8 a
Jacqueline Lee	16.3 bc	7.5 de	49.6 ab	1.3 a	22.4 b	2.5 b	52.9 a
MSI152-A	14.3 bc	8.8 de	44.2 ab	0.0 a	20.5 b	0.0 b	51.7 a
Pike	8.6 c	0.0 e	39.6 ab	0.0 a	15.1 b	0.0 b	47.5 a
$HSD_{0.05}$	30.63	34.32	42.50	37.59	28.92	25.70	25.0
2004							
MN15620	97.8 a	116.7 ab	104.4 a	33.7 a	125.1 a	107.0 a	39.1 bc
Torridon	91.2 ab	96.2 ab	110.2 a	19.8 a	116.1 ab	104.8 a	64.4 ab
FL1833	86.9 ab	138.7 a	126.3 a	1.2 a	75.3 a–c	79.7 a–d	50.7 a–c
MN98642	85.4 ab	114.3 ab	102.8 a	17.7 a	119.3 ab	58.2 a–e	37.5 c
ND5822C-7	85.1 ab	110.1 ab	107.9 a	1.7 a	94.8 a–c	96.2 a–c	54.9 a–c
Jacqueline Lee	84.4 ab	99.7 ab	101.2 a	13.6 a	101.8 ab	89.9 a–c	63.8 a–c
MSJ461-1	82.6 ab	100.3 ab	99.1 a	0.0 a	97.5 ab	98.4 ab	63.4 a–c
FL1867	77.9 ab	95.9 ab	121.5 a	19.7 a	82.0 a–c	48.1 b–e	52.8 a–c
ND2443	77.6 ab	96.6 ab	94.9 a	4.4 a	81.8 a–c	90.1 a–c	60.7 a–c
Atlantic	76.8 ab	83.6 b	85.3 ab	2.0 a	96.3 a–c	83.1 a–c	71.8 a
FL1879	73.6 ab	111.9 ab	80.8 ab	12.1 a	76.7 a–c	72.3 a–e	68.5 a
Megachip	73.3 ab	116.5 ab	111.4 a	0.0 a	84.4 a–c	26.2 de	54.0 a–c
MSI157-A	71.1 ab	85.3 b	98.6 a	1.1 a	88.8 a–c	49.3 b–e	61.0 a–c
MS317-1	70.6 ab	110.7 ab	91.0 a	1.3 a	64.8 bc	55.9 a–e	46.6 a–c
Snowden	57.1 ab	98.2 ab	27.4 b	13.6 a	60.5 bc	42.6 c–e	67.7 ab
Pike	55.4 b	77.2 b	96.3 a	0.0 a	37.2 c	22.0 e	60.4 a–c
$HSD_{0.05}$	41.18	49.08	59.69	58.09	59.36	54.16	29.19

[a] RAUEPC, relative area under the percent plant emergence progress curve calculated from 0–60 days after planting [full final emergence (max=100)] expressed as a percentage relative to the non-inoculated control

[b] Genotype classification according to Goodwin et al. (1995)

[c] Advanced breeding line

[d] Combined analyses of plant stand for all genotypes of *P. infestans* excluding data from non-inoculated control

[e] Values followed by the same letter are not significantly different at $P=0.05$ for comparisons of RAUEPC for different cultivar/ABL combinations within *P. infestans* genotypes (Tukey Multiple Comparison)

tuber was cut into two sections (longitudinally) with a sterile knife, ensuring the presence of viable sprouts on each seed piece. The exposed cut surface was placed face down on the homogenized mixture of mycelium and sporangia of *P. infestans* for 30 s (Lambert and Currier 1997; Kirk et al. 1999). Two experiments were established: a postinoculation seed tuber "re-storage" and a plant establishment

experiment that were carried out as controlled environment chamber studies and field experiments, respectively. The trials were conducted in 2003 and 2004. The non-inoculated control treatments were potato seed pieces from each cultivar/ABL that were cut and placed face down on homogenized rye agar media (no pathogen) for 30 s.

Seed Tuber Rot after "Re-storage"

Potato cultivars/ABLs used for the experiments were evaluated for tuber blight severity after inoculation and re-storage. In 2003, eight seed pieces per replicate per treatment from 12 cultivars/ABLs (Table 1) were inoculated with five different genotypes of *P. infestans* isolates (US-1, US-1.7, US-8, US-11 and US-14) onto freshly cut tuber surfaces and incubated for 30 days at 10 °C and 90% relative humidity (Lambert and Currier 1997; Lambert et al. 1998; Kirk et al. 1999). In 2004, 16 cultivars/ABLs were inoculated in the same manner as in the trial conducted in 2003 (Table 1).

Tubers were inoculated as described and were then stored in the dark in net bags within ventilated plastic boxes. Each treatment was replicated four times. Boxes were arranged in a complete randomized design and stored in environmental growth chambers (Chagrin Falls, Ohio 44022-0390) in darkness at 10 °C and 90% relative humidity. Disease development rates within tubers in relation to storage temperature were known from previous experiments (Kirk et al. 2001c) and a single sampling date was selected 30 days after inoculation (DAI). After incubation (30 DAI), seed pieces were cut 25, 50 and 75% from and parallel to the inoculated surface of $n=32$ inoculated seed pieces to assess tuber blight development in the tuber tissue. A digital image analysis technique was used to assess tuber tissue infection (Niemira et al. 1999; Kirk et al. 2001c). The area selection cut-off threshold was set to 10 light intensity units, effectively allowing the software to exclude all parts of the image darker than 10 light intensity units, e.g., the black background. The average reflective intensity (ARI) of all the pixels within the image gave a measurement of the severity of tuber tissue rot from each sample. The amount of late-blight-affected tissue per tuber was expressed as a single value (mean ARI) calculated as the average ARI of the three sections, described above.

Plant Establishment

In 2003 and 2004, eight seed pieces per replicate per treatment from 12 and 16 potato cultivars/ABLs in 2003 and 2004, respectively (Tables 2 and 3), were planted 5 DAI at the Muck Soils Research Farm (Laingsburg, MI, USA) separated by two guard plants (cv. Red Norland) at the ends of each plot. Both trials were arranged as a randomized complete block design with three replicates in 2003 (limited by seed availability) and four replicates in 2004. Each plot was 2.0 m (wide) × 3.0 m (long). Soils were prepared for planting with a mechanical cultivator in early May and fertilizers were applied during final bed preparation on the day of planting. Experiments were hand-planted on 15 May and 20 May in 2003 and 2004, respectively, in a sandy-loam soil with 3% organic matter content and pH 6.5. The preparations of non-inoculated control treatments for each cultivar/ABL were

described in "Culturing of *Phytophthora infestans* and Tuber Inoculations". Seed pieces were dropped into prepared hills (30 cm height × 45 cm width at the base of the hill) at a depth of 6 cm, 30 cm apart within single rows and 0.84 m between rows. Fertilizers were applied in accordance with results from soil testing carried out in the spring of each year. About 250 kg of N per ha (total N) was applied in two equal doses at planting and hilling in each year. Additional micronutrients were applied according to petiole sampling recommendations.

Climatic variables were measured with a CR10X measurement and control system (Campbell Scientific, Logan, UT, USA) equipped with soil temperature sensors located at 6 and 12 cm depth below the soil surface in the tuber-planting zone. Soil temperature and soil moisture were measured to estimate the conduciveness of the environment for late blight development in the planted tubers and to indicate when irrigation was necessary. When soil moisture was recorded below 80% of field capacity (measured with soil moisture sensors placed 6 and 12 cm below the soil; CR10X measurement and control system, Campbell Scientific), an irrigation system was turned on to maintain soil moisture at >80% of field capacity. Weeds were controlled by hilling and with metolachlor at 2.3 l ha^{-1} about 10 days after planting (DAP), bentazon salt at 2.3 l ha^{-1} about 20 and 40 DAP, and sethoxydim at 1.8 l ha^{-1} about 60 DAP. Insects were controlled with imidacloprid at 1.4 kg ha^{-1} at planting, carbaryl at 1.4 kg ha^{-1} about 30 and 55 DAP, endosulfan at 2.7 l ha^{-1} about 65 and 85 DAP and permethrin at 0.56 kg ha^{-1} about 50 DAP.

Statistical Analyses

Tuber rot severity was expressed relative to the ARI of the non-inoculated treatments for each cultivar/ABL. The relative ARI (RARI) of a treatment was calculated as follows:

$$\text{RARI}\ (\%) = \left(1 - \frac{\text{mean ARI treatment}}{\text{mean ARI control}}\right) \times 100,$$

where RARI (%) has a minimum value of zero (no visible symptoms) and a maximum value of 100 (tuber surface is completely black). As different cultivars/ABLs were evaluated across the two years, all data were analysed by year.

In the plant establishment experiment the number of emerged plants was recorded over a 60-day period after planting and final plant stand (%) and the relative area under the emergence progress curve (RAUEPC) were calculated (Wharton et al. 2007). The RAUEPC was calculated by modification of the method used to calculate the relative area under the disease progress curve (Campbell 1990), using the following equation:

$$\text{RAUEPC} = \frac{\sum (t_{i+1} - t_i)\left(\frac{E_{i+1}+E_i}{2}\right)}{T_{\text{total}} \times 100},$$

where t is the time in DAP and E is the measured percentage of plant emergence. As plant emergence was assessed at various time intervals, the area under the emergence progress curve (AUEPC) was calculated by adding the area under the linear progression of the number of emerged plants between consecutive estimation of

emergence from planting to full emergence. The RAUEPC was calculated by dividing the AUEPC by the maximum AUEPC (100 × duration of emergence period) from planting to full emergence. Plant stand and RAUEPC were measured as percentages relative to the values measured in the non-inoculated control plots. Data for both experiments were analysed by correlation analyses of related variables and analysis of variance (least squares method) using the JMP program, version 5.0.1 (SAS Institute, Cary, NC, USA).

Results

Seed Tuber Rot after "Re-storage"

Incubation of inoculated tubers at 10 °C resulted in significant tuber infection and tuber tissue discoloration within 30 DAI. As an example, tubers of the ABL ND2443 inoculated with *P. infestans* isolate *Pi*02-007 (US-8 genotype) and incubated at 10 °C for 30 days resulted in significant tuber infection and a range of RARI (%) values (Fig. 1). Significantly greater RARI (%) values were observed in the 2003 experiment compared with the 2004 experiment (Fig. 2). Non-inoculated control tubers remained free of potato late blight symptoms.

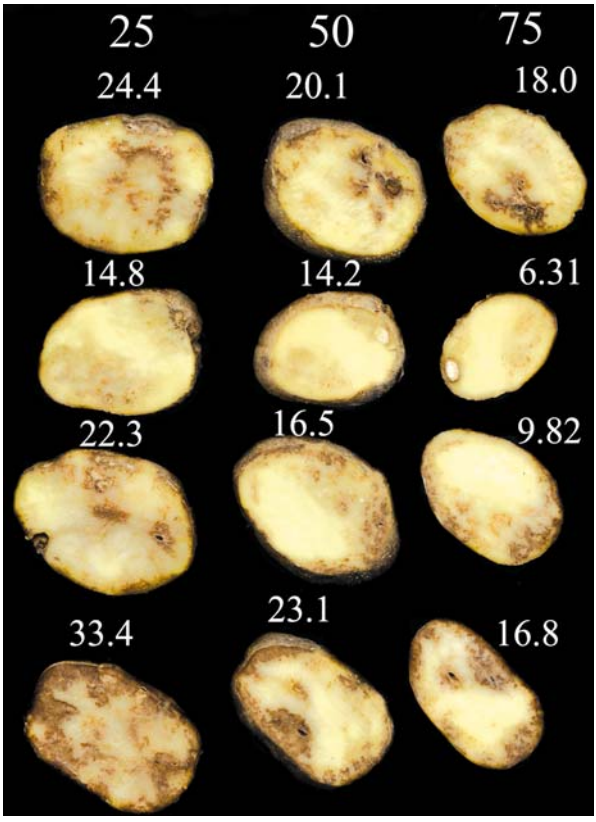

Fig. 1 Digital image of three tuber sections from four potato tubers of the advanced breeding line ND2443 inoculated with *Phytophthora infestans* isolate *Pi*-02-007 (US-8 genotype). Numbers indicate relative average reflective intensity [RARI (%)] for each tuber section cut at 25, 50 and 75% from and parallel to the inoculated surface; RARI values are relative to those of the non-inoculated control tubers of the same advanced breeding line

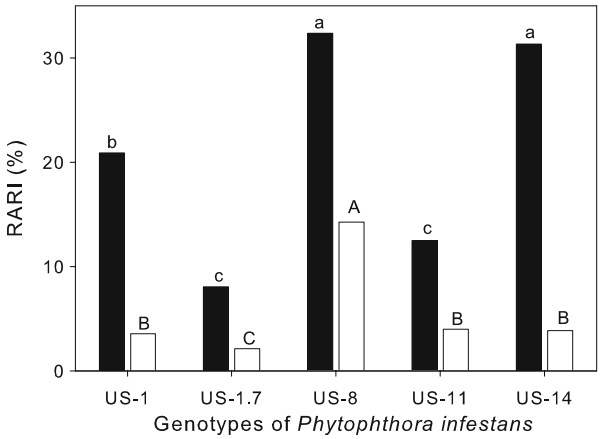

Fig. 2 Aggressiveness of different genotypes of *P. infestans* in tubers across all cultivars and advanced breeding lines tested in 2003 [*black bars* (*lower-case letters* for multiple range comparisons, values with the same letters are not significantly different at P=0.05)] and 2004 [*white bars* (*upper-case letters*)] expressed in terms of RARI (%) of inoculated tubers. The honestly significant difference at the 5% level ($HSD_{0.05}$) was 4.68 (2003) and 1.29 (2004), respectively, for comparisons between genotypes of *P. infestans*. High RARI (%) values indicate greater host tuber tissue darkening and greater aggressiveness of the pathogen

The US-8 genotype of *P. infestans* caused most tuber discoloration in terms of RARI (%) of scanned tuber sections in both 2003 and 2004 trials (Fig. 2). The US-14 genotype was the second most aggressive genotype in tubers and was not significantly different from the US-8 genotype (across all cultivars/ABLs) in the 2003 trial (Fig. 2), but in 2004 was not significantly different from the US-1 or US-11 genotypes. In 2003 and 2004, the US-1.7 genotype caused significantly less tuber tissue discoloration and rotting across all cultivars/ABLs tested (Fig. 2). The US-1 and US-11 genotypes caused moderate tuber rotting in both 2003 and 2004 trials, but US-1 caused more tuber rotting in 2003 than US-11.

Cultivars/ABLs demonstrated significant differences in the amount of necrotic tuber tissue expressed as tuber tissue discoloration after inoculation with different genotypes of *P. infestans*, and the responses of cultivars/ABLs were analysed in relation to the effect of the different genotypes of *P. infestans*. The cultivars/ABLs were ranked relative to susceptibility across all genotypes of *P. infestans* used to inoculate tubers (Table 1). Values of RARI (%) were higher in the 2003 trial compared with the 2004 trial. In 2003, values of RARI (%) ranged from 0.07 to 41.7, while in 2004 the values were between 0 and 28.3 (Table 1).

In 2003, cv. Pike had the highest RARI (%) across all *P. infestans* genotypes, followed by the cultivars/ABLs MSI152-A, MSJ317-1, MSJ319A, Jacqueline Lee, MSJ461-1, Torridon, MSJ319-7, FL1879, MSJ453-4Y, Atlantic and MSJ456-2Y, respectively. Significant differences among cultivars/ABLs with respect to RARI (%) within genotypes of *P. infestans* are detailed in Table 1 for 2003 and 2004 experiments.

In 2004, ABL MN98462 had the greatest tuber rot susceptibility across all *P. infestans* genotypes, followed by the cultivars/ABLs Snowden, MSJ461-1 and Pike,

MN15620, MSI152-A, FL1879, FL1833, Megachip, Torridon, ND2443, Jacqueline Lee, MSJ317-1, ND5822C-7, FL1867 and Atlantic, respectively.

Emergence

Final plant stand measured relative to the non-inoculated control across all cultivars/ABLs tested in 2003 was significantly less in plots planted with seed pieces inoculated with the US-8 and US-14 genotypes of *P. infestans* (Fig. 3), followed by the US-1 and US-11 genotypes, which had significantly decreased plant stand compared with the US-1.7 genotype and the non-inoculated control (Fig. 3). In 2004, final plant stand across all cultivars/ABLs was significantly less in plots planted with seed pieces inoculated with the US-8 genotype in comparison with the US-14 genotype of *P. infestans*, followed by the US-11 genotype, which had significantly decreased plant stand in comparison with US-1 and US-1.7 genotypes and the non-inoculated control (Fig. 3).

Seed pieces of cultivars/ABLs inoculated with different genotypes of *P. infestans* differed in final plant stand (%) measured relative to the non-inoculated control (Table 2). The cultivars/ABLs were ranked relative to final plant stand (%) across all genotypes of *P. infestans* used to inoculate tubers and the responses of cultivars/ABLs were analysed in relation to the effect of the different genotypes of *P. infestans* (Table 2). Plant stand in 2003 was 100% in all non-inoculated control plots for all cultivars/ABLs but was lower for most cultivars/ABLs in 2004. In 2003, cv. Atlantic had the greatest highest final plant stand (%) across all *P. infestans* genotypes and cv. Pike had the lowest. Significant differences among cultivars/ABLs with respect to final plant stand (2003) within genotypes of *P. infestans* are detailed in Table 2. In 2004, cv. Torridon had the highest plant stand across all *P. infestans* genotypes tested and cv. Snowden the least, although the differences were not significant. Significant differences among cultivars/ABLs with respect to plant stand (2004) within genotypes of *P. infestans* are detailed in Table 2.

The RAUEPC measured relative to the non-inoculated control across all cultivars/ABLs tested in 2003 was significantly less in plots planted with seed pieces

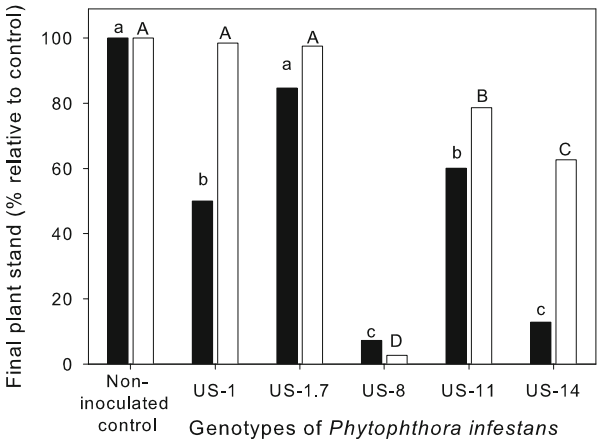

Fig. 3 Final plant stand (%) of potato cultivars and advanced breeding lines across different genotypes of *P. infestans* used in the study in 2003 [*black bars* (*lower-case letters* for multiple range comparisons, values with the same letters are not significantly different at $P=0.05$)] and 2004 [*white bars* (*upper-case letters*)] experiments. $HSD_{0.05}$= 18.25 (2003) and 35.41 (2004), respectively, for comparisons between genotypes of *P. infestans*

inoculated with the US-8 and US-14 genotypes of *P. infestans* (Fig. 4), followed by the US-1 and US-11 genotypes, which had significantly lower RAUEPC than the US-1.7 genotype and the non-inoculated control (Fig. 4). In 2004, the RAUEPC across all cultivars/ABLs was significantly less in plots planted with seed pieces inoculated with the US-8 genotype in comparison with the US-14 genotype of *P. infestans*, followed by the US-11 genotype, which did not differ in RAUEPC from the US-1 genotype and had a significantly lower RAUEPC than the US-1.7 genotype and the non-inoculated control (Fig. 4).

Seed pieces of different cultivars/ABLs inoculated with different genotypes of *P. infestans* differed in terms of RAUEPC. In 2003, cv. Atlantic had the greatest RAUEPC across all *P. infestans* genotypes, followed by the cultivars/ABLs Torridon, MSJ453-4Y, MSJ319-7, FL1879, MSJ456-2Y, MSJ461-1, MSJ319-A, MSJ317-1, Jacqueline Lee, MSI152-A and Pike. Significant differences among cultivars/ABLs with respect to RAUEPC (2003) within genotypes of *P. infestans* are detailed in Table 3. In 2004, ABL MN15620 had the highest RAUEPC across all *P. infestans* genotypes tested, followed by the cultivars/ABLs Torridon, FL1833, MN98642, ND5822C-7, Jacqueline Lee, MSJ461-1, FL1867, ND2443, Atlantic, FL1879, Megachip, MSI152-A, MSJ317-1, Snowden and Pike. Significant differences among cultivars/ABLs with respect to RAUEPC (2004) within genotypes of *P. infestans* are detailed in Table 3.

Foliar symptoms of potato late blight were absent on plants emerging from seed pieces inoculated with different genotypes of *P. infestans* in both 2003 and 2004 experiments.

During both seasons, the RAUEPC (measured relative to the non-inoculated control) was positively correlated with plant stand and the predicted RAUEPC was consistent across both years (Fig. 5). In 2004, there was more variability especially when plant stand was 0% (Fig. 5, bottom), owing to plants emerging then dying.

Emergence and Tuber Infection

RAUEPC values measured relative to the non-inoculated control were generally greater when RARI (%) values were lower in 2003 (Fig. 6a). Atlantic, Torridon and

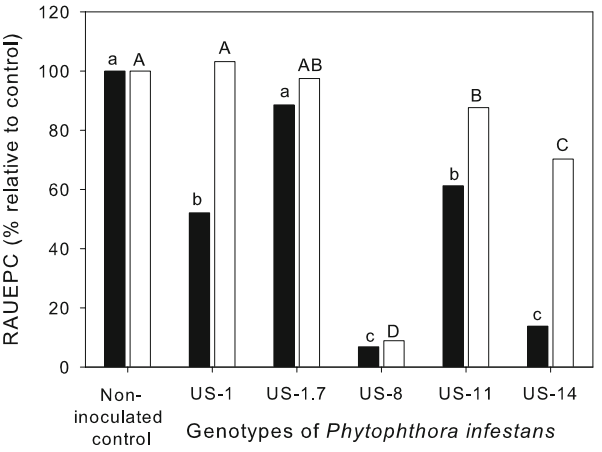

Fig. 4 Mean relative area under the emergence progress curve (*RAUEPC*) of potato cultivars and advanced breeding lines across different genotypes of *P. infestans* used in the study in 2003 [*black bars* (*lower-case letters* for multiple range comparisons, values with the same letters are not significantly different at $P=0.05$)] and 2004 [*white bars* (*upper-case letters*)] experiments. $HSD_{0.05}=12.88$ (2003) and 23.32 (2004), respectively, for comparisons between genotypes of *P. infestans*

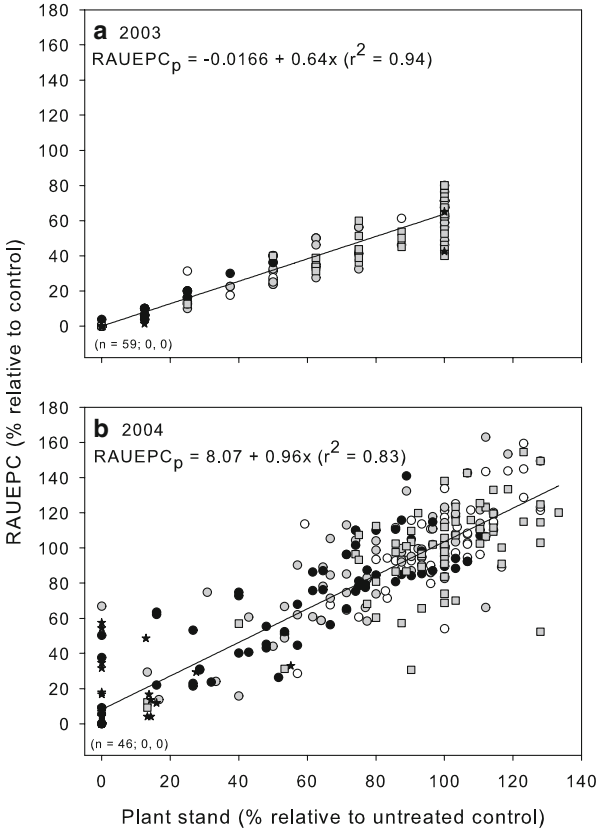

Fig. 5 Mean predicted relative area under the emergence progress curve ($RAUEPC_p$) expressed as a function of final plant stand (%) across potato cultivars and advanced breeding lines inoculated with different genotypes of *P. infestans* in 2003 (n=216) (*top*) and 2004 (n=384) (*bottom*), experiments. Symbols are for individual genotypes of *P. infestans*: *white circles* US-1, *squares* US-1.7, *grey circles* US-11, *stars* US-8, *black circles* US-14. In 2003 and 2004 there were n=59 and n=46 with RAUEPC=0 and final plant stand (%)=0, respectively expressed as n=59; 0,0 and n=46; 0,0

MSJ319-7 were most tolerant of US-1 and Jacqueline Lee, Pike, MSI157-A and MSJ461-1 were least tolerant of US-1 (Fig. 6a). Most of the cultivars/ABLs tested were tolerant of US-1.7, but two clear groups were apparent, with MSJ316-A and MSJ319-7 the most susceptible. All cultivars/ABLs were susceptible to US-8 and US-14. The relation between RAUEPC and RARI (%) in the US-11 genotype was similar to that of US-1, although Torridon was more susceptible to US-11, as were MSJ316-A and MSI152-A; Pike was the most susceptible cultivar (Fig. 6a). In 2004, all cultivars/ABLs tolerated US-1, US-1.7 and US-11, although Snowden despite having a fairly low RARI (%) still had a reduced RAUEPC (Fig. 6b). Pike was intolerant of the US-11 genotype of *P. infestans*. Although RARI (%) was lower relative to 2003, no cultivars/ABLs tolerated US-8, and Megachip, Pike and MN98642 were intolerant of US-14 (Fig. 6b).

Discussion

The significance of seed-borne inoculum of the late blight pathogen (*P. infestans*) in initiating late blight disease in the field has been reported in many studies (Wallin and Polhemus 1956; Boyd 1980; Doster et al. 1989; Dowley and O'Sullivan 1991;

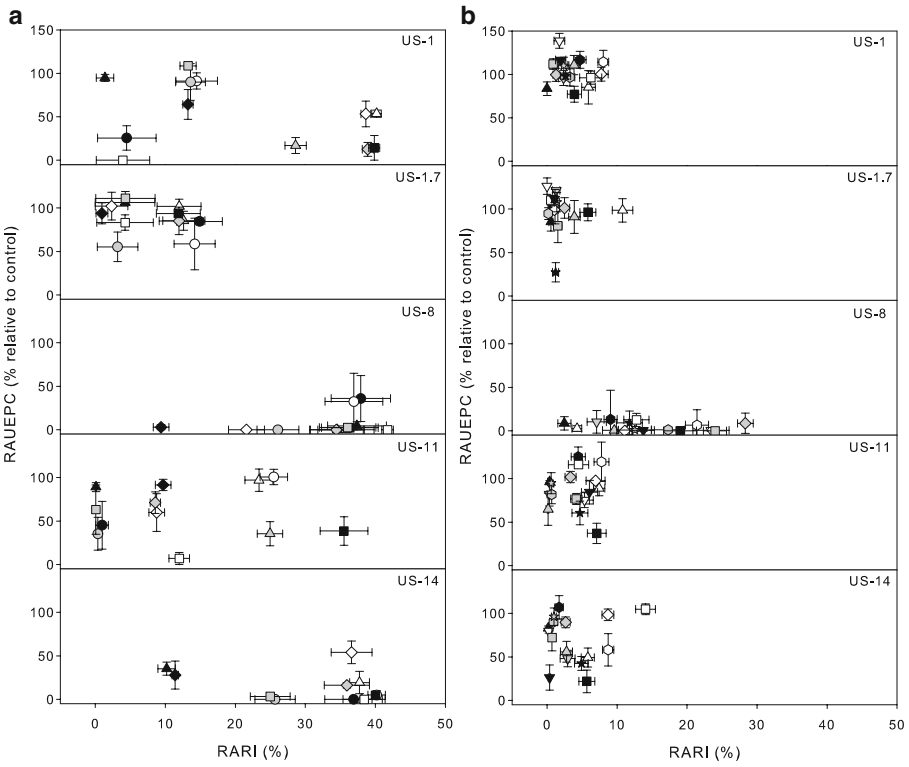

Fig. 6 RAUEPC expressed as a function of susceptibility to tuber late blight [measured as RARI (%)] across potato cultivars and advanced breeding lines inoculated with different genotypes of *P. infestans* used in **a** 2003 and **b** 2004 experiments. *Black upright triangles* Atlantic, *white upright triangles* MSI152-A, *grey upright triangles* MSJ317-1, *black circles* MSJ319-7, *white circles* MSJ316-A, *grey circles* MSJ453-4Y, *black diamonds* MSJ456-2Y, *white diamonds* MSJ461-1, *grey diamonds* Jacqueline Lee, *black squares* Pike, *white squares* Torridon, *grey squares* FL1879, *black inverted triangles* Megachip, *white inverted triangles* FL1833, *grey inverted triangles* FL1867, *black hexagons* MN15620, *white hexagons* MN98642, *grey hexagons* ND2443, *black stars* Snowden, *grey stars* ND5822C-7

Platt et al. 1999). However, the question of the frequency and rate of transmission from infected seed tubers to foliage is still unresolved and the more likely outcome is seed rot and reduced emergence. Van der Zaag (1956) evaluated 75 years of research on late blight epidemics and suggested that successful establishment of late blight in a crop from infected seed tubers occurred at a rate ranging from 0 to 2% of the infected tubers giving rise to foliar infections. In this study, in spite of using five different genotypes of *P. infestans* to inoculate 12 and 16 cultivars/ABLs in 2003 and 2004 experiments, respectively, no visible symptoms of late blight pathogen were observed on foliage from emergence to canopy closure. The inability to detect foliar late blight symptoms from inoculated seed tubers could be attributed to more than one factor, but most important is the small scale of the experiment, taking into consideration the estimated rate of this event to be less than 2% (Fry 1997). To account for this factor, we used an aggressive inoculation technique described as a realistic scenario during seed cutting procedures in the USA and Canada by Lambert

and Currier (1997) and Lambert et al. (1998). This technique achieved a 100% tuber inoculation rate; however, even at this rate no foliar symptoms of potato late blight were observed in either year of this study. Foliar potato late blight symptoms were detected in controlled greenhouse tests after seed tuber inoculations with US-8 (Kirk et al. 1999) and using molecular techniques by Appel et al. (2001). The emergence rate of shoots from tubers infected with US-8 was much lower than that from tubers infected with US-1 (Marshall and Stevenson 1996). Recently in 2007, in a similar experiment we observed one plant with foliar symptoms of potato late blight from a total population of n=4,000 inoculated tuber seed pieces (all cv. FL1879; Wharton, unpublished results).

The significant extent of tuber rotting and deterioration appears to be the primary symptom after inoculation with *P. infestans*. The results of the plant emergence experiment support this hypothesis since there was a strong negative correlation between the aggressiveness of *P. infestans* isolate and plant emergence rate. The results of this study demonstrated that exceptionally aggressive genotypes of *P. infestans* such as US-8 and US-14 resulted in poor emergence across all cultivars/ABLs evaluated. These results are in agreement with the findings of Platt et al. (1999) and Powelson et al. (2002), who reported that planting infected seed tubers rarely resulted in infected plants, especially with the aggressive genotypes of *P. infestans* (i.e. US-8 genotype) owing to extensive tuber rotting before emergence. Thus, it is likely that greater tuber pathogenicity lowers the rate of successful field establishment of late blight. The variability of susceptibility of tubers to different genotypes of *P. infestans* has implications for plant breeding efforts in that the major emphasis in the past was to breed for foliar resistance with limited emphasis on the reaction of the tuber.

Disease progressed through the tuber as seen in Fig. 1 through the serial slices made at 25, 50 and 75%. This technique could be used to better quantify cultivars/ABLs that differ in the degree of darkening of necrotic tissue in the slices relative to the genotype of *P. infestans*. Although inoculation in this experiment is somewhat artificial (i.e. from the centre of a cut tuber and disease moving outward rather than from an exterior entry through a wound and moving inward as seen in natural inoculations), Fig. 1 suggests differential aggressiveness and infected tubers could therefore potentially bear specific sprouts that have yet to be infected by the disease. Latent infection of sprouts may then result in a later appearance of the pathogen, but could still initiate a serious epidemic. Such a mechanism may explain why the more aggressive isolates of *P. infestans* remain predominant in North America.

The field experiment demonstrated that these cultivars/ABLs exhibited different responses to different genotypes of *P. infestans*. The cultivars/ABLs that had greatest tuber resistance included Atlantic, MSJ453-4Y, MSJ319-7 and FL1879, although Torridon, Atlantic, MSJ461-1 and Jacqueline Lee had the highest RAUEPC values. The difference in the RAUEPC values between 2003 and 2004 could be attributed to more than one factor, including differences in the prevailing weather conditions in the field between the two seasons in addition to isolate virulence and cultivar susceptibility. Isolates of *P. infestans* tend to lose some of their aggressiveness as well as pathogenicity over time during storage (Hodgson and Grainger 1964). It is likely that the differences between the 2003 and 2004 experiments in tuber responses of different cultivars/ABLs to different *P. infestans* genotypes is largely due to tuber and isolate factors since data from tuber rot severity (conducted in controlled

environment) had lower values in 2004 compared with 2003. This circumstance of inconsistency in cultivar responses to *P. infestans* among different experiments was also reported by Peters et al. (1999). Tubers of the same cultivars may vary in susceptibility over time, which could be the result of many factors, including physiological changes during storage such as the accumulation of reducing and non-reducing sugars and accumulation of stress-related metabolites (Bhatia and Young 1985). Nonetheless, some cultivars/ABLs that performed well did so in both experiments, such as cvs. Atlantic and Torridon, and some had poor emergence in both years, such as cv. Pike.

Inoculation with the US-8 genotype of *P. infestans*, which is the dominant genotype in North America (Young et al. 2009), resulted in significant reduction in plant emergence due to seed rot for all cultivars/ABLs tested. These findings are in agreement with those of Lambert and Currier (1997) and Lambert et al. (1998), who found that the US-8 genotype isolates were the most aggressive in tubers, causing rapid and significantly more tuber damage than any other genotype of *P. infestans.* The results of the tuber rot severity experiments demonstrated similar trends in cultivar susceptibility and genotype aggressiveness as the plant emergence experiment. Data from the two experiments were strongly negatively correlated, where cultivars/ABLs that demonstrated the highest level of plant emergence had the least tuber rotting and vice versa.

Tuber rot severity in the storage experiment demonstrated that cultivars/ABLs had different tuber susceptibilities to different genotypes of *P. infestans*. Generally cultivars/ABLs were most susceptible to the US-8 genotype of *P. infestans* and data from the tuber rot severity corresponded well to data from the plant emergence experiment; however, some exceptions occurred. For example, tuber rot severity in the ABL MSJ456-2Y inoculated with US-1 and US-14 genotypes was higher than in MSJ456-2Y inoculated with the US-8 genotype in 2003.

The results from this study circumstantially suggest that highly aggressive genotypes of *P. infestans*, such as the US-8 genotype, may produce limited primary inoculum owing to severe tuber rotting and deterioration of tubers before emergence. However, this scenario will depend mostly on the amount of inoculum of *P. infestans* found in or on potato tubers. In this study, tuber seed pieces were exposed to an excessive amount of inoculum and the results suggest that this amount of inoculum was sufficient to cause severe tuber rotting in some cultivars/ABLs. To determine the inoculum threshold required to cause significant tuber rotting and reduction in plant emergence, further studies are needed to establish the relationship between the amount of inoculum in potato seed tubers and the rate of tuber rot and its effect on plant emergence after planting. This would involve designing experiments in which seed tubers are inoculated with a series of concentrations of inoculum of *P. infestans* and evaluating the effect on tuber rot severity in storage and the rate of plant emergence after planting.

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