Am. J. Pot Res (2010) 87:509–520
DOI 10.1007/s12230-010-9156-1

Effect of Different Genotypes of *Phytophthora infestans* (Mont. de Bary) and Temperature on Tuber Disease Development

William W. Kirk · Alejandro Rojas · Pavani G. Tumbalam · Esther Gachango · Phillip S. Wharton · Firas Abu El-Samen · David Douches · Joseph Coombs · Christian Thill · Asunta Thompson

Published online: 13 July 2010

Abstract The interactions of different cultivars/Advance Breeding Lines (ABL) of potato with different genotypes of the potato late blight pathogen (*Phytophthora infestans*) at three storage temperatures on tuber late blight development were evaluated. The contribution of the medullar storage tissues was assessed rather than the periderm and outer cortical cell tissue. Tuber late blight severity measured as tuber darkening [mean Relative Average Reflectance Intensity [RARI (%)] generally increased with temperature. There was little difference in tuber late blight development between 7°C and 10°C treatments and in some combinations significantly more tissue darkening developed at 7 than at 10°C but little or no development occurred at 3°C. Resistance in tubers was observed only in Torridon and Stirling and to some extent Jacqueline Lee, but the cultivar Missaukee had weak tuber resistance. The US-8 genotype isolates were the most aggressive in tubers in most years causing rapid and significantly more tuber damage than any other genotype of *P. infestans* and similar to the US-6, US-10 and US-14 isolates used in 2006.

Resumen Se evaluaron las interacciones de diferentes variedades y líneas avanzadas (ABL) de papa con diferentes genotipos del patógeno del tizón tardío (*Phytophthora infestans*) a tres temperaturas de almacenamiento para el desarrollo del tizón tardío en tubérculo. Se analizó la contribución de los tejidos medulares de almacén en vez del peridermo y de tejido celular cortical más externo. La severidad del tizón tardío del tubérculo, medida como el oscurecimiento del tubérculo [media de la intensidad del promedio relativo de refractancia [RARI (%)], generalmente se incrementó con la temperatura. Hubo poca diferencia en el desarrollo del tizón tardío del tubérculo entre los tratamientos de 7 y 10°C, y en algunas combinaciones se desarrolló mayor oscurecimiento de tejido significativamente a 7 que a 10°C pero no se presentó a 3°C. La resistencia de los tubérculos se observó solo en Torridon y Stirling y hasta cierto punto en Jacqueline Lee, pero la variedad Missaukee tuvo débil resistencia de tubérculo. Los aislamientos del genotipo US-8 fueron los más agresivos en tubérculos en la mayoría de los años causando más daño en tubérculo rápida y significativamente que cualquier otro genotipo de *P. infestans* y similar a los aislamientos US-6, US-10, y US-14 usados en el 2006.

Keywords Breeding · Late blight · Cultivars · Advanced breeding lines

W. W. Kirk (✉) · A. Rojas · P. G. Tumbalam · E. Gachango
Department of Plant Pathology, Michigan State University, East Lansing, MI 48824, USA
e-mail: kirkw@msu.edu

D. Douches · J. Coombs
Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, USA

P. S. Wharton
University of Idaho Aberdeen Research & Extension Center, Aberdeen, ID 83210-1749, USA

F. A. El-Samen
Department of Plant Production Sciences, Jordan University of Science and Technology, P.O. Box 3030, Irbid 22110, Jordan

C. Thill
Department of Horticultural Science, University of Minnesota, St. Paul, MN 55108, USA

A. Thompson
Plant Sciences Department, North Dakota State University, Fargo, ND 58105, USA

Introduction

Potato late blight is the most important and most destructive disease of potato worldwide. The disease caused by the oomycete *Phytophthora infestans* (Mont. de Bary) is the greatest threat to the potato crop, accounting for significant annual losses in North America (Guenthner et al. 1999, 2001) and worldwide (Hijmans 2001). Tuber late blight results in tuber rotting both in the field and later in storage either in tubers intended for seed or consumption (Bonde and Schultz 1943; Johnson and Cummings 2009; Kirk et al. 1999; Lambert and Currier 1997; Murphy and McKay 1924, 1925; Olanya et al. 2009). 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; Kirk et al. 2009; Stevenson et al. 2007). The epidemiology of the foliar phase of the disease is correlated to 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; Fry 2008; Porter et al. 2005; Stevenson et al. 2007). Tubers can become blighted shortly after the disease is established on the foliage. *P. infestans* survives in tubers where it rots tubers intended for commercial use (Niemira et al. 1999) or acts as a primary source of inoculum for infection in the following growing season (Bonde and Schultz 1943).

Three major components contribute to late blight resistance in tubers; 1) a physical barrier consisting of several layers of phellem cells, known as the periderm; 2) the outer cortical cell layers that retard the growth of lesions and can completely block hyphal growth; and 3) medulla storage tissues characterized by reduced hyphal growth and sporulation of *P. infestans* (Flier et al. 1998, 2001; Pathak and Clarke 1987). Recent work has indicated that the new immigrant *P. infestans* clones, especially the US-8 genotype, are more aggressive in tubers and sprouts (Kirk et al. 2001d; Lambert and Currier 1997). Historically, studies of the late blight pathogen on tubers were conducted when *P. infestans* populations were dominated by US-1, a clonal lineage (Goodwin et al. 1994). Today, populations of *P. infestans* have changed and tuber resistance 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. The dynamics of potato blight development in tubers are largely influenced by temperature (Kirk et al. 2001d) and can result in decay in storage at currently used processing storage temperatures (e.g. 10°C for chip-processing) or non-emergence of plants due to seed and sprout rot (Kirk et al. 2009). The objectives of this study were to evaluate the interactions of different cultivars/Advanced Breeding Lines (ABL) of potato between different genotypes of *P. infestans* and storage temperature on tuber late blight development.

Materials and Methods

Germplasm Selection

Potato breeding efforts at Michigan State University and other potato breeding programs in the US have resulted in potato cultivars that are largely resistant to foliar late blight (Douches et al. 2004; Kirk et al. 2001b,c) but not significantly less susceptible than other cultivars in terms of tuber blight resistance (Kirk et al. 2001c). Potato late blight resistance estimates for the cultivars/ABL used in this study were breeders' estimates and are given as foliar and tuber ratings below, respectively. US cultivars are exclusively rated against the US-8 genotype of *P. infestans* and were Jacqueline Lee [Resistant (R), Susceptible (S); Douches et al. (2001)]; Kalkaska [R,S; Douches et al. (2009)]; Missaukee [R,I; Douches et al. (2010)]; MSL171-A (R,R); MSL211-3 (R,I); MSL757-1 (R,I); MSL766-1 (R, I); MSM051-3 (R,I); MSM137-2 (I,I); MSM171-A (R,I); MSM182-1 (I,I); MSM183-AY (R,I); MSN105-1 (R,S); MN98642 (S,S); MN15620 (S,S); ND2470-27 (S,S); Dakota Diamond [S,S; Thompson et al. (2008)]; White Pearl [S,S; Groza et al. (2006)] and Megachip [S,S; Groza et al. (2007)]. Both UK cultivars Stirling and Torridon have a NIAB 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 programs at Michigan State University, University of Wisconsin, Madison, University of Minnesota and North Dakota State University. Potato tubers from cultivars/ABL harvested during the previous growing seasons were stored at 3°C in the dark at 90% relative humidity until used. Tubers were warmed to 15°C in incremental steps of 2°C for 7 d before inoculation. 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 Multi-well kit (Alert Multiwell Kit—*Phytophthora sp.* Neogen Corporation, 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 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. After inoculation

tubers were returned to target temperatures by decreasing temperature by 2°C decrements over 2 d, 3 d and 4 d for storage treatments of 10°C, 7°C and 3°C, respectively.

Culturing of *Phytophthora infestans* and Tuber Inoculations

Cultures of *P. infestans* isolates corresponding to clonal lineages US-1 (Pi95-3), US-1.7 [Pi88 (2002–06)], US-6 [Pi95-2 (2006–07)], US-8 [Pi02-007 (2002–05), Pi06-02 (2006–07)], US-10 [SR83-84 (2005-06), Banam AK (2006–07)], US-11 (Pi96-1), US-14 [Pi98-1 (2002–05), Pi00-001 (2006–07)] were selected based on the aggressiveness criteria (Young et al. 2009). The selected isolates were from the collection of W. Kirk (Michigan State University). These isolates were acquired from field infections from 1995 to 2006 on foliage and tubers of potatoes of commonly grown in Michigan, USA. Pathogenicity was determined on foliage and tubers in tuber and detached leaf tests (Young et al. 2009). Since the genotypes US-1, US-1.7 and US-11 are rare in the US only single isolates representative of the range of genotypes were selected for this study. The experiments were carried out in controlled environment chamber studies. The trials were conducted from 2002 to 2007 (total of five experiments).

The isolates were grown in rye B media for 14 days in the dark at 18°C for sporangia production, and transferred to the light for 2 days to encourage sporulation. Sporangia and mycelium were harvested by flooding with cold sterile water (4°C) and gentle scraping of the surface of the culture using a rubber policeman. The mycelium/sporangia suspension was stirred with a magnetic stirrer for 1 h. The suspension was strained through four layers of cheesecloth and sporangia concentration was measured with a hemacytometer and adjusted to about 1×10^6 total sporangia ml^{-1} (discharged and non-discharged). The sporangial suspensions were stored for 6 h at 4°C to encourage zoospore release from the sporangia.

Whole Tuber Inoculation with *P. infestans*

Tuber late blight development caused by the different *P. infestans* genotypes on the cultivars/ABL were evaluated at different commonly used post-harvest potato storage temperatures (3°C, 7°C and 10°C) using whole tuber sub-peridermal inoculation. All tubers were washed in distilled H_2O to remove soil. The tubers were then surface sterilized by soaking in 2% sodium hypochlorite solution for 4 h. Tubers were dried in a controlled environment with forced air ventilation at 5,950 l min^{-1} at 15°C in dry air (30% relative humidity) for 4 h prior to inoculation.

The washed, surface-sterilized tubers were inoculated by a sub-peridermal injection of a sporangia suspension of 2×10^{-5} ml (delivering zoospores released from about 20 sporangia $inoculation^{-1}$) with a hypodermic syringe and needle at the apical end of the tuber about 1 cm from the dominant sprout to a maximum depth of 1 cm. Ten tubers of each cultivar/ABL were inoculated with each *P. infestans* genotype per temperature. Ten control tubers per cultivar/ABL were inoculated with cold (4°C) sterile distilled H_2O. After inoculation, tubers were placed in the dark in sterilized covered plastic crates and returned to controlled environment chambers [Percival Incubator (Model I-36LLVL, Geneva Scientific, LLC, PO Box 408, Fontana, WI)]. The chambers were set at 3°C, 7°C or 10°C and 95% humidity and the sample tubers were incubated for 40 days until evaluation. The tuber tissue inoculation experiments were conducted in December 2002 to January 2003 and annually through December to January 2003 to 2008.

Evaluation of Tuber Blight

A digital image analysis technique was used to assess tuber tissue infection. The method was previously used and standardized (Kirk et al. 2001a; Niemira et al. 1999). The image files were analyzed using SigmaScan V3.0 (Jandel Scientific, San Rafael, CA). The area selection cut-off threshold was set to ten light intensity units, limiting the determination to the non-dark parts of the image. The average reflective intensity (ARI) of all the pixels within the image gave a measurement of infection severity of the tuber tissue of each sample. The ARI was measured in sections from the apical, middle and basal regions of the tuber. The amount of late blight infected tissue per tuber was expressed as a single value (Mean ARI) calculated as the average ARI of the apical, middle and basal sections evaluated 40 days after inoculation (DAI).

Data Analysis

The presence of *P. infestans* in sample tubers was confirmed by ELISA (described above) and by isolating pure cultures of *P. infestans* from the infected tuber tissue and successful re-inoculation of potato tubers and leaves. The severity of tuber tissue infection was expressed relative to the ARI (described above) of the control tubers for each cultivar/ABL. The relative ARI (RARI) was calculated as:

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

RARI (%) has minimum value of zero (no symptoms) and maximum value of 100 (completely dark tuber surface).

Data for all experiments were analyzed by analysis of variance (least squares method) using the JMP program version 7.0 (SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513, USA). Treatment effects were

determined by three-way factorial ANOVA, where the main effects corresponded to: Cultivar/ABL, *P. infestans* genotype and temperature and multiple interactions among the main effects, including the three factor interaction. Data were not combined across years as different genotypes of *P. infestans* and different cultivars/ABL were used in each year.

Results

Factorial ANOVA analyses resulted in significant differences by year of the three main factors (Cultivar/ABL, *P. infestans* genotype, and temperature) and the multiple interactions among them (Table 1). Incubation of inoculated tubers at 10°C resulted in greatest tuber infection and tuber tissue discoloration within 40 DAI in 2003 regardless of genotype of *Phytophthora infestans* or cultivar/ABL although differences in some genotypes e.g. US-1.7 were not significant (Table 2). In 2004, there were no differences between 7°C and 10°C although no measurable disease developed at 3°C. In 2005, tuber late blight only developed at 10°C (data not shown). In 2006, there were only differences between storage temperature treatments in US-8 and very little disease developed at 3°C or 7°C (Table 2). In 2007, there was a general increase across all genotypes with increase in temperature.

The effect of genotype of *P. infestans* regardless of temperature in the different cultivars/ABL of potatoes showed a broad range of responses for each year (Tables 1, 2, 3, 4, 5, 6, 7). There were significant interactions in tuber late blight development [RARI (%)] among cultivar/ABL, genotypes and storage temperatures (Table 1).

The US-8 genotype was the most aggressive, regardless of temperature in all years although in 2007, US-6, US-10 and US-14 caused a significant amount of tuber late blight regardless of temperature or cultivar/ABL (Table 2).

Tuber Late Blight Development 2003

In 2003, 10 cultivars/ABL were tested to measure the tuber response to inoculation with different genotypes of *P. infestans* (Table 3). The RARI (%) varied in the different cultivars/ABL among genotypes and the responses were reported relative to each genotype of *P. infestans*. Among the tuber inoculations, the US-8 genotype was most aggressive, followed by the US-11 and US-14 genotypes. The ABL ND 2470-27 was the most susceptible to *P. infestans* genotypes with the highest RARI (%) value, and Kalkaska was the least susceptible cultivar/ABL in 2003 although still relatively susceptible to US-8 (Tables 2 and 3). Jacqueline Lee was particularly susceptible to US-1 and

Table 1 Three-way factorial ANOVA of the effect of cultivar/ABL, genotype of *Phytophthora infestans* and storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] by year. Variance ratio (F), degrees of freedom (df), and P-Value

Variables and interactions	2002–2003			2003–2004			2004–2005			2005–2006			2006–2007		
	F	df	P-Value	F	df	P-Value	F	df	P-Value	F	df	P-Value	F	df	P-Value
Variety	60.88	9	<.0001	75.68	8	<.0001	27.09	8	<.0001	57.52	8	<.0001	678.13	6	0.0000
Genotype	764.70	4	0.0000	1518.99	4	0.0000	509.84	4	<.0001	1036.63	4	0.0000	303.22	50	<.0001
Temperature	680.06	2	<.0001	1360.40	2	0.0000	ND[a]	0	ND	164.07	2	<.0001	192.23	1	<.0001
Variety X Genotype	27.12	36	<.0001	25.28	32	<.0001	16.01	32	<.0001	16.10	16	<.0001	24.18	13	<.0001
Variety X Temperature	16.44	18	<.0001	24.94	16	<.0001	ND	0	ND	39.68	32	<.0001	42.57	30	<.0001
Isolate X Temperature	76.01	8	<.0001	384.10	8	0.0000	ND	0	ND	123.15	8	<.0001	37.11	5	<.0001
Variety X Genotype X Temperature	11.08	72	<.0001	10.93	64	<.0001	ND	0	ND	6.58	64	<.0001	5.61	65	<.0001

[a] *ND* Not determined because tuber late blight developed only at 10°C

Table 2 Effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* by year

Year	Variety	Mean RARI (%)[a]		Genotype of *P. infestans*	Mean RARI (%)[a]		Temperature (°C)	Mean RARI (%)[a]	
2002–2003	ND2470-27	10.12	a[b]	US-8	14.59	a[b]	10	10.23	a[b]
	MSJ 461	9.38	ab	US-1	9.80	b	7	9.12	b
	Megachip	9.15	abc	US-14	6.76	c	3	4.00	c
	FL1879	8.50	bcd	US-1.7	4.64	d			
	Jacqueline Lee	8.30	cd	US-11	3.13	e			
	MN15620	7.67	de						
	White Pearl	7.57	de						
	ND 5822C-7	6.81	e						
	MN 98642	6.65	e						
	MSJ 371-1	3.69	f						
	LSD 0.05	3.164			2.728			2.344	
2003–2004	White Pearl	7.72	a	US-8	15.93	a	10	7.79	a
	MN15620	7.68	a	US-11	3.73	b	7	7.71	a
	FL1879	6.31	b	US-14	3.32	b	3	0.00	b
	ND2470-27	5.77	bc	US-1.7	1.49	c			
	MSJ 461	4.92	cd	US-1	1.38	c			
	Jacqueline Lee	4.38	de						
	MN5822C-7	3.76	def						
	MSJ317-1	3.20	ef						
	Megachip	2.78	f						
	LSD 0.05	3.103			2.729			2.345	
2004–2005	White Pearl	11.55	a	US-8	21.97	a	10	7.06	
	MN 15620	9.34	ab	US-11	5.51	b			
	ND2470-27	8.17	bc	US-14	4.39	b			
	FL1879	8.15	bc	US-1.7	2.13	c			
	MSJ 461	7.35	bcd	US-1	1.31	c			
	ND 5822C-7	6.00	cde						
	MSJ 371-1	5.56	de						
	Megachip	4.64	ef						
	Jacqueline Lee	2.79	f						
	LSD 0.05	3.107			2.732				
2005–2006	MSJ461-1	8.05	a	US-8	15.97	a	10	7.23	a
	MSM137-2	6.87	b	US-11	3.00	b	7	4.53	b
	MSM182	6.37	b	US-10	2.50	bc	3	3.63	c
	MSM171-A	5.94	b	US-1	2.11	c			
	MSL766-1	5.82	b	US-14	2.07	c			
	MSL757-1	4.28	c						
	Jacqueline Lee	3.21	cd						
	Torridon	3.03	d						
	Stirling	2.60	d						
	LSD 0.05	3.103			2.729			2.345	
2006–2007	MSN105-1	16.95	a	US-8	16.14	a	10	13.06	a
	MSM051-3	16.16	a	US-10	13.28	b	7	10.19	b
	MSJ461-1	15.90	a	US-14	12.71	b	3	7.76	c
	MSL 211-3	14.33	b	US-6	10.81	c			
	MSL 183-AY	6.82	c	US-11	7.04	d			
	Torridon	4.48	d	US-1	2.04	e			
	Jacqueline Lee	4.17	d						
	MSM171-A	3.89	d						
	LSD 0.05	3.032			2.850			2.344	

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of n=10 tubers per treatment combination

[b] Values followed by the same letter are not significantly different at p=0.05 for comparisons of mean RARI values within a) different *P. infestans* genotypes; b) cultivar/ABL combinations or c) temperature treatments (Based on Fishers protected LSD)

Table 3 The effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* (2002–2003)

Cultivar/ABL	Storage Temperature (°C)	Tuber tissue darkening caused by different genotypes of *P. infestans* [Mean RARI (%)[a]]									
		US-1		US-1.7		US-8		US-11		US-14	
Jacqueline Lee	3	5.71	h–m[b]	1.36	i–k	11.86	f–k	2.78	b–e	2.30	i–k
	7	18.47	ab	3.74	f–k	30.87	a	2.78	b–e	3.67	f–k
	10	10.67	e–h	0.90	jk	23.41	bc	2.77	b–e	3.25	g–k
Kalkaska	3	1.42	m	1.37	i–k	4.74	m	0.70	e	1.53	jk
	7	1.90	m	2.81	g–k	10.05	h–m	1.84	c–e	3.12	h–k
	10	1.78	m	2.01	h–k	14.74	d–h	2.17	c–e	5.17	e–k
Megachip	3	6.35	g–m	5.67	e–g	7.69	j–m	5.21	a–d	4.51	f–k
	7	8.83	f–l	12.65	a	15.28	d–h	3.42	b–e	14.80	b
	10	13.85	b–f	10.54	a–c	14.14	e–i	5.29	a–d	9.14	c–e
Missaukee	3	4.44	k–m	3.11	g–k	5.41	lm	2.70	b–e	2.49	i–k
	7	16.72	a–d	9.37	a–d	19.29	c–e	1.86	c–e	5.85	e–j
	10	18.89	ab	5.86	d–g	32.69	a	3.94	a–e	8.05	c–f
MN15620	3	3.25	l–m	0.65	k	8.42	i–m	2.30	b–e	0.86	k
	7	10.17	e–j	11.07	ab	15.73	d–h	3.57	b–e	6.38	d–i
	10	14.65	b–e	4.64	f–i	19.29	c–e	2.69	b–e	11.37	bc
MN98642	3	4.54	j–m	1.30	i–k	6.43	k–m	2.98	b–e	2.36	i–k
	7	9.46	e–k	5.17	e–h	15.18	d–h	2.26	b–e	7.75	c–g
	10	9.62	e–k	5.33	e–h	10.91	g–l	5.66	a–c	10.77	b–d
ND 2470-27	3	4.11	k–m	2.01	h–k	10.47	h–m	7.72	a	3.05	i–k
	7	11.64	d–g	3.75	f–k	19.83	c–e	1.94	c–e	10.57	b–d
	10	18.35	ab	1.92	h–k	28.58	ab	3.22	b–e	24.58	a
Dakota Diamond	3	5.14	h–m	4.42	f–j	10.20	h–m	1.37	de	1.42	jk
	7	12.21	c–f	7.16	c–f	8.69	i–m	2.31	b–e	3.25	g–k
	10	13.77	b–f	4.67	f–i	17.52	d–f	2.24	b–e	7.71	c–h
White Pearl	3	4.73	i–m	2.12	h–k	6.81	j–m	1.66	de	2.10	i–k
	7	10.23	e–i	10.48	a–c	12.39	f–j	3.90	a–e	9.53	c–e
	10	11.64	d–g	8.64	b–e	16.32	d–g	2.45	b–e	10.60	b–d

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of $n=10$ tubers per treatment combination

[b] Values followed by the same letter are not significantly different at $p=0.05$ for comparisons of mean RARI values within different *P. infestans* genotypes of cultivar/ABL combinations and temperature treatments (Based on Fishers protected LSD)

US-8 in 2003 but relatively resistant to other genotypes of *P. infestans*.

Tuber Late Blight Development 2004

The evaluation of *P. infestans* isolates in 2004 at different storage temperatures among different cultivars/ABL differed to that in measured in 2003. No disease was observed in inoculated tubers incubated at 3°C (Tables 2 and 4). There were no significant differences in tuber late blight development between 7°C and 10°C. Overall, US-8 was the most aggressive genotype and was significantly different from the other genotypes. White Pearl was the most susceptible cultivar overall and Megachip was the most resistant. Following US-8, genotypes US-14 and US-11 caused moderate tuber late blight and US-1.7 caused moderate disease development at 10°C in MN15620.

Tuber Late Blight Development 2005

In 2005, no tuber late blight developed at 3°C or 7°C and data were collected only at 10°C. The US-8 genotype was the most aggressive across the cultivars/ABL and genotypes US-11 and US-14 caused moderate tuber late blight (Tables 2 and 5). White Pearl was the most susceptible cultivar and Jacqueline Lee and Megachip

Table 4 The effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* (2003–2004)

Cultivar/ABL	Temperature (°C)	Tuber tissue darkening caused by different genotypes of *P. infestans* [Mean RARI (%)[a]]									
		US-1		US-1.7		US-8		US-11		US-14	
Jacqueline Lee	3	0.00	g[b]	0.00	f	0.00	i	0.00	f	0.00	f
	7	4.39	b	0.92	ef	21.28	ef	5.47	c–e	2.28	ef
	10	1.11	d–g	1.47	c–f	26.49	b–e	1.27	ef	1.06	f
Kalkaska	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	2.57	b–e	1.25	d–f	18.48	fg	1.50	ef	0.37	f
	10	0.89	e–g	1.35	d–f	12.14	h	9.14	b–d	0.24	f
Megachip	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	1.01	e–g	1.22	d–f	14.27	gh	1.56	ef	1.17	ef
	10	0.97	e–g	1.37	d–f	14.51	gh	2.59	ef	2.98	d–f
Missaukee	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	1.19	c–g	1.18	d–f	31.16	ab	1.89	ef	1.59	ef
	10	0.72	fg	0.76	ef	31.26	ab	1.35	ef	2.67	ef
MN15620	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	1.77	c–g	0.83	ef	27.38	b–d	16.33	a	1.50	ef
	10	7.03	a	8.42	a	34.34	a	10.22	bc	7.47	cd
ND2470-27	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	1.76	c–g	0.84	ef	24.28	c–f	13.11	ab	5.64	c–e
	10	1.39	c–g	1.06	ef	23.87	d–f	5.19	de	9.33	c
Dakota Diamond	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	2.02	c–f	1.84	c–f	19.73	fg	1.26	ef	1.58	ef
	10	1.77	c–g	3.13	b–e	19.78	fg	2.13	ef	3.18	d–f
White Pearl	3	0.00	g	0.00	f	0.00	i	0.00	f	0.00	f
	7	2.22	c–f	2.85	b–e	24.13	c–f	8.67	b–d	20.13	a
	10	2.92	b–d	3.53	b–d	27.50	b–d	8.41	b–d	15.36	b

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of n=10 tubers per treatment combination

[b] Values followed by the same letter are not significantly different at p=0.05 for comparisons of mean RARI values within different *P. infestans* genotypes of cultivar/ABL combinations and temperature treatments (Based on Fishers protected LSD)

were the most resistant. Missaukee was particularly susceptible to US-8 and not significantly different from White Pearl or MN15620.

Tuber Late Blight Development 2006

Very little late blight developed in inoculated tubers in 2006 at 3°C, 7°C or 10°C in cultivars/ABL inoculated with any genotype of *P. infestans* other than US-8. The US-8 genotype caused tuber late blight of which the severity increased with temperature from 3°C to 10°C (Table 2). The US-8 genotype was consistently aggressive on different cultivars regardless of temperature (Tables 2 and 6). The most susceptible cultivar in 2006 was Missaukee and the most resistant were Jacqueline Lee, Torridon and Stirling. Missaukee was very susceptible to US-8 but also moderately susceptible to US-11 in 2006.

Tuber Late Blight Development 2007

In 2007, new isolates of the US-10 and US-14 genotypes were used and largely tested on cultivars/ABL from the MSU breeding program. The amount of tuber late blight increased with temperature regardless of cultivar/ABL and the US-8, US-10 and US-11 genotypes were the most aggressive (Tables 2 and 7). The cultivars/ABL MSM171-A, Jacqueline Lee and Torridon were the most resistant and MSL211-3, Missaukee, MSM051-3 and MSN105-1 were the most susceptible.

Table 5 The effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* (2004–2005)

Cultivar/ABL	Temperature (°C)	Tuber tissue darkening caused by different genotypes of *P. infestans* [Mean RARI (%)[a]]									
		US-1		US-1.7		US-8		US-11		US-14	
Jacqueline Lee	10[c]	1.11	k[b]	1.47	k	9.02	f–i	1.27	k	1.06	k
Kalkaska	10	1.52	k	1.87	k	13.51	d–f	10.47	e–g	0.43	k
Megachip	10	0.97	k	1.37	k	14.51	d–f	2.59	jk	3.76	h–k
Missaukee	10	0.72	k	0.76	k	31.26	a	1.35	k	2.67	jk
MN15620	10	0.92	k	1.46	k	28.35	ab	15.50	de	0.49	k
Dakota Diamond	10	1.77	k	3.13	h–k	19.78	cd	2.13	jk	3.18	h–k
ND2470-27	10	1.39	k	1.06	k	23.87	bc	5.19	g–k	9.33	e–h
White Pearl	10	2.92	i–k	3.53	h–k	27.50	ab	8.41	f–j	15.36	de

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of $n=10$ tubers per treatment combination

[b] Values followed by the same letter are not significantly different at $p=0.05$ for comparisons of mean RARI values among all *P. infestans* genotypes of cultivar/ABL combinations (Based on Fishers protected LSD)

[c] No tuber tissue infection occurred at 3°C or 7°C in 2004–05 tests

Discussion

The significance of tuber late blight in initiating storage problems has been reported in many studies (Kirk et al. 1999, 2001d) and recently reviewed (Olanya et al. 2009). Infection of potato tubers by *P. infestans* may be initiated by zoospores, sporangia or oospores washed in precipitation or irrigation water from plant foliage and deposited in soil (Fry 2008). Although three major components contribute to late blight resistance in tubers; the phellem cells (periderm), the outer cortical cell layers and the medulla storage tissues characterized by reduced hyphal growth and sporulation of *P. infestans* (Pathak and Clarke 1987) in this study, only the contribution of the medullar storage tissues was assessed.

Temperature has a profound influence on the physiology of potato tubers (Kaur et al. 2009; Knowles et al. 2009; Kumar 2009) and also on the pathology of tubers as pertaining to late blight (Kirk et al. 2001d; Lambert and Currier 1997). The inclusion of the three temperature conditions was intended to simulate late blight development in tubers stored for seed, table-stock and processing, 3°C, 7°C and 10°C, respectively. In this study, tuber late blight severity measured as tuber darkening [RARI (%)] generally increased with temperature as previously reported (Kirk et al 2001d). However, in some years no late blight developed at 3°C or 7°C even in susceptible cultivars/ABL. Temperature in the controlled environments was measured through the season with data loggers and while the temperature in the 7°C environment was consistently between 6°C and 7°C in 2004–05 late blight developed only at 10°C, although in most other years disease developed at the 7°C storage treatment. The reason for the failure of late blight development in tubers is therefore unclear. However, acclimation of tubers may have varied depending on the size of the tuber and impacted initial and subsequent disease development after inoculation. Generally, there was little difference in tuber late blight development between 7°C and 10°C treatments and in some combinations significantly more tissue darkening developed at 7°C than at 10°C e.g. Jacqueline Lee by US-1 and US-11 (Table 4). In future experiments, it may be useful to incubate tubers from cooler temperatures at e.g. 10°C as seed used for planting would be warmed prior to planting and, as it is known that *P. infestans* can survive temperature exposure down to −3°C for 5 days (Kirk 2003), it is very likely that mycelium would spread through the tubers and infect sprouts. In addition, seed-borne inoculum of the late blight pathogen has been linked to the initiation of late blight disease in the field (Boyd 1974, 1980; Doster et al. 1989; Dowley and O'Sullivan 1991; Johnson and Cummings 2009; Johnson 2010; Keil et al. 2010; Kirk et al. 2009; Platt et al. 1999).

Unlike foliage resistance, the genetics of tuber blight resistance have not been extensively studied (Olanya et al. 2009). Generally, cultivars with foliage blight resistance show some tuber blight resistance (Collins et al. 1999), but this depends on plant genotype (Świeżyński and Zimnoch-Guzowska 2001) and in some instances the relationship does not hold (Kirk et al. 2001c; Platt and Tai 1998). In this study, the inoculation technique aimed to examine the resistance of medulla storage tissues which is characterized by mainly reduced hyphal growth of *P. infestans* and therefore tuber symptoms e.g. tissue necrosis (Pathak and

Table 6 The effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* (2005–2006)

Cultivar/ABL	Temperature (°C)	Tuber tissue darkening caused by different genotypes of *P. infestans* [Mean RARI (%)[a]]									
		US-1		US-8		US-10		US-11		US-14	
Jacqueline Lee	3	3.45	a–e[b]	5.20	h–k	3.37	b–d	1.89	cd	2.66	c–f
	7	2.22	a–f	7.19	h–k	2.47	b–d	3.18	b–d	2.14	c–f
	10	0.89	ef	11.30	f–i	1.02	cd	0.36	cd	0.75	ef
Missaukee	3	0.85	ef	19.32	d–f	1.97	b–d	2.74	cd	1.71	c–f
	7	0.08	f	26.91	a–d	1.99	b–d	3.77	bc	3.37	a–e
	10	1.04	d–f	35.27	ab	1.29	cd	18.14	a	2.22	c–f
MSL757-1	3	4.10	a–d	0.88	k	3.37	b–d	2.55	cd	1.28	d–f
	7	1.02	d–f	7.24	h–k	0.82	d	1.38	cd	0.41	f
	10	2.08	b–f	23.56	cd	7.48	a	2.64	cd	5.45	ab
MSL766-1	3	1.71	c–f	9.63	g–k	1.19	cd	1.01	cd	1.34	d–f
	7	2.88	a–f	26.21	b–d	2.76	b–d	3.70	bc	1.91	c–f
	10	0.30	ef	27.03	a–d	5.73	ab	1.35	cd	0.56	ef
MSM137-2	3	0.85	ef	22.03	de	1.05	cd	2.49	cd	0.64	ef
	7	0.44	ef	23.81	cd	1.59	cd	2.67	cd	1.02	ef
	10	4.33	a–c	31.46	a–c	3.42	b–d	2.66	cd	4.58	a–c
MSM171-A	3	5.39	a	9.00	h–k	1.81	b–d	2.26	cd	3.14	a–f
	7	3.12	a–f	21.67	de	5.04	a–c	2.29	cd	2.29	c–f
	10	1.94	b–f	26.26	b–d	2.87	b–d	1.08	cd	1.00	ef
MSM182-1	3	3.35	a–e	5.59	h–k	2.48	b–d	6.38	b	2.07	c–f
	7	1.86	b–f	10.76	f–j	1.75	b–d	2.76	cd	1.74	c–f
	10	4.99	ab	35.95	a	3.88	a–d	6.26	b	5.72	a
Stirling	3	3.10	a–f	1.63	jk	3.08	b–d	3.73	bc	1.90	c–f
	7	0.47	ef	4.36	i–k	0.61	d	0.71	cd	0.41	f
	10	1.67	c–f	14.27	e–h	0.91	d	1.47	cd	0.71	ef
Torridon	3	3.04	a–f	2.62	i–k	2.82	b–d	1.14	cd	1.54	d–f
	7	1.16	c–f	3.44	i–k	2.06	b–d	2.23	cd	4.11	a–d
	10	0.66	ef	18.47	d–g	0.72	d	0.22	d	1.22	d–f

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of $n=10$ tubers per treatment combination

[b] Values followed by the same letter are not significantly different at $p=0.05$ for comparisons of mean RARI values within different *P. infestans* genotypes of cultivar/ABL combinations and temperature treatments (Based on Fishers protected LSD)

Clarke 1987; Niemira et al. 1999; Flier et al. 2001). Such resistance may be linked to major gene resistance as recently reviewed by (Olanya et al. 2009). Park et al. (2005) analyzed tuber resistance in three mapping populations carrying *R* genes or a major QTL for foliar resistance to late blight. In one mapping population, tuber blight resistance was inherited independently of foliar blight and the other two populations tuber and foliage resistance were linked. In these two populations, the *R1* (or *R1-like*) gene acted on both foliage and tuber resistance. Resistance in both foliage and tubers is a very desirable trait in potatoes, but in this study only Torridon and Stirling appeared to have this quality and to some extent Jacqueline Lee (Douches et al. 2001). Jacqueline Lee and Missaukee (Douches et al. 2009) have strong foliar resistance to the US-8 genotype of *P. infestans*, but in this study Jacqueline Lee had only moderate, or in the case of Missaukee, weak resistance. This suggests that the genes responsible for foliage resistance are not present or at least active in the tubers.

Inoculation with the US-8 genotype of *P. infestans,* the dominant genotype in North America (Young et al. 2009), resulted in significant tuber late blight development for most cultivars and ABL tested. These findings are in agreement with Lambert and Currier (1997) and Lambert et al. (1998) who found that the US-8 genotype isolates were the most

Table 7 The effect of storage temperature on tuber tissue late blight as mean Relative Average Reflection Intensity [RARI (%)] in different cultivars and advanced breeding lines (ABL) of potatoes after inoculation with different genotypes of *Phytophthora infestans* (2006–2007)

Cultivar/ABL	Temperature (°C)	Tuber tissue darkening caused by different genotypes of *P. infestans* [Mean RARI (%)[a]]											
		US-1		US-6		US-8		US-10		US-11		US-14	
Jacqueline Lee	3	1.48	c–f[b]	4.10	fg	4.44	ij	3.17	j	1.90	fg	3.35	kl
	7	1.27	c–f	4.68	fg	5.56	i	5.09	ij	2.67	fg	2.97	kl
	10	2.32	b–f	4.84	fg	15.00	e–g	3.10	j	1.38	g	7.69	h–k
Missaukee	3	1.36	c–f[b]	13.09	de	17.44	d–f	18.40	c–e	3.41	f–g	12.14	e–h
	7	1.87	b–f	13.85	cd	20.74	cd	20.60	b–e	10.40	de	17.84	c–e
	10	5.60	a	27.15	a	33.11	a	32.47	a	12.55	b–d	24.15	ab
MSL183-AY	3	2.36	b–f	4.46	fg	11.42	gh	3.30	j	3.13	fg	6.63	h–l
	7	3.13	b–d	5.84	fg	14.73	fg	9.51	g–i	4.19	fg	7.60	h–k
	10	1.04	d–f	4.58	fg	24.42	b	7.91	h–j	2.51	fg	6.00	i–l
MSL211-3	3[c]	–		–		–		–		–		–	
	7	2.46	b–f	21.16	b	14.24	fg	19.91	b–e	5.00	fg	17.13	cf
	10	2.25	b–f	18.43	bc	32.09	a	22.04	bc	9.67	de	23.03	a–c
MSM051-3	3	0.94	d–f	8.63	ef	18.23	de	14.94	e–g	11.25	cd	14.44	d–g
	7	2.15	b–f	13.10	de	23.41	bc	20.85	b–d	15.86	ab	26.69	a
	10	2.93	b–e	18.14	bc	31.64	a	22.28	bc	17.37	a	28.00	a
MSM171-A	3	1.28	c–f	3.95	fg	7.79	hi	3.66	j	2.69	fg	2.33	kl
	7	0.94	d–f	3.00	g	7.15	i	3.07	j	3.60	fg	4.59	j–l
	10	0.54	f	1.82	g	6.29	i	2.35	j	3.14	fg	11.80	f–i
MSN105-1	3	3.39	a–c	21.90	b	18.47	de	15.31	d–f	9.84	de	15.48	d–g
	7	0.75	ef	22.71	ab	20.93	b–d	25.29	b	11.37	b–d	18.33	b–d
	10	3.92	ab	18.45	bc	30.67	a	25.59	b	15.57	a–c	27.10	a
Torridon	3	0.41	f	3.81	fg	1.45	j	2.94	j	2.12	fg	1.23	l
	7	1.74	b–f	5.39	fg	5.85	i	11.70	f–h	6.18	ef	1.99	kl
	10	1.39	c–f	4.10	fg	4.76	ij	10.45	f–i	4.76	fg	10.46	g–j

[a] Normalized tuber tissue darkening score expressed as 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 latitudinal at 25%, 50% and 75% from the apex of n=10 tubers per treatment combination

[b] Values followed by the same letter are not significantly different at p=0.05 for comparisons of mean RARI values within different *P. infestans* genotypes of cultivar/ABL combinations and temperature treatments (Based on Fishers protected LSD)

[c] Insufficient tubers of MSL 211-3 to inoculate and store at 3°C

aggressive in tubers causing rapid and significantly more tuber damage than any other genotype of *P. infestans.* In this study, the isolates of the US-10 and US-14 genotypes of *P. infestans* used from 2005 to 2007 were as aggressive as the US-8 isolates used throughout. Results of recent tuber rot severity experiments demonstrated similar trends in cultivar susceptibility and genotype aggressiveness on plant emergence (Kirk et al. 2009). Data from the two experiments conducted were strongly negatively correlated, where cultivars/ABL that demonstrated the highest level of plant emergence had the least tuber rotting and vice-versa. Results from this study and that of (Kirk et al. 2009) circumstantially suggest that highly aggressive genotypes of *P. infestans*, such as the US-8 genotype, may produce limited primary inoculum due 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 both studies, tuber seed pieces and stored tubers were exposed to an excessive amount of inoculum and results suggest that this amount of inoculum was sufficient to cause severe tuber rotting in some cultivars/ABL. The significant extent of tuber rotting and deterioration appears to be the primary symptom after inoculation with *P. infestans.* 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. It is clear that at least as much emphasis should be apportioned to the tuber resistance phenotype.

Acknowledgments This research was funded, in part, by the Michigan Agricultural Experiment Station GREEEN (Generating Research and Extension to meet Economic and Environmental Needs) Project GR 05/046, Michigan Potato Industry Commission, and supported in principal by the NCERA 211 (Quad State Potato Group) and CSREES Hatch Project Number MICL01966 and the Michigan Potato Industry Commission. Special thanks to Rob Schafer, Jarred Driscoll and Jay Estelle for technical expertise.

References

Andrivon, D. 1995. Biology, ecology, and epidemiology of the potato late blight pathogen *Phytophthora infestans* in soil. *Phytopathology* 85: 1053–1056.

Bain, R.A., R.W. Fairclough, S.J. Holmes, and G.L. Ligertwood. 1997. The role of *Phytophthora infestans* inoculum from stem lesions in the infection of tubers. *In* Proceedings of the Workshop on the European Network for Development of an Integrated Control Strategy of Potato Late Blight. Ed. Bouma, E. and H. Schepers, 98–105: PAV-Special Report No. 1.

Bonde, R., and E.S. Schultz. 1943. Potato cull piles as a source of late blight infection. *American Potato Journal* 20: 112–118.

Boyd, A.E.W. 1974. Sources of potato late blight (*Phytophthora infestans*) in the east of Scotland. *Plant Pathology* 23: 30–36.

Boyd, A.E.W. 1980. Development of potato-blight (*Phytophthora infestans*) after planting infected seed tubers. *The Annals of Applied Biology* 95: 301–306.

Collins, A., D. Milbourne, L. Ramsay, R. Meyer, C. Chatot-Balandras, P. Oberhagemann, W. de Jong, C. Gebhardt, E. Bonnel, and R. Waugh. 1999. QTL for field resistance to late blight in potato are strongly correlated with maturity and vigour. *Molecular Breeding* 5: 387–398.

Doster, M.A., J.A. Sweigard, and W.E. Fry. 1989. The influence of host resistance and climate on the initial appearance of foliar late blight of potato from infected seed tubers. *American Potato Journal* 66: 226–233.

Douches, D.S., K. Jastrzebski, J. Coombs, W.W. Kirk, K.J. Felcher, R. Hammerschmidt, and R.W. Chase. 2001. Jacqueline Lee: A late blight resistant table stock variety. *American Journal of Potato Research* 78: 413–420.

Douches, D., J. Coombs, K. Felcher, and W. Kirk. 2004. Foliar reaction to *Phytophthora infestans* in inoculated potato field trials in Michigan. *American Journal of Potato Research* 81: 443–448.

Douches, D.S., J. Coombs, R. Hammerschmidt, W.W. Kirk, and C. Long. 2009. Kalkaska: a round white chip-processing potato variety with common scab resistance. *American Journal of Potato Research* 86: 347–355.

Douches, D.S., J. Coombs, K. Felcher, W.W. Kirk, C. Long, and G. Bird. 2010. Missaukee: a round white potato variety combining chip-processing with resistance to late blight, Verticillium Wilt and Golden Cyst Nematode. *American Journal of Potato Research* 87: 10–18.

Dowley, L.J., and E.O. O'Sullivan. 1991. Sporulation of *Phytophthora infestans* (Mont.) de Bary on the surface of diseased potatoes and tuber-to-tuber spread of infection during handling. *Potato Research* 34: 295–296.

Flier, W.G., L.J. Turkensteen, and A. Mulder. 1998. Variation in tuber pathogenicity of *Phytophthora infestans* in the Netherlands. *Potato Research* 41: 345–354.

Flier, W.G., L.J. Turkensteen, G.B.M. van den Bosch, P.F.G. Vereijken, and A. Mulder. 2001. Differential interaction of *Phytophthora infestans* of potato cultivars with different levels of blight resistance. *Plant Pathology* 50: 292–301.

Fry, W.E. 2008. *Phytophthora infestans*: the plant (and *R* gene) destroyer. *Molecular Plant Pathology* 9: 385–402.

Goodwin, S.B., B.A. Cohen, and W.E. Fry. 1994. Panglobal distribution of a single clonal lineage of the Irish potato famine fungus. *Proceedings of the National Academy of Sciences of the United States of America* 91: 11591–11595.

Groza, H.I., B.D. Bowen, W.R. Stevenson, J.R. Sowokinos, M.T. Glynn, C. Thill, S.J. Peloquin, A.J. Bussan, and J. Jiang. 2006. White Pearl: a chipping variety with high level of resistance to cold sweetening. *American Journal of Potato Research* 83: 259–267.

Groza, H.I., B.D. Bowen, A.J. Bussan, W.R. Stevenson, F. Navarro, D. Kichefski, S.J. Peloquin, J. Palta, and J. Jiang. 2007. Megachip: a new potato variety for chipping. *American Journal of Potato Research* 84: 343–350.

Guenthner, J.F., M.V. Wiese, A.D. Pavlista, J.B. Sieczka, and J. Wyman. 1999. Assessment of pesticide use in the US potato industry. *American Journal of Potato Research* 76: 25–29.

Guenthner, J.F., K.C. Michael, and P. Nolte. 2001. The economic impact of potato late blight on US growers. *Potato Research* 44: 121–125.

Hijmans, R. 2001. Global distribution of the potato crop. *American Journal of Potato Research* 78: 408–412.

Johnson, D.A. 2010. Transmission of *Phytophthora infestans* from infected potato seed tubers to emerged shoots. *Plant Disease* 94: 18–23.

Johnson, D.A., and T.F. Cummings. 2009. Latent infection of potato seed tubers by *Phytophthora infestans* during long-term cold storage. *Plant Disease* 93: 940–946.

Kaur, A., N. Singh, R. Ezekiel, and N.S. Sodhi. 2009. Properties of starches separated from potatoes stored under different conditions. *Food Chemistry* 114: 1396–1404.

Keil, S.B., M. Benker, and M. Zellner. 2010. Double setting of potato seed tubers as a new approach to research primary stem blight (*Phytophthora infestans* (Mont.) de Bary). *American Journal of Potato Research* 87: 27–31.

Kirk, W.W. 2003. Tolerance of mycelium of different genotypes of *Phytophthora infestans* to freezing temperatures for extended periods. *Phytopathology* 93: 1400–1406.

Kirk, W.W., B.A. Niemira, and J.M. Stein. 1999. Late blight (*Phytophthora infestans* (Mont.) de Bary) development from infected potato seed pieces treated with fungicides. *Pesticide Science* 55: 1151–1158.

Kirk, W., B. Niemira, and J. Stein. 2001a. Influence of storage temperature on rate of potato tuber tissue infection caused by *Phytophthora infestans* (Mont.) de Bary estimated by digital image analysis. *Potato Research* 44: 87–96.

Kirk, W.W., K.J. Felcher, D.S. Douches, J. Coombs, J.M. Stein, K.M. Baker, and R. Hammerschmidt. 2001b. Effect of host plant resistance and reduced rates and frequencies of fungicide application to control potato late blight. *Plant Disease* 85: 1113–1118.

Kirk, W.W., K.J. Felcher, D.S. Douches, B.A. Niemira, and R. Hammerschmidt. 2001c. Susceptibility of potato (*Solanum tuberosum*) foliage and tubers to the US-8 genotype of *Phytophthora infestans*. *American Journal of Potato Research* 78: 319–322.

Kirk, W.W., B.A. Niemira, and J.M. Stein. 2001d. Influence of storage temperature on rate of potato tuber tissue infection caused by different biotypes of *Phytophthora infestans* (Mont.) de Bary estimated by digital image analysis. *Potato Research* 44: 86–96.

Kirk, W.W., F. Abu-el, P.W. Samen, D. Douches, P. Tumbalam, C. Thill, and A. Thompson. 2009. 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. *Potato Research* 51: 121–140.

Knowles, N.R., E.R. Driskill, and L.O. Knowles. 2009. Sweetening responses of potato tubers of different maturity to conventional and non-conventional storage temperature regimes. *Postharvest Biology and Technology* 52: 49–61.

Kumar, D. 2009. Changes in antioxidant system of potato tuber during low temperature storage in relation to sweetening development. *Journal of Food Science and Technology-Mysore* 46: 392–394.

Lambert, D.H., and A.I. Currier. 1997. Differences in tuber rot development for North American clones of *Phytophthora infestans*. *American Potato Journal* 74: 39–43.

Lambert, D.H., A.I. Currier, and M.O. Olanya. 1998. Transmission of *Phytophthora infestans* in cut potato seed. *American Journal of Potato Research* 75: 257–263.

Murphy, P., and R. McKay. 1924. The development of blight in potatoes subsequent to digging. *J Dep Lds Agric, Dublin* 24: 103–116.

Murphy, P., and R. McKay. 1925. Further experiments on the sources and development of blight infection in potato tubers. *J Dep Lds Agric, Dublin* 25: 10–21.

Niemira, B.A., W.W. Kirk, and J.M. Stein. 1999. Screening for late blight susceptibility in potato tubers by digital analysis of cut tuber surfaces. *Plant Disease* 83: 469–473.

Olanya, M.O., P.S. Ojiambo, R.O. Nyankanga, C.W. Honeycutt, and W. W. Kirk. 2009. Recent developments in managing tuber blight of potato (*Solanum tuberosum*) caused by *Phytophthora infestans*. *Canadian Journal of Plant Pathology* 31: 280–289.

Park, T.H., V.G.A.A. Vleeshouwers, J.B. Kim, R.C.B. Hutten, and R.G.F. Visser. 2005. Dissection of foliage and tuber late blight resistance in mapping populations of potato. *Euphytica* 143: 75–83.

Pathak, N., and D.D. Clarke. 1987. Studies on the resistance of the outer cortical tissues of the tubers of some potato cultivars to *Phytophthora infestans*. *Physiological and Molecular Plant Pathology* 31: 123–132.

Platt, H.W., and G. Tai. 1998. Relationship between resistance to late blight in potato foliage and tubers of cultivars and breeding selections with different resistance levels. *American Journal of Potato Research* 75: 173–178.

Platt, H.W., R.D. Peters, M. Medina, and W. Arsenault. 1999. Impact of seed potatoes infected with *Phytophthora infestans* (US-1 or US-8 genotypes) on crop growth and disease. *American Journal of Potato Research* 76: 67–73.

Porter, L.D., N. Dasgupta, and D.A. Johnson. 2005. Effect of tuber depth and soil moisture on infection of potato tubers in soil by *Phytophthora infestans*. *Plant Disease* 89: 146–152.

Stevenson, W.R., W.W. Kirk, and Z.K. Atallah. 2007. Management of foliar disease, early blight, late blight and white mold. In *Potato health management*, ed. D.A. Johnson, 209–222. St. Paul: APS.

Świeżyński, K.M., and E. Zimnoch-Guzowska. 2001. Breeding potato cultivars with tubers resistant to *Phytophthora infestans*. *Potato Research* 44: 97–117.

Thompson, A.L., B.L. Farnsworth, N.C. Gudmestad, G.A. Secor, D. A. Preston, J.R. Sowokinos, R. Glynn, and H. Hatterman. 2008. Dakota Diamond: an exceptionally high yielding chipping potato cultivar with long-term storage potential. *American Journal of Potato Research* 85: 171–182.

Young, G.K., L.R. Cooke, W.W. Kirk, P. Tumbalam, F.M. Perez, and K.L. Deahl. 2009. Influence of competition and host plant resistance on selection in Phytophthora infestans populations in Michigan State, USA and in Northern Ireland. *Plant Pathology* 58: 703–714.