SUSCEPTIBILITY OF POTATO VARIETIES AND ADVANCED BREEDING LINES (*SOLANUM TUBEROSUM* L.) TO *PHYTOPHTHORA INFESTANS* (MONT.) DE BARY IN GREENHOUSE SCREENINGS

David S. Douches, William W. Kirk, Kazimierz Jastrzebski, Christopher Long, and Ray Hammerschmidt[1]

Abstract

Late blight (*Phytophthora infestans* (Mont.) de Bary) has re-emerged as an important pathogen of the cultivated potato (*Solanum tuberosum* subsp. *tuberosum* L.) in North America. The purpose of this study was to evaluate the relative susceptibility of potato germplasm in the greenhouse in order to initiate a breeding program for resistance to the US-8/A2 mating type which is the more aggressive and prevalent strain of late blight. Whole plants of 147 cultivars and breeding lines were evaluated. Percent plant area infection was visually assessed. Seven days after inoculation, infection ranged from 0 to 100% and the overall mean was greater than 50%. Two-thirds of the cultivars and breeding lines tested were very susceptible to the US-8 genotype. The highest resistance was identified in the somatic hybrids between *S. tuberosum* and *S. bulbocastanum* and their backcross derivatives. Pike and Snowden were less susceptible than the other North American cultivars. Zarevo was most resistant among the European cultivars. Seven of the advanced breeding lines were equivalent to Zarevo in infection levels. The host plant resistance identified among the material tested in this study can be used by breeding programs to develop improved cultivars with resistance to US-8 genotypes of late blight.

Resumen

El tizón tardío (*Phytophthora infestans* (Mont.) de Bary) ha reemergido como un patógeno importante de la papa cultivada (*Solanum tuberosum* subsp. *tuberosum* L.) en América del Norte. El genotipo predominante en América del Norte en 1995 fue el tipo sexual US-8/A2. El objetivo de este estudio fue evaluar la susceptibilidad relativa del germoplasma para empezar un programa de mejoramiento para resistencia al tizón tardío. Se evaluaron las plantas completas de 147 cultivares y líneas de mejoramiento. El porcentaje del área de infección foliar fue determinado en forma visual. Siete días después de la inoculación el porcentaje de infección estaba en el rango de 0 a 100% y la media global era mayor al 50%. Las dos terceras partes de los cultivares y líneas de mejoramiento probados fueron muy susceptibles al genotipo US-8. La resistencia más alta fue identificada en los híbridos somáticos entre *S. tuberosum* y *S. bul-*

[1]Department of Crop and Soil Sciences and Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48824.

Accepted for publication January 9, 1997.

ADDITIONAL KEY WORDS: Late blight, disease testing, breeding.

bocastanum y los derivados de sus retrocruzamientos. Pike y Snowden fueron menos susceptibles que los otros cultivares norteamericanos. Zarevo fue el más resistente entre los cultivares europeos. Siete de las líneas de mejoramiento avanzadas mostraron niveles de infección equivalentes a los de Zarevo. La resistencia de las plantas hospedantes identificada en el material probado en este estudio puede ser usada por los programas de mejoramiento para desarrollar cultivares mejorados con resistencia a los genotipos US-8 del tizón tardío.

Introduction

During recent years, late blight (*Phytophthora infestans* (Mont.) de Bary) has re-emerged as the most important pathogen of the potato crop (*Solanum tuberosum* subsp. *tuberosum* L.) in North America. The disease is characterized by haulm destruction (Figure 1) and decay of the tubers. The US-1 genotype was most common in North America until 1994 (Deahl *et al.* 1995a; Tazelaar 1981). Since then, the most commonly reported genotype of late blight is US-8 (Stevenson, pers. comm.). The US-8 genotype of *P. infestans* is characterized by reduced sensitivity to metalaxyl and is A2 mating type (Deahl *et al.* 1993; Hamm *et al.* 1994). The potential for genetic recombination of A2 mating types of *P. infestans* with the historically more prevalent US-1 genotype/A1 mating type (Deahl *et al.* 1993) of late blight is of concern because of the potential for the production of oospores, which may survive in the soil to infect successive potato crops (Deahl *et al.* 1995a).

Little is known about the disease reaction of the North American cultivars to the US-8 genotype of *P. infestans.* Knowledge of late blight sensitivity of commercially important cultivars is needed to make decisions regarding late blight management. In addition, two preconditions for a successful breeding program are the existence of resistance sources and an efficient screening method.

The objectives of this study were to evaluate the relative susceptibility of germplasm using a greenhouse screening method. The results of initial greenhouse screenings of whole plants of commercial potato varieties from North America and Europe, of recently bred lines of *S. tuberosum* and of other breeding lines that are hybrids of the wild and cultivated *Solanum sp.* as potential sources of reduced sensitivity to the US-8 genotype of late blight are reported.

Materials and Methods

Plant Material

Tubers of cultivars and breeding lines were obtained from variety trials conducted at Michigan State University Montcalm Research Farm, Entrican, Michigan and Michigan State University Soils Farm, East Lansing, Michigan. These lines and their origin are listed in Table 1. Tubers of additional breeding lines were obtained from J.J. Pavek, USDA/ARS, Aberdeen, Idaho and the Michigan State University breeding program. The somatic fusion hybrids

TABLE 1.—*Potato germplasm tested for late blight susceptibility, it's geographical origin, and degree of infection measured by percent plant infection.*

Line	Ave. Rating*	Line	Ave. Rating
USDA/ARS Beltsville, Maryland		Michigan State University	
B0717-1	3.7**	MSG047-8	1.3
B0766-3	4.0	MSG050-2	1.3
USDA80-1	4.0	MSG163-1	1.3
B0763-15	4.7	MSE246-5	2.0
B9922-11	5.0	MSG007-2	2.0
		MSG012-1	2.0
Cornell University		MSF128-C	2.3
M28-3	2.0	MSC113-A	3.0
M19-4	3.3	MSE074-02	3.0
M39-4	3.3	MSE234-3	3.0
NY101	3.7	MSG047-1	3.0
NY103	4.0	MSA091-1	3.3
M14-1	4.3	MSB095-2	3.3
L235-4	5.0	MSD040-4RY	3.3
M14-6	5.0	MSE048-2Y	3.3
		MSE011-31	3.7
European cultivars		MSE080-4	3.7
ZAREVO	1.3	MSE228-1	3.7
SANTE	2.7	MSE228-9	3.7
BRODICK	3.0	MSB083-1	4.0
IS. SUNSHINE	3.3	MSE028-1	4.0
LILY	3.3	MSE028-4	4.0
SW88-109	3.3	MSE033-01RD	4.0
SW88-113	3.3	MSE037-4Y	4.0
LIBERTAS	3.7	MSE048-01Y	4.0
MATILDA	3.7	MSE263-10	4.0
DESIREE	4.0	MSE002-04	4.3
ESTIMA	4.0	MSE006-14	4.3
AGRIA	4.7	MSE011-25	4.3
ALPHA	4.7	MSE030-4	4.3
PENTA	4.7	MSE215-12	4.3
DORITA	5.0	MSE228-11	4.3
OFELIA	5.0	MSE228-3	4.3
		MSE228-5	4.3
USDA/ARS University of Wisconsin,		MSE250-2	4.3
Madison		MSE290-1Y	4.3
J101	0.0	MS702-80	4.7
J101K6A22	0.0	MSB076-2	4.7
J103	0.0	MSC010-20Y	4.7
J138	0.0	MSE001-28	4.7
J138A12	0.0	MSE011-11	4.7
J101K9	0.7	MSE018-1	4.7
J103K7	1.3	MSE041-1	4.7
J138A4	1.3	MSE192-8	4.7
PI203900	1.3	MSE213-2	4.7
J101A35	3.0		

Colorado State University			
C0083008-1	3.7	MSE220-3	4.7
		MSE221-1	4.7
North American Cultivars		MSE222-5Y	4.7
PIKE	2.3	MSE230-13	4.7
SNOWDEN	3.0	P88-13-4	4.7
KRANTZ	3.7	MSB106-8	5.0
PORTAGE	3.7	MSB110-3	5.0
MAINESTAY	4.0	MSE247-2	4.7
SHEPODY	4.0	MSE271-1	4.7
FRONTIER R	4.0	MSC148-A	5.0
CRESTONE R	4.3	MSE011-10	5.0
SAG. GOLD	4.3	MSE011-14	5.0
SPARTAN PEARL	4.3	MSE011-7	5.0
LEMHI RUSSET	4.7	MSE012-01	5.0
YUKON GOLD	4.7	MSE012-2	5.0
ATLANTIC	5.0	MSE015-2	5.0
CHALEUR	5.0	MSE021-4	5.0
GOLDRUSH	5.0	MSE040-6RY	5.0
ONAWAY	5.0	MSE149-5Y	5.0
PRESTILE	5.0	MSE226-4Y	5.0
R. BURBANK	5.0	MSE228-8	5.0
ST.JOHNS	5.0	MSE230-3	5.0
SUPERIOR	5.0	MSE230-6	5.0
		MSE263-3	5.0
USDA/ARS Aberdeen, Idaho		MSE273-8	5.0
A90586-11	1.0	P84-13-12	5.0
AWN86514-2	1.0		
G6582-3	1.0	North Dakota University	
AWN86524-5	1.3	ND2225-1R	4.3
A90587-5	3.3	ND860-2	4.3
A082611-7	3.7	ND2417-6	4.7
A7961-1	4.0	ND2471-8	5.0
A86102-6	5.0	ND01496-1	5.0
		J.R. Simplot	
		JS111-28	4.3
		JS91-95	4.7

* average of three replications; $LSD_{0.05} = 1.5$

** rating scale: 0 = 0 infection; 1 = 0.1 - 5% infection; 1 = 6-15% infection; 3 = 16-30% infection; 4 = 31-49%; 5 = 50-100%.

between *S. tuberosum* and *S. bulbocastanum* and their derivatives were obtained from J. Helgeson USDA/ARS University of Wisconsin, Madison.

Three tubers of each line were planted in 16 cm diameter clay pots in the greenhouse from February to April, 1996. Baccto Soil Mix was used as growing medium. Plants were grown under 16 hour daylength with supplemental lighting from high-pressure sodium lamps (400 watts). Daytime greenhouse temperature ranged from 18C to 25C. Whole plants at the age of 5 weeks (just prior to the appearance of flower buds) were tested for susceptibility to late blight.

FIG. 1. Leaf and stem infection from US-8 genotype of *Phytopthora infestans.*

Isolation of P. Infestans

Leaves infected with late blight (*P. infestans*) were collected from potato plants in Montcalm County, Michigan in 1995. A pure culture isolated from field infected tissue was prepared by a series of transfers from infected tissue to rye agar (Deahl 1993). Contaminating bacteria and other fungi were removed

by growing the infected tissues on rye agar amended with antibiotics (100 ppm each of penicillin G, pimaricin and polymixin) (Ribeiro 1978). The genotype was determined as US-8/A2 mating type by gel-acetate electrophoretic technique (Goodwin *et al.* 1995a) and the production of oospores when grown with an isolate known to be A1 mating type. This isolate was determined as metalaxyl insensitive using the method of Deahl, *et al.* (1995b). The isolate was named PAI 95-7. During this study, two re-isolations were made to ensure the continued pathogenicity of the inoculum. Potato plants were inoculated with a spore suspension of PAI 95-7.

Inoculum Production and Inoculation Procedure

Pure cultures of PAI 95-7 were started ten days in advance of each inoculation. The cultures were prepared by transferring 5 mm discs of *P. infestans* mycelium growing on rye agar from the leading edge of the culture onto rye agar (Deahl *et al.* 1993). The cultures were incubated at 20C in darkness for 10 days. Inoculum suspensions were prepared by washing the mycelium and spores from culture plates (80mm). Each plate was flooded with 10 ml of distilled water and the sporangial mycelium detached from the agar surface with a rubber policeman. The plates were rinsed with an additional 5 ml of distilled water. The suspension of mycelium and sporangial spores was stirred at low speed with a magnetic stirrer for one hour at room temperature. The suspension was strained through one layer of cheesecloth. We used water to adjust the concentration (10^5 sporangium ml^{-1}) which was measured with a hemacytometer. The suspension was then stored for four hours in a refrigerator at 4C to stimulate zoospore (8 zoospores/sporangium) release prior to inoculation.

The maximum floor space of plants to be inoculated was 3 m^2 (about 80 plants/3m^2). The number of cultures required to produce enough inoculum (at an inoculum rate of 10^5 sporangium ml^{-1}) to deliver 50 ml of inoculum to an area of 1 m^2 was calculated. Ten plates (80mm) of pure culture typically produced enough sporangia to yield 150 ml (50 ml/m^2) of inoculum suspension containing 10^5 spores ml^{-1}. The plants were placed on trays in an inoculation tent (1 meter x 3 meter x 1.5 meter). The relative humidity was maintained above 90% by misting the atmosphere for 15 minutes every $hour^{-1}$ (6 liters of deionized water per 24 hour period) with a gravity-fed humidifier (Herrmidifier Series 500). Six mill clear plastic sheets were used to enclose the inoculation tent. Relative humidity was checked periodically with a humidity sensor (Bandix psychrometer Model 566). Temperature was maintained between 18C and 25C within the inoculation tent by greenhouse computer sensors which control vents, shading and cooling. Lighting in the greenhouse was supplemented with high pressure sodium lamps at a 16 hr daylength.

The plants were inoculated in the evening (5 PM) when temperatures were between 18C and 22C by spraying each tray of plants with the appropriate amount of inoculum. The inoculum was applied with a hand-held sprayer. The

output of the sprayer per depression of the trigger was measured and equal amounts of inoculum applied to each tray of plants.

Disease Evaluation

Late blight infection was visually estimated as percentage plant (leaf and stem) area affected by blight lesions. The percent infected plant area was converted into a 1-5 scale where 1 was zero and 5 was greater than 50% infection (Table 1). Ratings were done at 4 and 7 days. Additional ratings were done at 10 and 14 days on the lines with low infection and up to four weeks on the most resistant lines. Each line was tested on three dates using a completely randomized design. Each plant represented a replication. Analysis of variance was conducted on the rating from day 7 using the ANOVA procedure of SAS (SAS 1988). Separation of means was based upon the least significant difference test.

Results and Discussion

The first stage of late blight infection was usually observed two days after inoculation as a downward curling of the leaves and petioles on the upper third of the plant. Lesion development was observed by the third day after inoculation. This ranged from small necrotic limited lesions on less sensitive plants to water-soaked lesions which then advanced to sporulating necrotic lesions on sensitive plants. On the fourth day after inoculation the range of infection observed was from 0 to 35% of the leaf area (or 0-4 using the rating scale in Table 1). Leaf area infection at day seven reached up to 100% in some lines (which was accompanied by stem collapse), and the overall average rating was greater than 50% (Table 1). Figure 2 shows the distribution according to the degree of infection while Figure 3 shows actual range of infection observed. Over two-thirds of the potato lines and cultivars were highly susceptible to US-8, while 17 demonstrated high resistance to the US-8 genotype of *P. infestans.*

Due to the large number of material tested, the screening was run over a three-month period. Susceptible cultivars (*i.e.* Atlantic, Goldrush, Russet Burbank, etc.) were included in each round of the screening. The high levels of infection observed in these susceptible cultivars suggested that variation between rounds of infection was not large. Plants with little or no infection (less than 20% of leaf area) were placed in the chamber, reinoculated and evaluated during the next week. This procedure separated resistant lines from those that escaped infection.

The lines tested in this study were separated into four arbitrary germplasm groups: North American cultivars, European cultivars, breeding lines, and *S. tuberosum* x *S. bulbocastanum* somatic hybrids (and derivatives) (Table 1). The breeding lines were from six US breeding programs with the majority of the lines (71%) from Michigan. This group of germplasm can be considered representative of the level of resistance to US-8 currently available among the cultivated germplasm of North America.

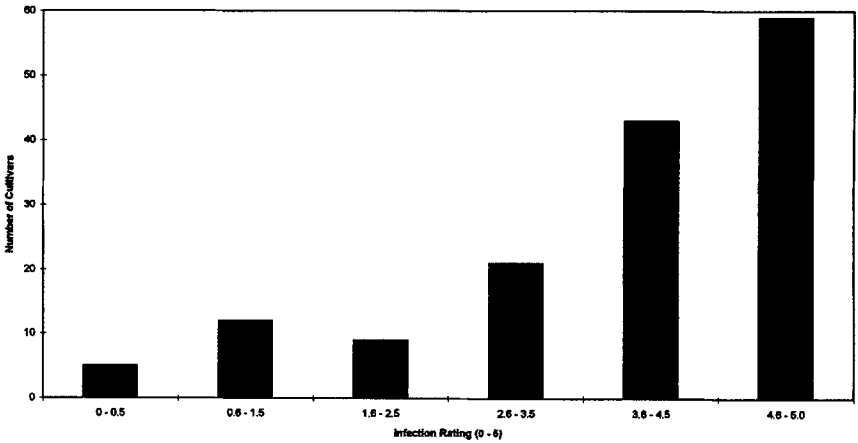

FIG.2. Late blight disease reaction (7 DAI) of potato cultivars and breeding lines infected with the US-8 genotype.

North American Cultivars

Twenty North American cultivars were evaluated in this study. Atlantic, Goldrush, Russet Burbank, Superior and Yukon Gold were highly susceptible to the PAI-95-7 US-8 genotype in the greenhouse test (late blight rating > 4.5). COO83008-1 had a significantly lower late blight rating (late blight rating = 3.7) as compared to highly susceptible cultivars at $P = 0.10$ (but not at $P < 0.05$). Inglis, *et al.* (1996), in field studies, found COO83008-1 to be more resistant than Russet Burbank, while GoldRush and Shepody were more susceptible. Some inconsistency between GoldRush assessments may be due to the genotypes of *P. infestans* found in the field studies (US-6, US-8 and US-11) or the severity of the inoculation tent. Further greenhouse tests may allow greater discrimination between COO83008-1 and the highly susceptible cultivars. Pike was least infected among the North American cultivars (late blight rating = 2.3). Both Pike and Snowden were significantly more resistant than the highly susceptible cultivars. In summary, only a few cultivars tested expressed any general resistance to the US-8 genotype of late blight.

European Cultivars

Sixteen European cultivars and advanced breeding lines, reported to have some resistance to late blight, were also evaluated. This group was, on average, similar to the North American cultivars in late blight susceptibility despite the fact that some of them were included into the test because they were reported to be resistant to late blight. The most susceptible European cultivars were Ofelia, Dorita, Agria, Alpha and Penta. Zarevo was confirmed to be highly resistant, while Sante and Brodick showed resistance similar to Snowden and Pike. Other lines with previous reports of late blight resistance were Libertas,

Matilda, Lily and Island Sunshine. In this study, these lines were classified as susceptible. The conflicting results may be attributed to the different genotypes of late blight predominant in Europe (Gisi *et al.* 1995), the severity of the environment within the inoculation tent, or the pathogenicity of the isolate.

Somatic Hybrids and Backcross Derivatives

The Mexican wild species, *S. bulbocastanum* (2n = 2x = 24), is resistant to late blight (Tazelaar 1981). Three somatic hybrids between *S. tuberosum* (PI 203900) and *S. bulbocastanum* (2n= 6x = 72), five backcross derivatives of these lines to *S. tuberosum* (J. Helgeson pers. comm.) and the tetraploid *S. tuberosum* parent of these somatic hybrids exhibited the highest resistance (Table 1, Figure 3) with the exception of J101A35. No infection was observed on five of these lines and they developed few or no lesions even when they were held for up to four weeks in the inoculation tent and reinoculated weekly. Two of these lines (J101K6A22 and J138A12) came from backcrosses to the Katahdin and Atlantic, respectively. These two lines were the most resistant to the PAI-95-7 US-8 genotype of late blight. PI 203900 also exhibited some resistance. These observations suggest that the resistance in the somatic hybrids and backcross lines may be contributed from both parents of the somatic hybrid.

US Breeding Lines

The largest group of material evaluated was from breeding lines developed in US breeding programs. The MSU lines comprised the majority of the material tested. The level of resistance observed in the breeding lines was, on average, similar to that of cultivars tested in this study. Four lines from the USDA/ARS Aberdeen and three lines from the MSU breeding programs exhibited higher resistance (Table 2). Four other lines from the MSU program also exhibited moderate resistance (similar to Pike).

TABLE 2.—*Pedigree of breeding lines with resistance to the PAI 95-7 US-8 genotype late blight.*

Line	Rating*	Pedigree
A90586-11	1.0	KSA195-90 x Ranger Russet
AWN86514-2	1.0	KSA195-96 x Ranger Russet
G6582-3	1.0	Scottish source
AWN86524-5	1.3	KSA195-96 x NDA848-3
MSG047-8	1.3	Pike x Zarevo
MSG050-2	1.3	Eramosa x L235-4
MSG163-1	1.3	W877 x Zarevo
MSE246-5	2.0	E55-27 x W870
MSG007-2	2.0	Atlantic x Zarevo
MSG012-1	2.0	MSB007-1 x Zarevo
MSF128-C	2.3	Hudson x W870
MSG047-1	3.0	Pike x Zarevo

* rating scale: 0 = 0 infection; 1 = 0.1 - 5% infection; 1 = 6-15% infection; 3 = 16-30% infection; 4 = 31-49%; 5 = 50-100%.

FIG.3. Range of late blight infection observed seven days after inoculation in the greenhouse tent.

There are two types of late blight resistance: general (horizontal) and race-specific (vertical) (Umaeros and Umaeros 1994). The purpose of this study was not to distinguish between the types of resistance, but observations from this study can be made. The somatic hybrids and their derivatives exhibited small limited necrotic lesions of which no sporulation was observed. Small localized necrotic lesions on a few of the hybrids and derivatives suggest a hypersensitive response from the host plant. Callousing on the leaves was also noted on many of these lines and suggests a type of hypersensitive reaction (Cuypers and Hahlbrock 1988). The high level of resistance could be partially contributed from PI 203900 which had less lesion spreading than many cultivars or breeding lines. All other lines exhibiting high levels of resistance did express limited lesion development. The foliage resistance could be due to factors such as infection efficiency and slower lesion development (van der Zaag 1959). Strong general resistance has been associated with later maturity of the lines (Swiezynski 1990); however, maturity was not evaluated in this study.

By examining the pedigrees of some of the lines tested, we can make some inferences regarding sources of late blight resistance and also give further support to the resistance observed among the parents. The pedigrees of 12 breeding lines with the highest late blight resistance are summarized in Table 2. Five of the selections from the MSU breeding program tested in this study were from crosses with Zarevo. Of these selections, only two had ratings equal to Zarevo (late blight rating = 1.3), while three had moderate resistance (late

blight rating = 2.0 - 3.0). The higher resistance observed in MSG047-8 and MSG163-1 may have been due to contributions from both parents (Table 3). Pike was the North American cultivar with the consistenly lowest infection. W877 is a full-sib of Snowden, and Snowden was reported to have some resistance in this study. MSG047-1, a full-sib of MSG047-8, did not have as high a resistance suggesting the late blight resistance factors segregate within the progeny. The other two breeding lines with Zarevo as a parent were more susceptible. Other MSU breeding lines also exhibited some resistance. The line MSF128-C is a selection from a cross between Hudson, noted to have some level of general resistance (Plaisted *et al.* 1973) and W870, another full-sib of Snowden. MSE246-5 is a selection from a cross between E55-27, a full-sib of Pike, and W870. The four lines from the USDA/ARS Aberdeen breeding program, A90586-11, AWN86514-2, G6582-3 and AWN86524-5, are selections from crosses between US lines and European lines with late blight resistance. G6582-3 has a Scottish breeding line as a late blight resistance parent, while the three others involved crosses to a breeding line from Poland (Pavek and Corsini, pers. comm.) (Table 2). These 12 lines, along with the parents contributing late blight resistance, are additional sources of resistance to consider in breeding for general resistance to late blight. These lines offer some agronomic and quality characteristics that are important for breeding (*i.e.* tuber type, internal quality and vine maturity).

The next step of this research is to compare the greenhouse assessment to a field assessment. In addition, exotic *Solanum* species should be evaluated as additional complementary sources of resistance. The results from this study also give direction for future studies to understand the mechanism of resistance in the high and moderately resistant lines. This germplasm should be tested against other genotypes of the *P. infestans* to better understand the value of these resistance sources.

Acknowledgments

This research was supported by the Michigan Agricultural Experiment Station, Michigan Potato Industry Commission and USDA special grant 95-34141-1399.

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