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Foliar and tuber assessment of late blight (*Phytophthora infestans* (Mont.) de Bary) reaction in cultivated potato (*Solanum tuberosum* L.)

D.S. DOUCHES[1]*, W.W. KIRK[2], M.A. BERTRAM[1], J.J. COOMBS[1] and B.A. NIEMIRA[2]

[1] Dept. of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, USA
[2] Dept. of Plant Pathology, Michigan State University, East Lansing, MI 48824, USA
* Corresponding author: douchesd@msu.edu

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Summary

Host plant resistance is an important component to the management of potato late blight, *Phytophthora infestans* (Mont.) de Bary. Assessment of potato lines (*Solanum tuberosum* L.) with various levels of resistance to *P. infestans* (US8, A2 genotype) were evaluated in field trials, greenhouse controlled environment chambers and inoculated tuber reactions. Five lines (AWN86514-2, B0692-4, B0718-3, Jacqueline Lee, and B0288-17) with strong foliar resistance to late blight were identified in these inoculated field trials. Greenhouse controlled environment chamber studies allowed resistant and susceptible lines to be distinguished, but the 1998 greenhouse results did not correlate well with field data. Four lines (A084275-3, Bzura, MSG007-1, and MSG297-4RD) evaluated by a digital image analysis technique demonstrated tuber resistance based upon average reflective index values in the inoculated tuber studies. Tuber resistance did not correlate with field foliar resistance. Based upon these results, field assessment of foliar reaction to *P. infestans* provides the best measure for assessing late blight resistance in potato. Tuber resistance to late blight can be identified among lines with varying levels of foliar resistance.

Introduction

Potato late blight, *Phytophthora infestans* (Mont.) de Bary, re-emerged in the mid-1980s and 1990s as a new threat to cultivated potato (*Solanum tuberosum* L.) production (Fry & Goodwin, 1997). Late blight had been successfully controlled with the systemic fungicide metalaxyl (Schwinn & Margot, 1991), but the migration of metalaxyl-resistant strains of *P. infestans* from central Mexico has caused serious potato production and economic problems worldwide (Fry & Goodwin, 1995). The most prevalent genotype of *P. infestans* in the United States is currently the US8 genotype (Fry & Goodwin, 1997); however, genotypes such as the original, metalaxyl-sensitive US1 and the metalaxyl-resistant US11 are also found, particularly in California, Washington and Oregon (Dorrance & Inglis, 1998; Goodwin et al., 1998).

Field screening of potato lines is an effective method to evaluate foliar resistance

to late blight. However, space and labour requirements, as well as seasonal limits and the risk of spread of inoculum of *P. infestans*, restrict large-scale field screening for determination of susceptibility of potato lines to late blight. Greenhouse testing can therefore be useful for determining susceptibility of potato lines to late blight. Environmental conditions such as humidity and temperature can be controlled to create uniform infections when performing repeated tests (Helgeson et al., 1998). Controlled conditions in enclosed environments minimize the risk of late blight spread in comparison to inoculated field trials (Colon et al., 1995) but impose conditions markedly different from the field. Therefore, it is possible that the controlled, optimal conditions and increased late blight pressure might overcome potato lines with good field tolerance. Resistance to tuber blight caused by *P. infestans* may (Platt, 1999) or may not (Black, 1970; Inglis et al., 1996; Dorrance & Inglis, 1997; Kirk et al., 2001) be correlated with foliar resistance. Therefore, it is essential to test the susceptibility of both the tubers and the foliage of breeding lines to *P. infestans*.

The primary objective of this study was to compare field and greenhouse late blight resistance evaluations on a set of germplasm with varying susceptibility to *P. infestans* (US8 genotype). The second objective of this study was to determine the levels of tuber resistance in selected lines with different degrees of foliar resistance and susceptibility in field and greenhouse screens and to compare tuber and foliar resistance within the lines.

Materials and methods

Plant material. Twenty-eight potato breeding lines were evaluated in each field trial and greenhouse experiment (Table 1). The potato breeding lines included were 1) National Late Blight Trial lines (Haynes et al., 1998); 2) susceptible commercial cultivars such as Atlantic, Russet Burbank, and Snowden; 3) European commercial cultivars imported for evaluation as potential late blight resistance sources; and 4) advanced breeding lines from university breeding programs in North America. Twenty-six of these lines were chosen to be included in the tuber resistance test. Tubers were hand-harvested from the 1998 foliage late blight trial field plots at the Muck Soils Research Farm (Michigan State University, Bath, MI) following haulm senescence in late September. Tubers, free from fungal and bacterial diseases (determined by culturing samples on selective agars) were stored at 4 °C for tuber tests or stored at about 20 °C until dormancy was broken for foliar greenhouse tests.

Preparation of P. infestans inoculum. Michigan isolates of *P. infestans* (US8, A2 mating type, Goodwin et al., 1995) were maintained on rye agar at 18 °C. A zoospore suspension of the US8 genotype of *P. infestans* (insensitive to metalaxyl, A2 mating type) was prepared from cultures grown on rye agar plates (Deahl et al., 1995) for 14 days in the dark at 18 °C. Sporangia were harvested from the Petri dishes by rinsing the mycelial/sporangial mat in cold (4 °C) sterile, distilled water and scraping the mycelial/sporangial mat from the agar surface with a rubber policeman. The mycelial/sporangial suspension was stirred with a magnetic stirrer for 1 hour.

The suspension was strained through four layers of cheesecloth and incubated at 4 °C for 4 hours to release zoospores. Prior to inoculation the concentration was adjusted to about 1×10^6 zoospores ml^{-1} based on hemacytometer readings.

Inoculum for the greenhouse screen was prepared from rye-agar cultures as described above, using the Michigan isolates of US8 (94–1, 94–3, 95–7, 97–1, 97–2, and 98–2) at 200 ml inoculum per chamber. This combination of isolates overcomes all known R-genes in detached leaf tests. For the field evaluation, the inoculum suspension was administered (100 ml/7.5 m row) through the field's irrigation system on 18 July, 1997 and 22 July, 1998.

Field evaluation. Field tests were conducted during the 1997 and 1998 growing seasons at the Michigan State University Muck Soils Research Farm, Bath, MI. Trials were planted on 3 June, 1997 and 5 June, 1998 in a randomized complete block design with three replications. Each 1.5 m plot contained four seed pieces at 30 cm spacing, with eight plots per row. A single Red Norland plant separated each plot in 1997, but in 1998 trial plots were separated by a 1 m space to facilitate evaluations. Following inoculation, the plants were mist-irrigated frequently with a sprinkler system to prevent plants from drying and to promote humidity within the canopy. No fungicides were applied to the plants.

Percent foliar infection caused by *P. infestans* was visually estimated every 3 to 7 d from 30 July, 1997 and 6 August, 1998 until susceptible control cultivars were 100% defoliated (about 28 DAI). To compare the reactions of the potato lines to late blight over time, the Relative Area Under the Disease Progress Curve (RAUDPC) was calculated for each line. RAUDPC is the Area Under the Disease Progress Curve (AUDPC, the area under the linear progression of percent foliar late blight from inoculation to the end of the evaluation period) (Colon et al., 1995) divided by the maximum AUDPC (100 ÷ the total number of days after inoculation) (Kirk et al., 1999).

Greenhouse evaluation. Greenhouse screening was conducted during the winter months of 1998 and 1999 according to the method described by Douches et al. (1997). Seed pieces were planted about 10 cm deep in 16 cm deep clay pots in the greenhouse and grown for approximately six weeks. Plants were then placed inside the controlled environment chamber in a completely randomized design with three replications. The controlled environment chamber consisted of a metal bench covered with 153 μm transparent polyethylethene to keep the atmosphere inside the chamber isolated from the surrounding greenhouse. The relative humidity in the chamber (3.4 m^3) was maintained at >90% by timer-controlled humidifiers (Herrmidifier model 500) and temperature ranged from 15 to 24 °C. Natural light was supplemented by high-pressure sodium lamps (400 W) 16 h day length. The potato plants were inoculated with the *P. infestans* zoospore suspension in the late afternoon. Plants were rated for percent foliar infection about seven days after inoculation (DAI).

Tuber disease evaluation. Cultures of *P. infestans* (Michigan US8 isolate, 97–1) were grown as described above. A homogenate of mature sporulating culture of *P. infes-*

tans with its rye agar substrate was prepared by removing the rye agar and growing culture into a sterile pyrex dish (10×10×2 cm) and blending the mix together with a sterile spatula. Approximately 0.1 ml of the homogenate was injected 3 to 5 mm into the periderm of sterilized tubers, adjacent to the apical meristem. Inoculated tubers were held in the dark at 12 °C and 95% relative humidity for 40 days. To provide a basis of reference for healthy tuber flesh, ten tubers of each line were punctured at the apical end with an identical sterilized hypodermic needle, inoculated with sterile water, and incubated as above.

The inoculated tubers were removed from storage and late blight was rated visually. Tubers were assessed visually for an estimate of surface degradation on a 1 to 9 scale of increasing disease severity (Niemira et al., 1999). The 1 to 9 scale used, relied on the characteristics of late blight as they developed on the surface of the tuber periderm. Tubers were evaluated for the first category (skin discoloration) and then evaluation of subsequent categories occurred only if the critical threshold of 10% was reached in the previous category. In cases where a more severe indicator (e.g. extensive physical degradation) was obtained before a critical threshold of a less severe indicator (e.g. 5 sprouts damaged), the higher rating was assigned to the tuber.

Each tuber was then sliced into sections approximately 2 cm from the apical and terminal ends and through the middle. The three tuber sections (apical, middle, and terminal) were placed immediately, cut surface down, on a transparent plate and scanned with a flatbed scanner (HP ScanJet 4c, Hewlett-Packard Co., Houston, TX). On the light intensity scale, pure black has an intensity of 0 light intensity units (LIU) and pure white an intensity of 255 LIU. Late blight infected tissue is darkened and uninfected tissue is light. On each grayscale tuber slice image, each pixel has a light intensity unit between 0 and 255 LIU. The average reflective intensity (ARI) is the mean LIU of all the pixels in the image. The resulting digital images were used to determine the ARI of each tuber slice as described by Niemira et al. (1999). An internal average was calculated by adding the reflective intensities of the apical, middle and terminal slices and dividing by three. To compensate for cultivar differences in flesh color, ARI of the diseased tubers were divided by the ARI of the control tubers. Thus, the higher the ARI value, the less darkened (diseased) tissue was present in the tuber slice.

Statistical methods. Analysis of variance was performed on the RAUDPC values of potato lines and cultivars for each field study; the percent foliar late blight infection values for each greenhouse study and the tuber late blight evaluations (ARI and tuber surface infection) using SAS general linear models procedure (SAS 2000). Mean comparisons were conducted using Fisher's Least Significant Difference (LSD, α=0.05). Spearman Rank Correlations were calculated using SAS (2000).

Results

Field results. In both years *P. infestans* infection spread evenly and rapidly throughout the field. The commercial cultivars used as susceptible controls, Atlantic and Russet Burbank, were 100% defoliated by late blight 28 DAI. Lesions were visible 9

DAI. Significant differences between breeding lines in susceptibility to late blight were found in 1997 ($P<0.01$) and 1998 ($P<0.01$). Five of the lines showed high levels of resistance in both 1997 and in 1998 (Table 1). The relative ranking of field performance remained consistent through two growing seasons (Table 2).

Table 1. Reaction of potato cultivars and advanced breeding lines by inoculation with potato late blight (*P. infestans*, US8 biotype) in field trials, greenhouse controlled environment chambers and tuber bioassays.

Potato line[e]	Field		Greenhouse		Tuber reaction	
	RAUDPC foliar reaction[a]		Percent foliar reaction[b]		Surface[c] infection	ARI[d] internal
	1997	1998	1998	1999		
B0692-4	0	5	48	2	3.1	158
AWN86514-2	1	5	57	2	4.0	152
B0288-17	3	14	47	12	5.7	170
Jacqueline Lee	4	4	10	11	4.2	152
B0718-3	6	8	82	3	6.4	147
Dorita	21	19	86	33	2.1	173
Bzura	23	10	73	30	3.1	183
A084275-3	26	19	57	50	3.5	190
Robijn	26	12	48	12	7.0	113
A080432-1	29	21	85	58	4.3	140
Stobrawa	29	17	63	22	4.3	127
B1004-8	30	27	32	28	5.0	166
Zarevo	30	16	2	22	5.2	171
Elba	31	17	95	4	5.5	125
Greta	32	21	90	8	5.8	129
A84118-3	34	21	48	18	–	–
B0811-13	34	22	34	13	–	–
Nordonna	35	25	85	35	5.8	112
Lily	36	26	78	30	4.6	166
MSE018-1	38	32	72	40	6.5	150
Snowden[f]	**39**	**35**	**65**	**60**	**6.0**	**153**
Matilda	40	29	40	37	4.6	166
MSG050-2	41	28	72	35	6.3	129
Atlantic	**46**	**35**	**34**	**77**	**4.3**	**170**
MSG007-1	47	35	32	28	6.1	188
MSG139-1	47	35	40	25	6.8	155
MSG297-4RD	47	36	38	8	4.5	189
Russet Burbank	**51**	**33**	**42**	**68**	**4.9**	**150**
Mean	29	22	56	28	5.0	155
LSD (α= 0.05)	10	5	45	31	0.9	17

[a] AUDPC, relative area under the disease progress curve (×100) calculated from the day of inoculation to the last evaluation of late blight (max = 100) (Kirk et al., 1999). Mean of three replications.
[b] Rating is a visual estimation of percent defoliation from 0–100%. Mean of three replications.
[c] Surface rating is on a 1–9 scale of increasing disease severity. Mean of six replications.
[d] ARI (average reflective index) rating (Niemira et al., 1999) represents the average light intensity of a scanned image with 0 = black (diseased flesh) and 255 = white (healthy flesh). Mean of three sections from six tubers.
[e] Table sorted by 1997 season.
[f] Susceptible control cultivars in bold.

Table 2. Spearman Rank Correlation Coefficients of the rank order in each evaluation of potato cultivars and advanced breeding lines in field trials, greenhouse controlled environment chambers and tuber bioassays.

	Spearman Rank Correlation Coefficients					
	Field foliar reaction RAUDPC		Greenhouse foliar reaction (% defoliation)		Tuber surface infection	Tuber ARI internal
	1997	1998	1998	1999		
Field foliar reaction RAUDPC 1997	–					
Field foliar reaction RAUDPC 1998	0.93 *	–				
Greenhouse foliar reaction (% defoliation) 1998	NS	NS	–			
Greenhouse foliar reaction (% defoliation) 1999	0.51 *	0.59 *	NS	–		
Tuber surface infection	0.43 *	NS	NS	NS	–	
Tuber ARI internal	NS	NS	–0.47 *	NS	–0.43 *	–

* Correlation coefficient is significant at $\alpha = 0.05$.
NS = Not significant at $\alpha = 0.05$.

Greenhouse results. Results from two separate runs of the experiment, one in 1998 and one in 1999, show significant differences between the most susceptible and most resistant lines (Table 1). No correlation was found between the relative resistance ranking and susceptibility of the lines based on 1998 greenhouse ratings and 1997 and 1998 field RAUDPC scores ranking (Table 2). However, there was a moderate correlation ($r=0.59$, $P<0.001$ and $r=0.51$, $P=0.006$) between the response of the 1999 greenhouse plants and the 1997 and 1998 field RAUDPC, respectively.

Tuber surface rating. Individual tubers displayed levels of disease ranging from 1 to 8 on the rating scale used, although mean values only varied between 2 and 7 across all potato lines (Table 1). Visual rating of tuber surface infection severity allowed detection of differences between potato lines, but there was no correlation between relative ranking of the tuber surface rating and field foliar late blight resistance (Table 2).

Internal section analysis. All potato lines showed signs of infection based on quantitative measurement of diseased flesh using the average reflective index (ARI (Table 1)). The internal tuber infection of a clone resistant to *P. infestans* (MSG297-4RD), a moderately susceptible line (MSG274-3), and a highly susceptible line (Nordonna) is illustrated in Fig. 1. To compensate for cultivar differences in flesh color, the ARI of the diseased tubers were divided by the ARI of the control tubers, which slightly altered the rankings of the lines. A moderate correlation (Table 2) was found between surface response ranking and ranking based on ARI ($r=-0.43$, $P=0.027$). There was no correlation between the resistance of the tubers and the resistance of their foliage from the previous field season ($P>0.05$).

Discussion

Five lines (AWN86514-2, B0692-4, B0718-3, Jacqueline Lee, and B0288-17) with strong foliar resistance to late blight were identified based on field trial results. Four lines (A084275-3, Bzura, MSG007-1, and MSG297-4RD) were classified as having tuber resistance to late blight that was not correlated with field foliar resistance. There were year-to-year differences between advanced breeding lines in their field reaction to late blight for each line, but the overall ranking of susceptibility and resistance remained stable. This suggests that field screening can provide an accurate assessment of the level of resistance to late blight in a range of advanced breeding lines and potato cultivars. When measured against standard cultivars, rating should remain consistent regardless of the conditions of the particular growing season (Colon et al., 1995; Dorrance & Inglis, 1997).

The greenhouse late blight resistance screen permitted the separation of resistant and susceptible lines based on percent infection. The 1998 greenhouse results did not correlate well with the field results. One contribution may be the unusually high disease severity in the 1998 greenhouse tests. However, when the 1999 greenhouse data alone were compared to the previous season's field ratings, moderate correla-

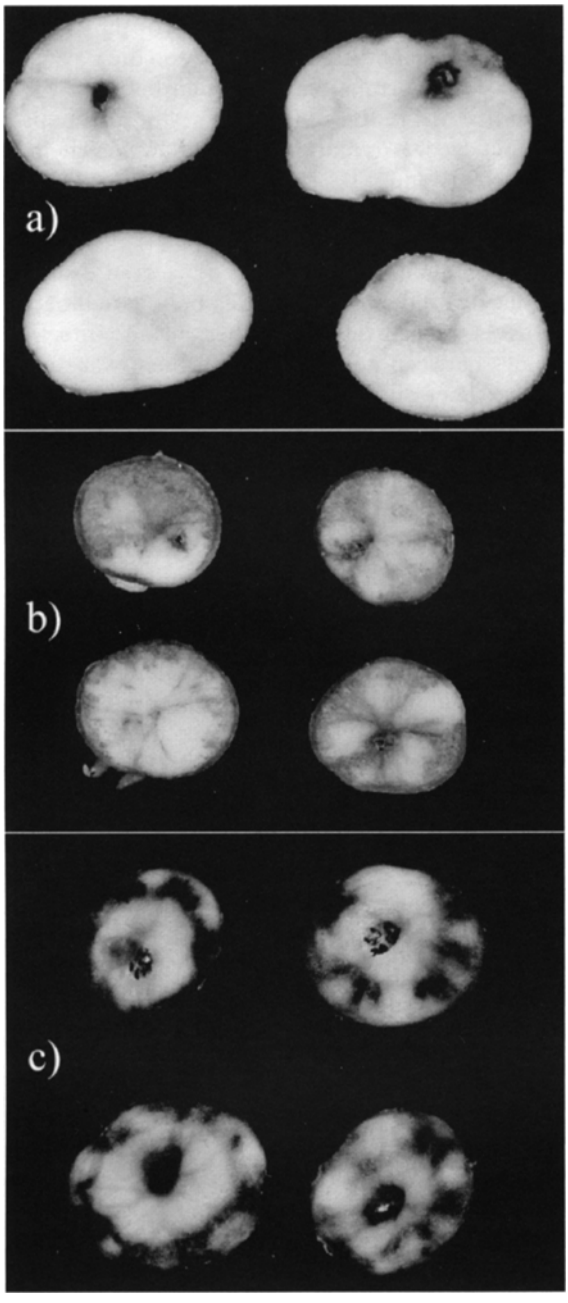

Fig. 1. Scanned apical sections of four sample tubers inoculated with *P. infestans* from a) MSG297-4RD (ARI=184), b) Jacqueline Lee (ARI=137), and c) Nordonna (ARI=102).

tions were found (r=0.51 and r=0.59 for 1997 and 1998, respectively) that was more consistent with an earlier greenhouse study (Douches et al., 1997).

The late blight reaction of the potato lines varied between the field and greenhouse experiments. Lines with strong foliar resistance in the field, AWN86514-2 and B0718-3, were intermediate for greenhouse defoliation. The strong resistance of Zarevo and its progeny MSG297-4RD in the greenhouse demonstrated intermediate resistance (Zarevo) or susceptibility (MSG297-4RD) under field conditions. Two other Zarevo progeny, MSG007-1 and MSG139-1, were intermediate in the greenhouse but highly susceptible in the field. The greater foliar resistance of this material may be due to its lower infection rate in the greenhouse (Dorrance & Inglis, 1997). This aspect of resistance may be negated under a month-long field evaluation. Stewart et al. (1983) discussed some of the factors that caused low correlation between greenhouse and field tests. Unpredictable disease severity was one of the main limitations of the greenhouse screening method.

Differentiation in internal tuber infection was observed between the clones tested in this study. The resistant clone MSG297-4RD is an advanced breeding line derived from Zarevo. Another line with tuber resistance, MSG007-1, is an advanced breeding line selected from a cross between Atlantic and Zarevo. The third progeny line from Zarevo, MSG139-1 (Snowden × Zarevo), was significantly more susceptible than its half-siblings as well as its resistant parent (based on internal mean). A more extensive tuber screen among progeny of Zarevo would be important to determine its value as a source of tuber resistance to *P. infestans*.

In the tuber analysis described in this study, the surface score did not correlate well (r=–0.43, P=0.027) with the internal rating since some lines darken through the center and in others the visible symptoms are confined to the surface; yet each rating gave valuable information about cultivar response to infection by *P. infestans*. The two assessments should be used to complement rather than predict one another.

Further work in this area needs to be conducted on tuber resistance on a wider range of cultivars and breeding lines, as well as progeny studies with lines that display high levels of resistance. This is especially important for cultivars, such as Zarevo, that also possess moderate or high foliar resistance, as there is some evidence that general combining ability for foliar and tuber resistance may be correlated (Stewart et al., 1994). For potato breeding programs, extensive screening is crucial to developing commercially acceptable cultivars with adequate resistance to late blight in both the foliage and tubers.

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