Assessment of Laboratory Methods for Evaluating Potato Tubers for Resistance to Late Blight

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ABSTRACT

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Two laboratory methods (whole tuber and tuber slice) were evaluated and compared with field assessment of potato tubers for resistance to late blight caused by *Phytophthora infestans*. Altogether, the resistance responses of 20 cultivars and advanced selections were compared by the three methods. All three assays separated materials into resistant and susceptible groups. The majority of cultivars and advanced selections did not react in the same way within the field and tuber-slice assays but did react similarly within the whole-tuber assay. Some cultivars were susceptible in the field at harvest but were resistant in the whole-tuber assay. The differences may be due to the extent of lenticel and eye development during tuber formation. In contrast, other cultivars resistant in the field at harvest were susceptible in the whole-tuber assay. In this case, placement in the hill may affect whether or not the tuber is exposed to inoculum or whether aging of tubers during storage affects susceptibility to tuber blight. Our study shows that high levels of tuber resistance are available in certain commercial cultivars and advanced potato selections. For laboratory assessments to be reliable, however, both pre- and poststorage evaluations may be necessary.

Additional keyword: *Solanum*

In 1995, approximately 20,000 metric tons of potatoes (*Solanum tuberosum* L.) were produced in the United States (21). Of these, nearly 58% were stored for 2 months or longer. Because of the value, and consequently the potential for economic loss, the tuber-borne phase of late blight caused by the fungus *Phytophthora infestans* (Mont.) de Bary has become increasingly important. In addition, newly identified migrant genotypes of *P. infestans* (12), US-6, US-7, and US-8, have been shown to be more aggressive in potato tubers compared with the previously existing US-1 genotype (18).

The release of cultivars with resistance to the tuber blight phase of the disease could reduce losses both in the field and in storage, as well as limit the amount of potential inoculum overwintering in tubers. Recently, using a standard set of cultivars, we compared greenhouse and laboratory screening methods designed to evaluate foliar resistance to late blight (8). Foliar

resistance to late blight, however, does not always correlate with resistance in tubers (6,14,28,29). Thus, reliable tuber-specific assays for screening cultivars and *Solanum* germ plasm for late blight resistance in tubers are needed.

Assays utilizing whole tubers, tuber slices, and tuber pieces have been developed to identify germ plasm resistant to tuber blight (Table 1), and some studies have shown some degree of correlation between lab and field results (5,7,19,20,25). These assays have also provided information on a genotype's response to the infection process. For example, the penetration, infection, and colonization of the periderm and cortical tissues can be evaluated by the whole-tuber assay; whereas in the tuber-slice method, resistance to colonization and R-gene recognition occurs (6,22,26). Swiezynski et al. (26) reported for genotypes originating from wild species that resistance not associated with single dominant genes was expressed in whole tubers but not in potato slices. Based on several years of data using the tuber-slice method, Darsow (5) reported that the fungus pathotype, inoculum concentration, and year of testing could influence a genotype's reaction to infection, and that variability in the reaction of potato clones indicated environmental dependence on the expression of resistance.

This study was carried out to determine if tuber-slice or whole-tuber inoculation could be employed under laboratory conditions as a rapid and accurate screening tool for tuber blight resistance.

MATERIALS AND METHODS

Germ plasm selection and field evaluation. In 1995 and 1996, 20 cultivars and advanced clonal selections from the Pacific Northwest Tri-State potato breeding program were selected based on their tuber reaction to late blight under field conditions. The germ plasm chosen for this study represented a range of reactions to tuber blight, from susceptible to resistant, as well as several maturity classes.

Cultivars were planted in a randomized complete block design with three replications. Ten seed pieces weighing 70 to 100 g each were planted in single-row plots spaced 107 cm apart. At the time of planting, fertilizer (10N-34P) at 806.4 kg/ha was applied approximately 5 cm below the seed piece using a planter-mounted fertilizer injection system. Four plots were bordered on the outside by spreader rows of cv. White Rose, which is intermediate in foliage resistance to late blight (14). Once the onset of disease occurred, naturally infected leaves from adjoining field trials were placed in the spreader rows to ensure uniform inoculum dosage. Two weeks prior to harvest, vines were mowed or hand cut to initiate vine kill. Tubers were harvested by hand, and late blight ratings were made on 13 September 1995 and 19 September 1996 as percentage by weight of tubers with late blight.

Healthy potato tubers, harvested by hand in 1995, were stored for 8 months in closed paper bags in a 4.4°C cooler until used later in the laboratory assays in 1996. Healthy tubers harvested in 1996 were held similarly for 3 and 4 months in a seed storage room where the temperature ranged from 4.5 to 15.5°C.

Inoculum production. One isolate, 95WWA (US-11 [8,14]), was maintained on rye agar. Cultures grown for 10 to 14 days were used in the tuber-slice laboratory assays. Inoculum for the whole-tuber assay was produced on potato leaves or leaflets, inoculated with a suspension of 1×10^4 sporangia per ml, and incubated in a moist

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chamber at 20°C under 12 h of light (Philips Fluorescent TL70 or Philips 60W Fluorescent F48T12 and Philips Tungsten 60W) for 7 days. Leaves with sporulating lesions were washed with distilled water, the sporangia counted with a hemacytometer, and final sporangial concentrations adjusted as needed.

Tuber-slice assay. Tubers were scrubbed with dish soap and water, rinsed thoroughly with water, soaked in 5% sodium hypochlorite for 20 min, rinsed under running water for 20 min, dipped in 70% ethanol for 1 min, and dried in a laminar flow hood. Seven-mm-thick sections from the middle of a tuber were sliced with a sterilized knife. The tuber slice was placed on top of two moistened filter papers in a plastic petri dish, and a 5-mm colonized agar plug of *P. infestans* was placed in the center of the tuber slice. Dishes were placed in plastic boxes lined with moist paper towels and incubated at 20°C in the dark for 7 days. Treatments were arranged in a randomized complete block design and replicated three times. Percent area of tuber slice colonized by *P. infestans* was estimated. The experiment was completed twice each year: 5 and 8 months (1996-1,

1996-2) and 3 and 4 months (1997-1, 1997-2) after harvest in 1995 and 1996, respectively.

Whole-tuber assay. Three tubers per cultivar were scrubbed under running tap water and placed on paper towels to dry. A sporangial suspension (8×10^4 per ml) was atomized onto each tuber, and tubers were turned to ensure complete coverage. Approximately 20 ml of the sporangial suspension was used for every 30 tubers. Tubers were placed in plastic boxes lined with moistened paper towels, and the boxes were then covered and placed in plastic bags to maintain high relative humidity. Boxes were stored for 7 days at approximately 18 to 20°C before being moved to a seed storage room for 4 weeks at 10°C. Based on our observations, the cooler temperature helped inhibit the growth of other tuber colonizers. Treatments were arranged in a randomized complete block design and replicated three times for 1996-1 and 1997-1, and four times for 1997-2. The tubers were evaluated visually for the presence or absence of external mycelium. Then 3- to 5-mm-thick peelings from each tuber were removed with a paring knife so that the percent in-

ternal surface area with dry brown corky rot could be estimated.

Data analysis. Field data (percent blighted tubers by weight) were transformed before analysis using square root of $x + 0.5$. Data were analyzed by analysis of variance (ANOVA) for differences between years, cultivars, and cultivar by year. If there was a significant *F* value, then means were separated by Fisher's least significant difference (LSD) (SAS Institute, Cary, NC). For the laboratory assays, nontransformed values for percent symptoms were analyzed for differences between years, tests within years, cultivars, cultivar by year interactions, and cultivar by test within year using ANOVA for 15 cultivars present in all tests. If *F* values were significant, means were separated by LSD. A separate ANOVA also was completed for each test, and if the *F* value was significant, means were separated by LSD.

RESULTS

Field evaluations. The amount of tuber blight at harvest was twofold higher in 1995 than in 1996. Foliage blight, as measured in the border spreader rows of White Rose, was 90 and 95% at the end of

Table 1. Summary of laboratory techniques used in screening tubers for late blight resistance utilizing tuber pieces (TP), tuber slices (TS) and whole-tubers (WT)

Tuber type	Inoculation	Environment ²	Rating/comments	Citation
TP, held at room temperature for 24-48 h, washed, surface sterilized, wounded	24-48 h after wounding 1 drop of 10,000 sporangia and zoospores/ml	96 h, petri dishes with moistened filter paper	Pieces were cut, measured fungal invasion through periderm	7
TS, held at room temperature for 24 h, washed, surface sterilized, 1 cm thick	10 µl of 20,000 zoospores/ml	7 days at 19°C, petri dishes with filter paper, dark	1-5 scale where 1 = resistant, 5 = susceptible	2
TS, 11 mm thick	Filter paper, zoospore suspension, after 24 h turned	7 days at 18-19°C	1-9 scale where 9 = no symptoms, 1 = fully colonized	5
TS, 5 double slices, each slice 10 mm thick	2,500 sporangia/50 mm ³ between slices	6 days at 16°C, high humidity, dark	Surface mycelium, 1-9 scale where 9 = no mycelium	26
WT	Sprayed	2 weeks at 15°C, high humidity	Percent disease	20
WT, US no. 1 grade	Sporangia sprayed on surface	1 day at 20°C, high humidity, then 14-15 d at 20°C, low humidity	Amount of tuber invaded, 0-5 scale	6
WT, 4 cm or greater in diameter	15,000 sporangia and zoospores/ml	6 & 14 days at 15°C, plastic boxes, peat & foam sheet	Amount necrotic area	19
WT, wounded	Sprayed, 10,000 zoospores/ml	18 h at 15°C, high humidity, then 13 days at 20°C, 90% RH, tubers placed on trays with wire bottoms	Large-scale production of diseased tubers, evaluated for the presence of other tuber-colonizing pathogens	32
WT	Dipped for 1 min, 5,000 sporangia/ml	35 days at 20°C, moist peat in plastic boxes, dark		9
WT, 10 tubers per progeny	40,000 zoospores/ml, complex race	24 h at 15°C, 100% RH, then 8 days at 12-18°C	Number of infected tubers	31
WT, 5 tubers/test, wounded crown end with 16 pins, 2 mm deep	24 h after wounding, sprayed with 2,500 sporangia/50 mm ³	14 days at 16°C, high humidity, dark	Average of surface and internal decay, graded on 1-9 scale, 9 = no damage	26
WT, stored 1 month, 80g +/-20 g, washed, blotted dry	Dipped for 1 min, 1,250 sporangia/ml	24 h at 18°C, high humidity, blotted dry, moved to open tray 20 weeks	Examined overwintering of metalaxyl resistant isolates	16
WT, wounded at bud end	Injected with homogenized suspension, wounds covered with Parafilm	7 days at 13°C, 87-92% RH	Tubers cut lengthwise, percentage of area affected, examined relative aggressiveness of <i>P. infestans</i> genotypes	18
WT, wounded	10,000 sporangia/ml, dip for 3 min	60 days at 5°C, 95% RH	Surface area of tuber affected, 0-4 scale where 0 = 0%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, and 4 = >50%	23

² RH = relative humidity.

the season for 1995 and 1996, respectively. There was a highly significant ($P = 0.0001$) cultivar by year interaction for tuber blight (Table 2). This indicated that tubers of the cultivars and advanced selections did not necessarily respond in a similar way between field studies in 1995 and 1996. For example, advanced selection Awn85540-1 and Katahdin had lower tuber blight ratings, and Ranger Russet, Elba, and TX1229-2RU had higher tuber blight ratings in 1995 than in 1996 (Table 3). Tubers of the cultivars and advanced selections could be separated into resistant and susceptible groups both years based on the transformed percent-by-weight of blighted tubers.

Tuber-slice assay. Results from two of the four tuber-slice assays are presented in Table 3. When all results from each of the four experiments were combined, there was a highly significant difference ($P = 0.0001$) among the cultivars for percent colonization, but there also was a highly significant ($P = 0.0001$) difference between years, tests within years, and cultivar by test within years (Table 2). The replicate within year by test interaction was also significant ($P = 0.03$). This indicated that tuber slices of the cultivars and advanced selections did not react similarly either between tests or between years, and there was variation within tests. Each assay was then analyzed separately, and the means for each assay were 68.3, 57.9, 18.3, and 43.9% colonization for 1996-1, 1996-2, 1997-1, and 1997-2, respectively. There was a significant difference in the amount of a tuber slice that was colonized among the cultivars and advanced selections in three of the four assays.

Whole-tuber assay. Results from two of the four whole-tuber assays are presented in Table 3. Fifteen cultivars and advanced selections responded similarly across tests and years (Table 2). There was a range of responses from resistant to highly susceptible in each assay. The overall test means from the three assays were 41.7, 50.0, and 20.3 for 1996-1, 1997-1, and 1997-2, respectively. However, the tests differed from one another significantly ($P = 0.001$). Two advanced selections were inconsistent

in their responses across tests: Awn85510-2 was more susceptible by about 50% in whole-tuber assay 1997-1 than in 1996-1, and A84118-3 was more susceptible in whole-tuber assay 1996-1 than in 1997-1 (Table 3).

DISCUSSION

The resistance responses of tubers in some of the cultivars and advanced selections planted in the field were not the same in 1995 and 1996, as indicated by a highly significant cultivar by year interaction. Therefore, we did not correlate the field response between years nor the laboratory methods with the field results. Stewart et al. (25) also reported cultivar by harvest date and cultivar by year interactions when tubers were evaluated for late blight in field trials.

The environmental component of variation is greater for tuber blight than for foliage blight (24). Dowley et al. (10) emphasized that the rating of tuber resistance in the field is "merely a guide," as field results may be conditioned by several factors. Timing of infection and distribution of inoculum can vary greatly from year to year and lead to disease escape. Tuber depth, distribution, and orientation in the hill; soil type (17); severity of the foliar epidemic; timing and amount of rainfall to wash sporangia into the soil (11, 27); and soil temperature can all influence the incidence and severity of tuber blight at harvest. Tuber blight ratings completed at harvest may only detect those infections that occurred 1 to 2 weeks prior to evaluation, i.e., when enough time has passed to allow for symptom development. Late infections that occur just prior to harvest may be undetectable because they are not yet visible. Tubers infected in the field early in the season may decompose by the time of tuber rating (W. Stevenson, *personal communication*; 30). The reasons outlined may account for some of the discrepancies between our 1995 and 1996 field tests and will continue to affect field assessments of tuber blight resistance.

Russet Burbank consistently has had relatively low tuber blight ratings in the

field at Mount Vernon (14; Table 3) but was one of the more susceptible cultivars (Table 3) when tested in the whole-tuber laboratory assay. Ranger Russet was relatively resistant in the field in 1996 but was susceptible in the 1995 field study and the whole-tuber assay. The physical placement of tubers in the hills, an architectural characteristic of different cultivars, can facilitate escape from infection (17). Resistance of Russet Burbank and Ranger Russet tubers in the field could be the result of depth in the tuber set or some other mechanism of escape. Substantial economic losses from tuber blight have occurred in these two cultivars after storage (14,15; D. Corsini, *personal communication*).

In contrast, Brador, Awn85542-1, and Awn85540-1 were susceptible in our field tests but resistant in the laboratory assays 3 to 8 months poststorage. Brador is a late-maturing cultivar (27), as are the other two advanced selections. Adams (1) reported that lenticels became more resistant to infection by *P. infestans* as tubers matured in the field. He proposed that cork barriers had formed and the cells beneath the lenticels had become suberized. Grinberger et al. (13) reported that young, immature tubers are more susceptible to tuber blight than are older, mature tubers.

The two laboratory assays compared in this study successfully separated resistant from susceptible cultivars. Due to the variation within and between individual experiments, however, the tuber-slice assay may not be suitable for screening large numbers of cultivars, advanced selections, or germ plasm for tuber resistance. Darsow (5) reported large amounts of variation in the tuber-slice assay by as many as six out of nine values in repeated experiments and recommended that germ plasm be tested for 3 years prior to a recommendation. While the whole-tuber assay requires a greater number of tubers than the tuber-slice method, it is more reliable; the cultivars and advanced selections we tested responded similarly in each repetition of the assay. We noted that many of the initial sites of infection were associated with lenticels or eyes. This is in agreement with

Table 2. Analysis of variance for field, tuber slice and whole tuber laboratory assays comparing cultivars and advanced selections, respectively, for response to inoculation with *Phytophthora infestans*^x

Source	Field assays			Tuber-slice assays ^y			Whole-tuber assays ^y		
	df	Mean square	F	df	Mean square	F	df	Mean square	F
Year	1	11.1	19.81***	1	46,095.8	82.63**	1	1,326.9	1.66
Block	5	1.10	1.96						
Test (year)	...	...	...	2	8,442.9	15.13**	1	9,289.9	11.63*
Cultivar × block	44	0.58	1.04	...	...	...	...	...	...
Block (year by test)	...	...	...	8	1,131.3	2.03*	11	455.8	0.57
Cultivar	19	9.59	17.13**	19	2,476.3	4.44**	14	3,663.4	4.59**
Cultivar × year	19	3.36	6.00**	19	897.9	1.61	14	851.5	1.07
Cultivar × test (year)	...	...	...	27	1,598.8	2.87**	14	934.2	1.17

^x Field tests were done in 1995 and 1996 and included 20 cultivars and advanced selections; laboratory assays in 1996 and 1997 compared 15 cultivars and advanced selections.

^y The tuber-slice assay was performed four times, and the whole-tuber assay was performed three times.

^z Numbers followed by one asterisk are significant at $P \leq 0.05$; numbers followed by two asterisks are highly significant at $P = 0.0001$.

Pathak and Clarke's (22) study, where they reported that the outer layers of the cortex, in some potato cultivars, were very resistant to colonization by *P. infestans*. They did note that this was not a permanent feature of the tissue, for this effect was reduced over time during storage. The whole-tuber assay was easier to set up and evaluate than the tuber-slice method under our conditions. In fact, a variation of this method was used to produce 8 tons of blighted tubers (32).

The age and maturity of tubers is reported to affect the response to inoculation with *P. infestans* in several laboratory studies (2,4,20,23). Bhatia and Young (2) reported that one cultivar was resistant when newly harvested but later was susceptible following storage; cultivars susceptible at harvest remained susceptible following storage. Chalenko et al. (4) reported a decline in resistance following storage due to changes in the ability of the tuber to produce wound periderm. In a laboratory test, Platt (23) reported more disease in October inoculations than in December and February in tubers taken from storage. Conversely, Boyd and Henderson (3) reported that resistance to late blight increased with maturity of the tubers.

From the results of the whole-tuber assay, there are sources of tuber resistance

available in certain commercial cultivars and advanced potato selections. Of those tested, in both field and whole-tuber assays, advanced breeding selections Awn85542-1 and Awn86514-2 were moderately resistant when evaluated with *P. infestans* US-11. Late-maturing cultivar Brador and advanced selections AO85165-1 and Awn85542-1 were resistant in the whole-tuber assays, but our field results indicate that the tubers may be susceptible to late blight, possibly because they were immature in the field at harvest.

Field evaluations regarding tuber resistance may continue to be important, in that physical placement of tubers in hills could be part of the cultivar response to the likelihood of tuber infection, and will need continual monitoring as new cultivars become available. Our conclusion from this study is that evaluation for tuber blight resistance also requires two separate laboratory assays. The first inoculation of potatoes with *P. infestans* is performed on whole tubers collected at the time of vine kill or at harvest to evaluate the effects of periderm development, skin set, or tuber maturity on the expression of resistance to late blight. The second inoculation is performed following storage of tubers collected at harvest to examine the effects of aging. At this time, the whole-tuber assay

is better suited for this purpose than the tuber-slice assay. It should be noted that, due to conflicting reports on physiological maturity from other studies, the final results of this type of testing may be cultivar dependent. However, producers could find this information useful in managing their fields and storages with regard to specific cultivars. Ideally, potato cultivars in the future will need to express resistance early in tuber development and then maintain high levels of resistance throughout the harvest and storage period.

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Table 3. Field and laboratory ratings for tuber blight resistance to *Phytophthora infestans* (US-11) in 20 potato cultivars and advanced selections from the Pacific Northwest Tri-State potato breeding effort

Cultivars and adv. selections	Field ratings ^a		Tuber-slice assays ^v		Whole-tuber assays ^w	
	1995	1996	1996-1	1997-2	1996-1	1997-1
Brador	9.4 ef	1.7 ab	25.0	50.0 cd	NT ^x	0.0 a
AO85165-1	15.4 f-h	11.1 f	100.0	41.7 cd	2.5 ab	3.7 a
AWN85542-1	0.55 a	3.0 a-e	56.7	NT	8.3 a-c	16.7 ab
AWN85540-1	1.3 ab	8.6 c-f	68.3	11.7 ab	0.0 a	31.7 a-c
AWN86514-2	0.1 a	0.6 a	30.0	8.3 ab	18.3 a-c	31.7 a-c
A84118-3	0.3 a	0.4 a ^y	56.7	NT	70.0 fg	34.2 a-c ^y
A81473-2	4.9 b-e	2.4 a-c	91.7	80.0 e-g	40.0 b-f	36.7 a-c
A86102-2	33.0 jk	8.1 ef	50.0	28.3 bc	51.7 d-g	40.0 a-c
Atlantic	0.0 a	1.9 ab	40.0	NT	83.3 g	43.3 a-c
Kennebec	7.1 de	7.3 c-f	NT	0.0 a	NT	50.3 a-c
Ranger Russet	22.8 h-j	3.5 a-e	100.0	83.3 fg	NT	57.5 bc
TX1229-2RU	45.4 k	6.6 b-f	95.0	86.7 g	45.0 c-g	63.3 bc
AO82611-7	0.8 ab	1.8 ab	75.0	1.7 a	73.3 fg	66.7 bc
Katahdin	1.6 a-d	6.5 b-f	NT	43.3 cd	20.0 a-e	66.7 bc
COO83008-1	2.7 a-d	1.8 ab	58.3	73.3 e-g	NT	70.0 c
Elba	10.3 e-g	2.6 a-d	85.0	60.0 de	NT	70.0 c
Shepody	19.0 g-i	21.2 g	60.0	NT	50.0 d-g	71.7 c
Russet Burbank	1.3 a-c	0.1 a	86.7	6.7 ab	80.0 g	75.0 c
AWN85510-2	2.3 a-d	0.2 a	61.7	63.3 d-f	13.3 a-d	76.7 c
ATX84706-2RU	28.1 ij	8.4 d-f	80.0	63.3 d-f	56.7 e-g	83.3 c
Mean	10.1	4.5	68.3	43.9	41.7	50.0
CV ^z	60.2	82.9	40.0	30.7	56.3	66.5

^a Field tuber blight ratings are percentage by weight of blighted tubers in a plot at harvest; percent data transformed before analysis using square root of $x + 0.5$. Numbers followed by the same letter are not significantly different from each other as indicated by LSD ($P \leq 0.05$) of the transformed data. Data back-transformed for presentation.

^v Tuber slice ratings are percent colonization of a tuber slice; data were not transformed prior to analysis. The *F* statistic was not significant ($P = 0.09$) for tuber slice assay 1996-1. The two assays with the highest mean percent tuber slice colonization of the four test results are presented.

^w Whole-tuber ratings are percent surface with symptoms of a whole tuber; data were not transformed prior to analysis. 1997-2 is not presented due to a low mean percent tuber colonized.

^x Not tested.

^y Average of entries from two different seed lots in 1996.

^z Coefficient of variation.

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