SCREENING TUBER-BEARING *SOLANUM* SPECIES FOR RESISTANCE TO *HELMINTHOSPORIUM SOLANI*

D. A. Rodriguez, G. A. Secor, N. C. Gudmestad, and K. Grafton[1]

Abstract

Silver scurf, caused by *Helminthosporium solani*, is an important disease of table stock and processing potatoes, for which few management strategies exist. Two hundred-twelve accessions of tuber-bearing *Solanum* species were screened for their response to *H. solani*. Tubers were inoculated in the laboratory with a spore suspension, incubated for 1 mo, and evaluated for infection using the number of conidiophore groups per square millimeter of sporulating tuber surface. Tubers with relatively low sporulation in the laboratory were retested using natural inoculum present in potato storages and assessed for infection. There were significant differences ($P < 0.05$) between accessions with both methods of inoculation. Some accessions of *Solanum demissum, S. chacoense, S. acaule, S. stoloniferum, S. oxycarpum,* and *S. hondelmannii* consistently demonstrated low sporulation in laboratory and storage, suggesting partial resistance. Both methods of inoculation, laboratory and storage, were found to be correlated (ranging from $r = 0.582$, $P = 0.006$; to $r = 0.925$, $P < 0.003$).

Compendio

La costra plateada de la papa, producida por *Helminthosporium solani*, es una enfermedad importante en papas para consumo fresco y procesamiento, con limitadas prácticas de manejo. Se evaluaron 212 entradas de *Solanum* tuberíferos por su respuesta a *H. solani*. Los tubérculos fueron inoculados en laboratorio con una suspensión de esporas, incubados por 1 mes, y evaluados por infección usando el número de grupos de conidióforos por milímetro cuadrado de superficie de tubérculo con esporulación. Los tubérculos con baja esporulación en el laboratorio fueron re-evaluados usando inóculo natural presente en almacenes de papa y analizados por infección. Se encontraron diferencias significativas ($P<0.05$) entre las entradas con los dos metodos de inoculación. Algunas entradas de S. *demissum, S. chacoense, S. acaule, S. stoloniferum, S. oxycarpum*, y *S. hondelmannii* mostraron consistentemente reducida esporulación en laboratorio y en almacen, lo cual sugiere una

[1]Research Assistant, Professor and Associate Professor of Department of Plant Pathology, and Professor of Department of Plant Science, North Dakota State University, Fargo, ND 58105. Permanent address of senior author - Fondo Nacional de Investigaciones Agropecuarias, Trujillo, Venezuela.

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resistencia parcial. Se encontró que ambos metodos de inoculación, laboratorio y almacen, estaban correlacionados (rango de r = 0.582, $P = 0.006$; a r = 0.925, $P < 0.003$).

Introduction

Silver scurf has become an important disease of fresh and processing potatoes (23, 35). During the last few years fresh and processing potatoes have been rejected due to heavy infection with silver scurf (35). The disease is caused by the imperfect fungus *Helminthosporium solani* Dur. and Mont. which is generally believed to be a seed-borne pathogen attacking only the periderm of potato tubers (3, 18). Some evidence, however, suggests the ability of *H. solani* to survive in the soil for short periods (20, 27).

The fungus spreads by means of conidia that germinate via a germ tube, "appressorium-like structure", and hyphae which can grow on or in the periderm (11). Hyphae penetrate either through lenticels or directly through the epidermis and grow within the peridermal cells. Eventually the hyphae shorten, thicken and mass together to form rudimentary stromata from which upward-growing groups of conidiophores rise to the outer surface of the tuber (11). The number of conidiophores per stroma is variable. Each conidiophore bears up to 20 or 30 conidia which are borne in a whorled fashion (11, 24).

In storage, the fungus sporulates and infects tubers, increasing the amount of potential inoculum as storage continues (32). The disease apparently had been controlled by benzimidazole fungicide treatment of seed and commercial stock entering storage (16), even though silver scurf was not the target disease. The appearance of resistance to benzimidazole fungicides (13, 25, 33) and the absence of an alternative, limit fungicidal control options.

Some cultivars were thought to be less susceptible to silver scurf (3, 15, 19), however, those cultivars frequently show high disease severity. In the present, the search for resistant cultivars has not been successful (28, 31). Potato cultivars grown in the United States have a narrow genetic base because most are derived from a common ancestor, the cv. Rough Purple Chili (2, 30). Cultivated and tuber-bearing wild *Solanum* species comprise an unexploited but potentially rich source of genetic diversity. Interspecific crosses are useful for cultivar improvement for resistance to diseases such as late blight, Verticillium wilt, early blight, Fusarium dry rot, wart, ring rot, and common scab (1, 8, 9, 10, 22, 30). Resistance to other skin diseases such as common scab and wart suggests the existence of resistance to silver scurf in potato germplasm. No wild or cultivated species, potentially useful to breeding programs, have been evaluated for silver scurf resistance.

This study was initiated to determine whether tuber-bearing *Solanum* species from the collection of the National Research Support Program-6, Sturgeon Bay, WI, respond differently to *Helminthosporium solani.*

Materials and Methods

Evaluation in Laboratory

Species —Three hundred-thirty accessions, comprising 82 *Solanum* species, were obtained as family tubers from the National Research Support Program-6, Sturgeon Bay, WI. Accessions were propagated in the greenhouse at 27±2 C (day) and 24±2 C (night), with natural sunlight during spring and summer and supplemental light at -12,000 $\mu E.m^{-2}\cdot s^{-1}$ during fall and winter. Harvested tubers were combined and stored at 3 to 4 C until inoculation, which was performed approximately 1 mo later. Two hundred-twelve accessions (Table 1) produced tubers and were used in the tests. Minitubers of cv Red Norland, Norchip, or Russet Burbank were produced either from tissue culture plantlets or plant cuttings grown in the greenhouse and used as positive (inoculated) and negative (sprayed with water only) controls in every test.

Inoculum —Four isolates of *Helminthosporium solani,* HSWS04, HSNB15, HSND18, and HSND24 (31), were grown on modified V8 medium containing 1.5% V8 juice, 2% agar (Difco Bacto-Agar) and 1.5 g $CaCO_3$ per liter and adjusted to pH 6.8. Cultures were incubated at 23 C in the dark for 1 or 2 mo before inoculation. Inoculum was prepared just before use as an aqueous suspension of 2.5 x 10^4 conidia per ml plus 150 µl/l of Tween 20.

Inoculation and Incubation —Tubers were inoculated with 0.9 ml of the spore supension per tuber using a hand-held plastic sprayer. Five tubers of each accession were inoculated with isolate HSNB15 in the first trial. Those accessions with low infection or no apparent infection were regrown and inoculated (up to 10 tubers) with a suspension of 2.5 x 10^4 conidia/ml of isolates HSWS04, HSNB15, HSND18, and HSND24.

Some accessions were repeated a third time. Positive and negative inoculation controls of the cultivars previously mentioned were included in each test. After inoculation, tubers were incubated for 1 wk in an intermittent mist chamber using a 12-sec duration at 30-min intervals. Tubers were placed in humid chambers for 4 wk. Humid chambers consisted of plastic boxes lined with wet paper towels and covered with aluminum foil.

After 1 mo, tubers were evaluated for infection by rating sporulation of *H. solani* on the tuber surface. Sporulation was observed to occur in patches with visually varied density of sporulation in the patches among accessions. Therefore, the surface of each tuber was scanned with a stereomicroscope at l0x magnification to find sporulating patches. When a sporulating patch was found, magnification was changed to 40x, and the number of conidiophore groups per field of view (NCV) was counted. The NCV was converted to the number of conidiophore groups per mm^2 (c/mm^2). Up to three random counts per tuber were taken, and the averaged c/mm^2 per tuber used for the analysis.

TABLE 1.—*Accessions of* Solanum *species evaluated for their responses to* Helminthosporium solani.

Species	Plant Introduction Number	Species	Plant Introduction Number	Species	Plant Introduction Number
S. albornozii	498206	*S. ambosinum*	365316	*S. demissum*	230579
S. acaule	186176	*S. ambosinum*	498207	*S. demissum*	310961
S. acaule	255501	*S. ambosinum*	498213	*S. demissum*	365380
S. acaule	310986	*S. avilesii*	498091	*S. demissum*	365382
S. acaule	472779	*S. brachycarpum*	230459	*S. demissum*	365391
S. acaule	473313	*S. brachycarpum*	243344	*S. doddsii*	442690
S. acaule	473326	*S. brachycarpum*	498021	*S. fendleri*	225661
S. acaule	473519	*S. bulbocastanum*	243345	*S. fendleri*	275158
S. acaule	498196	*S. bulbocastanum*	275185	*S. fendleri*	458409
S. andigena	160215	*S. brachistotrichum*	249927	*S. fendleri*	458422
S. andigena	161131	*S. brachistotrichum*	255529	*S. fendleri*	498239
S. andigena	214429	*S. brachistotrichum*	497993	*S. gourlayi*	320322
S. andigena	214443	*S. bukasovii*	365304	*S. gourlayi*	473055
S. andigena	230497	*S. bukasovii*	365353	*S. gourlayi*	473073
S. andigena	232041	*S. bukasovii*	458379	*S. gourlayi*	473091
S. andigena	233337	*S. bukasovii*	498222	*S. gourlayi*	473184
S. andigena	234592	*S. canasense*	246533	*S. gourlayi*	473342
S. andigena	243371	*S. canasense*	283074	*S. gourlayi*	500048
S. andigena	243377	*S. canasense*	442695	*S. gourlayi*	500024
S. andigena	243429	*S. canasense*	458377	*S. gourlayi*	500027
S. andigena	243436	*S. capsicibaccatum*	473458	*S. huancabambense*	458400
S. andigena	243452	*S. chacoense*	133073	*S. hjertingii*	186559
S. andigena	246547	*S. chacoense*	133659	*S. hjertingii*	251067
S. andigena	246554	*S. chacoense*	133713	*S. hondelmannii*	498281
S. andigena	258862	*S. chacoense*	195183	*S. hannemanii*	498405
S. andigena	258879	*S. chacoense*	230583	*S. hougasii*	239423
S. andigena	258885	*S. chacoense*	275136	*S. infundibuliforme*	472893
S. andigena	258929	*S. chacoense*	320289	*S. infundibuliforme*	472895
S. andigena	279291	*S. chacoense*	458312	*S. infundibuliforme*	472909
S. andigena	280888	*S. chacoense*	472819	*S. incamayoense*	473089
S. andigena	280919	*S. chacoense*	472827	*S. iopetalum*	275181
S. andigena	280948	*S. chacoense*	472828	*S. jamesii*	279278
S. andigena	280985	*S. chacoense*	472830	*S. jamesii*	458424
S. andigena	281001	*S. chacoense*	498317	*S. jamesii*	498407
S. andigena	281017	*S. chacoense*	500042	*S. kurtzianum*	442678
S. andigena	281036	*S. clarum*	275202	*S. kurtzianum*	458327
S. andigena	281078	*S. candolleanum*	498226	*S. kurtzianum*	472923
S. andigena	281192	*S. candolleanum*	498313	*S. kurtzianum*	472935
S. andigena	281200	*S. cardiophyllum*	184766	*S. kurtzianum*	472951
S. andigena	281243	*S. cardiophyllum*	251759	*S. kurtzianum*	472955
S. andigena	285008	*S. cardiophyllum*	283062	*S. kurtzianum*	472958
S. andigena	292097	*S. demissum*	160212	*S. kurtzianum*	473419
S. andigena	307743	*S. demissum*	161153	*S. kurtzianum*	498420

Species	Plant Introduction Number	Species	Plant Introduction Number	Species	Plant Introduction Number
S. andigena	324456	*S. demissum*	161166	*S. leptophyes*	320340
S. andigena	473250	*S. demissum*	161180	*S. leptophyes*	473451
S. andigena	473259	*S. demissum*	161365	*S. laxissimum*	498252
S. andigena	473270	*S. demissum*	161725	*S. matehualae*	498050
S. andigena	473507	*S. demissum*	201852	*S. microdontum*	218224
S. andigena	500057	*S. demissum*	205515	*S. microdontum*	320315
S. andigena	500058	*S. demissum*	218047	*S. microdontum*	458354
S. microdontum	473362	*S. pinnatisectum*	275235	*S. stoloniferum*	473534
S. microdontum	500035	*S. papita*	275229	*S. stoloniferum*	498053
S. microdontum	500064	*S. raphanifolium*	473465	*S. stoloniferum*	498287
S. megistacrolobum	473123	*S. sucrense*	290959	*S. tarijense*	217457
S. megistacrolobum	473149	*S. sanctae-rosae*	283089	*S. tarijense*	458366
S. megistacrolobum	473163	*S. sogarandinum*	365360	*S. tarijense*	473220
S. multidissectum	210052	*S. schenckii*	498410	*S. tarijense*	473242
S. multiinterruptum	275272	*S. spegazzinii*	472966	*S. tarijense*	500043
S. neorossii	473529	*S. spegazzinii*	472975	*S. tuberosum*	245935
S. oplocense	435080	*S. spegazzind*	473424	*S. toralapanum*	320302
S. oplocense	473188	*S. spegazzinii*	500051	*S. trifidum*	255536
S. oplocense	473189	*S. sparsipilum*	265871	*S. trifidum*	.255539
S. oplocense	498271	*S. sparsipilum*	458387	*S. verrucosum*	255544
S. oxycarpum	498272	*S. sparsipilum*	498305	*S. verrucosum*	320344
S. phureja	230586	*S. stenotomum*	234015	*S. verrucosum*	498010
S. phureja	320394	*S. stoloniferum*	160372	*S. venturii*	218220
S. polyadenium	347770	*S. stoloniferum*	161171	*S. vernei*	320329
S. polyadenium	498036	*S. stoloniferum*	161178	*S. vernei*	320332
S. polytrichon	255546	*S. stoloniferum*	253219		
S. polytrichon	279280	*S. stoloniferum*	275244		
S. polytrichon	279308	*S. stoloniferum*	275246		
S. pinnatisectum	253214	*S. stoloniferum*	365394		

Evaluation in Storage

Some of the accessions showing very low infection after two or three laboratory trials were exposed to the natural inoculum present in either a processing (10 to 15 C and 80 to 90% relative humidity) or table stock (3 to 5 C and 80 to 90% relative humidity) storage. Five tubers per accession were placed in mesh bags and either suspended in the storage hallway or placed on the potato pile and left for 1 or 4 mo. Greenhouse produced minitubers of cv Red Norland free of *H. solani* were used as positive (exposed) and negative (covered with a plastic bag) controls. Tubers were then recovered and incubated in the laboratory in humid chambers for 4 wk. Infection was evaluated as described previously .

Data Analysis

Analysis of variance was performed in every test using the general linear model procedure (SAS Institute Inc., Cary, NC). Some accessions had fewer tubers because they were not available or they rotted during incubation, therefore means were compared using the least-squares means procedure. Repeated experiments with the same accessions were combined for analysis when they showed homogeneous variances. Correlation analyses were performed on laboratory and storage methods to determine whether laboratory tests can be used to predict the reaction of the germplasm with natural inoculum.

Results

There was a significant ($P < 0.05$) differential response of the accessions to infection by *H. solani*. A group of 24 accessions and the cv Red Norland evaluated in the same repetitions in laboratory and storage are reported here (Table 2). Results of the total number of accessions evaluated are available on request from the authors. Sporulation ranged from 0.033 to 1.551 c/mm^2 in laboratory and from 0.549 to 6.407 c/mm^2 in storage (Table 2). Accessions with consistently low sporulation in laboratory and storage included *S. demissum* (PI's 161153, 160212, 218047, and 365391), *S. oxycarpum* (PI 498272), *S. acaule* (PI 310986), *S. stoloniferum* (PI's 160372, and 498287), *S. chacoense* (PI 498317), and *S. hondelmannii* (PI 498281).

Accessions with consistently high sporulation in laboratory and storage were *S. chacoense* (PI 133713), *S. microdontum* (PI's 500035, 500064, and 218224), *S. vernei* (PI 320332), *S. multiinterruptum* (PI 275272), and *S. iopetalum* (PI 275181) (Table 2). However, some accessions (*S. polyadenium,* PI 347770; *S. acaule,* PI 186176; *S. hannemanii,* PI 498405; *S. andigena,* PI's 500058 and 246554; *S. stoloniferum,* PI 275246; and *S. vernei,* PI 320329) had inconsistent results (Table 2). They showed relatively low sporulation in the laboratory but high sporulation in storage. Nonetheless, methods of inoculation, laboratory and storage, were found to be highly correlated among the species tested (Table 2). The correlation coefficient between sporulation found in the laboratory and the processing storage was $r = 0.691$ ($P < 0.001$), and between the laboratory and the table stock storage was $r = 0.616$ ($P = 0.001$).

Similar results were observed for the rest of accessions evaluated (data not show). Correlation coefficients between laboratory and storage tests among those other accessions ranged from $r = 0.582$ ($P = 0.006$) to $r = 0.925$ ($P < 0.003$).

Discussion

This is the first report of screening tuber-bearing *Solanum* species against *H. solani*. These tests demonstrate that accessions of wild and cultivated

TABLE 2.—Helminthosporium solani *sporulation on selected accessions of tuber-bearing* Solanum *species after laboratory and natural inoculation.*

Species/cultivar	Plant Introduction Number	Mean number of conidiophore groups per mm² of tuber surface (c/mm²)[a]		
		Lab.[b]	Stor.1[c]	Stor.2[d]
S. demissum	161153	0.033 a	0.839 ab	0.549 ab
S. demissum	160212	0.043 a	0.702 a	0.332 a
S. demissum	218047	0.053 a	0.357 a	0.382 a
S. polyadenium	347770	0.054 a	1.741 b	1.587 bc
S. acaule	186176	0.056 a	1.224 ab	1.076 b
S. hannemanii	498405	0.075 a	3.264 c	0.397 ab
S. oxycarpum	498272	0.093 a	0.583 a	0.310 a
S. acaule	310986	0.097 a	0.454 a	0.199 a
S. andigena	500058	0.155 a	4.210 c	1.199 b
S. stoloniferum	160372	0.157 a	0.114 a	0.320 a
S. stoloniferum	498287	0.158 a	0.474 a	0.183 a
S. chacoense	498317	0.176 a	0.496 a	0.291 a
S. demissum	365391	0.191 a	0.120 a	0.042 a
S. stoloniferum	275246	0.237 a	2.669 b	0.343 a
S. hondelmannii	498281	0.283 a	0.836 ab	0.296 a
S. vernei	320329	0.360 a	1.113 ab	2.041 c
S. andigena	246554	0.430 a	2.751 b	3.378 e
S. microdontum	218224	0.638 ab	1.748 b	1.473 bc
S. iopetalum	275181	0.698 ab	2.170 b	2.558 cde
S. microdontum	500064	0.706 ab	3.258 c	2.915 de
S. multiinterruptum	275272	0.791 ab	3.953 c	2.367 cd
S. vernei	320332	0.898 ab	3.665 c	3.639 e
S. microdontum	500035	1.058 ab	3.942 c	3.163 e
Red Norland		1.527 b	6.407 d	NE[f]
S. chacoense	133713	1.551 b	4.213 c	1.030 ab

[a]Means within each column with the same letters are not significantly different according to a least square means test (P=0.05). Correlation between Lab and Stor. 1 r=0.691, P<0.001; and between Lab and Stor. 2 r=0.616, P=0.001.

[b]Combining two laboratory tests.

[c]Accessions were exposed four months to inoculum present in a processing potato storage. Temperature ranged from 10 to 13 C and relative humiditiy from 80 to 95%.

[d]Accessions were exposed four months to inoculum present in a table stock potato storage. Temperatures ranged from 3 to 5 C and relative humidity from 80 to 95%.

[f]Not evaluated because of tuber rotting during incubation.

species of potato respond differently to the infection by the silver scurf pathogen. Significant differences were found among accessions of the same species. *Solanum demissum, S. oxycarpum, S. acaule, S. stoloniferum, S. chacoense,*

and *S. hondelmannii* were among the species with accessions with consistently low fungal sporulation. *Solanum microdontum, S. multiinterrruptum, S. iopetalum,* and *S. vernei* had accessions with consistently high fungal sporulation. Control cultivars inoculated with *H. solani* resulted in fungal sporulation equal or greater than several accessions.

Species such as S. *demissum, S. acaule, S. chacoense,* and *S. stoloniferum* have already been introgressed successfully into North American cultivars (30) and are listed as conferring resistance to various biotic and abiotic abnormalities (10). *Solanum demissum,* for example, has been used for its contribution of R genes for resistance to races of late blight (6). It is listed as a source of resistance to soft rot *(Erwinia carotovora ssp. carotovora* (Jones) Dye and *E. carotovora* ssp. *atroseptica* (van Hall) Dye) (10), potato virus Y (9, 10), and Colorado potato beetle *(Leptinotarsa decemlineata* Say) (9).

Solanum acaule is resistant to bacterial ring rot *(Clavibacter michiganensis* ssp *sepedonicus* (Spieck & Kott) Davis et al.) (21, 22), potato virus X, potato leaf roll virus, potato spindle tuber viroid, potato cyst nematode *(Globodera rostochiensis* (Wollenweber) Mulvey & Stone), frost, heat, and drought (10). Several common cultivars with wild or cultivated species in their background include Atlantic (*S. chacoense),* BelRus (*S. demissum),* Chieftain (*S. acaule),* Cascade (*S. demissum, S. andigena),* Conestoga (*S. andigena, S. acaule, S. chacoense, S. fendleri, S. microndontum, and S. toralapanum),* Crystal (*S. andigena, S. demissum),* Norchip (*S. acaule),* Norking Russet (*S. acaule, S. chacoense),* Raritan (*S. demissum),* Viking (*S. acaule),* and Yukon Gold (*S. acaule)* (30). Some of these cultivars, however, are reported to be very susceptible to silver scurf (G. Secor, unpublished data). The reason may be that they were not selected for silver scurf resistance or perhaps that the resistance character was not present in the accessions used to produce the cultivar.

The tests in this study were based on the ability of *H. solani* to sporulate on the tuber surface, which is a direct indication of the compatibility between pathogen and host. Fungal sporulation, instead of disease symptoms, was used for the screening because of the great variability of periderm color and smoothness among the species, which made differenciation of natural periderm characteristics of the species from silver scurf symptom difficult. In addition, infection by *Colletotrichum atramentarium* (Berk. et Br.) Taub (syn. *C. coccodes* (Wallr.) Hughes) produces a similar symptom on the tuber periderm, which can be frequently confused with silver scurf symptoms (1). Observation of sporulation is the most effective method to avoid the possibility of evaluating response to the wrong pathogen.

Primary infection by *H. solani is* characterized by a profuse sporulation under appropriate temperature and relative humidity in all susceptible cultivars. As lesions develop and age, sporulation is reduced and restricted to the edge of the lesions (17). Sporulation, thus, is a sign of a successful establishment of the pathogen and of potential disease development. Percentage of

eye plugs with *H. solani* conidiophores was used by Hide and Adams (12) to study the relationship between seed infection and infection of progeny tubers at harvest and after storage. Sporulation also was used by Merida *et al.* (28) to evaluate cultivar resistance to silver scurf in the laboratory, even though they did not find differences in sporulation among the cultivars evaluated, and to compare the virulence of different isolates of *H. solani* (26).

A reduction in pathogen reproduction in its hosts is recognized as a component of resistance (34, 36, 37). Pathogen reproduction as a means to assess cultivar susceptibility is used commonly in a number of host-pathogen systems. Determining the number of sporulating pustules in cereal rust diseases (29), the *Verticillium dahliae* colony count in potato stem sap (5), the number of conidia of *Fusarium oxysporum* f. sp. *lycopersici* per gram of stem tissue (4), and the colony forming units per gram of stem tissue and fluorescing cells of *Clavibacter michiganensis* ssp *sepedonicus* with the indirect fluorescent antibody staining technique in potato (7, 21, 22), are just a few examples.

Retesting the accessions by exposing them to the potato storage air resulted in a convenient method of natural inoculation. The presence of *H. solani* conidia in storage has been demonstrated previously (14, 32). The great variability of *H. solani* genotypes as well as the amount of inoculum present in the storage, constitute a suitable way for verifying the results obtained in the laboratory. Infection in the table stock storage was lower than in the processing storage (Table 2). This can be explained by a reduced amount of inoculum in the table stock storage which has been observed in another study (Rodriguez *et al.*, unpublished), and has been associated with differences in temperature.

Since a better control of fungal genotype and inoculum concentration can be achieved with laboratory inoculation, we propose that laboratory tests should be used for a preliminary screening of a large number of entries and the storage test be used for confirmation responses identified in the laboratory. Using a qualitative method of evaluation, such as high, moderate, and low sporulation intensity, instead of a quantitative method (such as the c/mm^2), would surely improve the efficiency of screening large numbers of entries. Species identified as potentially resistant are now being crossed to commercial cultivars and advanced selections by the North Dakota potato breeding program.

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