Genetics of Resistance to *Puccinia graminis* f. sp. *secalis* in Barley Line Q21861

Yongliang Sun, Brian J. Steffenson, and Yue Jin

First and second authors: Department of Plant Pathology, North Dakota State University, Fargo 58105; and third author: Plant Sciences Department, South Dakota State University, Brookings 57007.
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ABSTRACT

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Barley line Q21861 (PI 584766) possesses *rpg4*, a recessive gene that confers resistance to pathotype Pgt-QCCJ of *Puccinia graminis* f. sp. *tritici*, the wheat stem rust pathogen. Q21861 also possesses resistance to *P. graminis* f. sp. *secalis*, the rye stem rust pathogen. To determine the genetics of rye stem rust resistance in this line, a doubled haploid (Q21861/SM89010) and three different F_3 (Steptoe/Q21861, Q21861/SM89010, and Q21861/Klages) populations derived from Q21861 were evaluated to isolate 92-MN-90 of *P. graminis* f. sp. *secalis* at the seedling stage. The number of resistant and susceptible progeny in the doubled haploid population fit a 1:1 segregation ratio, indicating that a single gene conferred resistance to the rye stem rust pathogen. This result was confirmed from the 1:2:1 segregation ratio of homozygous resistant, segregating, and homozygous susceptible F_3 families in the three other populations. The resistance gene was partially dominant, based on the infection types of F_1 plants from the cross Q21861/Steptoe. Data for reaction to *P. graminis* f. sp. *secalis* were compared with those obtained in response to *P. graminis* f. sp. *tritici* (pathotype QCCJ) on remnant progeny from all four populations. Resistance to *P. graminis* f. sp. *secalis* cosegregated with resistance to *P. graminis* f. sp. *tritici*, suggesting that the gene conferring resistance to the former is at the *rpg4* locus in barley line Q21861.

Additional keywords: disease resistance, *Hordeum vulgare*.

In North America, barley (*Hordeum vulgare* L.) can be attacked by two different stem rust pathogens: *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn. (the wheat stem rust pathogen) and *P. graminis* Pers.:Pers. f. sp. *secalis* Eriks. & E. Henn. (the rye stem rust pathogen). Historically, *P. graminis* f. sp. *tritici* has been more important on barley in North America (11); however, yield losses ranging up to 30 to 40% have been reported due to *P. graminis* f. sp. *secalis* in British Columbia (3). The rye stem rust pathogen is a potential threat to barley production, because some isolates are virulent for *Rpg1* (16,17), a widely used stem rust resistance gene in Midwestern barley germ plasm (14).

Few studies have been conducted on rye stem rust resistance in barley, and this is probably because of the sporadic occurrence of *P. graminis* f. sp. *secalis* (16). The barley cultivars Black Hulless and Purple Nudum were reported to possess resistance to *P. graminis* f. sp. *secalis* in Canada (6) and Australia (1), respectively. A single recessive gene (designated now as *rpgBH*) was found to confer adult plant rye stem rust resistance in 'Black Hulless' by Steffenson et al. (16). In Australia, Babriwala (1) and Luig (7) identified a single dominant gene for resistance in the genotypes 'Purple Nudum' and 'Skinless', respectively.

The barley genotype Q21861 (PI 584766) possesses two genes for resistance to *P. graminis* f. sp. *tritici*: *Rpg1*, which has provided durable resistance for over half a century in Midwest barley cultivars (14), and *rpg4*, which confers resistance to pathotype Pgt-QCCJ of *P. graminis* f. sp. *tritici* (5,15). Pathotype QCCJ possesses virulence for *Rpg1* and has, over the past 5 years, become one of the most prevalent virulence types in the *P. graminis* f. sp. *tritici* population of the northern Great Plains (4,12). In a preliminary experiment, we found that Q21861 and a number of derived progeny had resistance to *P. graminis* f. sp. *secalis* at the seedling stage. All of the resistant progeny carried the *rpg4* gene, suggesting a possible relationship between this gene and resistance to *P. graminis* f. sp. *secalis*. The objectives of this study were to determine the genetics of resistance to *P. graminis* f. sp. *secalis* in Q21861 and to investigate the possible relationship of *rpg4* and rye stem rust resistance.

Corresponding author: B. J. Steffenson
E-mail address: bsteffen@badlands.nodak.edu

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MATERIALS AND METHODS

Plant materials. To determine the genetics of resistance to *P. graminis* f. sp. *secalis* in Q21861, an anther-culture-derived doubled haploid (DH) population from the cross Q21861/SM89010 was studied initially. This DH population (129 progeny total) previously had been evaluated for *rpg4* (15); thus, direct comparisons could be made regarding the relation between rye stem rust resistance and the presence of *rpg4* in the DH progeny. Preliminary results from this population indicated that resistance to *P. graminis* f. sp. *secalis* cosegregated with resistance to pathotype QCCJ of *P. graminis* f. sp. *tritici* as conferred by *rpg4*. To obtain additional data on the relationship between the gene for rye stem rust resistance and *rpg4*, additional populations (F_3 generation) involving Q21861 and three different susceptible parents were evaluated: Steptoe/Q21861, Q21861/SM89010 (provided courtesy of B. G. Rossnagel and K. N. Kao, Crop Development Centre and Plant Biotechnology Institute, respectively, Saskatoon, Saskatchewan), and Q21861/Klages (provided courtesy of D. M. Wesenberg, USDA/ARS, National Small Grains Germplasm Research Facility, Aberdeen, ID). Q21861 also was used as the female parent in a cross with Steptoe. The F_1 plants from this cross

were used to assess the relative dominance of the resistance gene(s) to the two rusts. Single F_1 plants from the three crosses were grown in a greenhouse to produce F_2 progeny. F_3 families were derived from individual F_2 plants.

The respective parents of each cross were included as controls in the rust evaluation tests. In experiments with *P. graminis* f. sp. *secalis*, the rye cultivar Prolific (CI 26) and the wheat cultivars McNair 701 (CI 15288) and Line E (PI 357308) were included as controls to verify the virulence of the culture and to detect possible contamination by *P. graminis* f. sp. *tritici* urediniospores, respectively (17). All F_3 families from the three crosses were split into two equal parts (25 to 30 seeds each) and evaluated for their infection types to both *P. graminis* f. sp. *tritici* (pathotype QCCJ) and *P. graminis* f. sp. *secalis* (isolate 92-MN-90).

Pathogen cultures. Isolate 92-MN-90 of *P. graminis* f. sp. *secalis* (obtained courtesy of A. P. Roelfs, USDA/ARS, Cereal Rust Laboratory, St. Paul, MN) was selected for this study, because Q21861 exhibits low infection types (0,0;) to it at low incubation temperatures (18 to 21°C). This isolate was purified by single uredinium isolation and then increased on 'Prolific' rye. Pathotype QCCJ (isolate QCC-2) of *P. graminis* f. sp. *tritici* was obtained courtesy of J. D. Miller (USDA/ARS, Northern Crop Science Laboratory, Fargo, ND). Urediniospores of both pathogens were partially dried in a desiccator containing $CaSO_4$ for 2 days and then stored in sealed glass tubes at –80°C until needed for inoculation.

Inoculation and assessment of infection types. A 3:1 peat moss/perlite potting mix (No. 1 Sunshine Mix; Fisons Horticulture, Vancouver, British Columbia, Canada) was used for growing all plant materials. Three to five seeds of the DH progeny, F_1 plants, and parents were sown in plastic cones (3.8 cm in diameter and 21 cm in depth). For the F_3 families, 25 to 30 seeds were sown in 10 × 10-cm plastic pots. Plants were grown at 22 to 26°C in a greenhouse with supplemental lighting provided by 1,000-W, metal halide bulbs (530- to 710-µmol photon m^{-2} s^{-1}) for 13 h per day. Fertilization was provided at planting with a controlled-release formulation (14-14-14, N-P-K, 2.2 g per container). When the primary leaves were fully expanded (7 days after planting), plants were inoculated with isolate 92-MN-90 of *P. graminis* f. sp. *secalis* or pathotype QCCJ of *P. graminis* f. sp. *tritici*. Stored urediniospores were removed from the freezer, heat shocked in water at 46°C for 6 to 7 min, and rehumidified at approximately 80% relative humidity for at least 3 h before being used for inoculation. Plants were inoculated with a suspension of urediniospores in a light-weight mineral oil (Soltrol 170; Phillips Petroleum Company, Bartlesville, OK). The inoculum concentration was 3.5 mg of urediniospores/0.65 ml of oil of which approximately 2 µl was applied per plant. After inoculation, plants were placed in front of an oscillating electric fan for 3 to 4 min to facilitate the rapid drying of the oil carrier from the plant surfaces. Plants were then moved to mist chambers maintained near saturation by intermittent mistings (32 s of mist every 16 min) from ultrasonic humidifiers. Plants were misted for 16 h at 21°C in complete darkness. After the misting period, plants were exposed to light from 430-W, high pressure sodium lamps (emitting 150- to 250-µmol photon m^{-2} s^{-1}) for 3 h. The chamber doors were opened halfway when the light was turned on to reduce the buildup of heat and to allow the leaf surfaces of plants to dry slowly.

After the infection period, plants were incubated in a growth chamber at 18 to 21°C with a 13-h photoperiod (115-W, very high output, cool-white bulbs emitting 120- to 225-µmol photon m^{-2} s^{-1}). Twelve to fourteen days after inoculation, the infection types (ITs) on plants were assessed using a modification of the 0 to 4 scale developed by Stakman et al. (13) for wheat. The scale used for barley was based primarily on uredinial size as described by Miller and Lambert (10). Infection types 0, 0;, 1, 2, or combinations thereof were considered as resistant responses, and infection types 3, 4, or combinations thereof were considered as susceptible responses. The chi-square statistic was used to test the goodness-of-fit to expected segregation ratios in all populations.

TABLE 1. Infection types of barley lines Q21861, SM89010, Klages, and Steptoe to isolate 92-MN-90 of *Puccinia graminis* f. sp. *secalis* and isolate QCC-2 (pathotype QCCJ) of *P. graminis* f. sp. *tritici* at 18 to 21°C

Barley line	Isolate 92-MN-90 of *P. graminis* f. sp. *secalis*	Isolate QCC-2 of *P. graminis* f. sp. *tritici*
Q21861	0,0;[a]	0,0;
SM89010	3⁻,2	3⁻,3
Klages	3⁻,2	3⁻,3
Steptoe	3⁻,2	3,3⁻

[a] Infection types are based on the 0 to 4 scale of Stakman et al. (13) as modified for barley by Miller and Lambert (10). The infection types observed on plants were recorded in order of their relative prevalence.

RESULTS

Genetics of resistance to isolate 92-MN-90 of *P. graminis* f. sp. *secalis*. Q21861 exhibited very low ITs (0,0;) and SM89010, Klages, and Steptoe mostly high ITs (3⁻, occasionally 2) in response to isolate 92-MN-90 of *P. graminis* f. sp. *secalis* (Table 1). Resistant and susceptible progeny were clearly recognizable in the Q21861/SM89010 DH population (Table 2). The number of resistant and susceptible progeny fit a 1:1 segregation ratio (P = 0.25), indicating that a single gene confers resistance to *P. graminis* f. sp. *secalis*. Infection types 0;, 1, and 2⁻ were observed on F_1 plants from the cross Q21861/Steptoe (data not shown). This

TABLE 2. Segregation of Q21861/SM89010 doubled haploid (DH) progeny and F_3 families from the crosses Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861 for resistance to isolate 92-MN-90 of *Puccinia graminis* f. sp. *secalis* at 18 to 21°C

Cross	Population	Homozygous resistant	Segregating	Homozygous susceptible	Expected ratio	X^2	Probability ($>X^2$)
Q21861/SM89010	DH	58	...	71	1:1	1.31	0.25
Q21861/SM89010	F_3	38	72	38	1:2:1	0.11	0.95
Q21861/Klages	F_3	49	111	63	1:2:1	1.76	0.41
Steptoe/Q21861	F_3	59	141	69	1:2:1	1.37	0.50

TABLE 3. Segregation of Q21861/SM89010 doubled haploid (DH) progeny and F_3 families from the crosses Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861 for resistance to isolate QCC-2 (pathotype QCCJ) of *Puccinia graminis* f. sp. *tritici* at 18 to 21°C

Cross	Population	Homozygous resistant	Segregating	Homozygous susceptible	Expected ratio	X^2	Probability ($>X^2$)
Q21861/SM89010[a]	DH	58	...	71	1:1	1.31	0.25
Q21861/SM89010	F_3	38	72	38	1:2:1	0.11	0.95
Q21861/Klages	F_3	49	111	63	1:2:1	1.76	0.41
Steptoe/Q21861	F_3	56	144	69	1:2:1	2.60	0.27

[a] Segregation data for the Q21861/SM89010 DH population are from Steffenson et al. (15).

suggests that the resistance gene is partially dominant, since the F_1 plants did not exhibit the predominantly low infection types of 0,0;, as with the resistant parent Q21861.

Resistant and susceptible plants were clearly recognizable within and among F_3 families in the crosses Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861 tested with isolate 92-MN-90. The range of ITs observed on resistant progeny was 0,0; to 0;,1 and for susceptible progeny was 2,3⁻ to 3⁻,3 (data not shown). Segregation for homozygous resistant, segregating, and homozygous susceptible F_3 families in all three crosses closely fit a 1:2:1 ratio (P = 0.41 to 0.95) (Table 2), thereby confirming the single gene ratio found earlier for the Q21861/SM89010 DH population. In segregating F_3 families, the number of resistant plants exceeded the number of susceptible plants by about 3 to 1 (data not shown). This indicates dominant gene action and corroborates the results found for F_1 plants of the cross Q21861/Steptoe.

Genetics of resistance to pathotype QCCJ of *P. graminis* f. sp. *tritici*. Q21861 exhibited low ITs (0,0;), whereas SM89010, Klages, and Steptoe exhibited high ITs (3⁻,3 to 3,3⁻) to pathotype QCCJ (Table 1). F_1 plants from the cross Q21861/Steptoe exhibited high ITs (3⁻,3 to 3⁻,2), indicating that resistance to pathotype QCCJ was recessive (data not shown). F_3 families from the crosses Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861 segregated in single gene ratios (1:2:1 with P = 0.27 to 0.95) for resistance to pathotype QCCJ (Table 3). Within segregating F_3 families, the plants segregated approximately 3:1 (susceptible/resistant), which indicated recessive gene action for *rpg4* (data not shown).

Relationship between *rpg4* and the gene conferring resistance to *P. graminis* f. sp. *secalis*. To determine the relationship between the gene identified for rye stem rust resistance and the *rpg4* gene for wheat stem rust resistance in Q21861, data for the reaction to the two rusts were compared in all segregating populations (Table 4). Resistance to the rye stem rust pathogen cosegregated with resistance to the wheat stem rust pathogen in the Q21861/SM89010 DH population (129 progeny), the Q21861/SM89010 F_3 population (148 families), and the Q21861/Klages F_3 population (223 families). Cosegregation for resistance also was found for 266 of 269 families from the Steptoe/Q21861 population. Three F_3 families that were classified as homozygous resistant to *P. graminis* f. sp. *secalis* appeared to be segregating in response to *P. graminis* f. sp. *tritici*.

DISCUSSION

A single gene was found to confer resistance to isolate 92-MN-90 of *P. graminis* f. sp. *secalis* in the barley line Q21861, based on four different segregating populations. The low (resistant) ITs of F_1 plants and the approximate 3:1 ratio of resistant/susceptible plants found in segregating F_3 families indicated that the gene was partially dominant. Monogenic inheritance for rye stem rust resistance previously was reported in the barley cultivars Purple Nudum (1), Skinless (7), and Black Hulless (16). Further studies should be made to determine the allelic relations among the reported genes for rye stem rust resistance in barley. Data from the evaluation of the Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861 F_3 populations to pathotype QCCJ were in agreement with those of Jin et al. (5) in that a single resistance gene, *rpg4*, acted in a recessive manner in Q21861. This gene was recently mapped to barley chromosome 7M (5H) using molecular markers (2).

In this study, the gene conferring resistance to the rye stem rust pathogen cosegregated with *rpg4* conferring resistance to pathotype QCCJ in 766 of 769 progeny tested (Table 4). Remnant seed from the three aberrant Steptoe/Q21861 F_3 families were retested with the two rusts. All three of these families were clearly homozygous resistant to *P. graminis* f. sp. *secalis* as before. To pathotype QCCJ of *P. graminis* f. sp. *tritici*, these families again appeared to be segregating, because several plants (from a total of about 30 additional plants examined) exhibited mostly high ITs (3⁻, 2 to 3⁻,3). Since *rpg4* is recessive, one would expect a 3 to 1 ratio of susceptible to resistant plants in segregating families. Instead, the number of resistant plants greatly exceeded the number of susceptible plants in these three families. It is likely that these F_3 families were, indeed, homozygous resistant to pathotype QCCJ. The reason why several plants exhibited susceptible ITs in the three Steptoe/Q21861 families is not known, but may be related to the genetic background contributed by the susceptible parent Steptoe.

The evidence reported here suggests that the gene for resistance to *P. graminis* f. sp. *secalis* is at the *rpg4* locus. Like *rpg4* (5), the gene conferring rye stem rust resistance also is temperature sensitive, because it gives low ITs at low temperatures (18 to 20°C) and high ITs at high temperatures (27 to 29°C) (Y. Sun and B. J. Steffenson, *unpublished data*). This characteristic is further evidence that the two genes are the same. Very large, segregating populations (perhaps >2,000 F_3 families), however, should be evaluated against the two rusts to unequivocally determine whether the genes are indeed at the same locus or are tightly linked. If the two genes are the same, they exhibit different gene action to the two formae speciales of *P. graminis*, partially dominant in response to *P. graminis* f. sp. *secalis* and recessive in response to *P. graminis* f. sp. *tritici*. It is certainly possible that a single host gene could confer resistance to two different formae speciales, because both could carry the same avirulence gene as hypothesized by Tosa (18). Single genes may also confer resistance to different species of rust. In wheat, the *Lr34* gene for resistance to leaf rust (*P. recondita* f. sp. *tritici*) is thought to be the same as the *Yr18* gene for resistance to stripe rust (*P. striiformis* f. sp. *tritici*) (9), and the *Lr20* gene is thought to be the same as the *Sr15* gene for resistance to stem rust (*P. graminis* f. sp. *tritici*) (8).

TABLE 4. Relationship between the *rpg4* gene for resistance to isolate QCC-2 (pathotype QCCJ) of *Puccinia graminis* f. sp. *tritici* and the gene conferring resistance to isolate 92-MN-90 of *P. graminis* f. sp. *secalis* in Q21861/SM89010 doubled haploid (DH) progeny and F_3 families from the crosses Q21861/SM89010, Q21861/Klages, and Steptoe/Q21861

Crosses	Number of DH progeny	Reaction to pathotype QCCJ[a]	Putative genotypes of DH progeny	Reaction to isolate 92-MN-90[a]
Q21861/SM89010[b]	31	S	*Rpg1Rpg1/Rpg4Rpg4*	S
	27	R	*Rpg1Rpg1/rpg4rpg4*	R
	39	S	*rpg1rpg1/Rpg4Rpg4*	S
	32	R	*rpg1rpg1/rpg4rpg4*	R
	Number of F_3 families		Putative genotypes of F_2 plants used to produce F_3 families	
Q21861/SM89010	38	HR	*rpg4rpg4*	HR
	38	HS	*Rpg4Rpg4*	HS
	72	SG	*Rpg4rpg4*	SG
Q21861/Klages	49	HR	*rpg4rpg4*	HR
	53	HS	*Rpg4Rpg4*	HS
	111	SG	*Rpg4rpg4*	SG
Steptoe/Q21861	56	HR	*rpg4rpg4*	HR
	69	HS	*Rpg4Rpg4*	HS
	141	SG	*Rpg4rpg4*	SG
	3	SG	*Rpg4rpg4*	HR

[a] S = susceptible, R = resistant, HR = homozygous resistant, SG = segregating, and HS = homozygous susceptible.

[b] Segregation data for the Q21861/SM89010 DH population are from Steffenson et al. (15).

Rye stem rust remains a potential threat to barley production in certain areas of North America (3,16). Thus, it is important to identify and characterize new sources of resistance to this disease. Several barley breeding programs in North America are transferring *rpg4* into elite germ plasm for resistance to the *Rpg1*-virulent pathotype QCCJ. This effort is being facilitated in some programs by the use of linked molecular markers (2). In the process of incorporating *rpg4*, breeders also will incorporate resistance to rye stem rust. This will have the added benefit of reducing or preventing future losses to this sporadic, but sometimes damaging disease.

LITERATURE CITED

1. Babriwala, G. T. 1954. Studies on rusts in barley. M.S. thesis. University of Sydney, Sydney, Australia.
2. Borovkova, I. G., Steffenson, B. J., Jin, Y., Rasmussen, J. B., Kilian, A., Kleinhofs, A., Rossnagel, B. G., and Kao, K. N. 1995. Identification of molecular markers linked to the stem rust resistance gene *rpg4* in barley. Phytopathology 85:181-185.
3. Green, G. J. 1974. Stem rust of wheat, rye and barley in Canada in 1973. Can. Plant Dis. Surv. 54:11-15.
4. Harder, D. E., Dunsmore, K. M., and Anema, P. K. 1994. Stem rusts on wheat, barley, and oat in Canada in 1993. Can. J. Plant Pathol. 16:329-334.
5. Jin, Y., Steffenson, B. J., and Miller, J. D. 1994. Inheritance of resistance to pathotypes QCC and MCC of *Puccinia graminis* f. sp. *tritici* in barley line Q21861 and temperature effects on the expression of resistance. Phytopathology 84:452-455.
6. Johnson, T., and Buchannon, K. W. 1954. The reaction of barley varieties to rye stem rust, *Puccinia graminis* var. *secalis*. Can. J. Agric. Sci. 34:473-482.
7. Luig, N. H. 1957. Inheritance studies of barley in reaction to disease resistance. M.S. thesis. University of Sydney, Sydney, Australia.
8. McIntosh, R. A. 1988. Catalogue of gene symbols for wheat. Pages 1225-1323 in: Proc. Int. Wheat Genet. Symp., 7th. T. E. Miller and R. M. D. Koebner, eds. Institute of Plant Science Research, Cambridge Laboratory, Cambridge.
9. McIntosh, R. A. 1992. Close genetic linkage of genes conferring adult-plant resistance to leaf rust and stripe rust in wheat. Plant Pathol. 41:523-527.
10. Miller, J. D., and Lambert, J. W. 1955. Variability and inheritance of reaction of barley to race 15B of stem rust. Agron. J. 47:373-377.
11. Roelfs, A. P. 1985. Wheat and rye stem rust. Pages 3-37 in: The Cereal Rusts. Vol. II. Diseases, Distribution, Epidemiology, and Control. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Inc., New York.
12. Roelfs, A. P., Long, D. L., and Roberts, J. J. 1995. Races of *Puccinia graminis* in the United States in 1993. Plant Dis. 79:969-972.
13. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiological races of *Puccinia graminis* f. sp. *tritici*. U.S. Dep. Agric. Agric. Res. Serv. E617.
14. Steffenson, B. J. 1992. Analysis of durable resistance to stem rust in barley. Euphytica 63:153-167.
15. Steffenson, B. J., Jin, Y., Rossnagel, B. G., Rasmussen, J. B., and Kao, K. 1995. Genetics of multiple disease resistance in a doubled haploid population of barley. Plant Breeding 114:50-54.
16. Steffenson, B. J., Wilcoxson, R. D., and Roelfs, A. P. 1984. Inheritance of resistance to *Puccinia graminis* f. sp. *secalis* in barley. Plant Dis. 68:762-763.
17. Steffenson, B. J., Wilcoxson, R. D., and Roelfs, A. P. 1985. Resistance of barley to *Puccinia graminis* f. sp. *tritici* and *Puccinia graminis* f. sp. *secalis*. Phytopathology 75:1108-1111.
18. Tosa, Y. 1992. A model for the evolution of formae speciales and races. Phytopathology 82:728-730.