Detection of the Stem Rust Resistance Gene *Rpg*1 in Barley Seedlings

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ABSTRACT

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The stem rust resistance gene *Rpg*1 has conferred durable resistance in barley (*Hordeum vulgare*) to *Puccinia graminis* f. sp. *tritici* (wheat stem rust pathogen) for nearly 50 yr in the northern Great Plains. Detection of *Rpg*1 at the seedling stage can be difficult because most barley genotypes show mesothetic reactions to the stem rust pathogen. Genotypes with and without genes for stem rust resistance were inoculated with pathotypes Pgt-TPM, -MCC, and -HPH of *P. g. tritici* in the seedling stage. After 12 days of incubation at 25–28 C, infection types were assessed on plants. With pathotype TPM, differences between barley genotypes with and without resistance genes were not distinct, since similar infection types were frequently observed on genotypes in both groups. In contrast, marked differences were observed among barleys to pathotypes MCC and HPH; genotypes with *Rpg*1 exhibited low infection types (0;, 0;1, 10;, occasionally 12 with pathotype HPH), whereas those with *rpg*1 (the recessive allele for susceptibility) exhibited distinctly higher infection types (mostly 3–3, 3–2, 33–, 33+, occasionally 23– with pathotype MCC). Genotypes carrying resistance gene *Rpg*2, *Rpg*3, or *rpg*BH displayed mostly intermediate (23–) to high (3–2, 3–3) infection types to these pathotypes. These data demonstrate the usefulness of pathotypes MCC and HPH in detecting barley genotypes with *Rpg*1. The reliability of this screening method, coupled with the short cycle (19 days) of seedling tests, will hasten the development of barley germ plasm with stem rust resistance and aid in subsequent genetic studies in this pathosystem.

The stem rust resistance gene *Rpg*1 (*T* gene) has provided durable resistance against the wheat stem rust pathogen, *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn., for nearly 50 yr in barley (*Hordeum vulgare* L.) cultivars grown in the Upper Midwest of the United States and the southern Prairie Provinces of Canada (15). In 1989, however, a pathotype of *P. g. tritici* (Pgt-QCC) with virulence on *Rpg*1 was detected throughout the northern Great Plains (2,9). Although pathotype QCC has caused only minor statewide yield losses (average of 1–3%) in barley during the past four seasons in the United States (15), the potential exists for a serious epidemic if inoculum of this pathotype increases and weather conditions favorable for disease development prevail. To maintain stable barley production in the Upper Midwest, it may be necessary to incorporate both *Rpg*1 and genes for resistance to pathotype QCC into new cultivars. Retention of *Rpg*1 in barley breeding lines is important because this gene has proved durable to *P. g. tritici* in the Great Plains (15).

In the field, genotypes with *Rpg*1 can be readily differentiated from those with *rpg*1 (the recessive allele for susceptibility) to some pathotypes of *P. g. tritici* (19). After the heading stage of plant development, barley genotypes with *Rpg*1 exhibit low rust severities and predominantly incompatible (low) infection responses, whereas those with *rpg*1 exhibit high rust severities and predominantly compatible (high) infection responses. The presence of the virulent pathotype QCC, now well established in the Great Plains (10), will confound field assessments for the identification of *Rpg*1 in barley. *Rpg*1 is difficult to detect in the seedling stage because most barley genotypes exhibit mesothetic reactions (different infection types on the same plant) to many pathotypes of *P. g. tritici*, especially at lower temperatures (5–7,19). Moreover, barley frequently exhibits uredinia that are associated with chlorosis (6,7,20)—an infection phenotype that can further complicate the unequivocal identification of *Rpg*1 in the seedling stage.

Development of effective methods for

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detecting *Rpg*1 or other genes for stem rust resistance at the seedling stage will facilitate the rapid improvement of barley germ plasm with stem rust resistance. The objective of this study was to evaluate the potential of several pathotypes of *P. g. tritici* in differentiating barley genotypes with and without resistance genes at the seedling stage. A preliminary report of this research has been published (17).

MATERIALS AND METHODS

Thirty barley genotypes were evaluated for their infection type to three pathotypes (Pgt-MCC, -HPH, and -TPM) of *P. g. tritici*. Included in the group of hosts were 22 cultivars (two- or six-rowed and malting or feed types) developed in or introduced to North America (Table 1). Twelve of these 22 cultivars are reported to possess *Rpg*1 and 10 to possess *rpg*1 (Table 2). Eight accessions were also included in the evaluation: Chevron and Peatland, the original sources of *Rpg*1 (8,13); Hietpas 5, the source of *Rpg*2 (*T*2 gene) (7); PI 382313, the source of *Rpg*3 (*T*3 gene) (4); Black Hulless, the source of *rpg*BH (*s* gene) (18); 80-TT-29 and 80-tt-30, the *Rpg*1/*rpg*1 near-isogenic lines (19); and Hiproly, a susceptible check that possesses *rpg*1. The recognized allele for stem rust reaction in each barley genotype (Table 2) is based on genetic studies or pedigrees. Pathotypes MCC (isolate A-5) and HPH (isolate A-14) were included because in a preliminary experiment they clearly differentiated the near-isogenic lines on the basis of the infection type. Pathotype TPM (isolate TNMK-SP1) also was included because it has been one of the most common pathotypes in the northern Great Plains from 1974 to 1989 (10).

Barley genotypes (four to six seeds) were sown in plastic cones (3.8 cm diameter and 21 cm depth) filled with No. 1 Sunshine Mix (Fisons Horticulture, Vancouver, Canada) and grown at 22–26 C in a greenhouse. Fertilization was provided at planting with a water-soluble formulation (Peters 15-0-15, N-P-K, stock solution of 45 g/L applied at a rate of 435–535 ppm per container) and a controlled-release formulation (Osmocote 14-14-14, N-P-K, 2.2 g per container). Supplemental lighting was provided by 1,000W metal halide bulbs (530–710 $\mu E \cdot m^{-2} \cdot s^{-1}$) for 13 hr per day. Plants were inoculated with pathotypes MCC, HPH, or TPM 7 days after planting when the primary leaves were fully expanded. A concentration of 6.0 mg of urediniospores per milliliter of light mineral oil (Soltrol 170) was applied at a rate of approximately 1.5 μl of oil per plant. Immediately after inoculation, plants were placed in front of an oscillating fan to facilitate the rapid drying of the oil carrier from plant surfaces; this was done to reduce the phytotoxic effects of excessive oil on the leaves.

After the oil had evaporated (about 2–5 min), plants were placed in chambers (94 cm long, 61 cm wide, and 114 cm high) maintained near saturation by intermittent mistings (32 sec of mist every 16 min) from ultrasonic humidifiers (16). Plants were incubated in the mist chambers for 16 hr at 20–21 C in the dark, exposed to sunlight in a greenhouse at 21–24 C, and allowed to dry slowly for approximately 4 hr before being placed in a growth chamber at 25–28 C (13-hr photoperiod supplied by 115W VHO cool-white bulbs, 120–225 $\mu E \cdot m^{-2} \cdot s^{-1}$). Twelve days after inoculation, infection types on each genotype (adaxial side of leaves) were assessed on a 0–4 scale. The infection type scale for barley is a modification of the one developed for wheat by Stakman et al (14) and is based primarily on uredinial size (6). This modification was necessary because chlorosis is invariably associated with larger uredinia (types 2, 3, and 4) on barley. Because most barleys exhibit mesothetic reactions to the stem rust pathogen, the infection type data were expressed as a mode (the one or two most common infection types observed on the leaves of genotypes among replicates within an experiment) and range (the lowest and highest infection types observed). For

Table 1. Barley genotypes used to evaluate the potential of pathotypes Pgt-MCC, Pgt-HPH, and Pgt-TPM of *Puccinia graminis* f. sp. *tritici* for detecting *Rpg*1 in the seedling stage

Genotype	PI or CI Number	Origin or description	Type
Andre	PI 469107	Washington Agricultural Experiment Station	Two-rowed malting
Azure	CI 15865	North Dakota Agricultural Experiment Station	Six-rowed malting
B1602	PI 502965	Busch Agricultural Resources, Inc.	Six-rowed malting
Betzes	CI 6398	Cultivar introduction from Poland	Two-rowed malting
Black Hulless	CI 666	Land race introduction from China	Six-rowed accession
Bonanza	CI 14003	Agriculture Canada, Brandon	Six-rowed malting
Bonneville	CI 7248	Utah and Oregon Agricultural Experiment stations	Six-rowed feed
Bowman	PI 483237	North Dakota Agricultural Experiment Station	Two-rowed feed
Chevron	CI 1111	Land race introduction from Switzerland	Six-rowed accession
Clark	CI 15857	Montana Agricultural Experiment Station and USDA-ARS	Six-rowed malting
Crystal	PI 531249	Idaho Agricultural Experiment Station and USDA-ARS	Two-rowed malting
Excel	PI 542047	Minnesota Agricultural Experiment Station	Six-rowed malting
Glenn	CI 15769	North Dakota Agricultural Experiment Station	Six-rowed malting
Harrington	...[a]	University of Saskatchewan, Saskatoon	Two-rowed malting
Hector	CI 15514	Agriculture Canada, Lethbridge	Two-rowed feed
Hietpas 5	CI 7124	Selection from Oderbrucker	Six-rowed accession
Hiproly	CI 3947	Land race introduction from Egypt	Two-rowed accession
Kindred	CI 6969	Selection from Wisconsin 37	Six-rowed malting
Klages	CI 15478	Idaho Agricultural Experiment Station and USDA-ARS	Two-rowed malting
Larker	CI 10648	North Dakota Agricultural Experiment Station	Six-rowed malting
Moravian III	CI 15812	Adolph Coors Company, Inc.	Two-rowed malting
Morex	CI 15773	Minnesota Agricultural Experiment Station	Six-rowed malting
Oderbrucker	CI 4666	Cultivar introduction from Germany	Six-rowed malting
Peatland	CI 5267	Land race introduction from Switzerland	Six-rowed accession/feed[b]
Primus II	CI 13796	South Dakota Agricultural Experiment Station and USDA-ARS	Six-rowed feed
Steptoe	CI 15229	Washington Agricultural Experiment Station	Six-rowed feed
Wisconsin 38	CI 5105	Wisconsin Agricultural Experiment Station	Six-rowed malting
80-TT-29	CI 16129	Backcross selection from (Wisconsin 38 × Chevron) × CCXI	Six-rowed experimental
80-tt-30	CI 16130	Backcross selection from (Wisconsin 38 × Chevron) × CCXI	Six-rowed experimental
...[c]	PI 3822313	Land race introduction from Ethiopia	Two-rowed accession

[a] No PI or CI number has been assigned for Harrington; Canadian Plant Gene Resource (PGR) number is 12181.
[b] Peatland was cultivated as a feed barley over a small number of hectares.
[c] No common name has been assigned for PI 382313.

ease of discussion, infection types were classified into the broad categories of low (types 0;, 1, 2, and combinations thereof), intermediate (type 23−), and high (types 3−2 or 3, 4, and combinations thereof).

The experiment was conducted in a randomized complete block design and was repeated twice; two replicates were included in experiment 1 and three in experiment 2. The identity and purity of pathotypes were verified according to the methods of Roelfs and Martens (11).

RESULTS

The mode and range of infection types on barley seedlings infected with pathotypes MCC, HPH, and TPM of *P. g. tritici* are given in Table 2. Marked differences were observed among barleys to pathotypes MCC and HPH; genotypes with *Rpg*1 exhibited low infection types (modes 0;, 0;1, and 10;, occasionally 12− with pathotype HPH), whereas those with *rpg*1 gave distinctly higher infection types (predominantly 3−3, 3−2, 33−, and 33+ with a 23− on Bonneville to pathotype MCC). These results were consistent among the different types of barley (e.g., two- vs. six-rowed and malting vs. feed) and between the two experiments. Moreover, the range of infection types on genotypes with *Rpg*1 or *rpg*1 was low and comprised, in most cases, only those infection types in the respective modes. With pathotype TPM, infection type differences between genotypes with *Rpg*1 and *rpg*1 were less distinct. Some genotypes with *Rpg*1 exhibited low infection types (e.g., modes of 21, 12, and 0;1), but others exhibited intermediate (23−) to high (3−2) infection types that were similar to those observed on genotypes with the recessive allele for susceptibility. In general, the range of infection types on individual host genotypes was greater with pathotype TPM than with MCC and HPH. The genotypes Black Hulless, Hietpas 5, and PI 382313, which possess genes for stem rust resistance that differ from *Rpg*1, exhibited mostly intermediate (23−) to high (3−2, 3−3) infection types to the three pathotypes; the exception was the low infection type 21 on Hietpas 5 to pathotype TPM in experiment 1.

DISCUSSION

The unequivocal identification of barley genotypes with *Rpg*1 can be difficult in the seedling stage. This is due, in part, to the association of chlorosis with large uredinia (6,7,20) and the frequency of mesothetic reactions (5–7,19) on barley to *P. g. tritici*. In this study, we demonstrated how barley genotypes with *Rpg*1 could be reliably detected at the seedling stage using pathotypes MCC and HPH. Genotypes with *Rpg*1 exhibited low infection types that were usually associated with necrosis, whereas those carrying *rpg*1, *Rpg*2, *Rpg*3, or *rpg*BH displayed high or intermediate infection types that were associated with chlorosis. Mesothetic responses were still observed on most of the genotypes with *Rpg*1 to pathotypes MCC and HPH, but the range of infection types was low (usually 0; to 1 or rarely 0; to 2−) and was always within the low infection type class. Some genotypes with *rpg*1 displayed a more variable infection phenotype that included both low and high infection types to the two pathotypes. However, in all cases but one (23− on Bonneville infected with pathotype MCC in experiment 1), the high infection type predominated in the mode. Similar reactions were observed on genotypes carrying *Rpg*2, *Rpg*3, and *rpg*BH, except for a higher frequency of intermediate

Table 2. Mode and range of infection types on barley seedlings to pathotypes Pgt-MCC, Pgt-HPH, and Pgt-TPM of *Puccinia graminis* f. sp. *tritici* at 25–28 C[a]

		MCC				HPH				TPM			
	Recognized allele for stem rust reaction[b]	Experiment 1		Experiment 2		Experiment 1		Experiment 2		Experiment 1		Experiment 2	
Genotype		Mode	Range (low/high)	Mode	Range (low/high)	Mode	Range (low/high)	Mode	Range (low/high)	Mode	Range (low/high)	Mode	Range (low/high)
Azure	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/1	0;1	0;/1	23−	1/3	23−	1/3−
B1602	*Rpg*1	0;	0;	0;1	0;/1	0;1	0;/1	10;	0;/1	12	1/2	3−2	2/3−
Bonanza	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/1	0;1	0;/1	23−	1/3−	23−	1/3−
Bowman	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/1	10;	0;/1	21	0;/2	23−	1/3−
Chevron	*Rpg*1	0;1	0;/1	0;1	0;/1	0;	0;	0;1	0;/1	21	1/2	21	1/2
Clark	*Rpg*1	0;1	0;/1	0;1	0;/1	12−	1/2−	10;	0;/1	23−	1/3−	3−2	2/3−
Excel	*Rpg*1	0;	0;	0;	0;	0;1	0;/1	0;1	0;/2	12	1/2	21	1/3−
Glenn	*Rpg*1	0;	0;	0;1	0;/1	0;1	0;/1	0;1	0;/1	21	1/2	23−	1/3−
Hector	*Rpg*1	0;1	0;/1	0;1	0;/1	10;	0;/2−	10;	0;/1	23−	1/3−	23−	2/3
Kindred	*Rpg*1	0;	0;	0;1	0;/1	0;1	0;/1	0;	0;	0;1	0;/1	21	1/2
Larker	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/1	0;1	0;/2	21	1/2	21	1/2
Morex	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/2−	0;1	0;/1	21	1/2	21	1/2
Peatland	*Rpg*1	0;	0;	0;1	0;/1	0;	0;	0;1	0;/1	21	1/2	21	1/2
Primus II	*Rpg*1	0;1	0;/1	0;1	0;/1	12−	1/2−	0;1	0;/1	23−	1/3−	23−	2/3−
80-TT-29	*Rpg*1	0;1	0;/1	0;1	0;/1	0;1	0;/1	0;1	0;/1	21	1/2	23−	2/3−
80-tt-30	*rpg*1	3−3	2/3	3−3	3−/3	33−	3−/3+	33+	3−/3+	3−3	2/3	3−2	2/3−
Andre	*rpg*1	33−	3−/3	3−3	3−/3	33+	3/3+	3−3	3−/3	3−2	1/3	23−	2/3−
Betzes	*rpg*1	3−2	2/3−	3−2	1/3−	33−	2/3+	3−3	2/3+	23−	1/3−	3−3	2/3
Bonneville	*rpg*1	23−	1/3−	3−2	2/3−	3−2	2/3	3−	3−	23−	2/3−	3−2	1/3−
Crystal	*rpg*1	3−2	2/3	3−2	2/3	3−3	2/3	3−3	2/3	3−2	2/3	3−2	2/3
Harrington	*rpg*1	3−2	2/3	3−3	2/3	3−3	3−/3	3−2	1/3	23−	1/3−	3−2	2/3
Hiproly	*rpg*1	33−	3−/3	3−3	3−/3	33+	3/3+	3−3	3−/3+	3−3	3−/3	33−	3−/3
Klages	*rpg*1	3−2	2/3−	3−3	2/3	33−	3−/3+	33−	3−/3	3−2	1/3−	3−2	2/3−
Moravian III	*rpg*1	3−3	2/3	3−3	3−/3+	3−2	2/3	33−	3−/3+	23−	1/3−	3−3	2/3
Oderbrucker	*rpg*1	3−2	2/3−	3−3	2/3	3−3	2/3	3−3	3−/3+	3−3	2/3	3−3	2/3
Steptoe	*rpg*1	3−2	2/3−	3−3	3−/3	33+	3/3+	3−3	3−/3+	3−3	2/3	3−3	3−/3
Wisconsin 38	*rpg*1	3−2	2/3−	3−2	2/3	3−3	2/3	3−3	3−/3+	23−	1/3−	3−2	2/3−
Hietpas 5	*Rpg*2	23−	1/3−	23−	1/3−	3−2	2/3	3−3	3−/3+	21	1/2	3−2	2/3
PI 382313	*Rpg*3	...[c]	...	23−	1/3−	...	...	3−3	2/3	...	...	23−	1/3−
Black Hulless	*rpg*BH	...	...	3−2	1/3−	...	...	3−3	3−/3	...	...	3−3	3−/3

[a] The mode represents the most common or two most common infection types observed on genotypes among replicates within an experiment, and the range represents the lowest and highest infection types observed on genotypes among replicates within an experiment. Infection types are based on a 0–4 scale and are listed in order of prevalence as observed on individual genotypes; + and − denote more or less sporulation, respectively.

[b] *Rpg*1 denotes the dominant homozygous resistant condition for the *T* locus, *Rpg*2 for *T*2, and *Rpg*3 for *T*3; *rpg*1 denotes the recessive homozygous susceptible condition for the *T* locus and *rpg*BH, the recessive homozygous resistant condition for the *s* locus.

[c] Genotype not included in first experiment.

infection types. The data we obtained for barley to pathotypes MCC and HPH agree with studies conducted by Andrews (1), Immer et al (3), and Sellam and Wilcoxson (12) in that genotypes with *Rpg*1 could be distinguished from those with *rpg*1 at the seedling stage. This, however, was not true for all pathotypes used in this study. With pathotype TPM, some genotypes with *Rpg*1 could not be readily differentiated from those with the recessive allele for susceptibility based on the infection type mode.

Our method for detecting genotypes with *Rpg*1 was effective across genetically diverse barleys and in different experiments conducted over time. Additionally, data analysis is simple using this protocol, since it only requires the comparison of distinct infection type modes as conferred by pathotypes MCC and HPH. This feature is a distinct advantage when one considers the quantitative methods that have been used to characterize the resistance of barley at the seedling stage. In several investigations, selection for stem rust resistance (i.e., detection of different genes for stem rust resistance) was based on weighted infection types (5,19) or seedling receptivity (R. Dill-Macky and R. G. Rees, *personal communication*). These procedures are laborious and time-consuming because the former requires an analysis of variance on transformed infection type data and the latter requires the use of semiquantitative inoculation techniques.

The infection phenotype of barley to *P. g. tritici* can vary under different temperature regimes at the seedling stage (6,7,19). Differences between genotypes with *Rpg*1 and *rpg*1 are usually most distinct at high incubation temperatures (25–28 C) because the former group generally exhibits only low infection types and the latter group exhibits high infection types (15). In this study, a high temperature regime was used during postinfection incubation. Results similar to the present study were obtained at lower incubation temperatures (18–22 C) in the greenhouse to pathotype MCC, although a higher frequency of low infection types was observed on barleys carrying *rpg*1 (B. J. Steffenson and Y. Jin, *unpublished*). The infection phenotype of barley may vary because of other environmental factors (e.g., light, fertility). Thus, standard protocols should be employed in all experiments to reduce variation.

In this investigation, alleles conferring the stem rust reaction in barley genotypes were known, either from genetic studies or from pedigrees. If an unknown genotype exhibits a low infection type to pathotype MCC or HPH, one cannot assume that it possesses *Rpg*1, because other undescribed genes may also confer a resistant reaction to these pathotypes. The identity of such genes can only be resolved through appropriate tests for allelism. Pathotypes MCC and HPH will be useful for detecting *Rpg*1 in progeny derived from parents known to carry the resistance gene. Indeed, pathotype MCC was effective for detecting individuals with *Rpg*1 from three doubled haploid and two conventional F_2 populations of barley (B. J. Steffenson and Y. Jin, *unpublished*). The reliability of this screening method coupled with the short cycle of seedling evaluations (19 days) will hasten the development of barley germ plasm with *Rpg*1 resistance and aid in subsequent genetic studies in this pathosystem.

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