

Inheritance of Resistance to *Puccinia hordei* in Cultivated and Wild Barley

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The inheritance of resistance to *Puccinia hordei* in several accessions of *Hordeum vulgare* and *H. spontaneum* was studied using leaf rust isolates whose combination of virulence genes would overcome resistance due to *Rph1*–*Rph12*. The results from this study indicated the presence of the *Rph3* resistance gene in cultivar Aim. This gene was dominant for resistance to isolate ND8702 but recessive for resistance to ND89-3. Allelism tests suggested that the *Rph3* allele occurred in a high frequency in barley originating from Egypt and the Mediterranean region. The following accessions of *H. vulgare* possess gene(s) that are likely different from *Rph1*–*Rph12*: CI 10506 (one dominant gene), PI 531849 (one dominant gene), and PI 531990 (a recessive gene in addition to *Rph3*). The *H. spontaneum* accessions were more diverse than the *H. vulgare* accessions, in both the number of genes for resistance to *P. hordei* and the types of interactions with rust isolates. Most of the *H. spontaneum* accessions tested had more than one resistance gene, with both dominant and recessive genes being common.

In the search for new sources of resistance to *Puccinia hordei* G. Oth, the barley leaf rust pathogen, we recently (Jin et al., in press) evaluated over 2,000 accessions of *Hordeum vulgare* L. and 885 accessions of *H. spontaneum* C. Koch to pathogen isolates with virulence for the known host resistance genes *Rph1*–*Rph12*. From this work, we found that effective resistance in the former species was rare and in the latter species fairly common (Jin et al., in press). The high frequency of resistant accessions in *H. spontaneum* has also been observed by others (Manisterski et al. 1986; Moseman et al. 1990), but studies on the genetics of resistance are limited. This lack of genetic information on resistance in *H. spontaneum* might account for the limited utilization of this species in barley improvement for leaf rust resistance. We report here on the inheritance of resistance in selected accessions of *H. vulgare* and *H. spontaneum* to several isolates of *P. hordei*.

Materials and Methods

Table 1 lists the virulence patterns of three *P. hordei* isolates (ND8702, ND89-3, and BRS76-12) on a set of differential host lines for barley leaf rust, along with the reactions of putative new sources of resistance (Jin et al., in press) from *H. vulgare*

and *H. spontaneum* to these isolates. The differential host lines for *P. hordei* consist of 12 barley lines (Steffenson and Jin 1992), each of which possesses a unique *Rph* gene or gene combination that confers resistance to certain pathotypes of the leaf rust pathogen. Pathotypes of *P. hordei* are identified based on their reaction (virulent or avirulent) on the differential host lines. By assessing the response (susceptible or resistant) of previously uncharacterized barley accessions to different pathotypes of *P. hordei*, one can postulate the probable resistance gene(s) carried by the host accessions.

Isolate ND89-3 is virulent for all known *Rph* genes except *Rph3* (Table 1). It is also virulent on many other new sources of resistance, as reported by Jin et al. (in press) and therefore possesses one of the widest virulence spectra known in *P. hordei*. Isolate BRS76-12 is also widely virulent and possesses a critical virulence gene for *Rph3* that is not found in isolate ND89-3. Together, isolates ND89-3 and BRS76-12 possess virulence for all known leaf rust resistance genes (*Rph1*–*Rph12*). Thus, any barley accession resistant to both isolates ND89-3 and BRS76-12 must have at least one resistance gene different from *Rph1*–*Rph12*, or a gene combination of *Rph3* with either *Rph7*, *Rph9*, or *Rph12*. Compared with the other two isolates,

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Table 1. Virulence patterns of isolates ND8702, ND89-3, and BRS76-12 of *Puccinia hordei* on differential lines of barley and other *Hordeum* accessions used for inheritance studies^a

Line/accession	Recognized <i>Rph</i> gene	Isolate of <i>P. hordei</i>		
		ND8702	ND89-3	BRS76-12
Differential lines^b of barley				
Sudan (CI 6489)	<i>Rph1</i>	H	H	H
Peruvian (CI 935)	<i>Rph2</i>	L	H	H
Estate (CI 3410)	<i>Rph3</i>	L	L	H
Gold (CI 1145)	<i>Rph4</i>	H	H	H
Magnif (CI 13860)	<i>Rph5</i>	L	H	H
Bolivia (CI 1257)	<i>Rph6+2</i>	L	H	H
Cebada Capa (CI 6193)	<i>Rph7</i>	L	H	L
Egypt 4 (CI 6481)	<i>Rph8</i>	H	H	H
Hor 2596 (CI 1243)	<i>Rph9</i>	L	H	L
Clipper BC8	<i>Rph10</i>	H	H	H
Clipper BC67	<i>Rph11</i>	H	H	H
Triumph (PI 290195)	<i>Rph12</i>	L	H	L
Other <i>Hordeum vulgare</i> accessions used as parents				
Aim (CI 3737)	unknown	L	L	H
Bowman (PI 483237)	none	H	H	H
Moore (CI 7251)	none	H	H	H
CI 10149	unknown	L	L	H
CI 10506	unknown	L	L	H
CI 11187	unknown	L	L	H
CI 11188	unknown	L	L	H
PI 531849	unknown	L	L	L
PI 531935	unknown	L	L	H
PI 531990	unknown	L	L	H
<i>Hordeum spontaneum</i> accessions used as parents				
HS 1 3351	unknown	L	L	L
PI 405305	unknown	L	L	L
PI 466245	unknown	L	L	L
PI 466247	unknown	L	L	L
PI 466323	unknown	L	L	L
PI 466324	unknown	L	L	L
PI 466373	unknown	L	H	L
PI 466450	unknown	L	L	H
PI 466453	unknown	L	L	L

^a Infection type ratings were based on the 0–4 scale of Levine and Cherewick (1952). Low infection types (L) 0, 0;, 1, 2 or combinations thereof were considered indicative of host resistance, whereas high infection types (H) 3 and 4 or combinations thereof, of host susceptibility.

^b Leaf rust differentials were based on Steffenson and Jin (1992). Gene designations for Clipper BC8 and Clipper BC67 were based on Feuerstein et al. (1990) and for Triumph on Jin et al. (1993).

Table 2. Reactions (infection types) of parents and F₁ plants, and segregation in F₂ populations from crosses among *Hordeum vulgare* accessions to isolates of *Puccinia hordei*

Cross	<i>P. hordei</i> isolate	Parental ITs ^a	F ₁ IT	No. of F ₂ plants		Ratio fit	χ ²	Prob. (>χ ²)
				Low IT	High IT			
Aim/Estate	ND8702	0;/0;	0;	278	0	no seg.		
Aim/Estate	ND89-3	1,2/1,2	1,2	311	0	no seg.		
Aim/Estate	BRS76-12	3/3	3	0	166	no seg.		
Aim/Bowman	ND8702	0;,1/3,4	1,2	247	79	3:1	0.10	.749
Aim/Bowman	ND89-3	1,2/4,3	3	54	204	1:3	2.28	.131
Aim/CI 10149	ND8702	0;/0;	0;	601	0	no seg.		
Aim/CI 11187	ND8702	0;/0;	0;	552	0	no seg.		
CI 11187/Bowman	ND8702	0;/3,4	0;,1	240	80	3:1	0.00	1.000
Aim/CI 11188	ND8702	0;/0;	0;	592	0	no seg.		
CI 11188/Bowman	ND8702	0;/3,4	— ^b	222	66	3:1	0.67	.414
Aim/PI 531990	ND8702	0;/0;	0;	530	0	no seg.		
Bowman/PI 531990	ND8702	3,4/0;	0;,1	460	109	13:3	0.06	.804
Bowman/PI 531990	ND89-3	3/1,2	1,2	57	196	1:3	0.82	.364
Bowman/PI 531990	BRS76-12	3,4/3	—	0	268	no seg.		
PI 531935/Bowman	ND8702	0;/4,3	0;	394	133	3:1	0.02	.900
Aim/CI 10506	ND8702	0;/0;	0;	159	15	15:1	1.67	.196
Aim/PI 531849	ND8702	0;/0;	0;	303	14	15:1	1.82	.177
Aim/PI 531849	BRS76-12	3/0;,1	1,2	237	66	3:1	1.67	.196
Bowman/PI 531849	ND8702	3/0;	0;,1	269	79	3:1	0.98	.322
Bowman/PI 531849	ND89-3	3,4/0;	1,0;	289	88	3:1	0.55	.457

^a ITs denote infection types (see Table 1 for IT classification).

^b Dash indicates not tested.

ND8702 possesses a narrow virulence spectrum (i.e., virulent for only a few *Rph* genes). This isolate was useful because it is avirulent on all the putative new sources of resistance used in this experiment.

We made crosses between selected resistant accessions and several cultivars—Aim (CI 3737), Bowman (PI 483237), and Moore (CI 7251). Cultivar Bowman was used as the “universal” susceptible parent for most of the crosses, and cultivar Moore was used as the alternative susceptible parent when Bowman was not available. Cultivar Aim was thought to carry *Rph3* based on its reaction to different pathotypes of *P. hordei* (Brückner 1971), but this had not been confirmed genetically. Aim was used for allelism testing with many of the new sources of resistance because they exhibited similar responses to several leaf rust isolates and shared several morphological characters (Jin et al., in press).

We then evaluated the reaction of parental, F₁, and F₂ plants from crosses to the selected leaf rust isolates. Specific combinations of crosses and leaf rust isolates were chosen to screen progenies based on parental reactions to the three leaf rust isolates. Seven-day-old plants were inoculated with a suspension of urediniospores in a lightweight mineral oil (Soltrol 170) and then incubated for 16 h at 20°C ± 1°C in a chamber with humidity maintained near saturation. After the incubation period, plants were allowed to dry off slowly before being placed in a greenhouse at 22°C ± 3°C. At 12–14 days after inoculation, we rated infection types on plants according to the 0–4 scale of Levine and Cherewick (1952). On this scale, infection types 0, 0;, 1, and 2 indicate resistance, whereas infection types 3 and 4 indicate susceptibility. Detailed procedures of inoculation and incubation can be found in our earlier report (Steffenson et al. 1993).

Results and Discussion

Inheritance of Resistance to *P. hordei* in *H. vulgare*

The infection types of parental and F₁ plants, and segregation in F₂ populations from crosses involving resistant accessions of *H. vulgare*, are listed in Table 2. F₂ populations from a cross between Estate, the source of the gene designated as *Rph3* (Robertson et al. 1965), and Aim were evaluated using isolates ND8702, ND89-3, and BRS76-12. All F₂ plants tested were resistant to isolate ND8702 and ND89-3 but

susceptible to isolate BRS76-12. This confirms that the resistance of Aim is due to *Rph3*, as postulated by Brückner (1971).

Segregation of F_2 plants for resistance and susceptibility in the Aim/Bowman cross fit a ratio of 3:1 (resistant:susceptible) when evaluated with isolate ND8702 and a ratio of 1:3 (resistant:susceptible) when evaluated with isolate ND89-3. These ratios indicate that *Rph3* had a dominant inheritance pattern for resistance to isolate ND8702 but a recessive inheritance pattern for resistance to isolate ND89-3. Incomplete dominance, where a slightly higher infection type occurs in the heterozygous condition, has been reported for *Rph3* and other *Rph* genes in barley (Jin et al. 1993; Parlevliet 1976); however, a reversal of the inheritance pattern from dominant to recessive has not been observed previously in the barley:leaf rust pathosystem. Such a reversal of inheritance pattern relative to different pathogen isolates has been reported for resistance in wheat to both stem rust (Knott and Anderson 1956) and stripe rust (Lupton and Macer 1962).

In a previous study (Jin et al., in press), we found a high frequency of barley accessions from Egypt and the Mediterranean region that were resistant to isolate ND89-3 and susceptible to isolate BRS76-12. This reaction pattern is similar to that of Estate and Aim (Table 1) and suggested the possible presence of the *Rph3* allele in these accessions. We therefore crossed a sample of accessions from this group—CI 10149, CI 10506, CI 11187, CI 11188, and PI 531990—with cultivar Aim to corroborate this hypothesis (Table 2). With the exception of the cross Aim/CI 10506, susceptible F_2 plants were not observed from these crosses when the F_2 populations were evaluated with isolate ND8702. The lack of segregation in the F_2 generation suggested that the resistance allele *Rph3* from Aim was present in CI 10149, CI 11187, CI 11188, and PI 531990. A single dominant gene was detected in PI 531935, another accession from Egypt. The gene in PI 531935 is likely *Rph3*, based on its response to the three *P. hordei* isolates (Table 1), but the allelic relation could not be confirmed due to the lack of a cross with a *Rph3* source.

Although the response of accession CI 10506 was similar to the *Rph3* sources to several *P. hordei* isolates as discussed previously, segregation for resistant and susceptible F_2 plants in the cross Aim/CI 10506 fit a ratio of 15:1. This suggested that CI 10506 possesses a dominant gene different from *Rph3*. Segregation in an F_2

Table 3. Reactions (infection types) of parents and F_1 plants, and segregation in F_2 populations from crosses of *Hordeum spontaneum* with *H. vulgare* accessions to isolates of *Puccinia hordei*

Cross	<i>P. hordei</i> isolate	Parental ITs ^a	F_1 IT	No. of F_2 plants		Ratio fit	χ^2	Prob. (> χ^2)
				Low IT	High IT			
Aim/PI 466450	ND8702	0,1/0;	— ^b	185	14	15:1	0.21	0.647
PI 466324/Aim	BRS76-12	0,1/3	—	93	38	3:1	1.12	0.290
PI 466323/Bowman	ND8702	0,1/3,4	—	102	19	13:3	0.74	0.390
PI 466323/Bowman	ND89-3	1,0/4,3	2,1	273	109	3:1	2.55	0.111
PI 466453/Bowman	ND8702	0/3	—	174	44	13:3	0.29	0.588
PI 466453/Bowman	ND89-3	0,1/3	—	233	96	3:1	3.07	0.080
PI 466453/Bowman	BRS76-12	0/3	—	109	32	3:1	0.40	0.527
Bowman/PI 466245	ND8702	3,4/0;	0;	298	73	13:3	0.21	0.648
Bowman/PI 466245	ND89-3	3,4/3N ^c	3N ^c	364 ^d	132	3:1	1.74	0.187
Bowman/PI 466245	BRS76-12	3,4/0;	0;	200	48	13:3	0.06	0.807
PI 466247/Bowman	ND8702	0/3,4	—	232	45	13:3	1.14	0.286
PI 466247/Bowman	ND89-3	1,2/3,4	—	182	55	3:1	0.41	0.524
Aim/PI 466247	BRS76-12	3/0;	0;	105	14	13:3	3.81	0.051
Aim/HS I 3351	ND8702	0,1/0;	—	194	4	63:1	0.27	0.603
Moore/PI 466373	ND8702	4,3/0;	0,1	625	37	15:1	0.49	0.483
Moore/PI 466373	BRS76-12	3/3N ^c	3N ^c	104 ^d	39	3:1	0.39	0.530
Aim/PI 405305	ND8702	0/0,1	0;	548	20	61:3	1.73	0.188
Aim/PI 405305	ND89-3	1,2/0,1	2,1	210	47	55:9	3.80	0.051

^a ITs denote infection types (see Table 1 for IT classification).

^b Dash indicates not tested.

^c 3N denotes an infection type of 3 with necrotic reaction.

^d Plants with infection type 3N were classified into the group with low infection types in the following cross-isolate combinations: Bowman/PI 466245 with ND89-3, and Moore/PI 466373 with BRS76-12.

population of the cross Bowman/PI 531990 revealed that this accession possesses a recessive gene in addition to *Rph3*. The recessive gene conferred resistance to isolate ND8702 but not to isolates ND89-3 and BRS76-12. Based on the segregation pattern observed in crosses CI 11187/Bowman and CI 11188/Bowman, it appears that no other genes for resistance to isolate ND8702 were present in CI 11187 and CI 11188 other than *Rph3*.

Accession PI 531849, an experimental line from the United Kingdom, was the only *H. vulgare* line resistant to all three isolates used in this study (Table 1). This unique resistance pattern suggested that this accession possesses gene(s) that are apparently different from the other tested sources. Evaluations of the F_2 populations from crosses of PI 531849 with Aim and Bowman to the three *P. hordei* isolates indicated that this accession had a dominant gene, and that this gene segregated independently from *Rph3* (Table 2). The allelic relation between the putative new gene in PI 531849 and other defined *Rph* genes is under investigation.

Inheritance of Resistance to *P. hordei* in *H. spontaneum*

Table 3 lists the infection types of parental and F_1 plants, and segregation in F_2 populations from crosses between several selected accessions of *H. spontaneum* and *H. vulgare*. The parental reactions to the three *P. hordei* isolates are given in Table 1. The extended maturation period and ex-

cessive shattering of F_1 plants limited the number of F_2 seeds available for rust evaluations in some crosses involving several *H. spontaneum* accessions. Thus, the degree of confidence was low for the goodness-of-fit tests, particularly in those crosses where multiple genes were involved.

Accession PI 466450 possesses a dominant gene for resistance to isolate ND8702, and PI 466324 possesses a dominant gene for resistance to isolate BRS76-12. Accessions PI 466323, PI 466453, PI 466245, and PI 466247 each possess a single dominant gene for resistance to isolate ND89-3, as well as two genes, one dominant and the other recessive, for resistance to isolate ND8702. Accessions HS-I-3351 and PI 466373 each possess two dominant genes for resistance to isolate ND8702. Segregation of F_2 plants to isolates ND8702 and ND89-3 from the cross Aim/PI 405305 indicates the presence of two genes, one dominant and the other recessive, in accession PI 405305. The *Rph3* gene from Aim accounted for one of the dominant genes for resistance to ND8702 and for one of the recessive genes for resistance to ND89-3 in this cross.

The inheritance pattern observed in PI 466245 and PI 466247 to isolate BRS76-12 was similar to that observed to isolate ND8702 (13 resistant:3 susceptible). The similarity in inheritance pattern to different *P. hordei* isolates in a particular accession may suggest that the same genes confer resistance to different pathotypes. For

instance, the genes in PI 466245 that confer resistance to isolate ND8702 may be the same as those that confer resistance to isolate BRS76-12. This hypothesis, however, was not tested in this study because the same F₂ plants were not evaluated with different pathogen isolates. The difference in inheritance patterns in PI 466245 for resistance to isolates ND8702 and ND89-3 obviously indicates the presence of an additional virulence gene in ND89-3.

The necrotic reaction of barley in response to leaf rust infection is generally associated with low (0; and 1) infection types (Levine and Cherewick 1952). In the interaction between accession PI 466245 and isolate ND89-3, however, a necrotic reaction occurred after the uredinia developed to full size (denoted by 3N—a 3-type uredinial size, but with necrosis). A similar reaction was also observed in the interaction between PI 466373 and BRS76-12. Segregation of F₂ plants indicated that the unique infection type was controlled by a dominant gene in each of the two accessions. These dominant genes may be different from each other because the necrotic reaction was observed in response to different rust isolates.

A comparative study for leaf rust resistance between cultivated and wild barley from a large germ plasm collection indicated that sources of resistance with ef-

fective genes are rather limited in *H. vulgare*, but fairly common in *H. spontaneum* (Jin et al., in press). Although the inheritance study for leaf rust resistance in *H. spontaneum* was based on only a small number of accessions, it is apparent that resistance in this wild species is much more diverse than in *H. vulgare* in several aspects: the number of genes involved, the spectrum of resistance conferred by these genes, and the phenotypic expression of resistance. The genetic diversity of resistance observed in this study explained, in part, the high frequency of resistance present in *H. spontaneum* populations and the broad spectrum of resistance that these accessions confer. Allelism studies and evaluations of other *H. spontaneum* accessions should reveal the diversity of resistance genes accumulated in *H. spontaneum* populations over the long history of coevolution between the host species and the leaf rust pathogen.

References

- Brückner F, 1971. Inheritance of the resistance to barley leaf rust and powdery mildew of cereals in some barley varieties. *Genet Slechteni* 7:95-102.
- Feuerstein U, Brown AHD, and Burdon JJ, 1990. Linkage of rust resistance genes from wild barley (*Hordeum spontaneum*) with isozyme markers. *Plant Breed* 104: 318-324.
- Jin Y, Statler GD, Franckowiak JD, and Steffenson BJ, 1993. Linkage between leaf rust resistance genes and

morphological markers in barley. *Phytopathology* 83: 230-233.

Jin Y, Steffenson BJ, and Bockelman HE, in press. Evaluation of cultivated and wild barley for resistance to pathotypes of *Puccinia hordei* with wide virulence. *Genet Res Crop Evol*.

Knott DR and Anderson RG, 1956. The inheritance of rust resistance: I. The inheritance of stem rust resistance in ten varieties of common wheat. *Can J Agric Sci* 36:174-195.

Levine MN and Cherewick WJ, 1952. Studies on dwarf leaf rust of barley. US Dept Agric Tech Bull No. 1057.

Lupton FGH and Macer RCF, 1962. Inheritance of resistance to yellow rust (*Puccinia glumarum* Erikss. & Henn.) in seven varieties of wheat. *Trans Br Mycol Soc* 45:21-45.

Manisterski J, Treeful LM, Tomerlin JR, Anikster Y, Moseman JG, Wahl I, and Wilcoxson RD, 1986. Resistance of wild barley accessions from Israel to leaf rust collected in the USA and Israel. *Crop Sci* 26:727-730.

Moseman JG, Nevo E, and El-Morshidy MA, 1990. Reactions of *Hordeum spontaneum* to infection with two cultures of *Puccinia hordei* from Israel and the United States. *Euphytica* 49:169-175.

Parlevliet JE, 1976. The genetics of seedling resistance to leaf rust, *Puccinia hordei* Otth in some spring barley cultivars. *Euphytica* 25:249-254.

Robertson DW, Wiebe GA, Shands RG, and Hagberg A, 1965. A summary of linkage studies in cultivated barley, *Hordeum* species: supplement III, 1954-1963. *Crop Sci* 5:33-43.

Steffenson BJ and Jin Y, 1992. Evaluation of barley genotypes for differentiating pathotypes of *Puccinia hordei*. In: Proceedings of the 8th European and Mediterranean Cereal Rusts and Mildew Conference, 1992 (Zeller FJ and Fischbeck G, eds). Weihenstephan, Germany: Verlag Th. Mann; 126-128.

Steffenson BJ, Jin Y, and Griffey CA, 1993. Pathotypes of *Puccinia hordei* with virulence for the barley leaf rust resistance gene *Rph7* in the United States. *Plant Dis* 77: 867-869.

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