Recessive Genes for Resistance to *Puccinia striiformis* f. sp. *hordei* in Barley

Xianming Chen and Roland F. Line

U.S. Department of Agriculture, Agricultural Research Service, Washington State University, Pullman 99164-6430.
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ABSTRACT

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Barley genotypes Abyssinian 14, BBA 2890, Grannelose Zweizeilige, PI 548708, PI 548734, PI 548747, and Stauffers Obersulzer are resistant to all races of *Puccinia striiformis* f. sp. *hordei* identified thus far in North America. Astrix, BBA 809, Bigo, Cambrinus, Emir, Heils Franken, Hiproly, I5, Mazurka, Trumpf, and Varunda have specific resistance to certain races, whereas Topper and Steptoe are susceptible to all races. Seedlings of parents and F₁, F₂, and F₃ progeny from crosses of resistant genotypes with Topper and Steptoe were tested for resistance to North American *P. striiformis* f. sp. *hordei* races PSH-1, PSH-4, PSH-10, PSH-13, and PSH-20. When tested with PSH-1, one recessive gene was detected in BBA 809, BBA 2890, Bigo, Hiproly, and Grannelose Zweizeilige; two recessive genes were detected in Emir, I5, PI 548708, PI 548734, PI 548747, Varunda, and Astrix; and one dominant gene and one recessive gene were detected in Abyssinian 14 and Stauffers Obersulzer.

In tests with PSH-4, one recessive gene was detected in BBA 809, two recessive genes were detected in Trumpf, and two partially recessive genes were detected in Astrix. In tests with PSH-13, one recessive gene was detected in BBA 2890, Grannelose Zweizeilige, I5, and PI 548708 and two recessive genes were detected in Abyssinian 14, Hiproly, PI 548734, and PI 548747. In tests with PSH-20, one recessive gene was detected in Bigo and a recessive gene and a dominant gene were detected in Heils Franken. A gene in Cambrinus for resistance to PSH-10 and a gene in Mazurka for resistance to PSH-20 were dominant on the basis of the response of the first seedling leaf but recessive on the basis of the response of the second leaf. Four different types of epistasis were detected. Information on the number of genes, mode of inheritance, and nonallelic gene interactions should be useful in understanding the host-pathogen interaction and in breeding barley for resistance to stripe rust.

Additional keywords: *Hordeum vulgare* L., race-specific resistance.

Stripe rust of barley (*Hordeum vulgare* L.), caused by *Puccinia striiformis* Westend. f. sp. *hordei* (syn. *P. glumarum* (J. C. Schmidt) Eriks. & E. Henn.), was first observed in the United States in 1991 at Uvalde, TX (33). Since then, the disease has been detected in other areas of Texas as well as in Oklahoma, New Mexico, Arizona, Colorado, Utah, California, Idaho, Montana, Oregon, and Washington (16). The disease is firmly established in the United States, especially in California and the Pacific Northwest, where the environment is very favorable for its development. Because most cultivars grown in the region are susceptible, the disease has a high potential for causing major losses if not controlled.

The use of resistant cultivars has been the most economical method of controlling rusts on cereals. However, information on the nature and genetics of resistance to stripe rust of barley is limited. Probably the earliest report on the genetics of barley stripe rust resistance was that by Murty (30) in 1942 in India. In that study, stripe rust resistance in the American cultivar Alpha was found to be conditioned by two dominant genes. Genetic studies of stripe rust resistance in nine barley genotypes conducted in India were reported during the 1960s (1-4,20,26,34,37). Eight loci for resistance to different Indian races in three barley genotypes, E.B. 145, E.B. 410, and E.B. 438, were named *Ps1* to *Ps8* with multiple alleles at the *Ps1* and *Ps3* loci (4). Among 11 resistant alleles at the eight loci, eight were dominant and three were recessive (4). Different types of epistasis, such as duplicate dominant, independent recessive, complementary recessive, and inhibitory genes, were reported (1-4,20,26,37).

In Europe, Nover and Scholz (31) studied resistance in Bigo, Abyssinian 14, BBA 2890, Abed Binder 12, and I5 to the European race 24 of *P. striiformis* (*P. striiformis* f. sp. *hordei*) and found that the resistance of all five genotypes was controlled by single recessive genes. Allelism tests suggested that Bigo, Abyssinian 14, and BBA 2890 had resistant alleles at the same locus, which was designated *yr*. A gene in Abed Binder 12 was designated *yr2*, and a gene in I5 was designated *yr3*. Johnson (21) reported another gene in cultivars Europa, Cambrinus, and Deba Abed designated *Yr4*.

Upadhyay and Prakash (36) studied the stripe rust resistance of barley genotypes to Indian races, including the Indian culture that they considered to be race 24. They reported that Bigo was susceptible to the Indian culture of race 24 and that Abyssinian 14 had one or more additional genes for resistance. In contrast to the study by Nover and Scholz (31), it is not clear whether the races used in India were *P. striiformis* f. sp. *hordei* or f. sp. *tritici*. It is also likely that the Indian race 24 was not the same as the European race 24. Most of the races used in the Indian studies were virulent on wheat genotype Michigan Amber, which is resistant to race 24 in Europe and all PSH races of *P. striiformis* f. sp. *hordei* detected in the United States (16,23,35).

We have reported 31 PSH races of *P. striiformis* f. sp. *hordei* (16,23) since barley stripe rust was first reported in 1991 in the United States (33), and we assume that there are probably additional races. The first genetic study of barley stripe rust resistance in North America was conducted by Chen et al. (7) at Oregon State University in cooperation with the International Wheat and Maize Research Center (CIMMYT) in Mexico. In that study, the stripe rust response of a doubled haploid population was evaluated in Mexico. Using molecular markers and quantitative trait loci mapping approaches, Chen et al. (7) mapped two quantitative trait loci conferring resistance in an elite six-row spring feed barley to the M arms of chromosomes 7 and 4.

Corresponding author: Xianming Chen; E-mail address: xianming@mail.wsu.edu

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In a previous study (16), we reported that barley genotypes PI 548708, PI 548734, PI 548747, BBA2890, Abyssinian 14, Grannelose Zweizeilige, and Stauffers Obersulzer were resistant to all PSH races of *P. striiformis* f. sp. *hordei* that have been detected in the United States so far and that Heils Franken, Emir, Astrix, Hiproly, Varunda, Trumpf, Mazurka, Bigo, I5, Cambrinus, and BBA 809 were resistant to some PSH races. Genes for resistance in these genotypes might be useful in breeding for resistance and in understanding host-pathogen interactions.

The objectives of this study were to determine the number of genes for resistance and their mode of inheritance in 18 resistant barley genotypes.

MATERIALS AND METHODS

The resistant and resistant/susceptible barley genotypes listed in Table 1 were crossed with the susceptible cultivars Topper and Steptoe by using the susceptible cultivars as the male parents. Reciprocal crosses were also made in which Steptoe was the female parent. F₂ progeny were obtained for all crosses, and F₃ progeny were obtained for the crosses by using Steptoe as the female parent.

Seedlings of parents and F₁, F₂, and F₃ progeny were planted, inoculated, and grown under controlled conditions described by Chen and Line (10,11,13). North American races PSH-1, PSH-4, PSH-10, PSH-13, and PSH-20 of *P. striiformis* f. sp. *hordei* were used to test the resistance. When possible, five to ten parental seedlings, one to three F₁ seedlings, 120 to 180 F₂ seedlings, and 89 to 120 F₃ lines with 12 to 25 seedlings from each line were tested.

Data on infection types were recorded 18 to 22 days after inoculation. A scale of 0 to 9, as described by Line et al. (24), was used. Infection types 0 to 3 were classified as resistant reactions, 4 to 6 as intermediate, and 7 to 9 as susceptible. Chi-square tests were used to determine the goodness of fit of the segregation ratios. For F₃ populations that were tested with two different races, chi-square tests were used to test the hypothesis of independent genes for resistance to each race. If the probability for the hypothesis was less than 0.01, we concluded that the genes controlling resistance to different races were either the same or linked.

RESULTS

Infection types of parents and F₁ progeny, observed resistant, intermediate, and susceptible F₂ plants, expected F₂ segregation ratios, and probabilities of chi-square tests for goodness of fit of the segregation ratios are shown in Tables 2 and 3. Numbers of homozygous resistant, segregating, and homozygous susceptible F₃ lines, expected ratios, and probabilities of chi-square tests for goodness of fit of the segregation ratios are shown in Table 4. In most cases, results were identical in the reciprocal crosses with Steptoe and the crosses with Topper, and therefore the pooled data are presented in Table 2. The F₃ data agreed with the F₂ data. F₁ plants from all crosses except the crosses with Astrix tested with PSH-4 had a high infection type (IT 8), which is a susceptible reaction. F₁ plants from the crosses with Astrix tested with PSH-4 had an intermediate infection type (IT 5). These results indicated that all cultivars except Astrix had resistance that was controlled by recessive genes.

Single recessive genes for resistance. The F₂ populations from crosses of BBA 809, BBA 2890, and Bigo with Topper and Steptoe and of Grannelose Zweizeilige with Steptoe segregated in a 1:3 (resistant/susceptible) ratio (Table 2). The F₃ populations of the four resistant genotypes crossed with Steptoe segregated in a 1:2:1 (homozygous resistant/segregating/homozygous susceptible) ratio (Table 4). These results indicated that BBA 809 had a single recessive gene for resistance to PSH-1 and PSH-4, Bigo had a single recessive gene for resistance to PSH-1 and PSH-20, and BBA 2890 and Grannelose Zweizeilige had single recessive genes for resistance to races PSH-1 and PSH-13 on the basis of the reciprocal crosses with Steptoe. The segregation of the Grannelose Zweizeilige × Topper cross tested with PSH-1 and PSH-13 best fit a 3:13 ratio, suggesting that Topper had a suppressor gene. Chi-square analyses for independent genes (Table 5) indicated that the genes in BBA 809 controlling resistance to PSH-1 and PSH-4 and the genes in Bigo controlling resistance to PSH-1 and PSH-20 were either the same or linked.

Resistance gene recessive in the second leaf and dominant in the first leaf. When tested with PSH-1 (Table 3), Mazurka had IT 2 on both the first (the bottom) and second leaves and Topper and Steptoe had IT 8 on both the first and second leaves. However, the

TABLE 1. Barley genotypes used in crosses, their identification numbers, origins, plant types, and reactions to specific races of *Puccinia striiformis* f. sp. *hordei* (PSH)

Genotype	Identification number ^a	Origin	Plant type ^b	Reaction to PSH races ^c					
				1	4	10	13	20	All races
Steptoe	CIHO 15229	United States	6-row	S	S	S	S	S	S
Topper	...	Netherlands	6-row	S	S	S	S	S	S
I5	PI 268187	Croatia	6-row	R	R	R	R	R	R
Hor 1428	PI 548708	Ethiopia	2-row	R	R	R	R	R	R
Hor 2926	PI 548734	Ethiopia	2-row	R	R	R	R	R	R
Hor 3209	PI 548747	Ethiopia	6-row	R	R	R	R	R	R
BBA 2890	BBA 2890	Germany	6-row	R	R	R	R	R	R
Abyssinian 14	PI 151789	Ethiopia	6-row	R	R	R	R	R	R
Grannelose Zweizeilige	PI 548740	Ethiopia	2-row	R	R	R	R	R	R
Stauffers Obersulzer	PI 467580	Germany	2-row	R	R	R	R	R	R
Heils Franken	PI 290183	Germany	2-row	S	S	R	S	R	R/S
Emir	PI 321787	Netherlands	2-row	R	R	S	S	S	R/S
Astrix	PI 339826	France	6-row	R	R	R	R	R	R/S
Hiproly	PI 060693	Egypt	2-row	R	S	S	R	R	R/S
Varunda	PI 410865	Netherlands	2-row	R	R	S	S	S	R/S
Trumpf	PI 548762	Germany	2-row	R	R	R	S	S	R/S
Mazurka	PI 399501	Netherlands	2-row	R	R	R	S	S	R/S
Bigo	PI 321857	Netherlands	6-row	R	R	R	S	R	R/S
Cambrinus	PI 321779	Netherlands	2-row	S	S	R	S	S	R/S
BBA 809	BBA 0809	Germany	6-row	R	R	S	S	R	R/S

^a PI = plant introduction number, and CIHO = cultivar identification number of *Hordeum*.

^b Astrix is a winter barley, and all other genotypes are spring barley. Grannelose Zweizeilige is awnless, and all other genotypes are awned. Grannelose Zweizeilige and Hiproly are hull-less, and all other genotypes are covered.

^c S = susceptible, R = resistant, and R/S = resistant to some of all races detected in the United States and susceptible to other races.

F₁ plants had IT 2 on the first leaves and IT 8 on the second leaves. When the infection type data of the first leaves were analyzed, the F₂ populations segregated in a 3:1 (resistant/susceptible) ratio. When the infection type data of the second leaves were analyzed, the F₂ populations segregated in a 1:3 (resistant/susceptible) ratio. Thus, the F₂ plants could be grouped into three classes: first and second leaves resistant, first leaf resistant and second leaf susceptible, and first and second leaves susceptible. A 1:2:1 ratio was obtained for the reciprocal crosses of Mazurka with Steptoe and with Topper. The F₃ plants from the Steptoe × Mazurka cross were also separated into the three classes. Plants that had IT 2 on the first leaf and IT 8 on the second leaf were observed only in the lines that were segregating. Segregation of the F₃ population fit a 1:2:1 ratio for resistant, segregating, and susceptible lines (Table 4). Similar results were obtained when the same crosses were tested with PSH-20. The results of the chi-square tests for independent genes (Table 5) indicated that the gene for resistance to PSH-1 and the gene for resistance to PSH-20 were either the same or linked. In tests with PSH-10 (Tables 3 and 4), the results of parents, F₁, F₂, and F₃ from crosses of Cambrinus with Topper and Steptoe were similar to those of the Mazurka crosses with Steptoe and Topper tested with PSH-1 and PSH-20. These results indicated that the genes in Mazurka and Cambrinus were expressed dominantly in the first leaf and recessively in the second leaf.

Two independent recessive genes for resistance. When tested with race PSH-1 (Table 2), the F₂ populations from crosses of PI 548734, PI 548747, PI 548708, and Astrix with Topper and Steptoe segregated in a 7:9 ratio. The F₃ lines from the crosses with Steptoe tested with the same race segregated in a 7:8:1 (resistant/segregating/susceptible) ratio. When tested with race PSH-13, the F₂ populations from crosses of PI 548734 and PI 548747 with Topper and Steptoe segregated in a 7:9 ratio, but the F₂ populations of PI 548708 with Topper and Steptoe segregated in 1:3 (resistant/susceptible) ratio. These results indicated that PI 548734 and PI 548747 each had two independent recessive genes for resistance to PSH-1 and PSH-13 and that PI 548708 had two independent recessive genes for resistance to PSH-1 but only one gene for resistance to PSH-13.

When tested with race PSH-1 (Table 2), F₂ segregation of crosses of I5 with Topper and Steptoe with I5 as the female parent fit a ratio of 7:9 (resistant/susceptible) plants, indicating that I5 had two independent recessive genes. The F₂ segregation of the cross of I5 with Steptoe in which I5 was used as the male parent best fit a 3:13 (resistant/susceptible) ratio, suggesting a recessive gene and a dominant gene, which were complementary, for resistance. The 1:8:7 F₃ ratio obtained from the same cross also showed that resistance to PSH-1 was conditioned by the complementary recessive and dominant genes (Table 4). When tested with race CDL-

TABLE 2. Stripe rust infection types produced on seedlings of the parents and F₁ plants by specific races of *Puccinia striiformis* f. sp. *hordei* (PSH), observed resistant, intermediate, and susceptible F₂ plants, expected F₂ segregation ratios, and probabilities of chi-square tests for goodness of fit to the segregation ratios

Cross ^a		PSH race	Infection type ^b			Observed no. of F ₂ plants ^c		Expected ratio ^d (R:S)	P ^e
R-parent	S-parent		R-p	S-p	F ₁	R	S		
BBA 809	Top, Ste(M), Ste(F)	1	2	8	8	124	357	1:3	0.69
BBA 809	Top, Ste(M), Ste(F)	4	1	8	8	111	352	1:3	0.61
BBA 2890	Top, Ste(M), Ste(F)	1	1	8	8	107	369	1:3	0.20
BBA 2890	Top, Ste(M)	13	1	8	8	76	248	1:3	0.52
Bigo	Top, Ste(M), Ste(F)	1	1	8	8	106	384	1:3	0.09
Bigo	Top, Ste(M), Ste(F)	20	2	8	8	130	352	1:3	0.32
G. Zweizeilige	Ste(M), Ste(F)	1	2	8	8	70	215	1:3	0.86
G. Zweizeilige	Top	1	2	8	8	24	142	3:13	0.16
G. Zweizeilige	Top	13	1	8	8	21	144	3:13	0.05
G. Zweizeilige	Ste(M)	13	1	8	8	32	101	1:3	0.80
PI 548734	Top, Ste(M), Ste(F)	1	1	8	8	218	269	7:9	0.65
PI 548734	Top, Ste(M)	13	1	8	8	137	180	7:9	0.85
PI 548747	Top, Ste(M), Ste(F)	1	1	8	8	192	299	7:9	0.04
PI 548747	Top, Ste(M)	13	1	8	8	139	200	7:9	0.31
PI 548708	Top, Ste(M), Ste(F)	1	1	8	8	184	243	7:9	0.78
PI 548708	Top, Ste(M)	13	1	8	8	97	243	1:3	0.13
I5	Top, Ste(M)	1	2	8	8	132	209	7:9	0.06
I5	Ste(F)	1	2	8	8	13	60	3:13	0.84
I5	Top, Ste(M)	13	2	8	8	82	253	1:3	0.83
Hiproly	Ste(M), Ste(F)	1	2	8	8	60	198	1:3	0.52
Hiproly	Top	1	2	8	8	26	136	3:13	0.38
Hiproly	Top, Ste(M)	13	1	8	8	21	229	1:15	0.16
Abyssinian 14	Top, Ste(M), Ste(F)	1	2	8	8	100	370	3:13	0.16
Abyssinian 14	Top, Ste(M)	13	0	8	8	23	281	1:15	0.34
Heils Franken	Top, Ste(M), Ste(F)	20	2	8	8	54	316	3:13	0.04
Emir	Top, Ste(M), Ste(F)	1	1	8	8	33	421	1:15	0.37
Varunda	Top, Ste(F)	1	2	8	8	25	309	1:15	0.35
Varunda	Ste(M)	1	2	8	8	13	96	3:13	0.07
Trumpf	Top, Ste(M), Ste(F)	1	2	8	8	38	428	1:15	0.09
Trumpf	Top, Ste(M), Ste(F)	4	2	8	8	30	353	1:15	0.20
Astrix	Top, Ste(M), Ste(F)	1	3	8	8	184	246	7:9	0.69
Astrix	Top, Ste(M), Ste(F)	4	2	8	5	142 (105)	188	5:4:7	0.81
St. Obersulzer	Top, Ste(M)	1	3	8	8	44	273	3:13	0.03
St. Obersulzer	Ste(F)	1	3	8	8	13	144	2:14	0.11

^a R-parent = resistant parent; G. Zweizeilige = Granellose Zweizeilige; St. Obersulzer = Stauffers Obersulzer; S-parent = susceptible parent; Top = Topper, used as male parent; and Ste = Steptoe, used as either male parent (M) or female parent (F).

^b R-p = the resistant parent, and S-p = the susceptible parent or parents.

^c R = resistant, and S = susceptible. The number of F₂ plants with intermediate resistance in crosses involving Astrix tested with race PSH-4 is in parentheses.

^d All ratios are for resistant (R) to susceptible (S) plants, except the tests of Astrix crosses tested with race PSH-4, for which the ratio is resistant to intermediate to susceptible plants.

^e Probability of chi-square test for goodness of fit.

^f Not tested.

TABLE 3. Infection types produced by specific races of *Puccinia striiformis* f. sp. *hordei* on seedlings of parents and F₁ progeny, number of F₂ plants that were resistant or susceptible on the first seedling leaf and second seedling leaf, the expected F₂ ratios, and probabilities of chi-square tests for the goodness of fit to the segregation ratios

Cross (female × male)	PSH race	Leaf position	Infection type ^a			No. of F ₂ plants ^b			F ₂ ratio	
			FP	MP	F ₁	R	S/R	S	R:(S/R):S	P ^c
Mazurka × Topper	1	1st	2	8	2	123		45	3:1	0.59
		2nd	2	8	8	43		125	1:3	0.86
		2nd/1st	2/2	8/8	8/2	43	80	45	1:(2):1	0.81
Mazurka × Steptoe	1	1st	2	8	2	125		37	3:1	0.53
		2nd	2	8	8	50		112	1:3	0.08
		2nd/1st	2/2	8/8	8/2	50	75	37	1:(2):1	0.10
Steptoe × Mazurka	1	1st	8	2	2	114		38	3:1	1.00
		2nd	8	2	8	40		112	1:3	0.71
		2nd/1st	8/8	2/2	8/2	40	74	38	1:(2):1	0.92
Mazurka × Topper	20	1st	1	8	2	127		37	3:1	0.47
		2nd	2	8	8	41		123	1:3	1.00
		2nd/1st	2/1	8/8	8/2	41	86	37	1:(2):1	0.75
Mazurka × Steptoe	20	1st	1	8	1	121		42	3:1	0.82
		2nd	2	8	8	43		120	1:3	0.68
		2nd/1st	2/1	8/8	8/1	43	78	42	1:(2):1	0.86
Steptoe × Mazurka	20	1st	8	1	1	121		40	3:1	0.96
		2nd	8	2	8	41		120	1:3	0.89
		2nd/1st	8/8	2/1	8/1	41	80	40	1:(2):1	0.99
Cambrinus × Topper	10	1st	2	8	2	132		38	3:1	0.43
		2nd	2	8	8	42		128	1:3	0.93
		2nd/1st	2/2	8/8	8/2	42	90	38	1:(2):1	0.76
Cambrinus × Steptoe	10	1st	2	8	2	134		43	3:1	0.83
		2nd	2	8	8	46		131	1:3	0.76
		2nd/1st	2/2	8/8	8/2	46	88	43	1:(2):1	0.95
Steptoe × Cambrinus	10	1st	8	2	2	132		38	3:1	0.43
		2nd	8	2	8	42		128	1:3	0.93
		2nd/1st	8/8	2/2	8/2	42	90	38	1:(2):1	0.76

^a FP = female parent, and MP = male parent.

^b R = resistant, S = susceptible, and S/R = susceptible reaction on the second leaf and resistant reaction on the first leaf.

^c Probability of chi-square test for goodness of fit.

TABLE 4. Total number of F₃ lines evaluated, number of F₃ lines that were homozygous for resistance, segregating for resistance (heterozygous), or homozygous for susceptibility when crosses of resistant genotypes with susceptible Steptoe were tested with North American races of *Puccinia striiformis* f. sp. *hordei* (PSH), expected ratios, and probability of chi-square tests for goodness of fit

Resistant parent	PSH race	Number of F ₃ lines				Expected F ₃ ratio ^a (RES:SEG:SUS)	P ^b
		Total	Resistant	Segregating	Susceptible		
BBA 809	1	120	21	68	31	1:2:1	0.15
BBA 809	4	120	32	61	27	1:2:1	0.80
BBA 2890	1	89	18	47	24	1:2:1	0.58
Bigo	1	109	37	59	13	1:2:1	0.01
Bigo	20	109	27	63	19	1:2:1	0.15
Grannelose Zweizeilige	1	93	23	45	25	1:2:1	0.91
Hiproly	1	105	21	55	28	1:2:1	0.53
Mazurka	1	89	18	52	19	1: 2:1	0.28
Mazurka	20	96	26	54	16	1:2:1	0.17
Cambrinus	10	112	27	56	29	1:2:1	0.96
I5	1	105	6	51	48	1:8:7	0.91
Abyssinian 14	1	99	7	54	38	1:8:7	0.56
Abyssinian 14	13	100	7	57	36	1:8:7	0.29
I 5	1	105	6	51	48	1:8:7	0.91
Abyssinian 14	1	99	7	54	38	1:8:7	0.56
Abyssinian 14	13	100	7	57	36	1:8:7	0.29
Emir	1	109	6	58	45	1:8:7	0.79
Varunda	1	111	8	61	42	1:8:7	0.45
Trumpf	1	114	8	62	44	1:8:7	0.54
PI 548708	1	111	47	56	8	7:8:1	0.90
PI 548734	1	100	43	48	9	7:8:1	0.52
PI 548747	1	120	49	60	11	7:8:1	0.39
Astrix	1	106	38	59	9	7:8:1	0.22
Heils Franken	20	110	9	65	36	1:8:7	0.06
Stauffers Obersulzer	1	111	8	56	47	1:8:7	0.90

^a RES = homozygous resistant, SEG = segregating, and SUS = susceptible.

^b Probability of chi-square test for goodness of fit.

13, the F₂ populations from crosses of I5 with Topper and Steptoe segregated in a 1:3 (resistant/susceptible) ratio, indicating that I5 had one recessive gene for resistance to race PSH-13 (Table 2).

Two complementary recessive genes for resistance. In crosses of Emir, Varunda, and Trumpf with Topper and Steptoe tested with PSH-1, of Trumpf with Topper and Steptoe tested with PSH-4, and of Hiproly and Abyssinian 14 with Topper and Steptoe tested with PSH-13, the F₂ populations segregated in a 1:15 (resistant/susceptible) ratio (Table 2) and the F₃ populations segregated in a 1:8:7 (homozygous resistant/segregating/homozygous susceptible) ratio (Table 4). The results indicated that the four genotypes each had two complementary recessive genes for resistance to the races with which they were tested. The F₂ population of the reciprocal crosses of Hiproly with Steptoe tested with PSH-1 (Table 2) segregated in a 1:3 (resistant/susceptible) ratio, indicating one recessive gene for resistance to PSH-1. The segregation of the Hiproly-Topper cross tested with PSH-1 best fit a 3:13 ratio, indicating that Topper had a suppressor gene. The F₂ population of Abyssinian 14 segregated in a 3:13 (resistant/susceptible) ratio when inoculated with PSH-1, indicating complementary interaction of a recessive gene and a dominant gene. The F₃ data (Table 4) of the female Steptoe crossed with Hiproly (1:2:1) and with Abyssinian 14 (1:8:7) tested with PSH-1 supported the F₂ results. Chi-square analysis for independent genes with the F₃ data of the Steptoe-Abyssinian 14 cross tested with PSH-1 and PSH-13 (Table 5) indicated that the genes in Abyssinian 14 for resistance to PSH-1 and PSH-13 were not independent.

One recessive gene and one dominant gene for resistance. When the Heils Franken crosses were tested with PSH-20 and the Stauffers Obersulzer crosses and the Varunda × Steptoe cross were tested with PSH-1, a 3:13 (resistant/susceptible) ratio was obtained for the F₂ populations (Table 2). When the cross Steptoe × Stauffers Obersulzer, in which Steptoe was the female parent, was tested with PSH-1, the segregation best fit a 2:14 ratio instead. The F₃ lines from crosses of the female Steptoe with Heils Franken and with Stauffers Obersulzer segregated in a 1:8:7 (resistant/segregating/susceptible) ratio (Table 4). These results indicated that Heils Franken had a recessive gene and a dominant gene for resistance to PSH-4, Stauffers Obersulzer had a recessive gene and a dominant gene for resistance to PSH-1, and the genes in both genotypes were complementary.

TABLE 5. Phenotypic reactions to different races of *Puccinia striiformis* f. sp. *hordei* (PSH), observed number of F₃ lines, and probabilities of chi-square tests for independent genes in Steptoe × BBA 809, Steptoe × Bigo, Steptoe × Mazurka, and Steptoe × Abyssinian 14

Phenotype ^a		Observed number of F ₃ lines from crosses of resistant genotypes with Steptoe ^b			
1st race	2nd race	BBA 809	Bigo	Mazurka	Abyssinian 14
RES	RES	18	22	17	1
RES	SEG	3	14	1	6
RES	SUS	0	0	0	0
SEG	RES	13	5	6	6
SEG	SEG	42	48	41	35
SEG	SUS	13	7	5	13
SUS	RES	0	0	0	0
SUS	SEG	16	1	8	16
SUS	SUS	15	12	11	22
Total		120	109	89	99
P for independent genes ^c		<0.001	<0.001	<0.001	0.006

^a The first race was PSH-1 for all tests, and the second race was PSH-4 for Steptoe × BBA 809, PSH-20 for Steptoe × Bigo and Steptoe × Mazurka, and PSH-13 for Steptoe × Abyssinian 14. RES = resistant, SEG = segregating, and SUS = susceptible.

^b Steptoe was used as the female parent in all crosses.

^c Probability of chi-square test for two independent recessive genes in the crosses of BBA 809, Bigo, and Mazurka. For the Abyssinian 14 cross, the chi-square test was for the hypothesis that the two genes (complementary dominant and recessive) for resistance to race PSH-1 are independent of the two genes (complementary recessive) for resistance to PSH-13.

Two partially dominant genes for resistance. When tested with race PSH-4 (Table 2), the F₁ plants from the reciprocal crosses of Astrix with Steptoe had an intermediate infection type (IT 5), and segregation in F₂ populations from crosses of Astrix with Topper and Steptoe fit a 5:4:7 ratio for resistant, intermediate, and susceptible plants. These results suggested that Astrix had two partially dominant genes for resistance to PSH-4 and that the susceptible alleles were epistatic.

DISCUSSION

Number of barley genes for resistance to stripe rust. Unlike the number of genes reported in wheat for resistance to *P. striiformis* f. sp. *tritici* (6,8–15,25,27,28), only a few genes in barley have been reported for resistance to *P. striiformis* f. sp. *hordei*. Eight loci (*Ps1* to *Ps8*), some with multiple resistant alleles, were reported by Indian scientists (4); four genes (*yr*, *yr2*, *yr3*, and *Yr4*) were reported by European scientists (21,31); and two unnamed genes were reported by Chen et al. (7) in North America. The genes detected in this study greatly increase the number of known genes for stripe rust resistance in barley.

Of the 18 barley genotypes investigated in this study, three have a single gene and 15 have two or more genes for resistance (Table 6). Data on the reactions to different races of *P. striiformis* f. sp. *hordei* (16) indicate that there are at least 20 different genes in the resistant genotypes.

Of the 18 genotypes, only five (Abyssinian 14, BBA 2890, Bigo, Cambrinus, and I5) have been previously studied. Nover and Scholz (31) reported that Bigo had a single gene, and Johnson (21) reported that Cambrinus had a single gene. Our data agree with their results. However, Nover and Scholz (31) reported that

TABLE 6. Number of and dominance (D), recessiveness (R), and partial recessiveness (P) of genes in barley genotypes for resistance to PSH races of *Puccinia striiformis* f. sp. *hordei*

Genotype	PSH race	Inheritance of resistance	
		Number of genes	Mode of inheritance ^a
BBA 2890	1	1	1R
	13	1	1R
Granellose Zweizeilige	1	1	1R
	13	1	1R
PI 548734	1	2	2R
	13	2	2R
PI 548747	1	2	2R
	13	2	2R
PI 548708	1	2	2R
	13	1	1R
I 5	1	2	2R
	13	1	1R
Emir	1	2	2R
Varunda	1	2	2R
Hiproly	1	1	1R
	13	2	2R
Bigo	1	1	1R
	20	1	1R
BBA 809	1	1	1R
	4	1	1R
Trumpf	1	2	2R
	4	2	2R
Astrix	1	2	2R
	4	2	2P
St. Obersulzer	1	2	1R,1D
Abyssinian 14	1	2	1R,1D
	13	2	2R
Heils Franken	20	2	1R,1D
Cambrinus	10	1	1R/D
Mazurka	1	1	1R/D
	20	1	1R/D

^a R = recessive, D = dominant, P = partially recessive, and R/D = recessive on the second leaf and dominant on the first leaf.

Abyssinian 14 and I5 each had a single gene, but we detected two genes in each of these genotypes. One of the two genes that we detected in Abyssinian 14 and I5 is probably the same as the gene in Nover and Scholz's report (31).

It is possible to determine whether the same gene or genes, linked genes, or different genes control resistance to different races by testing F_3 populations with different races. Because of the large number of crosses, we tested F_3 populations of the four resistant genotypes with two races. In these tests, the data suggest that either the same or linked genes confer resistance to both races. Further studies are needed to determine whether they are the same or linked genes. Race PSH-1, which is virulent on only two of the 11 differential genotypes (16), should detect the most resistance genes. This was true for all tests except tests of the progeny from crosses of Hiproly with Topper and Steptoe, which showed one gene for resistance to PSH-1 but two genes for resistance to PSH-13, a race that is virulent on seven of the eleven differential genotypes (16).

Effects of susceptible parents and reciprocal crosses on segregation ratios. In earlier genetic studies of wheat stripe rust resistance, we reported that gene interactions differed depending upon the susceptible parent used in the cross and differed even in some reciprocal crosses (10,11,14). In this study with barley, few such differences were detected. We crossed the 18 genotypes with susceptible Topper and Steptoe using Topper and Steptoe as the male parents and made reciprocal crosses with Steptoe as the female parent. Topper was developed in Europe. Steptoe was developed in Washington State of the United States and has been widely grown in the United States. Both cultivars are susceptible to all identified races of *P. striiformis* f. sp. *hordei*, which produce IT 8 on Steptoe and IT 9 on Topper. With a few exceptions, results of the crosses with Topper and the reciprocal crosses with Steptoe produced the same results. The reciprocal crosses of Granelose Zweizeilige with Steptoe tested with both races PSH-1 and PSH-13 showed a single recessive gene for resistance, whereas the cross with Topper showed that two genes were involved. The results indicate that Topper has a suppressor gene. This suppressor was also detected in the cross of Hiproly with Topper tested with PSH-1. In the tests with PSH-1, the F_2 segregation data from crosses of I5 with Topper and Steptoe when I5 was used as the female parent indicated that I5 has two independent recessive genes. When Steptoe was used as the female parent and tested with the same race, the F_2 and F_3 data indicated that one gene was dominant and one gene was recessive and that the interaction was complementary. These results suggest the possibility of maternal effects.

Nonallelic gene interactions. Four types of digenic interactions were detected: two independent recessive genes, two complementary recessive genes, complementary interactions of one recessive gene and one dominant gene, and two partially dominant genes. Two independent recessive genes (7:9 F_2 ratio and 7:8:1 F_3 ratio) were detected in crosses of PI 548708, PI 548734, PI 548747, I5, and Astrix with susceptible genotypes. Two complementary recessive genes (1:15 F_2 ratio and 1:8:7 F_3 ratio) were detected in crosses of Hiproly, Abyssinian 14, Emir, Varunda, and Trumpf with susceptible genotypes. The complementary interaction of a recessive gene and a dominant gene (3:13 F_2 ratio and 1:8:7 F_3 ratio) was detected in crosses of Abyssinian 14, Stauffers Obersulzer, and Heils Franken with susceptible genotypes. The interaction of two partially dominant genes (5:4:7 F_2 ratio) was detected in crosses of Astrix with susceptible genotypes, in which heterozygous plants produced an intermediate infection type. The first two types of gene interactions have been previously reported (4,20) for barley stripe rust, but the last two types have not. All these types of gene interactions have been reported for wheat stripe rust (10–14).

Recessive genes for resistance. In this study, most of the resistance genes were recessive. Such a large number of recessive

genes for resistance has not been reported for any other plant-pathogen system. The first report on the inheritance of resistance in wheat to *P. striiformis* f. sp. *tritici* was in 1905 by Biffen (6), who reported that a recessive gene controlled resistance. Recessive genes for resistance to plant pathogens have been reported in many plant species (5,17,19,22,29). In barley, dominant and recessive genes for stripe rust resistance have been reported in other genotypes (1–4,20,21,26,30,34,37). With findings similar to ours, Nover and Scholz (31) reported recessive genes in crosses of all five barley genotypes in their studies. Our results agree with Nover and Scholz's (31) reports that Bigo, Abyssinian 14, BBA 2890, and I5 have recessive genes. Our results from the reactions of the first leaves of the Cambrinus crosses agree with Johnson's (21) report that a gene in Cambrinus is dominant. We found that the gene in Cambrinus is dominant in the first leaf and recessive in the second leaf and that a gene in Mazurka is expressed in a similar manner. Changes in gene action from dominant to recessive have been reported in wheat resistance to *P. striiformis* f. sp. *tritici* (10–12,15,25,32).

Resistance is most often reported to be dominant in studies of the genetics of plant disease resistance. However, in natural plant-pathogen systems, recessive resistance may be as frequent as dominant resistance (5,18). The information on the recessive inheritance of the majority of resistance genes detected in this study is useful to breeders in applying special schemes in breeding programs. In breeding for resistance, backcrossing is the major approach for introducing resistance into an otherwise superior cultivar. More complex procedures can be used to incorporate a recessive resistance gene into a commercial cultivar. Selfing before or after each backcross can be used to select lines with a recessive resistance gene. Alternatively, progeny from each backcrossing to the recurrent parent can be test-crossed with the donor parent to determine whether the recessive resistant allele is present. Because many genes identified in this study are of a race-specific type and the durability of resistance in the genotypes resistant to all races has yet to be determined, caution should be taken in using the genes. Pyramiding, multiline, and gene deployment of these genes can be used to obtain durable resistance. The disadvantages of using recessive genes may bring more difficulties for pyramiding several recessive resistance genes into a cultivar or developing multilines. The problem may be overcome by marker-assisted selection. With molecular markers, selfing or test-crossing to the donor parent before or after each backcrossing to the recurrent parent should become unnecessary, and therefore incorporation of the recessive genes into new cultivars may be easier and faster. The large number of resistance genes detected in this study provide a good source of resistance. Allelism studies and genome mapping of these genes should be useful for identifying the genes, determining their relationships, locating the genes on chromosomes, and effectively using the genes for controlling stripe rust. The genes that are resistant to all races of *P. striiformis* f. sp. *hordei* are especially useful because they can provide resistance to a broad range of the pathogen population and may be durable if used in gene pyramiding, multilines, and gene deployment.

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