A Gene for Resistance to *Puccinia graminis* f. sp. *tritici* That is Present in Wheat Cultivar H-44 but not in Cultivar Hope

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ABSTRACT

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A backcross line of Marquis wheat carrying gene *Sr9d* from H-44 was more resistant to *Puccinia graminis* f. sp. *tritici* than was a second backcross line carrying *Sr9d* from Hope. The difference in reaction was caused by a second gene for resistance in the H-44 line. The gene was present in H-44 but was not present in Hope or the *Sr9d* (Hope) line. The nature of the resistance conferred by this second gene and the relationship of the gene to other genes for resistance in Hope and H-44 are discussed.

The stem rust-resistant wheat (*Triticum aestivum* L.) cultivars Hope and H-44 were produced by McFadden (7) by crossing the widely grown rust-susceptible cultivar Marquis and the resistant Yaroslav Emmer (*T. dicoccum*). Hope was used widely in breeding for resistance to *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. in the United States, and H-44 was used frequently in Canada.

Both Hope and H-44 carry stem rust resistance genes *Sr2, Sr9d,* and *Sr17* (1,3–6,8). In addition, Hope carries genes *Sr7b* (4) and *Sr18* (1). Various workers transferred single genes from each cultivar into lines of susceptible cultivars by backcrossing; those that carried "isolated" identified resistance genes soon were used as differential hosts to identify races of *P. graminis* f. sp. *tritici*. A line of Marquis carrying gene *Sr9d* from H-44 (*Sr9d* [H-44]) was chosen for use as a differential host in Canada; whereas, a line with *Sr9d* from Hope (*Sr9d* [Hope]) was selected for use in the United States. Although race identification results at Winnipeg, Manitoba, and St. Paul, Minnesota, have agreed remarkably well for many years, it rapidly became evident that the different *Sr9d* lines being used at the two locations produced different results. Seed of the *Sr9d* lines was exchanged and infection studies showed that line *Sr9d* (H-44) was resistant to several races that attacked line *Sr9d* (Hope). The difference in reaction was investigated by a genetic study of cultivars Hope and H-44, and lines *Sr9d* (Hope) and *Sr9d* (H-44).

MATERIALS AND METHODS

Results of preliminary investigations with seed stocks at Winnipeg revealed uncertainties concerning the origin and purity of stocks of cultivar H-44. Seedlings of three samples (a, b, and c) of H-44, one of Hope, and lines *Sr9d* (Hope) and *Sr9d* (H-44) were inoculated with 19 races of *P. graminis* f. sp. *tritici*. The infection types (9) produced by seven of these races (Table 1) showed that one sample (a) of H-44 was different from the other two, and that one sample (b) was impure. The single sample of Hope seemed pure and was more susceptible than H-44 (c) to five of the seven races. The *Sr9d* (Hope) line also was more susceptible to all races than the *Sr9d* (H-44) line. Apparently, H-44 either carried a different gene than *Sr9d* from Hope, or it carried another gene (or genes) that conferred additional resistance.

In view of the variable results obtained with H-44 in the preliminary trial, additional samples of seed of both Hope and H-44 were obtained from: W. Q. Loegering, University of Missouri, USA; R. A. McIntosh, University of Sydney, Australia; J. C. Craddock, U.S. Department of Agriculture, Beltsville, MD; and D. R. Knott, University of Saskatchewan, Canada. Ten samples of Hope and seven samples of H-44 were available from these sources and from Winnipeg seed stocks.

Crosses were made in growth cabinets by standard procedures. Seed of Hope was obtained from seed stock 9 and of H-44 from seed stock 17. The backcross line Pld/8*Mq was used as the susceptible parent. F_2 plants were grown in the field and harvested and threshed individually to provide seed of F_3 lines which were used to determine segregation ratios.

The races of *P. graminis* f. sp. *tritici* used in these tests were from the Canadian physiologic wheat race survey (2). Inoculum was produced on protected plants in the greenhouse and checked for purity on the differential hosts before being used to inoculate test plants.

All plants were inoculated in the greenhouse by atomizing an oil suspension of urediospores on the first seedling leaf and were incubated overnight in a chamber in the greenhouse. Greenhouse thermostats were set at 20 C during the day and 16 C during the night, but temperatures varied considerably according to the weather. Reactions were observed 12–14 days after inoculation and were classified according to infection type (9).

To verify the purity of the parents, progenies from all plants used in crossing were tested by inoculation with four races of the pathogen. All progenies produced infection types similar to those of the parent cultivars in earlier trials.

RESULTS

The infection types produced by seven races of *P. graminis* f. sp. *tritici* on seedlings grown from the various seed samples (Table 2) showed that most samples of Hope and line *Sr9d* (Hope) differed from most samples of H-44 and *Sr9d* (H-44) in reaction to races C1, C20, C30, and C34. Seven of the Hope samples (samples 1, 2, 3, 4, 8, 9, and 10) were similar in reaction to all races, but those of samples 5, 6, and 7 were mixed. The infection types of Hope sample 8 resembled those of the H-44 samples, but the seeds were old and reactions probably were affected by poor seedling growth. Samples 5 and 7 were identified as CI 8178 and sample 6 as CI 13133. Four samples of H-44 (12, 14, 16, 17) produced similar infection types with all races but samples 13 (CI 8177) and 15 (probably CI 8177), were mixed and sample 18 (an increase of sample 15), produced different infection types than the other samples. Sample 14 (CI 15091) seemed to be pure and representative of H-44. The samples shown to be segregating in Table 2 were badly mixed. Most other samples also contained a few off-type plants although this is not

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TABLE 1. Reaction of wheat seedlings grown from six Winnipeg seed stocks to infection by seven selected races of *Puccinia graminis* f. sp. *tritici*

P. graminis f. sp. *tritici* race	Infection types[a] produced on seedlings of lines:					
	Sr9d (Hope)	*Sr9d* (H-44)	H-44(a)	H-44(b)	H-44(c)	Hope
C5 (29-1)	4	23–	3±	2	2+	23+
C20 (11)	3±	2±	3+	3+,3±	2	3+
C32 (32)	3±	2+	3±	3+,2	2	23+
C34 (32)	3±	2+	3+	2+	2+	3+
C40 (32)	3±	2	3±	;	;	;
C41 (32)	3±	23–	3±	;2	;	;
C43 (32)	3±	23–	3+	2	2	3+

[a]Infection types as described by Stakman et al (9).

TABLE 2. Reaction of seedlings of 10 samples of wheat cultivar Hope, seven samples of H-44, and wheat lines *Sr9d* (Hope) and *Sr9d* (H-44) to infection with seven races of *Puccinia graminis* f. sp. *tritici*.

Wheat cultivar or line	Seed stock no.	Infection types[a] produced by seedlings inoculated with *P. graminis tritici* physiologic race:						
		C1	C5	C17	C20	C30	C33	C34
Hope	1	;2	23	;1	3±	3±	;1	4–
	2	–	23	;1	–	3±	;1	3+
	3	;2	23	;1	3±	3±	;1	4–
	4	;2	23	;1	3±	3±	;1	4–
	5	Seg.[b]	Seg.	;1	3±	Seg.	Seg.	4–
	6	Seg.	Seg.	;	3±	Seg.	;	4–
	7	23+	2+	Seg.	Seg.	23–	–	–
	8	;1	–	;1	23	2	;1	23–
	9	;2	23	;1	23+	3+	;1	4
	10	;1+	23	;1	3±	3±	;1	4–
Sr9d (Hope)	11	3±	–	2	3±	4	4–	4–
H-44	12	;1	2	;	23	2	;1	2+
	13	Seg.	Seg.	Seg.	Seg.	Seg.	Seg.	Seg.
	14	;1	2	;	2	2	;1	23–
	15	3±	Seg.	;	Seg.	2	Seg.	Seg.
	16	;	2	;	2	–	0	2+
	17	;	2	;1	2±	2	;	2+
	18	3±	–	;1	3+	3±	4	4–
Sr9d (H-44)	19	23	2	12	23–	23	4	23–

[a]Infection types as described by Stakman et al (9).
[b]Seg. indicates the sample was mixed.

indicated in Table 2. Evidently, precautions should be taken in genetic studies with these cultivars.

The seedling infection types produced on the parental cultivars by four races of *P. graminis* f. sp. *tritici* (Table 3) show the differences in disease reaction under investigation. Hope and H-44 were highly resistant to race C17 (infection type ;1). *Sr9d* (Hope) and *Sr9d* (H-44) were moderately resistant (infection type 2). The high resistance of Hope and H-44 to race C17 apparently was conferred by gene *Sr9d* and interacting genes. Both cultivars were highly resistant to races C18 and C41 and this resistance apparently was conferred by the *Sr17* present in both cultivars (4). It is clear that the *Sr9d* (H-44) line is more resistant to races C20 and C41 than the *Sr9d* (Hope) line. Apparently, *Sr9d* from Hope does not confer resistance to these races and the *Sr9d* (Hope) line is only moderately susceptible because of genes from Marquis which are carried by the susceptible parent Pld/8*Mq. Line *Sr9d* (H-44) may carry an additional gene (or genes) for resistance to races C20 and C41 or an allele at the *Sr9* locus that confers a different resistance than the Hope allele.

The F_3 segregation in the progeny of the cross Pld/8*Mq// *Sr9d* (H-44) to races C17 and C20 fitted a theoretical ratio of 1 resistant:2 segregating:1 susceptible (Table 4). Evidently segregation of gene *Sr9d* was detected by race C17. Segregation of a second gene, tentatively designated gene *H*, was detected by race C20. This gene segregated independently of *Sr9d* (linkage $\chi^2 = 2.0$; $P = 0.95–0.50$). The presence of gene *H* in H-44 was confirmed in other crosses involving H-44. The progeny of the cross Hope/H-44 failed to segregate either with race C17, which confirms previous reports

TABLE 3. Reaction of seedlings of parental cultivars and some close relatives to infection with four races of *Puccinia graminis* f. sp. *tritici*

Cultivars	Infection types[a] produced on seedlings inoculated with *P. graminis tritici* physiologic race:			
	C17	C18	C20	C41
Pld/8*Mq	3+	4–	3±	3±
Hope	;1	;1	3±	;1
H-44	;1	;1	23	;1
Sr9d (Hope)	2	4	3±	3±
Sr9d (H-44)	2	4	2±	23–
Renown Sel. (*Sr17*)	3+	;1	3±	;
Marquis	4	4	3±	3±
Prelude	3+	4	4	3+

[a]Infection types as described by Stakman et al (9).

that both cultivars carry gene *Sr9d*, or with race C41, which confirms the presence of *Sr17* in both cultivars. However, a single gene segregated when the progeny was tested with race C20 and the infection type (2 to 3–) indicated that it was gene *H*. The F_3 progeny of the cross Pld/8*Mq//Hope segregated in a ratio of 1 resistant:2 segregating:1 susceptible with races C17 and C18. Resistance to race C17 indicates the presence of gene *Sr9d*, and resistance to race C18, the presence of gene *Sr17* (Table 3). The progeny of the cross Pld/8*Mq//H-44 was tested with races C17 and C20 and here also gene *H* segregated independently of gene

TABLE 4. Segregation of genes for resistance to *Puccinia graminis* f. sp. *tritici* from the wheat cultivars Hope and H-44 in the F_3 of six crosses and the genotypes indicated by the segregation ratios

Cross		Number of F_3 lines:				
No. Coded description	Race	Resistant	Segregating	Susceptible	*P* for 1:2:1 ratio[a]	Gene(s)
1. Pld/8*Mq//*Sr9d* (H-44)	C17	31	53	24	.95–.50	*Sr9d*
	C20	25	53	30	.95–.50	*H*
2. Hope/H-44	C17	114	0	0		*Sr9d*
	C41	114	0	0		*Sr17*
	C20	28	56	30	.95–.50	*H*
3. Pld/8*Mq//Hope	C17	35	60	34	.95–.50	*Sr9d*
	C18	13	30	16	.95–.50	*Sr17*
4. Pld/8*Mq//H-44	C17	32	71	30	.99–.95	*Sr9d*
	C20	31	75	27	.50–.20	*H*
5. H-44/*Sr9d* (H-44)	C20	114	0	0		*H*
	C41	114	0	0		*Sr17, H*
6. Hope/*Sr9d* (H-44)	C20	23	67	36	.50–.20	*H*
	C41	56	66	4	.50–.20	*Sr17, H*

[a]Excepting cross 6 race C41 for which the ratio was 7:8:1.

TABLE 5. Reaction of wheat lines carrying *Sr9d* from Hope and H-44, line 577 carrying gene H, and Pld/8*Mq, the susceptible parent, to infection with six races of *Puccinia graminis* f. sp. *tritici*.

Physiologic race	Infection types[a] produced by *P. graminis tritici* on seedlings of lines:			
	577	*Sr9d* (Hope)	*Sr9d* (H-44)	Pld/8*Mq
C17	4–	2	2	3+
C18	3+	3+	4	4–
C20	23–	3+	2±	3±
C33	4	4–	4–	4–
C35	2±	1 to 3+	; to 3	1 to 3+
C41	X–	3+	23–	3±

[a]Infection types as described by Stakman et al (9).

Sr9d (linkage $\chi^2 = 3.7$, $P = 0.50–0.30$). The progeny of the cross H-44/*Sr9d* (H-44) did not segregate to races C20 and C41. In contrast, the progeny of the cross Hope/*Sr9d* (H-44) segregated to race C20 in a ratio of 1 resistant:2 segregating:1 susceptible which indicated the presence of gene *H*, and to race C41 in a ratio of 7 resistant:8 segregating:1 susceptible which indicated that gene *H* is independent of *Sr17*.

A comparison of the infection types on a line (577) from cross Pld/8*Mq//*Sr9d* (H-44) with those of line *Sr9d* (Hope) and line *Sr9d* (H-44) (Table 5) indicates that line 577 carries gene *H*, but not gene *Sr9d*. The susceptibility of line 577 to race C17, which is avirulent on lines *Sr9d* (Hope) and *Sr9d* (H-44), shows that line 577 does not carry gene *Sr9d*. All three lines are susceptible to races C18 and C33. Line 577 and line *Sr9d* (H-44) are moderately resistant to races C20, C35, and C41, but *Sr9d* (Hope) is susceptible or moderately susceptible. The moderate susceptibility of line *Sr9d* (Hope) to race C35 results from the moderately susceptible reaction of the background cultivar Marquis to this race. There is clear evidence, therefore, that a gene from H-44 is present in line 577 and that it is independent of gene *Sr9d*.

DISCUSSION

Knott (4) reported two genes in cultivar Hope and H-44 for resistance to race 56 (= C17); one conferred both seedling and adult plant resistance, and the other adult plant resistance only. The two genes interacted in both seedlings and adult plants to give high resistance similar to that of the parent. Separately both genes give less resistance than that observed in Hope and H-44. He identified the main gene as *Sr1* (since renamed *Sr9d*) and called the other gene for adult plant resistance *Sr2*.

There was good evidence for interaction between gene *Sr9d* and a second gene that is not gene *H* in the segregation of the F_3 from the crosses Pld/8*Mq//Hope and Pld/8*Mq//H-44 inoculated with race C17. The evidence for interaction was clear in the resistant lines from these crosses (Table 4) which were homozygous for gene *Sr9d*. In the Hope cross, the 35 resistant lines consisted of three groups. One group included lines in which all plants showed infection type ;1, the second group varied from type ;1 to 2, and the third group had lines with only type 2 plants. The observed ratio of the three groups was 9:20:6, suggesting that a single gene was interacting with *Sr9d* ($P = 0.95–0.50$). The lines in the resistant category of the H-44 cross acted similarly. The observed ratio of 11 lines having all plants type ;1, 11 lines with plants type ; to 2, and 10 lines with all plants type 2 fitted a one-gene ratio ($P = 0.30–0.20$). Lines in the segregating and susceptible categories also included plants that varied slightly in reaction but, when *Sr9d* was segregating or absent, gene action seemed unstable and categories of reaction were not clear. Both Hope and H-44 must have the gene that interacts with *Sr9d* and that confers a low degree of resistance. This gene seems to be unstable and it was difficult to study. It may be Knott's *Sr2* which he observed in seedling plants (4) as a modifier of *Sr1* (= *Sr9d*).

Gene *H* is unstable and often was difficult to detect in greenhouse experiments. Lines 577 and *Sr9d* (H-44), which carry gene *H*, occasionally appeared susceptible or moderately susceptible to races to which they normally are resistant (eg, C20, C35, and C41). Factors such as variable greenhouse temperatures and gene interactions seemed to alter the expression of resistance conferred by gene *H*.

The location of gene *H* is unknown and its instability which might increase in aneuploids, could make determination of its chromosomal location difficult. The present study shows that gene *H* is independent of genes *Sr9d* (chromosome 2B), *Sr17* (chromosome 7B), and the gene (*Sr2?*) that interacts with *Sr9d*. The nature of the resistance conferred by gene *H* and the pattern of races against which it is effective differ from those of any known gene. Apparently, it is not a previously described gene although it could be an allele.

The finding of gene *H* explains the differences between physiologic race identifications at Winnipeg and St. Paul and also the differences in reaction between Hope and H-44 described here. The importance of the gene from other points of view is uncertain. Its usefulness in seedlings is limited by its instability. It confers a low degree of resistance to a relatively small number of races of the stem rust pathogen in the 11-32-113 group described by Stakman (9). Unless further investigation demonstrates that its resistance is more effective in other genotypes or in adult plants, it does not appear promising for use in breeding for wheat rust resistance.

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