A Genetic Analysis of Leaf Rust Resistance in Red River 68 Wheat

Glen D. Statler

Assistant Professor, North Dakota State University, Fargo 58102.

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ABSTRACT

Genes conditioning resistance to wheat leaf rust incited by *Puccinia recondita* were investigated in Red River 68, a semidwarf hard red spring wheat resistant to prevalent races of leaf rust. Red River 68 was crossed and backcrossed to the susceptible variety Thatcher for the genetic analysis. The reactions of the parents, F_1 seedlings, F_2 seedlings and adults, and F_3 families, were explained by assuming that a single dominant gene conferred resistance to leaf rust culture 70-15 (race 15). Two dominant, independently inherited genes conferred resistance to culture 70-1 (race 1). Rust reactions of backcross-F_1 plants and backcross-F_2 families gave additional support for the hypotheses. The two genes are designated *Lr*RR-1 and *Lr*RR-2. *Lr*RR-1 conditions resistance to both culture 70-1 and 70-15. *Lr*RR-2 conditions resistance to culture 70-1.

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Additional key words: Triticum aestivum, reciprocal crosses, widely virulent, narrowly virulent, isogenic lines, genetic ratio.

Studies of the heritability of genes in *Triticum aestivum* spp. *vulgare* (Vill., host) MacKey conditioning resistance to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* are essential for determining which genes can be incorporated into a single wheat variety for more effective, long-term resistance. As early as 1926, Mains et al. (11) reported resistance due to independently inherited factors. Adams (1), in 1939, reported that a single factor conditioned resistance in Malakoff and Fulcaster. Monogenic inheritance was also detected by Caldwell & Compton (5) and by Wells & Swenson (18). Resistance to leaf rust in semidwarf wheat selections was found by Allan et al. (2) to be transmitted by a partially dominant and a recessive factor. Shaalan et al. (15) found resistance in Ottawa to race 9 controlled by one gene, whereas resistance in C.I. 13285 to race 15 was controlled by two genes. Two genes were found to condition resistance in Lee (19), several Mexican varieties (16), and certain differential varieties (13).

The identification of host genes is a prerequisite for testing the gene-for-gene hypothesis in *P. recondita* (14). Recently, genes determined by genetic analyses have been isolated and backcrossed into susceptible varieties. These isogenic lines have been assigned symbols (3, 6, 7, 8, 10, 12, 16).

The determination of genes for resistance is dependent on the virulence of the rust cultures used in the study (6). Berg et al. (4) speculated that more genes would be differentiated with a widely avirulent culture than with a more widely virulent one. Therefore, in the current study, progeny of Red River

68 X Thatcher crosses were tested with a widely avirulent culture 70-1 (race 1) and culture 70-15 (race 15) virulent on lines with *Lr*3 and *Lr*10.

MATERIALS AND METHODS.—Single pustuled uredial cultures of two physiologic races, 15 (culture 70-15) and race 1 (culture 70-1), were used to test all progeny. The two cultures were obtained from L. E. Browder, Manhattan, Kans. Both cultures were avirulent (0; to 0;1 infection type) on Red River 68 and virulent on Thatcher (4 infection type). Since F_1 plants of the cross Red River 68 X Thatcher and its reciprocal were resistant to both cultures, they were backcrossed to Thatcher, the susceptible parent. The F_1 plants and F_2 families from the backcross as well as F_2 plants and F_3 families from the cross were inoculated with cultures 70-1 and 70-15 and evaluated for seedling reaction. F_2 and backcross-F_1 plants were also inoculated in the adult stages.

I inoculated plants by dusting a mixture of urediospores of cultures 70-1 and talcum powder on the first leaves prior to development of the second leaf. The second leaf was inoculated similarly 5-6 days later with urediospores of culture 70-15.

Inoculated plants were held at ca. 100% relative humidity and 20 C for 20-22 hr. These plants were incubated for 12 days at 21-25 C in the greenhouse. Parent varieties and F_1 plants were included in all tests.

The rust reaction of each plant was scored after 12 days by the method proposed by Stakman et al. (17). The inoculated leaves were removed and placed in groups which differed in reaction types according to the method of Gough & Williams (9). The chi-square test for goodness of fit was used to analyze the segregating populations.

Red River 68 and lines containing host genes *Lr*1, *Lr*2, *Lr*2D, *Lr*3, *Lr*9, *Lr*10, *Lr*14, *Lr*16, *Lr*17, *Lr*18, or *Lr*19 were inoculated with several leaf rust cultures representing a wide range of pathogenicity. Reaction patterns on the isogenic lines were compared with those on Red River 68.

RESULTS AND DISCUSSION.—The F_1 progeny of the cross Red River 68 X Thatcher and its reciprocal were resistant (0; to 0;1 infection type) to culture 70-15 of *P. recondita*. The F_2 plants tested for reaction to culture 70-15 consisted of 156 plants derived from five F_1 plants of the Thatcher X Red River 68 cross and 152 plants derived from four F_1 plants of the reciprocal cross. The F_2 plants segregated into three phenotypic groups: 236 highly resistant (0; to 0;1):seven moderately resistant (2^- to 2^+); and 65 susceptible (3^- to 4). The seven moderately resistant types were combined with the highly resistant types. Chi-square tests indicated that the F_2 plants from the reciprocal crosses fit a 3:1 ratio ($P > .10$), indicating that resistance of Red River 68 to culture 70-15 of wheat leaf rust was conditioned by a single dominant gene (Table 1).

The chi-square test for heterogeneity indicated that the families were homogeneous ($P > .50$) and that there was no maternal influence. Seedling reaction was identical with adult reaction in all but a few cases which were probably escapes. This indicated that the gene conditioning resistance to culture 70-15 *P. recondita* was operative in both the seedling and adult stages.

TABLE 1. Reactions of F_2 plants and F_3 families from reciprocal Red River 68 X Thatcher wheat crosses to culture 70-15 of *Puccinia recondita*

F_2 plants	No. plants: Expected (3:1)	Observed: Seedling	Observed: Adult
Resistant (0; to 1)	231	243	236
Susceptible (3 to 4)	77	65	72
		$P >$ .10	.50

F_3 families	No. families: Expected (1:2:1)	Observed
Homozygous-resistant (0; to 1)	24	31
Segregating 3 (0; to 1): 1 (3 to 4)	48	49
Homozygous-susceptible (3 to 4)	24	16
		$P > .05$

Ninety-six F_3 families, consisting of about 20 plants each, when tested with culture 70-15, fit into one of three groups: 31 were homozygous resistant; 49 segregated three resistant:one susceptible; and 16 were homozygous susceptible (Table 1). Two families failed to fit any group and were probably misclassified for rust reaction. The data from the F_3 families fit a single factor ratio of 1:2:1 ($P > .05$).

The backcross-F_1 (Thatcher X Thatcher X Red River 68 and Thatcher X Red River 68 X Thatcher) segregated 58 resistant:46 susceptible. Chi-square tests indicated that the combined data from the backcrosses fit a 1:1 ratio ($P > .10$) (Table 2). The chi-square test for heterogeneity indicated that the families were homogeneous ($P > .10$). The adult backcross-F_1 plants also segregated 1:1 ($P > .50$).

The backcross-F_2 families derived from 96 backcross-F_1 plants segregated into two phenotypic groups as follows: 52 backcross-F_2 families from resistant backcross-F_1 plants segregated into a ratio of three resistant to one susceptible, and 44 backcross-F_2 families from susceptible backcross-F_1 plants were homozygous susceptible (Table 2). The number of families in the two groups fit a 1:1 ratio ($P > .25$), and thus support the hypothesis that a single dominant gene in Red River 68 conditions resistance to culture 70-15 of wheat leaf rust.

The five F_1 plants of the Thatcher X Red River 68 cross as well as four F_1 plants of the reciprocal cross were resistant to culture 70-1. The F_2 plants segregated into a ratio of 15 resistant to one susceptible ($P > .75$) (Table 3). The data were homogeneous ($P > .25$). Chi-square tests indicated that the F_2 plants also fit a 15:1 ratio ($P > .10$) when tested in the adult stage. The 15:1 ratio indicated

TABLE 2. Reactions of backcross-F_1 plants and backcross-F_2 families of crosses of Red River 68 and Thatcher wheat to culture 70-15 of *Puccinia recondita*

	Backcross-F_1 plants				Backcross-F_2 families	
	Seedling		Adult		Segregating	Homozygous-susceptible
	(0; to 1)	(3 to 4)	(0; to 1)	(3 to 4)	3 (0; to 1): 1 (3 to 4)	(3 to 4)
Expected (1:1)	52	52	52	52	48	48
Observed	58	46	55	49	52	44
	$P > .10$		$P > .50$		$P > .25$	

TABLE 3. Reactions of F_2 plants and F_3 families from reciprocal Red River 68 X Thatcher wheat crosses to culture 70-1 of *Puccinia recondita*

	No. plants		
	Expected	Observed	
F_2 plants	(15:1)	Seedling	Adult
Resistant (0; to 1)	290.625	290	286
Susceptible (3 to 4)	19.375	20	24
		$P >$ .75	.25

	No. families	
F_3 families	Expected (7:4:4:1)	Observed
Homozygous-resistant (0; to 1)	42.875	52
Segregating 15 (0; to 1): 1 (3 to 4)	24.500	23
Segregating 3 (0; to 1): 1 (3 to 4)	24.500	22
Homozygous-susceptible (3 to 4)	6.125	1
		$P > .05$

that resistance of Red River 68 to culture 70-1 (race 1) was controlled by two dominant independently inherited genes.

The 98 F_3 families from tested F_2 plants fit a two-factor ratio of 7:4:4:1 ($P > .05$) (Table 3). Fifty-two F_3 families from resistant F_2 plants were homozygous-resistant, 23 segregated 15 resistant:one susceptible, and 22 segregated three resistant:one susceptible. One F_3 family from a susceptible F_2 plant was homozygous-susceptible.

The 104 backcross-F_1 seedling plants tested segregated into a ratio of three resistant:one susceptible ($P > .25$) (Table 4). The chi-square tests indicated that the families were homogeneous ($P > .10$). The backcross-F_1 plants did not fit a 3:1 ratio ($P < .01$) when tested in the adult stage with culture 70-1. This failure to fit a genetic ratio may have been due to escapes or misclassification.

The 95 backcross-F_2 families tested segregated into five classes, three of which were expected. Thirty-one families segregated three resistant:one susceptible; 22 segregated 15 resistant:one susceptible; and 24 were homozygous-susceptible. The following two groups of families did not fit the expected groups. Eight families segregated approximately one resistant:one susceptible, and ten were homozygous-resistant. When the families that did not fit the expected classes were excluded, the remaining families fit the 2:1:1 ratio ($P > .10$).

Although two groups of families did not fit into the expected classes, all the susceptible backcross-F_1 plants were homozygous-susceptible when the F_2 families were tested. When only resistant and susceptible classes are considered, the data fits a 3:1 ratio very well ($P > .95$). Furthermore, the backcross-F_2 families that segregated 15:1 or 3:1 as well as the homozygous-resistant classes were from resistant F_1 plants. The homozygous-resistant backcross-F_2 families which were not expected may have been 15:1 groups which were not detected by the family size (20-25 plants) used. The backcross-F_2 families which segregated approximately 1:1 could have been 3:1 groups not detected by the family size

TABLE 4. Reactions of backcross-F_1 plants and backcross-F_2 families of crosses of Red River 68 with Thatcher wheat to culture 70-1 of *Puccinia recondita*

	Backcrosss-F_1 plants			Backcross-F_2 families		
	Resistant	Susceptible		Segregating	Segregating	Homozygous-susceptible
	(0; to 1)	(3 to 4)		3 (0; to 1):1 (3 to 4)	15 (0; to 1):1 (3 to 4)	(3 to 4)
Expected (3:1)	78	26	(2:1:1)	47.50	23.75	23.75
Observed	81	23	3/1 22/5 1/26	39.00	32.00	24.00
	$P > .25$				$P > .05$	

used, or which deviated from the 3:1 group by chance. With these assumptions, the data fit a 2:1:1 ratio ($P > .25$) (Table 4).

The virulence frequencies on Red River 68 did not match those found on any of the 11 isogenic lines when separately inoculated with 10 different leaf rust cultures representing a wide range of pathogenicity. The virulence of these cultures ranged from avirulent on all of the isogenic lines to virulent on eight of the 10 lines tested. Therefore, the two genes were assigned temporary symbols *Lr*RR-1 and *Lr*RR-2 in accordance with guidelines of the North American Leaf Rust Workers Committee.

The hypothesis was developed that *Lr*RR-1 was effective against both race 1 and race 15 because the same plants that were susceptible to culture 70-1 were also susceptible to culture 70-15. The few exceptions observed may have been due to misclassification. The fact that the plants which were susceptible to 70-15 were not all susceptible to culture 70-1 was further evidence for a second independent factor, *Lr*RR-2.

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