Resistance

The Relationship Between Slow Rusting and a Specific Resistance Gene for Wheat Stem Rust

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ABSTRACT

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Wheat cultivar Idaed 59 has specific resistance to *Puccinia graminis* f. sp. *tritici* conditioned by gene *Sr*Tt-1 that is associated with the resistance mechanisms of slow rusting and low receptivity to infection by rust races virulent for *Sr*Tt-1. The link between slow rusting and *Sr*Tt-1 purportedly was broken in a previous study in which a few progenies from Baart/Idaed 59 were characterized as having *sr*Tt-1 combined with slow rusting and *Sr*Tt-1 with fast rusting. The seedling responses of two such progenies were reexamined by infection tests with cultures of races 151-QSH and 15-TLM, which are avirulent and virulent on *Sr*Tt-1, respectively. The slow-rusting line resembled Idaed 59 in that it had the seedling resistance conditioned by *Sr*Tt-1 to race 151-QSH and low receptivity to infection by race 15-TLM. The fast-rusting line resembled Baart in that it was fully susceptible to both races. Thus, the resistance mechanisms in Idaed 59 have not been separated, and the relationships among them remain unclear.

Additional key words: general resistance, hypersensitive resistance, *Triticum aestivum*.

The specific resistance of gene *Sr*Tt-1 to *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn. found in wheat (*Triticum aestivum* L.) cultivars such as Idaed 59 is associated with adult plant characters for slow rusting (6) and low receptivity to infection (1,4) by putatively virulent races. Skovmand et al (6) found that the slow rusting of Idaed 59 was conditioned by one or more genes apparently linked to the dominant allele *Sr*Tt-1. Low receptivity in this cultivar is conditioned by a dominant gene that may be linked or identical to *Sr*Tt-1 (4), and this trait probably contributes to the slow-rusting type of resistance studied by Skovmand et al (6).

In seedlings of W2691SrTt-1, the differential line for the specific resistance conditioned by *Sr*Tt-1, a range of infection types is obtained with the races of *P. graminis* f. sp. *tritici* found in the United States (2). Generally, an infection type 0; is obtained with isolates of races 151-QSH, 56-MBC, and 32-RSH, but isolates of races 151-QFB and 151-QCB produce infection types ;1+ to X. A higher infection type than the foregoing is obtained with isolates of races 113-RKQ, 15-TNM, or 15-TLM and consists of a reduced

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number of type 3–4 infections with an occasional fleck. These latter races are considered virulent for the resistance of *Sr*Tt-1 (2), and no isolates producing a fully susceptible reaction on the differential for *Sr*Tt-1 have been found (1).

Histologic studies of the interaction of a single-spore culture of race 15-TLM with Idaed 59 and W2691SrTt-1 in adult (1) and seedling (3) plants indicated that the reduced infection is the result of a hypersensitive response between many penetrants of the rust fungus and the attacked host cells. Thus, W2691SrTt-1 and Idaed 59 could have a second gene for resistance that conditions low receptivity in adult plants and a mesothetic reaction in seedlings, characterized by infection type 40;, to races such as 15-TLM with virulence on the resistance of *Sr*Tt-1. This host reaction is not readily detected by the mass screening techniques used in routine race identification because of variation in inoculum deposition on the differential lines and the inconsistent appearance of the occasional fleck infection type. Furthermore, the resistant reaction conditioned by *Sr*Tt-1 is probably epistatic to the mesothetic reaction conditioned by the second gene. Hence, separation of these genes into individual lines is needed to resolve the diversity of infection types observed with different races on the differential line for the resistance conditioned by *Sr*Tt-1 and to evaluate the effectiveness of these resistances against the population of *P. graminis* f. sp. *tritici* in the United States.

A recent study (5) of the relationship between slow rusting and some genes for specific resistance to wheat stem rust identified a few progenies from Baart/Idaed 59 in which the characters governing slow and fast rusting in the field were found to be independent of the specific resistance of *Sr*Tt-1. The present report presents evidence from tests with cultures avirulent and virulent for the resistance of *Sr*Tt-1 that this separation was not achieved.

MATERIALS AND METHODS

Seed of four wheat lines descended from the cross Baart (CI 1697)/Idaed 59 (CI 13631) was obtained from R. D. Wilcoxson. Skovmand et al (5) characterized these lines as having different combinations of the alleles for *Sr*Tt-1 with characters for fast and slow rusting (Table 1).

Two rust cultures were used in infection tests: 151-QSH, which is avirulent for the resistance of *Sr*Tt-1 with infection type 0;, and 15-TLM, which is considered virulent for *Sr*Tt-1 with infection type 40;. Procedures described previously (3) were used for inoculation, environmental controls, histologic processing, and observations. The infection types observed on spaced plants grown in soil under these conditions differed slightly from those reported previously (2) for crowded plants grown in vermiculite.

Four seedling leaves were sampled 96 hr after inoculation for histologic examination. Percentages were converted to arc sines, and data were analyzed for variance. Direct comparisons of the number of uredia produced by the two cultures were not feasible because the inocula were not adjusted for equal numbers of infective spores. Uredial numbers produced by the two cultures were compared indirectly, however, by calculating the percentages of uredia each culture produced on Baart, which assumes that this cultivar had the same receptivity to infection by both cultures.

RESULTS AND DISCUSSION

Infection tests with cultures of races 151-QSH and 15-TLM (Table 2) indicated that the fast-rusting lines 128-2 and 132-5 resembled Baart in reaction and number of uredia produced. Contrary to the results of earlier work (5), therefore, line 128-2 has the allele *sr*Tt-1 for susceptibility and was unsuitable for studies of the relationship between the resistance of *Sr*Tt-1 and the associated character for the mesothetic reaction and low receptivity to infection.

The infection type and number of uredia the cultures produced on the slow-rusting lines 124-2 and 129-10 resembled the infection on Idaed 59. Although line 124-2 differed more from Idaed 59 in reaction to the culture of race 15-TLM than line 129-10, its reaction to the culture of race 151-QSH indicated that the resistance of *Sr*Tt-1 was present and that line 124-2 had been misclassified in the previous study (5).

A previous histologic study (3) of penetrant development of the culture of race 15-TLM in seedlings indicated that the significant features of the host-pathogen interaction in Idaed 59 and W2691SrTt-1 that differed from Baart were the frequency of aborted penetrants when the primary haustorial mother cell was attached to a necrotic host cell, the frequency of colonies with and without necrotic host cells, and the reduction in mean linear growth of colonies. These features of the pathogenicity of the two cultures on Baart, Idaed 59, and 124-2 were compared (Table 3). Susceptible Baart was significantly more compatible (ie, host cell necrosis was less and linear growth of colonies was greater) than Idaed 59 and 124-2 with both cultures. The culture of race 151-QSH on Idaed 59 and 124-2 was significantly less compatible than the culture of race 15-TLM: primary haustoria with necrotic host cells were more frequent, colonies without necrotic host cells were fewer, and linear growth of colonies was less, but the percentages of colonies with necrotic host cells did not differ. Thus, the incompatibility of the host-pathogen interaction for *Sr*Tt-1 and the gene conditioning the mesothetic reaction differ quantitatively but not qualitatively.

The significantly higher percentages of uredia and colonies without necrotic cells and a lower percentage of colonies with necrotic host cells indicated that the reaction of line 124-2 to the culture of race 151-QSH was weaker than that of Idaed 59. This less intense reaction of line 124-2 to race 151-QSH could explain the misclassification of its specific resistance in the previous study (5).

Idaed 59 and line 124-2 did not differ in number of uredia produced by the culture of race 15-TLM, but the latter line had more diversity in the type of infections present. In postpenetration development, the two wheats did not differ in the percentage of

TABLE 1. Test lines from Baart/Idaed 59 wheat identified as having different combinations of the alleles for *Sr*Tt-1 and characters for fast and slow rusting[a] caused by *Puccinia graminis* f. sp. *tritici*

Line	Postulated gene for specific resistance	Rusting characteristic[b]
Parents		
Baart	*sr*Tt-1	Fast
Idaed 59	*Sr*Tt-1	Slow
Progenies		
124-2	*sr*Tt-1	Slow
128-2	*Sr*Tt-1	Fast
129-10	*Sr*Tt-1	Slow
132-5	*sr*Tt-1	Fast

[a] From Skovmand et al (5).
[b] Based on the area under the disease progress curve.

TABLE 2. Infection type and number of uredia obtained with controlled inoculation of wheat seedlings of the parental and progeny lines from Baart/Idaed 59 with cultures of *Puccinia graminis* f. sp. *tritici* races 151-QSH and 15-TLM

Race	Host	Infection type	Uredia[a] per cm^2
151-QSH	Idaed 59	0;1=	0.07**
	129-10	0;1=	0.18**
	124-2	0;2	0.49**
	Baart	4+	2.69
	132-5	4+	2.99
	128-2	44−	2.37
15-TLM	Idaed 59	40;	0.53*
	129-10	4+0	0.54*
	124-2	X	0.49*
	Baart	4+	1.28
	132-5	4+	1.52
	128-2	4+	1.08

[a] * = Significantly less than Baart at $P = 0.05$; ** = significantly less than Baart at $P = 0.01$. For race 151-QSH, the least significant difference (LSD) at $P = 0.01$ was 1.25; for race 15-TLM, the LSD at $P = 0.05$ was 0.52.

TABLE 3. Infection type, uredial frequency, and penetrant development on Baart, Idaed 59, and line 124-2 of wheat inoculated with *Puccinia graminis* f. sp. *tritici* races 151-QSH and 15-TLM

Race	Host	Infection type	Uredia[x,z] (%)	Penetrant development[y,z] Primary haustoria with necrotic host cells (%)	Colonies with necrotic host cells (%)	Colonies without necrotic host cells (%)	Linear growth of colonies[z] (μm)
151-QSH	Baart	4	100 a	0 c	0 c	93.2 a	128.4 ab
	Idaed 59	0;1=	2.0 d	45.7 a	43.9 a	0.3 d	90.5 cd
	124-2	0;2	36.6 c	46.1 a	14.1 b	14.6 c	75.5 d
15-TLM	Baart	4	100 a	0 c	0 c	92.2 a	140.2 a
	Idaed 59	40;	76.5 b	5.9 b	43.5 a	41.2 b	120.5 b
	124-2	X	77.6 b	16.1 b	18.0 b	44.1 b	104.5 c

[x]Uredia per square centimeter expressed as a percentage of the number of uredia on Baart (assuming that Baart was equally receptive to infection by both cultures).
[y]Expressed as a percentage of all penetrants examined. Columns total less than 100 because of penetrants that aborted in other stages of development.
[z]Within columns, values followed by the same letter do not differ significantly, according to Duncan's multiple range test at $P = 0.05$.

aborted penetrants when the primary haustorial mother cell was attached to a necrotic host cell or in the percentage of colonies without necrotic host cells. Again, as with the culture of race 151-QSH, line 124-2 had significantly fewer colonies with necrotic host cells than Idaed 59. Furthermore, mean linear growth of colonies was significantly less in 124-2 than in Idaed 59. Although a higher percentage of penetrants formed colonies in Idaed 59 than in 124-2, the similar frequency of uredia on these two lines indicates that more colonies in Idaed 59 ceased to develop before uredia formed. The slower growth of colonies in 124-2 apparently resulted in the greater range in infection types than in Idaed 59.

The present results indicate that the characters for the resistances of *Sr*Tt-1, slow rusting, and the mesothetic seedling reaction were not separated in the tested lines. Thus, the question remains whether these resistances are conditioned by two closely linked genes or are pleiotropic expressions of a single gene. The small differences in the reactions of Idaed 59 and 124-2 to races virulent and avirulent for *Sr*Tt-1 could be caused by minor differences in the genetic background of the two lines.

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