Postpenetration Phenomena in Wheat Cultivars with Low Receptivity to Infection by *Puccinia graminis* f. sp. *tritici*

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ABSTRACT

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The characteristic low receptivity of wheat (*Triticum aestivum*) cultivars Marquis, Lee, Thatcher, and Idaed 59 to infection by *Puccinia graminis* f. sp. *tritici*, as shown by number of uredia in adult plants, was constant under different environments and with several cultures of diverse races identified as virulent on seedlings of these cultivars. Fungal penetrants of putative virulent cultures interacted either compatibly or incompatibly in all cultivars with low receptivity. Compatible colonies in cultivars with low receptivity were significantly smaller than those in plants of highly receptive cultivars Purdue 5481C1 and Baart. In Lee, Thatcher, and Idaed 59 the proportion of compatible to total penetrants reflected the reduced number of uredia produced on these hosts. In Marquis, however, the proportion of compatible penetrants did not differ significantly from that in Purdue 5481C1. The reduced colony size of compatible penetrants observed histologically at 65 and 96 hr in all hosts with low receptivity was generally reflected by the smaller uredia that appeared later. Highly incompatible colonies in cultivars with low receptivity were smaller than compatible ones and were associated with collapsed host cells. Thus, these incompatible penetrants produced a hypersensitive response similar to that associated with specific gene resistance and presumably failed to produce uredia.

Additional key words: wheat stem rust, general resistance, slow rusting, adult plant resistance.

Low receptivity to infection by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. is a major feature of the slow-rusting character of some wheats (*Triticum aestivum* L.). When inoculated uniformly with a virulent isolate, plants of such cultivars had significantly fewer primary uredia per unit of plant surface than did those of a fast-rusting cultivar (19). Why a unit of inoculum of a virulent race of the cereal rusts gives fewer infections on slow-rusting than on fast-rusting hosts is unclear. Reduced frequencies of pathogen penetration in slow-rusting hosts were reported for oat crown rust (10,13), oat stem rust (13), and wheat stem rust (5,6). Conversely, similar frequencies of penetration in slow-rusting and fast-rusting hosts were reported for barley leaf rust (8), oat stem rust (24), and wheat stem rust (15,17). Mechanisms that govern infection success may differ with host-pathogen combination. Mont and Rowell (17) concluded that differences in receptivity to infection of leaf blades from different wheats in which pathogen penetration rates were similar resulted from the failure of many penetrants to produce visible infections. The present histopathological study examined the postpenetration development of *P. graminis* f. sp. *tritici* in some wheats of high and low receptivity to ascertain why penetrants fail to form visible infections. A preliminary report (4) was made of some of these results.

MATERIALS AND METHODS

The test wheats, in decreasing order of receptivity determined in previous tests and their identified specific resistances (19), were: Purdue 5481C1 (P5481C1) *Sr7b, 10;* Marquis (CI 3641) *Sr7b, 18, 19, 20*; Lee (C I 12488) *Sr9g, 11, 16*; Thatcher (C I 10003) *Sr5, 9g, 12, 16;* and Idaed 59 (CI 13631) *SrTt-1.* P5481C1 is derived from the cross (Red Bobs)^2/Exchange and is resistant to race 151 of *P. graminis* f. sp. *tritici;* therefore, Baart (CI 1697) was used as a presumably fully recepetive and susceptible cultivar for the greenhouse tests. Observations in subsequent field tests by the second author have shown that Baart is similar to Marquis and less receptive than P5481C1 before the heading stage of development. The receptivity of W2691SrTt-1 (CI 17385), a single-gene differential wheat for *SrTt-1,* was compared in some tests to that of Idaed 59, which also has *SrTt-1* (19).

The avirulence/virulence formulae based on seedling tests of the cultures used of *P. graminis* f. sp. *tritici* were:

Race 15B-2 *Sr6,8,9a,9b,13,15,17/5,7b,9d,9e,9g,10,11,12,14,16, 18,19,20,Tt-1*
Race 32 *Sr9a,9e,13,Tt-1/5,6,7b,8,9b,9d,9g,10,11,12,14,15,16,17, 18,19,20*
Race 151 *Sr7b,9a,9e,13,Tt-1/5,6,8,9b,9d,9g,10,11,12,14,15,16, 17,18,19,20*

Inoculum of race 15B-2 was increased from a single uredospore isolate, but inoculum of races 32 and 151 was increased from single-pustule isolates.

Receptivity of P5481C1, Marquis, Lee, Thatcher, and Idaed 59 to infection in the field was determined in four replicates planted in April 1973 in a randomized complete block design at Rosemount, MN. Each plot consisted of a 1.8-m test row, bordered by rows of a resistant wheat to reduce inoculum drift, with an interplot distance of 1.8 m. Plots were sprayed with triazbutil (4-butyl-4*H*-1,2,4-triazole) at 1 kg/ha 23 days after planting for control of leaf rust (25). Cultivars were inoculated uniformly with the isolate of race 15B-2 by the method of Rowell and McVey (19) when growth by the Romig scale (7) ranged from stage 8 (flag leaf partially developed) in Marquis to stage 10 (boot stage) in Idaed 59. Uredia were counted and infection types were determined on a total of 20 penultimate leaves sampled from each plot 14 days after inoculation. Higgins and Schreiber's (11) method was used to measure the leaf area, and the average number of uredia per square centimeter was calculated.

Receptivity to infection in the greenhouse was determined with

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the three races on single plants in 10-cm-diameter pots with four replicates of each cultivar in a complete block design. Temperature in the greenhouse ranged from 21 to 30 C, and 8 hr of supplementary light, 11,000 lux at 25 cm, was provided with cool-white fluorescent lamps. The cultivars were inoculated with uredospores of the three races when growth ranged from stage 8 to stage 10 as in the field test. Inoculation was done by spraying 0.5 mg of uredospores in 0.5 ml of paraffinic oil onto the foliage of a rotating plant. The inoculated plants were incubated in a transparent polyethylene plastic dew chamber in the greenhouse from 1800 hours to 1200 hours the next day. Numbers of uredia and infection types were determined on the penultimate leaf blades 14 days after inoculation as in the field study.

Field samples for histological examination were obtained from test cultivars planted in hills and replicated nine times with a randomized block design at St. Paul, MN, in May 1974. Plants in each replicate were inoculated at growth stage 8 with race 15B-2 by spraying a suspension of 50 mg of uredospores in 5 ml of paraffinic oil onto the leaves. The inoculated plants were enclosed in a transparent polyethylene plastic chamber on the night of inoculation, and distilled water was continually atomized into the chamber until 1000 hours the next day.

Additional histological studies were made on Idaed 59, Thatcher, and Baart plants that were grown in the greenhouse and moved at growth stage 8 into a growth chamber programmed for 12-hr light periods (28,000 lux) at 27 C and 12-hr dark periods at 21 C. The plants were inoculated with races 15B-2,32, and 151 after 5 days of conditioning in the chamber. Inoculum was prepared by floating about 15 mg of uredospores on distilled water in a petri dish for 3 hr and then changing the distilled water twice to remove the germination self-inhibitor (1). The washed spores were applied heavily on the adaxial leaf surface with a clean glass rod. The inoculated leaves were inserted into a small, clear plastic chamber for a dew period from 1800 hours until 1000 hours the next day. Inoculated leaf samples were collected at 65 and 96 hr after inoculation.

Host-parasite interactions and fungal growth were observed by microscopic examination of cleared, stained leaf segments. Uredospore germination and stomatal penetration on leaf blades sampled 65 hr after inoculation were determined by the method of Anderson and Rowell (3). Samples with sufficient penetrations were then cut into 1-cm lengths for histological examination. Steps 1 through 4 inclusive in the method of Shobe and Lersten (20) were followed for fixing and clearing. McBryde's (16) method with omission of the picric acid was used for staining and mounting the cleared segments. Fungal colony length and width were measured with a calibrated eyepiece micrometer. Depth of penetration was measured by the graduations of the microscope fine focus adustment between the points of focus at the penetration peg and the deepest hypha that could be observed.

Data on number of infections, frequencies of host-parasite interactions, and hyphal measurements were subjected to analysis of variance. Duncan's (9) multiple range test was used to identify significant differences among cultivar means.

RESULTS

Receptivity to infection. The receptivity of the cultivars was determined in both the field and the greenhouse to test the reproducibility of receptivity under diverse conditions (Table 1). The field results confirmed the differences found on leaf blades of the cultivars in previous test (19) with race 15B-2. Purdue 5481C1 had significantly more infections than did the other cultivars; Lee, Marquis, and Thatcher had intermediate numbers of infections; and Idaed 59 had the least. Three races were used in the greenhouse tests to establish the consistency of the receptivity with cultures of different pathogenicity. In these tests, Baart was substituted for the highly receptive P5481C1 because the latter is resistant to race 151, and W2691SrTt-1 was added to compare a known line containing *SrTt-1* with Idaed 59. In general, the results with race 15B-2 were similar to those of the field tests. The receptivity of the cultivars resembled their receptivity in the field, except for Marquis, which had significantly fewer infections than did Lee in the greenhouse but not in the field. The receptivity to infection with different races was similar, except that Lee did not differ significantly from Baart with races 32 and 151. The very low amounts of infection on Marquis with race 151 and on Idaed 59 and W2691SrTt-1 with races 32 and 151 resulted from specific resistances of these wheats to these races.

Observations on the infection type (IT) in the field and greenhouse tests (Table 2) confirmed previous observations (19) that IT generally was lower on cultivars with low receptivity than on the controls. High ITs were observed on P5481C1 and Baart, and those on Marquis were only slightly lower, except for the low IT for race 151 resulting from the resistance of *Sr7b* (14). Lee and Thatcher were intermediate, with mixed ITs ranging from 1 to 3. The ITs with race 15B-2 on Idaed 59 and W2691SrTt-1 were predominantly 0, with an occasional fleck or uredia of IT 2 or 3. These two cultivars, however, were highly resistant, IT 0 to fleck, with races 32 and 151, which are avirulent for the resistance of *SrTt-1*.

Host-parasite interaction. Three types of compatibility interactions with race 15B-2 became evident during histopathological examination of field-grown adult plants (Table 3). These were: the fungal penetrant was compatible (it grew freely among host cells of normal appearance in an apparently compatible host-parasite relationship); the fungal penetrant was slightly incompatible (fungal development was moderately restricted, parasitized host cells stained more intensely than did nonparasitized cells, and the cell walls appeared to be thickened); and the fungal penetrant was highly incompatible (fungal development was restricted markedly and one or more fungal hyphae were in contact with collapsed host cells).

TABLE 1. Average number of primary uredia per square centimeter on penultimate leaf blades of adult wheat cultivars 14 days after uniform inoculation with uredospores of isolates of races 15B-2, 32, and 151 of *Puccinia graminis* f. sp. *tritici* in field and greenhouse

	Uredia/cm^2			
	Field	Greenhouse		
Cultivar	15B-2	15B-2	32	151
Purdue 5481C1	11.9 a[y]	...	...	...
Baart	...	3.3 a	2.4 a	2.5 a
Lee	3.0 b	1.1 b	1.9 a	2.0 a
Marquis	2.0 b	0.5 cd	1.2 b	0.6 c[z]
Thatcher	1.2 bc	0.9 bc	0.9 b	1.4 b
Idaed 59	0.2 c	0.1 d	0.0 c[z]	0.0 c[z]
W2691SrTt-1	...	0.2 d	0.0 c[z]	0.0 c[z]

[y] Within columns, values followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$.
[z] Cultivar with race-specific resistance to rust culture.

TABLE 2. Infection types of races 15B-2, 32, and 151 of *Puccinia graminis* f. sp. *tritici* on penultimate leaf blades of adult wheat plant cultivars 14 days after inoculation

	Infection types[a]			
	Field	Greenhouse		
Cultivar	15B-2	15B-2	32	151
Purdue 5481C1	4⁻3	–	–	–
Baart	–	4⁻3	4⁻3	4⁻3
Lee	231	231	23	32
Marquis	4⁻3	34	34	2[b]
Thatcher	123	23	23	32
Idaed 59	02	03	0[b]	0;[b]
W2691SrTt-1	–	0;3	0;[b]	0;[b]

[a] Infection types as described by Stakman et al (23) in which 0 = immune and 4 = very susceptible. Mixed infection types are indicated by two or more digits, which list the range of types present on a leaf blade in order of decreasing frequency.
[b] Cultivar with race-specific resistance to rust culture.

In the highly receptive P5481C1, virtually all penetrants developed compatibly, and no highly incompatible penetrants were observed. Marquis did not differ significantly from P5481C1, but a few highly incompatible infections were present. Although more slightly and highly incompatible penetrants were observed in Lee than in P5481C1 or Marquis, the percentages did not differ significantly. Thatcher had significantly fewer compatible and more highly incompatible penetrants than P5481C1, Marquis, and Lee. The fewest compatible and the most highly incompatible penetrants were observed in Idaed 59 and W2691SrTt-1. Thus, all cultivars except Marquis ranked similarly in the proportion of compatible penetrants observed and the degree of receptivity to infection.

Similar differences in compatibility of the host-parasite interaction were observed during histological examination of blades of adult plants of Baart, Thatcher, and Idaed 59 grown in a growth chamber (Table 4). In Baart, which was the most susceptible and receptive cultivar, no highly incompatible penetrants were found. This study revealed that more penetrants of the avirulent races 32 and 151 than virulent race 15B-2 were highly incompatible in Idaed 59, but incompatibility was expressed at an early stage of penetrant development, within 65 hr after inoculation, with all races. In Thatcher, the percentage of highly incompatible penetrants was similar for the three virulent races, but incompatibility of some penetrants was expressed at a later stage in Thatcher than in Idaed 59.

Fungal development. The length, width, and depth of the fungal colonies of race 15B-2 at 65 hr after inoculation were measured in cleared and stained leaf segments of field-grown adult plants (Table 5). Compatible colonies were larger than highly incompatible colonies. Colony development of highly incompatible penetrants was severely restricted and did not differ significantly in mean dimensions in Lee, Thatcher, Idaed 59, and W2691SrTt-1. The haustorial mother cell in contact with collapsed host cells often appeared to be weak, shrunken, or both, and similar disorganization sometimes extended into the hypha attached to the haustorial mother cell. Colonies of compatible penetrants in highly receptive P5481C1 were significantly wider than those in the less receptive cultivars and were significantly longer than those in all cultivars except Marquis. These dimensions did not differ significantly, however, among the cultivars with different levels of low receptivity. The reduced colony dimensions of compatible penetrants in cultivars with low receptivity corresponded roughly to the reduced sizes of uredia observed in the low IT on adult plants (Table 2).

Colonies also were measured in adult leaves of Idaed 59, Thatcher, and Baart that were inoculated with races 15B-2, 32, and 151 in a growth chamber (authors, *unpublished*). With race 15B-2 the differences in colony dimensions of compatible penetrants among cultivars were similar to those described previously in the field. Colony dimensions of highly incompatible penetrants did not differ significantly among the three races in Thatcher and Idaed 59, nor did they change between samples harvested at 40, 65, and 96 hr. These observations indicated that after a penetrant became highly incompatible, colony development ceased.

Haustoria were readily observed in the compatible colonies, but were obscured by the dense and darkly stained conditions of the collapsed host cells in the highly incompatible colonies. Occasionally, however, small spherical haustoria that failed to develop beyond the initial stage of formation were observed among the collapsed host-cell components. Haustoria in the compatible colonies were small and globose in the early stages of growth, but in advanced stages they were expanded into an elongated sac with some lobes or protrusions. The percentage of penetrants of race 15B-2 in which haustoria were observed was 78% in P5481C1, 62% in Marquis, 44% in Lee, 31% in Thatcher, 20% in Idaed 59, and 19% in W2691SrTt-1. Thus, the frequency of penetrants in which haustoria were observed approximated the frequency of compatible penetrants.

TABLE 3. Percentage of penetrants of an isolate of race 15B-2 of *Puccinia graminis* f. sp. *tritici* with various compatibilities at 65 hr after inoculation in field-grown adult wheat cultivars

Cultivar	Percentage of penetrants		
	Compatible	Slightly incompatible	Highly incompatible
Purdue 5481C1	94.6 a[z]	5.4 ab	0.0 c
Marquis	93.2 a	5.0 ab	1.7 c
Lee	79.2 a	14.2 a	6.6 c
Thatcher	55.9 b	12.9 a	31.2 b
Idaed 59	28.7 c	4.2 b	67.1 a
W2691SrTr-1	21.3 c	7.9 ab	70.8 a

[z]Within columns, values followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$.

TABLE 4. Percentage of highly incompatible penetrants of races 15B-2, 32, and 151 of *Puccinia graminis* f. sp. *tritici* 65 and 96 hr after inoculation of greenhouse-grown adult wheat plants

Race	Cultivar	Percentage of incompatible penetrants	
		65 hr	96 hr
15B-2	Baart	0.0 a[y]	0.0 a
	Thatcher	50.5 b	78.3 b
	Idaed 59	71.8 c	75.0 b
32	Baart	0.0 a	0.8 a
	Thatcher	52.5 b	75.1 b
	Idaed 59[z]	80.0 c	94.2 c
151	Baart	0.0 a	0.0 a
	Thatcher	51.7 b	72.5 b
	Idaed 59[z]	88.4 c	92.5 c

[y]In each triplet of data, values followed by the same letter are not significantly different as determined by Duncan's multiple range test at $P = 0.05$.

[z]Cultivar with race-specific resistance to rust culture.

DISCUSSION

Tests in field and greenhouse established that the receptivity to infection by virulent races of *P. graminis* f. sp. *tritici* in the tested wheat cultivars was reproducible under diverse conditions. Histopathological examination of the postpenetration development revealed that the degree of host-parasite compatibility and extent of colony development apparently was related to the receptivity of Lee, Thatcher, Idaed 59, and W2691SrTt-1. On these test cultivars the percentage of compatible penetrants decreased as the level of receptivity declined. This observation suggests that the reduced number of uredia produced on these cultivars developed from the

TABLE 5. Mean colony dimensions of penetrants of race 15B-2 of *Puccinia graminis* f. sp. *tritici* that had compatible and highly incompatible host-parasite interactions 65 hr after inoculation of field-grown adult wheat plants

Cultivar	Dimension (μm)					
	Compatible			Highly incompatible		
	Length	Width	Depth	Length	Width	Depth
Purdue 5481C1	110.6 a[y]	69.3 a	23.7 a	...[z]	...	...
Marquis	87.3 ab	53.1 b	16.6 ab	...	...	...
Lee	74.6 b	39.0 b	15.7 ab	59.0 a	14.8 a	2.9 a
Thatcher	70.3 b	32.7 b	13.6 ab	48.5 a	6.6 a	2.2 a
Idaed 59	63.0 b	27.7 b	9.7 b	49.9 a	7.0 a	3.2 a
W2691SrTt-1	73.3 b	29.4 b	12.2 b	50.8 a	7.6 a	2.5 a

[y]Within columns, values followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$.

[z]Observations of penetrants with collapsed host tissues in Purdue 5481C1 and Marquis were rare or absent, and data for these cultivars were not used in the statistical analysis.

compatible penetrants and that the highly incompatible penetrants failed to develop into uredia. This conclusion was supported by the observation that mean colony dimensions for highly incompatible penetrants were smaller than those for compatible penetrants and changed little between 65 and 96 hr. Thus, the quantitative differences in the receptivity of these cultivars apparently result from the rapidity and frequency of the incompatible interaction.

Colony dimensions of compatible penetrants were significantly larger in P5481C1 than in Lee, Thatcher, Idaed 59, and W2691SrTt-1. Although low receptivity in Marquis was not associated with a significant increase in incompatible colonies, the dimensions of compatible colonies resembled those in the low-receptivity cultivars more than those in P5481C1. The reduced size of compatible colonies in cultivars of low receptivity suggests that mechanisms other than host-cell collaspse restrict fungal development in these cultivars.

Mechanisms restricting colony development apparently are a common feature of the slow-rusting character. Reduced colony development in slow-rusting hosts has been reported for oat crown rust (10,13), oat stem rust (13,24), barley leaf rust (8), and wheat stem rust (15,26). The incompatible host-parasite interaction found in our test cultivars with low receptivity apparently is an uncommon feature of slow-rusting. Incompatibility in wheat stem rust was observed as an increased frequency of necrotic sites in slow-rusting hosts by Martin et al (15), but Kochman and Brown (13) reported that the hypersensitive response did not occur in slow-rusting hosts with oat crown and stem rusts.

The effect of the hypersensitive reaction of host cells on fungal growth and development is controversial. Király et al (12) questioned the causal relation of hypersensitivity in plant resistance to pathogen development, but Skipp and Samborski (21) reported an adverse effect of the hypersensitive reaction on pathogen development in wheat stem rust. Our results indicate that the rust penetrants in Idaed 59, Thatcher, and Lee that fail to produce uredia are those in which terminated pathogen development is associated with hypersensitive collapse of host cells.

In some respects, the observed resistances in these wheats of low receptivity to infection by *P. graminis* f. sp. *tritici* are similar to weak specific resistances. The high incompatibility observed in the low-receptivity hosts resembles the hypersensitive collapse of host cells and cessation of pathogen development described by Stakman (22) and Allen (2) for race-specific resistance in wheat stem rust. Low receptivity in adult plants is associated with a lower IT than that of the highly receptive and fully susceptible control. Furthermore, Rowell and McVey (19) reported that the characters for low receptivity to infection have relatively simple inheritance. In Idaed 59, a single dominant gene for low receptivity and the gene for specific resistance of *Sr Tt-1* are either identical or closely linked. In contrast, two complementary recessive genes for low receptivity in Thatcher and a third recessive gene for low receptivity in Lee appear to have no relation to the known genes for specific resistance in these cultivars.

No evidence was found in our limited tests, however, for race specificity of characters for low receptivity in these cultivars. Adult plants of Idaed 59 and W2691SrTt-1 had low receptivity and a low percentage of compatible penetrants in inoculation tests with all of 14 diverse isolates identified as virulent on *Sr Tt-1* in the annual race survey. The receptivity of Lee and Thatcher was constant with cultures of virulent races 15B-2, 32, and 151; and that of Marquis was constant with the cultures of virulent races 15B-2 and 32. Data of Mortenson and Green (18), however, indicate that the receptivity of Thatcher, but not Idaed 59, responded differentially with cultures of races 15B-1 and 15B-1L at 19 and 15 C. Thus, the role of specificity in stem rust resistances for low receptivity in these cultivars is unresolved.

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