Partial Resistance of Near-Isogenic Wheat Lines Compatible with *Erysiphe graminis* f. sp. *tritici*

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ABSTRACT

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Six near-isogenic lines of Chancellor winter wheat, differing in known powdery mildew resistance genes (*Pm*x), were evaluated relative to Chancellor for partial resistance to compatible isolates of *Erysiphe graminis* f. sp. *tritici* collected in central Pennsylvania. The variability due to the host always exceeded that due to the isolates for the parasitic fitness attributes that were investigated: latent period (LP), cumulative sporulation (CSP) per colony, and corrected infection efficiency (CIE). Fitness genes other than virulence genes, or multiple alleles of the virulence genes, caused significant differences in certain fitness attributes for different isolates of the same race when compared on the same host. In certain instances, lines carrying a particular *Pm*x gene were more susceptible than Chancellor. Significant isolate × host interactions and significant differences in isolate ranking were demonstrated for several near-isogenic lines, indicating the potential for erosion of partial resistance over time. Pooled data over all isolates indicated partial resistance for several near-isogenic lines carrying known *Pm*x genes relative to Chancellor: CI14122 with *Pm*3c (LP); CI14123 with *Pm*4 (CSP); and CI14122 with *Pm*3c, CI14123 with *Pm*4, and CI14033 with *Pm*x gene from cultivar Michigan Amber (CIE).

Additional key words: aggressiveness, epidemiology, horizontal resistance, stabilizing selection, *Triticum aestivum*, virulence.

Six near-isogenic soft red winter wheat (*Triticum aestivum* L.) lines, each possessing a different known powdery mildew resistance gene (*Pm*x), were evaluated by Nass (15) for residual effects against isolate 144 of *Erysiphe graminis* D.C. f. sp. *tritici* E. Marchal possessing the six virulence genes needed to confer compatibility to the six resistance genes. Residuality was considered to be the expression of partial resistance by a near-isogenic line with a particular *Pm*x gene, after having been overcome ("defeated") by a virulent isolate, compared to the Chancellor recurrent parent with no known *Pm*x genes (15). The study demonstrated that the near-isogenic lines with major resistance genes *Pm*3c, *Pm*4, and a gene known as *MA* from cultivar Michigan Amber could restrict certain parasitic fitness attributes that influence the rate of disease development. Martin and Ellingboe (12) demonstrated that the Chancellor line carrying *Pm*4 interacted differently with different compatible isolates of *E. graminis* relative to the development of elongating secondary hyphae. If the results of Nass (15) reflected a unique interaction with isolate 144 of *E. graminis*, then the ranking of partial resistance in the lines tested may change when evaluated with different isolates.

The presence of a differential interaction between components of rate-reducing resistance in the host and parasitic fitness attributes in the pathogen has been used as an indication of resistance gene stability and, thus, an indication of the longevity of resistance (10,16,17,19,26). A statistically significant difference in isolate ranking has also been used as an indication of the potential for erosion of resistance over time (10,16,17,19,26). These two measurements of the potential longevity of partial resistance have not been applied to near-isogenic wheat lines that contain known resistance genes and confer compatible infection types.

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Vanderplank (26) has reasoned that virulence genes in addition to those needed for virulence on a particular host cause isolates to be less fit. This logic was supported as a population average by Leonard and Czochor (11). However, the presence of different residual effects of "defeated" major genes seems incompatible with Vanderplank's theory as well as certain population genetic models when restricted to the equal and additive effects of gene action (11).

The purpose of this investigation was to study the ranking in partial resistance of certain near-isogenic lines with known powdery mildew resistance genes and possible differential host-isolate interactions with several isolates of *E. graminis*.

MATERIALS AND METHODS

Six near-isogenic lines of winter wheat were used as the host. Each resistance gene source was backcrossed eight times to Chancellor (hereafter designated as Cc), a winter wheat susceptible to all cultures of *E. graminis* in this study (2). The CI (USDA Cereal Investigation) number of the near-isogenic line and the source of each resistance gene follows: CI14118 (*Pm*2, Ulka); CI14119 (*Pm*2, CI12632); CI14122 (*Pm*3c, Sonora); CI14123 (*Pm*4, Khapli); CI14125 (*Pm*5, Hope); and CI14033 (*MA*, Michigan Amber).

Nine isolates of *E. graminis* collected from different commercial wheat fields in Pennsylvania were used to study the partial resistance of the near-isogenic wheat lines: isolates 10 and 13 (Landisville, 1979); isolates 136, 137, and 139 (Lewisburg, 1979); isolate 169 (Berwick, 1979); isolates 218 and 244 (State College, 1979); and isolate 144 (State College, collected between 1976 and 1978).

Primary leaves of the wheat lines were inoculated when plants reached the 1–2 leaf stage. The plants were then placed in environmental chambers for 8 days at 20 ± 2 C with a 12-hr photoperiod as outlined previously (21). The infection types presented in Table 1 were determined on primary leaves with the 0–4 scale (4). Isolates causing type 3– to 4+ reactions on a particular host were interpreted as possessing the virulence gene

matching the resistance gene in the host line. Therefore, the division between a compatible and incompatible relationship was between the 3− and 2+ infection type. This was the difference between a moderate amount of sporulation with no chlorosis and a small amount of sporulation with abundant mycelia and little or no chlorosis (4). Repetition of these tests produced the same infection types with the described environment.

All experiments were replicated four times and the general linear model Type IV SS (3) was used to analyze the data as a three-way analysis of variance. The least-significant-difference criterion (25, see page 106), computed with all host-isolate combinations, was used to make planned comparisons between Cc and each line for each isolate. Unpaired *t*-tests (25) were used to make pairwise comparisons between each line and Cc over all isolates and experiments as a test for average resistance, since variances and sample sizes were sometimes unequal for all measurements of fitness. Duncan's new multiple range test (25) was used as a test for significant differences in isolate ranking among isolates within lines. A randomized complete block design was used as a test for significant isolate effects.

Inoculation. The isoline seeds were sown in eight holes at two to three seeds per hole in 16.5 × 12 × 6-cm plastic flats containing a sterilized soil mixture of Hagerstown silty clay loam, peat, and sand (2:1:1, v/v). Ten to 15 primary leaves of 14-day-old seedlings were draped over an 8 × 15 × 10-cm wire grid, with the adaxial surface facing up, and were secured with masking tape.

A method of assuring similar infection densities was used to measure latent period and sporulation because the wheat lines differed in the number of colonies that formed from a given amount of inoculum. Therefore, it was necessary to plant one wheat line to a tray and expose all leaves to a gradient of relatively low inoculum density to increase the probability of obtaining at least a few leaves with less than five colonies. The trays containing the isolines were placed under a laminar flow hood (Environmental Air Control, Inc., Hagerstown, MD 21740) with the leaf blades perpendicular to the air flow. Cc plants that had been inoculated 8 days previously were shaken to remove older conidia and to synchronize conidial maturity 12 hr before they were used as a source of inoculum. After 12 hr, the plants were shaken 30 cm behind and 30 cm above the trays by hand to create a deposition gradient of conidia across the leaves with the air flow. This technique made it possible to choose two to five leaves with less than five colonies for further observation and therefore lessen both the depression of sporulation per colony (10,18) and the shortening of the latent period (10) with increasing colony number. The hood was sterilized with 10% Clorox and hands were washed between inoculations with different isolates. The trays were covered with plastic bags and transferred to a growth chamber that was maintained at 20 ± 2 C with illumination at the top of the trays at 80 μEinsteins·m^{-2}·sec^{-1} and a 12-hr photoperiod. The bags were removed after 2 days and the trays were moved closer to the lights with irradiation at the top of the trays at 170 μEinsteins·m^{-2}·sec^{-1}.

Latent period. On the fourth day after inoculation, all leaves were examined to choose one to two leaves with the fewest colonies. A modified vacuum sampler (23) was swept over all colonies on a given leaf on days 4 through 6. The greased slide upon which the spores were impacted was examined at ×100 to record the presence or absence of conidia. It was assumed that light suction (<138 mbar) would dislodge only mature conidia, and would be a more epidemiologically accurate method than microscopic examination for the presence of conidia on conidiophores.

On day 5, the leaves that were chosen on day 4 were examined. If the number of colonies exceeded five, other leaves with fewer colonies were selected and checked with the vacuum sampler for production of mature conidia. The procedure was repeated on day 6, and on day 7, leaves with five or fewer colonies were used to study sporulation for that replication. Latent period (LP) was therefore measured as the time from inoculation to when the first spore(s) could be dislodged.

Sporulation. Beginning on day 7 after inoculation, condia were removed every other day through day 13 by vacuuming conidia from all colonies on a leaf. Spore harvests were discontinued after day 13 due to the appearance of daughter colonies. The spore collection tube contained 5 ml of 0.1% Tween-20. The nozzle of the collection apparatus was coated with organosilane (Prosil-28, PCR Research Chemicals, Inc., SCM Corporation, Gainesville, FL 32602) to inhibit adhesion of the spores to the nozzle. One milliliter of distilled water was drawn through the nozzle of the collection apparatus into the collection tube to minimize spore carryover into the next sample. Twenty milliliters of a 1.0% NaCl solution was added to each tube, and four 0.5-ml aliquots were counted with a model zB Coulter Counter (Coulter Electronics, Inc., Hialeah, FL 33010). The counts for the aliquots were adjusted to compensate for the background count, then averaged and converted to the mean number of conidia per colony per day.

The sporulation data were analyzed as cumulative sporulation (CSP) through day 13. The $\log_{10}$ transformation was applied to the CSP data to normalize the variance.

Corrected infection efficiency. The plants were prepared for inoculation as described previously, but all isolines were planted in a tray for each inoculation. A modified version of the Melching settling tower (13), with dimensions of 40 × 73 × 73 cm was used for all inoculations. Infected leaves of Cc were placed in the inoculation funnel, and short blasts of nitrogen gas (690 mbar) were used to dislodge the conidia from the colonies. The trays were simultaneously rotated on a turntable at 7 rpm to permit a more uniform deposition of inoculum. Forty seconds were allowed for the conidia to settle, then the trays were bagged and placed in a growth chamber as described previously.

The inoculation funnel was removed and placed 8 cm under an

TABLE 1. Infection types of cultivar Chancellor wheat possessing different powdery mildew (*Pm*x) resistance genes to isolates of *Erysiphe graminis* f. sp. *tritici*[a]

		Near-isogenic line								
Isolate	CI[b] = / *Pm*x[c] =	14114 / 1	14118 / 2	14119 / 2	14120 / 3a	14121 / 3b	14122 / 3c	14123 / 4	14125 / 5	14033 / *MA*[d]
10		1	4	4	0	0	1+	4	4	1
13		0	3−	3−	0	0	0	0	2+	0
136		0	3	3	0	1	1	4	2+	0
137		0	4	4	0	0	0	0	4	1
139		0	4	4	0	0	3−	3	2+	1
144		0	4	4	0	0	3	4	4	4
169		0	4	4	0	0	0	2+	4	0
218		0	4	4	1	0	4	3−	4	3−
244		0	4	4	4	0	4	4	4	4

[a] Standard scale of 0–4 according to Finkner et al (4). Infection types from 3− to 4 were considered compatible and indicative of the presence of the virulence gene corresponding to the powdery mildew resistance gene in the host. Chancellor was "type 4" to all isolates.
[b] CI = USDA Cereal Investigation number.
[c] *Pm*x is the general powdery mildew resistance gene designation. The genes in the row are *Pm*1, *Pm*2, ... *Pm*5.
[d] Michigan Amber gene.

infrared bulb (2.675×10^4 ergs/sec) mounted on a ring stand. A portable electric heater (Market, model 61TS, Nutone Division, Scovill, Buffalo, NY 14207) (1.605×10^5 ergs/sec) was placed in the tower for 2.4 min to dessicate the few remaining conidia and to prevent contamination of the next inoculation. The temperature at the top of the tower was ~38 C at the end of the electrically timed heating period. The infrared bulb was simultaneously switched on during the heating cycle to kill the few remaining conidia in the funnel. The heater was then removed and the tower was allowed to cool to at least 26 C prior to the next inoculation. This procedure was adequate to kill conidia as determined from mock inoculations with the freshly "sterilized" funnel and chamber.

Segments from the center portions of inoculated leaves were excised 50–54 hr after inoculation and placed in test tubes containing 95% ethanol for 24 hr. The leaf segments were removed and further cleared in two fresh changes of 95% ethanol at 24-hr intervals. Leaf segments were mounted in lactophenol-methylene blue to stain the pathogen, and examined under the microscope at ×100 for germ tubes that had produced mature appressoria. Seven groups of 10 conidia with mature appressoria per replication were examined for each compatible host-isolate combination. The corrected infection efficiency (CIE) was calculated as the proportion of mature appressoria that had produced elongating secondary hyphae >30 μm (8). This "corrected" infection efficiency disregarded spores that were not viable, and was previously determined to be more reproducible than an infection efficiency based on total spores applied (24). Approximately 95–98% of all spores that were used as inoculum germinated on water agar, and therefore this method of examining infection may not have differed drastically from that used by others (6). The arc sine square-root function was used to normalize the variance of the CIE data.

RESULTS

Latent period. All colonies for all host-isolate combinations produced conidia by day 7. None of the treatments was significant in the analysis of variance for LP (Table 2).

A second analysis using the unpaired Student's *t*-test compared LP means across all isolates (Table 3). Only the line carrying *Pm*3 had a significantly longer LP than Cc.

Sporulation. All sources of variation were significant in the analysis of variance for cumulative sporulation (Table 2). Partial resistance relative to Cc, indicated by an underscore for each host-isolate combination, was detected for all lines except CI14118 (Table 4). Isolate 139 produced more conidia on CI14119 than on Cc, a phenomenon not previously found (15).

The statistics for lines over all isolates are presented in Table 3. Only CI14123 conferred partial resistance relative to Cc for CSP.

Corrected infection efficiency. All treatment effects were significant in the analysis of variance for CIE (Table 2), and partial resistance relative to Cc was detected for all lines except CI14118 (Table 5). The CIE for isolate 169 on Cc was significantly less than that on CI14125, an effect which was not previously found (15). The line with *Pm*2 from Ulka (CI14118) did not perform the same as the line with *Pm*2 from CI12632 (CI14119).

Isoline stability. Measurements of stability parameters (14) were attempted with respect to host susceptibility, with isolates as the environment term, but did not yield simple interpretations. Therefore, stability was expressed as the lack of significant differences in isolate ranking and the lack of a significant isolate effect in the analysis of variance for each fitness attribute and line.

Significant differences in isolate ranking have been suggested as a more sensitive measure of host-isolate interaction (26) than the *F*-statistic of the host-isolate interaction term in an analysis of variance. However, neither approach permits a numerical comparison of the degree of interaction among different hosts. It is for this reason that the interaction index is proposed. The number of significant differences between isolates determined from Duncan's new multiple range test when compared two at a time can be expressed relative to the maximum possible number. This index, which can take a value of 0 to 1, has several advantages: it is a single value to compare the degree of change in isolate rank on different hosts, it includes isolate ranking as a sensitive criterion beyond the *F*-statistic, it does not require a significant *F*-statistic to proceed with a mean-separation procedure (25) of isolates, and it is useful for comparing hosts that were tested with a different number of isolates. Further tests are needed to determine the accuracy of the index when hosts are tested with different isolates.

An index of 0 indicates maximum stability, and an index of 1 indicates minimal stability. For example, isolate 244 was significantly different from 144 and 218 for CIE on CI14033. The maximum possible number of differences between the three isolates tested on CI14033 taken two at a time is three. The index is therefore expressed as 2/3 = 0.67.

The variance ratio (*F*-statistic) of the isolate to the error term, the isolate ranking, and the interaction index are presented for each line in Tables 4 and 5, for CSP and CIE, respectively. The average index over all fitness attributes follows for each line: Cc = 0.07, CI14118 = 0.12, CI14119 = 0.08, CI14122 = 0.17, CI14123 = 0.22, CI14125 = 0.22, and CI14033 = 0.33. Note that the relatively few degrees of freedom in the error term for CI14122 and CI14033 may

TABLE 2. Analyses of variance for several parasitic fitness attributes of *Erysiphe graminis* f. sp. *tritici* that were used to evaluate the partial resistance of certain wheat lines[a]

		Parasitic fitness attribute[b]					
		LP		CSP		CIE	
Source	df	SS[c]	*F*	SS	*F*	SS	*F*
Total	183	120.52		16.20		12.31	
Experiment	3	18.56	12.11*	4.22	39.72*	0.05	1.51
Treatment	45	32.98	1.43	7.18	4.49*	10.90	23.89*
Line	6	5.52	1.80	3.85	18.07*	5.20	85.45*
Isolate	8	4.12	1.01	1.42	5.00*	0.80	9.87*
Line × isolate	31	20.92	1.32	2.34	2.12*	1.65	5.24*
Error	135	68.98		4.79		1.37	
R^2		0.43		0.70		0.89	

[a] Chancellor (Cc) winter wheat and six near-isogenic lines with race-specific powdery mildew (*Pm*x) resistance genes were tested with a number of isolates (Cc = 9, CI14118 = 9, CI14119 = 9, CI14122 = 4, CI14123 = 6, CI14125 = 6, and CI14033 = 3) and analyzed with a general linear model.

[b] LP = latent period in days, CSP = analyzed as $\log_{10}$ cumulative sporulation per colony 7–13 days from inoculation, and CIE = analyzed as arc sine (square root) function of corrected infection efficiency. Asterisks (*) indicate statistical significance, $P < 0.05$.

[c] Reduction in error SS due to adding a particular source of variation after all other terms have been added to the model except terms that contain the effect being tested.

TABLE 3. Statistics for several parasitic fitness attributes of *Erysiphe graminis* f. sp. *tritici* to Chancellor (Cc) winter wheat and six near-isogenic lines with specific powdery mildew (*Pm*x) resistance genes[a]

	Parasitic fitness attributes[b]					
	LP		CSP		CIE	
Line[c]	$\bar{x}$	*t*	$\bar{x}$	*t*	$\bar{x}$	*t*
Cc	5.52	...	50,119	...	0.93	...
CI14118	5.49	0.18	57,500	1.06	0.94	0.95
CI14119	5.68	0.88	47,863	0.38	0.91	1.06
CI14122	5.93	2.31*	39,800	1.50	0.36	13.83*
CI14123	5.54	0.09	20,400	6.59*	0.69	9.53*
CI14125	5.88	1.62	42,658	0.90	0.92	0.82
CI14033	6.08	1.85	36,300	1.15	0.57	4.49*

[a] $\bar{x}$ = mean of four replications, two leaves per replication, per host-isolate combination; *t* = Student's *t* (unpaired *t*-test) between each line and Cc, significant (*) at $P < 0.05$.

[b] LP = latent period in days, CSP = cumulative sporulation per colony 7–13 days from inoculation, analyzed after transformation to $\log_{10}$, and CIE = corrected infection efficiency, analyzed after transformation to arc sine (square root).

[c] Each line, designated by CI number except Cc, was tested with a number of isolates: Cc = 9, CI14118 = 9, CI14119 = 9, CI14122 = 4, CI14123 = 6, CI14125 = 6, and CI14033 = 3.

not permit accurate comparisons to other lines that were tested with more isolates.

Correlations between fitness parameters. Significant negative correlations existed between LP and CSP, and between LP and CIE (Table 6). Significant positive correlations were found between LP and CIE for one line, and between CSP and CIE for data pooled over lines. These correlations should not be interpreted as cause and effect relationships, and exceptions would be expected. For example, none of the lines demonstrated significant correlations singly between CSP and CIE, but only when the data were pooled.

Number of virulence genes and CSP or CIE. The number of virulence genes in each isolate were determined from the infection types on the lines presented in Table 1. Additional virulence genes may have been present but were not detectable with this set of differentials. When cumulative sporulation through day 13 and corrected infection efficiency were each regressed on the number of virulence genes in each isolate, none of the slopes was significantly different from zero at $P < 0.05$. Approximately half of the slopes were positive for CSP and CIE.

DISCUSSION

The powdery mildew resistance genes that were present in the lines used in this study may be referred to as race-specific genes, major genes, or vertical resistance genes by the criterion of infection type (26). The lines carrying these genes demonstrated significant differential interactions with respect to rate-limiting attributes with compatible isolates. Some of the resistance mechanisms that were expressed in the incompatible reaction (6,8,24) also seemed to be expressed to a lesser degree in the compatible reaction.

These observations support the interpretation (15,20) that race-specific resistance may also affect certain expressions of parasitic fitness that are influential in the rate of disease development. Parasitic fitness could be expressed in terms of the relative competitive abilities of biotypes, and these differences are the result of interactions among several components of fitness. Two particular components of fitness are CSP and CIE. Isolates may be compared with respect to these components, but an isolate with a greater CSP does not necessarily make it less fit than an isolate with a lesser CSP because interactions with other relevant fitness attributes would not be considered. The small correlation coefficients between the racial frequencies (21) of isolates 10, 137, 169, and 244, and certain fitness attributes on Cc demonstrate this point: LP = 0.33, CSP = 0.24, and CIE = 0.47. Another interpretation is that a small sample of isolates should not be expected to represent the range in fitness attributes that exists in particular genotypes such as races.

For example, if virulence genes in addition to those needed for

TABLE 4. Cumulative sporulation of several compatible isolates of *Erysiphe graminis* f. sp. *tritici* on cultivar Chancellor (Cc) winter wheat and six near-isogenic lines with race-specific powdery mildew (*Pm*x) resistance genes[a]

		Near-isogenic line[b]					
	Cc	14118[c]	14119	14122	14123	14125	14033
	F-statistic[d] = 0.57	3.26*	5.68*	3.23	3.24*	1.69	3.13
Isolate	Int. index[e] = 0.00	0.25	0.25	0.33	0.20	0.07	0.33
10	56,234 a	66,069 bc	58,888 bc		32,360 c	47,865 ab	
13	50,119 a	29,512 a	36,308 ab				
136	38,905 a	61,660 bc	36,315 b		*19,055* abc		
137	56,230 a	36,308 ab	*15,488* a			*26,303* a	
139	42,658 a	64,565 bc	*85,114* c	50,120 b	*18,198* abc		
144	63,096 a	74,130 c	67,608 bc	*24,548* a	*14,791* a	54,950 ab	*19,061* a
169	50,100 a	75,858 c	54,954 bc			45,701 ab	
218	44,668 a	63,090 bc	48,978 bc	40,738 ab	28,840 bc	35,483 ab	38,908 ab
244	52,481 a	64,565 bc	66,069 bc	48,980 b	16,218 ab	57,541 b	66,071 b

[a] Cumulative sporulation measured as the number of spores produced per colony on primary leaves 7–13 days from inoculation. Cumulative sporulation was analyzed after transformation to $\log_{10}$; values in table are back-transformed means of four replications.

[b] Letters indicate significant differences ($P <= 0.05$) among isolates within lines according to Duncan's new multiple range test; italics indicate a significant difference between Cc and line, $P < 0.05$, and LSD = 0.26.

[c] Line numbers designate USDA Cereal Investigation number.

[d] Variance ratio of isolate/error term from the analysis of variance by line, $P < 0.05$.

[e] Interaction index = number of significantly different isolate pairs/maximum number possible.

TABLE 5. Corrected infection efficiency of several compatible isolates of *Erysiphe graminis* f. sp. *tritici* on Chancellor (Cc) winter wheat and six near-isogenic lines with race specific powdery mildew (*Pm*x) resistance genes[a]

		Near-isogenic line[b]					
	Cc	14118[c]	14119	14122	14123	14125	14033
	F-statistic[d] = 10.51*	2.26	1.40	2.21	2.36	4.24*	50.63*
Isolate	Int. index[e] = 0.22	0.11	0.00	0.17	0.13	0.27	0.67
10	0.97 b	0.97 bc	0.97 a		*0.68* ab	0.96 c	
13	0.94 b	0.96 abc	0.92 a				
136	0.94 b	0.94 abc	0.93 a		*0.82* b		
137	0.97 b	0.91 ab	*0.85* a			0.95 bc	
139	0.94 b	0.94 abc	0.88 a	*0.26* a	*0.65* ab		
144	0.92 b	0.92 abc	0.89 a	*0.37* ab	*0.75* ab	0.91 abc	*0.31* a
169	0.74 a	*0.89* a	0.85 a			*0.94* bc	
218	0.94 b	0.96 bc	0.94 a	*0.31* ab	*0.62* a	*0.83* a	*0.41* a
244	0.93 b	0.97 c	0.94 a	*0.52* b	*0.61* a	0.88 ab	0.92 b

[a] Corrected infection efficiency was analyzed after transformation to arcsin (square root); values in table are back-transformed means of four replications.

[b] Letters indicate significant differences ($P < 0.05$) among isolates within lines according to Duncan's new multiple range test; italics indicate significant difference between Cc and line, $P < 0.05$, and LSD = 0.14.

[c] Line numbers designate USDA Cereal Introduction number.

[d] Variance ratio of isolate/error term from the analysis of variance by line, $P < 0.05$.

[e] Interaction index = number of significantly different isolate pairs/maximum number possible.

TABLE 6. Correlations between parasitic fitness attributes of *Erysiphe graminis* f. sp. *tritici* to Chancellor (Cc) winter wheat and six near-isogenic lines with race specific powdery mildew (*Pm*x) resistance genes[a]

Attribute[b]	Wheat line	Correlations[c] CSP	CIE
LP	Cc	−0.62*	0.00
	CI14118	−0.41*	0.25
	CI14119	−0.53	0.00
	CI14122	−0.14	−0.39
	CI14123	−0.60*	0.10
	CI14125	−0.55*	0.28
	CI14033	−0.58	0.66*
	Pooled	−0.46	−0.16*
CSP	Cc		0.07
	CI14118		0.04
	CI14119		0.14
	CI14122		0.13
	CI14123		−0.14
	CI14125		−0.06
	CI14033		0.55
	Pooled		0.29*

[a] Four observations for each host-isolate combination. Number of isolates tested on each line follow: Cc = 9, CI14118 = 9, CI14119 = 9, CI14122 = 4, CI14123 = 6, CI14125 = 6, and CI14033 = 3.
[b] Parasitic fitness attributes: LP = latent period in days, CSP = $\log_{10}$ cumulative sporulation per colony 7–13 days from inoculation, and CIE = arc sine (square root) function of corrected infection efficiency.
[c] *Significant at $P < 0.05$.

virulence on a particular host necessarily cause isolates to be less fit (26) or more fit (22) by the criteria of CSP or CIE, then the slope of zero for Cc from the regression of CSP or CIE on number of known virulence genes per isolate would not be expected. None of the other lines had slopes significantly different from zero. However, the presence of many unidentified virulence genes may make this analysis inadequate. Since many genes contribute to the fitness of a pathogen genotype, Leonard (11) has proposed that isogenic pathogens and hosts that differ only in virulence or resistance genes be used to address this hypothesis. A large number of isolates could also be used to test the above, provided the sample is large enough to detect the "cost" (11) of surplus virulence genes. Probably nine isolates of *Erysiphe graminis* is too small a sample to adequately test the hypothesis that unnecessary virulence genes reduce fitness.

This study demonstrated that isolate genotypes can influence the ability of the lines to express various degrees of partial resistance. Had any single attribute or isolate been used to evaluate the lines, there may have been a different conclusion. Nass (15) demonstrated that CI14122, CI14123, and CI14033 conferred partial resistance against isolate 144 for CSP. This study confirmed Nass's results (15). However, the isolates varied in response on any given line. For example, isolates 144 and 218 were of the same race, but 144 produced fewer spores on CI14123 while isolate 218 produced more spores on this line. Isolate 139 produced more conidia on CI14119 than on Cc, and isolate 169 had a larger CIE on CI14118 than on Cc. These examples demonstrate the variability in the expression of residuality, and the potential for greater disease on certain lines than on Cc.

There are four possible genetic sources of variation in the host-isolate interactions. These are the host resistance genes (*Pm*x), host background genes, pathogen virulence genes (*p*x), and pathogen background genes. If the wheat lines were not isogenic with respect to Cc, then differences in partial resistance may be expected due to the background differences of the lines as well as differences in isolate virulence (1). In one case, CI14118, possessing *Pm*2 from Ulka, did not perform the same as CI14119, possessing *Pm*2 from CI12632. This result underscored the importance of a gene's source in the expression of resistance (16) regardless of whether the "source effect" was due to linked modifiers (1) or unidentified multiple alleles of the gene in question.

A breeder would probably use the partial resistance of a line carrying a particular *Pm*x gene and would not be concerned if modifier genes tightly linked to the *Pm*x gene are responsible for the rate-limiting resistance. Evidence of such a single race-specific gene in use is the *Sr*Tt-1 gene (20) conferring rate-limiting resistance to compatible isolates of *Puccinia graminis*. The breeder may not be concerned with the recombination frequency between *Pm*x and modifiers, but may only want to be provided with a differential set of isolates of different races to identify the *Pm*x genes as well as a set to identify rate-reducing characters during the selection process.

It may not necessarily be impossible to separate infection type (IT) criteria (colony size, sporulation, etc.) from the same criteria that are used to measure rate-reducing resistance. Johnson et al (10) found a significant correlation between IT and sporulation, but small differences in the higher ITs occurred with large differences in sporulation for *P. striiformis*. The same general trend was observed in this study, with a greater variability in sporulation occurring with higher ITs. The variability in the measurements of partial resistance, relative to ITs greater than or equal to 3−, was large and the simple correlation coefficients were not significant between LP and IT ($r = -0.24$), CSP and IT ($r = 0.10$), and CIE and IT ($r = 0.12$). This variation may reflect the potential of the pathogen population to overcome small degrees of resistance in susceptible lines.

If significant host × isolate interactions or significant differences in isolate rank indicate the potential for erosion of resistance (26), then particular lines in this study may sustain a "breakdown" in residual resistance while others may not for any particular attribute. If LP exerts a major influence on the rate of epidemic progression (17), then CI14122 (with an interaction index of 0) may exert less selection pressure for isolates with shorter LPs than the other lines with greater interaction indices. However, LP was measured with the least precision of all the attributes ($R^2 = 0.43$), and future studies should check for sporulation more often. If sporulation is a major component in limiting the rate of disease increase (5,10,19), then CI14123 may retain residual resistance that would erode relatively slowly over time since the index = 0.20. If CIE is an important rate-limiting component (19), then the longevity of residual resistance may decrease in order for the following lines: CI14123 (index = 0.13), CI14122 (index = 0.17), and CI14033 (index = 0.67). Lines CI14122 and CI14123 may exert the strongest partial resistance overall (Student's "*t*" values greater than those for the other lines relative to Cc) but only until isolates with greater fitness on CI14122 or CI14123 increase in the population. Possibly CI14123 may retain more partial resistance than CI14122 for CSP after this event, since the greatest CSP for CI14123 is still less than that for Cc. Similarly, CI14122 may retain a smaller CIE than CI14123.

This interaction approach to predicting the longevity of resistance overlooks the possible longevity of rate-reducing resistance that may be associated with quantitative inheritance of particular rate-reducing resistance characters (16), as well as the quantitative inheritance of parasitic fitness (7). Alternatively, durable resistance may not be assured with knowledge of the mechanism of resistance, the genetic control, or the race-specificity as suggested by Johnson (10). The relationship of these results to field observations (9) should be investigated to account for inaccuracies of using a few isolates, plant phenology, environment, and geographic variability in pathogen fitness beyond virulence gene frequencies.

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