Resistance

Individual and Cumulative Effects of Long Latent Period and Low Infection Type Reactions to *Puccinia recondita* in Triticale

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ABSTRACT

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Triticale PI 429155 was selected as a possible source of leaf-rust resistance for wheat. This cultivar expresses an infection type (IT) 1^+ and a latent period (T_{50}) of about 14 days when inoculated with culture 7434-1-1T of *Puccinia recondita*. The effects of the incomplete hypersensitivity and slow-rusting resistance of PI 429155 were evaluated by separating the genetic factors for resistant IT and long T_{50} into different experimental cultivars, measuring the components of resistance on adult plants, and evaluating the resistances in epidemics. The derived cultivars possessed either no resistance factors (susceptible, SUSC), the factors for long T_{50} and susceptible IT (slow rusting, SR), the factors for resistant IT and moderately short T_{50} (hypersensitive resistance, HR), or factors for both forms of resistance combined (slow-rusting and hypersensitive resistances, SR + HR). SR, HR, and SR + HR all reduced the infection frequency on flag leaves. The IT, T_{50}, and uredinium areas of SUSC, SR, HR, and SR + HR were IT 4, 3, 2, and 1^+; 7.1, 13.0, 9.5, and 14.3 days; and 0.282, 0.124, 0.093, and 0.069 mm^2, respectively. The gamma distribution fit the pattern of spores produced per uredinium per day, measured from 7 to 30 days after inoculation. Cumulative spores produced per uredinium on SR, HR, and SR + HR were 27.5, 16.4, and 13.6% of that produced on SUSC. The long T_{50} of SR provided greater disease control than the reduced sporulation and smaller uredinia of HR in computer-generated models of rust epidemics and in hill plots in the field in 1986 and 1987.

Alien germ plasm is being used increasingly in wheat (*Triticum aestivum* L.) improvement. The gene pools of related species and genera are valuable sources of resistance to many pathogens. Transfers of resistance to *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* from alien species to wheat has exclusively involved genes that confer some degree of hypersensitivity (8–10,15,30, 33,37,40,44). Aside from the barriers encountered in the transfer of traits by wide hybridization (prefertilization incompatibility between parental species, postfertilization incompatibility in the hybrid, hybrid sterility, and lack of recombination), these genes can be manipulated rather easily. Their expression is similar to many of the known *Lr* genes in wheat that confer resistance to *P.*

recondita. Generally, these genes are dominant or partially dominant and are expressed in seedlings as well as in later growth stages (4).

In contrast to hypersensitive resistance, slow rusting can be recognized as another form of resistance. Pure-line cultivars with slow-rusting resistance exhibit susceptible infection type, but, compared with fully susceptible cultivars, they exhibit reduced infection frequencies, longer latent periods, smaller uredinia, and reduced sporulation (25) when infected with appropriate strains of the pathogen. "Slow-rusting resistance" as we use it here does not refer to the slow rate of rust increase on a resistant cultivar confronted by a fungus population heterogeneous for virulent and avirulent strains.

Inheritance of slow-rusting resistance in alien species has not been evaluated as extensively as hypersensitivity, in part because it

is more difficult to work with. In wheat, slow rusting and long latent period, a major component of slow rusting, are generally conferred by two or more partially recessive, additive genes (12,17,18) and are expressed to the greatest degree in adult plants (24).

Triticale (× *Triticosecale* Wittmack ex A. Camus) is a synthetic alien species that often exhibits high levels of resistance to common pathogens of wheat. In Indiana, several triticales were resistant to *P. recondita* in evaluations in the field and greenhouse (45). Studies on the inheritance of resistance to *P. recondita* indicated that these cultivars each possess one or two incompletely dominant factors that confer a resistant infection type, and an undetermined number of factors that confer a long latent period (Wilson and Shaner, *unpublished*).

These triticales were selected to be sources of resistance to *P. recondita*. Ideally, attempts to transfer the leaf-rust resistance from triticale to wheat should focus on all of the genes for resistance within the triticale cultivars because the race specificity of the resistances is unknown. The expression and inheritance of resistance will affect the strategy used to transfer the resistance, but the effectiveness of the resistance will dictate whether the transfer should be pursued. The objective of these experiments was to determine the value of the hypersensitive versus the nonhypersensitive resistances of PI 429155 in monocyclic and polycyclic infections.

MATERIALS AND METHODS

Development of experimental cultivars. PI 429155 was crossed to susceptible triticale PI 429007. The F_3 progeny were evaluated for resistance to *P. recondita*. Infection types (IT) (41) were determined for seedlings at the two-leaf stage (growth stage [GS] 12 [47]). Adult-plant infection types and latent periods were determined from inoculations performed when the spike was half emerged from the boot (GS 55). T_{50}s were calculated as the time required for 50% of the uredinia to erupt, as determined from the regression of the probit of the proportion of erupted uredinia on time (34). Seedlings in flats or the adaxial surface of the flag leaf of adult plants were misted with an aqueous spore suspension consisting of 50 mg of urediniospores of culture 7434-1-1T of *P. recondita* and 3 drops of Tween-20 per 100 ml. Culture 7434-1-1T is virulent toward *Lr* genes 2b, 2c, 2d, 3a, 3bg, and 9 and avirulent toward *Lr* genes 1, 2a, 3b, 10, 11, 12, 13, 17, 18, 19, 24, and 25. The plants were placed in a moist chamber overnight (18 hr) and then were returned to the greenhouse bench.

Selection began in the F_3 for plants with susceptible IT (IT 3 or 4) and short T_{50}, resistant IT (IT 1 or 2) and short T_{50}, or susceptible IT and long T_{50}. Two to three generations of selection, without crossing, for disease reaction among and within families (progeny derived from individual selections) were practiced. Selections 83907RC4-28-13-10 and 11 (83907RC4), collectively designated hereafter as the hypersensitive resistance (HR) cultivar, possessed the factors for resistant IT and moderately short T_{50}, and 83907RC1-5-16-6-11 (83907RC1), designated as the slow-rusting (SR) cultivar, possessed factors for long T_{50} but susceptible IT. PI 429007 (susceptible, SUSC), PI 429155 (slow-rusting and hypersensitive resistances, SR + HR), 83907RC4 (HR), and 83907RC1 (SR) were evaluated in the 1986 field experiment.

To insure separation of the resistances and to achieve greater uniformity among the experimental cultivars, additional crosses were made. Progeny of 83907RC4 (HR) were crossed to progeny of 83907RC2-1-35-17-29, a selection with susceptible IT and short T_{50} (SUSC), to select new HR and SUSC cultivars, and progeny of 83907RC1 (SR) were crossed to PI 429155 (SR + HR) to select new SR and SR + HR cultivars. The F_2 progeny of each F_1 plant were inoculated in the two-leaf stage (GS 12). The plants with resistant infection type were grown to maturity and allowed to self-pollinate without further evaluation. The plants with a susceptible infection type were reinoculated at GS 40–43, and their latent periods were determined. The latent period mean and variance of each F_2 population was calculated.

F_1-derived F_2 (F_1:F_2) populations were selected from the HR ×

SUSC and from the SR + HR × SR crosses. F_1:F_2 populations whose susceptible F_2 plants had the shortest T_{50} means were selected from the SUSC × HR crosses. The short T_{50} indicated that the HR parents of those crosses had few or no genes that conferred long T_{50}. F_1:F_2 populations whose susceptible F plants had the longest T_{50} means were selected from the SR × PI 429155 (SR + HR) crosses. The long T_{50} suggests that the SR parents from those crosses had more factors for long T_{50} than their sibs. Additional criteria for selection among all populations were similarities in plant height, flowering times, and seed quality.

The F_3 families of the selected F_2 populations were inoculated at GS 12. Within the HR × SUSC populations, F_3 families homozygous for resistant infection type were selected for the new HR cultivar, and the families homozygous for susceptible infection type were selected for the new SUSC cultivar. Within the SR + HR × SR populations, F_3 families homozygous for resistant infection type were selected for the new SR + HR cultivar, and the families homozygous for susceptible infection type were selected for the new SR cultivar. The components of resistance of these SUSC, HR, SR, and SR + HR cultivars were measured in the greenhouse experiment, from which the data for the computer simulation were derived.

Seed of the F_3 plants that were evaluated in the greenhouse were bulked within the SUSC, SR, HR, and SR + HR resistance groups. These bulks and PIs 429007 and 429155 were evaluated in the 1987 field experiment.

Greenhouse experiment and computer simulation. The flag leaves of plants at GS 44–55 (boots visibly swollen to spike half emerged) were inoculated in a settling tower (11) with 10 mg of urediniospores of culture 7434-1-1T of *P. recondita*. Five plants of each of the four resistance classes were inoculated in each of four inoculations. Within each inoculation, the cultivars were arranged in the settling tower in a randomized block design. Inoculated plants were incubated 18 hr overnight in a moist chamber where constant leaf wetness was maintained, and then they were placed on greenhouse benches in a randomized block design with five replications. Greenhouse temperatures were kept at approximately 26 C, and natural daylight was supplemented with 16 hr per day of about 20,000 erg · cm^{-2} sec^{-1} fluorescent lighting. Estimates of uredinia produced per viable spore deposited (infection frequency) were calculated from counts of spore deposition per unit area on greased microscope slides, spore germination on water agar, and final uredinium density per unit area on the inoculated leaves.

Erupted uredinia were counted within a 4-cm length of the flag leaves, beginning 6 days after inoculation. After uredinium eruption in the 4-cm section ceased, latent periods were calculated (34), and the lengths and widths of five randomly selected, relatively isolated uredinia per flag leaf were measured with a Bausch & Lomb measuring magnifier (Bausch & Lomb Inc., Rochester, NY). Uredinium area was calculated as (π × width × length)/4. Infection frequencies, latent periods, and uredinium areas of the resistance classes were analyzed for differences by analysis of variance.

Daily spore production on each line was measured by collecting into a common vial the spores produced on all replicates within an inoculation, by use of a cyclone spore collector. The spores were suspended in a 0.5% Tween-20 solution, and spore concentration in the suspension was determined from the average of the counts made in two hemacytometer preparations. Number of spores produced per uredinium per day was calculated from the spores collected per day divided by the estimated total number of uredinia erupted on all the leaves by that day. Total number of uredinia per leaf was calculated from the number of uredinia within the 4-cm length of leaf, the area of that length, and the total leaf area. Leaf area was calculated as follows:

$$AREA = \left\{ [(W1 + W2)/2] + [(W2 + W3)/2] + (0.5W3) \right\} \times (L/3)$$

in which L = the length of the leaf, and W1, W2, and W3 = the width of the leaf at the base of the leaf, at one-third, and at two-thirds of the length of the leaf, respectively.

A modified version of the computer program SLORUS (36) was

used to model disease progress on the experimental cultivars, by using the components of disease resistance measured in the monocyclic infection experiments described above. The original version of the program assumed that spore production per uredinium was constant (36). The models generated in this experiment were calculated with a version of the program that had been modified to accommodate the variable production of spores per uredinium per day that was observed. Various distributions were fit to the sporulation data, and the gamma distribution, $f(x) = kx^{(r-1)} e^{-\gamma x}$ (21), gave the closest fit. This distribution was incorporated into the program as an option for evaluating the effect of sporulation on epidemic development. The observed data for spore production were regressed with the following equation:

$$\ln(Y) = \ln k + (r-1)\ln x - \gamma x$$

in which Y = spores per uredinium, x = relative time in days after sporulation began, and k, r, and γ are constants derived from fitting the gamma distribution to the spore productions.

Variables required to run SLORUS models include some that are unaffected by cultivar resistance and some that are the components of resistance. Variables required that are unaffected by resistance and the values entered (in parentheses) were as follows: total leaf area (10,000 mm²), days for the epidemic to run (45 days), and proportion of spores that land on leaves, λ (models were initially run with values of 0.1, 0.2, 0.3, 0.4, and 0.5). An additional simulation was run in which the value of λ was selected by iteration such that the disease progress curve for SUSC corresponded closely to that for the progress of rust on flag leaves of SUSC in the field in 1987. This same value of λ (0.12) then was used to run simulations for the other three lines. Assumptions that are built into the model are that there are 10 primary infections, infections occur daily once secondary inoculum is produced, and the pathogen population is homogenous for phenotype with respect to virulence and aggressiveness.

Variables required by the model that are components of resistance included infection frequency (the proportion of spores landing on leaf tissue that give rise to uredinia). The values entered for the SUSC, SR, HR, and SR + HR models were 0.135, 0.112, 0.119, and 0.109, respectively. The values in Table 1 represent infections per viable spore deposited, whereas the values used in the model represent infections per total spores deposited. Other

variables were the latent period probabilities, P_j, or the noncumulative values of the proportion of uredinia that erupt on day j (see Fig. 1 for cumulative data), values derived from fitting a gamma distribution to the spore production distribution (intercept, ln k, 3.697, 4.078, 3.372, and 3.382; coefficient of log time, r − 1, 2.147, −0.277, 1.023, and 0.297; and coefficient of linear time, γ, −0.420, −0.087, −0.371, and −0.238), and the uredinium areas (data in Table 1). With these variables for each triticale line, SLORUS generated a disease progress curve and area under the disease progress curve (AUDPC) for each epidemic.

Field experiments. In the 1986 experiment, seedlings of PI 429155 (SR + HR), PI 429007 (SUSC), and their selected progeny lines 83907RC4 (HR) and 83907RC1 (SR) were transplanted into the field when at GS 12. Two disease environments were created for the experiment. The severe disease plots were planted approximately 20 m downwind (from the prevailing wind direction) of a wheat nursery that could serve as a source of inoculum. These plots were surrounded by a border row of the susceptible triticale PI 429049. Before the flag leaves of the plants in the border emerged (GS 30–36), the corner plants of the border were inoculated with urediniospores of culture 7434-1-1T of *P. recondita*. The mild disease plots were planted upwind of and separated from the nearest inoculum source by approximately 100 m of oat. These plots were surrounded by an uninoculated border row of the resistant triticale PI 429215.

Three plots were planted within each disease environment. Each plot was a 4 × 4 latin square, with one plant per hill. The hills were spaced 15 cm apart. Each latin square was arranged with a different permutation.

Leaf-rust severities on the flag leaves were estimated with the aid of standard diagrams (27). Disease severities were assessed five times at 5-day intervals. The AUDPCs for the 20-day intervals were calculated for each hill by the following equation:

$$\text{AUDPC} = \Sigma\left\{[Y_{(i+1)} + Y_i]/2\right\} \times [X_{(i+1)} - X_i]$$

in which Y_i = percent disease severity at time X_i. All of the tillers of four plants were killed by stem-boring insects. The AUDPCs for these missing plants were estimated (42), and the error degrees of freedom in the analysis of variance were reduced accordingly.

The AUDPCs were transformed to log (AUDPC + 1) before analysis to reduce the relationship between the means and variances of the AUDPCs. The transformed AUDPCs within the

TABLE 1. Effects of incomplete hypersensitivity and slow-rusting resistances from triticale PI 429155 on the components of resistance to culture 7434-1-1T of *Puccinia recondita* f. sp. *tritici*[u]

Cultivar resistance[v]	Infection frequency[w]	Latent period (days)[x]	Uredinium area (mm²)	Infection type	Cumulative sporulation (%)[y]
SUSC	0.793 a[z]	7.1 a	0.282 a	4	100
HR	0.702 b	9.5 b	0.093 c	2	16.4
SR	0.662 b	13.0 c	0.124 b	3	27.5
SR+HR	0.642 b	14.3 d	0.068 d	1+	13.6
Least significant difference (0.05)	0.066	0.9	0.015	...	...

[u] Values are the means of 20 replicates, except uredinium areas, which are the means of 100 measurements.

[v] SUSC, HR, SR, and SR + HR refer to cultivars that possess no resistance, incomplete hypersensitivity, slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, respectively. SUSC and HR were selected from the cross 83907RC4 × 83907RC2, and SR and SR + HR were selected from the cross 83907RC1 × PI429155.

[w] Number of uredinia produced per viable spore deposited.

[x] Time in days required for 50% eruption of uredinia on the regression line of probit of the proportion of erupted uredinia on time.

[y] Cumulative sporulation per uredinium from 7 to 30 days after inoculation, relative to SUSC.

[z] Means within a column followed by the same letter are not significantly different (P = 0.05) in pairwise comparisons.
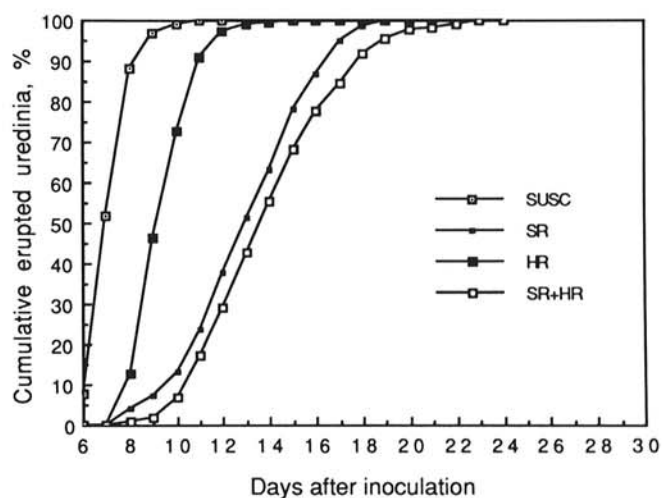

Fig. 1. Eruption of uredinia on flag leaves of triticale cultivars differing in latent period and infection type. The plants were inoculated in the greenhouse with culture 7434-1-1T of *Puccinia recondita*. Data are based on the number of uredinia erupted within a 4-cm length of the flag leaf of 20 plants per cultivar. SUSC, HR, SR, and SR + HR refer to cultivars that express no resistance, incomplete hypersensitivity, slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, respectively.

mild and severe disease environments were compared by nonorthogonal, single-degree-of-freedom linear comparisons.

In the 1987 experiment, five seeds of either the SUSC, HR, SR, or SR + HR bulks or PI 429007 and PI 429155 were planted in pots in the greenhouse. When the plants reached the four-leaf stage (GS 14), they were transplanted into the field into three 6 × 6 latin square plots. Each plot had a different permutation and was surrounded by a border of hill plots of the susceptible wheat cultivar Morocco. To assure adequate inoculum for early and severe disease pressure, the plants of the border were inoculated in the greenhouse with a urediniospore suspension of culture 7434-1-1T three days before transplanting them in the field. Two plants in each hill were tagged when the spike was half emerged from the boot. The average date on which the head was half emerged from the boot was designated the heading date for each cultivar.

Rust severities were determined for the flag, flag-1, and flag-2 leaves at 4-day intervals on each of the tagged tillers, and the average of the two evaluations was designated the severity for that leaf position at each hill. AUDPCs were calculated as above for the intervals of 24, 20, and 15 days after heading for the flag, flag-1, and flag-2 leaves, respectively. If a hill was not assessed on the day of truncation for the AUDPC determination, the severity values for the hill were transformed to logits and regressed against time by means of quadratic equations. The logit severities for the truncation dates were determined by extrapolation or interpolation, the estimated values were transformed back to percent severity values, and the AUDPCs then were calculated as described above. The AUDPC values were transformed to log (AUDPC + 1) before data analysis by analysis of variance. A different analysis of variance was used to analyze the AUDPCs for the different leaf positions.

RESULTS

Greenhouse experiment and computer models. Cultivar had a significant effect on the components of resistance to infection by *P. recondita* (Table 1). Proportionally more viable spores established uredinia on SUSC than on the cultivars with some form of resistance. Both SR and HR extended the latent period and reduced the uredinium area relative to SUSC. When the resistances were combined, the effects on latent period and uredinium areas were cumulatively expressed (Fig. 1, Table 1).

Spore production per uredinium per day increased rapidly to a maximum and then decreased gradually with time (Fig. 2). The infectious period did not terminate for any of the cultivars; sporulation continued at a gradually reduced capacity throughout the experiment. Among the resistant cultivars, spore production on SR decreased slowly, whereas sporulation on HR and SR + HR decreased more rapidly. It appeared that sporulation diminished as the leaf tissue supporting the uredinium senesced, which occurred more rapidly in the cultivars that possessed HR. More spores were produced on SR than on HR, and the resistances appeared to act together to further reduce cumulative sporulation (Table 1).

The AUDPCs calculated by SLORUS were large for SUSC at all levels of λ (proportion of spores that land on the leaves). AUDPCs of the cultivars with resistance were greatly reduced (Fig. 3). Across all λ levels, the ranks of the cultivars' AUDPCs were identical, but differences in effectiveness of resistance were more clearly seen at higher levels of λ. In all cases, SR gave greater disease control than HR, and disease suppression was greatest when the resistances were combined.

Field experiments. Leaf-rust severities on flag leaves of PI 429007 averaged 36 and 52% within the mild and severe disease plots in 1986. The ranking of the cultivars' AUDPCs was consistent across disease environments, and differences among AUDPCs were greater in the severe disease plots than in the mild disease plots (Fig. 4). Analysis of variance indicated that the effects of disease environment and cultivar resistance were significant (Table 2).

All forms of resistance reduced leaf rust compared to SUSC (Table 3). AUDPCs were significantly less for SR than for HR, and

the resistances acted cumulatively to confer greater protection when combined in SR + HR.

Leaf-rust severities on flag leaves of the susceptible cultivars PI 429007 and SUSC averaged 62 and 80%, respectively, in 1987. AUDPCs were less for the cultivars with some form of resistance
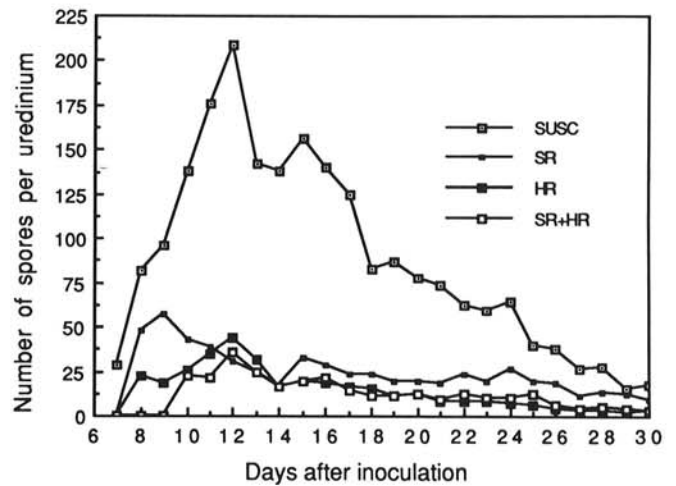

Fig. 2. Spores produced per uredinium per day on flag leaves of triticale cultivars differing in latent period and infection type. The plants were inoculated in the greenhouse with culture 7434-1-1T of *Puccinia recondita*, and urediniospores were harvested from five leaves of each cultivar. The number of spores collected was divided by the total number of uredinia on these leaves to obtain the number of spores per uredinium for each replicate. Data points are the mean of four replicates. SUSC, HR, SR, and SR + HR refer to cultivars that express no resistance, incomplete hypersensitivity, slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, respectively.
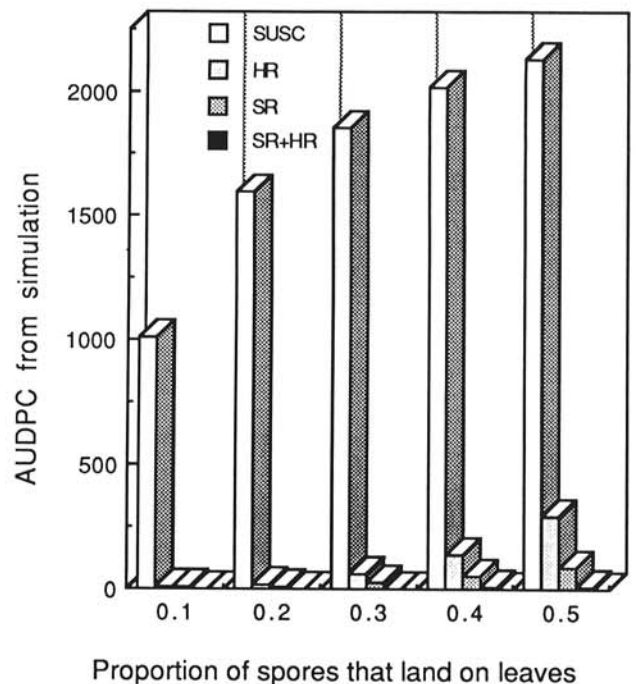

Fig. 3. Areas under the disease progress curve (AUDPCs) calculated from leaf-rust epidemics modeled with the computer program SLORUS. Data of the components of resistance to culture 7434-1-1T of *Puccinia recondita* of triticale cultivars differing in latent period and infection type were used to model the epidemics. The proportion of spores that land on the leaves is a variable in the model and refers to the proportion of the secondary inoculum produced on a cultivar that lands back on leaf blades of that cultivar and is not considered a component of resistance. SUSC, HR, SR, and SR + HR refer to cultivars that express no resistance, incomplete hypersensitivity, slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, respectively.

(Fig. 5). Within each leaf position, the ranks of the cultivars' AUDPCs were identical to those of the computer models and the 1986 field experiment.

Cultivar resistance was consistently a significant source of variation at all leaf positions (Table 4). Across all leaf positions, SR exhibited greater resistance than did HR. The derived SUSC cultivar had greater AUDPC values for the upper two leaves than did PI 429007; similarly, the derived SR + HR cultivar had greater AUDPCs for its upper two leaves than did PI 429155 (Table 5).

The computer models of disease increase that were generated with $\lambda = 0.12$ adequately fit the observed increase on SUSC but underestimated the rate of increase on the resistant cultivars (Fig. 6).

DISCUSSION

The low IT and long T_{50} reactions affected colonization in monocyclic infections and disease increase in polycyclic infections. The effects of the resistances were similar in many respects but differed in magnitude. Both reduced the infection frequency.
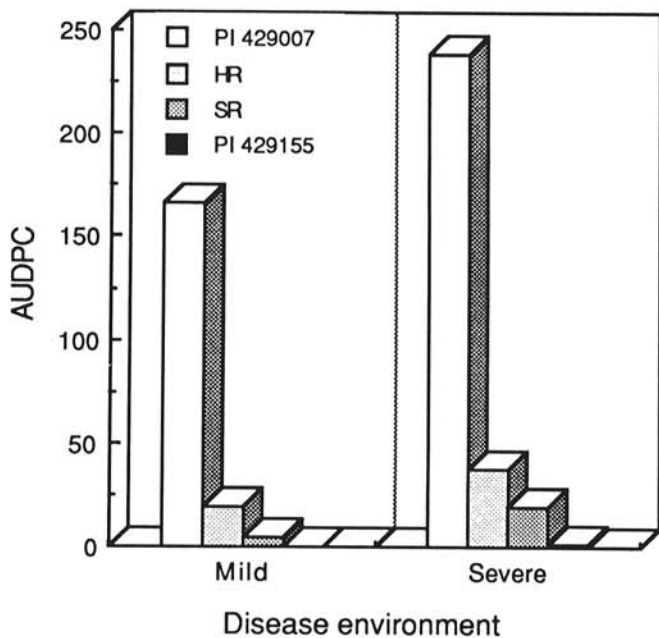

Fig. 4. Areas under the disease progress curve (AUDPCs) for flag leaves of triticales differing in latent period and infection type, evaluated in two leaf-rust epidemics at the Purdue Agronomy Farm in 1986. The triticale cultivar HR has incomplete hypersensitivity, SR has slow-rusting resistance, and both cultivars are derived from crosses between susceptible line PI 429007 and the SR + HR line PI 429155. Disease in the mild disease environment was the result of natural infection. The borders of the high disease plots were inoculated with culture 7434-1-1T of *Puccinia recondita*. AUDPC values are the means of 12 replicates.

TABLE 2. Analysis of variance of the effect of disease environment and cultivar resistance in triticale on AUDPCs[a] of leaf-rust epidemics observed at the Purdue Agronomy Farm in 1986

Source	df	Mean square
Disease[b]	1	4.345*[c]
Error (a)	4	0.362
Row (disease × plot)	18	0.122
Column (disease × plot)	18	0.126
Cultivar	3	18.220**
Disease × cultivar	3	0.300
Plot × cultivar (disease)	12	0.120
Error (b)	32	0.120

[a] Area under the disease progress curve. Values were transformed to log (AUDPC + 1) before analysis.
[b] Disease environment; inoculated versus uninoculated plots.
[c] * and ** indicate significant effects at $P = 0.05$ and 0.01, respectively.

Reduced infection frequency to rust pathogens of cereals could be the result of reduced appressorium formation (16), reduced penetration from established appressoria (29), abortion of fungal colonies at various stages of growth (2,22), or combinations of all these mechanisms. In the present experiments, chlorotic flecks

TABLE 3. Development of leaf rust in 1986 on triticale cultivars differing in resistance,[a] and nonorthogonal, single-degree-of-freedom linear contrasts

Cultivar[b] or contrast	Mild disease[c]	Severe disease
	Area under the disease progress curve	
SUSC	166.3	238.8
SR	4.4	19.0
HR	19.7	37.8
SR + HR	0.0	1.3
	Mean square[d]	
SUSC vs. SR, HR, and SR + HR	23.12**[e]	16.47**
SR vs. SR + HR	6.93**	5.73**
HR vs. SR + HR	4.81**	10.14**
SR vs. HR	0.54*	0.63*

[a] Experiment conducted at the Purdue University Agronomy Farm.
[b] Cultivar SUSC (PI 429007) has no resistance, SR (83907RC1) has slow-rusting resistance, HR (83907RC4) has incomplete hypersensitivity, and SR + HR (PI 429155) has both resistances, 83907RC is a cross between PI 429007 and PI 429155.
[c] Uninoculated versus inoculated plots.
[d] Mean value for cultivars in three 4 × 4 latin square plots within each disease environment. Values are untransformed data.
[e] * and ** indicate significant differences at $P = 0.05$ and 0.01, respectively. Contrasts were calculated with transformed values.
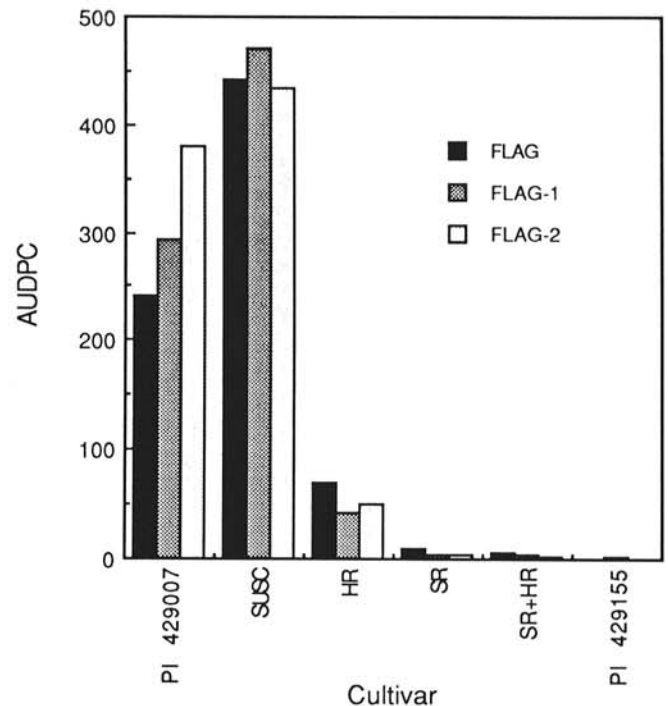

Fig. 5. Areas under the disease progress curve (AUDPCs) for the three uppermost leaves of triticale cultivars differing in latent period and infection type, observed in a leaf-rust epidemic at the Purdue Agronomy Farm in 1987. AUDPCs were calculated for 24, 20, and 15 days after heading for the flag, flag-1, and flag-2 leaves, respectively. SUSC, HR, SR, and SR + HR refer to cultivars that express no resistance, incomplete hypersensitivity, slow-rusting resistance, and incomplete hypersensitivity plus the slow-rusting resistance, respectively. These cultivars were derived from crosses between PI 429007 and PI 429155. The experimental cultivars are the bulked progeny of plants whose resistance components were evaluated and described in Table 1 and Figures 1 and 2. AUDPC values are the means of 18 replicates.

which did not give rise to uredinia were observed on the leaves, indicating that abortion of colonies before uredinium eruption occurred. The data suggest a cumulative effect on infection frequency when SR and HR were combined, but the effects were not significant.

Both resistances resulted in longer latent periods. By definition, a long T_{50} is expected in the slow-rusting cultivar, but incomplete hypersensitivity also extended the latent period. This effect is similar to what has been observed on Lr differential cultivars in Thatcher near-isogenic backgrounds (43). Although incomplete

separation of the genetic factors controlling IT and T_{50} may have produced this effect, the evidence suggests that the long T_{50} of HR is the result of the factor for low IT. In the 1987 field experiment, the derived SUSC cultivar was more susceptible than PI 429007.

TABLE 4. Analysis of variance of the effect of cultivar resistance on AUDPCs[a] of leaf-rust increase on the upper three leaves of triticale cultivars, observed at the Purdue Agronomy Farm in 1987

| Source | df | Mean square | | |
		Flag[b]	Flag-1	Flag-2
Plot	2	0.017	0.018	0.225
Row (plot)	15	0.079*[c]	0.043	0.041
Column (plot)	15	0.064	0.051	0.081
Cultivar	5	15.921**	16.920**	20.465**
Plot × cultivar	10	0.091*	0.095**	0.076
Error	60	0.040	0.028	0.073

[a] Area under the disease progress curve. Values were transformed to log (AUDPC + 1) before analysis.
[b] AUDPCs calculated for 24, 20, and 15 days after heading for the flag, flag-1, and flag-2 leaf positions, respectively.
[c] * and ** indicate significant effects at $P = 0.05$ and 0.01, respectively.

TABLE 5. Development of leaf rust in 1987[a] on the upper three leaves of triticale cultivars differing in resistance, and nonorthogonal, single-degree-of-freedom linear contrasts

Cultivar[b] or contrast	Flag	Flag-1	Flag-2
	Area under the disease progress curve[c]		
PI 429007	241.9	293.6	380.7
SUSC	442.8	471.9	435.3
HR	68.9	42.7	50.9
SR	9.6	4.5	3.8
SR + HR	5.6	4.4	1.9
PI 429155	0.9	1.5	0.9
	Mean square		
PI 429007 vs. SUSC	0.616**[d]	0.380**	0.030
HR vs. SR	9.653**	7.380**	9.607**
SR + HR vs. PI 429155	2.767**	0.986**	0.274

[a] Experiment conducted at the Purdue Agronomy Farm.
[b] PI 429007 and PI 429155 are the parental cultivars from which the others were derived. SUSC has no resistance, HR has incomplete hypersensitivity, and both cultivars were selected from crosses between 83907RC4 × 83907RC2. SR has slow-rusting resistance, SR + HR has both resistances, and both cultivars were selected from crosses between 83907RC1 × PI 429155.
[c] Calculated for 24, 20, and 15 days after heading for the flag, flag-1, and flag-2 leaf positions, respectively. Values are the means for the cultivars observed in three 6 × 6 latin square plots. Untransformed values are presented.
[d] * and ** indicate significant differences at $P = 0.05$ and 0.01, respectively. Contrasts were calculated with transformed data.
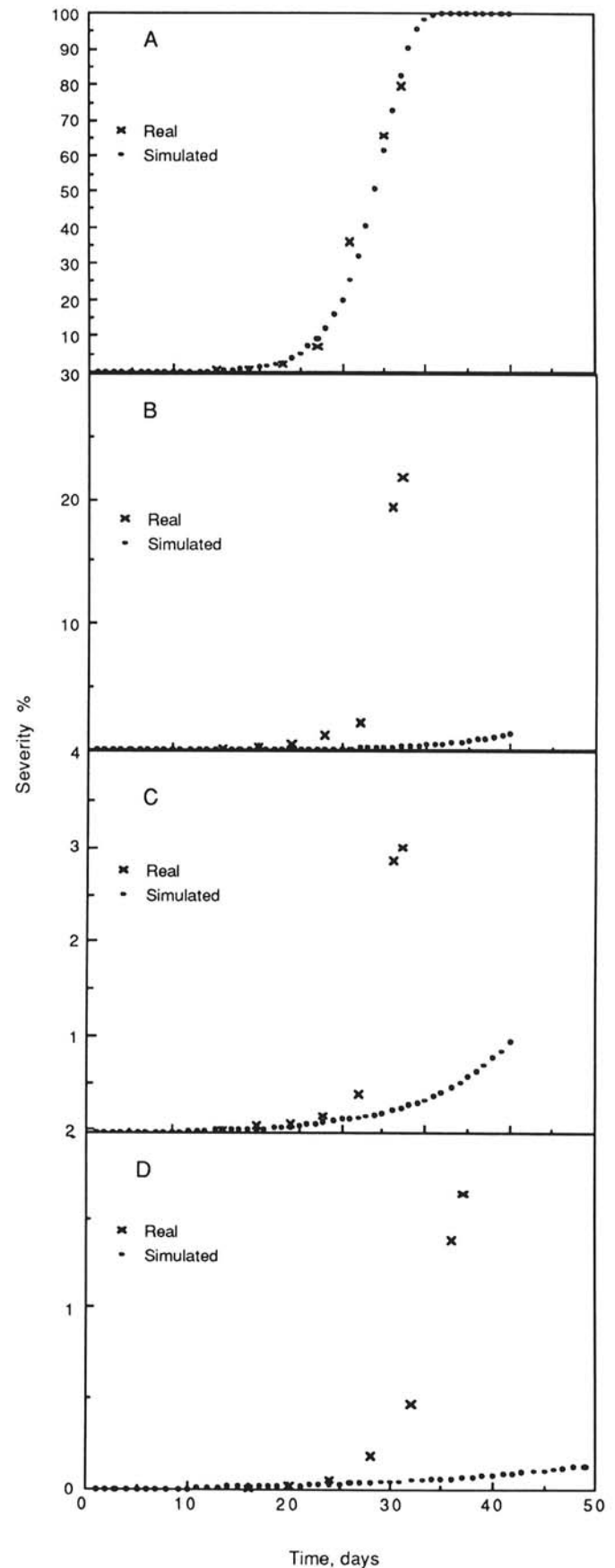

Fig. 6. Real and simulated disease progress curves for flag leaves of triticales that express no resistance (SUSC) (A), incomplete hypersensitivity (B), slow-rusting resistance (C), and incomplete hypersensitivity plus the slow-rusting resistance (D). The "real" curves are severities observed in hill plots in the 1987 field experiment, and the "simulated" curves are severities generated by SLORUS with the components of resistance measured in the monocyclic infection experiment in the greenhouse. The simulated curves were calculated with $\lambda = 0.12$. The time scale is relative; the real data points were shifted an additional 13 days after heading to align the appearance of leaf rust on SUSC to that of the simulated data.

The resistance of the HR cultivar differed from SUSC only by the factor for low IT, indicating that factors for long T_{50} were not present in either the SUSC or HR cultivars. The reduction of infection frequency and lengthening of T_{50} by both resistances support the view that classifying resistance as inoculum reducing or as rate reducing is often too simplistic (25).

Spore production distributions of the different cultivars, although differing in intercept, amplitude, and slope, were similar enough to be described by the gamma distribution. Greater sporulation by young uredinia, followed by a decrease in sporulation with age, has been observed on seedling leaves of small grains (13,16,20) and on primary leaves of bean (*Phaseolus vulgaris* L.) (46) infected by rust fungi. Sporulation patterns observed in this experiment resembled those produced at moderate temperatures on penultimate leaves of oat (*Avena sativa* L.) infected by *Puccinia coronata* f. sp. *avenae* Fraser and Ledingham (13). Examination of the latent periods of the cultivars in conjunction with the sporulation patterns in the monocyclic infection (Figs. 1 and 2) showed that the resistance affected the relative fecundity of individual uredinia differently. On the SUSC and HR cultivars, maximum sporulation per uredinium approximately corresponded to the time at which the greatest number of uredinia had erupted. On the SR and SR + HR cultivars, however, maximum sporulation per uredinium occurred before half of the uredinia had erupted. In the cultivars with slow-rusting resistance, uredinia that erupted later apparently produced fewer spores per day than the early erupting uredinia. A uredinium continued to sporulate until the tissue supporting the fungus senesced. The incorporation of the gamma function into SLORUS accommodated this pattern of spore production without requiring a defined infectious period for the uredinium.

The magnitudes of the AUDPCs differed between the SLORUS models and the epidemics observed in the hill plots. This situation is similar to what has been experienced in previous applications of the model (35); however, inoculum availability differed between the computer-generated and observed epidemics. SLORUS assumes that primary inoculum is the only exogenous inoculum. All secondary inoculum is derived from sporulating infections on the cultivar being evaluated. In this respect, SLORUS epidemics resemble epidemics in isolated fields. Interplot interference affected the AUDPCs in our field experiments. Movement of inoculum between the hills contributed to an "inoculum pool" in which the cultivars were evaluated. The inoculum in the pool originated from background inoculum, spores produced on the border, and spores produced on the experimental cultivars. The importance of exogenous inoculum in positive interplot interference is illustrated by the differences between the observed and expected epidemics on the resistant cultivars in Figure 6. Negative interplot interference, in which less disease develops on a susceptible cultivar as a result of a net spore from loss from a small plot compared to a large field (3), was not discernable in this hill-plot experiment. Epidemics like those we observed in the hill plots have been called reflected epidemics (48) because the level of disease on a cultivar reflects the level of inoculum available in the inoculum pool. Although SLORUS does not consider exogenous inoculum, the simulations reflected the relative ranking of the cultivars' resistance seen in the field.

The level of inoculum affected the magnitude of differences in resistance among the cultivars. In the computer models, in the 1986 field experiment, and in other studies (1,28), differences in the effectiveness of resistance were more clearly differentiated under severe disease pressure. In our evaluations, the resistance of SR controlled leaf rust more effectively than that of HR, regardless of the inoculum source. In the monocyclic infections, cumulative sporulation per uredinium was less on HR than on SR. Rust epidemics are polycyclic processes, however, and the effectiveness of a cultivar's resistance is ultimately measured by its ability to reduce the biotic potential of the rust population. Theoretical analyses of factors affecting population growth indicate that a population's biotic potential is influenced more by the age of an individual at first reproduction than by the number of offspring produced per individual (6). The time from birth to first

reproduction is analogous to the latent period of a rust infection site—the time from infection to sporulation—suggesting the importance of latent period in isolated epidemics on a pure-line cultivar. Long latent period is expected to be important in reflected epidemics as well. Uredinium eruption is delayed on slow-rusting cultivars, and in the absence of completely effective hypersensitivity, rust severities will be less on slow-rusting cultivars if evaluations are made before eruption is complete. In our experiments, the longer latent period of SR resulted in less severe leaf rust in hill plots than the shorter latent period of HR.

Although resistances of both the SR and HR expressions restricted leaf-rust development, the greatest suppression of disease occurred when the resistances were combined. Cumulative expression of combined resistance genes has been observed previously. Infection type is based not only on the presence or absence of chlorosis or necrosis, but also on uredinium area. Some genes that confer an intermediate hypersensitivity act cumulatively when combined to confer a more resistant infection type (31,32,38). Similarly, when slow-rusting cultivars are crossed, factors that confer long latent period can be combined to confer even longer latent periods (14,19,26). Histological studies of slow rusting and incomplete hypersensitivity in barley (*Hordeum vulgare* L.) infected with *Puccinia hordei* Otth indicate that these two types of resistance act independently during colonization of the host (5,23), suggesting that their effects would be expressed together. Higher levels of resistance to *P. graminis* in the field have been observed in cultivars that possess both types of resistance, compared to cultivars with either resistance alone (7,39). The present studies demonstrate the cumulative interactions of hypersensitive and nonhypersensitive resistances, both in the phenotypic components of resistance and in leaf-rust epidemics.

The cumulative effects of both the hypersensitive and nonhypersensitive resistances resulted in the high level of resistance in PI 429155. The single dominant gene for resistant infection type in PI 429155 probably could be easily backcrossed into wheat, but the results of this study indicate that the long latent period contributes substantially to the resistance of PI 429155. In both the experimental and computer-generated epidemics, the long T_{50} of SR provided protection greater than the smaller uredinia and reduced sporulation of HR. This effectiveness was expressed not only on the flag leaves but on the lower leaves as well. Although sterility barriers restrict free transfer of genes from triticale into wheat, backcrossing the factor for low infection type from PI 429155 to wheat, without consideration of the resistance factors for long latent period, will fail to exploit fully the leaf-rust resistance available in PI 429155.

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