Inheritance of the Leaf Rust Resistance of Four Triticale Cultivars

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ABSTRACT

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The inheritance of resistance to culture 7434-1-1T of *Puccinia recondita* f. sp. *tritici* was examined in four triticales that were selected as potential sources of resistance genes for wheat. The resistant triticales were each crossed to the susceptible triticale PI 429007. The parents and the F_1, F_2, and F_3 progeny were evaluated for segregation of infection type (IT) to determine the number and dominance of genes for resistant IT that each cultivar possesses. The resistant cultivars were crossed to each other and the F_2 and F_3 progeny were evaluated to examine the relationships of the resistance genes. The F_3 progeny with susceptible IT derived from the resistant × susceptible crosses were evaluated for the presence of genes for long latent period, an important component of slow-rusting resistance. PI 429120 possesses two independent, incompletely dominant genes that together confer a 0;n IT in the adult plant. PI 429155 possesses one incompletely dominant gene that confers a 12c IT. PI 429121 expresses a 0;1n IT, and PI 429215 expresses a 0;n IT. Both of these cultivars possess one incompletely dominant gene with a major effect and an additional minor gene that confers a nearly susceptible, mesothetic IT. The minor-effect gene in PI 429121 is recessive, whereas that in PI 429215 is partially dominant. The genes in PI 429120 are independent of those in the other cultivars. PI 429215 has a gene in common with PI 429121, and this major-effect gene is linked approximately nine map units from the gene in PI 429155. The four cultivars each possess an undetermined number of partially recessive genes for long latent period in addition to their genes for resistant IT. These triticales may be useful both as sources of leaf rust resistance for wheat and as examples for the directed use of genes for low-IT and slow-rusting resistances.

Additional keywords: alien germ plasm, general resistance, specific resistance, wheat.

The success of a cultivar depends in part on its yield potential and yield stability. Disease resistance and tolerance to environmental stresses are important in maintaining stable yields, yet, unlike environmental stresses, disease pressures from the pathogen populations confronting a cultivar may not remain stable over time. Disease pressures from pathogens such as rust fungi gradually change if a cultivar's resistance imparts greater reproductive fitness to particular pathogen strains. Although effective disease resistance can often be identified, in time it can be rendered ineffective by an increased frequency of virulence in the pathogen population (9,15). Genes for disease resistance may have limited usefulness in a succession of improved cultivars, and new sources of resistance must be identified as "old" genes lose effectiveness.

Alien germ plasm is a potential source of genes for disease resistance in crops. We selected several triticales (× *Triticosecale* Wittmack ex A. Camus) from the USDA Small Grains Collection because of the exceptional level of disease resistance they exhibited in a field nursery at Lafayette, IN. When evaluated in the greenhouse, four triticales expressed resistant infection types (IT) to *Puccinia recondita* Rob. ex. Desm. f. sp. *tritici* in the seedling stage. In the adult plant stage, two of these cultivars had 0;1n and 2c infection types and the delayed uredinium eruption characteristic of slow-rusting resistance (24).

These four accessions, which all originated from CIMMYT (Centro Internacional de Mejoramiento de Maiz Y Trigo), are potentially valuable sources of leaf rust resistance for wheat (*Triticum aestivum* L. em. Thell). Because transfer of traits between triticale and wheat is hindered by crossability barriers between the parents and sterility in the progeny, it was considered useful to determine how the resistance is inherited within these triticale cultivars. Genetic studies would indicate whether resistance in different cultivars is conferred by different or identical genes. Determining the dominance and number of genes for resistance would indicate the relative ease of transferring resistance. All other factors being equal, it would be easier to follow the transfer of a high level of resistance conferred by a single dominant gene than the transfer of a resistance controlled by a complex inheritance. The complexity of the inheritance affects the strategy used to transfer the resistance.

The following studies were conducted to determine the inheritance of resistance to *P. recondita* in selected triticales. The number of, and linkages between, genes that confer resistant IT were examined and the presence of genes for long latent period were determined. In this work we present evidence that the resistant IT of four resistant triticale lines is simply inherited and that genes for long latent period are present in the cultivars. The results of preliminary studies have been published previously (23).

MATERIALS AND METHODS

The resistant triticale PIs 429120, 429121, 429155, and 429215 were each crossed to the susceptible, fast-rusting triticale PI 429007, and to each other. These cultivars expressed ITs (17) of 0;1c, 0;1c, 0;1c, 0;1n, and 4 in the seedling stage, and infection types 0;n, 0;1n, 1+2c, 0;n, and 4 in the adult stage, respectively, when inoculated with culture 7434-1-1T of *P. recondita*. The mixed IT designation indicates that both types developed on the leaves, with the IT listed first being predominant.

Plants of each cultivar were selected for their reactions from inoculations in the greenhouse. Their progeny were bulked and used in crosses. Seeds of the parents and progeny were sown 1.5-cm deep in soil in flats, watered, and placed in a coldroom at 2 C for 3 days to promote uniform germination and emergence. The plants were grown on greenhouse benches under natural daylight supplemented with 16 hr day^{-1} of about 20,000 E cm^{-2} sec^{-1} from fluorescent lighting, except during June through August, when no supplemental lighting was provided. During all the experiments, the greenhouse temperatures ranged between 20 and 35 C, with a typical daily range of 21–29 C.

Plants were inoculated by misting them with an aqueous spore suspension consisting of 50 mg of urediniospores of culture 7434-1-1T of *P. recondita* and three drops of Tween 20 per 100 ml. Culture 7434-1-1T is virulent toward *Lr* genes 2b, 2c, 3a, 3b, 9, and 11 and avirulent toward *Lr* genes 1, 2a, 3bg, 10, 12, 13, 16, 17, 18, 19, 24, 25, and 26 (see reference 3 for information about these genes). This culture was used because it was originally collected from natural infection in the field in Indiana and is aggressive in both greenhouse and field. The plants were placed in a moist chamber overnight (15–18 hr) and were then returned to the greenhouse bench. Seedlings in flats were inoculated at the two-leaf stage (growth stage 12 [26]), and ITs were determined 9–14 days after inoculation, depending on the rapidity of uredinium formation as affected by temperature in the greenhouse. The adaxial surface of the flag leaves of adult plants was inoculated either when the flag leaf was fully emerged (growth stage 40–43), or, in some experiments, when the spike was half-emerged (growth stage 55).

The IT of the adult plant reaction was used to confirm ambiguous seedling ITs (i.e., mesothetic reactions and those bordering between resistance and susceptibility). When possible, the F_3 family reaction was used to confirm the hypothesized F_2 classification in all crosses except for the cross PI 429121/PI 429007, in which individual F_2 plant data inadvertently were not recorded. In this cross, the ambiguous ratio test (19) was used to delimit classes of segregating families based on the proportion of resistant plants within those families. Ratios of resistant (IT 0, 1, 2, or X) to susceptible (IT 3 or 4) plants in the F_2, and ratios of homozygous resistant to segregating (both resistant and susceptible plants) to homozygous susceptible F_3 families were compared to hypothesized ratios with the chi-square test. Expected F_3 ratios were based on the expected frequencies of F_2 genotypes and the expected classification (homozygous resistant, segregating, or homozygous susceptible) of the F_2-derived F_3 families. The Yates's correction (18) was used for tests that had one degree of freedom. Linkage estimates were determined by the method of maximum likelihood (1).

After the ITs of the F_3 plants were determined, individual plants of the susceptible parent PI 429007, the homozygous susceptible families, and the susceptible plants from the segregating families were transplanted to 10-cm-diameter pots and reinoculated in the adult plant stage to determine whether genes conferring long latent period were segregating in the portion of the population without the seedling-expressed low-IT resistance. The percentage of infection sites on the flag leaf with erupted uredinia was estimated at 1- to 2-day intervals, beginning 6 days after inoculation. Probits of the daily proportion of uredinia erupted were regressed on time (days). The latent period (T_{50}) was calculated from the regression equation as the time required for 50% of the uredinia to erupt (16). The latent period distributions of PI 429007 and of the F_3 plants with a susceptible IT were compared for differences with the Student's *t*-test for independent samples with unequal variances (19).

RESULTS

Resistant × susceptible. *PI 429120 × PI 429007.* The F_1 of PI 429120 × PI 429007 expressed a 1c IT. The F_2 segregated in an approximate ratio of 15 resistant to one susceptible (Table 1). A range of resistant ITs was observed in the F_2, which did not fit discrete Mendelian ratios. The 15:1 ratio suggested segregation of two dominant genes at independent loci. If this were the case, 7/16 of the F_2 individuals should be homozygous dominant at one or both loci, 8/16 should be heterozygous at both loci or heterozygous at one and homozygous recessive at the other, and 1/16 should be homozygous recessive at both loci. The F_3 family data segregated in an approximate ratio of seven homozygous resistant to eight segregating to one homozygous susceptible (Table 1). An apparent excess of homozygous resistant families probably resulted from a failure to detect segregation within small families (average family size was 18.6 plants). The results indicate that the resistant IT of PI 429120 is conferred by dominant genes at two independent loci. Because the heterozygous F_1 did not express as high a level of resistance as PI 429120, and because a range of ITs were obtained in the F_2, these genes apparently expressed incomplete dominance.

The susceptible F_3 population had plants with latent periods longer than those exhibited by PI 429007 (Fig. 1A). The latent period means of PI 429007 and the F_3 population differed significantly ($P < 0.0005$).

PI 429121 × PI 429007. The F_1 of PI 429121 × PI 429007 expressed a 2c IT. The F_2 segregated in an approximate ratio of three resistant to one susceptible ($\chi^2 = 1.14$, $P = 0.28$), and a range of resistant ITs were observed that did not fit discrete Mendelian ratios. The 3:1 segregation suggested that one dominant gene conferred the resistant IT of PI 429120. The F_3 results were contradictory to the interpretation from the F_2 data. While it was evident that one dominant gene segregated in the population, some families also segregated for a minor-effect gene that conferred a mesothetic (X) reaction. Plants that possessed this minor resistance allowed approximately 95% of the infection sites on the flag leaf to erupt into uredinia of a fully susceptible IT; the remainder developed ITs 0;n, 1, or 2. Near the completion of uredinium eruption, a small necrotic halo formed around some of the formerly susceptible infection sites, and, at times, a zone of green host tissue separated the edge of the uredinium from the necrotic halo. This very late-acting, low-IT resistance was reliably detected when the adult plants were periodically examined for latent period and was probably overlooked when the F_2 seedlings were evaluated. ITs of the F_2 were recorded only once, at 9 days after inoculation. Consequently, F_2 seedlings that might have shown this reaction were mistakenly classified as susceptible.

TABLE 1. Segregation of resistant and susceptible infection type in progeny derived from crosses between triticales inoculated with culture 7434-1-1T of *Puccinia recondita* f. sp. *tritici*

	F_2 plants[a]					F_3 families[c]					
Cross	Res.	Susc.	Expected ratio[b]	χ^2	Probability	Res.	Seg.	Susc.	Expected ratio	χ^2	Probability
PI 429120 × PI 429007	45	6	15:1	1.79	0.18	12	9	3	7:8:1	2.46	0.29
PI 429121 × PI 429007	91	38	13:3	9.02	0.003	19	34	5	7:8:1	2.98	0.22
PI 429155 × PI 429007	117	46	3:1	0.74	0.39	13	28	17	1:2:1	0.62	0.27
PI 429215 × PI 429007	138	14	15:1	1.80	0.18	15	23	2	7:8:1	0.91	0.64
PI 429120 × PI 429121	681	3	253:3	2.57	0.11	270	43	0	175:80:1	46.61	<0.001
PI 429120 × PI 429155	119	2	63:1	0.08	0.78	56	20	1	37:36:1	7.06	0.03
PI 429120 × PI 429215	307	3	255:1	1.38	0.24	233	48	2	175:80:1	27.20	<0.001
PI 429121 × PI 429155	796	2	61:3	34.18	<0.001	552	40	0	37:26:1	304.95	<0.001
PI 429121 × PI 429215	327	0	61:3	15.05	<0.001	144	0	0	37:26:1	105.08	<0.001
PI 429155 × PI 429215	254	0	63:1	3.08	0.08	93	4	0	37:26:1	57.64	<0.001

[a]Res. and Susc. refer to number of plants with resistant (0, 1, 2, or X) or susceptible (3 or 4) infection type (17).
[b]Ratio fit to data for chi-square test.
[c]Res., Seg., and Susc. refer to the number of homozygous resistant, segregating, and homozygous susceptible F_3 families, respectively.

The F_3 family data were consistent with a ratio of seven homozygous resistant to eight segregating to one homozygous susceptible (Table 1), indicating that genes for resistance were segregating at two independent loci in this population. One gene was dominant and had a major effect on resistance. A range of ITs in the F_2 and F_3 seedlings indicated that the resistance conferred by this gene was incompletely dominant. The dominance or recessiveness of the minor-effect gene could not be determined from the F_2 data or the 7:8:1 F_3 ratio, which is the expected ratio for segregation of either two dominant genes or one dominant and one recessive gene conferring resistance. The resistant-to-susceptible ratio (R:S) of F_2 plants was closer to (but was not fit by) 13R:3S than to 15R:1S (Table 1), and there was a greater proportion of susceptible plants than of resistant plants in a number of F_3 families. These facts suggested that the minor-effect gene is recessive.

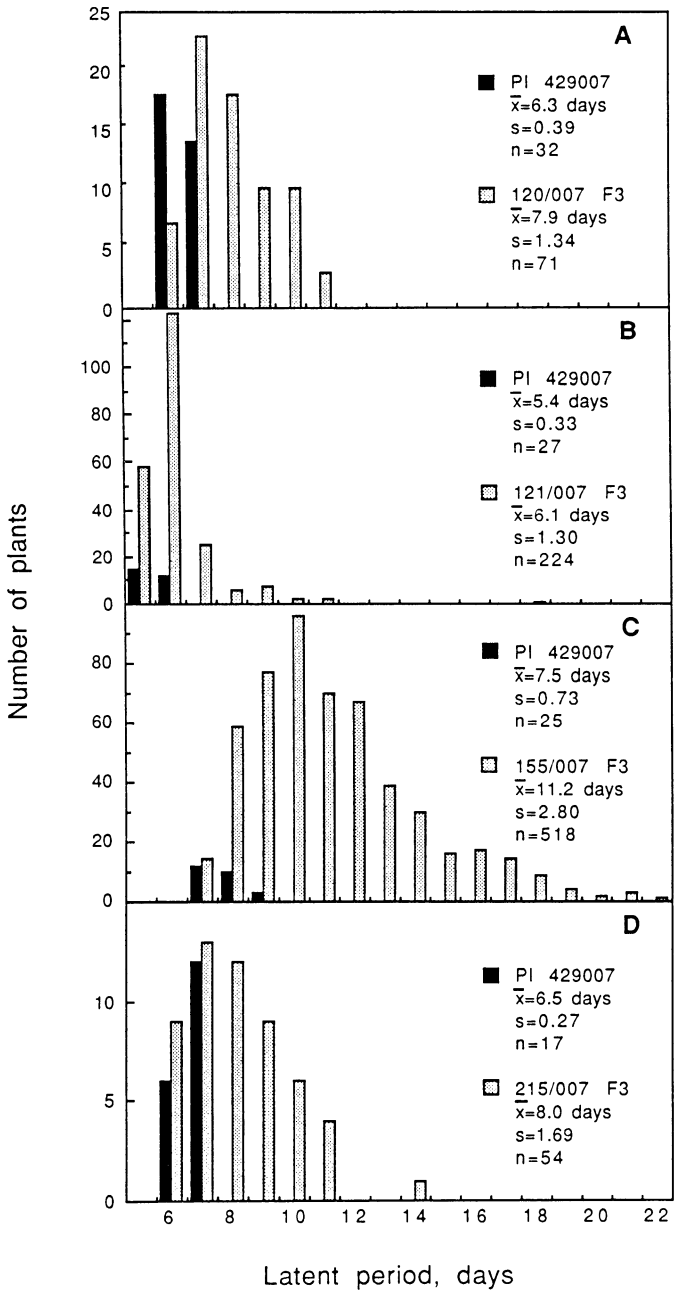

Fig. 1. Distributions of latent period of infection of susceptible triticale PI 429007 and of F_3 progeny with susceptible infection type (3 or 4) derived from crosses between PI 429007 and the resistant cultivars **A,** PI 429120; **B,** PI 429121; **C,** PI 429155; and **D,** PI 429215. Latent period was determined from uredinium eruption on flag leaves of plants inoculated in the greenhouse with culture 7434-1-1T of *Puccinia recondita*. $\bar{x}$ = mean, s = standard deviation, n = number of plants.

If the minor-effect gene is recessive, three fourths of the segregating families should segregate either 13R:3S or 3R:1S, and one fourth should segregate 1R:3S. Application of the ambiguous ratio test indicated that all families with less than 50% of the plants resistant should be classified as having a 1R:3S segregation. Of the 34 segregating families, 27 had a greater proportion of resistant plants, and seven had a greater proportion of susceptible plants. These numbers agreed with the expected 3:1 ratio ($\chi^2 = 0.16$, $P = 0.69$).

In the 27 families with a greater proportion of resistant plants, two thirds should segregate in a 13R:3S ratio and one third should segregate in a 3R:1S ratio. By further application of the ambiguous ratio test, families with less than 78.3% resistant plants were classified as having a 3R:1S segregation. Of the 27 families, 14 were included in the 13R:3S class, and 13 were included in the 3R:1S class. These numbers were consistent with the expected ratio of 2:1 ($\chi^2 = 2.04$, $P = 0.15$). The evidence suggests that the minor effect gene in PI 429121 is recessive.

The population of F_3 adult plants with fully susceptible IT had plants with latent periods longer than those of PI 429007 (Fig. 1B). The latent period means of PI 429007 and the susceptible F_3 population differed ($P < 0.005$).

PI 429155 × PI 429007. The F_1 of PI 429155 × PI 429007 exhibited a 2c IT. The F_2 segregated in an approximate ratio of three resistant to one susceptible, and a range of resistant ITs were observed that did not fit discrete Mendelian ratios. The F_3 family data were fit by a ratio of one homozygous resistant to two segregating to one homozygous susceptible (Table 1). These results indicate that the resistant IT of PI 429155 is conferred by one dominant gene. Because the resistance of the F_1 was not at as high a level as that of PI 429155, and because a range of ITs was observed in the F_2, the expression of resistance was evidently incompletely dominant.

The population of F_3 adult plants with high IT had plants with latent periods longer than those exhibited by PI 429007 (Fig. 1C). The latent period means of PI 429007 and the susceptible F_3 population differed ($0.010 < P < 0.025$).

PI 429215 × PI 429007. The F_1 of PI 429215 × PI 429007 expressed a 1c IT. The F_2 segregated in an approximate ratio of 15 resistant to one susceptible. Two levels of resistance were commonly observed, a highly resistant IT of 0;n and a mesothetic reaction; however, the observed numbers did not fit a discrete Mendelian ratio. The F_3 family data were fit by a ratio of seven homozygous resistant to eight segregating to one homozygous susceptible family (Table 1). The results indicate that the resistant IT of PI 429215 is conferred by two independent, dominant genes. Comparison of the F_2 and F_3 data indicated that one of the genes conferred a high level of resistance, and the other gene had a minor effect on IT and conferred a near-susceptible mesothetic reaction (X).

The susceptible F_3 population had plants with latent periods longer than those of PI 429007 (Fig 1D). The latent period means of PI 429007 and the susceptible F_3 population differed significantly ($P < 0.0005$).

Resistant × resistant. *PI 429120 × PI 429121.* The segregation of IT in the F_2 of PI 429120 × PI 49121 was consistent with the hypothesized ratio for four segregating loci in which the dominant alleles at three loci and the recessive allele at the fourth locus confer resistant IT (Table 1). The ratio of homozygous resistant to segregating to homozygous susceptible F_3 families did not fit the expected ratio for the hypothesis. The significant deviation from the expected ratio was due to an excess of apparently homozygous resistant families, probably resulting from a failure to detect segregation within small families (average family size was 15.1 plants). If the homozygous resistant and segregating families were combined into a single class, the F_3 data fit a 255:1 ratio ($\chi^2 = 0.43$, $P = 0.51$), even though none of the susceptible segregants in the F_2 evaluation survived or produced seed. The presence of susceptible progeny in many F_3 families indicated

that the loci of the genes conferring a resistant IT in PIs 429120 and 429121 are different. Although linkage relationships could not be unambiguously determined, the F_2 data indicated that the loci of the genes are probably independent.

PI 429120 × PI 429155. The F_2 of PI 429120 × PI 429155 segregated in an approximate ratio of 63 resistant to one susceptible, which was consistent with the expected ratio for segregation of three dominant genes for resistant IT. The F_3 family data did not agree with the expected ratio of 37 homozygous resistant to 26 segregating to one homozygous susceptible (Table 1). The significant deviation from the expected ratio was due to an excess of apparently homozygous resistant families, probably resulting from a failure to detect segregation within small families (average family size was 35.5 individuals). If the homozygous resistant and segregating families were combined into a single class, the F_3 data were consistent with a 63:1 ratio ($\chi^2 = 0.07$, $P = 0.78$). The results indicated that the two genes that confer resistant IT in PI 429120 were independent of the gene in PI 429155.

PI 429120 × PI 429215. The F_2 of PI 429120 × PI 429215 segregated in an approximate ratio of 255 resistant to one susceptible, which is the expected ratio for the segregation of four dominant genes for resistant IT. The F_3 family data were not consistent with the expected ratio of 175 homozygous resistant to 80 segregating to one homozygous susceptible (Table 1). The significant deviation from the expected ratio was due to an excess of apparently homozygous resistant families, probably resulting from a failure to detect segregation within small families (average family size was 16.8 plants). If the homozygous resistant and segregating families were combined into a single class, the F_3 data were fit by a 255:1 ratio ($\chi^2 = 0.14$, $P = 0.70$). The results indicated that the two genes for resistant IT in PI 429120 were independent of the two in PI 429215.

PI 429121 × PI 429155. The F_2 of PI 429121 × PI 429155 did not segregate in the 61 resistant to three susceptible ratio expected for independent segregation of one recessive and two dominant genes for resistance (Table 1). The rare recovery of susceptible recombinants and the frequent occurrence of a 0;n IT in the F_2 indicated that the major genes for resistant IT in PIs 429121 and 429155 were linked in repulsion.

If this were the case, F_1 gametes would most often contain the Ab or aB linkages, in which A and B are the dominant alleles that confer resistant IT in PIs 429121 and 429155. If C were the independent locus of the recessive allele that confers a resistant IT in PI 429121, susceptible F_2 progeny would have either genotypes ab/abCC or ab/abCc. If p is the recombination frequency between the major genes for resistance, the frequency of the susceptible class is $(p/2)^2(3/4)$. Equating the expression to 2/798, one obtains $p = 0.116$, and the distance between the two loci is 11.6 map units.

The F_3 data likewise did not fit the expected ratio for independent segregation of the genes for resistance, whether the families were compared to the expected ratio of homozygous resistant to segregating to homozygous susceptible families (Table 1) or the homozygous resistant and segregating families were combined into a single class ($\chi^2 = 8.41$, $P < 0.005$). Setting p equal to the recombination frequency between the major genes for resistance, the genotypes of the F_2 plants that would give rise to segregating F_3 families, and the probabilities of their occurrence, are:

Ab/ab Cc : $(2)[(1-p)/2](p/2)(1/2)$
aB/ab Cc : $(2)[(1-p)/2](p/2)(1/2)$
AB/ab Cc : $(2)(p/2)(p/2)(1/2)$
ab/ab Cc : $(p/2)(p/2)(1/2)$
Ab/ab cc : $(2)[(1-p)/2](p/2)(1/4)$
aB/ab cc : $(2)[(1-p)/2](p/2)(1/4)$
AB/ab cc : $(2)(p/2)(p/2)(1/4)$

The expected frequency of segregating F_3 families is the sum of the above probabilities, which reduces to $0.75p - (p^2/4)$. Equating this expression to 40/592, one obtains $p = 0.093$, and the distance between loci is therefore 9.3 map units.

When the F_2 and F_3 data were analyzed together by the maximum likelihood method, the recombination frequency was estimated to be 0.094, with a standard error of 0.0137.

PI 429121 × PI 429215. There was no segregation for susceptibility in the F_2 or F_3 progeny of PI 429121 × PI 429215 (Table 1). The observed ratios deviated significantly from the expected segregation of four genes for resistance, in which dominant alleles at three loci and the recessive allele at the fourth locus confer resistance. Results of crosses of each of these lines to the susceptible PI 429007, reported above, indicated that each of the resistant cultivars possesses a gene with a major effect and a gene with a minor effect of resistant IT. Among the F_2 plants, 311 expressed IT 0; and 16 expressed IT 1. The predominant IT among all the F_3 families was IT 0. The absence of susceptible plants in the segregating generations and the predominance of a high level of resistance in these populations indicated that the major-effect gene that confers a resistant IT to PI 429121 is allelic to, or the same as, the major-effect gene in PI 429215.

PI 429155 × PI 429215. There was no segregation for susceptibility in the F_2 of PI 429155 × PI 429215; however, the observed R:S did not deviate significantly from the ratio expected for the independent segregation of three dominant genes. Four out of 97 F_3 families, however, segregated (Table 1). The observed F_3 ratio did not fit the expected 37 homozygous resistant to 26 segregating to one homozygous susceptible. The significant deviation from the expected ratio was due to an excess of apparently homozygous resistant families, which may have resulted from a failure to detect segregation within small families (average family size was 20.3 plants). However, if the homozygous resistant and susceptible families were combined into a single class, the F_3 data were still not fit by a 63:1 ratio ($\chi^2 = 18.06$, $P < 0.005$). This suggests that the F_2 sample size was inadequate to determine whether the loci of the resistance genes were independent or linked. The infrequent occurrence of segregating F_3 families indicated that the major-effect genes for resistant IT in PIs 429215 and PI 429155 were not independent, but linked in repulsion. If p is the recombination frequency between the major genes for resistance, the expected frequency of segregating F_3 families is $0.75p - (p^2/4)$. Equating this expression to 4/97, one obtains a recombination frequency, p, of 0.056. Linkage estimates from the F_2 and F_3 data made by the maximum likelihood method gave a recombination frequency of 0.054, with a standard error of 0.0266.

When the F_2 and F_3 data from both the PI 429121 × PI 429155 and the PI 429155 × PI 429215 crosses are analyzed by the maximum likelihood method, a recombination frequency between the A and B loci of 0.089 is obtained, with a standard error of 0.0124. The chi-square test indicated that the data sets were homogeneous and supported the hypothesis that the recombination frequency was 0.089 ($\chi^2 = 1.65$, $P = 0.65$).

DISCUSSION

Our results suggest that the resistance of all the cultivars results from a combination of genes for low IT and long latent period. The four resistant triticales examined in this study originated from CIMMYT. Because of the selection and intercrossing approaches used at CIMMYT (4), combinations of low IT and slow rusting are likely to be present in material developed by this organization.

The resistant ITs of the cultivars were simply inherited as one or two genes expressing some degree of dominance. This mode of inheritance is similar to that found in other studies of leaf rust resistance in triticale (13,20) and is common to the inheritance of similar resistance to rust fungi in most plant species (5). Four genes with a major effect on IT were distributed among the cultivars, and genes with a minor effect on IT were detected in PIs 429121 and 429215.

Because all of the F_3 populations derived from the resistant susceptible crosses had progeny with susceptible ITs but latent periods longer than those of the susceptible parent, the long latent periods were the result of different genes and not pleiotropic expressions of the genes for resistant IT. The skewness of the

F_3 latent period distributions suggests that long latent period is a partially recessive trait, as is long latent period in wheat (8) and barley (11).

The number of genes that confer long latent period in these cultivars would be difficult to determine. Because some genes that confer a low or intermediate IT extend the latent period (21), plants with a resistant IT must be discarded from the analysis. Elimination of the plants with low IT not only reduces the population size evaluated, but may also eliminate genes for long latent period linked to those for low IT. The environmental variance associated with latent period also adds to the difficulty of determining the number of genes by an early generation analysis. Variances are larger for longer latent periods (8,24), but even the short latent period of the fast-rusting cultivar PI 429007 can be significantly affected by differences in environmental conditions from one date of inoculation to another (unpublished data).

Preliminary results of the genetic analysis of these cultivars (23) indicated that the IT of PI 429121 was conferred by two complementary genes and that the long latent period of PI 429155 was a partially dominant trait. Subsequent tests have shown that these hypotheses were incorrect. During various evaluations in the greenhouse, the ITs of plants grown from the seed stock of PI 429121 were found to vary from 0;n to 3. The cross was remade with a highly resistant selection, and the IT segregation of these progeny are the data reported here. The variation in IT in the original seed stock may be the result of environmental variance, heterogeneity in the original population, or the result of outcrossing, to which some triticales can be quite prone (6). Variation in the expression of the minor-effect gene, or inconsistent identification of its presence are other possible explanations. The dominance of the long latent period of PI 429155 in the preliminary study was inferred from the segregation of latent period in F_2 and BC_1 F_1 populations. Those distributions included latent periods of all plants, regardless of IT. There is evidence that some genes that confer a low IT can extend latent periods (21), and the dominant gene for low IT in PI 429155 also has this property (25).

Because a number of genes together confer the leaf rust resistance in each of the cultivars, it is unlikely that the complete resistance could be simply transferred to wheat. Often, backcrossing the resistance from one species to another will not transfer all of the resistance genes from the donor parent (2,7), and the partially recessive genes for slow-rusting resistance in these triticales would probably be lost unless care were taken to select for them. Segregants from crosses between wheat and these triticales could be selected for either low IT or long T_{50} and intercrossed to select for a higher expression of resistance. This approach may be successful because, when present alone, none of these genes completely prevented uredinium eruption, and the presence of genes for very long latent periods can be detected in plants that express ITs 1 or 2, as indicated by the results of this research. The resistance phenotypes of these cultivars, coupled with knowledge of the inheritance of resistance, has implications for the directed selection for combinations of resistance genes.

The resistance of a cultivar should be conferred by more than one gene to achieve a durable resistance. The consequence of relying on a single, highly effective gene for resistance to a rust fungus has again been recently illustrated in Australia with the selection of a race of *P. graminis tritici* virulent on Coorong triticale (10). Cultivars with a complex of genes for low IT often exhibit low rust severities in diverse environments, where pathogen populations possess different combinations and frequencies of virulence genes (14). "Gene stacking" is a recognized approach to developing widely effective rust resistance, and although the term usually refers to combinations of genes that confer a low IT, using a combination of genes for low IT and slow-rusting resistances is another approach to gene stacking. If strains of the pathogen that are virulent toward the low IT resistance are selected, some protection of the cultivar would be maintained by the slow-rusting resistance.

The results of this study indicate the value of genes that confer ITs 1 or 2 when a combination of slow-rusting and hypersensitive resistances is desired. PIs 429121 and 429155 expressed these ITs, and the presence of genes for long latent period was inferred from the adult-plant infection phenotype (24). PIs 429120 and 429215 also possess genes for long latent period as determined in this study, but this resistance was masked by the combinations of genes that together conferred an IT 0;. The presence of slow-rusting resistance can be detected in potential cultivars that express a 0 IT. Progeny derived from crosses to a susceptible cultivar could be evaluated in the greenhouse for segregation of IT and latent period, as in this and a similar study of barley cultivars (12), or evaluated in the field for segregation of IT and slow-rusting (22). But unless progeny tests are performed on potential cultivar releases, or unless a high level of slow-rusting resistance is well distributed in the elite germ plasm of a breeding program, it may be advantageous not to use genes that confer complete hypersensitivity. Because a long latent period can be detected in the presence of genes that confer an IT of 1 or 2, the combination of these resistances might be used successfully when polygenic resistance to disease is desired.

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