Genetics

Nonrandom Distribution of Virulence and Phenotypic Diversity in Two Populations of *Puccinia recondita* f. sp. *tritici* in Canada

J. A. Kolmer

Research scientist, Cereal Diseases Section, Agriculture Canada, Research Station, 195 Dafoe Road, Winnipeg, MB R3T 2M9 Canada.
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ABSTRACT

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The eastern and prairie populations of *Puccinia recondita* f. sp. *tritici* in Canada were examined for nonrandom distribution of virulence and phenotypic diversity. In the prairie region, where resistant cultivars have been grown and polymorphisms for unneeded virulences are low, virulence to *Lr1* and *Lr2a* appeared to be positively associated from 1960 to 1974 and was negatively associated from 1975 to 1987. Positive and negative virulence associations were also detected among virulences to *Lr1*, *Lr2a*, *Lr10*, *Lr16*, *Lr17*, *Lr18*, and *Lr24* in the prairie region. In the eastern region, where susceptible host cultivars are commonly grown and unneeded virulences are common, positive associations were found among virulences to *Lr2c*, *LrB*, *Lr3ka*, *Lr11*, and *Lr18*. Levels of phenotypic diversity between the two populations were compared with the Shannon index. Based on the infection types of the Unified Numeration differentials (*Lr1*, *Lr2a*, *Lr2c*, and *Lr3*), in the 3 yr examined, the eastern population had higher levels of phenotypic diversity than the prairie population. Most of the loss of diversity in both populations was caused by the departure of virulence frequencies from 0.5. The nonrandom distribution of virulence observed in both populations is characteristic of asexual cereal rust populations.

Additional keywords: linkage equilibrium, physiologic specialization, *Triticum*, virulence association.

The distribution of virulences among phenotypes and levels of phenotypic diversity are important parameters that characterize populations of cereal rust fungi. Previous work on these parameters has concentrated on differentiating between sexual and asexual populations (1,6,13,19). Sexually reproducing rust populations were shown to have near-random distribution of virulences and greater numbers of distinct phenotypes (races or virulence combinations) than did asexual populations, which have nonrandom distribution of the underlying virulences. Other factors, such as regional differences in host resistance and the ability of rust fungi to overwinter in certain regions, may also influence the effective size of rust populations (3) and, in turn, affect phenotypic diversity and distribution of virulence.

Distribution of virulence among phenotypes and phenotypic diversity are related attributes of pathogen populations. Sexual recombination in the absence of selective forces randomly distributes new mutations to virulence throughout the pathogen

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population. This should result in the maximum theoretical number of pathogen phenotypes for a given number of virulences. Mutations to virulence in asexual populations are effectively trapped in the genotypes in which they originated. This may result in a nonrandom distribution of virulence and a reduced number of phenotypes, although, with time, recurrent mutations are likely to distribute virulences throughout the entire pathogen population. However, in an agricultural context, the short-term distribution of virulence is the primary concern.

Browder and Eversmeyer (2) examined pathogenicity associations in regional populations of *Puccinia recondita*. Virulences to resistance genes *Lr1* and *Lr2a* were negatively associated throughout the central United States in 1972, but associations for *Lr1* and *Lr2a* differed elsewhere in the country. Virulences to *Lr1* and *Lr10* were positively associated in the eastern United States, and negative virulence associations were described for the pairs *Lr16* and *Lr17*, *Lr17* and *Lr18*, *Lr16* and *Lr18*. Alexander et al (1) examined pathogenicity associations in sexual and asexual populations of *Puccinia graminis* f. sp. *tritici*. Pathogenicity associations were stronger and more frequent in the asexual population than in the sexual population. They concluded that, in asexually reproducing populations of wheat stem rust, virulences and avirulences were effectively linked. Pathogenicity associations have also been examined in barley powdery mildew (17,18).

When nonrandom distributions of virulence are found in asexual populations of cereal rust fungi, it is difficult to ascertain the precise reason why certain virulences are positively or negatively associated. As Alexander et al (1) noted in studies on wheat stem rust, virulences may occur randomly in certain genotypes and be retained strictly within the original forms because of a lack of sexual recombination. This complete linkage of the pathogen genome makes it difficult to distinguish between associations that arise because of a reproductive advantage and those that occur strictly by chance. However, pathogenicity associations and nonrandom distribution of virulences are still valuable markers in defining and distinguishing asexual cereal rust populations.

Kolmer (9) recently examined Canadian records of the history of virulence and race dynamics of *P. r. tritici*, which reproduces asexually throughout North America (14). Eastern Canada (Ontario, Quebec), the prairies (Manitoba, Saskatchewan), and the Pacific region (Alberta, British Columbia) were recognized to have distinct populations of *P. recondita*. In the eastern region, where susceptible hosts are generally grown, virulence frequencies to *Lr2c* and *Lr3* fluctuated between 20 and 100%, whereas virulence to *Lr1* increased erratically after 1971. The Unified Numeration (UN) (11) race composition in this region was characterized by intermediate frequencies (20–60%) of races 2, 3, 5, 6, and 13 (Table 1). Intermediate levels of virulence have also been detected to a number of other resistance genes that have not been used in this region. In the prairies where resistant cultivars are generally grown, virulence frequency to *Lr3* has remained nearly fixed since 1960, and virulence to *Lr1* and *Lr2a* has increased rapidly from low initial levels since cultivars with these resistance genes were released in North Dakota. From 1960 to 1977, UN race 2 was the prevalent race detected in the prairie region. UN races 5, 13, and 17 have become more prevalent since 1978, when UN race 2 began to decline. Virulence and race frequencies of *P. recondita* in the prairies have been shown to be directly influenced by the use of resistant cultivars. Frequencies of virulence to resistance genes not deployed in this region are generally low. This article examines populations of *P. recondita* from the eastern and prairie regions for nonrandom associations of virulence and levels of phenotypic diversity to determine whether the two populations differ in their general population structure. The eastern and prairie regions differ in use of host resistance, and their populations of *P. recondita* have previously been shown to differ in levels of virulence polymorphisms and numbers of distinct phenotypes (8,9).

TABLE 1. Avirulence/virulence formulas of Unified Numeration (UN) races of *Puccinia recondita* f. sp. *tritici*

	Avirulence (A) and virulence (V) on UN differential host			
UN race	*Lr1*	*Lr2a*	*Lr2c*	*Lr3*
1	A	A	A	A
2	A	A	A	V
3	A	A	V	V
5	V	A	A	V
6	V	A	V	V
13	V	V	V	V
17	A	V	V	V

MATERIALS AND METHODS

The analyses of virulence distribution and phenotypic diversity in Canadian populations of wheat leaf rust are based on the annual physiologic race surveys conducted at the Winnipeg Research Station since 1931. The protocols used in the rust survey have been described by Samborski (14) and Kolmer (8). Collections of leaf rust throughout the surveys were obtained from nursery trap plots that contain resistant and susceptible wheat lines and from commercial cultivars that differ in resistance to leaf rust. This heterogeneity of host resistance may have an impact on the virulence frequencies and associations of the sampled rust populations and lead to artifactual results and conclusions. However, in the 1987 survey, Kolmer (8) found no correlation between host genotype and virulence of the corresponding leaf rust isolates.

The frequencies of individual virulence and virulence combinations, which are the primary data used in this paper, have been summarized by Kolmer (9). The prairie (Manitoba, Saskatchewan) and eastern (Ontario, Quebec, Maritimes) populations of *P. recondita* in Canada were analyzed by using various tests for nonrandom distribution of virulence and phenotypic diversity. The prevalent virulence combinations of leaf rust in the prairie population from 1960 to 1987 were analyzed to determine whether, during this period, their observed frequencies deviated significantly from expected frequencies, which are based on the random assortment of avirulence and virulence to *Lr1*, *Lr2a*, and *Lr3*. Avirulence or virulence to *Lr2c* was not included in the analysis because the same allele in the fungus conditions virulence to *Lr2a* and *Lr2c* (4). This analysis was split between the periods 1960–1974 and 1975–1987 because of the major increase in frequencies of virulence to *Lr1* and *Lr2a* that began in 1975 (9). Expected frequencies of virulence combinations were calculated by multiplying the appropriate individual avirulence or virulence frequencies. As an example, the expected frequency of isolates virulent only on *Lr3* in any year was obtained from the product of avirulence frequencies to *Lr1*, *Lr2a*, and virulence frequency to *Lr3* from that year. Actual frequencies of virulence combinations were subtracted from the expected frequencies for each year. The mean differences over the years 1960–1974 and 1975–1987 were tested to determine whether they were significantly different from zero by using a paired Student's t test. An arcsin (square root) transformation was applied to the expected and actual frequencies of the virulence combinations to normalize the variance of the mean differences. For example, the mean difference between the expected and actual frequencies of isolates virulent only on *Lr3* from 1975 to 1987 was −0.0589, with a standard deviation of 0.0658 (Table 2). With the arcsin (square root) transformation on the raw data, this difference was determined to be significant at the 0.05 level of confidence with 11 df by using the paired Student's t test. The prevalent virulence combinations in the eastern region from 1956 to 1987 were also examined in this manner.

Pathogenicity associations between selected pairs of virulences were examined in the prairie and eastern populations for selected years. 1977, 1984, and 1987 were chosen as representative years of the prairie population since the mid-1970s (9). In 1977, virulence to *Lr1* and *Lr2a* was at 20%; 1984 virulence to *Lr1* and *Lr2a* was 60 and 40%, respectively; 1987 virulence to *Lr1* and *Lr2a*

was 90 and 60%, respectively. Virulence to *Lr3* in all years was near 100%. Two-way contingency tables were set up with four categories of isolates: VV, virulent on resistance genes a and b; VA, virulent on resistance gene a, avirulent on gene b; AV, avirulent on resistance gene a, virulent on gene b; and AA, avirulent on resistance genes a and b. The *G* test of independence was used to test for significance of association at the 0.05 level of confidence with 1 df (1,15). If the expected number of any category in a table is less than five, the *G* test is not suitable and the association was not analyzed. This occurred in some cases in the prairie leaf rust population when only one or two phenotypes were dominant and with the eastern Canada population because a small number of isolates were usually surveyed.

The Shannon index of ecological diversity (12) was used to estimate the phenotypic diversity levels in the eastern and prairie populations in selected years. This measurement of diversity reflects the number of distinct phenotypes (virulence combinations) and the heterogeneity of phenotype frequencies. Use of the Shannon index in describing phenotypic variation in populations of plant pathogens has been examined by Groth and Roelfs (13).

RESULTS

In the prairie region from 1960 to 1974 (Table 2), virulence combinations VAV and AVV occurred at a significantly lower frequency than expected (mean differences of −0.0104 and −0.0117). Virulence combinations AAV and VVV did not differ significantly from expected frequencies. From 1975 to 1987, isolates virulent only on *Lr3* occurred at a frequency significantly lower than expected (mean difference of −0.0586), whereas virulence combination AVV occurred at a frequency significantly greater than expected (mean difference of 0.0569). Isolates virulent on *Lr1*, *Lr3* and *Lr1*, *Lr2a*, and *Lr3* did not differ significantly from expected frequencies during this time. These four virulence combinations accounted for 96 and 95% of the total leaf rust population in the prairies during the two periods examined.

In the eastern region from 1956 to 1987 (Table 2), only virulence combination AAA differed significantly from the expected frequency (mean difference of −0.0391). The five virulence combinations listed in Table 2 accounted for 87% of the leaf rust population in the eastern region during the period examined.

Two-way contingency tables were set up to examine the relationship between virulence to *Lr1* and virulence to *Lr2a* in the prairie region from 1956 to 1987. Only data from 1959, 1977, 1979, and 1980–1987 could be used in a *G* test for goodness of fit. Virulence to *Lr1* and *Lr2a* (Table 3) was positively associated in 1959 and 1977, not associated in either direction in 1979, and negatively associated from 1980 to 1987. The *G* statistic in all significant associations exceeded the value needed for the 0.001 level of confidence ($G = 10.28$, 1 df).

Virulence associations between other virulences in the prairies in 1977, 1984, and 1987 and the eastern region for 1984 and 1987 were also examined using two-way contingency tables and the *G* test (Table 4). Thirteen of the 18 tested virulence pairs in the prairie region and 13 of the 15 tested pairs for the eastern region were found to have significant associations.

Levels of phenotypic diversity were calculated for the eastern and prairie populations of *P. recondita* for 1977, 1984, and 1987 using the Shannon index (D) (Table 5). Two sets of differentials were used to measure diversity in both populations. Set A used differentials *Lr1*, *Lr2a*, and *Lr3*. Set B included the differentials in set A plus *Lr2c* and was used to measure the effect on diversity of adding *Lr2c* as a differential. Virulences to genes *Lr1*, *Lr2a*, and *Lr3* are conditioned by alleles at independent loci in the fungus. Virulence to *Lr2a* and *Lr2c* is conditioned by a single allele at one locus. A modifying gene in the fungus acts as an inhibitor of avirulence to the *Lr2c* allele (4). Cultures of leaf rust virulent to *Lr2a* are invariably virulent to *Lr2c*. Cultures of leaf rust avirulent to *Lr2a* and virulent to *Lr2c* are common in the eastern region and rare in the prairies.

Modified Shannon indexes were also calculated for each population using the expected phenotypic array, which was calculated under the assumption that virulences are randomly associated with each other. These values (D max fi) are used in determining the amount of diversity lost because of virulence frequencies (fi) that depart from 0.5, and in estimating the loss of diversity because of the presence of nonrandom virulence associations. Differential set A identifies eight possible phenotypes; differential set B will identify 12 possible phenotypes (10). The theoretical maximum Shannon index (D max) for set A is 2.079 and for set B is 2.484. The maximum value assumes that the virulences are randomly associated and that all virulences are present at a frequency of 0.5. The relationship between *Lr2a* and *Lr2c* violates the assumption of independence, but the addition of *Lr2c* as a differential is important in distinguishing the eastern and prairie populations in terms of relative diversity.

The percentage difference between D (max fi) and D (max) represents the diversity lost because of departure of virulence frequencies from 0.5. The effect of virulence association on loss of diversity was estimated by determining the percentage difference between D (max fi) and the actual value of D (Table 5). Using differential set A, the eastern and prairie populations were nearly

TABLE 3. Pathogenicity associations to *Lr1* and *Lr2a* in *Puccinia recondita* f. sp. *tritici* in the prairie region of Canada

Year	*G* value[a]	Direction of deviation
1959	31.27	+
1977	11.29	+
1979	1.55	NS
1980–1987	14.09–79.12	−

[a] *G* test for goodness of fit. + = significant positive association; NS = nonsignificant association; − = significant negative association.

TABLE 2. Mean deviations of expected minus actual virulence frequencies of the predominent virulence combinations of *Puccinia recondita* f. sp. *tritici* in the prairie and eastern regions of Canada from 1960 and 1956, respectively

Virulent (V) or avirulent (A) on			Prairie population				Eastern population	
			1960–1974		1975–1987		1956–1987	
Lr1	*Lr2a*	*Lr3*[a]	d[b]	sd[c]	d	sd	d	sd
A	A	V	−0.0008	0.0439	−0.0586*	0.0658	−0.0034	0.1825
V	A	V	−0.0104*	0.0119	0.0209	0.0634	0.0003	0.0660
V	V	V	−0.0004	0.0061	−0.0461	0.0573	0.0108	0.0369
A	V	V	−0.0117*	0.0145	0.0569*	0.0587	−0.0061	0.0509
A	A	A	...[d]	...	...	...	−0.0391*	0.0216
Mean percentage of total combinations			96		95		87	

[a] Resistance genes to which isolates in each group are virulent.
[b] Mean deviation of expected minus actual virulence combination frequencies. An arcsin (square root) transformation was applied to the frequency data. * = Significantly different from zero.
[c] Standard deviation of the means.
[d] Frequency <1%; too low for analysis.

equally diverse during 1984 and 1987 but not during 1977. When measured by set B, the eastern population had higher levels of diversity during each of the 3 yr. In both the prairie and eastern populations, based on set A differentials, departure of virulence frequencies from 0.5 accounted for nearly all of the total loss of diversity. Loss because of virulence association was relatively small with this set of differentials in all populations examined. Based on differential set B, the percent of diversity lost because of virulence associations relative to set A increased in all cases; loss of diversity because of deviation of virulence frequencies from 0.5 decreased in nearly all cases.

DISCUSSION

Distinct patterns of nonrandom virulence distribution characterize both the prairie and eastern populations of *P. recondita* in Canada. In the prairies, pathogenicity to *Lr1* and *Lr2a* appears to have been positively associated during the period when isolates avirulent on *Lr1* and *Lr2a* accounted for over 90% of the population (9). The frequency of virulence combinations AVV and VAV during this period were significantly lower than expected, and the *G* tests from 1959 and 1977 show that isolates with virulence to both *Lr1* and *Lr2a* occurred in numbers greater than expected. After isolates with virulence to *Lr1* and/or *Lr2a* increased in frequency, pathogenicity to both genes appears to have been negatively associated. Virulence combination AVV occurred in frequencies greater than expected during this period, and isolates avirulent on *Lr1* and *Lr2a* occurred in frequencies significantly lower than expected. The *G* tests from the period 1980–1987 indicate that isolates virulent on both *Lr1* and *Lr2a* occurred in smaller numbers than expected. A number of pathogenicity associations among resistance genes were also found (Table 4). Of the resistance genes listed in Table 4, only *Lr17* and *Lr18* are not used in cultivars grown in the Great Plains of North America. The selective influence of the resistance genes may be responsible for the observed associations. However, the positive association between *Lr17* and *Lr18* indicates that associations may also occur between unselected virulences.

The eastern population of *P. recondita* has been characterized by having intermediate frequencies of virulence to resistance genes *LrB*, *Lr2c*, *Lr3*, *Lr3ka*, *Lr11*, *Lr17*, *Lr18*, and *Lr30* (8,9). The associations among virulences to these genes (Table 4) are characteristic of this population. Virulence to *LrB* and *Lr3ka* is found almost exclusively in isolates avirulent to *Lr2a* and virulent to *Lr2c*. Virulence to *LrB* and *Lr18* was also associated in both years examined.

The nonrandom distribution of virulence observed in the eastern and prairie populations is characteristic of asexual cereal rust populations (1,13). Distinct virulence associations were found in the eastern population despite its having higher levels of virulence polymorphisms and diversity than the prairie population. Virulences to *Lr1* and *Lr2a* in the prairies were directly favored, starting in the late 1960s when cultivars with either *Lr1* or *Lr2a* were released in North Dakota. During the period of selection for virulences to *Lr1* and *Lr2a*, isolates with virulence to both genes occurred in significantly smaller numbers than expected, based on a random distribution of virulences. Stabilizing selection (16) is one possible explanation; isolates with virulence to both genes may have been at a selective disadvantage relative to those with virulence to only one resistance gene. However, other explanations may be equally valid (18). The asexual nature of the *P. recondita* population eliminates the chance of random genetic recombination and subsequent selection of the assorted genotypes. A larger than expected portion of the leaf rust population with virulence to either *Lr1* or *Lr2a* may have become established strictly by chance and continued to predominate. This "founder" effect (5) may also explain other characteristic virulence associations in the prairies and eastern region.

TABLE 4. Pathogenicity associations between virulences in the prairie and eastern populations of *Puccinia recondita* f. sp. *tritici* in Canada in 1977, 1984, and 1987

	Pathogenicity association[a]		
Virulence pair	1977	1984	1987
Prairie population			
Lr1 Lr16	S	+	S
Lr1 Lr17	+	+	S
Lr1 Lr18	S	+	NS
Lr1 Lr24	−	+	NS
Lr2a Lr16	S	−	S
Lr2a Lr17	NS	NS	S
Lr2a Lr18	S	+	+
Lr2a Lr24	S	S	−
Lr2a Lr10	NS	−	S
Lr17 Lr18	S	S	+
Lr24 Lr18	S	S	NS
Lr10 Lr17	−	S	S
Eastern population			
LrB Lr3	S	NS	S
LrB Lr3ka	S	+	+
LrB Lr11	S	NS	S
LrB Lr18	S	+	+
Lr3 Lr3ka	S	+	S
Lr3 Lr11	S	+	S
Lr3 Lr18	S	−	S
Lr2c Lr3ka	S	S	+
Lr2c LrB	S	S	+
Lr2c Lr18	S	S	+
Lr3ka Lr1	S	S	+

[a] Associations were determined using a *G*-test for goodness of fit. S = association was not tested, expected number in any cell was less than five; + = significant positive association ($G > 3.841$, 1 df); NS = nonsignificant association ($G < 3.841$, 1 df); − = significant negative association ($G > 3.841$, 1 df).

TABLE 5. Shannon indexes of diversity for the eastern and prairie populations of *Puccinia recondita* f. sp. *tritici* in Canada in 1977, 1984, and 1987 using differentials *Lr1, Lr2a,* and *Lr3* (Set A) and *Lr1, Lr2a, Lr2c,* and *Lr3* (Set B)

	Shannon indexes of diversity[a]				Diversity (%) loss to			
	D (actual)		D (max *fi*)		*fi*[b] ≠ 0.5		Virulence association	
Year	A	B	A	B	A	B	A	B
Eastern population								
1977	1.482	1.693	1.541	2.103	26	15	3	17
1984	1.219	1.361	1.297	1.492	38	40	4	5
1987	1.006	1.484	1.017	1.518	51	39	0.5	1
Prairie population								
1977	0.956	1.036	0.974	1.394	53	44	1	14
1984	1.191	1.343	1.398	1.806	33	27	10	18
1987	1.204	1.024	1.091	1.389	47	44	3	15

[a] Shannon index D (actual) was calculated from existing frequencies of virulence combinations. D (max *fi*) index was calculated assuming that virulences are randomly distributed (7). Maximum Shannon index for set A is 2.079 and for set B is 2.484. Maximum Shannon index was calculated assuming virulences are randomly distributed and are present at a frequency of 0.5.
[b] Frequency of virulence.

Virulence combinations typical of the prairie region are commonly found in the eastern region (8). This suggests the possibility of admixture occurring between the two populations. Virulence combinations typical of the eastern region are not commonly found in the prairies, suggesting a unidirectional movement between the two populations. Pathogenicity associations were found in the eastern population even though host resistance is not commonly used in this region. Certain virulence combinations may have a selective advantage on susceptible hosts or on those with noncorresponding resistance genes. Virulence associations were also found in the prairies, where resistance has been used in varying amounts since 1937 (14).

Phenotypic diversity was higher in the eastern region relative to that of the prairies in all 3 yr as measured by differential set B. The eastern population has been characterized by isolates avirulent on *Lr2a* and virulent on *Lr2c*. In the prairies, isolates avirulent to *Lr2a* are almost always avirulent to *Lr2c*. This characteristic difference between the two populations accounts for the higher diversity levels in the eastern population, using the differentials in set B. UN race 2 accounted for more 90% of the leaf rust population from 1960 to 1975 in the prairies. Diversity in this region increased after virulence frequencies to *Lr1* and *Lr2a* increased. By 1984 the prairies and the eastern population had nearly equal levels of phenotypic diversity as distinguished by both sets of differentials. Diversity in the prairies declined after virulence to *Lr1* continued to increase to nearly 90%.

When using set B differentials, the increase in proportion of diversity lost because of virulence associations most likely results from the association between virulence to *Lr2a* and virulence to *Lr2c*. The departure of virulence frequencies from 0.5 accounted for the majority of the reduction of diversity in both populations with both sets of differentials. This has also been found in sexual and asexual populations of wheat stem rust (6,7).

With the differentials in the *Prt* nomenclature (10), the eastern and prairie populations in the 1987 survey had Shannon index values of 2.96 and 2.37, respectively (8). The complete set of differentials further distinguishes the characteristic differences in virulence polymorphisms and diversity between the two populations. Total loss of potential diversity in both populations was 63%, with 23 and 16% lost because of virulence associations in the eastern and prairie populations, respectively. The use of additional differentials for which pathogenicity associations have been described increases the proportion of diversity lost because of virulence associations.

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