Phenotypic Diversity in Two Populations of *Puccinia recondita* f. sp. *tritici* in Canada During 1931–1987

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ABSTRACT

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The Canadian eastern and prairie populations of *Puccinia recondita* f. sp. *tritici* from race surveys conducted during 1931–1987 were assessed for phenotypic diversity within each population and phenotypic overlap between the two populations using four different indexes based on infection type on the modified Unified Numeration differentials. The indexes showed that the two populations had similar levels of absolute diversity during 1931–1959. Diversity in the prairie population was consistently lower than in the eastern population during 1960–1975, increased during 1976–1984, and decreased during 1985–1987. Levels of phenotypic diversity in the eastern population changed relatively little from the initial years. The degree of phenotypic overlap as measured by the Rogers index was highest during 1931–1946, after which the two populations diverged phenotypically. The changes in phenotypic diversity in the prairie population could be attributed to the directional changes in race frequencies due to the use of resistant cultivars in this region. The diversity indexes were regressed on the variables' sample size, number of races, and evenness of race frequencies to determine the proportion of variation in the diversity indexes that could be accounted for by the independent variables. The Gleason index was the most sensitive to number of races; the Shannon and Simpson indexes were the most sensitive to evenness of race frequencies. In general, the three indexes of absolute diversity showed little variation due to sample size. Differences in absolute phenotypic diversity within, and phenotypic overlap among, the eastern, prairie, and Pacific populations of *P. r. tritici* in 1988 were enhanced by using the 12 differentials in the *Prt* nomenclature.

Additional keywords: wheat leaf rust.

Puccinia recondita f. sp. *tritici* Rob. ex. Desm. (causal agent of wheat leaf rust disease) is found throughout the wheat-growing regions of North America. The fungus overwinters on winter wheat in the southern plains of the United States, and the urediniospores are carried each year to the northern plains states and prairie provinces by the prevailing southerly winds in late spring and early summer (20). Overwintering of wheat leaf rust also may occur less frequently in more northerly areas of wheat production, resulting in local inoculum sources. *P. r. tritici* is believed to reproduce only by asexual means in North America because susceptible alternate hosts have not been found (22). Leaf rust-resistant hard red spring wheat cultivars have been grown in the prairies of western Canada since 1937 (22). Susceptible soft white winter wheats generally have been grown in Ontario and parts of Quebec.

Different physiologic forms of *P. r. tritici* first were observed by Mains and Jackson in 1921 (18). Eight differential cultivars were used to identify International Standard races. Using these differentials, 15 races were identified in Canada during 1931–1940 (8); 18 races were identified in the United States during 1920–1929 (11). By 1966, 228 races had been described and added to the International Register of Physiologic Races of *Puccinia recondita* f. sp. *tritici* on the basis of infection type on the original eight differentials (10).

Johnston (9) and Basile (1) proposed removing three of the differentials that were temperature labile for infection type and grouping the International Standard races into Unified Numeration (UN) races that produced identical or similar infection types on the remaining five differential cultivars. Dyck and Samborski (2) examined the genetics of leaf rust resistance in the UN differential cultivars; they found resistance gene *Lr1* in Malakof, *Lr2a* in Webster, *Lr2c* in Loros, and *Lr3* in Mediterranean and Democrat. Dyck and Samborski (3) developed near-isogenic lines of wheat differing by single resistance genes in the Thatcher genotype. These lines have since been used to identify physiologic races of *P. r. tritici* (12). A modified UN nomenclature (17) used the Thatcher lines Tc*Lr1*, Tc*Lr2a*, Tc*Lr2c*, and Tc*Lr3* in place of the original UN differential cultivars. These differentials identified 12 UN races in the United States from 1978 to 1983 (17).

An expanded nomenclature (designated as *Prt*) for identifying distinct phenotypes of *P. r. tritici* in North America was proposed by Long and Kolmer (16). Twelve near-isogenic Thatcher lines arranged in three subsets of four are the primary differentials. Subset 1 has Tc*Lr1*, Tc*Lr2a*, Tc*Lr2c*, and Tc*Lr3*; subset 2 has Tc*Lr9*, Tc*Lr16*, Tc*Lr24*, and Tc*Lr26*; subset 3 has Tc*Lr3ka*, Tc*Lr11*, Tc*Lr17*, and Tc*Lr30*. Subset 1 contains the differentials in the modified UN system that have been used continuously in Canada since 1931 in either the original International Standard Differentials or in near-isogenic Thatcher lines to identify distinct phenotypes of *P. r. tritici*. Subset 2 is composed of resistance genes that have been deployed in wheats grown in the United States and Canada. Subset 3 is composed of resistance genes that have not been commonly used in North America, with the exception of *Lr11*, which has been used in winter wheats. Fifty-seven distinct phenotypes of *P. r. tritici* have been identified in North America using these differentials (16). In 1988, Kolmer (15) identified 44 distinct phenotypes in Canada using the *Prt* differentials with the supplemental differentials Tc*LrB* and Tc*Lr18*.

Indexes of species diversity have been used to describe the intraspecific diversity of races in populations of *P. graminis* f. sp. *tritici* (6,7,21) and other cereal rust fungi (5,13). Indexes of diversity can be used to describe the number of distinct phenotypes for a given number of sampled individuals, the frequency distribution of the unique phenotypes, and the degree of phenotypic overlap between two or more populations separated by either time or geography. Diversity as measured by the Gleason index takes into account the number of distinct phenotypes obtained from a given size sample (6,19):

$$H_g = (r - 1)/\ln(N)$$

where r = the number of distinct phenotypes and N = the number of individuals in the sample. The Shannon and Simpson indexes of diversity measure the number of distinct phenotypes and the

evenness of phenotype frequency distribution (6,19):

$$\text{Shannon: } H_w = -\sum_i p_i \ln(p_i)$$

$$\text{Simpson: } H_s = 1 - \sum_i [n_i(n_i - 1)/N(N - 1)]$$

where p_i = the frequency of the ith phenotype, n_i = the number of individuals of the ith phenotype, and N = sample size. The Gleason, Shannon, and Simpson indexes are measures of the absolute diversity within a population. The Rogers index of proportional phenotypic overlap accounts for differences in phenotypic frequencies between two populations (4,6):

$$H_r = 0.5 \sum_{i=1}^{m} | p_{i1} - p_{i2} |$$

where m = total number of phenotypes in both populations, p_{i1} = frequency of the ith phenotype in the first population, and p_{i2} = frequency of the ith phenotype in the second population. Use of these indexes and their various attributes in characterizing diversity in populations of plant pathogens have been discussed more fully by Groth and Roelfs (6). This study is intended to assess and compare the phenotypic diversity of *P. r. tritici* in the eastern and prairie regions of Canada from 1931 to 1987 using the above indexes of diversity. Races of *P. r. tritici* during these years were determined using the differentials in the modified UN nomenclature. The eastern, prairie, and Pacific populations in the 1988 virulence survey of *P. r. tritici* in Canada (12) also were analyzed and compared for phenotypic diversity and degree of similarity using the differentials in the *Prt* (16) nomenclature.

TABLE 1. Sample size, number of races, and standard deviation of race frequencies in surveys of *Puccinia recondita* f. sp. *tritici* in the eastern and prairie regions of Canada as identified on the modified Unified Numeration differential set

	Eastern population			Prairie population		
Year	Sample size	Races (no.)	Standard deviation of frequencies	Sample size	Races (no.)	Standard deviation of frequencies
1931	12	4	0.17950	31	7	0.17000
1933	9	5	0.11865	25	6	0.11840
1934	...[a]	...	...	10	5	0.10000
1936	29	7	0.11780	6	4	0.14610
1937	32	8	0.11310	39	7	0.11420
1938	53	7	0.12260	38	6	0.15130
1939	72	10	0.08600	62	6	0.12180
1940	54	9	0.09400	34	9	0.09860
1941	103	9	0.10610	58	9	0.10190
1942	84	7	0.12120	53	9	0.11650
1943	75	8	0.08650	58	9	0.14620
1944	70	9	0.09920	85	8	0.09940
1945	73	9	0.08390	118	9	0.11400
1946	98	7	0.10320	156	6	0.11930
1947	63	9	0.12800	128	8	0.12010
1948	52	10	0.15640	154	9	0.10240
1949	95	7	0.13970	238	9	0.13120
1950	93	5	0.20270	173	6	0.12700
1951	106	9	0.19080	240	8	0.12980
1952	107	7	0.19550	144	7	0.17690
1953	106	9	0.19230	74	3	0.20920
1954	134	9	0.13510	190	6	0.16320
1955	105	6	0.10710	172	7	0.17650
1956	29	5	0.18390	170	8	0.19110
1957	136	7	0.14580	184	9	0.11740
1958	116	6	0.21290	112	8	0.14660
1959	63	7	0.16380	254	7	0.17160
1960	109	4	0.17680	185	6	0.19650
1961	76	5	0.11920	47	4	0.17820
1962	70	6	0.14330	266	4	0.21030
1963	79	6	0.15170	152	6	0.21600
1964	100	7	0.14160	163	3	0.23690
1965	114	5	0.14420	219	5	0.22190
1966	25	3	0.15790	247	4	0.24120
1967	90	5	0.15690	132	3	0.21700
1969	18	3	0.13810	116	4	0.23109
1970	37	5	0.12530	158	5	0.23999
1971	45	5	0.12040	164	3	0.24520
1972	20	6	0.10560	124	2	0.24780
1973	29	4	0.14260	122	2	0.24760
1974	26	6	0.06600	114	5	0.22730
1975	12	5	0.11690	249	5	0.22000
1976	28	3	0.11410	199	5	0.21880
1977	27	6	0.08930	174	6	0.17380
1978	56	5	0.12760	167	5	0.19880
1979	39	7	0.12670	150	4	0.14760
1980	42	5	0.14470	245	6	0.13390
1981	79	7	0.09950	180	5	0.12900
1982	41	6	0.10900	248	7	0.14100
1983	48	6	0.10380	134	6	0.12280
1984	46	5	0.12260	222	5	0.13000
1985	54	9	0.09600	192	6	0.15120
1986	24	8	0.10550	176	4	0.15360
1987	48	6	0.12480	263	4	0.15560

[a]Samples were not obtained from the eastern region in 1934.

MATERIALS AND METHODS

The Agriculture Canada Research Station in Winnipeg, MB, has conducted annual physiologic race surveys of *P. r. tritici* since 1931. The methods employed in the surveys have remained essentially unchanged since their inception. Collections of rust-infected leaves are obtained from uniform nurseries and commercial fields throughout the country. The collections are increased on susceptible wheat seedlings (cultivar Little Club), and urediniospores from a single pustule are isolated and increased from each collection. The single-pustule isolates are evaluated for virulence on a set of differential wheat seedlings. Infection types are recorded 12 days later with the scale developed by Stakman and Levine (23). Infection types 0, 1, and 2 are considered to be avirulent, and infection types 3 and 4 are considered to be virulent.

The physiologic race designations of *P. r. tritici* in the surveys were converted to the modified UN system (14,15,17). Each UN race was regarded as a distinct phenotype for use in the intraspecific measures of phenotypic diversity. Gleason, Shannon, and Simpson indexes of diversity were calculated for the eastern and prairie populations for each year of the wheat leaf rust survey. Multiple regression analysis was performed with the diversity indexes as the dependent variables and number of races, sample size, and standard deviation of race frequencies as the independent variables that affect diversity. These independent factors previously have been shown to account for variation in diversity indexes in wheat stem rust populations (6). Rogers indexes measuring the degree of proportional phenotypic overlap between the eastern and prairie populations also were calculated.

The 1988 survey data were assessed for phenotypic diversity using the 12 differentials in the *Prt* nomenclature (12). Shannon and Gleason indexes were determined for the eastern, prairie, and Pacific regions using the three differential sets separately and in combination. Rogers indexes were determined for the pairings between the eastern, prairie, and Pacific regions for each of the three differential sets separately and in combination. A simplified Rogers index, which takes into account only the presence or absence of a phenotype in both populations, was used to measure the degree of distinct phenotypes in common between the three regions:

$$H_{rm} = 1 - x_{ij}/y_{ij}$$

where x = number of distinct phenotypes in common in populations i and j, and y = total number of distinct phenotypes in populations i and j. This modified index should be useful in comparing populations that differ in the magnitude of sample size because frequencies of distinct phenotypes are not taken into account. The modified Rogers index was calculated for pairings between the eastern, prairie, and Pacific regions using the three differential sets in combination.

RESULTS

The numbers of single-pustule isolates, numbers of distinct UN races, and standard deviation of race frequencies from each year of the survey in the eastern and prairie regions are listed in Table 1.

The eastern and prairie populations of *P. r. tritici* had similar levels of phenotypic diversity as measured by the Gleason, Simpson, and Shannon indexes (Fig. 1) from 1931 to 1959. Phenotypic diversity was consistently lower in the prairie population than in the eastern population for all three indexes from 1960 to the mid-1970s. Diversity in the prairie population increased from 1976 to 1984 and declined again from 1985 to 1987. Phenotypic diversity in the eastern population remained more constant, with only a slight decrease from 1960 to 1970.

The coefficients of determination (R^2) for the regression of the three indexes of variation on sample size were relatively small in both populations when compared with the R^2 obtained for the effects due to number of races and standard deviation of race frequencies (Table 2). The prairie population had higher values of R^2 than the eastern population for every combination of the independent variables. The Gleason index was the most sensitive to number of races. The Shannon and Simpson indexes were more sensitive to the standard deviation of race frequencies than the Gleason index.

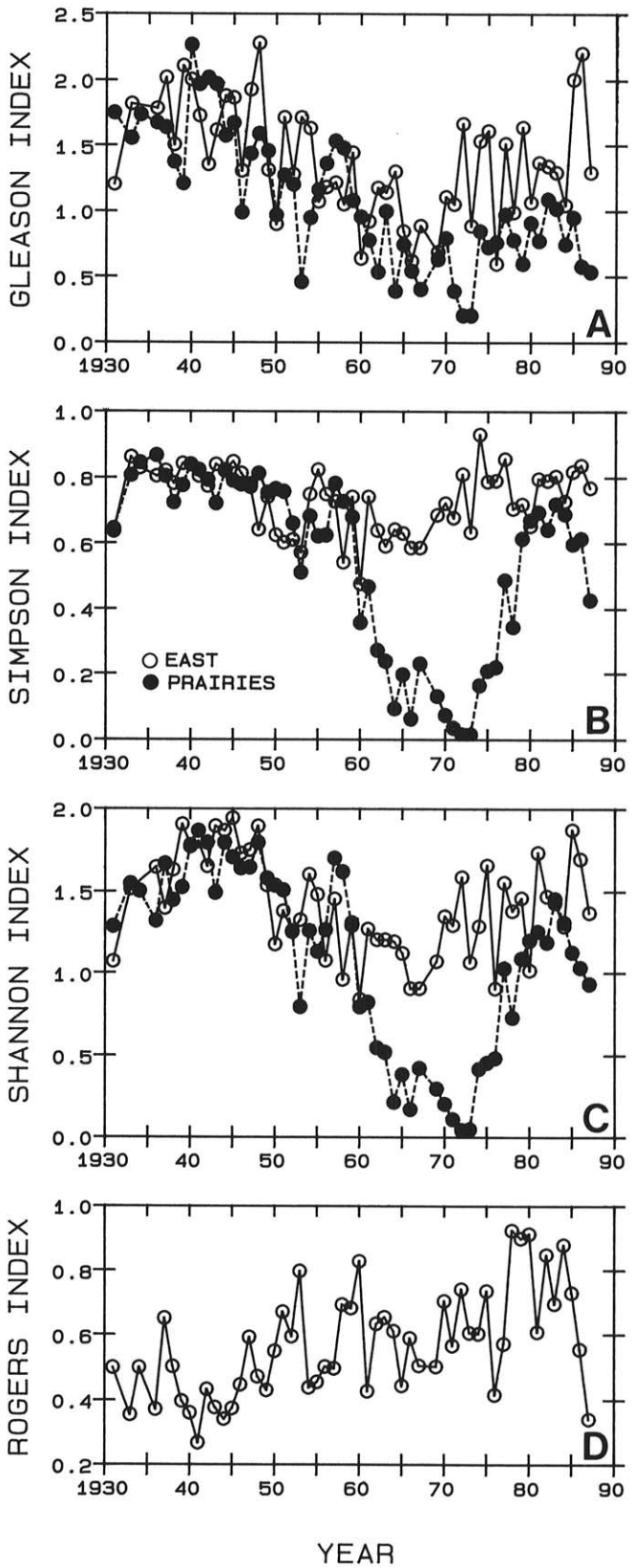

Fig. 1. Indexes of phenotypic diversity in the eastern (○) and prairie (●) populations of *Puccinia recondita* f. sp. *tritici* in Canada during 1931–1987.

TABLE 2. Coefficients of determination (R^2)[a] between independent components of diversity and three indexes of diversity from the eastern and prairie populations of *Puccinia recondita* f. sp. *tritici* in Canada during 1931–1987 identified on the modified Unified Numeration differential set[b]

		Components of diversity						
Diversity index	Population	Sample size (S)	Race number (R)	Standard deviation of race frequencies (E)	S and R	S and E	R and E	S, R, and E
Gleason	Eastern	0.0143 NS	0.7295	0.1496	0.9059	0.1170*	0.7611	0.9051
	Prairie	0.2368	0.7780	0.5217	0.9281	0.6249	0.7933	0.9296
Simpson	Eastern	0.0444 NS	0.0592*	0.5471	0.1747*	0.5406	0.5493	0.5666
	Prairie	0.0762*	0.5191	0.8996	0.5554	0.9008	0.9007	0.9047
Shannon	Eastern	0.0009 NS	0.6088	0.3708	0.6944	0.4153	0.8070	0.8212
	Prairie	0.0704*	0.6653	0.9180	0.6954	0.9199	0.9546	0.9590

[a]Adjusted $R^2 = 1 - (1 - R^2)(N - 1)$/degree of freedom error.
[b]All coefficients were significant at $P = 0.01$, except where indicated by NS (not significant) or * ($P = 0.05$).

Rogers indexes indicate that the eastern and prairie populations of *P. r. tritici* had the highest degree of phenotypic overlap during 1939–1945 (Fig. 1). After this period, the Rogers indexes generally increased, indicating that the populations were diverging phenotypically, although in a sporadic manner, until 1984, and then the indexes declined. Regression of the Rogers indexes on the years from 1931 to 1984 was significant ($R^2 = 0.72$, $P < 0.001$), indicating that the Rogers indexes increased significantly during this period.

The eastern and Pacific populations of *P. r. tritici* from the 1988 survey had the highest Shannon and Gleason indexes of phenotypic diversity using differential subset 3 (Tc*Lr3ka*, Tc*Lr11*, Tc*Lr17*, Tc*Lr30*) in the *Prt* nomenclature (Table 3) and the lowest indexes with differential subset 2 (Tc*Lr9*, Tc*Lr16*, Tc*Lr24*, Tc*Lr26*). The prairie population had the highest indexes of diversity using differential subset 2 and the least diversity with subset 3. Using all 12 of the *Prt* differentials, the Pacific population had the highest indexes of diversity, and the prairie population had the lowest indexes (Table 3).

Rogers indexes indicated that subset 3 distinguished the most variation and subset 2 the least variation between the eastern and Pacific populations (Table 4). Subset 1 distinguished the most variation and set 2 the least variation between the eastern and prairie populations, and the prairie and Pacific populations. Using the 12 differentials in total, the prairie-Pacific pairing had the highest Rogers index, indicating that these populations differed the most for identity and frequencies of distinct phenotypes. The eastern-prairie pairing had the lowest index, although it was still relatively high, indicating that these populations differed the least for identity and frequency of distinct phenotypes (Table 4). The modified Rogers index also indicated that the prairie-Pacific and the eastern-prairie pairings were the most and least different, respectively (Table 4).

TABLE 3. Shannon/Gleason indexes of phenotypic diversity of the eastern, prairie, and Pacific populations of *Puccinia recondita* f. sp. *tritici* in 1988 as measured on the three differential subsets in the *Prt* nomenclature (16), singly and in combination

	Populations of *P. r. tritici*		
	East	Prairie	Pacific
Subset 1[a]	1.205/1.3130	0.8902/0.5429	1.322/1.0277
Subset 2[b]	0.8455/0.9853	1.115/0.7239	0.1956/0.5138
Subset 3[c]	1.816/2.2990	0.4327/0.5429	1.452/2.0550
All sets	2.3646/3.6130	1.8145/2.5337	2.552/4.3681

[a]Tc*Lr1*, Tc*Lr2a*, Tc*Lr2c*, Tc*Lr3*.
[b]Tc*Lr9*, Tc*Lr16*, Tc*Lr24*, Tc*Lr26*.
[c]Tc*L43ka*, Tc*Lr11*, Tc*Lr17*, Tc*Lr30*.

TABLE 4. Rogers indexes of phenotypic overlap among the eastern, prairie, and Pacific populations of *Puccinia recondita* f. sp. *tritici* in 1988 as measured on the three differential subsets in the *Prt* nomenclature (16), singly and in combination

	Subset number			Complete set	
Population pairing	1[a]	2[b]	3[c]	Standard index	Modified index
East-Pacific	0.5231	0.2645	0.5785	0.9320	0.9375
East-Prairie	0.7949	0.4350	0.7145	0.8530	0.8965
Prairie-Pacific	0.8530	0.4695	0.6050	0.9545	0.9500

[a]Tc*Lr1*, Tc*Lr2a*, Tc*Lr2c*, Tc*Lr3*.
[b]Tc*Lr9*, Tc*Lr16*, Tc*Lr24*, Tc*Lr26*.
[c]Tc*L43ka*, Tc*Lr11*, Tc*Lr17*, Tc*Lr30*.

DISCUSSION

The eastern and prairie populations of *P. r. tritici* have had very dissimilar histories of phenotypic diversity as measured by the three indexes of absolute diversity. The large changes in phenotypic diversity since 1931 in the prairie region can be attributed to the directional changes in race frequencies that have been observed in this population (13,14). Phenotypic diversity in the eastern region has remained relatively constant due to the continued use of susceptible cultivars in this region.

The Rogers indexes from 1931 to 1945 indicate that the two populations generally had similar identities and frequencies of UN races during this period. Differences in the UN race composition of the two populations increased after the introduction of resistant cultivars in the prairie region in 1937 (13,22), and this is reflected in the gradual (although sporadic) increase in the Rogers indexes until 1984 when the indexes began to decline steeply. The sporadic increase in the Rogers indexes is probably a function of the directional selection of races in the prairie population and the more complex pattern of racial changes in the eastern population (13,14).

All three indexes of absolute diversity in the prairie population had a significant negative correlation with sample size, which is due to the small sample sizes (mean of 41.6, standard deviation of 22.8 during 1931–1944) in the early years of the survey and the higher levels of diversity during this period when the prairie population was relatively unselected and as diverse as the eastern population. The prairie population had very low diversity indexes during 1960–1980 when sample sizes were larger (mean of 169.6, standard deviation of 55.5). If sample sizes in the early years had been larger, the diversity indexes most likely would have remained the same or increased slightly. Conversely, if sample sizes had been smaller during 1960–1980, the indexes most likely would have remained unchanged or decreased slightly. None of the indexes in the eastern population were significantly affected by sample size.

The consistent difference in accountable variation within each index between the eastern and prairie populations is most likely due to the fundamental differences in race dynamics between the

two populations. The consistent, directional nature of race dynamics in the prairie population created greater and consistent variation in number of races and evenness of race frequencies when compared with the fluctuating nature of race dynamics in the eastern population.

Phenotypic diversity in the North American population of *P. g. tritici* as measured by the same indexes of diversity was found to decrease after eradication of the barberry alternate host (6). The sexual stage of *P. r. tritici* is not believed to contribute to the phenotypic variation in the North American populations of this fungus (22). Among the factors influencing phenotypic diversity in *P. r. tritici* in North America are cultivar usage and the overwintering ability of the fungus. Susceptible cultivars in the eastern region of Canada have maintained a more heterogeneous population of *P. r. tritici* than that observed in the prairie region (13). The fungus also has greater chance to overwinter in the eastern region, creating local populations that could be phenotypically dissimilar from one another and from the regional population found in the northern Great Plains of North America where overwintering of leaf rust would be expected to be infrequent (20).

The components of phenotypic diversity—number of races, evenness of race frequencies, and the independent variable sample size—influenced the indexes of diversity for *P. r. tritici* in generally a similar manner to their effects on diversity in *P. g. tritici* (6). Sample size had small effects on the diversity indexes of both rusts, with the effect generally smaller in *P. r. tritici*. The overall similar influence of the components of diversity was not necessarily expected, given the differences in the epidemiology and population structure between leaf and stem rust of wheat. Long-range transport of inoculum and large regional epidemics are in general more characteristic of wheat stem rust; one to three races usually account for more than 90% of the Great Plains population of wheat stem rust (6,21). The types of historical differential sets used to identify races in the two rust diseases are also quite different. The 12 differentials identified by Stakman that are used to identify races of wheat stem rust are cultivars now known to each possess various numbers of resistance genes (21). The four differential cultivars used in the UN nomenclature to identify races of wheat leaf rust are essentially single-gene lines and are more efficient on a per differential basis in identifying races than the Stakman differentials. A significant amount of potential phenotypic diversity in the wheat stem rust populations may be lost because of the clustering of resistance genes in the Stakman differentials (7). This also may partly explain the greater effect of sample size on the diversity indexes for wheat stem rust compared with wheat leaf rust.

The three subsets of differentials in the *Prt* nomenclature differ in ability to distinguish phenotypic variation within, and differences among, the three populations of *P. r. tritici* in Canada. This is due to the variable degree of virulence polymorphism to the differential resistance genes and also to the effect of nonrandom distribution of virulence in the leaf rust populations (13). When the entire set of *Prt* differentials is used, the absolute diversity as measured by the Gleason and Shannon indexes increases as do the phenotypic differences among the populations as measured by the Rogers index. Both the standard and modified Rogers indexes using the complete set of *Prt* differentials indicate very little overlap of distinct phenotypes among the three populations of *P. r. tritici* in Canada. No single phenotype was found in all three populations. The three populations currently are quite distinct in terms of identity and frequencies of distinct phenotypes.

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