Virulence and Diversity of *Puccinia recondita* f. sp. *tritici* in the United States in 1992

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ABSTRACT

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Isolates of *Puccinia recondita* f. sp. *tritici* were obtained from wheat leaf collections made by cooperators throughout the United States and from cereal rust field surveys of the Great Plains, Ohio Valley, and Gulf Coast states in 1992. Fifty-two virulence/avirulence phenotypes were found among 728 single uredinial isolates on 14 host lines that are near-isogenic for leaf rust resistance. The frequencies of virulence to lines with *Lr24* and *Lr26* during 1992 were greater than in previous years. Regional race distribution patterns again suggested that the central United States is a single epidemiological unit distinct from the eastern United States. The distinctive racial composition of collections from the Southeast, Northeast, and Ohio Valley indicate that populations of *P. r. tritici* in those areas are discrete, suggesting epidemics originate from localized overwintering sources. Although collections from nurseries were not significantly more diverse than collections from fields, they did differ substantially in some areas. In the Northeast, the racial composition of nursery collections showed little relationship to that in field collections.

Additional keywords: plant disease monitoring, rust epidemiology, wheat leaf rust

Wheat leaf rust, caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici*, occurs annually throughout most wheat-growing areas of the United States. In 1992, estimated losses in yield ranged from 0 to 11.3% in the 36 states that produced over 95% of the wheat (*Triticum aestivum* L.) crop. In the United States, losses in yield from leaf rust in winter wheat were estimated at 0.9, 2.2, 3.3, and 4.8% in 1989, 1990, 1991 and 1992, respectively (D. L. Long, *unpublished*).

Wheat leaf rust virulence surveys have been conducted by the Cereal Rust Laboratory since 1978 (12). Surveys have been conducted in Canada since 1931 (4), in Texas since 1985 (17), and in Mexico since 1988 (25). The Canadian survey data have been used to characterize virulence and race dynamics as well as phenotypic diversity within and among wheat-growing areas of Canada (3-6).

The objectives of this study were to characterize the virulence of the *P. recondita* population in the United States in 1992 to the North America Prt differentials (8) and other selected lines of wheat and to compare these results with those of previous surveys.

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MATERIALS AND METHODS

Leaf rust uredinial collections were made from wheat in surveys (approximately 26,000 km) of the Great Plains, Ohio Valley, and Gulf Coast states and by cooperators throughout the United States. The surveys followed predetermined routes through selected wheat-growing areas. Stops to collect leaf rust if present were made at commercial fields 32 km apart or at the first field thereafter. Additional collections were made at nurseries and trap plots along the route. Four collections were made from *Triticum cylindricum* L. (*Aegilops cylindrica* Host) growing near wheat fields in the southern Great Plains. A collection consisted of one to several leaves bearing uredinia from a single plant or cultivar. Collections from artificially inoculated nurseries were excluded from the survey.

Urediniospores from each collection were used to inoculate 7-day-old seedlings of the wheat cultivar Thatcher (CI 10003), treated at emergence with maleic hydrazide (1 g/3 L of H_2O) to enhance spore production. Plants were sprayed at a rate of approximately 0.5 ml per pot of 10-20 seedlings with a suspension of spores in lightweight mineral oil. Inoculated plants were placed in a dew chamber overnight at 18 C. The plants were then transferred to a greenhouse where temperatures varied between 18 and 28 C daily under natural light. After 12-15 days, three leaves were saved per collection, each bearing a single uredinium or pruned to a single uredinium. Six to nine days later, urediniospores were collected separately from one or two such uredinia per collection. If necessary, single uredinial isolates were increased through one uredinial generation on Thatcher before inoculating differential lines. Otherwise they were directly inoculated onto the differential host set (five to seven plants per line) consisting of near-isogenic, single gene lines of wheat known to possess resistance genes *Lr1, 2a, 2c, 3, 3ka, 9, 10, 11, 16, 17, 18, 24, 26*, and *30* in a Thatcher background (21). Sets of differential lines grown during June through September received no supplemental light. After September, natural daylight was supplemented with fluorescent lights from 0200 to 1400 (400-450 $\mu E \cdot m^{-2} \cdot s^{-1}$ at bench level). After 10-14 days, observations were recorded as either high or low infection type, as done in previous surveys (10-15).

Race designations and the wheat differentials used to define the races were those agreed upon by the North American Leaf Rust Workers Committee in 1986 (8). Differentials in the set were chosen because they provide clear distinctions between low and high infection types and because they account for a large part of the detectable diversity in virulence of *P. r. tritici* in North America.

Data were grouped by eight agroecological geographic areas (Fig. 1) based on the source of the collections: area 1

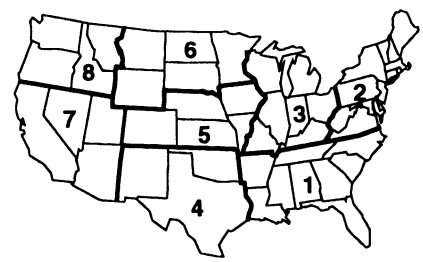

Fig. 1. Agroecological areas for *Puccinia recondita* f. sp. *tritici* in the United States. Area 1 = mainly southern-adapted soft red winter wheats; areas 2 and 3 = mostly northern-adapted soft red and white winter wheats that appear to be epidemiologically separated by geographic features; area 4 = a mixture of wheat types but primarily hard red winter; area 5 = hard red winter wheats; area 6 = mixed wheat types but primarily hard red spring wheat and durum; area 7 = spring wheats planted in late fall; and area 8 = a mixture of wheat types but primarily soft white winter.

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A second sample of spores from each rust collection was bulked with nine other collections made in the same area. Bulked collections were tested on a series of wheat lines resistant to common leaf rust races. This series consisted of Thatcher near-isolines *Lr19, 21,* and *29* (21); Aepoglom; Arapahoe; AZ-FH 50-4-1-1-1 (15); AZ-FH 51-2-2-1 (15); Buck Manantial (*Lr3, 13, 16, 17, 34*) (1); Ceruga 1 and 3 (9); CI 17906 (*Lr9, 24*) (15); CK 9877; CK 68-15/Skorospelka; Era/Lr19; Norm; RL 6059 (*Lr33, 34*) (22); E84018 (*Lr36*); RL 6081 (*Lr37*); Stoa; Siouxland/ProBrand 812; Tc*Lr26*/Tc*Lr29*//Tc*Lr19*/3/Tc*Lr26*/Tc*Lr21*; Tc*Lr29*/Tc*Lr21*//Tc*Lr25*/3/Stoa; Transec (*Lr25*); and Thatcher, a susceptible check. Each entry in the series consisted of five to seven plants. This series was inoculated separately with 68 bulked collections in 1992.

Data analysis. The Shannon index (2) of genetic diversity was calculated from data on race frequencies among field and nursery collections in areas 1 through 6

Table 1. Races of *Puccinia recondita* f. sp. *tritici* identified in leaf rust collections from commercial production fields (F) and experimental nursery plots (N) in the United States in 1992

	Percentage of isolates from indicated area[z] and source														
	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8
Prt code[y]	F	N	F	N	F	N	F	N	F	N	F	N	F	N	N
BBB-10	–	–	–	–	–	–	–	–	–	–	2	–	–	4	–
BGB-10	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
CCB-10	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–
DBB-10,18	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–
DBG-10	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–
FBM	6	–	–	–	8	–	–	–	–	–	–	–	–	–	–
FBM-18	–	–	–	–	8	4	–	–	–	–	–	–	–	–	–
FBM-10,18	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–
KBB-10	–	–	–	–	–	–	2	–	1	1	–	1	–	–	–
KBG-10	–	7	–	–	–	7	2	6	5	7	7	19	–	–	–
KCG-10	3	–	–	–	–	–	–	2	–	2	7	3	–	–	–
KDB-10	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
KDG-10	–	–	–	–	–	–	2	–	1	–	–	–	–	–	–
KFB-10	–	1	–	–	–	–	2	–	1	2	–	3	–	–	–
LBB-10	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–
LBB-10,18	–	–	–	27	–	–	–	–	–	–	–	–	–	–	–
LBD-10,18	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
MBB-10	3	1	–	–	8	4	5	2	1	–	5	1	–	12	–
MBD-10	–	–	–	–	–	–	5	2	–	–	–	–	–	–	–
MBG	6	6	–	–	25	–	–	–	1	1	–	–	–	–	–
MBG-10	36	39	–	–	25	40	5	–	10	6	5	9	100	–	–
MBJ	9	1	–	–	–	–	–	–	–	–	–	–	–	–	–
MBJ-10	3	2	–	–	–	–	–	–	–	1	–	–	–	–	–
MCB	–	–	–	–	–	–	–	–	–	–	–	–	–	23	–
MCB-10	–	1	–	13	–	–	5	–	–	–	–	1	–	42	–
MDB-10	–	–	–	–	–	2	11	2	4	5	5	3	–	–	–
MDG-10	3	–	–	–	–	2	–	–	–	1	–	1	–	–	–
MFB-10	–	3	–	7	–	7	15	43	18	27	18	15	–	–	–
MGB-10	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–
NBB-10,18	–	–	6	–	–	–	–	–	–	–	–	–	–	–	60
NBC-10	–	–	12	20	–	–	–	–	–	–	–	–	–	–	–
PBB-10,18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20
PBD-10	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–
PBG-10	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–
PBM-18	–	–	18	–	–	4	–	–	–	–	–	–	–	–	–
PBM-10,18	–	–	12	–	8	–	–	–	–	–	–	–	–	–	–
PBR-10	–	–	29	7	–	–	–	–	–	–	–	–	–	–	–
PGL-10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
PLM-10	3	1	12	–	–	–	2	–	–	–	–	–	–	–	–
PLM-18	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
SBD	–	–	–	–	–	–	5	–	2	–	–	–	–	4	–
TBB-10	–	–	–	–	–	–	3	–	5	1	7	3	–	–	–
TBG-10	3	22	–	7	8	18	16	28	25	26	34	27	–	4	10
TBJ-10	–	1	–	–	–	–	–	–	–	–	–	3	–	–	–
TBQ-10	–	1	–	7	8	–	–	–	–	–	–	–	–	–	–
TCG-10	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
TDB-10	6	1	–	–	–	–	10	6	15	9	5	3	–	–	–
TDG-10	–	–	–	–	–	2	2	–	3	4	7	1	–	–	–
TFB-10	6	–	–	–	–	4	6	6	5	5	–	8	–	–	–
TFG-10	–	–	–	–	–	–	2	2	–	1	–	–	–	–	–
TLD-10	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TLG-18	9	11	–	–	–	–	–	–	–	–	–	–	–	–	–
No. of isolates	33	148	17	15	12	55	62	53	92	82	44	78	1	26	10

[y] Prt code (8) plus *Lr10* and *Lr18* near-isogenic supplementals.
[z] See Figure 1.

and for nursery collections in areas 7 and 8. The Shannon index reflects both the number of races per population and the relative evenness of their frequencies. It is calculated by the equation $H_w = -\Sigma p_i \log_e(p_i)$, in which p_i is the frequency of the ith race. Standard errors were calculated, and paired Shannon indexes were compared statistically by the t test as described by Poole (20).

Rogers' index and an adapted Nei's standard genetic distance were calculated for all paired comparisons of populations in areas 1–8 as previously described (7). Rogers' index measures similarity of racial composition between populations. It is calculated by the equation $H_r = 0.5 \Sigma|p_{Ai} - p_{Bi}|$, in which $|p_{Ai} - p_{Bi}|$ is the absolute value of the difference between the frequencies of the ith race in populations A and B (2). Rogers' index varies from 0.0 for paired populations with identical races at identical frequencies to 1.0 for populations with no races in common.

Nei's (19) standard genetic distance measures similarity of frequencies of alleles at a number of genetic loci in the respective populations. Rogers' index is not sensitive to gene frequencies, because it treats all races as equally distinct, regardless of how many virulences they share. Therefore, Nei's standard genetic distance is a useful check against Rogers' index. It is possible for two populations to have similar frequencies of specific virulences (low Nei's distance) even if they do not have any races in common (high Rogers' index), if the races in the first population are genetically similar to those in the second population. Nei's standard genetic distance is calculated from the equation $D = -\log_e I$, in which $I = J_{AB}/(J_A J_B)^{0.5}$. For dimorphic loci, $J_{AB} = (1/L)\Sigma[p_{Ai}p_{Bi} + (1-p_{Ai})(1-p_{Bi})]$; $J_A = (1/L)\Sigma[p_{Ai}^2 + (1-p_{Ai})^2]$; and $J_B = (1/L)\Sigma[p_{Bi}^2 + (1-p_{Bi})^2]$, in which L is the number of loci, p_{Ai} and $(1-p_{Ai})$ are frequencies of the two alleles at the ith locus in population A, and p_{Bi} and $(1-p_{Bi})$ are frequencies of the two alleles at the ith locus in population B. $I = 0$ when the two populations share no alleles, and $I = 1$ when the two populations have identical allele frequencies over all the loci tested. Thus, D may vary between 0 and infinity.

Virulence tests with isolates of *P. r. tritici* provide phenotypic data but do not reveal whether the phenotypes are heterozygous or homozygous. Therefore, in adapting Nei's standard genetic distance to our data, we based the calculations of genetic distance on frequencies of phenotypes rather than alleles (7). For example, the frequency of virulence on the *Lr1* near-isoline was treated as the frequency of the allele for virulence corresponding to the *Lr1* resistance gene.

We calculated Rogers' index and the adapted Nei's distance for both field and nursery collections from areas 1–6 but for only nursery collections from areas 7 and 8 because of the lack of field isolates in those areas in 1992. Phenograms based on Rogers' index and Nei's distance were computed by the unweighted pair-group method with arithmetic mean (19) to display relationships among populations.

Table 2. *Puccinia recondita* f. sp. *tritici* race nomenclature code and corresponding virulence formula

Prt code[y]	Virulence formula[z]
BBB-10	*10*
BGB-10	*10, 16*
CCB-10	*3, 10, 26*
DBB-10,18	*2c, 10, 18*
DBG-10	*2c, 10, 11*
FBM	*2c, 3, 3ka, 30*
FBM-18	*2c, 3, 3ka, 18, 30*
FBM-10,18	*2c, 3, 3ka, 10, 18, 30*
KBB-10	*2a, 2c, 3, 10*
KBG-10	*2a, 2c, 3, 10, 11*
KCG-10	*2a, 2c, 3, 10, 11, 26*
KDB-10	*2a, 2c, 3, 10, 24*
KDG-10	*2a, 2c, 3, 10, 11, 24*
KFB-10	*2a, 2c, 3, 10, 24, 26*
LBB-10	*1, 10*
LBB-10,18	*1, 10, 18*
LBD-10,18	*1, 10, 17, 18*
MBB-10	*1, 3, 10*
MBD-10	*1, 3, 10, 17*
MBG	*1, 3, 11*
MBG-10	*1, 3, 10, 11*
MBJ	*1, 3, 11, 17*
MBJ-10	*1, 3, 10, 11, 17*
MCB	*1, 3, 26*
MCB-10	*1, 3, 10, 26*
MDB-10	*1, 3, 10, 24*
MDG-10	*1, 3, 10, 11, 24*
MFB-10	*1, 3, 10, 24, 26*
MGB-10	*1, 3, 10, 16*
NBB-10,18	*1, 2c, 10, 18*
NBC-10	*1, 2c, 10, 30*
PBB-10,18	*1, 2c, 3, 10, 18*
PBD-10	*1, 2c, 3, 10, 17*
PBG-10	*1, 2c, 3, 10, 11*
PBM-18	*1, 2c, 3, 3ka, 18, 30*
PBM-10,18	*1, 2c, 3, 3ka, 10, 18, 30*
PBR-10	*1, 2c, 3, 3ka, 10, 11, 30*
PGL-10	*1, 2c, 3, 3ka, 10, 16*
PLM-18	*1, 2c, 3, 3ka, 9, 18, 30*
PLM-10	*1, 2c, 3, 3ka, 9, 10, 30*
SBD	*1, 2a, 2c, 17*
TBB-10	*1 2a, 2c, 3, 10*
TBG-10	*1, 2a, 2c, 3, 10, 11*
TBJ-10	*1, 2a, 2c, 3, 10, 11, 17*
TBQ-10	*1, 2a, 2c, 3, 3ka, 10, 11*
TCG-10	*1, 2a, 2c, 3, 10, 11, 26*
TDB-10	*1, 2a, 2c, 3, 10, 24*
TDG-10	*1, 2a, 2c, 3, 10, 11, 24*
TFB-10	*1, 2a, 2c, 3, 10, 24, 26*
TFG-10	*1, 2a, 2c, 3, 10, 11, 24, 26*
TLD-10	*1, 2a, 2c, 3, 9, 10, 17*
TLG-18	*1, 2a, 2c, 3, 9, 11, 18*

[y] Prt code (8) plus *Lr10* and *Lr18* near-isogenic supplementals.

[z] Resistances evaluated: *Lr1*, *2a*, *2c*, *3*, *9*, *16*, *24*, *26*, *3ka*, *11*, *17*, *30*, *10*, and *18*.

RESULTS AND DISCUSSION

In 1992, a total of 728 single uredinial isolates were characterized. Fifty-two virulence phenotypes were identified (Tables 1 and 2) on the basis of the 12 differential host lines plus supplemental lines *Lr10* and *Lr18* (8), which are near-isogenic for leaf rust resistance genes. Virulence phenotypes are arranged in Tables 1 and 2 and Figure 2 by Prt code (8). Results are presented as percentages of isolates within areas separated into collections made from nurseries and fields. Thirty-four of the 52 races identified were collected from only one or two areas. The most frequently identified race in 1992 was TBG-10, which comprised

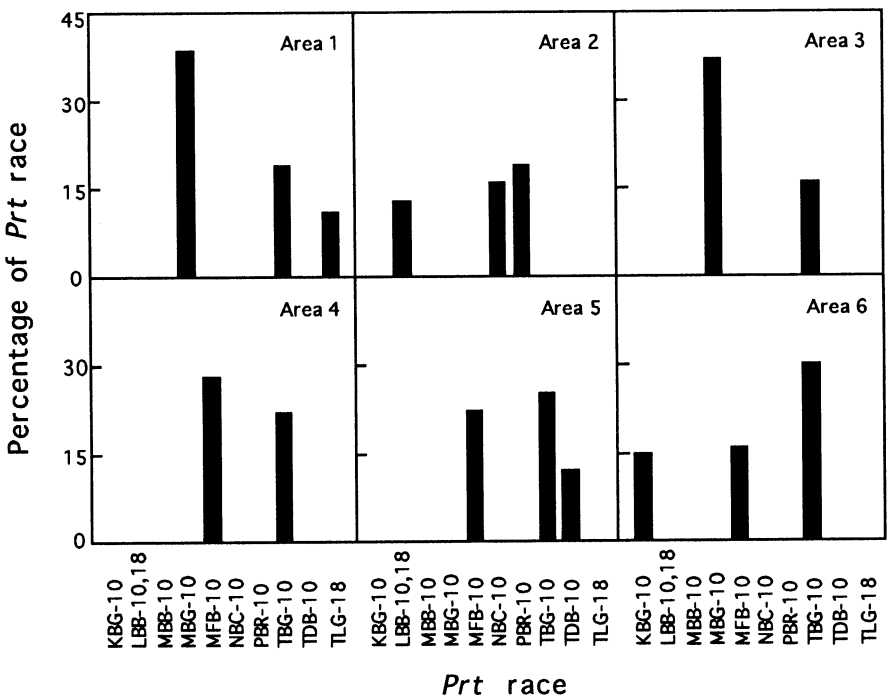

Fig. 2. Frequency of common races of *Puccinia recondita* f. sp. *tritici* among collections from areas 1–6 (Fig. 1) of the United States. Collections from fields and nurseries were combined, and races that occurred at >10% frequency in any area were included for the comparison.

21% of the nationwide population and was the only race found in all eight areas of the United States. In both 1990 and 1991 it comprised 17% of the total isolates. Race TBG-10 occurred at >18% frequency in areas 1, 3, 4, 5, and 6 (Fig. 2); it was the most frequent race in areas 5 and 6. The second most frequently identified race was MBG-10, which comprised 17% of the nationwide population in 1992 and 20% in 1991. MBG-10 was most common in areas 1 and 7 but was not found in area 2 or 8. Two of the other M- (virulent on *Lr1* and *3*) phenotypes, MDB-10 (virulent on *Lr24*) and MFB-10 (virulent on *Lr24* and *26*), together comprised 17% of the population nationwide. Race MFB-10 was common in areas 4, 5, and 6 (Fig. 2). Eleven other T- (virulent on *Lr1, 2a, 2c*, and *3*) phenotypes made up 16% of the population (12% in 1991 and 17% in 1990). Less common M- phenotypes were avirulent on *Lr10*. The wide distribution of M- and T- phenotypes throughout areas 4, 5, and 6 in 1992 (Table 1, Fig. 2) shows that these areas remain a continuous south-north epidemiological unit as previously proposed (7,10).

From 1981 to 1986 (12–14), the K- (virulent on *Lr2a, 2c*, and *3*) races were the most frequently identified phenotypes in the U.S. population. The frequency of this group has decreased from 39% in 1985 (13) to 8% in 1991 (10) and 9.8% in 1992 (Table 1). The K- races are currently found mainly in areas 4, 5, and 6 and less frequently in areas 1 and 3.

Most of the D- (virulent on *Lr2c*), F- (virulent on *Lr2c* and *3*), L- (virulent on *Lr1*), N- (virulent on *Lr1* and *2c*), and P- (virulent on *Lr1, 2c*, and *3*) phenotypes were found in the eastern soft winter wheat region (areas 1, 2, and 3) (Table 1). Race CCB-10 was found only in California (area 7). Races NBB-10,18, PBB-10,18, and PGL-10,18 were unique to Washington. Race TBG-10, the fourth race identified from Washington (area 8) was also common in other areas of the United States. Race groups B- (avirulent), C- (virulent on *Lr3*), and D- were less than 1.0% of all isolates identified. The B- phenotypes comprised 0.4% of the isolates and were found scattered from Louisiana to Minnesota to California. The D- phenotypes comprised over 14% of the isolates in New York but were not found outside area 2. The L- phenotypes made up 35% of the isolates identified from nursery collections made in North Carolina, Pennsylvania, and Virginia but were not found west of the Mississippi River or in area 3. The S- (virulent to *Lr1, 2a*, and *2c*) phenotype was identified from four *T. cylindricum* collections made in the southern Great Plains and one wheat collection in California and made up less than 0.8% of the isolates.

In general, the race collected most frequently from fields was also most common in nurseries in the same area. In area 2, however, race PBR-10 was most common in field collections but LBB-10,18 was most common in nursery collections (Table 1).

Table 3 summarizes the frequencies of virulence to each of the 14 differential lines among collections from the eight agroecological areas. Because of variations in greenhouse environments, temperature-sensitive genes *Lr3ka, 11, 17*, and *18* may have been occasionally misclassified. Incidence of virulence on lines with *Lr24* increased from 17% in 1990 to 28% in 1991 and 30% in 1992. Virulence to *Lr26* increased from 14% in both 1989 and 1990 to 20% in 1991 and 24% in 1992 (Table 2). Virulences to *Lr24* and *Lr26* were most common in areas 4, 5, and 6. Cultivars with *Lr24* are widely grown in the southern Great Plains (18). Combined virulence to *Lr24* and *Lr26* was found in KF-, MF-, and TF- phenotypes.

Virulence to *Lr11* was common throughout the United States and was identified in 18 virulence combinations in 1992, 22 combinations in 1991, and 20 combinations in 1990. In the 5 yr before 1990, *Lr11* combinations averaged 12 per year. This reflects a selective advantage of this virulence due to an increase in the hectarage of cultivars with *Lr11* (24). Phenotypes virulent to *Lr11* were the most common in the K-, M-, P-, and T- race groups.

Virulence to *Lr9* was identified in 6.1% of the U.S. population of *P. r. tritici* in 1991 (10) and 4.0% in 1992. Coker 9766 (*Lr2a* and *Lr9* resistance) is grown in area 1 (D. L. Long, *unpublished*), where 13.5% of the collections had *Lr9* virulence in 1991 (10) and 13% in 1992. Virulence to *Lr9* was also found in area 2 in 1992.

Virulence to *Lr16* decreased from 17% in 1986 to less than 0.6% in 1992 in the U.S. population. In Texas, the mean percentage of isolates virulent to *Lr16* averaged 18% from 1985 to 1987 (16) but only 1% from 1988 to 1990 (18), 0% in 1991, and 0.1% in 1992. This is primarily due to the discontinuation of growing ProBrand 812 in central Texas. In Canada, virulence to *Lr16* occurred in 6% of the isolates in 1987 (3) but was not found in 1989, 1990, and 1991 (6). Columbus and Kenyon, grown in Canada, have *Lr16* in combination with *Lr13*, and both are currently effective in Canada. Virulence to *Lr30* was low in all areas except 2 and 3.

Among the bulked collections, no virulence was found to 13 resistant series

Table 3. Percentage of *Puccinia recondita* f. sp. *tritici* isolates virulent to the single-gene differential lines used in the 1992 survey

Area[y]	Source[z]	No. of isolates	Percentage of isolates virulent to *Lr* gene													
			1	*2a*	*2c*	*3*	*3ka*	*9*	*10*	*11*	*16*	*17*	*18*	*24*	*26*	*30*
1	Field	33	91	30	39	100	9	15	70	73	0	15	9	15	9	9
	Nursery	148	91	44	45	98	1	12	82	90	1	5	13	5	7	1
2	Field	17	94	12	94	59	71	12	82	29	0	0	41	0	0	82
	Nursery	15	93	13	53	47	13	0	100	33	0	0	27	7	20	27
3	Field	12	83	17	42	100	33	0	58	67	0	0	17	0	0	25
	Nursery	55	85	33	45	100	13	2	91	71	0	0	13	16	13	13
4	Field	62	94	50	52	95	2	2	95	27	3	10	0	48	29	2
	Nursery	53	91	51	51	100	0	0	100	38	0	2	0	60	53	0
5	Field	92	91	65	65	98	0	0	97	46	0	2	0	49	25	0
	Nursery	82	87	59	59	100	0	0	99	50	0	1	0	54	38	0
6	Field	44	84	66	66	98	0	0	100	59	0	0	0	34	25	0
	Nursery	78	74	69	69	100	0	0	100	63	0	3	0	33	29	0
7	Field	1	100	0	0	100	0	0	100	100	0	0	0	0	0	0
	Nursery	26	88	8	12	88	0	0	69	4	0	8	0	0	69	0
8	Nursery	10	100	10	100	40	10	0	100	10	10	0	80	0	0	0
All fields		261	87	46	52	96	2	4	91	62	...	3	8	26	26	2
All nurseries		467	90	51	59	95	8	3	91	47	1	5	5	36	21	8
Total		728	88	48	54	96	4	4	91	57	...	4	7	30	24	4

[y] See Figure 1.
[z] Collections from commercial production fields and experimental nursery plots.

entries: Thatcher near-isolines *Lr19* and *29*, Tc*Lr26*/*29*//Tc*Lr19*/*3*/Tc*Lr26*/Tc*Lr21*, Tc*Lr29*/Tc*Lr21*//Tc*Lr25*/*3*/Stoa, Aepoglom, AZ-FH 50-4-1-1-1, AZ-FH 51-2-2-1, Buck Manantial, Ceruga 1, CI 17906, Era/*Lr19*, Norm, and Stoa.

With some exceptions, genetic diversity among field and nursery collections in 1992 as indicated by Shannon indexes (Table 4) were generally in the same range as in previous surveys during 1988–1990 (11) and 1991 (10). During 1988–1990, collections from both fields and nurseries in areas 2 and 3 showed high levels of diversity relative to areas 4, 5, and 6, which had intermediate diversity. In 1992, however, Shannon indexes for areas 2 and 3 were similar to those from areas 5 and 6. Shannon indexes for the Great Plains collections were most consistent with values for both field and nursery collections ranging between 1.7 and 2.3 from 1988 to 1992. An exception was the greater diversity (Shannon index 2.6) among field collections from area 4 in 1992. Collections from nurseries in areas 7 and 8 had low diversity in both the 1988–1990 and 1992 surveys.

In the 1988–1990 surveys, collections from nurseries in areas 1, 2, 6, and 7 were significantly more diverse than field collections from the same areas (11). This was also true for areas 1 and 2 in 1991 (10). In 1992, however, there were no significant differences in diversity between field and nursery collections except in area 4, where field collections were more diverse than nursery collections (Table 4). Thus, our previous conclusion that collections of leaf rust from nurseries tend to exhibit greater diversity of races than field collections (10,11) is not valid for all years or areas.

On the basis of racial composition, the field collections from areas 4, 5, and 6 from the Great Plains were similar (Figs. 3 and 4). In contrast, there were distinct differences among field collections from areas 1, 2, and 3 east of the Mississippi River. This pattern was also found in the 1988–1990 (11) and 1991 surveys (10). The similarity of racial composition of collections from areas 4, 5, and 6 suggests that these areas constituted a single epidemiological zone in 1992. In the Great Plains, *P. r. tritici* spreads so widely and in such large amounts that the selective effects of resistant genes in the wheats of areas 4, 5, and 6 must be taken into consideration as a whole when accounting for virulent frequencies in these regions. In contrast, the lack of similarity between the composition of races from field collections from area 2 and those from areas 1 and 3 suggests that these areas are not a single epidemiological zone. Apparently, overwintering of *P. r. tritici* occurred independently in areas 1 (Southeast), 2 (Northeast), and 3 (Ohio Valley), with limited movement of the pathogen among areas. Schafer and Long (23) reported evidence of overwintering of leaf rust in winter wheat in Pennsylvania, and Kolmer (6) showed that leaf rust overwinters in Ontario and Quebec.

In general, the phenogram for Rogers' indexes for nursery collections is similar to that for field collections (Fig. 3). The same similarity of nursery collections in areas 1 and 3 was also found in the 1988–1990 and 1991 surveys (10,11). In 1992, however, it was also noted that nursery collections from areas 1 and 3 were as similar as those from areas 4, 5, and 6 (Fig. 3).

Even though the phenograms for Rogers' indexes between areas were similar for field and nursery collections, the field and nursery collections within an area were not necessarily composed of similar races. For example, Rogers' index for the comparison between field and nursery collections within area 2 was 0.82, which indicates almost no relationship between the races collected in nurseries and those collected in fields. This value is almost identical to Rogers' index of 0.85 for the same comparison in 1991 (10). One explanation for the lack of similarity between nursery and field

Table 4. Shannon index of diversity for collections of *Puccinia recondita* f. sp. *tritici* from six agroecological areas of the United States in 1992

Area[x]	Shannon index[y] Field	Nursery	Significance[z]
4	2.64 a	1.66 cd	<0.05
5	2.22 b	2.19 ab	NS
1	2.22 b	1.91 bc	NS
6	2.06 b	2.21 a	NS
3	1.94 b	2.02 bc	NS
2	1.92 b	2.03 abc	NS

[x] See Figure 1.
[y] Collections were from commercial production fields and experimental nursery plots. Values within columns followed by the same letter are not significantly different at $P < 0.05$ according to t tests of paired isolates as described by Poole (20).
[z] Significance of the differences between values for field and nursery collections within the same area. NS = not significant.

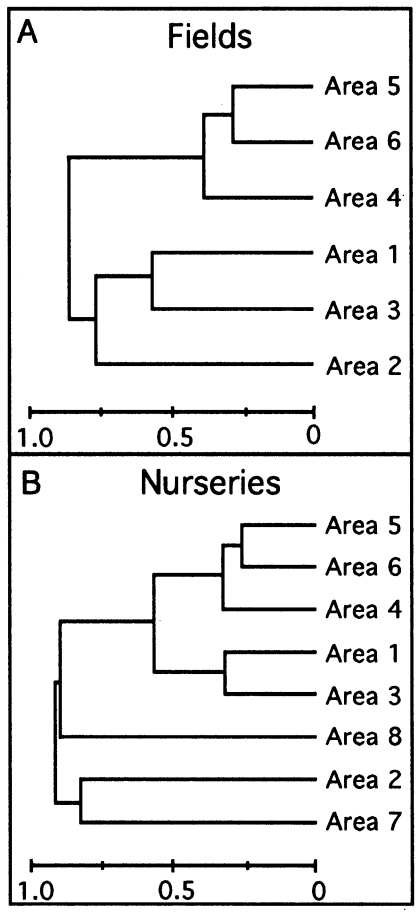

Fig. 3. Phenogram of similarities of racial compositions based on Rogers' index for collections of *Puccinia recondita* f. sp. *tritici* isolates in 1992 from **(A)** fields in areas 1–6 and **(B)** nurseries in areas 1–8 (Fig. 1). All isolates from areas 7 and 8 were collected in nurseries.

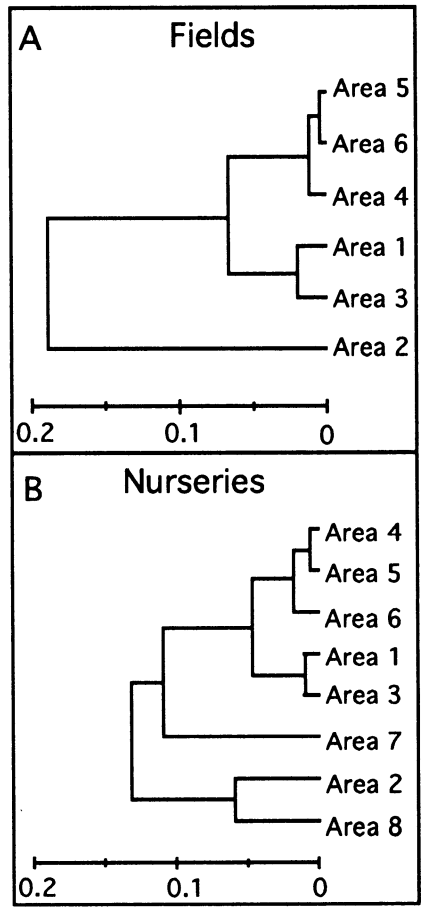

Fig. 4. Phenogram of similarities of racial compositions based on an adaptation of Nei's standard genetic distance between collections of *Puccinia recondita* f. sp. *tritici* in 1992 from **(A)** fields in areas 1–6 and **(B)** nurseries in areas 1–8 (Fig. 1). All isolates from areas 7 and 8 were collected in nurseries.

collections in area 2 may be that epidemiological zones in the Northeast are small. Thus, the collections from different fields and nurseries may represent largely independent populations of *P. r. tritici*.

Field and nursery collections in area 3 also differed substantially in racial composition. Rogers' index for this comparison was 0.60 in 1991 (10) and 0.59 in 1992. The lowest Rogers' index between field and nursery collections was 0.19 for area 5. This indicates close similarity of races and their frequencies in the two sets of collections. For areas 1, 4, and 6 the indexes between field and nursery collections were 0.41, 0.49, and 0.34, respectively. These values are similar to Rogers' indexes for field collections between areas 4, 5, and 6, which represent a single epidemiological zone (Fig. 3).

Nei's distance values provide another comparison between populations that reflects the frequency of individual virulences without regard to races. Obviously, populations composed of the same races in approximately the same frequencies will share the same pattern of frequencies of individual virulences. Thus, it is not surprising that areas 4, 5, and 6 with similar racial compositions in both field and nursery collections also show close similarity based on Nei's distances for both field and nursery collections (Fig. 4). As during 1988–1990 (11) and 1991 (10), virulence frequencies of field collections in areas 1 and 3 showed some similarity.

Virulence frequencies in field and nursery collections in area 2 were quite distinct from those in other eastern and Great Plains areas in 1992, although the nursery collections in area 2 showed some similarity to those in area 8. The same pattern was seen during 1988–1990 (11) but not in 1991 (10), when virulence frequencies in nurseries of area 2 were more similar to those of areas 1 and 3.

In 1992, 36 of the collections from areas 7 and 8 came from nurseries and one came from the field. As during 1988–1990 (11) and 1991 (10), collections from areas 7 and 8 were distinct from each other both in racial composition and in virulence frequencies (Figs. 3 and 4).

We are continuing to monitor populations of *P. r. tritici* in the United States to identify races with virulence combinations that will put currently grown wheat cultivars at risk. In addition, the analyses of diversity among collections from different areas of the country should lead to improved understanding of leaf rust epidemiology. Similar racial composition of collections throughout the Great Plains is consistent with rapid, long-distance spread of leaf rust annually through areas 4, 5, and 6. Our evidence from areas 1, 2, and 3 east of the Mississippi River and Kolmer's (6) evidence from Ontario and Quebec suggest that those *P. r. tritici* populations from those areas are much more discrete, as would be expected from localized overwintering of the pathogen and localized outbreak of epidemics.

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