Virulence and Diversity of *Puccinia recondita* f. sp. *tritici* in the United States in 1991

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ABSTRACT

Long, D. L., Roelfs, A. P., Leonard, K. J., and Roberts, J. J. 1993. Virulence and diversity of *Puccinia recondita* f. sp. *tritici* in the United States in 1991. Plant Dis. 77:786-791.

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 1991. Fifty-five virulence/avirulence phenotypes were found among 647 single uredinial isolates on 14 host lines that are isogenic for leaf rust resistance. The frequencies of virulence to lines with *Lr*24 and *Lr*26 during 1991 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.

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 1991, losses in yield ranged from 0 to 7.5% 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in winter wheat were estimated at 1.1, 0.9, 2.2, and 3.3% in 1988, 1989, 1990, and 1991, respectively (D. L. Long, *unpublished*).

Wheat leaf rust virulence surveys have been conducted at the Cereal Rust Laboratory since 1978 (11). Surveys have been conducted in Canada since 1931 (5), in Texas since 1984 (15), and in Mexico since 1988 (25). The Canadian survey data have been used to characterize virulence and race dynamics and 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 1991 to the North America Prt differentials (8) and other selected lines of wheat and to compare these results with those of previous surveys.

MATERIALS AND METHODS

Leaf rust uredinial collections were made from wheat in surveys (approximately 28,000 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 areas where small-grain cereals are important. Stops were made at commercial fields 32 km apart or at the first field thereafter. Additional stops were made at nurseries and trap plots along the route. A collection consisted of one to several leaves bearing uredinia from a single plant or cultivar.

Urediniospores from each collection were used to inoculate 7-day-old seedlings of wheat cv. Thatcher (CI 10003) treated at emergence with maleic hydrazide (1 g/3 L of H_2O) to enhance spore production. Plants were sprayed with spores suspended in lightweight mineral oil and 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. 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 differential lines were inoculated. Otherwise they were directly inoculated onto the differential host series (five to seven plants per line) consisting of wheat single-gene isolines known to possess resistance genes *Lr*1, 2a, 2c, 3, 3ka, 9, 10, 11, 16, 17, 18, 24, 26, and 30 in a Thatcher genetic background (20). 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 $\mu E \cdot m^{-2} \cdot s^{-1}$). After 10–14 days, observations were recorded as either high or low infection type, as was done in previous surveys (10–14).

Data are grouped by eight agroecological geographic areas (Fig. 1) based on the source of the collections: 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, a mixture of wheat types but primarily hard red spring and durum; area 7, spring wheats planted in late fall; and area 8, a mixture of wheat types but primarily soft white winter.

Paper No. 19,304, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul.

Accepted for publication 5 April 1993.

A second sample of spores from each rust collection was bulked with those from 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 isolines *Lr*19, 21, and 29 (20); Aepoglom; Anex; Arapahoe; AZ-FH 50-4-1-1-1 (14); AZ-FH 51-2-2-1 (14); Buck Manantial (*Lr*3, 13, 16, 17, and 34) (1); Ceruga 1, 2, 3, and 6 (9); CI 17906 (*Lr*9 and 24) (14); CK 9877; CK 68-15/Skorospelka; Probrand 812 (23); RL 6059 (*Lr*33 and 34) (21); Stoa; Siouxland/ProBrand 812; Transec (*Lr*25); and Thatcher, a susceptible check. Each entry in the series consisted of five to seven plants. This series was inoculated with 33 bulked collections in 1991.

Data analysis. The Shannon index of genetic diversity (2) was calculated from data on frequencies of races among field and nursery collections in areas 1 through 6, for which there were adequate isolates to measure diversity. The Shannon index reflects both the number of races per population and the relative evenness of their frequencies. The index 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 (19). Further information on uses and interpretations of the Shannon index of diversity in rust populations is presented by Groth and Roelfs (2) and Leonard et al (7).

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 (18) standard genetic distance (D) 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 *Lr*1 isoline was treated as the frequency of the allele for virulence corresponding to the *Lr*1 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 1991. Phenograms based on Rogers' index and Nei's distance were computed by the unweighted pair-group method with arithmetic mean (18) to display relationships among populations.

RESULTS AND DISCUSSION

In 1991, a total of 647 single uredinial isolates were characterized. Fifty-five virulence phenotypes were identified (Table 1) on the basis of the 12 differential host lines plus two supplemental lines, *Lr*10 and *Lr*18 (8), which are isogenic for leaf rust resistance genes. Virulence phenotypes are arranged in Table 1 and Figure 2 by Prt code (8), and results are presented as percentages of isolates within areas separated into collections made from nurseries and fields. Over 50% of the isolates had the M– (virulent on *Lr*1 and 3) phenotypes. The most frequently identified race in 1991 was MBG-10, which comprised 20% of the nationwide population and was the most widespread race in the United States. Race MBG-10 occurred at >10% frequency in areas 1, 2, 3, and 5 (Fig. 2) and was the most frequent race in areas 1 and 3. Two of the other M– phenotypes, MDB-10 virulent to *Lr*24 and MFB-10 virulent to *Lr*24 and *Lr*26, together comprised 20% of the population nationwide. Races MDB-10 and MFB-10 were most common in areas 4, 5, and 6 (Fig. 2). Another frequently identified race was TBG-10, which comprised the same percentage (17%) of the population in 1991 as in 1990. Race TBG-10 was the most common race in areas 5 and 6 and was also common in area 4 (Fig. 2). Ten other T– (virulent on *Lr*1, 2a, 2c, and 3) phenotypes made up 12% of the population (17% in 1990). Less common M– and T– phenotypes were avirulent on *Lr*10. The wide distribution of M– and T– phenotypes throughout areas 4, 5, and 6 in 1991 (Table 1, Fig. 2) shows that these areas remain a continuous south-north epidemiological unit, as previously proposed (7,10).

From 1981 to 1986 (11–13), the K– (virulent on *Lr*2a, 2c, and 3) races were the most frequently identified phenotypes in the U.S. population. The frequency of this group has decreased from the high of 39% in 1985 (12) to 8% in 1991 (Table 1).

Most of the C–, F–, N–, and P– phenotypes were found in the eastern soft winter wheat region, i.e., areas 1, 2, and 3 (Table 1). The exceptions were race CCB-10, which was found only in California (area 7), and NBG-10 and PBR-10, which were the only races identified from Washington (area 8). Race groups B–, D–, and L– individually were less than 3% of all isolates identified. The D– phenotype comprised over 50% of the isolates in New York and Michigan, and the L– phenotype was only identified from nursery collections made in Virginia.

Table 2 summarizes the frequencies of virulence to each of the 14 differential lines among collections from the eight agroecological areas. Because of variation in greenhouse environment, temperature-sensitive genes *Lr*3ka, 11, 17, and 18 may have been occasionally misclassified. Incidence of virulence on lines with *Lr*24 increased from 17% in 1989 and 1990 (10) to 28% in 1991. Most of the increased virulence to *Lr*24 occurred in areas 4, 5, and 6. Virulence to *Lr*26 increased from 14% in 1989 and 1990 to 20% in 1991 (Table 2). Cultivars with *Lr*24 are widely grown in the southern Great Plains (17). Combined virulence to *Lr*24 and *Lr*26 was found in KF–,

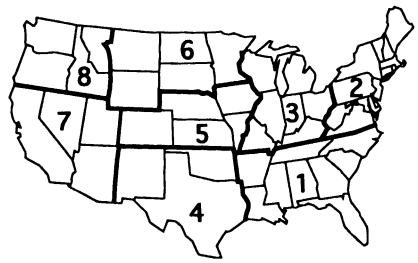

Fig. 1. Agroecological areas for *Puccinia recondita* f. sp. *tritici* in the United States. Area 1 = mainly southern-adapted soft red winter wheats; areas 2 and 3 = mostly northern-adapted soft red and white winter wheats that appear to be epidemiologically separated by geographic features; area 4 =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

MF–, and TF– phenotypes. The cultivar Siouxland has *Lr*24 and *Lr*26 (24) and is grown from central Texas to South Dakota; 90% of the isolates identified from 11 Siouxland collections had virulence to *Lr*24 and *Lr*26.

Virulence to *Lr*11 was identified in 22 virulence combinations in 1991, the same as in 1990 but 13 more than in 1989. This reflects a selective advantage of this virulence due to an increase in the acreage of cultivars with *Lr*11 (23). Phenotypes virulent to *Lr*11 were the most common in the K–, M–, and T– race groups.

Virulence to *Lr*9 was identified in 6.1% of the nationwide population in 1990 and 4.8% of the population in 1991. Coker 9766 (*Lr*2a and *Lr*9 resistance) is grown in area 1 (D. L. Long, *unpublished*), where *Lr*9 virulence was found in 13.5% of the collections in 1990 (10) and 10.4% of the collections in 1991.

Virulence to *Lr*16 has decreased from 17% in 1986 to 0.3% in 1991 in the U.S. population. In Texas, the mean percentage of isolates virulent to *Lr*16 averaged 18% from 1985 to 1987 (16) but only 1% from 1988 to 1990 (17) and none in 1991. This is primarily because ProBrand 816 is no longer grown in central Texas. In Canada, virulence to *Lr*16 occurred in 6% of the isolates in

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 1991

	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	N	N
BBD	–	–	–	–	–	–	1	–	–	–	–	–	–	–
BBG	–	–	–	–	5	–	–	–	–	–	–	–	–	–
CBB-10	–	–	–	–	3	–	–	–	–	–	–	–	–	–
CBG	–	3	–	–	–	–	–	1	–	–	–	–	–	–
CBM-10	–	–	–	–	5	–	–	–	–	–	–	–	–	–
CCB-10	–	–	–	–	–	–	–	–	–	–	–	–	100	–
CCG	–	–	–	–	–	1	–	–	–	–	–	–	–	–
DBB-18	–	–	–	7	3	–	–	–	–	–	–	–	–	–
DBB-10	–	1	–	–	5	–	–	–	–	–	–	–	–	–
DBB-10, 18	–	–	11	4	–	–	–	–	–	–	–	–	–	–
FBB-10	–	–	–	–	–	1	–	–	–	–	–	–	–	–
FBM-18	–	–	–	–	5	3	–	–	–	–	–	–	–	–
FBM-10, 18	–	1	–	–	–	–	–	1	–	–	–	2	–	–
FBR-18	–	–	–	–	–	3	–	–	–	–	–	–	–	–
FLM		–	–	–	5	–	–	–	–	–	–	–	–	–
KBB-10	–	–	–	–	–	–	–	–	–	5	–	–	–	–
KBG-10	–	1	–	–	–	1	5	8	–	3	23	22	–	–
KCG-10	–	1	–	–	–	–	–	–	–	3	–	–	–	–
KDG-10	–	–	–	–	–	–	3	–	–	–	–	–	–	–
KFB-10	–	–	–	–	3	–	6	4	–	–	–	2	–	–
LBB	–	–	–	7	–	–	–	–	–	–	–	–	–	–
LCB-10, 18	–	–	–	19	–	–	–	–	–	–	–	–	–	–
MBB	–	1	–	–	5	–	–	–	–	–	–	–	–	–
MBB-10	–	1	–	–	–	–	–	–	–	–	–	3	–	–
MBG	–	12	6	–	5	20	–	–	–	–	–	–	–	–
MBG-10	50	43	11	19	24	38	1	3	16	13	3	3	–	–
MCG	–	–	–	–	–	1	–	–	–	–	–	–	–	–
MCG-10	–	1	–	7	–	6	–	–	–	–	–	–	–	–
MDB-10	50	1	–	–	–	–	24	17	16	24	13	7	–	–
MDG-10	–	–	–	–	–	–	–	–	–	5	3	–	–	–
MFB	–	–	–	–	–	3	–	–	–	–	–	–	–	–
MFB-10	–	8	–	4	–	3	17	33	22	5	13	14	–	–
NBB-18	–	–	–	4	3	–	–	–	–	–	–	–	–	–
NBB-10	–	–	–	4	–	–	–	–	–	–	–	–	–	–
NBD-10, 18	–	–	–	–	–	–	–	–	–	–	–	–	–	60
NBG-10, 18	–	1	–	–	–	–	–	–	–	–	–	–	–	–
PBG-10	–	–	–	–	–	3	–	–	–	–	–	–	–	–
PBJ-10	–	–	–	–	–	–	–	–	–	–	–	–	–	40
PBL-10	–	–	–	–	13	–	–	–	–	–	–	–	–	–
PBM-18	–	–	28	–	3	1	–	–	–	–	–	–	–	–
PBR-18	–	–	33	–	–	–	–	–	–	–	–	–	–	–
PLM-10	–	3	11	–	5	10	–	–	–	–	–	–	–	–
PLM-10, 18	–	1	–	–	–	1	–	–	–	–	–	–	–	–
PLR-10, 18	–	–	–	19	–	1	–	–	–	–	–	–	–	–
TBB-10	–	2	–	4	–	–	13	4	7	3	5	–	–	–
TBG-10	–	11	–	–	3	–	22	19	31	29	28	37	–	–
TBJ-10, 18	–	1	–	–	–	–	–	–	–	–	–	–	–	–
TCB-18	–	1	–	–	–	–	–	–	–	–	–	–	–	–
TCB-10	–	–	–	–	–	–	1	3	–	–	3	–	–	–
TDB-10	–	1	–	–	–	–	1	4	7	3	–	5	–	–
TDJ-10, 18	–	–	–	–	–	–	–	–	–	–	5	–	–	–
TFB-10	–	1	–	–	–	–	4	1	2	8	3	3	–	–
TFG-10	–	–	–	–	–	1	1	–	–	–	3	–	–	–
TGB-10	–	–	–	–	3	1	–	–	–	–	–	–	–	–
TLG-18	–	3	–	4	3	–	–	–	–	–	–	2	–	–
No. of isolates	2	153	18	27	38	71	78	72	45	38	39	59	2	5

[y] Prt code (8) plus *Lr*10 and *Lr*18 isogenic supplementals.
[z] See Figure 1.

1987 (3) but was not found in 1989 (4). Columbus and Kenyon, grown in this area, have *Lr*16 in combination with *Lr*13, and both are currently resistant to leaf rust.

Among the bulked collections, no virulence was found to 13 resistant series entries: Thatcher isolines *Lr*19, 21, and 29; Aepoglom; Anex; Araphoe; AZ-FH 50-4-1-1-1; AZ-FH 51-2-2-1; Buck Manantial; Ceruga 1 and 3; CI 17906; and Stoa.

The levels of phenotypic diversity found within field collections were generally similar to those found in the previous survey (7). Shannon indexes were mostly in the range of 2.0–2.6, as in 1988–1990 (7). The greatest differences from the previous survey were for area 1, partly because of the few isolates and low diversity in 1991, and for area 2, which had Shannon indexes of 2.6 in 1988–1990 and only 1.62 in 1991 (Table 3). The cause of reduced diversity in field collections from area 2 in 1991 was not obvious. Yield losses to leaf rust in states in area 2 ranged from trace to 1% annually from 1988 to 1991 (D. L. Long, *unpublished*), and the numbers of isolates obtained from fields in area 2 were 19, 34, 22, and 18 for 1988, 1989, 1990, and 1991, respectively (10) (Table 2).

Collections from nurseries in 1991 in areas 1 and 2 were significantly more diverse (higher Shannon indexes) than those from corresponding field collections (Table 3), as in the 1988–1990 surveys. For area 3, the 1991 collections from fields were more diverse than those from nurseries. This is similar to results of the 1988–1990 surveys in which diversity in field collections from area 3 appeared slightly, although not significantly, greater than that in nursery collections. In 1991, there were no significant differences in diversity between field and nursery collections in areas 4, 5, and 6 of the Great Plains. In the 1988–1990 surveys, the nursery collections from area 6 were significantly more diverse than the field collections, whereas no significant differences were found between nursery and field collections in areas 4 and 5. The diversity of nursery collections relative to field collections appears to vary from area to area and from year to year. Kolmer (6) found that nursery collections in the Prairie Provinces of Canada had a significantly higher Shannon index than did field collections, indicating greater diversity, but Rogers' index between field and nursery collections was low, indicating that the common races were frequent in both sources of collections.

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 1988–1990 (7). The similarity of racial composition of collections from areas 4, 5, and 6 suggests that these areas constituted a single epidemiological zone in 1991. 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 1 and those from areas 2 and 3 suggests that area 1 has not contributed significantly to leaf rust development in areas 2 and 3. 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 the areas. Schafer and Long (22) reported evidence of overwintering of leaf rust in winter wheat

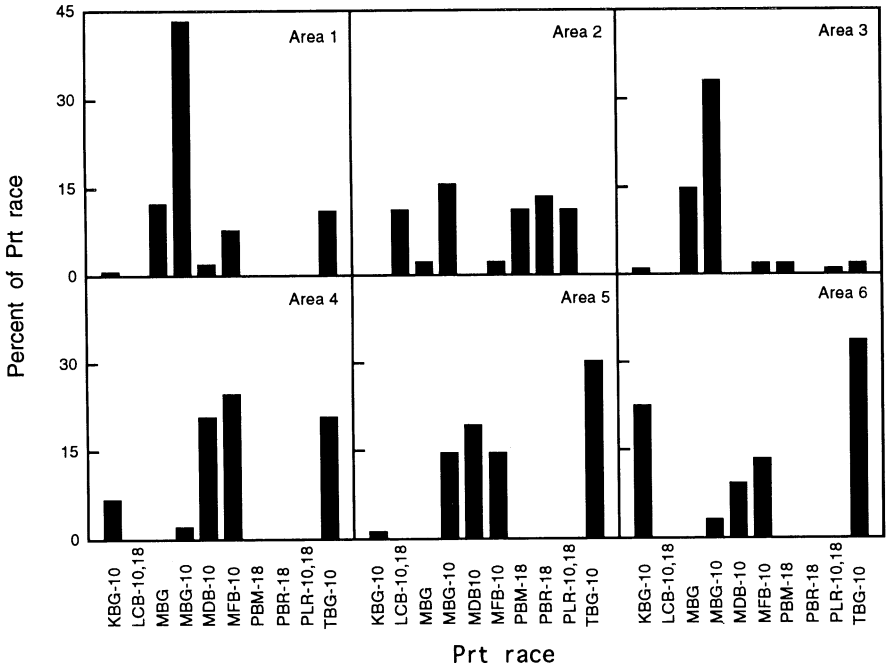

Fig. 2. Frequency of common races of *Puccinia recondita* f. sp. *tritici* among collections from areas 1–6 (Fig. 1) of the United States. Collections from fields and nurseries were combined, and races that occurred at >10% frequency in any area were included for the comparison.

Table 2. Percentage of *Puccinia recondita* f. sp. *tritici* isolates virulent to the single-gene differential lines used in the 1991 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	2	100	0	0	100	0	0	100	50	0	0	0	50	0	0
	Nursery	153	93	22	29	99	5	6	79	77	0	1	8	11	12	5
2	Field	18	89	0	83	89	72	11	33	50	0	0	72	0	0	72
	Nursery	27	89	7	44	56	18	22	78	48	0	0	56	4	30	18
3	Field	38	66	10	53	81	37	13	63	39	3	0	16	3	3	24
	Nursery	71	90	4	28	100	20	13	68	76	1	0	10	7	15	20
4	Field	78	85	56	56	99	0	0	99	32	0	1	0	56	29	0
	Nursery	72	85	44	46	100	1	0	99	32	0	0	1	60	42	1
5	Field	45	100	47	47	100	0	0	100	47	0	0	0	47	24	0
	Nursery	38	89	53	53	100	0	0	100	53	0	0	0	45	16	0
6	Field	39	77	69	69	100	0	0	100	64	0	5	5	38	20	0
	Nursery	59	74	71	73	100	2	2	98	64	0	0	3	31	19	2
7	Nursery	2	0	0	0	100	0	0	100	0	0	0	0	0	100	0
8	Nursery	5	100	0	100	40	0	0	100	40	0	100	60	0	0	0

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

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 main difference is that nursery collections from the Southeast (area 1) and Ohio Valley (area 3) were quite similar, whereas the field collections were distinct. This same similarity of nursery collections in areas 1 and 3 was also found in the 1988–1990 surveys (7).

The reason for the similarity of nursery but not field populations of *P. r. tritici* in areas 1 and 3 is unclear, but other evidence shows that field and nursery collections within the same area can differ substantially. Rogers' indexes for nursery × field population comparisons were 0.56, 0.85, and 0.60 for areas 1, 2, and 3, respectively. This means that in terms of racial composition, field collections showed little similarity to nursery collections from the same agroecological area when those collections were made in areas east of the Mississippi River. On the other hand, Rogers' index values for nursery × field population comparisons in the Great Plains were 0.28, 0.30, and 0.25 for areas 4, 5, and 6, respectively. These values are of the same magnitude as those for comparisons among field populations in areas 4, 5, and 6, which form a single epidemiological zone. Apparently, because of the more localized increase of leaf rust in the East, nursery collections in areas 1, 2, and 3 are less representative of overall field populations than are the nursery collections in the Great Plains. Perhaps the epidemiological zones in the East are much smaller than the agroecological areas shown in Figure 1.

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). Virulence frequencies of field collections in areas 1 and 3 showed some similarity, although not as much as in the 1988–1990 surveys (7). Virulence frequencies in nursery collections showed a close similarity between areas 1 and 3 in 1988–1990 and 1991. Virulence frequencies in field collections in area 2 were distinct from those of other areas in 1991, although the nursery collections in area 2 showed some similarity to those of areas 1 and 3 and, to a lesser extent, areas 4, 5, and 6.

All collections from areas 7 and 8 in 1991 came from nurseries. These collections differed from those of all other areas both in racial composition and in virulence frequencies (Figs. 3 and 4). The distinctiveness of collections in areas 7 and 8 was even more pronounced in 1991 than in the 1988–1990 surveys.

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 populations of the pathogen are much more discrete, as would be expected from localized overwintering and localized outbreak of epidemics.

Table 3. Shannon index of diversity for collections of *Puccinia recondita* f. sp. *tritici* from six agroecological areas of the United States in 1991

Area[x]	Shannon index[y] Field	Nursery	Significance[z]
3	2.61 a	2.12 ab	<0.05
4	2.06 b	1.96 ab	NS
6	2.00 bc	1.86 b	NS
5	1.72 cd	2.02 ab	NS
2	1.62 d	2.25 a	<0.05
1	0.68 e	2.15 ab	<0.05

[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 (19).
[z] Significance of the differences between values for field and nursery collections within the same area. NS = not significant.

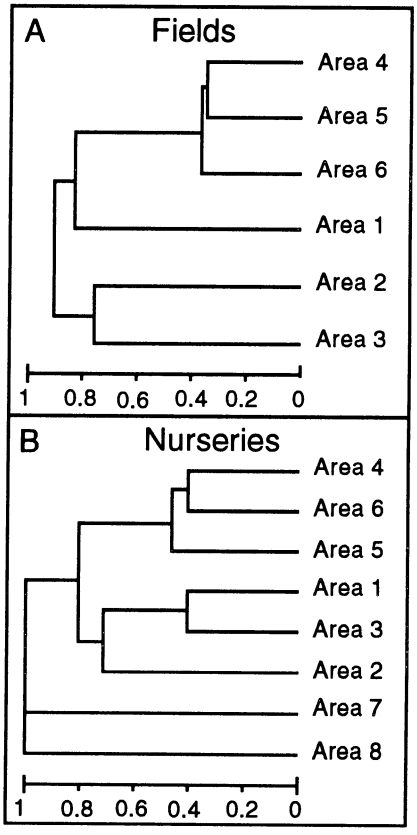

Fig. 3. Phenogram of similarities of racial compositions based on Rogers' index for collections of *Puccinia recondita* f. sp. *tritici* isolates in 1991 from **(A)** fields in areas 1–6 and **(B)** nurseries in areas 1–8 (Fig. 1). All isolates from areas 7 and 8 were collected in nurseries.

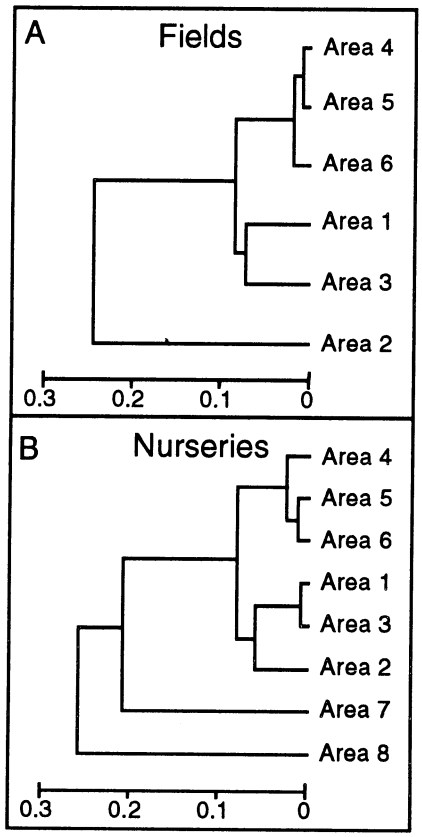

Fig. 4. Phenogram of similarities of racial compositions based on an adaptation of Nei's standard genetic distance between collections of *Puccinia recondita* f. sp. *tritici* in 1991 from **(A)** fields in areas 1–6 and **(B)** nurseries in areas 1–8 (Fig. 1). All isolates from areas 7 and 8 were collected in nurseries.

ACKNOWLEDGMENTS

We thank Shawn Eliason and Shawna Spindler for their technical assistance.

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