Physiologic Specialization of *Puccinia triticina* on Wheat in the United States in 2001

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ABSTRACT

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Collections of *Puccinia triticina* were obtained from rust-infected wheat leaves by cooperators throughout the United States and from surveys of wheat fields and nurseries in the Great Plains, Ohio Valley, Gulf Coast, California, Pacific Northwest, and Atlantic Coast States in order to determine the virulence of the wheat leaf rust fungus in 2001. Single uredinial isolates (477 in total) were derived from the wheat leaf rust collections and tested for virulence phenotype on lines of Thatcher wheat that are near-isogenic for leaf rust resistance genes *Lr1, Lr2a, Lr2c, Lr3, Lr9, Lr16, Lr24, Lr26, Lr3ka, Lr11, Lr17, Lr30, LrB, Lr10, Lr14a,* and *Lr18*. The isolates also were tested for virulence on adult plants with leaf rust resistance genes *Lr12, Lr13, Lr22a, Lr22b, Lr34, Lr35,* and *Lr37*. In the United States in 2001, 44 virulence phenotypes of *P. triticina* were found. Virulence phenotype MBDS, which is virulent to resistance gene *Lr17*, was the most common phenotype in the United States. MBDS was found in the Southeast, Great Plains, and Ohio Valley regions. Virulence phenotype THBJ, which is virulent to *Lr16* and *Lr26*, was the second most common phenotype, and occurred almost exclusively in the north-central Great Plains region. Phenotype MCDS, which is virulent to *Lr17* and *Lr26*, was the third most common phenotype and was found primarily in the Southeast, Ohio Valley, and Great Plains regions. The Southeast and Ohio Valley regions differed from the Great Plains region for predominant virulence phenotypes, which indicate that populations of *P. triticina* in those areas are not closely connected. The northern and southern areas of the Great Plains region differed for phenotypes with virulence to *Lr16*; however, the two areas had other phenotypes in common. Virulence to the adult plant resistance genes *Lr35* and *Lr37* was detected for the first time in North America in the MBDS, MCJS, and MCDS phenotypes.

Additional keywords: epidemiology, *Puccinia recondita* f. sp. *tritici*, specific virulence, wheat leaf rust

Wheat leaf rust, caused by the fungus *Puccinia triticina* Eriks., occurs wherever wheat is grown in the United States. Leaf rust is the most widespread and regularly occurring disease of wheat in North America and worldwide. The use of wheat cultivars with genetic resistance to leaf rust is the most practical method of controlling this disease. Effective leaf rust resistance in wheat cultivars is dependent on the virulence of the regional populations of *P. triticina*. The use of wheat cultivars with specific leaf rust resistance genes selects for phenotypes of *P. triticina* that have virulence to the resistance gene. Although over 45 leaf rust resistance genes have been described (21), many of the genes do not condition effective resistance because races of *P. triticina* with virulence to the genes are common. Distinct regional populations of *P. triticina* have evolved in North America due to the use of different leaf rust resistance genes in the different wheat classes that are grown across the continent (1,2,16).

Wheat leaf rust virulence surveys have been conducted by the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) Cereal Disease Laboratory, formerly known as the Cereal Rust Laboratory, since 1978 to detect new virulence phenotypes and to monitor shifts of virulence phenotypes in the major wheat-growing regions of the United States (15–17). Similar surveys have been done in Canada since 1931 (2,3,7,8,10) and in Mexico (26). In the United States (12) and Canada (3,4), data from leaf rust surveys have been used to characterize virulence, race dynamics, and phenotypic diversity within and between wheat-growing regions.

The objectives of this study were to characterize the virulence of populations of *P. triticina* in the United States in 2001 to the North American wheat leaf rust differentials (14) and to compare these results with those of previous surveys.

MATERIALS AND METHODS

Collections and virulence identification. Uredinial collections of leaf rust were made from wheat in annual surveys of the Great Plains, Ohio Valley, Gulf Coast, and southeastern states, and by cooperators throughout the United States. In 2001, field surveys of wheat were made in southern and central Georgia (late March through May); northern Texas and south-central Oklahoma (late April); southeastern Gulf Coast (mid-April to early May); southeastern states (late April to early May); Oklahoma and Kansas (mid-May); the Ohio River Valley (early June); north-central Kansas, Nebraska, western Iowa, South Dakota, and southern Minnesota (mid-June), and northern Plains states (early July and again in late July). Visual inspections for the presence of rust were made in commercial fields (4 to 50 ha in size) every 32 km or in the first field thereafter. Additional collections were made in wheat-breeding nurseries, trap plots, and demonstration plots along the route. Nurseries typically contain a wide array of leaf rust resistance genotypes, including breeding lines with leaf rust resistance genes not yet in commercial cultivars. Trap plots usually contain older cultivars of wheat no longer prominent in commercial production. A collection consisted of one to several leaves with uredinia from a single plant or cultivar. The leaves were air dried and stored at 4°C until spores were collected for inoculations. Collections from inoculated nurseries were not included in the study.

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 at approximately 0.01 g (dissolved in 30 ml of H_2O) per pot to enhance spore production. Plants were sprayed at a rate of approximately 0.5 ml per pot of 10 to 20 seedlings with a suspension of spores in Soltrol 170 (Phillips Petroleum, Bartlesville, OK) mineral oil. Inoculated plants were placed in a dew chamber overnight at 18°C. The plants then were transferred to a greenhouse where temperatures varied

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between 18 and 28°C daily under at least 8 h of natural light. After 12 to 15 days, three seedlings were saved per collection, each with the primary leaf trimmed to isolate a single uredinium. After 6 to 9 days, a cyclone spore collector was used to collect urediniospores separately from one to three single uredinia per collection. If the single uredinia were small and few spores were collected, the isolates were increased through one uredinial generation on seedlings of Thatcher before inoculating differential lines. Otherwise, spores from the single uredinia mixed with 0.5 ml of oil were directly inoculated by atomization onto 7- to 8-day-old plants of the differential host series (five to seven plants per line) of near-isogenic lines of Thatcher wheat with single resistance genes *Lr1*, *Lr2a*, *Lr2c*, *Lr3*, *Lr3ka*, *Lr9*, *Lr10*, *Lr11*, *Lr14a, Lr16*, *Lr17*, *Lr18*, *Lr24*, *Lr26*, *Lr30*, and *LrB*. Wheat lines with genes *Lr1, Lr2a, Lr2c, Lr3,* and *Lr11* were also in the early wheat leaf rust differential sets that were used in the United States and Canada from the 1930s to 1960s (2). The 16 differential lines in the current set detect most of the virulence diversity of *P. triticina* in North America. Sets of differential lines grown during June through September received no supplemental light. From October through May, natural daylight was supplemented with high-pressure sodium lamps from 0700 to 2300 (400 to 450 μE m^{-2} s^{-1} at bench level). After 10 to 14 days, infection types (IT) were recorded as either high (IT 3 to 4) or low (IT 0 to 2^+) as in previous surveys (15–19). Race designations were assigned as described by Long and Kolmer (14). A four-letter code describes the low or high infection types of each isolate to the 16 differential lines. Each letter corresponds to the infection types of four differentials. The Thatcher lines with genes *Lr1, Lr2a, Lr2c,* and *Lr3* were the four lines in the first set of differentials; lines with genes *Lr9, Lr16, Lr24,* and *Lr26* were the second set of differentials; lines with genes *Lr3ka, Lr11, Lr17,* and *Lr30* were the third set of differentials; and lines with genes *LrB, Lr10, Lr14a,* and *Lr18* were the fourth set of differentials. The same fourth set of differentials has been used in surveys of *P. triticina* in Canada (7,10).

Race and virulence frequencies were determined for collections from eight agroecological geographic areas (Fig. 1): area 1, mainly southern-adapted soft red winter wheats; areas 2 and 3, mostly northern-adapted soft red and white winter wheat; area 4, mixed wheat types but primarily hard red winter; area 5, hard red winter wheat; area 6, mixed wheat types but primarily hard red spring and durum; area 7, spring wheats planted in late fall; and area 8, mixed wheat types but primarily soft white winter.

Virulence to adult plant resistance genes. A group of isolates chosen to be representative of the most common virulence phenotypes were evaluated for virulence to adult plants of the Thatcher lines with *Lr12, Lr13, Lr22a, Lr35,* and *Lr37*, and Thatcher which has *Lr22b*. Plants were seeded in 15 cm (6-in.) pots filled with black topsoil, with four or two plants in each pot. Two pots with six adult plants in total were used for each isolate that was tested. Plants were grown at 15 to 25°C with supplemental metal halide lighting for 8 to 12 h per day and were fertilized with 20-20-20 NPK as needed. The plants were trimmed to two tillers each. Flag leaves were inoculated by atomizing a suspension of 1 to 2 mg of urediniospores from a single isolate of *P. triticina* in 350 μl of oil. Plants were placed in a dew chamber overnight after inoculation; removed from the chamber, and placed on a greenhouse bench under light. Fourteen days after inoculation, flag leaves were evaluated for IT using the same scale as for the seedling virulence tests.

Diversity measurements. The normalized Shannon index (24,25) of diversity calculated as $Sh(A) = -\Sigma p_i \ln(p_i)/\ln(n)$, where p_i = frequency of the ith virulence phenotype and n = total number of isolates in population A, was used to estimate diversity of virulence phenotypes of *P. triticina* in areas 1 to 7. The isolates in area 8 were not included in the diversity analysis due to the low sample size. The Kosman index of diversity (11), calculated as $KW(A) = Ass_{max}(A,A)/nk$, where Ass_{max} = the maximum value of the sum of distances between n matched pairs of isolates within a population A; n = total number of isolates in A; and k = number of differentials, also was used to estimate diversity within populations in areas 1 to 7. Both the normalized Shannon index and the Kosman index of diversity range from 0 to 1. The normalized Shannon index can be represented as a product of the evenness parameter $-\Sigma p_i \ln(p_i)/\ln(N)$ and the richness parameter $\ln(N)/\ln(n)$, where N is the total number of virulence phenotypes. Therefore, the normalized Shannon index accounts for the number and richness of virulence phenotypes and how evenly distributed they are in the population, without regard to their similarities in virulence. The Kosman index has some of the properties of the Shannon index and also takes into account the degree of similarity among isolates as a property of diversity. The Shannon and Kosman indexes were calculated using the bootstrap method with sample sizes set to 100 with replacement, by the KOIND program written by E. Kosman (23).

The Rogers' index of phenotypic distance (22), calculated as $R(A,B) = 0.5 \Sigma |p_{Ai} - p_{Bi}|$ in which p_{Ai} and p_{Bi} are the frequencies of the ith phenotype in populations A and B, respectively, was used to estimate the degree of phenotypic distance between the populations of *P. triticina* in areas 1 to 7. The Rogers' index measures the difference between two populations with regard to frequencies of identical phenotypes. The Kosman distance between populations A and B is determined as $KB(A,B) = Ass_{min}(A,B)/nk$ where Ass_{min} = the minimum value of the sum of distances between n matched pairs of an equal number of isolates from populations A and B; and k = number of differentials. The Kosman index takes into account the similarities in virulences between isolates in the two populations that are being compared. The Rogers' and Kosman distances also were calculated with the bootstrap procedure of the KOIND program (23) that generated random samples of 100 isolates based on the original data. Kosman (11) provides a more detailed description of the Kosman indexes of diversity and distance

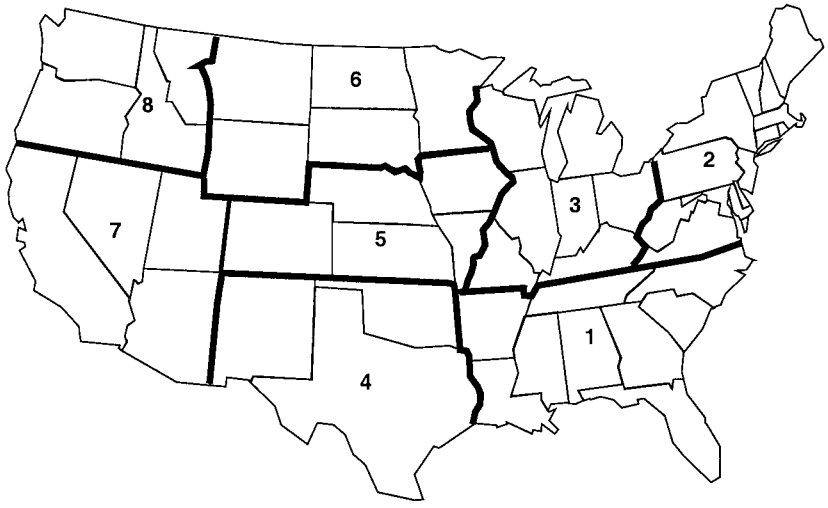

Fig. 1. Agroecological areas for *Puccinia triticina* in the United States. Winter wheat is grown in areas 1 to 5 and 8; spring wheat is grown in areas 6 and 7. Hard red winter wheat cultivars are grown in areas 4 to 6, soft red or white cultivars in areas 1 to 3, and mainly soft white cultivars in area 8. See text for greater details.

and how these compare with the Shannon and Rogers' indexes.

RESULTS

Incidence and severity of leaf rust. In the third week of March, trace amounts of leaf rust were observed on wheat cultivars and lines in southern Texas. By late April, leaf rust was severe on susceptible lines and cultivars in southern Texas, but was at light levels in fields in central Texas. In mid-May, 40% severities of leaf rust were reported on flag leaves of susceptible cultivars in northern Texas and southern Oklahoma. In late May, leaf rust was observed on *Aegilops cylindrica* L. (goat grass) growing along roadsides in Oklahoma. Throughout Texas and Oklahoma, temperatures in late winter and spring were much lower than normal, which delayed and reduced the development of leaf rust.

In the Gulf Coast of Georgia, Alabama, and Louisiana, trace levels of leaf rust were found in mid-April. Colder than normal winter temperatures greatly reduced the amount of leaf rust that overwintered in the southeastern states. In late April, leaf rust was light in plots in southern and central Georgia and Alabama. In early May, light leaf rust was found in fields in eastern Arkansas and South Carolina. In the third week of May, rust severities were 20% in plots of susceptible wheat in eastern North Carolina. Leaf rust incidence and severity was very light in the southeastern United States in 2002 compared with previous years.

In southern Kansas, traces of leaf rust were found in early May. In the last week of May, leaf rust was light in plots and only traces were found in fields from west-central Kansas to west-central Missouri. Leaf rust severity on cv. Jagger reached 20%, which was much lower than in previous years. As in Texas and Oklahoma, lower than normal temperatures delayed and reduced leaf rust development throughout Kansas.

In the second week of June, leaf rust severities were a trace to 10% in plots of winter wheat from Missouri to Ohio. Cool temperatures in the last two weeks of May slowed the development of leaf rust in the Ohio Valley region. In the last week of June, in New York, rust severities were 5 to 20% in winter wheat fields at the late milk stage. In the second week of May, traces of leaf rust were found in fields in central California. In the last week of May, leaf rust severities were 60% on wheat throughout the Central Valley of California.

In mid-June, light leaf rust was observed on flag leaves of hard red winter wheats in the eastern Dakotas. By late June, leaf rust severities were 20% on winter wheat and a trace on spring wheat in southern Minnesota and eastern South Dakota. In late June, leaf rust severities were 40% in winter wheat in eastern North Dakota. By mid-July, rust severities were 10% on winter wheat at grain-filling stage in eastern South and North Dakota. In late June, traces of leaf rust were found in spring wheat in southern and eastern North Dakota. By mid-July, leaf rust severities were 40% on susceptible spring wheats in southern Minnesota and eastern South Dakota, and 10% on the commonly grown spring wheat cultivars. By the last week in July, leaf rust was found in nearly every field in North Dakota and Minnesota. Heavy leaf rust infections were found in plots and fields in central North Dakota. Many wheat fields in this area had leaf rust severities of over 50% at the late milk to soft dough stage, and flag leaves were starting to senesce due to leaf rust. A complete summary of the 2001 leaf rust epidemic in the United States and estimates of yield losses in wheat due to leaf rust can be found at the USDA-ARS Cereal Disease Laboratory website (13).

Distribution of virulence phenotypes. Forty-four virulence phenotypes of *P. triticina* were found in the United States in 2001 (Table 1). The single uredinial isolates (477 in total) of *P. triticina* derived from collections made in the United States were tested for virulence to the Thatcher near-isogenic lines (Table 2). The number of single uredinial isolates tested for virulence phenotype was lower compared with previous years due to the colder spring and summer temperatures in the winter wheat areas, which slowed the development of leaf rust infections. Infections of stripe rust (*P. striiformis* Westend.) in the Ohio Valley and southern and middle Great Plains also reduced the number of leaf rust collections. Phenotypes MBDS (24.9%), THBJ (18.6%), and MCDS (10.5%) were the three most common phenotypes in the United States in 2001.

In the southeastern states (area 1), 15 virulence phenotypes were found among the 96 isolates tested in 2001 (Table 2). Phenotypes MBRK and TLGJ accounted for 45.8% of the isolates. None of the other virulence phenotypes in area 1 occurred at greater than 10%. In the Northeastern states (area 2), seven virulence phenotypes were detected among the 14 isolates. Four of the isolates were phenotype MCRK, four phenotypes occurred twice, and two phenotypes occurred once. In the Ohio Valley states (area 3), 13 virulence phenotypes were found among the 31 isolates that were tested. Phenotype MCDS at 22.6% was the most common, followed by MBRJ at 12.9%. None of the other phenotypes occurred at greater than 10%.

In the southern and middle Great Plains states (areas 4 and 5), MBDS was the most common virulence phenotype at 58.3 and 70.2%, respectively (Table 2). In area 4, MCDS was the second most common phenotype at 29.2%. In area 5, no phenotype other than MBDS occurred at greater than 10%. In all, 8 and 10 virulence phenotypes were detected in areas 4 and 5, respectively. In the northern Great Plains region (area 6), THBJ was the most common phenotype at 53.1%, followed by MBDS at 14.8%. Twenty-three virulence phenotypes were detected in area 6. In California (area 7), four virulence phenotypes were detected among the 39 isolates tested. MBGJ was the most common phenotype in area 7 at 46.3%, followed by MCDS at 28.2% and MBDS at 15.4%. In Washington state (area 8), six isolates of phenotype MDBJ were detected.

Virulence frequencies. Frequencies of virulence differed among populations of *P. triticina* in 2001 (Table 3). Virulence to *Lr2a* ranged from 0 to 21.4% in areas 2, 3, 4, 5, 7, and 8, and was 51.0 and 69.8% in areas 1 and 6, respectively. Leaf rust

Table 1. Virulence phenotype designations and virulences for isolates of *Puccinia triticina* from the United States in 2001 identified on 16 near-isogenic lines of Thatcher wheat[a]

Virulence phenotype	Virulences (ineffective *Lr* genes)
BBBD	*14a*
CBBD	*3,14*
CLLM	*3,9,3ka,B,18*
FCMT	*2c,3,26,3ka,30,B,10,14a,18*
FGBJ	*2c,3,16,10,14a*
FLLL	*2c,3,9,3ka,B*
LBBG	*1,10*
MBBJ	*1,3,10,14a*
MBDS	*1,3,17,B,10,14a*
MBGJ	*1,3,11,10,14a*
MBJJ	*1,3,11,17,10,14a*
MBRJ	*1,3,3ka,11,30,10,14a*
MBRK	*1,3,3ka,11,30,10,14a,18*
MCDS	*1,3,26,17,B,10,14a*
MCRJ	*1,3,26,3ka,11,30,10,14a*
MCRK	*1,3,26,3ka,11,30,10,14a,18*
MCRS	*1,3,26,3ka,11,30,B,10,14a*
MDBG	*1,3,24,10*
MDBJ	*1,3,24,10,14a*
MDRJ	*1,3,24,3ka,11,30,10,14a*
MFBJ	*1,3,24,26,10,14a*
MGBJ	*1,3,16,10,14a*
NBGT	*1,2c,11,B,10,14a,18*
PCRQ	*1,2c,3,26,3ka,11,30,B,10*
PLMR	*1,2c,3,9,3ka,30,B,10,18*
PNMR	*1,2c,3,9,24,3ka,30,B,10,18*
TBBS	*1,2a,2c,3,B,10,14a*
TBRJ	*1,2a,2c,3,3ka,11,30,10,14a*
TCBJ	*1,2a,2c,3,26,10,14a*
TCJS	*1,2a,2c,3,26,11,17,B,10,14a*
TCRJ	*1,2a,2c,3,26,3ka,11,30,10,14a*
TDBJ	*1,2a,2c,3,24,10,14a*
TDDS	*1,2a,2c,3,24,17,B,10,14a*
TFBJ	*1,2a,2c,3,24,26,10,14a*
TGBJ	*1,2a,2c,3,16,10,14a*
THBJ	*1,2a,2c,3,16,26,10,14a*
TKBJ	*1,2a,2c,3,16,24,26,10,14a*
TLGF	*1,2a,2c,3,9,11,14a,18*
TLGJ	*1,2a,2c,3,9,11,10,14a*
TLGS	*1,2a,2c,3,9,11,B,10,14a*
TLHS	*1,2a,2c,3,9,11,30,B,10,14a*
TLRJ	*1,2a,2c,3,9,3ka,11,30,10,14a*
TNMJ	*1,2a,2c,3,9,24,3ka,30,10,14a*
TNRJ	*1,2a,2c,3,9,24,3ka,11,30,10,14a*

[a] Thatcher lines with leaf rust resistance genes *Lr1, Lr2a, Lr2c, Lr3, Lr9, Lr16, Lr24, Lr26, Lr3ka, Lr11, Lr17, Lr30, LrB, Lr10, Lr14a,* and *Lr18.*

Table 2. Number and frequency (%) of virulence phenotypes of *Puccinia triticina* in the United States in 2001 identified on 16 lines of Thatcher wheat near-isogenic for leaf rust resistance genes

	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8		Total	
Phenotype	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
BBBD	0	0	2	14.3	1	3.2	0	0	0	0	6	3.7	0	0	0	0	9	1.9
CBBD	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
CLLM	0	0	0	0	1	3.2	0	0	0	0	0	0	0	0	0	0	1	0.2
FCMT	1	1.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
FGBJ	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
FLLL	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
LBBG	2	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
MBBJ	1	1.0	0	0	0	0	1	1.4	0	0	0	0	0	0	0	0	2	0.4
MBDS	4	4.2	0	0	3	9.7	42	58.3	40	70.2	24	14.8	6	15.4	0	0	119	24.9
MBGJ	0	0	2	14.3	3	9.7	0	0	0	0	2	1.2	18	46.2	0	0	25	5.2
MBJJ	0	0	0	0	0	0	0	0	0	0	0	0	4	10.3	0	0	4	0.8
MBRJ	8	8.3	2	14.3	4	12.9	0	0	1	1.8	0	0	0	0	0	0	15	3.1
MBRK	27	28.1	0	0	0	0	0	0	1	1.8	0	0	0	0	0	0	28	5.9
MCDS	3	3.1	0	0	7	22.6	21	29.2	3	5.3	5	3.1	11	28.2	0	0	50	10.5
MCRJ	0	0	0	0	0	0	2	2.8	0	0	0	0	0	0	0	0	2	0.4
MCRK	1	1.0	4	28.6	3	9.7	0	0	1	1.8	2	1.2	0	0	0	0	11	2.3
MCRS	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
MDBG	0	0	1	7.1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
MDBJ	0	0	0	0	1	3.2	0	0	0	0	0	0	0	0	6	100.0	7	1.5
MDRJ	0	0	0	0	0	0	2	2.8	1	1.8	1	0.6	0	0	0	0	4	0.8
MFBJ	0	0	0	0	0	0	0	0	2	3.5	0	0	0	0	0	0	2	0.4
MGBJ	0	0	0	0	0	0	1	1.4	1	1.8	3	1.9	0	0	0	0	5	1.0
NBGT	0	0	0	0	1	3.2	0	0	0	0	0	0	0	0	0	0	1	0.2
PCRQ	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
PLMR	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
PNMR	0	0	0	0	1	3.2	0	0	0	0	0	0	0	0	0	0	1	0.2
TBBS	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
TBRJ	5	5.2	0	0	0	0	0	0	4	7.0	0	0	0	0	0	0	9	1.9
TCBJ	0	0	0	0	3	9.7	0	0	0	0	4	2.5	0	0	0	0	7	1.5
TCJS	0	0	0	0	0	0	0	0	0	0	4	2.5	0	0	0	0	4	0.8
TCRJ	0	0	0	0	1	3.2	0	0	0	0	4	2.5	0	0	0	0	5	1.0
TDBJ	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	1	0.2
TDDS	0	0	0	0	0	0	0	0	2	3.5	0	0	0	0	0	0	2	0.4
TFBJ	0	0	0	0	0	0	2	2.8	0	0	8	4.9	0	0	0	0	10	2.1
TGBJ	0	0	0	0	0	0	0	0	0	0	2	1.2	0	0	0	0	2	0.4
THBJ	0	0	0	0	0	0	0	0	0	0	86	53.1	0	0	0	0	86	18.6
TKBJ	0	0	0	0	0	0	0	0	0	0	1	0.6	0	0	0	0	2	0.4
TLGF	8	8.3	2	14.3	0	0	0	0	0	0	0	0	0	0	0	0	10	2.1
TLGJ	17	17.7	0	0	0	0	1	1.4	0	0	2	1.2	0	0	0	0	22	4.6
TLGS	5	5.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1.0
TLHS	6	6.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1.3
TLRJ	2	2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
TNMJ	4	4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.8
TNRJ	0	0	1	7.1	2	6.5	0	0	0	0	0	0	0	0	0	0	3	0.6
Total	96	…	14	…	31	…	72	…	57	…	162	…	39	…	6	…	477	…

Table 3. Number and frequency (%) of isolates of *Puccinia triticina* in the United States in 2001 virulent on 16 lines of Thatcher wheat near-isogenic for leaf rust resistance

	Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8		Total	
Gene	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
Lr1	95	99.0	12	85.7	29	93.5	72	100.0	57	100.0	153	94.4	39	100.0	6	100.0	463	97.1
Lr2a	49	51.0	3	21.4	6	19.4	3	4.2	7	12.3	113	69.8	0	0	0	0	181	37.9
Lr2c	50	52.1	3	21.4	8	25.8	3	4.2	7	12.3	117	72.2	0	0	0	0	188	39.4
Lr3	94	97.9	12	85.7	29	93.5	72	100.0	57	100.0	156	96.3	39	100.0	6	100.0	465	97.5
Lr9	44	45.8	3	21.4	4	12.9	1	1.4	0	0	4	2.5	0	0	0	0	56	11.7
Lr16	0	0	0	0	0	0	1	1.4	2	3.5	93	57.4	0	0	0	0	96	20.1
Lr24	4	4.2	2	14.3	4	12.9	4	5.6	6	10.5	11	6.8	0	0	6	100.0	37	7.8
Lr26	5	5.2	4	28.6	14	45.2	25	34.7	7	12.3	116	71.6	11	28.2	0	0	182	38.2
Lr3ka	48	50.0	7	50.0	12	38.7	4	5.6	8	14.0	11	6.8	0	0	0	0	90	18.9
Lr11	81	84.4	11	78.6	14	45.2	5	6.9	8	14.0	17	10.5	22	56.4	0	0	158	33.1
Lr17	7	7.3	0	0	10	32.3	63	87.5	45	78.9	33	20.4	21	53.8	0	0	179	37.5
Lr30	54	56.3	7	50.0	11	35.5	4	5.6	8	14.0	10	6.2	0	0	0	0	94	19.7
LrB	19	19.8	0	0	13	41.9	63	87.5	45	78.9	38	23.5	17	43.6	0	0	195	40.9
Lr10	88	91.7	10	71.4	29	93.5	72	100.0	57	100.0	154	95.1	39	100.0	6	100.0	455	95.4
Lr14a	94	97.9	13	92.9	29	93.5	72	100.0	57	100.0	159	98.1	39	100.0	6	100.0	469	98.3
Lr18	37	38.5	6	42.9	6	19.4	0	0	2	3.5	3	1.9	0	0	0	0	54	11.3
Total	96	…	14	…	31	…	72	…	57	…	162	…	39	…	6	…	477	…

resistance gene *Lr2a* is found in the soft red winter wheats grown in area 1 and the hard red spring wheats in area 6. Virulence to *Lr2c* is highly associated with virulence to *Lr2a*. Virulence frequencies to *Lr2c* were higher than *Lr2a* in areas 1, 3, and 6, and were the same in the other regions. Virulence to *Lr9* ranged from 0 to 2.5% in areas 4, 5, 6, 7, and 8, and was 45.8, 21.4, and 12.9% in areas 1, 2, and 3, respectively. *Lr9* is common in the soft red winter wheat in areas 1, 2, and 3.

Virulence to *Lr16* was less than 4.0% in all areas except area 6, where it occurred at 57.4%. *Lr16* is found in the hard red spring wheat grown in area 6. Virulence to *Lr24* was low in all areas (0 to 14.3%) except in area 8, where all six isolates had virulence to this gene. Virulence to *Lr26* was 0 and 5.2% in areas 1 and 8, respectively; between 12.3 and 45.2% in areas 2, 3, 4, 5, and 7; and 71.6% in area 6. *Lr26* is found in the winter wheat grown in areas 1, 3, 4, and 5. Virulence to *Lr3ka* was at 0 to 6.8% in areas 4, 6, 7, and 8; and at 14.0 to 50.0% in areas 1, 2, 3, and 5. Winter wheat cultivars with *Lr3ka* have been grown in areas 4 and 5. Virulence to *Lr30* is highly associated with virulence to *Lr3ka*. Virulence frequencies to *Lr30* were the same as virulence to *Lr3ka* in areas 2, 4, 5, 7, and 8. In area 1, virulence to *Lr30* was slightly higher than virulence to *Lr3ka,* and in areas 3 and 6 virulence to *Lr30* was slightly lower than virulence to *Lr3ka*.

Virulence to *Lr11* was less than 6.9% in areas 4 and 8; between 10.5 and 56.4% in areas 3, 5, 6, and 7; and at 78.6 and 84.4% in areas 2 and 1, respectively. Many soft red winter wheat cultivars in area 1, 2, and 3 have *Lr11*. Virulence to *Lr17* ranged from 0 to 7.3% in areas 1, 2, and 8; between 20.4 and 53.8% in areas 3, 6, and 7; and was at 87.5 and 78.9% in areas 4 and 5, respectively. The hard red winter wheat Jagger, which has been commonly grown in areas 4 and 5, has *Lr17*. Virulence to *LrB* was at 0% in areas 2 and 8; between 19.8 and 43.6% in areas 1, 3, 6, and 7; and at 87.5 and 78.9% in areas 4 and 5, respectively. Virulence to *LrB* almost always occurred in isolates that had virulence to *Lr17*. Virulence to *Lr18* was at 0 to 3.5% in areas 4, 5, 6, 7, and 8; and 19.4 to 42.9% in areas 1, 2, and 3. *Lr18* is present in some winter wheat cultivars grown in areas 1, 2, and 3. Virulences to genes *Lr1, Lr3, Lr10,* and *Lr14a*, were greater than 90% in all areas except in area 2, where virulences to these genes ranged from 71.4 to 92.9%.

Table 4. Shannon and Kosman measures of phenotypic diversity for *Puccinia triticina* in seven geographical areas of the United States in 2001

Area	Shannon	Kosman
1	0.458	0.397
2	0.396	0.411
3	0.485	0.425
4	0.249	0.124
5	0.241	0.161
6	0.417	0.314
7	0.124	0.199

Diversity of populations of *P. triticina*. The population of *P. triticina* in areas 3, 1, and 6 were the most diverse for phenotypic diversity with Shannon index with values of 0.485, 0.458, and 0.417, respectively, and the population in area 7 was the least diverse at 0.124 (Table 4). Using the Kosman index, populations in areas 3, 2, and 1 were the most diverse, while the population in area 4 was the least diverse. The populations also were compared for differences among virulence phenotypes using the Rogers and Kosman distance indexes (Table 5). Using the Rogers' index, populations in areas 2 and 4, and in areas 2 and 5 differed the most with indexes of 0.984 and 0.976, respectively. Populations of *P. triticina* in areas 4 and 5; and 3 and 7, differed the least with Rogers indexes of 0.355 and 0.569. Using the Kosman distance index, populations in areas 1 and 4, and 2 and 4, differed the most, with indexes of 0.390 and 0.323, respectively. Populations in areas 4 and 5, and 4 and 7, differed the least, with values of 0.060 and 0.107, respectively.

Virulence to adult plant resistance genes. Seventy-eight isolates, consisting of 43 virulence phenotypes, were evaluated to the Thatcher lines with adult plant resistance genes (Table 6). All isolates were virulent to Thatcher with the adult plant resistance gene *Lr22b*. Thirty-three isolates, consisting of 22 different virulence phenotypes, had low IT of ; to ;2 to Tc*Lr12*. Seventeen isolates, of 14 different virulence phenotypes, had low IT of ; to 22^{+} to Tc*Lr13*. All isolates had low IT of ;2^{-} or IT 23 to Tc*Lr22a*. All isolates had low IT of ; to 23 to Tc*Lr34*. Seven isolates of phenotype MBDS, one isolate of MCDS, and one isolate of MCJS had high IT of 3 to 3^{+} to Tc*Lr35*. Seven isolates of MBDS, two isolates of MCDS, and one isolate of MCJS had high IT of 3 to 3^{+} to Tc*Lr37*.

DISCUSSION

The virulence phenotypes of *P. triticina* in 2001 in the United States showed a strong regional distribution caused by the presence of different leaf rust resistance genes in the various wheat classes that are grown across the country. In the southeastern states of area 1, MBRK was the most common phenotype, followed by TLGJ. These phenotypes have been selected by cultivars with *Lr2a, Lr9*, *Lr10,* and *Lr11*, which are very common in the soft red winter wheat grown in area 1 (J. A. Kolmer, *unpublished data*). Phenotypes of *P. triticina* with virulence to *Lr9* occurred almost exclusively in areas 1, 2, and 3, where soft red wheat winter wheat cultivars are grown. Virulence to *Lr9* occurred in 13 virulence phenotypes in 2001. In area 6, the most common phenotype was THBJ, virulent to genes *Lr2a* and *Lr16*, which are present in commonly grown hard red spring wheat in the Dakotas and Minnesota. Virulence to *Lr16* occurred at low levels in areas 4 and 5, and did not occur in areas 1, 2, 3, or 7. It is possible that phenotypes with virulence to *Lr16* overwinter on wheat in Nebraska and South Dakota, where winter and spring wheat cultivars with *Lr16* are grown. Virulence to *Lr16* occurred in FGBJ, MGBJ, TGBJ, THBJ, and TKBJ phenotypes in 2001. Virulence to *Lr24* occurred at low levels throughout most of the United States, which may reflect a decrease in wheat cultivars with this leaf rust resistance gene. Cultivars with *Lr26* are grown in the soft red wheat of areas 1, 2, and 3, and also in the hard red winter wheat of areas 4 and 5. Virulence to *Lr26* occurred at low to moderate levels in areas 1, 2, 3, 4, and 5 in 2001. Virulence to *Lr26* was at a high level in area 6, because the phenotype THBJ, which is virulent to *Lr2a* and *Lr16*, is also virulent to *Lr26*. Selection for virulence to *Lr2a* and *Lr16* in area 6 also has increased the frequency of virulence to

Table 5. Rogers (top diagonal) and Kosman (lower diagonal) measures of distance between virulence phenotypes in populations of *Puccinia triticina* in seven areas of the United States in 2001[a]

Area	1	2	3	4	5	6	7
1	…	0.841	0.848	0.913	0.866	0.929	0.937
2	0.159	…	0.611	0.984	0.976	0.931	0.861
3	0.216	0.193	…	0.661	0.838	0.781	0.569
4	0.390	0.323	0.193	…	0.355	0.744	0.591
5	0.302	0.310	0.181	0.060	…	0.785	0.810
6	0.295	0.319	0.220	0.235	0.239	…	0.817
7	0.269	0.264	0.150	0.107	0.130	0.239	…

[a] Top diagonal are measures of distance using Rogers index of phenotypic distance, and bottom diagonal are measures of distance using Kosman index of phenotypic distance.

Table 6. Infection types of isolates of *Puccinia triticina* from the United States in 2001 on near-isogenic lines of Thatcher wheat with adult plant resistance genes[a]

Isolate, state	Tc(*Lr22b*)	Tc*Lr12*	Tc*Lr13*	Tc*Lr22a*	Tc*Lr34*	Tc*Lr35*	Tc*Lr37*
BBBD 225 IN	3	;1	;2	2⁻	;	;1	;
BBBD 261 ND	3	;1	;2⁻	;	;	;2⁻	;
BBBD 228 NY	3⁺	;1	;	;2⁻	23	;	;
CBBD 267 MT	3⁺	;2	3⁺	;2⁻	23	;	;
CLLM 225 IN	3⁺	3⁺	3⁺	2⁻	23	;	;
FGBJ 207 ND	3⁺	3	;1⁻	2⁻	23	;1⁻	;
FCRT 21 AL	3⁺	3⁺	;1	;2⁻	23	;	0;
LBBG 11 AL	3⁺	;1	3⁺	2⁻	23	;	;
NBGT 349 KY	3⁺	;1⁻	3⁺	2⁻	23	;	;
MBBJ 2B TX	4	4	3⁺	2	23⁺	;	;
MBDS 107 KS	3⁺4	4	3⁺4	2⁻	23⁺	3⁺	3⁺
MBDS 121 OK	3⁺	;1	3⁺	22⁻	23	3⁺	3⁺
MBDS 135 KS	3⁺	;1	3⁺	2⁻	23	3	3
MBDS 152 NE	3⁺	3⁺	4	2⁻	23⁺	33⁺	33⁺
MBDS 203 MN	3⁺	3⁺	3⁺	2⁻	23	3	3
MBDS 1B TX	33⁺	3⁺	3⁺	2	23⁺	3⁺	3
MBDS 238 ND	3⁺4	3⁺4	;	2⁻	23	33⁺	33⁺
MBDS 250 MT	4	;12⁻	3⁺	2⁻	23	;	;
MBGJ 286 MN	3⁺	3⁺	3⁺	2⁻	23	;	;
MBGJ 61 CA	3⁺	3⁺	;	2⁻	22⁺	0	0
MBJJ 70 CA	3⁺	3⁺	33⁺	2⁻	23	;	0;
MBRJ 168BVA	33⁺	;1	3⁺	2⁻	2	;	0
MBRJ 84 NC	3⁺	;12⁻	3⁺	2	23⁺	0;	0;
MBRK 31 GA	3⁺	3⁺	3⁺	2⁻	23⁺	;	;
MBRK 36 AL	3⁺	3⁺	3⁺4	2⁻	23	;	;
MBRK 217 IA	3⁺	2⁺3	3⁺	;1⁻	;	;	;
MCDS 102 OK	3⁺	;1	3⁺	2⁻	;23	;	3⁺
MCDS 1A TX	3⁺	3⁺	3⁺	2⁻	23⁺	3⁺	3⁺
MCDS 71 CA	3⁺	;	;	2⁻	23	0;	0;
MCGJ 172 IN	3⁺	;12⁻	33⁺	23	23	0	0
MCJS 175 OH	3⁺	3⁺	3⁺	3⁺	23	3⁺	3⁺
MCRJ 44 TX	3⁺	;1⁻	33⁺	2⁻	23	;	;
MCRJ 168AVA	3⁺	3⁺	3⁺	23	23	0	0
MCRR 217 IA	3⁺	3⁺	3⁺	;2⁻	;2	;2⁻	;
MCRK 18 VA	33⁺	;12⁻	33⁺	23	23	0;	0;
MCRK 21B AL	3⁺	3⁺	3⁺	;2⁻	23	;	;
MDBJ 221 WA	3	;1	3	2⁻	23	;2⁻	;
MDBJ 106 KS	4	;12⁻	;	2⁻	23⁺	;	;
MDRJ 136 NE	4	2⁺	3⁺	2⁻	;23	;	;
MDRJ 6 TX	4	;12⁻	22⁺	2⁻	23⁺	;	;
MGBJ 110 KS	3⁺	;1	3⁺	2⁻	;1⁻	;1	
MGBJ 2A TX	3⁺	4	4	2	23⁺	;	;
PCRK 151 GA	3⁺	3⁺	;1⁺	2⁻	23	;2⁻	;
PCRQ 255 ND	3	3⁺	3	2⁻	23	;	;
PLMR 273 ND	3⁺	3⁺	;1⁻	;2⁻	23	;	;
PNMR 349 KY	3⁺	3⁺	;1	;2⁻	;23	;	;
TBBJ 130 MO	3⁺	;12	33⁺	2⁻	23	;	;
TBBS 294 ND	3⁺	3⁺	3	2⁻	23	;1	;1
TBRJ 98 NC	3⁺	;2⁻	33⁺	;2⁻	23⁺	0;	0;
TCBJ 134 SD	3⁺	;1	3⁺	2⁻	23	;	;
TCBJ 176 MO	3⁺	3⁺	3⁺	2⁻	23	;	;
TCRJ 298 ND	3⁺	3⁺	3⁺	2⁻	23	;	;
TCRJ 101 AR	3⁺	;2	3⁺4	22⁻	23	;1	;1⁺
TDDJ 162 KS	3⁺	;1	;1	22⁻	23	;1	;
TDDS 162 KS	4	;12⁻	;12	;	23⁺	;	;
TFBJ 184 SD	3⁺	3⁺	3⁺	2⁻	23	;2⁻	;1⁻
TGBJ 269 MT	3⁺	3⁺	3⁺	2⁻	23	;1⁻	;1
TGBJ 265 ND	3	3⁺	3⁺	2⁻	;	;1⁻	;1
THBJ 215 ND	3⁺	;1	3⁺	2⁻	23	;	;
THBJ 235 ND	3⁺	3⁺	3⁺	;2⁻	23⁺	;	;
THBJ 239 SD	4	4	4	2⁻	23⁺	;	;
THBJ 251 ND	3⁺	3⁺	3⁺	2⁻	23	;	;
THBJ 288 ND	3⁺	3⁺	3⁺	2⁻	23	;	;
THBJ 364 ND	3⁺	3⁺	3	2⁻	;	;2⁻	2⁻
TKBJ 260 ND	3⁺	3⁺	3⁺	2⁻	;2	;2⁻	;2⁻
TLGF 25 AL	4	;12	3⁺	2	23	;	;
TLGJ 19 LA	4	;12⁻	3⁺	2⁻	23⁺	;	;

(*continued on next page*)

[a] Infection types: 0 = no flecks or uredinia, 0; = faint hypersensitive flecks, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 2 = small uredinia with chlorosis, 3 = moderate size uredinia, 4 = large uredinia, ⁺ indicates slightly larger uredinia, ⁻ indicates slightly smaller uredinia, infection types with two symbols denote a range in infection type (i.e., 22⁺ indicates a mixture of 2 size uredinia with chlorosis and slightly larger uredinia with chlorosis).

Table 6. (*continued from preceding page*)

Isolate, state	Tc(*Lr22b*)	Tc*Lr12*	Tc*Lr13*	Tc*Lr22a*	Tc*Lr34*	Tc*Lr35*	Tc*Lr37*
TLGJ 26 AL	3+	;1−	33+	2	23	;	;
TLGJ 30 GA	3+	3+	3+	2−	23	;	;
TLGJ 32 FL	3+	;1	3+	2−	23+	;	;
TLGJ 56 LA	3+	;1+	;1+	2−	23	;	;
TLGJ 36 LA	3+	;1	;1	2−	23	0;	0;
TLGJ 8 GA	3+	3+	3+	;2−	23	;	;
TLGJ 88 NC	3+	3+	3+	2−	23	;	;
TLRJ 23 LA	3+	3	3+	2−	;23	;1−	;
TLRJ 23 LA	4	3+	3+	2−	23	;1−	;1−
TNMJ 58 LA	4	3+4	3+	2−	23	;	;
TNRJ 227 NY	3+	3+	3+	;2−	23	;	;

Lr26, even though wheat cultivars with *Lr26* are not grown in this region. The high leaf rust severities in fields and plots that were observed in area 6 indicated that many hard red spring wheat cultivars do not have good resistance to leaf rust.

Phenotype MBDS, which is virulent to *Lr17,* was common in areas 4, 5, and 6 in 2001. Phenotypes of *P. triticina* with virulence to *Lr17* have been selected and maintained in areas 4, 5, and 6 due to the presence of this gene in the Kansas wheat Jagger. The widespread distribution of phenotype MBDS from Texas and Oklahoma to North Dakota is caused by the south-to-north movement of airborne urediniospores across the Great Plains region of the United States. Virulence to *Lr17* occurred in MBDS, MCDS, MBJJ, TCJS, and TDDS phenotypes in 2001.

The predominant virulence phenotypes of *P. triticina* in 2001 were similar or identical to those in 2000 (15). MCRK was the most common phenotype in area 1 in 2000. MCRK differs from MBRK by having virulence to *Lr26*. TLGF was a common phenotype in area 1 in 2000 and differs from TLGJ by avirulence to *Lr10*. As in 2001, MBDS was the most common phenotype in 2000 in areas 4 and 5, and THBJ was the most common phenotype in area 6. Phenotypes with virulence to *Lr9* have historically (14–19) been found in the soft red winter wheat regions of areas 1, 2, and 3. Virulence to *Lr16* has occurred previously in the hard red winter wheat region of areas 4 and 5 (19), and especially in the hard red spring wheat region of area 6 (2,8). Virulence to *Lr24* and *Lr26* has fluctuated from low to high frequencies in the last 18 years in areas 1, 2, 3, 4, 5, and 6 (16,19,20).

Some minor differences in the relative ranking of phenotypic distance between populations of *P. triticina* in the different areas were measured with the Rogers' and Kosman indexes. The Rogers' index is based only on the frequencies of individual virulence phenotypes in the two populations that are being compared. The Rogers' index does not take into consideration how closely related different virulence phenotypes may be in the two populations. Thus, two phenotypes that differ by a single virulence would contribute equally to the Rogers' distance measurement with two phenotypes that differ by virulence to all 16 differentials. The Kosman index was developed to take into account differences in virulence between phenotypes as well as the frequencies of phenotypes (11). Using the Rogers' distance measurement, the greatest separation in populations of *P. triticina* was between areas 2 and 4 and areas 2 and 5. The leaf rust populations adapted to the northern soft red winter wheat in area 2 were the most different compared with the populations adapted to the hard red winter wheat of the southern and middle Great Plains region. With the Kosman distance, the populations of *P. triticina* in areas 1 and 2 differed the most compared with the population in area 4. The relatively small sample size of isolates in areas 2, 3, and 7, in 2001 may have influenced the phenotypic distances that were obtained. Both the Rogers' and Kosman indexes determined that the populations of *P. triticina* in areas 4 and 5 were the least different. Many of the same wheat cultivars are grown in both areas 4 and 5.

The populations of *P. triticina* in areas 3 and 1 were the most diverse for virulence phenotypes when measured with the Shannon normalized index. The Shannon index considers each phenotype equally, without regard to the differences in virulence among the phenotypes. Using the Kosman index of diversity, the populations of *P. triticina* in areas 3 and 2 were the most diverse. The Kosman diversity index takes into account the number and distribution of the unique phenotypes, in addition to similarity for virulence among the phenotypes. The small sample sizes in areas 2 and 3 may have affected the diversity index values. Previous work has shown that sample size can affect estimates of diversity in wheat leaf rust populations (3,4).

Virulence to the adult plant resistance genes *Lr35* and *Lr37* was detected for the first time in North America in leaf rust collections from the 2001 survey. Virulence to these genes was found in virulence phenotypes MBDS, MCDS, and MCJS. Virulence to *Lr35* and *Lr37* was found in isolates that were collected throughout the Great Plains, even though wheat cultivars with these genes have not been grown in this region. Phenotypes MBDS and MCDS became prevalent in the Great Plains region of the United States (areas 4, 5, and 6) and Canada starting in 1996 (6). In an earlier study (9), it was shown that phenotypes MBDS and MCDS also differed from the other phenotypes in the Great Plains by having virulence to *Lr3bg,* and *LrB,* and by avirulence to *Lr28*. Isolates of phenotypes MBDS and MCDS also had very different amplified fragment length polymorphism phenotypes (9) which, combined with the virulence differences, indicated that these recently prevalent isolates with virulence to *Lr17* were introduced to the Great Plains region of North America. In a group of 67 isolates of *P. triticina* from Canada that were collected in 1994 (5), none of the isolates were virulent to adult plants of Thatcher with *Lr35.* All of the isolates that were tested had a mesothetic resistance response on seedlings of the Thatcher line with *Lr37*. In field plots in the mid 1990s, the Thatcher lines with *Lr35* and *Lr37* had very low leaf rust severities, which also indicated that isolates of *P. triticina* with virulence to these genes were rare or nonexistent (J. A. Kolmer, *unpublished data*). Phenotypes MBDS and MCDS were most likely introduced to the Great Plains region in the mid 1990s and increased rapidly due to the selective effect of *Lr17* in Jagger wheat. Virulence to *Lr35* and *Lr37* has most likely been present in MBDS and MCDS phenotypes since they became prevalent. Two isolates, MBDS 250 MT and MCDS 102 OK, had low IT to either *Lr35* or *Lr37;* therefore, not all of the original introductions of this group of phenotypes of *P. triticina* may have had virulence to these two genes. It is possible that isolates with low IT to either *Lr35* or *Lr37* arose by mutation from isolates virulent to both genes, although this would seem unlikely given that most mutations convert avirulent isolates to virulent isolates. Gene *Lr37* has been used in the wheat cvs. Hyak and Madsen that have been grown in the Pacific Northwest. Gene *Lr35,* which was derived from *Triticum speltoides,* has not been used in a wheat cultivar in North America (21).

Populations of *P. triticina* in the different regions of the United States continue to change on a regular basis due to the cultivation of wheat cultivars with specific leaf rust resistance genes. As wheat classes with different leaf rust resistance genes are grown in the United States, it is likely that the regional populations of *P. triticina* will continue to differ for virulence phenotypes. Populations of *P. triticina* are extremely large; therefore, mutation that generates virulence variation is a recurrent event. Mutation and subsequent selection of specific virulence by host resistance genes has maintained diverse and dynamic populations of virulence phenotypes of *P. triticina* in North America.

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