Physiologic Specialization of *Puccinia triticina* on Wheat in the United States in 2006

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ABSTRACT

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Collections of *Puccinia triticina* were obtained from rust-infected leaves provided by cooperators throughout the United States and from surveys of wheat fields and nurseries in the Great Plains, Ohio River Valley, southeast, California, and Washington State in order to determine the virulence of the wheat leaf rust population in 2006. Single uredinial isolates (718 in total) were derived from the collections and tested for virulence phenotype on lines of Thatcher wheat that are near-isogenic for leaf rust resistance genes *Lr1, Lr2a, Lr2c, Lr3a, Lr9, Lr16, Lr24, Lr26, Lr3ka, Lr11, Lr17a, Lr30, LrB, Lr10, Lr14a, Lr18, Lr2*, and *Lr28* and winter wheat lines with genes *Lr41* and *Lr42*. In the United States in 2006, 56 virulence phenotypes were found. Virulence phenotypes TDBJG, TDBGG, and TDBJH were among the four most common phenotypes and were all virulent to resistance gene *Lr24*. These phenotypes were found throughout the Great Plains region. Phenotype MLDSD with virulence to *Lr9*, *Lr17,* and *Lr41*was also widely distributed in the Great Plains. In the soft red winter wheat region of the southeastern states, phenotypes TCRKG and MBRKG with virulence to genes *Lr11, Lr26,* and *Lr18* were among the common phenotypes. Virulence phenotypes with virulence to *Lr16* were most frequent in the spring wheat region of the northern Great Plains. Virulence to *Lr21* was not found in any of the tested isolates.

Leaf rust, caused by *Puccinia triticina* Erikss., is the most common disease of wheat in the United States and worldwide (20). *P. triticina* is spread throughout the United States by wind-dispersed urediniospores that average 20 μm in diameter and are carried in the atmosphere and usually deposited on wheat crops in rain events. The optimal conditions for leaf rust infection are 20°C with free water on the leaf surface for 8 h. Overnight dew periods are optimal for infection. The urediniospores germinate on wheat plants, producing the specialized infection structures of appressoria, germ tube, and penetration peg (1) that allow the fungus to penetrate the host stomata. Additional specialized structures, the substomatal vesicle and haustoria, are produced which allow the fungus to obtain nutrients from host mesophyll cells without killing them. Infectious hyphae of the fungus spread throughout the mesophyll layer. Leaf rust infections are initially visible as faint flecks on leaf surfaces 3 to 4 days after inoculation. Uredinia erupt and break through the epidermal leaf surface 8 to 10 days after initiation of the infection process. The clonally produced urediniospores can cycle indefinitely on wheat hosts. The optimal temperature for production of urediniospores is 25°C. Temperature and moisture conditions throughout much of the wheat-growing regions in the United States are suitable for the infection and spread of leaf rust (19). The abundance of susceptible wheat cultivars also facilitates the establishment and spread of the disease.

Urediniospores have a dikaryotic nuclear condition. Isolates of *P. triticina* can either be homozygous for genes that condition avirulence to leaf rust resistance genes in wheat, heterozygous for avirulence and virulence alleles, or homozygous for virulence alleles (8). An isolate of *P. triticina* heterozygous for an avirulence allele can be classified as avirulent yet still carry a virulence allele. Mutations of avirulence alleles in heterozygous isolates may lead to development of isolates with virulence to specific resistance genes. Because *P. triticina* populations in the United States are very large, it would be expected that random mutations occur in sufficient numbers to lead to the development of new leaf rust phenotypes with additional virulence to leaf rust resistance genes in wheat. Statler (22,23) conducted mutagenesis studies with *P. triticina* and described mutations from avirulence to virulence to specific resistance genes and mutations from virulence to avirulence.

At present, over 50 leaf rust resistance genes have been described in wheat (16). Most of the genes condition isolate-specific resistance in a gene-for-gene relationship with *P. triticina*. As a result of the isolate specificity of resistance genes, wheat cultivars often lose their effective resistance in a short period of time due to the selection and increase of isolates with virulence to the specific resistance genes. The highly dynamic nature of leaf rust phenotypes in North America caused by the constant use of wheat cultivars with specific resistance genes has resulted in a highly diverse population of *P. triticina*. On an annual basis, 50 to 70 phenotypes of leaf rust are described in the United States. This high level of virulence diversity has made highly effective and long-lasting leaf rust resistance in wheat very difficult to achieve.

Virulence surveys of the wheat leaf rust fungus 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 (14) to detect new virulence phenotypes and to monitor shifts of virulence phenotypes in the major wheat-growing regions of the United States. Earlier surveys of leaf rust virulence that started in 1926 were conducted by the USDA-ARS in Kansas and Indiana (3). Similar surveys have been done in Canada since 1931 (15) and in Mexico (21). In the United States (11) and Canada (4–6), data from leaf rust surveys have been used to characterize virulence dynamics and phenotypic diversity within and between wheat-growing regions. The objectives of this study were to characterize the virulence of *P. triticina* populations in the United States in 2006 to the North American wheat leaf rust differentials and to compare these results with those of previous surveys.

MATERIALS AND METHODS

Leaf rust occurrence and isolate collections. Uredinial collections of leaf rust

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were made from wheat plots and fields in surveys of the Great Plains, Ohio River Valley, southeastern states, and by cooperators throughout the United States. In 2006, field surveys of wheat were made in southern and central Texas (late March); northern Texas and south-central Oklahoma (late April); the southeastern states of Louisiana, Alabama, Mississippi, and Georgia (late April to early May); Oklahoma and Kansas (late May); the Ohio River Valley states of Illinois, Indiana, and Ohio (early June); north-central Kansas, Nebraska, western Iowa, South Dakota, and southern Minnesota (mid-June); and Minnesota, North Dakota, and South Dakota (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 breeding lines with various combinations of leaf rust resistance genes. Trap plots usually contain older, leaf-rust-susceptible wheat cultivars that are no longer prominent in commercial production. A collection consisted of from 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 inoculation and increase. Collections from inoculated nurseries were not included in the study.

Identification of virulence phenotypes. Urediniospores from each collection were used to inoculate 7-day-old seedlings of the wheat cv. Thatcher (CI 10003), that had been treated with a maleic hydrazide solution of approximately 0.01 g (dissolved in 30 ml of H_2O) per pot to enhance spore production. Each pot of 10 to 20 seedlings was sprayed with 0.25 ml of a suspension of spores in Soltrol 170 (Phillips Petroleum, Bartlesville, OK) mineral oil. After drying for 1 h, inoculated plants were placed in a dew chamber overnight at 18°C. The plants were then placed in individual plastic isolation chambers in a greenhouse where temperatures varied between 18 and 28°C daily under at least 8 h of natural light, with supplemental greenhouse lighting. After 12 to 15 days, three seedlings were saved per collection, each with the primary leaf trimmed to isolate a single uredinium. Then, 6 to 9 days later, 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 were mixed with 0.25 ml of oil and 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*, *Lr3a*, *Lr3ka*, *Lr9*, *Lr10*, *Lr11*, *Lr14a, Lr16*, *Lr17a*, *Lr18*, *Lr21, Lr24*, *Lr26*, *Lr28, Lr30*, and *LrB* and winter wheat lines with *Lr41* and *Lr42*. Wheat lines with genes *Lr1, Lr2a, Lr2c, Lr3a,* and *Lr11* were also in the early wheat leaf rust differential sets that were used in the United States (3) and Canada (2) from the 1930s to 1960s. 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 h. After 10 to 12 days, infection types (ITs) were recorded as either high (IT 3 to 4) or low (IT 0 to 2^+), as in previous surveys (12). A five-letter code described the low or high ITs of each isolate to the 20 differential lines. Each letter corresponded to the ITs of four differentials. The Thatcher lines with genes *Lr1, Lr2a, Lr2c,* and *Lr3a* 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, Lr17a,* and *Lr30* were the third set of differentials; lines with genes *LrB, Lr10, Lr14a,* and *Lr18* were the fourth set of differentials; and lines with genes *Lr21, Lr28, Lr41,* and *Lr42* were the fifth set of differentials. Sets 1 to 3 are the same as described by Long and Kolmer (12). The same first four sets of differentials have been used in *P. triticina* surveys in Canada (15). The fifth set of differentials was added for the first time in U.S. surveys in 2004. Phenotype and virulence frequencies were determined for collections from eight agroecological geographic areas, as shown and described in Figure 1.

Fig. 1. Agroecological areas for *Puccinia triticina* 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 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.

The leaf rust resistance genes present in the current soft red winter wheats, hard red winter wheats, and hard red spring wheats were postulated based on ITs to different virulence phenotypes of *P. triticina* using previously cited methods (7,17). The postulated leaf rust resistance genotypes of the cultivars are available at the USDA-ARS Cereal Disease Laboratory website in the germplasm evaluation section.

RESULTS

Onset and spread of leaf rust. In January 2006, drought conditions in Texas limited the early development of leaf rust. In early March in south Texas, low levels of leaf rust severity were present on flag leaves of winter wheat and, by mid-March, only trace levels of infection were observed in irrigated plots. In the second week of April, susceptible cultivars had high levels of rust severity in south Texas. In Oklahoma, dry conditions also limited leaf rust development and only trace levels of leaf rust were observed in wheat fields in the last week of March. In late April, trace levels of leaf rust were found in south Kansas in wheat plots that were under drought stress. By mid-May, low levels of leaf rust were present on wheat throughout Kansas. In central and eastern Nebraska, leaf rust was present at low levels by mid-May and increased to higher severity levels by early June. The widespread drought conditions throughout the southern Great Plains in 2006 limited leaf rust development in the hard red winter wheats.

Leaf rust infections that had overwintered were found on winter wheat in southern Minnesota in the first week of May. In early June, trace levels of leaf rust infections were found in eastern North Dakota on spring wheat. In late June, susceptible winter wheats had high levels of leaf rust severities in southern Minnesota and eastern South Dakota. In mid- to late July, high levels of leaf rust severities were found on susceptible spring wheats in Minnesota, South Dakota, and North Dakota.

Leaf rust was found on susceptible winter wheats in Louisiana in mid-February and reached high levels of severity by late March and early April. Leaf rust was common in east-central Arkansas in late April. In late April, leaf rust was common and severe on susceptible cultivars from central Mississippi to central Georgia. In mid-May, leaf rust was common and severe throughout the Coastal Plain region of North Carolina and the eastern region of Virginia. In early June, leaf rust was present at low levels in winter wheat in eastern Pennsylvania and was found at trace levels in upstate New York in mid-July. In early June, leaf rust was present on soft red winter wheats from central Missouri to central Illinois. By mid-June, high severities of leaf rust were found in Ohio and Indiana. A complete summary of the 2006 leaf rust epidemic in the United States can be found at the USDA-ARS Cereal Disease Laboratory website.

Distribution of virulence phenotypes. In total, 56 virulence phenotypes of *P. triticina* were found in the United States

from the 718 single-uredinial isolates that were tested for virulence on the Thatcher lines (Table 1). Phenotypes TDBJG (14.9%), MLDSD (9.1%), TDBGG (8.8%), and TDBJH (8.9%) were the four most common phenotypes in the United States in 2006. In the southeastern states (area 1), 26 virulence phenotypes were found among the 143 single uredinial isolates that were tested (Table 1). Phenotypes TDBJG (23.1%), MBRKG (6.3%), and TCRKG (6.3%) were the three most common phenotypes in this area. In the northeastern states (area 2), 10 virulence phenotypes were found among the 35 isolates that were tested. Phenotypes MFGJG (17.1%), MCPSB (14.3%), and MFDSB (14.3%) were the three most common phenotypes in this area. In the Ohio Valley states of area 3, 21 virulence phenotypes were found among the 27 isolates tested. Phenotypes TDBJG (18.6%), MCDSB (15.3%), and TCRKG (6.8%) were the three most common phenotypes in this area.

Table 1. Number and frequency (%) of virulence phenotypes of *Puccinia triticina* in the United States in 2006 identified by virulence to 20 lines of wheat with single genes for leaf rust resistance[a]

		Area 1		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7		Area 8		Total	
Phenotype	Virulences	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
BBBDB	14a	0	0	1	2.9	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
CBLSG	3,3ka,B,10,14a,28	0	0	0	0	0	0	1	0.5	0	0	0	0	0	0	0	0	1	0.1
LBBTG	1,B,10,14a,18,28	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	1	0.1
MBBJG	1,3,10,14a,28	2	1.4	0	0	0	0	1	0.5	0	0	1	0.4	0	0	0	0	4	0.6
MBDSB	1,3,17,B,10,14a	3	2.1	0	0	0	0	8	3.9	2	6.7	5	2.2	0	0	0	0	18	2.5
MBGJG	1,3,11,10,14a,28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	30	3	0.4
MBPSB	1,3,3ka,17,30,B,10,14a	2	1.4	0	0	1	1.7	1	0.5	0	0	2	0.9	0	0	0	0	6	0.8
MBPSG	1,3,3ka,17,30,B,10,14a,28	0	0	0	0	0	0	3	1.5	0	0	1	0.4	0	0	0	0	4	0.6
MBRKG	1,3,3ka,11,30,10,14a,18,28	9	6.3	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	11	1.5
MCBJG	1,3,26,10,14a,28	0	0	7	20	0	0	0	0	0	0	0	0	0	0	0	0	7	1
MCDSB	1,3,26,17,B,10,14a	8	5.6	0	0	9	15.3	4	1.9	1	3.3	9	3.9	2	50	1	10	34	4.7
MCDSG	1,3,26,17,B,10,14a,28	0	0	1	2.9	0	0	0	0	0	0	0	0	0	0	4	40	5	0.7
MCJJG	1,3,26,11,17,10,14a,28	0	0	0	0	1	1.7	0	0	0	0	0	0	0	0	0	0	1	0.1
MCPSB	1,3,26,3ka,17,30,B,10,14a	0	0	5	14.3	2	3.4	0	0	3	10	3	1.3	0	0	2	20	15	2.1
MCPSC	1,3,26,3ka,17,30,B,10,14a,42	2	1.4	0	0	0	0	4	1.9	0	0	6	2.6	0	0	0	0	12	1.7
MCRKG	1,3,26,3ka,11,30,10,14a,18,28	0	0	0	0	5	8.5	0	0	0	0	1	0.4	0	0	0	0	6	0.8
MDBJG	1,3,24,10,14a,28	2	1.4	0	0	0	0	0	0	0	0	2	0.9	0	0	0	0	4	0.6
MFBJG	1,3,24,26,10,14a,28	6	4.2	0	0	0	0	4	1.9	0	0	0	0	0	0	0	0	10	1.4
MFBKG	1,3,24,26,10,14a,18,28	1	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
MFDSB	1,3,24,26,17,B,10,14a	2	1.4	5	14.3	0	0	4	1.9	0	0	2	0.9	0	0	0	0	13	1.8
MFGJG	1,3,24,26,11,10,14a,28	2	1.4	6	17.1	2	3.4	0	0	0	0	0	0	0	0	0	0	10	1.4
MFPSC	1,3,24,26,3ka,17,30,B,10,14a,42	5	3.5	3	8.6	2	3.4	24	11.7	3	10	18	7.8	0	0	0	0	55	7.7
MFRJG	1,3,24,26,3ka,11,30,10,14a,28	0	0	0	0	1	1.7	0	0	0	0	0	0	0	0	0	0	1	0.1
MFRKG	1,3,24,26,3ka,11,30,10,14a,18,28	0	0	3	8.6	0	0	0	0	0	0	0	0	0	0	0	0	3	0.4
MFTJG	1,3,24,26,3ka,11,17,30,10,14a,28	0	0	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	2	0.3
MJBJG	1,3,16,24,10,14a,28	0	0	0	0	0	0	0	0	0	0	14	6.1	0	0	0	0	14	1.9
MJBJH	1,3,16,24,10,14a,28,42	0	0	0	0	0	0	0	0	0	0	2	0.9	0	0	0	0	2	0.3
MLDSD	1,3,9,17,B,10,14a, 41	6	4.2	0	0	2	3.4	33	16	6	20	16	6.9	2	50	0	0	65	9.1
PCMDG	1,2c,3,26,3ka,30,14a,28	2	1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.3
SBDGG	1,2a,2c,17,10,28	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	1	0.1
SBDJG	1,2a,2c,17,10,14a,28	0	0	0	0	0	0	1	0.5	0	0	1	0.4	0	0	0	0	2	0.3
TBBGG	1,2a,2c,3,10,28	0	0	0	0	0	0	1	0.5	0	0	1	0.4	0	0	0	0	2	0.3
TBBJG	1,2a,2c,3,10,14a,28	7	4.9	0	0	1	1.7	3	1.5	0	0	4	1.7	0	0	0	0	15	2.1
TBDSB	1,2a,2c,3,17,B,10,14a	3	2.1	0	0	0	0	0	0	0	0	7	3	0	0	0	0	10	1.4
TBNSB	1,2a,2c,3,3ka,17,B,10,14a	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	1	0.1
TBRKG	1,2a,2c,3,3ka,11,30,10,14a,18,28	5	3.5	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	7	1
TBTKG	1,2a,2c,3,3ka,11,17,30,10,14a,18,28	1	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
TCDSB	1,2a,2c,3,26,17,B,10,14a	4	2.8	0	0	0	0	0	0	0	0	4	1.7	0	0	0	0	8	1.1
TCRKG	1,2a,2c,3,26,3ka,11,30,10,14a,18,28	9	6.3	0	0	4	6.8	0	0	0	0	2	0.9	0	0	0	0	15	2.1
TCTDB	1,2a,2c,3,26,3ka,11,17,30,14a	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	1	0.1
TDBGG	1,2a,2c,3,24,10,28	6	4.2	0	0	0	0	20	9.7	0	0	37	16	0	0	0	0	63	8.8
TDBGH	1,2a,2c,3,24,10,28,42	0	0	0	0	2	3.4	2	1	0	0	4	1.8	0	0	0	0	8	1.1
TDBJG	1,2a,2c,3,24,10,14a,28	33	23.1	0	0	11	18.6	30	14.6	3	10	30	13	0	0	0	0	107	14.9
TDBJH	1,2a,2c,3,24,10,14a,28,42	8	5.5	0	0	1	1.7	31	15	6	20	18	7.8	0	0	0	0	64	8.9
TDDJG	1,2a,2c,3,24,17,10,14a,28	0	0	0	0	0	0	2	1	0	0	1	0.4	0	0	0	0	3	0.4
TDDSB	1,2a,2c,3,24,17,B,10,14a	0	0	0	0	0	0	3	1.5	0	0	0	0	0	0	0	0	3	0.4
TFBGG	1,2a,2c,3,24,26,10,28	0	0	0	0	0	0	2	1	0	0	2	0.9	0	0	0	0	4	0.6
TFBGH	1,2a,2c,3,24,26,10,28,42	0	0	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	2	0.3
TFBJG	1,2a,2c,3,24,26,10,14a,28	7	4.9	0	0	2	3.4	6	2.9	2	6.7	1	0.4	0	0	0	0	18	2.5
TFBJH	1,2a,2c,3,24,26,10,14a,28,42	0	0	2	5.7	0	0	2	1	4	13.3	0	0	0	0	0	0	8	1.1
TGBJG	1,2a,2c,3,16,10,14a,28	0	0	0	0	0	0	0	0	0	0	2	0.9	0	0	0	0	2	0.3
THBJG	1,2a,2c,3,16,26,10,14a,28	0	0	0	0	0	0	0	0	0	0	1	0.4	0	0	0	0	1	0.1
TJBGG	1,2a,2c,3,16,24,10,28	0	0	0	0	0	0	2	1	0	0	12	5.2	0	0	0	0	14	1.9
TJBJG	1,2a,2c,3,16,24,10,14a,28	0	0	0	0	0	0	1	0.5	0	0	12	5.2	0	0	0	0	13	1.8
TNRJJ	1,2a,2c,3,9,24,3ka,11,30,10,14a,28,41	6	4.2	2	5.7	1	1.7	7	3.4	0	0	1	0.4	0	0	0	0	17	2.4
TNRJK	1,2a,2c,3,9,24,3ka,11,30,10,14a,28,41,42	2	1.4	0	0	4	6.8	6	2.9	0	0	5	2.2	0	0	0	0	17	2.4
Total	...	143	...	35	...	59	...	206	...	30	...	231	...	4	...	10	...	718	...

[a] Lines tested were Thatcher lines with genes *Lr1, Lr2a, Lr2c, Lr3a, Lr9, Lr16, Lr24, Lr26, Lr3ka, Lr11, Lr17, Lr30, LrB, Lr10, Lr14a, Lr18, Lr21, Lr28*, and winter wheat lines with genes *Lr41*, and *Lr42*. Area 1 = Louisiana, Arkansas, Mississippi, Alabama, Georgia, Florida, South Carolina, and North Carolina; area 2 = Virginia, Maryland, Pennsylvania, and New York; area 3 = Missouri, Illinois, Kentucky, Ohio, Indiana, Indiana, Michigan, and Wisconsin; area 4 = Texas and Oklahoma; area 5 = Kansas, Iowa, and Nebraska; area 6 = Minnesota, North Dakota, South Dakota, and Montana; area 7 = California; and area 8 = Washington State.

In the southern Great Plains of Texas and Oklahoma (area 4), 27 virulence phenotypes were found among the 206 isolates tested. Phenotypes MLDSD (16%), TDBJH (15%), and TDBJG (14.6%) were the three most common phenotypes. In the central Great Plains of Kansas and Nebraska (area 5), 9 virulence phenotypes were found among the 30 isolates tested. Phenotypes MLDSD (20%), TDBJH (20%), and TFBJH (13.3%) were the three most common phenotypes. In the northern Great Plains of Minnesota, South Dakota, and North Dakota (area 6), 37 virulence phenotypes were found among the 231 isolates that were tested. Phenotypes TDBGG (16%), TDBJG (13%), and TDBJH (7.8%) were the three most common phenotypes.

In California (area 7), two isolates each of MCDSB and MLDSD accounted for all of the isolates. In Washington State (area 8), 4 virulence phenotypes were found among the 10 isolates tested. Phenotypes MCDSG, MBGJG, and MCPSB accounted for nine of the isolates.

Virulence frequencies. Frequencies of virulence to *Lr* genes differed among the regional populations of *P. triticina* in the United States (Table 2). Virulences to genes *Lr1, Lr3,* and *Lr10* were over 90% in all areas. Virulence to *Lr21* was not found in any area. Virulence to genes *Lr2a* and *Lr2c* was present in all areas except for area 7 and area 8, and was at the highest frequency in area 6 at 64% and area 1 at 63.6%. Virulence to *Lr9* was found in all areas except for area 8, and was at the highest frequency in area 7 at 50% and area 4 at 22.3%. Virulence to *Lr16* was found only in area 4 at 1.5% and area 6 at 18.6%. Virulence to *Lr24* was found in all areas except areas 7 and 8, and was at the highest frequency in area 4 at 70.9%. Virulence to *Lr26* occurred in all areas and was at the highest frequency in area 2 at 91.4%. Virulence to *Lr3ka* was found in all areas except for area 7 and was at the highest frequency in area 3 at 44.1%. Virulence to *Lr11* occurred in all areas except area 5 and area 7 and was at the highest frequency in area 3 at 40.7%. Virulence to *Lr17* occurred in all areas and was at the highest frequency in area 7 at 100% and area 5 at 50%. Virulence to *Lr30* was found in all areas except area 7 and was highest in area 3 at 44.1%. Virulence to *LrB* occurred in all regions and was at the highest frequencies in areas 7 (100%) and area 5 (50%). Virulence to *Lr14a* was found in all areas and was at 100% in areas 2, 5, 7, and 8. Virulence to *Lr18* occurred in areas 1, 2, 3, and 6 and was at the highest frequency in area 3 at 22%. Virulence to *Lr28* was found in all areas except area 7 and was at the highest frequency in area 1 at 75.5%. Virulence to *Lr41* was found in all areas except for area 8 and was highest in area 7 at 50% and area 4 at 22.3%. Virulence to *Lr42* was found in all areas except area 7 and area 8 and was highest in area 5 at 43.3%.

In area 1, the frequency of isolates with virulence to *Lr11, Lr18*, and *Lr26* has declined in recent years compared with 1996 to 2000, when phenotypes with these virulences were more frequent (Fig. 2A). Virulence to *Lr24* has increased rapidly to 55% in 2006 from less than 10% in 2004. Virulence to *Lr9* has decreased to near 10% in 2006 from nearly 50% in 2001. In area 4, virulence to *Lr17* reached nearly 90% of isolates in 2001 and has declined to nearly 40% in 2006 (Fig. 2B). Virulence to *Lr24* has increased steadily since 2001 to reach over 70% in 2006. Virulence to *Lr26* has varied from 15 to 40% from 1996 to 2006. Isolates with virulence to *Lr9* that are also virulent to *Lr41* have varied between 20 and 30% since 2002. In area 6, virulence to *Lr16* has varied between 15 and 40% since reaching over 50% in 2002 (Fig. 2C). Virulence to *Lr17* has varied between 20 and 55% since reaching over 60% in 2000. Virulence to *Lr2a* has been over 50% since 2001. Virulence to *Lr24* has increased from less than 10% from 2000 to 2003 to nearly 70% in 2006. Virulence to *Lr26* has declined from nearly 70% in 2000 to less than 25% in 2006.

DISCUSSION

In 2006, TDBJG, TDBGG, and TDBJH were among the four most common leaf rust virulence phenotypes in the United States. These virulence phenotypes are virulent to *Lr24* and were widely distributed throughout the Great Plains region. The commonly grown hard red winter wheat cvs. Jagalene (*Lr24*), Cutter (*Lr24*), and Ogallala (*Lr24*) have selected leaf rust phenotypes with virulence to *Lr24.* Leaf rust phenotype MLDSD was also common throughout the Great Plains region and had virulence to gene *Lr17* that is present in the commonly grown hard red winter wheats Jagger and TAM 111. MLDSD was also virulent to *Lr41* that is in the hard red winter wheat Overley. Phenotypes TDBGG and TDBJG were present in 2005 in the Great Plains but at lower frequencies (9). Leaf rust phenotypes MCDSB, with virulence to *Lr17* and *Lr26*, and MFPSC,

Table 2. Number and frequency (%) of isolates of *Puccinia triticina* in the United States in 2006 virulent to 20 lines of wheat with single genes for leaf rust resistance[a]

	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	143	100	34	97.1	59	100	205	99.5	30	100	231	100	4	100	10	100	716	99.7
Lr2a	91	63.6	4	11.4	30	50.8	119	57.8	15	50	148	64.1	0	0	0	0	407	56.7
Lr2c	93	65	4	11.4	30	50.8	119	57.8	15	50	148	64.1	0	0	0	0	409	57.0
Lr3	143	100	34	97.1	59	100	205	99.5	30	100	228	98.7	4	100	10	100	713	99.3
Lr9	14	9.8	2	5.7	7	11.9	46	22.3	6	20	22	9.5	2	50	0	0	99	13.8
Lr16	0	0	0	0	0	0	3	1.5	0	0	43	18.6	0	0	0	0	46	6.4
Lr24	80	55.9	21	60	30	50.8	146	70.9	18	60	161	69.7	0	0	0	0	456	63.5
Lr26	48	33.6	32	91.4	32	54.2	50	24.3	13	43.3	50	21.6	2	50	7	70	234	32.6
Lr3ka	43	30.1	13	37.1	26	44.1	46	22.3	6	20	41	17.7	0	0	2	20	177	24.7
Lr11	34	23.8	11	31.4	24	40.7	13	6.3	0	0	10	4.3	0	0	3	30	95	13.2
Lr17	36	25.2	14	40	19	32.2	87	42.2	15	50	78	33.8	4	100	7	70	260	36.2
Lr30	43	30.1	13	37.1	26	44.1	45	21.8	6	20	40	17.3	0	0	2	20	175	24.4
LrB	35	24.5	14	40	16	27.1	85	41.3	15	50	75	32.5	4	100	7	70	251	35.0
Lr10	141	98.6	34	97.1	59	100	206	100	30	100	230	99.6	4	100	10	100	714	99.4
Lr14a	137	95.8	35	100	55	93.2	179	86.9	30	100	174	75.3	4	100	10	100	624	86.9
Lr18	25	17.5	3	8.6	13	22	0	0	0	0	4	1.7	0	0	0	0	45	6.3
Lr21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Lr28	108	75.5	21	60	43	72.9	125	60.7	15	50	157	68	0	0	7	70	476	66.3
Lr41	14	9.8	2	5.7	7	11.9	46	22.3	6	20	22	9.5	2	50	0	0	99	13.8
Lr42	17	11.9	5	14.3	11	18.6	69	33.5	13	43.3	53	22.9	0	0	0	0	168	23.4
Total	143	...	35	...	59	...	206	...	30	...	231	...	4	...	10	...	718	...

[a] Area 1 = Louisiana, Arkansas, Mississippi, Alabama, Georgia, Florida, South Carolina, and North Carolina; area 2 = Virginia, Maryland, Pennsylvania, and New York; area 3 = Missouri, Illinois, Kentucky, Ohio, Indiana, Indiana, Michigan, and Wisconsin; area 4 = Texas, Oklahoma, and New Mexico; area 5 = Kansas and Nebraska; area 6 = Minnesota, North Dakota, South Dakota, and Montana; area 7 = California; and area 8 = Washington State.

with virulence to *Lr17*, *Lr24, Lr26,* and *Lr42*, were the two most common virulence phenotypes in the United States in 2005. These phenotypes were still present in 2006 but at lower frequencies compared with 2005.

The selective effects of leaf rust resistance genes in the different classes of wheat are also reflected in the common *P. triticina* virulence phenotypes in each area. In area 1, phenotypes MBRKG and TCRKG are both virulent to *Lr18* that is present in the soft red winter wheats SS520, CK 9803, Pioneer 2684, and FFR 524 that were grown in this area (7). Virulence to *Lr18* was highest in area 1. TCRKG is also virulent to *Lr11* and *Lr26* that are both present in the soft red winter wheats Choptank, SS MPV 57, and USG 3209. Soft red winter wheat cultivars MV5-46, Sisson, and AGS 2000 have *Lr26*. MBRKG is virulent to *Lr11* that is in many soft red winter wheat cultivars singly or in combination with other *Lr* genes. Virulence to *Lr11* was highest in the soft red winter wheat region of areas 1, 2, and 3. TCRKG and MBRKG were also common in the southeastern region in 2005 (9). The most common leaf rust phenotype in area 1, TDBJG, was virulent to *Lr24* which is in the soft red winter wheat McCormick. Virulence to *Lr9* has declined in area 1 from nearly 45% in 2003 to under 10% in 2006. This reduction is most likely associated with fewer current soft red winter cultivars with *Lr9*, because *P. triticina* isolates with virulence to *Lr9* declined in frequency in the absence of cultivars with this gene. The current cvs. Crawford, CK 9511, and Tribute have *Lr9.*

In area 6, the three most common virulence phenotypes, TDBGH, TDBJG, and TDBJH, were all virulent to *Lr2a*, which is present in the hard red spring wheat cvs. Alsen and Oxen (17). TDBGH was also a common phenotype in the northern spring wheat region in 2005. *Lr16* is present in the commonly grown hard red spring wheat cvs. Knudson, Briggs, and Freyr. Virulence to *Lr16* was highest in area 6. Leaf rust phenotypes TJBGG and TJBJG (each at 5.2% in area 6) had virulence to *Lr16* and also *Lr24*. The hard red spring wheat Banton was postulated to have *Lr24*.

Leaf rust resistance genes *Lr2a*, *Lr9, Lr11, Lr16, Lr17, Lr18, Lr24, Lr26, Lr41*, and *Lr42* have been used in recent years in the winter and spring wheats in the United States. Mutations for virulence produce new phenotypes with virulence to leaf rust resistance genes. In 1996, when virulence to *Lr17* first started to increase in the southern Great Plains region (13), two phenotypes, MCDSB and MBDSB, accounted for almost all of the isolates with virulence to *Lr17*. In 2006, virulence to *Lr17* was found in 28 virulence phenotypes. Virulence to other leaf rust resistance genes is widely distributed throughout the *P. triticina* population. In 2006, virulence to *Lr24* was found in 29 phenotypes and virulence to *Lr26* in 24 phenotypes. Virulence to *Lr9* was more restricted, being present in only three phenotypes, and virulence to *Lr16* was found in nine phenotypes. Hard red winter wheat cvs. with *Lr41* (Overley and Bullet) and *Lr42* (Fanin) are currently grown in the southern Great Plains. In 2006, 3 phenotypes had virulence to *Lr41* and 10 phenotypes had virulence to *Lr42*. Phenotypes with virulence to *Lr21* have not been found in the United States. This gene is present in the spring wheats Glenn and Steele; however, *Lr21* is not known to be present in any winter wheat cultivars. If winter

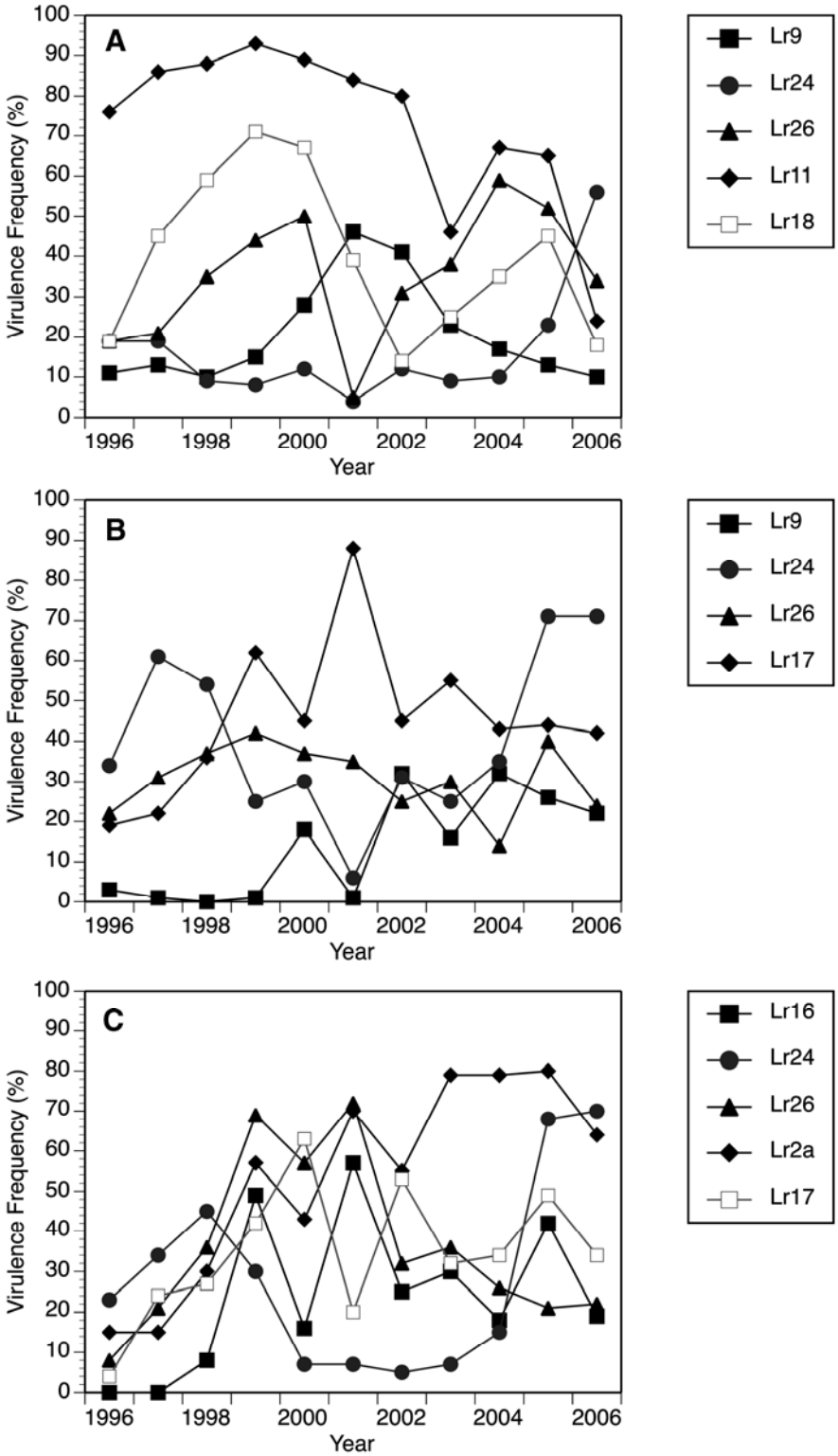

Fig. 2. Frequency (%) of *Puccinia triticina* isolates with virulence to selected leaf rust resistance genes in wheat from 1996 to 2006 in the **A,** southeastern states (area 1); **B,** southern Great Plains (area 4); and **C,** northern Great Plains (area 6).

wheat cultivars with *Lr21* were to be released in the region where *P. triticina* overwinters, leaf rust phenotype*s* with virulence to this gene would inevitably appear in the United States.

The widespread use of wheat cultivars in the United States with genes that are effective in seedlings and that condition resistance to specific leaf rust phenotypes has led to the development of a *P. triticina* population that is highly diverse for virulence. Cultivars with single specific genes for leaf rust resistance quickly select for virulent leaf rust phenotypes. Certain combinations of seedling resistance genes may condition high levels of resistance in widely grown wheat cultivars for a limited time. Given the large population size of *P. triticina* in the United States and the effects of mutation, it would be expected that isolates with combinations of virulence to the resistance genes would eventually appear. The spring wheat cvs. Norm and Knudson with combinations of effective seedling resistance genes *Lr16* and *Lr23* and the nonspecific adult plant resistance gene *Lr34* are highly resistant and have retained their resistance over a number of years (10,18) despite the highly dynamic *P. triticina* population.

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