Special Report

Physiologic Specialization of *Puccinia triticina* on Wheat in the United States in 2007

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ABSTRACT

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In 2007, leaf rust of wheat was severe throughout the Great Plains region of North America. Yield losses in wheat due to leaf rust were estimated to be 14% in Kansas. 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 2007. Single uredinial isolates (868 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*, *Lr21*, and *Lr28*, and on winter wheat lines with genes *Lr41* and *Lr42*. Fifty-two virulence phenotypes were found. Virulence phenotypes TDBJG, MFPSC, 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, with virulence to genes *Lr11*, *Lr26*, and *Lr18*, and MFGJH, with virulence to *Lr24*, *Lr26*, and *Lr11,* 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 phenotypes with virulence to *Lr11*, *Lr18*, and *Lr26* were most common in the soft red winter areas of the southeastern states and Ohio Valley. Virulence to *Lr21* was not found in any of the tested isolates.

Leaf rust, caused by *Puccinia triticina* Eriks., is the most common disease of wheat (*Triticum aestivum* L.) in the United States and worldwide (17). Leaf rust occurs on an annual basis throughout the wheat production regions east of the Mississippi and also throughout the Great Plains region. Infections of leaf rust become established in the fall and can survive and sporulate during the winter on winter wheat throughout the southeastern states, and also in the southern– to mid–Great Plains region. In the spring with temperatures of 20 to 25°C, new leaf rust infections rapidly develop and the urediniospores are carried in the southerly winds, which enables leaf rust to spread to wheat crops hundreds of kilometers distant within a few weeks (16).

Leaf rust resistance in winter wheat has traditionally relied upon the introgression and selection of germplasm with seedling resistance genes. Although seedling-based resistance has been easy to select and maintain in breeding programs, new phenotypes of *P. triticina* with virulence to the introgressed genes develop by mutation and increase rapidly in response to resistant wheat cultivars. The source of the introgressed resistance genes has made little difference in the long-term effectiveness of the resistance genes. Genes *Lr9* from *Aegilops umbellulata*, *Lr26* from *Secale cereale*, *Lr24* from *Thinopyrum ponticum*, and *Lr41*(=*Lr39*) from *Triticum tauschii* have proven to be no more durable for resistance than *Lr1*, *Lr2a*, *Lr11*, or *Lr17,* which were derived from common hexaploid wheat. For all of these genes, virulent phenotypes of *P. triticina* quickly increased, rendering the resistance genes largely ineffective. Wheat cultivars with combinations of leaf rust resistance genes have selected more complex leaf rust phenotypes that have combinations of virulence. When wheat cultivars with strongly selective seedling resistance genes are removed from cultivation, the virulent *P. triticina* phenotypes may also decline, which can restore the effectiveness of the resistance genes. Cyclical changes in frequency have been noted for virulence to genes *Lr9*, *Lr16*, and *Lr24* (3,6).

The soft red winter wheat cultivars that are grown in the southeastern states and the Ohio Valley area have the seedling leaf rust resistance genes *Lr1*, *Lr2a*, *Lr9*, *Lr11*, *Lr14a*, *Lr26*, and *Lr18* (J. A. Kolmer, *unpublished data*). None of these genes provide complete resistance, as phenotypes of *P. triticina* that have virulence to these genes have been detected in the annual virulence surveys of *P. triticina* in the United States (6). Adult plant resistance genes such as *Lr12*, *Lr13*, and uncharacterized resistance are also present in the soft red winter wheat cultivars (J. A. Kolmer, *unpublished data*). However, *Lr12* and *Lr13* are widely ineffective in this region and throughout the United States. The adult plant resistance gene *Lr34* that conditions phenotype nonspecific resistance is likely not present in this wheat class since a representative sampling of current and older soft red winter cultivars lacked the DNA marker allele associated with the presence of *Lr34* (8). The hard red winter wheat cultivars grown in the southern– to mid–Great Plains region have genes *Lr1*, *Lr16*, *Lr17*, *Lr24*, *Lr26*, and *Lr41* (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500). Leaf rust isolates with virulence to these different genes increased within a few years of cultivars with these genes being released in the Great Plains. A small number of current and older hard red winter wheat cultivars had the marker allele associated with *Lr34* (8). The hard red spring wheats that are grown in the north central Great Plains region have genes *Lr1*, *Lr2a*, *Lr14a*, *Lr16*, *Lr21*, *Lr23*, and the adult plant resistance genes *Lr13* and *Lr34*. Many of the hard red spring wheat cultivars have the marker allele associated with *Lr34* due to the introgression and selection of leaf rust resistant germplasm with adult plant resistance.

Virulence surveys of the wheat leaf rust fungus have been conducted by the 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. Earlier surveys of leaf rust virulence that started in 1926 were conducted by the USDA-ARS in Kansas (2) and Indiana (12). Similar surveys have been done in Canada since 1931 (1) and in Mexico (19). In the United

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States (11) and Canada (4), 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 2007 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. A total of 478 uredinial collections of leaf rust 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 2007, 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, Florida, and Georgia (late April to early May); Oklahoma, Kansas, and western Missouri (late May); the Ohio River Valley states of Illinois, Indiana, Ohio, and eastern Missouri (early June); north central Kansas, Nebraska, western Iowa, South Dakota, and southern Minnesota (mid-June), and Minnesota, North Dakota, South Dakota, and Wisconsin (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 one to several leaves with *P. triticina* 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 cultivar 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. Six 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 and Canada 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 700 to 2300 hours. After 10 to 12 days, infection types (IT) were recorded as either high (IT 3 to 4) or low (IT 0 to 2^+) as in previous surveys (9). A five-letter code describes the low or high infection types of each isolate to the 20 differential lines. Each letter corresponds to the infection types 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; and lines with genes *LrB*, *Lr10*, *Lr14a*, and *Lr18* were the fourth set of differentials; 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 (9). The same first four sets of differentials have been used in *P. triticina* surveys in Canada (13). The fifth set of differentials was added for the first time in U.S. surveys in 2004, since *Lr21* is present in spring wheats, *Lr41* and *Lr42* are present in winter wheats (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500), and *Lr28* differentiates *P. triticina* virulence phenotypes. Phenotype and virulence frequencies were determined for collections from eight agroecological geographic areas as shown and described in Figure 1.

The leaf rust resistance genes present in the current soft red winter, hard red winter, and hard red spring wheats were postulated based on infection types to different virulence phenotypes of *P. triticina* using previously cited methods (5,14). The postulated leaf rust resistance genes of the cultivars are available in the germplasm evaluation section at the USDA-ARS Cereal Disease Laboratory website (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500).

RESULTS

Leaf rust occurrence and isolate collections. Leaf rust was detected in wheat plots in central Texas in early February. By the second week of April, leaf rust severities were very high in wheat plots in south and central Texas with moderate severity levels in fields. In the first 2 weeks of May, high severity levels of leaf rust had developed in susceptible cultivars in central Oklahoma plots (Fig. 2). In late May, there were high levels of leaf rust in fields throughout Oklahoma. Leaf rust infections were found on lower leaves in Kansas in mid-March, likely the result of leaf rust overwintering in the central Great Plains during the winter of 2006–2007. Cool temperatures and a late freeze combined with high amounts of rainfall delayed development of the wheat crop in central and eastern Kansas in April and May. This delay allowed leaf rust to increase very rapidly on wheat before the crop had headed. Flag leaves of widely grown susceptible cultivars were heavily infected with leaf rust before grain filling had started. In mid-May, leaf rust was present at very high severity levels throughout Kansas. The widespread premature defoliation caused by leaf rust throughout central and eastern Kansas resulted in a 14% yield loss statewide (Kansas Department of Agriculture), the highest loss ever recorded for disease in wheat in Kansas.

At the end of May, leaf rust was found on winter wheat in Minnesota, North Dakota, and South Dakota (Fig. 2). Leaf rust was found on spring wheat in southern Minnesota in early June. Regular rainfall in the central and northern Great Plains in May allowed leaf rust to increase and spread throughout the region. By middle to late June, susceptible winter wheat culti-

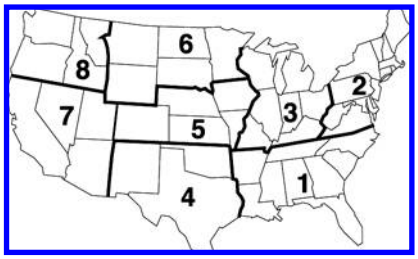

Fig. 1. Agroecological areas for *Puccinia triticina* in the United States. Area 1, mainly southern-adapted soft red winter wheats; areas 2 and 3, mostly northern-adapted soft red and white winter wheat; area 4, mixed wheat types but primarily hard red winter; area 5, hard red winter wheat; area 6, mixed 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.

vars had high severities of leaf rust in Minnesota, South Dakota, and Nebraska. In late June, leaf rust was very severe on spring wheats in southern and central Minnesota and central South Dakota. By the end of July, leaf rust was widespread and severe on spring wheat throughout Minnesota, South Dakota, and North Dakota.

In the soft red winter wheat areas, leaf rust was first found in southwestern Louisiana in late February. In late April, leaf rust was present along the Gulf Coast in southern Alabama and southern Georgia (Fig. 2). Dry conditions throughout the southeastern states in April and May limited the further increase and spread of leaf rust. Leaf rust was found in North Carolina in the first week of April. In late April, leaf rust was present at low levels in plots in North Carolina. By late May, leaf rust was increasing in fields in eastern Virginia and Maryland. Leaf rust was very common and at high severity levels in northeastern Missouri and southern Illinois fields in early

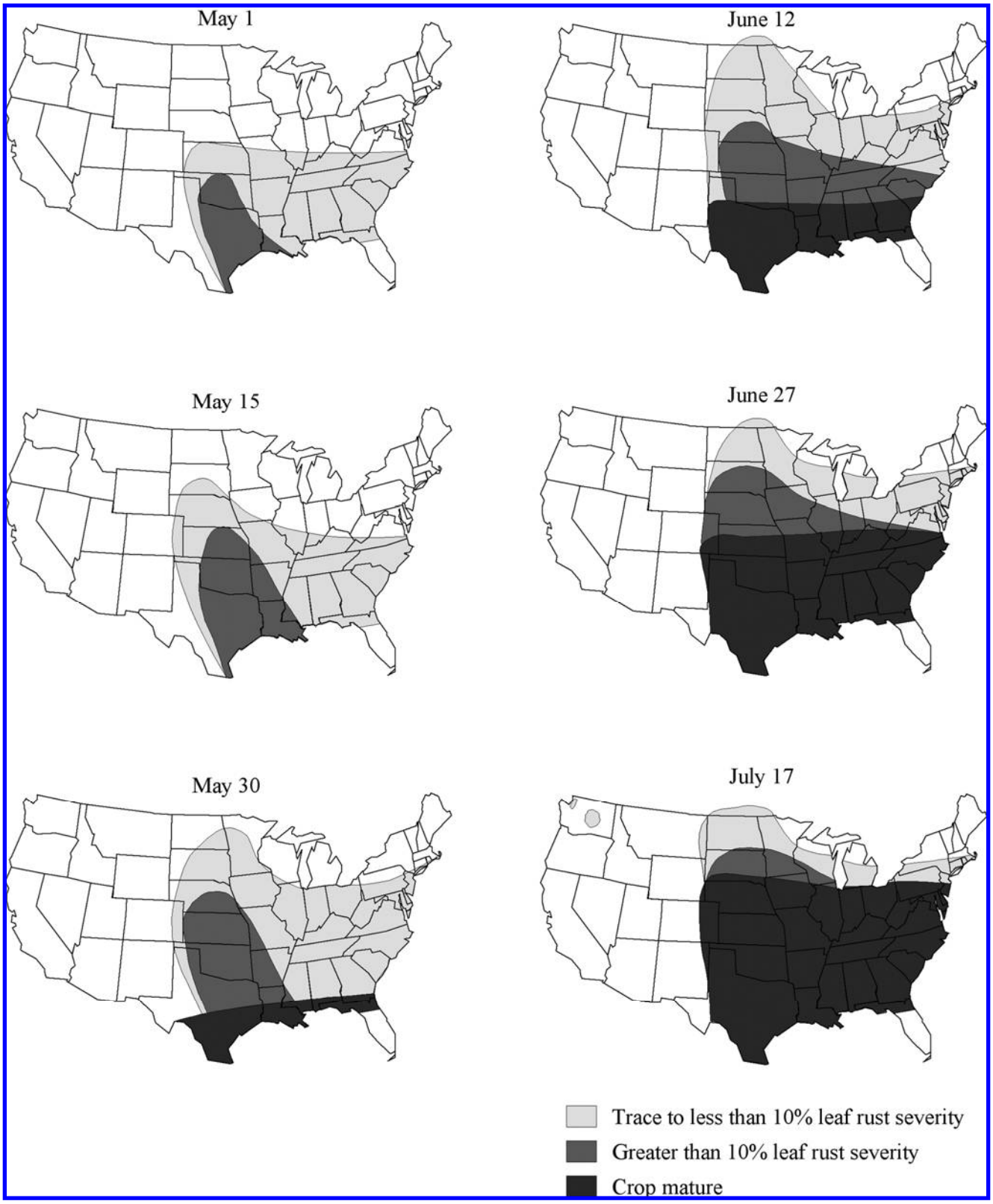

Fig. 2. Progression of leaf rust on wheat caused by *Puccinia triticina* in the United States in 2007.

June. In mid-June, leaf rust was very common in wheat fields in Ohio, Indiana, and Wisconsin. Leaf rust was present at low levels in mid-June in plots in central New York. A complete summary of the 2007 leaf rust epidemic in the United States can be found at the USDA-ARS Cereal Disease Laboratory website (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500).

Distribution of virulence phenotypes. In total, 52 virulence phenotypes of *P. triticina* were found in the United States from the 868 single-uredinial isolates that were tested for virulence on the Thatcher lines (Table 1). Phenotypes MFPSC (13.9%), MLDSD (12.2%), TDBGH (18.1%), and TDBJG (10.7%) were the

Table 1. Number and frequency (%) of virulence phenotypes of *Puccinia triticina* in the United States in 2007 identified by virulence to 20[a] lines of wheat with single genes for leaf rust resistance

		Area 1[b]		Area 2[c]		Area 3[d]		Area 4[e]		Area 5[f]		Area 6[g]		Area 8[h]		Total	
Phenotype	**Virulences**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**
BBBDB	14a	2	2.2	0	0	0	0	0	0	0	0	4	1.2	0	0	6	0.7
CCPSB	3,26,3ka,17,30,B,10,14a	0	0	2	2.9	0	0	0	0	0	0	0	0	0	0	2	0.2
LCDSB	1,26,17,B,10,14a	2	2.2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.2
MBDSB	1,3,17,B,10,14a	0	0	0	0	0	0	2	1	1	0.8	0	0	0	0	3	0.3
MBDTG	1,3,17,B,10,14a,18,28	0	0	2	2.9	0	0	0	0	0	0	0	0	0	0	2	0.2
MBGJG	1,3,11,10,14a,28	0	0	0	0	1	2.3	0	0	0	0	0	0	4	100	5	0.6
MBPSB	1,3,3ka,17,30,B,10,14a	0	0	0	0	0	0	0	0	0	0	6	1.8	0	0	6	0.7
MBRJG	1,3,3ka,11,30,10,14a,28	1	1.1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
MBTSB	1,3,3ka,11,17,30,B,10,14a	2	2.2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.2
MCDSB	1,3,26,17,B,10,14a	6	6.5	11	15.7	1	2.3	5	2.5	1	0.8	2	0.6	0	0	26	3
MCGJG	1,3,26,11,10,14a,28	4	4.3	0	0	0	0	0	0	0	0	0	0	0	0	4	0.5
MCRKG	1,3,26,3ka,11,30,10,14a,18,28	4	4.3	1	1.4	0	0	0	0	0	0	0	0	0	0	5	0.6
MCTSB	1,3,26,3ka,11,17,30,B,10,14a	0	0	3	4.3	0	0	0	0	0	0	0	0	0	0	3	0.3
MDGJG	1,3,24,11,10,14a,28	0	0	2	2.9	0	0	0	0	0	0	0	0	0	0	2	0.2
MDPSC	1,3,24,3ka,17,30,B,10,14a,42	0	0	0	0	1	2.3	0	0	2	1.6	1	0.3	0	0	4	0.5
MDSPC	1,3,24,3ka,11,17,B,14a,18,42	0	0	0	0	0	0	2	1	0	0	0	0	0	0	2	0.2
MFBJG	1,3,24,26,10,14a,28	5	5.4	0	0	0	0	0	0	0	0	0	0	0	0	5	0.6
MFGJH	1,3,24,26,11,10,14a,28,42	6	6.5	26	37.1	0	0	0	0	0	0	0	0	0	0	32	3.7
MFPSC	1,3,24,26,3ka,17,30,B,10,14a,42	15	16.1	7	10	8	18.2	28	14.2	18	14.4	45	13.4	0	0	121	13.9
MGBJG	1,3,16,10,14a,28	0	0	0	0	0	0	0	0	0	0	3	0.9	0	0	3	0.3
MJDSC	1,3,16,24,17,B,10,14a,42	0	0	0	0	0	0	2	1	2	1.6	0	0	0	0	4	0.5
MLDSD	1,3,9,17,B,10,14a,41	0	0	0	0	0	0	34	17.3	14	11.2	58	17.3	0	0	106	12.2
NBBFG	1,2c,14a,18,28	0	0	5	7.1	0	0	0	0	0	0	0	0	0	0	5	0.6
NBBKG	1,2c,10,14a,18,28	0	0	6	8.6	0	0	0	0	0	0	0	0	0	0	6	0.7
PBBGG	1,2c,3,10,28	0	0	0	0	0	0	0	0	2	1.6	0	0	0	0	2	0.2
PBDGG	1,2c,3,17,10,28	0	0	0	0	0	0	0	0	1	0.8	0	0	0	0	1	0.1
PCDSG	1,2c,3,26,17,B,10,14a,28	2	2.2	0	0	0	0	0	0	0	0	2	0.6	0	0	4	0.5
SBDGG	1,2a,2c,17,10,28	0	0	0	0	0	0	0	0	0	0	2	0.6	0	0	2	0.2
SBDSB	1,2a,2c,17,B,10,14a	0	0	0	0	0	0	0	0	0	0	1	0.3	0	0	1	0.1
SBJDG	1,2a,2c,11,17,14a,28	0	0	0	0	0	0	0	0	1	0.8	0	0	0	0	1	0.1
TBBJG	1,2a,2c,3,10,14a,28	6	6.5	0	0	0	0	0	0	0	0	1	0.3	0	0	7	0.8
TBRKG	1,2a,2c,3,3ka,11,30,10,14a,18,28	2	2.2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.2
TCBJG	1,2a,2c,3,26,10,14a,28	0	0	0	0	0	0	0	0	2	1.6	0	0	0	0	2	0.2
TCDSB	1,2a,2c,3,26,17,B,10,14a	0	0	0	0	2	4.5	0	0	0	0	1	0.3	0	0	3	0.3
TCMJG	1,2a,2c,3,26,3ka,30,10,14a,28	5	5.4	0	0	0	0	0	0	0	0	0	0	0	0	5	0.6
TCRJG	1,2a,2c,3,26,3ka,11,30,10,14a,28	0	0	0	0	2	4.5	0	0	0	0	0	0	0	0	2	0.2
TCRKG	1,2a,2c,3,26,3ka,11,30,10,14a,18,28	8	8.6	0	0	0	0	0	0	1	0.8	1	0.3	0	0	10	1.2
TCSJG	1,2a,2c,3,26,3ka,11,17,10,14a,28	0	0	1	1.4	0	0	0	0	0	0	0	0	0	0	1	0.1
TDBBG	1,2a,2c,3,24,28	0	0	0	0	2	4.5	0	0	0	0	0	0	0	0	2	0.2
TDBGG	1,2a,2c,3,24,10,28	4	4.3	2	2.9	2	4.5	10	5.1	2	1.6	21	6.3	0	0	41	4.7
TDBGH	1,2a,2c,3,24,10,28,42	0	0	0	0	10	22.7	16	8.1	43	34.4	88	26.3	0	0	157	18.1
TDBJG	1,2a,2c,3,24,10,14a,28	6	6.5	0	0	6	13.6	57	28.9	6	4.8	18	5.4	0	0	93	10.7
TDBJH	1,2a,2c,3,24,10,14a,28,42	4	4.3	0	0	7	15.9	14	7.1	6	4.8	11	3.3	0	0	42	4.8
TDDGH	1,2a,2c,3,24,17,10,28,42	0	0	0	0	0	0	0	0	2	1.6	6	1.8	0	0	8	0.9
TFBGH	1,2a,2c,3,24,26,10,28,42	0	0	0	0	0	0	4	2	7	5.6	5	1.5	0	0	16	1.8
TFBJG	1,2a,2c,3,24,26,10,14a,28	8	8.6	0	0	0	0	12	6.1	4	3.2	6	1.8	0	0	30	3.5
TGBJG	1,2a,2c,3,16,10,14a,28	1	1.1	0	0	0	0	6	3	0	0	0	0	0	0	7	0.8
TJBGH	1,2a,2c,3,16,24,10,28,42	0	0	0	0	1	2.3	2	1	3	2.4	30	9	0	0	36	4.1
TJBJG	1,2a,2c,3,16,24,10,14a,28	0	0	0	0	1	2.3	2	1	5	4	22	6.6	0	0	30	3.5
TLBJG	1,2a,2c,3,9,10,14a,28	0	0	0	0	0	0	0	0	2	1.6	0	0	0	0	2	0.2
TLGJG	1,2a,2c,3,9,11,10,14a,28	0	0	0	0	0	0	1	0.5	0	0	0	0	0	0	1	0.1
TNRJK	1,2a,2c,3,9,24,3ka,11,30,10,14a,28,41,42	0	0	2	2.9	0	0	0	0	0	0	1	0.3	0	0	3	0.3
Total		93		70		44		197		125		335		4		868	

[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*, and *Lr28*, and winter wheat lines with genes *Lr41* and *Lr42*. Virulence phenotypes were designated with hexadecimal coding system as in Long and Kolmer (9).
[b] States of LA, AR, AL, GA, FL, TN, SC, and NC.
[c] States of VA, WV, MD, PA, DE, NJ, NY, MA, CT, RI, VT, NH, and ME.
[d] States of MO, IL, KY, OH, IN, MI, and WI.
[e] States of TX, OK, and NM.
[f] States of KS, MO, IA, NE, and CO.
[g] States of MN, ND, SD, WY, and MT.
[h] State of WA.

four most common phenotypes in the United States in 2007. In the southeastern states (area 1), 20 virulence phenotypes were found among the 93 single uredinial isolates that were tested (Table 1). Phenotypes MFPSC (16.1%), TCRKG (8.6%), and TFBJG (8.6%) were the three most common phenotypes in this area. In the northeastern states (area 2), 13 virulence phenotypes were found among the 70 isolates that were tested. Phenotypes MFGJH (37.1%), MCDSB (15.7%), and NBBKG (8.6%) were the three most common phenotypes in this area. In the Ohio Valley states (area 3), there were 13 virulence phenotypes in the 44 isolates tested. Phenotypes TDBGH (22.7%), MFPSC (18.2%), and TDBJH (15.9%) were the three most common phenotypes in this area. In Texas and Oklahoma (area 4), there were 16 virulence phenotypes among the 197 isolates tested. Phenotypes TDBJG (28.9%), MLDSD (17.3%), and MFPSC (14.2%) were the three most common phenotypes in this area. In Kansas and Nebraska (area 5), there were 21 virulence phenotypes among the 125 isolates tested. Phenotypes TDBGH (34.3%), MLDSD (17.3%), and MFPSC (13.4%) were the three most common phenotypes in this area. In Minnesota, North Dakota, and South Dakota (area 6), there were 23 virulence phenotypes among the 335 isolates tested. Phenotypes TDBGH (26.3%), MLDSD (17.3%), and MFPSC (13.4%) were the three most common phenotypes in this area. In Washington State (area 8), the four isolates tested were all virulence phenotype MBGJG.

Virulence frequencies. Frequencies of virulence to *Lr* genes differed among the regional populations of *P. triticina* in the United States (Table 2). Virulence to genes *Lr1* and *Lr10* was over 90% in all areas. Virulence to *Lr3* was at 84.3% in area 2 and over 90% in the other areas. Virulence to *Lr21* was not found in any area. Virulence to *Lr2a* was highest in area 5 at 67.2% and lowest in area 2 at 7.1%. Virulence to *Lr2c* was highest in area 5 at 69.6% and lowest in area 2 at 22.9%. Virulence to *Lr9* was greater than 10% in areas 4, 5, and 6, and less than 5% in the other areas. Virulence to *Lr16* was highest in area 6 at 16.4%, and was less than 10% in the other areas. Virulence to *Lr24* was greater than 50% in all areas and was highest at 86.4% in area 3. Virulence to *Lr26* was greater than 10% in all areas and was highest in area 2 at 72.9%. Virulence to *Lr3ka* was 39.8% in area 1 and was greater than 10% in all other areas. Virulence to *Lr11* was highest in areas 1 and 2 at 29 and 50%, respectively, and greater than 10% in the other areas. Virulence to *Lr17* was highest in areas 2 and 4 at 37.1% and greater than 25% in the other areas. Virulence to *Lr30* was highest in area 1 at 39.8% and was greater than 10% in the other areas. Virulence to *LrB* was highest at 37.1% in area 4 and greater than 25% in the other areas. Virulence to *Lr14a* was highest in area 2 at 97.1% and greater than 50% in the other areas. Virulence to *Lr18* was at 15.1 and 20% in areas 1 and 2, respectively, and less than 5% in the other areas. Virulence to *Lr28* was highest in area 3 at 72.7% and greater than 50% in the other areas. Virulence to *Lr41* was greater than 10% in areas 4, 5, and 6 and less than 5% in the other areas. Virulence to *Lr42* was highest at 66.4% in area 5 and greater than 25% in the other areas.

In area 1, the frequency of isolates with virulence to *Lr26* increased from less than 40% in 2006 to 70% in 2007 (Fig. 3A). The frequency of isolates with virulence to *Lr24* and *Lr11* were 52 and 29%, respectively, close to 2006 levels. The frequency of isolates with virulence to *Lr18* declined from nearly 50% in 2005 to near 15% in 2007. Virulence to *Lr9* declined to 0% in 2007, continuing a decline from near 45% in 2001. In area 4, the frequency of isolates with virulence to *Lr24* and *Lr26* increased slightly compared to 2006, and isolates with virulence to *Lr17* and *Lr9* decreased slightly (Fig. 3B). In area 6, the frequency of isolates with virulence to *Lr24* and *Lr26* increased slightly compared to 2006, and the frequency of isolates with virulence to *Lr2a*, *Lr16*, and *Lr17* decreased slightly (Fig. 3C).

DISCUSSION

In 2007, TDBGH, MFPSC, and TDBGJ 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 hard red winter wheat cultivars Jagalene (*Lr24*), Cutter (*Lr24*), and Ogallala (*Lr24*) (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500) have se-

Table 2. Number and frequency (%) of isolates of *Puccinia triticina* in the United States in 2007 virulent to 20 lines of wheat with single resistance genes for leaf rust resistance

Resistance gene	Area 1[a]		Area 2[b]		Area 3[c]		Area 4[d]		Area 5[e]		Area 6[f]		Area 8[g]		Total	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
Lr1	91	97.8	68	97.1	44	100	197	100	125	100	331	98.8	4	100	860	99.1
Lr2a	44	47.3	5	7.1	33	75	124	62.9	84	67.2	214	63.9	0	0	504	58.1
Lr2c	46	49.5	16	22.9	33	75	124	62.9	87	69.6	216	64.5	0	0	522	60.1
Lr3	89	95.7	59	84.3	44	100	197	100	124	99.2	328	97.9	4	100	845	97.4
Lr9	0	0	2	2.9	0	0	35	17.8	16	12.8	59	17.6	0	0	112	12.9
Lr16	1	1.1	0	0	2	4.5	12	6.1	10	8	55	16.4	0	0	80	9.2
Lr24	48	51.6	39	55.7	38	86.4	149	75.6	100	80	254	75.8	0	0	628	72.4
Lr26	65	69.9	51	72.9	13	29.5	49	24.9	33	26.4	62	18.5	0	0	273	31.5
Lr3ka	37	39.8	16	22.9	11	25	30	15.2	21	16.8	54	16.1	0	0	169	19.5
Lr11	27	29	35	50	3	6.8	3	1.5	2	1.6	2	0.6	4	100	76	8.8
Lr17	27	29	26	37.1	12	27.3	73	37.1	42	33.6	124	37	0	0	304	35
Lr30	37	39.8	15	21.4	11	25	28	14.2	21	16.8	54	16.1	0	0	166	19.1
LrB	27	29	25	35.7	12	27.3	73	37.1	38	30.4	116	34.6	0	0	291	33.5
Lr10	91	97.8	65	92.9	42	95.5	195	99	124	99.2	331	98.8	4	100	852	98.2
Lr14a	89	95.7	68	97.1	29	65.9	165	83.8	65	52	183	54.6	4	100	603	69.5
Lr18	14	15.1	14	20	0	0	2	1	1	0.8	1	0.3	0	0	32	3.7
Lr21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lr28	66	71	47	67.1	32	72.7	124	62.9	87	69.6	217	64.8	4	100	577	66.5
Lr41	0	0	2	2.9	0	0	34	17.3	14	11.2	59	17.6	0	0	109	12.6
Lr42	25	26.9	35	50	27	61.4	68	34.5	83	66.4	187	55.8	0	0	425	49
Total	93		70		44		197		125		335		4		868	

[a] States of LA, AR, MS, AL, GA, FL, TE, SC, and NC.
[b] States of VA, WV, MD, PA, DE, NJ, NY, MA, CT, RI, VT, NH, and ME.
[c] States of MO, IL, KY, OH, IN, MI, and WI.
[d] States of TX, OK, and NM.
[e] States of KS, MO, IA, NE, and CO.
[f] States of MN, ND, SD, WY, and MT.
[g] State of WA.

lected leaf rust phenotypes with virulence to *Lr24*. Phenotype TDBGH is also virulent to *Lr42* that may be present in hard red winter wheat cultivar Fannin. 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 is also virulent to the gene *Lr41* that is in the hard red winter wheat cultivars Overley and Fuller (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500). Phenotypes MFPSC, MLDSD, and TDBJG were among the most common phenotypes in 2006 (6). TDBGH was present at a low frequency in 2006.

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 the different areas. In area 1, phenotypes MFPSC, TCRKG, TFBJG, MFGJH, and MCDSB are all virulent to *Lr26*, which is present in the soft red winter wheat cultivars USG 3209, Pioneer 26R61, AGS 2000, and Sisson (5). TCRKG is also virulent to genes *Lr11* and *Lr18* that are present in the soft red winter wheat cultivars SS520, CK 9803, Pioneer 2684, and FFR 524 (5; http://www.ars.usda.gov/main/site_main.htm?modecode=36400500). Isolates with virulence to *Lr11*, *Lr18*, and *Lr26* were most frequent in areas 1 and 2 where soft red winter wheat cultivars are grown. Phenotypes MFPSC, TFBJG, and MFGJH are also virulent to *Lr24*, which is present in the soft red winter wheat cv. McCormick (http://www.ars.usda.gov/main/site_main.htm?modecode=36400500). Virulence to *Lr9* has declined in area 1 from nearly 45% in 2003 to 0% in 2007. This reduction is likely associated with a concurrent reduction in acreage of soft red winter wheat cultivars with *Lr9*, since *P. triticina* isolates with virulence to *Lr9* have previously declined in frequency in the absence of cultivars with this gene. Isolates with virulence to *Lr16* were most frequent in area 6, where a number of hard red spring wheat cultivars have *Lr16* (14; http://www.ars.usda.gov/main/site_main.htm?modecode=36400500).

In 2007, some unique virulence phenotypes of *P. triticina* were detected. Phenotypes NBBFG and NBBKG, which were avirulent to *Lr2a* and virulent to *Lr2c,* were collected from soft white winter wheat cultivars in central New York, and were not found in any other region of the United States. These phenotypes may have overwintered in this region. Although NBBFG and NBBKG are relatively avirulent, the soft white winter wheats often lack any effective genes for leaf rust resistance. Similar phenotypes were previously found to overwinter in Pennsylvania (18). Phenotypes PBBGG and PBDGG were collected from triticale plots in Nebraska, and phenotype PCDSG was collected from triticale plots in Minnesota and Alabama. The P---- phenotypes are also avirulent to *Lr2a* and virulent to *Lr2c*, and may have some virulence adaptation to triticale. Phenotypes SBDGG, SBDSB, and SBJDG were collected from spring wheat cultivars in North Dakota and Minnesota, and from hard red winter wheat cultivars in Kansas, respectively. The S---- phenotypes are usually collected from *Aegilops cylindricum* (wild goatgrass) that grows as a weed in the south central Great Plains region (10). The S----- phenotypes are unique in being avirulent to *Lr3*, which is likely present in the hard red winter wheats.

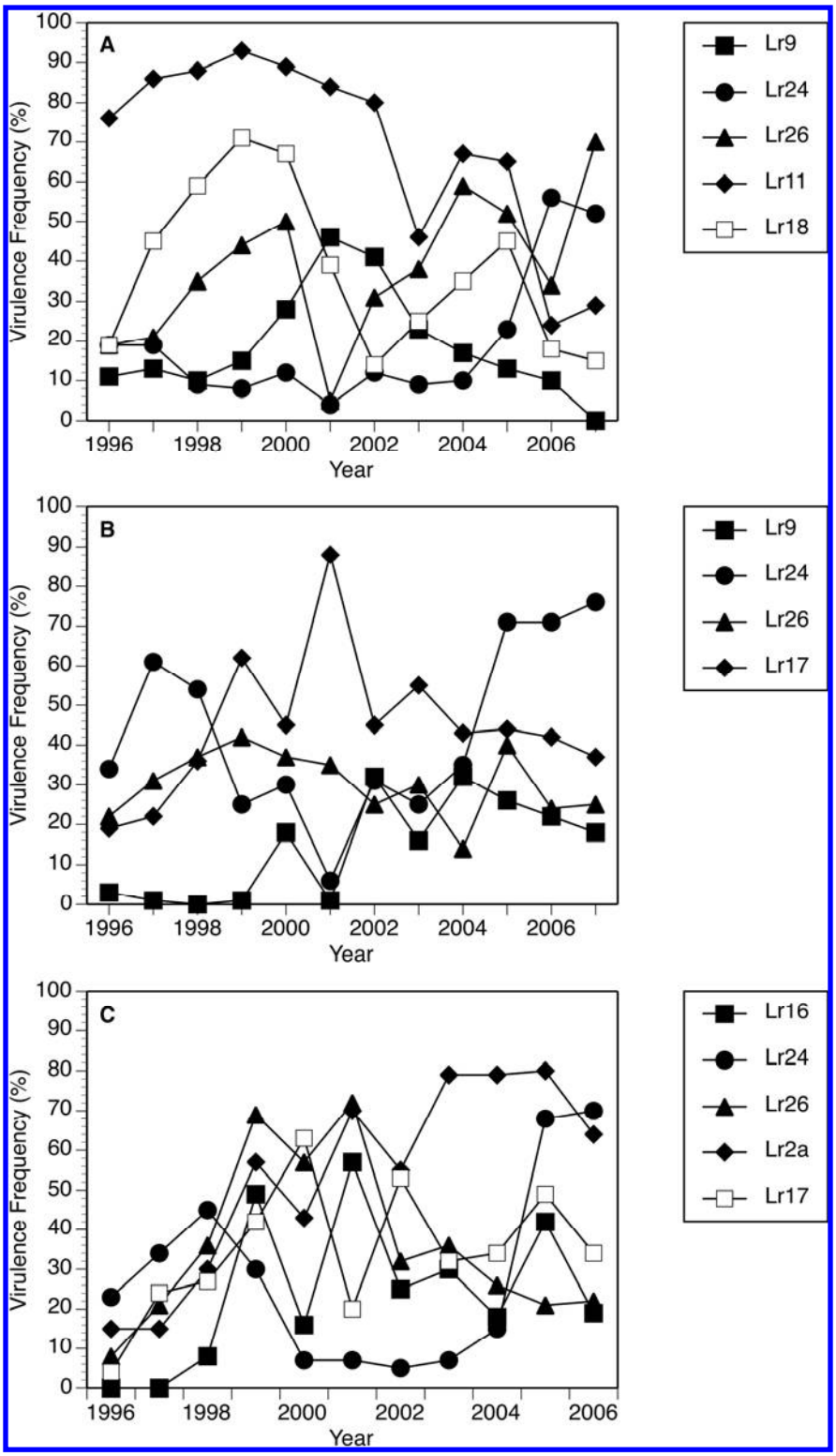

Fig. 3. Frequency (%) of *Puccinia triticina* isolates with virulence to selected leaf rust resistance genes in wheat from 1996 to 2007 in the **A,** southeastern states (area 1), **B,** southern Great Plains (area 4), and **C,** northern Great Plains (area 6).

Leaf rust resistance genes *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 (5,14; http://www.ars.usda.gov/main/site_main.htm?modecode=36400500). New phenotypes with virulence to resistance genes in wheat cultivars are continually produced by recurrent mutations in the *P. triticina* population. In 2007, 22 virulence phenotypes had virulence to *Lr17*. Virulence to *Lr17* was initially found in only a few phenotypes in 1996 when isolates with this virulence began to increase rapidly (10). Similarly, virulences to *Lr24* and *Lr26* are widely distributed in the *P. triticina* population, being found in 18 and 16 phenotypes respectively. In 2007, virulence to *Lr42* increased in frequency compared to 2006, and was found in all areas except area 8. In 2007, 11 phenotypes had virulence to *Lr42*. Some virulences have remained restricted to fewer phenotypes. Virulence to *Lr16* was found in five phenotypes, virulence to *Lr9* was found in four phenotypes, and virulence to *Lr41* was found in only two phenotypes. Virulence frequencies to both *Lr16* and *Lr9* have declined in recent years as cultivars with these genes occupy smaller acreages. Only five phenotypes were virulent to *Lr18*. In the late 1990s, over 70% of the isolates in area 1 had virulence to *Lr18*; however, the soft red winter wheat cultivars with *Lr18* are not currently widely grown. Gene *Lr21* is present in hard red spring wheat cultivars that are widely grown in Minnesota and North Dakota. Phenotypes with *Lr21* virulence have not been found in the United States. If winter wheat cultivars with *Lr21* are released in the region where leaf rust overwinters, leaf rust phenotypes with virulence to this gene would likely quickly 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 effects of mutation, it would be expected that isolates with combinations of virulence to the resistance genes would eventually appear. Wheat cultivars with combinations of genes that confer nonspecific resistance such as *Lr34* and possibly *Lr46* (20) combined with seedling genes such as *Lr16* and *Lr23* (7,15) have displayed highly effective levels of durable resistance in spring wheats.

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