Physiologic Specialization of *Puccinia triticina* on Wheat in the United States in 2010

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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 wheat fields and breeding plots by United States Department of Agriculture–Agricultural Research Service personnel and cooperators in the Great Plains, Ohio River Valley, southeastern states, Oregon, and Washington State in order to determine the virulence of the wheat leaf rust population in 2010. Single uredinial isolates (537 total) were derived from the collections and tested for virulence phenotype on 19 lines of ‘Thatcher’ wheat and a winter wheat line that are near-isogenic for 20 leaf rust resistance genes. In 2010, 38 virulence phenotypes

were described in the United States. Virulence phenotypes MLDSD, TDBJG, and TCRKG were the three most common phenotypes. Phenotype MLDSD is virulent to *Lr17* and *Lr39/Lr41* and was widely distributed throughout the United States. Phenotype TDBJG is virulent to *Lr24* and was found in both the soft red winter wheat and hard red winter wheat regions. Phenotype TCRKG is virulent to *Lr11*, *Lr18*, and *Lr26* and was found mostly in the soft red winter wheat region in the eastern United States. Virulence to *Lr21* was found for the first time in North America in isolates collected from spring wheat cultivars in North Dakota and Minnesota.

Leaf rust, caused by *Puccinia triticina* Erikss., is a common disease of wheat (*Triticum aestivum* L.) in the United States and worldwide (19). In the United States, *P. triticina* can overwinter in leaves of winter wheat that were infected in the fall by urediniospores from the previous summer's crop and survive to the spring. Leaf rust can overwinter regularly throughout the southern Great Plains from Texas to Nebraska and occasionally as far north as southern Minnesota. Leaf rust also overwinters regularly in the Gulf coast states and in the coastal plain from Georgia through Virginia.

Yield losses due to leaf rust have been heaviest in the winter wheat region from Pennsylvania to Kansas and Oklahoma (18). Years with the heaviest yield losses often had temperature and moisture conditions that also favored wheat yields. The widespread use of wheat cultivars that are susceptible to leaf rust allows *P. triticina* to overwinter over a wide area and can result in significant yield loss. In the last 20 years, leaf rust has caused an average loss of nearly 4% in Kansas, although annual losses can be much higher, as in 2007 (1), when leaf rust caused a 14% loss. In epidemic years, losses due to leaf rust in plots of susceptible spring wheat cultivars were as great as 40% (J. Kolmer, unpublished data).

In the United States, the different market classes of wheat have different genes for leaf rust resistance. The hard red winter wheat cultivars grown from Texas to South Dakota have genes *Lr3*, *Lr10*, *Lr14a*, *Lr17*, *Lr24*, *Lr26*, and *Lr39/41*. The soft red winter wheat cultivars grown in the southern, eastern, and Ohio Valley regions

have genes *Lr1*, *Lr11*, *Lr18*, *Lr24*, and *Lr26*. The hard red spring wheat cultivars grown in Minnesota, North Dakota, and South Dakota have genes *Lr1*, *Lr2a*, *Lr10*, *Lr16*, *Lr21*, and *Lr23*. These genes condition resistance to specific races or virulence phenotypes of *P. triticina*. Phenotypes with virulence to these genes have almost inevitably emerged within a few years after the genes were used in wheat cultivars. As a result, different virulence phenotypes are often found in the three different wheat regions.

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 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 (3) and Indiana (13). Similar surveys have been done in Canada since 1931 (2,14). In the United 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 2010 with 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. In 2010, USDA-ARS personnel and cooperators in the United States made a total of 336 uredinial collections of leaf rust from wheat plots and fields in surveys of the Great Plains, Ohio River Valley, and southeastern states. 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,

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South Dakota, and Wisconsin (early July and again in late July). Additional collections were made in wheat-breeding nurseries, trap plots, and demonstration plots along the route. Nurseries typically contain a wide array of regional cultivars and 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 at room temperature 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 'Thatcher' wheat (CI 10003) that had been treated with a maleic hydrazide solution of approximately 0.01 g (dissolved in 30 ml of H₂O) 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 plexiglass 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 two single uredinia per collection. The isolates were increased through one uredinial generation on seedlings of Thatcher before inoculating differential lines. Urediniospores of the single-uredinial isolates (2 to 3 mg) 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 a winter wheat line with the gene *Lr39* that had been previously designated as *Lr41*. A winter wheat line with *Lr42* was used in the surveys from 2004 to 2007; however, this line was dropped because it was later determined to also have *Lr24*, which greatly limited the effectiveness of this line as a differential.

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 previously described (12). A five-letter code describes the low or high ITs of each isolate to the 19 differential lines. Each letter corresponds to the ITs 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; lines with genes *LrB*, *Lr10*, *Lr14a*, and *Lr18* were the fourth set of differentials; and lines with genes *Lr21*, *Lr28*, and *Lr39/Lr41* were the fifth set of differentials. The fourth differential in the fifth set was not designated. Therefore, the fourth differential position was always designated as a low IT for coding phenotypes. Sets 1 to 3 are the same as described previously (12). The same first four sets of differentials have been used in *P. triticina* surveys in Canada (14). The fifth set of differentials was added for the first time in U.S. surveys in 2004, because *Lr21* is present in spring wheat cultivars, *Lr39/Lr41* is present in winter wheat cultivars, 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. Collections were not obtained from area 7 in 2010. A modified version of Nei's genetic distance (15) between isolates in areas 1, 2, 3, 4, 5, and 6 was calculated with NTSYS-pc v2.1 (Exeter Software, Seatauket, NY), in which the

frequency of isolates with virulence to a leaf rust resistance gene was used in place of allele frequency. The distance matrix of Nei's virulence distance between the areas was plotted with unweighted pair group method with arithmetic means clustering in NTSYS-pc v2.1.

The leaf rust resistance genes present in the current soft red winter wheat cultivars, hard red winter wheat cultivars, and hard red spring wheat cultivars were postulated based on ITs to different virulence phenotypes of *P. triticina* using previously cited methods (5,16). The ITs of the cultivars to different *P. triticina* isolates and the postulated leaf rust resistance genotypes of the cultivars are available at the USDA-ARS Cereal Disease Laboratory website in the germplasm evaluation section (<http://www.ars.usda.gov/Main/docs.htm?docid=9987>).

Results

Leaf rust occurrence and isolate collections. Leaf rust was found in winter wheat in south Texas in early February, and was present throughout the state by mid-March. In early April, leaf rust was increasing in severity in plots of commonly grown cultivars in south and central Texas. Leaf rust severity was generally low in fields throughout Texas. In late April, fields in southwest Oklahoma had severe leaf rust. In early May, leaf rust was found in several locations in south-central Kansas. In early June, leaf rust was severe in fields in eastern and central Kansas. Commonly grown hard red winter wheat cultivars such as 'Jagger' (*Lr17*), 'Overley' (*Lr39/41*), and 'Jagalene' (*Lr24*) were susceptible to leaf rust.

In late May, leaf rust was observed in winter wheat plots in southern Minnesota. In early June, leaf rust was observed at low levels in winter wheat plots in eastern South Dakota. In mid-June, plots of susceptible winter wheat in southern Minnesota and in central and eastern South Dakota had severe leaf rust. Trace levels of leaf rust were found in spring wheat fields in eastern South Dakota in early July. In mid-July, spring wheat plots and fields in eastern South Dakota and western Minnesota had moderate leaf rust severity. Leaf rust was at low levels in winter and spring wheat in North Dakota in mid-July. Susceptible spring wheat cultivars in plots in Minnesota and North Dakota at the end of July had moderate levels of leaf rust infection. Plots of spring wheat cultivars with *Lr21* had more leaf rust infection compared with previous years. Leaf rust was not present in farm fields due to the reduced levels of inoculum arriving from the southern plains and the extensive use of fungicide in the spring wheat area.

Leaf rust was at low levels in wheat plots and fields in southern Louisiana in early April. In early to mid-May throughout Louisiana, leaf rust was severe in wheat plots but low in fields. In mid-May, high levels of leaf rust were found in plots from Arkansas to Georgia; however, leaf rust was at low levels in fields in the same area. In mid-April, leaf rust was present on susceptible wheat cultivars in plots in eastern North Carolina. By the end of May, leaf rust was severe in plots throughout Virginia. In mid-May, susceptible

Fig. 1. Agroecological areas for *Puccinia triticina* in the United States. Area 1, mainly southern-adapted soft red winter wheat; areas 2 and 3, mostly northern-adapted soft red and soft 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 wheat planted in late fall; and area 8, mixed wheat types but primarily soft white winter.

cultivars in western Kentucky had moderate levels of leaf rust infection. In late May, moderate levels of leaf rust were present in fields in southern Illinois. In mid-June, fields in Indiana and Ohio had low to moderate severity levels. In mid-May, leaf rust was present in plots in Delaware, Maryland, and New York. Moderate levels of leaf rust were found in fields throughout New York in late June and July. In early July, moderate levels of leaf rust were present in fields in south-central Washington State. A complete summary of the leaf rust epidemic in 2010 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 2010, 38 virulence phenotypes of wheat leaf rust were identified in the United States from 537 single-uredinial isolates that were tested on the Thatcher lines (Table 1). Phenotypes MLDSB (29.8%), TDBJG (23.1%), and TCRKG (13.2%) were the only phenotypes with a frequency greater than 10% across the United States. MLDSB was found in

all areas, TDBJG was found in all areas except area 2, and TCRKG was found in all areas except areas 5 and 8. In the southeastern states (area 1), seven virulence phenotypes were found among the 52 isolates that were tested (Table 1). Phenotypes MLDSB (38.5%), TCRKG (23.1%), and TDBJG (13.5%) were the three most common phenotypes in this area. In the northeastern states (area 2), 11 virulence phenotypes were identified among the 58 isolates that were tested. Phenotypes TCRKG (31.0%), MCTSB (15.5%), and MCDSB (12.1%) were the three most common phenotypes in this area. In the Ohio Valley states (area 3), eight virulence phenotypes were identified among the 57 isolates that were tested. Phenotypes TCRKG (56.1%), MCTSB (14.0%), and TDBJG (14.0%) were the three most common phenotypes in this area. In Texas and Oklahoma (area 4), 12 virulence phenotypes were identified among the 135 isolates that were tested. Phenotypes MLDSB (48.1%), TDBJG (26.7%), and MFPSB (7.4%) were the three most common phenotypes in this area. In Kansas

Table 1. Number (*n*) and frequency (%) of virulence phenotypes of *Puccinia triticina* in the United States in 2010 identified by virulence to 19 differential Thatcher wheat lines with single genes for leaf rust resistance^a

Phenotype	Virulences	Area 1 ^b		Area 2 ^c		Area 3 ^d		Area 4 ^e		Area 5 ^f		Area 6 ^g		Area 8 ^h		Total	
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
BBBDB	14a	0	0	0	0	0	0	0	0	0	0	1	0.7	0	0	1	0.2
LBGJG	1,11,10,14a,28	0	0	0	0	0	0	0	0	0	0	0	0	1	3.6	1	0.2
LBRJG	1,3ka,11,30,10,14a,28	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	2	0.4
MBBJG	1,3,10,14a,28	0	0	0	0	0	0	1	0.7	0	0	0	0	0	0	1	0.2
MBDSB	1,3,17,B,10,14a	0	0	0	0	0	0	0	0	0	0	0	0	7	25.0	7	1.3
MCDJB	1,3,26,17,10,14a	0	0	0	0	0	0	0	0	0	0	0	0	2	7.1	2	0.4
MCDSB	1,3,26,17,B,10,14a	0	0	7	12.1	0	0	2	1.5	0	0	0	0	10	35.7	19	3.5
MCRKG	1,3,26,3ka,11,30,10,14a,18,28	0	0	3	5.2	0	0	1	0.7	0	0	0	0	0	0	4	0.7
MCTPB	1,3,26,3ka,11,17,30,B,14a,18	0	0	0	0	2	3.5	0	0	0	0	0	0	0	0	2	0.4
MCTSB	1,3,26,3ka,11,17,30,B,10,14a	0	0	9	15.5	8	14.0	0	0	1	1.7	0	0	0	0	18	3.4
MDTJG	1,3,24,3ka,11,17,30,10,14a,28	2	3.8	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
MFBJG	1,3,24,26,10,14a,28	3	5.8	2	3.4	0	0	0	0	0	0	0	0	0	0	5	0.9
MFPSB	1,3,24,26,3ka,17,30,B,10,14a	5	9.6	0	0	3	5.3	10	7.4	0	0	9	6	1	3.6	28	5.2
MGBGG	1,3,16,10,28	0	0	0	0	0	0	0	0	0	0	1	0.7	0	0	1	0.2
MLDSB	1,3,9,17,B,10,14a,39/41	20	38.5	4	6.9	1	1.8	65	48.1	12	20.7	55	36.9	3	10.7	160	29.8
MLFQD	1,3,9,17,30,B,10,39/41	0	0	0	0	0	0	0	0	0	0	1	0.7	0	0	1	0.2
SBDGG	1,2a,2c,17,10,28	0	0	0	0	0	0	0	0	0	0	1	0.7	0	0	1	0.2
SBJDG	1,2a,2c,11,17,14a,28	0	0	0	0	0	0	0	0	2	3.4	0	0	0	0	2	0.4
SCJDG	1,2a,2c,26,11,17,14a,28	0	0	0	0	0	0	0	0	2	3.4	0	0	0	0	2	0.4
TBBGG	1,2a,2c,3,10,28	0	0	0	0	0	0	1	0.7	2	3.4	1	0.7	0	0	4	0.7
TBBJG	1,2a,2c,3,10,14a,28	0	0	0	0	2	3.5	0	0	2	3.4	2	1.3	0	0	6	1.1
TBRKG	1,2a,2c,3,3ka,11,30,10,14a,18,28	3	5.8	2	3.4	0	0	2	1.5	0	0	0	0	0	0	7	1.3
TCBBB	1,2a,2c,3,26	0	0	0	0	0	0	2	1.5	0	0	0	0	0	0	2	0.4
TCGJG	1,2a,2c,3,26,11,10,14a,28	0	0	0	0	0	0	0	0	0	0	2	1.3	0	0	2	0.4
TCRJG	1,2a,2c,3,26,3ka,11,30,10,14a,28	0	0	2	3.4	0	0	0	0	2	3.4	0	0	0	0	4	0.7
TCRKG	1,2a,2c,3,26,3ka,11,30,10,14a,18,28	12	23.1	18	31.0	32	56.1	5	3.7	0	0	4	2.7	0	0	71	13.2
TCRKJ	1,2a,2c,3,26,3ka,11,30,10,14a,18,28,39/41	0	0	2	3.4	0	0	0	0	0	0	0	0	0	0	2	0.4
TDBGG	1,2a,2c,3,24,10,28	0	0	0	0	0	0	8	5.9	5	8.6	1	0.7	0	0	14	2.6
TDBJG	1,2a,2c,3,24,10,14a,28	7	13.5	0	0	8	14.0	36	26.7	22	37.9	47	31.5	4	14.3	124	23.1
TDDSB	1,2a,2c,3,24,17,B,10,14a	0	0	0	0	1	1.8	0	0	0	0	0	0	0	0	1	0.2
TFBGG	1,2a,2c,3,24,26,10,28	0	0	0	0	0	0	0	0	0	0	5	3.4	0	0	5	0.9
TFBGQ	1,2a,2c,3,24,26,10,21,28	0	0	0	0	0	0	0	0	0	0	9	6	0	0	9	1.7
TFBJG	1,2a,2c,3,24,26,10,14a,28	0	0	0	0	0	0	0	0	0	0	4	2.7	0	0	4	0.7
TFBJQ	1,2a,2c,3,24,26,10,14a,21,28	0	0	0	0	0	0	0	0	0	0	3	2	0	0	3	0.6
TGBJG	1,2a,2c,3,16,10,14a,28	0	0	0	0	0	0	0	0	0	0	1	0.7	0	0	1	0.2
TJBGG	1,2a,2c,3,16,23a,10,28	0	0	0	0	0	0	0	0	0	0	2	1.3	0	0	2	0.4
TLDSB	1,2a,2c,3,9,17,B,10,14a,39/41	0	0	0	0	0	0	0	0	4	6.9	0	0	0	0	4	0.7
TNRJJ	1,2a,2c,3,9,24,3ka,11,30,10,14a,28,39/41	0	0	7	12.1	0	0	2	1.5	4	6.9	0	0	0	0	13	2.4
Total	...	52	...	58	...	57	...	135	...	58	...	149	...	28	...	537	...

^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 a winter wheat line with gene *Lr39/41*.

^b States of Alabama, Arkansas, Georgia, Louisiana, Mississippi, and North Carolina.

^c States of New York, Pennsylvania, and Virginia.

^d States of Illinois, Indiana, Kentucky, Ohio, Pennsylvania, and Wisconsin.

^e States of Oklahoma and Texas.

^f States of Kansas and Nebraska.

^g States of Minnesota, Montana, North Dakota, and South Dakota.

^h States of Oregon and Washington.

and Nebraska (area 5), 11 virulence phenotypes were found among the 58 isolates that were tested. Phenotypes TDBJG (37.9%), MLDSB (20.7%), TLDSD (6.9%), and TNRJJ (6.9%) were the four most common phenotypes in this area. In Minnesota, South Dakota, and North Dakota, 18 virulence phenotypes were identified among the 149 isolates that were tested. Phenotypes MLDSB (36.9%), TDBJG (31.5%), MFPSB (6.0%), and TFBGQ (6.0%) were the four most common phenotypes in this area. In Washington State and Oregon (area 8), seven virulence phenotypes were found among the 28 isolates that were tested. Phenotypes MCDSB (35.7%), MBDSB (25.0%), and TDBJG (14.3%) were the three most common phenotypes in this area. A complete listing of the host cultivars and breeding lines, locations, and virulence phenotypes identified from the *P. triticina* collections in 2010 is available at the USDA-ARS Cereal Disease Laboratory website.

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*, *Lr3*, and *Lr10* was over 90% in all areas. Virulence to gene *Lr16* was found only in area 6 at 2.7%. Virulence to *Lr21* was found only in area 8 at 8.1%. Virulence to the remaining *Lr* genes was highly variable across the different areas. Virulence to *Lr2a* and *Lr2c* was lowest in area 8 (14.3%) and highest (77.6%) in area 6. Virulence to *Lr9* and *Lr39/41* was lowest in area 3 (1.8%) and highest in area 4 (49.4%). Virulence to *Lr24* was lowest in area 2 (15.5%) and highest in area 6 (53.7%). Virulence to *Lr26* was lowest in area 5 (8.6%) and highest in area 3 (78.9%). Virulence to *Lr3ka* and *Lr30* was lowest in area 8 (3.6%) and highest in area 3 (78.9%). Virulence to *Lr11* was lowest in area 8 (3.6%) and highest in area 2 (77.6%). Virulence to *Lr17* was lowest in area 3 (26.3%) and highest in area 8 (82.1%). Virulence to *LrB* was lowest in area 3 (26.3%) and highest in area 8 (75.0%). Virulence to *Lr14a* was 100% in areas 1, 2, 3, and 8 and between 85.9 and 91.9% in areas 4, 5, and 6. Virulence to *Lr18* was lowest in areas 5 and 8 (0.0%) and highest in area 3 (59.6%). Virulence to *Lr28* was lowest in area 8 (17.9%) and highest in area 3 (73.7%). The average of Nei's distance for virulence between isolates in areas 4 and 6 with isolates in area 5 was less than 0.03 (Fig. 2). The average virulence distance between isolates in area 1

with isolates in areas 4, 5, and 6 was 0.055. The average distance between isolates in areas 1, 4, 5, and 6 with isolates in areas 2 and 3 was 0.15.

In area 1 (Fig. 3A), the frequency of isolates with virulence to *Lr11*, *Lr18*, and *Lr26* declined from 2009. Isolates with virulence to *Lr9* and *Lr24* increased from 2009, and isolates with virulence to *Lr1* remained at 100%. In area 4 (Fig. 3B), isolates with virulences to *Lr9*, *Lr16*, *Lr17*, and *Lr26* remained relatively unchanged from 2009. In area 6 (Fig. 3C), isolates with virulences to *Lr2a*, *Lr24*, and *Lr26* increased slightly from 2009; isolates with viru-

Fig. 2. Unweighted pair group method with arithmetic means dendrogram of Nei's genetic distance adapted for virulence of *Puccinia triticina* isolates in areas 1, 2, 3, 4, 5, and 6 in the United States in 2010.

Table 2. Number (*n*) and frequency (%) of isolates of *Puccinia triticina* in the United States in 2010 virulent to 19 differential 'Thatcher' wheat lines with single resistance genes for leaf rust resistance

Gene	Area 1 ^a		Area 2 ^b		Area 3 ^c		Area 4 ^d		Area 5 ^e		Area 6 ^f		Area 8 ^g		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
<i>Lr1</i>	52	100.0	58	100.0	57	100.0	135	100.0	58	100.0	148	99.3	28	100.0	536	99.8
<i>Lr2a</i>	22	42.3	31	53.4	43	75.4	56	41.5	45	77.6	82	55.0	4	14.3	283	52.7
<i>Lr2c</i>	22	42.3	31	53.4	43	75.4	56	41.5	45	77.6	82	55.0	4	14.3	283	52.7
<i>Lr3</i>	52	100.0	56	96.6	57	100.0	135	100.0	54	93.1	147	98.7	27	96.4	528	98.3
<i>Lr9</i>	20	38.5	11	19.0	1	1.8	67	49.6	20	34.5	56	37.6	3	10.7	178	33.1
<i>Lr16</i>	0	0	0	0	0	0	0	0	0	0	4	2.7	0	0	4	0.7
<i>Lr24</i>	17	32.7	9	15.5	12	21.1	56	41.5	31	53.4	80	53.7	5	17.9	210	39.1
<i>Lr26</i>	20	38.5	43	74.1	45	78.9	20	14.8	5	8.6	36	24.2	13	46.4	182	33.9
<i>Lr3ka</i>	22	42.3	45	77.6	45	78.9	20	14.8	7	12.1	13	8.7	1	3.6	153	28.5
<i>Lr11</i>	17	32.7	45	77.6	42	73.7	10	7.4	11	19.0	6	4.0	1	3.6	132	24.6
<i>Lr17</i>	27	51.9	20	34.5	15	26.3	77	57.0	21	36.2	66	44.3	23	82.1	249	46.4
<i>Lr30</i>	22	42.3	45	77.6	45	78.9	20	14.8	7	12.1	14	9.4	1	3.6	154	28.7
<i>LrB</i>	25	48.1	20	34.5	15	26.3	77	57.0	17	29.3	65	43.6	21	75.0	240	44.7
<i>Lr10</i>	52	100.0	58	100.0	55	96.5	133	98.5	54	93.1	148	99.3	28	100.0	528	98.3
<i>Lr14a</i>	52	100.0	58	100.0	57	100.0	124	91.9	51	87.9	128	85.9	28	100.0	498	92.7
<i>Lr18</i>	15	28.8	25	43.1	34	59.6	8	5.9	0	0	4	2.7	0	0	86	16.0
<i>Lr21</i>	0	0	0	0	0	0	0	0	0	0	12	8.1	0	0	12	2.2
<i>Lr28</i>	27	51.9	38	65.5	42	73.7	56	41.5	41	70.7	83	57.7	5	17.9	295	54.9
<i>Lr39/41</i>	20	38.5	13	22.4	1	1.8	67	49.6	20	34.5	56	37.6	3	10.7	180	33.5
Total	52	...	58	...	57	...	135	...	58	...	149	...	28	...	537	...

^a States of Alabama, Arkansas, Georgia, Louisiana, Mississippi, and North Carolina.

^b States of New York, Pennsylvania, and Virginia.

^c States of Illinois, Indiana, Kentucky, Ohio, Pennsylvania, and Wisconsin.

^d States of Oklahoma and Texas.

^e States of Kansas and Nebraska.

^f States of Minnesota, Montana, North Dakota, and South Dakota.

^g States of Oregon and Washington.

lence to *Lr17* declined slightly; and virulence to *Lr16* remained very low.

Discussion

In 2010, the most common virulence phenotypes of *P. tritici* were selected by the leaf rust resistance genes present in the hard red winter and soft red winter wheat cultivars. The most common virulence phenotype, MLDS, was virulent to genes *Lr17* and *Lr39/Lr41* that have been postulated to be in the hard red winter wheat Jagger (*Lr17*), 'TAM 111' (*Lr17*), 'Santa Fe' (*Lr17*), Overlay (*Lr39/Lr41*), 'TAM 112' (*Lr39/Lr41*), 'Postrock' (*Lr39/Lr41*), and 'Fuller' (*Lr17* and *Lr39/Lr41*) that are grown in the southern and central Great Plains region. The second most common phenotype, TDBJG, is virulent to *Lr24* that was postulated to be present in hard red winter wheat such as 'TAM 113', Jagalene, 'Cutter', 'Ike', 'Hitch', and 'Ogallala'. The third most common phenotype, TCRKG is virulent to genes *Lr11*, *Lr18*, and *Lr26*. These genes were postulated to be present in soft red winter wheat such as 'Panola' (*Lr11*), 'Coker 9553' (*Lr11*), 'Saluda' (*Lr11*), 'S550' (*Lr26*), 'USG3209' (*Lr11*, *Lr26*), 'Jamestown' (*Lr11* and *Lr18*), and 'Shirley' (*Lr11*, *Lr18*, *Lr26*) that are grown in the southern and eastern United States.

Fig. 3. Frequency (%) of *Puccinia tritici* isolates with virulence to selected leaf rust resistance genes (*Lr1*, *Lr2a*, *Lr9*, *Lr24*, *Lr26*, *Lr11*, and *Lr18*) from 1996 to 2010 in the following areas of the United States: **A**, southeastern states (area 1); **B**, southern Great Plains (area 4); and **C**, northern Great Plains (area 6).

In 2010, phenotype MLDS was widespread across the United States, because it was the first or second most common phenotype in all areas except areas 2 and 8. This phenotype first increased and became common in the southern Great Plains region of areas 4 and 5 due to virulence to *Lr17* and *Lr39/Lr41* in 2005–06 (7,8). In recent years, MLDS has spread to the southern United States and has remained prevalent in the Great Plains region. Not all phenotypes were widely distributed because there were some strong geographic differences in phenotype distribution. Phenotypes TCRKG and TBRKG were prevalent in areas 1, 2, and 3 but occurred at low frequencies in the other areas. MCDSB was the most common phenotype in Oregon and Washington State (area 8) but occurred at lower frequencies in the other areas. In 2009 (10), MLDS (28.9%), TCRKG (16.8%), and TDBGG (14.4%) were the three most common phenotypes in the United States. From 2009 to 2010 there was relatively little change in the most prevalent phenotypes throughout the United States.

In 2010 in Minnesota and North Dakota spring wheat research plots, cultivars with *Lr21* had higher levels of leaf rust than observed in previous years. Phenotypes TFBJQ and TFBGQ, both with virulence to *Lr21*, were identified from these collections. As previously noted (6), this was the first confirmed virulence in *P. tritici* in North America on wheat lines with *Lr21*. Many of the spring wheat cultivars currently grown in North Dakota and Minnesota have *Lr21*. If phenotypes with *Lr21* virulence persist and spread in the North American *P. tritici* population, then cultivars with this gene will suffer increased leaf rust infection severity.

Previously (17), six distinct groups of *P. tritici* isolates in North America were described based on simple sequence repeat (SSR) genotypes that also differed for virulence phenotypes. In that study, isolates with MLDS phenotype were in the NA-3 SSR group. Phenotypes TCRKG and TDBJG were in the SSR group NA-5. Phenotypes TFBGQ and TFBJQ with *Lr21* virulence and other phenotypes with new combinations of virulence will be genotyped in future years and compared with the SSR genotypes of the previously characterized populations to determine whether any new introductions of *P. tritici* have occurred in North America.

As in previous years (9,10), two epidemiological zones of *P. tritici* phenotypes were evident from the 2010 virulence data. Isolates in areas 2 and 3 were nearly identical for virulence and differed for virulence compared with isolates in areas 1, 4, 5, and 6. In a change from previous years, isolates in area 1 were closer for virulence to isolates in areas 4, 5, and 6 due to the widespread occurrence of phenotype MLDS in these four areas. In 2008 and 2009, isolates in the soft red winter wheat region of areas 1, 2, and 3 were very similar for virulence, as were isolates in the hard red winter wheat region of areas 4, 5, and 6. The different *Lr* genes present in the soft red winter wheat cultivars and hard red wheat cultivars have contributed to maintaining different regional populations of *P. tritici* phenotypes in the United States.

The widespread use of wheat cultivars in the United States with genes that are effective in seedling plants and condition resistance to specific leaf rust phenotypes has led to the development of a *P. tritici* population that is highly diverse for virulence. Because populations of *P. tritici* in the United States are extremely large, it would be expected that recurrent mutations would generate new virulence phenotypes that would increase in response to leaf rust resistance genes in wheat cultivars. As new cultivars with leaf rust resistance are released, it will be important to characterize the resistance in these cultivars by gene postulation (5,16) or by molecular markers in order to determine whether leaf rust resistance genes in host cultivars have selected for new *P. tritici* virulence phenotypes as in the case of the newly emerged virulence for *Lr21*.

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