Physiologic Specialization of *Puccinia triticina* on Wheat in the United States in 2013

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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 USDA-ARS personnel and cooperators in the Great Plains, Ohio River Valley, and southeastern states in order to determine the virulence of the wheat leaf rust population in 2013. Single uredinial isolates (490 total) were derived from the collections and tested for virulence phenotype on 20 lines of Thatcher wheat that are near-isogenic for leaf rust resistance genes. In 2013, 79 virulence phenotypes were described in the United States. Virulence phenotypes MBTNB, TNBGJ, and MCTNB were the

three most common phenotypes. Phenotypes MBTNB and MCTNB are both virulent to *Lr11*, and MCTNB is virulent to *Lr26*. MBTNB and MCTNB were most common in the soft red winter wheat region of the southeastern states and Ohio Valley. Phenotype TNBGJ is virulent to *Lr39/41* and was widely distributed throughout the hard red winter wheat region of the Great Plains. Isolates with virulence to *Lr11*, *Lr18*, and *Lr26* were common in the southeastern states and Ohio Valley region. Isolates with virulence to *Lr21*, *Lr24*, and *Lr39/41* were frequent in the hard red wheat region of the southern and northern Great Plains.

Leaf rust, caused by *Puccinia triticina* Eriks., is a common disease of wheat (*Triticum aestivum* L.) in the United States (Kolmer and Jin 2007) and worldwide (Roelfs et al. 1992). The leaf rust fungus is well adapted to most continental and coastal climates where wheat matures in warm to hot conditions. Leaf rust is the most common rust on wheat in North America (Samborski 1985), South America (Germán et al. 2007), Central Asia (Morgounov et al. 2007), Russia (Morgounov et al. 2011), and central, eastern, and southern Europe (Chester 1946). In the United States, leaf rust infections can overwinter in the southern Great Plains region of Texas, Oklahoma, and Kansas and also in the southeastern states from Louisiana to Virginia (Roelfs 1989). As the winter wheat crop matures in spring, urediniospores are produced on infected winter wheat plants and are carried by the southerly winds to the wheat-producing regions in the Northern Great Plains, Ohio Valley, and northeastern states. Leaf rust can survive and spread easily in the United States since many of the most commonly grown hard red and soft red winter wheat cultivars are susceptible.

Populations of cereal rust fungi in large continental regions such as North America can vary for race or virulence phenotype due to various forces. Differences in sexual or asexual reproduction between populations in different regions can lead to clear differentiation of virulence phenotypes on a regional basis as is found for wheat stem rust (*P. graminis* f. sp. *tritici*) in North America (Roelfs and Groth 1980). However, because *P. triticina* reproduces throughout North America by the clonal production of urediniospores on wheat (Ordoñez and Kolmer 2009), any regional differentiation of populations cannot be due to differences in reproduction. Restricted movement of urediniospores and overwintering of rust infections can also result in regional populations of virulence phenotypes. In Pennsylvania (Schafer and Long 1988), New York, and Washington (Kolmer and Hughes 2014), distinct virulence phenotypes

of *P. triticina* have been collected from the soft red winter and soft white winter wheat cultivars that are grown in these states. These virulence phenotypes likely overwintered in these states and were not found in other regions of the United States in those years. Differences in host resistance genotypes can also lead to regional differences in virulence phenotypes. In the Great Plains region of Texas, Oklahoma, Kansas, and Nebraska, hard red winter wheat cultivars such as Jagger with *Lr17* (Long et al. 2000), Overlay (*Lr39/41*) (Kolmer et al. 2011), and Jagalene (*Lr24*) (Kolmer et al. 2007) have been associated with rapid increases of phenotypes with virulence to these cultivars. In Minnesota and North Dakota, phenotypes with virulence to *Lr21* are found (Kolmer and Hughes 2013) due to the presence of this gene in many spring wheat cultivars. In the southeastern and Ohio Valley states where soft red winter wheat cultivars with genes *Lr9*, *Lr11*, *Lr18*, and *Lr26* are grown (Kolmer 2003), phenotypes with virulence to these genes are common.

The USDA-ARS Cereal Disease Laboratory has conducted virulence surveys of the wheat leaf rust fungus since 1978 (Long et al. 1985) 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 (Johnston et al. 1968) and Indiana (Mains and Jackson 1926). Similar surveys have been done in Canada since 1931 (Johnson 1956; McCallum and Seto-Goh 2006). In the United States (Leonard et al. 1992) and Canada (Kolmer 1999), 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 2013 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 2013, USDA-ARS personnel and cooperators in the United States made a total of 271 uredinial collections of leaf rust from wheat plots and fields in surveys of the Great Plains, Ohio River Valley, northeastern states, and southeastern states. Field surveys of wheat were made by USDA-ARS personnel in Kansas and western Missouri (late May), southern Minnesota (mid-June), Ohio Valley (mid-June), and Minnesota, North Dakota, South Dakota, and Wisconsin (early July and again in late July). Additional collections were made in wheat breeding

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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.

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 the wheat cultivar Little Club, which were treated with a maleic hydrazide solution of approximately 0.01 g (dissolved in 30 ml 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 Plexiglas isolation chambers in a greenhouse where temperatures varied between 18 and 28°C daily with 16 h of supplemental greenhouse lighting. After 12 to 15 days, two to three seedlings were saved per collection, each with the primary leaf trimmed to isolate

Table 1. Number and frequency (%) of virulence phenotypes of *Puccinia triticina* in the United States in 2013 identified by virulence to 20 lines of wheat 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		Total	
		#	%	#	%	#	%	#	%	#	%	#	%	#	%
BBBQD	B,10,39/41	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
CCPSB	3,26,3ka,17,30,B,10,14a	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
FBPSB	2c,3,3ka,17,30,B,10,14a	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
FCPLB	2c,3,26,3ka,17,30,B	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
KFBIG	2a,2c,3,24,26,10,14a,28	0	0	0	0	1	1.2	0	0	1	1.1	0	0	2	0.4
LBBGG	1,10,28	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
MBDSB	1,3,17,B,10,14a	0	0	0	0	0	0	1	1.4	0	0	1	0.9	2	0.4
MBDSD	1,3,17,B,10,14a,39/41	0	0	0	0	0	0	5	7.2	6	6.5	13	11.5	24	4.9
MBPSB	1,3,3ka,17,30,B,10,14a	0	0	0	0	1	1.2	7	10.1	0	0	4	3.5	12	2.4
MBPSD	1,3,3ka,17,30,B,10,14a,39/41	2	1.6	0	0	0	0	1	1.4	1	1.1	1	0.9	5	1.0
MBTNB	1,3,3ka,11,17,30,B,14a	28	22.8	0	0	42	49.4	1	1.4	5	5.4	1	0.9	77	15.7
MBTSB	1,3,3ka,11,17,30,B,10,14a	4	3.3	0	0	1	1.2	0	0	3	3.2	0	0	8	1.6
MCDSB	1,3,26,17,B,10,14a	0	0	0	0	0	0	1	1.4	0	0	0	0	1	0.2
MCSDS	1,3,26,17,B,10,14a,39/41	0	0	0	0	1	1.2	0	0	1	1.1	2	1.8	4	0.8
MCPSD	1,3,26,3ka,17,30,B,10,14a,39/41	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
MCRHG	1,3,26,3ka,11,30,10,18,28	0	0	2	28.6	0	0	0	0	0	0	0	0	2	0.4
MCSQB	1,3,26,3ka,11,17,B,10	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
MCTNB	1,3,26,3ka,11,17,30,B,14a	20	16.3	0	0	7	8.2	2	2.9	2	2.2	0	0	31	6.3
MCTQB	1,3,26,3ka,11,17,30,B,10	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
MCTSB	1,3,26,3ka,11,17,30,B,10,14a	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
MDPSB	1,3,24,3ka,17,30,B,10,14a	0	0	0	0	0	0	2	2.9	0	0	0	0	2	0.4
MFBSB	1,3,24,26,B,10,14a	0	0	0	0	0	0	1	1.4	0	0	0	0	1	0.2
MFDSB	1,3,24,26,17,B,10,14a	0	0	0	0	0	0	0	0	0	0	2	1.8	2	0.4
MFNSB	1,3,24,26,3ka,17,B,10,14a	0	0	0	0	0	0	2	2.9	1	1.1	4	3.5	7	1.4
MFNSD	1,3,24,26,3ka,17,B,10,14a,39/41	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
MFPSB	1,3,24,26,3ka,17,30,B,10,14a	2	1.6	0	0	0	0	9	13.0	4	4.3	5	4.4	20	4.1
MFQHG	1,3,24,26,3ka,11,10,18,28	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
MHDNB	1,3,16,26,17,B,14a	1	0.8	0	0	1	1.2	0	0	1	1.1	0	0	3	0.6
MHDSB	1,3,16,26,17,B,10,14a	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
MJBIG	1,3,16,24,10,14a,28	0	0	0	0	0	0	0	0	2	2.2	0	0	2	0.4
MJPSB	1,3,16,24,3ka,17,30,B,10,14a	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
MLDSD	1,3,9,17,B,10,14a,39/41	0	0	2	28.6	0	0	2	2.9	1	1.1	0	0	5	1.0
MLPSD	1,3,9,3ka,17,30,B,10,14a,39/41	0	0	0	0	0	0	1	1.4	7	7.5	1	0.9	9	1.8

(continued on next page)

^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*, *Lr39/41*, and *Lr42*.

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

^c State of New York.

^d States of Illinois, Indiana, Michigan, eastern Missouri, Ohio, and Wisconsin.

^e States of Oklahoma and Texas.

^f States of Colorado, Iowa, Kansas, western Missouri, and Nebraska.

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

a single uredinium. When single uredinia began to form secondary rings, generally 9 to 14 days after inoculation, cyclone spore collectors were used to collect urediniospores separately from two to three single uredinia per collection. Urediniospores of the single-uredinal isolates 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*, *Lr3*, *Lr3ka*, *Lr9*, *Lr10*, *Lr11*, *Lr14a*, *Lr16*, *Lr17*, *Lr18*, *Lr21*, *Lr24*, *Lr26*, *Lr28*, *Lr30*, and *Lr39/41*, *Lr42*, and *LrB*. If an insufficient amount of urediniospores were obtained from the single uredinium to inoculate a differential set, the spores were increased on seedlings of the susceptible wheat cultivar Little Club prior to testing on the differential set.

Sets of differential lines were grown in the greenhouse and evaluated for rust infection type from April to June and from September through the end of January. Natural daylight was supplemented with high-pressure sodium lamps from 0800 to 2400 h. After 10 to 12 days,

infection types (IT) were recorded as either high (IT 3 to 4) or low (IT 0 to 2*) as previously described (Oelke and Kolmer 2004). A five letter code based on the original code proposed for *P. triticina* (Long and Kolmer 1989) describes the low or high infection types to the 20 differential lines. Each letter corresponds to the infection types of four differentials. The Thatcher lines with genes *Lr1*, *Lr2a*, *Lr2c*, and *Lr3* were the four lines in the first set of differentials; lines with genes *Lr9*, *Lr16*, *Lr24*, and *Lr26* were the second set of differentials; lines with genes *Lr3ka*, *Lr11*, *Lr17*, and *Lr30* were the third set of differentials; lines with genes *LrB*, *Lr10*, *Lr14a*, and *Lr18* were the fourth set of differentials; and lines with genes *Lr21*, *Lr28*, *Lr39/41*, and *Lr42* were the fifth set of differentials. Sets 1 to 3 are the same as described previously (Long and Kolmer 1989). The first four sets of differentials have been used in *P. triticina* surveys in Canada (Kolmer 1998). The fifth set of differentials was added for the first time in U.S. surveys in 2004, since *Lr21* is present in spring wheat cultivars, *Lr39/41* is present in winter wheat cultivars, and *Lr28* differentiates *P. triticina* virulence

Table 1. (continued from preceding page)

Phenotype	Virulences	Area 1 ^b		Area 2 ^c		Area 3 ^d		Area 4 ^e		Area 5 ^f		Area 6 ^g		Total	
		#	%	#	%	#	%	#	%	#	%	#	%	#	%
MMPSD	1,3,9,26,3ka,17,30,B,10,14a,39/41	0	0	0	0	0	0	1	1.4	0	0	1	0.9	2	0.4
NBBRG	1,2c,B,10,18,28	0	0	0	0	1	1.2	0	0	0	0	1	0.9	2	0.4
PBDBG	1,2c,3,17,28	0	0	0	0	0	0	1	1.4	0	0	0	0	1	0.2
PBDGG	1,2c,3,17,10,28	0	0	0	0	0	0	3	4.3	0	0	2	1.8	5	1.0
PBDGJ	1,2c,3,17,10,28,39/41	0	0	0	0	0	0	2	2.9	0	0	4	3.5	6	1.2
PBDQJ	1,2c,3,17,B,10,28,39/41	0	0	0	0	0	0	0	0	3	3.2	3	2.7	6	1.2
PCDGJ	1,2c,3,26,17,10,28,39/41	0	0	0	0	0	0	3	4.3	0	0	0	0	3	0.6
PCLQG	1,2c,3,26,3ka,B,10,28	0	0	1	14.3	0	0	0	0	0	0	0	0	1	0.2
SBDGG	1,2a,2c,17,10,28	2	1.6	2	28.6	0	0	2	2.9	3	3.2	0	0	9	1.8
TBBBJ	1,2a,2c,3,28,39/41	0	0	0	0	1	1.2	0	0	1	1.1	0	0	2	0.4
TBBGJ	1,2a,2c,3,10,28,39/41	0	0	0	0	2	2.4	4	5.8	8	8.6	10	8.8	24	4.9
TBBGS	1,2a,2c,3,10,21,28,39/41	0	0	0	0	0	0	1	1.4	0	0	10	8.8	11	2.2
TBBJG	1,2a,2c,3,10,14a,28	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
TBDJQ	1,2a,2c,3,17,10,14a,21,28	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
TBGJG	1,2a,2c,3,11,10,14a,28	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
TBJSB	1,2a,2c,3,11,17,B,10,14a	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
TBRFG	1,2a,2c,3,3ka,11,30,14a,18,28	2	1.6	0	0	0	0	0	0	1	1.1	0	0	3	0.6
TBRKG	1,2a,2c,3,3ka,11,30,10,14a,18,28	22	17.9	0	0	4	4.7	0	0	2	2.2	2	1.8	30	6.1
TCBJG	1,2a,2c,3,26,10,14a,28	0	0	0	0	0	0	0	0	0	0	2	1.8	2	0.4
TCDSB	1,2a,2c,3,26,17,B,10,14a	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
TCGJG	1,2a,2c,3,26,11,10,14a,28	3	2.4	0	0	0	0	0	0	0	0	0	0	3	0.6
TCJSB	1,2a,2c,3,26,11,17,B,10,14a	4	3.3	0	0	0	0	0	0	1	1.1	2	1.8	7	1.4
TCQJG	1,2a,2c,3,26,3ka,11,10,14a,28	0	0	0	0	0	0	0	0	0	0	3	2.7	3	0.6
TCRFG	1,2a,2c,3,26,3ka,11,30,14a,18,28	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
TCRKG	1,2a,2c,3,26,3ka,11,30,10,14a,18,28	16	13.0	0	0	9	10.6	0	0	2	2.2	0	0	27	5.5
TCTSB	1,2a,2c,3,26,3ka,11,17,30,B,10,14a	2	1.6	0	0	2	2.4	0	0	0	0	0	0	4	0.8
TDBGJ	1,2a,2c,3,24,10,28,39/41	0	0	0	0	1	1.2	1	1.4	2	2.2	3	2.7	7	1.4
TDBGQ	1,2a,2c,3,24,10,21,28	0	0	0	0	0	0	0	0	0	0	4	3.5	4	0.8
TDBJG	1,2a,2c,3,24,10,14a,28	0	0	0	0	0	0	1	1.4	1	1.1	2	1.8	4	0.8
TDBJJ	1,2a,2c,3,24,10,14a,28,39/41	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
TDBJQ	1,2a,2c,3,24,10,14a,21,28	0	0	0	0	0	0	3	4.3	0	0	2	1.8	5	1.0
TDBSB	1,2a,2c,3,24,B,10,14a	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
TDGJG	1,2a,2c,3,24,11,10,14a,28	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
TDPSB	1,2a,2c,3,24,3ka,17,30,B,10,14a	0	0	0	0	0	0	1	1.4	0	0	1	0.9	2	0.4
TFBGJ	1,2a,2c,3,24,26,10,28,39/41	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
TFBJQ	1,2a,2c,3,24,26,10,14a,21,28	0	0	0	0	0	0	0	0	1	1.1	0	0	1	0.2
TFKDB	1,2a,2c,3,24,26,11,17,30,14a	0	0	0	0	2	2.4	0	0	0	0	0	0	2	0.4
TFKNB	1,2a,2c,3,24,26,11,17,30,B,14a	0	0	0	0	1	1.2	0	0	0	0	0	0	1	0.2
TFPSB	1,2a,2c,3,24,26,3ka,17,30,B,10,14a	1	0.8	0	0	1	1.2	0	0	0	0	0	0	2	0.4
TJBJG	1,2a,2c,3,16,24,10,14a,28	0	0	0	0	0	0	0	0	0	0	1	0.9	1	0.2
TNBGJ	1,2a,2c,3,9,24,10,28,39/41	0	0	0	0	1	1.2	5	7.2	17	18.3	16	14.2	39	8.0
TNBJJ	1,2a,2c,3,9,24,10,14a,28,39/41	2	1.6	0	0	1	1.2	5	7.2	6	6.5	2	1.8	16	3.3
TNRJJ	1,2a,2c,3,9,24,3ka,11,30,10,14a,28,39/41	4	3.3	0	0	0	0	0	0	0	0	0	0	4	0.8
TPBGJ	1,2a,2c,3,9,24,26,10,28,39/41	0	0	0	0	0	0	1	1.4	2	2.2	3	2.7	6	1.2
TPBJJ	1,2a,2c,3,9,24,26,10,14a,28,39/41	0	0	0	0	0	0	0	0	2	2.2	0	0	2	0.4
TPRJJ	1,2a,2c,3,9,24,26,3ka,11,30,10,14a,28,39/41	1	0.8	0	0	0	0	0	0	0	0	0	0	1	0.2
Total		123		7		85		69		93		113		490	

phenotypes. Near-isogenic Thatcher lines with *Lr39/41* and *Lr42* were used for the first time in 2012. When possible, isolates with phenotypes that were recorded only once were tested a second time to confirm their phenotype.

Phenotype and virulence frequencies were determined for collections from six agroecological geographic areas as shown and described in Figure 1. Collections were not obtained from areas 7 or 8 in 2013. A modified version of Nei's genetic distance (Nei 1972) 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 UPGMA 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 infection types to different virulence phenotypes of *P. triticina* using previously cited methods (Kolmer 2003; Oelke and Kolmer 2004). The infection types 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.

Results

Leaf rust occurrence and isolate collections. In 2013, wheat leaf rust was widely distributed across the United States from the Great Plains to the east coast, but was generally found at low levels. Leaf

Table 2. Number and frequency (%) of isolates of *Puccinia triticina* in the United States in 2013 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		Total	
	#	%	#	%	#	%	#	%	#	%	#	%	#	%
<i>Lr1</i>	123	100.0	7	100.0	84	98.8	69	100.0	89	95.7	112	99.1	484	98.8
<i>Lr2a</i>	63	51.2	2	28.6	30	35.3	24	34.8	51	54.8	64	56.6	234	47.8
<i>Lr2c</i>	63	51.2	3	42.9	31	36.5	33	47.8	55	59.1	75	66.4	260	53.1
<i>Lr3</i>	121	98.4	5	71.4	84	98.8	67	97.1	88	94.6	112	99.1	477	97.3
<i>Lr9</i>	7	5.7	2	28.6	2	2.4	15	21.7	35	37.6	23	20.4	84	17.1
<i>Lr16</i>	1	0.8	0	0.0	1	1.2	0	0.0	4	4.3	2	1.8	8	1.6
<i>Lr24</i>	12	9.8	0	0.0	9	10.6	31	44.9	41	44.1	47	41.6	140	28.6
<i>Lr26</i>	54	43.9	3	42.9	27	31.8	20	29.0	20	21.5	28	24.8	152	31.0
<i>Lr3ka</i>	107	87.0	3	42.9	69	81.2	27	39.1	31	33.3	26	23.0	263	53.7
<i>Lr11</i>	110	89.4	2	28.6	72	84.7	3	4.3	16	17.2	8	7.1	211	43.1
<i>Lr17</i>	70	56.9	4	57.1	61	71.8	47	68.1	42	45.2	51	45.1	275	56.1
<i>Lr30</i>	105	85.4	2	28.6	72	84.7	25	36.2	30	32.3	18	15.9	252	51.4
<i>LrB</i>	69	56.1	3	42.9	59	69.4	37	53.6	40	41.9	46	40.7	253	51.6
<i>Lr10</i>	72	58.5	7	100.0	30	35.3	65	94.2	83	89.2	111	98.2	367	74.9
<i>Lr14a</i>	119	96.7	2	28.6	78	91.8	46	66.7	54	59.1	56	49.6	355	72.4
<i>Lr18</i>	41	33.3	2	28.6	15	17.6	0	0.0	5	5.4	3	2.7	66	13.5
<i>Lr21</i>	0	0.0	0	0.0	1	1.2	4	5.8	1	1.1	16	14.2	22	4.5
<i>Lr28</i>	54	43.9	5	71.4	25	29.4	32	46.4	56	60.2	71	62.8	243	49.6
<i>Lr39/41</i>	9	7.3	2	28.6	7	8.2	32	46.4	59	63.4	72	63.7	181	36.9
<i>Lr42</i>	0	0.0	0.0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total	123		7		85		69		93		113		490	

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

^b State of New York.

^c States of Illinois, Indiana, Michigan, eastern Missouri, Ohio, and Wisconsin.

^d States of Oklahoma and Texas.

^e States of Colorado, Iowa, Kansas, western Missouri, and Nebraska.

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

Fig. 2. UPGMA dendrogram of Nei's genetic distance adapted for virulence of *Puccinia triticina* isolates in agroecological areas 1, 2, 3, 4, 5, and 6 in the United States in 2013.

rust was present at high severity in plots in south central Texas in early February and at low levels in plots in southeastern Louisiana in early March. Cool spring weather delayed the planting of spring wheat and development of winter wheat in the Great Plains and many eastern states. Incidence and severity of leaf rust in the southern to northern Great Plains was low due to cooler spring temperatures, dry conditions, and the application of fungicides. Leaf rust was present in Minnesota in mid-June and was present at moderate levels in plots in North Dakota and northern Minnesota in late July. Because most of the leading wheat cultivars are susceptible to leaf rust, many wheat fields in the southeastern states, southern and northern Great Plains region, and Ohio Valley were sprayed with fungicide to prevent yield losses. Estimated losses of 1 to 2% in wheat due to leaf rust occurred in North Carolina, South Carolina, Mississippi, Missouri, Wisconsin, Illinois, Indiana, and Louisiana.

Estimated losses of less than 1% occurred in the other states. A complete summary of the wheat leaf rust incidence and severity in 2013 in the United States can be found at the USDA-ARS Cereal Disease Laboratory website (http://www.ars.usda.gov/SP2UserFiles/ad_hoc/36400500Cerealarustbulletins/13CRB9.pdf). Samples of leaf rust were obtained from 24 states in areas 1, 2, 3, 4, 5, and 6 from a total of 271 collections.

Distribution of virulence phenotypes. In 2013, 79 virulence phenotypes of wheat leaf rust were identified in the United States from 490 single-uredinial isolates that were tested on the Thatcher lines (Table 1). Phenotypes MBTNB (15.7%), TNBGJ (8.0%), and MCTNB (6.3%) were the three most common phenotypes across the United States. MBTNB was found in all areas except for the northeastern states of area 2. TNBGJ was found in areas 3, 4, 5, and 6, and MCTNB was found in areas 1, 3, 4, and 5. No virulence

Fig. 3. Frequency (%) of *Puccinia triticina* isolates with virulence to selected leaf rust resistance genes from 2004 to 2013 in the following areas of the United States: southeastern states (A, area 1); southern Great Plains (B, area 4); and northern Great Plains (C, area 6).

phenotypes were found in all areas. In the southeastern states (area 1), 24 virulence phenotypes were found among the 123 isolates tested (Table 1). Phenotypes MBTNB (22.8%), TBRKG (17.9%), and MCTNB (16.3%) were the three most common phenotypes in this area. In the northeastern states (area 2), four virulence phenotypes: MCRHG, MLDSB, PCLQG, and SBDGG were found among the seven isolates that were tested. In the Ohio Valley states (area 3), 24 virulence phenotypes were found among the 85 isolates that were tested. Phenotypes MBTNB (49.4%), TCRKG (10.6%), and MCTNB (8.2%) were the three most common phenotypes in this area. In Texas and Oklahoma (area 4), 28 virulence phenotypes were found among the 69 isolates that were tested. Phenotypes MFPSB (13%), MBPSB (10.1%), and MBDSD (7.2%) were the three most common phenotypes in this area. In Kansas and Nebraska (area 5), 34 virulence phenotypes were found among the 93 isolates that were tested. Phenotypes TNBGJ (18.3%), and TBBGJ (8.6%), and MLPSD (7.5%) were the three most common phenotypes in this area. In South Dakota, North Dakota, and Minnesota (area 6), 35 phenotypes were found among the 113 isolates tested. Phenotypes TNBGJ (14.2%), MBDSD (11.5%), TBBGJ (8.8%), and TBBGS (8.8%) were the four most common phenotypes in this area.

Virulence frequencies. Frequencies of virulence to the *Lr* genes differed among the regional populations of *P. tritici* in the United States and are listed in Table 2. Virulence to *Lr16* was found at very low levels in areas 1, 3, 5, and 6. Virulence to *Lr21* was found in areas 3, 4, 5, and 6. No isolates with virulence to *Lr42* were found. Isolates with virulence to *Lr1* and *Lr3* were >94% in areas 1, 3, 4, 5, and 6. Virulence to the other *Lr* genes was found at variable levels across the different regions. Virulence to genes *Lr11*, *Lr26*, and *Lr18* was highest in areas 1, 2, and 3. Virulence to *Lr24* and *Lr39/41* were highest in areas 4, 5, and 6. Based on frequencies of virulence to *Lr* genes, the areas split into three groups using Nei's genetic distance adapted for virulence (Fig. 2). Isolates in area 1 and area 3 were separated from isolates in areas 2, 4, 5, and 6 by 0.19 Nei's distance. Isolates in areas 1 and 3 and in areas 4, 5, and 6 were very closely related for virulence.

In area 1 (Fig. 3A), the frequency of isolates with virulence to *Lr11*, *Lr18*, and *Lr26* declined slightly from 2012, while isolates with virulence to *Lr9* increased slightly. In area 4 (Fig. 3B), the frequency of isolates with virulence to *Lr39/41* and *Lr24* decreased from 2012, while isolates with virulence to *Lr17* increased. In area 6 (Fig. 3C), isolates with virulence to *Lr2a* and *Lr21* declined from 2012, while isolates with virulence to *Lr16* remained at very low levels.

Discussion

In 2013 as in previous years, the leaf rust resistance genes that are present in the hard red winter and soft red winter wheat cultivars have likely selected the most prevalent virulence phenotypes of *P. tritici*. Phenotypes MBTNB and MCTNB, the most common and third most common phenotypes respectively, are virulent to *Lr11*, which is found in the soft red winter wheat cultivars that are grown in areas 1, 2, and 3 (Kolmer 2003). MCTNB is also virulent to *Lr26* that is also present in the soft red winter wheat cultivars. The second most common phenotype TNBGJ is virulent to *Lr39/41* that is present in many hard red winter wheat cultivars such as Armour, Fuller, TAM 112, PostRock, and Overlay that were widely grown in the southern Great Plains in 2013. The virulence of the *P. tritici* population in the United States did not change drastically in 2013 compared with the immediate previous years. In 2012, the three most common phenotypes were TNBGJ, TCRKG, and MBTNB (Kolmer and Hughes 2014).

There were strong geographical differences in distribution of the *P. tritici* phenotypes. Phenotypes MBTNB (virulent to *Lr11*), TBRKG (virulent to *Lr11* and *Lr18*), MCTNB (virulent to *Lr11* and *Lr26*), and TCRKG (virulent to *Lr11*, *Lr18*, and *Lr26*) were the most common phenotypes in the areas 1 and 3 where soft red winter wheat cultivars with genes *Lr11*, *Lr18*, and *Lr26* are grown. In the hard red wheat region of areas 4, 5, and 6, the common phenotypes TNBGJ, TBBGJ, and MBDSD are virulent to *Lr39/41* that is present

in many cultivars in areas 4 and 5. Phenotype MBDSD is also virulent to *Lr17*, as are MFPSB, MBPSB, and MLPSD that were present in areas 4 and 5. *Lr17* was postulated to be present in the cultivars TAM 111 and Jagger. Phenotypes with virulence to *Lr21* (TFBJQ, TDBJQ, TDBGQ, and TBBGS) had the highest frequency in the hard red spring wheat region of area 6, where wheat cultivars such as Faller, Prosper, and Barlow with *Lr21* are commonly grown. The geographic differences in phenotype distributions are also seen in the Nei's virulence distance between isolates in the different areas. Isolates from the hard red wheat areas 4, 5, and 6 of the Great Plains were highly similar for virulence and differed the most compared with isolates in areas 1 and 3, where soft red winter wheat cultivars are grown.

Some isolates with unusual virulence phenotypes were also found in 2013. A single isolate of phenotype BBBQD was found on Overlay wheat in Kansas. This isolate has a virulence phenotype identical to other isolates with high virulence to durum wheat that are found in the durum producing regions of Mexico, South America, the Middle East, and Europe (Ordoñez and Kolmer 2007). This isolate was determined to be virulent on commonly grown durum wheat cultivars (Kolmer 2014). Since this isolate is also virulent to *Lr39/41*, it may have sufficient virulence to survive on winter wheat in Great Plains region and spread north to the durum production region of North Dakota. Phenotypes FBPSB, FCPLB, PBDBG, PBDGG, PBDGJ, PBDQJ, and PCDGJ were found in the Great Plains region of areas 4, 5, and 6. These phenotypes are avirulent to *Lr2a*, virulent to *Lr2c* and *Lr17*, and vary for virulence to *Lr39/41*. Phenotypes that differ for virulence to *Lr2a* and *Lr2c* were previously mostly found in areas 2 and 8 where soft white winter wheat cultivars are grown. Isolates of phenotype SBDGG were found in areas 1, 2, 4, and 5. These isolates are identical for virulence to Race 9 that was the most common *P. tritici* phenotype in the 1930s to mid-1940s in North America (Johnson 1956). SBDGG isolates are only rarely found in recent years, likely due to avirulence to many leaf rust resistance genes that are present in modern wheat cultivars.

The hard red and soft red winter wheat cultivars that have various leaf rust resistance genes and are grown in different regions of the United States have continuously selected for a population of *P. tritici* that is highly diverse for virulence. In recent years, isolates with virulence to *Lr9* have decreased in the soft red wheat region of area 1; however, it would be expected that isolates with virulence to this gene would increase rapidly if cultivars with *Lr9* were to be grown on increased acreages. Similarly, isolates with virulence to *Lr11* and *Lr16* have been more frequent in past years in the Great Plains region of North America, but would likely increase again if cultivars with these genes were grown in greater amounts. The phenotype TBBGS with combined virulence to *Lr21* and *Lr39/41* has been found in Texas and North Dakota. Hard red winter wheat cultivars or germplasm with *Lr21* or *Lr39/41* will be vulnerable to this phenotype as are the many spring wheat cultivars with *Lr21*. As new leaf rust resistant cultivars are released, it will be important to characterize the resistance in these cultivars by gene postulation, molecular markers, or genetic analysis in order to determine if leaf rust resistance genes in host cultivars have selected for new *P. tritici* virulence phenotypes.

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