Virulence of *Puccinia triticina* on Wheat in the United States in 1999

D. L. Long, Plant Pathologist, K. J. Leonard, Research Plant Pathologist, and M. E. Hughes, Biologist, Cereal Disease Laboratory, USDA, Agricultural Research Service, Department of Plant Pathology, University of Minnesota, 1551 Lindig St., St. Paul 55108

ABSTRACT

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Isolates of *Puccinia triticina* were obtained from wheat leaf collections made by cooperators throughout the United States and from surveys of wheat fields and nurseries in the Great Plains, Ohio Valley, and Gulf Coast states in 1999. Pathogenic races were determined from virulence/avirulence phenotypes on 14 host lines that are near-isogenic for leaf rust resistance. We found 58 races among 1,180 isolates in 1999. As in previous surveys, regional race distribution patterns showed that the central United States is a single epidemiological unit distinct from the eastern United States. The distinctive racial composition of collections from the Southeast, Northeast, and Ohio Valley indicates that populations of *P. triticina* in those areas are not closely connected, suggesting epidemics originate from localized overwintering sources.

Additional keywords: plant disease monitoring, *Puccinia recondita*, rust epidemiology, wheat leaf rust

Wheat leaf rust, caused by *Puccinia triticina* Eriks. (1) (= *P. recondita* Rob. ex Desmaz. f. sp. *tritici*), occurs annually throughout most wheat (*Triticum aestivum*) growing areas of the United States. In recent years, yield losses to leaf rust in wheat have ranged from trace levels (<1%) in many states to 12% in California in 1996, 10% in Oklahoma in 1997, and 3.4% in Kansas and 4.0% in Minnesota and North Dakota in 1999 (7). Losses to leaf rust in winter wheat in the United States were estimated at 4.8, 4.8, 0.7, 2.4, 0.8, 2.9, 1.6, and 2.2% in 1992, 1993, 1994, 1995, 1996, 1997, 1998, and 1999, respectively (7). Losses in spring wheat were estimated at 0.5, 0.3, 0.0, 0.1, 0.0, 1.1, 0.8, and 2.7% for the same years. Except in 1999, leaf rust losses have been lower in spring wheat than in winter wheat in the United States, mainly because of more effective resistance in spring wheat cultivars and because *P. triticina* rarely overwinters in the northern Great Plains where most spring wheat is grown.

Wheat leaf rust virulence surveys have been conducted by the Cereal Disease

Laboratory, formerly known as the Cereal Rust Laboratory, since 1978 to detect new pathogenic races and to monitor shifts of race frequencies in major wheat growing regions of the United States (12). Similar surveys have been done in Canada since 1931 (3) and in Mexico (20). In the United States (6) and Canada (2–5), leaf rust survey data have been used to characterize virulence and race 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 1999 to the North America wheat leaf rust differentials (8) and other selected lines of wheat, and to compare these results with those of previous surveys.

MATERIALS AND METHODS

Collections and race identification.

Uredinial collections of leaf rust were made from wheat in annual surveys (over routes totaling approximately 20,000 km) of the Great Plains, Ohio Valley, and Gulf Coast and by cooperators throughout the United States. In 1999, field surveys of wheat were made in southern and central Georgia (late March through May); eastern and southern Texas (early April); northern Texas and south central Oklahoma (late April); southeastern Gulf Coast (mid-April to early May); southeastern states (late April); Oklahoma and Kansas (mid-May); the Ohio River Valley (early June); north central Kansas, Nebraska, western Iowa,

South Dakota, and southern Minnesota (mid-June); and northern Plains states (early July and again in late July). Visual inspections for the presence of rust were made in commercial fields (4 to 50 ha in size) every 32 km or in the first field thereafter. Additional collections were made in wheat breeding nurseries, trap plots, and demonstration plots (collectively referred to as nurseries in data analysis) along the route. Nurseries typically contain a wide array of leaf rust resistance phenotypes including breeding lines with leaf rust resistance genes not yet in commercial cultivars. Trap plots usually contain older cultivars of wheat no longer prominent in commercial production. Leaf rust was also collected from goat grass, *Triticum cylindricum* Ces. (= *Aegilops cylindrica* Host), growing near wheat fields in Oklahoma. A collection consisted of one to several leaves bearing uredinia from a single plant or cultivar. The leaves were air-dried and stored at 4°C until spores were collected for inoculations. No collections from inoculated nurseries were included in the study.

Urediniospores from each collection were used to inoculate 7-day-old seedlings of the wheat cultivar Thatcher (CI 10003), treated at emergence with maleic hydrazide at approximately 0.01 g (dissolved in 30 ml of H₂O) per pot to enhance spore production (18). Plants were sprayed with a suspension of spores in lightweight mineral oil at a rate of approximately 0.5 ml of spore suspension per pot of 10 to 20 seedlings. Inoculated plants were placed at 18°C in a dew chamber overnight. The plants were then transferred to a greenhouse where temperatures varied between 18 and 28°C daily under natural light. After 12 to 15 days, three seedlings were saved per collection, each with the primary leaf trimmed to bear a single uredinium. Six to 9 days later, a cyclone spore collector was used to collect urediniospores separately from one or two such uredinia per collection. If the single uredinia were small and few spores were collected, the isolates were increased through one uredinial generation on Thatcher before inoculating differential lines. Otherwise, spores from the single uredinia were directly inoculated onto 7- to 8-day-old plants of the differential host series (five to seven plants

Corresponding author: D. L. Long
E-mail: davidl@cdl.umn.edu

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per line) of near isogenic lines of Thatcher with single resistance genes *Lr1*, 2*a*, 2*c*, 3*a*, 3*ka*, 9, 10, 11, 16, 17, 18, 24, 26, and 30. Lines included in this standard set of differentials were chosen by the North American Leaf Rust Workers Committee (8) because they account for a large part of the detectable diversity in virulence of *P. tritici* in North America and because they react with distinct low or high infection types. 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 0200 to 1400 (400 to 450 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at bench level). After 10 to 14 days, infection types were recorded as either high (IT 3-4) or low (IT 0-2+) as in previous surveys (9-15). Race designations were assigned as described by Long and Kolmer (8).

Race and virulence frequencies were determined for collections from seven of eight agroecological geographic areas (Fig. 1): area 1, mainly southern-adapted soft

red winter wheats; areas 2 and 3, mostly northern-adapted soft red and white winter wheats that appear to be epidemiologically separated by geographic features; 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. There were no collections from area 8 in 1999.

RESULTS AND DISCUSSION

Races identified. Leaf rust infection was widespread in the southern and central Great Plains and much heavier than normal in the northern Great Plains in 1999. A total of 1,180 single uredinal isolates were characterized, and 58 races were identified in 1999 (Table 1) based on high/low infection types on the 12 differential host lines plus a Thatcher line with *Lr10* and one with *Lr18* (8). Races found in areas 1 to 7 are arranged by the North American wheat leaf rust code (8) in Table 2. Results are presented as percentages of isolates within areas separated into collections made from nurseries and fields.

The M-- race group (virulent on *Lr1* and 3*a*) comprised 59% of the total number of leaf rust isolates identified in 1999. The most frequently identified race group in 1999 was M_D (virulent on *Lr1*, 3*a*, and 17), which comprised 24% of the nationwide sample. The most common race MBD-10 was found in areas 2, 3, 4, 5, 6, and 7 of the United States in 1999 (Table 2). Race MBD-10 comprised 13, 9, 4, and 1% in 1999, 1998, 1997, and 1996, respectively (9). MBD-10 was not found in 1995 (10). MCD-10, the fourth most widely identified race in 1999 at 9% of the population, was found at 12, 8, 4, and 0.3% in 1998, 1997, 1996 (9), and 1995 (10), respectively. MCR-10,18 (virulent to *Lr1*, 3*a*, 3*ka*, 10, 11, 18, 26, and 30) was the third most widely identified race in 1999, and comprised 10% of the population. This race was identified from rust collections made only in areas 1, 2, and 3. MCR-10,18 was not identified in 1998 or 1996 but comprised 4% of the identified isolates in 1997 (9). MDR-10 (virulent on *Lr1*, 3*a*, 3*ka*, 10, 11, 24, and 30) comprised 6% of the nationwide sample in 1999, although it was the most frequently found race in 1997 and 1998, comprising 23% of the nationwide population in both years (9). MDR-10 comprised 3% of the population in 1996 and 0.3% in 1995 (9,10). Race MDR-10 was found in all areas of the United States except in area 7. MBR-10 and MBR-10,18 (virulent to *Lr1*, 3*a*, 3*ka*, 11, and 30) together comprised 13, 18, 23, and 44% of the nationwide sample in 1999, 1998, 1997, and 1996, respectively (9). In 1999, these two races were found in all areas of the United States except in area 7. The other 13 M-- races together comprised 9%

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

Table 1. North American wheat leaf rust nomenclature (Pt) code and corresponding virulence formula for races identified in 1999

Pt code ^a	Virulence formula ^b	Pt code	Virulence formula
FBM-10,18	2c, 3a, 3ka, 10, 18, 30	TBD-10	1, 2a, 2c, 3a, 10, 17
FBR-10,18	2c, 3a, 3ka, 10, 11, 18, 30	TBM-10	1, 2a, 2c, 3a, 3ka, 10, 30
FCM-10,18	2c, 3a, 3ka, 10, 18, 26, 30	TBR-10	1, 2a, 2c, 3a, 3ka, 10, 11, 30
KFB-10	2a, 2c, 3a, 10, 24, 26	TBR-10,18	1, 2a, 2c, 3a, 3ka, 10, 11, 18, 30
LCG-18	1, 11, 18, 26	TCB-10	1, 2a, 2c, 3a, 10, 26
MBB-10	1, 3a, 10	TCB-10,18	1, 2a, 2c, 3a, 10, 18, 26
MBD-10	1, 3a, 10, 17	TCD-10	1, 2a, 2c, 3a, 10, 17, 26
MBG	1, 3a, 11	TCM-10	1, 2a, 2c, 3a, 3ka, 10, 26, 30
MBG-10	1, 3a, 10, 11	TCM-10,18	1, 2a, 2c, 3a, 3ka, 10, 18, 26, 30
MBG-10,18	1, 3a, 10, 11, 18	TCR-10	1, 2a, 2c, 3a, 3ka, 10, 11, 26, 30
MBK-10	1, 3a, 10, 11, 17, 30	TDB-10	1, 2a, 2c, 3a, 10, 24
MBR-10	1, 3a, 3ka, 10, 11, 30	TDG-10	1, 2a, 2c, 3a, 10, 11, 24
MBR-10,18	1, 3a, 3ka, 10, 11, 18, 30	TDR	1, 2a, 2c, 3a, 3ka, 11, 24, 30
MCB-10	1, 3a, 10, 26	TDR-10	1, 2a, 2c, 3a, 3ka, 10, 11, 24, 30
MCD-10	1, 3a, 10, 17, 26	TDR-10,18	1, 2a, 2c, 3a, 3ka, 10, 11, 18, 24, 30
MCG-10	1, 3a, 10, 11, 26	TFB-10	1, 2a, 2c, 3a, 10, 24, 26
MCR-10	1, 3a, 3ka, 10, 11, 26, 30	TFG-10	1, 2a, 2c, 3a, 10, 11, 24, 26
MCR-10,18	1, 3a, 3ka, 10, 11, 18, 26, 30	TFM-10	1, 2a, 2c, 3a, 3ka, 10, 24, 26, 30
MCT-10	1, 3a, 3ka, 10, 11, 17, 26, 30	TFR-10	1, 2a, 2c, 3a, 3ka, 10, 11, 24, 26, 30
MDB-10	1, 3a, 10, 24	TGB-10	1, 2a, 2c, 3a, 10, 16
MDR-10	1, 3a, 3ka, 10, 11, 24, 30	THB-10	1, 2a, 2c, 3a, 10, 16, 26
MFB-10	1, 3a, 10, 24, 26	THD-10	1, 2a, 2c, 3a, 10, 16, 17, 26
MGB-10	1, 3a, 10, 16	THM-10	1, 2a, 2c, 3a, 3ka, 10, 16, 26, 30
MGD-10	1, 3a, 10, 16, 17	TJB-10	1, 2a, 2c, 3a, 10, 16, 24
PBR-10,18	1, 2c, 3a, 3ka, 10, 11, 18, 30	TKB-10	1, 2a, 2c, 3a, 10, 16, 24, 26
PNM-10,18	1, 2c, 3a, 3ka, 9, 10, 18, 24, 30	TLG-18	1, 2a, 2c, 3a, 9, 11, 18
SBD	1, 2a, 2c, 17	TLG-10,18	1, 2a, 2c, 3a, 9, 10, 11, 18
SBJ-10	1, 2a, 2c, 10, 11, 17	TLR-10	1, 2a, 2c, 3a, 3ka, 9, 10, 11, 30
TBB-10	1, 2a, 2c, 3a, 10	TNR-10	1, 2a, 2c, 3a, 3ka, 9, 10, 11, 24, 30

^a Race code plus *Lr10* and *Lr18* near-isogenic supplements.

^b Resistances evaluated: *Lr1*, 2*a*, 2*c*, 3*a*, 3*ka*, 9, 10, 11, 16, 17, 18, 24, 26, and 30.

of the nationwide sample in 1999 (Table 2).

Thirty T- races (virulent on *Lr1*, *2a*, *2c*, and *3a*) formed the second largest group of races and comprised 38% of the isolates in 1999. The races were found at 23, 21, and 15% of the nationwide sample in 1998,

1997, and 1996, respectively (9). Race THB-10 was the second most widely identified race in 1999 and comprised 12% of the isolates. Most THB-10 isolates were found in area 6. In 1998 and 1997, THB-10 comprised only 1 and 0.2% of the isolates nationally. Race group TC- (virulent to

Lr1, *2a*, *2c*, *3a*, *10*, and *26*) comprised 7% of the isolates identified in 1999. Race group TD- (virulent to *Lr1*, *2a*, *2c*, *3a*, *10*, and *24*) comprised 5% in 1999 (Table 2). The TLG-18 race was common in area 2 and comprised 4% of the isolates nationally in 1999 (Table 2). TLG-18 comprised

Table 2. Frequency and distribution of races of *Puccinia triticina* collected from fields (F) and nurseries (N) in agroecological areas 1 (Southeast), 2 (Northeast), 3 (Ohio Valley), 4 (Southern Plains), 5 (Central Plains), 6 (Northern Plains), and 7 (Southwest) of the United States in 1999

Pt code ^a	Isolates from indicated source (%)													
	Area 1 ^b		Area 2		Area 3		Area 4		Area 5		Area 6		Area 7	
	F	N	F	N	F	N	F	N	F	N	F	N	F	N
FBM-10,18	0	1	0	0	0	1	0	0	0	0	0	0	0	0
FBR-10,18	0	3	0	0	0	0	0	0	0	0	0	0	0	0
FCM-10,18	0	1	0	0	0	0	0	0	0	0	0	0	0	0
KFB-10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
LCG-18	0	1	0	0	0	0	0	0	0	0	0	0	0	0
MBB-10	0	0	0	0	0	0	0	0	0	0	1	0	0	0
MBD-10	0	0	0	14	5	4	8	24	33	18	20	19	0	20
MBG	0	0	0	0	0	4	0	0	0	0	0	0	0	0
MBG-10	13	3	0	14	0	4	0	3	0	0	0	0	100	80
MBG-10,18	0	1	0	0	0	0	2	1	0	0	0	0	0	0
MBK-10	0	0	0	0	0	0	6	6	0	0	0	0	0	0
MBR-10	19	10	0	0	9	0	0	4	0	18	2	3	0	0
MBR-10,18	13	18	75	21	9	16	0	1	0	0	1	1	0	0
MCB-10	13	0	0	0	0	2	0	0	0	0	0	1	0	0
MCD-10	0	0	0	0	7	12	38	24	0	28	6	8	0	0
MCG-10	0	1	0	0	0	0	0	0	0	0	2	1	0	0
MCR-10	0	2	0	0	5	0	0	1	0	0	0	0	0	0
MCR-10,18	13	34	0	21	2	16	0	0	0	0	0	0	0	0
MCT-10	0	0	0	0	0	0	2	0	0	0	0	0	0	0
MDB-10	0	1	0	0	0	0	0	0	33	0	2	* ^c	0	0
MDR-10	0	4	0	0	0	2	8	14	0	10	6	6	0	0
MFB-10	0	0	0	0	0	4	0	1	0	0	0	1	0	0
MGB-10	0	0	0	0	0	0	0	0	0	0	2	1	0	0
MGD-10	0	0	0	0	0	0	0	1	0	0	7	2	0	0
PBR-10,18	0	0	0	0	7	0	0	0	0	0	0	0	0	0
PNM-10,18	0	*	0	0	0	0	0	0	0	0	0	0	0	0
SBD	0	0	0	0	0	0	21	0	0	0	0	0	0	0
SBJ-10	0	0	0	0	0	0	4	0	0	0	0	0	0	0
TBB-10	0	0	0	0	0	2	0	1	0	0	2	1	0	0
TBD-10	0	0	0	0	0	0	0	1	0	0	0	*	0	0
TBM-10	0	0	0	0	4	0	0	0	0	0	0	0	0	0
TBR-10	13	*	0	0	0	0	0	0	0	0	2	1	0	0
TBR-10,18	0	0	0	0	7	2	0	0	0	0	0	0	0	0
TCB-10	0	1	0	0	4	4	2	1	0	0	0	2	0	0
TCB-10,18	0	1	0	0	0	0	0	0	0	0	0	0	0	0
TCD-10	0	0	0	0	0	0	0	0	5	0	0	0	0	0
TCM-10	0	0	0	0	0	2	0	0	0	0	0	3	0	0
TCM-10,18	0	1	0	0	4	0	0	0	0	0	0	1	0	0
TCR-10	0	2	0	0	11	20	0	3	0	8	2	4	0	0
TDB-10	0	*	0	0	0	0	0	0	13	3	2	0	0	0
TDG-10	0	0	0	0	0	0	2	1	0	0	0	0	0	0
TDR	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TDR-10	0	*	0	0	2	4	0	1	0	3	0	7	0	0
TDR-10,18	0	1	0	0	4	0	0	0	0	0	0	0	0	0
TFB-10	0	1	0	0	0	0	4	2	33	0	0	*	0	0
TFG-10	0	0	0	0	0	0	0	1	0	0	0	0	0	0
TFM-10	0	0	0	0	0	0	0	0	0	0	1	1	0	0
TFR-10	0	0	0	0	0	2	4	6	0	0	2	3	0	0
TGB-10	0	0	0	0	0	0	0	1	0	0	0	2	0	0
THB-10	19	0	0	0	5	0	0	0	0	0	42	23	0	0
THD-10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
THM-10	0	0	0	0	16	0	0	0	0	0	0	0	0	0
TJB-10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TKB-10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TLG-18	0	14	25	29	0	0	0	0	0	0	0	1	0	0
TLG-10,18	0	0	0	0	0	0	0	1	0	0	0	0	0	0
TLR-10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TNR-10	0	1	0	0	0	0	0	0	0	0	0	2	0	0
No. isolates	16	296	4	14	56	50	52	147	3	40	127	363	2	10

^a Races based on 12 North American leaf rust differential lines (11) plus supplemental lines with *Lr10* and *Lr18*.

^b Agroecological areas are shown in Figure 1.

^c * = less than 1%.

6, 4, and 3% of the nationwide sample in 1998, 1997, and 1996, respectively (9), and 1, 6, and 9% in 1995, 1994, and 1993, respectively (10). In the years from 1993 through to 1999, this race almost exclusively was identified from rusted soft red winter wheat collections (i.e., CK 9835) from areas 1 and 2 (Table 2) (9,10). The T- races (virulent to *Lr1*, *2a*, *2c*, and *3a*) are a very diverse group, with 15 of the 30 T- races identified in 1999 comprising less than 4% of the total nationwide sample (Table 2).

The M- races were common in all seven areas sampled in 1999. All of the isolates from area 7 were M- races, as were 74% of those from areas 1, 2, 4, and 5, and 45% from areas 3 and 6. The T- races were more common in area 6 (56%) and area 3 (46%) than in the other areas. Although overall M- races were less common in area 6 (northern plains) than in areas 4 (southern plains) and area 5 (central plains), the most common race, MBD-10, occurred at higher frequencies in areas 4, 5, and 6 than in other areas. This is consistent with earlier conclusions that leaf rust spreads freely throughout the Great Plains, but movement between other areas is less common (6).

In the 1999 nationwide survey, the combined race groups F- (virulent on *Lr2c*, *3a*), L- (virulent on *Lr1*), and P- (virulent on *Lr1*, *2c*, *3a*) represented 2% of all isolates identified (Table 2) and were found scattered throughout the eastern soft red winter wheat region.

The 11 isolates of race SBD and two isolates of SBJ-10, comprising 1% of the isolates nationwide, all came from central and southwestern Oklahoma and were from collections of rusted plants of *T. cylindricum* either on roadsides or in wheat fields.

Virulence frequencies. Frequencies of virulence on each of the 14 differential lines differed among collections from the

eight agroecological areas (Table 3). Due to variation in greenhouse environment, temperature sensitive genes *Lr3ka*, *11*, *17*, and *18* may have been misclassified occasionally. Avirulent isolates may give intermediate to susceptible reactions on lines with *Lr3ka*, *Lr11*, or *Lr18* at high (>25°C) temperatures, whereas resistant reactions on the lines with *Lr17* may be difficult to distinguish from susceptibility at abnormally low temperatures for some leaf rust isolates. These temperature effects were minimized by suspending race identification work in the greenhouse during July and August.

Incidence of virulence on lines with *Lr26* represented 47% of the total U.S. isolates in 1999 (Table 3), which had increased from 34% in 1998 (9). In 1986, less than 1% of isolates were virulent to *Lr26* (14). Virulence to *Lr24* has ranged from 2% in 1986 (14) to 41% in 1997 (9) and 17% in 1999 (Table 3). Virulences to *Lr24* and *Lr26* were most common in areas 4, 5, and 6 (Table 3). Cultivars with *Lr24* are widely grown in the southern Great Plains (16).

Virulence to *Lr11* was found in 51% of the race population throughout the United States and was identified in 28 races in 1999. From 1996 to 1998, the number of races virulent on *Lr11* increased from 16 to 34 (9). This reflects a selective advantage of this virulence due to an increase in the acreage of cultivars with *Lr11* (19). The number of races found with virulence to *Lr11* also suggests an accumulation of independent mutations to *Lr11* virulence in a variety of genetic lineages in the *P. triticina* populations. Virulence to *Lr11* was most frequent in M- and T- races, the two most common race groups.

Virulence to *Lr17* was identified in 27% of the nationwide sample of *P. triticina* in 1999. *Lr17* was found in 9, 16, and 21% of the nationwide sample in 1996, 1997, and 1998, respectively. In 1994 and 1995 (10),

Lr17 virulence was identified in only 2% of the nationwide population. This increase in virulence from 2% in 1995 to 27% in 1999 directly correlates with a significant increase in the acreage of Jagger, a hard red winter cultivar with *Lr17* (17) resistance.

Virulence to *Lr16* was identified in 17% of the nationwide sample in 1999 (Table 3). The last time there was such high virulence to *Lr16* was in 1986, when 17% of the race population was virulent to *Lr16* (14). Less than 1% of the U.S. population was virulent to *Lr16* in 1997 (9). In 1999, seven phenotypes (MGB, MGD, TGB, THB, THM, TJB, and TKB) were identified with virulence to *Lr16* (Table 1). In Canada, virulence to *Lr16* occurred in 6% of the isolates in 1987 (2) and 17.2% in 1998 (5), but it was not found from 1989 to 1994 (5). The increase in virulence to *Lr16*, particularly in area 6, may account for the leaf rust losses that were much higher than normal on spring wheat in the northern plains states in 1999 (7). Many of the currently grown spring wheat cultivars have *Lr16* as part of their resistance (17). Interestingly, none of the leaf rust isolates from the southern Great Plains and only 1% of those from the central Great Plains in 1999 were virulent on *Lr16* (Table 3).

Virulence to *Lr9* was identified in 5% in 1999 and 4, 5, and 3% of the nationwide sample of *P. triticina* in 1996, 1997, and 1998, respectively (9). In 1999, *Lr9* virulence was found only in the PN-, TL-, and TN- races and mainly in the eastern soft red winter wheat region (areas 1, 2, and 3). *Lr9* is found almost exclusively in soft red winter wheats (17).

Virulence to *Lr30*, which is associated with virulence to *Lr3ka*, increased from 16% in 1993 (10) to 46% in 1999 (Table 3). *Lr30* virulence was common in all areas of the United States in 1999 except area 7. The increase in virulence to *Lr30* is apparently due to selection for virulence to

Table 3. Percentage of isolates of *Puccinia triticina* virulent on the single-gene differential lines used in the 1999 survey

Area ^a	Source	No. of isolates	Isolates virulent on <i>Lr</i> gene (%)													
			1	2a	2c	3a	3ka	9	10	11	16	17	18	24	26	30
1	Field	16	100	31	31	100	56	0	100	69	19	0	25	0	44	56
1	Nursery	296	96	22	26	99	77	15	85	94	0	0	74	8	44	77
2	Field	4	100	25	25	100	75	25	75	100	0	0	100	0	0	75
2	Nursery	14	100	29	29	100	43	29	71	86	0	14	71	0	21	43
3	Field	56	100	55	63	100	79	0	100	55	21	13	32	5	54	79
3	Nursery	50	100	36	36	100	64	0	96	70	0	16	34	12	62	64
4	Field	52	100	37	37	75	13	0	79	27	0	79	2	17	50	19
4	Nursery	147	100	21	21	100	31	1	100	44	2	56	3	27	39	37
5	Field	3	100	33	33	100	0	0	100	0	0	33	0	67	33	0
5	Nursery	40	100	28	28	100	38	0	100	38	0	50	0	25	40	38
6	Field	127	100	52	52	100	13	0	100	15	51	33	1	13	54	13
6	Nursery	363	99	58	58	100	33	3	99	30	31	30	2	25	50	33
7	Field	2	100	0	0	100	0	0	100	100	0	0	0	0	0	0
7	Nursery	10	100	0	0	100	0	0	100	80	0	20	0	0	0	0
U.S.	Field	260	100	47	49	95	31	0	95	31	31	35	11	12	51	32
U.S.	Nursery	920	98	37	38	100	48	7	94	57	13	24	28	19	45	49
U.S.	Total	1,180	99	39	41	99	44	5	94	51	17	27	24	17	47	46

^a Agroecological areas are: 1 (Southeast), 2 (Northeast), 3 (Ohio Valley), 4 (Southern Plains), 5 (Central Plains), 6 (Northern Plains), and 7 (Southwest). See Figure 1.

Lr3ka, which has been used in Kansas wheat cultivars. *Lr30* does not occur in common wheat cultivars in the United States.

Leaf rust resistance genes *Lr1*, *2a*, *2c*, *3a*, and *10* have been used in wheat cultivars in the Great Plains for many years, during which virulence to these genes became common. Most races found in recent years are virulent to *Lr1*, *3a*, and *10*. Both the K-- races, which were common before 1985 (12,13), and the S-- races, which were found on wheat in the 1960s (2), are virulent to both *Lr2a* and *Lr2c*. By 1986, the M-- races replaced K-- races as the most prevalent races in the Great Plains. M-- races are virulent to *Lr1* and *3a* but avirulent to *Lr2a* and *2c*. The recent increase of T-- races may indicate another shift in the race pattern of the Great Plains and a return to increased virulence to *Lr2a* and *2c* as well as *Lr1* and *3a*.

The genes *Lr9*, *16*, *24*, and *26* are currently being used in combination with other resistance in many of the U.S. wheat breeding programs (17). During the past 20 years, these genes have lost effectiveness, especially when they were added one gene at a time to new wheat cultivars. *Lr24* and *26* were highly effective as late as 1985 (13), but now provide little protection. Incidence of virulence to lines with *Lr26* increased from less than 1% of the total U.S. isolates in 1986 to 47% in 1999 (Table 3). Virulence to *Lr24* has ranged from 2% in 1984 (13) to 17% in 1999 (Table 3). Cultivars with *Lr24* are widely grown in the southern Great Plains (16).

In the past 10 years, virulence to *Lr9* and *16* has increased when cultivars with these genes have been planted in significant acreage. In the past, virulence to *Lr16* has declined when cultivars with *Lr16* lost favor and were removed from production, which has allowed *Lr16* to be recycled in some breeding programs. For example, virulence to *Lr16* declined from 17% in the U.S. population in 1986 (14), when the cultivar ProBrand 812 was grown on sig-

nificant acreage, to less than 1% in 1997. In 1999, virulence to *Lr16* had again risen to 17% of the U.S. population, because many of the currently grown spring wheats have *Lr16* as part of their resistance (17). Since 1995, cultivars with *Lr17* (e.g., Jagger) have gained popularity, and there has been a corresponding increase in virulence to *Lr17*. By 1999, more than 27% of the U.S. leaf rust isolates could attack cultivars with *Lr17*.

The history of breeding for leaf rust resistance, especially in winter wheats, has shown that it is a continuous struggle. Whenever new resistant genes have been used alone over significant areas, the corresponding virulence has appeared and increased in the *P. trititica* population within a few years. Therefore, it is important to combine new genes for race-specific resistance with other effective genes for resistance.

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