Virulence, Frequency, and Distribution of Races of *Puccinia striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* Identified in the United States in 2008 and 2009

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Abstract

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Puccinia striiformis f. sp. *tritici* and *P. striiformis* f. sp. *hordei*, the causal agents of stripe rust on wheat and barley, respectively, can change rapidly in virulence, and such changes may overcome resistance in cultivars and result in severe epidemics. To monitor virulence changes in the pathogen populations, isolates obtained from stripe rust samples collected by the authors and collaborators from 17 U.S. states in 2008 and 13 states in 2009 were tested on 20 wheat and 12 barley differential lines to identify races of *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei*, respectively. In 2008, 33 *P. striiformis* f. sp. *tritici* (PST) races were detected, including a new race, PST-138, which was similar to previously identified PST-127 (virulent on wheat differentials 1, 2, 3, 4, 6, 8, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19, and 20) but not virulent on differential 8. The five most frequent races were PST-114 (virulent on differentials 1, 3, 4, 8, 9, 10, 11, 12, 14, 16, 17, 18, 19, and 20), PST-100 (virulent on differentials 1, 3, 8, 9, 10, 11, 12, 16, 17, 18, 19, and 20), PST-116 (similar to PST-114 plus virulent on differential 5), PST-101 (similar to PST-100 plus virulent on differential 2), and PST-98 (similar to PST-100 but not virulent on differential 9). In 2009, 26 *P. striiformis* f. sp. *tritici* races were identified,

including two new races, PST-139 and PST-140. PST-139 was similar to PST-127 but not virulent on differentials 16 and 20. PST-140 was similar to PST-114 but not virulent on differential 9. The five most frequent races were PST-139 (19%), PST-140 (14%), PST-114 (11%), PST-116 (10%), and PST-127 (9%). However, the most widely distributed races were PST-98 (in 10 of the 14 states) and PST-102 (in 7 of the 14 states). Differential genotype AvSYr5NIL (*Yr5*) was the only one among the 20 differentials that remained resistant to all of the identified races. Virulence diversity of the *P. striiformis* f. sp. *tritici* populations was higher west of the Rocky Mountains. For barley stripe rust, *P. striiformis* f. sp. *hordei* (PSH)-33 (virulent on barley differentials 1 and 7) was the most common (46%) of the 11 races detected in 2008, including a new race, PSH-82 (virulent only on barley differentials 1 and 11). In 2009, six previously identified races were detected, of which five (PSH-16, PSH-38, PSH-46, PSH-54, and PSH-71) were detected in Washington and two (PSH-54 and PSH-70) in Oregon. The information on *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* races should be useful in selecting genes for developing cultivars with effective stripe rust resistance.

Puccinia striiformis Westend. is a species of basidiomycete fungus causing stripe rust on wheat, barley, and many grass species. In the United States, wheat stripe rust, caused by forma specialis *P. striiformis* f. sp. *tritici* Erikss., has been most prevalent in states west of the Rocky Mountains but has become increasingly important in states east of the mountains since 2000 (5,19,21,26). In term of affected area and yield loss, stripe rust has been considered one of the most important diseases on wheat in the United States since the late 1950s (5,21,26,28). In the United States, barley stripe rust, caused by another forma specialis, *P. striiformis* f. sp. *hordei* Erikss., was first detected in Texas in 1991. It subsequently spread to Colorado, New Mexico, Arizona, California, Montana, Idaho, Oregon, and Washington, and caused severe damage in California and the Pacific Northwest (PNW) (Washington, Idaho, and Oregon; 2–4,17,30).

Growing resistant cultivars can be an effective, economical, and environmentally friendly means for control of stripe rust of wheat and barley. However, new races of *P. striiformis* with different

combinations of virulences can quickly evolve, making previously resistant cultivars susceptible and resulting in devastating yield loss (5,6,26,33,34,36). Monitoring such race changes is essential for more effective use of stripe rust resistance in breeding programs.

In the United States, race surveys using a set of differential lines have been conducted for *P. striiformis* f. sp. *tritici* since 1960 and for *P. striiformis* f. sp. *hordei* since 1993 (4,5,17,26,28). Virulence, aggressiveness, evolution, distributions, and frequencies of *P. striiformis* f. sp. *tritici* (PST) races from 1960 to 2007 and of *P. striiformis* f. sp. *hordei* (PSH) races from 1991 to 2007 have been previously reported (4–7,13,17,19–21,27–29). The objective of this study was to identify races of *P. striiformis* f. sp. *tritici* and *P. striiformis* f. sp. *hordei* and determine their frequency and distribution in the United States in 2008 and 2009.

Materials and Methods

Field monitoring of stripe rust and collecting samples of the rust. Stripe rust was monitored by plant pathologists, breeders, extension personnel, and growers in commercial fields and nurseries for monitoring diseases and screening germplasm and breeding lines in wheat- and barley-growing areas throughout the United States. Samples of stripe rust-infected leaves were collected by the authors and cooperators for identifying races in our laboratory. In general, samples consisted of one or more leaves with uredinia from a single cultivar or line at a field site and were sent in a glassine or paper envelope using overnight mail to our laboratory because the pathogen can lose viability quickly. Collection date, location (city, county, and state), host (wheat, barley, or grass), cultivar, growth stage, rust prevalence (percentage of plants infected), rust intensity (percentage of leaf area infected), and IT were recorded whenever possible. The samples were kept dry at 4°C before they were used to obtain isolates.

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Obtaining and storing isolates. ‘Nugaines’ wheat, which is susceptible at the seedling stage to all known *P. striiformis* f. *tritici* races in the United States, and ‘Steptoe’ barley, which is susceptible to all identified *P. striiformis* f. sp. *hordei* races, were used to increase urediniospores of the initial samples from wheat or barley, respectively. Nugaines and Steptoe were used to increase urediniospores of the initial samples from grasses, because many grass species can be infected by *P. striiformis* f. *tritici* or *P. striiformis* f. sp. *hordei*. Standard procedures and conditions were used for inoculation, growing plants before and after inoculation, and collecting and storing urediniospores, as previously described (19,21,28). Seedlings at the two-leaf stage were used for inoculation with urediniospores from sample leaves. Inoculated plants were kept in a dew chamber at 10°C for 24 h in the dark and then transferred to a growth chamber with a diurnal temperature cycle that gradually changed from 4°C at 2:00 A.M. to 20°C at 2:00 P.M. with a 16-h photoperiod, as described by Chen et al. (19,21). Plants inoculated with each sample were isolated using a booth to prevent cross-contamination. Generally, 16 days after inoculation, urediniospores were collected using a vacuum spore collector about once every 2 days until enough spores were obtained for further testing and storage.

If initial isolates did not produce typical reaction patterns of previously identified races when tested on the set of wheat or bar-

ley differentials, subisolates were obtained by increasing urediniospores on selected differential lines. If the reactions of differential lines indicated that an initial isolate was likely a new race or mixture of different previously existing races, the lines were considered to be key differentials during the process of race identification for the particular isolate.

A single-uredinium isolate was obtained from an original or subisolate by transferring urediniospores from a single uredinium onto leaves of a key differential line with a fine brush. In general, a single-uredinium isolate is considered purer than the original or subisolate and, therefore, was used as a type isolate for designating a new race.

Urediniospores were dried in a desiccator kept at 4°C for at least 2 days before keeping in sealed glass vials or foil bags at 4°C for short-term storage (up to 4 months) or in liquid nitrogen for long-term storage.

Determination of virulences of isolates and identifying races.

The 20 wheat lines in Table 1 and 12 barley lines in Table 2 were used to differentiate the *P. striiformis* f. *tritici* and *P. striiformis* f. sp. *hordei* races, respectively, as previously described (4,5,19,21). Fresh urediniospores or those kept at 4°C from an original, sub-, or single-uredinium isolate were used to inoculate the complete set of wheat or barley differentials. Infection types (ITs) were recorded at

Table 1. Wheat lines used to differentiate races of *Puccinia striiformis* f. sp. *tritici* and their genes for resistance to stripe rust

Differential number	Line		Type	Resistance gene ^b
	Name	ID number ^a		
1	Lemhi	CI 011415	Spring	<i>Yr21</i>
2	Chinese 166	CI 011765	Winter	<i>Yr1</i>
3	Heines VII	PI 201195	Winter	<i>Yr2</i> , <i>YrHVII</i>
4	Moro	CI 013740	Winter	<i>Yr10</i> , <i>YrMor</i>
5	Paha	CI 014485	Winter	<i>YrPa1</i> , <i>YrPa2</i> , <i>YrPa3</i>
6	Druchamp	CI 013723	Winter	<i>Yr3a</i> , <i>YrD</i> , <i>YrDru</i>
7	AvSYr5NIL ^c	YR 00004	Spring	<i>Yr5</i>
8	Produra	CI 017460	Spring	<i>YrPr1</i> , <i>YrPr2</i>
9	Yamhill	CI 014563	Winter	<i>Yr2</i> , <i>Yr4a</i> , <i>YrYam</i>
10	Stephens	CI 017596	Winter	<i>Yr3a</i> , <i>YrS</i> , <i>YrSte</i>
11	Lee	CI 012488	Spring	<i>Yr7</i> , <i>Yr22</i> , <i>Yr23</i>
12	Fielder	CI 017268	Spring	<i>Yr6</i> , <i>Yr20</i>
13	Tyee	CI 017773	Winter	<i>YrTye</i>
14	Tres	CI 017917	Winter	<i>YrTr1</i> , <i>YrTr2</i>
15	Hyak	PI 511674	Winter	<i>Yr17</i> , <i>YrTye</i>
16	Express	PI 573003	Spring	<i>YrExp1</i> , <i>YrExp2</i>
17	AvSYr8NIL ^c	YR 000008	Spring	<i>Yr8</i>
18	AvSYr9NIL ^c	YR 000009	Spring	<i>Yr9</i>
19	Clement	PI 518799	Winter	<i>Yr9</i> , <i>YrCle</i>
20	Compair	PI 325843	Spring	<i>Yr8</i> , <i>Yr19</i>

^a CI = crop index number, PI = plant identification number, and YR = yellow rust resistance gene line number.

^b Refer to Chen (5), Chen and Line (9–12), Chen et al. (8,15,16,18), Lin and Chen (25), and McIntosh et al. (31) for the *Yr* genes.

^c AvSYr5NIL, AvSYr8NIL, and AvSYr9NIL, developed by the Plant Breeding Institute, University of Sydney, Australia, are near-isogenic lines in the ‘Avocet Susceptible’ (AvS) background (35).

Table 2. Barley lines used to differentiate races of *Puccinia striiformis* f. sp. *hordei* and their genes for resistance to barley stripe rust

Differential number	Line		Resistance gene ^a
	Name	ID number	
1	Topper	BDPST 1	None ^b
2	Heils Franken	PI 290183	<i>Rps4</i> , <i>rpsHF</i>
3	Emir	CIho 13541	<i>rpsEm1</i> , <i>rpsEm2</i>
4	Astrix	CIho 13862	<i>Rps4</i> , <i>rpsAst</i>
5	Hiproly	CIho 03947	<i>rpsHi1</i> , <i>rpsHi2</i>
6	Varanda	PI 410865	<i>rpsVa1</i> , <i>rpsVa2</i>
7	Abed Binder 12	PI 327961	<i>rps2</i>
8	Trumpf	PI 548762	<i>rpsTr1</i> , <i>rpsTr2</i>
9	Mazurka	PI 399501	<i>Rps1.c</i>
10	Bigo	CIho 11795	<i>Rps1.b</i>
11	I 5	PI 288187	<i>Rps3</i> , <i>rpsI5</i>
12	Bancroft	PI 605474	<i>RpsBa^b</i>

^a Refer to Chen and Line (14) for resistance genes in the differential lines.

^b Topper is susceptible to all races and, therefore, has no effective genes for resistance to *P. striiformis* f. sp. *hordei*. The race-specific resistance gene or genes in Bancroft have not been genetically determined.

20 to 22 days after inoculation based on a 0-to-9 scale (28). IT data were converted to avirulence/virulence formulae. An isolate was considered avirulent on a specific differential line when there were either no symptoms (IT 0) or there were necrotic or chlorotic flecks (IT 1), necrotic or chlorotic blotches without sporulation (IT 2), or necrotic or chlorotic blotches with only a trace to slight sporulation (IT 3 to 4). An isolate was considered to be virulent if it caused moderate to abundant sporulation, with or without chlorosis or necrosis (IT 5, 6, 7, 8, or 9) (28).

If the virulence pattern of an isolate matched that of a previously designated race, the isolate was identified as that race. Repeated tests were conducted for isolates showing virulence patterns different from previously identified races. Two or more tests were done with sub- or single-uredinium isolates to designate new races.

Determination of race distribution, frequency, and diversity.

Race distribution and frequency were summarized as previously described by Chen et al. (19,21). Two measures of diversity were calculated from data on races from different regions within the United States (32). The relative Gleason index was calculated as $H_{GR} = (N_p - 1)/(N_i - 1)$, in which N_p is the number of races identified in the sample and N_i is the total number of isolates in the sample. The relative Shannon index was calculated as $H_{SR} = (1/\ln N_i) \{-\sum [p_j \ln(p_j)]\}$, in which p_j is the frequency of the j th race in the sample and N_i is the total number of isolates in the sample. The relative Gleason index and relative Shannon index values are the ratios of Gleason and Shannon indices relative to the maximum values possible for the given sample sizes if every isolate in the population were of a different race. The relative Gleason and relative Shannon indices were used to avoid bias in comparisons between populations of greatly different sample sizes (1). The Gleason index is especially sensitive to richness of diversity (i.e., number of races) in the population, whereas the Shannon index reflects both richness and evenness (similarity of race frequencies) in the population (22,23).

The Shannon and Gleason indices, which have been commonly used to determine diversity of plant pathogens, are based on the relative frequencies of different races. However, the indices treat nonidentical phenotypes as equally distinct and do not count for race similarities in virulence patterns (24). Thus, we used the Kosman index (24), which takes both phenotypic frequency and degrees of similarity among distinct phenotypes into consideration. The Kosman index, Ko , of the given population was calculated

using the equation $Ko = Ass_{max}(A,A)/nk$, where $Ass_{max}(A,A)$ is the maximum value of the sum of distances between matched pairs of isolates, k is the number of differentiating factors, and n is the number of isolates. For calculated Ko for each *P. striiformis* f. sp. *tritici* population, $Ass_{max}(A,A)$ was the maximum sum of the virulence differences between each pair of isolates, k was the number of differentials (20 in this study), and n was the number of isolates. Because of the small number of isolates and concentrated regions, diversity indices were not calculated for the barley stripe rust pathogen.

Results

Distributions and collections of wheat stripe rust. Wheat stripe rust collections were obtained from Alabama, Arkansas, California, Georgia, Idaho, Illinois, Indiana, Kansas, Kentucky, Louisiana, Missouri, Montana, Oklahoma, Oregon, South Dakota, Tennessee, Texas, Virginia, Washington, and Wisconsin in 2008, and from Arizona, California, Georgia, Idaho, Kansas, Louisiana, Michigan, Montana, Nebraska, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Virginia, and Washington in 2009. The distribution and magnitude of damage in 2008 and 2009 were similar to those in 2006 and 2007, and much less than in 2005 (*data not shown*).

Identification of *P. striiformis* f. sp. *tritici* races. In total, 294 and 265 *P. striiformis* f. *tritici* isolates were obtained in 2008 and 2009, respectively. The numbers of isolates obtained and races detected for each of the epidemic regions are summarized in Table 3. Based on these isolates, 42 *P. striiformis* f. *tritici* races (33 in 2008 and 26 in 2009, with 17 in common in the 2 years) were detected across the 2 years (Table 3), of which 15 were detected in 2008 but not in 2009, 9 were detected in 2009 but not in 2008, and 18 were identified in both 2008 and 2009 (Table 4). Virulence formulae of these races are shown in Table 4. Of the 42 races, 1 new race (PST-138) was identified in 2008 and 2 new races (PST-139 and PST-140) in 2009. PST-138 was virulent on differentials 1, 2, 3, 5, 6, 9, 10, 11, 12, 13, 15, 16, 17, 18, 19, and 20 and avirulent on differentials 4, 7, 8, and 14. PST-139 was virulent on 1, 2, 3, 5, 6, 8, 9, 10, 11, 12, 13, 15, 17, 18, and 19 and avirulent on 4, 7, 14, 16, and 20. PST-140 was virulent on differentials 1, 3, 4, 8, 10, 11, 12, 14, 16, 17, 18, 19, and 20 and avirulent on 2, 5, 6, 7, 9, 13, and 15. PST-138 was similar to PST-127 but not virulent on differential 8, and PST-139 was similar to PST-127 but not virulent on

Table 3. Number of isolates of wheat stripe rust (Isolates), number of races identified (Races), relative Gleason index (RGI), relative Shannon index (RSI), and Kosman diversity index (Ko) of *Puccinia striiformis* f. sp. *tritici* in each epidemiological region in the United States in 2008 and 2009^a

Regions ^b	2008					2009					Average		
	Isolates	Races	GRI	RSI	Ko	Isolates	Races	GRI	RSI	Ko	RGI	RSI	Ko
R1	118	16	0.13	0.44	0.20	169	12	0.07	0.36	0.39	0.10	0.40	0.30
R2	2	1	0.00	0.00	0.00	2	2	1.00	1.00	0.05	0.05	0.50	0.03
R3	5	3	0.50	0.66	0.10	5	5	1.00	1.00	0.14	0.75	0.83	0.12
R4	26	12	0.44	0.71	0.17	10	5	0.44	0.59	0.10	0.44	0.65	0.14
R5	45	14	0.30	0.62	0.40	40	14	0.33	0.55	0.28	0.32	0.59	0.34
R6	53	12	0.21	0.55	0.16	15	5	0.29	0.50	0.16	0.25	0.53	0.16
R1–R6	249	31	0.12	0.52	0.28	241	25	0.10	0.47	0.45	0.11	0.49	0.37
R7	11	4	0.30	0.43	0.06	8	3	0.29	0.50	0.08	0.29	0.47	0.07
R8	6	5	0.80	0.87	0.08	8	5	0.57	0.67	0.06	0.69	0.7	0.07
R9	...	...	...	...	...	...	...	...	...	...	...	...	...
R10	8	4	0.43	0.64	0.09	6	3	0.40	0.57	0.08	0.42	0.60	0.09
R11	18	8	0.41	0.66	0.11	...	...	...	...	...	0.41	0.66	0.11
R12	2	1	0.00	0.00	0.00	2	1	0.00	0.00	0.00	0.00	0.00	0.00
R7–R12	45	11	0.23	0.51	0.08	24	6	0.22	0.44	0.08	0.22	0.48	0.08
United States	294	33	0.11	0.49	0.25	265	26	0.10	0.47	0.42	0.10	0.48	0.34

^a Symbol ... indicates no samples or no data.

^b Wheat stripe rust epidemiological regions in the United States are as follows: Region 1 (R1) = eastern Washington, northeastern Oregon, and northern Idaho; R2 = western Montana and southern Alberta, Canada; R3 = southern ID, southeastern Oregon, northern Nevada, northern Utah, western Wyoming, and western Colorado; R4 = western Oregon and northern California; R5 = northwestern Washington and southwestern British Columbia, Canada; R6 = central and southern California, Arizona, and western New Mexico; and R7 = Texas, Louisiana, Arkansas, Oklahoma, and eastern New Mexico; R8 = Kansas, Nebraska, and eastern Colorado; R9 = South Dakota, North Dakota, Minnesota, eastern Montana, and southern Manitoba and southern Saskatchewan, Canada; R10 = Mississippi, Alabama, Florida, Georgia, South Dakota, North Dakota, Tennessee, and Kentucky; R11 = Missouri, Illinois, Indiana, Iowa, Wisconsin, Michigan, and Ontario, Canada; and R12 = Virginia, West Virginia, Ohio, Maryland, Pennsylvania, and New York (21).

differentials 16 and 20. PST-140 was similar to previously identified PST-114 (virulent on differentials 1, 3, 4, 8, 9, 10, 11, 12, 14, 16, 17, 18, 19, and 20) but not virulent on differential 9. Thus, the three new races have relatively narrow virulence spectra compared with some previously identified races.

Distributions and frequencies of *P. striiformis* f. sp. *tritici* races. In 2008, region 1 (eastern Washington, northeastern Oregon, and northern Idaho, the major wheat-growing area in the PNW) had 16 races, followed by region 5 (14 races) and regions 4 and 6 (12 races each) (Table 3). In contrast, only one race was detected in

Table 4. Races of *Puccinia striiformis* f. sp. *tritici* (PST) with their virulence formulae, first year of detection in the United States (Year), frequency, and distribution in U.S. epidemiological regions in 2008 and 2009^a

Race	Virulence formula ^b	Year	2008 Frequency (%)		2009 Frequency (%)	
			U.S.	Regions	U.S.	Regions
PST-21	2	1980	0.3	R1 (0.9)	...	...
PST-23	1,3,6,9,10	1981	0.3	R5 (2.2)	1.1	R5 (7.5)
PST-25	1,3,6,8,9,10,12	1982	1.4	R5 (8.9)	1.9	R5 (12.5)
PST-33	1,3,9,12,13	1984	...	...	0.4	R5 (2.5)
PST-35	1,10	1985	0.3	R5 (2.2)	0.4	R5 (2.5)
PST-46	1,3,6,9,10,11	1991	0.3	R1 (0.9)	...	...
PST-54	1,3,4,6,8,9,10,12	1994	3.4	R5 (22.2)	...	...
PST-67	1,2,3,11,12,16	2000	0.3	R6 (1.9)	...	...
PST-78	1,3,11,12,16,17,18,19,20	2000	0.3	R7 (9.1)	0.4	R8 (12.5)
PST-80	1,3,8,11,12,16,17,18,19,20	2000	...	...	0.4	R8 (12.5)
PST-91	1,9,10	2002	...	...	1.1	R5 (7.5)
PST-92	1,10,12	2002	2.4	R5 (15.6)	3.4	R5 (22.5)
PST-94	1,9,10,12	2002	1.0	R5 (6.7)	0.4	R5 (2.5)
PST-98	1,3,8,10,11,12,16,17,18,19,20	2002	6.1	R1 (5.1), R2 (100.0), R5 (4.4), R6 (9.4), R7 (18.2), R8 (16.7), R11 (5.6)	7.9	R1 (1.8), R4 (10.0), R6 (40.0), R7 (25.0), R8 (50.0), R10 (50.0), R12 (100.0)
PST-100	1,3,8,9,10,11,12,16,17,18,19,20	2003	14.6	R1 (11.9), R3 (40.0), R4 (3.9), R5 (4.4), R6 (9.4), R7 (63.6), R8 (33.3), R10 (37.5), R11 (27.8), R12 (100.0)	3.8	R1 (1.8), R2 (50.0), R6 (13.3), R7 (25.0), R8 (12.5), R10 (16.7)
PST-101	1,2,3,8,9,10,11,12,16,17,18,19,20	2003	6.5	R1 (1.7), R4 (7.7), R6 (24.5), R10 (25.0)	0.8	R1 (0.6), R4 (10.0)
PST-102	1,3,8,9,10,11,12,14,16,17,18,19,20	2003	4.4	R1 (2.5), R4 (11.5), R6 (3.8), R8 (16.7), R11 (22.2)	4.5	R2 (50.0), R6 (33.3), R7 (50.0), R10 (33.3)
PST-108	1,3,4,6,9,10,12	2003	...	...	1.5	R5 (10.0)
PST-109	1,4,8,10,12	2003	1.0	R5 (6.7)	...	...
PST-110	1,3,8,9,11,12,16,17,18,19,20	2004	0.7	R7 (9.1), R10 (12.5)	...	...
PST-111	1,3,5,8,10,11,12,16,17,18,19,20	2004	3.1	R4 (15.4), R6 (9.4)	1.1	R3 (20.0), R5 (2.5), R8 (12.5)
PST-113	1,2,3,8,9,10,11,12,14,16,17,18,19,20	2004	1.0	R1 (2.5)	...	...
PST-114	1,3,4,8,9,10,11,12,14,16,17,18,19,20	2004	19.4	R1 (37.3), R3 (40.0), R4 (3.9), R5 (8.9), R6 (7.6), R11 (11.1)	10.6	R1 (15.4), R3 (20.0), R5 (2.5)
PST-115	1,3,5,8,9,10,11,12,14,16,17,18,19,20	2004	4.8	R3 (20.0), R4 (19.2), R6 (7.6), R10 (25.0), R11 (11.1)	...	...
PST-116	1,3,4,5,8,9,10,11,12,14,16,17,18,19,20	2005	6.8	R1 (15.3), R4 (3.9), R5 (2.2)	10.2	R1 (15.4), R3 (20.0)
PST-117	1,3,6,8,9,10,11,12,14,16,17,18,19,20	2005	1.7	R1 (0.9), R4 (3.9), R8 (16.7), R11 (11.1)	...	...
PST-118	1,3,8,9,10,11,12,13,14,16,17,18,19,20	2005	...	...	0.4	R1 (0.6)
PST-119	1,3,4,8,9,10,11,12,16,17,18,19,20	2005	3.7	R1 (3.4), R4 (7.7), R5 (11.1)	0.4	R1 (0.6)
PST-122	1,2,3,6,8,9,10,11,12,14,16,17,18,19,20	2006	0.7	R6 (3.8)	...	...
PST-123	1,3,6,8,9,10,11,12,16,17,18,19,20	2006	1.0	R6 (1.9), R8 (16.7), R11 (5.6)	...	...
PST-127	1,2,3,5,6,8,9,10,11,12,13,15,16,17,18,19,20	2007	4.4	R1 (10.2), R6 (1.9)	9.1	R1 (13.6), R6 (6.7)
PST-128	1,2,3,6,8,10,11,12,16,17,18,19,20	2007	0.3	R4 (3.9)	...	...
PST-129	1,2,3,8,10,11,12,16,17,18,19,20	2007	3.4	R6 (18.9)	1.9	R4 (50.0)
PST-130	1,3,4,8,10,11,12,16,17,18,19,20	2007	2.0	R1 (3.4), R5 (4.4)	2.3	R1 (1.8), R3 (20.0), R4 (10.0), R5 (2.5)
PST-131	1,3,5,6,8,9,10,11,12,14,16,17,18,19,20	2007	1.4	R4 (7.7), R5 (2.2), R11 (5.6)	...	...
PST-132	1,3,6,8,9,10,12,13,15	2007	...	...	0.4	R5 (2.2)
PST-133	1,2,3,5,6,8,9,10,11,12,14,16,17,18,19,20	2007	1.7	R1 (1.7), R4 (11.5)	...	...
PST-136	1,3,9,10,12,13,15	2007	...	...	3.0	R5 (20.0)
PST-137	1,2,3,5,6,8,9,10,12,13,15,17,18,19,20	2007	0.7	R1 (1.7)	0.4	R1 (0.6)
PST-138	1,2,3,5,6,9,10,11,12,13,15,16,17,18,19,20	2008	0.3	R1 (0.9)	...	...
PST-139	1,2,3,5,6,8,9,10,11,12,13,15,17,18,19	2009	...	...	18.9	R1 (29.0), R6 (6.7)
PST-140	1,3,4,8,10,11,12,14,16,17,18,19,20	2009	...	...	13.6	R1 (18.9), R3 (20.0), R4 (20.0), R5 (2.5)

^a Distribution by epidemiological region. Region 1 (R1) = eastern Washington, northeastern Oregon, and northern Idaho; R2 = western Montana and southern Alberta, Canada; R3 = southern ID, southeastern Oregon, northern Nevada, northern Utah, western Wyoming, and western Colorado; R4 = western Oregon and northern California; R5 = northwestern Washington and southwestern British Columbia, Canada; R6 = central and southern California, Arizona, and western New Mexico; and R7 = Texas, Louisiana, Arkansas, Oklahoma, and eastern New Mexico; R8 = Kansas, Nebraska, and eastern Colorado; R9 = South Dakota, North Dakota, Minnesota, eastern Montana, and southern Manitoba and southern Saskatchewan, Canada; R10 = Mississippi, Alabama, Florida, Georgia, South Dakota, North Dakota, Tennessee, and Kentucky; R11 = Missouri, Illinois, Indiana, Iowa, Wisconsin, Michigan, and Ontario, Canada; and R12 = Virginia, West Virginia, Ohio, Maryland, Pennsylvania, and New York (21). The value following a region is the frequency of the race in the region and the value in bold is the most common race in the region; ... indicates there were no samples.

^b Virulence formulae are based on reactions on wheat differential lines: 1 = Lemhi, 2 = Chinese 166, 3 = Heines VII, 4 = Moro, 5 = Paha, 6 = Druchamp, 7 = AvSYr5NIL, 8 = Produra, 9 = Yamhill, 10 = Stephens, 11 = Lee, 12 = Fielder, 13 = Tyee, 14 = Tres, 15 = Hyak, 16 = Express, 17 = AvSYr8NIL, 18 = AvSYr9NIL, 19 = Clement, and 20 = Compair. Differential lines resistant to the race are not shown in the column of virulence formulae.

region 2 and region 12. Collectively, regions west of the Rocky Mountains (R1 to R6) had 31 races while regions east of the Rocky Mountains (R7 to R12) had 11. The same trend was found in 2009. Region 5 (northwestern Washington) had the highest number of races (15 races) followed by region 1 (12 races). Region 12 had only one race again. Collectively, the western regions (R1 to R6) had 25 races and the eastern regions had only 6 (Table 3).

The frequencies of the races ranged from 0.3% (identified from one isolate) to 19.3% in 2008, and ranged from 0.4% (one isolate) to 18.9% in 2009 (Table 4). In 2008, the five predominant races were PST-114 (19%), PST-100 (15%), PST-116 (7%), PST-101 (6%), and PST-98 (6%). In 2009, the five predominant races were PST-139 (19%), PST-140 (14%), PST-114 (11%), PST-116 (10%), and PST-127 (9%) (Table 4). In 2008, PST-21, PST-23, PST-35, PST-46, PST-67, PST-78, and PST-138 were identified from only one sample each and, in 2009, PST-33, PST-35, PST-78, PST-80, PST-94, PST-118, PST-119, PST-132, and PST-137 were detected from only one sample each. Most of the remaining races were detected at frequencies lower than 5%. In both 2008 and 2009, PST-98 (virulent on differentials 1, 3, 8, 9, 11, 12, 16, 17, 18, 19, and 20) and PST-100 (similar to PST-98 plus virulence on differential 10) had the widest distribution across the country. The races with virulences to differentials 13 and 15, such as PST-127, PST-132, PST-136, PST-137, PST-138, and PST-139, were found only in the regions west of the Rocky Mountains (R1 to R6). Most of the old races, such as PST-21, PST-23, PST-25, PST-33, PST-35, PST-46, and PST-54, were also detected only in the west, especially northwestern Washington (Table 4). PST-116, PST-127, PST-136, PST-139, and PST-140 had considerable increases ($\geq 3\%$) in frequency, whereas PST-54, PST-100, PST-101, PST-114, PST-115, and PST-119 decreased considerably ($\geq 3\%$) from 2008 to 2009.

Virulences and their distribution and frequency in *P. striiformis* f. sp. *tritici* populations. Virulences and their frequency in the United States and distribution in various epidemic regions are shown in Table 5. The frequencies of virulences to the 20 wheat differentials (Table 1) ranged from 0% (differential number 7 with Yr5) to almost 100% (differential number 1 with Yr21) in 2008 and from 0 to 100% for the same differential genotypes, respectively, in 2009 (Table 5). In 2008, virulences to differentials 2 (Yr1), 6 (Yr3a, YrD, YrDru), 13 (YrTye), and 15 (Yr17, YrTye) had low frequencies (<20%); virulences to differentials 4 (Yr10, YrMor), 5 (YrPa1, YrPa2, YrPa3), and 14 (YrTr1, YrTr2) had moderate frequencies (20 to 80%); and those to differentials 3 (Yr2, YrHVII), 8 (YrPr1, YrPr2), 9 (Yr2, Yr4a, YrYam), 10 (Yr3a, YrS, YrSte), 11 (Yr7, Yr22, Yr23), 12 (Yr6, Yr20), 16 (YrExp1, YrExp2), 17 (Yr8), 18 (Yr9), 19 (Yr9, YrCle), and 20 (Yr8, Yr19) had high frequencies (>80%). The frequency classes remained basically the same in 2009, except that virulences to differentials 2, 6, 13, and 15 increased from low to moderate and virulence factors to differentials 8, 9, 16, and 20 decreased from high to moderate. Virulences with moderate to high frequencies in both 2008 and 2009 were widespread across the country, whereas virulence factors in the low-frequency class, especially virulences to differentials 13 and 15, were basically limited to the western regions.

Diversity of rust populations in epidemic regions. Among regions with five isolates or more, region 8 had the highest relative Gleason index (RGI) (0.80) and relative Shannon index (RSI) (0.87), while region 1 had the lowest RGI (0.13) and region 7 had the lowest RSI (0.43) in 2008 (Table 3). In 2009, region 1 had the lowest RGI (0.07) and RSI (0.36), while region 3 had the highest (1.00) of both RGI and RSI. Diversities in various regions and nationally were similar in 2008 and 2009. Over the 2 years, on average, region 1 had the lowest diversity (0.10 RGI and 0.40 RSI) and region 3 had the highest diversity (0.75 RGI and 0.83 RSI). In general, the western population (R1 to R6) had a diversity (0.49) similar to the eastern population (R7 to R12; 0.47). For the whole country, the wheat stripe rust population had RGI of 0.10 and RSI of 0.48, which indicated a low level of diversity if the average diversity ranges (0.10 to 0.75 for RGI and 0.40 to 0.83 for RSI) of the various regions were used as references.

When Kosman index values were used in comparison, region 5 had the highest diversity (0.4), followed by region 1 (0.2), and regions 2 and 12 had the lowest (0); and the regions west of the Rocky Mountains (R1 to R6) had a higher diversity (0.28) than the regions east of the Rocky Mountains (R7 to R12; 0.08) in 2008 (Table 3). In 2009, region 1 had the highest diversity (0.39), followed by region 5 (0.28), and region 12 had the lowest (0). The diversity (0.45) of the west (R1 to R6) was much higher than that (0.08) in the east. Averaging the 2 years, the west had a diversity of 0.37, the east 0.08, and the whole country a moderate level (0.34) of diversity.

Barley stripe rust and *P. striiformis* f. sp. *hordei* races. Samples of barley stripe rust were obtained from California only in 2008 and from Washington and Oregon in both 2008 and 2009 (Table 6). The distribution and severity of barley stripe rust were low, except for western Oregon and western Washington, where stripe rust exceeded 90% intensity on susceptible barley cultivars. Only 33 isolates were obtained in 2008 and 12 in 2009.

In 2008, 11 races were identified (Table 6). An isolate from eastern Washington was identified as a new race (PSH-82), because it was virulent on only 2 of the 12 barley differentials (lines 1 and 11). PSH-33 (virulent on differentials 1 and 7) was predominant, comprising 46% of the isolates and occurring in all three states (California, Oregon, and Washington). In 2009, the 12 isolates were the same as six previously identified races (Table 6). Because of the small sample size, determination of the predominant race was not possible. Five (PSH-16, PSH-38, PSH-46, PSH-54, and PSH-71) of the six races were identified in Washington and two (PSH-54 and PSH-70) in Oregon. PSH-71 was detected from three isolates, and all other races were detected from one or two isolates.

Discussion

The distribution of wheat stripe rust in 2008 and 2009 was not as widespread as in 2005 but was similar to that in 2006 and 2007 (6,21). The estimated percentage of yield loss in Washington and California in both years was similar to that of 2007. The nationwide estimated yield losses were slightly lower in 2008 and 2009 than in 2007 and much lower than that in 2005 (<http://www.ars.usda.gov/mwa/cdl>). The possible reasons for the relatively low levels of stripe rust in 2008 and 2009 include low winter temperatures and high temperatures and dry conditions in the late growing season of each year, which were relatively unfavorable to the pathogen overwintering and to disease development in both growing seasons in several regions. For example, the monthly average temperatures of the Palouse region in eastern Washington and northern Idaho were 1.73 and 1.62°C lower than the long-term (normal) average temperatures for January 2008 and December 2009, respectively. The observed relatively low levels of stripe rust were in agreement with predictions for the disease based on winter weather conditions in this region in 2008 and 2009 (*data not shown*). Widespread drought conditions in the south-central states in the spring seasons of both 2008 and 2009 did not allow stripe rust to develop.

In this study, more *P. striiformis* f. *tritici* races were detected west of the Rocky Mountains than in the eastern regions. In 2008 and 2009, there were 9 and 6 races identified east of Rocky Mountains, whereas 31 and 25 races were detected west of the Rocky Mountains, respectively. This is generally in agreement with previous reports (4–6,21,26,28).

Historically, races first emerge in the western regions (5,21,26,28). One new race, PST-138, was identified in 2008, and two new races, PST-139 and PST-140, were identified in 2009. All three new races were identified in the west. These races, together with other races identified in the west in recent years, such as PST-127 and similar races with virulence factor to Hyak (Yr17, YrTye), may eventually spread to the eastern regions. For this reason, breeding programs in the eastern regions should pay attention to races increasing in the western regions. For example, virulence to Yr17, as indicated by the susceptibility of differential genotype Hyak, has been in the *P. striiformis* f. *tritici* population in the PNW

since the early 1980s (5). Although Hyak-virulent races decreased in frequency from the late 1990s until recent years, the virulence did not disappear and has reemerged in combination with many other virulence factors. In 2007, we detected PST-127, which has the virulence factor to Hyak, at very low frequencies in California and the PNW (21). As shown in the present study, PST-127 and similar races, such as PST-139, have increased in frequency in the west. This increase has made wheat cultivars and breeding lines bearing this resistance gene more vulnerable to the disease. In fact, *Yr17* virulence was confirmed from 2010 stripe rust samples collected from the eastern regions (A. Wan and X. M. Chen, *unpublished data*).

Two major factors have contributed to the development of new races and maintaining a high number of races in the PNW and California. First, a relatively large number of different cultivars are grown in these regions. In Washington, for instance, more than 70

different wheat cultivars with various stripe rust resistance genes are grown every year. Second, the cropping system and weather conditions are diverse, and the weather favors survival, growth, and reproduction of the stripe rust pathogen. Growing both winter and spring wheat with extended times for planting and harvesting provides a host for the pathogen all year long. These conditions favor the survival and reproduction of new races (5,21). For instance, PST-116, PST-127, PST-139, and PST-140 were only found in regions 1 and 6 of the western United States. Generally, the races identified east of the Rocky Mountains can be detected in the west, whereas not every race identified in the west has been found in the east (5,6,19,21,28). The spread of new races is generally correlated with the frequency and direction of prevailing winds, which explains why movement of wheat stripe rust inoculum and races in the United States is usually from west to east and from south to north (5,21). The large number of races in the west may also be

Table 5. Frequency of virulence (Fq.) of *Puccinia striiformis* f. sp. *tritici* isolates to specific wheat differential lines and distribution of those isolates in the United States in 2008 and 2009^a

Differential ^b	2008			2009		
	N	Fq. (%)	Distribution (number of isolates)	N	Fq. (%)	Distribution (number of isolates)
Lemhi	293	100	R1(117), R2(2), R3(5), R4(26), R5(45), R6(53), R7(11), R8(6), R10(8), R11(18), R12(2)	265	100	R1(169), R2(2), R3(5), R4(10), R5(40), R6(15), R7(8), R8(8), R10(6), R12(2)
Chinese 166	58	20	R1(23), R4(6), R6(27), R10(2)	82	31	R1(74), R4(6), R6(2)
Heines VII	279	95	R1(117), R2(2), R3(5), R4(26), R5(31), R6(53), R7(11), R8(6), R10(8), R11(18), R12(2)	251	95	R1(169), R2(2), R3(5), R4(10), R5(26), R6(15), R7(8), R8(8), R10(6), R12(2)
Moro	107	36	R1(70), R3(2), R4(4), R5(25), R6(4), R11(2)	102	39	R1(88), R3(4), R4(3), R5(7)
Paha	68	23	R1(35), R3(1), R4(15), R5(2), R6(10), R10(2), R11(3)	105	40	R1(99), R3(2), R5(1), R6(2), R8(1)
Druchamp	52	18	R1(19), R4(7), R5(16), R6(4), R8(2), R11(4)	88	33	R1(73), R5(13), R6(2)
AvSYr5NIL	0	0	...	0	0	...
Produra	277	94	R1(115), R2(2), R3(5), R4(26), R5(33), R6(52), R7(10), R8(6), R10(8), R11(18), R12(2)	184	69	R1(120), R2(2), R3(5), R4(10), R5(10), R6(14), R7(8), R8(7), R10(6), R12(2)
Yamhill	236	80	R1(107), R3(5), R4(21), R5(31), R6(32), R7(8), R8(5), R10(8), R11(17), R12(2)	182	69	R1(131), R2(2), R3(2), R4(1), R5(27), R6(9), R7(6), R8(1), R10(3)
Stephens	289	98	R1(117), R2(2), R3(5), R4(26), R5(45), R6(52), R7(9), R8(6), R10(7), R11(18), R12(2)	262	99	R1(169), R2(2), R3(5), R4(10), R5(39), R6(15), R7(8), R8(6), R10(6), R12(2)
Lee	264	90	R1(117), R2(2), R3(5), R4(26), R5(16), R6(53), R7(11), R8(6), R10(8), R11(18), R12(2)	229	86	R1(169), R2(2), R3(5), R4(10), R5(4), R6(15), R7(8), R8(8), R10(6), R12(2)
Fielder	290	99	R1(116), R2(2), R3(5), R4(26), R5(43), R6(53), R7(11), R8(6), R10(8), R11(18), R12(2)	258	97	R1(169), R2(2), R3(5), R4(10), R5(33), R6(15), R7(8), R8(8), R10(6), R12(2)
Tyee	16	5	R1(15), R6(1)	86	33	R1(74), R5(10), R6(2)
Tres	123	42	R1(71), R3(3), R4(16), R5(6), R6(12), R8(2), R10(2), R11(11)	104	39	R1(85), R2(1), R3(3), R4(2), R5(2), R6(5), R7(4), R10(2)
Hyak	16	5	R1(15), R6(1)	84	32	R1(73), R5(9), R6(2)
Express	261	89	R1(114), R2(2), R3(5), R4(26), R5(16), R6(53), R7(11), R8(6), R10(8), R11(18), R12(2)	178	67	R1(119), R2(2), R3(5), R4(10), R5(4), R6(14), R7(8), R8(8), R10(6), R12(2)
AvSYr8NIL	262	89	R1(116), R2(2), R3(5), R4(26), R5(16), R6(52), R7(11), R8(6), R10(8), R11(18), R12(2)	229	86	R1(169), R2(2), R3(5), R4(10), R5(4), R6(15), R7(8), R8(8), R10(6), R12(2)
AvSYr9NIL	262	89	R1(116), R2(2), R3(5), R4(26), R5(16), R6(52), R7(11), R8(6), R10(8), R11(18), R12(2)	229	86	R1(169), R2(2), R3(5), R4(10), R5(4), R6(15), R7(8), R8(8), R10(6), R12(2)
Clement	262	89	R1(116), R2(2), R3(5), R4(26), R5(16), R6(52), R7(11), R8(6), R10(8), R11(18), R12(2)	229	86	R1(169), R2(2), R3(5), R4(10), R5(4), R6(15), R7(8), R8(8), R10(6), R12(2)
Compair	262	89	R1(116), R2(2), R3(5), R4(26), R5(16), R6(52), R7(11), R8(6), R10(8), R11(18), R12(2)	229	68	R1(120), R2(2), R3(5), R4(10), R5(4), R6(14), R7(8), R8(8), R10(6), R12(2)

^a N = number of isolates. Distribution by regions. Region 1 (R1) = eastern Washington, northeastern Oregon, and northern Idaho; R2 = western Montana and southern Alberta, Canada; R3 = southern ID, southeastern Oregon, northern Nevada, northern Utah, western Wyoming, and western Colorado; R4 = western Oregon and northern California; R5 = northwestern Washington and southwestern British Columbia, Canada; R6 = central and southern California, Arizona, and western New Mexico; and R7 = Texas, Louisiana, Arkansas, Oklahoma, and eastern New Mexico; R8 = Kansas, Nebraska, and eastern Colorado; R9 = South Dakota, North Dakota, Minnesota, eastern Montana, and southern Manitoba and southern Saskatchewan, Canada; R10 = Mississippi, Alabama, Florida, Georgia, South Dakota, North Dakota, Tennessee, and Kentucky; R11 = Missouri, Illinois, Indiana, Iowa, Wisconsin, Michigan, and Ontario, Canada; and R12 = Virginia, West Virginia, Ohio, Maryland, Pennsylvania, and New York (21).

^b Virulence on differential.

explained by the current set of wheat differentials, which includes several cultivars grown in the western United States. However, such hypothesis is not supported by the use of a set of *Yr* isogenic lines to identify *P. striiformis* f. *tritici* races in 2010, because we have also identified more races in the west than in the east (A. Wan and X. M. Chen, unpublished data).

The RGI and RSI did not result in meaningful information about diversities in various regions, because they treat differences the same for any pair of races and ignore the differences and similarities of virulence factors among races. Using these indices, the populations in the east and west of the Rocky Mountains had similar diversity. However, the Kosman index values revealed much higher diversity in the west than in the east, especially in the eastern PNW (R1) and western Washington (R5). The results are in agreement with the large number of races and wide range of virulence factor combinations in races identified in this study and previous studies (5,6,19,21,26). The present study clearly shows that the Kosman index is more suitable than the RGI and RSI for assessing population diversity of rust fungi using virulence data, because the Kosman index takes into consideration not only the differences in sample sizes but also the similarity in virulence or avirulence of isolates.

The percentage of isolates virulent on differentials 1, 2, 4, 5, 8, 9, 10, 11, 12, 14, 16, 17, 18, 19, or 20 ranged from 23% (differential 5 in 2008) to 100% (differential 1 in 2009). Compared with the virulence frequencies in 2007 (21), there were big increases of virulence factors to differential 2 (*Yr1*), from 15.0% in 2007 to 30.9% in 2009; differential 6 (*Yr3a*, *YrD*, and *YrDru*), from 22 to 33%; differential 13 (*YrTye*), from 2 to 33%; and Hyak (*Yr17* and *YrTye*), from 2 to 32%. Together with the tests of representative isolates of 2008 and 2009 on *Yr* isogenic lines (data not shown), the results of the present study show that *Yr1*, *Yr2*, *Yr3a*, *Yr4a*, *Yr6*, *Yr7*, *Yr8*, *Yr9*, *Yr10*, *Yr17*, *Yr19*, *Yr20*, *Yr21*, *Yr22*, *Yr23*, *Yr24*, *Yr25*, *Yr26*, *Yr27*, *Yr28*, *Yr31*, *Yr43*, *Yr44*, *YrHVII*, *YrMor*, *YrPa1*, *YrPa2*, *YrPa3*, *YrDr1*, *YrDr2*, *YrPr1*, *YrPr2*, *YrSt1*, *YrSt2*, *YrYam*, *YrTye*, *YrTr1*, *YrTr2*, *YrExp1*, *YrExp2*, and *YrCle* were singly not effective against most to almost all isolates in 2008 and 2009. The results indicate that these genes should be avoided in the breeding programs. The large number of *Yr* genes that have become ineffective warrants the use of non-race-specific resistance. Although isolates were found to be virulent to *Yr32* and *YrSP*, the two genes were effective against most of the isolates. No isolates were found virulent to *Yr5* and *Yr15*. These genes should be used in combination to extend the life of each resistance source. It would be better to pyramid effective race-specific resistance genes with those for non-race-specific resistance to achieve more durable and highly effective resistance to stripe rust (5).

Similarly, barley stripe rust was generally low in severity and distribution in 2008 and 2009, except in experimental fields in

western Oregon and western Washington. The situation was similar to that of the years since the late 1990s, when stripe rust was severe in California and the PNW (4). In 2008 and 2009, no barley stripe rust was detected in eastern regions, even though this is where barley stripe rust was first identified in the United States (30). Barley stripe rust samples were obtained from North Dakota but we were unable to recover urediniospores from the samples. We do not know whether these were *P. striiformis* f. *tritici* or *P. striiformis* f. sp. *hordei* because some barley cultivars are susceptible to some *P. striiformis* f. *tritici* races (17). The low levels of barley stripe rust in 2008 and 2009 could be attributed to the decreased barley acreage in California and most of the PNW, and the use of more resistant cultivars. 'Baronesse' barley, with a moderate level of non-race-specific high-temperature adult-plant resistance, has replaced Steptoe, which is highly susceptible (4). Volunteer plants of spring barley Steptoe can survive during the winter and can be a source of *P. striiformis* f. sp. *hordei* in the spring in the PNW. The elimination of Steptoe could have contributed to the reduction of barley stripe rust in the PNW. The numbers of races detected in 2008 and 2009 were generally similar to those from 2000 to 2007 (4,7,20). In the 2 years of the present study, one new race (PSH-82) was identified, which has increased the number of *P. striiformis* f. sp. *hordei* races to 82 since the early 1990s (17).

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Table 6. Races of *Puccinia striiformis* f. sp. *hordei*, their virulence formulae, first year of detection (Year), and frequency (Fq.) and distribution in the United State in 2008 and 2009^a

Race	Virulence formula ^b	Year	2008			2009		
			N	Fq. (%)	Distribution (N)	N	Fq. (%)	Distribution (N)
PSH-16	1,3,5,7,8	1995	1	3.0	CA (1)	2	16.7	WA (2)
PSH-33	1,7	1996	15	45.5	CA (12), OR (1), WA (2)	...	...	...
PSH-37	1,2,4,7	1996	1	3.0	CA (1)	...	...	...
PSH-38	1,2,3,4,5,7,8	1996	...	...	...	2	16.7	WA (2)
PSH-46	1,7,8	1996	6	18.2	CA (6)	2	16.7	WA (2)
PSH-48	1	1997	2	4.4	CA (2)	...	...	...
PSH-54	1,7,8,12	2001	3	9.1	CA (1), WA (2)	2	16.7	OR (1), WA (1)
PSH-68	1,6,7,8,10,12	2003	1	2.2	CA (1)	...	...	...
PSH-70	1,7,10,12	2004	1	3.0	WA (1)	1	8.3	OR (1)
PSH-71	1,3,5,6,7,8,9,10,12	2004	1	3.0	OR (1)	3	25.0	WA (3)
PSH-77	1,3,5,7,8,9,10,12	2006	1	3.0	OR (1)	...	...	...
PSH-82	1,11	2008	1	3.0	WA (1)	...	...	...

^a N = number of isolates, CA = California, OR = Oregon, WA = Washington, and ... indicates there were no samples and no data available.

^b Virulence formulae are based on reactions on barley differential lines: 1 = Topper, 2 = Heils Frank, 3 = Emir, 4 = Astrix, 5 = Hiproly, 6 = Varunda, 7 = Abed Binder 12, 8 = Trumpf, 9 = Mazurka, 10 = Bigo, 11 = I 5, and 12 = Bancroft. Differential lines resistant to the race are not shown in the virulence formula column.

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