Population Race Structure of *Pyrenophora tritici-repentis* Prevalent on Wheat and Noncereal Grasses in the Great Plains

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ABSTRACT

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The fungus *Pyrenophora tritici-repentis*, cause of tan spot of wheat, is an important foliar pathogen worldwide. Genetic variation in the fungal population prevalent in the Great Plains was studied by analysis of 270 single-spore isolates of *P. tritici-repentis* recovered from wheat, durum, and 10 noncereal grasses: Alti wild rye, barnyard grass, crested wheatgrass, intermediate wheatgrass, needle and thread grass, quackgrass, smooth brome grass, sand reedgrass, slender wheatgrass, and wild barley. The isolates were grouped into five known races based on necrosis and/or chlorosis induction on standard differentials with two additional wheat genotypes ND495 and M-3. The isolates recovered from wheat were races 1, 2, and 4, while those from durum were races 1 and 5. Isolates from noncereal grasses were all race 4, except for the recovery of two isolates of race 1 from smooth brome grass. Race 3 was not found in this study. This is the first record of barnyard grass and slender wheatgrass as alternative hosts for *P. tritici-repentis*. The recovery from noncereal grasses suggests that the fungus has a fairly wide host range; however, predominance of a race that is avirulent on wheat on these grasses tends to eliminate their significance in the disease epidemiology of wheat. The results indicate that *P. tritici-repentis* has a diverse population on wheat and noncereal grasses. For durable resistance, wheat lines should be tested against all virulent races found in the field.

The fungus *Pyrenophora tritici-repentis* (Died.) Drechs., anamorph *Drechslera tritici-repentis* (Died.) Shoemaker (synonym *Helminthosporium tritici-repentis* Died.), causes tan spot, a foliar disease of wheat worldwide (18). The fungus produces lens-shaped necrotic lesions with a chlorotic halo on susceptible cultivars. The fungus is also pathogenic on many other members of the family Poae (11,18,24). The fungal isolates from wheat are cross-pathogenic on grasses and vice versa (18,20,22,23). The pathogen can over-season on diseased seed, infested crop residue, and overwintering grass hosts (11). Since the 1970s, the disease has become a serious problem and sporadically caused considerable losses (3 to 50%) in production in major wheat growing areas in the United States and elsewhere (18,31). The change in disease severity could be due to a change in pathogen virulence, wide adoption of no-till and conservation tillage practices, and/or introduction of susceptible cultivars.

In attempting to develop durable and resistant cultivars to combat plant diseases,

knowledge of the genetic diversity of plant pathogens is essential. The *P. tritici-repentis* population on wheat and alternative hosts shows variability in both virulence and aggressiveness (1,10,16,20,22,23,27,29,32,33). The fungal populations prevalent on durum were not included in these aforementioned studies. In most cases, virulence and/or aggressiveness was measured using a quantitative rating scale based on lesion size and/or necrotic leaf area. For example, 40 isolates collected from the United States and Canada were tested for their virulence on five spring wheat genotypes, one durum genotype, and one barley genotype (10). These isolates were grouped into 12 races, based on leaf area infected and lesion number produced per cm². Krupinsky (24) recovered 87 single-spore isolates of *P. tritici-repentis* from various grass species and barley and tested them on wheat. Isolates were statistically different in their aggressiveness as they induced variable necrotic lesion sizes. This indicated that other grass hosts could provide a potential reservoir for genetic variation in the pathogen population.

Two qualitative types of symptoms, tan necrosis (nec+) and extensive chlorosis (chl+) produced by *P. tritici-repentis* on susceptible wheat genotypes, were identified by Lamari and Bernier (26). *P. tritici-repentis* isolates have been grouped into five races based on their ability to induce necrosis and chlorosis (race 1), necrosis only (race 2), chlorosis only (races 3 and 5

both produce chlorosis, but on different genotypes), and lack of either necrosis or chlorosis (race 4) on appropriate wheat genotypes (26,28). Three host-selective toxins, Ptr ToxA, Ptr ToxB, and Ptr ToxC, have been isolated to date (7,9,11,30). These toxins are associated with typical tan spot symptoms, tan necrosis (ToxA) and chlorosis (ToxB and ToxC), on susceptible wheat cultivars. After the discovery of the three host-selective toxins and the demonstration of independent genetic mechanisms behind the interaction of hexaploid/tetraploid wheats and *P. tritici-repentis* races 1, 3, and 5 (14,15), the race classification system seems reliable for studying genetics of the fungal population.

In 1989, Lamari and Bernier (26) reported that a majority of isolates collected in western Canada grouped as race 1; however, in 1998, both races 1 and 2 were prevalent in the region (27). In another study, 59 isolates were obtained from wheat samples collected from nine counties of South Dakota and tested by inoculating them individually on wheat lines Celtic (susceptible to necrosis and chlorosis) and Erik (resistant) (1). Sixty-four percent of the isolates produced necrosis and chlorosis (i.e., race 1), and 12% produced chlorosis. Only 2% caused necrosis only, and the rest of the isolates produced small lesions without necrosis or chlorosis. The fungal population on durum has not been explored yet in North America.

It was hypothesized that the *P. tritici-repentis* populations prevalent on noncereal grasses in wheat cultivated areas, grasslands, state parks, and national parks in the northern Great Plains might differ from one another. The grasses prevalent in locations remote from wheat have only a small chance to be exposed to the pathogen population that exists on wheat and may represent an independent genetic reservoir with unique virulence profiles. The objective of this study was to characterize the *P. tritici-repentis* populations prevalent on durum, wheat, and noncereal grasses in the U.S. Great Plains. Results have been reported in brief (2-4,6).

MATERIALS AND METHODS

***Pyrenophora tritici-repentis* isolates.** Diseased leaf samples were collected from spring wheat (n = 10 samples from different locations), durum (n = 25), and 28 noncereal grass host species (n = 118), and processed for the recovery of *P. tritici-*

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repentis. The durum leaf samples were collected from 15 locations within the primary durum production area of north-eastern North Dakota on 24 and 25 July 1997. The noncereal grass host species samples were taken from North Dakota, Minnesota, Montana, South Dakota, and Wyoming. The grass samples were collected from wheat areas (n = 66), national grasslands (n = 30), and state and national parks (n = 22). These samples were collected in the second week of July 1998. The noncereal grass host species sampled and number of samples of each species are listed in Table 1.

To recover *P. tritici-repentis* from the samples, leaves of each sample were cut into 2-cm lengths, and 50 leaf pieces were plated, 10 per plate, in plastic petri dishes (9 cm diameter) containing three layers of dampened Whatman no. 1 filter paper. To dampen the filter papers, 3 ml of distilled sterilized water was added to each plate. The leaves were incubated in an alternating cycle of 24 h light at 22°C and 24 h in dark at 16°C for 96 h to induce conidiophore and conidia formation. Incubated leaf pieces were examined under a stereoscope, and conidia of the fungus were picked individually with a flamed steel needle that had been cooled in a plate of V8PDA (150 ml of V8 juice, 10 g of Difco potato dextrose agar, 3 g of CaCO₃, 10 g of Bacto agar, and 850 ml of distilled water) (26). This procedure produces a sticky needle tip for picking of a single conidium. Each conidium was transferred onto an individual V8PDA plate. The single-spore cultures were incubated at 21°C in the dark for 8 days or until the colony size reached about 7 cm in diameter.

Twenty-five isolates of *P. tritici-repentis* were obtained from wheat, 71 from durum, and 77 from alternative hosts. Additionally, 51 isolates collected from North Dakota, 9 from South Dakota, 10 from Kansas, 12 from Oklahoma isolated from wheat, and 15 isolates obtained from other grass hosts (bromegrass [n = 7], western wheatgrass [n = 5], and wild barley [n = 3] collected from northern Great Plains) were included in this study. The isolates from Kansas, Oklahoma, and 16 of 51 from North Dakota were recovered in late 1980s and were also included in the analysis of race structure. All isolates were stored until testing following the protocol developed by Jordahl and Francel (19).

Inoculum production. To produce inoculum, four colonies of each isolate of stored cultures were initiated on V8PDA. The plates were incubated at 21°C in darkness until the colonies were about 5 cm in diameter. The plates were then flooded with sterilized distilled water, and the mycelium was matted with a flamed test tube. Excess water was decanted, and plates were incubated in an alternating cycle of 24 h light at 22°C and 24 h dark at 16°C to induce the formation of conidiophores and

conidia. When conidia were formed, 30 ml of sterilized distilled water were added to each dish and conidia were dislodged using a looped wire. The conidial suspension was adjusted to 3,000 per ml following the procedure described by Jordahl and Francel (19). Tween 20 was added at one drop per 100 ml of spore suspension before inoculations to enhance adhesion.

Inoculations and characterization of the isolates. The 270 isolates were grouped into races by inoculating them individually on seedlings of wheat differentials (26) at the two-leaf stage. Two additional genotypes, ND495 (susceptible to tan spot) and M-3 (resistant), were added to the standard set of differentials to increase the chance of finding more variants in the fungal population. Seeds were planted in plastic cones (3.8 cm in diameter and 20 cm in length) containing Sunshine Mix no. 1 (Fison Horticulture, Vancouver, B.C.) and grown in the greenhouse at an average temperature of 21°C (20 to 23°C) with a 16-h photoperiod. Seven seedlings of each differential genotype were inoculated individually with a spore suspension, 3,000 spores per ml, of

each isolate until runoff. Inoculated seedlings were air-dried, moved to a mist chamber at 18°C for 24 h, and then transferred to a growth chamber at 21°C with 16-h photoperiod for 7 days. The seedlings were rated for symptom development using a qualitative rating scale (Table 2) (26). The isolates were grouped into the appropriate races based on lesion type, tan necrosis and chlorosis, and absence of both lesion types.

RESULTS

Recovery of *P. tritici-repentis* from the samples. *P. tritici-repentis* was recovered from 40% of 153 samples. All wheat (n = 10) and durum (n = 25) samples were infected with *P. tritici-repentis*; whereas only 22% (26/118) of noncereal grass samples produced the fungus (Table 1). Only 20% (6/30) of the smooth bromegrass samples produced *P. tritici-repentis*, with the rest of the samples infected with *P. bromi* (data not reported). Of the intermediate wheatgrass samples, 31% (5/16) produced the fungus, and *P. tritici-repentis* could be recovered from 14% (1/7) of the intermediate wheatgrass samples from wheat areas.

Table 1. Numbers of samples of noncereal grass species from which *Pyrenophora tritici-repentis* were recovered from wheat production areas, the Theodore Roosevelt National Grasslands, and several state and national parks

Common name	Scientific name	Numbers (<i>P. tritici-repentis</i> /total)		
		Wheat	Grasslands	Parks
Alti wild-rye ^a	<i>Leymus angustus</i> (Trin.) Pilg.	3/6	0/1	
Barnyard grass	<i>Echinochloa crusgalli</i> (L.) Beauv.	1/2	0/1	0/2
Basin wild-rye ^a	<i>Leymus cinereus</i> (Scribn. & Merr.) A. Love	0/1		
Big blue stem ^a	<i>Andropogon gerardii</i> Vitm.	0/6		
Canada wild-rye ^a	<i>Leymus canadensis</i> L.	0/1		
Crested wheatgrass ^a	<i>Agropyron cristatum</i> (L.) Gaertn.	1/1	0/3	
Fowl manna grass	<i>Glyceria striata</i> (Lam.) Hitchc			0/2
Green foxtail ^a	<i>Setaria viridis</i> (L.) Beauv.	0/5		0/1
Green needle grass ^a	<i>Stipa viridula</i> Trin.	0/2		
Indian grass ^a	<i>Sorghastrum nutans</i> (L.) Nash	0/2		
Intermediate wheatgrass ^a	<i>Thinopyrum intermedium</i> (Host) Barkw. & D. R. Dewey	1/7	1/4	3/5
June grass ^a	<i>Koeleria cristata</i> (L.) Pers.	0/1	0/1	
Meadow foxtail ^a	<i>Alopecurus paratensis</i> L.			0/1
Needle-and-thread grass ^a	<i>Stipa comata</i> Trin. & Rupr.	1/1		
Quack grass ^a	<i>Agropyron repens</i> (L.) Beauv.	1/3	0/1	
Reed Canary grass ^a	<i>Phalaris arundinacea</i> L.	0/1		
Russian wild-rye ^a	<i>Psathyrostachys juncea</i> (Fisch.) Nevski	0/2	0/2	
Sand reed grass ^a	<i>Calamovifla longifolia</i> (Hook.) Scribn.		1/1	
Slender wheatgrass	<i>Elymus trachycaulum</i> (Link) Malte	1/2	2/4	
Slender wood grass	<i>Cinna latifolia</i> (Trev.) Griseb.			0/1
Smooth bromegrass ^a	<i>Bromus inermis</i> Leyss.	1/11	4/10	1/9
Standard crested wheatgrass	<i>Agropyron desertorum</i> (Fisch. Ex Link) Schult.		0/1	
Switch grass ^a	<i>Penicum virgatum</i> L.	0/3		
Tall wheatgrass ^a	<i>Thinopyrum ponticum</i> (Podp.) Barkw. & D. R. Dewey	0/1		
Thickspike wheatgrass ^a	<i>Elymus lanceolatus</i> (Scribn. & Smith) Gould	0/2		
Timothy	<i>Phleum pratense</i> L.			0/1
Western wheatgrass ^a	<i>Agropyron smithii</i>	0/2		
Wild barley ^a	<i>Critesion jubatum</i> (L.) Nevski	3/3	1/1	
Wild oat	<i>Danthonia intermedia</i> Vasey	0/1		
Total samples		13/66	9/30	4/22

^a Previously reported as host (Hosford [17]; Krupinsky [20,24]).

In contrast, 44% (4/9) of the intermediate wheatgrass samples from parklands and grasslands were infected with the fungus. During this study, *Drechslera gigantea*, *D. dactylidis*, *Septoria* spp., and *Ascochyta* spp. were also observed on various samples (data not recorded).

***P. tritici-repentis* races.** Races 1, 2, and 4 on wheat, 1 and 5 on durum, and 1 and 4 on noncereal grasses were identified (Table 3). The majority of the isolates on wheat and durum were typed as race 1 (Table 3). Of 107 isolates from wheat in the northern Great Plains, only 3% of the fungal population was grouped as race 2. Five percent of the isolates did not produce any symptom and were grouped under race 4. In contrast to the fungal population on wheat and durum, almost all (90/92) of the isolates obtained from noncereal grasses were grouped as race 4, regardless of the area from which the sample was collected (Table 3). Race 3 and off-type races were not found in this study.

DISCUSSION

The recovery data for *P. tritici-repentis* indicate that species of alternative hosts can harbor the fungus regardless of location or habitat where they exist and that the fungus has a fairly wide host range. The results are in agreement with previous studies that showed the fungus could survive on, and be isolated from, field samples of various noncereal grasses (12,21,22,24). In this study, *P. tritici-repentis* was recovered from two noncereals, barnyard grass and slender wheat grass, which had not been previously reported as hosts (24). In addition, 8 of the

23 grass species previously reported as alternative hosts (24) produced the fungus (Table 1).

Smooth brome grass use as a pasture grass and its widespread natural population in the Great Plains make this grass a potential overwintering source of *P. tritici-repentis* and a potential source of physiological variation in the fungal population. In a previous study, smooth brome grass was found to be nearly equal in susceptibility to the fungus as wheat (20). In one study, 73% of the field samples collected during 1981 to 1983 produced *P. tritici-repentis* (21). However, in the present study, *P. tritici-repentis* was recovered from only 20% of the samples, with *P. bromi* recovered from the rest. The results confirm previous studies (20,21) that the fungus could survive and be recovered from smooth brome grass field samples.

P. bromi, which causes brown leaf spot of smooth brome grass, and *P. tritici-repentis* are morphologically very similar (34). *P. bromi* can be misidentified as *P. tritici-repentis* when isolated from smooth brome grass. Krupinsky (21) reported that the samples collected in 1984 produced more *P. bromi* isolates than those collected during 1981 to 1983. In this study, 80% of the smooth brome grass samples produced *P. bromi*.

A higher recovery rate of *P. bromi* isolates from the smooth brome grass samples may be expected, as the majority of the smooth brome grass wild population and all commercial cultivars are susceptible to this pathogen (8). *P. tritici-repentis* may not compete well with *P. bromi* on this host under field conditions. In addition, a low

recovery (20%) of *P. tritici-repentis* from the collected samples further strengthens the idea that smooth brome grass may not be a good source for *P. tritici-repentis* survival under field conditions.

De Wolf et al. (11) suggested that smooth brome grass should be included with the wheat differentials in order to differentiate race 4 from *P. bromi* if the fungal isolates need to be characterized into races. Otherwise, isolates may be grown on the differential medium "sucrose proline agar medium" as suggested by Shoemaker (34). In the present study, the samples were analyzed by placing them on three layers of dampened filter paper. This procedure decreases the chance of one species overgrowing another species, as only conidia develop during the incubation period. Also, single spores were transferred from the incubated leaves onto V8PDA, a medium that can discriminate between the two species based on their growth rate and the presence or absence of protothecia (5).

A high frequency of recovery of *P. tritici-repentis* was expected from intermediate wheatgrass samples collected from wheat areas because the fungal population prevalent on wheat is known to infect intermediate wheatgrass. In addition, *P. tritici-repentis* isolates from wheat were found to be equally virulent on noncereal grasses such as intermediate wheatgrass and smooth brome grass (22). In one study, 44% of field-collected intermediate wheatgrass leaf samples produced *P. tritici-repentis* (25), similar to the 31% found overall in this study. However, the majority (4/9) of the positive intermediate wheatgrass leaf samples were collected from parklands and grasslands.

P. tritici-repentis was recovered at a high frequency from Altı wild rye and wild barley (from 3 of 6 and 3 of 3 samples, respectively) collected from wheat areas (Table 1). These grasses exist as weeds in cultivated areas, ditches, and so on; however, since these isolates typed as race 4 (producing neither necrosis nor chlorosis), their epidemiological significance in tan spot on wheat is probably minimal.

Based on these results, noncereal grasses prevalent in wheat, grassland, and parkland areas varied in supporting the growth of *P. tritici-repentis*. There could be two reasons for this variation: first, the fungal population may not be aggressive on noncereal grasses; and second, these wild populations of noncereals may vary in reaction from susceptible to resistant. The natural populations of these grasses are not expected to be homogenous, as they are out crossing and responding to selection pressures. Moreover, no specific trend was observed in the fungal recovery from noncereal grasses based on areas from which the samples were collected. However, the low recovery of *P. tritici-repentis* from a small number of noncereal grasses indicates that most of these species support a minimal

Table 2. Wheat differentials used in this study and their reaction to known races of *Pyrenophora tritici-repentis*

Race	Wheat differentials					
	Glenlea	ND495	Katepwa	6B365	Salamouni	M-3 ^a
1	Necrosis	Necrosis	Necrosis	Chlorosis	Resistant	Resistant
2	Necrosis	Necrosis	Necrosis	Resistant	Resistant	Resistant
3	Resistant	Resistant	Resistant	Chlorosis	Resistant	Resistant
4	Resistant	Resistant	Resistant	Resistant	Resistant	Resistant
5	Resistant	Resistant	Chlorosis	Resistant	Resistant	Resistant

^a A synthetic wheat also designated as W-7976.

Table 3. Proportion of isolates of *Pyrenophora tritici-repentis*, collected from wheat, durum, and noncereal grasses in the U.S. Great Plains, that typed as races indicated

Source	Isolates tested ^a	Races (%) ^b				
		1	2	3	4	5
Bread wheat - Northern Great Plains ^c	85	92	3	0	5	0
Bread wheat - Southern Great Plains ^c	22	96	0	0	5	0
Durum	71	89	0	0	0	11
Noncereal grasses	92	2	0	0	98	0

^a Isolates from durum and spring wheat in North Dakota were obtained on 24 and 25 July 1997; isolates from Oklahoma and Kansas were collected in the late 1980s. Isolates from South Dakota were obtained in 1995; isolates from noncereal grasses were obtained in July 1998.

^b *P. tritici-repentis* isolates were grouped into different races as described by Lamari and Bernier (25).

^c Northern Great Plains = North Dakota and South Dakota; Southern Great Plains = Kansas and Oklahoma.

growth of the fungus. This finding and the 98% recovery of race 4 (avirulent on wheat) suggest these grasses may not have a significant role in tan spot epidemiology on wheat in the northern Great Plains. *P. tritici-repentis* races 1, 2, and 4 were observed on wheat in the northern Great Plains. All isolates from the southern Great Plains were race 1 except for one isolate of race 4. These results indicate that race 1 is the most prevalent race in the U.S. Great Plains. These findings are in agreement with previous work (1,26) in which race 1 was found as the predominant race in South Dakota and western Canada. Prevalence of race 1 in these regions could be due to: (i) lack of selection pressure because the majority of the wheat cultivars are susceptible; (ii) the production of multiple host-specific toxins such as Ptr ToxA and ToxC by race 1, which makes it more fit than the other races; and (iii) little chance to produce recombinants as the fungus is homothallic.

Race 2 of *P. tritici-repentis* was observed in a very low frequency (3%) in the northern Great Plains. Similarly, race 2 was observed infrequently in previous studies conducted in South Dakota (1) and western Canada (26). In western Canada, an increase in the proportion of race 2 over the years 1990 (9%) to 1994 (50%) has been reported (27). This increase was thought to be due to susceptibility of most of the wheat cultivars to both races 1 and 2. Host susceptibility to both races would be expected to exert minimal selection pressure on each race, and thus might provide equal chances for their survival (27). In the present study, the fungal isolates analyzed were collected in the 1980s and 1990s and from four states of the Great Plains. If the increase in race 2 population over the period of 1990 to 1994 was because of susceptibility of the cultivars (27), this is not the case in the U.S. Great Plains, where a majority of the cultivars used are at least moderately susceptible to both races and are sensitive to Ptr ToxA (S. Ali, unpublished). There could be three reasons that race 2 is still present in low frequency in this region: (i) the fungus is homothallic, which decreases the chances of recombinants; (ii) the fungus is multi-cyclic so even if both races reproduced equally during the wheat season, race 1 conidia would remain the most abundant, as it is the most prevalent race in the region; and (iii) the conidia are airborne and can be dispersed over kilometer distances so that races would mix rather than maintain isolated pockets (13).

In this study, 5% of the isolates obtained from wheat were grouped as race 4 but the origin of race 4 on wheat is unknown. The race 4 population may be coming from other grass hosts, in which 98% of the isolates were race 4. It is suspected that race 4 might be non-persistent in wheat fields because it

would not compete well with races virulent on wheat.

Eleven percent of the isolates obtained from durum were race 5. However, race 5 was isolated from a sample collected from an experimental research station at Langdon, ND. It is not surprising to find variation in the fungal population in an area where many wheat genotypes with diverse genetic backgrounds are grown for breeding and yield trials. The existence of race 5 in the northern Great Plains warns that the fungal population should be periodically screened for physiological specialization, especially for increased frequency of race 5. In addition, wheat genotypes should be tested for their reaction to race 5 to establish possible sources of resistance should the need arise.

Ninety-eight percent of the isolates obtained from noncereal grass hosts were grouped as race 4. This indicates that grass and wheat hosts carry completely different populations of *P. tritici-repentis*. These results contrast with all previous studies in which isolates from noncereal grass hosts were found to be pathogenic on wheat and vice versa (18,20,21); this contrast is likely due to a difference in sampling locations. In the previous studies, most of the samples were collected from areas where wheat and noncereals were grown in close proximity, which provides ample opportunity for the fungus to disperse from wheat and grow as a saprophyte on other hosts. In contrast, nearly half of the samples in this study were collected from areas remote from wheat production.

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