Stability of *Stagonospora nodorum* Isolates from Perennial Grass Hosts after Passage Through Wheat

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ABSTRACT

Krupinsky, J. M. 1997. Stability of *Stagonospora nodorum* isolates from perennial grass hosts after passage through wheat. Plant Dis. 81:1037-1041.

Eleven isolates of *Stagonospora nodorum* from smooth brome, western wheatgrass, intermediate wheatgrass, Altai wildrye, basin wildrye, and an *Agropyron* cross were passed through wheat five times using detached leaf inoculations. Lesion length, which was used as a measure of adaptation and aggressiveness, did not increase after passage through wheat. When the wheat-isolate check was removed from the analyses, the cultivar $\times$ isolate interactions were nonsignificant, indicating a lack of specificity among the original isolates and isolates passed through wheat. Inoculation of wheat seedlings in a glasshouse confirmed the results obtained with the detached leaf inoculations. These isolates showed no progressive adaptation to wheat and no significant change in their aggressiveness. This indicates that since most isolates from perennial grass hosts produce small lesions on wheat and do not easily adapt to wheat, they apparently would not cause severe symptoms on wheat.

Additional keywords: *Leptosphaeria nodorum*, *Phaeosphaeria nodorum*, *Septoria nodorum*

Phaeosphaeria nodorum (E. Müller) Hedjaroude (= *Leptosphaeria nodorum* E. Müller), anamorph: *Stagonospora nodorum* (Berk.) Castellani et E.G. Germano (= *Septoria nodorum* (Berk.) Berk. in Berk. & Broome) is a serious pathogen of wheat (*Triticum aestivum* L.). Wheat isolates of *S. nodorum* can infect and produce pycnidia on other grass species (1,21). The fungus has been isolated from many naturally infected gramineous hosts (4,7,8,10,14,19). Symptoms develop on various grasses when inoculated with isolates from wheat (1,6,9,21) or from other grass species (7,9). Isolates from perennial grasses were found to be pathogenic on wheat but, with few exceptions, they did not induce as much damage as did wheat isolates (7,8,10). Most isolates from perennial grasses were considered to be less aggressive types (8,10,14).

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Accepted for publication 22 May 1997.

Publication no. D-1997-0624-04R

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The possible adaptation of wheat isolates to other hosts after passage through those hosts has been indicated. Ao and Griffiths (1) inoculated several grasses with a wheat isolate of *S. nodorum*. When the fungus was reisolated and inoculated onto wheat, the majority of isolates produced less severe symptoms than the original wheat isolate, indicating a possible change in aggressiveness following a single passage through another host besides wheat. Harrower (6) reported on the repeated passage of a wheat isolate through three other grass hosts. The decrease in incubation time on the other host species with increased passages, and the increase in incubation time on the original wheat host, indicated a change in aggressiveness with increased passage through the other hosts. Skajennikoff and Rapilly (18), using reductions in 1,000-kernel-weight to measure aggressiveness, reported an increase in aggressiveness with the passage of a wheat isolate through rye. The possible adaptation of wheat isolates to barley and barley isolates to wheat after passage through the alternate host has been shown with barley-adapted and wheat-adapted isolates of *S. nodorum* (2,3,5).

Considering that isolates of *S. nodorum* from wheat and barley have shown some adaptation after passage through different hosts, a study was undertaken to determine if isolates from perennial grasses can adapt to wheat. Although a few isolates from perennial grass are comparable to isolates from wheat, the majority of grass isolates are less aggressive than wheat isolates (8,10,14). Perennial grass isolates that produced mild symptoms on wheat in ear-

lier studies (8,10,14) were tested by passage through wheat to determine if they would adapt to wheat and cause more severe symptoms with increased number of passages through wheat.

MATERIALS AND METHODS

Eleven isolates of *S. nodorum* (Table 1) were passed through wheat and tested for possible increased adaptation to wheat. Isolates were obtained from 6 grasses: smooth brome (*Bromus inermis* Leyss.), Altai wildrye (*Leymus angustus* (Trin.) Pilg.), basin wildrye (*L. cinereus* (Scribn. & Merr.) A. Löve), western wheatgrass (*Pascopyrum smithii* (Rydb.) Löve), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth and D.R. Dewey subsp. *intermedium*), and an *Agropyron* cross (*Agropyron repens* (L.) P. Beauv. $\times$ *A. desertorum* (Fisch. ex Link) Schultes). These isolates produced mild symptoms in earlier studies (8,10,14). Isolates were obtained from diseased leaves from plants in experimental plots, nurseries, and pastures at Mandan, North Dakota. All isolates were started from a single cirrus from one pycnidium. Isolates were obtained, grown, and stored, and inoculum prepared as previously reported (13).

Passage of isolates through wheat. Since cross-contamination of isolates should be considered where cycles of reselection are involved (15), a laboratory technique of inoculating detached seedling leaves of wheat (10,13) was used for passage of isolates through wheat leaves and for testing of isolates. Seedling wheat leaves of the susceptible spring wheat cultivar Fortuna were produced in a growth chamber with a 14-h light period. The temperature ranged from 23°C during the light to 17°C during the dark. Seeds were planted in a peat moss-vermiculite mixture (1:1, vol/vol) to which a balanced macro- and micro-nutrient fertilizer was added. Leaves were cleaned by spraying them with a 0.1% sodium hypochlorite solution, rinsed with sterile distilled water, and allowed to dry in a laminar flow cabinet (HEPA filters for supply air) before leaf samples were clipped for use. After discarding 2 cm from the distal end of the leaf, 5-cm pieces of seedling leaves were cut, and placed adaxial side up on water agar (0.5%) containing 150 mg/l of benzimidazole in 100 mm square plastic petri dishes (15 mm depth). One end of the leaf was inoculated with a 5- μ l spore suspension of *S. nodorum*. Inoculated leaves were

incubated for approximately 10 days at 21°C with a 12-h photoperiod to allow lesion development.

To reisolate isolates from inoculated wheat leaves, a leaf piece with the leading edge of a lesion furthest from the point of inoculation was surface sterilized for 3 min in a 1% sodium hypochlorite solution containing a surfactant, rinsed in sterile distilled water, plated on 2% water agar, and incubated. After sporulation, cirrhi were transferred to V8 juice agar containing an antibiotic (gentamicin sulfate, 50 mg/liter) to eliminate bacterial contaminants (13). Reisolated isolates were transferred to V8 juice agar, incubated to pro-

duce spores, and used for the next inoculation cycle. Each isolate was passed through wheat five times. Six isolates were obtained for each isolate and were numbered from WRE-0 (original isolate) through WRE-5 (five passages through wheat). All reisolated isolates were stored in 15% glycerol at -90°C for future comparisons. To revive isolates for inoculation experiments, transfers were made directly from the vials and streaked down the center of V8 agar plates. The remainder of the frozen suspension was placed back in the freezer for future use.

Detached leaf inoculations. With the exception of placing the inoculum at the

center of the leaf, the same detached leaf inoculation procedures described above were used to compare isolates. Six isolates (WRE-0 through WRE-5) of each original isolate and one wheat isolate, a standard check, were compared on detached leaves in the same microenvironment (petri dish). A surfactant (Tween 20, polyoxyethylene sorbitan monolaurate, 2 drops/50 ml) was added to the inoculum which was standardized (1.5×10^6 conidia/ml) for each isolate within a experiment. Occasionally, when an adequate spore concentration was not obtained for an individual isolate, the isolate was dropped from the experiment. Four replicates were maintained in the

Table 1. Isolates of *Stagonospora nodorum* from grasses used in reisolation studies

Detached leaf experiment ^b	Isolate	Source of isolate	Literature citations	Glasshouse experiment ^a
DL1	4841	Smooth brome	(10)	...
DL2	5154-1	Smooth brome	(10)	GH11
DL3	6011-2	Smooth brome	(10)	GH11
DL4	6369-1	Smooth brome	(10)	GH11
DL5	6377	Smooth brome	(10)	GH11
DL6	7600	Western wheatgrass	(14)	GH12
DL7	7584	Western wheatgrass	(14)	GH12
DL8	1021	Intermediate wheatgrass	(8,14)	GH12
DL9	1087	Agropyron cross	(8,14)	GH13
DL10	7706	Basin wildrye	(14)	GH13
DL11	5036	Altai wildrye	(14)	GH13

^a Each study included the original isolate (WRE0), the reisolated isolates (WRE1 through WRE5), and a wheat isolate.

^b Each study included the original isolate (WRE0), the fifth reisolated (WRE5), and a wheat isolate.

Table 2. Lesion length (mm) on detached wheat leaves following inoculations with isolates of *Stagonospora nodorum* reisolated after various numbers of passages through wheat^x

Experiment	Source of isolate	Number of passages through wheat						Wheat isolate
		0	1	2	3	4	5	
DL1	Smooth brome	2 ^y	2	3	3	... ^z	...	9
DL2	Smooth brome	2	3	3	2	2	2	9
DL3	Smooth brome	1	2	2	2	2	2	7
DL4	Smooth brome	1	2	2	1	2	2	7
DL5	Smooth brome	2	2	2	2	1	3	9
DL6	Western wheatgrass	2	3	3	3	2	3	8
DL7	Western wheatgrass	...	4	4	3	2	2	8
DL8	Intermediate wheatgrass	3	3	4	3	3	4	8
DL9	Agropyron cross	2	3	4	3	3	4	13
DL10	Basin wildrye	3	3	3	3	4	3	20
DL11	Altai wildrye	2	...	...	...	2	2	8

^x Six wheat cultivars (Butte 86, Eureka, Fortuna, Kitt, Olaf, and Red Chief) were used in all studies.

^y Lesion length, mm. Each datum is the average of 24 values (four replicates × six cultivars).

^z Missing values. Isolates were not included because of inadequate spore concentration for the inoculation of detached wheat leaves.

Table 3. Analyses of variance for lesion length (mm) on detached wheat leaves inoculated with *Stagonospora nodorum* after five passages through wheat^y

Experiment	Source of isolate	Source of variance			
		Rep	Cultivar	Isolate	Cultivar × isolate
DL1	Smooth brome	NS ^z	**	NS	NS
DL2	Smooth brome	NS	*	NS	NS
DL3	Smooth brome	NS	*	NS	NS
DL4	Smooth brome	*	NS	*	NS
DL5	Smooth brome	**	**	**	NS
DL6	Western wheatgrass	NS	**	**	NS
DL7	Western wheatgrass	NS	NS	**	NS
DL8	Intermediate wheatgrass	*	**	NS	NS
DL9	Agropyron cross	NS	**	**	NS
DL10	Basin wild rye	NS	*	*	NS
DL11	Altai wild rye	NS	**	*	NS

^y Six wheat cultivars (Butte 86, Eureka, Fortuna, Kitt, Olaf, and Red Chief) were used in all studies.

^z NS = not significant at $P = 0.05$, * = significant at $P = 0.05$, ** = significant at $P = 0.01$.

same incubator. Nine to ten days after inoculation, lesion length was measured and necrotic area was visually estimated as percentage of total leaf area. Seedling leaves from 6 cultivars of wheat (Fortuna, Red Chief, Butte 86, Kitt, Eureka, Olaf), which were produced in a growth chamber, were cleaned as above and used for the experiments. Eleven experiments (DL1 through DL11) were conducted (Table 1), one for each original isolate.

Possible differences in adaptation and aggressiveness were determined by the ability of isolates to cause significant differences in symptom severity with the detached leaf experiments, as measured by lesion length and percentage necrosis. Aggressiveness is defined as the amount of disease caused by a pathogen upon a host that contains only race nonspecific resistance to pathogenesis (17). Isolates that produced lesions statistically larger than other lesions in a particular experiment are referred to as high aggressive isolates, and

isolates that produced shorter lesions are referred to as less aggressive isolates, even though lesion length is a continuous quantitative variable.

Data from each experiment, with and without the wheat check isolate, were analyzed (split-plot design) with an analysis of variance procedure (SAS version 6.8, SAS Institute, Cary, NC). Statistical comparisons were made with Student-Newman-Keuls multiple range test (SAS). If an individual datum was missing, e.g. when an inoculation droplet spread along the edge of the leaf from the point of inoculation, data from that experiment were analyzed with a general linear model (GLM, SAS). Because of the similarity of results from the lesion length and percentage necrosis data, only the lesion length data are presented.

Glasshouse inoculations. WRE-5 isolates were compared with their original WRE-0 isolates and a standard wheat isolate in glasshouse inoculations of wheat

seedlings. Three experiments were conducted (Table 1): one with eight isolates from smooth brome (GH11), one with four isolates from western wheatgrass and two isolates from intermediate wheatgrass (GH12), and one with two isolates each from Altai wildrye, basin wildrye, and an Agropyron cross (GH13). Because only eight isolates from smooth brome were used in GH11, one smooth brome isolate was randomly dropped.

The same 6 wheat cultivars listed above were used in the glasshouse inoculations. Seeds were planted in plastic containers (4 cm diameter by 21 cm depth) containing the same potting media and fertilizer as above. The containers with 3 to 4 plants were used to replicate the experiments. Plants were grown in a glasshouse with a 12-h light and temperature cycle (13). The temperature ranged from 24°C during the light to 13°C during the dark.

Ten days after planting, plants were inoculated by spraying a conidial suspension (3×10^6 conidia per ml) onto the leaves (13). To avoid cross-contamination of isolates, inoculations were conducted in an exhaust hood that was washed with running water before each inoculation. After inoculation, 5 replicates were maintained in a high-humidity chamber for 48 h, then moved to a glasshouse bench. Ten days after inoculation, plants were clipped above the first leaf and the first leaves were visually assessed for the percentage of the leaf blade tissue that was necrotic. For each inoculation experiment, an analysis of variance was conducted on the arcsine-transformed percent necrosis data and statistical comparisons were made with the Student-Newman-Keuls test (SAS). Preliminary reports on some aspects of this study were made (11,12).

RESULTS

Passage of isolates through wheat. The detached leaf inoculations worked well as a method for passage of isolates through wheat. Eleven isolates from 6 different hosts were passed through wheat five

Table 4. Comparison of lesion length on detached wheat leaves following inoculations with isolates of *Stagonospora nodorum* obtained from perennial grasses and passed through wheat^x

Experiment	Isolate ^y	Source of isolate	Lesion length (mm) ^z
DL4	6369 WRE-0	Smooth brome	1.3 a
	6369 WRE-1		1.7 a
	6369 WRE-2		1.8 a
	6369 WRE-3		1.3 a
	6369 WRE-4		1.5 a
	6369 WRE-5		1.8 a
DL9	1087 WRE-0	Agropyron cross	2.4 b
	1087 WRE-1		3.3 ab
	1087 WRE-2		3.8 a
	1087 WRE-3		3.4 ab
	1087 WRE-4		3.3 ab
	1087 WRE-5		4.0 a
DL10	7706 WRE-0	Basin wildrye	3.4 ab
	7706 WRE-1		2.7 b
	7706 WRE-2		3.5 ab
	7706 WRE-3		3.3 ab
	7706 WRE-4		3.6 a
	7706 WRE-5		2.8 ab

^x Six wheat cultivars (Butte 86, Eureka, Fortuna, Kitt, Olaf, and Red Chief) were used in all studies.

^y A total of six cultures were obtained for each isolate and were numbered from WRE-0 (original culture) through WRE-5 (five passages through wheat).

^z Overall means within a study were compared with the Student-Newman-Keuls test; means followed by a letter in common are not significantly different at $P = 0.05$.

Table 5. Analyses of variance for lesion length on detached wheat leaves following inoculations with grass isolates of *Stagonospora nodorum* passed through wheat^z

Experiment	Source of isolate	Source of variation	Degrees of freedom	Mean squares
DL8	Intermediate wheatgrass with wheat check	Replicate	3	23.5**
		Cultivar	5	51.9**
		Error a	15	4.0
		Isolate	6	63.1**
		Cultivar $\times$ isolate	30	5.4**
		Error b	106	2.3
		Total	165	
DL8	Intermediate wheatgrass without wheat check	Replicate	3	22.2*
		Cultivar	5	32.6**
		Error a	15	4.4
		Isolate	5	4.9 NS
		Cultivar $\times$ isolate	25	1.9 NS
		Error b	88	2.2
		Total	141	

^z Length of lesion measured. Split plot design. NS = not significant at $P = 0.05$; * = significant at $P = 0.05$; ** = significant at $P = 0.01$. The total degrees of freedom adjusted for missing values.

Table 6. Percentage necrosis on wheat seedlings following inoculations with initial isolates of *Septoria nodorum* compared with the same isolates after five passages through wheat^y

Experiment	Isolate	Source of isolate	Initial isolates	Isolates resulting from five passages through wheat
GH11	5154-1	Smooth brome	2	2
	6011-2	Smooth brome	4	3
	6369-1	Smooth brome	... ^z	2
	6377-1	Smooth brome	2	2
GH12	7600	Western wheatgrass	2	4
	7584	Western wheatgrass	...	3
	1021	Intermediate wheatgrass	3	3
GH13	1087	Agropyron cross	3	3
	5036	Altai wildrye	...	3
	7706	Basin wildrye	2	3

^y Six wheat cultivars (Butte 86, Eureka, Fortuna, Kitt, Olaf, and Red Chief) were used in all studies. Each datum is the average of 30 values (five replicates $\times$ six cultivars). The average percentage of necrosis for the wheat check was 42, 23, and 35% for studies GH11, GH12, and GH13, respectively.

^z ... = missing values (cultures not included in study because of inadequate spore concentration).

times, producing a total of 55 reisolated isolates.

Detached leaf inoculations. The average lesion length for the wheat check was 9.6 mm in the 11 detached leaf inoculations (Table 2). The wheat isolate produced longer lesions than either the initial grass isolates, which had an average lesion length of 2.0 mm, or the reisolated isolates, which had an overall average lesion length of 2.6 mm. The average lesion length for the WRE-1 isolates was 2.7 mm, compared to 2.7 mm for the WRE-5 isolates (Table 2), indicating no progressive increase in lesion length with additional passages through wheat.

Analyses of variance were conducted with and without the wheat isolate for each experiment. When the wheat isolate was included in the analyses, the isolate effect was significant for all experiments. When the wheat check was not included in the analyses, the significance of the isolate effect was reduced (Table 3). With the comparisons in experiment DL4, isolate means could not be separated with the Student-Newman-Keuls multiple range test (Table 4), even when the isolate effect was significant. In the other experiments, when statistical differences were indicated, most isolate means could not be separated with the Student-Newman-Keuls multiple range test, and there was no consistent indication of a progressive increase in adaptation of isolates with passage through wheat (Table 4). Thus, excluding the standard wheat isolate, all isolates within most experiments produced lesions of similar length after passage through wheat and no progressive adaptation was demonstrated with these grass isolates.

When the standard wheat isolate was included in the analyses, the cultivar $\times$ isolate interaction was significant in all 11 analyses. When the wheat check was removed from the analyses, the cultivar $\times$ isolate interaction was nonsignificant for all 11 experiments (Table 3), for example, experiment DL8 (Table 5).

Glasshouse inoculations. The percentage of necrosis for the standard wheat check averaged 33%. The percentage of

necrosis for the WRE-5 isolates averaged 3%, similar to the 2% average for the initial isolates (Table 6).

DISCUSSION

In this study, the less aggressive grass isolates did not adapt to wheat after five passages through wheat, indicating that these isolates were stable. The use of less aggressive isolates provided a rigorous test of their adaptability to wheat. The glasshouse inoculations confirmed the results of the detached leaf inoculations; there was no increase in aggressiveness. When the wheat check was removed from the analyses, the cultivar $\times$ isolate interaction was nonsignificant for all 11 experiments. This would indicate a lack of specificity (20) among the original isolates and the isolates reisolated from wheat.

These results are in contrast to a study in which a wheat isolate showed an increase in aggressiveness toward 3 other grass hosts after the repeated passage of that isolate through the other hosts (6), and to studies in which wheat-type isolates adapted to barley and barley-type isolates adapted to wheat after passage through the opposite host (3,5). The lack of adaptation in this study is similar to the results with wheat and barley isolates reported by Berecket et al. (2) and Osbourn et al. (16). Berecket et al. found changes in aggressiveness, but they did not find dramatic adaptation of wheat isolates following three passages through barley (2). Osbourn et al. found instances of change in host adaptation rare after passage through detached leaves of wheat and barley (15,16).

Considering that less aggressive isolates make up the majority of isolates from perennial grasses (8,10,14), one can speculate that the majority of isolates from perennial grasses would not easily adapt to wheat and would not cause severe symptoms on wheat. Even though perennial grasses could be a source of inoculum and genetic variability for *S. nodorum*, only a minority of the isolates would initially be able to cause severe symptoms on wheat. Infested wheat stubble and infested seed would be the more effective sources of inoculum.

ACKNOWLEDGMENTS

I thank M. Geck and D. Wetch for technical assistance, and A. L. Scharen and D. E. Mathre for their constructive comments.

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