Aggressiveness of *Stagonospora nodorum* Isolates from Perennial Grasses on Wheat

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ABSTRACT

Krupinsky, J. M. 1997. Aggressiveness of *Stagonospora nodorum* isolates from perennial grasses on wheat. Plant Dis. 81:1032-1036.

Isolates of *Stagonospora nodorum* from 13 perennial grasses were tested on detached wheat leaves. Grass isolates that were consistently associated with large or small lesions were statistically differentiated. Some grass isolates were detected that were associated with large lesions on wheat (high symptom severity), but most isolates produced small lesions (mild level of symptom severity). The ability of grass isolates to cause significant differences in symptom severity, as measured by lesion length, was interpreted as differences in aggressiveness. Grass isolates that were associated with high symptom severity were found to be similar to selected wheat isolates in their level of aggressiveness. Results were confirmed with inoculations of seedling wheat plants in the glasshouse. Wheat cultivars were statistically differentiated from one another with all types of isolates. The cultivar $\times$ isolate interactions were, generally, not significant with unselected isolates, indicating a low possibility of specificity. In contrast, when isolates associated with large and small lesions were compared, the cultivar $\times$ isolate interaction was significant in most experiments, but the magnitude of the mean square for the interaction was low compared to the mean squares of the main effects. The ability of *S. nodorum* to infect perennial grasses would improve the likelihood of survival of this fungus between wheat crops. Because most isolates are not associated with severe symptom severity, their potential effect on wheat is probably less than would be expected considering the potential number of isolates available from the grasses.

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 pathogen of wheat, *Triticum aestivum* L. *Stagonospora nodorum* has been isolated from a number of naturally infected gramineous hosts (5,9-13,18,23,25). Symptoms have been produced on grasses with isolates from wheat (1,8,12,19,21,25,26), and with isolates from other grass hosts (10,12,25). Triticale and other species of *Triticum* and *Aegilops*

vary in symptom severity when tested for resistance to *S. nodorum* (2,6,7,16,17,27). Barley-type isolates of *S. nodorum* have been identified (5, 22).

In inoculations of wheat cultivars in the glasshouse with isolates from *Agropyron* species and wheat, *Agropyron* isolates were pathogenic on wheat, but they induced less symptom severity than wheat isolates (11). With one exception, similar results were found with isolates from smooth brome, *Bromus inermis* (13). In another study, 6 out of 7 isolates from other hosts besides wheat caused symptoms on wheat that were greater than symptoms on four grass hosts, but the symptom severity on wheat was less than the symptom severity caused by a wheat isolate (10). Wheat isolates can produce pycnidia and survive on other grass hosts (1,21,26).

This study was conducted to determine if perennial grass hosts could serve as sources of inoculum for wheat by assessing the ability of grass isolates to cause high symptom severity on wheat, to compare grass isolates with isolates from wheat, and to examine the possibility of cultivar $\times$ isolate interactions. A preliminary report on some aspects of this study was made (14).

MATERIALS AND METHODS

Isolates of *S. nodorum* were obtained from lesions on diseased grass leaves. Le-

sions were located on the leaf blade of most grasses, but with crested wheatgrass (*Agropyron desertorum*) a common symptom was a sheath lesion located at the base of the flag leaf. Most diseased leaves were obtained from plants in experimental plots, nurseries, and pastures at Mandan, North Dakota. Isolates were obtained, grown, stored, and inoculum was prepared as reported (15).

Detached leaf inoculations. Detached seedling leaves were inoculated to differentiate isolates of *S. nodorum* (13,15) based on symptom severity. With this method, grass isolates were compared on different leaves of a wheat cultivar in the same microenvironment (petri dish). Leaves were visually rated 7 to 10 days after inoculation for symptom severity, which was measured by lesion length and percentage necrosis. Seven cultivars of wheat (Fortuna, Red Chief, Butte, Kitt, Eureka, Olaf) were used unless noted otherwise, and plants were grown as in a previous study (15).

Glasshouse inoculations. Isolates associated with severe or mild symptom severity with the detached leaf inoculations were compared in glasshouse inoculations of seedling plants using described procedures (15). The same 7 wheat cultivars were inoculated as used in the detached leaf inoculations. Each isolate-cultivar combination was replicated with 5 containers (3 to 4 plants per container). Ten days after planting, plants were inoculated. Ten days after inoculation, plants were clipped above the first leaf, and first leaves were visually assessed for percentage of necrosis of the leaf blade tissue.

Experimental design. The inoculation experiments were conducted in phases, similar to an earlier study (15). A split-plot design with 5 to 7 isolates inoculated onto leaves of 1 cultivar per petri dish was used. A petri dish, as an experimental unit, was replicated four times in an incubator. For each experiment, analyses of variance were conducted on the arcsine-transformed percentage of necrosis and lesion length data (SAS version 6.08, SAS Institute, Cary, NC). Adjustments were made for missing data by analyzing those experiments with a general linear model (GLM, SAS). If a water control was a treatment, the control data were not included in the statistical analyses, but the control mean for the experiment is included with data presented in the tables. Analyses of variance were used to obtain a general pattern or statistical

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Accepted for publication 22 May 1997.

Publication no. D-1997-0624-03R

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trend for isolate and cultivar main effects, and cultivar $\times$ isolate interactions. Because results from the percentage of necrosis data were similar to results obtained with the lesion length data for the detached leaf experiments, only the lesion length data are presented. Statistical comparisons were made with the Student-Newman-Keuls test (SAS).

A significant isolate effect on disease symptom severity, as measured by lesion length or percentage necrosis, was interpreted as evidence for differences in aggressiveness. Aggressiveness is defined as the amount of disease caused by a pathogen upon a host that contains only race nonspecific resistance to pathogenesis (20). The apparent high aggressive isolates associated with lesions that are statistically longer and larger than lesions associated with other isolates in a particular experiment are referred to as high aggressive isolates, and the apparent low aggressive isolates associated with the shorter and smaller lesions are referred to as low or less aggressive isolates, even though lesion length is a continuous quantitative variable.

Phase one, initial inoculations. Twenty-seven isolates of *S. nodorum* were obtained from 12 grass species (Table 1) and compared in experiments G1 through G6 to determine if isolates could be differentiated statistically. To compare a larger number of *Agropyron* isolates than tested previously (11), 31 additional isolates were obtained from crested wheatgrass and compared in experiments C1 through C5. Fourteen isolates from smooth brome were compared in three studies. Five to seven unselected isolates were compared in each experiment. Because the number of isolates obtained from various hosts differed, isolates from more than one host were compared in some experiments. Some isolates were used in more than one experiment.

Phase two, selection of isolates. Grass isolates were retested in phase two to consolidate the results from phase one, to verify their consistency with symptom severity, and to select isolates associated with severe or mild symptom severity, as measured by large or small lesions. The grass isolates that produced small lesions were compared in experiments G7 through G9, and those that produced large lesions were compared in G10 through G13.

Phase three, differentiation of isolates. Isolates that produced large lesions were compared with isolates that produced small lesions to determine the consistency of this trait. Isolates associated with large and small lesions were compared in 9 detached leaf and 2 glasshouse inoculations. In four detached leaf experiments, G14 through G17, one isolate that produced large lesions was compared with one isolate that produced small lesions. In these four experiments, eight replications and three

cultivars (Fortuna, Eureka, and Olaf) were used. Seven leaves were inoculated in each petri dish, 3 with one isolate, 3 with another isolate, and 1 with distilled water for comparison. In the other five detached leaf experiments, G18 through G22, several isolates that produced large lesions were compared with several isolates that produced small lesions with all seven cultivars and four replicates. Isolates were also compared on wheat seedling leaves in glasshouse experiments GH3 and GH4.

Phase four, comparison of isolates from different hosts. Isolates from grasses that produced either large or small lesions

were compared with wheat isolates in experiments G23 and G24. The aggressiveness of the selected wheat isolates was determined in a previous study (15).

RESULTS

Isolates of *S. nodorum* from perennial grasses caused symptoms on wheat. In most experiments, isolates differed in the size of the lesions they induced.

Phase one, initial inoculations. Lesion size varied (Table 2) when testing different grass isolates. Isolate effects were significant in 5 out of 6 analyses, G1 through G6 (Table 3). Although isolates that produced

Table 1. Grass hosts from which *Stagonospora nodorum* was isolated

Source of isolate	Common name
<i>Agropyron cristatum</i> (L.) Gaertn.	Crested wheatgrass (Fairway) ^s
<i>Agropyron desertorum</i> (Fisch. ex Link) Schult.	Crested wheatgrass (standard) ^s
<i>Agropyron fragile</i> (Roth) Candargy subsp. <i>sibiricum</i> (Willd.) Meld. (Syn. = <i>Agropyron sibiricum</i> (Willd.) Beauvois)	Siberian wheatgrass
<i>Agropyron repens</i> (L.) P. Beauv. (Syn. = <i>Triticum repens</i> L., <i>Elytrigia repens</i> (L.) Nevski) $\times$ <i>A. desertorum</i> (Fisch. ex Link) Schultes	Agropyron cross ^s
<i>Bromus inermis</i> Leyss.	Smooth brome ^t
<i>Critesion jubatum</i> (L.) Nevski (Syn. = <i>Hordeum jubatum</i> L.)	Wild barley ^u
<i>Elymus canadensis</i> L.	Canadian wildrye ^v
<i>Leymus angustus</i> (Trin.) Pilg. (Syn. = <i>Elymus angustus</i> Trin.)	Altai wildrye ^w
<i>Leymus cinereus</i> (Scribn. & Merr.) A. Löve (Syn. = <i>Elymus</i> <i>cinereus</i> Scribn. & Merr.)	Basin wildrye ^w
<i>Leymus racemosus</i> (Lam.) Tsvelev subsp. <i>vacemosus</i> (Syn. = <i>Elymus giganteus</i> Vahl.)	Mammoth wildrye ^x
<i>Psathyrostachys juncea</i> (Fisch.) Nevski (Syn. = <i>Elymus juncea</i> Fisch.)	Russian wildrye ^y
<i>Pascopyrum smithii</i> (Rydb.) A. Löve (Syn. = <i>Agropyron smithii</i> Rydb.; <i>Elytrigia smithii</i> (Rydb.) Nevski; <i>Elymus smithii</i> (Rydb.) Gould)	Western wheatgrass ^z
<i>Thinopyrum intermedium</i> (Host) Barkworth & D. R. Dewey subsp. <i>intermedium</i> (Syn. = <i>Agropyron intermedium</i> (Host) Beauvois; <i>Elytrigia intermedia</i> (Host) Nevski subsp. <i>intermedia</i>)	Intermediate wheatgrass ^z

^s Previously reported as host (11).

^t Previously reported as host (10,13,18).

^u Previously reported as host (3,11).

^v Previously reported as host (4).

^w Previously reported as host (12).

^x Previously reported as host (4,12,23).

^y Previously reported as host (12,18).

^z Previously reported as host (11).

Table 2. Comparison of lesion length produced on detached leaves following inoculations with unselected isolates of *Stagonospora nodorum* obtained from perennial grasses^y

Experiment	Isolate	Source of isolate	Lesion length (mm) ^z
G1	9522	Wheat (check)	14 a
	7606	Western wheatgrass	12 ab
	7599	Western wheatgrass	10 b
	7588	Western wheatgrass	7 c
	1094-1	Western wheatgrass	5 cd
	7600	Western wheatgrass	2 de
G2	7584	Western wheatgrass	2 e
	9522	Wheat (check)	14 a
	7631	Altai wildrye	7 b
	7705	Basin wildrye	7 b
	8938	Canadian wildrye	7 b
	8937-2	Basin wildrye	7 b
	7651	Russian wildrye	6 b
	8877-2	Altai wildrye	6 b

^y Phase one inoculations, initial inoculations with unselected isolates. Six wheat cultivars used in all studies were Butte 86, Fortuna, Kitt, Red Chief, Eureka, and Olaf.

^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 $P = 0.05$.

large lesions were detected in phase one, most grass isolates produced small lesions.

Isolate effects were significant when comparing crested wheatgrass isolates (C1 through C5, Table 3) but statistical differences were mainly due to differentiation of the crested wheatgrass isolates from the wheat check, rather than differences among the crested wheatgrass isolates themselves. Because of the small lesions associated with the 31 crested wheatgrass isolates and the difficulty of finding distinct differences among them (data not shown), these isolates were not re-tested. Similarly, the 14 isolates from smooth brome produced only small lesions (data not shown).

Cultivar effects were significant in 10 of the 11 initial experiments (Table 3; excluding the 3 with smooth brome isolates). The cultivar $\times$ isolate interaction was not significant in 8 out of 11 analyses.

Phase two, selection of isolates. Isolate effects were significant in all 7 analyses (Table 3) when comparing isolates either associated with small (G7 to G9) or large (G10 to G13) lesions. Similar to the results in phase one, cultivar effects were significant in 6 out of 7 analyses, and the cultivar $\times$ isolate interaction was not significant in 6 out of 7 analyses (Table 3).

Phase three, differentiation of isolates.

In experiments G14 through G22, the isolates associated previously with large lesions produced higher symptom severity than the isolates associated previously for production of small lesions (Table 3 and Table 4).

Wheat cultivars were statistically differentiated in all nine experiments, G14 through G22 (Table 3). The cultivar $\times$ isolate interaction was significant in 8 out of 9 analyses of variance (Table 3); however, the magnitude of the mean squares for the interactions was low

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

Experiment	Isolate	Isolate designation ^y	Source of isolate	Lesion length (mm) ^z
G14	7606-23	A	Western wheatgrass	10 a
	7606-22	A	Western wheatgrass	10 a
	7606-21	A	Western wheatgrass	10 a
	7600-23	L	Western wheatgrass	1 b
	7600-22	L	Western wheatgrass	1 b
	7600-21	L	Western wheatgrass	1 b
	Control	...	...	0.2
G18	7599	A	Western wheatgrass	10 a
	7606	A	Western wheatgrass	10 a
	7651	L	Russian wildrye	6 b
	7706	L	Basin wildrye	3 c
	5036	L	Altai wildrye	1 d
	7584	L	Western wheatgrass	1 d
	7600	L	Western wheatgrass	1 d

^x Phase three inoculations, comparison of isolates that produced large lesions with isolates that produce small lesions. Six wheat cultivars used in all studies were Butte 86, Fortuna, Kitt, Red Chief, Eureka, and Olaf.

^y A = isolates that produced large lesions in an earlier study and considered to be highly aggressive; L = isolates that produced small lesions in an earlier study and considered to be less aggressive.

^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 3. Analyses of variance for lesion length on detached wheat leaves following inoculations by isolates of *Stagonospora nodorum* from grass hosts

Experiment	Isolate designation ^v	Phase	Source of variation ^w			
			Replicate	Cultivar	Isolate	Cultivar $\times$ isolate
G1	U	1	**	**	**	**
G2	U	1	**	**	**	NS
G3	U	1	NS	**	**	NS
G4	U	1	*	**	**	NS
G5	U	1	NS	**	**	*
G6	U	1	NS	*	NS	NS
C1 ^x	U	1	*	**	**	NS
C2 ^x	U	1	NS	NS	**	NS
C3 ^x	U	1	NS	**	**	**
C4 ^x	U	1	NS	**	**	NS
C5 ^x	U	1	NS	**	**	NS
G7	L	2	NS	**	**	NS
G8	L	2	NS	**	**	NS
G9	L	2	*	NS	**	NS
G10	A	2	NS	**	**	**
G11	A	2	NS	**	**	NS
G12	A	2	NS	**	**	NS
G13	A	2	NS	**	**	NS
G14 ^y	A-L	3	NS	**	**	**
G15 ^y	A-L	3	*	**	**	**
G16 ^y	A-L	3	NS	**	**	**
G17 ^y	A-L	3	NS	**	**	**
G18	A-L	3	*	**	**	**
G19	A-L	3	NS	**	**	**
G20	A-L	3	NS	**	**	**
G21	A-L	3	NS	**	**	**
G22	A-L	3	NS	**	**	NS
G23 ^z	A-L	4	*	**	**	NS
G24 ^z	A-L	4	*	**	**	*
GH3	A-L	3	NS	**	**	**
GH4	A-L	3	*	**	**	*

^v U = unselected isolate; A = isolate that produced large lesions in an earlier study and considered to be highly aggressive; L = isolate that produced small lesions in an earlier study and consider to be less aggressive.

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

^x Unselected crested wheatgrass isolates, wheat check included in all but one study.

^y Comparison of one isolate that produced large lesions with another isolate that produced small lesions. Each isolate was used three times in each study.

^z Isolates from wheat and grass that produced either large or small lesions.

compared to the mean square of the main effects (Table 5).

In glasshouse inoculations of seedling plants, isolates that produced large lesions on detached leaves induced higher symptom severity than isolates that produced small lesions on detached leaves (Table 6). Isolates that produced large lesions on detached leaves had overall percentage of necrosis ratings of 53%, compared to 3% for isolates that produced small lesions on detached leaves.

Wheat cultivars in the seedling inoculation experiments were statistically differentiated, and the cultivar $\times$ isolate interaction was significant in both experiments (Table 3). Similar to results with the detached-leaf inoculations, the magnitude of the mean squares for the interactions was low compared to the mean square of the main effects (Table 5), and cultivar $\times$ isolate interactions were not obvious in the data (Table 6).

Phase four, comparison of isolates from different hosts. Isolates from grass and wheat that produced large and small lesions were differentiated. Grass isolates that produced large and small lesions were comparable to wheat isolates that produced large and small lesions in experiments G23 and G24 (Table 7).

DISCUSSION

Differences were detected among 72 grass isolates in 96% (26 out of 27) of the detached wheat leaf experiments. Isolates that produced large and small lesions were differentiated. The ability of grass isolates to cause significant differences in symptom severity with the detached leaf experiments, as measured by lesion length, was interpreted as differences in aggressiveness. The isolates that produced large lesions on detached leaves consistently produced higher symptom severity in glasshouse inoculations of wheat seedlings than isolates that produced small lesions on detached leaves, confirming differences among grass isolates.

Grass isolates that produced large and small lesions were comparable to wheat isolates that produced large and small lesions. Thus, grass isolates were similar to wheat isolates in their range of aggressiveness, and grass isolates that produced large lesions, even if they were in a minority, were as aggressive as isolates from wheat that caused a high level of symptom severity.

Although grass isolates varied in symptom severity as measured by lesion length, most grass isolates produced small lesions. This is in contrast to wheat isolates, which

tend to produce large lesions (15). The small lesions associated with the crested wheatgrass isolates and the difficulty of finding distinct differences among them was similar to a study in which isolates from *Agropyron* species were pathogenic on wheat but induced less symptom severity than wheat isolates (11). These crested wheatgrass isolates were also included in a study of 48 crested wheatgrass isolates that were found to be nearly indistinguishable (by seven nuclear restriction fragment length polymorphism loci) from *S. nodorum* populations collected from wheat (B. McDonald, *personal communication*). The production of small lesions by the 14 isolates from smooth brome also confirmed the results of a previous study with isolates from this grass (13).

Wheat cultivars were statistically separated from one another in 93% (25 out of 27) of the experiments. This indicates that wheat cultivars can be differentiated with grass isolates associated with the production of large and small lesions.

When comparing unselected isolates in phase one and isolates associated with a similar level of aggressiveness in phase two, the cultivar $\times$ isolate interaction was not significant in 71% (15 out of 21) of the experiments, indicating a lack of physiological specialization (24). This is similar to results obtained in initial experiments with wheat isolates (15). When isolates associated with large and small lesions were compared in phase three and four, the cultivar $\times$ isolate interaction was significant in 82% (9 out of 11) of the experiments. This is in contrast to the nonsignificance of the cultivar $\times$ isolate interaction in phases one and two, when a number of the same isolates were compared. Apparently the selection and comparison of isolates associated with large or small lesions influences the significance of the cultivar $\times$ isolate interaction. This is similar to results obtained when differentiating wheat isolates (15). This significant interaction would be expected if some level of specificity is present among the isolates (24). It is hypothesized that the interactions should be at their highest level with this group of grass isolates, since the isolates tested were selected for the greatest differences. Con-

Table 5. Analyses of variance for lesion length on detached wheat leaves (G18) and for percentage of necrosis of seedling plants (GH3) following inoculations with isolates of *Stagonospora nodorum* obtained from grasses^y

Experiment	Source of isolate	Source of variation	Degrees of freedom	Mean squares
G18	Grasses	Replicate	3	21 *
		Cultivar	5	87 **
		Error a	15	5
		Isolate	6	623 **
		Cultivar $\times$ isolate	30	30 **
		Error b	80	6
		Total	139	
GH3 ^z	Grasses	Replicate	3	0.008 NS
		Cultivar	5	0.329 **
		Error a	15	0.004
		Isolate	5	3.217 **
		Cultivar $\times$ isolate	25	0.075 **
		Error b	90	0.009
		Total	143	

^y Split plot design. NS = not significant at $P = 0.05$; * = significant at $P = 0.05$; ** = significant at $P = 0.01$. The degrees of freedom were adjusted for missing values.

^z Analysis on arcsine-transformed percentage of necrosis data.

Table 6. Necrosis (percentage of first leaf area) on wheat seedlings following inoculations with isolates of *Stagonospora nodorum* obtained from grasses^w

Isolate ^x	Host ^y	Wheat cultivars					
		Fortuna	Eureka	Butte 86	Kitt	Olaf	Red Chief
7606-A	WWG	94	75	76	60	62	16
7599-A	WWG	70	53	45	36	33	12
7651-L	RWR	5	8	4	2	4	1
7706-L	BWR	4	7	3	1	3	2
1087-L	A $\times$	4	7	2	2	3	1
7584-L	WWG	3 ^z	3	1	1	2	1

^w Glasshouse inoculations of seedling plants. Each datum is the average of 10 observations, five replicates in each of two experiments, GH05 and GH06.

^x A = isolates that produced large lesions in an earlier study and considered to be highly aggressive; L = isolates that produced small lesions in an earlier study and considered to be less aggressive.

^y WWG = Western wheatgrass, RWR = Russian wildrye, BWR = Basin wildrye, A $\times$ = Agropyron cross.

^z Average of only five replicates; isolate 7584 was only included in GH03.

Table 7. Comparison of lesion length on detached wheat leaves following inoculations with isolates of *Stagonospora nodorum* obtained from perennial grasses and wheat^x

Experiment	Isolate	Isolate designation ^y	Source of isolate	Lesion length (mm) ^z
G23	7606	A	Western wheatgrass	12 a
	7599	A	Western wheatgrass	8 b
	8630	A	Wheat	8 b
	1087	L	Agropyron cross	2 c
	9076	L	Wheat	2 c
	9074	L	Wheat	2 c
	Control	...	...	0.04

^x Phase four inoculations, comparison of isolates from different hosts that consistently produced large or small lesions in earlier studies. Six wheat cultivars used in all studies were Butte 86, Fortuna, Kitt, Red Chief, Eureka, and Olaf.

^y A = isolates that produced large lesions in an earlier study and considered to be highly aggressive; L = isolates that produced small lesions in an earlier study and considered to be less aggressive.

^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 $P = 0.05$.

sidering that the magnitudes of the mean squares for the interactions were low compared to the mean squares of the main effects, it can be speculated either that specificity is present with the grass isolates but only at a low level, or that specificity is apparent only when isolate extremes are selected and may not be apparent when randomly testing isolates. This is similar to the results obtained from testing wheat isolates (15).

Considering that *S. nodorum* can survive on perennial grasses (1,21,26) and that some of the grass isolates were as aggressive as those isolated from wheat, grass hosts could provide a source of primary inoculum for wheat. The perennial habit of these grasses would improve the likelihood of overwintering and survival of *S. nodorum* between wheat crops. But because most isolates are not associated with severe symptom severity, the effect on wheat is probably less than would be expected considering the potential number of isolates available from the grasses. The perennial grasses are a potential source of high aggressive isolates, but considering that those isolates are in the minority, one could speculate that most isolates that cause high symptom severity on wheat probably originate from infested wheat residue and/or infested seed.

ACKNOWLEDGMENTS

I thank D. Wetch, J. Eide, and S. Heinert for technical assistance; and A. Bauer, D. Mathre, and A. L. Scharen for their constructive comments.

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