Comparative Pathogenicity of Isolates of *Sclerotinia trifoliorum* and *S. sclerotiorum* on Alfalfa Cultivars

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ABSTRACT

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Eight cultivars and one experimental population of alfalfa were artificially inoculated with five isolates each of *Sclerotinia trifoliorum* and *S. sclerotiorum*. Isolates of both species originated from different forage legume hosts and geographic areas in the United States. Inoculations were performed by dusting dried and comminuted mixtures of infested wheat and oat grain over foliage of 4-wk-old plants. Plants were maintained at 17–20 C with intermittent atmospheric saturation for 24 days after which plant survival was evaluated. Isolates of both *Sclerotinia* species differed significantly ($P < 0.01$) in virulence. Alfalfa cultivars differed significantly ($P = 0.02$) in susceptibility, and responses of cultivars to the two species were generally similar. Florida 77 was the most susceptible of the eight cultivars to both *Sclerotinia* species, and 5472 was the least susceptible. An experimental population (STR), previously selected from cultivar Delta for resistance to *S. trifoliorum*, expressed the least susceptibility to both *Sclerotinia* spp. Cultivar × isolate interactions were not significant for *S. sclerotiorum* but were significant ($P < 0.01$) for *S. trifoliorum*. These interactions appeared to be caused by differences in virulence of isolates and did not suggest the occurrence of pathogenic races. Significant ($P < 0.01$) experiment × cultivar and experiment × isolate interactions also occurred for both species; possible causes are discussed. Results indicate that responses of these alfalfa cultivars to *S. trifoliorum* and *S. sclerotiorum* are generally similar, that selection for resistance to *S. trifoliorum* in alfalfa may also confer resistance to *S. sclerotiorum*, that no evidence for different pathogenic races was detected among the isolates, and that host of origin is not an important determinant for the virulence of *Sclerotinia* isolates on alfalfa.

Sclerotinia trifoliorum Eriks. and *S. sclerotiorum* (Lib.) de Bary are both important pathogens of alfalfa and other forage legumes in North America. *Sclerotinia trifoliorum* is the more widespread and better known of the two pathogens on alfalfa and may cause extensive or complete loss of stands under favorable conditions (18,20). Apothecia of *S. trifoliorum* are produced mainly during late fall and early winter from over-summered sclerotia in soil, and disease development occurs primarily from winter through early spring in most locations. *S. trifoliorum* is primarily damaging on first-year, fall-planted crops in the southeastern and south-central United States. Cultivars of alfalfa differ in susceptibility to *S. trifoliorum* (21), but no cultivars with acceptable levels of resistance have yet been developed (18). Few or no methods for disease control are known other than the use of spring planting and plowing to bury sclerotia (18).

Sclerotinia sclerotiorum is primarily known as a pathogen of vegetable, oilseed, and ornamental crops. However, it also causes disease in forage legumes under favorable conditions. On alfalfa in North America, *S. sclerotiorum* has mainly been reported as a pathogen during the summer months in Canada (1,3) and the Pacific Northwest (4). The most detailed studies were made by Gilbert in irrigated alfalfa grown for seed production in Washington (4). He observed that apothecia were produced in spring and that infection and disease development occurred in spring and early summer. Gilbert (5) also found that fall burning of stubble after seed harvest was a highly effective control measure because sclerotia present in residue were destroyed or lost viability.

Sclerotinia sclerotiorum has also been observed as a pathogen of vetches, winter pea, and caleypea in several states of the southeastern United States (14), and on alfalfa in Georgia and berseem clover in Mississippi (R. Pratt, *unpublished*). Although details of the disease cycle have not been established on these forage legumes in the Southeast, symptoms in the field were identical to those caused by *S. trifoliorum* and appeared at the same time in early spring. In some instances, sclerotia of both pathogens were collected together from the same patches of parasitized plants (14). These observations and results indicate that *S. sclerotiorum* may be a pathogen on alfalfa, as on the other forage legumes, in the southeastern United States (18). Since symptoms caused by *S. trifoliorum* and *S. sclerotiorum* on alfalfa are similar, and sclerotia are similar or identical, it is possible that some disease attributed to *S. trifoliorum* might be caused by *S. sclerotiorum*.

Only a few studies have directly compared the pathogenicity of *S. trifoliorum* and *S. sclerotiorum* on alfalfa or other crops, and results have not been consistent. Cappellini (2) reported the most comprehensive study to date. He inoculated field plots of alfalfa, red clover, and white clover with isolates of *S. trifoliorum* from forage legumes and *S. sclerotiorum* from other crops. Isolates of *S. trifoliorum* were pathogenic to alfalfa and clovers, but isolates of *S. sclerotiorum* were nonpathogenic on alfalfa and red clover. Significant isolate × host interactions suggested the possible occurrence of pathogenic strains within *S. trifoliorum* (2). Held and Haenseler (7) inoculated forage legumes, vegetables, and other crops with *S. trifoliorum*, *S. sclerotiorum*, and *S. minor* Jagger in the greenhouse; all three species caused severe disease on alfalfa. Pratt and Rowe (15) inoculated stems of alfalfa plants with single isolates of *S. trifoliorum* and *S. sclerotiorum* in separate experiments. Plants differed in susceptibility to both pathogens, but host responses were not significantly correlated.

Recently, progress has been reported by several workers in efforts to screen and breed for resistance to *S. trifoliorum* in alfalfa (6,8,11,12,16,17). These reports suggest that germ plasms or cultivars of alfalfa with resistance to *S. trifoliorum* may become available for use by scientists and producers in the near future. However, it is not known whether host resistance developed in response to one isolate of *S. trifoliorum*, or in one location, will be effective against isolates or strains of the pathogen from other locations. It is also not known whether populations developed for resistance to *S. trifoliorum* also will manifest resistance to *S. sclerotiorum*. Therefore, the purposes of this study were 1) to compare the pathogenicity of five isolates each of *S. trifoliorum* and *S. sclerotiorum* from diverse locations and forage legume hosts on select alfalfa cultivars under controlled conditions, and 2) to com-

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pare the alfalfa cultivars and an experimental population on the basis of susceptibility to isolates of the two *Sclerotinia* spp.

MATERIALS AND METHODS

Growth and inoculation of plants. Seven alfalfa cultivars were selected from entries in the 1992 Southern Regional Variety Test on the basis of differences in susceptibility to an isolate of *S. trifoliorum* (R. Pratt, *unpublished*). Also included were cv. Delta and an experimental population termed "STR" that was selected from Delta by stem inoculations (16,17). The STR population expressed significant resistance to *S. trifoliorum* compared with Delta in artificial inoculation experiments and with natural infection in the field (16,17). Seed of the nine alfalfa entries were germinated for 2 days on water agar and planted individually in plastic cone-shaped cells (12 cm height, 45 cm^2 capacity) ("Fir Cell," Stuewe & Sons, Inc., Corvallis, OR) containing a greenhouse potting mixture (1:1, sand/peat + vermiculite + limestone [Pro-mix A, Premier Brands, Inc., Stamford, CT]). Inoculant of *Rhizobium* was dusted over seedlings and washed into soil shortly after planting. At 2 and 3 wk, plants were fertilized with 5-11-26 (N-P-K), and at 3 wk plants also received micronutrients and trace elements (Peter's S.T.E.M., W. R. Grace & Co., Fogelsville, PA). Plants were grown for 4 wk in the greenhouse prior to inoculation. Eight plastic cells containing plants of one entry were arranged in a clay pot (11 cm height, 10.5 cm diameter) and held upright with sand to provide a single experimental unit.

Inoculations were performed with five isolates of *S. trifoliorum* and five of *S. sclerotiorum* from forage legumes in the eastern United States. Two isolates from Wisconsin were kindly supplied by R. R. Smith; other isolates were collected by the first author (Table 1). Each isolate originated as a sclerotium formed on a parasitized plant in the field (14). Mycelial colonies were generated by surface disinfesting, bisecting, and plating sclerotia on agar, or by plating stored inoculum, as described previously (13,14). Inoculum consisted of an infested mixture of wheat and oat grain as devised by Kreitlow (9). The grain mixture was autoclaved in flasks, inoculated with individual isolates, incubated, air-dried, stored, comminuted, and sieved as described previously (13). Flasks of inoculum were inspected to ascertain complete colonization by *Sclerotinia* isolates prior to air-drying. New preparations of inoculum of all isolates were used for each experiment.

Plants were inoculated by dusting inoculum over foliage as in previous studies (13,17). Briefly, each pot with eight cones was placed in a plastic cup (8 cm height, 560 cm^3 capacity), and the cup and pot were placed in a translucent plastic bag (42 cm height, 4.3 L capacity) that was folded down below foliage. Approximately 180 ml of water was added to the bag external to the cup to prevent saturation of roots. Nine pots (one per entry) in cups and bags were randomized on a laboratory cart, and foliage of all plants was sprayed with 30 ml of a sticker solution (Pel-gel Nutrient Adhesive, Liphatech, Inc., Milwaukee, WI) in a fine mist. Inoculum of a single isolate (1.875 g per pot) was dusted evenly over foliage of all plants, and bags were pulled up over plants and sealed to create a saturated atmosphere for each pot. Experimental units were randomized on a growth bench and maintained at 17–20 C with fluorescent growth lights (80 $\mu E\ m^{-2} \cdot s^{-1}$ intensity) on a 12-h photoperiod. Bags were unsealed and folded down to expose plants to ambient air at 4 days after inoculation, re-sealed at 8 days, and folded down for a final time at 12 days. The number of plants alive in each pot was recorded at 24 days after inoculation.

Experimental design and statistical methods. A 9 × 11 factorial experiment was performed three times. This experiment consisted of the nine alfalfa entries each inoculated with the five isolates of *S. trifoliorum*, the five isolates of *S. sclerotiorum*, and with autoclaved colonized inoculum for controls. In each repetition of the experiment, four replicate pots of each treatment combination (entry × isolate) were arranged in a randomized complete block design in the growth room.

Analysis of variance (ANOVA) was performed by use of SAS procedures (19). Controls were not included in ANOVA because all plants survived. When an entry × isolate interaction occurred, the principle of extra sum of squares (10) was used to test the significance ($P = 0.05$) for each isolate within the interaction. When one of five isolates of *S. trifoliorum* caused a significant entry × isolate interaction, responses of alfalfa entries to this isolate and the remaining isolates were compared separately in mean separation tests. The similarities in entry responses to isolates of *S. trifoliorum* were evaluated by correlational analysis. All ANOVAs were performed with actual experimental data (numbers of live plants per pot). Means were separated by use of Duncan's new multiple-range test at $P = 0.05$ and are expressed as percentages of live or dead plants (see tables below).

RESULTS

Mean percentages of plants that survived inoculations with the 10 *Sclerotinia* isolates from three experiments are given

Table 1. Sources of isolates of *Sclerotinia trifoliorum* and *S. sclerotiorum* used to inoculate alfalfa cultivars

Sclerotinia sp.	Isolate no.	Source host and state[z]		Year collected
S. trifoliorum	1	Alfalfa (*Medicago sativa* L.)	Miss.	1987
	2	Red clover (*Trifolium pratense* L.)	Wis.	1992
	3	Hairy vetch (*Vicia villosa* L.)	La.	1987
	4	Berseem clover (*T. alexandrinum* L.)	Miss.	1987
	5	Winter pea (*Pisum sativum arvense* (L.) Poir.)	La.	1987
S. sclerotiorum	6	Alfalfa	Ga.	1992
	7	Red clover	Wis.	1992
	8	Hairy vetch	Ga.	1988
	9	Berseem clover	Miss.	1992
	10	Caleypea (*Lathyrus hirsutus* L.)	La.	1987

[z] Isolates from Wisconsin were kindly supplied by R. R. Smith, Jr.; all other isolates were collected by the first author.

Table 2. Mean percentages of alfalfa plants from three experiments that survived inoculation with isolates of *Sclerotinia trifoliorum* and *S. sclerotiorum*

	Percentages of surviving plants[z]												
	S. trifoliorum isolates						*S. sclerotiorum* isolates						
Alfalfa entry	1	2	3	4	5	Mean	6	7	8	9	10	Mean	Entry mean
Florida 77	16	1	5	2	84	22	8	8	28	19	16	16	19
Cimarron	20	3	14	14	93	29	16	4	42	21	24	21	25
Delta	26	6	6	11	89	28	8	6	42	27	29	23	25
WAMPR	34	3	11	15	92	31	7	14	42	22	29	25	28
DS 957	30	5	14	18	83	31	19	9	55	18	28	26	29
5373	30	10	18	15	88	32	15	9	57	29	24	27	30
Apollo Supreme	30	5	24	15	89	33	24	14	46	30	30	29	31
5472	50	7	21	17	94	38	28	16	58	34	43	36	37
STR	56	11	26	13	100	41	28	19	59	36	53	39	40
Isolate mean:	33	6	15	13	91		17	11	49	26	31		
Species mean:						32						27	

[z] Percentages based on a total of 96 plants inoculated for each entry × isolate combination in three experiments.

in Table 2. Sources of variation in these experiments, and their levels of significance, are given in Table 3. Differences in virulence of isolates are given in Table 4, and differences in susceptibility of alfalfa entries to isolates of the two pathogens are given in Table 5. Results with controls were not included in tables because 100% of these plants survived in all experiments.

Significant differences in virulence of isolates and in responses of alfalfa entries were observed with both *Sclerotinia* spp. For *S. sclerotiorum*, no significant differences were observed between repetitions of the experiment, and entry × isolate and repetition × entry × isolate interactions were not significant. However, repetition × entry and repetition × isolate interactions were highly significant (Table 3). The most virulent isolate originated from red clover, and the least virulent originated from hairy vetch (Tables 1 and 4), but the range of differences in virulence of isolates was more narrow than with isolates of *S. trifoliorum* (Table 4). Florida 77 was the most susceptible alfalfa entry, the STR population was the least susceptible, and numerous differences between the nine entries were significant (Table 5).

For *S. trifoliorum*, significant differences were observed between repetitions of the experiment, and entry × isolate, repetition × entry, and repetition × isolate interactions all were highly significant (Table 3). Isolate #1 was the source of the significant entry × isolate interaction; this interaction was not significant when the remaining four isolates were analyzed together. Therefore, responses of alfalfa entries were compared separately for isolate #1 and the remaining four isolates of *S. trifoliorum* (Table 5). The correlation coefficient for responses of alfalfa entries to isolate #1 of *S. trifoliorum* and their mean responses to the other four isolates was highly significant ($r = 0.83$, $P < 0.01$).

The most virulent isolate of *S. trifoliorum* originated from red clover and the least virulent originated from winter pea (Tables 1 and 4). The range of differences in virulence of isolates was broad compared with that of isolates of *S. sclerotiorum* (Table 4). Florida 77 was the most susceptible alfalfa entry, the STR population was the least susceptible, and numerous differences between entries were significant. The range of percentages of survival among plants of the different entries was greater for isolate #1 than for the other four isolates (Table 5).

DISCUSSION

Results of this study demonstrate that isolates of *S. trifoliorum* and *S. sclerotiorum* differ significantly in virulence on alfalfa cultivars. The most virulent isolates of both species originated from red clover; this indicates that occurrence on alfalfa is not an important determinant for high virulence of isolates on alfalfa. Cultivars of alfalfa differed in susceptibility, and differences between cultivars were generally consistent for the two *Sclerotinia* spp. Results obtained with the STR population and isolates of *S. sclerotiorum* suggest that breeding for resistance to *S. trifoliorum* may also give enhanced resistance to *S. sclerotiorum*.

With the five isolates of *S. sclerotiorum*, ANOVA revealed no significant isolate × entry interactions. This indicates that alfalfa entries were parasitized similarly by the five isolates of *S. sclerotiorum* despite the great diversity in locations and hosts of origin of these isolates. However, when the five isolates of *S. trifoliorum* were analyzed together, highly significant isolate × entry interactions were revealed (Table 3). When isolate #1 was excluded from the analysis, isolate × entry interactions were not significant. These results indicate that isolate #1 parasitized the alfalfa entries differently than did the other four isolates. Such differences could potentially indicate the occurrence of a different pathogenic race. However, this did not appear to be the case, because responses of alfalfa entries to isolate #1 closely paralleled their mean responses to isolates 2, 3, 4, and 5 (Table 5) and were highly significantly correlated with them ($r = 0.83$, $P < 0.01$). For all isolates, Florida 77 was the most susceptible cultivar, 5472 was the least susceptible cultivar, the STR population was the least susceptible entry, and most differences between remaining entries were similar. However, the range of values for alfalfa entry means with isolate #1 (16–56% survival of plants) greatly exceeded the ranges for the other four isolates (23–38%) (Table 5). Therefore, the isolate × entry interactions for *S. trifoliorum* appeared to be caused by differences in the ranges of values for plant survival among cultivars, and not by contrasting interactions between isolates and cultivars that might suggest the occurrence of pathogenic races.

For both *S. trifoliorum* and *S. sclerotiorum*, repetition × entry and repetition × isolate interactions were highly significant (Table 3). Experimental results do not provide direct evidence for causes of these interactions, but related observations suggest possible causes that might be tested by further experimentation. Repetition × entry interactions may have been caused by different responses of cultivars to changing environmental conditions during their growth in the greenhouse prior to inoculation. Plants for the three experiments were grown in February, March, and April, respectively, and daylength, light intensity, and temperature increased during these months. Plants grew more rapidly and produced more succulent foliage with the warmer temperatures and longer days, but cultivars did not respond uniformly to the changes in environmental conditions. Parasitism by the *Sclerotinia* isolates tended to be more severe on plants that had grown rapidly and produced succulent leaf and stem tissue. Therefore, varying differences in relative growth rates of cultivars prior to inoculations may have caused or contributed to the significant repetition × entry interactions.

The repetition × isolate interactions that were observed with *S. trifoliorum* and *S. sclerotiorum* may have been caused by dif-

Table 3. Sources of variation and their significance for mean plant survival for three repetitions of an experiment with five isolates of *Sclerotinia trifoliorum* and five isolates of *S. sclerotiorum* inoculated onto nine alfalfa entries

	S. trifoliorum isolates			*S. sclerotiorum* isolates		
Source of variation	df	Mean square	$P > F$[y]	df	Mean square	$P > F$[y]
Repetition	2	64.0	<0.01	2	7.8	NS[z]
Block (repetition)	9	6.1	NS	9	17.7	NS
Entry	8	12.6	<0.01	8	20.0	0.02
Isolate	4	821.0	<0.01	4	141.8	<0.01
Entry × isolate	32	2.2	<0.01	32	2.0	NS
Repetition × entry	16	3.0	<0.01	16	5.4	<0.01
Repetition × isolate	8	7.4	<0.01	8	10.5	<0.01
Repetition × entry × isolate	64	1.1	NS	64	1.5	NS
Error	395	1.2		395	1.4	

[y] Level of probability for a greater value of *F*.

[z] Not significant.

Table 4. Mean percentages of alfalfa plants killed by isolates of *Sclerotinia trifoliorum* and *S. sclerotiorum* and significant differences between isolates

Sclerotinia sp.	Isolate	Percentage of plants killed[z]
S. trifoliorum	5	9 a
	1	67 b
	3	85 c
	4	86 c
	2	94 d
S. sclerotiorum	8	51 a
	10	69 b
	9	73 b
	6	83 c
	7	88 d

[z] Means based on a total of 864 plants of nine alfalfa entries that were inoculated in three experiments. Means not followed by the same letter differ significantly at $P = 0.05$ according to Duncan's new multiple range test.

Table 5. Mean percentages of plants from nine alfalfa entries that survived inoculation with isolates of *Sclerotinia trifoliorum* and *S. sclerotiorum* and significant differences between entries

	Percentages of surviving plants[y]		
	S. trifoliorum[z]	*S. trifoliorum*	*S. sclerotiorum*
Alfalfa entry	**isolate 1**	**isolates 2, 3, 4, 5**	**isolates 6, 7, 8, 9, 10**
Florida 77	16 a	23 a	16 a
Cimarron	20 ab	31 bc	21 ab
Delta	26 ab	28 b	23 abc
WAMPR	34 b	31 bc	25 bc
DS 957	30 ab	32 bc	26 bc
5373	30 ab	33 bc	27 bc
Apollo Supreme	30 ab	33 bcd	29 c
5472	50 c	35 cd	36 d
STR	56 c	38 d	39 d

[y] Means based on a total of 96 plants inoculated for each entry × isolate combination in three experiments. Means not followed by the same letter differ significantly at $P = 0.05$ according to Duncan's new multiple range test.

[z] Results with isolate 1 of *S. trifoliorum* are compared separately because significant ($P < 0.01$) isolate × entry interactions occurred for combined results with all five isolates. No significant isolate × entry interactions occurred for combined results with isolates 2, 3, 4, and 5, or for results with the five isolates of *S. sclerotiorum*.

ferences in virulence of cultures used to prepare inoculum. For each isolate, the culture used to prepare inoculum for the first experiment was obtained from a stored sclerotium, and cultures used for subsequent experiments were obtained by plating infested grain prepared for the preceding experiment. This use of different cultures for inoculum production may have caused changes in the relative virulence of isolates. For example, virulence of isolate #5 appeared to decrease because 23, 3, and 2% of plants were killed in experiments 1–3, respectively. Virulence of isolate #10 appeared to increase because 59, 74, and 75%, respectively, of plants were killed. For other isolates such as #7, with 90, 90, and 88%, respectively, of plants killed, virulence was relatively stable among experiments.

Further research would be helpful to verify the principal results of this study with other isolates of the two *Sclerotinia* spp., with other cultivars of alfalfa, with other populations that are developed for resistance, and possibly by the use of other inoculation techniques or approaches.

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