Effects of Soil Temperature, Moisture, and Depth on Survival and Activity of *Sclerotinia minor, Sclerotium cepivorum,* and *Sporidesmium sclerotivorum*

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ABSTRACT

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High soil temperature and low soil moisture reduced survival and activity of sclerotia of *Sclerotium cepivorum* and *Sclerotinia minor* and macroconidia of *Sporidesmium sclerotivorum.* Fifty percent or more of the propagules of the three fungi in the soil were killed within 39 hr at 40 C, 6 hr at 45 C, or 2 hr at 50 C. When soil containing the propagules of these fungi was dried to a moisture level of −1,516 bars or lower for 7 days and remoistened to −0.2 bar, survival of the sclerotia and the viability of the macroconidia declined over a period of 6 wk. In the field, numbers of sclerotia of *S. minor* at the soil surface and at depths of 0–2 cm declined during the summer months, whereas numbers of sclerotia at depths of 2–8 and 8–14 cm increased slightly and then remained constant. Decline in numbers of sclerotia on the soil surface and at depths of 0–2 cm was assumed to be due to low soil moisture levels during the summer months. Apothecial initials (stipes) were formed on sclerotia during April through June at low levels (1–6%) at all soil depths. Natural infection of sclerotia of *S. minor* by *Sporidesmium sclerotivorum* in the field occurred irregularly and at low levels at the soil surface and at 0–2 cm. Infection of sclerotia was consistent and high at 2–8 and 8–14 cm. The implications of these findings for control of Allium white rot and lettuce drop are discussed.

Sclerotinia minor Jagger can produce more than 12,000 sclerotia on a single lettuce plant, with an average of about 3,500 (6). When these sclerotia are disked into soil over an area occupied by the plant, average inoculum density of the soil in theory would be 7.9 sclerotia per 100 g of soil above the background level. In reality, the inoculum density varies from 0 to 1,252 sclerotia per 100 g of soil (6). If survival is high, one would expect very high inoculum levels after several years of lettuce production. However, one rarely encounters a lettuce field with an inoculum density higher than five or six sclerotia per 100 g of soil (7). Natural biological control by mycoparasites such as *Sporidesmium sclerotivorum* Uecker, Ayers, & Adams could account for some of the natural decline in inoculum densities of these plant pathogens (9). However, New Jersey fields exist where lettuce is grown every year with less than 5% lettuce drop and no known mycoparasites have been detected (P. B. Adams, *unpublished*). Physical factors such as temperature and soil moisture could regulate inoculum densities of pathogens in production fields.

A few laboratory studies have shown the effects of soil temperature and moisture on survival of sclerotia; however, these results have not been demonstrated in the field. Smith (23) showed that sclerotia of two *Sclerotinia* species and *Sclerotium cepivorum* leaked nutrients, were rapidly colonized by microorganisms, and decayed when dried for short periods of time at 30 C and 30% relative humidity (RH) and then placed on moist soil. It was later shown that when soil containing sclerotia of *Sclerotinia minor* was air-dried for one or more days and remoistened, inoculum density declined by about 60% within two or more weeks (3). However, Papavizas (19) could not confirm these findings with sclerotia of *Sclerotium cepivorum.*

The purpose of this study was to investigate the effects of soil temperature and low soil moisture on survival and activity of propagules of *Sclerotinia minor, Sclerotium cepivorum,* and their mycoparasite *Sporidesmium sclerotivorum* and to further relate these findings to results obtained in the field. Results of such a study should provide a better understanding of the soil fungi and lead to improved methods of disease control.

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MATERIALS AND METHODS

Soil temperature studies. Effect of soil temperature on survival of sclerotia of *Sclerotinia minor* and *Sclerotium cepivorum* and macroconidia of *Sporidesmium sclerotivorum* was determined. Rumford loamy sand (pH 6.4) was infested with sclerotia of *Sclerotium cepivorum* (ATCC 56041) as described previously (10). Norfolk sandy loam (pH 6.3–6.5) was infested with sclerotia of *Sclerotinia minor* (ATCC 52583). Inoculum densities of both fungi were about 500–600 sclerotia per 100 g of soil, and moisture content was 11–12% (−0.15 bar). Test tubes (15 × 150 mm) were filled with 10 g of infested soil (50–60 sclerotia) and capped with plastic caps. Test tubes were sealed in plastic bags to reduce water loss from the soil and incubated at 25, 30, 35, 40, 45, and 50 C. At hourly intervals up to 6 hr and then at 6 and 12 hr and 1, 2, 4, 8, 16, and 32 days, four tubes were assayed from each temperature. All sclerotia were retrieved from each soil sample by sieving (4), and 20 were surface-sterilized and placed on a semiselective medium (10). Viability of sclerotia was determined after 14 days, by which time viable sclerotia were able to produce secondary sclerotia.

Macroconidia of *Sporidesmium sclerotivorum* (CS-5, ATCC 56894) were harvested from a vermiculite culture prepared by the Sylvan Spawn Laboratory, Inc. (Worthington, PA). Spores were put on 25-mm (0.45-μm pore size) membrane filters (26,500 spores per filter), and filters were buried in Norfolk sandy loam in crucibles as previously described (2). Soil moisture content was 7.6%. Crucibles were put in storage dishes containing water so as to reduce water loss from the soil. At 15, 30, 45, and 60 min and the intervals described before, a filter was removed from the soil at each temperature and placed on the surface of saturated Norfolk sandy loam in 5.5-cm-diameter petri dishes containing about 1,400 sclerotia of *Sclerotinia minor* per 100 g of soil. The macroconidia were incubated for 7 days at 25 C, at which time they were stained and their germinability (viability) determined as previously described (2). Four counts of germination of 100 spores each were made to assess viability.

Data obtained from the 25 C treatment were considered as a control. Viability of sclerotia at 25 C was 90% or greater after 32 days. Viability of macroconidia of *Sporidesmium sclerotivorum* at 25 C was 70–80%; thus all data were converted to the percentage of that at 25 C for that time period.

Laboratory soil moisture studies. Rumford loamy sand was infested with sclerotia of either *Sclerotinia minor* or *Sclerotium cepivorum*. Fifty-gram portions of moist soil in 250-ml beakers were placed in desiccators over a saturated solution to maintain a specified RH. Moist soil was also put in tared aluminum cups to determine the moisture content of the soil at the various RHs. The treatments in these experiments were as follows: 1) soil kept moist (about 10% moisture) and 2) soil over saturated solutions of potassium carbonate (43% RH), or 3) magnesium chloride (33.2% RH), or 4) lithium chloride (12% RH), or 5) sodium hydroxide (7% RH). Desiccators were kept at 25 C in an incubator to maintain the proper humidity. Soils were kept at the various humidities for 7 days, at which time the soil in the beakers was brought back up to about 10% moisture. Moisture content of soil in aluminum cups was determined and percent moisture was converted to soil matric potential using the following equation: water potential = $(RT/V) \log$ RH, where R is the ideal gas constant, T is the absolute temperature, V is the volume of a mole of water, and log is the natural logarithm (14,15) (Table 1). Immediately after soil moisture was raised to 10%, inoculum density of *Sclerotinia minor* or *Sclerotium cepivorum* was determined and the sclerotia surface sterilized and put on a semiselective medium (3,10) to determine their viability. At subsequent 7-day intervals up to 42 days, only inoculum density was determined. Norfolk sandy loam containing 250,000 *Sporidesmium sclerotivorum* (CS-5, ATCC 56894) macroconidia per gram of soil was placed under the same conditions as before to determine the effect of drying on the viability of the macroconidia. After drying, soil was brought back to the original soil moisture (8.5%) for 3 days. Macroconidia were then retrieved from soil samples (11) and germinability determined as described before.

Field studies. Two field plots were established (Rumford loamy sand at Beltsville, MD.) to determine the survival and activity of *Sclerotinia minor* and the activity of a natural population of *Sporidesmium sclerotivorum*. The two plots (3 × 3 m) were infested in the fall of 1984 with sclerotia of *Sclerotinia minor* grown on sand-cornmeal (12). One plot was rototilled to a depth of 15 cm in April 1985, whereas the second plot was so treated in early May 1985. From that time on, plots were not treated in any way except to rogue the weeds. Each plot was divided into four quadrants. Soil samples were collected from each quadrant of each field plot (eight samples) at 2-wk intervals to a depth of 14 cm. Samples were also collected from the soil surface. The samples were taken with a soil-sampling tube 5.2 cm in diameter (i.d.). The soil core was sectioned to obtain samples at depths of 0–2, 2–8, and 8–14 cm. The soil samples were air-dried, screened through a 2-mm sieve to remove stones, weighed, and assayed for the number of sclerotia by a wet-sieving method (4). Because some of the sclerotia had produced apothecial initials (stipes) in the field, the number of sclerotia with stipes was recorded for each soil sample. Sclerotia retrieved from each soil sample were divided into two equal portions and either placed nonaseptically on moist filter paper in 9-cm petri dishes (25 per dish) or surfaced-sterilized and placed on a semiselective medium to determine viability. Sclerotia on moist filter paper were observed for up to 2 wk for infection by *Sporidesmium sclerotivorum*. A maximum of 50 sclerotia (two petri dishes) were placed on moist filter paper and 20 sclerotia were placed on the agar medium. To compare the inoculum density in the samples with different amounts of soil, the number of sclerotia per soil sample was divided by the weight of air-dried soil and multiplied by 100 to obtain the number of sclerotia per 100 g of air-dried soil. Data on the number of sclerotia with stipes, number of sclerotia infected by *Sporidesmium sclerotivorum*, and number of viable sclerotia were all converted to a percentage of the sclerotia recovered from that sample.

In an adjacent area (within 3 m) a third noninfested field plot (3 × 12 m) was rototilled in early April 1985 and subsequently maintained like the other two plots. Each day, three replicate soil samples were taken as before, put in plastic bags, and immediately brought to the laboratory to record fresh weight. Samples were dried overnight at 95 C, and a dry weight was obtained to determine moisture content of the soil.

Air temperature and rainfall data were obtained from a site within 300 m of the field plots.

RESULTS

Soil temperature studies. Survival of

Table 1. Conditions under which infested Rumford loamy sand was dried and its moisture content

Chemical[a]	Temperature (C)	Relative humidity (%)	Soil moisture content (%)	Soil moisture content Matric potential (bars)
Untreated control	20–23	···	10.73	−0.2
Potassium carbonate	25	43.0	0.50	−1,160.0
Magnesium chloride	25	33.2	0.33	−1,516.0
Lithium chloride	25	12.0	0.20	−2,915.0
Sodium hydroxide	25	7.0	0.13	−3,656.0

[a] Soils were dried in a desiccator over a saturated solution with an excess of solute of the chemical.

propagules of the three fungi at 25 and 30 C after 30 days ranged from 88 to 100%. Survival was reduced by higher soil temperatures. Propagules of the three fungi were killed within 4 hr at 50 C and within 12 hr at 45 C. After 32 days at 35 C, 96% of sclerotia of *Sclerotium cepivorum*, 100% of macroconidia of *Sporidesmium sclerotivorum*, and 67% of sclerotia of *Sclerotinia minor* were killed. Time required to kill 50% of the sclerotia at each temperature (35, 40, 45, and 50 C) was determined. These results (Table 2) indicate that sclerotia of *Sclerotium cepivorum* are the most sensitive to heat, whereas those of *Sclerotinia minor* are the least sensitive.

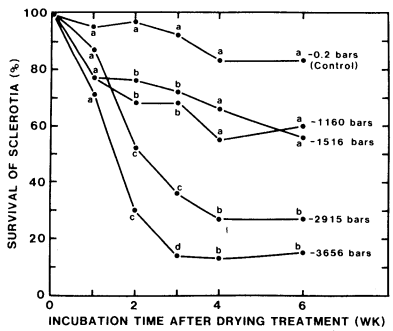

Fig. 1. Survival of sclerotia of *Sclerotinia minor* in soil after soil was dried to the indicated matric potentials for 7 days and remoistened to −0.2 bar for 6 wk. Data points at an incubation time with a common letter are not significantly ($P < 0.01$) different as determined by Duncan's multiple range test.

Soil moisture studies. When soil infested with sclerotia of *Sclerotinia minor* was dried to very low matric potentials for 7 days and remoistened to −0.2 bar, survival of sclerotia in soils dried to −2,915 bars or less was significantly ($P < 0.01$) less than soil dried to higher matric potentials (Fig. 1). This effect was apparent within 2 wk after the soil moisture was raised to −0.2 bar. These data were analyzed with the 0-wk assay data equal to 100% survival. The data for three fungi were analyzed at the 6-wk assay, and the survival for the control (−0.2 bar) for each fungus was made to equal 100%. Survival of macroconidia of *Sporidesmium sclerotivorum* was the most sensitive of the three fungi to the drying treatments and *Sclerotium cepivorum* the least sensitive to the treatments (Table 3). A significant ($P < 0.01$) reduction in survival was obtained for *Sporidesmium sclerotivorum* when the soil was dried to −1,160 bars, for *Sclerotinia minor* at −1,516 bars, and for *Sclerotium cepivorum* at −2,915 bars.

Field studies. Inoculum densities of *Sclerotinia minor* in the field plots at depths of 0–14 cm was 45–62 sclerotia per 100 g of soil in one plot and 52–167 sclerotia per 100 g of soil in the other plot at the beginning of the experiment. Viability of the sclerotia in the plots ranged from 70 to 90% through mid-July. After this time, viability of the sclerotia was no longer determined.

In late May, inoculum density of sclerotia in both plots at depths of 2–8 and 8–14 cm increased to 120–140% over that in early May and remained high through September (Table 4). Inoculum density at the soil surface and at 0–2 cm began to decline (Table 4) in early June and reached 32 and 53%, respectively, in September.

Between 8 May and 15 September 1985, the minimum and maximum temperatures were 6 and 37 C. During this period, the plots received 30.96 cm of rain, with 8.50 cm in May, 5.20 cm in June, 11.95 cm in July, 4.43 cm in August, and 0.88 cm in September. There were several dry periods during the summer months. From 16 June to 9 July, there was only 2.03 cm of rain. During this period, the soil moisture of the surface soil was below 0.5% (−1,160 bars) four times and was at 0.2% (−2,915 bars) twice. Percent soil moisture at depths of 2–8 and 8–14 cm never fell below 4.8% (−3 bars), whereas that at 0–2 cm was at intermediate levels.

Apothecial initials (stipes) were observed on sclerotia of *Sclerotinia minor* at the first soil assay on 19 April and continued in nearly all samples for the duration of the experiment. Stipes were found on sclerotia from all soil depths. Percentage of sclerotia with stipes was very low, ranging from 0 to 6%. There was no relationship between soil depth and production of stipes. It appeared that production of stipes stopped in the middle of June. On subsequent assay dates, stipes were dark brown compared with the lighter brown-tan stipes found in previous assays. Also, percentage of sclerotia with stipes decreased and remained low (0.1–1.2%) for the remainder of the summer. More than 380 stipes were found on sclerotia, but no apothecia were observed, either

Table 2. Time required to kill 50% of the propagules (LD_{50}) of three soilborne fungi in soil at various temperatures

Temperature (C)	LD_{50} (hr)		
	Sclerotium cepivorum (sclerotia)	*Sporidesmium sclerotivorum* (macroconidia)	*Sclerotinia minor* (sclerotia)
35	129.6	266.4	624.0
40	9.5	37.2	38.4
45	1.7	5.2	3.4
50	0.8	0.8	1.5

Table 3. Survival of sclerotia (based on inoculum density) of *Sclerotinia minor* and *Sclerotium cepivorum* in moist soil (−0.2 bar) 6 wk after infested soils were dried to the specified matric potentials for 7 days and viability (based on germinability) of macroconidia of *Sporidesmium sclerotivorum* 3 days after infested soils were dried to specified matric potentials for 7 days

Matric potential of dried soils	Survival based on percentage of control		
	Sporidesmium sclerotivorum	*Sclerotinia minor*	*Sclerotium cepivorum*
−0.2 bar (control)	100 a[z]	100 a	100 a
−1,160 bars	73 b	77 ab	90 ab
−1,516 bars	61 c	69 bc	80 ab
−2,915 bars	39 d	30 c	59 bc
−3,656 bars	24 e	19 c	28 c

[z] Values in a column followed by the same letter are not significantly ($P \leq 0.01$) different according to Duncan's multiple range test.

Table 4. Survival of sclerotia of *Sclerotinia minor* in the field at various depths in the soil profile during the summer of 1985

Sampling date	Percent survival of sclerotia at			
	Soil surface	0–2 cm	2–8 cm	8–14 cm
8 May	100	100	100	100
20 May	83 cdef[z]	114 abcde	120 abcd	124 abcd
30 May	99 abcdef	137 abc	140 ab	136 abc
20 June	85 bcdefg	109 abcde	126 abcd	126 abcd
5 July	53 fg	113 abcde	131 abc	144 a
18 July	83 cdefg	115 abcde	140 ab	138 abc
30 July	36 g	94 abcdef	140 ab	140 ab
16 August	32 g	62 efg	126 abcd	140 ab
27 August	44 fg	72 defg	113 abcde	142 ab
15 September	32 g	53 fg	130 abc	125 abcd

[z] Values followed by the same letter are not significantly ($P > 0.01$) different according to Duncan's multiple range test.

attached to stipes or free in the soil samples.

Plots were located in a field in which *Sporidesmium sclerotivorum* was originally detected. Sclerotia retrieved from plots in May were infected with *S. sclerotivorum* at very low levels (1%). Incidence of infection of sclerotia varied greatly from one sample to another and from one assay to the next. Infected sclerotia were detected more consistently at soil depths greater than 2 cm than at lesser soil depths. In one plot, starting in early July, all four replicates of soil samples at depths of 2–8 and 8–14 cm contained infected sclerotia. However, a reduction in inoculum density of sclerotia at 8–14 cm could not be detected until early November.

DISCUSSION

Soil temperature experiments indicated that all three fungi in this study were quite sensitive to constant soil temperatures of 40–50 C, with sclerotia of *Sclerotium cepivorum* being the most sensitive and sclerotia of *Sclerotinia minor* the least sensitive. All three fungi survived quite well at soil temperatures up to 35 C. Soil temperature alone does not appear to play a major role in the natural decline in populations of these fungi in temperate climates. However, if effects of high soil temperatures for short periods are additive, then short durations of temperatures above 35 C, over time, may have an effect.

Tarping fields with clear plastic (solarization) would raise the soil temperature sufficiently to effectively reduce the viability of the two plant pathogens and the beneficial fungus. It was shown in Australia that the average soil temperature under plastic at a depth of 20 cm can be 40 C, depending on the soil type and location (20,21). Solarization treatment was sufficient to provide 100% control of lettuce drop caused by *Sclerotinia minor*. In the same study, soil solarization provided only 17% control of onion white rot caused by *Sclerotium cepivorum*. In the onion experiment, average soil temperatures under plastic at depths of 5, 15, and 30 cm were 47, 37, and 28 C, respectively. Temperatures at depths 15 cm or more were not sufficient to kill a high percentage of the sclerotia. Crowe and Hall (16) showed that sclerotia of *S. cepivorum* placed 30 cm deep in soil could infect garlic bulbs. Also, if a field was infested with sclerotia at 30 cm and plowed after solarization treatment, sclerotia from the lower soil depths that were not killed by the solarization could be moved to the upper levels of the soil profile and cause infection of a host crop.

The data on survival of sclerotia in soils dried to moisture levels of $<-1,200$ bars ($<0.5\%$) seem to be unrealistic. However, soil at the surface and at 0–2 cm deep frequently dry to this moisture level or lower. With *Sclerotium cepivorum*, sclerotia are uniformly distributed to a depth of 20–25 cm (5), and any of these sclerotia are capable of causing white rot (16); thus, high mortality in the surface soils would not significantly reduce disease incidence. More than 90% of plant infections with lettuce drop caused by *Sclerotinia minor* occur from sclerotia in the top 2 cm of the soil profile (12,17). This moisture study may explain why only a moderate incidence of lettuce drop occurs in most fields. Field experiments showed that the inoculum density of *Sclerotinia minor* at depths of 0–2 cm declined during July and August to about 20–30% of the original level. Inoculum densities of sclerotia at depths greater than 2 cm remained reasonably constant during this period (Table 4). Soil moisture determinations at the soil surface and to a depth of 2 cm were 0.5% on many occasions and 0.2% at least twice in field plots. Results obtained in laboratory experiments would explain the decline in survival of the sclerotia close to the soil surface in the field plots. Field plots in this study were not cultivated during the experiment. Lettuce growers would normally cultivate their crop to 2 cm or deeper several times during the growing season. Cultivations would tend to dry the soil to low moisture levels ($>-1,200$ bars) more rapidly than occurred in this study. Rainfall and irrigations would provide the moisture necessary for the biological degradation of the dried sclerotia (23). If this phenomenon occurs in the high-rainfall and humid middle Atlantic states of the United States, the effect would be even greater in the drier western U.S. lettuce production areas of Arizona and California.

Results reported by Abawi et al (1) on survival of sclerotia in dried soils would appear to contradict those presented in this study. However, in most of the experiments reported by Abawi et al, they failed to remoisten and incubate their dried soils as was done in this and other studies (3,23). Futhermore, their lowest soil moisture treatment was not sufficiently low to adversely affect survival of their sclerotia.

In California, sclerotia of *Sclerotinia minor* were found to survive poorly but better near the soil surface than at lower soil depths (18). However, the conditions in the California study were different from those in this study. Sclerotia used in California were either produced in the laboratory or collected in the field and subsequently air-dried before they were put into the field. Drying is a treatment that reduces the survival of sclerotia once they are placed in moist soil (3,23). In the present study, sclerotia were produced in the laboratory and put into the field without drying in November 1984 and allowed to overwinter before the field test was initiated in the spring of 1985.

Apothecia of *Sclerotinia minor* are rarely seen in agricultural fields, perhaps because they are small and often the same color as the soil. During April, May, and June, 1–6% of the sclerotia formed apothecial initials or stipes, but none of the stipes produced apothecia. Soil depth had no effect on production of stipes. However, light is required for the development of apothecia on the stipes (22). Only stipes that reach the soil surface will develop apothecia. Stipes produced at depths of 8–14 cm would not be expected to reach the soil surface.

Sporidesmium sclerotivorum infected sclerotia of *Sclerotinia minor* in the field at all depths. However, at depths below 2 cm, infection of the sclerotia was more consistent and was higher than that at 0–2 cm. Effects of soil depth on the activity of the mycoparasite was probably due to the higher soil moisture levels at these depths (8).

Location of fungal propagules within the soil profile plays a major role in determining the function of those propagules, especially those of *Sclerotinia minor* and *Sporidesmium sclerotivorum*. In this study, it was shown that sclerotia of *Sclerotinia minor* survived poorly at soil depths of 2 cm or less. This depth corresponds to approximately the depth of planting and cultivation of lettuce. Sclerotia at depths greater than 2 cm (depth of disking and plowing) survived well. It was previously shown that only sclerotia at 0–2 cm deep initiate infection of lettuce (12,17). The present study also indicates that the mycoparasite *Sporidesmium sclerotivorum* is more active and effective at depths greater than 2 cm. It has also been reported that the larvae of the fungus gnat *Bradysia*, a preditor of sclerotia of *S. sclerotivorum*, is more active at 0–2 cm than at lower depths (13). This same preditor has been observed feeding on sclerotia of *Sclerotinia minor* (P. B. Adams, *unpublished*). When a lettuce plant infected by *Sclerotinia minor* is disked into soil to a depth of 14 cm, about 70% of the sclerotia produced on the plant are distributed in the upper 8 cm, and more than half of those in the upper 2 cm of the soil profile (6).

This information may be used to improve current strategies for control of lettuce drop. For example, in regions of low humidity and rainfall (i.e., Arizona and California) a farmer could prepare a field for planting lettuce in the off-season, wait 1–2 mo for the sclerotia in the upper 2 cm to die (as shown in this study), and then plant the crop. If a second crop of lettuce is to immediately follow the first crop, the farmer could apply a contact fungicide on the harvested field and plow both the crop refuse and fungicide to a depth below 2–3 cm. One could also apply a good mycoparasite such as *Sporidesmium sclerotivorum* either alone or in combi-

nation with an appropriate fungicide. The strategy in the control of lettuce drop should minimize the number of sclerotia in the top 2–3 cm of the soil profile at the time of planting the crop.

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