Sclerotial Survival and Apothecial Production by *Sclerotinia sclerotiorum* Following Outbreaks of Lettuce Drop

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ABSTRACT

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The number of sclerotia of *Sclerotinia sclerotiorum* gradually declined over the years following outbreaks of lettuce drop in four naturally infested fields. The rates of population decline did not differ significantly among the four fields tested. In two fields located in a semiarid region, 5.5 and 2% of the initial amounts of sclerotia were still viable after 7 yr. Sclerotia removed from soil samples were classified by weight into four groups: 14–40, 7–14, 3–7, and 1–3 mg per sclerotium. The frequency distribution of the four sclerotial weight groups changed over the years, as small sclerotia became increasingly predominant over large ones. This trend was significant according to a generalized logit model. The number of apothecia produced per sclerotium showed a significant nonlinear increase with increasing sclerotial weight. The percentage of apothecia-producing sclerotia decreased significantly with increasing depth of burial in the soil. In addition, apothecial production was delayed with depth. Of the apothecia produced by sclerotia in lettuce fields 80 days after planting, 94% were located in the top 5 cm of the soil. The highest relative frequency of carpogenically germinated sclerotia (24.6%) was found at a depth of 2 cm.

Additional keywords: inoculum density, inoculum potential, viability.

Lettuce drop caused by the fungus *Sclerotinia sclerotiorum* (Lib.) de Bary occurs between February and April and is the most serious problem affecting the lettuce crop in Israel (13). Ascospores are often the main source of inoculum (12,18). Lettuce drop is caused mainly by ascospores of *S. sclerotiorum* from apothecia in the same field and, to a lesser extent, by ascospores from distant sources (5). The inoculum density of this fungus is the lowest reported for soilborne pathogenic fungi (8). Fifteen

viable sclerotia in 10 kg of soil in a lettuce field caused severe yield loss, whereas one or two sclerotia appeared to be the threshold for economic yield loss (i.e., a loss of 4% of lettuce plants) (3). *S. sclerotiorum* survives mainly as sclerotia in soil for at least 2 or 3 yr (6,11,16). Little specific information is available, however, on the length of time that sclerotia survive in a particular field, or whether the ability to produce apothecia is age-dependent.

The objectives of this study were to determine the survival duration of sclerotia of *S. sclerotiorum* in fields following outbreaks of lettuce drop, measure changes in sclerotial size with time, assess the ability of recovered sclerotia of various sizes to produce apothecia when buried at various soil depths, and measure stipe lengths of germinated sclerotia in lettuce fields.

MATERIALS AND METHODS

Field sites, climate, and crop sequences. Sclerotial survival was studied over a period of 4–8 yr in four fields after a lettuce crop (*Lactuca sativa* L. 'Vanguard') was severely affected by lettuce drop. One field (A) was located in the Jordan valley, in an arid climate with 200 mm of annual rainfall. The other three fields (B, C, and D) were located in the northwestern Negev area, where the climate is semiarid and the average rainfall 300 mm (from November to February). Two additional fields (E and F), as well as five fields in which the length of sclerotial stipes was measured, were also located in the northwestern Negev. The annual mean number of days with temperatures ≥35 C was 114 in the Jordan Valley and 18 in the Negev. The area of each field was approximately 0.2 ha. Field A consisted of loamy clay (0.5% organic matter and 25% clay, pH 7.8; field capacity 32%, v/w); Fields B, C, D, E, and F consisted of loess (0.5% organic matter, pH 8.8; field capacity 21%, v/w). Survival of sclerotia was studied in fields A, B, C, and D, which were sampled over 4, 8, 7, and 6 yr, respectively. Sclerotia recovered from the soil samples obtained from the fields B, C, and D and from two additional fields, E and F, located in the same area were used to determine the effect of sclerotial age on apothecial production.

Crop sequences in fields A–F following the infested lettuce crops are shown in Table 1. Fields A, C, and D were cultivated with a disk plow to 10–15 cm once per year (field D in March, and fields A and C in October). Field B was cultivated two or three times per year, depending on the crop being grown. Irrigation volumes in the summer growth season for cabbage, peanut, potato, and tomato were 4,000, 6,000, 4,000, and 6,000 m^3/ha, respectively. In field B, although other crops susceptible to *S. sclerotiorum*, including cabbage, tomato, and potato, were grown in the crop sequence, disease was prevented by appropriate chemical treatments: for potato and tomato, mancozeb (2,000–3,000 g/ha) applied at weekly intervals during the growth season (10 sprays in potato and 15 in tomato); for cabbage, three benomyl sprays (500 g/ha) were applied during the last month of the growth season. During the study, crops and weeds were inspected for disease.

Soil sampling and extraction of sclerotia. Following incorporation of infected lettuce residues into soil, 10 composite soil samples, each weighing 10 kg, were collected from each field every year in October. Samples from fields A–D were each composed of 25 subsamples, taken with a small spade from the top 10-cm layer at random intervals along two diagonal transects. Each soil sample was wet-sieved through a 1-mm mesh sieve, and sclerotia were carefully separated from the remaining organic particles. In the years during which production of apothecia was examined, sclerotia were extracted from the soil at the beginning of November. Another 10 soil samples from each field (A–D) were stored dry in a shaded indoor area protected from rainfall, and sclerotia were extracted in March. Each soil sample was kept in a 10-L container.

Survival, viability, and production of apothecia. Viability of the extracted sclerotia (fields A–D) was examined according to the method of Ben-Yephet et al (5). Survival over time was calculated as a percentage of the initial viable population of sclerotia in each field. The effect of sclerotial age on apothecial production was studied each year from 1986 to 1988. In 1986, sclerotia were obtained from fields B, C, and D, in which the sclerotial ages were 3, 2, and 1 yr, respectively. In 1987, sclerotia were obtained from the same three fields, plus field E, in which lettuce drop had occurred in 1986, so that the sclerotial ages obtained were 4, 3, 2, and 1 yr. In 1988, sclerotia were obtained from fields B–E, plus field F, in which lettuce drop had occurred in 1987, and sclerotial ages of 5, 4, 3, 2, and 1 yr were thus obtained.

Following the occurrence of lettuce drop, the effect of time on sclerotial weight was examined in fields C and D. Sclerotia obtained from each field (i.e., from the 10 soil samples) were classified by weight into four groups: 14–40, 7–14, 3–7, and 1–3 mg (Fig. 1). The ability of sclerotia to produce apothecia was examined as follows. For each field, nine sclerotia were placed at each of four depths (2, 4, 6, and 8 cm) in each of five pots (8 × 8 × 15 cm) filled with steamed soil consisting of a mixture of sand and loam soils (1:1, v/v). Apothecial production was evaluated by counting apothecia at weekly intervals from day 30 to 107. The sclerotia were chosen from each of the four weight groups in numbers approximately proportional to their frequency in the soil samples from that field. In those cases for which the total number of sclerotia per field (i.e., per 10 soil samples) was less than the number needed (180) for a test of apothecial production, additional soil samples were collected and more sclerotia

TABLE 1. Crop sequences in fields following outbreaks of lettuce drop caused by *Sclerotinia sclerotiorum*

Field[a]	Season	Crop sequences									
		1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
A	Summer	...	Bare	Bare	Bare	Bare	...	...	...	...	...
	Winter	Lettuce	Corn	Corn	Corn	FA[b]	...	...	...	...	...
B	Summer	...	...	Bare	Bare	Bare	Tomato	Peanut	Tomato	Garlic	Peanut
	Winter	...	Lettuce	Tomato	Potato	Cabbage	Wheat	Wheat	Potato	FA	...
C	Summer	...	...	...	Bare	Bare	Bare	Bare	Bare	Watermelon	Bare
	Winter	...	....	Lettuce	Wheat	Wheat	Wheat	Wheat	FA	Wheat	...
D	Summer	...	...	...	...	Bare	Bare	Bare	Bare	Bare	Bare
	Winter	...	...	...	Lettuce	FA	FA	FA	FA	FA	...
E	Summer	...	...	...	...	...	Bare	Bare	...	...	...
	Winter	...	...	...	...	Lettuce	Wheat	Celery	...	...	...
F	Summer	...	...	...	...	...	...	Bare	...	...	...
	Winter	...	...	...	...	...	Lettuce	Wheat	...	...	...

[a]Field A was located in the Jordan Valley and fields B-F in the northwestern Negev. Field A was irrigated during the growth period of corn; fields C, E, and F received no irrigation. Field B was irrigated in the first three years during the winter only and in the remaining four years in the summer and winter.
[b]Fallow.

extracted. Nevertheless, the required number could not always be obtained.

All experiments were performed each year in the same shaded area at the Volcani Center, Bet Dagan. The pots were carefully watered each day to keep soil moist but avoid flooding and uncovering the sclerotia. Maximum and minimum air temperatures were recorded daily during the experiment, which extended from mid-November until mid-March each year (107 days). The appearance of apothecia was recorded weekly, starting 1 mo after sclerotia were placed in the soil.

Length of stipes produced by sclerotia in lettuce fields. At 80 days after planting of lettuce crops, stipes produced by sclerotia were collected by gentle removal of soil around apothecia that appeared under the lettuce canopy. Stipe length was measured only on those sclerotia for which stipes and apothecia were removed as complete units. A total of 100 sclerotia were successfully collected for measurement of stipe length in each of five lettuce fields, three in 1988 and two in 1989. All five fields were located in the northwestern Negev.

Statistical analysis. Data on sclerotial survival were analyzed by the SAS LIFEREG procedure (14); a Weibull distribution (9) was assumed. This procedure estimates the "intercept" parameters, μ and σ, which are related to the usual shape (c) and scale (b) parameters by $\sigma = 1/c$ and $\mu = (1/c)\log b$. In comparing different populations, we assumed that they have the same intercept μ, and the difference in the parameter σ was tested by a chi-square test. Generalized logit analysis was applied to other frequency data with the SAS CATMOD procedure (14). Both procedures obtain estimates by the maximum likelihood method. Analysis of variance by the SAS GLM procedure (14), which allows for unbalanced data, was applied to the other results after log transformation for the number of apothecia produced and arcsine transformation for the percentage of apothecia-producing sclerotia. Each field was first analyzed as a separate experiment. For combined analysis, a weighted analysis of variance is usually done with weights inversely proportional to the variances within experiments. For the two variables employed, weighted analysis of variance was not needed, because separate ANOVAs for the experiments yielded homogeneity of variance across experiments.

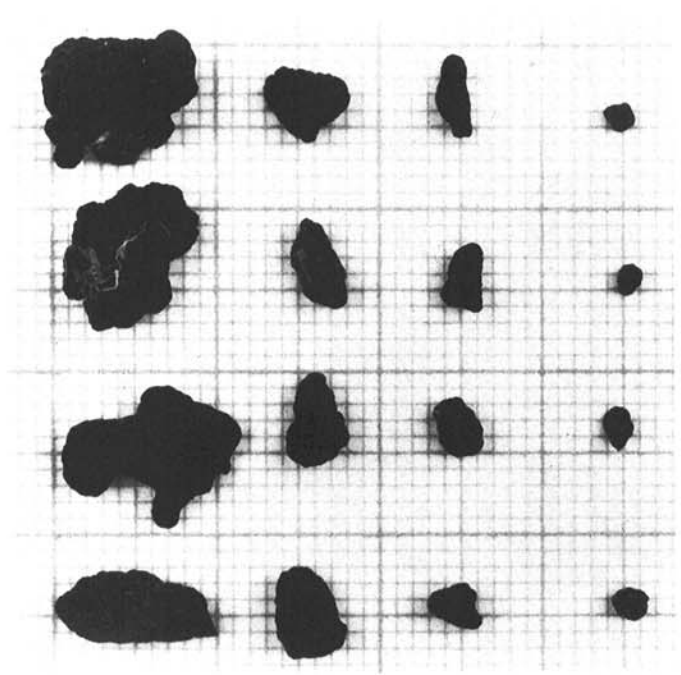

Fig. 1. Representative sclerotia of four sclerotial weights. Left to right: >14–40, >7–14, >3–7, and 1–3 mg per sclerotium. Scale: small square = 0.1 × 0.1 mm.

RESULTS

Survival of sclerotia in the field. Following outbreaks of lettuce drop, a similar trend in the rate of decline in numbers of viable sclerotia was observed in successive years in the four fields sampled (Fig. 2). The variance-to-mean ratio (r) of the 24 field-year combinations varied between 0.337 and 2.543, with only five instances of "overdispersion" ($r > 1$) and only one instance in which it was significantly greater than 1. Thus, sclerotial dispersion in soil could be fitted by a Poisson distribution. Weibull distributions were well suited to the survival data as judged by the residuals. Differences among the μ parameters of the fields were not significant. A common Weibull distribution fitted to all four fields yielded the estimates $\mu = 1.34 \pm 0.02$ and $\sigma = 0.459 \pm 0.012$. In fields B and C, the levels of viable sclerotia after 7 yr were 2 and 5.5%, respectively. After 8 yr, sclerotia were not detected in field B. The viability of sclerotia was similar for all four fields over the years of the study and fluctuated between 80 and 95%. No consistent differences in viability were noted among sclerotia of different sizes.

The relative frequency distribution of the four sclerotial weight groups from fields C and D changed over the years; most frequencies shifted from the larger groups toward the smallest one (1–3 mg) (Fig. 3). This trend was significant ($P < 0.01$) according to a generalized logit model. Fields C and D differed

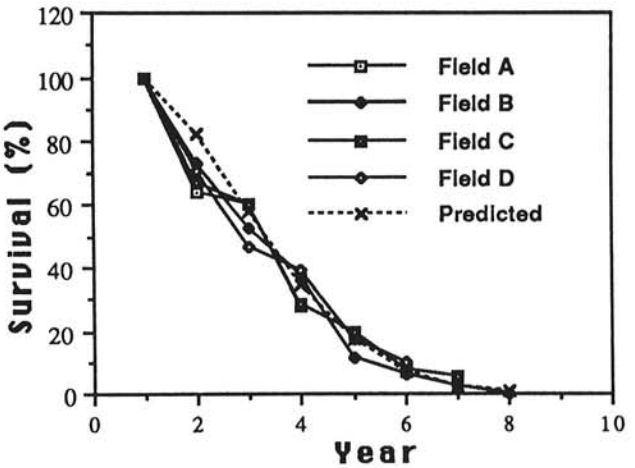

Fig. 2. Reduction of sclerotial populations over time following outbreaks of lettuce drop caused by *Sclerotinia sclerotiorum*. Ten 10-kg soil samples were collected in October every year from each field. The mean number of viable sclerotia one year after outbreaks of lettuce drop (considered as 100%) was 7.6, 22.6, 18.0, and 45.0 sclerotia per 10 kg of soil in fields A, B, C, and D, respectively.

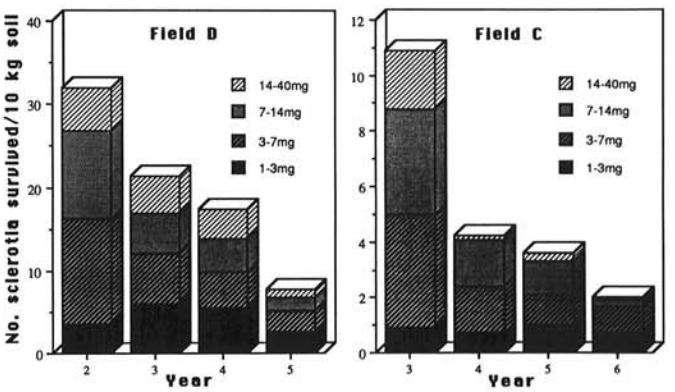

Fig. 3. Number of sclerotia of different weights recovered at various times following outbreak of lettuce drop. The number of sclerotia in each weight group was calculated from the total number of sclerotia recovered every year in 10 soil samples, 10-kg each. In field D, 320, 213, 175, and 78 sclerotia were recovered after 2, 3, 4, and 5 years, respectively; in field C, 108, 53, 36, and 15 sclerotia were recovered after 3, 4, 5, and 6 years, respectively.

significantly in their rate of change over the years ($P < 0.05$). Recovery of sclerotia in the last year (year 5 in field D and year 6 in field C), expressed as a percentage of recovery in the first year (year 2 in field D and year 3 in field C), for the four weight groups (from highest to lowest) was 17.6, 15.1, 21.1, and 71.4 in field C and 4.8, 5.3, 14.6, and 77.7 in field D. These results illustrate the predominance of the smaller sclerotia in later years.

Production of apothecia by sclerotia following lettuce drop. A decline in apothecial production was not correlated with sclerotial age (data not presented). Since depth × age and depth × weight group interactions were not significant for the variables measured, the tables and graph show the main effect only. Apothecial production at four depths by sclerotia recovered from the soil was recorded at weekly intervals (Fig. 4). Production of apothecia was earliest and greatest when sclerotia were buried at 2 cm. The percentage of sclerotia that produced apothecia during the 107-day burial decreased significantly with depth: 37.2, 24.2, 17.9, and 5.2% of sclerotia produced apothecia at depths of 2, 4, 6, and 8 cm, respectively (cumulative percentages from Figure 4). The deeper the sclerotia were buried, the later the appearance of apothecia. The number of days to 75% apothecial production were 51, 74, 92, and 101 for depths of 2, 4, 6, and 8 cm, respectively. For the 6- and 8-cm depths, the productive period could be extended even beyond 107 days. No significant interaction was observed between depth of burial and sclerotial weight or field or year of observation.

The effect of sclerotial weight on the number of apothecia per sclerotium was linear ($P < 0.001$). Both the linear and the quadratic effects of sclerotial weight on the percentage of sclerotia that produced apothecia were significant ($P < 0.05$) (Table 2).

Length of apothecial stipes in the field. Approximately 12% of the apothecia-producing sclerotia were located on the soil surface under the lettuce canopy, and stipes were less than 1 cm long. The longest stipes recovered were 9 cm, but 82% of sclerotia produced stipes between 1 and 5 cm long (Table 3).

Apothecial production in the field was previously found mainly in the top 2 cm of soil (1). Although some apothecia were produced from sclerotia located in the 5- to 9-cm soil layer, 94% of apothecia were produced in the 0- to 5-cm soil layer. The relative frequency of apothecial production was similar at depths of 0, 1, 4, and 5 cm, and the highest frequency was found at depths of 2 and 3 cm.

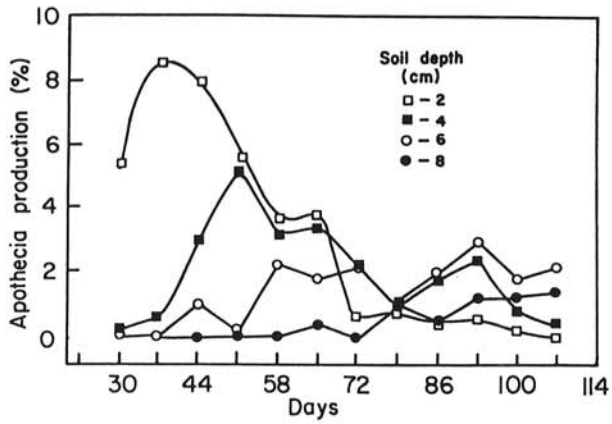

Fig. 4. Apothecial production (percentage of sclerotia tested) by sclerotia of *Sclerotinia sclerotiorum* buried at different soil depths and evaluated at various time intervals. Sclerotia were collected in three successive years: in 1986, from fields B, C, and D; in 1987, from fields B, C, D, and E; and in 1988, from fields B, C, D, E, and F. The frequency of apothecia-producing sclerotia at each time interval was calculated from the total number of sclerotia buried at each depth. The total numbers of sclerotia buried at 2, 4, 6, or 8 cm over the 3-yr period were 594, 549, 396, or 270, respectively. The total numbers of sclerotia that produced apothecia during the 107-day burial were 221, 133, 71, or 14 at 2, 4, 6, or 8 cm, respectively. Ambient air temperatures recorded during the 3 yr of study fluctuated between 8 and 12 C (minimum) and between 15 and 25 C (maximum). The monthly maximum and minimum temperatures varied each year by no more than 3.4 and 3.7 C, respectively.

TABLE 2. Effect of sclerotial weight on percentage of sclerotia that produced apothecia and number of apothecia per sclerotium

Sclerotial weight (mg)	No. of sclerotia tested[a]	Apothecia-producing sclerotia (%)[b]	Apothecia (mean no. per sclerotium tested)[c]	Sclerotia with multiple apothecia (%)[c]
14–40	393	31	0.55	14.3
7–14	603	29	0.39	6.9
3–7	631	21	0.25	4.1
1–3	182	11	0.12	0.5

[a]Sclerotia were removed from soil samples collected from fields during the years 1986, 1987, and 1988. Sclerotia were subsequently buried at depths of 2, 4, 6, and 8 cm and evaluated for production of apothecia over 107 days.
[b]Both the linear and the quadratic effects of sclerotial weight on the percentage of sclerotia that produced apothecia were significant ($P < 0.05$).
[c]Calculated as the number accumulated during the 3-yr study. The linear effect of sclerotial weight was significant ($P < 0.001$).

DISCUSSION

Soil in the different fields was cultivated every year to the same depth (10–15 cm), and sclerotial production was not detected on weeds or on susceptible crops. We therefore assumed that the decline in the number of sclerotia was due to loss of viability. Fitting of the Weibull distribution to the decline of viable sclerotia during successive years yielded a highly skewed distribution. After an outbreak of lettuce drop, the number of sclerotia that can be recovered at a given time from a particular field depends on both the number of sclerotia initially incorporated into the soil and the decline function. This function was found to be similar in the four fields tested (A–D). Thus, whereas sclerotia were recovered for as long as 7 yr after lettuce drop in fields B and C, sclerotia probably would be recovered for an even longer period in field D, where the initial number of sclerotia was higher than in fields B and C.

The decline in populations of sclerotia can probably be attributed to soil microorganisms that decompose sclerotia (19). Information available on the survival of sclerotia of *S. sclerotiorum* that were buried in soil and subsequently recovered at various times suggests that sclerotia can survive for longer than 3 yr (6). In a study of Sclerotinia wilt in sunflower (8), the germinability of sclerotia from different sites varied from 76 to 93%, with a mean of 80.4% for all sclerotia. In our study, although the number of viable sclerotia decreased with time, germinability

TABLE 3. Relative frequency of apothecia-producing sclerotia of *Sclerotinia sclerotiorum* with stipes of varying lengths formed in lettuce fields

Stipe length (cm)	Relative frequency of sclerotia (%)[a] Field number 1	2	3	4	5	SD[b]
<1	17	9	11	12	9	3.3
1	18	18	12	12	10	3.7
2	31	32	17	20	23	6.7
3	16	22	30	15	21	6.0
4	8	14	13	14	16	3.0
5	7	5	8	18	10	5.0
6	3	0	1	6	6	2.4
7	0	0	6	2	3	2.0
8	0	0	1	1	0	0.0
9	0	0	1	0	2	0.7

[a]Results are from three fields (1–3) in 1988 and two fields (4 and 5) in 1989. In each field, stipe length was determined for 100 apothecia-producing sclerotia 80 days after planting.
[b]Standard deviation calculated from the data from five fields.

of the recovered sclerotia was not affected and was similar at the various times tested. The increase in frequency of the smaller sclerotia accompanied by a decrease in incidence of the larger ones was probably due to higher survival rate of the small sclerotia, production of secondary sclerotia (19), and/or higher rate of shrinkage or apothecial production by the large ones relative to the small.

Our conclusion that a Poisson distribution fits sclerotial dispersion in soil is in contrast to the findings of Marois and Adams (10) and Dillard and Grogan (7), who reported that a negative binomial distribution most often fits the sampling distribution for *S. minor*. This discrepancy may be due to the difference in either the species or the sampling techniques used.

Reports on the effect of soil moisture on sclerotial survival in *S. minor* are contradictory: low soil moisture increased (4) or decreased (2) sclerotial decline. In our study, although the findings were not conclusive, sclerotial decline over 4–8 yr in the irrigated field (field B) apparently occurred more rapidly than in the nonirrigated fields (C and D).

The inoculum potential of sclerotia of *S. sclerotiorum* declined as a result of the decrease in both inoculum density and sclerotial weight. Sclerotia of smaller mass produced a smaller total number of apothecia and fewer apothecia per sclerotium. Our inability to demonstrate an age-related decline in apothecial production can probably be explained by the failure to obtain enough sclerotia, especially those aged 4–6 yr, for these experiments.

In a recent study of apothecial production by *S. sclerotiorum* conducted in pots (11), more apothecia were produced by sclerotia placed at a depth of 0–2 cm than by those buried deeper. The results of our study also showed a significant decrease in the percentage of sclerotia that produce apothecia, as well as a significant increase in the time required for production of apothecia and the number of apothecia produced, with increasing depth of burial.

In a previous study (5) conducted in the same two regions as the present work, one or two viable sclerotia per 10 kg of soil in lettuce fields caused approximately 4% incidence of lettuce drop. This inoculum density appears to be a threshold for economic yield loss. Similar inoculum levels were found in field A and in fields B and C after 4 and 6 yr, respectively. *S. sclerotiorum* survived better in cropped than in uncropped soils (15), whereas cropping sequence had no effect on reduction of inoculum density (3). Crop rotation may not be effective in the control of Sclerotinia diseases caused by the large sclerotial types (17). In our study, a similar decrease in viable sclerotia was noted in all four fields tested, whether cropped or fallow. Thus, under our conditions, inoculum density might be reduced below threshold levels by fungicides or crop rotations with nonhosts. The present findings with respect to sclerotial decline may enable growers to plan better strategies to control the pathogen.

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