Factors Affecting Survival of Sclerotia, and Effects of Inoculum Density, Relative Position, and Distance of Sclerotia from the Host on Infection of Lettuce by *Sclerotinia minor*

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We are grateful to A. S. Greathead, Monterey County Cooperative Extension Service, Salinas, for assistance with field plot studies.
Research supported in part by the California Iceberg Lettuce Research Advisory Board.
Accepted for publication 19 May 1980.

ABSTRACT

IMOLEHIN, E. D., and R. G. GROGAN. 1980. Factors affecting survival of sclerotia, and effects of inoculum density, relative position, and distance of sclerotia from the host on infection of lettuce by *Sclerotinia minor*. Phytopathology 70:1162-1167.

Inoculum densities of *Sclerotinia minor* found in surveys of lettuce (*Lactuca sativa*) fields in Salinas Valley, California, during 1978 and 1979 ranged from zero to three sclerotia per 70 ml (100 g) sample of soil. Sclerotia capable of eruptive germination and thus potentially able to cause infection (competent), ranged from 0 to 0.80 per 70 ml of soil. Within each field no significant differences were found among inoculum densities for different samples or sampling periods within a single crop season. Incidence of drop ranged from 0.5 to 18.5% and was proportional to both inoculum density of competent sclerotia ($r^2 = 0.80$) and total sclerotia ($r^2 = 0.76$). Sclerotia developed at all depths on newly infected lettuce tissue buried at 0 to 30 cm, but fewer were formed at greater depths than at or near the soil surface. Numbers of recoverable sclerotia formed on buried infected tissue and their percent germination decreased progressively with time of burial. Sclerotia survived better in dryer than in moist soil and better at shallower than at greater depths; washing and drying prior to burial had no effect on survival. Sclerotia survived better in a field with suppressive soil (without history of drop) than in a field with nonsuppressive soil (with a history of drop). *Trichoderma* spp. were isolated most frequently from retrieved ungerminated sclerotia and most isolates were parasitic on *S. minor*, but there was variability among isolates. Sclerotia in contact with the main lettuce stem on the soil surface caused the highest percent of infection; if located more than 1 cm from the plant, no infection resulted in most instances. Sclerotia in contact with the main root at greater depths were less effective in causing drop than those at shallower depths.

Additional key word: epidemiology.

After commercial harvest, lettuce residues infected by *Sclerotinia minor,* including those with sclerotia already formed, are disked into the soil. Brown and Butler (7) noted that discarded and rejected heads of lettuce infected with *Sclerotinia sclerotiorum* continued to produce large numbers of sclerotia on the surface and beneath the soil. However, they did not specify depth of burial or present data to quantify their observations.

Studies on survival of sclerotia of *Sclerotinia* spp. have been carried out under a wide range of soil conditions; results have been variable, ranging from less than 1 mo to 11 yr (2,7,9,19). A number of factors have been reported to affect survival of fungal sclerotia (8), such as mycoparasites (6,10,12,13,22,23), temperature (2,4,7,9,15,24), and soil moisture and gases (1,9,16,18–20,24).

Not all sclerotia of *S. minor* that survive in the field are competent to germinate eruptively or are in a position to infect susceptible hosts. To initiate disease without an extraneous food base, a sclerotium must be capable of eruptive germination (21) and must be located within a limited distance from the plant (11,14). Adams (3) reported the natural occurrence of inoculum densities of *S. minor* ranging from 0 to 82 sclerotia per 100 g of soil, but he did not present data on the corresponding incidence of lettuce drop.

In this study the relation of inoculum density to disease incidence, factors affecting survival of sclerotia, and the effect of relative position and distance of sclerotia of *S. minor* from lettuce on incidence of lettuce drop were examined.

MATERIALS AND METHODS

Survey of lettuce fields for inoculum density and disease incidence. Lettuce fields in the Salinas Valley, California, with and without previous history of lettuce drop, were chosen for survey, and survey periods covered the time from disking the land prior to planting until harvest of the next lettuce crop. An area of approximately 1/8 ha in each field was sampled monthly during the 1978 and 1979 cropping seasons, and the average of three assays are presented for each cropping season. Sampling techniques initially involved scooping soil from the surface to a depth of about 10 cm with a hand-trowel at random from about 30 spots in a selected area (1/8 ha) of each field. In the initial surveys, all soil samples from each field were thoroughly mixed and five 70-cm^3 subsamples were taken at random from each bulked sample after air-drying for 24 hr (samples actually were 100 g but are converted to volume). In later surveys, a sampler, 4.4 cm in diameter and 5.0 cm long, made from aluminum pipe was used to collect soil samples (78 cm^3) at random from 150 spots within the sampled area of each field and five subsamples from each bulked sample were assayed without drying. Subsamples were soaked in water for 30 min and wet-sieved onto stacked 0.5- and 0.25-mm sieves and residues retained on both sieves were collected on filter paper, air dried for 24 hr on the laboratory bench, and sclerotia from each sample were counted and tested for eruptive germination as described previously (15).

Percent lettuce drop was determined just prior to harvest by evaluating about 1,000 lettuce plants within the sampled area. Ten rows were selected at random and about 100 plants within each row were assessed for infection and drop by *S. minor*.

Effect of depth of burial of infected lettuce tissue on formation and survival of sclerotia. Lettuce crowns naturally infected or artifically inoculated with *S. minor* were buried in nonsterilized field soil in 10-cm-diameter plastic pots in a greenhouse prior to sclerotia formation; artificially inoculated lettuce crowns only were similarly buried in soil at the field site. All treatments were sampled for sclerotia at monthly intervals and recovered sclerotia were dried and tested for germination as described previously (15).

Ethylene contents of soil gas samples taken at monthly intervals in the treatment area described by Ioannou et al (17) were determined with a Carle 8000 gas chromatograph and a Carle 211 gas chromatograph (Carle, Inc., Fullerton, CA 92631). Soil water potential and water content were determined with a thermocouple psychrometer and by weighing and drying samples in the laboratory. Soil and gas samples usually were collected about 2–3 days after irrigation. Soil temperature was recorded with a thermograph.

Survival of sclerotia introduced into field soil. Twenty-five sclerotia either cultured on autoclaved oats moistened with nutrient broth (15) or collected from infected lettuce tissue in the

0031-949X/80/12116206/$03.00/0

field were buried in vials or test tubes containing nonsterilized field soil previously dried to various matric potentials on a pressure plate (15). Each ψ_m-depth treatment, incubated at 20 C in a temperature-controlled incubator, was replicated four times. Sclerotia were assessed weekly for survival and germination as described previously (15).

Three-month-old sclerotia produced on autoclaved oat seed and subjected to different treatments consisting of washing and drying in ambient air were tested for survival in nonsterilized field soil. Some of the sclerotia were washed and dried for 24 hr, others were not washed but dried for 24 hr, and others were washed but not dried; controls were neither dried nor washed. Twenty-five sclerotia from the different treatments were buried at different depths in vials or test tubes containing field soil adjusted to ψ_m of -1 bar. Each treatment was replicated four times and sclerotia were retrieved at weekly intervals to assess survival and germinability.

To examine survival in the field, 50 laboratory or field-collected sclerotia were buried in each of several 5-cm-diameter plastic pots at various field sites. Each treatment was replicated three times and sampled every 2 wk for sclerotial survival and germinability. Soil gas and soil samples were taken for determining ethylene content and moisture measurements from all depths at each sampling date.

Occurrence and parasitic ability of fungi on sclerotia of *S. minor* from lettuce field trials. Fungi growing in or sporulating on retrieved sclerotia that failed to germinate were isolated by transferring some spores or a piece of sclerotium to potato dextrose agar (PDA). Pure cultures of the fungi were tested for their efficacy as parasites of *S. minor*. Twenty-five sclerotia were placed on sterile moist quartz sand in 9.0-cm diameter glass petri plates and inoculated with spore suspensions of the various isolates obtained by adding 10 ml of sterile water to 1-wk-old cultures on PDA slants. Four plates with sclerotia were inoculated with each fungal isolate and incubated at room temperature (21 C). Sclerotia were observed daily to determine whether they had germinated; if they were covered with growth of another fungus or were water-soaked, they were probed with a needle to determine whether they were firm.

Effect of distance of sclerotia from lettuce on the incidence of drop. Lettuce plants were grown in a greenhouse in 20-cm-diameter plastic pots containing nonsterilized soil from a lettuce field. Sclerotia were placed on the soil surface at various distances from the main stem or at various depths in contact with the tap root of 8-wk-old plants. Each treatment consisted of 15 plants, and plants were assessed daily for 15 days for signs and symptoms of drop.

RESULTS

Natural inoculum density of *S. minor* and incidence of drop. Results of surveys of six fields in Salinas Valley, California, for naturally occurring inoculum density in 1978 and 1979 are presented in Table 1. Average numbers of sclerotia per 70 or 78 cm^3 of soil ranged between zero and three for all fields, and the differences among samples for each field and cropping season were not significant. The numbers of competent sclerotia per 70- or 78-ml volume of soil ([number of sclerotia] × [percent eruptive germination]) ranged from zero to six-tenths and drop infection from zero to 11.6%. In ten other fields included only in the 1979 survey (data not presented in Table 1), the number of competent sclerotia ranged from thirteen-hundredths to one per 78 ml of soil and drop infection ranged from 0.5 to 18.5%. The percentage of eruptive germination of all sclerotial samples from the 16 fields ranged from 17 to 35% and averaged 28.6 ± 4.7. The incidence of drop in all 16 fields was significantly correlated with numbers of

TABLE 1. Inoculum density (sclerotia) of *Sclerotinia minor* and incidence of drop occurring in lettuce fields in the Salinas Valley, California[a]

Field	Avg. total (and competent) sclerotia/70 cm^3 of soil[a]				Drop (%)[b]		
	Spring 78	Summer 78	Winter 79	Spring 79	Spring 78	Summer 78	Spring 79
1	2.2 (0.3)	1.4 (0.2)	2.1 (0.6)	1.6 (0.5)	7.1	N. D.[c]	N.D.
2	2.9 (0.5)	1.9 (0.4)	2.6 (0.5)	2.1 (0.6)	6.3	11.4	5.4
3	1.1 (0.2)	1.5 (0.3)	1.7 (0.5)	1.7 (0.4)	3.9	11.6	N.D.
4	0 (0)	0 (0)	0 (0)	0 (0)	0.0	0.0	0.0
5	0.5 (0.0)	0.6 (0.4)	0.8 (0.2)	1.1 (0.2)	N.D.	4.7	2.3
6[d]	3.0 (0.6)	2.4 (0.6)	1.3 (0.4)	1.6 (0.3)	N.D.	N.D.	2.8

[a] Soil samples were collected at monthly intervals starting from the time of disking the previous crop to harvesting of the next crop. Inoculum density of *S. minor* (sclerotia) was determined by wet sieving five 70–78 cm^3 subsamples taken randomly from each bulked field soil sample. Recovered sclerotia were washed, dried, and percent of eruptive germination was determined. In parentheses: (competent sclerotia) = (total sclerotia) × (percent germination).

[b] Percent lettuce drop was determined by evaluating 1,000 plants just prior to harvest within each sampled area; plants within 10 rows selected at random were included. Inoculum densities presented are averages of four sampling dates.

[c] Not determined because fields were not planted to lettuce.

[d] Field No. 6 had 10 sclerotia per 70 cm^3 of soil and 31% drop in the summer of 1977. It was fallowed in fall 1977 and winter 1978, planted to garlic in spring and summer 1978, fallowed again in fall 1978 and winter 1979, and lettuce was planted in spring 1979.

TABLE 2. Effect of depth of burial of incipiently infected lettuce crowns on sclerotial formation and survival in natural field soil in the greenhouse

Source	Depth of burial (cm)	Sclerotia recovered after: 1 mo		2 mo		3 mo	
		No. per crown	Germ. (%)	No. per crown	Germ. (%)	No. per crown	Germ. (%)
Greenhouse[a]	0	242 a	32.2	56 a	3.7	25 a	0
	5	209 a	36.7	3 b	9.0	1 b	0
	10	194 a	24.3	3 b	7.0	0 b	...
	20	66 a	38.3	0 b	0	0 b	...
Field[b]	0	92 a	20	29 a	10	11 a	0
	5	68 a	17	2 b	0	0 b	0
	10	35 b	5	2 b	0	0 b	0
	20	21 b	6	0 b	0	0 b	0

[a] Inoculated lettuce crowns, in 10.2-cm (4-inch) diameter plastic pots containing nonsterilized field soil, were buried prior to sclerotia formation at different depths in 120 × 90 × 25-cm wood boxes containing lettuce field soil in the greenhouse (about 21 C). Soil moisture was maintained at near field capacity. Each treatment was replicated five times.

[b] Infected lettuce crowns from a commercial field were collected and buried prior to sclerotia formation as described above.

[c] Values in the column followed by different letters are significantly different according to Duncan's multiple range test ($P = 0.01$).

both total and competent sclerotia ($r^2 = 0.76$ and 0.80, respectively).

Effect of depth of burial of infected lettuce crowns on the formation and survival of sclerotia. Infected lettuce crowns buried and retrieved from soil in the greenhouse at monthly intervals were wet sieved and the recovered sclerotia were dried and tested for germination. On both naturally infected or inoculated crowns, sclerotia were formed at all depths of burial, but more were formed near the soil surface than at the lower depths (Table 2). More sclerotia were formed on laboratory infected lettuce crowns than on those collected from commercial lettuce fields. By the end of the 2nd mo, numbers of recoverable sclerotia at the greatest depths tested had decreased to an average of two to three per crown regardless of whether the crowns were naturally infected in the field or artificially inoculated. No sclerotia were recovered after 3 mo burial at depths greater than 5 cm.

Laboratory-inoculated crowns also were used in field trials. Results from field and greenhouse tests were similar (Table 3); sclerotial production decreased with depth and fewer sclerotia were retrieved with increased time of burial. Germination of retrieved sclerotia also decreased with time and depth of burial of infected tissue in both the greenhouse and the field (Tables 2 and 3).

Survival of sclerotia introduced into natural field soil. The effects of three soil moisture tensions and five depths on sclerotial survival and germination were investigated in the laboratory (Fig. 1). At all ψ_m tested, sclerotia on the soil surface survived better than those that were buried, and survival was reduced at the lower soil moisture tensions. After 4 wk of burial, survival of both laboratory and field sclerotia decreased drastically, but survival of field-collected

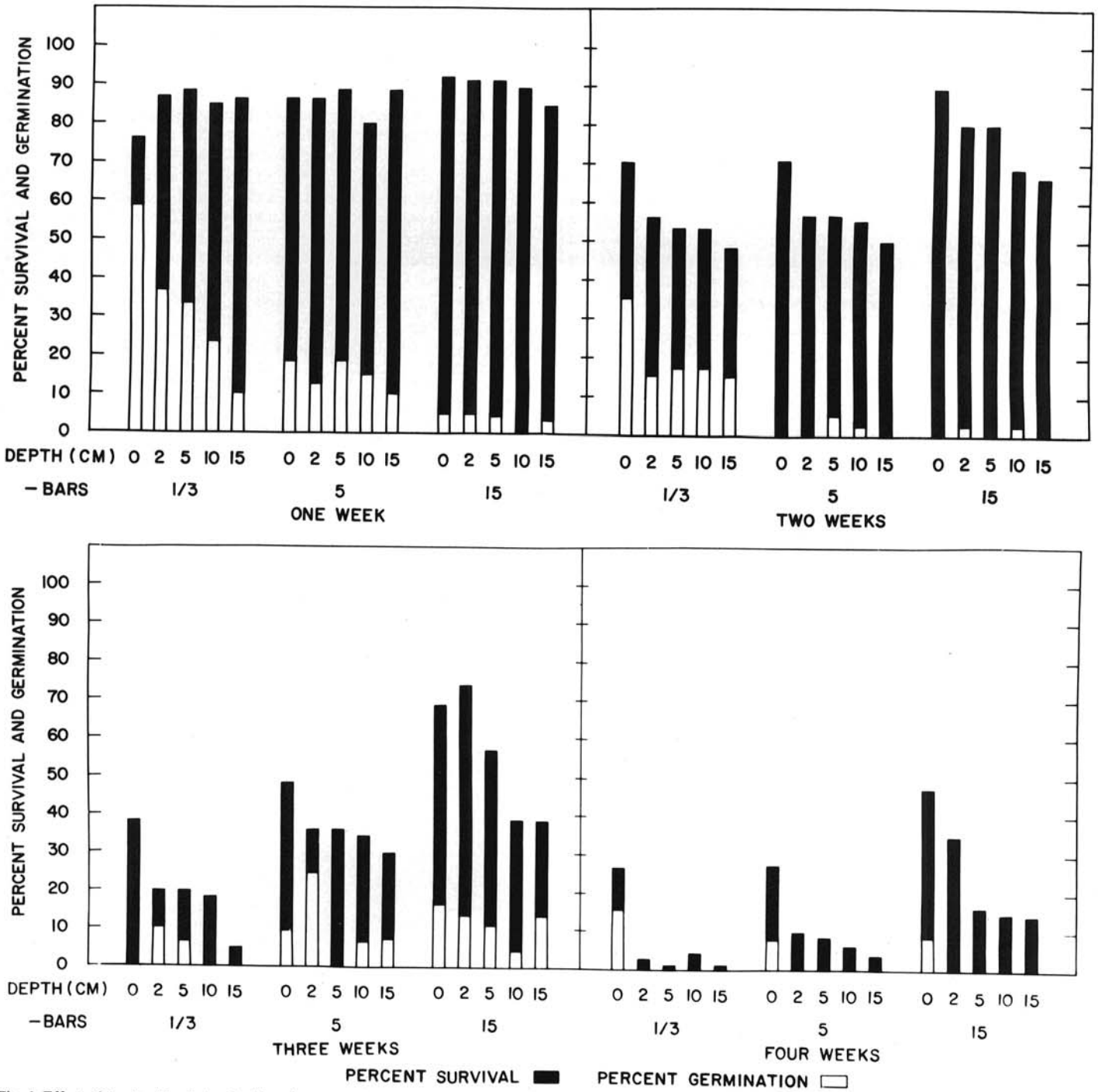

Fig. 1. Effect of depth of burial and soil moisture tension on survival and germination of sclerotia of *Sclerotinia minor*. Twenty-five sclerotia from cultures on autoclaved oat seed were buried in vials or test tubes containing soils adjusted to the various ψ_m and were incubated at 20 C. Each treatment was replicated four times. Similar tests with sclerotia from the field produced similar results.

sclerotia (not presented) was not significantly lower than that of laboratory-produced sclerotia. Percent germination of sclerotia also decreased with increased depth and time of burial.

The effect of washing and drying on survival of sclerotia of *S. minor* is presented in Table 4. Although survival of sclerotia was reduced with increased depth and duration of burial, there were no significant differences in survival of the differently treated sclerotia.

Sclerotia buried in two lettuce fields, one with suppressive soil (field 4, Table 1—no history of drop) and the other with nonsuppressive soil (field 3, Table 1) were retrieved at 2-wk intervals and assessed for survival and germination. Sclerotial survival decreased with depth and time of burial in both fields (Table 5). In the suppressive soil, sclerotia survival was significantly higher at all depths than in nonsuppressive soil, and there were no significant differences in survival of laboratory-produced and field-collected sclerotia in either field at any sampling time (Table 5).

Soil moisture and ethylene contents at various depths were determined at 1-mo intervals for 3 mo in the two fields. Ethylene concentration was about 1.5 μl/ L at all depths in both fields. Soil moisture tensions decreased with increase in depth from 0 to 30 cm, but were lower in the suppressive soil.

Occurrence and parasitic ability of fungi isolated from sclerotia. The frequency of isolation of fungi and results from tests of parasitism on sclerotia are presented in Table 6. Of the 122 isolates of fungi isolated from sclerotia, *Trichoderma* spp. were the most numerous (44 isolates) and most efficient in parasitizing sclerotia. The parasitic ability of other soil fungi on *S. minor* sclerotia ranged from 0 to 20%, indicating that some of the fungi were surface contaminants rather than parasites.

Effect of distance of sclerotia from lettuce on the incidence of drop. Competent sclerotia (one per plant) placed in contact with lettuce main stems or roots at 0 to 5 cm below the soil surface resulted in decrease in drop incidence with depth (Table 7). When sclerotia were placed on the soil surface 2 cm or more from the main stem, their ability to cause disease in the absence of bridging organic matter was nil (Table 7). Ability of sclerotia 1 cm from the main stem to cause disease was much reduced compared to those in contact with the stem.

TABLE 3. Effect of depth of burial of infected lettuce crowns on sclerotial formation and survival in the field

	Sclerotia formation and recovery after:			
	1 mo		2 mo	
Depth of burial (cm)	No. per crown[a]	Germ. (%)	No. per crown	Germ. (%)
0	266 a[b]	32	37 a	6.3
5	215 ab	22	4 b	0
15	142 b	11	2 b	0
30	131 b	0	0 b	0

[a] Laboratory-infected lettuce crowns were buried prior to sclerotia formation at different soil depths in the field. Buried tissues were retrieved twice at monthly intervals and sclerotia formation determined by wet sieving. Recovered sclerotia were washed, dried, and tested for germination on moist quartz sand.

[b] Values in the column followed by different letters are significantly different according to Duncan's multiple range test ($P = 0.01$).

DISCUSSION

After dormancy is relieved by aging followed by drying, sclerotia of *S. minor* can germinate eruptively and can infect lettuce directly without the need for an exogenous energy source. However, in

TABLE 4. Effect of washing and drying on survival of sclerotia

		Survival (%) after:			
Treatment[a]	Depth (cm)	1 wk	2 wk	3 wk	4 wk
Washed dried	0	90.5	75.2	62.9	49.5
Washed nondried	0	92.5	72.5	67.6	50.5
Unwashed dried	0	95.2	81.9	70.5	48.6
Unwashed nondried	0	92.4	80.0	68.6	45.7
Washed dried	5	87.6	72.4	38.4	11.4
Washed nondried	5	91.4	69.5	40.3	19.0
Unwashed dried	5	93.3	72.4	41.9	11.4
Unwashed nondried	5	94.3	74.3	42.9	17.1
Washed dried	10	89.5	63.8	30.5	9.5
Washed nondried	10	87.6	62.9	33.3	13.3
Unwashed dried	10	90.5	78.1	32.4	5.7
Unwashed nondried	10	94.3	63.8	37.1	18.1

[a] Twenty-five laboratory-produced sclerotia subjected to different treatments of washing and drying were buried at different depths in vials or test tubes containing nonsterilized field soil adjusted to −1 bar moisture tension. Some of the sclerotia were washed and dried for 24 hr, others were not washed but dried for 24 hr or were washed but not dried; controls were neither washed nor dried. Each treatment was replicated four times.

TABLE 5. Effect of depth of burial of sclerotia[a] of *Sclerotinia minor* in two lettuce fields (suppressive and nonsuppressive) on survival and germinability

	Percent survival and viability of sclerotia after:							
	2 wk		4 wk		6 wk		8 wk	
Sclerotia type and depth (cm)	Recovery (%)	Germ. (%)/ no. tested	Recovery (%)	Germ. (%)/ no. tested	Recovery (%)	Germ. (%)/ no. tested	Recovery (%)	Germ. (%)/ no. tested
Nonsuppressive soil								
F[b]-0	99.3	31/100	94.7	64/100	41.3	6/60	20.0	0
F-5	18.0	2/27	8.0	0/8	3.3	0	2.0	0
F-15	11.3	3/17	0	...	0	...	0	...
F-30	1.1	0	0	...	0	...	0	...
L[b]-0	96.0	28/100	96.7	66/100	38.0	12/57	32.0	4/48
L-5	29.3	5/28	20	9/30	5.3	0	1.0	0
L-15	12.0	2/12	2	1/3	0.7	...	0	...
L-30	5.3	0	0	...	0	...	0	...
Suppressive soil								
F-0	98.0	42/100	97.3	40/100	60.0	28/90	39.0	4/58
F-5	56.0	12/75	37.3	10/56	32.7	6/49	8.0	2/12
F-15	18.0	4/25	2.7	0	0	...	0	...
F-30	2.0	0	0	...	0	...	0	...
L-0	96.7	64/100	98.0	76/100	68.0	38/100	41.0	8/61
L-5	67.3	33/100	38.7	20/58	32.0	15/48	11.0	1/16
L-15	18.7	6/28	2	0	0.7	0	0	...
L-30	2.7	1/3	0.7	0	0	...	0	...

[a] Fifty laboratory or field-collected sclerotia, washed and dried for 24 hr, were put in 5-cm diameter plastic pots and buried at 0–30 cm depth in lettuce fields. Each treatment was replicated three times.

[b] F = field sclerotia from natural infection; L = cultures sclerotia produced in the laboratory.

agreement with other reports (4,11,18) only a portion of the sclerotia of *S. minor* that survive in soil between crops are competent to germinate eruptively (average 28.6 ± 4.7% in this study) and only a small fraction of these are located close enough to the crown or upper part of the root to cause drop (11).

Although lettuce has been grown in the Salinas Valley, California, for many years and often two crops per year are grown in the same field, the percent drop usually is low (0–10%). Furthermore, some fields consistently have less drop than others. Incidence of drop is influenced mainly by inoculum density of germinable sclerotia in the soil and by conditions that influence germination and infection. Inasmuch as sclerotia can germinate over a wide range of temperatures, O_2, CO_2, and ethylene concentrations (16), and at soil moisture tensions as great as −15 bars (15), it seems unlikely that the soil environment is usually limiting.

Inoculum density of *S. minor* in the 16 fields surveyed in 1978–1979 was low, ranging from zero to three total sclerotia and zero to eight-tenths competent sclerotia per 70–78 cm^3 of soil. Similar results reported by Adams (3) for California lettuce soils ranged from zero to six total sclerotia per 100 g of soil, whereas in the same report inoculum density of *S. minor* in soils from New Jersey and New York ranged from zero to 23 and 16 to 82 sclerotia, respectively, per 100 g of soil. Adams (3) did not report the amount of lettuce drop corresponding with the inoculum density data for California and other states. Beach (5), however, reported as much as 75% drop by *S. minor* in Pennsylvania, a much higher incidence than observed in California. Inasmuch as our results indicated that lettuce drop was significantly correlated with total sclerotia (r^2 = 0.76) and competent sclerotia (r^2 = 0.80) per sampling volume (70–78 cm^3), the differences in incidence of drop probably reflect the influence of different inoculum densities in the different lettuce-growing areas. The low inoculum densities of *S. minor* sclerotia in Salinas Valley soils apparently result from the relatively short survival time. For example, results presented herein indicate that sclerotia formed on infected lettuce tissue were ephemeral and that more than 97% of the sclerotia buried at or below 5 cm were not retrievable after 4 wk. In contrast, survival time in other reports ranged from 15 mo to 11 yr (2,7,9,19).

It has been suggested that other factors, such as mycoparasites, may influence survival of sclerotia (8,10,12,13,22,25). In the Salinas Valley, *Trichoderma* spp. were the most common and effective mycoparasites isolated from retrieved sclerotia and this parasite often was observed colonizing sclerotia that had formed on infected plants in the field.

Results from this study and those reported by Abawi et al (1) agree that survival of sclerotia buried in the suppressive soil was better than in the conducive soil. The factors involved in this apparently antithetic result are not known.

Various qualitative and quantitative differences in soil microflora and soil physical properties that need further study probably influence survival times and, consequently, inoculum density and subsequent percent drop in different fields in the Salinas Valley. In general, however, despite repeated cropping each year with lettuce, most fields in the Salinas Valley have maintained relatively low incidences of drop. Thus, the Salinas Valley seems to be a unique lettuce-growing area with a relatively efficient natural biological control of lettuce drop that possibly can be enhanced when the factors involved and their interactions have been identified.

TABLE 6. Frequency of isolation of fungi from retrieved field sclerotia that failed to germinate

Genera of fungi isolated[a]	Proportion of isolates	Range of parasitism (%)[b]
Trichoderma spp.	.36	8–89
Fusarium spp.	.18	0–22
Chaetophoma spp.	.15	0–12
Penicillium spp.	.14	4–21
Mucor spp.	.04	0–22

[a] One or two isolates of *Alternaria* spp., *Torula* spp., *Trichocladium* spp., *Cylindrocarpon* spp., *Ulocladium* spp., and *Paecilomyces* spp. also were isolated from retrieved sclerotia and their parasitic ability on sclerotia ranged from 0 to 20%.

[b] Four replicates of 25 sclerotia on moist quartz sand were inoculated with spore suspension of each fungus isolate and incubated for 7 days. Water-soaked sclerotia that were soft and disintegrated were considered to have been parasitized. Figures presented for each genus represent the range of percent sclerotia parasitized by all isolates of the genus.

TABLE 7. Effect of distance of sclerotia of *Sclerotinia minor* from lettuce crowns or roots on incidence of lettuce drop[a]

Distance from plant (cm)	Depth below soil surface (cm)	No. of plants	
		Total tested	No. with drop
0	0	15	13
1	0	15	3
2	0	15	1[b]
3	0	15	3[b]
4	0	15	0
5	0	15	1[b]
0	1	15	12
0	2	15	10
0	3	15	9
0	5	15	4
Noninoculated control		15	0

[a] Plants inoculated at 8 wk of age were assessed at daily intervals for 15 days. Each treatment was replicated 15 times.

[b] Infection resulting from colonization of lower senescent leaves on soil surface.

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