Effects of Irrigation and Tillage on Temporal and Spatial Dynamics of *Sclerotinia minor* Sclerotia and Lettuce Drop Incidence

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ABSTRACT

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The temporal and spatial dynamics of *Sclerotinia minor* sclerotia and the resulting incidence of lettuce drop were studied under furrow irrigation with conventional tillage and subsurface-drip irrigation with minimum tillage during 1993–95. Lettuce crops were grown each year during the spring and fall seasons. All plants were inoculated immediately after thinning in the spring of 1993. Grids of 24 contiguous quadrats (1 by 1 m^2) were demarcated in the centers of each 150-m^2 plot. Lettuce drop incidence in each quadrat was evaluated each season prior to harvest. One soil sample (100 cm^3) was collected from each quadrat at harvest and after tillage prior to planting of the next crop for both spring and fall crops and assayed for *S. minor* sclerotia using wet sieving. Lloyd's index of patchiness, the β-binomial distribution, and variance of moving window averages were used to evaluate the spatial patterns of sclerotia and lettuce drop incidence under the two irrigation systems and associated tillage treatments. Disease incidence remained significantly higher under furrow irrigation than under subsurface-drip irrigation throughout the study period, and was significantly higher on fall crops than on spring crops. Under furrow irrigation, the number of sclerotia at the end of a crop season increased significantly over that at the beginning of the season, but no significant changes were detected over years. In contrast, the number of sclerotia within a single season did not increase significantly under subsurface drip irrigation, nor was year-to-year accumulation of sclerotia statistically significant. The degree of aggregation of sclerotia increased significantly during a cropping season under furrow irrigation, but not under subsurface drip irrigation. The conventional tillage after harvest under furrow irrigation decreased the degree of aggregation of sclerotia after each season, but the distribution pattern of sclerotia under subsurface-drip irrigation changed little by the associated minimum tillage. Spatial pattern analyses suggested that the aggregation of *S. minor* sclerotia occurred at a scale of no more than 1 m, and distribution of diseased lettuce plants was random at a scale larger than 1 m. The combination of fewer sclerotia produced by each crop and its unaltered distribution under subsurface drip irrigation and associated minimum tillage makes it a valuable cultural practice for lettuce drop management.

Lettuce drop, an important soilborne disease worldwide, is caused mainly by *Sclerotinia minor* Jagger in the central coast of California (16). Soilborne sclerotia are the most important inoculum source. Survival of sclerotia is affected by the location of sclerotia in the soil profile, duration of burial, soil moisture, and soil temperature. Although sclerotia of the related *S. sclerotiorum* have been reported to survive in soil for up to 11 years (2), sclerotia of *S. minor* disintegrate or lose viability within 8 weeks in saturated soil (12). Sclerotia of *S. minor* primarily infect lettuce by direct germination (16,18), and carpogenic germination of *S. minor* rarely has been observed in nature (10). The optimal temperature and moisture for sclerotial germination is 15°C and –0.03 MPa (9). Under optimal conditions, sclerotia germinate eruptively, producing masses of hyphae that come in contact with lettuce roots, crowns, and senescent leaves, causing soft watery root, crown, and head rot. Large numbers of sclerotia then are produced from colonized lettuce tissues and are released into the soil to serve as inoculum for the next crop (16).

Lettuce drop incidence at harvest typically is correlated with the sclerotial density in the soils at planting, and plant-to-plant spread seldom occurs within a cropping season (7). Lettuce drop incidence also is affected by the spatial distribution of sclerotia because only the sclerotia in the top 8 cm of soil and within a horizontal distance of 2 cm from lettuce crowns are capable of infection (12). Thus, not only disease incidence and the density of viable sclerotia but also the spatial patterns of diseased plants and of soilborne sclerotia in soil are of great epidemiological importance. Knowledge of spatial patterns of sclerotia can be applied to improve sampling methods and to promote a better understanding of lettuce drop epidemics that, in turn, can be used to improve the management of this disease in coastal California and elsewhere.

As with most soilborne diseases, sclerotia of *S. minor* are mostly clumped or clustered in field soil. Their distribution is greatly affected by agricultural practices, such as irrigation and tillage. Irrigation can have a major impact on lettuce drop because of its influence on soil moisture and temperature, which are critical for the germination of sclerotia and subsequent infection of lettuce (9). Several different irrigation systems currently are employed in lettuce production in coastal California. Traditionally, furrow irrigation was used because of the low cost and the ease with which it can be operated. To increase water use efficiency and decrease salt accumulation caused by furrow irrigation, growers largely adopted sprinkler irrigation in the late 1960s (23). Sprinkler irrigation offered many advantages for lettuce production, such as higher and uniform seedling emergence, more efficient water use, and higher yields (5). However, under both furrow and sprinkler irrigation systems, a large volume of soil becomes saturated, which can facilitate germination of sclerotia and increase infection of lettuce (21). Since the late 1980s, subsurface drip irrigation has been used in lettuce production not only for conservation of water but also for pest management. Subsurface drip irrigation requires about half the water needed by furrow and sprinkler systems. Although initial costs for installation of subsurface drip systems are high, once the system is in place, operating costs are low. Soil

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moisture under subsurface drip irrigation is significantly lower at all depths and distances from the bed center after an irrigation event than under furrow irrigation (21). Soil temperature, in contrast, is significantly higher at both 5 and 15 cm of depth under drip irrigation than under furrow irrigation. These factors may reduce the germination of sclerotia and result in greater disintegration of sclerotia.

A comparative study of furrow and subsurface drip irrigation effects on disease of lettuce revealed that the reduction in incidence of lettuce drop under subsurface drip irrigation was superior to that under furrow irrigation plus application of registered fungicides (21). Disease suppression under subsurface drip irrigation was not related to any changes in soil microflora (4). Subsurface drip irrigation, in addition to crop rotation, is considered a potential agricultural practice for management of lettuce drop. Thus, it is critical to determine how lettuce drop and populations of *S. minor* sclerotia will change over seasons under different irrigation systems.

Minimum tillage always is employed in fields with a subsurface drip irrigation system because drip tapes, buried at 25 cm of depth and typically remaining in place for 3 to 4 years, would be damaged by conventional tillage. Thus, to understand the long-term effects of using this irrigation practice also requires considering the influence of the associated minimum tillage. Previously, deep plowing was considered to have the beneficial effect of reducing the number of *S. minor* sclerotia in the topsoil and resulting in reduced incidence of lettuce drop in the long term (22). Although deep plowing reduces the incidence of lettuce drop immediately after plowing, subsequent tillage practices following deep plowing redistributed sclerotia of *S. minor* to areas of the field that previously were devoid of them. This resulted in significantly greater incidence of lettuce drop on the second and third crops of lettuce following deep plowing (22). Prompted by this observation, the objectives of this study were to study the temporal and spatial dynamics of *S. minor* sclerotia and lettuce drop incidence under subsurface drip irrigation system with minimum tillage, and furrow irrigation with conventional tillage. Preliminary results have been published previously (20).

MATERIALS AND METHODS

Experimental site. Field experiments were conducted in a lettuce field at the Hartnell College East Campus in Salinas, CA during 1993–95. The soil in the field is an Antioch fine sandy loam (45% sand, 32% silt, 23% clay, and 2.2% organic matter). Each year, susceptible lettuce cvs. Salinas and Misty Day were sown in the spring and fall, respectively. The seed were directly sown in two rows per bed at a rate of 3 kg ha^{-1}. During both seasons each year, plots were fertilized according to best management practices with ammonium nitrate at the rate of 160 kg of N ha^{-1} in banded, split applications. Soon after planting and before thinning, all plots were irrigated with sprinklers to promote uniform emergence of lettuce seedlings. Three weeks after emergence, seedlings were thinned to a spacing of 30 cm. Preliminary assays of soil samples collected from the experimental plots revealed that the density of resident *S. minor* sclerotia was low in this field. Therefore, to establish a uniform distribution of initial inoculum, all lettuce plants in the experimental plots were inoculated with a monosclerotial isolate of *S. minor* in the spring of 1993, 1 week after thinning as described below. Immediately after thinning, two different irrigation treatments, subsurface drip and furrow, were imposed. The treatments were arranged in a randomized complete block design with four replications (one replication of subsurface drip irrigation subsequently was abandoned because of damage to drip tapes and extensive leaking). Each plot was 25 m in length and six beds (each 1 m wide) in width. Adjacent plots were separated by one bed of 12 m in length. In plots with subsurface drip irrigation, a single drip tape (0.5-mm-thick plastic; T-Systems International, San Diego, CA), with emitters spaced 20 cm apart, was buried 25 cm below the soil surface in the middle of the raised beds prior to sowing of the first lettuce crop in spring 1993. Although conventional tillage such as soil ripping, disking, and chiseling was used in furrow-irrigated plots, minimal tillage such as shallow (top 15 cm of soil) disking and rebedding was applied in the plots with subsurface drip treatment, where the drip tapes remained in the soil throughout the duration of the study. The frequency of irrigation was determined based on evapotranspiration rates and crop coefficients for lettuce. Subsurface drip irrigation was applied twice a week from 9:00 a.m. to 3:00 p.m. at a pressure of 0.56 kg/cm^2, and the furrow irrigation was applied once a week (starting at 9:00 a.m. and stopping when the furrows were three-fourths full).

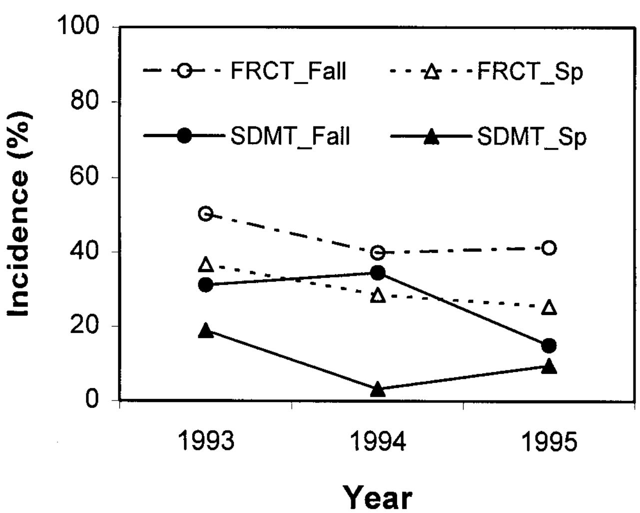

Fig. 1. Temporal dynamics of lettuce drop incidence caused by *Sclerotinia minor* in plots under subsurface drip with minimum tillage (SDMT) and furrow irrigation with conventional tillage (FRCT) during springs (Sp) and falls (Fall) of 1993 to 1995. Incidence in plots under subsurface drip in fall 1994 was unusually high because some drip tapes were damaged and released more water than usual.

Production of inoculum and inoculation. Rye seed (20 g) and 10 ml of distilled water were dispensed into 125-ml Erlenmeyer flasks and autoclaved twice at 121°C for 1 h each time. A monosclerotial isolate of *S. minor* from a commercial lettuce field in Salinas was plated on potato dextrose agar medium at 23 ± 5°C. After 2 days of incubation, two 4-mm-diameter mycelial plugs from the edge of this culture were dispensed into each of the flasks containing rye seed. The flasks were shaken to facilitate maximal colonization of rye seed by the pathogen after incubation on laboratory benches for 1 week. After 3 weeks of incubation, the rye kernels, as well as the associated mycelium and sclerotia,

TABLE 1. Analysis of variance of lettuce drop incidence (logit transformed) caused by *Sclerotinia minor* under subsurface drip and furrow irrigation with minimum and conventional tillage, respectively, on spring and fall crops during 1993–95

Effect	Numerator df	Denominator df	*F* value	*P* > *F*
Treatment[a]	1	28.0	64.48	<0.001
Year[b]	2	27.1	8.89	0.001
Year–treatment	2	27.1	1.13	0.339
Crop[c]	1	27.1	38.45	<0.001
Crop–treatment	1	27.1	3.8	0.062
Year–crop	2	27.1	3.76	0.036
Year–crop–treatment	2	27.1	4.66	0.018

[a] Treatments included furrow irrigation with conventional tillage and subsurface drip irrigation with minimum tillage.
[b] 1993, 1994, and 1995.
[c] Spring and fall crops each year.

were used as inoculum. One week after thinning in the spring of 1993, one *S. minor*-infested rye kernel was placed on the soil surface at 5 mm from the crown of each lettuce plant.

Data collection. At harvest of each spring and fall crop, an area 6 m long and four beds wide was demarcated in the center of each plot for collecting disease and pathogen propagule data. Within this area, grids of 24 (4 by 6) contiguous quadrats (1 by 1 m^2) were demarcated. The total number of plants and the number of plants showing lettuce drop symptoms were counted in each of the 24 quadrats, and disease incidence was calculated (except for the spring crop in 1993, when only an overall incidence was calculated for each plot). One 100-cm^3 soil sample was collected from each quadrat at harvest and after tillage (before sowing of the next crop) using a custom-designed soil auger during the 1993, 1994, and 1995 spring and fall crop seasons. Soil samples were assayed for sclerotia of *S. minor* using the wet sieving method (19). After enumerating the sclerotia, they also were tested for germination on water agar (19).

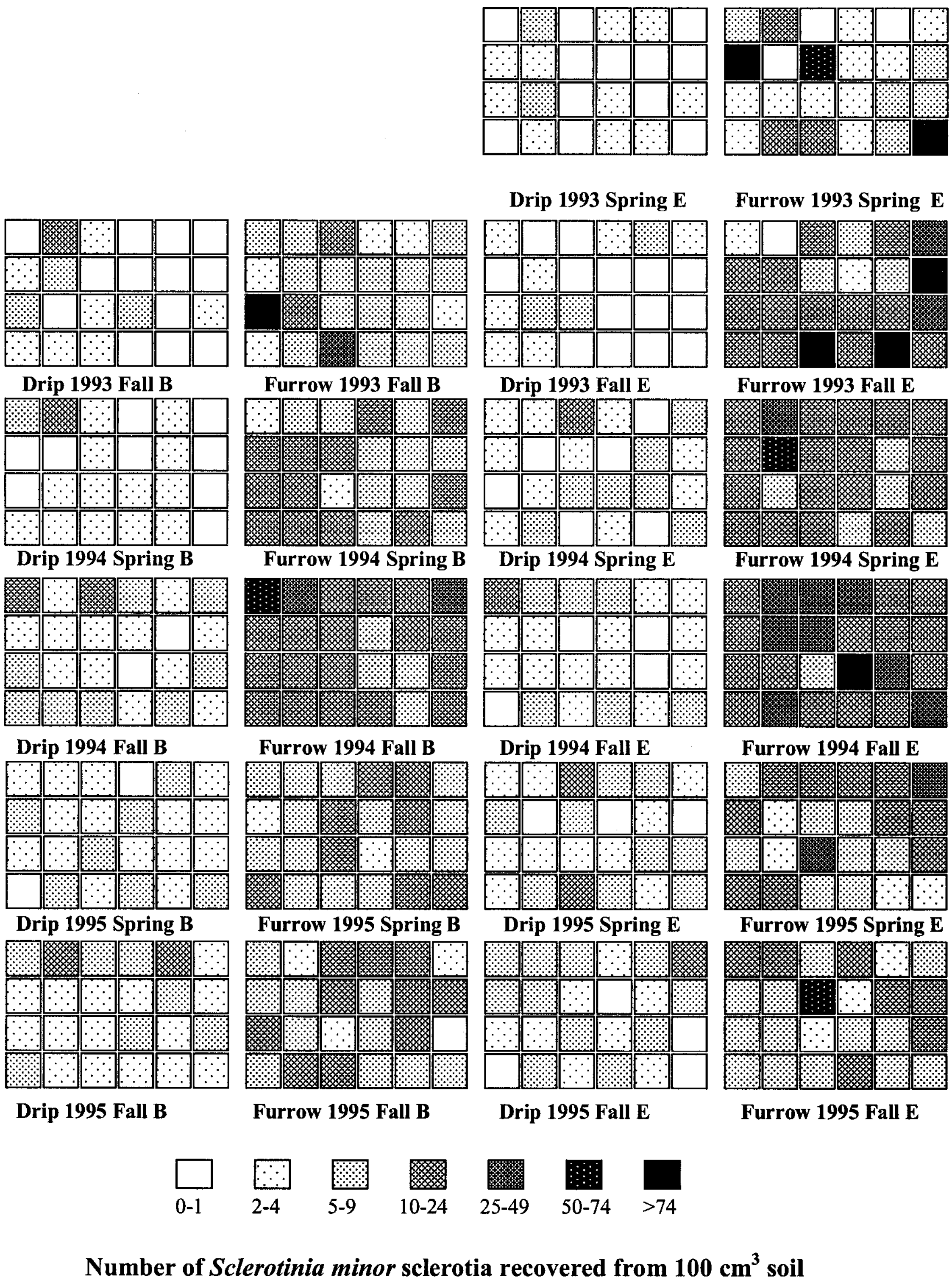

Fig. 2. Distribution of sclerotia of *Sclerotinia minor* in plots under subsurface drip with minimum tillage and furrow irrigation with conventional tillage during 1993 to 1995. Each square represents the data collected from a 1-by-1-m^2 quadrat at the beginning (B) and end of the seasons (E). Soil samples drawn from each quadrat were assayed for *S. minor* sclerotia by wet sieving. Data from all replications were similar; hence, data from only one replication is depicted.

Data analysis. To normalize the variances, disease incidence and number of sclerotia first were transformed using logit and natural log functions, respectively. Analysis of variance was conducted using a generalized, linear mixed model in SAS (release 8.0; SAS institute Inc., Cary, NC). Year, crop season, and sampling time were considered as subplot factors, while treatment was considered as main plot factor. For disease incidence, treatment, year, crop season, and their interactions were considered as fixed, while block, block–treatment, and block–treatment–year were considered as random. For the number of sclerotia, sampling time (beginning of crop season or at harvest) and its interaction with the other factors also were considered fixed, while interaction of block–treatment–year–crop season was taken as random, in addition to the random effects used in analysis of incidence. Spatial distribution maps were generated for disease incidence and sclerotial population in each plot. Lloyd's index of patchiness (LIP) was calculated for the distribution of sclerotia in each plot (13). Paired t tests were used to compare the LIP values before and after tillage in the same plots. The plots under the two irrigation systems were analyzed separately, and effects of crop and season were ignored. The same tests were used to determine the changes in spatial distribution of sclerotia from planting to the end of the crop season. Because LIP is not suitable for disease incidence data, the β-binomial distribution (BBD) was used to characterize the spatial pattern of lettuce drop incidence (11,14). Furthermore, a method based on variance of moving window averages (VMWA) also was used to assess the spatial distribution of disease incidence and number of sclerotia in each plot (6; B. M. Wu, K. V. Subbarao, F. J. Ferrandino, and J. J. Hao, *unpublished data*). The method determines an aggregation index at different lag distances based on the change in variance of the new data sets that are derived by moving a window and averaging data from different window sizes. A positive, zero, and negative index indicates a positive, weak, and negative association (aggregated, random, and dispersed distribution), respectively. In the analysis, the VMWA indices at lag distance 1 (1 m) were compared with LIP (number of sclerotia) or dispersion of BBD (disease incidence). The relationship between incidence of lettuce drop in each quadrat during each crop season and the density of *S. minor* sclerotia at the beginning of that season in the same quadrat was analyzed using the linear regression procedure in SAS (release 8.0l SAS Institute Inc.). Similarly, the density of sclerotia at the end of a season also was related to incidence of lettuce drop in the same crop season by linear regression analysis.

RESULTS

Disease incidence. Although a uniform distribution of sclerotia was established in all plots during spring 1993, lettuce drop incidence in plots under furrow irrigation was significantly higher than in plots under subsurface drip irrigation by the end of the season (Fig. 1). During the subsequent crop seasons, incidence of lettuce drop decreased and remained lower in plots under drip irrigation, whereas disease incidence in plots under furrow irrigation remained at higher over all seasons (Fig. 1). Analysis of variance revealed significant differences in lettuce drop incidence among treatments, years, and crop seasons (Table 1). Regardless of the irrigation system, fall crops showed significantly higher disease incidence than spring crops (Table 1; Fig. 1). In addition, overall incidence of lettuce drop tended to decrease (significant

TABLE 2. Analysis of variance on the number of *Sclerotinia minor* sclerotia (log-transformed) recovered from 100 cm^3 of soil under subsurface drip and furrow irrigation with minimum and conventional tillage, respectively

Effect	Numerator df	Denominator df	F value	$P > F$
Treatment[a]	1	10.6	21.02	0.001
Year[b]	2	10.1	4.48	0.040
Year–treatment	2	10.1	1.66	0.238
Crop[c]	1	11.9	2.61	0.132
Crop–treatment	1	11.9	0.59	0.457
Year–crop	2	12.4	0.72	0.504
Year–crop–treatment	2	12.4	3.05	0.083
Time[d]	1	22.8	61.40	<0.001
Time–treatment	1	22.8	36.74	<0.001
Year–time	2	22.8	7.58	0.003
Year–time–treatment	2	22.8	11.91	0.000
Crop–time	1	22.7	14.04	0.001
Crop–time–treatment	1	22.7	0.08	0.776
Year–crop–time	1	22.7	10.64	0.004
Year–crop–time–treatment	1	22.7	1.21	0.283

[a] Treatments included furrow irrigation with conventional tillage and subsurface drip irrigation with minimum tillage.
[b] 1993, 1994, and 1995.
[c] Spring and fall crops each year.
[d] Samples were collected at the beginning of a season (post tillage, before sowing) and at harvest.

TABLE 3. Analysis of variance on the number of *Sclerotinia minor* sclerotia recovered from 100 cm^3 of soil under subsurface drip and furrow irrigation with minimum and conventional tillage, respectively

	Furrow				Subsurface drip			
Effect	Numerator df	Denominator df	F	$P > F$	Numerator df	Denominator df	F	$P > F$
Year[a]	2	4.5	2.09	0.227	2	4.1	3.12	0.151
Crop[b]	1	6.3	2.61	0.155	1	5.8	0.45	0.530
Year–crop	2	6.6	1.11	0.385	2	6.0	3.25	0.111
Time[c]	1	13.4	76.89	<0.001	1	9.6	3.22	0.104
Year–time	2	13.4	14.76	<0.001	2	9.6	0.62	0.558
Crop–time	1	13.3	6.83	0.021	1	9.6	11.73	0.007
Year–crop–time	1	13.3	7.97	0.014	1	9.6	4.58	0.059

[a] 1993, 1994, and 1995.
[b] Spring and fall lettuce crops each year.
[c] Samples were collected at the beginning of a season (post tillage, before sowing) and at harvest.

difference among years) during the 3-year study period (Table 1; Fig. 1), except that the incidence in plots under subsurface drip was higher in the fall of 1994 than in the fall of 1993, likely due to the leakage of drip tapes.

Number of sclerotia. As with disease incidence, the density of sclerotia in plots under furrow irrigation was significantly higher than in plots under subsurface drip irrigation, while difference between sampling times (at the beginning or at the end of the growing season) and among years from 1993 to 1995 also were significant (Fig. 2; Table 2). The number of sclerotia increased significantly from the beginning of a crop season (after tillage) to the end of the season in plots under furrow irrigation (significant effects of sampling time), but accumulation of sclerotia over the 3 years was not significant under furrow irrigation (Table 3; Fig. 3A). Under drip irrigation with minimum tillage, in contrast, the density of sclerotia did not increase significantly within a cropping season, nor was the increase among years statistically significant (Table 3; Fig. 3A). When numbers of sclerotia at different sample times were analyzed separately, the inoculum level at the beginning of the fall crops was significantly higher than at the beginning of the spring crops, despite the lack of significant seasonal effects on the numbers of sclerotia at harvest (Table 4). The number of sclerotia showed a significant difference among years at the beginning of the season but not at harvest (Table 4). The numbers of sclerotia at the beginning of the season (post tillage) and at harvest both were affected significantly by the irrigation systems (Table 4), but the difference was slightly smaller at the beginning of crop season. This was, perhaps, because of the redistribution of sclerotia by conventional tillage associated with furrow irrigation, as indicated by the significant interaction of treatment–sampling time (Table 2). Under subsurface drip irrigation, the number of sclerotia at the beginning of a season was highly related to that at the end of the preceding crop season, and the number of sclerotia at the end of a crop season was also highly correlated with the number at the beginning of a crop season (Table 5). In contrast, under furrow irrigation, the number of sclerotia at the beginning of a season was not significantly related to the number of sclerotia at the end of the preceding crop season, even though a significant (but weaker than under subsurface drip) correlation between the number of sclerotia at the beginning of a crop season and the end of a season was observed (Table 5). The percent change (presumed to reflect the survival of sclerotia) in the number of sclerotia between the two successive crop seasons was higher under subsurface drip irrigation than under furrow irrigation, but the change in the number of sclerotia within a crop season was lower under subsurface drip irrigation than under furrow irrigation (Fig. 3B).

Spatial distribution of lettuce drop. As determined by BBD, the spatial distribution of diseased plants showed significant ($P < 0.05$) aggregation in 8 of 35 cases (five seasons by seven plots) (data not shown). The degree of aggregation measured by the index of dispersion (D) (Fig. 4A) from the BBD analysis did not differ significantly between treatments, but increased over the study period with a slope significantly differing from zero ($P < 0.05$) when combined. In contrast, the spatial patterns determined by the VMWA index at lag distance 1 (separated by 1 m) varied dramatically from plot to plot (showing large standard errors) and exhibited uniform (negative index), random (index = 0), and aggregated (positive index) distributions (Fig. 4B). Despite the in-

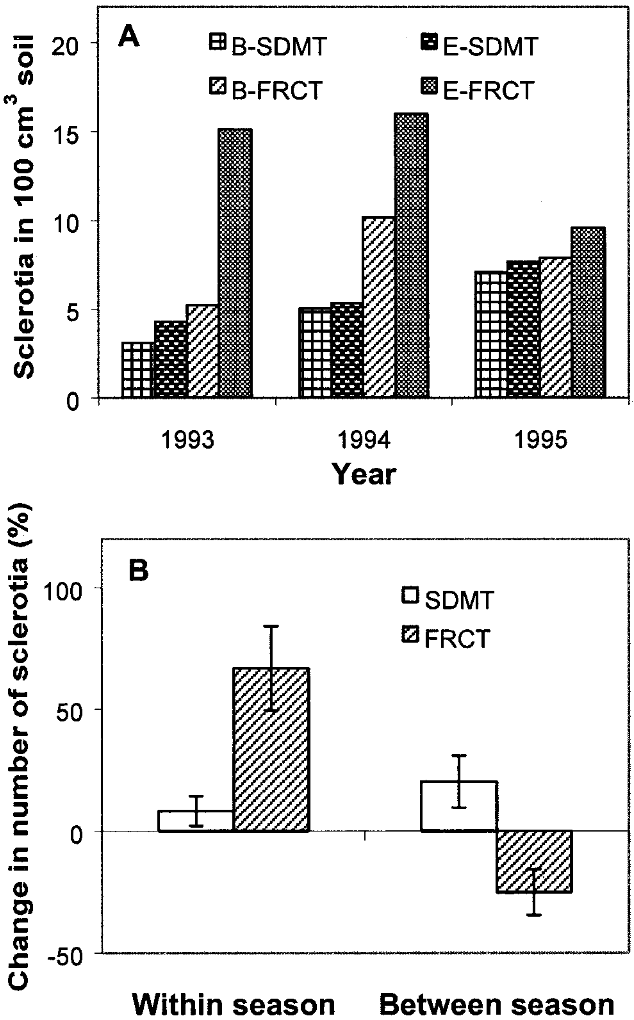

Fig. 3. A, Number of sclerotia of *Sclerotinia minor* under subsurface drip and furrow irrigation at planting (B-SDMT and B-FRCT) and at the end of cropping season (E-SDMT and E-FRCT) during 1993 to 1995, and **B,** percent change in the numbers of sclerotia within a cropping season and between two consecutive seasons under the two irrigation systems. Data points were averaged over all replications and years and the vertical bars represent the standard errors of the means.

TABLE 4. Analysis of variance on the number of *Sclerotinia minor* sclerotia recovered from 100 cm^3 of soil at the beginning and at the end of spring and fall lettuce crops under subsurface drip and furrow irrigation with minimum and conventional tillage, respectively, during 1993–95

	At harvest				Beginning of season			
Effect	Numerator df	Denominator df	*F*	*P* > *F*	Numerator df	Denominator df	*F*	*P* > *F*
Treatment[a]	1	10.7	34.99	<0.001	1	11.5	8.49	0.014
Year[b]	2	10.1	2.39	0.142	2	11.2	15.24	0.001
Year–treatment	2	10.1	3.20	0.084	2	11.2	1.14	0.354
Crop[c]	1	12.4	0.12	0.730	1	9.5	63.75	<0.001
Crop–treatment	1	12.4	0.95	0.348	1	9.5	1.61	0.235
Crop–year	2	12.4	0.03	0.966	1	9.5	38.83	<0.001
Year–crop–treatment	2	12.4	2.60	0.114	1	9.5	0.01	0.915

[a] Treatments included subsurface drip with minimum tillage or furrow with conventional tillage.
[b] 1993, 1994, and 1995.
[c] Spring and fall lettuce crops each year.

herent differences in the incidence of lettuce drop between the two irrigation systems, there was no consistent difference in VMWA indexes of diseased plants between the two irrigation systems, nor was there any consistent trend in the indexes over crop seasons during the study period (Fig. 4B).

Spatial distribution of sclerotia. Although the plants were inoculated uniformly during the spring 1993 crop (the first season), at the end of the crop season, LIP values indicated that sclerotia were highly aggregated under both subsurface drip and furrow irrigation systems (Fig. 5A). Nevertheless, aggregation of sclerotia, as measured by LIP, decreased dramatically at subsequent sampling times and remained low throughout the study period under subsurface drip irrigation (Fig. 5A). Aggregation of sclerotia in plots under furrow irrigation, however, was more dependent on the sampling time. Sclerotia were less aggregated at the beginning of a season and aggregation increased at the end of a season, followed by less aggregation at the beginning of subsequent seasons. As the experiment progressed, LIP values both at the beginning and end of seasons tended to decrease over the study period (Fig. 5A). Paired *t* tests revealed that LIP for the number of sclerotia increased significantly within crop seasons under furrow irrigation but not under subsurface drip irrigation (Table 6). The tests also showed a significant decrease of LIP from the end of a season to the beginning of the next season (post

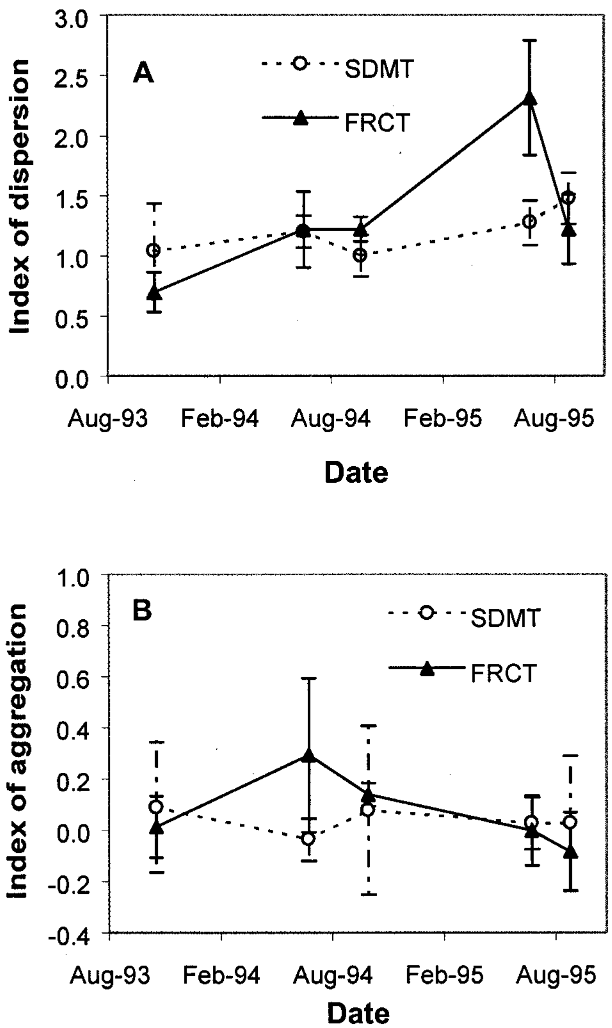

Fig. 4. Aggregation of incidence of lettuce drop-infected plants under subsurface drip with minimum tillage (SDMT) and furrow irrigation with conventional tillage (FRCT) during spring 1993 to fall 1995 calculated using **A,** β-binomial distribution method (showing index of dispersion), and **B,** the variance of moving window averages method (showing aggregation index at lag distance 1). The vertical bars represent the standard errors of the mean among plots.

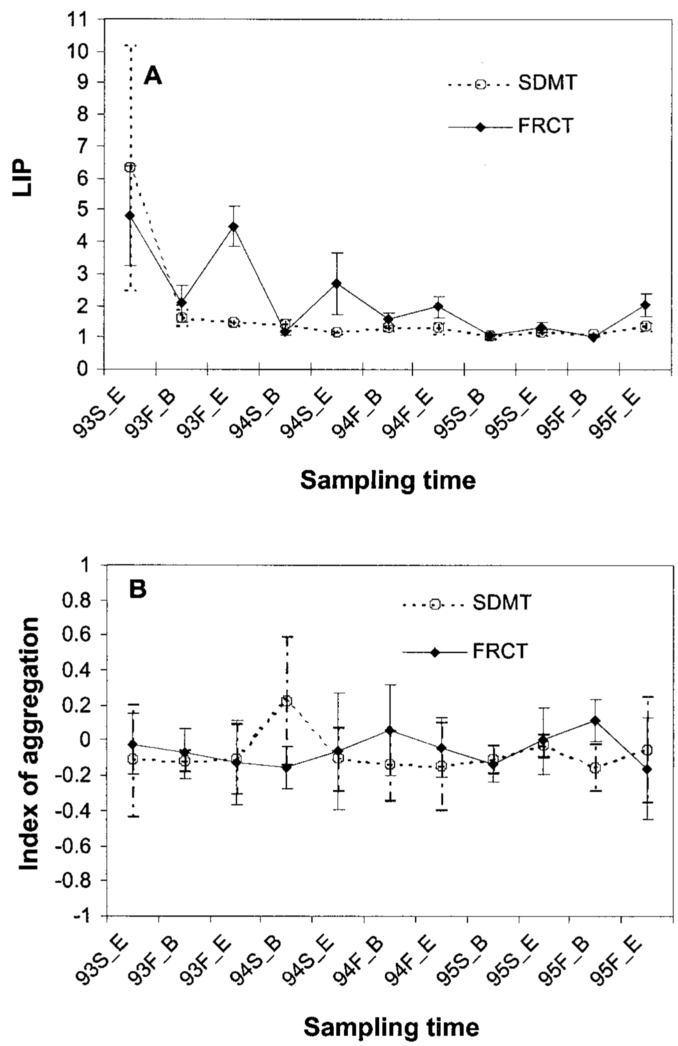

Fig. 5. Aggregation of *Sclerotinia minor* sclerotia under subsurface drip with minimum tillage (SDMT) and furrow irrigation with conventional tillage (FRCT) calculated using **A,** Lloyd's index of patchiness (LIP), and **B,** the variance of moving window averages method (showing the aggregation index at lag distance 1). The horizontal axis indicated the sample times during 1993–95 (B = beginning, E = end of crop season, S = spring, and F = fall). The vertical bars represent the standard errors of the mean among plots.

TABLE 5. Regression analysis on the changes in the number of sclerotia of *Sclerotinia minor* within a crop (from the beginning of a crop season to the end of the season) and between crops (from the end of a crop season to the beginning of the subsequent season) under subsurface drip with minimum tillage (SDMT) or furrow irrigation with conventional tillage (FRCT) during 1993–95

Regression	Treatment	Equation	r^2	n[a]	P
Within crop	SDMT	$y = 0.959x + 0.526$	0.94	15	<0.001
Within crop	FRCT	$y = 1.044x + 4.084$	0.37	20	0.006
Between drops	SDMT	$y = 1.011x + 0.742$	0.70	12	<0.001
Between crops	FRCT	$y = 0.062x + 8.077$	0.03	16	0.499

[a] Within crop: $n = 5 \times$ number of plots; between crop: $n = 4 \times$ number of plots.

tillage), reflecting the significant influence of conventional tillage on LIP.

As with disease incidence, the aggregation index determined using the VMWA method did not exhibit any consistent trend over the study period or between different irrigation systems (Fig. 5B). The number of sclerotia showed aggregated, random, and uniform distributions in plots under both irrigation systems, and varied considerably among plots and seasons.

Relationship between the number of sclerotia and incidence of lettuce drop. Under both irrigation systems, incidence of lettuce drop was closely related to the number of sclerotia at the beginning of the season for the spring crops, but not for the fall crops (Table 7). The incidence resulting from same numbers of sclerotia (reflected by the slope of the regression equation I) was much higher under furrow irrigation than under subsurface drip irrigation (Table 7). In contrast, the number of sclerotia at the end of seasons was related to the incidence of lettuce drop only for fall crops, but not for spring crops (Table 7). Similarly, the number of sclerotia produced per diseased plant (reflected by the slope of the regression equation II) also was higher under furrow irrigation than under subsurface drip irrigation (Table 7).

DISCUSSION

Lettuce drop epidemics differed significantly under the two irrigation systems studied. Under furrow irrigation and associated conventional tillage, even low sclerotial densities at the beginning of the season led to a very high incidence of lettuce drop. In contrast, under subsurface drip irrigation and associated minimum tillage, no lettuce drop was observed in some plots even when the inoculum was present. Subsurface drip irrigation with minimum tillage significantly reduced the incidence of lettuce drop compared with furrow irrigation. The lower lettuce drop incidence under subsurface drip irrigation compared with furrow irrigation presumably is the result of the combined effects of lower density of sclerotia in soil and the lower moisture at the different soil profiles under this system (21). Although there was a relatively constant (not statistically significant) year-to-year increase in density of sclerotia under subsurface drip irrigation, the density of sclerotia remained significantly lower than under furrow irrigation throughout the study period. The significantly smaller increase in the density of sclerotia within a season under subsurface drip irrigation presumably was the result of fewer diseased plants and fewer numbers of sclerotia formed on these infected plants. At similar inoculum densities, fewer plants became infected by *S. minor* in plots under subsurface drip irrigation than in plots under furrow irrigation, suggesting that subsurface drip most likely limited the eruptive germination of sclerotia and prevented infection of lettuce. Under subsurface drip irrigation, soil moisture in the top 5 cm throughout the bed surface is significantly lower than under furrow irrigation, which not only prevents germination of *S. minor* sclerotia and limits infection of lettuce, but also prevents the formation of a large number of sclerotia on infected tissues (21).

One interesting finding from this study was a relatively stable year-to-year accumulation of sclerotia under the subsurface drip irrigation system but not under the furrow irrigation system. Under the furrow irrigation system, even though the number of sclerotia increased significantly within a crop season, increases were not sustained over the years. On average, there was a 25% reduction in the number of sclerotia from the end of a season to the beginning of the subsequent season. Two factors may have been responsible for this. First, the conventional tillage under this irrigation system redistributed the sclerotia both horizontally and vertically, resulting in a dilution of the numbers of sclerotia added after an infected lettuce crop in the upper soil profile. This also explains the weak correlation between the densities of sclerotia in two consecutive crop seasons. Second, the between-season survival of sclerotia was likely low and even lower from the end of a fall crop to the beginning of the subsequent spring crop. This period is much longer than from the end of the spring crop to the fall crop, and coincides with the onset of the rainy season in coastal California. One possible explanation for the lower survival of sclerotia under furrow irrigation may be the increased microbial degradation of sclerotia in soil. In the top 5 cm of soil, high water potential of >–0.1 MPa occurred only in a very small area close to the bed center (where the drip tape is located) under subsurface drip irrigation, whereas the whole bed showed high water potential under furrow irrigation (21). Higher soil moisture under furrow irrigation may increase the microbial degradation of sclerotia of *S. minor* (3). Greater numbers of sclerotia of *S. minor* were infected by *Sporidesmium sclerotivorum* at higher water potentials, but colonization and infection of sclerotia were limited when water potential was lower than –3 MPa (3). Abawi et al. (1) also found that survival of sclerotia of *S. minor* was reduced in a

TABLE 6. Paired *t* test on the Lloyd's index of patchiness (LIP) for the number of *Sclerotinia minor* sclerotia recovered from soil before tillage (BT) versus post tillage (PT), and at the beginning of a crop season (BOS) versus at the end of the crop season (EOS), for spring and fall lettuce crops during 1993–95

Treatment[a]	Comparison	*n*	*t*	$P > t$
FRCT	BOS vs. EOS	19[b]	3.48	0.003
FRCT	BT vs. PT	19[b]	4.06	<0.001
SDMT	BOS vs. EOS	15	0.08	0.934
SDMT	BT vs. PT	15	1.16	0.267

[a] FRCT = furrow irrigation with conventional tillage, and SDMT = subsurface drip with minimum tillage.
[b] LIP in one plot was not included in the analysis because it was influenced by the unusually high number of sclerotia in one quadrat.

TABLE 7. Relationship between lettuce drop disease incidence (DI) and the number of *Sclerotinia minor* sclerotia at the beginning and end of season under furrow and subsurface drip irrigation systems during springs and fall seasons, 1993–95

Regression[a]	Treatment[b]	*n*[c]	Slope	Intercept	$P > F$
DI versus BOS					
Spring	Subsurface drip	144	0.518	3.786	0.007
	Furrow	192	1.322	17.587	0.001
Fall	Subsurface drip	216	0.466	24.439	0.138
	Furrow	288	0.156	41.892	0.318
EOS versus DI					
Spring	Subsurface drip	144	0.016	5.958	0.715
	Furrow	192	0.071	10.848	0.224
Fall	Subsurface drip	216	0.048	4.287	0.004
	Furrow	288	0.200	6.197	0.013

[a] BOS = number of sclerotia at the beginning of season and EOS = number of sclerotia at the end of season.
[b] Minimum and conventional tillage was practiced under subsurface drip and furrow irrigation, respectively.
[c] The quadrats in plots under the same treatments during 1993–95 were considered replications. Data were not available for spring 1993, and there were three and four plots under subsurface drip and furrow irrigation, respectively, during each crop season.

moistened soil compared with dry soils, and they attributed the decline to the biological activity of *Trichoderma* spp. In contrast, under the subsurface drip irrigation system with minimum tillage, more sclerotia could survive between seasons, and most remain in the top soil profile of the bed (where soil samples were collected), resulting in a stronger correlation between the density at the end of a season and the density at the beginning of the next season.

Regardless of the irrigation-tillage system, fall crops showed significantly higher disease incidence than spring crops throughout the study period. One likely explanation may be the significantly higher sclerotial density at the beginning of the crop seasons than at the beginning of spring crop seasons, which may have resulted from better sclerotium survival from spring crops to fall crops than from fall crops to the next spring crops, as discussed above. Other less likely causes include the more conducive conditions (alternative wet and dry cycles of the soil that encourages infection by *S. minor*) (16) during the fall season (ending between September and November) than during spring season (ending in July). Although cultivar differences between the two seasons potentially could be responsible for this seasonal difference in disease incidence, all currently available commercial cultivars are uniformly susceptible to *S. minor* (17). Hence, the cultivar difference is unlikely to have been the cause of this differential disease incidence between the two seasons.

Sclerotia of *S. minor* exhibited aggregation under both subsurface drip and furrow irrigation systems when it was measured by LIP, but not according to the VMWA method. This might have been due to the different bases of the two methods. Calculation of LIP is based on the distribution of the numbers of sclerotia at sample sites, which classifies the distribution as aggregated when occurrence of one sclerotium increases the occurrence of other sclerotia within the same sample unit. The VMWA method, however, is based on the relationship between the neighboring sample sites, which identifies an aggregation if the two nearby sample sites tend to have similar density of sclerotia (6). Combination of conclusions from the two methods suggested that the aggregation of sclerotia was limited to a small area within a sample unit, or less than one lag distance (1 m). The small-scale aggregation of sclerotia might have resulted from the aggregation of sclerotia produced by a diseased plant, as evidenced by the increase in aggregation from the beginning of a season to the end of the season. Therefore, the degree of aggregation of *S. minor* sclerotia was positively related to the mean number of sclerotia in the soil (22). The aggregation within a limited scale was consistent with the results obtained by Dillard and Grogan (7), who found that the distribution of sclerotia of *S. minor* in soil was aggregated when measured by variance to mean ratio. Disease incidence, determined by BBD, was aggregated in some plots that most likely resulted from the aggregated distribution of sclerotia. The result on disease incidence using the method based on VMWA was very similar to the previous results from ordinary runs analysis (7). Together, these results not only indicated insignificant plant-to-plant spread but also provided convincing evidence for the aggregation of sclerotia and the subsequent aggregation of infected lettuce plants on a small scale.

Paired *t* tests of LIP revealed that the degree of aggregation of sclerotia decreased significantly following a conventional tillage under furrow irrigation, but remained nearly the same after minimum tillage under drip irrigation. The results suggested that conventional tillage can redistribute the sclerotia by moving large amounts of soil and render the distribution of soilborne inoculum more uniform or random. Research on other pathosystems yielded similar results on the effects of conventional tillage on the distribution of pathogens (8,15). Olanya and Campbell (15) found that the aggregation of propagules of *Macrophomina phaseolina* decreased after one tillage operation, and this was most apparent when inoculum density and degree of aggregation were high. Gavassoni et al. (8) reported that a no-till system promoted aggregation of the *Heterodera glycines* population in soybean fields, whereas a conventional system reduced the degree of aggregation. This also was consistent with a previous study on deep plowing, in which deep plowing was found to reduce the aggregation of *S. minor* sclerotia in soil significantly (22).

In summary, the smaller increases in sclerotial density after each lettuce crop, the restricted movement of inoculum under the minimum tillage practiced with subsurface drip irrigation, and the concomitantly lower lettuce drop incidence offer a sustainable alternative for the management of the disease. Furthermore, subsurface drip irrigation also reduced the severity of corky root of lettuce (21), making it an even more attractive strategy for soilborne disease management in lettuce.

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