Septoria Leaf Spot Lesion Density on Trap Plants Exposed at Varying Distances from Infected Tomatoes

Francis J. Ferrandino, Associate Scientist, and **Wade H. Elmer,** Associate Plant Pathologist, Connecticut Agricultural Experiment Station, P.O. Box 1106, New Haven 06504

ABSTRACT

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Twelve trap plant experiments were conducted over 6 years to examine the spatial dispersal of conidia of *Septoria lycopersici* (causal agent of Septoria leaf spot) during and immediately following rain events. The leaf area of each trap plant was determined before exposure. Trap plants were placed out in the field for 1 to 5 days at perpendicular distances of 0.5 to 106 m from rows (29 to 67 m long) of inoculated tomato plants (*Lycopersicon esculentum).* Trap plants were retrieved and then incubated for 10 to 14 days in a greenhouse. Septoria leaf spot lesions were then counted, and disease severity was expressed as the number of lesions per unit leaf area (lesions/m^2). Disease severity was high (10^3 to 10^6 lesions/m^2) within a meter of the source and low (10 to 10^3 lesions/m^2), but detectable at distances of up to 106 m from the line source. The logarithm of the resulting disease severity on trap plants was found to be well correlated (r^2 = 0.59 to 0.98, df = 10 to 30) with the logarithm of distance from the line source, suggesting a dispersal function described by an inverse power law of distance. The observed transport at long distance suggests that at least some conidia are carried in very small rain droplets or secondary splash droplets. This long-range dispersal of spores may have a major impact on the epidemiology of this disease.

Septoria leaf spot of tomato (*Lycopersicon esculentum* Mill.) caused by *Septoria lycopersici* Speg. is a common late season disease in the northeastern U.S. The disease can result in serious defoliation during periods of cool wet weather and can cause up to a 50% reduction in fruit yield (16). The fungus primarily infects leaves, although stems, fruiting bracts, and the calyx can also be affected. After a latent period of 5 to 10 days, infection results in small (2 to 5 mm diameter) translucent lesions that darken as the plant tissue becomes necrotic. Spore-bearing pycnidia are formed within these lesions 2 to 4 days later. Water is required in the infection cycle to hydrate the pycnidia, force the cirrhus of spores out of the ostiole of the pycnidium, and dissolve away the mucilaginous matrix in the pycnidium (8,21). Fungi, such as *S. lycopersici*, that release spores within a surrounding mucilage are usually assumed to be carried in rain-splash droplets. Parker et al. (29) demonstrated rain splash dispersal for this pathogen up to 1.8 m from a source with steeply decreasing infection with increasing distance. Splash-dispersal is a common mechanism among plant pathogenic fungi, but is thought to be limited to transport distances of only a few meters (17).

The velocity of spread of a plant disease epidemic is extremely sensitive to the spatial distribution of dispersed propagules about a focus of disease (26). For splash-dispersed pathogens the form of the dispersal function is usually assumed to be given by a negative exponential function of distance (19,20,24,25). On the other hand, wind-borne spores travel farther, and dispersal has been better described by an inverse power law of distance (5,19,22,28), as well as by more complicated mathematical expressions (1,9,13,15,32,36–39).

The pertinent distance scale over which inoculum transport must be known is approximately given by the product of the observed velocity of disease spread and the mean time between generations of the pathogen. Measured disease velocities range from 0.2 to 4 m $days^{-1}$ (23). Assuming 10 days as a reasonable time between spore generations, then the mathematical description of such epidemics would require a knowledge of spore dispersal over a distance range of 2 to 40 m, depending on the pathogen. With the exception of two studies that measured spore dispersal beyond 5 m (19,31), most determinations of the spatial contact distribution have been limited to distances within a few meters of the inoculum source (1,2,4,6,7, 22,28,38). However, the overall shape of the contact distribution or, more precisely, the proportion of spores that travel great distances may play a large role in determining the velocity of disease spread (15) and can be critical to the nature of the ensuing epidemic (11,15,34) as well as the resulting impact of disease on final yield (14).

Our objective was to use trap plants to determine the dispersal of Septoria leaf spot inoculum over a large range of distance. This paper describes the results of a series of tomato trap plant experiments in which trap plants were exposed for 20 to 120 h at varying perpendicular distances (0.5 to 106 m) from rows (length between 29 and 67 m) of tomato plants infected with Septoria leaf spot.

MATERIALS AND METHODS

Tomato seeds (*Lycopersicon esculentum* Mill. 'Better Boy') were sown into 36-cell plastic trays filled with potting mix (Promix BX, Premier Brand, New Rochelle, NY) and germinated in the greenhouse (18 to 30°C). After 2 weeks, seedlings that had one true leaf were thinned to one plant per cell and fertilized with 40 ml of Peter's 20-8-16 soluble N-P-K (5 g/liter). Two weeks later, seedlings were transplanted into 1-liter plastic pots filled with Promix BX and grown for an additional month. Plants in the larger pots received approximately 100 ml of Peter's 20-8-16 soluble N-P-K (10 g/liter) solution weekly. Two-month-old seedlings 25 to 30 cm tall with 10 to 13 nodes were moved to a cold frame to acclimate for 1 week to outdoor conditions and then transplanted into the field on 21 May 1989, 5 June 1990, 26 June 1991, 4 June 1992, 11 June 1993, and 7 June 1994. Tomatoes were grown in single file rows from 30 to 67 m long at a spacing of 0.9 m mulched with 4 mil black plastic. In 1989, 1991, 1992, and 1993 plants were left unpruned and unsupported. In 1990 and 1994 plants were staked and pruned to two stems. Plots were treated with 10-10-10 (N-P-K fertilizer) at a rate of 1,120 kg ha^{-1} at planting, and an additional 500 kg ha^{-1} was applied in mid July, when the first fruit were about 3 cm in diameter. Dried tomato vine residues that were colonized by *S. lycopersici* and collected the previous year were crushed, and a total of 200 to 300 g was spread evenly around and on the leaves of the plants in these source plots on 2 July 1989, 24 June 1990, 6 July 1991, 3 August 1992, and 17 July 1994. The inoculated plants were covered with two layers of tobacco shade cloth and received daily overhead

Corresponding author: Francis J. Ferrandino
E-mail: fjferr@caes.state.ct.us

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irrigation (0.5 cm per day) for a period of 2 weeks. In 1993, plants were not artificially inoculated and disease occurred naturally. The source row of infected tomato plants was moved each year and was oriented along an east-west line in 1989 and 1993, and along a north-south line in 1990, 1991, 1992, and 1994. Trap plants were always placed out on land not previously (within 20 years) planted to tomatoes.

Additional monthly sowings of tomato were made each season to generate a continuous supply of trap plants. These plants were grown for 5 to 7 weeks in the greenhouse and then held in a lath house 500 m from the source row until needed. When disease had spread throughout the source row, disease severity was estimated by assaying between 15 and 30 randomly chosen stems. Trap plant leaf area, A_L, was estimated by measuring leaf length along the midrib, L (distance from first true leaflet to the distal end of the terminal leaflet), and maximum width, W, using the following relation: $A_L = 0.45\ L \times W$ obtained by linear regression ($r^2 = 0.97$, df = 112) (16). Plants were exposed in the field for 20 to 120 h during rain starting on 29 August 1989, 15 September 1989, 24 August 1990, 14 September 1991, 25 September 1992, 9 October 1992, 16 September 1993, 27 September 1994, and 16 October 1994. Plants were placed at perpendicular distances of between 0.5 and 100 m from the source row. In addition, 6 to 15 trap plants were placed out at least 500 m from any tomato planting during each experiment to assess the background exposure to inoculum from ambient sources. During exposure all farm equipment and personnel were kept out of the field. All exposed plants were then incubated in a greenhouse (18 to 23°C) for 10 to 15 days, after which the number of lesions on each individual leaflet was counted. Since leaf age can affect lesion development (12,21), the youngest and the oldest leaves on each plant were excluded in the assessment of disease severity.

Lesion counts and leaf area estimation were used to calculate mean lesion density ($S(x)$: lesions m^{-2}), a measure of disease severity, for each plant (total plant leaf area was between 0.05 and 0.08 m^2) that was placed at a perpendicular distance x (m) from the line source. The resulting data were analyzed by performing linear regression analyses in which the dependent variable was $\ln(S)$. The independent variable was either $\ln(x)$ or x, which correspond to contact distributions given by inverse power law or exponential functions of distance, respectively. The validity of the above linear models was tested by an examination of the behavior of the residuals.

In order to estimate the strength of the source row, 20 to 30 stems were assayed for Septoria leaf spot lesions and leaf area was estimated. Lesion counts and leaf area estimation were used to calculate mean lesion density per meter of source row, S_S (lesion m^{-1}). Rainfall amount, RA_B, and duration, RD_B, for the 24-h period before trap plants were placed out in the field, as well, as the rainfall amount, RA_D, and duration, RD_D, during plant exposure were monitored. Possible relations between measured source properties, meteorological variables and fitted disease severity at 1 m distance, $S(1\ m)$, and the fitted slope parameters for the power law, b, and exponential law models, B, were examined through correlation analysis.

RESULTS

The meteorological and epidemiological details of each of the 12 experiments are outlined in Table 1. Rainfall during the first experiment was due to a localized thunderstorm during which precipitation was quite intense (11 mm h^{-1}; Table 1). In all the rest of the experiments precipitation was due to large storms that affected the entire eastern seaboard. For five of the profiles (profiles 1, 2, 8, 10, and 11), source plants were dry when trap plants were placed out. For the remaining 7 profiles (3, 4, 5, 6, 7, 9, and 12), the rain had already started and source plants were wet for 3 to 20 h before trap plants were placed out in the field. Rainfall during exposure varied from 12 to 70 mm and lasted from 3 to 87 h. These experiments represent a wide range of rainfall conditions both before and during plant exposure. As the experiments progressed, we increased exposure time and increased the range of distance from the source row over which trap plants were placed (Table 1). Mean source severity varied from 1,450 to 6,730 Septoria leaf spot lesions m^{-1} over the course of the study. Early blight (causal agent, *Alternaria solani*) incidence was never greater than 2% in the source plantings and no lesions were ever observed on trap plants.

Exposed trap plants developed typical lesions of Septoria leaf spot after 5 to 10 days. Resultant lesion densities on the trap plants placed out 500 m from the source row to sample background exposure varied from 0 to 6 lesions m^{-2}. Since these observed lesion densities were never more than 10% of those observed on the trap plants placed farthest from the line source, the effect of background exposure was ignored in the following analyses. Trap plant lesion densities for each of the 12 experiments are presented in Figures 1 and 2. For profiles 1, 2, 3, 4, 6, 7, and 11, each data

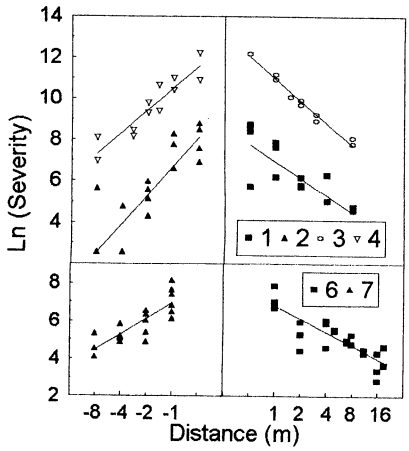

Fig. 1. Log-log plot of trap plant disease severity (lesions m^{-2}) versus perpendicular distance from the line source for experiments 1, 2, 3, and 4 (top panel) and for experiments 6 and 7 (bottom panel). Solid lines are the power law fits to the data (Table 2).

Table 1. Meteorological and source information for each of the nine experiments

Profile no.	Initial date	Exposure time T_T (h)[a]	Rainfall duration (h)[b] Before RT_B	Rainfall duration (h)[b] During RT_D	Rainfall amount (mm) Before RT_B	Rainfall amount (mm) During RA_D	Distance range (m)	Source length L_S (m)	Source severity S_S (103 lesions m^{-1})[c]
1, 2	29 August 1989	20	0	3	0	33	0.5 to 8	38	2.12
3, 4	15 September 1989	60	18	22	27	12	0.5 to 8	38	6.73
5	24 August 1990	72	20	25	32	39	1 to 32	29[d]	4.42
6, 7	14 September 1991	68	3	9	6	17	1 to 16	30	1.45
8	25 September 1992	58	0	32	0	13	1 to 32	57	3.43
9	9 October 1992	64	5	16	12	70	1 to 32	57	4.35
10	16 September 1993	72	0	27	0	24	1 to 16	43	3.02
11	28 September 1994	120	0	87	0	24	1 to 16	67[d]	3.64
12	19 October 1994	120	6	7	4	13	1 to 106	67[d]	2.42

[a] Total time trap plants were exposed.
[b] Rainfall duration and amount are reported for the 24-h period prior to exposure (before) and for the exposure period itself (during).
[c] Source severity is expressed as number of lesions per linear meter of source row (see text).
[d] Source rows in these years were staked and pruned (see text).

point represents the disease severity of a single trap plant. For profiles 5, 8, 9, and 10, each data point is the mean disease severity of two trap plants planted in the same pot. For profile 11, each data point represents the disease severity of three trap plants planted in the same pot. Maximum disease severity on trap plants was about 10^5 lesions/m^2 found on plants placed within a meter of the source. Some of the leaflets on these sample plants had as many as 300 lesions. Disease severity decreased very rapidly on plants that were placed farther and farther from the line source (Figures 1 and 2).

A comparison of a log-log versus a log-linear regression analysis was made to determine which model best fit the observed contact distribution. The power law regression lines presented in Table 2 are plotted in Figures 1 and 2. The power law model consistently gave a larger value of r^2 than the exponential model for every measured profile (Table 2). However, this difference was only significant for profile 5 (Fisher's z-test with $P < 0.05$) (33) and the distribution of the residuals from both the power law and the exponential law fit did not significantly ($P < 0.05$) differ from a normal distribution (Lilliefors test) (33).

Source lesion densities were well correlated with the predictions of both the power law and exponential law regressions evaluated at 1 m (Table 3). Note $S(1\text{ m})_{pow} = \exp(a)$ where a is the fitted value for the power law and $S(1\text{ m})_{exp} = \exp(A+B\cdot 1\text{ m})$, where A and B are the fitted values for the exponential law given in Table 2. Of the meteorological variables, rainfall amount (RA_B) and duration (RT_B) during the 24-h period prior to trap plant exposure were best correlated with S(1 m) and superior to rainfall amount and duration during the actual exposure of the trap plants (Table 3). The power law parameter, b, was not significantly correlated with any variables. However, the exponential law slope parameter, B, was positively correlated with the maximum distance between source and trap plants (r_{MAX}).

DISCUSSION

Rain events are essential in the development of Septoria leaf spot (8,21,29) for hydration and spore release from the pycnidium, and periods of leaf wetness greater than 16 h significantly increase conidial germination and infection (12,21). Furthermore, it is most likely that a large fraction of the spores released in the rain are disseminated within water droplets either splashed off or dripped from infected leaves. These waterborne conidia account for most of the disease spread within a plant and to adjacent plants within a few meters of the source lesion (17). However, the spread of disease is considerably enhanced if even a small fraction of the propagules (<10%) become airborne and are, therefore, able to travel much larger distances (>10 m) before infecting (15). Fitt et al. (17) cite numerous cases in which splash-dispersed spores were detected at greater distances from the source than expected (distances of 4 to 10 m at heights of 0.5 to 1 m above the source). Our findings suggest that windblown rain may be a vehicle for long-distance transport of *S. lycopersici*. Such a dispersal function causes a rapid increase in isopathic velocity as the epidemic spreads from foci (15). This property could dramatically affect the ensuing epidemics and the need for fungicide application (13).

One would expect that disease severity on trap plants would be a function of the overall amount of inoculum, so that the observed strong correlation between source strength and disease spread (Table 3) is reasonable. The importance of precipitation prior to exposure may be related to the difficulty in freeing conidia from the ge-

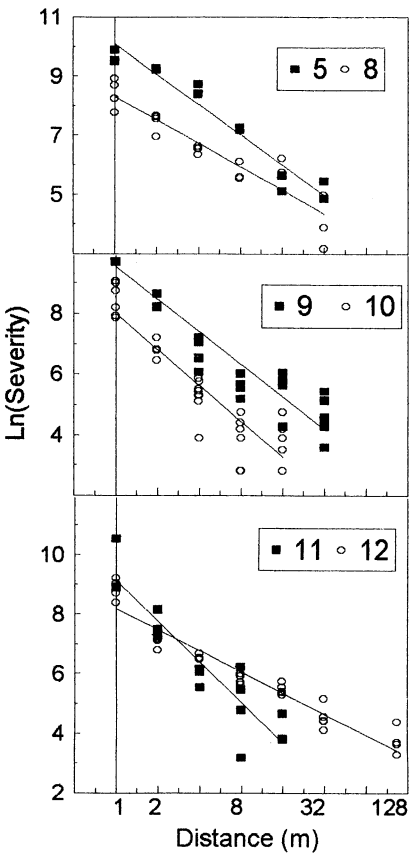

Fig. 2. Log-log plot of trap plant disease severity (lesions m^{-2}) versus perpendicular distance from the line source for experiments 5 and 8 (top panel), experiments 9 and 10 (middle panel), and experiments 11 and 12 (bottom panel). Solid lines are the power law fits to the data (Table 2).

Table 2. Log-log and log-linear regression results for disease severity, S, on trap plants versus distance, x, from focus for the experiments in Table 1

	Power law			Exponential law			
	$\ln(S) = a + b\ln(x)$ [a]			$\ln(S) = A + B\cdot x$ [a]			
Profile no.	a	b	r^2	A	B (m^{-1})	r^2	df
1	6.92	−1.18	0.59	7.33	−0.39	0.43	13
2	6.70	−2.00	0.81	7.51	−0.71	0.68	14
3	10.93	−1.55	0.98	11.26	−0.47	0.75	10
4	10.52	−1.55	0.86	10.86	−0.48	0.69	10
5	10.08	−1.47	0.94	9.09	−0.15	0.80	10
6	6.82	−1.02	0.69	6.28	−0.15	0.61	23
7	6.93	−1.20	0.69	6.93	−0.34	0.56	17
8	8.30	−1.14	0.88	7.56	−0.12	0.78	22
9	9.52	−1.54	0.88	8.25	−0.13	0.60	24
10	7.24	−1.42	0.84	7.01	−0.24	0.55	34
11	9.12	−1.97	0.84	8.07	−0.30	0.62	13
12	8.15	−1.00	0.91	6.67	−0.03	0.52	33

[a] S is disease severity (lesion/m^2) and x is distance (m) from source. A and a are the intercepts, and B and b are the slopes of the exponential and power law fits, respectively.

Table 3. Correlation coefficients between measured source properties, meteorological variables (Table 1) and fitted disease severity at 1 m distance, S(1 m), and the slope parameters for the power law, b, and exponential law models (B, Table 2)

	Power law		Exponential law	
Independent variable	S(1 m)[a]	b	S(1 m)[a]	B
Total exposure time (T_T)	+0.24[b]	−0.36	+0.11	+0.58
Source severity (S_S)	+0.90**	−0.35	+0.84**	+0.05
Length of source (L_S)	−0.08	+0.07	−0.10	+0.27
Maximum trap plant distance (x_{MAX})[c]	−0.20	−0.45	−0.30	+0.62*
Rainfall duration before exposure (RT_B)	+0.88**	+0.07	+0.72*	+0.01
Amount of rain before exposure (RA_B)	+0.87**	+0.10	+0.69*	+0.15
Rainfall duration during exposure (RT_D)	−0.01	−0.49	−0.01	+0.15
Amount of rain during exposure (RA_D)	−0.10	−0.27	−0.31	+0.26

[a] S(1 m) is defined by $S(1\text{m}) = e^a$ for the power law and by $S(1\text{ m}) = e^{A+B\cdot 1\text{m}}$ for the exponential law where a, A, and B are defined in Table 2.

[b] Significant correlation coefficients are followed by asterisks (* = $P < 0.05$; ** = $P < 0.01$).

[c] x_{MAX} is the distance between source of spores and most distant trap plants.

latinous matrix exuded by pycnidia. The relation between the duration of pycnidia wetting and the release of conidia has not been investigated. However, the fact that rainfall during exposure was not as good a predictor of disease spread as rainfall before exposure is harder to understand. Parker et al. (29) found a strong correlation ($r^2 = 0.86$, [$P < 0.001$]) between rainfall during exposure and the resulting trap plant disease severity but rainfall prior to exposure was not reported. One possible explanation for this difference is that a number of our experiments were conducted during periods of very heavy rainfall (in particular profiles 1, 2, 6, 7, 9, and 12; Table 1) quite in excess of the precipitation reported by Parker et al. (29). Perhaps, in very heavy rains, some conidia may wash off leaves before they have a chance to germinate.

The experimental determination of spore dispersal over a large range of distances can be difficult due to the rapid decrease in spore deposition away from a source (5,7). Basically, the long exposure times needed to measure spread at large distances tend to overload trap plants close to the source of spores. For a point source or an inoculum source confined to a small area, this dilution effect is complicated by the variation in wind direction over the course of exposure. These experimental difficulties were partially overcome by using long rows of uniformly infected plants (4). This source geometry tends to increase the relative amount of dispersal at distance while minimizing the effect of variable wind direction. In addition to variations in wind direction, changes in wind speed also complicate the processes of spore release (3), spore transport (10,15,27,30,35), and spore deposit (1,9,10). For this reason it is desirable to have a relatively long exposure of time (>1 day) to average out the effects of intermittency and more nearly approximate the causal spore dispersal pattern for an in situ epidemic. Trap plants serve the same purpose as spore traps but their use has the further advantage of assessing only the viable and ineffective spore population at any given distance from a source (18).

The use of relatively long rows of homogeneously infected plants as a source of inoculum combined with the long duration trap plant exposure method of inoculum detection has been shown to be well suited to describing the long-range dispersal of inoculum for the *Septoria*-tomato system. This method minimizes problems with variable wind direction and temporal variation in spore release. At large distances increased sensitivity was obtained by increasing the number of trap plants exposed. The small size and distinct appearance of the lesions of this disease make it easy to accurately determine disease severity using trap plants over a wide range of lesion densities with minimal output of expense and labor. The observed spore transport seems to be better described by an inverse power law of distance, a transport function usually attributed to wind-dispersed spores (17,19).

The experiments described above demonstrate that the spatial dispersal of the conidia of *S. lycopersici* during and immediately after rain is best described by a negative power law of distance from the source of inoculum. This disease is usually assumed to be splash dispersed, a process that is often thought to be limited to dispersal within a few meters of the source of inoculum. The long-range dispersal herein observed is suggestive of alternative dispersal mechanisms. Perhaps some spores are carried in very small droplets or are disseminated by dry dispersal. This behavior will tend to increase the rate of disease spread, which will have a major impact on successful management practices for the control of Septoria leaf spot on tomato.

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