Influence of Rain Events on Spatial Distribution of Septoria Leaf Spot of Tomato

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ABSTRACT

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Tomato seedlings spaced 30 cm apart were placed 30–180 cm from an inoculum source in the field for 24-hr periods on five rain dates and five non-rain dates. The mean number of lesions per leaf on plants exposed on rain dates ranged from 70 to 1,680, whereas only 0.0–0.46 lesions per leaf developed on plants exposed on non-rain dates. The mean number of lesions per leaf was linearly related to millimeters of rainfall during exposure periods ($b_0 = -224$, $b_1 = 528$, $R^2 = 0.86$, $P < 0.0001$). Percent defoliation within rows of tomato plants increased at the apparent infection rate of 0.282 units per day following spray inoculation of the center plant in each row. The study confirms that rain is a primary mechanism for spore dissemination and an important factor contributing to the development of Septoria leaf spot epidemics in tomatoes.

Additional keywords: *Lycopersicon esculentum,* disease forecasting, disease gradients

Much of the biological information concerning *Septoria lycopersici* Speg., causal agent of Septoria leaf spot of tomatoes (*Lycopersicon esculentum* Mill.), comes from in vitro studies of the morphology, nutrition, and biological requirements of the fungus conducted during the first half of this century (7,11,15,19). Later reports focused primarily on host resistance (3,4,26) and pathogen variation (6,14). Since acceptable tomato cultivars possessing resistance to Septoria leaf spot are not yet commercially available, management of the disease relies primarily on sanitation and frequent fungicide applications.

Although Septoria leaf spot occurs in virtually every country where tomatoes are grown (13), little quantitative information is available regarding the epidemiology of the disease, with the exception of recent work in Ontario (31) and Connecticut (8). Recently, commercial growers in the eastern U.S. and Canada have begun to use disease-warning models to improve the efficacy and economic efficiency of fungicide sprays for control of early blight (causal agent: *Alternaria solani* (Sorauer) (24,25), anthracnose (causal agent: *Colletotrichum coccodes* (Wallr.) S. J. Hughes), and Septoria leaf spot. Although existing tomato disease-warning models do not incorporate epidemiological data pertaining specifically to *S. lycopersici,* these models have been deployed with the assumption that they will provide acceptable control of Septoria leaf spot (10,25).

Early observations linked overhead irrigation and rainfall to disease occurrence. Levin (15) observed that new lesions appeared on greenhouse plants with infected lower leaves when plants were watered from above. Endrinal and Celino (7) also observed that plants placed near infected tomato plants and watered regularly by overhead irrigation and rainfall developed Septoria leaf spot symptoms after 3 wk. Because the role of rainfall on the temporal and spatial dynamics of the disease has not been elucidated, the objectives of our study were to determine the importance of rain events for the dispersal of *S. lycopersici* spores and to quantify the temporal and spatial progress of *S. lycopersici* in field-grown tomatoes.

MATERIALS AND METHODS

Field plots. Field experiments were conducted in 1992 at the Iowa State University Horticulture Farm near Gilbert, IA. Three 6.1-m × 18.3-m blocks were established in a 50-m × 25-m area that had not been planted previously to tomatoes. Rows were oriented east-west with 12.2-m strips of unmowed grass between plots. A herbicide (trifluralin, 0.33 L/ha) and 13-13-13 fertilizer (446 kg/ha) were applied before transplanting. Relative humidity, rainfall, wind speed, leaf wetness duration, and air temperature were recorded at hourly intervals by a CR-10 datalogger (Campbell Scientific, Inc., Logan, UT) installed for a nonrelated study in a tomato field 0.4 km from our site. Overhead irrigation was applied on two dates, 20 May (at transplanting) and 18 August.

Plants. Five-week-old seedlings of a determinate, fresh-market cultivar (New Yorker) were transplanted into the field on 20 May. Each replicate block contained a single 15-m row of 25 plants placed 60 cm apart; plants were not staked. Rows were side-dressed with 46-0-0 urea (155 g N/15 m row) on 16 June. Insects were controlled with esfenvalerate (Asana 0.66 EC, E. I. DuPont de Nemours and Company, Wilmington, DE) applied at a rate of 0.16 kg a.i./ha every 7–14 days beginning on 5 June.

In the greenhouse, seeds (cv. New Yorker) were sown in 72-cell flats at weekly intervals and transplanted to 15.2-cm-diameter plastic pots after 4 wk. Seedlings were watered with soluble fertilizer (Peters Peat-Lite Special, 315 ppm N) three times each week; $MgSO_4$ (100 ppm) was applied once each week. Greenhouse plants were used as live spore traps at 6 wk after sowing.

Inoculum. Three-week-old sporulating cultures of *S. lycopersici* grown on tomato leaf extract agar (C. Block, USDA Plant Introduction Station, Ames, IA, *personal communication*) on 10-cm-diameter petri plates were flooded with 15 ml of sterile water plus Tween 20 (1 drop/100 ml) for 10 min, then rubbed with a bent glass rod. The spore suspension was filtered through two Kimwipes (Kimberly-Clark Corp., Roswell, GA) to remove mycelial fragments. On 2 July the center plant in each row was inoculated by applying a suspension containing 1×10^6 spores per milliliter to the point of runoff (approximately 67 ml/plant) using a hand-trigger spray bottle. To minimize spray drift to adjacent plants during inoculation, each plant was surrounded by a cardboard shield.

Disease development. Experiments were conducted over a 5-wk period beginning 14 July. Sporulating lesions on plants in each 15-m row served as inoculum sources. Plants in the canopy were 30–60 cm tall during the experimental period. Potted plants (live spore traps) approximately 60 cm in height were placed in the field for periods of 24 hr on five rain dates and five non-rain dates. These dates represented five replications in time for both rain and non-rain conditions. In each block, ten trap plants were spaced 30 cm apart along a transect perpendicular to the row of established plants, to maximum distances of 150 cm both north and south of the center plant in each established row. Disease development in two directions was monitored,

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following the approach used by Minogue and Fry (22) and Nutter (23). After 1 August, the maximum distance was increased to 180 cm and twelve trap plants were used in each transect. Pots were set into shallow holes in the ground so that the soil line within pots was at ground level and the plants remained upright. After 24 hr in the field, trap plants were returned to the greenhouse and incubated in plastic mist tents for 50–60 hr to encourage spore germination and infection (19,21,31). Relative humidity levels close to 100% were maintained by intermittent operation of cool-mist vaporizers inside the tents. Hygrothermographs were used to record RH levels throughout the experiment. Temperature in the greenhouse averaged 25 C but occasionally fluctuated ±5 C during night and sunny periods. Septoria leaf spot lesions were identified based on observations of characteristic lesions, pycnidia, and conidia (15).

Disease assessment. Disease severity on trap plants was assessed 10–14 days after field exposure by *(1)* determining the number of Septoria leaf spot lesions occurring on one leaf located at mid-height on the plant and *(2)* visually estimating the percent diseased area per leaf for all leaves attached to the main stem of the plant. Values for percent diseased leaf area were plotted against distance from soil line to each leaf node, and the resulting area under the curve (AUC) was used as a summary measure of total disease on a plant. AUC was calculated using the equation

$$\sum_{i}^{n-1} [(y_i + y_{i+1})/2]\,(h_{i+1} - h_i),$$

where n = the number of leaves assessed per plant, h_i = height from soil line to leaf node for the ith leaf, and y_i = the proportion of symptomatic leaf area (5). Bias in the selection of single leaves for determining lesion number per leaf was reduced by systematically assessing the leaf closest to the oldest flower cluster; leaves at this position were similar with regard to leaf age and height on the plants.

Data for rain and non-rain dates were combined and used to quantify the effects of epidemic duration and hours of leaf wetness during exposure on trap plant disease severity. These data and the effect of rainfall amount on trap plant disease severity also were examined using rain-date information only. The experiment was treated as a split-plot design with trap plant positions as main-plot treatments and exposure dates (a repeated measure) as split plots.

Infection gradients on trap plants, representing *S. lycopersici* spore dispersal gradients, were quantified by relating lesion number and AUC to distance from the source of inoculum. Disease severity values and distances were transformed according to the power law, exponential, Berger and Luke, and Minogue and Fry models to achieve linearity (1). Model fit was evaluated on the basis of R^2 values and F tests for linearity and goodness-of-fit (1,5). The best-fit model was used to estimate equation parameters for individual gradients (north and south directions in each of the three blocks) for each rain exposure date. Differences in slopes and intercepts due to direction, date, and rainfall were then examined using PROC GLM (SAS Institute, Cary, NC).

Disease severity within the 15-m established rows was assessed by estimating percent defoliation (leaves either abscised or completely necrotic) per plant. Plants were assessed on five dates from 23 July to 14 August. Mean percent defoliation within each block (n = 25) was calculated for each assessment date. Preliminary analyses showed that temporal progress was best described by transforming disease severity (y) to logits [ln ($y/(1 - y)$)] to achieve linearity. Apparent infection rates were then estimated from combined data for all three blocks using least squares regression (5,29).

RESULTS

Disease development. The maximum number of lesions per leaf for trap plants exposed on the date with the greatest rainfall (30.0 mm) exceeded 2,000, as determined from actual counts (Fig. 1A). In contrast, the number of lesions per leaf on trap plants at all distances from the inoculum source was very low (0–10 lesions) for non-rain dates, indicating that spore dissemination was minimal in the absence of rain (Fig. 1B). For most dates, disease severity was greatest on lower leaves and on plants 30–60 cm from the source. After heavy rainfall (30.0 mm) the distribution of lesions on upper leaves of plants 150 cm from the source was similar to that on plants 30 cm from the source, suggesting that spores were disseminated beyond the 300-cm-long transect occupied by the trap plants (Fig. 2). AUC values for the majority of plants exposed on non-rain dates generally were

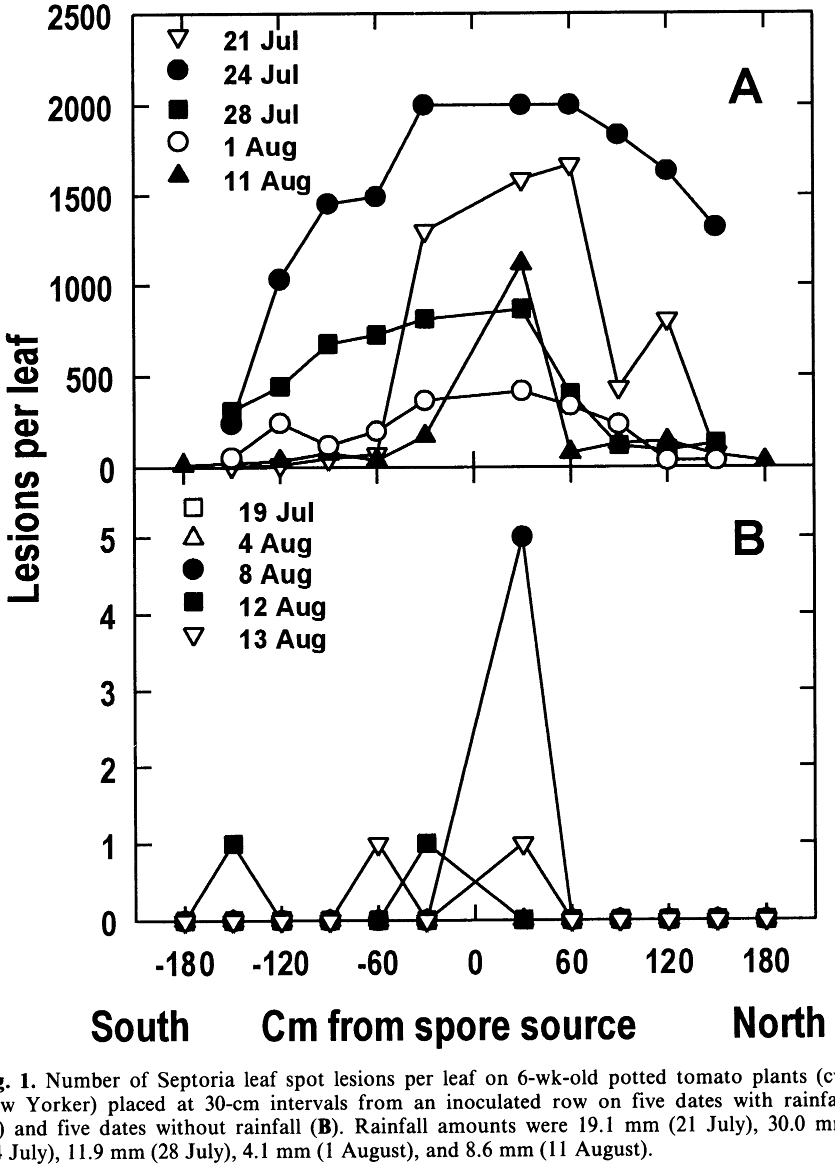

Fig. 1. Number of Septoria leaf spot lesions per leaf on 6-wk-old potted tomato plants (cv. New Yorker) placed at 30-cm intervals from an inoculated row on five dates with rainfall (A) and five dates without rainfall (B). Rainfall amounts were 19.1 mm (21 July), 30.0 mm (24 July), 11.9 mm (28 July), 4.1 mm (1 August), and 8.6 mm (11 August).

zero; plants occasionally had very low AUC values due to extensive chlorosis associated with one to several lesions per plant (data not shown).

Leaf wetness duration during exposure periods was 5.3–14.3 hr on the five non-rain dates and 3.7–19.1 hr on rain dates. Statistical analysis failed to detect a linear relationship between leaf wetness duration during field exposure and either $\log_e$ (lesion number) or AUC (data not shown). Maximum and minimum temperature and average wind speed during exposure had no significant effects on disease severity (data not shown). Date and date × plant position effects were significant (Table 1). Partitioning of sums of squares showed that the effect of date on disease severity for all plant positions and with regard to distance from the source was due to increasing rainfall amount rather than the number of days since spray inoculation. Block means for number of lesions per leaf on live trap plants (y), used as a summary of the total amount of disease resulting from a given exposure period, were linearly related to rainfall amount (x, in cm) by the equation $y = -224 + 528x$ ($R^2 = 0.86$, $P < 0.0001$). Mean AUC values for trap plants (y) were linearly related to rainfall amount (x) by the equation $y = 368 + 352x$ ($R^2 = 0.68$, $P < 0.0001$).

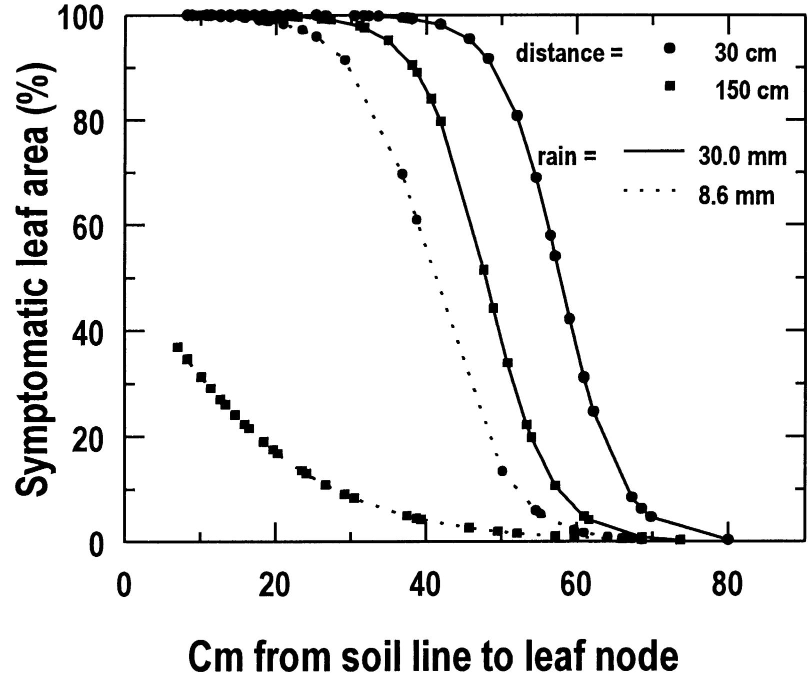

Fig. 2. Percent chlorotic or necrotic leaf area per leaf due to Septoria leaf spot in relation to distance between leaf node and soil line for trap plants placed 30 cm or 150 cm from an inoculum source on 11 August (rain = 8.6 mm) and 24 July (rain = 30.0 mm). On 24 July, rainfall was accompanied by strong wind gusts.

Table 1. Analysis of variance for Septoria leaf spot disease severity on trap plants placed 30–150 cm from an inoculum source in the field for 24-hr periods on five dates with rainfall[a]

Source[b]	df	MS	*F*	*P*>*F*
Plant position	9	1,307,001	25.4667	0.0001
Direction[c]	1	988,854	19.2676	0.0004
Distance from source[d]	4	2,561,700	49.9143	0.0001
Increasing distance[e]	1	10,194,426	198.6366	0.0001
Error	18	51,322		
Date	4	4,508,207	63.9362	0.0001
Date × position	36	176,819	2.5077	0.0003
Days past inoculation[e] × position	9	85,278	1.2094	0.3011
Mm rainfall[e] × position	9	1,445,781	20.5043	0.0001
Date × direction	4	855,573	12.1339	0.0001
Error	80	70,511		

[a] Data shown are based on disease severities for individual plants, calculated by integrating area under the curve (AUC) formed by plotting percent diseased leaf area against distance (cm) from soil line to leaf node for all leaves attached to the main stem of a plant.

[b] Experiment was analyzed as split-plot design with plant positions (distance from inoculum source) as whole plot treatments and field exposure dates as split plot factors. Sums of squares were subdivided to test significance of linear effects of rainfall amount and distance from inoculum source.

[c] North or south of inoculated, established row.

[d] Plants were placed 30, 60, 90, 120, and 150 cm from inoculum source.

[e] Linear effects.

Data from individual disease gradients were best described by the regression of non-transformed AUC values with distance from the source. Data fit to the resulting regression equations was acceptable ($R^2 > 0.60$, $P < 0.10$) for 17 of the 30 gradients examined (Table 2). Increase in rainfall explained 61.5% of the variation in intercept values for individual gradients ($F_{1,24\ \mathrm{df}} = 48.20$, $P < 0.0001$), whereas slope values were not significantly related to rainfall amount.

Epidemic progress in plantings. Numerous lesions were present on spray-inoculated plants 1 wk after inoculation. Two weeks after inoculation, lesions were observed on tomato plants adjacent to the inoculated plants. Nearly all plants were 100% defoliated by 14 August (Fig. 3). Disease increase with time was best described by the logistic model, which states that the apparent rate of infection is related to the logarithm of the ratio of the amounts of diseased and healthy tissue present (5). Apparent infection rates averaged 0.282 (SE = 0.015, $R^2 = 0.96$, $P < 0.0001$).

DISCUSSION

The high infection frequencies seen on trap plants exposed during rain events, in contrast to the sparse development of lesions and absence of disease gradients on trap plants exposed during non-rain periods, indicated that rain was a primary mechanism for spore dissemination and deposition of *S. lycopersici* and that rainfall contributed substantially to plant-to-plant spread (alloinfection). These findings agree with those obtained for other *Septoria* spp. An association between rainfall events and increases in disease severity was also found for *Septoria nodorum* (Berk.) Berk. and *S. tritici* Roberge in Desmaz. (12,28,30). Hess and Shaner reported that increases in severity of Septoria tritici blotch were associated with rainfall events occurring 14-16 days earlier (12). Royle et al (28) demonstrated that intense rainstorms distributed *S. nodorum* and *S. tritici* spores up to 60 cm within winter wheat canopies, and that disease levels in the field were predicted by the number of days with rainfall exceeding 5 mm. Although differences in crop-canopy structure and spore characteristics rule out direct comparison of pathosystems involving different *Septoria* spp., these studies all show that enhanced distribution of new infection sites is related to rain events. We demonstrated that rainfall directly influenced the amount of new infections by contributing to spore dissemination. It was possible to quantify this influence by relating rainfall amount to lesion frequency and to estimates of the strength of the inoculum source (given by the estimated y-intercept values for disease gradients) (5).

Statistical analysis indicated that disease progression with time in the established plantings did not significantly affect disease severity and gradient parameters. This finding eliminated the possibility that an increase in the total amount of diseased tissue in the field was a primary factor contributing to trap plant disease severity. It is possible that disease progression affected the shape of individual disease gradients once inoculated plants deteriorated and inoculum sources were no longer aligned in the same north-south transects as the trap plants. Direction effects and date × direction interactions were most likely related to meteorological variables not recorded, such as wind direction and gust velocity. Other environmental variables not recorded in our study may account for some of the unexplained variation in our disease gradients, and hence the poor fit of the empirical models. Without additional variables to account for wind speed, wind direction, rain intensity, etc., gradient models may not be adequate summaries of spore dissemination patterns for splash-dispersed pathogens under field conditions (5).

In our study, rapid epidemic development was accompanied by abundant and frequent rainfall (a total of 22.6 cm fell on 21 dates between 2 July and 19 August), which contributed to a high level of alloinfection in field plantings. This pattern of rapid disease increase has also been documented for *S. nodorum* and *S. tritici* epidemics on winter wheat, in which periods of heavy rain were associated with severe disease outbreaks (28,30). In contrast, in years in which little rainfall occurred during the growing season, disease progressed more slowly within the wheat canopy as infection resulting from contact with inoculum produced on lower leaves during dew periods was limited to adjacent leaves, resulting in a much lower frequency of alloinfection (28,30). The high apparent infection rates associated with our field tomato plantings show the explosive potential of Septoria leaf spot epidemics during wet years. In comparison, apparent infection rates for tomato early blight epidemics (causal agent: *Alternaria solani* (Sorauer), based on percent disease, were reported to be 0.074–0.136 units per day (20,24), which is less than half the average rate calculated for Septoria leaf spot in our plots.

Rainfall amount explained 86% of the variation in the number of lesions per leaf on trap plants and 68% of the variation in AUC values. Based on these findings, rainfall-facilitated dissemination of *S. lycopersici* spores is a critical limiting factor for disease increase. Therefore, to predict more accurately the risk of Septoria leaf spot epidemics, a disease-warning model should include rainfall as a contributing factor. Disease-warning models such as FAST (20) and TOM-CAST (25) were developed for an air-dispersed pathogen (*A. solani*) and emphasize the importance of temperature and wetness conditions conducive to sporulation and infection. TOM-CAST, a model developed from FAST, is widely used in Canada and the midwestern United States to estimate the risk of outbreaks of early blight, anthracnose, and Septoria leaf spot. However, TOM-CAST does not discriminate between causes of wetting periods such as dew, rain, and irrigation (25). In the case of Septoria leaf spot of tomato, wetness periods favorable for sporulation and infection may not result in significant disease increase unless rainfall or overhead irrigation is present to disseminate spores (9). Incorporating rainfall measurements as inputs to a model such as TOM-CAST could potentially enhance the model's accuracy in predicting when fungicide sprays are needed to control Septoria leaf spot, and thereby improve the system's efficacy in regions where this disease is a significant threat. Before this can be done, however, further research is needed to identify critical levels of rainfall and determine how environmental factors and cultural practices influence splash dispersal of *S. lycopersici* spores and disease progression.

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Table 2. Frequency of acceptable data fit to disease gradient models (5) applied to Septoria leaf spot disease gradients for five rain dates[a]

Severity measure	Model		Frequency[b]
Lesion count	Linear	$y = b_0$[c] $- b_1$[d]x	6
	Power law	$\ln(y) = \ln(b_0) - b_1\ln(x)$	12
	Exponential	$\ln(y) = \ln(b_0) - b_1x$	13
	Berger and Luke	$\ln[y/(1-y)] = \ln[b_0/(1-b_0)] - b_1\ln(x)$	13
	Minogue and Fry	$\ln[y/(1-y)] = \ln[b_0/(1-b_0)] - b_1x$	13
AUDPC	Linear	$y = b_0 - b_1x$	7

[a] Six gradients (north and south directions in three blocks) were examined for each date. Disease severity on single tomato plants spaced 30–150 cm from an inoculum source was represented either by number of lesions on one leaf per plant or by integration of the area under the curve (AUC) formed by plotting percent diseased leaf area per leaf against distance from soil line to leaf node. Models producing regression equations with R^2 values >0.60 and P values <0.10 were considered to be acceptable summaries of the data.

[b] Number of the 30 disease gradients examined that were adequately described by the model. Data for a particular gradient may be described appropriately by more than one gradient model.

[c] Disease severity at $x = 0$.

[d] Rate of change in disease severity per unit x.

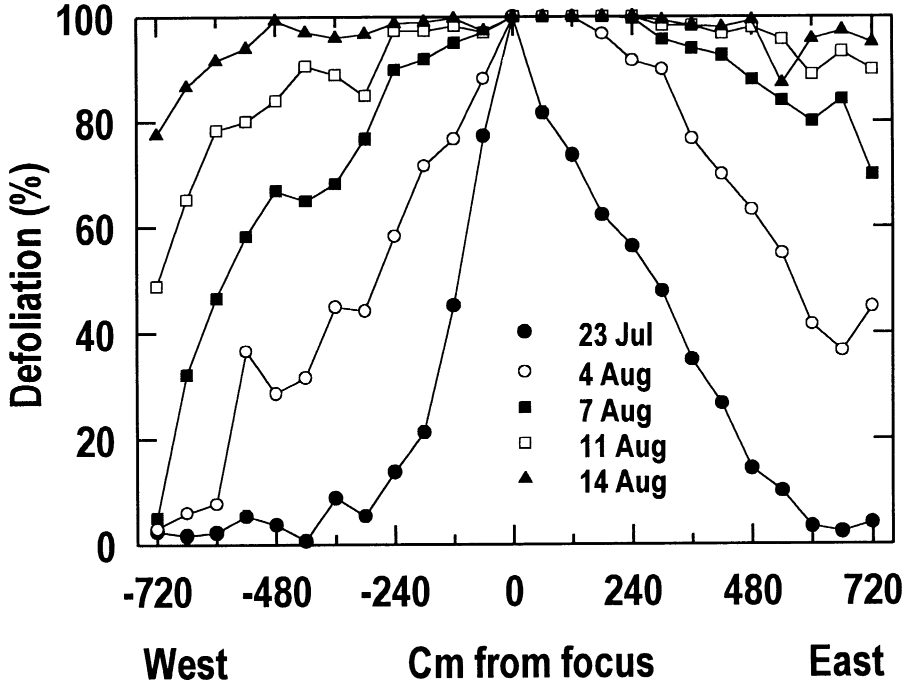

Fig. 3. Defoliation due to Septoria leaf spot, assessed as percentage of necrotic tissue per tomato plant (cv. New Yorker), at 60-cm intervals along a 15-m row. A suspension of *S. lycopersici* spores was sprayed on a single plant at the center of each row on 2 July. Values represent means from three plots.

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