

Reduction in Tomato Yield Due to Septoria Leaf Spot

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ABSTRACT

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In 1988 and 1989, unpruned tomato plants (cv. Better Boy) were grown on black plastic mulch in plots (four to six plants per plot). In early July, plots were artificially infested with tomato residues colonized by *Septoria lycopersici*. Control plots were not infested with residues and were sprayed weekly with mancozeb. The number of empty leaf nodes, attached dead leaves, diseased leaves, and healthy leaves were counted throughout the season. The rate of disease progress was 0.05–0.18 per day, and yields from diseased plots were 40–95% of the yields obtained from sprayed controls. In both years, final yield was negatively correlated with the square of the area under the disease progress curve (AUDPC) (1988, $R^2 = 0.70$; 1989, $R^2 = 0.80$ –0.83) and positively correlated with healthy leaf area duration (HAD) (1988, $R^2 = 0.76$; 1989, $R^2 = 0.83$ –0.89). The equations that best described the relation between final yield (Y) and AUDPC and HAD were: $Y = 9.9 - 0.0028 (\text{AUDPC})^2$, ($R^2 = 0.80$, $df = 47$) and $Y = 1.3 + 0.10 \text{HAD}$ ($R^2 = 0.82$, $df = 47$). Manual defoliation experiments conducted concurrently with these studies demonstrated that removal of 25 or 50% of the total number of leaves from sprayed plants did not significantly reduce yield, whereas removal of 75% of the leaves lowered yield by 34–53%. The relation between HAD and yield from manually defoliated plots was similar to that with nonsprayed plants that were defoliated by *Septoria* leaf spot. Measurements of HAD may be a better predictor of final yield than AUDPC because of its linear relation to yield.

Septoria leaf spot, caused by *Septoria lycopersici* Speg., is a common foliar disease of tomato (*Lycopersicon esculentum* Mill.) in the eastern United States (1–3,10–12,14). This disease has been routinely controlled by fungicide application (4,12,14). However, the recent concerns regarding fungicide usage on tomato have stimulated new interest in reducing the frequency of fungicide application and in searching for disease resistance (16).

A major challenge in plant pathology is to reduce fungicide inputs without appreciable reductions in yield or quality. Disease forecasting models developed for different crops have indicated that the number of fungicide sprays applied to control a specific disease can be reduced during certain seasons without economic crop loss (9,13,19).

These predictive models require knowledge of optimal environmental conditions for inoculum increase and release and an understanding of the relationship between disease progress and plant damage and yield (15). The yield-loss relation for the *Septoria* leaf spot–tomato system has not been well studied. This paper reports the relationship between disease progress of *Septoria* leaf spot and the resulting yield in tomato. A preliminary report has been published (7).

MATERIALS AND METHODS

Site and culture. Tomato (cv. Better Boy) seeds were sown into 36-cell plastic trays filled with potting mix (Promix BX) and germinated in the greenhouse (18–30 C). After 2 wk, seedlings had one true leaf and were thinned to one plant per cell and fertilized with 40 ml of Peter's 20-8-16 soluble N-P-K (5 g/L). At 4 wk, seedlings were transplanted into 1-L 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/L) solution weekly. Two-month-old seedlings 25–30 cm tall with 10–13 nodes were moved to a cold frame to acclimate for 1 wk, then transplanted into the field on 15 May 1988 and 21 May 1989.

Plot establishment. The trials were conducted at Lockwood Farm in Hamden, Connecticut, during 1988 and 1989 on a Cheshire fine sandy loam soil (57% sand, 33% silt, 10% clay, pH 6.2) that had been limed during the fall of 1987 at a rate of 500 kg/ha. Unpruned and unsupported tomatoes were planted through 4-mil black plastic at a spacing of 0.9 × 0.9 m in plots designed in a square grid pattern (hereafter designated as the “grid planting”). Plots consisting of four to six contiguous plants were treated with N-P-K fertilizer (10-10-10) at 112 kg/ha at planting and at 50 kg/ha in early July when the first set fruit were about 3 cm in diameter.

Dried tomato vine residues heavily colonized by *S. lycopersici* that had been collected during the previous year were crushed by hand, and 100–150 g was evenly spread in and around each plot on 7 July 1988 and 2 July 1989. Control plots were not infested with residues and were sprayed weekly with mancozeb (Manzate 200 80WP) at a rate of 0.88 kg a.i./ha beginning 12 July 1988 and 15 July 1989.

In 1989, an additional planting was established approximately 100 m away from the plots described above. This consisted of two single-file rows of tomato plants at a spacing of 0.9 m (hereafter designated as the “line planting”). One row (25 plants) extended to the north and the other (40 plants) to the east. Plots consisted of five contiguous plants along each row. At the southeast intersection of these two rows, 30 tomato plants were planted at high density within a 2 × 2 m region to act as primary foci of disease and source of inoculum. These plants had developed a dense canopy by 21 June and were then infested with the vine-residue inoculum, covered with two

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layers of tobacco shade cloth, and given overhead irrigation daily for 3–5 hr for 2 wk.

In order to assess the direct effect of defoliation on yield, four additional plots in a sprayed grid planting were each subjected to one of four defoliation treatments, i.e., no leaves (0%), every fourth leaf (25%), every other leaf (50%), or three of every four leaves (75%) were removed. These plots were immediately adjacent to the grid planting, and treatments were arranged in a randomized complete block design with four replicates. The 25% defoliation treatment had negligible effect in 1988 and therefore was not used in 1989. Manual defoliation was initiated when symptoms were first noted in nonsprayed plots (14 July 1988 and 8 July 1989) and was repeated on new growth every 2–3 wk until the final harvest in mid-September. Average daily rainfall and daily minimum and maximum temperatures were recorded each growing season from a weather station less than 200 m from the plots.

Disease and growth measurements.

The average area per leaf (A_L) was estimated by measuring leaf length (L , distance from first true leaflet to distal end of terminal leaflet) and maximum width (W) for 10 leaves on each sampled plant using the relation $A_L = 0.45 L \times W$, which was obtained by linear regression ($R^2 = 0.97$, $df = 112$). Total leaf area per plant was estimated biweekly by counting the total number of expanded leaves (>10 cm long) on sampled plants and multiplying that number by the average leaf area.

Foliar damage due to disease was estimated every 1–2 wk beginning mid-July. Two or three stems per plant were arbitrarily chosen from three arbitrarily selected plants in sprayed or nonsprayed plots. The number of empty leaf nodes, attached dead leaves, diseased leaves, and healthy leaves were counted. Disease damage was expressed as the fraction of total potential leaf area diseased for the sampled stems and included defoliated, attached dead, and diseased leaves. The leaf area of missing and dead leaves was estimated by multiplying the total number of dead and fallen leaves by the average tomato leaf area. Symptomatic leaves were grouped into one of six categories of leaf damage: 0, 1–5, 6–15, 16–25, 26–50, and >50% of the leaf area covered with lesions. Damage estimates were adjusted for the number of leaves that died from natural senescence by subtracting the average number of empty leaf nodes on stems in the sprayed plots. On the average, natural senescence accounted for less than 5–6% of the total defoliation.

Beginning in August, fruit was picked weekly at the first sign of red coloration, then counted and weighed. In the final harvest, all the remaining red and green fruit were picked, counted, and weighed.

Analysis of disease progress. Non-linear regression analysis was used to fit the fraction of the total leaf tissue that was damaged [$S(t)$] as a function of time (t) for each plot to the logistic equation in the following form: $S(t) = 1/\{1 + \exp[-r(t - t_{1/2})]\}$, where r is the rate of disease progress per day and $t_{1/2}$ is the number of days after first fruit set when 50% of the total leaf area is diseased, dead, or defoliated. Therefore, r and $t_{1/2}$ were estimated for each of 18 plots in 1988 (six sprayed and 12 nonsprayed plots on the grid planting) and 28 plots in 1989 (four sprayed and eight nonsprayed plots on the grid plantings and four sprayed and 12 nonsprayed plots in the line plantings). Area under the disease progress curve (AUDPC) was calculated as follows: $AUDPC_i = \sum_{j=2}^N (S_j^i + S_{j-1}^i)(t_j - t_{j-1})/2$, where N is the total number of observations in t and S_j^i is the fraction of the total leaf tissue that was damaged in plot i at time t_j . Because the disease

severity (S) was dimensionless and t was expressed in days, AUDPC was expressed in days. The plots with the maximum and minimum values of AUDPC as calculated above were used to show the range of disease progress among the nonsprayed plots. Healthy leaf area duration (HAD) (17) was computed for each plot by subtracting the amount of damaged leaf area from the total leaf area and integrating the difference over the entire season in analogy with the equation for calculating AUDPC. The relations between yield and AUDPC or HAD were examined by regression analysis.

RESULTS

Lesions of Septoria leaf spot were first noted on 14 July 1988 and 8 July 1989, and pycnidia were observed 8–12 days later. Microscopic examinations confirmed the presence of *S. lycopersici*. Lesions characteristic of early blight, caused by *Alternaria solani* Sorauer,

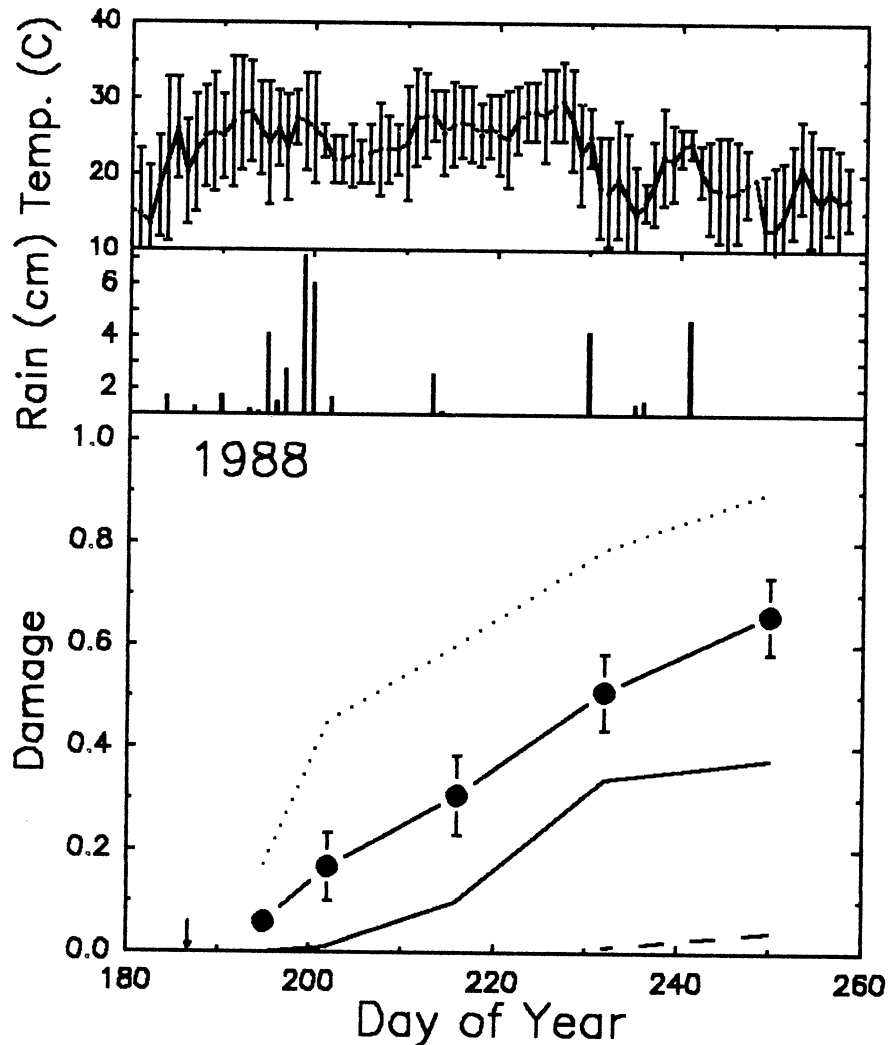


Fig. 1. Daily minimum and maximum temperatures (upper panel), daily rainfall (middle panel), and disease progress of Septoria leaf spot for nonsprayed tomato (cv. Better Boy) plots with maximum (dotted line) and minimum (solid line) values for AUDPC (bottom panel) in 1988. Also shown are averaged levels of leaf damage for nonsprayed (●) and sprayed (dashed line) tomato plots. Error bars represent selected standard deviations, and arrow indicates time of first fruit set.

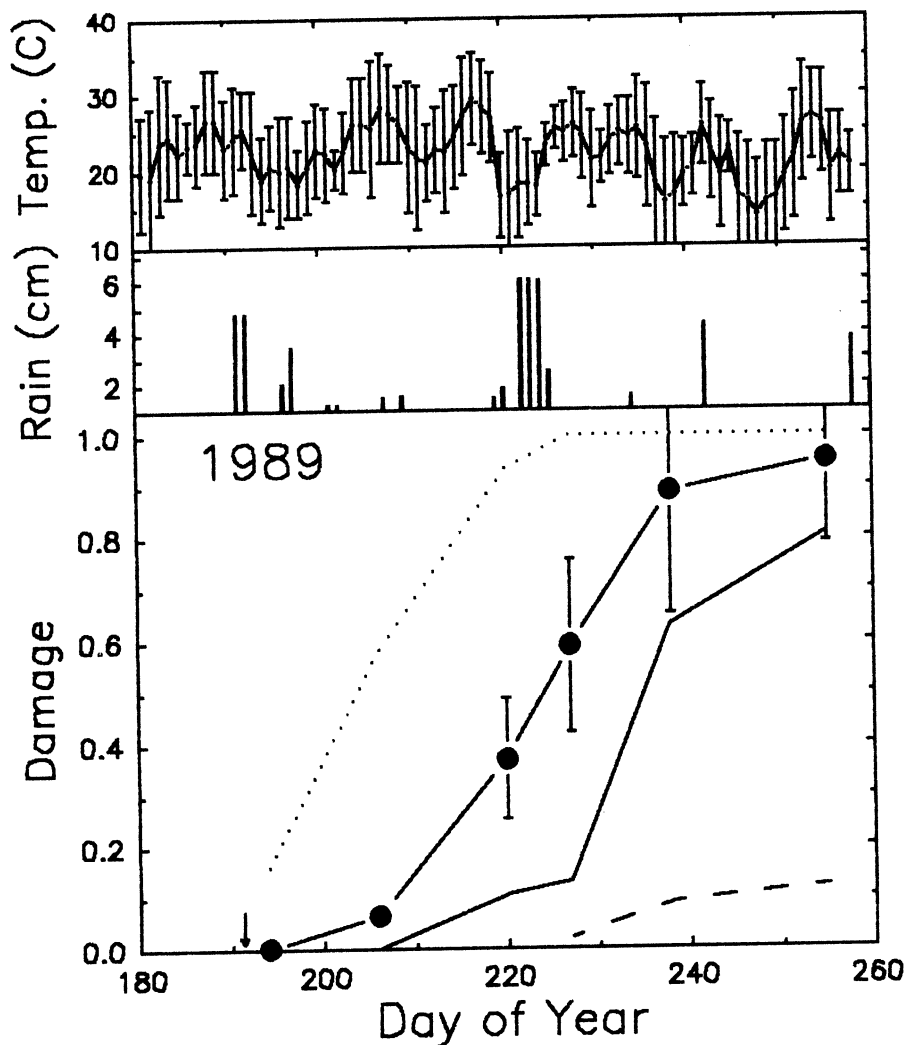


Fig. 2. Daily minimum and maximum temperatures (upper panel), daily rainfall (middle panel), and disease progress of Septoria leaf spot for nonsprayed tomato (cv. Better Boy) plots with maximum (dotted line) and minimum (solid line) values for AUDPC (bottom panel) in 1989. Also shown are averaged levels of leaf damage for nonsprayed (●) and sprayed (dashed line) tomato plots. Error bars represent selected standard deviations, and arrow indicates time of first fruit set.

Table 1. Effect of fungicide application and manual defoliation on yield, area under the disease progress curve (AUDPC), and healthy leaf area duration (HAD) on tomato plants infected with Septoria leaf spot

Year	Planting design ^y	Fungicide ^w	Defoliation ^x (%)	Yield (kg/plant)	AUDPC (days)	HAD (m/day)
1988	Grid	-	0	8.6 ab ^y	21.8 a	70
		+	0	9.6 a	1.2 b	87
		+	25	9.1 ab	— ^z	86
		+	50	7.9 ab	—	64
		+	75	6.3 b	—	50
1989	Grid	-	0	7.5 ab	28.3 a	59
		+	0	9.5 a	2.8 b	78
		+	50	6.8 ab	—	59
		+	75	5.4 b	—	44
		1989	Line	-	0	7.8 a
+	0			10.0 b	4.8 b	88

^y Grid = square (0.9 × 0.9 m), line = single file (0.9 m apart).

^w Weekly application of mancozeb (0.88 kg a.i./ha).

^x Removal of zero, one, two, or three leaves of every four on each plant.

^y Values followed by different letters are significantly different by Duncan's multiple range test at $P = 0.05$.

^z Not calculated.

were rare and were not enumerated. In general, damage from Septoria leaf spot was less severe in 1988 (Fig. 1) than in 1989 (Fig. 2). Rainfall was more frequent and temperatures were slightly lower in 1989 than in 1988. Disease progress was variable among the nonsprayed plots in both years. Nonlinear regression analyses yielded values of r ranging between 0.05 and 0.12 per day in 1988 and between 0.03 and 0.18 per day in 1989 for plants in the grid planting. Disease progressed faster in the line planting, and values of r were between 0.06 and 0.28 per day, with the larger values obtained for plots immediately adjacent to the focus. Foliar damage increased so rapidly in these plots that plants were almost completely defoliated by late July.

Yield loss was greater in 1989 than in 1988. In both years, sprayed plots had larger HADs and lower AUDPCs than nonsprayed plots (Table 1). Mean yield,

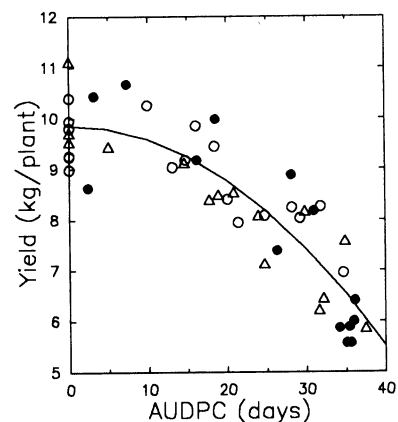


Fig. 3. Relation between yield and area under the disease progress curve (AUDPC) in nonsprayed and sprayed tomato plots in 1988 (○ = grid planting) and 1989 (△ = grid planting, ● = line planting). Overall quadratic regression is plotted.

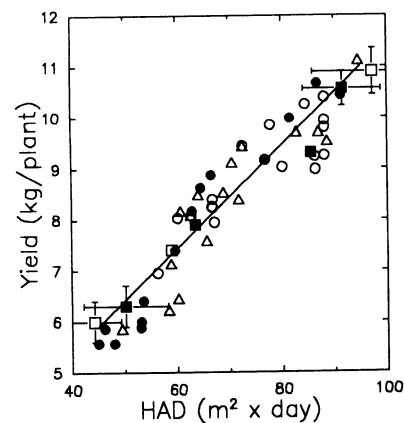


Fig. 4. Relation between yield and healthy leaf area duration (HAD) in nonsprayed and sprayed tomato plots in 1988 (○ = grid planting, □ = manually defoliated plots) and 1989 (△ = grid planting, ● = line planting, ■ = manually defoliated plots). Overall linear regression is plotted with selected standard deviations of HAD sums and yield means.

however, was not significantly affected by fungicide application because of the great variability in yield and disease progress among the nonsprayed plots. Manual removal of leaves did not significantly reduce the yield below the nondefoliated sprayed plots until 75% of the leaves were removed. Yields from plants in all manually defoliated plots were not significantly different from yields from plants defoliated by *Septoria* leaf spot. The early fruit harvest (before 20 August) in sprayed, nonsprayed, or manually defoliated plots did not differ significantly from nondefoliated sprayed controls (*data not shown*).

Final yield was positively correlated with $t_{1/2}$ ($R^2 = 0.79$) and negatively correlated with r ($R^2 = -0.68$) (*data not shown*). The relationship between yield (Y) and AUDPC was consistently curvilinear in both years (Fig. 3) and was fitted best by the quadratic model: $Y = Y_0 + A(\text{AUDPC})^2$, where the parameters Y_0 (kg/plant) and A (kg/plant/day) were fit by linear regression. Inclusion of the linear AUDPC term in this equation decreased the F value and therefore was discarded. The fitted equations describing the disease effect on yield in 1988 and 1989 in the grid plantings were $Y = 9.7 - 0.0020(\text{AUDPC})^2$, ($R^2 = 0.70$, $df = 17$) and $Y = 9.7 - 0.0027(\text{AUDPC})^2$, ($R^2 = 0.83$, $df = 13$), respectively. In 1989 the fitted equation in the line planting was $Y = 10.3 - 0.0033(\text{AUDPC})^2$, ($R^2 = 0.80$, $df = 15$). Because these equations did not significantly differ, they were combined, and the fitted equation for all plots was $Y = 9.9 - 0.0028(\text{AUDPC})^2$, ($R^2 = 0.80$, $df = 47$).

Yield in both years was linearly correlated with HAD ($Y = B + C \text{HAD}$), where the parameters B (kg/plant) and C (kg/plant/day) were fit by linear regression, and the equations from the 1988 and 1989 grid plantings and the 1989 line planting were not significantly different (Fig. 4). In addition, the equation describing the relation between yield and HAD from sprayed plots that were defoliated manually did not significantly differ from plots with *Septoria* leaf spot. The fitted equation that best described the overall relation between yield and HAD was $Y = 1.3 + 0.10 \text{HAD}$, ($R^2 = 0.82$, $df = 47$).

DISCUSSION

Estimates of disease progress based on the total potential leaf area yielded a quadratic relation between AUDPC and

yield (Fig. 3), which suggested that a certain level of leaf damage could be tolerated without appreciable yield loss. The AUDPC values above a threshold level of about 10–15 days (which corresponded to $t_{1/2}$ values of 45–55 days) were associated with less yield. In our experiments, the $t_{1/2}$ values indicated that *Septoria* leaf spot did not significantly reduce yields when leaf damage was less than 50% by mid-August. Further refinement and validation of this model may provide the basis for a fungicide spray schedule based on action thresholds (19) and conidial release predictions as seen for other diseases of tomato (13) and for other crops (9).

Yield loss due to *Septoria* leaf spot was mainly a late-season phenomenon, since early yield loss was negligible. This result is in agreement with the relative insensitivity of the yield from early-season determinant tomato plants to *Septoria* leaf spot damage (4). Part of this late-season phenomenon may be environmental, as cool, wet weather conditions favoring the spread of this disease often prevail late in the growing season in the northeastern United States. Also, increases in plant stress, light penetration, and/or fruit temperature due to the more open plant canopy may hasten ripening in defoliated plants and produce early yields similar to the sprayed plots.

The threshold-type yield response curve also may be partially due to the rapidly increasing leaf area over the course of the fruit-filling period, which may partially compensate for loss of leaves. In the 4 wk following first fruit set, leaf area increased fourfold, from about 0.8 m² to 3.0 m² per plant. The nonlinear yield response to *Septoria* leaf spot damage can hinder an accurate yield prediction when disease is not distributed homogeneously within a field (5,6).

Manual defoliation has been reported to increase the specific net assimilation in remaining tomato leaves (18). This may explain why in the present study 75% of the leaves had to be removed before yield loss occurred. This compensatory response might be the same for diseased plants, since the observed relation between tomato yield and HAD (17) was similar for plants defoliated either by hand or by *Septoria* leaf spot (Fig. 4). Although the rate of assimilate production in leaves was not measured, the similarity between the above yield relations suggests that this disease does not appreciably reduce the rate of carbon

assimilation via diffusible toxins released from the lesions (8). Therefore, the major effect of this disease on yield was the direct reduction of HAD, since both diseased and healthy leaflets are abscised when a partially diseased leaf is shed from the plant. For all of the above reasons, HAD appears to be the best predictor of yield.

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