Plant Mortality Distribution and Crop Losses in Flue-Cured Tobacco

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ABSTRACT

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Relationships between crop losses in flue-cured tobacco (*Nicotiana tabacum*) and the distribution of plant mortality due to black shank, caused by *Phytophthora parasitica* var. *nicotianae* race 0, or injection of glyphosate were investigated in Virginia during 1986–1987. The number of plants compensating for the yield of adjacent dead plants decreased as plant mortality became increasingly clustered. Plot yield and gross economic returns increased linearly with the number of compensating plants per plot. In 1986, relationships between plant mortality distribution and plot yield or gross economic returns were unaffected by cause of death (*P. p. nicotianae* vs. a 41% solution of glyphosate) or inoculation date (4 vs. 6 wk after transplanting). In 1987, injection of *P. p. nicotianae* or glyphosate 4 wk after transplanting had no effect on the relationships. Although yield and gross economic returns were reduced in 1987 by inoculation 6 wk after transplanting, yield and economic returns increased faster with decreased clustering of mortality when *P. p. nicotianae*, rather than glyphosate, was injected into treated plants. Compensating plants produced higher yields than individual plants from control plots, but yields from compensating plants were not affected by the number of neighboring dead plants. Lower grade indices were sometimes noted for compensating plants. Lower quality characteristics from compensating plants were also sometimes associated with the number of adjacent dead plants. Relationships between quality characteristics of compensating plants and adjacent plant mortality were more consistent for cv. K 326 than for cv. K 394 and when injections involved *P. p. nicotianae* rather than glyphosate. Although the 2–6% variation in plot yields resulting from changes in plant mortality distribution was statistically significant, it may not be large enough to require inclusion of mortality distribution in models for predicting yield losses resulting from reduced stands of flue-cured tobacco. The highly significant relationships between plot yield and gross economic returns and the number of compensating plants (rather than characteristics of individual compensating plants) suggest that reasonably accurate crop loss estimates could be based on stand counts performed during critical periods in the growing season.

Additional keywords: compensation, epidemiology

Phytophthora parasitica Dastur var. *nicotianae* (Breda de Haan) Tucker causes black shank, a root and stem rot that is one of the most economically important diseases of tobacco (*Nicotiana tabacum* L.) in the United States. Estimated annual losses attributed to this disease routinely exceed $10 million in North Carolina alone (20). Resistant cultivars (2), crop rotation (8,18), and early postharvest destruction of tobacco roots and stalks (17) reduce losses from tobacco black shank, but economically acceptable control of this disease frequently requires application of the systemic fungicide metalaxyl (4,16,22,26). Use of metalaxyl for control of black shank is expensive, costing producers an estimated $158/ha for the minimum rate of 1.12 kg a.i./ha.

Much of the epidemiological research on tobacco black shank has focused on predicting disease incidence based on inoculum density (5,6,9) and environmental variables such as soil moisture and soil temperature (7,13,19,23,25). A quantitative model of the relationship between disease incidence and subsequent crop losses would be useful in optimizing management of tobacco black shank.

Black shank induces crop losses primarily by reducing host populations. However, tobacco plants have the capacity to compensate significantly for the yield lost when adjacent plants have been killed (3). As might be expected, the earlier that adjacent plants die, the more compensation that can occur. The effects of spatial aspects of disease incidence or severity on expected crop losses have been discussed by Hughes and James (10–12,14). They concluded that increased aggregation of disease should result in increased crop losses when losses depend on the number of surviving plants in the host population that can produce compensatory yield. Effects of disease aggregation on crop losses may increase with increasing disease incidence (12). However, the black shank pathogen may infect but not kill plants of partially resistant cultivars (24). Such infection could reduce the compensatory yield otherwise produced by plants adjacent to disease foci. A detailed analysis of yield loss resulting from such "hidden black shank" has not been published. This report examines the effects of plant mortality distribution on crop losses in flue-cured tobacco. It also investigates the economic implications of reduced vigor in infected but surviving flue-cured tobacco plants.

MATERIALS AND METHODS

Experiments were conducted in 1986 and 1987 at the Southern Piedmont Agricultural Experiment Station, Blackstone, Virginia, in a field naturally infested with race 0 of *P. p. nicotianae*. Tobacco had been planted in the field continuously since 1974. The field was broadcast-fumigated with 560 kg/ha of a 67:33 mix-

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ture of methyl bromide and chloropicrin on 28 March 1986 and 10 April 1987. Fumigant was injected 15–20 cm deep through chisels spaced 30 cm apart. The field was covered with polyethylene for at least 72 hr after fumigation and cultivated after removal of the plastic.

The standard preplant pesticides fenamiphos, chlorpyrifos, aldicarb, and pebulate were applied each year for control of tobacco cyst nematodes (*Globodera tabacum* subsp. *solanacearum* (Miller & Gray) Behrens), soil insects, foliar insects, and weeds, respectively. An additional application of napropamide was made after the final cultivation to extend weed control throughout each growing season. Plots were fertilized by addition of 67, 45, and 134 kg/ha of nitrogen, phosphorus, and potassium, respectively. Plots were hand-transplanted on 13 May 1986 and 12 May 1987 and hand-harvested as leaves ripened. Leaves were cured in conventional stick barns. Other cultural practices conformed with those recommended for flue-cured tobacco by the Virginia Cooperative Extension Service (15).

A split-split-plot experimental design was used each year with four replications. Field plots consisted of three 12.3-m rows on 1.2-m centers. Plants were spaced 50.8 cm apart within each row, with the two end plants serving as guard plants. The center row of each plot was treated, while the adjacent two rows functioned as borders. Main plots consisted of flue-cured tobacco cultivars with either low (cv. K 326) or high (cv. K 394) levels of resistance to black shank. Subplots consisted of time of treatment application: 4 or 6 wk after transplanting. Sub-subplots consisted of an untreated control or stem injection of six of the 24 plants within the center row of each plot with 3 ml of a mycelial suspension of *P. p. nicotianae* race 0 or an equal quantity of a 41% formulation of glyphosate (Roundup). Injections were performed to create the following patterns of plant mortality: 1) six individual, but not adjacent, dead plants; 2) three groups of two dead plants each; 3) two groups of three dead plants each; and 4) one group of six consecutive dead plants (Table 1).

Fungal inoculum for the first inoculation date in 1986 was prepared by removing the aerial mycelium from 30 10- to 14-day-old cultures of *P. p. nicotianae* race 0 on oatmeal agar and incubating the mycelium from five 9-cm-diameter petri dishes in 5 ml of a 0.01 M KNO_3 solution for 4–5 days. On the day that inoculations were to be performed, the incubated mycelium was bulked, comminuted in 400 ml of cold deionized water, and diluted with additional cold deionized water to a final volume of 1 L. Fungal inoculum was stored in an iced bucket until use. Inoculum preparation methods were similar for other inoculations, except that 45 petri dishes of the pathogen were used to prepare 1.5 L of inoculum.

Inoculation procedures were adapted from those described by Shew (24). Plants to be inoculated were wounded by drilling a 0.28-cm-diameter hole at a 45° angle through the taproot approximately 2.5 cm below the soil line. A syringe-type repeating pipette was then used to introduce 3 ml of fungal inoculum into each inoculated plant. Fungal inoculations were performed 12 and 27 June in 1986 (30 and 45 days after transplanting, respectively). Herbicide injections employed 3 ml of a 41% solution of glyphosate in the same manner as described for the fungal inoculations. Glyphosate injections were delayed for 19–20 days after inoculations with *P. p. nicotianae* in an attempt to synchronize plant mortality from the herbicide and death from black shank. Inoculations in 1987 were performed on 8 and 22 June and 17 June and 10 July (26 and 40 days vs. 35 and 58 days after transplanting) for *P. p. nicotianae* and glyphosate, respectively.

Table 1. Plant mortality distribution treatments imposed on plots of flue-cured tobacco by stem inoculation with race 0 of *Phytophthora parasitica* var. *nicotianae* or by injection of glyphosate

Treatment	Plant mortality distribution[z]	Dead plants/focus	Potentially compensating plants/plot
1	ooooXooXooXooXooXooXoooo	1	12
2	ooooooXXoooXXoooXXoooooo	2	6
3	oooooooXXXooooXXXooooooo	3	4
4	oooooooooXXXXXXooooooooo	6	2

[z] o = Untreated plant, X = inoculated or injected plant.

Table 2. Length of time required for 90–100% mortality of plants after inoculation with *Phytophthora parasitica* var. *nicotianae* or injection of glyphosate

Year	Cultivar	Inoculation date (weeks after transplanting)[z]	Days between treatment and 90–100% mortality		Days between death from glyphosate vs. death from *P. p. nicotianae*
			P. p. nicotianae	Glyphosate	
1986	K 326	4	14	9	+14
		6	13	9	+15
	K 394	4	28	9	−7
		6	42	9	−14
1987	K 326	4	21	12	0
		6	21	12	+9
	K 394	4	44	5	−30
		6	30	12	0

[z] Inoculations 4 wk after transplanting were performed on 12 June and 1 July in 1986 and 8 and 17 June in 1987 for *P. p. nicotianae* and glyphosate, respectively. Stem injections of *P. p. nicotianae* vs. glyphosate 6 wk after transplanting were given on 27 June and 16 July in 1986 and 22 June and 10 July in 1987.

Number and location of permanently wilted or dead plants in each plot were recorded weekly throughout the growing season. Individual leaves from remaining plants were harvested when ripe. Cured leaves were weighed and graded by USDA marketing service inspectors. Cured leaf weights and grades were also obtained for two randomly selected plants adjacent to one or more inoculated or injected plants in the center row of treated plots. Weights and grades were also obtained from two randomly selected plants in the center row of control plots for comparison. Average market prices were obtained from USDA Agricultural Marketing Service–Tobacco Division market news reports distributed by the Virginia Department of Agriculture and Consumer Services. A 1–99 index that groups federal flue-cured tobacco grades according to equivalent economic value (27) was also used to estimate the quality of each harvest. Gross economic returns for each harvest were estimated as the product of the total cured leaf weight harvested from the plot and the average market price of the appropriate grade for that harvest. Gross economic returns for each plot were calculated as the sum of the gross economic returns from multiple harvests from the same plot. Data were evaluated by analysis of variance and linear regression with the Statistical Analysis System (21). Residual plots were obtained and examined for each regression model developed. Unless otherwise indicated, no systematic patterns were observed. Coefficients of determination (R^2) are presented for each regression model.

RESULTS

Within 14 days of inoculation with *P. p. nicotianae* in 1986, 90–100% of plants of K 326 were permanently wilted (Table 2). Mortality of K 326 occurred somewhat later in 1987. Plants of the more resistant K 394 took longer to die. In contrast to the variation in time between inoculation and mortality for plants inoculated with *P. p. nicotianae*, 100% of the plants injected with glyphosate in 1986 and 1987 were dead within 9 and

12 days, respectively. With the exception of K 394 inoculated 4 wk after transplanting in 1987, mortality was complete in plots containing glyphosate-injected plants within 1–2 wk of their counterparts inoculated with *P. p. nicotianae*. All inoculated or injected plants were dead before the first harvest and were not harvested. One noninoculated plant died of black shank in each of three plots in 1986 and in each of four plots in 1987.

Increased clustering of plant mortality resulted in decreasing numbers of compensating plants in each experimental plot (Table 1). Plot yield and gross economic returns increased linearly with the number of plants adjacent to a focus of plant mortality, i.e., with the number of compensating plants per plot (Figs. 1 and 2). Crop losses, therefore, increased as plant mortality distribution became increasingly clustered. The relationship between plot yield or gross economic returns and plant mortality distribution was linear for both cultivars and after inoculation with *P. p. nicotianae* or injection of glyphosate at either date in 1986 (Fig. 1). Plant mortality distribution also had a linear effect on plot yield and gross economic returns across cultivars and after inoculation with *P. p. nicotianae* or injection of glyphosate when inoculations were performed 4 wk after transplanting in 1987 (Fig. 2). Losses in plot yield and gross economic returns were similar across cultivars and treatments in 1986 and when inoculations or injections were performed 4 wk after transplanting in 1987, but losses increased faster ($P \leq 0.05$) when neighboring plants were injected 6 wk after transplanting with *P. p. nicotianae* rather than glyphosate (Fig. 2). All regression models were significant at $P \leq 0.05$ except for the model relating 1987 gross economic returns to the number of compensating plants after inoculation with glyphosate 6 wk after transplanting ($P \leq 0.09$). However, lack-of-fit tests for the model relating 1987 gross economic returns to mortality distribution indicated a significant fit to the data. Grade indices for experimental plots were unaffected by any of the experimental variables included in the study in 1986 or 1987.

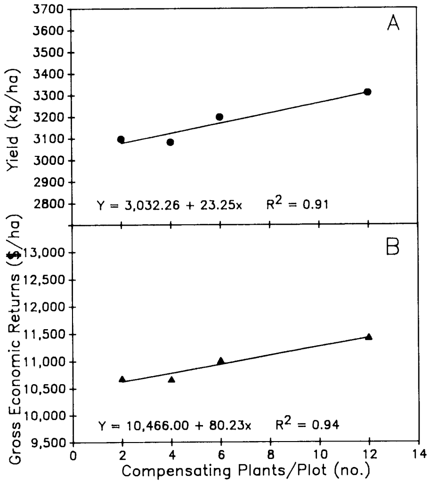

Fig. 1. Effect of mortality distribution on **(A)** yield and **(B)** gross economic returns for flue-cured tobacco in 1986. The fewer the number of compensating plants (those adjacent to a focus of mortality) in each plot, the more clustered the distribution of mortality.

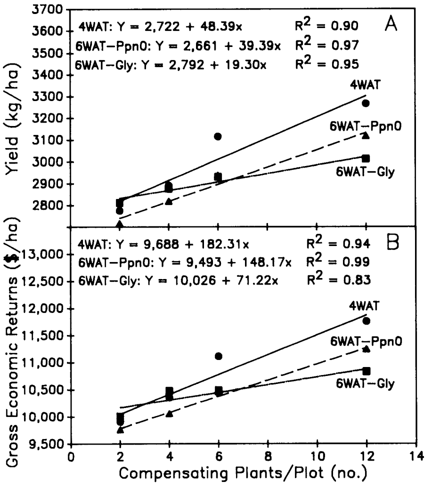

Fig. 2. Effect of mortality distribution on **(A)** yield and **(B)** gross economic returns for flue-cured tobacco in 1987. The fewer the number of compensating plants per plot (those plants adjacent to a focus of mortality), the more clustered the mortality distribution. 4WAT refers to data combined over inoculation or injection 4 wk after transplanting. 6WAT-Ppn0 and 6WAT-Gly refer to inoculation 6 wk after transplanting with 3 ml of a mycelial suspension of *Phytophthora parasitica* var. *nicotianae* race 0 and injection with a 41% solution of glyphosate, respectively.

Table 3. Effects of treatment on agronomic characteristics of compensating plants (individual flue-cured tobacco plants adjacent to a simulated disease focus)

Year	Cultivar	Time of treatment (weeks after transplanting)	Inoculum type	Yield (g/plant)	Grade index (1–99)
1986	K 326 and K 394	···	Untreated	237.49 b[z]	48.2 a
		4 and 6	Glyphosate	274.91 a	45.3 a
		4 and 6	*Phytophthora parasitica* var. *nicotianae*	276.67 a	41.5 b
1987	K 326	···	Untreated	283.49 b	47.8 a
		4	Glyphosate	335.53 a	39.6 b
		4	*P. p. nicotianae*	360.79 a	39.4 b
		···	Untreated	288.93 b	42.0 a
		6	Glyphosate	322.07 ab	43.5 a
		6	*P. p. nicotianae*	349.05 a	38.6 a
	K 394	···	Untreated	299.44 b	40.0 a
		4	Glyphosate	367.45 a	40.2 a
		4	*P. p. nicotianae*	376.89 a	42.2 a
		···	Untreated	262.46 b	54.0 a
		6	Glyphosate	325.40 a	43.0 b
		6	*P. p. nicotianae*	340.89 a	44.8 b

[z] Means within a column followed by the same letter(s) are not significantly different according to the Waller-Duncan test (*k*-ratio = 100). Comparisons are valid only within year and within cultivar and inoculation date in 1987.

Individual plants next to inoculated or injected plants yielded more than plants with apparently healthy neighbors (Table 3). Yields from compensating plants did not increase significantly ($P \leq 0.05$) with the size of an adjacent simulated disease focus. Grade indices for leaf harvested from compensating plants declined significantly ($P \leq 0.05$) when adjacent plants were killed by inoculation with *P. p. nicotianae* in 1986. Reduced grade indices were also noted for compensating plants in 1987 for cv. K 326 inoculated 4 wk after transplanting and for cv. K 394 inoculated 6 wk after transplanting. No significant relationship was observed between size of an adjacent disease focus and grade indices for leaf from compensating plants in 1986, but grade indices were related curvilinearly ($P \leq 0.11$) to increasing numbers of adjacent plants inoculated with *P. p. nicotianae* in 1987 (Fig. 3).

DISCUSSION

As expected, losses in flue-cured tobacco yield and gross economic returns increased as the distribution of plant

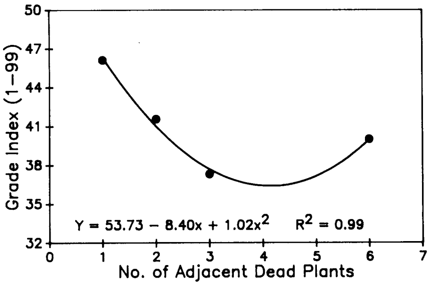

Fig. 3. Flue-cured tobacco grade index (25) vs. the size of an adjacent focus of mortality (number of adjacent dead plants) created by injecting race 0 of *Phytophthora parasitica* var. *nicotianae* in 1987.

mortality became increasingly clustered in both years of this study (10–12,14). This trend was consistent across inoculation with a biotic pathogen (*P. p. nicotianae*) vs. injection of a herbicide either 4 or 6 wk after transplanting and was detected for cultivars with both high and low levels of resistance to the pathogen. Plant mortality distribution influenced crop loss in these experiments by changing the number of individual plants contributing compensatory yield (Table 1). The linearity of the relationships between the number of compensating plants per plot and plot yields or gross economic returns (Figs. 1 and 2) and the lack of a significant effect of mortality focus size on the yield from adjacent compensating plants suggest that plant mortality distribution influenced crop losses solely by changing the number of compensating plants. The importance of the number of healthy plants surrounding a focus of disease also implies that location of disease foci within a field may be as important as the general distribution of mortality in altering disease losses, because concentrations of disease incidence along field edges would be bordered by fewer plants than clumps of disease within a field.

The apparent similarity in yield from plots inoculated with *P. p. nicotianae* or injected with glyphosate may be evidence against economically significant reductions in the yield of flue-cured tobacco plants not showing symptoms on aboveground plant parts. This result is important because partial damage to plants bordering dead neighbors could have reduced the role of compensatory yield in determining the effect of spatial heterogeneity on crop losses (11). Spatial distribution of mortality would have had no effect on crop losses if plants bordering mortality foci had produced the same yield as healthy plants surrounded by other healthy plants. Further yield reductions from plants adjacent to mortality foci would have caused crop loss to increase with decreasing aggregation of mortality because the total number of damaged plants would then increase with decreasing aggregation of mortality.

Quality is a critical component of crop value that could also have been affected by distribution of plant mortality (14). Although yields from plants adjacent to mortality foci increased, quality decreased. Grade indices from compensating plants sometimes declined even further with increasing numbers of adjacent dead plants, but this effect was often not large enough to be significant.

The absence of root damage on plants adjacent to mortality foci caused by *P. p. nicotianae* could be attributed to host resistance and unfavorable environmental conditions. Precipitation levels were low in both years of the study, particularly in July. However, irrigation brought total moisture levels close to the 30-yr average (Table 4). The lack of economically significant crop losses arising from reduced vigor rather than plant death suggests that models for adjusting flue-cured tobacco yields for reduced plant stands (3) could be adapted to accurately estimate crop losses caused by black shank and perhaps other stand-reducing diseases.

Although statistically significant, the increases in crop loss with increased clustering of plant mortality may not have been large enough to be important in a practical sense. Losses in flue-cured tobacco yield from a 30% incidence of black shank were altered by only approximately 2–6% (Figs. 1 and 2). Black shank usually occurs in commercial flue-cured tobacco fields at incidences much lower than 30%. Informal disease thresholds for black shank control only require disease incidences of 6% to justify application of the maximum fungicide rate. In addition, disease aggregation may exert a lesser effect on crop losses at low vs. high disease incidences (12). Research investigating the importance of plant mortality distribution at disease incidences below 10% may be necessary to confirm the importance of disease distribution in optimizing management of tobacco black shank.

Much of the delay in development of a crop loss model for tobacco black shank may be due to difficulties in predicting disease incidence based on pathogen propagule densities and/or environmental variables (1,6,7). The results of this study, together with those from a theoretical study of the relationship between spatial distribution of crop injury and crop losses (10), suggest that a model predicting yield losses based on plant stand (3) may provide a useful approach for estimating crop losses in infested flue-cured tobacco fields. Accurate crop loss models based on such easily obtainable data could facilitate development of more formal economic thresholds for management of a number of economically important wilt diseases of tobacco. A similar approach may be useful for wilt diseases of other row crops. Further work is necessary to examine the accuracy of estimating black shank incidence by various methods and to confirm the accuracy of stand-adjustment models in predicting losses in flue-cured tobacco yield and quality due to black shank.

Table 4. Annual monthly precipitation, irrigation, and number of days of measurable (0.13 cm) precipitation recorded at the Southern Piedmont Agricultural Experiment Station, Blackstone, Virginia, in 1986 and 1987 and 30-yr averages for monthly precipitation

	1986[x]			1987[x]			
Month	Total rainfall (cm)	Total irrigation (cm)[y]	No. of rain days[z]	Total rainfall (cm)	Total irrigation (cm)[y]	No. of rain days[z]	Av. for 30 yr
May	8.00	0	5	4.57	0	2	8.69
June	2.92	5.08	3 (2)	3.18	0	3	9.32
July	5.08	7.62	4 (3)	5.08	9.32	3 (3)	13.94
August	20.07	0	8	4.44	6.78	6 (2)	10.21
September	2.03	0	0	14.35	0	9	9.07
October	7.62	0	4	3.81	0	2	6.88

[x] Plants were inoculated with *Phytophthora parasitica* var. *nicotianae* on 12 or 27 June 1986 and on 8 or 22 June 1987. Glyphosate injections were given on 1 or 16 July 1986 and on 17 June or 10 July 1987.

[y] Irrigation was applied in 2.54- to 3.30-cm increments in 1986 and 1987 on an as-needed basis.

[z] Number of days rainfall exceeded 25 mm after the date of inoculation. Numbers in parenthesis are number of days the experiment was irrigated.

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