Progress and Spread of Dark Leaf Spot in Cabbage

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ABSTRACT

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The progress and spread of dark leaf spot (*Alternaria brassicicola*) in three cultivars of cabbage (*Brassica oleracea* var. *capitata*) were characterized in two seasons. The intensification of disease in time at each of six points along a gradient from a line source of diseased plants resulted in disease progress curves that were almost symmetrically sigmoidal. Three growth models (logistic, Gompertz, and Weibull) were fitted to the severity values by nonlinear regression. The shape parameter (c) for the Weibull function averaged 3.61 (ranged from 2.40 to 6.36). The average daily epidemic rates with the logistic model were $k_l = 0.06$ in the winter and $k_l = 0.11$ in the spring. Final disease severity (y_f) at the source averaged 0.52 in the winter and 0.97 in the spring. In both seasons, gradients of disease were very steep from the source to 1 m. The nearly flat gradients from 1 to 6.7 m were fit satisfactorily by each of eight gradient models, but the total gradient was described adequately only by the modified model of Gregory and the Hoerl function. Initial disease (time of appearance and amount), epidemic rate, and y_f were influenced by distance from the source of inoculum. The three cultivars of cabbage differed in apparent susceptibility to dark leaf spot as determined by average epidemic rates, y_f, isopathic rates, areas under disease progress curves (AUDPC) (temporal), and volumes under disease progress surfaces (VUDPS) (temporal and spatial); however, initial disease severities and slopes of disease gradients were similar for the three cultivars. In the spring, yield was correlated negatively with y_f and AUDPC.

Dark leaf spot of cabbage (*Brassica oleracea* L. var. *capitata* L.), incited by *Alternaria brassicicola* (Schwein.) Wiltshire, causes serious losses in production worldwide (1,5,9,14,23,28). Strategies for control of dark leaf spot include reduction of inoculum in seed (9,14) and application of fungicides (9,28). Improvement in control of disease in any pathosystem often can be made if knowledge of the intensification of disease in time (progress) and movement of disease in space (spread) is available. The most efficient determination of the probable effect of various control practices on the progress and spread of disease is by the use of models that use the range of values observed from natural epidemics.

Of the several models proposed to describe the progress of polycyclic diseases over time, the logistic and the Gompertz equations are used most widely (2). The proportions of disease (y) are linearized by $Y = \ln[y/(1-y)]$ and $Y = -\ln[-\ln(y)]$, respectively. A third model, the Weibull function (24,29), has received much attention recently because of its flexibility and simplicity. With this latter function, the disease proportions are linearized by $Y = \{\ln[1/(1-y)]\}^{1/c}$ (10).

The most popular model to explain disease spread is the power function of Gregory (12), which is $y = ax^b$, in which y is the proportion of disease at x units of distance from the source, a is the value of y at $x = 1$, and b is the rate of change in y with change in x; i.e., b is an estimate of the slope of the gradient and the value of b is usually negative. The transformation equation is $\log(y) = \log(a) + b \log(x)$. However, as originally proposed, this model cannot be used to predict disease at the inoculum source (distance $x = 0$), as log(0) has no definition (22). Gregory's model was modified by Mundt and Leonard (22) to include a truncation factor (m) [$y = a(x + m)^b$], which allows the estimation of disease at the source when $x = 0$. Values of m were approximately the radii of the sources (22).

Other models of gradients have been described. The model of Kiyosawa and Shiyomi (15) [$y = a \exp(-bx)$] was used to describe spore dispersal in multilines. Lambert et al (16) designed a generalized model [$y = a \exp(ax^n)$] with mixed power and exponential terms and a shape parameter n. Maffia (19) used Hoerl's function (7) to characterize hollow-shaped curves [$y = ax^b \exp(nx)$] to describe gradients of bean rust. Sometimes $\ln[y/(1-y)]$ or $-\ln[-\ln(y)]$ is plotted over $\log_{10}(x)$ or x (4,8,17,19,21) to linearize hollow-shaped curves.

In this study, the observed progress and spread of dark leaf spot in three cabbage cultivars during two seasons were evaluated by fitting three models for progress and eight models for spread. In addition, several epidemic variables were evaluated for their ability to detect differences in cultivar susceptibility to this disease. A preliminary report has been issued (11).

MATERIALS AND METHODS

Crop culture. Field trials were conducted at the Agricultural Research and Education Center, Hastings, FL, on a sandy loam soil. Plots (7.3 × 4.1 m) were assigned randomly in each of four replicates to three cultivars of cabbage: Abbott & Cobb No. 5 (Abbott and Cobb, Inc., Feasterville, PA), Gourmet (Ferry Morse Seed Co., Mountain View, CA), and Market Prize (Joseph Harris Co., Rochester, NY). Each plot contained four rows of plants and was buffered by 6 m of uncultivated land at the end of the rows (east and west of the plants) and 4.1 m parallel to the rows (north and south of the plants). Temperature, relative humidity, and rainfall in the plot area were recorded with a hygrothermograph and recording rain gauge.

Standard commercial practices were used to produce seedlings in outdoor seedbeds. Transplants were set 30 cm apart in rows 1.02 m apart on 8 October 1985 for the winter season and 2 April 1986 for the spring season. Applications of approved insecticides were made to the entire crop as needed.

Inoculation. Cultures of *A. brassicicola* were obtained from the Florida Type Culture Collection of the Florida Division of Plant Industry in Gainesville. The cultures were maintained on 20% V-8 juice agar (20). Six-day-old cultures were flooded with sterile deionized water containing 0.01% Triton X-100 (Rohm and Haas, Inc., Philadelphia, PA) and then rubbed with a curved glass rod. The concentration of suspended conidia was determined with a hemacytometer and diluted to about 5×10^4 conidia ml^{-1}. To create a line source of inoculum, the conidial suspension was sprayed on individual plants (5–7 sec $plant^{-1}$) on the border of each plot (east border in the

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winter, west border in the spring) with a CO_2-pressurized sprayer adjusted to 1.4 kg cm^{-2}. Inoculated plants were covered with polyethylene bags for 24 hr to prevent spore removal by wind or rain. Plants were inoculated when the transplants were 36 days old in the winter season and 26 days old in the spring season.

Evaluation of disease. Disease severity (proportion of leaf area with symptoms) was determined with the aid of the Horsfall-Barratt scale (13). In the winter season, six weekly observations were made from days 28 to 63 after inoculation. In the spring test, eight weekly observations were made from day 11 to day 60. Plants on the two inner rows were evaluated for disease at the line source (0 m) and at 0.3, 1.2, 2.7, 4.6, and 6.7 m from the line source. The Horsfall-Barratt rating scores were converted to disease proportions with conversion tables (26).

Characterization of disease in time and space. Curves for the progress of disease were constructed from estimates of disease severity over time for each observation point. A nonlinear curve-fitting program (3) was used to fit three models to the data: logistic (2), $y_t = 1/\{1 + \exp[-(a + k_l t)]\}$; Gompertz (2), $y_t = \exp[-a \exp(-k_g t)]$; and Weibull (24), $y_t = 1 - \exp\{-[k_w(t - a)]^c\}$. In these models, y_t is the disease proportion at time t, and k is the rate parameter. The a term in the three models is a parameter for initial disease; in the logistic model, $a = \ln[y_0/(1 - y_0)]$ and in the Gompertz model, $a = -\ln(y_0)$. In the Weibull function, a positions the curve on the time axis, and c is the curve-shape parameter. In these analyses, y_0 was the amount of disease at first observation, and the maximum amount of possible disease (y_{max}) was assumed to be 1.0. The R^2 and the residual sum of squares were used to evaluate the magnitude of variation among the data that was explained by the model (goodness of fit) (6,7). The pattern of scatter when residuals ($y_{observed} - y_{predicted}$) were plotted vs. time was used to confirm the appropriateness of the model (6). The progress of disease among cultivars was compared with observed initial disease (y_0), epidemic rate (k), final disease severity (y_f), and the area under the disease progress curve (AUDPC) (27).

Similar statistical methods were used to evaluate models for the spread of disease in space. A nonlinear curve-fitting program (3) was used to evaluate five gradient models: Gregory (12), $y = ax^b$; modified Gregory (22), $y = a(x + m)^b$; Kiyosawa and Shiyomi (15), $y = a \exp(-bx)$; Lambert et al (16), $y = a \exp(-bx^n)$; and Hoerl (7,19), $y = ax^b \exp(nx)$. In these models, y is the proportion of disease severity at x units of distance from the inoculum source and b is the slope parameter. In the model of Gregory (12), a is the disease proportion at one unit of distance from the source, whereas in the modified Gregory model (22), a is the disease proportion at $1 - m$ units of distance. In the models of Lambert et al (16) and Hoerl (7), n is a parameter that modifies the curve shape, and this parameter increases the flexibility and applicability of the models if curve shapes vary.

Three other gradient models were examined in their linearized form because the models contained logarithms both to the base e (ln) and to the base 10 (log), and the nonlinear equations were rather complex. These models were the logistic gradient model (4), $\ln[y/(1 - y)] = \ln[a/(1 - a)] - b \log(x)$; the Gompertz gradient model (8), $-\ln[-\ln(y)] = \ln[-\ln(a)] - b \log(x)$; and a variant of the logistic gradient model (21), $\ln[y/(1 - y)] = \ln[a/(1 - a)] - bx$. In these regressions, a was the average proportion of disease on the plants closest (0.3 m) to the inoculum source. These latter transformations were compared by the R^2 and for significance of the slope of the regression by Student's t statistic.

The volume under the disease progress surface (VUDPS), as suggested by Maffia (19), and the isopathic rate (rate of movement in space of a given level of disease severity) (4) were calculated from the progress and spread characteristics of the disease. The VUDPS was calculated from the AUDPCs at each point in space as: VUDPS $= \Sigma\{[(A_{i+1} + A_i)/2]\ [x_{i+1} - x_i]\}$; where A_i = the AUDPC at x_i units of distance from the source. The isopathic rates were calculated from the source to 6.7 m for the $y = 0.1$ isopath in the winter season and for the $y = 0.05$ isopath in the spring season.

Yield. Cabbage heads were hand-harvested and weighed individually on day 70 after inoculation in the winter and on day 73 in the spring. Yields were expressed as kilograms of fresh weight m^{-2}. Yields were regressed vs. y_f or AUDPC with a linear, exponential, or power equation.

RESULTS

The initial spread of disease away from the source was later in the winter season than in the spring season despite similar weather at the beginning of the epidemics in both seasons. In the 10 days after inoculation of the source plants in each season, there were two periods of rainfall with 2.5 mm of rain each, and the average daily mean temperature was 24 C. The intensification of disease in time was slower in the winter season presumably because of colder temperatures. The mean daily temperatures in the winter were 7–23 C, whereas in the spring, the mean temperatures were 17–32 C. In the winter at 28 days after inoculation, a

Table 1. Initial disease (y_0), final disease (y_f), and epidemic rates (k) for dark leaf spot (*Alternaria brassicicola*) on three cultivars of cabbage in two seasons[a]

Cultivar	Distance (m)	Winter 1985–1986					Spring 1986				
		y_0	y_f	k_l	k_g	k_w	y_0	y_f	k_l	k_g	k_w
Market Prize	0.0	0.14	0.65	0.030	0.016	0.016	0.04	0.99	0.095	0.049	0.026
	0.3	0.03	0.38	0.042	0.015	0.012	0.01	0.66	0.091	0.032	0.017
	1.2	0.02	0.30	0.044	0.014	0.011	0.00	0.17	0.128	0.026	0.010
	2.7	0.02	0.23	0.040	0.012	0.011	0.00	0.09	0.117	0.022	0.007
	4.6	0.01	0.15	0.051	0.013	0.009	0.00	0.07	0.112	0.020	0.007
	6.7	0.00	0.21	0.054	0.014	0.010	0.00	0.06	0.108	0.019	0.007
Abbott & Cobb No. 5	0.0	0.07	0.41	0.031	0.014	0.013	0.02	0.93	0.076	0.033	0.018
	0.3	0.03	0.30	0.034	0.012	0.011	0.01	0.59	0.080	0.026	0.015
	1.2	0.02	0.30	0.044	0.014	0.011	0.00	0.09	0.117	0.022	0.007
	2.7	0.01	0.21	0.047	0.013	0.010	0.00	0.08	0.112	0.021	0.007
	4.6	0.01	0.21	0.067	0.017	0.010	0.00	0.04	0.102	0.018	0.004
	6.7	0.00	0.16	0.121	0.024	0.009	0.00	0.04	0.103	0.018	0.005
Gourmet	0.0	0.07	0.50	0.034	0.016	0.013	0.03	1.00	0.102	0.050	0.025
	0.3	0.03	0.38	0.040	0.014	0.012	0.01	0.89	0.098	0.036	0.018
	1.2	0.01	0.35	0.052	0.016	0.013	0.00	0.42	0.145	0.033	0.015
	2.7	0.01	0.30	0.060	0.017	0.012	0.00	0.16	0.125	0.025	0.009
	4.6	0.00	0.33	0.132	0.028	0.012	0.00	0.13	0.122	0.024	0.009
	6.7	0.00	0.21	0.124	0.025	0.010	0.00	0.08	0.112	0.020	0.007

[a] Initial disease assessed 28 days (winter) and 11 days (spring) after inoculation. Epidemic rates (k) calculated with logistic (l), Gompertz (g), and Weibull (w) models by nonlinear regression.

disease severity of $y = 0.09$ was observed on plants at the source, and the average disease severity for the plots (three cultivars and six distances) was 0.009. Because the latent period may be as short as 3 days under optimum conditions (10), several cycles of disease likely occurred in the first 4 wk. In the spring, a disease severity of $y = 0.03$ at the source was observed 11 days after inoculation and the average severity for the plots was 0.004; the disease at the source increased to $y = 0.21$ by day 25. At harvest, the severity averaged over the three cultivars at all distances was 0.31 in the winter and 0.36 in the spring (Table 1).

Progress of disease in time at the 36 points (six distances, three cultivars, two seasons) was described most accurately by the Weibull function ($R^2 = 0.89$; range 0.79 to ≈1). The means (and ranges) of R^2 for the logistic and Gompertz models were 0.78 (0.20–0.98) and 0.71 (0.47–0.95), respectively. The shape parameter (c) of the Weibull function ranged from 2.59 to 4.69 (mean 3.60) in the winter and from 2.40 to 6.36 (mean 3.62) in the spring. For both seasons, the mean values of parameter c of the Weibull function were close to the c values for idealized logistic curves (24,29) and, indeed, 28 of 36 progress curves of dark leaf spot were fitted better by the logistic model than by the Gompertz model.

Of the 36 disease progress curves, an $R^2 > 0.85$ from nonlinear regression was obtained for 25 curves with the Weibull function, 13 curves with the logistic model, and 10 curves with the Gompertz model. Eight curves had a plateau of little increase in disease for a 2- to 3-wk period in midseason, and these curves were not fit well ($R^2 < 0.85$) by any of the three models. The average daily epidemic rate, calculated with the logistic model, was $k_l = 0.06$ in the winter and 0.11 in the spring. Twelve of the 36 curves had faster than average daily rates of disease progress in the final week of the season (mean $k_l = 0.19$ in the winter and 0.23 in the spring). These 12 curves were also characterized by Weibull c (curve shape) values >3.8. These higher c values were indicative of a distribution of daily increase of severity that was skewed to the left, or phytopathologically, by adult plant susceptibility or a period of weather more favorable for disease. The 24 curves with c values <3.8 had epidemic rates during the last week that were about half as fast ($k_l = 0.1$ winter and 0.12, spring) as those curves with $c > 3.8$.

Epidemic rates at different distances. The range and pattern of epidemic rates were subject to equivocal interpretations. Because the Weibull function provided the best statistical fit, the rates obtained with this model should allow optimum characterization of the epidemics. Although a wide range of curve shapes were found for epidemics of dark leaf spot, the epidemic rates of these curves can still be compared because the variability in curve shape parameter (c) has little influence on the rate parameter (k_w) (29). In the winter, the range of rates observed at six distances for three cultivars was rather narrow (k_w = 0.009–0.016) with only a slightly faster rate at the source (0 m) as compared with 6.7 m (0.014 vs. 0.01). In the spring, the range of rates was broad (k_w = 0.004–0.026, mean 0.012). In the spring, the epidemic rates (k_w) at the source were nearly four times as fast as at 6.7 m (0.023 vs. 0.006). Contrarily, if the rates were calculated with the logistic model (k_l), the epidemic was faster at 6.7 m than at 0 m in the winter (0.10 vs. 0.03) and similar at both distances in the spring (0.11 vs. 0.09) (Table 1). The interpretations of the rate of progress of dark leaf spot of cabbage based on the Gompertz model were intermediate between those based on the Weibull function and the logistic model.

Disease progress variables over distance. Because of the distinct gradients in both seasons, the disease at first observation (y_0), AUDPC, and final disease (y_f) decreased with distance from the source. For values averaged over the three cultivars, y_0 at the source was 0.092 (winter) and 0.031 (spring) and decreased to 0.002 and 0 at 6.7 m, respectively. The y_f averaged 0.52 (winter) and 0.97 (spring) at the source to 0.06 (both seasons) at 6.7 m (Table 1). In the winter season, the AUDPC averaged over the three cultivars was 9.51 units (disease proportion-days) at the source and decreased to 1.74 units at 6.7 m; whereas in the spring season, corresponding units were 21.1 and 0.87 (Table 2). In both the winter and spring seasons, y_f and AUDPC were highly correlated ($r = 0.93$, $P < 0.01$).

Disease spread. The disease severities for each observation time were considered as separate gradients with unique curves. Thus, 18 gradients (three cultivars, six dates) were evaluated in the winter and 24 gradients (three cultivars, eight dates) in the spring.

In both seasons, the gradients were very steep from the source to ≈1 m and very flat from ≈1 m to 6.7 m. Each of the eight gradient models fit the latter, more distant, and flatter gradients well in nonlinear or linear regression. Only the modified Gregory model ($0.63 < R^2 < 0.99$, mean 0.91) and the Hoerl function ($0.56 < R^2 < 0.99$, mean 0.89) adequately fit the total gradients. The poorest statistical fit was obtained with the model of Kiyosawa and Shiyomi ($0.60 < R^2 < 0.99$, mean 0.79), and disease at the source was considerably underestimated. The gradient slopes for the modified Gregory model were much steeper in the spring (mean, $b = 0.73$) compared with the winter (mean, $b = 0.39$) (Table 3). The values for the truncation factor (m) in the modified Gregory model were small, with means of 0.12 m (winter) and 0.11 m (spring).

Isopathic rates. Despite the faster progress of dark leaf spot and higher y_f observed in the spring experiment, the isopathic rates were faster in the winter (average 0.24 m day^{-1} vs. 0.16 m day^{-1} in the spring). The slowest isopathic rates were calculated for Market Prize in winter (0.17 m day^{-1}) and spring (0.15 m day^{-1}) (Table 4). The fastest isopathic rate (0.31 m day^{-1}) was observed for Gourmet in the winter season.

Comparison of cultivars. The three cvs., Abbott & Cobb No. 5, Market Prize, and Gourmet, were susceptible to dark leaf spot. However, the cultivars could be ranked based on several epidemic variables. For both seasons, Abbott & Cobb No. 5 had the lowest y_f at all distances, the slowest epidemic rates (by the Weibull function), the smallest AUDPC at most distances, and the smallest VUDPS (Tables 2 and 4).

Table 2. Areas under disease progress curves (AUDPC) for dark leaf spot on three cabbage cultivars in a gradient from a line source of inoculum with corresponding yield in two seasons

		Winter 1985–1986		Spring 1986	
Cultivar	Distance (m)	AUDPC (y-days)	Yield (kg m^{-2})	AUDPC (y-days)	Yield (kg m^{-2})
Market Prize	0.0	12.31	5.38	25.66	0.00
	0.3	4.54	6.45	8.09	2.10
	1.2	2.59	6.74	2.05	3.66
	2.7	2.37	6.88	1.31	4.22
	4.6	1.74	6.49	0.95	5.41
	6.7	1.82	8.47	0.86	6.60
Abbott & Cobb No. 5	0.0	7.74	7.29	13.00	0.40
	0.3	3.79	8.39	4.94	1.53
	1.2	2.67	8.40	1.46	3.23
	2.7	1.97	9.68	1.13	3.83
	4.6	1.90	7.14	0.85	5.36
	6.7	1.66	11.22	0.83	5.44
Gourmet	0.0	8.48	6.61	24.64	0.00
	0.3	3.94	8.55	9.43	0.77
	1.2	2.95	7.27	3.19	3.40
	2.7	2.26	7.16	1.65	3.83
	4.6	2.22	7.62	1.44	5.10
	6.7	1.74	9.40	0.92	5.10

Table 3. Gradients of dark leaf spot on three cabbage cultivars in two seasons[a]

	Winter 1985–1986					Spring 1986				
Cultivar	Day	b	a	m	R^2	Day	b	a	m	R^2
Market Prize	28	−0.48	0.02	0.12	0.92	25	−0.56	0.03	0.15	0.91
	35	−0.29	0.04	0.12	0.94	32	−0.41	0.03	0.09	0.94
	42	−0.45	0.05	0.12	0.97	39	−0.60	0.04	0.11	0.93
	49	−0.44	0.06	0.12	0.93	46	−0.84	0.06	0.10	0.98
	56	−0.42	0.15	0.11	0.89	53	−1.27	0.16	0.10	0.99
	63	−0.27	0.30	0.12	0.88	60	−1.02	0.26	0.11	0.99
Abbott & Cobb No. 5	28	−0.80	0.02	0.12	0.96	25	−0.43	0.02	0.13	0.98
	35	−0.23	0.04	0.13	0.98	32	−0.54	0.03	0.11	0.96
	42	−0.39	0.04	0.04	0.96	39	−0.41	0.04	0.11	0.93
	49	−0.49	0.06	0.11	0.97	46	−0.52	0.04	0.12	0.98
	56	−0.31	0.13	0.12	0.94	53	−0.92	0.08	0.10	0.95
	63	−0.20	0.27	0.13	0.80	60	−1.31	0.17	0.09	0.99
Gourmet	28	−0.90	0.01	0.12	0.96	25	−0.60	0.03	0.11	0.97
	35	−0.19	0.03	0.14	0.82	32	−0.49	0.03	0.12	0.97
	42	−0.24	0.03	0.12	0.95	39	−0.73	0.05	0.11	0.97
	49	−0.50	0.06	0.12	0.95	46	−0.57	0.06	0.10	0.91
	56	−0.38	0.14	0.12	0.96	53	−1.20	0.19	0.10	0.99
	63	−0.13	0.35	0.13	0.63	60	−0.80	0.47	0.14	0.99

[a] Gradients calculated with modified Gregory model [$y = a(x + m)^b$] by nonlinear regression of disease proportions for five distances from 0.3 to 6.7 m; where b = gradient slope, a = estimated disease at source, m = truncation factor, and R^2 = coefficient of determination.

Table 4. The isopathic rates[a] and volumes under disease progress surfaces (VUDPS) of dark leaf spot on three cabbage cultivars in two seasons

	Winter 1985–1986		Spring 1986	
Cultivar	Isopathic rate (m day^{-1})	VUDPS (y-m-days)	Isopathic rate (m day^{-1})	VUDPS (y-m-days)
Market Prize	0.17	17.10	0.15	16.19
Abbott & Cobb No. 5	0.25	15.53	0.17	11.14
Gourmet	0.31	17.27	0.16	19.85

[a] Rates calculated for isopath $y = 0.10$ in the winter and $y = 0.05$ in the spring.

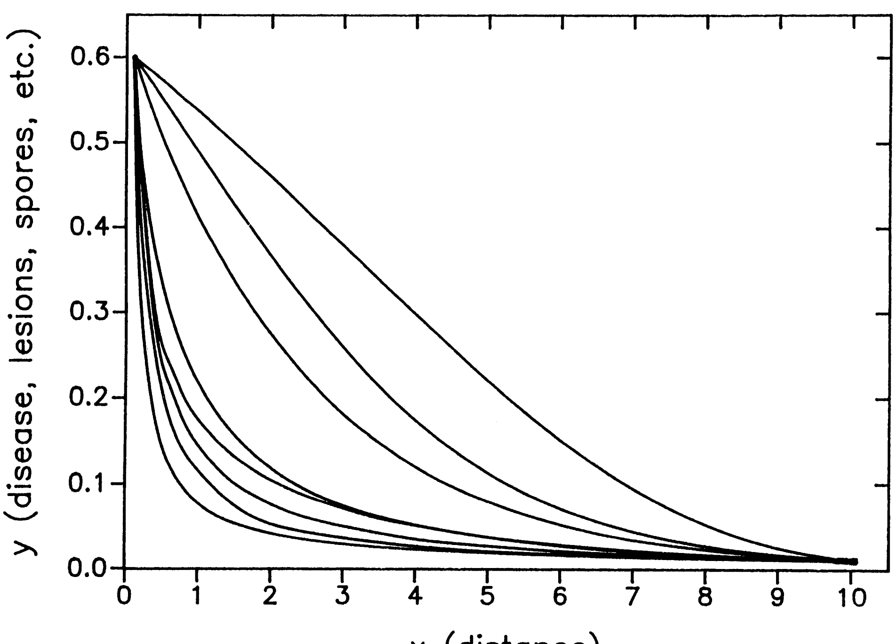

Fig. 1. Representative curves of eight gradient models. The curves from the bottom to the top of the figure at $x = 1.0$ were generated by the following models: $y = ax^b$ (Gregory); $\ln[y/(1 - y)]$ vs. $\log(x)$; $y = a \exp(bx^n)$, $n = 0.2$ (Lambert et al); $y = ax^b \exp(nx)$, $n = -0.2$ (Hoerl); $-\ln[-\ln(y)]$ vs. $\log(x)$; $y = a \exp(-bx)$ (Kiyosawa and Shiyomi); $\ln[y/(1 - y)]$ vs. x; and $-\ln[-\ln(y)]$ vs. x. All curves began with proportion $y = 0.6$ at distance $x = 0.1$ and decreased to $y = 0.01$ at $x = 10.0$. Different curve shapes are possible with the models of Lambert et al and Hoerl by using other values for the shape parameter (n). The curve shown for the Gregory model typifies many of the steep gradients observed for *Alternaria brassicicola* on cabbage in which y = disease proportion and x = meters.

The latter variable is the best measure of disease stress in the total plot area because it combined the effects of disease in both time and space. Gourmet usually had the highest y_f, the fastest average epidemic rates (Weibull and logistic), and a high VUDPS. In addition, Gourmet had the highest Weibull c values (average 3.98, $P < 0.05$) compared with 3.37 for Abbott & Cobb No. 5 and 3.49 for Market Prize. The high c values occurred in Gourmet because of the rapid, late-season increase of disease (adult plant susceptibility). Based on the interpretation for most variables, Market Prize exhibited slightly less susceptibility than Gourmet.

Yields. The average yields of the three cabbage cultivars in the winter season were more than double the yields in the spring (7.7 vs. 3.3 kg m^{-2}) (Table 2). In the winter, Abbott & Cobb No. 5 had the greatest yield (8.7 kg m^{-2}), followed by Gourmet (7.8), and Market Prize (6.7), all significantly different ($P < 0.01$). In the spring, Market Prize had the greatest average yield (3.7 kg m^{-2}), followed by Abbott & Cobb No. 5 (3.3) and Gourmet (3.0); all yields were significantly different ($P < 0.05$).

In the winter, yields at the inoculum source averaged 6.4 kg m^{-2}; these yields were significantly ($P < 0.05$) lower than the plot average. Yields of 9.6 kg m^{-2} were obtained at the 6.7 m distance; these yields were significantly ($P < 0.05$) higher than the plot average. Thus, a gradient of increasing yield occurred at points away from the source. However, the yields of plants at the selected distances along the gradient were only poorly correlated ($P > 0.1$) with disease at harvest ($r = 0.69$) and with AUDPC ($r = 0.60$).

In the spring, nearly all plants at the inoculum source had disease severities near 1.0 (dead); consequently, most plants at the source had no yield. For the three cultivars, there were distinct gradients of yield increasing with distance from the source. Yields of the three cultivars were significantly ($P < 0.01$) and linearly correlated with disease at harvest [yield (kg m^{-2}) = 5.25 − 5.3 y_f; $r = 0.95$]. The AUDPC values provided better prediction ($R^2 > 0.96$) of yields than y_f. The regression equations for estimating yield (Y) in the spring season were $Y = 5.2 \exp(-0.205$ AUDPC), $Y = 5.9 \exp(-0.196$ AUDPC), and $Y = 6.6 \exp(-0.187$ AUDPC) for Abbott & Cobb No. 5, Gourmet, and Market Prize, respectively.

DISCUSSION

The epidemics of dark leaf spot on cabbage in the winter and spring seasons were very different. Compared with the epidemic in winter, the disease in the spring began sooner after inoculation, intensified more rapidly, spread (in distance) more slowly, reached higher final disease near the source, had steeper gradients, and generally had higher VUDPSs. The steep gradients and relatively slow isopathic rates probably arose from very localized spore dispersal; i.e., predominantly rain-splash dispersal. During the last 20 days of the winter season, there were eight occasions of rain with a total rainfall of 90 mm. In the spring season, there were nine periods of rain in the last 20 days, but the total rainfall (146 mm) was much heavier than in the winter. The daily mean temperature averaged over the last 20 days of the season was colder in the winter (13.8 C) compared with the spring (30.5 C). Whether the actual spread of *A. brassicicola* is primarily attributable to rain-splash or windborne dispersal of spores remains undetermined (10).

The calculation of epidemic rates was problematical. Because many disease proportions were $y < 0.05$, particularly at sites distant from the inoculum source, an accurate estimation of epidemic rates with the logistic transformation was not possible because of the aberrations noted earlier (17) with this model. Hence, the logistic rates reported here should be interpreted with caution. Other transformations, such as the Weibull or Gompertz, seem more appropriate to estimate epidemic rates when many low values of disease intensity are encountered.

The researcher, when working with disease spread, has a choice of many models to analyze the gradients. To illustrate some possibilities, representative curves of several gradient models were calculated (Fig. 1). It is obvious that several models may provide a reasonably close statistical fit to certain gradients. The gradient models of Hoerl (7,19) and Lambert et al (16) have a term for curve shape, so these two models have more flexibility and, therefore, will fit many gradient types. The Hoerl model [$y = ax^b \exp(nx)$] is like the Gregory model ($y = ax^b$), but with an adjustment factor [$\exp(nx)$] for curve shape. Because most of the natural gradients of dark leaf spot of cabbage were fit well by the Gregory model, the adjustment factor of the Hoerl model was minimal ($1.0 < \exp(nx) < 1.5$).

For the modified Gregory model, Mundt and Leonard (22) estimated the m value (to allow estimation of disease at the source) to be the radius of the source. The actual radii of the source plants in our experiments were 0.1 m in the winter and 0.09 m in the spring. For the steep gradients of dark leaf spot, the estimated m values (0.12 m in the winter and 0.11 m in the spring) were similar to the actual radii of the sources. Also, with these small m values, the gradients with the Gregory and modified Gregory models were essentially identical.

Several workers (e.g., 12,18,30) have reported that disease gradients commonly flatten with the intensification of the epidemic in time. For the gradients of *A. brassicicola* on three cultivars of cabbage in two seasons, the gradients did not flatten in time; in fact, the gradients in the spring became steeper later in the season.

From the analyses of intensification of dark leaf spot in time and space, we conclude that for the disease to be severe in the field, early and numerous foci are required. From these foci, steep gradients of disease would occur and the spread of disease in space would likely be reasonably slow (unless frequent rains occurred). The intensification of dark leaf spot in time ($k_l \approx 0.1$) is somewhat slower than other common leaf spots ($0.15 < k_l < 0.3$) (25,30,31) and certainly much slower than epidemics of rusts as are commonly encountered ($0.3 < k_l < 0.6$) (4,17,18,30,31). The control of this disease should be rather easily accomplished by planting disease-free seed and avoidance of inoculum from debris. (These practices preclude the early appearance of disease.) Plants in seedbeds should be maintained disease-free by periodic applications of an effective fungicide. Occasional sprays of fungicide should be effective to slow any epidemic in the field.

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