

Potato Yield Loss Prediction and Discrimination Using Preplant Population Densities of *Verticillium dahliae* and *Pratylenchus penetrans*

L. J. Francl, L. V. Madden, R. C. Rowe, and R. M. Riedel

Postdoctoral research associate, associate professor, and professors, respectively, Department of Plant Pathology, The Ohio State University, Ohio Agricultural Research and Development Center, Wooster 44691 and Columbus 43210.

Salaries and research support provided by OSU/OARDC and by North Central Integrated Pest Management competitive grant 85-CRSR-2-2670. Journal Series Article 73-86.

Accepted for publication 3 October 1986 (submitted for electronic processing).

ABSTRACT

Francl, L. J., Madden, L. V., Rowe, R. C., and Riedel, R. M. 1987. Potato yield loss prediction and discrimination using preplant population densities of *Verticillium dahliae* and *Pratylenchus penetrans*. *Phytopathology* 77:579-584.

Reduced yields of potato, *Solanum tuberosum*, attributable to preplant population densities of *Verticillium dahliae* and *Pratylenchus penetrans*, pathogens involved in potato early dying disease, were quantified with linear regression models. Experimental microplot data consisted of controlled, factorial, pathogen inoculum levels in fumigated soil and resulting yields of potato cultivar Superior at two locations over a 5-6 yr period. Variation in yield relative to controls was explained best by regressions on the natural log of *V. dahliae* × *P. penetrans*. Population densities of pathogens at planting also were used in a discriminant analysis to predict yields above or below 90% of the control yield. A discriminant

function correctly classified 86% of the yields from a 3-yr subset of data from one location. The rate of correct classification was 70% when the same discriminant function was validated on data not used in model development. Erection of a third category, "between 80-90% of the control yield," resulted in an overall 6% misclassification rate for the "below 80% relative yield" category as "above 90% relative yield," and a 23% misclassification rate for "above 90% relative yield" as "below 80% relative yield." Discriminant models intentionally minimized "below 80% relative yield" misclassification in order to promote confidence in the management of potato early dying.

Additional key words: crop loss assessment, discriminant analysis, pest management, potato early dying.

Potato early dying is a serious disease problem in potato (*Solanum tuberosum* L.) production, particularly when the crop is monocultured or grown intensively. Potato early dying has long been associated with the soilborne fungus *Verticillium dahliae* Kleb. (8,22) but can occur as a disease complex that involves *V. dahliae* and the root-lesion nematode, *Pratylenchus penetrans* (Cobb) Filipjev & Schuur. Stekh. (17). Detailed studies of the epidemiology of potato early dying in Ohio (16,23,25) have shown that *V. dahliae* and *P. penetrans* can act synergistically, i. e., together they cause symptom development and yield reduction at population levels that individually have little or no effect. In Wisconsin, 55 propagules of *V. dahliae* per cubic centimeter of soil and 50 *P. penetrans* per 100 cm³ of soil had an additive effect on symptom expression when compared with *V. dahliae* alone (12). *Pratylenchus* spp. also had a statistically significant association with wilt severity in an Idaho study (3). Other nematode species, such as *Meloidogyne incognita* (Kofoid and White) Chitwood and *Globodera rostochiensis* (Woll.) Behrens, also appear to exhibit interactive effects with *V. dahliae* on potatoes (2,7,9).

Premature senescence of potato vines often results in markedly reduced yields. However, yield loss assessment for potato early dying has proven to be problematical (3,19,21,24). For example, the relationship between colony-forming units (cfu) of *V. dahliae* per gram of soil and tuber yield (19) or wilt incidence (3) was significant in some potato-growing areas but not in others. Problems in predicting yield loss most likely have arisen because of sampling and assay errors in estimation of pathogen populations, differing environmental conditions and cultural practices, unquantified soil properties (including, but not limited to, the nematode community), possible differences in virulence among pathogen isolates, and unexplained variability in tuber yield. In the Ohio microplot studies, pathogen isolates were held constant and carefully quantified, and two constant soil types provided similar

physicochemical soil conditions over 5-6 yr at two locations (25). These Ohio data were used in this assessment of yield loss.

A recent review (27) identified various approaches for assessment of yield reduction. The approach chosen in this analysis was an empirical, single-point model, wherein pathogen populations are measured once before planting the crop. This is a practical approach to the management of soilborne pathogens because most pest management decisions must be made before planting.

Pathogen population density can be related mathematically to yield in a variety of ways. The two methods chosen for this study were linear regression and discriminant analysis. The properties of linear regression parameters have been well described (5,18,27). Nonlinear analysis (20,26) was ruled out as an analytical tool because the levels of predictor variables within a single year were deemed insufficient (14) and because nonlinear models are difficult to verify in multiple pest situations (6). Although discriminant analysis has been used infrequently in pest management studies (1,11,15), interpretation of the analysis is straightforward. In discriminant analysis, observations, such as yield, are partitioned into nonoverlapping groups before the analysis. Then, one or more discriminating variables, such as pathogen population density, are used in a linear function to assign an observation to one of two or more groups with a minimum error rate (13). Discriminant analysis has a relative advantage over regression in that exact observed yields, which integrate many nonrecorded variables and may be highly variable, are not predicted, but only broad categories of yield are classified. The economic utility of this analysis is that decisions in pest management are implicitly dependent on a predictive categorization of yield above or below some threshold value.

MATERIALS AND METHODS

Microplot studies. Data used in model development were collected in microplot studies conducted at Wooster, OH, from 1980 to 1985 and at Celeryville, OH, over the same years except 1984. Details of experimental methodology from 1980 to 1983 have

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. § 1734 solely to indicate this fact.

been published (25). Differences in experimental protocol in 1984 and 1985 are discussed together with background information.

Each microplot consisted of a 25-cm internal diameter \times 31-cm long, unglazed, open-ended clay tile containing 8 L of soil. The soil at Wooster was a Wooster silt loam and that at Celeryville was a Rifle peat (25). Microsclerotia of *V. dahliae* and vermiforms of *P. penetrans* were mixed with fumigated soil singly or together at two to three population densities each year (Table 1). Microsclerotial densities of *V. dahliae* were reported on a per 10 g of soil basis from 1980 to 1983 and on a per cubic centimeter of soil basis during 1984–1985. To form an equivalent measure of density over all years, microsclerotia per soil weight was converted to a soil volume basis by using soil bulk density estimate of 1.3 g/cm³ for the silt loam and 0.33 g/cm³ for the organic soil. Densities of *P. penetrans* were reported as vermiforms per 100 cubic centimeters of soil in all years, and both pathogen populations were sampled after mixing with microplot soil just before planting.

One pathogen-free, *S. tuberosum* cultivar, Superior, single-eyed seed piece was planted in each microplot (25). Planting dates were 30 May 1985 for Celeryville and 4 June 1984 and 5 June 1985 for Wooster. Plants were harvested on 9 September 1985 at Celeryville and 5 September 1984 and 4 September 1985 at Wooster. Yield was determined as the total tuber weight in grams per plant. Pathogen inoculum densities were the two main effects in a factorial arrangement with 15 replicate microplot tiles per treatment. Relative yield data in this analysis were calculated as the mean yield of the treatment divided by the mean yield of the corresponding control grown in uninfested soil.

TABLE 1. Preplant population densities established in microplots and used in development of potato early dying yield loss models

Year	Plot location	<i>V. dahliae</i> cfu/cm ³ soil	<i>P. penetrans</i> vermiforms/100 cm ³ soil
1980	Wooster	2, 23	9, 30, 106
	Celeryville	3, 30	18, 56, 151
1981	Wooster	2, 23	8, 25, 143
	Celeryville	3, 30	47, 137, 362
1982	Wooster	2, 23	38, 84, 245
	Celeryville	3, 30	25, 92, 247
1983	Wooster	2, 23	3, 15, 30
	Celeryville	3, 30	12, 15, 70
1984	Wooster	4, 27, 139	30, 39, 57, 67, 86, 151 168, 256
1985	Wooster	2, 9, 59	4, 15
	Celeryville	2, 25	2, 13

TABLE 2. Regression estimates of tuber yield relative to an uninoculated control from potatoes in microplots infested with *Verticillium dahliae* (VD) and/or *Pratylenchus penetrans* (PP) and estimates of relative yield from regression on the natural log (ln) of *V. dahliae* \times *P. penetrans*

Plot location	Year	Best-fit regression equation	<i>F</i> ^a	Adjusted <i>r</i> ²	Regression on ln (<i>V. dahliae</i> \times <i>P. penetrans</i>)			
					Intercept (<i>B</i> ₀)	Slope (<i>B</i> ₁)	<i>F</i> ^a	Adjusted <i>r</i> ²
Wooster	1980	0.91 - 0.047[ln(VD \times PP)] - 0.121[ln(VD)]	18.9**	0.76	0.83	-0.084	18.7**	0.62
	1981	0.87 - 0.001(PP)	5.2*	0.28	No fit		1.2	0.02
	1982	No fit	No fit		2.7	0.14
	1983	1.03 - 0.0601[ln(VD \times PP)] - 0.007(PP)	32.8**	0.85	0.98	-0.075	32.3**	0.74
	1984	1.16 - 0.003(VD)	12.9**	0.52	No fit		3.8	0.20
	1985	0.95 - 0.065[ln(VD \times PP)] - 0.04[ln(VD)]	79.1**	0.93	0.91	-0.079	85.1**	0.88
Celeryville	1980	0.94 - 0.037[ln(VD \times PP)] - 0.029[ln(PP)]	40.8**	0.88	0.88	-0.046	48.0**	0.81
	1981	1.03 - 0.016[ln(VD \times PP)] - 0.068[ln(VD)] - 0.001(PP)	31.6**	0.93	0.94	-0.037	19.5**	0.70
	1982	1.04 - 0.029[ln(VD \times PP)]	22.3**	0.66	1.04	-0.029	22.3**	0.66
	1983	0.89 - 0.055[ln(VD \times PP)]	19.4**	0.63	0.89	-0.055	19.4**	0.63
	1985	1.02 - 0.033[ln(VD \times PP)] - 0.103[ln(VD)] - 0.014(PP)	103**	0.97	0.90	-0.096	27.7**	0.77

^aSignificance of the *F*-test value: * *P* < 0.05, ** *P* < 0.01.

Regression analyses. The relative yields from each year and location were regressed separately on the component pathogen population densities, their natural logarithm (ln) transformations, and ln(*V. dahliae* \times *P. penetrans*), to find the best predictors of relative yield. All population data were increased by a value of 1.0 before transformations so that a log of zero density could be calculated. The same independent variables were used in regression analyses of data from the entire 6 yr at Wooster and 5 yr at Celeryville and in a combined analysis. All regression equations were evaluated for overall significance (*F*-test, *P* < 0.05), significance of estimated coefficients (Student's *t* tests, *P* < 0.05), and pattern of the residuals (5). The coefficient of determination was adjusted for degrees of freedom (adjusted *r*²) to properly compare regression equations with different numbers of independent variables.

Discriminant analyses. The discriminant analysis program (7M) from BMDP Statistical Software uses an automatic stepwise procedure to select discriminating variables (4). A linear function was determined that would best categorize relative yields by using the same set of independent variables mentioned above as potential discriminating variables. Tuber yields were categorized as greater than or less than 90% of the control yield before the analysis. Yields were divided into three categories, >90%, 80–90%, and <80% of the control yield in a second discriminant analysis to reduce misclassifications between the “above 90% relative yield” and “below 80% relative yield” groups. In general, selection of yield loss categories was based on the desire to consider economically important losses while maintaining model simplicity. Discriminant functions were evaluated by calculating classification error rates. Wilks' lambda statistic was used to test the equality of group means for included discriminating variables.

RESULTS

Regression analyses. The regression equations that best fit each of the 11 data sets had a variety of predictor variables (Table 2). In eight of 11 cases, ln(*V. dahliae* \times *P. penetrans*) was a significant independent variable. In one case, yield loss could not be related to pathogen population density at planting, and in two other cases either *P. penetrans* or *V. dahliae* alone was the sole significant variable. The intercept coefficients (*B*₀), indicative of relative yields for the controls as well as for treatments having independent variables not included in the regression equations, were not significantly different from 1.0, except for the equation from Wooster, 1984. Also in Table 2 are statistics of the simple regression model: relative yield = *B*₀ + *B*₁ [ln(*V. dahliae* \times *P. penetrans*)]. *B*₁ coefficients in these equations are indicative of the degree of yield loss attributable to the combination of these two

pathogens. Intercept estimates were, of course, less precise and r^2 values were lower than the full, best-fitting regressions.

The regression equation with the independent variable $\ln(V. \text{dahliae} \times P. \text{penetrans})$ provided the best fit when data were combined over all years for each location (Fig. 1). Neither the estimated intercepts nor the slope coefficients were significantly different ($P = 0.05$) when the regression equations from the two locations were compared with one another; however, the intercept coefficient for the Celeryville regression equation was significantly ($P < 0.05$) less than 1.0. Coefficients of determination were low due to large year-to-year variation. The combined data from Wooster had more year-to-year variability than those from Celeryville (see also Table 2), producing a larger standard deviation for the B_1 coefficient and a smaller adjusted coefficient of determination. $\ln(V. \text{dahliae} \times P. \text{penetrans})$ was again the independent variable that best explained relative yield response when data sets from both locations over all years were combined (Fig. 1). The intercept term for this regression was not significantly different than 1.0. There was no pattern to the residual values of these three regression equations when residuals were plotted against their respective predicted values.

Discriminant analyses. The highest percentage of correct classifications in discriminant analysis was realized when the discriminant model was developed on 3 yr of data from Wooster (1980, 1983, and 1985). These years were chosen on the basis of having the same soil type and a similar, steep, significant ($P < 0.05$) slope of the regression line when relative yield was regressed on $\ln(V. \text{dahliae} \times P. \text{penetrans})$ (Table 2). Therefore, this data subset purposely contained observations of relative yield that showed a strong dose response to inoculation levels. Also, forcing independent variables into the automatic stepwise procedure of BMDP7M was necessary to determine the discriminating variables that would correctly classify the highest percentage of observations. Presumably, intervention was necessary because of

the intercorrelation between the $\ln(V. \text{dahliae} \times P. \text{penetrans})$ term and the individual pathogen terms. Derived discriminant models were validated on data from Celeryville and from Wooster in 1981, 1982, and 1984. These data were not used in developing the models.

The discriminant function that gave the most correct classifications used $\ln(V. \text{dahliae})$ and $\ln(V. \text{dahliae} \times P. \text{penetrans})$ as discriminating variables (Table 3). The classifications were 86% correct over all observations in the 3-yr Wooster data set from which the model was developed. The discriminant function correctly classified 80% of all observations for the 5-yr Celeryville data set and 56% for the remaining 3 yr of data at Wooster, for an average of 70% correct predictions. Over all data sets, 21% of the yields actually "below 90% relative yield" were misclassified as "above 90% relative yield." The misclassification rate of yields

TABLE 3. Classification matrix above and below 90% of potato tuber yields for controls and percentage of correct classifications from a discriminant analysis conducted on potato early dying data from Wooster microplots, 1980, 1983, and 1985 and validated on two data sets

Data set	Actual classification	Prediction ^a		Percent correct predictions
		Below 90%	Above 90%	
Wooster	Below 90%	18	4	82
1980, 1983, 1985	Above 90%	1	13	93
Celeryville	Below 90%	29	8	78
1980-1983, 1985	Above 90%	3	14	82
Wooster	Below 90%	9	3	75
1981, 1982, 1984	Above 90%	13	11	46

^a A relative yield below 90% is predicted if the quantity $[-3.593 + 1.404 \ln(V. \text{dahliae}) + 0.691 \ln(V. \text{dahliae} \times P. \text{penetrans})]$ is greater than the quantity $[-0.781 + 0.394 \ln(V. \text{dahliae}) - 0.041 \ln(V. \text{dahliae} \times P. \text{penetrans})]$.

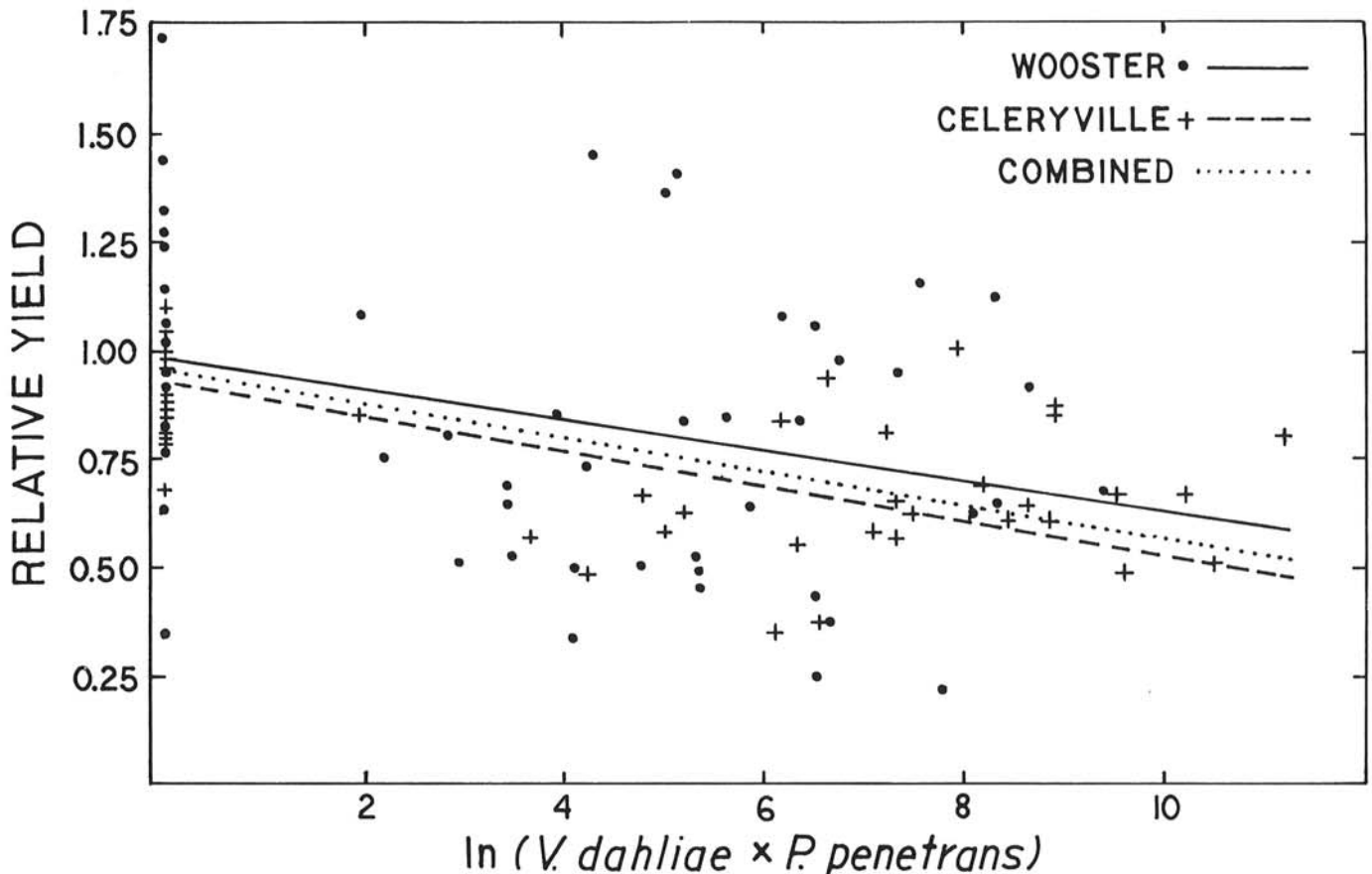


Fig. 1. Relationship between relative tuber yield and $\ln(\text{Verticillium dahliae} \times \text{Pratylenchus penetrans})$ population density plotted as regression lines and scatter of data points for Wooster and Celeryville microplot locations. Regression equations with coefficients \pm their standard deviations are: relative yield (Wooster) = $0.98 (\pm 0.045) - 0.036 (\pm 0.011) \times \ln(V. \text{dahliae} \times P. \text{penetrans})$, adjusted $r^2 = 0.12$; relative yield (Celeryville) = $0.91 (\pm 0.027) - 0.039 (\pm 0.006) \times \ln(V. \text{dahliae} \times P. \text{penetrans})$, adjusted $r^2 = 0.44$; relative yield (combined) = $0.95 (\pm 0.028) - 0.038 (\pm 0.007) \times \ln(V. \text{dahliae} \times P. \text{penetrans})$, adjusted $r^2 = 0.20$.

TABLE 4. Classification matrix for potato tuber yields less than 80%, 80–90%, and greater than 90% of control yields based on a discriminant analysis of potato early dying microplot data from Wooster 1980, 1983, and 1985 and validated on two data sets

Data set	Actual classification	Prediction ^a			Percent correct predictions	Percent severely incorrect predictions ^b
		<80%	80–90%	>90%		
Wooster 1980, 1983, 1985	Below 80%	16	2	2	80	10
	80–90%	0	2	0	100	...
	Above 90%	0	3	11	79	0
Celeryville 1980–1983, 1985	Below 80%	20	2	0	91	0
	80–90%	5	3	7	20	...
	Above 90%	2	5	10	59	12
Wooster 1981, 1982, 1984	Below 80%	3	2	1	50	14
	80–90%	5	0	1	0	...
	Above 90%	10	5	9	38	42

^a A relative yield below 80% is predicted if the quantity $[-4.848 + 1.308 \ln(V. \text{dahliae}) + 1.074 \ln(V. \text{dahliae} \times P. \text{penetrans})]$ is greater than the quantities $[-2.370 + 1.495 \ln(V. \text{dahliae}) - 0.309 (V. \text{dahliae} \times P. \text{penetrans})]$ (80–90%) and $[-1.184 + 0.381 \ln(V. \text{dahliae}) - 0.034 \ln(V. \text{dahliae} \times P. \text{penetrans})]$ (above 90%).

^b A prediction is severely in error when either <80% relative yield is predicted for actual relative yields >90%, or >90% relative yield is predicted for actual relative yields <80%.

TABLE 5. Preplant pathogen variables used in discriminant analyses of yield loss due to potato early dying and their average values within specified categories of tuber yield relative to an uninoculated control

Variable	Wilks' lambda	P ^a	Average value in group ^b		
			Relative yield		
			Below 90%	Above 90%	
Ln(<i>V. dahliae</i>)	0.470	<0.001	2.28	0.46	
Ln(<i>V. dahliae</i> × <i>P. penetrans</i>)	0.542	<0.001	3.76	0.14	
			Relative yield		
			Below 80%	80–90%	Above 90%
Ln(<i>V. dahliae</i>)	0.359	<0.001	2.34	1.70	0.46
Ln(<i>V. dahliae</i> × <i>P. penetrans</i>)	0.415	<0.001	4.13	0.00	0.14

^a Significance of Wilks' lambda statistic.

^b *V. dahliae* is measured as cfu/cm³; *P. penetrans* is measured as vermiforms per 100 cm³ of soil; natural logs of all values were taken before calculating the means.

actually "above 90% relative yield" as "below 90% relative yield" was 31%. Most of the former misclassifications occurred when either high densities of *P. penetrans* or low densities of *V. dahliae* resulted in a yield decrement. Most of the latter misclassifications were from the Wooster 1981–1982–1984 data set and occurred when the combination of *P. penetrans* × *V. dahliae* or *V. dahliae* alone sometimes failed to reduce yields.

These same data sets were similarly analyzed with three categories of relative yield (Table 4). A prediction was defined as being only slightly in error if the "80–90% relative yield" category was predicted rather than the "below 80% relative yield" or "above 90% relative yield"; or if the "80–90% relative yield" category was misclassified. A prediction was severely in error if "below 80% relative yield" was predicted as "above 90% relative yield" or the reverse misclassification occurred. Over all observations, only 6% of yields actually "below 80% relative yield" were misclassified as "above 90% relative yield." The reverse misclassification rate was 23%. The sources of these errors were, of course, the same as in the previous discriminant analysis. The "80–90% relative yield" category contained 20% of the total observations.

Wilks' lambda statistic, the significance of Wilks' lambda, and the average values in each group for the discriminating variables, $\ln(V. \text{dahliae} \times P. \text{penetrans})$ and $\ln(V. \text{dahliae})$, are presented in Table 5. The group means of the discriminating variables were significantly different in both discriminant functions.

Pathogen densities that reduced yields by 10%. Regression and

TABLE 6. Population levels of *Verticillium dahliae* and *Pratylenchus penetrans* that reduced potato yields to 90% of uninoculated controls in microplots as estimated by regression and discriminant models

Model	Population level ^a	
	Product of <i>V. dahliae</i> and <i>P. penetrans</i> (±1 standard deviation)	
Linear regression ^b		
Wooster	15 (8–54)	
Celeryville	12 (8–19)	
Combined	13 (8–24)	
Discriminant ^c	<i>V. dahliae</i>	<i>P. penetrans</i>
	0	— ^d
	1	17
	2	5
	3	2
	4	1
	15	0

^a *V. dahliae* in cfu/cm³ and *P. penetrans* in vermiforms per 100 cm³.

^b Assumes an intercept at 1.0 and uses slopes from Fig. 1.

^c From discriminant function in Table 3.

^d Not estimable from model. Data would suggest a population much greater than 17 vermiforms per 100 cm³.

discriminant equations were used to estimate population densities of *V. dahliae* and *P. penetrans* that would reduce yields to 90% of corresponding uninoculated controls (Table 6). The estimates from three regression analyses (Fig. 1) are single values ranging from 12 to 15, each of which is a multiplicative product of *V. dahliae* × *P. penetrans*. Separate estimates of component pathogen densities were possible to some extent from the discrimination function. In particular, the discriminant function estimated a 10% yield loss at 15 cfu per cubic centimeter of soil for *V. dahliae* in the absence of *P. penetrans*.

DISCUSSION

V. dahliae, at population densities commonly found in Ohio soils, usually reduced yields of potato only slightly in these microplot studies when it was the sole pathogen (16,25). Data collected in 1984 and 1985 as well as new, quantitative regression analyses of all data support this contention. *P. penetrans* also had little or no effect on yield when inoculated alone. Reduction in yield attributable to potato early dying was greatest when fumigated soil was infested with both pathogens. Preliminary results from microplot studies in unfumigated soil (Rowe, unpublished) indicate that this relationship is not restricted to fumigated soil. Clearly, assessment potential of potato yield loss and

pest management program design and implementation must consider the preplant population levels of both *V. dahliae* and *P. penetrans*.

Differences found in the choice of independent variables of the best-fitting regression equations, and in estimates of the B_1 coefficients for the simple regressions with $\ln(V. dahliae \times P. penetrans)$ (Table 2), suggest that the effect of potato early dying on yield is also affected by environmental and physiological factors that were not included in our analysis. There is evidence for a late-season temperature effect (25). Data from Celeryville exhibited a more consistent pathogen interaction effect on relative yield than those from Wooster because the former consistently had $\ln(V. dahliae \times P. penetrans)$ as a significant independent variable. A systems analysis of environmental factors together with pathogen population densities is under way to help explain yearly variation in relative yield.

An analysis of multiyear data by location and over both locations demonstrated that the combination of *V. dahliae* \times *P. penetrans* was the predominant determinant of relative yield. James and Teng (10) recommended multiyear and multilocation assessment of yield loss to measure the behavior of pathosystems under various environments. Though there was little variation in yield loss at Celeryville, the regression equation for the Wooster data essentially averaged 3 yr of mild and 3 yr of severe yield loss.

The intercept (B_0) in the regression equations should approximate 1.0 (i. e., no yield loss relative to the control). All but two estimates of B_0 did not differ significantly ($P < 0.05$) from 1.0. Potato early dying reduced yields only slightly at Wooster in 1984 and the natural log of *V. dahliae* \times *P. penetrans* was nonsignificant. It is possible that for the combined years at Celeryville, small, but consistently negative, effects on yield by *V. dahliae* or *P. penetrans* alone (Table 2) caused the underestimate in B_0 .

Logarithmic transformation of pathogen population density will improve the fit of the regression model if successively higher population levels cause less plant damage per unit, as was the case here. Unfortunately, using the product of population densities of *V. dahliae* \times *P. penetrans* as a model of interaction implicitly equates the damage caused by the two pathogens, albeit at a 100-fold difference in soil volume. These results indicate that the regression equations were adequate models of yield reduction due to potato early dying, but perhaps the issue of pathogen equivalency should be addressed in future work.

The first discriminant function, using 90% yield relative to the control as a threshold, had a higher rate of correct classifications on the 3 yr of data used in model development and on the Celeryville validation data than on validation data from Wooster, 1981-1982-1984. The model incorrectly predicted most "above 90% relative yield" classifications as "below 90% relative yield" for the latter data set because potato early dying only slightly reduced yields in those years. Because it was developed from years wherein yield loss was relatively high, the discriminant model intentionally minimized the misclassification of "below 90% relative yield" as "above 90% relative yield." For the same reason, the population density estimates of *V. dahliae* and *P. penetrans* that would reduce yields by 10% were lower than those estimated from regression equations (Table 6). This model equated damage from *V. dahliae* and *P. penetrans* to a lesser extent than did regression models based on $\ln(V. dahliae \times P. penetrans)$.

The second discriminant function improved the classification rate in the sense that it included a third category that essentially served as a hedge to avoid making severely incorrect predictions. Once again, the model was conservative in the misclassification of "below 80% relative yield" as "above 90% relative yield." The third category may also be construed as a buffer zone around the uncertain selection of a threshold.

Discriminant models use an approach to yield loss assessment that is different from both linear and nonlinear regression models because the discriminant function categorizes the yield response into discrete groups rather than predicting yield response on a continuous scale at every level of an independent variable. Therefore, discriminant analysis of yield reduction and crop loss assessment for pest management share a common conceptual

approach. In the former, some threshold value must be predefined to discriminate two groups, whereas in the latter an economic threshold is chosen between some pest management action and no pest management action. Although these data did not come from production fields, there is correspondence between some of our results and yield loss estimates from commercial potato fields (3,19). In particular, the estimate of a 10% yield loss at 15 cfu of *V. dahliae* per cubic centimeter of soil in the absence of *P. penetrans* (Table 6) is comparable to the 10% yield loss estimate at about 10 cfu of *V. dahliae* per gram of soil in some areas of Colorado (19). Therefore, these analyses should provide a realistic starting point for the development of mathematical pest management models for control of damage due to potato early dying. Further microplot studies in nonfumigated soil and studies in commercial fields are now under way.

LITERATURE CITED

1. Billings, R. F., and Bryant V., C. M. 1983. Developing a system for mapping the abundance and distribution of southern pine beetle in east Texas. *Z. Angew. Entomol.* 96:208-216.
2. Corbett, D. C. M., and Hide, G. A. 1971. Interaction between *Heterodera rostochiensis* Woll. and *Verticillium dahliae* Kleb. on potato and the effect of CCC on both. *Ann. Appl. Biol.* 68:71-80.
3. Davis, J. R., and Everson, D. O. 1986. Relation of *Verticillium dahliae* in soil and potato tissue, irrigation method, and N-fertility to Verticillium wilt of potato. *Phytopathology* 76:730-736.
4. Dixon, W. J., and Brown, M. B. 1983. BMDP Statistical Software. University of California Press, Berkeley.
5. Draper, N. R., and Smith, H. 1981. Applied Regression Analysis. 2nd ed. John Wiley & Sons, New York. 709 pp.
6. Duncan, L. W., and Ferris, H. 1983. Validation of a model for prediction of host damage by two nematode species. *J. Nematol.* 15:227-234.
7. Harrison, J. A. C. 1971. Association between the potato cyst nematode, *Heterodera rostochiensis* Woll. and *Verticillium dahliae* Kleb. in the early dying disease of potatoes. *Ann. Appl. Biol.* 67:185-193.
8. Isaac, I., and Harrison, J. A. C. 1968. The symptoms and causal agents of early dying disease (Verticillium wilt) of potatoes. *Ann. Appl. Biol.* 61:231-244.
9. Jacobsen, B. J., MacDonald, D. H., and Bissonnette, H. L. 1979. Interaction between *Meloidogyne hapla* and *Verticillium albo-atrum* in the Verticillium wilt disease of potato. *Phytopathology* 69:288-292.
10. James, W. C., and Teng, P. S. 1979. The quantification of production constraints associated with plant diseases. *Appl. Biol.* 4:201-267.
11. Kemp, W. P., Everson, D. O., and Wellington, W. G. 1985. Regional climatic patterns and western spruce budworm outbreaks. *U.S. For. Serv. Tech. Bull.* No. 1693.
12. Kotcon, J. B., Rouse, D. I., and Mitchell, J. E. 1985. Interactions of *Verticillium dahliae*, *Colletotrichum coccodes*, *Rhizoctonia solani*, and *Pratylenchus penetrans* in the early dying syndrome of Russet Burbank Potatoes. *Phytopathology* 75:68-74.
13. Lackenbruck, P. A. 1975. Discriminant Analysis. Hefner Press, New York. 128 pp.
14. Madden, L. V. 1980. Quantification of disease progression. *Prot. Ecol.* 2:159-176.
15. Madden, L. V., Knoke, J. K., and Louie, R. 1983. Classification and prediction of maize dwarf mosaic intensity. Pages 238-242 in: Proceedings International Maize Virus Disease Colloquium and Workshop. D. T. Gordon, J. K. Knoke, L. R. Nault, and R. M. Ritter, eds. Ohio State University. 266 pp.
16. Martin, M. J., Riedel, R. M., and Rowe, R. C. 1982. *Verticillium dahliae* and *Pratylenchus penetrans*: Interactions in the early dying complex of potato in Ohio. *Phytopathology* 72:640-644.
17. Morsink, F., and Rich, A. E. 1968. Interactions between *Verticillium albo-atrum* and *Pratylenchus penetrans* in the Verticillium wilt of potatoes. (Abstr.) *Phytopathology* 58:401.
18. Neter, J., Wasserman, W., and Kutner, M. H. 1983. Applied Linear Regression Models. Richard D. Irwin Inc., Homewood IL. 547 pp.
19. Nnodu, E. C., and Harrison, M. D. 1979. The relationship between *Verticillium albo-atrum* inoculum density and potato yield. *Am. Potato J.* 56:11-25.
20. Pennypacker, S. P., Knoble, H. D., Antle, C. E., and Madden, L. V. 1980. A flexible model for studying plant disease progression. *Phytopathology* 70:232-235.
21. Powelson, M. L. 1979. Verticillium wilt of potatoes in irrigated sands: The Oregon experience. *Oreg. Agric. Exp. Stn. Tech. Paper* 5106. 6 pp.
22. Reinke, J., and Berthold, G. 1879. Die Zersetzung der Kartoffel durch

- Pilze. Unters. Bot. Lab. Univ. Gottingen 1:1-100.
23. Riedel, R. M., Rowe, R. C., and Martin, M. J. 1985. Differential interactions of *Pratylenchus crenatus*, *P. penetrans*, and *P. scribneri* with *Verticillium dahliae* in potato early dying disease. *Phytopathology* 75:419-422.
 24. Rouse, D. I. 1985. Some approaches to prediction of potato early dying disease severity. *Am. Potato J.* 62:187-193.
 25. Rowe, R. C., Riedel, R. M., and Martin, M. J. 1985. Synergistic interactions between *Verticillium dahliae* and *Pratylenchus penetrans* in potato early dying disease. *Phytopathology* 75:412-418.
 26. Seinhorst, J. W. 1965. The relation between nematode density and damage to plants. *Nematologica* 11:137-154.
 27. Teng, P. S. 1985. Construction of predictive models: II. Forecasting crop losses. Pages 177-206 in: *Advances in Plant Pathology Vol. 3. Mathematical Modeling of Crop Disease*. C. A. Gilligan, ed. Academic Press, New York. 255 pp.