Effects of Three Soil Types on Potato Early Dying Disease And Associated Yield Reduction

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

First, second, and fourth authors: postdoctoral research associate, professor, and associate professor, respectively, Department of Plant Pathology, The Ohio State University (OSU), Ohio Agricultural Research and Development Center (OARDC), Wooster 44691; third author: professor, Department of Plant Pathology, OSU/OARDC, Columbus 43210.

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ABSTRACT

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Potato early dying is a serious soil-borne disease that occurs in many diverse soils in areas of commercial potato (*Solanum tuberosum*) production. *Verticillium dahliae* and *Pratylenchus penetrans*, causal agents in the early dying disease syndrome, were mixed at several factorial levels with Wooster silt loam, Spinks fine sand, or Rifle peat, and placed in microplots at a single location. The effects of soil type on disease development and yield reduction in potato cultivar Superior was measured over two seasons. Disease was measured as the area under the senescence progress curve (A) and day of senescence onset. Disease progress was greater when soils were infested with both pathogens together than when infested with either pathogen alone. Disease progress and senescence onset were more similar among soils than between years. Regression models that used preplant population levels of pathogens as determinant variables explained more variation in A in 1985 than in 1986. Senescence onset at high levels of *V. dahliae* and *P. penetrans* was 32–35 days sooner than controls in 1985 and 19–24 days earlier in 1986. Differences in disease onset and progress between years were associated with a greater soil moisture deficit and higher temperatures in the latter half of the 1986 season. Yield reduction, for separate years and without using measures of disease as predictors, was explained best by the model:

$$\text{Yield} = b0 - b1(\ln[V.\ dahliae \times P.\ penetrans]) - b2(\ln[V.\ dahliae]) + b3(P)$$

in which P = 1 if microplots contained Rifle peat and 0 otherwise. There was no evidence of interaction between soil type and pathogen population on yield reduction when years were analyzed separately, although estimates of the beta coefficients differed between years and *P. penetrans* consistently reduced yields in sand both years when it was the sole pathogen. Tuber yields in 1985 and 1986 were significantly ($P<0.01$) correlated with A ($r = -0.97$ and -0.76) and senescence onset ($r = 0.92$ and 0.76). A discriminant model that classifies yield relative to controls based on pathogen density at planting and had been developed using previously collected microplot data severely misclassified only 8% of these new data from three soil types. This suggests that soil type can be ignored in classifying relative yield reductions due to potato early dying.

The potato early dying syndrome is one of the most important uncontrolled diseases of potato (*Solanum tuberosum* L.) (17). Affected plants senesce approximately 1-4 wk earlier than the normal maturity for a given cultivar. In spite of the fact that early dying can cause yield reductions as high as 30–40% in commercial potato-growing areas across the United States, the disease often goes unrecognized because symptoms resemble natural senescence (17). Although early dying reduces productivity in virtually all soils in which potatoes are commercially grown, comparative effects of different soil types within a single environment have not been studied.

Verticillium dahliae (Kleb.) is a major pathogen in the potato early dying disease complex. *Pratylenchus penetrans* (Cobb) Filipjev and Schuur. Stekh., a commonly occurring plant-parasitic nematode with many crop hosts, including potato, can synergistically interact with *V. dahliae* to greatly increase the severity of early dying and subsequent yield loss (8,18). Potato early dying occurs in sandy river basin soils of the Pacific Northwest and in the sands, loams, and organic soils of midwestern and eastern states (14,17,18). *Verticillium* wilt of cotton, also caused by *V. dahliae*, occurs widely in coarse-, medium-, and fine-textured soils (1,19). *P. penetrans* often infests commercial potato fields (3), but damage to plants is particularly great in fine-textured soils. *P. penetrans* reduced yields of potato cultivar

Superior in potted, steam-sterilized sandy loam 20% at 38 nematodes per 100 cm^3 (2). Florini et al (4) found *P. penetrans* more prevalent than *P. crenatus* in the sandy loam and loam soils of Long Island, NY. Damage to potato was much greater when *P. penetrans* predominated in the species mix, and involvement of *V. dahliae* was suspected, although neither plants nor soil was assayed for the fungus (4). Other researchers have improved yields of potato in fine-textured soils by manipulating the population density of *P. penetrans*, but did not assay for *Verticillium* (3,6,11,12).

The severity of early dying and resulting yield reduction in susceptible cultivars are most likely affected by an interplay among physical and biological factors in the soil and agricultural practices. In previous microplot studies, we found a quantitative effect of soil populations of *V. dahliae* and *P. penetrans* at planting on subsequent tuber yield reduction (5,17) and a differential effect of *Pratylenchus* species on disease and yield reduction (16). Our objectives in this study were to compare plant response to *V. dahliae* and *P. penetrans* in three different soils in a single experimental setting and to quantify yield reduction responses in these soils. Answers to these questions would help determine the need for a soil factor in regression and discriminant models of potato yield reduction presently based on population densities of *V. dahliae* and *P. penetrans* at planting (5).

MATERIALS AND METHODS

Microplot technique. The methodology for using clay tile microplots (25 cm inside diameter × 30 cm long) in potato early dying research in Ohio and the methods for culturing disease-free potato seed tubers from tissue-cultured plantlets and producing inoculum of *P. penetrans* have been detailed elsewhere (18). Inoculum of *V. dahliae* was produced by growing the fungus in the dark at 20–24 C for 3–4 wk on minimal medium (15) overlaid with sterile cellophane. Following incubation, cellophane fragments, adhering mycelia, and microsclerotia from 400–600 petri plates were rubbed off the media and dispersed in water with a blender, and the mixture was poured through nested 250-, 75-, and 38-μm mesh sieves. Material retained on the latter two sieves was rinsed in place with additional water and resuspended in a large volume of water. This sieving procedure was repeated three times to concentrate the microsclerotia and wash out as many hyphal fragments and conidia as possible. After final sieving, the concentrated microsclerotia were resuspended in 1.5 L of water. As a final dry carrier for the microsclerotia, soil autoclaved twice 24 hr apart was oven-dried and sifted through a 821-μm mesh sieve. The concentrated microsclerotia were slowly pipetted onto 12 L of the screened soil, with continual hand mixing. The infested soil was then thoroughly mixed for 1 hr in a large twin-shell blender with an internal high-speed rotor bar. Infested soil was sampled, and colony-forming units (cfu) of *V. dahliae* were assayed by dilution plating on streptomycin-alcohol medium (9). Concentration of this inoculum was in the range of 10^5 cfu/g. Inoculum was stored in a plastic bag and refrigerated for 2–3 wk prior to use. A second, less-concentrated batch of inoculum was prepared from a portion of the first by further dilution with sterile, screened soil. After assay results were known, weighed amounts of either inoculum were calculated for addition to aliquots of fumigated field soil so that the ratio of inoculum to field soil was at least 1 g/L.

Field microplots were established in 1985 and 1986 on Wooster silt loam in northcentral Ohio at the Ohio Agricultural Research and Development Center, Wooster. Test soils were: Rifle peat, an organic soil (15% silt, 1% sand, 9% clay, and 75% organic matter, pH 5.2, CEC 52); Wooster silt loam (65% silt, 20% sand, 15% clay, and 2% organic matter, pH 5.4, CEC 14); and Spinks fine sand (4% silt, 95% sand, 1% clay, and 1% organic matter, pH 5.6, CEC 2). Rifle peat was fumigated in place with 465 kg/ha of methyl bromide:chloropicrin (3:2) to minimize variation caused by other soil pathogens. The fumigant was injected at a depth of 20 cm under a 2.1-m continuous plastic sheet in early May. The Wooster silt loam site was similarly fumigated at a rate of 392 kg/ha. Spinks fine sand was transported to the research site and placed on an asphalt surface, covered with plastic, and fumigated with the same mixture. Plastic was removed 3 wk after fumigation, and soils were brought to the laboratory for pathogen infestation. Pathogen inoculum was quantitatively mixed with soil at two or three controlled levels and sampled after mixing for final assays of populations of *V. dahliae* and *P. penetrans*, as previously described (18). These final assays were used in the analyses of results. Mixed soils were then moved to the test sites and placed into clay tile microplots (10 L of soil per tile) within 48 hr of infestation.

Planting dates were 5 June 1985 (day of year = 156) and 3 June 1986 (day 154). One single-eye tuber seed piece of cultivar Superior was planted in each of 15 replicate microplots per treatment. The experimental design was a $3 \times 3 \times 4$ factorial, with the three soils each placed in randomly arranged whole plots and pathogen infestation levels randomized within whole plots. A CR-21 data logger (Campbell Scientific, Logan, UT) monitored air temperature, soil temperature at 5-cm depth in each soil, and precipitation during the growing season. The sand and silt loam were fertilized with 10-20-20 N-P_2O_5-K_2O at 20 g per microplot 4 wk after planting. Plants were sprayed with azinphosmethyl (O,O-Dimethyl *S*-[(4-oxo-1,2,3-benzotriazin-3(4*H*)-yl)methyl] phosorodithioate for control of leafhoppers, primarily *Empoasca fabae* Harris, on day 219 in 1985 and on days 191, 209, and 238 in 1986. Tubers were harvested and weighed on 4 September 1985 (day 247) and 3 September 1986 (day 246).

Disease assessment. Symptoms associated with the potato early dying syndrome are generally indistinguishable from normal senescence (17). Therefore, we use the term senescence in this paper to describe measures of disease and normal aging. This does not imply, however, that control plants grown in noninfested soil or in soil infested only with nematodes were suffering from early dying disease. Senescence was evaluated approximately weekly, on a subjective 0–3 scale, in both years. A zero rating was given to plants with no visible foliar senescence, a rating of one indicated chlorotic lower leaves, a rating of two was given to generally chlorotic plants usually with some wilting, and a rating of three indicated a severely diseased or dead plant (18). A rating of zero at about 1 wk prior to the first rating (taken when symptoms were first noticeable) was added to the data to form a zero baseline.

Area under the senescence progress curve (A) was calculated by the method of trapezoids, using days of the year and senescence rating as the x and y axis, respectively. A was calibrated to a 0–3 scale by dividing the calculated area by the total length of the rating period. Mean dates on which senescence ratings first exceeded zero were estimated directly from the data as an empirical method to measure senescence onset. If a plant received a senescence rating of two as its first rating greater than zero, it was assumed to have a rating of one midway between the dates of that rating and the previous rating. Also, a senescence rating of one was invalidated if followed by two or more ratings of zero.

Analyses. Least-squares regression analysis was used because of its superiority to multiple comparison techniques in analyzing response to quantitative levels of pathogen population density (13). For each soil and year, A, senescence onset, and tuber yield (grams per plant) were regressed on inoculum level of one pathogen at a constant level of the other pathogen to test for linear trends. Also, these variables were regressed on inoculum densities of both pathogens together or their natural log plus 1.0 transformations for each soil type separately and for the three soils combined. To model plant response over all three soils, soil type was coded by two indicator variables that took on the value of one or zero to indicate presence or absence of a particular soil type (10). For instance, the variable P equalled one if the soil type was Rifle peat, and zero otherwise. Likewise, S equalled one if the soil type was Spinks fine sand, and zero otherwise. Wooster silt loam was represented with zero for variables P and S.

Average tuber yields within each soil and treatment were divided by their respective control means to form an index of relative yield. Expression of yield relative to controls minimizes effects of soil type that are independent of the reduction in yield caused by pathogens. Best-fitting regression equations were found by stepwise analysis, and coefficients and determinant variables were

compared with results from previous years (5). A previously developed predictive discriminant model (5) was also validated on these new data. The discriminant model classifies relative tuber yield into >90%, 80–90%, or <80% of the control by using preplant population densities of *V. dahliae* and *P. penetrans* as discriminating variables.

RESULTS

The 1985 and 1986 growing seasons presented quite different environments for potato growth and disease development. The 1985 season was characterized by moderate temperatures and well-dispersed rainfall (Fig. 1). The 1986 season, however, began with heavy rains for the first 6 wk after planting, followed by dry weather until harvest. Plants appeared stressed for water late in the 1986 season. Over the entire season, mean daily temperatures averaged 0.9 C more in 1986 than in 1985. In particular, the period from day 185 to day 215 averaged 1.6 C more in 1986 than in 1985. From planting to harvest in 1985, 1,228, 1,263, and 1,270 degree days accumulated in Wooster silt loam, Rifle peat, and Spinks fine sand, respectively; corresponding cumulative degree days in 1986 were 1,363, 1,400, and 1,392. Air temperatures were related to disease assessments because of the small differences between soils and because readily available air temperature data may allow future verification of our results.

Disease assessment. A was less different among soils than between years, especially if assayed pathogen densities are taken into account (Table 1). Overall, more senescence occurred in 1986 than in 1985. Increasing populations of *P. penetrans* in the absence of *V. dahliae* had no significant ($P = 0.05$) effect on A, as indicated by linear trend analysis; however, 31 significant linear trends were found in the remaining 36 regressions (Table 1). Several trends appeared to be curvilinear, but this response was less important than the linear trends and was not analyzed further.

In 1985, ln(*V. dahliae* × *P. penetrans*) was a significant ($P<0.05$) predictor of A in all soils and ln(*V. dahliae*) was significant in Rifle peat and Spinks fine sand (Table 2). Slope coefficients for ln(*V. dahliae* × *P. penetrans*) were very similar for the three soil types in 1985. No soil type indicator variable was significant in 1985 when all three soil types were analyzed together; therefore, soil did not have a large effect on A. In 1986, ln(*V. dahliae*) and ln(*V. dahliae* × *P. penetrans*) were significant predictors of A in all three soils. Regression coefficients in 1986 differed sufficiently among soils so that P and S, as well as $S \times$ ln(*V. dahliae*), were significant indicator variables in an equation that combined the three soils. Inclusion of $S \times$ ln(*V. dahliae*) suggests that the fungus had a larger effect on A in sand than in peat and silt loam. The marked increase of early dying due to combined soil infestation with *V. dahliae* and *P. penetrans*, measured as senescence at harvest and as reduced tuber yields in previous years (18), can be seen in the linear trend analysis of A (Table 1) and in regression analysis (Table 2).

For brevity, only the plant senescence curves for controls, *V. dahliae* alone, *P. penetrans* alone, and high levels of *V. dahliae* plus high levels of *P. penetrans* are presented in Figure 2. Senescence consistently progressed fastest in plants grown in soils infested with the highest levels of *V. dahliae* plus *P. penetrans*. There was an early increase in senescence in 1985 for *V. dahliae* plus *P. penetrans*, a slight leveling off, then rapid senescence during later weeks. However, in 1986, the leveling was reduced or absent. The progress of plant senescence was similar between controls and the high rate of *P. penetrans* alone (Fig. 2). Disease progress was faster in 1986 than in 1985 in all soils, particularly for controls and *P. penetrans* alone.

Mean dates of senescence onset depicted the earlier decline of

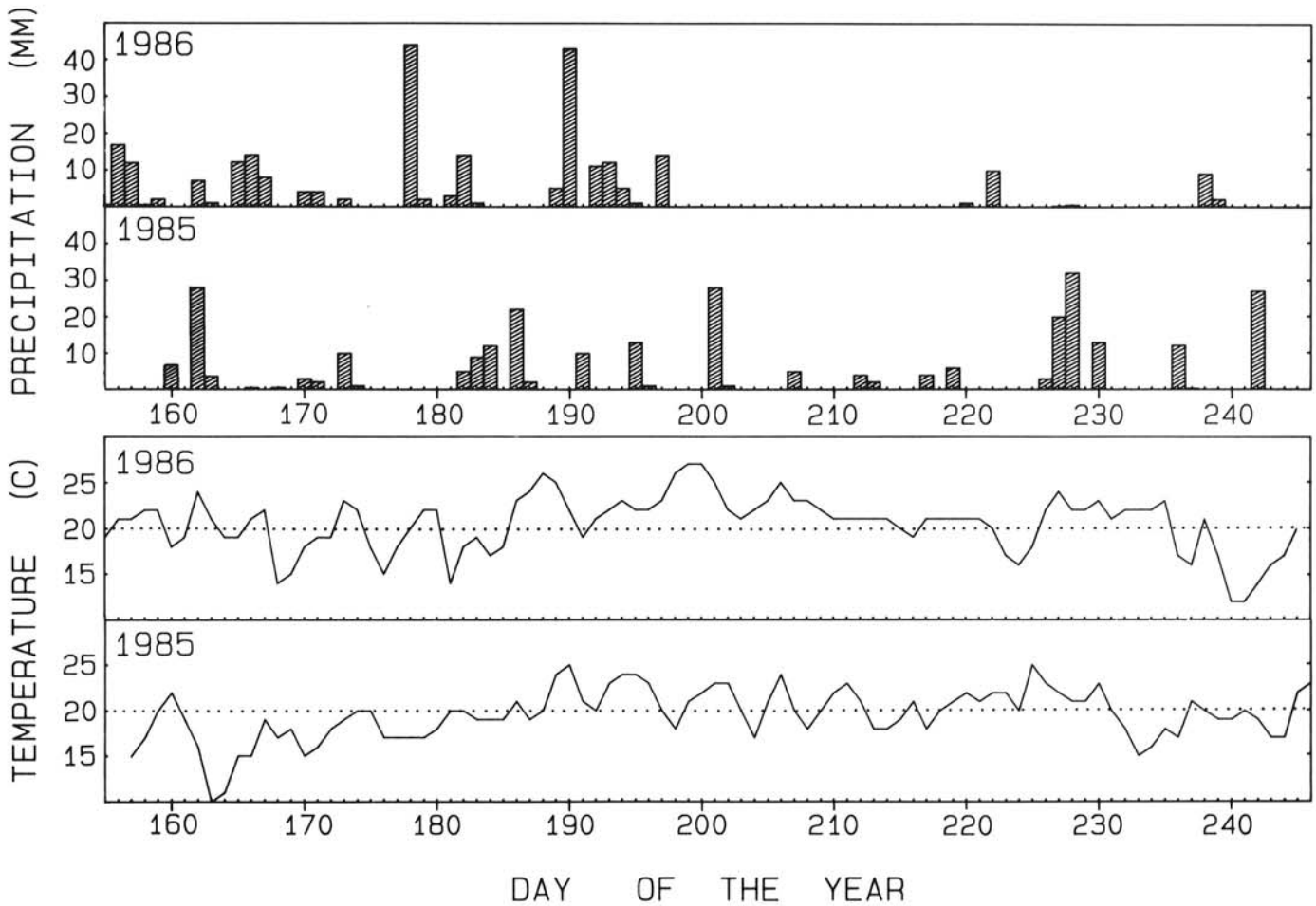

Fig. 1. Average daily air temperature and total daily precipitation in 1985 and 1986 at the experimental site, Wooster, OH.

TABLE 1. Effect of *Verticillium dahliae* and *Pratylenchus penetrans* in three soil types on areas under the senescence progress curve (0–3 scale) for the potato cultivar Superior grown in field microplots at Wooster, OH, in 1985–1986

	1985					1986				
Wooster silt loam										
P. penetrans[b]	*V. dahliae*[a] 0	0.1	3	56	*P*[c]		*V. dahliae* 0	0.5	2	10	*P*
0	0.4	0.7	1.1	1.3	0.03	0	0.7	1.0	1.5	1.6	0.00
4	0.4	1.1	1.7	1.7	0.10	11	1.0	1.1	1.7	2.0	0.00
15	0.6	1.4	1.8	2.0	0.05	50	0.8	1.7	2.1	2.3	0.00
P	0.07	0.03	0.13	0.06		*P*	0.98	0.00	0.00	0.00	
Rifle peat										
P. penetrans	0	2	7	34	*P*		0	0.5	3	8	*P*
0	0.2	0.6	1.1	1.2	0.01	0	0.9	0.8	1.1	1.3	0.01
4	0.3	1.2	1.6	1.7	0.03	11	0.9	1.0	1.4	1.7	0.00
15	0.3	1.4	1.7	1.9	0.02	50	0.9	1.5	1.8	2.0	0.00
P	0.24	0.03	0.04	0.01		*P*	0.84	0.00	0.00	0.00	
Spinks fine sand										
P. penetrans	0	4	16	72	*P*		0	0.3	1	2	*P*
0	0.3	1.0	1.2	1.2	0.03	0	0.7	0.8	1.1	1.3	0.00
4	0.6	1.1	1.6	1.7	0.01	11	0.8	1.0	1.3	1.5	0.00
15	0.5	1.6	1.8	2.0	0.03	50	0.7	1.0	1.3	1.8	0.00
P	0.54	0.00	0.04	0.02		*P*	0.55	0.56	0.30	0.00	

[a] Population levels of *V. dahliae* as colony-forming units per cm^3 of soil at planting.
[b] Population levels of *P. penetrans* as vermiforms per 100 cm^3 of soil at planting.
[c] *P* denotes linear trend significance level for the change in area with increasing levels of one pathogen at a constant population level of the other pathogen.

TABLE 2. Best-fitting regression equations for area under the senescence progress curve (0–3 scale) to population levels at planting of *Verticillium dahliae* (VD) and *Pratylenchus penetrans* (PP) in silt loam, peat (P), and sand (S) in 1985–1986

Soil type	Equation	Adjusted r^2 (%)
	1985	
Wooster silt loam	$0.87 + 0.19[\ln(VD \times PP)]$	62
Rifle peat	$0.44 + 0.21[\ln(VD)] + 0.15[\ln(VD \times PP)]$	89
Spinks fine sand	$0.58 + 0.17[\ln(VD)] + 0.11[\ln(VD \times PP)]$	89
Combined	$0.65 + 0.14[\ln(VD)] + 0.14[\ln(VD \times PP)]$	78
	1986	
Wooster silt loam	$0.94 + 0.27[\ln(VD)] + 0.14[\ln(VD \times PP)]$	87
Rifle peat	$0.86 + 0.16[\ln(VD)] + 0.13[\ln(VD \times PP)]$	93
Spinks fine sand	$0.71 + 0.55[\ln(VD] + 0.07[\ln(VD \times PP)]$	96
Combined	$1.00 + 0.24[\ln(VD)] + 0.12[\ln VD \times PP)] - 0.19[P] - 0.31[S] + 0.21[S \times \ln(VD)]$	90

green tissue in plants affected by early dying (Table 3). Significant ($P < 0.05$) linear trends were least frequent for the *P. penetrans*-alone treatment, but there was a consistent dose response to *V. dahliae*. Senescence onset for high levels of *V. dahliae* plus *P. penetrans* was 32–35 days sooner than for controls in 1985 and 19–24 days sooner in 1986. Senescence onset was highly ($P < 0.01$) correlated with ln(*V. dahliae* × *P. penetrans*) in 1985 ($r = -0.77$) and 1986 ($r = -0.85$). Senescence of control plants began 9–15 days sooner in 1986 than in 1985, when planting date was taken into account. This difference decreased to 1–6 days sooner, when based on cumulative air degree days (base, 7 C). Dates of senescence onset for comparable pathogen densities were much less different between years than dates of onset for controls.

Tuber yield. The combination of *V. dahliae* and *P. penetrans* reduced tuber yields in all three soils (Table 4) in a manner consistent with previous results (5,18). *V. dahliae* alone reduced yields from 0 to 31% of the control; *P. penetrans* caused, at most, a 16% yield reduction in Spinks fine sand. The combined effect of *V. dahliae* and *P. penetrans* drastically reduced yields up to 63% at high inoculum level. High plant-to-plant variability, rather than curvilinear responses, was largely responsible for the somewhat few significant linear trends for treatments having both pathogens. Tuber yields in 1985 and 1986 were significantly correlated ($P < 0.01$) with *A* ($r = -0.97$ and -0.76) and day of senescence onset ($r = 0.92$ and 0.76).

Yield was regressed on pathogen density for each soil type separately (Table 5). Pathogen effects on yield within soils varied from year to year and were different among soils within years. Ln(*V. dahliae* × *P. penetrans*) was a significant predictor in most instances. *P. penetrans* was a significant factor in sand both years and in Wooster silt loam and Rifle peat in 1986. Coefficients of determination (adjusted r^2) were generally higher in 1985 than in 1986, indicating that *V. dahliae* and *P. penetrans* accounted for more variation in yield in 1985.

Soil type was then used as an indicator variable in regressions of tuber yield on pathogen density (Table 5). Rifle peat increased yields by 60 g per plant in 1985 and 139 g per plant in 1986, relative to yields in Wooster silt loam and Spinks fine sand. There were no significant interactions between pathogen density and soil type.

Regression models (not shown) of yield as a percentage of controls within soils and for separate years had similar determinant variables and coefficients as models fit to previous data (5). *P. penetrans* was a significant determinant variable in both years for relative yield in Spinks fine sand; models predicted a 1% (1985) or 0.2% (1986) yield decline per assayed vermiform. *V. dahliae* caused a significant yield reduction in Spinks fine sand both years but only in 1985 for Rifle peat and Wooster silt loam.

A discriminant model (5) that had been developed with data from microplot experiments conducted in Wooster silt loam and used ln(*V. dahliae*) and ln(*V. dahliae* × *P. penetrans*) as discriminating variables was validated on these new data (Table 6). Severe misclassifications of predicted groupings of relative yields were few. For data over all soils, the model severely misclassified only 8% of the yields relative to the controls. A misclassification was considered severe when the prediction was >90% but actual yield was <80% of the control, or conversely, when the prediction was <80% and the actual yield was >90% of the control.

DISCUSSION

These results support the assertion (5,8,16,18) that the interaction of *V. dahliae* and *P. penetrans* creates a more acute disease situation and greater yield reductions than when either pathogen is present alone. This interaction proceeded in all three soil types tested, and though the effect of fungus and nematode on senescence onset, progress, and yield showed some quantitative differences among soils and between years, similarities appeared more often than substantial differences. Early dying disease symptoms appeared earlier and progressed faster when both *V. dahliae* and *P. penetrans* were present in the three soils than when *V. dahliae* or *P. penetrans* alone was added to soil. Disease progress was intermediate between the interaction treatments and treatments with *P. penetrans* when plants were grown in soil with *V. dahliae* alone (Fig. 2). Plants in soil infested with *P. penetrans* alone generally senesced similarly to control plants grown in fumigated soil. Differences among soils in onset and progress of senescence were much less than differences between years. The only demonstratable interaction between soil type and pathogens occurred in 1986, when *V. dahliae* in sand caused an increase in *A* (Table 2).

Use of a subjective rating scale of disease progress, which is liable to confound normal plant senescence with early dying disease symptoms, is less desirable than a more quantitative measure, such as disease incidence or percentage of infected tissue. However, given the nature of this disease as well as the microplot experimental method, quantitative measures would have been

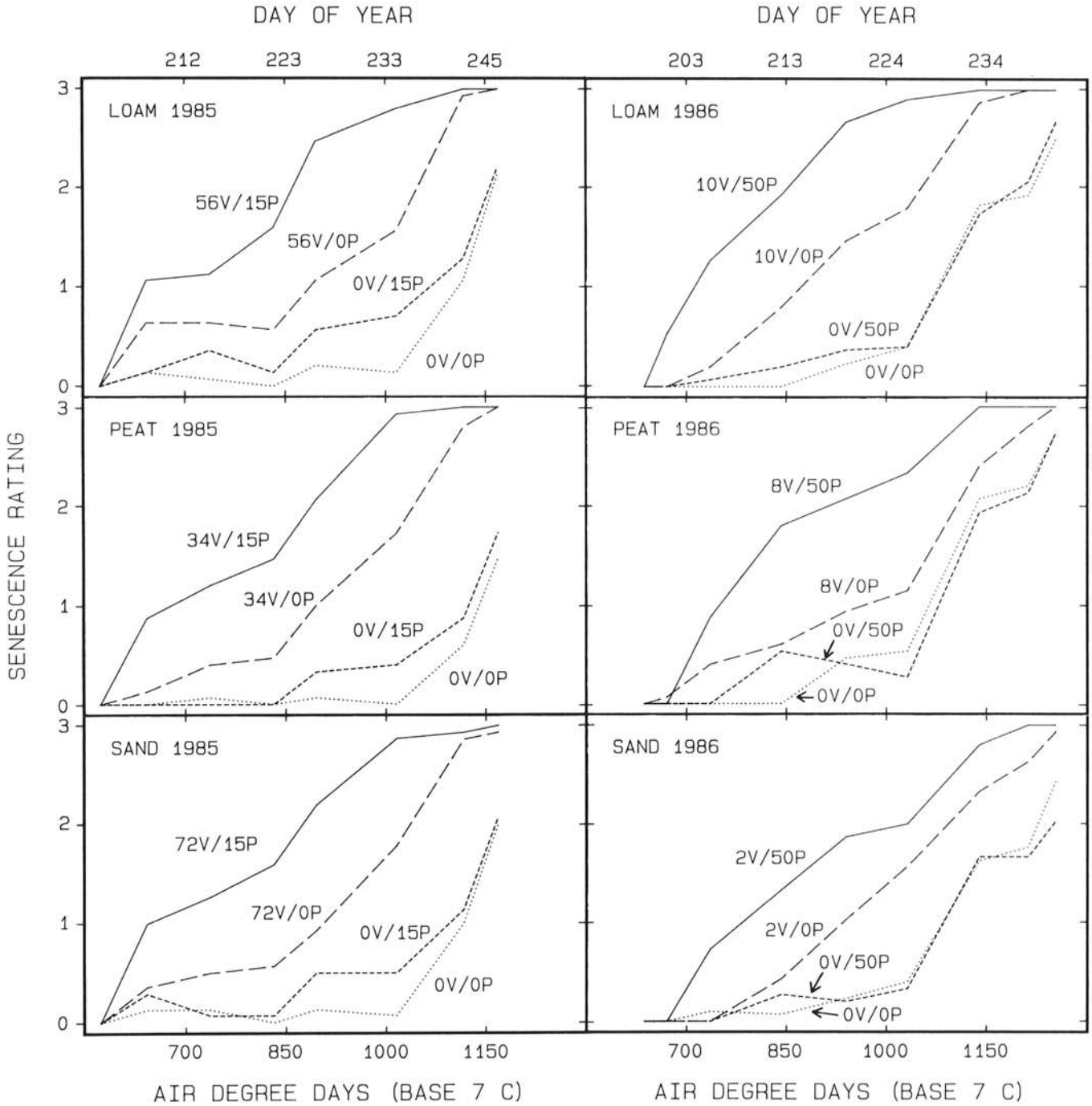

Fig. 2. Senescence progress curves for potato cultivar Superior in Wooster silt loam, Rifle peat, and Spinks fine sand, as affected by preplant population levels of *Verticillium dahliae* (V, cfu/cm^3) and *Pratylenchus penetrans* (P, vermiforms/100 cm^3) and expressed as either a day of the year or air degree day (base, 7 C).

extraordinarily difficult to obtain. Nevertheless, valuable information was drawn from available data by using semiquantitative ratings.

Although weather patterns were not the sole difference between experiments conducted in 1985 and 1986, it is useful to speculate on how much variation in disease severity can be accounted for by plant/pathosystem response to environment. Senescence in healthy potatoes is externally influenced by temperature, soil moisture, soil nutrient supply, and, in some cultivars, day length (20). The critical photoperiod for tuberization in cultivar Superior is longer than 20 hr (7), so day length was not a factor in this case. Temperature and soil moisture appeared to be the dominant forces driving onset of senescence for controls in these experiments, but senescence onset in plants grown in soil infested with comparable levels of *V. dahliae* and *P. penetrans* in both years appeared to be less dependent on environment (Table 3). Warmer temperature and drier soils in 1986 than in 1985 can reasonably be held accountable for observable differences between years in onset of senescence. A smaller difference in the apparent rate of senescence between controls and diseased plants in 1986 than in 1985 (Fig. 2) may have been due to the shortage of soil moisture experienced by all plants. Higher apparent rates of senescence development in

TABLE 3. Effect of *Verticillium dahliae, Pratylenchus penetrans*, and soil type on day of the year on which foliar senescence in the cultivar Superior was first observed in 1985–1986

	1985						1986				
Wooster silt loam											
	V. dahliae[a]						*V. dahliae*				
P. penetrans[b]	0	0.1	3	56	*P*[c]		0	0.5	2	10	*P*
0	239	227	221	213	0.00	0	228	222	215	213	0.00
4	237	217	208	208	0.00	11	225	221	210	206	0.00
15	228	212	209	207	0.00	50	225	210	206	204	0.00
P	0.00	0.00	0.00	0.00		*P*	0.15	0.00	0.00	0.00	
Rifle peat											
	0	2	7	34	*P*		0	0.5	3	8	*P*
0	243	233	221	220	0.00	0	226	227	222	217	0.00
4	240	218	210	209	0.00	11	223	220	215	210	0.00
15	235	214	210	208	0.00	50	225	213	208	207	0.00
P	0.00	0.00	0.00	0.00		*P*	0.94	0.00	0.00	0.00	
Spinks fine sand											
	0	4	16	72	*P*		0	0.3	1	2	*P*
0	240	222	218	218	0.00	0	227	226	221	218	0.00
4	229	221	209	208	0.00	11	224	218	216	213	0.00
15	232	210	207	207	0.00	50	226	223	216	208	0.00
P	0.07	0.00	0.00	0.00		*P*	0.83	0.31	0.09	0.00	

[a] Population levels of *V. dahliae* as colony-forming units per cm^3 of soil at planting.
[b] Population levels of *P. penetrans* as vermiforms per 100 cm^3 of soil at planting.
[c] *P* denotes linear trend significance level for the change in date of first foliar senescence with increasing levels of one pathogen at a constant population level of the other pathogen.

TABLE 4. Effect of *Verticillium dahliae* and *Pratylenchus penetrans* in three soil types on tuber yield (grams per plant) of the cultivar Superior grown in field microplots at Wooster, OH, in 1985–1986

	1985						1986				
Wooster silt loam											
	V. dahliae[a]						*V. dahliae*				
P. penetrans[b]	0	0.1	3	56	*P*[c]		0	0.5	2	10	*P*
0	980	880	820	770	0.24	0	790	830	760	700	0.11
4	940	740	520	520	0.17	11	860	900	760	550	0.00
15	980	630	500	370	0.08	50	830	630	500	480	0.01
P	0.98	0.13	0.20	0.07		*P*	0.79	0.00	0.00	0.02	
Rifle peat											
	0	2	7	34	*P*		0	0.5	3	8	*P*
0	1000	920	920	770	0.02	0	1020	920	900	840	0.07
4	1040	740	620	510	0.02	11	940	850	980	750	0.08
15	1030	760	500	400	0.02	50	910	790	760	760	0.11
P	0.76	0.31	0.03	0.03		*P*	0.19	0.07	0.06	0.54	
Spinks fine sand											
	0	4	16	72	*P*		0	0.3	1	2	*P*
0	1000	850	700	690	0.04	0	920	800	780	770	0.20
4	980	750	530	520	0.05	11	890	860	810	740	0.26
15	840	550	470	370	0.03	50	830	770	680	600	0.08
P	0.06	0.02	0.04	0.06		*P*	0.55	0.64	0.56	0.09	

[a] Population levels of *V. dahliae* as colony-forming units per cm^3 of soil at planting.
[b] Population levels of *P. penetrans* as vermiforms per 100 cm^3 of soil at planting.
[c] *P* denotes linear trend significance level for the change in yield with increasing levels of one pathogen at a constant population level of the other pathogen.

TABLE 5. Best-fitting regression equations that describe the effect of preplant population density of *Verticillium dahliae* (VD) and *Pratylenchus penetrans* (PP) on tuber yield (grams per plant) in silt loam, peat (P), and sand in 1985–1986

Soil type	Equation	Adjusted r^2 (%)
	1985	
Wooster silt loam	$848 - 76[\ln(VD \times PP)]$	76
Rifle peat	$1{,}011 - 61[\ln(VD)] - 67[\ln(VD \times PP)]$	96
Spinks fine sand	$980 - 74[\ln(VD)] - 27[\ln(VD \times PP)] - 10\,(PP)$	93
Combined	$898 - 37[\ln(VD)] - 60[\ln(VD \times PP)] + 60\,(P)$	84
	1986	
Wooster silt loam	$883 - 111[\ln(VD)] - 3(PP)$	70
Rifle peat	$994 - 72[\ln(VD)] - 28[\ln(PP)]$	59
Spinks fine sand	$913 - 184[\ln(VD)] - 2(PP)$	86
Combined	$843 - 58[\ln(VD)] - 32[\ln(VD \times PP)] + 139\,(P)$	72

TABLE 6. Classification matrix for potato (cv. Superior) tuber yields less than 80%, 80–90%, and greater than 90% of control yields in three soils based on a discriminant model developed with potato early dying microplot data from Wooster, OH, in 1980, 1983, and 1985[a]

Soil type	Actual classification	Prediction <80%	Prediction 80–90%	Prediction >90%	Percent severely incorrect predictions[b]
Wooster silt loam[c]	<80%	4	0	0	0
	80–90%	0	1	0	
	>90%	1	0	6	14
Rifle peat	<80%	9	1	1	9
	80–90%	0	2	2	
	>90%	1	2	6	10
Spinks fine sand	<80%	7	2	1	10
	80–90%	1	2	5	
	>90%	0	0	6	0

[a] From Francl, L. J., et al (5).
[b] A prediction is severely in error when either <80% relative yield is predicted for actual relative yields >90% or when >90% relative yield is predicted for actual relative yields <80%.
[c] Data from 1985 were used in the development of the discriminant model (5), so only data from 1986 are presented here.

1986 than in 1985 also corresponded to the general observation that potato early dying is more severe in dry years.

Soil type did not markedly affect yield reductions due to *V. dahliae* and *P. penetrans*, although yields in Rifle peat were consistently higher overall. There was a consistent yield reduction in both years for potatoes in Spinks fine sand with *P. penetrans* alone and, to a lesser extent, with *V. dahliae* alone. The reduction of yields relative to controls in these soils, as affected by *V. dahliae* and *P. penetrans*, was similar to microplot experimental results from previous years (5).

Tuber yield was highly correlated to disease assessments, but the magnitude of yield reductions for combinations of *V. dahliae* and *P. penetrans* in all soils was less in 1986 than in 1985. This is explainable, in part, by the larger difference between controls and combined pathogen treatments for onset of senescence and apparent rate of senescence (Table 3 and Fig. 2) in 1985 versus 1986. Regression models of A (Table 2) explained more experimental variability in 1986 than in 1985, whereas models of yield (Table 5) explained more variability in 1985 than in 1986. The influence of pathogens on yield, therefore, was less in 1986, because the environment exerted a stronger influence, effectively reducing variability in senescence ratings. Actual tuber yields of control plants were comparable between years in the three soils, which is somewhat surprising given the different environments during the growing seasons.

Our yield loss discriminant model (5) performed well when validated on these new microplot data. The model is general in that yield reductions within a given soil are expressed as a percentage of yield potential in that soil, which is estimated by the controls grown in noninfested soil. Thus, soil type was not needed to classify relative yield reductions, because using relative yields reduces the effect of soil productivity factors that do not interact with the early dying disease syndrome. Unless further evidence proves contradictory, these data show that no soil type indicator needs to be incorporated into this predictive model. The model can be refined further if the yield reduction caused by *P. penetrans* in sandy soils in the absence of *V. dahliae* is taken into account. Future validation studies will be made in commercial potato fields having various soil types, in our effort to deploy a predictive model to forecast yield reductions for potato early dying in an integrated pest management program.

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