Verticillium Wilt of Potato: A Model of Key Factors Related to Disease Severity and Tuber Yield in Southeastern Idaho

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ABSTRACT

In three years (1994, 1995, and 1996), a total of 100 commercial potato fields in southeastern Idaho were surveyed for soil variables, severity of Verticillium wilt, soil inoculum density of *Verticillium dahliae* and *Colletotrichum coccodes*, colonization of stems, root, and tubers by *V. dahliae* and *C. coccodes*, and tuber yield, size, and quality. As a generalization, factors related to soil integrity (organic matter, organic nitrogen, and increased nutrient availability) were most closely related to wilt suppression and higher tuber yields, whereas factors related to loss of soil integrity (sodium and reduced nutrient availability) were related to increased wilt and lower tuber yields. In a multiple regression analysis, three independent variables, feeder-root infections by *V. dahliae*, sodium content in soil, and soil organic content, were significant predictors of tuber yield. With these three factors, this model accounted for 49%, 53%, and 62% of the field variability related to total yield in 1994, 1995, and 1996, respectively. Throughout this investigation, *V. dahliae* root infections had the most direct effect on tuber yield, which emphasizes the importance of quantifying root infections in epidemiological studies of Verticillium wilt. Based on these results, organic matter may be one factor that can be manipulated for suppression of Verticillium wilt without reducing soil populations of the pathogen.

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INTRODUCTION

In the arid and semi-arid regions of the world, Verticillium wilt, caused by *Verticillium dahliae* Kleb., is a common limiting factor of potato production. In the western U.S., this disease is frequently referred to as potato early dying (Rowe *et al.* 1987). Severe early dying symptoms, however, can also result from interactions between *V. dahliae* and the root lesion nematode, *Pratylenchus penetrans*. The results of numerous soil assays have shown *P. neglectus* to be the most common root lesion nematode in Idaho potato fields (Davis *et al.* 1992), whereas *P. penetrans* has not been detected. To date, our studies have shown no relationship between *P. neglectus* and either wilt severity or potato yield (Davis *et al.* 1992).

Colletotrichum coccodes can cause aerial infections, premature vine death, and as a soilborne pathogen it can interact with *V. dahliae* to increase symptom expression and yield reduction (Mohan *et al.* 1987). In addition to yield reductions, certain *C. coccodes* isolates have also been found to reduce specific gravity and yields of larger tubers >280 g (Barkdoll and Davis 1992).

Soil inoculum densities of *V. dahliae* have been correlated with incidence and severity of Verticillium wilt and economic damage in potato (Nnodu and Harrison 1979). In southeastern Idaho, however, this has not been the case. A three-year quantitative survey of potato fields throughout southeastern Idaho showed no significant correlation between soil populations of *V. dahliae* and wilt severity (Davis and Everson 1986). Several cultural factors such as nitrogen (N), phosphate (P), and soil electroconductivity (EC) accounted for 71% of the field variability related to Verticillium wilt in cv. Russet Burbank.

Green manure studies at the University of Idaho Aberdeen Research Center also raised questions concerning the predictability of Verticillium wilt with *V. dahliae* soil inoculum levels (Davis *et al.* 1996). Large differences in disease incidence and severity as well as economic damage were observed among different green manure treatments in plots having essentially the same soil inoculum densities of the pathogen. A later study (Davis *et al.* 1999) showed control of Verticillium wilt with green manures (barley and corn) even though the inoculum densities of *V. dahliae* were 2 to 4 fold higher than weed free fallow areas. In contrast to soil populations of *V. dahliae*, root colonization by this pathogen early in the growing season was highly correlated with both wilt incidence (positively) and potato yield (negatively). Clearly, a number of soil physical, chemical and/or biological factors significantly influenced the ability of *V. dahliae* to colonize roots while compromising the relationship between soil inoculum density and disease incidence.

These recent findings suggested a possible explanation for the failure to find a significant correlation between soil inoculum density and wilt incidence in the earlier survey of grower fields (Davis and Everson 1986). In commercial fields, factors similar to those observed in our green manure studies could impact the ability of *V. dahliae* to colonize potato roots, and hence, weaken the relationship between soil inoculum density and disease incidence and severity. The availability of a reliable, quantitative assay for root colonization (Huisman 1988) permitted the evaluation of this possibility. In addition, the simultaneous quantification of other soil factors and potentially interacting microorganisms may provide leads on other factors influencing this host-pathogen interaction.

The objectives of this investigation were (1) to quantify both *V. dahliae* and *C. coccodes* in soil and in stems, roots, and tubers of potato and soil nutrients and soil physical factors in commercial potato fields and (2) to determine the relationships of pathogen inoculum densities and soil factors to wilt severity, yield, and tuber quality.

MATERIALS AND METHODS

Field Selections

Soil samples were collected from 100 commercial potato fields in southeastern Idaho during 1994-1996. None of these fields, which had been in potato production for an extended period of time, had been treated with green manures. Approximately 50% of the growers practice a three-year wheat, sugar beet, wheat rotation prior to potato. Depending on the region and year, survey fields were selected that had been planted with Russet Burbank on similar dates. Unlike the earlier study, all fields selected for the survey were under professional management. Many growers employ the services of crop-production advisors who make recommendations on fertilizer applications (based on soil and petiole analysis), irrigation scheduling, and other cultural practices. Selection of such supervised fields minimized many uncontrolled variables that different cultural practices can introduce. The constant oversight of field performance ensured that the survey fields received essentially similar cultural treatment throughout the growing season. For each time and area, potatoes in fields being compared were at similar growth stages. In the three production areas (Bingham County, Power County, and Magic Valley), similarity of growth stage at sampling time was verified by evaluating the plant height after emergence. At each sampling date, differences in plant height among locations were considered negligible. In each field, a 30.5-m-long two-row plot was staked. All evaluations of disease severity and collections of soil and plant material were taken from these plots.

Soil Assays

A total of 18 random soil samples were taken in late May with a 1.8-cm-diameter sampling tube to a depth of 23 cm from each plot and bulked. Samples from locations being compared were made within 24 hr. Soil samples were mixed thoroughly, divided, and analyzed the following day by Stukenholtz Labs (Twin Falls, ID) for the following: pH, electroconductivity (mmhos cm^{-1}), Na, cation exchange capacity (CEC), excess lime, organic matter, organic N, NO_3-N, P, K, Ca, Mg, S, Zn, Fe, Mn, Cu, and B. The remaining soil was slowly air dried for 4-5 wk in the laboratory at room temperature (about 20-25 C). Air-dried soil from each plot was separately remixed in plastic bags. From this sample, six subsamples totaling 80 g were randomly collected and mixed again. Samples from the third mixing were passed through a 250-μm (60 mesh) screen to remove large pieces of organic matter and to standardize particle size. Final samples were again mixed, and for each plot, five subsamples (50 mg each) were plated onto separate plates of NP-10 medium (Sorensen *et al.* 1991) with the Anderson air sampler (Butterfield and DeVay 1977). Plates were incubated at laboratory room temperature for 2 wk, washed under running tap water to remove soil particles, and colonies of *V. dahliae* and *C. coccodes* were counted with a binocular microscope and expressed as colony-forming units per gram of dry soil (cfu/g soil). Soil samples were independently assayed by both J.R. Davis and O.C.

Huisman at the University of Idaho, Aberdeen, and University of California, Berkeley, respectively.

Root Assays

Five core samples were taken with a bulb planter (6 x 10 cm) from the row in each plot that was not used for harvest. Soil samples were collected in early July of each year. Root infections by *V. dahliae* and *C. coccodes* were quantified by the procedure of Huisman (Huisman 1988). Feeder roots of at least 1 cm in length were collected with tweezers from the soil sample. Roots were washed thoroughly in root wash solution (1% sodium hexametaphosphate, 0.1 % Tergitol NP-10) and rinsed in sterile water. Roots were then plated on NP-10 medium (Sorensen, *et al.* 1991). After 2 wk, the number of colonies of *V. dahliae* and *C. coccodes* emerging from the root cortex were counted and expressed as number of colonies per meter of root (cfu/m root).

Disease Assessment

Wilt symptoms were expressed as the percentage of stems with symptoms in each plot (50 stems per plot). In 1994, symptom development was both earlier and generally more severe than in either 1995 or 1996. In view of this, wilt symptoms were expressed as the incidence of severe wilt (>75% of foliage with symptoms) as previously described (Davis *et al.* 1983). In 1995 and 1996, however, disease severity was noticeably less, and wilt symptoms were evaluated on the uppermost 15 cm of the stem. To separate Verticillium-like symptoms from other factors that may produce similar symptoms (e.g., drought stress, nutrient deficiency, or senescence), the terminal 8 cm of stem tissue was assayed for *V. dahliae* and *C. coccodes* as previously described (Davis *et al.* 1983). At harvest, 1-mm-thick slices from the stem ends of 30 tubers were bulked and assayed for each pathogen. Stem apices and tuber stem ends were air dried in the laboratory and ground with a Wiley mill using a 40-mesh screen. Samples (10 mg) were then plated onto NP-10 medium using the Anderson Sampler. Following incubation for several weeks, *V. dahliae* and *C. coccodes* colonies were counted under a stereomicroscope. Colonies from stem and tuber populations were estimated as colony-forming units per gram dry tissue (cfu/g tissue).

Tuber Harvesting and Grade

At season end, potatoes were harvested from a 3.0-m row length at each location. Following washing, tubers were graded according to standard methods (Anonymous 1971).

Data Analysis

All fungal soil, root, stem, and tuber population data were transformed [ln (x+1)]. Simple correlations were first determined for all data, which included 18 soil factors, eight pathogen variables (inoculum densities in soil of *V. dahliae* and *C. coccodes*, root colonization by *V. dahliae* and *C. coccodes*, stem colonization by *V. dahliae* and *C. coccodes*, and tuber colonization by *V. dahliae* and *C. coccodes*) and five yield variables (total yield, usable tubers, U.S. #1 tubers, tubers >280 g, and U.S. #1 tubers >280 g) (Steel and Torrie 1960). Years of data collection also were included in the model. Partial regression coefficients were calculated for each year, and yield data of each year were normalized (adjusted). This allowed for comparisons among growers within year, between years, and for the combined years.

These estimates were tested for generality by including other terms in the model – e.g. OM, Na, and ln cfu *V. dahliae* as predictors. Multiple regression equations (Myers 1986) and prediction models were determined based on the most commonly related factors.

RESULTS

The commercial fields exhibited a range of values for each of the biotic and abiotic factors (Table 1). For most factors, differences occurred among years. Since fields were selected *a priori* to data collection, such differences may be related to chance selection processes for soil physical factors or to environmental differences among years (for disease and tuber components).

Relationship Between Verticillium Soil and Root Populations and Wilt Severity and Tuber Yield

Analysis of within-year data yielded a number of significant correlations among the factors (Table 2). On the average (using pooled data correlated within years), the density of cortical root infections by *V. dahliae* correlated significantly ($P<0.05$) with wilt severity whereas soil inoculum density of *V. dahliae* did not. The correlation (0.529**) between the percentage of wilt and root cortical infections was also significant ($P<0.01$) (Table 2). Relationships, where they existed, either between soil populations of *V. dahliae* and feeder-root infections or between wilt severity and yield components were all negative (Table 2). Wilt severity and root colony densities correlated significantly ($P<0.01$) with all yield components; e.g., total yield, usable tubers, U.S. #1s, and tubers > 280 g. With the exception of the tubers in the >280-g class, correlation coefficients were higher for root colony density

TABLE 1—*Mean values and ranges of survey data by year of commercial potato fields.*

	1994		1995		1996	
	Mean	Range	Mean	Range	Mean	Range
% wilt	27.1	0-100	19.6	0-80	14.2	0-40
Ln cfu *Colletotrichum coccodes*/g stem	2.44	0-8.00	—		—	
Ln cfu *C. coccodes*/m root	1.66	0-3.14	.73	0-2.84	—	
Ln cfu *C. coccodes*/g soil	1.05	0-3.37	.41	0-3.21	.58	0-2.83
Ln cfu *C. coccodes*/g tuber	7.09	3.07-8.72	6.55	0-8.56	4.48	0-8.04
Ln cfu *Verticillium dahliae*/g stem	3.44	0-9.16	4.31	0-9.32	3.39	0-7.55
Ln cfu *V. dahliae*/m root	2.21	0-4.11	1.57	.59-3.03	1.47	0-3.03
Ln cfu *V. dahliae*/g soil	2.99	0-5.42	3.61	.69-4.98	2.49	0-4.23
Ln cfu *V. dahliae*/g tuber	6.29	3.71-8.22	5.76	3.04-7.74	5.54	0-8.14
% organic matter	1.60	.50-2.85	1.52	.85-2.30	1.78	1.45-2.35
ppm organic N	60.6	25.0-90.0	61.4	35.0-85.0	38.1	35.0-45.0
CEC[1]	13.4	7.0-17.0	17.1	7.2-22.5	16.9	11.7-21.2
EC[2]	1.57	.80-3.00	.93	.50-2.00	1.05	.40-2.00
% lime	4.51	0-12.80	3.41	.10-12.80	5.89	1.20-13.90
soil pH	7.57	6.00-8.10	7.78	6.9-8.2	7.97	7.40-8.20
ppm NO_3-N	26.6	14.0-39.0	26.5	10.0-38.0	33.2	13.0-45.0
ppm P	26.5	17.0-35.0	33.6	24.0-51.0	29.9	7.00-47.00
ppm K	286	140-510	308	130-810	330	95-1527
meg 100^{-1}g soil	.19	.05-.50	.13	.05-.40	.27	.20-.50
ppm Ca	10.0	4.9-12.7	12.8	4.3-18.5	12.6	8.7-16.3
ppm S	22.8	10.0-62.0	13.7	5.0-29.0	11.8	7.00-25.00
ppm Zn	3.81	.60-9.10	3.09	1.20-7.80	2.87	1.50-6.90
ppm Mn	8.83	2.20-18.30	5.82	2.40-14.50	7.88	4.00-13.00
ppm B	.63	.40-.90	.59	.50-.70	.66	.65-.70
t ha^{-1} total yield	43.4	30.5-56.2	41.9	26.7-56.3	46.0	15.9-62.51
t ha^{-1} usable tubers	31.4	20.1-42.4	28.4	10.5-43.2	30.9	10.3-53.4
t ha^{-1} U.S. #1 tubers	25.2	9.6-37.5	24.0	7.6-37.9	23.4	6.9-41.0
t ha^{-1} tubers >280g	9.5	2.0-22.1	6.4	0.8-20.6	12.5	2.1-29.4
t ha^{-1} U.S. #1 tubers >280g	10.4	2.0-22.1	4.9	0.0-15.6	8.3	0.5-22.5

[1] Cation exchange capacity
[2] Electroconductivity *coccodes.*

than for wilt severity (Table 2). Soil inoculum densities of *V. dahliae* were negatively correlated ($P<0.01$) with total yield, usable tubers, and yield of U.S. #1s, but not with tubers > 280 g. The correlation coefficients, however, were much lower than those found between root colony density and yield components. These data show that over the three-year study that feeder root infection was the best predictive value for both wilt severity and yield loss. Tuber infection was second to the feeder root infection in predictive value, followed by soil and apical stem populations.

Relationship of Abiotic Factors with Wilt Severity and Tuber Yield

Ten soil factors were negatively correlated with wilt severity (organic matter [OrgM], organic N [OrgN], cation exchange capacity [CEC], electroconductivity [EC], lime, NO_3-N, S, Zn, and B) (Table 2). Of these factors, OrgM and Org-N had the highest correlation coefficients and were collinear with CEC, EC, lime, NO_3-N, Ca, S, Zn, and B.

Sodium was negatively correlated with total yield, usable tubers and US #1s but not with large tubers (>280 g). Organic matter was positively correlated with three of the four yield components, with the exception of U.S. #1 tubers. Phosphorus was positively correlated with total yield and tubers > 280 g, but not with the other yield components. For the other soil factors, most correlations were insignificant with yield or significant with only a single yield component (Table 2).

Relationship of C. coccodes *with Wilt Severity and Tuber Components*

Wilt severity was the highest and occurred earlier in 1994 compared to 1995 and 1996. Apical stem populations of *C. coccodes* correlated significantly ($P<0.01$) with wilt severity (Table

TABLE 2—*Pooled within year correlations of biotic and abiotic factors with Verticillium wilt and tuber yield components of potato.*

Correlated factors	Pooled correlations for 3 year period[1]					
			Tuber yield			
	% wilt	Ln *V. dahliae* in soil	Total	Usable	U.S. #1	>280
% wilt			-.357**	-.412**	-.306**	-.486**
ln cfu *Colletotrichum coccodes*/g stem	+.560**[4,5]					-.497**
ln cfu *C. coccodes*/m root						
ln cfu *C. coccodes*/g soil			-.211*			
ln cfu *C. coccodes*/g tuber	+.257**			-.205*	-.223*	
ln cfu *Verticillium dahliae*/m root	+.529**	+.235*	-.514**	-.454**	-.400**	-.287**
ln cfu *V. dahliae*/g stem	+.376**		-.251**			
ln cfu *V. dahliae*/g soil			-.399**	-.311**	-.349**	-.093
ln cfu *V. dahliae*/g tuber	+.330**	+.425**	-.432**	-.363**	-.278**	-.235*
% Org-M		-.499**	+.226*	+.213*		+.362**
ppm Org-N		-.512**				+.301**
CEC[2]		-.385**				+.245*
EC[3]		-.309**				+.309**
% lime		-.299**	-.225*			
soil pH			-.207*			
ppm NO_3-N		-.219*				
ppm P			+.224*			+.229*
ppm K			+.256*			
ppm Na			-.409**	-.370**	-.366**	
ppm Ca		-.341**				+.265*
ppm S		-.268**				+.231*
ppm Zn		-.291**				+.269**
ppm B		-.297**				

[1]With exception of pathogen data in respect to wilt and yield of particular relevance, only correlation coefficients showing significant differences are presented in the table.
[2]Cation exchange capacity.
[3]Electroconductivity mmhos cm^{-1}.
[4]*indicates significance to P≤0.05, **indicates significance to P≤0.01.
[5]In 1994 wilt in upper stems was primarily correlated with *C. coccodes*.

2). This significant relationship between *C. coccodes* stem infections and wilt occurred in only one of the three years. When combined with the percent soil organic matter in a multiple regression equation, these two factors (stem colonization by *C. coccodes* and percentage of soil organic matter) accounted for 73% of the field variability related to wilt.

In 1994, apical stem populations of *C. coccodes* were negatively correlated (P<0.01) with yield of tubers >280 g, but not with total yield, usable tubers, or US #1 tubers. Although Mn alone showed no significant correlation with tuber size in 1994, both *C. coccodes* stem infections and Mn accounted for 80% of the field variability related to large tubers >280 g.

Although number of root infections by *C. coccodes* was higher in 1994 than 1995 or 1996 (Table 1) and disease was more severe, the number of root infections by *C. coccodes* were not correlated with wilt severity (Table 2). However, the number of root infections by *C. coccodes* in 1994 was highly correlated with the number of root infections by *V. dahliae*; e.g. the greater the number of root infections by *C. coccodes*, the greater the number of root infections by *V. dahliae*.

A Descriptive Model

For all four yield variables (total yield, usables, U.S. #1, and tubers >280 g), ln cfu *V. dahliae*/m feeder root showed higher negative correlations than either the ln cfu *V. dahliae*/g of soil or of tubers. Therefore, this variable was chosen as a better predictor than either soil inoculum density of *V. dahliae* or tuber colonization by this pathogen.

The severity of wilt differed from year to year (Table 1). Not only did symptoms occur earlier in 1994 compared to the other two years, disease was more severe. In 1994, wilt was recorded on basis of stems showing >75% wilt, whereas in 1995 and 1996 symptoms were less evident and data were taken if symptoms were present in the upper 15 cm of the stem. In spite of this, the percentage of stems with symptoms was still higher in 1994 than in either 1995 or 1996. To compensate for this, the year effect was included in the model. To do this, partial regression coefficients were adjusted for yearly effects. This allowed for comparisons among fields within each particular year. In this manner, the "pooled within year" estimates for generality were tested by holding other terms in the model constant. We further interpreted the model by the strength of the coefficient of determination (R^2) and by the significance of each of the partial regression coefficients.

Since both percentage of organic matter and Na were the most consistently related to tuber yield components, along with feeder-root infections by *V. dahliae*, they also were included as key variables in a descriptive mathematical model of our surveys. Common slopes were assumed for all years, e.g., only the y intercepts changed, and these changes were compensated for by partial regression coefficients. For example, for calculation of $\hat{y}$ = yield, the following calculations were used:

1994 $\hat{y} = 449.2 + 64.54\ OM - 293.93\ Na - 46.14\ LVDRT$

1995 $\hat{y} = 396.7 + 64.54\ OM - 293.93\ Na - 46.14\ LVDRT$

1996 $\hat{y} = 454.9 + 64.54\ OM - 293.93\ Na - 46.14\ LVDRT$

(where 449.2 = 454.9 – 5.7 and 396.7 = 454.9 – 58.2)

OM = % organic matter, LVDRT = ln cfu *V. dahliae*/m root

The model was as follows:

$$y_{ij} = \mu + a_i + B_1 X_{1\,ij} + B_2 X_{2\,ij} + B_3 X_{3\,ij} + e_{ij}$$

where y_{ij} = observation of j^{th} farm in the i^{th} year.

μ = overall mean

a_i = effect of i^{th} year

B_1 = partial regression coefficient of y on OM

B_2 = partial regression coefficient of y on Na

B_3 = partial regression coefficient of y on ln *V. dahliae* root colony density

e_{ij} = random error

This combination of three factors (organic matter, Na, and ln cfu *V. dahliae*/m root) provided the highest R^2 values. When other soil factors were included, the R^2 values were lower and not as consistent.

When tested in each of the three years, R^2 values for each of the yield components remained similar using the above three factors. For 1994, 1995, and 1996, respectively, these factors accounted for 49%, 53%, and 62% of the field variability related to total yield, 44%, 43%, and 50% for yield of usable tubers, and 44%, 43%, and 33% for yield of U.S. #1s. For U.S. #1 tubers >280 g, they accounted for 26%, 25%, and 35% of the field variability.

Analyses of Variance showed these three key factors related to yield and quality to be highly significant (Table 3). With the exception of the relationship of Na to U.S. #1 tubers >280 g in size, all four factors (year, organic matter, Na, and ln cfu *V. dahliae*/m root) were correlated with the four yield components. Using these data, the impact of number of root infections by *V. dahliae* and soil organic matter on wilt severity can be estimated (Table 4). The effect of these two variables on tuber yield is quite large (Tables 5 and 6). When the percentage of soil organic matter was maintained as a constant of 1.7% (the approximate mean organic level of fields surveyed), and the number of *V. dahliae* infections/m root were altered to a range from 1 to 36/m root, yield decreased with an increase in *V. dahliae* root infections. Similarly, when multiple-regression calculations considered the

TABLE 3—*Analysis of variance for factors related to tuber yield of potato.*

		Total		Usable		U.S. #1		Total >280 g		U.S. #1 >280 g	
Source	df	M.S.	P>F	M.S.	P>F	M.S.	P>F	M.S.	P>F	M.S.	P>F
Year	2	29,343	0.0001	31,916	0.0001	14,584	0.0181	19,609	0.0001	18,724	0.0001
Organic matter	1	51,039	0.0001	43,154	0.0003	22,249	0.0131	31,680	0.0001	24,913	0.0001
Na	1	79,068	0.0001	64,179	0.0001	57,253	0.0001	6,441	0.0512	3,328	0.1264
ln cfu *Verticillium dahliae*/m root	1	90,017	0.0001	66,970	0.0001	49,935	0.0003	12,333	0.0075	13,630	0.0024
Error	94	2,724		3,093		3,482		1,652		1,399	
Total	99										
R^2		0.496		0.406		0.304		0.382		0.361	
Mean		387.3		267.5		216.6		79.2		67.4	
Standard Deviation		52.2		55.6		59.0		40.6		37.4	

TABLE 4—*Calculated severity of Verticillium wilt based on* Verticillium dahliae *root infections and soil organic matter.*[1]

cfu *V. dahliae*/m root	Soil organic matter (%)	Wilt severity (%)		
		1994	1995	1996
1	1.7	20.7	7.6	8.6
6	1.7	22.1	22.1	19.5
12	1.7	22.9	30.4	25.7
24	1.7	23.8	39.6	32.6
36	1.7	24.4	45.3	36.8
12	0.8	63.4	39.3	41.8
12	1.3	40.9	34.4	32.9
12	1.7	22.9	30.4	25.7
12	2.0	9.4	27.5	20.4
12	2.3	0.0	24.5	15.0

[1] Multiple regressions for wilt predictions by year.
1994 y = 95.6 + 1.443 ln cfu *V. dahliae*/m root - 45.001 % organic matter
$R^2 = 0.491$ $s^2 yx = 579.3$
1995 y = 8.1 + 14.844 ln cfu *V. dahliae*/m root** - 9.871 % organic matter
$R^2 = 0.173$ $s^2 yx = 336.1$
1996 y = 26.8 + 11.108 ln cfu *V. dahliae*/m root** - 17.894 % organic matter**
$R^2 = 0.562$ $s^2 yx = 57.9$

number of infections/m root, the decrease in yield that resulted from an increase in number of root infections was diminished with increased soil organic matter.

Similarly, yields of tubers >280 g also showed large responses to root infections by *V. dahliae* and percentage of soil organic matter (Table 6). With the higher number of root infections, wilt was more severe in 1995 and 1996, whereas in 1994, when *C. coccodes* was more closely related to wilt incidence, the effect of number of root infections by *V. dahliae* was barely evident. As with total yield, yield of tubers >280 g was reduced with increased root infections by *V. dahliae* when percent organic matter was held constant. In contrast, yield of tubers >280 g was increased when root infections by *V. dahliae* were maintained constant and percentage of organic matter was increased.

DISCUSSION

When we did the early survey of grower fields during 1975-1978 (Davis and Everson 1986), we lacked a good technique for quantifying *V. dahliae* infection in potato roots. Since then, quantification of feeder root infection by *V. dahliae* is done routinely

TABLE 5—*Calculated tuber yield loss estimates of potato based on number of* Verticillium dahliae *root infections and percent soil organic matter.*

cfu *V. dahliae*/m root	% soil organic matter	Tuber yield (T ha⁻¹)[1]								
		1994			1995			1996		
		Mean	% decrease	Range	Mean	% decrease	Range	Mean	% decrease	Range
1	1.7	50	—	46-53	50	—	46-53	48	—	43-53
6	1.7	45	10.0	43-47	41	18.0	38-43	42	12.5	38-46
12	1.7	43	14.0	40-44	36	28.0	32-39	39	18.8	33-45
24	1.7	40	20.0	36-42	30	40.0	25-35	35	27.1	26-45
36	1.7	38	24.0	34-41	26	48.0	20-33	33	31.3	21-44
12	0.8	43	—	37-45	29	28.0	23-35	21	58.9	7-35
12	1.3	43	—	39-44	33	17.5	29-36	31	39.2	22-40
12	1.7	43	—	40-44	36	10.0	32-39	39	23.5	33-45
12	2.0	43	—	40-45	38	1.8	33-42	45	11.8	38-52
12	2.3	43	—	39-47	40	—	34-45	51	—	41-60

[1] Multiple regressions for yield predictions by year.
1994
y = total yield = 466 – 41.65 ln cfu *Verticillium dahliae*/m root + 12.25 organic matter.
$R^2 = 0.360$ $s^2 y \bullet x = 2{,}508$
1995
y = 425.3 – 81.14 ln cfu *V. dahliae*/m root + 62.29 organic matter.
$R^2 = 0.453$ $s^2 y \bullet x = 2{,}602$
1996
y = 192.5 – 53.87 ln cfu *V. dahliae*/m root + 175.02 organic matter.
$R^2 = 0.412$ $s^2 y \bullet x = 5{,}047$

TABLE 6—*Calculated estimates of tuber yield loss estimates of potato based on* Verticillium dahliae *root infections and soil organic matter.*[1]

cfu *V. dahliae*/m root	Soil organic matter (%)	1994		1995		1996	
		T ha^{-1} tubers >280g	% decrease	T ha^{-1} tubers >280g	% decrease	T ha^{-1} tubers >280g	% decrease
1	1.7	12.3	—	9.2	—	12.3	—
6	1.7	10.4	15	6.2	33	11.0	11
12	1.7	9.4	24	4.4	52	10.2	17
24	1.7	8.2	33	2.5	73	9.4	24
36	1.7	7.4	40	1.3	86	8.9	28
12	0.8	5.7	51	1.2	81	0	100
12	1.3	7.7	34	3.0	54	4.7	74
12	1.7	9.4	21	4.4	32	10.2	59
12	2.0	10.5	10	5.5	16	14.3	22
12	2.3	11.8	—	6.5	—	18.4	—

[1] Total T ha^{-1} of tubers >280 g
1994 y = 68.0 - 17.292 ln cfu *V. dahliae*/m root + 36.05 % organic matter *
R^2 = 0.251 $s^2 y \bullet x$ = 1,899
1995 y = 59.12 - 27.618 ln cfu *V. dahliae*/m root** + 31.21 % organic matter
R^2 = 0.202 $s^2 y \bullet x$ = 1,112
1996 y = -84.83 - 12.043 ln cfu *V. et*/m root + 122.12 % organic matter **
R^2 = 0.348 $s^2 y \bullet x$ = 2,269
* = $P \leq 0.05$, ** = $P \leq 0.01$

by several laboratories. This added step between soil and apical stem assays is a link for improving our understanding of the relationship between Verticillium wilt and tuber yield.

With the high number of *C. coccodes* root infections that occurred in 1994, *V. dahliae* root infections were also higher. Greenhouse studies have shown that symptoms were more severe and reduction in tuber yield was greater when both *C. coccodes* and *V. dahliae* were present. This study also demonstrates the close association between stem infections by *C. coccodes* and reduced tuber size. Although this relationship to tuber size has been demonstrated in field experiments (Barkdoll and Davis 1992), this is the first quantitative field survey showing a similar relationship. Although these relationships with *C. coccodes* were observed in only one out of three years, this is not surprising, since *C. coccodes* requires specific environmental conditions that are not required by *V. dahliae* for wilt development (Davis and Johnson, 2001). Wilt from *V. dahliae* results from infection of feeder roots, whereas wilt development from *C. coccodes* results from aboveground stem and foliage infections. The latter is favored by the movement of soil particles with high winds, warm temperatures (>30 C), and moisture, either from rains or sprinkler irrigation. Root infections by *V. dahliae* were correlated with wilt severity over the three-year period, whereas *C. coccodes* root infections were not (Table 2).

"Pooled within year" analyses, adjusting for the average value of each year, showed root infections by *V. dahliae* to correlate positively with wilt severity, whereas soil populations of V. *dahliae* did not (Table 2). This finding is consistent with earlier observations (Davis and Everson 1986). Based on our studies with green manures (Davis *et al.* 1996), we had postulated that root colonization levels, in contrast to soil populations, should correlate positively with wilt. As documented by this study, this was observed to be the case for commercial fields as well. This suggests that similar relationships are occurring in grower fields where green manure treatments were not applied. In our surveys, feeder root infections by *V. dahliae* accounted for only 24% of the field variability observed with wilt severity. This also is consistent with the earlier finding that cultural practices and nutrient levels showed a highly significant correlation with wilt severity. A number of soil physical and chemical components exhibited highly significant negative correlations with wilt severity (Table 2). This is consistent with the interpretation that the plant nutrient status, in turn influenced by the soil nutrient status, is a significant modulator of pathogen activity in the host and of wilt severity. Soil organic matter also was correlated negatively with wilt incidence and positively with yield. The earlier study (Davis and Everson 1986) failed to take soil organic matter into account. This study is the first to report on the role of soil organic content in the epidemiology of Verticillium wilt.

Potato yields also showed significant negative correlations with *V. dahliae* populations in the roots, tubers, soil, and stems. Correlations with root populations were the highest, followed by tuber, soil, and stem populations (Table 2). Feeder root infections explained 51% of the observed field variability in total yield, whereas soil populations explained only 40% of this variability. Again, these results indicate that a measure of the pathogen in the root system is a much better predictor of subsequent economic damage than are soil populations.

In addition to *V. dahliae*, other soil factors exhibited significant correlations, both negative and positive, with tuber yields (Table 2). Positive correlations with soil nutrient levels are not surprising given the role of nutrients in plant growth. However, three key factors (feeder root infections by *V. dahliae*, Na, and soil organic matter) explained a major portion (Table 3) of the observed field variability related to tuber yield. With economic subcomponents of yield, analogous values were lower but still highly significant. Other factors exhibited a high degree of covariance with the main factors.

The negative relationships of soil Na on tuber yield are consistent with reported negative effects of Na on plant growth (Richards 1954). Na in the soil may exert important secondary effects on plant growth by adversely modifying soil structure (McGeorge and Breazeale 1938).

The importance of soil organic matter on disease suppression has been previously described for the biological control of *Pythium*, *Phytophthora*, and *Rhizoctonia solani* in greenhouse potting soils (Hoitink and Boehm 1999). Hoitink and Boehm used composts to provide a food base for biocontrol agents in potting soils, which led to sustained biological control based on activities of microbial communities. Organic amendments (green manures, stable manures, and composts) have long been recognized to facilitate biological control if applied well ahead of planting (Baker and Cook 1974; Hodges and Scofield 1983; Lumsden *et al.* 1983).

Prior to 1950, farmers commonly used green manures in their fields, but with the increased use of synthetic inorganic fertilizers and fungicides it became possible to break the link between organic amendments, soil fertility, and disease control. Hoitink and Boehm (1999) suggest that with the introduction of modern agriculture, the soil structure has declined, and with this degradation, numerous diseases caused by soilborne plant pathogens eventually developed to epidemic proportions.

The content of soil organic matter is possibly the single best indicator of soil quality (Papendick and Elliott 1983). With a reduction in amount of organic matter, soil tilth and crop productivity are compromised. Similar relationships also have been shown with green manure studies (Davis *et al.* 1994, 1996, 1999). When field plots were maintained weed-free and fallow, soil organic matter was reduced, and with this reduction, Verticillium wilt was more severe. In contrast, among green manure treated plots, organic matter was higher and Verticillium wilt was less severe. Regardless of green manure treatment, *V. dahliae* soil populations were similar to those in the fallow. In this regard, the study described in this paper suggests that organic matter may be a factor that can be manipulated for suppression of Verticillium wilt without reducing soil populations of the pathogen.

LITERATURE CITED

Anonymous. 1971. United States Standards for Grades of Potatoes (35 F.R. 18257). Consumer and Marketing Service, Washington, DC.

Baker, K.F., and R.J. Cook. 1974. Biological control of plant pathogens. *In:* Kelman, A., and L. Sequiera (eds), The Biology of Plant Pathogens. Freeman, San Francisco. pp. 67-70.

Barkdoll, A.W., and J.R. Davis. 1992. Distribution of *Colletotrichum coccodes* in Idaho and variations in pathogenicity on potato. Plant Dis 76:131-135.

Butterfield, E.J., and J.E. DeVay. 1977. Reassessment of soil assays for *Verticillium dahliae*. Phytopathology 67:1073-1078.

Davis, J.R., and D.O. Everson. 1986. Relation of *Verticillium dahliae* in soil and potato tissue, irrigation method, and N-fertility to Verticillium wilt of potato. Phytopathology 76:730-736.

Davis, J.R., S.L. Hafez, and L.H. Sorensen. 1992. Lesion nematode suppression with the Butte potato and relationships to Verticillium wilt. Am Potato J 69:371-383.

Davis, J.R., O.C. Huisman, D.O. Everson, L.H. Sorensen, and A.T. Schneider. 1999. Control of Verticillium wilt of the Russet Burbank potato with corn and barley. Am J Potato Res 76:367.

Davis, J.R., O.C. Huisman, D.T. Westermann, S.L. Hafez, D.O. Everson, L.H. Sorensen, and A.T. Schneider. 1996. Effects of green manures on Verticillium wilt of potato. Phytopathology 86:444-453.

Davis, J.R., O.C. Huisman, D.T. Westermann, L.H. Sorensen, A.T. Schneider, and J.C. Stark. 1994. The influence of cover crops on the suppression of Verticillium wilt of potato. *In:* Zehnder, G.W., M.L. Powelson, R.K. Jannson, and K.V. Ramay (eds), Advances in Potato Pest Biology and Management. APS Press, St. Paul, MN. pp. 332-341.

Davis, J.R., and D.A. Johnson. 2001. Black dot. *In:* Stevenson, W.R., R. Loria, G.D. Franc, and D.P. Weingartner (eds), Compendium of Potato Diseases. APS Press, St. Paul, MN. (in press).

Davis, J.R., J.J. Pavek, and D.L. Corsini. 1983. A sensitive method for quantifying *Verticillium dahliae* colonization in plant tissue and evaluating resistance among potato genotypes. Phytopathology 73:1009-1014.

Davis, J.R., J.C. Stark, L.H. Sorensen, and A.T. Schneider. 1994. Interactive effects of nitrogen and phosphorus and Verticillium wilt of Russet Burbank potato. Am Potato J 71:467-481.

Hodges, R.O., and A.M. Scofield. 1983. Effect of agricultural practices on the health of plants and animal produce: A review. *In:* Lockeretz, W. (ed), Environmentally Sound Agriculture. Praeger, New York. pp. 3-34.

Hoitink, H.A.J., and M.J. Boehm. 1999. Biocontrol within the context of soil microbial communities: A substrate-dependent phenomenon. Ann Rev Phytopathol 37:427-446.

Huisman, O.C. 1988. Colonization of field-grown cotton roots by pathogenic and saprophytic soilborne fungi. Phytopathology 78:716-722.

Lumsden, R.D., J.A. Lewis, and P.D. Millner. 1983. Effect of composted sewage sludge on several soilborne plant pathogens and diseases. Phytopathology 73:1543-1548.

McGeorge, W.T., and J.F. Breazeale. 1938. Studies on soil structure: Effect of puddled soils on plant growth. Arizona Ag Expt Sta Tech Bul 72:413-447.

Mohan, S.K., J.R. Davis, L.H. Sorensen, and A.T. Schneider. 1992. Infection of aerial parts of potato plants by *Colletotrichum coccodes* and its effects on premature death and yield. Am Potato J 69:547-559.

Myers, R.H. 1986. Classical and Modern Regression with Applications. Duxbury Press, Boston.

Nnodu, E.C., and M.D. Harrison. 1979. The relationship between *Verticillium albo-atrum*, inoculum density, and potato yield. Am Potato J 56:11-25.

Papendick, R.I., and L.F. Elliott. 1983. Soil physical factors that affect plant health. *In:* Kommedahl, T. and P.H. Williams (eds), Challenging Problems in Plant Health. APS Press, St. Paul, MN. pp. 173-174.

Richards, L.A. (ed). 1954. Diagnosis and improvement of saline and alkali soils. Agriculture Handbook No. 60. U.S. Department of Agriculture. 159 pp.

Rowe, R.C., J.R. Davis, M.L. Powelson, and D.I. Rouse. 1987. Potato early dying: Causal agents and management strategies. Plant Dis 71:482-489.

Sorensen, L.H., A.T. Schneider, and J.R. Davis. 1991. Influence of sodium-polygalacturonate sources and improved recovery of *Verticillium* spp from soil (Abstr.). Phytopathology 81:1345.

Steel, R.G.O., and J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, Inc., San Francisco.