Relation of *Verticillium dahliae* in Soil and Potato Tissue, Irrigation Method, and N-Fertility to Verticillium Wilt of Potato

J. R. Davis and D. O. Everson

Professor, Department of Plant, Soil and Entomological Sciences, University of Idaho Research and Extension Center, Aberdeen, 83210, and professor, Department of Mathematics and Applied Statistics, University of Idaho, Moscow 83843, respectively.
We thank F. H. Nissley, M. N. Howard, and W. B. Jones for technical assistance; Ore-Ida Foods, American Potato, and Simplot Soilbuilders for assisting with plot locations and data collection; W. C. Schnathorst (University of California, Davis) and J. E. Puhalla (University of California, Berkeley) for verification and identification of strains of *Verticillium dahliae*; G. S. Santo for assay of soil for nematode populations; Analytical Services, Department of Plant and Soil Sciences, University of Idaho, Moscow, for nutrient evaluations; and W. C. Schnathorst and J. E. DeVay for valuable counsel throughout this investigation. This study was funded in part by the Idaho Potato Commission.
Accepted for publication 5 February 1986.

ABSTRACT

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.

Investigations of several potato-growing areas in Idaho showed inconsistent relationships between populations of *Verticillium dahliae* in soil and wilt severity. This lack of consistency was associated with cultural management practices. Increases in severity of Verticillium wilt were more highly correlated with furrow irrigation than with sprinkler irrigation. Irrigation method and N, K, and P applications accounted for as much as 71% of the field variability related to colonization of *V. dahliae* in potato stem tissue. Increased availability of nitrogen suppressed the incidence of Verticillium wilt on the cultivar Russet Burbank but had no effect on severity with the cultivar Norgold Russet. Wilt severity was also correlated positively with populations of soilborne *Pratylenchus* spp. Studies over several years provided no evidence to suggest direct associations for either increased wilt or reduced yield as a result of infection by *Colletotrichum atramentarium*.

Additional key words: disease suppression, epidemiology, plant nutrition, *Solanum tuberosum*.

In Idaho and other arid regions of the western United States, Verticillium wilt of potato (*Solanum tuberosum* L.) is caused by *Verticillium dahliae* Kleb. (5,6,8). The strain of *V. dahliae* that has been consistently associated with Idaho potatoes is similar in type to the nondefoliating strain (SS4) found on cotton (5) and has been further characterized (5,8,27) to be in the vegetative compatibility group P-4. Depending on disease severity, time of occurrence, and growing season, potato yields and tuber size may be substantially reduced by this pathogen. Yield losses of 5.6–11.2 t/ha are not uncommon, and losses as great as 46% have been documented in southeastern Idaho (5,8).

Many fumigants have been highly effective in controlling the Verticillium wilt disease of potato. However, all are relatively high in cost, and the question of need and justification for fumigation frequently occurs. The ability to predict potential problems with *Verticillium* spp. in soil would be of great economic value.

Using a procedure described by Butterfield and DeVay (3), a direct relationship was found between inoculum in the soil and wilt severity or stem colonization by *V. dahliae* on the cultivar Russet Burbank (11). Using a similar method to measure populations of *V. dahliae* in air-dried soil, Nnodu and Harrison (24) related the amount of soilborne inoculum to potato yield. They suggested that assays of *V. dahliae* in soil could provide a means for selecting fields that are either safe for planting potatoes or that may benefit by control procedures. Ashworth et al (2) established a direct relationship between *V. dahliae* in soil and infection (vascular discoloration) of cotton plants. In contrast, a survey study by DeVay et al (13) indicated no correlation between inoculum levels of *V. dahliae* in air-dried soils from 26 fields and the incidence of foliar symptoms of Verticillium wilt in cotton. They suggested that many other factors such as cropping history, nitrogen, soil moisture, air temperature, aeration of soil, plant populations, and changes of microbial population are partially responsible. In addition, the presence of suppressive soils (29) or other organisms such as *Pratylenchus penetrans* (Cobb) Filipjev & Schuurmans-Stekh. and *Colletotrichum atramentarium* (Berk. & Br.) Taubenh. might interact with *V. dahliae* (16,19,20,25,28,31).

In general, inoculum densities of *V. dahliae* of 10–20 colony-forming units (cfu) per gram of soil appear to cause economic loss in potato. Soil solarization studies indicated that *V. dahliae* at 10 cfu/g of air-dried soil produce a measurable incidence of Verticillium wilt and significantly reduce potato yields of cultivar Russet Burbank by more than 9.3 t/ha (8). Nnodu and Harrison (24) estimated the threshold for economic damage to lie between 18 and 23 cfu/g of air-dried soil. Powelson (26) demonstrated that 10–200 cfu/g of soil would cause severe Verticillium wilt of potato. Martinson and Horner (21) assayed soil from a potato field with a history of severe Verticillium wilt and found only 10–40 viable cfu of *V. dahliae* per gram of soil. Easton (14) found populations of 40–102 cfu/g of soil from Washington potato fields.

The purpose of this study was to evaluate the potential use of assays of populations of *V. dahliae* in field soils for the prediction of Verticillium wilt incidence. The relationships of cultural management factors, *C. atramentarium*, and *Pratylenchus* spp. to the incidence of wilt were also considered. Portions of this work have been reported previously (7,10).

MATERIALS AND METHODS

Field selection, survey, and quantitative soil assays. Soil samples were collected from 159 potato fields in southern Idaho and eastern Oregon during 1975–1978. Depending on the region and year, these collections were made from fields that had been planted with Russet Burbank on similar dates. In 1975 and 1976, soil samples were collected from each area before emergence. In 1977 and 1978, soil samples were collected within 1 wk of emergence. Planting dates ranged from 15 April to 25 May. For each time and area,

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.

potatoes in fields being compared were at similar stages of growth. In a given area and year, soil collection was within 24 hr for the locations being compared. In the four areas investigated (Bingham County, Magic Valley, Treasure Valley, and Egin Bench), the similarity of growth stage at the time of collection in each field was verified by evaluating the mean tuber sprout length in each field before emergence (1975 and 1976) or plant height after emergence (1977 and 1978). In accordance with dates of collection, sprout-length differences between fields were considered negligible (±2.5 cm from means).

In each field, a single row length of 30.5 m was staked out and mapped for future study; the distance between rows was about 0.9 m. All evaluations for disease incidence and collections of soil and plant material were taken from these defined areas. Twelve random samples from the upper 23 cm of soil profile were taken with a 1.8-cm-diameter sampling tube from each 30.5 m row location and bulked for each plot site. Soil samples were mixed thoroughly and slowly air-dried for 4–5 wk at laboratory room temperature (about 20–25 C). Populations (cfu) of *V. dahliae* in each plot were determined in accordance with the method described by Butterfield and DeVay (3).

Inoculum densities of *V. dahliae* for each plot represented mean values obtained from counts on five plates with 50 or 100 mg of air-dried soil per plate (depending on the year of collection). Populations of *C. atramentarium* in soil were quantified with a method described by Farley (15). This procedure involved mixing 200-g samples of air-dried soil with H_2O in a Waring Blendor, wet sieving, and diluting the resulting suspension containing *C. atramentarium* onto plates of a selective medium.

Wilt incidence determinations. The wilt index for each year was determined in all fields either by indexing the symptoms of Verticillium wilt on a scale of 1–12 as described by Horsfall and Barratt (18) or by evaluating the percentage of stems with wilt symptoms. As previously reported (11), the percentage of stems with typical Verticillium wilt symptoms was determined by evaluating 50 randomly selected stems per 30.5-m row. Wilt data were taken when symptoms in an area became clearly evident, with evaluation dates ranging from 20 August to 7 September. In a given area and year, the locations being compared were evaluated within 24 hr of each other. The degree of vascular discoloration was also determined by collecting about 30 stems per plot 2.5 cm above the soil line. At the laboratory, fresh cuts were made on stems at about 1.3 cm above the soil line and macroscopic evaluations were made.

Fungal assays from potato stem tissue. Colonization of *V. dahliae* in potato stem tissue was quantified as described previously (11) by plating air-dried potato stem tissue that passed a 40-mesh screen on a Wiley mill on a selective nutrient pectate medium (NPX). This procedure also made it possible to simultaneously identify and quantify the colonization of stems by *V. nigrescens* Pethybr. and *C. atramentarium*.

Fungal identification. Isolates of *V. dahliae* were routinely selected from NPX plates and transferred to potato-dextrose agar (PDA) for further characterization. Representative isolates (>100) from soil and stem tissue were submitted for identification of pathotypes of *V. dahliae* and several type cultures from this collection were submitted for characterization of vegetative compatibility groups among Idaho isolates. Isolates of *V. nigrescens* were subcultured from NPX to PDA for further evaluation of fungal morphology.

Type cultures were randomly selected from NPX plates and subcultured onto both PDA and a selective medium to compare culture morphologies of *C. atramentarium* (15). Samples of stroma from these isolates (>30) were selected randomly from NPX plates, embedded in paraffin, and sectioned at 10 μm for microscopic examination.

Pathogenicity determinations for isolates of *V. dahliae*. Thirty cultures of *V. dahliae* were selected randomly from isolates collected from soil throughout the potato-growing areas of Idaho and tested for pathogenicity. Russet Burbank seed potatoes, shown by isolations from tuber stem-ends to be free of *V. dahliae*, were obtained from the University of Idaho Tetonia Experiment Station (UITES). Before planting, the seed pieces were disinfested for 2 min in 0.5% NaOCL, rinsed in tap water, and planted in a U.C. mix potting soil. Seed pieces were sprouted in flats. Sprouts (about 10–15 cm high) were removed, rinsed, and held under wet paper towels for a maximum of 3 hr, until inoculation. During the process of sprout removal from mother tubers, care was taken to avoid root injury. Inoculations of each isolate of *V. dahliae* were made by dipping roots into inoculum suspensions of 10^6–10^7 viable conidia per milliliter, and roots were immediately planted in 15×17 cm pots. Control roots were dipped in water. Treated plants were arranged on a greenhouse bench in a randomized block design with four replicates (one plant per replicate). Plants were left for several weeks under greenhouse conditions where the normal photoperiod was about 11–13 hr of daylight and mean temperature conditions ranged from 15 to 25 C.

Nutrient analyses of plant tissue and soil. Petioles were collected for nutritional analyses from each year between 3 and 12 July. In 1978, petioles were also collected on 10 August. The petiole from the last fully matured leaf was selected from 30 or more plants per plot. Samples were oven-dried below 65 C and ground through a 250-μm-mesh screen in a Wiley mill. A minimum of eight subsamples of soil per plot were collected and, before analyses, were oven-dried and ground. Nutrient evaluations were made using standard colorimetric, atomic absorption, and flame photometry procedures.

Nematode assay. Soils were assayed for nematode populations by using standard procedures (4).

Harvesting and grading. Potatoes from plots of the Egin Bench area were harvested on 14 and 15 September 1978 by hand digging 9.2 m of row within the 30.5-m row that was used for field evaluations and assays. Potato tubers from these plots were washed and graded according to standard procedures (1).

Effect of nitrogen and soil fumigation treatments on Verticillium wilt. The effect of nitrogen on wilt incidence was investigated in a Declo silt loam soil. The year preceding this study, the soil had been planted with barley. For more than 30 yr the location of this investigation was cropped with barley, wheat, and potato and had a history of Verticillium wilt caused by *V. dahliae*. The last potato crop planted in this field area (2 yr earlier) had severe Verticillium wilt. For this reason and because residual nitrogen levels within the upper 30 cm of the soil profile were low (8.9 ppm), this field was selected to investigate the effect of nitrogen on Verticillium wilt of potato.

The plot design was a randomized block factorial with six replicates; variables consisted of 10 treatments involving fumigation vs. nonfumigation with five nitrogen treatments. Plot dimensions were 15.3 × 3.7 m with row spacings at 0.9 m.

On 17 April a mixture of 17% chloropicrin (Telone C, Dow Chemical Co., Midland, MI) was applied at 296 L/ha (±5%) to treated plots at a soil depth approximating 20 cm. Treatments were applied with a Gravity-Flo fumigator consisting of six shanks spaced 30 cm apart. At the time of fumigation, soil temperatures were 8–10 C at a depth of 15–25 cm. Immediately after application, the soil was sealed with a cultipacker.

On May 2, to eliminate residual fumigant before planting, the field was cultivated. On the same date, EPTC was applied for weed control at 3.4 kg/ha and disked to a depth approximating 13 cm.

Before planting and treating with fertilizers, core samples of 76 cm^3 were collected randomly from the upper 30 cm of the soil profile. Assays were made for NO_3-N, P, K, Mn, Mg, Ca, organic matter, and pH.

Seed potatoes of cultivars Russet Burbank and Norgold Russet were obtained from the UITES. Seed potatoes were cut to 57 ± 3 g and treated with 5% captan dust, applied at the recommended rate of 0.45 kg/45 kg of seed pieces.

Plots were planted 16 days after fumigating on 3 May. Within each plot, two rows, 1.8 × 15.3 m, were each planted with Norgold Russet and Russet Burbank. For insect control, disulfoton (Disyston) (3.4 kg/ha) was applied at planting by an endless belt applicator.

On 13 May fertilizer treatments of NH_4NO_3 were side-dressed with an endless belt applicator about 10 cm from each side of the potato seed pieces. Nitrogen was applied at five rates (0, 84, 168, 252, and 336 kg/ha). Broadcast applications of 146 kg of P_2O_5/ha were similarly side-dressed to all plots. Throughout the growing season, plots were irrigated by furrow irrigation.

On 3 July, petioles were collected from plots as described previously for nutritional evaluation. On 24 July and 5 August, 50 petioles (the top petiole on each plant) were collected from each Norgold Russet and Russet Burbank plot that had been fertilized at one of three N rates (0, 168, and 336 kg/ha) to determine the incidence of infection by *V. dahliae*. These collections were made before the onset of symptom development. Each petiole was dipped into 0.5% NaOCl, and isolations were made onto PDA. The percentage of wilt incidence in each plot was determined on 19 August by evaluating general symptoms.

On 5 August, petioles were collected from plots for nutritional analyses and at season's end, soil samples were collected from several profiles to evaluate possible differences of N leaching.

On 24 and 25 September, a total of 12.2 m of row was harvested from each plot.

Depending on the year and comparisons that were made, several analyses of variance were used. In 1975, simple random samples within each of three potato-growing areas (Treasure Valley, Bingham County, and Magic Valley) were taken, and simple linear regressions and correlations were calculated. Within each area, the stage of potato growth and time of collection were similar. These effects in all areas were also combined by using a stratified random sampling procedure. This combined sample consisted of 29 farms in Treasure Valley, 22 farms in Bingham County, and 18 farms in Magic Valley. A least-squares covariance analysis was used to describe the three dependent variables (cfu of *V. dahliae* per gram of soil, percentage of foliar wilt, and percentage of stems with vascular discoloration). The following models were fit:

$$y_{ijk} = \mu + G_i + A_j + \beta\,(X_{ijk} - \bar{X}\ldots) + e_{ijk}.$$

Factors described for analysis were: y_{ijk} = response of k^{th} farm in the j^{th} area and i^{th} irrigation method, μ = overall mean, G_i = effect of the i^{th} irrigation method (furrow or sprinkler), A_j = effect of the j^{th} area (Treasure Valley, Bingham County, or Magic Valley), and β = the partial regression coefficient of the response variable on *V. dahliae* in soil. Preliminary analyses of these data indicated neither a significant interaction of irrigation method × area nor a significant partial regression of the response variables on *Colletotrichum* spp. in stem tissues. Therefore, these terms were not included in the final analyses. The homogeneity of correlation coefficients among areas was tested using a chi-square test (30).

In 1976, a simple random sample of 32 Bingham County farms was taken, of which 28 had complete data. Stepwise multiple-regression equations were fit for the three dependent variables (cfu of *V. dahliae* in stem tissue, wilt incidence, and vascular discoloration), using the following independent variables as candidates: soil electrical conductivity at season's end, NO_3-N (ppm) in petioles (12 July), percentage of potassium in petioles (12 July), percentage of phosphorus in petioles (12 July), manganese (ppm) in petioles (12 July), NO_3-N (ppm) in upper 23 cm of soil profile at season's end, percent total nitrogen at season's end, and NH_4-N (ppm) in upper 23 cm of soil profile at season's end.

A simple random sample of 21 Bingham County farms was taken in 1977, and simple linear regressions and correlations were calculated. Additionally, in 1978, a simple random sample of 37 farms in the Egin Bench area was taken, and correlations were computed.

Analyses of variance among replicated plots involving the effect of N and soil fumigation treatments on yield and wilt incidence were determined in accordance with the experimental design that is described. Because petioles were collected from plots involving only three nitrogen treatments (0, 168, and 336 kg/ha), analyses were modified to accommodate this change. Analyses were made in accordance with a randomized complete block design with six replicates and a 2 × 3 factorial arrangement that involved two levels of fumigation and three levels of N.

TABLE 1. Linear correlations between inoculum density of *Verticillium dahliae* in field soil and symptoms of Verticillium wilt in three potato-growing areas of Idaho

Wilt incidence and severity	Primary irrigation	*V. dahliae* (cfu/g of air-dried soil)	Site comparisons (no.)	*r* Values
Western Idaho				
(Treasure Valley)	Furrow	0–50		
Wilt severity[a]			21	0.50*[c]
Wilt incidence[b]			29	0.72***
Central Idaho				
(Magic Valley)	Sprinkler	0–92		
Wilt severity			18	0.64**
Wilt incidence			18	0.62**
Eastern Idaho				
(Bingham Co.)	Furrow and sprinkler	0–106		
Wilt severity			22	0.16
Wilt incidence			22	0.24

[a] Based upon a wilt index score of 1–12 with higher values indicating greater disease severity.

[b] Percentage of stems with vascular discoloration.

[c] Correlation coefficients followed by *, **, or *** were significant at $P = 0.05$, $P = 0.01$, or $P = 0.001$, respectively.

RESULTS

Fields initially sampled during 1975 in the eastern, central, and western areas of southern Idaho, represented three distinct growing areas (Bingham County, Magic Valley, and Treasure Valley). Among fields from the west (Treasure Valley) and central regions (Magic Valley), inoculum densities in soil were correlated with wilt incidence but not from the east (Bingham County), a region with the highest inoculum densities (up to 106 cfu/g of soil) (Table 1). Within the eastern region, there were some fields with high inoculum densities (>46 cfu/g of soil) that did not develop wilt symptoms.

Isolates of *V. dahliae* collected from soil and stems were consistently identified as a strain related to the SS4 cotton strain and were later designated as the Rb5 strain (W. C. Schnathorst, *personal communication*). Subsequently this strain type was characterized by Puhalla and Hummel (27) to be in the vegetative compatibility group P-4.

When isolates of *V. dahliae* were selected randomly from soils throughout the potato-growing regions of Idaho, all were pathogenic on potato and produced severe wilt symptoms on cultivar Russet Burbank. There was no evidence of avirulent isolates of *V. dahliae* in soil samples.

In eastern Idaho, where the inoculum density in soil failed to correlate with either wilt severity or vascular discoloration, irrigation among fields was approximately equally divided between furrow and sprinkler. When the wilt index means for irrigation methods were averaged over three major growing regions, a highly significant trend existed ($P = 0.01$) for differences between fields irrigated by sprinkler and furrow. The least-square means of wilt indices for furrow-irrigated fields (4.16 ± 0.47) were higher than those for sprinkler-irrigated fields (1.96 ± 0.47).

Data from all three regions were analyzed by multiple-regression analyses. When the homogeneity of correlation coefficients among areas was tested using a chi-square test, no significant differences among areas were found between either wilt index and *V. dahliae* in soil or vascular discoloration and *V. dahliae* in soil. However, the correlation between colonization of *V. dahliae* in stem tissue and *V. dahliae* in soil was significantly higher ($P = 0.05$) in Magic Valley than in Bingham County or Treasure Valley. When the variables associated with wilt symptoms were considered as functions of the level of cfu of *V. dahliae* in soil with an analyses of covariance, there was little relationship. The greatest effect per cfu of *V. dahliae* in soil was on vascular discoloration of potato stems ($P = 0.01$). The mean effect of a cfu of *V. dahliae* per gram of soil on the percentage of stems with vascular discoloration was calculated to be 0.607 ± 0.161.

A separate 2-yr study (1976 and 1977) in eastern Idaho (Bingham County) also demonstrated a consistent lack of correlation between inoculum of *V. dahliae* in the soil and wilt severity (Table 2). Even with high inoculum densities (>70 cfu/g of soil), some fields had a negligible severity of wilt. In contrast, the relationship between cfu of *V. dahliae* in stem apices and wilt severity was significant ($P = 0.01$ to 0.001). During these 2 yr, the mean *V. dahliae* cfu per gram of soil was nearly the same (41–42 cfu/g) and the ranges of counts among fields were similar (0–138 cfu/g).

In addition to significant correlations between the cfu of *V. dahliae* in potato stems with wilt severity, a significant association with cultural management was found. In 1976, the severity of wilt incidence was positively related ($r = 0.62$, $P = 0.001$) with method of irrigation in 32 fields; wilt was more severe in fields irrigated with furrow than with sprinkler. Although the mean inoculum of *V. dahliae* was similar in sprinkler-irrigated and furrow-irrigated fields (40 [range of 0–138] and 47 [range of 8–74] cfu/g of soil, respectively), the incidence of wilt and cfu of *V. dahliae* in potato stems of furrow-irrigated fields were about four times greater than in sprinkler-irrigated fields. The mean incidence of potato stems with severe wilt was 13% in sprinkler-irrigated fields and 52% in furrow-irrigated fields. Similarly, the cfu of *V. dahliae* in potato stems were 152 cfu/g of stem-tissue in sprinkler-irrigated fields and 618 cfu/g of stem tissue in furrow-irrigated fields.

The electroconductivity of the soil profile was similarly positively correlated ($r = 0.60$, $P = 0.001$) with wilt. Certain nutrient levels in potato petioles (collected 12 July) were negatively related to the incidence of wilt (NO_3-N [$r = -0.544$, $P = 0.01$] and K [$r = -0.661$, $P = 0.001$]). In contrast to NO_3-N levels in the petioles, the NO_3-N from the soil at season's end was positively correlated with wilt ($r = 0.629$, $P = 0.001$). Among the nutritional factors, only NO_3-N in petioles yielded a significant negative correlation with the cfu of *V. dahliae*.

Several cultural factors may influence the degree of colonization by *V. dahliae* in potato stems, but these cultural relationships may not necessarily be the same in every region and every year. The relationship of cultural factors to the colonization of potato stems by *V. dahliae* was best predicted by the equation:

$$\text{Log}\, y = 24.06 - 1.521\, X_1 - 0.000266\, X_2 - 1.268\, X_3 - 10.551\, X_4$$

where y = cfu of *V. dahliae* per gram of apical stem tissue, X_1 = electrical conductivity of soil, X_2 = ppm NO_3-N in petioles, X_3 = percent K in petioles, and X_4 = percent P in petioles. During 1976, the management variables associated with this equation (electrical conductivity, NO_3-N, K, and P in petioles) accounted for 71% of the field variability related to colonization of *V. dahliae* in potato stem tissue. In contrast, a study in Bingham County during 1977 failed to account for colonization of *V. dahliae* by the same prediction equation. Nevertheless, cultural factors still continued to relate inoculum density of *V. dahliae* to wilt development. In 1976 and 1977, the colonization of potato stems by *V. dahliae* was still associated with the mode of irrigation. With furrow irrigation,

TABLE 2. Association of *Verticillium dahliae* in stem apices of potato and in soil samples with the severity of Verticillium wilt in Bingham County in eastern Idaho

V. dahliae	*r*-Value[a]	Fields compared (no.)
Field study 1		
cfu/g in stem apices	0.64***[c]	32
cfu/g in soil[b]	0.20	32
Field study 2		
cfu/g in stem apices	0.63**	21
cfu/g in soil[d]	0.11	21

[a] Regression with the percentage of stems showing severe Verticillium wilt (>75% yellowing and/or death).
[b] Range of cfu/g of soil was 0–138 with mean 42 cfu/g.
[c] Correlation coefficients followed by the symbol ** or *** were significant at $P = 0.01$ or $P = 0.001$, respectively.
[d] Range of cfu/g of soil was 0–124 with mean 41 cfu/g.

TABLE 3. Linear correlations among soilborne organisms, fungal colonization in potato stems, cultural management practices, wilt severity, yield, and tuber size in 37 fields of eastern Idaho (Egin Bench area, 1978)

	r-Values with dependent variables				
	Wilt (%)				
Independent Variables	9 August	23 August	Yield	Undersized[a] (%)	*Verticillium dahliae* (cfu/g of apical stem tissue)
Microorganisms					
V. dahliae cfu/g of					
soil	0.181	0.142	0.132	0.182	0.235
basal stem tissue	0.484**[b]	0.413*	−0.069	0.234	0.163
apical stem tissue	0.537***	0.555***	−0.548***	0.597***	...[c]
Colletotrichum atramentarium cfu/g of					
soil	− 0.160	−0.313	0.024	0.150	−0.137
basal stem tissue	−0.157	−0.226	−0.012	0.187	−0.104
apical stem tissue	−0.116	−0.069	−0.001	0.242	−0.070
V. nigrescens cfu/g of					
basal stem tissue	−0.218	−0.264	0.120	−0.309	−0.114
apical stem tissue	−0.101	−0.256	0.320	−0.061	−0.009
Pratylenchus/250 cm^3 of soil	0.332*	0.144	−0.076	0.107	0.218
Cultural factors					
Irrigation method (subirrigation and sprinkler)	0.192	0.332*	0.172	−0.049	0.090
Soil electroconductivity	0.129	0.181	0.054	−0.089	0.094
Petiole nutrients—6 July					
NO_3-N (ppm)	−0.446**	−0.523***	0.287	−0.408*	−0.541***
P (%)	0.062	0.029	0.067	0.363*	0.025
K (%)	0.316	0.115	−0.004	0.197	−0.009
Petiole nutrients—10 August					
NO_3-N (ppm)	−0.482**	−0.489**	−0.002	−0.200	−0.467**
P (%)	−0.402*	−0.430**	0.260	0.101	−0.259
K (%)	0.424**	0.212	−0.085	0.351*	0.261
Mn (ppm)	−0.300	−0.399*	0.120	−0.061	−0.257

[a] Tubers were counted as undersized if they weighed <113 g.
[b] Correlation coefficients followed by *, **, or *** were significant at $P = 0.05$, $P = 0.01$, and $P = 0.001$, respectively.
[c] Correlation coefficient not shown because values of *V. dahliae* cfu/g of apical stem tissue are the same as listed with variables under microorganisms.

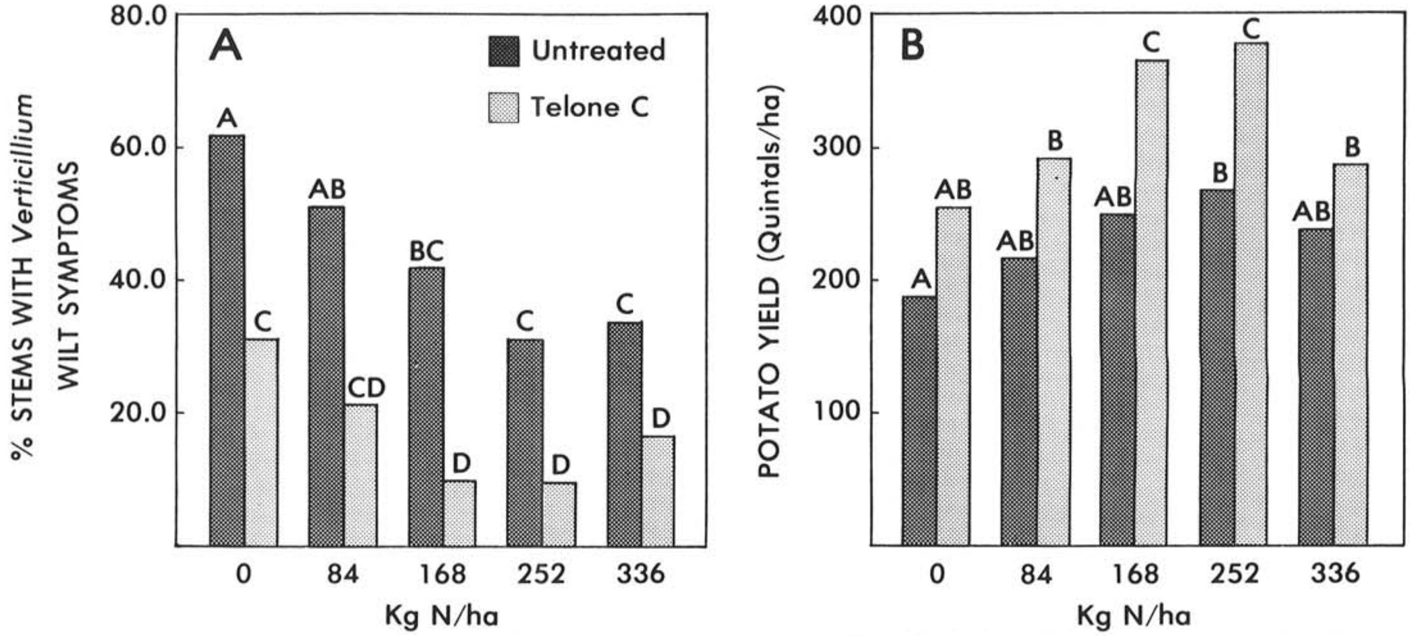

Fig. 1. Relation of severity of Verticillium wilt (**A**) and yield (**B**) on cultivar Russet Burbank with soil fumigation and nitrogen treatments. Different letters over bars denote significant differences to $P = 0.05$.

TABLE 4. Linear correlations between colony-forming units of *Colletotrichum atramentarium* in soil, microorganisms, wilt severity, yield, and tuber size in 37 fields in eastern Idaho (Egin Bench area, 1978)

Variables	*C. atramentarium* in soil r-Value[a]	*C. atramentarium* in soil r-Value[b]	Comparisons (no.)
Symptoms and yield			
Wilt (%)			
9 August	−0.160	0.004	37
23 August	−0.313	−0.366*[c]	37
Yield total	0.024	0.055	34
Undersized tubers (%)	0.150	0.160	34
Microorganisms			
V. dahliae cfu/g of			
soil	0.044	−0.143	37
basal stem tissue	−0.191	−0.297	37
apical stem tissue	−0.137	−0.188	37
C. atramentarium cfu/g of			
basal stem tissue	0.931***	0.859***	37
apical stem tissue	0.709***	0.671***	37
V. nigrescens cfu/g of			
basal stem tissue	−0.122	−0.428**	37
apical stem tissue	−0.074	−0.145	37
Pratylenchus/250 cm^3 soil	0.236	0.377*	36

[a] *C. atramentarium* cfu not transformed prior to correlating.
[b] *C. atramentarium* cfu transformed to $\log_{10}(X + 1)$.
[c] Correlation coefficients followed by *, **, or *** were significant at $P = 0.05$, $P = 0.01$, or $P = 0.001$, respectively.

there was a trend for greater colonization of *V. dahliae* of stems ($r = 0.473$, $P = 0.05$) than with sprinkler irrigation. In addition, the P levels in potato petioles continued to show a significant negative correlation with wilt ($r = -0.607$, $P = 0.01$).

As with other investigations in the eastern region during 1975–1977, the inoculum levels of *V. dahliae* in 37 field soils in 1978 did not correlate with the incidence of Verticillium wilt. Because inoculum densities of *V. dahliae* were considered high among all plot areas (ranging from 32 to 452 cfu *V. dahliae* per gram of soil, with the mean 183 cfu/g), the amount of inoculum was not considered to be a limiting factor. Nevertheless, as in previous years, plants in some fields with high inoculum levels did not develop severe disease. Table 3 illustrates simple linear relationships between wilt severity, yield, size, soilborne organisms, and cultural management factors.

Of 18 independent variables, the colonization of *V. dahliae* in potato stems was most consistently related to the incidence of wilt, tuber yield, and tuber size (Table 3). With higher colonization of apical stem tissue by *V. dahliae*, the incidence of wilt was higher, yield was lower, and the percentage of undersized tubers was higher. Among all factors, only NO_3-N in petioles correlated significantly ($P = 0.01$–0.001 depending on time of petiole collection) with the colonization of potato stems by *V. dahliae*. With increased N availability in petioles, colonization of apical stem tissue by *V. dahliae* was decreased.

Nutritional factors that involved N, P, and Mn correlated negatively with wilt (Table 3). When methods of irrigation were compared, the wilt incidence was correlated more positively in subirrigated fields than in those with sprinkler irrigation. NO_3-N in petioles correlated negatively with undersized tubers, whereas significant positive associations with the percentage of undersized tubers occurred with the presence of both P and K in petioles.

Throughout the 4 yr of this investigation, there was no indication of increased Verticillium wilt as cfu of *C. atramentarium* in soil increased. Inoculum of *C. atramentarium* in soil was highly correlated ($P = 0.001$) with the colonization of *C. atramentarium* in potato stem tissue (both basal and apical regions), suggesting a direct relationship between soilborne inoculum and infection (Table 4). In contrast to the positive relationship between stem infection and soilborne inoculum, *C. atramentarium* in soil was negatively correlated ($P = 0.05$) with the incidence of wilt and with the recovery of *V. nigrescens* in basal stem tissue (Table 4). Soil populations of *C. atramentarium* were positively related to the recovery of *Pratylenchus* spp. in soil. No significant adverse relationship existed between *C. atramentarium* in soil or stem tissue and yield.

From the epidemiology studies of 1976–1978 in eastern Idaho, the relationship of N availability to Verticillium wilt of the Russet Burbank potato was most consistent. The importance of N was further illustrated by the results of field studies at Aberdeen (Figs. 1 and 2). With treatments involving either N or chloropicrin, the severity of Verticillium wilt was significantly suppressed (Fig. 1). With wilt suppression by either fumigation or N, yield increases were consistent. Throughout these investigations, the incidence of wilt (Figs. 1 and 3) was highly correlated with the incidence of *V. dahliae* in potato petioles (Fig. 1 [$r = 0.657$, $P = 0.001$], Fig. 3 [$r = 0.750$, $P = 0.001$]).

The effect of N on wilt severity of the Russet Burbank potato was also verified with isolations from treatments involving the extreme and median N rates (Table 2). As the rate of N was increased, the incidence of *V. dahliae* significantly decreased ($P = 0.05$) and the incidence of *V. dahliae* was highly correlated with NO_3-N levels in potato petioles ($r = -0.600$, $P = 0.01$).

In contrast with Russet Burbank, N availability had no effect on the severity of Verticillium wilt in the Norgold Russet potato (Fig. 3), and the incidence of *V. dahliae* was not significantly correlated with NO_3-N levels in potato petioles ($r = -0.280$). These results indicate that response to N was associated with potato genotype.

DISCUSSION

The incidence of Verticillium wilt of the Russet Burbank cultivar was highly correlated with the colonization of apical stem tissue by *V. dahliae* (upper 5 cm of stem tissue). To a lesser extent, wilt severity also was related to the colonization of *V. dahliae* in basal stem tissue (about 2.5 cm above soil line). Additional studies have demonstrated highly significant correlations between the colonization of apical stem tissue with wilt, indicating that the threshold of colonization required for symptom development was about 100 cfu/g of air-dried apical stem tissue (11).

Although wilt severity was commonly found to be highly correlated with the cfu of *V. dahliae* in potato stem tissue, the same relationship frequently did not hold true with the inoculum density of *V. dahliae* in soil. The results of several years' study have shown no correlation between *V. dahliae* in soil with the severity of Verticillium wilt.

A slight, but significant, association was also found between populations of soilborne *Pratylenchus* spp. and wilt. Results suggest that *Pratylenchus* spp. had little, if any, influence on Verticillium wilt in the Egin Bench area of eastern Idaho. This could have been attributed to the fact that many fields may have been infested with *Pratylenchus* spp. having little, if any, virulence capability on potato. *Pratylenchus neglectus*, an avirulent root lesion nematode to potato, inhabits the fields of eastern Idaho (12).

Many questions have been raised concerning the possible role of *C. atramentarium* on potato production (16,19,31,32). In Idaho, the significance of *C. atramentarium* has been open to question (9). Although this pathogen has shown potential for increasing the severity of Verticillium wilt when inoculated in the presence of *V. dahliae*, evidence for the natural occurrence of this relationship with the Russet Burbank cultivar has not been found.

Our studies continue to support the view that the effect of *C. atramentarium* on early dying of cultivar Russet Burbank is of minor or no consequence. To the contrary, a significant negative correlation between wilt incidence and inoculum of *C. atramentarium* in soil (Table 4) suggests that this fungus may be suppressing the wilt problem. These results are in agreement with those of Mostafa (23), who reported that an isolate of *Colletotrichum* sp. reduced Verticillium wilt in cotton by producing phytotoxic diffusible substances.

Although no evidence existed that potato fields lacking soilborne *V. dahliae* would show severe wilt at season's end, the reverse was frequently true. In many instances, fields with high

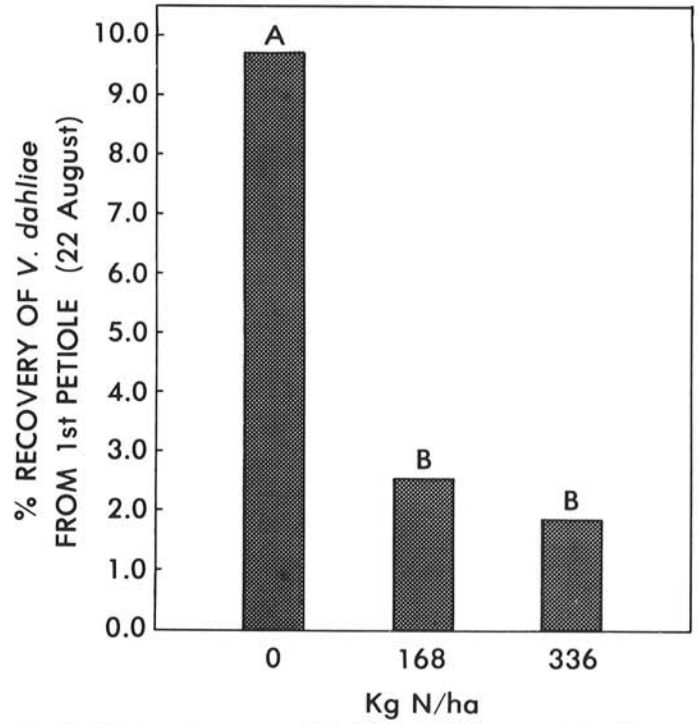

Fig. 2. Relation of recovery of *Verticillium dahliae* on cultivar Russet Burbank with nitrogen treatments. Different letters over bars denote significant differences ($P = 0.05$) determined by orthogonal contrasts for a 2×2 factorial design.

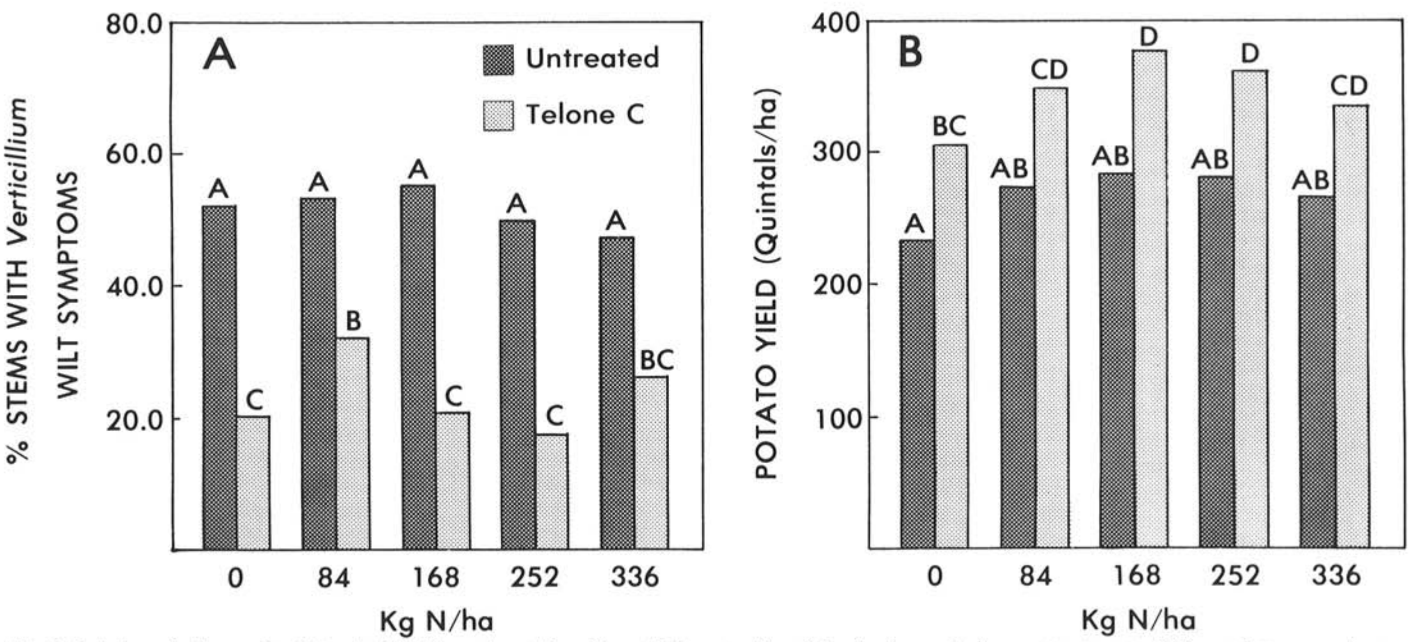

Fig. 3. Relation of wilt severity (**A**) and yield (**B**) on the cultivar Norgold Russet with soil fumigation and nitrogen treatments. Different letters over bars denote significant differences to $P = 0.05$.

levels of *V. dahliae* (>46 cfu/g of soil) produced potatoes with few, if any, symptoms.

Because investigations of strain types of *V. dahliae* have provided evidence suggesting a uniformity of type among Idaho potato fields and because isolates from soil have consistently been highly pathogenic on potato, it is doubtful that differences of strain and pathotype would account for the frequent lack of correlation with soilborne inoculum levels. The variability of wilt severity was closely associated with cultural management practices.

Increases of Verticillium wilt were highly correlated with furrow irrigation, compared with sprinkler irrigation. These observations agree with previous reports (17,22). In the Egin Bench area, where fields were not irrigated by furrow, there was more wilt in subirrigated fields than in those that were sprinkler irrigated. Although the explanation for relationships with methods of irrigation is not known, a relationship with N availability has been suggested (5). With furrow irrigation, N often accumulates within the upper 7.5–15.0 cm of the soil profile. In contrast, N may be more uniformly distributed throughout the soil with sprinkler irrigation. When N is less available to the plants' root systems because of leaching and poor distribution, disease incidence and severity may increase.

Among all cultural factors that were considered, N availability was most commonly associated with Verticillium wilt of potato. In both the Bingham County and Egin Bench areas of eastern Idaho, the colonization of *V. dahliae* in potato stems was negatively correlated with the NO_3-N levels in potato petioles. As the availability of N increased, colonization in plant tissue by *V. dahliae* decreased. With a deficiency of petiolar N, Verticillium wilt in cultivar Russet Burbank was more severe. As the availability of N approached the optimum for highest yield, disease severity was less and this relationship was inversely related to yield.

In contrast, the inverse relationship between available N and severity of Verticillium wilt has not been found with the Norgold Russet, which has a more determinant growth habit than Russet Burbank. These observations indicate a genotypic relationship associated with N response. It is also possible that other cultural factors may also counteract the effects of soilborne inoculum. This was suggested by studies of 1976, when cultural factors associated with soil electroconductivity (a measure of total salt content), and N, K, and P in petioles accounted for 71% of the field variability related to the colonization of *V. dahliae* in potato stems.

Our research exemplifies the importance of cultural management practices on the Verticillium wilt disease of potato. The use of optimal soil fertility may currently provide one of the most viable solutions to the management of Verticillium wilt in the Russet Burbank potato.

LITERATURE CITED

1. Anonymous. 1971. United States standards for grades of potatoes (35 F. R. 18257). Consumer and Marketing Service, Washington, DC, 19 pp.
2. Ashworth, L. J., Jr., Huisman, O. C., Harper, D. M., Stromberg, L. K., and Bassett, D. M. 1979. Verticillium wilt disease of cotton: Influence of inoculum density in the field. Phytopathology 69:483-489.
3. Butterfield, E. J., and DeVay, J. E. 1977. Reassessment of soil assays for *Verticillium dahliae*. Phytopathology 67:1073-1078.
4. Cobb, N. A. 1918. Estimating the nematode population of soil. U.S. Dep. Agric. Tech. Circ. 1.
5. Davis, J. R. 1981. Verticillium wilt of potato in southeastern Idaho. Univ. Idaho Curr. Inf. Ser. 564.
6. Davis, J. R. 1984. Approaches for the control of potato early dying caused by *Verticillium dahliae* (Abstr.) Am. Potato J. 61:519-520.
7. Davis, J. R. 1984. Relationships of plant nutrition and methods of irrigation to Verticillium wilt of the Russet Burbank potato. Pages 180-181 in: Abstr. Triennial Conf. Pap. Eur. Assoc. Potato Res., 9th., Interlaken, Switzerland.
8. Davis, J. R. 1985. Approaches to control of potato early dying caused by *Verticillium dahliae*. Am. Potato J. 62:177-185.
9. Davis, J. R., and Howard, M. N. 1976. Presence of *Colletotrichum atramentarium* in Idaho and relation to *Verticillium dahliae* and early dying of potato. (Abstr.) Am. Potato J. 53:397-399.
10. Davis, J. R., McMaster, G. M. 1979. Irrigation and nutritional relationships associated with Verticillium wilt of Russet Burbank potato. (Abstr.) Phytopathology 69:915.
11. Davis, J. R., Pavek, J. J., and Corsini, D. L. 1983. A sensitive method for quantifying *Verticillium dahliae* colonization in plant tissue and evaluating resistance among potato genotypes. Phytopathology 73:1009-1014.
12. Davis, J. R., Sorenson, L. H., Corsini, D. L., and Hafez, S. L. 1983. Effects of continuous cropping with potato genotypes on *Verticillium dahliae* and *Pratylenchus neglectus*. (Abstr.) Phytopathology 73:958.
13. DeVay, J. E., Forrester, L. L., Garber, R. H., and Butterfield, E. J. 1973. Characteristics and concentration of propagules of *Verticillium dahliae* in air-dried field soils in relation to the prevalence of verticillium wilt in cotton. Phytopathology 64:22-29.
14. Easton, G. D. 1967. The number of *Verticillium* propagules in field soils in Washington. (Abstr.) Phytopathology 57:1004.
15. Farley, J. D. 1972. A selective medium for assay of *Colletotrichum coccodes* in soil. Phytopathology 62:1288-1293.
16. Goodell, J. J., Powelson, M. L., and Allen, T. C. 1982. Interrelations between potato virus X, *Verticillium dahliae*, and *Colletotrichum atramentarium* in potato. Phytopathology 72:631-634.
17. Guthrie, J. W. 1960. Early dying (*Verticillium wilt*) of potatoes in Idaho. Univ. Idaho Res. Bull. 45. 24 pp.
18. Horsfall, J. G., and Barratt, R. W. 1945. An improved system for measuring plant diseases. (Abstr.) Phytopathology 35:655.
19. Kotcon, J. B., Rouse, D. J., and Mitchell, J. E. 1984. Interactions of *Verticillium dahliae*, *Colletotrichum atramentarium*, *Rhizoctonia solani*, and *Pratylenchus penetrans* in the early dying syndrome of Russet Burbank potatoes. Phytopathology 75:68-73.
20. 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.
21. Martinson, C. A., and Horner, C. E. 1962. Importance of nonhosts in maintaining the inoculum potential of *Verticillium* (Abstr.) Phytopathology 52:742.
22. McMaster, G. 1959. A new concept in sprinkler irrigation. Univ. Idaho Prog. Rep. 17. 12 pp.
23. Mostafa, A. K. M. 1967. Studies on the control of vascular wilt diseases of cotton by fungi associated with the cotton plant. Diss. Abstr. 27(11)B:3746.
24. 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.
25. Otazu, V., Gudmestad, N. C., and Zink, R. T. 1978. The role of *Colletotrichum coccodes* in the potato wilt complex of North Dakota. Plant Dis. Rep. 62:847-851.
26. Powelson, R. L. 1970. Significance of population level of *Verticillium* in soil. Pages 31-33 in: Root Diseases and Soil-borne Pathogens. T. A. Toussoun, R. V. Bega, and P. Nelson, eds. University of California Press, Berkeley. 252 pp.
27. Puhalla, J. E., and Hummel, M. 1983. Vegetative compatibility groups within *Verticillium dahliae*. Phytopathology 73:1305-1308.
28. 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.
29. Schneider, R. W., ed. 1982. Suppressive Soils and Plant Disease. American Phytopathological Society, St. Paul, MN. 88 pp.
30. Steel, R. G. D., and Torrie, J. H. 1980. Principles and Procedures of Statistics, 2nd ed. McGraw-Hill, New York. 633 pp.
31. Stevenson, W. R., Green, R. J., and Bergeson, G. B. 1976. Occurrence and control of potato blackdot root rot in Indiana. Plant Dis. Rep. 60:248-251.
32. Thirumalachar, M. J. 1967. Pathogenicity of *Colletotrichum atramentarium* on some potato varieties. Am. Potato J. 44:241-244.