Effects of Green Manures on Verticillium Wilt of Potato

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This study was funded in part by the Idaho Potato Commission and by a special grants program of the USDA-ARS.
We thank S. A. Wheeler for technical assistance.
Accepted for publication 10 February 1996.

ABSTRACT

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

Two field studies were conducted to investigate the effects of green manure treatments on Verticillium wilt of potato (cv. Russet Burbank) caused by *Verticillium dahliae*. Each study involved the use of a sudangrass (*Sorghum vulgare* var. *sudanense* 'Monarch') green manure treatment and a fallow treatment for either 2 or 3 years prior to growing potato. In addition to sudangrass, comparisons also were made with several green manure treatments, including Austrian winter pea (*Pisum sativum* 'Austrian winter'), two cultivars of rape (*Brassica napus* var. *napus* 'Dwarf Essex' and 'Bridger'), rye (*Secale cereale*), oat (*Avena sativa* 'Monida'), and corn (*Zea mays* 'Jubilee'). Verticillium wilt of potato was best controlled after green manure treatments of either sudangrass or corn; after these treatments, yields were increased above all other treatments. Wilt was most severe when potato followed the fallow treatment and intermediate following rape, Austrian winter pea, oat, and rye. Wilt incidence was positively correlated with *V. dahliae* colonization in apical stems but was not significantly related to other pathogens (*Pratylenchus neglectus*, *Colletotrichum coccodes*, *Rhizoctonia solani* Ag-3) or to effects of green manure treatments on preplant nutritional effects of N, P, or K.

Additional keywords: cropping relationships, early dying suppression, increased yield and quality, nutritional relationships.

Verticillium wilt of potato caused by *Verticillium dahliae* Kleb. is a serious economic problem in arid and semiarid regions of the world. In Idaho, Verticillium wilt reduces tuber yield by 5 to 12 metric tonnes ha^{-1} annually (11). Crop rotations that separate potato crops by up to 5 years have been ineffective in suppressing this disease (11,19). There are only two known methods for reducing soil populations of this pathogen within an acceptable time span: the use of fumigation and solarization. Of these approaches, only fumigation is widely used, in spite of its cost, environmental impact, and risk to workers. Even with the use of soil fumigation, however, a cost-effective yield response is not always possible. Earlier studies in Idaho showed no correlation between the inoculum density of *V. dahliae* in soil and potato stems (12). The influence of a variety of cultural factors on the development of *V. dahliae* in potato tissue accounted for this lack of correlation with soil inoculum.

Cultural factors involving N, P, and soil electroconductivity measurements have accounted for as much as 71% of the field variability of Verticillium wilt severity (12). Among nutritional factors, N is commonly related (negatively) to the severity and incidence of this disease (35). The combined effects of N and P on wilt severity are even greater (20) than their independent effects. The mode of irrigation also may affect the severity of Verticillium wilt. With sprinkler irrigation, the disease is generally less severe than with furrow irrigation (12). Cappaert et al. (9) reported that high soil moisture early in the growing season increased the severity of Verticillium wilt of potato.

In addition to cultural factors, other pathogens may affect disease development (32,39), and the presence of infection by these pathogens should be considered when evaluating treatment effects on Verticillium wilt of potato.

From the time of the ancient Inca culture, and probably before, the sustainability of potato cropping has been enhanced by the addition of organic materials to soil (41). To some extent, these practices are still followed using cover crops. Summer cover crops in Florida have been associated with the diminution of Verticillium wilt of potato. For over 100 years, potato growers of Hastings, FL, have grown summer cover crops to suppress weeds, use up excess fertilizer remaining from potato crops, and maintain soil organic matter. These cover crops are grown annually during the summer and fall prior to planting potato (33). In earlier years, Verticillium wilt of potato was present, but coincident with the more recent use of a sorghum-sudangrass cover crop, the expression of Verticillium wilt has mostly subsided (D. Weingartner, *personal communication*). In Washington, Verticillium wilt was suppressed and potato yield increased after precropping with a green pea-sudangrass rotation during the same year (21). It was not determined, however, if these responses were due to precropping with sudangrass or to the combined effect of both crops. With a pea rotation, an increase in N availability might explain both suppression of wilt and increased yield. In other studies, the incidence of Verticillium wilt of peppermint was reduced when following corn (23).

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Publication no. P-1996-0311-01R

Because green manures are effective for improving both soil tilth and organic matter, while providing nutrient benefits for plant growth, we chose to investigate the effects of green manures on Verticillium wilt of potato. Owing to the complexity of Verticillium wilt and the interactions of the many factors influencing this disease (36), it seemed essential that these factors be considered to understand the effect of treatments, particularly in the case of green manures. Not only are green manures a major source of plant nutrients, plant nutrition in turn can have a significant impact on the disease etiology of *Verticillium* (20). This paper reports the effect of green manure treatments on yield, quality, inoculum densities, infection, and symptoms of Verticillum wilt and describes the relationships of *V. dahliae* and other pathogens and plant nutrients in soil to the dependent variables of both disease symptoms and potato yield. A portion of this work has been published (15,16,17,25,26,42).

MATERIALS AND METHODS

The field used for this investigation was located at the University of Idaho Research and Extension Center, Aberdeen, and had a Declo loam soil type, pH 8.2. Prior to this study, the field was cropped to barley, wheat, potato, and other crops for more than 70 years. Barley was grown throughout the field in 1986 prior to initiating the green manure treatments in 1987. This field had a long history of Verticillium wilt on potato crops. Initial inoculum levels of *V. dahliae* within the upper 23 cm of the soil profile ranged from 40 to 70 CFU/g of air-dried soil.

Field study 1. Green manure crops were grown for three consecutive years (1987 through 1989) on the same plots. Cropping treatments consisted of a weedfree fallow treatment, Austrian winter pea (*Pisum sativum* L. 'Melrose'), sudangrass (*Sorghum vulgare* Pers. var. *sudanense* (Piper) Hitche. 'Monarch'), and two cultivars of rape (*Brassica napus* L. 'Dwarf Essex' and 'Bridger'). Plots, 7.3 × 19.8 m, were arranged in a 5 × 5 Latin-square design.

Field study 2. Cropping treatments were grown for two consecutive years (1988 through 1989) on the same plots. Treatments involved a weedfree fallow treatment, oat (*Avena sativa* L. 'Monida'), rye (*Secale cereale* L.), sudangrass ('Monarch'), and corn (*Zea mays* L. 'Jubilee'). Plots for study 2 were located adjacent to those for study 1, and the plot design and size of both studies were the same.

With the exception of 1987 when the area of the field used for study 2 was fallow, cultural practices were similar for both studies. Each year the green manure crops, with the exception of pea, were planted during the last week of May. Pea was planted several weeks earlier, during either April or early May. Throughout these studies, green manures were mechanically incorporated into soil between 4 and 19 August by either disking or rotovating. Prior to soil incorporation, above-ground plant samples were collected from an area 1 m^2 in the buffer regions of each plot to provide an estimate of the amount of residue incorporated into the soil. These residue samples were oven-dried at approximately 49°C before making weight determinations.

Metribuzin (dry flowable) was applied to pea plots at 0.18 kg ha^{-1} on 26 June 1987 for weed control. In subsequent years, metolachlor (emulsifiable concentrate on corn and sudangrass) was applied at 2.2 kg ha^{-1}. Trifluralin (emulsifiable concentrate) was applied on pea at 0.38 kg ha^{-1}. 2-4-D (water soluble amine) was applied on oat and rye at 0.56 kg ha^{-1}. Bromoxynil (emulsifiable concentrate) was applied on oat and rye at 0.42 kg ha^{-1}.

Based on yearly soil assays (University of Idaho Soils Lab, Moscow), fertilizers were broadcast with a Barber spreader as follows: 280 kg of N per ha and 196 kg of P per ha in 1987, 112 kg of N per ha in 1988, and no preplant fertilizer in 1989. N (45 kg ha^{-1}) was applied through sprinkler lines on 2 June 1988 and on 2 and 16 June and 7 July 1989. N (45 kg ha^{-1}) also was applied by sprinkler after residue incorporation during August to accelerate breakdown of organic matter.

Cultural practices for potato. During the first week of May 1990 and 1991, potato (Russet Burbank) was planted throughout all plots (0.9-m row spacing with plots separated by 3.0 m of fallow area). Seed was cut at approximately 59 ± 3 g per seedpiece and planted 30 cm apart with an assist-feed planter at a depth of 12 to 15 cm. All seed potatoes used in these studies met certification standards (3).

Aldicarb (3.4 to 3.9 kg a.i. ha^{-1}) was applied at planting for insect control. All irrigations, including the green manure treatments, were done with solid-set sprinklers. With the exception of 1990 when N was a treatment variable, cultural practices were as recommended by the University of Idaho for potato production (2,7,30,34,43). To avoid pathogens that commonly cause foliar symptoms and yield losses in potato (*Alternaria solani* and *Colletotrichum coccodes*) (2,33), aerial sprays of either mancozeb at 1.8 kg ha^{-1} or chlorothalonil at 1.25 kg ha^{-1} were applied at weekly intervals as flowable liquid between mid-July and 1 September.

Fertilizer treatments, 1990. To test the possibility of interaction effects between treatments and N levels, a split-plot experimental design was superimposed over all plot locations. Treatments involved a low N treatment (59 kg of N per ha) that was broadcast to all plots as NH_4NO_3 on 27 April. On 30 April, an additional 137 kg of N per ha was applied to plots receiving a high N treatment.

Plant tissue assays. *V. dahliae* was assayed in apical stems toward the end of the growing season (20 to 30 August) as previously described with an Andersen sampler after air-drying and milling (18,19). On 4 September 1991, stem bases from study 1 were assayed for *C. coccodes*. Thirty representative stem bases per plot were collected, and a 1-mm-thick cross-section from each was removed from an area 1.3 cm above the soil surface. Samples were disinfested, air-dried, ground, and assayed on Tergitol NP-10 (Union Carbide Co., Bound Brook, NJ) (NPX) media (8). During November 1990 and December 1991, 30 slices of potato peel, approximately 1.0 mm thick × 1 cm diameter, were taken from the stem ends of 30 tubers (113 to 280 g) for each plot of studies 1 and 2. After air-drying the tissue for several weeks, the tissue was ground and assayed on NPX agar for colonies of both *V. dahliae* and *C. coccodes*.

Soil assays for *V. dahliae*. Prior to planting during either April or May of each year, 24 soil samples (2-cm core) were collected from the top 23 cm of each plot during 1987 to 1991 for study 1 and during 1988 to 1991 for study 2. At time of collection, the core samples from each plot were bulked and separately mixed in a clean 8-liter container. These samples were air-dried for approximately 6 weeks at 20 to 25°C. Samples from each plot were separately remixed in 61 × 61-cm plastic bags. From this sample, six subsamples totaling 80 g were collected randomly and mixed again. Samples from the third mixing were passed through a 250-μm (60 mesh) screen to remove organic matter and standardize particle size. Final samples were mixed again, and for each plot, five subsamples (50 mg each) from the final mixing were plated, each onto a separate plate of NPX medium following the Andersen sampler procedure for soil assay (8).

Nematode assay. Soil collected from the field plots was divided for assay of *V. dahliae* and for assays of *Pratylenchus neglectus*. These assays were performed by the University of Idaho Nematology Laboratory, SW Idaho Research and Extension Center, Parma, by standard procedures (10,28).

Disease assessment. Wilt symptoms were evaluated each year at midseason (2 to 13 August) and later in the season (27 August to 5 September). Wilt data were expressed as the percentage of stems with wilt symptoms in each plot (50 stems evaluated per plot). Early August data expressed wilt symptoms on the uppermost 15 cm of the stem. Late-season evaluations determined the incidence of severe wilt symptoms (>75% of foliage with Verticillium symptoms) as previously described (18,19,20). To separate Verticillium-like symptoms from other factors that may produce similar symptoms (e.g., drought stress, nutrient deficiency, senescence, etc.), the terminal 8 cm of stem tissue was assayed for *V. dahliae* in the manner described previously. *Verticillium* infection of roots also was quantified by the procedure of Huisman (24).

On 23 and 24 July 1990, below-ground potato stems were harvested from 1.5 m of plot row in each plot. These stems were washed and evaluated for cankers/lesions caused by *Rhizoctonia solani* Ag-3 as previously described (13).

Nutrient analyses of soil. Prior to planting potato during the spring and prior to applying preplant fertilizers, soil samples were collected from each plot for nutrient analyses. Soil nutrients were measured in a minimum of eight soil cores (3.3 × 30 cm) per plot and were combined, air-dried, and ground before analyses. During 1990, whole-plant samples were collected from 1.5 m of plot row on 16 July and 21 August for study 1 and on 19 July and 23 August for study 2. Similarly, whole-plant samples were obtained

TABLE 1. Effect of green manure treatments on above-ground plant residues and preplant soil nutrients[x]

	Treatment	Plant residue (metric tonnes ha^{-1} [dry weight]) 1988	1989
Study 1	Austrian winter pea	9.2 A	7.0 B
	Sudangrass	10.3 A	10.6 A
	Dwarf Essex rape	10.4 A	9.5 A
	Bridger rape	10.3 A	9.5 A
Study 2	Oat	11.7 A	11.6 A
	Rye	6.7 B	7.0 B
	Sudangrass	10.1 A	11.4 A
	Corn	7.7 B	13.3 A

	Treatment[y]	Nutrient in soil[z] (ppm) NO_3-N	P	K	Mn	Zn	% Soil organic matter[z]
Study 1	Fallow	14.6 A	22.0 A	174 B	4.4 A	0.54 B	1.10 C
	Austrian winter pea	12.3 A	21.4 AB	178 B	4.6 A	0.56 B	1.19 BC
	Sudangrass	13.0 A	18.5 C	144 C	5.2 A	0.58 AB	1.38 A
	Dwarf Essex rape	30.4 B	19.9 AC	195 AB	5.0 A	0.68 A	1.31 AB
	Bridger rape	24.8 B	19.3 BC	207 A	4.8 A	0.56 B	1.24 AC
Study 2	Fallow	13.8 A	25.0 A	192 A	3.4 B	0.52 A	1.03 A
	Oats	16.2 A	20.8 B	205 A	4.1 A	0.56 A	1.15 A
	Rye	25.4 B	22.5 B	220 A	3.8 AB	0.56 A	1.14 A
	Sudangrass	13.9 A	21.6 B	188 A	4.0 A	0.58 A	1.22 A
	Corn	15.1 A	21.8 B	196 A	3.8 B	0.56 A	1.15 A

[x] Different letters denote significant differences within a column, $P \leq 0.05$.
[y] No plant residues were incorporated in the fallow treatment.
[z] Analyses were made during the spring of 1990 prior to planting and prior to adding preplant fertilizers.

TABLE 2. Effect of green manure treatments on inoculum densities of *Verticillium dahliae*, field study 1[y]

Treatment	*V. dahliae* log(CFU/g soil)[z] (mean) 1987 (1n)	1988 (1n)	1989 (1n)	1990 (1n)	1991 (1n)	Treatment mean (1n)
Fallow	3.74 A	3.46 AB	3.97 AB	3.97 A	3.83 A	3.80 A
Austrian winter pea	4.17 A	3.87 A	3.80 AB	3.52 A	2.47 C	3.57 A
Sudangrass	4.12 A	3.27 B	3.50 B	2.77 B	2.53 C	3.23 B
Dwarf Essex rape	3.67 A	3.15 B	4.11 A	3.76 A	3.40 AB	3.61 A
Bridger rape	3.73 A	3.36 AB	3.88 AB	3.65 A	3.18 B	3.56 AB

Source of Variation	df	Mean square	$P > F$
Treatment	4	1.029	0.042
Row	4	0.438	0.270
Column	4	0.691	0.115
Error (*a*)	12	0.297	
Year	4	2.750	0.001
Year × treatment	16	0.664	0.001
Year × row	16	0.333	0.064
Year × column	16	0.189	0.382
Error (*b*)	48	0.170	
Total	124		
Year			
Linear	1	5.645	0.001
Quadratic	1	0.901	0.060
Cubic	1	2.651	0.002
Lack-of-fit	1	1.821	0.006
Year linear × treatment	4	2.200	0.001
Year quadratic × treatment	4	0.205	0.453
Year cubic × treatment	4	0.053	0.858
Lack-of-fit	4	0.196	0.346

[y] Different letters denote significant differences within a column, $P \leq 0.05$.
[z] Cover crops were grown from 1987 to 1989, followed by potato from 1990 to 1991.

during 1991 for each study. Nutrient analyses were made as previously described (27), and N analyses of soil samples were made by the methods of Gavlak et al. (22).

Harvesting and grading. Potatoes were harvested each year between 25 September and 7 October from a total of 10.7 m of the center rows to avoid border effects in each plot. Tubers were washed and graded according to standard methods (1). During late July, whole plants were harvested from 1.5 m of row to evaluate the effect of treatments on plant growth and nutrient uptake.

Data analyses. Data involving stem assays of *V. dahliae* and *C. coccodes* were significantly, positively skewed. Therefore, the analysis of variance (ANOVA) of *V. dahliae* per gram of tissue was performed on transformed $\ln(y + 1)$ values. Data on percent infection were analyzed after arcsine-square root percent transformation. In all cases, means were calculated from the transformed data and reconverted to original units. The effect of treatments on changes in inoculum density per gram of soil over time was assessed according to a Latin-square split-plot repeated-measures analysis. To adjust for a nonrandom assignment of years, because years occurred in sequence, the Greenhouse-Geisser adjustment was used (29) to ensure that all comparisons among years were valid. All ANOVAs were conducted in accordance with the experimental design. Correlations were run between treatment means for the nutrient and pathogen variables. This resulted in tests of significance with only 3 df for correlations among means of the five green manures tested.

RESULTS

Green manure residues. Above-ground plant residues from green manure treatments ranged from 7 to 10 metric tonnes ha^{-1} (Table 1) when incorporated into soil. There were significant differences in plant residue weights between treatments. In 1988, corn and rye residue weights of study 2 were the lowest, whereas in 1989 Austrian winter pea of study 1 and rye residues of study 2 were the lowest. Prior to planting potato, the levels of soil organic matter differed significantly between treatments in study 1 but not in study 2 (Table 1). There was a slight but significant negative correlation ($r = -0.459$, $P < 0.05$) between the percentage of soil organic matter and wilt incidence in study 1 but not in study 2. After cropping of green manures, differences ($P \leq 0.05$) in nutrient concentrations in soil occurred between treatments. Although preplant differences of N and K concentrations in soil (Table 1) occurred in the 1990 potatoes, these differences did not relate to either the incidence of Verticillium wilt or the colonization of *V. dahliae* in apical stems. P did not appear to be a limiting factor among any of the plots. Although residual-soil P levels in sudangrass plots were lower than the fallow levels in both studies, the potato yields were consistently higher in the sudangrass plots when compared with fallow. Similarly, N was not a limiting factor for yield. On 1 July, petiole NO_3-N concentrations for both studies were adequate (ranging from 17,680 to 19,440 µg/g in all treatments) (data not shown).

Soil populations of *V. dahliae*. *Study 1.* Mean soil inoculum densities of *V. dahliae* ranged from 11 to 64 CFU/g of soil for 1987 to 1991 (Table 2). Although no significant differences were evident in 1987, differences ($P \leq 0.05$) did occur in later years. The main effects of treatments, years, and their interactions were significant ($P \leq 0.05$). Except for the Bridger rape treatment, sudangrass had a lower ($P \leq 0.05$) *V. dahliae* inoculum density than the fallow, Austrian winter pea, and rape treatments of Dwarf Essex. In 1988, *V. dahliae* populations were higher ($P \leq 0.05$) in Austrian winter pea plots than in plots of either sudangrass or Dwarf Essex. In 1989, *V. dahliae* inoculum densities were lower ($P \leq 0.05$) in sudangrass than in Dwarf Essex plots, and in 1990, the *V. dahliae* inoculum density in sudangrass-treated areas was lower ($P \leq 0.05$) than in all other treatments. In 1991, inoculum densities for treatments with either sudangrass or Austrian winter pea were lower ($P \leq 0.05$) than for all other treatments (Table 2).

The linear, cubic, and lack-of-fit components were significant in the year main effect. The years 1987 and 1989 had relatively high values, whereas a general decline in inoculum densities occurred over time (Fig. 1). This was shown by a significant year linear × treatment interaction. The differential negative slopes for sudangrass and Austrian winter pea were much steeper than for those of either Dwarf Essex or Bridger rape. In contrast, no noticeable decrease in the inoculum density occurred over time with the fallow treatment.

Study 2. For study 2, mean soil inoculum densities for *V. dahliae* ranged from 26 to 66 CFU/g of soil in 1990 and 1991 (Table 3). Although *V. dahliae* inoculum density means did not differ between green manures in 1990, the mean inoculum densities of corn and oat treatments in 1990 and 1991 had lower inoculum densities compared to the fallow treatment. The sudangrass treatment, on the other hand, in study 1 did not reduce soilborne populations of *V. dahliae* following 2 years of green manure treatment.

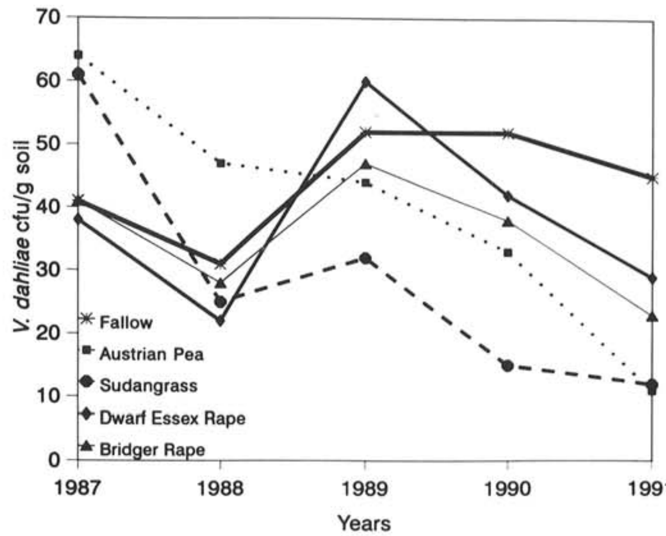

Fig. 1. Inoculum density of *Verticillium dahliae* in fallow and green manure treatments in 1987 to 1989. In 1990 and 1991 Russet Burbank potato was planted in all plots. Inoculum density was quantified during the spring of each year (April to May).

TABLE 3. Effect of green manure treatments on inoculum densities of *Verticillium dahliae*, field study 2

	V. dahliae (CFU/g soil)[z]		
	Mean		Treatment
Treatment	1990 (ln)	1991 (ln)	mean (ln)
Fallow	4.02 A	4.39 A	4.20 A
Oat	3.56 AB	3.88 C	3.72 B
Rye	3.66 AB	4.17 AB	3.92 AB
Sudangrass	3.52 AB	4.36 AB	3.95 AB
Corn	3.28 B	3.92 BC	3.60 B

Source of variation	df	Mean square	$P > F$
Treatment	4	0.528	0.029
Row	4	1.630	0.001
Column	4	0.201	0.264
Error (*a*)	12	0.134	
Year	1	3.572	0.001
Year × treatment	4	0.109	0.450
Year × row	4	0.781	0.004
Year × column	4	0.058	0.720
Error (*b*)	12	0.110	
Total	49		

[z] Different letters denote significant differences within a column, $P \leq 0.05$.

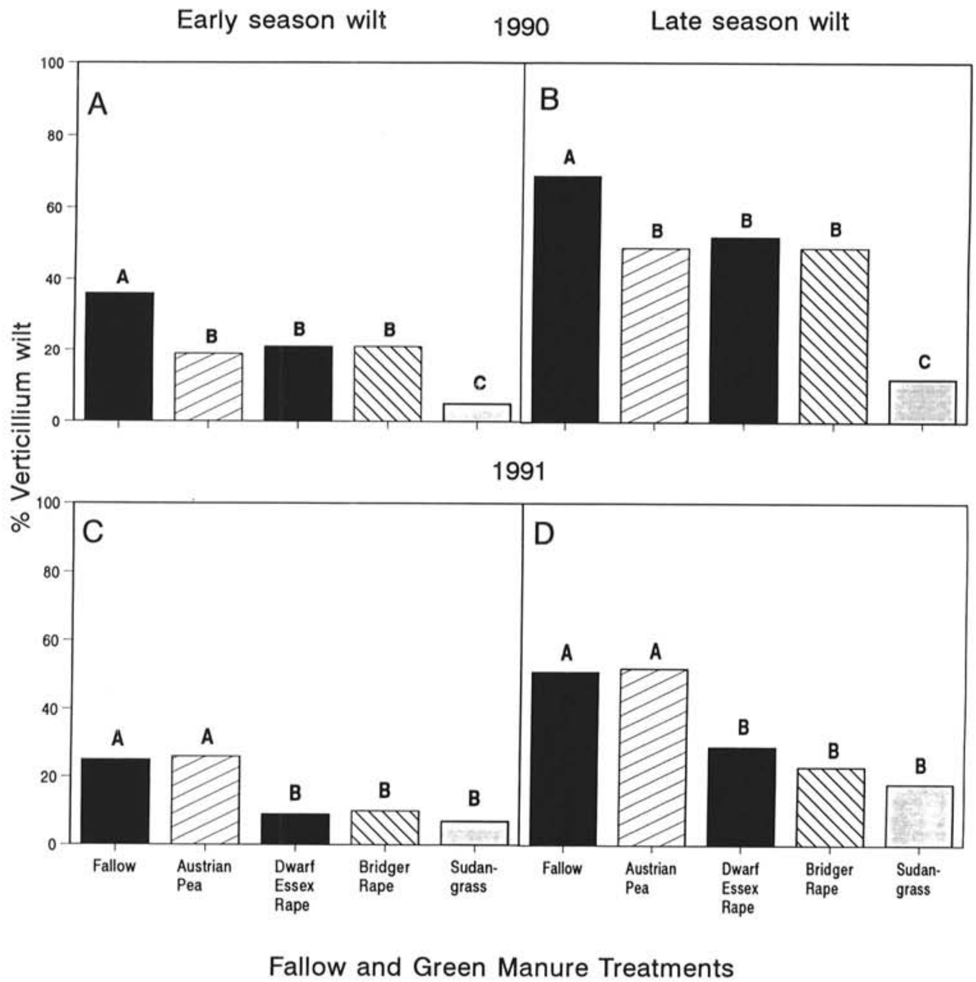

Fig. 2. Verticillium wilt incidence in study 1. **A,** Mean values of percent wilt incidence (in upper 8 cm of potato stems) observed early in the growing season of 1990 (2 through 13 August). **B,** Percent incidence of advanced wilt symptoms (dead to nearly dead) late in the growing season of 1990 (27 August through 5 September). **C,** Mean values of percent wilt (in upper 8 cm of potato stems) observed early in the growing season of 1991 (2 through 13 August). **D)** Percent incidence of advanced wilt symptoms (dead to nearly dead) late in the growing season of 1991 (27 August through 5 September). Different letters indicate significant differences between mean wilt percentages ($P \leq 0.05$) according to Duncan's multiple range test.

Wilt incidence. *Study 1.* Visible incidence of wilt, both early and late in the growing season, was lower ($P \leq 0.05$) in plots with previous green manure histories (Fig. 2). Sudangrass was most effective for suppression of wilt, and the fallow treatment had the highest wilt incidence. Wilt suppression with sudangrass continued into mid-September. Although the potatoes grown following fallow were almost completely dead, potatoes following sudangrass were still green and appeared relatively healthy (Fig. 3). Neither N nor the effect of cropping practice × nitrogen interactions affected wilt. Throughout these investigations, the incidence of wilt was highly correlated (Table 4) with the *V. dahliae* inoculum densities in the apical 8 cm of potato stems.

There were no positive correlations between Verticillium symptoms or yield and *P. neglectus*, *C. coccodes*, Rhizoctonia stem canker (caused by *R. solani* Ag-3), or combinations of these factors. Soil inoculum densities of *V. dahliae* were significantly correlated with both the incidence of wilt on several dates and with the inoculum densities of *V. dahliae* in potato stems (Table 5).

Wilt was not suppressed with increased P. The only minor elements to correlate negatively with wilt incidence were Mn and Zn. The correlation ($P \leq 0.05$) for Mn was only significant in the low N plots of both studies. Zn, on the other hand, correlated consistently ($P \leq 0.05$ to 0.01) with wilt incidence in both the low and high N plots of study 2 on each date.

When potato was planted for the second consecutive year over all the plots in 1991, wilt was suppressed in plots previously cropped with sudangrass, Dwarf Essex, and Bridger, but the effect of sudangrass did not differ from the two latter treatments as it had in 1990 (Fig. 2). The effect of Austrian winter pea on Verticillium wilt also differed. In 1990, after Austrian winter pea treatments, wilt was significantly reduced, whereas in 1991 wilt was not reduced with this treatment when compared with fallow. As in 1990, the amount of wilt in 1991 continued to be highly correlated with *V. dahliae* in potato stems (Table 4).

Study 2. In 1990, wilt incidence in study 2 for both the early (14 August) and late season (27 August to 5 September) was suppressed when green manure treatments were compared with fallow (Fig. 4). As with study 1, the sudangrass treatment had the lowest incidence of infection; this was lower ($P \leq 0.05$) than either the rye or fallow treatments. Neither N nor the N × previous-crop interactions had a significant effect on wilt incidence (data not shown). The 1990 stem-colonization data of study 1 for *V. dahliae* showed similar relationships that were comparable to the wilt data (Table 6). Although not significant, the treatment rankings for stem colonizations of study 2 were the same as the wilt incidence, and in both studies, the colonization of apical stems by *V. dahliae* was highly correlated with the incidence of Verticillium wilt on several dates (Table 4). With the exception of 1991 when wilt was no longer suppressed, the incidence of wilt throughout this investigation was highly correlated with both the arithmetic means and with ln values of *V. dahliae* densities in potato stems (Table 4). In 1990, soil

Fig. 3. Verticillium wilt on potato vines (Russet Burbank) **A,** on 12 September 1990 after three successive years of fallowing during the growing season and **B,** on 12 September 1990 after three successive green manure crops of sudangrass.

inoculum densities were positively correlated with both wilt and stem inoculum densities of *V. dahliae* in the low N plots (Table 5). Correlations with the root lesion nematode (*P. neglectus*) were not significant (Table 5).

Tuber yield and grade. In study 1, total yields of potato were increased from 15 to 30% in plots previously cropped with sudangrass compared to the other treatments (Table 7). Increases of U.S. #1 yields after sudangrass were 35% higher than after fallow and 17 and 23% higher than after Austrian winter pea and rape treatments, respectively. The yield of large tubers (>280 g), which may bring a premium price, also were increased with sudangrass over all other treatments, with yield increases ranging from 55 to 183%. Austrian winter pea produced 83 and 38% higher yields of large tubers than either the fallow or Dwarf Essex rape treatments, respectively. Although interaction effects between the N and cropping treatments were not significant, high N reduced ($P \leq 0.05$) total tuber yields by 6% and U.S. #1 yields by 13%.

As observed in study 1, the highest total tuber yields were produced after the sudangrass treatment. In study 2, however, the effect with corn was similar to sudangrass (Table 7). Corn and sudangrass increased total yields by 31 and 38%, respectively, compared to the fallow treatment and 13 and 20% compared to the oat and rye treatments. Total yields were 15% higher after oat and rye than after fallow. Similar results also occurred with either U.S. #1 or large tubers (>280 g). Sudangrass produced significant increases of 71, 41, and 33% in U.S. #1 tubers above the fallow, oat, and rye treatments respectively, but did not differ from the corn. The rye and corn treatments increased yields by 29 and 43%, respectively, above fallow. The effect on tuber size was similar. Again, sudangrass increased the yield of >280-g tubers from 22 to 267%. Corn, like sudangrass, increased yields of large tubers above the fallow, oat, and rye treatments from 50 to 200%. The oat and rye

TABLE 4. Correlations (*r* values) of percent wilt incidence of *Verticillium dahliae* CFU in potato stems

Date / Study	*r* values[z]				No. of comparisons
	13 Aug.	21 Aug.	27 Aug.	5 Sep.	
1990					
Study 1					
CFU/g	0.375**	0.575***	0.582***	0.446**	50
Log CFU/g	0.378**	0.449**	0.518***	0.508***	
Study 2					
CFU/g	0.456***	...	0.319*	0.280*	50
Log CFU/g	0.502***	...	0.435**	0.448**	
	20 Aug.	23 Aug.	28 Aug.	4 Sep.	
1991					
Study 1					
CFU/g	0.685***	0.698***	0.604**	0.642***	25
Log CFU/g	0.537**	0.667***	0.569**	0.577**	
Study 2					
CFU/g	0.066	0.066	0.150	0.021	25
Log CFU/g	0.113	0.127	0.173	0.064	

[z] *, **, and *** indicate $P = 0.05$, 0.01, and 0.001, respectively.

treatments, in turn, increased yields above fallow by 100%. As with study 1, the addition of N also reduced yield. Although interactions between cropping and N treatments were not significant, the main plot N treatment had a significant ($P \le 0.05$) effect on yield. The high N treatment reduced total and U.S. #1 yields and yields of >280-g tubers by 9, 19, and 25% respectively.

Adverse effects with the high N rate also occurred in the middle of the growing season in study 1 (24 July) and study 2 (7 August, data not shown). The high N treatment in study 1 reduced both the number and weight of tubers as well as the weights of above-ground plant parts. In contrast to the other treatments, sudangrass reduced both the number and weight of early tubers, while increasing the weights of above-ground plant parts. The effects of the rape treatments, on the other hand, which earlier had produced approximately twice the residual N concentration in soil as the fallow, Austrian winter pea, or sudangrass treatments (Table 1), produced intermediate effects between the sudangrass and fallow treatments. Early in the growing season, rape decreased tuber weights, while not increasing the above-ground stem and foliage weights, as was observed with sudangrass-treated areas. The total

TABLE 5. Correlations (*r* values) between ln values of green manure treatment means for *Pratylenchus neglectus* and *Verticillium dahliae* in soil with wilt incidence and *V. dahliae* reproduction in apical potato stems

	% Wilt[z]								ln *V. dahliae* in apical stems	
	Low N				High N					
Soil variable	13 Aug.	21 Aug.	27 Aug.	5 Sep.	13 Aug.	21 Aug.	27 Aug.	5 Sep.	Low N	High N
Study 1										
ln *P. neglectus*	−0.765	−0.513	−0.444	−0.506	−0.675	−0.468	−0.495	−0.428	−0.078	−0.227
ln *V. dahliae* in soil	0.784	0.934*	0.920*	0.974**	0.811	0.950*	0.995**	0.998**	0.892*	0.941*
	13 Aug.	27 Aug.	5 Sep.		13 Aug.	27 Aug.	5 Sep.			
Study 2										
ln *P. neglectus*	−0.720	−0.842	−0.862		−0.717	−0.693	−0.727		−0.402	−0.563
ln *V. dahliae* in soil	0.893*	0.881*	0.875*		0.942*	0.966**	0.975**		0.899*	0.774

[z] * and ** indicate $P = 0.05$ and 0.01, respectively.

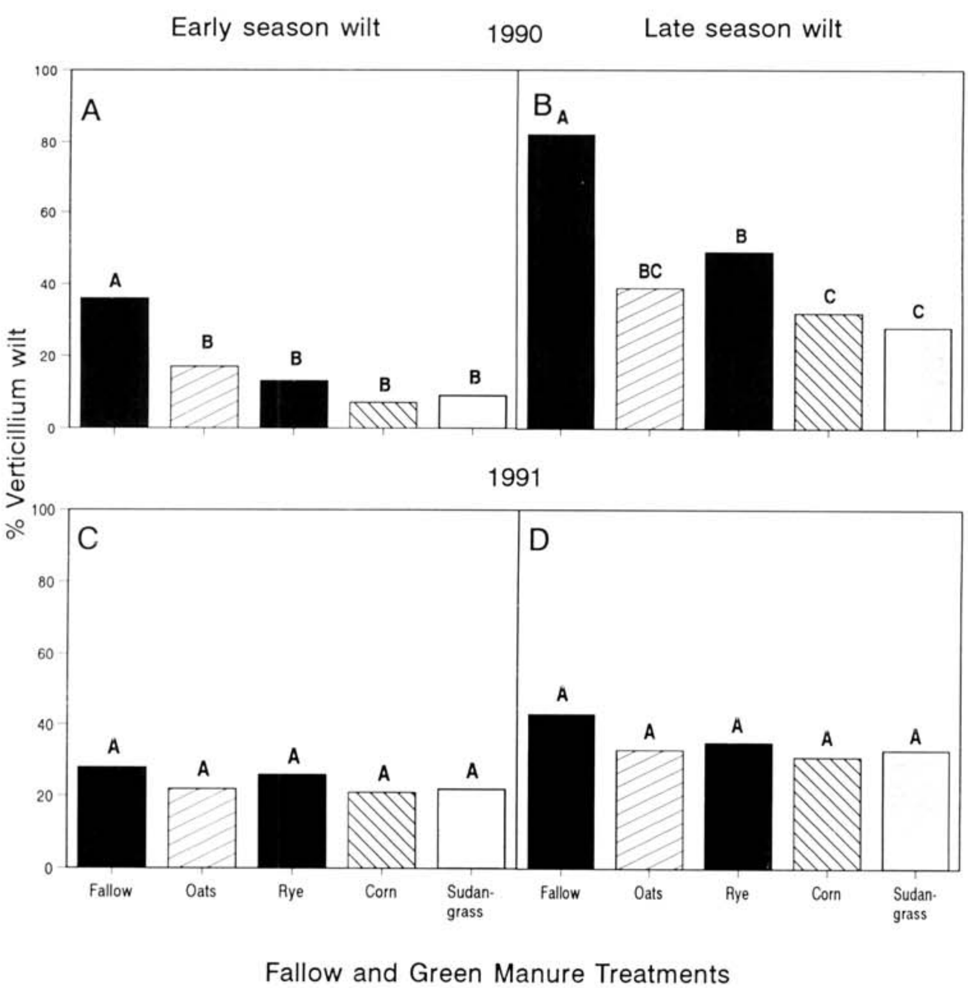

Fig. 4. Verticillium wilt incidence in study 2. **A,** Mean values of percent wilt incidence (in upper 8 cm of potato stems) observed early in the growing season of 1990 (2 through 13 August). **B,** Percent incidence of advanced wilt symptoms (dead to nearly dead) late in the growing season of 1990 (27 August through 5 September). **C,** Mean values of percent wilt (in upper 8 cm of potato stems) observed early in the growing season of 1991 (2 through 13 August). **D,** Percent incidence of advanced wilt symptoms (dead to nearly dead) late in the growing season of 1991 (27 August through 5 September). Different letters indicate significant differences between percent wilt ($P < 0.05$).

plant weight of potatoes grown in plots previously cropped to rape was significantly lower than those of potatoes grown after either Austrian winter pea or sudangrass.

When tubers were harvested early in study 2 (7 August, about 2 weeks after study 1), there was no evidence that either the N level or the previous crop influenced the number of tubers, but as with study 1, the high N treatment also reduced both total tuber weights and total plant weights. As in study 1, the effects of sudangrass increased ($P \leq 0.05$) above-ground stem and foliage dry weights when compared with fallow. The adverse effect of high N was further shown by the significant reductions in total potato yield.

When yield relationships were correlated with populations of pathogens in soil and disease symptoms and with inoculum densities of *V. dahliae* in potato stems (Table 8), the results were negatively correlated with factors involving *V. dahliae*, total yield, U.S. #1 yield, and the production of >280-g tubers. In contrast, these data were not significantly related with soilborne populations of *Pratylenchus*. There was, however, a negative relationship between the high N plots and indices of Rhizoctonia disease in study 2. In no other cases did significant relationships between *Rhizoctonia* and yield occur. The yields did not differ in 1991 for either study 1 or 2.

DISCUSSION

These results provide evidence that the suppression of Verticillium wilt of potato can be achieved with green manure treatments. Green manures from either sudangrass or corn were most effective of all the treatments studied. Although fallowing, particularly clean fallowing, is frequently reported to reduce the incidence of Verticillium wilt in succeeding crops of cotton (37), our studies showed no reduction of *V. dahliae* populations when land was left fallow. The level of wilt suppression we observed had practical significance because the soil inoculum density of *V. dahliae* in these studies was higher than the mean population levels observed in most commercial fields in Idaho (12).

Although sudangrass lowered soil populations of *V. dahliae* in study 1 and this treatment had the least disease, factors other than reduced inoculum also contributed to disease suppression. This was shown with study 2. In study 2, the inoculum densities in the sudangrass treatment did not differ significantly from the other treatments. Yet, the sudangrass green manure treatment reduced late-season wilt in 1990 to a lower value than either the rye or fallow treatments. Similar results have been observed with later studies (J. R. Davis, O. C. Huisman, D. T. Westermann, L. H. Sorensen, and A. T. Schneider, *unpublished data*).

Although the sudangrass treatment of study 1 showed a reduction of soil inoculum densities for *V. dahliae* after three consecutive years of treatment, this effect was not observed after 2 years in study 2. However, both experiments showed a similar degree of Verticillium wilt control and similar yield increases with sudangrass, whether the treatment was for 2 or 3 years. Although 1991 soil inoculum densities of both the Austrian winter pea and sudangrass treatments were lower ($P \leq 0.05$) than the other treatments (Table 2), the effects of these treatments on wilt were quite different. Treatment with sudangrass had significantly less wilt than with Austrian winter pea.

With the exception of Zn and Mn in the preplant-treated areas, we were unable to demonstrate a significant relationship between preplant nutrient concentrations and disease suppression (data not shown). Relationships between Mn and Zn and wilt suppression have been reported previously (6). Considerable work has been done in Russia on defining the relationships between Verticillium wilt resistance and minor elements, and from these studies, both Mn^{++} and Zn^{++} frequently have been associated with suppression of Verticillium wilt of cotton. Throughout our studies, soil levels of N failed to correlate with either wilt severity or *V. dahliae* colonization in potato stems. However, N was not deficient even at the lower rate. Rather than showing a beneficial effect with N, N application actually reduced yields in both studies. Increased N rates failed to affect either wilt incidence or growth of *V. dahliae* in the plant. The suppressive effect of high N on early-season yield reductions commonly occurs with potato (30) and is normally solved by applying N after the plants have formed tubers.

V. dahliae levels in soil and potato stems were correlated with incidence of wilt in both 1990 and 1991. Throughout our investigations, we were alert to the possibility that other pathogens might confound the interpretation of causal relationships. For this reason, frequent protective fungicide applications were applied to plots to minimize the severity of either early blight (*A. solani*) or aerial infections of *C. coccodes*. *C. coccodes* has been associated with both wilt symptoms and yield losses of potato (5,32). However, *C. coccodes* was not recovered from the apices of potato stems at any time. In certain locations and growing seasons, the recovery of *C. coccodes* from stem apices is associated with foliar infections of this pathogen and have been associated with severe wilt symptoms in Idaho (J. R. Davis, O. C. Huisman, L. H. Sorensen, and A. T. Schneider, *unpublished data*). Although the presence of this pathogen in field soils, stem bases, and roots has not been associated directly with early death of potato, it may interact with

TABLE 6. Effects of green manure treatments on infection of Russet Burbank potato by *Verticillium dahliae*

Treatment	*V. dahliae* (CFU/g apical stem)	
	22 Aug. 1990	20 Aug. 1991
Study 1		
Fallow	479 A[y]	1,352[z]
Austrian winter pea	291 A	2,628
Sudangrass	60 B	646
Dwarf Essex rape	290 A	1,352
Bridger rape	449 A	1,532
Study 2		
Fallow	894[z]	1,772[z]
Oat	792	1,936
Rye	656	1,604
Sudangrass	556	1,020
Corn	382	1,652

[y] Analyses of variance based on log values of CFU. Different letters denote significant differences within the column, $P \leq 0.05$.
[z] Differences not significant.

TABLE 7. The effect of green manure and N treatments on potato yield in 1990

Treatment	Yield (metric tonnes ha^{-1})[y]		
	Total	U.S. #1	Tubers >280 g
Field study 1			
Cropping treatment			
Fallow	30 B	20 B	6 C
Austrian winter pea	34 B	23 B	11 B
Sudangrass	39 A	27 A	17 A
Dwarf Essex rape	32 B	22 B	8 BC
Bridger rape	32 B	22 B	9 BC
Nitrogen rate			
Low (N_1)	34 A	24 A	11[z]
High (N_2)	32 B	21 B	9[z]
Field study 2			
Fallow	26 C	14 C	3 D
Oat	30 B	17 BC	6 C
Rye	30 B	18 B	6 C
Sudangrass	36 A	24 A	11 A
Corn	34 A	20 AB	9 B
Nitrogen rate			
Low (N_1)	33 A	21 A	8 A
High (N_2)	30 B	17 B	6 B

[y] Different letters denote significant differences within a column, $P \leq 0.05$.
[z] Interactions between N × green manures treatments not significant.

TABLE 8. Correlations (r values) between green manure treatment means for diseases and pathogens with yield and grade of potato tubers in 1990

Disease and pathogen variables	Total yield (metric tonnes ha^{-1})[w]		U.S. #1 (metric tonnes ha^{-1})[w]		Tubers >280 g (metric tonnes ha^{-1})[w]	
	Low N rate	High N rate	Low N rate	High N rate	Low N rate	High N rate
Study 1						
% Wilt incidence[x]	−0.929*	−0.993**	−0.880*	−0.774	−0.972**	−0.932*
V. dahliae CFU/g stem	−0.817	−0.944*	−0.809	−0.867*	−0.748	−0.903*
V. dahliae log CFU/g stem	−0.896*	−0.993**	−0.840	−0.783	−0.868*	−0.925*
V. dahliae CFU/g soil	−0.968*	−0.958**	−0.942*	−0.744	−0.986**	−0.963**
V. dahliae log CFU/g soil	−0.978*	−0.980**	−0.943*	−0.713	−0.994**	−0.971**
Rhizoctonia index[y]	−0.517	0.001	−0.598	0.379	−0.388	−0.315
% *Rhizoctonia*-free stems	−0.423	0.195	−0.511	0.656	−0.364	−0.122
% Stems with severe *Rhizoctonia*[z]	0.191	−0.539	0.170	−0.702	0.151	−0.407
Pratylenchus/500 cm^3 soil	−0.120	0.161	−0.208	0.465	0.037	−0.145
Log *Pratylenchus*/500 cm^3 soil	0.152	0.438	0.051	0.707	0.298	0.140
Study 2						
% Wilt incidence	−0.947*	−0.839	−0.928*	−0.740	−0.929*	−0.798
V. dahliae CFU/g stem	−0.659	−0.702	−0.640	−0.593	−0.596	−0.731
V. dahliae log CFU/g stem	−0.762	−0.951**	−0.730	−0.960**	−0.786	−0.961**
V. dahliae CFU/g soil	−0.872*	−0.861	−0.827	−0.701	−0.828	−0.817
V. dahliae log CFU/g soil	−0.832	−0.805	−0.776	−0.638	−0.764	−0.774
Rhizoctonia index	−0.426	−0.876*	−0.414	−0.949**	−0.484	−0.873*
% *Rhizoctonia*-free stems	0.543	0.396	0.561	0.534	0.650	0.370
% Stems with severe *Rhizoctonia*	−0.198	−0.698	−0.175	−0.703	−0.207	−0.624
Pratylenchus/500 cm^3 soil	0.398	0.059	0.392	−0.003	0.445	−0.032
Log *Pratylenchus*/500 cm^3 soil	0.692	0.376	0.674	0.335	0.669	0.335

[w] * and ** indicate $P = 0.05$ and 0.01, respectively.

[x] Percent stems that showed evidence of severe wilt (>75% of foliage dead to nearly dead).

[y] Higher values denote greater disease severity.

[z] Stems showing cut-off with severe infection.

V. dahliae and have an additive effect on potato early dying (32). However, when CFU of *C. coccodes* was quantified from basal stems and tuber stem ends, there was no significant relationship with the effects of green manure treatments.

Sholte and s'Jacob (39) reported that *P. neglectus* and *R. solani* may have a synergistic effect with *V. dahliae* on potato yield. They also concluded that *P. neglectus* may facilitate the infection process of *V. dahliae* (38). However, in our study there were no significant interactions between *V. dahliae*, *P. neglectus*, and the incidence of Rhizoctonia disease. Although aldicarb (an insecticide-nematicide) was used for insect control with these investigations, it is doubtful that this lack of relationship with *P. neglectus* can be explained by its use. Earlier field studies (14) on the effect of aldicarb have shown no significant relationships between *P. neglectus* and *V. dahliae* infections for either Russet Burbank or Butte potato. This lack of effect of *P. neglectus* and *V. dahliae* infection was further supported by the fact that the Russet Burbank cultivar is susceptible to *P. neglectus*, whereas Butte is highly resistant.

During 1990, both corn and sudangrass treatments increased yield and quality of potato tubers, while the fallow treatment consistently had the lowest yields. Although differences among these treatments in *Verticillium* severity continued into the second year of potato cropping in study 1, yields were not different. Plant pathogens are not the only factors influencing potato yield. Our studies have shown that *V. dahliae* root infections may account for about 39% of the field variability related to yield (J. R. Davis, O. C. Huisman, D. O. Everson, L. H. Sorensen, and A. T. Schneider, *unpublished data*). Sholte et al. (40) stated that growing potatoes at increasing frequencies in a rotation may lead to substantial yield losses even in the absence of pests or pathogens that are known to reduce yield. Both our current studies and previous investigations (19) support this supposition.

Although the explanation for the effect of green manures is not completely understood, in ecological studies accompanying this investigation several lines of evidence have suggested biological control: (i) the direct effects of treatments on soilborne *V. dahliae* populations alone do not account for disease suppression; (ii) root-colonization data consistently have shown *V. dahliae* suppression on potato roots with green manure treatments to be highly correlated with both disease incidence and potato yield (16,17,26), even though treatments have had no effect on inoculum densities of *V. dahliae* in soil; and (iii) disease reduction has been highly correlated with both nonspecific microbial activities and major changes in microbial populations, as evidenced by increases of nonpathogenic *Fusarium* spp. (e.g., *F. equiseti*) (17,25,26). These relationships will be discussed in a separate paper.

As pesticide and fumigant options are withdrawn, we will become increasingly dependent on alternative methods to manage Verticillium wilt of potato. In addition to resistant cultivars, soil solarization, and management of crop nutrition and irrigation, green manures may become an effective tool for suppression of this disease. Not only do green manures provide an alternate approach for disease control, they may increase nutrient availability (31), reduce groundwater contamination, and stimulate beneficial microflora in soil (4).

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