AN ABSTRACT OF THE THESIS OF

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Effect of a sudangrass green manure in two soil types on the activity, populations and community structure of soil microorganisms, populations of *Verticillium dahliae* in soil and on potato roots, and potato early dying, were evaluated in a field microplot experiment in the Columbia Basin. Potato cv. Russet Burbank was grown in identical green manure and fallow soil treatments transported from Idaho and Washington where sudangrass previously suppressed or enhanced early dying of potatoes, respectively. Incorporation of sudangrass increased total microbial activity (TMA) by 46.2 and 30.1 % in the Idaho soil in 1996 and 1997, and by 43.0 % in the Washington soil in 1996 only. Neither green manure or soil type, however, affected soil populations of *Fusarium*, total bacteria, or actinomycetes. Across soil type, fluorescent pseudomonad populations were unaffected or increased by 107 % in 1996 and 1997, respectively. Although not repeated across years, *Fusarium* root populations were 19.7 and 28.3 % higher in sudangrass treated soil from Washington in 1996 and Idaho in 1997, respectively, but the proportion

of *Fusarium* species were similar across soil types. Bacterial rhizosphere communities, based on sole-carbon-source utilization patterns on Biolog GN microplates, did not differ among the soil types or green manure treatments. Across soil type, *V. dahliae* soil and root populations were unaffected in 1996, but were lower by 20.4 and 41.2 % in Idaho sudangrass soil treatments in 1997. Apical stem populations of *V. dahliae* and disease severity, however, did not differ among the treatments. Although tuber yield in Washington soil was 31.5 % higher than Idaho soil in 1996, yield was not affected by a sudangrass green manure. Because suppression of early dying of potato observed in Idaho was not replicated in transported soil in the Columbia Basin, the macroenvironment may interact with the sudangrass green manure to regulate the effect, or lack of effect on disease. TMA is not an indicator of disease suppressive ability of a soil following sudangrass as activity increased despite a lack of effect on disease. Based on this study, there is no evidence for differences in microbial populations or communities between the Idaho and Washington soils that could explain the suppression or enhancement of early dying of potato by a sudangrass green manure.

Influence of a Sudangrass Green Manure on Microorganisms and Early Dying of Potatoes in Two Soils

by

Robin L. Parks

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CONTRIBUTION OF AUTHORS

Dr. Mary Powelson was involved in the study design, data interpretation, and writing of each manuscript. Marlys Cappaert was involved in the design, data collection and interpretation, and statistical analysis for the experiment. Dr. Ken Johnson assisted in the study design and writing of each manuscript.

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INTRODUCTION

GREEN MANURES

Green manures are crops grown specifically to be tilled into the soil as fresh organic matter. The agronomic benefits of green manures include improved soil physical structure, increased soil nutrient levels and organic matter, and in certain cases, plant disease suppression. Crops that produce abundant foliage or leguminous crops, which increase soil nitrogen content, are preferred as green manures. Decomposition of the organic matter yields humus which helps bind soil particles together and improve soil nutrient and moisture availability. Additional benefits of green manuring include protection of soil from wind or water erosion, interruption of continuous cropping sequences, and provision of an extra cash crop as feed or seed from some green manure crops. Economic profit can accompany these benefits when alternative agriculture practices such as green manures are combined with conventional agriculture (72).

POTATO EARLY DYING

The soilborne fungus *Verticillium* causes vascular wilt diseases in a variety of ornamental and agricultural crop hosts. The species *V. dahliae* Kleb. is the primary causal pathogen of potato early dying, also known as Verticillium wilt of potato, in most regions

of the United States. Potato early dying is a major constraint to potato production in many areas of the U. S. (74). *V. dahliae* can survive in soil as microsclerotia, microscopic resting structures, for at least 8 years in the absence of a susceptible host. These structures are produced within host tissue and released into the soil as the host tissues decay. *Verticillium* occurs naturally in soil or can be introduced to fields in infected plant material. In the presence of host roots, the microsclerotia germinate and germ tubes penetrate the growing root tip. The fungus colonizes xylem systemically, producing mycelium and conidia. Growth and enzyme activity by the pathogen blocks xylem vessels, causing acropetal progression of chlorosis and necrosis of leaves. The premature defoliation caused by the vascular wilt reduces net photosynthesis, and contributes to lower crop yields (79).

Recommended management strategies for potato early dying include soil fumigation, soil solarization, crop rotation, and resistant cultivars. These strategies, however, can be difficult to implement due to expense and practical limitations. For example, soil solarization is effective only in environments that can provide enough solar energy to heat the soil to a temperature high enough to reduce soil inoculum levels. Crop rotations are often impractical as the microsclerotia can survive for many years. Few resistant cultivars are accepted by the industry (75).

EFFECT OF GREEN MANURES ON PLANT DISEASES

Green manure crops are being investigated as alternative management tactics for Verticillium wilt of several crop hosts (14,18,87). If the improved soil health and nutrient levels (6,85) following a green manure crop can be combined with plant disease

suppression, crop yields can increase and agrochemical use can decrease. A variety of types of organic soil amendments have been reported to suppress diseases caused by fungi and nematodes whereas other amendments do not affect or even enhance disease severity. Diseases caused by nematodes have been suppressed by green manure crops of legumes (76), various cereals and vegetables (7), rapeseed (48,65), and sudangrass (64). Conversely, sudangrass and sorghum-sudangrass (58), as well as a variety of other vegetable crops (7) have not suppressed disease or nematode populations in other experiments.

Studies on the potential of a variety of organic soil amendments to suppress fungal plant disease have met with similar successes and failures. A corn cover crop or green manure decreased Rhizoctonia hypocotyl rot of snapbean whereas tomato, cabbage and pepper had no effect (60). Cabbage and cellulose amendments were among a variety of organic amendments that reduced *Thielaviopsis basicola* inoculum and bean root rot (73). Cabbage residue amendments combined with soil solarization reduced pathogen inoculum and severity of cabbage yellows (77) and gummy stem blight of watermelon (53). Even the addition of stable or fowl manure suppressed Sclerotinia soft rot of lettuce (1). Among a variety of crucifers, a white mustard green manure reduced *Aphanomyces euteiches* soil populations and severity of root rot of peas (66). Yet, if a green manure crop is a susceptible host to the pathogen, inoculum and disease severity can increase, as seen with lettuce drop, caused by *Sclerotinia minor* (56).

For potato early dying, a similar pattern of variable success has been obtained for suppression of this disease with organic amendments. In a greenhouse study, chitin, wheat, and green clover amendments decreased *V. dahliae* soil populations (50).

Suppression of Verticillium wilt of peppermint and potato followed a corn and a green pea-sudangrass rotation crop, respectively (25,39). A broccoli green manure decreased soil inoculum density and Verticillium wilt of cauliflower (87). Two recent field experiments investigating the potential of green manures to suppress potato early dying also illustrate the variable success of this management tactic. Davis et al (18) reported suppression of Verticillium wilt of potato in Idaho following a variety of green manures, with the largest reduction caused by sudangrass. However, when a sudangrass green manure, identical to the treatment used in Idaho, was grown in the Columbia Basin of Washington, the green manure increased Verticillium wilt in the subsequent potato crop (14). Reasons that may explain these conflicting results are the focus of our research project.

Because the studies were performed in different locations, under different environments, the main objective of the project was to determine whether the macroenvironment was the main regulator of the effect of sudangrass on potato early dying. The severity of potato early dying is known to be influenced by temperature, soil moisture, and soil nutrient levels (79). Green manure and fallow soil treatments in both Idaho and Washington, soil transportation from Idaho to the Columbia Basin, and a field microplot experiment allowed us to directly compare identical soil treatments under one environment and identical irrigation and fertilization practices.

A second objective of the study was to investigate the effect of this green manure on microbial populations, including *V. dahliae*, in both Idaho and Washington soil. Whether a sudangrass green manure affects *V. dahliae* inoculum is unclear. Similarly, the effect of soil type on this potential reduction in *V. dahliae* inoculum by sudangrass is also

unknown. Although sudangrass consistently suppressed the incidence of Verticillium wilt in Idaho, Davis et al (18) did not observe a consistent reduction of inoculum to account for the disease response. Cappaert and Powelson (14) observed no consistent effect of sudangrass on *V. dahliae* soil populations in the Columbia Basin while disease severity was increased.

Because inoculum reductions were not correlated with disease suppression following the use of a green manure and because total soil microbial activity was negatively correlated with disease incidence (19), Davis et al (18) proposed that some form of biological control may be responsible for disease suppression. The incorporation of a green manure is known to increase populations and activity of microorganisms in arable soil (11,55,63,82). Whether populations in the two soils differ or if populations of certain microorganisms are favored by the incorporation of a sudangrass biomass and if these populations affect *V. dahliae* or potato early dying is unknown. Due to on-going field experiments at the original field study locations in Idaho and Washington, a unique opportunity was available to directly compare the microbial populations in the Idaho and Washington soil and whether the influence of sudangrass on microbial populations or activity differs between the two soils when the soil are placed in a common environment.

CHAPTER 1

Influence of a Sudangrass Green Manure on Microbial Activity, Populations, and Community Structure in Two Soil Types

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ABSTRACT

The effect of a sudangrass green manure in two soil types on populations of *Verticillium dahliae*, total microbial activity, microbial populations and community structure was evaluated in a microplot field experiment in the Columbia Basin. Potato cv. Russet Burbank was grown in soil from Washington and Idaho subjected to identical sudangrass and fallow treatments. Compared to the fallow control, sudangrass increased total soil microbial activity by 46.2 and 30.1 % ($P \leq 0.05$) in the Idaho loam in 1996 and 1997, respectively. A similar increase was seen in Washington sandy loam, by an average 43.0 % ($P \leq 0.05$) in 1996. No increase was observed in 1997. Incorportation of sudangrass did not affect soil populations of *Fusarium*, total bacteria, or actinomycetes in either soil type, but increased fluorescent pseudomonad populations by 107 % ($P = 0.0008$) across soil types only in 1997. *Verticillium dahliae* soil and root populations were unaffected in 1996, but were decreased in Idaho treatments, by 20.4 and 41.2 % ($P \leq 0.05$), respectively, in 1997. Higher *Fusarium* root populations, by 19.7 and 28.3 % ($P \leq 0.05$) were recovered from sudangrass soil treatments from Washington in 1996 and Idaho in 1997, respectively. Similar increases in *Fusarium* species isolated from roots were observed between the soil types. Characterization of rhizosphere bacterial communities using a Biolog GN microplate technique revealed no differences among the soil types or green manure treatments. Because microbial activity increased in both soil types following sudangrass, and microbial populations and community structures did not differ between the soil types, whether microorganisms have a biological control role in regulating the response of potato early dying to a sudangrass green manure is unknown.

INTRODUCTION

Agricultural management practices can influence the size and activity of the microbial biomass in the soil. The addition of nutrients to soil, from inorganic fertilizers to organic residues, increases root biomass, root exudates, and crop residues, therefore providing more substrates for microbial growth and activity (82). Studies in arable soil demonstrate that green manures, a cropping practice in which green biomass of cover crops is tilled into the soil, can significantly change soil biological properties including increased populations and activity (11,55,63).

The incorporation and decomposition of green manure biomass, and this resulting change in soil biology, may directly or indirectly affect soilborne plant pathogens. Fungicidal breakdown products of cruciferous green manures can act as biofumigants to directly reduce the soil inoculum density (66,87). Alternately, if a green manure crop is a host to a pathogen, inoculum and disease severity in the following crop can increase (56). Non-cruciferous rotation crops, green manures, or crop amendments that are non-hosts to pathogens also have been observed in a variety of studies to influence fungal pathogen populations or disease severity, although the mechanism of these effects are unknown (1,10,50,53,60,73). As a cover crop or green manure, these crops may sustain or selectively encourage the growth and activity of non-pathogenic microorganisms that may compete with or be antagonistic to pathogens. Alternately, biological changes in the soil following crop rotations, plant residue incorporation, or soil solarization have been proposed to be beneficial to plant growth which could contribute to disease suppression

(10,51,53). Either mechanism could account for a green manure creating a disease suppressive soil.

Results of an Idaho study (18,19) suggested that changes in soil microbial populations or activity following a sudangrass green manure may be responsible for the suppression of Verticillium wilt of potato. Verticillium wilt, also known as potato early dying is a major constraint to potato production throughout the United States (74,75). This vascular wilt disease, characterized by early senescence and subsequent reduced yields, is caused by the soilborne fungus *Verticillium dahliae*. Potato early dying is particularly difficult to manage as the soilborne microsclerotia of *V. dahliae* can remain viable for many years in the absence of host plants. In the presence of host roots, microsclerotia germinate and germ tubes penetrate the root tip. The fungus can systemically colonize potato by producing mycelium and conidia which block vascular vessels, producing the characteristic unilateral wilt of leaves, reducing photosynthesis, and resulting in early senescence. As only a few of commercially grown potato cultivars have some resistance to *Verticillium*, reduction of soilborne inoculum density is the primary goal of management. Because the soilborne microsclerotia can survive for up to 8 years in the absence of a host, a short-term (< 4 year) crop rotation is not an effective management tactic. Irrigation management and soil solarization are known to suppress disease severity but the most widely used practice is soil fumigation. Because of the expense and increased government regulation of soil fumigants, and climatological restrictions for effective soil solarization, alternative management strategies are being sought. Theoretically, this disease could be suppressed if a cultural practice, such as a green manure, favored the activity of natural soil microflora which would either compete

with *V. dahliae* for root colonization sites or soil nutrients, or be directly antagonistic to the microsclerotia.

The effect of a green manure such as sudangrass on microorganisms may be analogous to the shifts in components of native soil microflora that have been proposed to follow soil solarization (35). These shifts may account for the long-lasting increased crop growth following a solarization treatment. For example, observed changes include increases in plant-growth promoting fluorescent pseudomonads with simultaneous decreases in plant growth suppressive organisms or minor root pathogens (35). Fluorescent pseudomonads may promote plant growth by suppressing the activity of soilborne pathogens or plant growth deleterious microorganisms through aggressive root colonization, antibiotic production (35), or nutrient competition (83). Changes in actinomycete populations, and differences between locations, may be responsible for increased plant growth in the presence of a root pathogen (10). *Fusarium* species also have been indicated to be involved in induced resistance (68) or correlated with disease reduction (19).

The results from the Idaho study (18) indicated that the suppression of Verticillium wilt following a sudangrass green manure may be due to similar shifts in soil microflora. A sudangrass treatment reduced pathogen soil populations in one of the Idaho studies, but not in another, although Verticillium wilt severity was reduced in both (18). Therefore, the disease suppression could not always be attributed to a reduction in inoculum density. Also, there was a significant, negative correlation between soil microbial activity and wilt severity in green manure treatments. Populations of *Fusarium*

equiseti in particular are believed to be associated with biological control in the Idaho studies (19).

Contrary results, however, were observed in a green manure study in Washington. Cappaert and Powelson (unpublished data) reported that sudangrass treatments identical to those used in Idaho, increased disease severity (14) and did not consistently affect *V. dahliae* soil populations. Still, as in Idaho, the green manure increased soil microbial activity in the Columbia Basin of Washington (14). Therefore, there was a positive correlation between soil microbial activity and wilt severity following sudangrass in Washington. If biotic soil factors are involved in this disease response, then perhaps the activity that is increased in the Washington soil is due to populations different from those in the Idaho soil such that no competitors or antagonists to *V. dahliae* are favored by a sudangrass green manure.

We therefore wanted to determine whether the soil microflora differ between the Idaho and Washington soils and whether sudangrass affects these variables in either soil. Due to on-going sudangrass green manure experiments in the original Idaho and Washington study sites, and a microplot field experiment technique, we took advantage of a unique opportunity to directly compare, in one location, the microbial activity and composition of the two soils after identical cropping sequences. Potatoes were grown in microplots containing soil from the original Idaho and Washington study sites. The objective of this study was to determine whether a sudangrass green manure affects microbial responses, including activity, populations, and community physiological characterization in either soil type. Because seasonal variations in activity and populations are common (55), measuring soil microbial responses at the same location on

the same dates could allow for more reliable comparisons between soils. Populations of *Verticillium dahliae* were measured to determine whether sudangrass affected inoculum density or potato root colonization in either soil. The rate of hydrolysis of fluorescein diacetate was used as a measure of microbial activity as in the original Idaho and Washington studies (14,19,81). Assuming that the activity of no single group of organisms, but rather the enhanced populations of an assortment of microorganisms would influence disease severity, broad categories of microorganisms were studied. By estimating soil populations, the effect of sudangrass was measured on bacteria, actinomycetes, *Fusarium*, and fluorescent pseudomonads, all of which have been proposed to be active in disease suppressive soils (10,12,50,51,68,83). Metabolic properties of the total rhizosphere microflora population in each soil treatment also was characterized using gram-negative Biolog microplates to further characterize potential differences between the Idaho and Washington soils, and if a sudangrass green manure treatment can change these properties.

MATERIALS AND METHODS

Soil treatment origins.

A microplot field experiment was conducted in 1996 at the Hermiston Agricultural Research and Extension Center in the Columbia Basin of northcentral Oregon and in 1997 at the AgriNorthwest Research Facility in the Columbia Basin of southcentral Washington. Treatments were created by the transfer of soil from established field experiment plots in southcentral Washington and southeastern Idaho to the

microplot field site. From these sites, soil was removed from plots that had been subjected to fallow or sudangrass green manure treatments (Table 1.1).

For the Idaho soil treatments, sudangrass (*Sorghum vulgare* var. *sudanense* variety HS-33) was grown as a green manure at the University of Idaho Research and Extension Center at Aberdeen, ID (elevation 1341 m, 130 day growing season, Delco loam soil type) in 1995. Sudangrass seed was drilled in late May and plants were disked in late August to constitute a 1 yr green manure treatment. In 1996, sudangrass was again grown in the same plots to establish a 2 yr green manure treatment. Weed-free fallow control plots also were maintained in 1995 and 1996. For the Washington soil treatments, sudangrass (*Sorghum vulgare* var. *sudanense*) was grown as a consecutive green manure in 1994, 1995, and 1996 at the AgriNorthwest Research Facility, Plymouth, WA (elevation 185 m, 150 day growing season, Quincy fine sandy loam soil type) along with weed-free fallow control plots. Sudangrass was drilled 15 May (99 kg/hA) and disked 15 August. In 1996, these field plots provided soil that had been cropped for 1 or 2 yr to sudangrass. In 1997, 2- and 3-yr green manure treatments were used.

Microplot establishment.

In early April 1996, fallow and 1 yr sudangrass green manure soil from Idaho was hand-shoveled into separate 730-L wooden crates and transported by a semi-truck to the study site in Oregon where it was transferred to cylindrical plastic pots (28-L, 35 cm high X 29 cm inside diameter) (Anderson DIE MFG® #6 Deep, OBC NW Inc., Canby, OR) with a hole 5.5 cm in diameter bored in the bottom for drainage. The fallow, 1 and 2 yr sudangrass green manure soil from Washington was hand-shoveled directly into the

plastic pots and transported to the Oregon experiment site in mid-April. The five treatments were arranged in a randomized complete block design and replicated fifty times. Pots were buried upright to an approximate depth of 30 cm in rows spaced 1.5 m apart on 0.61 m centers.

TABLE 1.1. Sudangrass green manure and fallow treatments established in Idaho and Washington and used in a microplot experiment in the Columbia Basin.

	Growing Season					
	Field Treatments			Columbia Basin Microplot Experiment[a]		
Field Plot	1994	1995	1996	Treatment	1996	1997
ID-F S1/S2[b]		Fallow	Fallow	ID-F	+	+
		Sudangrass	Sudangrass	ID-S1	+	-
				ID-S2	-	+
WA-F S1/S2[b]		Fallow	Fallow	WA-F	+	+
		Sudangrass	Sudangrass	WA-S1	+	-
S2/S3[c]	Sudangrass	Sudangrass	Sudangrass	WA-S2	+	+
				WA-S3	-	+

[a]Potatoes were grown in microplots in 1996 and 1997 in the Columbia Basin. Soil in microplots originated from green manure treatments in large scale field plots in Idaho (ID) and Washington (WA) established between 1994 and 1996.
[b]Plot yielded 1 yr (S1) and 2 yr (S2) sudangrass green manure treatments for microplots in 1996 and 1997, respectively.
[c]Plot yielded 2 yr (S2) and 3 yr (S3) sudangrass green manure treatments for microplots in 1996 and 1997, respectively.

During the second week of April 1997, fallow and 2-yr green manure soils from the Idaho location were transported to Washington as in 1996. Soil that had been fallow or cropped for 2 or 3 consecutive years to a sudangrass green manure at the Washington site was hand-shoveled directly into pots. A sixth treatment was created by mixing equal amounts of the Idaho 2 yr sudangrass soil and the Washington fallow soil in a 0.7 m^3 cement mixer. Experimental design and plot establishment were as described in 1996.

Generation III seed potatoes (*Solanum tuberosum* cv Russet Burbank), obtained from Madras Produce Co. in Madras, OR, were cut into single eye seed pieces with a 2.5 cm melon scoop. Seed pieces were presprouted for 10 days in sterile moist vermiculite at 20 C. During the last week of April in 1996, one seed piece was planted 8 cm deep in the center of each of 200 pots and two seed pieces were planted in each of 50 pots for early season destructive sampling in 10 blocks. During the first week in May in 1997, one seed piece was planted in 240 pots and two seed pieces in 60 pots for early season sampling. The field was irrigated with a line source in 1996 and with a lateral move system in 1997. In late May 1996, each pot was fertilized by hand with a soluble mixture of Peters Professional® 30-10-10 NPK fertilizer to provide 26.9 kg of N, 8.9 kg of P, and 8.9 kg of K per ha. In 1997, dry fertilizer was applied to the Washington plots in early April, prior to microplot establishment at a rate of 168 kg/ha N, 168 kg/ha P, 392.9 kg/ha K, 22.41 kg/ha Mg, and 2.23 kg/ha Bo. In early June, this same fertilizer mixture was applied by hand to the microplots containing Idaho soil. In 1997, a N-P-K solution (10-30-10) was injected into the irrigation system throughout the season.

In 1996, weeds were controlled in the interplot area by applying the herbicide metribuzin (Sencor®, Bayer Corp., Kansas City, MO) at planting, in early July, and in late July. Microplots were hand weeded weekly beginning in July. In early June, imidacloprid (Admire® 2 F, Bayer Corp., Kansas City, MO) was injected into each pot with a syringe at a rate of 3.36 kg/ha to prevent Colorado potato beetles. Metribuzin was sprayed prior to field establishment in 1997 and rows were hand weeded throughout the season. In late May, sethoxydim (Poast®, BASF, Research Triangle Park, NC) was sprayed between the rows to control volunteer corn. In early July, disulfoton (Di-

syston®, Bayer Corp., Kansas City, MO) was sprayed on the field to control a Colorado potato beetle infestation.

Sampling dates.

Twenty replicate microplots per treatment, for a total of 100 pots in 1996 and 120 pots in 1997, were designated for disease assessment, stem assay, and fresh tuber yield. Randomly selected plants and soil were harvested from the remaining microplots throughout the growing season. Soil was sampled at planting in 1996 and 1997 and both soil and plants were sampled at 3, 5, 7, and 9 wk (1997), and 11 wk (1996) following 80% emergence. The degree days after planting (DDAP) at each sampling date were calculated by the methods of Baskerville and Emin (5).

Soil and root sampling.

Soil samples were taken from the top 20 cm of randomly selected microplots with a hand trowel, placed in plastic bags and transported on ice to Corvallis, OR where they were stored at 5 C until processed within 48 hr for soil microbial activity and microbial populations. A total of five and seven treatment replicate samples were collected at each sampling date in 1996 and 1997, respectively. The entire root ball of potato in randomly selected microplots was harvested and placed in a paper bag. The roots were transported on ice to Corvallis, OR where they were stored at 5 C and processed within 24 hr. A total of 10 treatment replicate samples were represented. In 1996, two plants were sampled at the two early season sampling dates from each of five replicate pots per treatment. In

1997, at each of these early plant sampling dates, one plant was sampled from each of 10 replicate pots.

FDA hydrolysis.

Total soil microbial activity, represented by the rate of hydrolysis of flourescein diacetate (3', 6'-diacetylfluorescein [FDA]) in an aliquot of soil, was measured 24 hr after sampling following the procedures described by Schnurer (81). Briefly, the spectrophotometer was calibrated with two sets of standards per treatment using soil composites which contained an equal amount of soil (5 - 10 g) from each of five replicates per treatment. FDA (Sigma® Chemical Co., St. Louis, MO) was dissolved in acetone (reagent grade, Fisher Scientific, Atlanta, GA) and stored as a stock solution (2 mg/ml) at -15 C. To produce the set of standards, a series of FDA aliquots (0, 50, 100, 150, and 200μL) diluted in 5 ml of a phosphate buffer (K_2HPO_4 and KH_2PO_4) was boiled in test tubes for 1 hr to hydrolyze the FDA. The boiled FDA aliquots and 20 ml phosphate buffer were added to approximately 5 g of the soil composite for each treatment in 250-ml Erlenmeyer flasks. To determine the percent soil moisture, 15 g samples of each of the soil composites were dried for 10 days at room temperature and re-weighed. A total of 5 g of each of the five replicate soil samples was added to a 250 ml erlenmeyer flask containing 15 ml buffer and 200μL of FDA. The FDA was added simultaneously to all flasks which were then incubated for 30 min at 20 C on a rotary Lab-Line® Orbit Shaker at 200 rpm. The hydrolytic reaction was stopped by adding 20 ml of acetone to each sample and standard flask. The solution in each flask was filtered

through folded Whatman® #1 filters in glass funnels into glass test tubes. The filtrate was transferred to 4.5 ml disposable plastic cuvettes (Fisher Scientific, Atlanta, GA).

Amount of fluorescein, a product of FDA hydrolysis, in each sample was quantified as absorbance at 490 nm (A_{490}) with a spectophotometer (Model 8452A Diode Array, Hewlett® Packard, Palo Alto, CA). The spectrophotometer was calibrated with the set of standards for each treatment. Concentration of hydrolyzed FDA in each of the samples was calculated with spectrophotometer software (89532Q UV-VIS, Hewlett® Packard, Palo Alto, CA). Total soil microbial activity was calculated as grams FDA hydrolyzed per hour per gram of dry soil.

Microbial soil populations.

Soil samples were plated on selective media 48 hr after collection. One gram of soil from each microplot was serially diluted to 10^{-6} g/ml in 0.1% water agar. To obtain counts of approximately 10 to 200 colonies per plate, specific dilutions were chosen for each media type based on counts from previous experiments and the first sampling of each year. For each soil sample, 200 μL aliquots from each of two dilutions, were pipetted onto separate media plates and spread with a flame sterilized glass rod.

Soil was plated on Nash-Snyder agar medium modified with streptomycin sulfate to select for *Fusarium* species (67), on high pH water agar for actinomycetes (water agar adjusted to pH 10.5 with 1N NaOH), on 10% tryptic soy agar for culturable aerobic bacteria (61), and on King's B agar for fluorescent *Pseudomonas* species (54). Nash-Snyder and high pH water agar plates, and tryptic soy agar and King's B agar plates were incubated for 7 and 2 days, respectively, at room temperature (20-24 C). A short wave

lamp (UV - 254 nm, Mineralight®) was used to illuminate and count fluorescent pseudomonad colonies. Microbial populations were calculated as colony-forming-units per gram soil (CFU/g soil).

Verticillium dahliae. Approximately 20 g of each soil sample was dried for at least 14 days in plastic weigh boats at room temperature (20-24 C). The dried soil was ground with a ceramic mortar and pestle and two 0.20 g subsamples per sample were plated on Sorensen's modified NP-10 medium (86) using an Andersen air sampler (Andersen Samplers Inc., Atlanta, GA) (13). Plates were incubated at room temperature (20-24 C) in the dark for 10 days. Soil was washed from the agar surface under running tap water and *V. dahliae* colonies were counted under a stereoscope. *V. dahliae* soil populations were estimated as colony-forming-units per gram dry soil (CFU/g soil).

Microbial root populations.

Within 24 hr after sampling, root balls were rinsed with distilled water to remove adhering soil. Roots were hand-cut into 1 cm long segments and a total of 80 root segments per sample were plated on both NP-10 medium for *Verticillium* and Nash-Snyder medium for *Fusarium* sp.. Colonies of *Fusarium* sp. were counted after 7 days incubation at 20 C. *V. dahliae* colonies were enumerated after 10 days incubation at 20 C in the dark with the aid of a dissecting microscope (13). Root populations were estimated as colony-forming-units per root length (CFU/cm).

In 1997, at 5 wk post-emergence, a subsample of the recovered *Fusarium* sp. root colonies were characterized to species. Identifications were performed for four treatments: fallow and 2 yr sudangrass from both Idaho and Washington. Two to three

colonies on Nash-Snyder medium root plates from 10 randomly selected replicate plots per treatment were subsampled. These colonies were transferred to potato dextrose agar (Difco® Laboratories, Detroit, MI) and carnation leaf agar (31) and incubated under light 12 hr/day for 14 to 30 days at 20 C. Identification to species was performed using "*Fusarium* Species: An Illustrated Manual for Identification" (69).

Biolog assay.

Prior to washing with distilled water, approximately 1 g of root tissue from randomly selected plots (four replications per treatment) was cut from the root ball and placed in plastic baggies, stored at 5 C, and processed 48 to 72 hr after sampling using a procedure developed by George DiGiovanni (personal communication). Roots were cut into 1-cm pieces with flame sterilized scalpels and rinsed with 15 ml of 0.85% NaCl to remove adhering soil. Root samples (0.75 to 1.0 g) were placed in 14 ml sterile polypropylene test tubes (Falcon®, Becton Dickenson Labware, Lincoln Park, NJ) containing 10 ml of an extraction solution (0.2% sodium hexametaphosphate and 6μM Zwittergent detergent). Tubes were vortexed for 2 min on a high setting to extract microorganisms from the roots. Slurries were transferred to new sterile polypropylene test tubes and centrifuged at 2000x g for 10 min (at 3000 rpm in an IEC-HNS swinging bucket centrifuge). The supernatant was transferred to 10 ml of saline (0.85% NaCl) in glass test tubes. Percent transmittance in each sample tube was measured with a Biolog turbidimeter and adjusted with saline to a final percent transmittance between 70 and 85%. Biolog GN MicroPlates™ (Biolog Inc., Hayward, CA) were inoculated with the adjusted extracts using a multitip automatic pipettor. Plates were incubated at 28 C. The

optical density (OD) at 590 nm of the wells in each plate was read with a ThermoMax microplate reader and Biolog Microstation Software Version 350 (1996) or Version 370 (1997). Plates were read beginning at 18 - 20 h and at 2 h intervals to 36 - 40 h depending on when the plates bracketed the target average color well development (AWCD) value of 0.60 +/- 0.02 (38). This AWCD value for each plate was calculated by subtracting the OD of the control well from the average OD of all 95 substrate wells. The OD of each of the substrate wells were standardized following the procedure of Garland et al (38) [(OD – control well OD)/AWCD].

Nutrient analysis.

Soil samples at planting were analyzed for nutrients (calcium, magnesium, manganese, nitrate-nitrogen, phosphorous, potassium, sodium, zinc), pH, and percent organic matter by the Central Analytical Laboratory, Department of Crop and Soil Science, Oregon State University.

Data analyses.

All microbial population response variables underwent an analysis of variance (ANOVA) using SAS, version 6.12, PROC GLM (80) according to a one-way treatment structure (i.e. no interaction term for soil type x manure treatment). All soil microbial population and *V. dahliae* root population data were transformed (ln(x+1)) to conform to the ANOVA assumption of normal distribution of data. Means were separated by Fisher's protected least significant difference (LSD) test. Linear contrasts between treatment groups were performed if the ANOVA F-statistic was significant. Standardized

optical density Biolog data were subjected to a principal component analysis. These analyses were conducted with SAS, version 6.12 PROC FACTOR (80) using ones as prior communality estimates. The principal axis option was used to obtain the components and this was followed by a varimax (orthogonal) rotation.

RESULTS

Results will be presented in the same order for all response variables. Comparisons between soil types, across green manure treatments, will be followed by comparisons between fallow and sudangrass treatments, across soil types in 1996 and 1997. Within each soil type, differences between sudangrass and fallow treatments will then be presented. Lastly, the mixture soil treatment will be compared with its component soils. Responses in the Washington sudangrass treatments were not consistently different from each other. Therefore, treatment references to the number of years of a sudangrass green manure treatment was applied, will be omitted in the text unless consistently significant differences were observed. Idaho and Washington soil types will be referred to as loam and sandy loam, respectively.

FDA hydrolysis.

Incorporation of sudangrass as a green manure resulted in an increase in total microbial activity (TMA) in Idaho loam in both years and only in Washington sandy loam soil in 1996. The level of activity was relatively constant throughout the season in both years and significant differences among treatments tended to occur early and late in

the growing season. In 1996, TMA differed among treatments ($P \leq 0.08$) on 4 of 5 sampling dates and on 2 of 5 dates ($P \leq 0.09$) in 1997 (Table 1.2). Averaged over the season and treatments, TMA was 18.9 % higher ($P = 0.01$) in the Washington sandy loam compared to the Idaho loam in 1996, but in 1997 soil type had no effect on TMA. In 1996, TMA did not differ among the sudangrass treatments ($P > 0.05$), but the mean activity was 46.3 % higher in the sudangrass treatments than the fallow controls ($P = 0.0001$). In 1997, TMA in green manure soils did not differ significantly from the fallow.

The season average microbial activity in the loam green manure treatment was 46.2 and 30.1 % higher ($P \leq 0.05$) than the fallow in 1996 and 1997, respectively. However, sudangrass in the sandy loam soil increased TMA compared to the fallow only in 1996. Regardless of sampling date in 1996, TMA among the 1 yr and 2 yr sudangrass treatments did not differ. Averaged over the 1996 season, TMA was higher by 45.0 and 38.4 % ($P \leq 0.05$) in the two sandy loam sudangrass treatments compared to the fallow. Averaged over 1997, however, TMA in the Washington 2 yr sudangrass and fallow treatments were not different ($P > 0.05$), whereas TMA in the Washington 3 yr sudangrass treatment was 37.8 and 38.0 % lower ($P \leq 0.05$) than the 2 yr green manure and fallow, respectively. Microbial activity in the ID-WA mixture did not differ from the mean activity in either mixture component soils.

Microbial soil populations.

Although higher TMA was observed in soils to which sudangrass was incorporated, differences in component microbial soil populations between sudangrass

TABLE 1.2. Effect of a sudangrass green manure on total microbial activity measured as rate of hydrolysis of fluorescein diacetate (FDA) in microplots containing Idaho and Washington soil.

	FDA hydrolyzed (g/hr/g soil)											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	9.15 C[h]	10.22 AB	13.15 BC	12.44	10.62 C	11.06 B	3.96	8.73	8.02 C	10.35 C	14.06	9.24 B
ID-S1[c]	22.74 A	13.33 A	9.24 C	18.48	17.04 B	16.17 A	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	4.61	7.66	16.20 A	13.91 ABC	17.72	12.02 A
WA-F[b]	12.32 C	9.19 B	17.66 AB	10.85	13.27 BC	12.66 B	5.69	14.19	14.32 AB	10.86 BC	15.53	12.12 A
WA-S1[c]	18.31 AB	11.96 AB	18.45 AB	19.84	23.19 A	18.35 A	-	-	-	-	-	-
WA-S2[d]	13.67 BC	12.54 A	20.76 A	18.38	22.24 A	17.52 A	4.11	13.72	13.80 AB	15.00 A	13.86	12.10 A
WA-S3[e]	-	-	-	-	-	-	2.88	8.97	11.32 BC	10.74 BC	9.99	8.78 B
MIX[f]	-	-	-	-	-	-	5.21	13.64	11.96 ABC	14.45 AB	15.60	12.17 A
P value[g]	0.0003	0.0792	0.0247	0.1093	0.0001	0.0001	0.1222	0.4108	0.0806	0.0885	0.6274	0.0076

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

and fallow treatments or between soil types were seldom significant when averaged over the season. A sudangrass green manure did not affect population size of *Fusarium* (Table 1.3), total bacteria (Table 1.4), or actinomycetes (Table 1.5) in either soil type. Within sampling dates, some significant treatment differences among component populations were seen. But these differences were not consistent over time. In general, lower total populations of all microorganism groups were recovered in 1997 compared to 1996.

Unlike the *Fusarium*, bacteria and actinomycete soil populations, higher fluorescent pseudomonad populations were more consistently recovered from the green manure treatments regardless of soil type. In 1996 and 1997, the mean fluorescent pseudomonad population in the loam soil was 1.05 % smaller ($P > 0.05$) and 25.5 % larger ($P = 0.09$), respectively, than in the sandy loam soil (Table 1.6). Averaged across types, soils amended with sudangrass yielded 71.5 % and 107 % larger pseudomonad populations compared to the fallowed soils in 1996 and 1997, respectively ($P > 0.05$, $P = 0.0008$).

Microbial soil populations of *Fusarium*, bacteria, or actinomycetes in the ID-WA mixture treatment were not different from populations in the component soils at any date. Averaged over the season, the fluorescent pseudomonad population recovered from the mixture treatment was 25.9 % smaller than the average population in the sudangrass treatment in the loam ($P \geq 0.05$) but 134 % larger than in the fallow sandy loam population ($P \leq 0.05$).

Verticillium. Soil populations of *V. dahliae* fluctuated throughout the growing season and differences among treatments were not consistent across time. Regardless of soil type or green manure treatment, populations were highest at planting in early May.

TABLE 1.3. Effect of a suc *arium* in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	10.48	7.94	9.67	7.99	10.26 A[h]	9.27	6.33	4.81	6.11	6.75	6.99	6.66
ID-S1[c]	8.52	9.68	7.67	7.81	10.45 A	8.82	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	7.62	5.60	6.91	7.52	5.26	6.70
WA-F[b]	11.14	9.46	9.37	9.65	9.92 A	9.91	7.38	4.43	7.06	5.38	5.25	6.11
WA-S1[c]	11.32	9.73	7.95	9.37	10.47 A	9.77	-	-	-	-	-	-
WA-S2[d]	11.08	7.93	7.23	9.99	6.27 B	8.50	8.01	6.78	4.47	5.81	6.20	6.45
WA-S3[e]	-	-	-	-	-	-	7.45	3.50	6.91	6.55	6.73	6.71
MIX[f]	-	-	-	-	-	-	7.89	5.58	6.07	7.77	6.35	6.76
P value[g]	0.1913	0.6908	0.4273	0.6482	0.0987	0.3736	0.4056	0.8940	0.1930	0.4816	0.6287	0.9399

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

TABLE 1.4. Effect of a sudangrass green manure on population dynamics of culturable bacteria in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	12.18	16.69	15.94	16.17	16.54	15.50	10.88	13.96	9.85	13.70	12.28	12.44
ID-S1[c]	12.76	16.11	16.70	16.24	17.14	15.79	-	-	-	-	-	-
ID-S2[d]	-[h]	-	-	-	-	-	13.12	9.06	13.03	13.92	11.88	12.31
WA-F[b]	13.23	15.83	15.70	16.57	16.49	15.56	13.32	13.16	12.58	12.70	10.05	12.64
WA-S1[c]	12.84	16.72	16.58	16.72	16.87	15.94	-	-	-	-	-	-
WA-S2[d]	12.78	15.78	15.84	16.13	16.49	15.41	13.71	12.93	11.03	13.63	11.26	12.73
WA-S3[e]	-	-	-	-	-	-	13.61	13.28	12.32	13.49	12.74	13.05
MIX[f]	-	-	-	-	-	-	13.78	14.63	12.28	12.69	11.82	13.45
P value[g]	0.3470	0.4620	0.7402	0.8470	0.1216	0.8307	0.6995	0.2599	0.5259	0.1936	0.7088	0.7194

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq _{0.05}$.
[h]not evaluated.

TABLE 1.5. Effect of a sudangrass green manure on population dynamics of actinomycetes in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	10.48	13.61	13.07	13.77 B[h]	14.22	13.03	9.68	10.54	10.81	11.11	11.13 A	10.98
ID-S1[c]	8.52	13.36	13.18	13.73 B	14.39	12.64	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	11.46	10.82	11.11	11.31	11.12 A	11.28
WA-F[b]	11.14	13.86	13.61	14.10 AB	14.10	13.36	11.17	9.21	10.88	11.02	10.36 C	10.64
WA-S1[c]	11.32	14.27	13.81	14.24 A	14.54	13.64	-	-	-	-	-	-
WA-S2[d]	11.08	14.16	13.27	14.19 A	14.38	13.42	11.79	10.98	11.06	10.69	10.42 BC	10.92
WA-S3[e]	-	-	-	-	-	-	11.30	10.40	11.16	10.84	11.03 AB	11.23
MIX[f]	-	-	-	-	-	-	11.68	11.08	10.87	11.19	11.25 A	11.22
P value[g]	0.1913	0.2425	0.1409	0.0454	0.4543	0.3208	0.2314	0.9697	0.6356	0.2930	0.0669	0.8476

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

TABLE 1.6. Effect of a sudangrass green manure on population dynamics of fluorescent *Pseudomonas* in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	0.0	2.62	4.47	8.93 A[h]	7.02 AB	4.61	1.88	5.12	3.72	2.35 BCD	3.40	2.97 BC
ID-S1[c]	2.16	8.01	2.16	8.88 A	12.20 A	6.68	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	7.52	6.22	5.98	7.86 A	5.32	6.38 A
WA-F[b]	2.30	2.76	4.47	2.30 B	4.88 B	3.34	5.45	1.13	2.13	0.0 D	1.06	2.02 C
WA-S1[c]	0.0	2.76	7.07	11.37 A	11.93 A	6.63	-	-	-	-	-	-
WA-S2[d]	2.16	7.87	4.47	8.88 A	12.37 A	7.15	8.29	3.97	2.27	4.46 ABC	4.43	4.74 AB
WA-S3[e]	-	-	-	-	-	-	6.98	5.25	6.82	1.22 CD	2.37	4.41 AB
MIX[f]	-	-	-	-	-	-	7.71	0.62	3.19	6.56 AB	4.34	4.73 AB
P value[g]	0.7744	0.3400	0.8274	0.0873	0.0363	0.1148	0.1462	0.4542	0.1157	0.0642	0.9153	0.0046

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq _{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

Across green manure treatments, populations were smaller in the sandy loam compared to the loam in both years. Season average *V. dahliae* populations in the sandy loam soil treatments were 56.2 and 62.7% smaller ($P = 0.0001$ and $P = 0.0001$) than in the loam in 1996 and 1997, respectively. Within soil type, *Verticillium* populations in the fallow and sudangrass treatments differed only in the loam in 1997 (Table 1.7). Averaged over the 1997 season, the population in the sudangrass loam treatment was 20.4 % smaller ($P \leq 0.05$) than the fallow.

The mean soil population in the ID-WA mixture treatment did not differ at any date from populations in either of the components ($P > 0.05$). Averaged over the season, though, the population in the fallow sandy loam was 26.2% smaller ($P \leq 0.05$) than the mixture population.

Microbial root populations.

Fusarium. Although differences in soil populations of *Fusarium* were not detected, *Fusarium* was recovered more frequently from roots of potato grown in sudangrass compared to fallow treatments in both years. Population sizes within treatments were consistent over time, following a slight increase early in the season. Significant differences did not appear to depend on the length of time sudangrass was grown. In the Idaho loam soil, *Fusarium* root populations were increased by 28.3 % ($P \leq 0.05$), only after sudangrass was grown for 2 yr (Table 1.8). However, among the Washington sandy loam treatments, only the *Fusarium* population in the soil cropped to 1 yr of sudangrass was larger, by 19.7 % ($P \leq 0.05$), than the fallow.

TABLE 1.7. Effect of a sudangrass green manure on population dynamics of *Verticillium dahliae* in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	3.51 A[h]	1.81 AB	1.63 AB	2.27 A	2.96 A	2.62 A	3.49 A	3.02 A	1.95 A	1.67 A	2.41 A	2.54 A
ID-S1[c]	3.02 AB	2.46 A	2.85 A	2.32 A	2.88 A	2.75 A	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	3.46 A	1.88 BC	2.05 A	1.38 AB	1.53 B	2.02 B
WA-F[b]	2.69 BC	0.35 BC	0.72 B	0.0 B	1.71 AB	1.36 B	2.11 B	1.69 BC	1.32 AB	0.92 B	1.70 AB	1.53 C
WA-S1[c]	1.91 CD	0.0 C	1.02 B	0.84 B	0.93 B	1.10 B	-	-	-	-	-	-
WA-S2[d]	1.62 D	0.87 ABC	0.95 B	0.38 B	0.98 B	1.07 B	2.02 B	0.93 C	0.80 B	0.71 B	1.72 AB	1.23 C
WA-S3[e]	-	-	-	-	-	-	1.28 C	0.98 C	1.09 B	1.34 AB	1.92 AB	1.31 C
							-	-	-	-	-	-
MIX[f]	-	-	-	-	-	-	3.23 A	2.29 AB	2.03 A	0.87 B	2.10 AB	2.08 B
P value[g]	0.0001	0.0372	0.1236	0.0007	0.0098	0.0001	0.0172	0.0009	0.0016	0.0361	0.0878	0.0001

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

TABLE 1.8. Effect of a sudangrass green manure on population dynamics of *Fusarium* recovered from roots of potato cv. Russet Burbank grown in microplots containing Idaho and Washington soil.

	CFU/cm root									
	1996					1997				
Treatment	162[a]	231	344	656	Season Average	171	277	356	479	Season Average
ID-F[b]	0.24 D[h]	1.63	1.00 D	1.02 B	0.96 D	0.78 D	1.07 C	0.99 C	1.13 C	0.99 D
ID-S1[c]	0.46 CD	1.55	1.10 CD	1.09 B	1.06 CD	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	1.06 C	1.49 B	1.18 B	1.33 B	1.27 C
WA-F[b]	0.84 BC	1.78	1.30 BC	1.06 B	1.22 BC	1.36 AB	1.72 AB	1.55 A	1.53 A	1.54 A
WA-S1[c]	1.35 A	1.90	1.66 A	1.10 AB	1.46 A	-	-	-	-	-
WA-S2[d]	1.04 AB	1.76	1.51 AB	1.34 A	1.42 AB	1.47 A	1.78 AB	1.65 A	1.48 AB	1.59 A
WA-S3[e]	-	-	-	-	-	1.39 AB	1.90 A	1.64 A	1.38 AB	1.58 A
MIX[f]	-	-	-	-	-	1.32 B	1.49 B	1.49 A	1.30 BC	1.40 B
P value[g]	0.0019	0.3595	0.0001	0.0782	0.0001	0.0001	0.0001	0.0001	0.0043	0.0001

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

Compared to the loam, there were more *Fusarium* colonies per length of root in the sandy loam soil treatments. Averaged over the 1996 and 1997 seasons, populations on roots grown in sandy loam were 34.9 and 39.1 % larger ($P = 0.0001$ and $P = 0.0001$) than loam populations, respectively. Within soil type, larger populations tended to be recovered from soil cropped to a green manure. Averaged over the seasons, the mean population recovered from the sudangrass loam treatment was 11.2 and 27.9 % larger than the fallow ($P > 0.05$ and $P \leq 0.05$) in 1996 and 1997, respectively. Differences among sandy loam treatments were observed only in 1996. Populations did not differ at any time between the two sandy loam sudangrass treatments in either year. In 1997, the mean root population from the ID-WA soil mixture treatment did not differ from the mean of its two components at any date.

Based on identification of subsamples of *Fusarium* colonies recovered from potato roots, there were similar effects of a sudangrass green manure on the number of species present from each soil type. *F. solani*, *F. equiseti*, and *F. oxysporum* were the most abundant species in both soils (Table 1.9). Of these species, numbers of *F. equiseti* colonies were larger in the sudangrass soil compared to the fallow by 67 and 50 % in loam and sandy loam soil, respectively.

***Verticillium*.** Relative root populations of *V. dahliae* fluctuated throughout the season and significant differences among treatments, if any, were not consistent over time. In contrast to soil populations, root populations remained relatively stable over the season with no clear trends over time. Regardless of treatment, recovered root populations peaked late in the growing season in 1996 at 660 DDAP. But in 1997, at the last sampling date

TABLE 1.9. Effect of a sudangrass green manure on the percentage of *Fusarium* species isolated from roots of potato cv. Russet Burbank grown in microplots containing Idaho and Washington soil in 1997.

	% species[a]			
	Idaho loam		Washington sandy loam	
Fusarium sp.	Fallow	Sudangrass[b]	Fallow	Sudangrass[b]
acuminatum	4.5	9.5	0	9.5
equiseti	9.5	14.3	13.6	23.8
moniliforme	0	0	9.1	0
oxysporum	4.3	0	13.6	14.3
proliferatum	0	0	13.6	4.8
sambucinum	4.5	14.3	0	0
solani	76.2	61.9	50.0	47.6
Total # of isolates	21	21	22	21

[a]from a subsample of colonies isolated from roots plated on Nash-Snyder agar medium.
[b]green manure grown for 2 consecutive yr prior to potatoes.

at 470 DDAP, root population sizes were similar to those recovered at earlier dates.

Consistent with *V. dahliae* soil population sizes, smaller root populations were recovered from the sandy loam compared to loam soil treatments (Table 1.10). Averaged over the season, root populations in the sandy loam were 63.6 and 61.3% smaller ($P = 0.0001$ and $P = 0.0001$) than in the loam in 1996 and 1997, respectively. Only a sudangrass green manure grown for 2 yr in the Idaho loam soil affected root populations. The season average *V. dahliae* potato root population in this sudangrass treatment was 41.2% smaller ($P \leq 0.05$) than the fallow.

Averaged over the 1997 season, the *V. dahliae* root population in the ID-WA mixture treatment differed from the mean of the two components ($P = 0.0007$). Yet, the mixture population differed significantly only from the population in the fallow sandy loam component. Root populations from the loam and sandy loam soil components were 27.2 and 69.5 % smaller ($P > 0.05$ and $P \leq 0.05$) than the mixture.

TABLE 1.10. Effect of a sudangrass green manure on populations of *Verticillium dahliae* recovered from roots of potato cv. Russet Burbank grown in microplots containing Idaho and Washington soil.

	ln CFU/cm root									
	1996					1997				
Treatment	162[a]	231	344	656	Season Average	171	277	356	479	Season Average
ID-F[b]	0.10 B[h]	0.16 A	0.07 A	0.22 AB	0.14 A	0.18 A	0.11 A	0.18 A	0.10	0.14 A
ID-S1[c]	0.24 A	0.12 AB	0.07 A	0.36 A	0.20 A	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	0.09 B	0.05 B	0.09 AB	0.07	0.08 BC
WA-F[b]	0.0 B	0.01 C	0.03 AB	0.17 B	0.07 B	0.01 C	0.04 BC	0.01 B	0.09	0.03 D
WA-S1[c]	0.06 B	0.02 C	0.0 B	0.13 B	0.06 B	-	-	-	-	-
WA-S2[d]	0.01 B	0.05 BC	0.01 B	0.15 B	0.06 B	0.02 C	0.02 BC	0.03 B	0.13	0.05 CD
WA-S3[e]	-	-	-	-	-	0.01 C	0.01 C	0.02 B	0.11	0.04 D
MIX[f]	-	-	-	-	-	0.09 B	0.09 A	0.15 A	0.09	0.11 AB
P value[g]	0.0056	0.0289	0.0199	0.0243	0.0001	0.0001	0.0001	0.0053	0.7157	0.0001

[a]Degree days after planting.
[b]Weed-free fallow soil from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

Biolog assay.

Patterns of sole-carbon source utilization based on analysis of color response data from Biolog GN microplates were not replicable between samples or between years. Typically, only the first three principal components contributed to explaining a large amount, more than 5 %, of variance in the data. These first three components combined accounted for 53 to 58% and 59 to 69% of the total variance in color development data in 1996 and 1997, respectively. Two dimensional graphical displays of the first two principal components at each sampling date suggested different color development patterns between the loam and sandy loam soils in 1996 but not 1997 (Figure 1.1 - 1.2). There was no indication that patterns differed between green manure and fallow soil within soil type. Even within sampling date, variability was evident between replicates and treatments in the rates of average well color development (AWCD) (Figure 1.3 - 1.4). This variability could account for differences in utilization patterns described by the principal components rather than differences between soil origin or changes in microbial physiological groups due to incorporation of sudangrass.

Nutrient analysis.

The soil chemical characterization results were used for post-planting fertilization recommendations. The lower nitrate-nitrogen and phosphorous amounts in Idaho loam soil was due to a pre-plant fertilization of the Washington field soil prior to its transport to microplots (Table 1.11). The loam contained a higher percent organic matter than the sandy loam. Although a sudangrass green manure was grown in Idaho for 1 year and

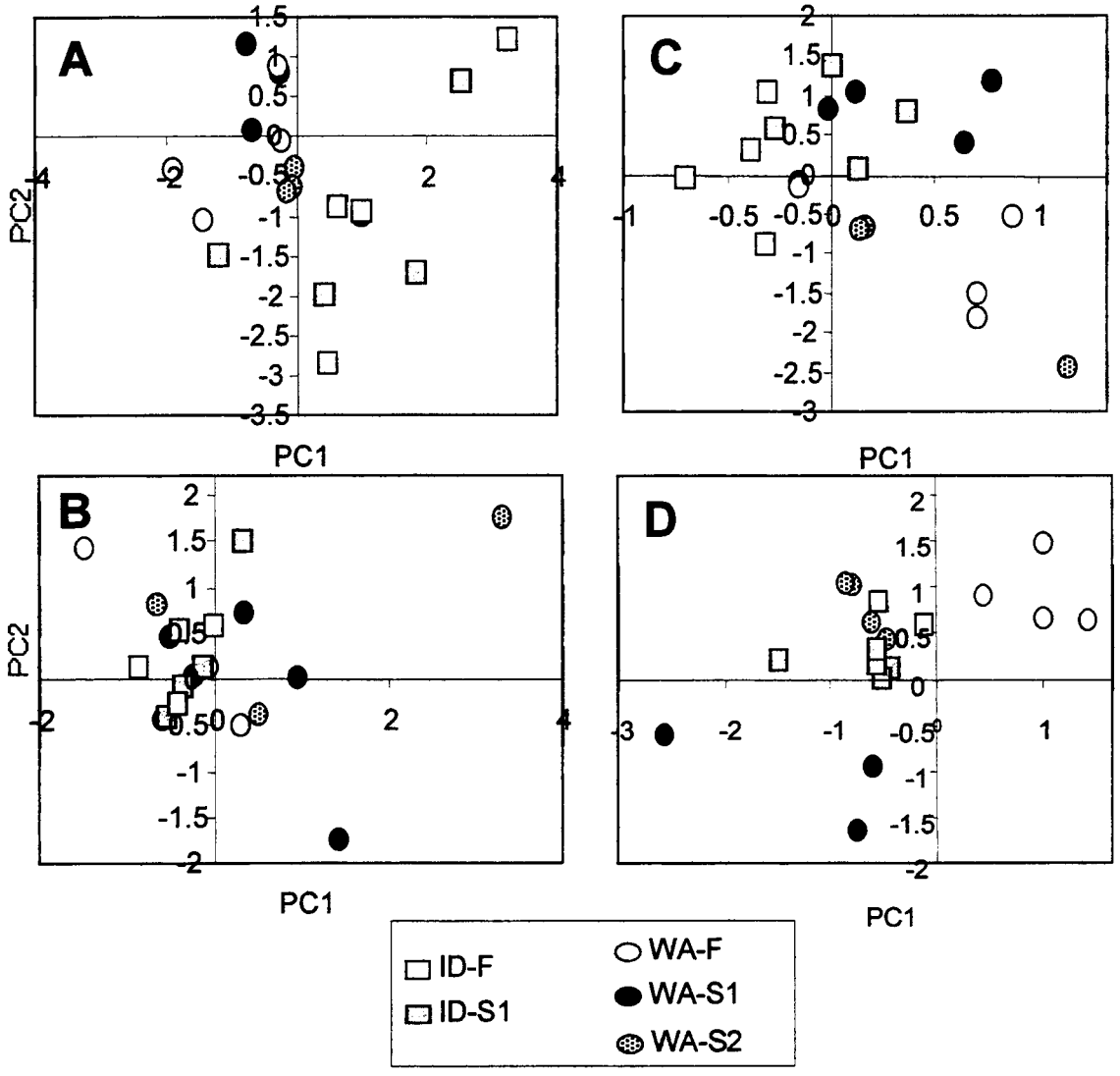

Figure 1.1. Ordination produced from principal components analysis of color well development on Biolog GN microplates from rhizosphere samples of potatoes grown in microplots in 1996. Four sampling dates from the 1996 season are represented: **A,** 162 degree days after planting (DDAP), **B,** 231 DDAP, **C,** 343 DDAP, **D,** 656 DDAP. Scores of each sample for the first and second principal components (PC) are plotted. Symbol type distinguishes soil type: Idaho Delco loam (ID) or Washington Quincy fine sandy loam (WA). Soil treatments include fallow (F) and sudangrass green manure grown for 1 (S1) or 2 (S2) consecutive years.

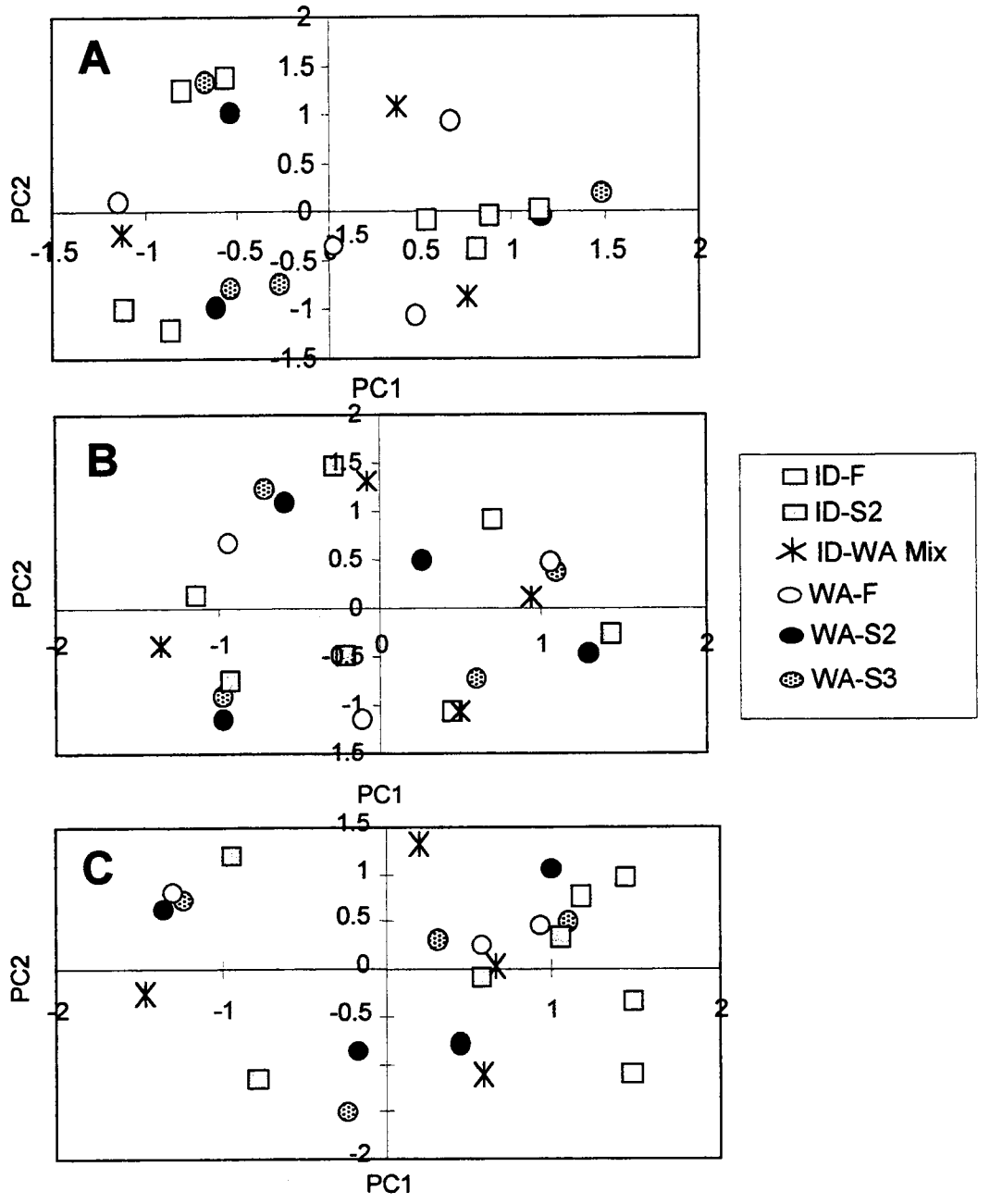

Figure 1.2. Ordination produced from principal components analysis of color well development on Biolog GN microplates from rhizosphere samples of potatoes grown in microplots in 1997. Three sampling dates from the 1997 season are represented: **A,** 171 degree days after planting (DDAP), **B,** 277 DDAP, **C,** 356 DDAP. Scores of each sample for the first and second principal components (PC) are plotted. Symbol type distinguishes soil type: Idaho Delco loam (ID) or Washington Quincy fine sandy loam (WA). Soil treatments include fallow (F) and sudangrass green manure grown for 2 (S2) or 3 (S3) consecutive years. ID-WA Mix treatment consists of equal proportions of ID-S2 and WA-F soil.

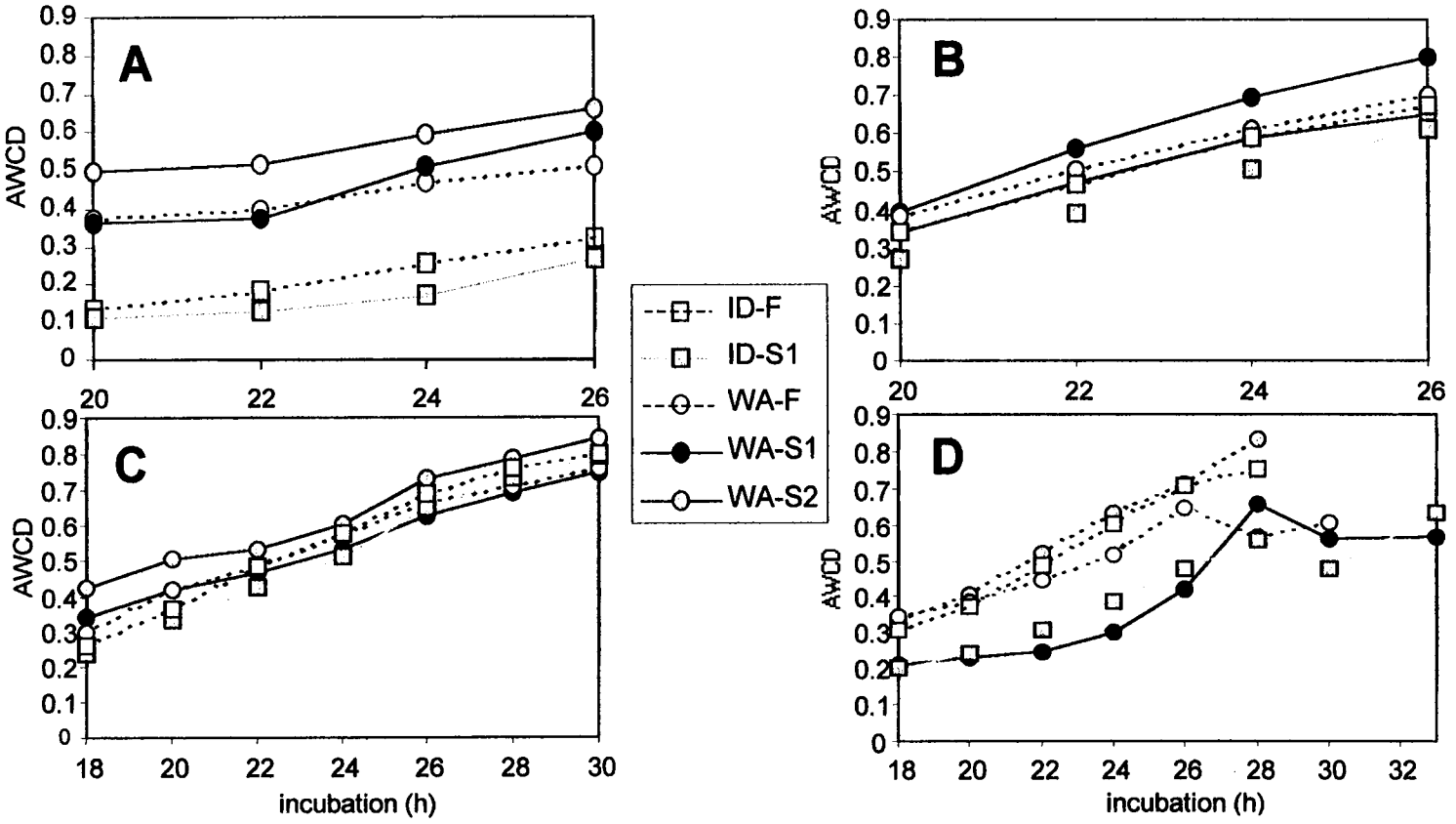

Figure 1.3. Color development of Biolog GN microplate wells in 1996 with incubation at 28 C. Lines represent the mean AWCD (average color well development) for 95 sole-carbon-source response wells from four replicate microplates per soil treatment. Four sampling dates are represented; **A**, 162 degree days after planting (DDAP), **B**, 231 DDAP, **C**, 343 DDAP, and **D**, 656 DDAP. The soil treatments include two soil origins, Idaho (ID) and Washington (WA). The WA soil treatments are fallow (F), 1 yr (S1) and 2 yr (S2) consecutive cropping of a sudangrass green manure. The ID treatments are fallow (F) and 1 yr (S1) of a sudangrass green manure.

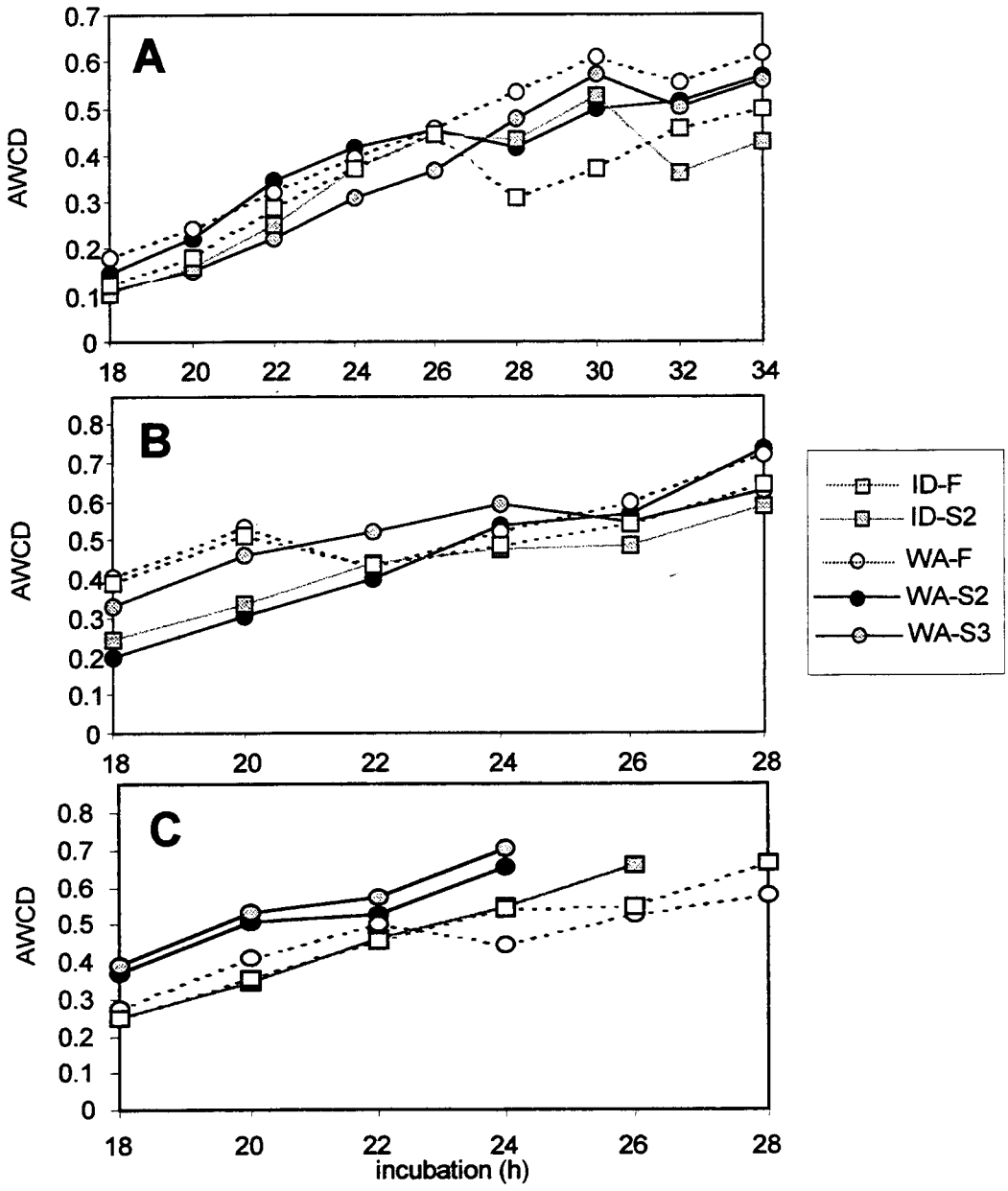

Figure 1.4. Color development of Biolog GN microplate wells in 1997 with incubation at 28 C. Lines represent the mean AWCD (average color well development) for 95 sole-carbon-source response wells from four replicate microplates per soil treatment. Three sampling dates are represented for 1997; **A**, 171 degree days after planting (DDAP), **B**, 277 DDAP, and **C**, 356 DDAP. The soil treatments include two origins, Idaho (ID) and Washington (WA). The WA soil treatments are fallow (F), 2 yr (S2) and 3 yr (S3) consecutive cropping of a sudangrass green manure. The ID soil treatments are fallow (F) and 2 yr (S2) of a sudangrass green manure.

Washington for 1 and 2 years, the percent organic matter in the soil types was not increased compared to the fallow soil in 1996. In 1997, higher organic matter was observed in all sudangrass treatments compared to the respective fallow although the differences in the sandy loam were slight. Larger amounts of nitrate-nitrogen were obtained following sudangrass amendments to both soils. Among the other soil nutrients, there were few consistencies in comparing sudangrass and fallow treatments in the sandy loam and loam soil in both 1996 and 1997.

TABLE 1.11. Nutrient composition of soil from southeastern Idaho and southcentral Washington that were fallowed or cropped to a sudangrass green manure for 1 to 3 consecutive years.

	Soil Chemical Composition[a]									
Treatment			(ppm)					(meq/g)		
1996	pH	% OM[b]	NO3-N	P	K	Mn	Zn	Ca	Mg	Na
ID-F[c]	8.1	3.77	7.9	31	343	5.2	1.24	35.0	3.0	0.11
ID-S1[d]	8.0	3.31	9.2	25	328	6.6	1.46	36.0	3.1	0.13
WA-F[c]	6.6	1.12	41.3	69	488	6.7	5.12	4.0	1.7	0.07
WA-S1[d]	7.2	1.18	54.6	42	335	9.4	6.40	4.4	1.5	0.06
WA-S2[e]	6.8	1.08	45.6	42	363	7.5	6.20	4.0	1.6	0.06
1997										
ID-F	8.4	3.72	8.6	6.0	367	5.5	1.28	33.0	2.9	0.09
ID-S2[e]	8.5	4.47	9.4	5.0	335	6.0	1.22	31.0	3.2	0.12
WA-F	5.6	1.27	34.5	89	441	6.3	4.84	2.9	1.1	0.03
WA-S2	5.5	1.28	46.4	94	410	7.9	4.42	2.9	1.1	0.04
WA-S3[f]	5.5	1.36	49.6	96	511	7.8	5.22	2.7	1.0	0.02
MIX[g]	8.2	2.94	21.2	5.0	382	5.8	2.34	28.0	2.6	0.09

[a]Soil nutrient analysis conducted on bulked soil samples collected at potato planting. Analyses were performed by the Central Analytical Laboratory, Department of Crop and Soil Science, Oregon State University.
[b]Percent organic matter lost on ignition.
[c]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[d]Soil cropped to a sudangrass green manure for 1 yr.
[e]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[f]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[g]Mixture treatment consists of equal proportions of ID-S2 and WA-F soil.

DISCUSSION

Sudangrass green manure treaments increased total microbial activity (TMA) in both Idaho loam and Washington sandy loam soil types in a microplot study in the Columbia Basin. Nevertheless, early dying of potatoes was not suppressed in either soil type (Chapter 2) and *V. dahliae* soil and root populations were reduced only by the Idaho 2-year sudangrass green manure treatment. Despite the increased microbial activity, *Fusarium*, bacteria, and actinomycete soil populations did not differ among treatments or between soil types. In only one year of the study, sudangrass increased *Fusarium* root populations and fluorescent pseudomonad soil populations in both the loam and sandy loam soils. Thus, this treatment had no consistent effect of sudangrass on microbial activity, or fungal and bacterial populations in the two soils.

Total microbial activity can indicate suppressiveness of a greenhouse soil mix to Pythium root rot (44). Based on this microplot study, however, TMA may not be a useful universal indicator of the potential for suppression of Verticillium wilt. In the original Idaho field study, there was a significant negative correlation between Verticillium wilt incidence and TMA following a sudangrass green manure, supporting the hypothesis that some biological control mechanism may be involved in disease suppression (18,19). Conversely, TMA was positively correlated with disease severity in the Washington field study (14), perhaps indicating a different relationship between disease and soil microflora than in Idaho. The rate of hydrolysis of fluorescein diacetate (FDA) to determine TMA is best used as a general indicator of heterotrophic microbial activity in soil rather than microbial biomass. A number of enzymes, including esterases, lipases, and proteases,

hydrolyze FDA. Some fungi, and most bacteria, both known plant tissue decomposers, hydrolyze FDA (81).

In general, crop amendments increase microbial activity (11,14,19,55,82). This is most likely due to the increased availability of organic matter following a green manure as Schnurer et al (82) reported a significant positive correlation between TMA and organic matter in agricultural soil. The incorporation of plant tissue provides carbon sources and increases soil water holding capacity, thus encouraging microbial activity. Even the addition of inorganic nitrogen fertilizer, encouraging plant root growth, can increase TMA (55). For this study however, the measured percent organic matter was not always larger in the soil cropped to sudangrass, regardless of soil type. There was a large increase in organic matter only in the loam soil after two consecutive years of sudangrass. This is unlike previous studies in agricultural soil with organic amendments (11,82) in which organic matter was up to 1.4 times larger following a green manure than a non-green manure crop. However, despite the small change in organic matter, sudangrass significantly increased TMA in the sandy loam soil in 1996, and loam soil in both years. In fact, despite a lower organic matter across treatments, TMA in the sandy loam was larger than the loam in 1996. In 1997, activity was unaffected by the 2 year sandy loam sudangrass treatment and decreased in the 3 yr sandy loam sudangrass soil. TMA in this latter treatment was consistently lower than that of the fallow throughout the season. These results were atypical of this soil as TMA was consistently and significantly increased by sudangrass in the original field study in Washington (14). There was no detectable error in treatment assignment to resolve this discrepancy nor did results from other variables suggest that treatments were not assigned or collected properly.

Although increased microbial activity may depend on soil depth, with most of the activity occurring to the depth of organic matter incorporation, ranging from 0 to 10 cm in one study (55), this should not have been a factor even when soil was transported. From both the Idaho and Washington study sites, soil was dug within the top few inches which should include the bulk of the incorporated residue. This soil was either shoveled directly into the microplots (Washington) or mixed further by transportation in wooden boxes before being shoveled into microplots (Idaho). Known problems with the TMA procedure are high or low pHs, which facilitate non-biological hydrolysis of FDA, or high adsorption of fluorescein to soil particles (81). As the adsorption rate is unknown, but the pH of the Washington sandy loam was similar in all treatments (Table 1.11), it is unknown why the TMA in the sudangrass treatments were lower or not different from the fallow. Despite this discrepancy, the results from our study indicate that TMA levels are not indicative of the suppressiveness of a sudangrass green manure soil to potato early dying.

Temperatures in the microplot soil may have determined the higher level of microbial activity in 1996. Mean air temperatures and resulting degree days after planting were very similar between 1996 and 1997. But, in 1996, weeds grew profusely between the microplots while soil was kept bare throughout the 1997 season. The weed cover would likely keep soil temperatures lower compared to bare soil and would more closely resemble row closure in a potato field. The weed cover may have also retained soil moisture, thus encouraging microbial activity. In addition, the exposed upper lip of the black microplot could conceivably conduct solar energy and heat the soil contained in the

pot especially when exposed to sun. If soil temperatures were too high, they may have constrained microbial activity or even reduced population sizes of microorganisms.

Soil populations of various groups of microorganisms were estimated to determine if changes in TMA corresponded to changes in population sizes of soil microflora. The groups studied were chosen to represent general soil microbial populations and specific groups thought to be responsible for biological control in disease suppressive soils. *Fusarium* populations were estimated as Davis et al (19) reported selective effects on soil and root populations of *Fusarium* species in the original Idaho study. While the percent of *F. equiseti* populations sampled from roots increased following this green manure, this effect was observed in both Idaho and Washington soil. In fact, a higher proportion of *F. equiseti* colonies were identified from Washington soil. Davis et al (19) has suggested that *Fusarium* sp. may be involved in the suppression of Verticillium wilt. One study (68) has indicated an active disease suppression role of non-pathogenic *Fusarium* in which isolates of *F. oxysporum* inoculated in soil induced resistance to Fusarium wilt of cucumber.

In our study, the effect of sudangrass on root populations of *Fusarium* species was not consistent in either Idaho loam and Washington sandy loam soil. Averaged over the season, only sandy loam 1 year and loam 2 year green manure treatments increased root populations of *Fusarium* in 1996 and 1997, respectively. The consistently higher *Fusarium* population in the loam 2 year treatment, may indicate an effect of the number of years a sudangrass green manure is cropped. Similarly, a decrease in *V. dahliae* populations was observed only after two years of a sudangrass crop in Idaho soil. This same time-dependent effect, however, was not seen in the sandy loam in which

differences were observed only after one year of sudangrass. Yet, in both 1996 and 1997, higher *Fusarium* root populations were recovered from the sandy loam treatments compared to roots in the loam. Despite this quantitative difference in populations between the soil types, there was little effect of sudangrass on the percent of *Fusarium* species recovered from the roots. Although higher percentages of *F. equiseti* colonies were isolated from roots grown in sudangrass soil treatments, the increased percentage was similar in both soil types.

Microplot soil populations of *Fusarium* did not correspond with the differences in root colonization. Averaged over the season, plate counts of *Fusarium* soil populations were not different among any of the treatments. Populations did not differ between soil types. The one treatment difference that occurred, with a lower population in the 2 year sudangrass treatment in sandy loam, on the last sampling date in 1996, was most likely due to seasonal population variation, common in soil population estimations (55). The lack of correspondence between root and soil populations may be due to higher microbial activity in the rhizosphere (52). Also, as plate counts consistently ranged from 0 to 50, there was large variability between replicates which could prevent the ANOVA from detecting significant differences. Yet, in both years of the microplot study, *Fusarium* soil populations in the sudangrass treatments were not consistently higher or lower than those in the fallow soils indicating the measurement method and seasonal variation had more influence on population estimates than the sudangrass treatment.

Few treatment differences were detected for bacterial and actinomycete soil populations, as well. Similar to TMA, increased microbial populations have been related to increased soil organic matter (11,55). Bloem et al (11) observed increased soil bacteria

and actinomycete populations following a green manure. Keinath (53), in contrast, reported that a cabbage residue amendment and solarization, or crop rotation, had no effect on actinomycete populations. As the role of both groups in biological control have been studied, their populations were monitored in our microplot study. Actinomycetes have been identified as possible biological control agents. Black and Beute (9,10) reported that increased actinomycete populations, favored by a soybean rotation, may be responsible for suppression of black rot of peanut, caused by microsclerotia-forming *Cylindrocladium crotalariae*. Greenhouse experiments indicated that this disease suppression may result from increased plant growth induced by actinomycetes. Soil microflora can affect plant growth by contributing plant growth hormones and organic and inorganic nutrients by affecting availability of nutrients (10). Broadbent et al (12) identified actinomycetes which controlled damping off by *Rhizoctonia* but did not affect pathogen population sizes. Increased populations of both bacteria and actinomycetes were associated with a reduction of *V. dahliae* inoculum density and severity of Verticillium wilt of strawberry following soil amendments (50).

In the loam and sandy loam soils, in which organic matter was not always increased after sudangrass, the green manure had no clear effect on populations of actinomycetes. Populations did not differ between soil types. Populations of recognizable actinomycete colonies were not significantly different when averaged over the season. Although they differed on one date in each year of the study this was most likely based on seasonal variability.

Bacterial plate counts in the microplot study in the Columbia Basin did not differ among treatments or between soil types. Increased bacterial populations have been

observed after green manure treatments (11) or specific crop rotations (10). Azad et al (3) reported that root exudates of potato cultivars with different susceptibilities to Verticillium wilt supported different populations of bacteria. Although the size of rhizosphere bacterial populations were not different between cultivars, antagonists to *V. dahliae* and nitrogen fixing bacteria tended to be more commonly associated with the disease resistant cultivar. As more severe Verticillium wilt is associated with lower soil nitrogen (22), an increased population of nitrogen fixing bacteria on roots may be associated with disease suppression (2,3). As bacterial and actinomycete populations did not differ among treatments in the microplot study, there is no evidence that they influence soil or root populations of *V. dahliae* in either the loam or sandy loam soil type.

Within a narrower bacterial group, sudangrass did increase fluorescent *Pseudomonas* populations in both soil types. Although differences between sudangrass and fallow treatments within soil type were significant only in 1997, there was a trend of higher populations in sudangrass treatments in 1996 as well. Fluorescent pseudomonads are a component of the beneficial *Pseudomonas* rhizobacteria group which are very heterogenous and have been found in both disease suppressive and conducive soils (83). Some have been identified as antagonists to pathogens (12). They share an ability to aggressively colonize plant roots and some can increase plant growth, through either exclusion of root pathogens or production of growth promoting substances (51,83). Fluorescent pseudomonads also produce secondary metabolites that can be antibiotic and possess siderophores that bind iron and could limit growth or activity of other soil organisms requiring iron, including pathogens (83). Nevertheless, populations increased in both soil types and disease severity did not differ among the treatments (Chapter 2). To

support this finding, changes in fluoresent pseudomonad soil populations have not always been found to correlate with disease suppression or increased yield following organic amendments (53).

Although plate counts did not reveal an effect of sudangrass on bacteria, actinomycete and *Fusarium* soil populations, while microbial activity was increased, there are a variety of possibilities of why significant differences in microbial populations did not accompany the incorporation of sudangrass. This technique offers a limited, biased view of the microbial community due to both the selectivity of the media and the non-culturability of many microorganisms (37). Variability between replicates may have been too large for ANOVA to detect significant differences. The number of replicates may have been too low to reduce variability, even after it was increased in 1997. If the effect of sudangrass on microbial populations is subtle, plate count estimation may not be sensitive enough to detect differences. The bacteria and actinomycete populations are broad classification categories which were chosen based on availability of selective media and to investigate whether sudangrass affects large portions of the soil microbial population. The selected culturing conditions, of incubation length and temperature, may not have been optimal to detect differences. Although sudangrass did not have a detectable effect on broad groups, differences may occur within genera or species. Yet, while population differences were observed within the narrower group of fluorescent pseudomonads, *Fusarium* species populations were similar in both Idaho and Washington soil types.

The patterns of sole-carbon source utilization obtained from Biolog GN microplates also indicate that sudangrass did not have a measurable effect on microbial

communities. The characterization of microbial communities based on the inoculation of rhizosphere samples on microplates is based on the pattern of color development, among the 95 sole carbon sources on the plate, which is a result of microbial respiration (37,38). Following a principal components analysis of standardized absorbance values from plates with similar average color well development, there was no clear separation of principal components between sudangrass and fallow treatments in either the loam or sandy loam types. Only in 1996 were there suggestive graphical patterns that microbial communities differed between the two soils although this was not consistent between sampling dates.

The lack of replicability between samples and between years may be due to the heterogeneity of soil microbial communities, temporal shifts in communities, or the limited ability of the technique to detect differences. Although the protocol used to inoculate the microplates attempted to adjust for differences in cell-density, no plate counts were performed to estimate bacterial populations in the inoculum suspension. The color response in the microplate wells appear to be related to the cell inoculum density of microorganisms able to use the substrates (38). It has been shown that differences in inoculum cell density can account for differences in color development rates and in utilization patterns even between replicates of the same treatment (41). The rate of color development varied between replicates within each treatment at each sampling date. Inoculum estimations should be performed in order to be able to attribute differences between AWCD values and utilization patterns to treatment rather than inoculum cell density. If this experiment was repeated, cell density estimations would be essential. Garland and Mills (37) reported that Biolog can detect temporal changes in rhizosphere microbial communities of potato cv. Norland under growth chamber conditions. As

rhizosphere samples were taken from different microplots over time in our study, a direct comparison to determine whether temporal shifts occurred is not valid. Yet, assuming that temporal shifts would occur in the field in potato cv. Russet Burbank, this would introduce more variablity into the technique, perhaps making detection of treatment or soil differences more difficult. While the use of Biolog microplates attempts to characterize a microbial community, therefore avoiding the bias of counting single artificial groups of organisms, it still is biased by requiring culturable organisms that can amplify under the given conditions to produce color changes (43). Because of these limitations, Biolog analysis most likely cannot differentiate between subtle changes that may occur following a sudangrass green manure.

Although the techniques used in this study did not detect consistent differences in microorganism populations or community physiological activity, differences in *V. dahliae* root and soil populations did occur between soil origins. Although soil population levels of *V. dahliae* varied between the two soils, the lack of consistent differences in microbial responses could not account for effects of sudangrass on *V. dahliae*. There was a lower density of natural inoculum in the Washington sandy loam compared to the Idaho loam but both levels were high enough to cause disease expression in the original field studies (14,18). Although the magnitude of differences varied throughout the season, soil populations in all treatments peaked early in the growing season. Seasonal variations in *Verticillium* soil populations have been reported by others (8,28,30,46,47). These variations in recovery of *V. dahliae* may be due to conidia production on senescent tissue (29), seasonal releases of microsclerotia from decomposing host plant debris in soil, mechanical damage to host plant tissue at harvest, or to antagonism and/or predation by

soil organisms (30). Joaquim et al (47) suggested that such seasonal differences in *V. dahliae* populations might differ with geographic location. While populations declined from spring to mid-summer and tended to increase in late July or August in our study, other studies have reported various seasonal dynamics. Two studies in California report that *Verticillium* populations in cotton fields declined from February to August and peaked in October (30), or increased beginning in July (46). Populations in potato fields peaked in July in an Ohio study (47), and in November at a southwestern Ontario site (28). These periodic changes in population sizes of *V. dahliae* should be considered when interpreting soil assay populations. Therefore, a strength of this microplot study was the ability to directly compare effects of sudangrass on *V. dahliae* populations in the Idaho and Washington soil types at one location throughout the growing season, with the same assay procedure.

Averaged over the season, *V. dahliae* soil populations from the microplot study reflect the inconsistent effects of a sudangrass green manure that were observed in the original Idaho and Washington field studies. In the original Washington field study a green manure had no consistent effect on *V. dahliae* soil populations throughout the season (Cappaert and Powelson, unpublished data). Our study supports these results as the microplot soil populations did not differ among any of the Washington sandy loam green manure treatments. In the original Idaho field study (18), a 3 year cropping of sudangrass decreased *V. dahliae* soil populations, whereas a 2 year sudangrass treatment in a second experiment had no effect on soil populations. In our study, the Idaho 2 year loam sudangrass treatment populations were lower than the fallow control when averaged over the season. Yet, soil populations were not lower following only 1 year of sudangrass

cropping in both the original Idaho study (18) and our study. The significantly lower *V. dahliae* soil populations with 2 year versus 1 year of sudangrass green manure in the loam indicates that the influence of the green manure on microsclerotia may be time dependent. This dependence on cropping length also was reported by Green (39) in which a suppression of Verticillium wilt of peppermint required at least 5 years of a corn rotation.

The differences in *V. dahliae* populations counted on roots, measured as colonies per length of root, reflected the different population levels between the soils. Inoculum density in the loam was 128 and 68 % larger than that of the sandy loam in the two years of the study. In turn, the root populations were 168 and 175 % larger in the loam compared to the sandy loam. A positive relationship between soil and root populations has been described previously with population dynamics of *V. dahliae* in California cotton fields (46). Both season average soil and root populations of *V. dahliae* were smaller in the 2 year loam green manure treatment compared with the weed-free fallow. A similar reduction in potato root colonization by *V. dahliae* was following 2 years of a sudangrass green manure was reported by Davis et al (19) in the Idaho field study. In contrast, no differences were detected among any of the sandy loam soil treatments. This concurs with results from the Washington field study (Cappaert and Powelson, unpublished data) in which sudangrass green manure crops had no effect on either soil or root populations of *V. dahliae*.

In addition, sudangrass did not affect the seasonal variation in *V. dahliae* root populations within soils in the microplot study. Root populations of *V. dahliae* over time differed between the Idaho and Washington soils only in 1997. Populations peaked in the

Columbia Basin microplot sandy loam treatments at the end of the season in both years after relatively stable populations throughout the season. Root populations in the loam soil also peaked at the last sampling date in 1996, but were relatively stable throughout the entire season in 1997. Benson and Ashworth (8) reported similar inconsistent root and soil population peaks of *V. albo-atrum* in cotton fields throughout a season. Huisman (46) reported increased cotton *Verticillium* root colony frequencies, which followed increased soil populations, beginning in July and continuing through the season. These increases could not be explained by a feasible type of inoculum dispersal (46) although variable explanations have been proposed for increased soil populations such as conidia production on senescent tissue on soil (29) or the formation of small secondary microsclerotia of *V. albo-atrum* (26).

Because the influence of the incorporation of a sudangrass green manure on *V. dahliae* microsclerotia is unknown, the inconsistent effects of sudangrass on soil and root populations within and between the soil types is not surprising. Sudangrass may decrease *V. dahliae* populations by inducing the germination of microsclerotia, since roots of plant species immune to systemic infection have reported to be colonized as frequently as susceptible species (27). *Verticillium* is not a good saprophyte (40) so germination in the presence of a non-host, without microsclerotia formation, could reduce soil populations. Therefore, two consecutive years of a sudangrass green manure may be long enough to significantly reduce soil populations in the Idaho loam. Sudangrass, however, never affected the low inoculum density of *V. dahliae* in the Washington sandy loam. Inconsistent effects of crop rotations, of varying types, lengths, and locations, on *Verticillium* soil populations or Verticillium wilt have been reported by others

(30,39,70,89). Although the discrepancy between the Idaho and Washington studies involves the same green manure and number of consecutive years of the green manure, it reflects this inconsistent effect of crop rotations on *V. dahliae*.

Aside from an effect of a non-host crop, the chemical composition of sudangrass leaves may directly decrease *V. dahliae* microsclerotia populations. One recent study (64) reported that *Meloidogyne* spp. were reduced following a sudangrass green manure and proposed that the reduction was due to hydrogen cyanide, a product of the ezymatic hydrolysis of dhurrin in disrupted leaf tissue. However, MacGuidwin and Layne (58) observed an increase in plant parasitic nematode populations following a sudangrass green manure. This inconsistency between studies was attributed to either the nematicidal activity being short-lived, or not effectively reaching all nematode populations. If incorporated sudangrass biomass is biocidal to microsclerotia of *V. dahliae*, then like the nematode studies, the direct effect on inoculum is not consistent even within the same soil and location. Because the inconsistent effects on population sizes was accompanied by a consistent reduction in Verticillium wilt incidence in potato following 2 or 3 years of sudangrass in the Idaho field study, Davis et al (18) proposed that changes in soil microbial activities or populations may account for the disease suppression, not a direct effect on *V. dahliae* inoculum.

The microbial responses to sudangrass measured in our microplot study did not indicate that microbial populations differ between the two soil types, and therefore could not account for the differences in disease response observed in the original field studies. While soil and root populations of *V. dahliae* were reduced by the sudangrass green manure after two years in the loam, the microbial populations and activity measured were

not different from those in the sandy loam. Sudangrass increased *Fusarium* root populations and fluorescent pseudomonad soil populations in both soil types as well. It is possible that the techniques used to measure microbial responses were not sensitive enough to differentiate subtle differences in microbial activity that could be responsible for the disease suppression in Idaho or the disease enhancement in Washington.

To try to determine whether microbial activity, and not only abiotic changes in the soil, is responsible for the suppression of Verticillium wilt in Idaho following sudangrass, a mixture treatment was created in 1997. It has been observed that conducive soils can be made suppressive by mixing with a suppressive soil suggesting that soil microflora are responsible for the disease suppression (12,83). To illuminate whether microflora may be involved in the suppressiveness of the Idaho sudangrass treatment, we created a mixture to test whether the suppressiveness could be transferred to the disease conducive Washington soil. The response variables measured in the mixture treatment were not consistently different from either of the components. Averaged over the season, *Fusarium* root populations in the mixture soil was the only microbial variable that was significantly different from either of the original components. This lack of difference from the source components indicates that an additive effect of the soil components was measured and no detectable shifts in microbial populations occurred when the soils were mixed.

If the suppression of potato early dying by a sudangrass green manure is regulated by a change in microbial populations or activities, the change is likely subtle. Just as Hornby (45) concluded that suppressive soils require a special set of circumstances, the suppression of potato early dying by a sudangrass green manure may require specific

native microflora, although the differences between soil may be too subtle to be detected by the methods used in this microplot study. There was no evidence from this microplot experiment in the Columbia Basin that total soil microbial activity or microorganism populations differ between the soil types from Idaho and Washington. In addition, there was no evidence that microbial populations or activity in the microplot soil were consistently affected by a sudangrass green manure. Therefore, because of the lack of differences, the microbial responses investigated cannot account for the suppression and enhancement of potato early dying observed in Idaho and Washington. Despite the inconsistent effect of a sudangrass green manure on potato early dying between these two locations, the use of green manures can be beneficial agronomically especially to improve soil health (6,72). The influence of a variety of green manure crops on potato early dying may have to be investigated in a variety of locations though in order for growers to make economically and ecologically profitable decisions in attempting to manage this disease with a green manure.

CHAPTER 2

Lack of Early Dying Suppression in Potatoes in the Columbia Basin by a Sudangrass Green Manure in Two Soil Types

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ABSTRACT

The effect of identical sudangrass green manure treatments on early dying of potatoes grown in soil from Idaho and Washington was evaluated in a field microplot experiment in the Columbia Basin. In previous field experiments, compared to a fallow control, a sudangrass green manure treatment suppressed potato early dying by 25 to 85 % in Idaho, but enhanced disease severity, by 8 to 29 %, in Washington. Potato cv. Russet Burbank was grown in identical sudangrass and fallow soil treatments from these original study sites in microplots in the Columbia Basin in 1996 and 1997. Washington soil populations of *V. dahliae* were 56.2 and 62.7 % ($P = 0.0001$) lower than in Idaho soil. *V. dahliae* root populations in Washington treatments were 63.6 and 61.3 % ($P = 0.0001$) lower than in Idaho treatments. Sudangrass did not affect pathogen populations among the Washington soil treatments. Compared to the fallow control, a sudangrass green manure in Idaho soil decreased *V. dahliae* soil and root populations, by 20.4 and 41.2 % ($P \leq 0.05$), in 1997. Measured as the area under the senescence progress curve (AUSPC), disease severity did not differ among treatments in either year. Accordingly, apical stem populations of *V. dahliae* did not differ among treatments. Yield was not affected by sudangrass and differed between soil types only in 1996 where yield in Washington soil was 31.5 % larger than in Idaho soil. Because a sudangrass green manure in Idaho soil did not affect disease severity, yield, or *V. dahliae* stem populations when potato was grown in the Columbia Basin, the macroenvironment may be interacting with the green manure to regulate the disease suppression in Idaho, and conversely, the lack of disease suppression observed in Washington.

INTRODUCTION

Potato early dying, caused primarily by the soilborne fungus *Verticillium dahliae* Kleb., is a constraint to potato (*Solanum tuberosum* L.) production in many areas of the United States (74). Recommended management strategies for this disease include soil fumigation, crop rotation, and resistant cultivars. In practice, however, these strategies can be difficult to implement. For example, soil fumigation is expensive and its use is likely to be restricted in the future (74), crop rotations are often impractical as microsclerotia of the pathogen can survive in soil for more than 8 yr, and few resistant cultivars are accepted by the industry (75).

Specific crop rotations and green manure crops are alternative management tactics for Verticillium wilt that are being investigated currently. The degree of disease suppression with rotations and green manures however, has been variable, with the reasons for this variability being only poorly understood. Nelson (70) reported no suppression of the disease in peppermint even after 12 years of fallow or non-host crops. In contrast, Green (39) reported a decrease in incidence of Verticillium wilt of peppermint following a 5 year corn rotation. Subbarao and Hubbard (87) observed lower incidence of wilt in cauliflower following a broccoli green manure in coastal California. A green pea-sudangrass green manure crop in Washington did not suppress Verticillium wilt of potato but did reduce stem populations of *V. dahliae* and increased tuber yield (25).

A recent field study in Idaho (18) reported that among a variety of green manure crops grown consecutively for 2 or 3 yr prior to cropping of potato, the incidence of

Verticillium wilt was most effectively suppressed by sudangrass (*Sorghum vulgare* var. *sudanese*) compared to a weed-free fallow. Davis et al (18) observed decreases in the incidence of late season Verticillium wilt symptoms of approximately 25 to 65% following 2 consecutive yr of a sudangrass green manure and 60 to 85 % following 3 yr of consecutive cropping of sudangrass. This disease suppression was correlated with a decrease in population size of *V. dahliae* in the stem apex. Following the 2- and 3-yr sudangrass green manures, total tuber yield increased 30 and 38%, respectively, compared to the weed-free fallow control.

Identical sudangrass green manure treatments in the Columbia Basin of southcentral Washington, however, increased disease severity (14). The addition of a sudangrass green manure for 1 or 2 yr increased disease severity in subsequent potato crops, measured by area under the senescence progress curve (AUSPC), by 29 and 8% compared to a fallow control (14). The green manure treatments had minimal effect on tuber yield as yield from the sudangrass treatments were not significantly ($P \leq 0.05$) different from the fallow.

The discrepancy in results between the two sites raises several questions. Because sudangrass field experiments were ongoing at both the Idaho and Washington locations, a unique opportunity was presented to determine whether the conflicting results from these studies were due to differences in the macroenvironments between the study sites. Field microplot experiments have been used successfully in previous studies on both potato early dying and green manure or cover crops. The effect of irrigation treatments (15,16), different soil types (33), and presence of *Pratylenchus penetrans* (59) on potato early dying are among previous field microplot experiments. The influence of green manures

and cover crops on the fungus *Cylindrocladium crotalariae* (9) and nematodes *Meloidogyne hapla* (7) and *M. chitwoodi* (64) also have been investigated using field microplots. The objective of our microplot study was to measure the effect of a sudangrass green manure on severity of potato early dying, population size of *V. dahliae* in soil, root, and stem apices, and tuber yield of potato grown in soil from Idaho and Washington at a common location in field microplots.

MATERIALS AND METHODS

Soil treatment origins.

A microplot field experiment was conducted in 1996 at the Hermiston Agricultural Research and Extension Center in the Columbia Basin of northcentral Oregon and in 1997 at the AgriNorthwest Research Facility in the Columbia Basin of southcentral Washington. Treatments were created by the transfer of soil from established field experiment plots in southcentral Washington and southeastern Idaho to the microplot field site. From these sites, soil was removed from plots that had been subjected to fallow or sudangrass green manure treatments (Table 2.1).

For the Idaho soil treatments, sudangrass (*Sorghum vulgare* var. *sudanense* variety HS-33) was grown as a green manure at the University of Idaho Research and Extension Center at Aberdeen, ID (elevation 1341 m, 130 day growing season, Delco loam soil type) in 1995. Sudangrass seed was drilled in late May and plants were disked in late August to constitute a 1 yr green manure treatment. In 1996, sudangrass was again grown in the same plots to establish a 2 yr green manure treatment. Weed-free fallow

control plots also were maintained in 1995 and 1996. For the Washington soil treatments, sudangrass (*Sorghum vulgare* var. *sudanense*) was grown as a consecutive green manure in 1994, 1995, and 1996 at the AgriNorthwest Research Facility, Plymouth, WA (elevation 185 m, 150 day growing season, Quincy fine sandy loam soil type) along with weed-free fallow control plots. Sudangrass was drilled 15 May (99 kg/hA) and disked 15 August. In 1996, these field plots provided soil that had been cropped for 1 or 2 yr to sudangrass. In 1997, 2- and 3-yr green manure treatments were used.

TABLE 2.1. Sudangrass green manure and fallow treatments established in Idaho and Washington and used in a microplot experiment in the Columbia Basin.

	Growing Season					
	Field Treatments			Columbia Basin Microplot Experiment[a]		
Field Plot	1994	1995	1996	Treatment	1996	1997
ID-F S1/S2[b]		Fallow Sudangrass	Fallow Sudangrass	ID-F	+	+
				ID-S1	+	-
				ID-S2	-	+
WA-F S1/S2[b]		Fallow Sudangrass	Fallow Sudangrass	WA-F	+	+
				WA-S1	+	-
S2/S3[c]	Sudangrass	Sudangrass	Sudangrass	WA-S2	+	+
				WA-S3	-	+

[a]Potatoes were grown in microplots in 1996 and 1997 in the Columbia Basin. Soil in microplots originated from green manure treatments in large scale field plots in Idaho (ID) and Washington (WA) established between 1994 and 1996.
[b]Plot yielded 1 yr (S1) and 2 yr (S2) sudangrass green manure treatments for microplots in 1996 and 1997, respectively.
[c]Plot yielded 2 yr (S2) and 3 yr (S3) sudangrass green manure treatments for microplots in 1996 and 1997, respectively.

Microplot establishment.

In early April 1996, fallow and 1 yr sudangrass green manure soil from Idaho was hand-shoveled into separate 730-L wooden crates and transported by a semi-truck to the study site in Oregon where it was transferred to cylindrical plastic pots (28-L, 35 cm high X 29 cm inside diameter) (Anderson DIE MFG® #6 Deep, OBC NW Inc., Canby, OR) with a hole 5.5 cm in diameter bored in the bottom for drainage. The fallow, 1 and 2 yr sudangrass green manure soil from Washington was hand-shoveled directly into the plastic pots and transported to the Oregon experiment site in mid-April. The treatments (5) were arranged in a randomized complete block design and replicated 50 times. Pots were buried upright to an approximate depth of 30 cm in rows spaced 1.5 m apart on 0.61 m centers.

During the second week of April 1997, fallow and 2 yr green manure soils from the Idaho location were transported to Washington as in 1996. Soil that had been fallow or cropped for 2 or 3 consecutive years to a sudangrass green manure at the Washington site was hand-shoveled directly into pots. A sixth treatment was created by mixing equal amounts of the Idaho 2 yr sudangrass soil and the Washington fallow soil in a 0.7 m^3 cement mixer. Experimental design and plot establishment were as described in 1996.

Generation III seed potatoes (*Solanum tuberosum* cv Russet Burbank), obtained from Madras Produce Co. in Madras, OR were cut into single eye seed pieces with a 2.5 cm melon scoop. Seed pieces were presprouted for 10 days in sterile moist vermiculite at 20 C. During the last week of April in 1996, one seed piece was planted 8 cm deep in the center of each of 200 pots and two seed pieces were planted in each of 50 pots for early season destructive sampling in 10 blocks. During the first week in May in 1997, one seed

piece was planted in 240 pots and two seed pieces in 60 pots for early season sampling. The field was irrigated with a line source in 1996 and with a lateral move system in 1997. In late May 1996, each pot was fertilized by hand with a soluble mixture of Peters Professional® 30-10-10 NPK fertilizer to provide 26.9 kg of N, 8.9 kg of P, and 8.9 kg of K per ha. In 1997, dry fertilizer was applied to the Washington plots in early April, prior to microplot establishment at a rate of 168 kg/ha N, 168 kg/ha P, 392.9 kg/ha K, 22.41 kg/ha Mg, and 2.23 kg/ha Bo per acre. In early June, this same fertilizer mixture was applied by hand to the microplots containing Idaho soil. In 1997, a N-P-K solution (10-30-10) was injected into the irrigation system throughout the season.

In 1996, weeds were controlled in the interplot area by applying the herbicide metribuzin (Sencor®, Bayer Corp., Kansas City, MO) at planting, in early July, and in late July. Microplots were hand weeded weekly beginning in July. In early June, imidiacloprid (Admire® 2 F, Bayer Corp., Kansas City, MO) was injected into each pot with a syringe at a rate of 3.36 kg/ha to prevent Colorado potato beetles. Metribuzin was sprayed prior to field establishment in 1997 and rows were hand weeded throughout the season. In late May, sethoxydim (Poast®, BASF, Research Triangle Park, NC) was sprayed between the rows to control volunteer corn. In early July, disulfoton (Di-syston®, Bayer Corp., Kansas City, MO) was sprayed on the field to control a Colorado potato beetle infestation.

Verticillium soil and root populations.

Plants and soil were harvested from randomly selected microplots throughout the growing season. Soil was sampled at planting in 1996 and 1997 and both soil and plants

were sampled at 3, 5, 7, and 9 (1997), and 11 wk (1996) following 80% emergence. Degree days after planting (DDAP) at each sampling date were calculated by the methods of Baskerville and Emin (5).

Soil samples were taken from the top 20 cm of randomly selected microplots with a hand trowel, placed in plastic bags and transported on ice to Corvallis, OR where they were stored at 5 C until processed within 48 hr for *V. dahliae* populations. A total of five and seven treatment replicate samples were collected at each sampling date in 1996 and 1997, respectively. The entire root balls of potato in randomly selected microplots were harvested and placed in a paper bag. The roots were transported on ice to Corvallis, OR where they were stored at 5 C and processed within 24 hr for *V. dahliae* populations. A total of 10 treatment replicate samples were represented. In 1996, two plants were sampled at the two early season sampling dates from each of five replicate pots per treatment. In 1997, at each of these early plant sampling dates, one plant was sampled from each of 10 replicate pots.

Approximately 20 g of each soil sample was dried for at least 14 days in plastic weigh boats at room temperature (20-24 C). The dried soil was ground with a ceramic mortar and pestle and two 0.20 g subsamples per sample were plated on Sorensen's modified NP-10 medium (86) using an Andersen air sampler (Andersen Samplers Inc., Atlanta, GA) (13). Plates were incubated at room temperature (20-24 C) in the dark for 10 days. Soil was washed from the agar surface under running tap water and *V. dahliae* colonies were counted under a stereoscope. *V. dahliae* soil populations were estimated as colony-forming-units per gram dry soil (CFU/g soil).

Within 24 hr after sampling, potato root balls were rinsed with distilled water to remove adhering soil. Roots were hand-cut into 1 cm long segments and a total of 80 root segments per sample were plated on NP-10 medium. *V. dahliae* colonies growing from root pieces were counted after 10 days incubation at 20 C in the dark using a dissecting microscope. Root populations were estimated as colony-forming-units per root length (CFU/cm).

Disease and yield.

Twenty replicate microplots per treatment, for a total of 100 pots in 1996 and 120 pots in 1997, were designated for disease assessment, stem assay for *Verticillium*, and fresh tuber yield. Beginning in early July, plants were rated weekly for percent of foliar senescent tissue. Senescence progress curves were produced using the percent senescence over time in degree days after planting (DDAP, base = 12.8 C) using the method of Baskerville and Emin (5). Area under the senescence progress curve (AUSPC) (84) was calculated using the equation:

$AUSPC=\Sigma[((\%\ \text{senescence}\ (\text{time}_{(x+1)}) + (\%\ \text{senescence}\ (\text{time}_{(x)}))/2*(\text{time}_{(x+1)} - \text{time}_{(x)})]$.

In mid September, microplots were lifted by hand, and the fresh weight of tubers was measured.

***Verticillium* stem populations.**

In early August 1996, and late July and mid-August 1997, the first three fully developed leaves from the top of the plant were sampled from the microplots on which

disease readings were taken. Because of the small amount of tissue, leaf petioles were bulked to form 10 replicate samples; each consisting of six petioles for each treatment. Petioles were stripped of leaves and dried in paper envelopes at room temperature (20-24 C) for 2 mo. The tissue was ground in a Thomas-Wiley™ Intermediate Mill (Arthur H. Thomas Co., Philadelphia, PA) with a #20 mesh screen. Ground tissue was plated on Sorensen's NP-10 medium using an Andersen air sampler. Plates were incubated at 20-24 C in the dark for 10 days. Colonies were counted and populations of *V. dahliae* were estimated as colony-forming-units per gram dried stem tissue (CFU/g).

Data analyses.

Response variables underwent an analysis of variance (ANOVA) using SAS, version 6.12, PROC GLM (80) according to a one-way treatment structure model (with no interaction term for soil type x manure treatment). Soil, root, and stem population data were transformed (ln(x+1)) to meet the ANOVA assumption of a normal distribution. Means were separated by Fisher's protected least significant difference (LSD) test. Linear contrasts between treatment groups were performed if the ANOVA F-statistic was significant.

Nutrient analyses.

Soil samples at planting were analyzed for nutrients (calcium, magnesium, manganese, nitrate-nitrogen, phosphorous, potassium, sodium, zinc), pH, and percent organic matter. In 1997, petioles were sampled for nutrient analyses. In late May and

again in mid August, one petiole (the fourth or fifth leaf from the top of the plant) was sampled from each of 10 replicate plants per treatment. Petiole samples were analyzed for nitrate nitrogen, total phosphorous and potassium by the Central Analytical Laboratory, Department of Crop and Soil Science, Oregon State University. Interpretation of nutrient concentrations in petioles were based on critical nutrient ranges established for potatoes (88).

RESULTS

Verticillium soil populations.

Soil populations of *V. dahliae* fluctuated throughout the growing season and differences among treatments were not consistent across time. Regardless of soil type or green manure treatment, populations were highest at planting in early May. Within soil type, populations in the fallow and sudangrass treatments differed only in the Idaho loam soil in 1997 (Table 2.2). Averaged over the 1997 season, the loam green manure treatment population was 20.4 % smaller ($P \leq 0.05$) than the fallow. Populations were smaller in the Washington sandy loam compared to the Idaho loam in both years. Season average *V. dahliae* populations in the sandy loam treatments was 56.2 and 62.7% smaller ($P = 0.0001$ and $P = 0.0001$) than in the loam in 1996 and 1997, respectively.

The mean soil population in the ID-WA mixture treatment did not differ at any date from populations in either of the component soils ($P > 0.05$). Averaged over the season, though, the population in the fallow Washington sandy loam was 26.2% smaller ($P \leq 0.05$) than the mixture population.

TABLE 2.2. Effect of a sudangrass green manure on the population dynamics of *Verticillium dahliae* in microplots containing Idaho and Washington soil.

	ln CFU/g soil											
	1996						1997					
Treatment	0[a]	162	231	344	656	Season Average	0	171	277	356	479	Season Average
ID-F[b]	3.51 A[h]	1.81 AB	1.63 AB	2.27 A	2.96 A	2.62 A	3.49 A	3.02 A	1.95 A	1.67 A	2.41 A	2.54 A
ID-S1[c]	3.02 AB	2.46 A	2.85 A	2.32 A	2.88 A	2.75 A	-	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	-	3.46 A	1.88 BC	2.05 A	1.38 AB	1.53 B	2.02 B
WA-F[b]	2.69 BC	0.35 BC	0.72 B	0.0 B	1.71 AB	1.36 B	2.11 B	1.69 BC	1.32 AB	0.92 B	1.70 AB	1.53 C
WA-S1[c]	1.91 CD	0.0 C	1.02 B	0.84 B	0.93 B	1.10 B	-	-	-	-	-	-
WA-S2[d]	1.62 D	0.87 ABC	0.95 B	0.38 B	0.98 B	1.07 B	2.02 B	0.93 C	0.80 B	0.71 B	1.72 AB	1.23 C
WA-S3[e]	-	-	-	-	-	-	1.28 C	0.98 C	1.09 B	1.34 AB	1.92 AB	1.31 C
MIX[f]	-	-	-	-	-	-	3.23 A	2.29 AB	2.03 A	0.87 B	2.10 AB	2.08 B
P value[g]	0.0001	0.0372	0.1236	0.0007	0.0098	0.0001	0.0172	0.0009	0.0016	0.0361	0.0878	0.0001

[a]Degree days after planting.
[b]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

***Verticillium* root populations.**

Relative root populations of *V. dahliae* fluctuated throughout the season and significant differences among treatments, if any, were not consistent over time. In contrast to soil populations, root populations remained relatively stable over the season with no clear trends over time. Regardless of treatment, recovered root populations peaked late in the growing season in 1996 at 660 DDAP. But in 1997, at the last sampling date at 470 DDAP, root population sizes were similar to those recovered at earlier dates.

Consistent with soil population sizes, smaller root populations were recovered from the Washington compared to Idaho soil treatments (Table 2.3). Averaged over the season, root populations in Washington sandy loam were 63.6 and 61.3% smaller ($P = 0.0001$ and $P = 0.0001$) than in Idaho loam in 1996 and 1997, respectively. Only a sudangrass green manure grown for 2 yr in the Idaho loam affected root populations. The season average *V. dahliae* root population in this 2 yr sudangrass treatment was 41.2% smaller ($P \leq 0.05$) than the fallow.

Averaged over the 1997 season, the *V. dahliae* root population in the ID-WA mixture treatment differed from the mean of the two components ($P = 0.0007$). Yet, the mixture population differed significantly only from the population in the Washington soil component. Root populations from the Idaho and Washington soil components were 27.2 and 69.5 % smaller ($P > 0.05$ and $P \leq 0.05$) than the mixture.

TABLE 2.3. Effect of a sudangrass green manure on the population dynamics of *Verticillium dahliae* recovered from roots of potato cv. Russet Burbank grown in microplots containing Idaho and Washington soil.

	ln CFU/cm root									
	1996					1997				
Treatment	162[a]	231	344	656	Season Average	171	277	356	479	Season Average
ID-F[b]	0.10 B[h]	0.16 A	0.07 A	0.22 AB	0.14 A	0.18 A	0.11 A	0.18 A	0.10	0.14 A
ID-S1[c]	0.24 A	0.12 AB	0.07 A	0.36 A	0.20 A	-	-	-	-	-
ID-S2[d]	-[i]	-	-	-	-	0.09 B	0.05 B	0.09 AB	0.07	0.08 BC
WA-F[b]	0.0 B	0.01 C	0.03 AB	0.17 B	0.07 B	0.01 C	0.04 BC	0.01 B	0.09	0.03 D
WA-S1[c]	0.06 B	0.02 C	0.0 B	0.13 B	0.06 B	-	-	-	-	-
WA-S2[d]	0.01 B	0.05 BC	0.01 B	0.15 B	0.06 B	0.02 C	0.02 BC	0.03 B	0.13	0.05 CD
WA-S3[e]	-	-	-	-	-	0.01 C	0.01 C	0.02 B	0.11	0.04 D
MIX[f]	-	-	-	-	-	0.09 B	0.09 A	0.15 A	0.09	0.11 AB
P value[g]	0.0056	0.0289	0.0199	0.0243	0.0001	0.0001	0.0001	0.0053	0.7157	0.0001

[a]Degree days after planting.
[b]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 1 yr.
[d]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[e]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[f]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[g]Probability of obtaining $F \leq_{0.05}$.
[h]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[i]not evaluated.

Symptom development.

Foliar symptoms of leaf chlorosis and necrosis were first observed at 344 and 356 DDAP in 1996 and 1997, respectively. AUSPC values did not differ among treatments in either year (P = 0.4641 and P = 0.2559, respectively) (Table 2.4).

Yield.

In 1996, mean tuber weight among treatments ranged from 0.97 to 1.44 kg/microplot (Table 2.4). Yield did not differ between the green manure and fallow treatments within a soil type, but mean yield of the Washington sandy loam treatments was 31.5% larger (P = 0.0001) than that of the Idaho loam treatments. In 1997, mean yield among all treatments ranged from 1.83 to 2.14 kg/microplot; however, there was no difference in yield among the treatments (P = 0.2959) within or across soil type.

***Verticillium* stem populations.**

Mean apical stem populations of *V. dahliae* among treatments ranged from 9.9 to 71.3 CFU/g dried stem tissue in 1996, and 16.5 to 240.3 CFU/g in 1997 (Table 2.5). Differences among soil treatments or types were not significant in either year (P = 0.3006 and P = 0.1310, respectively).

TABLE 2.4. Effect of sudangrass green manure on area under the senescence progress curve (AUSPC) and fresh tuber yield for Russet Burbank potatoes grown in microplots containing Idaho and Washington soil.

	AUSPC		Yield (kg/microplot)	
Treatment	1996	1997	1996	1997
ID-F[a]	28324 A[g]	19433 A	0.96 C	2.08 A
ID-S1[b]	25601 A	-[h]	1.12 BC	-
ID-S2[c]	-	18957 A	-	1.89 A
WA-F[a]	28669 A	20153 A	1.35 A	1.85 A
WA-S1[b]	32086 A	-	1.33 AB	-
WA-S2[c]	31883 A	16471 A	1.44 A	1.83 A
WA-S3[d]	-	17749 A	-	2.14 A
MIX[e]	-	20501 A	-	1.89 A
P value[f]	0.4641	0.2559	0.0004	0.2959

[a]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[b]Soil cropped to a sudangrass green manure for 1 yr.
[c]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[d]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[e]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[f]Probability of obtaining $F \leq_{0.05}$.
[g]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[h]not evaluated.

Nutrient analyses.

The soil chemical characterization results were used for post-planting fertilization recommendations. The lower nitrate-nitrogen and phosphorous amounts in Idaho loam soil was due to a pre-plant fertilization of the Washington field soil prior to its transport to microplots (Table 2.6). The Idaho loam contained a higher percent organic matter than the Washington sandy loam. Although a sudangrass green manure was grown in Idaho for 1 year and Washington for 2 years, the percent organic matter in these treatments was

not increased compared to the respective fallow soils in 1996. In 1997, higher organic matter was observed in all sudangrass treatments compared to the respective fallow

TABLE 2.5. Effect of sudangrass green manure on apical stem populations of *Verticillium dahliae* in potato cv. Russet Burbank grown in microplots containing Idaho and Washington soil.

	ln CFU/g dried apical stem	
Treatment	1996	1997
ID-F[a]	4.27 A[g]	3.71 A
ID-S1[b]	3.23 A	-
ID-S2[c]	-[h]	2.80 A
WA-F[a]	2.49 A	5.48 A
WA-S1[b]	2.31 A	-
WA-S2[c]	2.29 A	3.81 A
WA-S3[d]	-	5.21 A
MIX[e]	-	4.75 A
P value[f]	0.3006	0.1310

[a]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[b]Soil cropped to a sudangrass green manure for 1 yr.
[c]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[d]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[e]Mixture treatment in 1997 consists of equal proportions of ID-S2 and WA-F soil.
[f]Probability of obtaining $F \leq_{0.05}$.
[g]Means followed by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's protected least significant difference test.
[h]not evaluated.

although the differences in the sandy loam were slight. Larger amounts of nitrate-nitrogen were obtained from sudangrass treatments in both soil types. Among the other soil nutrients, there were few consistencies in comparing sudangrass and fallow treatments in the two soil types in both 1996 and 1997.

Although higher nitrate-nitrogen levels were obtained in the sudangrass amended soil, lower nitrate-nitrogen levels were present in potato petioles in the Idaho sudangrass

TABLE 2.6. Nutrient composition of soil from southeastern Idaho and southcentral Washington that were fallowed or cropped to a sudangrass green manure for 1 to 3 consecutive years.

Treatment			Soil Chemical Composition[a] (ppm)					(meq/g)		
1996	pH	% OM[b]	NO3-N	P	K	Mn	Zn	Ca	Mg	Na
ID-F[c]	8.1	3.77	7.9	31	343	5.2	1.24	35.0	3.0	0.11
ID-S1[d]	8.0	3.31	9.2	25	328	6.6	1.46	36.0	3.1	0.13
WA-F[c]	6.6	1.12	41.3	69	488	6.7	5.12	4.0	1.7	0.07
WA-S1[d]	7.2	1.18	54.6	42	335	9.4	6.40	4.4	1.5	0.06
WA-S2[e]	6.8	1.08	45.6	42	363	7.5	6.20	4.0	1.6	0.06
1997										
ID-F	8.4	3.72	8.6	6.0	367	5.5	1.28	33.0	2.9	0.09
ID-S2[e]	8.5	4.47	9.4	5.0	335	6.0	1.22	31.0	3.2	0.12
WA-F	5.6	1.27	34.5	89	441	6.3	4.84	2.9	1.1	0.03
WA-S2	5.5	1.28	46.4	94	410	7.9	4.42	2.9	1.1	0.04
WA-S3[f]	5.5	1.36	49.6	96	511	7.8	5.22	2.7	1.0	0.02
MIX[g]	8.2	2.94	21.2	5.0	382	5.8	2.34	28.0	2.6	0.09

[a]Soil nutrient analysis conducted on bulked soil samples collected at potato planting. Analyses were performed by the Central Analytical Laboratory, Department of Crop and Soil Science, Oregon State University.
[b]Percent organic matter lost on ignition.
[c]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[d]Soil cropped to a sudangrass green manure for 1 yr.
[e]Soil cropped to a sudangrass green manure for 2 consecutive yr.
[f]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[g]Mixture treatment consists of equal proportions of ID-S2 and WA-F soil.

treatment (Table 2.7). Compared to the fallow, slightly higher amounts of nitrate-nitrogen were obtained in potato grown in sudangrass amended soil from Washington. Although fertilization was identical for soil from both Idaho and Washington after planting, higher nitrate-nitrogen levels were found in plants grown in the Idaho loam. The petiole levels of phosphorous and potassium were similar between the two soil types. The percent of phosphorous and potassium in the petiole samples from sudangrass treatments was not consistently higher or lower than fallow treatments.

TABLE 2.7. Nutrient composition in petioles of potato cv. Russet Burbank grown in microplots containing fallow and sudangrass green manure soil treatments from southeastern Idaho and southcentral Washington.

	Petiole Nutrient Composition[a]		
	ppm	%	
Treatment	NO3-N	P	K
ID-F[b]	14951	0.430	7.21
ID-S2[c]	13994	0.495	7.05
WA-F[b]	11153	0.420	6.78
WA-S2[c]	12881	0.470	6.97
WA-S3[d]	11819	0.425	6.95
MIX[e]	10964	0.435	7.02

[a]Nutrient analysis conducted on bulked petiole samples collected 8/12/97. Analyses were performed by the Central Analytical Laboratory, Department of Crop and Soil Science, Oregon State University.
[b]Weed-free fallow soil treatments from Idaho (ID) and Washington (WA).
[c]Soil cropped to a sudangrass green manure for 2 yr.
[d]Soil cropped to a sudangrass green manure for 3 consecutive yr.
[e]Mixture treatment consists of equal proportions of ID-S2 and WA-F soil.

DISCUSSION

Severity of potato early dying was not affected by a sudangrass green manure in soil from either Idaho or Washington in this microplot study. Corresponding with this lack of a disease response, green manure treatments did not affect stem populations of *V. dahliae* or tuber yield. In addition, there was no difference in disease or stem populations between the soil origins, whereas a difference in tuber yield between the soils was observed only in 1996. These results were surprising given that in the Idaho field study (18), sudangrass suppressed disease, reduced pathogen stem populations, and increased tuber yield and in the Washington field study, disease severity was higher but yield was unaffected after a sudangrass green manure (14). Because sudangrass had no effect on these variables when potato was grown in Idaho soil treatments in the Columbia Basin, the macroenvironment may be interacting with sudangrass to regulate disease suppression in Idaho, and conversely, the lack of disease suppression observed in the Washington study.

The lack of effect of soil origin on yield in 1997 was consistent with a previous study with transported soils. In an Ohio microplot study involving three soil types in one location, including a silt loam and a fine sand type, Francl et al (33) reported little influence of soil type on severity of potato early dying or tuber yield. As no differences in disease severity were observed in the Columbia Basin microplot study, the significantly higher yield in the Washington soil in 1996 may be attributed to differences in the macroenvironment. The Ohio study indicated that among the treatments, differences in disease were larger between years based more on differences in soil moisture and air

temperatures between years of the study than on soil type. Higher temperatures and lower moisture levels favored higher disease severity and lower yields (33). Higher mean temperatures, by 1.2 C, were recorded in 1997 but monthly growing season mean temperatures in 1997 ranged from 1.2 C lower to 3.0 C higher than 1996. Although not measured, differences in soil moisture levels in this Columbia Basin microplot study, based on sprinkler and lateral move irrigation systems in 1996 and 1997 respectively, may have contributed to differences in yield between years.

Although there was no difference in *V. dahliae* stem populations, disease severity, or yield between the soils, larger soil and root populations of *V. dahliae* were recovered from Idaho sudangrass and fallow treatments compared with Washington. While sudangrass did not affect *V. dahliae* populations in the Washington soil, the 2 yr sudangrass green manure treatment in Idaho soil reduced both soil and root populations. Still, this reduction of soilborne inoculum in the Idaho soil was not reflected in significantly reduced disease severity or *V. dahliae* apical stem populations. Again, the macroenvironment of the Columbia Basin and southeastern Idaho may regulate the responses of potato early dying to a sudangrass green manure.

It has been shown in a variety of other studies that the severity of potato early dying and effects on yield can be influenced by external abiotic factors, particularly temperature and moisture (75). These field studies have reported that disease development and effects on yield may differ between years or between locations based particularly on air temperature. Corresponding to optimal growth temperature ranges of potatoes and *V. dahliae*, disease severity in potatoes increases as air temperature increases from 20 to 28 C (42,71). In a multilocation Ohio study (34), warmer late season

average temperature of 24 C resulted in more severe disease and lower tuber yields in soil infested with *V. dahliae*, compared to a cooler average temperature of 20 C which resulted in little change in tuber yields by the presence of *V. dahliae* (78). Similarly, Francl et al (34) reported that regression models based on field microplot studies in Ohio suggest that periods of high temperatures are negatively correlated with yield from infected plants. Johnson (49) demonstrated in a field study in Minnesota that under higher air temperatures (mean 23.3 C), the potato crop growth rate slows and potato early dying has a greater impact on yield. As the growing season mean air temperature in the Columbia Basin is 17.9 C compared to 15.7 C in southeastern Idaho (Table A.1), disease pressure may be greater at the Washington study site due to macroenvironment.

Because healthy potato senescence is influenced by environment, including temperature, soil moisture and soil nutrient levels, the effect of potato early dying on senescence rates can be secondary to environmental effects (33). In support of this suggestion, a study reported that very warm air temperatures may mask differences in severity of Verticillium wilt of cotton according to a field study with tolerant and susceptible cotton varieties in the San Joaquin Valley of California (36). In a year with more days of high temperatures (above 35 C) and higher daily temperatures, less disease occurred compared to a cooler year. In the warmer year of the study, disease severity in susceptible and tolerant cotton strains was not as clearly separated as in the cooler season year. A similar situation may occur between the field studies in the Columbia Basin and southeastern Idaho. During the growing season, mean daily temperatures in the Columbia Basin are higher, by an average 3.5 C, than the Idaho study site (Table A.1). Also, accumulated growing degree days (DDAY) are higher in the Columbia Basin, by 213 to

688 DDAY based on degrees Fahrenheit (Table A.1). If the influence of a sudangrass green manure on potato early dying is dependent on air temperatures, or if differences are extremely subtle, the longer season and warmer temperatures of the Columbia Basin of Washington compared to Idaho, may not allow separation of treatment effects. These warmer temperatures may be the reason no treatments differences were observed between the Idaho soils when located in the Columbia Basin.

This relation of disease severity and temperature may be explained by the biology of potato early dying and the difficulty in measuring disease as plant senescence rates. Vascular diseases tend to be favored by conditions of soil moisture and evapotranspiration conditions that allow a rapid flow of water which also carries conidia of the pathogen through the plant's vascular system (17). Harrison (42) proposed that the wilting associated with potato early dying is due to a reduction in transpiration in plants infected with *Verticillium*. As evapotranspiration is reduced under warmer temperatures in all plants, infected or not, differences between normal senescence and that due to *Verticillium* may be reduced, thus decreasing the level of detection of treatment differences.

Although soil nutrient concentrations have been reported to influence the severity of Verticillium wilt (19), there is no evidence from the original Idaho field experiment (18) or our microplot study to suggest a sudangrass green manure suppresses or enhances this disease based on changes in nutrient concentrations. Davis et al (18) could not demonstrate a significant relationship between pre-plant nutrient levels with disease suppression or *V. dahliae* stem colonization following green manure treatments. Because soil nutrient concentrations in soil in the microplots were not consistently higher or lower

than the fallow following a sudangrass green manure, no conclusions can be made whether nutrients are a regulator of the response of potato early dying to sudangrass. As petiole nutrient concentrations were within the marginal range for nitrate nitrogen and sufficient range for potassium and phosphorous for potato (88), no nutrient deficiencies were present that might mask or enhance differences in wilt severity estimation.

The lack of differences in *V. dahliae* stem populations between any of the treatments, regardless of soil type, corresponds with the lack of disease response to sudangrass in the microplot study. Although mean soil populations of *V. dahliae* in the Idaho soil were larger than the Washington populations, this inoculum density difference was not reflected in stem population sizes. This observation is consistent with a soil solarization study (20) in which there was no relation of *V. dahliae* stem populations to soil populations. A true test of the hypothesis that the macroenvironment influences the effect of a green manure on potato early dying would be to repeat the microplot study at the Idaho study site with Washington and Idaho soil treatments to observe whether Washington sudangrass treatment differences occur in the shorter, cooler Idaho season.

The conflicting results from the Idaho and Washington sudangrass studies resemble other recent sudangrass and nematode experiments. A field study attempting to suppress root lesion nematode, *Pratylenchus* spp., populations using a sudangrass green manure reported results that conflicted with other studies (58). While previous experiments (24,32,57) reported that sudangrass and sorghum-sudangrass green manures negatively affected root lesion nematode populations, no suppression of *Pratylenchus* spp. populations were reported following green manure treatments identical to the original studies. In fact, similar to results from the Washington study (14) in which potato

early dying severity increased following sudangrass, increased nematode populations were found in green manure soil discounting any nematicidal properties of sudangrass residue. MacGuidwin and Layre (58) speculated that the nematode studies could not be compared directly as theirs was a field study using indigenous nematode populations and different population density units compared with the greenhouse studies with inoculated nematode populations.

The strength of the Columbia Basin microplot study was that the effect of identical sudangrass green manures in two soils could be compared directly as the soil was in the same location, under the same environmental influences. As the suppression of potato early dying observed in Idaho was not replicated in the Columbia Basin of Washington in either Washington soil or transported Idaho soil, differences in the environment may explain why green manures do not affect disease or pathogens uniformly. Understanding the limitations of green manures to suppress plant diseases is key to their applicability in integrated pest management systems.

SUMMARY

Idaho and Washington soils revealed little difference in microbial activity, microbial populations, and physiological characterization. Although total microbial activity increased in soil cropped to sudangrass, populations of total bacteria, actinomycetes, and *Fusarium* were unaffected. Fluorescent pseudomonad populations in soils manured with sudangrass were higher in both Idaho and Washington soils, but significantly so only in one of the two years of the microplot study at each location. Although *Fusarium* root populations were larger in sudangrass soil from Idaho and Washington in separate years, this response was not replicable between years. There was little difference among soil types or treatments in the percentages of *Fusarium* species that were identified from root isolates. No differences in physiological characterization of rhizosphere bacteria communities, based on Biolog GN microplates, was evident among treatments.

Soil and root populations of the causal pathogen of potato early dying, *Verticillium dahliae*, were larger in Idaho soil compared with Washington. Sudangrass green manure treatments did not affect *V. dahliae* populations in the Washington soil. For the Idaho soil however, both soil and root populations of the pathogen were reduced by sudangrass, but only after 2 consecutive years of the green manure. Nonetheless, potato stem populations of *V. dahliae* in infected plants were not affected by soil or treatment in any season.

Under the environment of the Columbia Basin, severity of early dying of potatoes grown in microplots was not suppressed by a sudangrass green manure incorporated into

soils from Idaho or Washington. Because sudangrass did not affect disease severity in microplots in this common environment, differences in soil microbial properties owing to the incorporation of sudangrass could not be associated with differences in the disease response. Sudangrass green manures have suppressed potato early dying in the Snake Valley of Idaho, but did not when this soil was moved to the Columbia Basin. The warmer mean air temperatures in this latter location may increase the favorability of the environment to disease development and therefore reduce the suppressive response following a green manure treatment. A true test of the extent of regulation of symptom expression would be to repeat this experiment in the study site in southeastern Idaho.

Because the severity of potato early dying and its effect on yield are sensitive to environmental influences, the successful suppression of this disease by a sudangrass green manure may depend on location. Just as successful soil solarization requires a warm environment that receives sufficient amount of solar energy to heat the soil, disease suppression by a sudangrass green manure may require shorter and cooler growing areas such as southeastern Idaho. Sudangrass green manures increase total microbial activity in soil but this response variable does not necessarily differentiate between disease suppressive and disease conducive soils. Consequently, based on the results of this study, the role of a sudangrass green manure in the induction of microorganisms antagonistic to *V. dahliae* cannot be confirmed or discounted.

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APPENDIX

TABLE A.1. Historical maximum, minimum, mean temperatures and growing degree days (DDAY) data for green manure study locations in Idaho and the Columbia Basin of northcentral Oregon.

	Maximum (C)[a]		Minimum (C)[a]		Mean (C)		Growing DDAY[b]	
Month	ID[c]	CB[d]	ID	CB	ID	CB	ID	CB
Apr	13.9	18.1	-1.33	3.78	6.33	10.9		
May	19.3	22.7	3.05	7.67	11.2	15.2	273	401
Jun	24.6	27.2	7.22	11.6	15.9	19.4	685	911
Jul	29.9	31.1	9.72	13.9	19.8	22.5	1247	1563
Aug	29.2	30.7	8.22	13.3	18.7	22.0	1786	2184
Sept	23.2	25.6	3.22	8.56	13.2	17.1	2168	2643

[a]Maximum and minimum temperatures based on averages from 1961-1990 obtained from the Western Regional Climate Center.
[b]Average growing DDAYs accumulated from April based on average maximum-minimum temperatures (F) collected between 1914 and 1997 by Western Regional Climate Center.
[c]Data collected from University of Idaho Research and Extension Center in Aberdeen, Idaho.
[d]Data collected from Oregon State University Hermiston Agricultural Research and Extension Center, Hermiston, Oregon.

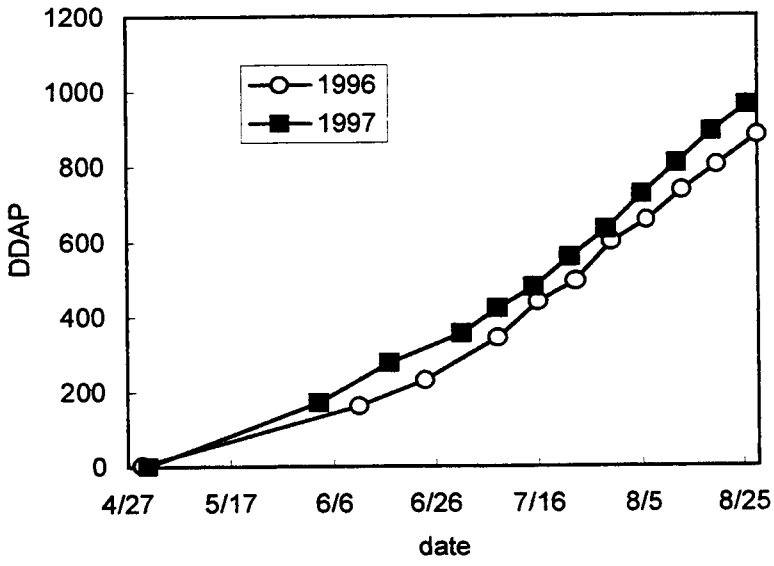

Figure A.1. Accumulated degree days after planting (DDAP, base 12.8 C) on sampling and disease reading dates for a microplot study in the Columbia Basin in 1996 and 1997.