Soil Biol. Biochem. Vol. 21, No. 3, pp. 403–408, 1989
Printed in Great Britain

0038-0717/89 $3.00 + 0.00
Pergamon Press plc

INFLUENCE OF HUMIC-RICH ORGANIC AMENDMENTS TO CONIFEROUS NURSERY SOILS ON DOUGLAS-FIR GROWTH, DAMPING-OFF AND ASSOCIATED SOIL MICROORGANISMS

D. A. SCHISLER* and R. G. LINDERMAN
Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331 and USDA-ARS, Horticultural Crops Research Laboratory, Corvallis, OR 97330, U.S.A.

(*Accepted* 1 *November* 1988)

Summary—*Fusarium* spp are absent from coniferous forest soils, yet are conspicous in conifer nursery soils. To test the hypothesis that loss of humus from nursery soils may affect *Fusarium* spp survival, three nursery soils were amended with four concentrations of three organic materials high in humic content. Amendment-induced increases and occasional decreases in tree growth varied with soil origin. A humic-rich amendment that stimulated tree growth in all soils also increased the numbers of several soil microbial groups ("total" bacteria, actinomycetes, extracellular-chitinase producers and facultative anaerobes). Fusarium-induced damping-off was reduced in one of the three soils by all amendments. Ectomycorrhizae were increased by only one type of amendment and then in only one of the soils. The complex nature of soil-humic interactions and the physiological action of these substances on roots and microbial cells complicates predicting the efficacy of humic-rich amendments to nursery soils.

INTRODUCTION

In 1967, Smith reported that *Fusarium oxysporum* (Schlect.), a pathogen of major economic importance on nursery-grown, first-year coniferous seedlings, did not persist on the roots of infected sugar pine (*Pinus lambertiana*) seedlings transplanted into a native pine forest. *Fusarium*, in fact, has not been reported as a pathogen of coniferous seedlings in forest soils and rarely reaches detectable populations in soils covered with a thick layer of needle litter (Toussoun, 1975, Schisler and Linderman, 1984). The inability of *Fusarium* to establish in forest soils has been attributed to the lack of annual plants in coniferous forest soils (Toussoun, 1975), to the germination and lysis effect of needle duff leachates (Menzinger, 1969; Toussoun *et al.*, 1969; Hammerschlag and Linderman, 1975), and to the effects of forest soil microbiota (Schisler and Linderman, 1984) on *Fusarium* macroconidia, chlamydospores and hyphae.

Coniferous forest soils frequently are higher in humic-rich organic matter than nursery soils due to humus additions to forest soils from needle litter decomposition and the loss of humus from nursery soils due to cultivation and lack of new inputs of organic substrates. Humic substances are involved in biochemical and physiological processes in plants and soil microbes which could indirectly influence the survival of *Fusarium* in forest soils. Humic and fulvic acids can complex with plant nutrients in the soil solution and stimulate enzyme-mediated uptake of nutrients by roots (Vaughan and Malcolm, 1985). This process often results in increased plant root and shoot growth and nutrition. Humic substances are also reported to improve soil structure (Chaney and Swift, 1986) and detoxify soil by adsorbing metals deleterious to plant growth (Schnitzer, 1986), processes which can improve plant health and resistance to pathogen attack.

Humic substances are known to increase microbial growth and activity. Visser (1985a) found that numbers of a wide range of taxonomic and functional groups of bacteria from soils increased on selective media if they contained humic acids extracted from soil. Humic substances apparently modify cellular activity and growth due to their influence as growth factors, their nutritive value or their influence on cell membrane permeability (Visser, 1985b). Microbial populations which increase due to humic substance amendments to soils include physiologic groups potentially deleterious to *Fusarium* survival.

Humic substances in forest soils may also contribute to the exclusion of *Fusarium* from coniferous forest soils due to their tendency to complex with soil enzymes. Purified soil enzymes are often easily degraded in laboratory studies, yet are extremely resistant to degradation when complexed with humic substances (Skujinš, 1976).

The feasibility of adding humic-rich substances to nursery soils in order to restore a microbially-mediated *Fusarium* suppressiveness similar to that of forest soils has not been investigated. Furthermore, the effect of humic substances on ectomycorrhiza development is not well studied. Our objective was to determine whether amendments of humic-rich organic compounds to nursery soils would affect: (1) soil suppressiveness to *Fusarium*; (2) populations of several microbial groups with potential for biocontrol; (3) ectomycorrhizae; and (4) Douglas-fir seedling growth.

*To whom all correspondence should be addressed at: USDA-ARS, Horticultural Crops Research Laboratory, Corvallis, OR 97330, U.S.A.

MATERIALS AND METHODS

Soil sites and preparation

Soils from three Pacific Northwest bareroot conifer nurseries in Oregon were sampled in early summer after seasonal rains had ceased. The soils were a clay loam from Brownsville, a coarse sandy loam from Mt Hood and a silt loam from Kellogg. These nursery soils were planted with Douglas-fir (*Pseudotsuga menziesii*) seedlings.

At each site, four or five samples of approx. 3 l. each were collected from the top 10 cm of soil, pooled and stored at 5°C. Sampling locations at each site were selected at random within a 25 × 25 m sampling area. Before experimental use, pooled samples were sieved (<2 mm) and mixed with pasteurized (60°C aerated steam for 30 min) river sand (3 soil:2 sand).

Humic-rich organic amendments

Three products known to be high in humic substances were selected for experimental use: (a) composted grape pomace (CGP) (ET100, Ortek, Bellevue, WA 98006); (b) Hypnum peat (HP), a high-humic-content hypnum (vs. sphagnum) based peat (The Bonaparte Company, Bellvue, WA 98004); and (c) powdered oxidized lignite coal (leonardite) (L) (Moms, Intertec Inc., Portland, OR 97217). Organic amendments were analyzed at the Oregon State University Soil Testing Laboratory for chemical and nutritional properties. Specific humic acid fractions were prepared (Stevenson, 1965).

Experimental treatments

Nursery soils were amended with 1, 2, 5 and 10% (by volume) of CGP, HP and L. Controls consisted of each nursery soil without amendments. Amended soil mixes were then sown with four surface-sterilized Douglas-fir seeds per 165 ml "supercell" container (Ray Leach Cone-tainers, Inc., Aurora, OR 97002). Tubes were top-dressed with 0.6 g of 18-6-12 Osmocote fertilizer and No. 2 gage chicken grit (crushed quartz which passes through a 4 mm sieve; to slow moisture loss from tubes during seed germination) and placed in a completely-randomized factorial design. Seedlings were grown at glasshouse temperature (23 ± 4°C) under ambient light supplemented with high pressure sodium vapor lamps (average = 350 μE m^{-2} s^{-1}).

The number of damped-off and healthy seedlings was recorded for six replicates of 28 trees per replicate up to the sixth week from seeding. The root systems of 15–25 damped-off seedlings from each soil were surface-sterilized and plated on peptone, pentachloronitrobenzene (PCNB) agar (PPA, Nash and Snyder, 1962) and selective V-8 agar (SV-8, Schmithenner, 1973) to determine whether *Fusarium* or *Phytophthora* and *Pythium*, respectively, were associated with seedling damping-off. Seedlings were then thinned to 1 per tube.

Twenty-six weeks after seeding, 15 seedlings per treatment were selected at random and the proportion of short roots with mycorrhizae, top height, stem caliper, root dry weight, shoot dry weight, root-to-shoot ratio, number of buds and number of lateral branches determined from each seedling. Analysis of variance was performed on a 3 × 3 × 4 factorial data set which resulted from the removal of the data from each control soil. Controls were then reinstated and data for each soil analyzed separately using a (3 × 4) + 1 analysis of variance. Means within each soil type were separated from their respective controls using Fishers protected L.S.D. test. After seedlings were harvested, samples of representative amended soil mixes were analyzed for chemical and nutrition properties at the Oregon State University Soil Testing Laboratory.

Analysis of microbial profiles

After seedling harvest, four tubes per treatment were selected at random for dilution plate analysis of soil microbial populations of the following toxonomic and functional microbial groups: bacteria, actinomycetes, extracellular chitinase producers, *Fusarium*, fluorescent pseudomonads and facultative anaerobes. Bacteria and actinomycete populations were assayed to indicate the total potential biological activity of the soils. Estimates of populations of soil microbial groups were made by dilution platings on selective media (Schisler and Linderman, 1989). Estimates of the populations of these same microbial groups were also made for the humic-rich organic amendments alone.

Extracts of the same soils were prepared to determine whether amended soils were suppressive to sporangia and zoospore production by *Phytophtora cinnamomi*, a sensitive indicator of general soil suppressiveness (Broadbent and Baker, 1974). Extracts were prepared by flooding 0.75 g dry weight equivalent of fresh soil in a 125 ml flask with 75 ml sd H_2O, and decanting the supernatant after 4 days at 23 ± 2°C. Five ml of extract were then used to flood three 5 mm dia by 1 mm thick disks of V-8 juice agar taken from the periphery of 2 day-old colonies of *P. cinnamomi* (Ribeiro, 1978) and placed in 5 cm dia Petri dishes. After 48 h, sporangia that had grown out from the disks were cold-shocked at 5°C for 40 min, warmed to room temperature, and appropriate serial dilutions of the extract containing released zoospores were plated on SV-8 agar. The number of viable *P. cinnamomi* zoospores ml^{-1} of extract were indicated by the number of colonies formed after dark incubation at room temperature for 2 days. Data for each soil type were analyzed using a (3 × 4) + 1 analysis of variance, and means of all microbial counts within each soil type were separated from their respective controls using Fisher's protected L.S.D. test.

RESULTS

Seedling growth and soil-amendment analysis

Humic amendments frequently increased and sometimes decreased seedling growth for those variables measured (Table 1). Significant soil × amendment interactions precluded pooling of the soil data to obtain overall humic amendment effects on tree growth. The CGP amendment often increased ($P < 0.01$, 0.05) seedling top heights, stem calipers, shoot weights and the number of buds and lateral branches per seedling at the 5 and 10% amendment rate. The HP amendment significantly ($P < 0.05$) increased seedling height and number of buds for

Table 1. Comparison of growth variables, percent mycorrhizae and damping-off of seedlings grown in three nursery soils amended with humic-rich organic materials

Soil/ blend	Top height (cm)	Stem caliper (mm)	Root dry weight (mg)	Shoot dry weight (mg)	Root-to-shoot	Buds (No.)	Lateral branches (No.)	Mycorrhizae (%)	Damping-off (%)	Germ. healthy (%)
Brownsville										
CGP 5%	6.6*	1.59	329	247	1.38	9.8**	2.6**	4.3	10**	68**
CGP 10%	6.9**	1.66*	308	269	1.19	8.2	2.3**	0.5	7**	69**
HP 5%	6.4	1.47	278	191	1.56	6.9	0.6	2.1	14**	61**
HP 10%	6.7*	1.47	322	218	1.52	8.7*	1.7	4.8	11**	60**
L 5%	5.9	1.42	259	187	1.54	6.2	0.7	1.5	2**	76**
L 10%	5.4	1.35	226**	178	1.64	5.5	0.2	3.1	7**	73**
Control	5.7	1.45	307	186	1.69	6.7	0.9	6.5	33	38
Mt Hood										
CGP 5%	6.7**	1.25	217	182**	1.27	4.1	0.5	2.7	17	28
CGP 10%	5.9**	1.25	225	185**	1.21	4.3	1.0	0.2	27	24
HP 5%	5.0	1.12	168	117	1.60	3.4	0.7	1.1	29	20
Hp 10%	5.1	1.14	185	138	1.48	4.8	0.8	0.4	16	33
L 5%	4.6	1.10	163	127	1.43	3.3	0.7	0.1	28	36
L 10%	4.6	1.24	209	143	1.58	4.2	1.3	2.7	23	33
Control	4.3	1.13	190	104	1.91	4.0	0.4	0.5	24	26
Kellogg										
CGP 5%	6.0*	1.34**	292**	166*	1.82	7.7**	0.9	8.0*	4	68
CGP 10%	7.7**	1.50**	431**	262**	1.75	9.0**	2.9**	0.0	8	62
HP 5%	5.2	1.13	182	116	1.65	4.1	0.7	1.1	5	65
HP 10%	5.0	1.17	159	114	1.52	3.9	0.5*	3.1	5	73
L 5%	4.8	1.06	162	89*	1.85	4.3	0.3*	0.8	4	64
L 10%	4.9	1.10	175	100	1.80	3.8	0.3*	1.1	9	63
Control	5.2	1.14	148	125	1.36	3.8	1.4	2.0	7	61

Values within the same column of a soil followed by *, or ** are significantly different from their associated control, $P < 0.05$, $P < 0.01$, respectively (Fishers's protected L.S.D. test).

seedlings grown in the Brownsville soil (Table 1), but otherwise did not stimulate tree growth in the soils tested. The L amendment did not increase, and at some amendment rates, decreased seedling growth (Table 1). The chemical and nutritional analysis of the amendments used and selected amended soils at the end of the experiment showed CGP to be higher in P and K than the other amendments (Tables 2 and 3). Of the three organic amendments, HP and L had the highest proportion of humic acid and fulvic acid, respectively (Table 2).

Ectomycorrhizae and seedling health

Soil origin was critical in determining the effect of amendments of mycorrhiza development, seedling damping-off and seedling health. Each amendment at every rate significant ($P < 0.01$) decreased seedling damping-off and increased the number of healthy seedlings ($P < 0.01$) in the Brownsville soil (Table 1), but had no effect in the other two soils. *Fusarium* populations in non amended soils were highest in the Brownsville soil (Table 4). *Fusarium* was the only

Table 2. Chemical and nutritional properties of humic-rich organic amendments

Amendment	pH	P	K	Ca	Mg	OM (%)	CEC	NH_4	NO_3	Humin (%)	Humic acid (%)	Fulvic acid (%)
		($\mu g\ g^{-1}$)						($\mu g\ g^{-1}$)				
CGP	7.2	334	15,900	4060	1560	41.4	69.5	254.1	10.9	91.0	1.5	7.5
HP	5.2	8	55	10,200	672	53.8	78.1	15.4	372.4	79.0	12.0	9.0
L	4.8	9	129	3980	492	14.4	32.0	79.8	1.0	85.5	4.5	10.0

Table 3. Chemical and nutritional properties of amended and control nursery soils at seedling harvest

Soil/amend	pH	P	K	Mg	OM (%)	CEC	NH_4	NO_3
Brownsville								
CGP 5%	5.7	29	417	327	1.95	16.4	2.8	5.8
HP 5%	5.5	24	179	360	2.33	18.4	2.4	5.6
L 5%	5.6	20	140	360	2.06	15.0	2.8	2.3
Control	5.4	26	152	348	1.08	16.8	2.8	11.7
Mt Hood								
CGP 5%	6.1	20	406	156	2.93	9.3	4.7	16.4
HP 5%	6.1	10	129	132	2.47	9.8	2.8	3.4
L 5%	5.9	10	129	132	2.58	9.3	2.4	6.7
Control	6.0	10	144	132	1.52	7.3	4.8	13.9
Kellogg								
CGP 5%	5.5	28	359	180	1.48	10.7	2.4	9.7
HP 5%	5.5	17	160	204	1.75	10.0	2.8	7.4
L 5%	5.4	18	179	216	1.70	10.5	2.8	4.5
Control	5.2	20	172	168	0.88	10.0	28.6	10.2

Table 4. Effect of humic-rich organic amendments of nursery soils on *Phytophthora* suppressiveness and the numbers of bacteria, actinomycetes, and *Fusarium* propagules (g^{-1} soil dry weight) isolated at seedling harvest

Soil/ blend	Bacteria	Actino	Chitin	Fusarium	Fluor. pseudo.	Facult. anaerobes	Phytoph. zoospores (ml^{-1} soil extract)
Brownsville							
CGP 5%	3.9E + 06[a]	2.1E + 06	2.1E + 05	3.3E + 03	5.8E + 03	1.3E + 06**	67
CGP 10%	5.9E + 06**[b]	2.6E + 06**	5.0E + 05	3.9E + 03	2.9E + 03	1.5E + 06**	95*
HP 5%	3.1E + 06	1.9E + 06	4.4E + 05	4.0E + 03	6.1E + 03	1.1E + 06	131**
HP 10%	4.1E + 06	2.0E + 06	3.0E + 05	4.2E + 03	8.0E + 03	1.0E + 06	120**
L 5%	2.9E + 06	1.6E + 06	1.5E + 05*	5.0E + 03	5.7E + 03	6.5E + 05	58
L 10%	2.4E + 06	1.8E + 06	1.8E + 05	4.5E + 03	2.7E + 03	8.7E + 05	43
Control	3.3E + 06	1.9E + 06	4.0E + 05	4.0E + 03	9.4E + 03	8.9E + 05	28
Mt Hood							
CGP 5%	5.2E + 06**	2.9E + 06	4.1E + 05*	1.8E + 03	1.1E + 03	2.6E + 06	6
CGP 10%	4.4E + 06*	2.6E + 06	3.4E + 05	1.2E + 03	9.8E + 02	2.6E + 06	3
HP 5%	3.8E + 06	2.5E + 06	4.2E + 05*	8.7E + 02	4.3E + 02	1.9E + 06	4
HP 10%	2.9E + 06	2.4E + 06	2.5E + 05	5.3E + 02	5.3E + 02	1.5E + 06*	12
L 5%	4.6E + 06**	3.2E + 06	5.1E + 05**	2.2E + 03	1.3E + 03	2.3E + 06	15
L 10%	4.3E + 006*	3.2E + 06	3.9E + 05*	1.6E + 03	6.7E + 01	1.9E + 06	2
Control	2.8E + 06	2.2E + 06	2.3E + 05	2.3E + 03	1.8E + 02	2.4E + 06	7
Kellogg							
CGP 5%	2.8E + 06	1.4E + 06**	2.8E + 05*	3.9E + 03	0.0E + 00	5.1E + 05	222
CGP 10%	5.2E + 06**	2.0E + 06**	3.4E + 05**	6.6E + 03*	4.3E + 03	9.8E + 05**	290
HP 5%	3.3E + 06	8.1E + 05	1.2E + 05	6.3E + 03*	1.7E + 02	3.6E + 05	158
HP 10%	1.9E + 06	7.8E + 05	1.5E + 05	3.3E + 03	3.3E + 01	7.6E + 05	158
L 5%	2.0E + 06	6.5E + 05	5.3E + 04	2.7E + 03	8.3E + 01	6.0E + 05	80
L 10%	1.7E + 06	7.5E + 05	9.8E + 04	4.7E + 03	3.3E + 02	6.2E + 05	22
Control	2.3E + 06	7.5E + 05	1.3E + 05	2.7E + 03	4.0E + 02	5.8E + 05	135

[a]Table values are in notation, i.e. 3.9E + 06 = 3.9 × 10^6.
[b]Values within the same column of a soil followed by *, or *** are significantly different from their associated control, $P < 0.05$, $P < 0.01$, respectively (Fisher's protected L.S.D. test).

pathogen isolated from the roots of damped-off seedlings grown in the Brownsville and Kellogg soils, while *Fusarium* and *Pythium* were isolated with equal frequency from the roots of damped-off seedlings grown in the Mt Hood soil. Ectomycorrhizae increased in Kellogg soil amended with 1 or 5% CGP, but amendments otherwise had little influence on ectomycorrhiza formation.

Microbial analysis, soil suppressiveness

Humic-rich organic amendments sometimes significantly increased and sometimes decreased the number of bacteria, actinomycetes, extracellular-chitinase-producing organisms, fusaria and facultative anaerobes recovered from amended soils (Table 4), while amendments had no effect on the numbers of fluorescent pseudomonads recovered from any soil. Although amendment effects on microbial populations varied, depending on the soil, CGP generally increased populations of bacteria, actinomycetes, extracellular-chitinase producers and facultative anaerobes, especially at the highest rates. Surprisingly, general soil suppressiveness to *Phytophthora* was decreased in 2 and 10% CGP-amended Brownsville soil, as measured by an increase in viable zoospores produced in soil extracts (Table 4).

Several amendment rates of HP increased ($P < 0.05$) populations of extracellular chitinase-producing organisms in the Mt Hood soil. In other soils, the highest rates of HP amendment increased ($P < 0.05$) the recoverable *Fusarium* population and decreased soil suppressiveness to *Phytophthora* (Table 4). Several amendment rates of HP decreased the population of faculatative anaerobes in the Mt Hood soil (Table 4).

Several rates of the L amendment increased the recoverable bacteria and chitinase producer populations in the Mt Hood soil, but decreased the number of chitinase producers in the Brownsville soil and the number of facultative anaerobes in the Mt Hood soil (Table 4).

Table 5. Number of colony-forming units of bacteria and actinomycetes recovered (g^{-1} material) from humic-rich organic amendments alone

Amendment	Bacteria	Actino	Chitin	Fusarium	Fluor. pseudo.	Facult. anaerobes
CGP						
Average	1.6E + 08[a]	6.9E + 07	5.3E + 05	0.0E + 00	5.8E + 04	1.2E + 06
SD	2.1E + 07	1.0E + 07	7.3E + 04	0.0E + 00	2.9E + 04	2.5E + 05
HP						
Average	1.6E + 07	5.0E + 05	6.9E + 04	0.0E + 00	7.3E + 03	1.6E + 05
SD	3.2E + 06	6.1E + 04	1.3E + 04	0.0E + 00	2.5E + 03	1.3E + 04
L						
Average	1.2E + 04	1.0E + 04	5.0E + 02	0.0E + 00	0.0E + 00	2.5E + 02
SD	3.2E + 03	5.5E + 03	5.5E + 02	0.0E + 00	0.0E + 00	8.7E + 01

[a] Table values are in notation, i.e. 3.8E + 06 = 3.8 × 10^6.

Bacterial and actinomycete populations as well as extracellular chitinase producers and facultative anaerobe populations considerably higher than those of control soils were recovered from the CGP amendment alone (Table 5). Populations of these groups were similar to or less than those of control soils for the HP and L amendments, respectively. Detectable populations of *Fusarium* were not present in any of the amendments used.

DISCUSSION

Humic amendments to nursery soils varied in their influence on soil microbial populations, depending on the kind of amendment and soil used. High background microbial counts for the CGP amendment (Table 5) would appear to at least partially account for the increased microbial populations in soil amended with 5 and 10% CGP, although microbial group populations in the HP and L amendments were too low to explain the microbial population increases occasionally seen in soils amended with these substances. Microbial population increases likely also resulted from the nutritive value of the amendments and perhaps from humic-mediated increases in microbial cell membrane permeability to nutrients (Visser, 1985b). Interestingly, high concentrations of the HP and L amendments occasionally decreased the populations of several microbial groups in amended soils (chitinase producers in Brownsville soil; bacteria, chitinase producers and facultative anaerobes in Mt Hood soil, Table 4). The concentration-dependent nature of the effects of humic substances on soil microbes was recorded by Visser (1985a).

The seedling growth enhancement frequently observed in humic-amended soils appears to be at least partially due to increased soil fertility, especially in CGP-amended soils (Tables 2 and 3). Humic substances are also known to improve soil structure, prevent the leaching of nutrients from soils, stimulate enzyme-mediated uptake of nutrients by roots and increase plant cell permeability to nutrients (Vaughan and Malcolm, 1985), processes which also could contribute to increased seedling growth. Humic substances (O'Donnell, 1973) also can have auxin-like qualities and inhibit and ezymatic oxidation of indoleacetic acid (Mato *et al.*, 1971). The inhibitory effect of high concentrations of the L amendment on some plant growth measurements parallels reported observations that humic substances can inhibit plant growth at high concentrations (Elgala *et al.*, 1978; Mylonas and McCants, 1980).

Several soil chemical, physical and microbiological factors may be involved in the variable influence of humic substances on ectomycorrhiza formation and seedling damping-off (Table 1). Clay colloids can absorb humic substances, thus modifying humic substance availability, depending on the quality and quality of clays present in a soil (Schnitzer, 1986). The growth and development of ectomycorrhizal fungi could, in turn, be affected (Tan and Nopamornbodi, 1979). Resident populations of root pathogenic fungi may have differed between soils, with differential responses of these fungi to humic substances accounting for different damping-off responses between soils. Nutrient differences between soils (Table 3) likely altered seedling nutrition which can affect ectomycorrhiza formation and seedling damping-off (Bloomberg, 1981). Lastly, the amount and relative proportions of inorganic ions in a soil can influence the quantity and quality of stable enzyme-humic complexes formed (Mayaudon, 1968; Maignan, 1982) which could affect the lytic nature of a soil.

Our results point to the difficulty in predicting the efficacy of adding high humic-content organic materials to nursery soils to control seedling damping-off and increase seedling growth and ectomycorrhiza formation. Reconstruction of a forest-like *Fusarium* suppressiveness in nursery soil via humic amendment is complicated by the fact that commerically-available humic products vary greatly from each other and undoubtedly from forest soils humus in type, content and availability of humic substances. The contribution of phenolic substances present in the leachates of coniferous needle litter (Blaschke, 1979; Hammerschlag and Linderman, 1975) to *Fusarium* exclusion from forest soils is another factor difficult to establish in nursery soils by the addition of humic-rich substances alone. Lastly, the high soil fertility of nursery soils and the resultant change in soil microbial population profiles (D. A. Schisler, unpublished results) defies reconstruction of a forest soil-like *Furarium* suppressiveness in nursery soils by the simple addition of humic-rich organic amendments.

Acknowledgement—We thank Gerald Barclay for determining the amounts of humic substances present in the organic amendments used in this study.

REFERENCES

Blaschke H. (1979) Leaching of water-soluble organic substances from coniferous needle litter. *Soil Biology & Biochemistry* **11**, 581–584.

Bloomberg W. J. (1981) Disease caused by *Fusarium* in forest nurseries. In *Fusarium: Diseases, Biology and Taxonomy* (P. E. Nelson, T. A. Toussoun, and R. J. Cook, Eds), pp. 178–187. The Pennsylvania State University Press, University Park.

Broadbent P. and Baker K. F. (1974) Behavior of *Phytophthora cinnamomi* in soils suppressive and conducive to root rot. *Australian Journal of Agricultural Research* **25**, 121–137.

Chaney K. and Swift R. S. (1986) Studies on aggregate stability. II. The effect of humic substances on the stability of re-formed soil aggregates. *Journal of Soil Science* **37**, 337–343.

Elgala A. M., Metwally A. I. and Khalil R. A. (1978) The effect of humic acid and Na_2EDDHA on the uptake of Cu, Fe and Zn by barley in sand culture. *Plant and Soil* **49**, 41–48.

Hammerschlag F. and Linderman R. G. (1975) Effects of five acids that occur in pine needles on *Fusarium* chlamydospore germination in nonsterile soil. *Phytopathology* **65**, 1120–1124.

Maignan C. (1982) Activite des complexes acides humiques invertase: influence du mode de preparation. *Soil Biology & Biochemistry* **14**, 439–445.

Mato M. C., Fábregas R. and Méndez J. (1971) Inhibitory effect of soil humic acids on indoleacetic acid-oxidase. *Soil Biology & Biochemistry* **3**, 285–288.

Mayaudon J. (1968) Stabilisation biologique des proteines ^{14}C dans le sol. In *Isotopes and Radiation in Soil Organic Matter Studies*, pp. 177–188. IAEA, Vienna.

Menzinger W. (1969) Zur keimungsphysiologie von *Fusarium*-chlamydosporen im Boden. *Bundesanstalt fur Land- und Forstwirtschaft*. Berlin-Dahlem **132**, 38–39.

Mylonas V. A. and McCants C. B. (1980) Effects of humic and fulvic acids on growth of tobacco. 1. Root initiation and elongation. *Plant and Soil* **54**, 485–490.

Nash S. M. and Snyder W. C. (1962) Quantitative estimations by plate counts of propagules of the bean root rot *Fusarium* in field soils. *Phytopathology* **52**, 567–572.

O'Donnell R. W. (1973) The auxin-like effects of humic preparations from leonardite. *Soil Science* **116**, 106–112.

Ribeiro O. K. (1978) *A Source Book of the Genus Phytophthora*. A. R. Ganter Verlag, K. G., Vaduz.

Schisler D. A. and Linderman R. G. (1984) Evidence for the involvement of the soil microbiota in the exclusion of *Fusarium* from coniferous forest soils. *Canadian Journal of Microbiology* **30**, 142–150.

Schisler D. A. and Linderman R. G. (1989) Selective influence of volatiles purged from coniferous forest and nursery soils on microbes of a nursery soil. *Soil Biology & Biochemistry* **21**, 389–396.

Schmithenner A. F. (1973) Isolation and identification methods for *Phytophthora* and *Pythium*. In *Proceedings of the First Woody Ornamental Disease Workshop*, pp. 94–110. University of Missouri-Columbia.

Schnitzer M. (1986) Binding of humic substances by soil mineral colloids. In *Interactions of Soil Minerals with Natural Organics and Microbes*, (P. M. Huang and M. Schnitzer, Eds), pp. 77–101. Soil Science Society of America, Madison.

Skujinš J. (1976) Extracellular enzymes in soil. *CRC Critical Reviews in Microbiology* **4**, 383–421.

Smith R. S. Jr (1967) Decline of *Fusarium oxysporum* in the roots of *Pinus lambertiana* seedlings transplanted into forest soils. *Phytopathology* **57**, 1265.

Stevenson F. J. (1965) Gross chemical fractionation of organic matter. In *Methods of Soil Analysis* (C. A. Black *et al.*, Eds), pp. 1409–1421. American Society of Agronomy, Madison.

Tan K. H. and Nopamornbodi V. (1979) Fulvic acid and the growth of the ectomycorrhizal fungus, *Pisolithus tinctorius*. *Soil Biology & Biochemistry* **11**, 651–653.

Toussoun T. A. (1975) Fusarium-suppressive soils. In *Biology and Control of Soil-borne Plant Pathogens* (G. W. Bruehl, Ed.), pp. 145–151. The American Phytopathological Society, St Paul.

Toussoun T. A., Menzinger W. and Smith R. S. Jr (1969) Role of conifer litter in ecology of *Fusarium*: stimulation of germination in soil. *Phytopathology* **59**, 1396–1399.

Vaughan D. and Malcolm R. E. (1985) Influence of humic substances on growth and physiological processes. In *Soil Organic Matter and Biological Activity*, (D. Vaughan and R. E. Malcolm, Eds), pp. 37–75. Martinus Nijhoff/Dr. W. Junk Publishers, Dordrecht.

Visser S. A. (1985a) Effects of humic acids on numbers and activities of micro-organisms within physiological groups. *Organic Geochemistry* **8**, 81–85.

Visser S. A. (1985b) Physiological action of humic substances on microbial cells. *Soil Biology & Biochemistry* **17**, 457–462.