Edaphic Factors Associated with the Incidence and Severity of Disease Caused by Fomes annosus in Loblolly Pine Plantations in Virginia

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ABSTRACT

Twenty circular 0.08-hectare (ha) plots were established in thinned loblolly pine, *Pinus taeda,* plantations with ten trees on high- and low-hazard disease (*Fomes annosus*) sites. The incidence of *F. annosus* was determined by aseptically removing six chips from each of two roots per tree and incubating the chips on ortho-phenyl-phenol medium at 23 C for two weeks in the dark. Average disease incidence for high-hazard plots (138 trees) and low-hazard plots (129 trees) was 32.6 and 7.8%, respectively. The difference in diameter between infected and noninfected trees was significant ($P = 0.05$) on all plots and at $P = 0.01$ on low-hazard plots. Fourteen soil parameters were measured at depths of 10 to 20 cm. Sand, noncapillary pores, and bulk density were positively correlated with disease incidence; clay, capillary pores, field capacity, permanent wilting percentage, and organic matter were negatively correlated. Of the soil parameters measured, sand, porosity, organic matter, and field capacity had the highest correlation when compared with disease incidence. In undisturbed loamy-sand and sandy-clay-loam soil cores, conidiospores were washed to a depth of 9.5 cm and 0.5 cm, respectively. Percent root infection tended to increase with soil depth in high-hazard soils, indicating the possible association between porosity, spore movement, and root infections in sandy soils.

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Additional key words: root rot, losses, spread.

Annosus root and butt rot is primarily a disease of conifers which is caused by the fungus *Fomes annosus* (Fr.) Karst. Since the first report of major damage in 1954, annosus root and butt rot has become the most important disease of thinned pine plantations in the southern United States (13, 25, 26). As with other root infecting pathogens, the effect of edaphic factors on infection and subsequent disease development is of primary importance.

In their southwide survey, Powers and Verrall (26) reported that disease severity was greatest on sandy soils with deep forest litter. Morris and Frazier (24) characterized such high-hazard sites as having greater than 70% sand at the 20-30 cm depth and a water table level below 45 cm. Froelich et al. (10) reported that severely damaged pine stands were growing on sandy soils of pH 5.4-5.9, with lower organic matter, grass cover, and clay content. However, the most severely damaged pine stands in England were found on alkaline soils (31, 36). Organic matter content of less than 10% in the top 20 cm has been reported to be associated with *F. annosus* infection (10, 31). Soil moisture has been shown to influence infection of loblolly pine roots by *F. annosus,* with low soil moisture enhancing, at least initially, the rate of penetration (34).

After initial infection of stumps by basidiospores, spread of the fungus occurs primarily via root contacts (15, 30). Kuhlman reported more root contacts, infected roots and dead trees on high-hazard sites (21). Spores of *F. annosus* have been found in sandy soils at depths to 90 cm (30). With the O horizon removed, spores of the fungus have been washed downward through a prepared column of Kershaw sand to a depth of 15 cm (19). Molin reported that *F. annosus* spores were washed through a sand column where they germinated and colonized blocks of wood. Direct stump root infection has been suggested (4) and reported (12). As few as 44 spores per root have been shown to cause infection of fine feeder roots (20).

The purpose of this study was to further characterize the principal edaphic factors associated with disease incidence and severity of *F. annosus* in thinned loblolly pine plantations located on deep sandy soils as compared to those located on clay soils. A concurrent objective was to further explain the success of the soil hazard rating system as described by Morris and Frazier (24) in Virginia.

MATERIALS AND METHODS.—Twenty loblolly pine plantations were selected using Morris and Frazier's (24) criteria as a guide, with 10 each on high- and low-hazard sites. The average age of the plantations were 31 and 34 years for high- and low-hazard stands, respectively. Original spacing averaged 1.8 × 1.8 m. Fifteen stands had been thinned twice and five had been thinned only once. Previous land-use had been general agriculture. *Fomes annosus* was determined to be present in selected stands by the location of conks on stumps or trees in all plantations regardless of hazard site.

Within each plantation a circular 0.08-ha plot was established. The soil within each plot was generally uniform in soil texture and conformed to the hazard rating for that plot. Each tree was numbered and the dbh (diameter, breast-high) measured. The crown of each tree was rated for symptom expression (disease severity).

The presence or absence of *F. annosus* in each tree was determined by the two-root method (TRM) (2). Each root was rated for symptom expression (disease severity). Six chips, each approximately 1 cm^3 in volume, were removed aseptically from opposite sides of each root, placed on OPP (ortho-phenyl-phenol) medium (4, 33), and incubated at 23 C for two weeks in the dark. This method was used for all isolations and incidence determinations unless otherwise noted.

The Parker Plantation was unique because it contained both high- and low-hazard soil sites, and the entire plantation was planted and thinned uniformly over both sides. A plot was established on each soil. The low-hazard site (PL) was characterized by sandy loam soil and the trees appeared to be healthy. The high-hazard site (PH), with loamy and sand soil, was located about 100 m from PL and showed considerable damage from *F. annosus*. Detailed studies were conducted on the incidence and severity of *F. annosus* in the Parker Plantation.

Soil parameters measured in all plots were sand, silt, clay, noncapillary pore space, capillary pore space, field capacity, phosphorus, potassium, and bulk density. Soil samples of approximately 3,000 g were collected at plot center at depths of 10,20, 30, 60, 90, and 120 cm. The air-dried soil was crushed and then seived through 2-mm mesh-size screen. Duplicate soil core samples were also collected at the six depths.

Particle size was determined by the pipette method (9, 17). Field capacity and permanent wilting percentage

TABLE 1. *Fomes annosus* on loblolly pine in Virginia (USA). Disease incidence and severity data collected from 20 plots

Hazard plots	Trees (no.)	Infected[a] (%)	Average DBH[b]		Crown symptom expression[c] (avg.)
			Infected (cm)	Noninfected (cm)	
High-hazard[d,f]					
PH	11	36	19.8	24.9	2.6
H	15	13	19.6	20.6	2.4
G	15	40	21.3	24.4	2.4
Sc	14	0	...	23.9	3.2
M	15	27	21.8	24.4	2.4
C	10	40	24.9	28.7	2.6
S	15	47	23.9	23.9	3.1
UC	13	31	15.8	19.1	3.0
PW	18	44	22.6	18.5	2.8
LOH	12	50	29.0	27.4	2.8
Average	14	33	22.1	23.5	2.7
Low-hazard[e,f]					
Cu	20	25	18.8	34.1	3.4
BC-1	11	9	30.0	26.4	3.4
BC-2	10	10	...	28.7	3.3
B	11	0	...	30.0	2.9
B-1	12	8	22.9	26.7	3.1
B-2	14	0	...	24.4	3.7
B-3	12	0	...	27.7	3.6
B-4	11	9	24.4	24.4	3.4
S-28	16	6	23.1	20.3	3.6
PL	2	0	...	...	3.6
Average	13	8	23.8	26.4	3.4

[a]Determined by two-root method.
[b]Diameter breast height.
[c]Rating scale: 4, healthy; 3, thin and green; 2, thin and chlorotic; 1, dead or dying.
[d]Based upon > 65% sand, 25 cm soil depth.
[e]Based upon < 65% sand, 25 cm soil depth.
[f]Coded plot designations are for plantation names and locations.

TABLE 2. *Fomes annosus* on loblolly pine. Root symptom expression and number of roots infected

Hazard plots	Trees sampled (no.)	Root Condition					
		Solid		Resin-soaked		Stringy	
		Roots observed (no.)	Roots with *F. annosus* (no.)	Roots observed (no.)	Roots with *F. annosus* (no.)	Roots observed (no.)	Roots with *F. annosus* (no.)
High-hazard[a]							
Totals	138	179	20	71	23	26	19
Percent			11		32		73
Low-hazard[b]							
Totals	129	230	2	19	6	9	5
Percent			1		32		56

[a]Based upon > 65% sand, 25-cm soil depth.
[b]Based upon < 65% sand, 25-cm soil depth.

were determined by the pressure-membrane method (28). Field capacity was measured at 0.1 bar for soils with more than 70% sand and at 0.33 bar for all other soils. Permanent wilting percentage was measured at 15 bars. Capillary and noncapillary pore space were determined by the difference method (35). Bulk density was based on the oven-dried weight per volume of soil (5). The pH was measured with a pH meter on a soil plus distilled water mixture (1:1, v/v). The North Carolina method of extraction was used to determine the amount of calcium, magnesium, phosphorus, and potassium in the soils (27). Percent organic matter was determined by wet digestion with sodium dichromate and sulfuric acid (27). A simple linear correlation was made to determine the degree of association between each soil parameter and disease incidence.

The complete root systems of five trees distributed within the PH and PL plots were excavated. Each root was numbered and its location at the root collar zone recorded. Top and bottom sides of each root were marked, and the depth of soil covering each root was recorded. All root contacts within and between trees were noted. Roots were then excised at the root collar, placed on ice and removed to the laboratory. Each root was diagrammed and root-chip isolations were made every 10 cm along the top and bottom sides of each root. Isolations were made also from the bark and feeder roots at selected points along the main roots.

TABLE 3. Soil characteristics associated with *Fomes annosus* in loblolly pine presented as a function of depth in high- and low-hazard plots [each value (%) represents the average of 10 plots]

Infection hazard and soil characteristics	Soil depth (cm)					
	10	20	30	60	90	120
High-hazard[a]						
Sand	78.1	74.9	72.6	64.5	66.8	68.9
Silt	17.5	18.9	20.7	20.9	15.6	12.1
Clay	4.3	6.0	6.7	14.5	17.4	19.0
Capillary pores	30.3	21.2	21.6	25.2	25.9	28.0
Noncapillary pores	23.1	26.4	15.7	13.8	13.7	12.6
Field capacity (0.1 bar)	9.9	10.4	10.4	12.5	13.4	15.5
Permanent wilting percentage (15.0 bars)	2.3	2.2	2.7	5.4	6.4	7.1
Available moisture	7.6	8.2	7.7	7.1	7.0	8.4
Organic matter	1.3	0.9	0.7	0.3	0.4	0.2
pH	4.6	4.8	5.0	5.2	5.2	5.1
Bulk density	1.51	1.63	1.67	1.70	1.68	1.66
Low-hazard[b]						
Sand	50.9	44.2	35.1	30.3	33.8	37.8
Silt	35.4	26.7	25.6	26.7	23.1	12.1
Clay	11.3	14.0	9.2	9.2	20.8	21.5
Capillary pores	35.9	38.4	42.0	43.0	43.0	44.0
Noncapillary pores	8.8	6.6	4.8	5.8	5.8	4.9
Field capacity (0.33 bar)	22.5	25.2	29.2	30.6	26.3	30.9
Permanent wilting percentage (15.0 bars)	9.0	11.3	16.3	19.4	18.8	15.4
Available moisture	13.5	13.9	12.9	11.2	7.5	15.5
Organic matter	3.3	2.1	1.4		0.8	0.8
pH	5.0	5.1	5.1	5.4	5.3	5.3
Bulk density	1.41	1.44	1.42	1.45	1.40	

[a]Based upon > 65% sand, 25-cm soil depth.
[b]Based upon < 65% sand, 25-cm soil depth.

TABLE 4. Soil characteristics averaged at 20- to 30-cm depths and percent infection of loblolly pine by *Fomes annosus* for 10 high-hazard plots

Soil characteristics	High-hazard plots[a]										
	PH	H	G	Sc	M	C	S	UC	PW	LOH	Avg.
Sand (%)	73	75	74	66	66	73	85	83	79	65	74
Silt (%)	23	17	15	28	27	22	10	12	17	25	20
Clay (%)	4	7	11	6	7	5	5	5	4	8	6
Noncapillary pores (%)	28	13	15	10	13	31	24	19	20	9	18
Capillary pores (%)	18	25	21	26	26	23	16	20	16	25	22
Field capacity (%)	8	10	10	13	11	10	6	10	7	12	10
Permanent wilting percentage (%)	2	4	4	3	4	2	2	3	2	3	3
Available moisture	6	6	6	10	7	8	4	7	5	9	7
Organic matter (%)	0.7	0.6	0.6	0.6	0.9	0.5	0.8	1.7	0.5	1.3	8
Bulk density (g/cc)	1.67	1.76	1.70	1.68	1.66	1.62	1.57	1.54	1.65	1.74	1.66
pH	4.6	4.7	4.9	4.9	4.8	4.9	4.8	5.4	5.2	5.1	4.9
Infection (%)	36	13	40	0	27	40	47	31	44	50	33

[a]Based upon > 65% sand, 25-cm soil depth. Coded plot designations are for plantation names and locations.

Experiments were conducted to determine the degree of movement of conidiospores of *F. annosus* through sand columns. Pyrex columns 18-cm long × 10 cm in diameter were packed with greenhouse potting sand, and then autoclaved for six hours at 1.14 atmospheres (18 psi) and 225 C. The void volume, determined with sterile distilled water, was 100 ml. Conidiospores used for percolation tests were harvested from 2-week-old cultures grown on malt extract agar medium, by washing with sterile distilled water, filtering the extract through cheesecloth, and centrifuging at 2,500 *g* for 20 minutes. Spores were resuspended in sterile distilled water. Centrifugation was repeated twice. The concentration of spores was determined by hemacytometer count. Fifty ml of spore suspension, containing 10^7 spores, were poured evenly over the column, followed by 650 ml of sterile distilled water. Seven 100-ml samples of percolated water were collected. A 1-ml aliquot of each sample was added to each of five plates of Kuhlman and Hendrix' medium (22). After seven days of incubation at 23 C in the dark, the number of colonies per plate were counted.

Following these tests, percolations tests were done with undisturbed columns of soil from plots UC-16, PH, G, BC, and PL. The percentage capillary and noncapillary pore space of UC-16, G and BC-1 was equal to the mean of all plots in their respective hazard group. PH and PL plots were selected to compare the downward movement of spores through soil columns of different hazard rating located within the same plantation.

Irrigation pipe, 10 cm in diameter, was cut into 30-cm lengths. Five 5.0-mm diameter holes were drilled every 5.0 cm along the length of the pipe. Core samples were taken at plot center by pounding the pipe sections into the soil and digging them out so as not to damage the integrity of the soil within the core. Each core was marked, wrapped in plastic, taken to the laboratory, and stored at 5 C until used.

Each soil core was suspended over a wire screen on a 15 cm diameter funnel. A total of 10^6 spores in 50 ml of sterile distilled water were sprinkled on top of the core to simulate rainfall. After the spore suspension had entered the soil, 450 ml of sterile distilled water was added. The

TABLE 5. Soil characteristics averaged at 20- to 30-cm depths and percent infection of loblolly pine by *Fomes annosus* for 10 low-hazard plots

Soil characteristics	Low-hazard plots[a]										
	Cu	BC-1	BC-2	B	B-1	B-2	B-3	B-4	S-28	PL	Avg.
Sand (%)	39	42	37	36	35	35	48	24	38	62	40
Silt (%)	25	21	33	39	32	43	28	28	30	26	30
Clay (%)	35	36	30	25	33	22	24	47	32	12	30
Noncapillary pores (%)	5	7	4	5	4	6	3	5	7	13	6
Capillary pores (%)	44	43	41	41	45	35	40	46	39	26	40
Field capacity (%)	29	28	25	31	31	23	30	35	24	13	27
Permanent wilting percentage (%)	15	18	14	12	14	13	11	24	15	4	14
Available moisture	14	10	11	19	17	10	19	11	9	9	13
Organic matter (%)	1.3	0.8	2.0	2.1	1.6	2.5	1.8	1.5	1.0	2.7	1.7
Bulk density (g/cc)	1.46	1.41	1.54	1.26	1.44	1.53	1.29	1.30	1.56	1.63	1.44
pH	5.1	5.0	4.9	4.8	5.2	5.6	5.4	5.3	5.1	4.9	5.1
Infection	25	9	10	0	8	0	0	9	6	0	8

[a]Based upon < 65% sand25-cm soil depth. Coded plot designations are for plantation names and locations.

TABLE 6. Simple linear correlation coefficients (multiple regression analysis) of soil parameters when compared with incidence of infection of loblolly pine by *Fomes annosus*

Variables	Soil depth (cm)					
	10	20	30	60	90	120
pH	−0.581**[a]	...[b]	...	−0.506*[c]	...	...
Sand	0.718**	0.724**	0.608*	0.625*	0.513*	...
Clay	−0.643**	−0.615**	−0.438*	−0.503*	...	...
Noncapillary pores	0.607**	0.618**	0.690**	0.659**	...	...
Capillary pores	−0.694**	−0.629**	−0.649**	−0.602**	−0.462*	...
Field capacity	−0.714**	−0.618**	−0.606**	−0.589**	−0.544*	...
Permanent wilting percentage	−0.601**	−0.567**	−0.525*	−0.544*	−0.480*	...
Bulk density	0.493	0.517*	0.463*	...	0.519*	0.542*
K	−0.601**	−0.556*	−0.511*	−0.579**	−0.542*	...
Mg	−0.510*	...	...	...	...	...
Ca	−0.490*	...	...	...	...	−0.570*
P	...	...	...	...	...	...
Organic matter	−0.944**	−0.611**	...	...	...	...

[a]** = Significant correlation, $P = 0.01$.
[b]... = Correlation value not significant.
[c]* = Significant correlation, $P = 0.05$.

total volume of 500 ml is equivalent to the average monthly rainfall of 6.25 cm.

Spores were added to one each of the cores from each plot. After all drainage had ceased, samples of soil from the 5.0 mm holes at different depths were removed, weighed, and placed in soil bottles. A volume of sterile distilled water, equal to the weight of the soil, was added to make a 1:1 (w:v) dilution. The soil bottles were then shaken by hand for 20 minutes and allowed to stand for one minute. A series of 10-fold soil dilutions were then made. Spores were detected by placing a 1 ml aliquot of each dilution in each of 10 plates containing Kuhlman and Hendrix' selective medium (18).

Two soil cores from each plot were used for controls. In one core, soil was removed from each of the five holes and soil dilution plates were made as before. To the second soil core, sterile distilled water was added until 100 ml was eluted. This sample was tested for conidiospores by the same method. All soil dilution plates were incubated at 23 C for 7-9 days. The presence of *F. annosus* colonies was determined by observation of the conidial stage of the fungus.

RESULTS.—The average number of trees per plot, number of infected trees and the average dbh and crown symptom expression for the high- and low-hazard plots are summarized in Table 1. The average infection incidence detected by the two-root method was four times higher in the high-hazard plots than in the low-hazard plots. Average dbh difference between infected and noninfected trees for the high- and low-hazard plots were found to be approximately 1.5 and 2.7 cm, respectively.

Symptom expression in excised roots, and the total number of roots infected on all plots, are shown in Table 2. Recovery of *F. annosus* was much higher from stringy roots.

Average values of soil characteristics at each of six soil depths are summarized in Table 3. Sand and noncapillary pore space values were highest at all depths in the high-hazard plots. Clay and capillary pore space were highest in the low-hazard plots. Silt was generally higher in the low-hazard soils only in the top 20 cm. The average values for FC and PWP generally increased with depth in both hazard soils, while available moisture remained approximately the same. Organic matter was higher in the low hazard, particularly at 10- and 20-cm depths. Calcium was higher in top 30 cm in the low-hazard soils than in the high-hazard soils, but lower at 60 to 120 cm. Bulk density was higher at all depths in the high-hazard soils. Difference in pH levels between the two soil types were very little at all depths, with the greatest difference at 10 cm.

Since the hazard rating system is based on soil texture at 20- to 30-cm depths, the average soil characteristics at these depths and the incidence of *F. annosus* detected for each plot are compared in Tables 4 and 5 for the high- and low-hazard plots, respectively. The sand values at these depths accurately reflected the hazard rating given to each plot by field observations. Differences in sand, porosity, and moisture values between the two disease-hazard soil types were more striking at 20- to 30-cm depths than at the individual depths. The average sand, silt, and clay values for all high- and low-hazard plots were 74, 20, and 6, and 40, 30, and 30, respectively.

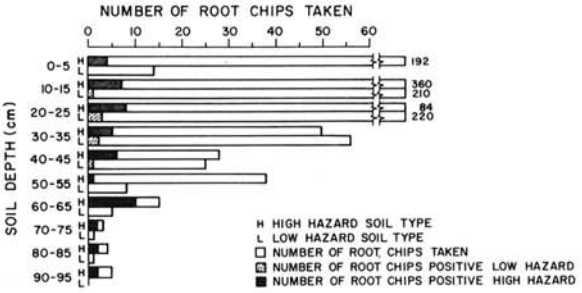

Fig. 1. Number of root chips isolated as a function of soil depth and number of root chips positive for *Fomes annosus* in excavation study of the root systems of 10 trees in the Parker Plantation (five trees per hazard soil type).

Soil and infection data for each of the soil depths from all plots were subjected to a multiple regression analysis. A simple linear correlation was determined for each soil parameter. The highest correlation was found with organic matter at the 10-cm depth. Sand and related parameters were also highly significant. A summary of the significant correlation coefficients is found in Table 6.

The relationship of level of infection to soil depth was measured by excavating root systems of five trees on the PH and PL plots. From a total of 1,552 and 1,073 root chips, *F. annosus* was isolated from 5.8 and 1.1% for the high- and low-hazard plots, respectively. Root chips are shown as a function of soil depth in Fig. 1. More chips were removed from roots located in the top 10 cm of the high-hazard soil, and more root chips were found positive for *F. annosus* at greater soil depths in high-hazard soils than in the low-hazard soil. A comparison between sampling two roots and all roots for these ten trees revealed twice as many trees infected *F. annosus* and 40% more infection with all roots sampled. No conks were found on any of the trees sampled on either hazard site.

The downward movement of spores by water through the soil may be an important factor in the spread of *F. annosus* in high-hazard soils. Conidia were washed through a prepared sand column 17.5 cm long with 1.25 to 8.74 cm of sterile distilled water. The number of spores per gram of soil for the five soil columns are summarized in Table 7. Spores moved through soil columns collected from UC-16 and G high-hazard plots to a depth of 9.5 cm.

TABLE 7. Downward movement of 10^6 *Fomes annosus* conidia by percolation through undisturbed field-collected soil cores[a] from loblolly pine plantations with 6.25 cm of water

Depth (cm)	Spores per gram of soil (no.)				
	High-hazard[b]			Low-hazard[c]	
	PH	UC-16	G	PL	BC-1
0 - 0.5	60	220	220	80	3,680
2.5 - 3.5	60	240	60	40	0
5.5 - 6.5	50	40	60	10	0
8.5 - 9.5	40	60	20	10	0
11.5 - 12.5	30	...[d]	...	0	...

[a] Soil cores were 10 cm in diameter, and 30 cm deep.
[b] Based upon > 65% sand, 25 cm soil depth.
[c] Based upon < 65% sand, 25 cm soil depth.

No spores were found below 0.5 cm in the soil column from BC-1. Spores were moved to a depth of 12.5 and 9.5 cm in the PH and PL soil columns, respectively. No spores were isolated from the control columns. It was extremely difficult to isolate *F. annosus* at 1:1 and 1:10 soil dilutions because of contaminating fungi and some bacteria. The best recovery occurred at 10^{-2} and 10^{-3} dilutions.

DISCUSSION.—Several investigators have reported on the incidence of *F. annosus* (8, 26, 32) and a comparison of the methods used has also been reported (3). The level of disease incidence found in this study was approximately the same as previously reported (1), which indicates that the disease incidence of annosus root rot may be higher than reported in other studies.

A possible loss in diameter growth has been shown in infected loblolly pine (2), and a growth loss suggested in infected Scots pine (*Pinus sylvestris* L.) (6). There was a significant difference in the diameters of infected and noninfected dominant and codominant trees, and a highly significant difference for the low-hazard plots. In the high-hazard plots, PH show the greatest difference; however, some plots indicated an opposite trend.

Determining disease severity by patterns of symptomatology of the crown is very difficult because trees may die from *F. annosus* infection without any outwardly visible signs of infection (17). The results of this study indicate that crown symptom expression can be used, but only as a rough estimate of disease severity. Stringy roots were found to be good symptoms of *F. annosus* infection; however, only about one-third of the resin-soaked roots revealed *F. annosus*.

Several investigators (10, 24, 26, 29) have noted the association of lighter textured soils with the presence of *F. annosus*. Soil parameters for the most part have been measured from soil samples taken from the top 30 cm (10, 24, 31). Soil samples used for analysis in the present study were taken at six depths, giving a better picture of the variation of the soil characteristics. Although most of the pine roots are located in the top 30 cm of the soil, significant numbers are found below this level as shown in Fig. 1.

In England, Rishbeth (29, 30, 31) and Wallis (36) found that in acid soils, *F. annosus* was more likely to be replaced by other fungi, and that the most severely damaged sites were on alkaline soils. In the southeastern United States, Froelich et al. (10) characterized severely damaged plots as having a pH range of 5.4 to 5.9. In this study, pH was found to be not associated with disease incidence or severity. The pH values for low- and high-hazard soils averaged about 4.8 to 5.1 for the top 30 cm, respectively (Table 3). It appears that from 4.5 to 6.0 pH plays no significant role in determining disease incidence or severity.

Organic matter, especially at the 10-cm depth (Table 6), was found to be significantly correlated with disease incidence. Other reports (10, 31) have associated low organic matter content with severely damaged areas. Field capacity and permanent wilting percentage were significantly correlated with disease incidence in this study. Trees subjected to moisture stress are more susceptible to infection by *F. annosus* (34), and this would occur most often on deep sandy soils. Bulk density values in Table 3 reflect the high sand content of the high-hazard plots. Bulk density was found to be highly significant at 10 cm. Calcium, phosphorus, potassium and magnesium values were generally not found to be correlated, $P=0.01$, with incidence. Porosity at soil depths of 10 to 60 cm was found to be significantly correlated with disease incidence, with noncapillary pore space positively related and capillary pore space negatively related to disease incidence (Table 6).

The downward movement of spores through the soil has been studied by several investigators (7, 11, 19, 23, 29). In this study, conidia were found to move downward through a prepared sand column 17.5 cm deep with as small an amount as 1.24 ml of water. However, in the sand column from BC-1 low-hazard plot, spores did not move below the top 0.5 cm of soil. With the PH soil core, spores were isolated at depths down to 12.5 cm, and with the PL soil core, spores were recovered at depths down to 9.5 cm. Although the percent recovery of *F. annosus* was somewhat low, the trend was quite evident. The results with the PL core seem to contradict the findings with the other low-hazard soil core, BC-1. However, a comparison of the values for the noncapillary pore space provides an answer to the differences.

From the soil data reported, it is possible to draw some inferences as to their influence on the incidence of disease caused by *F. annosus*. Sand and related parameters were significantly correlated with disease. Organic matter was highly and negatively correlated with incidence at the 10-cm depth, but not at lower depths. The greatest difference between high- and low-hazard sites occurred at the 10-cm depth. High sand values increase noncapillary pore space while silt, clay, and organic matter decrease noncapillary pore space. Noncapillary pores were postively correlated with incidence as was sand, but capillary pore values were negatively correlated.

Kuhlman (21) has stated that the factor which contributed the most to the difference in disease development was the greater frequency of root contacts on the high-hazard sites. This was not found in this investigation, and there were no root-to-root contacts showing infection. However, there were several pockets of infection located on roots with noninfected root tissue on both sides. This was found almost exclusively in the loamy sand soil.

A comparison of the noncapillary pore space values for PH and PL with the percent infection found in the root excavation study indicates a possible positive trend between spore movement, noncapillary pore space values and infection at depths down to 95 cm. These data suggest that on loamy-sand soils direct root infection by spores, if indeed it does occur, may be as significant as root infection via root contacts.

The significant correlation between noncapillary pore space and disease incidence found in this study, strongly suggest that the downward movement of *F. annosus* spores may contribute significantly to spread and infection on sandy soils, and therefore, should be considered as a plausible explanation for the effectiveness of the hazard-rating system.

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