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Fusarium species associated with rhizosphere soil and diseased roots of eastern white pine seedlings and associated nursery soil

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Fusarium species isolated from necrotic roots of eastern white pine (*Pinus strobus*) seedlings in two nurseries included *F. acuminatum*, *F. equiseti*, *F. oxysporum*, *F. oxysporum* var. *redolens*, *F. proliferatum*, *F. sambucinum*, *F. solani*, and *F. sporotrichioides*. In addition, all but *F. sambucinum* were isolated from the rhizosphere; all, in addition to *F. graminearum*, were also isolated from nonrhizosphere soil. *Fusarium oxysporum*, *F. oxysporum* var. *redolens*, and *F. proliferatum* were the most prevalent taxa in roots and nonrhizosphere soil. These three taxa plus *F. solani* predominated in rhizosphere soil. Species prevalence differed by site and date of collection, e.g. *F. proliferatum* was present at only one site. At least seven species of *Fusarium* were associated with seedling root rot and their prevalence differed according to site and time of year.

Additional key words: F. oxysporum. F. proliferatum, F. solani, Pinus strobus, root rot.

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Différentes espèces de *Fusarium* ont été isolées des racines nécrosées de jeunes plants de pin blanc (*Pinus strobus*) dans deux pépinières. Parmi ces espèces, on a retrouvé le *F. acuminatum*, le *F. equiseti*, le *F. oxysporum*, le *F. oxysporum* var. *redolens*, le *F. proliferatum*, le *F. sambucinum*, le *F. solani* et le *F. sporotrichioides*. De plus, toutes ces espèces, sauf le *F. sambucinum*, ont aussi été isolées de la rhizophère; toutes ces espèces, en plus du *F. graminearum*, ont aussi été isolées du sol non rhizosphérique. Le *F. oxysporum*, le *F. oxysporum* var. *redolens* et le *F. proliferatum* ont été les taxons les plus fréquemment retrouvés dans les racines et dans le sol non rhizosphérique. Ces trois taxons, en plus du *F. solani*, prédominaient dans le sol de la rhizosphère. La prédominance des espèces a varié avec les emplacements et les dates d'échantillonnage; par exemple, le *F. proliferatum* a été retrouvé à un seul emplacement. Au moins sept espèces de *Fusarium* ont été associées à la pourriture des racines des jeunes plants et leur prédominance a varié selon les emplacements et les périodes de l'année.

Mots clés additionels: F. oxysporum, F. proliferatum, F. solani, Pinus strobus, fonte des semis fusariose.

Fusarium root rot frequently causes severe losses of eastern white pine (*Pinus strobus* L.) seedlings in bareroot nurseries in the north central United States (Riffle & Strong 1960) and southern Ontario (Greifenhagen et al. 1990). In three surveys, mortality was 10–25% in white pine plots in Wisconsin State Forest Nurseries (Renlund 1980, Renlund 1981, Prey et al. 1983), and in another survey, up to 75% of the white pine seedlings had root rot (Prey et al. 1985). In 1986, 68% of the 571 000 white pine seedlings from one nursery were culled because of root rot (Prey et al. 1986). *Fusarium oxysporum* Schlechtend.:Fr. has been isolated from root lesions on white pine seedlings in Wisconsin, Michigan, and Ontario nurseries (Riffle & Strong 1960, Enebak 1988, Honhart & Juzwik 1988). *Fusarium moniliforme* J. Sheld. and *F. solani* (Mart.) Sacc. have been isolated from diseased eastern white pine seedlings; however these observations were limited to a single isolate (Riffle & Strong 1960), or the *Fusarium* species causing root rot were not reported in reference to eastern white pine (Wenner & Merrill 1984).

We conducted a study to identify and quantify *Fusarium* species associated with root lesions, rhizosphere soil, and nonrhizosphere soil of white pine seedlings. We wanted to determine if *F. oxysporum* was present in necrotic white pine roots and if other *Fusarium* species were also associated with this disease.

Materials and methods

Nursery fields. Operational fields in two nurseries were used as study sites: A14 at St. Williams Provincial Nursery, St. Williams, Ontario, Canada; and C50 at Wilson State Forest Nursery, Boscobel, Wisconsin, USA. The two nurseries are similar in latitude and species grown. Soils in both nurseries are loamy sands with 2–4% organic matter and 1.20 g/cm^2 average bulk density. The maximum water holding capacity was 20% in the Wisconsin field and 18% in the Ontario field; soil pH was 5.6 in the Wisconsin field and 5.4 in the Ontario field. Both fields have a history of root rot in white pine crops.

One-half (130 m × 42 m) of the Ontario field was fumigated with dazomet (400 kg product/ha) in August 1989; the other half was left unfumigated. Ten 130 m × 1.1 m bed-rows in both sections were seeded with stratified white pine in April 1990, and the field was maintained through each growing season according to standard nursery practices. One-half (168 m × 8 m) of the Wisconsin field was used in this study. This field was fumigated with methyl bromide—chloropicrin (MC-33, 393 kg product/ha) in August 1989, four 168 m × 1.1 m bed-rows were

seeded with white pine in October 1989, and the field was maintained through two growing seasons according to standard nursery practices.

Field sampling. Twelve 1.1-m^2 plots were established in each section of the Ontario field in April 1991, the beginning of the second growing season. Plots were placed according to a stratified random sample design with equal numbers of plots located in low, mid-slope, and high topographic areas of each section of the Ontario field. In the Wisconsin field, where little topographic variation was found, eight 1.1-m^2 plots were systematically located in each of three blocks (56 m × 8 m) that were situated successively along the length of the field; representing the successive decrease in irrigation pipeline diameter down the length of the Wisconsin field. All plots included the entire width of the seedbeds. All samples were collected during the second growing season for each field, i.e. when seedlings were 2 years old. Sample dates differed by nursery: 30 April, 2 July and 2 October 1991 in the Ontario field; and 14 May, 21 July and 8 October 1991 in the Wisconsin field. Ten randomly-selected living seedlings were carefully removed from each plot on each date in each location. The seedlings were placed in polyethylene bags and stored at 5°C until processed (approximately 1 week later). Rhizosphere soil was collected from each seedling: excess soil was removed by gently shaking roots, and rhizosphere soil was collected on clean paper by gently rubbing each root by hand. The rhizosphere soils collected from 10 seedlings from each plot were combined into one sample per plot as the result of the low yield of soil. Rhizosphere soil was then air-dried and stored at 5°C until processed (approximately 2 weeks later). Cores of nonrhizosphere (or bulk) soil were collected with a 2-cm-diameter Oakfield tube sampler soil probe (Forestry Suppliers Inc., Jackson, MS 39284) to a depth of 15 cm, yielding approximately 40 cm^3 of soil per core. Five soil cores were collected between seedling rows within each plot, combined by plot in a polyethylene bag, and stored at 5°C until processed (within 3 weeks).

Isolation of *Fusarium* species. Rhizosphere and nonrhizosphere soils were assayed using serial dilution plating with 0.1% water agar. A 10-g subsample of the nonrhizosphere soil was assayed from each plot; soil moisture content for each sample was determined by oven drying an additional 10-g sample for 48 h at 105°C. Rhizosphere soil from each plot was assayed in a similar manner. One half mL of each dilution was spread on each of four plates of a medium selective for *Fusarium* species. Nash and Snyder's pentachloronitrobenzene-peptone agar (Nash & Snyder 1962) supplemented with aureomycin (Kommedahl et al. 1979) was used for all samples; this medium was amended with oxgall for samples collected in Ontario (Papavizas 1967). Petri dishes were incubated for 7–14 days at 24°C under indirect lighting. Colonies of *Fusarium* species were transferred to acidified potato-dextrose agar (PDA) (Dhingra & Sinclair 1985) and incubated 12–20 days at 22°C under fluorescent lamps (three General Electric or Sylvania 40 W cool white tubes) supplemented with UV light (one Sylvania 40W tube, BLB series) with a 12-h photoperiod. Single-spore isolates were then obtained from each colony and stored on silica gel at 5°C (Windels et al. 1988).

Seedling root systems were washed with tap water and examined for necrosis. Fungi were isolated from symptomatic roots by excising 1-cm-long root segments from the necrotic-healthy root tissue interface, immersing them in 0.5% NaOCl solution for 1–3 min. followed by a sterile distilled water rinse, and placing pieces of the excised segments on the previously described *Fusarium*-selective medium. The petri dishes were held for 7–14 days at 22–24°C under indirect lighting. As before, colonies of *Fusarium* were transferred to acidified PDA; single-spore isolates of each colony were collected, and isolates were stored on silica gel.

Identification of *Fusarium* species. Identification of *Fusarium* to species was made by placing silica gel crystals on PDA and carnation leaf agar (Nelson et al. 1983). Cultures were incubated under the light and temperature regimes previously described. Each isolate was examined microscopically and identified to species according to the system of Nelson, Toussoun, and Marasas (1983).

Results

***Fusarium* species recovered.** When root lesion samples are compared, the greatest number of *Fusarium* taxa were isolated from root lesions on eastern white pine grown in the Wisconsin nursery whereas the fewest taxa were isolated from root lesions of trees grown in the nonfumigated Ontario plot (Table 1). Greater numbers of *Fusarium* taxa were isolated from nonrhizosphere soil samples than from roots in both the Wisconsin nursery and the nonfumigated Ontario plots. Rhizosphere soil samples yielded fewer taxa from fumigated Ontario plots relative to the number of taxa isolated from symptomatic roots, whereas the number of taxa was greater from rhizosphere samples than from lesion samples of seedlings grown in the Wisconsin nursery as well as in the nonfumigated plots located in Ontario. *Fusarium oxysporum* var. *redolens*, *F. oxysporum*, and *F. solani* were isolated from all three sources in both locations; *F. acuminatum* and *F. equiseti* were obtained from the two soil environments in both locations and differed in occurrence in root lesions by location; *F. sporotrichioides* and *F.*

Table 1. *Fusarium* species isolated from root lesions on 2-year-old eastern white pine seedlings, rhizosphere soil, and nonrhizosphere soil in two bareroot nurseries

	Root lesions			Rhizosphere soil			Nonrhizosphere soil		
Fusarium species	WI‡	Ontario-fum.	Ontario-nonfum.	WI	Ontario-fum.	Ontario-nonfum.	WI	Ontario-fum.	Ontario-nonfum.
F. acuminatum	+			+	+		+	+	+
F. equiseti		+		+			+	+	+
F. graminearum				+			+		
F. oxysporum	+	+	+	+	+	+	+	+	+
F. oxysporum var. *redolens*	+	+	+	+	+	+	+	+	+
F. proliferatum	+			+			+		
F. sambucinum		+							+
F. solani	+	+	+	+		+	+	+	+
F. sporotrichioides	+			+			+		

‡WI is a fumigated field in F.G. Wilson State Nursery, Boscobel, Wisconsin, USA; Ontario-fum. is a fumigated section in St. Williams Provincial Nursery, St. Williams, Ontario, Canada; and Ontario-nonfum. is a nonfumigated section in St. Williams Provincial Nursery, St. Williams, Ontario, Canada.

proliferatum were recovered from all three sources in the Wisconsin field; *F. graminearum* was isolated from the two soil environments only in the Wisconsin field; and *F. sambucinum* was recovered from root lesions and nonrhizosphere soil only in the Ontario field. The subgroup *F. oxysporum* var. *redolens* (Booth 1971, Gerlach & Nirenberg 1982) was delineated on carnation leaf agar, due to its prevalence, even though its status as a separate taxon is not universally accepted (Messiaen & Cassini 1981).

Not all plots yielded symptomatic seedlings in our samples. Generally, 50% of plots contained seedlings with root rot on the first sample date whereas nearly 90% of the plots yielded seedlings with diseased roots on the last sample date (Table 2). *Fusarium* species were not recovered from every seedling that exhibited root necrosis. Recovery was 30% to 98% of affected seedlings collected on the different dates.

Prevalence of *Fusarium* species in root lesions. *Fusarium oxysporum* var. *redolens* was the taxon most frequently associated with root lesions in the Wisconsin field, followed by *F. proliferatum* (Fig. 1). *Fusarium oxysporum* var. *redolens*, *F. oxysporum*, and *F. solani* were the most frequently isolated species from seedlings in both sections of the Ontario field. There was no qualitative difference in the *Fusarium* species isolated from both sections, but the number of seedlings with root lesions from which *Fusarium* species were obtained was greater in the nonfumigated section than in the fumigated section for the July and October sampling dates. The number of seedlings with root lesions that yielded *Fusarium* species increased throughout the growing season at both nurseries. Mixtures involving seven different pairs of *Fusarium* species were associated with root lesions on affected seedlings from both nurseries. *Fusarium* species mixtures were less prevalent than the predominant two or three *Fusarium* species isolated from root lesions in all sites and dates with one exception. In the October samples from the nonfumigated section of the Ontario field, different mixtures of *Fusarium* species were recovered from diseased seedling roots (Fig. 1): *F. oxysporum* and *F. oxysporum* var. *redolens* from seven seedlings, *F. oxysporum* var. *redolens* and *F. solani* from six, and *F. oxysporum* and *F. solani* from three seedlings.

Prevalence of *Fusarium* species in nonrhizosphere soil. Mean number of colony-forming units (cfu) of *Fusarium* species per gram of soil peaked in all fields in July: 3779 in the Ontario-nonfumigated field; 2695 in the Ontario-fumigated field; and 4671 in the Wisconsin field. The predominant *Fusarium* species in each field differed slightly by sampling date. In the Wisconsin field, *F. oxysporum* var. *redolens* was the taxon most frequently recovered in April, but *F. proliferatum*, present at low levels in April, was the predominant species in July and October (Fig. 2A). In the Ontario-fumigated field, only *F. oxysporum* var. *redolens* and *F. sambucinum* were found in April; *F. oxysporum* appeared in July

Table 2. Incidence of fusarium root rot of 2-year-old eastern white pine seedlings by plot and seedling basis in an Ontario and a Wisconsin bareroot nursery

Nursery field‡	Sampling date	Affected plots (%)	Affected seedlings (%)
Wisconsin-fumigated	14 May 1991	42	8
	21 Jul 1991	79	20
	8 Oct 1991	88	30
Ontario-fumigated	30 Apr 1991	50	8
	2 Jul 1991	67	24
	2 Oct 1991	92	22
Ontario-nonfumigated	30 Apr 1991	50	8
	2 Jul 1991	100	28
	2 Oct 1991	92	35

‡Wisconsin-fumigated is located in F.G. Wilson State Nursery, Boscobel, Wisconsin, USA and Ontario-fumigated and -nonfumigated plots are located in St. Williams Provincial Nursery, St. Williams, Ontario, Canada.

and was the most prevalent species in October (Fig. 2B). *Fusarium oxysporum* var. *redolens* and *F. oxysporum* were frequently recovered on two of the sampling dates in both the fumigated and nonfumigated sections of the Ontario field; however, *F. solani* was present throughout the season in the nonfumigated section but appeared only during the October sampling date in the fumigated section (Fig. 2B & 2C).

Prevalence of *Fusarium* species in rhizosphere soil. The mean number of colony-forming units encompassing all *Fusarium* species (cfu per gram of soil) in both sections of the Ontario field peaked in July. Data are not available to make a similar comparison in the Wisconsin field. *F. oxysporum* var. *redolens* and *F. oxysporum* were the predominant taxa in rhizosphere soil in both sections of the Ontario field on all three sampling dates and in the Wisconsin field in October (Fig. 2). However, *F. solani* was found at much higher frequencies on all three dates in the rhizosphere soil from the nonfumigated section of the Ontario field than in the fumigated section. *Fusarium proliferatum* predominated in the Wisconsin field rhizosphere soil in May, but the number of colonies of *F. oxysporum*, *F. oxysporum* var. *redolens*, and *F. solani* reached counts similar to those of *F. proliferatum* by October.

Discussion

Three *Fusarium* species were consistently associated with diseased roots of eastern white pine seedlings in our studies. These findings augment previous reports that *F. oxysporum* is associated with white pine root rot (Enebak 1988, Honhart & Juzwik 1988). Although we isolated eight species of *Fusarium, F. oxysporum, F. proliferatum,* and *F. solani* were the most prevalent on roots and in rhizosphere and nonrhizosphere soils. Also, we found *F. oxysporum* var. *redolens* to be consistently associated with root

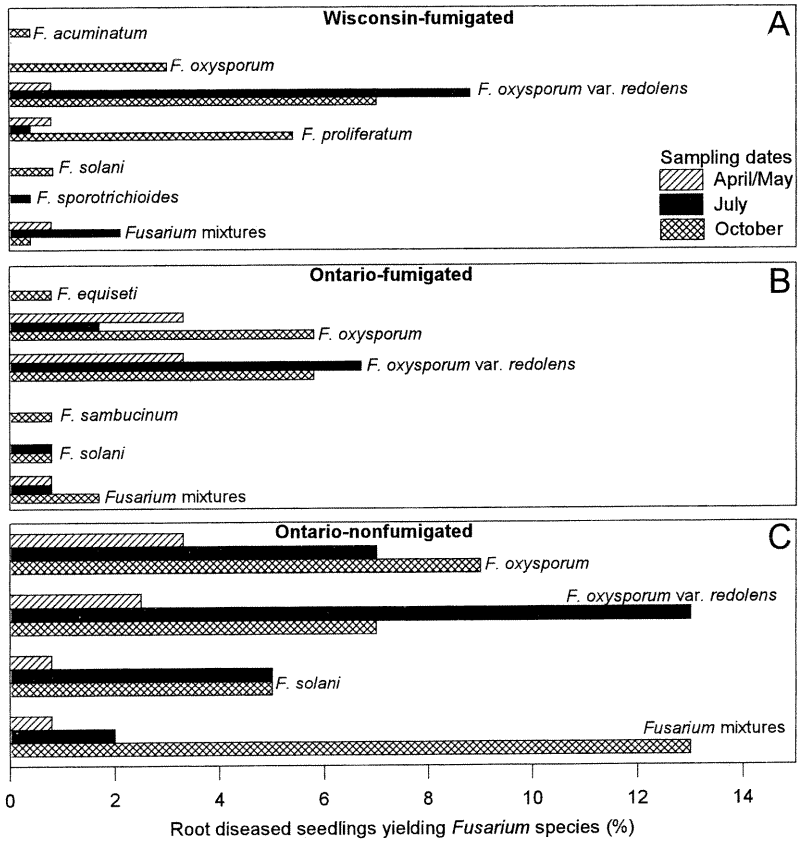

Figure 1. *Fusarium* species isolated from root lesions on 2-year-old eastern white pine seedlings in two bareroot nurseries. The Wisconsin-fumigated field is located in F. G. Wilson State Nursery, Boscobel, Wisconsin, USA. Ontario-fumigated and Ontario-nonfumigated are half sections of one field in St. Williams Provincial Nursery, St. Williams, Ontario, Canada. Samples were collected on 14 May, 21 July, and 8 October 1991 from the Wisconsin nursery. Samples were collected on 30 April, 2 July, and 2 October 1991 from the Ontario nursery.

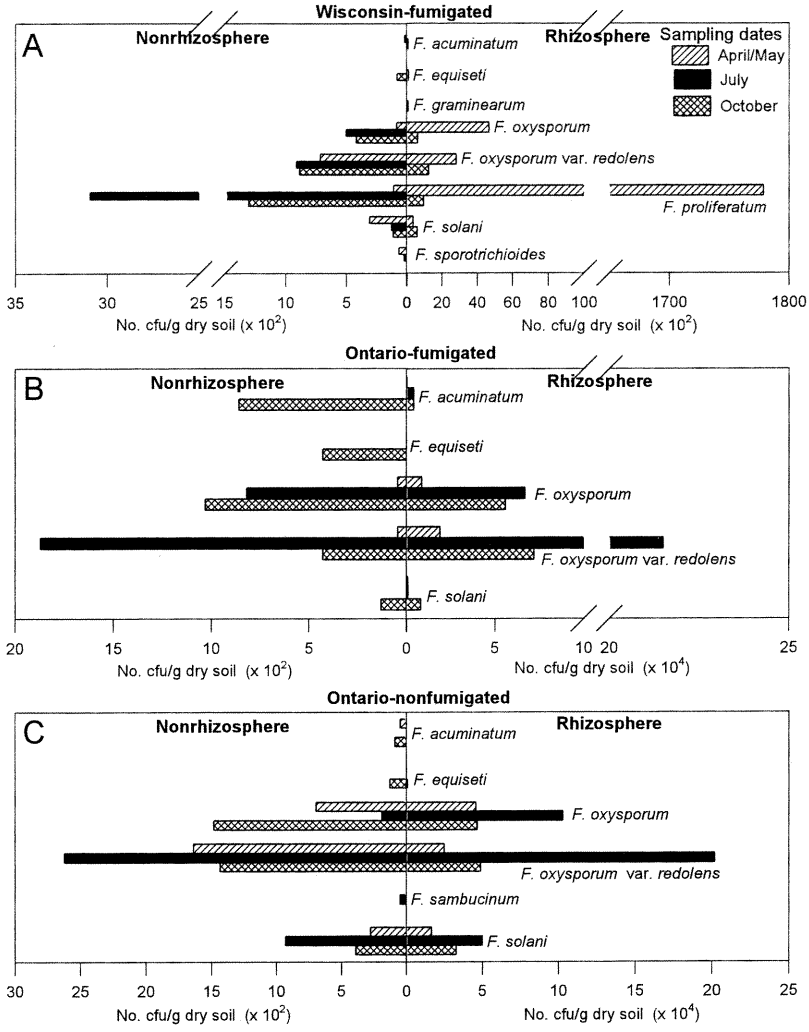

Figure 2. *Fusarium* species isolated from nonrhizosphere and rhizosphere soil collected from two eastern white pine bareroot nursery fields. The Wisconsin-fumigated field is located in F.G. Wilson State Nursery, Boscobel, Wisconsin, USA. Ontario-fumigated and Ontario-non-fumigated plots are half sections of one field in St. Williams Provincial Nursery, St. Williams, Ontario, Canada. Samples were collected on 14 May, 21 July, and 8 October 1991 from the Wisconsin nursery. Samples were collected on 30 April, 2 July, and 2 October 1991 from the Ontario nursery.

lesions in our study, confirming previous reports that a subgroup of *F. oxysporum* may play a significant role in root rot of conifers (Booth 1971, Matuo & Chiba 1966). Mixtures of *Fusarium* species were isolated from root lesions, but such mixtures were isolated less often than were single species of *Fusarium*. This suggests that, compared to single species of *Fusarium*, mixtures may be less important contributors to fusarium root rot of eastern white pine.

Riffle and Strong (1960) reported that *F. moniliforme* and *F. solani* were implicated in root rot of white pine, and our data support their conclusion. Since Riffle and Strong's report, *F. proliferatum* has been separated from *F. moniliforme* (Nirenberg 1976). Riffle and Strong may have reported *F. proliferatum* had they known of the existence of this species. This is the first report of *F. acuminatum*, *F. equiseti*, *F. sambucinum*, and *F. sporotrichioides* associated with diseased roots of eastern white pine seedlings. However, the low rate of isolation of these four species from symptomatic roots raises the question of whether these species are secondary rather than primary colonizers of white pine roots.

The species composition of *Fusarium* assemblages in white pine nursery fields apparently varies with season, geographic location, and management practices,

among other factors. Incidence of symptomatic seedlings that yielded *Fusarium* isolates increased as the growing season progressed; total number of colony-forming units of all *Fusarium* species, in rhizosphere and nonrhizosphere soil, peaked in July. Generally, the number of species of *Fusarium* detected was greater in October than in April/May. However, this may be attributed to secondary colonization by these minor species or increases in specific populations that enabled detection of the minor *Fusarium* species rather than migration of these minor species into the fumigated fields.

The Wisconsin site yielded a greater diversity of *Fusarium* species from rhizosphere and nonrhizosphere samples than did the Ontario location. In addition, a predominant *Fusarium* species in the Wisconsin nursery, *F. proliferatum*, was not detected at the Ontario nursery. A lessor diversity of *Fusarium* species was associated with diseased seedlings in nonfumigated plots than that found in fumigated plots. Fumigation frequency, type of fumigant, soil characteristics, and site characteristics may contribute to the diversity of *Fusarium* species present. These factors may influence when, where, how, and which *Fusarium* species recolonize fumigated soil

Many researchers have observed that if a single species is prevalent, that species is usually the pathogen and it competes successfully against other less pathogenic or saprophytic species (Bruehl 1987). Conversely, a single species or a combination of species occupying the rhizosphere may mediate root invasion by a pathogen, especially if the pathogen has a low competitive saprophytic ability demonstrated by its inability to colonize the rhizosphere (Ocamb & Kommedahl 1994). The role of each *Fusarium* species has yet to be resolved, and pathogenicity tests have been initiated to ascertain the primary cause of white pine root rot. Moreover, site and seasonal influences need to be determined in order to understand white pine root rot. Nevertheless, it is possible that multiple *Fusarium* taxa cause root rot of white pine in bareroot nurseries, and effective disease control measures are needed to produce healthy seedlings.

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