Armillaria species on small woody plants, small woody debris, and root fragments in red pine stands

K.W. Kromroy, R.A. Blanchette, and D.F. Grigal

Abstract: The incidence of *Armillaria* on small woody plants, small woody debris, and root fragments was estimated in red pine (*Pinus resinosa* Ait.) stands in northeastern Minnesota. Soil core samples 10 cm in diameter, and extending to a depth of either 16 or 25 cm, were collected from 13 stands belonging to three age-classes. Half of the youngest stands had been treated using herbicide. Mycelial fans or rhizomorphs of *Armillaria* were observed on 13% of the small woody plants and isolated from 8% of them. Including small woody debris and root fragments, 38% of 0–16 cm deep samples had *Armillaria*. *Armillaria* was observed on 3% and isolated from 1% of individual substrate units from 0 to 25 cm deep samples. Within a single stand, 0%–67% of the samples and 0%–9% of the individual units had evidence of *Armillaria*. All but one isolate were *Armillaria ostoyae* (Romagn.) Herink. Herbicide-treated and untreated red pine stands had similar *Armillaria* incidence, and there was a trend of incidence inversely related to stand age-class. Large numbers of small woody plants, woody debris, and root fragments were found in red pine stands; varying percentages of these substrates were contributing to the survival of *Armillaria* and could also be serving as sources of root disease inoculum.

Résumé : L'incidence d'*Armillaria* sur les plantes ligneuses de petite dimension, les petits débris ligneux et les fragments de racines a été évaluée dans des peuplements de pin rouge (*Pinus resinosa* Ait.) du nord-est du Minnesota. Des échantillons de sol sous forme de carottes de 10 cm de diamètre et atteignant une profondeur de 16 ou 25 cm ont été récoltés dans 13 peuplements représentant trois classes d'âge. La moitié des plus jeunes peuplements avaient été traités avec des herbicides. Des plaques mycéliennes en forme d'éventail ou des rhizomorphes caractéristiques de l'armillaire ont été observés sur 13 % et isolés sur 8 % des plantes ligneuses de petite dimension. Si on inclut les débris ligneux et les fragments de racines, l'armillaire était présent dans 38 % des échantillons de 0 à 16 cm de profondeur. L'armillaire a été observé sur 3 % et isolé sur 1 % des unités individuelles de substrat des échantillons de 0 à 25 cm de profondeur. Dans un seul peuplement, 0 % – 67 % des échantillons et 0 % – 9 % des unités individuelles montraient des signes d'armillaire. Tous les isolats à l'exception d'un correspondaient à *Armillaria ostoyae* (Romagn.) Herink. L'incidence de l'armillaire était similaire que les peuplements de pin rouge aient été traités à l'herbicide ou non et elle avait tendance à être inversement reliée à la classe d'âge du peuplement. Un nombre important de plantes ligneuses de petite dimension, de débris ligneux et de fragments de racines ont été observés dans les peuplements de pin rouge; différentes proportions de ces substrats contribuent à la survie de l'armillaire et pourraient aussi servir de sources d'inoculum pour cette maladie de racines.

[Traduit par la Rédaction]

Introduction

Armillaria root disease continues to cause significant economic and ecological damage to conifers growing in undisturbed areas in several regions of North America, as well as in stands under varying management (Rosso and Hansen 1998; Lundquist 2000; Morrison et al. 2000; McLaughlin 2001*a*; Rizzo and Slaughter 2001). One approach to managing armillaria root disease is to reduce the amount of inoculum on a site by removing substrates that serve as food bases for the fungus. Sanitation efforts are typically applied following harvest, but before regeneration, and usually focus on stumps and large-diameter roots of harvested trees (Hagle and Shaw 1991; Morrison and Mallet 1996; Sturrock 2000; Omdal et al. 2001). Even though small segments of stems and roots have been used successfully as inoculum for armillaria root disease in greenhouse experiments (Patton and Riker 1959; Rishbeth 1985; Whalstrom and Johansson 1992; Klein-Gebbinck et al. 1993), small materials dry and (or) become colonized by other fungi more quickly than larger units of substrate (Redfern and Filip 1991; Bruhn et al. 1998). Small materials usually are disregarded as important sources of inoculum in the field. For example, after removing 94% of the belowground stump and large-root biomass from *Armillaria* and *Heterobasidion annosum* infested sites in New Mexico, Omdal et al. (2001) estimated that, because over 50% of the remaining broken roots were less than 2.5 cm in diameter, the material would rapidly decay and not be a significant source of inoculum. Lung-Escarmant and Guyon (2004) only considered stumps from the original stand

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and recently killed trees in the regenerating stand as sources of inoculum in their assessment of inoculum density over time and space in a pine plantation in France.

There may be some scenarios in which small substrates are important in armillaria root disease. Root fragments colonized by *Armillaria ostoyae* (Romagn.) Herink. as small as 0.5 cm in diameter apparently served as sources of inoculum to infect naturally regenerating ponderosa pine (*Pinus ponderosa* Laws.) 12 years after site treatment in central Washington (Reaves et al. 1993). In conifer orchards in Ontario treated to remove residual roots and debris, the median-sized pieces of debris in the root zones of trees killed by *A. ostoyae* from sites that were fallow before planting for 1 and 5 years were 2 and 7 cm^3, respectively (Bruhn et al. 1998). Roth et al. (2000) reported that 20 years after ponderosa pine had been regenerated on infected sites, the only sanitation treatment consistently associated with reduced mortality from armillaria root disease was hand removal of roots following mechanical push-out logging.

In addition to residual woody debris and root fragments (DRF), current understory vegetation may provide substrates for *Armillaria* species and thus contribute to inoculum potential. *Armillaria* rhizomorphs and (or) lesions frequently are observed on roots of understory trees and shrubs (Adams 1974; Kile 1980; Pearce et al. 1986; Rizzo et al. 1995) and in south-western Australia *Armillaria luteobubalina* kills many species of understory plants in eucalyptus forests and coastal dune vegetation (Shearer and Tippett 1988; Shearer et al. 1997, 1998). In 10-year-old plantations of radiata pine (*Pinus radiata* D. Don) in New Zealand, Shaw et al. (1976) concluded that toetoe (*Cortaderia fulvida* (Buch.) Zotov), a perennial grass, played a role in the epidemiology of root disease caused by *Armillaria novae-zelandiae* (Stevenson) Boesewinkel. Almost 90% of dead toetoe clumps were infected with *Armillaria*, and in one plantation, pines with adjacent dead toetoe clumps had a significantly higher infection rate than pines that did not have toetoe within 30 cm. In Alberta, Canada, *Armillaria* rhizomorphs were identified on fireweed (*Epilobium angustifolium* L.), a perennial forb growing in stands of young lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) with armillaria root disease (Klein-Gebbinck et al. 1991). In follow-up greenhouse experiments, both *Armillaria mellea* (Vahl:Fr.) Kummer and *A. ostoyae* were able to infect fireweed and in turn infect the pine, suggesting a role for this forb in the epidemiology of armillaria root disease (Klein-Gebbinck et al. 1993).

While there are several references implicating small woody debris, root fragments, and understory vegetation in armillaria root disease, there are few quantitative studies on the occurrence of *Armillaria* on these substrates in North America and their potential to serve as sources of inoculum. This information would be useful in choosing methods for root disease management, and especially sanitation procedures. These procedures are expensive, may cause excessive disturbance to a site, and may leave varying amounts of residual inoculum to contribute to root disease (Hagle and Shaw 1991; Reaves et al. 1993; Bruhn et al. 1998; Roth et al. 2000; Sturrock 2000; Omdal et al. 2001).

We conducted a study to quantify the incidence of *Armillaria* species on understory plants — specifically woody species and small DRF in red pine (*Pinus resinosa* Ait.) stands in northeastern Minnesota. Red pine is widely planted in the northern United States and Canada (Rudolf 1990), and the red pine forest type accounts for about 4% of the 20 million ha of forestland in Minnesota, Wisconsin, and Michigan (Schmidt 2002). Although tree mortality was not assessed in this study, red pine is susceptible to armillaria root disease (Pronos and Patton 1977; Smith et al. 1994; McLaughlin 2001*a*), and Rizzo et al. (1995) reported mortality associated with *A. ostoyae* on red pine in a stand near those we sampled.

Materials and methods

Study stands

Study stands were located within the University of Minnesota Cloquet Forestry Center in northeastern Minnesota. The forest type cover of the center, an area of more than 1500 ha, is mostly upland forest of red, white (*Pinus strobus* L.), and jack pine (*Pinus banksiana* Lamb.), spruce–fir, and aspen–birch (Alm 1988). The soils in the study stands are of the Omega–Cloquet–Cromwell association (Lewis 1978), a well-drained glaciofluvial outwash. We sampled three age-classes and, within the youngest class, herbicide-treated and untreated stands. Six stands were 5–8 years old (young pine, YP) and had been planted following clearcuts of red pine – jack pine stands. Three of the YP stands had been treated using the herbicide glyphosate within 1–4 years after planting to control competition (young pine treated, YPTR), and three were untreated (young pine untreated, YPUT). Three stands, 68–78 years in age at the time of the study, were termed middle-aged (MID). These stands had been thinned within 6–10 years prior to the study. Four red pine stands ranging in age from 150 to 240 years were termed old (OLD). These stands were the result of natural regeneration after several fires that occurred in the area during the 1700s and 1800s. Some thinning had been done in one of these stands (OLD2) about 10 years prior to the study. Recent (within 3 years) red pine mortality was observed in two stands, YPTR3 (5%) and MID2 (10%), and *Armillaria* fans were present on roots and (or) root collars of dead standing trees. Stand size ranged from 0.25 to 0.9 ha. Other stand information is reported in Table 1.

Sample collection and processing

Substrates were defined as: (1) small woody plants, woody species other than red pine, with a stem diameter between 1 and 20 mm at ground level; and (2) small DRF, pieces of debris or roots (live and dead) at least 1 mm in diameter and 20 mm long. Using a completely randomized design, 15 points were located in each of 12 stands, and 25 points were located in one stand (YPTR1). This was the first stand to be sampled, after which the number of sampling points was reduced because of time constraints. Sampling occurred at the small woody plant that was closest to the randomly located point; we included hardwood sprouts and suckers as well as seedlings of both hardwoods and conifers (other than red pine). Multiple stems arising from a single root base were considered one plant. After recording the species, aboveground condition, and ground-level stem diameter(s), the sample plant was cut at the soil line. Next, a 10 cm diameter core, 16 cm long (1256 cm^3) and centered over the cut stem, was removed using a steel coring device

Table 1. Vegetation characteristics of 13 red pine study stands, Cloquet Forestry Center, University of Minnesota.

	Stumps[a]			Red pine ≥1.4 m tall		Small woody plants[b] (no./m^2)			DRF[c] in 0–25 cm deep samples	
Stand type[d]	ID No.	Avg.[e]	Range	Avg.[e]	Range	Avg.[f]	Range	% dead	Avg.[g]	Range
YPTR	1	6	4–7	8	4–12	13	8–17	46	28	20–42
	2	2	0–4	5	0–8	10	5–18	2	34	22–45
	3	6	0–9	10	10–11	22	17–28	3	25	22–45
YPUT	1	1	0–3	4	3–4	25	10–36	2	31	20–44
	2	2	0–3	5	2–7	17	12–27	1	25	19–32
	3	8	6–9	12	8–18	22	17–27	7	36	23–45
MID	1	7	2–14	6	4–8	7	2–14	6	10	6–15
	2	2	1–2	12	8–16	8	3–13	15	30	26–35
	3	3	0–6	6	5–7	4	0–6	6	21	16–33
OLD	1	0	0	3	1–5	8	3–14	19	46	39–60
	2	1	0–3	1	1	11	8–14	11	25	18–32
	3	1	0–4	3	0–7	4	1–10	0	18	15–23
	4	2	0–3	1	0–3	5	0–8	10	22	11–32

[a]All species.
[b]Woody plants other than red pine with 1–20 mm stem diameter at the ground.
[c]Debris and root fragments at least 1 mm in diameter and 20 mm long.
[d]Stand types are the following: YPTR, young pine (5–8 years) treated with herbicide; YPUT, young pine (5–8 years) no herbicide; MID, middle age (68–78 years); OLD, old (150–240 years).
[e]Average number and range per 0.01 ha, based on four or five randomly located 0.01-ha plots.
[f]Average number and range (live and dead) based on four to five randomly located 1-m^2 plots.
[g]Average number and range per core sample, 10 cm diameter and 25 cm long.

(Lever Action Hole Cutter, Par Aide Products Co., St. Paul, Minnesota). Each core, containing sample plant roots along with soil and other organic matter, was placed in a plastic bag. At five of the sample points in each stand, a second core was collected from 16 to 25 cm deep (706 cm^3). Collections were made during the summer and autumn of three consecutive years, beginning in 1995.

Samples were stored at 7–10 °C for 2–5 d before processing, at which time the contents of the plastic bag were placed on a 1 cm × 1 cm mesh screen, which rested on a second screen with a 3 mm × 3 mm mesh. Soil was washed from the roots and DRF by spraying with a garden hose. The material retained on both screens was assessed for the presence of *Armillaria*.

Assessment for *Armillaria*

The incidence (presence or absence) of *Armillaria* was measured by observation of, and by subsequent isolation from, mycelial fans and rhizomorphs associated with the substrate units (small woody plant or DRF). Incidence estimates of *Armillaria* were calculated as (1) the number of small woody plants with *Armillaria* per total number of small woody plants sampled; (2) the number of 0–16 cm deep samples with *Armillaria* on at least one DRF per total number of 0–16 cm deep samples; (3) the number of 0–16 cm deep samples with *Armillaria* on either a small woody plant or at least one DRF; and (4) the number of individual substrate units (i.e., pieces), including the sample plant root as one unit, with *Armillaria* in the 0–25 cm deep samples per total number of substrate units collected in those samples.

Each substrate unit with *Armillaria* was assigned a score based on the presence or absence of rhizomorphs, their apparent attachment and (or) penetration, and presence or absence of mycelial fans. Isolation was attempted from each substrate unit on which *Armillaria* was observed. Pieces of mycelial fans (5 mm or less in size) and (or) wood were taken from unexposed surfaces and plated both on water agar (15 g Difco agar/L) and on basidiomycete-selective medium (Harrington et al. 1992). Rhizomorphs that were attached to substrate units were removed carefully, and surface disinfected by soaking in an aqueous solution of 10% bleach and 20% ethanol for 3 min, then rinsed in sterilized water, and blotted on sterilized paper towel. These were cut into 1-cm segments and cultured. Plates were incubated under laboratory conditions (20–25 °C). Subculturing onto 1% malt extract agar (MEA) was done to obtain pure isolates.

Armillaria species identification

Diploid–haploid pairings, per Korhonen (1978), were used to identify the unknown *Armillaria* isolates to species. Each field isolate, presumably diploid, was paired with haploid tester isolates (two each of *A. ostoyae*, *Armillaria gallica* Marxmüller & Romagn., and *A. mellea*; one each of *Armillaria sinapina* Bérubé & Dessureault and *A. calvescens* Bérubé & Dessureault) obtained from Dr. David Rizzo, University of California, Davis. One 3-mm plug of the tester strain was placed on 1% MEA, 5 mm from a plug of the unknown. Plates were incubated under laboratory conditions for 5–7 weeks, at which time all pairings were subcultured (Harrington et al. 1992) and visually evaluated after 10–14 d. If the field isolate belongs to the same species as the haploid tester, the fluffy haploid mycelia of the tester isolate becomes converted to diploid mycelia with flat morphology (Rizzo and Harrington 1992). For each diploid–haploid combination, three pairings were made and subcultured.

Statistical analyses

Differences in *Armillaria* incidence within and between stand types were analyzed using generalized linear mixed models, with random effects due to stands. Model fits were compared with a likelihood ratio test — the difference between the [–2 log likelihood statistic] for the two models be-

Table 2. Incidence of *Armillaria* on small woody plants in four red pine stand types, Cloquet Forestry Center, University of Minnesota.

	No. of small woody plants[a]									
	YPTR		YPUT		MID		OLD		Total	
Species	Ex.	*Arm.*	Ex.	*Arm.*	Ex.	*Arm.*	Ex.	*Arm.*	Ex.[b]	*Arm.*
Corylus cornuta Marsh.	20	6, 4	10	2, 2	16	1, 0	28	3, 0	74 (5)	12, 6
Rubus L. spp.	13	0, 0	8	0, 0	8	0, 0	1	0, 0	30	0, 0
Vaccinium angustifolium Ait.	7	0, 0	10	4, 3	5	0, 0	3	0, 0	25 (1)	4, 3
Diervilla lonicera Mill.	3	0, 0	11	2, 0	4	0, 0	6	0, 0	24 (1)	2, 0
Acer L. spp.	1	1, 0	0	—	4	0, 0	15	0, 0	20 (1)	1, 0
Populus L. spp.	6	3, 3	1	0, 0	4	1, 0	0	—	11 (4)	4, 4
Comptonia peregrina (L.) J.M. Coult.	3	1, 0	3	0, 0	0	—	0	—	6	1, 0
Lonicera L. sp.	0	—	0	—	0	—	4	0, 0	4	0, 0
Abies balsamea (L.) Mill.	0	—	0	—	1	0, 0	2	0, 0	3	0, 0
Amelanchier sanguinea (Pursh) DC.	1	0, 0	0	—	1	1, 1	0	—	2 (1)	1, 1
Picea A. Dietr. sp.	0	—	0	—	1	0, 0	0	—	1	0, 0
Rosa L. sp.	1	0, 0	0	—	0	—	0	—	1	0, 0
Unknown	0	—	2	1, 1	1	1, 1	1	0, 0	4 (2)	2, 2
Total plants	55	11, 7	45	9, 6	45	4, 3	60	3, 0	205	27, 16
Plants with no live stems	7	3, 3	2	1, 1	3	1, 1	3	0, 0	15	5, 5

Note: YPTR, young pine (5–8 years) treated with herbicide; YPUT, young pine (5–8 years) no herbicide; MID, middle age (68–78 years); OLD, old (150–240 years). Ex., number of plants examined.; *Arm.*, number of plants on which *Armillaria* was observed and number on which *Armillaria* was observed and subsequently isolated; —, not applicable, since no plants of this species were examined.

[a]Includes both live plants and those with no live stems.

[b]Numbers in parentheses indicate the number of plants with no live stems.

ing compared has a χ^2 distribution with degrees of freedom equal to the difference in the number or parameters in the models. Both *t* test statistics and odds ratios were used in interpreting results of the final model. Analyses were conducted using SAS statistical software (SAS 9.1, SAS Institute Inc. 2003). Separate analyses were conducted for three measures of *Armillaria* incidence: (1) the number of 0–16 cm deep samples for which *Armillaria* was observed on either the small woody plant or at least one DRF; (2) the number of 0–16 cm deep samples from which *Armillaria* was isolated from either the small woody plant or at least one DRF; and (3) the number of individual substrate units on which *Armillaria* was observed out of the total number of units in 0–25 cm deep samples. Because the number of individual units from which *Armillaria* was isolated was so low, statistical tests were not performed on these data.

Results

Comparison among substrate components

A total of 205 small woody plants were sampled, representing 10 genera of broad-leaved species and two genera of conifer species (Table 2). Over one-third of the sampled plants were beaked hazelnut (*Corylus cornuta* Marsh.) This species, along with *Rubus* species, late low blueberry (*Vaccinium angustifolium* Ait.), northern bush-honeysuckle (*Diervilla lonicera* Mill.), maple species (mainly *Acer rubrum* L.), and aspen species (mainly *Populus tremuloides* Michx.) made up 90% of the sampled plants. Seven percent of the sampled plants had no evidence of a live stem.

Overall, mycelial fans or rhizomorphs of *Armillaria* were observed on the roots of 13% of the small woody plants that were sampled, representing seven genera, and *Armillaria* was isolated from 8% of the total number, representing four genera (Table 2). The highest incidence of *Armillaria* across all plants was on *C. cornuta* (observed on 12 of 205, isolated from 6 of 205), followed by *V. angustifolium* and *Populus* spp. Observations of *Armillaria* on *C. cornuta* occurred in all stand types, accounting for 22% (YPUT) to 100% (OLD) of the plants with *Armillaria*; the fungus was isolated from this host species in two of the stand types (YPUT, YPTR). For a single plant species, the highest percentage with *Armillaria* was *Populus*, with 36% showing signs and producing the fungus in culture; most of these were in the YPTR stand type. Of the plant species that were sampled in all four stand types (*C. cornuta*, *Rubus* spp., *V. angustifolium*, and *D. lonicera*), *Rubus* was the only one on which *Armillaria* was not observed in any stands. *Armillaria* was observed on the roots of small woody plants from 10 stands, and isolated from this substrate from six stands. The maximum incidence of *Armillaria* on small woody plants in a single stand was 40% based on observation and 33% based on isolation. All the isolates from the plants were identified as *A. ostoyae.*

Debris and root fragments were assessed for *Armillaria* presence or absence in 190 of the 0- to 16-cm-deep samples (12–15 per stand). The incidence of *Armillaria* overall, estimated as the percent of 0- to 16-cm-deep samples with the fungus on at least one DRF, was 33% (62 of 190) based on observation, and 13% based on isolation (Table 3). *Armillaria* was observed on DRF from 11 stands and isolated from DRF from eight stands. Among single stands, the maximum percentage of samples with *Armillaria* on DRF was 60% based on observation and 33% based on isolation (data not shown). All isolates, except one, were identified as *A. ostoyae.* The exception was *A. sinapina*, the identification being confirmed by PCR-based analysis (D. Rizzo, University of California, Davis, personal communication).

The percentage of 0- to 16-cm-deep samples in which *Armillaria* was observed on a substrate unit increased from 13% (24 of 190) based on the plants alone, to 38% when

Table 3. Comparisons among the numbers of 0–16 cm deep samples with *Armillaria* on small woody plants, small woody debris and root fragments (DRF) in four red pine stand types, Cloquet Forestry Center, University of Minnesota, based on observation (Obs.) alone and observation followed by isolation (isol.).

		No. of samples with *Armillaria* by substrate type					
		Small woody plants		DRF		Total[a]	
Stand type	No. samples examined	Obs.	Obs. + isol.	Obs.	Obs. + isol.	Obs.	Obs. + isol.
YPTR	45	8	4	25	10	28	14
YPUT	43	9	6	20	11	23	15
MID	42	4	3	11	3	14	6
OLD	60	3	0	6	0	7	0
Total	190	24	13	62	24	72	35

Note: YPTR, young pine (5–8 years) treated with herbicide, 3 stands; YPUT, young pine (5–8 years) no herbicide, 3 stands; MID, middle age (68–78 years), 3 stands; OLD, old (150–240 years), 4 stands.

[a]Total number of samples with *Armillaria* may be less than the sum of the number for each substrate because it was found on both substrates in some samples.

Fig. 1. Percentage of 0–16 cm deep core samples with *Armillaria* on at least one substrate unit (small woody plant, small woody debris, or root fragment (DRF)) in 13 red pine stands, Cloquet Forestry Center, University of Minnesota; 12–15 core samples per stand. Stand types were the following: (*i*) YPTR young pine (5–8 years) treated with herbicide; (*ii*) YPUT young pine (5–8 years) no herbicide; (*iii*) MID middle age (68–78 years) and; (*iv*) OLD (150–240 years).

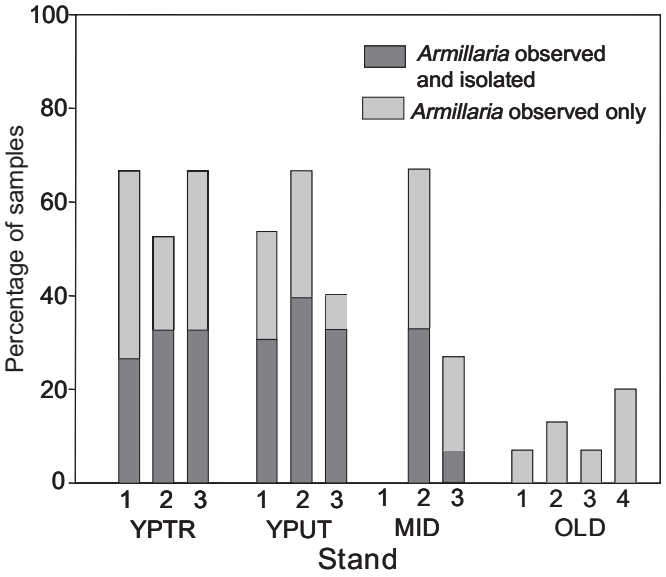
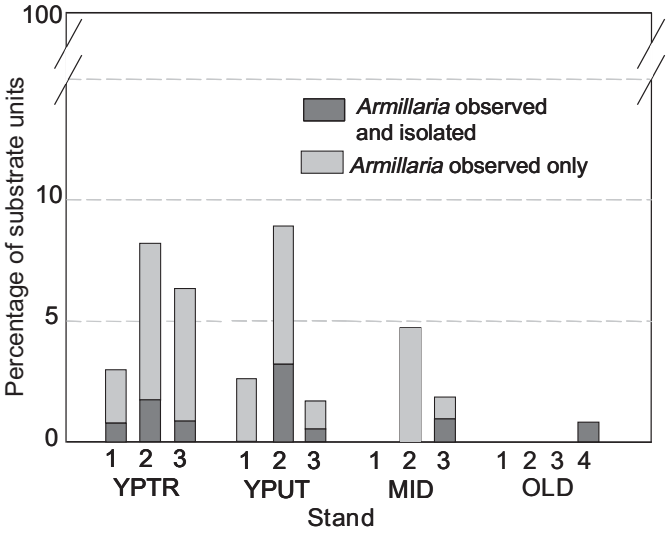


Fig. 2. Incidence of *Armillaria* on individual substrate units (small woody plants, small woody debris and root fragments (DRF)) in 0–25 cm deep core samples in 13 red pine stands, Cloquet Forestry Center, University of Minnesota; 300–550 units per stand. Stand types were the following: (*i*) YPTR young pine (5–8 years) treated with herbicide; (*ii*) YPUT young pine (5–8 years) no herbicide; (*iii*) MID middle age (68–78 years); and (*iv*) OLD (150–240 years).



DRF were included (Table 3). Based on isolation, the occurrence of *Armillaria* in the upper 16 cm was 7% for the plants alone and 18% for the plants and DRF combined. The percentages of 0- to 16-cm-deep samples with *Armillaria* on either a small woody plant or at least one DRF were used to compare stands and stand types (Fig. 1).

The numbers of individual DRF that were present in one 0- to 25-cm-deep sample (approx. 1960 cm^3) ranged from 6 to 60 (Table 1). Samples from 0–16 cm deep, which were almost twice the volume of samples from 16–25 cm deep, contained about 2.5 times as many DRF as the samples from the lower depth (data not shown). Sizes of individual pieces of DRF ranged from the minimum 1 mm × 20 mm (16 mm^3) to 2.5 cm × 20 cm (98 cm^3); most of the pieces were within 1–25 cm^3. The larger pieces were usually fragments of lateral roots of adjacent shrubs or trees. A total of 1685 DRF plus the small woody plants resulted in a combined total of 1750 individual substrate units that were collected and assessed in the 0- to 25-cm-deep samples. Overall, *Armillaria* was observed on 3% of individual substrate units in the upper depth (0–16 cm deep) and 3% in the lower depth (16–25 cm deep). *Armillaria* was isolated from less than 1% of the total number of substrate units in each depth. The percentage of individual units with *Armillaria* in a single stand ranged from 0% to 9% per 0- to 25-cm-deep sample based on observation, and 0%–3% based on isolation (Fig. 2). The percentage of core samples with *Armillaria* on at least one substrate unit was 32% (21 of 65) for 0- to 16-cm-deep sam-

Table 4. *Armillaria* isolation rate and score for small woody plants and small woody debris and root fragments (DRF) in 13 red pine stands, Cloquet Forestry Center, University of Minnesota.

	No. units with *Armillaria* observed, isolated					
	Score[a]					
Substrate type	1	2	3	4	Total	Isolation rate (%)[b]
Small woody plants	0, 0	1, 0	19, 9	7, 7	27, 16	60
DRF, 0–16 cm	1, 1	17, 1	34, 3	31, 17	83, 22	26
DRF, 16–25 cm	0, 0	3, 0	8, 1	4, 3	15, 4	27
Total	1, 1	21, 1	61, 13	42, 27	125, 42	34
Isolation rate (%)	100	5	21	64	34	

[a]Scores assigned as follows: 1, rhizomorphs growing on substrate surface, but attachment is not evident; 2, rhizomorph(s) attached to the substrate, but penetration is not evident; 3, rhizomorph(s) attached, and one or more penetration points are present; and 4, mycelial fans are present.

[b]Percentage of individual substrate units from which *Armillaria* was isolated based on total number of units from which isolation was attempted, which was all units on which it was observed.

ples and 42% (27 of 65) for 0- to 25-cm-deep samples, based on observation. Based on isolation, inclusion of the 16- to 25-cm depth increased the core samples with *Armillaria* from 12% to 15%. All isolates were identified as *A. ostoyae*.

Incidence estimates of *Armillaria* based on observation were higher than estimates based on isolation. Isolation success was related to the degree to which the fungus was established on, or in, the substrate unit (Table 4). Isolation rates ranged from a high of 100% (7 of 7) for small woody plants scored as 4 (mycelial fans present) down to 0% for substrate units scored as 2 (rhizomorphs attached but no penetration evident). Across all scores, the isolation rate was higher from the plants (60%) than from the DRF (26%–27%). For the four stands from which *Armillaria* was not isolated from sampled substrates (MID1, OLD1, OLD2, OLD3), additional material was collected, and the presence of *A. ostoyae* was ultimately confirmed by isolation from substrate located in or near each of these stands.

Comparison of *Armillaria* incidence within and between stand types

Results were similar for the three measures of *Armillaria* incidence that were analyzed. Variation in incidence due to random stand effects was not significant ($p > 0.05$) for any of the measures, and differences between the YPTR and YPUT were not significant ($p > 0.10$) for these measures. A final model with YPTR and YPUT combined and no random effects was fit to each data set. Statistical significance varied, but there was a trend of decreasing *Armillaria* incidence with older stand age-classes for the three measures. *Armillaria* incidence based on observation in 0- to 16-cm-deep samples was significantly different in the MID ($p = 0.0226$) and OLD ($p = 0.0002$) stand types than in the YP stand type, with the odds of observing *Armillaria* on a small woody plant or at least one DRF in the MID and OLD stand types about one-third and one-tenth the odds of observing *Armillaria* in the YP stand type, respectively. *Armillaria* incidence measured by isolation in 0- to 16-cm-deep samples was also less in the MID and OLD stand types than in the YP type; the difference between the MID and YP types was less significant ($p = 0.0537$) than for the observation data, and there were no isolations from 0- to 16-cm-deep samples from any of the OLD stands. Incidence measured as the number of individual substrate units on which *Armillaria* was observed in the MID stand type was lower than, but not significantly different from, the incidence in the YP stand type ($p = 0.1771$), while the incidence in the OLD stand type was significantly lower than in the YP stand types ($p = 0.0057$).

Discussion

Armillaria–substrate associations

Two new hosts for *A. ostoyae* were identified in this study: these are the first records of *A. ostoyae* on *Amelanchier sanguinea* and *Vaccinium angustifolium* since the distinction of *A. ostoyae* as separate from *A. mellea* (Korhonen 1978; Anderson and Ullrich 1979). Our findings of *Armillaria* on *C. cornuta* support those of Rizzo et al. (1995) from a nearby red pine – jack pine stand, except only 1 of 12 plants on which *Armillaria* was observed in our study was dead, and Rizzo reported that *A. ostoyae* had killed several *C. cornuta* stems. *Rubus* species are listed as hosts of *Armillaria mellea* (sensu lato) (Raabe 1962; Farr et al. 1989), but evidence of *Armillaria* was not observed on any of the sampled *Rubus*. *Armillaria ostoyae* has been identified on *Rosa* species (Klein-Gebbinck et al. 1991), *Abies balsamea*, and *Picea* species (Mallet 1990; Blodgett and Worrall 1992; Banik et al. 1995; Gerlach et al. 1997; McLaughlin 2001*b*), but no signs of *Armillaria* were evident on the few plants of those species that were sampled in this study.

The woody debris pieces in our samples were in various stages of light-colored, wet, stringy decay. Root fragments varied in condition from live (probably severed during sampling) to dead and somewhat decayed but still identifiable as part of a root (e.g., with fine roots). We did not classify the condition of DRF, but incidence of viable *Armillaria* in relationship to stage of decay may be important in assessing inoculum potential of these small substrates.

Armillaria ostoyae accounted for 98% of the isolates identified from these stands, consistent with findings in nearby stands by Rizzo et al. (1995). The single isolate of *A. sinapina* came from a piece of debris in YPUT3, and to our knowledge is the first report of this species in Minnesota. *Armillaria ostoyae* was identified from isolations from four other samples from the same stand; this is the first report of the co-occurrence of *A. ostoyae* and A. *sinapina* in

Minnesota. The co-occurrence of these two *Armillaria* species has been reported from sites in Wisconsin (Banik et al. 1995), New York (Blodgett and Worrall 1992), Alberta (Pankuch et al. 2003), and Ontario (McLaughlin 2001*b*). While less is known about this species, *A. sinapina* has been considered a less aggressive pathogen than *A. ostoyae* (Banik et al. 1995; Pankuch et al. 2003).

The low isolation rates in our study were most likely due to the difficulty of recovering pure, viable cultures of *Armillaria* from substrate units that were very small in size and, in the case of some of the debris pieces, in advanced stages of decay. We were conservative in our assessment, however, and observations that were not confirmed by isolation were only reported as positive for *Armillaria* if a mycelial fan and (or) rhizomorph were clearly evident on, or in, the substrate unit.

Armillaria incidence among stand types

Stressed and dying vegetation, such as that treated by herbicide, may be more vulnerable to colonization by *Armillaria* than untreated vegetation, because its defense capabilities have been altered (Wargo and Harrington 1991), and such material might become a significant source of inoculum for armillaria root disease (Whitney 1985; Hood et al. 1991). Our study did not identify significant differences in the incidence of *Armillaria* between the herbicide-treated and untreated young stands, whether incidence was based on plants and DRF combined, or the plants alone (Tables 1, 3). More uniformly timed herbicide application and a larger number of stands would strengthen the comparison between the two stand types.

A trend of *Armillaria* incidence inversely related to stand age-class was evident for all measures. Numbers of DRF substrate units that were present showed no clear trend with stand age-class (data not shown), but small woody plants were more abundant (Table 1) and somewhat more diverse (data not shown) in the YP stands than in either the MID or OLD stands. Of the species on which *Armillaria* was observed, three (*V. angustifolium*, *D. lonicera*, and *Comptonia peregrina*) were sampled more frequently in the YP stands than in the MID or OLD stands. Also, the YP stands contained varying numbers of jack pine and aspen (averages 5–35/0.01 ha, data not shown), while these species were rare or absent from the MID and OLD stands. Both jack pine and aspen are hosts to *A. ostoyae* (Rizzo et al. 1995; Pankuch et al. 2003) and, if they served to increase the total amount of *Armillaria* present in the young stands, they may have contributed to the higher *Armillaria* incidence on the small substrates as well. Rizzo et al. (1995) suggested that recently clear-cut stands contain larger amounts of "easily colonized substrates" compared with older stands, and roots of recently cut stumps are generally considered the primary source of armillaria root disease inoculum. While some of the root fragments examined in our study were likely from stumps, stumps were not evaluated for *Armillaria* directly. Stump densities in the OLD stands were lower than in the YP and MID stands (Table 1), and with the exception of OLD2, were older and less likely to have been created simultaneously in a given stand. Individually and combined, OLD stumps probably offered less suitable substrate for *Armillaria* than YP or MID stumps, contributing to the reduced incidence of the fungus in the OLD stands on other substrates as well.

Implications for *Armillaria* survival, root disease, and management

We know that wide host range, ability to colonize a succession of substrates, and production of rhizomorphs that grow through the soil from one substrate to the next enable species of *Armillaria* to persist for decades or even centuries within a forest (Redfern and Filip 1991; Smith et al. 1994; Ferguson et al. 2003). We present quantitative data on the occurrence of *Armillaria* on small woody plants, woody debris, and root fragments — substrates for which these data are generally lacking. Although we did not assess the potential for the *Armillaria* that we found to infect roots of the overstory red pine, we suggest that these substrates may serve as sources of inoculum. They may be relatively small in size but are found in potentially significant numbers and distribution, particularly in young stands. Using conservative values from our results in young pine stands, we estimate that in 1 ha (area equivalent to 1 200 000 points, 10 cm in diameter) 360 000 points, 10 cm in diameter, contain a small woody plant or DRF with *Armillaria* in the upper 16 cm of soil. Further, if 1% of the individual substrate units in the upper 25 cm of soil of a 1-ha stand carried viable *Armillaria*, there would be 250 000 colonized units at one point in time in this stand.

Roots of understory plants, woody and nonwoody, may contribute to armillaria root disease by providing substrate for colonization and subsequent inoculum (Shaw et al. 1976; Klein-Gebbinck et al. 1991, 1993) or by serving as "nonsusceptible carriers" of the fungus (Swift 1972). We focused on woody plants, the majority of which appeared relatively healthy, including those with *Armillaria*; 70% of the plants with *Armillaria* had attached and penetrating rhizomorphs without evidence of mycelial fans or extensive cambial attack. Although our observations were made at a single point in time, some of these plants may have been serving simply as carriers of the fungus. Knowledge of the relative susceptibility of understory species would aid in managing this substrate, whether in site selection based on existing understory composition, or in promotion of certain understory species. In the absence of this information, increasing diversity of understory species may reduce the amount of susceptible host substrate, as reduced conifer mortality caused by *A. ostoyae* has been associated with increasing overstory species diversity (Morrison and Mallet 1996; Gerlach et al. 1997; McLaughlin 2001*a*).

Site selection is the first opportunity to manage armillaria root disease, potentially reducing the need for disruptive treatments, consistent with ecosystem management of our forest lands (Hansen and Goheen 2000). Some treatments may reduce the overall amount of primary inoculum on a site, but may fragment and redistribute residual inoculum (Bruhn et al. 1996, 1998; Morrison et al. 1988). While volume rather than numbers of substrate units may become more important with time after planting (Morrison et al. 1988), Roth et al. (2000) suggested that in the short term, for example, the decade following site treatment, numbers, rather than size, of inoculum pieces are better indicators of the likelihood of infection. For seed orchards, Bruhn et al. (1996) suggest ranking potential sites based on the amount of woody residual present which could support root disease, rather than ranking based on current inoculum levels. If it is

necessary to use a site with large amounts of woody debris, a fallow period after harvest prior to regeneration may allow the majority of small units to lose their value as inoculum for *Armillaria* and reduce the incidence of root disease (Bruhn et al. 1998). Results of work by Bruhn et al. (1998) support a period of 8–10 years between site treatment and planting conifer seed orchards.

Conclusions

The incidence of *Armillaria* on small woody plants, woody debris, and root fragments reported here is further support for *Armillaria* as an integral component of many forest sites. The incidence of *Armillaria* on nonwoody understory vegetation, the relative susceptibility of understory species to *Armillaria*, and measures of the potential for all these substrates to serve as root disease inoculum are data that will further support integrated, ecologically sound disease management.

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References

Adams, D.H. 1974. Identification of clones of *Armillaria mellea* in young-growth ponderosa pine. Northwest Sci. **48**: 21–28.

Alm, A.A. 1988. Cloquet forestry center research papers and reports for the 75-year period from 1912–1987. Minnesota Agricultural Experimental Station, University of Minnesota, St. Paul, Minn.

Anderson, J.B., and Ullrich, R.C. 1979. Biological species of *Armillaria mellea* in North America. Mycologia, **71**: 402–414.

Banik, M.T., Paul, J.A., and Burdsall, H.H., Jr. 1995. Identification of *Armillaria* species from Wisconsin and adjacent areas. Mycologia, **87**: 707–712.

Blodgett, J.T., and Worrall, J.J. 1992. Distributions and hosts of *Armillaria* species in New York. Plant Dis. **76**: 166–170.

Bruhn, J.N., Mihail, J.D., and Meyer, T.R. 1996. Using spatial and temporal patterns of *Armillaria* root disease to formulate management recommendations for Ontario's black spruce (*Picea mariana*) seed orchards. Can. J. For. Res. **26**: 298–305.

Bruhn, J.N., Mihail, J.D., and Meyer, T.R. 1998. Armillaria root disease inoculum remaining in young Ontario conifer plantations following root raking or madge rotoclearing. North. J. Appl. For. **15**: 191–196.

Farr, D.F., Bills, G.F., Chamufis, G.P., and Rossman, A.Y. 1989. Fungi on plants and plant products in the United States. APS Press, St. Paul, Minn.

Ferguson, B.A., Dreisbach, T.A., Parks, C.G., Filip, G.M., and Schmitt, C.L. 2003. Coarse-scale population structure of pathogenic *Armillaria* species in a mixed-conifer forest in the Blue Mountains of Oregon. Can. J. For. Res. **33**: 612–623.

Gerlach, J.P., Reich, P.B., Puettmann, K., and Baker, T. 1997. Species, diversity, and density affect tree seedling mortality from *Armillaria* root rot. Can. J. For. Res. **27**: 1509–1512.

Hagle, S.K., and Shaw, C.G., III. 1991. Avoiding and reducing losses from Armillaria root disease. *In* Armillaria root disease. *Edited by* C.G. Shaw III and G.A. Kile. USDA Agric. Handb. 691. pp. 157–173.

Hansen, E.M., and Goheen, E.M. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. Annu. Rev. Phytopathol. **38**: 515–539.

Harrington, T.C., Worrall, J.J., and Baker, F.A. 1992. *Armillaria*. *In* Methods for research on soilborne phytopathogenic fungi. *Edited by* L.L. Singleton, J.D. Mihail, and C.M. Rush. APS Press, St. Paul, Minn. pp. 81–85.

Hood, I.A., Redfern, D.B., and Kile, G.A. 1991. *Armillaria* in planted hosts. *In* Armillaria root disease. *Edited by* C.G. Shaw III and G.A. Kile. USDA Agric. Handb. 691. pp. 122–149.

Kile, G.A. 1980. Behaviour of an *Armillaria* in some *Eucalyptus obliqua – Eucalyptus regnans* forests in Tasmania and its role in their decline. Eur. J. For. Pathol. **10**: 278–296.

Klein-Gebbinck, H.W., Blenis, P.V., and Hiratsuka, Y. 1991. Spread of *Armillaria ostoyae* in juvenile lodgepole pine stands in west central Alberta. Can. J. For. Res. **21**: 20–24.

Klein-Gebbinck, H.W., Blenis, P.V., and Hiratsuka, Y. 1993. Fireweed (*Epilobium angustifolium*) as a possible inoculum reservoir for root-rotting *Armillaria* species. Plant Pathol. **42**: 132–136.

Korhonen, K. 1978. Infertility and clonal size in the *Armillariella mellea* complex. Karstenia, **18**: 31–42.

Lewis, R.R. 1978. Soil survey of Carlton County, Minnesota. USDA Soil Conservation Service, Washington, D.C.

Lundquist, J.E. 2000. A method of estimating direct and indirect effects of Armillaria root disease and other small-scale forest disturbances on canopy gap size. For. Sci. **46**: 356–362.

Lung-Escarmant, B., and Guyon, D. 2004. Temporal and spatial dynamics of primary and secondary infection by *Armillaria ostoyae* in a *Pinus pinaster* plantation. Phytopathology, **94**: 25–131.

Mallet, K.I. 1990. Host range and geographic distribution of *Armillaria* root rot pathogens in the Canadian prairie provinces. Can. J. For. Res. **20**: 1859–1863.

McLaughlin, J.A. 2001*a*. Impact of Armillaria root disease on succession in red pine plantations in southern Ontario. For. Chron. **77**: 519–524.

McLaughlin, J.A. 2001*b*. Distribution, hosts and site relationships of *Armillaria* spp. in central and southern Ontario. Can. J. For. Res. **31**: 1481–1490.

Morrison, D.J., and Mallet, K.I. 1996. Silvicultural management of Armillaria root disease in western Canadian forests. Can. J. Plant Pathol. **18**: 194–199.

Morrison, D.J., Wallis, G.W., and Weir, L.C. 1988. Control of *Armillaria* and *Phellinus* root diseases: 20-year results from the Skimikin stump removal experiment. Can. For. Serv. Pac. For. Res. Cent. Inf. Rep. BC-X-302.

Morrison, D.J., Pellow, K.W., Norris, D.J., and Nemec, A.F.L. 2000. Visible versus actual incidence of Armillaria root disease in juvenile coniferous stands in the southern interior of British Columbia. Can. J. For. Res. **30**: 405–414.

Omdal, D.M., Shaw, C.G.I., and Jacobi, W.R. 2001. Evaluation of three machines to remove *Armillaria*- and *Annosum*-infected stumps. West. J. Appl. For. **16**: 22–25.

Pankuch, J.M., Blenis, P.V., Lieffers, V.J., and Mallet, K.I. 2003. Fungal colonization of aspen roots following mechanical site preparation. Can. J. For. Res. **33**: 2372–2379.

Patton, R.F., and Riker, A.J. 1959. Artificial inoculation of pine and spruce trees with *Armillaria mellea*. Phytopathology, **49**: 615–622.

Pearce, M.H., Malajczuk, N., and Kile, G.A. 1986. The occurrence and effects of *Armillaria luteobubalina* in the karri (*Eucalyptus diversicolor* F. Muell.) forests of western Australia. Aust. For. Res. **16**: 243–259.

Pronos, J., and Patton, R.F. 1977. Armillaria root rot of red pine planted on oak sites in Wisconsin. Plant Dis. Rep. **61**: 955–958.

Raabe, R.D. 1962. Host list of the root rot fungus, *Armillaria mellea*. Hilgardia, **33**: 25–88.

Reaves, J.L., Shaw, C.G.I., and Roth, L.F. 1993. Infection of ponderosa pine trees by *Armillaria ostoyae*. Northwest Sci. **67**: 156–162.

Redfern, D.B., and Filip, G.M. 1991. Inoculum and Infection. *In* Armillaria root disease. *Edited by* C.G. Shaw III and G.A. Kile. USDA Agric. Handb. 691. pp. 48–61.

Rishbeth, J. 1985. *Armillaria*: resources and hosts. *In* Developmental biology of higher fungi: Symposium of the British Mycological Society. *Edited by* D. Moore, L.A. Casselton, D.A. Wood, and J.C. Frankland. Cambridge University Press, Cambridge, UK. pp. 87–101.

Rizzo, D.M., and Harrington, T.C. 1992. Nuclear migration in diploid–haploid pairings of *Armillaria ostoyae*. Mycologia, **84**: 863–869.

Rizzo, D.M., and Slaughter, G.W. 2001. Root disease and canopy gaps in developed areas of Yosemite Valley, California. For. Ecol. Manage. **146**: 159–167.

Rizzo, D.M., Blanchette, R.A., and May, G. 1995. Distribution of *Armillaria ostoyae* genets in a *Pinus resinosa – Pinus banksiana* forest. Can. J. Bot. **73**: 776–787.

Rosso, P., and Hansen, E. 1998. Tree vigour and the susceptibility of Douglas fir to Armillaria root disease. Eur. J. For. Pathol. **28**: 43–52.

Roth, L.F., Shaw, C.G., III, and Rolph, L. 2000. Inoculum reduction measures to control Armillaria root disease in a severely infested stand of ponderosa pine in south-central Washington: 20 year results. West. J. Appl. For. **15**: 92–100.

Rudolf, P.O. 1990. *Pinus resinosa* Ait. Red pine. *In* Silvics of North America. Vol. 1. Conifers. *Technical coordinators* R.M. Burns and B.H. Honkala. USDA Agric. Handb. 654. pp. 442–455. Available from http://www.na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/pinus/resinosa.htm.

SAS Institute Inc. 2003. SAS online version 9.1 [computer program]. SAS Institute Inc., Cary, N.C.

Schmidt, T.L. 2002. Red pine in the Northern Lake States. *In* Proceedings of the Red Pine SAF Region V Technical Conference, Cloquet, Minn., 26–27 March 2002. *Edited by* D.W. Gilmore and L.S. Yount. Department of Forest Resources, University of Minnesota, St. Paul, Minn. Staff Paper Ser. No. 157. pp. 3–16. Available from http://www.cnr.umn.edu/FR/publications/staffpapers/Staffpaper157.pdf.

Shaw, C.G., III, Sinja, D., and MacKenzie, M. 1976. Toetoe (*Cortaderia fulvida*) — a new graminaceous host for Armillaria root rot. N.Z. J. For. **21**: 263–268.

Shearer, B.L., and Tippett, J.T. 1988. Distribution and impact of *Armillaria luteobubalina* in the *Eucalyptus marginata* forest of south-western Australia. Aust. J. Bot. **36**: 433–445.

Shearer, B.L., Byrne, A., Dillon, M., and Beuhrig, R. 1997. Distribution of *Armillaria luteobubalina* and its impact on community diversity and structure in *Eucalyptus wandoo* woodland in southern western Australia. Aust. J. Bot. **44**: 151–165.

Shearer, B.L., Crane, C.E., Fairman, R.G., and Grant, M.J. 1998. Susceptibility of plant species in coastal dune vegetation of south-western Australia to killing by *Armillaria luteobubalina*. Aust. J. Bot. **46**: 321–334.

Smith, M.L., Bruhn, J.N., and Anderson, J.B. 1994. Relatedness and spatial distribution of *Armillaria* genets in infected red pine seedlings. Phytopathology, **84**: 822–829.

Sturrock, R.N. 2000. Management of root diseases by stumping and push-falling. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C. Technology Transfer Note 16.

Swift, M.J. 1972. The ecology of *Armillaria mellea* Vahl (ex Fries) in the indigenous and exotic woodlands of Rhodesia. Forestry, **45**: 67–86.

Wargo, P.M., and Harrington, T.C. 1991. Host stress and susceptibility. *In* Armillaria root disease. *Edited by* C.G. Shaw III and G.A. Kile. USDA Agric. Handb. 691. pp. 88–101.

Whalstrom, K.T, and Johansson, M. 1992. Structural responses in bark to mechanical wounding and *Armillaria ostoyae* infection in seedlings of *Pinus sylvestris*. Eur. J. For. Pathol. **22**: 65–76.

Whitney, R.D. 1985. Herbicide-killed roots as inoculum sources of *Armillaria* root rot in Ontario spruce. *In* Proceedings of the 33rd Annual Western International Forest Disease Work Conference, Olympia, Wash., 24–27 September 1985. *Edited by* W. Theis. Oregon State University, Corvallis, Ore. pp. 68–70.