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Identification of *Armillaria* Species in the Chequamegon-Nicolet National Forest

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ABSTRACT.—Armillaria species were isolated from coniferous and deciduous overstory species in 17 of 22 stands in the Chequamegon area of the Chequamegon-Nicolet National Forest. Armillaria calvescens and A. sinapina were identified once each, and the remainder of the isolates were A. ostoyae. These findings are related to reports of Armillaria species from other areas of North America, particularly the western Great Lakes States, and to the potential role of Armillaria root disease in the Chequamegon.

KEY WORDS: *Armillaria*, root disease, Cheqamegon-Nicolet.

The Chequamegon area of the Chequamegon-Nicolet National Forest in northwestern Wisconsin covers 348,000 hectares, nearly 90 percent of which are classified as timberland (Haugen *et al.* 1998). In addition to wood and wood products, the lands are managed for wildlife habitat and numerous forms of recreation. Beginning in the late 1980s, USDA Forest Service personnel observed tree mortality and decline in some areas of the Chequamegon. *Armillaria* root disease, important in several areas of North America (Bruhn *et al.* 2000, Lundquist 2000, Mallett and Maynard 1998, McLaughlin 2001b, Morrison *et al.* 2001, Rizzo and Slaughter 2001), was suspected of contributing to these observed declines, but no mycological investigations had been done in this area.

The objectives of this study were to identify the species of *Armillaria* present in the Chequamegon, especially in declining stands, and to relate these findings to previously collected information about *Armillaria*,

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particularly in the western Great Lakes States, but also in other areas of North America. This is the first step in assessing the role of these fungi in the Chequamegon forest.

MATERIALS AND METHODS

Stands with dead and dying trees were selected first because the presence of Armillaria species was strongly suspected, and other stands were selected to represent the major overstory species of the forest. The root collars, butts, and one meter of lateral roots of recently killed or declining trees were examined for signs (mycelial fans or rhizomorphs) of Armillaria. The soil was carefully removed from around the base and lateral roots of these trees, and small areas of bark were lifted or peeled back. In stands where dying or declining trees were not observed, stumps and snags were examined. Samples of roots, root collars, and butts harboring Armillaria-like mycelial fans, rhizomorphs, or white stringy rot were collected for isolation, and the soil surrounding the sampled substrate was examined for rhizomorphs, which were collected if present. Host species, substrate type, and diameter at 1.3 m or at ground level, for trees and stumps, respectively, along with the location and form (fan, rhizomorph, decayed wood) of Armillaria observed were recorded for each sample. Overall condition of the tree, and the presence of decay, other fungi, and insect or disease problems were also noted. One or two samples for isolation were collected per stand. Sampled materials were placed in paper bags and stored in a cooler while traveling (1 to 2 days), then placed in cold storage (4 C°) for 1 to 4 days until isolations were completed.

Isolations were made following procedures described by Rizzo and Harrington (1993). Small (≤ 5 mm) pieces of mycelial fans and/or wood were taken from where the bark was removed and plated both on water agar (WA, 15 g Difco agar per L) and on basidiomycete-select agar (BSMA, 15 g malt extract and 15 g agar per L, amended with 4 ug/ml benomyl 50WP and 100 ug/ml streptomycin sulfate after autoclaving (Harrington et al. 1992)). Rhizomorphs were surface disinfected by soaking in an aqueous solution of 20 percent ethanol and 10 percent bleach for 2 minutes, then rinsed in sterile distilled water. These were cut into 1-cm segments and plated. Plates were incubated under laboratory conditions (20-25 C°). To obtain pure cultures, transfers onto 1 percent malt extract agar (MEA) were made 1 to 2 weeks after isolation, and, if necessary, a second transfer was made 4 weeks later.

Diploid-haploid pairings, per Korhonen (1978), were used to identify the unknown *Armillaria* isolates to species. Each unknown presumably diploid isolate was paired with 8-12 haploid testers (table 1), which were obtained from David Rizzo (Rizzo 1993). One 3-mm plug of the tester strain was placed on 1 percent MEA, 5 mm away from a plug of the unknown. Plates were

Table 1.—Tester isolates used in haploid-diploid pairings for identification of Armillaria species

Species	Isolates	
A. ostoyae A. gallica A. gemina A. sinapina A. calvescens A. mellea	A37 ¹ , A100 A74, A102, A103 A80, A78 ¹ A48, A52 ¹ A77 ¹ , A7 ¹ A72 ¹	

¹Listed in: Harrington, T.C.; Rizzo, D.M. 1993.

incubated under laboratory conditions for 5-7 weeks, at which time all pairings were subcultured. As described by Harrington *et al.* (1992), three 3-mm plugs were taken from the tester (haploid) side of the pairing—one from the margin of the tester advancing toward the outside of the plate (away from the plug), one from the middle of the tester growth area, and one from between these two—and transferred to new plates of 1 percent MEA. These were incubated for 10-14 days and then visually evaluated. Rizzo and Harrington (1992)

demonstrated that nuclear migration occurs from the diploid to the haploid in conspecific pairings and that, in most cases, this method should be considered a reliable means of identifying *Armillaria* to species. Mycelial growth of single-spore haploid isolates (the testers) is usually whitish and fluffy, with much aerial mycelia. Growth of diploid isolates (unknowns) tends to be flat, brown to dark brown, and becomes crustose in many cases. If the growth of the subcultured plug from the middle of the tester colony and at least one other subculture differed in morphology from the original tester strain, i.e., were flat and/or crustose rather than fluffy, the unknown was considered to be the same species as the tester strain.

RESULTS AND DISCUSSION

Twenty-two stands in the four ranger districts of the Chequamegon (Hayward, Glidden, Washburn, and Park Falls) were inspected for Armillaria between June and August 1992 (fig. 1). Stands varied in age and some were recently clearcut. While most stands were predominantly conifer overstory, stands of pure and mixed overstory were included. No fruiting bodies of Armillaria were observed during this survey, because their production occurs in the fall. However, Armillaria fans and/or rhizomorphs were observed in 86 percent of the stands and Armillaria species were isolated from material collected in 90 percent (17 of 19) of those stands (table 2, fig. 1). Although the distributions of Armillaria species are probably irregular throughout the Chequamegon, the genus is considered to be ubiquitous in forested areas, and a more thorough examination of potential substrates would be required to claim that Armillaria species were "absent" from a stand. Armillaria fans and/or rhizomorphs were observed on 78 percent of 37 samples collected and Armillaria species were isolated from 76 percent (23 of 29) of those samples. Whereas Armillaria species were isolated from both live and dead conifers, the fungi were isolated only from dead deciduous trees (table 3).

Of the 23 *Armillaria* isolates identified from the Chequamegon, 21 were *A. ostoyae*, 1 was *A. sinapina*, and 1 was *A. calvescens*. Since the late 1980s, each of these species has been identified in the western Great Lakes region, and root disease associated with *A. ostoyae* has been reported on several conifer and deciduous hosts (table 4). Species of *Armillaria* are not confirmed

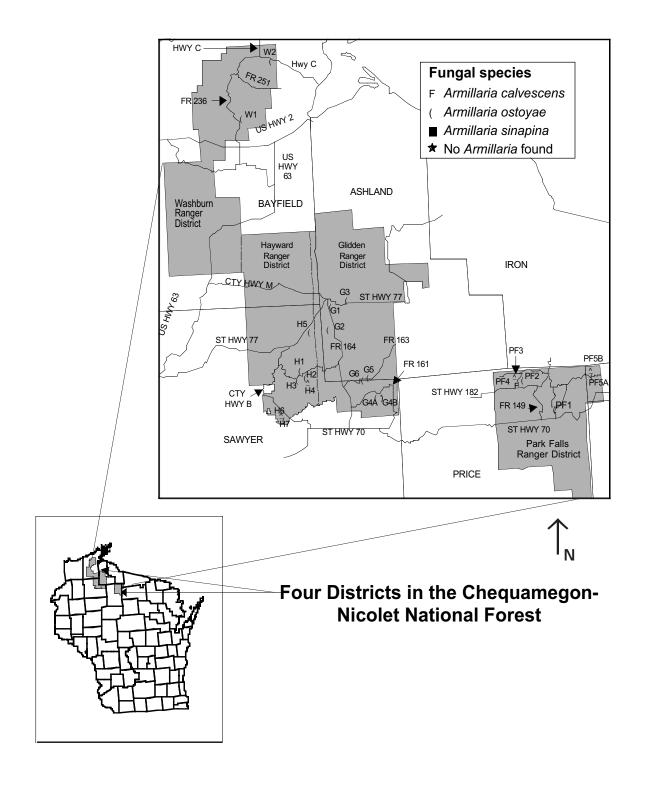


Figure 1.—Stands in the Chequamegon-Nicolet National Forest that were examined for the presence and identification of Armillaria species. Each stand is designated by a letter and number (e.g., H5 = Hayward Ranger District, stand number 5).

Table 2.—Numbers of stands and samples examined for Armillaria species by ranger district in the Chequamegon area of the Chequamegon-Nicolet National Forest

	Ranger district				
Stands	Hayward	Glidden	Park Falls	Washburn	Total
Total no. examined	7	7	6	2	22
No. with signs ¹ of A <i>rmillaria</i>	5	6	6	2	19
No. with symptoms ² only	0	1	0	0	1
No. from which Armillaria was isolated	5	6	4	2	17
Samples					
Total no. examined	12	10	13	2	37
No. with signs of Armillaria	9	8	10	2	29
No. with symptoms only	1	1	2	0	4
No. from which Armillaria was isolated	8	8	5	2	23

¹Only assessed belowground, signs are mycelial fans, rhizomorphs.

Table 3.—Numbers and condition of trees from which Armillaria species were isolated by ranger district in the Chequamegon area of the Chequamegon-Nicolet National Forest

		Ranger district				
Tree type	Condition	Hayward	Glidden	Park Falls	Washburn	Total
Conifer	Living	1	0	1	0	2
	Dead	3	4	1	1	9
	Stump, snag	4	1	2	0	7
	Total	8	5	4	1	18
Deciduous	Living	0	0	0	0	0
	Dead	0	3	1	1	5
	Stump, snag	0	0	0	0	0
	Total	0	3	1	1	5

for the earliest publications from this region, either because isolations were not made or because the work occurred before several intersterile groups were identified within the original *A. mellea* complex (Anderson and Ullrich 1979, Korhonen 1978, Shaw and Kile 1991, Volk and Burdsall 1995).

The finding of *A. calvescens* on *Acer saccharum* Marsh. is consistent with other reports from the western Great Lakes States, and from New York and Ontario (Banik *et al.* 1995, Blodgett and Worrall 1992, McLaughlin 2001a). Although most often causing a butt rot, *A. calvescens* has been identified as a factor in a decline of sugar maple in New York (Bauce and Allen 1992).

McLaughlin (2001a) reported *A. saccharum* as a host of *A. sinapina* in Ontario, but the identification from the

Chequamegon may be the first report of *A. sinapina* on this host from the western Great Lakes States. Banik *et al.* (1995) identified *A. sinapina* on several conifer and deciduous species in Wisconsin and Michigan, but not on *A. saccharum.* In both Ontario and New York, *A. sinapina* has been associated with cambial infection as well as butt rot (Blodgett and Worrall 1992, McLaughlin 2001a). More intensive sampling is required to suggest roles for either of these two *Armillaria* species in the Chequamegon forest.

The predominance of *A. ostoyae* in the Chequamegon is consistent with results of other collections of *Armillaria* from sites in the western Great Lakes States that are, or once were, dominated by conifers (Banik *et al.* 1995, Rizzo *et al.* 1995, Smith *et al.* 1994). In the Chequamegon, *A. ostoyae* was identified on five

²Only assessed belowground, the main symptom is white stringy rot of the wood.

Table 4.—Previously published accounts of Armillaria species in the western Great Lakes States

Reference	<i>Armillaria</i> spp.	Associated host or substrate	Vegetation on the site at the time / past (if known)	Location	
Kromroy 1999	A. ostoyae	Abies balsamea	8-yr-old conifer plantation / mixed hardwoods	Rhinelander, WI	
	A. ostoyae	Quercus rubra, Populus deltoides	30-40 yr-old <i>Pinus resinosa</i> plantation / <i>Quercus</i> spp.	Black River Falls, WI	
	A. ostoyae	Corylus cornuta, Vaccinium angustifolium, Populus spp., Amelanchier sanguinea	P. resinosa plantations / upland forest of P. resinosa, P. strobus, & P. banksiana, Picea-Abies & Populus-Betula	Cloquet, MN	
	A. sinapina	Debris in the soil	Same as above	Cloquet, MN	
	A. gallica	Rhizomorphs in the soil	20-60-yr-old <i>P. resinosa</i> plantation / <i>Quercus</i> spp.	Black River Falls, WI	
A. A.	A. calvescens	Acer saccharum, Betula papyrifera, Lonicera spp., Populus tremuloides, Quercus rubra, Q. velutina, Tilia americana, Ulmus spp.	Not described	Upper Peninsula (UP), MI; central MN; southwestern WI	
	A. gallica	A. balsamea, P. resinosa, P. strobus, Acer rubrum, A. saccharinum, A. saccharum, B. papyrifera, Carya ovata, Fraxinus pennsylvanica, P. tremuloides, Prunus serotina, Quercus alba, Q. ellipsoidalis, Q. macrocarpa, Q. rubra, Q. velutina, Ulmus spp., duff	Not described except for some collected in <i>P. tremuloides</i> stands	UP MI; eastern MN; WI	
	A. mellea	A. saccharum, Quercus spp.	Not described	UP MI; SE MN; west- central & southern WI	
	A. ostoyae	A. balsamea, Picea glauca, P. banksiana, P. resinosa, P. strobus, Thuja occidentalis, Tsuga canadensis, A. rubrum, A. saccharum, Betula alleghaniensis, B. papyrifera, Fraxinus nigra, P. tremuloides, Q. rubra, Q. velutina, Ulmus spp.	Not described except for some collected in <i>P. tremuloides</i> stands	UP, MI; central MN; NE & central WI	
	A. sinapina	A. balsamea, T. occidentalis, T. canadensis, A. rubrum, B. alleghaniensis, F. nigra, P. tremuloides, Q. rubra	Not described except for some collected in <i>P. tremuloides</i> stands	UP, MI; northern WI	

Reference	<i>Armillaria</i> spp.	Associated host or substrate	Vegetation on the site at the time / past (if known)	Location
Rizzo <i>et al.</i> 1995	A. ostoyae	P. banksiana; hardwood regeneration; conifer & hardwood stumps	Clearcut; <i>P. banksiana</i> planted / <i>P. resinosa - P.</i> banksiana	Cloquet, MN
	A. ostoyae	P. resinosa, P. banksiana, A. balsamea, A. rubrum, B. papyrifera	P. resinosa - P. banksiana with mixed deciduous / estab. after 1894 fire	Cloquet, MN
Smith <i>et al.</i> 1994	A. ostoyae	P. resinosa, A. rubrum, Populus sp., B. papyrifera stumps	P. resinosa seedling plantation / northern hardwood forest	Northern MI
	A. sinapina	Populus sp. stump	Same as above	Northern MI
Smith <i>et al.</i> 1992	A. bulbosa = A. gallica	Fruiting bodies & rhizomorphs in soil	Northern hardwood forest	Northern MI
Smith <i>et al.</i> 1990	A. ostoyae & A. bulbosa = A. gallica	Fruiting bodies	P. resinosa seedling plantation / northern hardwood forest	Northern MI
Proffer <i>et al.</i> 1987	A. ostoyae	Prunus cerasus, P. avium, P. persica, Malus pumila	Prunus orchards	Lower Peninsula, MI
	NABS¹ III = A. calvescens	P. cerasus	Prunus orchards	Lower Peninsula, MI
	A. mellea	P. cerasus , Quercus sp. stumps	Prunus orchards	Lower Peninsula, MI
Stanosz & Patton 1987	A. mellea sensu lato ² (no isolation)	Populus spp; suckers & stump	Short rotation <i>Populus</i> plots / mature <i>Populus</i> stand	Grand Rapids, MN
Livingston et al. 1982	A. mellea sensu lato	A. balsamea	A. balsamea plantation / 50-60-yr-old hardwood stand	Grand Rapids, MN
Pronos & Patton 1978	A. mellea sensu lato	Q. alba, Q. rubra	Natural <i>Quercus</i> stands, sprout origin, herbicide treated and untreated	Black River State Forest, WI
Pronos & Patton 1977	A. mellea sensu lato (no isolation)	P. resinosa	P. resinosa plantation, Quercus overstory, herbicide treated / natural Quercus stands, sprout origin	Northwest, northeast, & west-central WI

¹ North American Biological Species, an intersterile population identified within the original *A. mellea* complex. ² Refers to the original *A. mellea* complex before its separation into several species.

conifers—Abies balsamea (L.) Mill., Picea glauca (Moench) Voss, Pinus banksiana Lamb., P. resinosa Ait., and P. strobus L. and three deciduous species—A. saccharum, Populus tremuloides Michx., and Betula papyrifera Marsh (table 5). All have been previously reported as hosts of A. ostoyae in this region.

Although its pathogenicity toward deciduous species is less clear (Gregory *et al.* 1991), *A. ostoyae* is a serious pathogen of several conifer species (Blenis 2000, Cochran 1998, Rosso and Hansen 1998, Whitney 1995). It invades the roots of trees already stressed, but may also penetrate the bark and kill the cambium in the roots and root collar of healthy trees, resulting in their

death (Gregory et al. 1991, Kile et al. 1991). Root disease from Armillaria species is a contributing factor in several declines. "Decline" is a disease syndrome caused by interactions among predisposing (e.g., site quality, tree age), inciting (e.g., drought, insect defoliation) and contributing (e.g., two-lined chestnut borer) factors (Manion 1991). Some species in this genus, such as A. ostoyae, may also act as a predisposing factor by requiring a small but constant drain of host resources to defend against chronic low-level infections that occur on otherwise healthy roots (J. McLaughlin, personal communication). By also deriving nourishment saprophytically from stumps and debris, A. ostoyae can survive on a site for many years.

Table 5.—Armillaria ostoyae¹ and host associations from the Chequamegon area of the Chequamegon-Nicolet National Forest

Host species	Host condition	D.b.h. ² (cm)	Stand ³
Acer saccharum	Dead	10	G4A
Betula papyrifera	Dead, in clump with live	15	W2
Populus tremuloides	Dead	<1	G3
Abies balsamea	Dead Stump, broken	<1 31 32 30	G3 H2 H5 PF2
Picea glauca	Dead Stump, cut	38 NR⁴ NR 26 15	G5 H1 H1 H3 H3
Pinus banksiana	Live, declining Dead Snag	20 13 28 20	PF1 PF5A W1 PF5A
Pinus resinosa	Live, suppressed Dead Stump, cut	15 10 60 38	H7 G3 G2 H7
Pinus strobus	Dead	44	G1

¹ A single isolate of *A. calvescens* was collected from a dead stem of *A. saccharum*, 4 cm d.b.h., growing in a clump of live and dead, site PF4. A single isolate of *A. sinapina* was collected from a single dead *A. saccharum*, 13 cm d.b.h., site G4B.

² D.b.h.: Diameter at 1.4 m above ground for stems, at ground level for stumps.

³ Refers to the ranger district and stand number as shown in figure 1.

⁴ Not recorded.

The most notable mortality observed in this study was of the jack pine in stand 5A in the Park Falls district and the white spruce in stand 1 in the Hayward district. Although the exact role of *Armillaria* root disease in these stands was not clear, it probably contributed to the situation. Other factors in the jack pine mortality appeared to be the maturity of the trees, the exposure of the site, and the presence of bark beetles and other root and butt rot fungi. Factors in addition to *Armillaria* root disease that may have been contributing to the white spruce mortality were heart rot associated with *Phellinus pini*, premature needle loss and branch mortality associated with *Rhizosphaera kalkhoffii* (Juzwik 1993), drought stress, and poor soils (USDA 1990).

Between the 1983 and 1996 cyclic inventories, the USDA Forest Service, Forest Inventory and Analysis (FIA) unit reported that the total area of deciduous forest types in the Chequamegon increased by 23 percent while the total area of conifer forest types decreased by 18 percent, due largely to reductions in jack pine and white spruce forest types and reduced growing-stock volume for both these species (Haugen et al. 1998). Changes in harvest practices, natural forest succession, and weather patterns contributed to these changes, but most likely so did insect outbreaks and diseases, including Armillaria root disease. Evidence of the significance of A. ostoyae in forest succession and composition has been reported by McLaughlin (2001b) in areas of southern Ontario. Hardwood species are colonizing openings where A. ostoyae has killed the red pine. Although some mortality is occurring among the hardwoods, in general they appear less susceptible than the red pine and are expected to eventually dominate these sites.

CONCLUSIONS

The occurrence of *A. ostoyae* on eight overstory species, coniferous and deciduous, and its presence in most of the stands that were examined are consistent with other reports documenting the broad host range and widespread distribution of *A. ostoyae*, both in the western Great Lakes States and in other areas of North America. Although additional data are required to draw more definitive conclusions, based on the findings of this study, *A. ostoyae* should be viewed as an integral component of the Chequamegon forest landscape,

capable of causing root disease and thus a likely contributor to decline and mortality of overstory species, especially conifers.

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LITERATURE CITED

Anderson, J.B.; Ullrich, R.C. 1979.

Biological species of Armillaria mellea in North America. Mycologia. 71: 401-414.

Banik, M.T.; Paul, J.A.; Burdsall, H.H., Jr. 1995. *Identification of Armillaria species from Wisconsin and*

Identification of Armillaria species from Wisconsin and adjacent areas. Mycologia. 87: 707-712.

Bauce, E.; Allen, D.C. 1992.

Role of Armillaria calvescens and Glycobius speciosus in a sugar maple decline. Canadian Journal of Forest Research. 22: 549-552.

Blenis, P.V. 2000.

Post-spacing mortality of lodgepole pine from Armillaria root disease. Canadian Journal of Plant Pathology. 22: 181.

Blodgett, J.T.; Worrall, J.J. 1992.

Distributions and hosts of Armillaria *species in New York.* Plant Disease. 76: 166-170.

Bruhn, J.N.; Wetteroff, J.J., Jr.; Mihail, J.D.; Kabrick, J.M.; Pickens, J.B. 2000.

Distribution of Armillaria species in upland Ozark Mountain forests with respect to site, overstory species composition and oak decline. Forest Pathology. 30: 43-60.

Cochran, P.H. 1998.

Examples of mortality and reduced annual increments of white fir induced by drought, insects, and disease at different stand densities. Res. Note PNW-525. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 19 p.

Gregory, S.C.; Rishbeth, J.; Shaw, C.G., III. 1991.

Pathogenicity and virulence. In: Shaw, C.G. III; Kile, G.A., eds. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture, Forest Service: 76-87.

Harrington, T.C.; Rizzo, D.M. 1993.

Identification of Armillaria species from New Hampshire. Mycologia. 85: 365-368.

Harrington, T.C.; Worrall, J.J.; Baker, F.A. 1992.

Armillaria. In: Singleton, L.L.; Mihail, J.D.; Rush, C.M., eds. Methods for research on soilborne phytopathogenic fungi. St. Paul, MN: APS Press: 81-85.

Haugen, D.E.; Freeman, P.C.; Theisen, M.A. 1998.

The forest resources of the Chequamegon-Nicolet National Forest. Resour. Bull. NC-194. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 7 p.

Juzwik, J. 1993.

Morphology, cultural characteristics, and pathogenicity of Rhizosphaera kalkhoffii on Picea spp. in northern Minnesota and Wisconsin. Plant Disease. 77: 630-634.

Kile, G.A.; McDonald, S.E.; Byer, J.W. 1991.

Ecology and disease in natural forests. In: Shaw, C.G., III; Kile, G.A., eds. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture, Forest Service: 102-121.

Korhonen, K. 1978.

Infertility and clonal size in the Armillariella mellea *complex.* Karstenia. 18: 31-42.

Kromroy, K.W. 1999.

Studies on the identification and ecology of Armillaria species in Minnesota and Wisconsin. St. Paul, MN: University of Minnesota. 186 p. Ph.D. thesis.

Livingston, W.H.; Cromwell, W.H.; French, D.W.

1982. Armillaria mellea *infection in a balsam fir plantation in north central Minnesota.* Minnesota Forestry Research Notes. St. Paul, MN: University of Minnesota, Agricultural Experiment Station. 2 p.

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. Forest Science. 46: 356-362.

Mallett, K.I.; Maynard, D.G. 1998.

Armillaria root disease, stand characteristics, and soil properties in young lodgepole pine. Forest Ecology and Management. 105: 37-44.

Manion, P.D. 1991.

Tree disease concepts. Englewood Cliffs, NJ: Prentice Hall. 402 p.

McLaughlin, J.A. 2001a.

Distribution, hosts and site relationships of Armillaria spp. in central and southern Ontario. Canadian Journal of Forest Research. 31: 1481-1490.

McLaughlin, J.A. 2001b.

Impact of Armillaria root disease on succession in red pine plantations in southern Ontario. Forestry Chronicle. 77: 519-524.

Morrison, D.J.; Pellow, K.W.; Nemec, A.F.L.; Norris, D.J.; Semenoff, P. 2001.

Effects of selective cutting on the epidemiology of Armillaria root disease in the southern interior of British Columbia.

Canadian Journal of Forest Research, 31: 59-70.

Proffer, T.J.; Jones, A.L.; Ehret, G.R. 1987.

Biological species of Armillaria isolated from sour cherry orchards in Michigan. Phytopathology. 77: 941-943.

Pronos, J.; Patton, R.F. 1977.

Armillaria root rot of red pine planted on oak sites in Wisconsin. Plant Disease Reporter. 61: 955-958.

Pronos, J.; Patton, R.F. 1978.

Penetration and colonization of oak roots by Armillaria mellea in Wisconsin. European Journal of Forest Pathology. 8: 258-267.

Rizzo, D.M. 1993.

Genetics and ecology of Armillaria ostoyae. St. Paul, MN: University of Minnesota. 116 p. Ph.D. thesis.

Rizzo, D.M.; Blanchette, R.A.; May, G. 1995.

Distribution of Armillaria ostoyae *genets in a* Pinus resinosa - Pinus banksiana *forest.* Canadian Journal of Botany. 73: 776-787.

Rizzo, D.M.; Harrington, T.C. 1992.

Nuclear migration in diploid-haploid pairings of Armillaria ostoyae. Mycologia. 84: 863-869.

Rizzo, D.M.; Harrington, T.C. 1993.

Delineation and biology of clones of Armillaria ostoyae, A. gemina, and A. calvescens. Mycologia. 85: 164-174.

Rizzo, D.M.; Slaughter, G.W. 2001.

Root disease and canopy gaps in developed areas of Yosemite Valley, California. Forest Ecology and Management. 146: 159-167.

Rosso, P.; Hansen, E. 1998.

Tree vigour and the susceptibility of Douglas fir to Armillaria root disease. European Journal of Forest Pathology. 28: 43-52.

Shaw, C.G.; Kile, G.A., eds. 1991.

Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture, Forest Service. 233 p.

Smith, M.L.; Bruhn, J.N.; Anderson, J.B. 1992.

The fungus Armillaria bulbosa is among the largest and oldest living organisms. Nature. 356: 428-431.

Smith, M.L.; Bruhn, J.N.; Anderson, J.B. 1994.

Relatedness and spatial distribution of Armillaria genets in infected red pine seedlings. Phytopathology. 84: 822-829.

Smith, M.L.; Duchesne, L.C.; Bruhn, J.N.; Anderson, J.B. 1990.

Mitochondrial genetics in a natural population of the plant pathogen. Genetics. 126: 575-582.

Stanosz, G.R.; Patton, R.F. 1987.

Armillaria *root rot in aspen stands after repeated short rotations.* Canadian Journal of Forest Research. 17: 1001-1005.

USDA Forest Service. 1990.

Premature needle loss of spruce. Pest Alert NA-PR-01. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Area. 1 p.

Volk, T.J.; Burdsall, H.H.J. 1995.

A nomenclatural study of Armillaria and Armillariella species (Basidiomycotina, Tricholomataceae). Oslo, Norway: Fungiflora. 121 p.

Whitney, R.D. 1995.

Root-rotting fungi in white spruce, black spruce, and balsam fir in northern Ontario. Canadian Journal of Forest Research. 25: 1209-1230.