Site Relationships of *Armillaria* Species in New York

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ABSTRACT

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A statewide investigation was conducted to determine site relationships of *Armillaria* species in New York forests. *Armillaria* was found in 211 of 303 stands sampled. *A. calvescens* was found mainly at northern hardwood sites with *Acer saccharum*. *A. gallica* was found primarily at upland oak sites with soils that were low in organic matter and had high pHs. This species was found more frequently than expected by chance on dry sites. *A. ostoyae* occurred principally at spruce-fir sites with soils that were higher in sand, lower in silt and clay, higher in organic matter, and had lower pHs of the organic horizon than soils for most other species. *A. sinapina* showed no strong relationships with a forest type group but, compared with other *Armillaria* species, was found at sites with higher relative dominance and relative density of *Betula alleghaniensis*. It was found at sites with the same soil properties as those with *A. ostoyae*. *A. gemina* was a rare species found at hardwood sites and, compared with other *Armillaria* species, was found at sites with higher relative dominance of *Fagus grandifolia* and *Pinus* spp. *A. mellea* sensu stricto was not found in any of the study sites.

Much of the observed variability in host ranges, levels of pathogenicity, and site conditions associated with Armillaria root disease may relate to differences among species of *Armillaria*. Although some differences in distributions, host range, and levels of pathogenicity have been reported (7,11,16,21), ecological variations among *Armillaria* species are poorly understood. Quantitative data are needed to properly elucidate ecological differences among *Armillaria* species.

Site characteristics are important components of ecology. They help determine how suitable an area is for a species and how competitive a species will be at a site. The geographic distributions and host/substrate relationships of *Armillaria* species in New York were described previously (7). The objectives of this study were to determine differences in site relationships among *Armillaria* species in New York forests.

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MATERIALS AND METHODS

Sample plots. Three hundred and three sites were selected from New York State-owned forest lands. An attempt was made to nonrandomly select sites beforehand that were distributed evenly throughout the state. Study sites chosen had stand sizes greater than 3,600 m^2 and an average tree diameter at breast height greater than 12 cm (for trees with a diameter of 3 cm and greater). Sampling occurred from June to September 1988 and during May 1989.

After a distance of at least 25 m from a stand edge was reached, the stand was examined for *Armillaria*. *Armillaria* was considered present at a site if found within 25 min of searching (one person). Signs of *Armillaria* normally were found in less than 2 min. For sites in which *Armillaria* was not found (92 sites), only the location and forest type group (10) were recorded.

Where *Armillaria* was determined to be present (211 sites), square sample plots were established around the first live tree found to be colonized by *Armillaria* but at a distance of at least 25 m from the stand edge. Colonized living trees included trees where *Armillaria* was found infecting the cambium and/or causing a butt rot. Epiphytic associations were not considered colonization. If no live trees were found to be colonized, plots were established around the first substrate (snag, stump, or log) found to be colonized by *Armillaria*. If five or more trees were included, 10 × 10 m plots were established; otherwise, 15 × 15 m plots were used.

Isolations were obtained from field samples of rhizomorphs and wood and isolates were identified to species by matings in vitro with previously identified haploid *Armillaria* isolates (7).

Observations and measurements made within plots included forest type group (10); species and diameter at breast height for trees with a diameter of 3 cm and greater; number of stumps, snags, and logs with a diameter of 6 cm and greater; and slope percent (100% = 45°) and position (upper, middle, or lower). The frequency of rhizomorphs in the soil was assessed in 15 soil samples (including litter layer and mineral soil) measuring 8 × 8 × 8 cm taken at locations evenly distributed throughout the sample plots. Sites were classified as high if rhizomorphs were observed in greater than eight of the soil samples, moderate if observed in one to eight, and low if no rhizomorphs were observed within the soil samples.

For sites in which plots were established, calculations were made for the total basal area per hectare; average diameter; total number per hectare of trees, snags, stumps, and logs; relative dominance (total basal area of one species as a percentage of the total basal area of all species); and relative density (number of individuals of one species as a percentage of the total number of individuals of all species) for each tree species found within the sample plots.

Soils. Measurements were made of the thickness of the organic horizon. Fifteen

5 × 5 cm samples of the organic soils were collected at sites with an organic horizon thickness of 0.5 cm or greater. After removal of the organic layer, mineral soils were collected at a 8-cm depth from 15 soil cores measuring 2.54 cm in diameter. These were evenly distributed throughout the sample plots. Samples collected within a plot were combined into one composite organic and one composite mineral sample and air-dried in the laboratory at room temperature.

Air-dried soil samples were passed through a 2-mm sieve and stored in plastic-lined paper cans. An electrometric procedure was used to determine the pH of organic and mineral soils. Soil/water ratios used for organic and mineral soils were 10:1 and 2:1, respectively (6). The pH was converted to hydrogen ion concentration for statistical analysis. Organic matter content of the mineral soil was determined by loss on ignition (6). Soil texture was determined by the modified hydrometer method (6). For coarse- and fine-textured soils, 100 and 50 g of sample was used, respectively.

Soil drainage was designated as dry for upper- to midslope position sites with a slope greater than 25% and a percent sand greater than 50%. Drainage was classified as wet for lower slope position sites with a slope less than 6% and standing water at least part of the year. Sites that did not fit into either the dry or wet classes were placed in the moderate soil drainage class.

Analysis. In most cases, a single isolate was collected from within each sample plot. When more than one *Armillaria* species was found within a sample plot, the plot data were used for all *Armillaria* species found within the plot. When a single *Armillaria* species was found more than one time, the plot data were used only once for that species.

Quantitative data were subjected to one-way analysis of variance. If significant differences were found, means were separated using Fisher's protected least significant difference range test at the 95% confidence level. Chi-square goodness-of-fit analysis was used on frequency data. The expected frequencies used were $(S \cdot C)/N$, where S is the number of observations of an *Armillaria* species, C is the total number of observations of the category of interest, and N is the total number of observations. Differences were considered significant at probabilities of 0.05 or less.

RESULTS

Armillaria was found in 211 of 303 observed stands (Fig. 1). No apparent difference in geographic distribution was found between stands in which *Armillaria* was present and those in which it was not. *A. calvescens* Bérubé & Dessureault was found in 98 sample plots, *A. gallica* Marxmüller & Romagn. (= *A. bulbosa* (Barla) Kile & Watling, = *A. lutea* Gillet) in 67, *A. ostoyae* (Romagn.) Herink. in 22, *A. sinapina* Bérubé & Dessureault in 22, and *A. gemina* Bérubé & Dessureault in eight. *A. mellea* (Vahl:Fr.) P. Kumm. was not found in any of the sample plots.

At least one isolate was obtained from each of the sample plots. Two isolates were collected at each of 43 sites and three were collected at each of six sites. Three plots were found to have two different species, and one plot had three different species. *A. sinapina* was found in combination with either *A. calvescens* or *A. ostoyae*; *A. gemina* with *A. gallica*; and *A. calvescens* with both *A. sinapina* and *A. gemina*.

Significant differences from expected frequencies of association of *Armillaria* species with forest type groups occurred (Table 1). In northern hardwood forest types, *A. calvescens* and *A. sinapina* were found more frequently than expected by chance and the other species less frequently. In upland oak forest types, *A. gallica* was found more frequently than expected by chance and most others (except *A. gemina*) much less frequently or not at all. *A. gallica* also was the only species found infecting living trees in the upland oak forest types. In spruce-fir forest types, *A. ostoyae* and *A. sinapina* were found more frequently than expected by chance, whereas the other species were not found at all in this forest type group. *A. ostoyae* was the only species, of the two, found infecting living trees in these forest types. Conifers were present in 91% of the plots in which *A. ostoyae* was found. *Armillaria* species were found more frequently than expected by chance in northern hardwood plots and less frequently than expected in plantations.

Significant differences occurred among *Armillaria* species in their mean relative dominance for six tree species and for four tree groupings (Table 2). *A. calvescens*, *A. sinapina*, and *A. gemina* were found at sites with a higher mean relative dominance of *Acer saccharum* Marsh. than were other *Armillaria* species. *A. gallica* and *A. gemina* were found at sites with a higher mean relative dominance of *Quercus rubra* L. than were other *Armillaria* species, and plots with *A. gallica* had a higher mean relative dominance of other oak species than did other *Armillaria* species. *A. ostoyae* was found in plots with a higher mean relative dominance of *Abies balsamea* (L.) Mill., *Picea rubens* Sarg., and other conifer species. *A. ostoyae* and *A. gemina* were found in plots with a higher mean relative dominance of other pine species. *A. sinapina* was found in plots with a higher mean relative dominance of *Betula alleghaniensis* Britton (*B. lutea* F. Michx.), and *A. gemina* was found in plots with a higher mean relative dominance of *Fagus grandifolia* Ehrh.

Significant differences existed among *Armillaria* species in their mean relative density for six tree species and for two tree groupings (Table 3). Sites with *A. calvescens*, *A. sinapina*, and *A. gemina* had a higher mean relative density of *A. saccharum* than did sites with other *Armillaria* species. Sites with *A. calvescens*, *A. gallica*, and *A. gemina* had a higher mean relative density of *Fraxinus americana* L. than did sites with other *Armillaria* species. *A. gallica* and *A. gemina* were found at sites with a higher mean relative density of *Q. rubra* than sites of other *Armillaria* species, and sites with

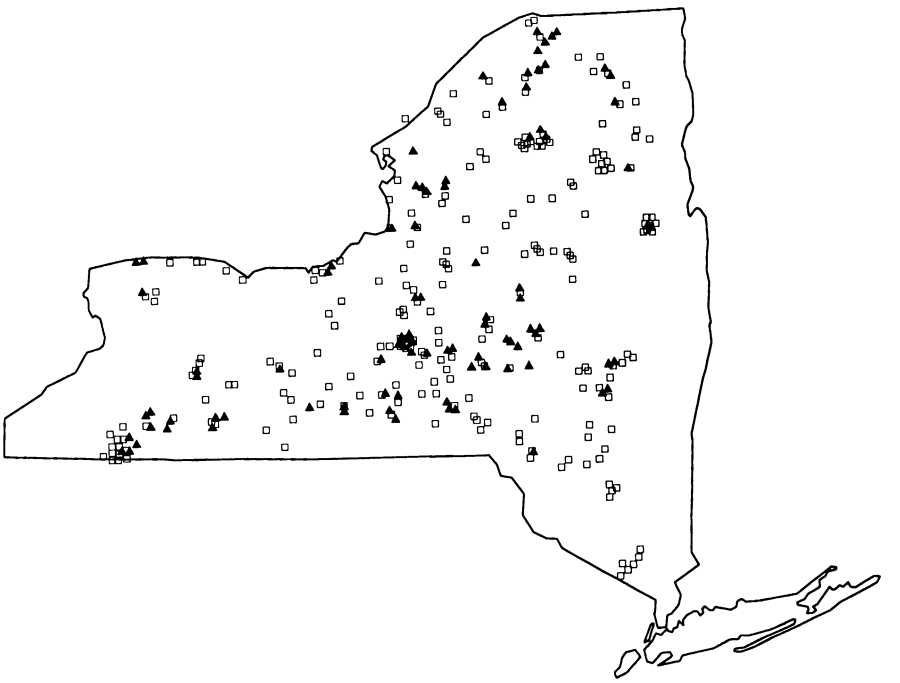

Fig. 1. Distribution of sites in New York State in which *Armillaria* was found (□) and in which *Armillaria* was not found (▲).

A. gallica had a higher mean relative density of other oak species than did sites of other *Armillaria* species. *A. ostoyae* was found in plots with a higher mean relative density of *A. balsamea* and other conifer species, and with *A. sinapina*, in plots with a higher mean relative density of *P. rubens*. *A. sinapina* was found in plots with a higher mean relative density of *B. alleghaniensis*.

Significant differences in mean values of soil variables existed among *Armillaria* species (Table 4). *A. calvescens* and *A. gallica* were found in plots with a lower percent sand and a higher percent silt and clay on average than were *A. ostoyae* and *A. sinapina*. *A. gallica* was found in plots with pHs (mineral and

Table 1. Number of plots of each forest type group occupied by each *Armillaria* species and in which *Armillaria* was not found

Armillaria spp.	No. of observations[t]	Forest type group[s]							
		Northern hardwood	Pine and hemlock	Upland oak	Spruce-fir	Plantations	Other hardwood[u]	Other mixed[v]	P[w]
A. calvescens	98	58	13	1	0	3	18	5	<0.01
A. gallica	67	14	9	21	0	4	16	3	<0.01
A. ostoyae	22	6	4	0	10	2	0	0	<0.01
A. sinapina	22	12	3	0	3	0	3	1	0.37
A. gemina	8	2	0	1	0	1	3	1	0.44
Not found[x]	92	12	12	4	4	39	20	1	<0.01
Total	309	104	41	27	17	49	60	11	
P[y]		<0.01	0.83	<0.01	<0.01	0.43	0.14	0.71	
P[z]		<0.01	0.88	0.09	0.57	<0.01	0.55	0.13	

[s] Forest type groups as defined in Forest Cover Types of the United States and Canada, Society of American Foresters, Washington, DC.
[t] Total number of observations for each species of *Armillaria* and for stands in which *Armillaria* was not found.
[u] Other hardwood types include unclassified hardwood types, and SAF types aspen (16), and cottonwood (63).
[v] Other mixed types include unclassified mixed hardwood/softwood types.
[w] Probability that there is no difference among the forest type groups, within a row, based on chi-square tests.
[x] Stands in which *Armillaria* was not found.
[y] Probability that there is no difference among the species of *Armillaria*, within a column, based on chi-square tests.
[z] Probability that there is no difference between sites in which *Armillaria* species were observed and sites in which it was not found based on chi-square tests.

Table 2. Mean relative dominance of each tree species in plots occupied by each *Armillaria* species

Armillaria spp.	No. of observations[u]	*Acer saccharum*	*Quercus rubra*	Other oaks[v]	*Abies balsamea*	*Picea rubens*	Other conifers[w]	Other pines[x]	*Betula alleghaniensis*	*Fagus grandifolia*	Other spp.[y]
A. calvescens	98	25.6 b[z]	1.0 a	0.1 a	0.5 a	0.3 a	0.3 a	1.7 a	2.5 a	9.5 a	58.5 c
A. gallica	67	10.7 a	16.7 b	8.7 b	0.0 a	0.0 a	0.0 a	2.0 a	1.9 a	5.2 a	54.8 bc
A. ostoyae	22	5.6 a	0.0 a	0.0 a	17.0 b	17.5 b	4.8 b	7.0 ab	8.0 a	2.1 a	38.0 ab
A. sinapina	22	20.6 ab	0.0 a	0.0 a	2.7 a	4.4 a	0.2 a	0.0 a	14.5 b	6.3 a	51.3 bc
A. gemina	8	22.9 ab	4.8 ab	0.0 a	0.0 a	0.0 a	0.0 a	14.3 b	1.0 a	32.5 b	24.5 a

[u] Total number of observations for each species of *Armillaria*.
[v] *Quercus alba*, *Q. bicolor*, *Q. palustris*, *Q. prinus*, and *Q. velutina*.
[w] Conifer species, except pines, that made up less than 1.5% of the total species and that show a significance level greater than 0.05 alone, including *Picea glauca*, *P. mariana*, *Taxus canadensis*, *Thuja occidentalis*, and *Larix* spp.
[x] Pine species that made up less than 1.5% of the total species and that show a significance level greater than 0.05 alone, including *Pinus resinosa* and *P. sylvestris*.
[y] All other species that show a significance level greater than 0.05 alone, including *Acer pensylvanicum*, *A. rubrum*, *A. saccarinum*, *Alnus rubra*, *Betula lenta*, *B. papyrifera*, *Carpinus caroliniana*, *Carya cordiformis*, *C. ovata*, *Castanea dentata*, *Fagus grandifolia*, *Fraxinus nigra*, *F. pennsylvanica*, *Juglans cinerea*, *J. nigra*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Ostrya virginiana*, *Picea abies*, *Pinus resinosa*, *P. strobus*, *P. sylvestris*, *Populus deltoides*, *P. grandidentata*, *P. tremuloides*, *Prunus serotina*, *Robinia pseudoacacia*, *Sassafras albidum*, *Tilia americana*, *Tsuga canadensis*, *Ulmus americana*, *Amelanchier* spp., *Cornus* spp., *Crataegus* spp., *Prunus* spp., *Rhododendron* spp., and *Ulmus* spp.
[z] Mean values in the same column followed by different letters are significantly different ($P < 0.05$) according to Fisher's protected LSD multiple range test.

Table 3. Mean relative density of each tree species in plots occupied by each *Armillaria* species

Armillaria spp.	No. of observations[v]	*Acer saccharum*	*Fraxinus americana*	*Quercus rubra*	Other oaks[w]	*Abies balsamea*	*Picea rubens*	Other conifers[x]	*Betula alleghaniensis*	Other spp.[y]
A. calvescens	98	30.5 b[z]	4.1 ab	0.6 a	0.2 a	0.9 a	0.5 a	0.3 a	3.1 a	59.8 a
A. gallica	67	16.0 a	7.6 b	6.9 b	2.8 b	0.0 a	0.0 a	0.1 a	1.7 a	64.9 a
A. ostoyae	22	8.8 a	0.5 a	0.0 a	0.0 a	27.6 b	9.9 c	4.0 b	4.0 a	45.2 a
A. sinapina	22	24.8 ab	1.5 a	0.0 a	0.0 a	2.3 a	6.6 bc	0.5 a	9.8 b	54.5 a
A. gemina	8	31.0 b	2.9 ab	2.6 ab	0.0 a	0.0 a	0.0 ab	0.0 a	1.0 a	62.5 a

[v] Total number of observations for each species of *Armillaria*.
[w] *Quercus alba*, *Q. bicolor*, *Q. palustris*, *Q. prinus*, and *Q. velutina*.
[x] Conifer species, except pines, that made up less than 1.5% of the total species and that show a significance level greater than 0.05 alone, including *Larix* spp., *Picea glauca*, *P. mariana*, *Taxus canadensis*, and *Thuja occidentalis*.
[y] All other species that show a significance level greater than 0.05 alone, including *Acer pensylvanicum*, *A. rubrum*, *A. saccarinum*, *Alnus rubra*, *Betula lenta*, *B. papyrifera*, *Carpinus caroliniana*, *Carya cordiformis*, *C. ovata*, *Castanea dentata*, *Fraxinus americana*, *F. nigra*, *F. pennsylvanica*, *Juglans cinerea*, *J. nigra*, *Liriodendron tulipifera*, *Nyssa sylvatica*, *Ostrya virginiana*, *Picea abies*, *Pinus strobus*, *Populus deltoides*, *P. grandidentata*, *P. tremuloides*, *Prunus serotina*, *Robinia pseudoacacia*, *Sassafras albidum*, *Tilia americana*, *Tsuga canadensis*, *Ulmus americana*, *Amelanchier* spp., *Cornus* spp., *Crataegus* spp., *Prunus* spp., *Rhododendron* spp., and *Ulmus* spp.
[z] Mean values in the same column followed by different letters are significantly different ($P < 0.05$) according to Fisher's protected LSD multiple range test.

Table 4. Mean values of soil variables in plots occupied by each *Armillaria* species

Armillaria spp.	No. of observations[x]	Mineral soil layer					Organic soil layer	
		Sand (%)	Silt (%)	Clay (%)	pH	Organic matter (%)	pH[y]	Organic horizon thickness (cm)
A. calvescens	98	47 a[z]	42 c	11 b	4.4 a	14.1 b	4.3 b	2.6 b
A. gallica	67	46 a	40 c	14 b	4.6 b	10.1 a	4.6 c	2.0 a
A. ostoyae	22	67 c	26 a	7 a	4.3 a	13.8 ab	4.0 a	5.0 d
A. sinapina	22	63 bc	30 ab	7 a	4.3 a	19.8 c	4.3 b	3.4 c
A. gemina	8	51 ab	39 bc	10 ab	4.2 a	14.3 ab	4.1 ab	2.8 a–c

[x] Total number of observations for each species of *Armillaria*.
[y] Total number of observations for each species of *Armillaria* in the organic pH column were 83, 50, 21, 20, and 6, respectively.
[z] Mean values in the same column followed by different letters are significantly different ($P < 0.05$) according to Fisher's protected LSD multiple range test.

Table 5. Frequency of plots in three rhizomorph abundance classes for each *Armillaria* species

Armillaria spp.	No. of observations[t]	Low[u]	Moderate[v]	High[w]	P^x
A. calvescens	98	11 L[y]	50 L	37 H	0.02
A. gallica	67	8 L	49 H	10 L	<0.01
A. ostoyae	22	19 H	3 L	0 L	<0.01
A. sinapina	22	4 L	9 L	9 H	0.34
A. gemina	8	1 L	4 L	3 H	0.77
Total	217	43	115	59	
P^z		<0.01	0.02	<0.01	

[t] Total number of observations for each species of *Armillaria*.
[u] Low frequency sample plots had no rhizomorphs within 15 soil cores.
[v] Moderate frequency sample plots had one to eight of 15 soil cores with rhizomorphs.
[w] High frequency sample plots had more than eight of 15 soil cores with rhizomorphs.
[x] Probability that there is no difference among the frequencies of rhizomorphs within a row based on chi-square tests.
[y] Letters indicate observed frequencies higher than expected (H) or lower than expected (L), although they may not indicate significant differences.
[z] Probability that there is no difference among the species of *Armillaria* within a column based on chi-square tests.

organic) higher than that of all other species. *A. ostoyae* was found in plots with pHs lower than most other species. *A. sinapina* was found in plots with a higher mean organic matter content (of the mineral soil) than that of all other species. *A. ostoyae* was found in plots with a thicker organic horizon on average than that of all other species. *A. gallica* was found on dry sites more frequently than expected by chance ($P < 0.01$) and on wet sites less frequently than expected by chance.

Significant differences in the frequency of rhizomorphs in the soil occurred among *Armillaria* species (Table 5). *A. calvescens* was found more frequently than expected by chance in plots that were ranked high in rhizomorph frequency, *A. gallica* was found more frequently than expected by chance in moderate plots, and *A. ostoyae* was found more frequently than expected by chance in plots ranked low in frequency. No significant deviations from expected frequency of the rhizomorphs were observed for plots with *A. sinapina* and *A. gemina*.

A. calvescens and *A. gallica* occurred on plots with significantly ($P = 0.02$) fewer snags per hectare on average (130 and 106 snags per hectare) than did *A. ostoyae* (233 snags per hectare).

No significant differences existed among *Armillaria* species in the following site characteristics: total basal area of trees per hectare; total numbers of trees, snags, stumps, or logs per hectare; average tree diameter; slope position; or slope percent (*data not shown*).

DISCUSSION

Although the ecology of *Armillaria* has been studied (13), little is known of site differences among the species. No single site characteristic can explain all the differences among *Armillaria* species, but the differences in site characteristics among the species can explain some of the variation previously associated with a single species.

A. calvescens was the most common species encountered in New York and was found mainly on maples and other hardwood hosts (7). It was found predominantly in northern hardwood stands and sites with *A. saccharum*, the most common forest cover and tree species in the state.

A. gallica previously was reported on oaks and other hardwoods (7,11,16,17). In this study, it often was found in upland oak stands. The relation to drainage class may be explained by the fact that upland oak type stands often occur on dry sites (10). In Europe, *A. gallica* was reported to produce abundant rhizomorphs in the field (17). In this study, it was found more frequently than expected by chance at sites with a moderate amount of rhizomorphs in the soil.

A. ostoyae was the most common *Armillaria* species found in montane spruce-fir forests in New Hampshire (12). It has been found primarily on conifers (7,9,16,17). In this study, it was found mainly in spruce-fir stands and was the only species found infecting living hosts in spruce-fir stands. In England, compared with other species, *A. ostoyae* was found killing trees growing in more acid soils (16). In this study, it often was found in acid soils, which are quite common in New York. *A. ostoyae* produces few rhizomorphs in New York forests as was observed in Europe (17).

A. sinapina previously showed no strong relationship to either hardwood or conifer hosts in New York (7). In this study, no strong relationship was found to a forest type group, but it was found at sites with higher relative dominance and relative density of *B. alleghaniensis* than were other *Armillaria* species.

A. gemina has been reported only in the northeastern United States, as a rare species, primarily on hardwoods (1,5,7). In the current study, it was found as a rare species in hardwood stands and, compared with most other *Armillaria* species, at sites with higher relative dominance of *F. grandifolia* and *Pinus* spp. The small sample size of *A. gemina* probably explains the lack of differences from other species for many of the site variables measured.

A. calvescens and *A. gallica* often were found under similar ecological conditions. They both were found in hardwood stands and at sites lower in sand and higher in silt and clay, on average, than were most other species. Both were reported on hardwood hosts (7,11,16,17). Studies of rDNA suggested that these species are more closely related than other *Armillaria* species (2,3,20). These species also are similar in basidiome morphology relative to other species (5). Although these species may be more closely related than other species, distinct differences in forest type group, forest composition, soil pH, soil organic matter percent, and organic horizon thickness were found in this study. Their geographic distributions and frequencies of host species also differ in New York (7).

A. ostoyae and *A. sinapina* also were

found under similar ecological conditions. Compared with other species, they both were found at sites higher in *P. rubens* stems, higher in organic matter and sand, and lower in silt and clay and were the only two species found in spruce-fir stands in New York. They were reported to have similar geographic distributions in New York (7) and similar basidiome morphology (4). *A. ostoyae* and *A. sinapina* both appear to be relatively northern species (11). However, differences in forest type groups, forest composition, soil organic matter percent, organic horizon thickness, and pH of the organic horizon were found in this study. Differences in host type preferences (hardwood vs. conifer) also were reported (7).

A. ostoyae and *A. gemina* were reported to have identical basidiome characteristics (5). They also belong to closely related rDNA classes (2,3). However, *A. ostoyae* is found primarily on conifers (7,9,14,16) and *A. gemina* was reported predominantly on hardwoods (1,5,7). In this study, *A. ostoyae* occurred primarily in conifer stands and *A. gemina* in hardwood stands. Distinct differences also were found in other site parameters.

The stands in which *Armillaria* was not found were mainly plantations and unclassified hardwood stands. *Armillaria* was not found in 80% of the plantations observed. Many of the plantations in New York were established by the Civilian Conservation Corps on abandoned farm fields. *Armillaria* was reported as a less common problem in plantations established on abandoned farms (19). Reduction in the amount of *Armillaria* inoculum had been reported in areas that were cut and then allowed to fallow (15,18). The unclassified hardwood stands were frequently composed of early successional species and may have become established on abandoned fields.

In this study, the present forest covers were used to describe the forest type groups (10), but the forests of today are different from the original mature forests (8). Some anomalous variation within the *Armillaria* species as to their forest type groups, host/substrate relationships, and other ecological characteristics could be explained by the fact that they became established in the original mature forests and persisted at the site despite some changes in overstory species composition.

The *Armillaria* species identified in New York forests have different forest cover associations and soil relationships. The frequency of rhizomorphs in the soil also differs among the species. These ecological differences can help to distinguish species and understand relationships among *Armillaria* species, site conditions, and disease. These are important steps in developing strategies for managing forest stands.

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