Determination of the Ecological and Geographic Distributions of *Armillaria* Species in Missouri Ozark Forest Ecosystems

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Abstract.—Armillaria root rot contributes to oak decline in the Ozarks. Three *Armillaria* species were detected in Ecological Landtypes (ELT's) representing south- to west-facing side slopes (ELT 17), north- to east-facing side slopes (ELT 18), and ridge tops (ELT 11). *Armillaria mellea* was detected in 91 percent of 180 study plots; was detected with equal frequency in all three ELT's; and was ubiquitous in block 3. *Armillaria gallica* was detected in 64 percent of the study plots; was detected least frequently in block 3; and was detected least frequently on ELT 17 in block 3. The distribution of *A. tabescens* remains incompletely resolved; it is the least abundant species and the most difficult to survey. *Armillaria mellea* was much more frequently associated with oak mortality than were *A. gallica* or *A. tabescens*, based on isolations from dying or recently killed trees. If these three species compete for substrate, oak decline levels may be influenced by landscape patterns of *Armillaria* species co-occurrence. We hypothesize that oak decline will be most severe in block 3, and especially on ELT 17, where *A. mellea* most often occurs in the absence of *A. gallica*.

Armillaria (Fr.:Fr.) Staude is a white-rot wood decay fungus genus (Fungi, Agaricales) comprising about 40 species worldwide (Volk and Burdsall 1995, Watling *et al.* 1991). Due to similarities in the morphology of *Armillaria* mushrooms, mycelial fans, and rhizomorphs, all annulate North American *Armillaria* were widely thought to belong to a single highly variable species (*Armillaria mellea*) until the late 1970's. Following Hintikka's (1973) description of a mating test for distinguishing *Armillaria* species using pedigreed single-basidiospore isolates, great progress has been made in clarifying biological, ecological and taxonomic issues concerning *Armillaria* species (Korhonen 1995). The name *Armillaria mellea* (Vahl:Fr.) Kummer now clearly represents a single *Armillaria* species, the type species of the entire genus (Watling *et al.* 1991). The exact number of *Armillaria* species in North America remains uncertain due to insufficient study. Unfortunately, much of the *Armillaria* literature well into the 1980's is of limited value because the correct identity of the *Armillaria* species studied was never established. This is the initial report of the first formal study of the *Armillaria* species influencing forest structure in upland Ozark oak-hickory forests. The three *Armillaria* species encountered were *A. gallica* Marxmüller & Romagnesi, *A. mellea*, and *A. tabescens* (Scop.) Emel.

A portion of the energy derived by *Armillaria* mycelia from wood decay (Garraway *et al.* 1991) is spent on sexual reproduction of airborne basidiospores on mushroom gills. Each spore that successfully germinates to colonize a suitable woody substrate (food base) generally mates with another sexually compatible germling to form a genetically unique individual ("genet," *sensu* Harper 1977) that may become established in the landscape as an agent of wood decomposition and perhaps of root disease and forest decline (Anderson and Kohn 1996, Guillaumin *et al.* 1991).

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Genets of all *Armillaria* species are functionally territorial, enlarging through sequential colonization of woody food bases by branching, cord-like rhizomorph systems and/or growth across root contacts and grafts (Gregory *et al.* 1991, Morrison *et al.* 1991, Redfern and Filip 1991). Rhizomorph growth is fueled with energy and nutrients derived from food base decay (Anderson and Ullrich 1982, Garrett 1956, Rishbeth 1972) and from the soil through which the rhizomorphs grow (Morrison 1975). *Armillaria* rhizomorph production is generally increased when using hardwood compared with conifer food bases (Redfern and Filip 1991). Because *Armillaria* species do not produce asexual spores, *Armillaria* genets are potentially continuous in the forest floor. *Armillaria* genets are also potentially long-lived and can achieve great size (Anderson and Kohn 1996, Bruhn *et al.* 1997, Korhonen 1978, Legrand *et al.* 1996, Rishbeth 1991, Shaw and Roth 1976, Smith *et al.* 1992), especially when compared with most vegetation.

Armillaria species differ in host preference and virulence; genets of the same species can also differ in virulence. Studies elsewhere of *Armillaria* species that also occur in the Ozarks have concluded that *A. mellea* is much more virulent than either *A. gallica* or *A. tabescens* (Gregory *et al.* 1991, Guillaumin *et al.* 1993, Redfern and Filip 1991, Rishbeth 1991). *Armillaria mellea* and *A. gallica* are generally considered to be much more common than *A. tabescens* (which can be locally abundant). *Armillaria mellea* is capable of attacking and killing a wide variety of hardwoods and a smaller range of conifers (mainly non-resinous species). *Armillaria gallica* is more restricted to colonizing dying or dead material and causing butt rot of hardwoods. In western Europe, *A. tabescens* is considered the least virulent of the three species, largely restricted to hardwood stumps. A notable exception is primary parasitism by *A. tabescens* of exotic *Eucalyptus* species in southwest France. North American *A. tabescens* has a large host range and may be somewhat more virulent than European *A. tabescens* (Sinclair *et al.* 1987). However, Rhoads (1925, 1956) indicated that exotic and cultivated tree species were much more susceptible than native tree species to North American *A. tabescens*, especially when planted on land previously cleared of oak forest.

Armillaria species (and genet) distributions are related to long-term vegetation and Ecological Land Type (ELT) characteristics (Bruhn *et al.* 1994, Korhonen 1978, Rishbeth 1982). The mechanisms by which neighboring *Armillaria* genets of the same or different species interact to allocate space among themselves are not yet clear. Where the perimeters of *Armillaria* genets meet or overlap, genets may interact as a result of niche overlap and competitive exclusion (Leibold 1995, Mohammed and Guillaumin 1989). Genets of different *Armillaria* species may circumvent each other as a result of different colonization strategies (Legrand *et al.* 1996). Nevertheless, the activity levels of *Armillaria* genets adjust to changes in the environment (*e.g.*, climate, defoliation, vegetation management) that affect the supply of food bases and the vulnerability of potential hosts (Bruhn *et al.* 1994, Lonsdale and Gibbs 1996, Wargo 1996, Wargo and Harrington 1991). The spatial arrangements and ecological attributes of *Armillaria* genets help shape long-term forest community structure in response to perturbations (Lundquist 1993, Worrall and Harrington 1988), because each extant combination of genets contributes differently to the regulation of stand structure and composition.

Armillaria species are often implicated as opportunistic root parasites contributing to forest declines incited by various stress events (Bauce and Allen 1992, Clinton *et al.* 1993, Houston 1992, Johnson and Law 1989, Kile *et al.* 1991, Wargo 1996). Both excess moisture and drought during the growing season are capable of inciting *Armillaria* root disease (e.g., Lonsdale and Gibbs 1996, Wargo and Harrington 1991). Rhoads (1956) found that droughty acidic sites predisposed trees to attack in Florida, whereas poorly drained soils on former oak sites predisposed grape plants to attack in Missouri (Rhoads 1925). A study of oak decline in upland Ozark forests showed that the growth rates of trees that eventually died did not recover following severe drought (compared to similar trees that remained healthy), and that growth of declining trees was further depressed with each succeeding drought (Dwyer *et al.* 1995). This scenario is consistent with a combined *Armillaria* + drought etiology. A relationship has been recognized between predisposing stress events (e.g., drought, late frost, defoliation), Armillaria root disease, and oak decline and mortality in the Missouri Ozarks (Johnson and Law 1989, Law and Gott 1987), though the identities of the *Armillaria* species involved and the nature and extent of their involvement and interactions were not determined. The black/

scarlet oak cover type occupies approximately 2 x 10^6 ha in Missouri. Affecting over 7.2 x 10^5 ha on the Mark Twain National Forest alone, oak decline has been most severe on Captina silt loam soils situated on broad ridges and moderately severe on Clarksville silt loam soils with west aspects (Law and Gott 1987). If predictions of greater climatic instability including more frequent summer droughts prove correct (Joyce *et al.* 1990, Kraüchi 1993, Rind *et al.* 1990), the resultant physiological stress to forest trees could heighten levels of *Armillaria* root disease and associated forest decline.

The shortage of previous knowledge about *Armillaria* distributions and activities in upland Ozark forests is related to the lack of attention paid to this geographic region by mycologists in the past and the difficulty of distinguishing the annulate *Armillaria* species in the field. Once the distributions and behaviors of Ozark *Armillaria* species are clarified, it will be possible to devise silvicultural programs that consider this pivotal genus of forest fungi.

Objectives

The goal of our study is to use ecological characteristics to explain the pre-treatment geographic distributions and behavioral patterns of all *Armillaria* species occurring in the nine MOFEP sites. Characteristics to be considered include forest vegetation cover and ELT variables describing geo-landform, soils, and climate. Data describing these variables for the permanent vegetation plots are gradually becoming available (Chen *et al.* 1997, Kabrick *et al.* 1997, Meinert *et al.* 1997). As a result, the pre-treatment distribution of *Armillaria* species with respect to oak decline occurrence and severity will be clarified.

Our initial research objectives are:

1. to identify all *Armillaria* species occurring in the nine MOFEP sites before treatment;
2. to test the hypotheses that each *Armillaria* species is initially uniformly distributed: (a) among the three silvicultural treatments, (b) among the three blocks of sites, and (c) among ELT's characterized by ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes; and
3. to formulate hypotheses based on field observations concerning the pre-treatment relationship of each *Armillaria* species to the occurrence of oak decline.

METHODS

Experimental Design

MOFEP is designed to evaluate the responses of forest vegetation (and other forest life-forms) to even-aged (EAM), uneven-aged (UAM), and no-harvest (NHM) management. Over 600 permanent 0.2-ha study plots (fig. 4 in Brookshire *et al.* 1997) have been established in nine sites of approximately 400 ha each. The nine sites are arranged in three blocks of three sites each. One site in each block has been allocated to each of the three types of management (fig. 1 in Brookshire *et al.* 1997). Approximately 10 percent of each EAM and UAM site have been set aside from harvest. Within each site, plots were allocated to ELT's approximately in proportion to site land area represented by each ELT. Three upland ELT's (designated 11, 17, and 18) dominate the study sites (Miller 1981). These three ELT's can be roughly described as ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes, respectively (fig. 2 in Brookshire *et al.* 1997). Overstory vegetation associated with these three ELT's is mostly mature second-growth oak, hickory, and shortleaf pine. Logging has not occurred in any of the nine sites for at least 40 years. Experimental cutting in the EAM and UAM sites began in the spring of 1996.

Because we plan to build on this *Armillaria* distribution study with studies of responses of *Armillaria* species and vegetation to silvicultural treatments, we anticipated need for at least six study plots (per ELT per site) that receive the treatment assigned to that site. Permanent vegetation plots representing each of the three dominant upland ELT's in each of the nine MOFEP sites were randomly selected for this study (fig. 5 in Brookshire *et al.* 1997). Because 11 of our originally selected plots are located in stands subsequently reserved from treatment (designated OG, "old growth"), and to include all permanent vegetation plots in which weather data are being collected (Chen *et al.* 1997), we now have *Armillaria* distribution data for 180 plots rather than the 162 plots originally selected (table 1). Of these, 64 plots received silvicultural treatment in 1996 (table 1). Although it would be difficult to confirm the absence of an *Armillaria* species from a study plot, we assume that the inability to detect a particular *Armillaria* species in the vicinity of a plot constitutes strong evidence that the species is ecologically much less influential than if it

Table 1.—*Distribution of* Armillaria *study plots among statistical blocks, forest sites, silvicultural systems, ecological land types, and type of harvest activity*

Block	Site	Silvic. system[1]	Harvest treatment[1]	ELT[2]	Total plots[3]	Harvested plots[3]
1	1	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
	2	UAM	S	11	7	7
			S	17	6	3
			S	18	8	5
	3	EAM	I	11	6	2
			I	17	8	1
			C	17	8	1
			I	18	6	4
			C	18	6	1
2	4	UAM	S	11	6	6
			S	17	7	5
			S	18	6	6
	5	EAM	I	11	7	4
			C	17	8	1
			I	18	8	1
			C	18	8	3
	6	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
3	7	UAM	S	11	7	5
			S	17	8	4
			S	18	6	2
	8	NHM	—	11	6	0
			—	17	6	0
			—	18	6	0
	9	EAM	C	11	6	1
				17	6	0
			C	18	8	2

[1] Silvicultural system: NHM indicates no-harvest management (—); UAM indicates uneven-aged management by single-tree and group selection (S); EAM indicates even-aged management by clearcutting (C) and thinning (I). None of the six ELT 17 *Armillaria* study plots in site 9 received harvest treatment in 1996.
[2] Ecological landtype, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).
[3] Total plots are the number of plots examined for *Armillaria* in the site. Harvested plots are the number of plots examined for *Armillaria* harvested by the indicated treatment.

were abundant enough for us to detect its presence. Thus, our experimental hypothesis was:

H_0: Each *Armillaria* species occurs with equal frequency irrespective of MOFEP block, ELT, or proposed silvicultural treatment.

This hypothesis was evaluated separately for *A. gallica* and *A. mellea* using the GLM algorithms of the SAS statistical package to perform analysis of variance (ANOVA). MOFEP block, ELT, and silvicultural treatment served as classification variables. The response variable was the transformed proportion of plots within a site in which the *Armillaria* species of interest was found. The transformation used was the arcsin of the square root of the calculated proportion (Steel and Torrie 1980). Because of the small number of plots per site, the response variable was weighted by the inverse of its variance: $[p(1-p)/n]^{-1}$. The treatment*block interaction was used as "error a," to evaluate the significance of differences among treatments and blocks. The treatment*ELT*block interaction was used as "error b," to evaluate significance of differences among ELT's and the treatment*ELT interaction. Occurrence data for *A. tabescens* will be analyzed after additional field isolates are collected and identified.

Because the ANOVA above combines the 5 to 8 binomial presence/absence data for each ELT/site combination into a single proportion, its ability to detect ELT differences is severely limited. Because of the pre-harvest timing of this evaluation, the silvicultural treatments can be set aside to examine the distributions of *A. gallica* and *A. mellea* among ELT's in each of the three blocks of sites using contingency table analysis of the raw data. We used the general association statistic (GA) of the Cochran-Mantel-Haenszel test (Agresti 1990) for this purpose.

Sampling

Each entire 0.2-ha plot was thoroughly searched at least once, depending on what was collected and what could be observed. The forest floor was scanned carefully for fruiting of *A. mellea* and *A. tabescens* during at least one visit when each species was known to be fruiting on the site. When fruiting was found on a plot, at least one collection was made representing each mushroom morphology type (based on color and stature) encountered. Fruiting at the base of trees was collected preferentially. During every visit, any imminent or recent tree mortality was noted and evaluated for presence of mycelial fans, and these were always collected. Living trees with abnormally few live leaves (and many of these abnormally small and chlorotic) were categorized as "dying." Dead trees retaining fine twig structure and any dead leaves were categorized as "recent-dead" (table 2). During at least one visit, all woody debris, stumps, and dead trees were carefully examined for presence of rhizomorphs. Several rhizomorph samples were collected from each plot whenever possible. Evaluation of a plot was considered complete only after it had been searched thoroughly for all these forms of evidence. The locations of all field collections were mapped for use in ensuing studies of the spatial relationships between *Armillaria* populations, tree vegetation, and oak decline.

Field estimation of an *Armillaria* genet's pathogenicity requires careful consideration of available evidence, including (1) the condition of the woody substrates from which isolates are taken, and (2) the source tissues of the isolate (Gregory *et al.* 1991, Morrison *et al.* 1991). The presence of an *Armillaria* mycelial fan in the root collar cambial region of a dying or recently killed tree constitutes strong evidence of pathogenicity, because mycelial fans represent lethal colonization of the invaded root cambium tissue. Mycelial fans under the bark of long-dead trees may represent necrotrophic colonization unrelated to pathogenicity. Although rhizomorphs are the organs of root infection, rhizomorphs alone are not strong evidence of pathogenicity. Rhizomorphs on root surfaces are either non-pathogenic or have not had appropriate opportunity (e.g., through host stress) to demonstrate their pathogenicity. Because *Armillaria* species fruit well on the forest floor and on woody debris in proximity to living trees, fruiting near a tree is not strong evidence of pathogenicity. Based on these considerations, all of the above structures were used to determine the presence/absence within plots of each *Armillaria* species, but only the presence of a mycelial fan in the root collar of a dying or recently killed tree was interpreted as strong evidence of pathogenicity.

Sample Analysis

Armillaria field isolates representing each study plot were derived from (1) mycelial fans on dying

Table 2.—*Sources of MOFEP* Armillaria *study isolates*[1].

Substrate	Source	*Armillaria* species *gallica*	*mellea*
Healthy			
red oaks (subgenus *Erythrobalanus)*			
	mycelial fan or wood	0	0
	mushroom	0	8
	rhizomorph	0	0
white oaks (subgenus *Leucobalanus*)			
	mycelial fan or wood	0	0
	mushroom	0	2
	rhizomorph	0	0
hickories (*Carya* species)			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	2	0
pine (*Pinus echinata*)			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
Total (healthy)		2	12
Dying or Recent-dead			
red oaks			
	mycelial fan or wood	3	32
	mushroom	0	41
	rhizomorph	5	1
white oaks			
	mycelial fan or wood	2	1
	mushroom	0	2
	rhizomorph	0	0
hickories			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	0	3
Total (dying or recent-dead)		11	80
Debris or Dead ≥ 2 yrs			
red oaks			
	mycelial fan or wood	3	39
	mushroom	0	68
	rhizomorph	29	2
white oaks			
	mycelial fan or wood	1	4
	mushroom	0	20
	rhizomorph	13	0
hickories			
	mycelial fan or wood	1	0
	mushroom	0	2
	rhizomorph	21	0
other hardwoods[2]			
	mycelial fan or wood	3	3
	mushroom	0	22
	rhizomorph	59	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	1	0
Total (debris or dead ≥ 2 yrs)		132	160
Total (all 3 categories)		145	252

[1] The 89 isolates not represented include: *A. gallica* - 15 rhizomorph isolates from unidentifiable woody debris, 1 isolate from a bait potato, and 1 fan isolate with incomplete data; *A. mellea* - 39 forest floor mushroom isolates, 1 fan isolate with incomplete data, and 1 isolate from unidentifiable woody debris; *A. tabescens* - all 31 isolates.

[2] Other hardwoods includes dogwood, red maple, unidentifiable oak, sassafras, and black walnut.

or dead trees, (2) rhizomorphs from dying or dead trees or woody debris on the forest floor, and/or (3) mushrooms. It was necessary to culture *Armillaria* isolates from field samples because reliable species and especially genet identifications are based on tests applied to pure cultures. Initial isolations were made by transferring fungal tissue to petri dishes containing 2-percent (w/v) water agar with 200 micrograms per milliliter streptomycin sulfate. Mushroom caps were torn radially, and internal cap trama tissue for isolation was taken from just above the gills. Mycelial fan isolates were derived using sections of colonized root with intact bark, by sterilizing the bark surface with 20-percent household bleach (1.05-percent NaOCl) and carefully removing a window of bark to expose the fan. Rhizomorph isolates were obtained by soaking 5+-cm rhizomorph lengths in 20-percent household bleach for 7 minutes, blotting them dry in a clean paper towel, and culturing from 1-mm-long sections. Bacterial contamination was eliminated using van Tieghem cells (Tuite 1969). Working cultures were maintained in petri dishes containing 2-percent (w/v) malt extract medium solidified with 2-percent (w/v) agar. Isolates were preserved for long-term storage in sterile distilled water (Richter and Bruhn 1989). The Center for Forest Mycology Research, USDA Forest Products Laboratory, Madison, WI, and the Field Museum of Natural History, Botany Department, Chicago, IL, as well as our own laboratory, serve as permanent repositories for representative *Armillaria* cultures and/or voucher mushroom specimens.

Field isolates were first identified to genet through vegetative incompatibility tests conducted in petri dishes on 3-percent (w/v) malt extract agar (MEA) (Guillaumin *et al.* 1996). Each genet was then identified to species by at least one of several means. The traditional means of determining *Armillaria* species identity is by mating tests in which single-basidiospore (haploid) isolates obtained from a mushroom representing an unidentified field genet are mated in petri dish culture with single-basidiospore "tester" isolates of known species identity (Guillaumin *et al.* 1991). For this purpose, we have used a set of tester isolates identified and provided to us by Dr. James B. Anderson (Dept. of Botany, University of Toronto). In compatible matings, characteristic morphological changes occur as the tester isolate becomes converted to a diploid condition. Although single-basidiospore isolates may be derived for some genets through *in vitro* fruiting of field isolates (Darmono *et al.* 1993, Garraway *et al.* 1991), other means of identification are required for the preponderance of genets that do not readily fruit in culture. In so-called "diploid-haploid" pairing tests, tester isolates are paired with unidentified field isolates (presumed diploid). Conversion of the haploid tester isolate to diploid morphology occurs if the paired isolates are conspecific (Korhonen 1978, Rizzo and Harrington 1992).

Because both types of mating test are time consuming and laborious, we also evaluated more efficient methods of speciation. All MOFEP isolates of our *Armillaria* species could be distinguished on the basis of their growth rate and culture morphology either or both (1) after 7 weeks incubation on 1.5-percent (w/v) MEA in the dark at 33°C, or (2) after 7 weeks incubation on tannic acid agar (Davidson *et al.* 1938) at 24°C in the dark. We also found it possible to distinguish nearly all of our MOFEP isolates on the basis of their esterase and polyphenoloxidase enzyme complements. Having developed these two supplementary systems for *Armillaria* isolate identification, we learned in late 1994 of a much faster new technique for *Armillaria* isolate speciation using RFLP and PCR analysis of genetic patterns in the intergenic spacer (IGS) region of the ribosomal RNA operon (Harrington and Wingfield 1995). We currently rely on either diploid-haploid pairings or PCR analysis of the ribosomal RNA operon to speciate field isolates.

Considering the potentially very large sizes of *Armillaria* genets (e.g., Shaw and Roth 1976, Smith *et al.* 1992), we evaluated the possibility that any of the detected genets might occupy a territory large enough to span more than one study plot. To do this, we conducted somatic compatibility tests between isolates representing all genets of each species occurring on neighboring plots. These tests involved 71 plots, and included 40 genets of *A. gallica* from 36 plots, 60 genets of *A. mellea* from 41 plots, and 7 genets of *A. tabescens* from 6 plots.

RESULTS

Sample Collection

Establishment of the large collection of MOFEP *Armillaria* field isolates required for this initial study is nearly complete. All of the 485 field isolates obtained in 1993-1995 from 180 of the

permanent MOFEP plots have been identified as representing 431 genets belonging to three *Armillaria* species (140 genets of *A. gallica*, 261 genets of *A. mellea*, and 30 genets of *A. tabescens*). No genet was encountered on more than one of our study plots. As many as four genets and three species have been recovered from individual plots.

Armillaria gallica was collected mostly as rhizomorphs (90 percent of collections), seldom as mycelial fans (9 percent); we have not yet found *A. gallica* fruiting in the study plots. *Armillaria mellea* has been collected rarely as rhizomorphs (2 percent), and mostly as mycelial fans (27 percent) or mushrooms (70 percent); *A. mellea* fruited well October 11-22, 1993, August 24 to September 13, 1994, and October 3-11, 1995. *Armillaria tabescens* has never been collected as rhizomorphs, but mostly as mycelial fans (52 percent) or mushrooms (48 percent); *A. tabescens* fruited well mid-August to September 8, 1993 and August 26 to September 7, 1994, but poorly in mid-October 1995. Final evaluation of *A. tabescens* distribution is postponed pending collection of additional field data during a year favorable for fruiting.

Isolates of *A. gallica*, *A. mellea*, and *A. tabescens*, respectively, were derived from mycelial fans at the root crowns of 5, 33, and 3 declining or recently killed hardwood trees (table 2, *A. tabescens* data not shown). This represents 4 percent, 13 percent, and 10 percent, respectively, of the isolates included in table 2 (*A. tabescens* data not shown). *Armillaria mellea* appears to be quite virulent, *A. tabescens* appears to be intermediate in virulence, and *A. gallica* appears to be relatively avirulent (though probably capable of butt rot).

Armillaria Species Distributions

Results of our 3-year survey clearly portray the pre-treatment distributions of *A. gallica* and *A. mellea* in MOFEP's upland forests (table 3).

Table 3.—*Frequencies of detection of* Armillaria gallica *and* A. mellea *on 180 randomly selected 0.2-ha permanent vegetation plots, by ELT within the nine MOFEP sites*[1].

Species	ELT[2]	Status	Site[3]									
			1	2	3	4	5	6	7	8	9	Total
A. gallica	11	Present	6	6	3	4	7	5	3	3	3	40
		Absent	0	1	3	2	0	1	4	3	2	16
	17	Present	3	3	5	4	5	5	1	0	2	28
		Absent	3	3	3	3	3	1	7	6	4	33
	18	Present	6	8	5	6	6	5	4	2	4	46
		Absent	1	0	1	0	2	1	2	4	3	14
A. mellea	11	Present	4	7	5	6	4	5	7	6	6	50
		Absent	2	0	1	0	2	1	0	0	0	6
	17	Present	6	5	7	6	6	5	8	5	6	54
		Absent	0	1	1	1	2	1	0	1	0	7
	18	Present	7	6	4	6	8	7	6	6	8	58
		Absent	0	2	1	0	0	0	0	0	0	3

[1] Tabular values are the numbers of plots for which evaluation is complete in which the specified *Armillaria* species has been detected (present) or has not been detected (absent).

[2] Ecological land type, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).

[3] Sites 1-3 comprise statistical block 1; sites 4-6 comprise statistical block 2; sites 7-9 comprise statistical block 3. Sites 1, 6, and 8 will remain uncut; sites 2, 4, and 7 are receiving uneven-aged management; sites 3, 5, and 9 are receiving even-aged management.

ANOVA detected significant distributional differences among the three statistical blocks for both *A. gallica* ($P = 0.036$) and *A. mellea* ($P = 0.046$) (table 4). Though *A. mellea* was common on all three ELT's in all nine sites (table 3), it was nearly ubiquitous in block 3 (i.e., sites 7-9, the Peck Ranch) compared with blocks 1 and 2. *Armillaria mellea* was detected in 86, 88, and 98 percent of the study plots in blocks 1, 2, and 3, respectively (table 5). In contrast, *A. gallica* was much less commonly detected in block 3 than in blocks 1 and 2. *Armillaria gallica* was detected in 75, 78, and 39 percent of the same study plots in blocks 1, 2 and 3, respectively (table 5). The distribution record for *A. tabescens* is only complete for the no-harvest management treatment (sites 1, 6, and 8), where *A. tabescens* was found in 39, 39, and 18 percent of the study plots in blocks 1, 2, and 3, respectively. ANOVA detected no differences in *Armillaria* species occurrence among treatments or ELT's.

When the distributions of *A. gallica* and *A. mellea* among the three study ELT's were examined for each block using contingency table analysis of the raw presence/absence data, the Cochran-Mantel-Haenszel test detected no difference in the frequencies with which *A. mellea* was detected on the three study ELT's (block 1: GA = 0.327, df = 2, $P = 0.849$; block 2: GA = 4.248, df = 2, $P = 0.120$; block 3: GA = 1.950, df = 2, $P = 0.377$). Significant differences were detected in the frequencies with which *A. gallica* was detected on the three study ELT's in blocks 1 and 3 (block 1: GA = 6.989, df = 2, $P = 0.030$; block 2: GA = 2.551, df = 2, $P = 0.279$; block 3: GA = 7.138, df = 2, $P = 0.028$). In block 1, *A. gallica* occurred on only 55 percent of south- to west-facing side slope plots, 79 percent of ridgetop plots, and 90 percent of north- to east-facing side slope plots. In block 3, *A. gallica* occurred on only 15 percent of south- to west-facing side slope plots, compared with 50 percent of ridgetop plots, and 53 percent of north- to east-facing side slope plots.

Table 4.—*Analysis of variance table for evaluating distribution of* Armillaria gallica *and* A. mellea *among MOFEP plots relative to block, silvicultural treatment, and ELT.*

Species	Source of variation[1]	df[2]	Type III SS[3]	F[4]	Pr > F[5]
A. gallica	Block	2	39.3	8.5	0.036
	Treatment	2	5.0	1.1	0.423
	Error a (Treatment*Block)	4	9.3	.	.
	ELT	2	0.7	0.2	0.839
	Treatment*ELT	4	13.6	1.7	0.222
	Error b (Treatment*ELT*Block)	12	24.5	.	.
A. mellea	Block	2	73.5	7.4	0.046
	Treatment	2	6.1	0.6	0.588
	Error a (Treatment*Block)	4	20.0	.	.
	ELT	2	19.1	0.2	0.844
	Treatment*ELT	4	38.8	0.2	0.947
	Error b (Treatment*ELT*Block)	12	664.5	.	.

[1] Silvicultural treatment: even-aged management, uneven-aged management, or no-harvest management; ELT, ecological landtype based on slope and aspect: ridges, south- and west-facing side slopes, or north- and east-facing side slopes.
[2] df: degrees of freedom.
[3] Type III SS: sums of squares values associated with the indicated sources of variation.
[4] F: F-statistic associated with the indicated source of variation.
[5] Pr > F: the probability of observing an F-statistic of greater magnitude by random chance.

Table 5.—*Distribution of* Armillaria gallica *and* A. mellea *among the three study ELTs*[1]*, in each block.*

Species	Status	Block 1			Block 2			Block 3		
		11	17	18	11	17	18	11	17	18
A. gallica	Present	15	11	19	16	14	17	9	3	10
	Absent	4	9	2	3	7	3	9	17	9
A. mellea	Present	16	18	17	15	17	21	19	19	20
	Absent	3	2	3	3	4	0	0	1	0

[1] Ecological landtype, based on slope and aspect: ridges (ELT 11), south- to west-facing side slopes (ELT 17), and north- to east-facing side slopes (ELT 18).

DISCUSSION

We have confirmed the presence of three *Armillaria* species on a stratified sample of the permanent vegetation study plots located in all nine MOFEP sites over the period 1993-1995. This represents the first demonstration of the occurrence of *A. gallica* and *A. mellea* (in the strict sense) in the Ozarks; *A. tabescens* was previously reported from southern Missouri by Rhoads (1925). The distribution of *A. tabescens* has proven more difficult to finalize than those of *A. gallica* or *A. mellea*, because *A. tabescens* (1) produces few or no rhizomorphs in the forest floor, (2) causes little mortality that would provide mycelial fans, (3) fruits less predictably than *A. mellea*, and (4) appears to be the least abundant of the three species. Depending on conditions for fruiting, we expect to complete the "pre-treatment" distribution record for *A. tabescens* over the next year or two, in conjunction with logging damage documentation. Because *Armillaria* genet establishment is a very slow process (in contrast to genet response to environmental change), we feel safe in assuming that genets detected in the next year or two will still reflect pre-operational distributions.

As the study progressed, it became apparent that an effective survey for all three species should involve a different search strategy for each species. Although *A. gallica* apparently did not fruit and was rarely virulent enough to provide mycelial fans on recently killed trees, it produced the vast majority of the rhizomorphs that were collected. *Armillaria mellea* fruited regularly in mid to late autumn, was commonly collected as mycelial fans from recently killed trees, but was rarely collected as rhizomorphs. Fruiting of *A. mellea* was associated with the advent of cold autumn nights as well as adequate moisture. *Armillaria tabescens* has taken the longest time to survey, in part because it appears to be the least common. Fruiting provided the majority of records for this species, which was recovered infrequently as mycelial fans and never as rhizomorphs. The timing and abundance of *A. tabescens* fruiting was quite unpredictable from year to year, apparently depending mainly on abundant moisture in mid to late summer. It can fruit in late summer if moisture is abundant, later in the autumn with *A. mellea*, or hardly at all. Both *A. mellea* and *A. tabescens* fruited exceptionally well in 1993, one of the wettest years on record. Dry weather in late August and September 1995 was apparently responsible for delayed and greatly diminished fruiting by *A. tabescens*. In general, annual fruiting of each species was restricted to a single 2- to 3-week window of time, and these windows did not necessarily overlap. Based on these considerations, we placed highest survey priority on searching for fruiting from mid-August through late-October, and focused on rhizomorph, mycelial fan, and decay collections when fruiting was not occurring. The differences among these three species in the relative abundance with which they produce rhizomorphs, mycelial fans, and mushrooms underscore major differences in their biologies and the need to search for them differently.

Armillaria mellea was the most widely distributed of the three species, detected in 91 percent of all plots examined. *Armillaria gallica* was detected in 64 percent of the plots examined, and *A. tabescens* was the least frequently detected species, although the survey of its

distribution is incomplete. No pre-treatment differences were detected in the distributions of either *A. gallica* or *A. mellea* among the sets of sites assigned to each silvicultural treatment, but significant differences were detected for both species among the three blocks of sites. Both *A. gallica* and *A. mellea* were frequently detected in blocks 1 and 2, but *A. mellea* was nearly ubiquitous in block 3 (the Peck Ranch) where *A. gallica* was detected on fewer than half of the studied plots. Further, no differences were detected in the distribution of *A. mellea* among the three study ELT's in any of the three blocks, whereas *A. gallica* was less frequently detected on south- to west-facing side slope plots in blocks 1 and (especially) 3 than on either ridgetop plots or north- to east-facing side slope plots. It therefore appears that *A. mellea* occurs in the absence of *A. gallica* most frequently in block 3, and especially on south- to west-facing side slopes.

If south- to west-facing side slopes in blocks 1 and (especially) 3 are generally drier, warmer, and/or rockier than the rest of the MOFEP sites, the *A. gallica* distributional differences may be explained by conditions for rhizomorph growth. Seasonal drying can affect *Armillaria* rhizomorph growth in upper soil layers. It has been shown that cellulose and lignin degradation rates in forest soils increase with rising soil moisture and temperature (Donnelly *et al.* 1990). Working with *A. gallica* and *A. mellea*, Morrison (1976) encountered few rhizomorphs below 30 cm depth, and found few rhizomorphs in the upper 5 cm of the soil at a dry site, whereas rhizomorphs were most abundant in the upper 5 cm of the soil at a moist site. It seems reasonable to anticipate that rhizomorph growth would generally be less robust on exposed south- to west-facing side slopes than on more protected north- to east-facing side slopes. The distribution of *A. mellea* appears to be less affected by ELT variables, perhaps because *A. mellea* is less dependent on rhizomorph spread than is *A. gallica*.

Our sample of 180 of the 0.2-ha MOFEP vegetation plots represents the rich variety of interactions occurring within MOFEP forest communities among stand structure, ELT, silvicultural treatment effects, and local patterns of *Armillaria* genet distribution. Studies elsewhere have shown that forest floor maps of genet distribution often indicate little or no map overlap of *Armillaria* genets belonging to species with similar "colonization strategies," but frequent overlap of genets belonging to *Armillaria* species with different colonization strategies (e.g., Bruhn *et al.* 1997; Kile *et al.* 1991; Legrand *et al.* 1996; Rizzo and Harrington 1993; Smith *et al.* 1992, 1994). Different colonization strategies can result from differences in virulence or host preference. The unique genetic potential of each *Armillaria* genet is expressed only within that genet's boundary, but when genets of the same or different *Armillaria* species occupy the same landscape they may influence each other's behavior in areas of genet contact. For example, Mohammed and Guillaumin (1989) found that when *A. gallica* and *A. mellea* occupied the same substrate, *A. mellea* inhibited *A. gallica*, without being inhibited in return by *A. gallica*. Since all three MOFEP *Armillaria* species are hardwood-specializing fungi, and *A. gallica* is by far the most prolific producer of rhizomorphs, *A. mellea* and *A. tabescens* may often have less access to food base resources suitable for all three species within the boundaries of competing *A. gallica* genets. Thus, as a result of niche overlap (Leibold 1995), *A. gallica* may mitigate the root disease activity of a co-occurring *A. mellea* or *A. tabescens* genet. Bruhn *et al.* (1997) found small *A. mellea* genets to occur commonly within larger *A. gallica* genets, suggesting that *A. mellea* had sole access to certain food base resources perhaps due to its greater virulence. The small size of the *A. mellea* genets may reflect their isolation by the surrounding *A. gallica* genet.

From the above discussion, it appears that south- to west-facing side slopes in MOFEP block 3 should have the highest risk of oak decline associated with *Armillaria* root disease in the MOFEP sites. Our long-term objectives involve mapping of representative spatial patterns of *Armillaria* genet distributions in selected study plots, experimental testing of *Armillaria* species interactions under selected sets of field conditions, and modeling of temporal and spatial projections of forest structure (e.g., Larsen 1997) including decline. Ultimately, we are interested in explaining the interactions among *Armillaria* populations and MOFEP forest structure, as influenced by MOFEP experimental silvicultural treatments.

Silvicultural operations can affect residual forest development in unexpected ways when interactions with the fungal and insect components of forest communities are not anticipated. The relative contributions of even-aged *vs.*

uneven-aged management to the risk of decline are not clear. Comparisons of these two systems from the standpoint of decline exacerbation should focus attention on the frequency of stand entry, the spatial and size distributions of stumps created (i.e., new *Armillaria* food bases), the extent of forest floor disturbance, and aboveground residual tree damage. We are documenting harvest effects on our study plots by mapping and characterizing stumps, residual stem injuries, and vehicle paths. Belowground root damage along vehicle paths is also being characterized. Although root wounds are not always necessary for host infection by *A. tabescens* (Rhoads 1956), they have been found to increase host vulnerability (Weaver 1974), probably in part because *A. tabescens* rhizomorph growth through soil rarely if ever occurs. It has also been shown that damaged roots are more vulnerable to *A. mellea* invasion than uninjured roots, and that this effect is not limited to the point of injury (Popoola and Fox 1996). Root collar and basal stem injuries may have similar physiological effects on host vulnerability to *Armillaria* root disease and/or butt rot. Maps of the juxtaposition of stumps, vehicle paths, residual trees, and *Armillaria* genets will provide unprecedented opportunities to interpret forest community dynamics.

Starkey *et al.* (1989) associated the risk of oak decline in southern upland hardwood forests with acute summer drought, recent or repeated spring defoliation, stand maturity, predominance of red oak group species, low site index, and xeric site conditions. Dwyer *et al.* (1995) found that oak decline in the Ozarks affected stressed trees regardless of age. Nevertheless, silvicultural options for maintaining healthy stands are more satisfactory than options for dealing with declining ones. Partial cutting in declining stands for any reason often results in acceleration of decline, and regeneration of declining stands can be complicated by the impaired condition of trees needed as vigorous seed or sprout sources (Starkey *et al.* 1989). As species composition shifts away from the red oak group in declining stands, managers will have to decide whether or not to augment natural hardwood regeneration by encouraging or planting shortleaf pine. In young high risk stands prior to the advent of decline, partial cuttings may reduce stress and shift species composition toward more resistant species (e.g., white oak, shortleaf pine, etc.). Shortening the rotation age may reduce stand vulnerability to decline if it reduces physiological stress levels.

Although *Armillaria* species are certainly not the only organisms that contribute to mortality or decline in the Ozarks, they are of particular interest because of the spatial stability of *Armillaria* genets (i.e., their long-term relationship with forest structure), and their pivotal role in mediating the influences of stress events and the activities of stress agents (Wargo 1996). Other relevant organisms and diseases include oak wilt, Hypoxylon canker of oak, the two-lined chestnut borer, and defoliating insects (e.g., the looper complex and gypsy moth). Oak wilt disease is widely distributed in the Ozarks (Jones and Bretz 1958). The oak wilt pathogen (*Ceratocystis fagacearum*) is a primary parasite capable of infecting and killing healthy oaks. Oak wilt is most severe in stands approaching pure red oak species composition, where root grafts connect a high proportion of the most susceptible trees (Bruhn *et al.* 1991). Because oak wilt epidemiology is independent of host stress (at least with red oak species), oak wilt and oak decline are not causally related. Hypoxylon canker of oak (caused by *Hypoxylon atropunctatum*) has been associated with other factors causing oak decline and mortality (Bassett and Fenn 1984, Law and Gott 1987). Bassett and Fenn (1984) showed that the pathogen occurs in branches and boles of healthy oaks without causing disease until the advent of stress; they were not able to cause disease with artificial inoculations. They isolated the pathogen with equal frequency from non-diseased branches and boles of healthy black or red oaks and white oaks, suggesting that the greater observed incidence of disease on black or red oaks was due to differences in susceptibility or exposure to drought. Although the two-lined chestnut borer (*Agrilus bilineatus*) is most often a secondary colonizer of severely stressed or dying trees, it can occasionally build to population levels capable of accelerating mortality. Borer activity in the Ozarks is commonly associated with formation of mortality pockets in conjunction with oak wilt, *Armillaria* root disease, and/or Hypoxylon canker (Law and Gott 1987). Although the gypsy moth has not yet arrived in the Ozarks, a very high proportion of Ozark land area supports forest stands comprising very high densities of tree species preferred by the gypsy moth (Liebhold *et al.* 1997).

It seems appropriate to close this consideration of relevant Ozark forest pathogens and insect pests with a brief mention of annosus root disease of shortleaf pine, caused by

Heterobasidion annosum. Once found widely distributed in the Ozarks (Berry and Dooling 1962), *Heterobasidion annosum* has become all but forgotten with the encroachment of oaks onto logged-over upland Ozark pine forest sites (Johnson and Law 1989) and the de-emphasis on pine regeneration. A substantial portion of the Ozark land area currently supporting black/scarlet oak forest was previously dominated by more drought-tolerant shortleaf pine (Law and Gott 1987). Although annosus and *Armillaria* root diseases share some important features (Sinclair *et al.* 1987), in the Ozarks annosus root disease does not noticeably affect hardwoods and pine is not appreciably affected by *Armillaria* root disease. Although the distribution and intensity of annosus root rot in preceding pine forests are unknown, there are no records of "pine decline" corresponding to more recent records of oak decline. It seems plausible that shortleaf pine is ecologically better adapted to the more stressful upland Ozark sites than are members of the red oak subgenus. Perhaps oak decline functions to shift forest vegetation on these sites toward greater compatibility with the long-term local environment.

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