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Population structure of *Armillaria* species in several forest types

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Abstract: Population structure of *Armillaria calvescens, A. gemina, A. gallica* and *A. ostoyae* in New York was studied in plots established at six sites and transects at three others. No significant differences among species in size or density of genets (identified by somatic incompatibility) was detected. The size distribution of genets revealed a high frequency of very small genets (mostly associated with single sample points) and a uniformly lower frequency of larger genets ranging up to 670 m^2 (44 m long). Density of genets (including all *Armillaria* species) was higher in plots with more species of *Armillaria.* There was little spatial overlap between genets regardless of species. Five of 33 pairs of isolates from within roots and from superficial, associated rhizomorphs consisted of different species; the other 28 pairs were comprised of single genets. The data suggest that expansion beyond the initial resource unit is a critical phase in the development of genets and are consistent with patchwise distribution of niches that differentiate *Armillaria* species in these stands. Evidence from two plots, in which *A. ostoyae* apparently colonized planted stands of conifers on sites previously unforested or supporting hardwoods, supports the concept that basidiospores are important in the population structure of *Armillaria* species and the epidemiology of the diseases they cause.

Key Words: basidiospores, clone, epidemiology, root rot, somatic incompatibility

INTRODUCTION

Knowledge of the population structure of fungi can provide important information on the epidemiology of diseases they cause. The size distribution, density and arrangement of individuals provides indirect information on frequency of establishment of new individuals, factors contributing to establishment and growth of individuals, and intraspecific interactions. These can then be related to the establishment of infections and disease spread, permitting the refinement of epidemiological models and approaches to management.

Armillaria species are of particular interest in this regard because they are abundant, widespread, and of great economic importance. Population structure of *Armillaria* species varies greatly (Kile et al., 1991). This variation is not unexpected because numerous species of *Armillaria* are found worldwide in areas that vary greatly in climate, forest type, and management history. Studies are needed to better characterize populations and factors that influence their structure.

In referring to population units of *Armillaria,* "clone" has been distinguished from "genotype" based on the occurrence of discrete centers of tree mortality, i.e., in some cases there may be several clones of one genotype (Kile, 1983). With fungi, physical continuity or lack thereof is difficult to demonstrate, and discrete centers of tree mortality are not always present. The term "genet" is used to refer to plant population units whose members have the same genotype (developed from a single seed), and seems appropriate for use here in the sense of genotype as used above. It does not imply physical continuity among sample points.

A variety of techniques is available for population studies in *Armillaria.* Cultural characters (Rishbeth, 1978), mating-type alleles (Anderson et al., 1979; Kile, 1983; Korhonen, 1978), isozymes (Rizzo and Harrington, 1993), and molecular-genetic analysis (Smith et al., 1992) have all been used successfully to distinguish individuals of *Armillaria* (in some cases identified as mycelial types, clones, or genotypes). However, the most widely used technique has been somatic incompatibility (SI), sometimes called intraspecific antagonism (Adams, 1974; Hood and Sandberg, 1987; Kile, 1983, 1986; Rishbeth, 1978, 1988, 1991; Rizzo and Harrington, 1993; Siepmann, 1985). Like most other techniques, SI tests may not distinguish some closely related genotypes (Kile, 1983; Korhonen, 1978), but investigators have found that in practice it, "reliably distinguishes members of different intercompatibility groups" (Hood and Sandberg, 1987) and that it was the, "only feasible means of identifying genotypes and studying clonal development on a large scale" (Kile, 1983). Rizzo and Harrington (1993) found that SI distinguished two groups not distinguished by isozyme analysis. Further, SI is presumably the mechanism that

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operates in nature to maintain the individuality of secondary mycelia of hymenomycetes (Rayner, 1991). For many purposes, therefore, genets may be best defined on that basis.

In this study, populations of locally common *Armillaria* species were characterized primarily in two northern hardwood stands, two conifer plantations, and two mixed conifer-hardwood stands to compare population structure among species and among stands.

MATERIALS AND METHODS

Sites were selected that had stands of forest types common in New York and where *Armillaria* was present. Plots were established at six sites and were at least 30 × 30 m (except for one at Newcomb, which was 45 × 15 m). Some plots were revisited and expanded by further sampling. The plots (named after nearby geographic features) and their areas (m^2) were Allegany (1076), Bear Swamp (1140), Boonville (5750), Newcomb (675), Tully (2246) and Westernville (10 620). In three other sites, transects were established at right angles to one another and sampled along at least 20 m. Transects were established at Bear Swamp South, Cranberry Lake and Finger Lakes National Forest. In addition, pairs of isolates from roots and associated rhizomorphs were collected at various sites in conjunction with another study (Blodgett and Worrall, 1992a).

In plots and along transects, root collars of all trees, snags and stumps were searched for mycelial fans, decay, basidiomes and rhizomorphs typical of *Armillaria* (except for the Christmas tree plantation in Westernville, where only dead and dying trees were examined). Rhizomorphs were also sought in soil in areas where no other tree-associated samples were found. Whenever the fungus was found, samples were taken and their locations mapped. Isolations were made from samples using the selective media BSMA or BDS (Worrall, 1991).

Somatic incompatibility tests were done by pairing isolates on modified Weinhold's glucose-asparagine medium with ethanol (without malt extract) and on Shaw and Roth's medium (Harrington et al., 1992). In some cases one medium was used and pairings with inconclusive results were repeated on the other medium, but in most cases pairings were done on both media simultaneously. Isolates to be paired were placed on the agar surface 5–10 mm apart. Two pairings, about 5 cm apart, were done per plate. Controls consisted of self pairings. Pairings were observed after 2, 3 and 5 wk.

When cultures were alike in appearance and fused where they met at their growing margins, they were considered somatically compatible. Somatic incompatibility was indicated by a line of demarcation (Adams, 1974; Mounce, 1929) that took the form of a disjunction between the cultures, sometimes including a sparse zone and sometimes additionally a pigmented line in the agar. The line of demarcation was maintained out into the margin as the colonies grew side by side, unlike the ephemeral sparse zone sometimes seen in compatible control pairings. Pairings giving inconclusive results were repeated.

When many isolates from one plot were studied, some of them were initially paired in all combinations to establish the identity of some genets. Two or three testers of these genets were used in pairings with the remaining isolates. Any isolates that remained unidentified with previously identified genets were paired with one another in all combinations. Additional pairings were done to verify previous results. The shortest outlines that enclosed all the included points were drawn around the genets as smoothed polygons on scaled maps. Their areas were calculated using Canvas (Deneba Software, Florida). Such an area or length represents not the actual surface area or length of the organism, but the maximum area or linear extent in which it was found. Genets with only a single sample point were assumed to be circles with a diameter of 3 m (roughly the diameter of the system of larger roots of one stump). Differences in size and density (genets/ha) were tested by analysis of variance ($P = 0.05$).

One or more representatives of every genet were identified to species by "haploid-diploid" crosses with known haploid testers (Blodgett and Worrall, 1992a; Harrington et al., 1992).

RESULTS

The four *Armillaria* species encountered, *A. calvescens* Bérubé & Dessureault, *A. gallica* Marxmüller & Romagn., *A. gemina* Bérubé & Dessureault, and *A. ostoyae* (Romagn.) Herink, are among the most common species in the area (Blodgett and Worrall, 1992a). In total, somatic incompatibility was studied with 280 isolates; data presented here are drawn from 197 isolates.

The species varied in the ease with which SI tests could be interpreted and in consistency among pairings. *Armillaria ostoyae* almost always gave very well-defined, clear results in which groupings were consistent among pairings. The other species occasionally gave unclear or inconsistent results, requiring repetition and the use of numerous testers of each genet to obtain a mutually consistent, reliable pattern of results.

Both length and area of genets were highly variable within species and did not vary significantly among species. The mean lengths of genets (and sample sizes) were *A. gemina*, 17.1 m (10); *A. calvescens*, 11.7 m (16);

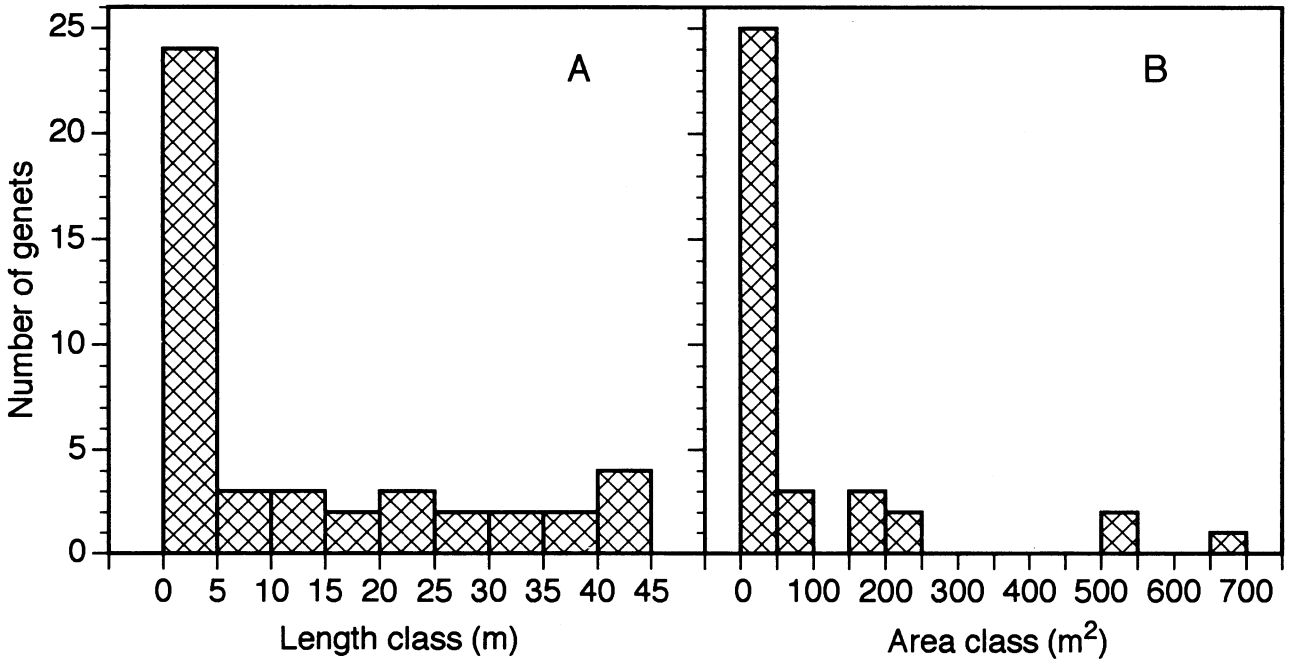

FIG. 1. Frequency distribution of length (A) and area (B) for genets of all species.

A. ostoyae, 10.6 m (16); and *A. gallica,* 18.5 m (4). The respective mean areas (and sample sizes, which were smaller because area could only be determined in plots) were 93.7 m^2 (7), 70.5 m^2 (12), 106 m^2 (16), and 7.1 m^2 (1).

Considering all the genets together, there was little variation in the frequency distribution of either length or area, with the exception that the smallest size class, mostly consisting of genets represented by single sample points, was much more frequent than the other classes (FIG. 1).

Density varied from 4.7 genets/ha to 65 genets/ha (FIG. 2). Plots with only one species of *Armillaria* had the lowest density of genets, and plots with three species had the highest density. Mean density of genets was calculated for each of the two species that occurred four times in the six area plots. *Armillaria ostoyae* had 11 ± 5 genets/ha (mean ± standard error) and *A. calvescens* had 24 ± 12 genets/ha. No significant difference could be detected between these samples.

Individual plots varied greatly in stand conditions as well as in population structure of *Armillaria* species. Tully (FIG. 3) was a typical northern hardwoods stand dominated by *Acer saccharum* Marsh. (sugar maple) with smaller amounts of *Fagus grandifolia* Ehrh. (beech) and *Prunus serotina* Ehrh. (black cherry). Maple and beech stumps were present from a commercial thinning in about 1980. *Armillaria gemina* and *A. calvescens* were found on the plot, and each had one or two relatively large genets (about 30 m long, consisting of 7–24 sample points) and several single-point genets. There was some overlap between the two larger genets of *A. calvescens,* but essentially none between the species.

Westernville was a Christmas tree plantation with *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) and a small number of *Pinus sylvestris* L. (Scots pine). A few dying Douglas-fir were found scattered in the plantation, and all successful isolations yielded *A. ostoyae* (FIG. 4). One genet was 520 m^2, but for four others only single sample points were found. A sample from the surrounding natural vegetation, a northern hardwood forest (outside the plot), yielded *A. calvescens.*

Armillaria ostoyae also dominated a 60-yr-old Scots pine plantation on sandy soil near Boonville, New York

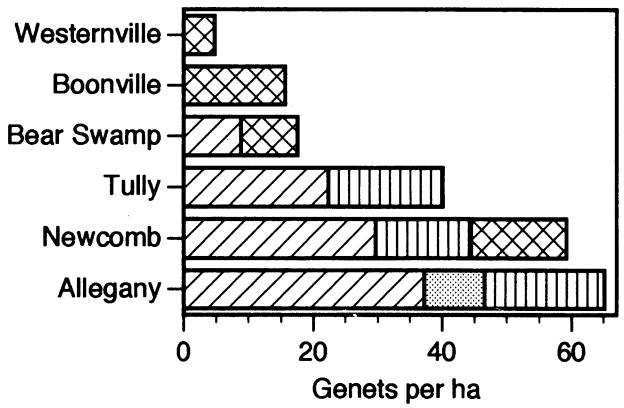

FIG. 2. Density of genets in six plots with one, two or three species per plot. Species are *Armillaria calvescens* (▨), *A. gallica* (□), *A. gemina* (▥), and *A. ostoyae* (▩).

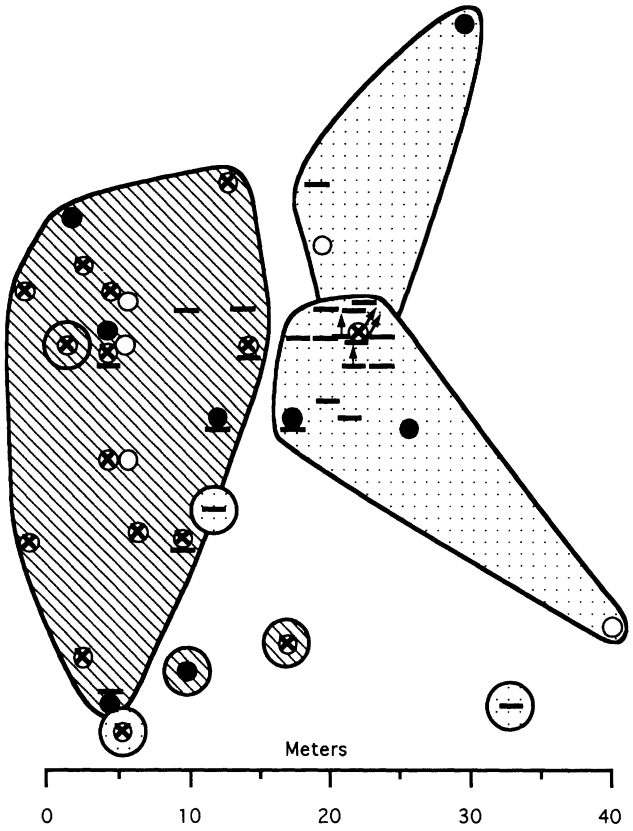

FIG. 3. Map of *Armillaria* isolates and genets from plot in northern hardwood stand in Heiberg Forest near Tully, New York. Species are *A. gemina* (▨) and *A. calvescens* (▩). Symbols represent live (○) and dead (●) trees, stumps (⊗), and rhizomorphs from soil (—). Isolates of a common genet (determined by somatic incompatibility) are enclosed in an outline. In the overlap between the two largest genets of *A. calvescens*, members of the genet nearer the upper edge of the figure are distinguished with arrows. The outline around each genet is drawn for clarity and does not indicate the presence or location of physical connections among the isolation points.

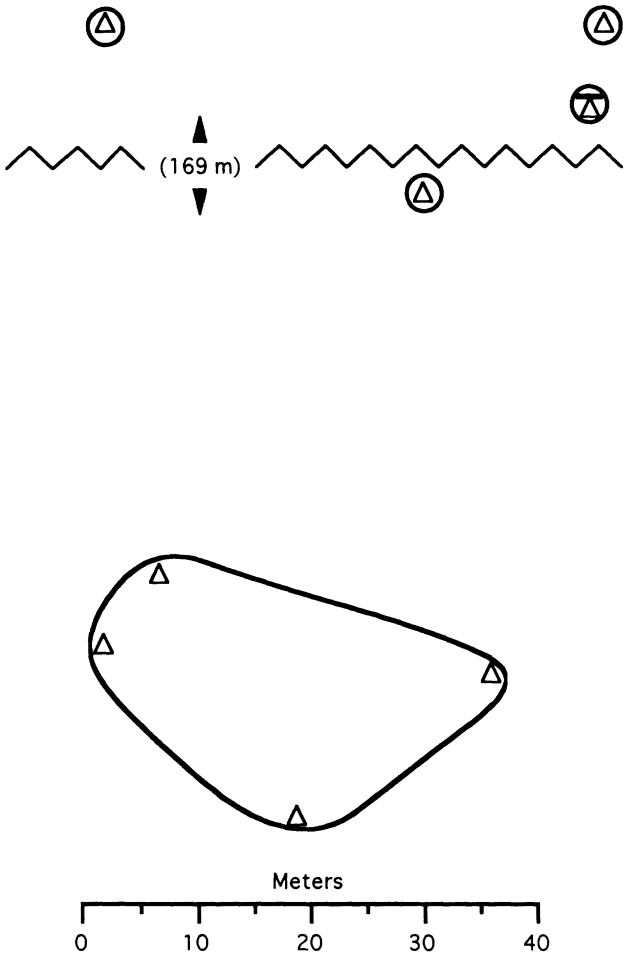

FIG. 4. Map of isolates and genets of *A. ostoyae* from plot in a plantation of Douglas-fir Christmas trees near Westernville, New York. Symbols represent live or recently killed trees (△) and rhizomorphs from soil (—). The zig-zag line indicates a distance of 169 m, not shown, in which no *Armillaria* was found. *Armillaria calvescens* was found in the adjacent hardwood stand.

(FIG. 5). The largest genet, 670 m^2, was adjacent to the access road. Smaller genets were found a bit farther into the stand and single-point genets were found scattered deeper into the stand. There was current mortality of both the overstory and of Scots pine regeneration caused by both large and small genets of *A. ostoyae*.

Bear Swamp (16 isolates, not shown) was a mixed conifer-hardwood stand supporting primarily *Abies balsamea* (L.) Mill. with some maple and cherry. One genet each of *A. calvescens* and *A. ostoyae* was found, one beside the other.

The Newcomb plot (11 isolates, not shown) was also a mixed stand. It supported 3 species of *Armillaria*. All isolates were from stumps, some of which were still alive, from a recent shelterwood cut. The largest genet (236 m^2) was *A. calvescens* and included several sound hardwood stumps and butt-rotted beech and sugar maple stumps. *Armillaria ostoyae* was found in a single, large, butt-rotted *Picea rubens* Sarg. (red spruce) stump. *Armillaria gemina* colonized several sound hardwood stumps in a small area. All cases of butt rot were apparently caused by the associated *Armillaria* sp.

Three *Armillaria* species were also found in the Allegany plot (13 isolates, not shown). The stand was dominated by sugar maple but also contained beech, cherry and hemlock. There was abundant mortality in the stand, not all of which could be attributed to *Armillaria*. The largest genet (77 m^2) was *A. gemina*. Several smaller genets of *A. calvescens* covered two or three trees, and *A. gallica* was found only as rhizomorphs near the edge of the plot.

In 33 cases, isolations were successful from both the

woody substratum and external rhizomorphs. This enabled a consideration of the frequency with which such pairs are the same species and the same genet. As expected, in most cases they were the same genet (13 pairs were *A. ostoyae,* 6 each *A. gemina* and *A. calvescens,* 2 *A. sinapina* Bérubé & Dessureault, and 1 *A. gallica*), but in five cases (15%) they were not. All of those cases involved pairs of different species. Three such cases involved *A. ostoyae* in the root and *A. calvescens* outside; these occurred in a stand of diseased balsam fir with a heavy admixture of hardwoods. In two cases *A. gemina* was found in the root, once with *A. calvescens* outside and once with *A. gallica.*

DISCUSSION

Sizes of genets determined here may be underestimates because of edge effects. However, it appears that the plots were sufficient to encompass the genets encountered. The largest genets found in the study, in the Westernville, Tully and Boonville plots, were about 5%, 20% and 12% of plot area, respectively, and their locations make it unlikely that they extended beyond plot boundaries.

Origin of new genets.—The frequency of small genets, especially those represented only by a single sample point, suggests that a mechanism operates to establish new genets. Diploid-haploid interactions could theoretically lead to genetic recombination, but evidence suggests that diploid nuclei simply replace haploid nuclei (Rizzo and Harrington, 1992), in which case any recombination would have to involve extranuclear genes. Mutation of established genets of *Armillaria* has been suggested to explain instances of anomalous variation in sexual or somatic incompatibility in nature (Korhonen, 1978; Rishbeth, 1991; Rizzo and Harrington, 1993). However, the large size of some apparently uniform genets has been cited as evidence against mutation as a source of new genotypes (Smith et al., 1992). Colonization by basidiospores, whose function in nature was once questioned, is now considered more likely (Hood and Sandberg, 1987; Kile, 1986; Korhonen, 1978; Rishbeth, 1970, 1978, 1988).

Although inoculation with basidiospores has met with poor or no success (Kile, 1986; Rishbeth, 1970), there are several lines of evidence for basidiospore establishment. Its occurrence in nature need not be frequent to dramatically influence distribution and population structure. The occurrence of unique, spatially isolated genets (Kile, 1986) is consistent with establishment via basidiospores. Colonization of wood during exclusion of rhizomorphs has been used as evidence for basidiospore establishment (Hood and Sandberg, 1987). The random distribution of isozyme

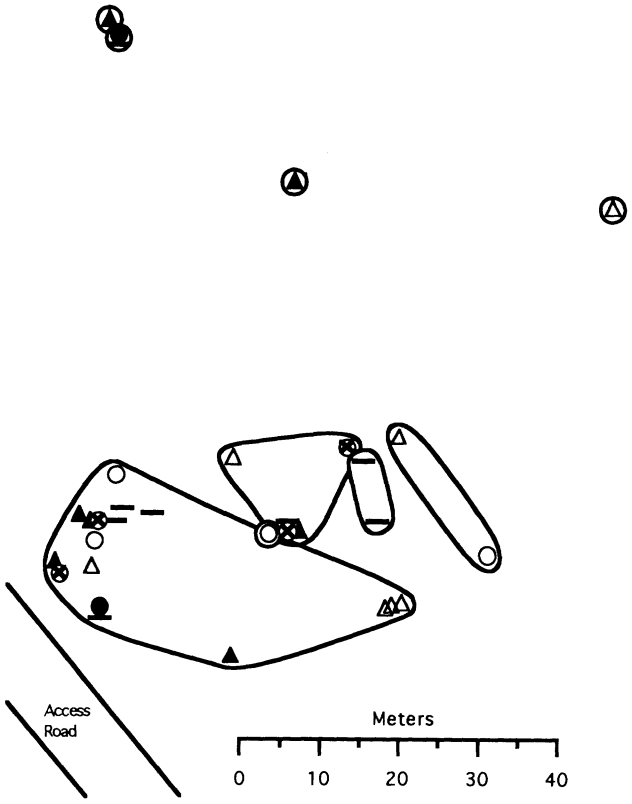

FIG. 5. Map of isolates and genets of *A. ostoyae* from plot in Scots pine stand near Boonville, New York. Symbols represent live (○) and dead (●) trees, live (△) and dead (▲) regeneration, stumps (⊗), and rhizomorphs from soil (—).

markers among SI groups is also consistent with basidiospore establishment (Rizzo and Harrington, 1993). Another source of evidence for basidiospore establishment is the occurrence of small, presumably young genets in areas putatively free of *Armillaria* in the recent past. Such evidence was found in the case of small genets in forests established on former agricultural or heathland (Rishbeth, 1978, 1988).

In the present study, two such stands were found. A Christmas tree plantation established on a hardwood site was infested with *A. ostoyae,* with mostly small genets. In New York, *A. ostoyae* is generally found only in stands with a high relative density of conifers (Blodgett and Worrall, 1992b), and *A. calvescens,* the most common species in northern hardwoods, was isolated from the adjacent natural vegetation. Although it is possible that *A. ostoyae* was present in association with scattered conifers in the hardwood stand before clearing, the small, widely distributed genets make basidiospore establishment a much more likely explanation.

The other stand providing evidence for basidiospore colonization, Boonville, also involved *A. ostoyae.* The area was all potato fields before 1930, although oc-

casional landscape trees cannot be ruled out. Pines were planted after the potato farms were abandoned. The first subsequent management activity was a thinning in 1977. There have been several partial harvests since then, partly in response to an epidemic of Scleroderris canker.

Although *Armillaria* has been noted on potato in rare circumstances (Hood et al., 1991), the long-term maintenance of multiple genets in this way must be considered very unlikely. Considering published estimates of radial growth rates of genets, which vary from 0.06 to 1.6 m/yr (Rishbeth, 1978; Smith et al., 1992), the largest and presumably oldest genet was probably initiated shortly after stand establishment. It was located along the access road, where unmanaged removals (e.g., for Christmas trees) would be most likely. The resulting stumps or dead roots would be suitable infection courts for basidiospores (Rishbeth, 1970, 1978). Over the years, occasional removals may have occurred somewhat deeper in the stand, leading to establishment of the genets there of generally intermediate size. Beginning in 1977, managed removals of dominant trees would permit establishment of the very small genets scattered deeper in the stand.

The occurrence of *Armillaria ostoyae* in these planted stands where its prior presence was unlikely, together with the frequent occurrence of small, single-point genets, supports the concept that basidiospores play a role in establishing new genets and shaping population structure.

Development of genets.—In the samples studied here, the frequency of genets of *Armillaria* species dropped abruptly above the smallest size class and was followed by a flat distribution. In general, it is assumed that genet size is related to age (Rishbeth, 1978; Smith et al., 1992). Because samples were taken from many different stands, a recent, unusual episode of genet establishment is unlikely as an explanation for the abundant, small genets. If the population is at a steady state, it appears that expansion of genets beyond the initial resource unit is a critical phase in their development. They may be exceptionally vulnerable before that point, so that survivorship drops very rapidly before expansion. Alternatively, the first step of expansion to a new resource unit may be a relatively rare event, and many persist on their initial resource unit until it is exhausted. However, the assumption that size is related to age is tenuous in this regard because small genets may represent remnants of old, formerly large genets. Further data, especially relating age to size for small and young genets, will be necessary to interpret this structure.

Interactions among genets and species.—The greater density of genets in plots with more species is consistent with the concept that the species occupy somewhat distinct niches (Rizzo and Harrington, 1993). Mixed conifers and hardwoods can explain niche differentiation between *A. ostoyae* and sympatric species. *A. gallica* is often associated with oaks in mixed stands, and *A. calvescens* is a regular associate of maples (Blodgett and Worrall, 1992a). *Armillaria gemina* is found in stands with relatively heavy amounts of beech (Blodgett and Worrall, 1992b). Niche differentiation by virulence, mode of host mortality, etc., is also possible.

In heterogeneous stands, the niches may be patchily distributed or may overlap to a larger extent. Considerable overlap among *Armillaria* species found in one plot in New Hampshire (Rizzo and Harrington, 1993) may represent intimately overlapping niches. In an extreme case, each species occupies its own "layer" of the forest with independent opportunities for establishment and growth.

In this study, the negligible overlap among species is consistent with patchy distribution of niches in these stands, i.e., niches are partitioned spatially to a greater degree. In this case, expansion of a genet would be limited by the patchiness of suitable niches. Because isolated, uncolonized patches of suitable niche may be most readily colonized via air, such discontinuity may increase opportunities for basidiospore establishment.

Rhizomorph-root pairs.—Since clones of *Armillaria* can enlarge to encompass many trees and stumps, my finding that isolates from within roots are usually the same as isolates from superficial rhizomorphs is expected. Cases in which different species were found inside vs. outside the roots, however, show that species may overlap locally at least to some extent but may remain differentiated by substrate. Siepmann (1985) and Rizzo and Harrington (1993) also found several cases in which one species was isolated from decay and another species was isolated from superficial rhizomorphs. Such cases also emphasize the importance of obtaining isolates from inside roots when attempting to isolate a pathogen.

Regional and stand factors.—In general, these genets are intermediate in size and density compared to those from other areas (Hood and Sandberg, 1987; Kile, 1983, 1986; Shaw and Roth, 1976; Smith et al., 1992). Genet densities in those studies range from about 1/ha or less to well over 50/ha. Observations suggest that high moisture levels may be critical to successful establishment of basidiospores (Rishbeth, 1970). In the arid conditions of portions of western North America (Adams, 1974; Shaw and Roth, 1976) and dry sclerophyll eucalypt forests of southern Australia (Kile, 1983), large, infrequent genets appear to be the common state. In wet sclerophyll eucalypt forests of Tasmania (Kile, 1986) and in New Zealand (Hood and Sandberg,

1987), small frequent genets predominate. In this study and in others from the northeastern United States (Rizzo and Harrington, 1993; Ullrich and Anderson, 1978), the population status was intermediate between those extremes, as is the climate.

In studies cited above, very low densities of clones correspond with very large clones. In this study, the lowest densities were in the two conifer plantations where most genets were fairly small and probably of recent origin. These stands are in the early stages of colonization by *Armillaria*. As time passes, the genets can be expected to get larger and/or more dense. Thus land use history and forest management can affect the population structure of *Armillaria* species.

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