Effects of defoliation and cutting in eastern oak forests on *Armillaria* spp. and a competitor, *Megacollybia platyphylla*

E.A. Burrill, J.J. Worrall, P.M. Wargo, and S.V. Stehman

Abstract: Gypsy moth (*Lymantria dispar* L.) and Armillaria root rot interact to cause extensive mortality in eastern oak forests. Defoliation by gypsy moth weakens trees and increases their susceptibility to Armillaria root rot. Partial cutting prior to defoliation has been proposed as a management technique because it may increase tree vigor and the ability to withstand defoliation stress. However, cutting could also increase inoculum potential of *Armillaria* by providing a resource, the residual stumps. *Megacollybia platyphylla* (Pers.:Fr.) Kotl. & Pouz. is a native, cord-forming, saprobic fungus that may compete with *Armillaria* for resources such as stumps, snags and debris. A factorial treatment design with three levels of cutting and three levels of defoliation was used to examine the effects of cutting and defoliation on the two fungi. Among uncut stands, defoliated stands had significantly greater colonization of resource units by *Armillaria* than nondefoliated stands. However, stands that were cut prior to defoliation had significantly less *Armillaria* colonization and significantly more *M. platyphylla* colonization than those that were not cut. *Armillaria* colonized snags better than stumps and colonized least well in debris, where *M. platyphylla* showed its best colonizing performance. The data suggest that cutting mitigates the effects of defoliation on colonization by *Armillaria* and are consistent with the hypothesis that *M. platyphylla* plays a role in such mitigation.

Résumé : La spongieuse (*Lymantria dispar* L.) et l'armillaire, en agissant conjointement, causent beaucoup de mortalité dans les forêts de chênes de l'Est. La défoliation par la spongieuse affaiblit les arbres et augmente leur susceptibilité à la carie de racine causée par l'armillaire. La coupe partielle avant une défoliation a été proposée comme méthode d'aménagement parce qu'elle peut augmenter la vigueur des arbres et leur capacité à supporter le stress causé par la défoliation. Cependant, la coupe peut également augmenter le potentiel d'inoculum de l'armillaire en lui procurant une source de nourriture dans les souches résiduelles. Le *Megacollybia platyphylla* (Pers.:Fr.) Kotl. & Pouz. est un champignon saprophyte indigène qui forme des rizomorphes et peut compétitionner avec l'armillaire pour des sources de nourriture comme les souches, les chicots et les débris. Un dispositif factoriel avec trois niveaux d'éclaircie et trois intensités de défoliation a été utilisé pour étudier les effets de l'éclaircie et de la défoliation sur les deux champignons. Parmi les peuplements non éclaircis, il y avait significativement plus d'unités de source de nourriture qui étaient colonisées par l'armillaire dans les peuplements défoliés que dans les peuplements non défoliés. Cependant, les peuplements qui avaient été éclaircis avant la défoliation étaient significativement moins colonisés par l'armillaire et significativement plus colonisés par le *M. platyphylla* que ceux qui n'avaient pas été éclaircis. L'armillaire colonisait mieux les chicots que les souches et moins bien les débris dans lesquels le *M. platyphylla* réussissait sa meilleure performance de colonisation. Les résultats suggèrent que l'éclaircie atténue les effets de la défoliation sur la colonisation par l'armillaire et supportent l'hypothèse que le *M. platyphylla* joue un rôle dans cette mitigation.

[Traduit par la rédaction]

Introduction

Defoliation by gypsy moth, *Lymantria dispar* L., is a major cause of tree stress in oak forests of the eastern United States. Although mortality may be caused by defoliation alone, it is usually due to colonization of weakened trees by secondary agents such as the two-lined chestnut borer, *Agrilus bilineatus* Weber, or *Armillaria* (Dunbar and Stephens 1975; Wargo 1977).

Various silvicultural treatments have been recommended to reduce susceptibility of oak stands to defoliation and vulnerability to damage. Partial cutting prior to defoliation can be used to render a stand less susceptible to defoliation (sanitation thinning) by altering the species composition, to improve the vigor of residual trees so they are less vulnerable to secondary organisms, and to remove trees likely to die (presalvage thinning) (Gottschalk 1993, 1997; Gottschalk et al. 1988). Cutting is not recommended if defoliation is expected within the next 5 years because trees can suffer from cutting shock for 3–5 years (Gottschalk 1987; Twery and Gottschalk 1989). During this time of recovery, trees may be

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more vulnerable to other stresses and mortality may occur after defoliation. There is also some concern that stumps left after cutting may support additional growth of *Armillaria*, increasing inoculum potential and subsequent mortality (Hood et al. 1991; Rishbeth 1972). Indeed, the consensus of foresters is that mortality following defoliation is higher in cut stands than in uncut stands (Gottschalk 1989). However, in a comparison of cut stands to uncut stands, cutting had no significant effect on post-defoliation mortality (Gottschalk 1989).

Biological control of root and butt rots has often been considered and has been successful in some situations (Rishbeth 1975). Indirect (or integrated) biological control, management of the ecosystem so as to favor naturally occurring antagonists, is more complex and less studied than direct application of antagonists but may have broader potential (Shaw and Roth 1978). The cord-forming fungus *Megacollybia platyphylla* (Pers.:Fr.) Kotl. & Pouz. (=*Tricholomopsis platyphylla* (Pers.:Fr.) Sing.) shows a similar distribution, occupies a similar ecological niche and spreads by means similar to *Armillaria* (Chapela and Boddy 1988; Rayner 1979; Thompson and Boddy 1983; Thompson and Rayner 1982). Both fungi can spread through soil, grow subcortically, and utilize dead woody material. *Megacollybia platyphylla* can overgrow *Armillaria gallica* Maxmüller & Romagn., and *Armillaria ostoyae* (Romagn.) Herink in vitro (Thompson and Boddy 1983). Evidence suggested that *Armillaria calvescens* Bérubé and Dessur. and *M. platyphylla* compete for stumps after thinning in a northern hardwood forest (Worrall 1991).

The objective of this study was to determine the effects of cutting and defoliation on the relative abundances of *M. platyphylla* and *Armillaria* in mixed oak stands.

Materials and methods

Region and forest types

Field work was conducted in southcentral Pennsylvania and adjacent portions of West Virginia and Maryland. The predominant forest cover in this region is upland oak–hickory, the most extensive forest cover type in the contiguous United States (Burns 1983). It is found on all topographic positions from dry, rocky ridges to deep coves and well-drained valley floors, and is on varied soil types. Oak–hickory in this sense is usually defined as stands in which upland oaks, red maple (when associated with central hardwoods) or hawthorn, singly or in combination, make up a plurality of the stocking (DiGiovanni 1990; Widman 1995). Common associates include maples, yellow-poplar (*Liriodendron tulipifera* L.), and hickories. All of the forests in this study fit this type. In an applied program of hardwood management in the Allegheny Mountains (Marquis and Ernst 1992), our stands fit into two types. The first, oak–hickory, is defined as stands in which at least 65% of the basal area is in any oak or hickory species. The second, transition hardwood, is defined as stands in which at least 65% of the basal area is in any species of the oak–hickory or northern hardwood types, but the stand qualifies for neither type alone. Northern hardwood stands have at least 65% of the basal area in sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), sweet birch (*Betula lenta* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), American basswood (*Tilia americana* L.), cucumber-tree (*Magnolia acuminata* L.), black cherry (*Prunus serotina* Ehrh.), white ash (*Fraxinus americana* L.), or yellow-poplar. Transition hardwood stands in some areas are referred to as Appalachian mixed hardwoods or cove hardwoods.

Detailed stand analysis was available from the USDA Forest Service Northeastern Forest Experiment Station in Morgantown, W.Va., for 19 of the 28 stands in our study. Primary species of the oak–hickory group in our stands were (in order of importance) chestnut oak (*Quercus prinus* L.), northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), hickory species, and scarlet oak (*Quercus coccinea* Muenchh.). Primary species of the northern hardwood group were red maple, yellow-poplar, black cherry, sugar maple, and birch species. In our stands of the oak–hickory type, relative basal area of the oak–hickory and northern hardwood species were 70–95% and 2–30%, respectively. In stands of the transition hardwood type, relative basal area of the oak–hickory species was 31–61%; that of the northern hardwood species was 30–54%. The remaining nine stands were classified based on cruise data of local foresters.

Study design

Twenty-eight stands were classified according to cutting and defoliation classes (Table 1). Twenty-four of these stands formed a 3 × 3 factorial treatment arrangement consisting of three levels of cutting (not cut, cut 1985–1990, and cut 1979–1984) and three levels of defoliation (no or light defoliation (<30%), 1 year moderate to heavy defoliation (>30%), and 2 or 3 years moderate to heavy defoliation with defoliation occurring from 1985 to 1989). Four additional stands received 2 years moderate to heavy defoliation in 1990–1991; these were not part of the factorial arrangement but were used in other analyses. The defoliation estimates were made from aerial photos and sketch maps by the U.S. Forest Service and (or) state forestry agencies. Stands designated as lightly defoliated were classified in the no or light defoliation class because <30% defoliation on a stand-wide basis is not always discernible from aerial estimates. Stands that were cut had acceptable growing stock above the B level (Roach and Gingrich 1968) before cutting and between B and C levels after cutting except for one stand (2-83BC1) that had acceptable growing stock below the C level after cutting.

For the purposes of study design, stand susceptibility to defoliation and defoliation can be considered to be the same factor. Because of gypsy moth host preferences, stands with a relatively high basal area of species from the northern hardwood group are less likely to be defoliated than stands with high basal area of oak–hickory species. In our treatment classification, therefore, the defoliated stands were Oak–hickory and most of the nondefoliated stands were transition hardwood. It is impractical and unrealistic to do an experiment in which intentional defoliation is applied to randomly selected stands of either type. As in all retrospective field studies, where it is impossible to assign the treatments to the experimental units in a randomized fashion, observed effects can only be regarded as associated with the treatment factors and directly establishing causality for the treatment factors is not possible.

Data collection

Six plots (10 × 10 m) were systematically located within each stand (Burrill 1994) and sampled in 1993. We recorded the diameter of all stumps and standing dead and dying trees (referred to here as snags) with a minimum diameter of 10 cm at approximately 15 cm above the soil line. In a band from 5 cm above the soil line to 10 cm below the soil line, we removed the bark and examined the subcortical region for evidence of colonization by *Armillaria* and *M. platyphylla*. Degree of colonization by each fungus was estimated as a percentage of the area of the inspected 15-cm band of each stump or snag. Woody debris units (downed material such as fallen branches and stems) with a diameter of at least 10 cm at some point of their length were also examined. Any

Table 1. Type, location, cutting, and defoliation classes of stands sampled for colonization and rhizomorph density of *Armillaria* and *Megacollybia platyphylla*.

		Defoliation 1985–1989 (>30%)		Defoliation 1990–1991 (>30%)
	No defoliation or light defoliation (<30%)	Defoliated 1 year	Defoliated 2 or 3 years	Defoliated 2 years
Not Cut	TWERY 2; TH; Monongalia, WV TWERY 5; TH; Monongalia, WV WLCR 167; TH; Mifflin, PA WLCR 168; OH; Mifflin, PA	BR 11; OH; Fulton, PA BR 12; OH; Fulton, PA	BEC 17; OH; Bedford, PA WT 36; OH; Fulton, PA WT 37; OH; Fulton, PA	TWERY 8; OH; Preston, WV TWERY 14; OH; Preston, WV
Cut 1985–90	SF 46; TH; Garrett, MD TWERY 1; TH; Monongalia, WV TWERY 3; TH; Monongalia, WV TWERY 9; TH; Monongalia, WV	4-86 BC1; OH; Somerset, PA 4-85 BC7; OH; Somerset, PA	NS	TWERY 7; TH; Preston, WV TWERY 13; OH; Preston, WV
Cut 1979–84	CH 2; TH; Bedford, PA CH 3; OH; Bedford, PA MC10; OH; Fulton, PA SF 36; TH; Garrett, MD	2-83 BC1; OH; Bedford, PA 4-81 BC3; OH; Somerset, PA 4-79 BC6; OH; Somerset, PA SF 41; OH; Garrett, MD	CH 7; OH; Bedford, PA	NS

Note: The first three columns form the 3 x 2 factorial treatment design that was analyzed. The final column is not part of the treatment design, but those stands were used in correlation analyses and in analysis of colonization by resource type (stumps, snags, or debris). Stand type and county and state are indicated for each stand. MD, Maryland; PA, Pennsylvania; WV, West Virginia; OH, oak–hickory; TH, transition hardwood. NS, no stands were located that fit this combination of cutting and defoliation status.

portion of the debris unit that was greater than 4 cm, in ground contact, and inside the plot boundaries was examined for colonization by *Armillaria* or *M. platyphylla* by overturning the unit and estimating the proportion of the length colonized by each fungus.

Estimates of the percent colonization of individual stump, snag, and debris units were averaged over each stand. The result is hereafter referred to as "mean degree of colonization (%)" or simply "colonization."

Armillaria was identified based on subcortical mycelial mats, rhizomorphs, and white rot with characteristic zone lines (Morrison et al. 1991). Although it was impractical to identify *Armillaria* to species in this extensive field study, several prior studies have shown that *Armillaria gallica* Maxmüller & Romagn. is by far the dominant species of *Armillaria* in this forest type and region. In surveys of oak–hickory forests, collections in 21 of 23 stands and isolations from 28 of 31 trees of *Quercus* spp. were *A. gallica* (Blodgett and Worrall 1992). In plots (100 × 200 m) in six stands of the Tuscarora State Forest of south-central Pennsylvania, the site of the WLCR plots in the current study (Table 1), *A. gallica* was the dominant or sole species of *Armillaria* (Wargo 1993; P.M. Wargo, unpublished data). All other plots used in the current study are in the same ridge and valley province and physiographic region and have a similar forest cover type. Indeed, branching patterns of rhizomorphs from plots in the current study were monopodial, also suggesting *A. gallica* as the dominant species. *Megacollybia platyphylla* was identified based on the presence of characteristic subcortical fungal mats, whitish rhizomorphs, and white rot. Although the mycelial cords produced by *M. platyphylla* do not fit some strict definitions of "rhizomorphs" (Rayner and Boddy 1988), we will use that term for simplicity of expression. Samples were taken of fungal growth in cases where identification was questionable. Isolations were made and cultures were identified by macroscopic and microscopic characteristics.

Rhizomorph sampling

Five soil samples per plot (20 × 20 cm), located at the four corners and plot center were excavated to a depth of 20 cm and examined for rhizomorphs of *Armillaria* and *M. platyphylla*. The rhizomorphs were removed from the soil, bagged, and labeled. Later they were separated by fungal type, cleaned with water, dried for 48 h in a fruit dryer, and stored. They were dried again for 2–3 h at 100°C before weighing. Total masses were summed for each plot and expressed as rhizomorph density ($kg \cdot ha^{-1}$). Mean density was calculated by averaging the six plot values for each stand.

Pairings in vitro

Two isolates each of *Armillaria gallica*, (Nos. 101 and 102, obtained from Finger Lakes National Forest, New York) and *M. platyphylla* (No. HU-2, from Hustontown, Pa., and No. WT1, from Wells Tannery, Pa.), were paired on malt extract agar (MEA; 1.5% w/v). Inoculum plugs were placed 5 cm apart. Five replicates were used; unpaired isolates were used as controls. Plates were incubated at 22°C in the dark. Observations were made on growth by each fungus and apparent interactions. Isolations from areas where *M. platyphylla* grew over *A. gallica* were taken randomly from the overgrown area.

Statistical analysis

The experimental unit for this study was a stand. Therefore, for analysis of variance (ANOVA) the response variables analyzed are percent colonization and rhizomorph density ($kg \cdot ha^{-1}$) averaged at the stand level. A square-root transformation was applied to percent colonization estimates to diminish the effect of unequal variances.

Because of the defoliation and cutting characteristics of available stands, one cell of the intended 3 × 3 factorial had no stands, and the treatments in the other cells were not equally replicated. To

Table 2. Effect of cutting and defoliation on percent colonization of all resource types (stumps, snags, and debris) by *Armillaria* and *Megacollybia platyphylla*: ANOVA for 2 × 2 factorial subset.

		Armillaria		*Megacollybia platyphylla*	
	df	Type III SS	*P*	Type III SS	*P*
Cutting	1	0.40	0.530	0.27	0.637
Defoliation	1	7.09	0.014	1.38	0.293
Interaction	1	10.33	0.004	4.50	0.066
Residual	20	19.53		23.68	

Note: Cutting levels were not cut and cut (combining both cutting periods). Defoliation levels were not defoliated and defoliated (combining both 1 year and 2 or 3 years defoliation, 1985–1989). Variates for this analysis were the square roots of stand means.

compensate for the empty treatment combination, the analysis focused on subsets of the treatment structure representing complete factorial arrangements (Stehman and Meredith 1995). One subset consisted of the 3 × 2 factorial when the stands defoliated 2 or 3 years were removed from the analysis. The second subset analyzed was created by collapsing the treatment structure into a 2 × 2 factorial in which the two 1985–1989 defoliation levels were combined and the two cutting levels (cut 1985–1990 and cut 1979–1984) were also combined. For both subsets, the main effects of the cutting and defoliation treatments, along with their interaction, were evaluated. The 3 × 2 subset analysis permits more detailed assessment of the defoliation treatment because it incorporates 3 levels of this treatment factor. The 2 × 2 subset analysis was selected because it uses more of the stands and consequently has more statistical power to detect treatment effects. This 2 × 2 factorial analysis permits comparison of cutting versus no cutting, and defoliated versus nondefoliated, along with the interaction of these two factors.

Because of the unequal replication feature, type III sums of squares were used to evaluate main effect and interaction contrasts. Statistically significant interaction effects ($\alpha = 0.20$) were followed by examination of simple effects. The high significance level for the interaction tests ($\alpha = 0.20$) was selected to improve power to detect interaction if present (Stehman and Meredith 1995). Because most of the biologically interesting simple effects were pairwise comparisons of means, Fisher's protected least squares difference was used to provide control of the experimentwise error rate at $\alpha = 0.05$ for each subset analysis.

Colonization was compared among the three resource types (stumps, snags, and debris), with a separate analysis conducted for *Armillaria* and *M. platyphylla*. Mean degree of colonization (%) of each resource type was computed for each experimental unit (stand). For each pair of resource types (e.g., stumps versus snags), the difference in colonization was evaluated via a paired *t* test. The paired *t* test accounts for any within-stand correlation of the colonization responses for the different resource types. Analyses were conducted using SAS (version 6.11) or SuperANOVA.

Kendall's nonparametric rank correlation analysis was performed to assess correlation between *Armillaria* and *M. platyphylla* colonization on all resources considered together. Similarly, the correlation between rhizomorph densities ($kg \cdot ha^{-1}$) of the two fungi at the plot level was also computed.

Results

Effects of cutting and defoliation on colonization

In the 2 × 2 analysis (Table 2), the significant interaction between cutting and defoliation for both *Armillaria* (p = 0.004) and *M. platyphylla* (p = 0.066) demonstrated that the effect of defoliation depended on whether the stand had been cut. Simple effect comparisons (Table 3) showed that, among uncut stands, the effect of defoliation was greater colonization by *Armillaria* (p < 0.01). This defoliation effect was reversed in the cut stands, where *Armillaria* colonization was higher in the nondefoliated stands (although this simple effect was not significant). Considering only defoliated stands, colonization by *Armillaria* was significantly lower in the cut than in the uncut stands (p = 0.02). However, in nondefoliated stands, the effect of cutting was greater *Armillaria* colonization, although the difference was not significant. For *M. platyphylla*, simple effect comparisons showed that defoliation was associated with a statistically significant (p < 0.01) increase in colonization in the cut stands, but the defoliation effect was not significant in the uncut stands. Cutting was associated with an increase in colonization of *M. platyphylla* in defoliated stands (p = 0.01), but the effect of cutting was not significant in the nondefoliated stands.

The 3 × 2 subset analysis permits a more detailed assessment of the cutting treatment because time of cutting enters the analysis. The significant interaction between cutting and defoliation for both *Armillaria* (p = 0.009) and *M. platyphylla* (p = 0.048) again demonstrated that the effect of defoliation depended on whether the stand was cut (Table 4). The nature of this interaction effect is revealed by the simple effect comparisons (Table 5). Among nondefoliated stands, the earlier cut (1979–1984) was associated with significantly higher *Armillaria* colonization than either the more recent cut (1985–1990) or the uncut stands. Among stands defoliated 1 year, higher *Armillaria* colonization occured in the uncut stands than in cut stands. The pattern in the effect of defoliation over the different cutting treatments matched that described in the 2 × 2 subset analysis. Defoliation was associated with a significant increase in *Armillaria* colonization in the uncut stands, but a significant effect of defoliation was not observed in either of the two cutting treatments.

The simple effect comparisons for *M. platyphylla* (Table 5) showed that in nondefoliated stands, the effect of cutting was not statistically significant, although the cutting treatments both had lower percent colonization than the uncut stands. For defoliated stands, cutting had a significant effect, with the earlier cut (1979–1984) associated with significantly higher colonization than the uncut stands. The more recent cut (1985–1990) also had higher colonization than the uncut stands, but the difference was not significant. The two cutting times produced nearly the same percent colonization. A significant increase in percent colonization was observed for the defoliated stands in the early cutting treatment (1979–1984), but the effect of defoliation was not significant within the other two levels of the cutting factor.

In summary, stands that were either defoliated or cut (but not both) had colonization by *Armillaria* that was generally greater than in stands that experienced no cutting and no defoliation. However, stands that were both defoliated and cut did not have greater *Armillaria* colonization than did uncut, nondefoliated stands. *Megacollybia platyphylla* generally showed an opposite pattern, i.e., stands that were only defoliated or only cut had lower colonization, but stands both defoliated and cut had higher colonization than other stands.

Table 3. Effect of cutting and defoliation on percent colonization of all resource types (stumps, snags, and debris) by *Armillaria* and *Megacollybia platyphylla*: means and simple effects for a 2 × 2 factorial subset.

	Armillaria		*Megacollybia platyphylla*	
	No defoliation	Defoliated	No defoliation	Defoliated
Not cut	3.1±1.7*a*	17.2±4.9*b*	16.1±2.5*yz*	14.6±4.5*y*
Cut	7.4±1.7*a*	5.4±0.5*a*	11.3±1.8*y*	23.3±4.4*z*

Note: Values are means ± SE. Cut stands include those from both cutting periods. Defoliated stands include both 1 year and 2 or 3 years defoliation, 1985–1989. For each fungus, means followed by the same letter are not significantly different (Fisher's Protected LSD, α = 0.05).

Table 4. Effect of cutting and defoliation on percent colonization of all resource types (stumps, snags, and debris) by *Armillaria* and *Megacollybia platyphylla*: ANOVA for a 3 × 2 factorial subset.

		Armillaria		*Megacollybia platyphylla*	
	df	Type III SS	*P*	Type III SS	*P*
Cutting	2	1.60	0.287	1.11	0.523
Defoliation	1	1.18	0.177	3.91	0.046
Interaction	2	7.95	0.009	6.22	0.048
Residual	14	8.19		11.4	

Note: Cutting levels were not cut, cut 1985–1990, and cut 1979–1984. Defoliation levels were not defoliated and defoliated 1 year 1985–1989. Variates for this analysis were the square roots of stand means.

Rhizomorphs

The ANOVA of rhizomorph density in the 3 × 2 analysis revealed weak interaction between cutting and defoliation for both *Armillaria* and *M. platyphylla* (p = 0.19 in both cases; ANOVA table not shown). As with colonization, however, the responses of the two fungi were generally opposite (Table 6). Nondefoliated stands that were cut early had much higher density of *Armillaria* than uncut (p = 0.03) or recently cut stands (p = 0.01). Similarly, among uncut stands, defoliated stands had more *Armillaria* rhizomorphs than nondefoliated stands (p = 0.05).

In contrast, defoliation and early cutting alone were not associated with an increase in *M. platyphylla* but rather a nonsignificant decrease, compared with stands with neither cutting nor defoliation. The main effect of cutting was significant for *M. platyphylla* (p = 0.01), primarily because recently cut stands had higher densities of rhizomorphs than other stands. This was especially true in recently cut stands that were defoliated, which had significantly more rhizomorphs than uncut, defoliated stands (p = 0.05).

Variation among resource types

The three resource types (debris, stumps, and snags) differed substantially in degree of *Armillaria* colonization, with snags being the highest and debris being significantly lower (Table 7). In contrast, *M. platyphylla* colonized debris more than other resource types and significantly more than stumps.

Correlations

The Kendall correlation between rhizomorph densities of *Armillaria* and *M. platyphylla* at the plot level was –0.14 (p = 0.01). The Kendall correlation between percent colonization by *Armillaria* and *M. platyphylla* on all resources was –0.07 (p < 0.01). These correlations are biologically weak, although statistically significant.

Pairings in vitro

In pairings between *M. platyphylla* and *Armillaria gallica*, both fungi initially formed circular colonies. *Armillaria gallica* colonies and surrounding agar were brownish. *Megacollybia platyphylla* colonies were whitish and grew faster than those of *A. gallica*. *Armillaria gallica* colonies remained circular, but *M. platyphylla* became invaginated on the side of the colony closest to *A. gallica* after 5 days, before contact between the two fungi. At about 8 days, when the colonies were 1–2 mm apart, *A. gallica* colony edges became a darker brown.

Megacollybia platyphylla colonies then overgrew *A. gallica* in all pairings within 2 weeks and ultimately covered them completely. Bleaching of *A. gallica* colonies frequently occurred when they were overgrown with *M. platyphylla*. No parasitism of *A. gallica* hyphae by *M. platyphylla* hyphae was observed by microscopic examination. *Armillaria gallica* and *M. platyphylla* hyphae were distinguishable because *M. platyphylla* had clamp connections and smaller hyphae; *A. gallica* lacked clamp connections. In 104 isolations from overgrown *A. gallica* colonies, *M. platyphylla* was isolated 88 times (85%) and *A. gallica* 6 times (6%).

Discussion

Colonization

The interdependence that we observed between cutting and defoliation in association with *Armillaria* colonization may have important implications for management and should be understood clearly. Whereas either factor alone was associated with greater *Armillaria* colonization than in undisturbed stands, the combination yielded generally lower levels of *Armillaria* colonization. In other words, defoliation was associated with an increase of *Armillaria* in uncut stands, but a decrease in cut stands. As a result, stands cut prior to defoliation had significantly less *Armillaria* colonization than those not cut.

Based on positive reports from eastern Africa, Redfern (1968) tested ring barking and poisoning trees years before felling to see if colonization by *Armillaria* was reduced compared with trees felled while alive. It was thought that exhaustion of carbohydrates in the treated trees would make them poor substrates for *Armillaria* and (or) that other fungi could better compete under those conditions. However, roots of treated trees were actually colonized more than control

Table 5. Effect of cutting and defoliation on percent colonization of all resource types (stumps, snags, and debris) by *Armillaria* and *Megacollybia platyphylla*: means for all treatments and simple effects for a 3 × 2 factorial subset analysis.

	No defoliation	Defoliated 1985–1989: Defoliated 1 year	Defoliated 1985–1989: Defoliated 2 or 3 years*	Defoliated 1990–1991, 2 years*
Armillaria				
Not cut	3.1±1.7*a*	13.2±4.9*b*	19.8±7.9	8.9±8.6
Cut 1985–1990	3.9±1.6*a*	5.2±0.5*ab*	NS	4.7±1.3
Cut 1979–1984	10.9±1.6*b*	5.1±0.7*ab*	7.2	NS
Megacollybia platyphylla				
Not cut	16.1±2.5*xyz*	12.5±8.0*xy*	15.9 ±6.5	15.2±13.6
Cut 1985–1990	13.8±3.1*xy*	24.8±5.6*yz*	NS	27.1±1.7
Cut 1979–1984	8.8±1.1*x*	26.7±5.9*z*	6.8	NS

Note: Values are treatment mean ± SE. For each fungus, means followed by the same letter are not significantly different (Fisher's Protected LSD, α = 0.05) for the 3 × 2 subset analysis. NS, no stands fit this combination of cutting and defoliation status.
*These columns were not included in the 3 × 2 subset and simple effect analysis.

Table 6. Effect of cutting and defoliation on mean rhizomorph densities (dry kg·ha^{-1}) of *Armillaria* and *Megacollybia platyphylla*.

	Armillaria: No defoliation	*Armillaria*: Defoliated 1 year	*Megacollybia platyphylla*: No defoliation	*Megacollybia platyphylla*: Defoliated 1 year
Not cut	19.6±5.7*a*	82.0±17.0*b*	4.3±1.4*y*	2.4±0.5*y*
Cut 1985–1990	7.2±2.9*a*	43.4±6.3*ab*	10.5±2.7*yz*	16.2±12.2*z*
Cut 1979–1984	76.6±31.6*b*	42.8±16.7*ab*	3.9±0.8*y*	6.9±3.4*yz*

Note: Values are treatment mean ± SE. For each fungus, means followed by the same letter are not significantly different (Fisher's Protected LSD, α = 0.05).

Table 7. Percent colonization of three resource types by *Armillaria* and *Megacollybia platyphylla*.

	Resource type: Debris	Stumps	Snags
Armillaria	4.4±0.7*a*	9.7±3.2*ab*	12.4±2.7*b*
Megacollybia platyphylla	18.9±2.3*y*	13.7±2.5*z*	14.2±2.8*yz*

Note: Values are means ± SE of resource units calculated over each stand. Within each row, means followed by the same letters are not significantly different by paired *t* test (α = 0.05; 27 df, except for comparisons involving stumps, which were based on 24 df because stumps were absent in some stands).

trees. Defoliation in our system may function much like ring barking in Redfern's study. Both deplete storage reserves in roots (Wargo 1972, 1981*a*, 1981*b*), and both increase *Armillaria* colonization (Wargo 1972, 1981*a*).

Colonization by *M. platyphylla* was analyzed to determine whether it tended to increase with decreased *Armillria* colonization. This would help explain why *Armillaria* colonization was low in cut, defoliated stands. The combination of cutting and defoliation may favor *M. platyphylla*, which excludes *Armillaria* from potential resources.

For *M. platyphylla*, interaction between cutting and defoliation was significant. However, in contrast to *Armillaria*, *M. platyphylla* colonization was higher in stands cut and defoliated than either uncut, defoliated or cut, nondefoliated stands. This pattern is the opposite of that for *Armillaria* colonization. Thus, in defoliated stands, cutting was associated with less *Armillaria* and more *M. platyphylla* than the absence of cutting.

The data suggest that cutting prior to defoliation mitigated the effects of defoliation on *Armillaria* colonization. Further, the results are consistent with the hypothesis that *M. platyphylla* replaced or excluded *Armillaria* in stands that were cut and defoliated.

Resource types

Armillaria did not colonize debris well. Stumps were a significantly better resource type, followed by snags. This is consistent with our understanding of *Armillaria* as a root pathogen and primary colonizer of roots and butts of dying trees (Thompson and Boddy 1983). Snags were the resource type most selective for *Armillaria*. It is the only resource type in which *Armillaria* colonization was as great as that of *M. platyphylla*. Because they can invade living trees, *Armillaria* spp. have a competitive advantage in stressed and dying trees relative to *M. platyphylla*, which is confined to dead material. In contrast, debris was the resource most heavily colonized by *M. platyphylla*, which is known to colonize a wide range of debris well, including small units such as twigs and beech cupules (Boddy 1993; Worrall 1991).

Rhizomorphs

Rhizomorph density of the two fungi followed the same general pattern as colonization of woody resources. By both measures, early cutting and defoliation individually were associated with significantly more *Armillaria* than no cutting and no defoliation. The recently cut stands had lower rhizomorphs densities than older cuttings. In an earlier study in the same forest type, defoliation led to increased rhizomorph density of *Armillaria* in 5 years but not in 1 year (Twery et al. 1990). In that study, older stumps (15–20 years old) did not support significant rhizomorph systems. Thus, *Armillaria* rhizomorphs in this system may peak between 8 and 15 years after cutting. In the case of *M. platyphylla*, our recently cut stands (3–8 years before sampling) had high rhizomorph densities, leading to a significant main effect even in the presence of significant interaction. Thus, after cutting, *M. platyphylla* may produce rhizomorphs more quickly than *Armillaria*. These results, particularly with respect to *Armillaria*, correspond well with the colonization results, but that is not a foregone conclusion. Redfern (1968) found that colonized roots of trees ring barked before felling produced far lower mass of *Armillaria* rhizomorphs than those of trees felled without ring barking. Thus, all wood is not equivalent as a resource for rhizomorph production. Also, varying chronology of colonization and rhizomorph production relative to sampling time may lead to noncorrespondence of colonization and rhizomorphs. These factors may explain, for instance, why rhizomorph production by *M. platyphylla* in nondefoliated stands shows a different pattern of variation with cutting than does colonization.

Correlations

Negative correlations between *Armillaria* and *M. platyphylla*, both in terms of resource colonization and rhizomorph density, support the hypothesis that *M. platyphylla* and *Armillaria* compete for the same resources, although the support is weak. Somewhat stronger negative correlations in the same comparisons were obtained previously in a northern hardwood forest (Worrall 1991). Such correlations may be weaker in more diverse communities, where competitive relationships involve more species.

Pairings in vitro

Thompson and Boddy (1983) reported that *M. platyphylla* grew over *A. gallica* (as *A. bulbosa*) and *A. ostoyae* in pairings on agar, but replacement was not confirmed by isolation. Observation of logs have also suggested that *M. platyphylla* was a strong combatant and could replace other fungi (Chapela et al. 1988). Based on extensive isolations in our experiment, it appears that *M. platyphylla* can replace *Armillaria* in vitro. Behavior of wood-decay fungi on malt agar often correlates surprisingly well with patterns of occurrence in the field (Rayner and Boddy 1988). In particular, a major study of interactions between *Armillaria luteobubalina* Watling & Kile and other wood-decay fungi found a close relationship between combative ability on agar and on wood (Pearce 1990). Thus, it is reasonable to suggest that *M. platyphylla* is capable of replacing *Armillaria* in occupied zones of wood. This is consistent with inverse patterns of colonization by the two fungi observed in the field. Experiments under more natural conditions will be necessary to confirm this ability.

Conclusions

Because *Armillaria* spp. spread rapidly in the cambial zone of freshly killed trees, it has been considered difficult to identify a good candidate for biological control (Rishbeth 1976). A successful competitor of *Armillaria* should have early contact with the pathogen and should be capable of subcortical growth and colonization of roots (Rayner 1979). Like *Armillaria*, a number of saprobic cord-forming fungi spread along the cambial zone before colonizing the outer wood (Rayner 1977; Thompson and Boddy 1983) and are in a position to compete directly with *Armillaria*. Cord-forming saprobes have thus been suggested as biocontrol agents for root pathogens (Boddy 1993; Thompson and Boddy 1983).

One such naturally occurring cord-former outperformed inoculated antagonists in a study of biological control in Australia. Freshly cut stumps of *Eucalyptus diversicolor* F. Muell. (karri) were inoculated with *A. luteobubalina* and three noncord-forming antagonists. However, a cord-forming *Hypholoma* sp., which infected the stumps naturally, excluded the pathogen from belowground portions of the stumps better than the inoculated antagonists (Pearce and Malajczuk 1990). In stumps treated with ammonium sulphamate, inoculation with cord-forming fungi significantly reduced colonization by *A. luteobubalina* (Pearce et al. 1995). Because such fungi have a similar niche to *Armillaria*, they have been considered an exciting prospect in biological control of Armillaria root rot (Hagle and Shaw 1991).

Megacollybia platyphylla, another such cord-former, is common in hardwood and mixed forests of northeastern North America, Europe, and other regions. Here we have shown that, although they use much the same resources, stand-changing events such as cutting and defoliation have differential effects on populations of the two fungi. This information may ultimately facilitate management approaches that reduce inoculum of the pathogen.

These data support the practice of cutting prior to defoliation (Gottschalk 1993, 1997; Gottschalk et al. 1988; Twery and Gottschalk 1989). The results suggest that a rationale for the practice, in addition to increasing host vigor, is reduction of inoculum potential of *Armillaria*. Colonization by an antagonist, *Megacollybia platyphylla*, is favored by the practice and may play a role in reducing colonization by *Armillaria*. The data further suggest that even a recent cutting may be beneficial.

The two fungi appear to compete for the same resources. Their niches overlap in snags and especially stumps, where *Armillaria* builds inoculum potential. The niche of *Armillaria* extends into living trees; that of *M. platyphylla* extends into debris. They may be further differentiated within stem bases and roots, but more intensive sampling will be necessary to determine this. Niche differentiation between the two fungi suggests that management activities that increase or decrease particular resources may be used to selectively regulate populations of the fungi.

The main effect of recent cutting on rhizomorphs of *M. platyphylla* suggests that this fungus proliferates quickly in response to the input of branches, twigs and roots during cutting. When defoliation occurs during this period, *Armillaria* may have minimal inoculum potential to attack stressed trees and maximal competition with fungi such as *M. platyphylla*.

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