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Effects of Forest Management Practices and Environment on Occurrence of *Armillaria* Species

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Abstract : Influences of environment (indicated by plant associations) and forest management practices on the distribution of *Armillaria* spp. and genets (vegetative clones) were investigated. A total of 142 isolates of *Armillaria* was collected from various host trees on pristine and managed sites (thinned and/or fertilized) growing in relatively wet and dry environments in eastern Washington, U.S.A. The incidence of *Armillaria* spp. was significantly higher in the relatively wetter sites than the relatively drier sites, as indicated by plant associations. However, no differences in *Armillaria* occurrence were found among different forest management practices (control vs. thinned vs. thinned and fertilized) within both wetter and drier sites. Incidence of *Armillaria* was significantly different among conifer and shrub species. The highest proportion with *Armillaria* was found on grand fir (*Abies grandis*). Based on pairing tests and rDNA sequencing, the 142 isolates were comprised in a total of 20 genets representing three *Armillaria* species. More diverse *Armillaria* spp. were found in both relatively wetter and relatively drier sites within the undisturbed control plots, compared to plots disturbed by forest management practices. The results from this study provide baseline information toward understanding how environment and forest management practices influence incidence and diversity of *Armillaria* species and genets.

Key words **:** *forest management, thinning, fertilization, Armillaria root disease, species identification, plant associations*

Introduction

Armillaria root disease has an extremely wide distribution in forests worldwide, with extensive occurrence in inland northwestern U.S.A./Canada and other parts of the world. Armillaria root disease occurs extensively in northern Idaho, Oregon, Washington, and western Montana, U.S.A. Previous studies demonstrate 16-40% growth/volume losses due to Armillaria root disease in areas of the inland northwestern U.S.A./Canada (Cruickshank, 2000; Wargo and Shaw, 1985). In general, the fungus expands radially from foci at an estimated rate of up to 2 m per year (Peet *et al*., 1996; Shaw and Roth, 1978). Infection of new root systems can eventually cause the death of surrounding trees, resulting in up to 55% volume loss over a 20-year period (Filip and Goheen, 1984). However, some *Armillaria* species are predominately saprophytic, and may act to sustain forest productivity by improving nutrient cycling through decomposition of organic matter. Previous studies also indicate that saprophytic *Armillaria* species may protect susceptible trees from attack by pathogenic *Armillaria* spp. (Bruhn *et al*., 2000).

Based on biological and morphological characteristics, *Armillaria* species in North America were initially grouped into 10 North American Biological Species (NABS). Recently, molecular tools (e.g., DNA sequencing, Amplified Fragment Length Polymorphisms) were developed to identify species, hybrids, populations, and genets of *Armillaria* (Kim *et al*., 2002; 2006; Klopfenstein *et al*., 2001). However, some saprophytic and secondary pathogenic *Armillaria* species remain difficult to identify due to high genetic similarities and potential hybridization among closely related species (Kim *et al*., 2006). These genetically similar species are *A. calvescens* (NABS III), *A. sinapina* (NABS V), *A. gallica* (NABS VII), and *A. cepistipes* (NABS XI) (Kim *et al*., 2006), hereafter referred to as "NABS III-V-VII-XI complex". They are genetically distant from pathogenic *A. solidipes* (NABS I=*A. ostoyae*; Burdsall and Volk, 2008) and other North American *Armillaria* spp. (Kim *et al*., 2006).

Well-defined associations of trees, shrubs, and herba-

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ceous plants, called plant associations, are strong indicators of site conditions as influenced by interactions of topography, soil properties, temperature, and precipitation patterns in western North America (McDonald *et al*., 2000). Data from random *Armillaria* plots throughout the western U.S.A. have shown that distribution and activity of *Armillaria* species are strongly correlated with plant associations (or habitat types) (McDonald *et al*., 1987; McDonald, 1998). In conifer forests, the overstory series reflects soil temperature, and the forest floor vegetation reflects soil moisture. Thus, plant associations reflect combined temperature-moisture regimes. Plant associations can be grouped together into plant association groups or sub-series based on previously defined criteria (Williams *et al*., 1995; Hall, 1998), analysis of plant distribution data (McDonald *et al*., 2000), or climate envelopes for indicator species derived from climate modeling (Simpson, 2007). Sub-series were used to organize and interpret *Armillaria* distribution and activity, fire severity and fire-return intervals, and other ecological processes in coniferous forests of the western U.S.A. (McDonald, 1998; McDonald *et al*., 2000; 2003).

Little progress has been made toward developing effective management methods for *Armillaria* species due to a lack of information about how pathogenic and saprophytic *Armillaria* species are influenced by host trees and other environmental factors (e.g., precipitation, soil properties, topographic characteristics, silvicultural practices – fertilizer application, reforestation practices, thinning, harvest methods, prescribed fire, etc.) across landscapes.

The objectives of this study were to 1) assess effects of forest management practices on genet (vegetative clone) and species diversity of *Armillaria*, and 2) determine the influence of plant associations on the occurrence of *Armillaria* genets and species.

Materials and Methods

1. Study site and plot selection

Armillaria isolates were surveyed and collected from BOISE® land, southwest of Chewelah, WA, U.S.A (Table 1). The criteria for the plot selection were based on wetness of the site, commercial pre-thinning, and fertilization variables (Table 1). For this study, we selected three plant associations: grand fir/ninebark [*Abies grandis*/*Physocarpus malvaceus* (ABGR/PHMA)], western hemlock/queen cup beadlily [*Tsuga heterophylla/Clintonia uniflora* (TSHE/CLUN)], and western redcedar/queen cup beadlily [*Thuja plicata/Linnaea borealis* (THPL/CLUN)] (Williams *et al*., 1995). These plant associations are contained in two sub-series (according to McDonald *et al*., 2000) as follows: 1) cool fir/dry herb sub-series - ABGR/PHMA and 2) cedar-hemlock/moist herb sub-series - TSHE/CLUN and THPL/CLUN. The cedar-hemlock/moist herb sub-series is relatively wetter (annual precipitation: 127 cm and temperature: 7.2ºC) than cool fir/dry herb sub-series (annual precipitation: 99 cm and temperature: 6.7ºC). A total of 18 plots (3 treatments of forest management practices × 3 replications × 2 sub-series; 0.04-ha size: 20 × 20 m) were surveyed for *Armillaria* isolates (Table 1). Plot boundaries and individual trees were mapped. GPS was used to establish a reference point, and a laser range finder and angle encoder were used to determine locations of individual trees.

2. Fungal collection and culture

We surveyed for *Armillaria* isolates from all tree/shrub species (at least 3 trees per species, of ca. large/medium/small Diameter at Breast Height) and representative shrubs present on each plot. At least three major lateral roots were excavated and examined for signs of *Armillaria* spp., such as rhizomorphs on the root/butt surface,

Table 1. Plot treatments and location for this study.

Sub-series[a]	Treatments	General Location of Plots		Comments
		Latitude	Longitude	
Cedar-hemlock /moist herb	Undisturbed control	48° 04.986'	118° 00.020'	Established 1920's
	Commercial pre-thinning (CPT, thinned)	48° 05.947'	117° 59.641'	Harvested by over-story removal in 1978, CPT in 1987, and selectively harvested in 1987
	Thinned and fertilized	48° 05.227'	118° 00.177'	CPT in 1987 and fertilized in 1999 (nitrogen, potassium)
Cool fir/dry herb	Undisturbed control	48° 07.881'	117° 57.767'	Established 1930's
	Commercial pre-thinning (CPT, thinned)	48° 06.212'	117° 59.423'	Harvested by over-story removal in 1985 and CPT in 1986
	Thinned and fertilized	48° 07.315'	117° 57.017'	CPT in 1978 and fertilized in 1995 (nitrogen, potassium, sulfur, boron)

[a]Cedar-hemlock/moist herb sub-series includes *Tsuga heterophylla*/*Clintonia uniflora* (TSHE/CLUN) and *Thuja plicata*/*Clintonia uniflora* (THPL/CLUN) plant associations and cool fir/dry herb includes *Abies grandis*/*Physocarpus malvaceus* (ABGR/PHMA) plant association

mycelial fans under the bark, or rotten wood containing mycelia of *Armillaria* spp. When found, *Armillaria* spp. samples were collected and established in culture. The following information was also collected with *Armillaria* isolates: 1) host information (species, overall health, growth, etc.); 2) ecological information associated with *Armillaria* isolates (rhizomorph, mycelial fan, substrate, etc.); 3) plant species present; and 4) topography, elevation, slope, aspect, and land form. We collected more than 200 isolates of *Armillaria* (ca. 10 to 20 isolates per plot, depending on the site), mostly from rhizomorphs. We surface-sterilized rhizomorphs, bark fans, and rotting wood to establish a total of 142 *Armillaria* isolates in culture. Isolates were grown on malt-agar medium (3% malt extract, 3% dextrose, 1% peptone and 1.5% agar) at 21°C in the dark.

3. Fungal species identification

Fungal isolates were condensed down to individual genets (vegetative clones) using somatic incompatibility tests (Mallett and Hiratsuka, 1986). Species identification of these genets was performed by a DNA sequencing method (intergenic spacer region; IGS-1) and verified by sequence similarity within GenBank. PCR products from nuclear rDNA (IGS-1) were obtained by a direct-PCR method (i.e., mycelium was scraped from pure culture and added directly to the PCR mixture to serve as DNA template) and primer sets (LR12R and O1) were used for amplification based on Kim *et al.* (2006).

4. Statistical analysis

The statistical significance of sub-series and forest management practices on *Armillaria* occurrence was tested using chi-square tests for independence, using Web Chi Square Calculator (http://www.physics.csbsju.edu/stats/chi-square.html).

Results and Discussion

1. Occurrence of *Armillaria* in association with different sub-series and forest management practices

Armillaria occurrence was significantly higher in the cedar-hemlock/moist herb sub-series than the cool fir/dry herb sub-series (Table 2). A total of 135 trees were inspected for *Armillaria* species in cedar-hemlock/moist herb sub-series and *Armillaria* samples were found and collected on 70% of inspected trees. In contrast, *Armillaria* samples were found and collected on 53% of trees out of 90 trees growing in the cool fir/dry herb sub-series (Table 2). No differences in *Armillaria* occurrences were found among different forest management practices within each sub-series, control vs. commercial pre-thinning (thinned) vs. thinned and fertilized (df=2, α=0.05, P=0.13). The ranges of *Armillaria* occurrence on different forest management practices were 60%-79% in the cedar-hemlock/moist herb sub-series and 40%-67% in the cool fir/dry herb sub-series (Figure 1). The "thinned" treatment showed the highest percent of *Armillaria* occurrence regardless of sub-series; however, no statistically significant differences were found among treatments (Figure 1).

McDonald *et al.* (1987) found that the occurrence of *Armillaria* is strongly correlated to the plant associations (habitat types). They installed 0.04-ha plots across widely ranging plant associations in the northern Rocky Mountains, U.S.A. and surveyed for *Armillaria* spp. In general, *Armillaria* spp. were absent from the somewhat extreme climates such as "hot and dry", "cold and dry", "cold and wet", and "frost pocket" of the Douglas-fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) series. Later, McDonald (1998) showed 19 of 26 plots in the cool fir/dry herb sub-series supported *Armillaria*

Table 2. Occurrence of *Armillaria* on conifers and shrubs growing on two different sub-series in eastern Washington, U.S.A.

Sub-series[a]	*Armillaria* occurrence No. of trees	No *Armillaria* occurrence No. of trees	χ^2
Cedar-hemlock/moist herb	94 (70%)	41 (30%)	6.36*
Cool fir/dry herb	48 (53%)	42 (47%)	

[a]See Table 1 for detailed sub-series information; *df=1, α= 0.05, P < 0.05

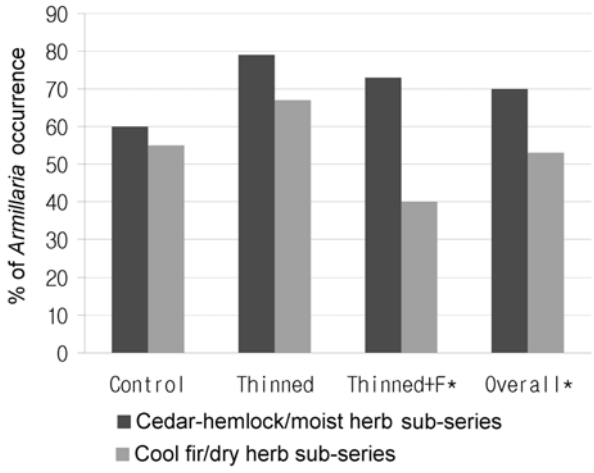

Figure 1. Occurrence of *Armillara* on conifers and shrubs growing on two different sub-series in eastern Washington, U.S.A. Cedar-hemlock/moist herb sub-series includes *Tsuga heterophylla*/*Clintonia uniflora* (TSHE/CLUN) and *Thuja plicata*/*Clintonia uniflora* (THPL/CLUN) plant associations, Cool fir/dry herb sub-series includes *Abies grandis*/*Physocarpus malvaceus* (ABGR/PHMA) plant association. Control, thinned: Commercial Pre-thinning, thinned+F: Commercial Pre-thinning and fertilized (See Table 1 for detailed treatments information);* df = 1, α= 0.05, P < 0.05.

spp., while 14 of 14 plots in the cedar-hemlock/moist herb sub-series supported the *Armillaria* spp. In this study, all plots (9 for cool fir/dry herb sub-series and 9 for cedar-hemlock/moist herb sub-series) supported *Armillaria* spp. Our results support the previous studies (McDonald *et al*., 1987; McDonald, 1998).

Several previous studies reported that severity of Armillaria root disease tends to increase as management intensifies. The activity of Armillaria root disease appears to increase on sites that are disturbed by management activities, such as partial cutting (Filip, 1977; Filip and Goheen, 1982; Redfern, 1978), excessive grazing (Bega, 1979), fire control (Shaw *et al*., 1976), and clear cutting (Redfern, 1978; Shaw and Roth, 1978). Singh and Richardson (1973) reported that method and quality of planting also can influence the disease activity. In contrast to other studies, Filip *et al.* (1989) indicated that pre-commercial thinning reduced tree mortality caused by Armillaria root disease in a ponderosa pine (*Pinus ponderosa*) stand in central Oregon, U.S.A. They noted that pre-commercial thinning may be the only feasible management option for a ponderosa pine stand affected by Armillaria root disease, because the eradication of this disease through chemical and physical (e.g., stump removal) controls is not economically practical.

2. Incidence of culturally verified *Armillaria* on conifers and shrubs

Incidence of *Armillaria* was significantly different among conifer species, ranging from 11% on lodgepole pine (*Pinus contorta*) to 87% on grand fir (Table 3). The occurrence of *Armillaria* on shrubs including oceanspray (*Holodiscus discolor*), serviceberry (*Amelanchier alnifolia*), ninebark, Rocky Mountain maple (*Acer glabrum*),

Table 3. Incidence of culturally verified *Armillaria* on conifers within two sub-series[a] located in eastern Washington, U.S.A.

Conifer species	No. of plants inspected	No. with *Armillaria*	Proportion with *Armillaria*	χ^2
Ponderosa pine (*Pinus ponderosa*)	18	6	33%	
Lodgepole pine (*P. contorta)*	9	1	11%	
Douglas-fir (*Pseudotsuga menziesii*)	44	29	66%	
Grand fir (*Abies grandis*)	44	39	87%	47.17*
Western larch (*Larix occidentalis*)	37	26	70%	
Western redcedar (*Thuja plicata*)	20	4	20%	
Western hemlock (*Tsuga heterophylla*)	10	8	80%	
Shrubs[b]	42	29	69%	

[a]See Table 1 for detailed sub-series information; *df = 6, α= 0.05, $P < 0.05$
[b]Oceanspray (*Holodiscus discolor*), serviceberry (*Amelanchier alnifolia*), ninebark (*Physocarpus malvaceus*), Rocky Mountain maple (*Acer glabrum*), willow (*Salix* sp.), redstem ceanothus (*Ceanothus sanguineus*), Pacific yew (*Taxus brevifolia*), buffaloberry (*Shepherdia canadensis*), blue elderberry (*Sambucus cerulean*)

Table 4. Incidence of culturally verified *Armillaria* on conifers within cedar-hemlock/moist herb sub-series.[a]

Conifer species	No. of plants inspected	No. with *Armillaria*	Proportion with *Armillaria*	χ^2
Ponderosa pine (*Pinus ponderosa*)	2	2	100%	
Lodgepole pine (*P. contorta*)	7	1	14%	
Douglas-fir (*Pseudotsuga menziesii*)	16	12	75%	
Grand fir (*Abies grandis*)	32	30	94%	45.35*
Western larch (*Larix occidentalis*)	27	22	81%	
Western redcedar (*Thuja plicata*)	20	4	20%	
Western hemlock (*Tsuga heterophylla*)	10	8	80%	

[a]See Table 1 for detailed sub-series information; *df = 6, α = 0.05, $P < 0.05$

Table 5. Incidence of culturally verified *Armillaria* on conifers within cool fir/dry herb sub-series.[a]

Conifer species	No. of plants inspected	No. with *Armillaria*	Proportion with *Armillaria*	χ^2
Ponderosa pine (*Pinus ponderosa*)	16	4	25%	
Lodgepole pine (*P. contorta*)	2	0	0%	
Douglas-fir (*Pseudotsuga menziesii*)	28	17	61%	10.69*
Grand fir (*Abies grandis*)	12	9	75%	
Western larch (*Larix occidentalis*)	10	4	40%	

[a]See Table 1 for detailed sub-series information; *df = 4, = 0.05, $P < 0.05$

Table 6. *Armillaria* isolates/genets/species derived from northeastern Washington, U.S.A.

Sub-series[a]	Treatments[b]	No. of isolates	Genet[c]	Species Identification
Cedar-hemlock/ moist herb	Undisturbed control	32	P	*A. solidipes*
			N	NABS[d] III-V-VII-XI complex
			O	NABS X
	Commercial pre-thinning (thinned)	33	R, S	NABS III-V-VII-XI complex
			T	NABS X
	Thinned and fertilized	29	N, Q	NABS III-V-VII-XI complex
Cool fir/dry herb	Undisturbed control	18	D	*A. solidipes*
			A, B, E	NABS III-V-VII-XI complex
			C	NABS X
	Commercial pre-thinning (thinned)	18	F, G, H, I	NABS III-V-VII-XI complex
	Thinned and fertilized	12	D	*A. solidipes*
			J, K, L, M	NABS III-V-VII-XI complex

[a]See Table 1 for detailed sub-series information; [b]See Table 1 for treatments information; [c]Vegetative clone; [d]North American Biological Species

willow (*Salix* sp.), redstem ceanothus (*Ceanothus sanguineus*), Pacific yew (*Taxus brevifolia*), buffaloberry (*Shepherdia canadensis*), and blue elderberry (*Sambucus cerulean*) was quite high (69%) (Table 3). Incidence of *Armillaria* varied among conifer species within the cedar-hemlock/moist herb and cool fir/dry herb sub-series, but the relative rates of occurrence may vary by species (Tables 4 and 5). No western hemlock or western redcedar were found in cool fir/dry herb sub-series, as expected (Table 5).

Previous study by McDonald *et al.* (1987) showed very similar results for the incidence of *Armillaria* spp. on conifers in the northern Rocky Mountains, U.S.A. In that study, the highest proportion with *Armillaria* spp. was found on grand fir (64%), followed by Douglas-fir (54%), western larch (*Larix occidentalis*) (43%), western hemlock (36%), ponderosa pine (33%), lodgepole pine (31%), and western redcedar (20%). The high incidence of *Armillaria* spp. on plots is not a direct indicator of root disease or tree mortality because both pathogenic and saprophytic *Armillaria* spp. are included in these results. Therefore, it is critical to identify pathogenic species of *Armillaria* collected from each plot as well as saprophytic species.

3. Identification of *Armillaria* genet and species

A total of 20 (A-T) genets were identified from the 142 isolates using somatic incompatibility tests (Table 6). Each treatment had a different number of genets. Overall, the cool fir/dry herb sub-series contained more genets than the cedar-hemlock/moist herb sub-series (13 vs. 7) (Table 6). Since *Armillaria* incidence on hosts was higher on the cedar-hemlock/moist herb sub-series, we can infer *Armillaria* genets were occupying larger areas in cedar-hemlock/moist herb sub-series.

Three *Armillaria* species were identified among the 20 genets using IGS-1 rDNA sequences - *A. solidipes,* NABS III-V-VII-XI complex, and NABS X (Table 6). Two genets (*A. solidipes* genet "D" and NABS III-V-VII-XI complex genet "N") occurred on two different treatment sites. For example, *A. solidipes* genet D was collected in undisturbed cool fir/dry herb sub-series, control and thinned, fertilized sites (Table 6). The three species (*A. solidipes*, NABS III-V-VII-XI complex, and NABS X) identified from the study sites are commonly found *Armillaria* species within the inland northwestern U.S.A. Undisturbed, control plots (both sub-series) had more diverse *Armillaria* spp. than the disturbed (managed) plots (Table 6). Noticeably, NABS X, which is a potential protector against pathogenic *A. solidipes*, did not occur in disturbed (managed) plots except the cedar-hemlock/moist herb sub-series, thinned treatment site (Table 6). Our previous study indicated that *A. solidipes* appears to be limited within areas dominated by NABS X (McDonald *et al.*, 1998) in northern Idaho, U.S.A. We observed similar trends in our cedar-hemlock/moist herb sub-series control site – *A. solidipes* genet (represented by triangles) was surrounded by a NABS X genet (represented by circles) (Figure 2). In addition, we did not observe any *A. solidipes* that were derived from pathogenic mycelial fans (an indication of pathogenicity). These observations raise the question as to whether some *Armillaria* species can protect a site from invasion by pathogenic species. In our study, NABS X did not occur in thinned and fertilized plots. We can speculate that these managed sites are perhaps more vulnerable to future infection from pathogenic *Armillaria* species. More studies are needed to understand the interactions among *Armillaria* species, genets, and hosts under different forest management practices and environments. This study also suggests that small differences in site moisture (annual precipitation: 99 cm for cool fir/dry

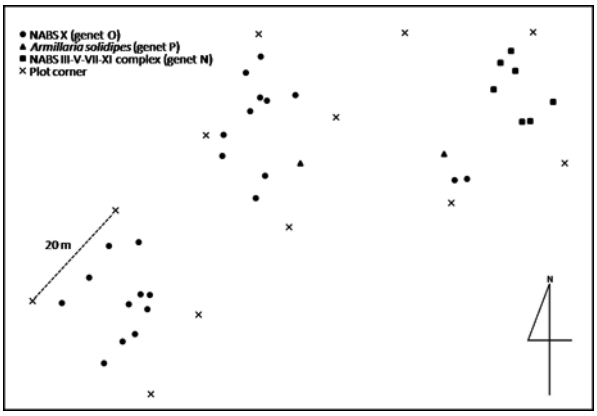

Figure 2. Map of *Armillaria* occurrence in cedar-hemlock/moist herb sub-series control plots (plot size: 0.04 ha, 20 × 20 m). Three plots were installed for cedar-hemlock/moist herb sub-series control treatment. Individual trees that collected *Armillaria* isolates were mapped and each *Armillaria* species and genet was indicated by cireles (NABS X – genet O), triangles (*A. solidipes* – genet P), and squares (NABS III-V-VII-XI complex – genet N). Cedar-hemlock/moist herb sub-series includes *Tsuga heterophylla*/*Clintonia uniflora* and *Thuja plicata*/*Clintonia uniflora* plant associations. NABS: North American Biological Species of *Armillaria*.

herb sub-series vs. 127 cm for cedar-hemlock/moist herb sub-series) and temperature (annual temperature of 6.7ºC for cool fir/dry herb sub-series vs. 7.2ºC for cedar-hemlock/moist herb sub-series) relationships could lead to unpredictable behavior of resident *Armillaria* species and genets. Data regarding temperature and moisture should be collected to better predict the influences of soil temperature and moisture on *Armillaria* spp. distribution.

The DNA sequencing method was used to identify *Armillaria* species in this study. The use of molecular genetic tools including DNA sequencing for species identification provides critical baseline information for characterizing, mapping, and predicting occurrence and pathogenicity of *Armillaria* species in managed forest ecosystems across the landscape. Such information should help develop prediction models for the site-specific occurrence and behavior of individual *Armillaria* species and facilitate management decisions to minimize the harmful effects and maximize the beneficial effects of *Armillaria* species. These models could also potentially be adapted to estimate site-specific growth losses due to Armillaria root disease.

In conclusion, this study provides baseline information toward understanding how incidence and behavior of *Armillaria* species and genets are associated with environment and forest management practices. This approach can be applied to 1) predict distribution of different *Armillaria* species, hybrids, and genets across forest landscapes; 2) determine appropriate management practices for specific forest sites to increase beneficial effects of saprophytic *Armillaria* species, and minimize detrimental effects of pathogenic *Armillaria* species, and 3) assess the potential impacts of climate change on *Armillaria* spp. distribution.

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