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Armillaria in the Northern Rockies: Pathogenicity and Host Susceptibility on Pristine and Disturbed Sites

G. I. McDonald
N. E. Martin
A. E. Harvey

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Intermountain Research Station
324 25th Street
Ogden, UT 84401

Armillaria in the Northern Rockies: Pathogenicity and Host Susceptibility on Pristine and Disturbed Sites

G. I. McDonald
N. E. Martin
A. E. Harvey[1]

ABSTRACT

Over all plots (disturbed and pristine), incidence of pathogenic Armillaria *showed a strong tendency to decrease as habitat type productivity increased. This trend gave rise to a clear separation of plots by climax series. The relatively less productive subalpine fir and Douglas-fir series exhibited high incidence of root disease and the relatively more productive grand fir, western redcedar, and western hemlock series significantly less. Within these productivity groups, other patterns emerged. Disturbance appeared to be related to a dramatic increase in incidence of pathogenicity, but not occurrence, within the high-productivity grouping of communities. Also, the ability of disturbance to elicit pathogenicity seemed to decline as site productivity increased. Conversely, the pristine plots within the low-productivity series exhibited high incidence of the pathogen in a pathogenic state. This condition seemed to be related to a community structure characteristic of transition between cold-dry to cool-moist and warm-dry to warm-moist. Predicting risk of* Armillaria*-caused mortality, occurrence of pathogenic species and clones of* Armillaria*, a possible role for host stress in expression of pathogenicity by* Armillaria*, and risk rating of host species are discussed.*

KEYWORDS: habitat types, host stress, root rot management, root rot risk, risk rating, disease hazard

Armillaria commonly occurs as rootlike rhizomorphs growing on plant debris or epiphytically attached to root systems of dead, diseased, or healthy host plants (Garrett 1960; Kile 1980; Leach 1939; Raabe and Trujillo 1963; Redfern 1973). Isolates obtained from such rhizomorphs, as well as isolates obtained from mycelial fans, decayed wood, and sporophores, can belong to clones or species whose apparent pathogenicity varies from very high to obligately saprophytic (Kile 1983; Rishbeth 1982; Wargo and Shaw 1985).

Severity of this *Armillaria*-caused root disease tends to increase as management intensifies. Partial cutting (Filip 1977; Filip and Goheen 1982; Redfern 1978), excessive grazing (Bega 1979), and fire control (Shaw and others 1976) all appear to increase activity of *Armillaria*. In Queensland, Australia, *Armillaria* was found in nearly all stumps after clearcutting of a first-rotation introduced pine forest (Anon. 1982). Chemical and mechanical killing of hardwood brush or timber is linked to increased activity (Pronos and Patton 1977; Swift 1972). Conifer plantations replacing clearcut conifer or hardwood forests have experienced significant *Armillaria*-related mortality (Redfern 1978; Shaw and Roth 1978). Even method and quality of planting (Rykowski 1981) can influence damage caused by this organism (Singh and Richardson 1973). There are several interactions between *Armillaria* root rot and the actions of insects and other diseases (Dunbar and Stephens 1975; Madziara-Borusiewicz and Strzelecka 1977; Singh and Raske 1983; Wargo 1977, 1981). Slash disposal methods may also affect *Armillaria*; woody debris incorporated into the soil can be a significant food base increasing the inoculum potential and thereby becoming a source of new infections (Garrett 1960; Raabe and Trujillo 1963).

Many researchers have reported ubiquitous distribution and host ranges of *Armillaria* spp. (Ehrlich 1939; Hobbs and Partridge 1979; Hubert 1950; Swift 1972). The primary objective of these studies, however, was to determine degree of damage to affected hosts rather than extent of occurrence of the fungus. Other examples are Carey and others (1984), Williams and Marsden (1982), and James and others (1984), wherein sample points were selected by first locating symptomatic trees or root disease centers. We recently demonstrated that *Armillaria* distribution, as determined by randomly located plots, is related to habitat type (McDonald and others in press).

No information is presently available regarding probability of encountering, from randomly selected forest locations, the genus *Armillaria* in pathogenic mode on any host. Such information is important because probability of occurrence (at quantitative level, for instance, proportion of 0.04-ha plots) of pathogenic *Armillaria* in relation to stand attributes can serve to classify forest lands for options and risk to host species given specific management actions.

[1]Principal plant pathologist, plant pathologist, and principal plant pathologist, respectively, located at Intermountain Station's Forestry Sciences Laboratory, Moscow, ID.

We began a study of population-level genetic and ecologic interactions between *Armillaria* and its conifer and hardwood hosts in 1983. One objective was to predict the probability of *Armillaria*-caused damage to hosts by geographic location, host species, and stand management history. A major concern addressed by this study was the association of pathogenic *Armillaria* with habitat type and management history, as judged by signs of the fungus and disease symptoms found on randomly located plots.

This paper reports on the occurrence of pathogenic *Armillaria* by host species, plot vegetation—community type (habitat type), and the effect of human disturbance on culturally verified rhizomorph and fan collections of *Armillaria*.

MATERIALS AND METHODS

The root systems of at least one living and apparently healthy representative of all major hardwood and conifer species on each plot were inspected for fans, decayed wood, and (epiphytic) rhizomorphs. The inspection consisted of exposing the root collar and major roots to a depth of about 0.3 m and a lateral spread of 0.5 to 1 m, then looking for decay and fans by chopping away the bark. This inspection required 1 to 3 hours per plot. Evidence of man's activity, such as road building or previous cutting, within 75 m of a plot was recorded. Finally, any unhealthy or recently dead trees (from seedlings to mature) were inspected for the cause of their condition. Trees with fans and root resinosis, fans and green needles, or fans and red needles were recorded as *Armillaria*-killed or damaged, and isolates of fans were taken.

Pathogenic *Armillaria* was said to have been encountered if a dead tree exhibited enough resinosis to soak the soil in the area of the root crown, or if the cambium showed a wound reaction common in living trees at the site of *Armillaria* fan attachment. Fans alone on a dead tree were not considered adequate evidence that *Armillaria* had been instrumental in death of a tree. Fans alone were taken as positive evidence of pathogenicity if the tree was healthy in appearance, declining, or recently dead (red-brown needles). Tree size was not considered. Pathogenic encounter was recorded if signs and symptoms, or both, were found on plants within 25 m of the 400-m^2 plot.

All plots were classified by habitat type according to appropriate dichotomus keys based on lists of indicator plants and by study of plot photos and plant lists by an experienced ecologist (Neiman 1984). Habitat type of the few plots that occurred on recent or regenerated clearcuts was determined by inspection of adjacent stands. Plots were pooled by climax series for analyses. The expected site index for each series was obtained from series descriptions (Cooper and others in press; Steele and others 1981; Pfister and others 1977). Plots were further classified as nondisturbed and human-disturbed. The proportion of each class within each series and of some individual habitat types was calculated. For those plots supporting saprophytic or pathogenic *Armillaria*, or both, on a specific host species, we computed the proportion of that host species that was damaged.

RESULTS

Distribution of Pathogenic *Armillaria*

When plots supporting pathogenic *Armillaria* were classified by climax indicator species, the heterogeneity chi-square was significant at 8 percent (table 1). Second, the likelihood of encountering pathogenicity appeared to decrease with increasing productivity (site index) among the series (table 1). The relationship between community stability, community productivity, disturbance, and pathogenicity was investigated (table 2). The comparison for occurrence of pathogenicity on disturbed and undisturbed low-productivity sites yielded a nonsignificant heterogeneity chi-square (table 2). But disturbed high-productivity plots compared to undisturbed high-productivity plots showed a heterogeneity chi-square significant at 0.005 (table 2). Undisturbed-low and undisturbed-high were also significantly different (table 2). Thus, disturbed high-productivity plots had more pathogenicity than undisturbed high-productivity plots. Undisturbed low-productivity plots showed more pathogenicity than undisturbed high-productivity plots, and undisturbed low-productivity plots were not different from disturbed high-productivity plots.

Rankings of Conifer Species

The proportion of pathogenic *Armillaria* on particular hosts was computed for the 10 most common host species in each series (table 3). The proportion was calculated only from plots where both *Armillaria* and the host were present. The species sorted into three groups: (1) Western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western white pine (*Pinus monticola*) that did not support pathogenic *Armillaria*, (2) ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), and western redcedar (*Thuja plicata*) that exhibited moderate levels of pathogenicity, and (3) Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) that exhibited a high incidence of pathogenic encounter, particularly when they were climax.

Table 1—Incidence of pathogenic *Armillaria* in habitat types known to support *Armillaria*. Plots are classified by climax vegetation and listed in order of increasing productivity site index

Climax species	Site index	Number of plots	Proportion of pathogenic *Armillaria*
Subalpine fir	16.15	15	0.53
Douglas-fir	16.46	[1]6	.67
Grand fir	19.81	42	.309
Western redcedar	21.95	10	.20
Western hemlock	22.56	15	.13

χ^2 = 8.32, d.f. = 4, prob. of larger χ^2 = 0.08.
[1]Includes the single ponderosa pine series plot.

Table 2—Incidence of pathogenic *Armillaria* on 78 randomly selected 0.04-ha plots having *Armillaria* in some form. Plots were classified by plot productivity (high and low) (see table 1) and man-caused disturbance[1]

Disturbance-productivity combination	Number of plots	Proportion with *Armillaria*	$^2\chi^2$	$P \leq \chi$
Disturbed-low	4	0.25		
Undisturbed-low	17	.65	0.78	0.4
Disturbed-high	17	.59		
Undisturbed-high	40	.18	7.86	.005
Disturbed-low	4	.25		
Disturbed-high	17	.59	.44	.6
Undisturbed-low	17	.65		
Undisturbed-high	40	.18	10.22	.005
Undisturbed-low	17	.65		
Disturbed-high	17	.59	0	1.0
Disturbed-low	4	.25		
Undisturbed-high	40	.18	1.24	.3

[1]Undisturbed = pristine plots 75 or more meters from human disturbance. Disturbed = in or within 75 meters of thinning, clearcut, or roadside.

[2]Chi square calculated according to Snedecor (1956) for 2 by 2 contingency table with correction for continuity.

DISCUSSION

Our conclusions about pathogenicity are: (1) incidence of pathogenic *Armillaria* decreases as primary productivity among series increases; (2) incidence of pathogenic *Armillaria* decreases as productivity of habitat types within the ABGR, THPL, and TSHE series (see definitions in table 3) increases; (3) incidence of pathogenicity was high (59 percent) on disturbed plots in the ABGR, THPL, and TSHE series; (4) incidence of pathogenicity was low (18 percent) on undisturbed plots in the ABGR, THPL, and TSHE series; (5) incidence of pathogenicity was high (65 percent) on undisturbed plots in the PSME and ABLA series; and (6) incidence of pathogenicity was low (25 percent) on disturbed plots in the PSME and ABLA series. Because the undisturbed plots represent the natural situation, we conclude that human activities have increased the incidence of pathogenicity threefold within the ABGR, THPL, and TSHE series.

A conclusion about human activities within the PSME and ABLA series is not possible because of the small number of plots in the disturbed class. Nevertheless, *Armillaria* clearly is exhibiting considerable pathogenic behavior on some habitat types within these series even in the absence of human activity. These plots appear to represent transitional zones between moist-cool to moist-warm sites on the one hand, and either cold-dry or warm-dry on the other. They probably occurred in our sample as undisturbed because they tend to be low-quality sites and are unattractive harvesting targets.

New evidence presented by Morrison and others (1985) links *A. ostoyae* to damage on conifers throughout southern British Columbia. These authors point out that knowledge of geographic range of the pathogen species does not explain damage differences between coastal and interior forests. Their explanation is variation in pathogenicity between coastal and interior forms of a single species—*Armillaria ostoyae*. If we can accept that pathogenic situations observed in our study were caused only by *A. ostoyae*, then our results suggest variation in pathogenicity of this species is linked to site productivity, host adaptation, or stress.

The hypothesis that is preferred by the authors to explain all relevant observations about *Armillaria* behavior in western North America is that the fungus, perhaps *A. ostoyae*, acts as a facultative pathogen that causes the most damage on stressed conifers. This is the proposed mode of action for *Armillaria* (species unknown) in forests

Table 3—Rankings of conifer species susceptibility to *Armillaria* within plant community climax series on plots in 15 Northern Rocky Mountain National Forests

Host species	Series					
	ABLA	PSME	ABGR	THPL	TSHE	All
PIPO[1]	— —	1/3 = 33	0/9 = 0	— —	— —	1/2 = 8
PICO	[2]1/8 = 13	0/5 = 0	2/14 = 14	0/2 = 0	0/4 = 0	3/33 = 9
PIMO	— —	— —	0/8 = 0	0/2 = 0	0/6 = 0	0/16 = 0
PSME	2/8 = 25	36 = 50	6/29 = 21	1/8 = 13	1/8 = 13	13/59 = 22
LAOC	0/5 = 0	0/5 = 0	0/22 = 0	0/4 = 0	0/10 = 0	0/46 = 0
TSHE	— —	— —	— —	— —	0/14 = 0	0/14 = 0
THPL	— —	— —	— —	1/10 = 10	0/11 = 0	1/21 = 5
PIEN	3/14 = 21	0/2 = 0	4/17 = 24	0/2 = 0	1/5 = 20	8/40 = 20
ABGR	— —	— —	7/31 = 23	2/9 = 22	0/9 = 0	9/49 = 18
ABLA	6/15 = 40	— —	0/7 = 0	0/2 = 0	1/3 = 33	7/27 = 26
All	12/50 = 24	4/21 = 19	19/137 = 14	4/39 = 10	2/70 = 3	

[1]PIPO = *Pinus ponderosa*, PICO = *Pinus contorta*, PIMO = *Pinus monticola*, PSME = *Pseudotsuga menziesii*, LACO = *Larix occidentalis*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, PIEN = *Picea engelmannii*, ABGR = *Abies grandis*, ABLA = *Abies lasiocarpa*.

[2]Number of pathogenic occurrences (by plot) on specified host/number of occurrences within series when both species and *Armillaria* were present.

of the Eastern United States (Wargo 1979, 1984; Wargo and Shaw 1985).

Our hypothesis would explain the following: (1) The habitat types where *Armillaria* appears to cause high damage to undisturbed subalpine fir and Douglas-fir are transitional between relatively stable cold-dry and cool-moist regions and between hot-dry and warm-moist regions. Thus, these two damaged species may represent maladapted transitional populations, even though they are growing in their "natural environment." (2) Within the relatively more stable environments represented by the ABGR, THPL, and TSHE series, a slightly different mechanism may work. Here the physiologic traits of most species have the acclimative tolerances to withstand natural stresses, but these tolerances are exceeded for grand fir, Douglas-fir, lodgepole pine, Engelmann spruce, and possibly western redcedar and ponderosa pine when human-caused perturbations result in severe site modification as discussed by Likens (1985). In accordance with this hypothesis, two of the tolerant species (PIMO, LAOC) are known to possess shallow adaptive clines (Rehfeldt 1982; Rehfeldt and others 1984). Also, in any stressful situation, additions of anthropogenic inputs such as lead (Smith 1984) could tip the balance in favor of a pest. As productivity of the site increases, the impact of the perturbation lessens. When a highly productive state, as represented by the most productive sites in northern Idaho and like sites west of the Cascade crest, is reached, adaptive tolerances are not exceeded.

CONCLUSIONS

Pathogenic behavior, within the ecological range of the fungus, depends on specific combinations of habitat type and stand development history. Hypothesized patterns of occurrence must be validated before being put to general use in predicting risk to *Armillaria*. Validation is important because risk prediction has potential for extension to other parts of the Western United States, both for *Armillaria* and for other endemic diseases of forest trees. This approach should be highly effective for root pathogens of woody plants. The occurrence and function of many of these fungi are likely tied to long-term soil and climatic conditions, just as is the case with occurrence of the indicator plants.

Armillaria species and clones are known to encompass nonpathogenic saprophytes, secondary pathogens, amd primary pathogens (Morrison 1982; Rishbeth 1982; Shaw 1977). Hypotheses that could explain such varied behavior are site-specific stressing of hosts or varying geographic distribution patterns of pathogenic and nonpathogenic forms. A most important avenue of future research is the determination of which hypotheses or combinations give the best explanation. The results presented in this paper are based solely on host responses and point to existence of an *Armillaria* (perhaps *A. ostoyae*) that functions as an ecosystem scavenger or secondary pathogen which works mostly on stressed hosts. Nevertheless, our results do not rule out the existence of an *Armillaria* that functions as a primary pathogen with geographic clines varying in pathogenicity (Morrison and others 1985). To answer this question will require much data about the geographic and host range of individual *Armillaria* clones.

Regardless of ultimate explanations, results presented in this paper indicate that forest managers will need to know habitat type and management history of Northern Rocky Mountain stands to make informed decisions relating expected *Armillaria* damage to species selection and seed source after disturbance.

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