Preliminary Report on the Ecology of *Armillaria* in Utah and the Inland West

Geral I. McDonald,
USDA Forest Service, Rocky Mountain Research Station,
1221 South Main Street,
Moscow, Idaho 83843, USA.
E-mail: gimcdon@forest.moscowfsl.wsu.edu

Introduction

Shoestring root rot of conifers, caused by species of the basidiomycetous genus *Armillaria*, damages conifers in forests throughout the western United States. Most conifers are hosts to one or more species of *Armillaria*. Host range, aggressiveness, and other ecological behaviors of this fungus vary with locality. In coastal forests of western Oregon and Washington, occasional damage to Douglas-fir (*Psudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) is not significant. In the wet inland forests of northern Idaho, eastern Washington, and western Montana, Douglas-fir and grand fir (*Abies grandis*) mortality can be severe in size classes ranging from seedlings to mature trees. In higher elevation forests, damage to subalpine fir (*A. lasiocarpa*) and Englemann spruce (*Picea englemannii*) can be significant. The fungus is seldom found in dry forests dominated by ponderosa pine (*Pinus ponderosa*). Is ecological behavior and occurrences of *Armillaria* predictable or unpredictable at specific locations in conifer forests of the western United States?

In 1983, a study of the ecological genetics of the *Armillaria* - conifer pathosystem was initiated to answer this question. First, 120 plots (0.04 hectares) were established at random on 15 national forests within a 300-mile radius of the Intermountain Research Station Laboratory located at Moscow, Idaho (McDonald and others 1987). Habitat type of each plot was determined to associate occurrence and behavior of *Armillaria* with plant communities (McDonald and others 1987). Data from these investigations suggested that *Armillaria* behavior and occurrence could be mapped (predicted) over large geographic areas, if the number of map units were reduced by combining habitat types into ecologically similar Potential Vegetation Groups (PVGs). This idea was given an initial test with the establishment of 48 plots randomly located on national forests in Utah.

Phytosociology: the ecological context

Davis and others (1980) combined habitat types expected to exhibit similar fire behavior into fire behavior ecoclasses. We reasoned a similar tactic should facilitate the understanding of ecological aspects of *Armillaria* behavior. If ecosystem roles of *Armillaria* were to be understood, a less subjective method of combining habitat types would be needed. Thus, a system to group defined habitat types was constructed on the premise that conifer climax species indicate a temperature gradient and that shrubs and herbs indicate a moisture gradient (McDonald 1991). This idea was recently expanded to encompass all the conifer forests of Utah, Idaho, Oregon, Washington, and Montana (McDonald unpublished data). Before discussing this new classification effort, we need to define plant association and habitat type. A plant association is simply an abstract taxonomic unit described by the ecologist who has formulated a specific classification system based on distribution of native plants (Pfister 1989). After the associations are defined, a dichotomous key can be constructed to define potential climax communities (plant associations) at a particular site – the habitat type (Pfister 1989).

To obtain an ecologically consistent west-wide classification of habitat types into PVGs, we used the classification of north Idaho forest vegetation (Cooper and others 1991) as a model for defining temperature and moisture gradients. We reasoned that the mix of heterogeneous mountainous topography and climate of north Idaho has created environments representative of most of the forested environments in the west. There were notable exceptions in that the dry and warm ponderosa pine and pinyon-juniper communities were missing. Nevertheless, the dichotomous keys to habitat types in northern Idaho (Cooper and others 1991) were constructed to reflect a moisture gradient in a heterogeneous environment. We hypothesized that under-story plants presented in the north Idaho classification defined water availability bands. Further, when augmented with additional plants found in other regions, moisture bands could be extended over the total range of annual soil temperatures found in conifer forests of the west (Figure 1). Since temperature and moisture interact to limit niches, not all indicators extend over the complete range of temperatures (Figure 1). The idea applied to this

classification is that the maximum drought tolerance of the indicators defines the moisture band in question over the entire temperature gradient (Figure 2). For example, *Clintonia uniflora* was hypothesized to define 30 to 35 inches of annual water availability in cold environments and *Polystichum munitum* defines this same amount of water in a warmer environment. Although indicator species tend to occur in wetter ecosystems (Figure 2), their explicit dry limit could be determined by appropriate drought tolerance experiments. Amounts and pattern of water input, evapotranspiration, and storage capacity of the soil profile also influence the dry limit. Application

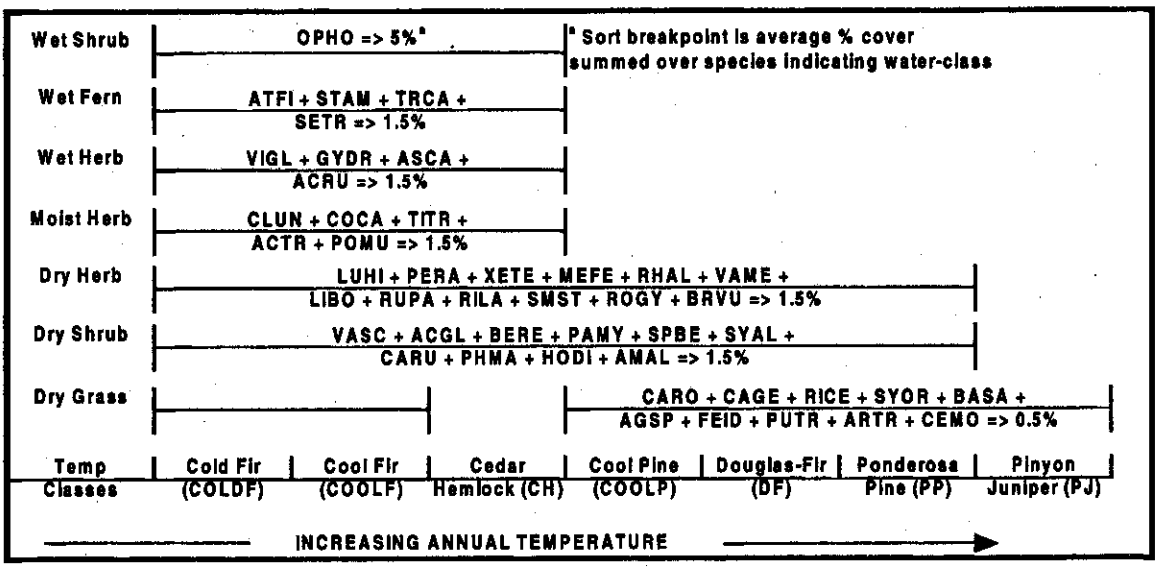


Figure 1. Distribution of water-class indicator species over a temperature gradient defined by climax conifer species

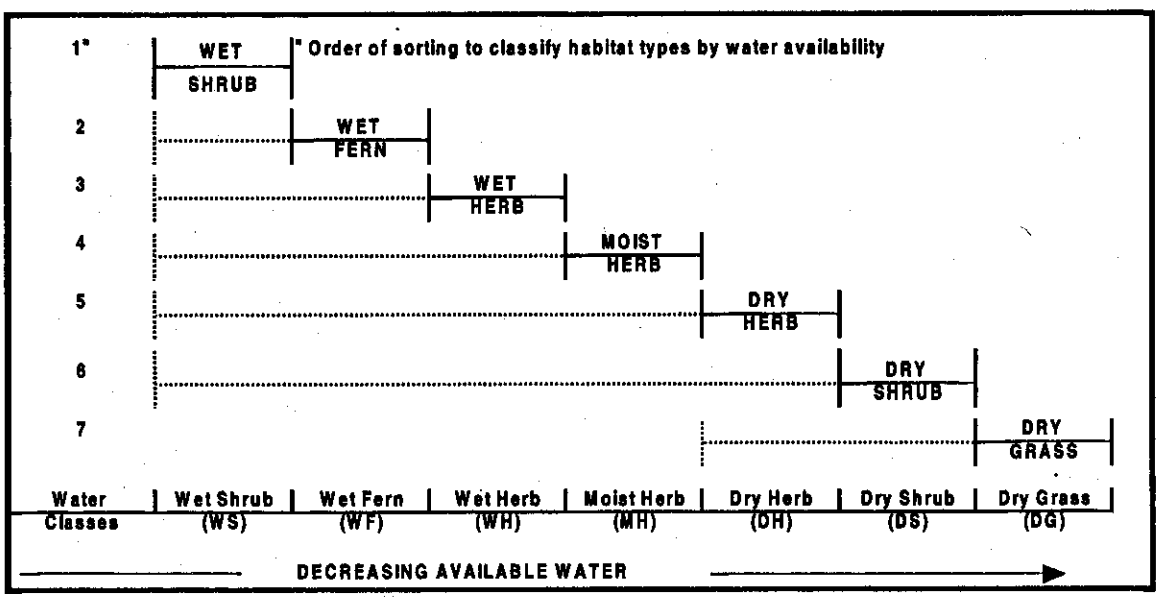


Figure 2. Distribution of water-class indicatore species over water-classes

of this approach also requires the assumption that populations of assumed ecological synonyms do not exhibit geographic variation of their ecophysiological traits. We know that this assumption may not hold with some plants. Nevertheless, the assumption can be tested for important indicator plant species.

Inspection of the dichotomous keys to habitat types produced seven moisture-class groups. These groups were Wet Shrub (WS), Wet Ferns (WF), Wet Herbs (WH), Moist Herbs (MH), Dry-Herbs (DH), Dry-Shrubs (DS), and Dry-Grass (DG) (see Table 1 for list of species in each group). In all, 12 habitat type manuals covering the states of Oregon and Washington east of the crest of the Cascade Mountains, all of Montana, all of Idaho, and all of Utah were utilized. Next, these groups of assumed ecological synonyms (indicators) were used to classify habitat types and phases. Average cover, as given in constancy tables published in the 12 classifications, were extracted to produce a matrix of 631 habitat types (records) x 61 species (fields). Coverage was summed across fields for all members of an indicator group to produce a moisture index for each habitat type. Then all records having an index above a threshold value were removed to form each respective moisture class in an order from wet to dry (Figure 2). Index threshold was set at 1.5% for each class, except the first and last. The threshold for the wettest class (WS) was set at 5% because the class was based on a single relatively large shrub. The threshold for the most dry class (DG) was set at 0.5% because plant coverage is uniformly low at low levels of available soil moisture. In this fashion, each of the 631 habitat types was assigned to a moisture class.

The same logic was applied for establishing a temperature gradient defined by conifer climax species (Figure 3). The association of climax species with temperature is widely accepted but not well proven. However, this assumption can be tested by measuring soil temperature at each plot at a depth of 50cm. A single measurement at 50cm anytime throughout the year gives the average annual temperature of the first meter of soil depth (USDA Soil Conservation Service, 1975). The conifer climax species at any location will be the species exhibiting the most shade tolerance at a specific temperature x moisture intersection. Climax species were grouped into COLD Fir (COLDF), COOL Fir (COOLF), Cedar-Hemlock (CH), COOL Pine (COOLP), Douglas-Fir (DF), Ponderosa Pine (PP), and Pinyon-Juniper (PJ) (see Table 1).

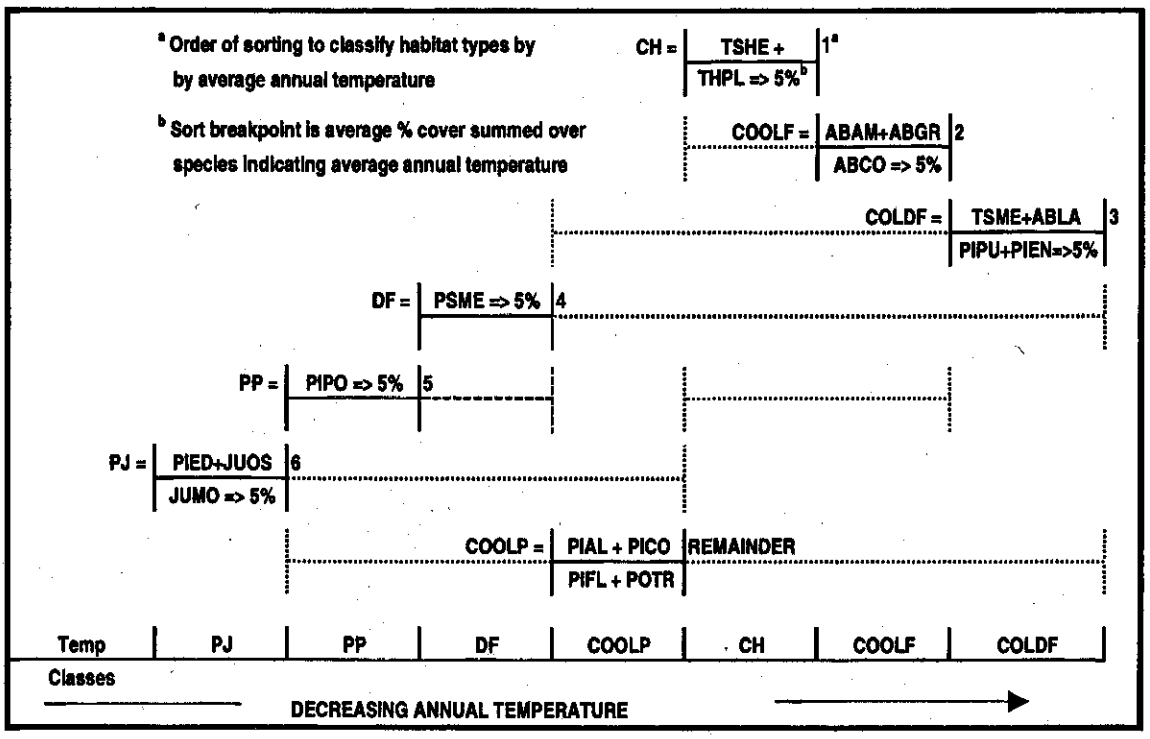


Figure 3. Distribution of temperature-class indicator species over temperature classes

The average-cover matrix was sorted with group removal as described above, except removal was based on a temperature index obtained by summing the average cover values for each climax group. Order of removal from the matrix was decreasing shade tolerance and increasing cold tolerance, then by increasing shade and heat tolerance (Figure 3). The accumulated average-cover threshold for these sorts was 5%. Finally, habitat types that did not reach the summed 5% average-cover index were placed into the remainder class, COOLP (Figure 3). In this fashion, each of the 631 habitat types was assigned to one of seven temperature-class designations. The moisture-class and temperature-class designations were combined to produce 31 distinct PVGs. The 631 habitat types defined in the 12 habitat type manuals were reduced to 30 PVGs (Table 2). One PVG, COOLF/WS, was not represented in the 631 defined habitat types, but it has theoretical existence (the classification is available from the author).

WET SHRUB		**DRY SHRUB**		**CEDAR-HEMLOCK**	
OPHO	*Oplopanax horridum* (Devil's Club)	VASC	*Vaccinium scoparium* (Grouse whortleberry)	TSHE	*Tsuga heterophylla* (Western hemlock)
		ACGL	*Acer glabrum* (Rocky Mountain maple)	THPL	*Thuja plicata* (Western red cedar)
WET FERN		BERE	*Berberis repens* (Creeping Oregon grape)		
ATFI	*Athyrium filix-femina* (Ladyfern)	PAMY	*Pachistima myrsinites* (Myrtle boxwood)	**COOL PINE**	
STAM	*Streptopus amplexifolius* (Twisted-stalk)	SPBE	*Spiraea betulifolia* (Shiny-leaf spirae)	PIAL	*Pinus albicaulis* (Whitebark pine)
TRCA	*Trautvetteria caroliniensis* (False bugbane)	SYAL	*Symphoricarpos albus* (Common snowberry)	PICO	*Pinus contorta* (Lodgepole pine)
SETR	*Senecio triangularis* (Arrowleaf groundsel)	CARU	*Calamagrostis rubescens* (Pinegrass)	PIFL	*Pinus flexilis* (Limber pine)
		PHMA	*Physocarpus malvaceus* (Ninebark)	POTR	*Populus tremuloides* (Quaking aspen)
WET HERB		HODI	*Holodiscus discolor* (Ocean-spray)		
VIGL	*Viola glabella (Pioneer violet).*	AMAL	*Amelanchier alnifolia* (Serviceberry)	**DOUGLAS-FIR**	
GYDR	*Gymnocarpium dryopteris* (Oak fern)			PSME	*Pseudotsuga menziesii* (Douglas-fir)
ASCA	*Asarum caudatum* (Wild ginger)	**DRY GRASS**			
ACRU	*Actaea rubra* (Baneberry)	CARO	*Carex rossii* (Ross sedge)	**PONDEROSA PINE**	
		CAGE	*Carex geyeri* (Elk sedge)	PIPO	*Pinus ponderosa* (Ponderosa pine)
MOIST HERB		RICE	*Ribes cereum* (Squaw currant)		
CLUN	*Clintonia uniflora* (Queen cup beadlily)	SYOR	*Symphoricarpos oreophilus* (Mountain snowberry)	**PINYON-JUNIPER**	
COCA	*Cornus canadensis* (Bunchberry dogwood)	BASA	*Balsamorhiza sagittata* (Arrowleaf balsamroot)	PIED	*Pinus edulis* (Pinyon pine)
TITR	*Tiarella trifoliata* (Coolwart foamflower)	AGSP	*Agropyron spicatum* (Bluebunch wheatgrass)	JUOS	*Juniperus osteosperma* (Utah juniper)
ACTR	*Achlys triphylla* (Vanilla leaf)	FEID	*Festuca idahoensis* (Idaho fescue)	JUMO	*Juniperus monosperma* (One-seed juniper)
POMU	*Polystichum munitum* (Western swordfern)	PUTR	*Purshia tridentata* (Bitterbrush)		
		ARTR	*Artemisia tridentata* (Mountain big sagebrush)		
DRY HERB		CEMO	*Cercocarpus montanus* (Alderleaf mountain mahogany)		
LUHI	*Luzula hitchcockii* (Smooth woodrush)				
PERA	*Pedicularis racemosa* (Sickletop lousewort)	**COLD FIR**			
XETE	*Xerophyllum tenax* (Beargrass)	ABLA	*Abies lasiocarpa* (Subalpine fir)		
MEFE	*Menziesia ferruginea* (Mock azalea)	TSME	*Tsuga mertensiana* (Mountain hemlock)		
RHAL	*Rhododendron albiflorum* (White rhodoendron)	PIEN	*Picea engelmannii* (Engelmann spruce)		
VAME	*Vaccinium membranaceum* (Big huckleberry)	PIPU	*Picea pungens* (Blue spruce)		
LIBO	*Linnaea borealis* (Twinflower)				
RUPA	*Rubus parviflorus* (Western thimbleberry)	**COOL FIR**			
RILA	*Ribes lacustre* (Prickly current)	ABAM	*Abies amabilis* (Pacific silver fir)		
SMST	*Smilacina stellata* (Starry Solomon-seal)	ABGR	*Abies grandis* (Grand fir)		
ROGY	*Rosa gymnocarpa* (Baldhip rose)	ABCO	*Abies concolor* (White fir)		
BRVU	*Bromus vulgaris* (Columbia brome)				

Table 3. List of moisture class and temperature class indicator plants used to classify habitat types

Armillaria distribution and behavior in the Inland Northwest

The 120 plots installed in 1983 were classified by PVG and the results (Table 3) show some clear patterns. First, although sampling was sparse in the DG moisture band, 17 plots fell into the DS band and none supported *Armillaria* (Table 3). The next wettest band was DH, which included 54 plots. Of these, 65% supported only *A. ostoyae* (McDonald unpublished data). The remainder of the 1983 plots fell into the more moist bands. Forty-four of 46 plots (96%) supported both *A. ostoyae* and North American Biological Species

(NABS) X (McDonald unpublished data). Only two plots were located in the COLDF/WF PVG and none supported *Armillaria*. This may indicate an upper limit of soil moisture for the genus.

These findings support the following three hypotheses. First, DG and DS moisture classes are not suitable habitats for any *Armillaria* species. Second, *A. ostoyae* has at least a 0.65 probability of occurring on DF or cooler /DH PVGs. Third, the probability of finding the two *Armillaria* species on 0.04-hectare plots in MH or WF ecosystems is 0.96. These data also indicate that wetter ecosystems may not support *A. ostoyae* and NABS X.

Temp Classes	Water Classes						
	Dry Grass	Dry Shrub	Dry Herb	Wet Herb	Wet Herb	Wet Fern	Wet Shrub
PJ	1						
PP	24	29	1				
DF	19	101	35	2			
COOLP	13	11	11	1			
CH			4	24	10	8	5
COOLF	2	18	45	24	6	8	0
COLDF	30	43	110	13	5	27	1

Table 2 Distribution of 631 inland west habitat types

Temp Classes	Water Classes						
	Dry Grass	Dry Shrub	Dry Herb	Wet Herb	Wet Herb	Wet Fern	Wet Shrub
PJ	0						
PP	0/1	0	0				
DF	0	0/8	6/9	0			
COOLP	0	0	0	0			
CH			0	14/14	7/7	4/4	0
COOLF	0	0/1	18/25	11/12	4/4	0	0
COLDF	0	0/8	11/20	4/5	0	0/2	0

Table 3 Fraction of inland northwest plots with *Armillaria*

Variation of genet behavior in the CH/WH PVG was demonstrated by results from an intensive sampling study on the Priest River Experimental Forest in northern Idaho (McDonald and others 1998). About 1300 isolates were collected from a 2-acre site. These isolates sorted into 7 genets belonging to *A. ostoyae* and NABS X. One NABS X genet dominated the site, occurring as more than 900 isolates. *A. ostoyae* genets varied in their ecological behavior. One genet was found as fans on 114 of 129 trees, while 77% of the occurrences of another genet appeared as epiphytic rhizomorphs. Nearly 100% of the isolates belonging to NABS X were obtained from epiphytic rhizomorphs. After 10 years of observation, none of the NABS X genets have produced basidiomata and only one of the *A. ostoyae* genets has. These multiple individuals also exhibit variation in rhizomorph production, pathogenic aggressiveness, frequency of basidiome production, and potentially, host specificity. Based on these findings, we can hypothesize that highly variable multiple genets of *A. ostoyae* are present in wet ecosystems. The idea of multiple genets is further supported by the initial delineation of genets obtained from the 120 random Inland Northwest plots (McDonald and Martin 1988).

Armillaria in Utah

In 1992, 16 plots were established during a preliminary inspection of Utah forests. These plots were established by stratification of forest type and without regard for expression of disease. Plots were inspected for *Armillaria* signs and symptoms and indicator plants as previously described (McDonald and others1987). In 1993, 32 plots were established at random on four national forests (8 plots per forest) as previously described (McDonald and others1987). A few nonrandom collections made by others augmented the random plots. Our complete collection of plots (Figure 4) are representative of most of the conifer forest ecosystems in Utah. Preliminary determination of genets and their species affiliation shows one genet per plot and all Utah collections belong to *A. ostoyae* (McDonald unpublished data).



Figure 4. Locations of Utah *Armillaria* plots

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	0/3						
PP	0/4	0	0				
DF	0	0/5	0	0			
COOLP	0/2	0/1	0	0			
CH			0	0	0	0	0
COOLF	0/1	1/6	1/1	0	0	0	0
COLDF	1/7	5/12	3/6	0	0	0	0

Table 4. Fraction of Utah plots with *Armillaria*

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	0/3						
PP	0/5	0	0				
DF	0	0/13	6/9	0			
COOLP	0/2	0/1	0	0			
CH			0	14/14	7/7	4/4	0
COOLF	0/1	1/7	19/26	11/12	4/4	0	0
COLDF	1/7	5/20	14/26	4/5	0	0/2	0

Table 5. Fraction of all Inland plots with *Armillaria*

With regard to distribution across ecosystems, Utah *Armillaria* shows both similarities with and differences from the Inland Northwest experience (Table 4). Seventeen randomly located plots fell within the DG moisture band in the PJ, PP, COOLF, and COLDF temperature bands. One of 7 COLDF plots supported *A. ostoyae*. This finding mostly agrees with the Inland Northwest findings. In the case of the DS band, a statistically significant difference (Table 6) may exist, since 5 of 20 COLDF/DS plots supported *A. ostoyae*. On the other hand, in ecosystems one step wetter (COLDF/DH) and one or two steps warmer (DF and COOLF/DS), a regional difference is not apparent (Tables 3, 4, and 6). Distributions across ecosystems for the total data are intriguing (Table 5). *Armillaria* appears to inhabit a band of environments bordered by parallel lines from COLDF/DG to CH/WH and from COLDFF/MH to CH/WF.

Armillaria behavior: Utah vs. Inland Northwest

Are disagreements in distribution by ecosystem in the two regions due to sampling variation or are they due to ecotypic variation of *A. ostoyae*? In light of demonstrated variation among genets at the Priest River Experimental Forest, it seems prudent to consider that ecotypic variation can cause differences in ecological behavior across PVGs. A genetic hypothesis could include genet by genet variation caused by selection for specific environments from preexisting gene pools via spore-rain, phenotypic plasticity, or classic mutation and

recombination. This hypothesis can be tested by measuring reaction norms, which are graphs of environment vs. genotype (Stearns, 1989). They allow visualization of population x treatment interaction, tendency for similar patterns of plasticity, amount of environmental sensitivity of traits, and amount of additive genetic variation (Figure 5). A reaction norm can be measured for any quantitative trait. Some potential *Armillaria* traits are

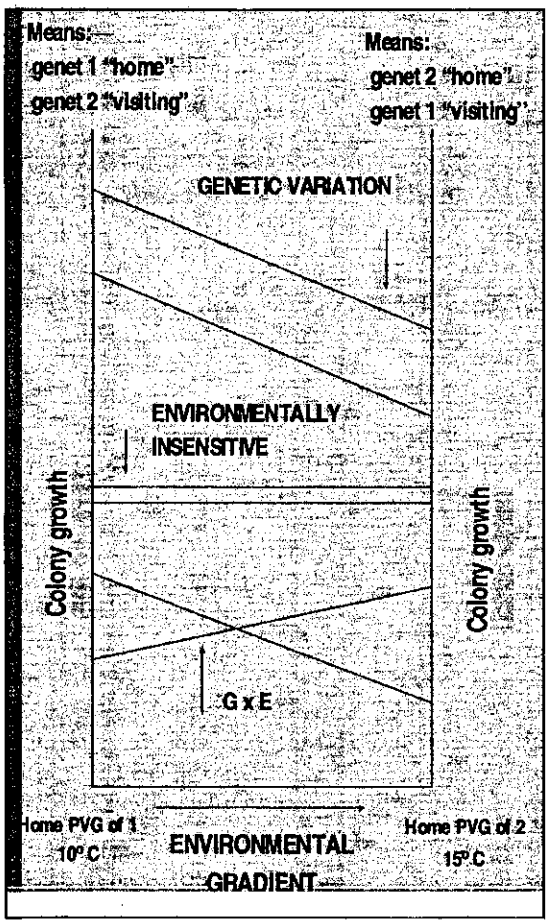


Figure 5. Interpretation of a phenotypic plasticity experiment

		Armillaria Present			
Potential Veg Group	Location	yes	no	% Present	Fisher's Chi SQ
DF/DS	NW	0	8	0	
	Utah	0	5	0	no test
COLDF/DS	NW	0	8	0	
	Utah	5	7	42	0.1
COLDF/DH	NW	11	9	55	
	Utah	3	3	50	1

Table 6. Comparison of *Armillaria* occurrence in overlapping northwest and Utah PVGs (Fisher's exact chi Square)

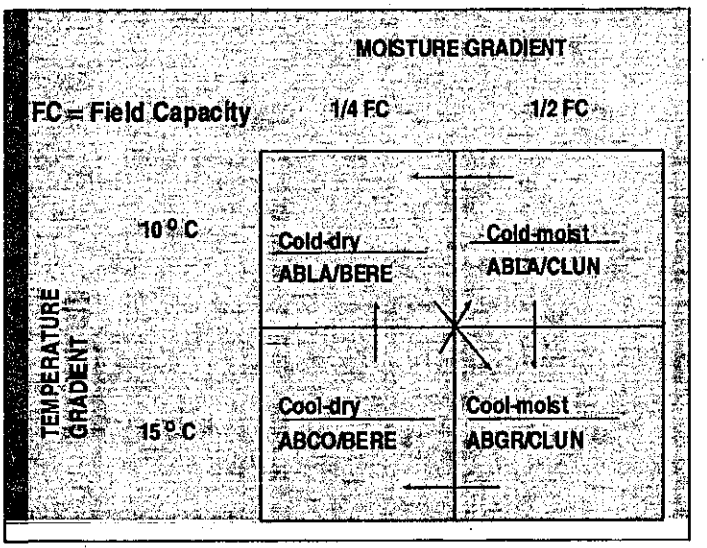


Figure 6. A possible phenotypic plasticity experiment designed to assess ecological genetics of *Armillaria*

respiration, colony growth, rhizomorph production, germ tube growth rate, percent of germination, cold tolerance, heat tolerance, pH tolerance, and nutrient requirements. A potential experiment (Figure 6) could be performed with the addition of soil temperatures taken at a 50cm depth on plots where the *Armillaria* was collected.

Conclusions

This preliminary analysis comparing *Armillaria* populations raises some interesting questions. First, does the limited data collected so far accurately show the true distribution of this important genus over western conifer ecosystems? If it does, then mapping of ecosystems (PVGs) will provide an accurate baseline for managing the fungus – whether to lessen disease impacts or to insure ecosystem function. If distribution is sufficiently limited by environmental constraints, then mapping of current distributions will provide reliable information for the future. On the other hand, if the fungus is expanding its range, explicit knowledge about that expansion will be needed. The suggested genetic experiment is the first step toward obtaining such an understanding of the biology of *Armillaria*. Finally, we have discussed potential new distribution only into more dry ecosystems.

But, new distribution may be similarly limited or mediated into more wet ecosystems. For example, we have observed *A. cepistipes* (*A. sinapina*?) behaving as an aggressive pathogen on dominant Sitka spruce (*Picea sitchensis*) in very wet ecosystems on the Oregon coast (McDonald unpublished data). In addition, *A. ostoyae* was observed causing mortality in Douglas-fir in a wet ecosystem near Lake Quinault on the Washington coast (McDonald unpublished data). Do these instances represent the limited occurrence of relatively rare pathogenic variants that have fitness for unusual environments? Effective management of forested ecosystems will require answers to these questions.

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