

## FIRE, COMPETITION AND FOREST PESTS: LANDSCAPE TREATMENT TO SUSTAIN ECOSYSTEM FUNCTION

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### ABSTRACT

Fire, competition for light and water, and native forest pests have interacted for millennia in western forests to produce a countryside dominated by seral species of conifers. These conifer-dominated ecosystems exist in six kinds of biotic communities. We divided one of these communities, the Rocky Mountain Montane Conifer Forest, into 31 subseries based on the ability of shrubs and forbs to predict soil-moisture regimes and conifers to predict soil-temperature regimes. This classification facilitated correlation of fire regimes, ecophysiological theory, and genetic theory to create an analytical framework for assessing ecological change. Using this tool we assessed likely ecologic impacts resulting from the introduction of white pine blister rust. Because large-scale disturbance, fire and cutting, have been greatly reduced in western ecosystems most heavily impacted by blister rust, their restoration will require large-scale replacement of the role of fire. Reduced net primary productivity is a natural consequence of forest succession. As forests age, photosynthetic and water use efficiencies decline, while decomposition in the standing biomass increases. Most forests reach a point where carbon release exceeds carbon sequestration—the “pathologic rotation.” Effective management of these forces will require exact knowledge, ecosystem by ecosystem, of resource availability and system processing efficiencies. Using the classification presented, theories of competition, ecophysiology, genetics and pest behavior can be combined to examine site-specific ecosystem behavior. Finally, a preliminary plan to achieve process sustainability is presented.

Keywords: Fire regimes, root rot, blister rust, western white pine, habitat types, biotic communities

### INTRODUCTION

Fire, competition for light and water, insects, and microbes have interacted for millennia in the western

United States to produce a forested landscape dominated by the seral or pioneering conifers. Some important species are: ponderosa pine (*Pinus ponderosa*), pinyon pines (*P. monophylla* and *P. edulis*), western white pine (WWP) (*P. monticola*), whitebark pine (*P. albicaulis*), lodgepole pine (*P. contorta*), and western larch (*Larix occidentalis*). Fuels, topography, and weather, in association with wind, insects, and disease produce unique fire regimes (Agee 1997). Either large or small fires, in a geographic sense, can release energy at high or low rates (Agee 1997). Large or small, as well as high or low intensity fires can cause low to high ecological damage, as measured by death to ecosystem dominants (large conifers). Fire regimes vary dramatically over time and space. These regimes are influenced by local conditions. For example, islands of wet sites in a sea of dry sites will take on some of the characteristics of the dry forest and the opposite holds as well (Agee 1998). Since fire has been the dominant recurring historic disturbance in western forests, the key to maintenance of ecosystem function is a full understanding of time-space interactions among fire, management activities, insects, and disease.

The most widespread soil-inhabiting organism causing mortality of forest plants is the shoestring fungus. Root rot of woody plants caused by species of the basidiomycetous genus *Armillaria* damages conifers in forests throughout the western United States. Most conifers and many hardwoods 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, the genus causes occasional damage to Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (McDonald 1991a). 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 all size classes (McDonald 1991a). In higher elevation forests, damage to subalpine fir (*A. lasiocarpa*) and Englemann spruce (*Picea englemannii*) can be significant

(McDonald 1991a). The fungus is seldom found in dry forests dominated by ponderosa pine (McDonald 1991b). Are ecological behavior and occurrence of *Armillaria* predictable at specific locations in conifer forests of the western United States? To examine this question, about 200 plots (0.04 hectares each) were established at random throughout the western United States (McDonald 1998). Habitat type of each plot was recorded to associate occurrence and behavior of *Armillaria* with plant communities (McDonald et al. 1987). Data from these investigations showed that *Armillaria* behavior and occurrence could be predicted over large geographic areas.

During establishment of the *Armillaria* plots, an appreciation of the ecosystem impact of introduced white pine blister rust (WPBR) (*Cronartium ribicola*) was developed. Much of the interior wet forest of northern Idaho was at one time dominated by WWP (Neuenschwander et al. 1999). Introduction of WPBR in 1910 (see McDonald and Hoff 2000) has nearly eliminated WWP from much of its range (Neuenschwander et al. 1999). To understand the overall ecological impact of this introduction, an efficient method for studying the simultaneous ecological interactions among hosts, insects, pathogens, fire, and forest management at scales from local to landscape is needed. In this document, we augment and connect existing ecological frameworks dealing with regimes of fire (Agee 1993), soil temperature (Meurisse 1991), soil moisture (Meurisse 1991), and root rot (McDonald 1991b) to facilitate site-specific management for sustainability of ecosystem function in western forests historically dominated by five needle pines. Our goal is to foster a management philosophy that will ensure maintenance of ecological roles at historic levels for the principal disturbances – fire, native insects, native pathogens, and other microbes.

### **PHYTOSOCIOLOGY: THE ECOLOGICAL CONTEXT**

An ecological context can be achieved through application of ideas embodied in hierarchical classifications of plant communities (Kent and Coker 1992). Much has been published about various methods of community classification (Brown et al. 1998). Ecological classifications have been produced to cover most of the conifer forests of the western United States (Wellner 1989). Most classifications in current use are based on climatic, edaphic, topographic, and topoedaphic climax as outlined for north Idaho (Cooper et al. 1991). These classifications are based on the idea that

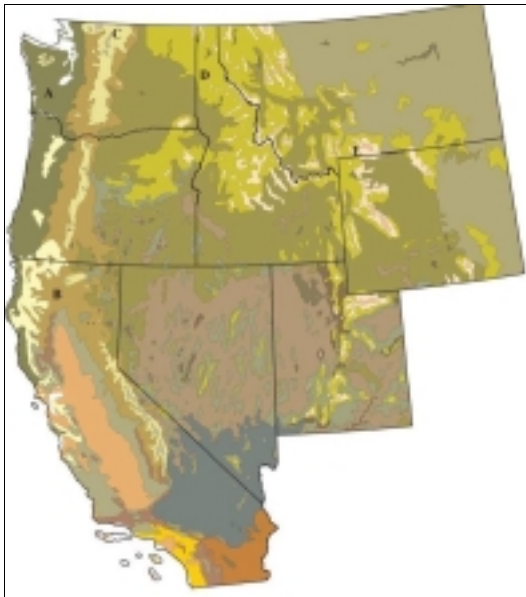
a community of forest plants proceeds through paths of succession to a potential climax association that is typical of a specific site. Key elements are the series or alliance and plant associations or habitat types (Brown et al. 1998). A plant association is simply an abstract taxonomic unit, or plant community, defined by a list of indicator plants compiled by the ecologist who has formulated a specific classification system. The classification is based on plot data collected to assess distributions of native plants. After 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). Since fire usually interrupts succession, potential climax forests are rarely achieved (Fischer and Bradley 1987, Shiplett and Neuenschwander 1994).

These ideas have been used in various ways to assess and understand forested ecosystems. Potential Vegetation Types (PVT), formed by grouping similar habitat types, provided a biophysical link to enable the creation of individual succession models and the mapping of their output (Keane et al. 1996). Potential Natural Vegetation (PNV), mapped by Kuchler (1964), was used as the basis for mapping six historic fire regimes of western North America (Hardy, et al. 1998). Davis et al. (1980) grouped habitat types occurring in the northern Rocky Mountains into fire behavior ecoclasses. Arno (1980) linked fire history to climax series for forests of the Northern Rocky Mountains. We reasoned a similar tactic should facilitate the understanding of ecological aspects of *Armillaria* behavior (McDonald 1991b).

Nevertheless, if ecosystem roles of *Armillaria* were to be understood, an unbiased rationale for grouping habitat types was needed. Thus, a method designed to group previously defined habitat types was constructed on the premise that conifer climax species indicate a temperature gradient and that shrubs and herbs found on the forest floor indicate a moisture gradient (see McDonald 1991b for rationale). Distribution of dominant conifers was loosely connected to specific definitions of soil moisture and temperature regimes (Meurisse et al. 1991). Three regimes representing increasing available moisture (XERIC, USTIC, and UDIC) were paired to three temperature regimes representing increasing temperature (MESIC, FRIGID, and CRYIC). A 3x matrix did not supply enough categories to encompass readily apparent variation in *Armillaria* behavior so we expanded to a 7x matrix (McDonald 1998). In attempting to expand the grouping of habitat types to cover plot data collected in west-

ern Oregon and Washington (McDonald unpublished data), we became aware that connection to an even larger scale was needed.

A system was needed to place behavior of *Armillaria* and other aspects of ecosystem function of specific sites, as describe, by plant association, into a continental context. Plot data describing plant associations needed to be connected to a continental hierarchy. Brown et al. (1998) tied previously described plant associations to continental biotic communities through an eight-level hierarchy. Brown et al. (1998) began at the continental level with “nearctic” and “neotropical” biographical realms (level 1). Our target forests fit into the “natural upland vegetation” hydrologic regime (level 2) of the nearctic biographical realm. The appropriate formation is “forest and woodland” (level 3). Climate zone is “warm-temperate” (level 4) and biotic province is “Rocky Mountain” (level 5). Thus, we will discuss the potential vegetation of the Rocky Mountain Montane Conifer Forest (RMMCF) biotic community (Figure 1). Eighty-two biotic communities, each occupying over 100 km<sup>2</sup>, were mapped (Reichenbacher et al. 1998).



**Figure 1. North American biotic communities in western United States (Brown et al. 1998): (A) Oregonian Coastal Conifer Forest, (B) Cascade Sierran Montane Conifer Forest, (C) Cascade Sierran Subalpine Conifer Forest, (D), Rocky Mountain Montane Conifer Forest. (E) Rocky Mountain and Great Basin Subalpine Conifer Forest. Base map: Environmental Protection Agency, U. S. Department of Energy.**

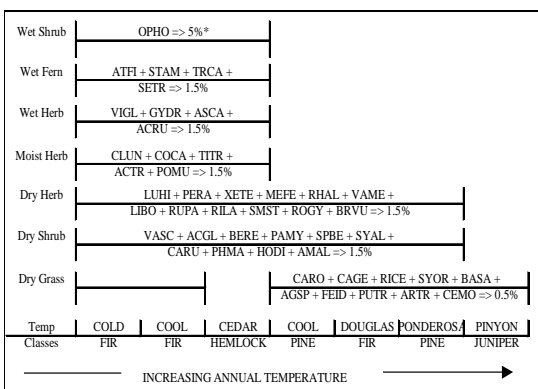
Brown et al. (1998) utilized series for level 6 and associations for level 7. However, here we encounter a problem of number of groups and of confounding interpretation among groups. Over 650 habitat types have been defined for the RMMCF (McDonald unpublished data). If series (level 6) and habitat types (level 7) were used as defined, that would require the mapping and ultimately the management of 650 different ecological units. In addition, habitat types defined by various ecologists may carry identical names yet function differently or carry different names and function the same. Habitat types needed to be correlated across regions (Bourgeron 1989). Strict adherence to the system of Brown et al. (1998) would confound moisture and temperature gradients. In turn, ecosystem processes such as fire, decomposition, and pest activity, influenced by temperature and moisture, would be confounded and therefore not predictable across the landscape. Our suggested solution is to use climax species of conifer dominants to define a temperature gradient and to use understory indicator plants to define a moisture gradient as they do now (see Cooper et al. 1991 Figure 52). Groups of habitat types then become subseries. That is, each series or related groups of series would be putatively subdivided into behaviorally consistent classes, which, in turn, could be mapped under biotic communities in the hierarchical classification. We suggest combining levels 6 and 7 (Brown et al. 1998) into a maximum of 49 classes called subseries.

### Collating Habitat Types to Subseries

To obtain ecologically consistent assemblages of habitat types, we used the classification of northern Idaho forest vegetation (Cooper et al. 1991) as a model for defining temperature and moisture gradients. We reasoned that the mix of heterogeneous mountainous topography and climate of northern Idaho has created a biophysical environment representative of most western forests and the dichotomous key to habitat types in northern Idaho (Cooper et al. 1991) was constructed to reflect a moisture gradient in a heterogeneous environment.

We interpret the key to mean that understory plants presented in the northern Idaho classification indicate water availability bands. Since temperature and moisture interact to limit niches, not all indicators extend over the complete range of temperatures (Figure 2). These bands could be augmented with plants found in other regions (landscapes covered by other classifications) defining the same range of available water (ecological synonyms). In this way, moisture bands could

be extended over the total range of annual soil temperatures found in conifer forests of the RMMCF biotic community (Figure 2). The assumption here is that the maximum drought tolerance of the indicator plant defines the moisture band in question over the entire temperature gradient (Figure 3). For example, we hypothesize that *Clintonia uniflora* defines 30 to 35 inches of annual water availability in cold environments and that *Polystichum munitum* defines the same in a warmer environment. As illustrated (Figure 3), an indicator species value is on the dry limit of its ecological amplitude. Explicit dry limits of indicator plants could be determined by appropriate drought tolerance experiments. Amounts and pattern of water

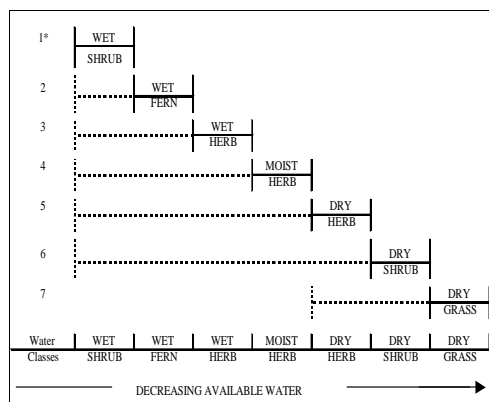


**Figure 2. Distribution of soil-moisture indicator species over a temperature gradient defined by climax conifer species. (\*) Canopy coverage determined from constancy tables of habitat type manuals (see text) summed over all species listed for a moisture class. (see Tables 1 and 2 for species names).**

input, evapotranspiration, and storage capacity of the soil profile also influence the dry limit.

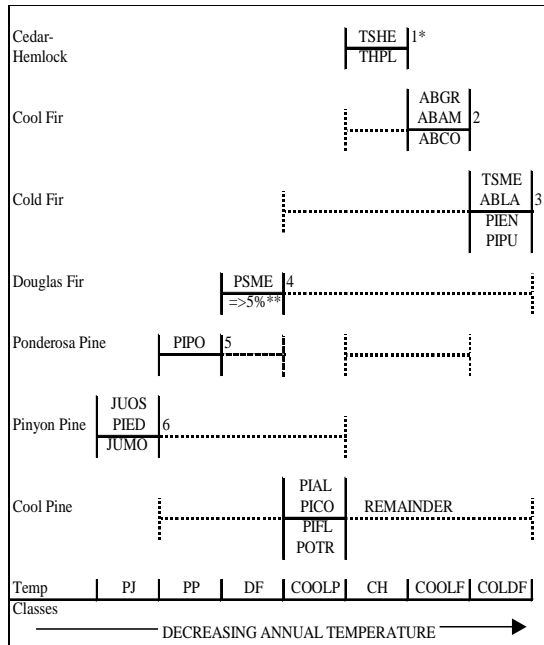
Inspection of the dichotomous keys to habitat types produced seven moisture regimes and seven temperature regimes. Moisture regimes were Wet Shrub (WS), Wet Ferns (WF), Wet Herbs Shrubs (DS), and Dry Grass (DG) and temperature regimes were cold-fir, cool-fir, cedar-hemlock, cool pine, Douglas-fir, ponderosa pine, and pinyon-juniper (see Tables 1 and 2 for list of species in each group). In all, we used 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 (Pfister et al. 1977, Williams et al. 1990, Williams and Lillybridge 1983, Johnson and Clausnitzer 1992, Johnson and Simon 1987, Cooper et al. 1991, Topik et al. 1988, Williams and Smith 1991, Steele et al. 1981, Steele et al. 1983; Youngblood and Mauk 1986; Mauk

and Henderson 1984). Even though manuals for the east slope of the Cascade Mountains belong to the Cascade-Sierran biotic province (Figure 1), we did not apply the distinction for this exercise. 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 3). 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 driest 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.



**Figure 3. Distribution of soil-moisture indicator species by soil-moisture class illustrates ecological amplitude and importance of sort order to define class. (\*) Order of sorting canopy coverage data obtained from combined constancy tables (see text for references).**

The same logic was applied for establishing a temperature gradient defined by conifer climax species (Figure 4). The association of climax species with temperature is widely accepted but not well-proven. Measurement of soil temperature at each plot at a depth of 50cm (Meurisse et al. 1991) would test this assumption. The 50 cm temperature is one of the parameters used to define soil-temperature regimes. 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



**Figure 4. Distribution of soil-temperature indicators by soil-temperature class illustrates ecological amplitude of shade tolerance over putative soil-temperature gradient. (\* = sort order to define class, \*\* = canopy coverage sorting index computed from data obtained from constancy tables -see text for references).**

grouped into cold-fir, cool-fir, cedar-hemlock, cool-pine, Douglas-fir, ponderosa pine, and pinyon-juniper (see Table 2). 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. Records were removed from the matrix by decreasing shade tolerance and increasing cold tolerance, then by increasing shade and heat tolerance (Figure 4). 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 4). In this fashion, each of the 631 habitat types was assigned to one of seven temperature-class designations.

Moisture-class and temperature-class designations were combined to produce 31 distinct subseries. The 631 habitat types defined in the 12 habitat type manuals were reduced to 30 sub-series (Table 3). One sub-series, CoolF/WS, was not represented in the 631 defined habitat types, but it has theoretical existence. The classification is available from the authors. It is important to note that mapping of subseries would enable geographic mapping of ecological function, in-

<b>WET SHRUB (WS)</b>	
OPHO	<i>Oplopanax horridum</i> (Devil's Club)
<b>WET FERN (WF)</b>	
ATFI	<i>Athyrium filix-femina</i> (Ladyfern)
STAM	<i>Siretopus amplexifolius</i> (Twisted-stalk)
TRCA	<i>Trautvetteria carolinensis</i> (False bugbane)
SETR	<i>Senecio triangularis</i> (Arrowleaf groundsel)
<b>WET HERB (WH)</b>	
VIGL	<i>Viola glabella</i> (Pioneer violet).
GYDR	<i>Gymnocarpium dryopteris</i> (Oak fern)
ASCA	<i>Asarum caudatum</i> (Wild ginger)
ACRU	<i>Actaea rubra</i> (Baneberry)
<b>MOIST HERB (WH)</b>	
CLUN	<i>Clintonia uniflora</i> (Queen cup beadlily)
COCA	<i>Cornus canadensis</i> (Bunchberry dogwood)
TITR	<i>Tiarella trifoliata</i> (Coolwart foamflower)
ACTR	<i>Achlys triphylla</i> (Vanilla leaf)
POMU	<i>Polystichum munitum</i> (Western swordfern)
<b>DRY HERB (DH)</b>	
LUHI	<i>Luzula hitchcockii</i> (Smooth woodrush)
PERA	<i>Pedicularis racemosa</i> (Sickletop lousewort)
XETE	<i>Xerophyllum tenax</i> (Beargrass)
MEFE	<i>Menziesia ferruginea</i> (Mock azalea)
RHAL	<i>Rhododendron albiflorum</i> (White rhododendron)
VAME	<i>Vaccinium membranaceum</i> (Big huckleberry)
LIBO	<i>Linnaea borealis</i> (Twinflower)
RUPA	<i>Rubus parviflorus</i> (Western thimbleberry)
RILA	<i>Ribes lucustre</i> (Prickly current)
SMST	<i>Smilacina stellata</i> (Starry Solomon's-seal)
ROGY	<i>Rosa gymnocarpa</i> (Baldhip rose)
BRVU	<i>Bromus vulgaris</i> (Columbia brome)
<b>DRY SHRUB (DS)</b>	
VASC	<i>Vaccinium scoparium</i> (Grouse whortleberry)
ACGL	<i>Acer glabrum</i> (Rocky Mountain maple)
BERE	<i>Beberis repens</i> (Creeping Oregon grape)
PAMY	<i>Pachistima myrsinites</i> (Myrtle boxwood)
SPBE	<i>Spiraea betulifolia</i> (Shiny-leaf spiraea)
SYAL	<i>Symphoricarpos albus</i> (Common snowberry)
CARU	<i>Calamagrostis rubesens</i> (Pinegrass)
PHMA	<i>Physocarpus malvaceus</i> (Ninebark)
HODI	<i>Holidiscus discolor</i> (Ocean-spray)
AMAL	<i>Amelanchier alnifolia</i> (Serviceberry)
<b>DRY GRASS (DG)</b>	
CARO	<i>Carex rossii</i> (Ross sedge)
CAGE	<i>Carex geyeri</i> (Elk sedge)
RICE	<i>Ribes cereum</i> (Squaw current)
SYOR	<i>Symphoricarpos oreophilus</i> (Mountain snowberry)
BASA	<i>Balsamorhiza sagittata</i> (Arrowleaf balsamroot)
AGSP	<i>Agropyron spicatum</i> (Bluebunch wheatgrass)
FEID	<i>Festuca idahoensis</i> (Idaho fescue)
PUTR	<i>Purshia tridentata</i> (Bitterbrush)
ARTR	<i>Artemisia tridentata</i> (Mountain big sagebrush)
CEMO	<i>Cercocarpus montanus</i> (Alderleaf mountain mahogany)

**Table 1. List of plant species used to indicate soil-moisture regimes in the Rocky Mountain Montane Conifer Forest biotic community.**

cluding behavior of fire, insects, diseases, and decomposition.

**FIRE-ECOLOGY AND SUBSERIES**

Agee (1993) classified fire behavior in western forests into three regimes based on moisture and temperature gradients determined by plant associations. Davis et

<b>COLD FIR</b>	
ABLA	<i>Abies lasiocarpa</i> (Subalpine fir)
TSME	<i>Tsuga mertensiana</i> (Mountain hemlock)
PIEN	<i>Picea engelmannii</i> (Engelmann spruce)
PIPU	<i>Picea pungens</i> (Blue spruce)
<b>COOL FIR</b>	
ABAM	<i>Abies amabilis</i> (Pacific silver fir)
ABGR	<i>Abies grandis</i> (Grand fir)
ABCO	<i>Abies concolor</i> (White fir)
<b>CEDAR-HEMLOCK</b>	
TSHE	<i>Tsuga heterophylla</i> (Western hemlock)
THPL	<i>Thuja plicata</i> (Western red cedar)
<b>COOL PINE</b>	
PIAL	<i>Pinus albicaulis</i> (Whitebark pine)
PICO	<i>Pinus contorta</i> (Lodgepole pine)
PIFL	<i>Pinus flexilis</i> (Limber pine)
POTR	<i>Populus tremuloides</i> (Quaking aspen)
<b>DOUGLAS-FIR</b>	
PSME	<i>Pseudotsuga menziesii</i> (Douglas-fir)
<b>PONDEROSA PINE</b>	
PIPO	<i>Pinus ponderosa</i> (Ponderosa pine)
<b>PINYON-JUNIPER</b>	
PIED	<i>Pinus edulis</i> (Pinyon pine)
JUOS	<i>Juniperus osteosperma</i> (Utah juniper)
JUMO	<i>Juniperus monosperma</i> (One-seed juniper)

**Table 2. List of conifer species used to indicate soil-temperature regimes.**

Temp Classes	Soil-Moisture Classes						
	DG	DS	DH	MS	WH	WF	WS
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 3. Classification of 631 habitat types (see text for references) into 31 subseries (defined in text). (\* 1 = number of Pinyon-Juniper/Dry-Grass habitat types out of 631 habitat types listed in constancy tables, i. e. the ColdF/Dry Herb subseries contained 45 habitat types).**

al. (1980) grouped habitat types occurring on the Lolo National Forest in western Montana into fire groups. Habitat types occurring in Montana east of the continental divide (Fischer and Clayton 1983), in central Idaho (Crane and Fischer 1986), in western Montana (Fischer and Bradley 1987), in the woodland of Utah (Bradley et al. 1992a) and in eastern Idaho and western Wyoming (Bradley et al. 1992b) were subsequently grouped. This list included several of the habitat type manuals used in this study.

**Resource Competition Classes**

To understand the connections among fire, pests, and conifer ecophysiology, let's turn to an ecological theory about competition. When we reduced the RMMCF fire groups described for Montana, Idaho, and Utah to Agee's (1993) three regimes, three kinds of competition emerged that could be attributed to subseries on the basis of the thinning effects of fire. The light-water-tradeoff theory states that plants cannot simultaneously have high tolerance for low levels of both water and light (Smith and Huston, 1989). This means that ongoing processes of natural selection and phenotypic plasticity (Stearns, 1989; Nijhout, 1999) can create different sorts of populations depending on selection environment through time. Thus, low intensity-high frequency fire regimes should stimulate dominant conifers to compete for water first and light second. High intensity-low frequency fire regimes should foster competition for light. Then the moderate intensity-moderate frequency regimes should be highly variable and therefore a more difficult evolutionary problem. Thus, putative genetic responses could have created three discernible ecophysiological structures on the landscape: water-limited, light-limited, and transitional or water regulated (Table 4).

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	1*						
PP	24	29	1				
DF	19	101	35	2			
CoolP	13	11	11	1			High Intensity Fires
CH			4	24	10	8	5
CoolF	2	18	45	24	6	8	0
ColdF	30	43	110	13	5	27	1
Water Competition	Transition		Light Competition				

**Table 4. Connection between resource competition (water, transition, and light) and fire regimes (low, moderate, and high severity).**

We postulate that moisture and temperature regimes characteristic of a particular environment interact through time with a fire regime to produce a characteristic range of conifer phenotypes. To consider how fire, genes, and climate interact to create particular phenotypes, we need to consider additional theories. Ecologists have developed the notion that ecophysiological aspects of individual plants can be thought of as a factory (Bloom, et al. 1985). This theory is known as ecological econometrics. Trees acquire resources (water, nutrients, and light). They produce revenue (fixed carbon); they build new factories (replacements and additions). Trees save resources and revenue in storage and incur losses and forced transfers. They have pest-mediated extractions (Harvey et al. 1994), pest and mycorrhizae support payments, and mycorrhizae mediated forced transfers to competing plants (Simard et al. 1997).

We conclude that natural selection and/or phenotypic plasticity generate factories (in the sense of Bloom et al. 1985) designed for specific environments. Selection and phenotypic plasticity are constrained by existing genes, so species and ecotypes within species will respond to environmental pressures differently. Finally, some plastic physiological traits, such as sapwood/heartwood and root/shoot ratios may become fixed. The distribution of subseries for the RMMCF biotic community into resource classes is depicted in Table 4.

**Water-limited Forests**

Water-limited subseries forests include the classic open western forests dominated by ponderosa pine. These include the pure ponderosa pine series as well as the dry portions of the Douglas-fir, grand fir, white fir, subalpine fir and lodgepole pine series. Large size, short fire return interval, and low fire intensity characterize this fire regime. Patch size (opening large enough to sustain regeneration) is very small (0.25 ha or less) (Agee, 1998). The common result in these ecosystems is an all-aged stand of a fire-resistant dominating seral species. So long as the fires continue, the stands are thinned and competition for water is reduced. Individual trees that develop in this environment can maximize the ecological factory to compete for a limited water resource and contend with other environmental stresses such as insect and fungal pests. *Armillaria* is rarely found in these subseries (Table 5), but bark beetles are of prime importance (Keen 1936). One possible scenario is that as trees age various econometric efficiencies decline and at about 400 to 500 years of age they lose their ability to repel pest attacks. In

the water-limited subseries, most fire patches occur where pest-killed old growth burns (Agee 1998). Agee (1993) provides an excellent discussion of the interaction of fire and stand development in this sub-series.

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	1*		Transition				
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
	Water Limited		Light Limited				

Legend	Armillaria NABSI			Armillaria NABSX		
	Seral	2nd Seral	Climax	Seral	2nd Seral	Climax
Low impact	Rare	Rare	Rare	None	None	None
<i>A. ostoyae</i> climax	Tolerant	None	Diseased	None	None	None
Armillaria complex	Tolerant	Diseased	Tolerant	Tolerant	Diseased	Diseased
Both climax	Tolerant	Tolerant	Diseased	Tolerant	Diseased	Diseased

**Table 5. Regimes of *Armillaria* root disease (McDonald unpublished) in the Rocky Mountain Montane Conifer Forest.**

**Water-regulated Forests**

All but two of the transitional subseries have moderate severity fires. Most upland stands are even-aged serals in 20 to 200 ha patches. A fire return interval of 25 to 75 years can create multi-aged stands of fire-resistant seral species. Some multi-aged climax stands may survive in riparian zones. If upland fires burn with sufficient intensity, riparian zones may be consumed (Agee 1998). The interaction of location with fire regime is evident (Table 6) where one transitional sub-series, Cedar Hemlock/Dry Herb is mixed-severity while another, CoolFir/Dry Herb, is moderate severity. The first is found as dry islands in a sea of wet while the second occurs as wet islands in a sea of dry. *Armillaria* is found in many subseries of the regime (Table 5) and defoliators are very active (McDonald 1985).

**Light-limited Forests**

Agee (1993) does not segregate his discussion to biotic community and lumps together behavior of forests residing in the Oregonian Coastal Forest, Cascade-Sierran Montane Forest, and Rocky Mountain Montane Conifer Forest biotic communities (see Figure 1). Regarding the interaction of fire, climate, and genes, the three communities may behave similarly. Although Agee's (1993) book provides an excellent discussion

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	1*		Moderate				
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
	Low		Mixed		High		Rare
Legend							
Fire Regime	Under-burn	Mixed severity	Replacement	Size			
Low	5-20 yr	Rare	Rare	1-2000 ha			
Moderate	25-75 yr	25-75 yr	150-300 yr	20-100 ha			
Mixed	few	50-100 yr	150-300 yr	200-2000 ha			
High	Rare	100+ yr	300-400 yr	500-50,000 ha			
None	none	Rare	600+ yr	Variable			

**Table 6. Five fire regimes defined by severity and patch size mapped to 31 subseries within the Rocky Mountain Montane Conifer Forest biotic community. (\*) = number of habitat types grouped to subseries.**

about fire ecology of most of the subseries in our proposed classification, the wet inland forests of the RMMFC were neglected.

Agee’s (1993) inclusion of these cedar/hemlock and wet grand fir forests in his chapter on mixed conifer forests highlights a problem with his classification and discussion of fire ecology in Pacific Northwest forests. Our more detailed classes point to an important distinction. We think three regimes are needed to describe fire behavior in the light-limited subseries. Because our classification of forest ecosystems divides series along a moisture gradient we can clearly distinguish dry to wet gradients in the western hemlock/western red cedar, grand fir/white fir, and spruce/sub-alpine fir/mountain hemlock series.

Agee (1993) discusses a wet western hemlock high severity fire regime characterized by a 900-year fire return interval. A dry western hemlock variable severity regime characterized by a 130 to 150-year stand replacement interval and a 65-75 year return for patchy occurrence of fire somewhere in the stand is discussed. This regime describes the mixed severity regime presented by Zack and Morgan (1994). In addition, Agee (1993) and Zack and Morgan (1994) state that certain very wet forest ecosystems see very little fire. Thus, we divide the light-limited subseries into three fire regimes: mixed severity, high severity, and none. The mixed severity regime falls midway between Agee’s

moderate severity and high severity. Moderate severity regimes have almost as much underburning as low severity regimes (Agee 1998), while mixed severity regimes have little. On the other hand, high severity regimes create large patches (Agee 1998), while mixed severity regimes create small patches (Zack and Morgan 1994). Now, we simply place Agee’s three regimes and the two additional regimes, mixed severity and none, on the classification table (Table 6).

**WESTERN WHITE PINE FORESTS: MESIC LIGHT-LIMITED SUBSERIES**

A major unnatural disturbance has impacted the mesic subseries of the RMMCF. Introduction of WPBR and the subsequent removal of a vital component from these forests is the most important forest health problem in the RMMCF and several other biotic communities as well (McDonald and Hoff 2000). We will use the tools developed above to examine this issue.

The mesic portion of the light-limited competition group (Table 7) is located in a region that has heavy winter snow, a deep ash cap, and little rain in July and August. On about 2.5 million ha of this region, WWP was a modifier keystone species prior to the introduction of WPBR (Neuenschwander et al 1999). Modi-

Temp Classes	Water Classes						
	DG	DS	DH	MH	WH	WF	WS
PJ	1*		Moderate				
PP	24	29	1				Westen White Pine Subseries
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
	Low		Mixed		High		Rare

**Table 7. Habitat types capable of supporting western white pine and their association with moderate, mixed and high severity fire regimes. (\*) = number of habitat types grouped to each subseries.**

fier keystones are those species whose loss leads to significant changes in ecosystem structure, materials, and energy flows (see Mills et al. 1993 for further discussion of modifier keystone species). WPBR and salvage logging (in this case, total removal of WWP stems and very little else), has reduced the area to about 100,000 ha (Neuenschwander et al. 1999). Historic mixed and high severity fires in these light-limited ecosystems created a landscape dominated by 200 ha to 40,000 ha even-aged stands of seral species. On the



uplands, succession in even-aged stands was usually interrupted by stand replacement fire at about 200 years (Zak and Morgan 1994) (Figure 5).



**Figure 5. Interruption of stand succession by stand replacement fire at an upland site on the Clearwater National Forest. USFS photo taken August 13, 1925.**

The CoolF/Dry Herb subseries, the most dry of the light-limited group, is associated with two situations. In the Blue Mountains of northeastern Oregon and the northern Rocky Mountains of western Montana, this sub-series occurs as islands of wet forests in a sea of dry forest where the moderate severity regime and its associated under-burning tends to remove WWP. Thus, the fire resistant species (ponderosa pine, western larch, and Douglas-fir) gain a competitive advantage. Although present in these situations, WWP does not dominate.

However, if CoolF/Dry Herb is located in a sea of wet forests, as in northern Idaho, then the mixed severity regime will be most prevalent. In this situation, most of the stand could be dominated by WWP and the fire-resistant seral species would dominate in a few relatively small patches. Seral species in these northern Rocky Mountain forests are tolerant of root rot organisms, especially members of the genus *Armillaria*. Meanwhile, secondary serals such as Douglas-fir and grand fir are highly susceptible to *A. ostoyae*. One report states that Douglas-fir seldom reaches 100 years in age (Rockwell 1917). The climax species western hemlock and western red cedar are very susceptible to a host of butt and heart rots, especially *Armillaria* North American Biological Species X (Table 5). In northern Idaho sawtimber, 18% of the western red cedar, 66% of the grand fir, and 100% of the western hemlock stems were not merchantable due to rot columns (Rockwell, 1917).

WWP is a species that requires full sun for optimum growth and establishes very efficiently on highly disturbed surfaces, especially after a stand replacement fire (Figure 6). Seeds are wind-disseminated up to 800 m. They can survive up to four years in duff and they germinate well on both burned and unburned mineral soil (Graham 1990). Recent comparisons of 25-year-old blister-rust resistant WWP stands with development of neighboring stands without WWP show some potentially interesting influences of canopy structure. A young WWP-dominated stand lets enough light through the canopy for rich shrub and lichen layers to develop; yet, establishment of more shade-tolerant competing conifers is suppressed, as observed by one of us (GIM). This difference in canopy structure may also impact the dynamics of snow-pack accumulation and removal, such that landscape hydrologic processes could change in the absence of WWP. The historic landscape composed of forests in this group of subseries presented mostly even-aged stands 200 to 2000 ha in size. They included mixtures of Douglas-fir, grand fir, western larch, and WWP. Many stands also included suppressed western hemlock and western red cedar. Western white pine composition varied from 15% to 100% and average composition in number of stems was about 32% (Rockwell 1917). The landscape would have included some small patches (0.5 to 10 ha) of multi-aged stands of fire-resistant Douglas fir and western larch. An occasional upland stand would have escaped stand replacement fire and succession would have continued to typical old, uneven-aged climax structure. In riparian zones, small 1 to 100 ha patches of all-aged stands of climax species would have escaped stand replacement fire.



**Figure 6. Rapid and complete western white pine regeneration after a stand replacement fire. USFS photo taken in 1939.**

WWP forests generally have sufficient moisture to support light-limited competition. Before introduction of WPBR, closed, single-layer canopies were common in forests 30 to 300-years old (Figure 7, 8, 9, and 10). Transitional and water-limited ecosystems are found in patches of thin ash cap, at low elevations, in areas of low precipitation on the eastern, southern and west-



**Figure 7. Light-limited competition illustrated in a naturally regenerated 35-year-old white pine stand in northern Idaho. USFS photo taken in 1935.**



**Figure 8. Even-aged, light-limited upland succession illustrated in an 80-year-old white pine stand in northern Idaho. USFS photo taken in 1935.**

ern edges, and/or steep south-facing slopes. Many riparian zones have sufficient moisture to prevent burning and these developed classic all-aged stands of climax species. As stated above, succession of the even-aged WWP stands was usually interrupted by stand replacement fire at about 200 years. Sometimes upland sites escaped stand replacement fire long enough for climax species to dominate (Figure 11). These species require more resources than seral species (Harvey et al. 1998) and they are more prone to heart and butt rots (Rockwell 1917, Maloy and Gross 1963). This means that they are subject to elevated rates of decom-



**Figure 9. Even-aged, light-limited upland succession illustrated in a 160-year-old white pine stand in northern Idaho. USFS photo taken in 1935.**

position in live stems. Reduced photosynthesis efficiency, coupled with the elevated rate of decomposition, leads to rapid onset of the pathologic rotation (see Baxter 1952) where decomposition in live and standing trees exceeds carbon fixation. In central Idaho, stands dominated by climax species had more disease at 90 years of age than stands dominated by seral species had at 150 years of age (Kolb et al. 1998).

On the dry portion of these subseries, small patches of multi-aged fire-resistant species dominated. WWP experiences high mortality in prescribed burns after harvest or in underburns before harvest (Figure 12), because its bark is thin. Studies designed to measure the tolerance of WWP to fire were not found. We conclude that WWP will be removed where mixed severity fire visits and seral competitors such as western larch, ponderosa pine and Douglas-fir would be favored. All-aged stands of climax species dominated on the wettest subseries where little fire occurred (Table 7).



**Figure 10. Late seral stage in a light-limited 400 year-old western white pine stand in northern Idaho. USFS photo taken in 1930.**

#### **Classic Silviculture in the Western White Pine Subseries**

For many years the preferred management of WWP was a 40 to 200 ha clearcut. In the mid-70s, size was reduced to about 20 ha (Figure 13). All snags were felled and then the cut was burned. The idea was to emulate the ecological effects of a stand replacement fire. Early on, plantations were established among the snags, but fear of re-burns (Figure 14) and concerns about safe logging eliminated the practice of leaving snags. In terms of landscape ecology, the classic clearcut demonstrated several problems. Its regular shape draped over the landscape without regard to topographic features did not match the pattern of a stand replacement fire. Riparian areas were not given any special consideration. Most biomass was removed and that remaining was placed directly on the forest floor. Road density was high and not generally designed to any exacting ecological standards. One of the most



**Figure 11. Endpoint of succession, upland climax stand that has moved well into the “pathologic rotation,” on the Coeur d’Alene National Forest in northern Idaho. USFS photo taken in 1934.**



**Figure 12. High fire-caused mortality in a controlled underburn (no crown fire) in a natural northern Idaho western white pine stand. USFS photo taken in 1927.**

serious flaws was size. Placing 20 ha patches across the entire landscape would produce much fragmentation. An additional ecological process that might be lost is site disturbance caused by falling snags. This action can lead to significant mixing of soil horizons, as shown for wind throws in Alaska (Bormann et al. 1995).



**Figure 13. Classic clearcut on the Coeur d'Alene National Forest in northern Idaho. USFS photo taken in 1952.**



**Figure 14. Re-burn of a stand after a stand replacement fire in the Pack River drainage of northern Idaho. USFS photo taken in 1934.**

### THE FUTURE

We now stand at a crossroad. Direct mortality caused by the foreign microbe and indirect mortality caused by salvage logging designed to capture expected mortality has removed sufficient WWP individuals to alter its ecological role as a keystone species over significant portions of its former range. Canopy openings of historic proportions (200 to 40,000 ha) have been curtailed. Source of seed is so reduced that even a much increased regeneration opportunity afforded by a large fire may not be a sufficient remedy. Blister rust remains a daunting problem that needs consideration (Hoff et al. 2000). Attainment of near-historic landscape patterns in these light-limited ecosystems requires significant restoration of the type suggested by Tomback et al. (2000) for whitebark pine ecosystems. Such management, while biologically feasible, demands political will and public resources.

The alternative to restoration is to allow these forests to continue along current successional pathways to an all-aged climax condition. Relative to restored forests; these forests would fix less photosynthate and si-

multaneously release more carbon from accelerated decomposition in standing live trees. Because less light (energy) would reach the forest floor, the rate of decomposition of down woody biomass would slow enough to increase fuel loads. Increased mortality caused by root rots and other pests would also increase fuel loads. The all-aged climax forest structure will have more fuel ladders and place a larger portion of site nutrient capital in the canopy (Harvey et al. 1998) than the restored forest.

Increased numbers of standing dead, dead and down, standing decomposing, and living trees would likely cause a shift in the fire regime of these forests. A historic regime dominated by high severity fire (see Table 6) with some mixed severity fire would most likely shift to mostly mixed severity fire with moderate severity fire on the drier sites. Such a shift is potentially damaging to impacted ecosystems. With WWP at its historic density, the stand replacement interval was about 200 years and the fire return interval somewhere in the stand was about 50 years. If ignition frequency remained the same without WWP, stand-replacement fires should happen about every 100 years because the increased fuel loads and ladders should lead to more crown fires. Increased heat on the forest floor, caused by increased amounts of downed fuel, and increased nutrient capital in the canopy would both accelerate ecological damage caused by burning. The loss of the ability of WWP to rapidly recapture the burned landscape could lead to an increased occurrence of shrub fields and a further decrease in the ability of the 2.5 million ha to fix carbon, stabilize soil, and contribute high quality water. Restoration of WWP to its modifier keystone role seems to be the prudent path. Restoration is, in the final analysis, an effective strategy of fuel management.

### A Suggested Restoration Strategy

Fire behavior models could be applied to define a potential burn pattern (Figure 15). Regeneration cutting would emulate these patterns to provide for WWP establishment. Ragged cuts encompassing about 200 ha would be characterized by a complex pattern of leave-trees and only riparian areas expected not to burn would be protected. We know this suggestion is in disagreement with current guidelines in INFISH and PACFISH (Quigley 1996). However, current regulations that require leave strips on all intermittent and live streams may result in leaving so much fuel as to place restoration efforts at risk. For example, applying current regulations to the burned area depicted (Figure 15) would remove about 50% of the burned area from treatment.



**Figure 15.** Landscape view of a 200 ha fire in northern Idaho showing complex burn pattern. B-1 = burned hot enough to destroy most of the duff layer, M-1 = most of the duff did not burn (duff damage estimated by production of *Ribes* plants. USFS photo taken in 1933.

A more prudent strategy that could reduce erosion in the long run would be to simulate the burning of riparian areas in an entire drainage as depicted and then prevent all disturbance for 150 to 200 years. This approach would come closest to mimicking historic patterns for large watersheds.

Until we learn how to substitute for the beneficial ecological effects of fire (see Harvey et al. this volume), the regeneration area would need to be broadcast burned. Following burning, an appropriate rust-resistant stock (Hagle et al. 1989) should be planted among the snags (Figure 16). Principles of integrated blister



**Figure 16.** Western white pine plantation established in 1916 after a stand replacement fire at Cedar

**Creek on the St. Joe National Forest in northern Idaho. USFS photo taken in 1932.**



**Figure 17.** Landscape view of pristine 100-year-old western white pine stand in northern Idaho. USFS photo taken in 1932.



**Figure 18.** Pristine 250-year-old stand dominated by western white pine on the Clearwater National Forest in northern Idaho. USFS photo taken in 1933.

rust management (Hagle et al. 1989) should also be applied, as needed for the next 100 years. The developing stand should be left to normal successional processes for another 50 to 100 years (total age 150 to 200 years). Such a program could restore the landscape near to what it once was (Figure 17). This action would produce individual stands with historic canopy structures (Figure 18), sustain near-historic levels of productivity, and minimize erosion. The end result of restoration would create suitable habitat for lynx, grizzly bear, salmon, and other animals that made their home in these forests.

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