United States
Department of
Agriculture

Forest Service

Pacific Northwest
Region

**Umatilla National
Forest**

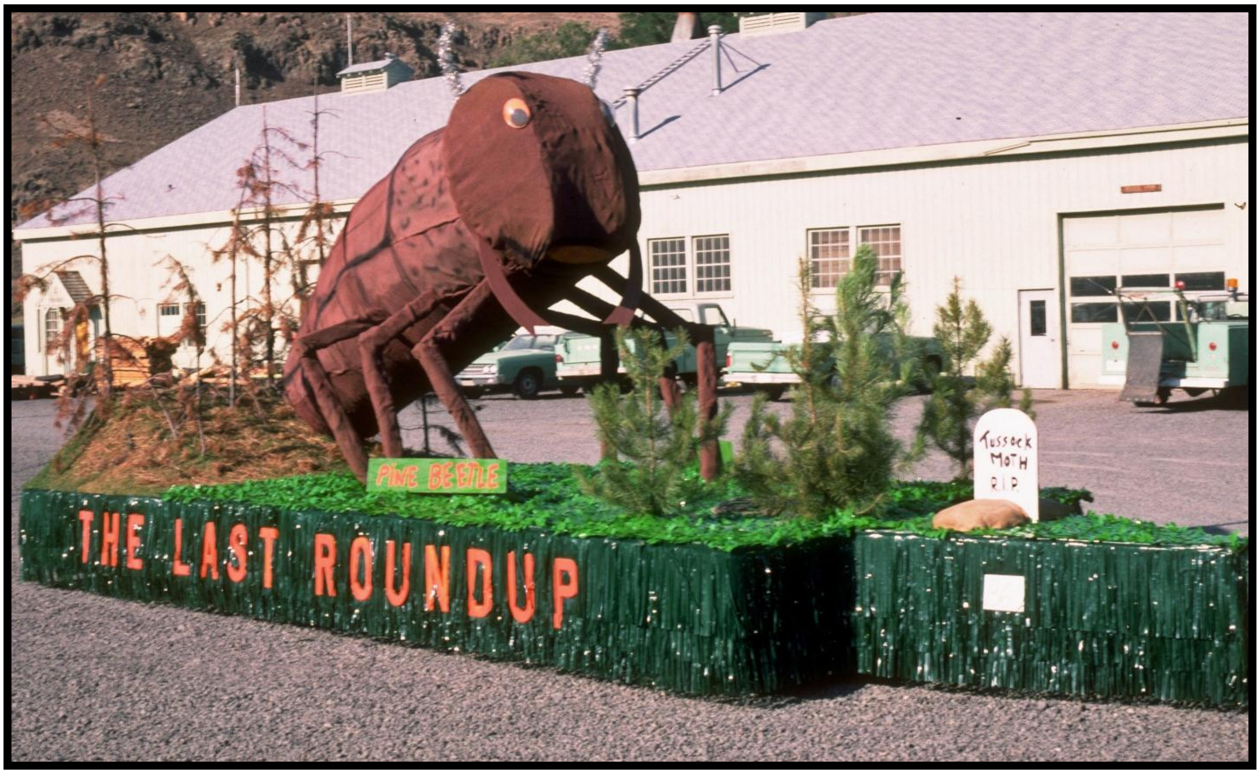
F14-SO-TP-09-00
May 2000

Potential Vegetation, Disturbance, Plant Succession, and Other Aspects of Forest Ecology

David C. Powell

Potential Vegetation, Disturbance, Plant Succession, and Other Aspects of Forest Ecology

David C. Powell



USDA Forest Service
Pacific Northwest Region
Umatilla National Forest
2517 SW Hailey Avenue
Pendleton, OR 97801

Technical Publication F14-SO-TP-09-00
May 2000

AUTHOR

DAVID C. POWELL is a silviculturist, USDA Forest Service, Umatilla National Forest, 2517 SW Hailey Avenue, Pendleton, Oregon 97801.

ABSTRACT

Historically, a dominant perspective in ecology viewed forests as stable ecosystems existing in harmony and balance with their environment. Many land managers were educated during an era when college instruction emphasized this steady-state view of the natural world. The last three decades saw a period of rapid ecological change for literally millions of acres in the Blue Mountains. Some of this change was related to normal growth and maturation (e.g., plant succession), but much of it resulted from insect and disease impacts. Initially, the high impact levels caused land managers to question the health of ecosystems, but eventually they began to realize that these disturbance processes were not producing the catastrophic results that would have been predicted by their education and training. With the advent of ecosystem management in 1992, and as a result of changing attitudes about disturbance processes, land managers began to think about plant succession, competition, and other aspects of forest ecology in a different way. The primary objective of this document is to describe the historical perspective (an equilibrium or balance-of-nature philosophy) and compare it with the current paradigm (a non-equilibrium or dynamic equilibrium concept).

Keywords: Ecological amplitude, competition, disturbance, plant succession, Blue Mountains, old-forest, relay floristics, initial floristics, seral status, vegetation classification, potential vegetation, management implications, historical range of variability, landscape ecology, forest health.

TITLE PAGE PHOTOGRAPH

The Last Roundup. Each fall during the second week in September, Pendleton, Oregon is home to the Pendleton Round-Up rodeo. During Round-Up week, Pendleton holds several parades in which the Umatilla National Forest traditionally entered a float. In 1975, the Forest's parade float commemorated two disturbance events – an outbreak of Douglas-fir tussock moth in mixed-conifer forests, and a mountain pine beetle infestation in lodgepole pine forests. Over 350,000 acres of the Umatilla National Forest were rapidly defoliated by tussock moth between 1972 and 1974, at which point the outbreak collapsed on its own after a native virus spread through the insect population. In 1974, DDT was applied to some of the defoliated area, although a relatively small proportion of the Umatilla's outbreak was treated (32,706 acres). On the parade float, the small grave in the lower right portion of the photograph has a tombstone that reads 'Tussock Moth R.I.P.' When this photograph was acquired, mountain pine beetle was just assuming preeminence as a landscape-level disturbance agent; an outbreak that began in 1968 on the Wallowa-Whitman National Forest (near Johnson Rock Lookout) grew steadily from there – by the fall of 1975, almost one and ½ million acres of lodgepole pine in the Blue Mountains were infested with pine beetles. This Round-Up float reflects prevailing attitudes of that era – disturbance processes were viewed as an aberration and it was predicted they would diminish in importance once forest management successfully transformed overmature (decadent) stands into vigorous, pest-free communities. Subsequent developments – an intense spruce budworm outbreak and numerous landscape-scale wildfires – suggest that these predictions may have been optimistic, eventually causing managers to reevaluate their preconceptions about the role of disturbance processes in forest ecosystems.

ACKNOWLEDGEMENTS

This report benefited from reviews by PAUL HESSBURG (Pacific Northwest Research Station, Wenatchee Forest Sciences Laboratory) and CHARLIE JOHNSON (Area Ecologist for the Malheur, Umatilla, and Wallowa-Whitman National Forests).

TABLE OF CONTENTS

FIGURES

TABLES

Introduction

A distant summer view of the Blue Mountains shows a dark band of coniferous forest occurring above a lighter-colored grassland zone. Each of the two contrasting areas seems to be homogeneous, and the border between them appears sharp. A closer view, however, reveals great diversity within each zone and borders that are poorly defined. Herbaceous communities and stands of deciduous trees are scattered throughout the coniferous forest, and the species of dominant conifer changes from one site to another. At the foot of the mountains, fingers of forest and ribbon-like shrub stands invade the grassland zone for varying distances but become progressively less common before eventually disappearing altogether.

The Blue Mountains province, then, is actually broken up into a myriad of small units, most of which are repeated in an intricate, changing pattern. Making sense of this landscape pattern is possible using a concept called potential vegetation (PV). Potential vegetation implies that, in the course of time and in the absence of future disturbance, similar types of plant communities will develop on similar sites. The concept of potential vegetation is not always well understood, so one of the objectives of this document is to explain it along with other related aspects of forest ecology.

Historically, a dominant perspective in ecology viewed forests as stable ecosystems existing in harmony and balance with their environment. Disturbance was viewed as an unnatural and unexpected intrusion into these equilibrium systems. Many individuals in the current cohort of public land managers were educated during an era when college instruction emphasized this steady-state view of the natural world.

Blue Mountain forests recently experienced three decades of continual disturbance – Douglas-fir tussock moth in the early 1970s, mountain pine beetle from the late 1960s to the late 1970s, western spruce budworm in the 1980s and early 1990s, and stand-replacing wildfire in the late 1980s and throughout the 1990s. During this prolonged period of ecological change, land managers initially questioned the health of ecosystems – perhaps disturbance, like disease in a human body, was an indicator of poor health. Eventually, however, they began to realize that these disturbance processes were not producing the catastrophic results that would have been predicted by their education and training.

In 1992, the U.S. Forest Service adopted a new paradigm called ecosystem management, which emphasizes an ecological approach to management of the national forests and grasslands. With the advent of ecosystem management, and as a result of their changing attitudes about disturbance, land managers began to think about forest ecology in a different way. An important objective of this document is to describe the historical perspective, an equilibrium or balance-of-nature philosophy, and compare it with the current paradigm, a non-equilibrium or dynamic equilibrium concept.

Ecological Amplitude

The genetic characteristics of a plant species allows it to be adapted to a specific range of environmental conditions, which is called its ecological amplitude (Daubenmire 1968). Ecological amplitude can be related to a variety of site factors such as elevation, aspect, geology, and soil type. Together these factors create the underlying foundation, or a geomorphic template, upon which the biological landscape is constructed. Does this mean that a particular species, plant community, or vegetation zone is influenced directly by a certain elevation or soil type? In general, the answer to this question is no.

While it is fairly easy to list individual site factors, it is very difficult to predict their integrated effect on plants. The biophysical components of a plant's environment interact to form a temperature and moisture regime based primarily on gradients of elevation, slope, and aspect (Swanson et al. 1988). These components can either balance or offset each other – an example is the situation where a species switches aspect with changes in elevation. At the lower edge of its elevational distribution, the species will be found on a northerly aspect; in the middle or zonal portion it occurs on east- or west-facing exposures; and at the upper elevational limit it occupies a southerly aspect (Blumer 1911).

A plant species whose distribution switches from one aspect to another may seem unusual, but it really is not because both situations may provide a similar temperature and moisture setting (fig. 1). Some ecologists have referred to this concept as an effective environment because it demonstrates that one set of site factors (a south aspect at 6,000 feet) can be ecologically equivalent to another (a north aspect at 5,000 feet). Differing combinations of site factors can have a similar influence on an ecosystem due to the ecological principle of compensating effects (Allen and Hoekstra 1992; Larsen 1923, 1930).

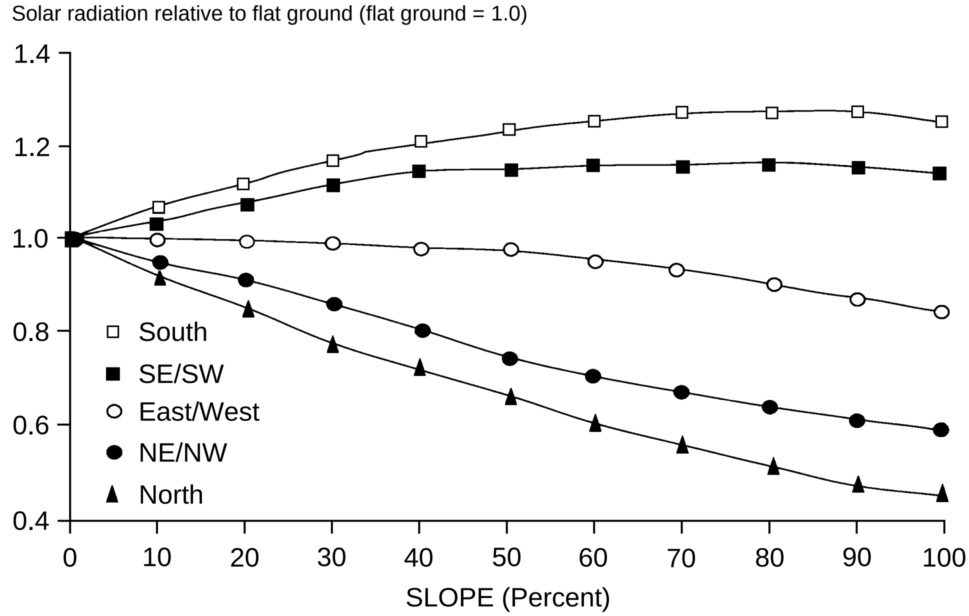


Figure 1–Effect of slope and aspect on solar radiation at 50° north latitude (redrawn from Stathers et al. 1998). Slope and aspect have a major influence on the amount of solar radiation received above a vegetation canopy. Latitude affects day length and the intensity of incoming solar radiation, so the relationships shown in this figure would vary slightly for lower latitudes. This figure illustrates why vegetation composition can differ significantly on a steep slope as compared to a gentle slope for the same aspect, and from one aspect to another for the same slope gradient.

Some plants have wide ecological amplitude and tend to be common – they are generalists and can occupy a great variety of ecological niches (or a very wide niche, depending on how a niche is defined). A good example of an ecological generalist is common yarrow,[1] which is found from hot dry sites at low elevations to cold moist grasslands in the alpine zone. Obviously, it has wide ecological amplitude for both temperature and moisture.

Other plants have narrow ecological amplitude and are found only in certain environments. Mountain alder and bluejoint reedgrass are examples of plants with rather narrow amplitude; both are restricted almost exclusively to wet sites. Since species with narrow amplitude are good indicators of specific environmental conditions, they are often used as indicator plants when classifying potential vegetation.

Ecological amplitude can be scale dependent. At a broad geographical scale, for example, lodgepole pine is considered to have wide ecological amplitude (Lotan and Critchfield 1990). Such a characterization is not necessarily accurate at a lower level – in the Blue Mountains physiographic province, lodgepole pine is restricted almost exclusively to frost pockets and other cool or cold sites, most often at high elevations. These sites have volcanic ash-cap soils overlying residual soils or Columbia River Basalt geologic substrates; the ash-cap soils are deeper and hold more moisture than the residual basaltic soils. In the Blue Mountains, lodgepole pine is seldom found on south aspects or steep slopes, presumably because the ash deposits have been eroded from these areas (Trappe and Harris 1958), although the warm dry climatic regime associated with south- or west-facing exposures undoubtedly has an influence as well.

Lodgepole pine developed interesting adaptations to cope with the environmental variation presented by its broad geographical range. In the central and northern Rocky Mountains, for example, lodgepole pine evolved a closed-cone trait (serotiny) in response to a disturbance regime dominated by infrequent, stand-replacing wildfires. Since lodgepole pine seed disperses for a relatively short distance (about 200 feet; see table 14 in appendix 2), serotiny is an effective adaptation for restocking large fire areas because it stores millions of seeds per acre in cones whose scales are sealed with resinous bonds just waiting to be broken by the heat of a fire. In the Blue Mountains, however, lodgepole pine has a very low percentage of closed cones (fig. 2), although it is a prolific seed producer with good cone crops occurring almost every year (Trappe and Harris 1958).

As is often the case with ecological phenomena, the temperature and moisture relationships of plant species are more complex than one might suspect. An example is Engelmann spruce, which has relatively narrow ecological amplitude because it is found primarily on cool or cold sites with abundant moisture, often at high elevations. Research has shown, however, that temperature at night, not during the day, was the most important factor controlling all aspects of Engelmann spruce growth except terminal bud formation. Surprisingly, Engelmann spruce tolerated, and grew better under, warmer night and day temperatures than redwood (*Sequoia sempervirens*) – a species adapted to the mesic coastal environments of northwestern California and southwestern Oregon (Hellmers et al. 1970).

Ecological amplitude dictates whether a plant can tolerate the environmental conditions of a particular site. But action of the environment on an individual plant or the overall community is neither uniform nor consistent because unusual events are quite normal (a severe frost episode every few years; a prolonged drought every few decades). For example, dendrochronology studies indicate that droughts of varying magnitude have been common in eastern Oregon over the

---

[1] Scientific plant names are provided in appendix 1.

last 300 years (Graumlich 1987, Keen 1937). Extreme conditions often have a greater influence on the long-term welfare of an individual plant or the community to which it belongs than average conditions (fig. 3) (Taylor 1934).

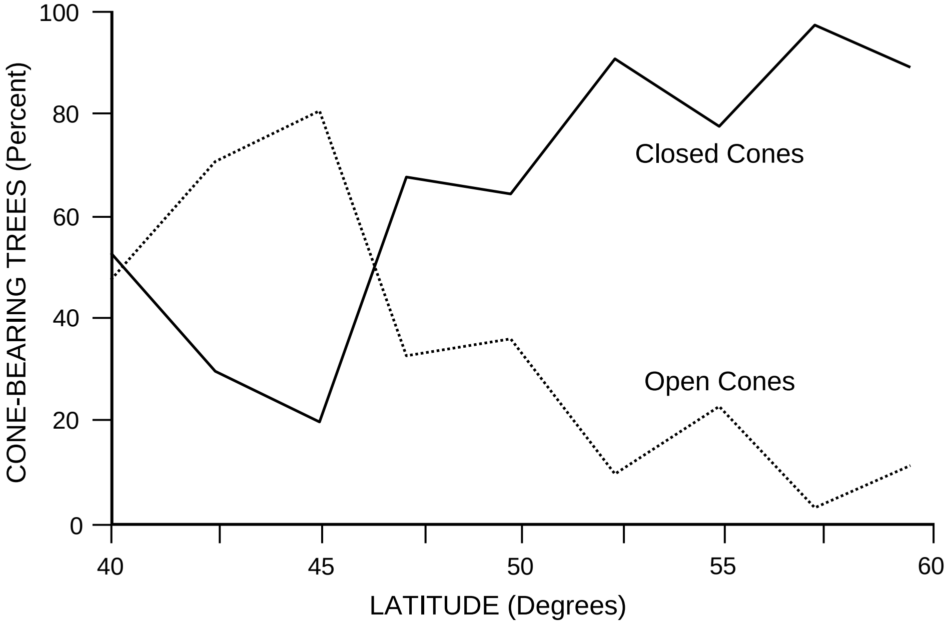


Figure 2–Variations in cone serotiny for lodgepole pine (redrawn from Koch 1996). Lodgepole pine serotiny (the closed cone trait in this figure) varies with latitude. Note that the lowest serotiny percentage in western North America occurs at a latitude of 45° North, which happens to coincide with the central Blue Mountains. Since serotiny is presumed to represent an adaptation to fire (Lotan 1976), the trends displayed in this figure suggest that crown fire exerted less genetic selection pressure in the Blue Mountains than in other parts of lodgepole's range. Serotiny also varies with stand age and other factors – the closed-cone trait is more common in old trees (and stands) than in young trees (and stands) (Lotan 1976, Mason 1915). Variations in the percentage of serotinous trees can have an important influence on landscape heterogeneity (Turner et al. 1997).

Mountainous regions have a diversity of landforms, topography, climate, soils, slope exposure, geology, and other abiotic factors. Each combination of these factors affects a site's temperature and moisture status. Since plant distributions are influenced primarily by temperature and moisture (as controlled by their ecological amplitude), any significant change in abiotic factors causes a change in plant composition. On the Umatilla National Forest, temperature and moisture varies somewhat predictably with changes in elevation, aspect, and slope exposure (fig. 4).

Tolerance and Competition

An individual plant species will survive and prosper only if it is more competitive than other species that can tolerate the same environmental conditions. Certain aspects of the ability of one species to compete with another are referred to as its tolerance. Tolerance refers to a plant's ability to withstand the effects of one or more limiting factors such as unusually high or low temperatures, a deficit of soil moisture during the growing season, or environments with a deficiency of sunlight or nutrients. In forestry, the tolerance receiving the most emphasis is shade tolerance – the capacity of a species to survive and grow in the shade of other trees (Harlow et al. 1996).

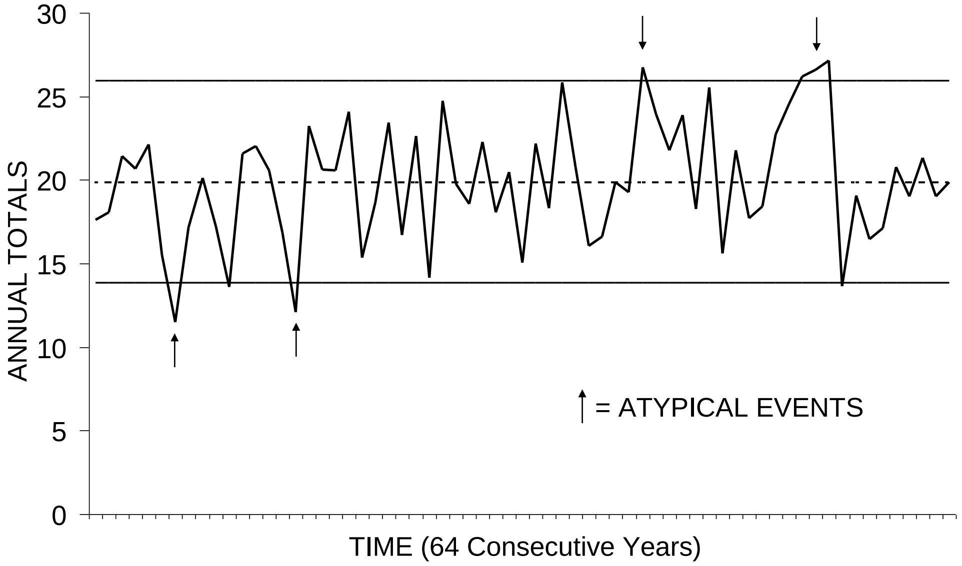


Figure 3–Extreme or unusual environmental events have an important influence on ecosystems. Action of the environment on an individual plant or its overall community is neither uniform nor consistent because unusual events are quite normal (periodic frost events, episodic droughts, etc.) (Taylor 1934). This figure illustrates the concept by using the precipitation record from a weather station in the Blue Mountains. Two lines delineate a zone containing 90% of the variation around the record's 64-year mean (the dashed line midway between the two lines is the mean). Since the 90% was based on statistics (standard deviation), a different zone could have been established by selecting another value (67%, 80%, 95%, etc.). By selecting 90%, it was assumed that on average, 9 years out of 10 would have normal precipitation and the other year would be abnormal (either unusually high or low). In this figure, 4 periods escaped the 90% threshold zone and, by definition, would be considered unusual (arrows denote the unusual periods). Plant species exposed to this precipitation regime would need sufficient ecological amplitude to survive the unusual periods; otherwise, they may be able to successfully colonize an area in the short term, but would not persist over the long term. Note that 90% was used as an example only; in actuality, each species would have its own particular definition of what constitutes extreme or unusual conditions.

Plant species vary in their capability to tolerate either an abundance or a deficit of sunlight, and these differences have an important influence on community development patterns and successional relationships (Shirley 1929). Trees that can tolerate shade, for example, are assumed to be the climax species; intolerant species are considered to be early-seral colonizers who will ultimately be replaced by shade-tolerant climax trees. This statement implies that characteristics conferring success in late succession are the best indicators of a species' competitive ability, although such an assumption ignores the fact that rapidly-growing early-seral species, which shade and suppress their 'superior' late-seral competitors, are most successful during early and middle succession (Drury and Nesbit 1973, Huston and Smith 1987).

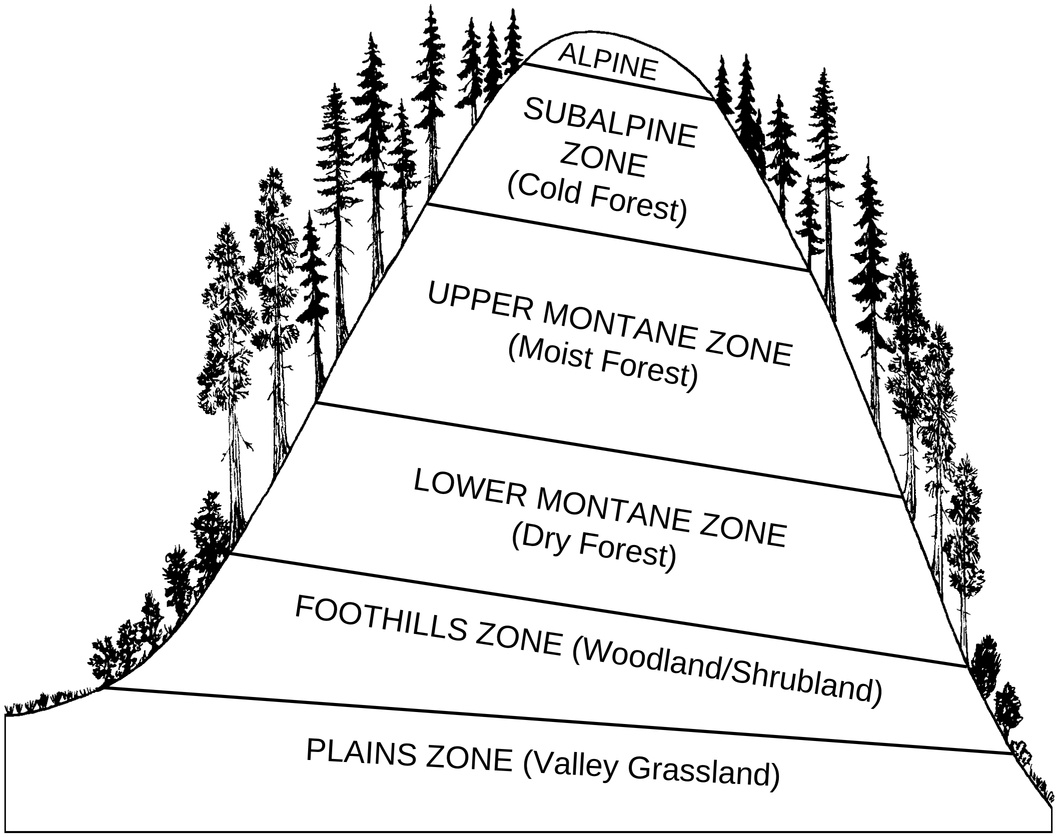


Figure 4–Vegetation zones of the Blue Mountains. Vegetation types tend to occur in zones as one moves up or down in elevation. In the northern hemisphere, a south-facing slope receives more solar radiation than a flat surface, and a north-facing slope receives less. Thus the same temperature conditions found on a plateau or bench may occur higher on an adjacent south-facing slope, and lower on a north aspect. Because of this, a particular vegetation type will be found above its ordinary elevational range on south slopes and below it on north slopes (Bailey 1996). The end result is shown above – vegetation zones arranged vertically in response to elevation (moisture), and sloping downward from south to north in response to slope exposure (temperature). Each of the three forest zones typically occupies about 2,000 feet of elevation, with the upper edge of a zone controlled by tolerance to low temperatures and the lower edge by tolerance to a lack of moisture (Daubenmire 1943, Pearson 1920). Note that these effects can be modified by the direction of moisture-bearing winds, by variations in fog or cloud cover, and by latitude since the maritime climatic influence gradually deteriorates from north to south in the Blue Mountains. Also, fire suppression has blurred the historical zonation of forest vegetation; Douglas-fir, grand fir and Engelmann spruce have all expanded their ranges to lower elevations over the last 90 years. **Valley grasslands** occur at low elevations where moisture is too limiting to support trees except along waterways. The **foothills zone** tends to be dominated by western juniper in the central and southern Blue Mountains, although shrublands (serviceberry, black hawthorne, common chokecherry, etc.) occupy this zone in the northern Blues where a maritime climate prevails. **Dry forests** occur on hot and warm dry sites where ponderosa pine, Douglas-fir, or grand fir are the climax species. These sites were historically dominated by ponderosa pine because it is well adapted to survive a natural disturbance regime featuring low-intensity wildfires occurring every 8 to 20 years. The **moist forest zone** is relatively common, especially in the northern Blue Mountains. It includes moist, mixed-conifer sites where Douglas-fir, grand fir, or subalpine fir are the climax species. Lodgepole pine and western larch are common early-seral species. Western white pine occurs in this forest zone. These mixed-conifer forests often have maximum species diversity because the Blue Mountains function as a transverse bridge between the Cascade Range to the west and the Rocky Mountains to the east, allowing tree species and other floristic elements from both areas to commingle. **Cold forests** occur at high elevations in the subalpine zone and are dominated by subalpine fir and Engelmann spruce. Lodgepole pine or whitebark pine often forms persistent plant communities there. Above the cold-forest zone is a treeless **alpine zone**, although alpine environments are uncommon in the relatively low-elevation Blue Mountains.

Trees develop differently when growing in full sunlight versus shade. In the short term, these differences are related more to the environment than to species – the physiological changes experienced by a shade-tolerant species growing in full sunlight are similar to those for a shade-intolerant species (changes such as a greater number of branches per whorl, more sharply angled branches, a high proportion of sun leaves, greater apical control, greater crown depth, and needles positioned on all sides of the branches) (Bates 1926, Williams et al. 1999, Zon 1907, Zon and Graves 1911). In the long term, however, a genetically-controlled suite of life history characteristics (see appendix two) has the most influence on how a species responds to light, temperature, moisture, nutrients, and the other components of its environment (Huston and Smith 1987, Oliver and Larson 1996).

In low light conditions, shade-tolerant species exhibit greater changes in crown morphology than shade-intolerant species. For conifers, an example of this morphological plasticity is provided by the 'leader height to lateral branch growth' ratio, which helps explain the pronounced change in crown shape exhibited by shade-tolerant conifers growing in light-limited environments. These light-starved crowns evolve from the conical shape produced in full sunlight to a flat-topped or umbrella form commonly found in low-light conditions. Shade-intolerant conifers are less able to reduce their height growth relative to lateral branch extension and are seldom found with the umbrella growth form (Oliver and Larson 1996, Williams et al. 1999).

By maintaining a limited number of healthy branches in their live crown and by allocating more resources to lateral growth than to apical growth, shade-tolerant species increase the probability of intercepting sunflecks and capturing light that would otherwise go to undergrowth vegetation such as shrubs and herbs (Oliver and Larson 1996, Williams et al. 1999). Tree species that are very shade tolerant can persist on the diffuse light provided by short-lived sunflecks (those lasting an average of 6-12 minutes), which may provide from one- to two-thirds of the total seasonal photosynthetically-active radiation in moist temperate forests (Canham et al. 1990, Chazdon and Pearcy 1991).

Deeply shaded forest floors virtually devoid of plants are common in mesic coniferous forests of the Pacific Northwest. Ecologists refer to such sites as depauperate. It is often assumed that a depauperate undergrowth is the result of excessive shading (e.g., a lack of sunlight). However, trenching experiments where ditches or trenches prevented the roots of overstory trees from affecting the growth of established seedlings and other understory vegetation showed that under a dense forest canopy, root competition may actually limit plant growth more than a lack of sunlight (McCune 1986, Zon 1907). For this reason, tolerance is now believed to reflect the capability of a plant to complete its life cycle under a forest canopy, from seedling to adult, regardless of whether this ability is derived from tolerance to shade, root competition, or a combination of the two (Harlow et al. 1996).

A lack of regeneration in many forest stands, particularly by tolerant species such as Engelmann spruce and true firs, may not be related to shade. An interesting study examined the lethal and nonlethal effects of the organic horizons (the O horizon in soil classification terminology) of forest soils on seed germination for several associated conifer species (Daniel and Schmidt 1972). The investigators found that Engelmann spruce O-horizon (e.g., the O horizon formed beneath a pure canopy of Engelmann spruce trees) was not only lethal to Engelmann spruce seeds, but also to seeds of subalpine fir, Douglas-fir, and lodgepole pine. Subalpine fir O-horizon was lethal to its own seeds but only marginally harmful to other species. Douglas-fir O-horizon had a significant adverse impact on its own seeds and was moderately harmful to seeds of other species. Lodgepole pine O-horizon was essentially neutral for all seeds.

In this study, which factors contributed to a lack of seed germination? The failure of conifer seed to germinate was attributed primarily to the action of pathogenic fungi. Non-sterilized O-horizons supported huge masses of fungal hyphae after 90 days, whereas sterilized O-horizons had no fungal activity. These results help to explain why a mineral-soil seedbed has beneficial effects on seed germination and tree regeneration. They also provide an important reason for why Engelmann spruce and subalpine fir seedlings are frequently found on rotting logs and stumps, and the exposed soil of uprooted (windthrown) trees, rather than on the forest floor itself (Daniel and Schmidt 1972, Zhong and van der Kamp 1999).

It must be emphasized that the ability of a plant to endure shade or root competition is considered a tolerance for good reason. There are few examples of trees that seem to require shade for their development. After initial establishment, when light shade is beneficial for most species, many shade-tolerant trees attain their highest vigor when growing in full sunlight (Harlow et al. 1996). Tolerant species are often found beneath intolerant species, but it's usually because overstory shade helps conserve soil moisture and serves to moderate air temperatures near the ground. Or to put it more simply, the presence of tolerant trees in the understory is for temperature and moisture reasons, not because they have a physiological requirement for shade (Bates 1926, McMinn 1952).

One exception to this generalization involves forest sites in the southern Rocky Mountains. At high elevations in the southern Rockies, sunlight is intense – above 10,000 feet, there is twice as much ultraviolet radiation and 25% more total light than at sea level (Zwinger and Williard 1972). Research found that intense sunlight at high elevations results in irreversible damage to the photosynthetic mechanism of planted seedlings. Damaged seedlings became chlorotic as a result of solarization damage, and many of them eventually died. Related studies found that water stress (drought) had little or no influence on damage levels and that seedling mortality was related exclusively to solarization (Ronco 1970).

Shade tolerance is related to the maximum leaf area supported by mature stands (the leaf area carrying capacity of a site). Leaf area is largely dependent upon moisture and nutrient availability, and the relative efficiency with which different tree species can convert water, nutrients, and sunlight into foliage (Waring 1983). The maximum leaf area index for shade-intolerant species is lower than that associated with shade-tolerant species (see table 9 in appendix two), indicating that shade-intolerant species may be less efficient than shade-tolerant trees at converting nutrients and moisture into foliage.

Vegetational Variation

Environmental conditions vary continuously across a landscape, so the resulting plant composition also varies. For this reason, a plant association is not an exact assemblage of species from one location to another, or even in the same place from year to year. Although the plant composition can vary, the variation occurs within relatively narrow limits. For example, a particular plant species is often found in more than one plant association, but its frequency or abundance (canopy cover) will differ between them.

Plant compositions are also regional – the Douglas-fir/mountain snowberry plant association (PSME/SYOR), for example, occurs in the forests of central Idaho (Steele et al. 1981), the Blue and Ochoco Mountains of northeastern Oregon and southeastern Washington (Johnson and Clausnitzer 1992), and the Wallowa-Snake province of northeastern Oregon (Johnson and Simon 1987). In each of these areas, the floristic composition associated with PSME/SYOR differs slightly from the others.

In a local geographical area, sites in the same plant association exhibit less variation than sites in different associations (Daubenmire 1961, 1973). For example, two widely separated areas supporting the grand fir/queencup beadlily plant association may have differing proportions of Engelmann spruce or western larch in their tree canopies, or Scouler willow or twinflower in their undergrowths, but they still represent equivalent ecological environments because both sites have a similar temperature and moisture regime (cool moist).

Vegetational variation is derived from two main sources – physical or abiotic site factors, and historical factors related to an area's disturbance history. Abiotic factors have the most influence in situations with strong topographic controls, so they tend to be important in the northern Blue Mountains where landform, topography, aspect and other factors exhibit great variation (Clarke and Bryce 1997). In the northern Blues, it is not uncommon for the landform to change from a gentle plateau to a deep, steep-sided canyon within a relatively short distance.

Historical factors are an important source of variation on topographically-benign sites such as plateaus or benches. These areas tend to be similar with respect to soil physical and chemical properties (Geist and Strickler 1978), so forest composition varies primarily as a consequence of plant succession (disturbance history) and not because of differences in ecological site potential (Schimpf et al. 1980). Since much of the central and southern Blue Mountains has relatively gentle topography, disturbance history and stochastic (random) events are major sources of vegetational variation for this area.

How much of the floristic composition of an area is due to abiotic site factors versus historical factors? A fascinating study examined this question by sampling mesic, old-growth forests in eleven adjacent canyons along the east front of the Bitterroot Range in western Montana (McCune and Allen 1985). The sampled areas had no evidence of recent disturbance and were sites with low environmental variability – each old-growth stand occurred on granitic parent material and experienced a similar climatic regime, so it was assumed that site factors and vegetation were largely independent of each other (e.g., vegetational variation was ostensibly unrelated to variation in site factors).

Surprisingly, McCune and Allen (1985) found that only 10 percent of the floristic composition associated with old-growth forests in the Bitterroot canyons was due to abiotic site factors, with the other 90 percent presumably related to historical factors. These results have interesting implications because a basic tenet of the climax concept is that once plant succession has progressed to the point of a climax community, there should be a high degree of floristic similarity from one stand to another because climax vegetation is supposed to represent a faithful and consistent expression of abiotic site potential (Whittaker 1953).

Since McCune and Allen (1985) found that major differences in climax vegetation can be unrelated to site factors, one could infer that the climax concept should be applied with caution. As they concluded: "if similar sites need not develop similar communities, then we should be cautious in using climax vegetation as a standard for comparisons that rest upon the assumption that composition at climax is solely determined by site characteristics" (McCune and Allen 1985, page 368). Their work also provides strong evidence of the dominant role that chance (random events) plays in vegetational development, and it clearly demonstrates that succession can have multiple endpoints.

Disturbance

Disturbance, the primary initiator of plant succession, is an important and integral process in many forest ecosystems. A disturbance is defined as a relatively discrete event that disrupts the structure of an ecosystem, plant community, or population, and changes resource availability or the physical environment. Disturbances happen over relatively short time intervals: windstorms occur over hours to days, fires occur over hours to weeks, and volcanoes erupt over periods of days or weeks (Turner 1998).

Ecologists often distinguish between a discrete disturbance event – like an individual windstorm or wildfire – and the disturbance regime that shapes an ecosystem or landscape. A disturbance regime refers to the spatial and temporal dynamics of disturbance events over a long time period (Turner 1998). Characterization or description of a disturbance regime would typically include the following items:

- *Area or size* – the area disturbed, expressed as area per event or area per time period.
- *Distribution* – spatial distribution.
- *Frequency* – mean number of disturbance events per time period.
- *Magnitude* – expressed as either intensity (energy release rates for a fire) or severity (tree mortality related to fire effects).
- *Return interval* – the inverse of frequency, or the average time interval between successive disturbance events.

Disturbances come in all shapes and sizes, ranging from relatively minor to relatively major events. They can be caused by biotic agents (insects, diseases, animal damage, etc.) or by abiotic factors (wind, fire, flood, etc.). Since disturbances vary in both frequency and magnitude, the spatial and temporal impact of any particular disturbance event depends upon the hierarchical scale being considered (fig. 5). An example is the burrowing activity of pocket gophers (*Thomomys* spp.) and other small mammals, which may be viewed as a disturbance at one spatial scale but not at another (White 1979).

Disturbances are fundamentally important in controlling landscape pattern and ecological function. Peter White (1987) described seven general principles regarding disturbance processes and their effects:

- **Disturbances occur on a variety of temporal and spatial scales** – disturbances act at small and large spatial scales, and affect ecosystems for either short or long periods.
- **Disturbances affect many levels of biological organization** – disturbances can disrupt ecosystem development, return areas to earlier seral stages, and change habitat mosaics.
- **Disturbance regimes vary, both regionally and within any particular landscape** – disturbance regimes commonly vary with potential vegetation: 80% of individual tree mortality in cold-forest types is typically related to wind, whereas 20% or less may be wind-related in dry-forest types.
- **Disturbances overlay environmental gradients, both influencing and being influenced by these gradients** – disturbances behave differently depending on which physical or environmental gradients they interact with (dry sites versus moist sites).

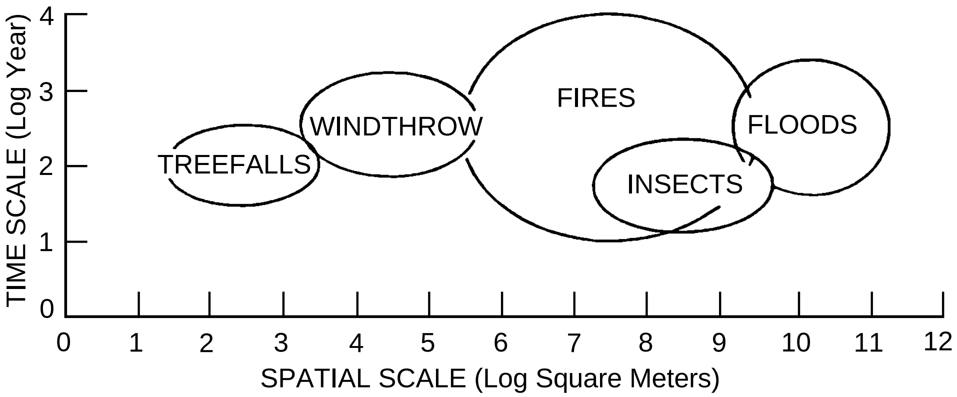


Figure 5–Idealized temporal and spatial relationships among selected disturbance regimes (redrawn from Urban et al. 1987). This figure illustrates the concept that disturbance is implicitly scaled. For example, if disturbance is defined as events that kill trees prematurely (the treefalls regime in this figure), then disturbance is confined to a relatively narrow timeframe (temporal scale) when considered in the context of the typical or maximum longevity of Blue Mountain tree species (see table 17, appendix two). Large-scale disturbances such as fires, hurricanes, and volcanoes are spatially heterogeneous; whether a large disturbance is qualitatively different from numerous small disturbances remains an unresolved issue in ecology (Turner et al. 1997).

- **Disturbances interact and can be synergistic** – lodgepole pines weakened by a slow-moving fungus *(Polyporus schweinitzii)* are attacked by mountain pine beetles and the resulting dead trees eventually contribute to a forest fire. The fire causes basal wounds on surviving trees, which provide new infection points for the fungus and the cycle begins again (fig. 6) (Geiszler et al. 1980).
- **Disturbances may result from feedback between the state of a plant community and its vulnerability to disturbance** – the composition and structure of dry-site forests was a direct result of low-severity, high-frequency fire, ensuring a sustainable forest by reducing vulnerability to crown fire and by preventing succession to the late-seral tree species.
- **Disturbances produce variability in communities** – disturbances promote plant and animal diversity by influencing the species composition, age, edge characteristics, and distribution of structural stages across the landscape.

A disturbance, and the recovery period that follows it, can have an important influence on ecosystem functions and processes. On the one hand, destabilizing forces (disturbance processes) are important for maintaining ecosystem diversity and resilience. On the other hand, stabilizing forces (growth and maturation) are important for maintaining inherent productivity and biogeochemical cycles (Holling 1996). It must be emphasized, however, that ecosystems are not equally resilient – that is, they do not possess an equal ability to recover from disturbance.

Knowing the intensity and frequency of disturbance processes shaping an ecosystem is important because species (both plant and animal) are adapted to the effects of disturbance (e.g., the spatial pattern of vegetation composition and structure at a landscape scale). The species diversity of an area depends on the balance between disturbance frequency and intensity, and the level of competition that exists between species (Parminter 1998). The composition of plant communities reflects complex interactions between species life history characteristics, disturbance intensity and frequency, and chance events – suggesting that both deterministic and stochastic factors have an influence on ecosystem variation (Halpern 1989).

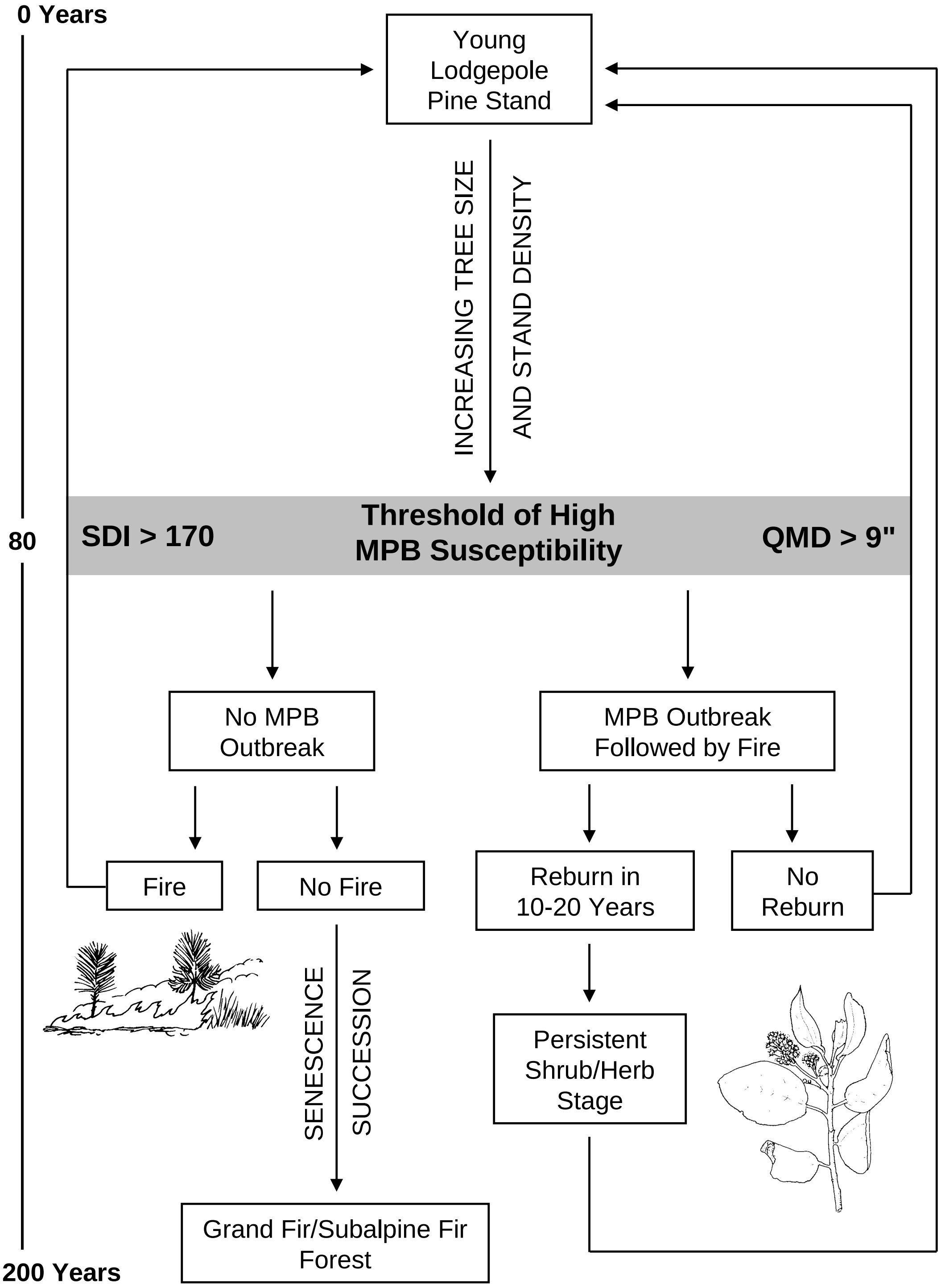


Figure 6–Generalized interactions between mountain pine beetle, fuel accumulation, stand density, tree size, and stand-replacing wildfire. This diagram depicts lodgepole pine development and its relationship to wildfire and bark beetles, two disturbance agents that essentially combine to perpetuate this forest type at a landscape scale. Although this diagram is simplistic, it does show that disturbance processes interact – their combined effect may influence landscape patterns more than either process acting alone. Bark beetles transmit fungi between trees, and fungi reduce trees' ability to resist bark beetles. When these processes result in a preponderance of lodgepole pine forest across large landscapes or watersheds, some degree of fragmentation might be beneficial as a way to circumvent landscape-scale insect outbreaks and their associated wildfires (Perry 1988).

Some disturbance events have been characterized as catastrophic – a recent example was an outbreak of western spruce budworm (*Choristoneura occidentalis*) in the Blue Mountains between 1980 and 1992. Such characterizations are often inaccurate, since true catastrophes are rare and destructive events not repeated with regularity (Rogers 1996). Catastrophe, like beauty, may be in the eye of the beholder. Although the budworm outbreak might qualify as a severe disturbance event for areas such as the North Fork John Day River Basin, where host-type forests sustained substantial impacts, it was not a catastrophe because species extirpations and other enduring ecological changes were not a result (Shlisky 1994).

Disturbances frequently have a renewal effect by helping to recycle nutrients. Fire used to be the predominant recycling force in forests of the interior Northwest (fig. 7) because it decomposed fallen litter and other biomass, rejuvenated many herb and shrub species while selecting against others, thinned young tree stands, and regulated tree species composition (Agee 1993, Hall 1976, Harvey 1994, Johnson et al. 1994a). In many interior Northwest forest ecosystems, the average interval between fire events was historically less than the life span of an individual member of the dominant species (table 1).

Table 1 demonstrates that a disturbance process generally varies along an environmental gradient. The fire-return intervals in table 1 describe a fire-free interval for each PVG; they show that the average fire-free interval decreases from cold to dry sites. Conversely, typical and maximum tree longevity increases from cold to dry sites, with early- or mid-seral species generally living longer than late-seral species. Table 1 indicates that with a fully-functioning fire regime, forests dominated by late-seral or climax species would develop infrequently, particularly on dry-forest sites (Romme and Knight 1981).

Because disturbances create and maintain the vegetation patterns we see on a landscape, intentional or unintentional shifts in a disturbance regime may cause dramatic changes, particularly for wildlife species whose welfare is influenced by the distribution and juxtaposition of vegetative habitat components (Turner 1998). In this respect, a lack of disturbance can be as damaging to biological diversity and ecological integrity as too much disturbance (Noss 1983).

Some effects of an altered disturbance regime are insidious, initiating successional changes occurring over decades or more (Sloan 1998). Frequently, these changes are so difficult for people to recognize that they have been referred to as the ‘invisible present’ (Magnuson 1990), resulting in a perception of forest tranquility due to the seemingly timeless nature of large trees (Shugart and West 1981). Perhaps the reason that many contemporary writings still focus on disturbance as an unnatural or aberrant phenomenon is that it often functions at a longer temporal scale than a human lifetime (Parminter 1998).

When humans alter a disturbance regime, it can eventually lead to simplification (homogenization) of a landscape (Lehmkuhl et al. 1994, Turner 1998). When a landscape in the Blue Mountains undergoes simplification, the first elements to be affected are often limited vegetation components such as quaking aspen clones; riparian forests of cottonwood, alder, birch, or willows; western white pine stands; and certain types of shrubland. In some instances, humans altered the disturbance regime by introducing a management practice such as livestock grazing; in others, alteration resulted from suppression of a native disturbance process such as frequent surface fire (Irwin et al. 1994, Mutch et al. 1993).

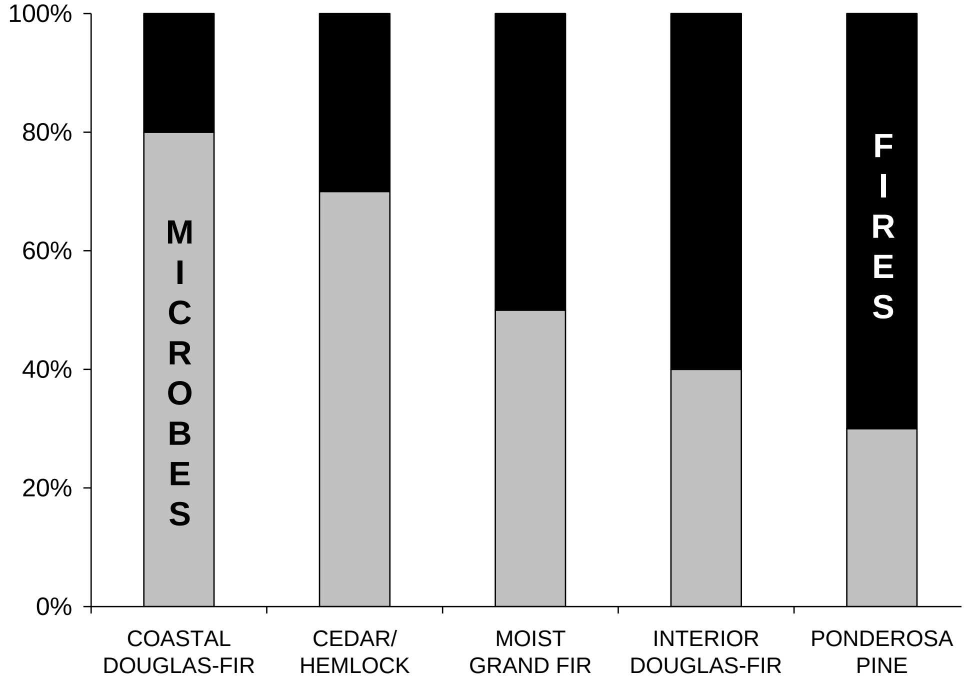


Figure 7–Microbes and fire as decomposition agents (adapted from Harvey et al. 1994). For forests of the Pacific Northwest, fire (black portion of the bars above) and microbes (gray portion) are important agents of decomposition and nutrient cycling. Wildfire was traditionally viewed as an undesirable disturbance event, but in dry forests of the interior Northwest it was important for nutrient cycling. Microbial decomposition effectively recycles nutrients in coastal Douglas-fir forests and other areas with a humid, temperate climate, but microbes are relatively ineffective in dry ecosystems. After surface fires were suppressed following settlement of the Blue Mountains, microbial decomposition has been unable to keep up with the organic debris accumulating beneath forests (needles, twigs, branches, etc.). A disturbance event will eventually reset these systems by converting their accumulated biomass back to its elemental constituents (carbon, phosphorus, etc.). For many forest types, stand-replacing wildfire functions as a reset agent.

Table 1: Comparison of fire return interval and tree longevity, in years.

PVG	Fire Return Interval	Seral Status	Predominant Tree Species	Tree Longevity (Years) Typical	Tree Longevity (Years) Maximum
Dry Forest	15 Years	Early	Ponderosa pine	300	725
		Mid	Douglas-fir	200	500
		Late	Grand fir	200	400
Moist Forest	30-50 Years	Early	Western larch	300	915
		Mid	Western white pine	400	615
		Late	Grand fir	200	400
Cold Forest	80-110 Years	Early	Lodgepole pine	100	300
		Mid	Engelmann spruce	250	550
		Late	Subalpine fir	150	250

Sources/Notes: Potential vegetation group (*PVG*) is described in Powell (1998) and in figure 18 on page 40. *Fire-return interval* is from Agee (1993; table 1.2, page 13). *Seral status* is derived from table 15 in appendix 2. *Tree species* shows the predominant species, by seral status, on upland forest sites for each PVG. *Tree longevity* values are from table 17 in appendix 2.

Left unchecked, a trend toward landscape simplification can ultimately result in impoverished vegetation diversity – extensive areas devoid of aspen, cottonwood, ninebark, park-like ponderosa pine, huckleberry, western white pine, and other early- or mid-seral stages (Case and Kauffman 1997). Losing these stages is unfortunate because they contribute to biological diversity, scenic beauty, wildlife habitat, and recreational opportunities. Without properly-functioning disturbance regimes to continually create new ecological niches for these biotic components, they cannot survive and prosper (Sloan 1998). And since disturbance regimes are responsible for a landscape's structural and compositional complexity, their disruption can eventually degrade both plant and animal diversity (Hansen et al. 1991).

A good example of the changes resulting from landscape simplification involves the quaking aspen ecosystem. Where aspen communities occur in the western United States, they are second only to riparian areas in species diversity and abundance. Fire suppression on western landscapes, when coupled with excessive browsing of young aspen trees by livestock and wildlife, has led to rapid displacement of aspen communities by conifer forests. Since conifer forests transpire more water than aspen and support a sparse undergrowth with relatively few plant species, aspen displacement results in water yield reductions and declines in the number and kinds of plants and animals (Bartos and Campbell 1998).

Anthropogenic disruptions of historical disturbance regimes resulted in wildlife conditions that bear little resemblance to the presettlement situation. These changes indicate a shift in foraging habitat from one favoring grassland/savanna species (e.g., pronghorn antelopes, grasshoppers, bluebirds, and turkeys) to one favoring species that feed in dense forests (porcupines, bark beetles, pygmy nuthatches, and perhaps pileated woodpeckers) (Covington and Moore 1994). Human activities have also contributed to emergence of invigorated species that are apparently doing better now than they did in the past. Examples of invigorated species might include coyote, raccoon, house sparrow, red-winged blackbird, bull thistle, western juniper, and western spruce budworm, to name just a few (Powell 1994).

If historical disturbance regimes had been allowed to maintain an appropriate range of ecological conditions (composition and structure) in Blue Mountain landscapes, then they could have played an important role in perpetuating both species and genetic diversity (Haufler 1994). This approach has been referred to as a coarse filter for conservation of biological diversity (AKA biodiversity); it is based on the premise that native species are adapted to indigenous disturbance regimes and their resulting range of habitat patterns (Hunter 1990). A coarse filter reflects the fact that we cannot even name or enumerate all of the species in a landscape, much less rationally plan for their habitat needs or account for their ecosystem functions (Cissel et al. 1994).

When wildlands are managed to produce water, wood, and other commodities required by a human society, an underlying assumption is that the greater the similarity between the effects of an indigenous disturbance regime and the effects of management activities, the higher the probability that inherent ecological processes will continue with minimal adverse impact. "The only way to satisfy the popular demand for preserving biodiversity is to practice silviculture and harvesting within large regions in ways that maintain landscape ecosystems in mosaic patterns which approximate or mimic natural mosaic patterns" (J.S. Rowe, as quoted in Parminter 1998).

Cissel et al. (1994) recently described a six-step process to analyze disturbance processes at a landscape scale and to use the analysis results to generate potential management actions:

1. Assess historical and current disturbance regimes for terrestrial and aquatic ecosystems.
2. Integrate this information using an appropriate mapping and/or narrative technique and define a desired landscape condition and associated management approach for sub-areas, or strata, with similar disturbance regimes, potential vegetation, and human use patterns.
3. Project this management approach into the future using a geographical information system; assume no natural disturbances, but allow for plant succession; model vegetation manipulation activities that approximate the historical disturbance regime.
4. Analyze the resulting landscape pattern to see if adjustments are needed to meet established objectives – current conditions may be outside the range of desired conditions.
5. Adjust the frequency, intensity, or location of future harvesting units as required; change the amount or shape of reserves; prescribe ecosystem restoration practices.
6. Identify management actions encouraging development of a desired landscape condition.

Old Forest Structure in Dynamic Landscapes

During the last decade, few issues in the Pacific Northwest were more contentious than preservation of late-seral or old-growth forests, an issue eventually culminating in the northern spotted owl being listed as a threatened species under the Endangered Species Act. Although it might have peaked in the 1990s, concern about old-growth has existed for much longer than that: "it is a pity to have all this majesty of antiquity (the shadowy aisles of an untouched Oregon forest) wholly destroyed. Man cannot restore it. It cannot be rebuilt by Nature herself in less than a thousand years, nor indeed ever, for it never is renewed the same" (C.E.S. Wood, Portland intellectual 'gadfly,' as quoted in The Oregonian newspaper, 1908).

In the interior Northwest, old forest structure occurs in two forms, and each form was developed and maintained by a different disturbance regime. In dry forest areas, plant succession toward a climatic climax was historically interrupted by frequent surface fires that maintained forest stands in an early-seral condition. These successional communities were very stable because ecosystems with frequent disturbances exhibit only a narrow range of plant communities (Steele and Geier-Hayes 1995). The old forest structure associated with early-seral conditions is referred to as old forest single stratum (table 2).

Some moist or cold forest areas, by virtue of their topographic position, soil type, or a combination of environmental conditions and vegetation attributes, are less frequently affected by stand-replacing disturbances than the surrounding landscape. These areas may be thought of as semi-stable elements in a dynamic landscape because their environmental settings allow them to function as disturbance refugia. Disturbance refugia are often associated with specific physiographic settings such as upper headwalls, the confluence of two stream channels, areas with perched water tables, and valley bottoms immediately adjacent to perennial streams (Camp et al. 1997, Taylor and Skinner 1998).

Disturbance refugia typically differ from the surrounding landscape matrix in species composition, or in structural attributes such as tree height, stand density, or diameter distribution. Refugia may harbor plant and animal species that would otherwise be absent if an entire landscape was subjected to the same disturbance regime. Whereas fire was the predominant disturbance agent for matrix areas in the landscape, disturbance refugia were more often affected by insects and diseases that created soft snags and other biotic components missing from the surrounding forest (Camp et al. 1997).

Table 2: Description of forest structural stages.

	**Stand Initiation (SI)**. Following a stand-replacing disturbance such as wildfire or tree harvest, growing space is occupied rapidly by vegetation that either survives the disturbance or colonizes the area. Survivors survive the disturbance above ground, or initiate new growth from their underground organs or from seeds on the site. Colonizers disperse seed into disturbed areas, the seed germinates, and then new seedlings establish and develop. A single canopy stratum of tree seedlings and saplings is present in this stage.
	**Stem Exclusion (SECC** or **SEOC)**. In this structural stage, trees initially grow fast and quickly occupy all of their growing space, competing strongly for sunlight and moisture. Because trees are tall and reduce light, understory plants (including smaller trees) are shaded and grow more slowly. Species that need sunlight usually die; shrubs and herbs may become dormant. In this stage, establishment of new trees is precluded by a lack of sunlight (stem exclusion closed canopy) or by a lack of moisture (stem exclusion open canopy).
	**Understory Reinitiation (UR)**. As the forest develops, a new age class of trees (cohort) eventually gets established after overstory trees begin to die or because they no longer fully occupy their growing space. This period of overstory crown shyness occurs when tall trees abrade each other in the wind (Putz et al. 1984). Regrowth of understory seedlings and other vegetation then occurs, and trees begin to stratify into vertical layers. This stage consists of a low to moderate density overstory with small trees underneath.
	**Young Forest Multi Strata (YFMS)**. In this stage of forest development, three or more tree layers have become established as a result of minor disturbances (including tree harvest) causing progressive but partial mortality of overstory trees, thereby perpetuating a multi-layer, multi-cohort structure. This stage consists of a broken overstory layer with a mix of sizes present (large trees are scarce); it provides high vertical and horizontal diversity (O'Hara et al. 1996).
	**Old Forest (OFSS** or **OFMS)**. Many age classes and vegetation layers mark this structural stage and it usually contains large old trees. Decaying fallen trees may also be present that leave a discontinuous overstory canopy. The illustration shows a single-layer stand of ponderosa pine that evolved under the influence of frequent, recurring surface fires (old forest single stratum). On cold or moist sites without frequent fires, multi-layer stands with large trees in the uppermost stratum may be present (old forest multi strata).

Sources: Based on O'Hara et al. (1996), Oliver and Larson (1996), and Spies (1997).

Old forest structure associated with disturbance refugia typically consists of late-successional species occurring in multi-cohort, high-density stands (e.g., stands of grand fir, Engelmann spruce, or subalpine fir with multiple canopy layers and high crown closure). The old forest structural class associated with disturbance refugia is referred to as old forest multi strata (table 2).

A common misconception is that old-growth is synonymous with late-seral or climax conditions. For forests of the interior Northwest, this generalization is seldom true because old-forest stands often feature an overstory with tall, large-diameter trees of early- or mid-seral species (western larch, western white pine, or ponderosa pine) (Hall 1984). As a result of fire suppression and selective timber harvests over the last 75 years, there has been a shift from open ponderosa pine forest to closed pine and Douglas-fir stands in dry ecosystems, and in moist forests, the change has been from tall white pine-western larch stands to relatively short grand fir-spruce-subalpine fir stands (Graham et al. 1999, Hessburg et al. 1999b, Lehmkuhl et al. 1994, Powell 1994).

Several recent bioregional assessments indicate that old forest structure is substantially reduced in most of eastern Oregon and Washington since the Euro-American settlement era (Hessburg et al. 1999b, Lehmkuhl et al. 1994). Information about historical amounts and distribution of old forests is scarce, however, so it is unclear whether a reduction has actually occurred and what its magnitude might be. Camp et al. (1997), for example, found that old forests historically occupied a relatively small proportion of the landscape (9 to 16 percent) in the Wenatchee Mountains of eastern Washington.

Old forests can contribute significantly to local and regional biodiversity. For this and other reasons, there is strong interest in restoring old forest structure to a level that approximates its historical abundance. Any restoration approach should incorporate the following concepts relating to the landscape ecology of eastern Oregon (Camp et al. 1997, Everett et al. 1994):

- Current anomalous landscapes and disturbance regimes need to be restored to a more sustainable state to conserve old-forest remnants and to maintain old-forest networks.
- Today, many old-forest remnants are surrounded by a mosaic of young forest types with heightened fire and insect hazard.
- Given the limited contribution from any individual old-forest patch, additional old-forest stands need to be continually created to maintain a dynamic balance through time.
- Efforts to conserve old forest should not sacrifice contributions from other structures or components in the landscape.
- Conserving the disturbance processes influencing ecosystems is every bit as important as conserving individual plant and animal species or old forest structure – a lack of disturbance can be as threatening to biological diversity as excessive disturbance (Noss 1983).
- Management of old forest patches should be integrated with the disturbance regimes characteristic of their associated landscape.
- Any plan to sustain old forests must first sustain the landscape of which they are a part.
- In managing old forests, a landscape perspective is needed that coordinates species requirements with ecological processes and other functional attributes of ecosystems.
- Forest ecosystems of the interior Pacific Northwest are in a constant state of change, and it must be recognized that the successional pathway of a high proportion of the forest stands will be interrupted by fire, windthrow, insect attack, or disease before they can reach an old-forest condition.

A restoration strategy for old forests could include the following considerations (Camp et al. 1997, Everett et al. 1994):

- Conservation of the remaining old-forest patches is the cornerstone of any management scheme, if for no other reason than it best maintains future options.
- Sites that do not have a full complement of old forest characteristics can partially function as old forest for those attributes that are present.
- In some parts of the landscape it might be necessary to designate areas of younger forest as old-forest management areas in order to meet desired future objectives with respect to a seral stage distribution.
- Silvicultural practices can be used to accelerate development of old-forest characteristics in young stands, particularly those influencing regeneration density, stocking levels, or competing vegetation (Spies et al. 1991). Research has shown that tree size increases rapidly after stand density levels are reduced (Barrett 1979, Seidel and Cochran 1981).
- The potential for increasing the amounts and distribution of old forest multi strata stands is present on the landscape in the form of mid- to late-seral structural classes (specifically, the understory reinitiation and young forest multi strata classes; see table 2).
- Although mid- to late-seral stands are in the pipeline to replace old forests lost to natural disturbances, we still do not know the appropriate ratio of late-seral to old forest patches to ensure that current or desired levels of old forest are maintained in perpetuity.
- Evaluating historical amounts of old forest (as is often done when analyzing the historical range of variability for forest structural classes) can provide a first approximation of old forest abundance that was sustainable and with which plant and animal species evolved.
- Ideally, historical evaluations should incorporate several reference points in time and at a sufficient spatial scale to ensure that major disturbance regimes have been accounted for.
- A successful old forest strategy allows flexibility in specific ground locations over time. The shifting mosaic landscape concept suggests a dynamic framework in which old forest patches are lost and created in equilibrium at appropriate spatial and temporal scales.
- Restoration of old forests carries with it long-term management costs with little expectation of substantial commodity production. Creation of an old-forest network explicitly assumes that biological diversity and other old-forest values are specifically desired by human society.
- A dynamic ecosystems philosophy should be the foundation of any old-forest strategy – an ecologically sustainable representation of old forest structure in the landscape is more important than preservation of individual old forest patches.

Plant Succession

Landscapes and the ecosystems that comprise them age through time. The series of changes resulting in forest aging is called plant succession. Plant succession, which begins with colonization or reoccupation of a disturbed area by vegetation, refers to temporal changes in both species abundance and vegetation structure (fig. 8). Once initiated, plant succession may follow a variety of pathways (directions) and can occur at varying rates of speed (Drury and Nesbit 1973, McCune and Allen 1985). Since the composition, structure, and function of an ecosystem can change as plant succession progresses, it is important that land managers understand the many ways in which succession influences forest development to ensure that management activities are placed on a sound ecological foundation.

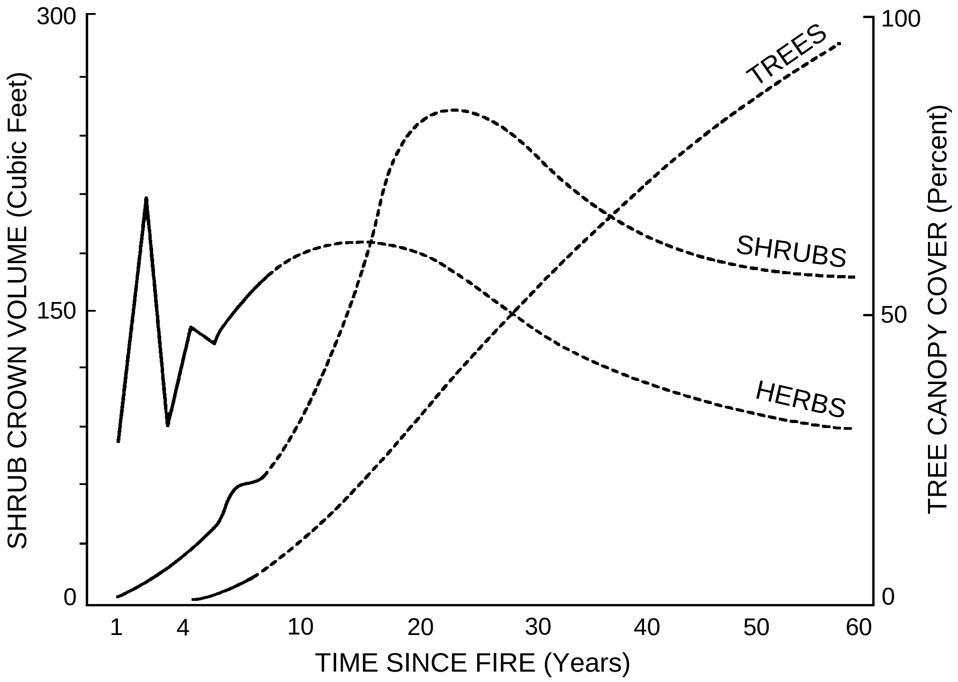


Figure 8–Plant succession following a prescribed, stand-replacing crown fire in south-central Idaho (adapted from Lyon 1971). For at least the last several thousand years, fire has been the principal initiator of plant succession in the interior Northwest. Holocaustic fire (stand-replacing crown fire) represents one of the most severe disturbance events that a forest ecosystem ever experiences (Stickney 1990). Plants comprising the initial community after a holocaustic wildfire have been classified as survivors, residual colonizers, or offsite colonizers, depending on how they regenerate following severe disturbance. Initially a stand-replacing wildfire area will be dominated by herbaceous plants such as forbs and graminoids (grasses and sedges; see table 27 in app. 2). As succession progresses, woody plants eventually predominate, with shrubs peaking by the second decade and trees assuming dominance between 30 and 40 years after the fire. On this site, dominant post-fire shrubs were snowbrush ceanothus, Scouler willow, and Rocky Mountain maple. Post-fire succession is controlled by broad-scale gradients in cone serotiny (see fig. 2), by mid-scale variation in fire intensity and pattern, and by fine-scale variability in soil conditions, slope steepness, and aspect (Turner et al. 1997). Note that even though trees may not predominate until the third decade, they were already established in the post-fire community by the fourth year after the fire – this is a good example of the initial floristics developmental pattern, which is explained later in this section (page 28).

Equilibrium Paradigm

The first generation of American ecologists was led at the start of the twentieth century by Nebraska scientist Frederic Clements. Clements and his University of Nebraska collaborators (particularly Charles Bessey and Rosco Pound) believed that plant succession caused ecosystems to develop in a predictable sequence of steps – much the same way as a human infant matures into an adult. Proponents of this super-organism philosophy maintained that individual species were linked together in mutually beneficial systems exhibiting properties greater than the sum of their parts (Clements 1916, Egerton 1973, Wu and Loucks 1995).

Clements contended that nature was orderly, and that its order was for the most part stable and self-regulating. He assumed that the normal condition of ecosystems was a state of homeostasis or equilibrium – a forest grows to a mature climax stage that becomes its naturally permanent condition (Clements 1916). Disturbance was a transitory phenomenon, a foreign intrusion into an otherwise balanced and harmonious community that in a healthy ecosystem was quickly disposed of in the same sense that a healthy organism disposes of disease (Perry 1994).

Many contemporary ideas about the environment are based on Clements' notion that nature is capable of retaining its inherent balance more or less indefinitely if only humans could avoid disturbing it (Cronon 1996, Shugart and West 1981). Clementsian ideology about the balance of nature is still espoused today: "we must not disturb the hierarchical balance of nature and the food chain. The earth has a natural system of interacting homeostatic mechanisms similar to the human body's. If one system is diseased, then other systems develop abnormalities in function" (Caldicott 1992).

Clements and his followers viewed disturbance as a rare phenomenon and believed that most sites in North America supported climax vegetation prior to Euro-American settlement. Their classical equilibrium paradigm of plant succession, a dominant ecological philosophy for at least 40 years, was based on the following principles (Clements 1916, 1936; Cook 1996, Odum 1969, Pickett and Ostfeld 1995):

- Plant succession was orderly, unidirectional, always passed through the same phases, and was therefore predictable and deterministic.
- Ecosystems were viewed as closed, self-regulating, and subject to a single stable equilibrium.
- Plant succession occurred only when one plant community modified the physical environment to an extent allowing another community to get established.
- Plant succession always culminated in a relatively stable community (the climax plant association).
- The stable end-point of plant succession (climax) was the norm, with disturbances being nothing more than aberrant disruptions of the normal successional process.
- Humans were not included on the roster of normal ecological factors, either as an ecosystem component or as a process (disturbance agent, etc.).

Contrary to Clements' claims, subsequent work has shown that the normal state of nature is not one of balance; the normal situation is to be recovering from the last disturbance. Change and turmoil, rather than constancy and balance, seems to be the rule. We now know that the concept of a forest evolving to a stable (climax) stage, which then becomes its naturally permanent condition, is incorrect (Botkin 1990, Stevens 1990). In many areas and particularly in the interior Pacific Northwest, large-scale disturbances are common and development to a truly stable climax is rare or absent (O'Hara et al. 1996).

Foresters have long embraced a steady-state view of the natural world, one that embodied concepts such as the 'regulated' forest and a systems approach to management (silvicultural 'systems,' regeneration 'systems,' etc.). Many of these attitudes had their basis in European or Germanic precedents (Weetman 1996). Until the late 1980s or early 1990s, forest planners continued to use linear programming techniques (e.g., FORPLAN) to calculate non-declining 'even flow' timber harvest levels and a long-term 'sustained yield' capacity in their quest for the 'fully regulated' forest. In fact, it was only recently that concerted attempts were made to explicitly incorporate the dynamic effects of disturbance processes in growth-and-yield models and linear programming algorithms (Beukema and Kurz 1996).

Foresters were not alone in embracing a steady state paradigm. In 1950, Carl O. Sauer wrote in the Journal of Range Management that “ecology has instructed us that plant societies may strike such happy balance with their environment and between their members as to form a stable, indefinitely reproducing order, called a climax vegetation.” But Sauer questioned this concept with respect to grassland communities, particularly after observing the effects of aboriginal burning on plant succession. “Plant associations are contemporary expressions of historical events and processes,” he wrote, further noting that “a real science of plant ecology must rest not only on physiology and genetics, but on historical plant and physical geography” (Sauer 1950).

Many of the world’s wildlife and fish populations have been managed by using a balance of nature philosophy that assumes when a population is disturbed, it will return to its former state (size) by following a logistic growth curve (Kay 1994). This classic incarnation of the homeostasis concept was based on two primary assumptions: (1) ecosystems are balanced and have a natural equilibrium, and (2) when disturbed, they will always seek to return to this equilibrium (Drury and Nesbit 1973, Huston and Smith 1987). In nature, however, there is no steady state and no true equilibrium (Botkin 1994), so it might be difficult to provide essentially constant levels of habitat for some plant or animal species, particularly in the dynamic, non-equilibrium landscapes of the inland West (Shugart and West 1981).

The ‘balance of nature’ is a poorly articulated idea that is a cultural metaphor rather than an exact scientific concept. It has deep historical roots, is held in high esteem, and is often invoked as apparently irrefutable dogma during discussion. Tempting as it may be to play nature as a trump card, it quickly becomes a self-defeating strategy because adversaries simply refuse to recognize each other’s trump and then go off to play by themselves (Cronon 1996). And because the balance-of-nature idea is not scientific, it is unclear just what its assumptions are, where and when it might apply, what mechanisms might lead to it, and how one could experimentally test it (Egerton 1973, Pickett and Ostfeld 1995).

The balance-of-nature metaphor, however, can represent some valid scientific ideas. It points toward the ecological principle that there are limitations in natural systems. No component of an ecological system, at whatever level of organization, grows without limit (Pickett and Ostfeld 1995). A good example is the many density-dependent processes in nature, as demonstrated by development of a single-cohort (even-aged) forest stand. These stands experience an initial period of unfettered free growth before eventually entering a self-thinning zone where density-related competition causes some of the trees to die (Cochran et al. 1994, Powell 1999).

In ecology, the relationship between population density and plant size has been referred to as self-thinning or the ‘–3/2’ rule (fig. 9). This rule states that after a stand enters the self-thinning zone, an increase in plant mass (size) must be accompanied by a corresponding decrease in plant density. The self-thinning phenomenon has been observed in a wide variety of species and life forms, including mosses, spike-rushes, sedges, reeds, and trees (Zeide 1987). Although early work by Japanese scientists suggested that one size-density relationship existed for all species (expressed as a logarithmic line with a –3/2 slope), later work found that both the slope and the intercept values of the maximum-density line showed considerable variation within and between species (Weller 1987, Westoby 1984, Yoda et al. 1963).

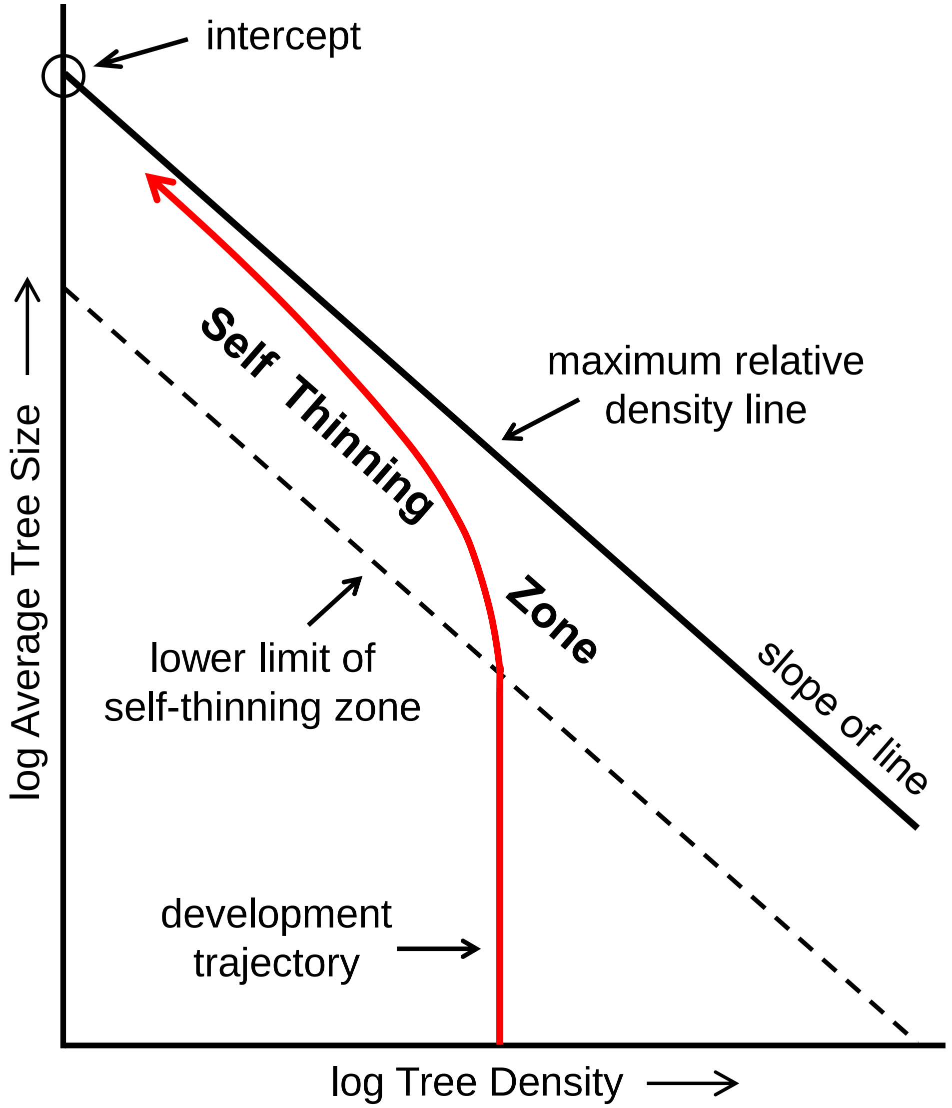


Figure 9–Schematic representation of important concepts related to self thinning (after Jack and Long 1996). This figure portrays an upper boundary or maximum size-density line which varies not only by tree species, but by plant association for the same species. The upper-boundary line is a logarithmic relationship with a negative slope (it's sloping downward rather than upward), which means that more trees are associated with a smaller size and less trees with a larger mean size. This negative relationship between mean size and density exists for all self-thinning plant populations, regardless of their life form (tree, shrub, herb). The self-thinning trajectory line shows a typical development pattern for an individual even-aged tree stand that eventually experiences density-dependent mortality. After self-thinning begins, a stand is constrained by the upper boundary and its future trajectory will then remain below, but track along, this line. The lower dashed line shows the lower limit of the self-thinning zone; stands beyond this line experience density-related, competition-induced mortality. For many tree species, the lower boundary coincides with 75% of the full-stocking level (Cochran et al. 1994, Powell 1999).

Henry A. Gleason was one of the first ecologists to challenge the equilibrium paradigm when he presented evidence showing that the dynamics of plant communities can be understood primarily as the sum of its individual species (Gleason 1926, 1927). Where Clements saw cooperation in nature, Gleason observed competition; where Clements looked for organized wholes, Gleason found loose pieces; and where Clements hoped for stability and order, Gleason saw a jostling of species – each seeking its own advantage in obvious disregard for the welfare of others in the community (Worster 1996). Many other scientists eventually challenged the equilibrium paradigm (Botkin 1990 and 1995, Cobb et al. 1993, Cook 1996, Cooper 1926, Egerton 1973, McCune and Allen 1985, O'Hara et al. 1996, Oliver 1981, Oliver and Larson 1996, Sprugel 1991, Stevens 1990, Tansley 1935, Whittaker 1953, et al.).[2]

Non-Equilibrium Paradigm

Ecological research conducted over the last 50 years has clearly demonstrated that the natural world is far more dynamic, far more changeable, and far more entangled with human history than was reflected in Clements' simplistic explanation of plant succession as a closed, self-contained process (Cronon 1996, Stevens 1990). Change is not only inevitable and universal, it is also variable – but not all changes are created equal. Some changes are cyclical, others are linear. Some changes occur in an afternoon, others over a millennium. And some changes are gradual or continuous (plant succession) whereas others are episodic (disturbance events) (Worster 1996).

By the mid 1950s, ecologists began to realize that natural systems are not nearly so balanced or stable as Clements would have us believe, and his habit of talking about ecosystems as if they were organisms, with a life cycle much like that of a living plant or animal, was far more metaphorical than real (Cronon 1996, Egerton 1973, Wu and Loucks 1995). This change in attitude gradually led to a modern non-equilibrium or dynamic equilibrium paradigm of plant succession. The non-equilibrium model considers ecosystem structure to be determined by long-term forces such as ecological (plant) succession and fluctuations in climate, and by the more immediate effects of disturbance events.

Individual communities that have reached a stable condition (the climax end-point of plant succession) are rare (Niering 1987), although a mosaic of different communities at a landscape scale can exhibit a stable frequency distribution of vegetative states. For example, many landscapes exist as a shifting mosaic of patch types (Bormann and Likens 1979). This concept suggests that an overall balance of patch births and deaths can produce a dynamic equilibrium – there is local change, but the total number of young and old communities remains relatively constant in response to disturbance processes and plant succession (Drury and Nesbit 1973, Pickett and Ostfeld 1995, Voller and Harrison 1998, White 1987).

With the advent of the non-equilibrium paradigm, the emphasis has shifted from viewing disturbance as a rare and unpredictable event to treating it as a natural process operating at a variety of spatial and temporal scales (Pickett et al. 1989, Wu and Loucks 1995). Non-equilibrium conditions are particularly common when the spatial scale of a disturbance process approaches or exceeds the size of a typical landscape unit. In areas where landscape-scale fires, windstorms (hurricanes), disease epidemics, or insect outbreaks occur regularly, forests are unlikely to reach a steady state.

---

[2] It was not the intent of this discussion to denigrate Frederic Clements or his contributions in any way. He was a true pioneer of plant ecology and one of the first ecologists in the United States to apply the principles and methods of plant ecology to a forestry problem – see his excellent bulletin entitled *The life history of lodgepole burn forests* (Clements 1910) for the results of that work.

The non-equilibrium model is based on the following principles (Cook 1996, Pickett and Ostfeld 1995):

- Disturbance is frequent enough to exert a significant influence on vegetation dynamics, with the result that many ecosystems will never reach a climax state.
- Random influences (chance events) play a significant role in plant succession.
- Life history characteristics (see appendix two) can have a direct bearing on plant succession, causing it to vary whenever the species that occupy a disturbed area change.
- Different ecological mechanisms may drive plant succession on closely-related sites or at different points during a sere's development.

Humans were not considered to be part of the equilibrium paradigm of plant succession because they violated many of its basic assumptions (Pickett and Ostfeld 1995). This attitude was explicitly incorporated into many of our federal lands policies. The Wilderness Act of 1964, Public Law 88-577, defines wilderness as "an area where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain" (Drury 1998). This attitude of setting humans apart from nature is inconsistent with archaeological evidence, which shows that ecosystems of the interior Columbia River basin have been inhabited by humans for at least 15,000 years (Knudson 1980).

Many people assume that when Europeans arrived in the New World, the land was sparsely occupied by American Indians, the impacts of native peoples were relatively minor, and the landscape was pristine. Recent investigations have shown this assumption to be a myth – American Indians were far from the passive hunters and gatherers depicted in western movies and novels. Their actions had a profound influence on the structure and composition of western ecosystems, a not unexpected result when considering that they used hundreds of plants and animals for food, fiber, shelter, forage, and medicine. Fire was often their main tool for creating and maintaining the habitats required by these plants and animals (Denevan 1992, Kay 1994, Robbins 1997).

In the non-equilibrium paradigm, humans are emerging as just one of many sources of ecological disturbance that keeps nature in a continual state of change. The question of whether humans should intervene in natural processes is moot, since humans and their near-human ancestors have been doing so for eons and ecosystems around the world bear their indelible imprint.

Because ecosystems with native peoples differ markedly from those lacking an aboriginal influence, a hands-off approach by today's managers will not duplicate the conditions under which presettlement ecosystems developed (Botkin 1995, Christensen et al. 1996, MacCleery 1992, Stevens 1990). On the other hand, it is important to recognize that the technologies used by Native Americans to manipulate landscapes for thousands of years were far different than those employed by Euro-American emigrants (Aplet and Keeton 1999, Cronon 1996).

Historically, ecologists largely ignored forests that had been burned or blown down because in an equilibrium system, disturbance was thought to be the exception rather than the rule. Once studies of forest succession began in earnest, they showed that a single group of tree species is not predestined to inhabit an area, that recruitment of new trees into a forest often follows a disturbance event rather than being a constant occurrence, and that disturbance severity has a major influence on which tree species will dominate afterward (Bloomberg 1950, Cobb et al. 1993, Drury and Nesbit 1973, O'Hara 1995, O'Hara et al. 1996, Oliver 1981, Oliver and Larson 1996, Spurr 1952).

Instead of seeking an elusive or nonexistent equilibrium, we should be looking for the trajectory over which an ecosystem is most likely to travel in the future. Rather than trying to maintain a forest ecosystem in one particular state, for example, we should be asking whether or not an action (or no-action) will allow it to stay within a set of bounds that seem either normal or preferred (Botkin 1994, Steele 1994).

Perhaps the concept of homeorhesis, which is the tendency of a perturbed system to return to its pre-perturbation trajectory or rate of change, is a more ecologically appropriate paradigm than homeostasis – the tendency to return to some pre-disturbance state (fig. 10) (Budiansky 1995, Christensen et al. 1996, Wu and Loucks 1995). The concept of homeorhesis recognizes that when an inappropriate landscape configuration is produced, whether by anthropogenic activities or by alteration of a disturbance regime, it will not revert to its former state when left alone; it will remain in an undesirable state (or on an undesirable trajectory) until actively transformed to some other state (Shugart and West 1981).

Plant succession was historically characterized as a change in species composition following replacement of one species by another – bull thistle is replaced by lupines, which are in turn replaced by pinegrass – but it can also refer to changes in vegetation physiognomy (fig. 11). Forest succession is characterized by progressive and often dramatic changes in physiognomy resulting from increasing tree size, decreasing tree density, and changing species dominance. During their development, forests generally occupy most of the following physiognomic classes – stand initiation, stem exclusion, understory reinitiation, and old forest (see table 2; O'Hara et al. 1996, Oliver 1981, Oliver and Larson 1996, Spies 1997).

After a stand-replacing wildfire event, forest sites experience a short post-fire period with high tree recruitment, followed by low and sporadic recruitment during the remainder of a stand's life. The initial post-fire cohort has a much lower mortality rate than subsequent cohorts; very few, if any, of the overstory trees will ever be replaced by trees from the understory – understory trees are born there and tend to die there as well (Johnson et al. 1994b).

Relay Floristics

Historically, many ecologists believed that plant succession follows a relay floristics pattern (Clements 1936). In relay floristics, a group of species invades after a disturbance and becomes dominant. As the early species mature, they cast shade, add organic matter to the soil, and otherwise modify the environment, which has the ironic effect of setting the stage for their eventual replacement by another species or group of species (in effect, they foul their own nest, creating an environment where they can no longer persist) (Drury 1998). This progression continues until a species or group invades and is able to replace itself rather than being supplanted by another species or group (fig. 12).

The term relay floristics was coined because like a relay race at a track and field meet, one floristic group relays the site to another until some relatively stable stage is eventually reached (Drury and Nesbit 1973). After a major disturbance destroys the forest, relay floristics predicts that grasses and forbs would first invade the site, followed by shrubs that crowd out the herbs. Soon, certain tree species would displace the shrubs, and in the shade of the first trees other species would come in and eventually eliminate the pioneering trees.

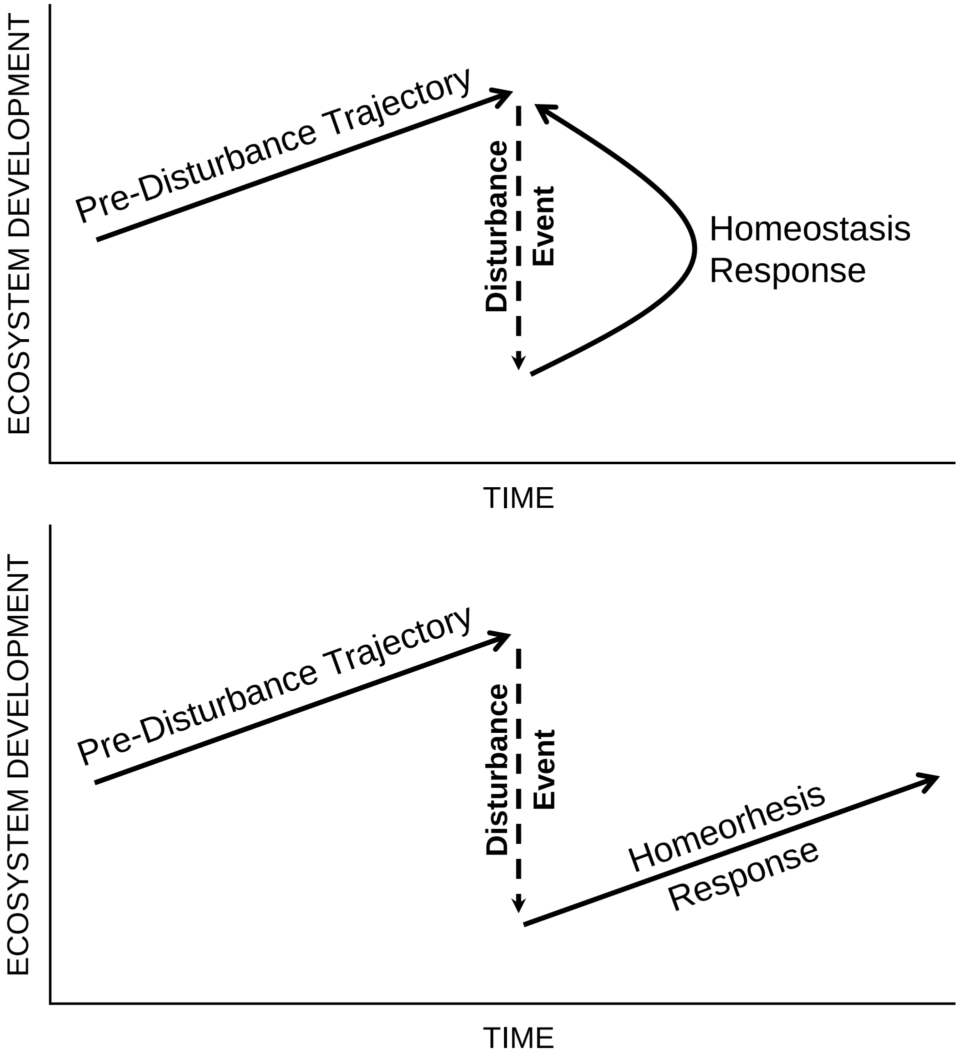


Figure 10–Two models of ecosystem response to disturbance. Homeostasis (upper half of figure) assumes that a disturbed ecosystem will attempt to return to its pre-disturbance equilibrium (the undisturbed state). Homeorhesis (bottom half) assumes that a disturbed ecosystem will attempt to return to its pre-disturbance trajectory or rate of change (rhesis is Greek for 'preserving the flow'). Homeorhetic stability implies a return to intrinsic ecosystem dynamics following disturbance, rather than a return to an artificial undisturbed state or equilibrium condition (Budiansky 1995, Christensen et al. 1996, Wu and Loucks 1995). The concept of homeorhesis also recognizes that when an inappropriate landscape configuration is produced, it will not revert to its former state when left alone; it will remain in an undesirable state (or on an undesirable trajectory) until actively transformed to some other state (Shugart and West 1981).

The ecological principle underlying relay floristics is one of facilitation – except for the first one, each stage in this progression depends on changes caused by the previous stage. What's important here is to recognize that the changes are not random or accidental – without the environmental modifications provided by an earlier stage, it is assumed that the plants associated with a later stage could not get established or survive.

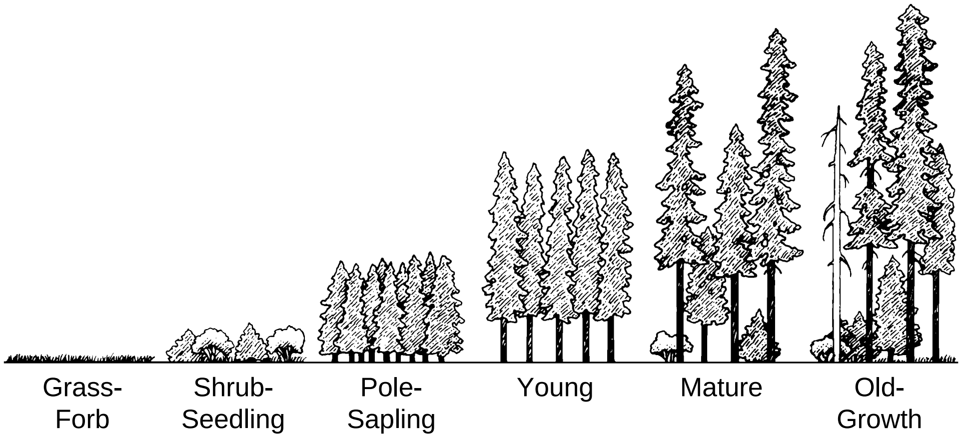


Figure 11–Physiognomic succession in a conifer forest (adapted from Thomas et al. 1979). After stand-replacing disturbance, a new forest develops by passing through successive and predictable stages. These changes result in a progression of vertical structure (physiognomy) through time. This figure shows a six-stage chronosequence, beginning with a grass-forb stage and culminating in a late-seral, old-growth stage. In this example, the first two stages are dominated by non-tree lifeforms (herbs and shrubs); the last four are dominated by trees. Forest structure has recently been classified into four to seven stages using a process-based approach (O'Hara et al. 1996, Oliver 1981, Oliver and Larson 1996, Spies 1997); table 2 (page 17) describes these structural stages in more detail.

In 1977, biologists Joseph Connell and Ralph Slatyer published an article in which they refuted Clements' claim that an invading community of pioneering species, constituting the first stage in plant succession, worked to prepare the ground for its successors. The first comers, according to Connell and Slatyer (1977), managed in most cases to stake out their claims and defend them successfully – they did not give way to a later group of long-term settlers. Only when the pioneers died or were damaged by subsequent disturbance processes, thus releasing the site resources they had monopolized, did late-comers find a foothold and get established (Connell and Slatyer 1977, Johnson et al. 1994b, Worster 1996). Connell and Slatyer's work demonstrates that disturbance processes can provide an important ecosystem service by reallocating nutrients, sunlight, moisture, and the other essentials of life.

Initial Floristics

Some sites support many different plant species following disturbance and plant succession then progresses according to an initial floristics pattern. In initial floristics situations, dominance is not determined by which species can invade first, but by the growth rates and development patterns (e.g., life history characteristics) of the species themselves (Halpern 1989, Oliver and Larson 1996). Since plants get established at approximately the same time in an initial-floristics situation (Johnson et al. 1994b), the development and structure of these communities is directly related to how well each individual species can capitalize on the post-disturbance environment.

Frank Egler (1954) was one of the first American ecologists to notice that tree species did not always invade a disturbed site in a relay fashion – a mix of species often occurred on a site initially and then assumed dominance in a sequential pattern (fig. 13). It was noted (1) that many species either survive a disturbance or colonize the area shortly thereafter, and (2) that long-term changes in composition occur through gradual expansion and decline of species (e.g , changing dominance), rather than through sequential recruitment and replacement (Halpern 1989).

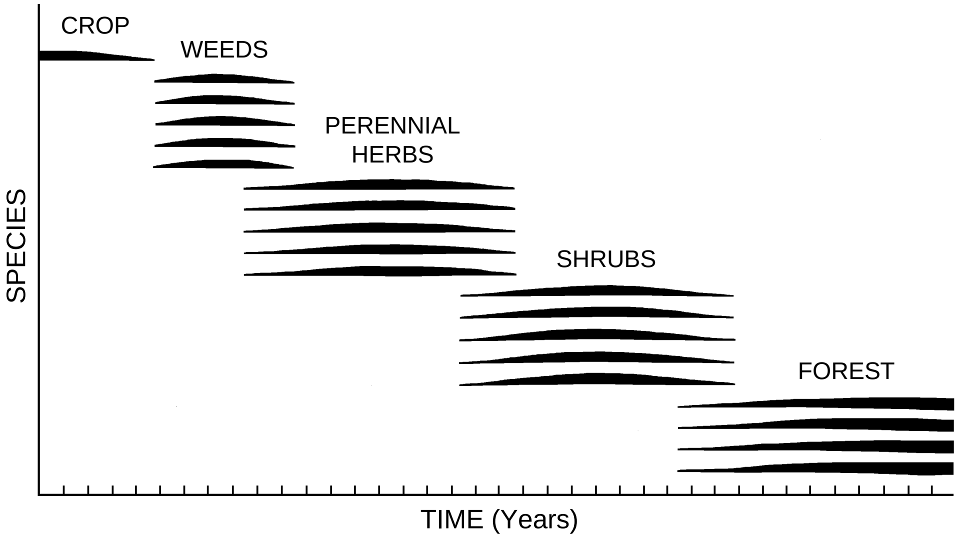


Figure 12–Relay floristics model of plant succession (adapted from Egler 1954). Succession refers to temporal changes in both species abundance and vegetation structure following a disturbance event. In the relay floristics model, it is assumed that changes in species composition occur because plants colonize a disturbed area at different times. Relay floristics also assumes that the early species act as facilitators, modifying environmental conditions to an extent that allows the later species to eventually get established. This relay floristics model formed the basis for early descriptions of the plant succession concept (Clements 1916).

The initial floristics pattern results in physiognomic succession (changes in vertical stand structure due to differential growth patterns) rather than species succession (lodgepole pine invades and is replaced by Douglas-fir, which in turn is replaced by grand fir, and so forth). Species exhibit a changing pattern of abundance or dominance based on differences in their life history traits, or because they have a different response or tolerance to disturbance processes. One group of species may consist of winter annuals, another of biennials or short-lived perennials, and a third of long-lived perennials, with each one responding to the post-disturbance environment in a slightly different way (Halpern 1989). Some species find optimum habitat in early-successional conditions, others in mature plant communities, and some in both environments. For this reason, significant changes in disturbance levels as compared to historical conditions (either increases or decreases) can ultimately degrade biological diversity (White et al. 1999).

A good example of initial floristics is mixed, single-cohort (even-aged) forests containing a mix of early- and late-seral species. Since trees grow and develop at different rates, these stands gradually develop a multi-storied, stratified structure with the fast-growing western larches and lodgepole pines in the upper stratum, and the slower-growing Douglas-firs and grand firs in a lower stratum (Cobb et al. 1993, O’Hara 1995). Although stratified stands are typically assumed to be uneven-aged because of the relay floristics paradigm, the multi-layered structure of initial-floristics stands is actually the result of differing height growth rates between the shade-tolerant and shade-intolerant tree species (Larson 1986; fig. 14).

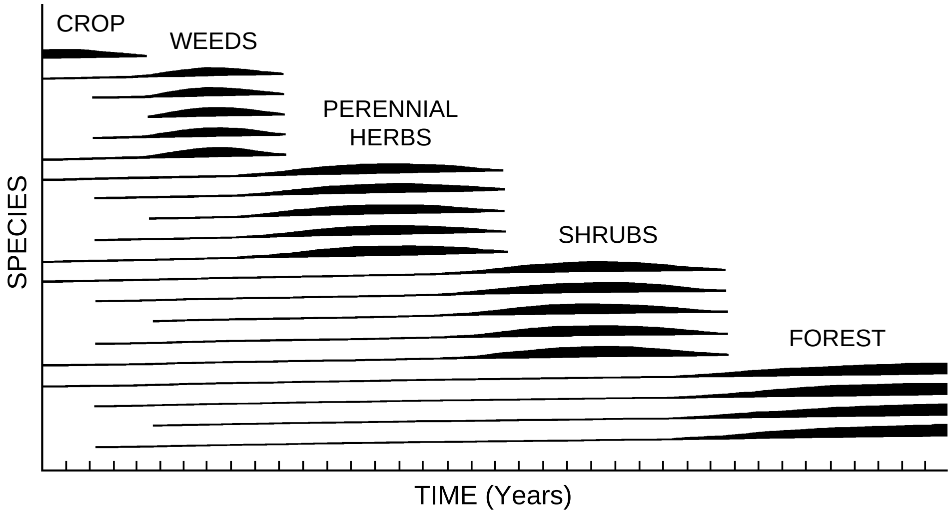


Figure 13–Initial floristics model of plant succession (adapted from Egler 1954). Succession refers to temporal changes in both species abundance and vegetation structure following a disturbance event. In the initial floristics model, it is assumed that changes in species dominance occur because plants grow and develop at different rates. Rather than different species arriving on a disturbed site at different times (as is assumed by the relay floristics model in fig. 12), the initial floristics model assumes that most species were already present or got established soon after a disturbance. In this model, the vegetation progresses through a series of structural changes, with the rates of change controlled by the life history characteristics of individual species in the plant community (e.g., annual herbs will develop in a different way, and at a different rate, than woody perennials). Appendix 2 provides 20 tables summarizing life history characteristics with important implications for forest succession.

Now, which of these concepts is correct, relay floristics or initial floristics? Actually, both of them are valid since both patterns occur in nature. Relay floristics is predominant in situations experiencing primary succession, such as vegetation colonizing bare rock, landslides, glacial deposits, lava flows, sand dunes, and other areas that never supported plant life before. Since these substrates are relatively uncommon, relay floristics is not a widespread development pattern (fig. 15) (Drury and Nesbit 1973). Primary succession generally occurs over a timeframe spanning hundreds to thousands of years.

Initial floristics is associated with secondary succession, which occurs after a disturbance event has modified the vegetation of a site without seriously affecting the physical, chemical, or biological characteristics of its soil. Forest clearcuts, burned areas, windthrow pockets, insect-killed stands, and abandoned agricultural fields are just a few examples of sites undergoing secondary succession. Since these types of disturbance events are relatively common, initial floristics is a frequent development pattern (Drury and Nesbit 1973). Secondary succession generally occurs over a timeframe spanning tens to hundreds of years – figure 8 (page 20) shows a 60-year successional progression following stand replacement wildfire.

Seres and Seral Stages

When plant succession is initiated by disturbance, the resulting sequence of plant communities is known as a sere; each of the individual communities in a sere is a seral stage (Kimmins 1997). It is important to make a distinction here – succession is an ecological process, and the plant communities it creates (the sere and its stages) are nothing but a product of the process.

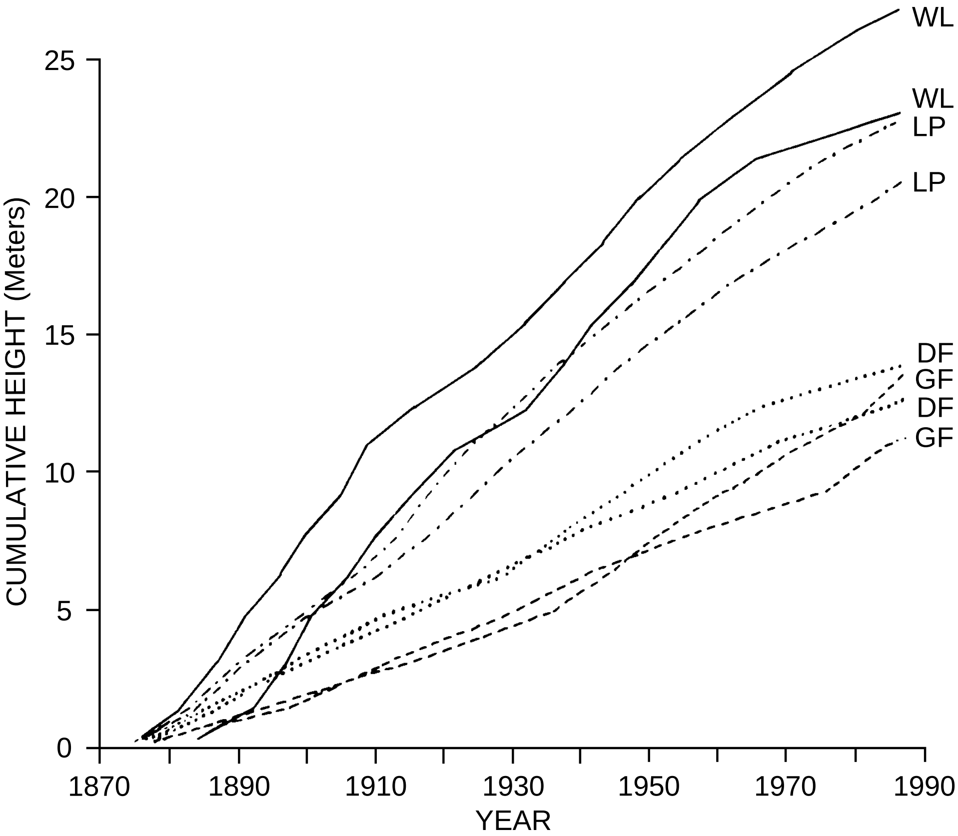
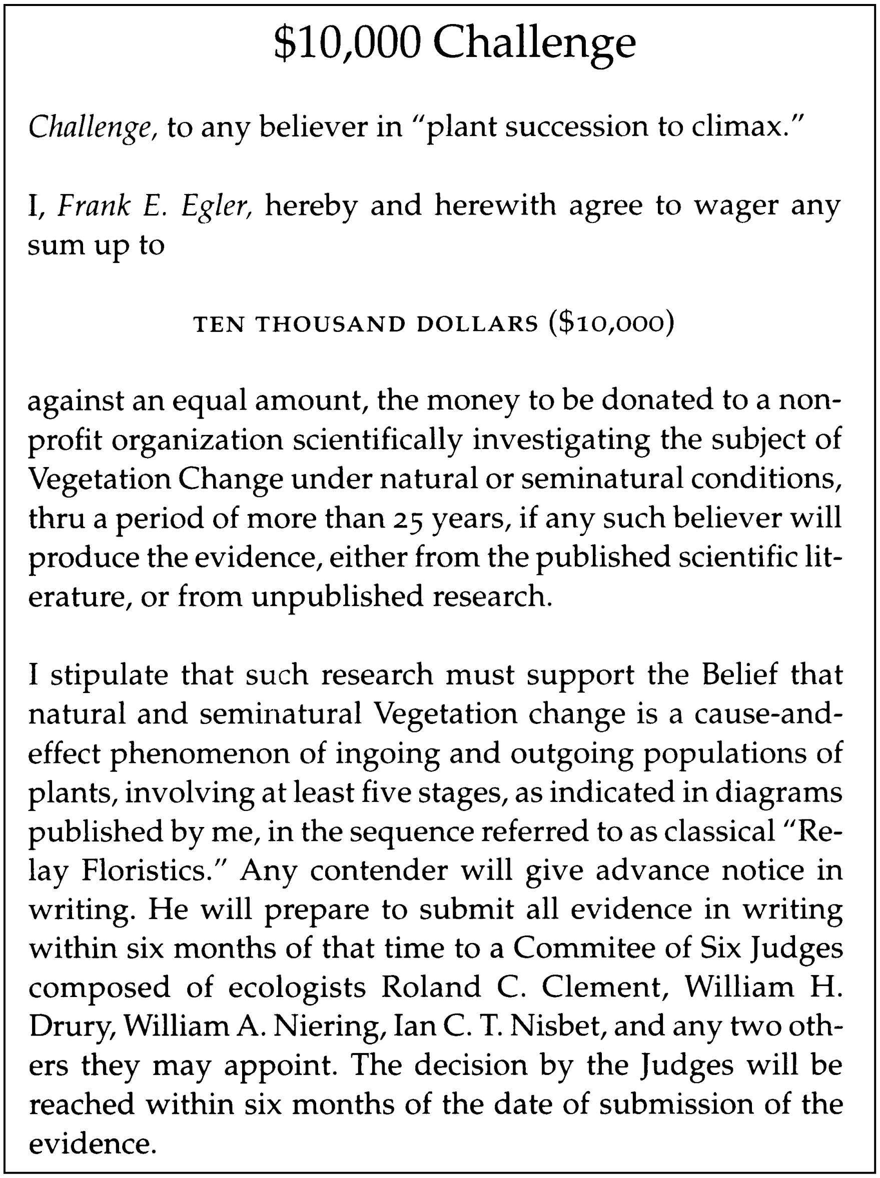


Figure 14–Development of mixed-species, single-cohort forests (adapted from Cobb et al. 1993). Different tree species grow and develop at different rates. This figure shows that early-seral species (western larch, WL, and lodgepole pine, LP) grow faster than mid- or late-seral associates (grand fir, GF, and Douglas-fir, DF) when both groups are present in a single-cohort (even-aged) stand. The end result is a multi-storied structure sometimes mistaken for an uneven-aged condition, even by silviculturists who neglect to use an increment borer to check whether a stratified structure is even- or uneven-aged (Bloomberg 1950, Larson 1986, O'Hara 1995). After timber harvest or insects and diseases remove the dominant overstory trees, the physiognomy of these stands can change from a relatively open structure featuring tall-stature, early-seral species to a dense structure with a predominance of short-stature, late-seral species (Graham et al. 1999).

Seral vegetation is that which has not attained a steady state; current populations of some species are being replaced by others. Seral communities are categorized as early-seral, mid-seral, or late-seral, depending on how much time has passed since the disturbance event (Hall et al. 1995). Often, the plant composition varies for each of the seral stages. For example, table 3 portrays the composition associated with early-, mid-, and late-seral stages developing on grand fir plant associations in the Blue Mountains.

The interaction between ecological amplitude and plant succession results in tree species being able to fill several seral roles. Ponderosa pine is a good example. On hot dry sites at low elevations, it is often climax because other species do not have the ecological amplitude to survive in these environments. On warm dry sites where Douglas-fir or grand fir is climax, ponderosa pine is a long-lived, early-seral dominant. On cool moist sites where grand fir or subalpine fir is climax, it is a minor or accidental species. And on cold dry sites at high elevations, ponderosa pine doesn't occur at all because it cannot survive in these ecological environments (Powell 1998).



$10,000 Challenge

Challenge, to any believer in "plant succession to climax."

I, *Frank E. Egler,* hereby and herewith agree to wager any sum up to

TEN THOUSAND DOLLARS ($10,000)

against an equal amount, the money to be donated to a nonprofit organization scientifically investigating the subject of Vegetation Change under natural or seminatural conditions, thru a period of more than 25 years, if any such believer will produce the evidence, either from the published scientific literature, or from unpublished research.

I stipulate that such research must support the Belief that natural and seminatural Vegetation change is a cause-and-effect phenomenon of ingoing and outgoing populations of plants, involving at least five stages, as indicated in diagrams published by me, in the sequence referred to as classical "Relay Floristics." Any contender will give advance notice in writing. He will prepare to submit all evidence in writing within six months of that time to a Commitee of Six Judges composed of ecologists Roland C. Clement, William H. Drury, William A. Niering, Ian C. T. Nisbet, and any two others they may appoint. The decision by the Judges will be reached within six months of the date of submission of the evidence.

Figure 15–A challenge issued by ecologist Frank Egler seeking evidence that the relay floristics successional pattern actually occurs (from Drury 1998). In the 1950s (and republished in 1975), Egler offered a $10,000 prize to anyone who could present verifiable evidence supporting the relay floristics pattern of plant succession. When he died in 1997, no one had met Dr. Egler's challenge over a 40-year period. [Note: many Forest Service employees might know of Frank Egler because when Jack Ward Thomas was Chief, he often quoted him: "ecosystems are not only more complex than we think, they are more complex than we can think."]

Table 3: Seral composition associated with grand fir plant associations of the Blue Mountains.

	EARLY SERAL SPECIES			MID SERAL SPECIES			LATE SERAL SPECIES		
	TREE	SHRUB	HERB	TREE	SHRUB	HERB	TREE	SHRUB	HERB
ABGR/ TABR/ CLUN	LAOC PIPO	CEVE RIVI	CIVU RUOC	PSME	SASC ALSI	THMO PTAQ FRVE	PIEN ABGR	LIBO2 TABR	ARCO THOC CLUN
ABGR/ ACGL	LAOC PIPO	CEVE RIVI	CIVU AGUR	PSME	SASC ALSI	ASCA7 PTAQ FRVE	PIEN ABGR	SYAL VAME ACGL	ARCO VIOR2
ABGR/ CLUN	PICO LAOC PIPO	CEVE RIVI	CIVU CARO RUOC	PSME	SASC ALSI	PTAQ FRVE	PIEN ABGR	VAME LIBO2	ARCO VIOR2 CLUN
ABGR/ LIBO2	PICO LAOC PIPO	CEVE ARNE RIVI	CIVU CARO	PSME	SASC ALSI	ASCA7 FRVE	PIEN ABGR	VASC VAME LIBO2	ARCO VIOR2
ABGR/ VAME	PICO LAOC PIPO	CEVE ARNE RIVI	CIVU CARO	PSME	SASC AMAL	LUPIN PTAQ FRVE	PIEN ABGR	SPBE VASC VAME	CAGE CARU THOC
ABGR/ VASC-LIBO2	PICO LAOC	ARNE SHCA	CIVU CARO	PSME	SASC ALSI	LUPIN FRVE	PIEN ABGR	VASC LIBO2	CAGE CARU
ABGR/ VASC	PICO LAOC PIPO	ARNE SHCA	CIVU CARO	PSME	SASC	LUPIN FRVE	PIEN ABGR	VASC	CAGE CARU
ABGR/ SPBE	PICO LAOC PIPO	CEVE ARNE	CIVU CARO	PSME	SASC	LUPIN PTAQ FRVE	ABGR	AMAL SPBE	CAGE CARU
ABGR/ CARU	PICO LAOC PIPO	CEVE ARNE RICE	CIVU CARO	PSME	SASC	LUPIN FRVE	ABGR	SYOR	CAGE CARU
ABGR/ CAGE	LAOC PIPO	CEVE ARNE	CIVU	PSME	CELE SASC	CARO	ABGR	SYOR	CAGE

Sources/Notes: From Clausnitzer (1993). This table includes some, but not all, of the plant associations in the grand fir series for the Blue Mountains (the leftmost column contains plant association symbols). Refer to appendix 1 for the scientific and common names of plants whose alphanumeric symbols are included in this table.

Some seral communities are very stable, especially if they developed in response to recurrent disturbance. Disturbance frequency determines the length of successional cycles for a particular ecological system. Ecosystems with frequent disturbances have continually interrupted successions and exhibit a narrow range of plant communities and vegetation structure (Steele and Geier-Hayes 1995). A good example of a plant community maintained by high-frequency disturbance is park-like ponderosa pine, a forest cover type featuring large, widely-spaced trees growing above an undergrowth of dense grasses.

Blue Mountain landscapes dominated by open, park-like ponderosa pine forest had been created and maintained by frequent, low-intensity surface fires occurring every 8 to 20 years (Hall 1976). When Oregon's ponderosa pine forests were examined in 1910-1911, an open stand condition was clearly evident: "In pure, fully stocked stands in the Blue Mountains region there are commonly from 20 to 30 yellow pines per acre over 12 inches in diameter, of which but few are over 30 inches. Over large areas the average number per acre is ordinarily less than 20" (Munger 1917). [Note that 20 trees per acre results in an equilateral (triangular) spacing of 50 feet between trees, which certainly qualifies as an open condition.]

Because cyclic fire remained relatively constant, park-like pine forests were stable ecosystems that came to depend on a particular fire frequency and intensity (Sloan 1998). Fire frequency must be maintained at an appropriate level if park-like pine is to persist and this is the reason why fire frequency, not occurrence, is so important. Species presence remembers fire but abundance forgets (Allen and Wyleto 1983).

On most sites historically supporting park-like pine, suppression of the native disturbance regime – frequent surface fires (underburning) – had the unintended consequence of allowing late-seral grand firs and Douglas-firs to replace the pines. By the late 1970s, it was believed that at least 25% of the ponderosa pine type had been replaced with mixed-conifer forest (Barrett 1979); the reduction was apparently greater than that for the southern Blue Mountains, where ponderosa pine declined by more than half between 1936 and 1980 (Powell 1994). These declines resulted in old-growth ponderosa pine forests of the Rocky Mountains being declared a threatened ecosystem of the United States (Noss et al. 1995).

Replacement of park-like ponderosa pine with mixed-conifer forest was caused by human alteration of a disturbance regime. After frequent surface fires were suppressed, and following removal of mature pine trees with partial-cutting timber harvest practices, multi-storied stands dominated by late-seral species (grand fir and Douglas-fir) got established (Powell 1994, Sloan 1998). Thick layers of organic matter accumulated beneath the invading fir trees, tying up nitrogen and other nutrients that are cycled slowly without fire (Harvey 1994). Little natural thinning occurred, and the trees that died were usually the small pines and larches that succumb to suppression before the firs (fig. 16). Fuels accumulated at an alarming rate (Hall 1976). Herbage production declined substantially, affecting both native and introduced ungulates (Hedrick et al. 1968, Irwin et al. 1994). And loss of the park-like stand structure apparently had a detrimental impact on nesting success for blue grouse (Pelren and Crawford 1999).

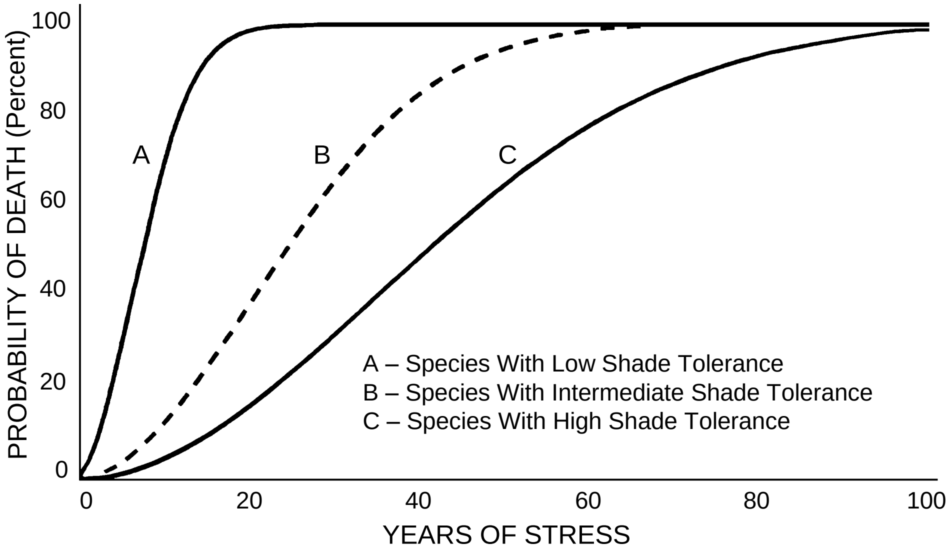


Figure 16–Tree resistance to stress varies with shade tolerance (adapted from Keane et al. 1996). Tolerance refers to a plant's ability to withstand the effects of one or more limiting factors such as unusually high or low temperatures, a deficit of soil moisture during the growing season, or environments with a deficiency of sunlight or nutrients. In forestry, perhaps the tolerance that has received the most emphasis is shade tolerance – the capacity of a species to survive and grow in the shade of other trees (Harlow et al. 1996). Intolerant tree species (lodgepole pine, ponderosa pine, western larch) die relatively quickly when exposed to chronic stress associated with overcrowding (high stand density), drought, root disease, and other factors. Trees with intermediate tolerance (Douglas-fir and western white pine) can withstand a longer period of stress without dying. Shade-tolerant species (Engelmann spruce, grand fir, subalpine fir) can endure relatively long stress periods before experiencing mortality.

How did fire suppression and partial cutting timber harvest contribute to ecosystems that are out of balance? Both practices had a detrimental effect on ecosystem resilience by altering vegetation diversity and complexity, particularly at a landscape scale. The alterations resulted in forests at risk, and the forests most at risk are those under the most stress because they contain too many trees, or too many of the wrong kind of trees, to continue to thrive. As these forest stands get older and denser, the competition between trees intensifies, stress increases, and the probability of significant ('catastrophic') change goes up dramatically (Sampson et al. 1994, Sloan 1998).

Over-protection from fire can render a forest susceptible to serious soil damage when a fire eventually does occur (Grier 1975). Where historical wildfire regimes have been altered because society is not prepared to accept fire-related risks to life and property, land managers should attempt to design thinnings and other management treatments that emulate the desirable characteristics of presettlement fire regimes (Kimmins 1997). Table 4 describes how some silvicultural treatments could be used to emulate certain aspects of native disturbance processes.

Historically, spatial variation in fire severity was important for providing diversity in landscape patterns. Under the recent fire regime (suppression), the influence of fire as an ecological process has been dramatically reduced – resulting in more homogeneous landscape patterns (Hessburg et al. 1999b, Lehmkuhl et al. 1994, Taylor and Skinner 1998).

Table 4: Silvicultural practices that can be used to mimic certain aspects of disturbance processes.

PRACTICE	DISTURBANCE PROCESSES BEING EMULATED
Clearcutting (with reserve trees)	• Stand replacing fires on sites where they are characteristic (e.g., on cold-forest and on upper-elevation moist-forest sites). • Mountain pine beetle outbreaks in pure, even-aged forest of lodgepole pine. • Windthrow occurring in pure, even-aged forest.
Overstory Removal (with reserve trees)	• Western pine beetle affecting uneven-aged ponderosa pine forest. • Douglas-fir beetle in multi-layered Douglas-fir forest. • Spruce beetle in forests with spruce in the overstory and spruce and true firs in the understory (Veblen et al. 1991). • Mountain pine beetle in multi-layered lodgepole pine forest (particularly when shade-tolerant species exist in the understory). • Subalpine fir mortality caused by balsam woolly adelgid. • Windthrow in subalpine forest with an overstory of lodgepole pine and an understory of spruce and fir (Veblen et al. 1989).
Salvage Cutting (removing some proportion of dead trees only)	• A reburn event in which a second fire consumes trees killed by the first burn, typically after they topple over. • A wildfire event after insect-caused mortality – insects kill the trees, they topple over, and their stems are then consumed by fire.
Selection Cutting	• Root disease centers in mature, mixed-species forest (emulated by group selection). • Dwarf-mistletoe parasitism in mature, mixed-species forest (emulated by individual-tree selection). • Lightning-caused tree mortality on upper-slope physiographic positions (emulated by individual-tree selection). • Senescence (tree death) related to old age in overmature forest.
Shelterwood or Seed-Tree Cutting	• Bark beetle outbreaks in mature, even-aged, mixed-species forest. • Mixed-severity wildfire in mature, mixed-species forest. • Avalanche chutes on steep slopes in the subalpine zone (emulated by the strip variant of the shelterwood cutting method). • Douglas-fir tussock moth defoliation in mixed-conifer forest.
Thinning	• Low-intensity surface fires in multi-layered forest of ponderosa pine, or in mixed forest of ponderosa pine and Douglas-fir/true fir. • Budworm damage in dense, even-aged, mixed-conifer forest. • Low-intensity wildfire in areas with a mixed-severity fire regime.
Understory Removal	• Budworm damage caused by the ‘feeding ladder’ effect where larvae rain down from taller trees onto shorter trees. • Surface fires in mixed forest with fire-resistant overstory species (ponderosa pine, larch, Douglas-fir) and fire-susceptible understory species (lodgepole pine, true firs, spruce).

Sources/Notes: Silvicultural practices are defined in the glossary and Helms (1998).

Defoliators and other landscape-scale insects often respond to increased homogeneity. For example, when reduced fire frequency caused changes in forest structure and composition at a landscape scale, outbreaks of the western spruce budworm increased in both duration and intensity, but not in frequency (Anderson et al. 1987).

Current ecological conditions in forests of the interior Northwest suggest that immediate management action may be warranted. This management intervention needs to be intensive and to cover wide areas of the landscape, but to be effective it must be substantially different in both impact and appearance from what was done historically (Sampson et al. 1994). Management intervention should use an adaptive approach that considers the forest as a fully-functioning ecosystem. Ecological principles form the basis of this approach assuming that if the effects of forest management activities closely resemble those of indigenous disturbances, then the risk of losing native species and altering ecosystem processes is greatly reduced (Aplet and Keeton 1999, DeLong and Tanner 1996, Rowe 1992).

If the scale of forest harvesting does not emulate the scale of native disturbance processes, then we can expect ecological changes that decrease biological diversity and interfere with other ecosystem processes such as energy and nutrient cycling (Baydack et al. 1999, Eng 1998). Using a variety of cutting patterns is important to avoid uniform landscapes; grouping cut blocks reduces the total amount of edge, minimizes fragmentation, and maintains larger patches of old forest. It is important that management action focuses on the effects of disturbance processes and the function of biological legacies (fig. 17), rather than attempting to directly replicate a particular disturbance agent.

Deciding to take immediate action can result in a philosophical shift toward proactive management to curtail excessive fire and insect impacts, and a shift away from reactive management in response to landscape-scale disturbance events. The solution could start with thinnings and understory removals to reduce stand density in overcrowded forests, particularly on warm dry sites where overcrowding was a rare phenomenon before the onset of anthropogenic fire suppression (Oliver et al. 1994). No single silvicultural practice, however, can hope to precisely reproduce the inherent variability of a landscape because forests and other ecosystems are shaped by a variety of disturbance processes (Voller and Harrison 1998).

Society’s response to deteriorated ecological conditions in the interior Northwest has lacked consensus. Some groups advocate a passive hands-off approach, believing that active intervention would make an unfortunate situation even worse. Others maintain that active intervention in combination with natural processes would be appropriate for restoration of ecosystem sustainability. An eminent group of fire ecologists cautioned that a status quo solution for the Blue Mountains “will leave us with seriously degraded ecosystems offering little value in an ecological, aesthetic, or economic sense. This option goes counter to the values and concerns of society today, such as biological diversity, beautiful and ‘natural’ landscapes, healthy plant and animal communities, and long-term productivity” (Mutch et al. 1993).

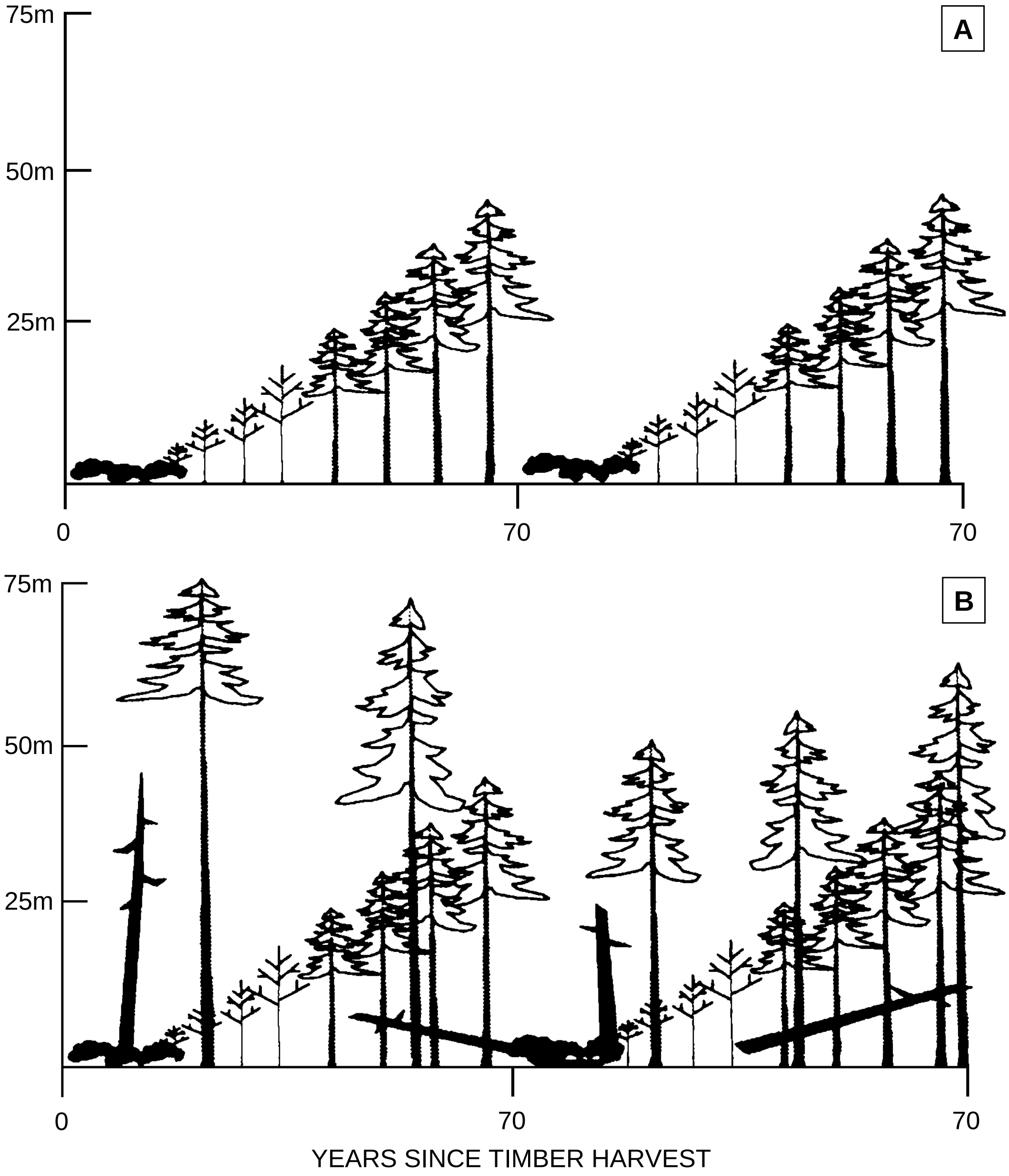


Figure 17–Comparison of idealized development in stands designed for (A) maximum wood production and (B) both structural diversity and wood production (adapted from Hansen et al. 1991). Traditional management practices for maximizing wood production tended to create tree plantations that were relatively simple with respect to structure, habitat diversity, and retention of so-called biological legacies. Contemporary practices that better mimic natural forest patterns, processes, and interactions can maintain biological diversity while simultaneously providing an opportunity for wood production. In addition to a young (regenerating) tree cohort, the contemporary stand (B) features these legacies derived from one or more of the previous forest generations: remnant old, live trees; downed dead wood; and standing dead wood (snags). Providing legacies recognizes that the effects of stand-replacing disturbance were heterogeneous, creating a variety of patch sizes, shapes, ages, and intra-patch structural elements (shrubs, snags, decaying wood, live conifers and hardwoods, etc.) (Aplet and Keeton 1999, Rochelle et al. 1999).

Vegetation Classification

It is important to recognize that forests are more than timber stands – they are complexes of living organisms that interact not only with each other, but with their environment. These complexes are called an ecosystem. There are many kinds of ecosystems but not an infinite number, and ecologists soon learned that similar ecosystems occur repeatedly across the landscape. Vegetation and indicator plants are readily observed components of an ecosystem. They can be used to help recognize different ecosystems and to delineate their boundaries (e.g., map them). The process of identifying and characterizing different ecosystems is called vegetation classification.

Potential vegetation has been classified using a taxonomic approach based on extensive sampling of stands with climax or near-climax plant composition (Pfister and Arno 1980). All of the vascular plant species found in the sampled communities are recorded and used when developing a classification. Grouping of similar communities results in a taxonomic hierarchy. Forest vegetation has been organized as two hierarchies; the highest level of the fine-scale hierarchy is based on the projected climax dominant tree species and is called the series. The subalpine fir series, for example, includes all plant associations where subalpine fir is presumed to be the dominant tree species at climax (fig. 18).

The middle level of the fine-scale hierarchy is a combination of an overstory tree dominant and one or more indicator species (or groups of ecologically similar species called unions) in the undergrowth vegetation layer. These units are called a plant association.[3] Forested plant associations are named for their dominant overstory (tree) and undergrowth (shrub or herb) plants, such as the *Abies grandis/Clintonia uniflora* plant association (abbreviated ABGR/CLUN). From an ecological perspective, it is assumed that the dominant tree species (*Abies grandis*) reflects an area's macroclimate, whereas the undergrowth indicator plant (*Clintonia uniflora*) represents a site's microclimate and soils.

The lowest level of the fine-scale hierarchy is called a phase, which represents a subdivision of a plant association. Phases reflect minor environmental differences within a plant association and are named for an indicator plant species, such as the pinegrass phase of the Douglas-fir/birchleaf spirea plant association (Steele et al. 1981). Although commonly used elsewhere in the Rocky Mountains (Pfister and Arno 1980), phases have not been included in vegetation classifications for the Blue Mountains (Crowe and Clausnitzer 1997, Johnson and Clausnitzer 1992, Johnson and Simon 1987).

Potential vegetation information is also valuable for land-use planning, ecosystem analysis at the watershed scale (e.g., watershed analysis; REO 1995), bioregional assessments such as the Interior Columbia Basin Ecosystem Management Project (Johnson et al. 1999), and for a variety of other mid- or broad-scale purposes. To meet these needs, a mid-scale hierarchy of potential vegetation was recently developed (fig. 18). The mid-scale hierarchy consists of plant association groups[4] and potential vegetation groups. A link between the fine- and mid-scale hierarchies is provided by the plant association.

---

[3] In many areas of the western U.S., this level of the potential vegetation hierarchy is called a habitat type.

[4] Plant association groups (PAGs) are often assumed to be equivalent to biophysical environments. This assumption is seldom true because biophysical environments generally incorporate physical factors such as geology or geomorphology (Jensen et al. 1997), whereas PAGs are based on potential vegetation only.

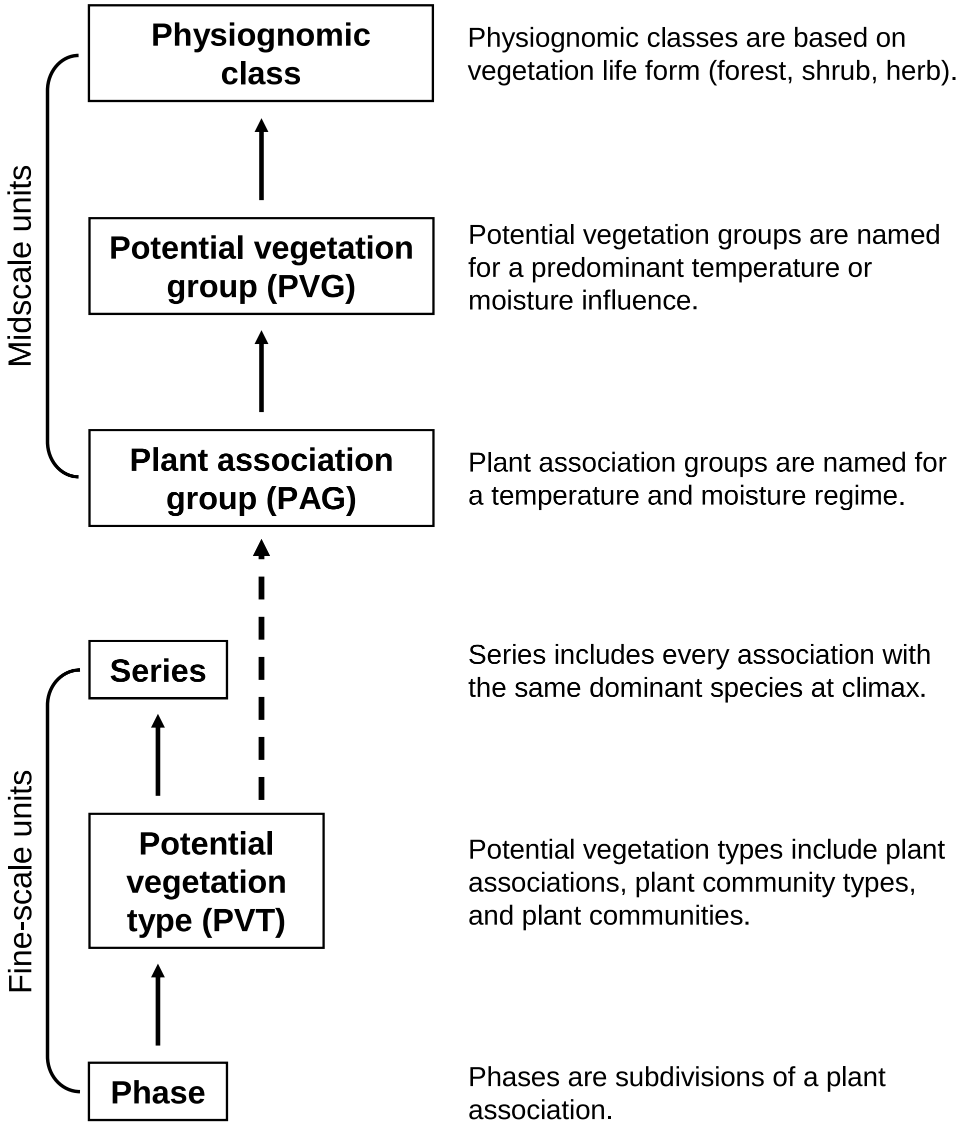


Figure 18–Hierarchies of potential vegetation for upland forests. Potential vegetation can be organized as both a fine-scale and a mid-scale hierarchy. The fine-scale taxonomic units are described in vegetation classifications and their associated keys. Series is the highest level of the fine-scale hierarchy; phase is the lowest level (Pfister and Arno 1980). For analysis purposes, a mid-scale hierarchy was recently developed. Potential vegetation groups (PVGs) are the highest level of the mid-scale hierarchy; plant association groups (PAGs) are the lowest level. A link between the fine-scale and mid-scale hierarchies is provided by the plant association because associations are aggregated to form PAGs. For the Umatilla National Forest in the central and northern Blue Mountains, the composition of PAGs and PVGs is described in Powell (1998).

Some late-seral (successional) vegetation types persist on the landscape and have been referred to as plant community types in vegetation classifications. Plant community types can include vegetation that might be climax, but about which there is uncertainty. Forested plant community types have one or more dominant tree species in the overstory, and a well-developed undergrowth. The undergrowth may reflect the climax composition, but the overstory dominants are often long-lived seral trees that exist because a previous disturbance event favored their establishment instead of the climax species.

Tree species occur in either pure or mixed stands called cover types. Cover types are classified using existing tree composition, regardless of whether it represents the potential vegetation of a site. Cover types reflect the forests as they exist today – what a land manager finds on the ground and must deal with on a daily basis. Cover type classifications have a long history and are commonly used for management purposes, not just for forests but also for rangelands and other non-forest vegetation (Shiflet 1994). Forest cover types of the United States and Canada are described in Eyre (1980).

Management Implications

Why are some plant communities found only in certain situations (subalpine fir forests at high elevations)? Why are some structural stages associated most often with particular environmental conditions (the old forest single stratum stage (table 2) with warm dry sites)? And why do certain disturbance agents have a dramatically different impact depending on which ecological type they occur in (a short flame-length fire tends to be lethal to forests on cold sites but not on dry sites)? The response of an ecosystem to a management practice or a disturbance agent has been termed a management implication.

Potential vegetation (PV) has an important influence on ecosystem processes. It is the engine that powers vegetation change – it controls the speed at which shade-tolerant species get established beneath shade-intolerant trees, the rate at which forests produce and accumulate biomass, and the impact that fire, insects, pathogens, and other disturbance agents have on forest composition and structure. The implications of these processes are predictable, at least to some extent, because they can be related to PV, and research has shown that sites with the same PV behave in a similar way (Cook 1996, Daubenmire 1961).

Because of its predictive power, PV is useful for estimating the impact of disturbance agents and management activities on different ecological environments. For example, a prescribed fire with a flame length of 2 feet and an intensity of 25 BTU/ft/sec has relatively benign, nonlethal results when used on warm sites where the overstory trees have thick bark (ponderosa pine, Douglas-fir, western larch). This same treatment has dramatically different results (high tree mortality) on cold sites dominated by thin-barked subalpine firs and lodgepole pines.

Once an area has been classified and mapped into potential vegetation units (plant associations), then management of the forest can be simplified somewhat while simultaneously putting it on a sound ecological foundation. Although simplification has potential pitfalls (over-simplification often does more harm than good), it can provide clarity and foster strategic thinking: “we must learn how to aggregate and simplify, retaining essential information, without getting bogged down in unnecessary detail” (Levin 1992).

Historically, forest management was based on classification of existing cover types. Although a cover-type map provides valuable information about existing tree species and size classes, it provides little information about productivity or other ecological site potentials. The problem with this situation is that “any map that provides only an inventory of a highly perishable resource is short-lived, whereas a map which portrays the productive capacity of the land is as permanent as the land itself” (Daubenmire 1973).

A polygon on a cover-type map delineating lodgepole pine (the ‘perishable resource’ mentioned above) could obviously support another stand of the same species after being disturbed, but the map would provide no hint about which species could replace lodgepole pine in the absence of future disturbance (grand fir? subalpine fir?), whether or not the site is suitable for western white pine, whether prescribed fire would stimulate good browse for big-game animals, and whether the lodgepole is growing under marginal or optimal conditions for its growth and development (Daubenmire 1973).

Potential vegetation maps are useful for a variety of purposes and have been developed for some areas in the western United States. Since soil maps exist for many wildland areas, attempts have been made to correlate PV types with soil mapping units as a way to extend PV mapping. Correlation efforts were not successful because "closely similar stands of climax forest occur on soils with very different profile characteristics, and different climax forests may have similar profiles" (Daubenmire and Daubenmire 1968).

Useful vegetation classifications provide more than just the capability to determine which types are present in an area – they allow land managers to better predict vegetation response to a variety of management activities such as regeneration cutting or prescribed fire. Some examples of how potential vegetation (PV) has been used to develop management implications are described below:

- **Developing reforestation recommendations**. In the old days, foresters often planted the same species that had been harvested, perhaps not realizing that late-seral trees are poorly adapted to postharvest conditions. Sometimes, they planted a commercially valuable species where it wasn't well adapted ecologically, such as ponderosa pine on cold or wet sites. As early as 1683, foresters in Germany recognized that every tree species would not be acceptable on every forest site (Boerker 1916). Knowing the successional status of each tree species occurring in a plant association can greatly improve reforestation success, with early-seral species best adapted to open conditions and mid-seral species suitable for partially-shaded environments (table 5).
- **Prescribing silvicultural treatments**. One of the most challenging aspects of silviculture is the choice of a regeneration cutting method because it controls canopy openings, shading, and ultimately the species composition of a new stand. Many management implications pertaining to silviculture, including natural regeneration probabilities and seed-seedling ratios have been summarized by plant association or by habitat type (White et al. 1992).
- **Anticipating response to fire**. The vegetative response to wildfire or another disturbance will vary, but can be predicted with relative certainty (Crane and Fischer 1986). Consider a ponderosa pine vegetation type – burning could create delightful stands of grass, all of the browse that deer and elk could ever want, an abundance of little pine trees, or an understory free of invading grand fir. It mostly depends on which plant association is being burned!
- **Responding to insect and disease risk**. Research has shown that some plant associations are more susceptible than others to Armillaria root disease, western spruce budworm, and other insects or diseases (Carlson 1989, Daubenmire 1973). Western dwarf mistletoe *(Arceuthobium campylopodum)*, for example, is much more common on the dryer end of the ponderosa pine series (PIPO/AGSP) than on the moister end (PIPO/SYAL) (Daubenmire and Daubenmire 1968). When dealing with susceptible associations, managers can minimize future insect and disease risk by favoring resistant species or by modifying the treatment parameters (Steele et al. 1996).
- **Identifying site capability and productivity**. PV may be more appropriate than site index for characterizing productivity because it can be determined regardless of overstory tree

composition, tree size, and stand density (Cook 1996). For this reason, the Forest Vegetation Simulator (FVS) and certain other computer models require that plant association be supplied as an input variable. Height growth rates and relative productivity for ponderosa pine were found to be positively correlated with habitat type (plant association) in eastern Washington and northern Idaho (Daubenmire 1961).

- **Stratifying land on an ecological basis**. PV may be an ideal tool for land stratification because similar plant associations encompass a relatively narrow range of ecological potential. Relatively simple strata that emphasize dominant landscape components and processes, and that explain variability in stand composition and structure, are appropriate for most purposes. The main purpose of an ecological classification system is to identify and describe land areas with similar ecological potentials so that possible responses to management actions can be predicted (ECOMAP 1993).
- **Assessing tree stocking**. Manipulation of stocking levels has important impacts on stand development and the appearance of future forest landscapes. Suggested stocking levels were recently developed for upland-forest plant associations occurring in the Blue-Ochoco and Wallowa-Snake physiographic provinces (Cochran et al. 1994, Powell 1999). Plant associations are also valuable for identifying sites with limited capacity for tree growth – a situation called low inherent stockability.
- **Responding to animal damage risk**. Research has shown that some plant associations provide more desirable habitat for small mammals than others (Hoffman 1960, Rickard 1960). Although small mammals play important roles in forest ecosystems and are a critical component of biodiversity, they can be problematic with respect to reforestation. When tree plantations are established on plant associations for which pocket gophers, voles, porcupines, and certain other small mammals have an affinity, it can be difficult to obtain adequate seedling survival or to achieve long-term stocking-level objectives (Crouch 1982, Smith 1982).

Historical Range of Variability

A recurring theme in recent forest ecology literature is the historical range of variability (HRV).[5] This concept is used to characterize the fluctuations or variations in ecosystem conditions or processes over a period of time (fig. 19). It is now understood that ecosystem conditions change over time as they are affected by disturbance processes; when disturbances act with a characteristic frequency and magnitude, ecosystems respond by exhibiting a particular behavior and complexity (Aplet and Keeton 1999, Morgan et al. 1994). As commonly used in the interior Northwest, HRV refers to a range of conditions as they existed prior to settlement by Euro-American emigrants (a time period generally defined as the mid 1800s).

---

[5] Some authorities refer to this analytical technique as the natural range of variability (Hessburg et al. 1999a, Swanson et al. 1994). Natural is an ambiguous term, but it is frequently used to signify something of esthetic or spiritual importance (Christensen et al. 1996). I will use historical rather than natural, primarily to avoid the ambiguity and because historical conveys a sense of time, an essential quality of the HRV concept.

Table 5: Seral (successional) status of tree species by plant association and potential vegetation group.

PVG	PLANT ASSOCIATION	JUOC	PIPO	PSME	LAOC	PICO	PIMO	PIEN	ABGR	ABLA2
COLD FOREST	ABLA2/MEFE									PNC
	ABLA2/VASC			MS	ES	ES		LS		PNC
	ABLA2/VASC/POPU			MS	ES	ES		LS		PNC
	ABLA2/CAGE					ES				PNC
	ABGR/VASC		ES	MS	ES	ES		LS	PNC	
	PICO/CARU					PNC				
MOIST UPLAND FOREST	ABGR/TABR/CLUN		ES	MS	ES			LS	PNC	
	ABGR/TABR/LIBO2			MS	ES		MS	LS	PNC	
	ABGR/GYDR								PNC	
	ABGR/POMU-ASCA3				ES			LS	PNC	
	ABGR/TRCA3				ES			LS	PNC	
	ABLA2/TRCA3					ES		LS		PNC
	ABLA2/CLUN				ES			LS		PNC
	ABLA2/LIBO2				ES			LS		PNC
	ABLA2/VAME				ES	ES		LS		PNC
	ABGR/CLUN		ES	MS	ES	ES	MS	LS	PNC	
	ABGR/LIBO2		ES	MS	ES	ES	MS	LS	PNC	
	ABGR/VAME		ES	MS	ES	ES		LS	PNC	
	ABGR/VASC-LIBO2			MS	ES	ES		LS	PNC	LS
	ABGR/ACGL		ES	MS	ES		MS	LS	PNC	
	ABGR/BRVU			MS	ES			LS	PNC	
	PSME/ACGL-PHMA		ES	PNC						
	PSME/HODI		ES	PNC						
DRY UPLAND FOREST	ABGR/SPBE		ES	MS	ES	ES			PNC	
	ABGR/CARU		ES	MS	ES	ES			PNC	
	ABGR/CAGE		ES	MS	ES				PNC	
	PSME/PHMA		ES	PNC	ES					
	PSME/SPBE		ES	PNC						
	PSME/SYAL	A	ES	PNC	ES					
	PSME/SYOR		ES	PNC						
	PSME/VAME		ES	PNC						
	PSME/CARU		ES	PNC					A	
	PSME/CAGE		ES	PNC					A	
	PIPO/SYAL	A	PNC							
	PIPO/SYOR		PNC							
	PIPO/CARU	A	PNC							
	PIPO/CAGE	A	PNC							
	PIPO/CELE/CAGE		PNC							
	PIPO/PUTR/CAGE		PNC							
	PIPO/PUTR/CARO		PNC							
	PIPO/CELE/FEID-AGSP		PNC							
	PIPO/PUTR/FEID-AGSP		PNC							
	PIPO/FEID	LS	PNC							
	PIPO/AGSP	A	PNC							

Sources/Notes: Adapted from Clausnitzer 1993, Hall 1973, Johnson and Clausnitzer 1992, and Steele et al. 1981. Seral status codes (ES, MS, LS, PNC) are described in the glossary; A = accidental occurrence. Appendix 1 provides names for plant symbols in this table. Potential vegetation group (PVG) is described in Powell 1998.

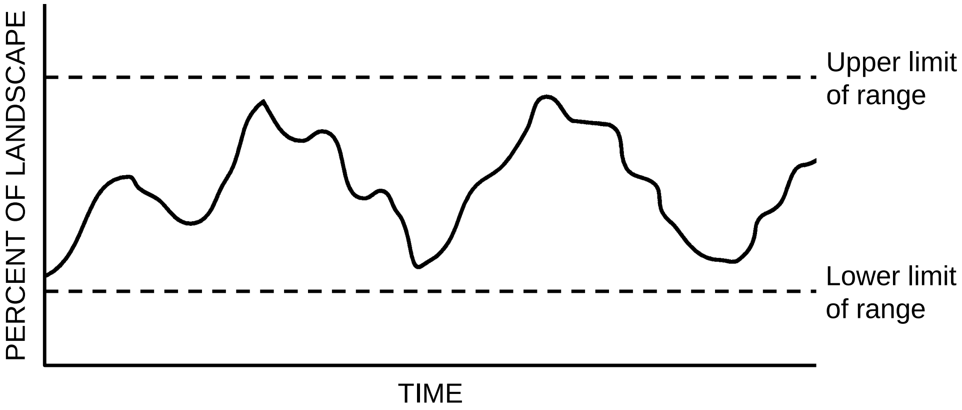


Figure 19–The historical range of variability (HRV) is used to characterize fluctuations in ecosystem components (composition, structure, and function) through time (Aplet and Keeton 1999, Morgan et al. 1994, Swanson et al. 1994). As commonly used in the interior Northwest, HRV refers to a range of conditions as they existed prior to settlement by Euro-Americans (a timeframe generally defined as the mid 1800s). When land managers decide to actively intervene by mimicking a native disturbance process (see table 4), it is important that management activities not cause an ecosystem element to surpass the adaptational thresholds shown here as upper and lower limits. Note that this diagram also portrays varying rates of change through time because the phrase 'range of variability' is meant to encompass more than just the extreme values (the upper and lower limits). Assume this figure shows hypothetical fluctuations in old forest structure within a watershed. Over time as stands mature, old-forest acreage increases until disturbance eventually transforms some of it to another condition, at which point the acreage declines. Small acreage declines are caused by fine-scale processes such as root disease; large declines result from wildfire or insect defoliation. The dynamics caused by disturbance in this hypothetical ecosystem describe a range of variability for old-forest structure.

HRV is an analytical technique to characterize inherent variation in ecosystem composition, structure, and function, reflecting recent evolutionary history and the dynamic interplay of biotic and abiotic factors. Composition refers to the relative abundance of ecosystem components such as water, nutrients, and species. Structure refers to their physical arrangement in an ecosystem, and function refers to the processes through which composition and structure interact, including predation, decomposition, and disturbances such as fire and floods (Aplet and Keeton 1999).

HRV is meant to reflect ecosystem properties free of major influence by Euro-American humans, providing insights into ecosystem resilience (Kaufmann et al. 1994, Landres et al. 1999). It helps us understand what an ecosystem is capable of, how historical disturbance regimes functioned, and inherent variation in ecosystem conditions and processes – the patterns, connectivity, seral stages, and cover types produced by ecological systems at a landscape scale (USDA Forest Service 1997). "Study of past ecosystem behavior can provide the framework for understanding the structure and behavior of contemporary ecosystems, and is the basis for predicting future conditions" (Morgan et al. 1994).

HRV is not intended to portray a static, unchanging condition. It should relate to ecological processes that have important implications on ecosystem behavior, such as the capacity to function effectively in a constantly changing environment. Ecosystems of the interior Northwest evolved with a steady diet of fires, insect outbreaks, disease epidemics, floods, landslides, human uses, and weather cycles. Change was, and still is, the only constant in their existence. HRV is designed to characterize the range of vegetation composition and structure resulting from these agents of change (Morgan et al. 1994).

The past can teach us what worked and what lasted – how resilient ecosystems sustained themselves through time (Swetnam et al. 1999). The type and frequency of presettlement disturbances can serve as a management template for maintaining sites within their historical range of plant communities and vegetation structures – if landscapes can be maintained within HRV, they stand a good chance of maintaining their biological diversity and ecological integrity over time (Aplet and Keeton 1999). This approach ensures that management treatments are consistent with the conditions under which native species, gene pools, communities, landscapes, and ecosystem processes have evolved (DeLong and Tanner 1996).

HRV is intended to serve as a benchmark from which change can be measured; it is not a specific condition that ecosystem management strives to attain (USDA Forest Service 1997). A common misconception is that it might be appropriate to use HRV as a management objective by linking desired future conditions directly to HRV, but a better approach is to let historical data inform an analyst about ecosystem behavior and potential management consequences (Millar 1997). Helping to identify opportunities to restore an ecosystem's resilience – its capacity for regeneration and renewal – is perhaps the most important contribution that HRV information can offer to an assessment or planning effort.

Even if land managers wished to turn back the clock to some idealized presettlement era, the current reality of dams, roads, human settlements, fire suppression, and mounting demands on wildland resources to meet societal needs would make this goal problematic. Clearly, we cannot turn all our wheat fields back into bluebunch wheatgrass prairies, no matter how inadequate they may now seem from an ecological perspective. We simply cannot go back in time and undo all that has happened and, in that sense at least, we are prisoners of time and our own history (Worster 1996). A recent scientific assessment for the interior Columbia River basin suggests that presettlement conditions could not be restored even if that was an explicit objective (Quigley and Arbelbide 1997).

An ecosystem analysis should recognize that "ecosystems are moving targets, with multiple potential futures that are uncertain and unpredictable. Therefore management has to be flexible, adaptive, and experimental at scales compatible with the scales of critical ecosystem functions" (Walters 1986). After acquiring an understanding about the HRV of a particular ecosystem variable (e.g., soil conditions, animal population sizes, plant community or seral stage composition, stream sediment loads, air quality, forest structural stages, etc.), an analyst can use this information to:

- Assess current departures from HRV and then estimate whether present trends are within or outside the historical ranges.
- Determine where current conditions or trends depart from HRV, thereby identifying areas that might require active intervention to restore ecosystem resilience and sustainability.
- Develop an appreciation for how ecosystem patterns, processes, and interactions operate, and then use this insight when formulating desired future conditions.

HRV began to be widely used as an analytical technique with the advent of ecosystem management, a new paradigm adopted by the U.S. Forest Service in 1992. An ecosystem-based approach to management exhibits many of these characteristics (Christensen et al. 1996):

- Long-term sustainability is a fundamental value.
- Clear, operational goals are vitally important.
- Sound ecological models and understanding are evident.
- An understanding and appreciation of ecosystem complexity and interrelations are incorporated.
- Recognition of the dynamic character of ecosystems is apparent.
- An attention to context and scale is obvious.
- An acknowledgment of humans as ecosystem components is explicit.
- A commitment to adaptability and accountability is included.

Caraher et al. (1992) used an expert panel approach to establish historical ranges, which were then used to assess departures and trends for several ecosystem components in the Blue Mountains (e.g., structural stages, stream shrub cover, streambank stability, etc.). They found that several ecosystem elements are currently outside the historical range of variability because of activities such as fire suppression and fish stocking (Caraher et al. 1992).

Lehmkuhl et al. (1994) derived historical ranges empirically, and then compared the historical and current condition of several landscape variables and indices for forests of eastern Oregon and eastern Washington. For their assessment effort, they used the standard error of the stratified mean to establish a range of variability that encompassed 68% of the variation around the means computed for each of their historical variables (Lehmkuhl et al. 1994).

The comparison effort by Lehmkuhl et al. (1994) included two watersheds in the Wenaha-Tucannon Wilderness (both are located in the Grande Ronde River basin). They found that substantial declines in ponderosa pine, grass/forb, and other early-seral patch types had occurred. This result reflects an important impact of long-term fire suppression – the landscape had become more homogeneous, with fewer vegetation types (particularly early-seral stages), larger patches at lower patch densities, and less total edge than would have been produced by the historical fire regime (Lehmkuhl et al. 1994).

The use of HRV for several recent bioregional assessment efforts (Hessburg et al. 1999b, Lehmkuhl et al. 1994) may be problematic due to the temporal baseline that was used. Early aerial photography was interpreted to establish an historical baseline for these assessments; however, the oldest photography dates from the late 1930s to the late 1940s and this resulted in a temporal comparison period of only 50 years or less (aerial photography from the late 1980s was used to characterize current conditions). The concern about this situation is that by the late 1930s, substantial changes in species composition and forest structure had already occurred or were well underway, particularly changes resulting from overgrazing in the late 1800s and early 1900s (Irwin et al. 1994, Skovlin and Thomas 1995).

Forest Health

The HRV concept has recently been proposed as a way to assess forest health. Although forest or ecosystem health may not be an appropriate term in some respects (Wicklum and Davies 1995), it can be valuable for communication because people identify with the concept by drawing an analogy to human health. Since a key premise of HRV is that native species have evolved with, and are adapted to, the disturbance regime of an area, ecosystem elements occurring within their historical range are believed to represent healthy situations (Aplet and Keeton 1999, Swanson et al. 1994). At a landscape scale, for instance, a forest might be considered healthy if the spatial and temporal patterns of species composition, structure, and seral stages are within the historical range for this landscape type.

The last twenty to forty years saw a period of rapid ecological change for literally millions of acres in the Blue Mountains. Some of this change was related to normal growth and maturation (e.g., plant succession), but much of it resulted from abnormally high levels of insects and diseases, including significant outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), western spruce budworm, Douglas-fir tussock moth (*Orgyia pseudotsugata*), Douglas-fir beetle (*Dendroctonus pseudotsugae*), and fir engraver (*Scolytus ventralis*) (Gast et al. 1991). Largely in response to these insect outbreaks, the Blue Mountains region gained national notoriety for its forest health problems (Wickman 1992).

Insect and disease problems were just one symptom of a possible decline in forest health; perhaps a more dramatic one was a proliferation of stand-replacing wildfires in the 1980s and 1990s (Canal, Corral Basin, Glacier, Sheep Mountain, Snowshoe, Tepee Butte, Tower, Wheeler Point, Whiting Springs, and many others). Many of these fires occurred in areas with previous damage from insect outbreaks or disease epidemics, both of which contributed to unusually high fuel accumulations. A recent survey conducted by Oregon State University found that many Blue Mountain residents perceive their forests to be unhealthy, which is probably a response to insect, disease, and wildfire impacts (Shindler and Reed 1996).

Do wide-ranging insect and disease outbreaks indicate that ecosystems are unhealthy? And what do large, landscape-scale wildfires indicate in an ecological sense? Since ecosystems are constantly changing, we need to evaluate their health in a similar context. Healthy forests not only tolerate periodic disturbance, they might depend on it for rejuvenation and renewal (Johnson et al. 1994a). However, significant changes in the magnitude (extent), intensity, or pattern of disturbance can serve as indicators of impaired forest health (Sampson and Adams 1994).

Insects, pathogens, and parasites are not only important disturbance agents, but they also play a vital role in ecosystem function (Franklin et al. 1987, Harvey 1994, Wickman 1992). These agents cause dead or dying trees, which in turn affects plant succession and the diversity of animal communities in an area. In particular, dead wood provides critical habitat for a wide variety of wildlife species (Bull et al. 1997), and it is a key factor influencing the total species diversity of an area (Franklin and Forman 1987). In the Blue Mountains, standing dead trees (snags) are used for nesting or shelter by 39 bird and 23 mammal species; downed dead trees are used by at least 179 wildlife species (Thomas 1979).

Forest insects can also have an important influence on nutrient cycling and site productivity. In a study conducted near Mammoth Lakes, California, it was found that the radial growth of trees defoliated by Douglas-fir tussock moth (DFTM) was significantly greater than that of non-defoliated trees, even 40 years after the outbreak had subsided (Wickman 1980). It is hypothesized that the enhanced growth was related to increased nutrient cycling from insect frass (excrement) and litter fall, in combination with the thinning effect (e.g., selective tree mortality) caused by DFTM defoliation (Wickman 1990).

Altered disturbance regimes are often expressed as forest health problems such as stand-replacing wildfires or insect outbreaks, but the conditions that give rise to these problems take decades or even centuries to develop. For example, when the U.S. Fish and Wildlife Service analyzed 146 threatened, endangered, or rare plant species for which conclusive fire effects information is available, it was found that 135 of them benefit from fire or are found in fire-adapted ecosystems, suggesting that historical fire suppression may have had a detrimental impact on their abundance or persistence (Leenhouts 1998).

Plant succession in combination with human influence and extremes in weather are the primary ingredients of forest health problems; insect outbreaks and disease epidemics may be little more than symptoms of an underlying problem (Sloan 1998, Steele 1994). Forest ecosystems will adjust to altered disturbance regimes with the only tools available – insects, diseases, wildfire and, to a limited extent, microbial decomposition (Harvey 1994; also see figure 7).

Perhaps the best yardstick for addressing forest health is historical variation – are the changes caused by insects, diseases, and wildfire consistent with what would be expected (the HRV) for similar ecosystems and vegetative conditions? For most of the dry forest environments in the Blue Mountains, and for some of the moist-forest ones as well, the answer to this question would probably be ‘no’ (Caraher et al. 1992, Gast et al. 1991, Hessburg et al. 1994, Mutch et al. 1993, Oliver et al. 1994, Sampson and Adams 1994, Wickman 1992).

Without application of needed restoration treatments in the near future (15-30 years), there is a high probability that the Blue Mountains’ legacy into the next century will be large, homogenous landscapes recovering from wildfires and other ecosystem setbacks on a scale unprecedented in recent evolutionary history (Sampson et al. 1994). Simply reintroducing native disturbance processes (landscape-scale surface fire, for example) may produce effects outside of any historical precedent, moving the ecosystem farther away from, rather than closer to, the HRV. In such situations, some type of restoration treatment (reductions in tree biomass or big-game populations, for example) may be needed before a disturbance process could be reintroduced (Aplet and Keeton 1999, Case and Kauffman 1997, Graham et al. 1999).

Both now and in the future, a desirable landscape condition for the Blue Mountains province is a diverse, heterogeneous vegetation mosaic that is more consistent with the historical range of variability, less susceptible to wide-area disturbances, and thus more sustainable (Mutch et al. 1993, Sampson et al. 1994). Using an HRV approach to help reach this goal means providing a full diversity of structural elements in variable configurations and quantities, with the ultimate objective being maintenance of the dynamic patterns and processes that are integral to healthy ecosystems (Aplet and Keeton 1999).

Landscape Ecology

Ecologists refer to landscapes as large areas comprised of interconnected or repeated patterns of habitats or ecosystems (Forman 1997, Turner and Gardner 1991). The science of landscape ecology studies the biological functions and interactions of vegetation patterns across large areas, assuming that there are strong links between ecosystem pattern and ecological function and process. Landscape structure has a strong influence on the flow of energy, nutrients, water, and disturbances, as well as organisms and their genes (Diaz and Apostol 1992, Gustafson 1998).

A single drainage basin may be considered a landscape if it is large enough to contain a variety of repeating patterns, but often a landscape will include more than one watershed. To be considered a landscape, an area must contain a variety of components that interact over time and space to provide ecological functions and processes (Forman and Godron 1986, Turner 1998).

Some landscape ecologists use a simple, three-component model as a conceptual tool to classify a landscape's spatial elements. The most common element in a landscape is referred to as the matrix. The matrix in many landscapes of the Pacific Northwest would be a continuous forest cover of conifers. In grass-tree mosaic landscapes of the northern Blue Mountains, however, the matrix would consist of grassland dominated by bluebunch wheatgrass, Idaho fescue, and prairie junegrass.

An important quality of the matrix is that it is the most connected element in the landscape; there are no inherent barriers to movement from one portion of the matrix to another. Like the open space in a pinball machine, energy, animals, or objects can move freely within the matrix area. Because it tends to be the most uniform of the three landscape elements, the matrix exerts the greatest control over landscape function (Diaz and Apostol 1992, Eng 1998).

An area within the landscape that is distinct from the matrix and isolated from other similar areas is called a patch. Patches are the second element in a conceptual model of landscape structure. Discrete patches result from disturbance events and from variation in the physical (abiotic) environment. Like the pins in a pinball machine, patches lack the connectivity of the matrix. A patch may consist of a single opening in a forest, or it could be a remnant stand of mature forest in a landscape matrix dominated by young trees or agricultural development (Diaz and Apostol 1992, Eng 1998).

The third element in a conceptual model of landscape structure is the corridor. Corridors are linear features or strips that differ from their surroundings on both sides. Corridors in a forested landscape can provide important connections between patches or non-adjacent portions of the matrix. Natural features such as riparian habitats along streams or rivers often function as corridors, providing connectivity between upper elevations or mid-slopes and the valley bottoms (Harrison and Voller 1998).

As important as corridors are, however, much of the connectivity in mature and old forests is through the matrix (Voller and Harrison 1998). In many landscapes and for numerous organisms, the matrix will be as important as, or more important than, corridors for connectivity. Since landscape patterns differ significantly from one ecosystem type to another, the type and degree of connectivity that exists in the natural landscape should serve as the primary blueprint when managers develop plans to provide corridors in managed landscapes (Franklin 1993).

Most connectivity objectives should be met using a coarse-filter approach (Aplet and Keeton 1999). Semi-permanent corridors (e.g., those with a relatively fixed location through time) are simple and flexible management tools that, because of their carefully chosen locations, can be more biologically effective than shifting or transient corridors. Semi-permanent corridors are often implemented as buffers adjoining streams, rivers, or other biologically sensitive components of the landscape (Harrison and Voller 1998).

Buffers provide some flexibility in terms of their characteristics (width, tree density, etc.) but are often inflexible with respect to their geographical location. Corridors should be designed to maintain continuity through time; therefore, it is important to consider buffer longevity in light of both native disturbance processes (such as wildfire- and insect-caused tree mortality) and planned disturbances such as timber harvesting or road building. If shifting corridors are to be used, then it is important to ensure that replacement corridors have the necessary attributes before existing corridors are exposed to planned disturbances such as timber harvest (Harrison and Voller 1998).

Riparian areas represent a dynamic interface or ecotone between water- and land-based ecosystems, where components of both systems interact. Native disturbance events (e.g., flooding, erosion, and sedimentation) are regular and predictable phenomena in these areas, causing fluctuations in plant communities, and in fish and wildlife populations. Some wildlife species use riparian corridors as a way to migrate from one area to another, but others find their primary habitat in a riparian zone because its greater diversity of plant species provides a wide variety of habitat conditions and niches (Voller and Harrison 1998).

Landscape patterns can have an important influence on human perceptions of scenic beauty. People value highly scenic landscapes, which research has shown to be those with a natural appearance based on their landform and water attributes and a characteristic or distinctive vegetation mosaic (Lucas 1991, Magill 1992, USDA Forest Service 1995).

In some managed landscapes, inherent vegetation patterns have been altered by previous timber harvest practices, particularly regarding the effects of small-patch clearcutting. Often, the result of clearcutting was a visual pattern whose texture, form, line, and color were out of scale with natural landscapes. Natural landscapes are those whose elements – texture, form, line, color, etc. – were produced by a disturbance regime without timber harvests, fire suppression, and other anthropogenic influences.

Historical patch sizes were recently analyzed for the Desolation watershed, a drainage within the North Fork John Day River subbasin. Aerial photographs from the late 1930s were used to assess reference (historical) conditions for the watershed. It was found that lodgepole pine, a disturbance-dependent forest cover type in this instance, comprised over one third of the watershed, occurring as 59 discrete patches ranging from 1 acre to 18,126 acres in size. Average lodgepole pine patch size was 434 acres (USDA Forest Service 1999).

On national forest system lands, the size of patches created by anthropogenic disturbances such as timber harvest is limited to no more than 40 acres by the National Forest Management Act of 1976 (Public Law 94-588) and its implementing regulations (36 CFR 219). When considered from a landscape perspective, patches of 40 acres or less are often inconsistent with vegetation patterns resulting from the inherent disturbance regime (DeLong and Tanner 1996). The Desolation analysis described above, for example, indicates that limiting patch size to 40 acres is inappropriate for lodgepole pine, particularly if anthropogenic patches are intended to mimic the vegetation mosaic associated with native disturbance processes (see table 4 for additional information about using anthropogenic practices to mimic disturbance processes).

Future activities in managed landscapes could attempt to rehabilitate undesirable visual conditions by restoring a natural vegetation pattern, e.g., a pattern in synchrony with, or analogous to, one produced by the native disturbance regime. As an example, existing clearcut units could eventually be expanded and shaped in such a way as to approximate the pattern, juxtaposition, and size of patches created by historical occurrences of stand-replacing wildfire. At a minimum, visual rehabilitation efforts should attempt to modify the unnatural, geometrically-regular pattern resulting from square or rectangular clearcuts.

Landscape patterns also affect how wildlife and other organisms use large land areas. Wildlife ecologists recognize that an important way to meet the habitat needs of certain species is to ensure that various habitat components are well connected to each other (Harrison and Voller 1998). Characteristics of landscape pattern, such as connectivity or the quality and quantity of edges between different landscape elements, can be measured and described to reveal how well different plant and animal species may use or disperse through an area (Gustafson 1998).

The spatial heterogeneity of a landscape can be described as (1) the number of patch types, (2) the proportion of each type, (3) the spatial arrangement of patches, (4) patch shape, and (5) the contrast between adjacent patches (Gustafson 1998). Ecosystems occur at a variety of spatial scales, with different processes operating at each scale to produce the patterns we see on a landscape. Therefore, how we analyze pattern is a function of the scale of observation (Aplet and Keeton 1999). FRAGSTATS (McGarigal and Marks 1995) and other computer programs (Ager 1997) have been developed to aid in the analysis of landscape pattern.

Four guidelines were recommended for effective analysis of spatial pattern when conducting integrated vegetation planning (Gustafson 1998):

1. Get the scale right by understanding the scale of the ecological processes of interest.
2. Choose descriptive metrics relevant to the spatial heterogeneity of the analysis area.
3. Choose an analytical method based on the analysis objectives and the inherent characteristics of the landscape being analyzed.
4. Formulate a relationship between a spatial index and the ecological process it is meant to represent so that empirical evidence can be related to the analysis results.

Scale

Understanding scale is central to an understanding of ecology because ecosystem structure and function are scale dependent (Levin 1992). Hierarchy theory helps explain the connections between complex landscape patterns and the scale of the many processes that influence the patterns (Eng 1998). This concept of interrelatedness is important in hierarchy theory, which divides multi-scaled systems such as a forested landscape into an ordered progression of spatial scales or levels. Table 6 demonstrates this concept by providing example hierarchies of terrestrial and aquatic units; figure 20 illustrates it using a simple, four-level forest hierarchy (Urban et al. 1987).

This concept demonstrates that ecological systems at every level are functional entities that also exist as part of a larger whole. Like the layers of an onion, each spatial level is embedded within another (Eng 1998). No one scale is best for all management applications; the scale selected will depend on the questions being asked and the resolution of the available data (White et al. 1999).

Forest vegetation reflects the interaction of ecosystem elements called components (composition), structures, and processes (functions), all of which occur as multi-level hierarchies (table 7). Components are the kinds and numbers of organisms that make up an ecosystem (Manley et al. 1995). Depending on the hierarchical level being considered, forest vegetation components include individual trees, aggregations of trees called cover types, or combinations of cover types called life forms (table 7).

Structure includes the physical arrangement or spatial distribution of ecosystem components (Manley et al. 1995). Structures can occur both horizontally (the spatial distribution of structural classes across a landscape) and vertically (trees of varying height growing together in a multi-layered arrangement). Depending on the hierarchical level being considered, examples of forest structure include size classes, structural classes, or physiognomic groups (table 7).

Table 6: Hierarchies of terrestrial and aquatic ecological units.

UNIT	DESIGN CRITERIA OR DESCRIPTION	SIZE RANGE
HIERARCHY OF TERRESTRIAL ECOLOGICAL UNITS		
Domain	Broad climate zones or groups (dry, humid, tropical)	1,000,000s of square miles
Division	Regional climate zones; vegetational affinities; soil orders	100,000s of square miles
Province	Dominant potential natural vegetation; mountains with complex vertical climate-vegetation-soil zonation	10,000s of square miles
Section	Geomorphic provinces; regional climate zones; soil order phases; potential vegetation groups	1,000s of square miles
Subsection	Geomorphic processes; elevation classes; soil subgroup phases; local climate zones; potential vegetation groups	10s to 1,000s of square miles
Landtype Association	Surficial geology; elevation classes; phases of soil families or series; local climate zones; plant association groups	1,000s to 10,000s of acres
Landtype	Landform, elevation, aspect, slope gradient, slope position; soils; rock types; plant association groups	100s to 1,000s of acres
Landtype Phase	Landform and slope position; soil mapping units; potential vegetation types	100s of acres
HIERARCHY OF AQUATIC ECOLOGICAL UNITS		
Subzone	Fish family patterns	1,000,000s of square miles
Region	Fish community patterns	100,000s of square miles
Subregion	Fish community subpatterns	100,000s of square miles
River Basin	Fish species assemblages (including endemism)	10,000s of square miles
Subbasin	Physiography and species groups	1,000s of square miles
Watershed	Hydrography and fish genetics	10s to 100s of square miles
Subwatershed	Local factors: topography or distinctive features or uses	100s to 1,000s of acres
Valley Segment	Geomorphology, climatic regime, hydrologic regime	100s of acres

Sources/Notes: Adapted from Cleland et al. (1997) and ECOMAP for the terrestrial hierarchy, and from McCammon (1994) for the aquatic hierarchy. These hierarchies represent alternative classification approaches, so the delineations produced by each system could differ for the same geographical area.

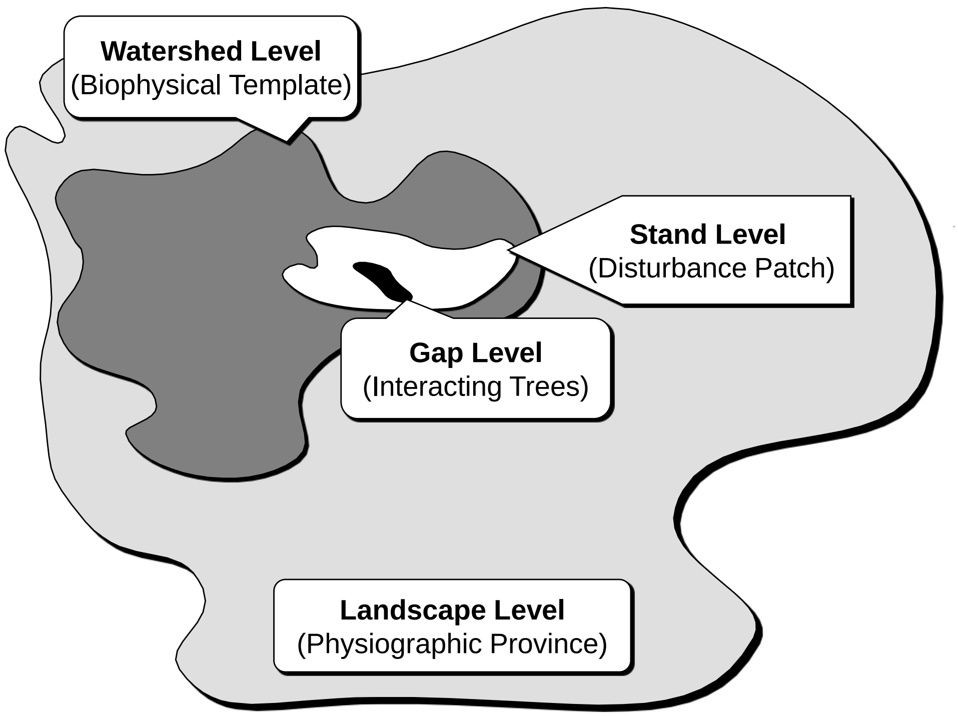


Figure 20–Four levels of a forest hierarchy (based on Urban et al. 1987). It is now widely recognized that ecosystems occur at a variety of spatial scales, with smaller systems nested within larger ones in a hierarchical fashion. This figure depicts a forested landscape as a hierarchy of gaps, stands, and watersheds. Trees within a gap interact more among themselves than with trees beyond the gap. By extension, a larger forest area can be considered as a mosaic of gap-sized patches, with each gap developing somewhat independently. Stands are comprised of contiguous gaps having similar characteristics. Stands in one drainage share a similar biophysical template and interact more with each other than with stands in other watersheds. At a higher level, landscapes can be defined as aggregations of similar, interacting watersheds (Urban et al. 1987).

Table 7: Examples of forest ecosystem components.

	ECOSYSTEM SCALE (HIERARCHICAL LEVEL)		
COMPONENTS	**FINE**	**MID**	**BROAD**
Composition	Individual tree	Cover type	Lifeform (tree/shrub/herb)
Structure	Tree size class	Structural stage	Physiognomic class
Process	Photosynthesis	Disturbance	Climate regime

Sources/Notes: Although they are shown individually in this table, it is important to note that ecosystem elements are interrelated – from an ecological perspective, they do not operate independently. See figure 20 for an example of a forest ecosystem hierarchy.

Processes are the flow or cycling or energy, materials, and nutrients through space and time (Manley et al. 1995). Forest processes can include everything from photosynthesis and nutrient cycling to stand-replacing wildfires and climatic cycles (table 7). In the interior Northwest, disturbance processes have influenced forest vegetation conditions to a greater degree than other ecosystem processes (Clark and Sampson 1995, O’Hara et al. 1996, Oliver and Larson 1996).

One rule of thumb for hierarchical analysis is to look up in scale for context and down in scale to understand process (Haynes et al. 1996). As an example, assume that an HRV analysis has identified a particular watershed as a candidate for harvest of old forest structure because it is over-represented there (i.e., old forest abundance exceeds the upper limit of HRV). However, without evaluating HRV at the next highest hierarchical level (the subbasin scale in this example), an analyst would be unaware of the watershed's contribution to old-forest structure in the context of the subbasin – and such knowledge might have an important influence on the timber harvest decision.

In this example, if the subbasin also exceeds HRV for old-forest structure, or if it occurs within the historical range but at the high end, then targeting the watershed for timber harvest may be appropriate and reasonable. On the other hand, if the subbasin is deficient in old-forest structure, then deferring timber harvest in the watershed may be prudent until old forest abundance at the subbasin scale is restored to an ecologically appropriate level (as evaluated using HRV as a benchmark).

This same approach can be used across all hierarchical levels – HRV could be assessed at the broadest scale first, then stepped down to the next lowest level, reassessed, and so forth down to the site or stand level (Aplet and Keeton 1999). It could also be used with a full suite of ecosystem components or categories of interest – a forest landscape in synchrony with HRV would not only provide old forest at an appropriate abundance and configuration, but it would also contain young and mid-age patches with size, shape, composition, and structure all falling within HRV for these ecosystem elements (Aplet and Keeton 1999, Morgan et al. 1994).

When we think about scale, we typically envision a spatial example. But ecosystems are also influenced by temporal scales. The time scales associated with landscape pattern and structure typically range from years to centuries, although variations in stream flow or bank structure can sometimes be measured in days, and biome-level changes may span millennia. Forest vegetation often requires hundreds of years to develop to its full expression, and soil erosion processes frequently span thousands of years (Eng 1998).

An appropriate temporal perspective is important because "how can human communities manage landscape change that takes place over a hundred years or more, when people's perceptions and priorities change from generation to generation, or even from election to election? Humans may not have the right 'attention span' to manage environmental change, and this may be the species' fatal flaw. Perhaps this is the value of history – as an attempt to extend the time frame of our memory beyond the human lifetime. The only problem is that history represents selective memory" (Spirn 1996).

Fragmentation

The loss of landscape connectivity, often described as habitat or forest fragmentation, is considered by some landscape ecologists to be among the greatest threats to biological diversity (Noss and Cooperrider 1994). It is generally recognized that fragmenting an area of contiguous forest into smaller patches diminishes both the quantity and quality of the remaining forest interior habitat. Fragmentation is also believed to increase the risk of some types of 'catastrophic' disturbance such as windthrow, fire, pests and pathogens, and landslides (Franklin and Forman 1987).

As described above, corridors are a natural feature of landscapes that provide important connectivity between landscape elements. Maintaining landscape connectivity is an essential aspect of forest management for biological diversity (Baydack et al. 1999, Voller and Harrison 1998). For this reason, it was recommended that networks of corridors or matrix areas be retained within managed landscapes to enhance inter-patch movement of species and for biodiversity reasons (Franklin and Forman 1987). Matrix lands may serve three critical roles for conserving biological diversity: (1) providing critical wildlife habitat at smaller spatial scales; (2) increasing the effectiveness of reserved areas via buffering; and (3) providing for connectivity (Franklin 1993).

One possible response to concerns about fragmentation and conservation of biological diversity is to establish a network of unmanaged reserves. Noss and Cooperrider (1994) suggest that an average of 50 percent of an area (±25%) should be in reserves, with as much as 99% reserved in situations such as the interior Northwest where landscapes are heterogeneous and dynamic. This unmanaged-reserve suggestion differs from recent whole-unit or emphasis-use approaches (Everett and Lehmkuhl 1996, 1999) considering landscapes as holistic units with a primary management objective of ecological integrity, where ecosystem conditions exist in synchrony with inherent disturbance regimes.

Everett and Lehmkuhl’s (1996, 1999) approach would reduce administrative fragmentation by combining or integrating compatible land-use allocations, resulting in greater connectivity of ecological conditions and disturbance regimes. Their proposal retains allocation differences for areas with widely divergent objectives (cattle grazing and riparian habitat conservation areas, for example), but it allows allocations with similar goals (big-game habitat and timber management) to be consolidated at a landscape scale.

Adopting Everett and Lehmkuhl’s (1996, 1999) approach could reverse the trend of carving up the national forests into progressively smaller pieces (via management allocations). It explicitly recognizes the dynamic nature of forest succession and the need to manage vegetation on a broad geographical scale. And it not only increases managerial flexibility, but also results in more congruence between inherent patterns of ecological site potential (e.g., potential vegetation) and native disturbance regimes.

In November 1998, a scientific conference convened in Portland, Oregon to examine forest fragmentation issues, including consideration of its consequences on wildlife populations in the western United States and Canada. A book containing 15 peer-reviewed chapters was published to summarize findings from the conference (Rochelle et al. 1999).

The conference discussed fragmentation in the context of island biogeography theory that considers forest patches as islands separated from each other by a sea of hostile habitat. Much of the island biogeography paradigm was derived from research conducted in the midwestern and eastern United States in situations where forest habitat had been converted to agricultural or urban uses (Harris 1984, MacArthur and Wilson 1969). Conference findings drew a clear distinction between forest fragmentation, where older and younger patches are juxtaposed on the landscape, and habitat loss, which occurs when forest is converted to a completely different land use (such as paved parking lots).

Key findings from the fragmentation conference included these items (Rochelle et al. 1999):

- The response of vertebrate populations to fragmentation differ, but for most species the effects of habitat loss are more significant than changes in habitat pattern.
- Some research suggests that vertebrate survival will be affected if the area of suitable habitat falls below a threshold of 20-30 percent.
- The negative effects on vertebrates occurring after forest land was converted to agricultural or suburban development are not apparent in western forests fragmented by timber production.
- Northwest forests were naturally fragmented by disturbance processes; in drier east-side forests, fire suppression has been de-fragmenting the indigenous patterns of fuel distribution and accumulation, thereby increasing the potential for large wildfires.
- Discussions of forest fragmentation are only meaningful if made in the context of historical landscape conditions.
- Connectivity of the landscape is not uniformly important to forest vertebrates because they vary in their gap-crossing abilities – there was little evidence that lack of connectivity is a threat in forests of the Pacific Northwest.
- There is little evidence from the Pacific Northwest to indicate the degree to which animal movements are affected by corridors – either limited by their absence or enhanced by their presence.
- The abundance of birds doesn’t change significantly in a forest stand from 40 years old to maturity; although some vertebrate species are restricted to old-growth, there are no apparent old-growth dependent communities (groups of species) among amphibians, reptiles, birds, or mammals (with the possible exception of bats).
- Leaving relatively small amounts of habitat structure (shrubs, snags, decaying wood, live conifers, and hardwoods) after timber harvest apparently makes the matrix area between patches more hospitable, suggesting that most late-successional species can be maintained in managed stands by retaining these structural elements (see figure 17, part B, on page 34).
- Riparian areas are often richer in species and more densely inhabited than are upland areas, but few forest-dwelling species are restricted to riparian areas.
- More vertebrate species are positively than negatively associated with edge habitat, although research has documented a few species that are consistently associated with forest interior habitat.
- The increased predation and nest parasitism observed when forest edge is surrounded by agricultural or suburban development are not evident when forest lands remain in forest use.
- There is no ideal patch size – management approaches resulting in a variety of habitat conditions and patch sizes on the landscape will meet the needs of the greatest number of species.
- Forest managers in the Pacific Northwest should not blindly apply the results of research studies from other regions such as the eastern and central United States.
- Forest fragmentation can best be understood from the perspective of individual species – “a landscape is not inherently connected or fragmented; the same landscape may be both from the perspective of two different species.”

Glossary

Abiotic. The nonliving components of the environment, not currently part of living organisms, such as soils, rocks, water, air, light, and nutrients (Dunster and Dunster 1996). Compare with biotic.

Allelopathy. A competitive strategy of plants in which there is the production of chemical compounds (allelochemicals) by such plants that interfere with the germination, growth, or development of another plant (Dunster and Dunster 1996).

Autecology. The study of relationships of individual organisms or species to environmental conditions. Autecology differs from synecology, which is the study of the ecology of groups of organisms (i.e., communities) in relation to environmental conditions (Dunster and Dunster 1996).

Biodiversity. A term which gained popularity in the late 1980s; used to describe all aspects of biological diversity including species richness, ecosystem complexity, and genetic variation (Allaby 1998).

Biome. A biological subdivision that reflects the ecological and physiognomic character of the vegetation. Biomes are the largest geographical biotic communities that it is convenient to recognize; they correspond broadly with climatic regions (Allaby 1998).

Biotic. Any living component of an ecosystem, including plants and animals (Dunster and Dunster 1996). Distinct from the abiotic physical and chemical components (Allaby 1998). Compare with abiotic.

Clearcutting. A regeneration cutting method in which essentially all trees have been removed from an area in one operation. Depending on management objectives, a clearcut may have reserve trees left to attain goals other than regeneration (provision of future snags, biological legacies, etc.) (Helms 1998).

Climax. The culminating seral stage in plant succession for any given site where, in the absence of catastrophic disturbance, the vegetation has reached a highly stable condition and undergoes change very slowly (Dunster and Dunster 1996). A self-replacing community that is relatively stable over several generations of the dominant plant species, or very persistent in comparison to other seral stages (Kimmins 1997).

Competition. The extent to which each organism maximizes fitness by both appropriating contested resources from a pool that is not sufficient for all, and adapting to an environment altered by all participants in the community or population. For trees, competition results in a density-related scarcity of certain environmental factors that are related to tree growth (Helms 1998).

Cover type. The plant species forming a plurality of the composition across a given land area, e.g., the Engelmann spruce-subalpine fir, ponderosa pine-Douglas-fir, or lodgepole pine forest cover types (Helms 1998). Forest cover types of the United States and Canada are described in Eyre (1980).

Depauperate. An area that has biodiversity (plant composition and canopy cover) reduced to relatively few plant and animal species (Helms 1998). Low canopy cover in a life-form resulting from dense woody cover by trees or shrubs. Both shrub and herb layers may be depauperate in the stem exclusion stage of forest stand development (Hall et al. 1995).

Disturbance. A relatively discrete event that disrupts the structure of an ecosystem, community or population, and changes resource availability or the physical environment. Disturbances include processes such as fires, floods, insect outbreaks, disease epidemics, and windstorms (Dodson et al. 1998).

Disturbance regime. The spatial and temporal dynamics of disturbance events over a long time period. Description of a disturbance regime would include characteristics such as the spatial distribution of disturbance events; disturbance frequency (number of disturbance events in a specified time interval, or the probability of a disturbance event occurring within a particular time interval); return interval (average time between successive disturbance events); rotation period (length of time until an area equivalent to the size of an analysis area would be affected in one disturbance event); disturbance size; and the magnitude, or intensity, of a disturbance event (Dodson et al. 1998).

Ecological amplitude. The degree to which an organism can tolerate variations in environmental conditions (Dunster and Dunster 1996). Also see tolerance.

Ecological environments. The composite temperature and moisture conditions resulting from a combination of edaphic and physiographic factors (soil, aspect, elevation, topographic position, etc.). Due to compensating factors, a steep, south-facing slope at 5,000 feet elevation can represent an ecological environment that is equivalent to a moderate, north-facing slope at 4,000 feet.

Ecological niche. An organism's actual place within a community, including its tolerances for the physical environment, its interactions with other organisms, and the manner in which it uses the component parts of its habitat. Ecological niche is analogous to ecological range, which describes the range of environmental conditions within which an organism can live and survive (Dunster and Dunster 1996).

Ecology. The branch of biology that deals with intenelationships. The name was coined in 1866 by Ernst Haeckel. But the study of ecology is much older than the name; its roots lie in earlier investigations of the 'economy of nature.' The major theme throughout the history of ecology, and the ideas that underlie it, has been the interdependence of living things. An awareness, more philosophical than purely scientific, of this quality is what has generally been meant by an 'ecological point of view.' Thus, the question of whether ecology is primarily a science, or a philosophy or world view, has been a persistent identity problem (Worster 1996).

Ecosystem. A spatially explicit, relatively homogeneous unit of the earth that includes all interacting organisms and components of the abiotic environment within its boundaries (Helms 1998). This term was first used by A.G. Tansley in 1935 to describe a discrete unit consisting of living and non-living components, interacting to form a stable system (Allaby 1998).

Ecosystem management. Management driven by explicit goals, executed by policies, protocols, and practices, and made adaptable by monitoring and research based on our best understanding of the ecological interactions and processes necessary to sustain ecosystem composition, structure, and function (Christensen et al. 1996).

Ecotone. A zone of transition along the edges of two adjacent ecological communities. Such edge communities are typically rich in species. Ecotones can arise naturally, such as the interface between terrestrial and aquatic habitats, but they can also reflect human intervention (the transition between an agricultural development and an adjacent wildland, for example) (Allaby 1998).

Forest health. The perceived condition of a forest based on concerns about such factors as its age, structure, composition, function, vigor, presence of unusual levels of insects or disease, and resilience to disturbance. Note that perception and interpretation of forest health is influenced by individual and cultural viewpoints, land management objectives, spatial and temporal scales, the relative health of stands that comprise the forest, and the appearance of the forest at a particular point in time.

Fragmentation. The process of creating an increasingly complex mosaic of patches as a result of disturbances, including human activities; the fragmentation process breaks apart a given area into smaller, more geometrically simple pieces (Rochelle et al. 1999, Voller and Harrison 1998).

Growing space. An intangible measure of the total resources of a site (sunlight, moisture, nutrients, etc.) that are available to a plant (Helms 1998).

Habitat type. A basic ecological unit in classifying lands based on potential vegetation. It represents, collectively, all parts of the landscape that support, or have the capability to support, the same plant association (Alexander 1985). In effect, habitat types are mapping or land classification units; plant associations are their descriptors or map-unit labels. See plant association and potential natural community.

Historical range of variability. A characterization of the fluctuations in ecosystem conditions or processes over time. An analytical technique used to define the bounds of ecosystem behavior that remain relatively consistent through time (Morgan et al. 1994).

Homeorhesis. The tendency of a biological system to return to its pre-disturbance trajectory or rate-of-change following a perturbation or disturbance event (Budiansky 1995, Christensen et al. 1996). Compare with homeostasis.

Homeostasis. The tendency of a biological system to resist change and to maintain itself in a state of stable equilibrium (Allaby 1998). Compare with homeorhesis.

Indicator plant. Plant species that convey information about the ecological nature of a site, such as the nitrogen content of a soil and its alkalinity or acidity. These plant species have a sufficiently consistent association with some environmental condition or another species that their presence can be used to indicate or predict the environmental condition or potential for the other species (Kimmins 1997).

Initial floristics. A pathway of secondary succession in which the pattern of seral stages is determined by the particular mixture of species that arrive, or are already present, in an ecosystem after disturbance. The later successional species do not require environmental alteration by the early successional species (Kimmins 1997). Compare with relay floristics.

Landscape. A heterogeneous land area composed of interacting ecosystems that are repeated in similar form throughout. Landscapes can vary in size, ranging down to a few kilometers in diameter (Forman and Godron 1986).

Landscape ecology. A study of the structure, function, and change in a heterogeneous land area comprised of interacting ecosystems (Forman and Godron 1986). Some landscape ecologists classify the spatial elements of a landscape using a three-component model:

> **Matrix**: the most extensive and most connected landscape element; it plays a dominant role in landscape function. Also, the matrix is the landscape element surrounding a patch.
>
> **Patch**: a nonlinear surface area differing in appearance from its surroundings. A landscape element that is distinct from the matrix and isolated from other similar areas (patches).
>
> **Corridor**: a narrow, linear strip of land that differs from the matrix on either side. Riparian habitats along streams or rivers often function as corridors (Forman and Godron 1986).

Management implication. An index or attribute that can be quantified to determine the success of implementing land management planning guidelines. An example is the use of wildlife indicator species (Dunster and Dunster 1996).

Overstory. In a forest with more than one story (layer), overstory is that portion of the trees forming the uppermost canopy layer; in a two-storied forest (stands with two clearly defined canopy layers), the tallest trees form the overstory, the shortest trees the understory (Helms 1998). Compare with understory.

Overstory removal. A regeneration cutting method in which trees constituting an upper canopy layer are removed to release trees or other vegetation in an understory or subordinate layer. Depending on management objectives, an overstory removal may have reserve trees left in the overstory layer to attain goals other than regeneration (provision of future snags, biological legacies, etc.) (Helms 1998).

Phase. A level in the potential vegetation hierarchy representing minor environmental differences within a plant association (habitat type). A phase is named for an indicator plant species, such as the ninebark phase of the grand fir/mountain maple habitat type in central Idaho (Pfister and Arno 1980, Steele et al. 1981).

Physiognomy. The form and structure of vegetation in natural communities (Allaby 1998, Dunster and Dunster 1996).

Physiography. Pertains to factors influencing the development of landforms or a landscape, such as relief and topography, bedrock geology and structure, and geomorphological history (Dunster and Dunster 1996).

Plant association. A plant community with similar physiognomy (form and structure) and floristics; commonly it is a climax community (Allaby 1998). It is believed that 1) the individual species in the association are, to some extent, adapted to each other; 2) the association is made up of species that have similar environmental requirements; and 3) the association has some degree of integration (Kimmins 1997). See also habitat type and potential natural community.

Plant association group. Groupings of plant associations representing similar ecological environments; sometimes considered to be synonymous with ecological settings or biophysical environments.

Plant community type. An aggregation of all plant communities with similar structure and floristic composition. A vegetation classification unit with no particular successional status implied (Dunster and Dunster 1996).

Plant succession. The process by which a series of different plant communities and associated animals and microbes successively occupy and replace each other over time in a particular ecosystem or landscape location following a disturbance to the ecosystem (Kimmins 1997).

Potential natural community. The community of plants that would become established if all successional sequences were completed, without interference by people, under existing environmental conditions, including the current climate and eroded or damaged soils (Hall et al. 1995). See also habitat type and plant association.

Potential vegetation. The vegetation that would develop if all successional sequences were completed under the present site conditions (Dunster and Dunster 1996). See also potential natural community.

Potential vegetation group. An aggregation of plant association groups (PAGs) with similar environmental regimes and are dominated by similar types of plants. Groupings typically consist of PAGs representing similar temperature or moisture relationships.

Primary succession. Successional development of an ecosystem beginning after a disturbance removes all of the modifications to microclimate and the geological substrate produced by the previous succession. Succession on bare rock, in shallow lakes, after glacial retreat or volcanic eruptions, or on parent soil materials are examples of primary succession (Kimmins 1997). Compare with secondary succession.

Relay floristics. A pathway of primary succession in which early-seral communities alter the soil and microclimate in a way that facilitates the invasion and growth of subsequent successional communities. The early stages of this developmental pattern are typically considered to be predictable and invariable. Mid-seral stages often require prior occupancy of the site by pioneer stages before they can become established (Kimmins 1997). Compare with initial floristics.

Reserve. A generic term used to define areas protected or managed to maintain their natural values. Reserves range in size from small to extremely large (Voller and Harrison 1998). Large reserves are believed to represent one potential way of maximizing and maintaining interior forest habitat (Noss and Cooperrider 1994).

Salvage cutting. An intermediate cutting method in which trees are removed because they are dead, damaged, or dying due to injurious agents other than competition (insects, diseases, parasites, fire, etc.), or to recover economic value that would otherwise be lost (Helms 1998).

Secondary succession. Succession beginning in an environment that has already been more or less modified by a period of occupancy by living organisms. Secondary succession can be progressive (proceeding from an early stage to a later one) or retrogressive (proceeding from a later stage back to an earlier one) (Hall et al. 1995). Forest clearcuts and abandoned agricultural fields are examples of secondary succession (Kimmins 1997). Compare with primary succession.

Seed-tree cutting. A regeneration cutting method in which most of the overstory is removed except for a small number of widely dispersed trees retained for seed production and to produce a new seedling cohort adapted to a fully exposed microenvironment. Depending on management objectives, the seed trees may be reserved (left on site) to satisfy goals unrelated to regeneration (provision of future snags or biological legacies, etc.) (Helms 1998).

Selection cutting. A regeneration cutting method designed to maintain and perpetuate a multi-aged structure by removing some trees in all size (age) classes either singly (single-tree selection) or in groups (group selection) (Helms 1998).

Seral stage (status). The identifiable stages in the development of a sere, from an early pioneer stage, through various early- and mid-seral stages, to late-seral, subclimax, and climax stages. The stages are identified by different plant communities, different ages of the dominant vegetation, and by different microclimatic, soil, and forest conditions (Kimmins 1997). Four seral stages were described (Hall et al. 1995):

> **Early Seral (ES)**: clear dominance of early-seral species (western larch, ponderosa pine, lodgepole pine, etc.) is obvious; PNC species are either absent or present in very low numbers.
>
> **Mid Seral (MS)**: PNC species are increasing in the forest composition as a result of their active colonization of the site; PNC species are approaching equal proportions with the early- or mid-seral species.
>
> **Late Seral (LS)**: PNC species are now dominant, although long-lived, early-seral species (ponderosa pine, western larch, etc.) may still persist in the plant community.
>
> **Potential Natural Community (PNC)**: the biotic community that one presumes would be established and maintained over time under present environmental conditions; early- or mid-seral species are scarce or absent in the plant composition.

Sere. A characteristic sequence of developmental (seral) stages that occurs during plant succession (Allaby 1998). See seral stage.

Series. A level in the potential vegetation hierarchy representing major environmental differences reflected by distributions of tree species at climax. A series is named for the projected climax tree species – the subalpine fir series includes all plant associations where subalpine fir is presumed to be the dominant tree species at climax (Pfister and Arno 1980).

Shade tolerance. The capacity of trees to grow satisfactorily in the shade of, and in competition with, other trees (Helms 1998). Also see tolerance.

Shelterwood cutting. A regeneration cutting method in which many of the overstory trees are removed, leaving those needed to produce sufficient shade and seed to produce a new seedling cohort in a moderated microenvironment. Depending on management objectives, a shelterwood may have reserve trees left to attain goals other than regeneration (provision of future snags, biological legacies, etc.) (Helms 1998).

Silviculture. Techniques that are used to manipulate vegetation and to direct stand and tree development to create or maintain desired conditions. Silvicultural practices influence rates of tree growth and stand development, stand composition, stand structure, and biodiversity. Silviculture is based on an ecosystem concept that emphasizes the need to evaluate the many abiotic and biotic factors influencing the choice and outcome of silvicultural treatments and their sequence over time, and the long-term consequences and sustainability of management regimes. [Definition derived from multiple sources.]

Structural stage. A stage or recognizable condition relating to the physical orientation and arrangement of vegetation; the size and arrangement (both vertical and horizontal) of trees and tree parts. The following structural stages have been described (see table 2) (O’Hara et al. 1996, Oliver and Larson 1996):

> **Stand Initiation**: one canopy stratum of seedlings and saplings is present; grasses, forbs, and shrubs typically coexist with the trees.
>
> **Stem Exclusion**: one canopy stratum comprised mostly of pole-sized trees (5-8.9″ DBH) is present. The canopy layer may be open (stem exclusion open canopy) on sites where moisture is limiting, or closed (stem exclusion closed canopy) on sites where light is a limiting resource.
>
> **Young Forest Multi Strata**: three or more canopy layers are present; the size class of the uppermost stratum is typically small trees (9-20.9″ DBH). Large trees may be absent or scarce.
>
> **Understory Reinitiation**: two canopy strata are present; a second tree layer is established under an older overstory. Overstory mortality created growing space for the establishment of understory trees.
>
> **Old Forest**: a predominance of large trees (>21″ DBH) is present in a stand with one or more canopy strata. On warm dry sites with frequent, low-intensity fires, a single stratum may be present (old forest single stratum). On cool moist sites without recurring underbums, multi-layer stands with large trees in the uppermost stratum may be present (old forest multi strata).

Thinning. An intermediate cutting method designed to reduce stand density in order to improve growth of the residual trees, enhance forest health, or recover potential mortality resulting from inter-tree competition (Helms 1998). Two types of thinning are recognized – commercial thinning where the trees being removed are large enough to have economic value and can be sold to a timber purchaser, and noncommercial thinning where trees are too small to be sold for conventional products and the excess trees are left on site after being cut.

Tolerance. A forestry term expressing the relative ability of a plant (tree) to complete its life history, from seedling to adult, under the cover of a forest canopy and while experiencing competition with other plants (Harlow et al. 1996). In general ecology usage, tolerance refers to the capacity of an organism or biological process to subsist under a given set of environmental conditions. Note that the range of conditions under which an organism can subsist, representing its limits of tolerance, is termed its ecological amplitude (Helms 1998).

Undergrowth. Herbaceous and shrubby plants growing beneath a forest canopy; undergrowth does not include small trees such as seedlings or saplings. Compare with understory.

Understory. All of the vegetation growing under a forest overstory. In some applications, understory is only considered to be small trees (e.g., in a forest comprised of multiple canopy layers, the taller trees form the overstory, the shorter trees the understory); in other instances, understory is assumed to include herbaceous and shrubby plants in addition to trees. When understory is assumed to refer to trees only, other plants (herbs and shrubs) are often called an undergrowth to differentiate between the two (Helms 1998). Compare with overstory and undergrowth.

Understory removal. An intermediate cutting method used in multi-storied stands, typically those with an overstory of early-seral tree species and an understory of late-seral species. When used on dry-forest sites, the objective is to remove a high proportion of the understory trees to improve overstory vigor by reducing inter-tree competition and to increase the probability that mature ponderosa pines and western larches (generally the early-seral species on these sites) will survive into the future.

Union. A group of plant species used to represent a particular ecological environment or micro-climatic condition; usually consisting of species with a similarity in life-form, phenology, stature, or a somewhat coextensive distribution in a local vegetation mosaic. The union includes only a fraction of the total floristic composition for a vegetation type – only the combination of species that is useful for vegetation classification purposes is designated as a union (Daubenmire 1968).

Watershed. Any area of land that drains to a common point. A watershed is smaller than a river basin or subbasin, but is larger than a drainage or site. The term generally describes areas that result from the first subdivision of a subbasin, often referred to as a fifth-field watershed (REO 1995).

Appendix 1: Plant Names

This appendix provides scientific and common names for plants mentioned in the text or its associated tables or figures. Names and symbols were taken from Botanical Resources Group 1998, Clausnitzer 1993, Johnson and Clausnitzer 1992, and Johnson and Simon 1987.

COMMON NAME	SCIENTIFIC NAME	SYMBOL
arrowleaf grounsel	*Senecio triangularis*	SETR
big huckleberry	*Vaccinium membranaceum*	VAME
birchleaf spirea	*Spiraea betulifolia*	SPBE
bitterbrush	*Purshia tridentata*	PUTR
black cottonwood	*Populus trichocarpa*	POTR2
black hawthorne	*Crataegus douglasii*	CRDO
bluebunch wheatgrass	*Agropyron spicatum*	AGSP
bluejoint reedgrass	*Calamagrostis canadensis*	CACA
bracken fern	*Pteridium aquilinum*	PTAQ
bull thistle	*Cirsium vulgare*	CIVU
Canada milkvetch	*Astragalus canadensis*	ASCA7
Cascade mountain-ash	*Sorbus scopulina*	SOSC2
Columbia brome	*Bromus vulgaris*	BRVU
common chokecherry	*Prunus virginiana*	PRVI
common snowberry	*Symphoricarpos albus*	SYAL
common yarrow	*Achillea millefolium*	ACMI
creambush oceanspray	*Holodiscus discolor*	HODI
creeping hollygrape	*Berberis repens*	BERE
curlleaf mountain-mahogany	*Cercocarpus ledifolius*	CELE
Douglas-fir	*Pseudotsuga menziesii glauca*	PSME
elk sedge	*Carex geyeri*	CAGE
Engelmann spruce	*Picea engelmannii*	PIEN
false bugbane	*Trautvetteria caroliniensis*	TRCA3
fool’s huckleberry	*Menziesia ferruginea*	MEFE
grand fir	*Abies grandis*	ABGR
grouse huckleberry	*Vaccinium scoparium*	VASC
heartleaf arnica	*Arnica cordifolia*	ARCO
horsemint	*Agastache urticifolia*	AGUR
Idaho fescue	*Festuca idahoensis*	FEID
lady fern	*Athyrium filix-femina*	ATFI
lodgepole pine	*Pinus contorta*	PICO
lupine	*Lupinus* spp.	LUPIN
mallow ninebark	*Physocarpus malvaceus*	PHMA
mountain alder	*Alnus incana*	ALIN
mountain snowberry	*Symphoricarpos oreophilus*	SYOR
mountain thermopsis	*Thermopsis montana*	THMO

COMMON NAME	SCIENTIFIC NAME	SYMBOL
oakfern	*Gymnocarpium dryopteris*	GYDR
Pacific yew	*Taxus brevifolia*	TABR
pinegrass	*Calamagrostis rubescens*	CARU
pinemat manzanita	*Arctostaphylos nevadensis*	ARNE
ponderosa pine	*Pinus ponderosa*	PIPO
prairie junegrass	*Koeleria macrantha*	KOMA
quaking aspen	*Populus tremuloides*	POTR
queencup beadlily	*Clintonia uniflora*	CLUN
Rocky Mountain maple	*Acer glabrum*	ACGL
Ross sedge	*Carex rossii*	CARO
Round-leaved violet	*Viola orbiculata*	VIOR2
russet buffaloberry	*Shepherdia canadensis*	SHCA
Scouler willow	*Salix scouleriana*	SASC
serviceberry	*Amelanchier alnifolia*	AMAL
Sitka alder	*Alnus sinuata*	ALSI
snowbrush ceanothus	*Ceanothus velutinus*	CEVE
sticky currant	*Ribes viscosissimum*	RIVI
subalpine fir	*Abies lasiocarpa*	ABLA2
sword fern	*Polystichum munitum*	POMU
thinleaf alder	*Alnus incana*	ALIN2
true firs	*Abies* spp.	ABIES
twinflower	*Linnaea borealis*	LIBO2
twisted stalk	*Streptopus amplexifolius*	STAM
water birch	*Betula occidentalis*	BEOC2
wax currant	*Ribes cereum*	RICE
western coneflower	*Rudbeckia occidentalis*	RUOC
western juniper	*Juniperus occidentalis*	JUOC
western larch	*Larix occidentalis*	LAOC
western meadowrue	*Thalictrum occidentale*	THOC
western needlegrass	*Stipa occidentalis*	STOC
western white pine	*Pinus monticola*	PIMO
whitebark pine	*Pinus albicaulis*	PIAL
wild ginger	*Asarum caudatum*	ASCA3
Woods strawberry	*Fragaria vesca*	FRVE

Appendix 2: Life History Information

There are two basic philosophies with respect to plant succession – one is based on population or community dynamics, and the other is rooted in the interactions between individual plants or species (Huston and Smith 1987). The community-based model shares many similarities with the relay floristics pattern of plant succession; the individual-based model has much in common with initial floristics (see pages 26-30 for a description of relay and initial floristics). A community model was favored early in the twentieth century, an era when mutualism and inter-species dependencies were emphasized in ecology. Beginning with the latter half of the twentieth century, succession has been viewed primarily as a plant-by-plant or species-by-species replacement process and its dynamics understandable in those terms.

If one assumes that succession is controlled mainly by the life history characteristics of plants comprising a community, then it is important to understand these traits to comprehend how succession might progress. Forest succession, for example, is controlled largely by five traits that influence competition among trees: maximum growth rate, maximum size, maximum longevity, maximum rate of seedling establishment, and shade tolerance. Each of these traits may have an important bearing on a species' capability to compete for site resources that are collectively referred to as growing space. However, there is no such thing as absolute competitive ability nor any trait that confers competitive superiority under every condition – what may be important in one situation may not be in another (Huston and Smith 1987).

This appendix provides twenty tables that summarize life history strategies with important implications on plant succession in forest ecosystems. It is important to examine a suite of life history strategies because any individual trait offers physiological or morphological trade-offs that would prevent a species from being optimally adapted to every environment or condition. An example is competition for sunlight – the most important factor is a tree's position relative to the light source because a tall plant has a great advantage over a shorter competitor, regardless of their shade tolerances (Huston and Smith 1987).

In addition to a detailed autecological summary prepared by Minore (1979), helpful life history information is provided by the North America silvics manuals (Burns and Honkala 1990a, b), the USDA Fire Effects Information System (Fischer et al. 1996), and many on-line databases available through the National Biological Information Infrastructure (NBII).

Table 8: Minimum, optimal, and maximum photosynthesis temperatures for common tree species of the Blue Mountains.

TREE SPECIES	MINIMUM	OPTIMAL	MAXIMUM
Douglas-fir	28.4°	68.0°	105.8°
Engelmann spruce	24.8°	64.4°	98.6°
Grand fir	30.2°	69.8°	105.8°
Lodgepole pine	23.0°	69.8°	104.0°
Ponderosa pine	30.2°	78.8°	113.0°
Subalpine fir	19.4°	62.6°	100.4°
Western larch	26.6°	68.0°	100.4°
Western white pine	30.2°	68.0°	104.0°

Sources/Notes: Keane et al. (1996), Table 2, variables BS12, BS13, and BS52. All temperature values are expressed in degrees Fahrenheit.

Table 9: Maximum leaf area indexes, and leaf retention periods, for common tree species of the Blue Mountains.

TREE SPECIES	MAXIMUM LEAF AREA INDEX	LEAF RETENTION PERIOD (YEARS)
Douglas-fir	10	5
Engelmann spruce	12	6
Grand fir	12	6
Lodgepole pine	7	3
Ponderosa pine	8	3
Subalpine fir	12	6
Western larch	6	1
Western white pine	8	3

Sources/Notes: Keane et al. (1996), Table 2, variable BS22 (maximum leaf area index) and BS23 (leaf retention periods). Leaf area index is the amount of leaf surface area (calculated using all sides of the leaves) in a forest canopy over a given area of ground below it, expressed as a proportion (ratio) of leaf surface to ground area. An LAI of 8 means that there is 8 square feet of canopy foliage for every square foot of ground surface covered by the canopy.

Table 10: Ratio of projected leaf area to sapwood cross-sectional area at breast height for selected tree species of the Umatilla National Forest.

TREE SPECIES	RATIO OF LEAF AREA TO SAPWOOD AREA
Douglas-fir	250
Engelmann spruce	350
Grand fir	480
Lodgepole pine	150
Ponderosa pine	250
Quaking aspen	100
Subalpine fir	750
Western juniper	180

Sources/Notes: Waring and Running (1998, table 2.3, page 40), and Waring (1983, table 1, page 347). These ratios are expressed in m^2/m^2. A ratio of 750 for subalpine fir means that it can support 750 m^2 of canopy leaf area for each m^2 of sapwood (sapwood is the outer, living portion of a tree stem that supplies the foliage with water). Leaf area and sapwood are physiologically interdependent – transpirational water loss from foliage requires that water be resupplied by the sapwood conducting tissue in the outer stem. Leaf area is limited by the capacity of sapwood to supply water, and sapwood volume is affected by the leaf area available to produce dry matter for stem accretion (Kaufmann et al. 1982).

Table 11: Period when abundant seed crops begin to be produced, and periodicity of a good seed crop, for common tree species of the Blue Mountains.

TREE SPECIES	PERIOD WHEN ABUNDANT SEED CROPS ARE PRODUCED	PERIODICITY OF GOOD SEED CROPS
Black cottonwood	10-20 years of age	1-2 years
Douglas-fir	20-40 years of age	3-10 years
Engelmann spruce	40-60 years of age	2-6 years
Grand fir	40-60 years of age	3-5 years
Lodgepole pine	10-20 years of age	1-2 years
Mountain alder	10-20 years of age	3-5 years
Ponderosa pine	40-60 years of age	3-10 years
Quaking aspen	10-20 years of age	3-5 years
Subalpine fir	40-60 years of age	2-3 years
Water birch	10-20 years of age	1-2 years
Western juniper	[Not Reported]	1-2 years
Western larch	10-20 years of age	3-5 years
Western white pine	40-60 years of age	3-5 years
Whitebark pine	40-60 years of age	[Not Reported]

Sources/Notes: Daniel et al. (1979), Tables 8-2 and 8-3. The ‘periodicity of good seed crops’ item shows the average number of years between good seed crops.

Table 12: Flowering, ripening, and dispersal dates for common tree species of the Blue Mountains.

TREE SPECIES	FLOWERING PERIOD	RIPENING PERIOD	DISPERSAL PERIOD
Black cottonwood	April-June	June	June
Douglas-fir	May-June	July-August	August-September
Engelmann spruce	June-July	August-September	September-October
Grand fir	March-June	August	August-September
Lodgepole pine	June-July	August-September	September-October
Mountain alder	February-April	[Not Reported]	[Not Reported]
Ponderosa pine	April-June	August-September	August-September
Quaking aspen	March-May	May-June	May-June
Subalpine fir	June-July	August	September
Western juniper	April-May	September	Persists 2 years
Western larch	April-June	August-September	September-October
Western white pine	June-July	August	August-September
Whitebark pine	July	August-September	Not Shed

Sources/Notes: Young and Young (1992).

Table 13: Minimum reproductive age (years), and cleaned seed weight (seeds per pound), for common tree species of the Blue Mountains.

TREE SPECIES	MINIMUM REPRODUCTIVE AGE (YEARS)	CLEANED SEED WEIGHT (SEEDS PER POUND)
Douglas-fir	20	43,545
Engelmann spruce	25	136,078
Grand fir	15	22,680
Lodgepole pine	15	93,894
Ponderosa pine	20	11,975
Quaking aspen	[Not Reported]	3,583,377
Subalpine fir	25	34,473
Thinleaf alder	[Not Reported]	666,780
Western juniper	[Not Reported]	12,247
Western larch	15	136,078
Western white pine	15	26,989
Whitebark pine	60	2,585

Sources/Notes: Minimum reproductive age column: Keane et al. (1996), Table 2, variable BS38; cleaned seed weight column: Young and Young (1992). The cleaned seed weight item was included as a relative measure of seed size – species with the greatest number of seeds per pound have the smallest seeds, and vice versa. Species with small seeds typically produce more of them, on a numerical basis if not by volume or weight, than large-seeded species. Seed size can have an important influence on regeneration success since small seeds generally disperse farther from a parent tree than large seeds.

Table 14: Effective seed dispersal distances (in feet), and pollination agents, for common tree species of the Umatilla National Forest.

TREE SPECIES	SEED DISPERSAL DISTANCE (FEET)	POLLINATION AGENT
Douglas-fir	300-330 feet (1)	Wind
Engelmann spruce	490-750 feet (2)	Wind
Grand fir	200 feet (1)	Wind
Lodgepole pine	200 feet (1)	Wind
Mountain alder	500 feet or more (1)	Wind
Ponderosa pine	100-120 feet (1)	Wind
Quaking aspen	500 feet or more (1)	Wind
Subalpine fir	50-100 feet (1)	Wind
Western juniper	[Not Reported]	Wind
Western larch	120-150 feet (1)	Wind
Western white pine	400 feet (1)	Wind
Whitebark pine	[Dispersed by birds, not wind]	Wind

Sources/Notes: Source codes for seed dispersal distance (noted in parentheses next to each range of values) are: (1) Nyland (1996), table 13-1, page 270; and (2) Fryer and Johnson (1988). For pollination agent, source is Burns and Honkala (1990a and 1990b). Dispersal distances are maximums for the majority of seed; for example, at least 50% of grand fir seed will fall within 200 feet of the windward edge of an opening, although up to 10% may be dispersed at least twice that far.

Table 15: Seed germination on an ash/charcoal substrate, and seral status, for common tree species of the Blue Mountains.

TREE SPECIES	SEED GERMINATION ON ASH/CHARCOAL	SERAL STATUS
Douglas-fir	Increased	Mid Seral
Engelmann spruce	Reduced	Mid Seral
Grand fir	Increased	Late Seral
Lodgepole pine	No Effect	Early Seral
Ponderosa pine	Increased	Early Seral
Subalpine fir	[Not Reported]	Late Seral
Western larch	No Effect	Early Seral
Western white pine	Increased	Mid Seral

Sources/Notes: Seed germination on an ash/charcoal substrate is from Fisher (1935); it is one factor influencing regeneration success following wildfire. Seral status is from Keane et al. (1996, Table 1, page 10); it refers to the seral stage in which a species predominates – ponderosa pine and other early-seral species may be found in mid-seral or late-seral stands, but typically predominate only in early-seral communities.

Table 16: Shade tolerance ratings for common tree species of the Blue Mountains.

TREE SPECIES	SHADE TOLERANCE RATING ACCORDING TO:		
	BURNS	DANIEL	KEANE
Black cottonwood	Very Intolerant	Very Intolerant	[Not Reported]
Douglas-fir (interior)	Intermediate	Intermediate	Intermediate
Engelmann spruce	Tolerant	Tolerant	Tolerant
Grand fir	Tolerant	Tolerant	Tolerant
Lodgepole pine	Very Intolerant	Intolerant	Very Intolerant
Pacific yew	Very Tolerant	Very Tolerant	[Not Reported]
Ponderosa pine	Intolerant	Intolerant	Very Intolerant
Quaking aspen	Very Intolerant	Very Intolerant	[Not Reported]
Subalpine fir	Tolerant	Very Tolerant	Tolerant
Western juniper	Intolerant	Intolerant	[Not Reported]
Western larch	Very Intolerant	Very Intolerant	Very Intolerant
Western white pine	Intermediate	Intermediate	Intolerant
Whitebark pine	Intermediate	Very Intolerant	Intolerant

Sources/Notes: Burns column: Burns and Honkala (1990), page 646; Daniel column: Daniel et al. (1979), Table 13-2; Keane column: Keane et al. (1996), Table 2. Shade tolerance is defined as the capacity of trees to grow satisfactorily in the shade of, and in competition with, other trees (Helms 1998).

Table 17: Maximum and typical longevity (in years) for common tree species of the Blue Mountains.

TREE SPECIES	MAXIMUM LONGEVITY	TYPICAL LONGEVITY
Douglas-fir	500 (5)	200 (3)
Engelmann spruce	550 (4)	250 (2)
Grand fir	400 (4)	200 (4)
Lodgepole pine	300 (4)	100 (8)
Pacific yew	350 (4)	250 (4)
Ponderosa pine	725 (4)	300 (6)
Subalpine fir	250 (4)	150 (1)
Western juniper	900 (4)	300 (4)
Western larch	915 (4)	300 (7)
Western white pine	615 (4)	400 (4)

Sources/Notes: Typical longevity is the expected maximum age of individuals across a range of sites; maximum longevity is the absolute maximum age recorded for rare individuals. Source codes (noted in parentheses next to each value) are: 1: Alexander et al. 1990; 2: Alexander and Shepperd 1990; 3: Hermann and Lavender 1990; 4: Loehle 1988; 5: McCune and Allen 1985; 6: Oliver and Ryker 1990; 7: Schmidt and Shearer 1990; and 8: Trappe and Harris 1958.

Table 18: Maximum tree dimensions for common species of the Umatilla National Forest.

TREE SPECIES	MAXIMUM DIAMETER (INCHES)	MAXIMUM CIRCUMFERENCE (INCHES)	MAXIMUM HEIGHT (FEET)
Black cottonwood	68.0	213.6	140
Douglas-fir	79.8	250.7	180
Engelmann spruce	67.5	212.1	207
Grand fir	81.8	257.0	204
Lodgepole pine	41.5	130.4	120
Mountain alder	29.9	94.0	72
Pacific yew	22.4	70.4	39
Ponderosa pine	70.0	219.9	192
Quaking aspen	36.0	113.1	115
Subalpine fir	46.0	144.5	153
Water birch	25.0	78.5	58
Western juniper	60.7	190.7	73
Western larch	67.6	212.4	192
Western white pine	63.1	198.2	200
Whitebark pine	39.5	124.1	57

Sources/Notes: These dimensions pertain to champion trees in the Umatilla National Forest's big-tree program, which has existed since 1989. They were taken from Powell (2000). Diameter and circumference measurements were collected at breast height (4½ feet above the ground surface).

Table 19: Tree resistance and susceptibility ratings for Armillaria root disease.

TREE SPECIES	RESISTANCE	SUSCEPTIBILITY
Western larch	1 (Most Resistant)	Low
Ponderosa pine	2	Low
Lodgepole pine	[Not Reported]	Moderate
Western white pine	3	[Not Reported]
Douglas-fir	4	High
Grand fir	5 (Least Resistant)	High

Sources/Notes: Resistance ratings are from Entry et al. (1992); susceptibility ratings are from Morrison and Mallett (1996).

Table 20: Susceptibility to laminated and annosus root diseases, and Indian paint fungus stem decay, for common tree species of the Blue Mountains.

TREE SPECIES	LAMINATED	ANNOSUS	INDIAN PAINT
Douglas-fir	High	Tolerant	Resistant
Engelmann spruce	Intermediate	Intermediate	Resistant
Grand fir	High	High	High
Lodgepole pine	Tolerant	Intermediate	Immune
Ponderosa pine	Resistant	Intermediate	Immune
Subalpine fir	Intermediate	High	High
Western larch	Intermediate	Resistant	Immune
Western white pine	Tolerant	Tolerant	Immune

Sources/Notes: Laminated root disease: Filip and Schmitt (1979) and Thies and Sturrock (1995); all others: Williams et al. (1995), Table 5.

Table 21: Frost tolerance, drought tolerance, and snow damage resistance ratings for common tree species of the Blue Mountains.

TREE SPECIES	FROST TOLERANCE	DROUGHT TOLERANCE	SNOW DAMAGE RESISTANCE
Douglas-fir	Low	Moderate	Low
Engelmann spruce	High	Low	High
Grand fir	Moderate	Moderate	Moderate
Lodgepole pine	High	Moderate	Moderate
Ponderosa pine	Low	High	Low
Subalpine fir	Moderate	Low	High
Western larch	Moderate	Moderate	Moderate
Western white pine	High	Moderate	Moderate

Sources/Notes: Williams et al. (1995), Table 2.

Table 22: Specific wood density values for common tree species of the Blue Mountains.

TREE SPECIES	WOOD SPECIFIC GRAVITY
Black cottonwood	0.32
Douglas-fir	0.51
Engelmann spruce	0.31
Grand fir	0.45
Lodgepole pine	0.43
Pacific yew	0.67
Ponderosa pine	0.42
Quaking aspen	0.34
Subalpine fir	0.31
Western larch	0.48
Western white pine	0.42
Whitebark pine	0.34

Sources/Notes: Taken from Loehle (1988) or Mullin and McKnight (1981). Note that a weak correlation exists between wood specific gravity and species-specific longevity.

Table 23: Critical foliar nutrient concentrations for selected conifers of the Blue Mountains.

NUTRIENT	DOUGLAS-FIR	TRUE FIRS	LODGEPOLE PINE	PONDEROSA PINE	ENGELMANN SPRUCE	WESTERN WHITE PINE
Nitrogen (%)	1.40	1.15	1.20	1.10	1.50	1.00
Phosphorus (%)	0.12	0.15	0.12	0.08	0.18	0.15
Potassium (%)	0.60	0.58	0.50	0.48	0.60	0.70
Sulfur (%)	0.11	0.08	0.09	0.08	N.R.	0.20
Calcium (%)	0.15	0.12	0.08	0.05	0.15	0.30
Magnesium (%)	0.08	0.06	0.09	0.05	0.10	0.10
Manganese (ppm)	15	100	293	60	15	400
Iron (ppm)	25	50	58	50	100	40
Zinc (ppm)	10	10	52	30	10	15
Copper (ppm)	2	3	2.7	3	2.6	5
Boron (ppm)	10	10	4.3	20	5	10

Sources/Notes: Taken from Garrison and Moore (1998, page 17). See that document for a complete list of sources from which these nutrient concentration values were derived. N.R. = Not Reported. Note that for the Blue Mountains, ‘true firs’ includes grand fir and subalpine fir.

Table 24: Fire resistance characteristics for major conifer species of the Blue Mountains.

TREE SPECIES	Bark Thickness	Rooting Habit	Bark Resin (Old Bark)	Branching Habit	Foliage Flammability	Fire Resistance	Survival Strategy
Western larch	Very thick	Deep	Very little	High and very open	Low	Very high	Resister
Ponderosa pine	Very thick	Deep	Abundant	Moderately high & open	Medium	High	Resister
Douglas-fir	Very thick	Deep	Moderate	Moderately low & dense	High	High	Resister
Grand fir	Thick	Shallow	Very little	Low and dense	High	Medium	Avoider
Western white pine	Medium	Medium	Abundant	High and dense	Medium	Medium	Resister
Lodgepole pine	Very thin	Medium	Abundant	Moderately high & open	Medium	Low	Evader
Engelmann spruce	Thin	Shallow	Moderate	Low and dense	Medium	Low	Avoider
Subalpine fir	Very thin	Shallow	Moderate	Very low and dense	High	Very low	Avoider

Sources/Notes: Adapted from Flint (1925) and Starker (1934). Species rankings reflect the predominant situation for each trait. Tree species generally achieve fire tolerance by developing thick bark to protect their cambium, and by self-pruning to raise their lower crown above average flame height in the event of a fire. Species traits can vary during the lifespan of an individual tree, and from one individual to another in a population. For example, grand fir's bark is thin when young, but relatively thick when mature. Fire was ubiquitous on virtually all dry-forest sites, and on many of the moist-forest ones as well (see table 1, page 12). Some plants are considered to be fire adapted because they evolved strategies to maintain viable populations on sites where fires commonly occurred; other species are not well adapted to frequent fire. A Canadian ecologist (J.S. Rowe) classified the specific functional adaptations of plants to deal with fire, and he distinguished five primary strategies after studying boreal forests (Rowe 1983):

Invader: these plant species are early arrivers, and they depend on copious amounts of light, wind-disseminated seed to invade a fire from areas outside of it (fireweed and Scouler willow are good examples of the invader group).

Evader: these plant species store their seeds in the canopy, humus, or mineral soil to avoid high fire temperatures, and they respond to fire with rapid seed germination and establishment. The parent plants are generally killed by fire, so evader species produce a new generation from an onsite seed bank. Common examples are snowbrush ceanothus (regenerates from a soil seed bank), and lodgepole pine (regenerates from a canopy seed bank stored in serotinous cones).

Avoider: these plant species arrive late in plant succession, and they prosper where fire cycles are relatively long (such as fire regimes 3 and 4). They essentially lack effective adaptations to either survive a fire, or to regenerate quickly after one. Avoiders are generally the late-seral, shade-tolerant species found in old forests that haven't been disturbed for a long time. [Some species like grand fir have fairly wide ecological amplitude, which means they can function in a different way from one biophysical setting to another].

Resister: these plants tend to be early-seral, shade-intolerant species with effective adaptations for surviving low-severity fire. Good examples of resisters are thick-barked species with high crowns, such as ponderosa pine and western larch, because these life history traits protect the stem from damage (thick bark) and elevate the tree's heat-sensitive foliage well above the flames (high crown). Douglas-fir and western white pine are mid-seral species with relatively low fire tolerance when young (they are avoiders in this stage), but older trees are reasonably good resisters.

Endurer: these plant species handle fire by resprouting after it occurs; fire consumes or kills the above-ground portion of the plant, but they promptly revegetate by sprouting from the root system, root collar, rhizomes, or other below-ground organs protected from heat damage. A good example is quaking aspen, a clonal species with low fire resistance (for the existing stems), but it easily survives fire by sprouting from the root system using sucker shoots.

Table 25: Water use efficiency for selected tree and large-shrub species of the Blue Mountains.

Whitebark pine (highest)
Engelmann spruce
Douglas-fir (interior)
Subalpine fir
Western white pine
Ponderosa pine
Lodgepole pine
Quaking aspen
Scouler willow
Black cottonwood
Grand fir
Rocky Mountain maple
Cascade mountain-ash
Serviceberry
Water birch
Western larch (lowest)

Sources/Notes: Marshall and Zhang (1994). Water use efficiency is a measure of water use during photosynthesis. Species are ranked from highest efficiency (most efficient use of water during photosynthesis) to lowest efficiency. These rankings do not necessarily indicate which species are using the most water on an absolute basis because they are relative to the crown volume that is transpiring and photosynthesizing. For example, western larch had the lowest water use efficiency, but it would typically use less water on an absolute basis than grand fir because larch has much less crown volume than grand fir. Why do we care about water-use efficiency? Recent study results are consistent with the notion that in an environment where water is scarce, plants may compete effectively by increasing their potential water-use efficiency and that species abundance is controlled primarily by competition-driven water depletion. Appendix 1 provides scientific names for these plant species.

Table 26: Plant species of the Umatilla National Forest with known or suspected allelopathy.

COMMON NAME	SCIENTIFIC NAME
Bearberry	*Arctostaphylos uva-ursi*
Bottlebrush squirreltail	*Elymus elymoides*
Bracken fern	*Pteridium aquilinum*
Cheatgrass	*Bromus tectorum*
Columbia brome	*Bromus vulgaris*
Elderberry	*Sambucus* spp.
Foxtail fescue	*Vulpia myuros*
Japanese brome	*Bromus japonicus*
Meadow brome	*Bromus commutatus*
Medusahead	*Taeniatherum caput-medusae*
Mountain brome	*Bromus carinatus*
Rabbitfootgrass	*Polypogon monspeliensis*
Rattlesnake brome	*Bromus briziformis*
Ripgut brome	*Bromus diandrus*
Smooth brome	*Bromus inermis*
Soft brome	*Bromus hordeaceus*
Sumac	*Rhus* spp.
Timothy	*Phleum pratense*
Western coneflower	*Rudbeckia occidentalis*
Western wheatgrass	*Pascopyrum smithii*

Source/Notes: Allelopathy refers to a competitive strategy in which certain species produce chemical compounds that interfere with the germination, growth, or development of competing species. Allelopathic status was taken from Ferguson (1991), Ferguson and Boyd (1988), Fisher (1980), McDonald (1986), Stewart (1975), and Urban (1996). Plant names follow Botanical Resources Group (1998).

Table 27: Fire response mode and seedling competition risk ratings for shrubs and herbs commonly found after moderate- or high-severity forest fires, Umatilla National Forest.

PLANT SPECIES	RESPONSE MODE	COMPETITION RISK
Bearberry *(Arctostaphylos uva-ursi)*	Survivor	Moderate
Birchleaf spiraea *(Spiraea betulifolia)*	Survivor	Low
Bracken fern *(Pteridium aquilinum)*	Survivor	High
Bull thistle *(Cirsium vulgare)*	Offsite Colonizer	High
Canada milkvetch *(Astragalus canadensis)*	Residual Colonizer	Low
Canada thistle *(Cirsium arvense)*	Survivor	High
Common chokecherry *(Prunus virginiana)*	Survivor	Low
Common snowberry *(Symphoricarpos albus)*	Survivor	Moderate
Dandelion *(Taraxacum officinale)*	Offsite Colonizer	Low
Dogbane *(Apocynum androsaemifolium)*	Survivor	Low
Dwarf rose *(Rosa gymnocarpa)*	Survivor	Low
Elk sedge *(Carex geyeri)*	Survivor	High
Fireweed *(Epilobium angustifolium)*	Offsite Colonizer	Moderate
Heartleaf arnica *(Arnica cordifolia)*	Survivor	Low
Lanceleaf figwort *(Scrophularia lanceolata)*	Residual Colonizer	Low
Low Oregongrape *(Mahonia repens)*	Survivor	Moderate
Miners lettuce *(Claytonia perfoliata)*	Residual Colonizer	Low
Northwestern sedge *(Carex concinnoides)*	Survivor	Moderate
Oregon boxwood *(Paxistima myrsinites)*	Survivor	Low
Pearly everlasting *(Anaphalis margaritacea)*	Offsite Colonizer	Low
Pinegrass *(Calamagrostis rubescens)*	Survivor	High
Red fescue *(Festuca rubra)*	Survivor	High
Ross sedge *(Carex rossii)*	Survivor	High
Scouler willow *(Salix scouleriana)*	Residual Colonizer	Moderate
Showy aster *(Aster conspicuus)*	Survivor	Low
Snowbrush ceanothus *(Ceanothus velutinus)*	Residual Colonizer	High
Sticky currant *(Ribes viscosissimum)*	Residual Colonizer	Moderate
Tailcup lupine *(Lupinus caudatus)*	Residual Colonizer	Low
Watson willowherb *(Epilobium ciliatum)*	Residual Colonizer	Low
Wax currant *(Ribes cereum)*	Survivor	Moderate
Western hawkweed *(Hieracium albertinum)*	Offsite Colonizer	Low
Western yarrow *(Achillea millefolium)*	Offsite Colonizer	Low
Woods strawberry *(Fragaria vesca)*	Survivor	Low

Sources/Notes: ‘plant species’ include those observed to be abundant in the post-fire plant community following moderate- or high-severity burns in the central Blue Mountains; ‘response mode’ assignments were based on Strickler and Edgerton (1976) and other sources; ‘competition risk’ ratings were based on local experience. For the ‘response mode’ item, survivors are sprouters and other plants capable of regrowth; colonizers are post-fire plants established from seed, with residual colonizers originating from onsite (burned) sources and offsite colonizers originating from non-burned sources (Stickney 1990). Species with a high competition risk are capable of killing conifer seedlings directly; species with a moderate risk may cause limited seedling mortality, but more commonly cause growth losses; plants with a low risk cause limited growth losses and no seedling mortality. Plant nomenclature follows Botanical Resources Group (1998) and other sources.

Literature Cited

Agee, James K. 1993. Fire ecology of Pacific Northwest forests. Washington, DC: Island Press. 493 p.

Ager, A. 1997. UTOOLS: microcomputer software for spatial analysis and landscape visualization. Gen. Tech. Rep. PNW-GTR-397. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 15 p.

Alexander, Robert R. 1985. Major habitat types, community types, and plant communities in the Rocky Mountains. Gen. Tech. Rep. RM-123. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 105 p.

Alexander, Robert R.; Shearer, Raymond C.; Shepperd, Wayne D. 1990. *Abies lasiocarpa* (Hook.) Nutt.; subalpine fir. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 60-70.

Alexander, Robert R.; Shepperd, Wayne D. 1990. *Picea engelmannii* Parry ex Engelm.; Engelmann spruce. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 187-203.

Allaby, Michael, ed. 1998. The concise Oxford dictionary of ecology. 2nd edition. New York: Oxford University Press. 440 p.

Allen, Timothy F.H.; Hoekstra, Thomas W. 1992. Toward a unified ecology. New York: Columbia University Press. 384 p.

Allen, T.F.H.; Wyleto, E. Paul. 1983. A hierarchical model for the complexity of plant communities. Journal of Theoretical Biology. 101: 529-540.

Anderson, Leslie; Carlson, Clinton E.; Wakimoto, Ronald H. 1987. Forest fire frequency and western spruce budworm outbreaks in western Montana. Forest Ecology and Management. 22: 251-260.

Antos, Joseph A.; Habeck, James R. 1981. Successional development in *Abies grandis* (Dougl.) Forbes forests in the Swan Valley, western Montana. Northwest Science. 55(1): 26-39.

Aplet, Gregory H.; Keeton, William S. 1999. Application of historical range of variability concepts to biodiversity conservation. In: Baydack, Richard K. [et al.], eds. Practical approaches to the conservation of biological diversity. Washington, DC: Island Press: 71-86.

Bailey, Robert G. 1996. Ecosystem geography. New York: Springer-Verlag. 204 p.

Barrett, James W. 1979. Silviculture of ponderosa pine in the Pacific Northwest: the state of our knowledge. Gen. Tech. Rep. PNW-97. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 106 p.

Bartos, Dale L.; Campbell, Robert B., Jr. 1998. Water depletion and other ecosystem values forfeited when conifer forests displace aspen communities. In: Potts, Donald F., ed. Proceedings of the AWRA Specialty Conference, Rangeland Management and Water Resources. TPS-98-1. Herndon, VA: American Water Resources Association: 427-434.

Bates, Carlos G. 1926. Some relations of plant ecology to silvicultural practice. Ecology. 7(4): 469-480.

Baydack, Richard K.; Campa, Henry; Haufler, Jonathan B., editors. 1999. Practical approaches to the conservation of biological diversity. Washington, DC: Island Press. 313 p.

Beukema, Sarah J.; Kurz, Werner A. 1996. Vegetation dynamics development tool user's guide. Version 2.0. Vancouver, BC: ESSA Technologies, Ltd. 80 p.

Bloomberg, W.J. 1950. Fire and spruce. Forestry Chronicle. 26(2): 157-161.

Blumer, J.C. 1911. Change of aspect with altitude. Plant World. 14: 236-248.

Boerker, R.H. 1916. A historical study of forest ecology: its development in the fields of botany and forestry. Forestry Quarterly. 14: 380-432.

Borman, F.H.; Likens, G.E. 1979. Pattern and process in a forested ecosystem. New York: Springer-Verlag. 264 p.

Botanical Resources Group. 1998. A pocket guide to plants of the Umatilla National Forest, Oregon and Washington. F14-S0-03-98. Pendleton, OR: USDA Forest Service, Pacific Northwest Region, Umatilla National Forest. 205 p.

Botkin, Daniel B. 1990. Discordant harmonies: a new ecology for the twenty-first century. New York: Oxford University Press. 241 p.

Botkin, Daniel B. 1994. Preface. In: Sampson, R. Neil; Adams, David L., eds. Assessing forest ecosystem health in the inland West. Binghamton, NY: Food Products (Haworth) Press: xxi-xxiv.

Botkin, Daniel B. 1995. Our natural history: the lessons of Lewis and Clark. New York: G.P. Putnam's Sons. 300 p.

Budiansky, Stephen. 1995. Nature's keepers: the new science of nature management. New York: Free Press. 310 p.

Bull, Evelyn L.; Parks, Catherine G.; Torgersen, Torolf R. 1997. Trees and logs important to wildlife in the interior Columbia River basin. Gen. Tech. Rep. PNW-GTR-391. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 55 p.

Burns, Russell M.; Honkala, Barbara H. 1990a. Silvics of North America; Volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service. 675 p.

Burns, Russell M.; Honkala, Barbara H. 1990b. Silvics of North America; Volume 2, hardwoods. Agric. Handb. 654. Washington, DC: USDA Forest Service. 877 p.

Caldicott, Helen. 1992. If you love this planet: a plan to heal the earth. New York: W.W. Norton & Company. 232 p.

Camp, Ann; Oliver, Chad; Hessburg, Paul; Everett, Richard. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. Forest Ecology and Management. 95: 63-77.

Canham, C.D.; Denslow, J.S.; Platt, W.J. [et al.]. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical rainforest. Canadian Journal of Forest Research. 20: 620-631.

Caraher, David L.; Henshaw, John; Hall, Fred [et al.]. 1992. Restoring ecosystems in the Blue Mountains: a report to the Regional Forester and the Forest Supervisors of the Blue Mountain forests. Portland, OR: USDA Forest Service, Pacific Northwest Region. 14 p.

Carlson, Clinton E. 1989. Influence of habitat types on forest pests of the northern Rocky Mountains. In: Ferguson, Dennis E.; Morgan, Penelope; Johnson, Frederic D., comps. Proceedings–land classifications based on vegetation: applications for resource management. Gen. Tech. Rep. INT-257. Ogden, UT: USDA Forest Service, Intermountain Research Station: 186-192.

Case, Richard L.; Kauffman, J. Boone. 1997. Wild ungulate influences on the recovery of willows, black cottonwood and thin-leaf alder following cessation of cattle grazing in northeastern Oregon. Northwest Science. 71(2): 115-126.

Chazdon, Robin L.; Pearcy, Robert W. 1991. The importance of sunflecks for forest understory plants. BioScience. 41(11): 760-766.

Christensen, Norman L.; Bartuska, Ann M.; Brown, James H. [et al.]. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications. 6(3): 665-691.

Cissel, J.H.; Swanson, F.J.; McKee, W.A.; Burditt, A.L. 1994. Using the past to plan the future in the Pacific Northwest. Journal of Forestry. 92(8): 30-31, 46.

Clark, Lance R.; Sampson, R. Neil. 1995. Forest ecosystem health in the inland West: a science and policy reader. Washington, DC: American Forests, Forest Policy Center. 37 p.

Clarke, Sharon E.; Bryce, Sandra A., editors. 1997. Hierarchical subdivisions of the Columbia Plateau and Blue Mountain ecoregions, Oregon and Washington. Gen. Tech. Rep. PNW-GTR-395. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 114 p.

Clausnitzer, Rodrick R. 1993. The grand fir series of northeastern Oregon and southeastern Washington: successional stages and management guide. Tech. Pub. R6-ECO-TP-050-93. USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 193 p.

Cleland, David T.; Avers, Peter E.; McNab, W. Henry [et al.]. 1997. National hierarchical framework of ecological units. In: Boyce, Mark S.; Haney, Alan, eds. Ecosystem management: applications for sustainable forest and wildlife resources. New Haven, CT: Yale University Press: 181-200.

Clements, F.E. 1910. The life history of lodgepole burn forests. Bull. No. 79. Washington, DC: USDA Forest Service. 56 p.

Clements, Frederic E. 1916. Plant succession: an analysis of the development of vegetation. Pub. No. 242. Washington, DC: Carnegie Institution of Washington. 512 p.

Clements, Frederic E. 1936. Nature and structure of the climax. Journal of Ecology. 24: 252-284.

Cobb, David F.; O'Hara, Kevin L.; Oliver, Chadwick D. 1993. Effects of variations in stand structure on development of mixed-species stands in eastern Washington. Canadian Journal of Forest Research. 23: 545-552.

Cochran, P.H.; Geist, J.M.; Clemens, D.L. [et al.]. 1994. Suggested stocking levels for forest stands in northeastern Oregon and southeastern Washington. Res. Note PNW-RN-513. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 21 p.

Connell, Joseph H.; Slatyer, Ralph O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist. 111(982): 1119-1144.

Cook, James E. 1996. Implications of modern successional theory for habitat typing: a review. Forest Science. 42(1): 67-75.

Cooper, William S. 1926. The fundamentals of vegetational change. Ecology. 7(4): 391-413.

Covington, W.W.; Moore, M.M. 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. Journal of Sustainable Forestry. 2(1/2): 153-181.

Crane, Marilyn F.; Fischer, William C. 1986. Fire ecology of the forest habitat types of central Idaho. Gen. Tech. Rep. INT-218. Ogden, UT: USDA Forest Service, Intermountain Research Station. 86 p.

Cronon, William, editor. 1996. Uncommon ground: rethinking the human place in nature. New York: W.W. Norton & Company. 561 p.

Crouch, Glenn L. 1982. Pocket gophers and reforestation on western forests. Journal of Forestry. 80: 662-664.

Crowe, Elizabeth A.; Clausnitzer, Rodrick R. 1997. Mid-montane wetland plant associations of the Malheur, Umatilla and Wallowa-Whitman National Forests. Tech. Pub. R6-NR-ECOL-TP-22-97. Baker City, OR: USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 299 p.

Daniel, Theodore W.; Helms, John A.; Baker, Frederick S. 1979. Principles of silviculture. 2nd edition. New York: McGraw-Hill Book Company. 500 p.

Daniel, T.W.; Schmidt, Josef. 1972. Lethal and nonlethal effects of the organic horizons of forested soils on the germination of seeds from several associated conifer species of the Rocky Mountains. Canadian Journal of Forest Research. 2: 179-184.

Daubenmire, R.F. 1943. Vegetational zonation in the Rocky Mountains. Botanical Review. 9(6): 325-393.

Daubenmire, R. 1961. Vegetative indicators of rate of height growth in ponderosa pine. Forest Science. 7(1): 24-34.

Daubenmire, Rexford. 1968. Plant communities: a textbook of plant synecology. New York: Harper and Row. 300 p.

Daubenmire, R. 1973. A comparison of approaches to the mapping of forest land for intensive management. Forestry Chronicle. 49(2): 87-91.

Daubenmire, R.; Daubenmire, Jean B. 1968. Forest vegetation of eastern Washington and northern Idaho. Tech. Bull. 60. Pullman, WA: Washington State University, College of Agriculture and Home Economics, Agricultural Research Center. 104 p.

DeLong, S. Craig; Tanner, David. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodiversity and Conservation. 5: 1191-1205.

Denevan, William M. 1992. The pristine myth: the landscape of the Americas in 1492. Annals of the Association of American Geographers. 82(3): 369-385.

Diaz, Nancy; Apostol, Dean. 1992. Forest landscape analysis and design: a process for developing and implementing land management objectives for landscape patterns. Tech. Pub. R6 ECO-TP-043-92. Portland, OR: USDA Forest Service, Pacific Northwest Region. 94 p.

Dodson, Stanley I.; Allen, Timothy F.H.; Carpenter, Stephen R. [et al.]. 1998. Ecology. New York: Oxford University Press. 433 p.

Drury, William Holland, Jr. 1998. Chance and change: ecology for conservationists. Berkeley, CA: University of California Press. 223 p.

Drury, William H.; Nisbet, Ian C.T. 1973. Succession. Journal of the Arnold Arboretum. 54(3): 331-368.

Dunster, Julian; Dunster, Katherine. 1996. Dictionary of natural resource management. Vancouver, BC: UBC Press. 363 p.

ECOMAP. 1993. National hierarchical framework of ecological units. Washington, DC: USDA Forest Service. 21 p.

Egerton, Frank N. 1973. Changing concepts of the balance of nature. Quarterly Review of Biology. 48: 322-350.

Egler, F.E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio. 4: 412-418.

Eng, Marvin. 1998. Spatial patterns in forested landscapes: implications for biology and forestry. In: Voller, Joan; Harrison, Scott, eds. Conservation biology principles for forested landscapes. Vancouver, BC: UBC Press: 42-75.

Entry, J.A.; Martin, N.E.; Kelsey, R.G.; Cromack, K., Jr. 1992. Chemical constituents in root bark of five species of western conifer saplings and infection by *Armillaria ostoyae*. Phytopathology. 82(4): 393-397.

Everett, R.; Hessburg, P.; Lehmkuhl, J. [et al.]. 1994. Old forests in dynamic landscapes: dry-site forests of eastern Oregon and Washington. Journal of Forestry. 92(1): 22-25.

Everett, Richard L.; Lehmkuhl, John F. 1996. An emphasis-use approach to conserving biodiversity. Wildlife Society Bulletin. 24(2): 192-199.

Everett, Richard L.; Lehmkuhl, John F. 1999. Restoring biodiversity on public forest lands through disturbance and patch management irrespective of land-use allocation. In: Baydack, Richard K. [et al.], eds. Practical approaches to the conservation of biological diversity. Washington, DC: Island Press: 87-105.

Eyre, F.H., editor. 1980. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters. 148 p.

Ferguson, Dennis E. 1991. Allelopathic potential of western coneflower *(Rudbeckia occidentalis)*. Canadian Journal of Botany. 69: 2806-2808.

Ferguson, Dennis E.; Boyd, Raymond J. 1988. Bracken fern inhibition of conifer regeneration in northern Idaho. Res. Pap. INT-388. Ogden, UT: USDA Forest Service, Intermountain Research Station. 11 p.

Filip, Gregory M.; Schmitt, Craig L. 1979. Susceptibility of native conifers to laminated root rot east of the Cascade Range in Oregon and Washington. Forest Science. 25(2): 261-265.

Fischer, William C.; Miller, Melanie; Johnston, Cameron M. [et al.]. 1996. Fire Effects Information System: user’s guide. Gen. Tech. Rep. INT-GTR-327. Ogden, UT: USDA Forest Service, Intermountain Research Station. 131 p.

Fisher, George M. 1935. Comparative germination of tree species on various kinds of surface-soil material in the western white pine type. Ecology. 16(4): 606-611.

Fisher, Richard F. 1980. Allelopathy: a potential cause of regeneration failure. Journal of Forestry. 78: 346-350.

Flint, Howard R. 1925. Fire resistance of northern Rocky Mountain conifers. Idaho Forester. 7: 710, 41-43.

Forman, Richard T.T. 1997. Land mosaics: the ecology of landscapes and regions. Cambridge, UK: Cambridge University Press. 632 p.

Forman, Richard T.T.; Godron, Michel. 1986. Landscape ecology. New York: John Wiley & Sons. 619 p.

Franklin, Jerry F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications. 3(2): 202-205.

Franklin, Jerry F.; Forman, Richard T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology. 1(1): 5-18.

Franklin, Jerry F.; Shugart, H.H.; Harmon, Mark E. 1987. Tree death as an ecological process. BioScience. 37(8): 550-556.

Fryer, G.I.; Johnson, E.A. 1988. Reconstructing fire behaviour and effects in a subalpine forest. Journal of Applied Ecology. 25: 1063-1072.

Garrison, Mariann T.; Moore, James A. 1998. Nutrient management: a summary and review. Supp. Rep. 98-5. [Moscow, ID]: Intermountain Forest Tree Nutrition Cooperative. 48 p.

Gast, William R., Jr.; Scott, Donald W.; Schmitt, Craig [et al.]. 1991. Blue Mountains forest health report: "new perspectives in forest health." Portland, OR: USDA Forest Service, Pacific Northwest Region, Malheur, Umatilla, and Wallowa-Whitman National Forests.

Geist, J. Michael; Strickler, Gerald S. 1978. Physical and chemical properties of some Blue Mountain soils in northeast Oregon. Res. Pap. PNW-236. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 19 p.

Geiszler, D.R.; Gara, R.I.; Driver, C.H. [et al.]. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of south-central Oregon. Oecologia. 46: 239-243.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club. 46: 7-26.

Gleason, H.A. 1927. Further views on the succession concept. Ecology. 8(3): 299-326.

Graham, Russell T.; Harvey, Alan E.; Jain, Theresa B.; Tonn, Jonalea R. 1999. The effects of thinning and similar stand treatments on fire behavior in western forests. Gen. Tech. Rep. PNW-GTR-463. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 27 p.

Graumlich, Lisa J. 1987. Precipitation variation in the Pacific Northwest (1675-1975) as reconstructed from tree rings. Annals of the Association of American Geographers. 77(1): 19-29.

Grier, Charles C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Canadian Journal of Forest Research. 5: 599-607.

Gustafson, Eric J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems. 1: 143-156.

Haig, Irvine T.; Davis, Kenneth P.; Weidman, Robert H. 1941. Natural regeneration in the western white pine type. Tech. Bull. No. 767. Washington, DC: U.S. Department of Agriculture. 98 p.

Hall, Frederick C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southeastern Washington. R6 Area Guide 3-1. Portland, OR: USDA Forest Service, Pacific Northwest Region. 62 p.

Hall, Frederick C. 1976. Fire and vegetation in the Blue Mountains – implications for land managers. In: Proceedings of the Annual Tall Timbers Fire Ecology Conference No. 15; 1974 October 16-17; Portland, Oregon. Tallahassee, FL: Tall Timbers Research Station: 155-170.

Hall, Frederick C. 1984. Vegetation diversity in managed versus unmanaged ecosystems and effects on various resources. In: Cooley, James L.; Cooley, June H., eds. Natural diversity in forest ecosystems. Proceedings of the Workshop; 1982 November 29-December 1; Athens, Georgia. Athens, GA: University of Georgia, Institute of Ecology: 251-262.

Hall, Frederick C.; Bryant, Larry; Clausnitzer, Rod [et al.]. 1995. Definitions and codes for seral status and structure of vegetation. Gen. Tech. Rep. PNW-GTR-363. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 39 p.

Halpern, Charles B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology. 70(3): 704-720.

Hansen, A.J.; Spies, T.A.; Swanson, F.J.; Ohmann, J.L. 1991. Conserving biodiversity in managed forests: lessons from natural forests. BioScience. 41(6): 382-392.

Harlow, William M.; Harrar, Ellwood S.; Hardin, James W.; White, Fred M. 1996. Textbook of dendrology. 8th edition. New York: McGraw-Hill. 534 p.

Harris, Larry D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. Chicago, IL: University of Chicago Press. 211 p.

Harrison, Scott; Voller, Joan. 1998. Connectivity. In: Voller, Joan; Harrison, Scott, eds. Conservation biology principles for forested landscapes. Vancouver, BC: UBC Press: 76-97.

Harvey, Alan E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland western United States: past, present and future forest health. Journal of Sustainable Forestry. 2(1/2): 211-220.

Harvey, Alan E.; McDonald, Geral I.; Jurgensen, Martin F.; Larsen, Michael J. 1994. Microbes: driving forces for long-term ecological processes in the inland northwest's cedar-hemlock-white pine forests. In: Baumgartner, David M.; Lotan, James E.; Tonn, Jonalea R., comps. Interior cedar-hemlock-white pine forests: ecology and management. Symposium Proceedings; 1993 March 2-4; Spokane, Washington. Pullman, WA: Washington State University, Department of Natural Resource Sciences: 157-163.

Haufler, Jonathan B. 1994. An ecological framework for planning for forest health. Journal of Sustainable Forestry. 2(1/2): 307-316.

Haynes, Richard W.; Graham, Russell T.; Quigley, Thomas M., technical editors. 1996. A framework for ecosystem management in the interior Columbia Basin including portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-374. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 66 p.

Hedrick, D.W.; Young, J.A.; McArthur, J.A.B.; Keniston, R.F. 1968. Effects of forest and grazing practices on mixed coniferous forests of northeastern Oregon. Tech. Bull. 103. Corvallis, OR: Oregon State University, Agricultural Experiment Station. 24 p.

Hellmers, H.; Genthe, M.K.; Ronco, F. 1970. Temperature affects growth and development of Engelmann spruce. Forest Science. 16(4): 447-452.

Helms, John A., editor. 1998. The dictionary of forestry. Bethesda, MD: Society of American Foresters. 210 p.

Hermann, Richard K.; Lavender, Denis P. 1990. *Pseudotsuga menziesii* (Mirb.) Franco; Douglas-fir. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 527-540.

Hessburg, Paul F.; Mitchell, Russel G.; Filip, Gregory M. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. Gen. Tech. Rep. PNW-GTR-327. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 72 p.

Hessburg, Paul F.; Smith, Bradley G; Salter, R. Brion. 1999a [July]. Using estimates of natural variation to detect ecologically important change in forest spatial patterns: a case study, Cascade Range, eastern Washington. Research Paper PNW-RP-514. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 65 p.

Hessburg, Paul F.; Smith, Bradley G.; Kreiter, Scott D. [et al.]. 1999b [September]. Historical and current forest and range landscapes in the interior Columbia River basin and portions of the Klamath and Great basins. Part 1. Linking vegetation patterns and landscape vulnerability to potential insect and pathogen disturbances. Gen. Tech. Rep. PNW-GTR-458. 357 p.

Hoffman, George R. 1960. The small mammal components of six climax plant associations in eastern Washington and northern Idaho. Ecology. 41(3): 571-572.

Holling, C.S. 1996. Surprise for science, resilience for ecosystems, and incentives for people. Ecological Applications. 6(3): 733-735.

Hunter, Malcolm L., Jr. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Englewood Cliffs, NJ: Regents/Prentice Hall. 370 p.

Huschle, Gary; Hironaka, M. 1980. Classification and ordination of seral plant communities. Journal of Range Management. 33(3): 179-182.

Huston, Michael; Smith, Thomas. 1987. Plant succession: life history and competition. American Naturalist. 130(2): 168-198.

Irwin, Larry L.; Cook, John G.; Riggs, Robert A.; Skovlin, Jon M. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystems. Gen. Tech. Rep. PNW-GTR-325. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 49 p.

Jack, Steven B.; Long, James N. 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. Forest Ecology and Management. 86: 205-220.

Jensen, Mark; Goodman, Iris; Brewer, Ken [et al.]. 1997. Biophysical environments of the basin. In: Quigley, Thomas M.; Arbelbide, Sylvia J., tech. eds. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. Volume 1: 99-320.

Johnson, Charles Grier, Jr.; Clausnitzer, Rodrick R. 1992. Plant associations of the Blue and Ochoco Mountains. Tech. Pub. R6-ERW-TP-036-92. Portland, OR: USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 164 p.

Johnson, Charles G., Jr.; Clausnitzer, Roderick R.; Mehringer, Peter J.; Oliver, Chadwick D. 1994a. Biotic and abiotic processes of eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. Gen. Tech. Rep. PNW-GTR-322. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 66 p.

Johnson, Charles G., Jr.; Simon, Steven A. 1987. Plant associations of the Wallowa-Snake province. Tech. Pub. R6-ECOL-TP-225b-86. Baker City, OR: USDA Forest Service, Pacific Northwest Region, Wallowa-Whitman National Forest. 272 p.

Johnson, E.A.; Miyanishi, K.; Kleb, H. 1994b. The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta–Picea engelmannii* forest. Journal of Ecology. 82: 923-931.

Johnson, K. Norman; Swanson, Frederick; Herring, Margaret; Greene, Sarah, eds. 1999. Bioregional assessments: science at the crossroads of management and policy. Washington, DC: Island Press. 398 p.

Kaufmann, Merrill R.; Edminster, Carleton B.; Troendle, Charles A. 1982. Leaf area determinations for subalpine tree species in the central Rocky Mountains. Research Paper RM-238. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Kaufmann, Merrill R.; Graham, Russell T., Boyce, Douglas A., Jr. [et al.]. 1994. An ecological basis for ecosystem management. Gen. Tech. Rep. RM-246. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 22 p.

Kay, Charles E. 1994. Aboriginal overkill: the role of Native Americans in structuring western ecosystems. Human Nature. 5(4): 359-398.

Keane, Robert E.; Morgan, Penelope; Running, Steven W. 1996. FIRE-BGC – a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. Res. Pap. INT-RP-484. Ogden, UT: USDA Forest Service, Intermountain Research Station. 122 p.

Keen, F.P. 1937. Climatic cycles in eastern Oregon as indicated by tree rings. Monthly Weather Review. 65(5): 175-188.

Kimmins, J.P. 1997. Forest ecology; a foundation for sustainable management. 2nd edition. Upper Saddle River, NJ: Prentice Hall. 596 p.

Knudson, Ruthann. 1980. Ancient peoples of the Columbia plateau. Journal of Forestry. 78(8): 477-479.

Koch, Peter. 1996. Lodgepole pine in North America. Volume 1, part 1: background. Madison, WI: Forest Products Society. 343 p.

Larsen, J.A. 1923. Association of trees, shrubs, and other vegetation in the northern Idaho forests. Ecology. 4(1): 63-67.

Larsen, J.A. 1930. Forest types of the northern Rocky Mountains and their climatic controls. Ecology. 11(4): 631-672.

Larson, B.C. 1986. Development and growth of even-aged stands of Douglas-fir and grand fir. Canadian Journal of Forest Research. 16(2): 367-372. doi:10.1139/x86-063

Leenhouts, Bill. 1998. Assessment of biomass burning in the conterminous United States. Conservation Ecology [online]. 2(1): http://www.consecol.org/vol2/iss1/art1

Lehmkuhl, John F.; Hessburg, Paul F.; Everett, Richard L. [et al.]. 1994. Historical and current forest landscapes of eastern Oregon and Washington. Part 1: Vegetation pattern and insect and disease hazards. Gen. Tech. Rep. PNW-GTR-328. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 88 p.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology. 73: 1943-1967.

Loehle, Craig. 1988. Tree life history strategies: the role of defenses. Canadian Journal of Forest Research. 18: 209-222.

Lotan, James E. 1976. Cone serotiny–fire relationships in lodgepole pine. In: Proceedings of the Annual Tall Timbers Fire Ecology Conference Number 14 and the Fire and Land Management Symposium; 1974 October 8-10; Missoula, MT. Tallahassee, FL: Tall Timbers Research Station: 267-278.

Lotan, James E.; Critchfield, William B. 1990. *Pinus contorta* Dougl. ex. Loud.; lodgepole pine. In: Burns, Russell M.; Hankala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 302-315.

Lucas, Oliver W.R. 1991. The design of forest landscapes. Oxford, UK: Oxford Univ. Press. 381 p.

Lyon, L. Jack. 1971. Vegetal development following prescribed burning of Douglas-fir in south-central Idaho. Res. Pap. INT-105. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 30 p.

MacArthur, R.H.; Wilson, E.O. 1969. The theory of island biogeography. Princeton, NJ: Princeton University Press. 224 p.

MacCleery, Douglas W. 1992. American forests: a history of resiliency and recovery. FS-540. Durham, NC: USDA Forest Service; Forest History Society. 59 p.

Magill, Arthur W. 1992. Managed and natural landscapes: what do people like? Res. Pap. PSW-RP-213. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 28 p.

Magnuson, John J. 1990. Long-term ecological research and the invisible present. BioScience. 40(7): 495-501.

Manley, P.N.; Brogan, G.E.; Cook, C. [et al.]. 1995. Sustaining ecosystems: a conceptual framework. San Francisco, CA: USDA Forest Service, Pacific Southwest Region. 216 p.

Marshall, John D.; Zhang, Jianwei. 1994. Carbon isotope discrimination and water-use efficiency in native plants of the north-central Rockies. Ecology. 75(7): 1887-1895.

Mason, D.T. 1915. The life history of lodgepole pine in the Rocky Mountains. Bull. No. 154. Washington, DC: U.S. Department of Agriculture. 35 p.

McCammon, Bruce P. 1994. Recommended terminology for watershed hierarchy. Portland, OR: USDA Forest Service, Pacific Northwest Region. 5 p.

McCune, Bruce. 1986. Root competition in a low-elevation grand fir forest in Montana: a trenching experiment. Northwest Science. 60(1): 52-54.

McCune, B.; Allen, T.F.H. 1985. Will similar forests develop on similar sites? Canadian Journal of Botany. 63: 367-376.

McDonald, Philip M. 1986. Grasses in young conifer plantations – hindrance and help. Northwest Science. 60(4): 271-278.

McGarigal, Kevin; Marks, Barbara J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 122 p.

McMinn, Robert G. 1952. The role of soil drought in the distribution of vegetation in the northern Rocky Mountains. Ecology. 33(1): 1-15.

Merritt, Melvin L. 1911. Lodgepole pine in the Whitman National Forest. Unpub. Rep. Sumpter, OR: [USDA Forest Service, Whitman National Forest]. 18 p.

Millar, Constance I. 1997. Comments on historical variation & desired condition as tools for terrestrial landscape analysis. In: Proceedings of the Sixth Biennial Watershed Management Conference. Water Resources Center Rep. No. 92. Davis, CA: Univ. of California: 105-131.

Minore, Don. 1979. Comparative autecological characteristics of northwestern tree species – a literature review. Gen. Tech. Rep. PNW-87. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 72 p.

Morgan, Penelope; Aplet, Gregory H.; Haufler, Jonathan B. [et al.]. 1994. Historical range of variability: a useful tool for evaluating ecosystem change. Journal of Sustainable Forestry. 2(1/2): 87-111.

Morrison, Duncan; Mallett, Ken. 1996. Silvicultural management of armillaria root disease in western Canadian forests. Canadian Journal of Plant Pathology. 18: 194-199.

Mullin, E.J.; McKnight, T.S. 1981. Canadian woods, their properties and uses. Toronto: Univ. of Toronto Press.

Munger, Thornton T. 1917. Western yellow pine in Oregon. Bull. No. 418. Washington, DC: U.S. Department of Agriculture. 48 p.

Mutch, Robert W.; Arno, Stephen F.; Brown, James K. [et al.]. 1993. Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems. Gen. Tech. Rep. PNW-GTR-310. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 14 p.

Niering, William A. 1987. Vegetation dynamics (succession and climax) in relation to plant community management. Conservation Biology. 1(4): 287-295.

Noss, Reed F. 1983. A regional landscape approach to maintain diversity. BioScience. 33: 700-706.

Noss, Reed F.; Cooperrider, Allen Y. 1994. Saving nature’s legacy: protecting and restoring biodiversity. Washington, DC: Island Press. 416 p.

Noss, Reed F.; LaRoe, Edward T., III; Scott, J. Michael. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Rep. 28. Washington, DC: U.S. Department of the Interior, National Biological Service. 58 p.

Nyland, Ralph D. 1996. Silviculture: concepts and applications. New York: McGraw-Hill Companies, Inc. 633 p.

Odum, Eugene P. 1969. The strategy of ecosystem development. Science. 164: 262-270.

O’Hara, Kevin L. 1995. Early height development and species stratification across five climax series in the eastern Washington Cascade Range. New Forests. 9: 53-60.

O’Hara, Kevin L.; Latham, Penelope A.; Hessburg, Paul; Smith, Bradley G. 1996. A structural classification for inland Northwest forest vegetation. Western Journal of Applied Forestry. 11(3): 97-102.

Oliver, Chadwick Dearing. 1981. Forest development in North America following major disturbances. Forest Ecology and Management. 3: 153-168.

Oliver, Chadwick D.; Ferguson, Dennis E.; Harvey, Alan E. [et al.]. 1994. Managing ecosystems for forest health: an approach and the effects on uses and values. Journal of Sustainable Forestry. 2(112): 113-133.

Oliver, Chadwick D.; Irwin, Larry L.; Knapp, Walter H. 1994. Eastside forest management practices: historical overview, extent of their applications, and their effects on sustainability of ecosystems. Gen. Tech. Rep. PNW-GTR-324. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 73 p.

Oliver, Chadwick D.; Larson, Bruce C. 1996. Forest stand dynamics. 2nd edition. New York: John Wiley. 520 p.

Oliver, William W.; Ryker, Russell A. 1990. *Pinus ponderosa* Dougl. ex Laws.; ponderosa pine. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 413-424.

Parminter, John. 1998. Natural disturbance ecology. In: Voller, Joan; Harrison, Scott, eds. Conservation biology principles for forested landscapes. Vancouver, BC: UBC Press: 3-41.

Pearson, G.A. 1920. Factors controlling the distribution of forest types. Ecology. 1(3): 139-159, 289308.

Pelren, Eric C.; Crawford, John A. 1999. Blue grouse nesting parameters and habitat associations in northeastern Oregon. Great Basin Naturalist. 59(4): 368-373.

Perry, D.A. 1988. Landscape patterns and forest pests. Northwest Environmental Journal. 4: 213-228.

Perry, D.A. 1994. Forest ecosystems. Baltimore, MD: Johns Hopkins University Press. 649 p.

Pfister, Robert D.; Arno, Stephen F. 1980. Classifying forest habitat types based on potential climax vegetation. Forest Science. 26(1): 52-70.

Pickett, S.T.A.; Kolasa, J.; Armesto, J.J.; Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos. 54(2): 129-136.

Pickett, S.T.A.; Ostfeld, Richard S. 1995. The shifting paradigm in ecology. In: Knight, Richard L.; Bates, Sarah F., eds. A new century for natural resources management. Washington, DC: Island Press: 261-278.

Powell, David C. 1994. Effects of the 1980s western spruce budworm outbreak on the Malheur National Forest in northeastern Oregon. Tech. Pub. R6-FI&D-TP-12-94. Portland, OR: USDA Forest Service, Pacific Northwest Region. 176 p.

Powell, David C., comp. 1998. Potential natural vegetation of the Umatilla National Forest. Unpub. Rep. Pendleton, OR: USDA Forest Service, Umatilla National Forest. 31 p.

Powell, David C. 1999. Suggested stocking levels for forest stands in northeastern Oregon and southeastern Washington: an implementation guide for the Umatilla National Forest. Tech. Pub. F14-SO-TP-03-99. Pendleton, OR: USDA Forest Service, Pacific Northwest Region, Umatilla National Forest. 300 p.

Powell, David C. 2000. Big tree program. Pendleton, OR: USDA Forest Service, Pacific Northwest Region, Umatilla National Forest. 9 p.

Putz, F.E.; Parker, G.G.; Archibald, R.M. 1984. Mechanical abrasion and intercrown spacing. American Midland Naturalist. 112(1): 24-28.

Quigley, Thomas M.; Arbelbide, Sylvia J., tech. eds. 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins: volume II. Gen. Tech. Rep. PNW-GTR-405. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 4 volumes: 337-1055.

REO (Regional Ecosystem Office). 1995. Ecosystem analysis at the watershed scale: federal guide for watershed analysis. Version 2.2. Portland, OR: Regional Ecosystem Office. 26 p.

Rickard, W.H. 1960. The distribution of small mammals in relation to the climax vegetation mosaic in eastern Washington and northern Idaho. Ecology. 41(1): 99-106.

Robbins, William G. 1997. Landscapes of promise: the Oregon story, 1800-1940. Seattle, WA: University of Washington Press. 392 p.

Rochelle, James A.; Lehmann, Leslie A.; Wisniewski, Joe, editors. 1999. Forest fragmentation: wildlife and management implications. Leiden, Netherlands: Brill Academic Publishers. 301 p.

Rogers, Paul. 1996. Disturbance ecology and forest management: a review of the literature. Gen. Tech. Rep. INT-GTR-336. Ogden, UT: USDA Forest Service, Intermountain Research Station. 16 p.

Romme, W.H.; Knight, D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology. 62: 319-326.

Ronco, Frank. 1970. Influence of high light intensity on survival of planted Engelmann spruce. Forest Science. 16(3): 331-339.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W.; MacLean, D.A., eds. The role of fire in northern circumpolar ecosystems. New York: John Wiley & Sons Ltd: 135-154.

Rowe, J. Stan. 1992. The ecosystem approach to forestland management. Forestry Chronicle. 68(1): 222-224.

Sampson, R. Neil; Adams, David L., editors. 1994. Assessing forest ecosystem health in the inland West. Binghamton, NY: Food Products Press (Haworth Press). 461 p.

Sampson, R. Neil; Adams, David L.; Hamilton, Stanley S. [et al.]. 1994. Assessing forest ecosystem health in the inland West. Journal of Sustainable Forestry. 2(1/2): 3-10.

Sauer, Carl O. 1950. Grassland climax, fire, and man. Journal of Range Management. 3(1): 16-21.

Schimpf, David J.; Henderson, Jan A.; MacMahon, James A. 1980. Some aspects of succession in the spruce-fir forest zone of northern Utah. Great Basin Naturalist. 40(1): 1-26.

Schmidt, Wyman C.; Shearer, Raymond C. 1990. *Larix occidentalis* Nutt.; western larch. In: Burns, Russell M.; Honkala, Barbara H., tech. coords. Silvics of North America; volume 1, conifers. Agric. Handb. 654. Washington, DC: USDA Forest Service: 160-172.

Seidel, K.W.; Cochran, P.H. 1981. Silviculture of mixed conifer forests in eastern Oregon and Washington. Gen. Tech. Rep. PNW-121. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 70 p.

Shiflet, Thomas N., editor. 1994. Rangeland cover types of the United States. Denver, CO: Society for Range Management. 152 p.

Shindler, Bruce; Reed, Michelle. 1996. Forest management in the Blue Mountains: public perspectives on prescribed fire and mechanical thinning. Corvallis, OR: Oregon State University, Department of Forest Resources. 58 p.

Shirley, Hardy L. 1929. The influence of light intensity and light quality upon the growth of plants. American Journal of Botany. 16(5): 354-390.

Shlisky, Ayn J. 1994. Multiscale analysis in the Pacific Northwest. Journal of Forestry. 92(8): 32-34.

Shugart, Herman H., Jr.; West, Darrell C. 1981. Long-term dynamics of forest ecosystems. American Scientist. 69(Nov-Dec): 647-652.

Skovlin, Jon M.; Thomas, Jack Ward. 1995. Interpreting long-term trends in Blue Mountain ecosystems from repeat photography. Res. Pap. PNW-GTR-315. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 102 p.

Sloan, John P. 1998. Interruption of the natural fire cycle in a grand fir forest of central Idaho: changes in stand structure and composition. In: Pruden, Teresa L.; Brennan, Leonard A., eds. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tallahassee, FL: Tall Timbers Research Station. Tall Timbers Fire Ecology Conference Proceedings. 20: 250-257.

Smith, Graham W. 1982. Habitat use by porcupines in a ponderosa pine/Douglas-fir forest in northeastern Oregon. Northwest Science. 56(3): 236-240.

Spies, Thomas. 1997. Forest stand structure, composition, and function. In: Kohm, Kathryn A.; Franklin, Jerry F., eds. Creating a forestry for the 21st century: the science of ecosystem management. Washington, DC: Island Press: 11-30.

Spies, Thomas A.; Tappeiner, John; Pojar, Jim; Coates, Dave. 1991. Trends in ecosystem management at the stand level. Transactions of the 56th North American Wildlife and Natural Resources Conference. 56: 628-639.

Spirn, Anne Whiston. 1996. Constructing nature: the legacy of Frederick Law Olmstead. In: Cronon, William, ed. Uncommon ground: rethinking the human place in nature. New York: W.W. Norton & Company: 91-113.

Sprugel, Douglas G. 1991. Disturbance, equilibrium, and environmental variability: what is ‘natural’ vegetation in a changing environment? Biological Conservation. 58: 1-18.

Spurr, Stephen H. 1952. Origin of the concept of forest succession. Ecology. 33(3): 426-427.

Stathers, R.J.; Trowbridge, R.; Spittlehouse, D.L. [et al.]. 1998. Ecological principles: basic concepts. In: Lavender, D.P.; Parish, R.; Johnson, C.M. [et al.], eds. Regenerating British Columbia’s forests. Vancouver, BC: UBC Press: 45-54.

Steele, Robert. 1994. The role of succession in forest health. Journal of Sustainable Forestry. 2(1/2): 183-190.

Steele, Robert; Geier-Hayes, Kathleen. 1995. Major Douglas-fir habitat types of central Idaho: a summary of succession and management. Gen. Tech. Rep. INT-GTR-331. Ogden, UT: USDA Forest Service, Intermountain Research Station. 23 p.

Steele, Robert; Pfister, Robert D.; Ryker, Russell A.; Kittams, Jay A. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Steele, Robert; Williams, Ralph E.; Weatherby, Julie C. [et al.]. 1996. Stand hazard rating for central Idaho forests. Gen. Tech. Rep. INT-GTR-332. Ogden, UT: USDA Forest Service, Intermountain Research Station. 29 p.

Stevens, William K. 1990. New eye on nature: the real constant is eternal turmoil. New York: New York Times, Science Column for Tuesday, July 31, 1990. 2 p.

Stewart, R.E. 1975. Allelopathic potential of western bracken. Journal of Chemical Ecology. 1(2): 161-169.

Stickney, Peter F. 1990. Early development of vegetation following holocaustic fire in northern Rocky Mountain forests. Northwest Science. 64(5): 243-246.

Strickler, Gerald S.; Edgerton, Paul J. 1976. Emergent seedlings from coniferous litter and soil in eastern Oregon. Ecology. 57(4): 801-807.

Swanson, F.J.; Jones, J.A.; Wallin, D.O.; Cissel, J.H. 1994. Natural variability – implications for ecosystem management. In: Jensen, M.E.; Bourgeron, P.S., eds. Volume II: Ecosystem management: principles and applications. Gen. Tech. Rep. PNW-GTR-318. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 80-94.

Swanson, F.J.; Kratz, T.K.; Caine, N.; Woodmansee, R.G. 1988. Landform effects on ecosystem patterns and processes. BioScience. 38(2): 92-98.

Swetnam, Thomas W.; Allen, Craig D.; Betancourt, Julio L. 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications. 9(4): 1189-1206.

Tansley, A.G. 1935. The use and abuse of vegetational concepts and terms. Ecology. 16(3): 284-307.

Tausch, Robin J.; Wigand, Peter E.; Burkhardt, J. Wayne. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? Journal of Range Management. 46(5): 439-447.

Taylor, Alan H.; Skinner, Carl N. 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management. 111: 285-301.

Taylor, Walter P. 1934. Significance of extreme or intermittent conditions in distribution of species and management of natural resources, with a restatement of Liebig's law of minimum. Ecology. 15(4): 374-379.

Thies, Walter G.; Sturrock, Rona N. 1995. Laminated root rot in western North America. Res. Bull. PNW-GTR-349. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 32 p.

Thomas, Jack Ward, tech. ed. 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. No. 553. Washington, DC: USDA Forest Service. 512 p.

Thomas, Jack Ward; Maser, Chris; Rodiek, Jon E. 1979. Edges. In: Thomas, Jack Ward, tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. No. 553. Washington, DC: USDA Forest Service: 48-59.

Trappe, James M.; Harris, Robert W. 1958. Lodgepole pine in the Blue Mountains of northeastern Oregon. Res. Pap. 30. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 22 p.

Turner, Monica G. 1998. Landscape ecology: living in a mosaic. In: Dodson, Stanley I.; Allen, Timothy F.H.; Carpenter, Stephen R. [et al.]. Ecology. New York: Oxford University Press: 77-122.

Turner, Monica G.; Dale, Virginia H.; Everham, Edwin H., III. 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. BioScience. 47(11): 758-768.

Turner, Monica G.; Gardner, Robert H., editors. 1991. Quantitative methods in landscape ecology. New York: Springer-Verlag. 536 p.

Urban, Dean L.; O'Neill, Robert V.; Shugart, Herman H., Jr. 1987. Landscape ecology. BioScience. 37(2): 119-127.

Urban, Karl. 1996. Problematic grasses, and ecological distribution of western white pine, for the Tower Fire analysis area. Unpub. Rep. Pendleton, OR: USDA Forest Service, Pacific Northwest Region, Umatilla National Forest. 2 p.

USDA Forest Service. 1995. Landscape aesthetics: a handbook for scenery management. Agric. Handb. Number 701. Washington, DC: USDA Forest Service. Irregular pagination.

USDA Forest Service. 1997. Considering all things: summary of the draft environmental impact statements. R6-P&EA-UP-007-97. [Place of publication unknown]: USDA Forest Service; USDI Bureau of Land Management. 57 p.

USDA Forest Service. 1999. Desolation ecosystem analysis. Pendleton, OR: USDA Forest Service, Pacific Northwest Region, Umatilla National Forest. 206 p.

Veblen, Thomas T.; Hadley, Keith S.; Reid, Marion S.; Rebertus, Alan J. 1989. Blowdown and stand development in a Colorado subalpine forest. Canadian Journal of Forest Research. 19: 1218-1225.

Veblen, Thomas T.; Hadley, Keith S.; Reid, Marion S.; Rebertus, Alan J. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology. 72(1): 213-231.

Voller, Joan; Harrison, Scott, eds. 1998. Conservation biology principles for forested landscapes. Vancouver, BC: UBC Press. 243 p.

Walters, C.J. 1986. Adaptive management of renewable resources. New York: MacMillan. 374 p.

Waring, R.H. 1983. Estimating forest growth and efficiency in relation to canopy leaf area. Advances in Ecological Research. 13: 327-354.

Waring, Richard H.; Running, Steven W. 1998. Forest ecosystems: analysis at multiple scales. 2nd edition. San Diego, CA: Academic Press. 370 p.

Weetman, G.F. 1996. Are European silvicultural systems and precedents useful for British Columbia silviculture prescriptions? FRDA Rep. 239. Victoria, BC: Canadian Forest Service, Pacific Forestry Centre. 31 p.

Weller, Donald E. 1987. A reevaluation of the –3/2 power rule of plant self-thinning. Ecological Monographs. 57(1): 23-43.

Westoby, Mark. 1984. The self-thinning rule. Advances in Ecological Research. 14: 167-225.

White, Diane E.; Atzet, Tom; Greenup, Mel. 1992. Predicting planting success and natural regeneration potential using plant associations. Grants Pass, OR: Siskiyou National Forest. 31 p.

White, Peter S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review. 45(3): 229-299.

White, Peter S. 1987. Natural disturbance, patch dynamics, and landscape pattern in natural areas. Natural Areas Journal. 7(1): 14-22.

White, Peter S.; Harrod, Jonathan; Romme, William H.; Betancourt, Julio. 1999. Disturbance and temporal dynamics. In: Szaro, R.C. [et al.], eds. Ecological stewardship: a common reference for ecosystem management; volume II. Kidlington, Oxford, UK: Elsevier Science, Ltd: 281-312.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecological Monographs. 23: 41-78.

Wicklum, D.; Davies, Ronald W. 1995. Ecosystem health and integrity? Canadian Journal of Botany. 73: 997-1000.

Wickman, Boyd E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. Journal of Forestry. 78: 31-33.

Wickman, Boyd E. 1990. Old-growth forests and history of insect outbreaks. Northwest Environmental Journal. 6(2): 401-403.

Wickman, Boyd E. 1992. Forest health in the Blue Mountains: the influence of insects and disease. Gen. Tech. Rep. PNW-GTR-295. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 15 p.

Williams, Clinton K.; Kelley, Brian F.; Smith, Bradley G.; Lillybridge, Terry R. 1995. Forested plant associations of the Colville National Forest. Gen. Tech. Rep. PNW-GTR-360. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 375 p.

Williams, Harry; Messier, Christian; Kneeshaw, Daniel. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Canadian Journal of Forest Research. 29: 222-231.

Worster, Donald. 1996. Nature's economy: a history of ecological ideas. 2nd edition. Cambridge, UK: Cambridge University Press. 507 p.

Wu, Jianguo; Loucks, Orie L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Quarterly Review of Biology. 70(4): 439-466.

Yoda, K.; Kira, T.; Ogawa, H.; Hozumi, K. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (intraspecific competition among higher plants XI). Journal of the Institute of Polytechnics, Osaka City University, Series D. 14: 107-129.

Young, James A.; Young, Cheryl G. 1992. Seeds of woody plants in North America. Portland, OR: Dioscorides Press. 407 p.

Zeide, Boris. 1987. Analysis of the 3/2 power law of self-thinning. Forest Science. 33(2): 517-537.

Zhong, Jianwen; van der Kamp, Bart J. 1999. Pathology of conifer seed and timing of germination in high-elevation subalpine fir and Engelmann spruce forests of the southern interior of British Columbia. Canadian Journal of Forest Research. 29: 187-193.

Zon, R. 1907. A new explanation of the tolerance and intolerance of trees. Proceedings of the Society of American Foresters. 2: 79-94.

Zon, Raphael; Graves, Henry S. 1911. Light in relation to tree growth. Bull. 92. Washington, DC: USDA Forest Service. 59 p.

Zwinger, Ann H.; Willard, Beatrice E. 1972. Land above the trees: a guide to American alpine tundra. New York: Harper & Row Publishers. 487 p.