Rim 209

Old Growth and Forest Dynamics in the Douglas-Fir Region of Western Oregon and Washington

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ABSTRACT: Changes in the structure and function of Douglas-fir forests as they develop from young stands to old growth are examined. Old-growth Douglas-fir/western hemlock forests are a long-lived phase of a potentially very long successional sequence. After disturbance, some ecosystem attributes, such as leaf area and water quality, recover relatively quickly, while others, such as live and dead woody structures, which are important for wildlife, return to predisturbance maxima and toward a relative steady state only after four or five centuries. The gradual and variable nature of succession and stand development make the task of precisely defining old growth difficult. We propose an index of "old-growthness" or structural diversity that may be a useful tool in maintaining and managing successional diversity in forest landscapes.

INTRODUCTION

Public lands in western Oregon and Washington contain many acres of old-growth forests even after a century of logging. The forests of this region are dominated by Douglas-fir (*Pseudotsuga menziesii*), a species that can live more than 1000 years and grow to 3 m in diameter and more than 90 m in height (Harlow and Harrar 1969). The Northwest is truly a land of giant conifers where more than twenty species attain their maximum generic sizes and ages in a climate of dry, warm summers and mild, wet winters (Waring and Franklin 1979).

In the early part of this century, most of the forested area west of the crest of the Cascade Range was covered by old-growth forests consisting of Douglas-fir, western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), and several other large, long-lived conifer species. Most of these forests were probably more than 300 years old and many exceeded 750 years. Today, most of the original old growth has been logged or burned, and what remains is almost exclusively on public land. The fate of the remaining old-growth forests, which have high economic value, is a subject of intense public debate. Concern is mounting about the loss of biological diversity as the old growth is logged and the replacement forests are managed on rotations of less than 100 years.

Old-growth Douglas-fir forests are among the most studied old-growth forests in the world (e.g., Franklin et al. 1981), yet much remains to be learned about their structure and function, including their role as habitat. Information about their structural and compositional variability is lacking, and ecological definitions of old growth incorporating this information are needed for inventory and management.

Our purpose is to characterize successional changes in the structure and function of Douglas-fir forest ecosystems, particularly in the later stages. We will discuss the concept of old growth and its definition, estimate the amount and distribution of remaining old growth, and summarize recent information on the ecological characteristics of older forests. Finally, we will suggest an approach to characterizing ecological diversity associated with succession and discuss the role of natural disturbance in ecological dynamics.

Our discussion examines forests dominated by Douglas-fir occurring at low to middle elevations in the mountain ranges of western Oregon and Washington. Old-growth forests at higher elevations, dominated by *Abies* spp., or east of the Cascade Range, which are dominated by ponderosa pine (*Pinus ponderosa*), are also extensive and subject to the same public concerns. The changes that occur during succession in these forests are often similar to those in Douglas-fir forests, although the structure, dynamics, and function of these other forest types are not as well known.

THE CONCEPT AND DEFINITION OF OLD GROWTH

Old growth, a concept pertaining to successionally advanced forests, is difficult to define precisely. In one sense, a definition is implicit in the term "old growth," but how old a forest must be to qualify as "old" or what the "growth" must be like depend on one's point of view. Early definitions of old growth in the Pacific Northwest were largely from a timber perspective: old growth was defined on many national forests as trees past rotation age or trees larger than a certain diameter class. As ecological science has developed and as the popular awareness of the environment has changed over the last twenty to thirty years, other definitions of old growth based on ecology and esthetics have emerged and are finding their way into land-management debates.

An Ecological Perspective

Ecological characterizations of old-growth Douglas-fir forests (Franklin et al. 1981) recognize that old growth is more than just old or large trees. Large standing dead trees, large accumulations of fallen tree boles, and small- and intermediate-sized shade tolerant trees are also important components of old growth. These components and other characteristics combine to produce unique habitat and influence ecosystem processes.

Unfortunately, taking an ecological perspective does not make the task of defining old growth for land-management purposes much easier. A precise definition of old growth may be unrealistic: nature is just too complex and variable to fit into neat conceptual boxes. Within the Douglas-fir region, variation n environment, species composition, and listurbance history create a landscape in vhich no two stands are exactly alike. No iscrete points occur in stand evelopment to indicate when old growth achieved.

ge often is used to define old growth. ge may be the best single indicator — because it is simple and because so many of the attributes commonly associated with old growth are to some degree correlated with age — but age alone indicates nothing about the ecological structure of the forest. Because forests develop at different rates depending on environmental conditions and disturbance history, stand age may be a poor predictor of ecological characteristics. For example, Douglas-fir forests may develop old-growth characteristics between 150 and 250 years at most locations in the region. A 100-year range of uncertainty is not acceptable for management purposes and, furthermore, it only defines the initiation of old-growth characteristics.

Despite the difficulties in defining old growth in precise ecological terms old-growth forests can be characterized and contrasted with young natural and managed forests. These characterizations and comparisons provide the basis for a workable definition of old growth.

An Interim Definition

Research thus far (Franklin et al. 1981, Spies et al. in press) indicates that the old-growth forest is an ecologically diverse system that possesses unique features and can be defined on the basis of multiple characteristics. This particular diversity of structures and functions distinguishes old growth from younger successional stages. Interim definitions for old growth in the Douglas-fir region cover three old-growth Douglas-fir site types and the Sierra mixed-conifer forests (Table 1); they are based on minimal numbers and sizes of large live trees, canopy structure, snags, and logs (Old Growth Definition Task Group 1986). These definitions recognize some of the geographic and plant community variation found in old growth. They are based on minimal criteria rather than average values to encompass all old-growth forests for which data exist. A minimum stand size was not included because of objections that minimum acreages will depend on management objectives and the nature of the surrounding areas.

Several cautions must be observed in developing definitions of old-growth forests. First, old growth is part of a continuum of ecosystems that varies in both space and time. In defining old growth we are putting somewhat arbitrary limits on a continuous, highly variable system. Second, to one degree or another, the old growth we see today is a consequence of a unique set of environmental, ecological, and disturbance conditions in the past that are not precisely reproducible. Thus, in trying to define old growth precisely, we may be characterizing the form and function of a transitory phenomenon. In effect, if today's definition of old growth is too exact, it cannot serve as a model for tomorrow's old growth. This does not mean that nature (with or without human activities) cannot continue to produce old-growth forests, only that the forests are likely to be different to some degree from today's old growth. Finally, we need to make some subjective judgments about which characteristics will be used to define the system. We emphasize characteristics known to be ecologically important, such as number and sizes of snags and logs or tree size and variation in tree size. The use of these and other ecological features as a basis for defining old growth assumes that they are (1) important in distinguishing old growth from natural or managed forests in other successional stages and (2) related to the distinctive ecological functions of old-growth forests. The ecological functions that are considered are habitat for organisms and ecosystem productivity, including nutrient and hydrological cycling. We know considerably more about the structure of forests than about their function or how structure relates to function. Consequently, we need to make many assumptions, based on limited data, about what structural and readily visible and measurable features are important to ecosystem function.

An alternative to relatively precise definitions of old growth is to develop a general index of structural or habitat diversity. In such an approach the "old-growthness" of forests of all ages,

TABLE 1. Interim minimum standards for old-growth Douglas-fir and mixed conifer forests in western Washington and Oregon and in California* (from Old-Growth Definition Task Group 1986).

Stand Characteristic	Douglas-fir on western hemlock sites (western hemlock, Pacific silver fir)	Douglas-fir on mixed conifer sites (white fir, Douglas-fir)	Douglas-fir on mixed evergreen sites (tanoak, Douglas-fir)	Sierra mixed conifer (white fir)
Live trees	Two or more species with wide range of ages and tree sizes	Two or more species with wide age range and full range of tree sizes	Douglas-fir and evergreen hardwood (tanoak, Pacific madrone, and canyon live oak) associates (40 to 60% of canopy)	Two or more species with wide age range and full range of tree sizes
	Douglas-fir ≥8 per acre of trees >32 inches in diameter or >200 years old	Douglas-fir, ponderosa pine, or sugar pine 30 inches in diameter or >200 years old	Douglas-fir and pine ≥6 per acre of trees >32 inches in diameter or >200 years old	Douglas-fir, sugar pine, or ponderosa pine ≥8 per acre of trees >32 inches in diameter or >200 years old
	Tolerant associates (western hemlock, western redcedar, Pacific silver fir, grand fir, or big-leaf maple) ≥12 per acre of trees >16 inches in diameter	Intermediate and small size classes are typically white fir, Douglas-fir, and incense cedar, singly or in mixture	Intermediate and small size classes may be evergreen hard-woods or include a component of conifers (e.g., Douglas-fir or white fir)	Intermediate and small classes are typically white fir with Douglas-fir, or incense cedar, or both in some stands
Canopy	Deep, multilayered canopy	Multilayered canopy	Douglas-fir emergent above evergreen hard-wood canopy	Multilayered canopy
Snags	Conifer snags ≥4 per acre that are >20 inches in diameter and >15 ft. tall	Conifer snags ≥1-1/2 per acre that are >20 inches in diameter and >15 ft. tall	Conifer snags ≥1-1 1/2 per acre that are >20 inches in diameter and >15 ft. tall	Conifer snags ≥3 per acre that are 20 inches in diameter and >15 ft. tall
Logs	Logs ≥15 tons per acre including 4 pieces per acre ≥24 inches in diameter and >50 ft. long	Logs ≥10 tons per acre including 2 pieces per acre ≥24 inches in diameter and >50 ft. long	Logs ≥10 tons per acre including 2 pieces per acre ≥24 inches in diameter and >50 ft. long	Logs ≥10 tons per acre including 2 pieces per acre ≥24 inches in diameter and >50 ft. long

* Major series are shown in parentheses

whether natural or managed, could be compared. We discuss this approach more fully later in this paper.

HOW MUCH OLD GROWTH REMAINS?

Accurate information on the amount of old growth in Oregon and Washington at the time of non-native settlement and at present is unavailable. Franklin and Spies (1984) estimate that 60 to 70 percent of the commercial forest land in the Douglas-fir region was covered by old growth in the early 1800's. This percentage translates to about 6 million ha of old growth at the time of non-native settlement, based on an estimate of 10 million ha for the total amount of commercial forest land in the region. Haynes (1986) estimated the acreage of old growth in the Douglas-fir region at about 1.3 million ha, based on timber inventories of public and private commercial forest lands from the early to mid-1970's. For the inventory of national forest lands, old growth was defined as stands at least 10 acres in size, older than 250 years, with less than 10 percent entry. On other lands only the age criteria was used in the inventory. We estimate that perhaps 25 percent of the remaining old growth has been cut since these inventory data were collected, which would leave about 1 million ha or about 17 percent of the original area of old growth. A lower estimate would result if the definition of old growth was restricted to larger stands without any logging activity and a higher estimate would result if old growth was defined as stands older than 175 years, an age when many old-growth characteristics begin to appear.

Of the remaining old growth, about 270,000 ha exist in protected status in national parks and monuments in Washington (Haynes 1986). Additional acreage of old growth exists in wilderness areas and research natural areas; however, there is little old-growth Douglas-fir in wilderness because most of these forests are at high elevations.

Most of the old-growth Douglas-fir is on the west slope of the Cascade Range in Washington and Oregon. Little old growth remains in the Coast Ranges because of logging and wildfires (Juday 1976); existing stands in the Oregon Coast Ranges are concentrated on eastern slopes of Bureau of Land Management lands. The Siskiyou Mountains to the south of the Coast Ranges contain some of the largest remaining unroaded blocks of old growth in the region, although most of it is not Douglas-fir/western hemlock but mixed conifer old growth.

The size distribution of old-growth stands is as important as the total amount. For example, the majority of the old-growth patches on the Siuslaw National Forest are less than 16 ha (Harris 1984). The size distribution of old-growth patches on other national forests may follow a similar pattern with many small patches and few large patches, although many forests have a higher percentage of total old growth in large patches. Because a forest less than 10 ha may be entirely edge habitat (Harris 1984, Franklin and Forman 1987), many areas of old growth in the region cannot be considered ecologically viable, and estimates of the amount of old growth need to be adjusted downward accordingly. The minimum stand size for old growth varies depending on species composition, management objectives, location of the stand in the landscape, and successional stages of neighboring stands.

OLD GROWTH IN ECOLOGICAL SUCCESSION: STRUCTURE AND FUNCTION

Old-growth Douglas-fir is one phase of forest development, a process with many pathways and variable rates that is marked by interruptions and shifts from disturbances. We will examine what is known about differences between old-growth and young Douglas-fir ecosystems in composition, function, and structure.

Composition

Relatively little is known about the compositional changes that accompany the middle to latter stages of succession in Douglas-fir forests. Most research has concentrated on successional changes immediately after catastrophic disturbance and during the reestablishment of a closed canopy of Douglas-fir (Dyrness 1973, Long 1977, Halpern 1987). Long (1977) found that the greatest change in plant-community diversity came during the first seventy years of Douglas-fir stand development and predicted that after seventy years understory composition would reach a dynamic equilibrium exhibiting only gradual changes as western hemlock became a dominant in the understory and overstory. No studies have identified the plant-community changes that would occur as western hemlock becomes a dominant in the old-growth forest, although several are underway. Stewart (1986) found that cover and species richness were lower under western hemlock canopies in old-growth forests than under Douglas-fir canopies. This difference suggests that understory communities become more depauperate in latter stages of forest succession than in mid-stages. It also suggests that the spatial pattern of understory communities becomes more fragmented and heterogeneous in old-growth forests as the canopy becomes a mosaic of shade-tolerant and shade-intolerant trees.

Late in succession, stands become dominated by western hemlock and other shade-tolerant species. In the absence of large canopy disturbances, Douglas-fir does not regenerate and drops out of the stand. This process is slow, however, and 1200 years can pass before the last Douglas-fir dies (Franklin and DeBell 1988); fire is likely to destroy the stand before Douglas-fir disappears. The structural and compositional diversity of western hemlock forests is probably lower than their immediate precursors in which Douglas-fir is still a major component. These forests are still considered old growth and often contain large, well-decayed Douglas-fir snags and logs.

We know of no plant species that occur exclusively in old growth, although analyses of recent surveys are not yet complete. Observations, however, suggest that some vascular plants occur more frequently in old growth than in young forest stages. For example, Pacific yew (*Taxus brevifolia*), a very slow-growing, shade-tolerant species that does not mature for 250 to 300 years (Harlow and Harrar 1969), appears to reach its best development in the understories of old-growth forests. Little is known about the distribution of nonvascular plants — mosses, lichens, and liverworts — during succession in Douglas-fir forests. Many, such as *Lobaria oregana*, a foliose canopy lichen, appear to find optimal habitat in the environmental conditions of old-growth stands, and some may require old-growth habitat (Franklin et al. 1981).

The relationships of vertebrate species to Douglas-fir forest development are better known, although relatively few species have been studied in detail. The most familiar example is the northern spotted owl (*Strix occidentalis*), which appears to depend on the availability and distribution of old-growth stands for its survival (Gutierrez and Carey 1985). Seventy-six other wildlife species use old growth as their primary breeding habitat and sixty-five other species use old growth as their primary feeding habitat (Brown 1985). Species with particular preference for old growth include Vaux's swift (*Chaetura vauxi*), fisher (*Martes pennanti*), western red-backed vole (*Clethrionomys californicus*), and the Olympic salamander (*Rhyacotriton olympicus*).

Ecosystem Productivity

Gross primary productivity, the radiant energy fixed by photosynthesis per unit land area, is high early in Douglas-fir stand development and appears to stay at about the same rate through old growth (Grier and Logan 1977). Net primary productivity (NPP), which is the gross primary productivity minus losses through plant respiration, is usually calculated as the biomass increment (annual biomass accumulation minus branch, stem, and root mortality) plus litterfall (including above- and belowground mortality) and plant parts removed by grazers. NPP is also similar in young and old-growth Douglas-fir forests, although with an important difference: in young Douglas-fir forests most of the NPP is in biomass increment, but in old-growth forests tree mortality and litterfall constitute almost all of the NPP (Grier and Logan 1977).

The net wood production of these forests is of primary interest in timber management. Volume production in Douglas-fir reaches a maximum by ninety years or less and can stay high for another 100 years, depending on site conditions, before declining to low values in old-growth stands (McArdle 1961). In an analysis of a thirty-six-year record of gross and net growth in old-growth Douglas-fir (DeBell and Franklin 1987), gross wood-volume growth was relatively high, but it was nearly balanced by high tree mortality. Net growth was minimal, and total stand volume remained nearly constant.

The accumulation of live biomass in these forests appears to peak around 400 to 500 years and stay high without declining through 700 to 900 years (Spies et al. submitted). Changes in how that biomass is allocated among species do occur, but these are gradual: a slow decline in the dominance of Douglas-fir and an increase in the proportion of western hemlock and other shade-tolerant species.

Cycling and Storage of Materials

Nutrient cycles vary with succession, but few detailed studies have been conducted in Douglas-fir forests. Study results indicate that nutrient losses from the ecosystem can be high during clearcutting and for as long as fifteen years after (Fredriksen and Harr 1979); however, with the recovery of the vegetation and canopy cover, losses of elements such as nitrogen and phosphorus can become low in stands as young as thirty-seven years (Cole et al. 1967). Nutrient losses are also low in old-growth forests (Sollins et al. 1980).

The "tight" nutrient cycles of closed-canopy forests, including old growth, mean that water quality from these ecosystems is high compared with recently clearcut and burned forest areas (Fredriksen and Harr 1979). Soil erosion is also typically high immediately after clearcutting and low in closed-canopy forests, including old growth.

Another aspect of material cycling is water yield. Immediately after clearcutting water yields from watersheds in southwestern Oregon increased because evapotranspiration was reduced and surface runoff was increased (Harr et al. 1979). Yields of water decline and probably reach a steady state when fine-root and foliage biomass levels off in young stands, usually by the time of canopy closure (Turner and Long 1975, Vogt et al. in press). Where fog and low clouds are common, water yields from old-growth forests may be up to 30 percent higher than in clearcuts because more water condenses and precipitates from the tall canopies and larger amounts of needle and twig surfaces in old growth than in young forests (Harr 1982). At what age young forests begin to intercept substantial amounts of fog is not known.

Structures and Their Ecological Roles

The most obvious and well-known changes in Douglas-fir forests are in structures — the trees, snags, and fallen trees that create habitat for a variety of organisms and influence nutrient cycling. Contrasts between old growth and younger growth are large for coarse woody debris and aboveground tree biomass (Spies and Franklin 1985, Spies et al. in press).

The large old-growth Douglas-firs and western hemlocks provide unique habitat structure in several ways. First, by virtue of the great height of the trees — more than 70 m in many stands — the volume of the old-growth ecosystem is large, resulting in a long habitat gradient from the cool, moist forest floor, where climatic extremes are buffered, to the top of the canopy, which is exposed to bright sun, high winds, fog, rain, ice, and snow during the course of the year. Thus habitat is provided for many different organisms, including epiphytic lichens and mosses that grow in tree crowns on fan-shaped branches, bats and birds that feed on insects above the canopy, mammals and birds that feed on the abundant foliage, bark-gleaning birds that search the extensive surface of tree trunks for insects, and salamanders that dwell in moist organic matter covering the forest floor. The large crowns with stiff branches also intercept large amounts of snow, much of which melts in the canopy, keeping snow depths low in mature and old-growth stands and allowing herbivores to forage during the winter.

Many of the large live trees have broken tops, cavities, and gnarled branches protected by foliage that provide preferred nesting sites for bird species such as the spotted owl (Forsman et al. 1984). Large trees also support abundant epiphytic lichen and moss communities, including *Lobaria oregana*, a nitrogen fixing leafy lichen that can contribute nitrogen to the ecosystem (Franklin and Hemstrom 1981). Large live trees are the source of the large snags and logs that play important ecological roles.

With time, shade-tolerant trees — such as western hemlock, western redcedar, and Pacific silver fir — increase in abundance, and stands develop a multi-layered canopy. In younger Douglas-fir stands, Douglas-fir typically develops a relatively continuous single canopy layer (Figure 1). As mortality increases the spacing between Douglas-firs in the older stands, the Douglas-firs emerge above a canopy of western hemlock (Figure 1). Variation in tree size is one of the more distinctive features of old-growth Douglas-fir forests (Spies and Franklin 1985) and is readily evident in comparisons of diameter distributions in Douglas-fir stands of different ages (Figure 2). Variation in tree size contributes to the diversity of microhabitats, both vertically and horizontally.

Snags are abundant in all stages of succession in Douglas-fir forests, although the size of snags changes greatly. Large snags more than 50 cm in diameter at breast height (dbh) and 15 m tall are most abundant in the first few decades after wildfire in old growth and in latter stages of forest development (Spies et al. in press). Large dead trees are valuable to cavity-excavating birds such as the pileated woodpecker (*Dryocopus pileatus*). The underside of sloughing bark also provides habitat for at least twelve vertebrate species (Brown 1985). Because large-diameter snags maintain bark longer than small-diameter snags (Graham 1981), old-growth forests have more of this potential habitat than young ones (Brown 1985). Large snags also provide good foraging habitat for many woodpecker species.

Logs in Douglas-fir forests are created when trees fall to the forest floor or, more commonly, when snags or portions of snags fall. Like snags, fallen trees are common in all stages of natural forest succession, but the highest numbers and volume of large logs occur soon after catastrophic disturbance and in old-growth forests (Spies et al. in press). As logs decay they change structurally, providing habitat for 150 or more species of vertebrate organisms and many hundreds of species of invertebrates (Brown 1985, Harmon et al. 1986). Douglas-fir logs decay less rapidly than western hemlock logs (Graham 1981) and large logs decay less rapidly than small ones (Harmon et al. 1986) so large Douglas-fir logs provide the most stable habitat. Large Douglas-fir logs also provide germination sites for western hemlock and other plant species. In forest streams, logs become habitat for vertebrates and invertebrates, trapping organic matter and storing inorganic sediments (Harmon et al. 1986).

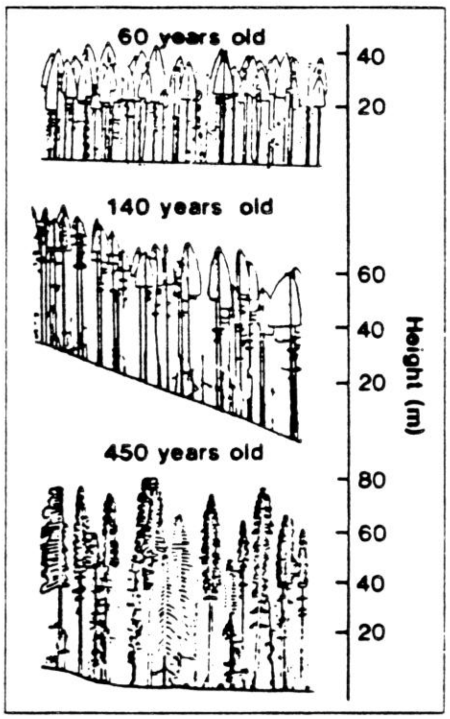

FIGURE 1. Profiles for a young, a mature, and an old-growth Douglas-fir forest. Crowns outlined in solid lines are Douglas-fir; crowns with dashed lines are western hemlock. Modified from figures drawn by Kuiper (unpublished data).

Both logs and snags are important in the functioning of both terrestrial and aquatic ecosystems in the Douglas-fir region. Coarse woody debris (CWD) provides storage for essential nutrients such as nitrogen. In one study (Sollins et al. 1980) in an old-growth forest, 21 percent of the aboveground nitrogen was stored in CWD, although only 4 percent of total-system nitrogen was in that form because of the high amounts of nitrogen in the soil. In old-growth forest streams, logs are sites of nitrogen fixation and, along with fine woody debris, store most of the nitrogen (Triska et al. 1984). On drier sites in the region, decayed logs may serve as sources of moisture for mycorrhizal and plant growth during dry periods, as has been observed in the Rocky Mountains (Harvey et al. 1976, 1979).

GENERAL TRENDS IN DOUGLAS-FIR STAND DEVELOPMENT

Old-growth forests are part of a continuum in which many aspects of structure and function change. Much of this change is a consequence of the development of the dominant trees in the canopy and the dead structures they ultimately produce. We can view ecological succession in Douglas-fir forests, and perhaps also in other forests, in terms of the waxing and waning of structural features related to dominant trees such as Douglas-fir. Theoretically, structural changes in the Douglas-fir region follow two general pathways with time (Figure 3). The first pathway has a U-shaped pattern, with high values immediately after catastrophic disturbance in old growth, declining to low values midway through succession, and then increasing to moderately high values again in old-growth forests. The curve then will decline somewhat as stands become climax or near-climax, losing their Douglas-fir component. We know that several characteristics follow this general pathway (Table 2) including amounts of CWD and numbers of large snags and logs that are carryover from the previous old growth (Spies et al. in press). The other pathway is more S-shaped and related primarily to growth and development of live trees; it has low values early in succession and increases to an asymptote later in succession in old growth and may stay high for several hundred years before declining (Figure 3). Characteristics following this pattern, to one degree or another, include stand biomass (Spies et al. submitted), tree size, and diversity of tree sizes (Table 2). These curves really represent families of curves that deviate to different degrees from these patterns, depending on the characteristic. They also represent those features that our research and intuition suggest take the longest time to reach a maximum and a relatively steady state. Other types of changes in structures and functions also occur, such as a decline in the density of Douglas-fir with time, decline in net wood production, and increase in foliage and fine root biomass. Here we have emphasized structural changes that do not reach relatively maximal values until late in succession.

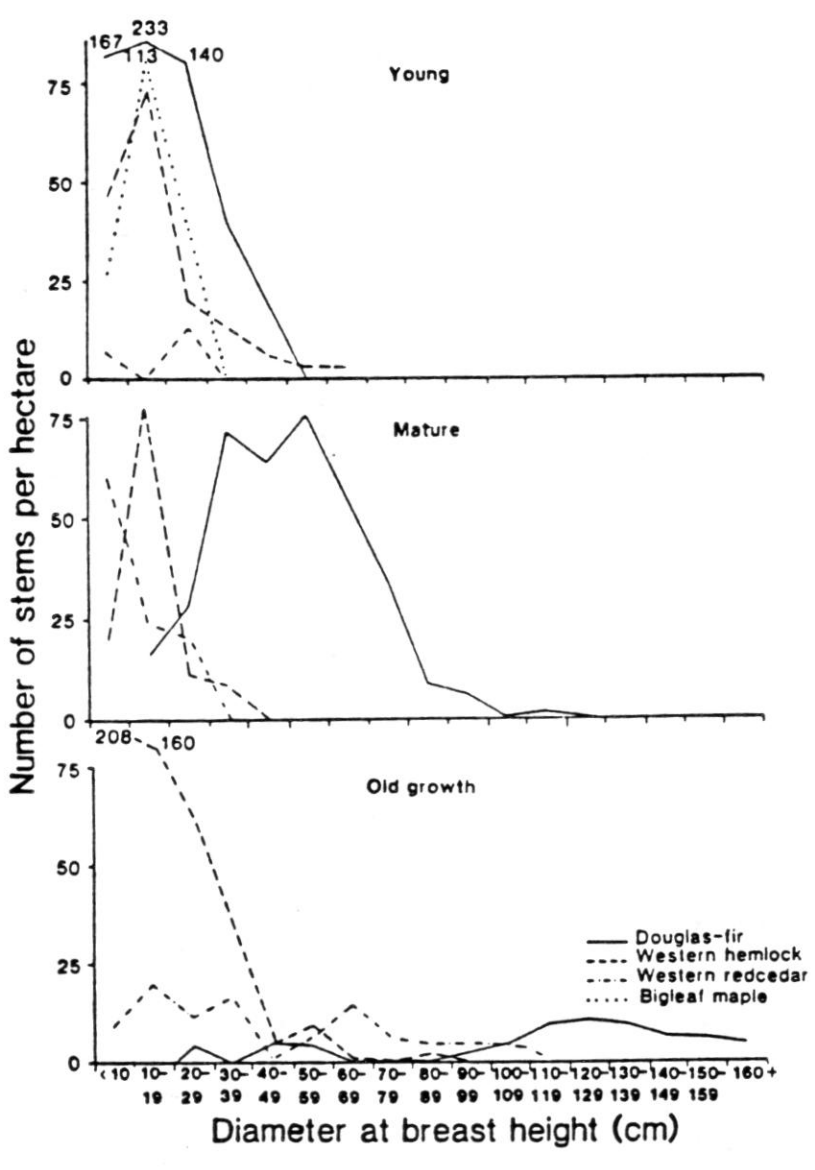

FIGURE 2. Diameter distributions by species for young, mature, and old-growth Douglas-fir forests in the central western Cascade Range. Numbers above the curves indicate stem densities exceeding seventy-five stems per hectare.

The ecological succession represented by Figure 3 does not include intermediate disturbances of various intensities but is one scenario in which a major fire occurs in an old-growth forest and no major disturbances occur again. We know this pattern is idealized; in nature, disturbances interrupt the process. Wind, insects, and fire often create openings in stands without completely destroying them. We believe the concept is useful, however, because (1) many stands or portions of stands approximate it, (2) it represents the general course of ecological change after most natural disturbances, and (3) it sets a standard in terms of potential maximal development of live and dead structures after disturbance. For example, if a fire destroyed a 100-year-old stand, curve one (CWD dynamics) would follow a similar pattern after the disturbance but would have lower initial values because less CWD would be present after the disturbance.

STRUCTURAL DIVERSITY INDEX

Old growth is one phase of forest succession that has high values for some, and unique combinations of many,

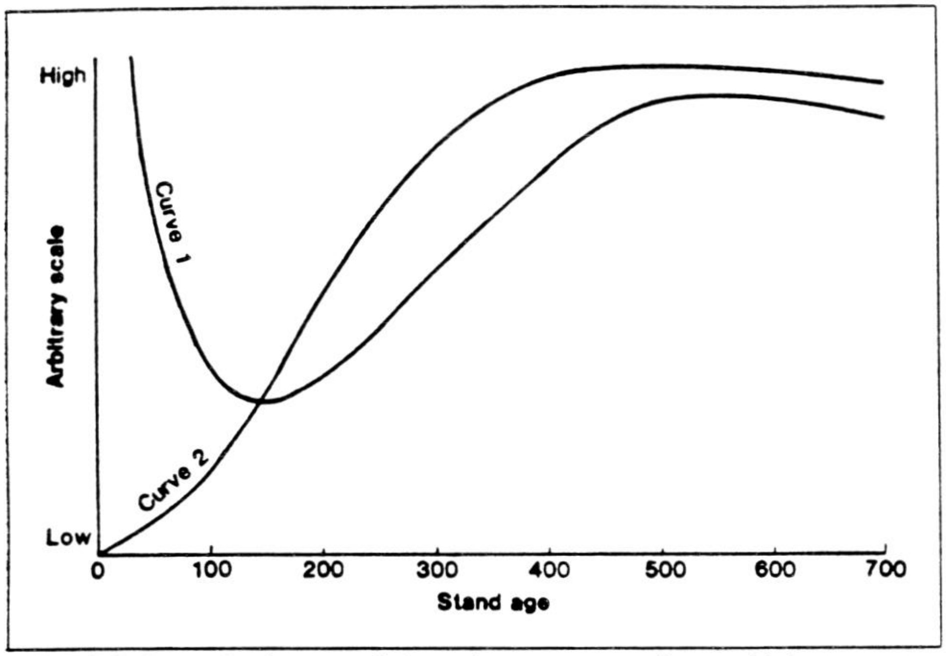

FIGURE 3. Generalized curves of change in ecosystem attributes with long recovery periods after disturbance in old-growth Douglas-fir forests.

TABLE 2. Classification of ecosystem characteristics according to their expected pattern of change (Figure 3) during succession in Douglas-fir forests.

Characteristics following a "U-shaped" curve (Curve 1)	Characteristics following an "S-shaped" curve (Curve 2)
Amount of coarse woody debris	Average tree size
Number of large snags	Diversity of tree sizes
CWD as percentage of total ecosystem biomass	Incidence of broken tops
Heterogeneity of understory	Forest floor depth
Plant species diversity	Surface area of boles and branches
Mammal diversity	Wood biomass

ecologically important characteristics. The loss of within-stand structural diversity (i.e., the variety of types and sizes of trees, snags, logs, and understory vegetation and their ecological functions) is one of the main issues mentioned in the debate over loss of successional diversity in managed forest landscapes (Franklin et al. 1986). Given the continuous nature of ecological succession, thinking in terms of a structural diversity index or an index of "old-growthness" may be more reasonable than identifying one point on the continuum to separate old growth from mature, young, or managed stands. We propose that such an index be composed of the characteristics that change most during succession and are most ecologically important to the habitat and functional characteristics of the ecosystem. Using the two general patterns of development discussed above (Figure 3), an old-growth index might be constructed by simply summing the values of characteristics so the highest values occur in the latter stages of Douglas-fir stand development (Figure 4). For example, a stand with high densities of large Douglas-firs and smaller western hemlocks and large amounts of CWD might have an index value above 0.75; a young stand with relatively high amounts of CWD inherited from the previous old stand might have an index value of 0.5; and a young stand lacking both CWD and large trees would have a value below 0.25. Other, more complex weighting schemes also could be used to emphasize stand characteristics important to particular functions.

A stand structure diversity index might prove useful for simple evaluations of the within-stand conditions of a forest landscape. Of course, indices have their limitations in that much complexity is boiled down into one number, and two stands with different structures may have the same index value. For many purposes in broad-scale landscape and old-growth management, however, an index of old growth may be useful. Laymon et al. (1985) have indexed spotted owl habitat suitability based on characteristics of live trees. To meet more specific objectives in wildlife-habitat management, different types of old-growth indices could be developed in which important habitat characteristics are given extra weight. As more information about the variation in old-growth structure becomes available and management objectives become more specific, different old-growth indices can be developed.

DISTURBANCES AND THE ROLE OF OLD-GROWTH DOUGLAS-FIR IN LANDSCAPE DYNAMICS

So far we have examined ecosystem change in terms of growth and

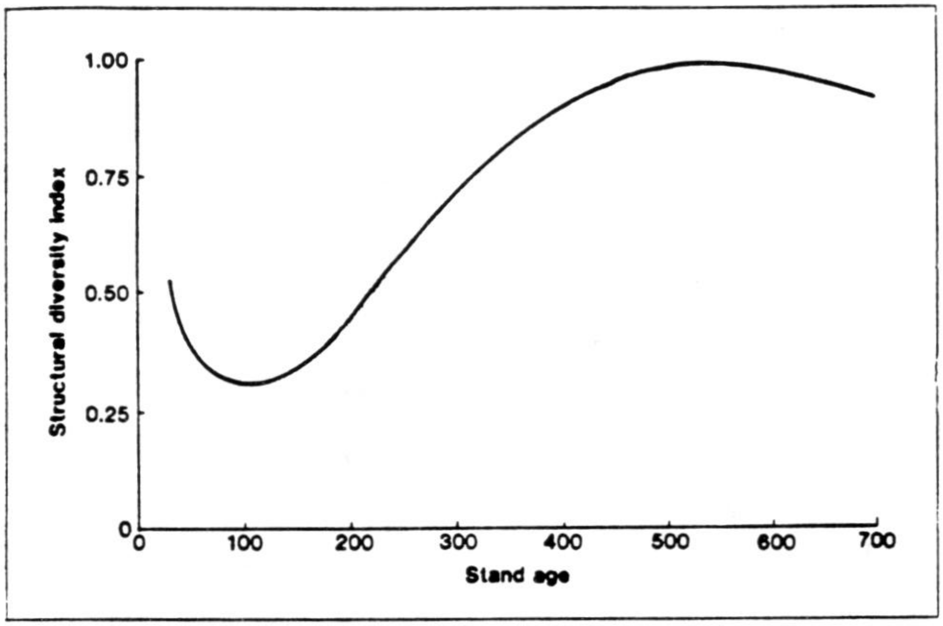

FIGURE 4. Hypothetical index of structural diversity in relation to stand age after disturbance in old-growth Douglas-fir forests.

development of stands and ecosystems. Disturbance is another important dynamic in these forests that can accelerate the development of structural and ecological complexity or bring ecological succession full circle by converting old-growth ecosystems to young-growth ecosystems.

Natural disturbances to old-growth Douglas-fir forests have occurred across a range of size, frequency, and severity. At the coarse end of the range are major catastrophic fires that kill trees in patches of hundreds of thousands of hectares. The Yacolt burn, which killed vegetation and consumed organic matter over 100,000 ha of forest in southwestern Washington in 1902, is one of several historical examples. Return intervals in the northern part of the region for such fires are 400 to 500 years, based on research in Mount Rainier National Park (Hemstrom and Franklin 1982). Because many of the current old-growth stands in the western Cascade Range are 400 to 500 years old, we suspect that many of them became established after a series of large fires around 500 years ago. These large fires probably were very patchy in their severity, killing all of the overstory in some areas, thinning some stands by underburning, and skipping other areas. Given the extensive nature of these fires and reburns in young stands, establishment of Douglas-fir may have been slow as a result of low seed availability. A low rate of reestablishment, partially as a result of limited seed source, may explain the wide age range of Douglas-fir (100 years or more) in many old-growth stands (Franklin and Hemstrom 1981).

In the southern part of the region, increasing evidence has been found (Morrison and Swanson in press) that smaller, less severe but more frequent fires also occurred in existing old-growth forests and earlier successional stages. These fires may have burned in association with larger, more severe fires or with fires on dry sites that have a fire frequency of around 100 years (Means 1982). When these fires burned in young stands, Douglas-fir trees would be killed, allowing establishment of a new cohort of Douglas-fir — another possible explanation for the wide age range in old-growth forests. When fires burned in old-growth forests, many large Douglas-firs would not be killed, leaving a canopy under which more shade-tolerant species would probably regenerate.

Finer scale disturbances result from wind, insects, and pathogens. Wind storms in fall and winter typically kill trees in a dispersed pattern of mortality. Large-scale disturbances from wind also occur at less frequent intervals and can destroy the canopies in patches of many hectares. The frequency and distribution of this scale of windstorm is not known for the region. Outbreaks of Douglas-fir bark beetle have occurred periodically, often in association with wind damage. These insect outbreaks kill trees in small groups that may be clustered or widely dispersed over an area. Pathogens, such as *Phellinus weirii*, also cause patchy mortality in Douglas-fir stands from young trees through old growth. Although this disease spreads slowly, it is widely distributed and may affect 10 percent or more of stands throughout the region.

Fine-scale disturbances accelerate the changes from young or mature stands to old growth by increasing: (1) woody debris in the stand, (2) vertical and horizontal heterogeneity, and (3) the proportion of shade-tolerant associates. In contrast, large-scale disturbances caused by fire return stands of any age to early successional stages by providing conditions for the establishment of Douglas-fir in large patches. Interestingly, large-scale disturbances caused by wind accelerate compositional changes toward shade-tolerant species because most of the new stand will come from advance regeneration.

Catastrophic wildfire has been the primary recycler of ecosystems in much of the region. Although wildfire can kill all the trees in a stand, it removes relatively little of the large wood, so the young regenerating stand has tremendously high amounts of CWD, perhaps over 800 t/ha on some sites (Spies et al. in press). This debris provides what may be an important inheritance for the young, regenerating forest. The standing dead trees provide a light, protective shade that may improve seedling survival on hot, dry sites. The large accumulation of wood and litter provides a source of organic matter that plays a role in site productivity (Harmon et al. 1986), as well as habitat for vertebrates and invertebrates. Through their persistent structures, old-growth ecosystems provide a strong linkage or legacy to postdisturbance ecosystems that may facilitate the recovery of those ecosystems. Viewed in this way, old-growth ecosystems play important ecological roles both when they are intact and when they are transformed by natural disturbances.

Although natural disturbances have been, and will continue to be, important in the dynamics of Douglas-fir landscapes, clearcutting and burning are the primary disturbances today. The staggered-setting system of clearcutting removes all of the aboveground tree biomass and large portions of the CWD in 12- to 16-ha patches dispersed on the landscape. Clearcutting differs from natural disturbance in at least three ways. First, unlike fire, clearcutting removes all of the live wood leaving an ecosystem with very little large wood debris and little structural diversity. Under the shorter rotations that follow, CWD in tree plantations declines still more (Spies and Cline in press). Second, the dispersed pattern of clearcuts results in smaller, more uniform patch sizes compared to wildfire patches. This change and other characteristics of this pattern of disturbance can have important effects on wildlife habitat and increase disturbance probabilities (Franklin and Forman 1987). Third, the frequency of clearcutting under 70- to 100-year rotations truncates succession well before old-growth characteristics begin to develop.

CONCLUSIONS

Old-growth Douglas-fir/western hemlock forests are a long-lived phase of a potentially very long successional sequence. Structural and functional changes common to shorter seres in many other forests take much longer in Douglas-fir forests. The long life spans and large sizes attained by Douglas-fir and other conifers and the slow decay rates of the wood also mean that woody structures persist over much longer periods than in many other forest systems. These factors, along with the often coarse-grained pattern of disturbance, have made successional changes in these forests conspicuous as well as ecologically significant. Many of the ecosystem changes depend strongly on the growth and development of the canopy-dominant Douglas-firs and associated shade-tolerant trees. Major changes in the live and dead structures and the habitats they create do not appear to slow until 500 years, after which the system moves slowly toward equilibrium.

The gradual and variable nature of succession and stand development make the task of precisely defining old growth difficult. Nevertheless, a workable set of definitions is possible. An index of structural diversity may be more useful and realistic than a search for one point in succession that separates old growth from other successional stages. This index of "old-growthness" might better estimate the successional diversity of a landscape and its capacity to support late-successional wildlife populations than measures based on two or three successional classes. Such an approach is also useful in characterizing the structure of managed forests and integrating them into ecological management of entire landscapes. Because most of the forested acreage in the Douglas-fir region will come under some degree of timber management, recognizing these areas as opportunities for enhancing ecological diversity is essential.

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