



Part 3

Douglas-Fir Forests of
Oregon and Washington

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Composition, Function, and Structure of Old-Growth Douglas-Fir Forests

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Abstract

Ecological characteristics of old-growth Douglas-fir forests are examined in terms of compositional, functional, and structural features. Old-growth forests typically include distinctive animal and plant species—that is, organisms that are most abundant in such forests. Functional behavior of old-growth forests differs from functional behavior under other forest conditions. Productivity is typically high, but most energy is used to maintain the large mass of living material; growth and mortality are in approximate balance over long periods. Nutrient and sediment yields from old-growth forests are typically very low. Old-growth forests also differ from younger forests in their effects on hydrologic cycles in areas where cloud or fog precipitation, rain-on-snow events, or both are important. The structural characteristics of old-growth forests are the basis for most of their unique compositional and functional attributes. Specifically, important structural components are large individual old trees—

whether live, dead and standing (snags), or dead and fallen (logs)—in both terrestrial and associated aquatic environments. Old-growth forests also have stand attributes that are very different from younger and, especially, from managed forests. The distinctive communities of microbes, invertebrates, higher plants, and animals that occur in old-growth forests are integrally related to the collective structural attributes.

Introduction

In the Pacific Northwest, the term “old-growth forests” typically connotes stands 200 to over 1000 years of age that contain large, coniferous trees, especially Douglas-fir. Such forests once covered millions of acres, but have been drastically reduced by logging and other forest clearing (Marcott and others, this volume; Morrison 1988). The remaining acreage is in high demand for a variety of conflicting uses, such as a source of merchantable logs and as habitat for animals and plants. As a result, the disposition of unreserved old-growth Douglas-fir has recently become very controversial.

A clearer understanding of the major ecological characteristics of old-growth Douglas-fir forests is relevant to the ultimate resolution of this controversy. Until about 20 years ago, little was known about the ecological nature of these forests. For example, foresters and wildlife managers have sometimes referred to old-growth stands as “cellulose

cemeteries” and “biological deserts.” Research over the last two decades has dispelled such notions, however, and provided insights into the distinctive ecological qualities of old-growth forests. Scientific studies, sponsored largely by the National Science Foundation (for example, Edmonds 1982, Franklin and others 1981) and, more recently, the USDA Forest Service’s Old-Growth Forest Wildlife Habitat Program (this volume), have documented many important differences between younger and older forests and, especially, between managed and unmanaged forest ecosystems.

In this paper, we provide an overview of the key ecological features of old-growth Douglas-fir forests. Our paper is divided into three sections: composition, function, and structure. Composition receives relatively little attention here, however, because it is the primary focus of many of the papers in this volume. We emphasize the structural characteristics of old-growth Douglas-fir forests because they determine many of the distinctive compositional and functional features of these forests. Structure is also the element that foresters manipulate to achieve specific functional or compositional goals.

Composition

Old-growth Douglas-fir forests are now known to have high biological diversity in groups as varied as plants (see Franklin and others 1981; Spies, this volume), vertebrates (see this volume), invertebrates (see Moldenke and Lattin, this volume; Schowalter 1989), and aquatic organisms (see Gregory and others, in press).

Alpha (species) diversity of both plants and animals is often highest early in succession before tree-canopy closure occurs, lowest in the heavily shaded young forest, and recovers to intermediate as the forest matures and evolves into old growth (fig. 1). High diversity of plant species early in succession is a combined result of the survival of forest species and the addition of weedy generalist species (Halpern 1988, Schoonmaker and McKee 1988); this combination may also occur with other classes of organisms. Habitats and environmental resources appear to be relatively limited in a fully stocked young forest (Spies and Franklin, this volume). As a result, species diversity, as well as structural and functional diversity, is probably lowest in this stage of forest development. Old-growth forests contain many highly specialized species, and several of these organisms appear to have clear preferences for old-growth habitats, based on their patterns of abundance. Ruggiero and others (1988) have argued that such preference should be interpreted to reflect a dependence on that habitat for survival over the long term.

Mammal diversity by forest stage

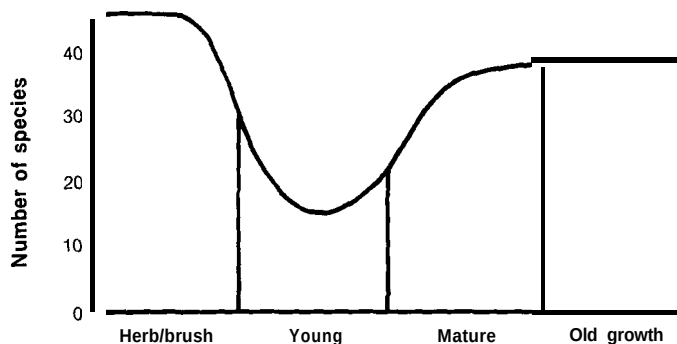


Figure 1-Generalized relationship of mammal species diversity to successional stage in Douglas-fir forests.

The major point here is that old-growth forests are biologically diverse ecosystems with several constituent species that appear to be closely associated with these forests. From a biological standpoint, such a conclusion is not surprising. Many species would be expected to become adapted to a habitat (old-growth forest) that has occupied large areas for long periods. That some of these species would become sufficiently specialized to require old-growth conditions for their survival also seems reasonable.

Function

Function refers to the work that an ecosystem does and the rate at which it is carried out. Examples of forest ecosystem functions are production, the capture of the sun’s energy through photosynthesis and its conversion to organic substances; regulation of nutrient cycling, including accumulation and conservation of nutrients; regulation of hydrologic cycles; and provision of habitat for organisms. We will briefly consider production and nutrient and water cycling; the habitat function of old-growth forests is covered in the section on old-growth structure.

Production

Old-growth forests are productive ecosystems, fixing and processing large amounts of solar energy. The huge foliar surfaces—the greenness-of typical old-growth Douglas-fir stands makes this evident; trees do not retain leaves that are respiring more energy than they are fixing through photosynthesis. Stand leaf areas are often very high in old-growth stands, commonly with 9 to 15 m² of leaf surface per square meter of ground surface. Young stands are typically in the

range of 6 to 8 m² (Franklin and Waring 1980). Individual old-growth trees may have 60 to 70 million needles with 4000 m² of leaf surface (Pike and others 1977). Obviously, such large photosynthetic factories could not be maintained if they were failing to support themselves.

Distinguishing between productivity as measured by biologists and that measured by foresters is important. Gross production in ecological terms is equivalent to the amount of energy fixed photosynthetically per unit area per unit time. Ecologists define net primary production as the biomass increment plus mortality, including litterfall and materials removed by grazing. Foresters define productivity as wood biomass increment, which describes only a portion of the ecosystem's total net productivity. Comments on the low productivity of old-growth forests therefore refer only to the relatively low rates of new wood production. Available data indicate that productivity of old and young forests is typically comparable but that the vast majority of production in old-growth forests is used in respiration and maintenance (Grier and Logan 1977).

Despite high respiration rates, most old-growth forests appear to maintain or increase their amounts of wood. Only one long-term study of timber growth and yield in an old-growth Douglas-fir forest is available (DeBell and Franklin 1987). Over 36 years, wood volumes remained constant even though the stand was subjected to serious attacks by several pests. Live-tree volume losses were high because of mortality, but this loss was offset by substantial stand growth. A high annual wood increment [15.8 m³/ha (1582 bd ft/acre)] was measured in a 10-year study of growth and mortality in a 250-year-old Douglas-fir stand on the Mount Hood National Forest (Bemtsen 1960). Even an extraordinarily high annual mortality of 14.1 m³/ha (1156 bd ft/acre) resulting from a major windstorm and bark beetle outbreak that occurred during this period failed to completely offset growth.

The conclusion that old-growth forests are generally stable in biomass or board foot accumulations is logical. That foresters have long recognized the basic stability of wood accumulations in old-growth forests is evident in their expression of "storing wood on the stump." We have also begun to realize that significant tree and forest growth occurs well beyond culmination of mean annual increment (for example, Williamson and Price 1971). Indeed, by cutting forests before or at culmination, we are cutting them at the transition from ecologically young to mature forests; growth and biomass accumulation are very far from complete at this stage.

Nutrient and Water Cycling

More data are available on the protective functions of old-growth forests-their effects on nutrient and water cycling and on soil erosion-than on any other functional aspect. Old-growth forest systems are highly retentive of nutrients. Large amounts are tied up in both living and dead organic material. Although the release of energy and nutrients from dead organic materials is often slow, it makes old-growth forests extremely conservative-nutrients are tightly retained within the ecosystem. Typically, only small amounts of nutrients leach into the ground water and subsequently appear in streams (for example, Fredriksen 1972, Sollins and others 1980). Soil erosion is also low in old-growth forests relative to rates typical of early stages in forest succession (Swanson and others 1982). The combination of low losses of dissolved nutrients and of particulate matter results in the high water quality of old-growth watersheds.

We are learning that old-growth forests have distinctive and often unexpected effects on hydrologic cycles. At the time of an earlier synthesis of old-growth characteristics (Franklin and others 1981), old and young forests were assumed to have similar net effects on water cycles, but this assumption has not proved true. One example is in effects on condensation of cloud or fog moisture. In a study at mid-elevations in the northern Oregon Cascade Range, fog drip from old-growth foliage was found to contribute up to 30 percent (89 cm or 35 in) of measurable precipitation per year (Harr 1982). This discovery came after clearcutting of some experimental watersheds reduced, rather than increased, water yields. Because old-growth forests typically have deep, multilayered canopies and comparatively high leaf areas, we can expect them to be more effective than young forests at condensing and precipitating moisture and atmospheric particulates. The differences between age-classes will probably be most profound where low clouds or fog are an important part of the microclimatic environment.

The snow hydrology of old-growth forests is also distinct from that of younger stands and, especially, clearcuts. Differences result mainly from a reduction in the potential for rain-on-snow flood events (Harr 1986). Several factors are responsible, including reduced snow accumulation in old-growth stands because of canopy interception, and protection of accumulated snow from the direct impacts of warm air masses and rain.

Structure

Structural characteristics of old-growth forests are extremely important whether the concern is with the ecology of these forests or their management. Many, and probably most, of the distinctive compositional and functional characteristics of old-growth forests are a direct consequence of their structural features (fig. 2). Hence, structure is the key to understanding the ecosystem dynamics of old-growth forests. Also, structure is what the forest manager can manipulate to achieve various objectives; this structural manipulation is what silviculture is about.

Old-growth forests, and unmanaged forests in general, tend to exhibit high structural diversity. In fact, structural diversity offers some of the strongest contrasts between unmanaged forests and intensively managed, commercial timber stands. Some key structural elements of old-growth forests are obvious: wide ranges in tree sizes, including trees of large diameter and height; deep, dense tree canopies; and abundant dead wood (Franklin and others 1981, Spies and others 1988) (fig. 3). Some of these attributes consist of individual structures (for example, large live trees, large snags, and large logs) and others are stand attributes (for example, multiple canopy layers and understory heterogeneity).

Individual Structural Features

Large live trees, large snags, and large logs are individual structural features that have been identified as key elements of old-growth Douglas-fir forests (for example, Franklin and Spies, this volume; Franklin and others 1981; Maser and others 1988; Old-Growth Definition Task Group 1986; Spies and others 1988). We will consider each briefly.

Large old-growth trees—The most conspicuous of the individual structural components of old growth are the large, and very old, live trees. These old trees are typically Douglas-fir, although many other species—such as western redcedar, Sitka spruce, and noble fir—may play similar roles depending on site conditions and stand history. Although size varies with site conditions and age, old-growth Douglas-fir trees are very large, with diameters of 1 to 2 meters and heights of 50 to 90 meters. Because individual trees are often 350 to 750 years old, their long and unique histories give them highly individual forms, in contrast to the uniformity of trees in young (40–80 yr) or mature (80–250 yr) stands.

The large, deep, irregular crown, that is characteristic of many old-growth Douglas-fir trees, is as ecologically important as the massive trunk. Branches are typically irregularly distributed and include large, multiple, fan-shaped arrays. Surfaces of these large branches or branch arrays are covered by thick organic accumulations, which play important roles as habitat for both plants and animals.

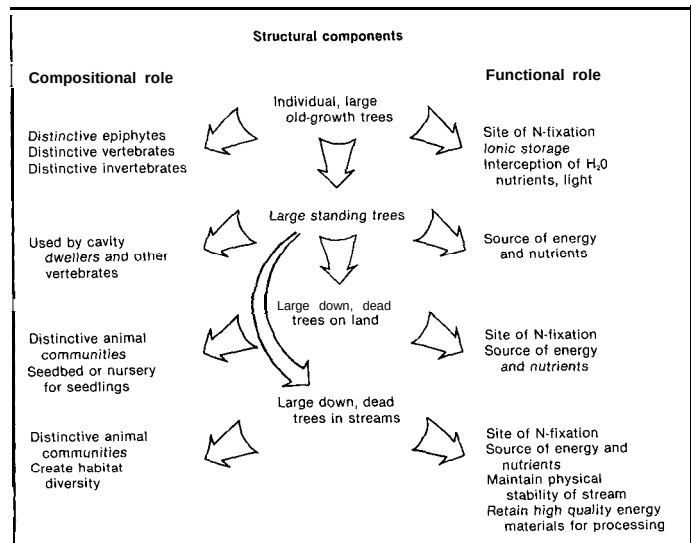


Figure 2—Relationship of some structural components of old-growth forest to distinctive habitat and ecosystem functions (from Franklin and others 1981).

The large, old, live trees are important contributors to the distinctive functions of old-growth forests. Canopies are sites for nitrogen-fixing foliose lichens, such as *Lobaria oregana* (Franklin and others 1981). They are also locales for condensation of moisture, precipitation of other atmospheric materials, and interception of snow. Large trees provide diverse habitats for a myriad of organisms, including epiphytic plants, birds, and mammals. Invertebrate communities are especially rich—an old-growth stand may contain more than 1500 species. A comparative study of canopy arthropods in an old-growth forest and in an adjacent plantation illustrates this richness (Schowalter 1989). Sixty-one species occurred in the old-growth canopy and one arthropod in four (individuals, not species) was a predator or parasite on another arthropod. In contrast, the plantation canopy supported only 16 species and only one in a thousand individuals was a predator or parasite; most individuals were herbivores, mainly aphids. Large trees also serve the important function of providing a source for the large snags and logs that are two other important forest structures.

Large snags—Most old-growth forests contain significant numbers of tall, large-diameter snags >50 cm d.b.h. and >20 m tall (Franklin and Spies, this volume; Franklin and others 1981; Spies and others 1988). Snags have a variety of functional roles in forests but are probably best known as essential habitat for many species of vertebrate and invertebrate animals (this volume, Brown 1985, Maser and others 1988, Thomas 1979). Large snags are particularly important for primary cavity excavators, such as the pileated woodpecker (see Part IV, this volume).



Figure 3—Structural features of old-growth Douglas-fir forests include a range in tree sizes (including large, old trees), large snags, and abundant logs.

Large logs—Logs are nearly as conspicuous in old-growth forest stands as are large live trees. In numbers, as well as in volume and weight of organic matter, they are an important structural component of natural stands (Spies and others 1988). Large logs typically persist for very long periods—up to several centuries for some species, such as Douglas-fir and western redcedar. Logs gradually decompose, undergoing a variety of physical and chemical changes. For these reasons, logs are present in a variety of decay states in most natural stands (Harmon and others 1986).

Large logs are important contributors to the distinctive compositional and functional features of old-growth stands (Harmon and others 1986). Logs represent major long-term sources of energy and nutrients as well as sites for nitrogen fixation. Logs may also provide physical stability by protecting sites from erosion and other geomorphic processes. Large woody debris is a dominant element in aquatic ecosystems associated with unmanaged Douglas-fir forests, controlling the distribution of habitats, providing substrate, and helping to retain materials within stream reaches.

Large logs provide essential habitat for many plant and animal species (see Parts V and VI, this volume). In addition to microbial and fungal species, many vascular plants use logs as habitat. A classic example is the reproduction of tree species on rotting logs (“nurse logs”), which is particularly well represented in the coastal rainforests (Harmon and Franklin 1988). Invertebrate communities are currently not well known but certainly include hundreds of species in a typical old-growth stand. And, as this volume documents, many vertebrate species use logs as habitat to a considerable extent.

Stand Structural Features

Old-growth forests also have important stand-scale structural features. Unfortunately, our emphasis on individual structures has tended to obscure the existence and importance of such stand features. We emphasize, however, that the character of old-growth forests is not reducible to a few individual structures or characteristics.

Tree size-class distributions provide a simple example of stand-scale structure. Because of the large number of small trees found in old-growth forests, average diameters and heights in old-growth stands may be similar to those in

young stands. The range of values, however, is much greater in old growth, and size-class distributions tend strongly towards much larger numbers of the smaller trees.

Multiple canopy layers or, more specifically, the continuous distribution of foliar surfaces from the top of the crown to the ground, is another stand-scale structural feature. Such canopy distributions are significant in creating greater quantities and greater diversity of animal habitat.

Understory heterogeneity is another stand-scale characteristic that is highly variable in old-growth stands. Understories in old-growth stands tend to be much patchier than in younger forest stands. This variability is partially a response to varied overstory conditions. Gaps are important structural features of old-growth stands and typically persist for long periods (Spies and others 1990). Well-developed understories of herbs, shrubs, and small trees characterize such open habitats. Heavily shaded sites (“antigaps”), also characteristic of old-growth forests, produce areas of bare litter from which green plants may be almost totally absent. Interestingly, except on dry sites, the distribution of gaps and antigaps in old-growth stands appears to be controlled primarily by the canopy density of western hemlock and other shade-tolerant codominants and not by the canopy distribution of dominant Douglas-firs.

Any consideration of old-growth forest structure must include both individual and stand structural features. Better understanding and quantification of the roles of known structural elements are needed along with basic research designed to identify additional stand-scale attributes.

Conclusions and Management Implications

Old-growth forests in the Douglas-fir region appear to provide specialized habitat for a unique array of species. These forests are also very productive in an ecological sense. Major contrasts in compositional, functional, and structural features exist between old-growth and managed young-growth stands. Differences between old-growth and unmanaged young-growth stands are less pronounced, however, because many structural features—such as large snags and logs—are carried over from the old stand to the new under natural disturbance regimes (Spies and others 1988).

Several management strategies can be used to accommodate plant and animal species associated with old-growth forests and to sustain old-growth forests as ecosystems. Retaining existing old-growth forests is, in many respects, the safest strategy. Much is still unknown about the composition, structure, and function of these ecosystems. How can we propose to recreate replicas of existing old-growth forests if we are still ignorant of many of the parts and how they are related? Furthermore, the existing old-growth forests are, at least to some degree, unique products of historical events; they are thus not completely reproducible. Any approach that emphasizes preservation of existing old growth must also include some strategy for replacing the stands that will inevitably be lost to natural catastrophes, such as fire, windstorm, and volcanic eruption.

Managing forest stands on long rotations is a second strategy for maintaining old-growth-like habitats. Natural developmental sequences (Franklin and Spies, this volume) show that old-growth conditions typically begin to emerge at 175 to 225 years (fig. 4). Silvicultural treatments could accelerate the development of old-growth structural and compositional features, such as the presence of large trees and intermediate canopy layers.

Partial cutting (sometimes referred to as partial or green-tree retention) is another approach to recreating old-growth-like forest structures in managed stands (fig. 4c). **Cuttings** of this type typically retain 10 to 40 percent of the living trees

(fig. 5), as well as snags and logs. Proposals for this type of cutting practice have been reinforced by observations of mixed-age-structure stands (see here illustrated in fig. 4b), such as Douglas-fir forests originating after the 1902 wildfires in southwestern Washington and a 1921 blowdown on the Olympic Peninsula. These naturally developed forests show that many of the structural elements of old growth can develop in less than 100 years if large structural “legacies” remain from the previous stand. Partial cutting can be used as either a substitute for or supplement to long rotations; that is, the strategies are not mutually exclusive.

Providing a low density of individual structures, such as large live trees, large snags, and large logs on clearcut areas is another strategy. This approach can be used to provide habitat for animal species that depend on specific types of structures, such as snags, but are otherwise tolerant of cutover habitats. Such approaches, which are designed to provide for a continuing supply of large snags and logs, are currently being widely applied on State and Federal forest lands (fig. 6).

Developing sound management strategies obviously requires dramatically expanded knowledge of natural forest ecosystems and how they work, including but not confined to old growth. The relationships of forest structure and function to various plant and animal species are critical and must include considerations of “lesser” organisms, such as invertebrates and fungi, as well as the vertebrates.

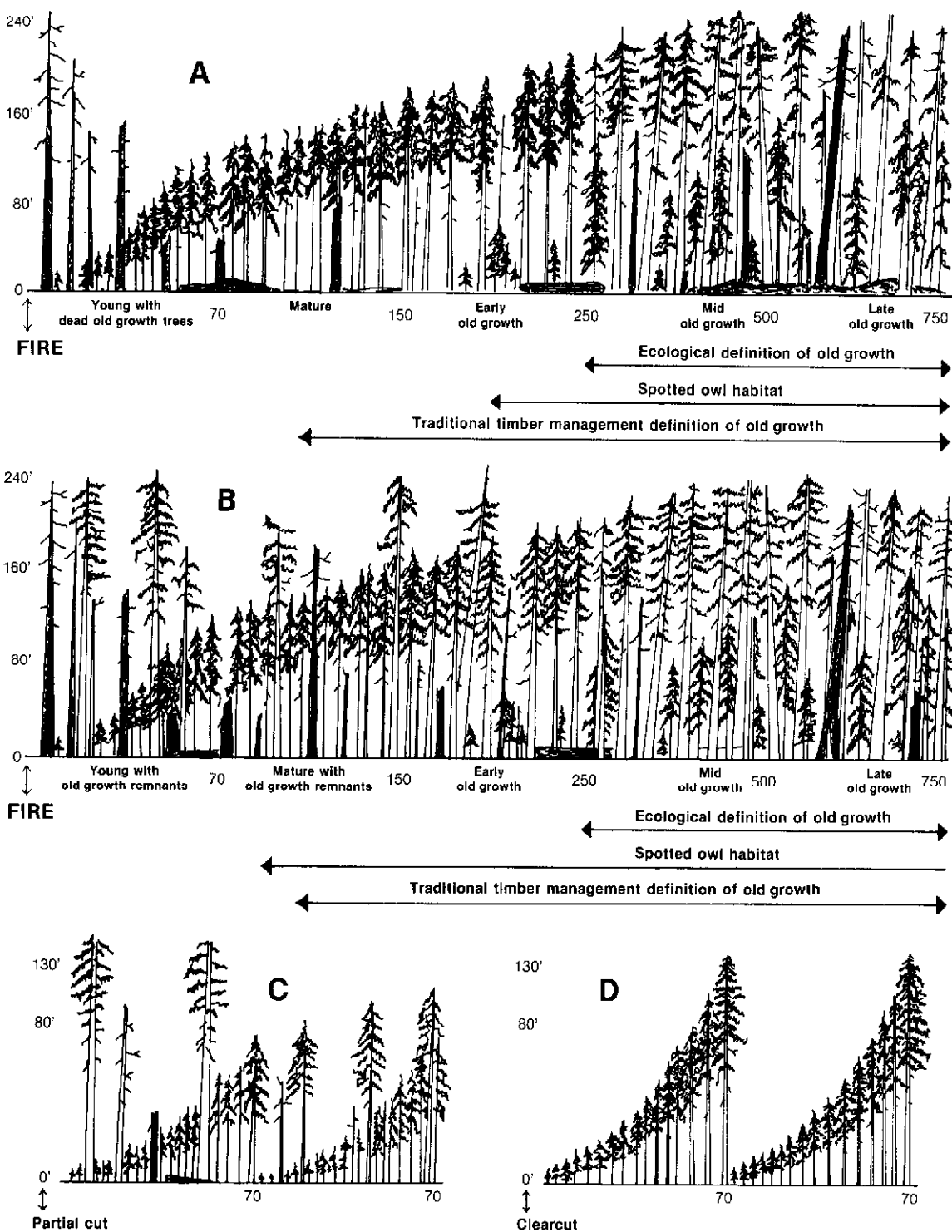


Figure 4—Structural diagrams for successional seres associated with: (A) natural succession after total destruction of an old-growth forest stand; (B) natural succession after partial destruction of an old-growth forest stand; (C) succession under a partial cutting regime to maintain two tree size- and age-classes; and (D) succession under a clearcutting regime with a single age-class. Note the similarity in structures between (B) and (C).

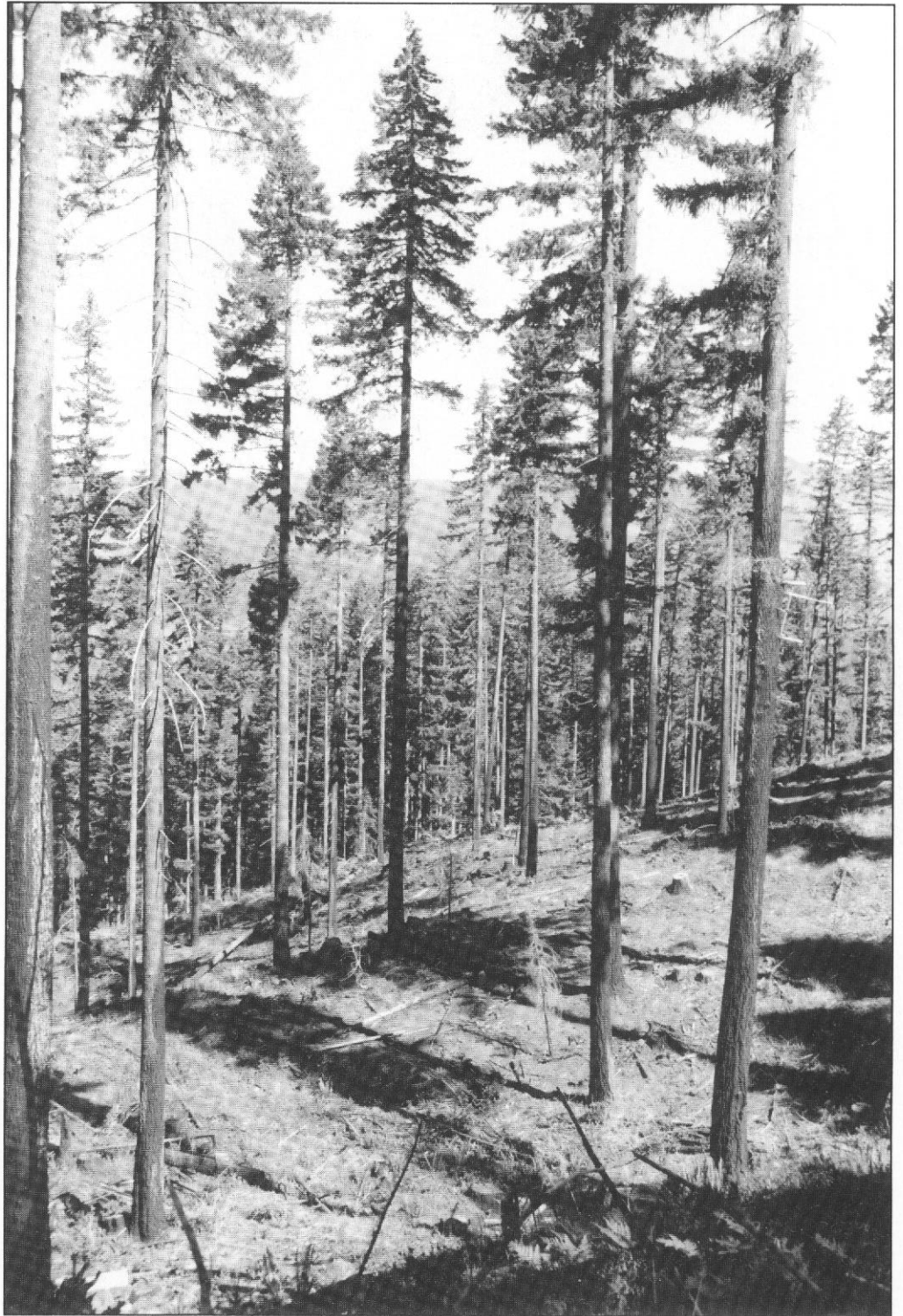


Figure 5—Partial cutting is one strategy for recreating old growth-like forest structures in shorter periods (such as 80-120 years) than would be required after clearcutting; 8 to 12 dominant mature (about 120 years) Douglas-fir trees were retained for the next rotation on this cutover (H. J. Andrews Experimental Forest, Blue River Ranger District, Willamette National Forest).



Figure 6—Retention of individual structural features—such as a few large green trees, snags, and logs—on clearcut areas, provide suitable habitat for some wildlife species; such practices are becoming common on commodity lands on northwestern National Forests (Innis Block, Blue River Ranger District, Willamette National Forest).

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