

## 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

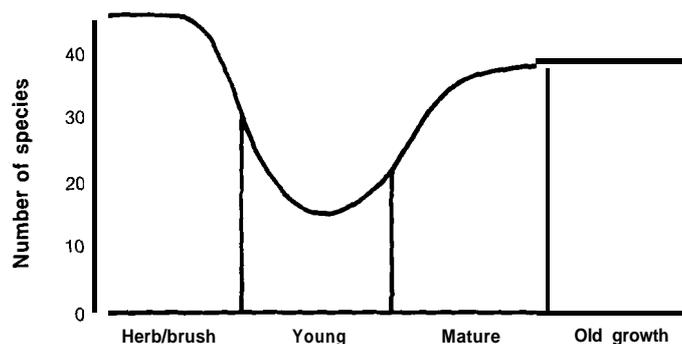


Figure 1-Generalized relationship of mammal species diversity to successional stage in Douglas-fir forests.

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 m<sup>2</sup> of leaf surface per square meter of ground surface. Young stands are typically in the

range of 6 to 8 m<sup>2</sup> (Franklin and Waring 1980). Individual old-growth trees may have 60 to 70 million needles with 4000 m<sup>2</sup> 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 m<sup>3</sup>/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 m<sup>3</sup>/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.

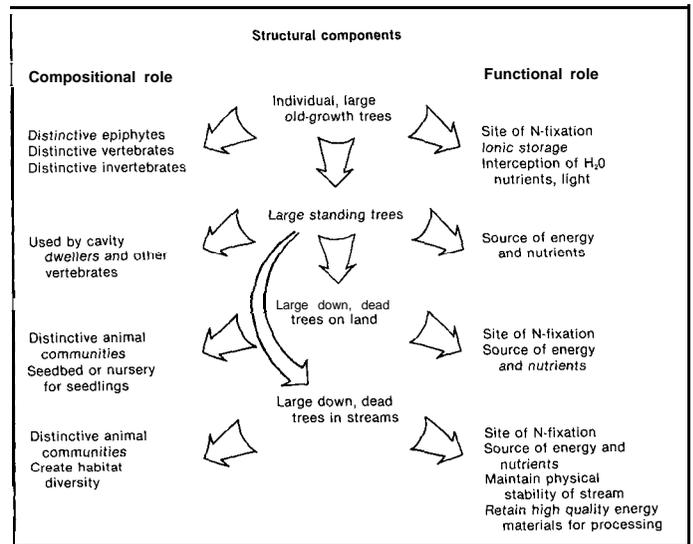


Figure 2—Relationship of some structural components of old-growth forest to distinctive habitat and ecosystem functions (from Franklin and others 1981).

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 sere illustrated in fig. 4b), such as Douglas-fir forests originating after the 1902 wild-fires 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.

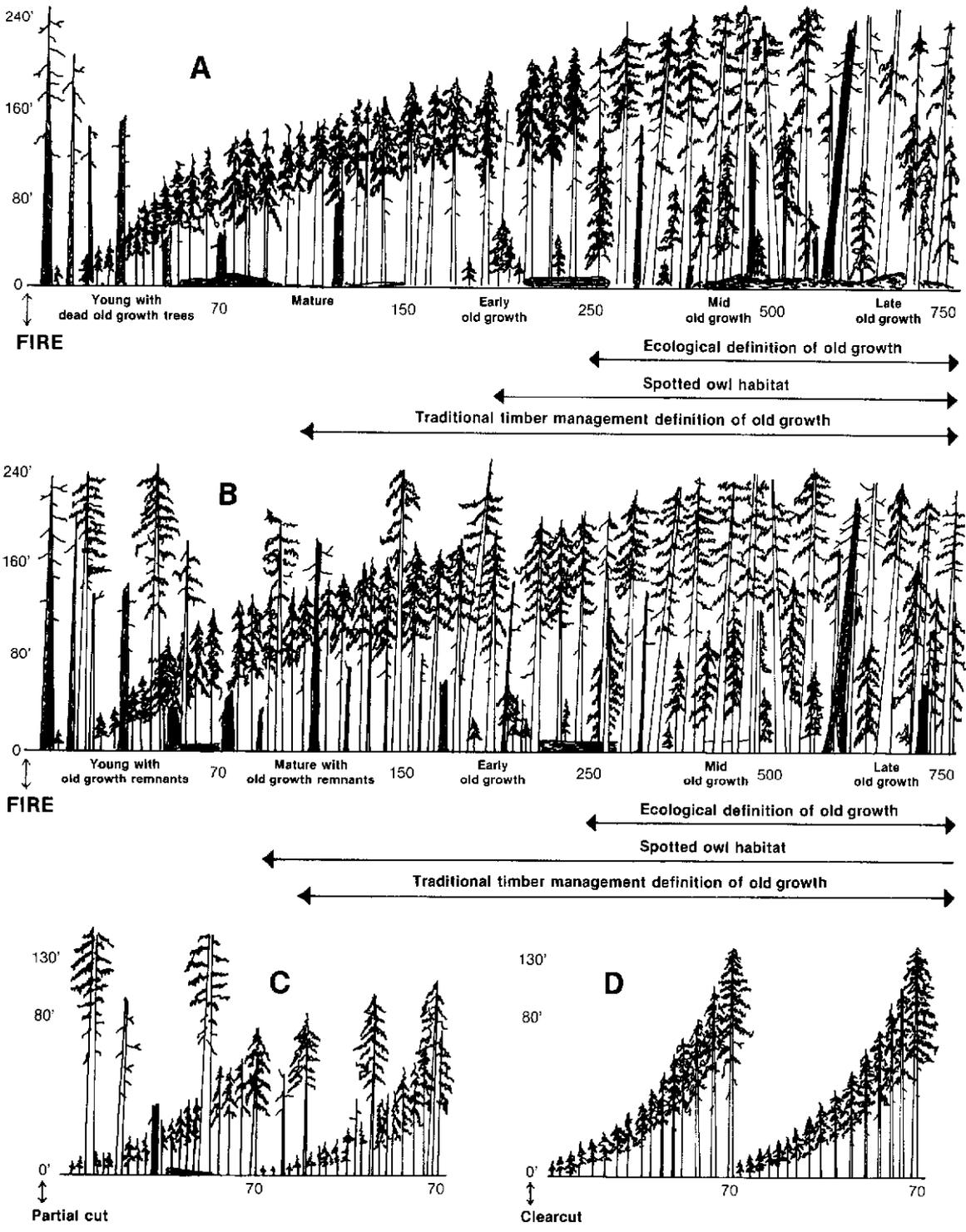


Figure 4—Structural diagrams for successional seres associated with: (A) natural succession after total destruction of an old-growth forest stand; (B) natural succession after partial destruction of an old-growth forest stand; (C) succession under a partial cutting regime to maintain two tree size- and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

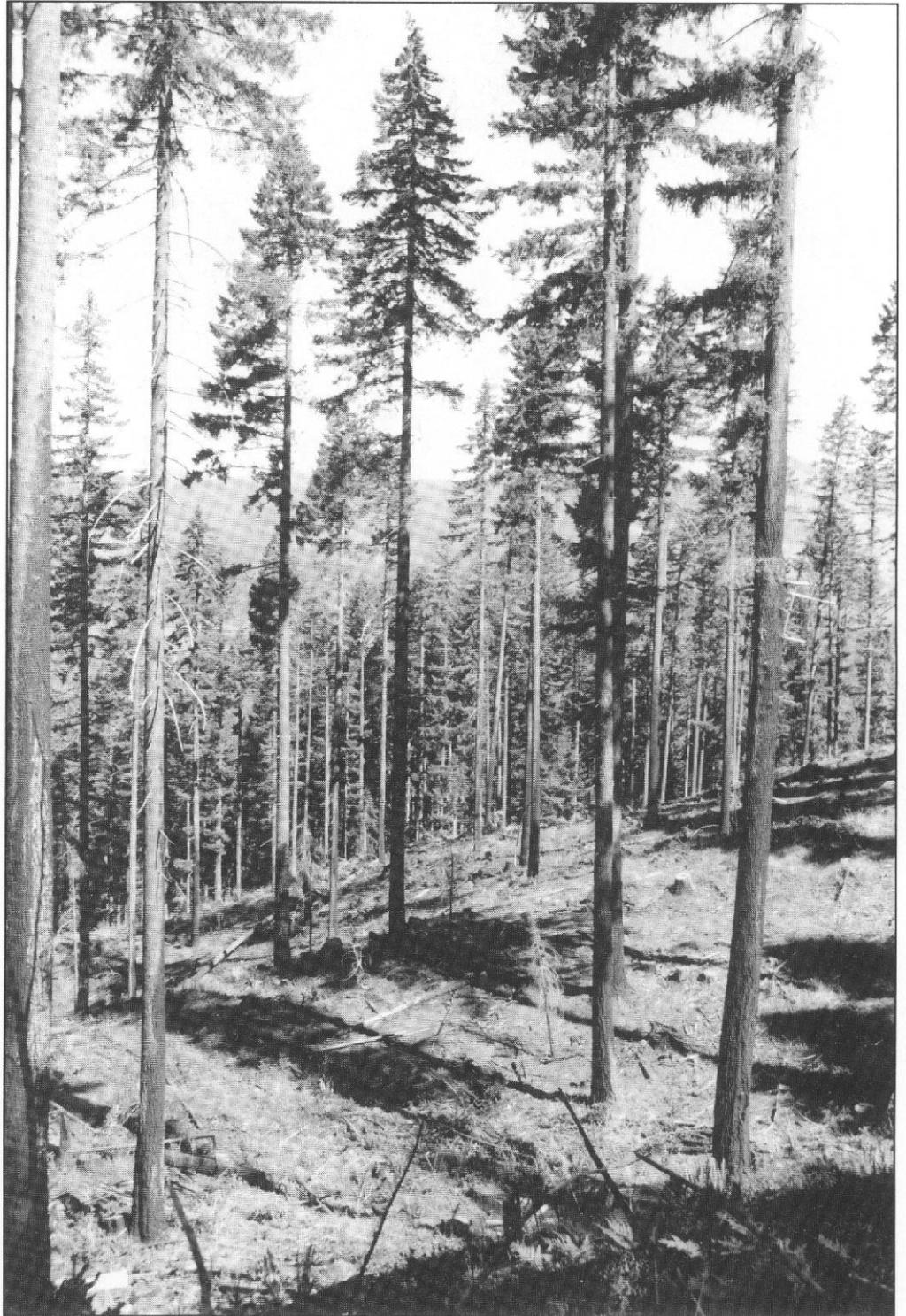


Figure 5—Partial cutting is one strategy for recreating old growth-like forest structures in shorter periods (such as 80-120 years) than would be required after clearcutting; 8 to 12 dominant mature (about 120 years) Douglas-fir trees were retained for the next rotation on this cutover (H. J. Andrews 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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Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

# Annual Changes in Seasonal Production of Hypogeous Sporocarps in Oregon Douglas-Fir Forests

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## Abstract

Sporocarps of hypogeous ectomycorrhizal fungi were harvested from 10 Douglas-fir stands representing a variety of natural habitats. Results are presented in a landscape context by assuming that the reported sporocarp production is representative of Western Hemlock Zone forests in the central western Cascade Range of Oregon. Over all stands, sporocarps were harvested from 5400 m<sup>2</sup> and yielded a total dry standing biomass equivalent to 1.3 kg per ha. The maximum single-stand sample biomass equaled 9.9 kg per ha. Forty-seven species of hypogeous fungi were recorded. *Elaphomyces granulatus*, *Gautieria monticola*, *Hysterangium coriaceum*, *Leucogaster rubescens*, and *Rhizopogon parksii* accounted for 73 percent of the biomass.

In contrast to epigeous species in the study area, hypogeous sporocarp production was higher in spring than in fall. Individual fungal species showed strong seasonal trends; most had spring production peaks. Year-to-year variation in relative biomass for individual species was greater in spring than in

fall. The major species in this study were also major species in studies from young Douglasfir stands in the Oregon Coast Range. *Gautieria monticola*, in particular, seems to be a widespread dominant species in Western Hemlock Zone forests of western Oregon.

## Introduction

Cooke (1972) defines mycocoenologists as "mycologists with ecological orientation, [or] ecologists with mycological interests." Arnolds (1981) considers a mycocoenological approach to ecological research as one that usually uses sample plots (quadrats) to inventory macrofungi in stands of well-defined plant communities or selected habitats. The goals of such research are to describe the fungal composition of a particular plant community and to draw conclusions about relationships between fungi and vegetation on a quantitative and qualitative basis.

Vegetation has long been used to assess site quality and to help identify the importance of various environmental factors (Cajander 1949). In the Pacific Northwest, quantification and classification of vegetation in combination with autecological observations has furthered development of the plant association and habitat type concepts (Daubenmire 1968, Hemstrom and others 1987, Zobel and others 1976). The prevailing regional system of plant community classification in the

Pacific Northwest greatly facilitated the execution of mycoecological research by freeing the investigator of the need to conduct elaborate vegetation studies to classify sample stands. This study was part of a regional characterization of Douglas-fir forests from which Spies and others (1988) provided the habitat classification.

Studies of the community ecology of macrofungi have lagged far behind those of vascular plants. Several daunting challenges face the would-be mycocoenologist. Arnolds (1981) provides a summary of some of these difficulties: fungal species concepts are often poorly understood and defined; collections are difficult to identify morphologically and often require considerable research to reach independent taxonomic decisions; research is limited to the study of sporocarps (fruiting bodies), which are strongly seasonal (Hueck 1953), are subject to yearly variation caused by variable weather patterns, and exhibit varying, largely unknown, rates of decay and predation; sporocarp production is not necessarily related to the abundance or activity of the mycelial colony; and, autecological research is lacking both in the field, where it is hampered by the concealed nature of the fungal colonies and in the laboratory where it is constrained by the investigators' inability to relate the conclusions to field situations with confidence.

Fungi that produce hypogeous (belowground) sporocarps (broadly referred to as truffles) pose additional challenges. The sporocarps are not only hidden from view, but are also often preferentially sought and consumed by small animals (Ure and Maser 1982). Although quantitative community studies of epigeous (fruiting above the ground) fungi have been reported since at least 1933 (Haas), Fogel (1976) was the first to provide a quantitative assessment of hypogeous sporocarp production. Most of the fungal species producing hypogeous sporocarps are thought to be ectomycorrhizal (fungi which develop mutually beneficial associations in the exterior layers of the roots of certain plants) (Castellano and others 1989; Trappe 1962, 1971). Mycorrhizal fungi act as extensions of the root system in forest trees and are thus important to their nutrition (Trappe and Fogel 1978).

Currently, the only practical way to compare the relative functional importance of species of ectomycorrhizal fungi in an ecosystem is by estimating sporocarp production. Potential functional roles of hypogeous species range from essential symbiosis with the roots of over-story trees (Harley and Smith 1983) to provision of sporocarps as food for animals (Vogel and Trappe 1978).

Several recent studies focused on sporocarp production by hypogeous fungal species in the Coast Range of western Oregon. Fogel (1976) was the first to quantitatively analyze

the seasonal distribution of hypogeous sporocarps; he used sporocarp dry weight and number to calculate mid-dates of fruiting for individual species and populations.

In a 13-month study including the end of a severe winter drought, Fogel and Hunt (1979) observed a strong fall peak in total sporocarp dry weight. Fogel (1981) reviews techniques for quantifying hypogeous sporocarps and correlates sporocarp production with temperature and moisture. Hunt and Trappe (1987) point out that documenting all species of hypogeous fungi in a forest stand requires longterm collecting over several years. Underestimation of species richness due to small stand samples and infrequent fruiting of some species was noted by Hunt and Trappe (1987). After 32 months of collection with a total sample area of 1536 m<sup>2</sup>, their species-area curve still had not stabilized.

The cited studies were confined to single, similar, second-growth Douglas-fir stands on Marys Peak in the Oregon Coast Range, which had all developed over 35 to 65 years after clearcut logging and burning. An obvious need existed to characterize the occurrence of hypogeous sporocarps in a landscape context from a variety of natural habitats over a wider forest area.

This research aims at broadening the data on year-to-year changes in the seasonal distribution of sporocarp production and reports the sporocarp abundance of major species (Hering 1966) of hypogeous fungi found in 10 forest stands in the H. J. Andrews Experimental Forest (Oregon Cascade Range physiographic province). Standing crop sporocarp biomass was measured within five Douglas-fir forest habitats covering a range of moisture- and age-classes. To obtain a representative sample of the major species and to document the differences in sporocarp production that are largely induced by year-to-year changes in weather patterns, the study spanned a 4-year period. Seasonal variation in fruiting pattern was anticipated through intensive spring and fall sampling. The following specific objectives were addressed: identification of the major fungal species that produce hypogeous sporocarps in Douglas-fir stands typical of the central Oregon Cascades; characterization of the seasonal fruiting aspect as determined by the major species; and determination of year-to-year changes in the seasonal distribution of each major species as measured by sporocarp biomass.

## Materials and Methods

### Study Area

The H. J. Andrews Experimental Forest occupies the 6400-ha drainage of Lookout Creek, a tributary of the McKenzie River (see frontispiece). Elevations range from 420 to 1630 m. The area is typical of the western slopes of the central Cascade Range in Oregon. The experimental forest

has been administered by the USDA Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948.

A cool-summer Mediterranean climate prevails in the study area. Average annual precipitation ranges from about 2300 to 2800 mm, depending on topography. About 90 percent of the precipitation occurs from October through April; summers are dry. Above 900-m elevation, winter snowpacks accumulate to a depth of 1 m or more. Temperatures are moderate and range from -2 (mean January minima) to 28 °C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Bierlmaier and McKee 1989, Franklin and Dymess 1971).

Inceptosols dominate the three general soil types that are characteristic of the experimental forest (Bemtsen and Rothacher 1959, Brown and Parsons 1973, Dymess and others 1974, Franklin and Dymess 1973). Steeper slopes and ridgetops often support a residual Brown Podzolic gravelly clay loam formed from andesite or basalt. Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams associated with breccia and tuff parent material are commonly found on midslopes. Gentle slopes and benches are often occupied by a colluvial clay loam.

The study area lies generally within the Western Hemlock Zone of Franklin and Dymess (1973). Studies of forest communities within the Western Hemlock Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Zobel and others 1976). Characteristic understory vascular plant species are used to describe the community types. For example, abundant sword fern and Oregon oxalis typify moist sites. Mesic sites may be occupied by Oregon grape and Pacific rhododendron. Towards the dry end of the scale, salal increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities of the Douglas-fir series. In these communities, Douglas-fir is often considered climax and oceanspray is an important shrub (Hemstrom and others 1987). A temperature gradient reflecting elevation is also noted (Zobel and others 1976). The coolest extreme is represented by the Western Hemlock-Pacific Silver Fir/Twinflower association, transitional to associations in the Pacific Silver Fir Zone.

### Sampling

Ten Douglas-fir forest stands were selected for sampling by age and moisture status. Age-classes were <80, 80 to 199, and 2200 years of age and are referred to in this paper, respectively, as young, mature, and old-growth. Relative moisture-classes prevailing at these sites were identified by generalized vascular plant habitat or community types by Spies and others (1988).

Five habitat combinations were selected (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young); two stands of each were sampled. Each stand, occupying about 5 ha of relatively homogeneous forest, represented a subset of typical stands originally located by other researchers as part of a regional forest characterization (Spies and others 1988). Stand locations (see frontispiece) and selected descriptive characteristics of each stand (table 1) are presented.

Stands were sampled in each season over 6 to 7 weeks. In spring, stands on lower elevation south slopes were sampled first, those on higher elevation north slopes last. We thereby condensed the sample period relative to temperature and moisture conditions that strongly influence fruiting. The fall sampling strategy was reversed with stands on higher, northerly slopes sampled first. Field work was initiated in the spring of 1983 and continued through spring of 1986.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps because fruiting differs so much by species and abundance in time and space. Additionally, Fogel (1976, 1981) and States (1985) report the clustered distribution of fruit bodies. Accordingly, well-distributed small plots were used in the conduct of this study.

For each stand sample, sporocarps were harvested from 25 circular 4-m<sup>2</sup> plots for a total sample area of 100 m<sup>2</sup>. Plots were placed systematically about every 25 m along three transects running parallel to the slope contour and spaced about 75 m apart. New transects were established for each stand sample; no plots were resampled. In western Oregon conifer forests, most hypogeous sporocarps are produced at or above the mineralorganic soil interface (M. Castellano, G. Hunt, D. Luoma, J. Trappe, pers. obs.). In each plot, the forest floor was raked back to a 5- to 10-cm depth, thereby exposing sporocarps in the upper soil layers. The number of sporocarps from each collection in a plot was recorded. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain <15 percent relative humidity, and weighed to the nearest 0.01 g to determine biomass. Major species are those with 25 percent of the total biomass in the study (Hering 1966).

The terms "dominant" and "subdominant" within categories refers to sporocarp biomass as an indicator of a species' importance relative to other species. Cooke (1955) measured the dominance of epigeous sporocarp by estimating fruiting body volume, and concluded his measure had "physiognomic rather than competitive significance." Cain and Castro (1959) note that the term "dominance" is applied to different phenomena but argue against restrictive meanings because the

Table 1—Selected characteristics by habitat of 10 Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon

Habitat <sup>a</sup>	Stand (#)	Age <sup>b</sup> (yr)	Basal area <sup>b</sup> (m <sup>2</sup> /ha)	Stem density <sup>b</sup> (#/ha)	Coarse soil <sup>b, c</sup> (% vol.)	Median elevation (m)	Aspect	Slope <sup>d</sup> (deg.)
WOG	2	450	81	280	47	550	NNE	30-35
	3	450	101	526	19	800	N	0-35
MOG	15	450	146	392	8	800	SW	0-15
	17	450	108	670	13	770	SSE	10-30
DOG	25	200	49	443	55	550	W	30-35
	29	200	47	463	52	700	SW	30-40
MM	36	130	71	408	33	1160	W	15-30
	90	84	38	433	25	930	SSW	10-30
MY	48	69	58	1410	48	1050	NW	20-30
	86	79	52	1535	59	930	NW	20-30

<sup>a</sup> WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

<sup>b</sup> Unpublished data from T. Spies (see Spies and others 1988).

<sup>c</sup> Fragments >2 mm.

<sup>d</sup> Wet old-growth stand 3 occupied a series of slumps causing high slope variability.

differences are clear enough in context. Dominance (also co- and subdominance) of a species indicates predominance as expressed by some measure that may or may not reflect ecological influence in the dynamics of the community.

The term "stand sample" refers to the total 100-m<sup>2</sup> collection area (from 25 plots) for a given stand at a given seasonal harvest in a given year. This report uses data collected from 54 stand samples over 4 years, 28 stand samples in spring and 26 in fall. Seasons were defined by equinox and solstice calendar dates. Twelve stand samples were taken in wet old growth, 10 in mesic old growth, 12 in dry old growth, 8 in mesic mature, and 12 in mesic young habitats.

### Analysis

Because of the unequal number of stand samples in the various seasonal categories, sporocarp biomass values were standardized to equivalent biomass, expressed in grams per hectare, and used to report seasonal results and relative values. The total biomass for a species in a category was divided by the appropriate fraction of a hectare sampled in that category to obtain equivalent biomass. Relative annual biomass of each species by season was calculated as a percentage of a species' total seasonal biomass (equivalent g/ha within each year).

## Results

### Total sporocarp production

Sporocarps were harvested from 5400 m<sup>2</sup> and yielded a dry weight biomass of 697 g, equivalent to a standing biomass of 1.3 kg per ha. The maximum single-stand-sample total biomass was 99 g dry weight or 9.9 kg per ha. Forty-seven

species of hypogeous fungi were recorded during the study. Fourteen species accounted for 94 percent of the total biomass. Five major species—*Elaphomyces granulatus* Fr., *Gautieria monticola* Harkn., *Hysterangium coriaceum* Hesse, *Leucogaster rubescens* Zeller & Dodge, and *Rhizopogon parksii* Smith—accounted for 73 percent of the biomass.

### Year-to-year variation

Spring fruiting was dominated by a different fungus each year: *Hysterangium coriaceum* in year one, *Gautieria monticola* in year two, and *Elaphomyces granulatus* in year three (table 2). Eighty percent of the spring biomass of *Elaphomyces granulatus* in year three was attributable to one extreme stand sample of 99 g. This value represents a particularly interesting outlier because it was obtained from a single 4-m<sup>2</sup> plot containing 54 sporocarps. If a more "reasonable" (for this sample size, 1000 m<sup>2</sup>) stand-sample value of 35 g for *E. granulatus* were assumed, then *Gautieria* would have been the spring biomass dominant in year three also. *Elaphomyces granulatus* was a subdominant in year two. *Rhizopogon parksii* was not found in spring.

Fall sporocarp production was dominated by *Rhizopogon parksii* with >50 percent of the total biomass (table 2) in all years. In each year, one stand sample contributed a large proportion of *R. parksii*'s fall biomass (29, 36, and 70 percent in years 1, 2, and 3, respectively). *Elaphomyces granulatus* was a fall subdominant in years one and two. *Leucogaster rubescens* was a fall subdominant in year three. *Hysterangium coriaceum* was not found in fall. Year one, with the least biomass, had relatively equal distribution of fall and spring biomass (table 2).

Table 2—Annual sporocarp biomass (equivalent g per ha) of major species by season in a 5400-m<sup>2</sup> total sample from 10 Douglas-fir stands, H.J. Andrews Experimental Forest, Oregon

Species	YEAR 1		YEAR 2		YEAR 3	
	Spring (n = 8)	Fall (n = 8)	Spring (n = 10) <sup>a</sup>	Fall (n = 9)	Spring (n = 10)	Fall (n = 9)
<i>Elaphomyces granulatus</i>	65	109	231	82	1234	87
<i>Gautieria monticola</i>	4	30	790	19	525	19
<i>Hysterangium coriaceum</i>	293	—	142	—	80	—
<i>Leucogaster rubescens</i>	10	21	84	43	13	131
<i>Rhizopogon parksii</i>	—	170	—	672	—	491
Seasonal g per ha	372	330	1247	917	1852	728
Yearly g per ha	351		1091		1319	

<sup>a</sup> 3 spring stand samples from a 4th year were included.

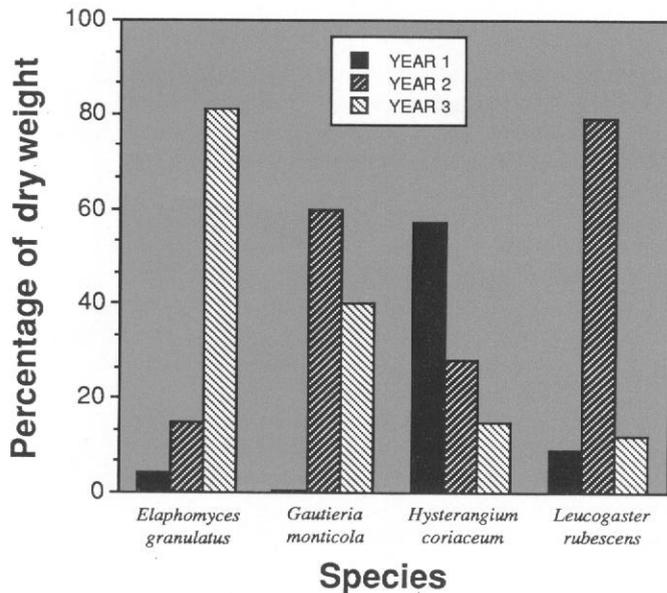


Figure 1—Major species year-to-year variation in spring relative sporocarp biomass in a 2800 m<sup>2</sup> total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

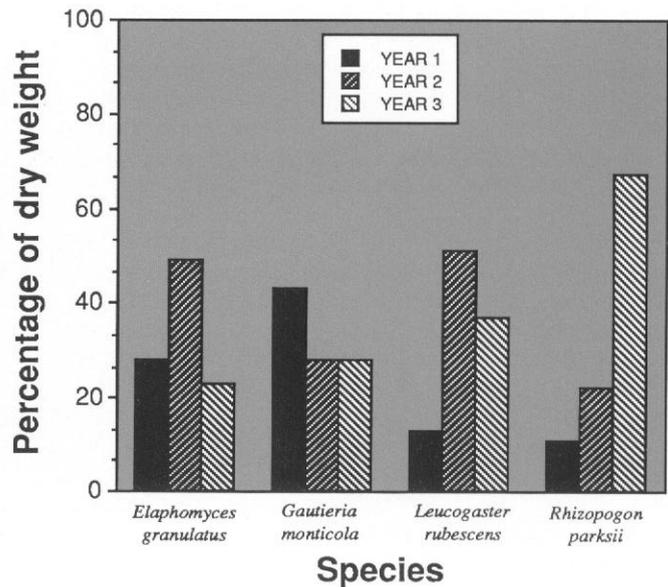


Figure 2—Major species year-to-year variation in fall relative sporocarp biomass in a 2600 m<sup>2</sup> total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The yearly proportion of each species seasonal sporocarp biomass is shown (figs. 1, 2). Variation in relative biomass from year to year for individual species was greater in spring than in fall. Three spring species had one year with >60 percent of their total seasonal biomass. In fall, only *Rhizopogon parksii* had such a strong single-year dominance.

## Discussion

This paper seeks to put the results in a landscape perspective by generalizing seasonal sporocarp production as being representative of Western Hemlock Zone forests in the central Cascade Range of Oregon. The most extensive previous

studies of hypogeous sporocarp production were confined to single stands (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). Their major goals were to quantitatively estimate sporocarp production, to determine phenology of production, and to characterize the hypogeous fungal-species community composition.

Fogel (1976) and Hunt and Trappe (1987) show that sporocarp biomass production of single species differs from year to year. In a 3-year study with small (50-m<sup>2</sup>) monthly samples, Fogel (1976) had four major species in common with this study. The species and biomass ranges of the annual

standing crop were as follows: *Elaphomyces granulatus*, 0 to 90 g per ha; *Gautieria monticola*, 13 to 432 g per ha; *Hysterangium coriaceum* (as *H. separabile* Zeller), 294 to 572 g per ha; and *Rhizopogon parksii*, 89 to 252 g per ha. Other major species of Fogel's (1976) study include: *Hymenogaster parksii* Zeller & Dodge, 76 to 435 g per ha; *Hysterangium setchellii* Fischer (as *H. crassum* [Tul. & Tul.] Fischer), 517 to 1206 g per ha; *Truncocolumella citrina* Zeller, 30 to 2336 g per ha; and *Tuber* spp., 0 to 380 g per ha. *Hysterangium setchellii* and *Truncocolumella citrina* were moderately important, while *Hymenogaster parksii* and *Tuber* spp. were minor species in Luoma (1988).

Fogel (1976) provides seasonal information on *Hysterangium coriaceum* by reporting fruiting period (monthly range) and mean calendar day of fruiting with number of days standard deviation. *Hysterangium* taxonomy was not well known at the time of his study so that *H. separabile* is the species reported and may not entirely equate with what is now accepted as *H. coriaceum*. Fogel (1976) made collections of *H. separabile* throughout the year and lists it as an "opportunistic" species. The mean fruiting date, however, in each of 3 years was in April with a standard deviation of 11 days—the smallest of the eight species reported. Fogel (1976) lists *Rhizopogon parksii* as a characteristic fall species.

Data from Dinner Creek, Oregon (Fogel and Hunt 1979, Hunt and Trappe 1987), gathered over 2 years, revealed five major species. *Three-Gautieria monticola*, 8 to 85 g per ha; *Leucogaster rubescens*, 316 to 338 g per ha; and *Rhizopogon parksii*, 116 to 463 g per ha—were also major species in the current study. *Two-Leucophleps magnata* Harkn., 21 to 189 g per ha; and *Truncocolumella citrina*, 0 to 749 g per ha—had moderate importance in Luoma (1988).

Hunt and Trappe (1987) sampled sporocarp production in a 1.5-ha stand for 21 months. Monthly production was estimated from twelve 4-m<sup>2</sup> plots. Major species in common with the present study were *Gautieria monticola*, 769 to 1527 g per ha and *Hysterangium coriaceum*, 106 to 204 g per ha. Other major species were *Hysterangium setchellii*, 746 to 842 g per ha and *Melanogaster* sp. nov., 108 to 225 g per ha.

Hunt and Trappe (1987) also report fruiting middate mean, and standard deviation for selected species. Over 2 years, *Hysterangium coriaceum* was collected from February to December but its middate was in April with a standard deviation of 8 days. *Rhizopogon parksii* was found only from September to December.

In this study, total spring equivalent biomass ranged from 0.4 to 1.8 kg per ha. These values were consistently greater than or equal to the fall range of 0.3 to 0.9 kg per ha (table 2) and contrast with Fogel and Hunt's (1979) marked fall biomass peak in the 1st year of sampling at Dinner Creek. Hunt and Trappe (1987) found comparable biomass between spring and fall during the 2d year of sampling at Dinner Creek. Fogel (1976) reports that spring and fall biomass were comparable but data in Hunt and Trappe (1987) show that Fogel had a marked spring biomass peak in each of 3 years. The single-sample maximum biomass of 9.9 kg per ha reported here supplants the unpublished values (1.4, 1.7 kg per ha) of Luoma and Hunt cited in table 6 of Hunt and Trappe (1987).

Total sporocarp biomass was substantially less in both spring and fall of year one compared to the other years. The low spring values may have been influenced by record high temperatures in May 1983. A 14-day period with only a trace of rain encompassed 12 days in which high temperatures reached more than 25 °C (mean monthly high = 18.7 °C) and included the highest May temperature (40°C) recorded at the H. J. Andrews station. Low sporocarp production in fall was coincidental with well below average September and October precipitation in 1983 (Bierlmaier and McKee 1989; F. Bierlmaier, unpubl. data).

Year one had the maximum production for one species in spring and another species in fall (figs. 1.2). Year two showed highest relative sporocarp biomass for two species in spring and two species in fall. One species had maximum spring biomass and one species had maximum fall biomass in year three. *Hysterangium coriaceum* was not found in the fall and *Rhizopogon parksii* was not found in spring; otherwise, no strong trends were in these data. In this data set, a single year with maximum relative biomass of two species occurring in the same season is the nominal distribution. Year two had both such species maximums for spring and fall.

Weather patterns (particularly the timing and duration of drought periods) likely account for much of the year-to-year seasonal variation observed in this and other studies (Fogel 1981). Although it is ecologically meaningful for a given year, such variation detracts from attempts to characterize general trends in importance or dominance (as measured by sporocarp biomass) by season and habitat. Such a characterization will be presented elsewhere in the scientific literature (Luoma and others, in press).

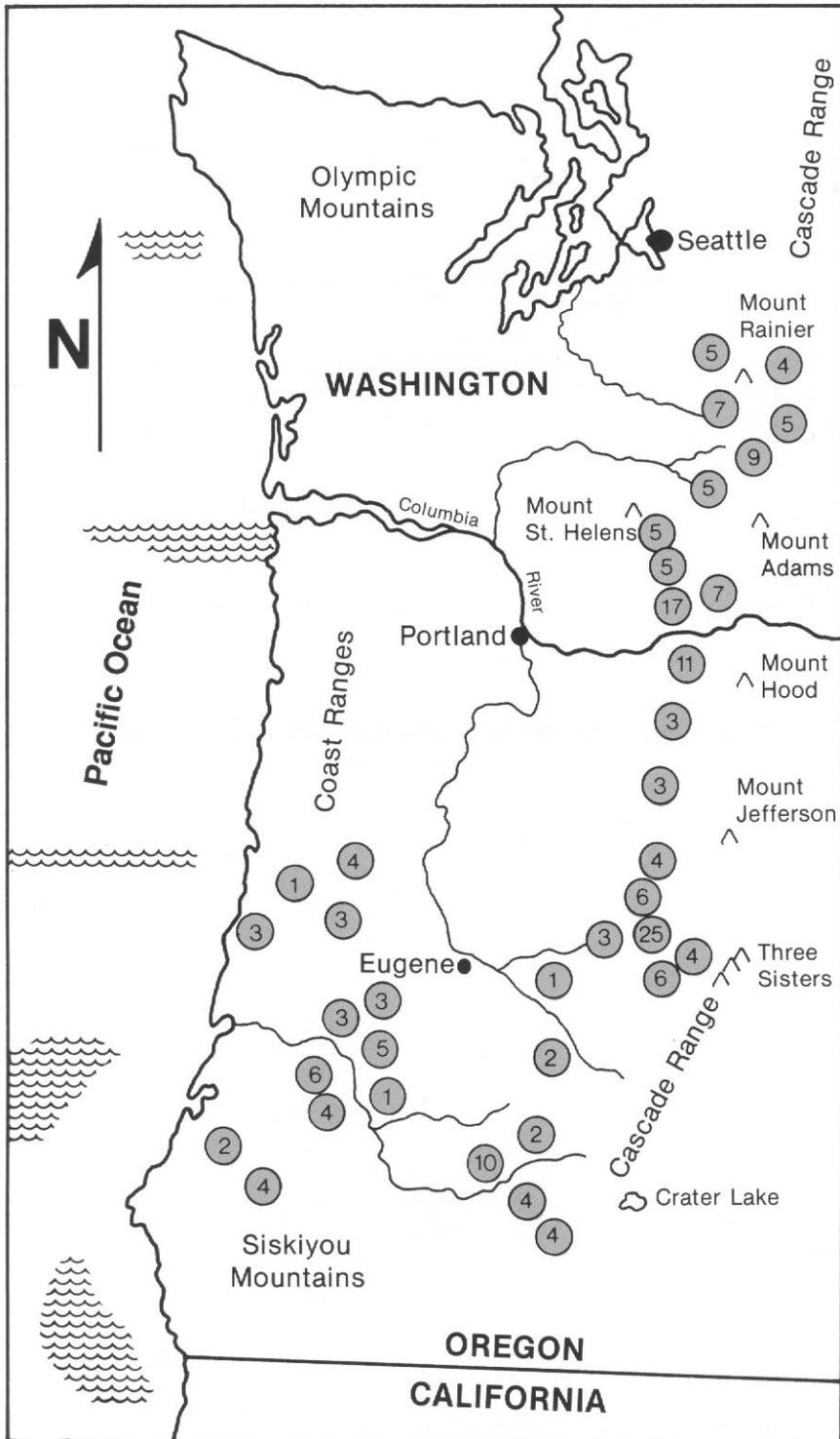
## Conclusions

Relatively few species (five) of hypogeous fungi accounted for most of the total biomass (73 percent). Many species showed strong seasonal variation in relative biomass production. For the major species, spring had greater year-to-year variation in sporocarp production and higher total biomass production than did fall. The range of standing biomass values for the species reported in this study is similar to the values reported for hypogeous sporocarps by other researchers. All of the major species in this study were also major species in one or more of the studies from young Douglas-fir stands in the Oregon Coast Range (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). In Western Hemlock Zone forests of western Oregon, *Gautieria monticola* seems to be a widespread sporocarp dominant, *Hysterangium coriaceum* a predominantly spring species, and *Rhizopogon parksii* characterizes the fall fruiting aspect. In contrast to epigeous mycorrhizal fungi, hypogeous sporocarp production is generally higher in spring than in fall (Fogel 1976; Hunt, unpubl. data).

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Location of stands in western Oregon and Washington. Numbers indicate total number of stands in an area.

# The Structure of Natural Young, Mature, and Old-Growth Douglas-Fir Forests in Oregon and Washington

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## Abstract

Structural characteristics of forest overstories, understories, and forest floor and coarse woody litter accumulations were related to stand age, geography, and relative site moisture in 196 Douglas-fir stands in western Oregon and Washington. Stands ranged in age from 40 to 900 years and typically originated after wildfire. A series of multivariate analyses was used to identify structural attributes that distinguished old-growth (>195 years old) from mature (80-195 years old) and young (40-80 years old) age-classes. Separate analyses of four attribute sets—overstory, stand condition (degree of damage and disease), understory vegetation, and forest floor and coarse woody litter indicated that the age-classes differed in numerous attributes. Discriminant models that used overstory characteristics, such as tree density, density of large Douglas-firs, and variation in tree diameter, and models combining variables from the four different attribute sets were most successful in distinguishing the age-classes. Age-classes represent portions of a continuous gradient of structural

variation associated with age, based on ordinations with canonical discriminant analysis. Old-growth stands from different geographic provinces and relative site moisture-classes differ considerably in structure. Much of this variation in old-growth structure was associated with variation in densities of shade-tolerant trees and characteristics of the understory vegetation. Variation in old-growth-forest structure strongly suggests that low to moderate disturbance during the life of the stands has had an important influence on stand structure. The study provides a basis for defining and taking inventory of old-growth conditions as well as for managing the natural diversity of old-growth and earlier successional Douglas-fir forests in western Oregon and Washington.

## Introduction

Douglas-fir forms dense, long-lived coniferous forests that dominate the mountainous landscapes of western Oregon and Washington. The structure and habitat quality of these forests varies greatly as a consequence of forest succession, disturbance, and plant community and environmental factors. The loss of the habitat structure associated with natural and old-growth Douglas-fir forests is a matter of intense public debate. The range of variability in the ecological structure of these forests is becoming more and more limited as the majority of forest lands are committed to short rotations for wood products. Information about natural Douglas-fir forest structure, its variability, and the processes that determine it are needed to identify wildlife habitat relationships, to

inventory critical habitat conditions, and to provide management targets for silvicultural manipulations, habitat reserve areas, and the maintenance of biological diversity.

Little quantitative information has been available on variation in natural Douglas-fir forests over a wide range of ages. Franklin and others (1981) describe the general ecological characteristics of old-growth Douglas-fir forests. They identify large live trees, large snags, and large logs as major distinctive features of these old ecosystems. Juday (1976) examines the species composition and some structural attributes in old-growth forests in the Oregon Coast Range. Alaback (1984) compares the structure of old-growth and second-growth western hemlock-Sitka spruce forests in southeastern Alaska. Most quantitative studies in Douglas-fir forests have focused on woody-debris components (Agee and Huff 1987, Graham and Cromack 1982, Sollins 1982, Spies and others 1988) or live tree components (Grier and Logan 1977; Franklin and DeBell 1988; Spies and others, unpubl. manuscript) in detailed studies of relatively few stands.

The major objectives of this study were to identify distinctive attributes and contrast the ecological structures of old-growth, mature, and young Douglas-fir forests; and to contrast the old-growth forest structure of different physiographic provinces and relative site moisture-classes in western Oregon and Washington. Several general questions were addressed: Are overstory, understory, and debris components equally distinctive among age-classes? Do different structural components change at the same rate and in the same manner with stand development and succession? How similar is old-growth forest structure among site moisture-classes from different physiographic provinces?

## Study Area

Douglas-fir-dominated forests were studied in Washington and Oregon in three physiographic provinces: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Coast Ranges of Oregon (Franklin and Dymess 1973). These provinces are characterized by steep, deeply dissected terrain with well-developed soil. Parent materials are Tertiary basalts and andesites in the Cascade Range, and early Tertiary sedimentary rocks in the Coast Range. The climate is wet in winter and dry in summer. Annual precipitation is heavy, ranging from 800 to over 3000 mm. Highest amounts of precipitation occur near the upper western slopes of the Coast Range and in the Cascade Range in Washington and northern Oregon (Franklin and Dymess 1973). Lowest precipitation occurs on the eastern slopes of the Coast Range and in the southern Oregon Cascades.

The study area encompasses two major vegetation zones: the Western Hemlock Zone and the lower elevational portion of the Pacific Silver Fir Zone (Franklin and Dymess 1973). Western hemlock and Pacific silver fir are the climax species on most sites in these zones; on dry sites, Douglas-fir may be climax. In southern Oregon, the northern margin of the Mixed Conifer Zone was sampled. In the Coast Range, the eastern margin of the Sitka Spruce Zone was sampled.

Most Douglas-fir stands in the region originated after catastrophic wildfire (Franklin and Hemstrom 1981); see Franklin and Dymess (1973) for a generalized, natural successional sequence. Young stands originating from wildfires are typically dominated by Douglas-fir, although western hemlock or red alder may dominate in some areas. By 200 years, many stands exhibit old-growth characteristics (Franklin and others 1981, Spies and Franklin 1988), such as codominance of western hemlock in the overstory, diverse vertical distribution of foliage, and large accumulations of woody debris (Spies and others 1988). True climax forests are rare because pioneer Douglas-fir can persist in stands for over 1000 years (Franklin and DeBell 1988; Franklin and others 1988; Spies and others, unpubl. manuscript), and wildfires occur more frequently than 1000 years on most sites.

## Methods

### General Design

A total of 196 Douglas-fir stands in Washington and Oregon representing different ages (40 to 900 years) and site conditions were sampled during 1983 and 1984 (see frontispiece). All stands originated after wildfires, which killed all or nearly all the overstory trees. We sampled along two gradients: a chronosequence of Douglas-fir stands on sites with moderate moisture, and a full range of site-moisture conditions for old-growth Douglas-fir stands (>200 years old). Resources were not available to sample extremes of site moisture for stands <200 years old. Consequently, the results of the Chronosequence analyses are based only on moderate or mesic sites (from young through old growth), and site-moisture analyses are based only on old-growth stands. To maintain a similar geographic distribution among ages of sampled stands, sampling was concentrated in areas in each province that contained all three of the following broad age-classes: young (<80 years), mature (80-195 years), and old growth (2195 years).

### Site Moisture Classification

Stands >200 years were tentatively assigned during field reconnaissance into three broad moisture-classes—dry, moderate, and moist—based on observations of vegetation composition (Franklin 1979, Zobel and others 1976), physiography, and soils. Dry sites occur on steep upper slopes of southerly aspects, commonly with skeletal soils. Plant communities of