Ecological Characteristics of Old-Growth Douglas-Fir Forests

Jerry F. Franklin, Kermit Cromack, Jr., William Denison,
Arthur McKee, Chris Maser, James Sedell, Fred Swanson,
and Glen Juday

Authors

Jerry F. Franklin
Pacific Northwest Forest and Rang e Experiment Station
Forest Service, U.S. Department of Agriculture
Corvallis, Oregon

Kermit Cromack, Jr.
Department of Forest Science
Oregon State University
Corvallis, Oregon

William Denison
Department of Botany
Oregon State University
Corvallis, Oregon

Arthur McKee
Department of Forest Science
Oregon State University
Cowallis, Oregon

Chris Maser
Bureau of Land Management, U.S. Department of the Interior
Corvallis, Oregon

James Sedell
Pacific Northwest Forest and Rang e Experiment Station
Forest Service, U.S. Department of Agriculture
Cowallis, Oregon

Fred Swanson
Pacific Northwest Forest and Rang e Experiment Station
Forest Service, U.S. Department of Agriculture
Cowallis, Oregon

Glen Juday
Alaska Ecological Reserves System
University of Alaska
Fairbanks, Alaska

Summary

The major ecological features of old-growth coniferous forests in the Douglas-fir region are reviewed. Special attention is given to characteristics that distinguish old-growth forests from managed and unmanaged (natural) young stands. The primary exemplary type is 350- to 750-year-old Douglas-fir-western hemlock forest typical of the western slopes of the Cascade Range, but other types and locales are discussed. Management techniques for maintenance of old-growth forests are also considered. Major conclusions are:

1. Approximately 175 to 250 years are required to develop old-growth forests under natural conditions in both Coast and Cascade Ranges. Development of old growth is faster on good sites than on poor sites.

2. Few plant or animal species are solely confined to old-growth forests, although many species-including several vertebrates, saprophytic plants, and epiphytic lichens-find optimum habitats in such forests. Some organisms, however, may require old growth to maintain viable populations. Moreover, there are substantial differences in composition and relative abundance of species between young- and old-growth forests.

3. Gross productivity is maintained at high levels in most old-growth stands, but mortality generally balances growth. Thus, the merchantable board-foot volume tends to remain constant for several centuries or gradually decreases because the amount of defect increases. Total organic matter keeps increasing because of accumulated masses of dead tree boles, mostly as down logs.

4. Old-growth forests are highly retentive of nutrients; large amounts are incorporated into living and dead organic matter. Losses of limiting nutrients, such as nitrogen, are low.

5. Nitrogen-fixing epiphytes are abundant in old-growth trees, and bacterial nitrogen fixation appears to be common in the large woody debris characteristic of old-growth forests.

6. Small- to medium-size streams in old-growth forests depend mainly on forest litter for an energy base. These materials are invariably partially utilized before they are exported downstream.

7. The structure of old-growth forest is more heterogenous than that of young forests; coefficients of variation in tree sizes are greater, and understory patchiness is much higher than in young-growth stands.

6. Most of the distinctive features of old-growth forests can be related to four structural features: (1) large, live old-growth trees, (2) large snags, (3) large logs on land, and (4) large logs in streams. The structural features are related over time.

9. A large, old-growth Douglas-fir is individualistic and commonly has an irregularly arranged, large, coarse branch system, and often, a long crown. It is ideal habitat for specialized vertebrates, such as the red tree vole, northern spotted owl, and northern flying squirrel, as well as nitrogen-fixing lichens.

10. Large snags are valuable as habitat for a variety of vertebrates and invertebrates and as a future source of logs.

11. Logs on the forest floor are important habitats for small mammals, including species that disperse spores of mycorrhiza-forming fungi. They also are sites for substantial bacterial nitrogen fixation and are essential as seedbeds for some trees and shrubs.

12. Logs are critical to maintenance of physical and biological stability in headwater streams. Debris dams create stepped stream profiles that dissipate energy otherwise used for transporting sediment and lateral-cutting and downcutting of stream channels. Such dams, with their associated plunge pools and beds of trapped gravels and fine sediments, provide a range of habitats needed to maintain a full array of stream and stream-margin organisms. Logs are an important source of energy, and the bulk of the ntirogen supply of a stream comes from woody debris.

13. Foresters wishing to maintain or create ecosystems with old-growth characteristics can tie management schemes to maintenance or develop ment of the four key structural components-large live, old-growth trees, large snags, and large logs on land and in streams.

14. Watersheds are probably best suited as management units for old-growth ecosystems. A small drainage usually has greater terrestrial habitat variability than occurs in a single stand, as well as a complete stream system. The size of a management unit will vary but probably should be at least 300 acres (120 hectares) to reduce effects of edges and susceptibility to damaging agents, such as wind, as well as to maintain viable populations of some birds and small mammals.

15. Buffer or leave strips along streams are also useful areas to manage as old-growth sites because woody debris is provided to the stream, and the riparian zone, a particularly rich and critical wildlife habitat, is protected. Such buffers, along with roadside strips of old-growth forest, also provide migration routes for wildlife between otherwise isolated patches of mature or old-growth forest.

16. Some ecological aspects of old-growth forests can be maintained by managing for individual attributes; for example, leaving scattered old-growth trees, rotten logs, or snags on cutover lands. The linked nature of these key structural components, as well as the requirements of some organisms for the total environment of an old-growth stand, makes management of entire stands a simpler approach to retention of such ecological features.

Abstract

Old-growth coniferous forests differ significantly from young-growth forests in species composition, function (rate and paths of energy flow and nutrient and water cycling), and structure. Most differences can be related to four key structural components of old growth: large live trees, large snags, large logs on land, and large logs in streams. Foresters wishing to maintain old-growth forest ecosystems can key management schemes to these structural components.

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Old-growth forests-forest ecosystems that have developed over a long period essentially free of catastrophic (including human) disturbance-are in increasingly short supply. In the Pacific Northwest, coniferous forests dominated by large, old trees occupied large expanses of the presettlement landscape, despite periodic episodes of wildfire. These forests represented both a valuable resource (large volumes of high quality wood) and a hindrance to agricultural development. Consequently, their elimination began early and has progressed to the point where, today, most of the remaining old-growth forests are on Federal lands, including the National Forests.

At current harvest rates, old-growth stands will not be completely cut over for at least four decades, even on National Forest lands where timber production is a primary objective. And many tracts of old-growth forest are permanently protected in National Parks, Wilderness, Research Natural Areas, and similar reserves. Nevertheless, these reserves occupy less than 5 percent of the original landscape, and the end of the unreserved old-growth forests is in sight. The public, scientists, and land managers are increasingly concerned about whether species, communities, and functions are in danger of being eliminated. Are there unique features, species, or important values associated with old-growth forests? Foresters are responding to such concerns by considering longer forest rotations on some areas or preserving specimen groves within the managed forest landscape.'

' As an example, the preferred management alternative in the draft environmental statement for the Hebo Planning Unit of the Siuslaw National Forest (USDA Forest Service Region 6 1977) commits 6,400 acres (2 560 ha) to maintenance of older forest. Under a 300-year rotation, approximately 3,000 acres (800 ha) of this would be maintained in the 200- to 300-year age class.

The expanded interest in old-growth forests surfaces many unanswered questions. Clearly, an old-growth forest is more than a collection of some large, old trees; but what else characterizes these forests? How are old-growth forests distinguished from natural second-growth forests that follow fire or result from managed stands? Once key attributes of old-growth forests are defined, further practical questions remain, such as: What characteristics should be sought by foresters attempting to perpetuate or recreate such ecosystems? What size tracts are essential to maintain a viable ecological unit, and what is the best geographic distribution of areas?

A group of scientists and land managers gathered at a work session sponsored by the USDA Forest Service in February 1977 to address these questions. The objective was to identify the ecological characteristics of old-growth coniferous forests and how they differ from young-growth and/or managed forests to provide suggestions for management strategies, and to identify areas for future scientific research.

This report represents current knowledge about the characteristics of an old-growth conifer forest in the Douglas-fir region of the Pacific Northwest. Special attention is directed to management problems, selection of old-growth reserves, development of old-growth stands by long rotations, and perpetuation of attributes of old growth in areas under intensive forest management. Much more research will be necessary, however, to provide definitive guidance in such topics as distribution and necessary size of old-growth management areas.

Old-growth Douglas-fir-western hemlock forests are the primary example of old-growth ecosystems in western Oregon and Washington. (Scientific names of trees are listed on page 44.) These forests, generally 350 to 750 years old, are the most common type of old-growth forest, particularly on western slopes of the Cascade Range. They are, in fact, the type of ecosystem commonly associated with the term "old growth," although forests as young as 200 years and as old as 1,000 years are also known as old growth. Other species and types also occur as old growth, such as Sitka spruce-western hemlock forests of coastal Oregon and Washington and the subalpine true fir-hemlock forests found the length of the Cascade Range. These will be commented on to the extent that available data permit.

In the strict sense, 350- to 750-year-old forests in the Douglas-fir region are generally not climax forests. Most stands of this age retain a significant component of long-lived Douglas-fir in the dominant tree canopy and will continue to do so for several more centuries. Because Douglas-fir is a subclimax species on most sites, subject to replacement by western hemlock and other more tolerant associates, stands of this type are technically in a subclimax condition. The structure and composition of the understory (as opposed to the tree canopy) are thought to be essentially the same as in a climax forest. The point is that old-growth Douglas-fir forests are not climax forests. True climax forests lack the large dominant Douglas-firs that give the forests much of their character and have tree layers of one or two shade-tolerant tree species (for example, western hemlock) which usually do not get as large. Other old-growth forests typically have long-lived pioneer species that attain large sizes, giving them much of their character, but which are generally lost in a climax forest. Examples are noble fir in subalpine environments, Sitka spruce along the coast, and sugar pine in southwestern Oregon.

Coast redwood forests are one type that apparently do retain very large dominant specimens in a true climax condition (Franklin and Dyrness 1973). If Cupressaceae, such as western recedar and Alaska-cedar, are present, very large dominant trees may remain in stands otherwise dominated by western hemlock or Pacific silver fir for yet another millenium beyond the disappearance of the Douglas-fir; members of this family have extremely long lifespans and some ability to reproduce under closed forest conditions.

In this report, the stream component of an old-growth ecosystem is considered along with the terrestrial component. Stream conditions depend strongly on the nature of associated forests. In fact, streams in old-growth forests contain several of the most distinctive features of these ecosystems.

Attributes of forest ecosystems are composition, function, and structure. Composition refers primarily to the array of plant and animal species present in an ecosystem. We also considered dominance an element of composition; that is, shifts in abundance as well as presence or absence of species. Function refers to how various ecological processes, such as production of organic matter and cycling of nutrients (through pathways and compartments), are accomplished and the rates at which they occur. It is well known that, as ecosystems develop or age, the relative size of various compartments, complexity of pathways, and transfer rates change (Odum 1971). Increased complexity in routing dead organic material (development of a system based on detritus) is one characteristic example of a functional change with succession. We considered types and rates of ecological processes as functional features of an ecosystem. Structure refers to the spatial arrangement of various components of the ecosystem, such as heights of various canopy levels and spacing of trees.

Finally, we define some terms and determine age limits for old-growth forests. It is difficult to define a lower age limit for old growth. The transition from mature to old-growth forest is gradual, and the age limit varies with site conditions (trees take different times to reach comparable size or physiological age on different sites) and with the type of stand (initial density and composition) that develops after the last disturbance. We would expect earlier development of old-growth characteristics on better Douglas-fir sites, in coastal environments, and in understocked stands and delayed development on poor sites, on many (but not all) subalpine environments, and in overstocked stands.

Forests typically begin exhibiting old-growth characteristics at about 175 to 250 years. Forests up to about 75 to 100 years old can generally be considered ecologically young in the Douglas-fir region. This is the period of very rapid growth or "adolescence." Mature forests are those in the period between culmination of maximum growth (peak of the growth curve) and the development of old-growth characteristics; that is, generally between 100 and 200 years. Federal foresters normally select the culmination of mean annual wood increment (end of youth) as the rotation or cutting age in managed forests. Substantial net growth (or net accumulation of live biomass) does continue in the mature forest although at a slower rate than in the young stand.[2] There

is typically little net gain or loss of live biomass in most old-growth forests over the long run, barring some catastrophe. This may change in extremely old forests (>750 years), but few examples of such old forests exist, even in the Pacific Northwest.

In this report, we distinguish between natural young-growth forests (such as those that have followed wildfires) and managed young-growth forests. Contrasts are very sharp between natural and managed young growth in several ecological attributes, such as the number of snags and rotten logs. Our concept of managed stands is based on current USDA Forest Service plans of prompt establishment of fully stocked young conifer forests after cutting of natural stands and major efforts to dispose of residue. We assume that such forests will typically have moderate levels of management (for example, thinning) and will have an 80- to 90-year rotation- a somewhat more conservative strategy than is currently practiced on the most intensively managed industrial forest lands in the Pacific Northwest.

We have attempted to contrast the features of old-growth and second-growth forests. Surprisingly, some aspects of younger forests have not yet been studied, so comparable data are not always available. In such cases, we have described the old-growth condition; future research on young growth should provide comparisons. When reading this report or drawing inferences from it, the reader is cautioned to be careful in distinguishing natural second- or young-growth stands from managed young-growth forests in any comparisons with old-growth forests.

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*Williamson and Price (1971) show some very high rates of growth in stands at or beyond average current rotation ages. Seven plots in unthinned Douglas-fir stands 90 to 150 years of age averaged a net growth of 114 ft³/acre (690 board feet (fbm) per acre or 8 m³/ha) per year.

Some general attributes of an old-growth forest are immediately apparent to an observer with even a moderate background in natural history (fig. 1). Trees typically vary in species and size; dominant specimens are truly impressive. Some large species differ in color and texture as well as in size. The multi-layer canopy produces a heavily filtered light, and the feeling of shade is accentuated by shafts of sunlight on clear days. The understory of shrubs, herbs, and tree seedlings is often moderate and is almost always patchy in distribution and abundance. Numerous logs, often large and in various stages of decay, litter the forest floor, creating some travel routes for wildlife and blocking others. Standing dead trees, snags, and rotted stubs are common, although a visitor gazing toward the ground will often mistake dead trees in early stages of decay for live trees. It is quiet; few birds or mammals are seen or heard except perhaps the melody of a winter wren (*Troglodytes troglodytes*), the faint songs of golden-crowned kinglets (*Regulus satrapa*) in the tree canopies, or a chickaree (*Tamiasciurus douglasi*).

Figure 1. Old-growth Douglas-fir—western hemlock forest showing diversity of tree sizes and heterogeneity of understory.
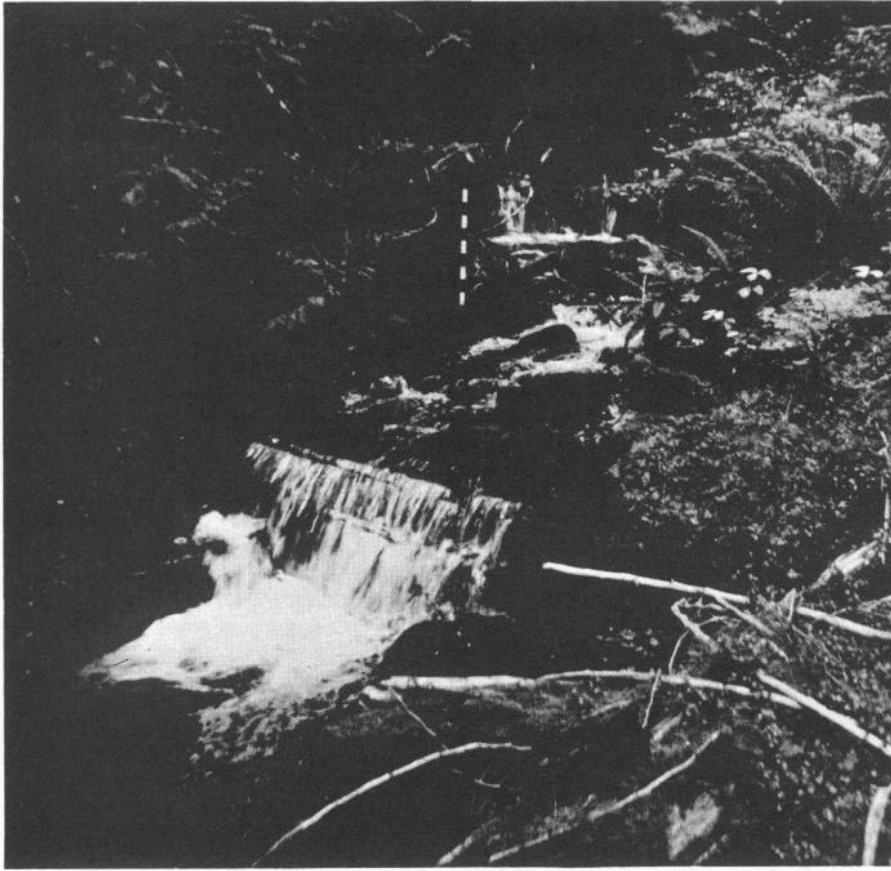
Figure 2. Small streams within old-growth forests depend heavily on terrestrial vegetation for energy and physical integrity.

Small to moderate size streams flowing through old growth (fig. 2) are shaded, often completely shielded from the sun by the canopies of adjacent trees. The smallest streams may be choked with organic debris; as size and volume of streams increase, clear, cool water runs through gravel beds behind old log dams and spills into plunge pools. Organic debris—for example, leaves, needles, twigs, bud scales— floats on the surface and accumulates in backwaters.

Some of these impressions represent important, distinctive aspects of an old-growth forest ecosystem that we will discuss as composition, function, and structure. Structural aspects of old-growth forests are the major unifying element since the peculiar compositional and functional features are mainly related to the distinctive structure of old growth. We discuss composition and function first, however, so that these aspects are not completely overshadowed by that of old-growth structure. We discuss composition and function again in the sections on habitat and cycling roles of live old-growth trees, standing dead trees or snags, logs on land, and logs in streams.

Old-growth forests obviously differ in composition from young stands. Ecological succession produces changes in the array of plant and animal species as well as in their relative abundance. Hence, there is a change from pure or nearly pure young forests of Douglas-fir to mixtures of old-growth Douglas-fir, western hemlock, western redcedar, and other species. Thomas et al. (1979c) outlined the changes in animal species associated with plant community successional stages in the Blue Mountains of eastern Oregon. These principles apply equally to Douglas-fir–western hemlock forests, as shown by Gashwiler (1970) and others. The most sterile successional stage, in diversity of both plant and animal species, is a dense, rapidly growing young conifer forest (Edgerton and Thomas 1978, Long 1977, Meslow 1978).

Few vascular plants appear confined to old-growth ecosystems in the Douglas-fir region. Lists of species from old-growth Douglas-fir–western hemlock stands in the H.J. Andrews Experimental Forest (Dyrness et al. 1974) show none that are confined to old-growth forests.

Some vascular plants do find optimum habitat (or most frequently— suitable environments) in old-growth Douglas-fir ecosystems. These are often saprophytic[3] plants belonging to the orchid and heather families— for example, phantom orchids (*Cephalanthera austinae*), pinesap (*Monotropa hypopitys* L.), woodland pinedrops (*Pterospora andromeda* Nutt.), and candystick (*Allotropa virgata*)— which favor heavily shaded environments rich in organic debris. Again, these vascular plants are not confined to old-growth ecosystems but often find suitable environments there.

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[3] Saprophytic plants obtain all or part of their energy from decomposition of dead organic materials rather than by photosynthesis. Most vascular plants characterized as saprophytic have fungal associates essential to their survival (Furman and Trappe 1971).

For lower plants-including mosses, lichens, liverworts, algae, and bacteria-there currently is no way of systematically addressing the question of dependency of a species on old growth. Many species find optimum habitat in old-growth forests, and some probably require old-growth habitat for survival. As in the case of vascular plants, more species probably find their optimum habitat in old growth, however. For example, snags in old-growth forests have a rich flora of Caliciales (lichens). Species that occur in old growth rarely occur on the drier snags found in younger forests. The rich communities of epiphytes found in the canopies of old-growth Douglas-fir include the foliose lichen Lobaria *oregana* (seldom found elsewhere), as well as Lobaria *pulmonaria* and *Alectoria sarmentosa* (also found in younger stands).

More is known about the relationship of vertebrate animals to old growth than any other group of organisms. Much of the interest in old growth is as habitat for the vertebrates primarily found there (Thomas 1979, DeGraaf 1978). Although many vertebrates utilize old-growth forests, some (table 1) exist mainly in old-growth ecosystems. The degree to which the listed species depend on old-growth forest ecosystems varies, but all find optimum breeding or foraging habitat there. Whether any species depends totally on old growth for survival is not clear; however, the fact that a species can survive in other age classes of a forest does not necessarily mean it can survive once the

Table l-Vertebrate animals that find optimum habitat for foraging or nesting or both in old-growth Douglas-fir-western hemlock forest ecosystems'

Group	Common name	Scientific name
Birds	Goshawk	*Accipiter gentilis*
	Northern spotted owl	*Strix occidentalis*
	Vaux's swift	*Chaetura vauxi*
	Pileated woodpecker	*Dryocopus pileatus*
	Hammond's flycatcher	*Empidonax hammondii*
	Pine grosbeak	*Pinicola enuclea for*
	Townsend's warbler	*Dendroica townsendi*
Canopy mammals	Silver-haired bat	*Lasionycteris noctivagans*
	Long-eared myotis	*Myotis evotis*
	Long-legged myotis	*Myotis volans*
	Hoary bat	*Lasiurus cinereus*
	Red tree vole	*Arborimus longicaudus*
	Northern flying squirrel	*Glaucomys sabrinus*
Ground mammals	California red-backed vole	*Clethrionomys californicus*
	Coast mole	*Scapanus orarius*
	Marten	*Martes americana*

* On the Olympic Peninsula, fisher *(Martes pennanti)* exists only in old-growth forests and should be added to this list for at least the peninsula. Habitat changes caused by cutting, rather than trapping, are probably responsible for elimination of this species from other sites. (Personal communication from Bruce Moorhead, Research Biologist, Olympic National Park, May 16, 1978.)

major reservoir of optimum habitat is gone. The factors responsible for a species' orientation toward old growth (food source, suitable nesting sites, protection from competition) also vary between species and provide a key to the management of a particular species (for example, providing snags for cavity dwellers).'

[4] Meslow (1978) reported that of 84 birds found in Douglas-fir forests, 49 nest in mature stands, and 3 of those (goshawk, northern spotted owl, and Vaux's swift) nest almost solely in mature stands. Sixteen of 20 hole nesters are found in mature forests.
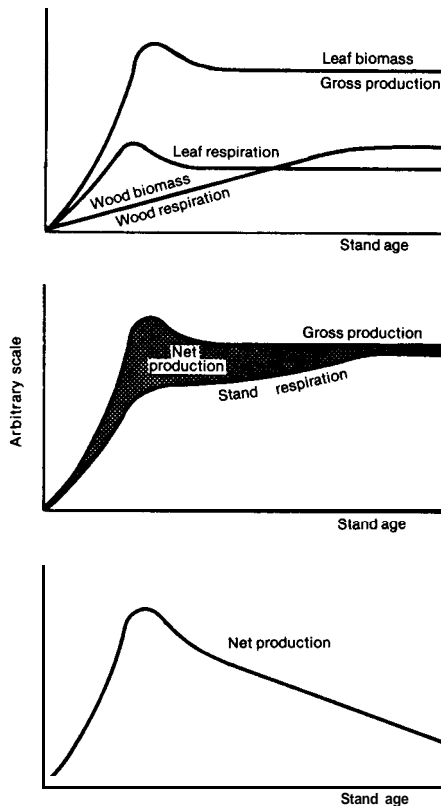
Figure 3. *Trends in biomass, respiration, and production in forest stands; note increasing amounts of ener y used in respiration (based on   and Kira 1977).*

Primary ecological functions within a forest ecosystem include primary production, energy flow, conservation and cycling of nutrients, and regulation of waterflow.

Forests. Primary production in old-growth forests is typically high. Leaf area and biomass accumulate rapidly and stabilize fairly early in the life of a stand (Long and Turner 1975), but there is little evidence for a substantial decline in either in old-growth stands. Foliage biomass values of 6.2 to 11.6 tons per acre (14 to 26 tonnes/ha) and ratios of projected leaf areas per unit of ground area ranging from 7 to 16 were reported in 14 old-growth Douglas-fir forests (Franklin and Waring 1960); leaf areas were affected by environmental conditions (Gholz et al. 1976). Values for coastal and subalpine types of old growth are comparable. These values exceed those found in mature (second-growth) forests 90 to 130 years in age. The large leaf areas in many old-growth stands indicate shade-tolerant associates, such as western hemlock. The long-crowned Douglas-firs also contribute substantial leaf area, however, and the multilayered canopy of an old-growth forest is well suited to efficient capture of energy. In summary, the-"factory" for photosynthetic production is generally large and intact in an old-growth forest.

Production of photosynthate may be high in mature and old-growth stands, but total energy used in respiration is also high. A hypothetical example of trends in biomass, respiration, and production rates (fig. 3) shows the increasing energy cost (in respiration) of simply maintaining, as living tissue, the increasing accumulations of biomass. Grier and Logan (1977) estimated gross respiration in one old-growth forest to be 67 tons per acre (150 tonnes/ha) per year-over 90 percent of the gross production.

On a more practical level, substantial growth in the form of wood and other increments of biomass occurs in old-growth forests. Much, but not all, of this increment is on the western hemlocks, western redcedars, and other shade-tolerant associates. But little or no increase of additional living biomass-or cubic feet-is occurring in an old-growth stand because of mortality and, in some stands, disease. Over the long run, living biomass appears to fluctuate around a plateau in response to episodes of heavy and light mortality.

This pattern of subtantial growth or increment in old-growth stands which is largely offset by mortality has been documented by the few available studies of growth. Annual wood increment was 1,582 board feet or 226 cubic feet per acre (15.8 m^3/ha) over a lo-year period in a 250-year-old Douglas-fir stand in the Clackamas River drainage of Oregon (Berntsen 1960). The annual mortality of 1,156 board feet or 201 cubic feet per acre (14.1 m^3/ha) did not completely offset this large amount of growth even though the measurement period was one of heavy loss; over 15 percent of the original 48 Douglas-firs per acre (119/ha) were lost in the lo-year period, mainly to bark beetles and windthrow. An old-growth[5] Douglas-fir-western hemlock forest in the Wind River drainage of the southern Washington Cascade Range grew 699 board feet or 106 cubic feet per acre (7.4 m^3/ha) per year over a 12-year period.

[5] King (1961) indicated that the age of the stand was 350 years. Subsequent stump counts in adjacent clearcuts, which had comparable forests before the cutting, suggest that the stand originated closer to 450 years ago.

Epidemics of bark beetles in Douglas-fir and western white pine were major contributors to the average annual mortality of 614 board feet or 96 cubic feet per acre (6.7 m^3/ha). Despite these large losses, the stand registered a small net gain. Neither Berntsen (1960) nor King (1961) took into account losses from decay in living trees, so some further reduction from the net growth figures is necessary in calculating net production of sound wood. Grier and Logan (1977) report losses in aboveground biomass in trees in a 25-acre (lo-ha), 450-year-old stand because of high mortality in a 2-year study period.

Old-growth forests, as well as much younger ones, apparently do experience periods of high mortality from bark beetle epidemics, severe windstorms, and so forth. There is also evidence that infection and losses caused by heart rots (and perhaps other types of diseases) are cyclic (Boyce and Bruce Wagg 1953). The limited data available indicate, however, that neither leaf mass nor total live biomass show regular reductions with age, at least up to 600 or 700 years.

Regardless of whether the volume of living trees is level or declining, there is evidence that total organic matter-living and dead-continues to increase in old-growth forests. This is mainly in the form of coarse woody debris, such as logs, which accumulates much more rapidly than it decomposes. In the absence of wildfire or other major disruption, the ultimate consequences of this

continuing accumulation of organic matter are not clear; few stands are old enough to indicate when accumulations of organic matter will peak, and even fewer have been analyzed. Limited data suggest that total accumulations of organic matter may peak at 800 to 1,000 years (Franklin and Waring 1980).

Development of large accumulations of dead organic matter relates to a major distinction in nutrient cycling between young-growth and old-growth stands. Specifically, Odum (1971) refers to carbon and nutrient cycling in old-growth forests as a "closed cycle, detrital-based system." Nutrient paths are complex and involve large amounts of detritus. Detritus decomposes slowly through the efforts of heterotrophic organisms; for example, fungi, bacteria, and invertebrates. Although release of energy and nutrients from the dead organic materials is slow, ecosystems functioning in this way are extremely conservative-nutrients are tightly retained within the system (Fredriksen 1970, 1972; Fredriksen et al. 1975). The low level of nutrients and other dissolved and suspended materials in water from old-growth ecosystems reflects this conservatism. The low level of erosion and the nature of the streams also contribute to the low losses of nutrients from old-growth forests (Sollins et al. 1980).

The development of a strongly conservative carbon and nutrient cycle based on detritus is a gradual and continuing process from the time a forest becomes established until its ultimate destruction by a natural catastrophe or human intervention; such features are not solely confined to old-growth forest. Old-growth forests usually have greater amounts and larger sizes of dead organic matter than young and mature stands of natural origin, however, and much more than managed forests.

In addition to being highly retentive of nutrients, old-growth forests have other means that provide nutrients as more and more nutrients become bound in wood and other materials. Trees meet larger and larger proportions of their annual requirements of nutrients by internal redistribution (Waring and Franklin 1979). Nitrogen (N) is a particularly critical nutrient; in an old-growth forest, substantial annual increments of N are provided by foliose lichens in tree crowns and by bacterial fixation in coarse woody debris. These biological fixation processes may provide inputs of 6 to 9 pounds of N per acre (7.5 to 9.5 kg/ha) or more per year to old-growth systems-more than in natural young growth and, especially, intensively managed forests.

The net effects of hydrologic cycling in old-growth and younger forests are similar. Water usage by plants and, therefore, streamflow quickly return to near the original level (of the natural forest) after a cutting (Anderson et al. 1976). There may be minor contrasts between young growth and old growth in that deep crowns of the old growth may have some advantage in intercepting fog and other aerosols. Perhaps the major hydrologic contrasts between young and old forests are in effects on erosion and on the biological and physical natures of streams.

Table P-Annual transfer of inorganic and organic matter under old growth on watershed 10 to a channel by hill slope processes, and export from the channel by channel processes, H. J. Andrews Experimental Forest, western Oregon Cascade Range[1]

Process	Inorganic matter		Organic matter	
	Tonnes	Tons	Tonnes	Tons
Hill slope:				
Solution transfer	3.0	3.3	0.3	0.3
Litter fall	0	0	.3	.3
Surface erosion	.5	.6		.3
Soil creep	1.1	1.2	.04	.04
Root throw	.1	.1	.1	.1
Debris avalanche	6.0	6.6	.4	.4
Slump and earthflow	0	0	0	0
Total	10.7	11.6	1.4	1.4
Channel:				
Solution transfer	3.0	3.3	.3	.3
Suspended sediment-				
Gross	.8	.9	.1	.1
Net		.7		.1
Bedload	.6	.7	.1	.3
Debris torrent	4.6	5.1	.3	.3
Total	6.9	10.7	1.0	1.0

[1] Adapted from Swanson et al. (1981a).

A broad spectrum of geomorphic processes transports organic and inorganic materials down hill slopes and through stream channels in old-growth ecosystems. Swanson et al. (1961a) estimate rates of material transfer for seven hill slope and four channel processes in one old-growth watershed (table 2). Surprisingly, greatest transfer of inorganic material occurs by the most episodic processes-debris avalanches and torrents from hill slopes and down stream channels. For example, only one debris avalanche moving more than 2,625 cubic feet (75 m^3) of soil is estimated to occur in three or four centuries of forested conditions in this steep, 25-acre (10-ha) watershed. Yet, this process moves more material, averaged on an annual basis, from hill slopes than more persistent and pervasive processes, such as surface erosion and solution transfer. Comparable data for second-growth forests are not available, but Swanson et al. (1981a) review and discuss variations in importance of erosion processes during the first 10 to 15 years after clearcutting.

The most important physical influence of old-growth forests on erosion is the provision of large organic debris which slows the routing of sediment through the channel system and dissipates the energy of streams.

Streams. The food base or energy supply of a stream in an old-growth stand is mostly litter from the adjacent forest-leaves, needles, cones, twigs, wood, and bark, all known as allochthonous material to the aquatic biologist (table 3). Large boles require special consideration since they (1) enter streams infrequently rather than annually, (2) physically shape the small stream, and (3) move downstream only by the rare debris torrent and must, therefore, be biologically processed or broken down in place. Input of allochthonous material to streams and their export from streams are predictable. Of the organic material that falls or slides into small streams each year, only 18 to 35 percent is exported or

Table 3—Particulate organic budget of a small stream of the H. J. Andrews Experimental Forest in the western Oregon Cascade Range, watershed 10, 1973-74 water year

Input			Standing crop			Export		
Source	Amount per stream per year		Source	Amount per stream per year		Source	Amount per stream per year	
	Pounds	Kilo-grams		Pounds	Kilo-grams		Pounds	Kilo-grams
Lateral movement[1]	428	194	Large detritus[2]	9,984	4 530	Dissolved organic matter	408	185
Dissolved organic matter	408	185	Small detritus[2]	1,587	720	Particulate organic matter	372	169
Litter fall and throughfall	251	114	Fine detritus[2]	115	52	Detritus respiration	205	93
Moss primary production	15	7	Primary producers	26	12	Primary producer respiration	33	15
Algal primary production	2	1	Macroinvertebrates	1	.3	Macroinvertebrate respiration	4	2
Total	1,104	501	Total	11,713	5 314	Total	1,022	464

[1] Lateral movement refers to materials sliding downslope into streams.
[2] Large detritus = >4 inches (10 cm); small = 0.4 inch to 4 inches (1 to 10 cm); fine = <0.4 inch (1 cm).

flushed downstream. These streams under old-growth forests retain materials; they are not mere conduits for quick export from the system—60 to 70 percent of the annual organic inputs are retained long enough to be biologically used by stream organisms. Large dams of woody debris effectively act as sieves and deposit zones for fine organic matter, allowing time for microbial colonization and consumption of the material by insects.

The amount of various inputs of debris processed in a defined section or "reach" of a stream depends on (1) the quantity and quality of nutrients in the debris and (2) the capacity of the stream to retain finely divided debris for the time required to complete processing.
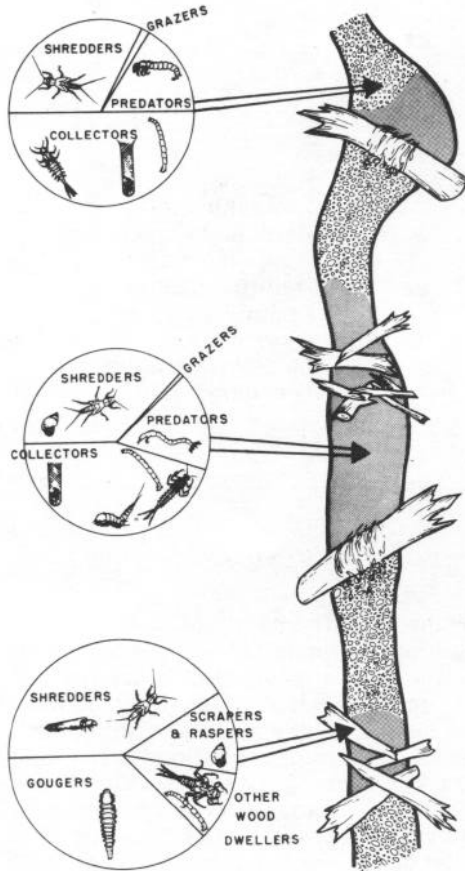
Debris may be fully utilized by the biotic community within a reach of stream or may be exported downstream. Since export from one reach constitutes an input to downstream reaches, processing continues as small debris moves through the system. Processing of organic matter includes metabolic utilization by bacteria and fungi, consumption of debris by insects, and physical abrasion. In all cases, debris is broken into smaller pieces which increases the surface-to-volume ratio and makes the debris particles increasingly susceptible to microbial attack. The length of stream required for complete processing of organic material may be longer in years when water is high than when it is low; the same is true in streams with lower capacity for retaining fine debris, such as streams lacking sufficient debris dams.

The point of this discussion is that small first- and second-order streams feed larger streams with a partially prepared food resource.[a] The stream is a continuum in which transported food materials become progressively smaller. In small streams under old growth, a large proportion of the basic food resource is derived from wood.
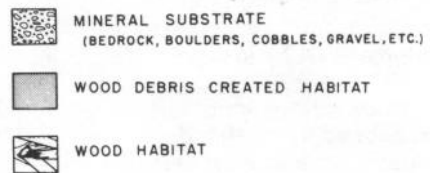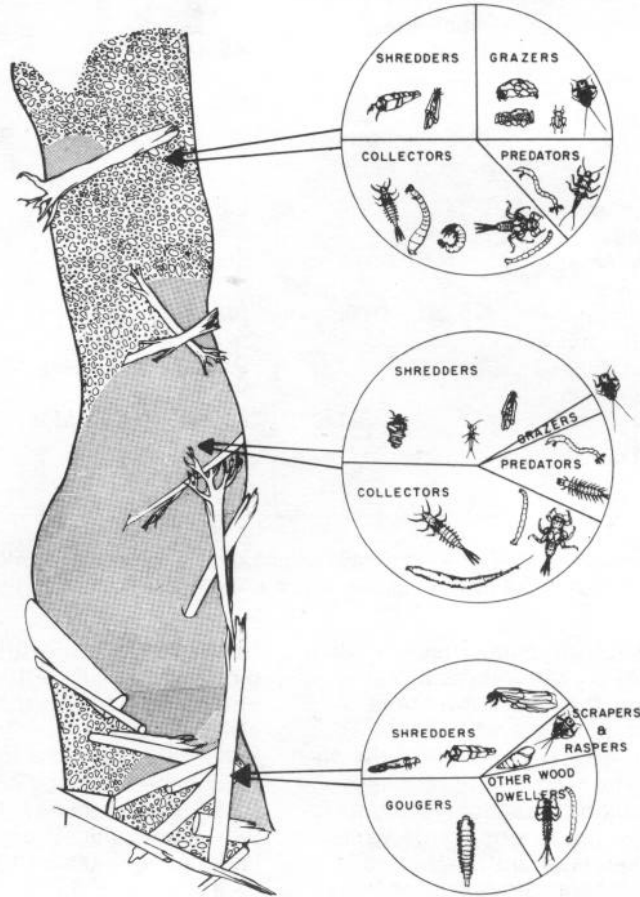
[a] As defined by Strahler (1957), first-order streams are smallest streams with no tributaries; junctions of first-order stream segments mark the upstream end of a second-order stream segment; the junction of two second-order segments marks the head of a third-order segment, and so on.

FORESTED STREAM HABITATS

(1-2 ORDER)
VERY SMALL STREAMS

(3-4 ORDER)
SMALL—INTERMEDIATE STREAMS

SHREDDERS GRAZERS
PREDATORS
COLLECTORS

SHREDDERS GRAZERS
COLLECTORS PREDATORS

SHREDDERS GRAZERS
PREDATORS
COLLECTORS

SHREDDERS
GRAZERS
PREDATORS
COLLECTORS

SHREDDERS SCRAPERS & RASPERS
GOUGERS OTHER WOOD DWELLERS

SHREDDERS SCRAPERS & RASPERS
GOUGERS OTHER WOOD DWELLERS

MINERAL SUBSTRATE
(BEDROCK, BOULDERS, COBBLES, GRAVEL, ETC.)

WOOD DEBRIS CREATED HABITAT

WOOD HABITAT

A

10

Figure labels:

METERS

STREAM ORDER

Stream Order	Meters
1	0.5
2	1-2
3	4-8
4	10
5	10-15
6	
7	50
8	

WOOD DEBRIS
MICROBES
CPOM
PRODUCERS (MOSSES)
FPOM EXPORT
P:R < 1
DEBRIS DAMS
PRODUCERS (PERIPHYTON)
FPOM INPUT
CPOM
WOOD DEBRIS
PRODUCERS (PERIPHYTON)
P:R > 1
FPOM INPUT

DEVILSCLUB CREEK
58% 23% 7% 12%

COLLECTORS
PREDATORS
SHREDDERS
GRAZERS

MACK CREEK
18% 17% 45% 20%

LOOKOUT CREEK
34% 19% 22% 25%
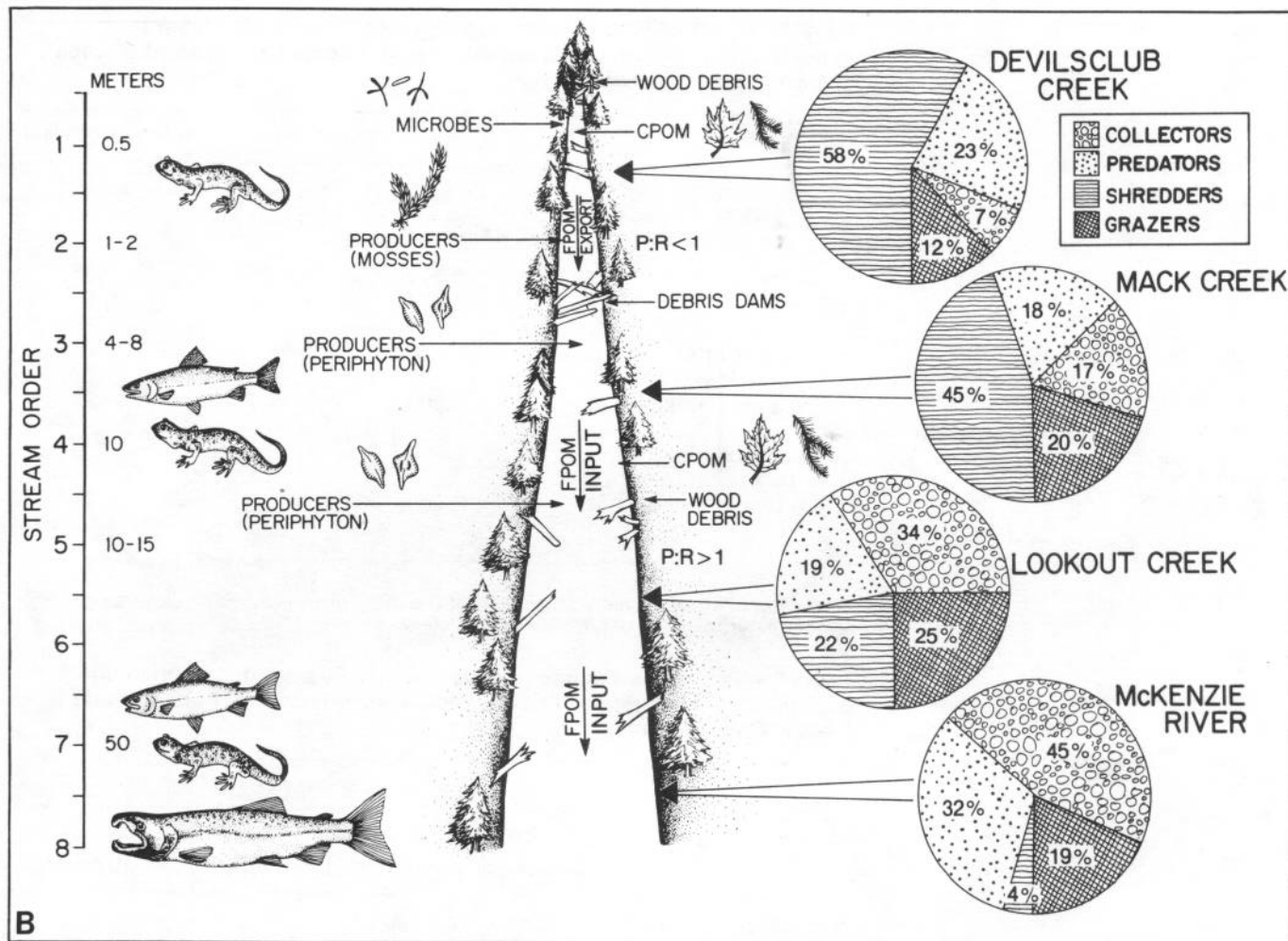
McKENZIE RIVER
45% 32% 19% 4%

B

Figure 4. Streams in old-growth forests have a rich, invertebrate fauna which gouge, shred, and scrape the larger organic material and collect the fine organics carried in the water. The type of fauna shifts with size of stream, however, and third- to fourth-order streams are generally richer in numbers, biomass, species, and functional types than are smaller streams.
A. Comparison of very small and intermediate streams, showing contrasting proportions of various functional groups by substrate (Anderson and Sedell 1979).
B. Diagram of first- to eighth-order streams, showing width (meters), dominant predators, producer groups, P:R (production:respiration) ratios, importance of wood, and proportion of invertebrate functional groups (adapted from Anderson and Sedell 1979). CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter.

The influence of the forest diminishes as the stream gets larger. The energy base of the stream is derived more from algae and less from forest litter (fig. 4, A and B). The greatest influence of the forest is found in the very small streams, whereas the most diversity in inputs and habitats is found in the intermediate (third- to fifth-order) streams. The invertebrates reflect these downstream shifts with fewer shredders (leaf eaters) and more grazers (algal feeders) in the larger streams (fig. 4, A and B). As the size of a stream in an old-growth forest changes, there are shifts in dominant organisms and the role each group of organisms plays in using available organic materials (fig. 4, A and B).

Table 4—Inputs of litter (excluding bole wood) to a small stream in watershed 10 in old-growth Douglas-fir, H. J. Andrews Experimental Forest, western Oregon Cascade Range[1]

Type of litter	Weight		Percent of total
	Ounce per square foot	Grams per square meter	
Leaf:			
Hardwood	0.0005	0.166	7.6
Conifer	.0016	.489	22.5
Fine woody litter (<1-centimeter or 0.4-inch diameter)	.0032	.972	44.7
Coarse woody litter (1- to 10-centimeter or 0.4- to 4-inch diameter)	.0018	.548	25.2

[1] Woody debris totals nearly 70 percent of the litter, even though the large weight of wood greater than 10 centimeters in diameter is excluded.

Table 5—Input of particulate organic nitrogen to a small stream in old-growth forest (watershed 10), H. J. Andrews Experimental Forest, western Oregon Cascade Range

Source	Amount per year			
	Ounce per square foot	Gram per square meter	Pounds	Kilogram
Deciduous leaf litter	0.0014	0.44	0.68	0.31
Coniferous leaf litter	.0030	.91	1.41	.64
Fine woody litter (<1-centimeter or 0.4-inch diameter)	.0023	.71	1.10	.50
Coarse woody litter (1- to 10-centimeter or 0.4- to 4-inch diameter)	.0003	.08	.13	.06
Nitrogen fixation in wood less than 10-centimeter or 4-inch diameter	.0023	.70	1.07	.49

The percent of each type of food available to microbes and invertebrates in small streams under old growth is presented in table 4. Woody material constitutes 50 to 70 percent of the total organic material, including very fine particles derived almost exclusively from bole wood; these data do not include bole wood, however, because it would completely overwhelm the other categories in table 4.

Invertebrates in the smallest streams flowing through old-growth forests have evolved to gouge, shred, and scrape wood and leaves and to gather fine organic particles. These first- and second-order streams are loaded with wood and have many wood-gouging beetle larvae and leaf-shredding stoneflies and snails. The small particles of organic material trapped by the large wood are gathered and fed on by a benthic copepod. These streams are noted for their uniqueness in that each is predominantly a beetle-stonefly-copepod-miniature snail invertebrate community (fig. 4A), not for an abundance of invertebrate populations.

Third- to fourth-order streams are generally richer in kinds, numbers, and biomass of organisms than are smaller streams-including a rich variety of insects and a continuous population of vertebrates, such as cutthroat trout *(Salmo c/arki)* tailed frog; and Pacific giant salamander. The richness and abundance are due, in part, to the increased importance of algae as a source of energy.

The green plants or primary producers in streams also vary widely by size of stream. In first- and second-order streams, moss cover is generally greater than 20 percent of the stream area and is located primarily on wood, bedrock, and boulders. The moss community generally occupies 5 percent or less of the stream area in third- and fourth-order streams-mostly on wood, bedrock, and large boulders. The algal community-primarily diatoms, green algae, and a few blue-green algae-is well developed and widely spread throughout larger streams. Small streams have a sparse diatomaceous flora and a patchy blue-green algal community which is intimately associated with the mosses.

Large woody debris is responsible for two types of habitat within each stream-wood and wood-created environments, such as depositional pools. Each of these habitats, as well as those not related to wood (mineral sediments in streambed formations not created by wood or bedrock), has a different faunal composition. Relative proportions of wood-related and other habitats vary markedly with size of streams. In the smallest streams, 50 percent or more of the area may be occupied by wood and wood-related habitats compared with 25 percent for third- and fourth-order streams.

Coarse woody debris also functions as a major source of N. Although the content of N in wood is small, large amounts of N are fixed in and on woody debris. In one small watershed in the western Oregon Cascade Range, input of N in wood or fixed in wood accounts for 52 percent of the total input of N to the stream, not counting N in woody material over 4 inches (10 cm) in diameter (table 5).
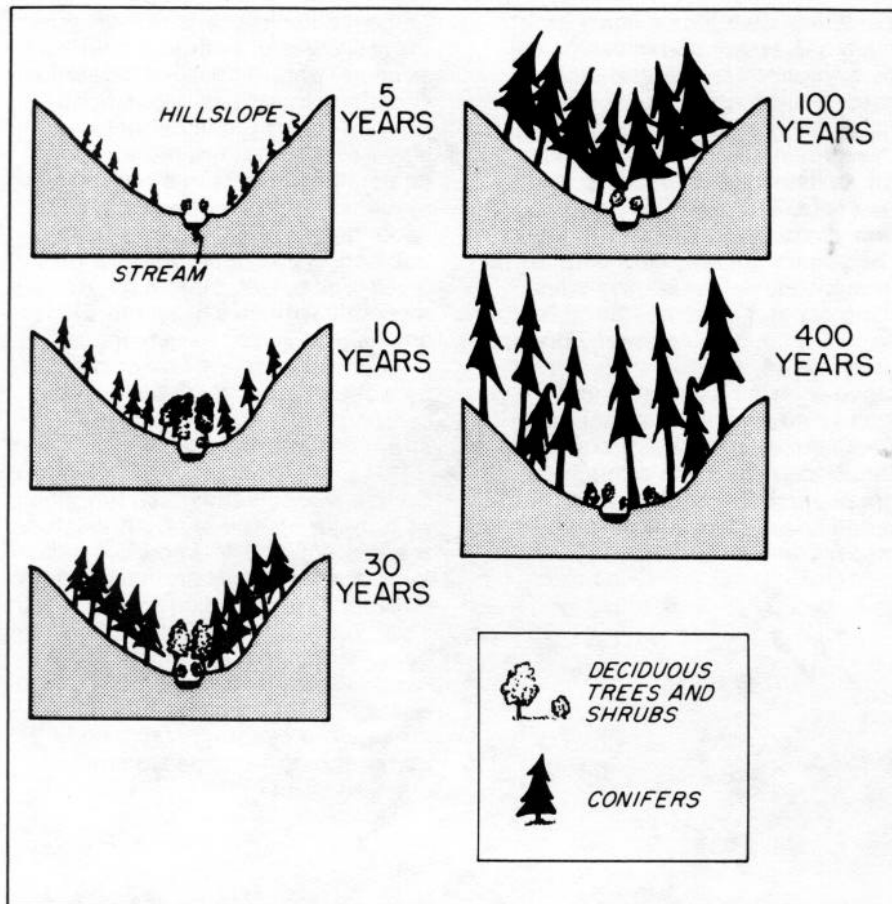
Figure 5. Hypothetical changes in the riparian zone through succession in Douglas-fir—western hemlock forests (Swanson et al. 1981b; from Analysis of Coniferous Forest Ecosystems in the Western United States *US/IBP Synthesis Series, V. 14, edited by R. L. Edmunds. Copyright © 1981 by Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa. Reprinted by permission of the publisher.)*

The environment of streams dominated by forest varies with stand age in response to changes in structure of streamside vegetation as it develops through time. A hypothetical succession of streamside vegetation is shown in figure 5. In small streams in the western Cascade Range, dense riparian stands of deciduous shrubs and small trees develop in one to two decades. Beyond that point in development, upslope conifers begin to overtop the deciduous streamside vegetation. Stands 50 to several hundred years old have a dense canopy of deciduous trees with little understory vegetation. Older stands have a multilayered structure, and more light penetrates to streams.

These variations in structure of the stand through time are reflected by shifts in both energy base and habitat in streams up to about fourth order. Although little is known about actual productivity of streams through succeeding stand structures, algae are known to be a dominant source of energy before the canopy closes; they continue to be an important contributor in small to intermediate streams as long as there is a hardwood canopy cover. When the stream is completely enclosed by a conifer canopy, the ecosystem shifts to a food base of conifer litter which is of lower quality than algae. The more open canopy of old growth provides greater diversity of nutrient inputs, including algae and litter of herbs, shrubs, hardwoods, and conifers.

Murphy (1979) measured populations of vertebrate and invertebrate predators, including salamanders in streams in recent clearcuts (less than 10 years old), in 20- to 30-year-old, second-growth stands, and in old-growth forests. He found that numbers and biomass of predators in the total stream, particularly cutthroat trout, were highest in recent clearcuts, lowest in second growth, and intermediate in old growth. Aho (1976), studying cutthroat trout, and

Lyford and Gregory (1975), studying algae and insects, found similar contrasts in populations between clearcut and old-growth forested sections of the same stream but did not examine stream systems in second-growth forests. Riparian habitats are also critical for mammals and birds (Thomas et al. 1979b).

In summary, old-growth forests dominate both the composition and the function of associated streams. Terrestrial litter is the primary source of energy and nutrients. Woody debris also functions as a major site for fixation of N and as habitat for a broad array of organisms. Logs are also the structural key to the physical and biological stability of a stream. In undisturbed forest, streams are highly retentive of organic materials and nutrients; little escapes without being at least partially processed (consumed and decomposed). Exported material provides downstream reaches with prepared food resources.

The large diameters and heights of the old-growth trees are the most striking structural attributes of these forests. Heterogeneity in diameter and spacing contributes, however, to the variety in an old-growth forest. The pioneers—predominantly Douglas-fir—continue to enlarge in diameter and height over time, while natural thinning reduces their numbers (table 6 and fig. 6). Shade-tolerant species, such as western hemlock, invade the stand and provide smaller trees.

Table 6—Density of all trees and Douglas-fir, mean d.b.h. of Douglas-fir, and stand basal area in age sequence of old-growth Douglas-fir-western hemlock stands in the Cascade Range

| Forest | Stands sampled | Density[1] | | | | Mean d.b.h., Douglas-fir | | Stand basal area | |
		All trees		Douglas-fir					
Years	Number	Number per acre	Number per hectare	Number per acre	Number per hectare	Inches	Centi-meters	Square feet per acre	Square meters per hectare
250	3	156	389	50	124	32	81	444	83
250[2]	9	NA	NA	52	130	NA	NA	NA	NA
430[2]	7	NA	NA	31	78	NA	NA	NA	NA
450	7	163	407	24	60	47	119	444	102
850	3	222	556	3	8	71	180	362	83

NA = not available.
[1] Trees>2-inch (5-cm) d.b.h.
[2] From Boyce and Bruce Wagg (1953).
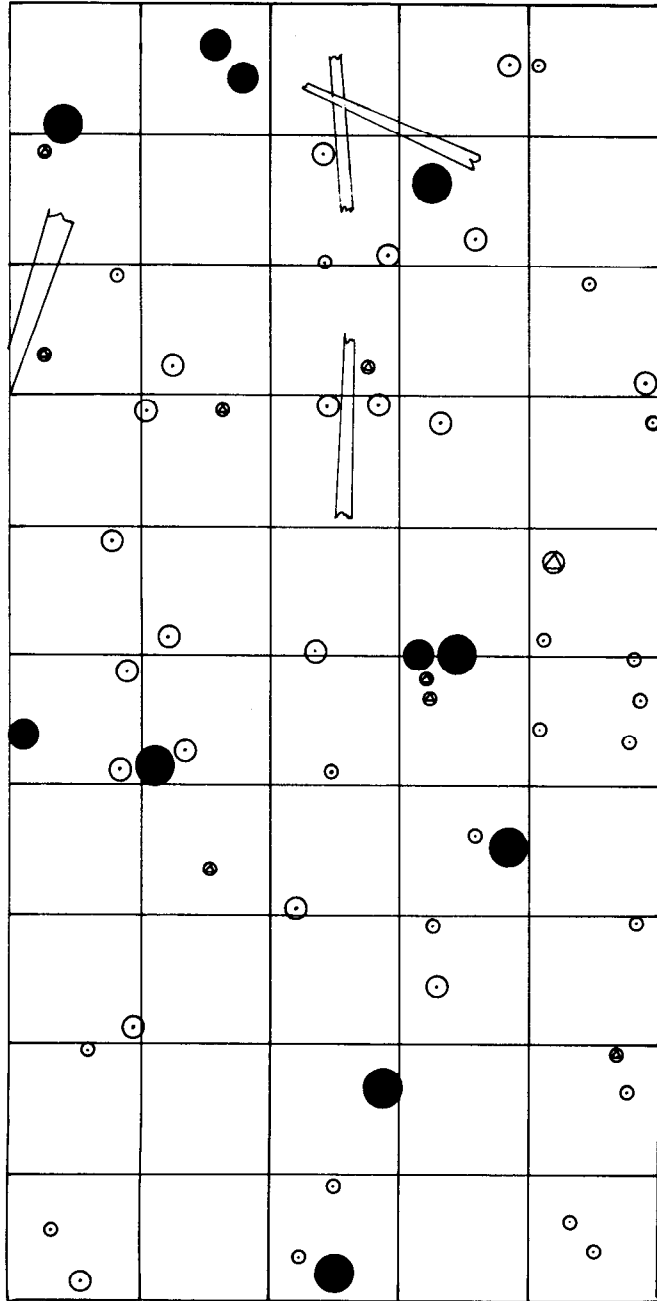
Tree density in age series of stands
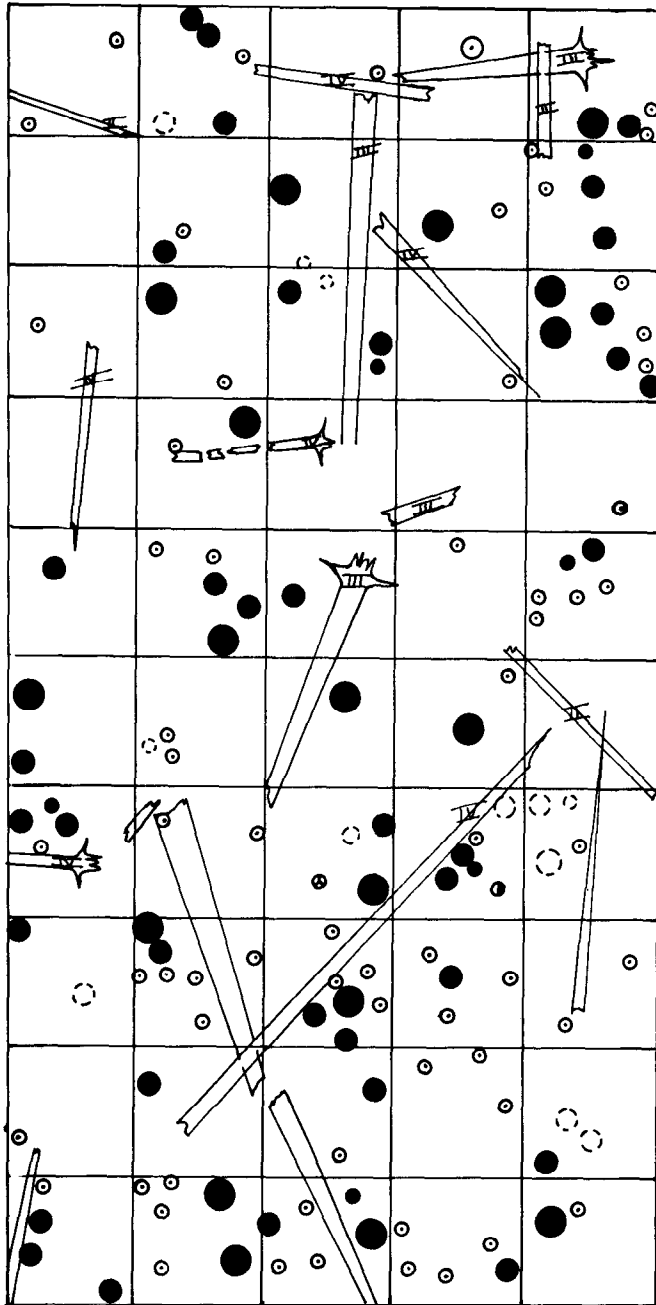
125
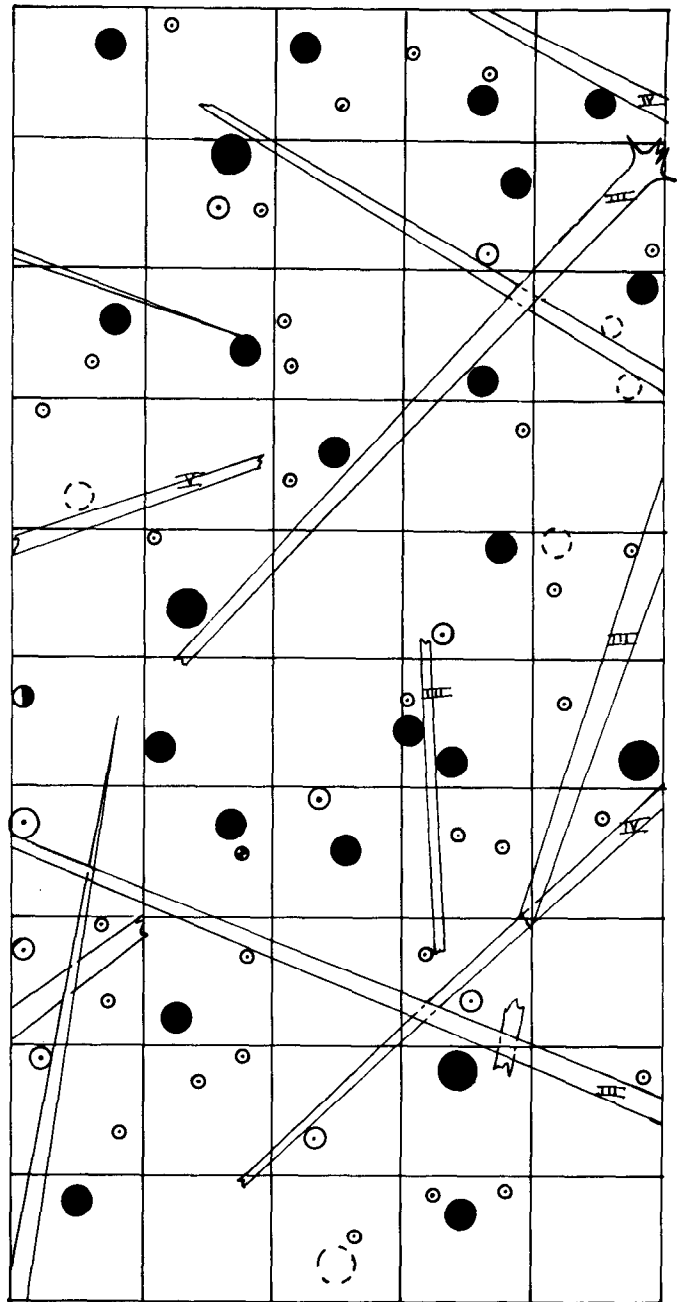
250

Figure 6. Stem maps of forest stands approximately 125, 250, 450, and 1,000 years of age, suggesting the increased range of tree sizes, reduced densities of Douglas-fir, and shift to shade-tolerant tree associates related to aging of the forest (all live trees greater than 2-inch (5-cm) d.b.h.).

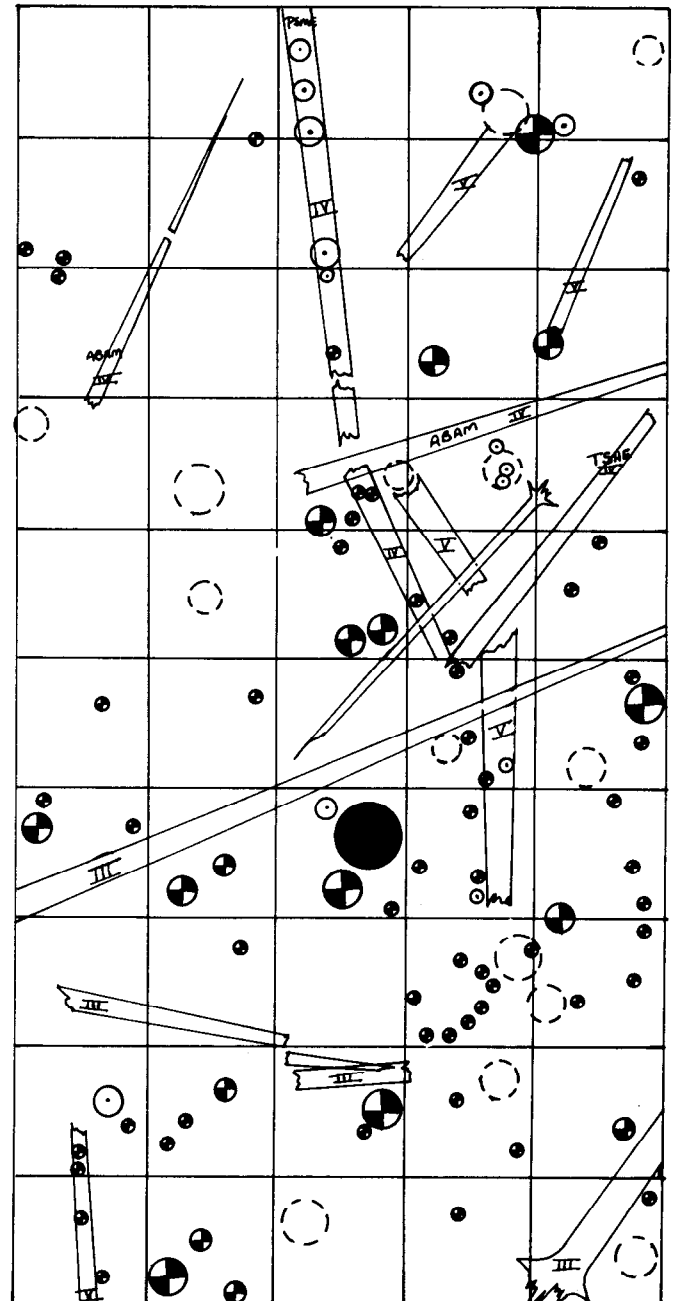# Tree density in age series of stands

450

1,000

Species code:
- ● Pseudotsuga menziesii
- ☉ Tsuga heterophylla
- ◑ Abies amabilis
- ◐ Thuja plicata
- △ Taxus brevifolia

Stem size class (centimeters):
- ○ 0-25
- ○ 26-50
- ○ 51-100
- ○ 100 +
- ⟳ Standing dead
- ⤳ Logs

Table 7—Mean diameters and coefficients of variation for all trees in excess of 12-centimeter (5-inch) d.b.h. for 7 young-growth stands and 7 old-growth stands on a wide variety of sites in the central Oregon Cascade Range

Young growth			Old growth		
Mean diameter		Coefficient of variation	Mean diameter		Coefficient of variation
Inches	Centi-meters	Percent	Inches	Centi-meters	Percent
11.5	28.7	77	10.8	27.0	131
12.5	31.3	80	12.3	30.8	112
13.3	33.3	84	14.4	36.1	100
13.6	34.0	69	15.8	39.5	91
16.9	42.2	48	17.4	43.5	114
20.8	51.9	53	21.7	54.2	92
25.7	64.2	39	29.2	73.1	61
Overall mean 16.3	40.8	64	Overall mean 17.4	43.5	100

Figure 7. Densities of all trees and Douglas-fir for stands illustrated in figure 6, showing the relatively constant level of density of all trees greater than 2-inch (5-cm) d.b.h. and declining densities of Douglas-fir.

Comparison of old-growth stands (450-year) with young-growth stands (125-year) in the Cascade Range of Oregon shows mean diameter of all trees over 12-inch (5-cm) d.b.h. to be close (table 7). The range of diameters is much greater in the old-growth stands, however, and this is reflected in the larger coefficients of variation (table 7). Total tree density (number of stems >2-inch d.b.h./acre or 5-cm/ha) does not appear to change much after a stand reaches 250 years of age (table 6 and fig. 7). Texture of bark changes with age and size, which, with the associated variation in diameter, undoubtedly reinforces the impression of greater heterogeneity in old growth.

There are few data to support the intuitive prediction that spatial heterogeneity of old-growth forests is greater than that of young growth. Moreover, variation in original stocking levels and site productivity from site to site would obscure any pattern in spacing. We tried to reduce some of this variation by pairing three young-growth and old-growth stands on the same habitat types in the Cascade Range. An analysis of distance to nearest tree was performed on the paired stands and on old-growth stands in the Coast Ranges of Oregon. Mean distance to the nearest tree and coefficients of variation in stands in the Cascade Range are somewhat greater in old-growth forests than in young growth (table 8). Because of unequal size of samples and their small numbers, the differences are not statistically significant at even the 10-percent level. The small size of the sample may also be obscuring trends. Mean spacing is significantly greater in stands of the Coast Ranges than in the Cascade Range (5-percent level), however, and the coefficients of variation tend to be larger (table 8).
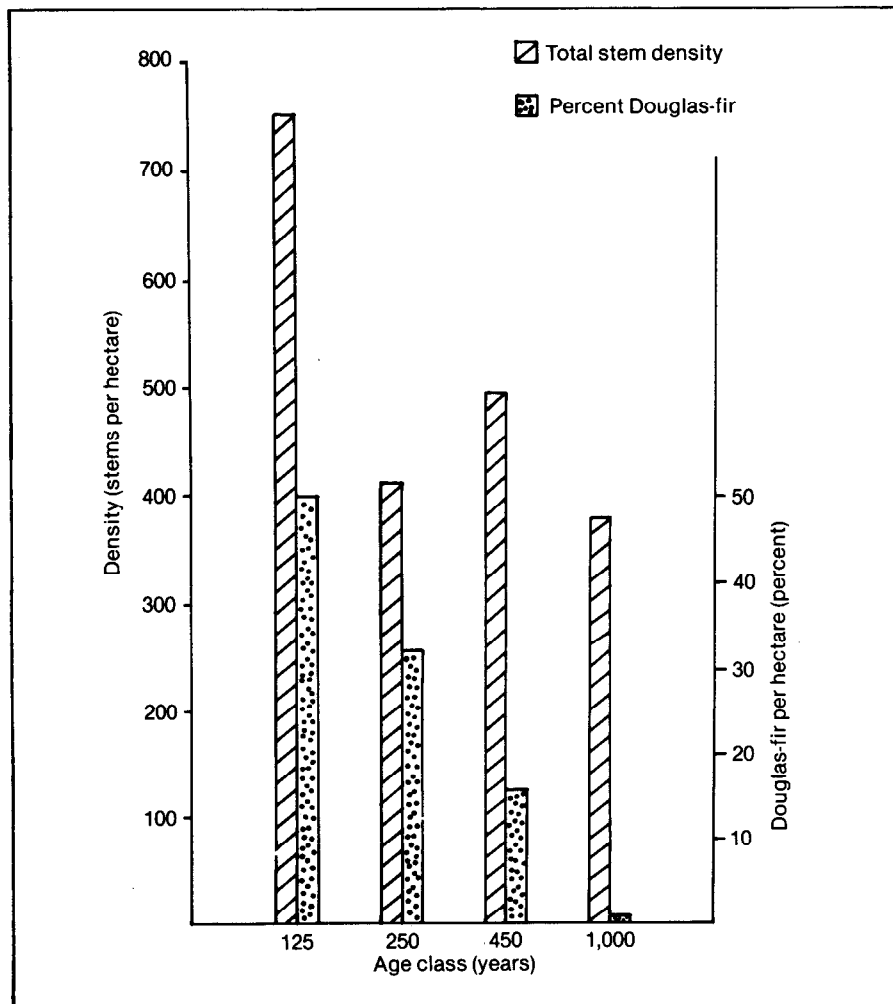
Another way to examine diversity is to plot histograms of numbers of trees in distance to nearest tree classes for the stands (fig. 8). Distributions are skewed much more toward smaller distances to nearest tree in the young-growth stands than in the old growth.

A commonly used index of diversity (H' or the Shannon-Weaver index) was calculated for the stands shown in figure 8 from the histogram data. Higher values of this index indicate greater diversity—the young-growth stands have H' values of 2.037 and 2.212; old-growth stands, 2.332 and 2.443.
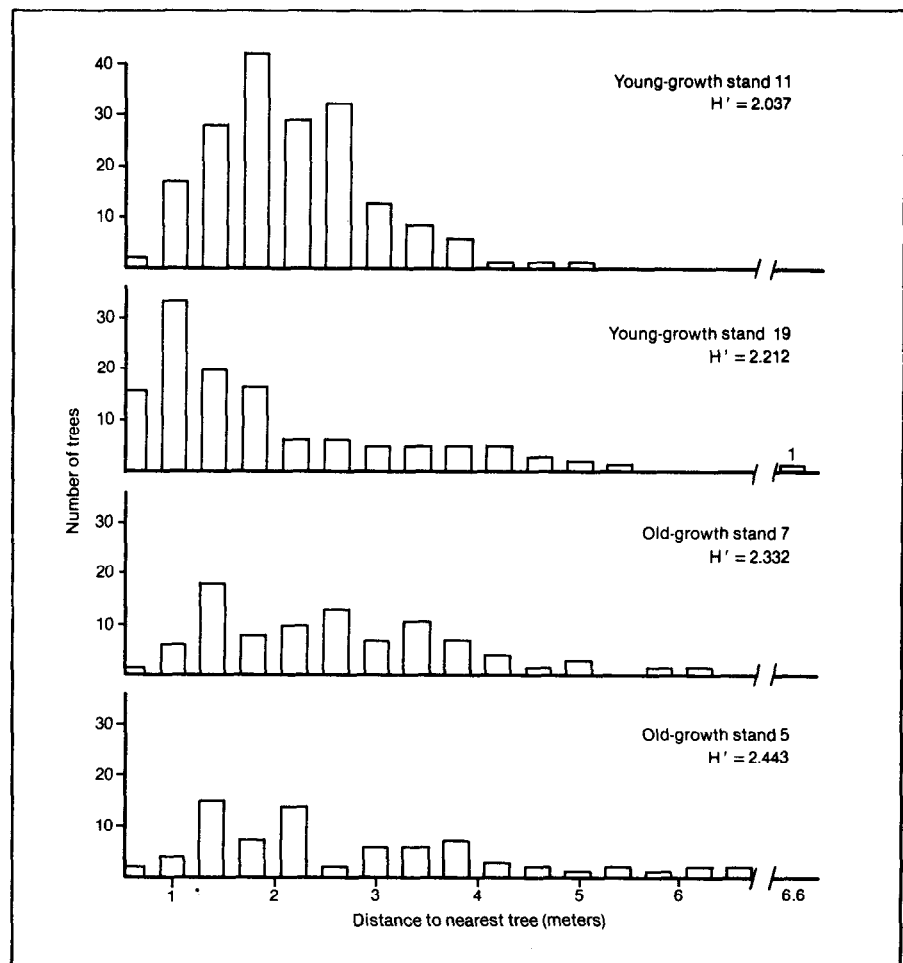
Conclusive demonstration of trends toward increased spatial heterogeneity in old-growth forests will require a much larger number of samples along a chronosequence of Douglas-fir stands, as well as in other coniferous forest types.

Diversification of tree structure may begin early. Many 90- to 130-year-old stands begin to show greater ranges in size of trees and a multilayered canopy. Time for development can also vary substantially with site conditions; stands on moist, productive sites develop a wider range of sizes earlier than do stands on dry, less productive sites. The broad range of sizes and varied canopy (as opposed to the monolayer of Douglas-fir canopies in young-growth stands) do not generally become well developed, however, until stands reach 200 to 250 years of age.

Figure 8. Number of trees greater than 12-inch (5-cm) d.b.h. by distance to nearest tree classes in two young-growth (125 years) and two old-growth (450 years) stands in the Cascade Range of Oregon.

Table 8—Mean distance to nearest tree and coefficient of variation for all trees over 2-inch (5-cm) d.b.h. in 3 young-growth and 3 old-growth stands on comparable habitat types in the Oregon Cascade Range and in 7 old-growth stands in the Oregon Coast Ranges

Location	Young growth (125 years)			Old growth (450 years)		
	Mean distance		Coefficient of variation	Mean distance		Coefficient of variation
	Feet	Meters	Percent	Feet	Meters	Percent
Cascade Range	7.00	2.12	37	9.14	2.77	53
	6.30	1.91	67	8.58	2.60	46
	9.24	2.80	49	9.47	2.87	45
Coast Ranges				9.14	2.77	53
				7.00	2.12	63
				9.11	2.76	55
				7.19	2.18	57
				10.56	3.20	65
				10.43	3.16	59
				10.00	3.03	58

Structural components

COMPOSITIONAL ROLE   FUNCTIONAL ROLE

Individual, large
old-growth trees

Distinctive epiphytes
Distinctive vertebrates
Distinctive invertebrates

Site of N-fixation
Ionic storage
Interception of H_2O
nutrients, light

Large standing
trees

Used by cavity
dwellers and other
vertebrates

Source of energy
and nutrients

Large down, dead
trees on land

Distinctive animal
communities
Seedbed or nursery
for seedlings

Site of N-fixation
Source of energy
and nutrients

Large down, dead
trees in streams

Distinctive animal
communities
Create habitat
diversity

Site of N-fixation
Source of energy and
nutrients
Maintain physical
stability of stream
Retain high quality energy
materials for processing

Figure 9. Most of the special habitat and ecosystem functions of old-growth conifer forests can be related to four structural components.

STANDING DEAD

INSECTS
FIRE
DISEASE

RECENT DEAD → DEAD → HARD SNAG → SOFT SNAG → STUB

LIVE
OLD-GROWTH
TREES

WIND, GRAVITY

FOREST
FLOOR

WIND

DECAY CLASS 1 → DECAY CLASS 2 → DECAY CLASS 3 → DECAY CLASS 4 → DECAY CLASS 5

DOWN DEAD

Figure 10. Routing of tree stems from live through various dead organic compartments; many pathways are possible.

A phenomenon related to diversification of stand structure is the development of greater patchiness in understory tree seedlings, shrubs, and herbs. Many young stands have relatively uniform understories—whether extremely depauperate, as in very dense stands, or with continuous cover of some dominant understory species, such as salal or swordfern. Homogeneity in the understory vegetation and forest floor gradually disappears as a stand develops. Many factors are responsible—shifting patterns of openings and heavily shaded areas and provision of new substrate, such as windthrown tree trunks and root wads. Understory patchiness seems characteristic of old growth in other forest types (coastal and subalpine), as well as Douglas-fir stands.

Three structural components (or four, counting logs on both land and in streams) are of overwhelming importance in an old-growth forest. These are the individual, live, old-growth trees; the large, standing, dead trees or snags; and the large, dead, down trunks or logs. Logs are at least as important (and possibly more so) to the stream component of the ecosystem as they are to the terrestrial component. It is these structural features that are, in large measure, unique to an old-growth forest ecosystem, setting it apart from young growth and, especially, managed stands. Furthermore, most of the unique, or at least distinctive, compositional and functional features of old-growth forests can be related to these structural features (fig. 9); that is, these structural components make possible much of the uniqueness of the old-growth forest in terms of flora and fauna (composition) and the way in which energy and nutrients are cycled (function).
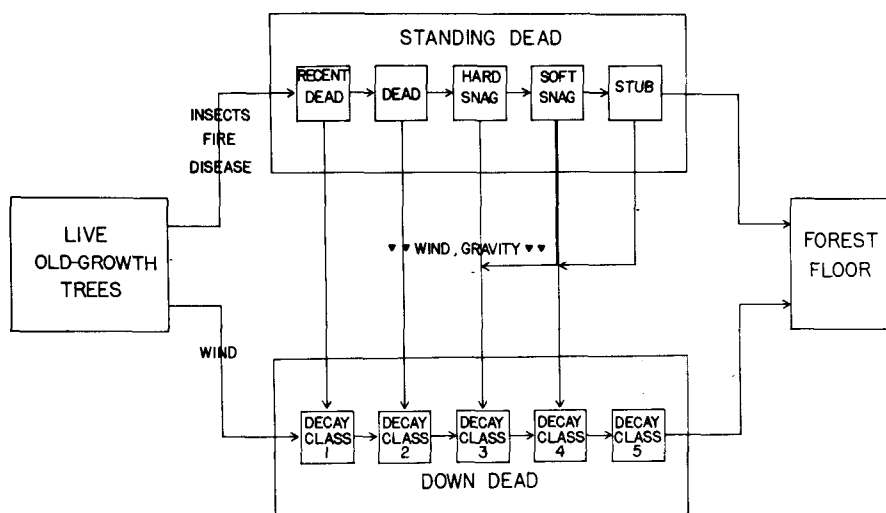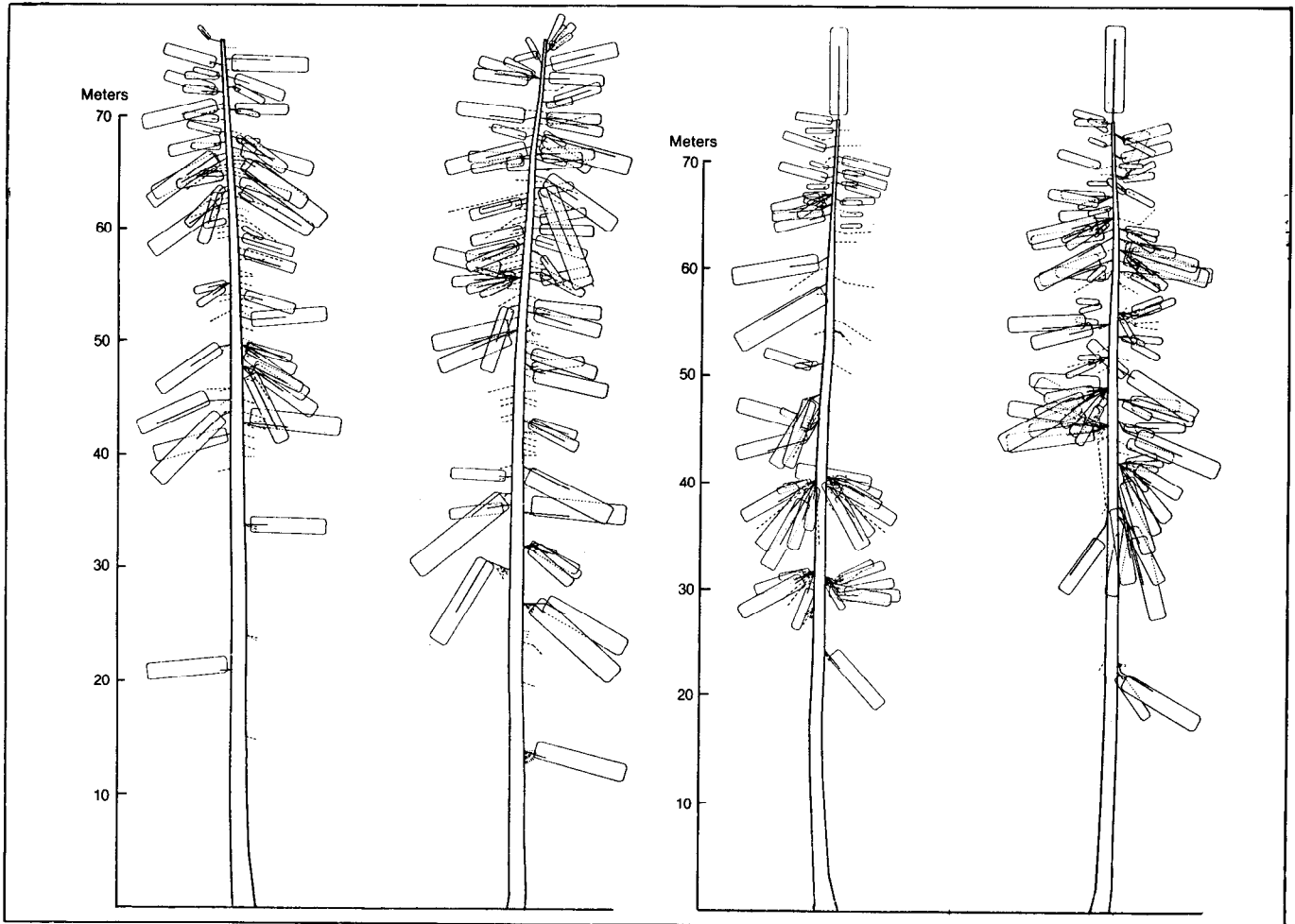
It is important to recognize that the four structural components are related (fig. 10). The dead organic structures—large snags and logs—are derived from the live old-growth trees. The tree thus plays a progression of roles from the time it is alive through its transformation to an unrecognizable component of the forest floor.

Live Old-Growth Trees. The most conspicuous of the four key structural components is probably the live, old-growth Douglas-fir trees. These trees are large; though size varies with site conditions and age, diameters of 3 to 6 feet (1 to 2 m) and heights of 165 to 295 feet (50 to 90 m) are typical. They are highly individualistic, much less uniform than trees in a 50- to 150-year-old stand. Each has been shaped over

the centuries by its genetic heritage, site conditions, competition with nearby trees, and the effects of storms, diseases, insects, and, possibly, soil mass movement.

The large, deep, irregular crown, characteristic of many old-growth Douglas-fir trees, is as ecologically important as the massive trunk (fig. 11). A 450-year-old tree typically has the overall shape of a bottle brush (albeit one with many missing bristles), with a cylindrical crown beginning 65 to 130 feet (20 to 40 m) above the ground and composed of

Figure 11. Schematic profiles of two old-growth Douglas-fir trees illustrating their individualistic nature and deep asymmetric crowns; several fan-shaped branch clusters are identifiable on the lower bole of both trees (diagrams courtesy W. Denison).

Figure 12. Many lower branches on old-growth Douglas-firs are large, horizontally flattened, fan-shaped arrays arising from the stub of an older branch; these provide extensive horizontal surfaces (photo courtesy W. Denison).

slender branches up to 6-inch (15-cm) diameter.[7] Branches are irregularly scattered through the lower two-thirds of the canopy; often there are gaps of many meters on one side of a tree (fig. 11). Many lower branches are horizontally flattened, fan-shaped arrays arising from the stub of an older branch and showing evidence of repeated breakage (fig. 12). Such massive irregular branch systems may be on one side of the trunk, but their follicled parts can spread out to surround over three-quarters of the circumference of the trunk. Upper surfaces of large branches are covered by organic "soil" (several centimeters thick), which is perched on the branches and supports entire communities of epiphytic plants (mainly mosses and lichens) and animals. Large branches are the home of myriad invertebrates, as well as birds and arboreal mammals. Branches in the upper third of the canopy are more numerous and regular in shape; they resemble those of younger trees.

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[7] The deep crowns of many old-growth Douglas-firs in old-growth forests of the Cascade Range have been the subject of considerable discussion among the authors. Douglas-fir crowns in many natural 75- to 150-year-old stands are quite short; live branch systems are confined to the upper one-third to one-fourth of the bole. It is hard to imagine how these trees could develop crowns similar to those of existing old-growth trees, even after several centuries. Epicormic branching is probably one factor. We also think that existing old growth originally developed in stands that were understocked; under such conditions, branch systems might persist much lower in the crown. A wide range in ages of dominant old-growth Douglas-firs in many stands does provide some evidence of low densities in original stands (Franklin and Waring 1980). If our inference about low tree densities being a factor in old-growth crown forms is correct, one implication would be that dominant Douglas-firs in many existing second-growth stands would not develop the "classical" old-growth form of crown. They might, however, develop the alternate form of crown often observed in the Coast Ranges and discussed later in this report.
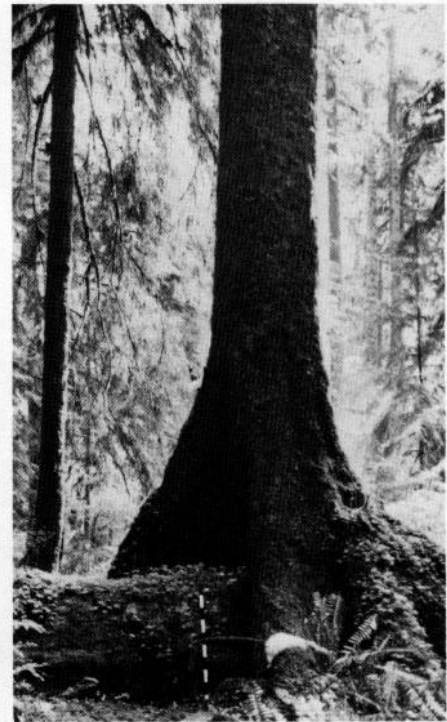

Figure 13. Long-lived species in the other forest types can attain the sizes of old-growth Douglas-fir and fulfill comparable ecological roles: Old-growth Sitka spruce (A) in coastal forests attain diameters of 60 inches (150 cm) or more and have massive epiphyte-laden branch systems. Noble fir (B) attains the largest size of any subalpine species but lacks a deep crown and dense branch system. Old-growth western redcedar (C) and Port-Orford-cedar (D) can be large specimens functionally comparable to old-growth Douglas-fir in many respects.

Old-growth trees frequently have broken tops, in which case one or several lateral branches may have grown upward and assumed leadership. Lateral branches of these secondary tops resemble those in the upper portion of an intact top.

Most stands have occasional old trees with their crowns concentrated at the top of the trunk in a spherical rather than a cylindrical form. Such
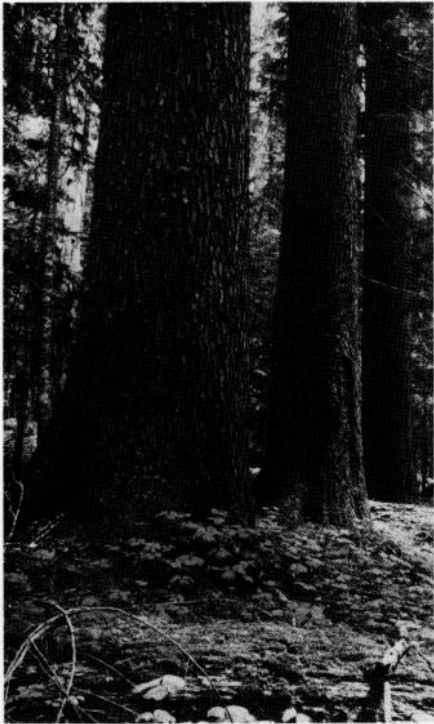
trees often overtop the adjacent canopy. The crowns of these trees are dominated by much larger limbs than are found in cylindrical crowns. This spherical form of crown seems more characteristic of old-growth stands in the Coast Ranges than of those on the west side of the Cascade Range and may reflect crowns developed in a denser stand (see footnote 7).

Few old-growth Douglas-firs have vertical trunks. The lower trunk leans away from the hillside but becomes nearly vertical where it extends above the surrounding canopy. Trunks on level sites appear to slope almost at random. Even a slight inclination of a trunk results in an important differentiation of habitat on its two sides. The upper
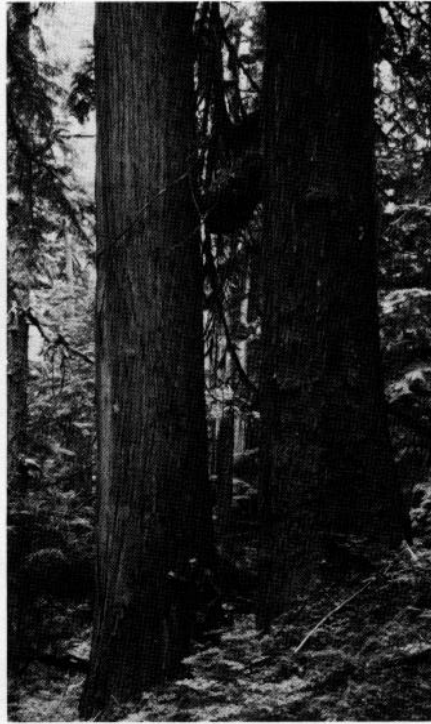
side gets almost all the moisture, both from direct precipitation and from stem flow and throughfall. Consequently, it is colonized by epiphytic plants (plants that grow on other plants) with relatively high moisture requirements, chiefly mosses. The lower side is a "desert" occupied by scattered colonies of lichens (Pike et al. 1975) that form a crust over the bark surface. The bark on the wet upper side is soft and easily eroded, sometimes appearing to be held in place by its mantle of mosses and lichens, whereas the bark on the lower side is hard and deeply furrowed, indicating that it remains in place for longer periods.

Old specimens of other tree species can play a role comparable to that of Douglas-fir to at least some degree, although none have been as thoroughly studied (fig. 13). Sitka spruce attains comparable sizes in coastal regions; irregular crown systems and heavy, epiphyte-laden branch systems are characteristic of
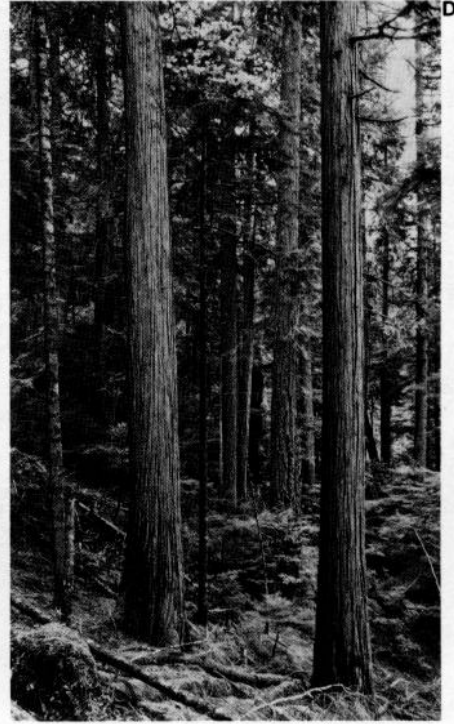
older specimens. Noble fir and western white pine are subalpine species with some, but not all, of the distinctive characteristics of Douglas-fir, as is sugar pine in southwestern Oregon. The so-called cedars—western redcedar, Alaska-cedar, Port-Orford-cedar, and incense-cedar—are capable of attaining sizes and fulfilling roles comparable to Douglas-fir in their respective types. These species have the additional advantage of fostering improved soil conditions through their base-rich litter. The major climax species—western hemlock, Pacific silver fir, and grand fir—appear, on the other hand, to lack the ability to completely fulfill the ecological roles of these long-lived pioneers.

Table 9—Temperature regime in an old-growth Douglas-fir tree canopy as related to precipitation during the current and preceding day[1]

Precipitation, current and preceding day	Days		Maximum daily temperature		Daily temperature range	
	Sept. 1976 to Aug. 1977	Sept. 1977 to Aug. 1978	Mean	Standard error	Mean	Standard error
Millimeters	——Number——		——————°Celsius——————			
0	195	124	18.8	± 11.2	13.1	± 6.8
0.1- 10.0	91	111	11.7	± 7.8	7.8	± 4.8
10.1- 20.0	35	48	9.5	± 6.0	5.8	± 4.0
20.1- 30.0	18	34	8.8	± 4.8	5.3	± 3.3
30.1-100	26	48	7.5	± 3.7	4.0	± 1.9

[1] An increasingly wet canopy results in lower minimum temperatures and a smaller diurnal range in temperature.

What ecological roles does a live, old-growth tree fulfill? There are many, but the most important are related to: (1) provision of habitat for the distinctive epiphytic plant and animal communities found in an old-growth forest; (2) effects on carbon, nutrient, and water cycling, especially the N budget of the site; and (3) source material for the other key structural components—standing dead trees, logs on land, and logs in streams.

Habitat Function. Many of the distinctive compositional features of old-growth forests—plants and animals—are related to the tree canopies. Almost every surface of an old-growth Douglas-fir is occupied by epiphytic plants; more than 100 species of mosses and lichens function as these epiphytes. The dry weight of mosses and lichens on a single old-growth tree ranges from 33 to 66 pounds (15 to 30 kg) (Pike et al. 1977), of which less than half is mosses; this excludes the ubiquitous crust-forming lichens which cannot be separated for weighing. In forests below 3,500-foot (1 000-m) elevation, about half the total weight of epiphytes is usually due to a single leafy or "foliose" lichen, *Lobaria oregana*, which is an active N fixer. Although lichens are found over almost all surfaces, many species are restricted to particular habitats (see table 1 in Pike et al. (1975) for an excellent illustration of this point). *Lobaria oregana*, for example, occurs chiefly on the upper sides of branches and twigs. *Lepraria membranacea*, on the other hand, prefers the lower trunk and the underside of branches. Nearly all mosses occur on the bottom half of a tree.

Epiphytic communities remove soluble mineral nutrients from water flowing over them. They also trap dust and litter fragments, including needles. This accumulation, augmented by decomposition of the epiphytes themselves, is most evident on the upper sides of large branches where it results in the formation of perched "soils."

When moist, the old-growth forest canopy is an important climatic buffer, a fact that may explain some of the special compositional and functional features of the canopy. Air temperatures in the canopy of an old-growth Douglas-fir stand in the western Cascade Range of Oregon can range as high as 104°F (40°C) during the summer and as low as 14°F (−10°C) during dry periods in the winter. When the canopy is wet, however, temperatures range from 32°F to 60°F (0°C to 15°C) (table 9). As precipitation increases, daily maximum temperatures and the daily temperature range decrease. This buffering reflects the large water-holding capacity of the canopy—about 264,000 gallons per acre (3×10^6 liters/ha)—equivalent to 1¼ inches (3 cm) of precipitation.

This environmental regime is important to survival of *Lobaria oregana* and may be to other canopy inhabitants. *Lobaria*, the dominant epiphytic lichen in old-growth stands on the west slope of the Cascade Range, is metabolically active when wet and dormant when dry. One-half to 1 inch (1 to 2 cm) of rainfall will wet the canopy sufficiently to raise the water content of the *Lobaria* above 70 percent. Below this moisture level, the lichen ceases to

fix N and is presumably protected against temperature extremes by dormancy. A moistened thallus would never be subjected to high temperatures because of the canopy's buffering (fig. 14). *Lobaria oregana* appears to be limited to habitats where moist conditions are always associated with cool temperatures, such as is characteristic of an old-growth canopy. When *Lobaria* thalli are transplanted to stands of young growth or mixed conifer-hardwood, they deteriorate rapidly, presumably because air temperatures exceed 60 °F (15 °C) and thalli are hydrated. *Lobaria oregana* usually does not occur in young Douglas-fir stands, possibly because their canopies hold insufficient moisture for adequate thermal buffering. It may be abundant on individual young trees in old-growth stands, however, where the surrounding mature trees provide an appropriate microclimate.

The canopy of an old-growth Douglas-fir forest harbors large numbers of invertebrates of many species. A single stand may have more than 1,500 species. A minority of species spend their entire cycle in the canopy: Araneida, Acarina, Homoptera, Collembola, Neuroptera, Thysanoptera, and Psocoptera. Other species of Lepidoptera, Hymenoptera, Diptera, and Coleoptera occur as eggs, larvae, and pupae in the canopy; but the adults can and do move out of the canopy. The majority of species encountered in the canopy are adults that spend their immature stages on the forest floor or in streams. In their canopy studies, Drs. George Carroll (University of Oregon) and William Denison (Oregon State University) discovered overwintering caddisfly adults in Douglas-fir canopies. Many adults of species of Mycetophilidae (fungus gnats) trapped in the canopy occur as larvae in the abundant mushrooms on the forest floor.
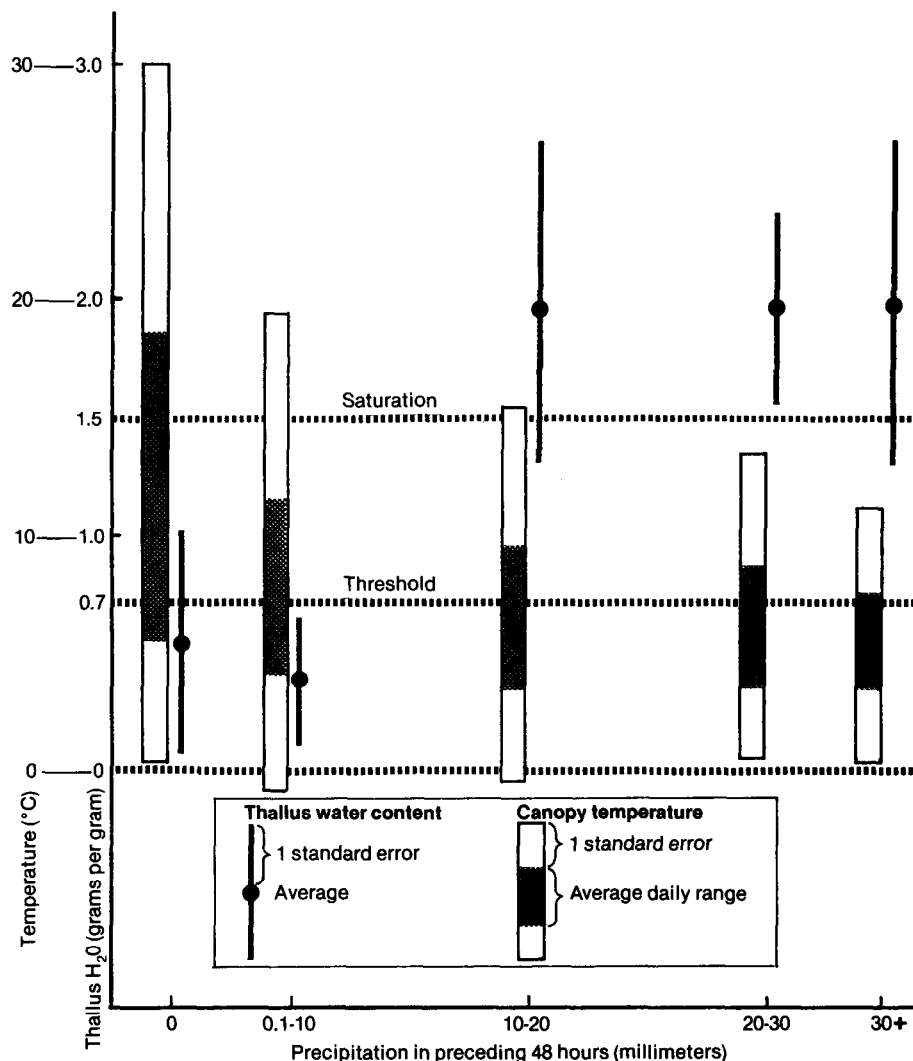

Figure 14. Relationship between canopy temperature, lichen (Lobaria oregana) thallus water content, and precipitation in the preceding 48 hours. Several thresholds are indicated: 0°C which is the lower thermal limit for nitrogen fixation; 70-percent thallus water content which is the lower moisture limit for nitrogen fixation; and 16°C which is the upper thermal limit (tolerance) for a saturated Lobaria thallus.

Although primary consumers (insects-such as sawflies, scales, or aphids-which feed on foliage or beetles which feed on wood) do occur in the canopy, they are not abundant. The most abundant arthropods are predaceous spiders, which belong to families such as Salticidae and Thomisidae. The large numbers of flies found in the canopy probably provide food for the spiders. Other arthropods feed on debris or on bacteria and fungi on surfaces of the canopy or are predators of other invertebrates. During one sampling period, invertebrates washed from foliage samples included:

Food source	*Invertebrates*
Needles	1 species of scale
	1 species of mealy bug
	1 species of Lepidoptera
Bacteria and fungi living on needles	6 species of mites
	4 species of flies (as larvae)
	5 species of Collembola
Other invertebrates	2 species of mites
	2 species of spiders

The canopy of an old-growth forest provides several insect habitats, both vertically and horizontally. Some species are found in the upper canopy, others in the lower; some species occur on major limbs and others among twigs and foliage.

Several vertebrates depend heavily on the old-growth canopy as sites for nesting, feeding, and protection. Well-known examples are the northern spotted owl, northern flying squirrel, and red tree vole. The vole may live for many generations in the same tree. The role that the large branch systems and organic accumulations play in providing suitable habitat should not be overlooked.

Cycling Function. Old-growth trees are one of the primary sites for photosynthesis, or production of the food base, on which the rest of the system depends. In this sense, they are the same as younger trees, except that each tree represents a large accumulation of organic material and nutrients (a "sink" in the short run and a "storehouse" in the long run) as well as a large photosynthetic factory. A single old-growth tree can have over 60 million individual needles with a cumulative weight of 440 pounds (200 kg) and a surface area of 30,000 square feet (2 800 m^2) (Pike et al. 1977). Total leaf areas in old-growth stands are probably not much different from those in younger stands, but the leaves are concentrated on fewer individuals. Fluctuations in production and live biomass strongly reflect mortality of these large dominant trees, which are both factory and storehouse, and the rate at which other trees occupy the vacated space.

A distinctive and unusual functional role of an old-growth tree is its contribution to the nitrogen economy of low-elevation to midelevation sites. Lichens that inhabit the canopy fix significant amounts of N which ultimately become available to the whole forest through leaching, litter fall, and decomposition. Estimates of fixed N range from 2.5 to 4.5 pounds per acre (3 to 5 kg/ha) per year. Most of the fixation is accomplished by *Lobaria oregana,* although several other large foliose lichens, such as *L. pulmonaria, Pseudocyphellaria rainierensis,* and *Peltigera aphthosa,* are also *azoto*-desmic[8] and, therefore, capable of fixing atmospheric *N. Lobaria ore-gana* accounts for half the total epiphytic biomass in the western Oregon Douglas-fir stands that have been studied. *Lobaria* and most N-fixing epiphytes are not common in young-growth stands, and this may be related to the microclimate of the old-growth forest canopy. Significant epiphytic inputs of N are, therefore, largely confined to old growth. Nitrogen-fixing bacteria on Douglas-fir foliage have not been found in the Pacific Northwest, even though they have been reported in Europe.

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[8] Azotodesmic lichens contain a blue-green alga, either as a primary plant symbiont or a secondary one, and therefore are capable of fixing N. Nonazotodesmic lichens contain a green alga as the sole algal symbiont and are not capable of fixing N.

Standing Dead Trees or Snags. In any old-growth stand there are substantial numbers of standing dead trees or snags (fig. 15). Indeed, snags were the first dead component of natural forests of which foresters were made aware—initially because of the fire and safety hazard they represent and, more recently, because of their value to wildlife (Bull and Meslow 1977, Bull 1978, Thomas et al. 1979a, Mannan et al. 1980). Some representative data for old-growth stands are provided in table 10. The only comprehensive study on dynamics of snags is by Cline et al. (1980), who studied 30 stands from 5 to 440 years old in the Coast and Cascade Ranges. Densities of snags decrease with stand age, but mean d.b.h. of snags increases from 5 to 29 inches (13 to 72 cm) between stand ages 35 and 200; larger snags survive longer. Cline et al. (1980) report mean densities of snags over 3.6-inch (9-cm) d.b.h. at 13.8 per acre (34.6/ha) and 7.3 per acre (18.3/ha) in stands 120 and 200 years old, respectively. These values, as well as a life table (model) estimate of 9.2 snags per acre (23/ha) for a 200-year-old stand, are substantially below the densities in table 10; all six of the old-growth stands of Cline et al. (1980) are located in the Coast Ranges.

Figure 15. Large numbers of standing dead trees or snags are characteristic of old-growth forests. A. The volume and numbers of standing dead trees may not be apparent to the casual observer in this 250-year-old Douglas-fir stand in the Bagby Research Natural Area, Mount Hood National Forest; dead stems are marked with an X. B. Heavily decomposed snags in old-growth Douglas-fir–western hemlock stand.
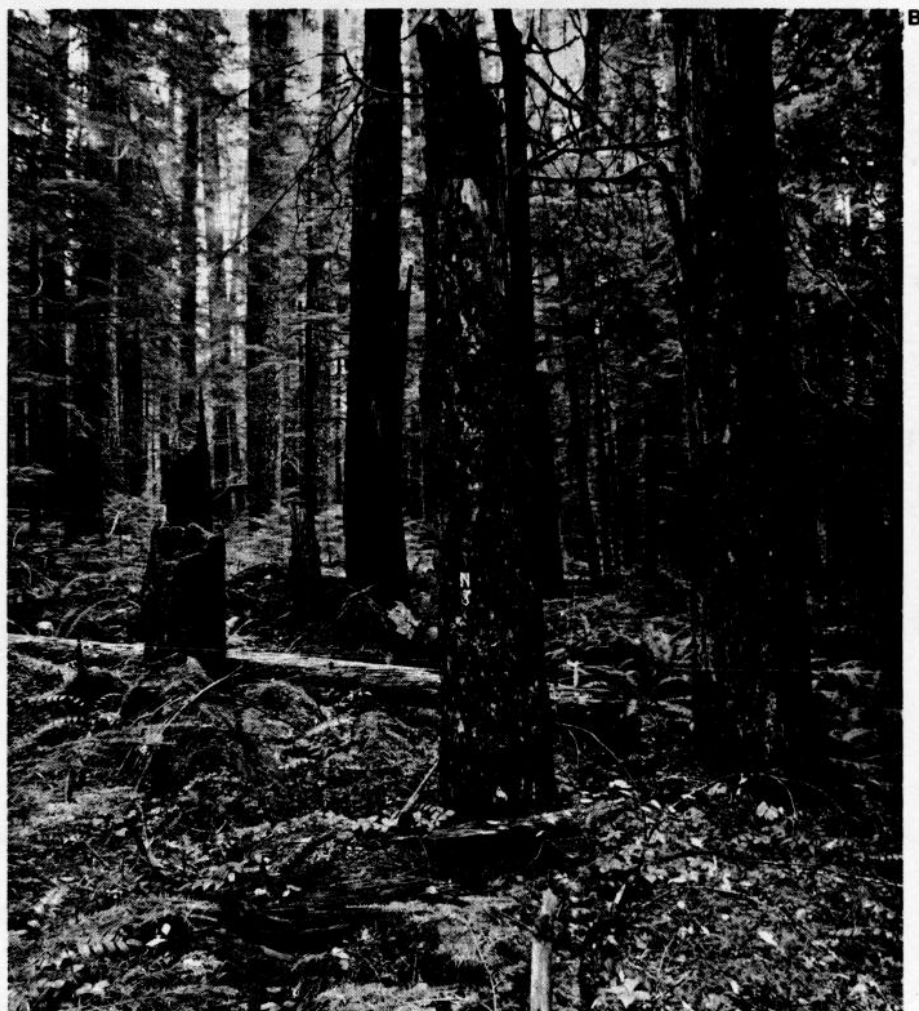
Table 10—Numbers of standing dead trees >13 feet (>4 m) in height and mean d.b.h. in age sequence of old-growth Douglas-fir-western hemlock stands in the Cascade Range[1]

| Forest age | Stands sampled | Height | | | All | Mean d.b.h. |
		13-31 feet (4-9 m)	32-64 feet (10-19 m)	>65 feet (>20 m)		
Years	Number	—— Number/acre (number/ha) ——				Inches (centimeters)
250	2	10 (26)	9 (22)	5 (12)	24 (60)	16 (42)
450	6	6 (16)	4 (10)	2 (6)	13 (32)	22 (57)
850+	3	7 (17)	5 (12)	2 (4)	13 (33)	25 (64)

[1] Short snags or stubs (<13 ft or <4 m in height) average about 61 per acre (152/ha) in 7 old-growth stands ranging from 250 to 1,000 years old; there is no apparent trend in numbers with age of stand in this small sample.

The large standing dead stems in excess of 20-inch (50 cm) d.b.h. and 65-foot (20-m) height are most valuable to wildlife (Scott 1978). Mannan et al. (1980) found hole-nesting birds usually used snags over 24-inch (60-cm) d.b.h. and 50 feet (15 m) tall in western Oregon. Density and diversity of species of hole-nesting birds were significantly related to mean diameter of snags. Smaller snags apparently do not provide suitable habitat for some animal species, and some tree species are preferred by hole-nesters (McClelland et al. 1979). Under natural conditions, large snags are not strictly a unique attribute of old-growth stands. Young-growth forests developing after wildfires have large residual snags from the original stand for various lengths of time. Cline et al. (1980) found residual or remnant snags in young-growth forest up to the oldest (110-year) age class they studied. Our experience is that large Douglas-fir snags typically persist for 50 to 75 years before being reduced to stubs less than 35 feet (10 m) in height; snags of western redcedar may remain essentially whole and standing for 75 to 125 years.

Large snags result from large trees; so they are a special product of old-growth forests. Managed young stands lack the residual snags of postwildfire stands unless snags are specifically planned. Natural stands appear to require about 150 years to develop snags 20 inches (50 cm) in diameter (Cline et al. 1980). Cline et al. (1980) suggest a life table approach for predicting densities and sizes of snags and recommend retention of large, defective trees for future snags in second-growth forests.

Various classifications, based on external features, have been developed for snags (Cline 1977, Cline et al. 1980, Thomas et al. 1979a); in general, these describe a time sequence in decomposition and disintegration of a dead tree (fig. 16). It is important to differentiate the stages of a snag since these are associated with changing values for wildlife. Both the path (stages) and the rate of disintegration of snags vary widely, however, depending on such factors as tree species, incidence and extent of decay at time of death, and environmental conditions. Douglas-fir snags typically disintegrate from the top down, losing the top and bark first. The trunk finally breaks off in large chunks, leaving a short snag or stub. Western redcedar and western white pine, on the other hand, often form bark-free, gray "buckskin" snags and remain essentially entire until they rot away at ground level and fall.

Habitat Function. A primary role of standing dead trees is the provision of habitat for wildlife. This has been discussed by Thomas et al. (1979a) for the Blue Mountains of Oregon and Washington. Snags in that area are the primary location for cavities that are used by 63 species of vertebrates—39 birds and 24 mammals. Uses include sites for nesting and overwintering, locations for courtship rituals, and food sources.

Thomas et al. (1979a) indicate a direct correlation between numbers of snags and related populations since suitable nesting sites are generally thought to limit populations; Mannan et al. (1980) confirm this for hole-nesting birds in western Oregon. The large, hard snags required by primary excavators, such as the pileated woodpecker (*Dryocopus pileatus*), are especially important. Such snags will be hard to perpetuate in managed stands (because of smaller trees and programs for salvaging wood and reducing fire and safety hazards); yet such snags are also suited to other wildlife species and will produce soft snags through the process of deterioration. Snags representing a variety of decay classes are needed in a stand to meet the differing requirements of vertebrates since not all use the same material. One special attribute of old-growth and large (natural), second-growth stands is that they provide the necessary array of snags with varying levels of decay, whereas young stands on cutover areas do not.

Cycling Function. Most of the functional roles (in energy and nutrient cycling, including sites for microbial nitrogen fixation) of standing dead trees are the same as those of logs and will be considered in the discussion of logs.
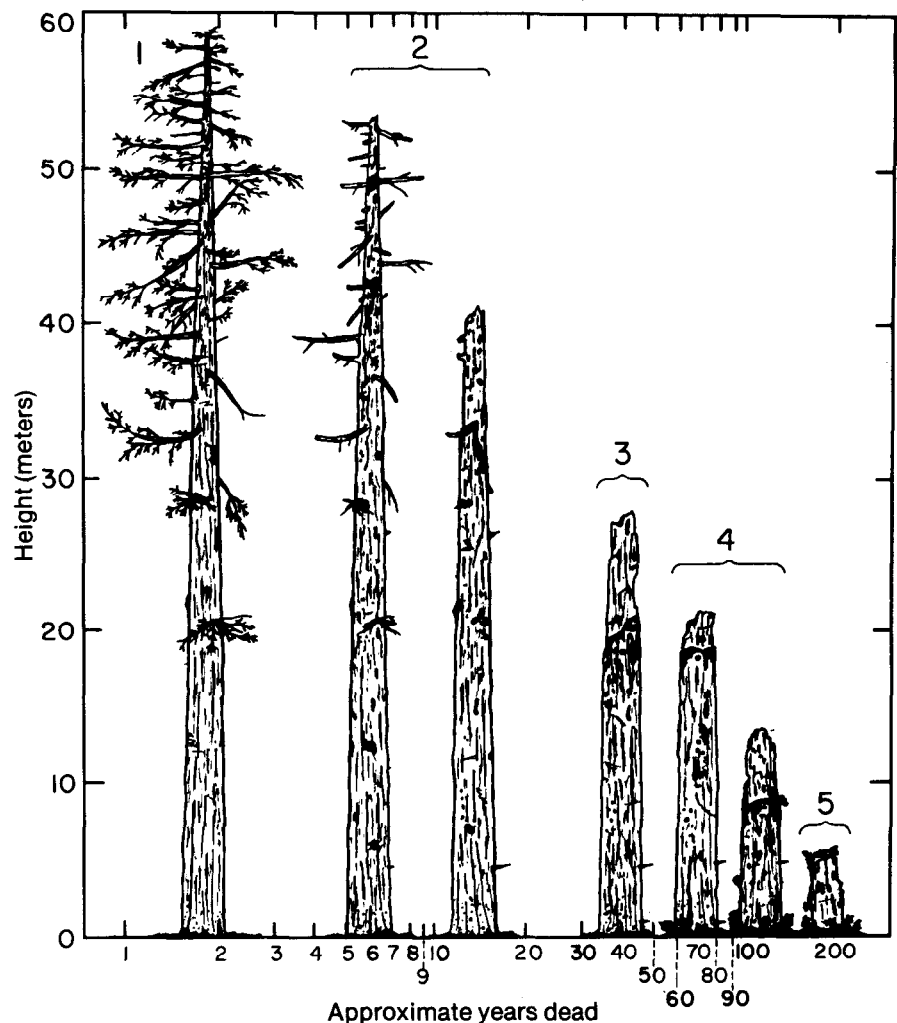
Standing dead trees do not necessarily disintegrate at the same rate or in the same way as logs and cannot be considered simply as vertical, dead trees (or vice versa) in terms of decay rates and agents. An old-growth Douglas-fir that dies standing appears to deteriorate much more rapidly if it remains standing than a tree of comparable size that dies by windthrow. The activity of invertebrate and vertebrate animals, gravity, wind, and the effect of rapidly alternating environmental conditions may all be factors involved in the more rapid disintegration of snags. This difference in the rate and nature of decomposition is, perhaps, the primary functional contrast between down trees and snags.

Figure 16. Successional or decompositional evolution of a standing dead Douglas-fir tree (courtesy Steve Cline).

Figure 17. Large masses of logs can be a dominant feature of old-growth forests, as illustrated in these stands with near-maximal accumulations: A. Midelevation stand of old-growth Douglas-fir in the western Cascade Range of Oregon. B. Old-growth stand of noble fir near Mount St. Helens, Washington.

Logs on Land. Logs, also describable as down dead trees or coarse woody debris, are nearly as conspicuous as the large, live trees. Large masses of logs can be the dominant feature of old-growth forests (fig. 17), and, in numbers, volume, and weight of organic matter, they constitute an important component. From 38 to 85 tons per acre (85 to 190 tonnes/ha) are typical values that have been reported. Down logs averaged 85 tons per acre over a 25-acre (10-ha) watershed covered with old-growth Douglas-fir–western hemlock forest (Grier and Logan 1977). Amounts within the watershed ranged widely —the lightest weights (24 tons/acre or 55 tonnes/ha) on a dry ridgetop and the heaviest (259 tons/acre or 581 tonnes/ha) on a lower slope, streamside area. Losses by downslope transfer had occurred on the ridgetop, and substantial amounts of debris had accumulated on the lower slope. In a 10-acre (4-ha) midelevation stand of Douglas-fir, western hemlock, and true firs, there were 82 tons of debris per acre (182 tonnes/ha),[9] 55 percent as recently fallen trees. Logs occupied 29 percent of the forest floor in this stand (fig. 18).

The average weight of down logs in seven old-growth stands, from 250 to over 900 years old, was 53 tons per acre (118 tonnes/ha);[10] the range was 38 to 70 tons per acre (85 to 156 tonnes/ha).[11] The largest accumulation of down wood recorded for a stand thus far is in the Carbon River Valley at Mount Rainier National Park; a hectare plot contains 188 tons per acre (418 tonnes/ha) of logs that covered 23 percent of the plot.

Logs are also major pools of important nutrients, such as N and phosphorus (P). In the old-growth watershed, the log component contained 192 pounds per acre (215 kg/ha) of N and 6.0 pounds per acre (6.7 kg/ha) of P (Grier and Logan 1977). In the midelevation stand, coarse woody debris contained 485 pounds per acre (544 kg/ha) of N (see footnote 9).
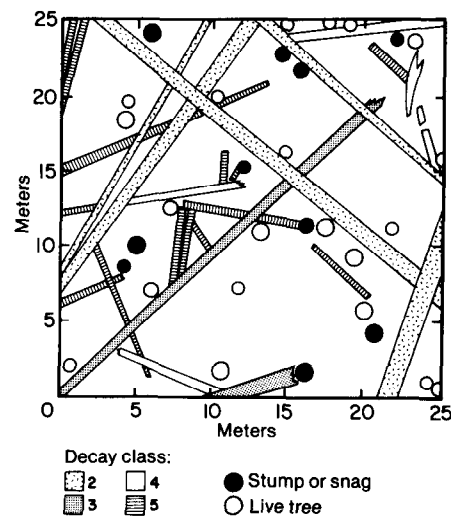

Figure 18. Down logs in midelevation stand of old growth in the H. J. Andrews Experimental Forest. Logs occupied 29 percent of the forest floor in this stand.

[9] MacMillan, Paul C., Joseph E. Means, Kermit Cromack, Jr., and Glenn M. Hawk. Douglas-fir decomposition, biomass, and nutrient capital in the western Cascades, Oregon. 65 p. Unpublished manuscript on file at Forestry Sciences Laboratory, Corvallis, Oreg.

[10] Unpublished data on file at Forestry Sciences Laboratory, Corvallis, Oreg. Stands are at low to middle elevations in the northern Oregon and southern Washington Cascade Range (from H. J. Andrews Experimental Forest, Oregon, to Mount Rainier National Park, Washington).

[11] Weights of down logs and stand age are only loosely correlated. Natural young Douglas-fir stands (about 100 years old), surveyed at the same time as the old growth, had masses of logs as large as some found in old-growth stands—primarily material carried over from previous stands as snags and logs. Large volumes of coarse woody debris are apparently characteristic of our natural forest ecosystems, adding credence to the concept of coarse woody debris as a mechanism to provide continuity of habitat from one forest generation to another (Maser et al. 1979) and for conserving large masses of organic matter and nutrients in major disturbances. It also suggests that the long-term ecological effects of nearly complete removal of woody debris in cutover stands and the prevention of new accumulations in intensively managed stands should be carefully examined.

Table 11—A 5-class scheme for rating decomposition of Douglas-fir logs[1]

Characteristic	Decay class				
	1	2	3	4	5
Bark	intact	mostly intact	partially intact to sloughing	absent	absent
Twigs, 1.2-inch (3-cm)	present	absent	absent	absent	absent
Large branches	present	present	present	present	absent
Exposed wood texture	intact	intact to partly soft	large, hard pieces	small, soft, blocky pieces	soft and powdery (when dry)
Portion of log on ground	support points	support points and slightly sagging	log is sagging	all	all
Exposed wood color	original	original	original to red-brown	light brown to reddish	red-brown to dark brown
Epiphytes	none	none	conifer seedlings (≤3 years old)	moss and hemlock seedlings	moss and hemlock seedlings
Log shape	round	round	round	round	oval
Invading roots	none	none	confier seedlings	in sapwood only	in sapwood and heartwood
Characteristics not used that also apply:					
Fungal fruiting bodies	none	*Cyathus, Tremella, Mycena, Collybia, Polyporus, Fomitopsis, Pseudohydnum*	*Polyporus, Polyporellus, Pseudohydnum, Fomitopsis*	*Cortinarius, Mycena, Marasmius*	*Cortinarius, Collybia, Cantharellus*
Mycorrhizae	none	none	none	in sapwood	in sapwood and heartwood

[1] Adapted from Fogel et al. (1972).

Figure 19. These logs are representative of several stages of decay or "decay classes."
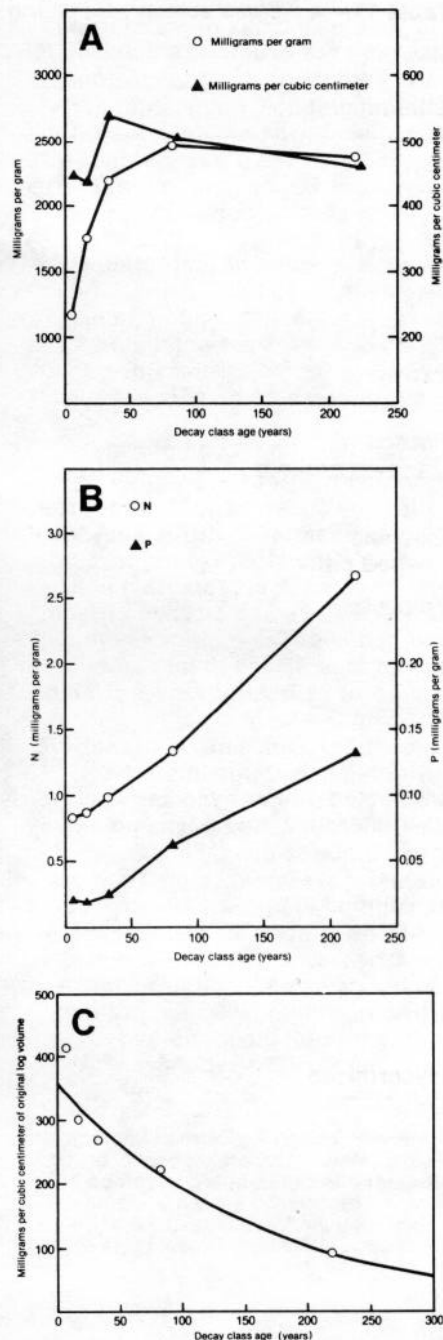

Figure 20. Important physical and chemical changes are associated with the progression of decomposition in logs. A. Changes in percent of water and volume of water per unit of wood with time; note the rapid increase in percent water early in decomposition. B. Changes in content of nitrogen (N) and phosphorus (P) with time. C. Changes in density of wood with time.

Like standing dead trees, logs go through recognizable stages of disintegration. One system for classifying the stage of decay of down logs is a five-class scheme based on easily recognized physical characteristics (table 11); some classes are shown in figure 19. As indicated in figure 10, standing dead trees may directly enter any of the first four log decay classes, depending on their condition when they fall. For example, a live tree, uprooted or broken off in a windstorm, becomes a decay class 1 log, whereas a very rotten snag might collapse into a decay class 3 or 4 log.

Important physical and chemical changes are associated with the progression of decomposition (fig. 20). Logs increase in moisture content at a very early stage in decomposition and retain significant quantities of water thereafter. This is an important factor in their suitability as wildlife habitat and as sites for establishment of tree seedlings and for N fixation. Nitrogen becomes concentrated in logs as decay progresses; over threefold increases occur between class 1 and 5 stages of decay. The concentrations of phosophorus and calcium show patterns similar to N.

Large logs disappear slowly. In one old-growth Douglas-fir stand at mid-elevation, for example, a class 5 log had charcoal on surfaces in contact with mineral soil, suggesting that it had fallen at the time of the wildfire that initiated the present stand-470 years ago! Decomposition rates can be expressed as decreases in log density (fig. 20c). Logs lose only about 40 percent of their original density after 150 to 200 years. Based on decomposition models, 480 to 580 years are estimated for a 30-inch (80-cm) diameter Douglas-fir log to become 90 percent decayed.'[?]

Habitat Function. Logs provide essential habitat for a variety of invertebrates (Deyrup 1975) and vertebrates (Maser et al. 1979). They are used as sites for lookouts, feeding and reproduction, protection and cover, sources and storage of food, and bedding. The high moisture content of logs makes them particularly important as habitat for amphibians.

Maser et al. (1979) reported that 178 vertebrates use logs in the Blue Mountains-14 amphibians and reptiles, 115 birds, and 49 mammals; they tabulated use by log decay classes for each species. Logs are considered important in early successional stages as well as in old-growth forests. The persistence of large logs has special importance in providing wildlife with habitat continuity over long periods and through major disturbances.

Logs may contribute significantly to reestablishment of animal populations by providing pathways along which small mammals can venture into clearcuts and other bare areas. This has relevance to the reestablishment of tree seedlings on bared areas since survival and growth of new trees depend on development of appropriate mycorrhizal associations. Surprisingly, fungal symbionts apparently disappear from cutover areas shortly after their host trees are removed (Harvey et al. 1978a), and the sites must be reinoculated with their spores. Many mycosymbionts have underground fruiting bodies and completely depend on animals for dissemination of spores. Small mammals are the vectors. They consume the fungus and carry spores to new areas, thereby inoculating tree seedlings (Maser et al. 1978a, 1978b; Trappe and Maser 1978).

Logs also serve as sites for reproduction of tree species, especially western hemlock (fig. 21). This is clearly an important function in natural stands since these seedlings and saplings supply replacements as openings appear in the overstory canopy. In one old-growth stand at midelevation in the Cascade Range, over 64 percent of the western hemlock and 4 percent of the Pacific silver fir reproduction were rooted in rotten wood.[13] The phenomenon of nurse logs is widespread in the forest types of the Pacific Northwest. Minore (1972) found that seedlings of both Sitka spruce and western hemlock were more numerous and taller on rotten logs than on the adjacent forest floor at Cascade Head Experimental Forest

in the Sitka Spruce Zone (Franklin and Dyrness 1973) on the Oregon coast. In the South Fork Hoh River Valley of Olympic National Park, also in the Sitka Spruce Zone, reproduction of spruce and hemlock is essentially confined to rotten wood substrates;[14] different species of logs also vary in their suitability as nurse logs as evidenced by differences in densities of seedlings. In subalpine environments, such as the Pacific Silver Fir Zone, successful reproduction of western hemlock is inevitably associated with rotten logs which are also heavily colonized by Pacific silver fir (Thornburgh 1989, Franklin 1988). Rotten logs as seedbeds or "nurseries" may have practical significance in a variety of situations; for example, as sites for natural reproduction after shelterwood or selective cuttings or for planting in cutover areas. Wood substrates appear to have particular silvicultural importance in coastal environments and where reproduction of western hemlock is desired. Rotten logs can also be of key significance in perpetuating campgrounds in old-growth forests in the Cascade and the Coast Ranges by providing seedbeds for tree reproduction.[15]

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[12] Means, Joseph E., Kermit Cromack, Jr., Paul E. MacMillan, and Alfred T. Brown. Models of Douglas-fir lo in a 450-year-old forest. 25 p. Unpublished manuscript on file at Forestry Sciences Laboratory, Corvallis, Oreg.

[13] Means, Joseph E. Personal communication. USDA Forest Service, Forestry Sciences Laboratory, Corvallis, Oreg.

[14] LaRoi, George H., and Jerry F. Franklin. 1979. *Picea sitchensis* and *Tsuga heterophylla* recruitment and survivorship in alluvial rain forests of the Hoh River Valley, Olympic National Park. Unpublished manuscript on file at Forestry Sciences Laboratory, Corvallis, Oreg.

[15] Moehring, Janis, and Jerry F. Franklin. 1977. Ohanapecosh camp round rehabilitation study. 51 p. Unpublished report for the National Park Service, Mount Rainier National Park.

Rotten wood is also critical as substrate for ectomycorrhizal formation. In one coniferous forest stand, over 95 percent of all active mycorrhizae were in organic matter—of which 21 percent were in decayed wood (Harvey et al. 1976b). In another study in the northern Rocky Mountains, decayed wood in soil was important in moist, mesic, and arid habitat types (Harvey et al. 1979); it was the most frequent substrate for active ectomycorrhizae on the dry site, probably because of high moisture levels in the wood. Mycorrhizal fungi can colonize logs, presumably using them as sources of water and nutrients (Harvey et al. 1978). The mycorrhizal relationships may be important factors in establishment of seedlings on nurse logs; they are also important to mature trees.

Just as quality and special properties of wood products vary by tree species, the natural ecological characteristics of logs also vary by species. Average size of logs and slow rates of decay make some species, such as Douglas-fir and redcedar, more persistent. Differences in value of species as nurse logs may relate to physical and chemical properties of the log or the type of wood rot infesting it; the inferior performance of western hemlock in the role of nurse log is one example.

Figure 21. Decaying logs are important habitat for the reproduction of tree species; this "nurse log" has seedlings of western hemlock, western redcedar, and Sitka spruce.

Cycling Function. Based on current knowledge, the most important cycling functions of logs are as sinks or storage compartments for energy and nutrients and as sites for N fixation. In addition, logs may provide physical stability, protecting the site from surface erosion.

The accumulations of carbon and nutrients represented by logs can be very large. In the short-term view, this material is a sink since it is made available so slowly. On the other hand, it is a significant source of stored energy and nutrients and one that can "bridge" major disturbances (can be continuous from an old-growth forest through a wildfire to a young-growth stand). Trunks of live trees, snags, and logs are structures in which N is retained through a wildfire; whereas in more easily burned organic components (leaves, forest floor) substantial N is volatilized and lost from the system.

The discovery of significant bacterial N fixation in coarse woody debris is recent; it occurred simultaneously in the forests of the Northeastern, Southeastern, and Northwestern United States. The most thorough study reported to date is Roskoski's (1977) in northeastern hardwood forests. Greater decay and higher moisture contents were associated with a higher incidence of N fixation in woody debris. Fixation occurred in an average of 25 percent of the wood samples >0.4 inch (1 cm) in diameter. Larger woody debris was probably more favorable for N fixation because of better moisture conditions (and consequent low oxygen levels) and because larger pieces last longer, disintegrate more slowly, and, therefore, provide greater opportunity for inoculation by the appropriate bacteria. Larsen et al. (1978) and Roskoski (1977) found higher rates of N fixation in logs at advanced stages of decay and higher moisture content.

Roskoski (1977) estimated total N fixation in hardwood stands of different ages. The largest amounts were in the youngest (14 years old-l.25 ± 1.80 kg/ha per year) and oldest (200 years old-0.96 ± 0.77 kg/ha per year) stands. The amounts of N fixed were directly related to the weight of coarse woody debris which was 17 tons per acre (38 tonnes/ha)-all from the previous old-growth forest-and 15 tons per acre (34 tonnes/ha) in the 4- and 200-year-old stands, respectively.

Amounts of N fixation have not yet been estimated for old-growth coniferous forests in the Pacific Northwest, although N fixation has been detected. Substantially greater amounts are expected than those estimated for eastern hardwood forests, based on the large tonnage of woody debris present (5 to 15 times that reported by Roskoski 1977), and the much larger average size of material in the Douglas-fir region. We estimate approximately 4 pounds per acre (4.4 kg/ha) per year of N fixed in an average old-growth stand;[16] a daily rate from Larsen et al. (1978) of 2.0×10^{-9} moles per gram of logs is assumed in all decay classes throughout the year in the more moderate year-round climate on the west coast.

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[16] Our typical old-growth stand has 65 tons per acre (145 tonnes/ha) of logs and 20 tons per acre (45 tonnes/ha) of snags.

Decaying logs and decayed wood in soil are also of overwhelming importance as sites for nonsymbiotic N fixation in forests in the northern Rocky Mountains (Harvey et al. 1978); this is especially true of dry sites and during dry periods. Nitrogen fixation may occur in standing dead trees, even with their wider fluctuations in moisture content and aeration, but the amounts are unknown. Fixation is also associated with development of heart rots in live trees (Aho et al. 1974). Harvey et al. (1978) provide examples of both situations-N fixation associated with *Fomes pinicola* (a saprophytic fungus) in dead Douglas-fir and with *Echinodontium tinctorium* (a heart rot) in live western hemlock.

Logs have numerous important roles in cycling nutrients and maintaining site productivity. Complete removal of wood residues by harvesting and broadcast burning eliminates logs as reservoirs of nutrients and water and as entities whose physical effects may have a positive influence on the quality of a site (Jurgenson et al. 1977). Increased commercial use of wood residues or complete yarding of unmerchantable residues reduces the amount of sound or partially decayed logs. Since the products of decay and fire (humus, decayed wood, and charcoal) are important to quality and function of forest soils (Harvey et al. 1978, Jenny 1980), future forest management must consider logs as "parent material" for soil organic matter.

Logs in Streams. Large, woody debris in streams is a dominant element in aquatic ecosystems of old-growth forests. Debris largely controls the distribution of aquatic habitats, stability of streambeds and streambanks, and routing of sediments and water through the stream system.

Large, organic debris enters streams by a variety of mechanisms, some of which are interrelated and occur as a chain reaction. Principal mechanisms of input are blowdown, slides, avalanches, deep-seated mass movements from adjacent slopes, and undercutting of streambanks. Large debris is exported from sections of streams by flotation at high streamflow; in massive debris torrents involving the rapid down-channel movement of a slurry of soil, alluvium, and large organic debris; and by movement of fine particulates and dissolved material produced by biological and physical breakdown of logs.

The general character of large debris in small (first to second order) and intermediate-size (third to fourth order) streams in old-growth Douglas-fir is shown in figures 22 and 23. The first-order stream (fig. 22) is choked with debris, located essentially where it fell. The third-order stream (fig. 23) is large enough to float and redistribute some of the debris, forming accumulations along the channel. The third-order stream is still narrow relative to the length of individual pieces of debris, so accumulations of debris affect the width of the entire channel. In fifth-order and larger rivers, debris from old-growth forests accumulates high on streambanks at high flow, and, therefore, plays only a minor direct role in the physical and biological character of the river (Keller and Swanson 1979).
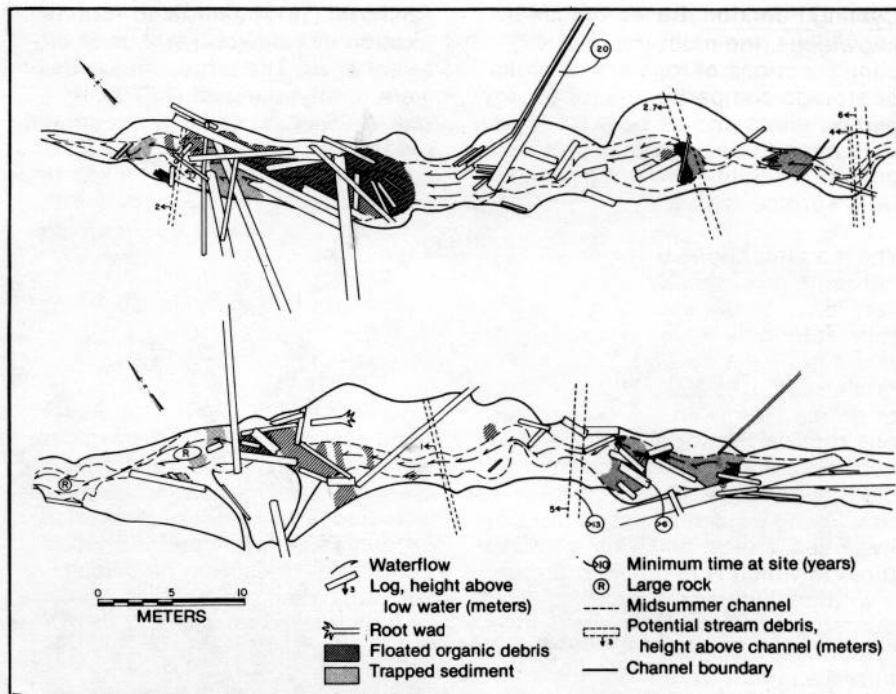

Figure 22. Small, first-order streams in old-growth forests are often choked with coarse woody debris as in these mapped sections of a stream in the H. J. Andrews Experimental Forest, western Oregon Cascade Range.
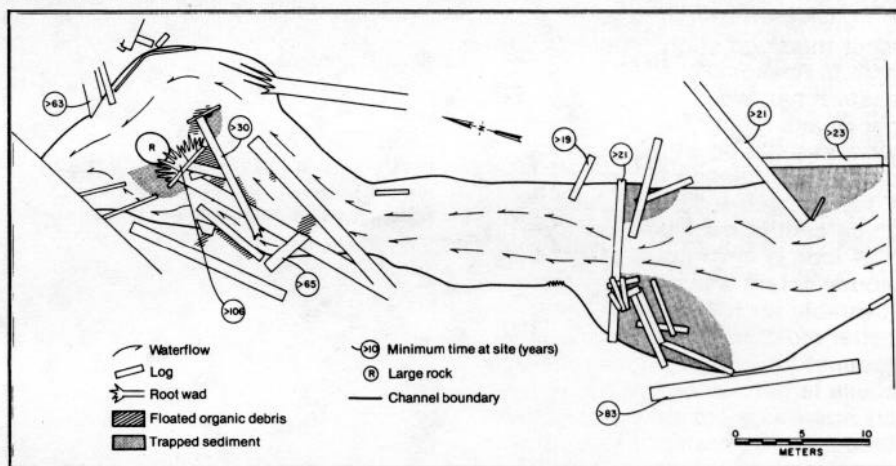

Figure 23. Third-order streams are large enough to float and redistribute much of the woody debris, forming distinct accumulations as in this section of Mack Creek in the H. J. Andrews Experimental Forest, western Oregon Cascade Range.

Table 12—Loading of coarse (>4-inch or 10-cm diameter) debris in sections of 5 streams flowing through old-growth Douglas-fir forests in the McKenzie River system, western Oregon[1]

Stream	Loading of coarse debris		Length of sample area		Width of channel		Gradient of channel	Stream order	Watershed area	
	Pounds per square foot	Kilograms per square meter	Feet	Meters	Feet	Meters	Percent		Square miles	Square kilometers
Devilsclub Creek	8.7	43.5	297	90	3.3	1.0	40	1	0.08	0.2
Watershed 2 Creek	7.6	38.0	445	135	8.6	2.6	26	2	.32	.8
Mack Creek	5.7	28.5	990	300	40	12	13	3	2.4	6.0
Lookout Creek	2.3	11.6	990	300	79	24	3	5	24.2	60.5
McKenzie River (Rainbow)	.1	.5	2,640	800	130	40	.6	6	410	1 020

[1] Specific gravity of wood is assumed to be 0.50 gram per cubic centimeter.

The relationship between size of debris and size of stream controls the arrangement and concentration of large debris at different points in a river system. In a downstream sequence, conditions change from (1) abundant, randomly distributed debris to (2) moderate loading of debris in a clumped distribution, and finally, to (3) a low concentration of widely distributed debris. The general decrease in loading of coarse debris downstream is exemplified in the McKenzie River system where headwater tributaries may have nearly 10 pounds per square foot (50 kg/m²) of coarse woody debris, whereas the mainstream McKenzie River at Rainbow has only 0.1 pound per square foot (0.5 kg/m²) (table 12).

Quantities of large debris in streams flowing through old-growth forest are large and variable. Froehlich (1973) measured large organic debris (>10-cm or 4-inch diameter and >0.3-m or 1-foot length) in 10 relatively undisturbed streams draining from 6 to 120 acres (2.4 to 49 ha). Values ranged from 7.1 to 24.8 tons per 100 feet (21 to 73.9 tonnes/100 m); mean was 13.8 tons per 100 feet (41.1 tonnes/100 m) and standard deviation, 6.6 (19.7). In five streams draining 282 to 1,593 acres (114 to 645 ha), loadings of large debris were 5.7 to 14.2 tons per 100 feet (17 to 43 tonnes/100 m); mean was 10.3 tons per 100 feet (30.7 tonnes/m) and standard deviation, 3.6 (10.7).

Expressed on an area basis, concentration of large debris averaged 10.1 pounds per square foot (50.6 kg/m²) in the small streams draining less than 120 acres (48 ha) of old growth. In contrast, large debris in four natural, second-growth stands initiated by wildfire 75 to 135 years ago averaged only 3.8 pounds per square foot (19.1 kg/m²). Furthermore, 75 percent of the coarse debris loading in these streams was made up of large diameter, decomposed pieces derived from the prefire, old-growth stand. Structural elements inherited from preexisting old-growth stands may persist in a stream through much of the development of second growth. Swanson and Lienkaemper (1978) hypothesized that streams flowing through managed, short-rotation forests will have very low loadings of coarse debris because management activities, such as harvesting and thinning, remove the source of large debris.

Loading of debris may be abruptly reduced by debris torrents, or "sluice-outs." Debris torrents are rare occurrences in old-growth ecosystems; the return period of torrents in a 25-acre (10-ha), old-growth watershed in the H. J. Andrews Experimental Forest has been estimated to be from 500 to 600 years. Torrents may reduce loading of debris to less than 1.0 ton per 100 feet (3.0 tonnes/100 m) of stream. As torrents move past forested streamside areas, however, banks are undercut, destabilizing trees and leading to a several-decade post-torrent period of relatively high inputs of coarse debris and reestablishment of stable debris dams and associated stream habitat. Where streamside stands are very young (less than 30 or 40 years), pieces of debris after a torrent may not be large enough to form stable accumulations and associated habitat.

The history of large debris in streams has been examined by dendrochronological methods (Swanson et al. 1976, Swanson and Lienkaemper 1976). Large pieces of debris commonly have been in streams for 25 to more than 100 years and have, therefore, weathered extreme events, such as the December 1964 flood in the Pacific Northwest. Western redcedar is particularly long lasting, followed, in order of increasing rate of breakdown, by Douglas-fir, western hemlock, and riparian hardwoods. This long residence time results from both the characteristic predominance of slowly decomposing Douglas-fir and western redcedar and the large debris provided by old-growth stands.

Large debris in streams strongly influences morphology of the channel and routing of sediment and water. In first-order through about third-order streams, debris helps to form a stepped longitudinal stream profile. Much of the energy of a stream is dissipated at falls or cascades created by debris. This pattern of dissipation in a small proportion of total stream length results in less energy available for erosion of bed and banks, more storage of sediment in the channel, slower routing of organic detritus, and greater diversity of habitat than in straight, even-gradient channels.

In small and intermediate streams in the Pacific Northwest, large debris may be the principal factor determining the characteristics of aquatic habitats. The important role of debris in creating habitat for fish has been reviewed by Narver (1971), Hall and Baker (1975), and others. The wood itself is a habitat or substrate for much biological activity by microbial, invertebrate, and vertebrate organisms.

The general influence of woody debris on aquatic habitat has been measured in several streams in the H. J. Andrews Experimental Forest (Swanson and Lienkaemper 1976). In an 800-foot (240-m) section of Mack Creek, which flows through old growth, 11 percent of the stream area is woody debris, 16 percent is wood-created habitat (primarily depositions of sediments behind woody debris), and 73 percent is nonwoody habitat-mainly cascades dominated by boulders. This section occurs in a third-order stream channel draining about 1,500 acres (600 ha). Woody debris occupies 25 percent and wood-created habitat another 21 percent of the stream area of Devilsclub Creek, a first-order tributary of Mack Creek draining 25 acres (10 ha). Much of the biological activity in the processing of detritus and other consumer organisms is concentrated in the wood and wood-created habitats.

Over half the inputs of N are associated with woody debris, including N fixation on wood. Quantitatively, woody debris is also the major energy input.

Distinctions between stream ecosystems in old-growth and second-growth stands are less clear than those between stream orders. Large organic debris plays the dominant role in streams in old-growth forests and clearly does not in managed second-growth forests. Natural, second-growth stands have residual debris dams as well as residual large stems for new dams that help span the period until the, young stand begins producing larger diameter woody debris. Analysis of the overall response of aquatic communities to long-term changes in structure and nutrient sources, such as those resulting from reduced concentrations of large, organic debris, is an important research problem.

In summary, coarse woody debris Is extremely important to streams In old-growth coniferous forests. Debris dams and associated plunge pools and trapped sediments, such as gravel bars, provide a great diversity of habitats for organisms. The resulting stepped stream profiles provide for greater physical and biological stability by dissipating energy otherwise used in cutting channels and moving sediment. Debris dams also slow the routing of other organic inputs, allowing organisms time to more fully process these materials before they are exported downstream. Finally, the woody debris is itself a major source of energy and nutrients for the stream ecosystem.

Old-growth forests provide highly specialized habitats and are neither decadent, unproductive ecosystems nor biological deserts. In this paper, we have contrasted the compositional, functional, and structural features of old growth with those of young-growth forests wherever data permit. It is clear that there are major contrasts between old-growth and managed, young-growth stands; structures, species, and patterns and rates of material (carbon and nutrient) flows and cycles characteristic of old growth will be absent from managed lands unless specifically provided for in silvicultural prescriptions. Differences between old-growth stands and natural, second-growth stands often appear to be one of degree; however, this is often because of material carried over from the old to the new stand, such as large snags and logs, which provide woody debris and animal habitat and serve other functions.

Alternatives for managing old-growth forest ecosystems or attributes include management to: (1) perpetuate existing old-growth stands, (2) recreate ecosystems with old-growth characteristics by long rotations, and (3) provide for individual features of old-growth forests. The first two alternatives involve a relatively small percentage of the commercial forest land in the Pacific Northwest; various acreages have been proposed in Federal land-use planning exercises, including spotted owl management plans, generally totaling 5 percent or less of the land base. Perpetuation of existing stands is the surest course since the old-growth conditions exist and can be expected to persist

for several additional centuries. This assumes viable sites (appropriate size and shape with boundaries that can be protected) are selected and catastrophic fire and windthrow are avoided. Recreation of old-growth conditions through long rotations is theoretically possible but clearly unproved at this time. Site selection is important, though perhaps not as critical as it is where perpetuation of an existing old-growth forest is the objective.

The third alternative-providing for individual features-involves applying the information from this report to the main body of commercial forest land in the Pacific Northwest, not simply to the small enclaves managed for old growth. Our knowledge of old-growth forests and how they work can be used to advantage in managing millions of acres of forest for timber production by improving their ability to provide additional ecological benefits. Some of the most important ecological features of old-growth forests, and, indeed, the entire natural forest sere, can be duplicated on these lands with relatively small sacrifice of production of timber. Knowledge of old growth, such-as that about snags and coarse woody debris, is widely applicable to forest management.

If the forest manager decides to retain, maintain, or recreate some forest ecosystems with old-growth characteristics several questions require attention. How should the old-growth allocation be distributed over the landscape? Which management practices should be followed in areas selected for retention of old growth and on areas to be managed on long rotations? Size and shape of old-growth enclaves are, distributional concerns. Structural features are the management key in either perpetuating or recreating old-growth stands.

Distribution of Old-Growth Management Areas. Having decided to maintain a certain percentage of a management unit as old-growth forest, a land manager must decide how it is most effectively distributed. Should a small stand be maintained in each drainage or compartment or fewer large tracts reserved? Where are boundaries best located? The history of natural wildfires is somewhat instructive, at least in indicating the landscape patterns in which existing old-growth stands originated. Stands were typically established in blocks of hundreds of acres. Boundaries most often were along topographic features, such as ridges or streams. "Feathering" of boundaries, resulting in large areas of mixed stands (residual old growth scattered through a young stand), was common. Fires often skipped large patches of trees, particularly on lower slopes and stream bottoms, or stands protected by natural barriers.

How large a drainage unit or stand is essential for a viable old-growth ecosystem is a difficult question. Generally, an area of 300 to 500 acres (120 to 200 ha) is sufficient for most plants and animals. This size has been suggested as essential to a pair of breeding northern spotted owls, for example, one of the most wide-ranging species dependent on old growth. McClelland et al. (1979)

suggest 50 to 100 acres (20 to 40 ha) for the nesting and feeding areas of cavity-dwelling birds. Generally, 500 to 1,000 acres (200 to 400 ha) are needed for a third-order stream drainage. Areas much smaller than 500 acres (200 ha) can, on the other hand, preserve many attributes of old-growth forests, particularly if the boundaries chosen for the area prevent rapid deterioration of the stand.

Entire drainage basins, even for small first- or second-order streams, are ecologically the most desirable units for old-growth forest management. Such drainages have natural topographic boundaries that often provide superior protection from windthrow and other external influences for the reserved stand. A variety of ecological conditions are present, along with a stream system in which natural land-water interactions (for example, woody debris inputs to the stream) can continue. Plant and animal diversity will also be higher in a drainage basin than in an isolated upland forest stand of the same size.

Another useful location for old-growth management areas is along streams. Streamside strips (buffer zones) were originally conceived for shading streams and minimizing increases in water temperatures; a more valuable function in streams up through at least third order is in providing essential energy, structural inputs (for debris dams), and stability of banks. Debris dams must be continually created to replace broken dams; this is particularly important after infrequent debris torrents that remove all, or most, pieces of large debris. Streamside strips of old-growth forest will provide for continued physical and biological stability of the aquatic ecosystem.

Streamside and roadside strips of old growth have the additional advantage of providing migration routes for organisms dependent on mature forests. The strips skirt managed stands and provide continuity between otherwise isolated pockets of natural and old-growth forest. Such migration routes may be important for avoiding loss of species as "islands" of habitat suited to a species become more limited and isolated MacClintock et al. 1977). The protected travel routes provided by these strips allow organisms to migrate in response to shifts in location of suitable habitat.

Reserve strips must be in appropriate locations and of sufficient size to survive normal windstorms. Streamside strips have often been narrow (since shading the stream was the primary objective) and sharp edged; consequently, they are extremely susceptible to blowdown. The wetter soils on lower slopes and streamsides do not make retention of strips any easier, and up slope harvesting often intensifies this problem. Regular programs to salvage logs on roadside or streamside strips are inappropriate because they accelerate deterioration of the stand and remove the essential structural components. Retention of dead wood is especially important for streams where it is the source of stabilizing debris dams. Salvage logging may be appropriate if losses from catastrophic windthrow or other causes occur. Even then, the salvage should not be complete; some down material should be selected and left on the land and in the stream. A 200-foot-wide (60-m) streamside or roadside strip is not a viable unit in most cases; considerable ingenuity and effort will be necessary to identify and lay out viable reserve strips.

Areas with problems that limit potential for management may also be appropriate sites for perpetuating old-growth ecosystems and organisms. An example could be steep landslide-prone headwall areas that depend on a strong and continuing root mantle for stability.

Structural Attributes in Perpetuating or Re-creating Old Growth. The distinctive structural features-the large, old-growth trees, snags, and logs on land and in streams-provide the major key to management strategies. The unique, important compositional and functional features of an old-growth forest usually accompany these structural elements.

An old-growth forest is much more than simply a collection of large trees. The dead, organic component is as important as the highly individualistic, large trees. Decaying snags and logs, particularly in streams, are beneficial and must be provided for in management schemes; they should not be viewed solely as waste, fire hazards, or impediments to management. Snags and logs play important roles as habitat for various organisms and in conserving and cycling nutrients and energy. To a large degree, success in managing forests for old-growth attributes will depend on learning to manage the dead, organic material as cleverly as the live trees.

There are implications here for management of old-growth stands selected for perpetuation. Salvage logging is inappropriate since it removes at least two of the major structural components-dead and down-that are key elements of the system. In all likelihood, some of the more decadent, live trees would also be removed. Salvage logging is also inappropriate because of the damage inevitably done to root systems and trunks of the residual stand which results in accelerated mortality of trees and overall deterioration of the stand.[17]

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[17] When stands are selected for preservation (for example, as roadside or streamside strips), the first (and frequently repeated) management activity is often a salvage program. If a manager wants to retain an old-growth ecosystem or a mature forest stand, entries should be avoided or at least minimized. Trees viewed as safety or fire hazards may better be felled and left in place than

There are also implications if the manager wishes to create an old-growth environment (after a stand is cut) by using a long rotation. Initially, foresters may retain larger amounts of woody residues, especially down logs, from the previous stand. Retention of scattered individual, old-growth trees may be useful as sources of epiphytic flora and eventually of large, dead standing trees and down logs.

Rapid development of large, long-crowned trees as early as possible is a key objective of management that can be aided several ways. Selection of understocked stands of reproduction as sites for creating old-growth stands is one approach since individuals will grow faster and lose lower branches more slowly under open-grown conditions. Many existing old-growth stands may have regenerated slowly (Franklin and Waring 1980); growth patterns of individual trees suggest growing conditions essentially free from competition for a century or more. If initial densities of stands are moderate-at current recommended levels for managed stands -precommercial and commercial thinnings will be necessary during the first 100 years of a long-rotation forest management cycle. Growth rates of individual trees will be too low at high densities, or at moderate densities on less productive sites, to produce desired sizes of stems even after 200 years; thinnings and partial cuttings are essential under those conditions. Great care must be taken, however, to minimize damage to residual trees.

Creation of appropriate types and amounts of standing dead and down trees is a specific management objective. Snags and logs from the original stand should be avoided during intermediate cuttings. Up to about 100 years, the size of snags and logs produced by the young stand is probably not of particular ecological importance. Some of this material could be removed along with excess live trees-those that will die before reaching significant diameter (50 cm or 20 inches). Openings for development of shade-tolerant species can also be created this way; if these species do not come in naturally, they could be artificially introduced, possibly by underplanting. The large snags, logs, and any live old growth left from the original stand should not be removed during salvage operations.

After about 100 years, partial cutting of any type becomes increasingly inappropriate. There are fewer live dominants, and their loss, either directly by cutting or gradually through damage to roots and trunks, is undesirable. Standing dead trees and logs now being recruited from the live stands are of sufficient size to fully perform desired habitat and cycling functions.

To summarize, if the objective is perpetuation of an old-growth forest ecosystem, a minimum amount of disturbance should be allowed. Snags and logs perform important functions and are essential structures. When the objective is to create an old-growth forest from scratch, large individual trees with large crowns should be grown as quickly as possible. Scattered old-growth trees and rotten logs from the original stand should be retained and reproduction of western hemlock, western redcedar, and other shade-tolerant associates under the Douglas-fir canopies encouraged. Partial cuttings may be useful and will be necessary in moderate to heavily stocked stands of reproduction if large trees are to be attained as quickly as possible. After trees are about 100 years old, such cuttings are increasingly inappropriate, however.

For multiple-use objectives, an increased awareness of the nature and nontimber value of individual trees is important; for example, potential or current value as habitat for epiphytic communities and wildlife. Knowledge of the ecological roles of standing, dead trees and logs beyond their value as wildlife habitat is also desirable.

There is considerable logic in managing entire stands or small drainages for old-growth attributes. The old-growth ecosystem is a system of many interlinked components, including organisms. The serial relationship of the key structural components has been discussed-from a large, old-growth tree to a nearly decomposed, rotten log (fig. 10). Further, some organisms or functions may depend on an intact old-growth forest for their perpetuation.

Nevertheless, a forester may wish to manage for some individual old-growth attributes. This is, in fact, how the forester can put some of the information on old growth to work to increase ecological benefits from intensively managed timberlands. The structural components again provide the key. Perhaps most obvious is providing for large snags and logs. This can be done in the first-generation managed forest by retaining some of this material from the virgin stand. The tendency has been to remove all such materials as a safety measure and to reduce logging residues, which are viewed as fire hazards and impediments in regeneration and other siivicuiturai activities. in second- and third-generation stands, a forester will have to create appropriate materials since neither large snags nor logs will usually be present.

The need for snags was recognized first by wildlife managers, and they have more recently recognized the value of logs (Maser et al. 1979, Thomas et al. 1979a). Thomas et al. (1979a) led in developing guidelines on sizes and numbers of such material needed to provide for vertebrates; although their research was conducted in the Blue Mountains of eastern Oregon and Washington, the same principles apply on the west side of the Cascade Range, as shown by Mannan et al. (1980) and Cline et al. (1980). These authors suggest that snags be created from defective, living trees and urge maintenance of large snags covering the spectrum of decomposition. Densities of snags in natural, old-growth stands are proposed as an interim management guide until more data are developed. Cline et al. (1980) also suggest leaving snags in groups to reduce problems of safety and fire control. It is important to remember that much more than habitat for vertebrate animals is involved in preserving snags; standing dead trees and logs serve other functions as well.[18]

There are currently no good guides to the number and sizes of logs that should be left on cutover areas. Removal of ail coarse woody debris is not the best ecological practice. Costs and benefits of some practices (such as yarding unmerchantable material) are not known; negative impacts on long-term site productivity, wildlife, and erosion may offset the benefits to fire protection and ground accessibility. it does appear that at least several larger logs per acre are needed for wildlife, especially small mammals. Defining the types and sizes of logs and other woody debris desired in managed stands is a major problem for research.

Retention of small groups of old-growth trees, or scattered individual trees, may be a useful practice. This was conceived as a technique for providing a source of epiphytic "inoculum" for adjacent young trees. Lack of such a source may be a factor in the absence of the N-fixing epiphytes on trees less than 150 years old. Leaving occasional old-growth trees has another advantage -it will, in the long run, provide a source of large snags and logs. This may be the easiest strategy for perpetuating these structural components into second- and even third-generation managed stands.

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[18] The role of dead wood in cycling and conserving nutrients, especially N, is an outstanding example. Ten years ago nothing was known about sources of N in old-growth stands, other than the atmospheric input. In the interim, epiphytic lichens and wood-dwelling bacteria have been identified as significant sites for fixation. There are several important sources for additions of N in both the early stages of forest succession-nonleguminous N fixers, such as alder (**Alnus** spp.) and ceanothus (*Ceanothus* spp.)-and in old-growth forests. Existing management strategies call for quick establishment of conifer canopies and short rotations-which effectively eliminate these additions of N to intensively managed sites.

Trees Mentioned in This Report

Common name	Scientific name
Alaska-cedar	*Chamaecyparis nootkatensis* (D. Don) Spach
Coast redwood	*Sequoia sempervirens* (D. Don) Endl.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Grand fir	*Abies grandis* (Dougl. ex D. Don) Lindl.
Incense-cedar	*Libocedrus decurrens* Torr.
Noble fir	*Abies procera* Rehd.
Pacific silver fir	*Abies amabilis* (Dougl.) Forbes
Port-Orford-cedar	*Chamaecyparis lawsoniana* (A. Murr.) Parl.
Sitka spruce	*Picea sitchensis* (Bong.) Carr
Sugar pine	*Pinus lambertiana* Dougl.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western redcedar	*Thuja plicata* Donn
Western white pine	*Pinus monticola* Dougl. ex D. Don

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Old-growth coniferous forests differ significantly from young growth forests in species composition, function (rate and paths of energy flow and nutrient and water cycling), and structure. Most differences can be related to four key structural components of old growth: large live trees, large snags, large logs on land, and large logs in streams. Foresters wishing to maintain old-growth forest ecosystems can key management schemes to these structural components.

Keywords: Ecosystems, old-growth stands, stand composition, stand structure, Douglas-fir, *Pseudotsuga menziesii,* western hemlock, *Tsuga heterophylla.*