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Distinctive Features of the Northwestern Coniferous Forest: Development, Structure, and Function

Jerry F. Franklin and Richard H. Waring

INTRODUCTION

The coniferous forests of the Pacific Northwest, those found on the slopes of the Cascade and Coastal ranges of Oregon, Washington, northern California, and British Columbia, are known throughout the world. This is the region renowned for Douglas-fir (*Pseudotsuga menziesii*) stands and western red cedar/western hemlock (*Thuja plicata*/*Tsuga heterophylla*) climaxes. Surely these forests, observed by foresters and botanists since the time of von Humboldt and Douglas, are well understood and can hold few surprises. Indeed, when the Coniferous Forest Biome Project of the U.S. International Biological Program (US/IBP) started more than 10 years ago, we thought we knew about all we needed to know about the natural forests of this region. The U.S. Forest Service had already reduced their studies of older forests in order to concentrate on younger stands. Biome program designers seriously debated the wisdom of studying natural, older forests when major questions seemed to revolve around managed stands.

During the last 10 years, however, we have made gigantic advances in our knowledge of these forest ecosystems. We have learned how they are structured, their functional behavior, and controlling factors. Research on these systems has evolved into tests of specific hypotheses as relevant questions have become apparent. Many results presented in this and other Colloquium papers are from these first- and second-generation ecosystem studies--i.e., biomes and sons and daughters of biomes!

Increasing knowledge has brought continual surprises--counterintuitive finds that make clear how little we really know about these coniferous forests. The high productivity and rapid turnover found below-ground in forests, for example, is outlined by Harris and Santantonio (this volume),

and the extent and importance of coarse woody debris in terrestrial and stream ecosystems is outlined by Triska and Cromack (this volume). The nitrogen cycle has been the source of one unexpected discovery after another. Ten years ago no clear idea existed of nitrogen sources in these forests; fixation by nonleguminous woody plants such as red alder has been widely known only since the mid-1950's. Textbooks hypothesized that free-living blue-green algae might be a source of nitrogen inputs along with precipitation. In the last decade at least two major sources of nitrogen have been identified: (1) the crown and ground dwelling lichens with a blue-green algal symbiont and (2) microbial activity in some types of organic matter such as coarse woody debris (logs). Almost certainly the nitrogen cycle will be the source of many further surprises.

Our objective in this paper is to highlight some findings on the structure and function of these coniferous forests. We also hope to transmit some sense of the progress and existing directions of current research and stimulate you to reexamine what you think you already know about these forests. We will cover: (1) biomass and productivity; (2) factors responsible for evergreen dominance and massiveness; (3) successional oriented studies of age structure and coarse woody debris; and (4) aspects of the old-growth systems.

Several topics highlighted in this paper are discussed more thoroughly elsewhere in this volume (see Waring, Triska, and Cromack on coarse woody debris, Swanson on erosion, Carroll on tree canopy ecosystems, and Cummins on stream ecosystems).

BIOMASS AND PRODUCTIVITY

Over the last decade scientists have documented what we have always suspected about northwestern forests--they contain the largest biomass accumulations in the world and are very productive. Trees have been dissected and equations developed and applied, and the results have shattered many theories about forest maxima which were based upon studies of temperate forests in other regions of the world.

Biomass

Biomass accumulates to record levels in large, long-lived species from dense coniferous forests. Maximal values in the Pacific Northwest contrast most strongly

with maximal biomass values from other regions of the world (Table 1). The analysis of a coast redwood (*Sequoia sempervirens*) stand in Humboldt State Park in California provides the greatest accumulation ever recorded, with a basal area of 343 m²/ha and a stem biomass of 3,461 ton/ha (Fujimori, 1977). Addition of branch, leaf, and, particularly, root biomass would increase the estimate of standing crop to well in excess of 4,000 ton/ha--very close to Fujimori's (1972) earlier estimate of 4,525 ton/ha for a coast redwood grove. These figures are larger but are consistent with the biomass of 3,200 ton/ha reported by Westman and Whittaker (1975) for three redwood stands on alluvial flats. Superlative stands are not confined to coast redwood, however (Table 1); maximum values

Table 1. Maximal biomass values for three coniferous forest types in the Pacific Northwest and comparable data for different forest formations elsewhere in the world.

Formation, type, and stand location	Stem volume	Basal area	Total biomass
	m ³ /ha	m ² /ha	mt/ha
<u>Coniferous forests, Pacific Northwest</u>			
<u>Sequoia sempervirens</u> ¹ (> 1,000 years old)	10,817	338	3,461 ⁴
<u>Pseudotsuga menziesii</u> - ² <u>Tsuga heterophylla</u> (450 years old)	3,600	127	1,590 ⁴
<u>Abies procera</u> ² (325 years old)	4,106	147	1,562 ⁴
<u>Evergreen hardwood</u> ³ (<u>Quercus cinnamomum</u> in Nepal)	n.a.	n.a.	575
<u>Deciduous hardwood</u> ³ (<u>Quercus prinus</u> in USA)	n.a.	n.a.	422
<u>Temperate conifer</u> ³ (<u>Tsuga sieboldii</u> in Japan)	n.a.	n.a.	730
<u>Conifer plantation</u> ³ (<u>Cryptomeria japonica</u> in Japan)	n.a.	n.a.	1,200

¹Fujimori, 1977.

²Fujimori et al., 1976.

³Art and Marks, 1971.

⁴Stem mass only.

for noble fir (*Abies procera*) and Douglas-fir are about half those for redwood, but they still greatly exceed maxima for temperate and tropical forests in other parts of the world. The contrast is further emphasized by the fact that biomass figures for the Pacific Northwest (Table 1) include stem biomass only, while those from other regions are for total biomass.

Current studies in the Pacific Northwest continue to gather evidence that large biomass accumulations are the rule rather than the exception. Average values contrast as greatly with those for other regions as the maximal values (Table 2). High values are characteristic of young (100 to 150 years old) as well as old Douglas-fir stands and of subalpine forests (noble fir) as well as temperate forests. Coastal stands of young-growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) tend to be particularly high (Table 2). One of the more extensive analyses available is for a 10-ha watershed in the Cascade Mountains of western Oregon (Grier and Logan, 1978):

Item	Biomass (ton/ha)
Foliage	12.4
Aboveground in living plants	718.0
Total in living plants	870.0
In logs and standing dead trees	215.0
Total ecosystem organic matter	1,249.0

The amount of biomass in living trees is quite remarkable, given the apparent decadence of the stand as evidenced by the large weight of dead trees and logs.

One noteworthy biomass component is foliage. Leaf biomass and surface area in the Pacific Northwest develop slowly, taking 30 years or more to reach a maximum (Long and Turner, 1975); in the eastern United States and other temperate regions of the world, equilibrium is achieved much earlier, reportedly in as little as 4 years (Marks and Bormann, 1972). Projected canopy surface areas in the Pacific Northwest typically reach $10 \text{ m}^2/\text{m}^2$ and may reach as much as $20 \text{ m}^2/\text{m}^2$, which is very close to the theoretical maximum (Gholz, 1979).

Table 2. Biomass values in representative stands of various types.

Type and age class ¹	Number of stands	Aboveground biomass	
		Average	Range
mt/ha			
Douglas-fir 70 to 170 years	10	604	422-792
Douglas-fir/western hemlock 250 to 1,000 years	19	868	317-1,423
Sitka spruce/western hemlock 121 to 130 years	3	1,163	916-1,492
Noble fir 130 years	1	880	---
Temperate deciduous forest Mature	19	243	87-422
Tropical rain forest Mature	9	318	67-415

¹See appendix for data sources for stands from the Pacific Northwest which include aboveground tree biomass only; source for temperate deciduous and tropical rain forests is Art and Marks (1971) and includes shrubs and herbs.

Leaf mass values are also very high, with an average of nearly 20 tons/ha (Table 3). These leaf mass and projected area values are much higher than those in temperate deciduous hardwood and evergreen hardwood stands. Values for temperate conifer stands in other parts of the world range near the low values for coniferous forests in the Pacific Northwest (Table 3). Interestingly, the values for leaf area and mass in northwestern coniferous forests also far exceed leaf areas developed by red alder (*Alnus rubra*), one of the most common and productive of the northwestern deciduous hardwoods; values in red alder stands, converted from biomass values, represent less than $10 \text{ m}^2/\text{m}^2$ (which is very high for a deciduous hardwood stand).

Productivity

Productivity of the northwestern American temperate forests is generally comparable to forest stands in other temperate regions. Biomass in young stands probably accumulates at 15 to 25 tons/ha annually in fully stocked stands on better than average

sites. Mature or old-growth stands have lower net productivities (Table 4).

Annual net productivity can be very great on the best sites. Fujimori (1971) reported a net production of 36.2 ton/ha in a 26-year-old coastal stand of western hemlock. Young forests of coast redwood also have high early productivities on good sites (Fujimori, 1972, 1977). Maximum values are substantially lower for temperate deciduous forests (24.1 ton/ha for tulip poplar, *Liriodendron tulipifera*) and temperate evergreen hardwood forests (28.0 ton/ha) (Art and Marks, 1971). Conifer plantations, with a reported maximum of 29.1 ton/ha for *Cryptomeria japonica*, approach the higher productivity values for northwestern stands.

In many other mesic temperate forests, however, annual productivity in early years typically equals or exceeds that in the Pacific Northwest. The key to the larger biomass accumulations in the Pacific Northwest is clearly the sustained height growth and longevity of the dominants, not the differences in productivity rates. This growth is aided by the trees' ability to accumulate and maintain a large amount of foliage. Northwestern tree species continue

Table 3. Leaf biomass and projected leaf areas for four forest types in the Pacific Northwest, three forest formations in Japan, and tropical rain forest.

Type ¹	Number of stands	Leaf mass	Projected leaf area
		mt/ha	m^2/m^2
Douglas-fir (young)	10	19	9.7
Douglas-fir/western hemlock (old)	19	23	11.7
Sitka spruce/western hemlock	4	21	13.2
Noble fir	1	18	10
Deciduous hardwood forest (Japan)	14	3.1	3 to 7
Evergreen hardwood forest (Japan)	40	8.6	5 to 9
Conifer (Japan) ²	66	16.9	6 to 10
Tropical rain forest	6	9.4	7 to 12

¹Data sources: Pacific Northwest, see appendix; Japan, Tadaki, 1977; tropical rain forest, Art and Marks, 1971.

²No stands of pine or Cupressaceae included.

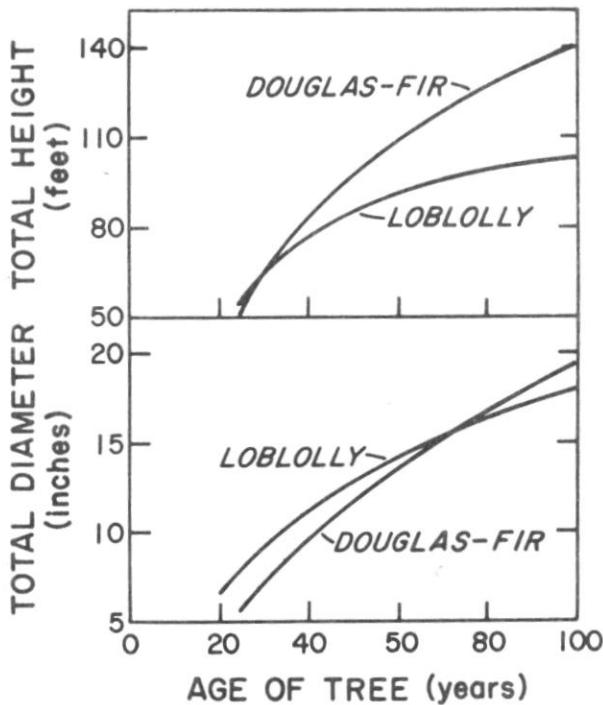


Figure 1. Comparison of the growth rates of Douglas-fir and loblolly pine. Pine has a faster earlier growth rate, but the sustained growth of the Douglas-fir results in the latter eventually overtaking the former.

to grow substantially in diameter and height, and stands in biomass, long after those in other temperate regions have reached equilibrium. This is well illustrated by comparing growth of loblolly pine (*Pinus taeda*) in the southeast and Douglas-fir in the Pacific Northwest (Worthington, 1954). Initially, the pine outgrows the Douglas-fir, being 100 percent taller at 10 years; however, Douglas-fir overtakes the pine in diameter growth at 25 years and in height growth at 30 years (Figure 1). Wood production from a single (100-year) rotation of Douglas-fir is about 22 percent greater than yields from two 50-year rotations of pine. Recent studies of height growth patterns for higher elevation Douglas-fir, noble fir, and mountain hemlock have further documented sustained height growth of northwestern species into their second and third centuries (Curtis et al., 1974; Herman et al., 1979; Herman and Franklin, 1977).

Table 4. Aboveground net primary production estimates for coniferous forests in the Pacific Northwest (west of the crest of the Cascade Range)

Community type	Stand age	Biomass	Net primary productivity	Source
	<u>years</u>	<u>mt/ha</u>	<u>mt/ha/yr</u>	
Coast redwood	"old"	3,200	14.3	Westman and Whittaker, 1975
Western hemlock	26	192	36.2	Fujimori, 1971
Western hemlock/Sitka spruce	110	871	10.3	Fujimori et al., 1976
Sitka spruce/western hemlock	130	1,080	14.7	Gholz, 1979
Western hemlock/Sitka spruce	130	1,492	12.3	Gholz, 1979
Douglas-fir	150	865	10.5	Gholz, 1979
Douglas-fir	125	449	6.6	Gholz, 1979
Douglas-fir/western hemlock	100	661	12.7	Fujimori et al., 1976
Douglas-fir/western hemlock	150	527	9.3	Gholz, 1979
Noble fir/Douglas-fir	115	880	13.0	Fujimori et al., 1976
Douglas-fir/western hemlock	450	718	10.8	Grier and Logan, 1977

Gross productivity rates are probably greater in many tropical rain forests and in warm-temperate evergreen broadleaf forests, but lower respiration rates in the Pacific Northwest result in greater net productivity. However, total autotrophic respiration appears much higher in northwestern coniferous forests than in temperate deciduous forests. Grier and Logan (1978) estimated respiration by a 450-year-old Douglas-fir stand at 150 ton/ha/year; estimates for a mixed oak and pine forest in New York and a tulip poplar forest in Tennessee were 15.2 and 15.9 ton/ha (Woodwell and Botkin, 1970; Sollins et al., 1973). The large respiration cost reflects the much larger foliar biomasses and the presence of respiring foliage during the relatively warm winters. The net effect of the high levels of autotrophic respiration is to accentuate differences in productivity between northwestern conifer and temperate deciduous hardwood forests, making the contrast in gross production even greater than that in net primary production.

In summary, the coastal regions of the Pacific Northwest are dominated by coniferous forest stands having biomass accumulations far exceeding forests in other northern temperate forest regions. Leaf masses and projected leaf areas greatly exceed those found in temperate deciduous hardwood forests. The large biomass values result from sustained growth of tree species with long lifespans rather than from greatly superior net annual productivities.

EVERGREEN CONIFER DOMINANCE

Another outstanding feature of the forests of the Pacific Northwest is their dominance by evergreen coniferous trees. Typically, forests in moderate environments in north temperate regions are dominated by deciduous hardwoods or by a mixture of hardwoods and conifers. This is true of natural forests in Asia, Europe, and the eastern United States. Yet, in the Pacific Northwest the ratio of conifers to hardwoods is more than 1,000:1 (Kuchler, 1946), a unique phenomenon. Furthermore, the few hardwoods that are present tend to occur as pioneer species (e.g., red alder) or occupy environmentally marginal or severe habitats (e.g., oaks), while in other temperate regions conifers tend to pioneer or be pushed toward more severe environments (see e.g., Regal, 1977).

What factors have been responsible for the evolution of these temperate forests in which conifers so completely dominate hardwoods? Scientists have speculated about this since the time of von Humboldt in the

mid-1800's. Some suggest that many hardwood genera were eliminated by cold temperatures during glacial epochs (Kuchler, 1946; Gray and Hooker, 1882). Most hardwood extinctions actually occurred during the Pliocene, however, eliminating glaciation as a factor. Furthermore, some scientists (Silen, 1962) feel that favorable Pleistocene environments in the Pacific Northwest, including the availability of migration routes, were factors contributing to the survival of the outstanding conifer gene pool.

Moisture and temperate deficiencies have also been proposed as important factors in eliminating hardwoods. Chaney and others (1944) suggest that arid periods were responsible for hardwood losses. Daubenmire (1975, 1976) identifies the annual distribution of the heat budget, i.e., summer heat deficiencies coupled with an inability to utilize the frequent warm days in the spring and fall. Regal (1977) proposes that gymnosperms survive as dominants only in environments that are, in some way, harsh or rigorous, but he concedes uncertainty as to how the coniferous forests of the Pacific Northwest conform to this hypothesis.

Research conducted under the auspices of the Coniferous Forest Biome clearly indicates that existing forests are very well adapted to the current climatic regime. In a variety of ways, the evergreen coniferous habit appears superior to that of a deciduous hardwood within the macroclimatic regime of warm, relatively dry summers and mild, wet winters. Since comparable climatic regimes have existed for several epochs, we propose that these were also key factors in the evolution of the northwestern coniferous forests and the competitive elimination of much of the original hardwood flora.

Climate

The climatic regime in the Pacific Northwest has striking contrasts to the climate in other temperate forest regions. Salient elements shown in Figures 2, 3, and 4 illustrate the temperature regime, precipitation pattern, and vapor pressure deficits for several stations in the Pacific Northwest and in temperate forest regions of the eastern United States and Europe.

Climatically, the region experiences wet, mild winters and warm, relatively dry summers. The dormant season, when shoot growth is inactive, is characterized by heavy precipitation with daytime temperatures usually above freezing. The growing season has warm temperatures associated with clear days, relatively little precipitation, and frequent vapor pressure defi-

cits, except directly on the Pacific Coast (i.e., in the *Picea sitchensis* Zone of Franklin and Dyrness, 1973). Water storage in snowpack, soils, and vegetation, as well as pulses of fog, clouds, or cool maritime air which reduce evaporation, are obviously important during the summer drought period experienced in the Pacific Northwest.

Climate in the region varies consider-

ably because of interactions between maritime and continental air masses and mountain ranges. Along the coast, where the maritime influence is strongest, mild temperatures are associated with prolonged cloudiness and narrow diurnal and seasonal fluctuations in temperature (6 to 10°C). Winters are extremely wet and freezing temperatures are rare. Summers are cool and relatively dry, but extended periods of cloudiness and fog greatly reduce evaporation. Valleys located in the lee of the Coast Ranges are drier and subject to greater temperature extremes and evaporative demand. For example, Eureka on the California coast contrasts with Roseburg in Oregon's Umpqua Valley, which is located between the Cascade and Coastal ranges (Figures 2, 3, and 4). On the western slopes of the Cascade Range, precipitation again increases and temperature regimes moderate until subalpine environments, with their cooler temperatures and deep winter snowpacks, are encountered. Similar patterns occur elsewhere in the

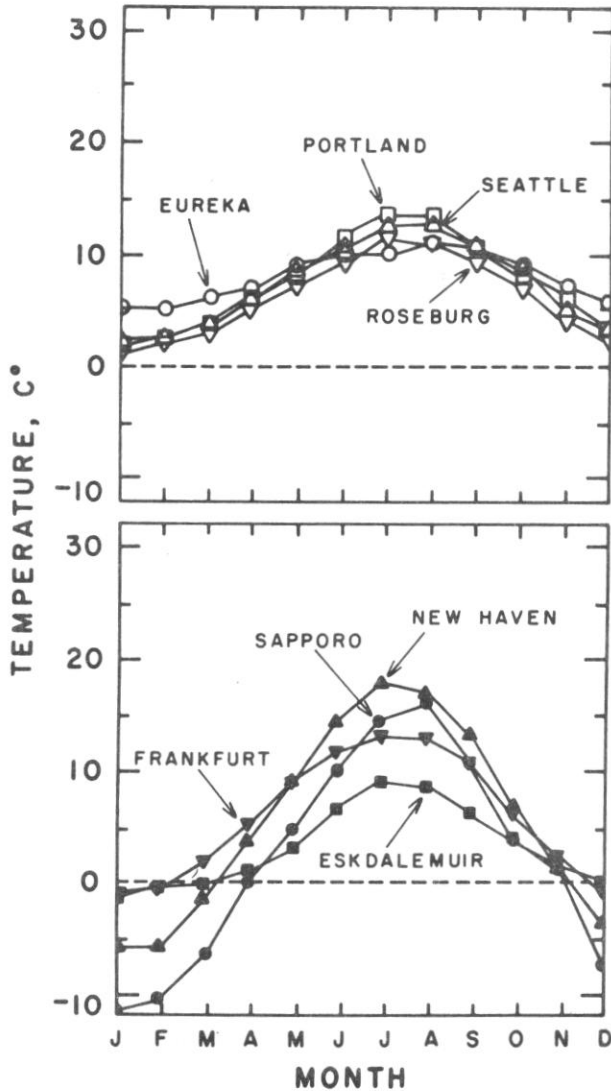


Figure 2. Temperature patterns that illustrate the contrast between the Pacific Northwest and other temperate forest regions of the world. Four stations in the Pacific Northwest are illustrated in section A, including one (Eureka) on the immediate coast. Stations from the eastern United States (New Haven), Japan (Sapporo), Scotland (Eskdalemuir), and Europe (Frankfurt) are illustrated in section B. Note the higher winter temperatures in the Pacific Northwest.

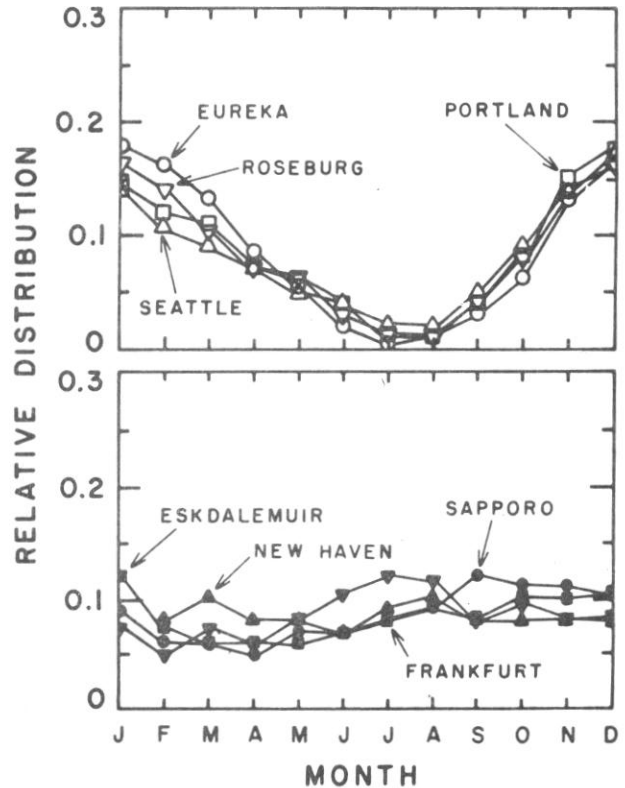


Figure 3. Relative distribution of precipitation in the Pacific Northwest (section A) and other temperate forest regions throughout the world (section B). Note the relatively dry summer period in section A and the equitable distribution of precipitation in section B.

region, although areas to the south are, of course, warmer and drier while those to the north are cooler and moister.

The climatic contrasts with other temperate forest regions are striking (Figures 2, 3, and 4). Major forest regions in the eastern United States, eastern Asia, and Europe have precipitation more evenly distributed with no reduction during the growing season (Figure 3). Throughout most of the Pacific Northwest, less than 10 per-

cent of the total precipitation falls during the growing season. In other temperate forest regions, summers are typically hotter and more humid, and winters are colder. Night temperatures during the growing season in the Pacific Northwest generally remain below 12°C. Near the coast, or along cold air drainages in the mountain valleys, nights often experience 10°C. Cool nights may create dew, but this quickly evaporates on clear warm days and evaporative demands are ultimately much higher than those experienced at similar temperatures in other temperate forest regions. Past regional comparisons have underestimated evaporative differences by failing to consider differences in humidity. This method underestimates evaporation in the Pacific Northwest by 25 to 60 percent for July and August, as seen by comparing maximum temperatures (Figure 2) with maximum vapor pressure deficits (Figure 4).

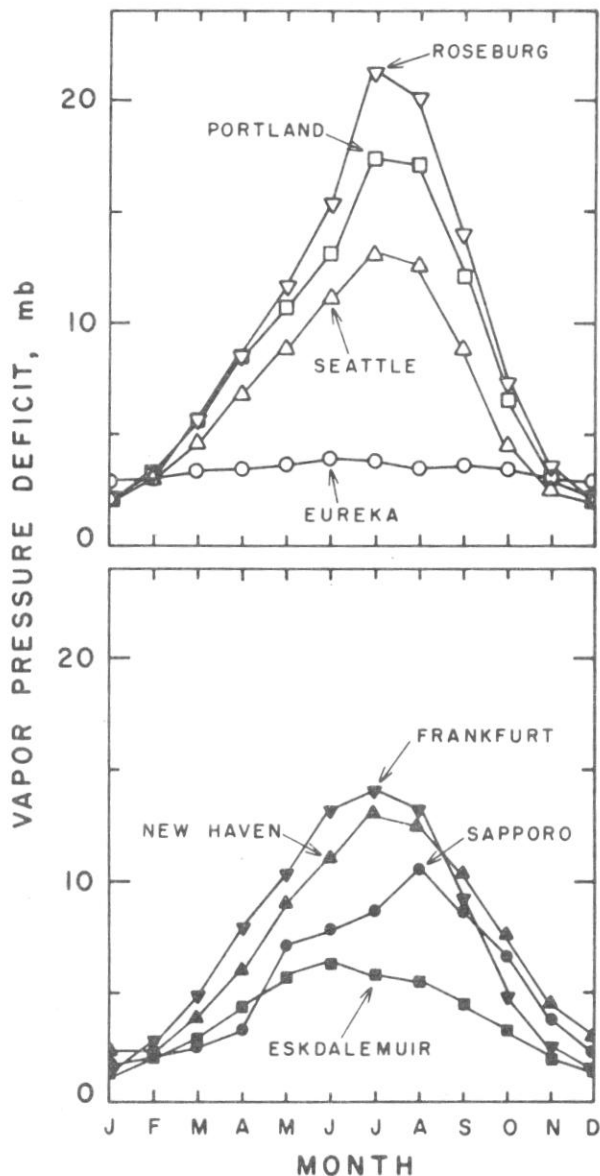


Figure 4. Monthly vapor pressure deficits for selected stations in the Pacific Northwest (section A) and other temperate forest regions of the world (section B). Summer deficits are generally much higher in the Pacific Northwest; the Eureka station is located on the immediate Pacific Coast.

How Environment Favors Evergreen Conifers

Almost all structural features of the northwestern forests are functionally advantageous under the moisture, temperature, and nutrient regimes of the Pacific Northwest—massiveness, evergreenness, conifer wood structure, and needle leaves. Factors favoring these habits can be aggregated into three categories:

- (1) Possibility of nongrowing season assimilation,
- (2) Constraint of photosynthesis by unfavorable moisture regimes in the summer, and
- (3) Peculiarities of the nutrient regime.

Nongrowing Season Assimilation. Mild temperatures permit substantial photosynthesis during the so-called dormant season of fall, winter, and spring. Conifers can assimilate over a broad temperature range. Considerable carbon uptake is possible below freezing (Ungerson and Scherdin, 1968) even by coastal species such as Sitka spruce (Neilson et al., 1972). Significant winter accumulations of dry matter by conifers have been documented in climates as diverse as those of western Norway and Great Britain (Hagem, 1947, 1962) (Rutter, 1957; Pollard and Wareing, 1968). Sitka spruce seedlings in Scotland actually doubled their dry weight between late September and mid-April (Bradbury and Malcom, 1979).

Substantial net photosynthesis occurs over a wide range of environments during the dormant season in the Pacific Northwest. Winter temperatures are mild and sub-

freezing day temperatures uncommon, even in montane environments. This is equally true of soil and air temperature; frozen soils are extremely uncommon even in subalpine environments, so water uptake is not a major problem. Model simulations indicate that as much as half of the annual net carbon assimilation by Douglas-fir occurs between October and May (Emmingham and Waring, 1977) (Figure 5). This long period of favorable temperature (and moisture conditions, as will be seen) is entirely lost to the deciduous hardwoods. The winter photosynthetic opportunity of the evergreen conifers is further enhanced by their long, conical crowns that intercept greater amounts of light during the low angles of the winter sun.

Unfavorable Summer Moisture Regimes.
 Now we can consider the second of the factors--constraint of summer or growing season photosynthesis by unfavorable moisture regimes. Extended periods of vapor pressure deficits during the summers force stomata on leaf surfaces to close, reducing water loss and subsequent carbon dioxide uptake. Effects of summer drought are particularly evident on dry sites, where nearly 70 percent of the annual net photosynthesis probably occurs outside of the growing season. Such site-to-site variations are apparent in Figure 5, where the effects of summer drought are compared in such contrasting sites as the coastal Sitka spruce zone environment and a hot, dry habitat type in the Cascade Mountains where Douglas-fir is the climax species.

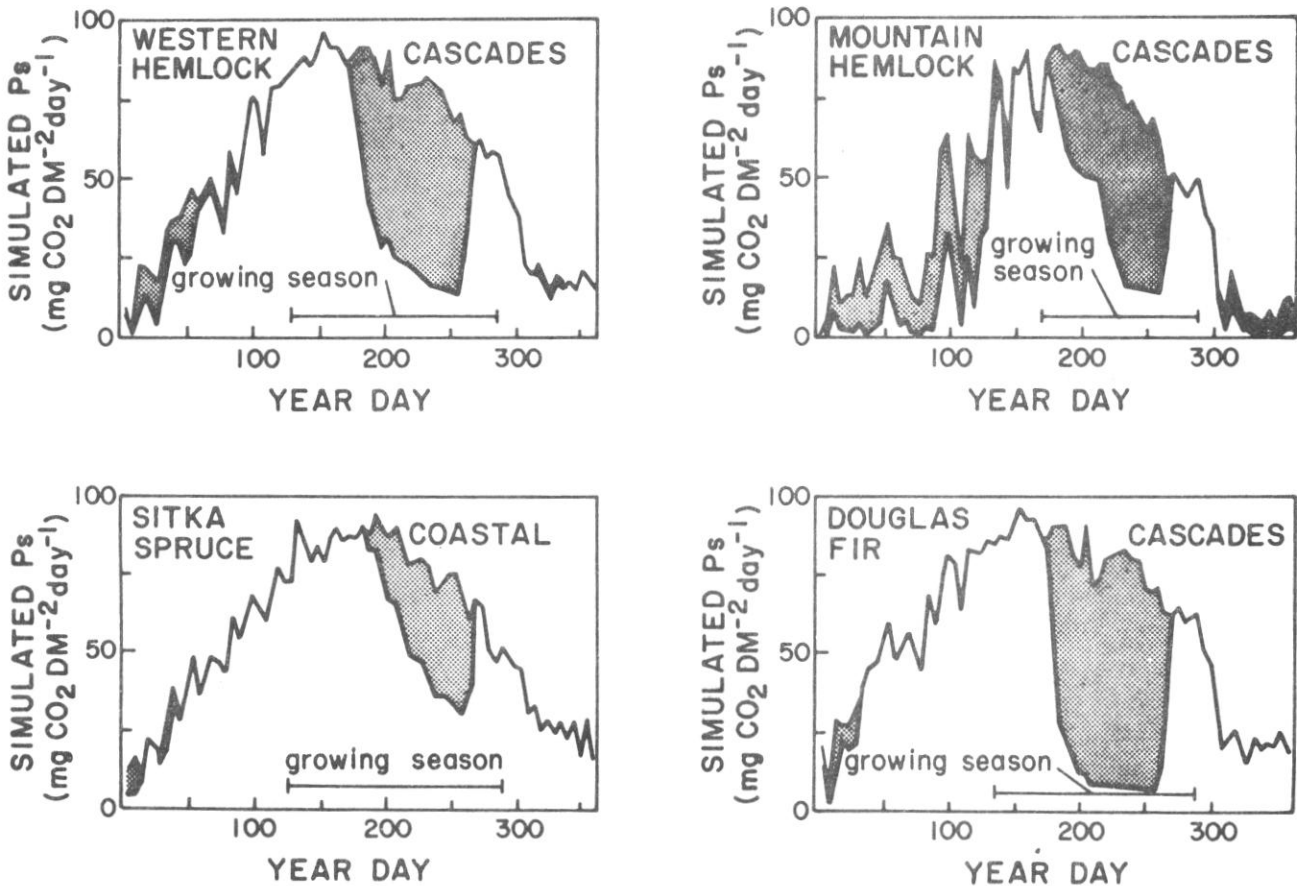


Figure 5. Simulated photosynthetic rates for Douglas-fir growth (1 to 2 m tall) in different forest environments characteristic of the Pacific Northwest. Maximal (upper) line shows potential photosynthesis without constraints due to moisture stress, frost, or low soil temperature; lower line incorporates these constraints, with the difference between the two projections shaded. A high proportion of the yearly photosynthesis occurs outside the "growing season" on all of these sites. "Western Hemlock Cascades" is for a moderate forest site, "Mountain Hemlock Cascades" for a very cold and snowy subalpine forest site, "Sitka Spruce Coastal" for a very favorable coastal site, and "Douglas-fir Cascades" for a very dry site.

Stomatal closure results from both soil moisture deficiencies and high evaporative demand (Hallgren, 1977; Running et al., 1975). Seasonal reductions in available soil water cause plant water deficits in many locations and will limit the degree to which stomata may open (Running et al., 1975). Increasing evaporative demand, measured by the water vapor deficit of the atmosphere, can also bring about stomatal closure, even in the presence of adequate soil water (Figure 6). Hundreds of field measurements reveal that both conifers and hardwoods are affected.

Evergreen conifers still have significant advantages over hardwoods during periods of moisture deficiency even though stomatal closure reduces photosynthesis in both groups. Heat exchange is less inhibited in needle-shaped than broad leaves, maintaining closer to ambient temperatures (Gates, 1968), particularly when stomata

are completely closed. Because evaporative demand usually exceeds critical limits during the growing season over much of the Pacific Northwest, the environment is obviously less than optimum for plants dependent upon this season for carbon uptake. Cool temperatures at night during the summer months also mean that evergreens are not penalized as severely by respiration losses as might be the case in temperate regions with warm summer nights.

Large volumes of sapwood are a structural feature of conifer forests that also helps dampen the effect of dry summer days. Both hardwoods and conifers utilize some water from conducting tissues to help meet daily transpiration requirements (Gibbs, 1958). However, the conifers have cells that are easier to recharge and that, because the trees grow larger, store much more water (Figure 7). A single 80-m Douglas-fir tree may store 4,000 liters of water

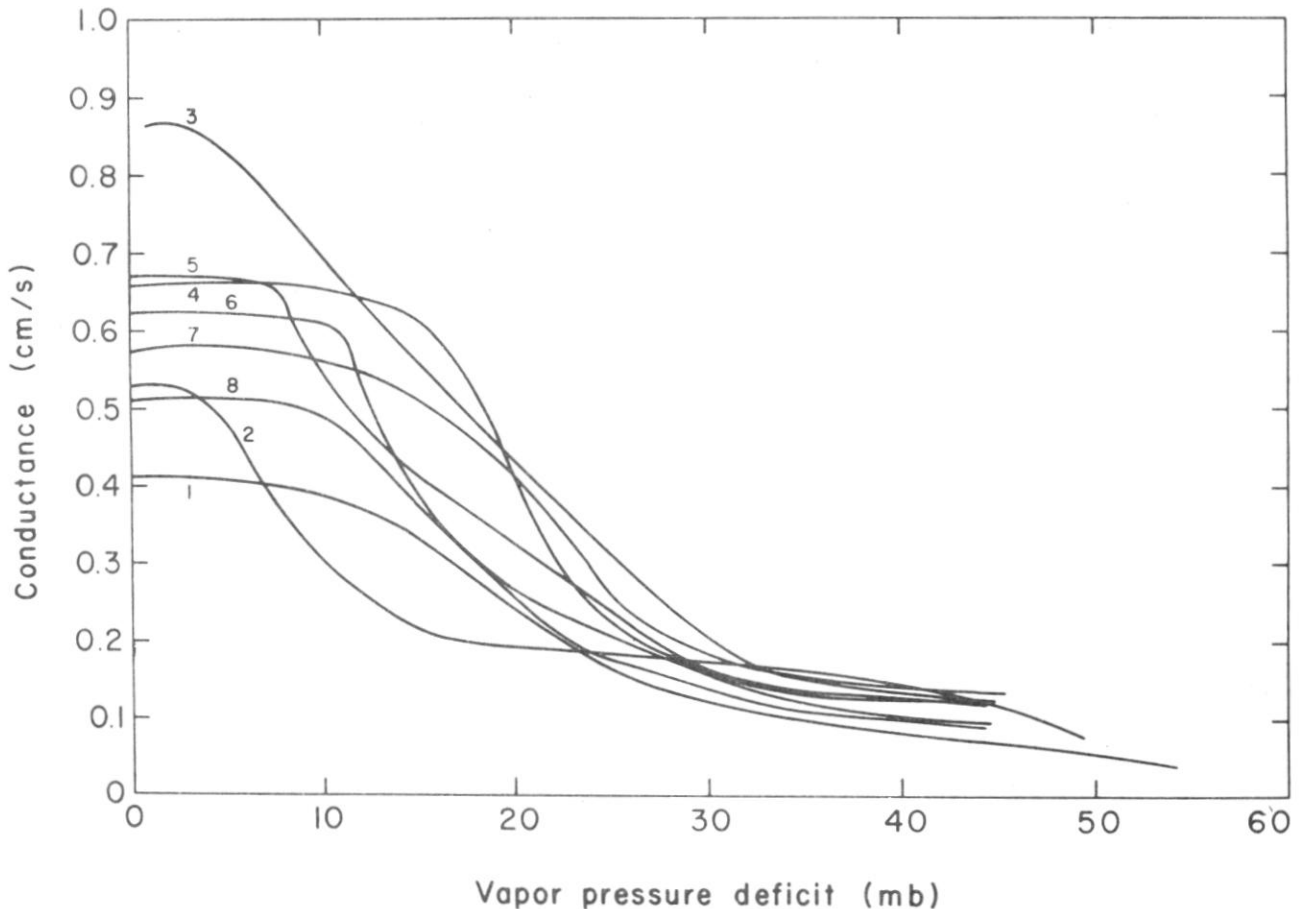


Figure 6. Maximum stomatal conductances recorded at different evaporative demands (vapor pressure deficits) for a variety of native species growing under conditions with adequate soil water. Conifers: 1 is Douglas-fir ($n = 312$), 2 is western hemlock ($n = 404$). Deciduous trees: 3 is Pacific dogwood ($n = 402$), 4 is bigleaf maple ($n = 68$). Evergreen broadleaf trees: 5 is golden chinkapin ($n = 159$). Deciduous shrub: 6 is vine maple ($n = 429$). Evergreen broadleaf shrubs: 7 is Pacific rhododendron ($n = 451$), 8 is salal ($n = 435$).

(Running et al., 1975). A forest stand can have more than 250 m³/ha of water available, enough to supply up to half the daily water budget (Waring and Running, 1978). Therefore, the sapwood represents a significant buffer against extremes in transpiration demand and helps offset the disadvantage of lifting water to great heights. Furthermore, although full hydration occurs during the winter, conifers may partially recharge sapwood after summer rain showers. Many hardwoods have no mechanism for effectively refilling the larger evacuated vessels until the next spring.

Large leaf areas may provide additional structural advantages for evergreen conifers in the dry summer climate of the Pacific Northwest. Water is sorted on and in the foliage in proportion to its area. The large needle mass also serves as a condensing surface for fog or dew, thus supplementing summer precipitation.

Summarizing contrasts in conifer-hardwood response to summer moisture deficiencies, both groups suffer stomatal closure and reduction in photosynthesis. Conifers have excellent control of water loss without increasing their leaf temperatures, however. They also can develop greater water storage capacities than hardwoods and utilize these adaptations to reduce the impact of stress common during the growing season.

Adaptations to Nutrient Regime. We can now consider the last of the three environmental influences--the distinctive nutrient regime of the Pacific Northwest. Nutrients clearly rank below temperature and moisture in their influence on the evolution of these forests, but they are still an important factor. The region has a nutrient regime that contrasts with that characteristic of other temperate forest regions, partially because of the winter-wet, summer-dry climate.

Decomposition and subsequent nutrient release from the organic layer occurs mostly during the cool, wet "dormant" season in the Pacific Northwest and may essentially cease during the relatively dry summer (Figure 8). Slow summer decomposition has been reported from such diverse sites as Douglas-fir and western hemlock forests at low to middle elevations and subalpine fir forests at high elevations in the Cascade Range (Fogel and Cromack, 1979; Turner and Singer, 1976). In the western Oregon Cascade Range almost no measurable decomposition occurs in July and August (Fogel and Cromack, 1979).

The massiveness of the forests also contributes to the uniqueness of the nutrient regime by binding large amounts of nutrients into standing crops. Over the long

sequences between disturbances organic matter accumulates on the forest floor, particularly as slowly decomposed coarse woody debris--large logs and branches. Ultimately, this creates conditions for large episodic losses of nitrogen and other nutrients as a result of wildfires.¹

The peculiarities of these nutrient regimes combine to favor plants that have relatively low nutrient requirements, conservatively use acquired nutrients, and can accumulate nutrients during the wet season when decomposition is most active. Evergreen conifers appear to have advantages over deciduous hardwoods on all scores.

Conifers generally have lower nutrient requirements and use nutrients more efficiently than most hardwoods. Foliage retention for several years is obviously advantageous in reducing annual nutrient requirements; current foliage may be only 15 to 16 percent of the total in Douglas-fir forests (Overton et al., 1973; Pike et al., 1977). The relatively low levels of nutrients found in foliage are also evidence of lower conifer requirements. Nitrogen in healthy foliage of 450-year-old Douglas-fir rarely exceeds 0.8 percent (dry weight basis), less than half the level of most hardwoods (Rodin and Bazilevich, 1967). Similar contrasts have been demonstrated with calcium.

Northwestern conifers also meet increasing proportions of their total nutrient requirements by redistribution from older tissue, especially senescent needles. Half of the nitrogen required by a 100-year-old stand of Douglas-fir (down to 30 kg/ha/yr from a high of 50) is met by translocation

¹ There are a large array of organisms associated with nitrogen fixation in the Pacific Northwest. Successional pioneers in the genera of *Alnus* and *Ceanothus*, as well as other higher plants, have nitrogen-fixing microbial associates. Large amounts of nitrogen--50 to 300 kg/ha/yr--can be fixed by such plants during early stages of forest development, partially or completely balancing losses associated with catastrophic fires. Foliose lichens endemic to the old-growth forests provide further, continuing nitrogen inputs of 3 to 5 kg/ha/yr. Finally, large boles which, as snags and down logs, survive major disturbances, are a source of slowly available nitrogen as well as the site for substantial microbial fixation. All of these pathways for fixation and retention of nitrogen may represent adaptations to catastrophic wildfires and related nitrogen deficiencies in a region otherwise favorable to vegetative growth.

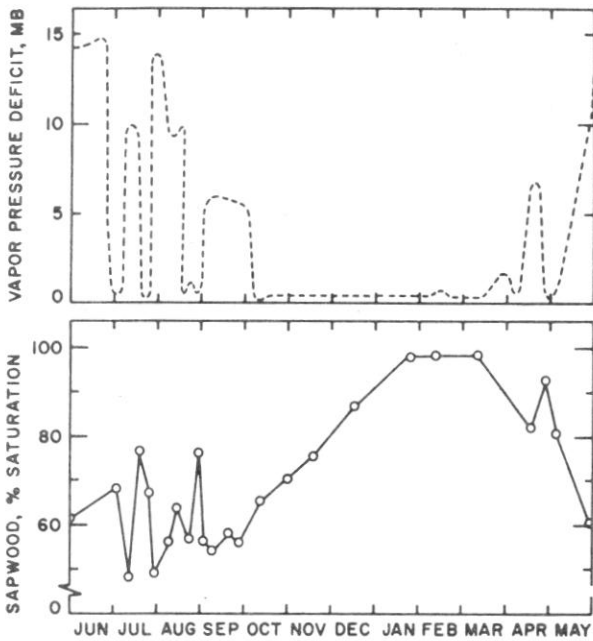


Figure 7. Seasonal variation in sapwood water storage of old-growth Douglas-fir (section B) in relation to evaporative demand (section A). Periodic summer storms totaling less than 10 cm precipitation reduced the evaporative demand, but clear weather following the storms encouraged a partial recharge before depletion began again. With the onset of fall precipitation, the evaporative demand remained below 2 ml and sapwood recharged at a constant rate until January when filled. In April 1976 the average evaporative demand exceeded 5 ml; some water columns in the sapwood were broken and the water was utilized for transpiration. Recharge is still possible after April, but only under abnormally low evaporative demand.

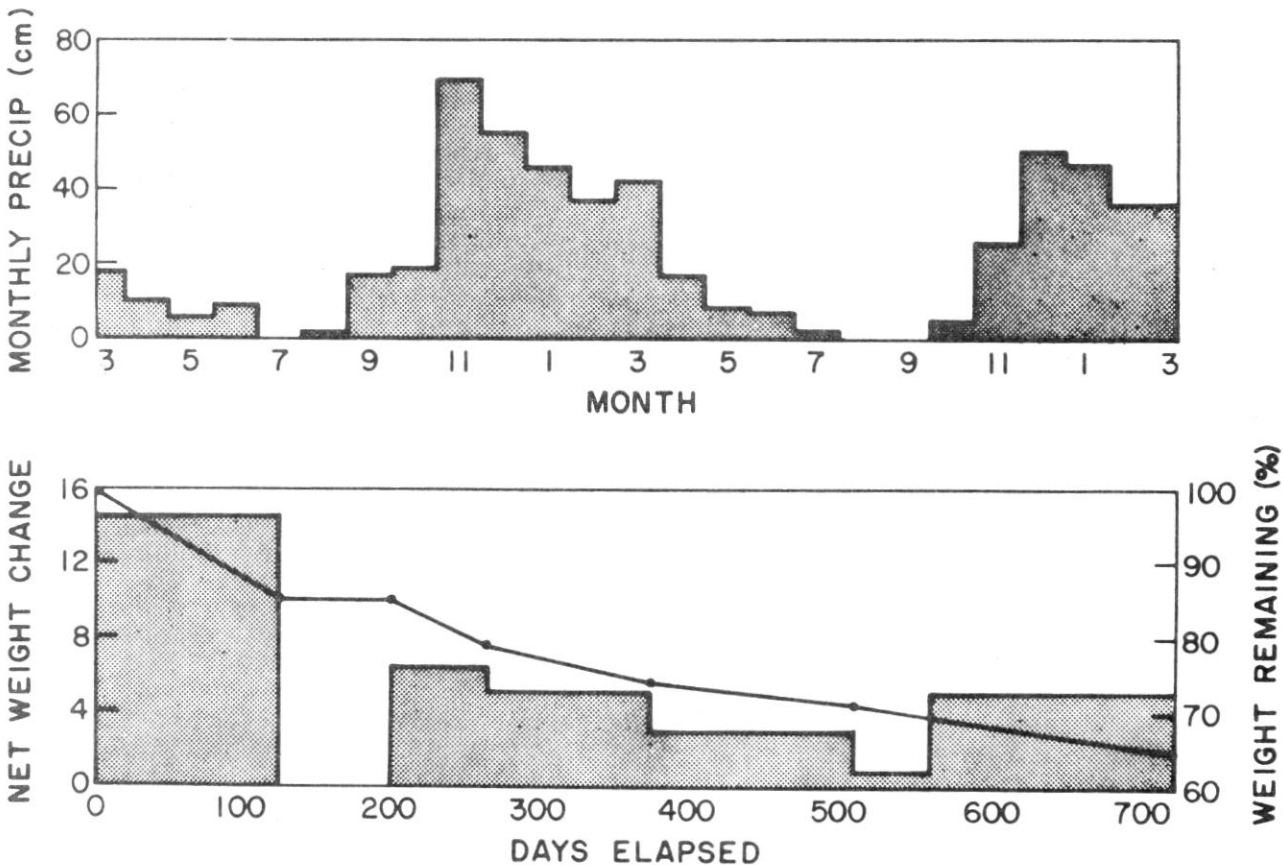


Figure 8. Decomposition rate for leaf litter stored in litter bags for two years, illustrating the highly seasonal nature of decomposition in the Pacific Northwest and its relation to precipitation (courtesy Kermit Cromack, Jr.)

(Cole et al., 1975). Other northwestern conifers behave similarly and may be even more conservative.

Deciduous hardwoods also redistribute substantial amounts of nutrients from foliage prior to leaf fall, but their total requirements are higher. Mature hardwoods reportedly require 70 kg/ha of nitrogen to develop their canopy each year, and less than one-third of this can be met by translocation from storage sites within the tree (Bormann et al., 1977).

Nutrient cycles also tighten during succession accentuating problems for a deciduous hardwood. Trees are increasingly dependent upon the forest floor, rather than the soil, for nutrients (Cole et al., 1975). Yet litter quality declines and litter decay slows, making this a poorer source of nutrients.

Hence, nutrient regimes in the Pacific Northwest again appear to be penalizing hardwoods. Total nutrient requirements are higher for hardwoods than evergreen conifers. Requirements must be largely met by absorption from soil and forest floor since hardwoods cannot provide as much of their nutrient requirements by internal redistribution. Yet decomposition and nutrient release are lowest during summer months when hardwood nutrient demand is high; the large pulses of nutrients during the wet fall and winter seasons is of less value for deciduous trees since they are less capable than evergreens of absorbing nutrients during the dormant season (Mooney and Rundel, 1979).

In summary evergreen coniferous trees are well adapted to the existing moisture, temperature, and nutrient regimes in the Pacific Northwest. Deciduous hardwood species have, on the other hand, numerous disadvantages in competing with conifers. First, they cannot utilize the "dormant" season for photosynthesis. Second, they are dependent upon assimilation during the growing season, a time when photosynthesis is frequently constrained by atmospheric and soil moisture deficiencies. Third, hardwoods have higher nutrient requirements and a higher proportion must be met by uptake from the soil and litter layers; again, this must be done during the growing season when decomposition and nutrient release are at minimal levels due to reduced soil moisture. Dominance by evergreen conifers appears to be an evolutionary response to a climate with cool, wet winters and warm, dry summers.

FOREST MASSIVENESS

The advantages of being massive are not as clear as those of being evergreen. Massiveness is, to a degree, related to some of the same environmental factors that favor evergreenness, however.

Size or massiveness results from the sustained growth and longevity of the tree species that occur in the Pacific Northwest. The fact that many species sustain their height and diameter growth for more than two or three centuries has already been mentioned. It is also important to recognize that every coniferous genus represented in the Pacific Northwest (save only *Juniperus*) has its largest and often longest-lived representative here--and often its second and third largest as well (Table 5).

Such a circumstance requires at least two conditions. First, there must be species' gene pools that favor persistent growth and long life. Second, there must be environmental conditions that allow the expression of this genetic potential--or at least do not select against such genotypes. Such environments are not necessarily pervasive in the temperate zone of the world. Periodic storms with high winds (hurricanes and typhoons) are, in fact, characteristic of most temperate forest regions. Indeed, Fujimori (1971) suggests that infrequent strong winds, such as those that disturb or weaken forest communities, are a key factor in the development of massive, long-lived forests in the Pacific Northwest. Less favorable conditions for development of pathogens is one of several alternative hypotheses. Neither explanation seems completely satisfactory.

Large size and longevity have adaptive advantages. Competitively, they obviously allow a species to overtop one of smaller structure or out-persist a species of short lifespan, or both. Long-lived species classed as pioneers or shade-intolerant are able to span the long periods between destructive episodes. Forest sites in the Pacific Northwest can go for many centuries between disturbances sufficient to allow regeneration of shade-intolerant species. For example, Hemstrom (1979) calculated the average fire-return period for Mount Rainier National Park, a site typical of much of the Cascade and Coastal ranges, to be more than 400 years. A short-lived, shade-intolerant species is clearly at a disadvantage under such disturbance regimes.

As with many organisms large size allows for buffering against adverse environmental conditions and stresses of various types. The value of the large sapwood storage areas in conifers in reducing

Table 5. Typical and maximum ages and dimensions attained by selected species of forest trees on better sites in the Pacific Northwest¹

Species	Typical			Maximum	
	Age	Diameter	Height	Age	Diameter
	<u>years</u>	<u>cm</u>	<u>m</u>	<u>years</u>	<u>cm</u>
Silver fir (<i>Abies amabilis</i>)	400+	90-110	44-55	590	206
Noble fir (<i>Abies procera</i>)	400+	100-150	45-70	>600	270
Port-Orford-cedar (<i>Chamaecyparis lawsoniana</i>)	500+	120-180	60	--	359
Alaska yellow-cedar (<i>Chamaecyparis nootkatensis</i>)	1,000+	100-150	30-40	3,500	297
Western larch (<i>Larix occidentalis</i>)	700+	140	50	915	233
Incense-cedar (<i>Libocedrus decurrens</i>)	500+	90	120	>542	368
Engelmann spruce (<i>Picea engelmannii</i>)	400+	100+	45-50	>500	231
Sitka spruce (<i>Picea sitchensis</i>)	500	180-230	70-75	>750	525
Sugar pine (<i>Pinus lambertiana</i>)	400	100-125	45-55	--	306
Western white pine (<i>Pinus monticola</i>)	400+	110	60	615	197
Ponderosa pine (<i>Pinus ponderosa</i>)	600+	75-125	30-50	726	267
Douglas-fir (<i>Pseudotsuga menziesii</i>)	750+	150-220	70-80	1,200	434
Coast redwood (<i>Sequoia sempervirens</i>)	1,250+	150-380	75-100	2,200	501
Western redcedar (<i>Thuja plicata</i>)	1,000+	150-300	60+	>1,200	631
Western hemlock (<i>Tsuga heterophylla</i>)	400+	90-120	50-65	>500	260
Mountain hemlock (<i>Tsuga mertensiana</i>)	400+	75-100	35+	>800	221

¹Typical values mainly from Franklin and Dyrness, 1973; maximum diameters from

effects of high moisture deficiencies has already been pointed out. The large mass of various organs, such as leaves, are also valuable for storage of nutrients and carbohydrates for use during times of high demand (the growing season) or stress.

SUCCESSIONAL ASPECTS OF NORTHWESTERN FORESTS

The lack of quantitative data on various aspects of forest succession in the Pacific Northwest is astounding. Foresters and botanists have been observing these forests for nearly a century, yet most successional analyses are either anecdotal (e.g., Munger, 1930, 1940) or based upon inferences drawn from current size class distributions (e.g., Franklin, 1966). Quantitative data have been especially scarce for older forests. Some data have been collected on compositional and structural changes in recently logged or burned areas (Dyrness, 1973).

This situation is rapidly changing and there are many interesting new findings in regard to changes in diversity, leaf and biomass development, and nitrogen budgets during forest succession (Long and Turner, 1975). Another interesting development is the increased recognition of multiple pathways in the development of stands on a given site, i.e., several possible species series as contrasted with a single sequence of pioneer and climax species.

We will consider briefly two aspects of forest succession which have been explored in recent studies: (1) age structures in old-growth Douglas-fir/western hemlock forests and (2) dynamics of coarse woody debris in a Douglas-fir forest chronosequence.

Age Structures in Old-Growth Douglas-fir Stands

Foresters and ecologists have always assumed that the old-growth forests dominated by Douglas-fir are even-aged. The Douglas-firs in these stands presumably were established over short time periods following major fires or other disturbances. In part, these assumptions were based upon observations of forest development and Douglas-fir regeneration following the extensive fires in the mid and late 1800's as well as in the Yacholt and Tillamook Burns of the twentieth century (Munger, 1930, 1940). For a time it was even believed that new Douglas-fir forests sprang almost instantly from seed stored in the litter layers (Hofmann, 1971), a hypothesis later disproved by Isaac (1943). No one bothered to analyze age structures of any old-growth stands, however, to test their hypothesized even-aged nature.

In 1975, an age structure analysis was conducted in an old-growth Douglas-fir stand at H. J. Andrews Experimental Forest in the western Cascades of Oregon. Experimental Watershed No. 10, a 10-hectare drainage, was clearcut. Previously, all of the trees in this drainage more than 15 cm diameter at breast height (dbh) had been stem mapped, recorded by dbh and species, and tagged at stump level. Following clear-cutting, rings were counted on stumps of more than 600 of the 2,700 inventoried stems, including a large proportion of the dominant Douglas-firs.

The age distribution of the counted Douglas-fir trees on Watershed No. 10 is shown in Figure 9A. A disturbance in about 1800 is obvious from a wave of younger Douglas-firs; this partial burn is also apparent in the age distribution of hemlocks, most of which date from 1800. The surprising result is the very wide range in ages of dominant, old-growth Douglas-firs in this stand--from 275 to 540 years of age. Furthermore, there is no evidence of multiple peaks or waves of establishment--just a gradually increasing number of individuals followed by a broad-crested peak and gradually declining period of establishment (Figure 9B). Analysis of separate habitat segments on this diverse watershed (Hawk, 1979), such as the moist lower slope and dry ridgetop situations, provided no explanation for the forest age pattern; a similar age distribution was found on all habitats.

Watershed No. 10 might be considered an aberrant situation, especially in view of the overall decadence of the stand (Grier and Logan, 1977) and relatively low site quality. Subsequent age structure analyses, however, have revealed similar patterns elsewhere. Joseph Means (pers. comm., 1979) analyzed a dense, thrifty Douglas-fir stand at about 1,000 m on a cool, moist habitat type. The same pattern, with a 125-year age range in the dominant Douglas-firs, is present (Figure 10). Ring counts on several clearcuts surrounding Thornton T. Munger Research Natural Area in the Wind River drainage of the southern Washington Cascade Range reveal an even more extended age range (200 years) in the dominant Douglas-firs (Figure 11); this stand is at around 500 m. The Douglas-fir age structures reported by Boyce and Bruce-Wagg (1953) are further evidence for wide ranges of age in old-growth stands; the implications of these early data were apparently overlooked.

The conclusion from all of these analyses is that many of the old-growth Douglas-fir forests are not even-aged. For some reason, many of these stands did not

close up rapidly following the disturbance or series of disturbances that destroyed the previous stands. Douglas-fir has apparently taken a long period (100 to 200 years) to fully reoccupy many of these sites. There are several possible explanations. The disturbance or disturbances that gave rise to these stands, many of which are 400 to 500 years of age, may have been so extensive as to eliminate seed source; gradual recolonization of the area would have been required, with a few individuals becoming established and eventually providing the seed source for development of a closed stand. The age structure patterns fit Harper's (1978) hypothesized sequence of this type. Competing vegetation may have delayed establishment of trees. Multiple disturbances subsequent to the first one may have wiped out portions of young stands, creating open spaces for establishment of even younger cohorts; reburns of young Douglas-fir stands occur, with survival of individual and small patches of trees.

In any case, the assumed pattern of forest succession with early establishment of even-aged Douglas-fir stands does not

appear to be the pattern followed by many of the old-growth stands. Successional studies during coming years should provide evidence of additional patterns and the responsible factors. Indeed, a recent study of tree ages in the Cowlitz River drainage of Mount Rainier National Park shows that establishment of shade-intolerance tree species, such as Douglas-fir and western white pine, is still taking place more than 80 years after the last wildfire (Figure 12) (Hemstrom, 1979).

Coarse Woody Debris in a Forest Chronosequence

Structural changes associated with successional development of forest stands in the Douglas-fir region are currently under study. These studies were stimulated, in part, by an analysis of old-growth forests (Franklin et al., 1979) that revealed precious little knowledge of northwestern forest structure beyond measurements of wood volumes and production. A series of nine Cascade Range stands have been studied thus far, ranging in age from about 100 years to more than 1,000 years. A major structural feature is the amount and distribution of coarse woody debris as standing dead (snags) and down (logs and chunks) (Table 6).

One of the most surprising findings from this survey was the large amount of dead wood in young stands. Much wood is being carried from the old into the new stand. Wildfire or windthrow may kill the previous stand but consumes very little of the wood; indeed, one or, more probably, several subsequent fires would be required to eliminate the large snags and down logs. Consequently, large amounts of woody debris bridge the disturbance and remain important structural features of the young stand for several centuries because of their slow rate of decomposition. By the time the woody debris carried over has largely disappeared, stems in the young stand are sufficiently large to provide an input of large woody debris. As a result, there seems to be a rather high level of woody debris found at all stages in forest succession. The large amount of coarse woody debris provides a major structural contrast between the natural "second-growth" stands and the managed forests created after logging.

A second interesting feature is the suggestion of greater amounts of woody debris with stand age. There is a trend toward greater absolute amounts as well as a higher ratio of dead/live organic matter in the stands more than 750 years of age (Figure 13). Amounts of coarse woody debris

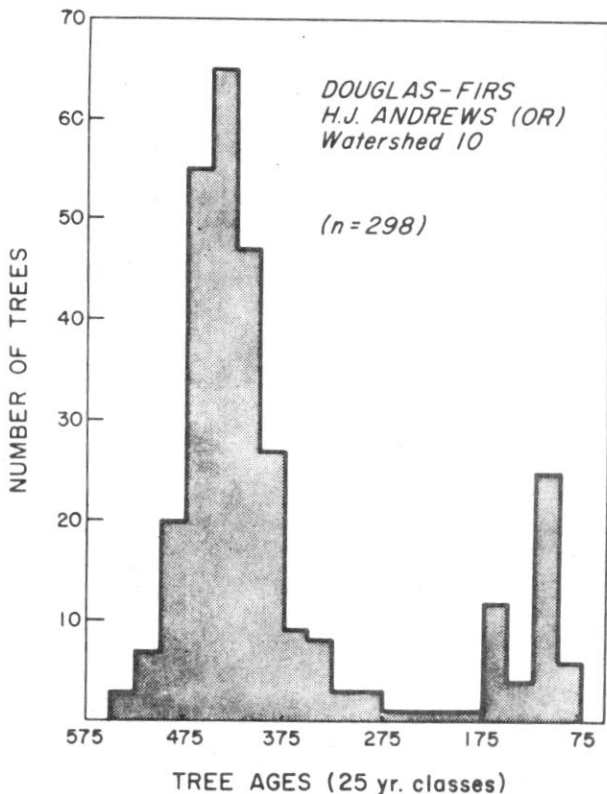


Figure 9A. Age class distribution of Douglas-fir trees on Watershed No. 10 at the H. J. Andrews Experimental Forest in the western Oregon Cascade Range. Tabulation of all counts by 25-year age classes.

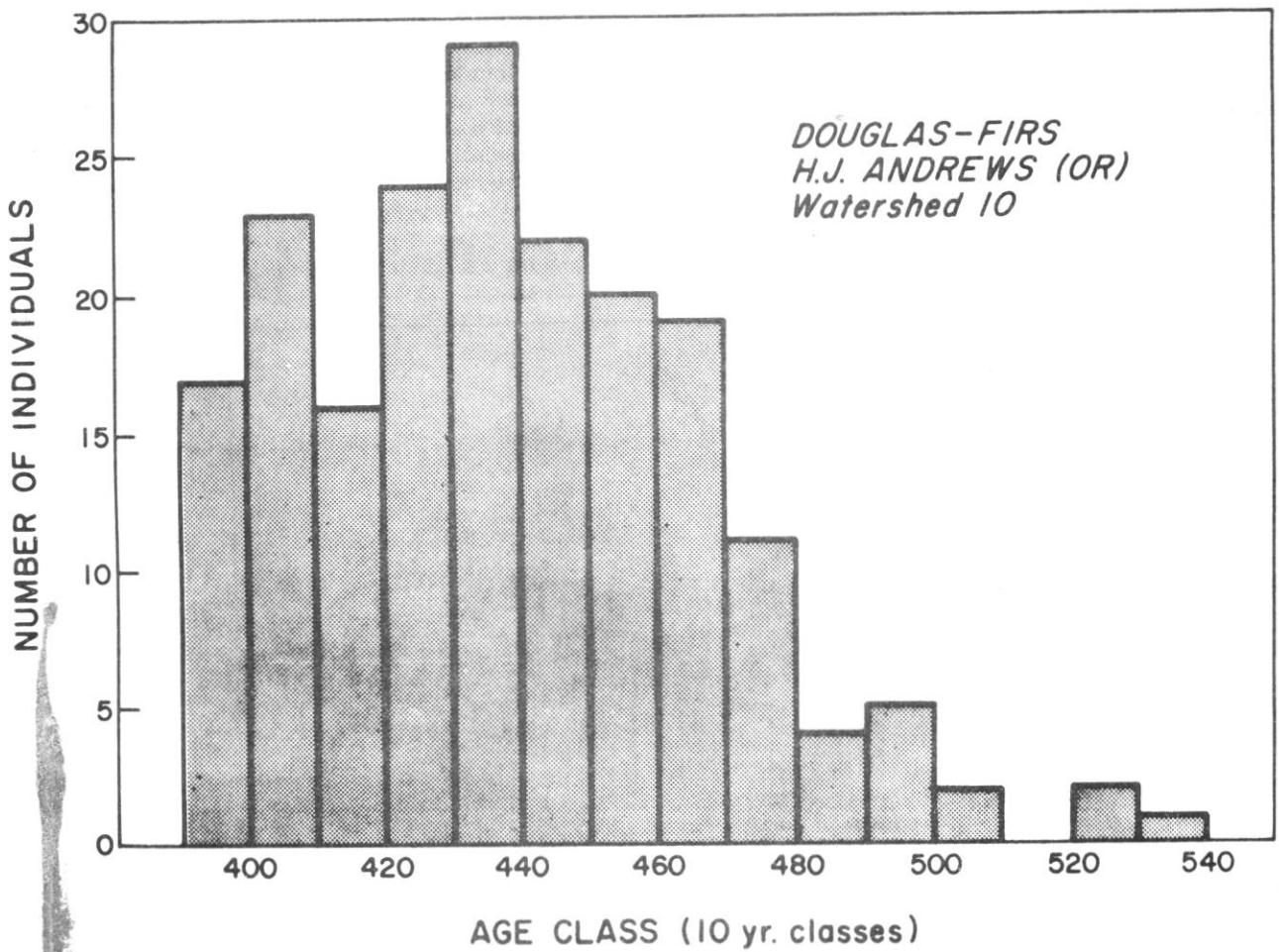


Figure 9B. Age class distribution of Douglas-fir trees on Watershed No. 10 at the H. J. Andrews Experimental Forest in the western Oregon Cascade Range. Tally of old-growth trees by 10-year age classes.

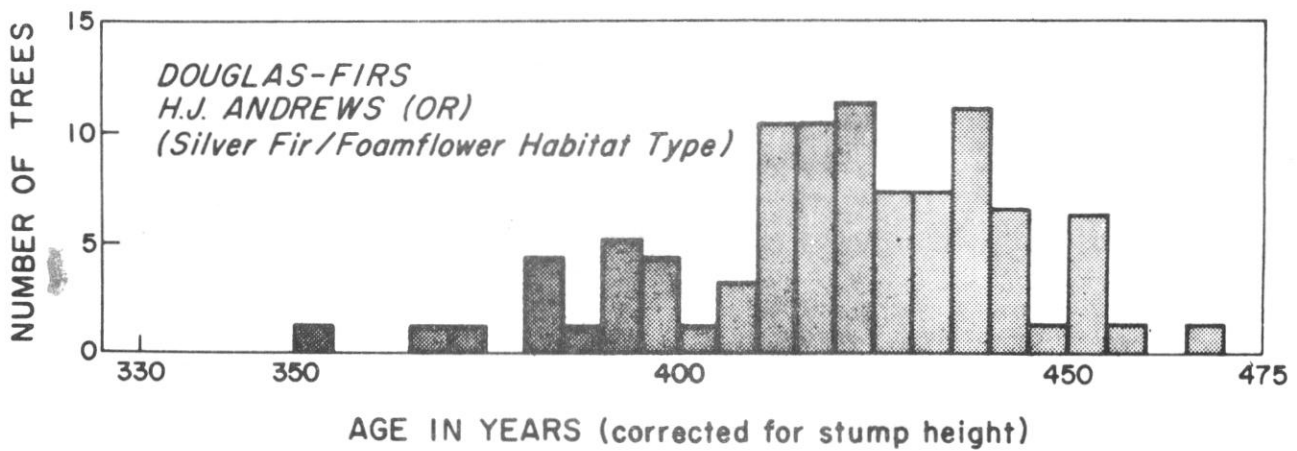


Figure 10. Age-class distribution of Douglas-fir trees in an old-growth stand located at about 900 m in the H. J. Andrews Experimental Forest on the Oregon Cascade Range.

at a given age vary widely, almost certainly because of peculiarities in development of individual stands. This variability makes it difficult to substantiate any statistical trends associated with stand age. There is, however, some corollary evidence from an analysis of old-growth stands at Mount Rainier National Park that suggests reduced

amounts of live biomass in very old stands (Table 6). A current hypothesis is that live organic biomass in a stand may peak at around 300 to 400 years, total biomass (live and dead) at around 750 years, and dead (coarse woody debris) at 800 to 1,000 or more years. Many more stand analyses are required, however, given the variability in patterns of stand development.

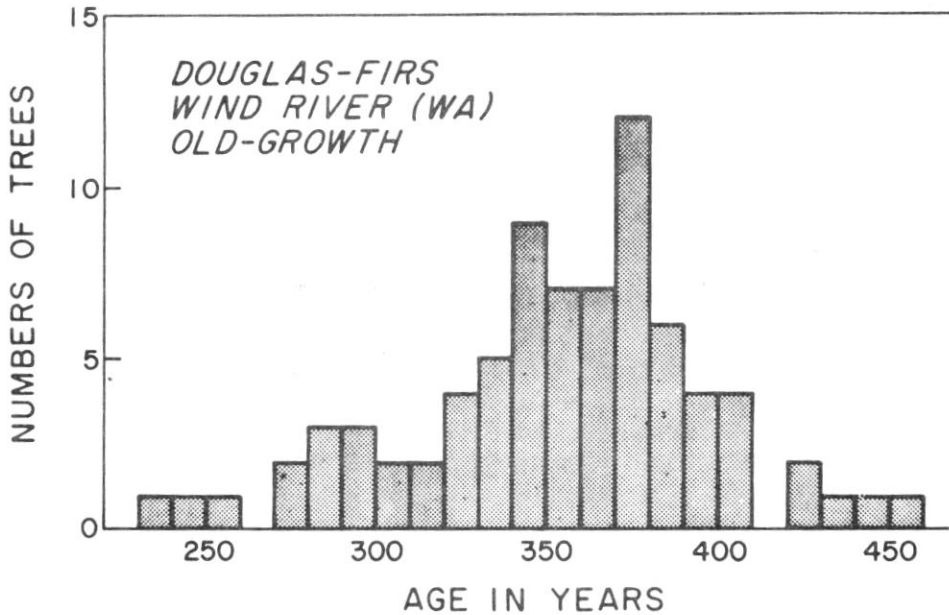


Figure 11. Age-class distribution of Douglas-fir trees in old-growth stands located around the periphery of the Thornton T. Munger Research Natural Area in the Wind River valley of the southern Washington Cascade Range.

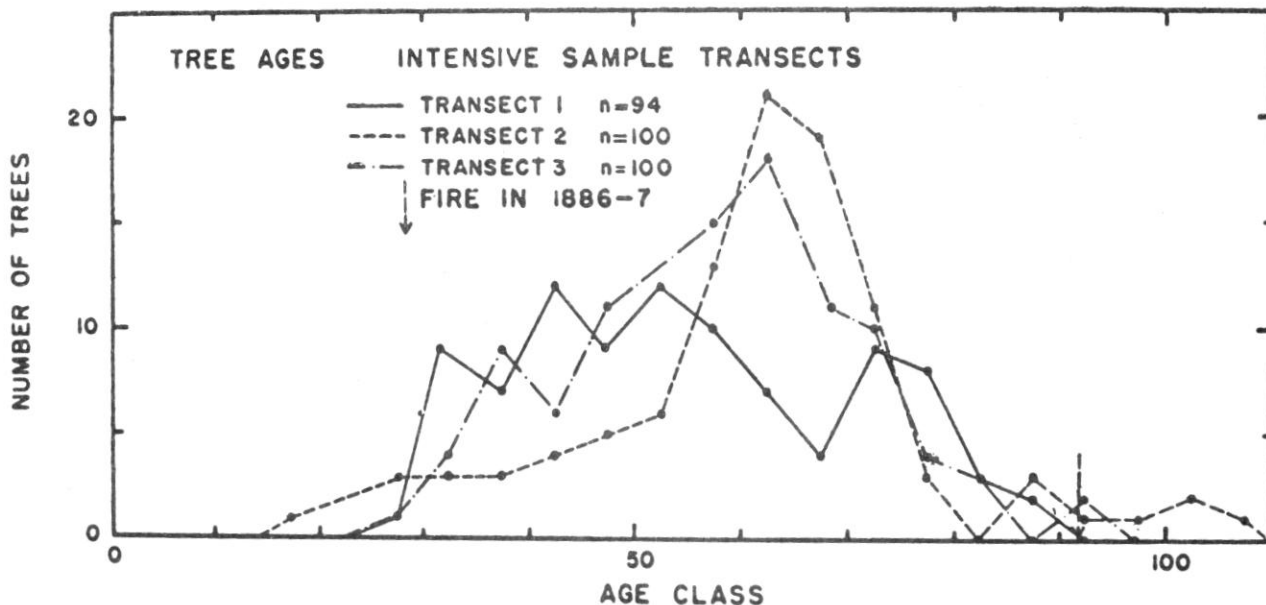


Figure 12. Age-class distribution of trees in stands developed following wildfires in the later 1800's in the Cowlitz River drainage, Mount Rainier National Park, Washington (from Hemstrom, 1979).

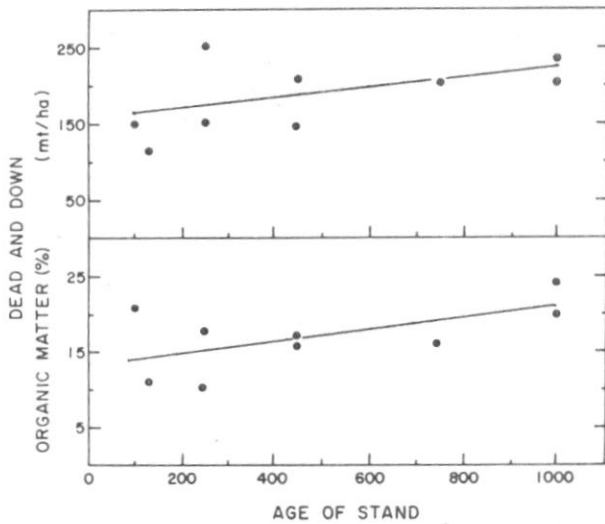


Figure 13. Total amounts (mt/ha) and percent of the total organic matter provided by coarse woody debris (standing dead trees and down logs) in a chronosequence of Douglas-fir/western hemlock forests located in the Cascade Range of Oregon and Washington; only a weak relationship with age is apparent in this preliminary data set.

Table 6. Coarse woody debris in a chronosequence of stands from mid-elevations in the northern Oregon and southern Washington Cascade Range¹

Stand ²	Age	Live biomass ³	Coarse woody debris			Dead/total biomass
			Snags	Logs	Total	
	<u>yrs</u>	<u>mt/ha</u>		<u>mt/ha</u>		<u>%</u>
HJA RS 24	100	564	37	113	150	21
HJA RS 26	130	934	48	70	118	11
MR 1	250	1,318	67	85	152	10
Bagby	250	1,069	122	129	251	19
HJA RS 2	450	1,189	58	90	148	11
HJA RS 3	450	991	79	131	210	17
Squaw	750	1,094	85	119	204	16
MR 2	1,000+	638	48	156	204	24
MR 3	1,000+	931	120	112	232	20

¹Unpublished data on file at the Forestry Sciences Laboratory, Corvallis, Oregon.

²"HJA RS" refers to hectare "reference stands" or permanent sample plots at H.J. Andrews Experimental Forest in the western Cascades of Oregon. "MR" stands are similar plots in Mount Rainier National Park, Washington. Bagby and Squaw are located in the northern Oregon Cascade Range.

³Including 20 percent of live aboveground biomass as estimate of live belowground biomass.

OLD-GROWTH FOREST ECOSYSTEMS

Old-growth forests are distinctive ecosystems that have not been well understood by either foresters or the lay public. Indeed, no one was really very interested in them until recently. Some viewed these forests as biological deserts although, insofar as biologic diversity is concerned, that description is most applicable to the dense, productive young forest. Others viewed them solely in aesthetic or religious terms. In any case, with their broadened sense of land stewardship, foresters are thinking increasingly in terms of maintaining and recreating such systems in order to provide a diversity of habitats and organisms. Questions have arisen as to the essential features of old-growth forests, however. What are their key characteristics and how do they differ from managed stands or from the natural second-growth forests that follow wildfire?

General features of old-growth (>200 years old) forest stands in the Douglas-fir region now have been described (Franklin et al., 1979). We have extracted a few highlights from that characterization and will briefly examine the compositional (what is there), functional (how it runs), and structural (how it's put together) features of old-growth forests. The emphasis will be on structure, since this provides a major key to the distinctiveness of old-growth stands.

Composition

The composition of old-growth forests is obviously different from that of young stands. Changes in composition--the array of plant and animal species--is, after all, a keystone of ecological succession. Many species, including some saprophytic plants, some epiphytic lichens, and several vertebrates, find optimum habitat conditions in old-growth forests. There are relatively few species of plants or animals that are found only in old-growth forests, however. Some organisms may require old-growth for maintenance of viable populations, although that is not yet clear. Currently, vertebrate/old-growth relationships are best understood, and a list of 14 birds and nine mammals finding their optimum habitat in old-growth Douglas-fir forests has been compiled (Franklin et al., 1979). Several of these, such as the northern spotted owl (*Strix occidentalis*) and the red tree vole (*Arborimus longicaudus*), may be examples of species that require a reservoir of their optimum habitat in old-growth forest to survive.

Function

Functional aspects of forests include primary production and the cycling of nutrients and energy. Productivity in old-growth forests is typically high, despite statements to the contrary. The large leaf areas and masses found in northwestern forests were mentioned earlier, and there is no indication that levels decline significantly in older stands. A single long-crowned old-growth Douglas-fir tree may have as many as 66 million needles and 2,800 m² of needle surface area. With such large and intact photosynthetic factories, production values are maintained at comparable levels over many centuries. However, respiration costs are high in old-growth stands because of their large live biomasses, greatly reducing the amount of net production.

On the more practical level, little accumulation of additional live biomass or board feet occurs in most old-growth stands. Substantial wood increment is taking place on individual trees, including associated western hemlock and other shade-tolerant species. Typically, this wood growth is largely offset by mortality and decay losses in living trees. In a 250-year-old Douglas-fir stand in the Mount Hood National Forest annual wood increment over 10 years was 15.8 m³/ha; an episode of heavy mortality (14.1 m³/ha/yr) caused by bark beetles and windthrow nearly offset this large growth. In the Thornton T. Munger Research Natural Area in the Gifford Pinchot National Forest a 450-year-old Douglas-fir/western hemlock stand grew 7.4 m³/ha/yr over 12 years; the average annual mortality was 6.7 m³/ha/yr. Hence, both stands registered small net gains. Over the long run, living biomass in stands in old stands probably fluctuates around a plateau in response to episodes of heavy and light mortality.

Old-growth forests are known to be highly retentive of nutrients. Complex detrital pathways exist in such stands and the release of energy and nutrients from dead organic matter is slow. This is reflected in the low levels of nutrients and other dissolved and suspended materials in streams from old-growth forests (see Fredriksen, 1970, 1972). Mechanisms for fixation of atmospheric nitrogen are also well developed in old-growth forests, providing for substantial increments by foliose lichens in tree crowns and by microbial fixation in coarse woody debris (see Carroll, this volume; Triska and Cromack, this volume).

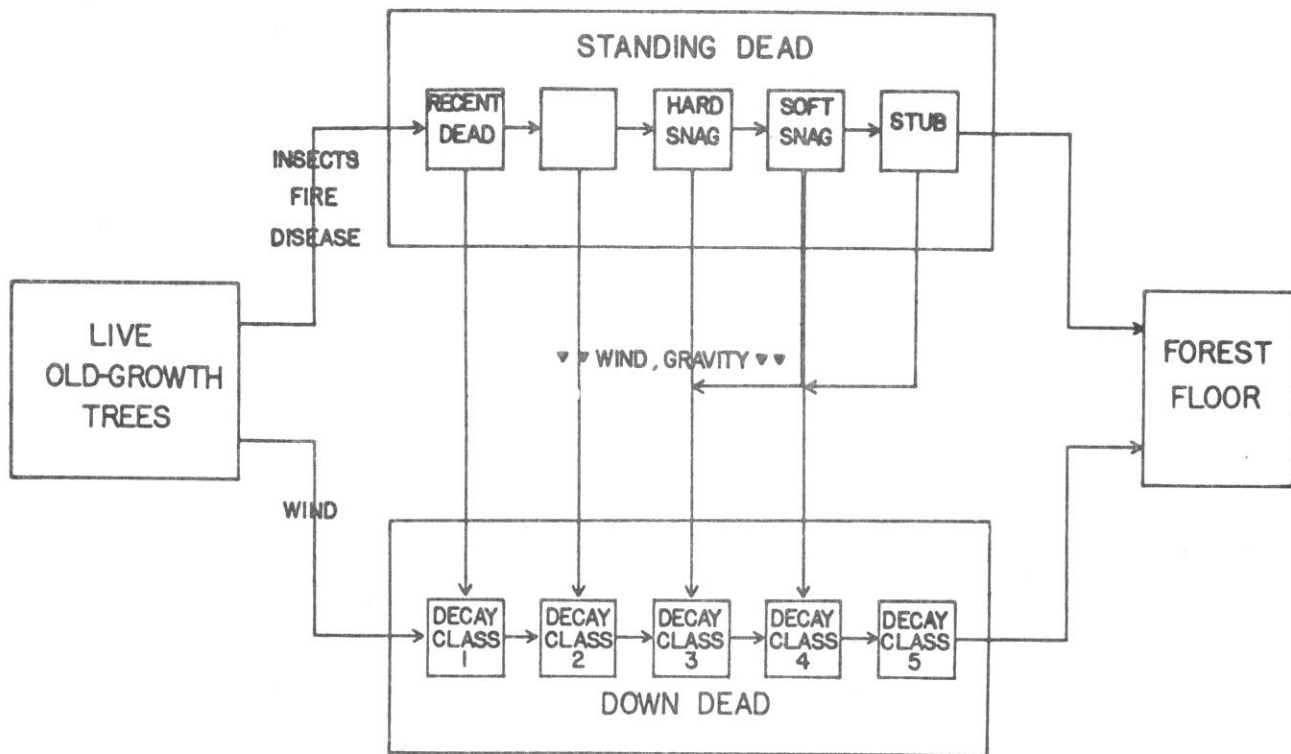
Structure

Structural diversity is characteristic of old-growth forests. There is, for example, a large range in tree sizes, a more varied canopy, and greater patchiness in the understory.

There are, however, three structural components of overwhelming importance--the individual, large, old-growth tree, the large, standing dead tree or snag, and the large, dead, down trunks or logs. These structural components are, in large measure, unique to an old-growth forest ecosystem, setting it apart from young growth and, especially, managed stands. These components are all related (Figure 14), with the tree playing a progression of roles from the time it is alive through its routing to an unrecognizable component of the forest floor. Further, most of the unique (or at least distinctive) compositional and functional features of old-growth forests can be related to these structures (Table 7); that is, these structural components make possible much of the uniqueness of old-growth forests in terms of flora and fauna

and the way in which energy and nutrients are cycled. Finally, logs are at least as important (and possibly more so) to the stream component as they are to the terrestrial component of the ecosystem (see Triska and Cromack; Swanson; and Cummins, all this volume).

The most conspicuous structural component is probably the live, old-growth Douglas-fir tree. Diameters of 1 to 2 m and heights of 50 to 90 m are typical. The trees are highly individualistic, having been shaped over the centuries by a wide range in forces. The large, deep, irregular crown is an important ecological feature (Figure 15). Live branch systems often extend two-thirds of the length of the bole. Flattened, fan-shaped branch arrays are characteristic and provide extensive horizontal surfaces for the development of epiphytic communities and wildlife habitat. Carroll (this volume) discusses the role of such canopies in nutrient cycling and the importance of canopy lichens (especially *Lobaria oregana*) in nitrogen fixation.



ROUTING OF FOREST TREES FROM LIVE THROUGH VARIOUS DEAD ORGANIC COMPARTMENTS

Figure 14. Diagrammatic illustration of the relationships between the key structural features (live trees, snags, and down logs) of old-growth forest stands.

Standing dead trees or snags are well known for the fire and safety hazards they represent and, more recently, as critical habitat for wildlife (Cline et al., 1979). Thomas and others (1979) have thoroughly analyzed the role of snags as sites for nesting, food sources, and other uses by wildlife. In the Blue Mountains of Oregon, snags are the primary location for 39 birds and 24 mammals species that utilize the cavities. Furthermore, a direct correlation is indicated between numbers of snags and related wildlife populations. Snags undergo a steady process of decay and disintegration, and a variety of standing dead size and decay classes are necessary to meet differing animal requirements. Snags also play the same functional roles as down logs.

Down dead trees, also known as logs or coarse woody debris, are nearly as conspicuous as the large live trees. Large masses of logs constitute an important component of old-growth forests (Table 6). In addition to their volume and weight, these logs can occupy 10 to 20 percent of the ground surface area. Logs provide several important habitat and functional roles (Table 7). Many animals utilize logs as food sources, protection, and living sites. The logs provide important pathways for small mammals that may be important in providing for the spread of mycorrhizal-forming fungi (Maser et al., 1978). Down logs also serve as habitat for reproduction of some tree species, especially western hemlock. In natural stands this is important in providing seedlings and saplings for potential canopy replacements. Logs, of course, represent large storehouses of energy and nutrients and, as pointed out by Triska and Cromack (this volume), are sites where significant bacterial fixation of nitrogen takes place.

These structural features of old-growth forests provide one handle for foresters to use in perpetuating or mimicking natural processes. Silvicultural methods can be developed for creating stands with these characteristics as well as individual structural (and, hence, compositional and functional features) of the virgin forests. It will be a challenge for foresters to see if they can learn to manage dead wood as imaginatively as they do live! Or, to put it another way, to manage for decadence as well as board feet! There certainly is evidence that they can--for example, in the new snag management policies.

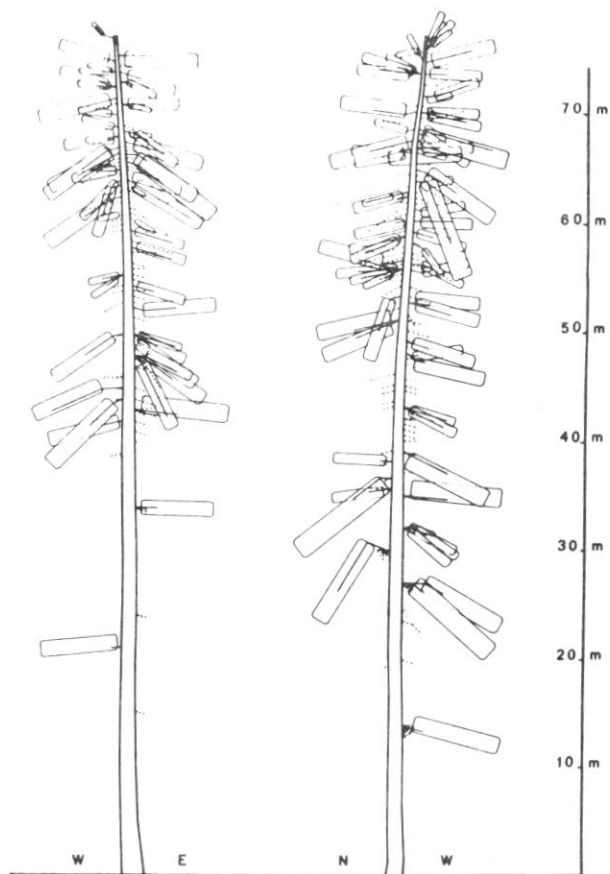


Figure 15. Schematic illustration of the branch systems of an old-growth Douglas-fir tree, illustrating the deep crown characteristic of many of the trees (courtesy Wm. Denison and G. Carroll).

CONCLUSIONS

Studies of our forest ecosystems during the last decade have produced many significant new insights into the structure and functioning of forests in the Pacific Northwest. We have much improved understandings of how forests are adapted to their environment and how they respond to various natural and man-created disturbances. These findings contribute to improved management of forest lands, and the development of applicable results can be expected to accelerate as we enter our third generation of ecosystem-level studies. I strongly suspect that, however much we currently think we know, we are going to be in for many more surprises.

Table 7. Relationship of the key structural components of old-growth Douglas-fir forests to compositional and functional attributes of these forests

Compositional role	Structural element	Functional role
Distinctive epiphytes Distinctive vertebrates Distinctive invertebrates	Individual, large old-growth tree	Site of N-fixation Ionic storage Interception of H ₂ O nutrients, light
Utilized by cavity dwellers and other vertebrates	Large standing dead	Energy and nutrient source
Distinctive animal communities Seedbed or nursery for seedlings	Large down dead on land	Site of N-fixation Energy and nutrient source
Distinctive animal communities Creates habitat diversity	Large down dead on stream	Site of N-fixation Energy and nutrient source Maintains physical stability of stream Retains high-quality energy materials for processing

ACKNOWLEDGEMENTS

This work is aggregated from that of many others. The discussion of evergreen conifer dominance is taken largely from Waring and Franklin (1979) and that on the old-growth forest from Franklin and others (1979), which includes contributions by K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. W. Moir has been a contributor to these ideas and directed studies at Mount Rainier which provided data utilized here. The dissertation research of H. Gholz and M. Hemstrom provided data and ideas. J. Means provided data and assistance on the age structure analyses, and S. Lewis provided data from her analysis of the Wind River stand. T. Thomas and M. James collected the data on dead and down coarse woody debris in the chronosequence stands. Additional input has been provided by P. Sollins, G. Carroll, G. Hawk, W. Emmingham, and R. Lambert.

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Appendix 1. Data sources for biomass and leaf area in stands in the Pacific Northwest

Dominant species	Stand age	Basal area	Aboveground biomass			Projected leaf area	Source and plot identification ²
			Total	Wood ¹	Foliage		
	yrs	m ² /ha		mt/ha		m ² /m ²	
Douglas-fir	70	60	422	406	16	8.1	Santantonio (Dry)
Douglas-fir	110	63	661	650	11	5.6	Fujimori et al., 1976
Douglas-fir	100	56	478	466	12	6.1	Franklin (RS 24)
Douglas-fir	120	72	531	509	22	11.2	Santantonio (Wet)
Douglas-fir	125	54	449	437	12	6.1	Gholz, 1979 (III)
Douglas-fir	130	90	792	772	20	10.2	Franklin (RS 26)
Douglas-fir	150	72	527	509	18	9.2	Gholz, 1979 (IV)
Douglas-fir	150	84	865	849	16	7.4	Gholz, 1979 (II)
Douglas-fir	150	90	786	762	24	12.2	Franklin (MR 13)
Douglas-fir	170	72	532	510	22	10.2	Santantonio (Modal)
Group average		71	604	585	19	9.7	
Noble fir	130	98	880	862	18	9.9	Fujimori et al., 1976
Sitka spruce/hemlock	121	100	916	908	8	5.1	Grier, 1976 (Plot 12)
Sitka spruce/hemlock	130	118	1,080	1,057	23	14.1	Gholz, 1979 (IA)
Sitka spruce/hemlock	130	111	1,492	1,460	32	20.2	Gholz, 1979 (IB)
Group average		110	1,163	1,142	21	13.4	
Western hemlock	26	49	192	171	21	13.4	Fujimori, 1971
Douglas-fir/hemlock	250	106	1,117	1,094	23	11.7	Franklin (MR 1)
Douglas-fir/hemlock	250	99	991	968	23	11.7	Franklin (Bagby)
Douglas-fir/hemlock	450	68	715	701	14	7.1	Franklin (RS 1)
Douglas-fir/hemlock	450	84	911	893	18	9.2	Franklin (RS 2)
Douglas-fir/hemlock	450	92	826	801	25	12.7	Franklin (RS 3)
Douglas-fir/hemlock	450	99	1,223	1,203	20	10.2	Franklin (RS 28)
Douglas-fir/hemlock	450	118	1,237	1,208	29	14.7	Franklin (RS 29)
Douglas-fir/hemlock	450	116	1,137	1,107	30	15.2	Franklin (RS 30)
Douglas-fir/hemlock	450	92	1,039	1,018	21	10.7	Franklin (RS 31)
Douglas-fir/hemlock	450	129	1,423	1,392	30	15.2	Franklin (RS 27)
Douglas-fir/hemlock	500	50	317	303	14	7.1	Franklin (MR 6)
Douglas-fir/hemlock	500	81	590	567	23	11.7	Franklin (MR 5)
Douglas-fir/hemlock	500	76	585	559	26	13.2	Franklin (MR 8)
Douglas-fir/hemlock	500	65	606	586	19	9.7	Franklin (MR 4)
Douglas-fir/hemlock	500	89	957	933	24	12.2	Franklin (MR 11)
Douglas-fir/hemlock	750	79	927	908	18	9.2	Franklin (Squaw)
Douglas-fir/hemlock	1,000	69	541	520	21	10.7	Franklin (MR 2)
Douglas-fir/hemlock	1,000	98	789	760	29	14.7	Franklin (MR 3)
Douglas-fir/hemlock	1,000	74	563	539	24	12.2	Franklin (MR 14)
Group average		89	868	845	23	11.7	

¹Bole, bark, and branches.²Daniel Santantonio: personal communication; stands located on wet, modal, and dry sites in McKenzie River drainage of Oregon Cascade Range. J. F. Franklin: data on file at Forestry Sciences Laboratory, Corvallis, Oregon. "RS" plots are hectare reference stands or permanent sample plots located at elevations between 360 and 1,200 m on the H. J. Andrews Experimental Ecological Reserve in the Western Cascades of Oregon. "Bagby" is a plot in the Bagby Research Natural Area, Mount Hood National Forest, Oregon. "Squaw" is located in the Squaw Creek drainage, a tributary of the South Fork of the Santiam River, Willamette National Forest, Oregon. "MR" plots are hectare reference stands or permanent sample plots located at elevations below 1,200 m in Mount Rainier National Park, Washington.