Evergreen Coniferous Forests of the Pacific Northwest

Massive long-lived conifers dominating these forests are adapted to a winter-wet, summer-dry environment.

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Summary. The massive, evergreen coniferous forests in the Pacific Northwest are unique among temperate forest regions of the world. The region's forests escaped decimation during Pleistocene glaciation; they are now dominated by a few broadly distributed and well-adapted conifers that grow to large size and great age. Large trees with evergreen needle- or scale-like leaves have distinct advantages under the current climatic regime. Photosynthesis and nutrient uptake and storage are possible during the relatively warm, wet fall and winter months. High evaporative demand during the warm, dry summer reduces photosynthesis. Deciduous hardwoods are repeatedly at a disadvantage in competing with conifers in the regional climate. Their photosynthesis is predominantly limited to the growing season when evaporative demand is high and water is often limiting. Most nutrients needed are also less available at this time. The large size attained by conifers provides a buffer against environmental stress (especially for nutrients and moisture). The long duration between destructive fires and storms permits conifers to outgrow hardwoods with more limited stature and life spans.

Along the Pacific Coast of northwestern America, the dominant vegetation consists of dense forests of evergreen conifers, which clothe the landscapes from northern California to the panhandle of Alaska (Fig. 1). The forests are unrivaled both in the size and longevity of individual trees and in the accumulations of biomass of individual stands. Furthermore, the massive evergreen canopies of these forests contrast with the deciduous hardwood or mixed hardwood-conifer stands typical of the North Temperate Zone.

The degree of conifer dominance is impressive. In the Cascade Mountains and Coast Range of the Pacific Northwest, the biomass of conifers is 1000 times that of the hardwoods. Of the 25 coniferous species in these forests many represent the largest, and often the longest-lived, of their genera (Table 1). Still represented are arboreal evergreen and deciduous taxa—such as species of tanoak (*Lithocarpus*), chinquapin (*Castanopsis*), maple (*Acer*), oak (*Quercus*), and alder (*Alnus*)—which can achieve some local importance. However, conifer-hardwood roles in the Pacific Northwest largely are the reverse of those in eastern North America. For example, northwestern hardwoods often play pioneer roles [such as red alder (*Alnus rubra*)] or occupy habitats whose environmental features significantly differ from the regional norm [for example, Oregon white oak (*Quercus garryana*) on droughty habitats].

What factors favored the evolution of these massive, conifer-dominated forests in contrast to the deciduous hardwood forests in other temperate regions? Scientists since Von Humboldt in the mid-1800's have speculated on this topic. Although some have suggested that cold temperatures during glacial epochs eliminated many hardwood genera (*1*), this is clearly not the case. Most hardwood extinction actually occurred during the Pliocene, much earlier than the Pleistocene when relatively mild environments and good north-south routes for propagation may have been major factors in maintaining the conifer gene pool in the Pacific Northwest (*2*).

Environmental features have also been proposed as major factors in conifer dominance. Chaney *et al.* (*3*) suggest that arid periods caused hardwood losses. Daubenmire (*4*) identifies cool summers, coupled with the inability of deciduous hardwoods to utilize frequent warm days in spring and fall. Regal (*5*) proposed that gymnosperms survive as dominants only in environments that are, in some way, harsh or rigorous; however, he concedes uncertainty as to how the coniferous forests of the Pacific Northwest conform to this hypothesis.

The steep mountainous topography of coastal northwestern America might suggest youthful, thin soils as a factor, but regional soils are, in fact, at least as deep and as fertile as those of other temperate forest regions. Hence, while harsh climates, thin soils, and periodic wildfires are probably factors in the development of the conifer forests of intermountain western North America in the rain shadow of the coastal mountains, these factors fail to explain conifer dominance in the coastal region.

Knowledge of the structure and function of the northwestern coniferous forest has been greatly extended by studies conducted as part of the International Biological Program. In this article, we apply these data to examine the relative merit of evergreen conifer and deciduous hardwood habitats under existing climatic conditions. Because regional climatic regimes have been similar for several epochs, we propose that the advantages enjoyed by evergreen conifers in such environments have been key factors in competitively eliminating much of the original hardwood flora. In addition, we document the large biomass and productivity values of the forests and suggest how massiveness is advantageous.

Paleobotanical Record

During the early and middle Miocene 18 to 28 million years ago, more than 40 genera of woody dicotyledons extended from Oregon north through Alaska and Siberia to Japan (*6, 7*). A pure coniferous forest existed only in the uplands, above 500 meters in Japan and above 700 meters in Oregon. Thus, the areas dominated by conifers—mostly fir, spruce, and hemlock—were highly disjunct during the early and middle Miocene in northwestern North America and northeastern Asia (*7, 8*).

By the late Miocene 12 to 18 million years ago, coniferous forests began to

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occupy large areas in the uplands. Floras at intermediate elevations throughout the western United States contained moderate to large amounts of fir, spruce, and hemlock (*6*). For the first time, a coniferous forest extended continuously from the uplands of Oregon northward through British Columbia and into Alaska (*7*).

During the late Miocene or early Pliocene some 10 to 12 million years ago, a rich boreal forest of spruce, pine, and hemlock—with smaller quantities of larch, fir, beech, oak, and elm—was established in northeastern Siberia (*9*). A similar trend was occurring in Alaska. However, in Oregon, the early Pliocene floras west of the Cascade Mountains contained an impoverished deciduous flora with hickory, elm, and sycamore still represented (*3*). Thus, more hardwood species became extinct during the late Pliocene than during any period since.

By the early Pleistocene, some 1.5 million years ago, and before major glaciation, the flora of the Pacific Northwest was essentially established as it appears today. Major components of the original widespread deciduous hardwood forest still persist in Japan, China, Europe, and parts of the eastern United States. Their extinction from the Pacific Northwest probably was related to changes in climate that favor the conifers present today.

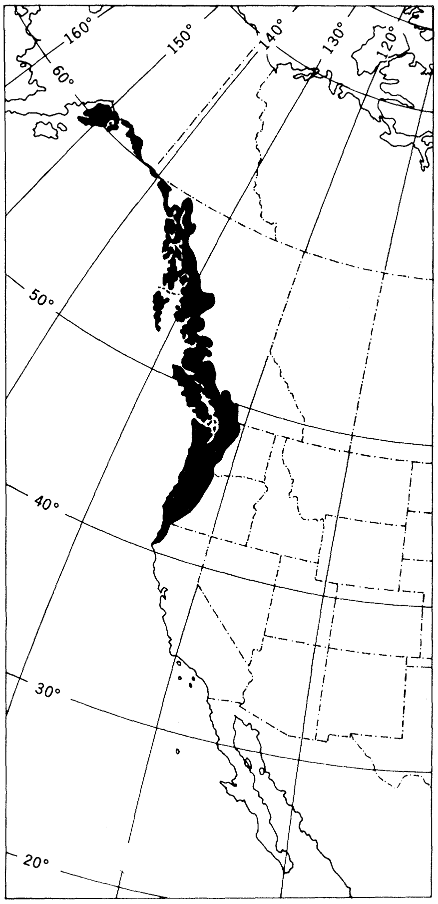

Fig. 1. The Pacific Northwest region, dominated by massive coniferous forests, extends from northwestern California to the southwestern coast of Alaska. The crest of the Coast Range or Cascade Mountains forms the eastern boundary of the region.

Present Climate

Climatically the region experiences wet mild winters and warm dry summers. The dormant season, when shoot growth is inactive, is characterized by heavy precipitation with daytime temperatures usually above freezing. Away from the coast, the growing season is characterized by warm temperatures, clear days, and little precipitation. Water storage in snowpack, soils, and vegetation—as well as pulses of fog, clouds, or cool maritime air which reduce evapotranspiration—obviously are more important during a summer drought.

The climate varies considerably as a consequence of the interplay 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 (6° to 10°C) in temperature. Winters are extremely wet, and freezing temperatures are rare. Summers are cool and relatively dry, but extended periods of cloudiness and fog often greatly reduce evaporation. Valleys in the lee of the Coast Range are drier, subject to greater temperature extremes and evaporative demand as are the lower elevation sites in the Cascades. On the western slopes of the Cascade Mountains, precipitation increases, and temperature regimes moderate until subalpine environments, with their cooler temperatures and deep winter snowpacks, are encountered. This pattern is similar throughout the region although areas to the south are warmer and drier than those to the north. Immediately to the east of the mountain crest begins another region with a more arid and continental climate, as well as sparser and shorter forests (*10*).

The climate contrasts strikingly with that of other temperate forest regions. Major forest regions in the eastern United States, eastern Asia, and Europe have more evenly distributed precipitation throughout the year with no reduction during the growing season (Fig. 2B). Throughout most of the Pacific Northwest, less than 10 percent of the total precipitation falls during the summer (Fig. 2A). In other temperate forest regions, summers are typically hotter and more humid, and the winters are much colder. During the growing season in the Pacific Northwest, night temperatures usually remain below 12°C, often dropping to 10°C near the coast or along cold air drainages in the mountain valleys. Dew may form on cool nights, but clear warm days cause the water to evaporate quickly, resulting in evaporative demands much higher than those experienced at similar temperatures in other temperate forest regions. Past regional comparisons have underestimated evaporative differences by using a simple estimate of potential evaporation (*11*) that does not consider differences in humidity (*12*). This method for assessing evaporation in the Pacific Northwest leads to values 25 to 60 percent too low for July and August.

Another significant climatic difference from other temperate forest regions may be the absence of typhoons and hurricanes that frequent eastern Asia and eastern North America. Frequent destructive storms presumably would inhibit evolution toward massiveness, regardless of other potential benefits (*13*, *14*).

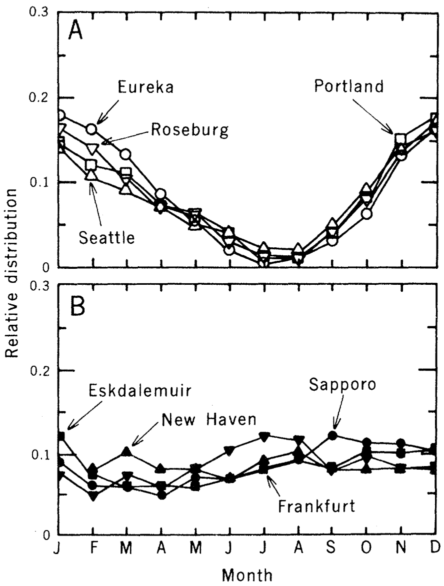

Fig. 2. Monthly distribution of precipitation for selected stations: (A) In the Pacific Northwest: Eureka, California, 41°N, 124°W, 101 cm annual precipitation; Seattle, Washington, 48°N, 122°W, 85 cm annual precipitation; Portland, Oregon, 45°N, 123°W, 106 cm annual precipitation; Roseburg, Oregon, 43°N, 123°W, 82 cm annual precipitation. (B) In other north temperate climates: Eskdalemuir, Scotland, 55°N, 3°W, 159 cm annual precipitation; New Haven, Connecticut, 41°N, 30°W, 104 cm annual precipitation; Sapporo, Japan, 43°N, 141°E, 104 cm annual precipitation; Frankfurt, Germany, 50°N, 8°E, 61 cm annual precipitation. [Adapted from (*63*)].

Forest Structure

The huge accumulations of biomass which typify the forests of the Pacific Northwest amaze everyone encountering them. In natural forests, numerous individual trees 100 to 200 centimeters in diameter at breast height (1.37 m) extend their crowns 60 to 80 m into the air. Such stands are rivaled only by a few of the eucalyptus forests of Australia. Biomass accumulates to record levels because these large, long-lived species dominate rather than occur as isolated individuals. Fujimori's (*15*) nondestructive analysis of a coast redwood forest in Humboldt State Park in California revealed a basal area of 343 square meters per hectare and a stem biomass of 3461 tons per hectare. Addition of branch, leaf, and particularly root biomass would increase the estimate of standing crop to well in excess of 4000 ton/ha—very close to Fujimori's (*16*) earlier estimate of 4525 ton/ha for a coast redwood grove. These figures are larger but consistent with the stem biomass of 3200 ton/ha reported for three redwood stands on alluvial flats (*17*).

Table 1. Typical and maximum ages and dimensions attained by selected species of forest trees on better sites in the Pacific Northwest. Typical values mainly from Franklin and Dyrness (*10*); maximum diameters from American Forestry Association (*61*); maximum ages from Fowells (*62*); or our own observations.

Species	Typical			Maximum	
	Age (years)	Diameter (cm)	Height (m)	Age (years)	Diameter (cm)
Silver fir *(Abies amabilis)*	>400	90 to 110	44 to 55	590	206
Noble fir *(Abies procera)*	>400	100 to 150	45 to 70	>500	270
Port-Orford-cedar *(Chamaecyparis lawsoniana)*	>500	120 to 180	60		359
Alaska-yellow-cedar *(Chamaecyparis nootkatenis)*	>1000	100 to 150	30 to 40	3500	297
Western larch *(Larix occidentalis)*	>700	140	50	915	233
Incense-cedar *(Libocedrus decurrens)*	>500	90 to 120	45	>542	368
Engelman spruce *(Picea engelmannii)*	>400	>100	45 to 50	>500	231
Sitka spruce *(Picea sitchensis)*	>500	180 to 230	70 to 75	>750	525
Sugar pine *(Pinus lambertiana)*	>400	100 to 125	45 to 55		306
Western white pine *(Pinus monticola)*	>400	110	60	615	197
Ponderosa pine *(Pinus ponderosa)*	>600	75 to 125	30 to 50	726	267
Douglas fir *(Pseudotsuga menziesii)*	>750	150 to 220	70 to 80	1200	434
Coast redwood *(Sequoia sempervirens)*	>1250	150 to 380	75 to 100	2200	501
Western redcedar *(Thuja plicata)*	>1000	150 to 300	>60	>1200	631
Western hemlock *(Tsuga heterophylla)*	>400	90 to 120	50 to 65	>500	260
Mountain hemlock *(Tsuga mertensiana)*	>400	75 to 100	>35	>800	221

Analyses of superlative stands are not confined to redwood nor to very old forests (Table 2). Maximum values for Douglas fir and noble fir forests appear to be about half those for redwood, but they still greatly exceed accepted norms for other temperate forests (*18*).

Continued data collection increasingly shows that large biomass accumulations are the rule rather than the exception. Aboveground biomass in 11 forests dominated by Douglas fir, western hemlock, and noble fir situated along moisture and temperature gradients in the Oregon Cascade Range (*19*) averaged 1070 ton/ha and ranged from 734 to 1773 ton/ha (*20*). The most detailed analysis available is for a 450-year-old Douglas fir forest on a 10-ha watershed in the Cascade Mountains of western Oregon (*21*) (Table 3). 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.

These biomass values are in sharp contrast to those in other forest regions—boreal, temperate, or tropical. Art and Marks (*22*) tabulated maximum aboveground biomass values of 422, 575, and 415 ton/ha for temperate deciduous, temperate evergreen hardwood, and tropical forests. Biomass of cool temperate hemlock forests in Japan and the northeastern United States reportedly exceeds 600 ton/ha, a value still below biomass accumulations in the Pacific Northwest.

One biomass component worthy of special note is foliage. Leaf biomass and surface area in the Pacific Northwest develop slowly, taking 50 years or more to reach a maximum (*23*); in the eastern United States, development occasionally peaks in as little as 4 years after germination (*24*). Projected canopy surface areas in the Pacific Northwest usually reach a

Table 2. Biomass and productivity values for some young- and old-growth coniferous forest stands in the Pacific Northwest.

Dominant species, age, and location	Source	Basal area (m^2/ha)	Stem volume (m^3/ha)	Biomass (ton/ha)	Net productivity (ton/ha/ per year)
Western hemlock and Sitka spruce; 110 years; Oregon Coast	(*18*)	98	1,987	871	10.3
Douglas fir and western hemlock; 100 years; Oregon Cascades	(*18*)	63	1,406	661	12.7
Noble fir and Douglas fir; 115 years; Oregon Cascades	(*18*)	98	1,989	880	13.0
Coast redwood; >1000 years; northern California Coast	(*15*)	338	10,817	3,461*	
Coast redwood; "old-growth"; alluvial flats, California Coast	(*17*)	247	9,500	3,200	14.3
Douglas fir and western hemlock; >400 years; Oregon Cascades	(*18*)	127	3,600	1,590*	
Noble fir; 400 years; Washington Cascades	(*18*)	147	4,106	1,562*	

*Stems only.

leaf area index of 10 m^2 of leaf surface area per square meter of ground surface (m^2/m^2) and often exceed 15 (*17, 25*). Leaf area index in the series of 11 reference stands mentioned earlier averaged 15, ranging from 10 to 20 m^2/m^2. These leaf areas are much greater than those in most temperate hardwood forests which rarely exceed 6 m^2/m^2 (*26, 27*). They also far exceed leaf areas reached by red alder in the Pacific Northwest (*28*) that, converted from biomass figures, represent less than 10 m^2/m^2. If the density of aboveground biomass is limited (*27*), the heights of northwestern conifers may be a factor in the high values for leaf biomass and area.

Productivity

Productivity of the Pacific Northwest temperate forests generally is comparable to forest stands in other temperate regions. Biomass in young stands probably accumulates at 15 to 25 ton/ha annually in fully stocked stands on better-than-average sites. Mature or old-growth stands have lower net productivities (Table 2); net productivity was 10.8 ton/ha in an old-growth stand dominated by Douglas fir (*21*).

Annual net productivity can be very great on the best sites. Fujimori (*13*) reported annual 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 (*15, 17*). Maximum values reported are substantially lower for temperate deciduous forest (24.1 ton/ha per year for tulip poplar), temperate evergreen hardwood forests (28.0 ton/ha per year), and conifer plantations (29.1 ton/ha per year for *Cryptomeria*) (*22*).

In early years, however, annual productivity in many other mesic temperate forests typically equals or exceeds that in the Pacific Northwest. The key to the larger biomass accumulations in the Pacific Northwest is clearly in the sustained height growth and longevity of the dominants, coupled with their ability to accumulate and maintain a large amount of foliage. These tree species continue to grow substantially in diameter and height, and stands accumulate biomass long after those in other temperate regions have reached equilibrium. This is well illustrated by comparing growth of loblolly pine in the Southeast and Douglas fir in the Pacific Northwest (*29*). Initially, the pine grows faster than 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. Wood production from a single (100-year) crop rotation of Douglas fir is about 22 percent greater than from two 50-year rotations of pine. Recent studies of height growth patterns for higher-elevation Douglas fir, noble fir, and hemlock have further documented that substantial height growth of these species may be sustained into their second and third centuries (*30*).

Table 3. Biomass for a 450-year-old Douglas fir forest in the Cascade Mountains (*26*).

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	1249.0

Gross productivity rates (per unit of leaf area) are probably greater in many tropical rain forests and warm-temperature evergreen-broadleaf forests, but the lesser respiration rates in the Pacific Northwest often show up in superior net productivity (*13*). However, total respiration for the massive northwestern coniferous forests is much higher than in temperate deciduous forests. Grier and Logan (*21*) estimated autotrophic respiration by a 450-year-old Douglas fir stand at 150 ton/ha per 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 per year (*31*). The net effect of the high levels of autotrophic respiration is to make the contrast in gross productivity between northwestern conifer and eastern hardwood forests much greater than the contrast in net primary productivity.

To conclude this section, the coastal regions of the Pacific Northwest are dominated by evergreen coniferous forests with biomass accumulations far exceeding those of forests in other north temperate regions. This mainly results from sustained growth of tree species with long life spans, rather than from greatly superior annual net productivities.

Adaptations to Temperature

All these structural characteristics—massiveness, evergreenness, large leaf areas, and even the needle-shaped leaf—are functionally advantageous under the moisture, temperature, and nutrient regimes of the Pacific Northwest. Mild winter temperatures permit substantial winter photosynthesis, and cool summer nights make large leaf and other biomass components less costly to maintain than in other temperate forest regions.

Conifers can assimilate over a broad

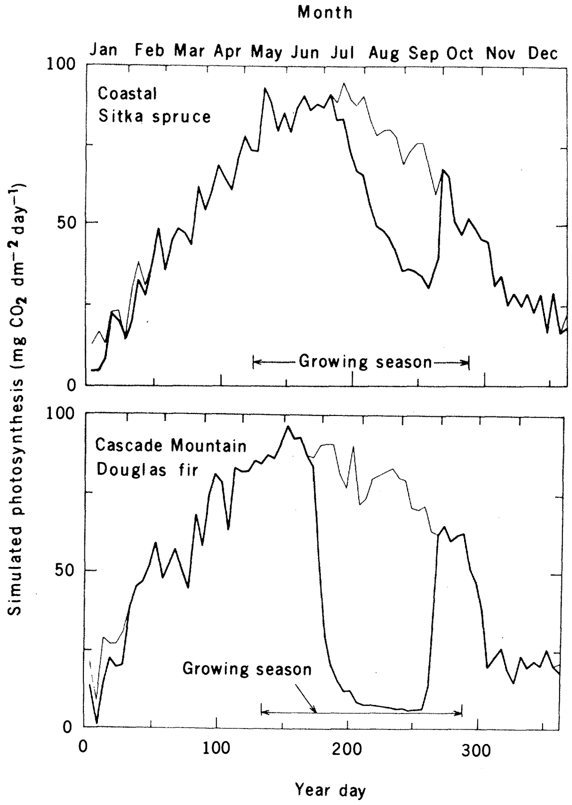

Fig. 3. Simulated photosynthetic rates for 1- to 2-m tall *Pseudotsuga menziesii* growing in a coastal Sitka spruce forest (upper) and a drier Douglas fir forest in the western Cascade Mountains of Oregon (*20*). Thin line shows potential photosynthesis without constraints due to moisture stress, frost, or low soil temperature; thick line incorporates these constraints. A high proportion of yearly photosynthesis occurs outside the "growing season" on all of these sites.

temperature range. Considerable carbon uptake is possible below freezing (*32*), even by coastal species such as Sitka spruce (*33*). Significant winter accumulations of dry matter by conifers have been recorded in maritime climates (*34*). Sitka spruce seedlings in Scotland actually doubled their dry weight between late September and mid-April (*35*).

During the dormant season for trees in the Pacific Northwest, substantial net photosynthesis occurs over a wide range of environments. Winter temperatures are mild and subfreezing day temperatures are uncommon, even in montane environments (*36*). Model simulations indicate that as much as half of the annual net carbon assimilation by Douglas fir occurs between October and May (*37*) (Fig. 3). This long period of favorable temperature (and moisture conditions, as seen below) is mostly lost to the deciduous hardwoods. The winter advantage of the evergreen conifers is further enhanced by their long, conical crowns that intercept greater amounts of diffuse light common during the winter when the sun angles are low (*38*).

Adaptations to the Moisture Regime

Photosynthesis is constrained by unfavorable moisture regimes during the summer months—the "growing season" upon which deciduous plants are so dependent. The dry summers cause stomata on leaf surfaces to close, reducing water loss and subsequent carbon dioxide uptake. Effects of summer drought are particularly apparent on dry sites where nearly 70 percent of the annual net photosynthesis occurs outside the growing season. For example, Fig. 3 contrasts a site in a coastal zone with Sitka spruce and western hemlock where the moisture regime is most favorable with a hot dry zone where Douglas fir dominates the western slopes of the Cascade Mountains.

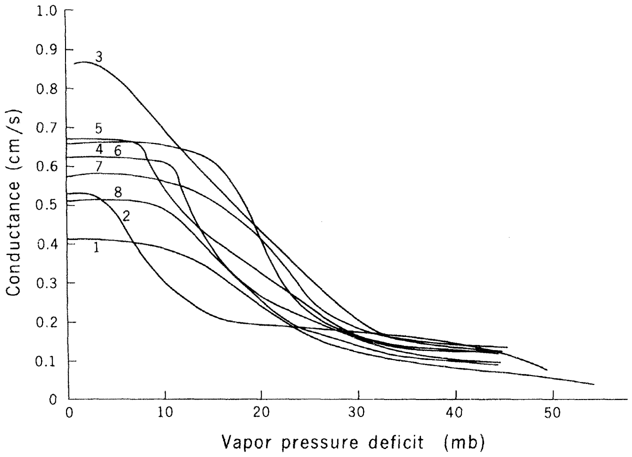

Fig. 4. Maximum stomatal conductances recorded at different evaporative demands (vapor pressure deficits) for a variety of native species growing under conditions with adequate soil water. Conifers: 1, Douglas fir (N = 312); 2, western hemlock (N = 404); deciduous trees: 3, dogwood (N = 402); 4, big leaf maple (N = 68); evergreen broadleaf tree: 5, chinquapin (N = 159); deciduous shrub: 6, vine maple; evergreen broadleaf shrubs: 7, rhododendron (N = 451); 8, salal (N = 435) [data from (*44*)].

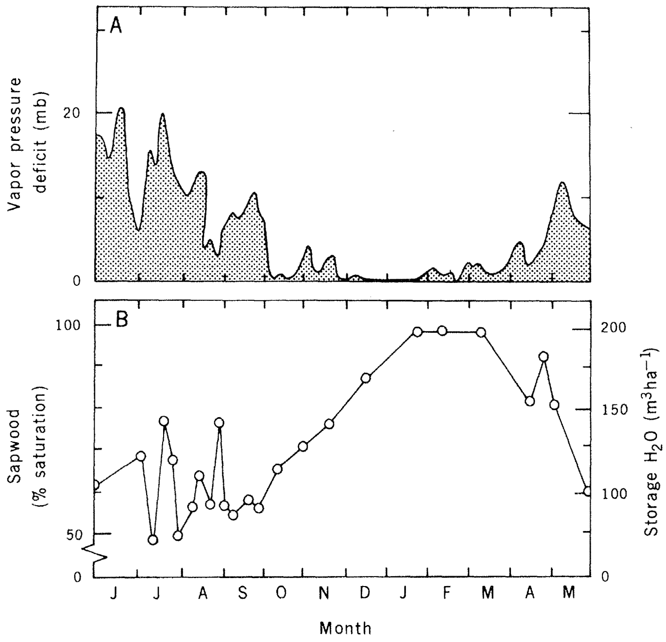

Fig. 5. Evaporative demand (A) in relation to seasonal variation in sapwood water storage of old-growth Douglas fir (B). Depletion begins in April well before the "growing season" and declines to minimum levels during the warm, dry summer months. Occasional summer rains provide for partial recharge, but complete recharge occurs during the fall and is completed in midwinter (*42*).

During the growing season, stomatal closure is induced by both soil drought and high evaporative demand (*39-41*). Seasonal reductions in available soil water cause plant water deficits in some locations and limit the degree and duration to which stomata open (*41*). Likewise, increasing evaporative demand, as measured by the water vapor deficit of the atmosphere, can by itself bring about stomatal closure by both conifers and hardwoods (*40, 42-44*). From hundreds of field measurements on diverse plants native to the Pacific Northwest, we found none able to maintain open stomata at high evaporative demands, regardless of the availability of soil water (Fig. 4).

Evergreen conifers tend to have significant advantages over deciduous hardwoods during periods of moisture deficiency even though photosynthesis is adversely affected in both groups. The needle-shaped conifer leaves remain closer to ambient temperatures than broad leaves (*45*) because heat exchange is less inhibited. As a result, respiration and transpiration are likely to be higher for broadleaf species than for conifers. Because evaporative demand usually exceeds critical limits throughout much of the area during the growing season, the environment is obviously less than optimum for plants that depend on this season for their major carbon assimilation.

The large volume of sapwood, a structural feature of conifer forests, dampens the effect of dry summer months. Both hardwoods and conifers utilize some water from conducting tissues to help meet daily transpiration requirements (*46*). However, the conifers have cells that apparently are easier to refill and that, because the trees grow larger, store more water (Fig. 5). A single 80-m Douglas fir may store 4000 liters of water (*41*). A forest stand can have water available exceeding 250 m^3/ha which may supply up to half the daily water budget (*42*). Hence, sapwood represents a significant buffer against extremes of negative water potential in foliage and stem. Although full hydration usually occurs during the winter, conifers may partially recharge sapwood after summer rain showers. Hardwoods, particularly ring porous species, have no mechanism for effectively refilling vessels in large trees.

In summary, the conifers have excellent control of water loss without increasing their leaf temperatures. Moreover, they can develop water storage to a greater extent than hardwoods and utilize these adaptations during severe conditions common during the growing season.

Adaptations to Nutrient Regimes

The temperate coniferous forests of the Pacific Northwest are evolutionary responses not only to moisture and temperature conditions, but also to distinctive nutrient regimes. Many features of these regimes contrast with those of more typical, temperate hardwood regions in the north, partially because of the winter-wet, summer-dry climate.

For example, most decomposition and subsequent nutrient release from organic litter occurs during the cool, wet "dormant" season and may essentially cease during the dry summer. Slow summer decomposition has been reported from such diverse sites as Douglas fir and western hemlock forests at low and middle elevations (*47*) and subalpine fir forests in the Cascade Range (*48*). In Montana forests of Douglas fir, more than 90 percent of the weight loss by litter takes place under winter snow despite subzero air temperatures (*49*). In western Oregon, almost no measurable decomposition occurs in July and August (*47*).

The massiveness of the forests also contributes to the uniqueness of the nutrient regimes by binding large amounts of nutrients into standing crops. Without frequent ground fires, organic matter—particularly large logs and branches—accumulates on the forest floor. Both the climate and forest combine to create conditions where large episodic losses of nitrogen (*50*) and other nutrients result from infrequent wildfires and subsequent leaching.

The peculiarities of these nutrient regimes combine to favor plants that have low nutrient requirements, that conservatively use acquired nutrients, and that can accumulate nutrients during the wet dormant season when decomposition is most active. In these ways, evergreen conifers appear to have distinct advantages over deciduous hardwoods.

Conifers generally require fewer nutrients and use them more efficiently than most hardwoods do. Foliage retention for several years, reducing annual nutrient requirements (*51, 52*), is obviously advantageous. The low levels of nutrients in foliage also give evidence of the lower requirements of conifers. Nitrogen in foliage of 450-year-old Douglar fir rarely exceeds 0.8 percent (dry weight basis), less than half that of most hardwoods (*53, 54*), yet needles appear healthy (*51*). Although Pacific Northwest conifers hold greater foliage biomass than hardwood forests, less than 20 percent is replaced each year so that the total requirement is usually less than that for the more demanding hardwoods. Coniferous forests require half the calcium of hardwood forests grown on similar soils for 100 years (*54*), in part because conifer wood has only about 20 percent of the calcium content of deciduous hardwoods (*53*). Conifers are also believed to more efficiently extract nitrogen and phosphorus from various sources (*55*).

Northwestern conifers meet increasing proportions of their total nutrient requirements by redistribution from older tissue, especially senescent needles. For example, half the nitrogen required by a 100-year-old stand of Douglas fir is met by redistribution from older foliage (*56*). At 100 years, the annual nitrogen requirement drops from a peak demand of about 50 kilograms per hectare to around 30 kilograms per hectare. Other northwestern conifers behave similarly and may be even more conservative (*57*).

Deciduous hardwoods also generally redistribute substantial nutrients from foliage before leaf fall, but their total requirements are higher. The nitrogen requirement of mature hardwoods in the eastern United States is reportedly 70 kg/ha each year for the canopy to develop, and less than one-third of this can be met by redistribution from storage sites within the trees (*58*). This should apply equally to hardwoods in the Pacific Northwest.

Hence, most hardwoods that compete with conifers in the Pacific Northwest either having nitrogen-fixing abilities (for example, alder) or are at a disadvantage on most sites. Their total nutrient requirement is higher than for associated conifers and must be met largely by uptake from the soil and litter. Yet decomposition and nutrient release are at low levels during the summer months when hardwood nutrient demand is high. The large pulses of nutrients leached during the wet fall and winter season are more available to conifers than to deciduous trees that have shed their leaves (*59*).

The binding of nutrients into biomass during succession again stresses deciduous hardwoods more than conifers. As they age, forest trees increasingly depend on the litter rather than on the soil for nutrients. For example, a 20-year-old forest of Douglas fir obtains 55 percent of its nitrogen from the litter while a 100-year-old forest may, on some sites, take essentially all of its nitrogen from this source (*56*). Yet the quality of the litter declines and litter decay rates slow, making dependence upon this nutrient source disadvantageous (*60*).

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50. An interesting feature of the Pacific Northwest is the large array of organisms associated with nitrogen fixation. Nitrogen, an important nutrient and one to which young forests typically show a growth response, is also the nutrient most severely affected by the wildfires typical of the region. A broad array of higher plants have nitrogen-fixing microbial associates [H. J. Evans, *Enhancing Biological Nitrogen Fixation* (National Science Foundation, Washington, D.C., 1975)], mostly successional pioneers such as *Alnus rubra* and *Ceanothus velutinus*. Large amounts of nitrogen—50 to 300 kg/ha per year—can be fixed during early stages of forest development, thereby balancing major losses associated with forest destruction by fire. Foliose lichens endemic to the large, massive crowns of old-growth trees provide further nitrogen inputs of 5 kg/ha per year. Finally, large boles contain substantial nitrogen; as snags and logs, these structures survive major disturbances, providing a slowly available source of nitrogen as well as sites for bacterial fixation [B. W. Cornby and J. B. Waide, *Plant Soil* **39**, 445 (1973); M. J. Larson, M. F. Jurgensen, A. E. Harvey, *Can. J. For. Res.*, **8**, 341 (1978)]. All 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.
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