



Part 2

The Environmental Setting

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Climate Change and the Origin of Old-Growth Douglas-Fir Forests in the Puget Sound Lowland

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Abstract

The vegetation and climate history of the Pacific Northwest is best understood from fossil pollen records and climatic simulations by general circulation models of the Earth's atmosphere. Paleoclimatic simulations by these models provide a physical explanation of the climate associated with past vegetation changes. During the maximum of the North American continental glaciation (30,000 to 18,000 years Before Present (years BP)), the Pacific Northwest experienced dry-cold easterly airflows from a strong high-pressure system centered above the massive continental ice sheet. Vegetation west of the Cascade Range consisted of open forest-tundra parklands with lodgepole pine, Engelmann spruce, and mountain hemlock interspersed with tundra communities. By about 10,000 years BP, the continental ice sheet had collapsed, and summer insolation increased because of changes in the Earth's orbital features. These changes brought warm-dry summers to the Pacific Northwest, and pollen records in the southern Puget Lowland indicate a predominance of Douglas-fir, oak, alder, and prairie herbs. Fires became more frequent, as lake sediments show a marked increase in charcoal concentrations. The closest modern analog to this vegetation may be the oak savannas and Douglas-fir forests of the

Willamette Valley. By 6,000 years BP, modern climatic conditions were established, and pollen records in this region show decreases in Douglas-fir, alder, oak, and grass pollen and increases in western redcedar and western hemlock pollen. Charcoal concentrations in sediments decrease rapidly at this time.

Pollen evidence indicates, therefore, that the modern forest composition of the Puget Lowland was established about 6,000 years BP. Although structural properties of these forests cannot be inferred from the pollen record, both the structure and composition of old-growth Douglas-fir forests can reasonably be assumed to have first established at this time. No compelling evidence in pollen data and paleoclimatic simulations suggests that this forest type existed elsewhere before 6,000 years BP. Old-growth Douglas-fir forests thus developed relatively recently on an evolutionary time scale and probably do not represent a coevolved complex of species bound together by tightly linked and balanced interactions.

Introduction

Pacific Northwestern forests have changed profoundly over the past 30,000 years in response to climate variations driven by changes in large-scale controls of the Earth's climate system (such as solar radiation, sea surface temperature, extent of land and sea ice, and atmospheric trace gases and particulates) (Barnosky and others 1987). Both fossil pollen records of past vegetation and physical models of global

atmospheric circulation clearly show that climate variations follow unique paths as new combinations of boundary conditions establish and disappear with varying periodicities (COHMAP members 1988, Huntley and Webb 1989). As a result, the climate history of the Pacific Northwest, as in other regions of the world, should not be viewed as a simple sequence of latitudinal or elevational displacements of modern climatic zones.

Plants have, therefore, not been able to escape climatic change by migrating within zones of climate that are simply displaced in space. Species continually face new conditions and must adjust to them by evolutionary, ecological, or phenotypic mechanisms (Brubaker 1986). Genetic change in long-lived species such as Northwestern conifers is probably too slow to keep pace with rates of climatic change (Bartlein and Prentice 1989). Thus, these species are probably not perfectly adapted to current climates and should retain some "memory" of past conditions in their current genetic make-up. The short-term responses of Pacific Northwest conifers to climatic change primarily involve ecological mechanisms (for example, altered reproduction and establishment rates) and physiological adjustments (for example, drought avoidance or tolerance mechanisms) that affect tree establishment and survival.

Pollen preserved in lake and bog sediments have provided most of the empirical evidence of past vegetation and climate in the Pacific Northwest (see Baker 1983, Bamosky and others 1987, Heusser 1986). Pollen data accurately reveal the general composition of regional forests but are less precise for reconstructing fine-scale forest features such as the composition and structure of individual stands. Stand conditions are generally inferred from knowledge of stand characteristics in modern forest zones thought to be similar to ancient forests. Plant macrofossils (such as leaves, seeds, and cones), which are often present in such sediments, have been invaluable for confirming and refining interpretations of pollen records (for example, Cwynar 1987, Dunwiddie 1986).

Fossil pollen records in the Puget Sound region indicate that Western Hemlock Zone forests (Franklin and Dyrness 1973) first established about 6,000 years ago. By inference, old-growth Douglas-fir forests date from this time. Because no evidence has been found that Douglas-fir forests existed as a zonal forest type elsewhere in the Pacific Northwest before this time, this forest association is young on an evolutionary time-scale and may not represent highly coevolved species-interactions.

In this paper, I will discuss forest and climate change in the lowlands west of the Cascade Range over about the past 30,000 years, with emphasis on the Holocene (the present interglacial, from 10,000 years ago to the present) because

pollen and plant macrofossil records are most abundant and old-growth Douglas-fir forests first became dominant during this period.

Sources of Paleoenvironmental Information

Pollen and Plant Macrofossils

Pollen and macroscopic plant parts are well preserved in anaerobic lake and bog sediments. Pollen is much more abundant than plant macrofossils because pollen (particularly of trees) is often produced in large amounts and widely dispersed by the wind. Owing to its ubiquitous occurrence, pollen has been the most important source of information about past vegetation in the Pacific Northwest (Baker 1983, Bamosky and others 1987, Heusser 1986). Pollen data have been supplemented in several studies by plant macrofossils, however, to increase the taxonomic and spatial resolution of vegetation reconstructions (Bamosky 1981, 1985, Cwynar 1987). Plant macrofossils provide finer taxonomic information than pollen because seeds and leaves typically can be identified to species, but pollen is generally identified to the genus for trees and shrubs and only to family for some important herbs (such as grasses and sedges) (Birks and Birks 1980). Macrofossils also reveal the local occurrence of plants near the collecting site because leaves and seeds fall close to the parent plant. Pollen, on the other hand, is often carried several kilometers before falling to the ground and, therefore, reveals the general composition of regional vegetation.

Fossil pollen data are interpreted primarily by making comparisons between modern and fossil pollen assemblages (Birks and Birks 1980). Researchers look for pollen assemblages in modern sediments that match those found in fossil sediments. If a close match is found, the modern vegetation is considered to be a good analog for past vegetation. Fine features of the vegetation, such as stand structures or local variation in stand composition, are inferred to have been the same as in the modern vegetation.

Radiocarbon dates or well-dated volcanic ash layers establish the timing of past vegetation change. Ash from the eruption of Mt. Mazama (about 6800 years BP, S. Porter, pers. comm.) forms a well-defined layer in lakes and bogs throughout the Pacific Northwest and provides an important time marker in Holocene sediments of the region.

Because lakes are formed primarily by the action of glaciers (such as glacial scouring and kettle formation), the spatial coverage of lake pollen records in the Pacific Northwest is related to the limits of continental and alpine glaciation (for example, see Barnosky and others 1987). Although alpine glaciers covered most of the Olympic Mountains and the Cascade Range, only one study (Dunwiddie 1986) has been done at high elevation, and the vegetation history in most of these mountains remains unknown. Continental glaciers

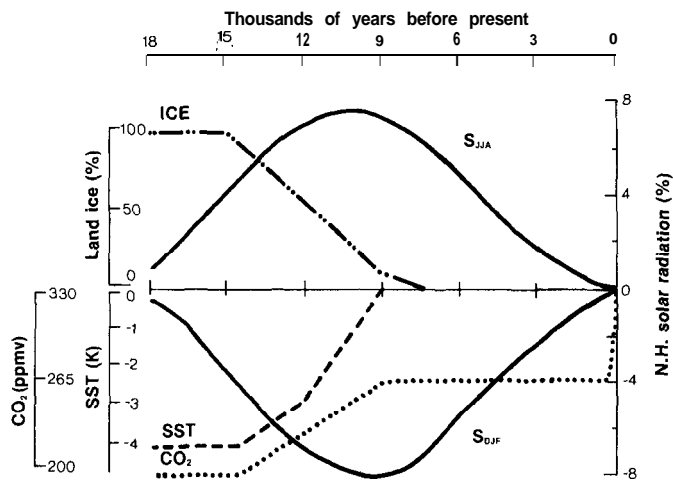


Figure 1—Major changes in external and internal boundary conditions of the Earth's climate system since 18,000 years BP (after Kutzbach and Guetter 1986). S_{JJA} , S_{DJF} : Northern Hemispheric solar radiation in June-August and December-February, respectively, as Percentage difference from present. Land ice as percentage of present. SST: global mean sea surface temperature as departure from the present. CO_2 as concentration in parts per million.

extended as far south as the central Puget Lowlands in Washington (Waitt and Thorson 1986). Consequently, lowland pollen records are relatively abundant from central Washington to southern British Columbia but are scarce in southern Washington and Oregon. Several excellent reviews of the vegetation history of the Pacific Northwest have recently been published (Baker 1983, Bamosky and others 1987, Heusser 1986).

Paleoclimatic Simulations by General Circulation Models

Over the past two decades, physical models of atmospheric circulation have been developed to examine the interactions of the major external and internal controls of global climate (for example, Hansen and others 1984, Kutzbach and Guetter 1986, Schlesinger and Zhao 1988, Wetherald and Manabe 1988). These models represent the current understanding of Earth's climate system and are being used to assess the characteristics of past and potential changes. The Community Climate Model (CCM) of the National Center for Atmospheric Research (NCAR) (Kutzbach and Guetter 1986) has been used to examine the ability of one model to reconstruct past climate change as recorded by fossil data (COHMAP members 1988). The major boundary conditions of this model are seasonal solar radiation, sea surface temperature, atmospheric aerosol and carbon dioxide concentrations, and the volumes of land and sea ice (fig. 1). The degree of agreement between paleoclimatic simulations and empirical evidence of past climate measures the success of the model. The model has been tested with paleovegetation and lake-level records from North America, Europe, and tropics of Africa and Asia. In general, the agreement has been good, and the model is presently considered to be a reasonable

mechanistic explanation of the climatic variations that drove past vegetation change. The comparison of these simulations with vegetation history in the Pacific Northwest is described in greater detail in Bamosky and others (1987) and COHMAP members (1988).

Definition of Old-Growth Douglas-Fir Forests and Their Identification in the Fossil Pollen Record

Old-growth Douglas-fir forests of the Western Hemlock Zone (Franklin and Dymess 1973) are defined by a combination of compositional and structural characteristics (Old-Growth Definition Task Group 1986). Old-growth forests generally may be identified by the presence of two or more tree species with large diameters (typically Douglas-fir plus one or more shade-tolerant associates, such as western hemlock or western redcedar); a wide range of sizes and ages and a deep, multilayered canopy; and substantial woody debris in the form of logs and standing snags.

Because pollen records reveal the compositional aspects of the vegetation, they indicate whether tree species that currently characterize old-growth stands were common in the past. They cannot, however, provide definitive evidence that those trees grew together in the same stands, or that past stands had the structural characteristics of modern old-growth forests. In this paper, I assume that structural characteristics follow compositional characteristics, and thus that old-growth Douglas-fir stands were first established in the Pacific Northwest when fossil pollen assemblages first matched pre-settlement pollen percentages of the modern Western Hemlock Zone. Because of the poor resolution of pollen data, the terms "old-growth Douglas-fir forests" and "Western Hemlock Zone forests" are used interchangeably in this paper.

Full- and Late-Glacial Vegetation and Climate (30,000 to 10,000 years BP)

The last ice age in the Pacific Northwest culminated in the Fraser Glaciation about 25,000 to 10,000 years BP (Waitt and Thorson 1983). Mountain glaciers covered the Cascade Range and Olympic Mountains from 29,000 to 22,000 years BP (Porter and others 1983), but lowland areas remained ice free until about 18,000 years BP, when ice advanced from southern British Columbia into the coastal Olympic Peninsula and the Puget Lowland (Waitt and Thorson 1983). These ice lobes coalesced and reached their maximum extent in the southern Puget Lowland south of Olympia, Washington. Lowland ice began to retreat about 15,000 years BP.

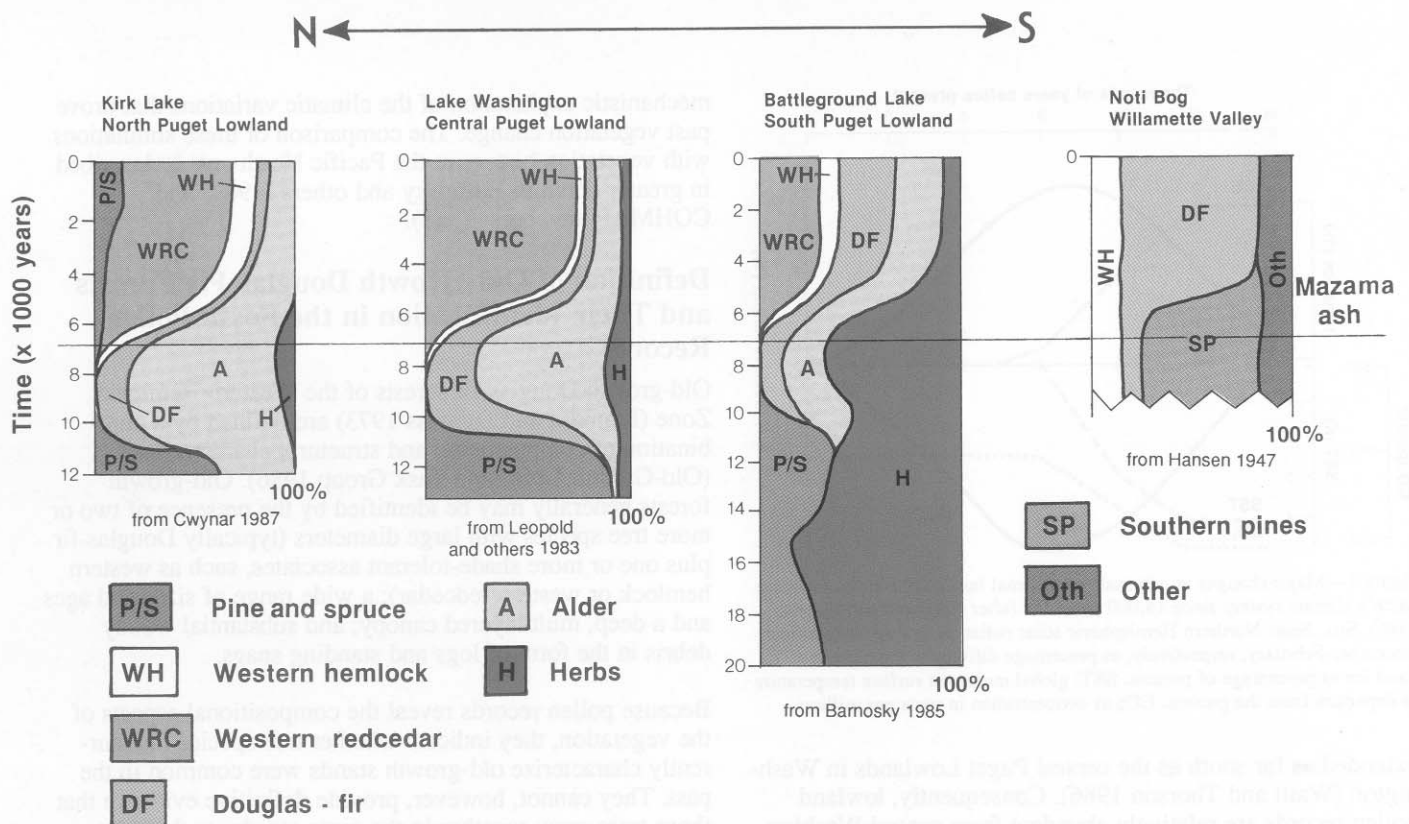


Figure 2—Schematic summary pollen diagrams from selected sites in the Puget Lowland and Willamette Valley. Each panel summarizes the percentage changes of major pollen taxa over time. Sources of data are indicated at the base of each panel.

Full-glacial vegetation (about 30,000 to 20,000 years BP) is recorded by several pollen diagrams south of the ice margin in the Olympia Peninsula and southern Puget Lowland (see Barnosky and others 1987). Unfortunately, no full-glacial pollen records are available for Oregon, so the vegetation south of the Columbia River during this period is unknown. Before 17,000 years BP, pollen assemblages of the southern Puget Lowland were dominated by grass, sedge, and sagebrush, but also showed moderate amounts of mountain hemlock, spruce, and pine (fig. 2) (Barnosky 1985). Needle fragments of Engelmann spruce and lodgepole pine have been found in sediments of this age (Barnosky 1981, Barnosky 1985). The abundance of both herb and tree pollen suggests that a parkland vegetation of tundra interspersed with trees covered the lowland landscapes. The presence of conifer needles indicates that trees survived in protected areas around lake basins. The full-glacial vegetation of the southern Puget Lowland may have resembled modern treeline associations in the Rocky Mountains of Idaho and southern Alberta (Barnosky and others 1987).

Climatic warming at the end of the last glaciation initiated a series of rapid vegetation changes (Barnosky and others 1987). Pine pollen (presumably lodgepole pine) increased between about 17,000 and 15,000 years BP. At one site, the increase in pine was associated with macrofossils of

Douglas-fir and Sitka spruce. Tundra communities must have been rapidly invaded by trees because herb pollen declined sharply during this period. Between 15,000 and 12,000 years BP, Sitka and Engelmann spruce, lodgepole pine, mountain hemlock, and true fir (species unknown) were the most important conifers in the southern Puget Lowlands. From 12,000 to 10,000 years BP, western and mountain hemlock, Douglas-fir, Sitka spruce, grand fir, red alder, and Sitka alder characterized the regional vegetation. These late-glacial pollen records reveal interesting mixtures of montane and lowland tree species with both dry and mesic site requirements (Barnosky and others 1987). Under late-glacial climates, local substrate and topographic variations may have caused strong moisture and temperature gradients, resulting in a complex mosaic of differing forest types. Regardless of the cause, similar assemblages of species are rare on the modern landscape. Furthermore, no evidence exists that old-growth Douglas-fir forests were present south of the ice sheet in western Washington during late-glacial times.

Climate simulations for the full-glacial period (represented by 18,000 years BP) show that atmospheric circulation over North America was strongly influenced by the large Laurentide ice sheet that covered much of the continent (Kutzbach and Guetter 1986, COHMAP members 1988. See fig. 3). Air descended from the upper atmosphere above the ice sheet

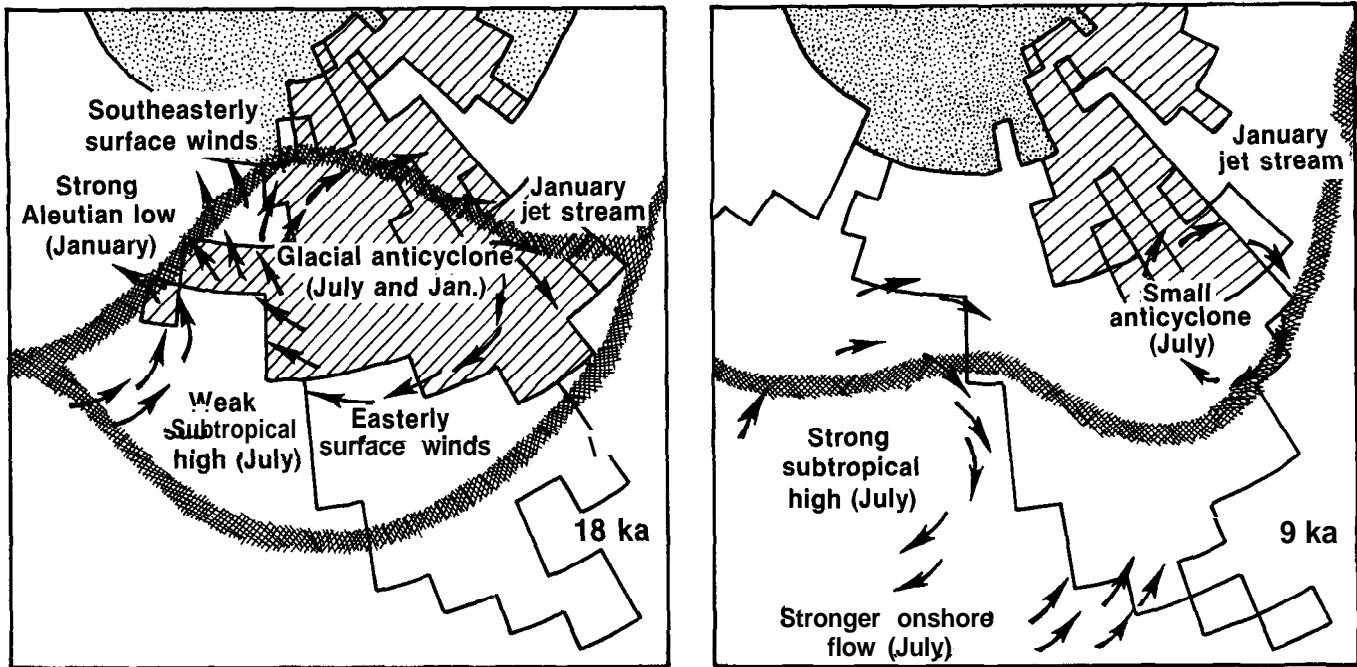


Figure 3-Paleoclimatic conditions for the Pacific Northwest as simulated by the NCAR CCM model for 18,000 and 9,000 years BP (after Bamosky and others 1987).

causing a strong high-pressure system, “the glacial anticyclone,” centered over the ice cap. Anticyclonic circulation brought prevailing easterly airflows across the Pacific Northwest, particularly in winter. Because of cold-dry airflow from the mid-continent ice cap, simulated temperatures, precipitation, and precipitation-minus-evaporation for 18,000 years BP were substantially lower than at present. These simulations agree with fossil pollen and macrofossil records that show tundra and xeric treeline species such as Engelmann spruce in the Puget Lowland during the full-glacial period.

Interglacial Vegetation and Climate (10,000 Years BP to Present)

The present interglacial is called the Holocene. By convention, it is defined as the period from 10,000 years BP to the present. By 10,000 years BP, lowland glaciers had receded from the Puget Lowland into southern British Columbia, and alpine glaciers were restricted to very high elevations in the Cascade Range and Olympic Mountains (Burke and Birkeland 1982, Thorson 1980).

Early Holocene (10,000 to 6,000 years BP)

Tree species indicative of cold climates had disappeared from the Puget Lowland by the beginning of the Holocene. Rapid changes in pollen and macrofossils suggest the onset of substantially warmer and drier climate than at present. Between about 10,000 and 6,000 years BP, pollen diagrams

from southern British Columbia to the central Puget Lowland showed maximum percentages of Douglas-fir, red alder, grass, and prairie herbs (Barnosky 1981, Leopold and others 1982, Mathewes and Rouse 1975, Tsukada 1982, Tsukada and others 1981). Pollen diagrams from the southern Puget Lowland show less Douglas-fir and alder but more grass and oak pollen (Bamosky 1985), suggesting a north-south vegetation gradient with a higher frequency of open, xeric communities in southern areas. Pollen of mesic tree species, such as western redcedar and western hemlock, was rare throughout the region. In addition, charcoal concentrations increased dramatically and spores of bracken fern became abundant in sediments.

Old-growth Douglas-fir forests were not important at the regional scale during the early Holocene because pollen assemblages of this period differed substantially from pre-settlement pollen spectra in modern forests in the Western Hemlock Zone (Barnosky 1981, Heusser 1977, 1986). The general importance of oak and grass pollen and the scarcity of mesic taxa in early Holocene pollen assemblages suggest that ancient vegetation may have been similar to modern oak savanna and Douglas-fir woodlands in the southern Willamette Valley of Oregon (Bamosky and others 1987). This hypothesis must be tested with modern pollen data from Oregon, however.

The most compelling climatic interpretation of the fossil pollen data is that warm-dry climates dominated the Puget Lowland during the early Holocene. Summer droughts were probably more severe and fires more frequent than today. Grassy areas, oak savannas, Douglas-fir woodlands, and riparian alder stands probably characterized the regional vegetation, with strong north-south gradients in the predominant community types. Southern areas may have been characterized by extensive grasslands and oak savannas, and northern areas by a shifting mosaic of dry Douglas-fir forests in early successional stages. This vegetation gradient was probably maintained by interactions of climate and fire.

Summer droughts were probably most severe in the southern Puget Lowland, resulting in discontinuous tree cover and sparse, dry fuels. These conditions would have favored frequent low-intensity fires, which can maintain savannas and grasslands effectively. Oregon white oak was probably common because it readily resprouts after fire. The thick bark of mature Douglas-fir probably allowed old trees to survive fire at scattered locations. The establishment of Douglas-fir would have been difficult, however, because of the sensitivity of young trees to even low-intensity fires (Agee, this volume). The distribution of parent materials (coarse outwash, till, pro-glacial lake sediments) may have controlled major spatial patterns of plant communities in the southern Lowland. In particular, extensive areas of coarse outwash were deposited south of the lowland ice sheet during late-glacial times (Thorson 1980). The soils of these areas were undoubtedly exceedingly droughty during the early Holocene and probably supported only grassland vegetation. Woodlands and savannas probably occupied finer textured soils in the region. Small modern prairies south of Olympia, Washington, may be remnants of extensive early Holocene grasslands. Prairies also may have been maintained in part by fires set by Native Americans who were present in the Northwest during the early Holocene.

The greater abundance of tree pollen in sediment records from the central and northern Puget Lowland (fig. 2) suggests that these areas were more heavily forested. The northern forests may have experienced fires of variable intensity (Agee, this volume) that were less frequent than in the savannas and grasslands to the south. Fire effects would have varied depending on fire intensity. Low-intensity fires would have removed understory plants but caused little tree mortality. Moderate fires would have killed some trees and opened growing space within stands, but intense fires would have killed most of the trees in a stand, thereby reinitiating succession. This type of variable fire regime characterizes dry Douglas-fir forests of southwestern Oregon and results in patchy mosaics of young and old stands of various tree densities. These forests may be reasonable modern analogs to those growing in the northern Puget Lowland during the early Holocene.

Pollen diagrams from coastal areas of the Olympic Peninsula also show maximum values of Douglas-fir and alder pollen in the early Holocene, but western hemlock pollen was more common than in the Puget Lowland (Bamosky and others 1987, Heusser 1986). Oak and grass pollens were rare in these diagrams. Apparently, maritime influences caused more mesic densely forested vegetation along the Pacific coast than farther inland. Coastal diagrams are nevertheless consistent with records from the Puget Lowlands, in that they show forest types with drier affinities in the early than in the mid- to late-Holocene.

The only pollen records from Oregon were published nearly 50 years ago by Hansen (1947), who pioneered palynological research in the Pacific Northwest. Hansen worked before techniques such as radiocarbon dating and fine taxonomic discrimination of pollen were developed. His diagrams, therefore, provide only very general descriptions of past vegetation. Nevertheless, they remain invaluable to current understanding of the forest history of the Pacific Northwest.

Hansen (1947), fortunately, identified the Mazama ash layer at several sites. It is now dated and can be used as a basis for comparing early- and late-Holocene pollen assemblages. High pine-pollen percentages are a striking feature of early-Holocene pollen diagrams from the central Willamette Valley. Although the pine species comprising this peak are not known, the conclusion seems reasonable that they were species currently more abundant to the south (such as ponderosa pine, Jeffrey pine, sugar pine, knobcone pine) rather than lodgepole pine, which typically characterizes full- and late-glacial pollen assemblages in the Northwest. This interpretation implies warmer-drier climates during the early-Holocene than at present and is thus consistent with interpretations of pollen records farther north. Regardless of their climatic significance, early-Holocene assemblages in western Oregon do not match mid- to late-Holocene spectra from the same area or from sites in Washington and southern British Columbia. One must conclude, therefore, that old-growth Douglas-fir forests were not common in Oregon during the first half of the present interglacial period.

Climate simulations for the early-Holocene are represented by the model for 9,000 years BP, when summer insolation at 40° N. latitude was 8 percent greater than present, the Laurentide ice sheet was greatly reduced, and the influence of the glacial anticyclone had essentially disappeared (COHMAP members 1988, Kutzbach and Guetter 1986). The simulated July temperature was higher, and precipitation-minus-evaporation was lower than at present, because of increased insolation. At 9,000 years BP the Earth was closest to the sun during the summer and the tilt of the Earth's axis was more extreme than at present, both of which increased

the intensity of solar radiation, Paleoclimatic simulations, therefore, agree with pollen data for warmer and more xeric forest associations during the early-Holocene.

Mid- to Late-Holocene (6,000 years BP to Present)

Holocene pollen records from the Pacific Northwest generally show the establishment of modern forest composition about 6,000 years BP (Baker 1983, Bamosky and others 1987, Heusser 1986. See fig. 2). Pollen of western hemlock and western redcedar increased, and pollen of Douglas-fir, grass, and alder decreased about that time at sites from the central Puget Lowland to southern British Columbia. Pollen changes were similar in the southern Lowland, except that Douglas-fir pollen increased during the mid-Holocene. The changes in both areas suggest a shift to more mesic forest communities and thus a trend toward a cooler and moister climate. This interpretation is supported by decreases in charcoal and bracken fern spores at about 6,000 years BP. Fire frequencies certainly decreased, favoring the expansion of fire-sensitive species such as western hemlock and western redcedar, and most parts of the region became densely forested by communities that were similar to those of the present.

Pollen changes in other parts of western Washington and Oregon also suggest a more mesic condition in the mid- and late-Holocene. For example, on the Olympic Peninsula, Douglas-fir and alder pollen decreased, while western hemlock and western redcedar pollen (not identified in some diagrams) increased (Bamosky and others 1987, Heusser 1977, 1986). In the Willamette valley, pine pollen decreased and Douglas-fir pollen increased in the mid-Holocene (Hansen 1947).

Although pollen data do not provide evidence of the structural features of the forests of about 6,000 years BP, the simplest interpretation of these data is that old-growth stand characteristics developed with the shift to modern forest composition. Structural changes may have lagged somewhat behind compositional changes, however, because features such as large woody debris and standing snags require time to develop. The length of time would have varied depending on forest type. For example, only a few hundred years would have been required for old-growth Douglas-fir stands to develop, but possibly more than a thousand years were needed for old-growth structures to develop in western redcedar stands. Northwest Indian cultures that depended on wood from massive western redcedars developed 2,000 to 3,000 years after the expansion of western redcedar on the Olympic Peninsula and Vancouver Island (Hebda and Mathewes 1984), suggesting that the establishment of old-growth conditions lagged considerably behind the first increase in western redcedar in these areas.

Pollen records from the Pacific Northwest provide convincing evidence for a climatic cooling and an increase in moisture during the second half of the Holocene. This interpretation is supported by geologic evidence showing the expansion of mountain glaciers (Burke and Birkeland 1983) and by paleoclimatic simulations. Models for 6,000 years BP are based on climatic boundary conditions similar to the present (COHMAP members 1988, Kutzbach and Guetter 1986). Summer insolation was slightly greater than today, but other boundary conditions were at modern values. By 6,000 years BP, simulations for the Northwest show the summer precipitation increased and summer temperature decreased by comparison with 9,000 years BP and thus they corroborate the climatic interpretation of the pollen data.

Discussion

No pollen evidence indicates that old-growth Douglas-fir stands were an important component of Pacific Northwestern forests before 6,000 years BP. Additional data are needed to confirm this statement, however, because the vegetation history of western Oregon is very poorly documented. The lack of data from Oregon is a particular problem for interpreting forest composition during full-glacial times. Douglas fir forests did not exist south of the ice sheet in western Washington, but no data exist to assess whether such forests occurred farther south. Circumstantial evidence from climatic simulations suggests that western Oregon was too cold and dry for the large-scale survival of Douglas-fir forests, and pollen records from northern California indicate xeric pine and possibly juniper woodlands during this period (Adams 1986). Thus, for old-growth Douglas-fir forests to have survived full-glacial conditions as an important forest type in the Pacific Northwest is unlikely.

A sufficient number of well-dated pollen diagrams are available from western Washington and southern British Columbia to conclude that old-growth Douglas-fir forests were rare or absent during the early-Holocene. Even the less-detailed and undated diagrams from western Oregon provide convincing evidence that old-growth forests did not exist south of the Puget Lowland in the early-Holocene. Even if Douglas-fir forests occupied western Oregon during full-glacial times, they must have disappeared as a zonal forest type during the warm, dry climates of the early-Holocene and then reassembled about 6,000 years BP.

During the early-Holocene, mesic late-successional conifers such as western hemlock and western redcedar may have formed small populations in moist topographic depressions or in stable riparian sites. These fire-sensitive species would have been relatively protected from fire in such environments. Both species presently occur in similar settings in warm, dry summer climates east of the Cascade Range (Franklin and Dymess 1973). At the onset of the cooler, wetter climate

of the mid-Holocene, such populations would have provided seeds for the rapid colonization of upland areas. With this expansion, modern zonal forests were established.

As in other parts of the world, the interpretation of forest history in the Pacific Northwest is limited by the coarse spatial resolution of pollen data. Extensive old-growth forests typical of the modern Western Hemlock Zone were clearly absent from western Washington before the mid-Holocene, but pollen data cannot evaluate the possibility that local old-growth stands occurred at restricted, scattered locations. Future research should address this question by examining pollen and macrofossil records from small collecting basins because such sites could provide records of local stand composition (Dunwiddie 1986).

Conclusion

Modern forests in the Western Hemlock Zone were established in western Washington about 6,000 years ago. These forests did not migrate into the region as intact communities from the south. Instead, dominant tree species of this forest zone had differing late-glacial and early-Holocene histories and responded individually to climate change.

Because climate is driven by a complex set of boundary conditions that do not change in unison, new conditions constantly arise and disappear on time scales of several thousand years. Over these broad time scales, tree species continuously reassemble in different combinations that follow the rhythm of changing climate.

Fire History of-Douglas-Fir Forests in the Pacific Northwest

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Abstract

The fire history of Pacific Northwest Douglas-fir forests is varied and complex because Douglas-fir exists in a variety of forest types over a wide range of environments. Douglas-fir has been dominant over this region because of disturbance by fire and the species' adaptations to fire. Human-caused fires have been locally important, but lightning appears to be most significant in explaining fire history. A lightning fire model based on climate suggests a strong north-south gradient in lightning ignitions. The western Olympic Mountains have a very low probability of ignition by lightning; the southern Washington Cascades have twice as much; the western Oregon Cascades have another 60 percent more; and the Siskiyou Mountains have twice, again as much. Our knowledge of fire return intervals based on forest age-class data shows a parallel history, ranging from fire return intervals over several centuries in the Olympics to several decades in the Siskiyou. Most Olympic forests have developed as first-generation stands after historic fires; Siskiyou forests are usually multi-aged stands that have experienced several fires. Almost all of the old-growth Douglas-fir resource is a product of fire: it not only has created and maintained such

stands but has destroyed them as well. In the short term, management strategies to perpetuate old growth can focus on protection against fire. In the long term, we will be forced to recognize a more dynamic management strategy, sensitive not only to historic fire regimes, but also to those expected with future climatic change.

Introduction

The fire history of Douglas-fir forests is varied and complex because Douglas-fir exists in a variety of forest types with a wide range of environmental conditions and associated species. Classical Pacific Northwest Douglas-fir forest is characterized by those low- to mid-elevation forestswest of the crest of the Cascade Range extending into the coastal and Klamath Mountain regions of California. This area is commonly known as the Douglas-fir region, and is the area to which this paper is applicable.

Although the region has been named after Douglas-fir because of the dominance of this one tree species over a wide area, Douglas-fir is a late-successional or climax species over only a small portion of the area for which it is named. Its dominance at the time of European settlement was largely due to disturbance, primarily by fire, for many centuries before such settlement. Pollen records establish that Douglas-fir dominance in past millenia often coincided with charcoal peaks in the pollen profile (Brubaker, this volume).

Such disturbance by fire was neither a unique event nor one easily characterized. Fire can occur at various frequencies, intensities, and extents. Severity, defined as the effect on the tree or the stand, varied because of these factors as well as because of the age and composition of the stands. These variables, although initially introducing a great deal of confusion, can be used to order our knowledge of the ecological effects of fire in Douglas-fir forests. In particular, they can be used to understand how old-growth Douglas-fir forests across this wide region have been created, maintained, and destroyed by this powerful agent of disturbance.

Disturbance as an Ecological Factor

The role of disturbance in ecosystems can be characterized by describing the type of disturbance and its frequency, magnitude, extent, and variability (Pickett and White 1985, White 1979). Moving from this simplistic characterization to the field application, however, is often quite difficult because of the problems associated with separating these various factors and the lack of independence between them. For Douglas-fir, which can live 750 to 1000 years or more, a millennium of history may have to be unravelled to understand the evolution of present species composition, structure, and pattern.

Many disturbances in addition to fire may also be important in stand history. Wind can cause catastrophic damage to stands (Franklin and Forman 1987, Ruth and Yoder 1953). Disease and insects can create locally patchy stands (DeBell and Franklin 1987, Russell and others 1986). Landscape-wide, however, fire appears to be the primary large-scale disturbance factor. Across the region, one estimate of average fire return interval is 230 years (Fahnestock and Agee 1983), about one-fifth the potential longevity of an individual tree (Franklin and Dymess 1973). Fire, therefore, is likely to disturb this "average" stand long before Douglas-fir disappears from the stand, even where Douglas-fir is an early seral species.

Relative Adaptations to Fire

Douglas-fir has long been characterized as a species adapted to fire (Flint 1925, Starker 1934). Its ability relative to other species to adapt to the presence of fire is critical to understanding the ecological impacts of fire. The fire strategy (for example, Rowe 1981, Wright and Bailey 1982) of major tree species of the Douglas-fir region is summarized in table 1. The relative success of Douglas-fir compared to its competitors depends on which other "players" are part of the stand. Where western hemlock and western redcedar are the only other species in a mature stand and a fire kills all the trees but does not consume all the organic mat (which would encourage the invader red alder along with Douglas-fir), Douglas-fir is likely to be a dominant in the new stand. Douglas-fir is also likely to be a dominant after fire in a mature stand where Pacific madrone and tanoak are understory

Table 1-Relative adaptations to fire of major species in the Douglas-fir region

Species	Life-history strategy ^a to fire when:		
	Young/small	Intermediate	Old/large
Douglas-fir	Avoider	Resister	Resister
Western hemlock	Avoider	Avoider	Avoider
Western redcedar	Avoider	Avoider	Avoider
Red alder	Invader	Avoider	Avoider
Black cottonwood	Invader	Endurer	Endurer
White/grand fir	Avoider	Avoider	Resister
Sugar pine	Avoider	Avoider	Resister
Knobcone pine	Invader	Evader	Evader
Pacific madrone	Invader	Endurer	Endurer
Tanoak	Invader	Endurer	Endurer
Ponderosa pine	Invader	Resister	Resister
Pacific silver fir	Avoider	Avoider	Avoider

^a Invaders = highly dispersive pioneers, rapid early growth; evaders = species with long-lived propagules stored in soil or canopy; avoiders = fire-sensitive individuals, even to low-intensity surface fires; resisters = able to resist fires of low to moderate severity; and endurers = resprouting species.

species. In a mature state in the presence of a moderate fire, Douglas-fir generally exhibits a "resister" strategy; and madrone and tanoak are "endurers" that are top-killed and will have to resprout from the ground. If a young stand with the same species mix is burned again in 20 years, however, Douglas-fir as a small tree will not be fire tolerant, and as an "avoider" will be killed, leaving the madrone and tanoak to resprout again and dominate the post-fire stand.

This system (table 1) treats the species as a variable, but it assumes that fire is something of a constant. As the examples above illustrate, the frequency of fire can create different ecological effects, as can different fire intensities. Over the region, fire frequency, intensity, and extent vary considerably, which helps to explain the myriad ecological effects of fire.

Regional Fire Patterns

Ignition Patterns

Ignitions by humans-Ignitions by humans are known to have been important in certain forest and grassland types of the Pacific Northwest. The dry Douglas-fir and ponderosa pine forests of the eastern Cascades may have been burned frequently by Native Americans (Barrett and Amo 1982). West of the Cascades, however, the role of aboriginal burning is much less clear for Douglas-fir forests. Burning by Native Americans was a common practice in the Willamette Valley grasslands and oak woodlands (Boyd 1986), and they apparently burned the valley bottoms of at least some of the major tributaries of the Willamette River (Teensma 1987). Norton (1979) and White (1980) make a strong case for aboriginal

ignitions in prairies adjacent to the relatively dry Puget Lowland Douglas-fir forests. Botanical (Habeck 1961, Kertis 1986, Thilenius 1968) and pedological (Ugolini and Schlichte 1973) evidence suggest that prairie-forest ecotones frequently burned and that forest area has expanded over the last century at the expense of prairie. Outside of these dry lowland prairie and woodland areas, little convincing evidence exists that aboriginal ignitions were a significant ignition source, although future investigations may shed more light on the debate.

Some of the earliest evidence for Native American fire-setting in the Douglas-fir region was collated by Morris (1934), who first documented the accounts of large historical fires in the Pacific Northwest. Although Native Americans are implicated in anecdotal accounts as the source of several large fires, the evidence is not overwhelming that they ignited many fires in upland forests. The coastal Oregon Native Americans were the victims of some of these fires, having been driven to the waters of the Pacific Ocean to survive (Morris 1934). The source of these fires is never clearly identified or placed in a cultural context. Legends tell of two other fires, both in Washington, that occurred in prehistoric times. The Quinault tribe has a legend of a great fire that swept down from the Olympic Mountains perhaps 500 years ago, pushing the people into the sea, but the ignition source is not identified (Anon. 1983). In an area roughly bounded by Mount St. Helens, Mount Rainier, and Centralia, a 500 000-ha fire is rumored to have occurred about 1800. This so-called "Big Fire" was supposedly set by the Cowlitz tribe against the Nisqually tribe, or was set by the Nisqually tribe as a means of generating rain during a drought (Clevinger 1951). The existence of two stories about the same fire make both suspect; alternatively, either or both could be true. At present, the case for widespread aboriginal fires throughout the Douglas-fir region is not convincing.

Lightning ignitions—The variability in regional lightning ignition patterns is illustrated by the application of a fire-cycle model based on climate. The Olympic fire-cycle model (Agee and Flewelling 1983) generates both significant fire ignitions and sizes based on climatic parameters of the site. For this application, only the ignition portion of the model is presented because the size (and fire-cycle) portion of the model is based on historic relations between fire size and climate not available regionally. The ignition portion of the model presents the expected ignitions exceeding 1 ha within a 175 000-ha area over a given period.

The model requires four inputs, each used by the model in one of twelve 10-day periods during the fire season: probabilities of long-term drought, a rain exceeding 0.25 cm, occurrence of a thunderstorm, and an east wind. The model was applied to four regional locations: the western Olympic Mountains, the Wind River area in southern Washington, the



Figure 1—Location of the sites used to simulate lightning ignitions in the fire-cycle model.

McKenzie River area in the central Oregon Cascade Range, and the eastern area of the Siskiyou Mountains (Jacksonville-Kerby) (fig. 1). The probability of long-term drought, defined as below-average annual precipitation, was set at 0.5, with additional cumulative years of drought at lower probabilities defined similarly to the Olympic model. Short-term drought was defined as 1 minus the probability of significant precipitation during 10-day summer periods and was gathered for each area based on records from nearby stations (Munger 1925). Thunderstorm probability was determined from Pickford and others (1980) for the Olympics and from Morris (1932) for the other sites.

As for any stochastic model, long-term expected averages are best calculated using many model repetitions; here, each simulation is based on averages from a 10,000-year run of the model. This represents not the Late-Quaternary period, but only a long-term average (or expected value) of the effects of 20th-century weather on ignition patterns. The results should be interpreted as relative rather than absolute values, although the model predicted well the proportional seasonal distribution of Olympic fires (fig. 2).

The probability of ignitions exceeding 1 ha increases as location shifts east and south from the western Olympics (fig. 3). The Wind River area has twice as many ignitions as the western Olympics, McKenzie River has about 60 percent more than Wind River, and the Siskiyou Mountain area has more than twice the number of ignitions as McKenzie River.

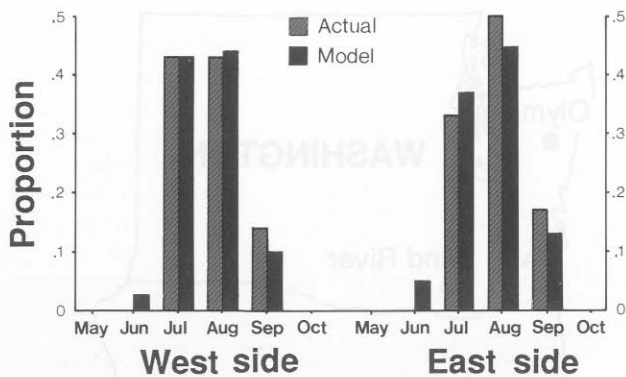


Figure 2—Seasonal distribution of simulated and actual (20th century) lightning ignitions for the western and eastern Olympics (from Agee and Flewelling 1983).

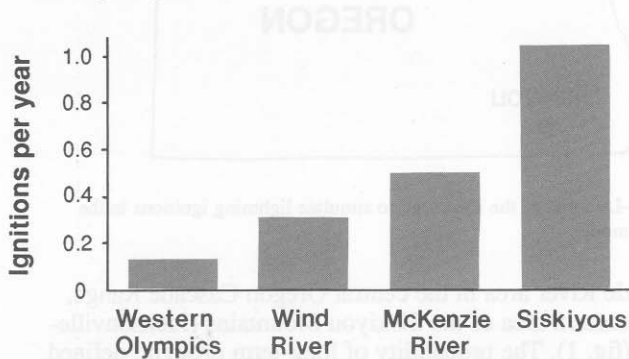


Figure 3—Simulated lightning ignitions for the locations shown in figure 1, from the fire-cycle model. Ignitions are simulated for a 175 000-ha area at each site. The figures should be interpreted as relative numbers between sites, rather than an absolute estimate at any one site.

The differences are largely due to increased frequency of lightning and decreasing summer precipitation patterns from northern Washington to southern Oregon. In each area, July and August are the months of greatest ignition activity, but September in the two southerly areas contains a higher proportion of total ignitions than in the two northerly areas. The model, which was initially designed for the Olympic Mountains, does not include October ignitions, which would likely increase the total ignitions for the southerly stations even more.

The patterns of ignition clearly support the hypothesis of higher fire activity towards the southern end of the Douglas-fir region. Ignition, however, is but one of the factors influencing fire activity; spread is another significant component.

Spread Patterns

We have little, if any, regional data on which to compare regional patterns of fire spread. Modern fire suppression activities have largely prevented fires from burning free in the forest, as they once did. The pattern of fire spread in the

Olympic Mountains is typically a period of relatively rapid spread during periods of east wind until the onset of significant precipitation. Although longer droughts and longer burning fires have likely occurred in the past, the typical fire of this century has burned for a few days before being naturally suppressed by onshore marine airflow and precipitation.

In the southern Douglas-fir region, fires most likely spread over periods of weeks to months. Morris (1934) quotes the Jacksonville Sentinel in September 1864: "...during the past few weeks...the fire [in the Siskiyou] has been raging with increasing fury." During the large wildfires of 1987, so many lightning-caused fires started that control actions were ineffective in stopping them. The fires, which started August 30, burned into November, with 39 fires burning over 75 000 ha. This event has been superceded twice in the recorded history (since 1907) of the Siskiyou National Forest (Atzet and others 1988, Helgerson 1988), however, suggesting that 1988 was an unusual but not unprecedented year. Similar examples of long-burning fires in different forest types can be found in areas with prescribed natural fire plans: red fir forests of Crater Lake and in the southern Sierra have sustained fires for several months (Kilgore 1971; F. Van Horn, pers. comm.).

In a relative sense, then, the spread patterns of fires across the Douglas-fir region probably mimic the ignition patterns. Although no long-term records are available for any area of the region, the lower probability of precipitation towards the south probably allows fires to die down but not be extinguished during periods of low winds or moderate weather, and remain capable of renewed spread under patterns of windy or warmer weather.

Fire Return Intervals

Regional fire patterns can also be deduced from records of vegetation. Fire scars on living trees are one source of fire presence in the past. Age-classes of trees that either resist or endure fire or invade after fire are another source of information about fire history (Agee, in press). The mosaic of even-aged and multi-aged stands across the landscape can provide clues about fire severity as well as fire presence.

A regional average fire return interval for forests where Douglas-fir is a dominant in the stand has been estimated at 230 years, based on an analysis of forest survey records from the 1930s (Fahnestock and Agee 1983). Considerable spatial variability is included in this estimate, as suggested by results of the fire-cycle model. Significant temporal variability is also characteristic of these fire return intervals, so that the 230-year average is of limited utility as a parameter of fire frequency across the region.

The notion of a “fire cycle,” or a return interval of regular frequency, is not as meaningful as in drier forest types, where with some measure of variability a roughly cyclic occurrence of fire can be assumed (compare mixed-conifer forest, as in McNeil and Zobel 1980). Rarely in a Douglas-fir stand is the fire record long enough or regular enough to infer a cyclic pattern of fire, particularly in the presence of climatic shifts that would alter any cycle in operation. Different patterns of historic fire have clearly affected the Douglas-fir forests of the region, however.

Moist Douglas-fir forests—In the moist Douglas-fir forests of the Coast Range of Oregon, the Washington Cascade Range, and the Olympics, most forests are first-generation post-fire forests less than 750 years old. This pattern would suggest a fire return interval somewhat less than 750 years. The fire-cycle model of Agee and Flewelling (1983) could not reproduce a natural fire rotation (essentially a fire cycle) of less than 3500 years using 20th-century climate patterns, and even with significant alteration in climate input to the model, fire return intervals could only be brought down to about 900 years. They suggested that perhaps much larger than average events may have occurred in the past (also suggested by Henderson and Peter (1981) for the southeastern Olympics) as a result of short-term but very extreme changes in two or more of the climate parameters that drive the model.

Our knowledge of the dates of old-growth forest establishment is so weak as to preclude firm hypotheses about disturbance pulses of the past. The forests around Mount Rainier appear to have had a major fire about 750 years ago (Hemstrom and Franklin 1982), and similar-aged stands have been identified in the southern and western Olympics (Agee, pers. obs.). A series of about 650-year-old or 450- to 500-year-old fires—or both—are apparent from the data of Henderson and Peter (1981) in the southern Olympics, Franklin and Hemstrom (1981) and Yamaguchi (1986) in the southern Washington Cascade Range, and Huff (1984) in the western Olympics. Although the forest age-class data are sparse, these are also times of sunspot minima identified by Stuiver and Quay (1980), using tree-ring analysis of carbon-14 activity. If large fires are associated with these periods of general global cooling, they may represent periods where altered synoptic weather patterns, particularly during the growing season, contained higher frequency of lightning and foehn (east) wind patterns.

In moist Douglas-fir forests, long early seral tree recruitment (for example, 75-100 years for Douglas-fir) has been documented after disturbance by fire (Franklin and Hemstrom 1981). This pattern is not characteristic of all prehistoric fires. For example, Huff (1984) shows a 60-year recruitment interval for a fire in about 1465 in the western Olympics, and Yamaguchi (1986) shows that about 95 percent of Douglas-fir

was recruited within 40 years after a fire in about 1300 near Mount St. Helens. Even on these sites, however, the regeneration period is decades long and probably represents some regeneration from trees that initially colonized the burn and grew large enough to produce viable seed to help completely restock the stand. Lack of seed source, brush competition, and reburns—or a combination of these factors—have been identified as delaying regeneration on such sites (Franklin and Hemstrom 1981). Patterns of reburns on the Tillamook fire of 1933 at 6-year intervals (1939, 1945, 1951; Pyne 1982), at Mount Rainier in the late 19th century, and at the southern Washington Yacolt burn of 1902 (A. Gray, unpubl. data) are evidence these sites will reburn. High surface fire potential during early succession in Douglas-fir forest was identified by Isaac (1940) as a “vicious cycle” of positive feedback, encouraging rhizomatous bracken fern; this pattern was quantified by Agee and Huff (1987, fig. 4). Given sufficient sources for reignition (the original Yacolt and Tillamook burns and all reburns are thought to have been human-ignited), the reburn hypothesis is likely to be true in certain areas. Whether reburns were a common event before European settlement in the moist portion of the Douglas-fir region is not clear, however.

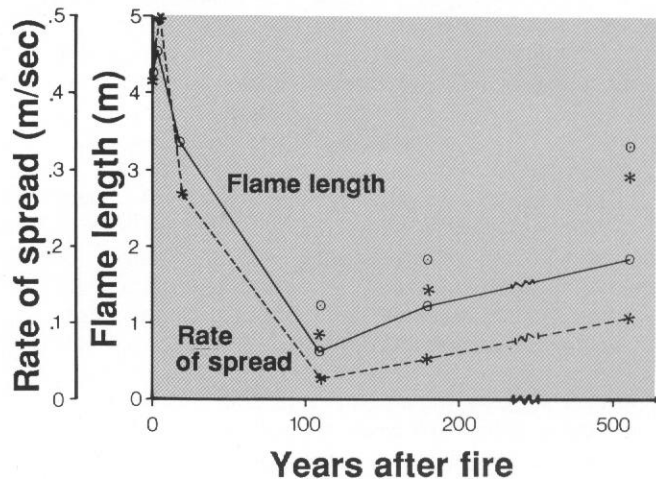


Figure 4—Rate of spread and flame length by stand age for a sere in the western Olympic Mountains. Wind speed is 268 m per minute, and dead fuel moisture contents are 6, 7, and 8 percent for 1-hour, 10-hour, and 100-hour timelag fuels at stand ages 1, 3, and 19. Connected points represent microclimate buffering at stand ages 110, 180, and 515; wind speed is reduced to 134 m per minute and fuel moisture increases to 10, 11, and 12 percent. Unconnected points at these ages represent constant microclimate across all sites.

After disturbance and over time, potential surface-fire behavior declines, particularly after crown closure, and then gradually increases in the old-growth seral stage (Agee and Huff 1987). Returns in roughly 100-year-old stands during the late 1400's suggested by Henderson and Peter (1981) suggest that independent crown-fire behavior in these thick-canopied stands may be an additional significant type of fire. Our present state of knowledge is insufficient to tell.

Mesic-to-dry Douglas-fir forest—For many years, the pattern of stand-replacement fire summarized above was a paradigm for the Douglas-fir region. Recent work, particularly in the Oregon Cascades, suggests a higher fire frequency, and different ecological role, for fire in mesic-to-dry Douglas-fir forest, reinforcing the output of the fire-cycle model (fig. 3). A site in the western Oregon Cascades (Stewart 1986) near the H.J. Andrews Experimental Forest regenerated after a stand-replacement fire in about 1530, but it has had three partial-mortality fires since then, in about 1660, about 1860, and about 1890. Some of these fires were in the settlement period and probably reflect human-caused fires, but the partial mortality associated with them is significant. Over a broader area several kilometers to the southeast, encompassing similar forest types, Morrison and Swanson (1990) suggest a natural fire rotation of 95 to 145 years over the last five centuries, well below that of the moist Douglas-fir forests of Washington. The patchiness of at least some of the fires is illustrated by a fire-severity map from Morrison and Swanson (1990; fig. 5A). A similar fire regime was noted by Means (1982) on dry sites in the western Oregon Cascades and by Agee and Dunwiddie (1984) for dry Douglas-fir forests in Washington's San Juan Islands (fig. 5B). Another fire-frequency analysis was completed by Teensma (1986), near the area studied by Morrison and Swanson. Using conservative methods that did not recognize underburns with no resulting regeneration or substantial fire scarring of trees, Teensma estimated a natural fire rotation of 100 years over the last five centuries. If fires of moderate severity are removed from the analysis, a stand-replacement mean fire return interval is 130 to 150 years, suggesting that intense fires are a significant part of the natural fire regime in this area, but that fires of lower severity also occur. Other stands 500 years old or older exist without much evidence of recurrent fire.

These studies strongly indicate that a variable fire regime with much higher frequency than found in the typical, moist, Washington Douglas-fir forest occurs in the central Oregon Cascades, and in other mesic-to-dry Douglas-fir forests.

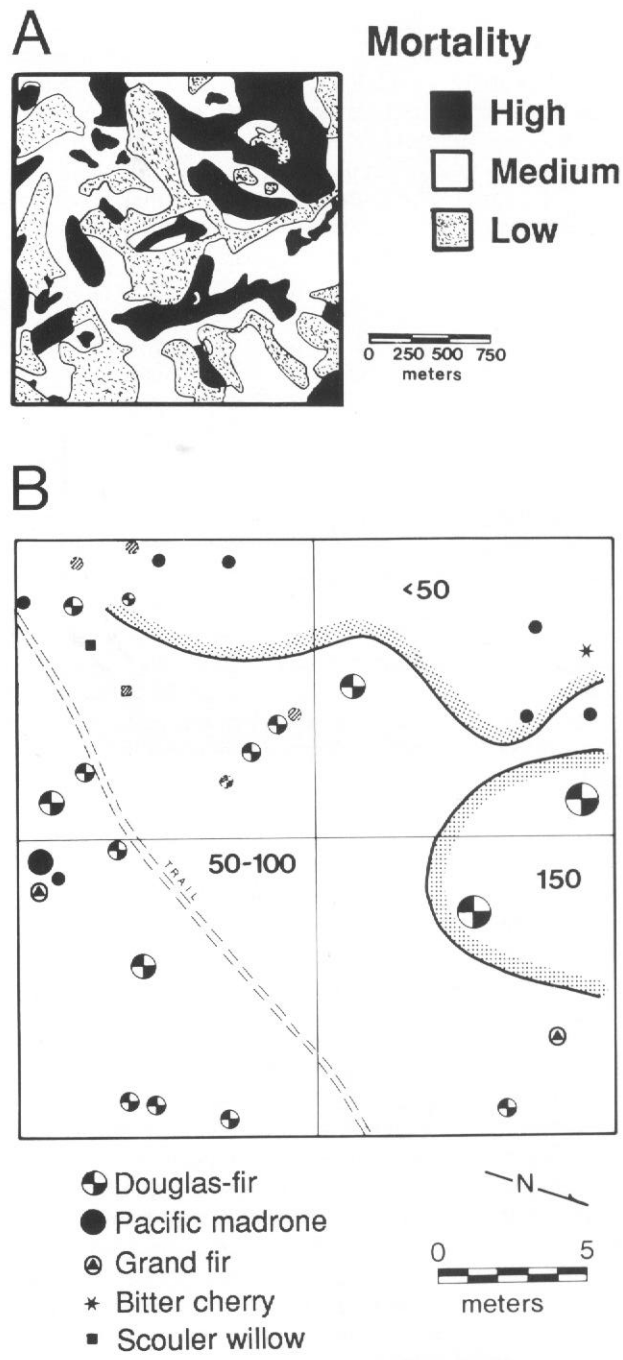


Figure 5—A. Reconstructed fire severity for a site in the central western Cascades, redrafted from data of Morrison and Swanson (1990). More area in this particular fire burned with moderate-to-low severity than high severity, but high-severity fire remains an important disturbance process in the mesic-to-dry portion of Douglas-fir forests. B. Stem map of an intensive plot on Yellow Island in the San Juan Islands (from Agee and Dunwiddie 1984). Three age-classes (<50, 50-100, and 150 years) are distinct. Relative diameter of stems is shown by the size of the symbol: smallest symbols are 0 to 20 cm, and largest symbols are >100 cm. Dead stems are shown by parallel lines within symbols.

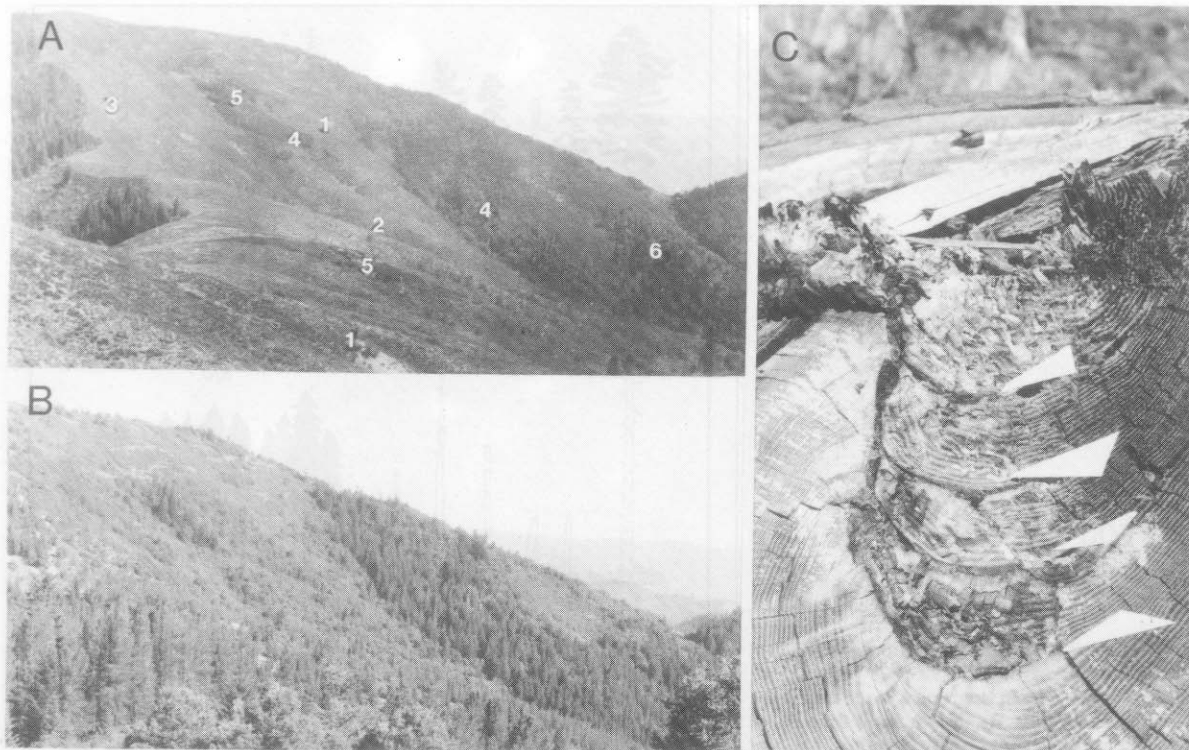


Figure 6—A. The south-facing slope of Kinney Creek, near the Applegate River in southwest Oregon, photographed in 1917 (Hofmann 1917). The numbers correspond to fire dates of: 1 = 1915; 2 = 1914; 3 = 1910; 4 = 1897; 5 = 1886; 6 = 1854. B. The same landscape photographed in 1988. C. A fire-scarred Douglas-fir in a clearcut just north of the ridgeline (see arrow in B); each of the white marks identifies a distinct fire scar.

Very dry Douglas-fir forests—The Douglas-fir forests of the central-to-eastern Siskiyou Mountains are among the driest forest types in which Douglas-fir is a dominant and where old-growth Douglas-fir is recognized (Old-Growth Definition Task Group 1986). The complex geology, land-use history, steep environmental gradients, and variable fire history of this area have prevented generalizations about fire history and its ecological effects. Native Americans may have significantly affected these drier Douglas-fir forests, but their effect is largely unknown. Miners, settlers, and trappers altered the patterns of burning in the 19th century, and fire suppression has altered burn patterns in the 20th century (Atzet and Wheeler 1982, Atzet and others 1988). From the coastal forests of southwest Oregon and inland to the crest of the Coast Range, fire frequency decreases from perhaps between 90 and 150 years to about 50 years. Frequencies averaging 20 years have been found in the eastern Siskiyou Mountains (Atzet and others 1988) in the area where fire ignitions were simulated by the fire-cycle model.

An example of frequent fires in the eastern Siskiyou is shown by the Kinney Ridge landscape west of the Applegate River, originally photographed by Hofmann (1917) (fig. 6A)

and rephotographed in 1988 (fig. 6B). In the area shown by the arrow in figure 6A, fire scars on stumps in a recent clearcut (fig. 6C) in old-growth Douglas-fir indicated a fire return interval of about 18 years between 1740 and 1860, although most of the fires indicated by Hofmann (1917) on the photograph after 1860 are not recorded in the sampled scars on the north (left) side of the ridgeline.

Species Composition and Structural Effects of Fire

Old-growth Douglas-fir forests are biologically defined on the basis of species composition and structural characteristics (Old-Growth Definition Task Group 1986). Among these characteristics are criteria for size, density, and age of Douglas-fir; generally multilayered canopies; snags; and logs. The interim minimum standards are slightly different between the major plant series (western hemlock, Pacific silver fir, Douglas-fir, tanoak, white fir) where old-growth Douglas-fir exists. Given that the fire regimes are probably different between these plant series, it is not intuitively obvious how apparently similar species composition and structural characteristics developed.

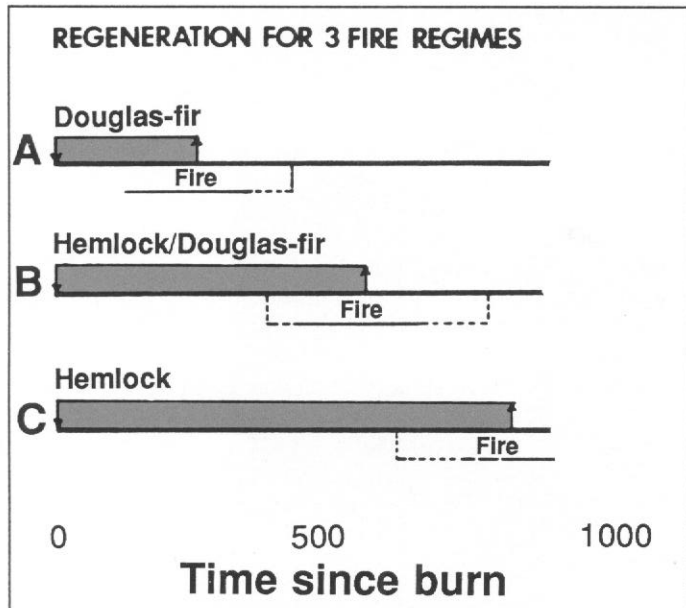


Figure 7—Species responses to changes in fire frequency (from Huff 1984). These fire regimes represent fire return intervals of about 100+ years (A) to about 1000+ years (C). The solid-to-dashed lines underneath each thick line represent the average range of fire return intervals, and the paths denoted by the arrows above the thick line represent occurrence of a fire, along with the species likely to dominate after disturbance.

Huff (1984) has summarized the species response to disturbance regimes for a range of wet-to-dry Douglas-fir forests (fig. 7). If fire is absent for 700 to 1000 years on wet sites, Douglas-fir will drop out of the stand, and western hemlock or Pacific silver fir will be the primary seed source for postfire regeneration (fig. 7C). On sites with fire return intervals in the 300- to 600-year range—well within the longevity of individual Douglas-fir—mixed dominance of Douglas-fir and western hemlock or Pacific silver fir will result from a typically severe stand-replacement fire (fig. 7B). A stand-development sequence will occur as illustrated in figure 8 (modified from Huff 1984). At age 200+, the characteristics of old growth are usually present. The Douglas-fir component, having developed after the previous centuries-old fire, provides the live-tree criterion, and those large Douglas-fir and western hemlock begin to supply the large-log component.

When fire return intervals are reduced to 30 to 70 years in drier and warmer environments, western hemlock may not even be present on the site (fig. 7A), and a stand-development sequence similar to that shown in figure 9 may occur. Beginning after a stand-replacement fire, the Douglas-fir regenerating on the site may survive several moderate-severity fires that thin the Douglas-fir (“resisters”), remove the understory

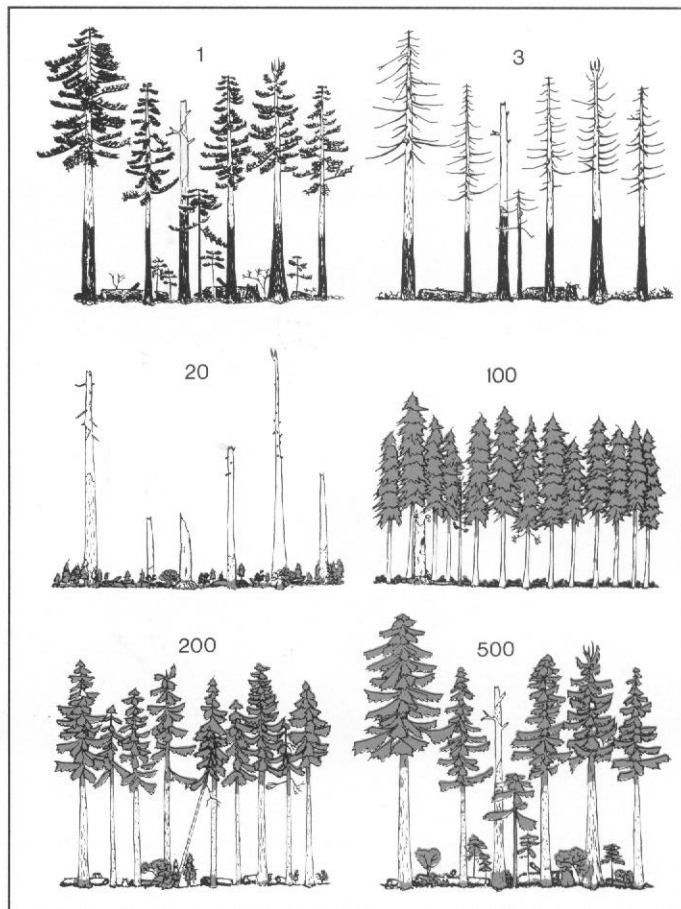


Figure 8—Stand-development sequence for wet Douglas-fir forests, illustrating the creation of old-growth character. Fire return interval is 500 years or more, and the old-growth character is found after about 200 years. Even after 500 years, the old-growth character remains a function of the previous disturbance that initiated the Douglas-fir.

white or grand fir (“avoiders”), and topkill the associated hardwoods, such as madrone and tanoak (“endurers”). Several reoccurrences of such fires will create a stand with several age-classes of Douglas-fir (some of which are large), and an age-class of Douglas-fir and hardwoods representing regeneration after the last disturbance. Understory-tolerant conifers of other species will also be represented in this most-recent regeneration. Large logs are provided by residual Douglas-fir or sugar pine that have died from insect, disease, or the last fire, or have blown over. At age 250+, the structure of this stand may meet the old-growth criteria, having developed in a very different way than the wet-site Douglas-fir stand. Such stands will usually be intermixed with others that have experienced a stand-replacement event during one of the intermediate fires, so that the landscape is more patchy than in the wetter Douglas-fir forests.