Fire and the Forest History of the North Cascade Range
Author(s): Les C. Cwynar
Reviewed work(s):
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1938350

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FIRE AND THE FOREST HISTORY OF THE NORTH CASCADE RANGE

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Abstract. Postglacial vegetation changes are often ascribed to the direct effects of climate change. I studied pollen, plant macrofossils, and sediment charcoal in order to determine the potential role of changes in the disturbance (fire) regime in the postglacial development of local vegetation at Kirk Lake in the foothills of the North Cascade Range in northwestern Washington. Five pollen assemblage zones are recognized: a Pinus—Populus zone >12 000 BP, a Picea—Alnus sinuata zone from >12 000 to 11 030 BP, an Alnus rubra—Pteridium zone from 11 030 to 6830 BP, a Cupressaceae zone beginning at 6830 BP, and a late Holocene Pinus—Alnus rubra zone from 2400 to 900 BP.

The first forests (>12 000 BP) were an open mixture of conifers and deciduous trees, chiefly Tsuga mertensiana, Abies, Pinus contorta, and Populus on a landscape subject to erosion. Just before 12 000 BP, the pioneer species Picea sitchensis, Alnus rubra, and A. sinuata became important constituents of the forest. Although pollen accumulation rates were high, the abundance of Alnus sinuata indicates an open-canopy forest. Beginning ≈11 200 BP, climatic warming initiated major changes in forest composition and the fire regime. Tsuga heterophylla migrated into the region, rapidly expanded, then declined shortly thereafter, while Pseudotsuga menziesii, Alnus rubra, and Pteridium expanded, and Pinus contorta, Picea sitchensis, Populus, and Alnus sinuata declined. The abundance of Pseudotsuga, Alnus rubra, and Pteridium between 11 030 and 6830 BP corresponds with increased influxes of charcoal into the sediment; this zone is interpreted as a closed forest with a relatively high fire frequency and composed of a mosaic of postfire successional communities in which fire-adapted Pseudotsuga and Alnus rubra predominated over firesensitive Tsuga heterophylla. Pinus monticola became locally important ≈8000 BP. Between 6800 and 6400 BP Thuja plicata arrived, Tsuga heterophylla expanded, and Alnus rubra, Pseudotsuga, and Pteridium declined. These changes are accompanied by a reduced fire frequency, inferred from lower charcoal accumulation rates, and they indicate a shift to wet-temperate climate similar to today’s. The late Holocene fossil record shows the development of the adjacent peatland, which Pinus contorta eventually invaded.

Key words: Cascade Range; charcoal; fire; forest history; paleoecology; palynology; plant macrofossils; Quaternary studies.

INTRODUCTION

Recent studies of vegetation emphasize the importance of disturbance (White 1979, Mooney and Godron 1983, Pickett and White 1985). The composition of forests is partly determined by the disturbance regime, which includes average rates, distribution in space, and severity of disturbances (Loucks 1970, Mooney and Godron 1983, Shugart 1984, Pickett and White 1985, Runkle 1985). In forests, disturbances occur on various scales, ranging from small gaps created by the death of one or a few trees, leading to gap-phase regeneration, to large gaps created by a variety of external factors, such as fire or wind, leading to secondary succession (Runkle 1985).

Delcourt et al. (1983) developed an hierarchical model of how vegetation patterns arise from the interaction of physical and biological processes on three time scales: micro (1−5000 yr, 1−10^5 m²), macro (5 × 10^2−10^6 yr, 10^6−10^12 m²), and mega (>10^6 yr, >10^12 m²). They concluded that “the Quaternary paleoecological record demonstrates the importance of climatic change as the dominant influence upon vegetational processes and patterns at the macro-scale of spatial-temporal resolution” and that “even at the micro-scale, prevailing disturbance regimes that affect plant succession must be viewed within the context of their prevailing macroclimate.” When macroclimate changes, vegetation may therefore be expected to respond not only to the direct effects of change in climate, but also to the indirect effects of change in the disturbance regime.

Although fire is an important agent of disturbance in the modern evergreen coniferous forests of the Pacific Northwest (PNW) and some forest types depend on it for their regeneration (Franklin and Dyrness 1973, Agee 1981, Hemstrom and Franklin 1982), the post-glacial development of PNW forests is generally inter-
interpreted as resulting from the direct effects of climate change. The general sequence of postglacial vegetation change at lowland sites in the northern Puget Trough (Hansen 1938, 1947, 1948, Hansen and Easterbrook 1974, Baker 1983, Heusser 1983, Barnosky 1984) begins with open forests of various admixtures of temperate lowland (Pinus contorta, Populus) and montane taxa (Abies lasiocarpa, Tsuga mertensiana). At \( \approx 11 \) 200 BP temperate lowland species began to replace montane species so that by 10 000 and 6000 BP, and then the development of the modern humid climate after 6000 BP.

The role of fire in either maintaining plant communities or in initiating vegetation change has increasingly attracted the attention of Quaternary paleoecologists, especially since charcoal is abundant in lake sediments and easily quantified (Waddington 1969, Swain 1973, Cwynar 1978, Green 1981, Grimm 1983, Lamb 1985, Winkler 1985a, b, Dunwiddie 1986). Some researchers have recognized the potential significance of fire in the postglacial development of PNW forests (Hansen 1947, Heusser 1973a, Mathewes 1973, Leopold et al. 1982), but only Sugita and Tsukada (1982) and Dunwiddie (1986) have provided detailed studies of charcoal from lake sediments, and Mathewes (1985) has stressed the need for direct evidence of past fire regimes from sedimentary charcoal profiles for a full understanding of postglacial vegetation change in the PNW. My primary objective in this paper is to reconstruct the history of local vegetation around Kirk Lake, Washington in relation to disturbance by fire. I specifically address the following questions: (1) Are postglacial changes in vegetation associated with changing fire regimes? (2) What was the nature of the vegetation between 10 000 and 6000 BP and what was the relative importance of change in climate vs. the disturbance regime in initiating the development and maintenance of this vegetation, which has generally been interpreted as an open Pseudotsuga woodland possibly maintained by fire and resulting from the direct effects of a much drier climate relative to modern? I argue that the vegetation was a closed forest, but more importantly, that a change in the fire regime and not the direct effects of climate change initiated and maintained this forest.

**SITE DESCRIPTION**

Kirk Lake is small (0.6 ha), relatively deep (7.6 m), and is on the western flank of the North Cascade Range at 190 m altitude (Fig. 1; 121°37′ W, 48°14′ N; Section 23 N/P, Township 32 N, Range 9 E). It lies just within the maximum extent of the Cordilleran Ice Sheet (Waitt and Thorson 1983) of the Fraser Glaciation (circa 25 000–10 000 BP). The North Cascades near Glacier Peak were deglaciated before 12 250 BP (Beget 1984). The vicinity of Kirk Lake was deglaciated before \( \approx 11 \) 500 BP, and the lake probably formed as a kettle in outwash or kame terrace (J. E. Beget, personal communication). Glaciers in the region re-advanced in the early Holocene \( \approx 8400–8300 \) BP (Beget 1984). No bedrock is exposed within the drainage basin of Kirk. Surrounding mountains are composed of crystalline rocks, principally schists (McKee 1972).

The lake lies within the Tsuga heterophylla Zone (Franklin and Dyrness 1973), which regionally is dominated by Pseudotsuga menziesii (Douglas-fir), Tsuga heterophylla (western hemlock), and Thuja plicata (western red cedar). Abies amabilis (Pacific silver fir), A. grandis (grand fir), Picea sitchensis (Sitka spruce), Pinus contorta (lodgepole pine), and P. monticola (western white pine), are minor constituents. The most common deciduous tree is Alnus rubra (red alder). Near the lake, Thuja plicata and Tsuga heterophylla are the most common trees together with some Pseudotsuga menziesii. A peatland on the east side supports a stand of Pinus contorta with scattered Picea sitchensis and a shrub understory of Ledum groenlandicum (Labrador tea) and some Alnus sinuata (Sitka alder). A small stand of Typha latifolia (cattail) grows at the north end of the lake.

**METHODS**

I collected a 12.44-m core from peat on the west shore of the lake with a 5 cm diameter modified Livingstone piston sampler (Wright 1967) and help. I removed samples of 0.5 cm\(^3\) with a calibrated brass sampler (Birks 1976) for pollen analysis (at 20-cm intervals above 9 m, and 5- or 10-cm intervals below 9 m) and to determine percent mass-loss on ignition (LOI) at 550°C. Tablets of Eucalyptus pollen or Lycopodium spores were added to pollen samples for determination of pollen concentration and pollen accumulation rates (PARs). I prepared samples for pollen analysis using standard methods (Faegri and Iversen 1975) and, in addition, sieved basal inorganic sediments to remove fine particles (Cwynar et al. 1979). I tallied a minimum sum of 300 upland pollen types (trees, shrubs, terrestrial herbs, pteridophyte spores, and unknowns) for each sample and used it to calculate pollen percentages. The Haploxylon/Diploxylon determination of pine pollen was based on a minimum of 25 grains per sample. I zoned the pollen diagrams using constrained cluster analyses (Gordon and Birks 1972). Charcoal was analyzed by the method of Waddington (1969). Clark (1984) has shown that charcoal counts derived from pollen preparations are sensitive to the preparation techniques used; I treated all samples identically during sample preparation.

For plant macrofossil analysis, I removed 5 cm long
core segments, measured their volumes (generally 60–80 cm$^3$) by displacement in a graduated cylinder, wet-
sieved each through screens of 1000-, 425-, and 106-
$\mu$m mesh (clayey or silty samples were disaggregated
in a 5% sodium pyrophosphate solution), and then
picked, identified, and enumerated all seeds, fruits, co-
nifer needles, and other recognizable plant parts from
the residues. Identifications were based on modern ref-
eree material. I embedded in wax several conifer
needles from basal sediments and sectioned them for
critical identifications. I included only samples with
a minimum of 20 conifer needles in the preparation of
the percentage diagram of conifer macrofossils (Dun-
widdie 1987), with the exception of two samples from
the early postglacial period; I amalgamated some sam-
bles in order to raise the needle sum to 20.

**Stratigraphy**

Numerous coarse roots and wood fragments pre-
vented the collection of the uppermost 1 m of sedi-
ment. None of the core reacted with 10% HCl, indi-
cating the absence of carbonates. The sediment
stratigraphy was as follows (Munsell Color descriptions
[Munsell Color 1975] are given in parentheses):

<table>
<thead>
<tr>
<th>Depth below surface (cm)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>100–360</td>
<td>Peat, well-decomposed at the bottom and coarser at the top (7.5 YR 3/4).</td>
</tr>
<tr>
<td>360–715</td>
<td>Coarse gyttja grading to decomposed peat (5 YR 4/3).</td>
</tr>
</tbody>
</table>
| 715–1151                | Fine detritus gyttja grading upward to coarse gyttja. (Grading in color from 7.5
|                         | YR 2/1 to 5 YR 2/3.) A volcanic ash occurred between 775–771 (2.5 YR 8/1). |
| 1151–1184               | Predominantly silt (N 4/0) with complex banding of thin sand and clay layers and
|                         | some brownish, slightly organic layers. A couplet of volcanic ash layers occurred at
|                         | 1151–1153 cm; each layer was ≈2 mm thick and formed a sharp contact with adjacent
|                         | sediment. Slightly organic, brownish silt lay between the ash layers. |

**Table 1.** Radiocarbon dates from Kirk Lake, Washington.

<table>
<thead>
<tr>
<th>Sediment depth interval (cm)</th>
<th>Radiocarbon age (BP ± 1 sd)</th>
<th>Laboratory number</th>
</tr>
</thead>
<tbody>
<tr>
<td>865.0–870.0</td>
<td>8600 ± 40</td>
<td>QL-1614</td>
</tr>
<tr>
<td>960.0–965.0</td>
<td>9580 ± 60</td>
<td>QL-1615</td>
</tr>
<tr>
<td>1060.0–1065.0</td>
<td>10 510 ± 60</td>
<td>QL-1616</td>
</tr>
<tr>
<td>1105.0–1110.0</td>
<td>11 180 ± 60</td>
<td>QL-1617</td>
</tr>
<tr>
<td>1125.0–1130.0</td>
<td>11 500 ± 160</td>
<td>QL-1618</td>
</tr>
<tr>
<td>1153.5–1158.0</td>
<td>13 250 ± 90</td>
<td>QL-1649</td>
</tr>
<tr>
<td>1165.0–1173.0</td>
<td>14 610 ± 220</td>
<td>QL-1619</td>
</tr>
</tbody>
</table>

1200–1244 Banded sandy clay with some silt. Coarse
sand at the very bottom (N 3/0). Inorganic.

Below the ash couplet LOI was <6% (see Fig. 3),
whereas above the ash LOI rose rapidly to 40–75% through-
out most of the core, increasing to a maximum of 94% in the upper peat.

**Chronology**

Seven radiocarbon dates (Table 1) were obtained
from the lower half of the core where most of the pollen
stratigraphic events occur. The geographic distribution
of Holocene tephra layers (Sarna-Wojcicki et al. 1983),
the pollen stratigraphy, and radiocarbon dates indicate
that the tephra at 771–775 cm is from Mount Mazama.
Its age of ≈6800 BP (S. Porter, personal communi-
cation) is used as another point on the age-depth curve.
Deposition times were calculated by linear interpola-
tion (Fig. 2). The two oldest dates (14 610 and 13 250
BP) may not be reliable because the sediment dated
has a low organic content (<6%), which may result in
spuriously old dates (Olsson 1979). If these dates are
correct, the sedimentation rate would have been very
slow, which seems unlikely because of the many small
layers of sand, which probably sedimented rapidly. An
 hiatus below the ash couplet is an alternative to slow
continuous sedimentation. In either case, reliable de-
nosition times cannot be based on the two oldest dates.
Therefore, I extrapolated deposition times downward
only to the top of the ash couplet at 11.51 m and
upward to the change in sediment type from fine to
coarse detritus gyttja.
RESULTS AND INTERPRETATION

Five local pollen assemblage zones are informally recognized on the basis of constrained cluster analysis (Fig. 3). The chief features of these zones and their associated PARs (Fig. 4), charcoal accumulation rates (CHARs; Fig. 4), and plant macrofossils (Figs. 5 and 6) are summarized in Table 2.

Although it is clear from the superposition of the pollen zone boundaries onto the macrofossil concentration diagram (Fig. 5) that there is excellent agreement between the pollen and macrofossil data, there are, nevertheless, several important local changes in the vegetation that are not as evident in the pollen profiles as in the macrofossil record. In the mid-Holocene there is a shift from Diploxyylon to Haploxylon pine pollen, although the overall abundance of pine remains low. The macrofossil record, however, shows that *P. monticola* became important in the local vegetation when this shift occurred. Similarly, when *Picea* pollen appears consistently in the late Holocene at values <2% (a subtle change that occurs at other sites and is generally disregarded in vegetation reconstructions), leaves of *Picea sitchensis* recur indicating its local reappearance.

The percentage macrofossil diagram for conifers (Fig. 6) indicates several interesting trends. *Pseudotsuga* was clearly the dominant conifer in the early Holocene, but *Tsuga heterophylla* was important locally despite its

![Figure 2](image-url)  
**Fig. 2.** Age-depth curve for Kirk Lake. ■ Mazama tephra (6800 BP), ○ radiocarbon dates used in the calculation of deposition times in years per centimetre, ○ dates that are not considered reliable.

![Figure 3](image-url)  
**Fig. 3.** Pollen percentage diagram for Kirk Lake.
low pollen percentages. Furthermore, *Pseudotsuga* declined in local abundance in the mid-Holocene as *Tsuga heterophylla* and *Thuja plicata* increased. The percentage diagram highlights these trends, but in general there is little difference between the concentration (Fig. 5) and percentage (Fig. 6) macrofossil diagrams. When interpreting these diagrams, however, we should bear in mind that nothing is known about the potential for differential preservation of macrofossils and that deciduous species were important (*Populus* and *Alnus rubra*) early in the postglacial period.

*Basis for interpretation*

Paleoecologists now often use quantitative methods to compare fossil pollen assemblages with pollen assemblages produced by modern vegetation so that vegetation reconstructions may be refined (MacDonald and Ritchie 1986). This approach was not possible in this study for two reasons. First, pollen spectra from different types of deposits are not directly comparable (e.g., Ritchie 1974, Birks 1977). Most samples of modern pollen spectra from the PNW are derived from moss polsters (Heusser 1973b, 1978a, c, d) and therefore cannot be compared with the fossil spectra from the lake muds of Kirk Lake. Second, *Pseudotsuga* and other conifers have been selectively logged so that sediments show a striking decrease of conifer pollen and an increase of *Alnus* pollen, attributable to *A. rubra*, which colonizes disturbed environments (Davis 1973, Heusser 1978a, c, Barnosky 1981, Sugita and Tsukada 1982, Dunwiddie 1987). Pollen spectra immediately below the settlement horizon better describe the pollen rain of the natural forests of the region (Davis 1973, Heusser 1978d), but they are too few in number to form an adequate basis for comparison.

Kirk Lake is small, so most of the pollen it receives is derived from local or extra-local sources, i.e., from plants growing within several hundred metres of the lake (Jacobson and Bradshaw 1981). Plant macrofossils are also derived from local source areas, but areas smaller than those for pollen (Watts 1978, Birks 1980). The reconstructions possible from the record at Kirk are therefore of the local vegetation, but because of the lack of modern pollen and macrofossil samples for comparison with the fossil assemblages, the reconstructions are necessarily qualitative and based on the abundances of various taxa in the pollen and macrofossil records. When interpreting the pollen record, I have

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**Fig. 3.** Continued.
FIG. 4. Pollen and charcoal accumulation rate diagram.

FIG. 5. Concentration diagram of plant macrofossils from Kirk Lake. For the trees and shrubs, all macrofossils are leaves unless otherwise shown. For all other plants, they are fruits or seeds, unless otherwise indicated. The concentration data are plotted on a log scale.
borne in mind that _Pseudotsuga_ and _Tsuga heterophylla_ are generally under-represented and _Alnus rubra_ over-represented in modern pollen spectra relative to their abundance in the vegetation (Heusser 1973b, 1978a, c, d). Dunwiddie (1985, 1987) has shown that in the PNW, conifer needles can be identified to species and are abundant in the sediments of small lakes and ponds; their abundance in recent sediments is proportional to the importance of the species in the local vegetation (within 30 m of the site). Therefore, although I have considered the pollen and macrofossil records together, I have relied more on the specific determinations and abundances of macrofossils to reconstruct the local vegetation. The pollen record has been primarily used to correlate the record at Kirk with the records at other sites.

Swain (1973) showed that past fires around a lake could be identified by the presence of distinct charcoal peaks in the sediments of the lake. Changes in the amount of charcoal accumulating in lake sediments (CHARS) may therefore be taken as an indication of changes in the fire regime. However, it is not possible to determine whether the fire regime is changing with respect to the frequency or magnitude of fires.

### Paleoeocological reconstructions

**Pinus–Populus zone (KL-1).**—This zone is present at most sites in the PNW (Barnosky 1981) and is generally interpreted as representing a pine woodland dominated by _Pinus contorta_ (confirmed at Kirk Lake by the predominance of Diplolaxon-type pollen and macrofossils), _Populus_, and _Tsuga mertensiana_. The inorganic nature of the sediment indicates that the vegetation cover was probably too sparse to stabilize the fresh soil surfaces. The occurrence of _Alnus sinuata_, which today grows in the Cascade Range on inorganic soils where forest canopies are open (Oliver et al. 1985), also indicates that the forests were open.

**Picea–Alnus sinuata zone (KL-2).**—Similar pine-dominated pollen assemblages from western Washington have generally been interpreted as representing open, woodland vegetation. This interpretation is particularly appropriate for sites farther south in the glaciated areas of southwestern Washington (e.g., Barnosky 1981, Tsukada and Sugita 1982) where PARs are comparatively low (5000–10 000 grains·cm⁻²·yr⁻¹), the sediment organic content is low, and open-ground taxa are common (_Thalictrum_, _Epilobium_, _Saxifraga_...
tricuspidata-type). At Kirk Lake the abundance of Alnus sinuata indicates that the forest canopy must also have been partially open. The higher PARs at Kirk, however, suggest that forests there were less open than those in southwestern Washington. Because PARs are a function not only of pollen productivity by vegetation but also of pollen transport to the lake by streams (Peck 1973, Bonny 1976, Pennington 1979), other explanations for these high PARs are possible, although they seem improbable. For example, erosion of polleniferous soil into the lake may have inflated the PARs somewhat. However, it is unlikely that that is solely responsible for the high PARs, because PARs remain high at the end of the zone where the organic component (LOI) of the sediment reaches 60% of sediment dry mass, in comparison with 6% at the beginning of the zone. Another possible explanation is that these high PARs result from changing patterns of sediment deposition within the lake (Davis et al. 1984). Multiple cores would be needed to test this hypothesis rigorously, but it seems unlikely because the core was recovered from the side of the basin, far from the presumed center of deposition where the water is 7.6 m deep today.

The local vegetation around Kirk Lake during this period was, therefore, a well-developed but nonetheless somewhat open coniferous forest of Pinus contorta, Picea sitchensis, Tsuga mertensiana, and Abies lasiocarpa. The abundance of Picea sitchensis probably reflects its ability to colonize open habitats. At present, both Picea sitchensis and Pinus contorta colonize dunes along the PNW coast and invade prairie in southwestern Washington (Franklin and Dyrness 1973). Populus and Alnus rubra were important deciduous trees. A. sinuata was most prominent during this time, probably growing in canopy gaps. Fire was a minor influence on this vegetation. CHARs in this zone are moderate relative to the rest of the record and are consistent with dominance by P. contorta ssp. contorta, the coastal type that occurs in the PNW today. It differs from ssp. latifolia, the inland or Rocky Mountain type, in having open cones that shed their seeds seasonally (Critchfield 1980). This is generally regarded as an adaptation to a less severe fire regime than that experienced by ssp. latifolia in the drier interior.

Alnus rubra-Platydium zone (KL-3).—This zone has been variously interpreted as representing "structurally open forest, unlike the forest of today" (Heusser 1978b), unstable transitional open woodlands (Tsukada et al. 1981), woodland (Barnosky 1981, Sugita and Tsukada 1982), or either open woodland or a forest mosaic (Leopold et al. 1982, Barnosky 1984). The interpretation

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**Fig. 6.** Percentage diagram of conifer-leaf macrofossils.
that this zone represents an open forest community is commonly based on two observations. First, *Pteridium* is a heliophytic fern in which sporulation decreases with increasing shade (Conway 1957, Page 1976). Its spores are abundant in this zone, implying the presence of an open community. Secondly, the percentages for *Pseudotsuga* pollen in this zone are maximal for the postglacial period, and they exceed considerably percentages found in surface samples from modern closed forests in the Puget Lowland and adjacent areas (Heusser 1973b, 1978a, c, d). Since trees generally flower most profusely when grown in open stands (Faegri and Iversen 1975), and the highest values for *Pseudotsuga* pollen in surface samples come from *Pseudotsuga* woodlands in the rainshadow of the Olympic Mountains (Heusser 1978a), a woodland hypothesis was widely accepted. There are several difficulties with this hypothesis.

First, the analogy with open, dry rainshadow communities is not compelling because *Alnus rubra* and *Pteridium*, both of which increase in this zone together with *Pseudotsuga*, are infrequent in these communities (Franklin and Dymess 1973, Fonda and Bernardi 1976). This analogy is also linked with the climatic interpretation that increased *Pseudotsuga* implies greater aridity, but it seems paradoxical that pollen of *Alnus rubra*, a species of moist habitats, increases in abundance simultaneously with that of *Pseudotsuga*. Secondly, the low percentages of *Pseudotsuga* pollen in surface samples may be an artifact of selective logging of *Pseudotsuga* coupled with the over-representation of *Alnus rubra* pollen.

Several lines of evidence suggest that the forest was closed. First, at Lake Washington, where the natural presettlement forest was dominated by closed stands of *Pseudotsuga menziesii, Thuja plicata,* and *Tsuga heterophylla* (Davis 1973, Scott 1980), pollen spectra from sediment immediately below the settlement horizon contain 5–60% *Pseudotsuga* pollen (Davis 1973, Leopold et al. 1982). Similarly, at Mineral and Hall Lakes, presettlement *Pseudotsuga* percentages are ≈15 and 9%, respectively (recalculated from Figs. 4 and 5 in Sugita and Tsukada [1982] using the total pollen and spores of upland plants as the pollen sum, as at Kirk Lake). Dunwiddie (1987) found 20% *Pseudotsuga* pollen in the surface sediment of a pond on Mount Rainier located within a dense old-growth stand of *Pseudotsuga* that formed 80% of the total basal area. The 10–17% *Pseudotsuga* pollen at Kirk Lake is therefore consistent with expected percentages for *Pseudotsuga* in closed forests.

Secondly, at sites where total PARs have been calculated for this zone, they are high: 20 × 10³ grains·cm⁻²·yr⁻¹ at Kirk Lake, 20–45 × 10³ grains·cm⁻²·yr⁻¹ at Davis Lake in the southern Puget Lowland (Barnosky 1981), 10 × 10³ grains·cm⁻²·yr⁻¹ at Mineral Lake, and ≈16 × 10³ grains·cm⁻²·yr⁻¹ at Hall Lake (Sugita and Tsukada 1982). There is no change to a more-minerogenic sediment in this zone, so these high PARs do not result from increased erosion associated with an open forest. Presettlement PARs for *Pseudotsuga* at Mineral and Hall Lakes (1200 and 2500 grains·cm⁻²·yr⁻¹, respectively [Sugita and Tsukada 1982]), where closed forests dominated by *Pseudotsuga, Thuja plicata,* and *Tsuga heterophylla* grew before settlement, are similar to the mean values for this zone at Kirk (2050 ± 920 grains·cm⁻²·yr⁻¹). Such a correspondence indicates that this zone represents a closed forest.

Thirdly, as previously mentioned, *Alnus sinuata* does

<table>
<thead>
<tr>
<th>Pollen zone</th>
<th>KL-1</th>
<th>KL-2</th>
<th>KL-3</th>
<th>KL-4</th>
<th>KL-5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Informal name</td>
<td><em>Pinus—Populus</em></td>
<td><em>Picea—Alnus sinuata—type</em></td>
<td><em>Alnus rubra—Pteridium</em></td>
<td><em>Cupressaceae</em></td>
<td><em>Pinus—Alnus rubra—type</em></td>
</tr>
<tr>
<td>Depth (cm)</td>
<td>1180-1157.5</td>
<td>≈1157.5—1097.5</td>
<td>1097.5—777.5</td>
<td>772.5—275</td>
<td>≈275—100</td>
</tr>
<tr>
<td>Age (BP)</td>
<td>&gt;12000</td>
<td>≈12000—11030</td>
<td>11030—6830</td>
<td>6830—&lt;2400</td>
<td>≈2400—900</td>
</tr>
<tr>
<td>Major palynomorphs</td>
<td><em>Pinus, Populus,</em></td>
<td><em>Pinus, Alnus sinuata—type,</em></td>
<td><em>Alnus rubra—type,</em></td>
<td><em>Tsuga heterophylla,</em></td>
<td><em>Pinus, Alnus rubra—type,</em></td>
</tr>
<tr>
<td></td>
<td><em>Tsuga mertensiana</em></td>
<td><em>Picea, Alnus rubra—type,</em></td>
<td><em>Pteridium</em></td>
<td><em>Cupressaceae,</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Tsuga heterophylla,</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Alnus rubra—type,</em></td>
<td></td>
</tr>
<tr>
<td>Total PARs (10³ grains·cm⁻²·yr⁻¹)</td>
<td>30–65</td>
<td>15–30</td>
<td>15–25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Major terrestrial plant macrofossils</td>
<td><em>Pinus contorta</em> (rare)</td>
<td><em>Picea sitchensis,</em></td>
<td><em>Pseudotsuga,</em></td>
<td><em>Thuja plicata,</em></td>
<td><em>Pinus contorta,</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Abies (lasiocarpa),</em></td>
<td><em>Tsuga heterophylla,</em></td>
<td><em>Pseudotsuga,</em></td>
<td><em>Ledum, Thuja plicata,</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Pinus contorta,</em></td>
<td></td>
<td><em>Tsuga heterophylla,</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Alnus rubra,</em></td>
<td></td>
<td><em>Pinus monticola,</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Alnus sinuata,</em></td>
<td></td>
<td><em>Picea sitchensis</em></td>
<td></td>
</tr>
<tr>
<td>CHARs (10⁶ μm³·cm⁻²·yr⁻¹)</td>
<td>...</td>
<td>2–4</td>
<td>&lt;1–8</td>
<td>&lt;1–2</td>
<td>...</td>
</tr>
</tbody>
</table>
not grow in closed forests (Oliver et al. 1985). *A. sinuata*-type pollen declines as *Pseudotsuga* increases at the beginning of this zone, implying that the forest canopy became closed.

How can the evidence for both closed and open forests be reconciled? Hansen (1948), Heusser (1973a, 1978a), Barnosky (1981), Leopold et al. (1982), Mathews (1973, 1984, 1985), and Tsukada et al. (1981) argued that fire has been important for maintaining open communities during this time. The charcoal profile from Kirk Lake clearly shows increased charcoal accumulation rates in this zone. Similarly, at Hall Lake, \( \approx 80 \) km southwest of Kirk Lake, high percentages and PARs of *Pseudotsuga, Alnus*, and *Pteridium* in the early Holocene are accompanied by postglacial maximum CHARs (Sugita and Tsukada 1982). Thus, disturbance by fire was more important during this time.

Both *Pseudotsuga* and *Alnus rubra* are well adapted to survive and regenerate after fire (Fowells 1965), and they are the most important trees following disturbance in the *Tsuga heterophylla* Zone (Munger 1940, Franklin and Dyrness 1973). In contrast, *Tsuga heterophylla* is especially sensitive to fire owing to its thin bark and shallow roots, which are often exposed (Fowells 1965). *Pteridium* is also abundant during early successional stages following logging or fire, particularly during the 1st 5 yr after disturbance (McMinn 1951, Franklin and Dyrness 1973).

Repeated fires leave an irregular, patchy distribution of vegetation on the landscape in various stages of succession. A higher fire frequency would result in a higher proportion of patches in relatively young successional stages, and thus a greater abundance of *Alnus rubra* and *Pteridium* on the landscape. In addition, pollen percentages of fire-sensitive *Tsuga heterophylla* declined early in this zone and remained at low values as the percentages of *Pseudotsuga* pollen increased.

In the absence of disturbance, *T. heterophylla* invades stands of *Pseudotsuga*, replacing it in late seral stages. Because of the higher fire frequency during zone KL-3 time, however, the development to later successional stages was preempted more frequently so that *Pseudotsuga* was less often replaced by *T. heterophylla*, except probably at the wettest sites in the drainage where fire frequency remained relatively low.

I interpret this zone as representing a closed forest dominated by *Pseudotsuga, Alnus rubra*, and *Tsuga heterophylla* as a mosaic of postfire seral communities of different ages. These forests were similar to modern closed forests of the region except that they lacked *Thuja*, *Tsuga heterophylla* was less abundant, and the proportion of landscape patches in early successional stages was relatively high because of a higher frequency of disturbance by fire.

**Cupressaceae zone (KL-4).**—The increased abundances of *Thuja plicata* and *Tsuga heterophylla* pollen and macrofossils indicate the development of forests similar to those of today in which *Pseudotsuga, Thuja plicata*, and *Tsuga heterophylla* trees predominate. The coincident increase of *Thuja* and decline of *Alnus* (both of which grow in moist habitats) in both the pollen and macrofossil records suggest that *Thuja plicata* replaced *Alnus rubra* trees on the wettest sites least prone to fire. *Pinus monticola*, a tree of well-drained sites, became a minor but consistent local component of the forest.

The greater particle size of the sediment in the upper part of this zone and the occurrence of *Ledum* and *Gaultheria shallon* macrofossils indicate the encroachment of the growing peatland toward the coring site. Both *Pinus contorta* and *Picea stichensis* once again grew locally. They were probably restricted to the developing peatland, as they are today at Kirk and other similar sites in western Washington (Franklin and Dyrness 1973).

**Pinus–Alnus rubra zone (KL-5).**—The initiation of peak deposition indicates the growth of the peatland over the coring site. The most extensive peatland in the basin is on the east side of the lake opposite the coring site. The increase in Diploxylon pine pollen and of *Pinus contorta* macrofossils reflects the continued colonization of the peat by pine as well as its greater proximity to the coring site. The increased amplitude in the abundance of pollen of most taxa, such as *Alnus*, probably results from greater local heterogeneity of fossil deposition on peat surfaces relative to lakes. It is not clear, for example, whether *Alnus rubra* or *Pteridium* were actually more abundant at this time. The vegetation changes of this period can be attributed to local peat growth and expansion, and the forests of surrounding uplands may not have changed.

**DISCUSSION**

Pickett (1976) developed an evolutionary model of succession in which he viewed landscapes as “mosaics of successional habitats, generated by random periodic disturbance.” In this model, vegetation on the scale of landform units depends in part on the frequency of disturbance. Hansen (1947) argued that the postglacial development of vegetation in the Puget Lowland was influenced “regionally by fire and locally by soil conditions, and to a limited extent by climate.” Although the ultimate cause of postglacial vegetation change was climate change, the charcoal record at Kirk indicates that change in the fire regime was a proximate cause for some of the postglacial changes in vegetation. Specifically, the increase of *Pseudotsuga, Alnus rubra*, and *Pteridium* coincident with a decline of *Tsuga* is readily explained in terms of a shift to a relatively younger mosaic of postfire successional communities as a consequence of more frequent fires. The trend to warmer and/or drier climate in the PNW during zone KL-3 time is well established (Heusser 1983, Barnosky 1984), but if greater dryness itself were the proximate cause of these changes from zone KL-2 to KL-3, then the increase of *A. rubra*, which grows in moist habitats,
would be paradoxical. Rather, a small change to drier climate probably triggered a relatively large change in the disturbance regime by increasing fire frequency. Similarly, the later increased abundances of Tsuga heterophylla and Thuja plicata in the vegetation and concomitant decreases of Pseudotsuga and A. rubra may be attributed to less frequent fires.

The importance of the disturbance regime itself as a factor influencing forest composition is apparent in the PNW where forests have recently changed drastically in response to an altered disturbance regime dissociated from climate change. Logging has artificially elevated the frequency and severity of disturbance. The result is a mosaic of relatively young successional communities in which A. rubra and Pteridium are abundant. Recent pollen spectra contain abundant A. rubra-type pollen and Pteridium spores (Davis 1973, Heusser 1978d), and they are remarkably similar in this respect to spectra from zone KL-3 (Davis 1973, Heusser 1978d).

ACKNOWLEDGMENTS

I thank W. A. Watts for the opportunity to do this research. Detailed reviews by C. Barnosky and E. Grimm greatly improved an earlier version of this paper. P. W. Dunwiddie, G. M. MacDonald, R. W. Mathewes, J. C. Ritchie, S. Sugita, and W. A. Watts made useful suggestions on the manuscript. C. Barnosky, P. W. Dunwiddie, E. Grimm, and W. A. Watts helped to core the site. P. W. Dunwiddie helped to identify some of the macrofossils. M. Stuiver kindly supplied the radiocarbon dates. A. Christmas provided clerical assistance. This work was funded by a National Science Foundation grant to E. B. Leopold and an Operating Grant (U0242) to me from the Natural Sciences and Engineering Research Council of Canada.

LITERATURE CITED


