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Vegetational and Climatic History of the Pacific Northwest during the Last 20,000 Years: Implications for Understanding Present-day Biodiversity

Cathy Whitlock[1]

Introduction

During the last 20,000 years, the world climate system has moved from a glacial state into the present interglaciation, known as the Holocene. In the course of the transition, the vast continental ice sheets disappeared, sea level rose worldwide, land and ocean surfaces warmed, and moisture became redistributed (Ruddiman and Wright 1987). These global events also set in motion a series of adjustments to regional climate that caused changes in vegetational composition, the formation of new plant communities, and shifts in the biogeographic range of particular species. The legacy of these events is the present diversity—species richness or number of taxa—of plants and their distribution on the landscape. Thus, a knowledge of the environmental history of a region is important in understanding present and future landscape change.

In the Pacific Northwest, the retreat of glacial ice created a landscape of stagnant ice and glacial meltwater debris in northern Washington, Idaho, and western Montana. This region was colonized by the biota that survived in the unglaciated region to the south, along the exposed coastal shelf, and in the highlands. What was the nature of vegetation in the unglaciated region? How did glacial-age communities respond as climates changed, deglaciated terrain became available, and new species entered the region? What environmental controls shaped the subsequent development of modern forests within both the glaciated and unglaciated regions? In what ways have present-day vegetation and plant communities in the Pacific Northwest been influenced by long-term changes in climate, substrate, biological interactions, and natural disturbance?

Present patterns of biodiversity in the Pacific Northwest represent the culmination of

[1](Formerly Cathy W. Barnosky), Department of Geography. University of Oregon, Eugene, Oregon 97403.

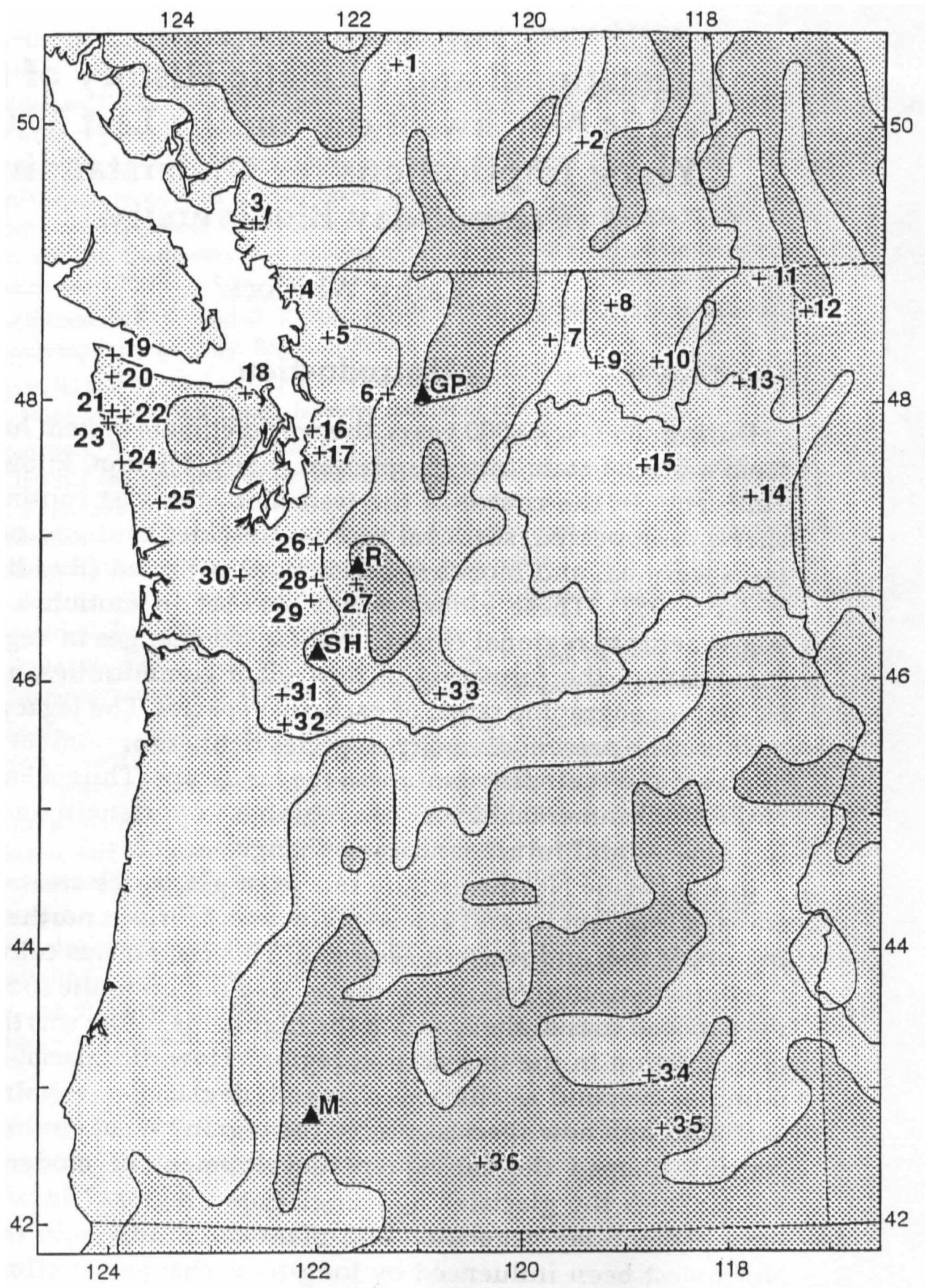

Fig. 1. Location of radiocarbon-dated pollen sites in the Pacific Northwest. 1. Pinecrest Lake (Mathewes and Rouse 1975); 2. Kelowna Bog (Alley 1976); 3. Marian and Surprise lakes (Mathewes 1973); 4. Pangborn Bog (Hansen and Easterbrook 1974); 5. Mosquito Lake (Hansen and Easterbrook 1974); 6. Kirk Lake (Cwynar 1987); 7. Mud Lake (Mack et al. 1979); 8. Bonaparte Meadows (Mack et al. 1979); 9. Goose Lake (Nickmann and Leopold 1985); 10. Simpsons Flats (Mack et al. 1978b); 11. Big Meadow (Mack et al. 1978c); 12. Hager Pond

(Mack et al. 1978d); 13. Waits Lake (Mack et al. 1978a); 14.

ecological, climatological, and geological processes spanning several time scales. Ecological research provides information on recent responses of vegetation to disturbance and rapid environmental change; the fossil record, however, offers complementary information by disclosing ways in which vegetation has responded to large-scale environmental perturbations in the past. The insights gained from paleoecology take on particular importance with the prospect of a 4-5° C warming in the next century as a result of increasing greenhouse gases (Houghton et al. 1990). To appreciate the changes in vegetation and plant communities that will ensue from a warming of this magnitude necessitates an examination of the paleoecologic record, and the limitations and assumptions associated with it.

The objective of this paper is to describe the vegetational and climatic history of the Pacific Northwest during the late-Quaternary period from 20 ka (kiloannum = 1,000 years before present) to the present day. My remarks are confined to Washington State and southern British Columbia, where the fossil record is richest and our understanding of the landscape history is most refined (Fig. 1). A broader discussion of the late-Quaternary vegetational history of the western United States (U.S.) can be found in review papers by Baker (1983), Heusser (1983), Mehringer (1985), Barnosky et al. (1987), and Thompson et al. (in press).

The Nature of the Paleoecologic Record in the Pacific Northwest

The Pacific Northwest features a large number of lakes and bogs suitable for paleoecologic research. Wetlands that formed after late- Pleistocene glaciers melted contain Holocene sediments rich in pollen and plant macrofossils. Localities beyond former ice margins record conditions before and during the period of glaciation. Pollen

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Williams Fen (Nickmann 1979); 15. Creston Fen (Mack et al. 1976); 16. Hall Lake (Tsukada et al. 1981); 17. Lake Washington (Leopold et al. 1982); 18. Manis Mastodon site (Petersen et al. 1983); 19. Wentworth Lake (Heusser 1973); 20. Wessler Bog (Heusser 1973); 21. Soleduck Bog (Heusser 1973); 22. Bogachiel River site (Heusser 1978); 23. Hoh River Valley site (Heusser 1974); 24. Kalaloch (Heusser 1972); 25. Humptulips (Heusser 1983); 26. Nisqually Lake (Hibbert 1979); 27. Jay Bath (Dunwiddie 1986); 28. Mineral Lake (Tsukada et al. 1981); 29. Davis Lake (Barnosky 1981); 30. Zenkner Valley section (Heusser 1977); 31. Fargher Lake (Heusser 1983); 32. Battle Ground Lake (Barnosky 1985a); 33. Carp Lake (Barnosky 1985b); 34. Diamond Pond (Wigand 1987); 35. Fish Lake (Mehringer 1985); 36. Chewaucan Lake (Hansen 1947). M = Mount Mazama; SH = Mount St. Helens; R = Mount Rainier; GP = Glacier Peak.

data, extracted from sediment cores at individual sites, provide a picture of local vegetational change through time. When such vegetational reconstructions are compared from several sites, researchers can infer broader changes in regional vegetation and climate. A chronologic framework for the paleoecologic record is established by a series of radiocarbon dates obtained from bulk sediment or organic fossils within the sediment. Volcanic ashes from eruptions of Mount St. Helens (in southwestern Washington State), Glacier Peak (in the northern Washington Cascade Range), and Mount Mazama (southwestern Oregon) are regularly found in lake sediments; when the ash can be traced to an eruption of known age, its occurrence in the sedimentary record provides another useful dating tool. Mazama ash, for example, is recovered in the sedimentary record of nearly every site, and the eruption is believed to have taken place between 6.7 and 7 ka (Sarna-Wojcicki et al. 1983).

Most paleoecologic research in the Pacific Northwest has focused on broad patterns of climatic and vegetational change that occur on time scales of centuries or millennia. The spatial scale of the reconstruction is determined by the size of the lake or wetland, which in turn defines the pollen-collecting area within the surrounding vegetation. Small- to medium-sized lakes (1—50 ha) collect pollen from an area of 100—1,000 km^2 (Jacobson and Bradshaw 1981). The temporal resolutions of the reconstruction are determined by the number and stratigraphic spacing of pollen samples collected from the sediment cores (Grimm 1988). Pollen samples are usually taken at a stratigraphic interval that represents one sample for every 300—1,000 years of sediment accumulation. This temporal resolution is sufficient to disclose changes in vegetation associated with large-scale changes in climate and disturbance regime (Birks and Birks 1980; Grimm 1988). A sampling interval this coarse, however, is less instructive in identifying short-term changes or site-specific disturbances.

The vegetational reconstruction is greatly improved when stratigraphic records of plant macrofossils are examined in association with pollen data derived from the same strata. Seeds, needles, and other plant remains often provide species identifications in cases where pollen data cannot; they also confirm the local presence of a species at a particular time in the past. When analyzed, particulate charcoal in lake cores provides direct data on past fires (Sugita and Tsukada 1982; Dunwiddie 1986; Cwynar 1987).

Pollen records from the Pacific Northwest were first described in the 1930s and 1940s (e.g., Hansen 1938, 1947). Using a simple peat sampler, H. P. Hansen cored several wetland sites in the Pacific Northwest and provided pollen evidence that plant communities had changed continuously since the last ice age. Hansen (1947) attributed the pollen sequence to stages of natural succession from tundra to modern forest during a steadily warming postglacial climate. He also noted a period in the middle Holocene when the occurrence of xerophytic (dry-loving) taxa suggested a climate that was warmer and drier than the present. These early studies (e.g., Hansen 1947) are of limited use today, inasmuch as only a few pollen taxa were identified and radiocarbon dating was not available to establish an independent chronology. Nonetheless, they laid the foundation for subsequent paleoecologic research in the Pacific Northwest by showing that the region's vegetation and climate had changed significantly since the last ice age.

Vegetational and Environmental History

Vegetation and Climate During the Last Glaciation (ca. 20-14 ka)

In the Pacific Northwest, the period from 20 to 16 ka was characterized by extensive alpine glaciation, but the Cordilleran ice sheet was relatively small and there was little glacial ice in the lowlands (Waitt and Thorson 1983). In contrast, the Laurentide ice sheet was at its greatest extent in northeastern North America between 20 and 16 ka (Mickelson et al. 1983), and its effect on the climate of the Pacific Northwest was considerable, as we shall see. The Cordilleran ice sheet did not reach its greatest size until 15—14 ka, when glaciers were present in the Puget Trough and the Straits of Juan de Fuca (Waitt and Thorson 1983). Cordilleran ice lobes east of the Cascade Range were probably also at their greatest southern position at ca. 15-14 ka, although the glacial chronology of eastern Washington and Idaho is poorly known. When the Cordilleran ice sheet was at its maximum, alpine glaciers were actually smaller than earlier, and large areas of the Cascade and Coast ranges were already ice free (Waitt and Thorson 1983).

Paleoclimates can be quantitatively simulated with the use of general circulation computer models (GCMs). The model simulations provide insights into the large-scale climatic controls during the last 20 ka and the environmental response to them. When a full-sized Laurentide ice sheet is used as input in a GCM model, the simulations suggest that the climate of the northwestern United States was affected by the ice sheet in three ways (Broccoli and Manabe 1987; COHMAP 1988). First, the Laurentide ice sheet caused a general cooling throughout the northern mid-latitudes. Second, it split the North American jet stream, and the southern branch was located south of the present position of the jet. This displacement apparently shifted winter storm tracks south of their present position, and the Pacific Northwest was essentially robbed of its source of winter moisture during the full-glacial period. The third way in which the ice sheet affected climate was through the anticyclonic (clockwise) circulation generated over the Laurentide ice sheet. This circulation pattern created stronger easterly surface winds along the southern margin of the ice sheet, which probably enhanced cold and arid conditions in the Pacific Northwest.

Vegetation in the Pacific Northwest from 20 to 16 ka was strongly influenced by the large-scale controls of climate described above. The west side of the Olympic Peninsula was covered by a mixture of tundra and parkland vegetation during this period (Heusser 1977, 1978, 1983). *Picea* (spruce), *Alnus* (alder), *Pinus* (pine), *Tsuga mertensiana* (mountain hemlock), and *T. heterophylla* (western hemlock) were present in lowland communities that closely resemble modern subalpine parkland in the Olympic Mountains. Areas close to alpine glacier margins were covered by grass (Gramineae), *Artemisia* (sagebrush or wormwood), and alpine herbs. Overall, vegetational data from the Olympic Peninsula imply a cooler climate that was maritime in character between 20 and 16 ka.

Concurrently, the Puget Trough supported tundra and subalpine parkland, and the major species were grass, sedge (Cyperaceae), *Artemisia,* and tundra herbs (Barnosky 1981, 1985a). Plant macro-fossils of *Picea engelmannii* (Engelmann spruce), *Pinus contorta* (lodgepole pine), *Abies lasiocarpa* (subalpine fir), and *Taxus brevifolia* (Pacific yew) were recovered in the Puget Trough and southern Fraser Lowland in sediments dating between 21 and 17 ka (Barnosky 1981, 1985a; Hicock et al. 1982). The presence of *Picea engelmannii* macro-fossils is significant to our understanding of the climate at this time because today it is generally found in mountainous areas east of the Cascade crest (Fowells 1965). The closest modern analog for the Puget Trough vegetation is believed to be modern subalpine parkland in the northern Rocky Mountains (Barnosky et al. 1987). The occurrence of *P. engelmannii* at low elevations west of the Cascade Range in full-glacial time suggests that the climate there was colder and drier than in the Puget Trough today. Paleoclimatic reconstructions based on pollen data from Battle Ground Lake (Fig. 2) in the southern Puget Trough indicate that mean annual temperature was 5-7° C cooler than today, and annual precipitation was 1,000 mm less during the period from 20—16 ka (Whitlock et al. 1990).

Carp Lake, a crater-lake site east of the Cascade Range, provides information on full-glacial conditions in the southwestern Columbia Basin. High percentages of grass and *Artemisia* pollen, low rates of pollen accumulation, and pollen of alpine herbs indicate a period of tundra and steppe between 23.5 and ca. 10 ka (Barnosky 1985b). Apparently, conditions were colder and drier than today, and lower treeline lay above its present elevation throughout the glacial period. It seems unlikely from the Carp Lake data that Cascade conifers grew in the southwestern Columbia Basin, but they may have been present in Oregon or in protected mountain enclaves of the Washington Cascades.

Comparison of Full-glacial Vegetation in the Lowland Areas

A regional comparison of paleoecologic records from the Pacific Coast, the Puget Trough, and the Columbia Basin helps to clarify the environment during the glacial period (Fig. 3). Between 20 and 16 ka, conditions were colder than today, and west of the Cascade crest, upper treeline was lowered by as much as 1,000 m, allowing for the spread of tundra and subalpine communities to Low elevations. The presence of xerophytic taxa in the Puget Trough and Columbia Basin suggests that winter storms were less frequent and unable to penetrate inland. Only the west side of the Olympic Peninsula features taxa that indicate conditions as humid as today. The absence of Puget Sound in full-glacial time also may have enhanced aridity in the Puget Trough because this marine embayment has an important moderating influence on local climate. In many ways, the full-glacial environment of the Puget Trough would have more resembled modern intermontane basins to the east than the coastal plain to the west.

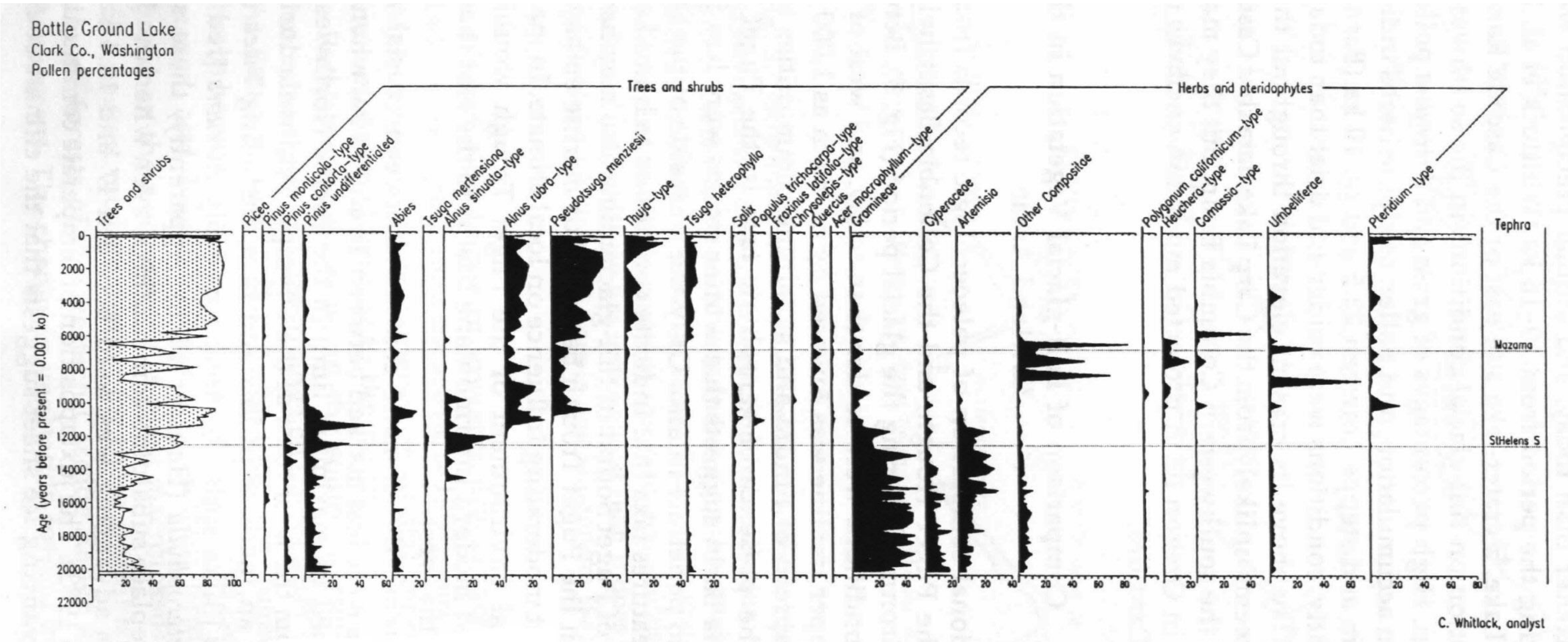

Fig. 2. Pollen abundance of selected plant taxa obtained from the analysis of a sediment core from Battle Ground Lake, Clark County, Washington. Changes in pollen percentages through time at Battle Ground Lake and other sites provide evidence of vegetational changes in the southern Puget Trough during the last 20,000 years (see text for further discussion). The vertical scale represents years before present (yr B.P.; 1,000 yr B.P. = ka), based on radiocarbon age determinations and the occurrence of known-age volcano debris (tephras) in the core (after Barnosky 1985*a*).

In general, the climatic contrasts between coastal and interior lowlands were less marked between 16 and 14 ka, when Cordilleran ice reached its maximum limit in the Pacific Northwest. Pollen records from the west coast of the Olympic Peninsula during this time indicate an increase in lowland taxa, including *Picea* (probably *P. sitchensis* [Sitka spruce]), *Alnus* (probably *A. rubra* [red alder]), and *Tsuga heterophylla* (Heusser 1978). Apparently, these species were able to replace subalpine communities, even when the Juan de Fuca lobe was advancing westward between 17 and 14.4 ka (Waitt and Thorson 1983). The juxtaposition of temperate communities adjacent to an advancing ice sheet suggests that the climate south of the ice sheet had already begun to warm. Sea-surface temperatures at 15—14 ka were higher than before (Mix 1987), and a warmer ocean must have been a stronger influence on coastal vegetation than the presence of an ice sheet just to the north.

Parkland communities in the southern Puget Trough took on a more mesophytic (wet-loving) character after ca. 16—15 ka (Fig. 3). At Battle Ground Lake in the southern Puget Trough, grass and herbs become less dominant than before and *Picea sitchensis, P. engelmannii,* and *Tsuga mertensiana* (mountain hemlock) were present, based on their occurrence as plant macrofossils and pollen (Fig. 2). The nearest modern analog for these assemblages is found in subalpine forests of the western Cascade Range and eastern Olympic Mountains. The change in vegetation toward more mesophytic taxa is believed to be associated with the onset of cool humid conditions at 16—15 ka. A paleoclimatic analysis suggests that temperatures were 2-6° C below the present, but that precipitation was comparable to present-day values (Whitlock et al. 1990).

The introduction of wetter conditions at 16—15 ka suggests that winter storms were more frequent in the Pacific Northwest than before. Increased precipitation may have promoted the advance of Cordilleran ice into Washington State, as well as shifted the vegetation toward assemblages of species more typical of a maritime climate (Hicock et al. 1982; Barnosky 1984). The onset of wetter conditions suggests that Laurentide ice had diminished to a size that no longer split the jet stream (Barnosky et al. 1987; Thompson et al., in press). As the ice sheet shrank, the southern branch of the jet shifted northward and directed winter storms into the Pacific Northwest. Independent evidence to support this climatic scenario comes from the pluvial lake chronology of the Great Basin. A period of high lake levels between 16 and 13 ka implies that the shift of the southern branch of the jet occurred then (Thompson et al., in press).

Appearance of Temperate Taxa During Deglaciation (ca. 14-10 ka)

Paleoclimate simulations of 12 ka incorporate a smaller ice sheet, which no longer creates a split jet or stronger surface easterlies in the northwestern U.S. (COHMAP 1988; Thompson et al., in press). Consequently, temperature and precipitation differences

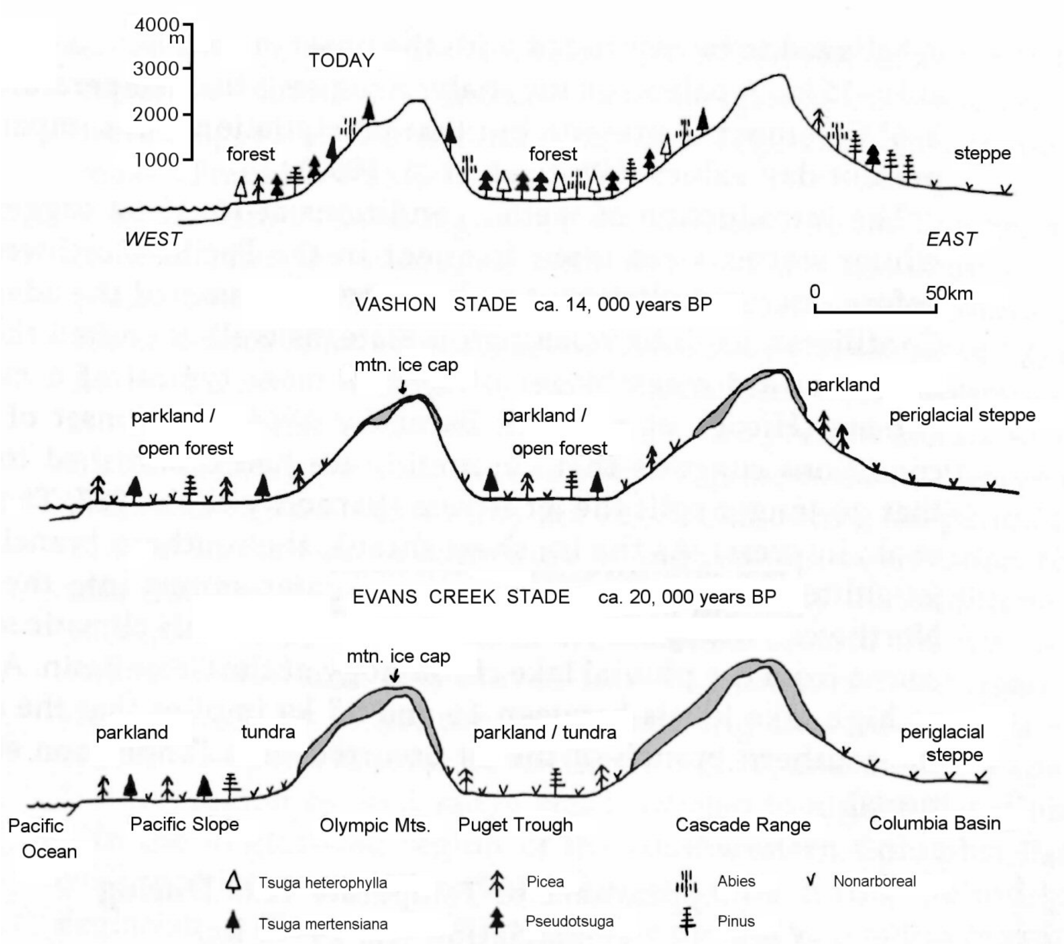

Fig. 3. Schematic transects across southwestern Washington show dominant vegetation and ice distribution today, during the full-glacial period (Evans Creek Stade, Ca. 20 ka), and during the maximum advance of Cordilleran ice (Vashon Stade, ca. 14 ka). During the Vashon Stade, Cordilleran ice occupied lowlands north of this transect, and throughout glacial time the coastline lay 20—50 km farther west than it does today (from Barnosky 1984). Note: 1,000 yr B.P. equals one kiloannum (ka).

(relative to the present) in the Pacific Northwest were not so severe at 12 ka as before, and the simulated climate was warmer and wetter than in the 18 ka simulation (COHMAP 1988).

The period from 14 to 10 ka is the most interesting ecologically because the environmental changes that occurred resulted in the formation of new plant communities in the deglaciated areas and changes in the vegetation of the unglaciated regions. After 14 ka, *Pinus contorta* grew in the region formerly occupied by the Puget and Juan de Fuca lobes and became the major tree species for the next 2,000 years. *Pinus contorta* is well-suited to colonize infertile soil (Fowells 1965), and it apparently was able to establish with little delay on landscapes of stagnant ice and glacial meltwater debris (outwash). Between 12 and 10 ka, *P. contorta* was joined by *Picea sitchensis, Pseudotsuga,* and *Tsuga heterophylla* to form a more closed forest. *Alnus rubra* was also present and presumably grew in riparian and disturbed settings. In the rainshadow region of the northeastern Olympic Peninsula, communities of herbs and shrubs rather than forest were present between 12 and 10 ka (Petersen et al. 1983). Drier conditions and coarse-textured soils on glacial outwash probably were responsible for maintaining open vegetation, just as they are today (Franklin and Dyrness 1973).

In the unglaciated region of the southern Puget Trough, vegetational changes associated with warming are not shown in the pollen record until 11.2 ka (Barnosky 1985a). At Battle Ground Lake, *Tsuga heterophylla, Picea sitchensis, Pseudotsuga, Abies grandis* (grand fir) or *A. amabilis* (Pacific silver fir), *Populus balsamifera* (cottonwood), *Alnus rubru,* and *A. sinuata* (Sitka alder) are present at 11.2 ka (Fig. 2). These taxa grew near the site with *Tsuga mertensiana, Abies grandis,* and *Alnus sinuata.* Apparently the vegetation during the period from 11.2 to 9.5 ka was an admixture of high- and low-elevation forest taxa that has no modern counterpart. It is likely that montane and subalpine species survived in wet habitats around the site, while temperate lowland taxa moved into and colonized disturbed and dry settings. By 10 ka, continued warming allowed temperate conifers to expand around Battle Ground Lake, and montane species left the region as their range was restricted to higher elevations.

In the unglaciated region of the southwestern Columbia Basin, communities around Carp Lake changed little during the course of deglaciation (Barnosky 1985*b),* and the upland vegetation remained treeless. Farther north, however, areas affected by the retreat of glacial ice and by catastrophic Scabland floods were invaded by an open parkland vegetation. In the Okanogan Highlands and Channeled Scablands, the vegetation was predominantly grassland, as evidenced by high percentages of *Artemisia* and grass pollen (Fig. 4). These communities have been interpreted as tundralike (Mack et al. 1978*a*, *b, c;* Nickmann 1979), although the warming trend evident elsewhere suggests that they were probably more steppelike than tundralike in character. *Pine* (presumably *Pinus albicaulis* [white-bark pine] and *P. monticola* [western white pine]), fir, and spruce were present in small numbers, implying that the climate was still cooler than today (Mack et al. 1978a, *b, c, d,* 1979; Nickmann 1979).

Introduction of Xerothermic Communities in the Early Holocene (ca. 10-5 ka)

The height of postglacial warming in the Pacific Northwest occurred in the early Holocene as a result of an amplification in the seasonal cycle of solar radiation between 12 and 6 ka. Summer radiation was greater and winter radiation was less in the early

Holocene than today because the tilt of the earth's axis was greater then and the earth was closest to the sun (perihelion) in summer instead of winter, which is the present situation (Kutzbach and Guetter 1986). The amplification was greatest between 10 and 9 ka, when radiation values were 8% higher in summer and 10% less in winter in the Pacific Northwest (Kutzbach 1987). Computer model simulations suggest that the direct effects of greater summer radiation in the northwestern U.S. were increased temperature and decreased effective moisture (Barnosky et al. 1987; Kutzbach 1987; COHMAP 1988). Indirectly, greater summer radiation also caused an expansion of the eastern Pacific subtropical-high pressure system off the Pacific Northwest, which intensified summer drought (Heusser et al. 1985; Barnosky et al. 1987). In model simulations for 6 ka, the increase in summer radiation is less than at 9 ka and intensity of summer warmth and aridity in the Pacific Northwest is attenuated (Kutzbach 1987; COHMAP 1988).

Evidence of early Holocene drought abounds in the Pacific Northwest. On the Olympic Peninsula *Pseudotsuga, Pteridium* (bracken fern), and *Alnus rubra* were abundant within forests predominantly of *Tsuga heterophylla* and *Picea* (Heusser 1977). This interval occurs between ca. 10 and 8-6 ka. Forests throughout the Puget Trough and southern Fraser Lowland featured more *Pseudotsuga, Alnus rubra,* and *Pteridium* than today (e.g., Mathewes 1973; Mathewes and Rouse 1975; Tsukada et al. 1981; Leopold et al. 1982; Cwynar 1987). Local prairies in the central Puget Trough also expanded their range during the early Holocene (Tsukada et al. 1981). Fire was apparently important in maintaining these forests, as evidenced by the abundance of charcoal in sediments of this period (Sugita and Tsukada 1982; Cwynar 1987). Both *Pseudotsuga* and *Alnus rubra* are adapted to fire and thus better able to regenerate than *Tsuga heterophylla* or *Picea sitchensis* (Munger 1940; Franklin and Dyrness 1973). Cwynar (1987) argues that repeated fires during this interval left a mosaic of forest in various stages of succession. *Alnus rubra* and *Pteridium* were favored in early successional stages; *Pseudotsuga* domininated intermediate stages; a few areas of the forest developed into late successional stages of *Tsuga* and *Picea* forest.

In the southern Puget Trough, high percentages of *Pseudotsuga, Alnus,* and *Pteridium,* as well as significant amounts of *Quercus, Chrysolepis* (chinkapin), and herbs are registered between 9.5 and 5 ka at Battle Ground Lake (Fig. 2). The vegetation is interpreted as an open forest or savannah, similar to the historic vegetation of the Willamette Valley to the south (Barnosky 1985a). Apparently, during the early Holocene, xerophytic communities were able to shift their range northward into the southern Puget Trough. Paleoclimatic reconstructions based on pollen data from Battle Ground Lake suggest that annual precipitation was 40—50% less than today between 9.5 and 4.5 ka, and annual temperature was 1-3° C higher (Whitlock et al. 1990).

The southwestern Columbia Basin remained treeless during the early Holocene, although the presence of Chenopodiineae (Chenopod and amaranth families) and temperate aquatic taxa at Carp Lake indicate that conditions were warm and dry rather

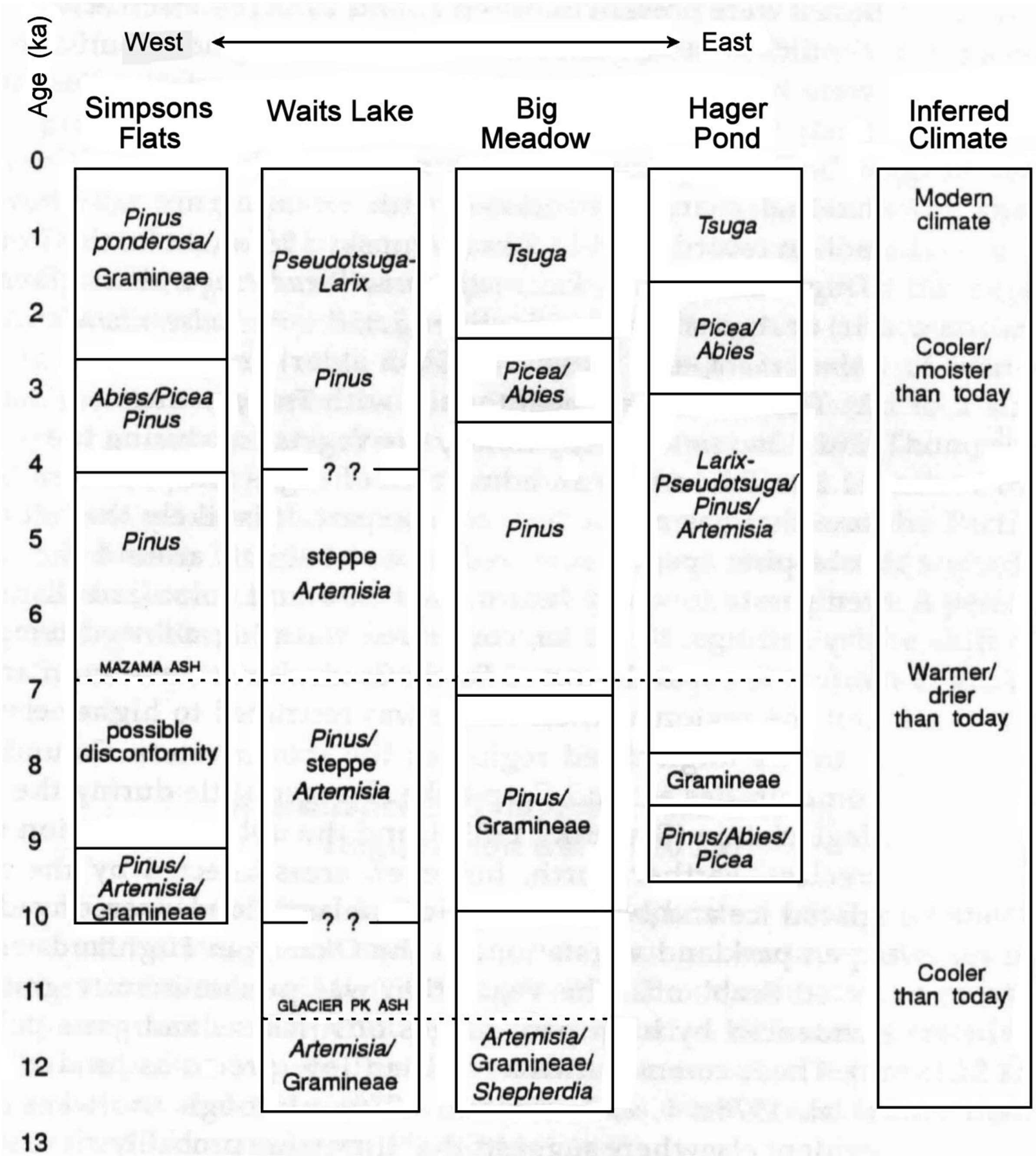

Fig. 4. Vegetational changes and inferred climatic conditions in northeastern Washington and northern Idaho during the last 10,000 years, based on pollen analysis (after Mack et al. 1978a).

than cold and dry as in the glacial period (Barnosky 1985b). Lake levels at Carp Lake were low during the early Holocene, and the site probably dried intermittently (Barnosky 1985*b*). Increased summer drought is evident in the Okanogan Highlands and Channeled Scablands beginning between 10 and 9 ka (Fig. 4; Mack et al. 1978*a, b, c, d,* 1979; Nickmann 1979; Nickmann and Leopold 1985). Drought is inferred from increasing pollen percentages of *Pinus* (attributed to either *P. contorta* or *P. ponderosa),* grass, and *Artemisia. The* assemblages resemble modern pollen spectra from the steppe vegetation in the Columbia Basin, which suggests that the forest/steppe ecotone lay at least 100 km north of its present position in the early Holocene (Mack et al. 1978*a*).

Establishment of Modern Vegetation Patterns in the Late Holocene (ca. 5 ka-present)

After 6—5 ka, summer drought was less intense, as a result of lower temperatures and greater precipitation than before. The vegetational response to wetter conditions varies from place to place. Some sites record pollen assemblages that suggest a shift to mesophytic taxa as early as ca. 7 ka. In the southern Puget Trough, *Thuja*-type pollen is more abundant in sediments at Battle Ground Lake and presumably represents the spread of *Thuja plicata* in humid and riparian settings (Fig. 2). *Thuja*-type pollen and macrofossils are recorded in the northern Puget Trough between 6 and 5 ka and on the north-central coast of British Columbia at ca. 4 ka (Hebda and Mathewes 1984). On the Olympic Peninsula and in the Puget Trough and southern Fraser Lowland, the spread of *Thuja* was accompanied or closely followed by an increase in *Tsuga heterophylla* and *Picea sitchensis. Pinus monticola* also became more common in the late Holocene at some sites (Barnosky 1981; Cwynar 1987). Prairies shrank in size during the last 5,000 years (Hibbert 1979), and peat and fen margins expanded at many sites.

A 6,000-year pollen record obtained from the sediments of a small lake on Mount Rainier (at ca. 1,400 m elevation) suggests ways that climate affected plant succession in middle-elevation forests (Dunwiddie 1986). Between 6 and 3.5 ka, seral species, including *Abies lasiocarpa, Pseudotsuga, Pinus monticola, Abies procera* (noble fir), and *Pinus contorta,* were abundant. The assemblage suggests warmer conditions than today and more frequent fires. After 3.5 ka, late-successional species predominated, including *Tsuga mertensiana, T. heterophylla,* and *Chamaecyparis nootkatensis* (Alaska cedar). The transition correlates with the onset of Neoglaciation (Burbank 1981; Graumlich and Brubaker 1986), when the climate was cooler and moister. Cooler conditions and reduced fire frequency apparently allowed mature forest stands to develop in the last three millennia (Dunwiddie 1986).

In eastern Washington, early Holocene communities with abundant *Artemisia* and grass shifted to *Pinus* parkland and then mixed forest in response to cooler wetter conditions in the late Holocene (Mack et al. 1978*a*, *b, c, d,* 1979; Nickmann 1979; Nickmann and Leopold 1985). In the western Columbia Basin, this transition occurred quite early, between 8.5 and 7 ka, when steppe vegetation was rather dramatically replaced by *Pinus ponderosa* parkland (Barnosky 1985b; Leopold and Nickmann 1985). In the last 4,000 years, *Pinus* forest has been invaded by mesophytic conifers (e.g., *Pseudotsuga/Larix,* *Abies, Tsuga, Picea)* and in some places by *Quercus* (Barnosky 1985b). Some sites from the Okanogan Highland indicate a brief cooling between 3.5 and 1.7 ka when pollen percentages of *Picea* and *Abies* increased (Fig. 4). In general, however, modern forests dominated by *Pseudotsuga, Abies, Tsuga heterophylla,* and *Picea* were established in the Okanogan Highlands after 2.5—1.7 ka.

Implications of the Paleoecologic Record for Ecology and Biogeography

The vegetational history of the Pacific Northwest represents the response of plants to a hierarchical set of environmental controls that vary through time. At a relatively broad scale, variations in latitudinal and seasonal distribution of solar radiation and in ice-sheet size have governed the overall pattern of change during the last 20,000 years. These controls have led to major vegetational changes in the Pacific Northwest that have occurred at approximately the same time and in a comparable direction climatically. For example, the establishment of xerothermic subalpine vegetation (including *Picea engelmannii* and *Artemisia)* between 20 and 16 ka accords well with large-scale changes in circulation invoked by the presence of Laurentide ice. Cold conditions in the mid-latitudes occurred in response to a cold ice sheet (Broccoli and Manabe 1987). Aridity resulted from the southerly displacement of the jet stream and the enhancement of surface easterlies. The development of mesophytic subalpine vegetation (including *Tsuga mertensiana, Picea sitchensis,* and *Alnus sinuata)* after 16 ka implies a northward shift in the winter storm track, which likely occurred as the Laurentide ice sheet shrank in height along its western margin. The appearance of thermophilous (warm-loving) taxa after ca. 12 ka and drought-adapted vegetation at 10—9 ka owes its explanation to the amplification of the seasonal cycle of solar radiation and the enhancement of the subtropical high between 12 and 6 ka. The response to these controls included the formation of forests dominated by *Pseudotsuga* and *Alnus,* prairie, and grassland, as well as shifts in the position of the forest/steppe ecotone.

In contrast to the Laurentide ice sheet's influence on glacial vegetation and climate in the Pacific Northwest, the direct influence of Cordilleran ice seems to have been minimal. For example, when glacier lobes extended to the coast, local vegetation included temperate taxa, probably as a result of a climatic warming brought about by higher sea surface temperatures. Neither did the advance of the Puget lobe effect a major change in vegetation. A site located a few kilometers south of the Puget lobe features high percentages of *Alnus* and *Pinus* (Heusser 1977), suggesting that trees were present near and perhaps on the glacier surface. If present at all, periglacial tundra was restricted at the time of the Cordilleran advance.

The insensitivity of vegetation to local glacial conditions is also evident in differences between the timing of vegetational changes and the chronology of ice retreat. Glaciers receded rapidly after 14.5 ka, whereas the appearance of temperate taxa did not occur until ca. 2,000 years later. This discrepancy implies that communities south of the ice margin were more responsive to large-scale changes in circulation, such as those described by paleoclimate model simulations, and less responsive to local glacier position.

On shorter time scales and finer landscape scales, the distribution of biota is further influenced by local variations in environment and climate. Changes in fire frequency, for example, have been an agent of vegetational change in many Northwest forests (Hemstrom and Franklin 1982; Cwynar 1987; Dickman and Cook 1989; Morrison and Swanson 1990). Fires were probably more frequent in the Pacific Northwest during the early Holocene warm / dry period than they are today, and as a result early-successional species and forest openings would have been more abundant than today. The possibility that Native Americans deliberately set fire to maintain prairie and open areas for hunting and berry gathering has been suggested by historical documents (see Johannessen 1971; Towle 1982; Leopold 1987) but whether Paleoindians and early Archaic people used fire to alter early-Holocene landscapes needs to be explored further. Unfortunately, Holocene fire history is based on only a few charcoal records; more information is needed to assess the long-term fire frequency and its controls.

Substrate conditions have also been important in shaping vegetation on a local scale. Prairie and oak woodland in the central Puget Trough, San Juan Islands, and northeastern Olympic Peninsula are favored by summer drought and the coarse-textured soils that have developed on outwash (Franklin and Dyrness 1973). The early dominance of *Pinus contorta* in deglaciated regions also reflects its superior ability to establish seedlings in the favorable edaphic (soil) conditions that existed during ice recession. Just like the late-glacial spread *of Juniperus* in northwestern Europe (Huntley and Birks 1983), *Pinus contorta* was able to succeed on poorly developed soils in areas of little competition.

The paleoecologic record of the Pacific Northwest sheds some light on the nature of ice-age refugia in the western U.S., although the exact location of temperate conifers during the glacial maximum is unknown. The fact that geographically separate coastal and interior subspecies of *Pseudotsuga* are recognized today (Fowells 1965), each with distinctive morphologic and genetic characteristics, suggests that western and eastern populations of *Pseudotsuga* were isolated from each other during glacial periods (Tsukada 1982; Critchfield 1984). Present-day *Pseudotsuga* populations in Washington may have come from one or several coastal refugia, whereas *Pseudotsuga* in the northern Rocky Mountains probably had an interior distribution during the last glaciation. In the Puget Trough and Fraser Lowland, *Pseudotsuga* appears in the pollen record of all sites at approximately the same time, suggesting that glacial-age populations were not far from their present range or that their spread was very rapid. It seems likely that populations occupied protected habitats at low elevations in the Coast Range and Cascade Range, which enabled them to colonize the Olympic Peninsula, Puget Trough, and Fraser Lowland in less than 500 years once the climate warmed (Barnosky 1985a). A similar scenario may explain the rapid appearance of *Tsuga heterophylla, Abies grandis,* and *Picea sitchensis* in the late-glacial, although the fossil record of these taxa is sparse. So far, the only example of species migration from south to north is the spread of *Thuja plicata,* which occurred in response to cooler, moister conditions in the late Holocene. Additional pollen data from Oregon and the unglaciated parts of Washington may help locate the range of temperate taxa during the last glaciation. However, if these taxa occurred as scattered individuals on the glacial-age landscape, their exact whereabouts will remain elusive.

The development of modern forest communities did not occur until the last few millennia, and there are compelling climatic reasons as to why they could not form before then. Apparently, *Tsuga heterophylla, Abies grandis,* and *Picea sitchensis* were present in western Washington and southwestern British Columbia shortly after deglaciation. However, during the early Holocene, intensified drought restricted their range in favor of more xeric-adapted species. For example, in the early Holocene, *Alnus rubra* probably occupied the riparian niche that *Thuja* now holds. The eastward extension of Pacific coastal species into northeastern Washington, northern Idaho, and northwestern Montana also could not have occurred until the late Holocene. Conditions in the Okanogan Highlands and northern Rocky Mountains were too cold for these taxa in late-glacial time and too warm and dry in the early Holocene. It was probably not until the late Holocene, when summer radiation was reduced and the subtropical high weakened, that Pacific air could penetrate. into the interior from the coast.

When the climatic history and vegetational history of the Pacific Northwest are compared, it is clear that vegetation has responded continuously to a varying array of climatic conditions during the last 20,000 years. The temporal lags between the vegetational response and the climatic forcing seem to have been comparatively short: less than 1,000 years, and probably less than 500 years. On time scales shorter than this, edaphic factors and changes in disturbance regime and competition also have been important. In terms of both the climate and the vegetation, no millenium has been exactly like any other during the last 20,000 years. Paleoecologic data from the Pacific Northwest and elsewhere suggest that modern communities are loose associations composed of species independently adjusting their ranges to environmental changes on various time scales (e.g., Davis 1976; Prentice 1986; Huntley and Webb 1988; Schoonmaker and Foster 1991).

What are the implications of the Quaternary record for questions of biodiversity in the Pacific Northwest? Clearly, diversity in terms of species number / area has varied during the last 20,000 years. Periods of rapid environmental change in the past are generally characterized by increases in species richness, and analogs for these intervals are often modern ecotones between communities or vegetation types. For example, the late-glacial transition was a period of high species richness that developed as subalpine communities were invaded by temperate taxa. Species with life histories suitable for frequent disturbance and stressed environments have fared well during periods of rapid climatic change (Brubaker 1988; Graham 1988). In the Pacific Northwest, *Alnus rubra, Pseudotsuga, Pinus contorta,* and possibly *P. ponderosa* were most abundant during periods of major climatic change in the past, and these taxa will probably be equally successful in colonizing rapidly changing and disturbed environments in the future.

A conservation strategy that seeks to preserve areas of high species richness in the face of future global warming fails to recognize the ephemeral nature of such associations to climate changes of similar magnitude in the Quaternary. Likewise, conservation efforts that emphasize the preservation of communities or vegetation types will probably be unsuccessful because future climate changes quite likely will dismantle the community or vegetation type of concern (Brubaker 1988; Davis 1989; Overpeck et al. 1991). Present-day reserves will likely be the source area for many of the taxa that will comprise future communities. But these reserves will probably not be the final residence for the communities that form as taxa respond to increasing drought and warming (Franklin et al. 1991).

Rather than focus on the preservation of communities, Hunter et al. (1988) propose that conservation plans identify and preserve environments with enough variability to permit species to adjust their range locally in the face of climatic change. The emphasis on environmental diversity, rather than species richness, is based on the vegetational changes of the last 20,000 years. In the Pacific Northwest, environmentally diverse reserves should include an elevational range that can encompass temperature and precipitation gradients within the region. Reserves along north-south mountain ranges, for example, would allow species to shift to higher elevations and higher latitudes during periods of warming and increased drought. Franklin et al. (1991) note that maintenance of diversity in such areas will entail a comprehensive approach that includes wildlands as well as commodity lands. On a broader scale, reserves should be connected by corridors to enable species to shift their range, without depending on island-hopping as a sole means of range adjustment (Graham 1988). Reserves also should include unusual habitats to sustain species that are limited by edaphic conditions (Hunter et al. 1988). Among such areas would be the prairies of western Washington and Oregon, the loess plateaus of eastern Washington, and the serpentine regions of southwestern Oregon and eastern Washington.

The need for paleoecologic data becomes more urgent as we attempt to predict the vegetational changes that will occur in the future. Although the *rate* of future climatic change will be faster than any in the Holocene record, the *magnitude* of change may be similar to that during the late-glacial to Holocene transition when temperatures warmed by 4-5° C (Overpeck et al. 1991). The fossil record thus provides us with a series of sensitivity tests to study the range of vegetational responses under different climatic scenarios. Paleoecologic studies can be used to predict which species will grow in a region under different climatic regimes, as well as the disturbance mechanisms that will accompany and effect vegetational change.

The paleoecologic record offers the opportunity to study biologic change over longer time scales and broader spatial scales than is possible in most ecologic studies. This extended framework creates an opportunity to consider the importance of climate, local environment, and human activity in shaping vegetational patterns in the past, present, and future. In the Pacific Northwest, the database still contains some critical information gaps that need to be filled. For example, few paleoecologic records exist from Oregon, which has the greatest climatic and vegetational diversity of the region today, and potentially the greatest sensitivity to climatic variations in the past and future. Sites that have annually laminated (varved) sediments offer the opportunity to study past changes in vegetation on very fine time scales. Such sites need to be studied in the Pacific Northwest to understand better the sensitivity of vegetation to rapid environmental changes occurring over decades and centuries. Finally, further information is needed on fire history, soil development, and past human activity to determine the importance of these factors in shaping vegetation.

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