Paleoecology of a Montane Peat Deposit Near Lake Wenatchee, Washington[1]

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INTRODUCTION

The interpretation of montane post-Pleistocene forest succession by fossil pollen analysis of peat bogs is somewhat complicated by proximity of the deposits to several life zones. The marked differences in elevation of adjacent areas permits the existence of forests representing several climatic provinces within range of pollen dispersal to the accumulating sediments. It also results in the preservation of a larger number of species of pollen from forest trees, thus making interpretations more general. In areas of slight relief subjected to Pleistocene glaciation, forest succession apparently consisted of a gradual transition from the pioneer forests to those that followed. When one type of forest had given way to the changing environment and was replaced by another, its pollen was no longer recorded in the peat to any extent. Montane bogs, however, may record by their pollen the forests of several life zones or climatic provinces. The biota of a life zone may have moved to lower or higher altitudes because of climatic change or other reasons, but it may still be recorded by the pollen of its forest, together with that of other life zones which may have migrated into adjacent areas. These factors tend to make the picture of postglacial forest succession less definite, although the proportion of significant tree pollen should be indicative of the nearest and most extensive life zone.

LOCATION AND ORIGIN OF PEAT DEPOSIT

The peat deposit of this study accumulated at the west end of Fish Lake, Chelan County, Washington, on the east slope of the Cascade Mountain Range. The bog lies at an elevation of about 1880 feet above sea level, and its greatest part is in sect. 21, T. 27 N., R. 17 E., on the Chiwaukum, Washington, Quadrangle. It occupies an area of about 500 acres. Lake Wenatchee, which is much larger than Fish Lake, lies about one mile to the southwest. Both of these lakes owe their origin to glaciation. The Wenatchee and Chiwawa glaciers united in the vicinity of Fish Lake just east of Lake Wenatchee, and the combined icebody moved down the Wenatchee Valley for several miles (Russell, 1900). Fish Lake is retained chiefly by lateral and irregular ground moraines left by the Wenatchee Valley glacier. A deep valley fill extends for many miles downstream from the lake, in which the Wenatchee River has intrenched itself in regaining its preglacial gradient. Lateral moraines in this area occur from about 1200 to 1800 feet above the present level of Lake Wenatchee, indicating that the ice was at least 2000 feet thick. The higher ridges were not glaciated and may have been forested during the latter part of glaciation. The chronological correlation of the glaciers on the east slope of the Cascades with the continental ice sheet is not possible with the data now at hand (Antevs, 1929). It seems probable, however, that in general the recession of the two were concurrent, and the peat deposit represents most of postglacial time.

Several intermittent streams feed Fish Lake from the north, but most of its water is probably received from

[1]Presented before the meeting of the Ecological Society of America, Seattle, Washington, June 20, 1940. Published with the approval of the Monographs Publication Committee, Oregon State College, as Research Paper No. 46 of the School of Science, Department of Botany.

subterranean sources. A single stream drains it into the Wenatchee River a mile to the south. That most of the valleys at higher elevations to the west carried glaciers, is evidenced by U-shaped valleys, hanging glacial troughs, and cirques at the sources of some of the tributaries. The topography in areas adjacent to the bog is very rugged, with many of the peaks and ridges rising to an elevation of 6000 feet or more. Glacier Peak, about 27 miles northwest, attains an elevation of 10436 feet, and Mt. Stuart, the same distance southwest, has an elevation of 9470 feet. Both mountains support living glaciers.

FORESTS IN ADJACENT AREAS

The bog is located within and near the eastern edge of the Canadian life zone, although most of Fish Lake is in the Arid Transition (timbered) zone (Piper, 1906). The rapid rise in elevation immediately to the northwest causes the latter zone to grade abruptly into the Canadian zone. As a high ridge a few miles farther east also supports the Canadian zone, the timbered Transition zone extends up the Wenatchee River valley as a peninsula into the Canadian zone. At higher elevations, in all directions except the southeast, the Canadian zone grades into the Hudsonian zone, and the higher peaks and ridges rise above timberline into the Alpine zone. At much lower elevations near the mouth of the Wenatchee River, the timbered Transition zone grades into the Upper Sonoran in the Columbia River valley. There are three life zones within 10 miles and five life zones within 25 miles of the bog. It is probably within range of pollen dispersal from all of these vegetation provinces, but the Canadian and Transition (timbered) zones comprise the largest part of the area within a 25 mile radius.

The Canadian life zone in the state of Washington is not well defined, but western white pine (*Pinus monticola*) is probably more restricted to and representative of this zone than any other tree (Piper, 1906). On the eastern slope of the Cascades other trees present, but not confined to this zone, include Douglas fir (*Pseudotsuga taxifolia*), western hemlock (*Tsuga heterophylla*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmanni*), western red cedar (*Thuja plicata*), lodgepole pine (*Pinus contorta*), lowland white fir (*Abies grandis*), silver fir (*A. amabilis*), and noble fir (*A. nobilis*). The latter two are not common on the east slope of the Cascades. Lodgepole pine is chiefly a disclimax species and may invade areas that have been disturbed by lumbering and fire.

The timbered Transition zone is characterized chiefly by western yellow pine (*Pinus ponderosa*), which usually exists in open pure stands because of its intolerance for shade. Other trees in order of their importance are Douglas fir, western larch, lodgepole pine, western hemlock, western red cedar, and white fir. The latter two occur chiefly on protected sites near stream courses. Broadleaf species which thrive locally on favorable sites but are not common include cottonwood (*Populus trichocarpa*), mountain birch (*Betula fontinalis*), mountain alder (*Alnus tenuifolia*), late alder (*A. sitchensis*), and several species of willows. These species are not necessarily confined to this zone.

The Hudsonian zone lying just above the Canadian, supports sparse forests of subalpine fir (*Abies lasiocarpa*), mountain hemlock (*Tsuga mertensiana*), white bark pine (*Pinus albicaulis*), lodgepole pine, Alaska cedar (*Chamaecyparis nootkatensis*), and alpine larch (*Larix lyallii*). Near timberline the trees become prostrate and assume the characteristic Krummholz form. Reproduction often occurs by layering because of the adverse conditions for seedling development and the failure of the trees to produce seed during the short growing season. The amount of pollen produced by these forests is probably relatively small, but some pollen apparently drifts to lower elevations, as is evinced by its presence in the bog. It is to be noted that lodgepole pine occurs in all three forested life zones, and the presence of its pollen in the peat may not be indicative of forest succession, but rather of its adaptability and disclimax status.

Clements' classification of the major North American vegetation climaxes places the area in which the bog lies in the larch-pine association of the Coast Forest (Weaver and Clements, 1938). This forest lies between the subalpine and grassland formations and includes most of the Canadian and timbered Transition zones. The larch-pine forest is a transition type between the Cedar-hemlock formation of the coast forest and the montane forest of the Rocky Mountains. It reaches its maximum development in northern Idaho. Zon (1924) includes the zone of the bog in the yellow pine-Douglas fir forest, with the spruce-fir forest adjacent immediately above, and the bunch-grass prairie adjoining below. The yellow pine-Douglas fir forest includes all of the timbered Transition zone and a large part of the Canadian zone, and the spruce-fir forest includes the remainder of the Canadian and all of the Hudsonian zone according to the latter classification.

The ruggedness and great relief of the surrounding terrain, with its accompanying diversity of slope, exposure, soil, and climate, permit the existence of many localized associations, faciations, and consociations near the bog. This range of environmental factors and its expression by the forest cover may perhaps best be portrayed by the number of forest types within a small radius to the bog. The peat deposit lies approximately in the center of the township, which includes eight distinct forest types (Forest type map, 1936). The greater part of the township is covered with yellow pine of four types, including small and large trees and ranging in volume from 50 to 80 per cent. This is to be expected, because two-thirds of the township lies within the Transition zone. Other more localized types include Douglas fir, both large and small, comprising 60 per cent of the stand by volume; lodgepole pine, comprising 50 per cent; and a pine mixture consisting of yellow and white pine, western larch, Douglas fir, and white fir. Adjoining townships to the north and west are covered largely with upper-slope types composed of subalpine, noble, and lovely fir, mountain and western hemlock, western larch, Douglas fir, Engelmann spruce, and white and lodgepole pines. Subalpine types consisting of Alaska cedar, mountain hemlock, alpine larch, and white bark pine also exist, but these are sparsely forested. The forests and their component species have been discussed here somewhat in detail in order to show the large number of conifers present and their distribution in relation to the bog, as well as the sources of the many species of pollen in the peat.

The mean annual precipitation recorded a few miles west of the bog, in the Canadian zone, at an elevation of 1990 feet is about 38 inches. Less than 15 per cent of this occurs during the growing season. Thornthwaite (1931) in his classification of the climates of North America designates this area as having a humid microthermal climate, with adequate precipitation at all seasons. His description of the seasonal distribution of precipitation, however, does not seem to be correct in view of the dearth of rainfall during the growing months, but as his classification is general, it does not include local deviations within the larger climatic provinces. To correlate the climatic provinces of Thornthwaite with Clements' climax formations, the larch-pine forest coincides in general with the humid microthermal climatic zone along the eastern flank of the Cascade Range. The timbered Transition zone is partly included in this climatic province, and the adjoining one is designated as subhumid microthermal, with a deficiency of precipitation at all seasons. There necessarily must be a gradual transition from one climatic province to the next, and as the bog is near the line of junction, it seems reasonable to consider areas of the same elevation near the bog as having an inadequate summer precipitation. It is realized that the interplay of temperature and precipitation brings about a physiological compromise and is an index to the amount of water available to the plant.

FLORA ON THE BOG

A marginal ditch surrounding the bog retains water during most of the year. This zone supports a rather nondescript community of swamp plants including *Cyperus inflexus, Juncus regelii, Typha latifolia, Sparganium eurycarpum, Potamogeton alpinus, Lysichitum americanum, Bidens cernua, Equisetum fluviatile, Carex* spp., *Salix* spp., *Alnus tenuifolia, Spiraea menziesii,* and *Cornus stolonifera.* At the west end of the lake several stages of hydrarch succession are present, including a floating plant hydrosere characterized chiefly by yellow pond lily (*Nymphozanthus polysepala*), and followed on the bog by poorly defined zones of cattail, bulrush, sedge, and rush. Most of the surface of the bog is in the sedge-meadow stage at present, but inundation during part of the year allows the persistence of many hydrophytic plants. The more common plants are several species of sedge, *Eleocharis acicularis, Eriophorum gracile, Viola palustris, Bidens cernua, Epilobium alpinum, Potentilla palustris, Menyanthes trifoliata, Drosera rotundifolia, Spiraea menziesii,* and a shrubby willow. Widely scattered patches of *Sphagnum* sp. are present, but *Drepanocladus aduncus*[2] seems to be the most abundant and widely spread moss. A single dead specimen of lodgepole pine was noted near the margin. The bog apparently never existed in the Sphagnum-ericad stage, as is evidenced by the scarcity of sphagnum leaves and the entire absence of ericad pollen in the peat.

METHODS AND TECHNIQUE

Peat samples were obtained at quarter-meter intervals with a Hiller peat sampler. The thickness of the pollen-bearing sediments in the area of sampling is 8.5 meters. The lowest three-quarter meter consists of gray sand, underlain with coarser sand and gravel of such compactness as to prevent penetration with the peat sampler. It was not possible to secure samples at the 7.5 and 7.25 meter levels because of the liquid nature of the sediments. Sandy silt at the next three higher levels grades into gray limnic peat at 6.5 and 6.25 meters. An olive-green, colloidal limnic peat is present from 6 to 3 meters, which grades into brown fibrous sedge peat present to the surface. Volcanic ash crystals occur from 3.75 to 3.25 meters but are most abundant at 3.5 meters. Volcanic ash is present usually as a single layer in peat and other lake sediments in the Pacific Northwest (Rigg and Richardson, 1938, Hansen 1938, 1939a, 1939b, 1939c, 1940b, 1941a, 1941b, 1941c). A bog located near New Westminster, British Columbia, likewise shows no definite stratum of ash, but pollen analysis revealed the presence of crystals dispersed throughout a half meter of peat (Hansen, 1940a). In other post Pleistocene sediments of the Pacific Northwest which lack a layer of ash, the presence of crystals may be disclosed upon microscopic examination. The presence of an ash stratum in lake sediments in the lower Willamette Valley of Oregon, and the occurrence of pumice layers in peat deposits on the east slope of the Cascade Range in Oregon suggests that there may have been several sources for these deposits. Those described in Washington may have come from Glacier Peak in the northern part of the state,[3] while the pumice in bogs lying north and east of Crater Lake may have come from the eruption of Mt. Mazama which apparently occurred long after the maximum of Pleistocene glaciation (Williams, 1939).

In preparation for study, about 2 cc. of peat or pollen-bearing sediments were boiled 15 minutes in a weak solution of potassium hydrate with gentian violet stain, strained through cheesecloth, washed several times with water, and mounted in glycerin jelly. Exactly 200 significant pollen grains were identified from each level. The nonsignificant pollen was also identified but was not used in the computation of percentages (table 1). The method used in the identification of Pacific Northwest fossil conifer pollen has been described in recent papers (Hansen, 1940b, 1941a, 1941b). Fossil pollen is identified by measuring the cell or grain and assigning it to that species within whose size-range it falls. If the dimensions are within the limits of overlap of the size-ranges of smaller or larger pollen of other species it is discarded as an unknown and listed under its generic name (table 1). The number of these pollen grains is not used in computing the percentages for the pollen profiles. It seems impossible to separate the pollen of species whose size-ranges are within those of larger or smaller species or that of a single species. In this paper pollen designated as that of *Pinus ponderosa* and *P. monticola* may include some of *P. albicaulis* whose pollen size-range is within that of the first. Likewise, pollen identified as *Abies grandis* and *A. nobilis* may include some of *A. amabilis,* while *Larix occidentalis* may constitute some of *L. lyallii.* Pollen of *Tsuga heterophylla* may be readily separated from that of *T. mertensiana* because of the presence of bladders on the pollen of the latter. Pollen of *Pseudotsuga taxifolia* is distinct, and offers no difficulties in its separation. The author realizes that there may be some error in this procedure, but it is believed that this method of pollen identification involves no more error than is present in the whole problem of pollen statistics.

FOREST SUCCESSION

The forests existing in areas adjacent to the bog when the earliest pollen-bearing sediments were deposited consisted chiefly of western yellow, lodgepole, and white pine, with a preponderance of the first (Fig. 1). They recorded 36, 19, and 12.5 per cent of the significant pollen respectively. Pollen of other conifers present are Douglas fir, western and mountain hemlock, Engelmann spruce, and lowland white and noble fir (table 1). As previously suggested, it is possible that forests existed on adjacent unglaciated ridges during the latter part of the glacial period, and that forest succession had advanced beyond the pioneer stage at the time the lowest pollen-bearing sediments were deposited. This is further suggested by the low proportion of lodgepole pine and the presence of some Douglas fir and western hemlock pollen in the bottom level. In most of the bogs analyzed to date in the Pacific Northwest, lodgepole pine was the dominant pioneer postglacial invader and was recorded by its pollen from 34 to 78 per cent in the lower levels (Hansen, 1938, 1939a, 1939b, 1940a, 1940b, 1941a). These bogs lie within the glaciated region and the initial forest invasion as recorded

[2]Identified by Miss Clara Chapman, St. Helens Hall, Portland, Oregon.
[3]Information from Dr. A. C. Waters, Department of Geology, Stanford University.

TABLE 1. PERCENTAGES OF FOSSIL POLLEN

Depth in meters	8.5	8.25	8.0	7.75	7.0	6.75	6.5	6.25	6.0	5.75	5.5	5.25	5.0	4.75	4.5	4.25	4.0	3.75[1]	3.5[1]	3.25[1]	3.0	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.50	0.25	0.0
Pinus contorta	19	17	16	15	14	11	10	5	5	6	7	10	9	9	7	6	7	8	9	9	10	14.5	11	9	10	9	5	8	10	11	10.5	9	15
P. monticola	12.5	20	24	28	35	38	35	38	48	50	46	44	36	40	42	43	39	40	40	40	39	38	29	30	29	36	47	42	28	18	18	20	13
P. ponderosa	36	36	32	24	10	12	14.5	10	7	7	6	8	9	13	13	16	12	18	18	15	17.5	27	34	36	32	27	20	19	22	35	35	35	37
Pseudotsuga taxifolia	6	5	8	8	11.5	10	14	13	11	11	13	13	9.5	11	9	5	10.5	9	10	9	8	2	6	4.5	5	3.5	6	8	9	6	3	6	9
Tsuga heterophylla	7	7	6	11	8	8	11	12	12	6	11.5	5	12	12	10	10	7.5	6	11	11	7.5	6.5	3	4	4.5	7	8.5	4.5	10	12	15	9	10
T. mertensiana	1	4	2	0.5	3	5.5	2	6	2.5	6	2	2	7	3.5	4	2	6.5	2.5	1.5	0.5	3	1	1.5		3	3		3	2.5		3	1.5	2.5
Picea engelmanni	5	1	2	1.5	5	2	1.5	2	1.5	2.5	2	1.5	2		2	1.5	0.5	1	0.5	1	2.5	1.5	1	0.5	1	2.5		1.5	2	2	1.5	1	2
Abies grandis	8	5	5	5	3.5	6	6	7	4.5	5	6	5	6.5	5	7	3.5	9	7	2	3.5	5	3	5	3	4	3.5	9.5	5.5	9	7.5	8.5	9	5.5
A. lasiocarpa	5	2	3	3	7	4	2	4	1	3	1.5	2.5	3.5	3	2	6	2.5	3	2	2.5	1	2.5	0.5	3	2	1.5	1	3	2.5	2.5	1.5	2	2
A. nobilis		2	2	3	2	3.5	2	2.5	2	2.5	1.5	4.5	2.5	2.5	2.5	4	1	3	1	3	2	1.5	2.5	2.5	1.5	2	2.5	2	3	2	2	5	2.5
Larix occidentalis		0.5					0.5					2	1	1	1	1	1.5	2	4	4	4.5	2	5.5	6.5	7	4		3	2	2	0.5	1	1.5
Pinus spp.[2]	12	17	19	13	18	21	11	23	9	11	13	15	12	13	14	18	19	21	17	8	12	13	15	18	22	21	17	16	17	22	19	16	12
Abies spp.[2]	2	1	1	3	5	3	2	1		2		5	6	3	2	1	3	4	1			1	1	2	2	1	5	3	1	2	3	5	2
Gramineae	0.5	0.5		1	0.5		0.5	0.5	5.5		3	2.5	2		0.5	1.5	3	0.5	1	1.5		0.5		1	0.5	1				1.5	1	1.5	
Compositae					0.5		1									0.5							0.5		0.5		0.5	0.5		0.5	0.5		
Chenopod-Amaranth										1	0.5												0.5										
Alnus[3]	10	7	16	17	12	7	20	16	18	10	22	14	14	20	23	20	12	20	8	5	23	10	4	12	15		1	1	2	9	14	2	9
Betula[3]						1							1	1		1														1			1
Acer[3]	1		1	2		1				1	1	3		2		1	2	1	1	1		1	1					25	1	2	3	6	1
Salix[3]		3	2	1	3		2	1	2				1		4	12	8	3	1	3	4	1	1	1				1	1	3			4
Cyperaceae[3]		2		2	2		2				1		1								14	36	70	31	16		60	23	70	53	34	9	11
Nymphozanthus polysepala[3]																									1								
Typha latifolia[3]	1	1	1	1												1	1	1		1	2	1		1	1		1	1	3	2	3		1

[1]Volcanic ash crystals.
[2]Number of discarded pollen grains of **Pinus** and **Abies**, not computed in percentages.
[3]Number of pollen grains, not computed in the percentages.

probably occurred on primary denuded terrain. In a bog within, but nearer the edge of the timbered Transition zone in the same general region, western yellow pine is likewise recorded by the highest proportion of pollen in the lowest level (Hansen, 1939c). This bog apparently was formed in a landslide depression in an unglaciated area, and it may not record all of postglacial forest succession. In Oregon bogs located well beyond the limits of Pleistocene glaciation, lodgepole pine is similarly recorded by low proportions of pollen in the lowest levels (Hansen, 1941b, 1941e). This substantiates the theory that established forests were in existence during the glacial period and at the time the lowest sediments were deposited. Although lodgepole pine is abundant along the Oregon Coast, bogs in this region record extremely low proportions of this species at the bottom as well as throughout their entire profiles.

If the unglaciated ridges adjacent to the bog of this study were not forested during the glacial period, there is an alternative explanation for the low representation of lodgepole pine in the lower levels. The earliest pollen-bearing sediments may not have been deposited immediately upon the recession of the ice, and the forest succession may have already advanced beyond a pioneer lodgepole pine-invasion. Yellow pine decreases sharply from 36 per cent at the lower two levels to 10 per cent at 7 meters, and then declines more gradually to 6 per cent at 5.5 meters, its lowest proportion in its pollen profile. White pine rapidly increases from 12.5 per cent at the lowest level to 50 per cent at 5.75 meters, from which point it gradually declines to 29 per cent at 2.5 meters. Concurrently, yellow pine increases from its lowest proportion of 6 per cent at 5.5 meters to 36 per cent at 2.25, where it supersedes white pine. The latter again shows a sharp increase to 47 per cent at 1.5 meters, and then makes a final decrease to 13 per cent at the surface. Conversely, yellow pine diminishes to 19 per cent at 1.25 meters and then records a final increase to 37 per cent at the surface. Lodgepole pine gradually declines to 5 per cent at 6.25 meters from its highest proportion at the bottom, and then fluctuates between this and 15 per cent at the surface. It is to be noted that the final percentages of lodgepole, white, and yellow pine approximate those at the bottom level. The highest proportion of pollen recorded throughout the profile is that of white pine with 50 per cent at 5.75 meters (fig. 1).

Douglas fir, western hemlock, and lowland white fir are the best represented of the other conifers by their pollen profiles. These species show slight fluctuations from bottom to top, and do not seem to denote any modification of the forest succession as is suggested by the pollen profiles of yellow, white, and lodgepole pine. Douglas fir fluctuates from 2 to 14, western hemlock from 3 to 15, and lowland white fir from 2 to 9.5 per cent (table 1). In the lower levels of other bogs that have been analyzed in the Pacific Northwest, Douglas fir and hemlock are recorded by their pollen only slightly or not at all. This fact suggests that they do not appear with the pioneer invaders in early postglacial forest succession in the glaciated region. Either no seed-bearing specimens existed sufficiently close to the ice-front to make possible an initial invasion, the environmental conditions were not favorable, or they could not compete with the more adaptable and aggressive lodgepole pine. When the environmental conditions left in the wake of the glacier were sufficiently ameliorated, these species were able to enter. In the Puget Lowland they gradually replaced the earlier forests and competed with

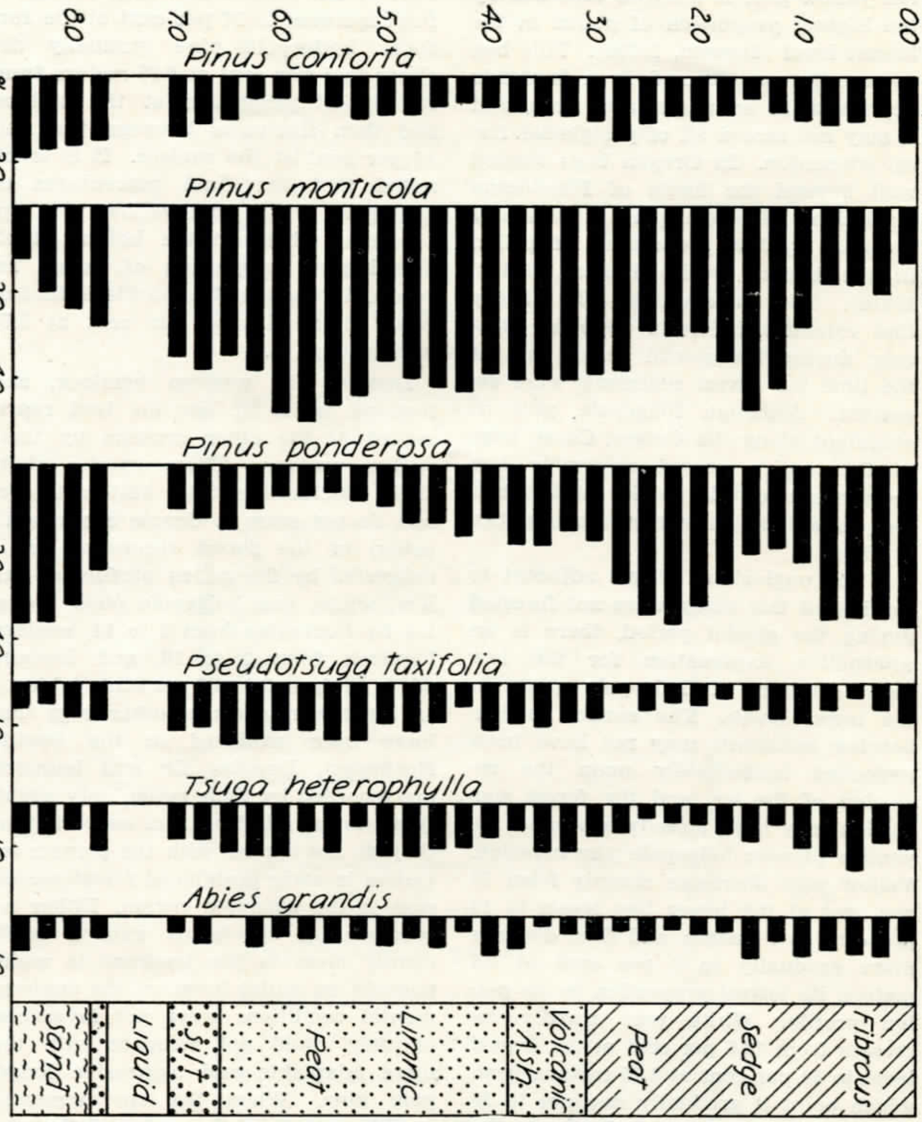

FIGURE 1. Pollen Profiles of Fish Lake bog.

each other for predominance (Hansen, 1938, 1940a, 1941a). In the Fish Lake bog the presence of their pollen in the lowest level supports the theory that the pioneer postglacial forest of this area may have not been recorded even in the earliest pollen-bearing sediments.

The pollen of Engelmann spruce, alpine and noble fir, mountain hemlock, and larch is present at most horizons, but the maximum attained by any one is only 7 per cent. With the exception of western larch, pollen of these species probably drifted down from the Canadian and Hudsonian zone forests at higher altitudes, or possibly was carried into the lake by incoming streams rising at much higher elevations. Their slightly higher proportions in the lower half of the profile, however, suggest that these subalpine species existed at lower altitudes during this time, which reflects a cooler climate. It is also possible that the pollen of larch includes some of alpine larch, and that of western white pine a goodly proportion of white bark pine, which would further substantiate the latter interpretation. Pollen analysis of subalpine bogs may help to solve this problem by showing to what extent subalpine species is recorded in such peat deposits.

Alder is represented at most horizons. A maximum of 23 pollen grains is recorded at 4.5 and 3 meters. Other broadleaf species are represented by sporadic occurrences of their pollen and include mountain birch, vine, largeleaf, and dwarf maple, and willow (table 1). The increase in sedge pollen in the upper levels is correlative with the gradation of limnic peat into fibrous peat in the upper levels.

CLIMATIC CONSIDERATIONS

In recent papers the author has expressed the belief and attempted to show that climate has not been the major, if even an important factor, in the control of post-Pleistocene forest succession in the Pacific Northwest. This is perhaps more true west of the Cascade Range than to the east. The successional relationships of the many coniferous species seem to be largely controlled by their reaction upon the environment and their coaction with one another as well as other species of plants and animals. This is evinced by the subclimax status of Douglas fir in the Cedar-hemlock association of the coast forest, and of western white pine in the Hemlock-cedar-lowland white fir formation in northern Idaho (Huberman, 1935). Fire is also an important element in altering the environmental conditions, changing the forest composition and course of normal forest succession, allowing invasion by disclimax species, permitting the persistence of subclimax seres, and inhibiting the culmination of the climax formation. Prehistoric fires doubtless played an important role in interrupting postglacial forest succession. This generalization is without proof in the area of this study, but pollen analysis and the presence of several charred-peat layers in a bog in the Coast Range of Oregon shows that fire has apparently been responsible for the persistence of Douglas fir as the predominant species in this area during the post-Pleistocene (Hansen, 1941b). During the summer of 1939, the United States Forest Service reported 1273 forest fires in Oregon and Washington as having been caused by lightning. There seems to be no reason to believe that fires caused in this way were less common in the past. An example of how the results of fire might be reflected in the pollen record of montane forests is the burning of an extensive area within a single life zone or forest type. The pollen from these forests would be reduced in quantity, while that from forests in adjoining unburned areas would remain the same.

The latter, however, would record a higher proportion and thus falsely denote an increment in the species of that zone. This would probably be more true in rugged montane regions with several life zones than in regions with slight relief and extensive expanses of a single association.

Insect depredations on the forests are an important biotic factor which materially influence the course of forest succession. The damage of insects to the forests is less precipitate and spectacular than that caused by fire, but it may be of tremendous magnitude. In the western forests the pines have the most insect enemies, and of these the bark beetles are the most numerous and destructive (Keen, 1939). They destroy more standing timber than all other insects combined. Pine, spruce, fir, and hemlock are most severely subjected to insect damage in the order named, but larch is comparatively free from insect pests. Their differences in degree of susceptibility to insect attack cause the normal forest succession toward a climax to be radically upset and deferred, or perhaps inhibited entirely. In western white pine and lodgepole pine forests of the northern Rocky Mountain region, bark beetles so affect the proportion of species as to convert stands to entirely different composition (Keen, 1939). In Yosemite National Park, lodgepole pine stands completely destroyed by bark beetles have been succeeded by forests of hemlock and fir. In other areas bark beetle epidemics in mixed stands of yellow pine and white fir have killed all of the pine and changed the stand into pure fir. Insect depredations in prehistoric times probably have been as common and effective as today, and the postglacial forest succession doubtless was appreciably influenced by this factor. Fungal disease also perhaps played a somewhat parallel role in altering postglacial forest succession.

Snowslides and landslides are additional nonclimatic factors which may have disrupted and modified postglacial forest succession. This is especially true in rugged montane regions, and one may see large denuded areas where snowslides have removed much of the forest. Landslides are also common in areas of tilted rock strata and on talus slopes at the base of columnar basalt cliffs. The accumulated soil and vegetative cover is removed, and plant succession is interrupted and must begin anew. Soil formation is modified and controlled in its many aspects by the vegetative cover. The type, texture, structure, and depth of the soil, and the parent rock from which it is derived, however, have a profound effect upon the course and rate of plant succession. Soil erosion in a topographically young montane region is rapid. Mature soil profiles consequently develop slowly, and a soil climax may not be attained until a region has been planed down and the rate of erosion reduced. Fire also may augment the rate of erosion. Piper (1906) stated that western yellow pine tends to avoid soils that have been derived from basalt, and favors the granitic types. This is one example of the many edaphic factors regulating forest succession and determining the climax in the area of this study, because the basaltic strata of the Columbia Plateau abut against the eastern slope of the Cascade Range in this region.

White and yellow pine seem to be the best climatic indicators of successional and climatic trends in this study, from the standpoint of both their present ranges and of recorded pollen. They are the only species showing sufficient fluctuation upon which to base an interpretation of climatic trends, and they are more distinct and restricted in their respective ranges than the other species concerned. As previously stated white pine is generally confined to the

Canadian zone except where favorable localized areas may support a few isolated trees. Yellow pine is largely limited to the timbered Transition zone, but also occurs in adjacent zones where local conditions enable it to thrive. The present range of white pine indicates that it thrives best under moister and cooler conditions than does yellow pine, and that it is more tolerant of shade. White pine usually exists as a subclimax species, because it is less tolerant of shade than the climax dominants in the area where it makes its maximum development (Larsen, 1929). Yellow pine usually occurs in pure stands, and it is the climax tree within the range of its best growth. It seems to re-enter without a disclimax or subclimax sere after having been removed by fire or cutting (Shantz and Zon, 1924). In its present range the annual precipitation is apparently too low to permit competition and replacement by other species. It seems reasonable to infer from these facts that an increase in yellow pine pollen marks a warming and drying climate, while an increase in white pine pollen denotes a cooler and moister climate in the area of this study. The small fluctuation of the other conifers is significant, because it means that yellow and white pine vary conversely with respect to each other. This fact suggests that their fluctuation may be more a direct result of climate than of normal forest succession controlled largely by the biotic, edaphic, and physiographic factors.

There are four general trends of increase and decrease for yellow and white pine; and increase of one being concurrent with a decrease of the other and vice versa (fig. 1). Climatically these fluctuations suggest a long initial period of increasing coolness and moisture, followed by a warmer and dryer period of perhaps equal length. A third and shorter period of increased coolness and humidity is marked by the increase and decrease of white and yellow pine respectively. This was succeeded by a final dryer and warmer period, which has existed to the present. The third period, however, was brief and poorly defined, and the fluctuation in the proportion of pollen may be the result of forest succession interrupted by factors other than climate. If this is true, the first period was followed by one of warming and drying to a maximum which has persisted to the present. This alternative interpretation would be more correlative with that of the previously mentioned bog within the timbered Transition zone and one in northern Washington (Hansen, 1939c, 1940b). The early, gradual increment in white pine suggests a downward movement of the Canadian to replace the timbered Transition zone, which apparently existed near the bog at the time the lowest pollen-bearing sediments were deposited. The reverse of this sequence of events then followed, and upon the basis of the proportion of pollen in the highest horizon, the composition of the present forest is similar to that which existed at the beginning of its record. The limited record and fluctuation of the Hudsonian zone species suggest that the climate did not vary sufficiently to cause their marked increase or decrease in areas adjacent to the bog. As previously stated, however, it is possible that the pollen of larch and pine may include more or less of the subalpine species of the same genera. If this is true it would tend to indicate even a greater degree of cooling than suggested by the maximum proportions of western white pine pollen. An increase in moisture probably would cause an increase in white pine at the expense of yellow pine without necessarily a decrease in temperature. White pine would then be able to compete with yellow pine because of its advantage of greater tolerance for shade.

SUMMARY

At least eleven species of conifers are recorded by their pollen in a montane peat deposit, located within but on the edge of the Canadian life zone on the east slope of the Cascade Range in Washington. The time of origin of the pollen-bearing sediments is indefinite, but they probably represent most of post-Pleistocene time. The stage of forest succession as recorded by pollen suggests that some postglacial time had elapsed when the initial pollen-bearing stratum was deposited, or that adjacent ridges and highlands were forested during the latter part of the glacial epoch.

Several life zones and climatic provinces, represented by many distinct forest types existing within a small area around the bog, tend to complicate the interpretation of forest succession and climatic trends. The major trends of succession and movement of life zones seem to be best indicated by the pollen profiles of western yellow and western white pine. The limited representation and fluctuation of other species of the Transition, Canadian, and Hudsonian zones minimizes their importance as indicators.

The earliest forests recorded consisted chiefly of yellow, white, and lodgepole pine, with a preponderance of the first. A gradual and constant increase in white pine suggests a cooling and humidifying of the climate, succeeded by a final warmer and dryer period as evidenced by the increase of yellow pine and decrease of white pine. A minor fluctuation in the upper levels may be a result of factors controlling forest succession other than climate. The composition of the present forests is similar to the first forests recorded, as based upon the interpretation of pollen analysis. The author has pointed out some nonclimatic factors that may have influenced forest succession.

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Reprinted from August, 1941, issue of Northwest Science