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POSTGLACIAL FOREST SUCCESSION AND CLIMATE IN THE PUGET SOUND REGION

POSTGLACIAL FOREST SUCCESSION AND CLIMATE IN THE PUGET SOUND REGION

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Fossil pollen analysis and its correlation with postglacial forest succession and climate have been well developed in Europe and the Middle West of the United States by various workers. As far as the writer has been able to ascertain there has been little or no work done in this field in the Pacific Northwest. Erdtmann, of Sweden, collected peat samples from a bog located a few miles north of Seattle, in 1931, but there is no record of his having made an analysis of these samples.[1] Pollen analyses of two bogs near Kodiak, Alaska were made by Bowman ('34), in which incomplete results were obtained because of the inability to secure samples from the upper levels of the bogs. The physical and floristic characteristics of the bogs in the Pacific Northwest have been well worked out by Rigg (1916, '17, '18, '22, '25, '34, '38).

The term "Puget Sound Region" is used to denote the southern part of the Puget Sound Basin, which is generally considered as a physiographic division. It is used here to include an area extending from Everett, twenty-five miles north of Seattle, to the southern terminus of the area subjected to glacial or glaciofluvial action, about twenty-five miles south of Tacoma. East and west this region extends from the Cascade to the Olympic Mountains (fig. 1), and is more or less homogeneous in regard to its ecologic and physiographic features. It is not to be assumed, however, that the forest succession as recorded by the pollen in the bogs of this study, is necessarily indicative of the entire region, or of this region only. All of the Puget Sound region was glaciated during the Pleistocene, and the topography is almost wholly a result of the erosion and deposition by glacial ice and water. There were two periods of glaciation (Bretz, '13). The first, known as the Admiralty, was followed by the Puyallup interglacial period, and the second is known as the Vashon which has been correlated with the Middle Wisconsin glaciation of the Middle West (Antevs, '29).

FORESTS OF THE PUGET SOUND REGION

In the Puget Sound region Douglas fir, *Pseudotsuga taxifolia,* western red cedar, *Thuja plicata,* and western hemlock, *Tsuga heterophylla,* reach their greatest development. Although the Douglas fir is codominant it is

[1] Personal information from Prof. G. B. Rigg.

considered to be a subclimax species, because of the intolerance of its seedlings, while those of cedar and hemlock readily develop on the forest floor and form an understory, which if allowed to continue without interruption

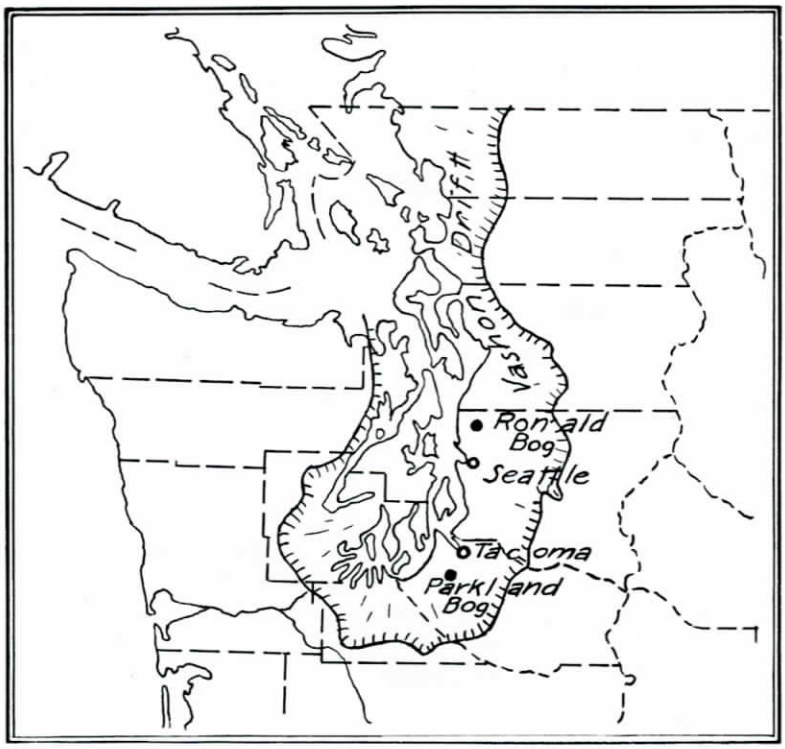

FIG. 1. Map of a portion of western Washington showing the approximate borders of the Vashon glaciation, and the location of the Ronald and Parkland bogs. Drift border from maps by Antevs and Bretz.

by fire, disease, or lumbering, will eventually crowd out the Douglas fir (Hofmann, '24). This would evidently culminate in a climax formation of hemlock-cedar with old and mature Douglas firs scattered throughout. Other subdominant species include white fir, *Abies grandis,* white pine, *Pinus monticola,* lodgepole pine, *Pinus contorta,* and an occasional specimen of Sitka spruce, *Picea sitchensis,* in lowland areas and on floodplains.

The floodplain association consists chiefly of large-leaf maple, *Acer macrophyllum,* red alder, *Alnus oregona,* cottonwood, *Populus trichocarpa,* aspen, *P. tremuloides,* Oregon ash, *Fraxinus oregana,* and casacara, *Rhamnus purshiana.* The principal shrubs include *Cornus pubescens, C. occidentalis, Acer circinatum, Corylus californica, Osmaronia cerasiformis, Sambucus callicarpa, Symphoricarpos albus, Pyrus diversifolia, Salix scouleriana,* and several species of *Ribes* and *Rubus.*

South and west of Tacoma are prairie-like areas sparsely timbered with groves of oak, *Quercus garryana,* and young stands of Douglas fir. Small stands of lodgepole pine and occasionally a specimen of yellow pine, *Pinus ponderosa,* are also found, and many of the herbaceous plants on these "prairies," including several species of grasses, are xeric types. The rainfall in Tacoma is greater than that of Seattle, but the sterile, gravelly soil contains little or no clay and provides efficient subdrainage. The rapid loss of water through subdrainage during the season of heavy precipitation, and the relatively dry summers produce a xeric habitat during the growing season. Another reason suggested for the persistence of these prairies within the hemlock-cedar climax area is said to be the former annual burning by the Indians in order to preserve their hunting grounds and the production of their food plant, the camas (Jones, '36). At present it appears that the Douglas fir is encroaching on the open areas and the groves of oak, causing modification of the xeric conditions. Eventually a more mesophytic condition will develop, which if left undisturbed will probably result in the normal Douglas fir subclimax, followed by the ultimate hemlock-cedar climax.

The Ronald Bog

The Ronald bog is located several miles north of the city of Seattle in Section 8, T. 26 N., R. 4 E. in King county (fig. 1) in an area of rolling hills composed of glacial material deposited by the Vashon ice.

The extent of the bog is about twenty-five acres. The present vegetation consists chiefly of *Sphagnum* spp., *Hypnum* sp., *Ledum groenlandicum, Kalmia polifolia, Vaccinium oxycoccus, Drosera rotundifolia,* and a few grasses and sedges. On the eastern side of the bog is a hydrophytic association consisting of cat-tail, sedges, and hardhack, *Spiraea douglasii.* Trees on the bog include white pine, western hemlock, lodgepole pine, Sitka spruce, and western red cedar. Most of these have been burned or cut down. At present the peat is being removed for commercial purposes, and a large part of the surface has been so completely burned that little of the virgin aspect remains. Burned areas show an invasion by *Polytrichum* sp. and fireweed, *Epilobium angustifolium.*

The average profile of several borings in the central part of the bog shows a varied succession of peat types underlain with 0.2 of a meter of blue clay in which pollens and phytoplankton abound. The blue clay is overlain with 1.2 meters of brown sedimentary peat, the upper layers of which contain some sedge. The next 0.3 m. consists of brown sedge peat, followed by 2.9 m. of hypnum moss peat, the upper part of which contains some sedge. The topmost 1.9 m. is composed of sphagnum peat, of which the upper half-meter is very raw. In general the profile in the area of sampling shows that the peat is raw and only slightly decomposed throughout. Sphagnum leaves are present throughout from 6.0 meter level, but do not

become abundant until the 1.5 meter level. Woody peat occurs at 4.0 m. and again at 3.5 m., and charred moss peat at 2.9 m. A layer of volcanic ash about one-half inch thick occurs at 2.3 m., which also occurs in most of the bogs of the Puget Sound region. The ash layer is found at varying depths in the same bog and in different bogs.

The Parkland Bog

This bog is located several miles south of Tacoma, and about one mile west of the village of Parkland in Pierce county in Sections 7, 8, 17, and 18, T. 19 N., R. 3 E. Samples were obtained from Section 7, and in the area of sampling the bog was 10.5 meters in depth. During the late winter and early spring the bog is almost entirely covered with water but in the summer, parts of the surface become sufficiently dry to permit the cutting of the almost pure stand of sedge for hay. The bog occupies some 120 acres. It lies in a depression in a terraced outward plain formed by streams which flowed southward from the retreating Vashon ice-sheet. Clover Creek flows through the bog, but has done little downcutting thus preventing the drainage of the original lake and the subsequent bog. The type and homogeneity of the peat indicate that the original lake was not deep, but as the bog developed the water table was constantly raised as the accumulation of peat continued.

The flora on the bog consists almost entirely of *Carex* spp., with a small amount of *Juncus effusus, Eleocharis palustris, Alisma plantago-aquatica, Salix lasiandra, S. scouleriana, Spirea menziesii,* and *Alnus oregona,* the latter occurring on some parts of the bog and in low adjacent areas.

A study of the peat profile shows that the peat types are entirely different from those of the Ronald bog. The peat is underlain with about 0.2 meter of blue clay, over which lie 3.5 meters of slightly fibrous sedimentary peat, then 3.6 m. of slightly oxidized sedge peat, succeeded by a layer of sedimentary peat from the 5.4 to the 2.6 m. level. The volcanic ash layer is present at the 2.8 meter horizon. Less oxidized peat grading into raw peat is found from the 2.6 m. level to the surface. There is no evidence that this bog ever existed in the sphagnum-ericad stage.

Methods

Peat samples from the deepest parts of each bog were obtained with a Hiller peat sampler at decimeter intervals. Because of limited time it seemed better to make an analysis of one boring from each of two bogs, rather than two borings from a single bog. In preparing the slides for pollen identification, deflocculation of the peat was effected by boiling in a weak solution of KOH, washing several times with water, and then centrifuging. The residue was mixed with glycerine jelly and gentian violet stain, and mounted on slides. A total of 150 to 250 pollens was counted from each half meter

level. A mechanical stage was used for counting. Fresh pollens of all of the species involved were obtained and used for study and reference during the process of identification. Sources of error involved in pollen statistics have been recognized and adequately discussed by Erdtmann ('31); Fuller ('35); Sears ('30); and Voss ('34).

Significance and Correlation of Pollen Spectra

The recession of the glacier from the Puget Sound Region left an area which was probably entirely devoid of vegetation. The first species to invade this denuded area must have been those which were able to withstand the somewhat adverse conditions and gain a foothold in the sterile and gravelly soil left by the ice and water. The initial forests were succeeded by less hardy species, when the climatic and edaphic conditions had become somewhat moderated by the further retreat of the ice, and the presence of the pioneer forests. It is rather difficult to state with certainty to what extent the post-glacial forest succession has been a direct result of climatic change, and how much has been due to normal plant succession. It seems logical to assume that the initial invasion was a direct result of the existing climate, while several later fluctuations may have been due to changes in other environmental conditions. It seems quite definite, however, that the initial climate in the Puget Sound Region was not as cold as that in the Lake States at the time of the recession of the ice there, because it must have been considerably modified by its proximity to the Pacific Ocean.

Pinus contorta

The pollen spectra show that lodgepole pine was the dominant pioneer tree in the area vacated by the ice. In the lowest level (10.5 m.) of the Parkland bog the frequency of this species is 78 per cent, and in the next two levels, the frequencies reach 74 and 78 per cent respectively (fig. 2*A*). Likewise in the Ronald bog the frequency is high in the lower levels, with 50 and 48 per cent at 6.5 and 6.0 meters respectively. There is a gradual decrease in the pollen frequencies to the surfaces of the bogs, which indicates a gradual decline in the abundance of lodgepole but the tree is now commonly found on many of the bogs in the Pacific Northwest (Rigg, '18). Its early maturation and prolific seed production would enable it to invade and persist under the constantly changing conditions caused by an oscillating ice-front. Lodgepole pine is very intolerant of shade, and would make its maximum development in the absence of competition by more tolerant species. The greater abundance of lodgepole on the Tacoma prairies than in the vicinity of Seattle, as indicated by the pollen spectrum, was probably due to the better suited soil conditions on the gravelly plains than the poorly drained and irregular topography in the latter area. Here, pine probably occupied the higher and better drained areas.

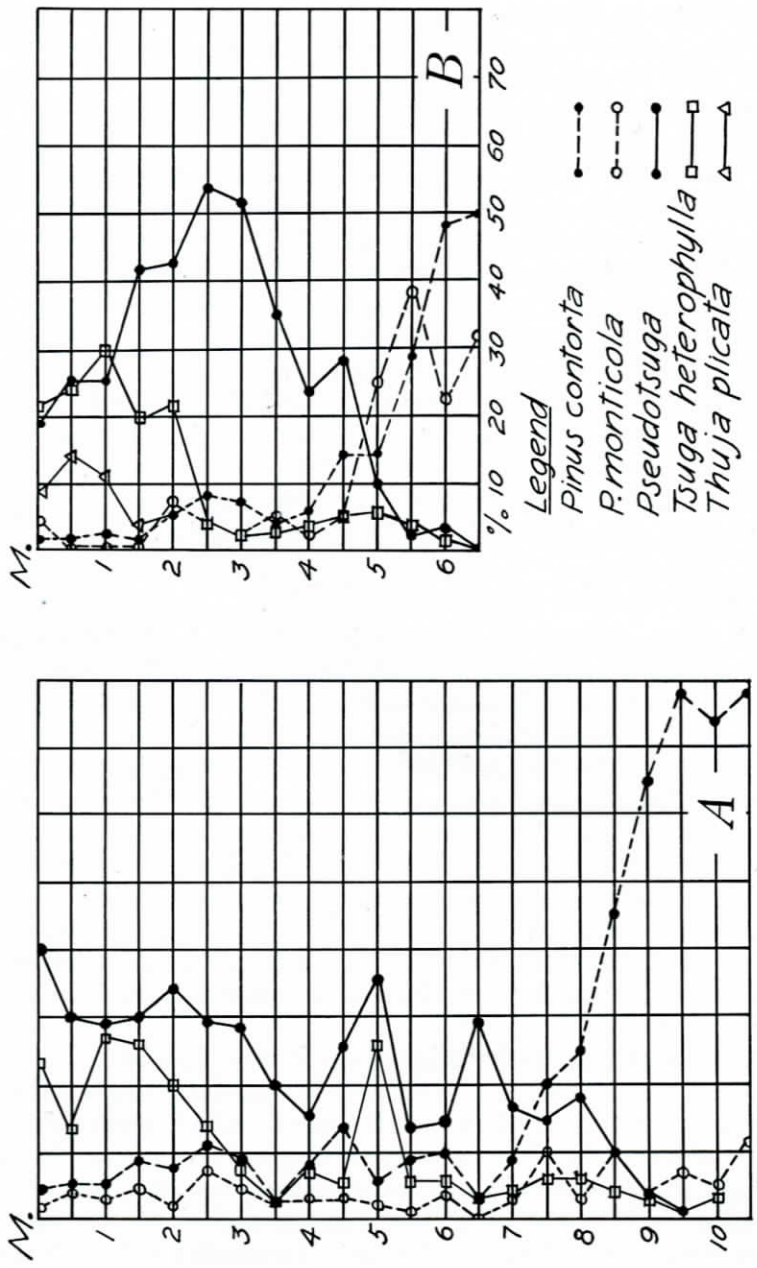

FIG. 2. Pollen diagrams of Parkland and Ronald bogs.

Pinus monticola

Western white pine was also an early invader but did not become immediately as abundant as lodgepole pine. The frequency in the lowest level of the Ronald bog is 32 per cent, with 23 and 36 per cent occurring at 6.0 and 5.5 meters respectively (fig. 2*B*). The lowest level of the Parkland bog shows a frequency of only 11 per cent with 10 per cent occurring at both 8.5 and 7.5 meters. The percentages decrease rapidly from these points and remain more or less constant throughout the rest of the spectrum. The presence of an appreciable amount of white pine early in postglacial time and its relatively rapid decline may well be due chiefly to climatic influences. It apparently was abundant until the climate became warmer, and then migrated to higher elevations as the mountain glaciers receded. Competition by later invading species such as Douglas fir and hemlock probably was also a contributing factor. The pollen spectrum indicates that it was less abundant on the Tacoma prairies than in the Seattle region, due perhaps to the unfavorable edaphic conditions which better supported an initial forest of lodgepole pine. Favorable conditions for the development and persistence of white pine did not exist long in the Puget Sound region.

Pseudotsuga taxifolia

There is no trace of Douglas fir pollen in the lowest level of the Ronald bog nor in the lower two levels of the Parkland bog (fig. 2). Apparently the conditions were too variable and severe for its existence in the area adjacent to the ice during glaciation, and later for the immediate invasion into the area vacated by the ice. In the Ronald bog there is a sharp and almost constant increase from 3 per cent at 6.0 meters to 54 per cent at 2.5 meters, from which there is a rather sharp and constant decrease to the surface. At the time when Douglas fir reached its highest frequency, hemlock began to increase rapidly and apparently at the expense of the fir, until at 1 meter the frequency of hemlock exceeds that of fir. Douglas fir is more tolerant of shade than lodgepole pine (Sudworth, '08), and consequently the pine was crowded out by competition of the fir, and in turn the fir by the hemlock.

The spectrum of Douglas fir indicates that it never became as abundant on the Tacoma prairies as it did farther north, and that it fluctuated considerably from time to time. The same is true of hemlock which correlates quite closely with fir, although at no level does it exceed fir. A sharp increase to 36 per cent at 5.0 meters with a conversely sharp decrease in oak, grasses and composites is indicative of a change in the ecological conditions, or perhaps the result of fire, disease, or insects. It seems likely that this sharp increase is due to increased precipitation which would be favorable for rapid development of fir and hemlock and detrimental to the existence of oak, grasses, and composites, all three groups of which are xerophilous and would

be crowded out by the shade of the conifers. A sharp decrease in the frequency of alder at the same level, however, could hardly be attributed to increased moisture, because it prefers the moist floodplains. Another decrease in Douglas fir and hemlock at 4.0 m. and an increase in grass to a frequency of 19 per cent may be indicative of another climatic change. This same decrease in fir is to be noted in the Ronald bog, so it is improbable that it is merely an incidental fluctuation. It may possibly represent a brief xerothermic period. There is a gradual increase in Douglas fir and hemlock to the 1 meter level, which is followed by a decrease at 0.5 m., from which they both increase markedly at the surface. The final decrease may be attributed to the aforementioned burning by the Indians, while the final increase down to the present represents the invasion of Douglas fir and hemlock since the cessation of the burning in historical times. This recent and continued invasion by Douglas fir is further verified by old residents who have spent most of their lives in this region (Jones, '36).

Tsuga heterophylla and Thuja plicata

The theory advanced by taxonomists and foresters that Douglas fir is a subclimax species in the Puget Sound region is well borne out by the correlation of its spectrum with that of the western hemlock (fig. 2). Hemlock is absent from the lowest level of both bogs. In the Ronald bog the frequencies of hemlock lag considerably behind those of Douglas fir until 2.5 meters at which point Douglas fir apparently reached its greatest development in the region. At this point hemlock rapidly increases while fir decreases until finally hemlock exceeds the fir at the 1 m. level, from which point both species decrease to the surface. This final decrease might well be due to the deforestation which has been extensively carried on since the advent of white man. Much the same story is indicated by the spectrum of the western red cedar. This species does not record its presence until the 2.0 m. level in the Ronald bog, and not at all in the Parkland bog. In the former its initial frequency is 5 per cent from which it decreases to 3 per cent at 1.5 m., and then increases to 11 and 14 per cent at 1.0 and 0.5 m. respectively, and finally decreases to 9 per cent at the surface. Both western red cedar and hemlock were asserting their supremacy and rapidly assuming the role of the dominants in effecting the culmination of the hemlock-cedar climax formation which would normally occur, but were interrupted by the appearance of a disturbing biotic factor, namely man.

On the Tacoma prairies hemlock was unable to overcome Douglas fir because of the several climatic fluctuations which occurred in postglacial time, allowing Douglas fir to keep ahead with each renewal of favorable conditions. These changes seem to have been felt more on the gravelly prairies than in the Seattle area, because the precipitation had a more direct effect on the former. Here the rapid subdrainage due to the porosity of

the soil, prevents the maintenance of a high water table throughout the growing season in spite of the moderately heavy annual mean precipitation.

Oaks, Grasses, and Composites

According to the pollen spectra, this group plays a more important role in plant succession on the Tacoma prairies than in the areas adjacent to the Ronald bog. There is a trace of oak pollen in several levels of the Ronald bog (table I). Composites likewise show only a trace, but grasses have several high frequencies. These, however, are not to be considered as in-

TABLE I. *Percentages of principal pollens from the Ronald bog*

Depth in meters	6.5	6.0	5.5	5.0	4.5	4.0	3.5	3.0	2.5	2.0	1.5	1.0	0.5	S
Pseudotsuga taxifolia	0	3	2	10	28	24	35	52	54	43	42	26	26	19
Tsuga heterophylla	0	1	3	6	5	4	3	2	4	22	20	30	24	22
Pinus contorta	50	48	29	15	15	6	4	7	8	5	2	3	2	2
Pinus monticola	32	23	38	25	5	3	5	2	4	7	1	1	1	4
Abies grandis	2	2	3	5	1	1	2	2	2	2	5	5	4	1
Picea sitchensis	3	0	1	2	1	0	0	0	0	1	0	1	0	2
Gramineae	0	0	1	1	18	2	3	3	0	7	5	3	4	12
Compositae	1	0	1	0	0	1	0	0	0	1	0	0	0	0
Quercus	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Alnus	10	17	14	35	23	32	40	14	22	27	20	20	21	26
Salix	1	3	1	0	1	9	2	5	2	0	1	0	0	0
Betula	0	0	1	1	1	16	5	6	84*	1	1	1	1	2
Acer	0	2	1	1	2	1	0	3	1	1	2	1	1	0
Thuja plicata	0	0	0	0	0	0	0	0	0	5	3	11	14	9
Fraxinus oregana	0	0	0	0	0	0	1	1	0	1	0	0	3	0
Ericaceae	0	0	0	0	4*	1*	7*	2*	0*	2*	6*	20*	41*	11*

* Number and not computed in percentages.

dicative of climatic fluctuations. The high frequency of 18 per cent at 4.5 meters may be due to an increase in bog grasses at that time, while the frequency of 12 per cent at the surface may be indicative of an increase of grass in the region in recent times because of the deforestation.

On the Tacoma prairies these three groups seemed to have been an important factor in the postglacial plant succession. All these groups show low frequencies from the lowest level to 7.0 meters which represents the time during which lodgepole pine was the dominant species in the area. At 7.0 and 6.5 m., oak records frequencies of 14 per cent, grass records 15 per cent at 6.5 m., and composites show a frequency of 13 per cent at 6.0 m. Lodgepole pine and hemlock show low frequencies at 6.5 m., but Douglas fir reaches one of its highest frequencies of 29 per cent at the same level. It apparently represents the period when the initial lodgepole pine consocies had become fairly well replaced by Douglas fir, oak, hemlock, and grasses. The frequencies of the three xerophilous groups remain relatively high for the 6.0 and 5.5 m. levels, while lodgepole pine increases to 10 per cent, and Douglas fir shows a sharp decrease to 14 per cent at 5.5 m. (fig. 2*A*). As previously stated, these fluctuations may indicate a dryer period, which was

unfavorable for Douglas fir, and permitted lodgepole pine to re-establish itself temporarily to some extent. At 5.0 m. the xerophilous groups and lodgepole pine decrease in frequency to less than 6 per cent, while Douglas fir and hemlock increase sharply to 36 and 26 per cent respectively. This converse fluctuation of the xerophilous and coniferous groups is indicative of an increase in humidity which was favorable for the rapid encroachment of the conifers upon the areas occupied by the oak, grasses, and composites.

An increase in oak and grasses at 4.0 m. and a corresponding decrease in Douglas fir and hemlock is evidence of another brief period of desiccation, or at least of physiological dryness. The frequencies of the xerophilous groups remain more or less constant from 4.0 m. to the surface, while the fir and hemlock increases, followed by a decrease, and finally increase again to the surface or down to the present day, the cause of which has been previously discussed, namely the burning by the Indians.

Alnus, Salix, Acer, and Fraxinus

These four genera cannot be considered as critical groups as far as climatic change and plant succession are concerned. *Alnus* is very abundant throughout the spectrum of each bog, and at many levels has the highest frequency. Alder is an early invader in the Puget Sound region, and probably occupy the moist lowlands, such as floodplains and drained lake beds, while lodgepole and white pine occupied the higher and better drained areas. In the Ronald bog alder makes its greatest appearance between the 5.0 and 3.5 m. levels, and in the Parkland bog between the 8.0 and 5.5 m. levels. The entrance of alder in such abundance was at the expense of lodgepole pine in the Tacoma area, and at the expense of both lodgepole and white pine in the Seattle area, while Douglas fir evidently increased at the expense of alder.

Associated with the alder was also to be found willow, maple, and ash, all of which exist in similar habitats. In the Ronald bog willow remains low and static generally throughout, but shows a frequency of 31 per cent at 3.5 m. in the Parkland bog. Willow is present on the bog today and the pollen spectrum is no doubt a record of willow as it occurs in the bog complex, and consequently is insignificant as an indicator of forest succession. Largeleaf maple and ash are also floodplain types, and appear in the limited percentages throughout most of the spectrum of each bog (tables I and II).

Betula and Ericaceae

Birch pollens in the bogs were probably from small and scattered stands of western birch, *Betula occidentalis* (tables I and II). At the present time this birch does not extend as far south as Seattle (Piper and Beattie, '15). The frequency of this genus does not become very high at any level in either bog, with the exception of 16 per cent at 4.0 m. in the Ronald bog. A total

TABLE II. *Percentages of principal pollens from the Parkland bog*

Depth in meters	10.5	10.0	9.5	9.0	8.5	8.0	7.5	7.0	6.5	6.0	5.5	5.0	4.5	4.0	3.5	3.0	2.5	2.0	1.5	1.0	0.5	S
Pseudotsuga taxifolia	0	0	1	4	10	18	15	17	29	15	14	36	26	16	20	28	29	34	30	29	30	40
Tsuga heterophylla	0	3	1	3	4	6	6	5	4	6	6	26	6	7	3	7	14	20	26	27	14	23
Pinus contorta	78	74	78	65	45	25	20	9	4	10	9	6	14	8	3	9	11	8	9	6	6	5
Pinus monticola	11	5	7	4	10	3	10	3	0	4	1	2	3	3	3	5	7	2	5	4	5	2
Pinus ponderosa	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1
Abies grandis	0	4	6	5	4	3	5	6	5	2	3	3	3	2	1	4	4	1	5	2	5	4
Picea sitchensis	0	2	0	0	5	3	4	4	2	0	0	1	1	1	1	1	2	0	1	0	1	1
Gramineae	5	4	0	2	2	2	2	5	15	10	12	4	9	19	9	4	5	8	3	3	5	7
Compositae	0	1	0	1	2	3	2	2	1	13	4	1	6	4	1	8	3	9	2	2	6	2
Quercus	0	0	0	1	1	3	1	14	14	10	5	1	1	4	2	2	0	1	1	2	1	2
Alnus	3	8	5	13	13	34	30	33	26	22	31	4	24	20	19	9	14	7	11	14	15	9
Acer	0	0	0	0	0	0	2	0	1	1	4	4	4	10	2	5	2	2	2	2	2	1
Salix	0	1	2	0	1	3	1	1	2	5	4	12	1	3	31	16	7	7	2	8	5	2
Betula	0	0	0	0	0	0	0	0	0	1	2	4	2	2	5	1	2	0	1	2	2	0
Fraxinus oregana	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	2

of 84 birch pollens was counted at 2.5 m. in the Ronald bog, but the pollens were smaller than those of western birch. They are probably from bog birch, *Betula glandulosa,* which is rather common on bogs in the vicinity of Seattle at the present time. The number of these pollens was not used in the computation of the percentages for this level, because it would tend to distort the other frequencies. Bog birch was a part of the bog complex rather than a factor in the forest succession in the area.

Ericaceous pollens are present in the Ronald bog from the 4.5 m. level to the surface, indicating the presence of ericaceous shrubs growing on the bog and also perhaps on higher ground adjacent to the bog. The number of these pollens was not used in computation of the frequencies, because they came from plants which were a part of the bog complex (table I). No ericaceous pollens were present in the Parkland bog.

Abies grandis and Picea sitchensis

White fir is present in low and rather constant frequencies throughout the spectra of both bogs (tables I and II). White fir is a subdominant species in the Puget Sound region, and generally grows best on moist and protected sites. Apparently it is present in the region today in much the same proportion as it has been throughout most of postglacial time.

A trace of Sitka spruce occurs at various levels in both bogs (tables I and II). It is more abundant in the Parkland bog than in the Ronald bog. Sitka spruce is a fog belt tree of the coast where it is a co-dominant with the western ~~red cedar~~ hemlock to form the spruce-~~cedar~~ hemlock climax formation (Jones, '36). An occasional specimen may be found in low and moist places in the Puget Sound region, but apparently spruce never played a conspicuous role in postglacial forest succession in this region.

A trace of yellow pine pollen is found at three levels in the Parkland bog (table II). A few scattered specimens of yellow pine are present on the prairies in the vicinity of Tacoma. As evidenced by the pollen analysis, yellow pine never became abundant in the Puget Sound region during postglacial time.

Postglacial Forest Succession

The first stage of forest succession in the Puget Sound region is represented by the initial invasion of lodgepole and white pine into the area upon the recession of the ice. This stage is also marked by an abundance of alder in the vicinity of Seattle.

The second stage is indicated by Douglas fir and some hemlock, which tended to replace the initial forests of lodgepole and white pine. On the Tacoma prairies this stage consisted of an invasion of Douglas fir which was shortly followed by an invasion of oak, grasses, composites, with some alder.

The third stage seems to have been a brief period of interruption in the development of the Douglas fir and hemlock forests. On the Tacoma prairies

this is correlated with distinct increases in grasses and composites, which might be indicative of a period of desiccation.

The fourth stage shows a resumption of the development of Douglas fir with a slight increase in hemlock. During this stage Douglas fir evidently reached its greatest development in postglacial time. On the Tacoma prairies Douglas fir seems to have suffered a brief period of unfavorable conditions before it resumed its final development.

The fifth and final stage which takes us down to the present day is one of gradual decline in the Douglas fir subclimax dominancy, and the beginning of the hemlock-cedar climax development, which in time would no doubt assume a dominant role if it had not been interrupted by the activities of man. On the Tacoma prairies the edaphic conditions and the biotic factors have prevented the hemlock-cedar climax formation from reaching as great a development. Here Douglas fir and hemlock have apparently just entered the last stage which had been retarded by the annual burning by the Indians, while western red cedar has not yet entered the areas. The volcanic ash evidently had no detrimental effect upon the forests because the layer deposited was too thin.

Climatic Considerations

The initial climate in the Puget Sound region was probably cool and moderately dry, with an abundance of soil moisture. It definitely was not a boreal climate such as existed in Wisconsin upon the recession of the ice (Hansen, '37). There are several evidences and reasons why the initial climate could not have been boreal. The first is the absence of pollens of subalpine species such as white bark pine, *Pinus albicaulis,* and alpine fir, *Abies lasiocarpa.* The second is the proximity of the Pacific Ocean to this region which must have had a moderating influence upon the climate even while the region was in the process of glaciation.

The initial cool and moderately dry climate was followed by a period of increase in temperature and humidity as the influence of the retreating glacier became less. A brief period of desiccation may be indicated by the influx of the xerophilous groups in the Tacoma area. The xerothermic period was followed by one of much increased humidity resulting in the most extensive postglacial development of Douglas fir. A final period consisted of possibly slightly decreased temperature and humidity similar to the cool and humid marine climate of today.

As previously stated, it is rather difficult to state whether the postglacial forest succession in the Puget Sound region has been a result of climatic changes or merely normal plant succession. The wide climatic range of the species under consideration, the extreme amount of overlapping of their ranges, their apparent adaptability to extremes of moisture and temperature, their shade enduring relationships, and their differences in longevity of life, all these factors cause one to hesitate in making any hard and fast

statements as to climatic fluctuation during postglacial time, based on the evidence supplied by fossil pollen analysis and forest succession.

Summary

Fossil pollen analyses were made of two bogs in the Puget Sound region of the Pacific Northwest of America. One of the bogs is located a few miles north of Seattle, and the other is located several miles south of Tacoma. Both are situated within the limits of the region affected by Pleistocene glaciation.

The Ronald bog has been formed in a depression in the ground moraine left by the Vashon ice. The Parkland bog has been developed in a kettle-hole or depression formed on the outwash plain deposited by streams which drained the ice and later the lakes of the Vashon glaciation.

Pollen analysis shows the following sequence of five stages of postglacial forest succession in the Puget Sound region: (1) A pioneer stage of lodge-pole pine, white pine, and alder; (2) An early invasion of Douglas fir with some hemlock; (3) A period of maximum development of Douglas fir; (4) A period of decline of Douglas fir and the beginning of the dominancy of hemlock; and (5) Continued increased development of hemlock and the entrance of western red cedar to form the hemlock-cedar climax formation, which was interrupted in historical time due to deforestation.

On the Tacoma prairies this sequence was somewhat modified in that the second stage consisted of Douglas fir and oak, while the third stage evidently consisted of a large proportion of oak, grasses, and composites.

In terms of climate this sequence seems to indicate an initial period of coolness and moderate dryness, followed by a warmer and more humid period. The third stage of succession indicates a possible xeric period, which resulted in an increase of xerophilous species on the Tacoma prairies, but which is less definitely reflected in the vicinity of Seattle. The fourth period was one of much increased humidity which has gradually moderated down to the present time, which is characterized by a cool and humid climate.

The deposition of volcanic ash apparently had little effect upon the forest succession, as there are no marked changes indicated by the pollen spectra.

As evidenced by this preliminary work, the postglacial climatic fluctuation is not as well defined in the Puget Sound region as in the Lake States, nor was the initial climate of a boreal type.

The climatic interpretation is tentative, and cannot be considered as definite until more work has been done in this region.

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