

## Late Quaternary Dynamics of Pollen Influx at Mineral Lake, Washington

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Pollen influx analysis at Mineral Lake, Washington, indicates that immediately south of the Puget Lobe of the Fraser Glaciation, tundra was a characteristic vegetation until 16,300 years ago. Invasion of *Pinus contorta* began 17,500 years B.P., and boreal climax conifers (*Abies*, *Picea* and *Tsuga mertensiana*), 16,300, but was temporarily interrupted by the Vashon advance (14,500-14,000 yr B.P.). *Pseudotsuga menziesii* began to grow in population 10,750 years ago, and woodland was established within a time span of 1,000 years. Modern lowland coniferous forests began to form 7,000 years ago. Logistic analysis of pollen abundance changes show that the intrinsic growth rate,  $r$  ( $\text{yr}^{-1}$ ), of pioneer species (e.g. 0.024-0.026 in *Pteridium aquilinum*) is higher than that of climax species (e.g. 0.003 in *Thuja plicata*). *P. menziesii*, a subclimax species, shows an intermediate  $r$  value (0.013) between these two ecologically different taxa. The absolute  $r$  value of *P. contorta* (-0.011) is only slightly lower than that of *P. menziesii*, although their replacement began almost simultaneously. Thus competition between these species was intense before the inflection point of *Pinus* curve 10,100 years ago. At this time, forest gaps became abundantly available for *Pseudotsuga*, as indicated by a peak of the diagnostic factor (the reciprocal of the pollen influx).

Key words: Logistic analysis — Plant population — Pollen influx — *Pseudotsuga menziesii* — Quaternary population ecology.

The Pacific Northwest is distinguished by a Mediterranean climate which permits various species of conifers to outgrow hardwoods with more limited stature and life span (Waring and Franklin, 1979). In particular, the Puget Lowland, located between the Cascades and the Olympic Mountains, is relatively dry, having about 1,000 mm of annual precipitation, most of which falls from September to April. This climatic regime encompasses cool-temperature coniferous forests consisting of *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* along with subordinate *Taxus brevifolia* (Franklin and Dyrness, 1973).

However, these forests were undoubtedly forced farther south between about 15,000 and 13,000 years ago, when the Puget Lobe of the Cordilleran ice sheet (during the Vashon Stade of the Fraser Glaciation) extended as far south as 46°47'N latitude (Fig. 1) (Crandell and Miller, 1974; Thomson, 1980). During the Fraser Glaciation on Mt. Rainier, mountain glaciers also grew and descended down valleys toward lowlands. They extended down to an altitude of some 300 m at the time of maximum development from about 25,000 to 18,000 years ago (the Evans Creek Stade) (Porter, 1976, 1977).

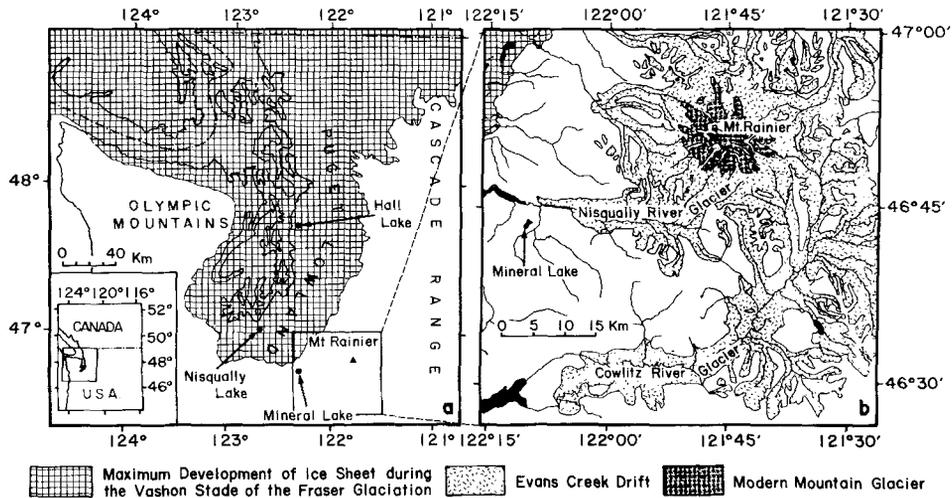


Fig. 1. Sketch map of the Pacific slope of Washington outlining the approximate cover of the Puget Lobe during the Vashon Stage of the Fraser Glaciation (a), and glaciers on Mt. Rainier during the Evans Creek Stage (b) (Crandell and Miller, 1974; Thornson, 1980). Mineral Lake is indicated on each map. Sites for Nisqually and Hall Lakes, from which a 13.3-m and a 12.1-m core were collected respectively, are also indicated; at each site a preliminary pollen diagram has been published (Tsukada, 1974; Tsukada, Sugita and Hibbert, 1981).

Pollen analysis should provide direct evidence of the effect of the Vashon advance and its subsequent retreat. This study describes the vegetational history around Mineral Lake ( $46^{\circ}43'N$  lat.,  $122^{\circ}10'W$  long.; alt. 443 m), located immediately south of Mt. Rainier, in response to the behavior of the continental and mountain glaciers and to the subsequent postglacial warming. Furthermore, in this short paper, we will examine late-glacial and early postglacial increasing and decreasing phases of fossil pollen assemblages by means of logistic analysis to assess meaningfully vegetational changes at the site.

#### Mineral Lake and Its Sediments

Mineral Lake lies approximately 15 km southeast of the maximum limit of the Puget Lobe of the continental Vashon ice, 6 km west of the Nisqually River glacial terminal, and 25 km north of the Cowlitz River glacial terminal, both of which originated from Mt. Rainier (Fig. 1). It yielded a 17.75-m core below 11 m of water. Eight  $^{14}C$ -dates determined are as follows: The 17.27–17.17 m level is  $17,500 \pm 400$  yr B.P. (Y-2662); the 16.55–16.45-m level,  $16,000 \pm 400$  (Y-2661); the 16.05–15.95-m level,  $14,550 \pm 220$  (QL-1276); the 15.75–15.65-m level,  $12,950 \pm 300$  (Y-2660); 12.90–12.80-m level,  $9,760 \pm 70$  (QL-1275); the 9.35–9.25-m level (immediately below the Mazama tephra),  $7,100 \pm 120$  (Y-2659); 9.15–9.05-m level (immediately above the Mazama tephra),  $6,800 \pm 180$  (Y-2658); and the 5.00–4.90-m level (just below the Mt. St. Helens' YN ash),  $3,700 \pm 120$  (Y-2657).

By using these dates, a plot of the age-depth relations shows four sedimentary phases which are expressed by the equations in parentheses ( $D$  is sediment depth in meters on the Y-axis, subtracting the thickness of the tephra layers described below, and  $t$  time in millennia on the X-axis), i.e. (1) a period of slow sedimentation rate ( $0.376 \text{ mm yr}^{-1}$ ) at the early phase of the lake development from ca. 19,000 to 14,000 years B.P. ( $D=10.42+0.38t$  for a layer from 17.75 to 15.75 m); (2) a shifting period of the sedimentation rate (from  $0.376 \text{ mm yr}^{-1}$  ca. 14,000 yr B.P. to  $1.276 \text{ mm yr}^{-1}$  ca. 11,000 yr B.P.) ( $D=-45.14+12.53t-0.89t^2+0.02t^3$  from 15.75 to 13.10 m); (3) a steady postglacial accumulation period ( $1.295 \text{ mm yr}^{-1}$ ) from ca. 11,000 to 100 years B.P. ( $D=0.14+1.30t$  from 13.10 to 0.20 m); and (4) an anthropogenic period of the rapid sedimentation rate ( $2.5 \text{ mm yr}^{-1}$ ) for approximately the last 100 years ( $D=0.08+2.50t$  for the top 0.20 m). The sharp increase in sedimentation rate from ca. 14,000 to 10,000 years B.P. resulted from favorable environmental conditions for organic production both in the lake and the surrounding upland; this ignition loss was doubled during this period.

The core contains four tephra units from Mt. St. Helens: M (17.165–17.160 m), two unnamed ones (the lower layer is here named FW; 16.730–16.715 m and the upper layer, GW; 16.695–16.605 m) and YN (4.89–4.88 m); and one from Mt. Mazama, O (9.24–9.16 m). The approximate date for each tephra fall is estimated by the curvilinear interpolation and extrapolation of the eight  $^{14}\text{C}$ -dates. The M tephra fall was ca. 17,400 years B.P., the unnamed Mt. St. Helens FW, 16,250 years B.P. and the GW, 16,200 years B.P., Mazama tephra, 6,950 years B.P., and the YN tephra, 3,650 years B.P.

### Pollen Influx for the Past 19,000 Years

The pollen diagram (Fig. 2) is divided into six major pollen assemblage zones, T, LI, LII, PI, PII and PIII (Tsukada *et al.*, 1981; Sugita and Tsukada, 1982). These zones are further divided into subzones by considering major key taxa (the left column of Fig. 2). The validity of this subzoning is shown by the difference of pollen deposition rate (PDR in  $\text{gr cm}^{-2} \text{ yr}^{-1}$ ) (Table 1). Here, the vegetation history in these zones is only briefly described to facilitate understanding logistic analysis of pollen abundance changes from late- to postglacial time.

*Zone T* (earlier than 16,300 yr B.P.; T stands for tundra) covers the middle part of the Fraser Glaciation (Crandell and Miller, 1974; Porter, 1977; Thornson, 1980) from the bottom of the core to ca. 16,300 B.P. The PDR is extremely low, being  $327 \pm 61$  (mean and standard error) ( $N=11$ ) in nonarborescent pollen (NAP) and  $173 \pm 44$  in arboreal pollen (AP), and the NAP percentage value is  $67 \pm 5$ ; for the percentage calculation, the basic sum includes all of pollen and spore types, but arborvitae, pine, alder and hazel pollen numbers are divided by four before being added to it. Grass (30–35%), sedge (15–20%), *Artemisia* (6–15%), *Salix* (2–10%) and *Betula* (2%) were of characteristic occurrence in this zone. *Polygonum bistortoides* and *Epilobium alpinum* types and *Valeriana*, which commonly grow in the alpine zone of the Pacific Northwest today, occurred frequently (the tundra elements are summed in the summary diagram

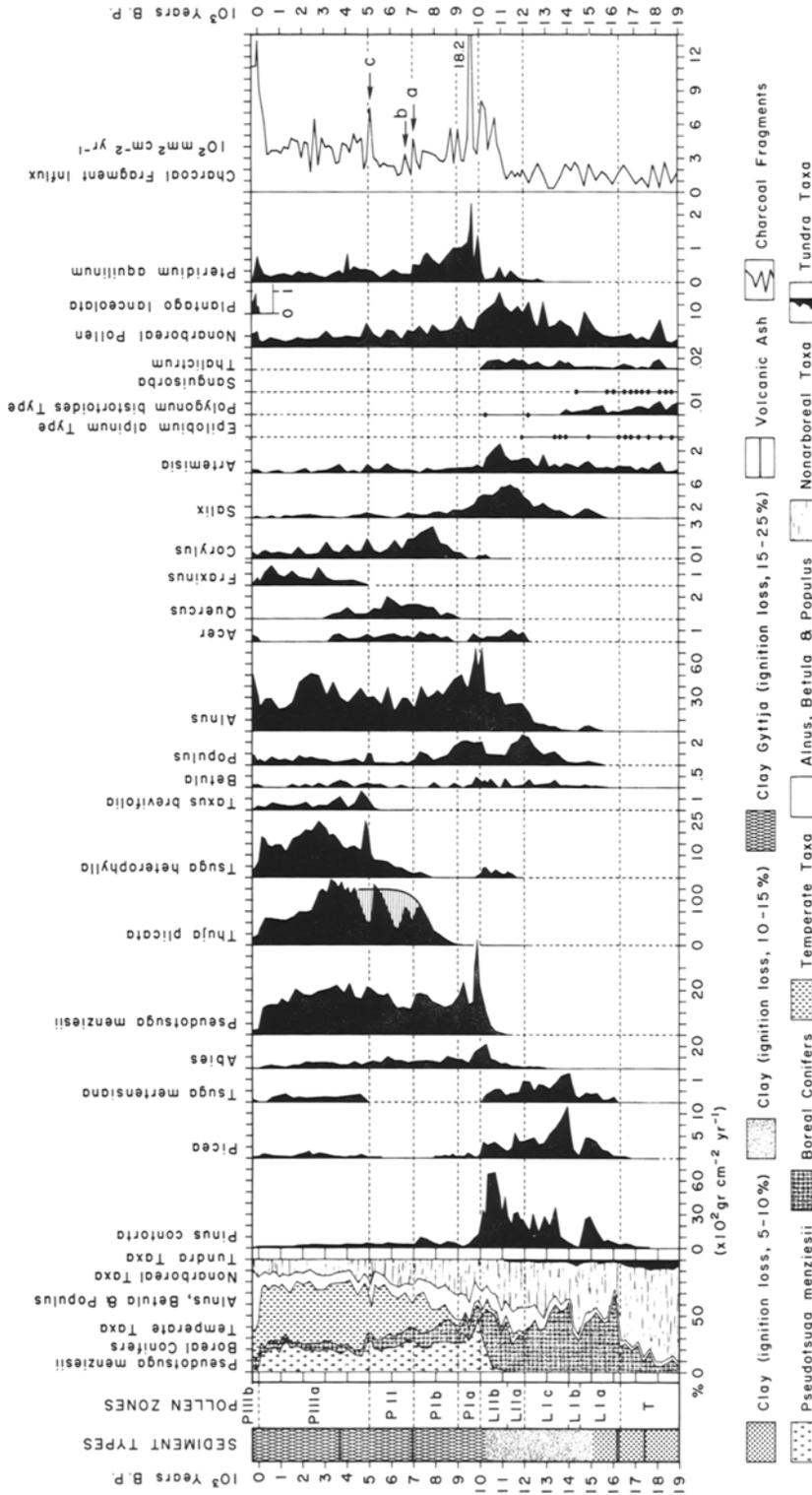


Fig. 2. The pollen influx diagram of a 17.75-m core collected from Mineral Lake, Washington. A smooth curve for *Thuja* is obtained by calculating the logistic equation in which  $r$  is 0.003 and  $K$ , 11,600 (Table 2). A summary pollen diagram in relative frequency is shown on the left column; in percentage calculation, the basic pollen sum includes AP, NAP and fern spores, but the original count of the large pollen producers, *Pinus*, *Thuja*, *Alnus* and *Corylus* is divided by four. Solid lines and dots (the latter are put only on records of *Epilobium*, *Sanguisorba* and *Polygonum*) indicate that the pollen influx value is  $20 \text{ gr cm}^{-2} \text{ yr}^{-1}$  or lower.

in Fig. 2). These assemblages indicate that the Mineral Lake area was surrounded by tundra vegetation at least earlier than 16,300 years ago. This conclusion is supported by the additional evidence that *Eurycercus glacialis*, a chydorid cladoceran species common in lakes of arctic tundra environments, was a dominant species in Mineral Lake until about this time (Jones and Tsukada, 1981).

Zone LI (16,300–12,000 yr B.P.; L stands for late-glacial) is distinguished by abundant pollen fallout of *Picea* ( $441 \pm 76$  gr cm<sup>-2</sup> yr<sup>-1</sup>; N=18) and *Pinus contorta* ( $1,492 \pm 280$ ). Even the NAP deposition rose to  $661 \pm 82$ , about a two-fold increase from that in the T zone due to somewhat increased productivity in LI time. A leaf of *Pinus contorta* is identified at the 14.35-m, and two attached to a fascicle, at the 13.95-m levels, implying strongly that this species along with spruce (probably *Picea engelmannii*) was prevalent during the late-glacial period. *Abies* and *Tsuga mertensiana* also began to increase significantly from the beginning of this zone (Fig. 2).

About 14,500 years ago, *P. contorta* sharply decreased from  $655$  gr cm<sup>-2</sup> yr<sup>-1</sup> to 19 between 15.95 and 16 m (ca. 14,500 yr B.P.), and *Picea* from 472 to 69 as well as total AP from 3,805 to 219. This level of decrease establishes the LIa/LIb zonal boundary. The sudden decline of *Picea* was not as much as that in *Pinus*, and the former began to increase about 300 years later, and attained an even higher level ( $651 \pm 117$ ) than before about 14,000 years ago (Fig. 2). The beginning of *Pinus* increase is also used for delineating the LIb/LIc boundary. *Pinus* reached the previous level in its abundance about 13,500 years ago, and maintained this value until 11,250 years ago (Fig. 2 and Table 1).

During the LIb period (14,500–14,000 yr B.P.), chronologically corresponding to the Vashon Stade, tundra plants increased percentagewise (NAP= $50 \pm 7.1\%$ ), but their PDR remained virtually the same as that in previous LIa and subsequent LIc times, and also the PDR of *Pinus* ( $132 \pm 41$ ), that in T time. These facts imply that while pine stands in valley floors were affected by the glacial advance, the tundra plants were not severely damaged around the lake. Since the recovery of *Picea* began late in LIb time, its PDR is much higher ( $248 \pm 143$ ), with higher standard error, than that of *Pinus* ( $132 \pm 41$ ). The reason that *Pinus* was more adversely affected than *Picea* was probably that these two taxa were preferentially growing in rather different habitats after the retreat of the Evans Creek glaciers; *Pinus* was on the fresh drift of the former glaciers, and *Picea*, on the better-developed soils on slopes and hills. The readvance of glaciers during the Vashon Stade was more or less taking the same course as before, and overrode pine-dominated stands. Stands of *Picea* on the unglaciated slopes and hills were able to restore the valley floors as soon as the glaciers retreated about 14,300 years ago near the Mineral Lake area. However, the establishment of *Picea* populations did not follow the modern successional sequence, i.e. from *Alnus* to *Picea* as observed at Glacier Bay, Alaska (Crocker and Major, 1955). *Picea* was in most cases invading tundra which had persisted for a long period of time, presumably improving nutrient levels in the soils (Davis, 1981). The spruce decline was probably due to the climatic warming, and pioneer tree taxa rapidly invaded newly created open habitats. This

Table 1. Averaged pollen deposition (gr cm<sup>-2</sup> yr<sup>-1</sup>) and charcoal

Pollen zones	<i>Pinus contorta</i>	<i>Picea</i>	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i>	<i>Thuja plicata</i>
PIIIb	115±9	34±3	439±26	828±46	2373±127
PIIIb <sub>2</sub>	117±32	33±5	263±29	547±56	1641±141
PIIIb <sub>1</sub>	114±9	34±4	486±21	902±41	2565±122
PIIIa	250±18	50±7	1662±92	1755±106	8617±759
PII	381±16	40±9	1509±120	524±84	7768±942
PI	516±51	66±7	1914±165	89±13	1949±568
PIb	542±61	57±10	1507±94	109±22	3873±903
PIa	493±83	74±11	2290±269	71±11	173±42
LII	3989±419	307±29	241±95	159±37	154±20
LIIb	4497±511	283±31	332±123	184±49	180±23
LIIa	2666±215	372±60	2±2	93±24	87±20
LI	1492±280	441±76	0±0	3±2	11±3
LIc	1988±405	651±117	1±1	4±3	16±6
LIb	132±41	248±143	0±0	0±0	4±2
LIa	1738±409	289±68	0±0	4±3	9±2
T	129±38	20±3	0±0	1±0	4±1

The rounded standard error,  $\sigma/\sqrt{N}$ , where  $\sigma$  is the standard deviation, and  $N$ , the B.P.; LI, 16,300–12,000 (LIa, 16,300–14,500; LIb, 14,500–14,000; and LIc, 14,000–10,000–7,000 (PIa, 10,000–9,000; and PIb, 9,000–7,000); PII, 7,000–5,000; PIIIa, 50 years).

pollen diagram (Fig. 2) seems to show that *Picea* invaded directly onto the tundra plant communities, and the vegetation was spruce-pine parkland in LIa (NAP=24±3.4%) and LIc (NAP=23±2%) times. Around the Mineral Lake area, *Alnus* and *Populus* began to increase almost simultaneously after *Picea* showed a declining trend about 12,500 years ago.

Zone LII (12,000–10,000 yr B.P.) begins with a rapid fall of *Picea* and *Tsuga mertensiana*, and in response to this, *P. contorta* increased further, reaching 3,989±419 (N=18). The PDR of *Tsuga heterophylla* rose considerably from 3±2 in LI time to 159±37 in LII time; it perhaps grew sporadically around the lake. This temporary abundance is also shown in pollen diagrams of Hall Lake (Tsukada *et al.*, 1981) and Nisqually Lake (Tsukada, 1974), suggesting that the late-glacial increase of the species was a wide-spread phenomenon in the Puget Lowland. *Abies* and *Alnus* also show a steady increase from the beginning of this zone. The NAP deposition rate was doubled from 661±82 to 1,185±55. Characteristic features of two tentative subzones are that (1) LIIa (ca. 12,000–11,250 yr B.P.) shows no sign of *Pseudotsuga* growth around the lake; (2) LIIb (ca. 11,250–10,000 yr. B.P.), the first arrival of a few *Pseudotsuga* trees, followed by the sudden expansion, and the rise of *Abies* (Fig. 2). Table 1 represents clearly the difference of *Pseudotsuga*'s PDR, i.e. 2±2 in LIIa time and 332±123 in LIIb. *Pteridium aquilinum* shows almost a tenfold increase from LI to LII time, from 17±7 to 169±28. The NAP percentage is still high (16±1%). The abundant NAP occurrence would suggest that the vegetation was *Pinus-Alnus* woodland, and associated with some *Pseudotsuga* after LIIb time. *Abies* and *Picea* were also scattered in moist places. At the end of the LII period, *Pinus contorta* and *Picea* became insignificant in the vegetation.

fragment deposition ( $\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$ ) rates for each discrete pollen zone

<i>Alnus rubra</i>	<i>Pteridium aquilinum</i>	AP	NAP	Charcoal fragments	N
3310±224	614±50	7394±187	477±23	13.53±0.75	24
4825±460	215±35	7727±675	519±42	8.06±0.44	5
2911±161	719±31	7306±166	466±26	14.96±0.59	19
3612±198	333±29	16787±968	335±24	3.97±0.20	33
2767±290	310±45	14072±1281	391±32	2.67±0.23	13
4220±264	1026±99	9863±703	619±38	4.42±0.68	25
3740±273	718±72	10985±1148	597±40	3.64±0.50	12
4664±413	1310±138	8828±793	638±65	5.14±1.21	13
3037±301	169±28	8872±675	1185±55	3.21±0.50	18
3271±402	176±34	9858±770	1227±69	3.80±0.62	13
2428±34	152±52	6307±248	1077±66	1.65±0.15	5
347±99	17±7	2547±403	661±82	1.50±0.19	18
619±168	32±13	3688±457	857±117	1.34±0.33	8
35±11	1±0	515±220	384±83	2.03±0.30	4
193±96	10±6	2380±587	584±134	1.37±0.32	6
6±2	0±0	173±44	327±61	1.48±0.27	11

number of separate counts (levels), is attached. Zone T covers ca. 19,000–16,300 yr (12,000); LII, 12,000–10,000 (LIIa, 12,000–11,250; and LIIb, 11,250–10,000); PI, 5,000–100; and PIIIb, after 100 (PIIIb<sub>1</sub>, 100–20; and PIIIb<sub>2</sub>, approximately the last

*Zone PI* (10,000–7,000 yr B.P.: P stands for postglacial) is labeled by an early postglacial *Pseudotsuga-Alnus* (Sugita and Tsukada, 1982) (NAP=15.0±1.5%) which is a transitional vegetation from late-glacial boreal parkland to mid- and late-postglacial cool-temperature coniferous forests. *Pseudotsuga*, which began to increase at the end of LII time, reached a maximum level early in the PI period. The colonization of the species was extraordinarily rapid; and its pollen deposition rate rose from 11 about 11,250 years ago to 4,306 about 9,900 years ago.

The open woodland community of *Pseudotsuga*, i.e. only a few hundred trees per hectare, existed in the Puget Lowland during the early and mid-Holocene (Heusser, 1978). It is reasoned that in an open woodland, crown volumes and consequently production of staminate cones increase, and that an isolated tree produces more pollen than a tree in the closed forest (Faegri and Iversen, 1975).

*Pseudotsuga* pollen could be dispersed to the lake from the crown of its tall trees which thrust above the general height of alder forests (Tsukada, 1982a). No obstacle was found for the liberation of *Pseudotsuga* pollen at that time. Meanwhile, the pollen influx data (Table 1) suggest that the tree frequency of *Pseudotsuga*, which was about 55% in lowland coniferous forests in the Mineral Lake area before man's disturbance of the forest (Tsukada, 1974) was able to produce as much pollen as in the PI period. This means that the open space in the *Pseudotsuga* woodland equals or is slightly more than the area which was occupied by *Tsuga heterophylla* and *Thuja plicata* just before European settlement in the area.

*Pseudotsuga* populations suddenly declined about 9,700 years ago. Forest fires were associated, and charcoal fragments and *Pteridium* spores show maximum occurrence, i.e. the former is 18.27  $\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$  (Fig. 2), and the latter, 2,397  $\text{gr cm}^{-2} \text{yr}^{-1}$ ;

their average values for the PIa zone are  $5.14 \pm 1.21 \text{ mm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$  ( $N=13$ ), and  $1,310 \pm 138 \text{ gr cm}^{-2} \text{ yr}^{-1}$ , both of which are the highest throughout the late-glacial and postglacial periods. Red alder, a pioneer species, shows maximum development during this period, as recorded by its abundant pollen occurrence. Forest fires were frequent throughout this region, and occurred several times near the site in the last 12,000 years, since large charcoal fragments (over 250 microns long) were found at each peak (the right column of Fig. 2). Generally, their individual size is less than  $50 \mu$  when the forest fire occurs in distant areas (Tsukada, unpublished).

*Tsuga heterophylla* was still insignificant throughout this period after declining about 10,000 years ago in LII time. *Thuja plicata* began to rise exponentially from the middle of this zone at which the PIa/PIb zonal boundary is placed (9,000 yr B.P. at Mineral Lake). It was preferentially occupying moister places such as edges of lakes and along stream banks. In PIb time, *Pseudotsuga* and *Pteridium* were slightly less abundant than before. *Quercus* and *Corylus* show small increases at the boundary but their pollen are probably from a distant origin in the more dry Nisqually area (Fig. 1) (Tsukada, 1974).

Zone PII (7,000–5,000 yr B.P.) opens with the beginning of the gradual rise of *Tsuga heterophylla*. *Abies* still maintained a moderate population level. *Pteridium* and *Alnus* declined ( $\text{NAP}=8.0 \pm 1.1\%$ ), indicating that forest closure was increasing. *Pinus monticola* grew to some extent (50–70 PDR; it is not shown in Fig. 2 and Table 1) during this period. Although the substantial rise of *Thuja plicata* is seen ( $7,768 \pm 942$ ), *Pseudotsuga* did not decrease much in its pollen production ( $1,509 \pm 120$ ). *Tsuga* together with *Thuja* was further increasing in response to *Alnus* decline but without affecting *Pseudotsuga* population heavily. About 5,000 years ago, a local forest fire destroyed *Thuja* stands extensively, and some increase of *Alnus* and the sudden explosive rise of *Tsuga* support the assertion that *Thuja* was growing in the moist watershed of the Mineral Lake area.

Zone PIII (after 5,000 yr B.P.) is the final developmental stage of modern climax forests. *Tsuga heterophylla* was firmly established after showing a considerably long phase of population growth in PII time. It superseded *Pseudotsuga* in the late Holocene (Hansen, 1947). However, around the Mineral Lake site, *Tsuga* pollen did not exceed *Pseudotsuga* significantly. The first continuous appearance of *Taxus* and *Fraxinus* was also from this period. Due to the cooling climate of the neoglacial period, furthermore, populations of subalpine species such as *Picea* and *Tsuga mertensiana* increased at higher elevations, and thus their pollen grains were continuously recorded during the PIII period.

The total pollen deposition increased, especially during the first two-thirds of this period. The deposition rate is forcibly influenced by *Thuja* even after its number is divided by four before the percentage calculation (Sugita and Tsukada, 1982), as large fluctuations of the total PDR roughly correspond to those of *Thuja*. This fact further suggests that *Thuja* was abundant along the lakeshore. The forest was further closed in PIII time until man's deforestation began about 120 years ago. So, NAP dropped to

the lowest level ( $6.0 \pm 0.3\%$ ) since the last glacial period. We must now realize that the codominance of three major conifer species (*Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* along with a newly arrived species *Taxus brevifolia*) has a history of only approximately the last 5,000 years.

The pollen accumulation of climax forest species declined dramatically in the uppermost part of the PIII zone. This decline was caused by intensive lumbering initiated by Euro-American settlers from the late 1800's to 1900's (Davis, 1973; Tsukada, 1974). This change establishes the zonal boundary, PIIIa and PIIIb. PIIIa is characterized by the *Pseudotsuga-Tsuga-Thuja* climatic climax forest community, and PIIIb, by the man-induced *Alnus* woodland associated with abundant bracken ferns, and by the first introduction of *Plantago lanceolata*, a species endemic to Europe. The increase of *Pteridium* and *Alnus* was markedly significant; the abundance of the former ( $719 \pm 31$ ) preceded slightly that of the latter ( $4,825 \pm 460$ ). This phenomenon distinguishes between subzones PIIIb<sub>1</sub> and PIIIb<sub>2</sub> (Table 1). The latter value is almost the same order of magnitude as that in the woodland during the PI period, suggesting that alder forests in PI time were as abundant as those of today.

### Logistic Rise and Decline of Pollen Abundance

Pollen analysis is the method predominantly employed to quantitatively reconstruct succession in past vegetation, and climatic inferences are then drawn from these reconstructions. The reconstructions themselves are based on the assumption of uniformitarianism of natural phenomena, i.e., the present is the key to the past. With this concept in mind, a number of pollen diagrams and climatic curves covering the late Quaternary have been produced in many parts of the world. However, pollen analysis is still far from an exact science unless the quantitative interpretation of pollen assemblages is made in terms of vegetation cover or biomass, and population ecology. Key features of the dynamics of populations often can only be perceived from a long-term perspective, one that immensely exceeds the lifetime of investigators. Pollen analysis is, in this sense, the powerful science with which to clarify the dynamic nature of plant populations through a long time of period.

#### *Positive Population Growth*

Pollen successions which show sigmoid growth-curve are countless. Some examples of these are *Pinus strobus* in the eastern United States (Brubaker, 1975; Craig, 1972), *Pinus sylvestris* in Finland (Hyvärinen, 1975, 1976), *Picea jezoensis* in central Japan (Tsukada, 1967). *Quercus* and *Fagus* at Lake Nojiri, Japan (Tsukada, 1972), *Ambrosia* and Chenopodiaceae around Lake Superior (Maher, 1977), and many others. Recently, postglacial changes in the abundance of *Cryptomeria japonica* pollen after its trees were established in near-optimal growing conditions were first approximated by an ordinary logistic equation (Tsukada, 1981, 1982b),

$$\frac{1}{p} \cdot \frac{dp}{dt} = r \left( 1 - \frac{p}{K} \right) \quad (1)$$

where  $p$  is the pollen influx number ( $\text{gr cm}^{-2} \text{ yr}^{-1}$ ) at a given time  $t$  ( $\text{yr}$ );  $r$ , the intrinsic growth rate ( $\text{yr}^{-1}$ ); and  $K$ , the upper limit of a population (in pollen analysis, the maximum carrying capacity in  $\text{gr cm}^{-2} \text{ yr}^{-1}$ ). This equation shows the relative growth rate to be a linear function of size, with gradient  $-r/K$  and intercept  $r$ . Clearly, relative growth rate is nowhere constant, but declines linearly with increasing population size. The growth function obtained by solving the differential equation is

$$p = \frac{K}{1 + ke^{-rt}} \quad (2)$$

where  $k=e^\beta$ ,  $\beta$  being the constant of integration. The equation is useful for describing the population growth of an organism in terms of biological parameters (Colinvaux, 1973; Hallam and Clark, 1981; Tsukada, 1982b), although it has some deficiencies due to several assumptions established to simplify the equation (May, 1981; Pielou, 1977; Murray, 1974).

A pollen assemblage of anemophilous species contains pollen from two major plant sources, i.e. that derived from nearby vegetation, and that from more distant sources. Thus, fossil pollen succession shows that a low frequency is observed long before the beginning of a sigmoid rise. If one applies this equation to negative population growth for the sake of comparison with synchronously increasing species, the lower asymptote of the decreasing species approaches zero; this is an inherent characteristic feature of the equation. Thus, Eq. 2 can be rewritten by adding the value of the lower asymptote  $K'$  [in pollen analysis, representing pollen and spores derived from distant refugial populations and/or from a few trees sparsely scattered in nearby source forests; generally less than 5% of overrepresented species in the forest vegetation, and thus consisting of two different populations in the equation (Tsukada, 1982b)], as,

$$p = \frac{K}{1 - ke^{-rt}} + K' \quad (3)$$

In pollen analysis, the intrinsic growth rate should be determined by the reproductive strategy (including germination and growth) of individual species in natural plant communities, which is strongly influenced by environmental conditions. Among physical environments, climatic and soil conditions, and among biological, intra- and interspecific competition, are the important factors that control the growth of plant population. If these conditions are optimal, the  $r$  value of an increasing species becomes high. In a declining species, the larger the absolute  $r$  value, the more severe are the environmental conditions. The asymptote of a plant species is regulated by availability of environmental resources, and that of pollen, by the size of plant population, physical environmental conditions (e.g. wind speed, size of catchment basin), pollen productivity, and pollen dispersion ability.

However, it is difficult to distinguish factors influencing the  $r$  and  $K$  values in fossil pollen assemblages. For example, in a declining population, it is not yet

known if the  $r$  value is specific to biological effect (e.g. man's disturbance or disease on plants) or even to climate. At present, when applying the logistic analysis to changing fossil pollen assemblages, the meaning of calculated  $r$  and  $K$  values must be sought from comparative studies of the invading and declining species together.

Let us first examine logistically the increasing phase of the pollen of major species at the lake. Table 2 shows four constants for Eq. 3, and the curves of selected species are drawn by using these constants (Fig. 3). The  $r$  value is the main concern in this discussion. Among the boreal species, *Pinus contorta* was the first invading species in the tundra vegetation 17,500 years ago, and it increased in abundance again after the retreat of the Vashon advance 14,000 years ago; both increases (though not shown in Fig. 3) were sigmoidal, and the  $r$  values are high (0.0065 for the former and 0.0040 for the latter), suggesting that the initial colonization of the species was rapid because there was no competition at that time. The  $r$  value for the

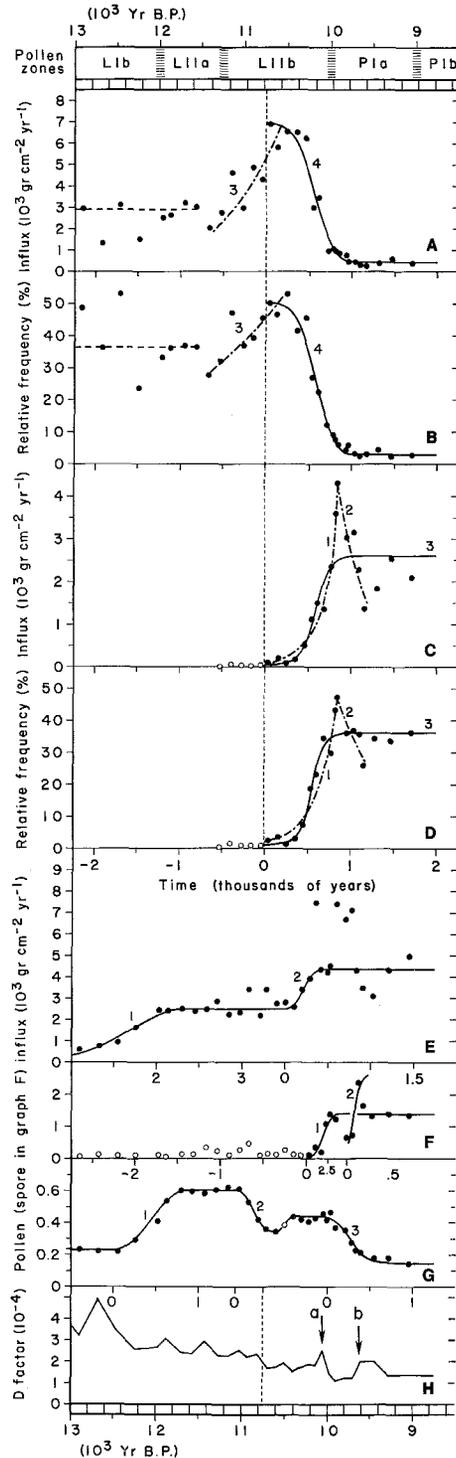


Fig. 3. Results of logistic and diagnostic factor analyses of rising and declining phases of major selected species at Mineral Lake from late-glacial to early postglacial time. Four empirical constants of the ordinary logistic equation are listed in Table 2. Graph A=*Pinus contorta* (pollen influx in  $\text{gr cm}^{-2} \text{yr}^{-1}$ ); B=*P. contorta* (%); C=*Pseudotsuga menziesii* (influx); D=*P. menziesii* (%); E=*Alnus rubra* (influx); F=*Pteridium aquilinum* (influx); G=*Salix* (influx); and H=the diagnostic D factor (the reciprocal of the total pollen influx, in which *Pinus*, *Thuja* and *Alnus* pollen influx numbers are divided by four. The beginning of pollen increase is set at year zero (Table 2).

Table 2. Four constants in an ordinary logistic equation (Eq. 3) for changes of pollen (spores in *Pteridium aquilinum*) assemblages at Mineral Lake, Washington

Species Name	Date of Yr Zero	$r$	$K$	$K'$	$k$	Graph in Fig. 3
<i>Pinus contorta</i> 1	17,500	0.0065	2845	50	$1.61 \times 10^6$	—
<i>Pinus contorta</i> 2	14,300	0.0040	2383	50	$3.78 \times 10$	—
<i>Pinus contorta</i> 3	11,100	0.0040	10712	50	3.23	—
<i>Pinus contorta</i> (%)	11,100	0.0020	66	5	1.07	—
<i>Pinus contorta</i> 4	10,750	-0.0113	6430	400	$3.16 \times 10^{-3}$	A
<i>Pinus contorta</i> (%) 4	10,750	-0.0096	46	5	$6.99 \times 10^{-3}$	B
<i>Pseudotsuga menziesii</i> 3	10,750	0.0133	2564	40	$2.13 \times 10^3$	C
<i>Pseudotsuga menziesii</i> (%) 3	10,750	0.0146	35	1	$2.68 \times 10^3$	D
<i>Abies</i>	14,300	0.0017	183	25	$1.29 \times 10$	—
<i>Picea</i> 1	16,300	0.0039	499	25	$3.00 \times 10$	—
<i>Picea</i> 2	14,300	0.0197	980	25	$2.47 \times 10^3$	—
<i>Tsuga mertensiana</i> 1	16,500	0.0015	174	5	$3.78 \times 10$	—
<i>Tsuga mertensiana</i> 2	14,500	0.0222	115	5	$4.99 \times 10^2$	—
<i>Thuja plicata</i> 1	9,000	0.0030	11607	80	$5.37 \times 10$	—
<i>Thuja plicata</i> 2	6,500	0.0031	15770	80	5.99	—
<i>Thuja plicata</i> 3	5,100	0.0029	16037	80	4.91	—
<i>Alnus rubra</i> 1	14,000	0.0039	2460	100	$5.02 \times 10^2$	E
<i>Alnus rubra</i> 2	10,500	0.0062	4500	100	9.49	E
<i>Salix</i> 1	13,150	0.0034	625	23	$3.05 \times 10$	G
<i>Salix</i> 2	11,700	-0.0175	264	340	$5.73 \times 10^{-3}$	G
<i>Salix</i> 3	10,400	-0.0113	300	140	$1.98 \times 10^{-2}$	G
<i>Pteridium aquilinum</i> 1	10,250	0.0241	1324	30	$1.16 \times 10^2$	F
<i>Pteridium aquilinum</i> 2	9,800	0.0256	2562	30	8.30	F

In this table,  $r$ —the intrinsic growth rate of pollen abundance;  $K$ —the upper asymptote of pollen or spore influx  $\text{gr cm}^{-2} \text{yr}^{-1}$ , or relative frequency;  $K'$ —the lower asymptote which is defined to be low but constant occurrence of pollen or spores which are principally derived from distant populations and/or a few trees scattered nearby source forests; and  $k$ —the integration constant. The constants of *Pinus* and *Pseudotsuga* are shown both in influx data and in relative frequency; the latter is only indicated after the species name. The number listed after the species name corresponds to that indicated for each curve in Fig. 3.

last major rise of the species was the same as that of the 2nd rise (Table 2); in this last instance the space became available for the growth of the species due to improved environmental conditions, but intra- and interspecific competition prevented the rapid growth of *P. contorta*. It was an increase in the abundance of the species already present on the landscape, not the invasion of a new one (the initial pollen abundance for the third rise was  $2,472 \pm 723$ ;  $N=9$ ; from 13,000 to 11,300 yr B.P.). Thus the population could quickly reach the maximum asymptote even in the low  $r$  value.

The late-glacial increase of subalpine climax species after the first arrival of their trees at the site from glacial refugia is characterized by moderate  $r$  values (e.g. *Picea*—0.0039, *Abies*—0.0017, and *Tsuga mertensiana*—0.0015). The  $r$  values were almost the same as those of other temperate climax species (Tsukada, 1982a), because not only environmental conditions were already favorable for the growth of these species, but because competition with other species (mainly *Pinus contorta*) was rather keen. Some uncertainty, however, remains with regard to logistic analysis of these species. In this analysis, the expected asymptote is not clear because these species were suddenly

decimated by the Vashon glacial advance. Additional analysis is needed for the late-glacial rising phase of the boreal species at sites where the invading trees were not directly influenced by the glaciation. The rise of *Picea* ( $r=0.020$ ) and *Tsuga mertensiana* ( $r=0.022$ ) was much faster after the retreat of the Vashon ice than that in the initial populations, simply because environmental conditions were optimal for the growth of both species after 14,300 years. It was warmer than before the Vashon advance, and open spaces were abundantly available because *P. contorta* did not prevent their expansion on unglaciated hills (Sugita and Tsukada, 1982).

*Alnus rubra* first arrived at the site 15,300 years ago, reaching  $454 \text{ gr cm}^{-2} \text{ yr}^{-1}$  just before a sudden crash 14,500 years ago. The next increase of the *Alnus* populations, which began 14,000 years ago, was not quick ( $r=0.0039$ ) and the asymptote is low ( $2,460 \text{ gr cm}^{-2} \text{ yr}^{-1}$ ). It was still too cold for the rapid, full expansion of the species. However, by 10,500 years ago, the climate was sufficiently improved for the third *Alnus* rise (Curve 2) to be rapid ( $r=0.0062$ ), as would be expected for a pioneer species. During the second rise of *Alnus*, two peaks are observed far above the general trend of the curve for a short interval, i.e. the first was in the midst of the *Pinus* decline (10,150 yr B.P.), and the second, after the complete decimation of pine forests 9,900 years ago. Analytical levels are too few to calculate reliable constants for the logistic equations incorporating these peaks, but the rises should be characterized by extraordinarily high  $r$  values.

*Pseudotsuga* also has a high  $r$  value (0.0146 in relative frequency and 0.0133 in influx). The  $r$  value is higher when calculated for relative frequency than it is for the influx rate. The reason for this is that the percentage change reflects increases and decreases of not only the species subject to the logistic analysis, but also others on the landscape. *Pseudotsuga*, in this case, quickly increased in abundance by replacement of *Pinus contorta*. This period coincides with the middle part of the logistic growth phase of *Pseudotsuga*. *P. contorta* further declined. As soon as *P. contorta* reached the lower asymptote, populations of other postglacial species (mainly *Pteridium aquilinum*) were simultaneously increasing along with *Pseudotsuga*. Thus, despite the fact that it was rising in real pollen production, the relative pollen frequency of *Pseudotsuga* failed to show an increasing trend. As a result of this, pollen of the species only appears to have reached an asymptotic level in relative frequency.

The observed changes of *Pseudotsuga* pollen abundance differs significantly from the calculated logistic curve (Fig. 3C, D; Table 2). The population rise of *Pseudotsuga* was so rapid, and its decline was so sudden before reaching a stable asymptote, that the increasing and decreasing phases can be approximated separately by exponential equations. The positive growth rates (Curve 1 in Fig. 3C, D) are 0.0045 in relative frequency and 0.0053 in influx rate, and the negative rates (Curve 2),  $-0.0016$  and  $-0.0033$ , respectively. The growth rate in the exponential equation is much lower than that in the logistic equation, because the former is not controlled by the asymptote.

The logistic curve indicates that it took approximately 1,000 years for *Pseudotsuga* to attain the asymptote level of maximum stable pollen productivity and influx, and the

population crash occurred at this time. This time period corresponds closely to the natural longevity of the species (Franklin and Dyrness, 1973), implying that the initial tree populations of the same age class spread on the landscape, and almost suddenly died out after the completion of their life-span. It is worth noting that *Pseudotsuga* cannot reproduce below a closed canopy forest. However, it is not denied that forest fires indicated by a large peak of charcoal fragments ( $1826 \text{ mm}^2 \text{ cm}^{-2} \text{ yr}^{-1}$  9,700 years B.P.) in Fig. 2 were the main causal factor for the sudden decline of *Pseudotsuga* populations.

*Pteridium* began to invade the vicinity of Mineral Lake about 13,000 years ago (Fig. 2), but showed no significant increase until 10,250 years ago. It began to increase with extraordinary speed at the end of the *Pinus* decline, and reached its first peak in the midst of the *Pseudotsuga* rise. This suggests that pockets of open space suitable for *Pteridium* were scattered in the early postglacial *Pseudotsuga* forests. *Pteridium* then declined drastically (Fig. 3F), as *Pseudotsuga* re-expanded to reach a stable population of carrying capacity immediately after its initial population crash. The  $r$  value of *Pteridium* is 0.0024 for the first rise, and 0.026 for the second.

*Thuja plicata* shows two major sudden declines due to forest fires (indicated by small peaks of charcoal fragments on the far right column of Fig. 2) 7,100 years ago (Arrow a), 6,700 (Arrow b) and 5,200 (Arrow c). After each decline of the species, it immediately increased asymptotically. This pattern is very similar to a theoretical population growth of mixed  $r$ - and  $K$ -phases in natural environments with disasters and resource limits (Harper, 1977). The  $r$  values for major asymptotic rises, i.e. the initial, 9,000 yr B.P.; the second, 6,500 yr B.P.; and the third, 5,100 yr B.P., were essentially identical (0.003) (Table 2; the  $r$  value for the small rise starting 7,000 yr B.P. was not calculated). In the last two instances *Thuja* still had significant population stocks ( $2,257 \text{ gr cm}^{-2} \text{ yr}^{-1}$  for the 2nd rise and 2,713 for the 3rd) nearby at the beginning of each rise, but the slopes were not influenced by different, initial population sizes represented by fossil pollen. Thus, integrated biological and climatic environments did not greatly change for the growth of *Thuja* from the first invading time 9,000 years ago to the early part of asymptotic reach in the third rise 4,000 years ago. However, the relatively moist modern climate did not prevail until *Tsuga heterophylla*, which is presumed to be a rapidly migrating species, began to immigrate into the *Pseudotsuga*-*Thuja* forest 7,000 years ago. The intrinsic growth rate of 0.003 is a plausible value for a postglacial climax species. Thus, if one uses this value and there were no forest disturbance, *Thuja* would have increased following the smooth curve shown in Fig. 2.

Here, one should also note that the  $r$  value is not affected by different pollen production rates inherent among different plant taxa. Despite the fact that the *Thuja* pollen influx number is divided by four to approximate its tree abundance due to high pollen production per unit vegetation cover (Tsukada *et al.*, 1981), the  $r$  value is still 0.003, which is exactly the same as that calculated by employing the original influx number (Table 2). This is one of the important characteristic features of logistic analysis as applied to pollen assemblages. Therefore, this analysis should provide

critical information on the population dynamics of the total pollen-bearing biomass in a given area, but is independent of different pollen productivities of individual species. If the  $r$  value and the time required to reach the asymptotic level in pollen influx rates of two different species is identical, then the pollen productivity becomes the only controlling factor determining their respective asymptotes, provided that the accumulation rate of pollen is proportional to the productivity.

### *Population Decay*

In pollen succession, some taxa decline either rapidly or gradually, as others increase in abundance. The declining trend of an observed pollen assemblage is reasonably approximated by the survival and/or finite difference functions. However, in particular, the rapid decrease of boreal species at the end of late-glacial time in temperate regions is one of the noteworthy features that deserves critical mathematical analysis. In nature, the decline of some fossil pollen taxa likely follows a reverse sigmoidal curve which is merely a mirror image of that of the asymptotically increasing population. It is also imperative to obtain  $r$  values for declining pollen assemblages which can be meaningfully compared with those of the simultaneously increasing species on a basis of the absolute value of the intrinsic negative growth rate. One can then look into niche availability, (Hutchinson, 1957; Whittaker *et al.*, 1973) and see whether or not an increasing species was actively taking over niches of decreasing species. To obtain the logistic constants of decreasing species, therefore, one can use the same ordinary logistic equation as defined previously, but setting the beginning of the decline from the upper asymptote as year zero, and the  $r$  value negative, as the abundance begins to decline. This is a workable assumption because seed germination rates and maturing rates of seedlings in established forests are lower than in initial populations, and thus the population declines asymptotically, reaching a final equilibrium state with the environment.

The calculated fall of *Pinus contorta* began slightly before reaching the asymptote. This is because the values of maximum occurrence from 10,750 to 10,500 years B.P., whose average is presumed to be the asymptote, had to be used for the logistic calculation of both increasing and declining abundances, although the lower asymptote is higher in the former than that in the latter. In Fig. 3A and B, the final rise of the species (Curve 3) is approximated by the exponential equation for both pollen influx and relative frequency, and the logistic constants are given in Table 2.

It can be clearly seen, however, that the onset of unidirectional decline of *Pinus* was almost at the same time as that of the *Pseudotsuga* rise, and the decline was so dramatic that the negative  $r$  value was high ( $-0.0113$  in pollen influx and  $-0.0096$  in relative frequency; Fig. 3A, B, Table 2), but it did not reach a final lower asymptotic level even when *Pseudotsuga* attained its peak. The fact that the absolute  $r$  value of *Pseudotsuga* is slightly higher than that of *P. contorta* indicates that even though the latter species was contributing abundant pollen into Mineral Lake sediments in the latest late-glacial period, scattered open spaces for *Pseudotsuga* were still available when it arrived at the site. However, *Pseudotsuga* was not able to rise in its population size

immediately because it could not compete efficiently with quickly increasing *P. contorta*. The decline of *P. contorta* was probably independent of the invasion of *Pseudotsuga*; it was set by the negative  $r$  value about 10,750 years ago, which in turn was fixed by threshold conditions imposed by the warming climate. Beyond the midpoint of the declining logistic curve of *Pinus*, the diagnostic factor D (the reciprocal of the pollen influx at each analytical level; Tsukada, 1982a) shows a conspicuous peak (indicated by Arrow a in Fig. 3H) about 10,100 years ago, just before *Pseudotsuga* attained its maximum abundance. This peak also implies that pine populations indeed continued to fall steeply before *Pseudotsuga* occupied the open space after 10,100 years ago. Another rise of the D factor (Arrow b) was caused by the sudden decline of *Pseudotsuga* and *Alnus* pollen 9,700 years ago.

*Salix* shows two stepwise declines (Fig. 3G), although they are hidden in the percentage diagram (Tsukada *et al.*, 1981). The first logistic decline ( $r=-0.018$ ) of the species was when *Pinus* was increasing. *Salix* increased slightly together with *Pseudotsuga* 10,750 years ago, but began to decline when *Pseudotsuga* was reaching its early postglacial maximum abundance. Thus, *Salix* populations were affected by available niches which were mainly determined by the coverage of *Pinus* and *Pseudotsuga*.

Changes of fossil pollen abundance are diversely expressed by the influx value, yet logistic analysis shows that pioneer species (as  $r$ -strategists) have higher  $r$  values than climax species (as  $K$ -strategists). The reason is clearly because the pioneer species have a faster reproductive cycle than the climax species. For example, *Pteridium* not only produces an enormous number of spores per frond in open habitats, but it also effectively reproduces by means of rhizomes once the plant is established. Since the intrinsic growth rate is high, the climatic tolerance range is wide, and the reproductive cycle begins with minute spores which can be easily carried by wind, the species complex has become a typical  $r$ -strategist. However, climax species invade a site after the establishment of pioneer species, in these examples during the early and mid-postglacial periods, and so must compete with other invading climax species. The climax species have longer life-spans than pioneer species and also emit pollen during the later years of their reproductive cycle.

### Conclusions

The pollen influx sequence of a 17.75-m Mineral Lake core spanning the last 19,000 years indicates two intervals of tundra vegetation. The earlier tundra period (>19,000–16,300 yr B.P.) around Mineral Lake corresponds to the latter part of the Evans Creek of the Fraser Glaciation (ca. 25,000–17,000 yr B.P.). Boreal coniferous forests (consisting initially of *Pinus contorta*, and after 16,300 years B.P. *Abies*, *Picea* and *Tsuga mertensiana* immigrated into this monospecific pine forest) were temporarily established before the second short episode of tundra environments (ca. 14,500–14,000 yr B.P.). This period corresponds to the maximum Vashon ice advance in the Puget Lowland.

The developmental and declining phases of fossil pollen abundances from the late-glacial through postglacial periods basically follow logistic law. Application of logistic analysis to fossil pollen sequences is a powerful method for assessing meaningfully these vegetational changes. The intrinsic growth rate ( $r$  in  $\text{yr}^{-1}$ ) is clearly related to  $r$ - and  $K$ -strategists. The  $r$  value of pioneer species is higher than that of climax species.

*Pseudotsuga menziesii* invaded scattered open spaces which were initially available in the late-glacial *Pinus contorta*-dominated forests, as indicated by a high diagnostic factor earlier than 10,750 years ago. The decline of *P. contorta* was probably determined by the late- and postglacial warming climate. The  $r$  value for declining *Pinus* pollen influx is  $-0.0113$ , which as an absolute value is slightly lower than that of the invading species, *Pseudotsuga* ( $0.0133$ ), indicating that both species were intensively competing for the space. At the inflection point (ca. 10,100 yr B.P.) of logistically declining *Pinus* forests, the diagnostic factor shows a conspicuous peak. This is because *Pinus* was reaching the lower asymptote, and suddenly released space for the growth of *P. menziesii*. *Pseudotsuga*, *Alnus* and *Pteridium* were dominant vegetational components in early postglacial time (pollen zone PI), but the climate favorable for the growth of cool-temperate conifers such as *Tsuga heterophylla*, *Thuja plicata*, *Pseudotsuga menziesii*, and *Taxus brevifolia* began about 7,000 years ago, and full development of the modern lowland coniferous forests was in the last postglacial PIIIa period, simply because the former two climax species have low  $r$  values requiring a long period of time to reach their respective asymptotic levels. Since they reached their own levels, the natural forest community has been stable for the past 5,000 years.

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