POLLEN TRANSPORT AND REPRESENTATION IN THE COAST MOUNTAINS OF BRITISH COLUMBIA

by

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POLLEN TRANSPORT AND REPRESENTATION

IN THE COAST MOUNTAINS OF BRITISH

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ABSTRACT

The study attempts to identify important variables affecting the quantitative relationship between dispersed pollen and the composition of vegetation surrounding two lakes in a coastal forest of British Columbia. Aerial and fluvial pollen influxes were recorded approximately bi-weekly in 22 samplers from March 15, 1977 to September 13, 1978 at Marion Lake, a medium-sized lake with a major inflowing stream and at Surprise Lake, a small enclosed basin. In addition, 25 surface samples were analyzed from Marion Lake and 4 from Surprise Lake to compare the relative pollen frequencies of trees with percentage basal area of each taxon around the lakes, as estimated from about 900 sampling points. A short sediment core (0.50 m) was analyzed from Marion Lake to calculate an annual sedimentation rate of 0.32 cm yr^{-1}, based on pollen evidence of dated historical disturbance.

Aerial pollen influx at both basins is dominated by regionally deposited types such as *Alnus* in spring and grasses in summer. These grains are produced mostly at elevations below the study area and deposited in quantities sufficient to obscure the aerial influx from study area vegetation. Fluvially transported pollen at Marion Lake is more representative of study area vegetation because most stream pollen is recruited by stream erosion of catchment soils, thus minimizing aerial dispersal differences of the various pollen types. Pollen eroded from the drainage basin make up about 80% of the annual stream-borne pollen load and aerial deposition accounts for the rest.

Pollen spectra from lake surface samples show little variation within the two basins except in stream influenced areas where the deposition of larger grains is favoured. Pollen concentrations (grains cm^{-3}) vary by factors of 3 to 4x within Marion Lake, probably due to the effects of lake currents.

A pollen budget was calculated for Marion Lake. Approximately 67% of the pollen spectrum is fluvially derived and the remaining 33% is derived from the atmosphere.

R-values for trees at Marion and Surprise Lakes are, respectively; Cupressaceae 0.33 and 0.74, *Alnus* 9 and 11, *Tsuga heterophylla* 0.38 and 0.35, *Pseudotsuga* 0.16 and 0.48, *Pinus* 36 and 30, *Abies* 1.4 and 2.5, *Acer* 0.80 and 0.30 and *Betula* 0.57 and 0.27. Variations in R-values are attributed to differences in pollen recruitment at the two sites and to differential corrosion and dispersion. In view of theoretical problems involved in the application of R-values for the correction of fossil pollen spectra, the major taxa were classified into three depositional groups (Regional, Extralocal and Local) according to their dispersive characteristics.

The representation and indicator value of each of these taxa is discussed and it is recommended that a separate pollen sum be constructed for the Extralocal group (*Pseudotsuga*, *Tsuga heterophylla*, *Abies*, *Picea*, and *Tsuga mertensiana*) to provide information on vegetation within the biogeoclimatic zone in which the depositional site is located. Problematic taxa, notably *Alnus* and *Pinus* are seriously over-represented whereas Cupressaceae representation may be altered in an unpredictable manner due to high corrosion susceptibility. All taxa in the Regional group are dispersed across zonal boundaries and are of limited indicator value.

The study emphasizes the complexity of pollen recruitment in different depositional basins and points out the importance of such information for paleoecologic interpretation.

DEDICATION

This thesis is dedicated to my wife, Catherine.

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I would like to acknowledge the patience and encouragement of my senior supervisor, Dr. R. W. Mathewes, who suggested the topic of this thesis and provided constructive feedback and guidance throughout the study.

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CHAPTER 1 INTRODUCTION

1.1 Aims and Objectives

A primary goal of pollen analysis is to reconstruct past vegetation from a study of the pollen and spores produced by these plant assemblages and subsequently preserved in peats and lake sediments. Such reconstructions must ultimately be based on an understanding of the present-day relationships between vegetation composition and the pollen grains and spores released from these assemblages. Differences in pollen production, dispersion, deposition and preservation create a complex situation which is poorly understood, especially in mountainous areas.

This study was conceived to contribute information critical for the understanding of the relationship between vegetation composition and sedimentary pollen deposition in the coniferous montane forests of southwestern British Columbia. Hopefully, the results will allow for more precise interpretations of pollen diagrams from the Pacific Northwest, where paleoecological research is currently experiencing renewed activity.

The University of British Columbia Research Forest was selected as a study area because the existing data base on plant ecology, geology, hydrology, climate and paleoecology would provide important information for the interpretation of the data.

The detailed aims and objectives are as follows:

(1) To compare pollen recruitment in a pond with closed drainage to recruitment in a lake with an active inflow and outlet stream in order to assess the relative importance of aerial and stream-borne pollen in the bottom sediments.

(2) To describe the relationship between phenology and aerial pollen influx in the study area, with the purpose of estimating the effective dispersal distance of the important pollen producers.

(3) To establish the quantitative relationships (R-values) between present-day abundance of tree species and their representation in surface samples at the two sites.

(4) To compare my findings with previously published research on pollen-vegetation relationships in mountainous regions.

1.2 Literature Review

Some research on vegetation representation has been carried out in mountainous regions of western North America using pollen contained in moss polsters and other surface samples (Heusser 1969, 1973, 1978, Birks 1977, Potter and Rowley 1960, Maher 1964). However, these studies do not provide quantitative data on modern pollen influx rates in relation to vegetation composition, nor do they evaluate pollen transport and sedimentation processes in lake sediments which are currently favoured by palynologists. Ebell and Schmidt (1964) and Schmidt and Hamblett (1962) have examined aerial pollen transport on Vancouver Island with regard to the establishment of seed orchards and their observations are very valuable for this study. Markgraf (1980) has recently studied pollen dispersal in the mountains of Switzerland.

This study emphasizes the importance of pollen recruitment strategies in different basins but comparable studies have all been performed in lowland situations (Peck 1973, Bonny 1977, Tauber 1977). For this reason the following review of relevant literature is primarily from outside mountainous areas but these studies provide a foundation for the present study.

The most common approach examining pollen representation has been to compare pollen captured in natural pollen traps with the surrounding vegetation. This method is extremely convenient and Heusser (1969, 1973, 1978) has been able to distinguish vegetational zones from polsters in the mountains of Washington. This method has two serious drawbacks which undermine its applicability to pollen analysis in limnic sediments. First, the samples are usually taken within forest stands and therefore most of the pollen captured represents vegetation within approximately 30M of the sample point (Andersen 1970). The pollen spectra which accumulate on the bottoms of lakes, however, represent a much larger source area (Berglund 1973). Second, pollen captured in natural pollen traps is much more susceptible to corrosion than pollen deposited in lakes and, because this process is taxonomically selective, the resulting pollen frequencies may be seriously altered (Sangster & Dale 1964). It is worth mentioning that Janssen (1967, 1972), Andersen (1970) and others have successfully utilized polster samples to study pollen dispersion and to estimate relative pollen production but the applicability of this information to limnic sediments is limited.

Samples from the uppermost sediments of lakes are more directly applicable to pollen analysis because the variables which control their deposition and the vegetational source area they represent are very similar to fossil pollen grains. Lichti-Federovich and Ritchie (1968) conducted a detailed study of this nature in western Canada. They concluded that pollen spectra deposited in medium-sized lakes can distinguish vegetation units at the formation level. When such "surface analogs" can be matched to fossil pollen spectra, a vegetation type similar to the one that produced the surface sample can be inferred.

A number of researchers have attempted to define a more objective interpretation of pollen evidence by calculating factors which correct for the over- or underrepresentation of the individual taxa in a pollen assemblage. These 'R-values' are calculated by dividing the percentage occurrence of a taxon in a surface pollen spectrum by the percent abundance of that taxon in the surrounding vegetation. Davis and Goodlett (1960) did pioneer work on R-values in eastern North America. The problems of applying such objective correction factors to pollen diagrams are discussed by Davis (1963) and by Livingstone (1968). Besides the errors involved in determining the pollen and vegetation percentages, another problem is the change in R-values for a taxon as its relative importance changes in the forest. Faegri and Iversen (1975) and Andersen (1970) discuss this problem at length. Given the problems involved in the objective application of R-values for each taxon, Faegri and Iversen (1975) recommend the establishment of a scale whereby taxa are placed into three or four major depositional groups for correcting pollen diagrams. They also point out that it is impossible to generate R-values of general usefulness, with values being applicable only to the immediate areas for which they were determined.

Another approach to understanding pollen-vegetation relationships is through an examination of pollen dispersal and deposition. Pollen grains are minute particles, most grains ranging in diameter from 15 to 90 microns. The terminal velocity of pollen grains is one or two orders of magnitude less than the force of wind in a natural situation so that their dispersal is a direct function of atmospheric turbulence. The atmosphere near the earth's surface moves in an irregular series of inter-locking wind eddies and the pollen which is suspended in these eddies will be impacted onto vegetation, land or water as they contact these surfaces. Wright (1952) studied the deposition of pollen from isolated trees and presented a general curve describing a very rapid attenuation of pollen grain numbers away from source trees. This general curve has been described by many researchers. The slope of this curve varies according to differential productivity by different species (strength of source), wind speed, atmospheric turbulence, height of the source and the slope of the terrain at the particular site. Although this type of research is important for understanding the theoretical mechanisms of pollen dispersal and deposition, Faegri and Iversen (1975) point out that these experiments do not apply to pollen released in a forest. Although pollen is released above the ground in a forest canopy, the denseness of the canopy means that these grains are effectively being released at zero elevation.

Pollen released by a forest stand behaves differently and Janssen (1967, 1972) has used transects of surface samples to analyze the deposition of pollen grains in natural situations. He describes three major depositional groups:

(A) <u>Local Deposition</u>: Surface samples collected under vegetation are dominated by pollen of the taxa present at the sample site because of their very rapid attenuation from source vegetation. In addition, much of the pollen released in the canopy is impacted onto the surrounding vegetation and subsequently washed onto the ground by precipitation. This type of pollen deposition accounts for the extremely local representation of moss and duff samples taken from within forest stands.

(B) <u>Extralocal Deposition</u>: Janssen showed that in some cases, as the sample transect moved 100 - 200 meters away from the stand, the attenuation of deposition was not as rapid as strictly theoretical studies would predict. He suggested that this effect may be due to lateral transport by wind in the trunk space of the stand as described by Tauber (1967, 1976). Another explanation is the different dispersal behaviour of heavy versus lighter pollen types. Maher (1963) was able to illustrate this type of deposition for Picea in small lakes in Colorado.

(c) Regional Deposition: At a distance of a few hundred metres from a vegetation stand, pollen deposition from that source is generally indistinguishable from "background" levels of regional pollen deposition. Janssen has shown that this background pollen is deposited relatively evenly over a given vegetation unit but becomes overshadowed by local or extralocal deposition in proximity to vegetation stands. The representation of vegetational units at the formation level, as determined by Lichti-Federovich and Ritchie (1968) and others supports this concept of regional deposition.

Janssen's work emphasizes the importance of basin size with regard to the source area represented by the surface pollen spectrum. Small basins will receive a higher percentage of locally and extralocally deposited grains than larger basins, and Berglund's (1973) work in southern Sweden emphasizes this point. Tauber (1967, 1976) constructed a pollen dispersal model describing three more-or-less independent transfer routes for aerial pollen. He states that 60% of aerial pollen deposited in a small lake in Denmark had been transported through the trunk space of the surrounding hardwood stand and represented vegetation composition within 200 metres of the basin. He also estimated that 35% of aerial deposition came from directly above the canopy and represented vegetation within 400 metres of the sample site. Only 5% was truly regional being deposited as the nuclei of raindrops or as rain-scoured pollen. Courrier and Kapp (1974) decided that transfer over the canopy dominated pollen transported through the trunk space at a small lake in Michigan. The apparent conflict between these two results may be a function of vegetation at the two sites. The basin studied by Courrier and Kapp was ringed by a dense coniferous stand which effectively filtered out pollen travelling below the canopy whereas in Tauber's study the trunk space was very open and wind speed was not significantly different above and below the canopy. This comparison emphasizes the complexity of the pollen recruitment situation at a given site by implicating vegetation structure as another in an already imposing list of variables.

Tauber (1977) also estimated that about 50% of the pollen deposited on the lake bottom was transported to the site by an intermittent inflow stream. This result is supported by similar studies of Peck (1973) who determined that 95-98% of total pollen was water-transported. Bonny (1977) also estimated a high water-transported fraction of between 70 and 90%. These results underscore the traditional choice of closed basins as preferred sites for palynological investigation since such high percentages of fluvially-derived grains would be expected to alter the pollen spectrum in favour of riparian taxa. However, in many situations, these ideal, medium-sized, enclosed basins are not available in the area to be studied and the vegetation represented by stream-derived pollen becomes an important unknown in basins with inflowing streams.

Pollen grains fall within the size range of particles for which Stokes' Law should be applicable, but differences between theoretical and observed rates of fall preclude a simple description of their behaviour in water (Heathcote 1978). Brush and Brush (1972) have studied the behaviour of pollen grains in a flume and were unable to find satisfactory explanations for different fluvial behaviours by using the physical characteristics of the grains. They attribute this to minor changes in specific gravity which can drastically alter the terminal velocities of the grains. For practical purposes Stanley (1969) states that although the size range of most pollen grains is that of medium to coarse silt (16 - 62 microns) they behave in the manner of fine to very fine silt (4 - 16 microns). Particles in this size range are transported by streams as washload and Muller (1959) recorded Alnus in the delta of the Orinoco River which must have travelled at least 800 kilometres. Cross, Thompson and Zaitleff (1966) showed that the highest concentrations of pollen grains in the surface sediments of the Gulf of California were at the mouths of inflowing rivers. McAndrews and Power (1973) have shown the influence of individual river basins in pollen spectra in the surface sediments of Lake Ontario. These studies indicate that pollen is transported very efficiently as part of the washload of rivers and may be transported over long distances in great quantity by this process.

Once deposited at a lake, the energy of internal currents easily transports sedimentary particles in the size range of pollen grains and, if these grains are then differentially deposited according to their diameters, pollen spectra may differ according to where in the basin the sample is taken. Davis (1968) first described the process of resuspension where pollen grains, after initial deposition are subsequently resuspended by lake currents and redeposited. This resuspension of pollen grains reduces year-to-year variations in pollen production but causes differences in pollen influx in different parts of the basin. Davis and Brubaker (1973) showed that lighter grains were more suceptible to the effects of resuspension because of their slower settling rates, whereas heavier grains settled directly to the bottom and were deposited relatively uniformly throughout the basin. Other investigators (Dodson 1977, Davis _et_. _al_. 1969, Tutin 1973, Terasmae and Mott 1964) have come to the similar conclusion that pollen grains are deposited in lakes as a function of the interaction between their physical properties and the physical limnology of the site. The distribution of pollen grains in lake sediments is only secondarily related to source vegetation and to differences in pollen influx at the lake surface. The activity of benthic invertebrates is another factor affecting the pollen chronology and Davis (1967) has shown how these organisms may burrow to a depth of up to 8 cm in Maine lakes. The activity of these benthic invertebrates effectively limited the temporal resolution of pollen cores from such organic sediments. All of these factors affect both the influx and the ratios of pollen grains in different regions of the lake basin.

Although most of these studies have not been performed in mountainous areas, they do provide valuable information on aerial and fluvial transport processes, estimates of pollen production and variables of pollen deposition. These results can be compared in a general way to the results of the present study.

1.3 The Study Area

Geology

The study area (Figure 1) is located almost entirely within the University of British Columbia Research Forest, 25 km east of Vancouver in the Coast Mountains of British Columbia. Topography is dominated by a series of north-south ridges whose rounded crests reflect glacial overriding. Figure 2 is a computer-generated block diagram of the study area illustrating the major topographic features. Relief in the study area ranges from 250 m south of Marion Lake to 1059 m on the western flanks of unglaciated Mount Blanshard, northeast of Marion Lake. The study area is hereafter defined as that area within the drainage basin of Marion Lake plus the area included by two overlapping circles 4 km in diameter centered on Marion and Surprise Lakes (Figure 3).

Dominated by plutonic and metamorphic rocks, the Coast Mountains form the southern end of the Coast Crystalline Complex which extends from Alaska to Vancouver (Eisbacher 1972). Roddick (1965) has mapped the most frequent rock types in the area as quartz diorite, diorite, and gabbro. The Vashon Stade of the Fraser Glaciation was the last glacial event to cover the study area. Mathewes (1973) reports continuous sedimentation in Marion Lake starting with deglaciation about 12,350 radiocarbon years B.P. The advance of Vashon ice compacted existing surficial materials into an impermeable basal till which was subsequently overlain by a coarse ablation till during glacial recession. Parent material for soil development is composed of either this ablation till or colluvial material although some organic and alluvial materials also occur (Lacate 1965).

Present Climate

Climate of the area is designated by Köppen as (Cfb), marine, west coast, mesothermal with a small range of temperature, wet and mild winters and relatively dry summers. Although there is no distinct dry season, 87% of total annual precipitation falls from October to April when a zone of eastward-moving frontal storms migrates to this latitude and sends

Figure 1 Map showing location of study area.

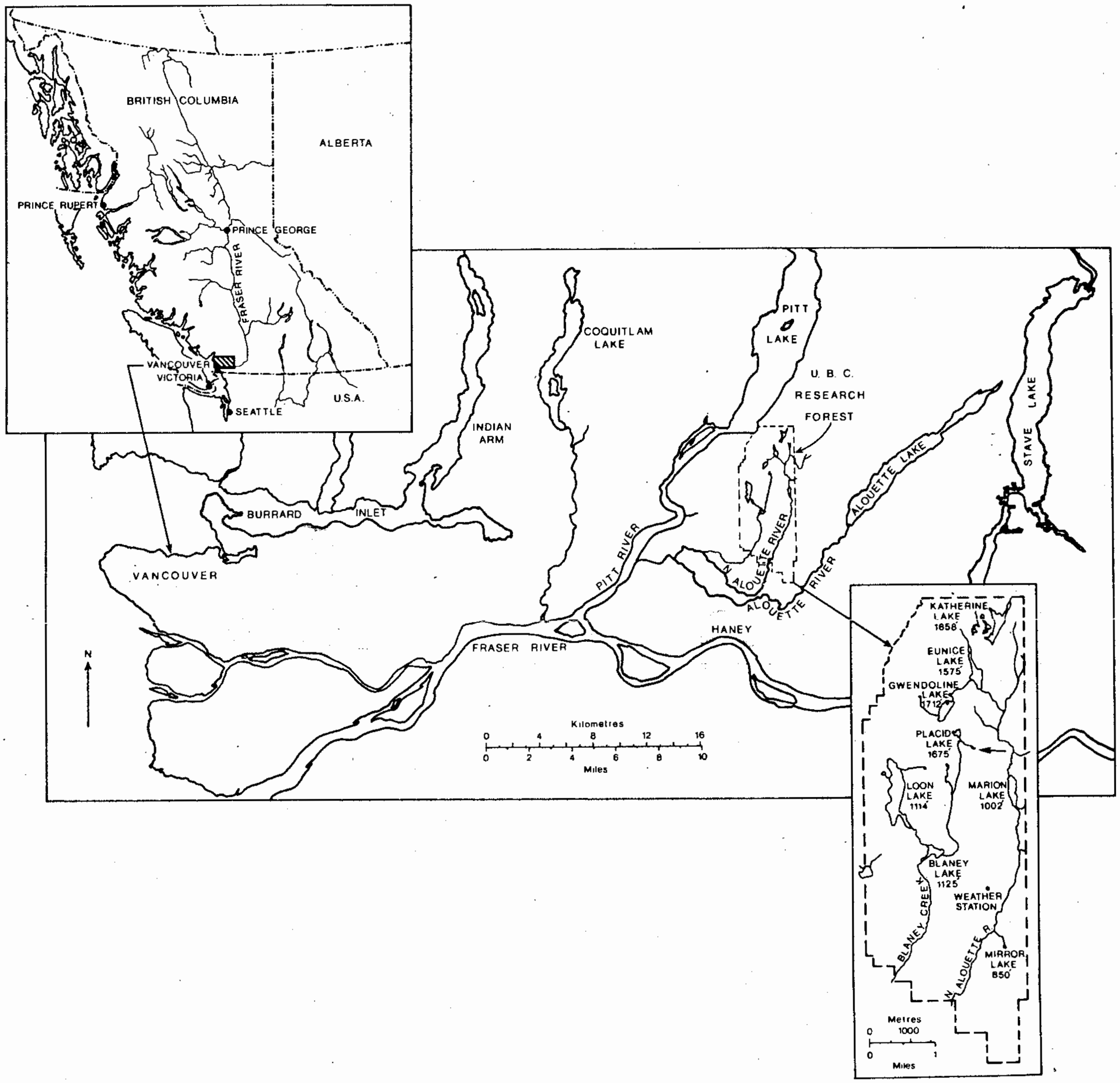
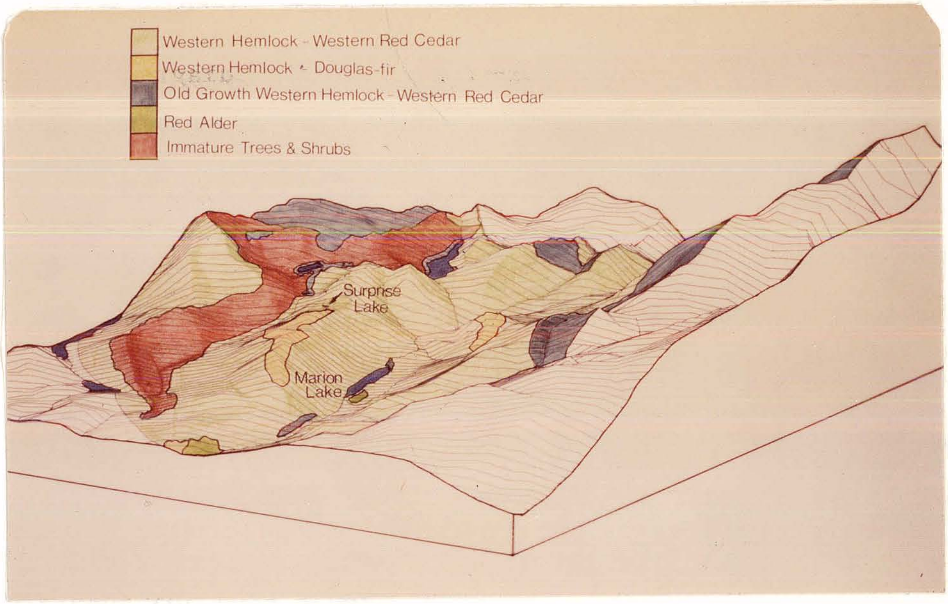

BRITISH COLUMBIA
ALBERTA
PRINCE RUPERT
PRINCE GEORGE
FRASER RIVER
VANCOUVER
VICTORIA
SEATTLE
U.S.A.
COQUITLAM LAKE
PITT LAKE
U. B. C. RESEARCH FOREST
INDIAN ARM
STAVE LAKE
ALOUETTE LAKE
BURRARD INLET
PITT RIVER
N. ALOUETTE RIVER
ALOUETTE RIVER
VANCOUVER
HANEY
FRASER RIVER
N
Kilometres
0 4 8 12 16
0 2 4 6 8 10
Miles
KATHERINE LAKE 1658′
EUNICE LAKE 1575′
GWENDOLINE LAKE 1712′
PLACID LAKE 1675′
LOON LAKE 1114′
MARION LAKE 1002′
BLANEY LAKE 1125′
WEATHER STATION
BLANEY CREEK
N. ALOUETTE R.
MIRROR LAKE 850′
Metres
0 1000
0 1
Miles

Figure 2 Computer-generated block diagram of study area topography and vegetation units.


Western Hemlock - Western Red Cedar
Western Hemlock - Douglas-fir
Old Growth Western Hemlock - Western Red Cedar
Red Alder
Immature Trees & Shrubs
Surprise Lake
Marion Lake

unstable air onto the mountainous coastline. An average precipitation of 30? $\mathrm{cm.yr}^{-1}$ is recorded for the Marion Lake drainage basin (Efford 1967). During the summer months this zone of frontal activity dissipates and clear skies may prevail for several weeks without interruption. The majority of arboreal anthesis in the study area occurs during the spring months when climatic conditions are transitional between these two extremes.

Wind was not measured in the study area although data obtained from Vancouver International Airport provide information on regional wind patterns. Winds from the east and southeast make up more than 50% of annual frequency with winds from the west and northwest accounting for another 25% (Hay and Oke 1970). It is important to note that local winds are channeled around topographic obstacles, so that north-south trending topography in the study area directs regional winds in these two directions. Furthermore, it has been pointed out by Ebell and Schmidt (1964) that pollen release in the Coastal Western Hemlock Zone occurs massively during rain-free days with high air temperature and low humidity. This weather is associated with the development of high pressure systems when gradient winds are light and locally-generated mountain-valley winds are likely to predominate. (Hay and Oke 1970 , Ebell and Schmidt 1964). Under this wind regime air movement is upslope during the day and downslope at night. The modification of regional wind pattern by local topography and the overriding of light gradient winds by local gravity flow during high pressure weather are significant for this study.

Sampling Sites

Marion Lake, located 300 m above sea level, is 800 m long and 200 m at its widest point with a surface area of 13.3 ha. Mean depth is 2.4 m, reaching a maximum depth of 7 m in an elongated trough near the northern inlet of Jacobs Creek. The Marion Lake drainage basin has an area of 13.08 km^2 and includes two lakes (Eunice and Gwendoline) above Marion Lake. Discharge in the basin has been monitored by the Water Survey of Canada since 1967. The combination of permeable soils overlaying an impermeable basal till and extreme basin relief means that discharge in the drainage basin responds rapidly to precipitation events. Large spates of water enter Marion Lake during heavy rainfall and lake volume has been observed to double within 24 hours (Efford 1967). This often dramatic discharge of water by the inflow stream causes the development of internal currents within Marion Lake. An additional aspect of the stormflow character of the basin is the expansion of the drainage network into intermittent channels on steep slopes which flow only during storm events and for a short time thereafter. For this reason channel length varies considerably between low and high discharges.

Surprise Lake is small (30 m at its widest point) peat-ringed basin with a maximum depth of 5.6 m. It occupies a depression in a bedrock ridge 1.1 km due northwest of Marion Lake at an elevation of 540 m. It has no significant inflow and is drained by an intermittent outflow at the western end. Sedimentation began about 11,270 radiocarbon years B.P. (Mathewes 1973).

Vegetation

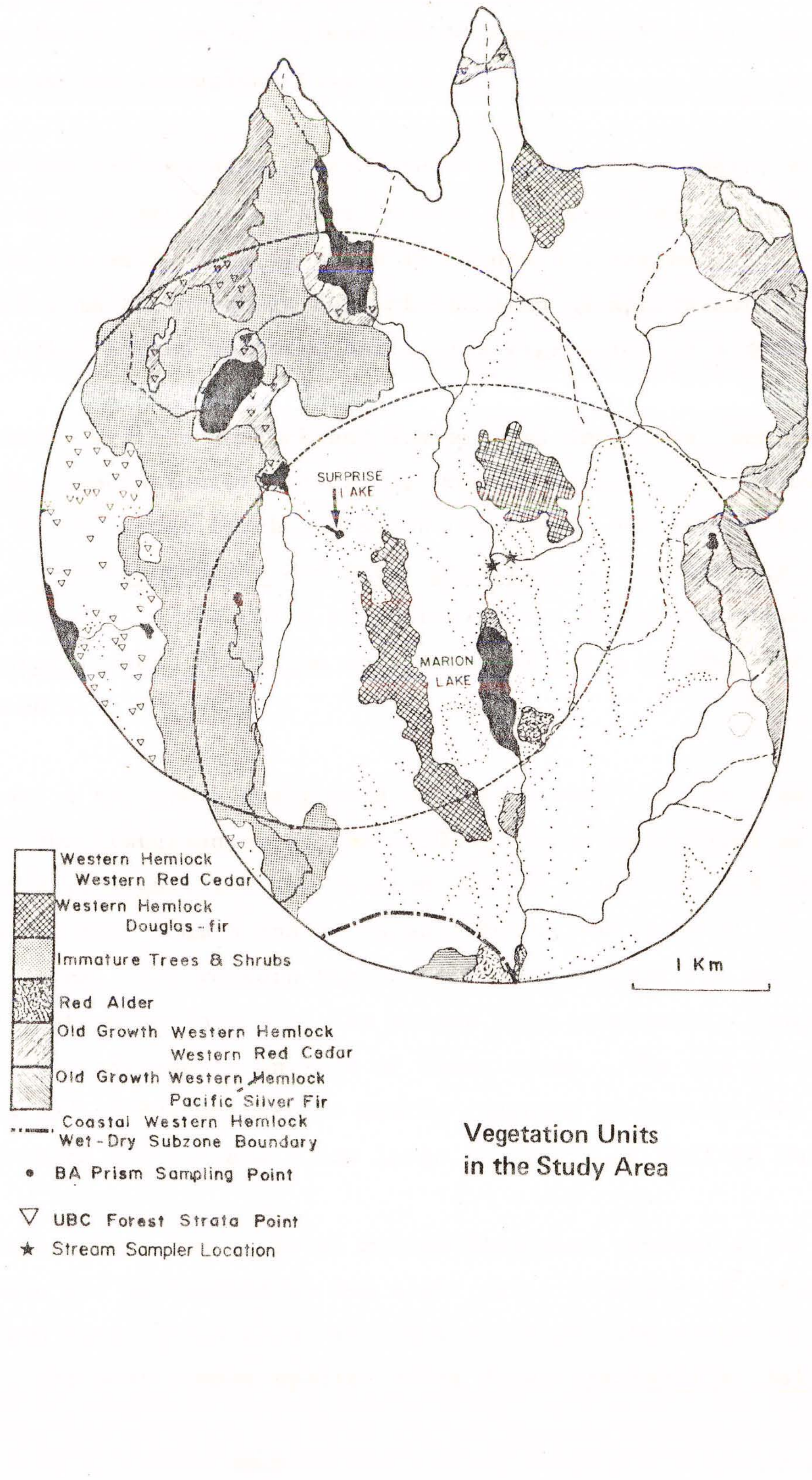
Common names and latin binomials of vascular plants follow Taylor and MacBryde (1977). Both latin and common names are used the first time that trees are mentioned--thereafter, only common names are used. Shrubs and herbs are referred to by latin names only throughout the text.

The study area lies almost completely within the wet subzone of the Coastal Western Hemlock biogeoclimatic zone although part of the southern portion is located within the dry subzone (Klinka 1976). This zone occupies elevations from about 300 to 1000 m where total annual precipitation exceeds 280 cm (Klinka 1976). Western Hemlock (*Tsuga heterophylla*) is considered the climatic climax species on mesic sites. Douglas-fir (*Pseudotsuga menziesii*) is a successional species in this subzone, occurring mainly on previously disturbed sites. Western Red Cedar (*Thuja plicata*) and Pacific Silver Fir (*Abies amabilis*) prefer moist sites with a rich supply of seepage water. Western White Pine (*Pinus monticola*) is found mostly on organic substrates whereas Lodgepole Pine (*Pinus contorta*) is restricted to rocky outcrops. Western Yew (*Taxus brevifolia*) occurs as scattered individuals on mesic soils under the canopy. Yellow Cedar (*Chamaecyparis nootkatensis*) is present in small numbers and illustrates the transitional nature of this subzone into the forested subzone of the Mountain Hemlock biogeoclimatic zone (Klinka 1976). Red Alder (*Alnus rubra*) prefers disturbed, moist sites and forms a border along most of the alluvial habitats in the study area. Black Cottonwood (*Populus balsamifera* subsp. *trichocarpa*) is present with occasional Paper Birch (*Betula papyrifera*) on moist sites, often with Bigleaf Maple (*Acer macrophyllum*) and Red Alder. Sitka Mountain Alder (*Alnus viridis* subsp. *sinuata*) and Vine Maple (*Acer circinatum*) occur throughout the zone on talus slopes or in streambank communities.

The present vegetational mosaic in most of the study area is the result of severe disturbance by logging and fire and is illustrated in Figure 3. The vegetation units have been compiled from University of British Columbia Research Forest Topography and Cover Maps (Sheets 2 and 3) and aerial photographs of the study area. Most stands are in various states of recovery following intensive logging from 1920 to 1931, accompanied by major fires in 1925, 1926 and 1931 which destroyed soil organic horizons and early forest regeneration (Klinka 1976). Mesic and hygric sites have shown the best recovery, being characterized by stands of Western Hemlock and Western Red Cedar with some Douglas-fir. These stands make up the largest percentage of the vegetation in the study area and are mapped in Figure 3 as the Western Hemlock - Western Red Cedar unit. Vegetation under these coniferous stands varies with site characteristics. Shrubs on mesic soils include *Vaccinium alaskaense*, *Menziesia ferruginea*, *Gaultheria shallon*, and *Vaccinium ovalifolium* while on more hygric sites Vine Maple, *Sambucus racemosa* and *Rubus spectabilis* are common. Herb species include the ferns *Polystichum munitum*, *Athyrium felix-femina* and *Blechnum spicant* and the angiosperms *Cornus canadensis*, *Clintonia uniflora*, *Trillium ovatum*, *Trientalis latifolia*, *Montia sibirica* and *Linnaea borealis*. Deciduous arboreal taxa such as Paper Birch, Red Alder, Black Cottonwood, Vine Maple and Sitka Mountain Alder form patches throughout this predominately coniferous area, especially in moist sites or where disturbance has been severe. Understory shrub species in these areas include *Rubus spectabilis*, *Rubus parviflorus*, and *Sambucus racemosa*.

Regeneration on xeric ridges has been less successful and patches of immature Douglas-fir are interspersed here with sparsely-vegetated rocky

Figure 3 Map of study area showing vegetation units, tree basal area sampling points, upstream fluvial sampler locations and circles 4 km in diameter used for R-value calculations.



Vegetation Units in the Study Area

knolls. Less xeric sites between these outcrops support isolated patches of mature Douglas-fir and Western Hemlock. These areas are mapped as the Western Hemlock - Douglas-fir unit in Figure 3 and their predominance on ridgetops is illustrated in this figure and in Figure 2. *Gaultheria shallon*, *Vaccinium ovalifolium* and *Vaccinium alaskaense* are the dominant species in the shrub layer. Stunted individuals of Lodgepole Pine are restricted to the rocky knolls throughout this area.

Much of the western side of the study area has been logged recently and, as a result, pollen production here is low. The areal extent of this vegetation in the study area is shown in Figure 3. Regeneration ranges in height from 8 m in the southern half of the area to approximately 4 m in the more recently logged northern half. The vegetation is a dense tangle of immature coniferous and deciduous growth with Douglas-fir being the most common conifer. Western Hemlock and Western Red Cedar are locally present throughout in association with decaying wood or seepage. Deciduous taxa include Red Alder, Paper Birch and Black Cottonwood and shrubs include *Salix spp.*, *Rubus spectabilis* and *Rubus parviflorus*. Understory vegetation is not abundant due to the thick regeneration but *Epilobium angustifolium*, *Anaphalis margaritacea*, *Pteridium aquilinum* and *Rubus ursinus* are present in small amounts.

There are a few areas designated as "Old Growth" in the study area that escaped the disturbances of the 1920's. These are mapped as two distinct units in Figure 3. The Western Hemlock - Western Red Cedar category is the most common and is established around many of the lakes in the study area. The Western Hemlock - Pacific Silver Fir unit occurs only on the eastern periphery of the Marion Lake catchment. Douglas-fir occurs as large individuals in both of these areas. The old growth area at the northern end of Marion Lake is mostly composed of Western Red Cedar with some Western Hemlock and a few large specimens of Western White Pine.

There are only a few areas of mature deciduous vegetation in the study area and these are designated as Red Alder units in Figure 3. Black Cottonwood and Paper Birch occur with Red Alder and the shrub layer is often dense, the most common species being *Rubus spectabilis*, *Salix spp.*, *Physocarpus capitatus* and *Rubus parviflorus*.

Riparian habitats with coarse-grained alluvium directly adjacent to watercourses dissect all of the above vegetation types. Red Alder, Sitka Mountain Alder and Black Cottonwood are the predominant arboreal species with a dense shrub community made up of *Rubus spectabilis*, *Spiraea douglasii*, *Aruncus dioicus*, *Salix spp*. and *Physocarpus capitatus* with occasional *Lonicera involucrata* and *Viburnum edule*. Streambank communities under the forest canopy include Vine Maple, *Oplopanax horridus*, *Lysichiton americanum* and many fern species. Lakeshore vegetation at Marion Lake is quite different compared to Surprise Lake. Marion Lake is surrounded by an emergent shrub-grass community composed of *Myrica gale*, *Spiraea douglasii*, *Calamagrostis canadensis*, *Pyrus fusca*, *Physocarpus capitatus*, *Salix spp*. and *Carex spp*. Surprise Lake is ringed by *Sphagnum* peat in which ericaceous shrubs such as *Ledum groenlandicum* and *Kalmia polifolia* grow with *Eriophorum chamissonis* and *Drosera rotundifolia*.

CHAPTER 2 METHODS

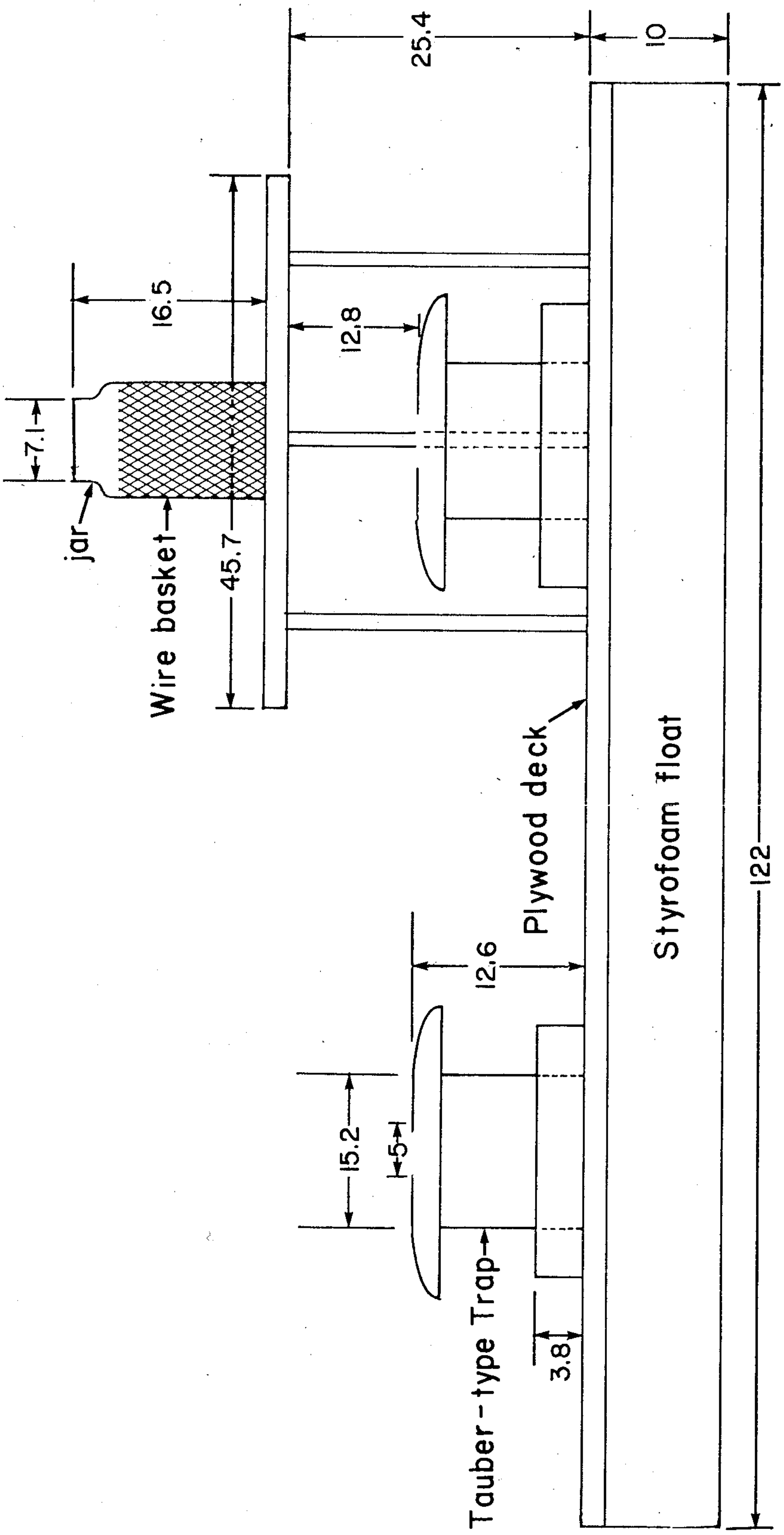
2.1 Field Methods

Aerial Pollen Sampling

Two types of aerial pollen samplers were utilized in this study. The first of these was a modified Tauber trap as described and tested by Tauber (1967, 1974). This sampler consists of a cylindrical plexiglas container covered with a circular, aerodynamic topplate with a central circular orifice 5 cm in diameter. Due to time limitations a commercial "frisbee" was used as a topplate on my traps instead of the aerodynamic collar described by Tauber. This type of trap was used because it has been demonstrated by Tauber (1974) that this sampler collects all grain sizes equally at natural wind speeds (around 2 m sec^{-1}) and requires little maintenance in the field. In addition, other investigators (Berglund 1973, Bonny 1977, Markgraf 1980) have used Tauber traps so that the results of this study will be comparable with existing studies. Kryzwinski (1977a) has criticized the use of Tauber traps for the estimation of pollen influx because of the inwashing of grains from the surface of the topplate. The second type of aerial sampler was a 32 oz glass jar with an opening 7.1 cm in diameter. A 10% glycerol solution was employed as a trapping medium to prevent dessication.

The samplers were mounted on plywood rafts as illustrated in Figure 4. A circular roof was placed 12.8 cm above the topplate of one of the Tauber traps in order to evaluate the importance of rain-scouring as a factor in the deposition of aerial pollen. In addition to the two Tauber-type traps a glass jar was placed on this roof in order to compare sampling results in the two types of aerial samplers. Rafts were anchored in the centre of Marion Lake and Surprise Lake in March 1977 directly above the coring sites of Mathewes (1973) so that aerial data could be related to information from these cores. This central position was also meant to provide a comparison between aerial influx in two different sized basins. A third raft was placed in the southern end of Marion Lake in the spring of 1978 to provide a comparison with the raft in the north end of the basin (Figure 5).

Figure 4 Design specifications for aerial sampling raft showing positions of Tauber-type samplers and glass jar sampler. All measurements are in centimeters.


jar
Wire basket
45.7
16.5
7.1
12.8
25.4
10
Plywood deck
Styrofoam float
122
12.6
15.2
5
Tauber-type Trap
3.8

Glass jar samplers were also placed on the east and west shores of Marion Lake to assess the importance of local and extralocal deposition compared to the middle of Marion Lake. The sampler on the east shore (A3) was placed on a high stump at a height of 3 m. The sampler on the west shore (A2) was positioned below the level of shrub vegetation on that shore (0.5 m). The purpose of this positioning was to compare aerial pollen influx above and below shoreline vegetation. The locations of all aerial samplers at Marion Lake are shown on Figure 5.

Aerial samplers were serviced approximately bi-weekly throughout the flowering period (February to mid-September) and monthly or longer during the non-flowering period (October to February). By collecting information at two week intervals the trapping results could be compared with phenological observations and pertinent climatic data.

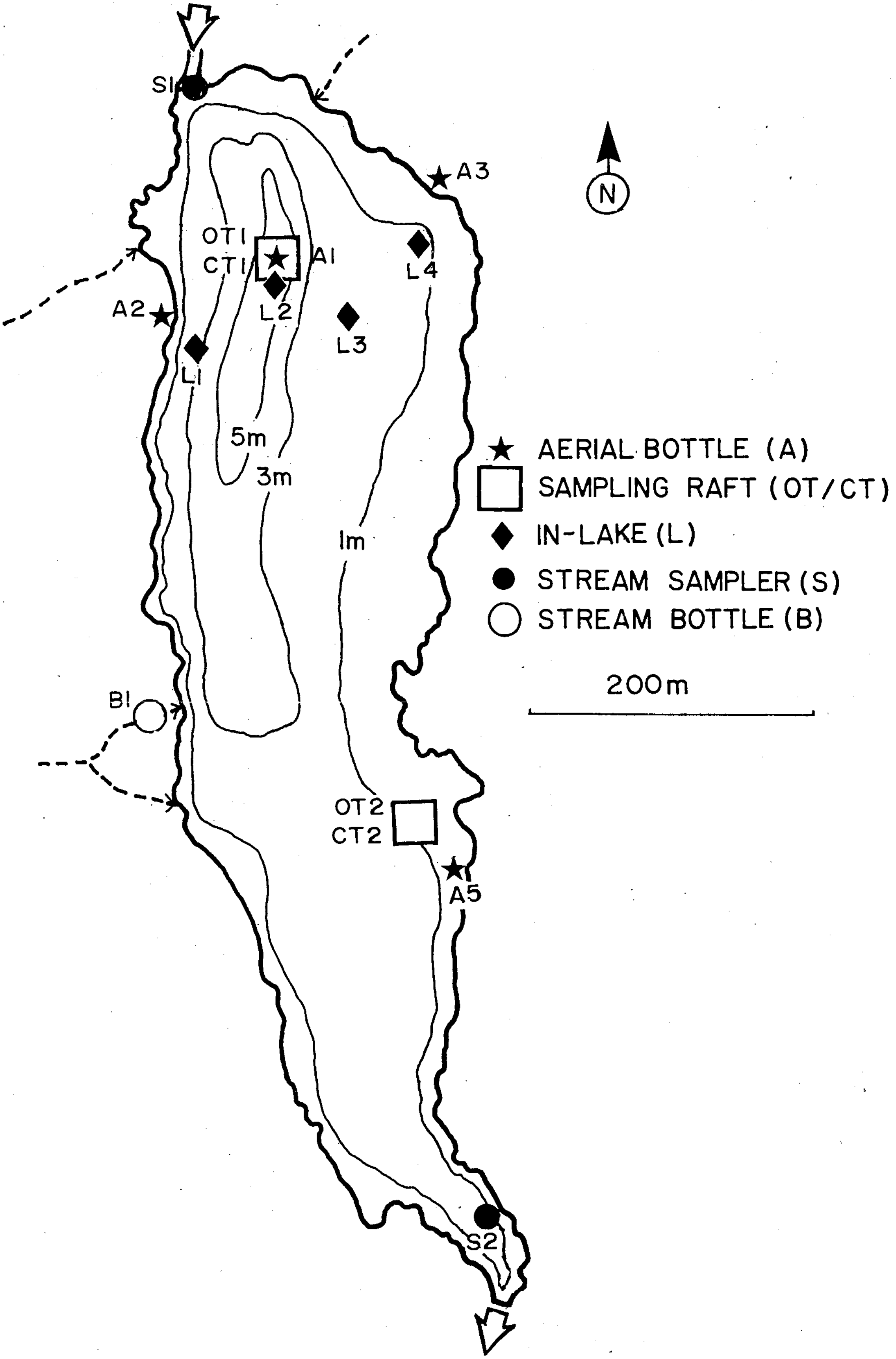
Fluvial Pollen Sampling

(1) Stream Samplers: In order to sample pollen transported by streams I used Tauber traps similar to those described above, but with the plexiglas cylinder deepened by a factor of three. The long cylinders encourage settling of suspended material as discussed by Peck (1973). This sampler was tested by Peck (1972) who showed that although large grains are sampled more efficiently than smaller ones at low water velocities, this difference is reduced at higher water velocities. Peck (1972) also showed that sampler efficiency decreases with increasing stream velocity.

Stream samplers were placed in the inflow and outflow streams at Marion Lake on March 15, 1977 and were taken out on September 13, 1978. These samplers were emptied concurrently with aerial traps although during very high rainfall periods this procedure had to be delayed until water levels dropped. Two additional samplers were installed alongside those already in place in order to examine the variation in stream sampling data. These additional stream samplers were subsequently removed and placed at two different locations in the stream above Marion Lake (see Figure 3).

The glass jars utilized for aerial sampling were also used to sample

Figure 5 Morphometric map of Marion Lake showing locations of aerial, fluvial and in-lake pollen samplers.


S1
A3
N
OT1
CT1
A1
L4
L2
A2
L3
L1
5m
3m
1m
★ AERIAL BOTTLE (A)
□ SAMPLING RAFT (OT/CT)
◆ IN-LAKE (L)
● STREAM SAMPLER (S)
○ STREAM BOTTLE (B)
200m
B1
OT2
CT2
A5
S2

stream pollen. They were submerged in two small impoundments and sampled pollen deposited by small intermittent streams entering Marion Lake on the west shore (see Figure 5). These samplers were emptied on a monthly basis and provided information on the pollen carried by these streams, which drain the western slope of Marion Lake.

(2) <u>In-Lake Samplers</u>: Glass jars were also suspended from poles in a transect across Marion Lake (Figure 5) and from the sampling rafts in the centre of Marion and Surprise Lakes. These samplers recorded the behaviour of pollen grains suspended in the water column and provide the basis for estimates of resuspension and annual sedimentation. In-lake samplers were changed monthly during the flowering period and with all other samplers outside of the flowering period.

(3) <u>Surface Samples</u>: Twenty-four surface samples were collected from Marion Lake and four from Surprise Lake. An Ekmann Grab was used to collect the samples and 1 cm^3 subsamples were skimmed from the surface of the lake mud. Sampling sites were chosen to provide coverage over the entire basin and to examine the effect of local vegetation.

Pollen sampling in the field was periodically interrupted by "natural disasters". Ice-rafting once caused the Marion Lake sampling raft to be dragged to shore. Beavers on several occasions gnawed off the wooden stakes supporting the stream samplers and incorporated them into their dam. Samplers on occasion would simply not be there and the raft at Surprise Lake was once found to be overturned without obvious explanation. These problems are to be expected and the only insurance against these calamities is to provide enough sampling coverage so that critical information is not totally lost.

Vegetation Sampling

(1) <u>Basal Area</u>: The relative abundance of the major arboreal taxa was estimated in order to compute R-values for these species. Basal area ($m^2 . ha^{-1}$) was measured using the Bitterlich variable-radius technique (Dilworth and Bell 1978). A "Cruise-master" prism angle gauge with a metric

basal area factor of 6 was used to convert tree counts from 884 sampling points to basal area. Sample points were chosen systematically along access roads within two overlapping 4 km circles around Marion and Surprise Lakes (see Figure 3). Subjectively-chosen transects were surveyed systematically along and across physiographic gradients in order to cover the complete range of habitats in the study area.

(2) Phenology: Phenological observations were made for selected plant species within the study area to provide interpretative information for the pollen sampling data. Details of flowering were estimated according to the legend in Figure 6 and are presented according to the method of Ritchie (1977). Species in which flowering was erratic or difficult to estimate were not tabulated. In the spring of 1978 phenological lapse-rates were recorded and isolines of flowering development were drawn for Red Alder (Figure 9).

2.2 Laboratory Methods

Aerial pollen samples were passed through a 250 µm sieve to remove any allochthonous detritus in the sample. The presence of insects or flower parts was noted. Samples were then concentrated by centrifugation in 50 ml centrifuge tubes at 2300 rpm for 5 minutes. The pollen and other material formed a visible cake in the bottom of the tube without adding $CaCO_3$ as a congealing agent, as has been suggested by Jorgensen (1967). After each centrifugation the supernatant was carefully poured off until approximately 5 ml remained in the bottom of the tube. Periodic examination of supernatant water ensured that grains were not being poured off. Samples were then transferred to 10 ml tubes for processing by the standard procedure described by Faegri and Iversen (1975). A 5 minute hot KOH treatment was followed by the addition of a known quantity (16,180 ± 1460) of Eucalyptus grains in tablet form (Benninghoff 1962). Carbonates were then dissolved by 10% HCl in a hot water bath for 10 minutes followed by transfer to glacial acetic acid, hot acetolysis for 1 minute and dehydration with butanol. Samples were mounted in silicone oil for microscopic examination and storage. Pollen was counted using a Wild M11 binocular microscope at 400X magnification. Critical determination of difficult types was performed under oil immersion at 1000X magnification. Pollen sums of not less than 200 grains were tabulated. During the summer months and during the non-flowering period influx rates were often so low that reaching this total was impossible.

Fluvial samples often contained large volumes of sediment and were passed through a 250 μm sieve to separate the pollen grains from the larger detritus. The larger detritus was centrifuged and a total volume of this material was recorded. The filtrate was allowed to settle for 48 hours after which most of the water was siphoned off. The remaining suspension was then centrifuged at 2300 rpm for 5 minutes and supernatant water poured off. This process was repeated until all of the sample was concentrated in the centrifuge tubes. The total volume of this sediment was added to the volume of the larger detritus in order to estimate the total volume of sediment trapped during the sampling period. A 0.5 cm^3 aliquot was processed for pollen analysis. Except for treatment with hydrofluoric acid to dissolve sand in these fluvial samples, the processing was identical to aerial samples.

Known numbers of <u>Eucalyptus</u> grains were added to both aerial and fluvial samples to estimate the number of pollen grains caught during each sampling period. For the aerial samples all grains present in the samplers were processed chemically for counting. In the case of the fluvial samples a 0.5 ml aliquot was taken from the sample for processing and from this sub-sample a concentration (pollen grains .cm^{-3}) was calculated. This concentration was then multiplied by the total volume of sediment trapped in the sampler to estimate the total number of pollen grains captured by the sampler over that sampling period. The total number of pollen grains in each sampler was divided by the number of days that the sampler was in place and by the cross-sectional area of the orifice of the sampler. This permitted the calculation of pollen influx rates (grains . cm^{-2} . day^{-1}) in each sampler. Dividing by the area of the orifice in order to calculate an influx rate involves the assumption that trapping efficiency is proportional to the area of the orifice. Tauber (1974) stated that this is true for the aerial Tauber traps but this assumption is untested for the aerial glass jar samplers. This assumption has been verified by Pennington (1973) for in-lake glass jars.

Pollen and spores encountered in this study were identified using a modern reference collection of Pacific Northwest species. Keys presented by Kapp (1969), Faegri and Iversen (1975) and McAndrews, Berti and Norris (1973) were also consulted. In the text of this study the term "pollen grain" is taken to mean both pollen grains of spermatophytic species and the spores of cryptogams.

CHAPTER 3 RESULTS AND DISCUSSION

3.1 Vegetation Analysis

Basal Area and Relative Frequency

The abundance of arboreal taxa was calculated as their percentage of the total basal area of all species estimated from 884 sampling points throughout the drainage basin of Marion Lake, and within circles 2 km in radius around both Marion Lake and Surprise Lake. This data was supplemented by information from 60 sample plots made available by the Univeristy of British Columbia Research Forest. A grid of 964 sample plots was therefore used for calculation of basal areas. Table 1 lists these frequencies for local vegetation (within 100 m of the site) and for more regional distances (1000 m and 2000 m). The local vegetation surrounding Marion Lake has three taxa not recorded locally at Surprise Lake. These are Black Cottonwood, Silver Fir and Paper Birch which make up only a small percentage of the vegetation within 100 m of Marion Lake. Douglas-fir and Red Alder are found in low amounts at both sites. Within all circles the data describe a vegetation which is dominated by Western Hemlock and Red Cedar. Their combined frequency accounts for more than 80% of total basal area although their roles in local vegetation are reversed at the two sites. Within 100 m of Marion Lake Red Cedar is the most important species (56%) with hemlock secondary (34%) while at Surprise Lake the situation is reversed with hemlock most common locally (57%) and cedar secondary (38%). The frequencies of these two taxa become almost equal (about 40%) in the 2 km circles, pointing out the shared dominance of these two species in the study area as a whole. The remaining 20% of the forest is composed primarily of five coniferous and four deciduous tree species. Douglas-fir is locally present in low percentages at both sites (2 - 3%), and increases away from the lakes (8 - 11%), reflecting its preference for more xeric habitats. Paper Birch follows this pattern as well. Silver Fir shows the opposite trend because the only recorded individuals occur in the valley occupied by Marion Lake so that its frequency declines drastically away from these rich sites. Black Cottonwood prefers moist sites and follows the same general pattern as Silver Fir. Red Alder is most common in the study area

Table 1. Relative frequencies (% of total basal area) of trees within circles of increasing radius around Marion and Surprise Lakes.

	MARION LAKE			SURPRISE LAKE		
	100 m	1000 m	2000 m	100 m	1000 m	2000 m
Thuja plicata	56	47	41	38	32	42
Tsuga heterophylla	34	37	41	57	53	40
Pseudotsuga menziensii	2.3	6.7	7.8	3.4	8.9	11
Alnus rubra	3.1	3.2	4.0	1.6	1.1	2.4
Betula papyrifera	0.1	3.0	3.5	-	3.4	2.3
Populus balsamifera	3.2	2.1	1.4	-	0.3	1.1
Abies amabilis	2.8	0.9	0.9	-	0.6	1.4
Acer macrophyllum	-	0.05	0.02	-	0.3	0.07
Pinus monticola	*	0.3	0.14	*	0.01	0.27
Picea sitchensis	-	-	-	-	-	0.03

* = present but not encountered during sampling.

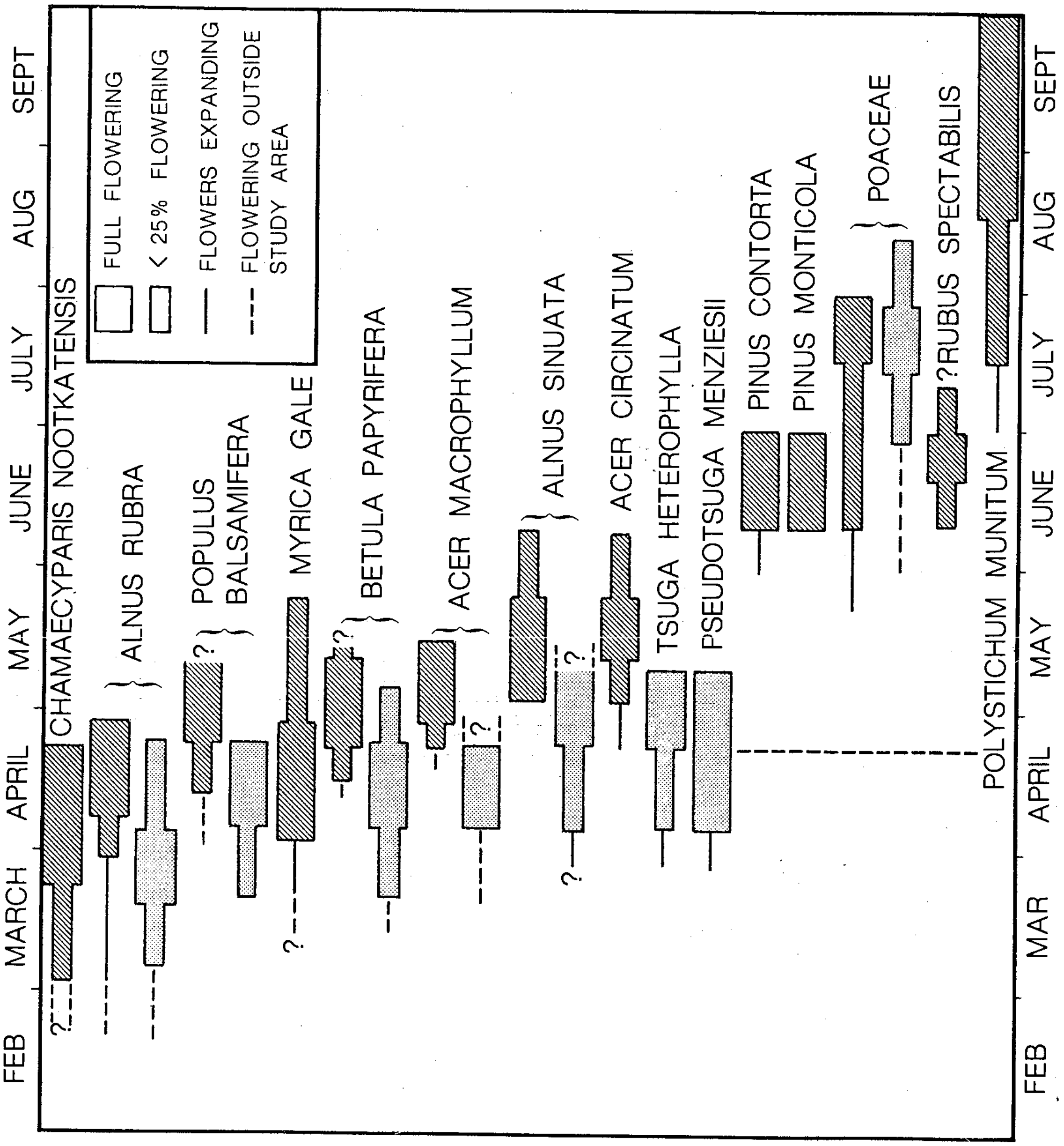
on alluvial soils along streams although some individuals do occur on moist upland sites. White Pine and Bigleaf Maple are present in low amounts and represent isolated individuals on moist sites in the study area. Lodgepole Pine although present on rocky knolls throughout the study area, was not recorded by the basal area prism because the stems of this species were usually less than 5 cm in diameter at breast height and therefore not wide enough to be recorded. This is important because these stunted individuals were observed to be producing pollen in abundance. The small frequency reported for Sitka Spruce (Picea sitchensis) is based on the observation of one individual.

Phenology

Figure 6 records phenological information and is based on field observations in 1977 and 1978. Phenology was recorded approximately every two weeks on the same dates as aerial sampler collection. The solid line preceding the two recorded flowering stages point out when flowers were first seen to be enlarging in response to environmental signals. Flowering in the study area occurred somewhat later than at lower elevations and this difference is indicated for some taxa by the dotted lines preceding bar graphs in Figure 6. Questionable starting and finishing points are indicated in the figure. This phenological information has been used to help interpret pollen dispersal distances. Anthesis does not begin abruptly either on a single tree or within the study area as a whole so that a breakdown into two flowering periods is necessary. The "<25% flowering" category describes a situation where some shedding of pollen has occurred but less than 1/4 of anthers were mature at the time of observation.

In general, flowering occurred about two weeks later in 1977 than in 1978, this pattern being observed in Red Alder, Paper Birch, Black Cottonwood, Bigleaf Maple and Sitka Alder. It was observed in 1978 that by April 23 the deciduous taxa had fully-developed canopies so that any dispersion advantage gained by releasing pollen grains into an open canopy would only be enjoyed by species whose anthesis preceded this date. In 1978 these species were Red Alder, Black Cottonwood, Paper Birch and Bigleaf Maple. Flowering dates of two important coniferous taxa, Western Hemlock

Figure 6 Summary of phenological observations in 1977 and 1978 in the study area. Dark bars indicate 1977 and light bars 1978 observations. Vertical dashed line represents date for full development of deciduous canopy in 1978.


FEB
MARCH
APRIL
MAY
JUNE
JULY
AUG
SEPT
FEB
MAR
APRIL
MAY
JUNE
JULY
AUG
SEPT
FULL FLOWERING
< 25% FLOWERING
FLOWERS EXPANDING
FLOWERING OUTSIDE STUDY AREA
CHAMAECYPARIS NOOTKATENSIS
ALNUS RUBRA
POPULUS BALSAMIFERA
MYRICA GALE
BETULA PAPYRIFERA
ACER MACROPHYLLUM
ALNUS SINUATA
ACER CIRCINATUM
TSUGA HETEROPHYLLA
PSEUDOTSUGA MENZIESII
PINUS CONTORTA
PINUS MONTICOLA
POACEAE
?RUBUS SPECTABILIS
POLYSTICHUM MUNITUM
?
?
?
?
?
?
?

and Douglas-fir straddle this date. Except for the two species of *Pinus* there is a natural division approximately at the end of May, after which the observations record primarily herbaceous taxa. This distinction is apparent in Figure 6 from the flowering of Poaceae pollen in June and July. *Rubus spectabilis* is one of the most common representatives of the Rosaceae family and observations of this species record a peak in the last two weeks of June. Sporangia of *Polystichum munitum* were observed and, although no clear endpoint was discernible, the majority of fronds examined were shedding by the middle of August.

3.2 Aerial Pollen

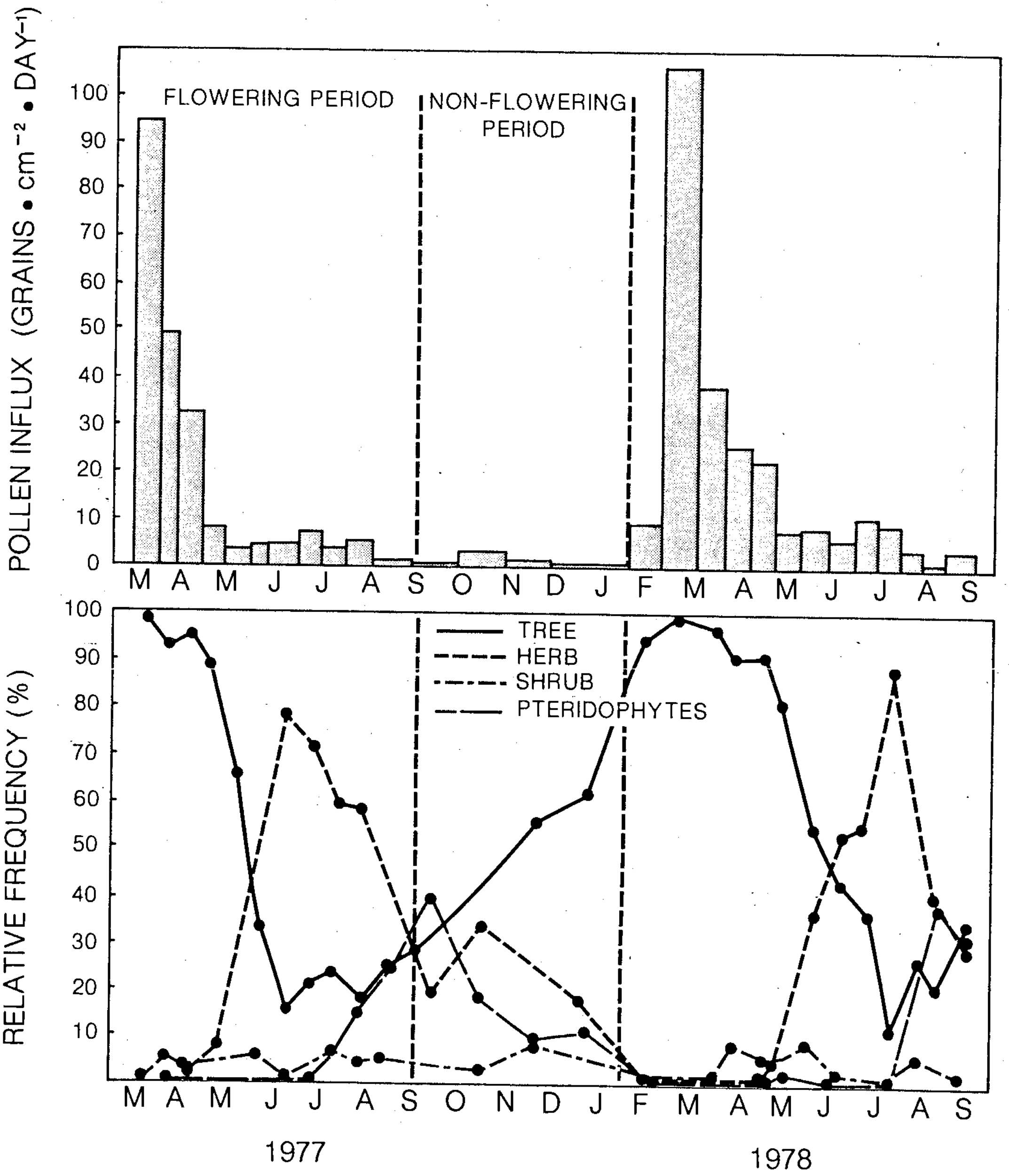
Seasonal Distribution of Aerial Pollen Deposition

The seasonal distribution of aerial pollen influx was investigated to evaluate the effects of changing weather phenomena on pollen dispersion. Pollen deposition at Marion and Surprise Lakes corresponds closely with local phenological observations for most taxa studied. In some species, however, aerial pollen deposition at the lakes preceded their anthesis in the study area and these examples are discussed later in this chapter. An evaluation of the seasonal character of pollen deposition thus provides a framework for understanding how pollen is transported and deposited.

Basic trends in total pollen influx and relative frequencies for all sampling periods are very similar at both Marion and Surprise Lakes. Figure 7, therefore, which is compiled from Marion Lake data, is representative of the basic pattern of aerial deposition throughout the study area. Pollen influx in 1977 and 1978 is dominated by peaks of about 100 grains . cm^{-2} . day^{-1} in March which decline to values around 10 grains . cm^{-2} . day^{-1} during May through August. Aerial pollen influx rates outside of the flowering period (September to January) are in the order of 1 grain . cm^{-2} . day^{-1}.

By comparing Figure 7a and 7b it is apparent that the early peaks of aerial influx are coincident with spectra dominated by tree pollen and that the later, lower values are mostly pollen of herbaceous taxa. In 1978

Figure 7 Seasonal changes in total pollen influx and relative frequencies of tree, herb, shrub and Pteridiophyte types.


POLLEN INFLUX (GRAINS • cm⁻² • DAY⁻¹)
FLOWERING PERIOD
NON-FLOWERING PERIOD
100
90
80
70
60
50
40
30
20
10
0
M A M J J A S O N D J F M A M J J A S
RELATIVE FREQUENCY (%)
TREE
HERB
SHRUB
PTERIDOPHYTES
M A M J J A S O N D J F M A M J J A S
1977
1978

the onset of the flowering period is marked by an increase from less than 1 grain . cm^{-2} . day^{-1} to 9.2 grains . cm^{-2} . day^{-1} at the beginning of February, due primarily to Cupressaceae pollen. The following sampling period, ending March 17, records the highest influx for all sampling periods (106 grains . cm^{-2} . day^{-1}) and the spectrum on this date is 48.2% *Alnus* pollen and 49.6% Cupressaceae pollen. This peak represents the coincident maximum influx values for these two taxa. Influx declines sharply after this maximum as Western Hemlock, Douglas-fir and Paper Birch attain their highest values between April 4 and May 5. After May 5 influx drops below 10 grains . cm^{-2} . day^{-1} marking the termination of anthesis for the major arboreal taxa. From June until September influx fluctuates between 1 and 10 grains . cm^{-2} . day^{-1} and Poaceae pollen is the major contributor, reaching its regional maximum at the end of June. Other herbs present in low but consistent amounts include *Plantago lanceolata* and *Rumex acetosella*, with Asteraceae and Cyperaceae occurring only sporadically. *Pinus* reaches its maximum during the first half of July. Beginning at the end of August, fern spores are released. They dominate the spectrum for a brief period at the end of September when palynomorph deposition from other sources is very low. *Abies*, *Picea* and Bigleaf Maple occur sporadically in the aerial spectrum throughout the year. Shrub pollen recorded throughout the year in low amounts include *Myrica gale*, *Salix*, *Acer circinatum*, *Corylus cornuta*, *Spiraea*, *Taxus*, Ericaeae and *Lonicera*.

Table 2 summarizes the proportions of aerial pollen influx over the flowering and non-flowering periods shown in Figure 7.

Table 2. Seasonal proportions of aerial pollen influx at Marion and Surprise Lakes for the depositional year September 9, 1977 to September 13 , 1978.

	MARION LAKE	SURPRISE LAKE
Flowering Period (Early) 2.2.78 - 27.5.78	86.1%	82.5%
Flowering Period (Late) 27.5.78 - 13.9.78	10.5%	13.5%
Non-flowering period 9.9.77 - 2.2.78	3.4%	4.0%

It is not surprising that some pollen is deposited onto the lake surfaces outside of the flowering period. Tauber (1977) records significant amounts of aerial deposition outside of the flowering season in a small Danish lake and has postulated that this phenomenon is the result of pollen grains being refloated from the twigs and leaves of vegetation surrounding the basin. Markgraf (1980) has also recorded deposition outside of the flowering season. However, she concluded that this influx is not due to refloatation but represents washout of pollen grains with a long residence time in the atmosphere. The results of this study support the hypothesis of Tauber. The maximum influx during the non-flowering period occurs during November when heavy wind and rain buffeted the study area. The local source of this pollen is indicated by the fact that influx into the aerial sampler on the shore of Marion Lake was 2.44 grains . cm^{-2} . day^{-1} compared to 1.33 grains . cm^{-2} . day^{-1} in the sampler in the centre of the lake. A Wilcoxin Paired-T-test between total numbers of each taxon in these two samplers reveals a significant difference at the 0.05 level. This implies that the heavy wind and rain during the sampling period removed pollen grains adhering to lakeshore vegetation and redeposited some of them into Marion Lake.

The spectrum during the non-flowering period is composed of 39.2% Alnus pollen, 20.6% Grass pollen and 14.4% fern spores with Pinus, Myrica gale, Picea and Western Hemlock all recording frequencies between 2 and 3%. Myrica gale forms low stands on the shore of Marion Lake and its representation in the refloatation spectrum supports the notion of a local source for this out-of-season influx. However, it is surprising that Cupressaceae comprises only 1.8% of this spectrum because Western Red Cedar forms dense stands on the shore of Marion Lake and Cupressacae pollen contributes 30% of the total annual aerial deposition in the study area. This anomaly is probably a result of extreme sensitivity to corrosion for pollen of this family. Moss polster samples taken from beneath stand composed totally of Western Red Cedar contained no recognizable Cupressaceae grains. Sangster and Dale (1964) have shown experimentally that pollen grains of the Cypress family are extremely susceptible to corrosion.

Compared to Tauber (1977), who measured values of refloated pollen ranging from 9.8 to 55.1% of total annual influx, pollen deposited in this manner accounts for only 3.4% of total annual influx at Marion Lake and 4.0% at Surprise Lake. These calculations only include pollen which is redeposited during the non-flowering period and therefore do not account for refloatation and redeposition outside the period of anthesis for a particular species, but within the flowering period as defined earlier. Refloatation within the flowering period was evaluated for Alnus because it makes up the largest percentage of the refloatation spectrum and good phenological information is available to define the period of anthesis. Recalculation increases the annual refloatation value for Alnus from 2.5 to 3.3% at Marion Lake and from 1.4 to 3.3% at Surprise Lake. Clearly, pollen deposited outside of the flowering period is quantitatively unimportant in the study area and these results support the estimates of Berglund (1973) and Markgraf (1980).

Aerial Pollen Transport and Deposition

Rain-out of Aerial Pollen

Differences between roofed and unroofed samplers (Figure 4) were examined in order to evaluate the quantitative importance of rain-scoured pollen, as was done by Tauber (1977) in Denmark. In order to determine if this sampling arrangement includes any sampling bias, pollen catches in all three sets of roofed and unroofed samplers were compared for the June 23 - July 7 sampling period. This was the only sampling period during which no precipitation was recorded in the study area. Therefore, there could be no rain-out component and trapping efficiencies in the roofed and unroofed samplers can be compared. Table 3 lists total grains captured for each taxon in sets of roofed and unroofed samplers at Marion and Surprise Lakes. A Wilcoxin Paired T-test reveals a significant difference only at Surprise Lake where the roofed sampler trapped six times as many grains as the unroofed sampler. Table 4 shows total grains captured in roofed and unroofed samplers during the 1977 and 1978 flowering periods. Again, the only samplers for which a significant difference is recorded are those at Surprise Lake in 1978. This rather surprising result suggests that the roofed sampler at Surprise Lake is more efficient at trapping pollen

Table 3. Total grains captured in roofed and unroofed Tauber-type traps at Marion and Surprise Lakes for the sampling period June 23, 1978 to July 13, 1978, the only sampling period in which no rainfall was recorded in the study area, compared by Wilcoxin Paired T-test.

(OT = unroofed, CT = roofed)

	MARION LAKE				SURPRISE LAKE	
	OT1	CT1	OT2	CT2	OT3	CT3
Abies	-	84	25	-	-	45
Cupressaceae	26	-	50	-	-	-
Picea	156	357	400	150	190	405
Pinus	806	945	475	950	660	765
Pseudotsuga	-	42	-	25	-	45
Tsuga heterophylla	78	273	200	75	50	225
Alnus	312	63	500	225	70	1035
Other Arboreal Pollen	104	-	25	-	-	90
Poaceae	3328	2835	3025	3475	1050	9450
Cyperaceae	26	-	25	-	-	135
Plantago lanceolata	208	63	150	75	50	405
Fern spores	26	63	50	75	10	225
Other Non-Arboreal Pollen	260	63	125	225	60	90
	5330	4788	5050	5275	2140	12915
	$p \leq 0.50$		$p \leq 0.2$		$p < 0.001$	

Table 4. Total grains captured in roofed and unroofed Tauber-type traps over the 1977 and 1978 flowering periods at Marion and Surprise Lakes compared by Wilcoxin Paired T-tests. OT = unroofed, CT = roofed)

	MARION LAKE						SURPRISE LAKE			
	1977		1978		1978		1977		1978	
TAXON	OT1	CT1	OT1	CT1	OT2	CT2	OT3	CT3	OT3	CT3
Abies	8	51	202	105	371	114	-	-	66	45
Cupressaceae	11769	9533	40110	33096	2226	3720	48388	57003	24250	38145
Picea	291	475	762	1078	1077	618	26	175	607	801
Pinus	562	1648	2960	2466	3151	3141	1230	1230	2429	2433
Pseudotsuga	101	10	641	1263	1074	1703	224	21	2734	2726
Tsuga heterophylla	1820	1480	5186	9168	9009	15922	2165	1893	10920	13003
Alnus	12862	7464	44972	31961	15922	28407	21375	12587	24291	42899
Betula papyrifera	3275	2050	559	1729	1028	2213	4786	1913	1547	3162
Other Arboreal Pollen	900	173	310	527	157	683	-	390	191	690
Poaceae	4519	8661	7971	6660	10897	9375	4587	3727	4153	16720
Plantago lanceolata	383	428	523	321	589	445	184	369	225	789
Rumex acetosella	93	60	209	76	302	173	18	-	40	82
Fern spores	561	797	1354	675	1609	824	624	288	1204	701
Myrica gale	883	1547	259	949	177	346	-	-	-	-
Other Non-Arboreal Pollen	715	827	822	412	918	2121	1218	538	1285	1285
TOTAL	38742	35204	106840	90486	48507	69805	84843	80134	73942	123481
	$p \leq 0.5$		$p \leq 0.5$		$p \leq 0.2$		$p \leq 0.1$		$p \leq 0.02$	

than the unroofed sampler so that any influx due to rain-scoured pollen in the roofed sampler could be negated.

Although sampling efficiences at the two rafts at Marion Lake are not significantly different, an analysis of individual taxa reveals that the roofed sampler is more efficient at that site as well. Table 5 summarizes total grains of Alnus and Cupressaceae pollen in roofed and unroofed samplers at Marion and Surprise Lakes. Both of these taxa reach their maxima during the February 25 to March 17 sampling period at both lakes. During this period the dry weather which initiated anthesis was suddenly terminated by heavy rainfall. The unroofed sampler at Marion Lake captured a higher number of both Alnus and Cupressaceae pollen than the roofed sampler during this sampling period but this is one of the only times that this occurred. It appears that during this sampling period the rain-out component was sufficiently heavy to compensate for the higher efficiency of the roofed samplers. At Surprise Lake the significantly higher efficiency of the roofed sampler (Tables 3 and 4) masks the contribution of the rain-out component.

The results from my Tauber-type traps may not be comparable to those used by Tauber (1967, 1974, 1977) because a commercial "frisbee" was substituted for his machined aerodynamic topplate. However, there are three points which support the comparibility of my findings. First, I recorded an annual aerial influx of 5685 grains . cm^{-2} . yr^{-1} in the unroofed sampler in the middle of Marion Lake and this value is very similar to deposition rates recorded in similar basins by other researchers (Bonny 1977). Second, a Wilcoxin Paired T-test shows that the unroofed Tauber-type samplers at Marion Lake and Surprise Lake trapped significantly more pollen grains than the glass jars set on the same raft. This suggests that, because of its aerodynamic shape, the topplate which I utilized increases sampling efficiency in a manner similar to that described by Tauber (1974) for his samplers. Third, my data in Chapter 3.4 show that there is a threefold difference in pollen trapping efficiency between the Tauber-type sampler and the lake surface. This is the exact correction factor which Tauber (1977) uses for his traps.

Table 5. Total grains captured for *Alnus* and Cupressaceae in roofed and unroofed samplers at Marion and Surprise Lakes from February 2, 1978 to May 8, 1978.

ALNUS (Total Grains)

	Surprise Lake		Marion Lake	
Sampling Period	Roofed	Unroofed	Roofed	Unroofed
Feb. 2 - Feb 24	54	243	22	230
Feb 25 - Mar 17	13608	8446	10350	39794
Mar 18 - Apr 4	12816	5076	5883	2205
Apr 5 - Apr 21	9860	8280	13104	572
Apr 22 - May 8	1505	1581	1484	729
	37843	23626	30843	43530

CUPRESSACEAE (Total Grains)

	Surprise Lake		Marion Lake	
Sampling Period	Roofed	Unroofed	Roofed	Unroofed
Feb 2 - Feb 24	3492	6021	4510	4140
Feb 25 - Mar 17	25110	10168	13050	34542
Mar 18 - Apr 4	7632	4982	5353	750
Apr 5 - Apr 21	1275	2829	9594	234
Apr 22 - May 8	172	204	583	378
	37681	24204	33090	40044

Thus it is questionable whether a comparison of roofed and unroofed samplers can provide a reliable estimate of the amount of rain-scoured pollen. Results summarized in Table 5 indicate that some pollen is deposited by the rain-scouring process but any estimation of its quantitative importance is not possible from this data.

Aerial Pollen Transport

Aerial pollen influx was compared among jar samplers at three Marion Lake locations (see Figure 5) and in the centre of Surprise Lake. These locations were selected firstly to examine differences in aerial pollen influx between basins of different size, by comparing samplers from the centres of Marion Lake (A1) and Surprise Lake (A4). Secondly, shoreline (A2, A3) and mid-lake (A1) sampling locations at Marion Lake were compared in order to evaluate the importance of local, extralocal and regional deposition. Table 6 lists the relative frequencies of the major taxa trapped in the aerial samplers at Marion and Surprise Lakes. The similarities of pollen spectra from different sampling locations shown in Figure 6 are emphasized by the very high correlation coefficients between the total numbers of taxon pairs in these samplers (Table 7). The total pollen influx for each sampling period was also examined for the same comparisons described above, using a Wilcoxin Paired T-test. The results reveal no significant differences in the total numbers of pollen grains deposited in the glass jar samplers. If local or extralocal deposition were dominant at any of these sampling sites then this should be apparent from differences in the relative frequency of different taxa and from different pollen influx values, but this is not the case. Sampling results implicate regional deposition as the major process controlling the aerial influx of pollen grains in the study area.

Table 6. Relative pollen and spore frequencies of major taxa at Marion and Surprise Lakes totalled over all common sampling periods in glass jar samplers.

	A1*	A2	A3	A1	A4
Abies	0.01	0.04	0.04	0.03	0.06
Cupressaceae	25	29	27	32	21
Picea	0.05	0.20	0.10	0.46	0.11
Pinus	0.31	0.36	0.70	0.82	1.0
Pseudotsuga	0.09	0.14	0.14	0.38	0.86
Tsuga heterophylla	2.1	3.8	3.2	4.9	7.5
Alnus	67	56	64	55	60
Betula	3.3	3.6	1.7	1.8	2.4
Other Arboreal Pollen	0.19	0.11	0.31	0.07	0.17
Corylus	0.27	0.67	0.12	0.05	0.35
Ericaeae	0.01	0.01	0.04	0.02	0.02
Myrica gale	0.34	3.6	0.68	0.11	0.02
Salix sp.	0.18	0.14	0.23	--	0.26
Rosaceae > 20 um	0.05	0.15	0.18	0.07	0.09
Spiraea	0.24	0.15	0.04	0.41	0.26
Other Shrubs	0.10	0.05	0.05	--	0.04
Poaceae	0.92	0.92	1.0	2.8	3.5
Cyperaceae	0.03	0.03	0.01	0.04	0.07
Compositae	0.03	0.08	0.04	0.07	0.09
Plantago lanceolata	0.09	0.05	0.08	0.18	0.15
Rumex acetosella	0.001	0.05	0.01	0.08	0.05
Other Herbs	0.02	--	0.01	0.03	0.07
Fern Spores	0.09	0.46	0.24	0.15	0.35
Pteridium	0.01	0.03	0.02	0.02	0.05
Other Spore	--	--	0.003	--	0.01
Unknown	0.37	0.50	0.44	0.33	0.51

* A1 = Marion Lake centre, A2 = Marion Lake west shore, A3 = Marion Lake east shore, A4 = Surprise Lake.

Table 7. Correlation coefficients calculated for total numbers of pollen grains captured in glass jar samplers and totalled over all common sampling periods at Marion Lake and Surprise Lake 1977/1978.

Sampler I	Sampler II	Correlation Coefficient
jar Marion L. centre (A1)	jar Marion L. east shore (A3)	0.998
jar Marion L. centre (A1)	jar Marion L. west shore (A2)	0.991
jar Marion L. east shore (A3)	jar Marion L. west shore (A2)	0.995
jar Marion L. centre (A1)	jar Surprise L. (A4)	0.979

This conclusion can be examined more thoroughly by comparing the depositional behaviour of individual taxa in the aerial samplers. Statistically significant differences in aerial pollen influx occur for Western Hemlock when results are compared for the samplers in the centre of Marion (A1) and Surprise (A4) Lakes and between the lakeshore sampler (A2) and the mid-lake sampler at Marion Lake (A1). Western Hemlock influx in these samplers is shown in Figure 8, and the rapid attenuation of pollen influx with distance from the Marion Lake shore emphasizes the non-regional depositional behaviour of this species.

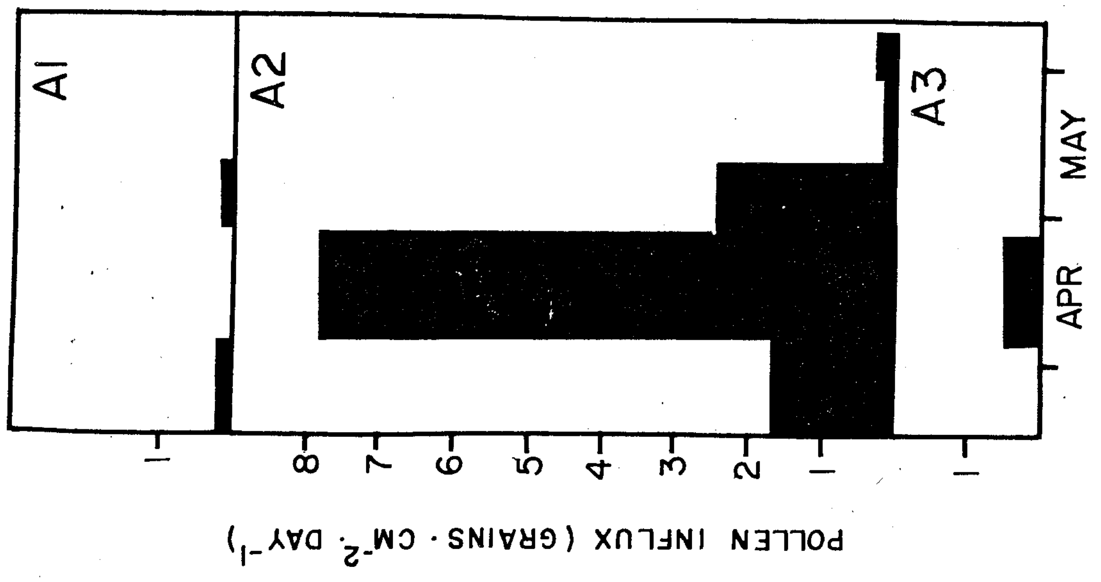
A similarly poor dispersion is expected for Douglas-fir pollen because Ebell and Schmidt (1964) state that it is not as well dispersed as Western Hemlock and Wright (1952) has estimated that Douglas-fir deposition is insignificant beyond 20 m from a source tree. However, no significant difference is recorded between the different sampling stations for this species. This is probably because Douglas-fir is not abundant within 100 m of either lake (Table 1, Chapter 3.1) so that Douglas-fir deposition is reduced to regional values in the lake sampler.

Myrica gale is a major component of the shoreline vegetation at Marion Lake and significant influx differences are indicated between the shore sampler (A2) and the mid-lake sampler (A1). Myrica influx is also significantly different between the two shore samplers at Marion Lake, one placed below the level of *Myrica* shrubs (A2) and the other positioned above the *Myrica* stand (A3) (Figure 8). These results provide an example of local deposition where pollen influx declines to regional values immediately above the *Myrica* stand and in the centre of Marion Lake. Another example of local deposition by *Calamagostis canadensis* is discussed later with reference to dispersal distances.

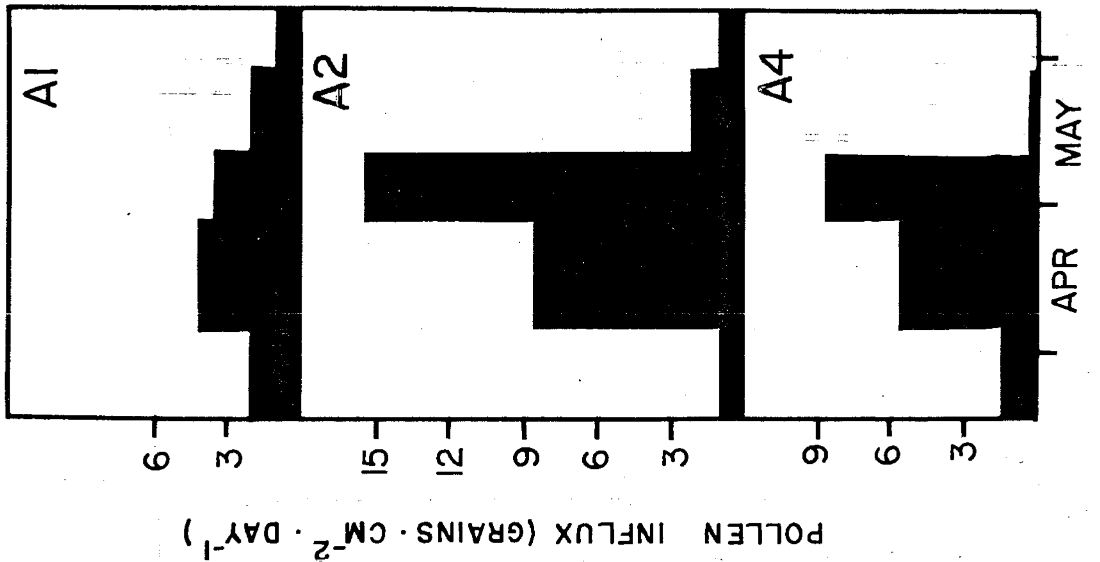
Deposition in the different aerial samplers is shown for Cupressaceae in Figure 8 and *Alnus* in Figure 9. *Pinus* and *Betula* influxes show similar trends in smaller amounts. No significant influx differences are indicated for any of these taxa in the different samplers and this relatively uniform deposition at all sampler locations points to a regional source for these grains.

Having proposed that most pollen deposited in aerial samplers in the study area is the result of regional transport, it is of interest to estimate how far pollen is travelling by this process. Figure 9 uses the observed lapse rate of Red Alder flowering times to demonstrate a minimum distance for pollen transport of that species. Red Alder forms significant stands away from alluvial habitats only outside the study area at lower elevations. Within the study area it occurs mostly on alluvium although isolated individuals do grow in upland situations. Only one Red Alder individual was observed within 100 m of Surprise Lake. Of particular interest is a stand of Red Alder adjacent to the south-eastern shore of Marion Lake (Figure 3) because it was expected that local depositional effects of this stand would be recorded in the samplers at Marion Lake. The maps in Figure 9 show isolines of flowering development for Red Alder based on field observations at the locations indicated on the maps. Phenological observations for Red Alder and *Alnus viridis* are also included in Figure 9 and point out that Red Alder pollen influx is responsible for the large increases in *Alnus* pollen influx. The graphs in Figure 9 show pollen influx histograms for the samplers at Marion and Surprise Lakes. Maximum influxes are recorded at all samplers (except on the west shore of Marion Lake) during the February 24 to March 17 sampling period which is before Red Alder comes into full flower in the study area. This pollen, therefore, must have been transported at least 2 km and probably much

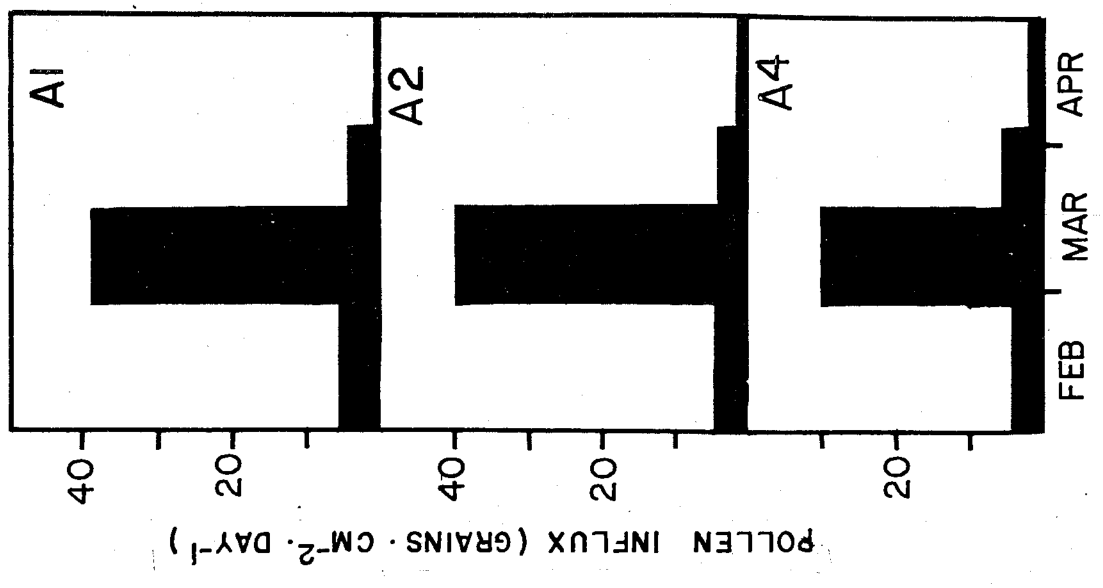
Figure 8 Aerial pollen influx histograms for *Myrica gale*, Western Hemlock, and Cupressaceae in selected glass jar samplers at Marion and Surprise Lakes. A1 = Marion Lake centre, A2 = Marion Lake west shore, A3 = Marion Lake east shore, A4 = Surprise Lake.



Myrica gale

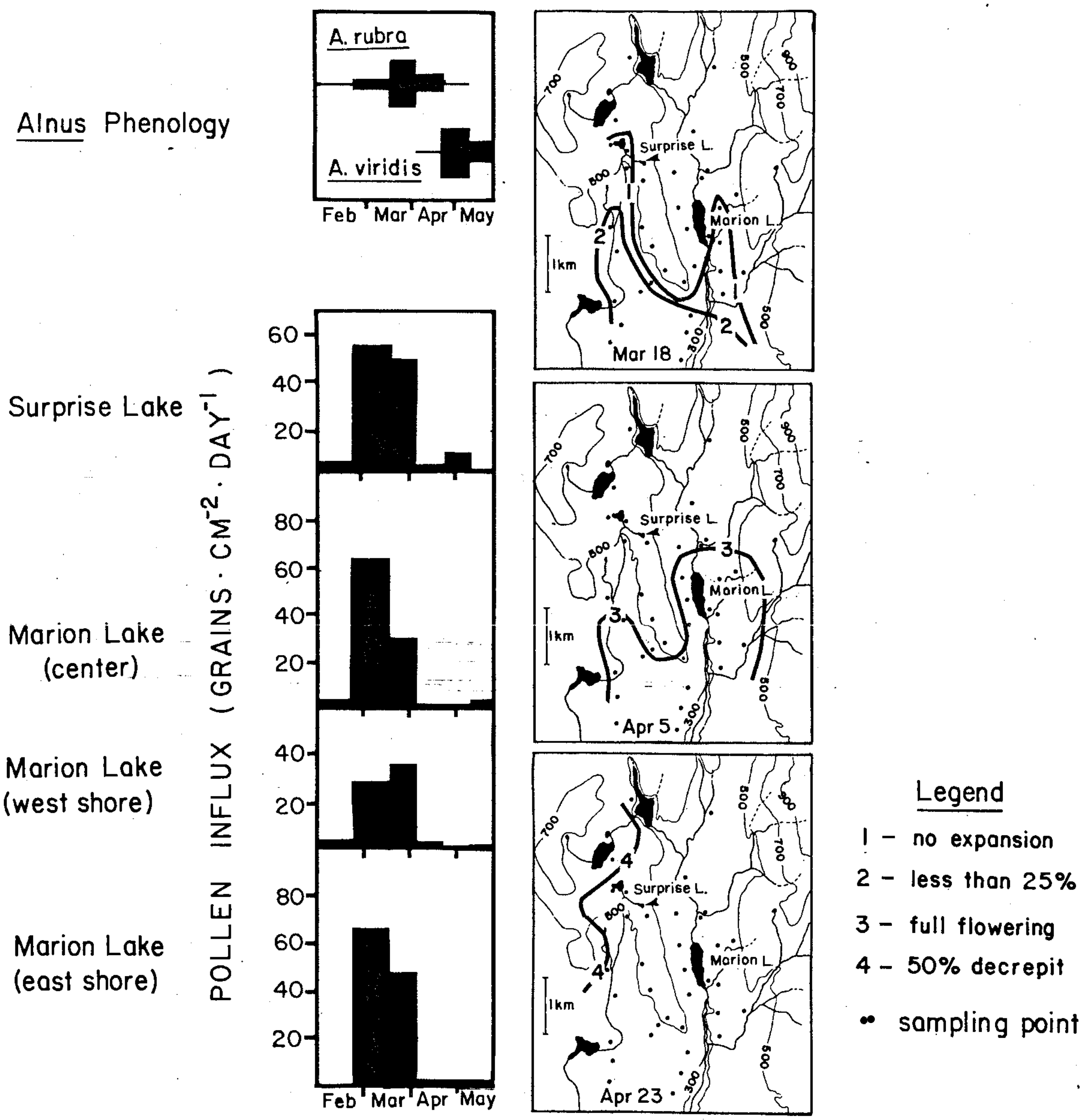


Tsuga heterophylla



Cupressaceae

Figure 9 Alnus pollen influx at Marion and Surprise Lakes compared with isolines of observed Red Alder flowering status on aerial pollen sampler collection dates.


Alnus Phenology
A. rubra
A. viridis
Feb Mar Apr May
Surprise Lake
Marion Lake (center)
Marion Lake (west shore)
Marion Lake (east shore)
POLLEN INFLUX (GRAINS · CM^{-2} · DAY^{-1})
60
40
20
80
60
40
20
40
20
80
60
40
20
Feb Mar Apr May
Surprise L.
Marion L.
1km
700
800
900
300
500
Mar 18
Apr 5
Apr 23
1
2
3
4
Legend
1 – no expansion
2 – less than 25%
3 – full flowering
4 – 50% decrepit
• sampling point

further because Red Alder forms large successional stands throughout the Fraser Valley. The similarity in influx between Marion and Surprise Lakes gives some idea of the evenness of the *Alnus* pollen concentration in the atmosphere over the study area for this period. During the sampling period ending April 4, Red Alder reaches full anthesis in the study area while influx declines in almost all aerial samplers, emphasizing the lack of quantitative impact of the *Alnus* stand adjacent to Marion Lake, compared to pollen transported from outside the study area.

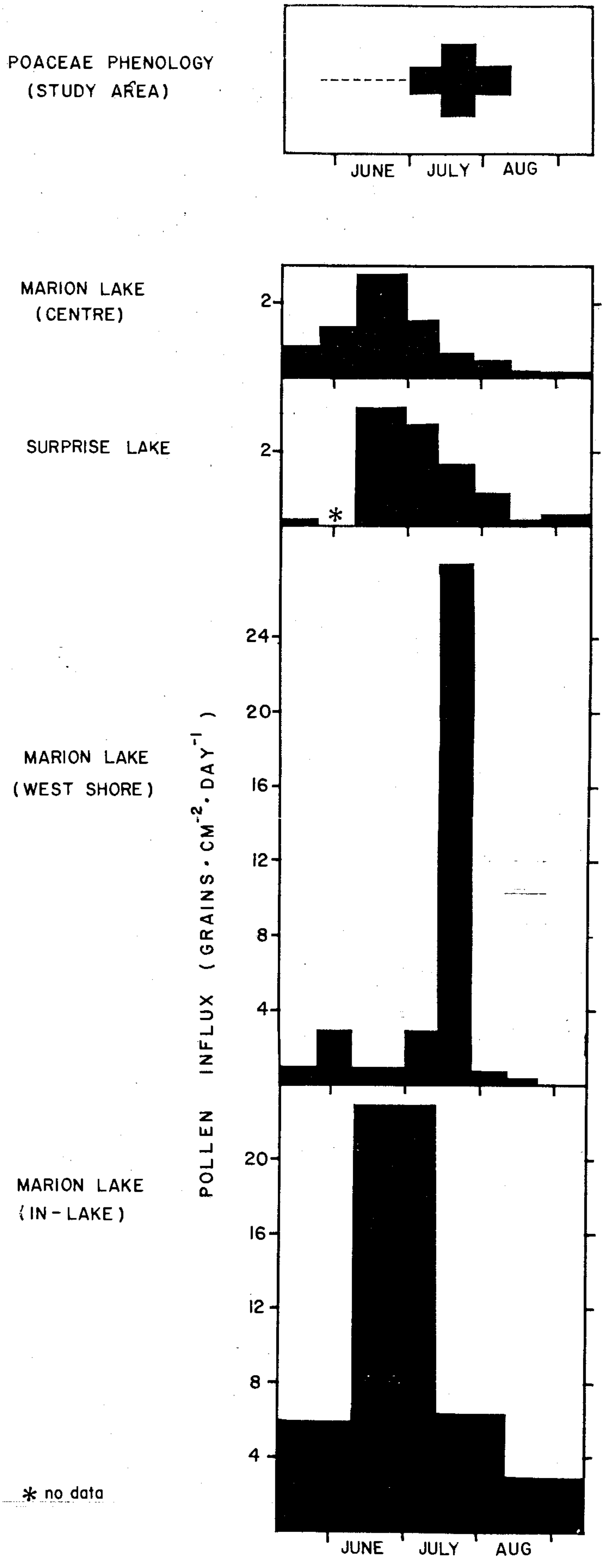
Figure 10 compares pollen influx histograms and phenological observations for grasses. The peak values at the centres of Marion and Surprise Lakes during the latter half of June must have a source outside of the study area because grasses were in a pre-flowering state at this time. The nearest source is agricultural land in the Fraser Valley 6 km to the southwest and 8 km to the south. The dramatic influx peak of 28.5 grains $cm^{-2} . day^{-1}$ recorded on the west shore of Marion Lake at the end of July can be confirmed as local by phenological records on *Calamagrostis canadensis*, and by the observation that this increase is absent in the mid-lake sampler at Marion Lake. Figure 10 also demonstrates the lack of impact that this local deposition has on the in-lake samplers suspended in Marion Lake. The peak for grass influx in the submerged samplers at Marion Lake is coincident with peaks in regional grass influx in the aerial samplers and returns to background levels as the local *Calamagrostis* reaches full flower.

These examples indicate that pollen is transported upslope in quantity over a minimum distance of 2 km for *Alnus* pollen and, in much smaller amounts, at least 6 km for grass pollen. They also emphasize the fact that this regional deposition is of sufficient magnitude to obscure effects of local vegetation at the two sampling sites.

Depositional Groups

The major pollen-producing taxa in this study have been organized into three depositional groups (Table 8) adapted from Janssen (1967) on the basis of aerial pollen sampling observations. For some taxa such as

Figure 10 Poaceae pollen influx recorded in aerial and in-lake samplers at Marion and Surprise Lakes and observations of *Calamagrostis canadensis* flowering at Marion Lake.


POACEAE PHENOLOGY
(STUDY AREA)
JUNE
JULY
AUG
MARION LAKE
(CENTRE)
2
SURPRISE LAKE
2
*
MARION LAKE
(WEST SHORE)
24
20
16
12
8
4
POLLEN INFLUX (GRAINS · CM⁻² · DAY⁻¹)
MARION LAKE
(IN-LAKE)
20
16
12
8
4
JUNE
JULY
AUG
* no data

Abies and *Picea*, it was not possible to describe any particular type of depositional behaviour and, in these cases, information from the palynological literature has been utilized to help classify the pollen types.

Table 8. Classification of important pollen-contributing taxa into depositional groups.

REGIONAL	EXTRALOCAL	LOCAL
Alnus	*Tsuga heterophylla*	*Myrica gale*
Cupressaeae	*Pseudotsuga menziesii*	Filicales
Pinus	*Abies*	*Pteridium*
Poaceae	*Picea*	Compositae
Rumex acetosella	*Tsuga mertensiana*	Cyperaceae
Plantago lanceolata	*Acer macrophyllum*	*Salix*
Betula		Ericaceae
Corylus		Rosaceae

Regional types include taxa which are well represented outside of the particular life-zone in which they occur. In this study and others (Heusser 1973, Markgraf 1980) regional types are dispersed from low to high elevations although Schmidt and Hamblett (1962) warn that this is not always the case. No significant differences in pollen influx at the various sampling locations have been demonstrated for *Alnus*, Cupressaceae, *Betula*, and *Pinus*. Grasses, *Rumex acetosella* and *Plantago lanceolata* most likely have their origin in the agricultural and urban areas of the Fraser Valley. These regional taxa account for 83% of annual aerial influx at Marion Lake. This regional dispersion across biogeoclimatic boundaries has obvious implications for the interpretation of fossil pollen assemblages in mountainous areas. Markgraf (1980) has come to a similar conclusion in her study of changes in pollen influx with elevation in Switzerland.

Extralocal taxa may be very important for the interpretation of fossil pollen assemblages in the Coast Mountains of British Columbia. They are usually not well represented outside of the vegetation zone in which they occur because of reduced dispersal capacity or low pollen production. In this study significant differences in aerial influx were demonstrated for Western Hemlock (Chapter 3.2) and, although I have not been able to illustrate this for the other taxa in the group, their physical properties and low representation suggest that they should be considered as extralocal types. This has already been mentioned for Douglas-fir. Heusser (1977) uses Abies, Mountain Hemlock, Western Hemlock, Picea, and Douglas-fir as indicators of vegetation zones on the basis of moss polster studies (Heusser 1969, 1973). Heusser (1977) does not use Alnus, Cupressaceae and Pinus pollen as zonal indicators because they are either "overrepresented and/or low pollen producers". Maher (1963) has demonstrated extralocal behaviour for Picea in small lakes in the mountains of Colorado. Barnosky (pers.comm.) has collected surface samples in a series of lakes in an elevational transect in the Cascade Mountains of Washington. Her data show a pollen representation which reflect vegetational distributions for Western Hemlock, Mountain Hemlock, Abies, Douglas-fir and Picea. Pinus, Cupressaceae and grasses show a regional trend. Considering the overrepresentation of regional taxa, the use of extralocal depositional types as indicators of biogeoclimatic zones may present a solution to this problem. This is discussed further in Chapter 4.

Many pollen types in the local category are entomophilous so that pollen production is low and dispersion is poor. Local deposition was demonstrated earlier for the wind-dispersed pollen of Myrica gale. Ferns are included in this group as are many of the shrub and herb taxa represented in the pollen rain in the study area. The representation of local types is increased by fluvial transport processes and this is discussed in Chapter 3.3.

Summary

Aerial pollen deposition in the study area is dominated by regionally-dispersed pollen types, predominantly Alnus and Cupressaceae. Regional taxa are transported upslope during dry spring weather suitable for anthesis and deposited in a relatively even "pollen rain" over the study area. The similarity of pollen influx rates throughout the study area emphasizes the evenness of aerial pollen deposition throughout the study area. Rain-scouring is responsible for some of this deposition although its quantitative significance has not been estimated in this study. Although examples of local and extralocal deposition have been observed for some taxa most of these effects are diluted by the large quantities of pollen grains transported from lower elevations. The lack of downslope transport in the study area is indicated by the poor representation of Mountain Hemlock pollen even though this species is abundant and flowering successfully directly above the two sampling sites.

3.3 Stream Pollen

Recruitment and Representation of Stream-Transported Pollen

Previous research by Peck (1973), Bonny (1977), and Tauber (1977) has indicated that stream-fed lakes derive a significant proportion of sedimented pollen from stream transport. In this chapter the quantitative importance and pollen recruitment strategy of the fluvial component is analyzed at Marion Lake.

Figure 11 shows seasonal changes in pollen influx (grains . cm^{-2}. day^{-1}) in the inflow sampler at Marion Lake. Average discharge(m^3/sec) for each sampling period in the inflow stream is also indicated, as compiled from data collected by the Water Survey of Canada at the Jacobs Creek above Marion Lake gauging station. Figure 11 demonstrates that pollen influx in the inflow stream does not reflect the same trends shown for aerial pollen influx. Rather, influx in the inflow stream sampler varies as a linear function of stream discharge as shown by the regression line in Figure 12. The high positive correlation ($r = 0.934$) is unusual in that, according to hydrologic theory, there should be a curvilinear relationship between discharge and suspended load (Leopold and Miller 1956). This apparent anomaly is probably a result of the reduction in sampling efficiency with increasing water velocity for these samplers as determined by Peck (1972). This conclusion can be supported by comparing the stream sampler in the Marion Lake inflow with another stream sampler positioned about 1 km upstream from the inlet to Marion Lake, at the Water Survey of Canada gauging station. The stream narrows at this point, therefore stream velocity increases, and, although there is still a strong linear relationship between pollen influx and discharge ($r = 0.974$) pollen influx is always between two and five times lower than in the sampler positioned in the Marion Lake inflow.

Figure 11 Changes in pollen influx(histograms, in the inflow stream sampler compared with stream discharge (line graph).

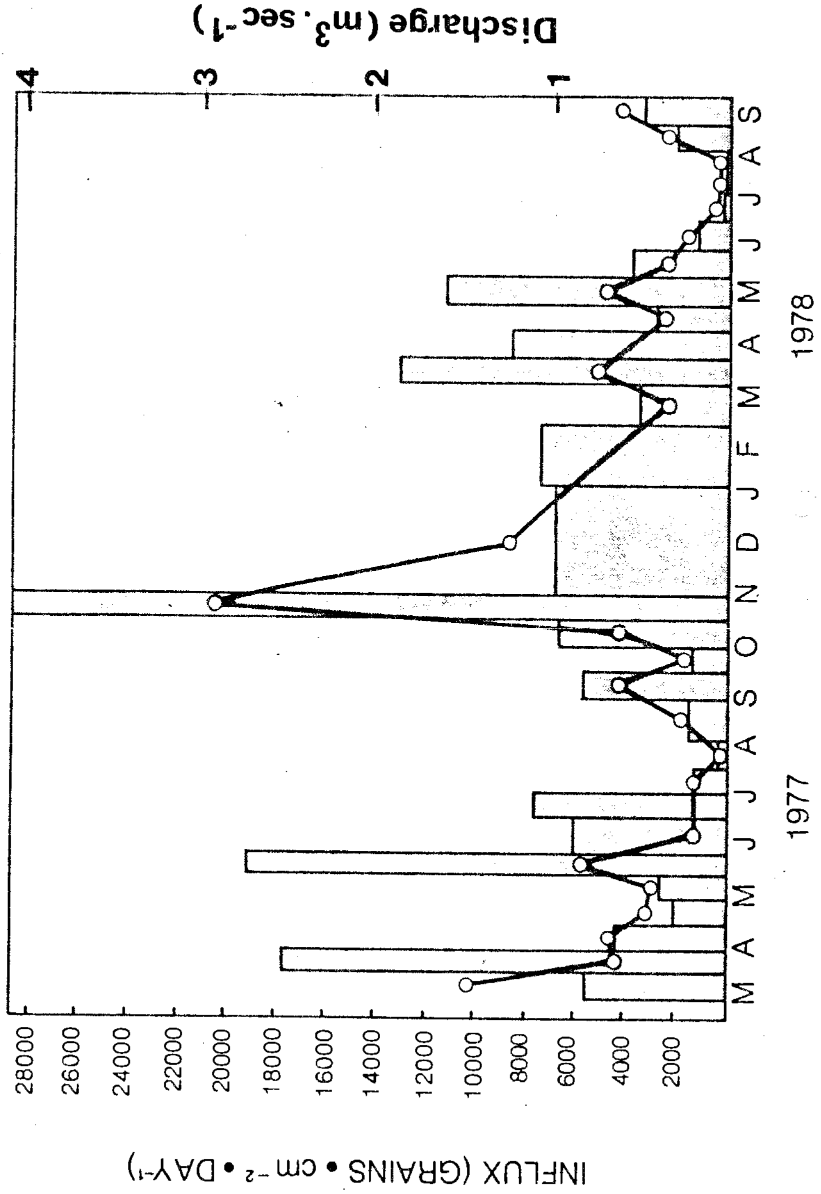
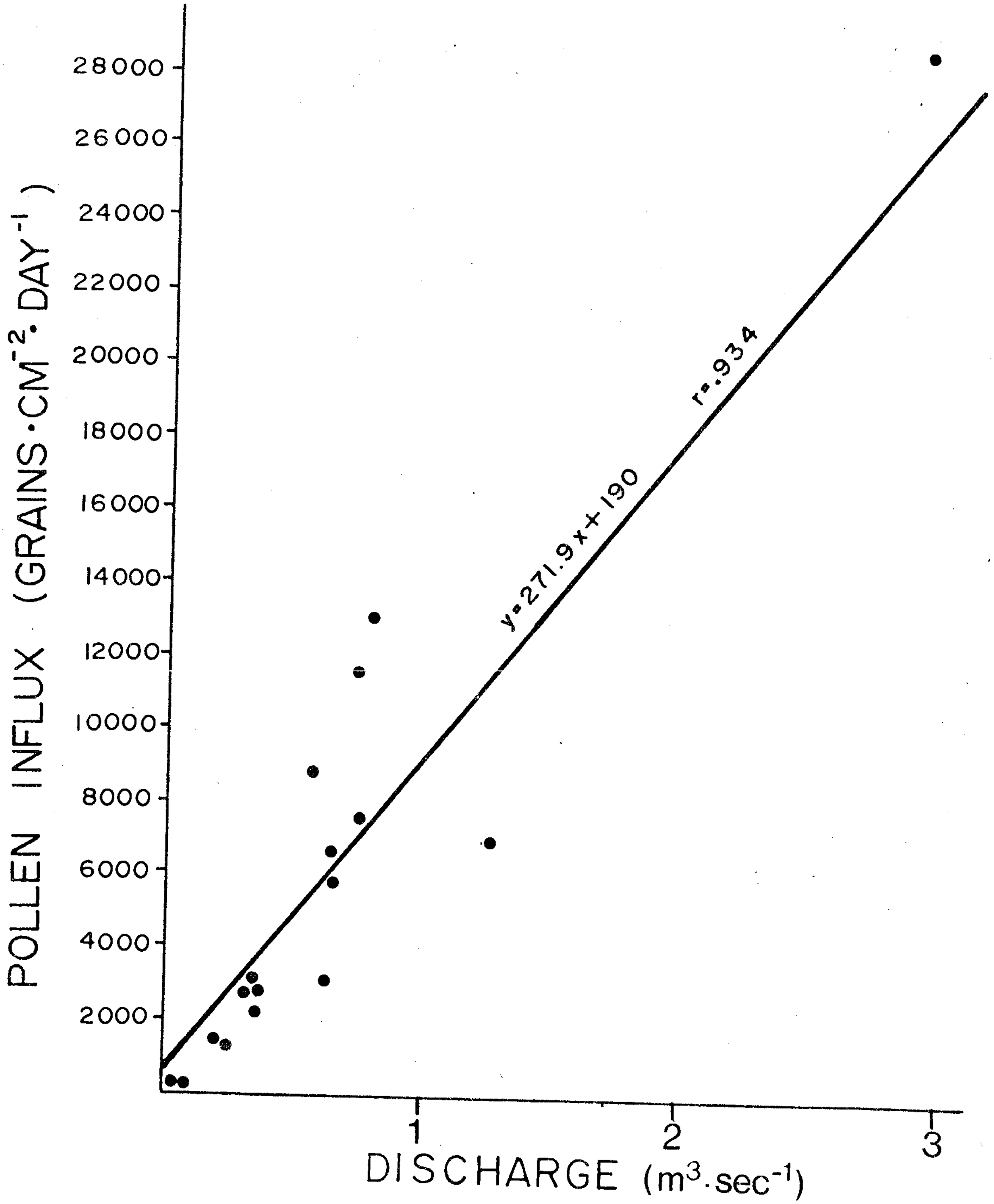

Discharge (m³. sec⁻¹)
4
3
2
1
INFLUX (GRAINS • cm⁻² • DAY⁻¹)
28000
26000
24000
22000
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
M A M J J A S O N D J F M A M J J A S
1977
1978

Figure 12 Linear regression comparing pollen influx in the Marion Lake inflow stream sampler with stream discharge.

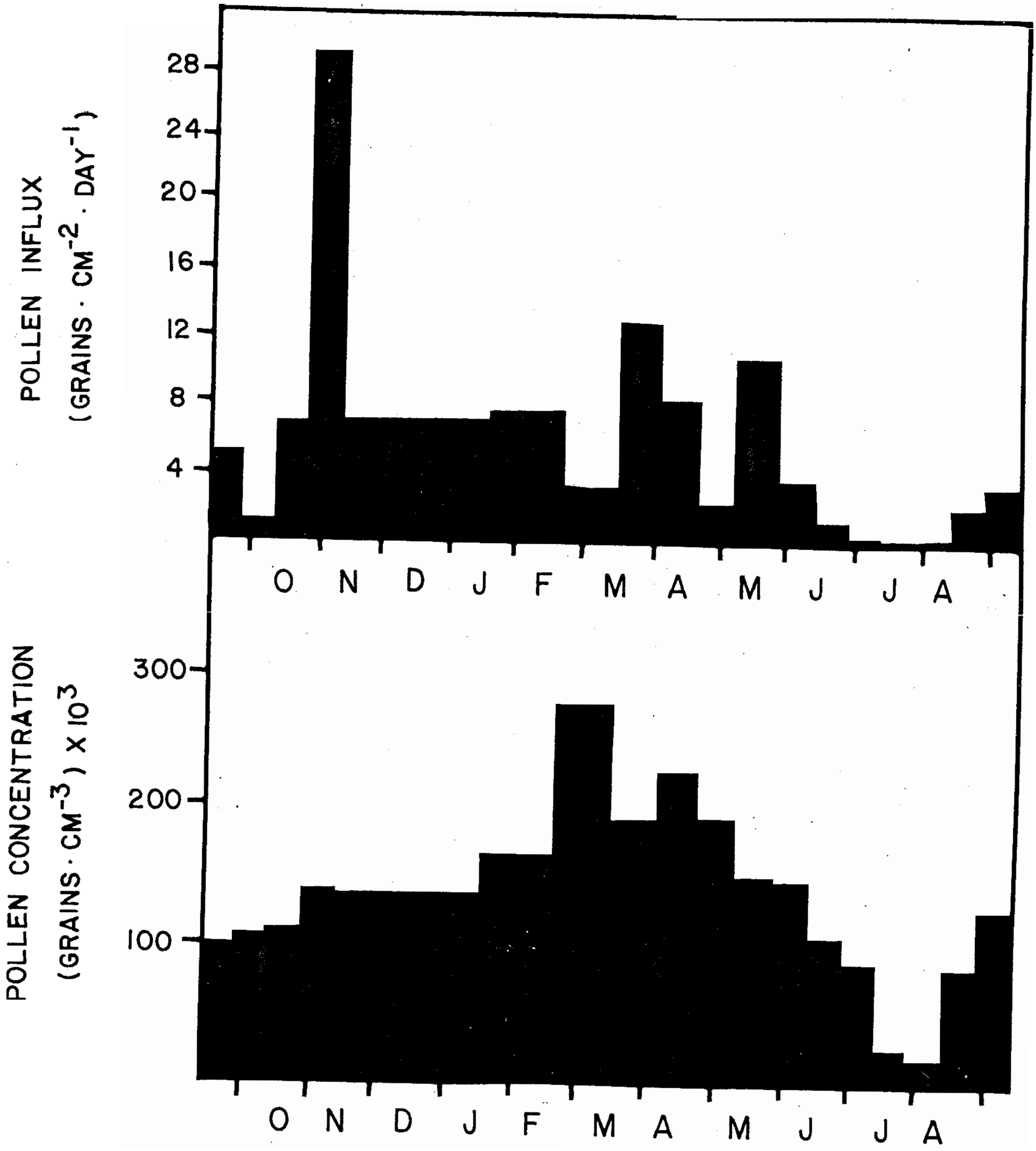

POLLEN INFLUX (GRAINS·CM^{-2}· DAY^{-1})
28000
26000
24000
22000
20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
DISCHARGE (m^3·sec^{-1})
1
2
3
y=271.9x+190
r=.934

Excluding the possibility that the higher influx recorded in the Marion Lake inflow sampler is recruited in the 1 km distance between the two samplers, the lower values in the upstream sampler must be caused by the decreasing sampling efficiency of the stream samplers as a function of differences in stream velocity at the two sampling points. This implies that the high pollen influxes recorded during the winter months actually underestimate the quantity of stream pollen input into Marion Lake during these high discharge periods. Regardless of changes in sampler efficiency, the high positive correlation between discharge and pollen influx in the inflow samplers implicates erosion in the drainage basin as the major process responsible for stream pollen recruitment.

Figure 13 presents changes in total pollen concentration in the sediment trapped by the inflow sampler at Marion Lake. Unlike pollen influx, high stream dicharges have little effect on the concentration of pollen grains in the suspended load of study area streams. The highest concentrations occur during the February 24 - March 17 sampling period and the stream pollen spectrum during this period is predominantly composed of *Alnus* and Cupressaceae. It was shown in Chapter 3.2 that *Alnus* pollen in the atmosphere over the study area at this time is dispersed from low-elevation stands and deposited in an even pollen rain throughout the study area. It is, therefore, this regional aerial deposition which is responsible for the increase in pollen concentration in the suspended sediment, and not aerial input from study area vegetation. The two lakes above Marion Lake (Eunice and Gwendoline, see Figure 3) must act as large pollen-collecting surfaces for this regional aerial influx and some of these grains are subsequently exported via the outflow streams of these basins into the inflow stream of Marion Lake. Although this aerial influx is of sufficient magnitude to cause changes in pollen concentration, it is obvious from Figure 13 that these concentration increases have little effect on the quantity of palynomorphs entering Marion Lake by the inflow stream. The highest peak in concentration (February 24 to March 17 period) is coincident with a very low pollen influx in the inflow sampler.

The relative importance of erosion and direct aerial input has been estimated by calculating the correlation coefficient ($r = 0.977$) between

Figure 13 Changes in pollen influx and pollen concentration in the inflow stream sampler at Marion Lake.


POLLEN INFLUX
(GRAINS · CM^{-2} · DAY^{-1})
28
24
20
16
12
8
4
O
N
D
J
F
M
A
M
J
J
A
POLLEN CONCENTRATION
(GRAINS · CM^{-3}) X 10^{3}
300
200
100
O
N
D
J
F
M
A
M
J
J
A

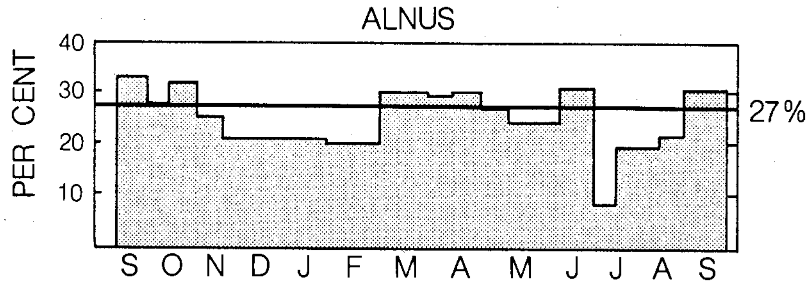
discharge and pollen influx in the inflow sampler for the non-flowering period when aerial influx is minimal in the study area. Due to this high correlation, expected influx can then be calculated for discharge values during the flowering period from this regression line. Any "surplus" influx above that expected from discharge during the flowering period, can then be attributed to direct aerial input. By this procedure it is estimated that erosive processes account for 80.1% of stream pollen with direct aerial input making up the remaining 19.9%

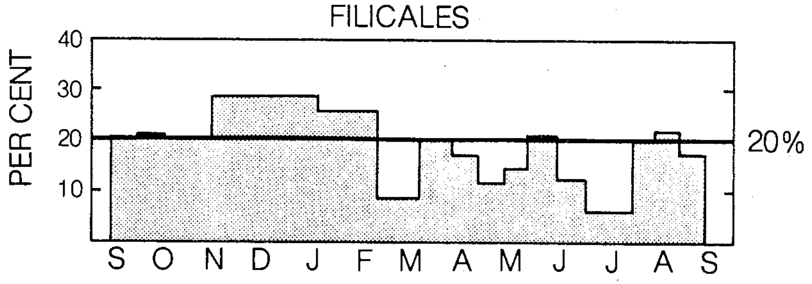
Erosion is therefore the most important recruitment process contributing pollen grains to the streams of the Marion Lake drainage basin. It is important to identify source areas of suspended sediment in the catchment if we are to understand what vegetation is represented by the pollen spectrum in the stream sampler. The Marion Lake catchment is mantled by very coarse soils which have developed from loose ablation till overlying impermeable lodgement till or bedrock. Relief is extreme in many areas of the catchment and these factors combine to create a dynamic fluvial environment where discharge responds very rapidly to precipitation. The hydrologic model which best describes the stormflow behaviour of streams in mountainous areas is that proposed by Hewlett and Hibbert (1967). It has been utilized to describe fluvial behaviour in a nearby watershed by Plamondon (1972). This model is based on the concept of a "variable source area" whereby precipitation rapidly infiltrates soils and travels downslope by subsurface flow until the capacity of soils to transport it is reached. At this point the water is forced to the surface and, as a result, channel lengths grow and the drainage net "reaches out" to more elevated regions of the catchment. Therefore, at low discharges the channel network is much shorter than during storms when the drainage net expands as a function of the amount of precipitation. Overland flow is very rare in this situation and occurs over only a very limited area adjacent to streams. Because of the lack of overland flow, sheet erosion is not an important erosive process in the study area and this implies that erosion from surface flow during drainage net expansion and erosion from streambanks are the predominant sources of eroded pollen in catchment streams. Recruitment by streambank erosion will collect pollen from different areas of the catchment as precipitation varies. During large storms the drainage net is increased so that pollen is eroded from a larger area than during periods of low precipitation.

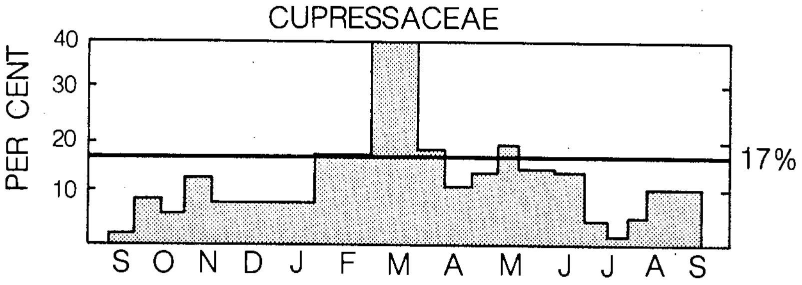
On the basis of these arguments the following model is put forward to describe the processes of pollen recruitment by the streams of the Marion Lake catchment. Stream erosion is the major pollen-recruiting process in the study area, accounting for approximately 80% of all grains delivered to Marion Lake by fluvial transport. The area of the drainage basin which contributes pollen in this manner changes as a function of drainage net fluctuations in response to precipitation events in the watershed. During heavy rainfall the drainage net extends via intermittent streams to higher elevations in the catchment and pollen is eroded from a wide area of the Marion Lake drainage basin. During low summer dischages, erosion is dramatically reduced as flow occurs only in the centre of streambeds over a limited area of the watershed. The direct aerial input of pollen grains accounts for the remaining 20% of pollen transported by the inflow stream and much of this is regional influx captured by two lakes above Marion Lake and transported to the inflow sampler by the stream network. A portion of the direct aerial input must be from grains washed from foliage by precipitation and redeposited onto the stream surface (Kryzwinski 1977b) but no attempt was made to measure this process. In the discussion which follows I shall utilize this model to interpret the seasonal changes in the relative pollen frequencies of some important taxa.

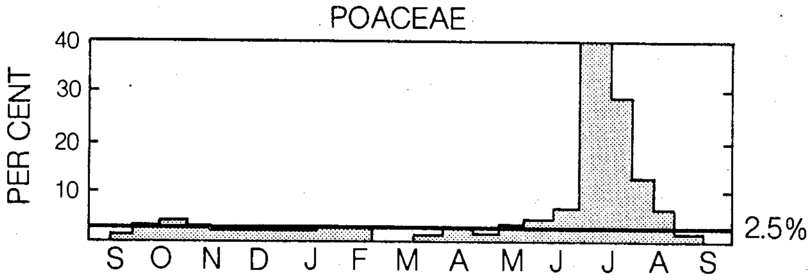
Figure 14 illustrates changes in the relative frequencies of selected taxa in the inflow sampler at Marion Lake from September 9, 1977 to September 13, 1978. Average annual frequency for each taxon is indicated by the horizontal line in each graph and these annual values are compared with average frequencies for these taxa during the non-flowering period (September 9, 1977 to January 16, 1978) in Table 9. The stream spectrum during the non-flowering period represents pollen eroded from catchment soils. It is apparent from Table 9 that the average annual frequencies deviate very little from the average frequency of those taxa during the non-flowering period. This point emphasizes the importance of erosion as the major recruitment process employed by the streams of the Marion Lake catchment. One notable exception is for Cupressaceae whose relatively poor

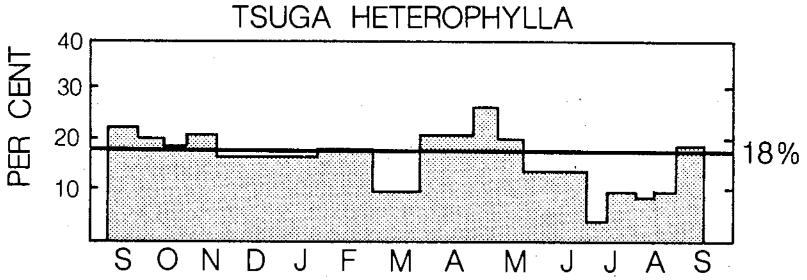
Figure 14 Changes in the relative frequencies of selected taxa in the inflow stream sampler at Marion Lake from September 9, 1973 to September 13, 1978. The average annual frequency for each taxon is indicated by the horizontal line in each graph.


ALNUS


FILICALES


CUPRESSACEAE


POACEAE


TSUGA HETEROPHYLLA

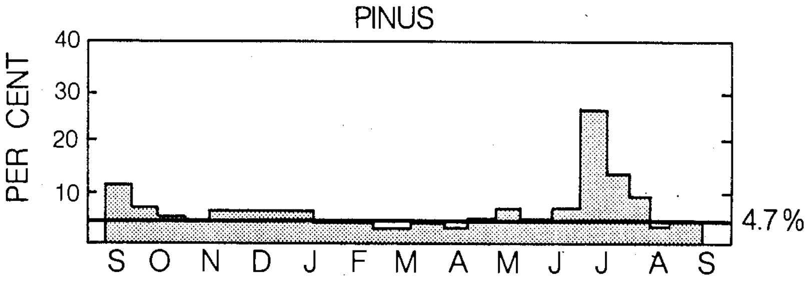

PINUS

Table 9. Comparison of average annual frequencies with frequencies during the non-flowering period in the inflow stream sampler at Marion Lake.

	NON-FLOWERING PERIOD (Sept 9/77 - Jan 16/78) (%)	ANNUAL (Sept 9/77 - Sept 13/78) (%)
Alnus	27.3	27.0
Cupressaceae	7.1	17.0
Tsuga heterophylla	19.2	18.0
Filicales	22.0	20.0
Poaceae	2.3	2.5
Pinus	6.5	4.7

representation during the non-flowering period is increased almost threefold by its direct aerial input during the flowering period. It is postulated in Chapter 3.2 that Cupressaceae pollen is very susceptible to corrosion and this probably explains its low frequency during the non-flowering period. All taxa show an increase in relative frequency during that part of the flowering period when they are present in the aerial spectrum. In all cases other than Cupressaceae this direct deposition is not sufficient to significantly alter their representation in the average annual fluvial spectrum. This effect is illustrated by the dramatic increases in the relative frequencies of Poaceae and *Pinus* during June and July when these taxa are in flower. During this period discharge is very low in catchment streams and pollen concentration in the inflow stream at Marion Lake is reduced by the lack of erosion in the drainage basin. In this situation the aerial influx of *Pinus* and Poaceae permits them to briefly dominate the stream spectrum. These large percentage increases have little effect on average annual values and for most of the year *Pinus* and Poaceae pollen is present at low and very constant background levels which closely parallel average annual frequencies. These observations support the pollen-recruitment model which has been presented above in which pollen eroded from the Marion Lake catchment is the most important source of pollen in the inflow stream.

The inflow spectrum can be compared to the aerial spectrum by examining the average annual frequencies for the most important pollen-contributing taxa. These are listed in Table 10. Two important points are revealed by this analysis:

(1) Almost all taxa listed as regional depositional types in Chapter 3.2 have lower average annual frequencies in the stream spectrum than in the aerial spectrum. *Alnus* frequency is only slightly lower but the representation of other regionally-dispersed types, such as Cupressaceae, *Betula*, and grasses is decreased between two and four times in the stream-transported pollen spectrum.

(2) Conversely, the relative frequency of the important extralocal and local depositional types increase their representation in the fluvial spectrum. This difference is recorded for Western Hemlock, Douglas-fir, *Abies*, *Pteridium* and especially fern spores.

The increase in representation for extralocal and local types in the fluvial spectrum indicates that the stream pollen spectrum represents a different vegetational area than the aerial spectrum. Pollen for the fluvial spectrum is derived primarily from the erosion of streambanks throughout the catchment, therefore, to understand what vegetation is represented by this pollen information, we must consider the deposition of pollen on the forest floor along streams. Although I have not examined this process, Andersen (1970) has studied the representation of surface samples from within forest stands in Denmark and his general conclusion is that the majority of pollen deposited at any point has a source in vegetation within 30 m of that point. This value cannot be applied directly to the situation in our study area because local stand characteristics, such as canopy height and slope effects in mountains could alter this distance but it does provide an estimate which has been widely accepted. It explains the increased representation of local and extralocal pollen types in the fluvial spectrum because their deposition would dominate the regional deposition in the development of soil pollen spectra along streambanks. The vegetation represented by the Marion Lake inflow pollen spectrum, therefore, is dominated by pollen from an approximate 30 m enlargement of the stream network. Superimposed on this local and extralocal deposition from catchment vegetation is a background component of regional deposition. The predominance of local and extralocal types in the stream pollen spectrum emphasizes the point that their poorer representation in the aerial spectrum is a result of their poorer dispersion.

I stated in Chapter 3.2 that extralocal types may be very important for the interpretation of fossil pollen assemblages in mountainous areas. Because of their poor dispersion their representation is not extended very far beyond the biogeoclimatic zone in which they occur. The heightened representation of extralocal types in the stream pollen spectrum supports the conclusions reached by Peck (1973) Cushing (1964) and Bonny (1977), namely that the fluvial component can provide a more accurate representation of vegetation around the sampling site than the aerial component. This is extremely important in mountainous areas where biogeoclimatic boundaries can be in close proximity to one another and regional deposition from lowland vegetation has been shown to dominate the aerial spectrum.

Table 10. Relative frequencies of major taxa in the inflow stream sampler (S1) and the aerial sampler (OT1) at Marion Lake.

TAXON	INFLOW STREAM (%)	AERIAL (%)
Abies	2.5	0.43
Cupressaceae	17	30
Picea	0.77	1.9
Pinus	4.7	4.5
Pseudotsuga	1.2	0.82
Tsuga heterophylla	18	7.2
Alnus	27	34
Betula	0.40	1.1
Corylus	0.21	0.14
Myrica	0.25	1.2
Ericaceae	0.09	0.10
Rosaceae > 20	0.91	0.32
Spiraea	0.19	0.67
Taxus	0.09	-
Poaceae	2.5	12
Plantago lanceolata	0.10	0.78
Rumex acetosella	0.04	0.23
Fern spores	20	3.8
Pteridium	3.4	0.12

There is one important objection which cautions against the utilization of depositional sites where fluvial transport is quantitatively important. Pollen grains and organic carbon from soils, peats and sedimentary rock, often of uncertain age, may be recruited by drainage basin streams and deposited out of chrono-sequence. This would complicate paleoecological investigations and radiocarbon dating. This objection is important only if such sites are interpreted without a careful examination of catchment geology and, more importantly, without comparing the results obtained from closed basins. In view of the many important alluvial facies as well as freshwater and oceanic sediments where fluvially-transported grains are an important determinant in the composition of the pollen spectrum, an understanding of how fluvial pollen is recruited, transported and deposited is mandatory for the proper interpretation of these fossil pollen sequences.

3.4 In-Lake Pollen

In-Lake Samplers

Total pollen influx rates (grains . cm^{-2} . day^{-1}) in the four submerged samplers have been compared for all sampling periods using a Wilcoxin Paired T-test and no significant influx differences have been established. The pollen spectra in these samplers are also very similar and the correlation coefficients comparing the total numbers of taxon pairs in these samplers points out the degree of similarity (Table 11).

Table 11. Wilcoxin T-scores and correlation coefficients for in-lake samplers at Marion Lake. (N.S. = not significant)

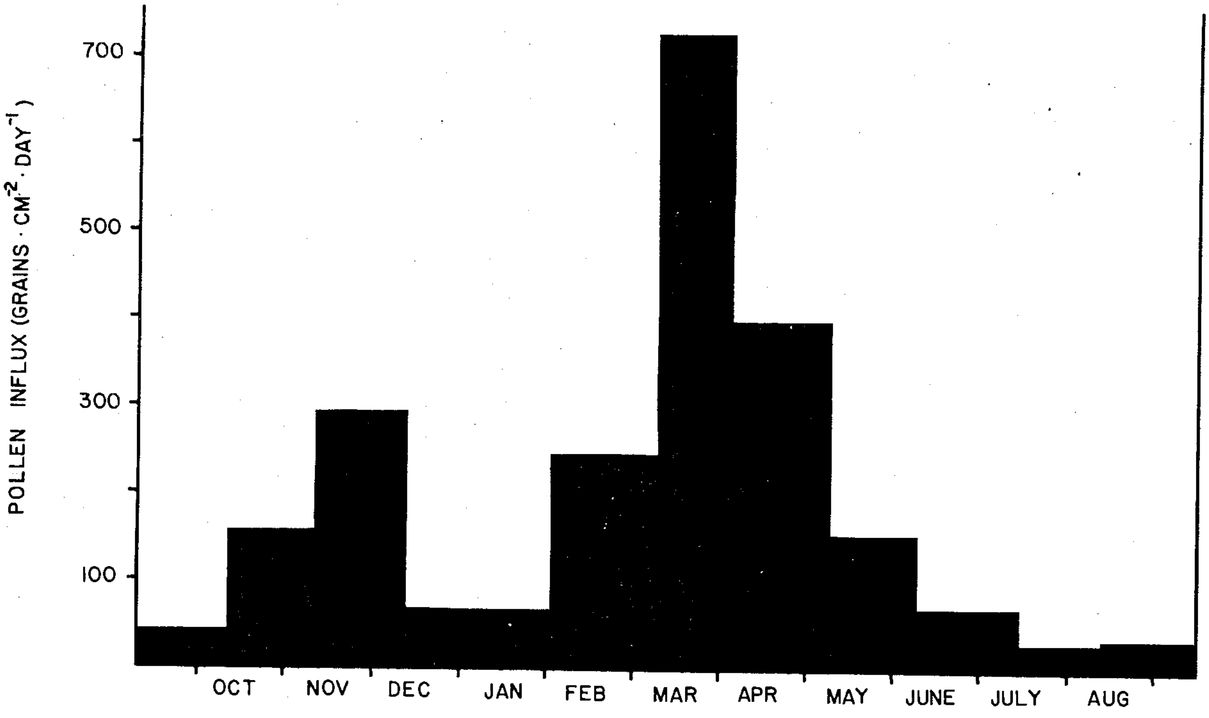
SAMPLERS COMPARED		T-SCORE	CORRELATION COEFFICIENT
L1	L2	41(N.S.)	0.995
L1	L3	43(N.S.)	0.994
L1	L4	32(N.S.)	0.976
L3	L2	35(N.S.)	0.996
L2	L4	54(N.S.)	0.994
L3	L4	62.5(N.S.)	0.956

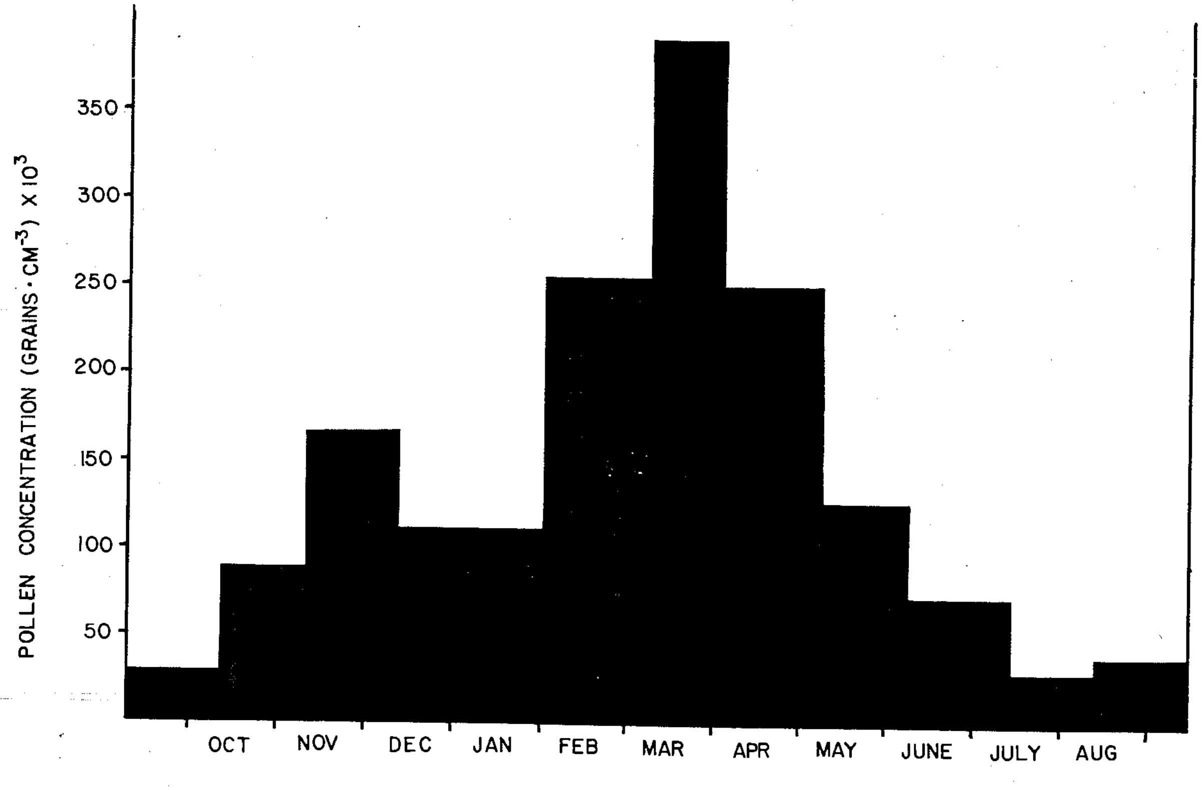
These results indicate that pollen in Marion Lake forms a relatively uniform suspension and support the findings of Brush and Brush (1972) and Davis (1968) who found a very homogenous mixture of suspended pollen types in their experiments. This does not necessarily imply that pollen deposition is uniform throughout Marion Lake. Brush and Brush (1972) have shown that, even with an homogeneous suspended component, the ratios of pollen deposited may differ. This is examined later in the discussion of surface samples.

Given the similarity of pollen influx and pollen ratios in the submerged samplers, Figure 15 was compiled by averaging all influx values (grains . cm^{-2} . day^{-1}) and all pollen concentration (grains . cm^{-3}) for all in-lake samplers at Marion Lake. The most obvious relationship in Figure 15 is that influx in the in-lake samplers varies directly ($r = 0.940$) with the concentration of pollen. This is in contrast to stream-transported pollen where concentration bears little relationship to pollen influx in the inflow stream sampler.

Pollen influx in the submerged samplers shows a minor peak (294 grains . cm^{-2} . day^{-1}) in November but the largest peak occurs in March (728 grains . cm^{-2} . day^{-1}) during the flowering period. This result is surprising in that the huge pollen influxes recorded in the inflow stream during the non-flowering period were expected to totally dominate pollen deposition in Marion Lake. Apparently the high stream discharges which deliver large amounts of pollen to Marion Lake during the winter create a situation where pollen is held in suspension and deposited in the southern half of Marion Lake or lost via the outflow stream. Pollen influx in the submerged samplers during a typical high discharge sampling period (Nov 11 - Dec 12) are relevant. Most of Marion Lake was frozen during this period except for an elongated trough in the middle of the basin which was maintained in an ice-free condition by the current generated by the inflow stream. The L3 sampler (see Figure 17) was the only one positioned in the ice-free portion of the lake (the L2 sampler was dislodged by ice) and it captured 5 to 6 times more pollen than the L1 or L4 samplers. During this period the inflow stream apparently continued as a stream through the ice channel and disappeared under the ice in the central area of the Marion Lake basin.

Figure 15 Pollen influx and pollen concentration recorded in in-lake samplers at Marion Lake from September 9, 1977 to September 13, 1978.


POLLEN INFLUX (GRAINS · CM^{-2} · DAY^{-1})
700
500
300
100
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG


POLLEN CONCENTRATION (GRAINS · CM^{-3}) X 10^{3}
350
300
250
200
150
100
50
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUNE
JULY
AUG

Marion Lake has been described as a "toilet bowl" which is flushed at regular intervals by violent stormflow in the Marion Lake catchment (Efford 1967). The extremely high pollen influxes recorded in the inflow stream sampler during these periods are not effectively deposited in the north end of Marion Lake because of the channeling of this stream discharge through the centre of Marion Lake. This subject is discussed later in the interpretation of Marion Lake surface samples.

The majority of in-lake pollen influx at Marion Lake is recorded during the flowering period and this suggests that aerial influx at Marion Lake is the most important pollen-contributing source. However, the spectra captured by the in-lake samplers during the flowering period reflect the influence of both fluvial and aerial inputs. For example, fern spores never comprise greater than 1% of the aerial spectrum during the flowering period yet their representation in the submerged samplers ranges from 3 - 13%. This is partially the result of stream pollen influx in which fern spores vary between 9 and 26% and indicate that the lower discharge in the inflow stream during the flowering period may be responsible for depositing more grains in Marion Lake than the high pollen influxes recorded in the inflow samplers during high winter discharges. Resuspended pollen may be important as well and the relative importance of this component as well as the aerial and fluvial components is estimated in Chapter 3.5.

Pollen influx in Marion Lake declines during the summer months when influx from all sources is very low.

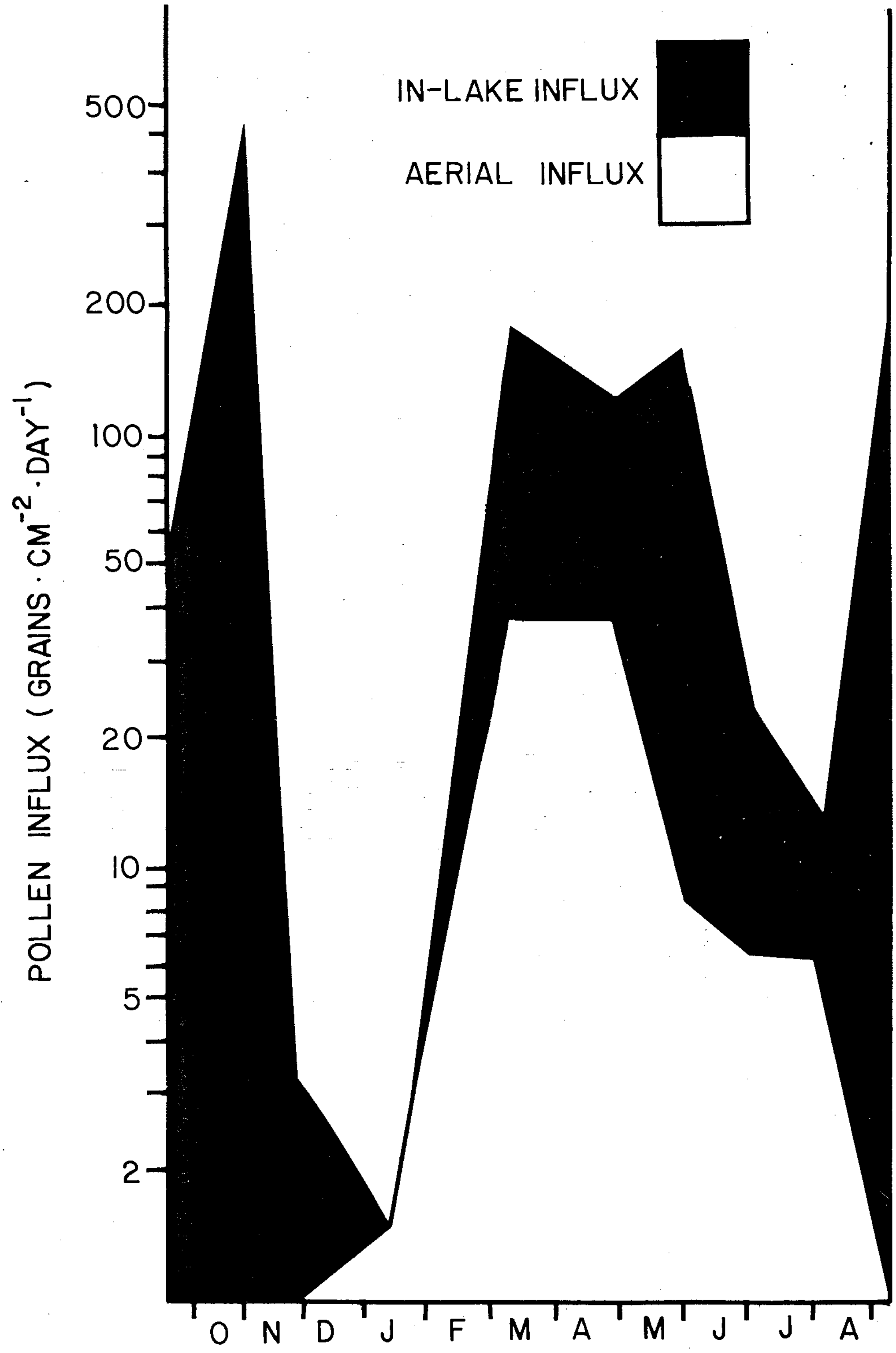
Surprise Lake

The annual pollen-depositional cycle at Surprise Lake is presented in Figure 16. Both aerial influx and in-lake influx have been included in order to relate deposition in the submerged samplers to aerial pollen deposition.

During the flowering period in-lake pollen influx in Surprise Lake increases with aerial influx suggesting that aerial influx is predominant from February to the end of July. Differences in the quantity of pollen grains during the flowering period in the two samplers may be a function of the difference in trapping efficiency between an aerial sampler and a lake surface as suggested by Tauber (1977). If aerial pollen influx is the main source of in-lake pollen then the pollen spectra in the two samplers should be very similar. A comparison of the spectra in the in-lake and aerial samplers was made by determining the correlation coefficients for the total numbers of the various taxa over common sampling periods. In general, correlation coefficients are very low indicating that even during much of the flowering period, much of the in-lake pollen influx does not have an aerial source. The highest correlation (r = 0.959) occurs during the April 4 to May 8 sampling period when the aerial sampler (unroofed Tauber-type) recorded a pollen influx of 38.5 grains . cm^{-2} . day^{-1}. The in-lake sampler recorded an influx of 123 grains . cm^{-2} . day^{-1} for the same period. It can be assumed from this strong positive correlation that influx in the submerged sampler over this period is caused primarily by aerial influx. This means that the difference in pollen influx between the submerged sampler and the aerial sampler can be attributed to differences in the trapping efficiency of the Surprise Lake surface and the Tauber-type aerial sampler which we used. According to these results, the lake surface is 3.2 times as efficient in trapping aerial pollen influx as the Tauber-type trap. Tauber (1977) utilized a 3X correction factor to compensate for differences in the trapping efficiency of his samplers compared to the lake surface. This correction factor becomes important for the determination of a pollen budget in Marion Lake and is discussed in Chapter 3.5. The close correspondence between my aerial sampling results and Tauber's correction factor also indicates that the aerial trapping efficiency of my Tauber-type sampler is directly comparable to results using conventional Tauber traps.

In-lake pollen influx increases dramatically after the flowering period, attaining a maximum of 530 grains . cm^{-2}. day^{-1} during the sampling period ending Nov 14, 1977. Two factors are important during this sampling period. Heavy rainfall and strong winds prevailed throughout, and the resulting wave action may have eroded pollen grains from the peat bank that rings Surprise Lake. In addition, water levels were very high in the boggy depression surrounding the basin, possibly resulting in soil pollen

Figure 16 Pollen influx in the unroofed Tauber-type aerial sampler and the in-lake sampler at Surprise Lake from September 9, 1977 to September 13, 1978.


IN-LAKE INFLUX
AERIAL INFLUX
POLLEN INFLUX (GRAINS · CM^{-2} · DAY^{-1})
500
200
100
50
20
10
5
2
O
N
D
J
F
M
A
M
J
J
A

being transported to the lake as water levels subsided. The increases in fern spores in the submerged samplers during high water periods supports the likelihood of soil pollen transfer. Resuspended pollen is probably an important component of pollen influx in the in-lake samplers as well but no attempt has been made to assess these variables in Surprise Lake. The aerial spectrum deposited during the 1978 flowering period illustrates a very high correlation with the spectrum in the surface samples at Surprise Lake ($r = 0.954$). This suggests that the large influx in the submerged samplers recorded during the non-flowering period is not qualitatively important.

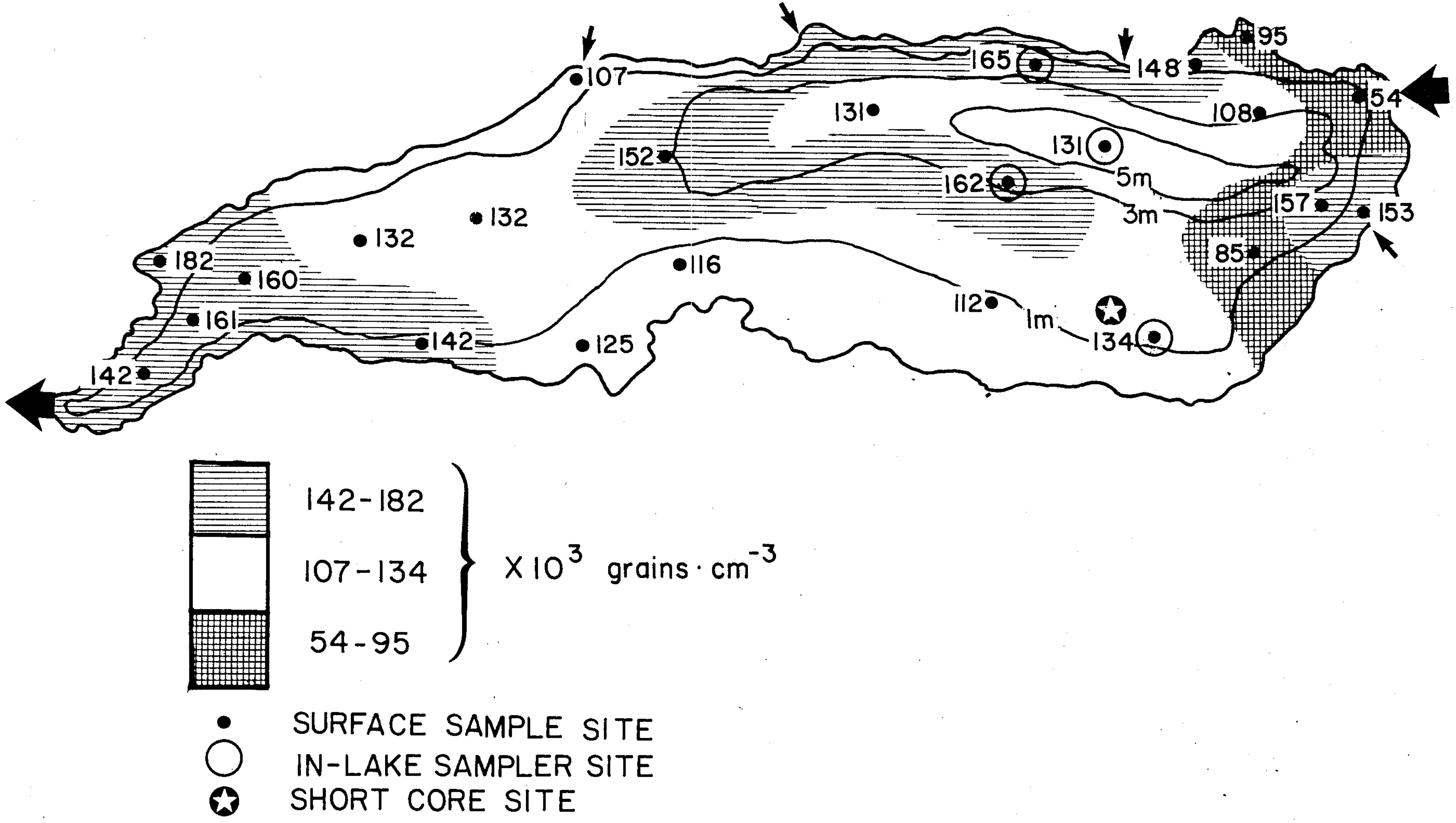
Pollen influx falls dramatically during December and January when Surprise Lake is ice-covered and both aerial influx and soil erosion are negligible.

Surface Samples

In Figure 17 the locations of 24 surface samples from Marion Lake are shown by dots, together with their pollen concentration values. In general, pollen concentrations increase from lows of 54,000 - 95,000 grains . cm^{-3} near the inflow stream to highs of 142,000 - 182,000 grains . cm^{-3} at the south end of the lake. At the north end, relatively high concentrations occur in a u-shaped area surrounding the deep trough, and near the mouth of an intermittent stream. This pattern can be explained on the basis of strong currents generated by the inflow stream which transport most grains towards the southern end of the basin. The u-shaped area may reflect scouring of pollen from the deep central trough and their deposition on the adjacent less-disturbed bottom. Pollen entering by the intermittent inflow at the north end of the basin is apparently quickly deposited due to weak current action.

Table 12 compares pollen concentrations of taxon pairs from samples near shore and in stream-influenced areas to their average concentrations for the entire basin. The high correlation coefficient between pollen concentrations in shore samplers and the Marion Lake average ($r = 0.998$) indicates that the local and extralocal aerial pollen deposition, previously demonstrated for *Myrica* and Western Hemlock

Figure 17 Map of Marion Lake showing locations and pollen concentrations of 24 surface sediment samples, positions of in-lake samplers, and location of the short core site.


107
165
148
95
154
131
108
131
152
162
5m
157
153
132
3m
132
85
182
160
116
161
112
142
1m
134
125
142
142-182
107-134
54-95
X 10^3 grains · cm^{-3}
● SURFACE SAMPLE SITE
○ IN-LAKE SAMPLER SITE
✪ SHORT CORE SITE

are not reflected in the composition of surface samples. This is not surprising given the degree of sediment mixing which must occur in Marion Lake during periods of heavy runoff. Those areas most effected by the influence of strong currents show a lower correlation with the Marion Lake average. This difference is characterized by a higher than average representation of heavy grains such as Western Hemlock, Abies, Picea, Pinus and fern spores. Currents apparently resuspend a higher proportion of light grains and remove them, thus increasing the representation of heavier types. Also, Brush and Brush (1972) determined experimentally that heavier pollen are more readily sedimented than lighter grains at the same water velocity. Their prediction that such differential deposition should occur under field conditions is supported by this study.

In four surface samples from Surprise Lake, pollen concentrations ranging from 116,000 - 170,000 grains . cm^{-3} are of the same magnitude as in Marion Lake. Little within-basin variation is indicated.

Summary

At the northern end of Marion Lake, in-lake pollen influx peaks during the spring flowering period when aerial deposition is at a maximum and stream discharge is moderate. Pollen influx decreases in the winter when high stream discharges periodically create a turbulent environment where pollen transport and resuspension is more prevalent than deposition. In summer, pollen influx from all sources is low.

Analysis of surface samples indicates threefold differences in pollen concentrations, probably due to sorting and differential deposition by lake currents. Pollen influx rates provide important information for the pollen analyst and our data show that threefold increases in pollen concentrations can be brought about by the influence of limnological factors alone. These differences are of the same magnitude as those reported by Davis (1973). It is worth reiterating that pollen influx changes of this magnitude in fossil pollen records should not be interpreted as indicators of vegetational changes, especially in lakes with stream inputs.

Table 12. Relative frequencies (%) of selected taxa in surface samples from Marion Lake adjacent to shoreline vegetation, in stream-influenced areas, and for all surface samples. Correlation coefficients comparing taxon concentrations are centred between the samplers compared.

TAXON	SHORELINE	MARION LAKE AVERAGE	STREAM-INFLUENCED AREAS
	(n=6)	(n=24)	(n=5)
Abies	2.0	1.7	2.8
Cupressaceae	11	12	12
Picea	0.7	0.9	1.5
Pinus	5.4	5.5	7.2
Pseudotsuga	1.4	1.3	2.1
Tsuga heterophylla	14	14	20
Alnus	35	35	24
Betula	2.0	1.9	1.3
Herb	5.5	4.2	3.2
Spore	18	18	21

0.998 0.926

Mathewes (1973) has interpreted forest changes in the study area on the basis of a core taken near the L2 sampler. The pollen spectrum in the surface sample from this location is identical to the Marion Lake average, and the pollen concentration is 131,000 grains . cm^{-3} which is almost identical to the average concentration of all surface samples (132,000 grains . cm^{-3}). It appears, therefore, that a core from this locality is representative of the basin as a whole.

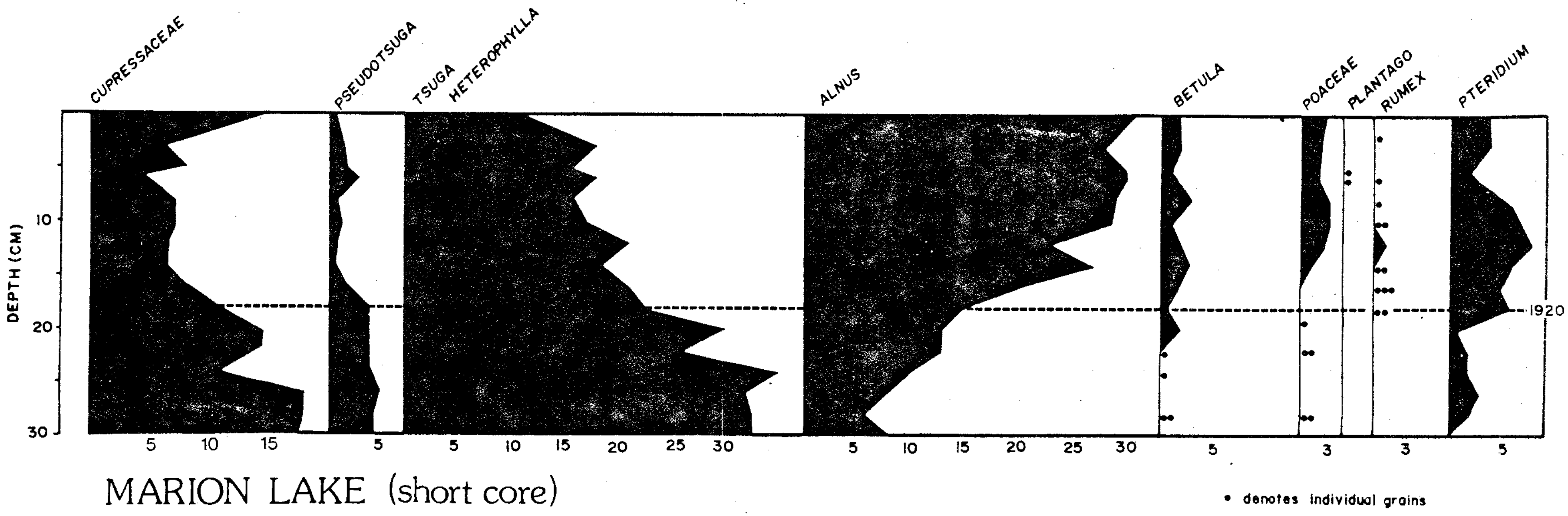
3.5 Marion Lake Pollen Budget

The calculation of an annual budget for Marion Lake is complicated by the fact that pollen captured by the in-lake samplers has three sources. In addition to new input from both aerial and fluvial origins, pollen resuspended from surface lake sediments is also known to be deposited in submerged samplers (Davis 1967, 1968). Pollen in lake samplers will therefore over-estimate annual pollen influx due to this resuspension component.

To determine what percentage of pollen influx is contributed by resuspension a short core 50 cm long was taken from Marion Lake, and analyzed to estimate an average annual pollen influx rate. This value can then be subtracted from the gross annual pollen influx recorded in the submerged samplers, and the difference should represent the amount of resuspended pollen.

The short core was taken with a Brown corer (Mott 1966) at the location indicated in Figure 17. The core was extruded and 0.5 cm^3 subsamples were taken at 2 cm intervals for pollen analysis after addition of a known quantity of exotic marker pollen grains (Eucalyptus), subsamples were prepared for microscopic examination by standard chemical procedures (Faegri and Iversen 1975) and 500 fossil pollen grains were counted on each slide. The relative frequencies of the most important taxa are presented as a pollen diagram (Figure 18). Fossil pollen concentrations (grains . cm^{-3}) were determined from the number of marker grains encountered while tabulating the fossil sum of 500 grains, according to the method of Benninghoff (1962).

Figure 18 Pollen diagram presenting changes in frequencies of important pollen types in a short core from Marion Lake. The clearance horizon is indicated at 18 cm by the horizonal line and is dated at 1920 from historical records.



MARION LAKE (short core)
Pollen Percentage Diagram

In order to estimate a sedimentation rate for this core, some dateable event must be identified, and the amount of sediment added since that date determined. Because the logging and fire history of the study area is known, forest clearance evidence was sought in the pollen diagram. In Figure 18 the level of forest clearance has been placed at the 18 cm level of the short core on the basis of the following changes in pollen frequencies.

(1) This level shows a marked decline of the two most important taxa with extralocal representation in the study area, Western Hemlock and Douglas-fir. They are important lumber species and their decline in the pollen diagram probably records havesting within the study area. In addition, spores of _Pteridium aquilinum_ increase at this level. Bracken is a common participant in post-logging succession in the U.B.C. Research Forest (McMinn 1951) and its increase is expected following forest clearance.

(2) Regionally dispersed taxa, such as _Alnus_ and _Betula_ begin their increase a few centimeters below the 18 cm horizon and illustrate the impact of earlier human disturbance at lower elevations. Cupressaceae, another regionally dispersed type, also records a gradual decline which precedes the local forest clearance horizon.

(3) The increase in agricultural and urban herb pollen (Grasses, _Plantago_ and _Rumex_) is apparent from 18 cm to the surface.

Klinka (1976) states that major logging began in 1920 in the study area and that fires in 1925 and 1931 destroyed post-logging regeneration. Therefore, the forest clearance horizon identified in Figure 18 has been taken to represent this 1920 disturbance and from this date a sedimentation rate of 0.32 cm . yr^{-1} was calculated. Pollen concentrations were determined in nine 0.5 cm^3 subsamples and these values were averaged to estimate the average pollen concentration in the sediment above the clearance horizon (156,199 grains . cm^{-3}). This value was then divided by the sediment deposition time (yr . cm^{-1}) during this period and an average annual pollen influx of 49,984 grains . cm^{-2} . yr^{-1} was calculated. An annual pollen influx rate of 63,942 grains . cm^{-2} . yr^{-1} was recorded in the in-lake samplers. The difference between these two figures (13,958 grains . cm^{-2} . yr^{-1}) represents the resuspension component and if this value is taken as a percentage of the gross pollen influx, the resuspension component is estimated to contribute 22% of the pollen deposited in the submerged samplers. New aerial and fluvial input accounts for the remaining 78%.

The average annual pollen influx (49,984 grains . cm^{-2} . yr^{-1}) can also be used to estimate the relative importance of the fluvial and aerial components in the Marion Lake pollen spectrum. An annual total aerial pollen influx of 5,685 grains . cm^{-2} . yr^{-1} was recorded by the Tauber-type sampler in the centre of Marion Lake. Tauber (1977) recommended a 3X factor to correct for the difference in pollen trapping efficiency between his sampler and the lake surface. A comparison between aerial pollen influx and pollen influx in the submerged sampler at Surprise Lake (Chapter 3.4) indicates that this correction factor is a reliable approximation of the relative trapping efficiency of the aerial samplers as compared to a lake surface. The use of this correction factor at Marion Lake may lead to an overestimate of aerial pollen influx because it does not account for the export of aerial pollen by the outflow stream. However, the 3X correction factor provides a more realistic evaluation of aerial pollen influx than that derived assuming that differences in trapping efficiency between the aerial sampler and the lake surface are negligible. Multiplying the aerial pollen influx at Marion Lake by 3 gives a corrected annual aerial influx of 17,055 grains . cm^{-2} . yr^{-1}, or 34% of the average annual influx of 49,984 grains . cm^{-2} . yr^{-1}. Fluvially transported pollen must account for the remaining 66% presently being deposited on the bottom of Marion Lake.

The estimate of 66% confirms the importance of fluvial pollen as previously suggested by other researchers. Peck (1973) estimated that the fluvial component contributed 95 - 98% of pollen deposited at two sites in Yorkshire. Bonny (1977) predicted a water-transported fraction between 70 and 90% and Tauber (1977) estimated that about 50% of pollen deposited at a small lake in Denmark was delivered by the lake inflow.

3.6 R-Values

In North America Davis and Goodlett (1960) were the first to attempt to calculate correction factors to compensate for differences in pollen representation among species. For any taxon, they divided the pollen percentage in a surface sample by the percent abundance in surrounding vegetation. The resulting ratios were termed R-values.

I calculated R-values for the major arboreal taxa from surface samples and the basal areas of all species in 964 basal area plots, totalled within 2 km and 4 km circles centred on Marion and Surprise Lakes (see Figure 3). The frequency of each taxon within these circles was estimated by expressing its basal area as a percentage of the total basal area of all arboreal species and these percentages were divided into the relative frequency of that taxon in the surface sample spectra at Marion and Surprise Lakes. Table 13 lists the R-values calculated. Pollen of taxa recognized as regional types in Chapter 3.2 were compared to vegetation in the 4 km circles (Alnus, Betula, Pinus and Cupressaceae) and extralocal types (Western Hemlock, Abies and Acer) were compared to vegetational representation in 2 km circles in an attempt to compensate for dispersal differences between these two groups.

The R-value for Cupressaceae pollen is more than twice as high at Surprise Lake (R = 0.74) than at Marion Lake (R = 0.33). It was concluded in the preceding section that this was the result of low representation of Cupressaceae pollen in the stream pollen spectrum at Marion Lake. This susceptibility to corrosion exhibited by Cupressaceae pollen may alter pollen ratios in pollen diagrams in an unpredictable manner. Once incorporated into sediment, Mathewes (1973) has shown that Cupressaceae pollen is well-preserved.

R-values for Western Hemlock are similar at both lakes and this reflects equal representation for this species in the surface spectra of Marion Lake (15%) and Surprise Lake (14%). I have shown that aerial influx of hemlock is significantly higher at Surprise Lake and attributed this to the different sizes of the basins. The fluvial spectrum increases the representation of Western Hemlock at Marion Lake so that its frequency, and consequently its R-values, are very similar at both lakes.

Table 13. R-values for important arboreal taxa in the study area at Marion and Surprise Lakes.

TAXON	MARION LAKE	SURPRISE LAKE
Cupressaceae	0.33	0.74
Tsuga heterophylla	0.38	0.35
Alnus	9	11
Pseudotsuga	0.16	0.48
Pinus	36	30
Abies	1.40	2.50
Acer macrophyllum	0.80	0.30

Alnus pollen deposition seriously overrepresents the abundance of Alnus throughout the study area, as indicated by R-values of 9 at Marion Lake and 11 at Surprise Lake.

Douglas-fir is underrepresented in the pollen spectrum at both Marion (R = 0.16) and Surprise Lakes (R = 0.48). At Marion Lake, Douglas-fir percentages are low in both the aerial (0.82%) and the fluvial (1.2%) spectra whereas at Surprise Lake it is somewhat higher at 3.3%. This difference may be the result of an extralocal effect as was the case for Western Hemlock.

Pinus has extremely high R-values at both lakes (R = 36,30) and points out its high production and excellent dispersal capacity. These values are exaggerated because Pinus contorta occurs as stunted individuals on rocky outcrops, but their stems were too small to be included in the vegetation survey. Although these individuals produced pollen in abundance, the fact that their presence is not accounted for exaggerates their true R-values.

Abies appears to be only slightly overrepresented on the basis of R-values of 1.4 at Marion Lake and 2.5 at Surprise Lake. Pacific Silver Fir accounts for approximately 1% of the total basal area in the study area, matching closely its pollen representation.

Betula is more underrepresented at Surprise Lake (R = 0.27) than at Marion Lake (R = 0.57) although its representation in surface spectra at the two lakes is almost identical. The difference in R-value is the result of different vegetational representation by Betula in 4 km circles around each lake.

The differences in R-values for each taxon at Marion and Surprise Lakes complicates their direct application to fossil pollen spectra. The difference in pollen recruitment at the two sites alters R-values and this has been illustrated for Cupressaceae, Abies, Pseudotsuga, Acer and Betula. Other factors, such as corrosion in the case of Cupressaceae and unrecorded pollen-contributing vegetation in the case of Pinus also alter R-values in the present study.

There are other variables which also effect the direct application of R-values to pollen assemblages. Andersen (1970) has discussed the changes in R-values for any taxon as its importance changes in the particular vegetational assemblage under consideration. In the present study I estimated an R-value of 0.16 at Marion Lake and 0.48 at Surprise Lake for Douglas-fir. Hansen (1949) provided data from which an R-value of 0.95 can be calculated for Pseudotsuga in stands in Oregon where it occurs with Garry Oak (Quercus garryana). These R-value differences illustrate the change in representation for any taxon as a function of the pollen production of associated species. For this reason R-values cannot be applied to pollen assemblages with different species combinations than those present in the calculation of these correction factors.

The application of R-values even within a given area of uniform species makeup is also complicated. Faegri (1966) pointed out the problems associated with differential transport of pollen grains with regard to the application of R-values. This is an important factor in the evaluation of R-values in this study because most aerial pollen is produced outside of the study area. For example, it was demonstrated that the major source of Alnus pollen at Marion and Surprise Lakes is from vegetation outside of the study area, yet basal area measurements for Alnus within the study area were used to estimate R-values. The difficulties of applying R-values as correction factors led Faegri (1966) to state, " . . . that both a calculation of the primary conversion factors and their later application in a strict mathematical sense meets with insuperable difficulties".

Although R-values determined in this study show variation at the two sites they do provide a rough estimate of the relative representation of important tree species. If these values are to be used to correct fossil pollen records in the Pacific Northwest the factors discussed in this chapter should be considered.

Given the difficulties involved in the direct application of R-values Janssen (1970) recommends the subjective interpretation of pollen records based on a knowledge of the pollen dispersal and production differences of the taxa involved. Also, Faegri and Iversen (1975) have proposed that important taxa be classified into groups on the basis of their dispersal and production characteristics and I presented such a classification in Chapter 3.2.

CHAPTER 4 DISCUSSION AND CONCLUSIONS

The floristic composition of the study area is poorly represented by the modern pollen spectra in Marion and Surprise Lakes. Whereas Klinka (1976) lists 240 species of vascular plants, 160 bryophyte species and 49 lichen species within the U.B.C. Forest, the present pollen spectrum at Marion Lake records only 47 pollen types. Furthermore, 5 of these pollen taxa account for 93% of all grains encountered in 25 pooled surface samples at Marion Lake, which represent a sum of 12,500 pollen grains. Part of the problem is an inability to identify most pollen types past the Genus level, and in some cases past even the Family level (eg. Cupressaceae, Poaceae) so that taxonomic differentiation is limited. The largest factor is the disproportionate representation of wind-pollinated (anemophilous) taxa compared to that of insect-pollinated (entomophilous) species. The pollination strategy of anemophilous taxa requires the liberation of large numbers of pollen grains into the atmosphere in order to ensure fertilization. Anemophilous plants are therefore well represented in the pollen deposited in limnic sediments and entomophilous taxa are correspondingly very poorly represented.

Palynologists have long been aware that the pollen spectrum presents a distorted picture of study area vegetation and that the overrepresentation of anemophilous species is the prime factor in this distortion. Fortunately, the most common trees in the Pacific Northwest are anemophilous, and are therefore well-recorded in sedimentary deposits. However, the representation of these arboreal taxa is complicated by the variables of pollen production, dispersion and deposition as discussed in this study. Palynologists must be aware of how these variables interact in a given physiographic area in order to interpret fossil pollen assemblages.

The major distortion of arboreal pollen frequencies in the study area is caused by the transport of large quantities of regionally dispersed types from lower elevations up to the study area, often obscuring the influence of vegetation within the study area. Upslope transport has been demonstrated for Alnus pollen during the early flowering period and I have postulated that most Cupressaceae pollen may be transported from outside the study area as well. Grass pollen from the Fraser Valley and Pinus pollen are regional types that dominate aerial pollen deposition during the latter half of the flowering period. The overrepresentation of lowland pollen at higher elevations is not a new observation, as Markgraf (1980) and Maher (1964) demonstrated in other mountainous areas.

To overcome this problem I suggested that extralocal types can be used to indicate vegetational composition in the neighborhood of the coring site because their relatively poor dispersal characteristics do not permit their transport in large quantity outside the vegetational zone in which they occur. In order to achieve this the important taxa were classified into depositional groups in that chapter and these groups are discussed below.

Regional Types

Regional pollen types are well represented outside the areas where they occur. Regional pollen originating at low elevations is transported upslope and deposited as a relatively even "pollen rain" throughout the study area. Aerial pollen influx rates for these taxa show no significant differences in samplers positioned around Marion Lake and at Surprise Lake. This lack of spatial differentiation points to a regional source for these grains. Regional pollen types discussed earlier have similar physical properties. Grain diameter is always less than 45 µm and in most cases falls between 25 and 35 µm.

Alnus

Alnus pollen is contributed by two species, Red Alder and Sitka Mountain Alder (Alnus viridis subsp. sinuata) although Heusser (1969) separates these species on the basis of pore numbers I have not done so in this study. Phenological observations confirm that the majority of Alder pollen comes from Red Alder. Red Alder occurs primarily on alluvium in the study area and accounts for only 4% of total basal area. Alnus pollen comprises 34% of the pollen spectrum at Marion Lake and 37% at Surprise Lake and therefore grossly exaggerates the abundance of Red Alder in the study area. Most Alnus deposition is clearly dispersed from lower elevations where Red Alder forms extensive stands after disturbance. Hansen (1949) commented on the high pollen production of alder and Heusser (1969, 1973) recorded the domination by Alnus pollen in high elevation moss polsters. The fact that moss polster spectra usually reflect vegetation in the immediate vicinity of the sample point (Anderson 1970) serves to emphasize the magnitude of regional dispersion by Red Alder. Mathewes (1973) reports Alnus frequencies ranging between 30 and 50% at Marion and Surprise Lakes throughout post-glacial time. These high percentages of Alnus pollen probably have their source on disturbed sites and alluvium in the Fraser Valley. Pollen of Red Alder obscures the representation of more climatically-controlled species and therefore complicates the reconstruction of paleovegetational assemblages.

Cupressaceae

Western Red Cedar and Yellow Cedar both contribute to the Cupressaceae pollen deposition in the study area, although Western Red Cedar forms 40% of total basal area whereas only two Yellow Cedar trees were recorded. Most Cupressaceae pollen must therefore be derived from Western Red Cedar. The aerial influx of Cupressaceae pollen is very similar in all samplers in a pattern similar to Alnus deposition. Good dispersion for pollen of Western Red Cedar is also indicated by the results of Ebell and Schmidt (1964) who illustrate the overlapping of Cupressaceae pollen deposition at different elevations on Vancouver Island. This overlapping effect does not occur for larger grains such as Western Hemlock and Abies. Barnosky (pers.comm.) collected surface samples in lakes along an elevational transect in Washington and Cupressaceae pollen is represented relatively evenly along the transect. All of these examples support the concept of regional pollen deposition for Cupressaceae pollen.

Although I recorded aerial influx for Cupressaceae (1719 grains . cm^{-2} . yr^{-1}) that is comparable to Alnus influx (1943 grains . cm^{-2} . yr^{-1}), the surface sample spectra of Marion Lake contained only 12% Cupressaceae pollen compared to 34% Alnus. Cupressaceae reach 37% at Surprise Lake and I suggest that these differences are due to greater sensitivity to corrosion for Cupressaceae pollen. This conclusion can be supported by the following results:

(1) Cupressaceae frequency in the stream spectrum is 17% and considering the high aerial influx of Cupressaceae pollen and the fact that Western Red Cedar comprises 40% of total basal area in the study area, this low representation can only be the result of poor preservation in the soil from which the fluvial spectrum is largely derived.

(2) Although Cupressaceae pollen makes up 30% of the aerial spectrum, its frequency in the refloatation spectrum is less than 1%. This can be explained by the corrosion of Cupressaceae pollen on the surface of lakeshore vegetation which is the source of the refloatation spectrum.

(3) Representation in the surface sample at Surprise Lake (37%) closely reflects the aerial dominance of Cupressaceae pollen (32%). Surprise Lake is a small, enclosed basin where aerial influx is the only important pollen source and this site must present a more favourable environment for the preservation of Cupressaceae pollen.

(4) Moss polster samples taken from within stands of Western Red Cedar contained no recognizable Cupressaceae grains.

This final example is supported by the results presented by Heusser (1969, 1973) in which he showed sporadic representation of Cupressaceae pollen in polsters.

As a result of its susceptibility to corrosion Cupressaceae representation may be altered in different basins by factors related to its differential preservation in different depositional environments. This complicates its interpretation in fossil pollen profiles. Interpretations are complicated further by its regional dispersion across biogeoclimatic zone boundaries and both of these factors should be considered in the investigation of pollen assemblages involving Cupressaceae pollen.

Pinus

Both Lodgepole Pine and Western White Pine contribute to the deposition of *Pinus* pollen in the study area. I combined counts of these species although they were separated where possible. Each species contributes approximately equally to total *Pinus* pollen influx. Western White Pine contributes only 0.14% of total basal area in the study area and the abundance of Lodgepole Pine, which is represented by stunted individuals with very high pollen production, could not be evaluated. Despite the extremely low vegetational importance of these two species, Pinus pollen has a frequency of 5 - 6% in Marion and Surprise Lakes and therefore its pollen representation greatly exagerrates the contribution of these species to study area vegetation. Both pines flower during the summer months when high pressure weather prevails and conditions for pollen dispersal are optimal.

High pollen production and excellent dispersion of Pinus pollen has been demonstrated and discussed by many authors (McAndrews and Wright 1969, Mack and Bryant 1974) and its overrepresentation in the present study reaffirms this behaviour in the Coast Mountains of British Columbia.

Other Regional Types

The majority of grass pollen influx in the study area has its origins in the Fraser Valley. Grass pollen is transported upslope and dispersed evenly throughout the study area. Pollen of two weedy agricultural taxa, Plantago lanceolata and Rumex acetosella are present in much lower but still consistent amounts throughout the summer months. Betula and Corylus are tentatively classified with the regional group. Both are amentiferous, producing relatively small grains on an annual basis and both have been considered as regional types by Markgraf (1980).

Extralocal Types

All taxa considered as extralocal types have characteristics that reduce their representation outside of the area where they occur. These grains range in diameter from 70 to 115 µm and are therefore larger than regional types. Heathcote (1979) measured settling velocities of these genera and the values range from 19 to 45 m per day. Heathcote (1979) provides data for the settling velocity of one regional taxon, Alnus, for which she measured a settling velocity of only 3.0 m per day. The poorer dispersive character which is indicated by the physical properties of extralocal types are supported by the following observations from this study.

(1) The representation of all extralocal types is higher in the fluvial spectrum than in the aerial spectrum at Marion Lake. This is a function of the equalization of dispersal differences in stream pollen recruited from under the forest canopy.

(2) Current-influenced areas within Marion Lake record a higher frequency of all extralocal types and this is the result of heavier grains being preferentially deposited in areas of higher fluvial energy.

(3) Significant differences in aerial influx have been recorded in the aerial samplers for Western Hemlock pollen although I have not been able to demonstrate this for other extralocal taxa because of their low pollen influxes.

Western Hemlock

Western Hemlock accounts for 40% of total basal area in the study area and is the dominant species on mesic sites. Krajina (1965) uses this species to define the Coastal Western Hemlock Biogeoclimatic Zone within which the study area is located. It occupies elevations intermediate between the Coastal Douglas-fir Zone below and the Subalpine Mountain Hemlock Zone above. Climatic conditions in the Coastal Western Hemlock Zone are defined by Krajina (1969). Annual temperature is above 10° C for 5 to 6 months and annual mean precipitation is 1550 to 4400 mm. Western Hemlock is therefore, a valuable indicator of climatic conditions.

Significant differences in aerial influx occur for Western Hemlock pollen between the shore and mid-lake samples at Marion Lake and between samplers in the middle of Marion Lake and Surprise Lake. These differences demonstrate the relatively poor dispersal characteristics of this species. The pollen of Western Hemlock is relatively large (70 - 80 μm) and Heathcote (1979) measured a settling velocity of 19.0 m per day. Heightened Western Hemlock representation in the stream spectrum (18%) where dispersal differences are minimized, has the effect of compensating for the differences in aerial deposition at the two basins (7.2% at Marion Lake and 14% at Surprise Lake) so that Western Hemlock frequencies in the surface sediments at Marion Lake (15%) and Surprise Lake (14%) are very similar. Ebell and Schmidt (1964) do not record an overlap of hemlock pollen deposition between sampling stations at different elevations on Vancouver Island. Heusser (1968, 1973) shows a high pollen representation in moss polsters taken within Western Hemlock vegetation units although some transport across zonal boundaries does occur. Barnosky (pers.comm) showed that Western Hemlock is well represented in lake surface samples and reflects vegetation composition in the vegetation surrounding the basin.

These examples illustrate that Western Hemlock pollen is poorly dispersed compared to regional types. Therefore it is not well represented outside of the biogeoclimatic zone in which it occurs. When this fact is combined with the climatic indicator value of Western Hemlock it can be seen that Western Hemlock pollen can provide valuable information for pollen analysis in the Pacific Northwest.

Douglas-fir

Douglas-fir is a climax tree at low elevations in the Coast Mountains and Krajina (1969) has defined the climatic characteristics of the Coastal Douglas-fir biogeoclimatic zone.

In the study area Douglas-fir accounts for 8% of total basal area and occurs as isolated individuals on mesic and especially more xeric sites. It comprises only 1% of the pollen spectrum at Marion Lake and 3.3% at Surprise Lake and although it has not been possible to demonstrate significant differences in its aerial influx at the two basins, there are many reasons to suggest that pollen of Douglas-fir is dispersed less efficiently than that of Western Hemlock. Wright (1952) has studied pollen deposition from isolated sources and concluded that Douglas-fir deposition falls to insignificant levels within 20 m of the source tree. Ebell and Schmidt (1964) state that Douglas-fir is transported less efficiently than Western Hemlock and this difference is probably due to its larger size (110 - 115 μm) and resultant faster settling velocity (44.5 m per day) measured by Heathcote (1978). Lower pollen production is probably another important factor which reduces the representation of Douglas-fir in pollen profiles. This combination of relatively poor dispersal efficiency and excellent climatic indicator value means that the interpretation of Douglas-fir pollen in pollen assemblages can provide valuable information on climatic changes in the area. Mathewes (1973) used changes in Douglas-fir pollen frequencies to infer climatic changes.

Abies

Pacific Silver Fir is the only member of this genus in the study area although I cannot rule out the possibility that *Abies grandis* or *Abies lasiocarpa* may be contributing some long-distance pollen as well. (Krajina 1969) utilizes Pacific Silver Fir as an indicator of the wet subzone of the Coastal Western Hemlock biogeoclimatic zone.

Pacific Silver Fir accounts for only 0.9% total basal area, growing in enriched lowland sites in the study area. Its slightly higher representation at Marion Lake (1.7%) compared to Surprise Lake (1.0%) is probably the result of better representation in the fluvial spectrum (2.5%) at Marion Lake. These values indicate a slight overrepresentation for *Abies* pollen in the two basins which is surprising given its diameter (90 - 100 µm) and rapid settling velocity of 24.4 m per day (Heathcote 1979). Both Barnosky (1980) and Heusser (1969, 1972) demonstrated that changes in *Abies* pollen frequencies in surface samples reflect change in the abundance of *Abies amabilis* in modern vegetation.

Although *Abies* pollen overrepresents the abundance of Pacific Silver Fir in the study area the magnitude of this factor is small compared to that of regional types. Like Western Hemlock and Douglas-fir, the pollen of this species is a valuable indicator of climatic conditions in the neighborhood of the sampling sites where it occurs.

Other Extralocal Types

Low numbers of *Picea* pollen at Marion and Surprise Lakes probably originate from Sitka Spruce which is much more frequent at lower elevations. Its low representation in the study area and its good representation in areas where it is abundant (Heusser 1978, Barnosky pers.comm.) point out that *Picea* pollen provides a relatively accurate representation of its vegetative abundance. These examples can also be used to describe the behaviour of Mountain Hemlock pollen, a species utilized by Krajina (1969) to define subalpine vegetation in the Coast Mountains of British Columbia. In all cases the relatively poor dispersion characteristics and excellent climatic indicator value of these species may permit the pollen analyst to reconstruct vegetational assemblages at the level of the biogeoclimatic zone.

Local Types

Surface samples taken directly beneath vegetation stands often reveal high percentages for taxa with little or no representation at a short distance away from these sites (Janssen 1973) and these are considered as Local types. Many of the insect-pollinated shrubs and herbs in the study area fall into this catgory, and also include anemophilous species such as *Myrica gale* at Marion Lake. Fern spores have a high representation in the fluvial spectrum at Marion Lake (20%) and this occurs because drainage basin streams erode fern spores from the stream-bank areas where many fern species predominate. This local deposition, however, limits the representation of zoophilous plant species and is the major reason for the distorted picture of study area vegetation by anemophilous taxa. These taxa are represented by their sporadic occurrence in the aerial spectrum--the most common in this study being *Salix*, Rosaceae, *Spiraea*, *Aruncus*, *Lysichiton*, Compositae (Liguliflorae and Tubuliflorae), Leguminosae, Cyperaceae, Ericaceae, *Epilobium*, *Equisetum* and *Sphagnum*. Local types can be very valuable as climatic indicators if they can be keyed to the species level. For example, Mathewes (1979) has used the presence of *Polemonium caeruleum* pollen to indicate a high elevation environment for the Vancouver area around 24,000 years B.P. The fluvial recruitment of Filicales spores is an example of additional vegetational information on local types which can be provided by stream-transported pollen.

The classification of the more important pollen-contributing taxa into depositional groups can assist in the interpretation of pollen assemblages in the Pacific Northwest. The recognition of problematic taxa such as *Alnus* and Cupressaceae assists in understanding changes in the frequencies of fossil pollen spectra. By determining changes in the frequencies of those taxa which best represent individual vegetation zones (extralocal types) more detailed conclusions can be drawn from pollen records. Janssen (1970) states that rather than utilizing R-values to correct pollen percentages a more productive exercise may be to construct an additional diagram in which pollen types which are transported from outside the area are eliminated. This conclusion agrees with that of Faegri (1966) and can be applied to fossil pollen assemblages in mountainous areas by constructing a separate pollen diagram in which only those taxa which have been identfied as extralocal types are considered in the abbreviated pollen sum. By this process the distorting effects of high Alnus influx and the unpredictable representation of Cupressaceae grains can be overcome and the frequencies of important arboreal grains which may have an important climatic indicator value, can be compared.

I have shown that the fluvial component is responsible for approximately 2/3 of the pollen grains presently being deposited at Marion Lake. The fluvial spectrum records increases in the frequencies of all extralocal types and I have emphasized the importance of these types as indicators of vegetation zones and climatic parameters. For this reason the contribution of stream-transported pollen is a positive one at Marion Lake and this conclusion is similar to that of Peck (1973), Bonny (1977) and Cushing (1964) in which they found that pollen sequences with a stream-derived component provided information about local vegetation which was not available in the aerial spectrum. With an understanding of how pollen is recruited in a given depositional site, the stream spectrum can be utilized to advantage in mountainous areas for two reasons: (1) it increases the representation of extralocal types as discussed above, and, (2) it collects pollen from an area that is "fixed in space", i.e. the drainage basin, and because of this the areal extent of pollen-contributing vegetation can be more easily visualized. These are important factors in mountain palynology where the pollen analyst must attempt to account for unpredictable aerial dispersal effects. The rich macrofossil assemblage transported by the inflow stream at Marion Lake is another factor in favour of depositional sites with fluvial inputs. The more negative implications of inflowing streams and sedimentary sequences are discussed in Chapter 3.3.

The pollen recruitment regimes at Marion Lake and Surprise Lake are very different but the representation of taxa at the two sites is not as divergent as the differences in pollen recruitment would suggest. This is because differences in aerial input resulting from size differences at the two sites are compensated for by the increased representation of poorly-dispersed types in the fluvial spectrum at Marion Lake. This example emphasizes the complexity of pollen-recruitment variables and their interactive effects in different basins and these should be considered by the pollen analyst.

The purpose of this study has been to illuminate some of the variables involved in the interpretation of fossil pollen assemblages in the mountains of the Pacific Northwest. In doing so I have arrived at some understanding of the complexity of the relationship between pollen assemblages and the vegetation that produces them. This information will be useful to those involved in palynology in the Pacific Northwest in particular, and to mountain palynology in general.

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