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Evaluating terrestrial-aquatic linkages in the Canadian Rocky Mountains: Eiffel Lake and Sentinel Lake, Banff National Park

by

Diana Tirlea

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Examining Committee

Rolf D. Vinebrooke, Biological Sciences, U of A, Supervisor

Alwynne B. Beaudoin, Quaternary Environments, Royal Alberta Museum, Co-supervisor

Marianne Douglas, Earth and Atmospheric Sciences, U of A, External Examiner

Randolph S. Currah, Biological Sciences, U of A, Internal Examiner

This thesis is dedicated to my mother, Viorica Normand, whose aspirations in life always involved the success and happiness of her daughters. I will always remember the sacrifices she made for us.

Abstract

This study examined if nutrient loading of phosphorus-rich pollen into small mountain lakes has a significant impact on lake productivity. Increased pollen input into lakes due to changes in vegetation (*e.g.,* timberline advance) may increase lake production. Deteriorated pollen was recorded for frozen and freeze-dried sediment samples to determine if storage method effects pollen preservation. There were no strong relationships between pollen accumulation rates (PAR) and pigment concentrations for Sentinel Lake and Eiffel Lake. A lagged response of pigment concentrations to increased PAR was illustrated for Eiffel. Examination of pollen ratios and stomata suggests recent timberline advance for Eiffel, but pollen ratios were a poor indicator of timberline for Sentinel. Sediment storage methods did not play a significant role in differential preservation of pollen grains. Further investigation of the potential effect of PAR on lake productivity is required because timberline advance may alter lake productivity through increased pollen input.

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1 INTRODUCTION

Mountain lakes are an important source of services such as potable water, recreational opportunities, and aesthetic quality (Vinebrooke & Leavitt 2005). As the negative impacts of human activities (*e.g.,* irrigation practices) and climate warming escalate, changes in high-elevation headwater systems are likely to lead to water shortages (Barnett *et al.* 2005), reduced water quality and alterations in lake community composition (Hauer *et al.* 1997; Parker *et al.* 2008; Schindler 2000, 2001). This study examines the effects of recent climate change on the relationship between nutrient inputs from pollen (from terrestrial plants) and aquatic productivity of two small mountain lakes in Banff National Park, Alberta.

Interactions between terrestrial and aquatic ecosystems can play an important role in the productivity of small lakes (Cole *et al.* 2006; Graham *et al.* 2006). For example, terrestrial inputs (*i.e.,* dissolved organic matter, litterfall) can stimulate relatively unproductive aquatic ecosystems (Schindler & Scheuerell 2002; Vinebrooke & Leavitt 1998), increasing both primary and secondary production (Graham *et al.,* 2006). Pollen may be an important nutrient supplement to lakes because it is a source of limiting nutrients and carbon (*i.e.,* phosphorus, nitrogen, dissolved organic carbon) (Doskey & Ugoagwu 1992; Newman 1995). Further, climate change may affect the productivity of small unproductive lakes because of its effect on pollen production (Lee *et al.* 1996b) and phenology (Walther 2003). As treeline encroaches on small unproductive mountain lakes in response to climate change (Danby & Hik 2007a; Danby & Hik 2007b; Walther 2004),

increasing pollen input may play a more important role in the nutrient budget of these lakes. For instance, changes in the catchments may increase nutrient flux into lakes altering lake community structure (Hede *et al.* 2010; Reuss *et al.* 2010).

Atmospheric deposition of organic matter (*e.g.,* leaves, seeds, twigs) was a significant source of nutrients increasing phytoplankton production in a small lake (Lake Wingra) in Wisconsin (Gasith & Hasler 1976). Terrestrial input of organic matter (*e.g.,* plant material, insects) may be a significant source of phosphorus to lakes (Cole *et al.* 1990). However, pollen was not considered a significant contributor of organic matter input because atmospheric deposition traps were deployed and sampled after peaks in pollen production (Cole *et al.* 1990). Sedimentary profiles investigating long-term pollen input (pollen accumulation rates) and fluctuations in pigment concentrations may better reveal if there is a relationship between pollen-derived nutrients and lake productivity.

Large production of pollen and rapid assimilation of pollen-derived nutrients suggests that pollen may play a significant role in the nutrient budget of ecosystems (Lee & Booth 2003). For example, large amounts of jack pine pollen (16-25 kg/ha) was deposited in a mixed boreal forest (Manitoba) in June during a short period (10-14 days) (Lee *et al.* 1996a). Pollen was considered a significant source of nutrients in a pine stand in Korea, where an average of 18-28 kg/ha pine pollen (*Pinus densiflora, P. rigida, P. banksiana*) fell in 1998 (Lee & Booth 2003). An ectomycorrhizal fungus (*Paxillus involutus*) effectively transferred

25% and 29% of phosphorus and nitrogen respectively to birch seedlings (*Betula pendula*), resulting in 8.3 times greater plant development (dry shoot and root weights) in pollen amended microcosms (400mg pollen, equivalent to deposition of 178 kg pollen / ha) versus non-pollen amended microcosms (Perez-Moreno & Read 2001). Graham *et al.* (2006) found that phytoplankton chlorophyll and abundance in boreal lakes (Ontario) were positively related to pollen-derived nutrients. Also, nutrient-enriched mesocosms increased zooplankton abundance, which was attributed to an increase in edible phytoplankton abundance due to addition of pollen (Graham *et al.,* 2006). Pollen input may contribute an estimated 45% of mean annual total phosphorus in small lakes as shown by studies at Crystal Lake, Wisconsin and may be sufficient to stimulate lake productivity, especially in phosphorus-limited lakes (Doskey & Ugoagwu 1989). Therefore, pollen can be a significant component of atmospheric deposition of nutrients entering lake ecosystem.

Temporal changes in whole-lake primary production can be quantified paleolimnologically by measuring variations in taxonomically diagnostic algal pigments (*e.g.,* chlorophylls, carotenoids) preserved in lake sediments (Wolfe *et al.* 2006). High-performance liquid chromatography (HPLC) can be used to separate lipid-based pigments preserved in sediment samples to quantify and detect temporal changes in phototrophic community composition (Millie *et al.* 1993). Historical changes in pigments coupled with measurements of terrestrial dynamics (*e.g.,* pollen) can be used to assess algal dynamics through time.

Therefore, HPLC analysis of sedimentary pigments can be useful in comparative studies dealing with high-resolution sampling; however, interpretations of sedimentary pigments must address their biochemical diagenesis (Millie *et al.,* 1993). For example, rapid diagenesis of sedimentary pigments in an alpine lake (Pipit Lake, Banff National Park) resulted in the loss of fucoxanthin, chlorophyll a and pheophytin pigments below 2cm core depth (Hobbs *et al.* 2010).

Pollen and stomata analysis has played a key role in the investigation of past vegetation changes (MacDonald 2001; Bennett 1994; Faegri *et al.* 1989). As pollen disperses from the parent plant, a portion becomes deposited and incorporated in sediment and thus the proportion of different types of pollen in sediment reflects the vegetation composition of the area (local and regional) at a specified temporal and spatial scale (Bennett & Willis 2001; Birks & Birks 2004). Further, fossil pollen assemblages in lake sediments can be used to determine changes in pollen input into lakes (Bennett 1994; Faegri *et al.,* 1989). Lignified stomata remain well-preserved in sediment and are typically dispersed over short distances as part of leaf fragments (MacDonald 2001). The presence (and abundance) or absence of Pinaceae stomata in lake sediments are useful in assessing occurrence of local forest species and interpreting treeline dynamics (Hansen 1995; MacDonald 2001; Yu 1997). Today, pollen analysis is often a component of multi-proxy studies (Hede *et al.,* 2010; Reuss *et al.,* 2010; Smol & Douglas 2007; Street-Perrott *et al.* 2007) because of its strength for investigating climatic and ecological changes. Together sedimentary pollen and stomata can be

used to investigate recent treeline dynamics (Beaudoin 1986; Evans 1997; MacDonald 2001).

Chapter two is an investigation of the potential effect of allochthonous pollen input on primary production in two relatively small unproductive mountain lakes in the Canadian Rockies. This chapter investigates past terrestrial (changes in vegetation) and lake ecosystem dynamics (algal abundance and composition) through examination of sedimentary pollen and algal pigments. Small lakes better represent local pollen input and therefore can be used to investigate local changes in past vegetation (Jackson 1990; Jacobson & Bradshaw 1981). Small lakes are also more responsive to small changes in nutrients (Cole *et al.,* 2006). By examining the factors contributing to the productivity of mountain lakes, we may be better able to forecast the future impacts of global change on these highly sensitive environments.

Chapter three is a study of treeline dynamics based on pollen ratios (*Picea:Pinus*) and stomata data (Beaudoin 1986; MacDonald 2001) in light of warming and cooling periods modeled from dendrochronological data (Luckman & Wilson 2005). This study will help determine if stomata and pollen ratios are suitable indicators of treeline dynamics in subalpine and alpine environments. This study will determine if using multiple proxies reliably infers past treeline fluctuations versus using a single indicator of treeline dynamics. Pollen ratios obtained from lake sediments are based on local (*Picea*) and regional (*Pinus*)

sources of pollen and are calibrated against modern pollen assemblages (surface samples) to infer shifts in timberline (Beaudoin 1986). Therefore, low ratios infer timberline retreat and high ratios infer timberline advance (Beaudoin 1986).

Chapter four investigates the effect of storage methods for sediment cores (frozen, freeze-dried) on preservation of pollen grains. There are no known studies that address whether storage method leads to differential preservation of pollen. Sediments intended for pollen analysis are typically kept frozen to reduce microbial activity (Faegri *et al.,* 1989; Moore & Webb 1991) whereas paleolimnological researchers typically freeze-dry their samples (Reuss *et al.* 2005). The amount of sporopollenin in the pollen wall, a mechanically and chemically resistant biopolymer (Blackmore *et al.* 2007), varies among taxa (Kwiatkowski & Lubliner-Mianowska 1957) and can lead to differential pollen preservation (Havinga 1967). If processes used to store sediment samples lead to further deterioration of the exine then it may affect the reliability of data derived from these samples. Hence, it would be preferable to use processes that have the greatest level of preservation. If there is no significant difference in deterioration of pollen grains between storage methods then freeze-dried sediment cores may be another useful storage method for cores intended for pollen analysis. This would provide researchers with the opportunity to use the same type of samples (*i.e.,* freeze-dried) for pollen and pigment analysis, increasing available stored sediment samples and minimizing the amount of coring needed.

The concluding chapter, **Chapter five,** reviews some of the difficulties in singling out factors responsible for stimulating lake productivity and touches on the limitations of this research and future potential research directions.

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2 TERRESTRIAL-AQUATIC LINKAGES OF TWO SMALL MOUNTAIN LAKES IN BANFF NATIONAL PARK

2.1 INTRODUCTION

Input of limiting nutrients (*i.e.*, phosphorus and nitrogen) into mountain lakes and rivers due to anthropogenic stressors has been well documented and studied (Baron *et al.* 2009; Murphy *et al.* 2010; Schindler 2000; Sickman *et al.* 2003). Allochthonous input of plant material into lakes can also play an important role in lake productivity (Gasith & Hasler 1976) influencing relatively unproductive lake ecosystems (Ask *et al.* 2009). Few studies have looked at the importance of pollen as a source of nutrients. Graham *et al.* (2006) determined that conifer pollen is a source of dissolved nutrients and organic matter to boreal lake ecosystems, stimulating primary and secondary production. Because small changes in nutrient loading into small mountain lakes may have a significant impact on their productivity (Hauer *et al.* 1997; Parker *et al.* 2008; Vinebrooke & Leavitt 1998), it is important to identify all terrestrial sources of nutrients that may be influenced by the increasing impacts of climate warming.

Pollen grains are an allochthonous source of macronutrients, which can be used by phytoplankton (Doskey & Ugoagwu 1992) in phosphorus-limited lakes (Schindler 1977). About 60% of phosphorus in pollen grains is water-extractable (Doskey & Ugoagwu 1992) and therefore pollen input may be an important factor in primary productivity. Due to long-distance dispersal and large production of

pollen grains (Davis *et al.* 1991), conifer pollen constitutes the majority of pollen deposited in lake sediments in northern temperate and boreal ecosystems (Janssen 1966). Some pollen types can be potentially transported hundreds to thousands of kilometers away from their origin (Campbell *et al.* 1999; Rousseau *et al.* 2003). Allochthonous input from conifer pollen may provide a large proportion of macronutrients to lake ecosystems where other nutrient sources are sparse. Whole-lake primary production can be quantified paleolimnologically by investigating changes in taxonomically diagnostic algal pigments (*e.g.,* chlorophylls, carotenoids) preserved in lake sediments (Millie *et al.* 1993). Pollen input (pollen accumulation rate) can be quantified by concentrating fossil pollen grains in sediment where chronological control is available (Birks & Birks 2004).

The objective of this research is to determine if there is a significant positive relationship between pollen accumulation rates (PAR) and algal pigment concentrations in sediment from two mountain lakes. Therefore, I am interested in understanding how the surrounding terrestrial ecosystem may impact the aquatic ecosystem, through amendments of pollen-derived nutrients (phosphorus, nitrogen) and organic carbon into mountain lakes. Further, I am interested in determining if warming and cooling periods in the Canadian Rockies during the last millennium are a significant predictor of pollen accumulation rates, which may impact lake production. I hypothesized that small subalpine and alpine lakes supplemented with atmospheric input of phosphorus-rich pollen will respond with increased lake productivity (increased pigment concentrations) over a temporal

scale. Therefore, I predict that increases in pollen input (increased PAR) will correspond to increases in total algal abundance (increased pigment concentration) in both lakes.

2.2 METHODS AND MATERIALS

2.2.1. Study Site

Sediment cores were taken from Eiffel Lake (51º19' N, 116º14' W) and Sentinel Lake (51º20' N, 116º13' W) in Banff National Park, Alberta. Sentinel Lake and Eiffel Lake are accessible via hiking trails from the Moraine Lake parking lot. The lakes are approximately 5.7 km west and 4.7 km northwest (trail distances) of the trailhead respectively (Fig. 2.1). The lakes are similar in geographical locations. Both Eiffel Lake and Sentinel Lake are relatively small lakes (13.5 ha and 2.8 ha respectively) (Mayhood & Anderson 1976). Recorded maximum elevations taken during site visits were 2240m a.s.l. for Eiffel Lake (east shoreline) and 2424m a.s.l. for Sentinel Lake (south shoreline).

The subalpine forest in the area is composed of mature *Picea engelmanni* Parry ex Engelmann (Engelmann spruce) and *Abies bifolia* A.Murray (Rocky Mountain subalpine fir) at elevations around 1996m a.s.l. With increased elevation the forest opens up with increased rocky and sediment patches and meadows vegetated with low-lying herbaceous and woody species including *Juniperus communius* L. (common juniper), *Salix* L. (willow), *Phyllodoce glanduliflora* (Hooker) Coville (yellow heather) and *Cassiope mertensiana* (Bongard) G.Don (mountain heather).

Larix lyallii Parlatore (alpine larch) appears between 2219-2377m a.s.l. with occurrence increasing as elevation increases. Patches of *L. lyallii* occur along the east/northeast and west (to a lesser extent) perimeters of Eiffel Lake (2240m a.s.l.) (Fig. 2.1). Sentinel Lake (2424m a.s.l.) area is characterized by alpine meadows, bare areas (rocky, sediment patches) and some krummholz trees.

Sentinel Lake is a fishless alpine lake located at the base of Pinnacle Mountain with a catchment (74 ha) comprised of carbonate (59%) and quartzite (41%) bedrock and dominated by rocky areas, moraine landforms and sparse low-lying vegetation (Holland & Coen 1983; Mayhood & Anderson 1976). The vegetation around the lake is dominated by *P. glanduliflora* and *C. mertensiana*, with less frequent occurrence of *Salix*, *Dryas octopetala* L. (white mountain avens), Asteraceae (asters), Ranunculaceae (buttercups), Poaceae (grasses) and Cyperaceae (sedges) and some krummholz trees. The phytoplankon composition has consisted mainly of diatom taxa including *Cyclotella* (Kütz) de Brebisson (524 cells / ml) and *Nitzschia* Hass. (152 cells / ml). Chrysophyceae (chrysophyceans), Chlorophyta (green algae) and Cryptophyta (cryptomonads) taxa were encountered at a lesser degree (<55 cells / ml) (Mayhood & Anderson 1976). Recent surveys of Sentinel Lake detected planktonic diatoms (*Asterionella formosa* Hass., *Fragilaria crotonensis* Kitton, *Stephanodiscus* Ehrenb., *Cyclotella*), dinoflagellates (*Gymnodinium* Stein, *Peridinium* Ehrenb.) and cryptophytes (*Cryptomonas*, *Rhodomonas minuta* Skuja). Diatoms (*Gomphonema* Ehrenb., *Cymbella* C.A. Agardh, *Eunotia* Ehrenb., *Pinnularia* Ehrenb., *Tabellaria*

Ehrenb.) and cyanobacteria (*Merismopedia glauca* (Ehr.) Naegeli, *Oscillatoria* Vaucher Ex Gomont, *Phormidium* Kuetzing Ex Gomont) were the dominant benthic taxa (Graham, M., unpublished data, University of Alberta).

Eiffel Lake is a fishless subalpine lake located in a depression at the base of Eiffel Peak in Banff National Park with a catchment area (360 ha) consisting of carbonate (20%) and quartzite (80%) bedrock and dominated by rocky areas, moraine landforms, sparse low-lying vegetation and trees and shrubs (Holland & Coen 1983; Mayhood & Anderson 1976). The arboreal vegetation includes *P. engelmanni*, *L. lyallii* and *A. bifolia*, with *L. lyallii* predominantly surrounding the west/northwest and east (to a lesser extent) margins of the lake. The low-lying vegetation is dominated by *Salix*, *P.glanduliflora, C. mertensiana* and *Hedysarum sulphurescens* Rydb. (yellow hedysarum) with less frequent occurrence of *Potentilla diversifolia* Lehm. (varileaf cinquefoil), *Castilleja occidentalis* Torr. (western paintbrush), *Antennaria lanata* (Hook.) Greene, *D. octopetala*, Asteraceae, Ranunculaceae and Poaceae species. In the 1970's, the phytoplankon composition was dominated by Chrysophytes (*Chromulina* Cienkowski (73 cells / ml), *Ochromonas* Vysotskii (21 cells / ml)) and Cryptophyte algae (*Rhodomonas minuta* (92 cells / ml)), as well as diatoms and green algae occurring in lower numbers (<14 cells / ml) (Mayhood & Anderson 1976). A recent survey (July 13, 2007) indicated that diatom species (*Fragilaria* Lyngb., *Achnanthes* Bory, *Navicula* Bory) dominated the assemblage (Graham, M. & Hobbs, W., unpublished data, University of Alberta).

The Lake Louise meteorological station (14.1 km from Moraine Lake) recorded an estimated average January and July temperatures of -13.4°C (SD 3.5) and 12.0°C (SD 1.3) respectively and an average 569.3 mm/yr of precipitation (Climate Normals 1971-2000) (Environment Canada 2010).

2.2.2. Coring, Sampling and Storage

Sediment cores were taken from approximately the deepest sections of Sentinel Lake basin (6.7m) and Eiffel Lake basin (13.5m) using a Glew gravity piston corer (Glew 1989). Coring locations were selected using bathymetric maps (Mayhood & Anderson 1976) and a submersible water depth sensor. Eiffel Lake (Core 1) was cored in March 2007, Sentinel Lake was cored in August 2007 (Cores 1, 2) and July 2008 (Core 3P).

The cores were extruded and sectioned by placing the coring tube vertically on a stand and subsequently lowering the piston at a set increment and scraping the sediment with a spatula into a labelled sterile plastic bag. For Eiffel Lake (Core 1) and Sentinel Lake (Cores 1, 2) sectioning commenced at the top of the core (sediment surface) in 0.25cm increments from 0-10cm, 0.5cm increments from 10-20cm, and 1.0cm increments from 20-30cm. For Sentinel Lake (Core 3) the sediment below 10cm was sampled in 0.5cm increments. Samples were kept in a cooler with ice during transportation.

Surface pollen samples were taken along the trails leading to the lakes at approximately 500m intervals and approximately 50m off of the hiking trail and from around the lake's perimeter in July 2008 (Fig. 2.1). The sampling areas were cleaned of any leaf litter and plant debris and a metal knife, first cleaned and sterilized with alcohol, was used to take a surface soil sample (0-1cm depth). Samples were placed into a labelled sterile plastic bag, sealed and kept in a cooler with ice during transportation.

To optimize preservation of algal pigments and pollen, sediment and pollen surface samples were frozen and stored in a freezer at -80ºC, until further processing (Faegri *et al.* 1989; Moore & Webb 1991; Reuss *et al.* 2005). Prior to subsampling core sediment for pigment and pollen analysis, samples were thawed for approximately half an hour, manually homogenized for approximately 5 minutes and vacuum freeze-dried (VirTis Freeze Mobile 24 Freeze Dryer, approximately -60°C) for 24 hours or until samples were dried (based on visual inspection). Freeze-dried samples were then stored in an -80ºC freezer until use. Eiffel Lake Core 1 was used for algal pigment analysis, pollen analysis, loss on ignition and ^{210}Pb dating. Sentinel Lake Cores 1-2 were used for pollen analysis, Core 1 was used for ^{210}Pb dating, and Core 3P was used for algal pigment analysis, ^{14}C dating and loss on ignition.

2.2.3. Processing and Statistical Analyses for Pollen

Freeze-dried sediment (lake core) samples were manually homogenized and subsampled for pollen analysis using a 1.25cm^3 measuring stainless-steel utensil (calibrated mean volume 1.28 cm^3, SD 0.05). Where samples of 1.25cm^3 were not attainable due to limited available sediment, volume was measured using disposable 3ml plastic syringes, with discrete volume readings (uncalibrated). All sampling tools were rinsed with distilled water in between sampling. Samples were taken in concordance with the intervals at which the core was sectioned where possible. Where material was limited (*i.e.,* top 2.5cm) intervals were combined in order to obtain volumes required for analysis and maintain resolution where possible. Frozen surface pollen samples were weighed, volumes were recorded and samples were then rinsed and sieved. Samples were filtered (300µm mesh filter) and rinsed with distilled water into a beaker three times. Filtered samples were weighed (wet weight), recorded for volume and processed. Anthers and microstrobilus from local vegetation were collected to establish a reference collection for confirming identifications of subfossil pollen.

All sediment subsamples, surface pollen samples, anthers and microstrobilus were chemically processed to concentrate pollen and spores following Faegri *et al.* (1989). Sediment subsamples and surface pollen samples were inoculated with a "spike" of *Lycopodium* spores (Batch # 710961 (2 tablets, 27,822+/-975 spores) or Batch # 414831 (2 tablets, 24,153+/-1197 spores)) prior to chemical processing (Stockmarr 1971). The "spike" was tallied along with pollen grains for each

sample and was used in equation (pollen concentration = spike added x pollen counted / spike counted) to determine fossil pollen concentrations (Stockmarr 1971). Processed samples were stained with safranin to enhance structural contrasts and suspended in silicone oil. Samples were manually homogenized for 5 minutes and mounted onto slides for counting. Using a transmitted light microscope, equally spaced transverses were counted at a magnification of 400X for each sample for the entire slide (22X40mm, 22x22mm and/or 18x18mm cover slip) to eliminate bias from differential sorting on the slide (Brookes & Thomas 1968). Magnification of 1000X was used for critical identification of pollen grains. No fewer than 500 identifiable pollen grains were counted with average counts of 1334 grains (SD 362) and 1317 (SD 562) for Sentinel Lake and Eiffel Lake sediment samples respectively and 1660 (SD 521) for surface samples. Of this pollen sum at least 200 or more pollen grains were taxa other than *Pinus*. Trilete spores, monolete spores, stomata and charcoal fragments were also recorded. Taxonomic identification of pollen grains, spores and stomata were made using published keys and glossaries (Bassett *et al.* 1978; Crompton & Wojtas 1993; Habgood & Simons 1985; Hansen 1995; Kapp *et al.* 2000; McAndrews *et al.* 1973; Punt *et al.* 2007) and pollen reference collections at the Royal Alberta Museum (Quaternary Environments) and from the University of Alberta (Palynology Lab, Department of Anthropology), supplemented by collections made from local site vegetation. Stomata were all identifiable as genera of Pinaceae using a published key (Hansen 1995). Key characteristics used to identify stomata included shape and proportion of upper and lower woody

lamellae on the guard cells and the angle of junction between the stem and medial boarder to the upper woody lamellae (Hansen 1995). When positive identification of stomata to genus was not possible, they were categorized as undifferentiated Pinaceae stomata. Charcoal fragments were sorted into three size categories; 12µm-36µm, 36µm-72µm or greater than 72µm.

Pollen sum determined for sediment and surface samples was inclusive of all identifiable pollen grains. Spores and indeterminate pollen grains were not included because inclusion of indeterminate pollen grains could artificially increase or decrease the pollen sum, as found by Hall (1981). Pollen percentages, concentrations and/or pollen accumulation rates were calculated and used to construct pollen diagrams for sediment samples and surface samples. Pollen diagrams were constructed using developed TILIA software and TG View computer packages available at http://www.ncdc.noaa.gov/paleo/tiliafaq.html (Grimm 1991-1993). Pollen accumulation rates below 3.5cm for Eiffel Lake were based on average sedimentation rates from the upper part of the core, as chronological controls for Eiffel Lake were not available down core due to limited material (refer to section 2.3.1 for more details). To identify significant relationship between pollen concentration and sedimentation rates, simple linear regressions were completed on untransformed data (SPSS 2007) for Eiffel Lake and Sentinel Lake.

2.2.4. Processing and Statistical Analyses for Algal Pigments

Freeze-dried samples were manually homogenized and subsampled for pigment analysis. Subsamples had average weights of 0.17g (SD 0.02g) and 0.15g (SD 0.07g) for Sentinel Lake and Eiffel Lake respectively. Pigments were extracted from sediment using an 80:20 acetone-methanol solution for 24 hours under darkness in an approximately -20°C refrigerator. Samples were decanted and the supernatant was filtered (0.2µm pore nylon) into a four dram vial. Samples were dried under nitrogen gas and pigment residuals were reconstituted with injection solution (70:25:5 acetone-ion-repairing agent-methanol, internal reference) and then transferred into amber vials with glass sleeves. Samples were analyzed with high-pressure liquid chromatography (HPLC) following Vinebrooke and Leavitt (1998), to quantify algal pigments in solution. Purchased commercial standard pigment values (DHI Water and Environment, Denmark) along with sample pigment and loss on ignition values (2 hr burn, 550ºC) were used in equation to calculate pigment concentrations per grams of organic matter. Concentrations of taxonomically diagnostic carotenoid and chlorophylls (reference Jeffrey & Vesk 1997) were used to determine whole-lake algal abundance and composition (Vinebrooke & Leavitt 1999). Major groups identified based on detected pigments include cryptophytes (alloxanthin), chromophytes including diatoms, dinoflagellates, chrysophytes (chl c, fucoxanthin, diadinoxanthin, diatoxanthin), chlorophytes (lutein), cyanobacteria (zeaxanthin), and zooplankton (astaxanthin). Lutein pigment could not be separated from zeaxanthin pigment and therefore lutein-zeaxanthin is interpreted as incorporating chlorophytes and cyanobacteria.

2.2.5. Pollen Accumulation Rates and Pigment Concentrations

To detect significant relationships between pollen accumulation rates (PAR) and pigment concentrations, simple linear regressions were completed (SPSS 2007) on log-transformed data for Eiffel Lake and Sentinel Lake. Correspondence analysis (CA) of major taxonomically diagnostic pigments and major pollen taxa was completed to detect changes in the community assemblage within the lake (algal pigments) and around the lake (pollen) in relation to core depth. Ordinations were completed on log-transformed data using CANOCO version 4.0 software (Ter Braak 1990).

Diagrams were constructed using TILIA software and TG View computer packages (Grimm 1991-1993) to illustrate historical sedimentary pigment concentrations, PAR and loss on ignition (LOI). Total carotenoid pigments excluded astaxanthin because the absorption coefficient used in calculating astaxanthin concentrations is much higher than other pigment absorption coefficients. Concentration ratios of chlorophyll (chl a) to total pheophytins were calculated to determine the stabilization of pigment diagenesis for both lakes. Statistical analysis between PAR and algal pigments and for algal pigments alone excluded samples where pigment diagenesis was unstable.

2.2.6. Radionuclide Dating and Loss on Ignition

Freeze-dried sediment subsamples were placed in labelled sterile bags or plastic vials, sealed and shipped to Flett Research Ltd. (Winnipeg, MB) for analysis and

interpretation of ^{210}Pb in the upper sediment (0-10cm) for Sentinel Lake. For Eiffel Lake (sampled by Hobbs, W., University of Alberta) analysis of ^{210}Pb was completed by MyCore Scientific Inc. (Deep River, ON). Frozen sediment from Sentinel Lake was thawed and sampled for bulk organic matter from the lower sediment (26.5-27cm), dried in a desiccator, weighed, placed in a sterile bag, sealed and shipped to Beta Analytic Inc. (Florida, USA) for analysis (accelerated mass spectrometry) and interpretation of ^{14}C. Due to limited material, Eiffel Lake was not sampled and analyzed for ^{14}C.

To calculate loss on ignition (LOI) freeze-dried sediment subsamples were first placed into pre-weighed labelled crucibles. Crucibles and dry subsamples were then weighed to obtain initial sample weight. Subsamples were then burned in a 550°C oven for 2 hours and afterwards weighed to obtain ashed sample weight. LOI was calculated following Heiri *et al.* (2001) to estimate organic content for Sentinel Lake. LOI values for Eiffel Lake were provided by Vinebrooke, R. D. (University of Alberta).

2.3 RESULTS

2.3.1 Sediment Core Radionuclide Dating

Radionuclide dating indicates that Sentinel Lake has a fairly slow rate of sediment accumulation. ^{210}Pb and ^{14}C results for Sentinel Lake indicates a near surface date of 128 yrs BP (^{210}Pb, 6.5cm depth, on freeze-dried sediment samples) and near bottom date of 2450+/- 40 yrs BP (^{14}C, Beta-251122, 2480 CAL yrs, 27cm depth,

on bulk organic material). These results indicate significant changes in sediment accumulation during the last 2500 years. An age model for Sentinel Lake was completed. This model combined a quadratic polynomial model (age=4.001+(-2.909 X depth) + (3.39 X depth^2); R^2=0.99, F(2,3)=1235, p<0.00) for the upper ^{210}Pb dated samples (6.5-0cm) and a linear model (age=-617.757+114.732 X depth; based on two samples only (R^2=1.00)) for the lower dated samples (^{210}Pb, 6.5cm and ^{14}C, 27cm). Calendrical equivalent dates for ^{14}C and ^{210}Pb were used to provide the same frame of reference for the linear model. ^{210}Pb results for Eiffel Lake indicate a near surface date of 133 yrs+/-16.6 yrs BP (3.5cm depth). ^{14}C dates were not available for Eiffel Lake due to limited material, and hence no age extrapolations past 3.5cm depth were made. Extracting of an additional sediment core from Eiffel Lake for dating purposes was unsuccessful because of the rocky lake bottom.

2.3.2 Loss on Ignition

Loss on ignition (LOI) was calculated to estimate organic content (Heiri *et al.* 2001). Missing LOI values were filled with values obtained from running a quadratic regression based on 3.5cm to 5cm depth for Eiffel Lake (y=56.849 + (-21.657x) + (2.312x^2)) and a cubic regression based on the top 6cm for Sentinel Lake (y=40.342 + (-14.258x) + (2.948x^2) + (-0.188x^3)). The regression models were a good predictor of LOI for Eiffel Lake (R^2 = 0.95, $F_{df(2,5)}$=56.49, p<0.00) and Sentinel Lake (R^2 = 0.91, $F_{df(3,17)}$=59.26, p<0.00). Both Eiffel and Sentinel

lakes had relatively low organic matter content below 2.5cm (< 19% and < 29% respectively).

2.3.3 Comparing Pollen Accumulation Rates and Pigment Concentrations Between Lakes

Pollen accumulation rates (PAR) were similar for both lakes and had equal variances ($F_{1,93}$=3.07, p=0.08) (Table 2.1). There was no statistical difference ($t_{0.05(2),93}$ = 1.36, p=0.178) between Eiffel Lake PAR and Sentinel Lake PAR. Total pigments were similar for Eiffel Lake and Sentinel Lake (Table 2.1). For total pigments, chlorophyll, and β-carotene the assumption of equal variances was violated ($F_{1,93}$ =9.57, <p=0.00, $F_{1,93}$=72.18, p<0.00, $F_{1,93}$=8.14, p<0.00 respectively) and therefore the data were natural log-transformed. There was no statistical difference ($t_{0.05(2),93}$ = 1.22, p=0.23) between log-transformed total pigments for Eiffel Lake and Sentinel Lake. Total chlorophyll and β-carotene were statistically different ($t_{0.05(2),93}$ = -18.78, p<0.00, $t_{0.05(2),93}$ = -10.98, p<0.00 respectively) with higher (untransformed) average chlorophyll and β-carotene concentrations for Sentinel Lake (Table 2.1).

2.3.4 Comparing Pollen Accumulation Rates and Pigment Concentrations Within Lakes

2.3.4.1 Eiffel Lake

Regression analyses were completed on log-transformed PAR and pigment concentration data (top 2.5cm data set excluded) for Eiffel Lake (Fig. 2.2). There were no strong relationships between chlorophyll, β-carotene or total pigments and PAR for Eiffel (Fig. 2.2). Regression analyses were also completed after removing an outlier at 8.25-8cm (Fig. 2.2). Still, there were no strong relationships revealed. Results (top 2.5cm data set and outlier excluded) revealed a higher R^2 value for total pigments and PAR (R^2=0.24, p=<0.00) compared to total chlorophylls and PAR (R^2=0.15, p=0.005) and β-carotene and PAR (R^2<0.00, p=0.744). These weak trends between pigment concentrations and PAR were mainly driven by high astaxanthin pigment concentrations. However, total pigment concentrations did appear to lag behind increases in PAR (Fig.2.3). Peaks in PAR occurred between 18-17cm, 12-10.5cm, 7-5cm and 3.25-0cm (Fig.2.3). There was a lagged response in increases of zooplankton (astaxanthin) and chromophyte abundance (diatoxanthin, fucoxanthin) suggesting a positive relationship with PAR between 25-2.5cm. This lagged response was less evident for cyanobacteria, green algae (zeaxanthin / lutein) and β-carotene (Fig. 2.3).

There was an increase of chlorophyll a and fucoxanthin (chromophytes) pigments up core (Fig. 2.3). Chlorophyll a, chromophytes (fucoxanthin, diadinoxanthin) and cryptophytes (alloxanthin) all increased from 2.5-0.75cm, while diatoxanthin,

zeaxanthin / lutein and β-carotene gradually decreased from 2.25-0cm (Fig. 2.3). Zooplankton (astaxanthin) increased upcore until 2.75cm and was absent from the top core samples (Fig. 2.3). Absorption peaks during this period were composed of astaxanthin and other unidentifiable pigments. As astaxantin could not be singled out from other pigments during this period, no peak values were recorded for the top core samples. Chlorophyll c only occurs between 2.25-0.25cm (Fig. 2.3). Periods where alloxanthin (cryptophytes) is absent from the record correspond with increases in astaxanthin (zooplankton) concentrations (Fig. 2.3). For Eiffel Lake pigment diagenesis declined rapidly over the upper 2.5cm of the sediment core and stabilized afterwards for the remaining core depth (Figs. 2.3).

2.3.4.2 Sentinel Lake

Regression analyses on log-transformed PAR and pigment concentration data (excluded the top 2.5cm and bottom 30-29cm) did not reveal any significant and strong relationships between chlorophyll, β-carotene or total pigments and PAR for Sentinel Lake (Fig. 2.4). Total pigments and PAR and β-carotene and PAR had lower R^2 values (R^2 =0.001, p=821, R^2 =0.006, p=603 respectively) compared to chlorophyll and PAR (R^2 =0.049, p=0.149) (Fig. 2.4).

Sentinel Lake did not demonstrate any strong trends between total pigments or total chlorophylls and PAR (Fig. 2.5). There was an increase in PAR upcore that corresponded with an increase in chlorophyll a and fucoxanthin pigment

concentrations (Fig. 2.5). Zeaxanthin / lutein, β-carotene and astaxanthin concentrations all decreased in the upper core samples (Fig. 2.5)

Total carotenoid and total chlorophyll pigment concentrations fluctuated throughout most of the record (Fig. 2.5). There was a general increase in total chlorophyll (chl a) upcore and cyanobacteria and green algae (zeaxanthin/lutein) dominated the phototropic community for the majority of the record (Fig. 2.5). Astaxanthin (zooplankton) was present throughout the record and appeared fairly stable. (Fig. 2.5). Periods of higher concentrations of chlorophyll a, fucoxanthin (chromophytes), astaxanthin (zooplankton), and total carotenoids occur between 2.5-0cm (Fig. 2.5). Diatoxanthin (chromophytes) occurs between 1.5-0.75cm and chlorophyll c (chromophytes, cryptophytes) occurs between 1.75-0cm (Fig. 2.5). Pigment diagenesis declined rapidly over the upper 2.5cm of the sediment core and stabilized until the last two samples (30-29cm), where all pigment concentrations dropped significantly or were absent (Figs. 2.5).

2.3.5 Correspondence Analysis

Correspondence analysis (ordinations) was completed for major taxonomically diagnostic pigments and for pollen accumulation rates of major pollen taxa in relation to sample depth for both lakes. Samples tended to form groupings based on depth, where near-surface samples clustered together apart from further down core samples (Figs. 2.6, 2.7). Distance between pigments and samples (core depth) represents how related individual pigments and samples are. For example,

pigments and samples in close proximity are more interdependent than pigments and samples far from one another.

Ninety-five percent and 100% of the variance in pigment concentrations for Eiffel Lake and Sentinel Lake respectively were captured by axis one and two (Fig. 2.6). Major pigments for both lakes are not greatly separated from one another and cluster near 0 (intersect of axis 1 and 2); however, fucoxanthin tends to be separated out slightly (Fig. 2.6). All major pigments were closest to sample 16 and 20, which corresponded to 6.5-6.25cm and 7.75-7.5cm respectively for Eiffel Lake (Fig. 3.15). Fucoxanthin was closest to sample 28 (16-15.5cm) and zeaxanthin and astaxanthin was closest to sample 7 (6-5.75cm) for Sentinel Lake (Fig. 2.6).

Ninety-five percent and 80% of variance in pollen accumulation rates for Eiffel Lake and Sentinel Lake respectively, were captured by axis one and two (Fig. 2.7). *Alnus* and all tree taxa were closest to sample 24 (9-8.5cm) and *Artemisia* was closest to sample 32 (12.5-12cm) for Eiffel (Fig. 2.7). *Alnus* and all tree taxa were closest to sample 33 (18.5-18cm) and *Artemisia* was closest to sample 17 (10.5-10cm) for Sentinel (Fig. 2.7).

2.3.6 Vegetation History of Eiffel Lake and Sentinel Lake

2.3.6.1 Sedimentation Rates and Pollen Concentration Relationship

Linear regressions were used to determine any significant positive relationship between sedimentation rates and pollen concentrations. If a positive relationship exists, then we can conclude that pollen accumulation rate is a result of changes in sedimentation rate (Beaudoin & Reasoner 1992). For Sentinel Lake, results indicated a weak negative relationship between pollen concentration and sedimentation rates with only 9.86% ($F_{df(1,45)}$=4.811, p=0.034) of the variation in pollen concentration explained by the model (Fig. 2.8). Radionuclide dating was not complete down-core for Eiffel Lake, and therefore sedimentation rates for sections below 3.5cm were based on an average sedimentation rate for the top section (0-3.5.cm). Linear regression was therefore completed on the top 3.5cm sections for Eiffel Lake. Results indicated that there was a strong positive relationship between pollen concentration and sedimentation rates with 97.77% of variation in pollen concentration explained by the model (Fig. 2.8). However, the large F-ratio was not significant (F(1,1)=43.403, p=0.095) and therefore we cannot conclude that pollen concentrations were entirely affected by sedimentation rates (regression based on three samples only).

2.3.6.2 Surface Pollen Samples

Pollen percentages for *Pinus* (x=62%, SD=11), *Abies* (x=5%, SD=3%) and *Alnus* (x=5%, SD=2%) did not show any obvious trends along an elevation gradient

(Fig. 2.9). *Picea* percentages increased with lower elevation and Ericad and trilete spore percentages decreased with lower elevation (Fig. 2.9). Seventy percent of stomata were identified as *Picea* (likely *Picea engelmannii*) and the remaining as undifferentiated (Pinaceae). Stomata frequency corresponded with *Picea* pollen percentages increasing in frequency with lower elevation (Figs. 2.9). There were no stomata in samples taken at the highest elevation (2417m) and the greatest amount of stomata (27) occurred at the second lowest elevation (1996m) (Fig. 2.9). Stomata percentages (percentage of the pollen sum) ranged from 0.68% to 2.15% for lower elevation (closed mature forest), from 0% to 0.40% for moderate elevations (open forest), and from 0% to 0.09% for higher elevations (open alpine meadows).

2.3.6.3 Eiffel Lake

Zonation distinguishes major zones of distinct pollen assemblages, which reflects changes in vegetation composition in the area. Zonation based on visual inspection can be subjective and therefore numerical zonation is generally used to characterize zones. Pollen percentages are generally stable for the entire core with no distinct zonation occurring throughout the core upon visual inspection (Fig. 2.10). The lack of any obvious changes in the assemblages for these records does not warrant numerical zonation.

Arboreal pollen dominates the pollen assemblage (x=98%, SD=0.74) throughout the record, with major contributors being *Pinus*, *Picea* and *Abies* (Fig. 2.10).

Pollen percentages range from 49-72% (x=60, SD=5.7) for *Pinus,* from 9-25% (x=16%, SD=3.5) for *Picea* and from 10-27% (x=16, SD=3.3) for *Abies.* A less significant contributor to the pollen assemblage is *Alnus*, with percentages ranging from 1-13% (x=6, SD=2.9) (Fig. 2.10). Between 7.25-4cm, there is an increase in *Picea* and *Abies* pollen percentages and a decrease in *Pinus* percentages (Fig. 2.10). Pollen percentages for *Alnus* generally decrease up core with percentages generally below 3% between 6.25-0cm (x=2.2, SD=0.7) and percentages generally greater than 3% between 25-6.25cm (x=6.8, SD=2.5) (Fig. 2.10). *Larix* and *Tsuga* appear in the record after 16cm as minor contributors to the pollen assemblage (<2%) (Fig. 2.10). The non-arboreal pollen is indicative of an alpine ecosystem and includes several alpine and sub-alpine taxa such as *Thalictrum, Silene, Saxifraga, Valeriana,* and *Oxyria* (Fig. 2.10). Less than 4% of the pollen assemblage was undeterminable pollen grains.

Charcoal fragment sums (>72μm) do not appear to display any strong trends. Three samples between 4.5-3.25cm have values greater than 1000 fragments, where all other samples have less than 1000 charcoal fragments (x=50, SD=18) (Fig. 2.10). Sedimentary microscopic charcoal fragments can be used to reconstruct past fire events, where large quantities of large charcoal fragments is an indicator of local fire (Whitlock & Larsen 2001). Pinaceae stomata occur through out most of the core, with no apparent trends in abundance or occurrence (Fig. 2.10). Two occurrences of *Larix* stomata (9-9.25cm, 2 stomata and 6.5-

6.75cm, 1 stoma) correspond with rare occurrences of *Larix* pollen in the top 12cm of the core.

Pollen concentrations for major taxa (>2 % composition of total pollen sum) were related to percent organic matter (LOI), where periods of low organic matter correspond to lower percentages and concentrations and vice versa (Fig. 2.11). An increase in *Picea* and *Abies* pollen concentrations between 7.25-4cm was associated with overall stable *Pinus* concentrations. Increases in *Alnus* pollen percentages correspond with decreases of *Pinus, Picea* and *Abies* pollen percentages between 25-13cm (Fig. 2.11). Charcoal concentrations (fragments > 72µm) decreased between 16-13.5cm and 9-6cm (Fig. 2.11).

Total pollen accumulation rate (PAR) fluctuated from 25-9cm, followed by a notable decrease in PAR at 9cm (Fig. 2.12). PAR had similar patterns in the pollen assemblage as pollen concentrations, as would be expected (Fig. 2.12). Charcoal accumulation rate fluctuated through the record and was influenced by percent organic matter (Fig. 2.12).

2.3.6.4 Sentinel Lake

Upon visual inspection there are no apparent zones or major trends illustrated in the pollen percentages for the Sentinel Lake record (Fig. 2.13). Arboreal taxa dominate the pollen assemblage (x=97%, SD=1.22) with *Pinus* pollen percentages ranging from 67-83% (x=75%, SD=4.1), *Picea* percentages ranging from 6-23%

(x=12%, SD=3.5) and *Abies* percentages ranging from 2-10% (x=5, SD=1.8). Occurrence of *Alnus* in Sentinel's record was similar to Eiffel, ranging from 1-11% (x=5, SD=2.2). Pollen percentages for *Alnus* generally increased up core (Fig. 2.13). *Artemisia* pollen has the highest occurrence up core (6-5.75cm, 2.5% and 3.5-2.5cm, 3.3%), which spans between 108-18 yrs BP (Fig. 2.13). The pollen assemblage includes several alpine taxa including *Thalictrum, Silene, Saxifraga, Zigadenus,* and *Oxyria* (Fig. 2.13). Typically, less than 6% of the pollen assemblage was undeterminable pollen grains. Abundance of charcoal fragments (>72µm) does not appear to display any trends (Fig. 2.13). Occurrence of Pinaceae stomata (75% *Picea,* 25% undifferentiated Pinaceae) appears in the record after 18.5cm (before 1505 yrs BP), with a maximum occurrence of 8 stomata at 8.5-8cm (357 yrs BP) (Fig. 2.13).

Pollen concentrations fluctuate with changes in percent organic matter (Fig. 2.14). *Pinus, Picea,* and *Abies* pollen concentrations have similar patterns throughout the record with no major trends in the data set. *Alnus* pollen concentration pattern is similar to that seen in the percentage data, but a general increase in *Alnus* pollen concentrations up core is less pronounced. Between 17.5-15.5cm (1390-1161 yrs BP) there is an increase in *Alnus,* Chenopodiaceae / Amaranthaceae, Poaceae, Cyperaceae and Other Trees and Shrubs concentrations and a decrease in all major tree taxa. This period overlaps with higher concentrations of charcoal fragments between 19-17cm (1562-1390 yrs BP) (Fig. 2.14). There is a peak in Ericad concentration at 7.5cm (243 yrs BP) (Fig. 2.14).

For total and most taxa, PAR generally increases up core and corresponds with increased sedimentation rate (Fig. 2.15). Similar to the concentration data there is an increase in Chenopodiaceae / Amaranthaceae, Poaceae and Other Trees and Shrubs PAR and a decrease in tree taxa between 17-15.5cm (1333-1161 yrs BP) (Fig. 2.15). Charcoal accumulation rates (CAR) increases between 19-17cm, but are less pronounced than the concentration data and increases between 4.5-2.5cm (60-18 yrs BP) (Fig. 2.15).

2.4 DISCUSSION

This study was designed to determine if there is a relationship between pollen accumulation rates (PAR) and algal pigment concentrations. The results did not support the hypothesis that small alpine lakes supplemented with atmospheric input of phosphorus-rich pollen will respond with increased primary production as inferred using sedimentary algal pigments. There were no strong relationships between chlorophyll, β-carotene or total pigments and PAR for Eiffel Lake and Sentinel Lake (Figs. 2.2, 2.4). However, PAR was associated with a lagged response in increases in total algal pigments, zooplankton and chromophyte abundance in Eiffel Lake (Fig. 2.3). Correspondence analysis (CA) formed groupings based on depth, with deeper samples being closely related and shallower samples being closely related (Figs. 2.6, 2.7). CA did not reveal any substantial changes in communities both around the lake (pollen) and within the lake (pigments) (Figs. 2.6, 2.7). Rapid rates of change in diagenesis are evident in

the near surface sediments (2.5-0cm) in both lakes (Figs. 2.3, 2.5) and in the bottom samples (30-29cm) for Sentinel Lake (Figs. 2.3, 2.5).

2.4.1 Response of Whole-Lake Algal Communities and Abundance in Response to Pollen Input

Lack of strong relationships between PAR and pigments suggests that pollen-derived phosphorus and organic carbon contributions to these two lakes are either, a) not a major player in regulating lake productivity, or b) contributions of pollen nutrients are not detectable due to a combination of factors influencing lake productivity. For example, input of pollen-derived nutrients may not be sufficient to increase primary production in lakes co-limited by nitrogen and phosphorus (Davidson & Howarth 2007; Elser et al. 2007) .

Peaks in PAR were associated with lagged increases in zooplankton and chromophyte abundance and less so for cyanobacteria and green algae in Eiffel Lake (Fig. 2.3). This lagged response is unexpected because pollen macronutrients are water soluble within 24hrs (Lee *et al.* 1996) are readily available for uptake within a short period (Graham *et al.* 2006, Doskey & Ugoagwu, 1992). Therefore, pollen-derived nutrients should be utilized by efficient phytoplankton and cyanobacteria. Further, dissolved organic matter both protects (from UV light) and provides nutrients to algae, increasing diatom abundance in alpine lakes (Vinebrooke & Leavitt 1998; Vinebrooke & Leavitt 1999). Pollen macronutrients are largely composed of nitrogen (Lee & Booth

2003); however, water-extractable nitrogen is less significant than water-extractable phosphorus (Doskey & Ugoagwu 1992). Nitrogen-fixing cyanobacteria may out-compete phytoplankton in low nitrogen environments (Schindler 1977; Tilman *et al.* 1986) and become poor competitors with increased phosphorus levels (Tilman *et al.,* 1986). From 8500-7900 cal yr BP, cyanobacteria was the dominant taxon in HØjby SØ Lake (Denmark), rapidly removing incoming nutrients (terrestrial organic matter) from surface water and the water column (Hede *et al.,* 2010). Pollen-amended mesocosms in boreal lakes (Ontario) mainly increased benthic diatoms and filamentous green algae abundance (Graham *et al.,* 2006). Therefore, increases in green algae and diatoms at the same time as peaks in PAR would be expected.

There was a statistically significant difference for total chlorophyll and β-carotene between lakes, where Sentinel Lake on average had larger chlorophyll and β-carotene concentrations (Table 2.1). This may be partly explained by a greater abundance of zooplankton occurring in Eiffel Lake compared to Sentinel Lake (Figs. 2.3, 2.5). Further, an increase in zooplankton (astaxanthin) abundance associated with a decrease in cryptophytes (alloxanthin) for Eiffel Lake may be indicative of grazing pressure increases during peaks in cryptophytes followed by collapse in secondary producers (Fig. 2.3). This suggests that zooplankton may be indirectly affected by nutrients entering the lake due to an increase in nutrients available for phytoplankton production (Graham *et al.,* 2006). Between 3.5-2.5cm (^{210}Pb 133±17 to 82±22 yrs BP) increases in PAR and pigments (Fig. 2.3) were

associated with recent warming (increase of 1.5°C mean annual temperatures) in the Canadian Rockies over the past century (Luckman & Wilson 2005).

The relationship between PAR and total pigment concentrations was weak for both lakes; however, Eiffel Lake had a larger and significant R^2 value (R^2=0.24, $p<0.00$) compared to Sentinel Lake (R^2=0.001, p=0.821) (Figs. 2.2, 2.4). Lake eutrophication is often more pronounced in lakes with large catchment areas (Hall & Smol 1993) and phosphorus export is positively related to catchment size (Prairie & Kalff 1986). The catchment area of Eiffel Lake (360 ha) is almost 5X larger than the catchment of Sentinel Lake (74 ha) (Mayhood & Anderson 1976). During the hemlock decline in Ontario (approximately 4,800 yrs BP), lakes with larger catchments and flatter topography had increased input of allochthonous and organic matter, resulting in increased algal abundance (Hall & Smol 1993). Catchments slope may be of little consequence to pollen-derived phosphorus and organic carbon input because atmospheric conditions and wind play a larger role in the distribution of pollen at higher elevations (Solomon & Silkworth 1986). Long-distance pollen from conifers (*e.g., Pinus*) contributed significantly to the pollen assemblage in both lakes (Figs. 2.12, 2.15). If pollen is a key nutrient source to lakes, pollen input will likely influence lake productivity where local forests are composed mainly of conifer trees (Graham *et al.,* 2006).

2.4.2 Comparing Algal Pigments of Whole-Lake Abundance and Assemblage within and between lakes

The main findings of the pigment profiles are a) increased total chlorophyll up core for both lakes (more pronounced in Eiffel); b) dominance of cyanobacteria and green algae (zeaxanthin/lutein) for the majority of the records for both lakes; c) relatively high levels of secondary production (astaxanthin) throughout the record for both lakes; and d) diagenesis of pigments in the upper sediment samples for both lakes (Figs. 2.3, 2.5).

Chlorophyll a is the only chlorophyll pigment contributing to the record for Eiffel Lake and Sentinel Lake below 2.5cm and 1.75cm (>17yrs BP) respectively (Figs. 2.3, 2.5). This may indicate that cyanobacteria was the dominant producer for the majority of the record (Hede *et al.,* 2010). This is supported by the fairly constant and significant contributions of zeaxanthin/lutein in the lake records (Figs. 2.3, 2.5). Furthermore, increased diatom abundance in relation to decreased chysophytes may indicate increased lake productions (Smol 1985). This trend is illustrated in the Eiffel Lake record between 6-3cm, where absence of alloxanthin is related to an increase in fucoxanthin suggesting a period of increased lake production (Fig. 2.3). In both lakes, cyanobacteria and green algae dominated the phototropic community (zeaxanthin/lutein) for the majority of the record (2cm down core). Other high altitude mountain lakes have yielded similar results (Vinebrooke & Leavitt 1999).

An increase in chromophytes including diatoms (fucoxanthin, diatoxanthin, chlorophyll c and a decrease in cyanobacteria and green algae (zeaxanthin/lutein) occurred in near surface samples (2-0cm) for both lakes (Figs. 2.3, 2.5). This suggests a reversal in the dominant primary producers from cyanobacteria and chlorophytes to diatoms. This fairly recent change (last century) is supported by algal surveys undertaken in the 1970's and 21st century for Eiffel Lake and Sentinel Lake. Thirty years ago Eiffel Lake's algal community was dominated by chrysophytes and cryptophytes, with diatoms and green algae occurring in low numbers (Mayhood & Anderson 1976). A recent survey (2007) indicated Eiffel Lake and Sentinel Lake were composed of mainly diatom taxa (*Fragilaria*, *Achnanthes*, *Navicula*) (Graham, M. & Hobbs, W., unpublished data, University of Alberta). Also, β-carotene, a fairly stable indicator of algal lake abundance (Leavitt 1993) decreased in the upper sediment samples along with the decrease in zeaxanthin/lutein (cyanobacteria and green algae), further supporting a decrease in cyanobacteria and green algae during this period (Figs. 2.3, 2.5).

2.4.3 Inference of vegetation history and fire history from pollen diagrams

2.4.3.1 Surface samples

Surface samples revealed an increase of *Picea* percentages and a decrease in Ericad pollen percentages and trilete spore percentages from high to lower elevations (Fig. 2.9). Presence and higher abundance of stomata corresponded well with an increase in *Picea* pollen at lower elevations (Fig. 2.9). Association

between low surface pollen percentages of major arboreal taxa and high percentages of Ericads was found in lower elevations in British Columbia's coastal mountains (Evans 1997). This was attributed to local abundant Ericad species overloading the pollen record resulting in depressed pollen percentages for major arboreal species (Evans 1997). This was not evident in our samples (Fig. 2.9). For our sites, based on vegetation surveys *Phyllodoce glanduliflora* and *Cassiope mertensiana* dominated higher elevations and *Picea engelmannii* was more dominant at lower elevations. This was represented by the surface pollen percentages and by an increase in stomata abundance (70% identified as *Picea*) in lower elevation samples (closed conifer forest) (Fig. 2.9). Further, *Pinus contorta* is a regional source of pollen and the pollen percentages remained fairly stable throughout the record and were not affected by increased Ericad percentages (Fig. 2.9). *Pinus albicaulis* was not encountered in the area during vegetation surveys. Further, the surface pollen assemblage and sedimentary subfossil pollen assemblage were similar in composition, indicating that modern and past vegetation are similar in the area (Figs. 2.9, 2.10, 2.13).

2.4.3.2 Eiffel Lake

Pollen percentages had low standard deviations for the major contributors to the total pollen sum (*Pinus, Picea, Abies*), which suggests that there is little change in pollen percentages over time for Eiffel Lake (Fig. 2.10). Further, minor contributors (mostly herbaceous taxa) are typically rare (<2%), sporadic and/or highly variable (Fig. 2.10). Therefore, results from these minor taxa do not offer

any other interpretative value other than being indicative of an alpine ecosystem. Also, pollen concentrations and pollen accumulation rates (PAR) for major taxa (>2 % composition of total pollen sum) are related to percent organic matter (LOI) for most of record (Figs. 2.11, 2.12). Charcoal concentrations and CAR fluctuated in relation to percent organic matter (Figs. 2.11, 2.12). The microscopic charcoal data and lack of correspondence to peaks of post-fire vegetation does not provide any indication of past local fires.

Although no zonation is evident, two main observations are notable (Figs. 2.10-2.12). Firstly, *Alnus* pollen generally decreases up core and secondly increases in *Picea* and *Abies* correspond to stable *Pinus* percentages and stable LOI between 7-4cm (Fig. 2.10). As *Pinus* is the regional pollen source and *Picea* and *Abies* are a local pollen source, this suggests timberline advance independent of LOI. Also, a decrease in *Alnus* pollen supports a decrease in open and shrubby areas. Timberline advance during this period is supported by pollen ratios (refer to Chapter 3). Further, occurrence of Pinaceae stomata occurs throughout most of the core, which supports proximity of forest species to the site (Fig. 2.10). Two occurrences of *Larix* stomata correspond well with rare occurrence of *Larix* pollen in the top 12cm of the core (Fig. 2.10). It is surprising that *Larix* stomata are not more represented in the record since *Larix lyallii* sheds its leaves annually and because of its proximity to the lake. For instance, *Larix* stomata represented local occurrence of *L. laricina* in the Northwest Territories (Yellowknife area) (Hansen *et al.* 1996) and local occurrence of *L. sibirica* in all treed sites in Siberia

(Clayden *et al.* 1996) defining tundra-forest gradients in both areas where *Larix* pollen was underrepresented in sediment. These results indicate that *Larix* stomata may not be a good indicator of *Larix lyallii* occurrence for the Eiffel Lake area.

As evident in the results, the relationship between organic matter and pollen is pronounced for pollen concentrations and PAR, which is accounted for by the sedimentation rate and sample volume (Figs. 2.11, 2.12). Pollen concentrations and PAR from Eiffel Lake were similar in pattern, which is not a surprise. Sedimentation rate for Eiffel was based on the average sedimentation rates for the top 3.5cm. Therefore, the interpretive value of the Eiffel Lake record is limited.

2.4.3.3 Sentinel Lake

The Sentinel Lake record did not display any distinct zonation upon inspection of the percentages and concentrations (Figs. 2.13, 2.14). In general *Alnus* increases up core and arboreal species dominate the pollen assemblage. For most taxa PAR generally increases up core and corresponds with increased sedimentation rate (Fig. 2.15). A peak in Ericads occurred at 7.5cm (243 yrs BP) and is most likely not a result of a real increase in pollen production or density of Ericads because of the singular record of high occurrence and entomophilous nature of Ericads.

Alnus demonstrates precocious flowering, where catkin development precedes spring leaf emergence. Reduced *Alnus* pollen percentages in the record have been

shown to be associated with prolonged winters and late spring frost associated with cooling events (Hede *et al.,* 2010). *Alnus* generally increases up core and *Artemisia* has the highest occurrence up core spanning the last century (108-18 yrs BP) (Figs. 2.13-2.15), which is associated with a warming period in the Canadian Rockies (Luckman & Wilson 2005). A prolonged cooling period from approximately 1450 to 1900 (Luckman & Wilson 2005) corresponds with lower *Alnus* PAR (Figs. 2.13-2.15).

Pinaceae stomata appear in the record at 18.5cm (1505 yrs BP), with a maximum occurrence at 8.5-8cm (357 yrs BP) (Fig. 2.13), may correspond to advance of *Picea* krummholz trees (75% *Picea* stomata) (refer to Chapter 3). Also, from 7-4.5 there is an increase in *Picea* and *Abies* percentages and a decrease of *Pinus* (Fig. 2.13), also suggesting timberline advance or increased pollen production in light of recent warming periods in the Canadian Rockies (refer to Chapter 3).

A period between 19-15.5 cm (1562-1161 yrs BP) exhibits increased charcoal fragment input followed by an increase in pollen from herbaceous taxa, including Poaceae, Cyperaceae and Chenopodiaceae / Amaranthaceae and a decrease in pollen from major tree taxa (Figs. 2.13-2.15). This may signify increased local fires followed by post-fire succession of grasses, sedges and shrubs and a decline in arboreal species. Although microscopic charcoal reflects regional and local fires (MacDonald *et al.* 1991), the pollen data here suggests a more local event represented by peaks in pollen from post-fire succession taxa between 19-15.5cm.

Post-fire periods in the boreal forest (Rainbow Lakes region, Wood Buffalo National Park, Alberta) have been associated with an increase in Poaceae and Cyperaceae pollen and decreased conifer pollen (MacDonald *et al.,* 1991). Conclusions that many species of Cyperaceae are aquatic (lake's edge) in this boreal forest region and therefore pollen from Cyperaceae taxa may contribute significantly to the pollen assemblage in absence of terrestrial succession post-fire have been made (MacDonald *et al.,* 1991). However, in the alpine many species of Cyperaceae are found on rocky, dry slopes, (Kershaw *et al.* 1998; Moss & Packer 1983) where succession of sedges with wind-dispersed pollen may contribute significantly to the post-fire pollen record. Between 4.5-2.5cm (*ca.* 60-18 yrs BP) CAR increases in correspondence with sedimentation rate (Fig. 2.15). However, the period between 19-15.5 cm (1562-1161 yrs BP) is associated with low and fairly stable sedimentation rates, and therefore we can assume changes in PAR is not strongly influenced by sedimentation rates during this period. Further, there was no significant relationship between sedimentation rates and pollen concentrations for Sentinel Lake, which supports that pollen accumulation rates are not a result of sedimentation rates (Fig. 2.8).

2.4.4 Implication of Study and Further Research

The cumulative effects of natural sources of nutrients and other environmental factors on alpine lakes may obscure effects of PAR on lake productivity. Therefore, similar studies on other alpine lakes should be undertaken to determine if any real relationship between PAR and pigment concentrations exists. Potential

long-term study of the effect of PAR on lake communities may include deploying pollen catchers set directly over lakes. Long-term sampling of pollen and lake water during the spring and summer months in conjunction with sediment sampling may be useful in determining the effect of pollen on lake communities. Also, these types of studies may be useful in further investigation of pigment and pollen degradation.

Further investigation into possible lagged responses of algal communities to pollen is needed. Measuring multiple terrestrial sources of nutrients (woody debris, leaves, pollen) in a more controlled environment (*e.g.,* mesocosms) may help determine the mechanisms controlling lake production and if pollen is an important factor. These controlled experiments can be followed by examination of temporal changes of sedimentary pollen and macrofossil input (*e.g.,* leaf fragments, seeds, insects) and sedimentary pigments. Also, studies examining pollen input and lake productivity in fishless lakes and lakes with fish can be undertaken to determine if intensive grazing by zooplankton on algae in fishless lakes suppresses the response of primary producers to pollen input.

2.5 TABLES AND FIGURES

Table 2.1. Pollen accumulation rates (PAR) and pigment concentrations averages and standard errors for Eiffel Lake and Sentinel Lake. Excludes values between 0-2.5cm for both lakes and 29-30cm for Sentinel Lake.

	Eiffel Lake				**Sentinel Lake**			
	PAR (grains / cm^2 /yr)	**Total Pigments (µg/g organic)**	**Total Chlorophyll (µg/g organic)**	**Total β-carotene (µg/g organic)**	**PAR (grains / cm^2 / yr)**	**Total Pigments (µg/g organic)**	**Total Chlorophyll (µg/g organic)**	**Total β-carotene (µg/g organic)**
Mean	3,420	13,594	53	32	2,821	11,582	277	59
Max.	7,550	30,531	144	57	11,872	23,038	493	120
Min.	322	3307	6	10	1,232	3,838	118	27
Std. Error	295	926	3	1	331	638	14	2

Figure 2.1. Location of Eiffel Lake and Sentinel Lake area in Banff National Park, Alberta. Filled circles indicate locations where surface samples and tree transects and / or vegetation surveys were completed.

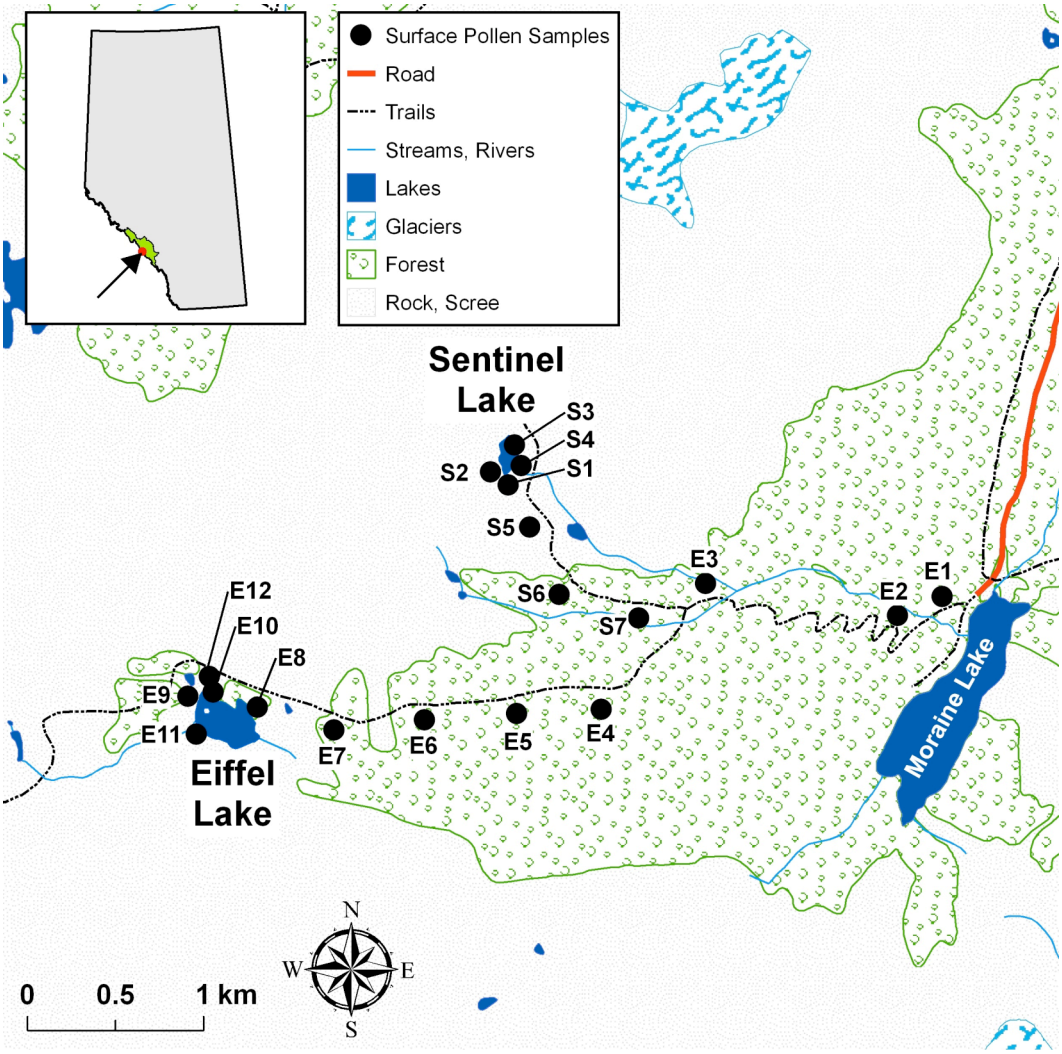


Figure 2.2. Total pigments (a), chlorophyll (b) and β-carotene (b) concentrations in relation to pollen accumulation rates for Eiffel Lake.

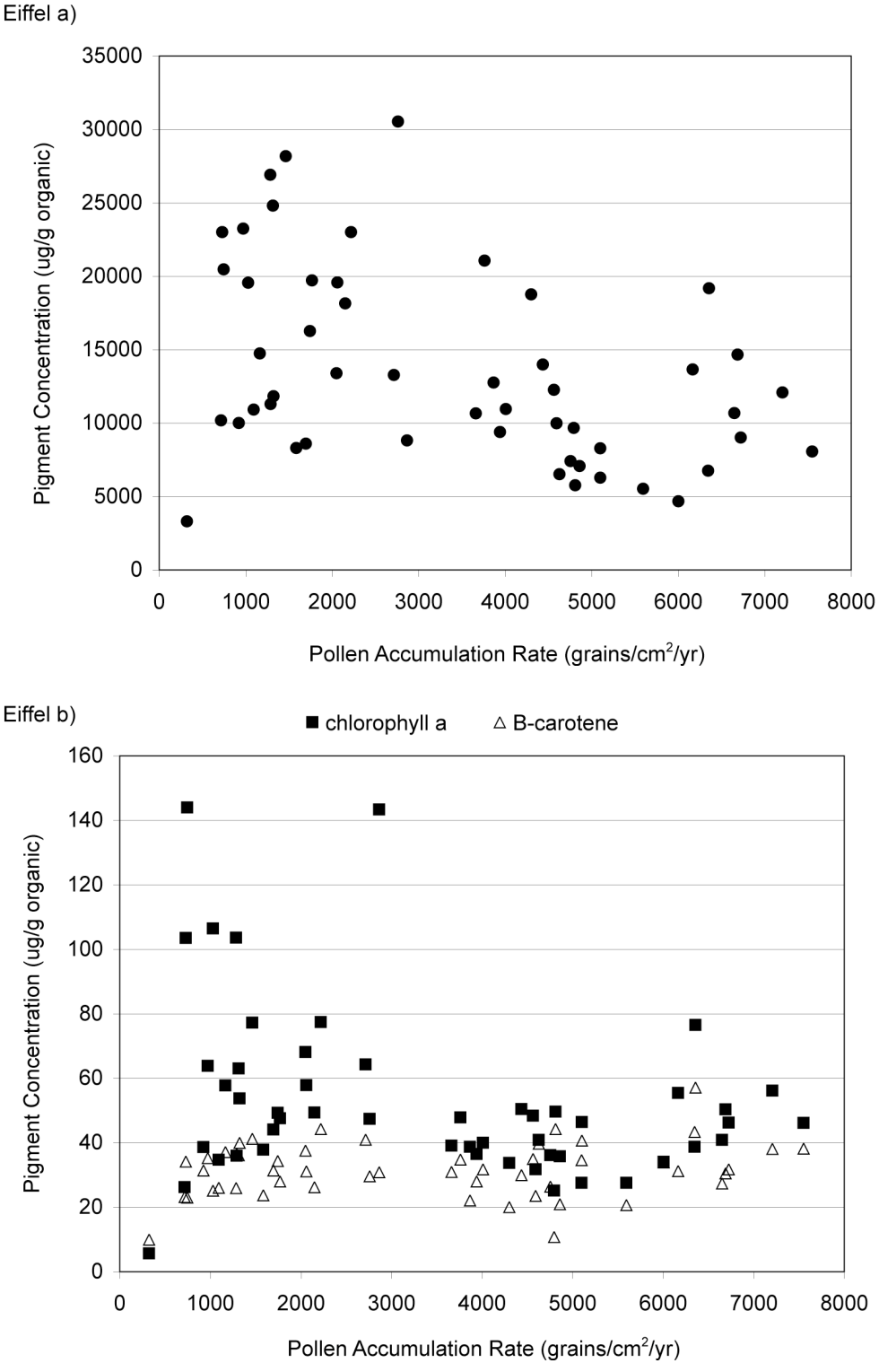


Figure 2.3. Eiffel Lake pigment concentrations, total pollen accumulation rates, percent organic matter (LOI) and chlorophyll a:pheophytin ratios.

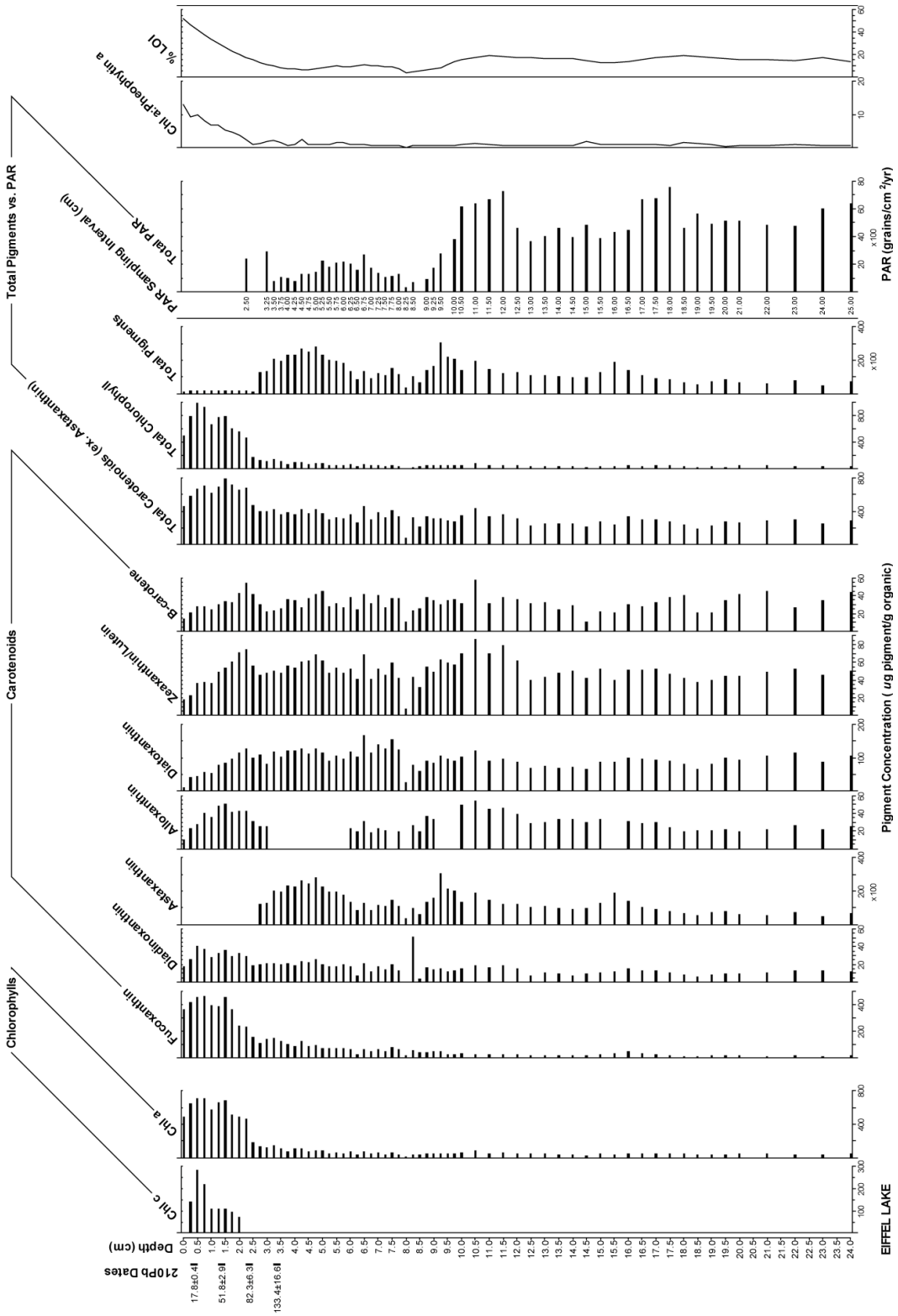
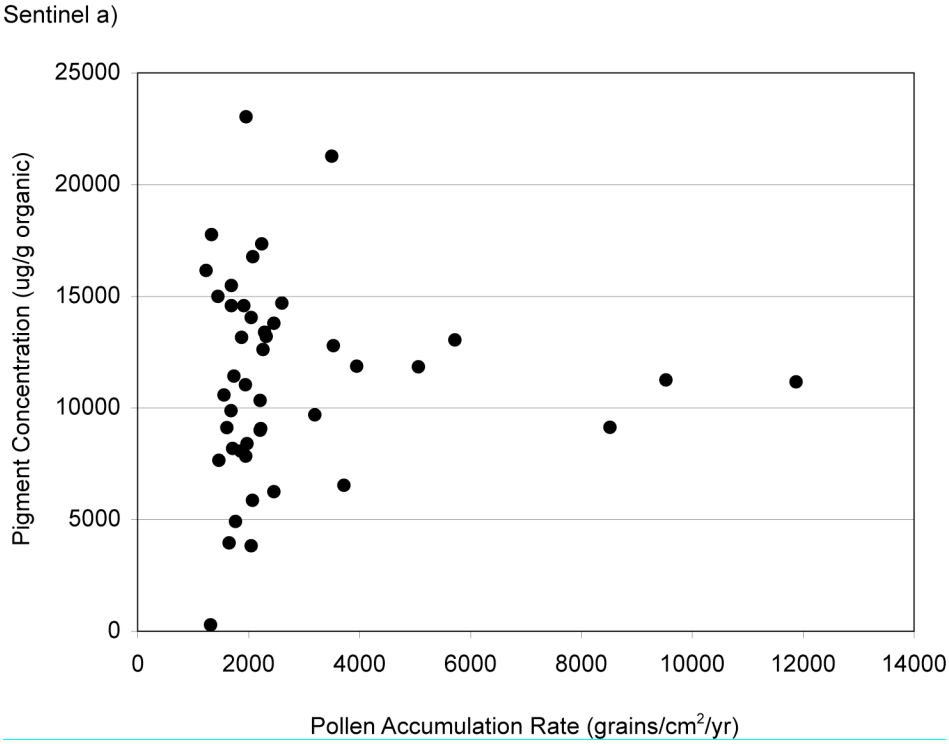


Figure 2.4. Total pigments (a), chlorophyll (b) and β-carotene (b) concentrations in relation to pollen accumulation rates for Sentinel Lake.



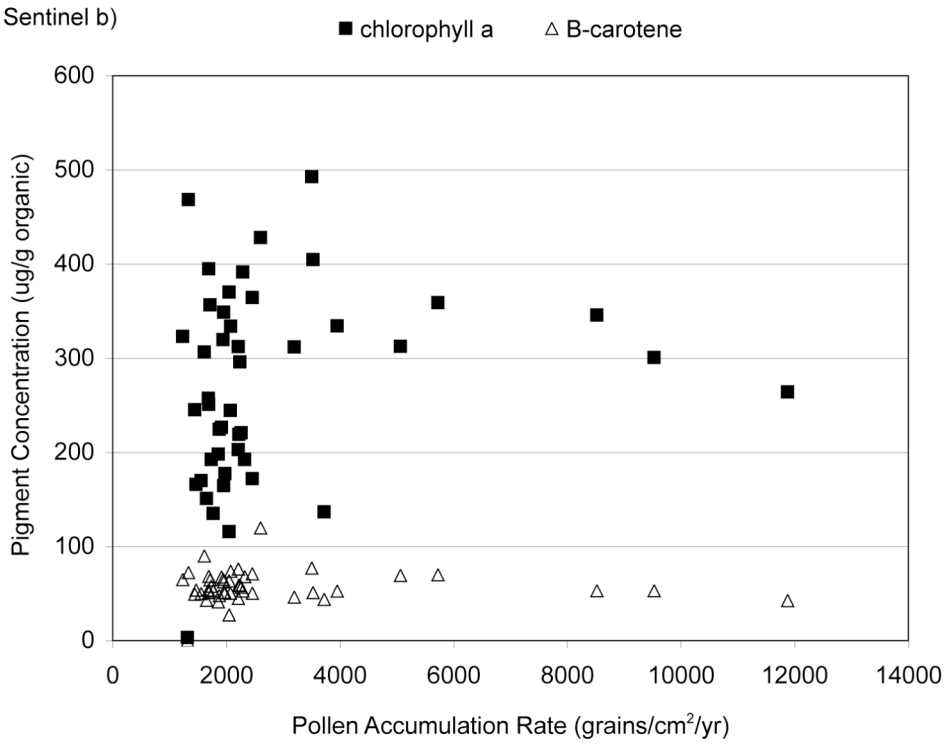


Figure 2.5. Sentinel Lake pigment concentrations, total pollen accumulation rates, percent organic matter (LOI) and chlorophyll a:pheophytin ratios.

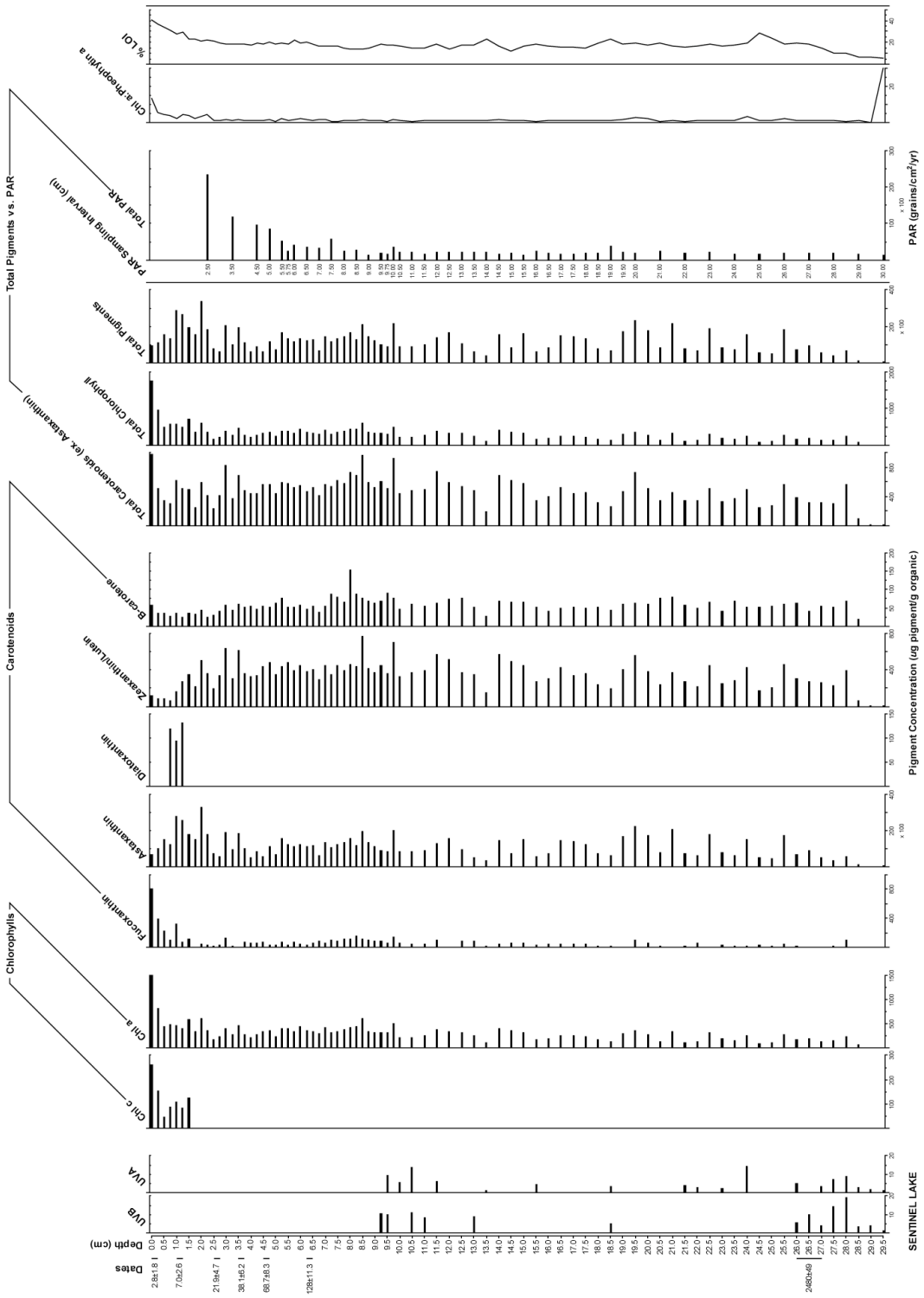
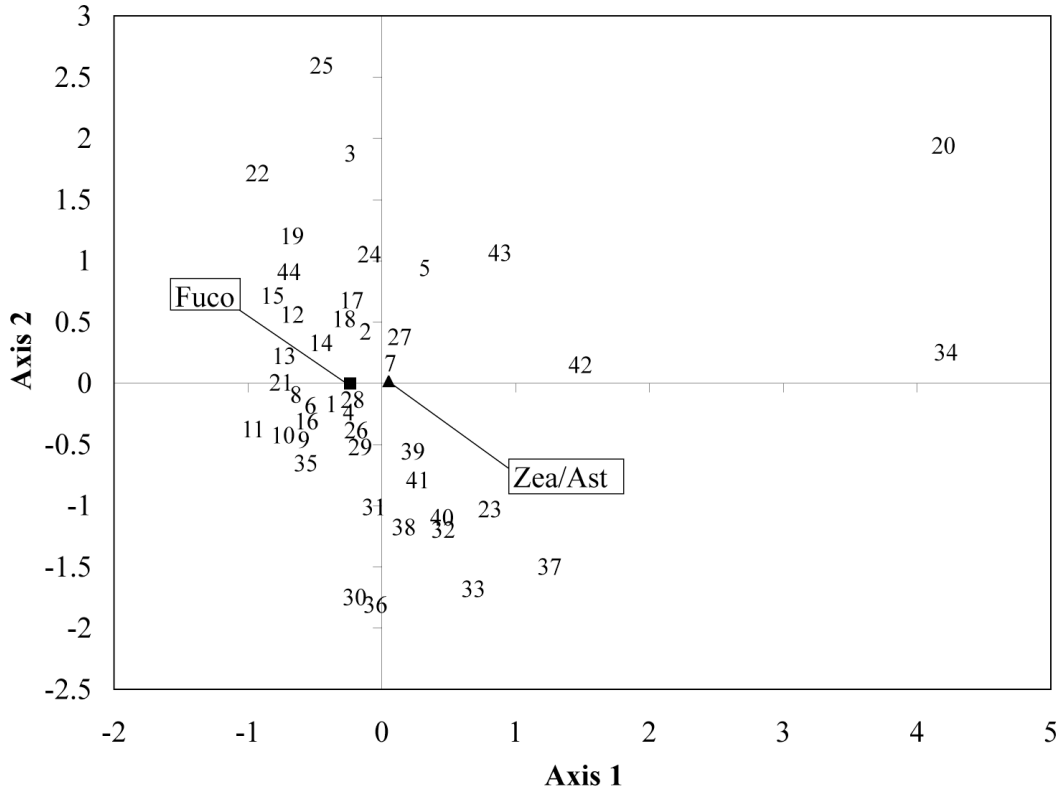


Figure 2.6. Eiffel Lake and Sentinel Lake ordination (correspondence analysis) results for major taxonomically diagnostic pigments. Sample numbers refer to depth profile, with lower numbers being upper depths and higher number being deeper depths. Pigment label lines are provided (lines are not indicating a directional influence). Pigment values that overlap are combined into one label box and are represented by one symbol. Zea = zeaxanthin, Diato = diatoxanthin, Asta = astaxanthin, Fuco = fucoxanthin, Diadin = diadinoxanthin.

Sentinel Lake Pigments (CA)



Eiffel Lake Pigment (CA)

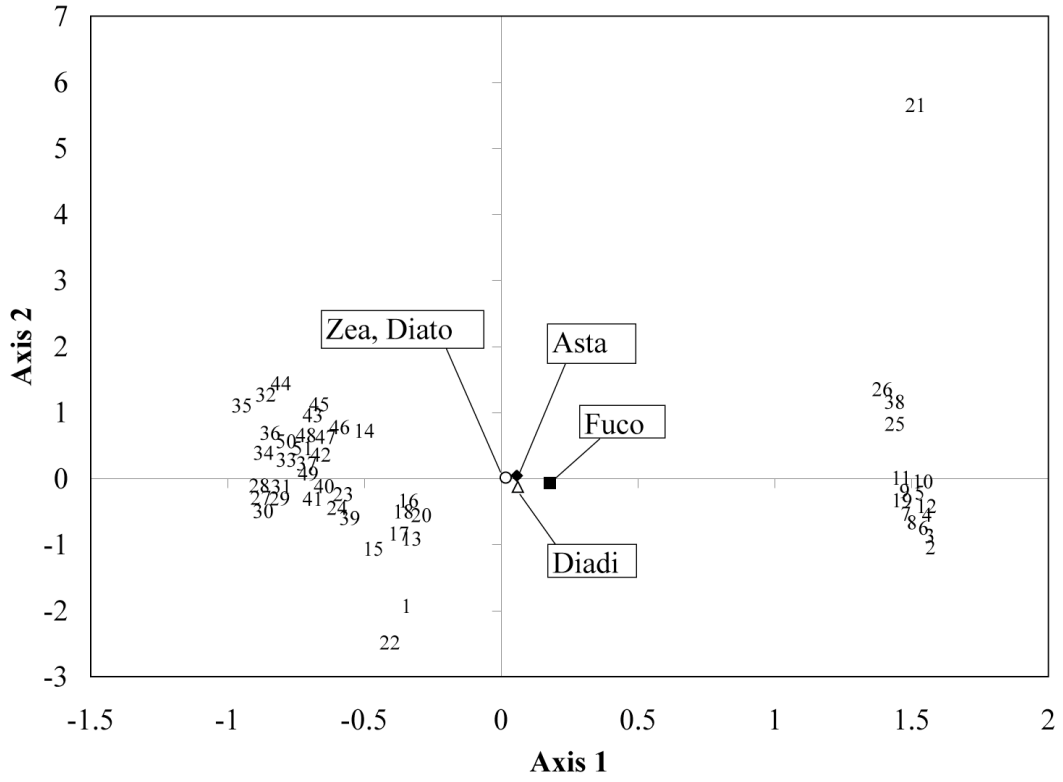
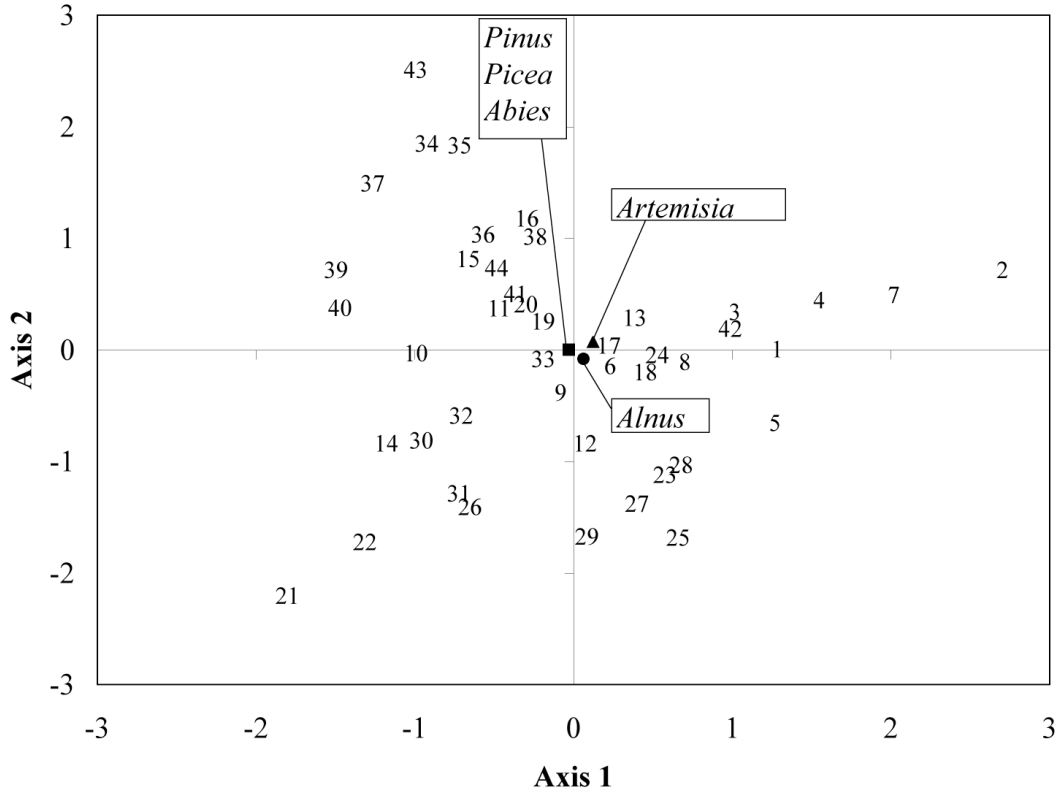


Figure 2.7. Eiffel Lake and Sentinel Lake ordination (correspondence analysis) results for pollen accumulation rates of major pollen taxa. Sample numbers refer to depth profile, with lower numbers being upper depths and higher number being deeper depths. Pollen taxa label lines are provided (lines are not indicating a directional influence). Pollen taxa values that overlap are combined into one label box and are represented by one symbol.

Sentinel Lake PAR (CA)



Eiffel Lake PAR (CA)

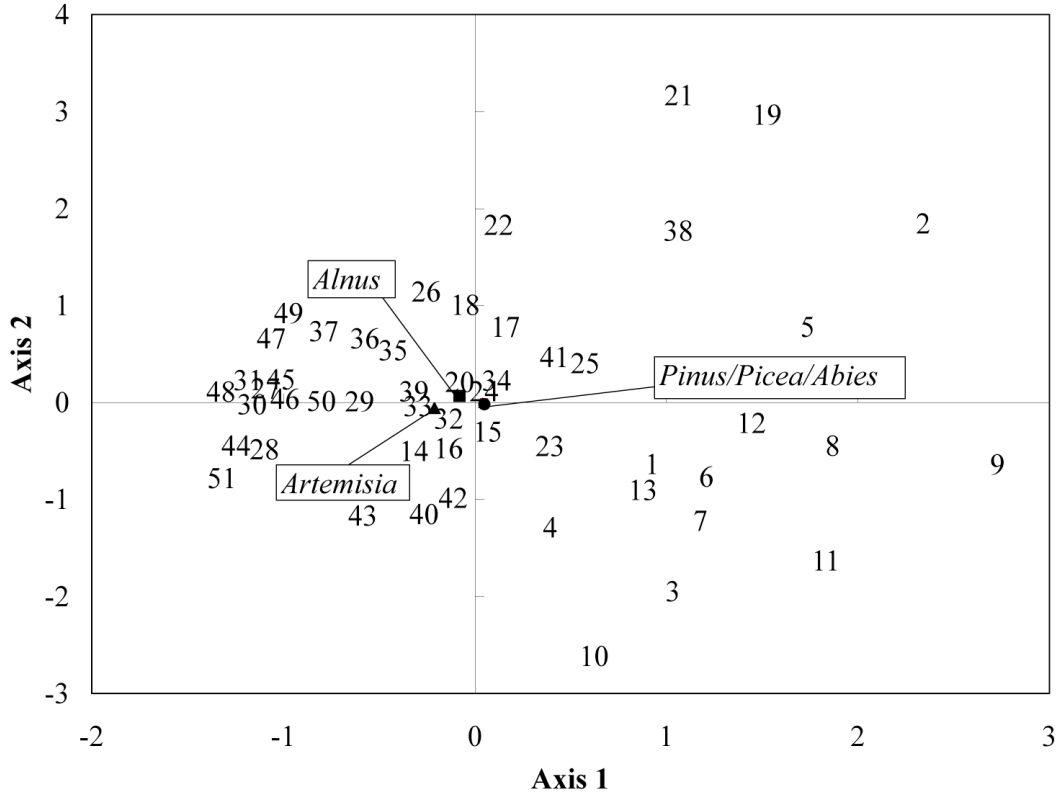
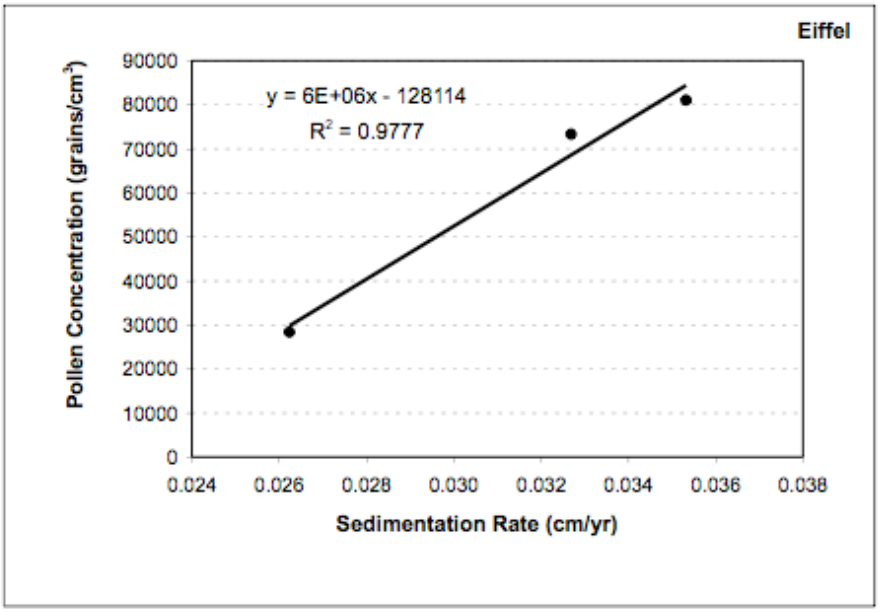


Figure 2.8. Regressions of sedimentation rate on pollen concentrations for a) Eiffel Lake and b) Sentinel Lake. Eiffel Lake only included sediment rates from the upper sediment samples, as no down core radionuclide dates were available to determine accurate rates downcore.


Eiffel
y = 6E+06x - 128114
R² = 0.9777
Pollen Concentration (grains/cm³)
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
0.024
0.026
0.028
0.030
0.032
0.034
0.036
0.038
Sedimentation Rate (cm/yr)

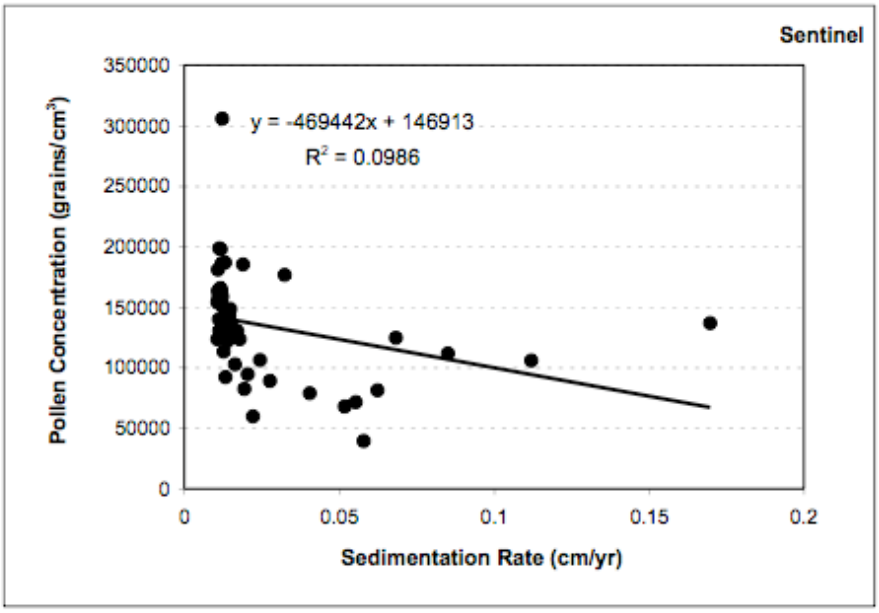

Sentinel
y = -469442x + 146913
R² = 0.0986
Pollen Concentration (grains/cm³)
350000
300000
250000
200000
150000
100000
50000
0
0
0.05
0.1
0.15
0.2
Sedimentation Rate (cm/yr)

Figure 2.9. Pollen percentages for surface samples taken along an elevation gradient. Site numbers 1 to 7 correspond to sample numbers E1A, E2A, E3A, E9A, E5A, S5A, and S4A respectively (refer to Figure 2.1 for site locations).

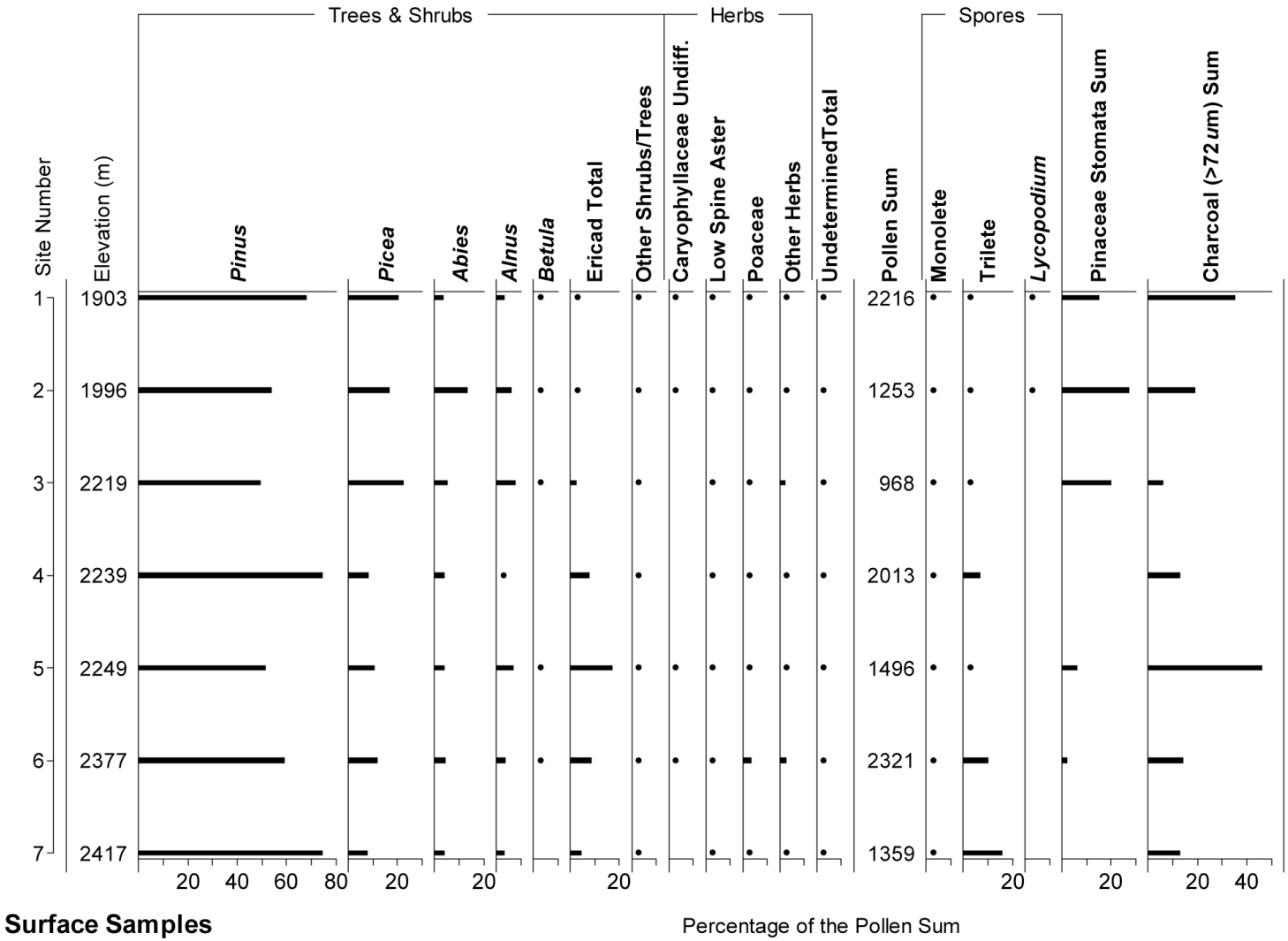

Trees & Shrubs
Herbs
Spores
Site Number
Elevation (m)
Pinus
Picea
Abies
Alnus
Betula
Ericad Total
Other Shrubs/Trees
Caryophyllaceae Undiff.
Low Spine Aster
Poaceae
Other Herbs
UndeterminedTotal
Pollen Sum
Monolete
Trilete
Lycopodium
Pinaceae Stomata Sum
Charcoal (>72um) Sum
1 1903 2216
2 1996 1253
3 2219 968
4 2239 2013
5 2249 1496
6 2377 2321
7 2417 1359
20 40 60 80
20
20
20
20
20
20
20 40
Surface Samples
Percentage of the Pollen Sum

Figure 2.10. Pollen percentages for Eiffel Lake inclusive of pollen and spore percentages, charcoal fragment and Pinaceae stomata sums, and total pollen concentration. Rare values (<2%) are indicated with a filled circle.

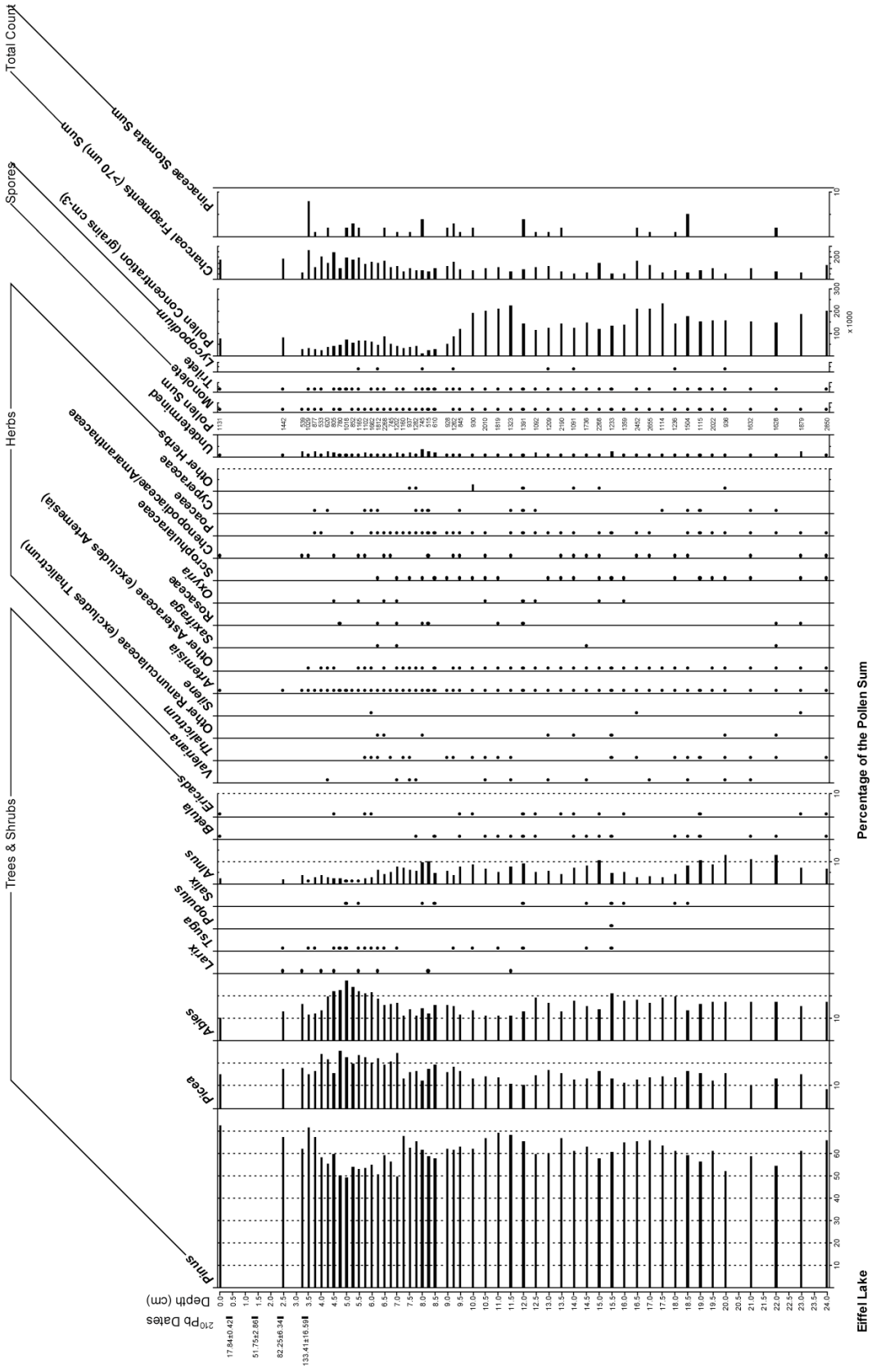

Eiffel Lake
Percentage of the Pollen Sum
Depth (cm)
210Pb Dates
17.84±0.42
51.75±2.86
82.25±6.34
133.41±16.55
Trees & Shrubs
Herbs
Spores
Total Count
Pinus
Picea
Abies
Larix
Tsuga
Populus
Salix
Alnus
Betula
Ericales
Valeriana
Thalictrum
Other Ranunculaceae (excludes Thalictrum)
Silene
Artemisia
Other Asteraceae (excludes Artemisia)
Saxifraga
Rosaceae
Oxyria
Scrophulariaceae
Chenopodiaceae/Amaranthaceae
Poaceae
Cyperaceae
Other Herbs
Undetermined
Pollen Sum
Monolete
Trilete
Lycopodium
Pollen Concentration (grains cm-3)
Charcoal Fragments (>70 um) Sum
Pinaceae Stomata Sum
x1000

Figure 2.11. Pollen concentrations and charcoal fragment concentrations for Eiffel Lake. Percent organic matter (LOI) is also presented. Only major taxa (>2% of the pollen sum) are included. Note the scale difference amongst taxa.

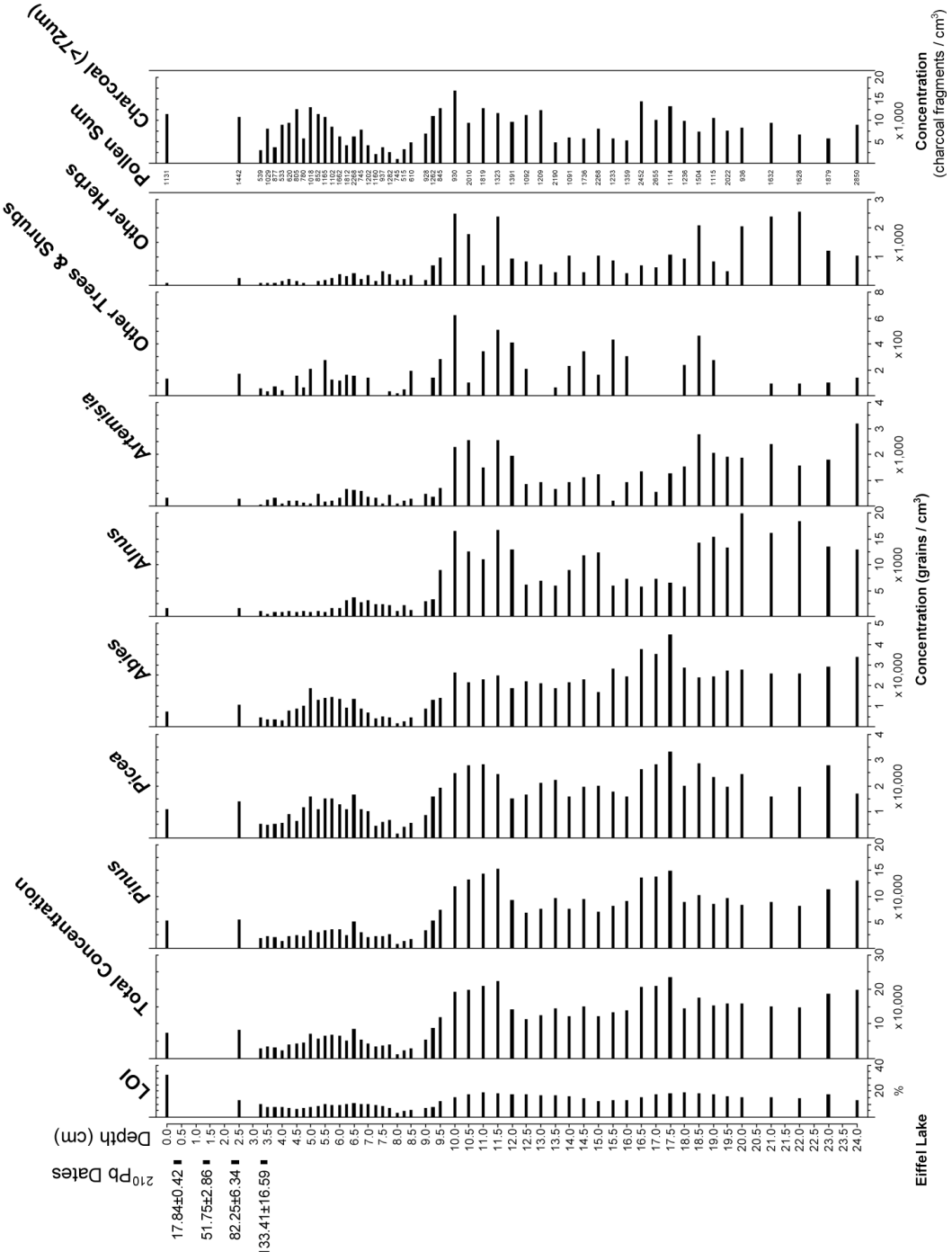

Eiffel Lake
Depth (cm)
210Pb Dates
17.84±0.42
51.75±2.86
82.25±6.34
133.41±16.59
LOI
Total Concentration
Pinus
Picea
Abies
Alnus
Artemisia
Other Trees & Shrubs
Other Herbs
Pollen Sum
Charcoal (>72um)
Concentration (grains / cm3)
Concentration
(charcoal fragments / cm3)

Figure 2.12. Pollen accumulation rates and charcoal accumulation rates for Eiffel Lake. Percent organic matter (LOI) is also presented. Only major taxa (>2% of the pollen sum) are included. Note the scale difference amongst taxa.

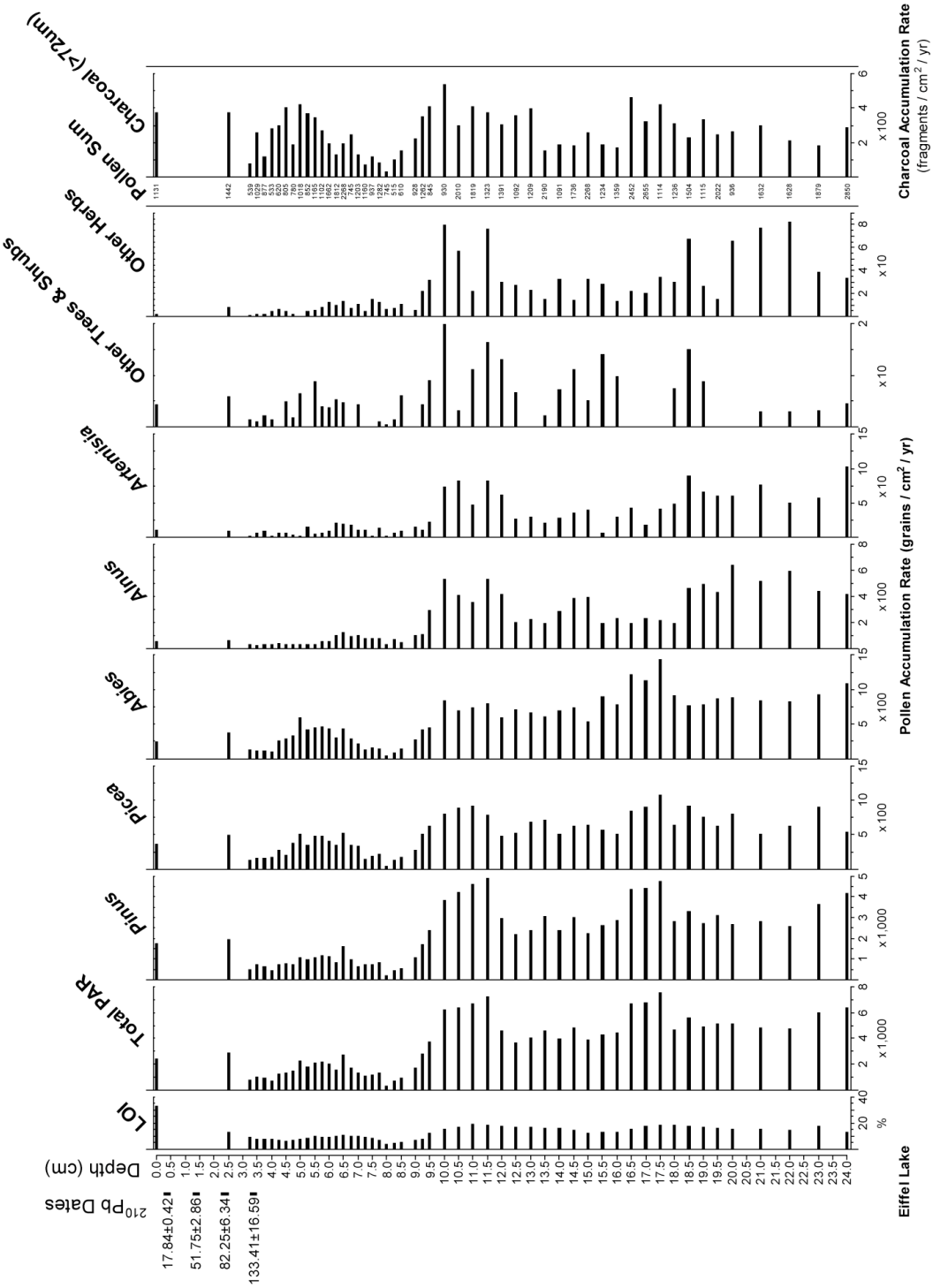

Eiffel Lake
Depth (cm)
^{210}Pb Dates
17.84±0.42
51.75±2.86
82.25±6.34
133.41±16.59
LOI
Total PAR
Pinus
Picea
Abies
Alnus
Artemisia
Other Trees & Shrubs
Other Herbs
Pollen Sum
Charcoal (>72um)
Pollen Accumulation Rate (grains / cm^2 / yr)
Charcoal Accumulation Rate
(fragments / cm^2 / yr)

Figure 2.13. Pollen percentages for Sentinel Lake inclusive of pollen and spore percentages, charcoal fragment and Pinaceae stomata sums, and total pollen concentration. Estimated age is presented based on linear and polynomial regression equations for radionuclide dates. Rare values (<2%) are indicated with a filled circle.

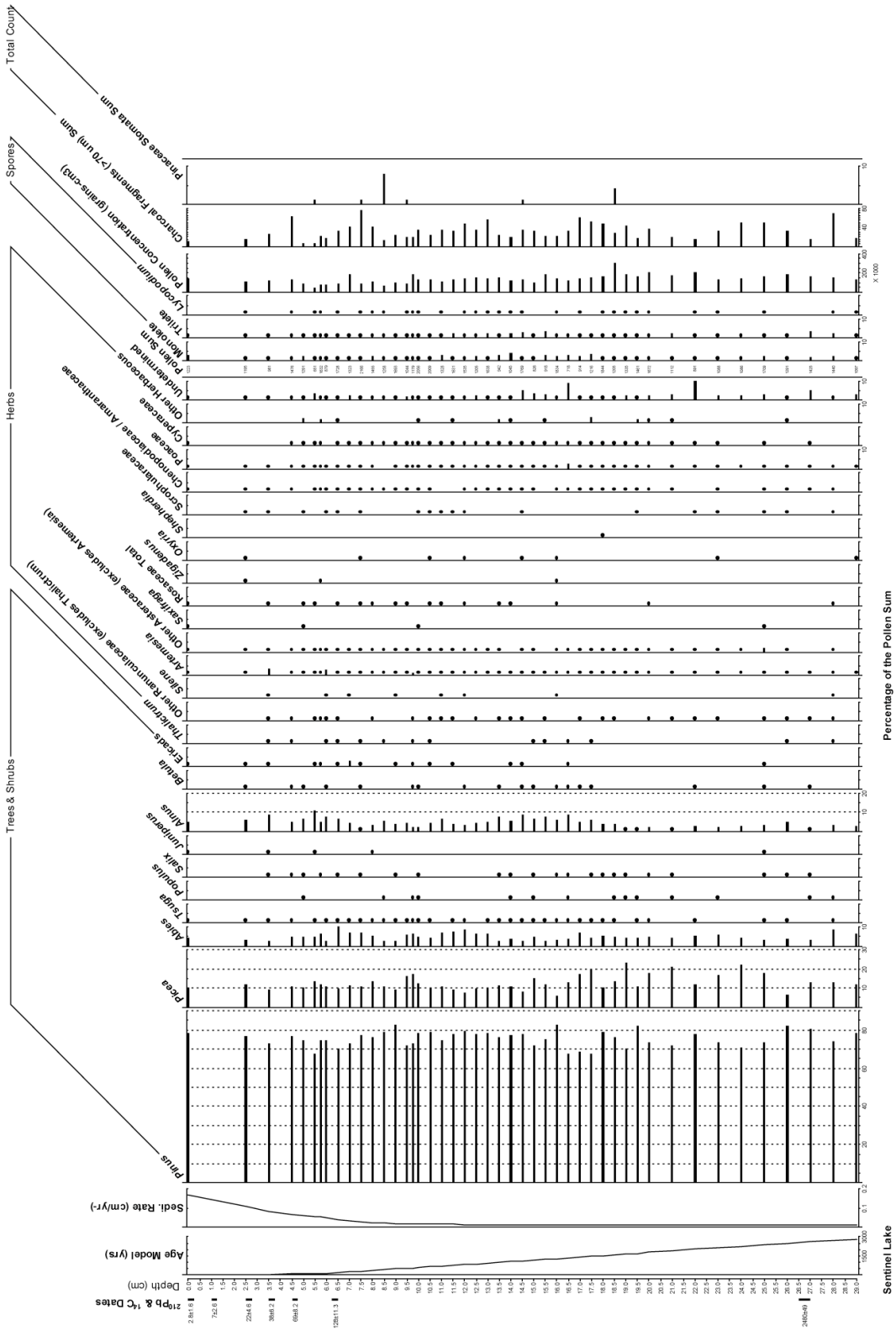

Total Count
Spores
Herbs
Trees & Shrubs
Phacaee Stomata Sum
Charcoal Fragments (grains-cm3)
Pollen Concentration (grains-cm3)
Lycopodium
Tilia
Monolete
Pollen Sum
Undetermined
Other Herbaceous
Cyperaceae
Poaceae
Chenopodiaceae / Amaranthaceae
Sphagnum
Oxyria
Zygadenus
Rosaceae Total
Saxifraga
Other Asteraceae (excludes Artemesia)
Artemesia
Stellaria
Other Ranunculaceae (excludes Thalictrum)
Thalictrum
Ericads
Betula
Alnus
Juniperus
Salix
Populus
Tsuga
Abies
Picea
Pinus
Sedi. Rate (cm/yr-)
Age Model (yrs)
Depth (cm)
210Pb & 14C Dates
Percentage of the Pollen Sum
Sentinel Lake

Figure 2.14. Pollen concentrations and charcoal fragment concentrations for Sentinel Lake. Percent organic matter (LOI) is also presented. Estimated age is presented based on linear and polynomial regression equations for radionuclide dates. Only major taxa (>2% of the pollen sum) are included. Note the scale difference amongst taxa.

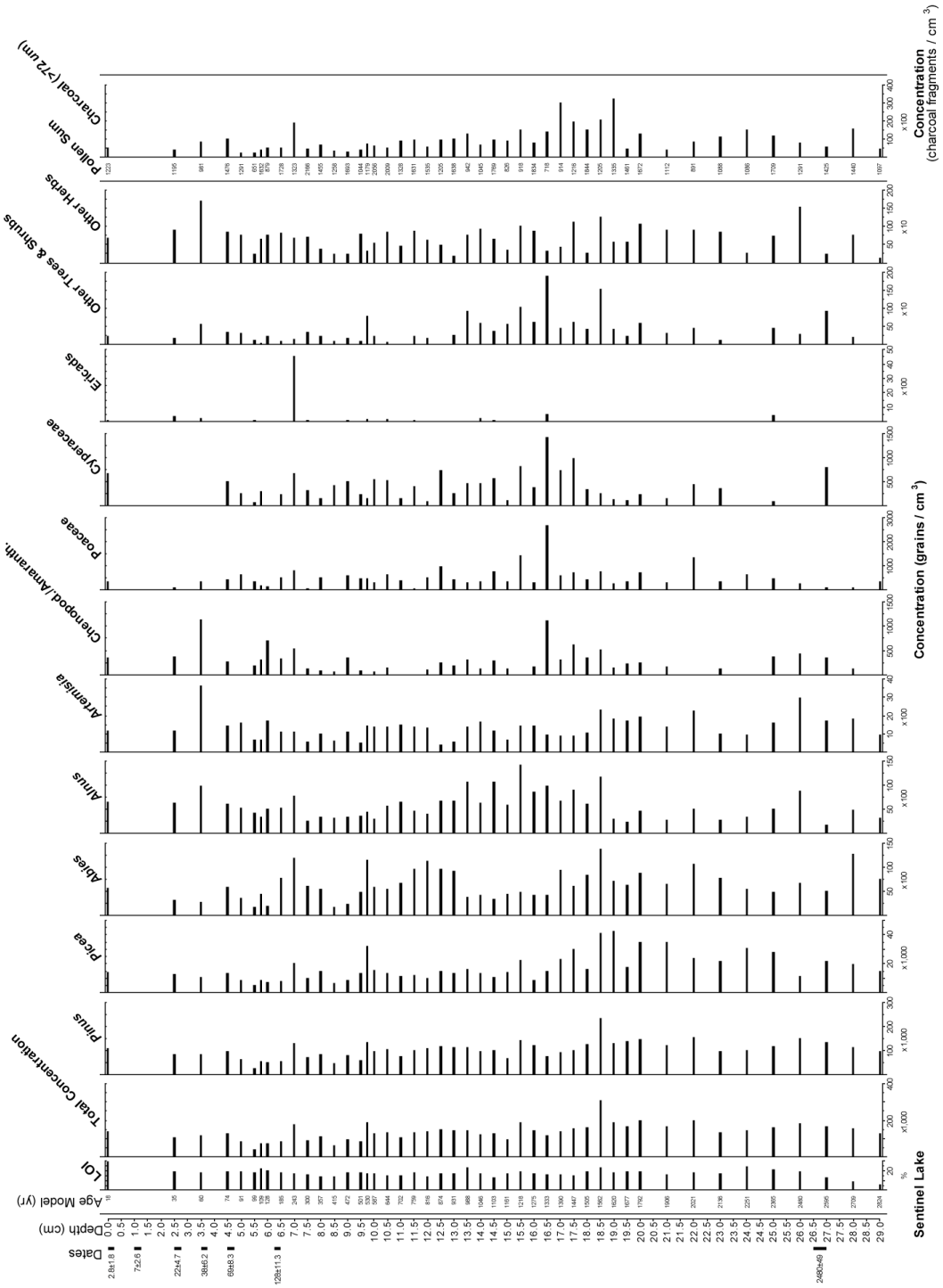
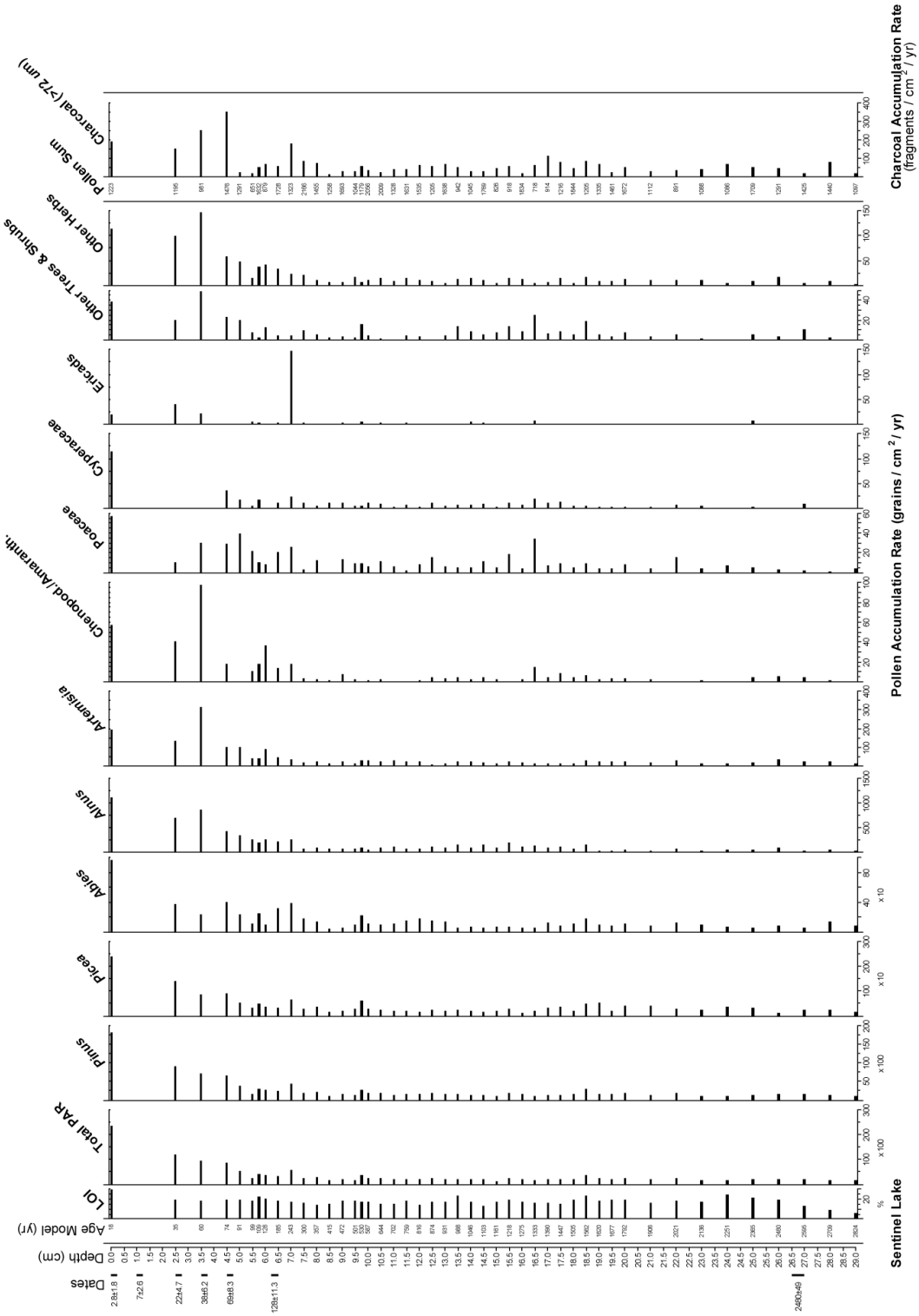

Sentinel Lake
Concentration (charcoal fragments / cm 3)
Concentration (grains / cm 3)
Dates
Depth (cm)
Age Model (yr)
LOI
Total Concentration
Pinus
Picea
Abies
Alnus
Artemisia
Chenopod./Amaranth.
Poaceae
Cyperaceae
Ericads
Other Trees & Shrubs
Other Herbs
Pollen Sum
Charcoal (>72 um)

Figure 2.15. Pollen accumulation rates and charcoal accumulation rates for Sentinel Lake. Percent organic matter (LOI) is also presented. Estimated age is presented based on linear and polynomial regression equations for radionuclide dates. Only major taxa (>2% of the pollen sum) are included. Note the scale difference amongst taxa.


Sentinel Lake
Pollen Accumulation Rate (grains / cm 2 / yr)
Charcoal Accumulation Rate (fragments / cm 2 / yr)
Dates
Depth (cm)
Age Model (yr)
LOI
Total PAR
Pinus
Picea
Abies
Alnus
Artemisia
Chenopod./Amaranth.
Poaceae
Cyperaceae
Ericads
Other Trees & Shrubs
Other Herbs
Pollen Sum
Charcoal (>72 um)
x 100
x 10
%

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3 DETERMINING TREELINE DYNAMICS FROM TWO MOUNTAIN LAKES USING PICEA:PINUS *POLLEN RATIOS AND STOMATA*

3.1 INTRODUCTION

Upslope migration of treeline in subalpine areas has been attributed to an increase of 1.5°C (mean annual temperatures) over the last century in the Canadian Rockies (Luckman & Kavanagh 2000; Reasoner & Hickman 1989). Other alpine ecosystem studies in the Yukon (Danby & Hik 2007a; Danby & Hik 2007b) and European Alps (Cannone *et al.* 2007; Walther *et al.* 2005) have also reported upslope migration of vegetation, as well as increased vegetation density. Walther (2004) has reviewed changes in vegetation related to climate warming. Fossil pollen assemblages obtained from lake cores can be calibrated by modern pollen assemblages to infer shifts in timberline in mountain regions, as demonstrated by Beaudoin (1986) and Evans (1997). Fluctuations in *Picea:Pinus* pollen ratios can be used as an indicator of timberline because changes in environmental conditions along an elevation gradient correspond with changes in vegetation (Maher 1963). However, pollen percentages alone may not be indicative of modern and past treeline dynamics because some dominant subalpine forest taxa (*e.g., Pinus*) contribute significantly to local and regional input into lakes making it difficult to discern between transitional zones of lower and upper treelines due to similar pollen ratios (Pisaric *et al.* 2000). Hence, interpretation of treeline dynamics is stronger when supported by multiple indicators (Pisaric *et al.,* 2000).

Nevertheless, pollen data provide useful information on treeline dynamics. The presence or absence of Pinaceae stomata in sediment can also be a useful indicator of the local occurrence of Pinaceae taxa (MacDonald 2001). Analysis of stomata is useful for determining local vegetation where lake sediment cores contain limited macrofossil remains and where certain pollen types are underrepresented due to poor preservation and dispersal (Hansen 1995; Yu 1997).

I was interested in determining if late Holocene timberline has moved upslope in the Eiffel Lake and Sentinel Lake area as a response to recent increased temperature trends. I hypothesized that timberline has shifted upward in the area in response to cooling and warming trends that have occurred in the Canadian Rockies over the past millennium, especially driven by a warming trend during the past century (Luckman & Kavanagh 2000; Luckman & Wilson 2005). Basing shifts in timberline on pollen ratios entails the acceptance of several assumptions. Firstly, reliable interpretation of pollen ratios is dependent on past vegetation composition being the same as modern vegetation compositions (Beaudoin 1986). I predict that pollen ratios will be a good indicator of treeline dynamics for both Eiffel Lake and Sentinel Lake, which are located in the same geographical area (approximately 2-3km apart). Secondly, the pollen record is assumed to be composed of a regional pollen type (denominator of the ratio) and a significant local pollen type (numerator) in order to reliably predict timberline fluctuations (Beaudoin 1986; Evans 1997; Maher 1963). The location of the study sites and the local vegetation (Holland & Coen 1983) suggest that these assumptions apply

here and therefore this approach should be appropriate. Further it is assumed that *Pinus* (mostly lodgepole pine) pollen contributes to the regional source, whereas *Picea* (mostly Engelmann spruce) pollen represents the local assemblage. Dispersal distance of *Picea* (~3% average regional percentage) pollen is much shorter than *Pinus* (~78% average regional percentage) and rapidly decreased from the coniferous-deciduous forest edge (Janssen 1966) with the majority of local pollen being dispersed within 300m (Faegri *et al.* 1989). Hence, low *Picea:Pinus* pollen ratios will correspond to timberline being further away from the site (timberline retreat), whereas high ratios are indicative of timberline advance (Beaudoin 1986; Evans 1997). Pollen ratios and stomata can be used to determine if these methods are useful in predicting treeline dynamics of similar sites within a specified geographical area. Also, these results will provide a better understanding of the impact of warming and cooling periods and their affect on treeline dynamics in the area.

3.2 METHODS AND MATERIALS

3.2.1. Study Site and Sampling

A detailed description of the study site, sampling, processing and enumeration of pollen and stomata is provided in Chapter 2. Sediment cores were taken from Eiffel Lake (51º19' N, 116º14' W) and Sentinel Lake (51º20' N, 116º13' W) in Banff National Park, Alberta. Eiffel Lake and Sentinel Lake are small fishless lakes (13.5ha and 2.8ha respectively) located above 2200m a.s.l. (Mayhood & Anderson 1976). Recorded elevations taken during site visits were 2240m a.s.l.

for Eiffel Lake (east shoreline) and 2424m a.s.l. for Sentinel Lake (south shoreline). Treeline in the area ranges between 2100-2300m a.s.l., with alpine lakes typically located greater than 2200m a.s.l. and subalpine lakes located between 1600-2200m a.s.l. (Vinebrooke & Leavitt 1999).

For this study, timberline is defined as the transitional zone from forests with erect growing trees to the sparsely distributed and dwarfed (krummholz) trees. Therefore, timberline can be abrupt or it can form a broad ecotone (Holtmeier 2009). Treeline is defined as the upper limit of krummholz (stunted trees) (Arno & Hammerly 1984). Hence timberline and treeline are closely tied. Treeline dynamics concern the movement of the treeline limit and timberline limit, as well as the difference between the continuous forest upper limit and krummholz upper limit.

Pinus contorta Douglas ex Loudon (lodgepole pine) was encountered once during site surveys and was represented by a single tree along the Eiffel Lake trailhead (~ 2 km east of lake, Fig. 3.1) and hence is not a major component of the local forest. The dominant forest species in the immediate area (sampling sites, Fig. 3.1) includes *Abies bifolia* A. Murray (Rocky Mountain subalpine fir), *Picea engelmanni* Parry ex Engelmann (Engelmann spruce) and *Larix lyallii* Parlatore (alpine larch).

Surface pollen samples of sediment were taken along an elevation gradient at approximately 500m intervals and at least 50m south, north or west of the hiking trail (Fig. 3.1.). Vegetation surveys were also conducted along these transects to determine dominant forest species and the extent of the treeline zone in the area. All sediment subsamples and surface pollen samples were chemically processed (Faegri *et al.* 1989), residues were stained with safranin and stored in silicone oil. Prior to processing, sediment subsamples and surface pollen samples were inoculated with *Lycopodium* spores "spike" (Batch # 710961 (2 tablets, 27,822+/-975 spores) or Batch # 414831 (2 tablets, 24,153+/-1197 spores) to estimate pollen and spore concentrations (Stockmarr 1971). Samples were manually homogenized for 5 minutes, mounted onto slides, and pollen grains were counted and identified using published and unpublished keys, identification guides (Bassett *et al.* 1978; Crompton & Wojtas 1993; Habgood & Simons 1985; Hansen 1995; Kapp *et al.* 2000; Mcandrews *et al.* 1973; Punt *et al.* 2007) and reference collections (Royal Alberta Museum's Quaternary Environments Pollen Reference Collections, University of Alberta Palynology Lab, study site reference collection). No less than 500 identifiable pollen grains were counted for sediment and surface samples, and of this pollen sum at least 200 or more pollen grains were taxa other than *Pinus.* All stomata were identifiable as Pinaceae, but whenever preservation permitted, stomata were identified to the genus level (Hansen 1995; MacDonald 2001).

3.2.2. Pollen Ratios and Treeline Dynamics

Investigation of treeline dynamics was undertaken by examining the presence (and abundance) and absence of stomata in surface and sediment pollen samples and by calculating surface and sediment pollen ratios (*Picea:Pinus* (spruce:pine)). Surface pollen ratios for samples E1-E3, E5, E9, S4 and S5 (Figs. 3.1, 3.2) were used to calibrate present timberline for the Eiffel Lake and Sentinel Lake area. Sediment pollen ratios were then used to compare apparent site elevation with present site elevation to infer shifts in timberline. This was completed by matching sediment pollen ratios with the appropriate surface sample elevations and corresponding ratios. Chronological control for the record of inferred treeline fluctuations was provided by radiometric dating Eiffel Lake and Sentinel Lake. The dating results were compared to recent temperature reconstructions for the Canadian Rockies compiled by Luckman & Wilson (2005).

3.3 RESULTS

3.3.1. Radiometric Dating

Detailed description of sampling, methods and results for radiometric dating is provided in Chapter 2. Radiometric dating (^{210}Pb and ^{14}C) for Sentinel Lake indicated a slow rate of sediment accumulation, near surface date of 128 yrs BP (^{210}Pb, 6.5cm depth) and near bottom date of 2450+/- 40 yrs BP (^{14}C, Beta-251122, 2480 CAL yrs, 27cm depth). For Eiffel Lake only ^{210}Pb radiometric dating indicates a near surface date of 133 yrs+/-16.6 yrs BP (4.5cm depth). ^{14}C

dates were not available for Eiffel Lake, and hence no ages were extrapolated past 3.5cm depth.

3.3.2 Stomata in the Surface Pollen Record

For surface pollen samples, most stomata (70%) were from *Picea* (likely *Picea engelmannii* based on site inspection) and the remaining (30%) were identified as Pinaceae stomata. Higher stomata abundance corresponded with higher *Picea* pollen percentages and low abundance corresponded with low *Picea* pollen percentages in the surface pollen samples (Figs. 3.2). There were no stomata in samples taken at the highest elevation (2417m a.s.l.) and most (27) occurred at the second lowest elevation (1996m a.s.l.) (Fig. 3.2). Stomata percentages (percentage of the pollen sum) ranged from 0.68% to 2.15% for lower elevation (closed mature forest), from 0% to 0.40% for moderate elevation (open forest), and from 0% to 0.09% for higher elevation (open alpine meadows). Stomata abundance (Pinaceae) corresponded well with surface pollen ratios where greater abundance occurred in surface samples taken from closed mature forest and lower abundance occurred in samples taken from alpine meadows or open forests (Fig. 3.3). These results suggest that the presence of *Picea* stomata is a good indication of local occurrence of upper subalpine spruce-dominated forest.

3.3.3 Calibration of Modern Timberline

Natural log transformed surface pollen ratios were used to calibrate modern timberline in relation to Eiffel Lake and Sentinel Lake (Fig. 3.3). There was a negative relationship between surface pollen ratios and elevation (R^2=0.33) obtained from seven surface pollen samples (Fig. 3.3). Ratios generally > 0.30 were from samples obtained from a closed mature forest and ratios generally < 0.20 were from samples obtained from an open forest or alpine meadow (Fig. 3.3). Closed forests were characterized by stands of mature *P. engelmannii* and *A. bifolia* (Fig. 3.3). Open forests were characterized by stands of *P. engelmannii*, *A. bifolia* and *L. lyallii* with some open areas of bare sediment and rocky patches and meadows with low-lying herbaceous vegetation and low-lying shrubs (*e.g., Salix* L. (willow)). Alpine meadows are characterized by low-lying herbaceous vegetation (*e.g, Phyllodoce glanduliflora* (Hooker) Coville (yellow heather), *Cassiope mertensiana* (Bongard) G. Don (mountain heather), *Salix*), sparse stunted trees (krummholz), bare sediment and rocky areas.

3.3.4 Timberline fluctuations inferred for Eiffel Lake and Sentinel Lake

Eiffel Lake and Sentinel Lake local vegetation assemblage and regional pollen records showed no significant changes in overall vegetation composition as the sediment records encompass relatively short time period (late Holocene). *Pinus* pollen is a major component of the pollen assemblages for Eiffel Lake (x=60%, SD=5.7%) and Sentinel Lake (x=75%, SD=4.1%). The pollen record indicates that *Picea* (likely *Picea engelmannii*) is a significant local source of pollen.

Sediment pollen ratios and apparent site elevation were plotted against depth for Eiffel Lake and Sentinel Lake (Figs. 3.4, 3.5). The apparent elevation was determined by using the top sediment sample (0-2.5cm) pollen ratio with the calibration (regression) equation. Predicted apparent site elevations for Eiffel Lake and Sentinel Lake were 35m (2205m a.s.l. predicted, 2240m a.s.l. actual) and 132m (2292m a.s.l. predicted, 2424m a.s.l. actual) lower than actual site elevations, respectively. Apparent site elevations for Eiffel Lake ranged between 2026-2295m a.s.l. (x=2157m a.s.l., SD=62) and pollen ratios ranged between 0.13-0.51 (x=0.28, SD 0.09). Sentinel Lake apparent site elevations ranged between 2114-2416m a.s.l. (x=2256, SD=68) and pollen ratios ranged between 0.07-0.33 (x=0.17, SD 0.07).

For Eiffel Lake, the sediment pollen ratios reveal two distinct patterns of timberline fluctuations (Fig. 3.4). Below 10cm core depth, apparent site elevations (25 samples) fluctuate above (timberline retreat) and below (timberline advance) present apparent site elevation (2205m a.s.l.) with ratios between 0.13-0.30 (x=0.22, SD=0.04) (Fig. 3.4). Above 10cm core depth, apparent site elevations (27 samples) generally remain below present apparent site elevation (timberline advance) with ratios between 0.19-0.51 (x=0.33, SD=0.10) and only one sample slightly above present apparent elevation (7.5-7.25cm, 2220m a.s.l.) (Fig.4.4). Between 7.25-4.75cm (10 samples) and 4.5-4cm (2 samples) ratios are higher than 0.3 (x=0.42, SD=0.06) denoting apparent site elevations between 2026m-

2111m a.s.l. (Fig. 3.4). Stomata are found throughout the sediment record with a maximum occurrence of 8 stomata at 3.75-3.5cm (Fig. 3.4).

For Sentinel Lake, the sediment pollen ratios do not reveal any apparent trends (Fig. 3.5). Apparent site elevations (46 samples) fluctuate above and below present apparent site elevation throughout the core (Fig. 3.5). Pollen ratios are highly variable between 27-16cm (x=0.21, SD=0.08, 15 samples) and less variable above 16cm core depth (x=0.15, SD=0.03, 28 samples) (Fig. 3.5). Stomata appear in the record at 19-18.5cm and are more commonly encountered between 9.75-5.5cm (Fig. 3.5).

3.4 DISCUSSION

3.4.1 Inferring timberline fluctuations for Eiffel Lake Area

Changes in apparent site elevations were compared with present apparent site elevation to infer timberline position. Apparent site elevations below present apparent site elevation (higher ratios) indicate timberline advance whereas values above present apparent site elevation (lower ratios) indicate timberline retreat. The predicted present apparent site elevation was close to actual elevation (35m lower than actual) for Eiffel Lake (Fig. 3.4). Based on *Picea:Pinus* ratios and stomata data, timberline has been advancing upslope during the interval represented by 10-0cm section for Eiffel Lake (Fig. 3.4). Overall, *Picea:Pinus* ratios suggest higher-than-present apparent timberline recorded in the upper 10cm of the core (Fig. 3.4.).

Eiffel Lake is a subalpine lake located near treeline, with *L. lyallii* (dominant species) and some *A. bifolia* trees found on the east and west (to a lesser extent) perimeter of the lake, and with *P. engelmannii* approximately 0.5-1 km east of the lake. It is not surprising that stomata can be found through most of the core (Fig. 3.4). However, it was surprising that there were only two occurrences of *Larix* stomata (2 stomata at 9-9.25cm and 1 stoma at 6.5-6.75cm). Studies have found that underrepresented pollen of locally abundant species are often represented by a large number of stomata representing that species (Hansen 1995; Yu 1997). *Larix* stomata and pollen corresponded well with apparent timberline advance in the interval represented by 10-0cm core sections (Fig. 3.4). Yet it is surprising that *Larix* stomata are not more represented in the record since *L. lyallii* sheds its leaves annually and because of its proximity to the lake. For instance, *Larix* stomata (presumably *L.laricina*) in surface samples better represented local occurrence of *L. laricina* and defined tundra-forest borders in the Northwest Territories (Yellowknife area), whereas *Larix* pollen were infrequently encountered (Hansen *et al.* 1996). *Larix* stomata (representing *Larix sibirica*) was also present in all treed sites along a Siberian tundra-forest gradient, whereas *Larix* pollen was underrepresented (Clayden *et al.* 1996). Therefore, frequently abundant *Larix* stomata are thought to be a good proxy of local occurrence of *Larix* (Clayden *et al.,* 1996; MacDonald 2001). Despite this, the results indicate that *Larix* stomata may not be a good indicator of *Larix lyallii* occurrence for the Eiffel Lake area and illustrates the potential limitation of stomata analysis in

certain areas. Some potential reasons for these findings may be differential preservation of stomata from different *Larix* species and varying environmental conditions in these mountain lakes. Therefore *Larix* stomata analysis should be further investigated in these areas.

The top 3.5cm inferred interval of timberline advance, calibrated by available radiometric controls, spans the last 133 yrs BP (3.5cm) for Eiffel Lake (Fig. 3.4). Evidence from the Canadian Rockies suggests an interval of climate warming in the last century (Luckman & Kavanagh 2000; Luckman & Wilson 2005), which correlates well with the top 3.5cm interval of timberline advance identified for the Eiffel core (Fig. 3.4). This suggest that upslope timberline advance in the study area is likely driven by warmer temperatures during this period. Evans (1997) differentiated between periods of high versus lower treeline position from a small montane lake core, which correlated well with warmer and cooler periods. Between *ca.* 4000-4500 yrs BP, timberline retreat implied by low pollen ratios corresponded well with cooler temperatures onset by glacial advance in Jasper National Park (Sunwapta and Wilcox Passes) (Beaudoin 1986). Also, changes in vegetation density and treeline fluctuations in the alpine Yukon corresponded well to warmer periods (Danby & Hik 2007b). A limitation to this interpretation is that Eiffel Lake was not dated down core and therefore inference of climatic changes in relation to treeline dynamics cannot be interpreted past 3.5cm.

Fluctuation of pollen ratios in the interval represented by 25-10cm suggests four periods of treeline advance and four periods of treeline retreat (Fig. 3.4.). Eight out of 10 occurrences of stomata correspond with greater-than-present ratios, supporting timberline advance during these periods (Fig. 3.4). However, 2 out of 10 occurrences of stomata occur where ratios are lower-than present, suggesting variability of the dataset around the apparent present site elevation, which is apparent upon visual inspection (Fig. 3.4.). Treeline advance may be rapid in some areas depending on local environmental conditions and species response to climate change (Luckman & Kavanagh 1998). Whereas, significant tree mortality due to extreme cooling periods is needed for significant treeline retreat where long-living acclimatized mature trees have reached higher elevations (Luckman & Kavanagh 1998). Therefore, marked treeline retreat in the span of the record is not likely due to the timescale indicated by the cores and typical slow rate of retreat. Alpine treeline and tree establishment is strongly influenced by diverse site-specific factors such as topoclimates, large temperature gradients, snow accumulation and drainage (Luckman & Kavanagh 1998), whereas northern treeline may react differently. Significant post-glacial upslope migration of *Pseudotsuga menziesii* (Douglas fir) was not evident in the pollen and macrofossil record with northern migration of *P. menziesii* into the Canadian Rockies (from populations north of the Great Divide Basin in the US) being estimated to occur between 50-220 m/yr (Gugger & Sugita 2010). The subarctic alpine treeline (*Picea glauca* (white spruce)) advanced 10m and 20m in the MacKenzie Mountains (NWT) and Yukon mountain ranges respectively, over the past 150

years, but had more significant increases in tree density (Szeicz & MacDonald 1995). Increased forest stand density and upslope migration were recorded in the subarctic alpine (Kluane Ranges, Saint Elias Mountains, Yukon) in relation to warming temperatures in the 20th century (Danby & Hik 2007b), which was also observed in aerial photographs (encompassing 40-41 years) in the same area (Danby & Hik 2007a). Therefore, fluctuations in ratios between 25-10cm may be interpreted as changes in pollen production and / or vegetation density (leading to increase of pollen) rather than upslope migration of trees.

3.4.2 Pollen ratios and Sentinel Lake

An unexpected result of this study is that Sentinel Lake's highly variable pollen ratios are not a good predictor of timberline fluctuations for this site (Fig. 3.5). Sentinel Lake (2424m a.s.l.) differs from Eiffel Lake (2240m a.s.l.) being situated at a higher elevation with open terrain, alpine meadows composed of low-lying vegetation, and sparse krummholz trees. Eiffel Lake is composed of more wind-protected terrain and open or closed (lower elevations) forested areas with erect tree forms. Due to topography (*i.e.,* slope and topography) and other environmental factors (such as moisture and temperature gradients) that may limit tree growth and establishment (Danby & Hik 2007b; Shafer *et al.* 2001), expansion of the upright forest may never be possible in the Sentinel Lake area where exposed terrain, bare rock and wind-exposed topography may limit tree establishment. For example, persistent high-velocity winds may play a role in limiting tree establishment due to its direct impact on snow relocation, soil

erosion, and soil and air temperatures (Holtmeier & Broll 2010). Hence, treelines are controlled by various climatic and other environmental factors at the global to the site scale (Holtmeier & Broll 2005). For instance, topography and permafrost (presence or absence) were partly responsible for *Picea glauca* advancing 65-85cm in the subarctic south-facing slopes, whereas *P. glauca* only increased in density on the north-facing slopes (landscape and local scales) (Danby & Hik 2007b). This illustrates how topographical variation between relatively close and geographically similar study sites can influence treeline and timberline advance and density differently.

Where timberline advances are not possible based on topography, *Picea:Pinus* ratios may not be a reliable proxy of timberline fluctuations. Other dominant plant species may be a more reliable indicator of vegetation advance versus timberline advance. For example, relatively small climatic changes (*e.g.,* 1-2°C mean annual temperature) and a decrease in snow cover days in the European Alps has resulted in the expansion and invasion of high alpine shrubs (Cannone *et al.,* 2007). The Canadian Rockies have experienced a similar temperature increase of 1.5°C (mean annual temperature) (Luckman & Kavanagh 2000). *Alnus* pollen percentages, concentrations and PAR all increase up core, and are most pronounced in the PAR data and less pronounced in the concentration data (refer to Chapter 2). Further and more extensive vegetation surveys are needed to determine if *Alnus* is a major component of the vegetation around the lake site, as alder was not identified immediately surrounding the lake or in the immediate

area (along the trail, Fig. 3.1). Past vegetation surveys of the area revealed that *Alnus incana* subsp. *tenuifolia* (Nutt.) Breitung (mountain alder, also called *A. tenuifolia*) is the species of alder occurring in the area (Holland & Coen 1983). If *Alnus* is a major component of the vegetation, *Alnus* pollen may be a more reliable indicator of vegetation advance for Sentinel Lake because alder often grows in disturbed areas (such as screes and rocky slopes) in this region (Holland & Coen 1983).

Stomata do not occur in the Sentinel Lake record until 19-18.5cm (estimated 1562 yrs BP), are more commonly encountered between 9.75-5.5cm (estimated 501-91 yrs BP) and are absent from an estimated age of 91 yrs BP to present (Fig. 3.5). The stomata record does not correspond well with increases in *Picea* pollen percentages, pollen concentrations or PAR for Sentinel Lake (refer to Chapter 2). However, the presence of stomata during these periods may still correspond to treeline advance of sparsely distributed krummholz trees. These stunted trees are still capable of producing pollen (Evans 1997); however, pollen production may be reduced or limited at such high elevations due to unfavorable conditions (Hicks 2006), such as lower temperatures and shorter growing seasons in alpine ecosystems. For example, critical mean July temperatures correlated well with *Pinus* (12°C) and *Picea* (13°C) pollen accumulation rates (PAR) and the northern limits of these species (Huusko & Hicks 2009). If critical temperatures needed for pollen production are not reached, PAR will be low (Huusko & Hicks 2009); therefore, treeline or vegetation biomass may not be indicated through

examination of the pollen record. Also, macrofossil (or stomata) remains that are not supported by the pollen record may be explained through the presence of sparse trees in the area and not because forest expansion (Hicks 2006), which may explain the disjunction between the pollen record and stomata record for Sentinel Lake.

3.4.3 Appropriate Use of Proxies to indicate Treeline Dynamics and Future Research

Upslope migration of alpine species (*e.g., Picea glauca*, *Betua papyrifera*) in relation to increased mean temperatures (of the coldest month) has been recorded (Danby & Hik 2007b). Whereas, other high-altitude species may have their distributions limited due to increased mean annual temperatures (Shafer *et al.,* 2001), disappearance of colder mountainous habitats (*i.e,* reduced snowpack and permafrost) (Beniston 2003; Cannone *et al.,* 2007), genetic variability, ability to adapt to environmental changes and interspecific competitions (Dukes & Mooney 1999). Therefore, it is important to investigate how vegetation in different alpine areas maybe affected by climatic changes and the impact changes in mean annual temperatures and precipitation will have on these ecosystems.

Conifer taxa may be overrepresented (*e.g, Pinus* spp.) or underrepresented (*e.g., Larix* spp.) in the subfossil pollen assemblage; therefore, it is important to use other indicators of treeline dynamics besides pollen percentages alone (MacDonald 2001). Lignified stomata preserves well in lake sediments and can be

quantified along with pollen to reconstruct past local vegetation and infer past treeline position (Hansen 1995). Based on these results, using presence or absence of stomata was a good method to determine how reliable the timberline calibration (surface pollen ratios) was (Fig. 3.3). An increase in stomata abundance indicated a lower elevations (closed forest) and decreased stomata abundance indicated higher elevations (alpine meadow or open forest) (Fig. 3.3). This method may be useful when limited samples are available for calibration. If stomata occurrence and abundance do not agree with surface pollen ratios and elevation changes in forest type, one should question using such a method for inferring treeline dynamics. However, this method does not ensure that pollen ratios are appropriate for every site. This may be determined by investigating variability in fluctuations in sediment pollen ratios. Where pollen ratios are not suitable, (*i.e.,* for Sentinel Lake) other proxies should be investigated in order to accurately infer treeline dynamics. Uncertainties in interpretation of pollen ratios in relation to warming and cooling periods for Eiffel Lake can be resolved by also obtaining radiometric dates down core. Also, increasing the number of surface samples used to calibrate apparent timberline would be beneficial and may result in stronger relationship between elevation and pollen ratios (increase R^2). Also, increasing the number of surface samples would allow better assessment of sample-to-sample variability in pollen ratios derived from Sentinel Lake and Eiffel Lake samples.

3.5 FIGURES

Figure 3.1. Location of Eiffel Lake and Sentinel Lake area in Banff National Park, Alberta. Filled circles indicate locations where surface samples and tree transects and / or vegetation surveys were completed.

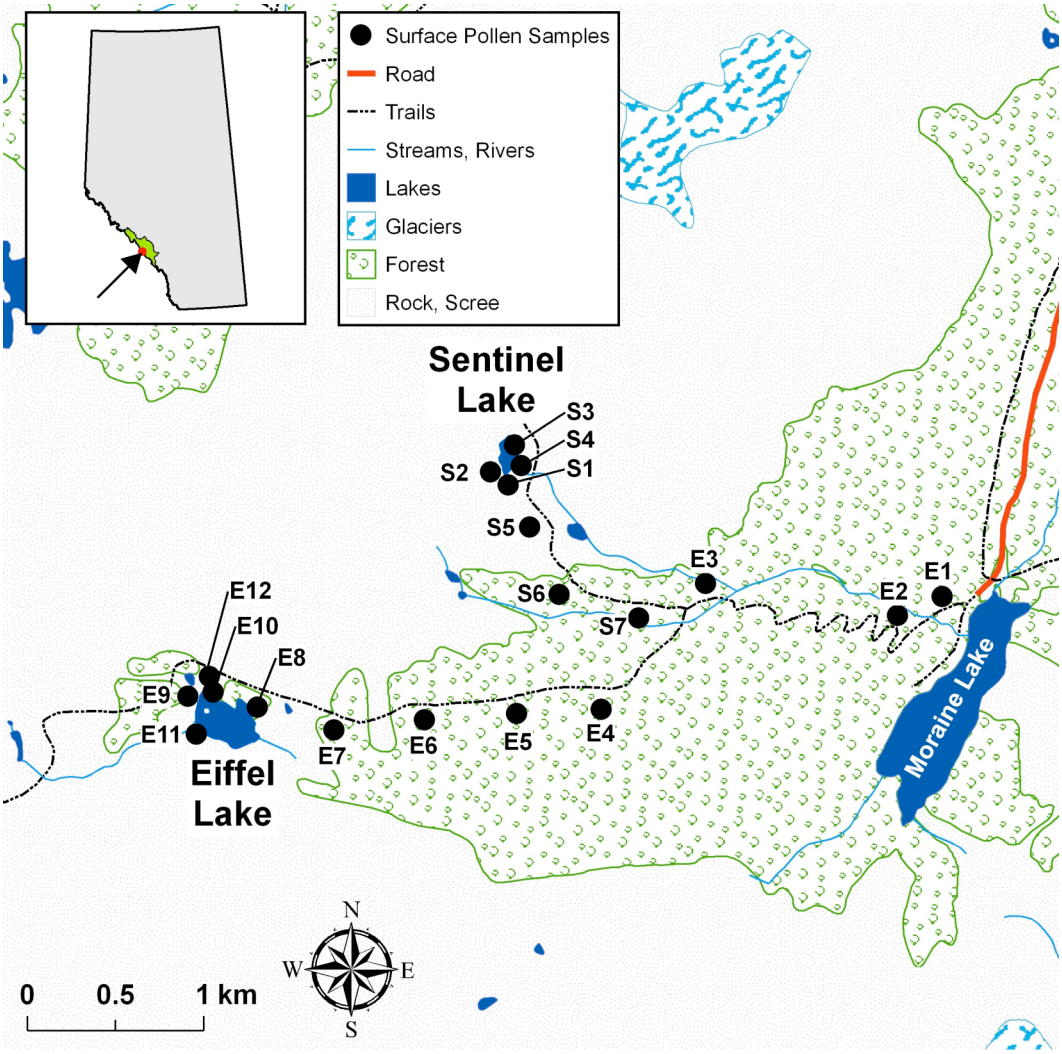


Figure 3.2. Pollen percentages for surface samples taken along an elevation gradient. Site numbers 1 to 7 correspond to sample numbers E1A, E2A, E3A, E9A, E5A, S5A, and S4A respectively (refer to Figure 4.1 for site locations).

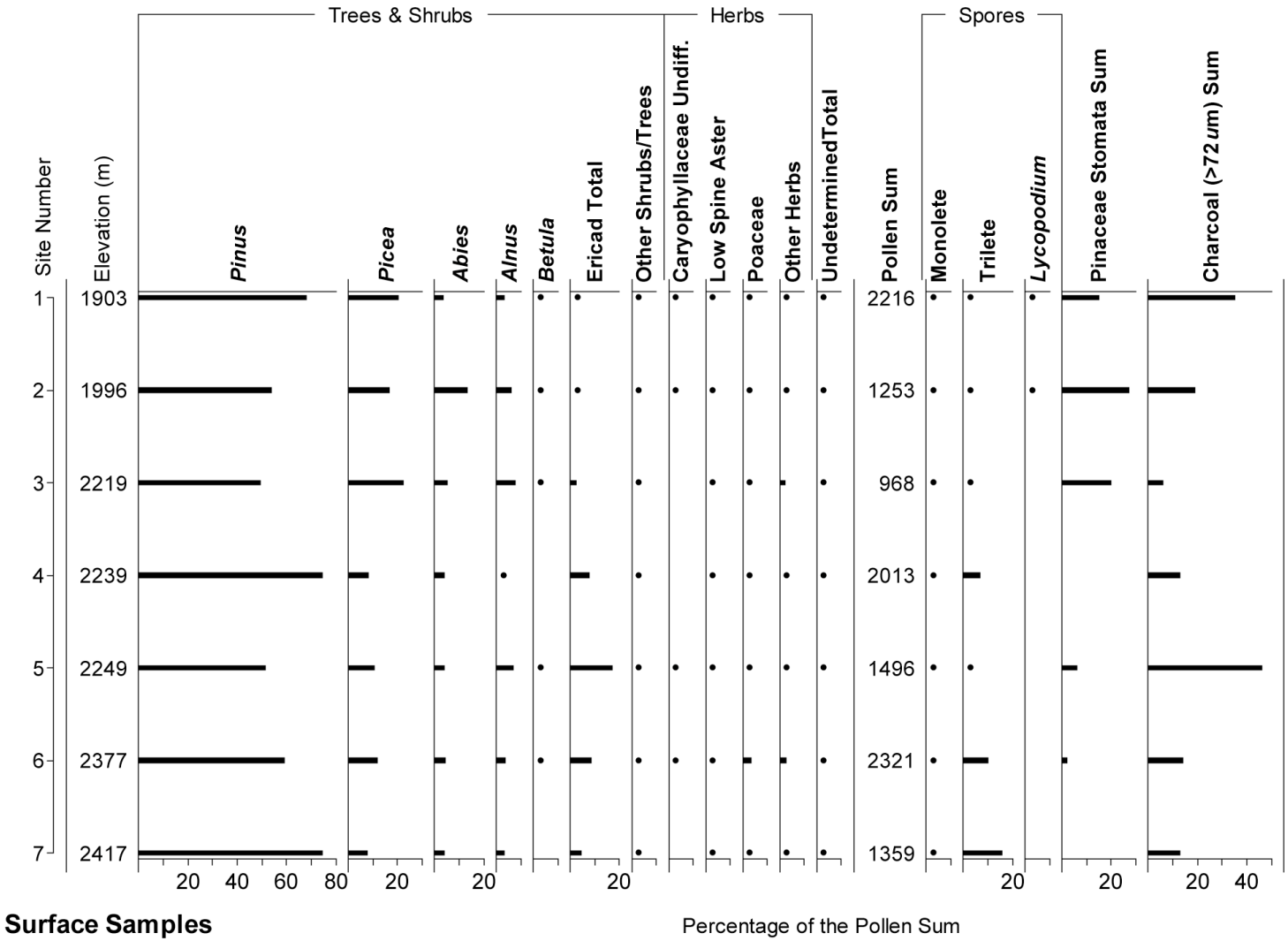

Trees & Shrubs
Herbs
Spores
Site Number
Elevation (m)
Pinus
Picea
Abies
Alnus
Betula
Ericad Total
Other Shrubs/Trees
Caryophyllaceae Undiff.
Low Spine Aster
Poaceae
Other Herbs
UndeterminedTotal
Pollen Sum
Monolete
Trilete
Lycopodium
Pinaceae Stomata Sum
Charcoal (>72 um) Sum
1 1903 2216
2 1996 1253
3 2219 968
4 2239 2013
5 2249 1496
6 2377 2321
7 2417 1359
20 40 60 80
20
20
20
20
20
20
20 40
Surface Samples
Percentage of the Pollen Sum

Figure 3.3. *Picea:Pinus* ratios (untransformed ratios are plotted) for surface pollen samples taken along an elevation gradient (1903m to 2417m). Corresponding elevations and stomata abundance (in brackets) are given for each point. Two distinct groupings (closed mature forest vs. alpine meadow/open forest) were noted. Dashed lines represents the 95% confidence intervals that a predicted value (elevation) for a given pollen ratio will fall within this range. The reported regression equation (based on natural log transformed ratios, y=apparent elevation, x=sediment pollen ratio) was used for predicting apparent site elevations from Sentinel Lake and Eiffel Lake pollen ratios.

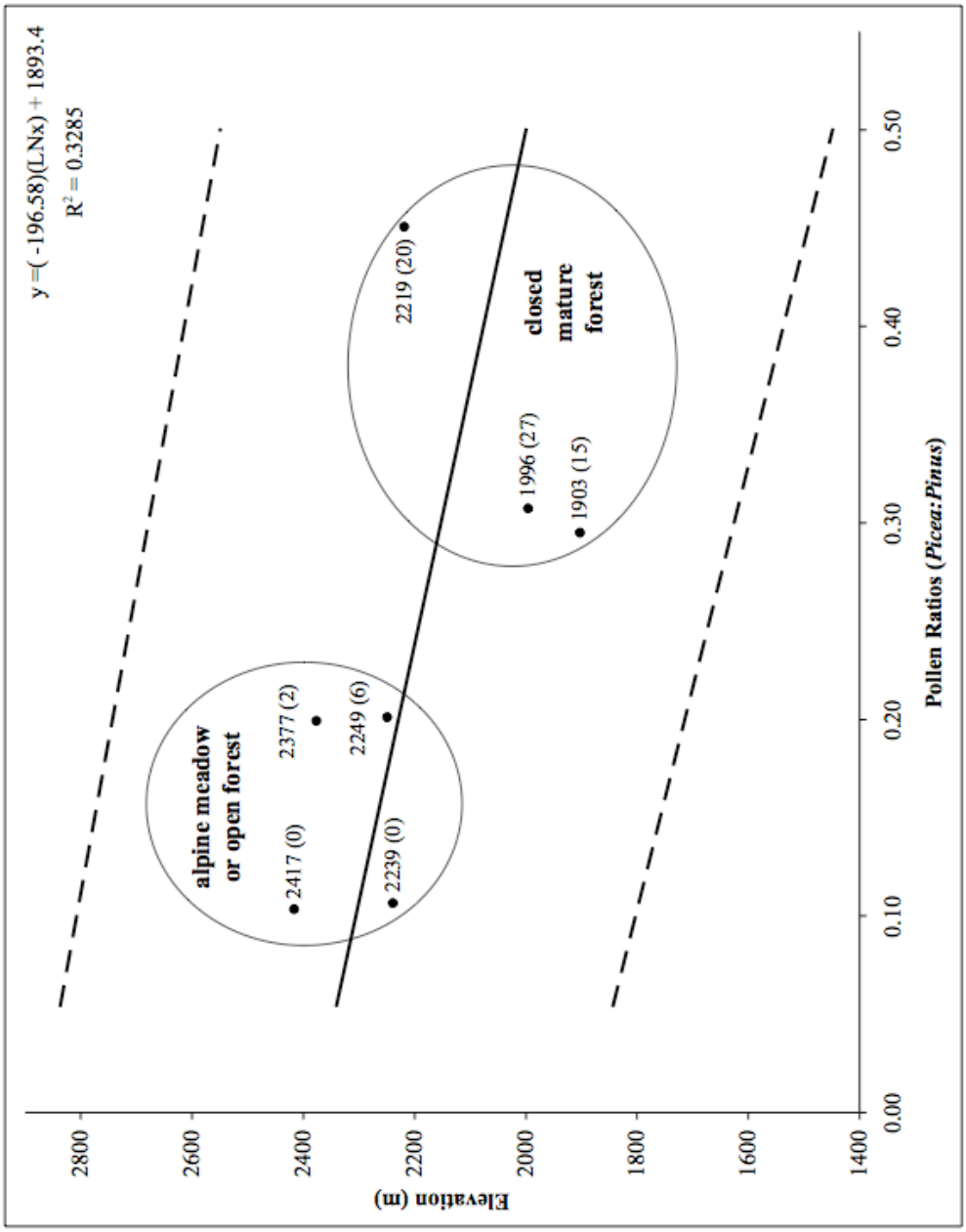

y =(-196.58)(LNx) + 1893.4
R² = 0.3285
alpine meadow or open forest
2417 (0)
2377 (2)
2249 (6)
2239 (0)
closed mature forest
2219 (20)
1996 (27)
1903 (15)
Elevation (m)
2800
2600
2400
2200
2000
1800
1600
1400
0.00
0.10
0.20
0.30
0.40
0.50
Pollen Ratios (Picea:Pinus)

Figure 3.4. Sediment pollen ratios (*Picea:Pinus*) and corresponding apparent site elevations for **Eiffel Lake**. The dashed line indicates apparent present site elevation for Eiffel Lake. Apparent site elevations are based on the surface pollen ratio calibration regression equation determined from surface pollen ratios (transformed). Numerical values adjacent to sample points (filled circle) correspond to the number of stomata in that sample, where present (no value reported = no stomata recorded for that sample).

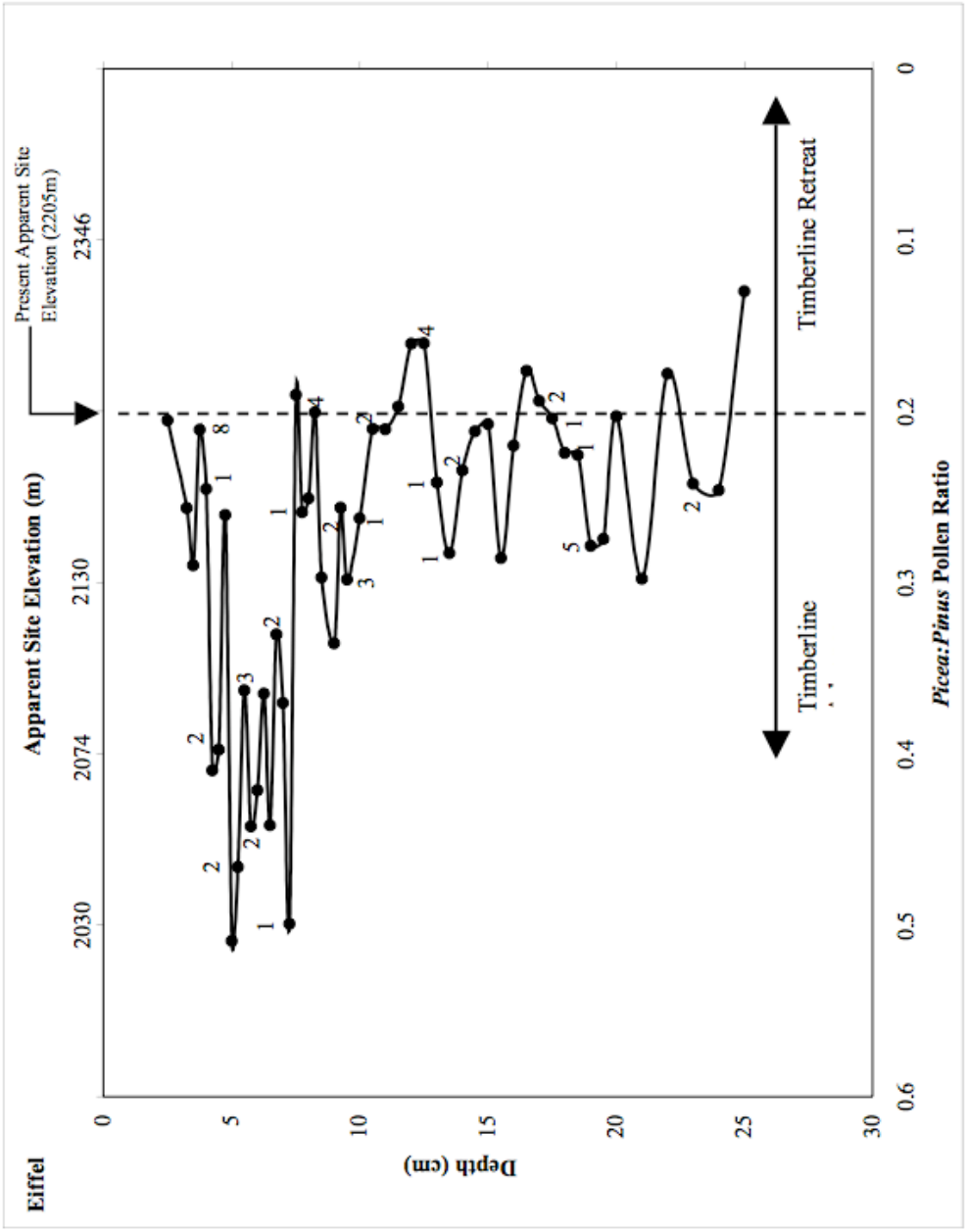
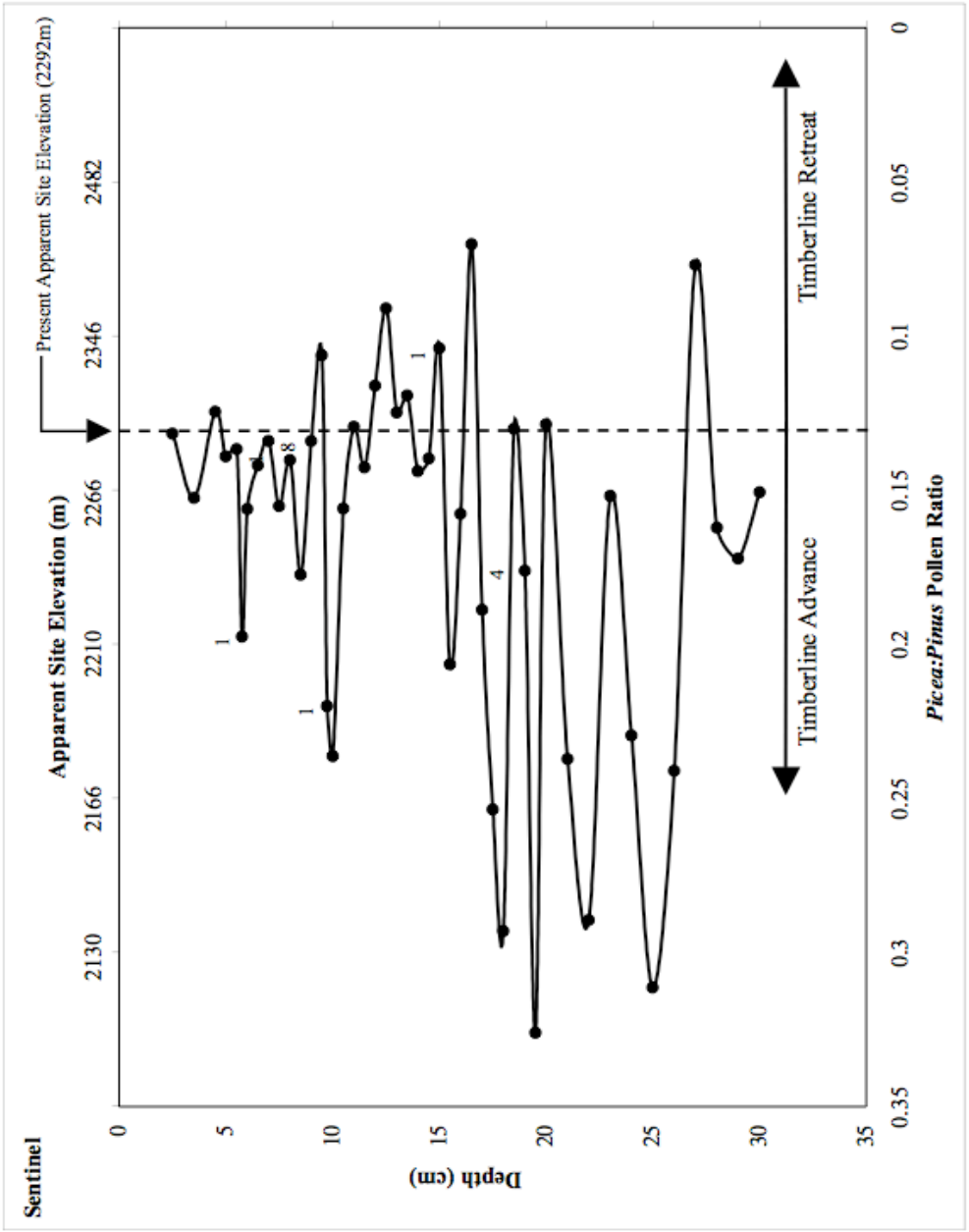

Eiffel
Apparent Site Elevation (m)
2030
2074
2130
2346
Present Apparent Site Elevation (2205m)
Depth (cm)
0
5
10
15
20
25
30
Timberline Retreat
Timberline
0.6
0.5
0.4
0.3
0.2
0.1
0
Picea:Pinus Pollen Ratio

Figure 3.5. Sediment pollen ratios (*Picea:Pinus*) and corresponding apparent site elevation for **Sentinel Lake**. The dashed line indicates apparent present site elevation for Sentinel Lake. Apparent site elevations are based on the surface pollen ratio calibration regression equation determined from surface pollen ratios (transformed). Numerical values adjacent to sample points (filled circle) correspond to the number of stomata in that sample, where present (no value reported = no stomata recorded for that sample).


Sentinel
Depth (cm)
0
5
10
15
20
25
30
35
Apparent Site Elevation (m)
2130
2166
2210
2266
2346
2482
Present Apparent Site Elevation (2292m)
Timberline Advance
Timberline Retreat
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Picea:Pinus Pollen Ratio
1
1
8
1
4

3.6 LITERATURE CITED

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4 DIFFERENTIAL PRESERVATION OF POLLEN GRAINS IN STORED LAKE SEDIMENTS: FROZEN VERSUS FREEZE-DRIED

4.1 INTRODUCTION

As pollen grains are dispersed and become incorporated in sediment, they may be subjected to deterioration and affect the reliability of interpretation of pollen records (Bennett & Willis 2001; Hall 1981; Havinga 1967; Holloway 1989; Jacobson & Bradshaw 1981; Janssen 1966; Jones *et al.* 2007; Moore & Webb 1991). Factors including pollen exine thickness, structure and sporopollenin content may all influence pollen preservation (Delcourt & Delcourt 1980; Havinga 1967; Havinga 1984; Sangster & Dale 1964). Therefore, taxonomically unidentifiable pollen grains may comprise a significant proportion of a counted assemblage. To obtain information encoded in this component of the assemblage, some researchers tally unidentifiable grains (Delcourt & Delcourt 1980) as well as assigning and tallying deterioration classes for identifiable pollen grains (Campbell 1991; Cushing 1967; Hall 1981). The abundance of indeterminable pollen grains can provide a means to evaluate the degree of pollen preservation within sediment (Jones *et al.,* 2007), whereas deterioration classes can be used to assess the cause of pollen deterioration (*e.g.* mechanical versus chemical deterioration).

In addition to fossilization processes that affect deterioration characteristics of the entire assemblage, certain pollen types may also be affected by "differential

preservation" due to sporopollenin content and pollen structure differences. The process of "differential preservation", where some pollen types preserve better (*e.g., Pinus, Picea*) than others (*e.g., Quercus, Populus*) depends on various factors intrinsic to the pollen types and can vary among different environments of deposition (Campbell 1999; Hall 1981). Havinga (1967, 1984) investigated the effects of oxidation and microbial activity (corrosion) on pollen preservation by manipulating soil types (field and laboratory experiments). Results showed that pollen characteristics and soil types influenced differential preservation (Havinga 1967, 1984). These findings highlight the importance of accounting for differential pollen preservation when interpreting palynological data. Reliable taxonomic determination becomes more difficult and pollen abundance decreases with pollen deterioration (Hall 1981). Therefore it is important to limit additional deterioration of pollen through sediment storage processes. Also, it is important to distinguish between deterioration of pollen due to storage methods of sediment and deterioration incurred through sedimentary processes.

Limited information is available on the impact of different sediment storage methods (such as freezing, freeze-drying, or vacuum-drying) on pollen preservation. The effect of different storage protocols on pollen viability has been investigated from the perspective of agriculture, horticulture, and genetic studies (Jett *et al.* 1993; Kozlowski 2002). For example, a study investigated the long-term effect of freeze-drying on the germination success rate of stored palm pollen used for artificial pollination (Boughediri *et al.* 1995). However, these studies do

not explicitly investigate the effects on the pollen exine and therefore have marginal relevance to the study of pollen extracted from sediments.

Sediment storage methods vary across disciplines; limnologists often store sediments in freezers or by freeze-drying, whereas palynologists often freeze sediments only (Faegri *et al.* 1989; Reuss *et al.* 2005). Optimal storage conditions for sediments intended for pigment extractions are -20°C or colder, followed by freeze-drying prior to pigment extractions, and afterwards freeze-dried samples should be frozen (Reuss *et al.,* 2005). Sediments intended for pollen analysis are typically wrapped and kept frozen in order to reduce any microbial activity (Faegri *et al.,* 1989; Moore & Webb 1991). So far, no studies are available that explore whether mechanical damage from freeze-drying of sediments lead to greater proportion of deteriorated pollen grains compared to pollen in frozen sediments. It is this question that the present study is designed to explore.

This study assesses the level of deterioration of pollen grains obtained from frozen and freeze-dried sediment subsamples to determine if there is a significant difference of the pollen assemblage data between storage methods. Specifically, this study was designed to investigate whether freeze-drying sediments leads to greater proportion of deteriorated pollen grains. By comparing the number of indeterminable pollen grains between storage methods, we can determine which method provides the least amount of information loss due to pollen deterioration. The purpose of this study is to determine a) if there are any significant differences

in overall pollen preservation between sample storage methods; b) if there are any differences in the number of palynomorphs observed in subsamples processed from frozen versus freeze-dried sediments; and c) if the frequency of indeterminable pollen grains is significantly different between sediment storage methods.

4.2 METHODS AND MATERIALS

4.2.1. Study Site and Sample Preparation

A sediment core was obtained from the deepest (6.7 m) section (roughly the center) of the Sentinel Lake basin (51º20' N, 116º13' W), in Banff National Park using a Glew gravity piston corer (Glew 1989). Coring location was selected using a bathymetric map (Mayhood & Anderson 1976) and a depth sensor. The core was extruded in the field and sectioned by placing the piston vertically on a stand and subsequently lowering the piston at a set increment and scraping the sediment with a spatula into a pre-labelled sealed sterile plastic bag. Sectioning commenced at the top of the core (sediment surface) with 0.25cm sections from 0cm-10cm down the core, 0.5cm sections from 10cm-20cm down the core, and 1.0cm sections from 20-30cm down the core. Samples were kept in a cooler with ice during transportation. In order to optimize preservation of algal pigments and pollen, samples were frozen and stored at -80ºC in a freezer, until freeze-drying (Faegri *et al.,* 1989; Moore & Webb 1991; Reuss *et al.,* 2005).

4.2.2. Radiometric Dating

Chronologic control (refer to Chapter 2 for details) provided by ^{210}Pb and radiocarbon (^{14}C) dates suggest that the core spans the last 2500 years.

4.2.3. Sediment Subsampling and Processing

Samples were removed from the freezer, thawed for approximately half an hour and manually homogenized for approximately 5 minutes. Ten frozen subsamples were obtained from 10 sections along the core's length (Table 4.1). Ten freeze-dried subsamples were then obtained from the same levels as those used for frozen samples (Table 4.1). Samples were vacuum freeze-dried using the VirTis Freeze Mobile 24 Freeze Dryer for approximately 24 hours at approximately -60°C or until samples were dried (based on visual inspection). Subsample weights and volumes varied (Table 4.1) due to sample storage method (dry versus wet samples) and limited material available from the core. Frozen and freeze-dried sediment subsamples were chemically processed to concentrate pollen and spores (following (Faegri *et al.,* 1989). In order to compare sample concentrations, samples were inoculated with a "spike" of *Lycopodium* spores (Batch # 710961 (2 tablets, 27,822+/-975 spores) or Batch # 414831 (2 tablets, 24,153+/-1197 spores)) (following (Stockmarr 1971). Processed subsamples were stained with safranin to enhance structural contrasts, and suspended in silicone oil. Subsamples were manually homogenized for 5 minutes and mounted onto slides for counting. Using a transmitted light microscope, equally spaced transverses were counted at magnifications of 400X, with 1000X used for critical identifications, for each

subsample (10 frozen, 10 freeze-dried, Table 4.1). For each subsample, an entire slide (22x22mm or 18x18mm cover slip) was counted to eliminate bias from differential sorting on the slide (Brookes & Thomas 1968). The pollen sum of corresponding frozen and freeze-dried samples (*e.g.,* 5.5cm frozen sample and 5.5cm freeze-dried sample) had a difference of less than 100 pollen grains (Table 4.1). For frozen samples S4 (14, 14.5cm), S6 (17-17.5cm), S7 (18.5-19cm), S8 (23-24cm), S10 (32-33cm), additional slides were required to increase the sum and reduce the difference between frozen and freeze-dried sample counts. Counting of these additional slides was only partial and was stopped when the difference was less than 100 pollen grains.

4.2.4 Deterioration Categories

To determine both mechanical and chemical deterioration eight deterioration categories were defined according to Cushing (1967) and Campbell (1991), with some modifications (Figs. 4.1, 4.2). Corroded pollen grains exhibited pitting and thinning of the exine. Degraded pollen grains exhibited extreme thinning of the exine, with surface sculpturing and grain structures poorly discernable. Less distinct, but intact pores and furrows, characterized both corroded and degraded pollen grains. Due to the difficulty in separating corroded from degraded grains, these two categories were combined into one deterioration category. Crumpled pollen grains were either folded or collapsed. Torn (broken) pollen grains were characterized by ruptures and tearing of the exine. Torn pollen grains were subdivided into five further categories in an attempt to isolate damage incurred by

mechanical stresses associated with storage methods (Figs. 4.1, 4.2). Preserved grains did not show any prominent deterioration and were wholly intact, including surface sculpturing and apertures.

Taxonomic identification of pollen grains, spores and stomata were made using published and unpublished keys and glossaries (Bassett *et al.* 1978; Crompton & Wojtas 1993; Habgood & Simons 1985; Hansen 1995; Kapp *et al.* 2000; McAndrews *et al.* 1973; Punt *et al.* 2007) and pollen reference collections at the Royal Alberta Museum (Quaternary Environments) and from the University of Alberta (Palynology Lab, Department of Anthropology), supplemented by additional collections made from local site vegetation. Most pollen grains were identified at the genus or family level. Each pollen grain counted and identified was assigned to one or more of the eight deterioration categories (D1-D8) (Figs. 4.1, 4.2). Pollen grains that were indeterminable due to deterioration or concealment were also recorded. D1 represented pollen grains that were either corroded or degraded. D2 represented grains that were crumpled. D3 represented grains in Tear Class A, with one tear being less than half the length of the grain. D4 represented grains in Tear Class B, with one tear being greater than half the length of the grain. D5 represented grains in Tear Class C, having multiple tears and/or large fragments missing. D6 represented grains in Tear Class D, with a tear between the bladders of bisaccate grains. D7 represented grains in Tear Class E, with bisaccate grains being completely torn in half. D7 was based on total bladder counts of identified bisaccate grains divided by two. D8 represented grains that

were well preserved. Pollen percentages for each deterioration category and sample were determined for four key taxa: (*Pinus* (Pine)*, Picea* (Spruce)*, Abies* (Fir)*, Alnus* (Alder)), non-arboreal (NAP, low-lying herbaceous and shrub taxa), arboreal (AP, trees and alder shrubs) and total pollen grains. The four key taxa were selected because they comprised the majority of identifiable pollen within the samples and occurred in every sample.

4.2.5 Presentation of Pollen Data

Pollen diagrams were constructed using developed TILIA software and TG View computer packages available at http://www.ncdc.noaa.gov/paleo/tiliafaq.html (Grimm 1991-1993) (Figs. 4.3-4.9). Pollen diagrams showing deterioration percentages were constructed for all pollen grains, key taxa, NAP, and AP for all 10 samples (frozen and freeze-dried). Sample one is the core top (5.5-5.75cm) and sample 10 is the core bottom (32-33cm). All pollen sums used to calculate the percentages excludes spike, spores and unidentifiable grains. Deterioration categories for all pollen grains (inclusive of all taxa) are expressed as a percentage of the pollen sum 1 for each sample. Pollen sum 1 is defined as the total number of all identifiable pollen grains per sample. For example, 5.6% pollen grains were well preserved in Frozen Sample 1 (15 pollen grains / 267 total grains counted in sample 1). Deterioration categories for arboreal pollen are expressed as a percentage of the pollen sum 2 for each sample. Pollen sum 2 is defined as the total number of all identifiable arboreal pollen grains per sample. For example, 20% of arboreal grains had multiple tears in Frozen Sample 1 (53 arboreal grains

in Tear Class C / 261 total arboreal grains counted in sample). Deterioration categories for non-arboreal pollen are expressed as a percentage of the pollen sum 3 for each sample. Pollen sum 3 is defined as the total number of all identifiable non-arboreal pollen grains per sample. For example, 33% of non-arboreal grains had multiple tears in Frozen Sample 1 (2 non-arboreal grains in Tear Class C / 6 total non-arboreal grains counted in sample). Deterioration categories for each key taxon (*Pinus, Picea, Abies, Alnus*) are expressed as a percentage of the pollen sum 4 for each sample. Pollen sum 4 is defined as the total number of all identifiable specified taxon pollen grains per sample. For example, 21% *Pinus* grains were torn between the bladders in Frozen Sample 1 (41 *Pinus* within Tear Class D / 197 total *Pinus* grains counted in sample). As noted in the pollen diagrams, some percentages are higher than 100%. This is because individual pollen grains were scored in one or more deterioration categories, and therefore a particular deterioration category could have a higher total count than the total pollen sum.

4.2.6. Statistical procedures

Multivariate analysis of variance (MANOVA) was completed for the key taxa (*Pinus, Picea, Abies, Alnus*), NAP, and AP in order to determine any significant differences and interaction effects between pollen deterioration percentages, groups tested and storage method (SPSS 2007). To confirm results of MANOVA, analysis of variance (ANOVA) was completed for each dependent category of key taxa, NAP, AP and deterioration categories. Two-tailed t-tests were

completed to determine any significant differences between storage methods for pollen sum, number of taxa encountered, and indeterminable grains.

4.3 RESULTS

4.3.1 Indeterminable Pollen Grains

A pollen diagram for indeterminable grains was not generated, because the difference between storage methods for indeterminable grains was less than 10% for all samples. The percentage of indeterminable pollen grains for frozen samples ranged from 5%-13% (10% average), and for freeze-dried samples ranged from 5%-16% (10% average). The average number of indeterminable grains counts per sample was 11 for frozen samples, and 15 for freeze-dried samples, with no discernable downcore pattern (Table 4.1).

4.3.2. General Patterns in Pollen Percentages and Differences between Storage Methods

Pollen diagrams were constructed (Grimm 1991-1993) in order to visualize any marked differences between storage method affect on pollen deterioration and any general patterns in pollen percentages with core depth (Figs. 4.3-4.9). Marked differences greater than 25% were noted between paired samples (*e.g.,* frozen sample 1 vs. freeze-dried sample 1) (Table 4.2).

4.3.2.1 Patterns and Comparison of Whole Assemblage

Whole assemblage (all pollen counted) pollen percentages for all deterioration categories showed no marked differences greater than 25% between storage methods (Fig. 4.3). Degraded and corroded pollen grains (D1) increased from near the top of the core (5.5-5.75cm) to the bottom of the core (32-33cm), for both frozen and freeze-dried samples (Figs. 4.3).

4.3.2.2 Patterns and Comparison of AP and NAP

No marked differences were noted between storage methods and deterioration categories for arboreal pollen percentages (Fig. 4.4), whereas marked differences (greater than 25%) between storage methods and deterioration categories were noted for non-arboreal pollen (Table 4.2, Fig. 4.5). For arboreal and non-arboreal pollen, degraded and corroded pollen grains (D1) increased from near the top of the core (5.5-5.75cm) to the bottom of the core (32-33cm), for both storage methods (Figs. 4.4-4.5).

Non-arboreal samples 1, 3, and 7-10 showed marked differences greater than 25% between storage methods (Table 4.2, Fig. 4.5). Freeze-dried samples with marked differences had higher percentages of the specified deterioration category 67% of the time (8/12) versus frozen samples (Table 4.2, Fig. 4.5). Non-arboreal frozen samples showed a gradual increase in crumpled pollen grains (D2) and total deteriorated pollen (D1-D5) from near the top of the core to near the bottom of the core with some fluctuation between samples (Fig. 4.5).

4.3.2.3 Patterns and Comparison of Key Taxa

No marked differences were noted between storage methods and deterioration categories for *Pinus* (Fig. 4.6), whereas marked differences (greater than 25%) between storage methods and deterioration categories were noted for *Picea, Abies,* and *Alnus* (Table 4.2, Figs. 4.7-4.9). For all investigated taxa (*Pinus, Picea, Abies, Alnus*), degraded and corroded pollen grains (D1) increased from near the top of the core (5.5-5.75cm) to the bottom of the core (32-33cm), for both storage methods (Figs. 4.6-4.9).

Picea samples 4, 8, and 9 showed marked differences greater than 25% between frozen and freeze-dried samples (Table 4.2, Fig. 4.7). Frozen samples with marked differences had higher percentages of the specified deterioration category 80% of the time (1/5) versus freeze-dried samples (Table 4.2, Fig. 4.7).

Abies samples 1, 2, 3, 5, 7, 9, and 10 showed marked differences greater than 25% between frozen and freeze-dried samples (Table 4.2, Fig. 4.8). Frozen samples with marked differences had higher percentages of the specified deterioration category 67% of the time (6/9) versus freeze-dried samples (Table 4.2, Fig. 4.8). Near the bottom of the core, there was increase in occurrence of crumpled (D2) and torn (D3) grains for *Abies* freeze-dried samples, and an increased of torn (D4) grains for *Abies* frozen samples (Fig. 4.8).

Alnus samples 1, 3, 4, 6, 7, 8, and 9 showed marked differences greater than 25%

between frozen and freeze-dried samples (Table 4.2, Fig. 4.9). Frozen and freeze-dried samples with marked difference were equal (50%), with no difference in then number of times one storage method had a higher percentage than the other storage method (Table 4.2, Fig. 4.9). Near the bottom of the core, there was increase in occurrence of torn (D3) grains for *Alnus* (Alder) frozen and freeze-dried samples, and torn (D5) grains for *Alnus* (Alder) frozen samples (Fig. 4.9). Also, near the bottom of the core there was a decrease of occurrence of torn (D4, D5) grains *Alnus* freeze-dried samples (Fig. 4.9).

4.3.2 Statistical Results

4.3.2.1 Comparing Pollen Sum, Number of Taxa, and Indeterminable Pollen

To verify assumptions for subsequent statistical analysis, Levene's test for equality of variance was used to determine if frozen and freeze-dried samples had equal variance (Zar 1999). Levene's test for pollen sum, number of taxa per sample and indeterminable pollen grains were all non-significant, therefore we assumed equal variances for the t-test statistics (Table 4.3).

Two-tailed t-test statistics were used to test if there was any significant difference between frozen and freeze-dried samples and their mean pollen sum (determinable pollen grains), number of indeterminable pollen grains and number of taxa encountered per sample (Table 4.3). There was no significant difference of the pollen sum between storage methods (frozen vs. freeze-dried samples), which

was expected as count criteria, was predetermined (Table 4.3). The number of taxa encountered in the frozen samples was slightly lower (x=11.2, SE 0.8), than the freeze-dried samples (x=10.8, SE 0.6), with no significant difference of the number of taxa between storage methods (frozen vs. freeze-dried samples) (Table 4.3). The number of indeterminable pollen grains in the frozen samples was slightly higher (x=16.5, SE 1.2), than the freeze-dried samples (x=15.1, SE 2.0), with no significant difference between samples (Table 4.3).

4.3.2.2 Comparing Storage Methods and Deterioration of Whole Assemblage

Values with unequal variances between storage methods (significant Levene's value) were transformed (natural log) prior to completing multivariate analysis of variance (MANOVA). Bonferroni correction was used to reduce Type I error (α=0.05 / 35 tests = α=0.001). MANOVA was completed to compare differences between storage methods and test for significant interaction effects of storage method on deterioration categories for all pollen types, NAP, AP, *Pinus, Picea, Abies,* and *Alnus*. Pillai's trace statistic is used as an indicator of explained variance due to the experimental factor, where large Pillai's values reject the null hypothesis (Zar 1999). Pillai's trace value is considered robust when sample sizes are equal (Field 2005), as in this case.

Initially MANOVA was completed between storage methods and deterioration categories **for all pollen grains**. There were no significant differences or interaction effects between deterioration classes and storage methods for all

categories (*e.g.,* D1 vs. D2 vs. D3 vs. D4 vs. D5 vs. D6 vs. D7), and for all deteriorated pollen versus preserved pollen (*e.g.,* D1-D7 vs. D8) (Table 4.4).

4.3.2.3 Comparing Storage Methods and Deterioration Within Groups

MANOVA was completed between storage methods and deterioration categories **within groups** for *Pinus, Picea, Abies*, *Alnus*, NAP, and AP categories (*e.g., Alnus* D1 vs. *Alnus* D2 vs. *Alnus* D3 vs. *Alnus* D4 vs. *Alnus* D5, *Pinus* D1-D7 vs. *Pinus* D8, or NAP D1-D5 vs. NAP D8). There were no significant differences or interaction effects within groups for all tests run (Table 4.4).

4.3.2.4 Comparing Storage Methods and Deterioration Between Groups

MANOVA was completed between storage methods and deterioration categories **between groups** for key taxa, NAP, and AP (*e.g.,* D7 Pine vs. D7 Spruce vs. D7 Fir or D3 NAP vs. D3 AP). There were no significant differences for all tests run (Table 4.4).

4.3.2.5 Follow-up Analysis

Levene's test was completed between storage methods and deterioration categories for all four key taxa, NAP and AP (Table 4.5). Values with unequal variances (bolded, $p<0.05$) were natural log transformed prior to completing analysis of variance (ANOVA) (Table 4.5). ANOVA was completed for all

dependent variables to verify that no real group differences existed between storage methods (frozen versus freeze-dried) and deterioration categories for all pollen grains, key taxa, NAP, and AP. (Table 4.5). There were no significant differences for all ANOVA tests run (Table 4.5).

4.4 DISCUSSION

4.4.1. Arboreal and Non-Arboreal Pollen Deterioration

There were no statistically significant differences in pollen deterioration between samples from different storage methods (frozen versus freeze-dried) for arboreal pollen (AP) and non-arboreal (NAP) pollen (Tables 4.4, 4.5). There were no marked differences in pollen deterioration and between storage methods greater than 25% for AP (Fig. 4.4). Marked differences (>25%) between storage methods for NAP were mostly concentrated near the bottom of the core (below 23cm core depth, samples D1, D2, D3, D5), and near the top (above13cm core depth, sample D8) (Table 4.2, Fig. 4.5). This may suggest that the storage method influences pollen preservation at different depths of the core. However, there is no consistent pattern as to which storage method affects pollen deterioration more or less. For example, the percentage of corroded/degraded (D1) pollen grains was higher for freeze-dried sample 8, while the percentage was higher for frozen sample 9 (Fig.4.5). We can conclude based on statistical analysis and visual inspection of pollen values that storage method does not affect the differential preservation of NAP and AP. Similar results for AP and *Pinus* were not unexpected because a large percentage of AP was comprised of *Pinus* pollen grains (>71% on average).

4.4.2. Key Taxa Pollen Deterioration

There were no statistically significant differences in pollen deterioration between storage methods for all grains counted, and between and within key taxa (Tables 4.4, 4.5). *Pinus* had no marked differences (>25%) between storage methods for all deterioration categories (Fig. 4.6). Sample-to-sample variability of 25% or more occurred between storage methods for *Picea*, *Abies*, and *Alnus* (Table 4.2, Figs. 4.7-4.9). Some sample-to-sample variability was also reported between sediment cores from Lake O'Hara (Yoho National Park, BC), but overall, pollen percentages were consistent across lake core samples (Beaudoin & Reasoner 1992). Further, less abundant taxa (*e.g., Alnus*) demonstrated greater sample-to-sample variability than did more abundant taxa (*e.g., Pinus*) (Beaudoin & Reasoner 1992).

Pinus and *Picea* have been shown in several studies to resist deterioration and occur in higher concentrations than other palynomorphs. For example, after repeated wet-dry cycles (Holloway 1989) or exposure to varying environmental conditions and soil types (Havinga 1984; Sangster & Dale 1960) *Pinus* spp. and *Picea* spp. pollen grains showed lower percentages of degradation than pollen from herbaceous species and/or other arboreal species.

Holloway (1989) noted that freezing temperatures (below -10°C) might cause mechanical damage to the pollen exine. Our samples were stored in a freezer at -80°C with only approximately two thawing periods for subsampling and

homogenizing purposes. The thick exine and greater amount of the sporopollenin present in bisaccate pollen grains may explain the low percentages of total degradation for these grains.

4.4.3. Sporopollenin, Pollen Sum, and Differential Pollen Preservation

The amount of sporopollenin in the exine of pollen grains varies among taxa (Kwiatkowski & Lubliner-Mianowska 1957), which can lead to differential pollen preservation (Havinga 1967). Based on other findings (Kwiatkowski & Lubliner-Mianowska 1957; Sangster & Dale 1964) the exine of *Pinus* pollen in this assemblage likely had greater sporopollenin content than the other taxa, which likely accounts for the greater abundance of well-preserved *Pinus* grains counted.

Also, the high content of sporopollenin found in bisaccate taxa, including *Pinus, Picea,* and *Abies*, can partially explain why there are few marked differences in the assemblage data between storage methods, compared to NAP (Table 4.2). *Pinus* showed no marked differences (Fig. 4.6), while *Picea* and *Abies* showed some marked differences between storage methods (Table 4.2, Figs.4.7-4.8). Both *Picea* and *Abies* have high sporopollenin content and *Abies* in particular has a thick exine with heavy sculpturing. Li *et al.* (2005) noted correlation between pollen grains that were heavily sculptured and had thick exine and overall representations and preservation in sediment. For instance, in their study pollen grains with thicker and sculptured exines (*i.e., Artemisia, Ephedra,* Chenopodiaceae, Compositae), were well-represented near-bottom of the

sediment, and *Artemesia, Betula*, and Chenopodiacaeae pollen percentages were significantly and positively correlated with sediment depth (Li *et al.* 2005). Taxa with thinner and smoother exines (*i.e.,* Cyperaceae and Gramineae) were well represented in near-surface samples and the Cyperaceae pollen percentage was significantly and negatively correlated with sediment depth (Li *et al.,* 2005). Moreover, the overwhelming abundance of *Pinus* pollen in assemblages in our study likely also influences its distribution among deterioration classes. *Pinus* on average was present in greatest abundance in all samples counted (381 frozen, 372 freeze-dried), followed by *Picea* (63 frozen, 80 freeze-dried), followed by *Alnus* (29 frozen, 29 freeze-dried), and lastly *Abies* (24 frozen, 25 freeze-dried). Therefore, total sporopollenin content, as well as total pollen count for *Pinus* may be the main reason why *Pinus* showed no marked differences between storage methods (Fig. 4.6), compared to the other key taxa (Table 4.2, Figs. 4.7-4.9).

4.4.4. Depth in Sediment and Differential Pollen Preservation

Change in pollen concentration based on depth in sediment is dependent on environmental factors, pollen morphology, pollen physiology, and sediment type. Li *et al.* (2005) found a change in pollen concentrations in the sediment profile based on pollen morphology and pH levels. They also noted higher occurrence of broken pollen grains in oxidative and microbial rich environments (Li *et al.,* 2005). Hall (1981) reported "progressive pollen deterioration" referring to an increased concentration of deteriorated pollen with increased sediment depth.

There were some notable patterns of increased pollen deterioration with increased depth of sediment in this study. Degraded and corroded pollen grains (D1) increased from core-top to core-base for both storage methods and for all investigated groups (Figs. 4.3-4.9). Crumpled pollen grains (D2) increased with core depth for non-arboreal frozen samples and *Abies* freeze-dried samples (Figs. 4.5, 4.8). Torn pollen grains, Tear Class A (Fig. 4.1, D3) increased with core depth for *Abies* freeze-dried samples and *Alnus* frozen and freeze-dried samples (Figs. 2.8, 2.9). Torn pollen grains, Tear Class B (Fig. 4.1, D4) increased with core depth for *Abies* frozen samples and decreased in occurrence with core depth for *Alnus* freeze-dried samples (Figs. 4.8, 4.9). Torn pollen grains, Tear Class C, (Fig. 4.1, D5) increased with core depth for *Alnus* frozen samples, and decreased in occurrence with core depth for *Alnus* freeze-dried samples (Fig. 4.9). Total deterioration (D1-D5) increased with core depth for non-arboreal frozen samples (Fig. 4.5).

The pattern of increased occurrence of some deterioration classes of both frozen and freeze-dried samples near the bottom of the core suggest that there is differential pollen preservation occurring with increased depth in sediment and therefore with increased sediment age (Fig. 4.3-4.9). These results do not appear to be related to the type of storage methods, but with other factors relating to pollen morphology or environmental factors (Figs. 4.3-4.9). To determine which environmental factors might be important would require additional studies of sediment characteristics such as pH, oxidation levels and microbial activity. Also,

future studies can record differential pollen preservation of the samples prior to processing the cores for storage, as well as after preparing the cores for storage. This will help to isolate differential pollen preservation solely due to storage methods versus other factors such as environmental and processing factors.

4.4.5. Summary, Relevance, and Future Studies

Freeze-drying sediment samples helps maintains the overall integrity of pollen by reducing microbial activity, enzyme activity, and water content. However, rapid removal of water through vacuum freeze-drying can increase denaturing of proteins (Ching & Ching 1964), resulting in mechanical deterioration of the pollen grain, specifically crumpled grains (Delcourt & Delcourt 1980). Freezing alone can increase mechanical damage through the formation of intracellular ice that can cause tear the cell wall (Matthews & Kraus 1981; Oldrich 1996). If storage methods played a factor in differential pollen preservation, an increase of crumpled grains and deteriorated grains due to mechanical stresses (*i.e.,* broken grains) should have resulted in the freeze-dried samples compared to frozen samples.

Our study found that there was no significant difference between the percentage of crumpled pollen grains in frozen versus freeze-dried samples, or any other deterioration categories (Tables 4.4, 4.5; Figs. 4.3-4.9). Based on this study, differential pollen preservation is not affected by varying storage methods of freezing or freeze-drying sediment cores (Tables 4.2-4.5, Figs. 4.3-4.9). The

results of this study indicate that freeze-drying can be a useful method for storing sediments that are intended to be later used in palynological studies. Further, this will increase the number of available stored (freeze-dried) sediment samples to be used by both paleolimnological and palynological studies and will minimize the amount of coring needed.

Further studies are needed to investigate if sediment cores should be kept cool (above freezing), prior to freeze-drying, in order to maintain morphological characteristics. Therefore, an extension to this experiment would be to measure water content and to freeze-dry sediment cores for analysis of pollen deterioration, prior to storing in a freezer. Also, investigating the effect of using different vacuum pressures, variable freeze-drying temperatures and periods, and variable storage periods of samples (frozen and freeze-dried), on pollen preservation quality would be an extension to this study. Increasing the counts for this analysis, especially for non-arboreal species, and counting continuous samples down the length of the core might help to refine these results further. These investigations are beyond the limits of this present study.

4.5 TABLES AND FIGURES

Table 4.1. Frozen (4.1a.) and freeze-dried (4.1b.) pollen subsample (S1 to S10) position in sediment, weights and volumes taken from a single sediment core obtained from Sentinel Lake in Banff National Park, Alberta. The pollen sum indicates total determinable pollen grains counted per sample. All determinable pollen grains were identified and assigned to one or more deterioration category (see Figs. 4.1, 4.2). Indeterminable grains indicate total pollen grains that could not be classified due to grain deterioration or grain concealment (minerals, organic debris). Indeterminable grains were assigned to one of the indeterminable categories (corroded/degraded, crumpled, broken, concealed). Palynomorphs indicates the number of unique taxa identified per sample.

4.1a. Frozen subsamples

Sample ID	Section Top (cm)	Section Bottom (cm)	Weight (g) (wet)	Volume (ml)	Pollen Sum	Indeterminable Grains	Palynomorphs
S1	5.5	5.75	0.197	0.15	267	19	9
S2	9.5	9.75	0.313	0.4	307	12	12
S3	12.5	13	0.802	0.8	668.5	17	13
S4	14	14.5	0.795	0.8	722	21	14
S5	15	15.5	0.604	0.6	426.5	8	12
S6	17	17.5	0.716	0.8	857.5	17	10
S7	18.5	19	0.302	0.4	550	17	8

Sample ID	Section Top (cm)	Section Bottom (cm)	Weight (g) (wet)	Volume (ml)	Pollen Sum	Indeterminable Grains	Palynomorphs
S8	23	24	0.617	0.65	521.5	19	12
S9	29	30	0.746	0.8	266.5	16	9
S10	32	33	0.831	0.8	536.5	19	9

4.1b. Freeze-dried Subsamples

Sample ID	Section Top (cm)	Section Bottom (cm)	Weight (g) (dry)	Volume (ml)	Pollen Sum	Indeterminable Grains	Palynomorphs
S1	5.5	5.75	0.0344	0.3	320	11	12
S2	9.5	9.75	0.1160	0.6	350	15	11
S3	12.5	13	0.3544	1.275	667.5	24	8
S4	14	14.5	0.3432	1.275	713	17	13
S5	15	15.5	0.1797	1	498.5	22	12
S6	17	17.5	0.1484	0.8	856	12	14
S7	18.5	19	0.3308	1.275	567	13	14
S8	23	24	0.3240	1.275	541	7	12
S9	29	30	0.3431	1.275	216	23	6
S10	32	33	0.3521	1.275	524	7	10

Table 4.2. Noted differences (greater than 25%) between paired frozen and freeze-dried samples for NAP, *Picea, Abies,* and *Alnus.* The percentage of deteriorated pollen is listed for paired samples, as well as the difference between these percentages. Values not bolded indicate a difference between 25-50%. Bolded values indicate a difference greater than 50%. All other groups, taxa or samples not listed in this table had a difference of less than 25% between paired samples. Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

Group	**Deterioration Category**	**Sample Number**	**Freeze-Dried (%)**	**Frozen (%)**	**Difference Between Freeze-Dried & Frozen (%)**
NAP	D1	8	33	5	28
NAP	D1	9	0	40	40
NAP	D2	9	66	0	**66**
NAP	D3	9	33	0	33
NAP	D3	10	33	0	33
NAP	D5	9	33	0	33
NAP	D5	10	0	29	29
NAP	D1-D5	3	81	50	29
NAP	D1-D5	9	133	60	**73**
NAP	D1-D5	7	38	71	33
NAP	D8	1	46	17	29

Group	Deterioration Category	Sample Number	Freeze-Dried (%)	Frozen (%)	Difference Between Freeze-Dried & Frozen (%)
NAP	D8	3	18	50	32
Picea	D1	9	0	26	26
Picea	D6	8	42	11	31
Picea	D6	9	15	50	35
Picea	D1-D7	4	101	126	25
Picea	D1-D7	9	96	121	25
Abies	D3	9	28	0	28
Abies	D5	5	43	84	41
Abies	D5	10	12	41	29
Abies	D6	2	0	46	46
Abies	D6	3	4	41	37
Abies	D7	1	64	26	38
Abies	D7	2	57	8	49
Abies	D1-D7	3	62	89	27
Abies	D1-D7	7	78	112	34
Alnus	D1	1	4	31	27
Alnus	D1	4	2	38	36
Alnus	D1	6	0	27	27
Alnus	D1	7	1	48	47
Alnus	D1	8	50	19	31

Group	Deterioration Category	Sample Number	Freeze-Dried (%)	Frozen (%)	Difference Between Freeze-Dried & Frozen (%)
Alnus	D2	1	64	31	33
Alnus	D2	3	82	39	43
Alnus	D2	9	33	6	27
Alnus	D1-D5	3	90	56	34
Alnus	D1-D5	7	66	100	34

Table 4.3. Homogeneity of Variance (Levene's Statistic) and two-tailed t-test (p=0.05) results comparing frozen versus freeze-dried samples for pollen sum, number of taxa per sample, and number of indeterminable pollen grains.

	Homogeneity of Variance		**T-Test**	
Group Tested	**F(df1,df2)=Levene's**	**Significance**	**F(df)=t-value**	**Significance**
Pollen Sum (raw)	F(1,18)=0.061	0.808	F(18)=-0.148	0.884
Taxa (raw)	F(1,18)=0.087	0.771	F(18)=-0.385	0.705
Indeterminable (raw)	F(1,18)=3.460	0.079	F(18)=0.602	0.555

Table 4.4. MANOVA (p=0.001) results comparing frozen versus freeze-dried samples for the four key taxa, NAP and AP and between deterioration classes. Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

Groups Tested	Pillai's Value	F(df1,df2)=Value	Significance
All D1-D7 vs. D8	0.303	F(2,17)=0.744	0.643
All D1 to D7	0.302	F(7,12)=0.741	0.643
Pine D1-D7 vs. D8	0.046	F(2,17)=0.405	0.673
Pine D1 to D7	0.395	F(7,12)=1.120	0.411
Spruce D1-D7 vs. D8	0.08	F(2,17)=0.743	0.491
Spruce D1 to D7	0.436	F(7,12)=1.326	0.318
Fir D1-D7 vs. D8	0.017	F(2,17)=0.149	0.862
Fir D1 to D7	0.404	F(7,12)=1.161	0.391
Alder D1-D5 vs. D8	0	F(2,17)=0.002	0.998
Alder D1 to D5	0.313	F(5,14)=1.276	0.328
AP D1-D7 vs. D8	0.067	F(2,17)=0.613	0.553
AP D1 to D7	0.29	F(7,12)=0.700	0.672
NAP D1-D5 vs. D8	0.059	F(2,17)=0.532	0.597
NAP D1 to D5	0.331	F(5,14)=1.388	0.287
D1 (P vs. S vs. F vs. A)	0.184	F(4,15)=0.845	0.518
D1 (P vs. S vs. F)	0.132	F(3,16)=0.810	0.507
D2 (P vs. S vs. F vs. A)	0.214	F(4,15)=1.014	0.431
D2 (P vs. S vs. F)	0.092	F(3,16)=0.537	0.663

Groups Tested	Pillai's Value	F(df1,df2)=Value	Significance
D3 (P vs. S vs. F vs. A)	0.3	F(4,15)=1.606	0.224
D3 (P vs. S vs. F)	0.299	F(3,16)=2.277	0.119
D4 (P vs. S vs. F vs. A)	0.148	F(4,15)=0.654	0.633
D4 (P vs. S vs. F)	0.022	F(3,16)=0.119	0.948
D5 (P vs. S vs. F vs. A)	0.13	F(4,15)=0.559	0.696
D5 (P vs. S vs. F)	0.116	F(3,16)=0.703	0.564
D6 (P vs. S vs. F)	0.15	F(3,16)=0.940	0.445
D7 (P vs. S vs. F)	0.146	(F3,16)=0.911	0.458
D8 (P vs. S vs. F vs. A)	0.18	F(4,15)=0.826	0.529
D8 (P vs. S vs. F)	0.159	F(3,16)=1.008	0.415
D1 AP vs NAP	0.111	F(2,17)=1.059	0.369
D2 AP vs NAP	0.077	F(2,17)=0.706	0.507
D3 AP vs NAP	0.178	F(2,17)=1.845	0.188
D4 AP vs NAP	0.086	F(2,17)=0.803	0.464
D5 AP vs NAP	0.044	F(2,17)=0.392	0.681
D8 AP vs NAP	0.034	F(2,17)=0.302	0.743

Table 4.5. Homogeneity of Variance (Levene's Statistic) and one-way ANOVA (p=0.05) results comparing frozen versus freeze-dried samples for the four key taxa, NAP and AP and between deterioration classes. Significant values for Levene's Homogeneity of Variance analysis (bolded values, 0.05), were transformed (natural log) prior to ANOVA analysis. Results indicated as n/a did not have sufficient levels of data (*i.e.,* too many zeros in data set) in order to perform statistical tests.

	Homogeneity of Variance		**ANOVA**	
Group Tested	**F(df1,df2)=Levene's**	**Significance**	**F(df1,df2)=t-value**	**Significance**
Pine D1	F(1,18)=0.442	0.514	F(1,18)=0.572	0.459
Pine D2	F(1,18)=0.190	0.668	F(1,18)=0.176	0.680
Pine D3	F(1,18)=6.427	**0.021**	F(1,18)=1.817	0.194
Pine D4	F(1,18)=1.313	0.267	F(1,18)=0.211	0.651
Pine D5	F(1,18)<0.000	0.988	F(1,18)=0.512	0.483
Pine D6	F(1,18)=0.320	0.579	F(1,18)=0.076	0.786
Pine D7	F(1,18)=0.612	0.444	F(1,18)=0.171	0.684
Pine D8	F(1,18)<0.000	0.987	F(1,18)=0.704	0.412
Pine D1-D7	F(1,18)=0.188	0.670	F(1,18)=0.041	0.842
Spruce D1	F(1,18)=3.418	0.081	F(1,18)=1.925	0.182
Spruce D2	F(1,18)=0.807	0.381	F(1,18)=0.64	0.434
Spruce D3	F(1,18)=0.467	0.503	F(1,18)=0.329	0.574
Spruce D4	F(1,18)=0.765	0.393	F(1,18)=0.039	0.849
Spruce D5	F(1,18)<0.000	0.997	F(1,18)=1.432	0.247

	Homogeneity of Variance		ANOVA	
Group Tested	**F(df1,df2)=Levene's**	**Significance**	**F(df1,df2)=t-value**	**Significance**
Spruce D6	F(1,18)=0.009	0.927	F(1,18)=0.911	0.353
Spruce D7	F(1,18)=0.034	0.855	F(1,18)=0.051	0.823
Spruce D8	F(1,18)=1.443	0.245	F(1,18)=0.875	0.362
Spruce D1-D7	F(1,18)=0.490	0.493	F(1,18)=0.768	0.392
Fir D1	F(1,18)=0.017	0.897	F(1,18)=0.008	0.928
Fir D2	F(1,18)=0.266	0.613	F(1,18)=0.689	0.417
Fir D3	F(1,18)=6.096	**0.024**	F(1,18)=2.208	0.155
Fir D4	F(1,18)=1.540	0.231	F(1,18)=0.253	0.621
Fir D5	F(1,18)=0.959	0.341	F(1,18)=0.971	0.338
Fir D6	F(1,18)=1.618	0.220	F(1,18)=1.783	0.198
Fir D7	F(1,18)=9.276	**0.007**	F(1,18)=2.819	0.110
Fir D8	F(1,18)=8.041	**0.011**	F(1,18)=0.049	0.826
Fir D1-D7	F(1,18)=0.469	0.502	F(1,18)=0.08	0.781
Alder D1	F(1,18)=0.928	0.348	F(1,18)=0.848	0.369
Alder D2	F(1,18)=0.057	0.814	F(1,18)=2.289	0.148
Alder D3	F(1,18)=1.738	0.204	F(1,18)=0.296	0.593
Alder D4	F(1,18)=10.578	**0.004**	F(1,18)=3.06	0.097
Alder D5	F(1,18)=1.231	0.282	F(1,18)=0.731	0.404
Alder D8	F(1,18)=1.237	0.281	F(1,18)=0.004	0.952
Alder D1-D5	F(1,18)=0.280	0.603	F(1,18)<0.000	0.994
AP D1	F(1,18)=0.562	0.463	F(1,18)=1.25	0.278

	Homogeneity of Variance		ANOVA	
Group Tested	**F(df1,df2)=Levene's**	**Significance**	**F(df1,df2)=t-value**	**Significance**
AP D2	F(1,18)=0.058	0.812	F(1,18)=0.686	0.418
AP D3	F(1,18)=5.803	**0.027**	F(1,18)=0.972	0.337
AP D4	F(1,18)=0.412	0.529	F(1,18)=0.08	0.780
AP D5	F(1,18)=0.014	0.909	F(1,18)=0.405	0.533
AP D6	F(1,18)=0.433	0.519	F(1,18)=0.029	0.867
AP D7	F(1,18)=0.077	0.784	F(1,18)=0.152	0.701
AP D8	F(1,18)=0.073	0.790	F(1,18)=0.631	0.437
AP D1-D7	F(1,18)<0.000	0.992	F(1,18)=0.376	0.547
NAP D1	F(1,18)=0.297	0.592	F(1,18)=0.129	0.724
NAP D2	F(1,18)=0.087	0.771	F(1,18)=0.914	0.352
NAP D3	n/a	**n/a**	F(1,18)=3.789	0.067
NAP D4	F(1,18)=16.371	**0.001**	F(1,18)=1.503	0.236
NAP D5	F(1,18)=0.018	0.894	F(1,18)=0.372	0.549
NAP D8	F(1,18)=0.665	0.426	F(1,18)=0.022	0.883
NAP D1-D6	F(1,18)=2.231	0.153	F(1,18)=0.303	0.589
All D1	F(1,18)=0.477	0.499	F(1,18)=1.126	0.303
All D2	F(1,18)=0.419	0.525	F(1,18)=0.776	0.390
All D3	F(1,18)=11.177	**0.004**	F(1,18)=0.954	0.342
All D4	F(1,18)=0.092	0.766	F(1,18)=0.026	0.873
All D5	F(1,18)=0.011	0.916	F(1,18)=0.462	0.505
All D6	F(1,18)=0.599	0.449	F(1,18)=0.024	0.879

	Homogeneity of Variance		ANOVA	
Group Tested	**F(df1,df2)=Levene's**	**Significance**	**F(df1,df2)=t-value**	**Significance**
All D7	F(1,18)=0.051	0.824	F(1,18)=0.153	0.700
All D8	F(1,18)=0.793	0.385	F(1,18)=0.541	0.471
All D1-D7	F(1,18)=0.088	0.770	F(1,18)=0.335	0.570

Figure 4.1. Schematic diagram showing eight deterioration categories used for this study (D1-D8). **D1 (corroded/degraded)** represents pollen grains that are either heavily corroded or pitted. **D2 (crumpled/folded)** represents grains that are crumpled. **D3 (1 tear < $^1/_2$ of length)** represents grains in Tear Class A, with one tear being less than half the length of the grain. **D4 (1 tear > $^1/_2$ of length)** represents grains in Tear Class B, with one tear being greater than half the length of the grain. **D5 (> 1 tear)** represents grains in Tear Class C, having multiple tears, including large fragments missing. **D6 (bet. bladders)** represents grains in Tear Class D, with a tear between the bladders of bisaccate grains. **D7 (torn in half)** represents grains in Tear Class E, with bisaccate grains being torn in half. **D8 (preserved)** represented grains that are well preserved.

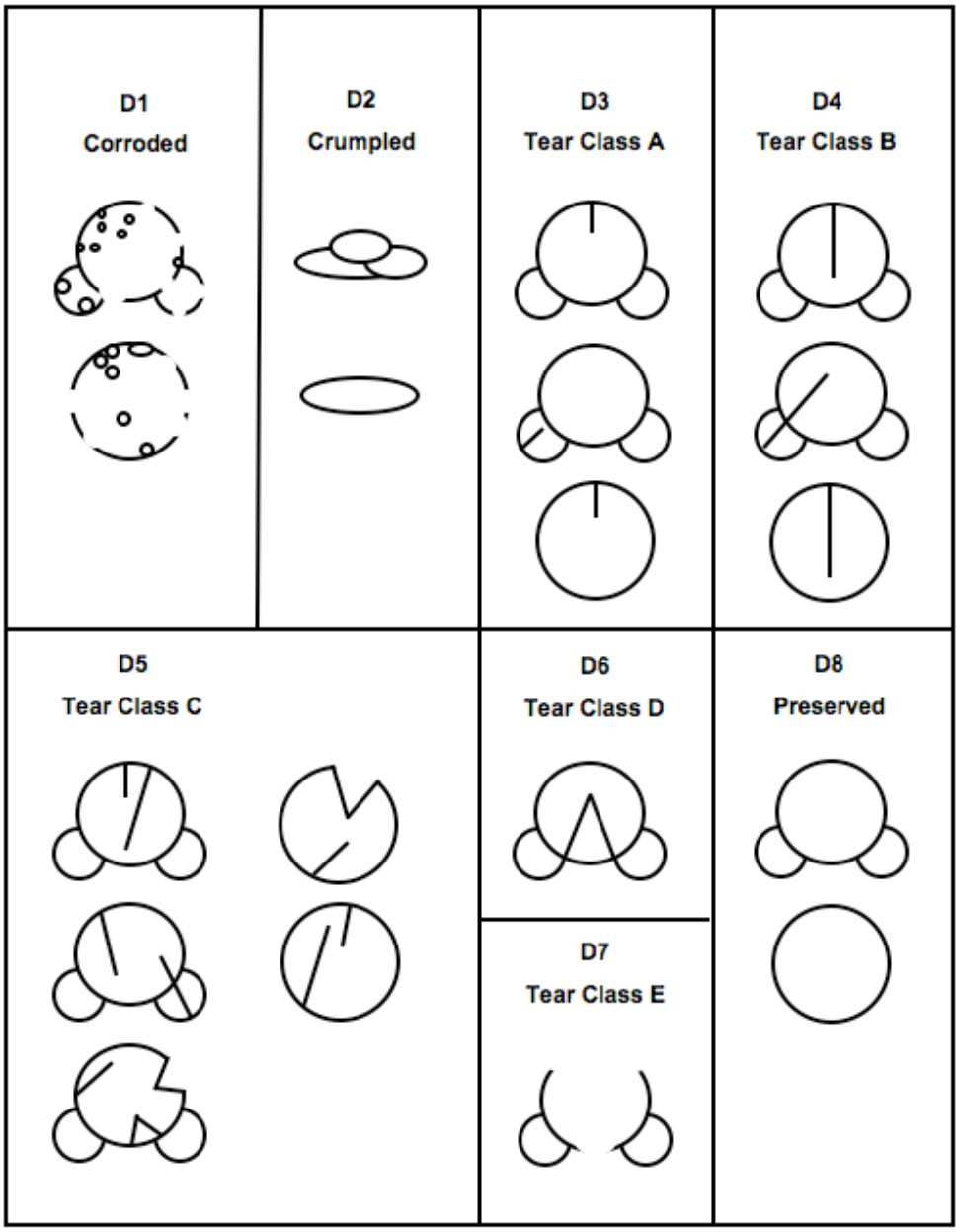
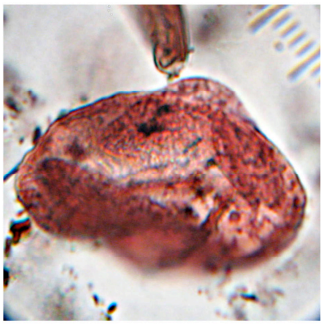
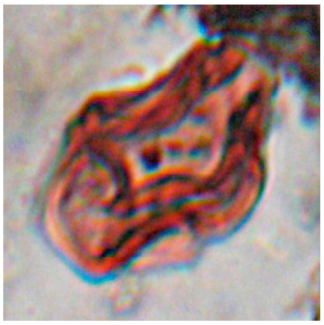

D1
Corroded
D2
Crumpled
D3
Tear Class A
D4
Tear Class B
D5
Tear Class C
D6
Tear Class D
D7
Tear Class E
D8
Preserved

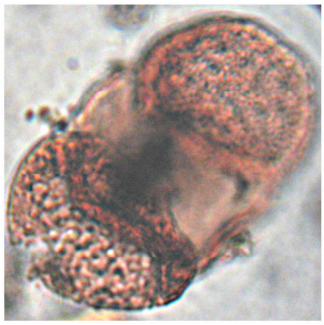
Figure 4.2. Select photographs showing pollen grain representatives of each of the eight deterioration categories. All grains are less than 100μm in maximum dimension. Refer to Figure 4.1, for schematic diagrams and description of deterioration categories.



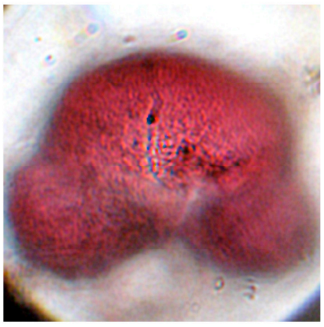
Pine: D1
(Degraded/Corroded)



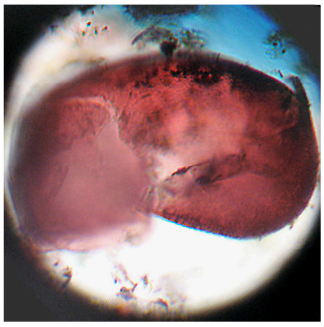
Alder: D2
(Crumpled)



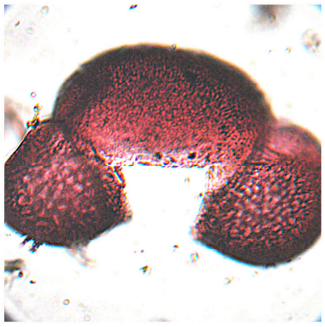
Pine: D3
(Tear < 1/2 Grain)



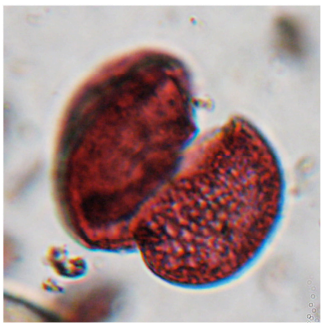
Pine: D4
(Tear > 1/2 Grain)



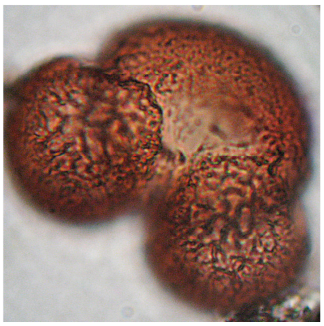
Spruce: D5
(More Than 1 Tear)



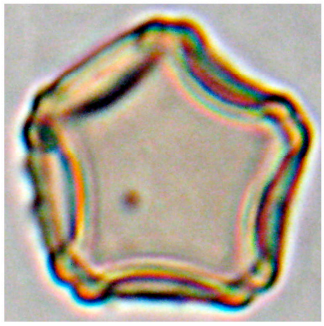
Fir: D6
(Tear Between Bladders)



Pine: D7
(Single Bladder)



Pine: D8
(Preserved)



Alder: D8
(Preserved)

Figure 4.3.

Percentage pollen diagram of **all pollen grains (**based on pollen sum 1), showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations. Circles denote rare values (< 5%).

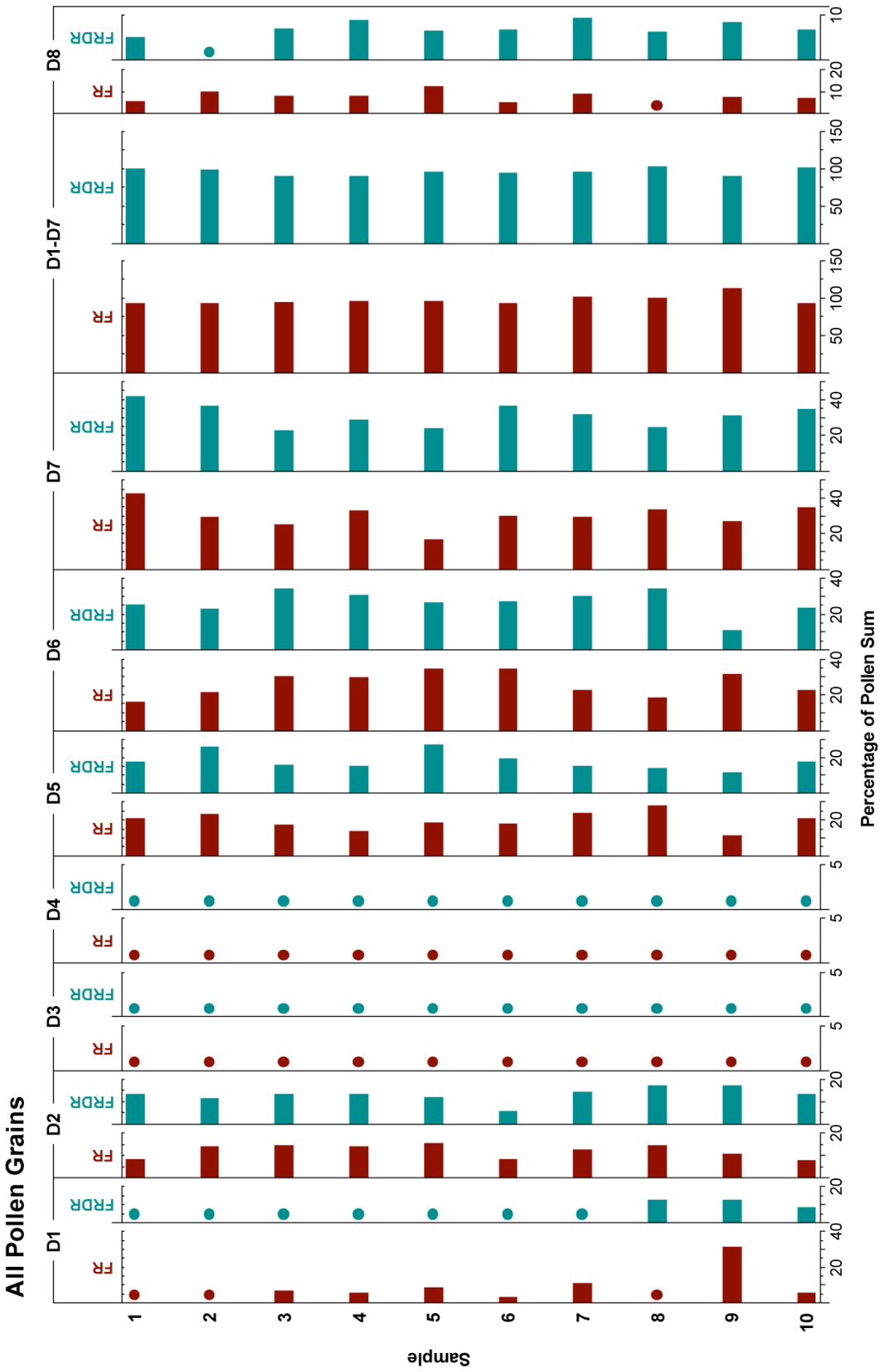

All Pollen Grains
D1
D2
D3
D4
D5
D6
D7
D1-D7
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.4.

Percentage pollen diagram of **AP** (arboreal pollen, based on pollen sum 2) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

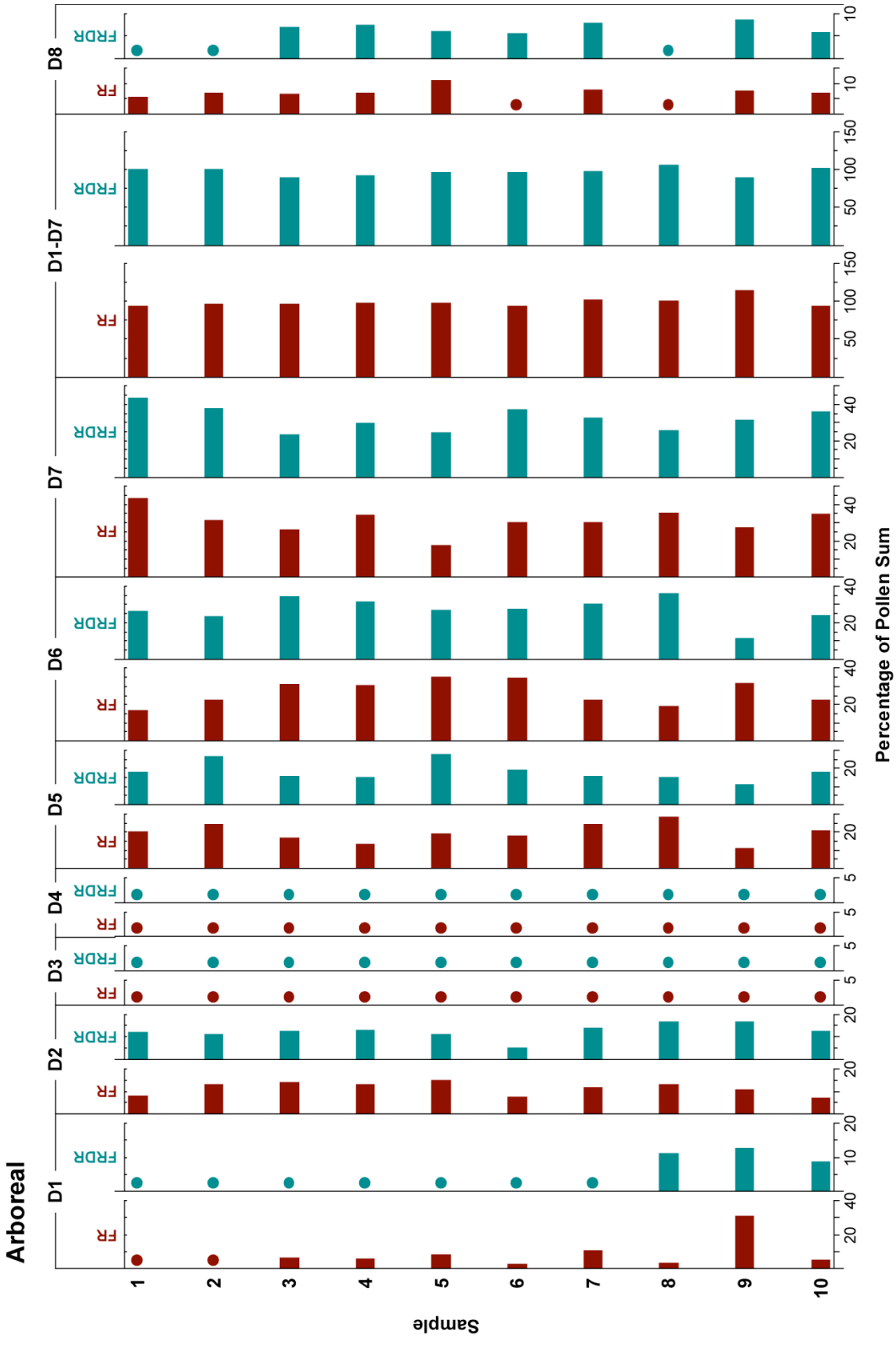

Arboreal
D1
D2
D3
D4
D5
D6
D7
D1-D7
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.5. Percentage pollen diagram of **NAP** (non-arboreal pollen, based on pollen sum 3) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

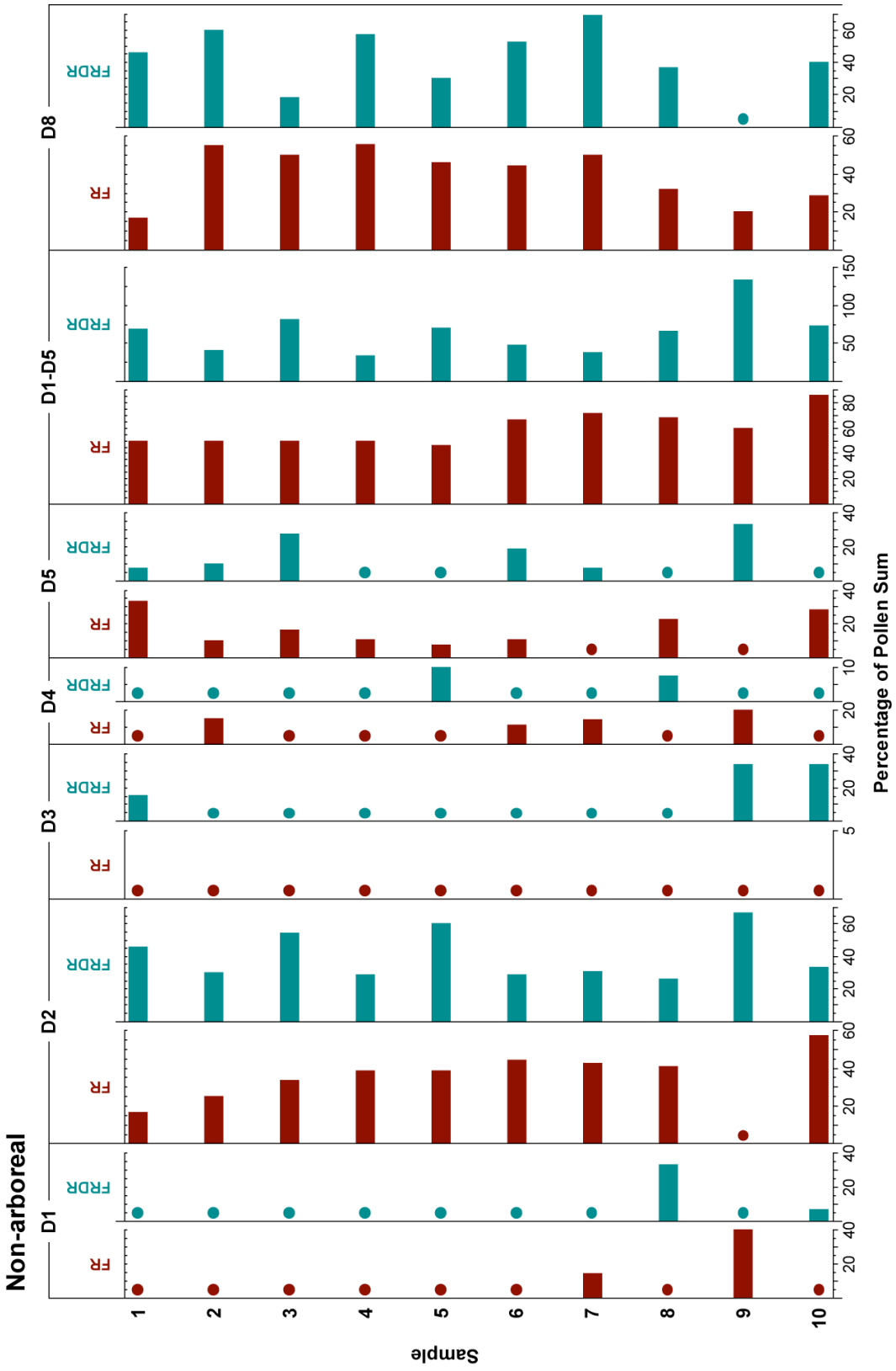

Non-arboreal
D1
D2
D3
D4
D5
D1-D5
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.6. Percentage pollen diagram of ***Pinus*** **sp.** (based on pollen sum 4) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

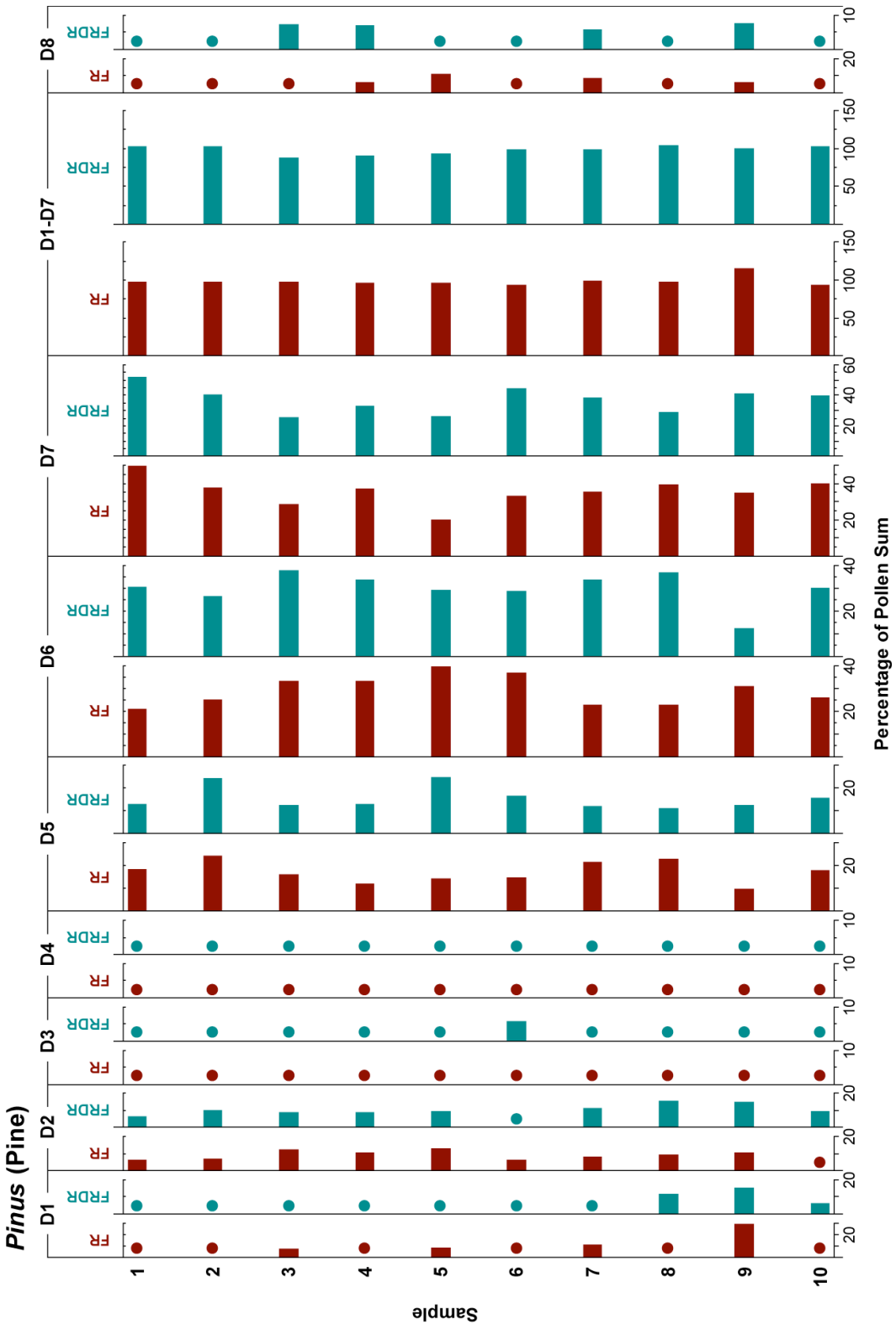

Pinus (Pine)
D1
D2
D3
D4
D5
D6
D7
D1-D7
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.7. Percentage pollen diagram of ***Picea*** **sp.** (based on pollen sum 4) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.

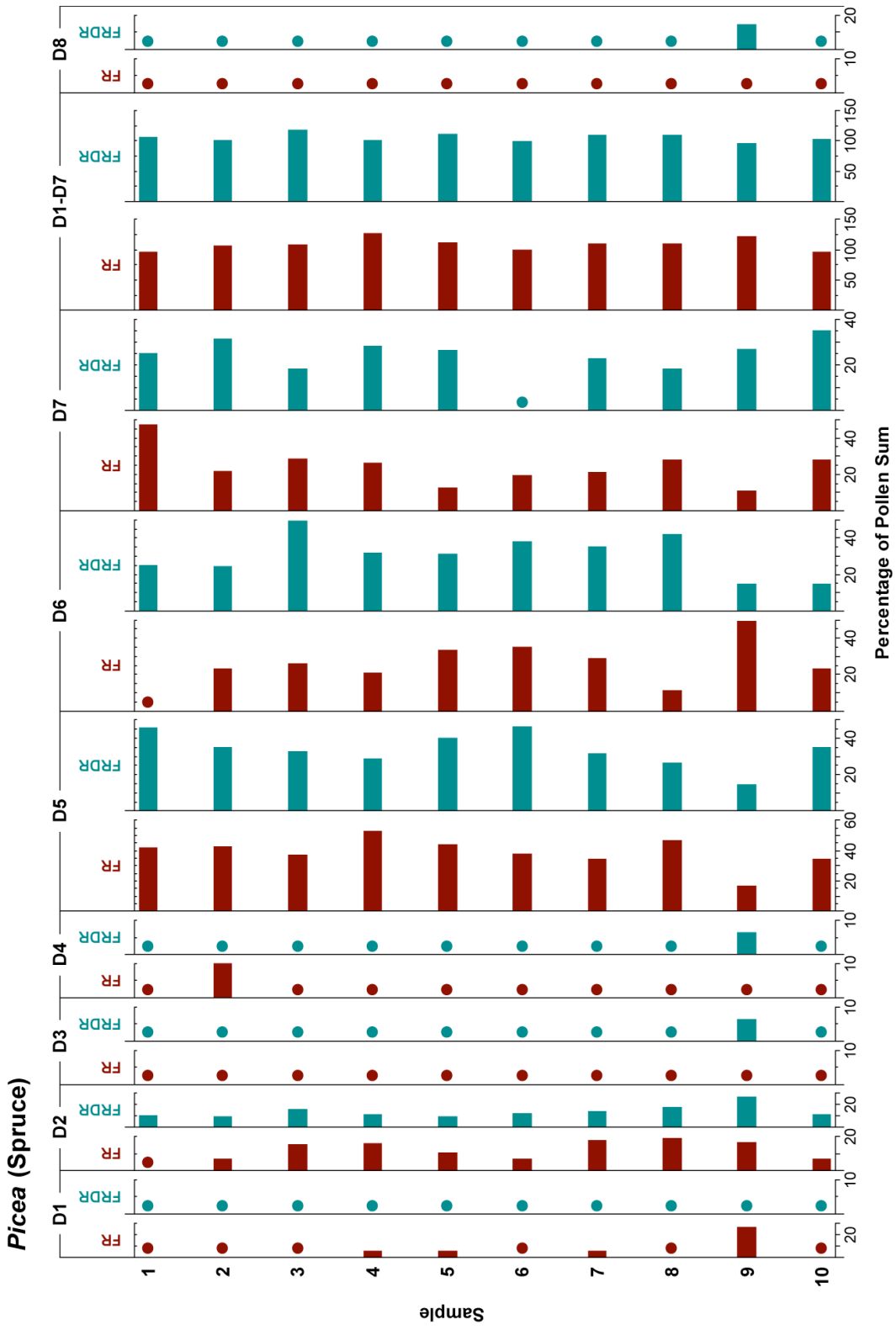

Picea (Spruce)
D1
D2
D3
D4
D5
D6
D7
D1-D7
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.8. Percentage pollen diagram of ***Abies*** **sp.** (based on pollen sum 4) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.8 caption for explanation of deterioration category abbreviations.

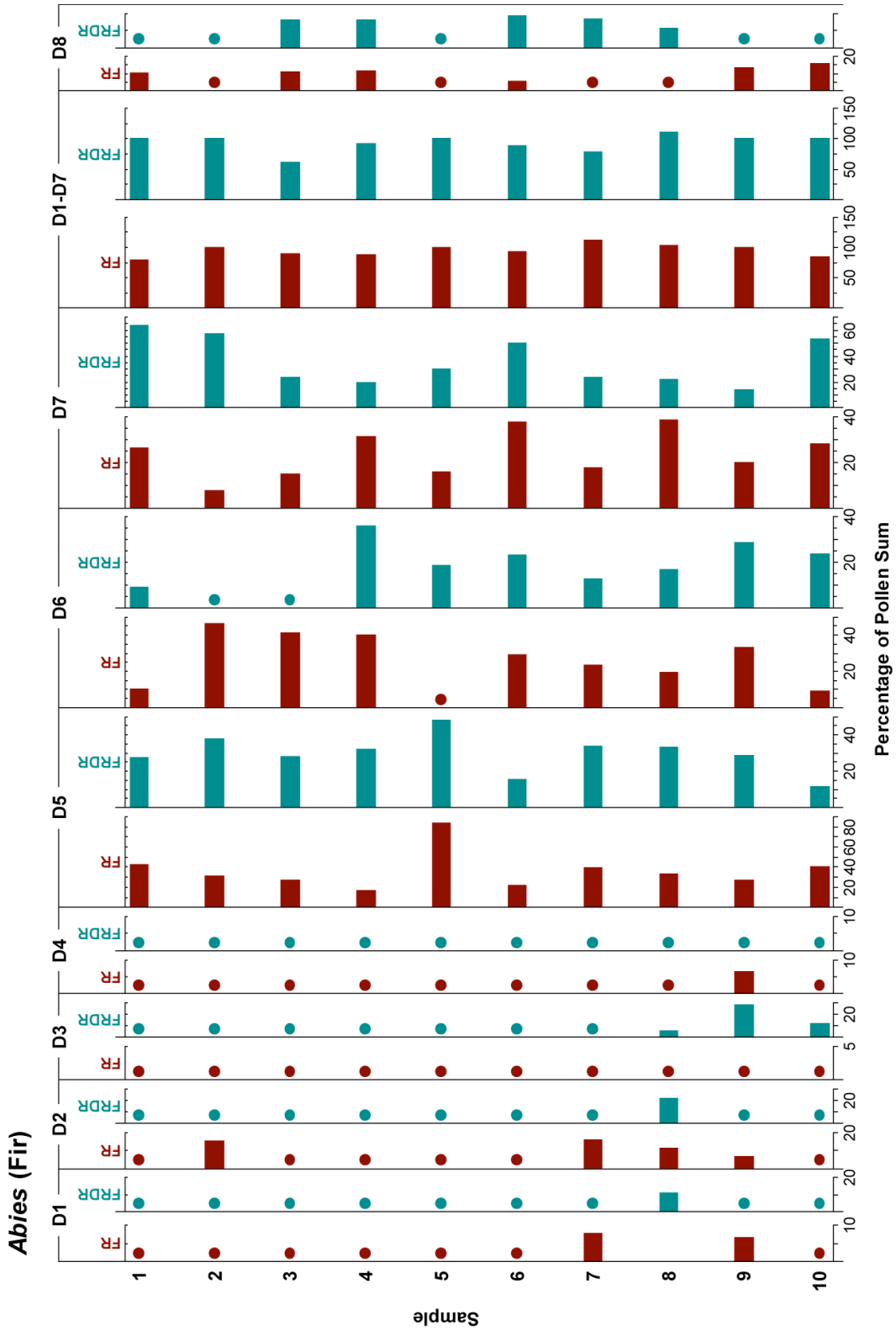
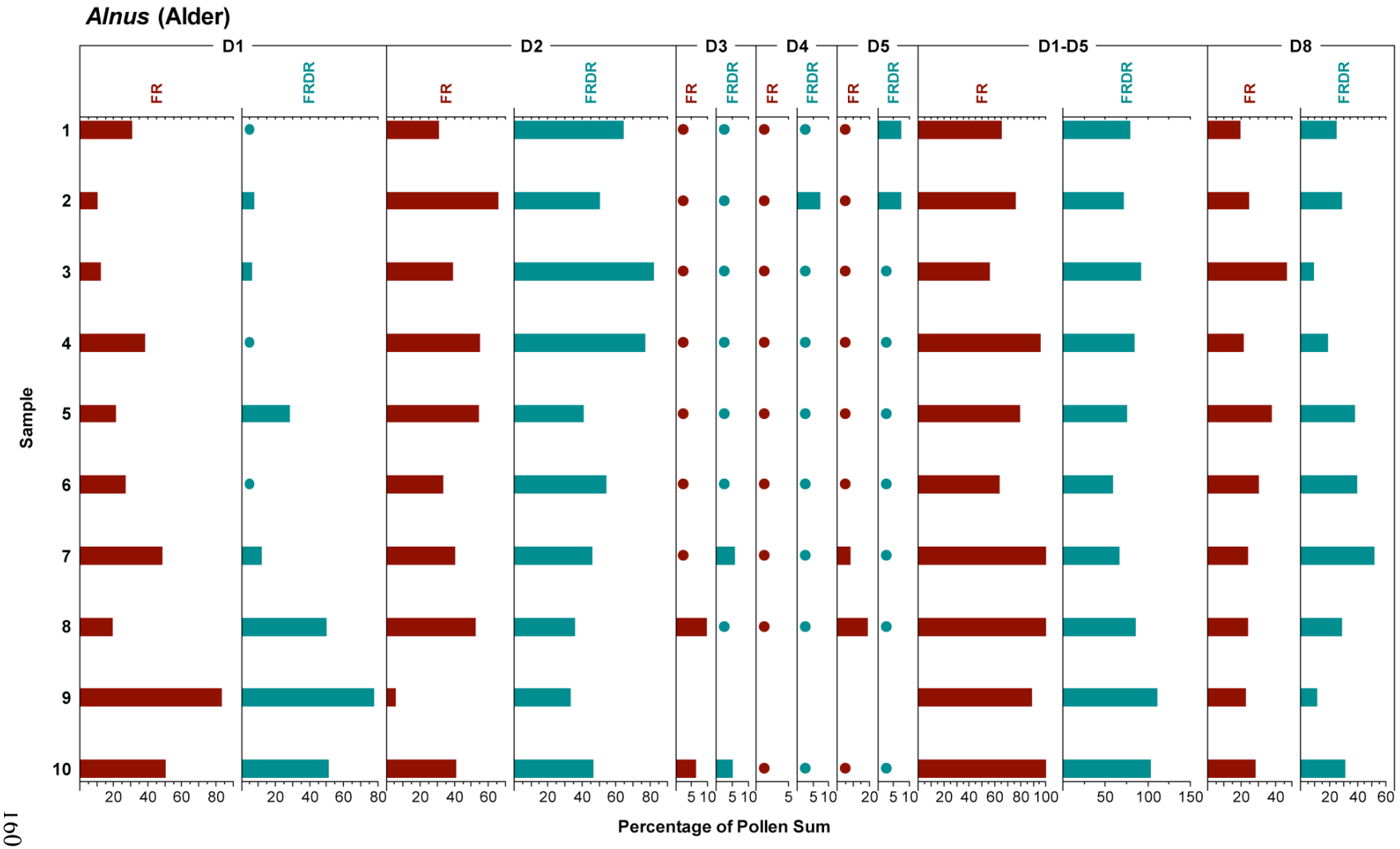

Abies (Fir)
D1
D2
D3
D4
D5
D6
D7
D1-D7
D8
FR
FRDR
Sample
Percentage of Pollen Sum

Figure 4.9. Percentage pollen diagram of ***Alnus* sp.** (based on pollen sum 4) showing deterioration classes for frozen and freeze-dried samples from Sentinel Lake, Banff National Park, AB. Teal green bars represent freeze-dried samples (FRDR) and maroon red bars represent frozen samples (FR). Refer to Figure 4.1 caption for explanation of deterioration category abbreviations.


Alnus (Alder)
D1
D2
D3
D4
D5
D1-D5
D8
FR
FRDR
Sample
1
2
3
4
5
6
7
8
9
10
20 40 60 80
20 40 60 80
20 40 60
20 40 60 80
5 10
5 10
5
5 10
20
5 10
20 40 60 80 100
50 100 150
20 40
20 40 60
Percentage of Pollen Sum

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5 CONCLUSION

Studies on the impact of natural allochthonous input of nutrient on lake ecosystems are complicated by the relatively long temporal scale and by several environmental factors masking distinct effects of the individual factors under investigations (Hall & Smol 1993). Our results may be indicative of accumulative effects regulating lake productivity and ultimately masking the magnitude of PAR contributions to algal production. Alternatively, input of pollen may not be the major player influencing lake algal abundance, but instead in-lake processes or other sources of organic matter (*e.g.,* leaves) may be responsible for increases in algal abundance (Vinebrooke *et al.* 1998). For example, release of sedimentary phosphorus may be stimulating algal communities in these lakes. Therefore, the lagged relationship between pigment concentrations and PAR for Eiffel Lake maybe due to independent effects of climate changes on PAR and lake biomass and abundance.

Climatic change has been correlated with upslope movement of treeline and increased vegetation density in the alpine (Danby & Hik 2007; Luckman & Kavanagh 2000; Walther *et al.* 2005). As treeline approaches the margins of these sensitive lakes pollen input may increase because of changes in vegetation density, proximity and phenology (Shafer *et al.* 2001; Walther 2003). Past treeline dynamics may be inferred by using sedimentary pollen ratios. Concurrence between several proxies of treeline fluctuations, such as *Picea:Pinus*

ratios (Beaudoin 1986; Evans 1997) and stomata data (MacDonald 2001; Oswald *et al.* 2007) is important to accurately interpret treeline dynamics especially when faced with more variable data. Where treeline advance may not be possible due to environmental conditions and topography of an area, inference of vegetation expansion using shrub species near higher elevation lakes may be more appropriate.

Effects of climate change on vegetation, pollen production and lake productivity is complex. For example, increased CO_2 levels contributed to the early onset of tree maturation in an experimental plot, resulting in increased pollen production per stand versus control plots (Ladeau & Clark 2006), which may significantly increase nutrient loads into lakes via increase pollen input. Further, changes in the vegetation, such as a drastic decline or increase in the dominant species, may have profound effects on lake communities through an increase of nutrients (Hall & Smol 1993). Effects of warming temperatures may also lead to reduced snowpack, increasing the likelihood of flowering alpine plants being exposed to late frost (Inouye 2008), which may reduce the amount of pollen entering the lake ecosystem. However, wind-pollinated taxa, such as *Pinus*, contribute to the majority of pollen entering the lake system (Faegri *et al.* 1989) in our alpine and subalpine study sites. Pollen production of wind-pollinated taxa (*i.e.,* Poaceae) is influenced by precipitation (Alba-Sánchez *et al.* 2010), which is predicted to increase in winter and decrease in summer and result in more extreme events (*e.g,* droughts) (Beniston 2005). These changes may result in increased or decreased

pollen influx into alpine lakes. At the same time, climatic changes in temperatures and precipitation will affect the length of ice-free growing period resulting in changes in lake algal communities (Parker *et al.* 2008; Smol & Douglas 2007).

A complication to this is the individualistic behaviour of tree species to climate change. For example, species (*i.e., Larix* spp.) that are able to reproduce vegetatively may remain fairly stable during climatic changes (Luckman & Kavanagh 2000), and may continue to contribute to the pollen influx entering alpine lakes. These changes in pollen accumulation rates may be difficult to capture for taxa (*i.e., Larix*) that are often underrepresented in sediment pollen records (Hansen *et al.* 1996) due to poor pollen dispersal (Jackson 1990) and preservation. Pollen and algal pigment diagenesis is an important factor that may affect our interpretations.

Studying the effects of storage methods on sediment cores to determine appropriate methods can be easily done to discriminate deterioration of pollen due to sedimentary processes versus storage methods. Shared pollen and pigment banks (stored sediment cores) could potentially service many researchers and reduce costs of core extraction and sediment processing. This may be possible if the same stored sediment cores (*e.g.,* freeze-dried) can be utilized by various techniques (*i.e.,* pollen analysis, pigment analysis) with minimal loss of information. Further investigation into sediment processing prior to and during storage (*e.g.,* pollen water content, vacuum pressures during freeze-drying) are

needed to determine how to best retain key morphological characters for accurate identification.

These studies demonstrate the complexities of teasing out individual factors affecting lake dynamics. Important factors such as co-limitation of lakes (Elser *et al.* 2007) and response of lake communities to input of terrestrial organic carbon or macronutrients (phosphorus, nitrogen) (Cole *et al.* 2006; Morris & Lewis 1988) must be considered. Additional multi-proxy studies investigating the long-term effects of pollen input to mountain lake productivity are needed. Phototrophic aquatic organisms are important bioindicators of past lake alterations in the face of environmental changes (Vinebrooke *et al.,* 1998), therefore an understanding of factors that may impact lake communities will allow us to build more accurate models that may benefit management practices in protected areas. For example, controlled forest burns and harvesting may be concentrated in areas where timberline advance has occurred to reduce the impact that increased pollen input may have on mountain lake ecosystems. By measuring the response of lake communities to multiple factors in a variety of lakes (*i.e,,* small versus large catchments) we will better understand the magnitude of each factor in relation to lake characteristics.

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APPENDIX A: **SITE PHOTOGRAPHS**

1) Eiffel Lake

Photo Credit: D. Tirlea, 2008

Photo Credit: D. Tirlea, 2008

2) Sentinel Lake

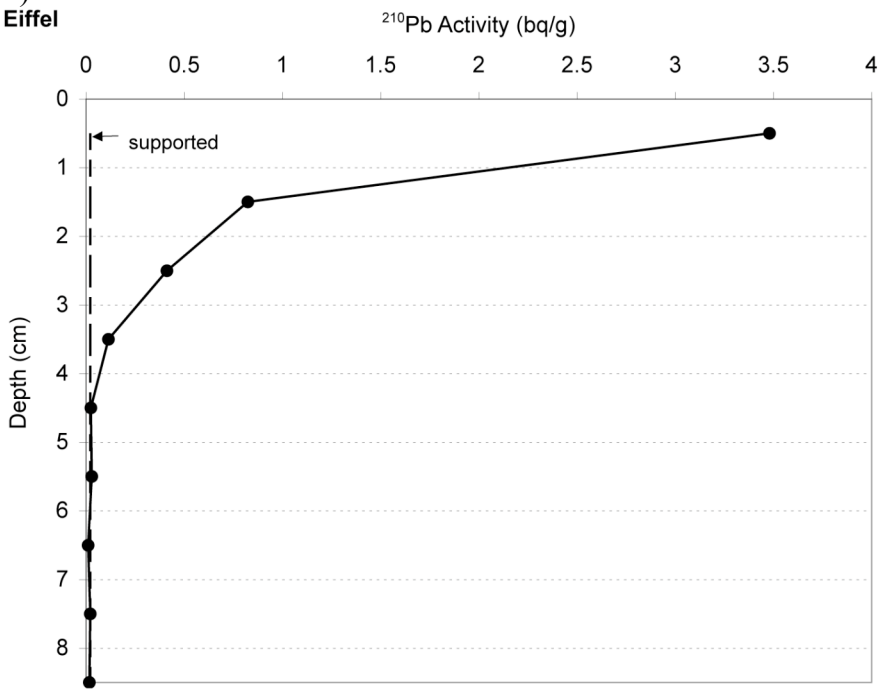
Photo Credit: unknown, field trip 2008 (Mireia, Conrad, Amanda, Diana)

Photo Credit: D. Tirlea, 2008

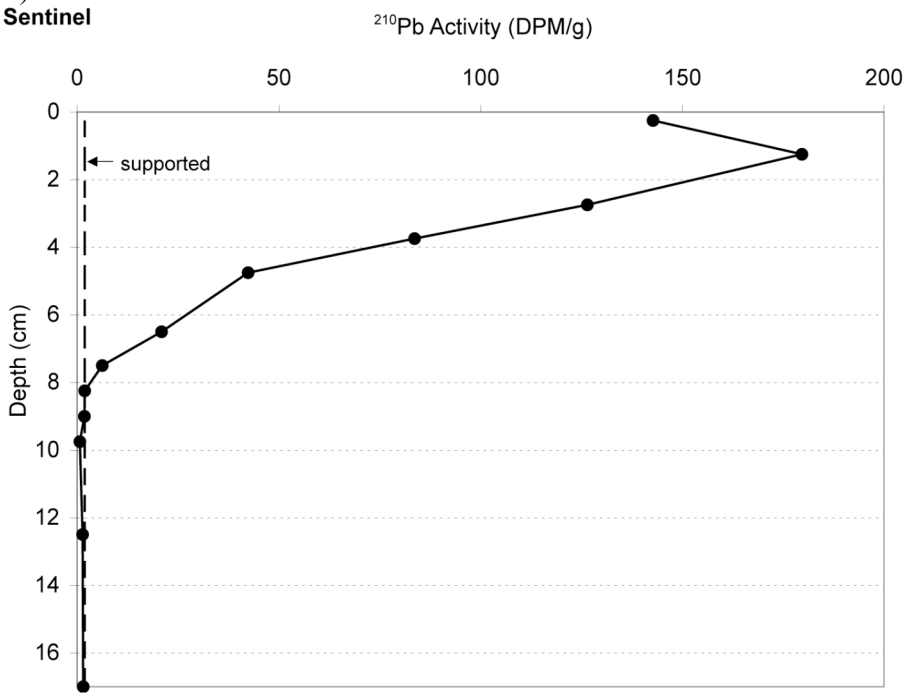
APPENDIX B: **^{210}PB DATING**

Sediment core profiles of total ^{210}Pb activity and supported ^{210}Pb (dashed line) for Eiffel Lake and Sentinel Lake.

1)



2)



APPENDIX C: **POLLEN IDENTIFICATION**

The following list consists of taxa encountered (pollen, spore and stomata) in Eiffel Lake and Sentinel Lake sediment samples and site surface samples. Only taxa presented in the pollen diagrams are described here. For each taxon key characteristics and references used in the identification of the taxon are given. A glossary of terminology used in the descriptions follows the list. Occurrence of taxa in sediments and surface samples are abbreviated as EF (Eiffel Lake sediment), SEN (Sentinel Lake sediment) and/or SU (surface samples). References used are abbreviated as follows:

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KAP: Kapp, R. O., O. K. Davis & J. E. King. 2000. Pollen and Spores, Second ed, S. C. I. Hall, American Association of Stratigraphic Palynologists Foundation, Texas, U.S.A, 279.

MCA: McAndrews, J. H., A. A. Berti & G. Norris. 1973. Key to Quaternary Pollen and Spores of the Great Lake Region, Life Sciences Miscellaneous Publication, Royal Ontario Museum, Toronto, Ontario, Canada, 61.

POL: Pollen reference collection from local site vegetation (Banff National Park), Royal Alberta Museum, Edmonton, Alberta.

RAM: Pollen reference collection, Quaternary Environments, Royal Alberta Museum, Edmonton, Alberta.

UOA: Pollen reference collection, Palynology Lab, Department of Anthropology, University of Alberta, Edmonton, Alberta.

Abies: Bisaccate (two bladders attached to the body), attachment point of bladders to body is well-defined division forming a constriction (distinct angle) between bladder and body. Bladders are heavily reticulate and sculpturing is distinct from the rugulate or striate sculpturing of the body. The cappa exine is very thick, with notable thinning near the centre (pole), large grain (body > 70µm lengthwise). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

***Alnus*:** Stephanoporate, psilate to scabrate (speckled appearance), arci present, pores vestibulate with pore cavity forming, annuli present around pores, typically 5 pores are present but 4 and 6 pore variants occur. References: HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Artemisia: Tricolporate, colpi broad, pores may be indistinct, sculpturing microechinate with blunt-tipped spines, exine thick (3-4µm) with distinct columns, grain small (20-30µm). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Asteraceae: echinate with small spines (length equal to less than base of spine), spine tips blunt, *e.g., Ambrosia* or spines large (length greater than base of spine), spine tip sharp *e.g., Arnica*. References: BAS, HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

Betula: Triporate, pores vestibulate with a protruding or enlarged appearance, pores with annulus, sculpturing psilate to scabrate, grain small (< 30µm). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Caryophyllaceae undifferentiated: Periporate, large distinct pores (~8-10 in encountered grains), sculpturing scabrate or appearing microreticulate, exine thick (3-4µm) with distinct columns, shape spheroid *e.g., Cerastium.* References: HAB, KAP, RAM, UOA. Occurrences: EF, SEN, SU.

Chenopodiaceae / Amaranthaceae: Periporate, pores annulate, more than 30 pores typically, sculpturing psilate or granulate, exine < 2µm, shape spheroid, size ranges between approximately 20-35 µm. References: BAS, HAB, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Cyperaceae: inaperature, tetrahedral (triangular), psilate surface, thinning of the wall in areas forming what may appear as indistinct pores (~1-6, referred as periporate or having a poroid area by MCA, KAP). BAS, HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

Ericad (includes Ericaceae, Pyrolaceae, Empetraceae): tetrad, tetrahedral arrangement with overall unit triangular. Individual pollen grains tricolporate. References: BAS, HAB, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

***Juniperus*:** Inaperturate, sculpturing psilate with scattered gemmae, exine thin, shape spheroid, grain small (20-30µm). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: SEN, SU.

Larix: Inaperturate, sculpturing psilate, exine thin, often ruptured or crumpled, grain large (typically > 60µm), References: BAS, HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SU.

***Oxyria* (Polygonaceae)** References: tricolporate, pores not very distinct, colpi long and slit-like, sculpturing finely scabrate, shape spherical, size 20-25µm References: BAS, RAM, UOA. Occurrences: EF, SEN.

Picea: Bisaccate (two bladders attached to the body), attachment point of bladders to body is not defined division, where bladders appear to merge into the body with no distinct angle between bladder and body. Bladder sculpturing is reticulate. Sculpturing transitions from reticulate bladders to scabrate body with no abrupt distinction between the sculpturing of the body and bladders. The cappa exine is thin. References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Pinus: Bisaccate (two bladders attached to the body), attachment point of bladders to body is well-defined division, forming a constriction (distinct angle) between bladder and body. Bladders are reticulate and sculpturing is distinct from the finely rugulate or granulate sculpturing of the body. The cappa exine is thin. (body between 45-65µm lengthwise). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Poaceae: monoporate, pore with annulus, psilate or scabrate sculpturing, grain spheroid, References: BAS, HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

***Populus*:** Inaperturate, sculpturing with dense scabrate to verrucate elements, grain spheroid, exine thin. References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

Ranunculaceae: Tricolpate, colpi membrane often granular or verrucate, sculpturing scabrate, microechinate or verrucate, shapes range from spheroid to prolate, exine thick and forming distinct columns in the ektexine, *e.g., Anemone*, *Ranuculus* References: BAS, HAB, KAP, RAM, UOA. Occurrences: EF, SEN, SU.

Rosaceae: Tricolporate, poroidal area (pores may not be distinct in some taxa, *e.g., Potentilla, Fragaria*) with or without an operculum, poridal area may be protruding (*Fragaria*), sculpturing typically striate or rugulate. Encountered taxa in the Rosaceae includes *Fragaria, Dryas, Rosa, Potentilla*. References: HAB, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

***Salix*:** Tricolpate or tricolporate, reticulate with transition from coarse reticulum to a finer reticulum nearing the apertures, margo present, grain small (~ 20-30µm). References: BAS, HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

***Saxifraga*:** Tricolpate, striate, no poroidal area, colpi without constriction, sculpturing striate, shape prolate typically, References: HAB, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

Scrophulariaceae: tricolpate or tricolporate, colpi long and broad with no membrane, sculpturing finely scabrate or reticulate *e.g., Castilleja, Penstemon*, *Veronica,* some members have two colpi that appear fused *e.g., Pedicularis* References: HAB, KAP, MCA, POL, RAM, UOA. Occurrences: EF, SEN, SU.

***Shepherdia*:** Tricolporate, colpi slit-like, pores appear annulate (slightly protruding), colpi lack constriction, sculpturing scabrate, shape prolate, grain small (20-35µm). References: HAB, RAM, UOA. Occurrences: SEN, SU.

***Silene*:** same as description for Caryophyllaceae descriptions except with 20-30 pores and sculpturing scabrate. References: HAB, KAP, RAM, UOA. Occurrences: EF, SEN, SU.

Spores: Monolete spores have a single slit-like scar and trilete spores have a triradiate (Y-shaped) scar. ***Lycopodium*:** triangular with pointy corners, thick muri, exine with distinct and raised 'feet', pronounced trilete scar, stained amber. ***Lycopodium* ('SPIKE'):** triangular with smooth corner, thin muri, exine with raised 'feet', trilete scar is weak, stained light amber to pink. References: HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

***Thalictrum*:** Periporate, pores with granules or verrucae, pores not annulate, shape spheroid, grains small (< 25µm). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

***Tsuga*:** Saccate (one bladder) marginal, grain spheroid, bladder with distinct projects (feet and ankle like shapes) creating a fringe around the grain. Center of grain appears depressed. Grain large (> 40µm). References: BAS, HAB, KAP, MCA, RAM, UOA. Occurrences: EF, SEN, SU.

***Valeriana*:** Tricolpate, colpi membrane with granules, echinate but with small spines, colpi with granules, exine thick, grain large (~ > 40µm) References: HAB, RAM. Occurrences: EF, SU.

***Zigadenus*:** Monocolpate, sculpturing reticulate (often fine and not very distinct), shape prolate. References: HAB, POL, RAM. Occurrences: SEN, SU.

Other Herbs: Infrequently encountered herbaceous plant pollen of several taxa were grouped into this category. This includes *Apiaceae, Urtica, Viola, , Polygonum, Rumex* Polygonaceae, Fabaceae, *Galium, Draba, Oxytropis,* Brassicaceae*,* ***Epilobium c.f. E. latifolium*** **(Onagraceae):** triporate, pores vestibulate and protruding / enlarged with distinct pore cavity formed, shape triangular, grain large (60-80µm). References: BAS, CRO, HAB, KAP, MCA, RAM, UOA.

GLOSSARY

Plural forms (pl._____) and synonyms (syn._____) are provided in brackets where appropriate. Definitions are based on the following sources:

Habgood, T. & E. P. Simons. 1985. A key to pollen and spores of Alberta, Third ed, Paleoenvironmental studies laboratory, Anthropology Department, University of Alberta, Unpublished key, Edmonton, Alberta, Canada, 31 pages.

Kapp, R. O., O. K. Davis & J. E. King. 2000. Pollen and Spores, Second ed, S. C. I. Hall, American Association of Stratigraphic Palynologists Foundation, Texas, U.S.A, 279.

Punt, W., P. P. Hoen, S. Blackmore, S. Nilsson & A. Le Thomas. 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology **143:** 1-81.

Arcus: (pl. arci) arches or ridges formed between pores.

Aspidate: protruding apertures.

Annulus: (pl. annuli) a thickening or thinning of the adjacent walls surrounding pore margin.

Cappa: (pl. cappae) the proximal regions of the corpus that is thickened.

Colpus: (pl. colpi) elongated apertures (sometimes referred to as furrow) with a length : breadth ratio greater than 2.

Corpus: central body of vesticulate (saccate) pollen grains, *e.g.,* pine.

Echinate: pollen wall sculpturing with sharp or blunt points or spines.

Exine: the outer portion of the pollen wall that is chemically resistant. The exine consists of the inner layer (endexine) and the outer layer (ektexine). Structures (pores, furrows) and sculpturing (*e.g.,* spines) of the outer wall are morphological

characteristics that aids in identification of pollen taxa. Sculpturing ranges from indistinct (smooth surface) to prominent (spiny surface).

Gemma: (pl. gemmae) sculpturing element that is constricted at the base and is equal to or wider than its height.

Inaperturate: no apertures present.

Margo: a thickening or thinning of the adjacent walls surrounding the colpi.

Monoporate: pollen grains having one pore.

Periporate: (syn. pantoporate) more than three pores; pores scattered or evenly distributed but not solely arrange along the equator

Pore: a circular aperture with a length : breadth ratio of less than 2.

Psilate: pollen wall sculpturing smooth.

Rugulate: pollen wall sculpturing elements irregularly shaped horizontal lines with no distinct pattern.

Reticulate: pollen wall sculpturing forming a network with walls (ridges) enclosing irregularly shaped spaces, network ranges in size and pattern.

Rugulate: pollen wall sculpturing elements irregularly shaped horizontal lines with no distinct pattern.

Saccate: (pl. sacci), bladder-like projection from the corpus of vesticulate (or saccate) pollen grains, *e.g.,* pine.

Scabrate: pollen wall sculpturing with small speckled or granular appearance and with no distinct pattern.

Stephanoporate: (syn. zonoporate) more than three pores; pores arranged along the equator.

Striate: pollen sculpturing consistent of long linear horizontal lines with groupings or all lines running parallel to one another.

Tetrad: four pollen grains or spores joined as one unit. Grains / spores may be aligned along one plane (linear, rhomboidal, tetragonal) or multiple 'stacked' planes (tetrahedral).

Triaperature: having three colpi (tricolpate) or three pores (triporate).

Tricolporate: pollen grains having three pores and three colpi.

Verrucate: pollen wall sculpturing with bump-like (verruca (pl. verrucae)) projections.

Vestibulate: (sing. vestibulum pl. vestibula) separation of the outer and inner layers of the pollen wall (see exine definition) forming a pore cavity.

APPENDIX D: **RAW POLLEN DATA**

1) Sentinel Lake, sediment samples

Raw Pollen Data
Sentinel Lake, Banff National Park

Core	Top Depth (cm)	Bottom Depth (cm)	Section Dry Wt. (g)	Pollen Sample Dry Wt.(g)	Pollen Sample Volume (cm3)	LOI % (550 burn)	Mean Lycopodium Spores Added to Sample	Spike Sum	Pollen Sum	Pinus
1	0	2.5		0.341	1.275	28.9454	27822	195	1222.5	957
1	2.5	3.5		0.313	1.275	19.3825	27822	246	1195	915
1	3.5	4.5		0.388	1.275	18.4416	27822	191	980.5	714.5
1	4.5	5		0.345	1.275	19.4848	27822	258	1475.5	1133
2	5	5.5	0.2796	0.107	0.6	18.8471	27822	737	1290.5	962
2	5.5	5.75	0.1056	0.0344	0.3	18.3133	27822	1526	651	438
2	5.75	6	0.1648	0.0874	0.6	21.9396	27822	1059	1632	1214.5
2	6	6.5	0.4258	0.1636	0.8	20.0018	27822	449	878.5	651.5
2	6.5	7	0.397	0.1705	0.8	17.9136	27822	761	1728	1212
2	7	7.5	0.4575	0.1546	0.4	16.6115	27822	521	1323	964
2	7.5	8	0.5115	0.2187	1	15.6004	27822	677	2166	1669
2	8	8.5	0.5619	0.2212	1	14.2251	27822	380	1454.5	1107.5
2	8.5	9	0.5287	0.2105	1	14.3897	27822	583	1257.5	992.5
2	9	9.5	0.4837	0.2641	1.2	17.8881	27822	414	1692.5	1393
2	9.5	9.75	0.2869	0.116	0.6	17.8593	27822	586	1044	747.5
2	9.75	10	0.3647	0.102	0.4	17.4409	27822	442	1178.5	855
2	10	10.5	0.5523	0.32	1.275	16.674	27822	363	2055.5	1609
2	10.5	11	0.6005	0.3736	1.275	14.6272	27822	337	2008.5	1576.5
2	11	11.5	0.5021	0.2131	1	14.4522	27822	359	1327.5	985
2	11.5	12	0.5835	0.3075	1.275	18.2571	27822	275	1631	1266.5
2	12	12.5	0.6075	0.3449	1.275	13.9786	27822	247	1534.5	1219
2	12.5	13	0.4886	0.3544	1.275	17.3594	27822	177	1205	933.5
2	13	13.5	0.8843	0.4308	1.275	17.2128	27822	250	1637.5	1283
2	13.5	14	0.9065	0.4044	1.275	22.9785	27822	142	941.5	716.5
2	14	14.5	0.4109	0.3432	1.275	16.701	27822	187	1045	805.5
2	14.5	15	0.5789	0.3464	1.275	12.5293	24153	266	1769	1375
2	15	15.5	0.5617	0.1797	1	16.6864	27822	249	825.5	593.5
2	15.5	16	0.7649	0.3958	1.275	18.7351	24153	93	918	688
2	16	16.5	0.7937	0.393	1.275	16.6187	24153	242	1833.5	1516.5
2	16.5	17	0.567	0.3654	1.275	15.7835	24153	120	718	482
2	17	17.5	0.4288	0.1484	0.8	15.6443	27822	237	914	623
2	17.5	18	0.6233	0.3889	1.275	15.0555	24153	153	1215.5	815.5
2	18	18.5	0.5751	0.3768	1.275	19.466	24153	220	1843.5	1452.5
2	18.5	19	0.4681	0.3308	1.275	23.0555	27822	86	1204.5	917
2	19	19.5	0.5496	0.3259	1.275	18.0881	24153	136	1335	934
2	19.5	20	0.4416	0.2989	1.275	19.3373	24153	169	1461	1201
2	20	21	1.0989	0.3651	1.275	18.617	24153	160	1672	1226.5
2	21	22	1.1566	0.323	1.275	16.0537	24153	127	1111.5	798
2	22	23	1.1447	0.3187	1.275	17.6107	24153	85	891	691.5
2	23	24	0.8512	0.324	1.275	17.3004	24153	158	1088	795
2	24	25	0.8775	0.2587	1.275	23.9814	24153	147	1086	764.5
2	25	26	1.3814	0.3124	1.275	21.136	24153	205	1708.5	1255
2	26	27	1.4413	0.3703	1.275	18.9928	24153	135	1291	1060.5
2	27	28	1.5336	0.3454	1.275	12.3857	24153	165	1424.5	1144.5
2	28	29	1.4712	0.3717	1.275	8.45616	24153	177	1439.5	1063
2	29	30	1.1261	0.3431	1.275	5.74513	24153	168	1097	859.5

Top Depth (cm)	Picea	Abies	Tsuga	Populus	Salix	Juniperus	Alnus	Betula	Thalictrum	Anemone
0	126	50.5	1			1	58			
2.5	139.5	36.5	1				70	1		
3.5	89	23	2		2	1	87		1	2
4.5	157.5	68	1		1		72	2	2	
5	131.5	57		2	2		84	1		
5.5	86.5	28.5	1			1	70			
5.75	189.5	100			1		78			1
6	92.5	23.5	2				65	1	1	1
6.5	162.5	170.5	1		1		115		1	
7	149.5	88.5	1				58			
7.5	234	149	5		2		61	1	1	
8	196.5	73.5	2			1	46			1
8.5	133	34	1	1			69		1	
9	148	39.5	2		1		59			
9.5	164.5	60	1				45			
9.75	202	72.5	1	3			28	1	1	
10	251	96.5	1	1	1		48	1		
10.5	204	83	1				88		1	
11	140.5	87					83			
11.5	147	120.5	3				59			
12	111	126.5	1				46	1		
12.5	116.5	78					54			1
13	153	104.5	3				76			
13.5	103	25	2		2		70	2		
14	112.5	36	3	1	1		54			
14.5	143	46	1				151	4		
15	122.5	38.5	2	1	1		52	1	1	
15.5	108.5	23.5	5				70		1	3
16	106.5	52.5	1		5		110	2		
16.5	91	27	3	4	4		62	1	1	
17	158	64	2				46	1		
17.5	239	48	3		1		73	1	1	
18	189	97	4		1		72			
18.5	161.5	54	2	1	3		46			
19	304.5	51.5		1	2		21			
19.5	154.5	56.5	1	1			21			
20	291	74.5	1		4		40			2
21	231	43.5		1	1		18			1
22	105	47.5	1				23	1		
23	182.5	63.5		1			24			
24	238	42.5					27			
25	302.5	51	2		1	1	55	1		1
26	81.5	47	1		1		63		2	
27	185.5	43.5		5	1		15	2		
28	183	119.5	1	1			46		1	
29	129.5	67					29			

Top Depth (cm)	Ranunculaceae Undiff.	Silene	Artemisia	Fenestrate Asteraceae	Low Spine Asteraceae	High Spine Asteraceae	Saxifraga	Onagraceae
0			10		4		1	
2.5			13		3			
3.5	5	2	32		1			
4.5	2		17		3	3		
5			25		1	2	3	2
5.5	2		11		1			
5.75			15		8	2		
6	1	3	22			3		
6.5	1		24		8	1		
7		1	8		3	1		
7.5			13		7	1		
8	2		13			1		
8.5			12		4			
9		1	19		1	1		
9.5			6	1	6	2		
9.75	1		9					
10			23		4	2	1	
10.5	3		21			3		
11	2	1	19			1		
11.5	1		17		7			
12		1	15		2			
12.5			3		1	2		
13			6		1	1		
13.5	1		9	1				
14	3		14					
14.5	1		16			5		
15			6		1	1		
15.5			7					
16		1	18		1	4		
16.5			6			1		
17	1		6		2			
17.5			7		3	1		
18	1		12		1			
18.5	1		9		3	1		
19			13		1	3		
19.5			15		2			
20			16		1	1		
21	1		9		1	2		
22	1		10			1		
23	1		8			3		
24			7		1	1		
25			17	1		2	1	
26	2		21			5		
27	2		15					
28	1	1	17	2				
29			8					

Top Depth (cm)	Apiaceae	Fragaria	Dryas	Rosa	Potentilla	Rosaceae Undiff.	Zigadenus	Oxyria	Polygonum
0		1							
2.5							1	1	
3.5		1				1			
4.5									
5						1			
5.5					1				
5.75							2		
6									
6.5				1		1			
7									
7.5			3			2		1	
8						1			
8.5									
9						1			
9.5						1			
9.75									
10									
10.5						3		2	
11			1						
11.5									1
12		1				1		1	
12.5									
13									
13.5		1							
14		2				2			
14.5								2	
15									
15.5									
16		1	2				1	1	
16.5									
17									
17.5	1								
18									
18.5									
19									
19.5									
20		2			2				
21									
22									
23								1	
24									
25									
26									
27									
28		1							
29								1	

Top Depth (cm)	Rumex	Polygonaceae Undiff.	Fabaceae	Galium	Draba	Oxytropis	Brassicaceae Undiff.	Shepherdia
0								
2.5								
3.5								
4.5								
5			2					
5.5								
5.75	1	1						
6								
6.5					1			
7								
7.5								
8								
8.5								
9								
9.5								
9.75								
10		1						
10.5								
11								
11.5								
12								
12.5								
13								
13.5					2			
14	1							
14.5								
15								
15.5							1	
16								
16.5								
17								
17.5						3		
18								1
18.5								
19								
19.5			1	1				
20							1	
21							1	
22								
23								
24								
25								
26							1	
27								
28								
29								

Pedicularis	Top Depth (cm)	Castilleja	Penstemon	Scrophulariaceae Undiff.	Veronica	Chenopodiaceae/ Amaranthaceae Undiff.	Poaceae	
	0					2	3	
	2.5			4	1	4	1	
	3.5	1		1		10	3	
	4.5					3	5	
	5	1					10	
	5.5					3	6	
	5.75					6	4	
	6			1		9	2	
	6.5	1		3		7	11	
	7					3	6	
2	7.5					2	2	
	8					1	7	
	8.5					1		
	9					6	11	
	9.5						6	
	9.75						3	
	10			1			5	
	10.5			1		2	10	
1	11						5	
1	11.5			1			1	
	12			1		1	6	
	12.5					2	8	
	13					2	5	
	13.5					2	2	
	14					1	3	
	14.5			1		4	11	
	15					1	3	
	15.5						7	
	16					2	4	
	16.5					7	17	
	17					2	4	
	17.5					5	6	
	18					4	5	
	18.5					1	3	
	19					1	2	
1	19.5					1	3	
	20					2	6	
	21					1	2	
	22			2			6	
	23	2				1	3	
	24						5	
	25			3		4	5	
	26		1			3	2	
	27					3	1	
	28			1		1	1	
	29						3	

Top Depth (cm)	Cyperaceae	Ericad Morph 1	Ericad Morph 2	Ericad Undiff.	Typha	Alder 4 pore	Alder 5 pore	Alder 6 pore	Charcoal 12-36 um
0	6	1				5	50	3	281
2.5		3	1			4	65	1	362
3.5		1	1			3	83	1	525
4.5	6					2	68	2	420
5	4					8	71	5	419
5.5	1	1				9	58	3	381
5.75	7		1		1	7	68	3	424
6						5	59	1	515
6.5	5	1				11	103	1	535
7	5	34				9	46	3	433
7.5	8	2				10	49	2	454
8	2					3	42	1	685
8.5	9					7	62		397
9	9		1			11	46	2	345
9.5	3					5	38	2	311
9.75	1			1		4	22	2	499
10	9					5	43		406
10.5	8	2				4	82	2	461
11	2					16	65	2	904
11.5	5			1		8	48	3	380
12	1					1	39	6	540
12.5	6					4	50		444
13	3					10	62	4	427
13.5	3					11	58	1	790
14	4		1	1		5	49		396
14.5	8			1	1	6	145		817
15	1					4	48		385
15.5	4					6	63	1	473
16	5					18	92		468
16.5	9			3		6	50	6	337
17	5					6	40		806
17.5	8					9	63	1	890
18	4					5	66	1	1151
18.5	1					3	43		439
19	1					4	16	1	77
19.5	1						21		140
20	2					4	36		376
21	1						18		149
22	2						23		88
23	3					1	23		318
24						4	23		396
25	1			5		3	51	1	450
26						7	55	1	230
27	7					9	3	3	565
28						2	44		450
29						1	28		135

Top Depth (cm)	Char 36-72 um	Char >72um	Stomata c.f. Picea	Stomata Pinaceae Undiff.	Spore /Egg?	Monolete	Trilete	Lycopodia	Concealed Unidentified
0	44	10				31	7		5
2.5	46	15				15	6	2	3
3.5	72	26				11	6		8
4.5	119	61				10	16	3	5
5	36	6				29	15		2
5.5	39	6	1			12	9	6	4
5.75	92	21				6	23	2	4
6	64	17				9	11		1
6.5	112	31			1	29	25	6	8
7	142	41				24	15		8
7.5	111	75	1		1	21	23	3	4
8	87	41				30	24	1	2
8.5	65	12	8			19	18	2	2
9	48	24				21	18		2
9.5	47	18	1			10	14	7	7
9.75	45	19				16	15	5	4
10	101	33				13	14	1	4
10.5	73	23				25	18		5
11	117	34				40	14	2	
11.5	117	32				16	34		4
12	65	46				18	13	3	4
12.5	76	33				24	15	1	7
13	114	56				24	37	1	5
13.5	84	24				25	12	2	1
14	57	19				38	24	5	4
14.5	132	34		1		32	50	7	19
15	80	31				12	12		4
15.5	73	21				28	29		3
16	97	21				39	27	1	1
16.5	88	32				20	11		18
17	203	60				22	17	8	4
17.5	155	52				42	15		5
18	175	46				24	33	3	6
18.5	80	28	1	3		20	17	1	10
19	232	42				14	15	6	12
19.5	40	17				6	4	1	10
20	107	36				25	15	1	11
21	25	19				15	24		11
22	37	15				8	15	2	53
23	92	31				6	11	1	12
24	117	50				5	18		10
25	127	50				40	30	3	18
26	54	32				22	18		14
27	48	14				28	49		32
28	143	69			2	32	31	1	20
29	41	17				3	12	1	21

Top Depth (cm)	Crumpled Unidentified	Torn Unidentified	Degraded Unidentified	Unknowns
0	2	4		4
2.5	3	3	1	0
3.5	7	3	1	2
4.5	8	2	3	2
5	4	9	2	3
5.5	12	4	1	1
5.75	7	5	3	2
6	5		1	4
6.5	1	7	1	3
7	18	3	3	7
7.5	8	2	1	0
8	13	4	2	9
8.5	11	3	1	12
9	9	4		2
9.5	9	5		1
9.75	8	3		5
10	11	2	2	1
10.5	7	1		4
11	5	2		3
11.5	10	10	1	2
12	4	3	1	0
12.5	13	3	3	1
13	7	3	2	1
13.5	14		2	2
14	10	2	1	1
14.5	27	21	18	13
15	13	3	6	2
15.5	8	3	10	7
16	15	3	6	3
16.5	15	6	26	0
17	7		1	9
17.5	6	4	8	11
18	14	4	2	1
18.5	6		1	2
19	8	2	7	1
19.5	4			0
20	17	4	5	1
21	14		6	2
22	9	5	21	4
23	8		4	0
24	12	1	2	3
25	20	3	6	8
26	2	1	4	1
27	19	6	17	0
28	5	1		1
29	2	3	4	0

2) Eiffel Lake, sediment samples

Raw Pollen Data		Effiel Lake (Core 1), Banff National Park					
Top Depth (cm)	Bottom Depth (cm)	Pollen Sample Dry Wt.(g)	Pollen Sample Volume (cm3)	LOI % (550C burn)	Mean Lycopodium Spores Added to Sample	Spike Sum	Pollen Sum
0	2.5	0.3146	1.275	32.633875	24153	292	1131
2.5	3.25	0.5855	1.275	12.8320397	24153	337	1442
3.25	3.5	0.5697	1.275	9.33996413	24153	360	539
3.5	3.75	0.5909	1.275	7.64655905	24153	611	1029
3.75	4	0.6742	1.275	7.35538962	24153	551	877
4	4.25	0.6437	1.275	7.06422018	24153	446	532.5
4.25	4.5	0.7048	1.275	6.31798045	24153	295	620
4.5	4.75	0.6902	1.275	5.57174071	24153	374	805
4.75	5	0.7278	1.275	6.58900235	24153	325	779.5
5	5.25	0.6676	1.275	7.60626398	24153	280	1017.5
5.25	5.5	0.5739	1.275	8.49063199	24153	294	851.5
5.5	5.75	0.6995	1.275	9.375	24153	345	1164.5
5.75	6	0.5716	1.275	9.04099322	24153	313	1102
6	6.25	0.4789	1.275	8.70698644	24153	495	1661.5
6.25	6.5	0.4954	1.275	9.55956697	24153	698	1811.5
6.5	6.75	0.4715	1.275	10.4121475	24153	510	2267.5
6.75	7	0.4771	1.275	10.0217694	24153	268	745
7	7.25	0.2617	0.6375	9.6313912	24153	1110	1202
7.25	7.5	0.4401	1.275	8.99711153	24153	649	1160
7.5	7.75	0.4818	1.275	8.36283186	24153	491	936.5
7.75	8	0.5136	1.275	6.8852459	24153	607	1282
8	8.25	1.0178	1.275	3.17683881	24153	1413	745
8.25	8.5	1.017	1.275	4.33560819	24153	439	515
8.5	9	0.9546	1.275	5.44811321	24153	404	610
9	9.25	0.7345	1.275	6.79078952	24153	325	928
9.25	9.5	0.7323	1.275	7.68535262	24153	279	1261.5
9.5	10	0.6389	1.275	12.1151366	24153	137	844.5
10	10.5	0.5635	1.275	15.2986363	24153	92	929.5
10.5	11	0.4888	1.275	17.0055413	24153	193	2010
11	11.5	0.5742	1.275	18.7124464	24153	166	1819
11.5	12	0.4939	1.275	18.0963807	24153	112	1322.5
12	12.5	0.4794	1.275	17.480315	24153	186	1390.5
12.5	13	0.3827	1.275	16.955223	24153	182	1091.6
13	13.5	0.3922	1.275	16.430131	24153	184	1208.5
13.5	14	0.3832	1.275	16.2106029	24153	291	2189.5
14	14.5	0.3999	1.275	15.9910747	24153	169	1091
14.5	15	0.5496	1.275	14.0964132	24153	221	1736
15	15.5	0.5284	1.275	12.2017517	24153	358	2267.5
15.5	16	0.4725	1.275	12.5783455	24153	175	1233
16	16.5	0.4459	1.275	12.9549393	24153	187	1358.5
16.5	17	0.483	1.275	15.132802	24153	225	2451.5
17	17.5	0.3905	1.275	17.3106646	24153	241	2654.9
17.5	18	0.3777	1.275	17.8889672	24153	90	1113.5
18	18.5	0.3739	1.275	18.4672698	24153	163	1235.5
18.5	19	0.3895	1.275	17.665747	24153	164	1503.5
19	19.5	0.3611	1.275	16.8642241	24153	140	1115
19.5	20	0.3172	1.275	16.0957734	24153	242	2021.5
20	21	0.3491	1.275	15.3273226	24153	112	936
21	22	0.3269	1.275	14.9432955	24153	207	1631.5
22	23	0.335	1.275	14.0537663	24153	209	1628
23	24	0.3542	1.275	17.1573973	24153	191	1879
24	25	0.4025	1.275	12.9757785	24153	274	2849.5

Raw Pollen Data												
Top Depth (cm)	Undetermined Sum	Pinus	Picea	Abies	Larix	Tsuga	Populus	Salix	Alnus	Betula	Valeriana	Urtica
0	13	818.5	168	113.5					23	1		
2.5	17	967	248	186	1	2			29			
3.25	13	333	96.5	87.5	1				19			
3.5	15	731	154	117		1			17			
3.75	20	587	144	107		2			26			
4	10	309	126.5	72	1				19			
4.25	15	341	135.5	121.5					16		1	
4.5	18	478	124.5	175.5	1	1			17			
4.75	11	388	197.5	174		1			16			
5	18	497	231.5	274		2		1	11			
5.25	7	457.5	166	204					15			
5.5	6	614	271.5	254	1	2		2	14			
5.75	24	586.5	247	233.5		1			26			
6	10	911.5	332.5	354.5		2			42			
6.25	32	914	403.5	339	2	4			114			
6.5	23	1334	440.5	363		4			99			
6.75	9	417.5	154.5	123					39			
7	27	592	295.5	199.5		4			91		1	
7.25	8	783	149	130					82			
7.5	19	583.5	151	130					58		1	
7.75	14	833.5	209	142.5					71	1	2	
8	26	456.5	91.5	107				1	70			
8.25	12	301.5	89.5	63	1				50			
8.5	12	352	118	96				2	27	2		
9	16	574	147	146					50			
9.25	6	773	230.5	192		2			49			
9.5	5	528	138.5	99					65	1		
10	5	575.5	121	127		1			80			
10.5	15	1336	281	220					128	1	1	
11	20	1252.5	247	200.5		1			97	2		
11.5	19	901	144.5	147	1				98	2	1	
12	8	905.5	145	181		1		1	127	1		
12.5	22	648.5	156.6	210.5					58	1		
13	21	720	203.5	202					67		2	
13.5	20	1454.5	341	286					90			
14	5	661.5	140	191.5					79	1		
14.5	22	1085	225	266		1		1	138	2	2	
15	37	1304	372.5	314					232	2		1
15.5	32	743.5	163.5	257		1	1	1	55	1		
16	9	879	155	237.5				1	71			
16.5	12	1601	310.5	447					69			
17	19	1747	356.5	445.4					91		1	
17.5	5	702.5	157.5	211.5					31			
18	23	750	169	243.5				1	50	1		
18.5	22	883.5	246	205				1	123	3	1	
19	19	627	172	180					113	1		
19.5	18	1227.5	249	345					170			
20	11	487	145	163					118		1	
21	23	952	169.5	282					175	1	2	
22	12	884	214	281					203	1		
23	43	1140	280.5	291.5					136			
24	36	1867.5	242.5	489.5					187	1		

Raw Pollen Data									
Top Depth (cm)	Viola sp.	Thalictrum	Anemone	Ranuculus	Ranunculaceae Undiff.	Silene sp.	Artemisia	Fenestrate Asteraceae	Low Spine Asteraceae
0							5		
2.5							5		4
3.25							1		
3.5							7		
3.75							9		
4							2		1
4.25							3		
4.5							4		1
4.75							2		
5							1		
5.25							7		
5.5							3	1	
5.75		1					3		1
6		1				1	8		1
6.25		4		1			24		
6.5				1			16		1
6.75		1					8		
7							10		2
7.25		1					11		3
7.5	1	3					2		2
7.75							13		2
8					1		5		3
8.25							5		
8.5							6		1
9		1					8		
9.25		1					5		1
9.5							5		1
10		1					11		2
10.5		2					26		1
11		1					13		2
11.5		1					15		1
12							19		1
12.5							8		2
13				1			9		
13.5							10		
14			2	1			8		1
14.5							13		
15							23		2
15.5		1	2				2	1	1
16							9		1
16.5		1				1	16	1	
17							7		3
17.5							6		2
18		2					13		1
18.5		2					24		3
19		2					15		
19.5							24		2
20		1			2		11		1
21		2					26		7
22		2			2		17		10
23						1	18		5
24		4					46		1

Raw Pollen Data										
Top Depth (cm)	High Spine Asteraceae	Saxifraga sp.	Epilobium latifolium	Apiaceae	Fragaria virginiana	Dryas	Rosaceae Undiff.	Oxyria	Polygonaceae Undiff.	
0										
2.5										
3.25										
3.5	1									
3.75										
4										
4.25	1									
4.5								1		
4.75					1					
5										
5.25										
5.5								1		
5.75										
6										
6.25		1			1					
6.5	2							2		
6.75										
7	1	1				1		1		
7.25										
7.5										
7.75										
8	1				3					
8.25					1					
8.5	2									
9										
9.25	4									
9.5										
10	1								3	
10.5	4							1		
11							1			
11.5										
12	1		1		1			1		
12.5	1							1		
13	1									
13.5	2									
14	1								1	
14.5	1	1								
15	2							2		
15.5										
16	1							1		
16.5	2									
17	2									
17.5	2									
18	2									
18.5	4									
19										
19.5	1									
20	2									
21	1									
22	2	2			1		3			
23							1			
24	3									

Raw Pollen Data									
Top Depth (cm)	c.f. Hedysarus	Galium	Brassicaceae Undiff.	Pedicularis	Castilleja	Penstemon	Scrophulariaceae Undiff.	Veronica	Chenopod undiff.
0									1
2.5									
3.25									1
3.5									1
3.75									
4									
4.25									
4.5									1
4.75									
5									
5.25									
5.5									1
5.75									1
6									
6.25				1					
6.5									1
6.75									1
7							1		
7.25									
7.5							1		
7.75	1								
8							1		
8.25									1
8.5						2			
9							1		
9.25									1
9.5				1					1
10							1		
10.5							2		2
11							2		
11.5									1
12									
12.5									
13							1		
13.5								1	1
14							1		1
14.5									1
15		1			1		2	1	2
15.5							1		
16							1		
16.5									2
17									1
17.5									
18							2		1
18.5									1
19						1	1		
19.5								1	
20			1	1			1		
21					8				1
22									
23						1			1
24						1			2

Raw Pollen Data											
Top Depth (cm)	Poaceae	Cyperaceae	Ericad Morph 1	Ericad Morph 2	Ericad Undiff.	Typha	Ulmus	Alder 4Pore	Alder 5Pore	Alder 6Pore	Charcoal 12-36 um
0			1					1	22		440
2.5									29		293
3.25								2	16	1	108
3.5									16	1	993
3.75	1	1						1	24	1	288
4	2							1	18		817
4.25		1						1	15		320
4.5			1					2	15		578
4.75								1	14	1	127
5									11		211
5.25	2								15		648
5.5								1	13		308
5.75		1	1					1	25		276
6	5	2	1					4	37	1	274
6.25	1	1						5	108	1	233
6.5	4							1	98		320
6.75	1								38	1	367
7	2					1	1		91		362
7.25	1							2	78	2	201
7.5	3							2	55	1	460
7.75	3	4						2	69		302
8	4	1						4	64	2	387
8.25	2	1						6	42	2	336
8.5	2							1	26		321
9	1							3	47		499
9.25	3							3	46		418
9.5	3	1	1					5	60		347
10	3		2					1	74	5	689
10.5	5							9	117	2	465
11								3	94		291
11.5	8	1						5	91	2	408
12	2	2	1					8	118	1	361
12.5	2	1	1					2	56		215
13	2								65	2	277
13.5	3		1					8	80	2	152
14	1		1					11	66	2	196
14.5								8	126	4	299
15	5		1					19	211	2	489
15.5	2						1	5	48	2	169
16			1	1				5	66		174
16.5	1							2	66	1	318
17	1							6	82	3	160
17.5		1						1	30		118
18								2	46	2	162
18.5	5	1						7	110	6	156
19	1	1	1					6	105	2	198
19.5	2							13	156	1	182
20	2							6	112		206
21	3	1						16	154	5	288
22	3	3						9	191	3	274
23	1			1				6	127	3	67
24	3		1					10	172	5	253

Raw Pollen Data									
Top Depth (cm)	Char 36-72 um	Char >72um	Stomata c.f. Abies	Stomata c.f. Picea	Stomata Pinaceae Undiff.	Monolete	Trilete	Lycopodia	Concealed Unidentified
0	162	175				2	6		9
2.5	124	188				1	5		9
3.25	43	56				2			7
3.5	231	256			8	5	2		9
3.75	114	104			1	3	4		4
4	285	207				2	1		6
4.25	115	144			2				10
4.5	204	245				1	4		4
4.75	84	99				1	1		5
5	133	192		2			2		12
5.25	114	177		2	1	2	2		5
5.5	117	194		1	1	4	9	2	3
5.75	84	137				2			10
6	120	158				3	1		4
6.25	126	147				2	4	1	8
6.5	153	163	1		1	11	33		10
6.75	110	109				1			4
7	138	119			1	4	4		8
7.25	70	74				6	5		4
7.5	157	94			1	3			4
7.75	78	82				6	2		5
8	110	75		4		6	5	1	10
8.25	100	74				6	3		7
8.5	125	101				3	1		5
9	112	117	2				1		6
9.25	118	159		3		8	3	2	3
9.5	87	92		1		6	2		2
10	134	81		2		13	1		1
10.5	110	94				12	3		7
11	80	111				21	2		13
11.5	120	69				15	4		8
12	142	93			4	5	2		2
12.5	64	107			1	2	2		12
13	89	120			1	9	2	1	19
13.5	76	73			2	6	2		13
14	53	52				4	2	1	2
14.5	83	65				8	4		8
15	131	150				10	3		11
15.5	77	53				7	1		24
16	42	52				8			3
16.5	101	169		2		1	3		10
17	89	126			1	10	3		13
17.5	57	62				1			4
18	72	83			1	4	2	1	19
18.5	57	62			5	9	3		19
19	56	77				6	3		11
19.5	102	97				8	1		11
20	75	48				8	4	1	7
21	95	102				12	3		18
22	84	72		2		9	3		4
23	31	57				3			31
24	112	128				3	3		27

Raw Pollen Data			
Top Depth (cm)	Crumpled Unidentified	Torn Unidentified	Degraded Unidentified
0	2	1	1
2.5	2	4	2
3.25	4	2	
3.5	4	2	
3.75	4	10	2
4	3	1	
4.25	5		
4.5	7	5	2
4.75	6		
5	4	2	
5.25	2		
5.5	1	2	
5.75	6	5	3
6	4	2	
6.25	8	10	6
6.5	9	2	2
6.75	4	1	
7	6	10	3
7.25	3	1	
7.5	8	5	2
7.75	5	3	1
8	12	4	
8.25	2	3	
8.5	5	2	
9	4	5	1
9.25	3		
9.5	2	1	
10	3	1	
10.5	6	2	
11	4	3	
11.5	9	2	
12	4	2	
12.5	7	3	
13	2		
13.5	5	2	
14	3		
14.5	10	4	
15	21	2	3
15.5	6		2
16	6		
16.5	1	1	
17	5	1	
17.5			1
18	4		
18.5	3		
19	5	1	2
19.5	1	5	1
20	3	1	
21	5		
22	6	2	
23	6	3	3
24	6		3

3) Sentinel Lake, freeze-dried samples and deterioration categories

FREEZEDRIED SAMPLES RAW NUMBERS, Sentinel Lake, Core 2													
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
5.5	5.75	Spike	711										
5.5	5.75	Pine	220	1	14			28	67	114	110	224	3
5.5	5.75	Spruce	48		5			22	12	12	39	51	
5.5	5.75	Fir	11					3	1	7	4	11	
5.5	5.75	Alder	28	1	18	0	1	2	0		22	22	7
5.5	5.75	Juniper	1		1	1					2	2	
5.5	5.75	Asteraceae Low Spine	1		1						1	1	
5.5	5.75	Asteraceae Artemisia	5		1	1					2	2	3
5.5	5.75	Asteraceae Undiff.	6	0	2	1	0	0	0		3	3	3
5.5	5.75	Cyperaceae Carex	1		1			1			2	2	
5.5	5.75	Chenopodiaceae / Amar.	1		1						1	1	
5.5	5.75	Poaceae	1		1						1	1	
5.5	5.75	Ranunculaceae	2	0	0	0	0	0	0		0	0	2
5.5	5.75	Rosaceae	1	0	0	0	0	0	0		0	0	1
5.5	5.75	Pollen	320	2	43	2	1	56	80	133	184	317	16
5.5	5.75	Monolete	4								0	0	
5.5	5.75	Trilete	2								0	0	
5.5	5.75	Lycopodiaceae Lycopodium	4								0	0	
5.5	5.75	Spores	10								0	0	
5.5	5.75	Indet Concealed	2								0	0	
5.5	5.75	Indet Crumpled	6								0	0	
5.5	5.75	Indet Torn	3								0	0	
												0	
9.5	9.75	Spike	167									0	
9.5	9.75	Pine	238.5	4	23			58	63	95.5	148	243.5	6
9.5	9.75	Spruce	65.5		6			23	16	20.5	45	65.5	
9.5	9.75	Fir	21	1				8		12	9	21	1
9.5	9.75	Pinaceae Tsuga	1		1						1	1	
9.5	9.75	Alder	14	1	7	0	1	1	0		10	10	4
9.5	9.75	Asteraceae Fenestrate	1								0	0	1
9.5	9.75	Asteraceae High Spine	1								0	0	1
9.5	9.75	Asteraceae Low Spine	1								0	0	1
9.5	9.75	Asteraceae Artemisia	4					1			1	1	3
9.5	9.75	Poaceae	2		2						2	2	
9.5	9.75	Rosaceae Undiff	1		1						1	1	
9.5	9.75	Pollen	350	6	40	0	1	91	79	128	217	345	17
9.5	9.75	Monolete	4								0	0	
9.5	9.75	Trilete	5								0	0	
9.5	9.75	Lycopodiaceae Lycopodium	7								0	0	
9.5	9.75	Spores	16								0	0	
9.5	9.75	Indet Concealed	5								0	0	
9.5	9.75	Indet Crumpled	7								0	0	
9.5	9.75	Indet Corroded / Degraded									0	0	
9.5	9.75	Indet Torn	3								0	0	
12.5	13	Spike	91								0	0	
12.5	13	Pine	496.5	17	42	3		62	187	125.5	311	436.5	36
12.5	13	Spruce	77		12		1	25	38	14	76	90	2
12.5	13	Fir	50		2		1	14	2	12	19	31	4

Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
12.5	13	Alder	33	2	27	1	0	0	0		30	30	3
12.5	13	Asteraceae	2	0	0	0	0	0	0		0	0	2
12.5	13	Cyperaceae Carex	5		2			3			5	5	
12.5	13	Chenopodiaceae / Amar.	1		1						1	1	
12.5	13	Poaceae	3		3						3	3	
12.5	13	Pollen	667.5	19	89	4	2	104	227	151.5	445	596.5	47
12.5	13	Monolete	14								0	0	
12.5	13	Trilete	11								0	0	
12.5	13	Lycopodiaceae Lycopodium	1								0	0	
12.5	13	Spores	27								0	0	
12.5	13	Indet Concealed	6								0	0	
12.5	13	Indet Crumpled	12								0	0	
12.5	13	Indet Corroded / Degraded	3								0	0	
12.5	13	Indet Torn	3								0	0	
											0		
14	14.5	Spike	135								0	0	
14	14.5	Pine	532	11	45	1		70	179	174	306	480	36
14	14.5	Spruce	88		10	1		25	28	25	64	89	4
14	14.5	Fir	25			1		8	9	5	18	23	2
14	14.5	Pinaceae Tsuga	3		1	1					2	2	1
14	14.5	Salicaceae Poplar	1		1			1			2	2	
14	14.5	Alder	43	1	33	2	0	0	0		36	36	8
14	14.5	Asteraceae Artemisia	9	0	0	0	0	1	0		1	1	6
14	14.5	Cyperaceae	3								0	0	3
14	14.5	Chenopodiaceae / Amar.	1		1						1	1	
14	14.5	Ericad	1	0	0	0	0	0	0		0	0	1
14	14.5	Polygonaceae Rumex	1		1						1	1	
14	14.5	Ranunculaceae Caltha	2		2						2	2	
14	14.5	Rosaceae Undiff	2								0	0	2
14	14.5	Rosaceae cf Fragaria	2		2						2	2	
14	14.5	Pollen	713	12	96	6	0	105	216	204	435	639	63
14	14.5	Monolete	33								0	0	
14	14.5	Trilete	14								0	0	
14	14.5	Lycopodiaceae Lycopodium	5								0	0	
14	14.5	Spores	53								0	0	
14	14.5	Indet Concealed	4								0	0	
14	14.5	Indet Crumpled	10								0	0	
14	14.5	Indet Corroded / Degraded	1								0	0	
14	14.5	Indet Torn	2								0	0	
14	14.5	Indetermined	17								0	0	
15	15.5	Spike	144								0	0	
15	15.5	Pine	340.5	11	32		1	85	99	87.5	228	315.5	15
15	15.5	Spruce	87	1	8	3		35	27	23	74	97	1
15	15.5	Fir	27		1			13	5	8	19	27	1
15	15.5	Pinaceae Tsuga	2				1	1			2	2	
15	15.5	Alder	32	9	13	1	1	0	0		24	24	12
15	15.5	Salicaceae Salix	1								0	0	1
15	15.5	Asteraceae High Spine	1		1						1	1	
15	15.5	Asteraceae Artemisia	2								0	0	2

15	15.5	Cyperaceae Carex	1				1				1	1	
15	15.5	Chenopodiaceae / Amar.	1		1						1	1	
15	15.5	Poaceae	3		3						3	3	
15	15.5	Ranunculaceae Thalictrum	1		1						1	1	
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
15	15.5	Pollen	498.5	21	60	4	4	134	131	118.5	354	472.5	32
15	15.5	Monolete	8								0	0	
15	15.5	Trilete	8								0	0	
15	15.5	Lycopodiaceae Lycopodium									0	0	
15	15.5	Spores	18								0	0	
15	15.5	Indet Concealed	4								0	0	
15	15.5	Indet Crumpled	9								0	0	
15	15.5	Indet Corroded / Degraded	6								0	0	
15	15.5	Indet Torn	3								0	0	
15	15.5	Indetermined	22								0	0	
											0	0	
17	17.5	Spike	237								0	0	
17	17.5	Pine	623	14	3	36	3	103	177	278	336	614	21
17	17.5	Spruce	100		12	2	1	46	38	0	99	99	2
17	17.5	Fir	64					10	15	32	25	57	6
17	17.5	Pinaceae Tsuga	2		2						2	2	
17	17.5	Alder	46	0	25	0	1	1	0		27	27	18
17	17.5	Betula	1								0	0	1
17	17.5	Asteraceae Low Spine	2								0	0	2
17	17.5	Asteraceae Artemisia	6								0	0	6
17	17.5	Cyperaceae Carex	5		1			2			3	3	2
17	17.5	Chenopodiaceae / Amar.	2		2						2	2	
17	17.5	Poaceae	4		3			1			4	4	
17	17.5	Ranunculaceae Undiff	1					1			1	1	
17	17.5	Pollen	856	14	48	38	5	164	230	310	499	809	58
17	17.5	Monolete	22								0	0	
17	17.5	Trilete	17								0	0	
17	17.5	Lycopodiaceae Lycopodium	8								0	0	
17	17.5	Spores	54								0	0	
17	17.5	Indet Concealed	4								0	0	
17	17.5	Indet Crumpled	7								0	0	
17	17.5	Indet Corroded / Degraded	1								0	0	
17	17.5	Indet Torn									0	0	
											0	0	
18.5	19	Spike	86								0	0	
18.5	19	Pine	408	7	46	2	3	49	136	155	243	398	23
18.5	19	Spruce	85.5	3	12	1	1	27	30	19.5	74	93.5	1
18.5	19	Fir	23.5		1		1	8	3	5.5	13	18.5	2
18.5	19	Pinaceae Tsuga	1		1						1	1	
18.5	19	Salicaceae Populus	1	1	1						2	2	
18.5	19	Alder	35	4	16	2	0	1	0		23	23	18
18.5	19	Salicaceae Salix	1								0	0	1
18.5	19	Asteraceae Ambrosia	1								0	0	1
18.5	19	Asteraceae Artemisia	5								0	0	5
18.5	19	Cyperaceae	1		1			1			2	2	
18.5	19	Chenopodiaceae / Amar.	1		1						1	1	

18.5	19	Poaceae	2		2					2	2	
18.5	19	Ranunculaceae Undiff	1							0	0	1
18.5	19	Rosaceae Undiff.	1							0	0	1
18.5	19	Pollen	567	15	81	5	5	86	169	180	361	541	53
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
18.5	19	Monolete	14								0	0	
18.5	19	Trilete	6								0	0	
18.5	19	Lycopodiaceae Lycopodium	1								0	0	
18.5	19	Spores	22								0	0	
18.5	19	Indet Concealed	8								0	0	
18.5	19	Indet Crumpled	5								0	0	
18.5	19	Indet Corroded / Degraded									0	0	
18.5	19	Indet Torn									0	0	
23	24	Spike	83								0	0	
23	24	Pine	378.5	44	59			42	139	109.5	284	393.5	16
23	24	Spruce	102.5	4	18	2		27	43	18.5	94	112.5	3
23	24	Fir	18	2	4	1		6	3	4	16	20	1
23	24	Salicaceae Poplar	1					1			1	1	
23	24	Alder	14	7	5	0	0	0	0		12	12	4
23	24	Asteraceae High Spine	2	1							1	1	1
23	24	Asteraceae Artemisia	5				1				1	1	4
23	24	Cyperaceae	1				1				1	1	
23	24	Chenopodiaceae / Amar.	1								0	0	1
23	24	Poaceae	3	1	1						2	2	
23	24	Ranunculaceae Undiff	1		1						1	1	
23	24	Scrophulariaceae Castilleja	2	1							1	1	1
23	24	Pollen	541	66	93	3	2	76	185	132	425	557	34
23	24	Monolete	5								0	0	
23	24	Trilete	8								0	0	
23	24	Lycopodiaceae Lycopodium	1								0	0	
23	24	Spores	14								0	0	
23	24	Indet Concealed	1								0	0	
23	24	Indet Crumpled	2								0	0	
23	24	Indet Corroded / Degraded	4								0	0	
29	30	Spike	22								0	0	
29	30	Pine	130.5	20	19	4	2	16	16	53.5	77	130.5	10
29	30	Spruce	48		13	3	3	7	7	13	33	46	7
29	30	Fir	3.5			1		1	1	0.5	3	3.5	
29	30	Alder	9	7	3	0	0	0	0	0	10	10	1
29	30	Poaceae	2		2			1			3	3	
29	30	Polygonaceae Oxyria	1			1					1	1	
29	30	Pollen	216	27	37	9	5	25	24	67	127	194	18
29	30	Trilete	2								0	0	
29	30	Lycopodiaceae Lycopodium	1								0	0	
29	30	Spores	3								0	0	
29	30	Indet Concealed	18								0	0	
29	30	Indet Crumpled									0	0	
29	30	Indet Corroded / Degraded	2								0	0	
29	30	Indet Torn	3								0	0	

32	33	Spike	65								0	0	
32	33	Pine	355.5	22	34	2	1	55	106	141.5	220	361.5	15
32	33	Spruce	103	1	12	3	2	36	15	36	69	105	2
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
32	33	Fir	8.5			1		1	2	4.5	4	8.5	
32	33	Pinaceae Tsuga	3	1		1	2				4	4	
32	33	Alder	39	20	18	2	0	0	0	0	40	40	12
32	33	Asteraceae High Spine	1			1					1	1	
32	33	Asteraceae Low Spine									0	0	
32	33	Asteraceae Artemisia	3			1					1	1	2
32	33	Cyperaceae	2			2					2	2	
32	33	Chenopodiaceae / Amar.	1								0	0	1
32	33	Ericad	3								0	0	3
32	33	Poaceae	5	1	5	1					7	7	
32	33	Pollen	524	45	69	14	5	92	123	182	348	530	35
32	33	Monolete	10								0	0	
32	33	Trilete	6								0	0	
32	33	Lycopodiaceae Lycopodium	1								0	0	
32	33	Spores	22								0	0	
32	33	Indet Concealed	2								0	0	
32	33	Indet Crumpled	3								0	0	
32	33	Indet Corroded / Degraded									0	0	
32	33	Indet Torn	2								0	0	
											0	0	

4) Sentinel Lake, frozen samples and deterioration categories

FROZEN SAMPLES RAW NUMBERS, Sentinel Lake, Core 2													
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
5.5	5.75	Spike	595								0	0	
5.5	5.75	Pine	197	4	12	1		36	41	97	94	191	8
5.5	5.75	Spruce	28.5		1			12	1	13.5	14	27.5	
5.5	5.75	Fir	9.5					4	1	2.5	5	7.5	1
5.5	5.75	Alder	26	8	8	0	0	1	0		17	17	5
5.5	5.75	Asteraceae Artemisia	1								0		
5.5	5.75	Cyperaceae	1					1			1	1	
5.5	5.75	Chenopodiaceae/Amar.	1					1			1	1	
5.5	5.75	Poaceae	2		1						1		
5.5	5.75	Pollen	267	12	22	1	0	55	43	113	133	246	15
5.5	5.75	Monolete	3								0	0	
5.5	5.75	Trilete	8								0	0	
5.5	5.75	Lycopodiaceae Lycopodiur	9								0	0	
5.5	5.75	Spores	20								0	0	
5.5	5.75	Indet Concealed	8								0	0	
5.5	5.75	Indet Crumpled	9								0	0	
5.5	5.75	Indet Corroded / Degraded									0	0	
5.5	5.75	Indet Torn	2								0	0	
9.5	9.75	Spike	190								0	0	
9.5	9.75	Pine	220	5	15	2	1	53	55	82	131	213	12
9.5	9.75	Spruce	30.5		2	1	3	13	7	6.5	26	32.5	
9.5	9.75	Fir	6.5		1			2	3	0.5	6	6.5	
9.5	9.75	Pinaceae Tsuga	1		1			1			2	2	
9.5	9.75	Alder	29	3	19	0	0	0	0		22	22	7
9.5	9.75	Asteraceae Low Spine	1				1				1	1	
9.5	9.75	Asteraceae Artemisia	6		2		1				3	3	4
9.5	9.75	Cyperaceae	7		1		1	1			3	3	4
9.5	9.75	Chenopodiaceae / Amar.	1								0	0	1
9.5	9.75	Poaceae	2		2						2	2	
9.5	9.75	Polygonaceae Oxyria	1								0	0	1
9.5	9.75	Ranunculaceae Anemone	2					1			1	1	1
9.5	9.75	Pollen	307	8	43	3	7	71	65	89	197	286	30
9.5	9.75	Monolete	12								0	0	
9.5	9.75	Trilete	12								0	0	
9.5	9.75	Lycopodiaceae Lycopodiur	9								0	0	
9.5	9.75	Spores	35								0	0	
9.5	9.75	Indet Concealed	6								0	0	
9.5	9.75	Indet Crumpled	3								0	0	
9.5	9.75	Indet Corroded / Degraded	1								0	0	
9.5	9.75	Indet Torn	2								0	0	
12.5	13	Spike	156								0	0	
12.5	13	Pine	524	36	64	4	2	83	174	150	363	513	18
12.5	13	Spruce	46	1	7			17	12	13	37	50	
12.5	13	Fir	36.5	1	1			10	15	5.5	27	32.5	4
12.5	13	Pinaceae Tsuga	3		2						2	2	1
12.5	13	Alder	41	5	16	2	0	0	0		23	23	19
12.5	13	Asteraceae High Spine	1								0	0	1
12.5	13	Asteraceae Low Spine	1								0	0	1

Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
12.5	13	Asteraceae Ambrosia	1		1						1	1	
12.5	13	Asteraceae Artemisia	6								0	0	6
12.5	13	Cyperaceae	1					1			1	1	
12.5	13	Poaceae	6		5			1			6	6	
12.5	13	Rubiaceae cf Galium	1					1			1	1	
12.5	13	Scrophulariaceae Undiff	1								0	0	1
12.5	13	Pollen	668.5	43	96	6	2	113	201	168.5	461	629.5	51
12.5	13	Monolete	20								0	0	
12.5	13	Trilete	5								0	0	
12.5	13	Spores	28								0	0	
12.5	13	Indet Concealed	6								0	0	
12.5	13	Indet Crumpled	6								0	0	
12.5	13	Indet Corroded / Degraded	3								0	0	
12.5	13	Indet Torn	2								0	0	
14	14.5	Spike	148								0	0	
14	14.5	Pine	603.5	21	62	2	1	71	199	222.5	356	578.5	35
14	14.5	Spruce	38	2	6	2		20	8	10	38	48	1
14	14.5	Fir	17.5					3	7	5.5	10	15.5	2
14	14.5	Pinaceae Tsuga	2			1	1				2	2	
14	14.5	Alder	42	16	23	0	1	0	0		40	40	9
14	14.5	Betulaceae	1		1						1	1	
14	14.5	Asteraceae Fenestrate	1								0	0	1
14	14.5	Asteraceae High Spine	2								0	0	2
14	14.5	Asteraceae Artemisia	5		1			2			3	3	3
14	14.5	Cyperaceae	2		1						1	1	1
14	14.5	Poaceae	5		5						5	5	
14	14.5	Rosaceae Undiff	1								0	0	1
14	14.5	Rosaceae Type 6	1								0	0	1
14	14.5	Scrophulariaceae Undiff	1								0	0	1
14	14.5	Pollen	722	39	99	5	3	96	214	238	456	694	57
14	14.5	Monolete	15								0	0	
14	14.5	Trilete	4								0	0	
14	14.5	Spores	19								0	0	
14	14.5	Indet Concealed	9								0	0	
14	14.5	Indet Crumpled	5								0	0	
14	14.5	Indet Corroded / Degraded	5								0	0	
14	14.5	Indet Torn	2								0	0	
											0	0	
15	15.5	Spike	139										
15	15.5	Pine	321	25	42	4	2	45	127	63	245	308	35
15	15.5	Spruce	57	3	6	2	1	25	19	7	56	63	1
15	15.5	Fir	9.5					8		1.5	8	9.5	
15	15.5	Pinaceae Undiff.	2	2							2	2	
15	15.5	Alder	24	5	13	1	0	0	0		19	19	9
15	15.5	Salicaceae Salix	1								0	0	1
15	15.5	Chenopodiaceae / Amar.	1								0	0	1
15	15.5	Poaceae	4		4						4	4	
15	15.5	Rosaceae Type 6	1								0	0	1
15	15.5	Scrophulariaceae Castilleja	1								0	0	1
15	15.5	Herbaceous	12	0	5	0	0	1	0	0	6	6	5

15	15.5	Pollen	426.5	35	66	7	3	79	146	71.5	336	407.5	51
15	15.5	Monolete	8								0	0	
15	15.5	Trilete	5								0	0	
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
15	15.5	Lycopodiaceae Lycopodiun	2								0	0	
15	15.5	Spores	15								0	0	
15	15.5	Indet Concealed	4								0	0	
15	15.5	Indet Crumpled	1								0	0	
15	15.5	Indet Corroded / Degraded	3								0	0	
17	17.5	Spike	199								0	0	
17	17.5	Pine	646	17	41	1	1	96	236	213	392	605	26
17	17.5	Spruce	115		8	1		43	40	22	92	114	1
17	17.5	Fir	54.5		2			12	16	20.5	30	50.5	3
17	17.5	Pinaceae Tsuga	3		3						3	3	
17	17.5	Alder	30	8	10	0	0	1	0		19	19	9
17	17.5	Salicaceae Salix	1		1						1	1	
17	17.5	Woody Shrub	31	8	11	0	0	1	0		20	20	9
17	17.5	Asteraceae Artemisia	5				1				1	1	4
17	17.5	Cyperaceae	1		1			1			2	2	
17	17.5	Chenopodiaceae / Amar.	1		1						1	1	
17	17.5	Poaceae	1		1						1	1	
17	17.5	Pollen	857.5	25	68	2	2	153	292	255.5	542	797.5	43
17	17.5	Monolete	10								0	0	
17	17.5	Trilete	9								0	0	
17	17.5	Spores	20								0	0	
17	17.5	Indet Concealed	9								0	0	
17	17.5	Indet Crumpled	5								0	0	
17	17.5	Indet Corroded / Degraded	2								0	0	
17	17.5	Indet Torn	1								0	0	
18.5	19	Spike	156								0	0	
18.5	19	Pine	389	40	31	4	2	84	88	136	249	385	31
18.5	19	Spruce	96.5	5	17	3		33	28	20.5	86	106.5	4
18.5	19	Fir	25.5	2	4	1	1	10	6	4.5	24	28.5	
18.5	19	Alder	25	12	10	1	0	2	0		25	25	6
18.5	19	Asteraceae Artemisia	8		1		2				3	3	6
18.5	19	Poaceae	3	2	3						5	5	
18.5	19	Oxyria Scroph	1								0	0	1
18.5	19	Ranunculaceae Undiff.	2		2						2	2	
18.5	19	Herbaceous	14	2	6	0	2	0	0	0	10	10	7
18.5	19	Pollen	550	61	68	9	5	129	122	161	394	555	48
18.5	19	Monolete	4								0	0	
18.5	19	Trilete	5								0	0	
18.5	19	Lycopodiaceae Lycopodiun	2								0	0	
18.5	19	Spores	14								0	0	
18.5	19	Indet Concealed	9								0	0	
18.5	19	Indet Crumpled	2								0	0	
18.5	19	Indet Corroded / Degraded	5								0	0	
18.5	19	Indet Torn	1								0	0	
23	24	Spike	160								0	0	

23	24	Pine	335	12	31	1	1	76	75	131	196	327	11
23	24	Spruce	105.5	1	20	4		49	12	29.5	86	115.5	2
23	24	Fir	36		4			12	7	14	23	37	
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
23	24	Pinaceae Tsuga	2			1		1			2	2	
23	24	Alder	21	4	11	2	0	4	0		21	21	5
23	24	Salicaceae Salix	1								0	0	1
23	24	Asteraceae High Spine	2								0	0	2
23	24	Asteraceae Low Spine	2					1			1	1	1
23	24	Asteraceae Artemisia	2								0	0	2
23	24	Cyperaceae	3					3			3	3	
23	24	Chenopodiaceae / Amar.	4		2			1			3	3	1
23	24	Poaceae	8	1	7						8	8	
23	24	Pollen	521.5	18	75	8	1	147	94	174.5	343	517.5	25
23	24	Monolete	11								0	0	
23	24	Trilete	4								0	0	
23	24	Lycopodiaceae Lycopodiun	1								0	0	
23	24	Spores	19								0	0	
23	24	Indet Concealed	13								0	0	
23	24	Indet Crumpled	2								0	0	
23	24	Indet Corroded / Degraded	3								0	0	
23	24	Indet Torn	1								0	0	
											0	0	
											0	0	
29	30	Spike	50								0	0	
29	30	Pine	186	54	19	2	1	18	57	64	151	215	11
29	30	Spruce	42.5	11	7		1	7	21	4.5	47	51.5	2
29	30	Fir	15	1	1		1	4	5	3	12	15	2
29	30	Alder	18	15	1	0	0	0	0		16	16	4
29	30	Asteraceae Artemisia	1								0	0	1
29	30	Cyperaceae	1				1				1	1	
29	30	Chenopodiaceae / Amar.	1	2							2	2	
29	30	Ranunculaceae Thalictrum	1								0	0	
29	30	Ranuncluaceae Type 5	1					1			1	1	
29	30	Pollen	266.5	83	28	2	4	29	83	71.5	229	300.5	20
29	30	Monolete	3								0	0	
29	30	Trilete	2								0	0	
29	30	Lycopodiaceae Lycopodiun	1								0	0	
29	30	Spores	7								0	0	
29	30	Indet Concealed	10								0	0	
29	30	Indet Crumpled	2								0	0	
29	30	Indet Corroded / Degraded	4								0	0	
29	30	Indet Torn									0	0	
32	33	Spike	134								0	0	
32	33	Pine	390	11	19	2	4	70	100	155	206	361	19
32	33	Spruce	73.5		5	3		25	17	20.5	50	70.5	1
32	33	Fir	32		1	1		13	3	9	18	27	5
32	33	Pinaceae Tsuga	2	1							1	1	1
32	33	Alder	32	16	13	2	0	1	0		32	32	9
32	33	Asteraceae High Spine	1		1						1	1	
32	33	Asteraceae Low Spine	2								0	0	2

32	33	Asteraceae Artemisia	3		2			2			4	4	
32	33	Ranunculaceae Undiff	1		1						1	1	
32	33	Pollen	536.5	28	42	8	4	111	120	184.5	313	497.5	37
Section Top (cm)	Section Bottom (cm)	Family/Genus	Sum	D1	D2	D3	D4	D5	D6	D7	Sum D1-D6	Sum D1-D7	D8
32	33	Monolete	14								0	0	
32	33	Trilete	11								0	0	
32	33	Spores	25								0	0	
32	33	Indet Concealed	9								0	0	
32	33	Indet Crumpled	5								0	0	
32	33	Indet Corroded / Degraded	1								0	0	
32	33	Indet Torn	4								0	0	
											0	0	