

Holocene Ecosystem Dynamics of a Central Vancouver Island Wetland:  
Development, Vegetation Change, and Carbon Accumulation

by

Kyle Beer  
B.Sc, University of Victoria, 2015

A Thesis Submitted in Partial Fulfillment  
of the Requirements for the Degree of

MASTER OF SCIENCE

in the Department of Biology

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## **Supervisory Committee**

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Dr. Terri Lacourse, Department of Biology  
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Dr. Joseph Antos, Department of Biology  
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## Abstract

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A multi-proxy paleoecological study that included pollen, microfossil, carbon (C), and nitrogen (N) analyses was conducted at a central Vancouver Island wetland near Courtenay British Columbia to reconstruct the site's history, C and N accumulation rates, and surrounding vegetation over the last 14,000 years. The paleoecological record shows that the lake that occupies the southeast corner of the wetland today was much larger during the late glacial period. Peat accumulation began through terrestrialization of the site, leading to vegetation and edaphic conditions characteristic of a bog or fen with variable water table depth inferred from testate amoebae and other microfossil remains. C accumulated with maximum and time-weighted mean accumulation rates of 81 and 19 g C/m<sup>2</sup>/cal yr, respectively. The highest C accumulation occurred during the accumulation of herbaceous peat in the early Holocene, which, given the similarity to other Northern Hemisphere peatlands, suggests a strong climate forcing of C accumulation. N accumulated with a time-weighted mean of 0.55 g N/m<sup>2</sup>/cal yr. Forest community composition was also affected by the changing climate. *Pinus contorta* dominated open forests near the site between at least 13,900 and 11,200 cal yr BP. *Picea* and *Abies* increased during Younger Dryas cooling (12,900-11,700 cal yr BP). *Pseudotsuga menziesii* was the most abundant tree species in the area during the early Holocene

(11,200-7500 cal yr BP). Around 7000 cal yr BP there was a shift to *Tsuga heterophylla* dominated forest, which continues to the present. This multi-proxy 14,000-year record provides evidence of the importance of climate and local factors in bog development, C and N accumulation, and vegetation history since the last glaciation.

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## **Introduction**

### **Peatlands**

Peat is material of at least 30% organic matter formed predominantly by incompletely decomposed plant remains (Joosten and Clarke, 2002). The organic material may come from any plant type but is often composed of sedges or mosses as they tolerate the high water tables present in wetlands. Peatlands are ecosystems where organic deposits have accumulated to a depth greater than 40 cm (National Wetlands Working Group, 1997) and fall into three categories (i.e., bogs, fens, and swamps), which are differentiated primarily based on their hydrology and hydrochemistry. Northern peatlands are most often either fens, which are fed at least partially by ground water or surface runoff, or bogs, which receive water almost exclusively through precipitation. The characteristic in common to all peatlands is that production from plants exceeds decomposition at and below the surface. This imbalance is caused more by incomplete decomposition than by high primary productivity (Laiho, 2006). Surface vegetation and climate may help to accelerate or slow succession between wetland categories (Belyea, 2009).

Peatlands cover about 3% of Earth's land area (3.2 M km<sup>2</sup>) and are most abundant in the Northern Hemisphere (Loisel et al., 2017), generally in wet areas or those with high precipitation. Peatlands form on sloping or flat terrain along maritime coastlines and in continental interiors as long as plant productivity exceeds decomposition. The differing conditions drive a varying rate of primary production and organic matter accumulation. Peatlands do not necessarily have high precipitation if water loss is sufficiently slow.

Cold temperatures at continental and northern sites balance the shorter growing season by reducing decomposition during the winter. Increases in temperature and/or growing season at these sites will directly increase the primary production of the peatland (Charman et al., 2013).

Peatland formation is a result of the interaction between plant species and the abiotic environment. Given high water saturation, peatlands form through one of three general processes: (1) terrestrialization, (2) paludification, and (3) primary peat formation (Rydin and Jeglum, 2013). Terrestrialization (infilling) occurs when peat forms at the edges of streams or lake basins. This process may include floating mats of vegetation that extend across the water's surface or organic accumulation near margins, extending the wetland surface into lacustrine or fluvial environments until the aquatic environment is completely infilled. Paludification is the development of a peatland on previously drier sites. Paludification may occur either as peatlands spread through a raising of the water table or by pedogenic processes that decrease the permeability of the soil and drown out established vegetation (Rydin and Jeglum, 2013). Primary peat formation occurs as peat-forming plants become established on soils previously devoid of vegetation on poorly drained and wet sites.

The development of wetland ecosystems generally follows a trend toward more terrestrial environments. Vegetation communities are often similar among coastal British Columbia wetlands, which suggests that plant succession is as important as climate in bog development (Hebda, 1977). Wetland expansion often occurs as a combination of the above three formation processes simultaneously (Rydin and Jeglum, 2013). The spread of shrubs and sedges facilitates paludification along the wetland margins (Hebda, 1977).

Though transition between swamps/marsh, fens, and bogs often occur in that order, reversions are possible given significant changes to site hydrology, vegetation, climate, or disturbance (Belyea, 2009; Rydin and Jeglum, 2013).

Change in wetland vegetation to plants with different ecological requirements suggests a change in the surrounding physical environmental. During terrestrialization, limnic peat forms below the water level as organic material settles to the bottom of standing water in shallow water marshes/swamps or along lake margins (Faegri and Iverson, 1975; National Wetlands Working Group, 1997; Rydin and Jeglum, 2013). Swamp or marsh-like margins are high in plant nutrients with vegetation often characterized by aquatic plants (e.g. *Typha*, *Nuphar*) and shrubs (e.g. *Myrica*, *Spiraea*) (Rydin and Jeglum, 2013). Peat formation in this setting gradually decreases the local relative water depth as material accumulates. When the level of peat exceeds the water level, conditions for peat forming sedges are met and the environment may transition to a fen-like ecosystem. If enough peat accumulates to separate the wetland surface from mineral water, a rapid transition to ombrotrophic plant assemblages may occur (Belyea, 2009).

Though the general pattern of development can be similar between maritime and continental peatlands, peat accumulation rates generally differ. In contrast to continental sites, maritime peatlands generally have longer or even year-round plant growth as a result of an oceanic climate, leading to higher total productivity. However, since microbial activity in maritime peatlands is less limited by cold winters, these ecosystems also have year-round decomposition. The more consistent temperature means that coastal wetlands accumulate peat at a lower rate compared to more seasonal continental or arctic

sites (Asada and Warner, 2005). Regardless of location however, peatlands store vast amounts of carbon that is of significance to global climate and the carbon cycle (Loisel et al., 2014).

### **Climate, Peatlands, and the Carbon Cycle**

Global temperatures are closely linked to concentrations of both CO<sub>2</sub> and CH<sub>4</sub> in the atmosphere (Petit et al., 1999). Anthropogenic carbon (C) transfer to the atmosphere from land use changes and the combustion of fossil fuels contributes significantly to the global C budget. As global temperature increases there is a chemical and vegetation response that may provide a stabilizing (if C sink strength increases) or destabilizing effect on temperature (if C sinks change to net sources). Overall peatland response to climate change is weakly understood as it depends on temperature, insolation, and precipitation. These affect peatland productivity and ultimately their ability to sequester and store C due to growth and decomposition rate changes (Charman et al., 2013; Rydin and Jeglum, 2013; Yu, 2006).

Much of the C fixed by plants in terrestrial ecosystems is stored aboveground in living tissue, with a smaller fraction input directly into the soil in the form of root exudates or decomposing biomass. Decomposition and microbial respiration release the majority of this C back into the atmosphere in the form of CO<sub>2</sub> (Trumbore, 2009), though the rate is dependent on specific ecosystem properties and is highly variable. The rate of C sequestration depends on plant growth rates and species longevity but this does not completely explain long-term storage and separation from the active C pool (Torn et al., 2009). Most terrestrial ecosystems store C in living tissue, soils, dead wood and litter;

however, mortality and subsequent decomposition result in low long-term rates of C accumulation (Bridgham et al., 2006). In contrast to other biomes, peatlands store ~98.5% of their C as peat below the surface, with only ~1.5% in the live vegetation (Gorham, 1991) due to near surface anoxic conditions. This provides a key difference between peatlands and most terrestrial ecosystems.

Peatlands interact with the C cycle in a more complex way than simply sequestering C, as they emit both CO<sub>2</sub> and CH<sub>4</sub> as a result of decomposition by bacteria, fungi, and soil invertebrates (Rydin and Jeglum, 2013). Much of the decomposition and therefore emissions occurs in the acrotelm, where aerobic bacteria are most active and C is released primarily as CO<sub>2</sub>. Successive burying results in the plant remains moving to below the water table, where most of the emissions occur as CH<sub>4</sub>. Though the rate of decomposition in the catotelm is low (due to anoxic conditions), most of the peat resides in this layer and so the low rate of decomposition acts across peat generated over millennia, making peatlands a significant global source of CH<sub>4</sub> (Gorham, 1991). The concentration of organic matter and depth of the deposits result in peatlands containing 25-30% of Earth's soil organic C (Bridgham et al., 2006; Gorham, 1991; Loisel et al., 2014; Yu et al., 2010).

Peatland response to anthropogenic climate change has been the focus of much research, which is based on their response to past climate (e.g. Charman et al., 2013; Loisel et al., 2014), simulation studies (e.g. Frey and Smith, 2005), and modern experiments (e.g. Boardman et al., 2011; Silvola et al., 1996). Increased plant growth in some northern peatlands is predicted to balance the increased decay below the surface and result in increased carbon accumulation (Charman et al., 2013). Other climatic

variables besides temperature will likely determine if this will be the case. Hydrological regime is of the utmost importance, as lowering water tables cause an increase in CO<sub>2</sub> release but also controls surface productivity: if summer water tables drop below a threshold many hydrophilic species will be outcompeted by more rapidly growing species (Rydin and Jeglum, 2013). Beyond surface emissions there is an indication that peatlands will transfer increased dissolved organic C into waterways, which will be transferred to the atmosphere from lakes or the ocean surface (Frey and Smith, 2005). Local conditions play a critical role for all these factors and highlight the need for research on wetlands across environmental gradients.

Over the Holocene, boreal and subarctic peatlands have been a small but constant C sink accumulating on average 29 g C/m<sup>2</sup>/yr (Gorham, 1991). Of the global estimated 612 Gt of peatland C, 547 Gt are stored in northern peatlands, which account for 80-90% of the total peatland area (Loisel et al., 2017; Yu et al., 2010). In the Northern Hemisphere the greatest peatland expansion occurred after continental ice sheet retreat; however, total peatland area might have been similar due to wetland expansion onto exposed areas of continental shelves during the last glacial maximum (Kaplan et al., 2006). As eustatic sea level increased to present day, the submergence of those areas was compensated for by ice sheet retreat that exposed continental sites (Gregory, 1978; Kaplan et al., 2006). Rapid expansion of peatlands and accumulation of C is thought to be a result of higher seasonality during the early Holocene that would have increased summer growth while decreasing winter decomposition (Yu et al., 2010, 2014). This trend is relatively consistent despite vegetation differences and highlights the importance of climate in C accumulation.

## **Peatlands as paleoecological records**

Peatlands are particularly useful ecosystems for the study of environmental change as they contain several records that may be used as proxies: (1) fossil pollen, (2) plant macrofossils, (3) carbon and its  $^{13}\text{C}$  isotope, (4) nitrogen and  $^{15}\text{N}$  isotope, (5) testate amoebae, and (6) non-pollen microfossil remains from plants, algae and other organisms. The combination of these proxies allows for the inference of developmental history and provides a detailed record of vegetation and environmental conditions. The diversity of information that can be gained demonstrates the value of multi-proxy peat studies.

Fossil pollen has been used extensively to determine changes in vegetation communities over longer time periods than can be observed directly (e.g. Brown and Hebda, 2002b, 2003; Huntley et al., 2013; Lacourse et al., 2012; Pellatt et al., 2001). Since plant community composition varies along environmental gradients it is also possible to infer past climatic conditions such as temperature and precipitation (e.g. Brown and Hebda, 2002b). The movement and migration of plant species becomes apparent over millennia in response to gradually shifting biotic and abiotic factors. Though fossil pollen analysis is an important tool for reconstructing past vegetation, plants such as conifers produce abundant pollen that is effectively dispersed, often masking the signature of local plants and low pollen producers. This regional pollen signal is amplified when analysis is based on lake sediments as the catchment and lake surface collect a much greater quantity of pollen grains. While still having abundant pollen from regional sources, peatlands have a larger pollen proportion derived from local vegetation. Pollen and spores derived from local plants (e.g. aquatic plants, mosses)

help to determine nearby physical landscape features, such as the amount of standing water, using their environmental requirements.

Plant macrofossils are un-decomposed plant parts that become incorporated into sediment or peat (Warner, 1990b). Macrofossil remains are common in peat and confirm local species presence since they are not often transported long distances. Another advantage of plant macrofossils is that they can often be identified with higher taxonomic resolution than pollen or spores (Warner, 1990b). Plant macrofossils are important in the study of wetland dynamics since they reflect peat composition and provide key information about species dynamics at the local scale.

Carbon content provides a measure of bulk C storage and allows an inference on the rate of CO<sub>2</sub> sequestration. Relating environmental conditions to past C accumulation rates gives information on the relationship between climate and peatland C dynamics. Further, if peat composition is analysed, these records connect local vegetation, climate, and C accumulation. When information from single sites is combined with multiple studies in large scale surveys (e.g. Charman et al., 2013), it is possible to better predict their response to future climate change. Analysis of nitrogen content provides information about nutrient status at the time of deposition. Carbon-nitrogen ratios also reflect general plant community composition (Pendea and Chmura, 2012), changes in hydrology, and relative contributions from algae (Meyers and Teranes, 2001). Lacustrine environments have higher nitrogen accumulation and a lower C:N ratio compared to terrestrial wetlands, due to the contribution of algal material to the organic matter (Meyers and Teranes, 2001). Woody, herbaceous, and moss-dominated peat also differ

substantially in their nitrogen content and C:N ratio, reflecting the attributes of their component plant remains (Loisel et al., 2014).

Non-pollen palynomorphs, including the microfossil remains of testate amoebae are often preserved in peat. Testate amoebae are protozoa that inhabit the surface peat layers where they account for 5-30% of the total microbial biomass (Booth and Zygmunt, 2005), though they have also been found in lake sediment (Charman et al., 2000). The abundance of individual taxa is controlled by environmental variables including water table height and thus provides information allowing for an inference of past conditions. These protozoa create a test that functions as protection from predation and the external environment (Charman et al., 2000). The organic material inside the test decays quickly, leaving only the decay resistant test, which can be identified long after death (Charman et al., 2000). Species have been shown to have different tolerances to temperature, incoming UV radiation, hydrology, and nutrient regimes (Booth and Zygmunt, 2005; Charman et al., 2000).

Plant, algal and other microfossils (non-pollen palynomorphs) give information on the hydrology, nutrient status and water chemistry near the wetland surface (Rydin and Jeglum, 2013). Plant microfossils are useful when studying species with low pollen production. Their advantage over macrofossil remains is that they may be more abundant and also allow for the analysis of pollen and microfossils simultaneously in pollen slides. Microalgae vary along the rich-poor gradient of water chemistry and allow an inference of hydrological source. Like macrofossils and testate amoebae, these indicators are not well dispersed and provide information about local depositional conditions. A large

variety of microfossils are preserved in peat and these allow researchers to relate changes in concentration to changes in local environmental conditions.

### **Paleoecological Studies on British Columbia Peatlands**

In British Columbia, peatlands are common in a 30-100 km wide strip along the north coast where they often cover more than 40% of the land area (Maynard, 1988). Vancouver Island peatlands are mostly clustered near the northern edge of the island where they are abundant ecosystems. Central and southern Vancouver Island peatlands are generally smaller and often occupy small depressions where runoff accumulates, as precipitation is reduced by the rainshadow effects of the Olympic and Vancouver Island mountain ranges (Golinski, 2004; Maynard, 1988).

Though many studies on peatland C dynamics and paleoenvironmental history have been done in Europe, the arctic, and continental North America (e.g. Charman et al., 2013; Loisel et al., 2014), few studies have been conducted on British Columbia peatlands. Peat-based paleoenvironmental studies in coastal British Columbia have largely focused on reconstructing past vegetation communities (Banner et al., 1983; Brown and Hebda, 2002b; Fitton, 2003; Hansen, 1950; Hebda, 1983; Heusser, 1960; Huntley et al., 2013). Heusser (1960) studied many peatland sites on a transect from Alaska to California, providing information principally on changes in forest community composition. Hansen (1950) categorised Holocene vegetation change near three bogs on the southern half of Vancouver Island. While these studies describe major changes in forest communities through time, there is little detail in the analyses: pollen identification was limited to a few tree species and there was no radiocarbon dating. More recent

studies (e.g. Brown and Hebda, 2002b; Fitton, 2003; Hebda, 1977, 1983) provide records of wetland development and surrounding forest community change over the Holocene with radiocarbon-based chronologies and complete pollen datasets.

Wetland development and carbon accumulation rates have been the focus of only a few studies in coastal British Columbia. Raised bog formation has been extensively studied through the analysis of peat composition and plant communities to evaluate successional changes and transitions from salt marsh to ombrotrophic bog at Burns Bog in metro-Vancouver (Hebda, 1977). Carbon dynamics have been studied on surface peat (Asada and Warner, 2005), but few studies span the Holocene (Lacourse and Davies, 2015; Turunen and Turunen, 2003). Asada and Warner (2005) investigated C balance and dynamics of surface peat containing several vegetation types and over several microtopographic areas. They found that the rate of C accumulation varied across microcommunities but was overall lower in comparison to continental sites (Asada and Warner, 2005). Turunen and Turunen (2003) determined the rate of long-term C accumulation over the last 12,000 years in a multi-proxy study of a slope bog on the north coast of British Columbia, finding the highest rates (21 g C/m<sup>2</sup>/yr) during the early Holocene. Lacourse and Davies (2015) analysed fossil pollen, macrofossil remains, and carbon and nitrogen accumulation and their isotopes over the last 14,000 years in a bog near Port McNeill on northern Vancouver Island. The mean C accumulation rate at Port McNeill Bog was 16.1 g/m<sup>2</sup>/cal yr, i.e., nearly double the rate at Turunen and Turunen's (2003) site on the north coast of B.C. Again, the highest rate (48.7 g C/m<sup>2</sup>/cal yr) occurred during the early Holocene. Nitrogen accumulation was, on average, 0.4 g/m<sup>2</sup>/cal

yr with the highest rates during accumulation of herbaceous peat in the early Holocene and lowest in *Sphagnum* peat during the middle to late Holocene.

### **General Paleoenvironmental History of Vancouver Island**

During the last glacial maximum, the Cordilleran and Laurentide ice sheets covered much of northern North America. Along the north Pacific coast of North America, ice was still expanding about 22,000 cal yr BP (Clague and James, 2002; Clark et al., 2009) with lobes of ice extending across Vancouver Island and as far south as Puget Sound (Clague and James, 2002). The volume of ice on land meant that global sea level was reduced by approximately 130 m (Lambeck et al., 2014). Locally, sea levels were also influenced by isostatic pressure. Ice sheet weight depressed the nearby land and resulted in a highly variable sea level along the British Columbia coast; the maximum sea level on the coast of Vancouver Island was 150 m higher than present (Hutchinson et al., 2004). Glacial retreat proceeded quickly and by about 10,000 cal yr BP ice was restricted to high elevations and was similar in extent to the modern environment (Clague, 1981). Sea level decreased at a rate of approximately 11 cm/yr along the central coast of Vancouver Island to reach present day levels around 9000 cal yr BP (Hutchinson et al., 2004).

### **Research Questions and Objectives**

The aim of my research is to produce a multi-proxy record of the developmental history and C accumulation of Grant's Bog, a wetland on central Vancouver Island. To accomplish this, a peat core was collected from the site and radiocarbon dated. I use

fossil pollen and spores to reconstruct local and regional vegetation since site formation. I use non-pollen palynomorphs including fungal, algal remains and testate amoebae to infer local hydrological conditions. Total organic matter and bulk carbon and nitrogen with  $^{13}\text{C}$  and  $^{15}\text{N}$  isotopes were analysed to determine C accumulation rates, local vegetation types, and nutrient status. The value in this record is to document the dynamics of this wetland on central Vancouver Island, a region where few comprehensive paleoenvironmental peat studies have been done.

## Materials and Methods

### Study site

Grant's Bog (informal name) is a wetland complex located on east central Vancouver Island (49° 47.2' N, 125° 07.6' W, 80 m above sea level) near Courtenay, British Columbia (Figures 1 and 2). The site is part of the Black Creek watershed in the Nanaimo Lowlands and is in the rainshadow of the Vancouver Island Ranges. Black Creek weather station, which is located approximately 6.5 km to the north, indicates a mean July temperature of 17.1 °C and mean January temperature of 2.8 °C (Environment Canada, 2017). Mean annual precipitation is 1645 mm/yr, which falls mainly as rain between October and March; the site receives very little snow (Figure 3). Grant's Bog is located in the very dry maritime subzone (CWHxm1) of the Coastal Western Hemlock biogeoclimatic zone (B.C. Ministry of Forests and Lands, 2016; Pojar et al., 1987). This zone is characterized by abundant *Pseudotsuga menziesii* and *Tsuga heterophylla* with a lower abundance of *Thuja plicata*. Common shrubs include *Gaultheria shallon*, *Mahonia nervosa* and *Vaccinium parvifolium* (Pojar et al., 1991).

The wetland complex is approximately 46 ha and consists of a shore bog with a small lake (1.8 ha) in its south-eastern corner (Figure 2). The complex sits in a small topographic depression and is connected to wetlands to the north (14.8 ha) and west (7.5 ha) for a total combined area of 68 ha. The water table depth fluctuates throughout the year between 6.5 and 81.5 cm (Golinski, 2004) and was 16 cm below the surface at the coring location at the time of sampling (July 2013).

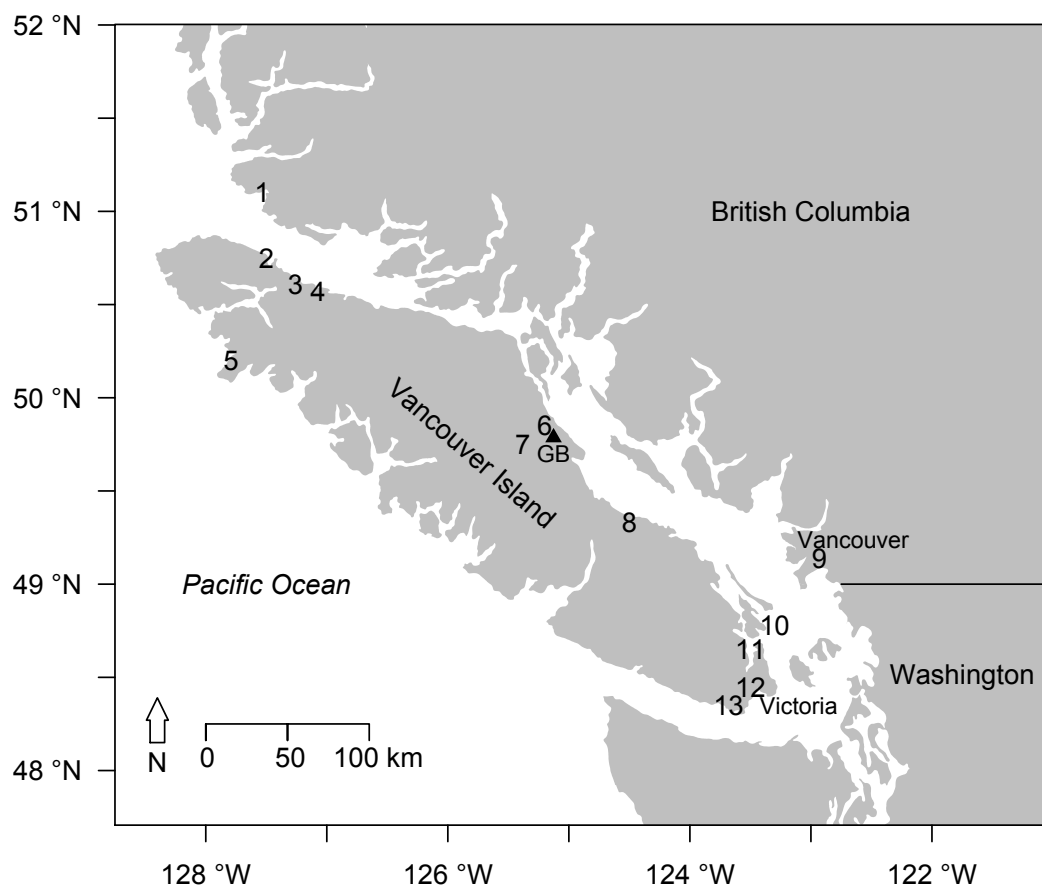


Figure 1. Location of Grant's Bog (GB) in southwestern British Columbia, Canada, and other sites mentioned in the text. 1 – Two Frog Lake (Galloway et al., 2007), 2 – Bear Cove Bog (Hebda, 1983), 3 – Misty Lake (Lacourse, 2005), 4 – Port McNeill Bog (Lacourse and Davies, 2015), 5 – Cottongrass Hollow (Hebda and Haggarty, 1997), 6 – Black Creek Bog (Hansen, 1950), 7 – Harris Lake Ridge Bog (Fitton, 2003), 8 – Qualicum Beach Bog (Hansen, 1950), 9 – Burns Bog (Hebda, 1977), 10 – Roe Lake (Lucas and Lacourse, 2013), 11 – Saanich Inlet (Pellatt et al., 2001), 12 – Langford Lake (Hansen, 1950), 13 – East Sooke Fen (Brown and Hebda, 2002b).



Figure 2. Aerial overview of Grant's Bog, British Columbia (Bing, n.d.). The star denotes the coring location.

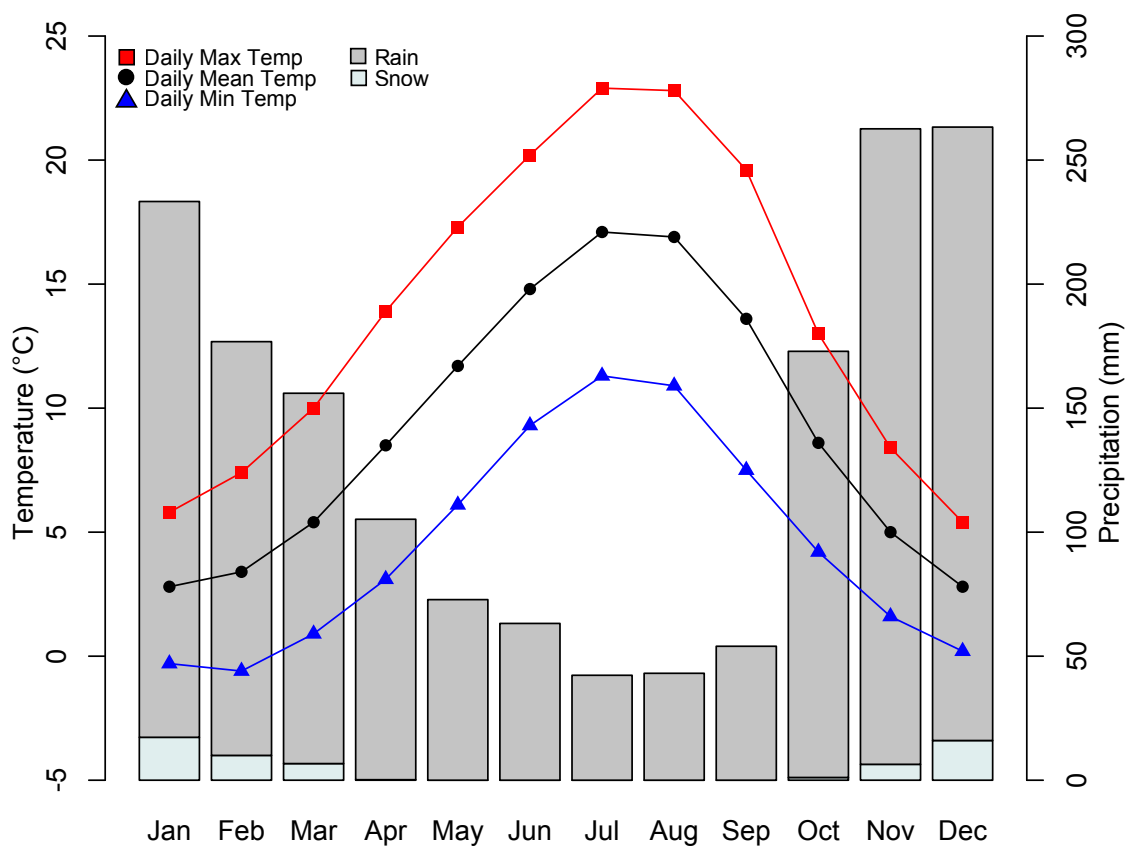


Figure 3. Temperature and precipitation at Black Creek climate station ( $49^{\circ} 50' N$ ,  $125^{\circ} 08' W$ ; 46 m asl) for 1988-2005 (Environment Canada, 2017). Snow is shown in water equivalent.

The wetland vegetation is dominated by *Sphagnum* mosses (*S. fuscum* and *S. palustre*) and *Rhododendron groenlandicum* and *Vaccinium uliginosum* shrubs (Golinski, 2004). Other common species include mosses (*Pleurozium schreberi*, *S. capillifolium*, *S. angustifolium*), shrubs (*Kalmia microphylla* spp. *occidentalis*, *V. oxycoccus*, *Rubus chamaemorus*), and sedges (*Eriophorum chamissonis*). *Pinus contorta* var. *contorta* and *Empetrum nigrum* are present in low abundance. *Tsuga heterophylla*, *Salix sitchensis*, *Carex* spp. and *Pteridium aquilinum* are present near the bog and lake edge.

### **Core collection**

In July 2013, a 810-cm core was collected from Grant's Bog using a Russian sampler. Two parallel coring holes, 25 cm apart, were used to extract 50-cm long sections with 10 cm of overlap across sections. The uppermost peat (0-24 cm) was also collected as a large solid block. The core was sectioned at 1 cm intervals and stored at 4 °C at the University of Victoria.

### **Radiocarbon dating**

To establish a chronology for the Grant's Bog core, peat and plant macrofossils from nine depths were submitted for AMS radiocarbon dating to Beta Analytic Inc. (Miami, Florida). Radiocarbon ages were calibrated to calendar years (cal yr) using the IntCal13 calibration dataset (Reimer et al., 2013). An age-depth model was constructed by T. Lacourse based on the calibrated radiocarbon ages and the top of the core (−63 cal yr BP) with 10,000 iterations of a smooth spline model (0.3 smoothing parameter) using the 'clam' package (Blaauw, 2010) in R (R Core Team, 2017).

### **Loss on ignition and carbon accumulation rates**

Loss on ignition (LOI) provides an estimate of organic matter content by comparing weights of dried samples to their weight after combustion (Dean, 1974; Heiri et al., 2001). Samples of 1 or 2 cm<sup>3</sup> were taken at 2-4 cm intervals along the length of the core (n=262) using a 1-cm diameter calibrated brass sampler. Samples were weighed in ceramic crucibles using a Mettler Toledo XSE105DU balance and then dried in a Thermoscientific Heratherm OGH60-S oven at 105 °C for 20 hr. Samples were transferred to a desiccator for 30 min to return to room temperature before weighing. Water content (%) was calculated based on the difference between wet and dry weights (g). Samples were then combusted in a Vulcan 3-550 Burnout Furnace at 550 °C for 4 hr to burn off all organic material. Samples were again placed in a desiccator before weighing. Organic matter content (%) was calculated from the dry weight and the weight of samples after combustion. Ash-free bulk density (g/cm<sup>3</sup>) was determined from the initial wet volume (cm<sup>3</sup>), and the weights of the sample after drying and combustion.

### **Carbon and Nitrogen analyses**

Samples of 2-3 cm<sup>3</sup> (n=98) were taken at depths where bulk density was determined with the aim of achieving a temporal resolution of <150 cal yr between samples. Samples were dried for 48 hr at 55 °C and transferred to a desiccator for 30 minutes until reaching room temperature. Samples were homogenized and ground to a fine powder (<125 µm) with a Retsch MM 200 ball mill at 25 Hz for 4-12 min and stored in glass vials.

Samples of 3–5 mg were packed into 5×8 mm tin capsules and weighed on a Sartorius ME5 microbalance. The samples were analysed with a Costech elemental

combustion system (model 4041) and a ThermoFisher Finnigan Delta-V mass spectrometer at the University of Victoria. Replicate analyses were conducted on 15% (n=15) of samples to assess homogeneity. Acetanilide (%C 71.09±1.5, %N 10.36±1.5), caffeine ( $\delta^{13}\text{C}$  -42.22±0.09‰,  $\delta^{15}\text{N}$  -0.94±0.05‰), and DORM ( $\delta^{13}\text{C}$  -17.27±0.01‰,  $\delta^{15}\text{N}$  14.33±0.13‰) standards were included in every run. Sample values were: acetanilide (%C 71.09±0.57, %N 10.36±0.11), caffeine ( $\delta^{13}\text{C}$  -42.3±0.17‰,  $\delta^{15}\text{N}$  -0.95±0.05‰), and DORM ( $\delta^{13}\text{C}$  -17.18±0.14‰,  $\delta^{15}\text{N}$  14.33±0.02‰). Carbon and nitrogen accumulation rates ( $\text{g/m}^2/\text{cal yr}$ ) were calculated using ash-free bulk density ( $\text{g/cm}^3$ ) and percent carbon or nitrogen along with the peat deposition times ( $\text{cal yr/cm}$ ). Correlations between the physical records were calculated using Pearson's product moment correlation coefficient.

### **Pollen and non-pollen palynomorph analyses**

Samples of 1-2  $\text{cm}^3$  were taken along the length of the core (n=102). A single tablet of  $18,584 \pm 829$  *Lycopodium* spores (Batch # 177745) was added to each sample to estimate pollen and non-pollen palynomorph (NPP) concentrations. Samples were treated with 10% KOH in a hot water bath (75 °C) for 8 min, sieved through 150  $\mu\text{m}$  mesh, and treated with acetolysis solution (9:1 acetic anhydride to sulphuric acid) in a hot water bath (75 °C) for 2.5 min. Five samples below 744 cm were also treated with hydrofluoric acid (HF) to remove inorganic material and sieved with 10  $\mu\text{m}$  Nitex mesh to remove small particles. Since HF destroys most NPP remains these samples were excluded from NPP analysis. Samples were then dehydrated with 95% ethanol and stored in 2000-cc

silicon oil for mounting and identification. The >150  $\mu\text{m}$  fraction was used for estimating peat composition by Craig (2016).

Identification of fossil pollen and NPPs was done under light microscopy using a Zeiss A2 light microscope at 400-630 $\times$  magnification. A minimum sum of 400 terrestrial pollen and spores was identified in each sample. Pollen and spore identification was performed using published dichotomous keys and photographs (e.g. Faegri and Iversen, 1989; Knapp et al., 2000; McAndrews et al., 1973; Moore et al., 1991) and modern reference material at the University of Victoria. *Alnus rubra* and *A. viridis* type pollen were differentiated according to May and Lacourse (2012). Ericaceae pollen were differentiated using Warner and Chinnappa (1986) and Moore et al. (1991). *Sphagnum* spores were identified according to Cao and Vitt (1986), although most could not be differentiated below genus.

Pollen percentages were calculated using the sum of all terrestrial pollen and spores (main sum). *Sphagnum* spore and aquatic pollen percentages were calculated using a sum that included these groups in addition to the main sum (main sum + *Sphagnum*; main sum + aquatics). Cluster analysis, based on taxa exceeding 5% of the main sum, was used to identify pollen assemblage zones, *Sphagnum* spores and the pollen from aquatic taxa were not included in the cluster analysis. The percentage data were analyzed using optimal splitting by sum-of-squares in 'psimpoll' 4.26 (Bennett, 1996) after square-root transformation. Splitting with binary sum-of-squares produced identical divisions. Information content indices (i.e. binary information content, optimal information content, and constrained incremental information content) resulted in identical splits with the exception of the uppermost pollen zone, which was not deemed statistically significant. A

broken stick model was used to test the statistical significance of the pollen assemblage zones.

Non-pollen palynomorphs identified in pollen slides include fungal spores, algal remains, and aquatic plant microfossils (Chambers et al., 2010; Pals et al., 1980; van Geel, 1978, 2001; van Geel et al., 1981). Testate amoebae tests were identified using Charman et al. (2000), Clarke (2003), and Payne et al. (2012). Numerical zonation of the NPP data was based on taxa that were present in five or more samples using optimal splitting by information content after square-root transformation and a broken stick model in 'psimpoll' 4.26.

## Results

### **Radiocarbon dating and chronology**

The age-depth model (Figure 4) was built using calendar age probability distributions for each AMS radiocarbon age (Table 1) and an age of  $-63$  cal yr BP (2013) for the top of the core. The base of the organic sediments at 744 cm is predicted to be 13,316 cal yr BP (12,390–13,658 cal yr BP). The radiocarbon age at 726.5-727 cm (wood fragment) was rejected from the age-depth model due to being out of order compared to the other radiocarbon dates. This is likely a result of this fragment being displaced during core extraction.

The accumulation rates calculated from the age depth model range from 0.03-0.24 cm/cal yr with a mean deposition time of 18 cal yr/cm (Figure 5). The lowermost organic sediment (700-744 cm; 11,800-13,300 cal yr BP) accumulated at a rate of 0.03 cm/cal yr. The accumulation rate underwent a major increase to its maximum of 0.24 cm/cal yr at  $\sim 8900$  cal yr BP followed by a major decrease to  $<0.08$  cm/cal yr at  $\sim 8000$  cal yr BP where it remains for most of the sequence. Between 3600 cal yr BP and the present, peat accumulation increases slightly to reach 0.08 cm/cal yr at the surface.

### **Stratigraphy**

The sequence collected from Grant's Bog extends to a depth of 810 cm (Figure 6). The sequence consists of terrestrial peat from the surface to 628 cm. The core gradually transitions to limnic peat around 628 cm, then to organic lake sediment around 690 cm. Clay occurs below 744 cm. Diatom analysis suggests that clays between 744 and

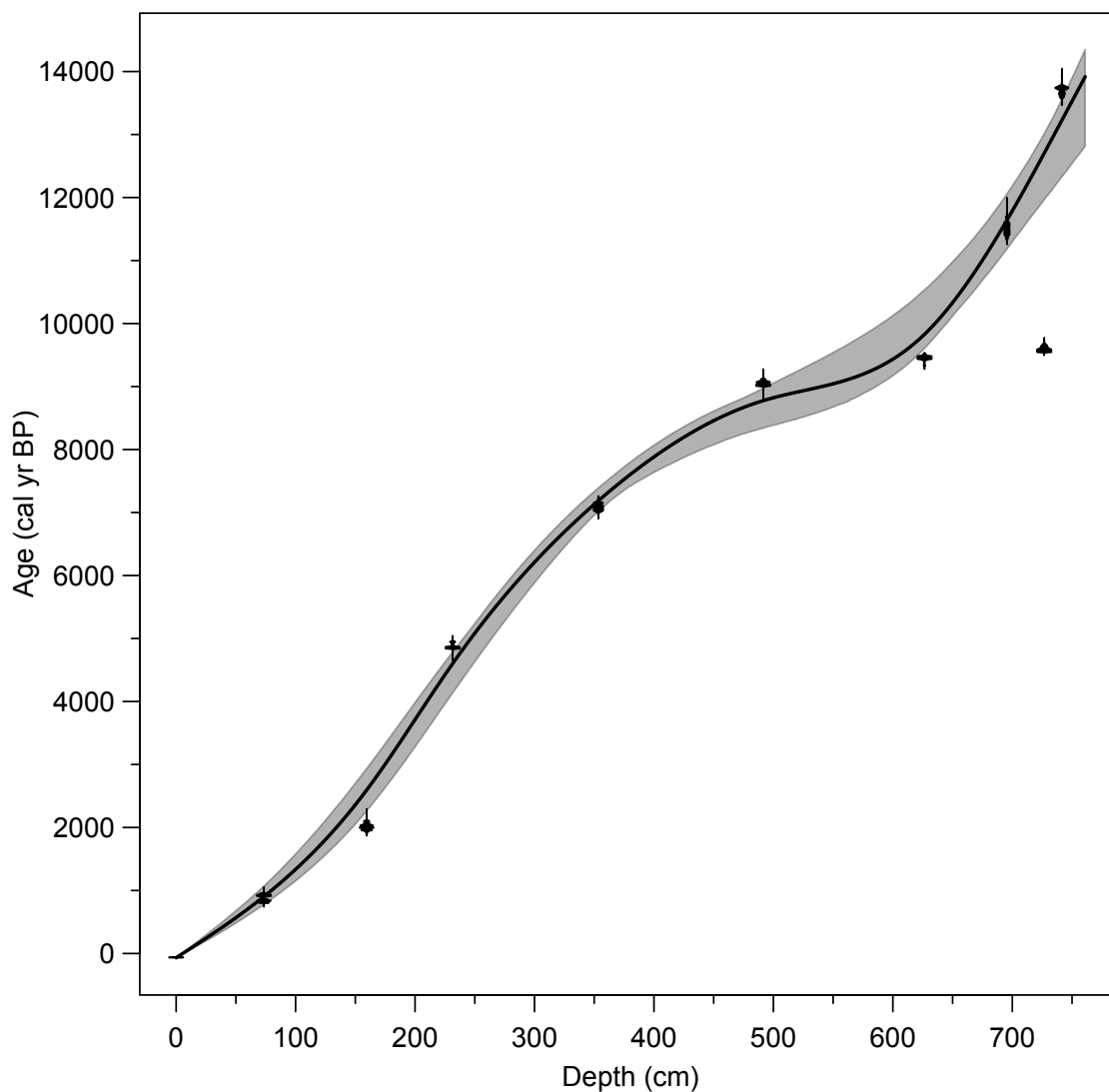


Figure 4. Age-depth model relating depth to calendar years before present for Grant's Bog, British Columbia. Model was constructed by T. Lacourse using 10,000 iterations of a smooth spline model using the 'clam' package (Blaauw, 2010) in R (R Core Team, 2017). Grey shaded area denotes the 95% confidence intervals as an indication of model precision. The date at 727 cm was rejected and was not used in model construction.

Table 1. AMS radiocarbon and calibrated calendar ages for Grant's Bog, British Columbia.

Depth (cm)	Material	Radiocarbon age ( $^{14}\text{C}$ yr BP $\pm 1\sigma$ )	Calendar Age Range <sup>a</sup> (cal yr BP)	Lab number
73–74	wood	990 $\pm$ 30	900-960	Beta-439738
159–160	peat	2050 $\pm$ 30	1930-2070	Beta-463068
231–232	wood	4300 $\pm$ 30	4830-4890	Beta-439739
353–354	peat	6190 $\pm$ 30	6990-7180	Beta-463069
491–492	wood	8110 $\pm$ 30	9000-9100	Beta-439740
626–627	wood	8420 $\pm$ 30	9410-9520	Beta-439741
695–696	bulk sediment	10,020 $\pm$ 30	11,330-11,700	Beta-480750
726.5–727	wood	8640 $\pm$ 30 <sup>b</sup>	9540-9670	Beta-439742
741–742	bulk sediment	11,900 $\pm$ 40	13,570-13,790	Beta-475650

<sup>a</sup> 2 $\sigma$  age range rounded to the nearest 10 yr

<sup>b</sup> rejected age

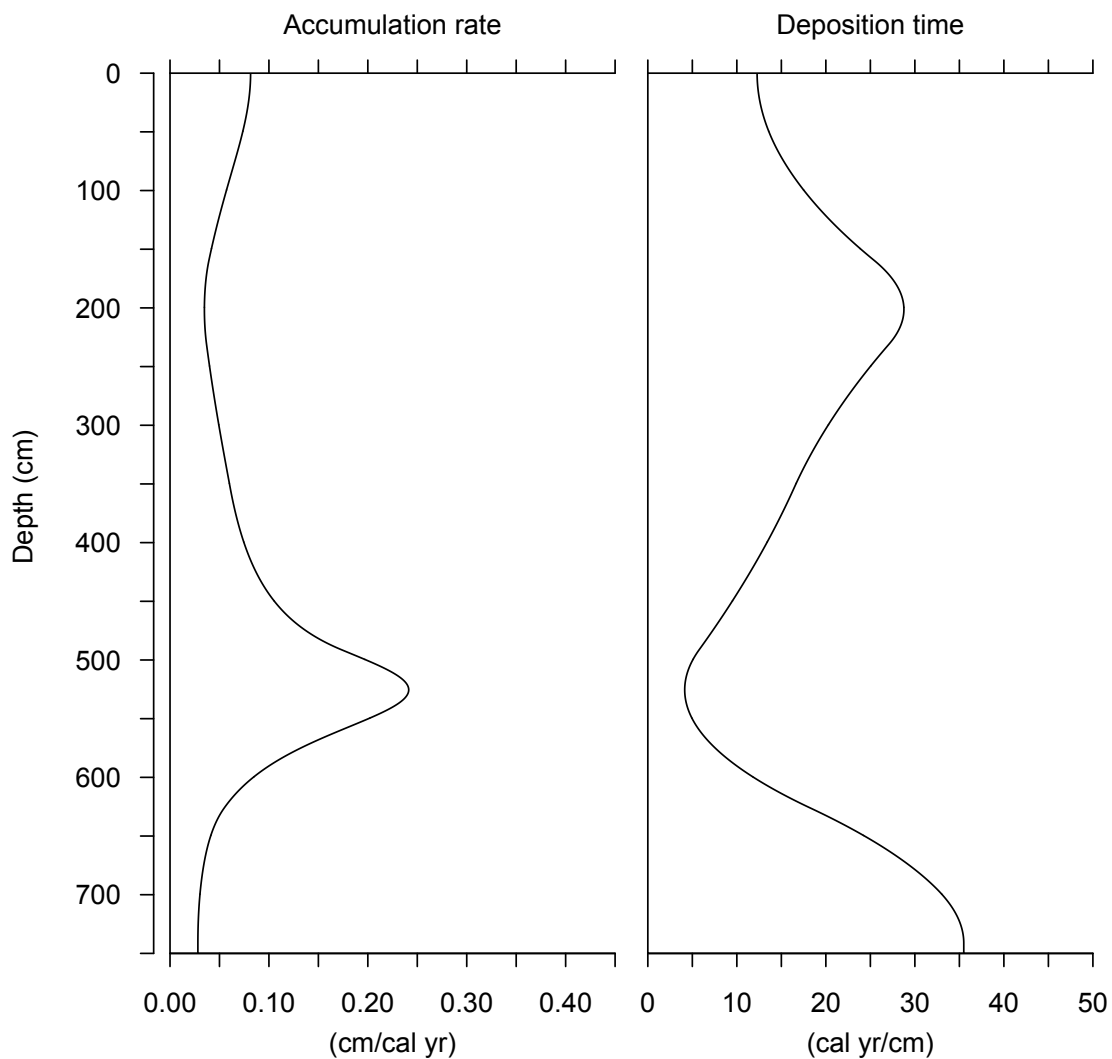


Figure 5. Model-predicted rates for the Grant's Bog core: accumulation rate of peat and lake sediment and the time over which they accumulated or were deposited.

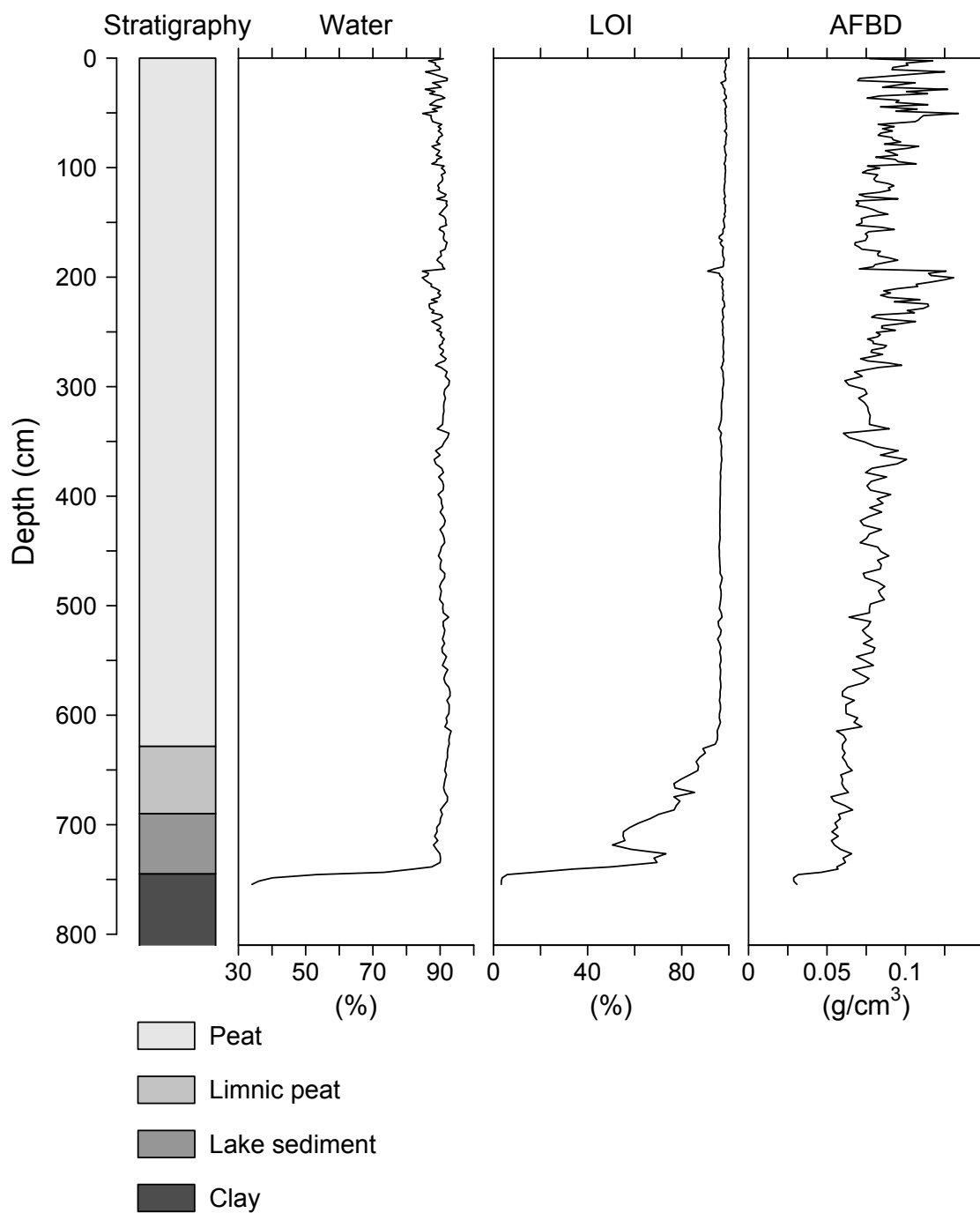


Figure 6. Physical records for the Grant's Bog core: stratigraphy, water content, mass loss on ignition (LOI), and ash-free bulk density (AFBD).

765 cm were deposited in a freshwater to brackish environment with a gradually increasing marine influence (Lacourse, unpublished data). Only marine diatoms are present below 765 cm. At this depth and below, the core is composed of fine marine clays characteristic of a brackish to marine environment.

Peat composition analysis of the Grant's Bog core by Craig (2016) shows varying amounts of ericaceous, *Sphagnum*, and herbaceous remains during the accumulation of terrestrial peat. *Sphagnum* leaves are present to 744 cm but increase substantially above 500 cm (Craig, 2016).

### **Loss on ignition (LOI) and bulk density**

Water content follows changes in core composition, remaining relatively constant throughout the peat and organic sediments, and then decreasing as sediments increase in inorganic content. From 0 to 739 cm (~13,100 cal yr BP), water content is  $\geq 85\%$  (Figure 6). Below 739 cm, water content decreases, reaching 34% in the basal clays.

LOI is generally constant throughout much of the core though it decreases slightly with depth; the values are highest in the surface peat and lowest in the basal clay (Figure 6). From the surface to a depth of 627 cm (~9800 cal yr BP), LOI remains relatively constant around 97%. A localised dip in LOI occurs at 194 cm where the value descends to 91% corresponding to an increase in charcoal (Craig, 2016). Between 627 and 718 cm (9800-12,400 cal yr BP), LOI decreases to 51%. The percentage increases to 73% at 726 cm (12,700 cal yr BP) and then declines to 3% in the basal clays.

There is higher variability in ash-free bulk density (AFBD) between adjacent samples compared to the water content and LOI (Figure 6). Sediment below 744 cm

(13,300 cal yr BP) has low bulk density ( $\sim 0.03 \text{ g/cm}^3$ ). The bulk density gradually increases between 727-200 cm (12,700-3700 cal yr BP) from 0.07 to  $0.13 \text{ g/cm}^3$ . AFBD decreases between 200 and 168 cm (3700-2800 cal yr BP). From 168 cm to the surface there is a gradual increase in AFBD (mean= $0.09 \text{ g/cm}^3$ ).

### **Carbon and nitrogen content, isotopes and accumulation rates**

Estimated carbon (C) content follows stratigraphic changes in core composition (Figure 7). Mean C is 30% at the base of the lake sediment. The transition to peat brings about an increase in C to about 45%, where it remains fairly constant until the surface. The uppermost sample from Grant's Bog has 51% C.

Percent nitrogen (N) also varies with the stratigraphy (Figure 7). N in the lake sediment is 2–3%. The gradual change from limnic to terrestrial peat around 628 cm (9900 cal yr BP) corresponds with a decrease in N to generally 0.5-1.5%, except for the increase between 3500-2200 cal yr BP (2–3%).

Carbon to nitrogen mass ratio (C:N) varies more among samples than either C or N separately (Figure 7). The limnic peat and lake sediment have a low C:N ratio of  $<17$ . The ratio is characterized by an increase to a mean of 50 between about 8400-4000 cal yr BP. Peat younger than 3500 cal yr BP has a lower C:N ratio compared to samples from the mid-Holocene.

Large changes in C and N isotopes occur alongside changes in stratigraphy (Figure 7).  $\delta^{13}\text{C}$  is low in the lake sediments at  $-30\text{‰}$ . The transition to peat brings an increase to a mean of  $-27.4\text{‰}$  for the remainder of the sequence. The uppermost two samples have low  $\delta^{13}\text{C}$ .  $\delta^{15}\text{N}$  in the lake sediment and limnic peat is around  $0\text{‰}$ . The

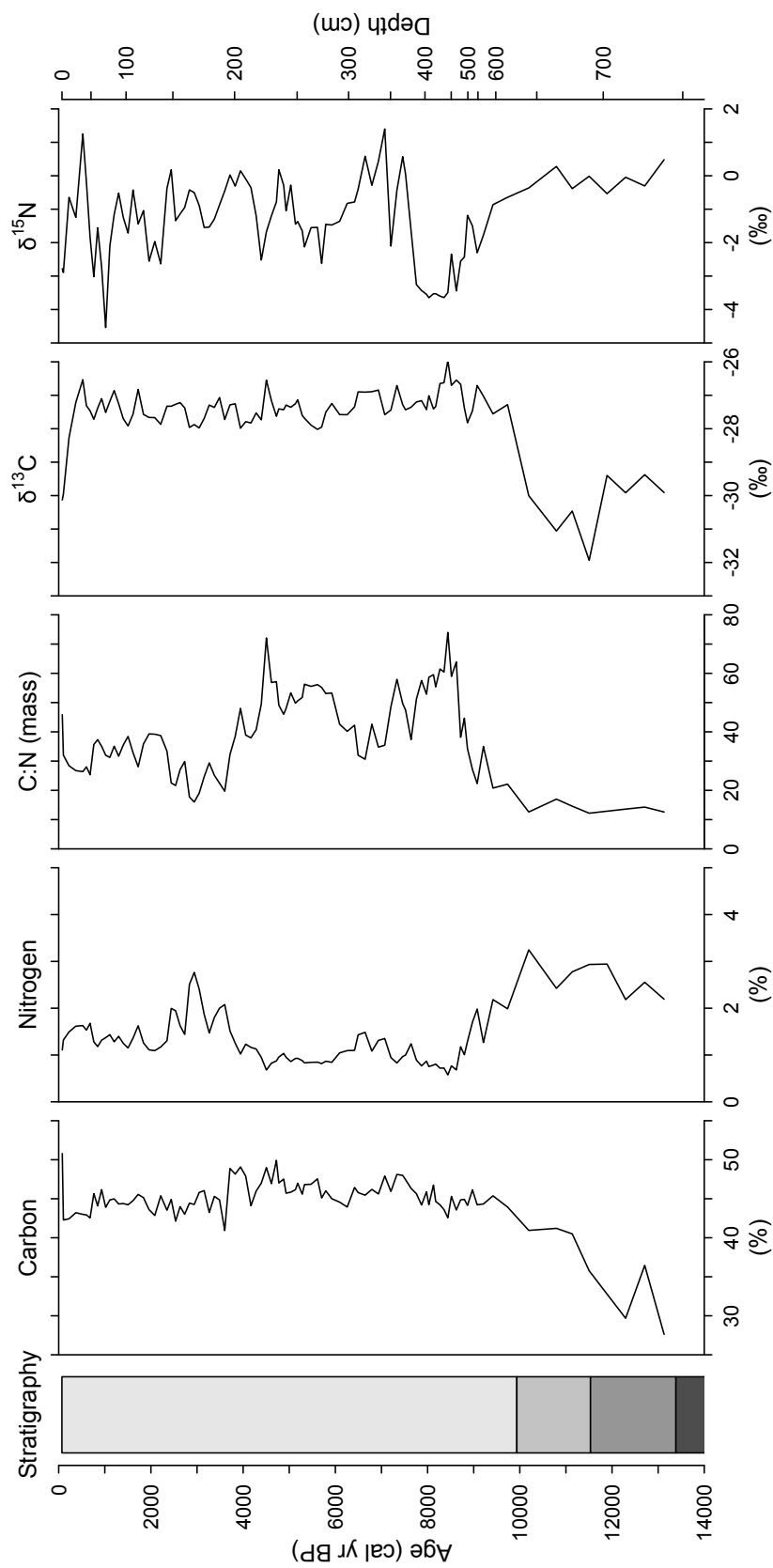


Figure 7. Physical records for the Grant's Bog core: stratigraphy, percent carbon, percent nitrogen, carbon to nitrogen ratio,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ . See Figure 6 for stratigraphy legend.

transition to a more terrestrial environment around 9600 cal yr BP begins a reduction of  $\delta^{15}\text{N}$  leading to  $-3.6\text{‰}$  at 8210 cal yr BP. By 7000 cal yr BP  $\delta^{15}\text{N}$  has increased to  $1.4\text{‰}$ . Peat younger than 7000 cal yr BP has a mean  $\delta^{15}\text{N}$  of  $-1.1\text{‰}$ , with significant variability between samples.

The carbon accumulation rate (CAR) follows a similar trend to the peat accumulation rate estimated with the age-depth model (Figures 5 and 8). CAR was low in lake sediment ( $5.2 \text{ g C/m}^2/\text{cal yr}$ ). Accumulation in the limnic peat increases to  $11.2 \text{ g C/m}^2/\text{cal yr}$  by 10,200 cal yr BP. The transition to terrestrial peat brings a rapid increase to  $81 \text{ g C/m}^2/\text{cal yr}$  at 8900 cal yr BP. Carbon accumulation then decreases until 7000 cal yr BP where it becomes stable between  $10\text{-}20 \text{ g C/m}^2/\text{cal yr}$ . Peat younger than 2000 cal yr BP is characterized by an increasing rate of carbon accumulation of up to  $43 \text{ g C/m}^2/\text{cal yr}$  in the surface peat.

The nitrogen accumulation rate (NAR) follows a similar trend to carbon, with reduced magnitude but similar percent variability (Figure 8). The lake sediment has a low accumulation rate of  $\sim 0.4 \text{ g N/m}^2/\text{cal yr}$ . The rate increases during the accumulation of limnic peat and the start of the terrestrial peat phase to reach  $3.0 \text{ g N/m}^2/\text{cal yr}$  at  $\sim 8900$  cal yr BP. NAR follows CAR and drops significantly to remain  $< 1 \text{ g N/m}^2/\text{cal yr}$  for the majority of the sequence. Peat younger than 2000 cal yr BP has an increasing accumulation rate to present.

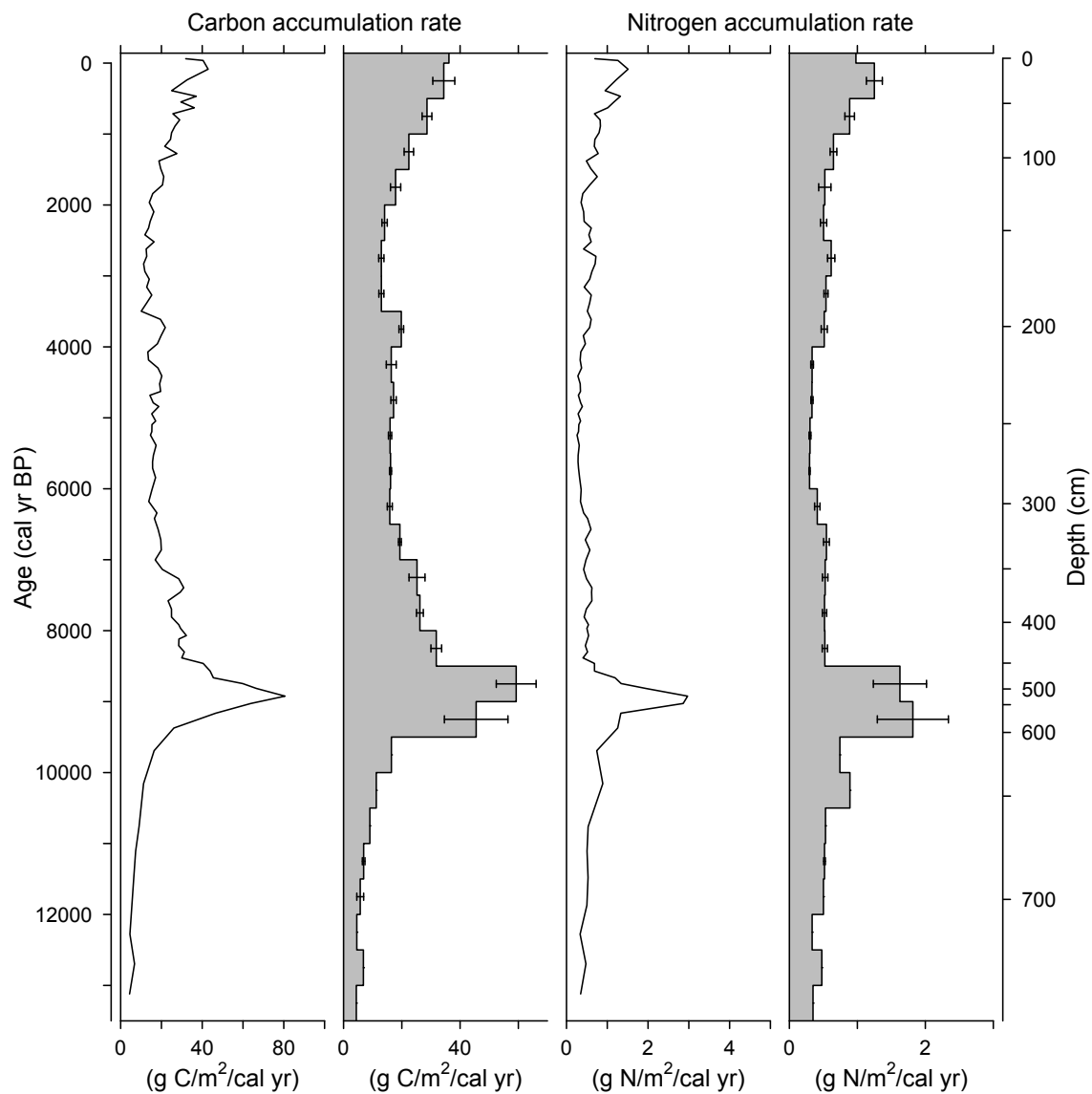


Figure 8. Estimated carbon and nitrogen accumulation rates for Grant's Bog, British Columbia. Instantaneous rates and mean rates in 500 cal yr bins are presented. Error bars are the standard error of the binned means for those constructed from multiple measurements. Bins without error bars are based on single measurements.

## **Pollen and spore assemblages**

Pollen and spores from 56 plant taxa were identified in the Grant's Bog sequence. Each sample accumulated over 4-35 cal yr based on the age depth model (Figure 5) with an average spacing of 138 cal yr between samples. The number of terrestrial pollen and spores identified range from 404-688 palynomorphs/sample (excluding *Sphagnum*). The numerical zonation identified six statistically significant zones, which are described below. Complete pollen and spore diagrams containing the infrequent taxa are included as supplemental figures (Figures A1-A3).

### Pollen Zone 1: 760-744 cm, >13,300 cal yr BP

Pollen spectra in the basal clays are characterized by abundant *Pinus contorta* that comprise 40-60% of the pollen sum (Figure 9) with a mean concentration of ~10,000 grain/cm<sup>3</sup> (Figure 10). Undifferentiated *Pinus* pollen accounts for another 15-40% and relates to a large number of broken *Pinus* grains that were not identified to species. *Picea* pollen accounts for <2%. *Alnus viridis* type pollen is relatively constant during this zone and makes up about 10% of the sum (Figure 11). Cyperaceae pollen range from 3 to 10%. Other herbaceous plants account for <3%. Fern spores, mostly Polypodiaceae, contribute <2%. A few tetrads of *Typha* pollen were also observed. The total pollen and spore concentration is low throughout this zone (16,000-27,000 grains/cm<sup>3</sup>) and progressively increases from the base of the sequence (Figure 10).

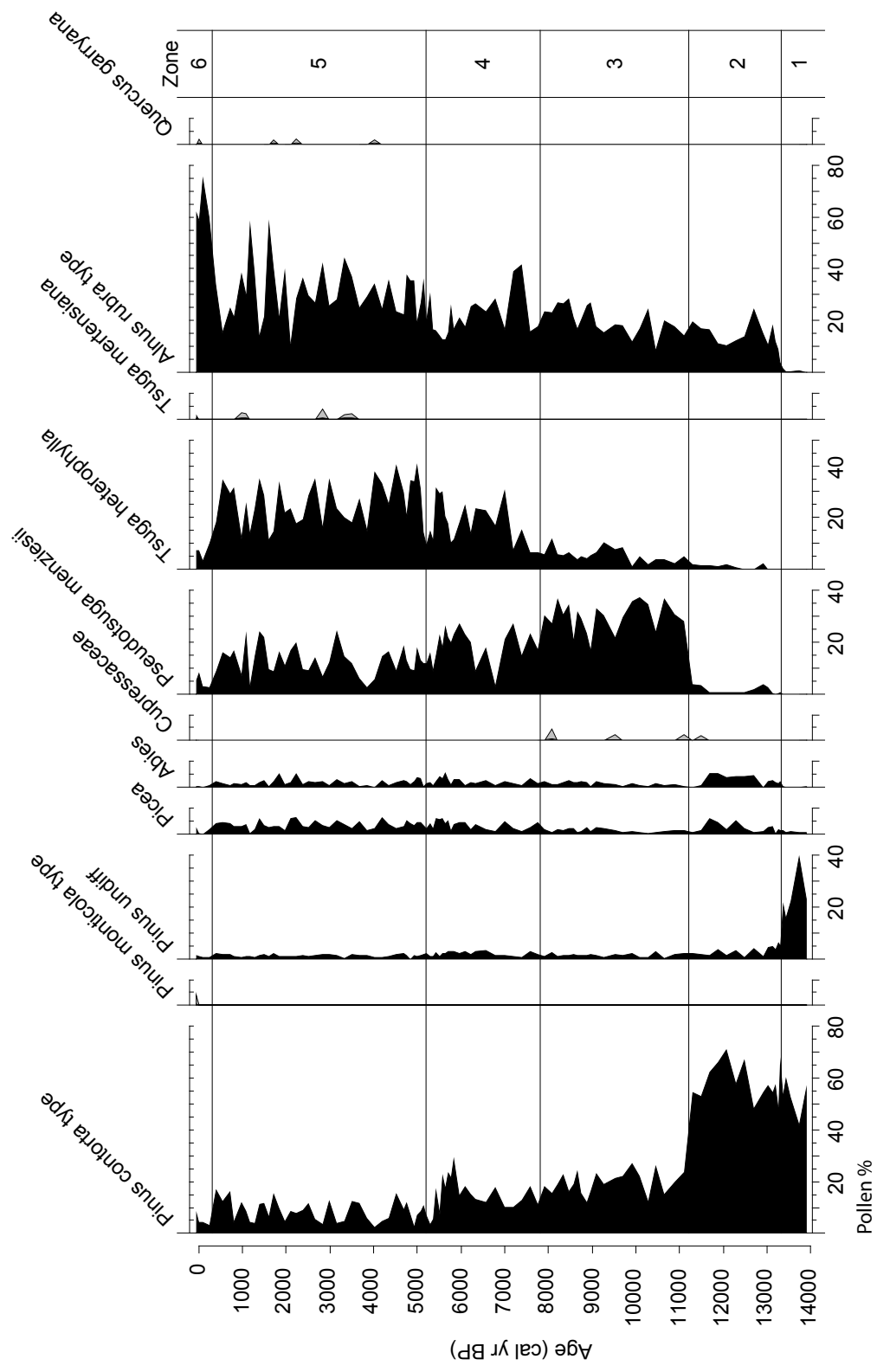


Figure 9. Arboreal pollen percentages from Grant's Bog, British Columbia. Light grey represents 10x exaggeration.

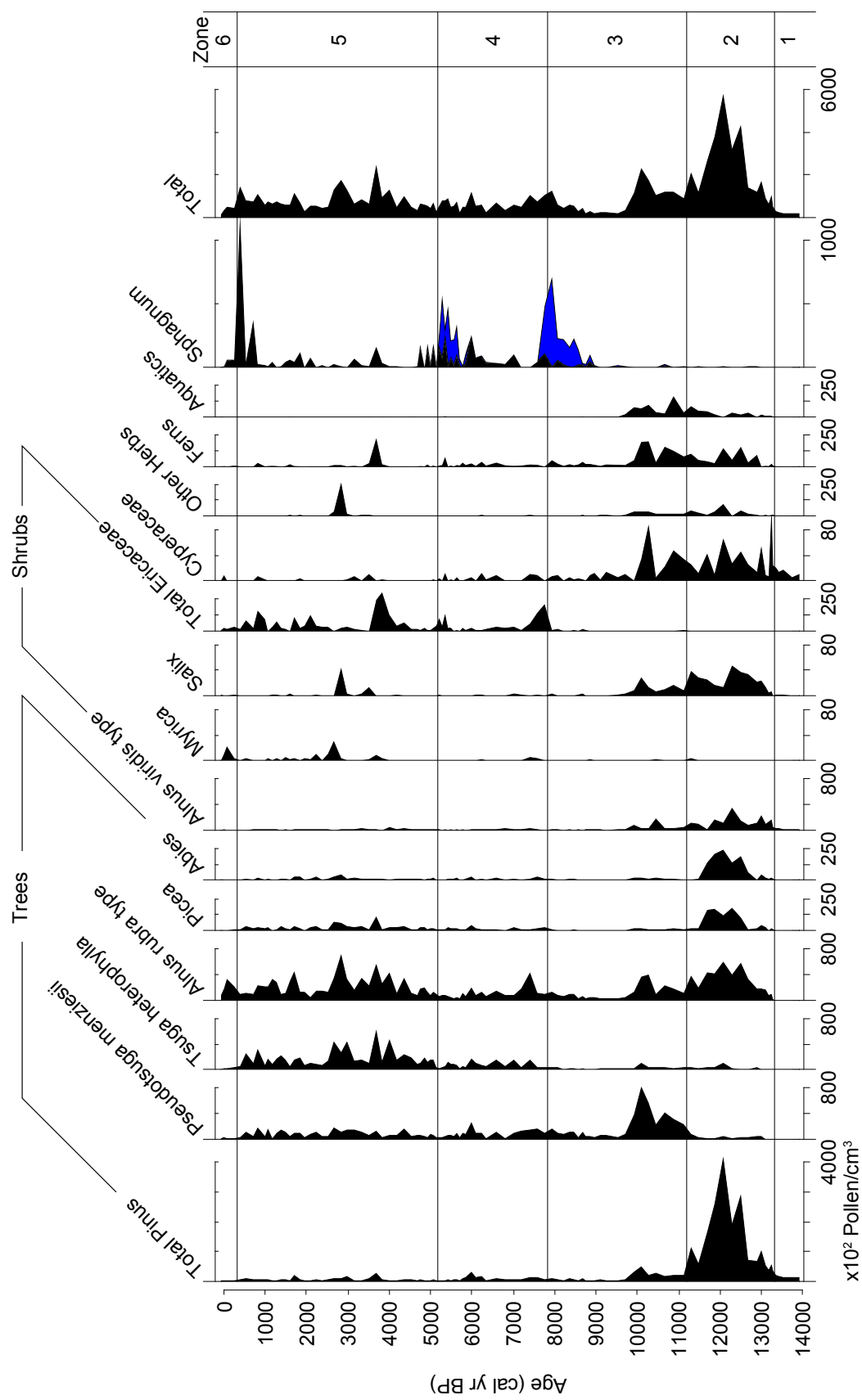


Figure 10. Pollen and spore concentrations of select taxa from Grant's Bog, British Columbia. In the *Sphagnum* plot, black is undifferentiated *Sphagnum* and blue is *Sphagnum fuscum* type. Total is based on the sum of all pollen and spores including *Sphagnum*. Note changes in scale.

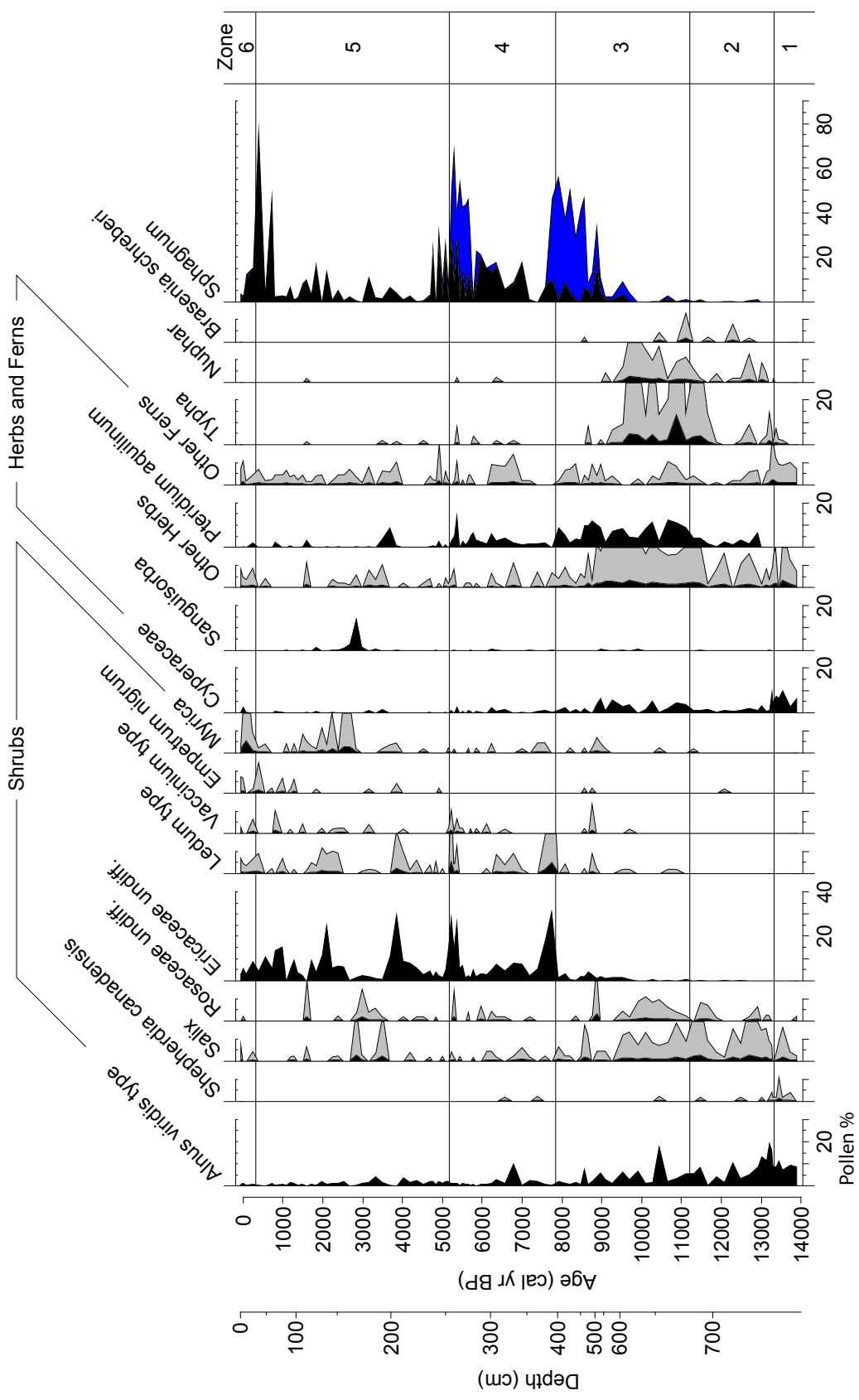


Figure 11. Shrub, herb, fern, and aquatic pollen and spore percentages for Grant's Bog, British Columbia. Light grey represents *Sphagnum fuscum* type. Blue is undifferentiated *Sphagnum* and black is *Sphagnum fuscum* type.

Pollen Zone 2: 744-681 cm, 13,300-11,200 cal yr BP

In this zone, *Pinus contorta* continues to dominate the pollen assemblages at 50-70% (Figure 9) and a mean concentration of  $\sim 130,000$  grains/cm<sup>3</sup> (Figure 10). *Pinus contorta* reaches a maximum concentration of  $\sim 410,000$  grains/cm<sup>3</sup> at 708 cm (12,100 cal yr BP) and then decreases towards the end of the zone. *Abies* and *Picea* pollen increase compared to pollen zone 1, though remaining <6%. *Pseudotsuga menziesii* pollen first appears in the record at 744 cm (13,300 cal yr BP) and composes <4% of the sum during the remainder of this zone. *Tsuga heterophylla* pollen is first observed in the record at 733 cm (12,900 cal yr BP) and comprises <3% throughout the zone. *Alnus rubra* type increases abruptly to account, on average, for 14%. *Alnus viridis* type is similar to the previous zone at about 10% (Figure 11). Cyperaceae pollen values decrease near the beginning of the zone to make up <3% of the sum. Other herbaceous plants continue to account for a small percentage, similar to pollen zone 1. *Pteridium aquilinum* spores increase but are low in relative abundance with an average of 2%. Pollen from aquatic taxa (*Nuphar*, *Brasenia*, and *Typha*) are present in low relative abundance (<5%). The total pollen and spore concentration increases during this zone with a deposition of 49,000-583,000 grains/cm<sup>3</sup> and is attributed primarily to a spike in *Pinus* pollen.

Pollen Zone 3: 681-396 cm, 11,200-7800 cal yr BP

At the start of this zone, *Pinus contorta* pollen decreases from the preceding zone to <30% (Figure 9), with a mean concentration of 25,000 grains/cm<sup>3</sup> until 630 cm (9900 cal yr BP) where it further decreases to <10,000 grains/cm<sup>3</sup> (Figure 10). *Pseudotsuga menziesii* increases to 20-35% of the sum, and remains in this range to the end of the zone

with concentrations generally between 10,000-15,000 grains/cm<sup>3</sup>. *Tsuga heterophylla* increases to 5-10% and is relatively constant throughout this zone. *Abies* and *Picea* maintain low and similar percentages of <5%. There are scattered Cupressaceae grains (<1%) present in this zone. *Alnus rubra* type increases and varies from 20-30%. *Alnus viridis* type reaches a maximum of 20% at 654 cm (10,400 cal yr BP) and then decreases over the rest of the zone (Figure 11). Ericaceae pollen has a relative abundance of about 5% for the majority of the zone with a sharp increase to ~40% at 390 cm (7700 cal yr BP). Cyperaceae pollen is present usually at <5%. *Pteridium aquilinum* continues to increase from levels in the previous zone to about 5-15% of the total. Pollen from aquatic taxa reaches maximum abundance during this zone (~15%) but becomes present only intermittently in samples above 535 cm (9000 cal yr BP). *Sphagnum* spores increase from 630-396 cm (9900-7800 cal yr BP) with *S. fuscum* type exceeding 50% at 402 cm (7900 cal yr BP). Undifferentiated *Sphagnum* spores account on average for <4%. Total pollen and spore concentration decreases from the previous zone to between 18,000-230,000 grains/cm<sup>3</sup>.

#### Pollen Zone 4: 396-254 cm, 7800-5200 cal yr BP

This zone marks the transition between *Pseudotsuga menziesii* dominated assemblages characteristic of zone 3, and *Tsuga heterophylla* and *Alnus rubra* dominated assemblages of zone 5. In this zone there are similar pollen concentrations of *Pinus*, *P. menziesii*, and *T. heterophylla* (9000, 8800, 7800 grains/cm<sup>3</sup> respectively), with a high concentration of *Alnus rubra* (10,500 grains/cm<sup>3</sup>) (Figures 9 and 10). Ericaceae pollen rises in abundance compared to the previous zone. *Pteridium aquilinum* spores become less abundant

(<10%) and are intermediate between the zones above and below. Undifferentiated *Sphagnum* and *S. fuscum* type spores are common during this period with average abundance of 10 and 17% respectively. Total pollen and spore concentration for this zone is between 22,000-122,000 grains/cm<sup>3</sup>.

#### Pollen Zone 5: 254-30 cm, 5200-300 cal yr BP

The defining species during this period is *Tsuga heterophylla*, which accounts for up to 35% (Figure 9) and has a mean concentration of about 20,000 grains/cm<sup>3</sup> (Figure 10).

This increase in percentage is matched by higher *T. heterophylla* concentrations.

*Pseudotsuga menziesii* decreases slightly but continues to account for 10-25% of the sum with a mean concentration of 8500 grains/cm<sup>3</sup>. *Pinus contorta* accounts for 5-20%, a decrease compared to the previous zone. *Abies* and *Picea* pollen remain similar to zone 4 (<4%). *Alnus rubra* type increases slowly through the zone to comprise up to 60% of the total. Ericaceae pollen varies with two large peaks where relative abundance exceeds 30%, though usually it is <10% in this zone (Figure 11); peaks in Ericaceae percentages are generally matched by increases in Ericaceae concentration (Figure 10). Pollen from herbaceous plants typically accounts for <4%, although there is an isolated peak in *Sanguisorba* pollen to 15% at 168 cm (2800 cal yr BP). *Myrica* pollen rises in relative abundance though remaining <3%. *Pteridium aquilinum* is present only intermittently and in low abundance. *Sphagnum* spores generally make up 5-20%. The increase in total pollen and spore concentration from the previous zone to 27,000-245,000 grains/cm<sup>3</sup> is largely attributed to increases in *Alnus rubra* and *Tsuga heterophylla*.

Pollen Zone 6: 30-0 cm, 300 cal yr BP to present

The surface peat is characterized by a decrease in the relative abundance and concentration of arboreal pollen with the exception of *Alnus rubra* type, which makes up 60-75% of the sum (Figure 9) and has a mean concentration of 20,000 grains/cm<sup>3</sup> (Figure 10). *Pinus contorta*, *Pseudotsuga menziesii* and *Tsuga heterophylla* each account for <10% of the sum. Ericaceae and *Myrica* pollen are present in low abundance (~5%) (Figure 11). Undifferentiated *Sphagnum* spores comprise 5-20% of the combined sum (Figure 11). The total pollen and spore concentration decreases to 15,000-50,000 grains/cm<sup>3</sup>.

**Non-pollen palynomorphs (NPPs)**

A total of 26 different NPPs were identified. Numerical zonation of the NPP data resulted in the identification of six significant zones (Figures 12 and 13). Complete NPP diagrams containing infrequent taxa are presented as supplemental figures (Figures A4 and A5). Based on compositional similarity, two of these zones were deemed subzones i.e., NPP-2a and 2b.

Zone NPP-1: 744-624 cm, 13,300-9800 cal yr BP

This zone is characterized by abundant pennate diatoms (Figure 12) with a mean concentration of ~65,000 frustules/cm<sup>3</sup>. Other algal remains (e.g. *Pediastrum*, *Closterium* and Zygnemataceae) are present intermittently in this zone. *Filinia* type and other rotifer eggs are abundant with mean concentrations of 1200 and 360 eggs/cm<sup>3</sup>, respectively. Nymphaeaceae leaf hair basal cells are restricted to this zone. Fungal spores (Type 124),

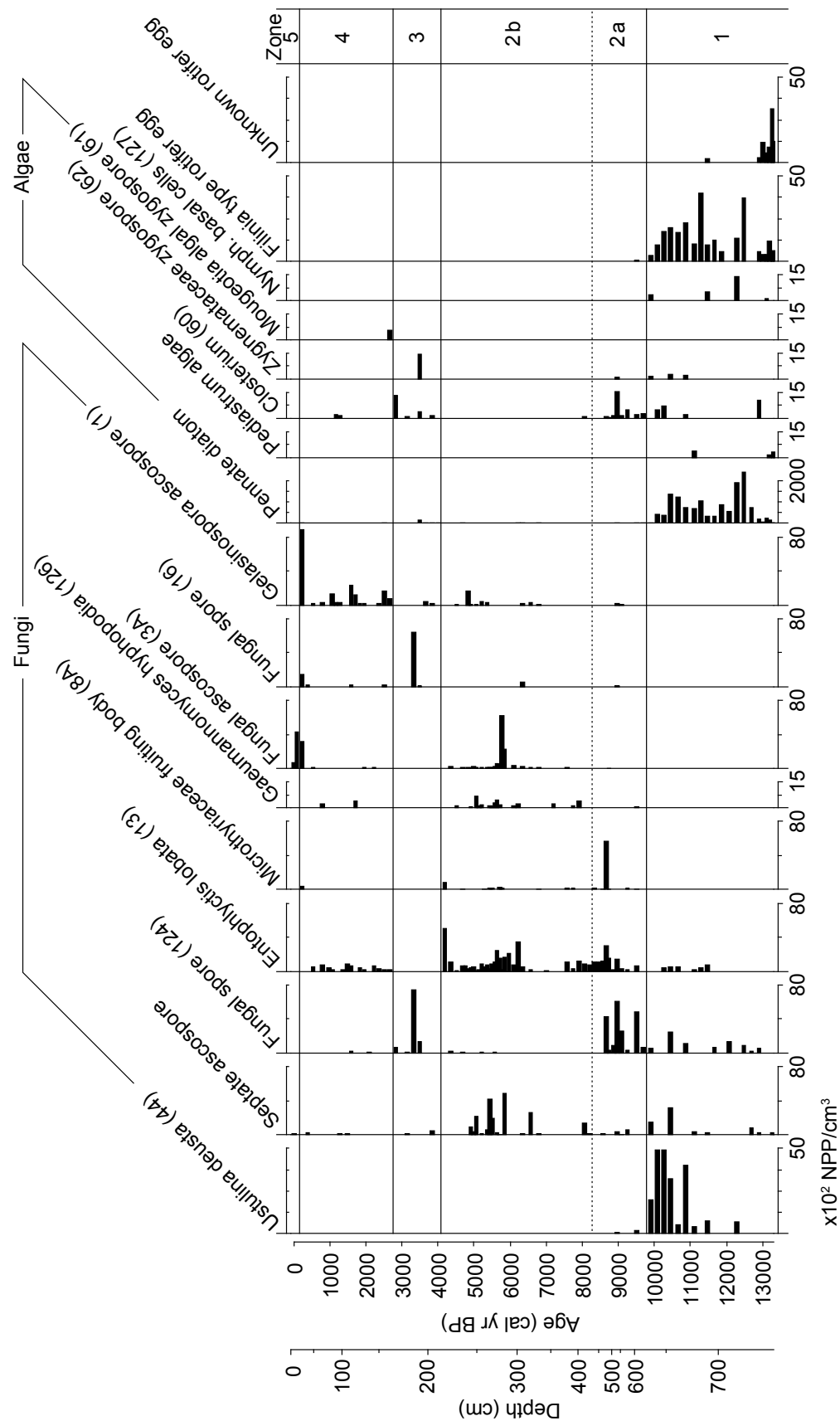


Figure 12. Concentrations of select non-pollen palynomorphs (NPP) from Grant's Bog, British Columbia. Numbers in parentheses refer to NPP types (Pals et al., 1980; van Geel, 1978). Note changes in scale.

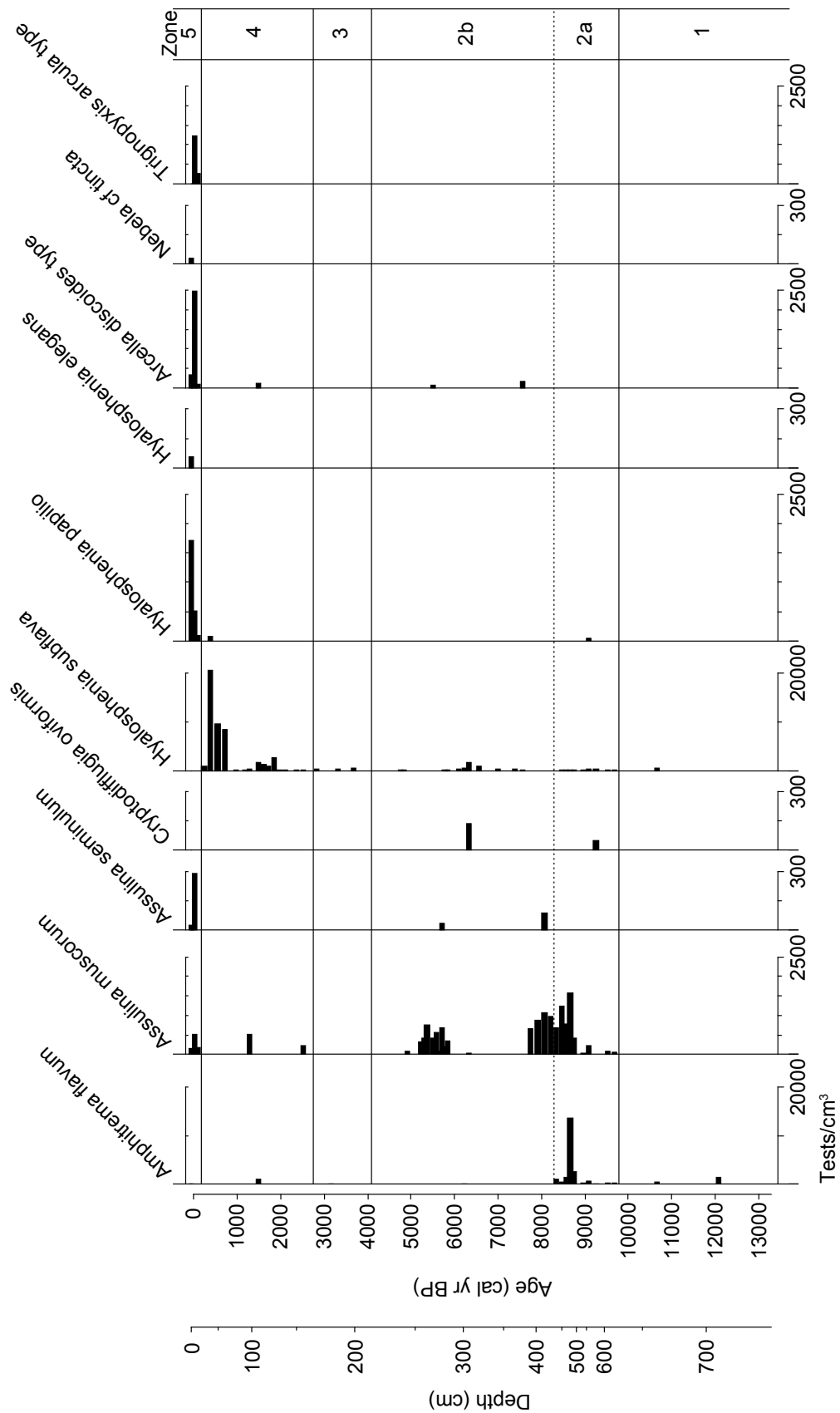


Figure 13. Testate amoebae concentrations from Grant's Bog, British Columbia. Note changes in scale.

septate ascospores, and *Ustulina deusta* are also present. *Entophlyctis lobata* is present above 690 cm (11,500 cal yr BP). Testate amoebae (*Amphitrema flavum* and *Hyalosphenia subflava*) were only observed in two samples in this zone (Figure 13).

Zone NPP-2: 624-213 cm, 9800-4100 cal yr BP

Fungal remains dominate the microfossils of NPP-2. *Entophlyctis lobata* is present throughout most of NPP-2 with a mean concentration of 950 sporangia/cm<sup>3</sup> (Figure 12). Microthyriaceae remains do not exceed 100 fruiting bodies/cm<sup>3</sup> with the exception of a peak of 5600 fruiting bodies/cm<sup>3</sup> at 474 cm (8700 cal yr BP). Testate amoeba remains tend to have sporadic occurrence with high concentrations over generally short time periods. *Assulina muscorum* is present from 630-390 cm (9900-7700 cal yr BP) and 379-279 cm (7600-5800 cal yr BP) (Figure 13). *Hyalosphenia subflava* is present in low abundance throughout the zone.

The NPP-2a subzone contains *A. flavum*, fungal spores (Type 124), and *Closterium* in higher abundance than subzone 2b. *Amphitrema flavum* is most abundant in subzone 2a with a mean concentration of ~1700 tests/cm<sup>3</sup>. Other testate amoebae occur in low concentrations. Fungal spores (Type 124) are present until 474 cm (8700 cal yr BP). *Closterium* is present in low abundances, with a mean concentration of 250 remains/cm<sup>3</sup>.

NPP subzone 2b contains septate ascospores throughout much of the subzone but are most abundant between 282 and 243 cm (5800-4900 cal yr BP). Fungal ascospores (Type 3A) are present in low concentrations in NPP-2b with an increase to ~6200

ascospores/cm<sup>3</sup> at 5800 cal yr BP. *Gaeumannomyces* is consistently present in low concentrations. *Gelasinospora* ascospores are present only intermittently in this subzone.

Zone NPP-3: 213-165 cm, 4100-2700 cal yr BP

This zone is characterized by an increase in algal remains, including *Closterium* with concentrations similar to those in subzone NPP-2a (Figure 12). Fungal spores (Type 16) are present infrequently with a single large peak in concentration. Type 124 fungal spores are also present infrequently with isolated peaks where concentrations are similar to NPP-2a. *Hyalosphenia subflava* continues in very low abundance (Figure 13).

Zone NPP-4: 165-18 cm, 2700-150 cal yr BP

Zone NPP-4 is characterized by an increase in fungal microfossils. *Entophlyctis lobata* and *Gelasinospora* concentrations reach up to 850 and 8900 remains/cm<sup>3</sup>, respectively, and are present in most samples (Figure 12). Pennate diatoms and most other algal remains are not present in this zone. *Hyalosphenia subflava* maintains low abundance until 66 cm (800 cal yr BP) and reaches a maximum concentration of 21,000 tests/cm<sup>3</sup> at 36 cm (400 cal yr BP) after which it decreases (Figure 13). Fungal ascospores (Type 3A) increase dramatically at 24 cm (250 cal yr BP), near the end of the zone.

Zone NPP-5: 18-0 cm, 150 cal yr BP to present

NPP-5 consists of the three uppermost samples. In this zone, a number of testate amoebae are recorded for the first time (*Hyalosphenia elegans*, *Trignopyxis arcula* type, *Nebela* cf. *tincta*) or increase substantially (*Assulina seminulum*, *Hyalosphenia papilio*, *Arcella*

*discoides* type). Fungal ascospores (Type 3A) are present with the exception of the uppermost sample.

## Discussion

### Site History and Development of Grant's Bog

Late-glacial climate has been interpreted as cool and humid in southwestern British Columbia (Mathewes, 1973). The Cordilleran Ice Sheet was in retreat, leaving coastal areas ice-free by ~14,000 cal yr BP (Hutchinson et al., 2004). Sea level reconstructions based on fossil diatoms and marine shells indicate that relative sea level reached 85 m above current levels between ~15,000-13,500 cal yr BP in the area around Courtenay (Hutchinson et al., 2004). This is similar to the elevation of Grant's Bog and is in close enough proximity that isostatic differences should be minimal (Clague and James, 2002; James et al., 2009). Fine marine clays are present at the base of the Grant's Bog core. The presence of marine diatoms in these clays suggests a brackish to nearshore marine environment. Sea level reconstructions (Hutchinson et al., 2004) and the Grant's Bog age-depth model suggest these marine sediments were deposited before 14,000 cal yr BP. Falling sea level isolated the basin from marine influence and lead to a gradual transition toward a freshwater lake. Similar lake formation is documented on the surrounding coast and nearby islands (Hutchinson et al., 2004).

Sediment at the study site deposited between ~14,000-13,300 cal yr BP consists of freshwater lacustrine clays low in organic matter (Figure 6) suggesting a significant influx of sediment from the catchment area. Influx of inorganic sediment reflects the erosional state of the surrounding landscape and suggests low soil stability and vegetation cover (Edwards and Whittington, 2001). Local vegetation on the lake margin consisted mainly of *Salix*, Rosaceae and herbaceous plants belonging to Cyperaceae,

Chenopodiaceae, and Asteraceae (Figures A1, A2). Low-lying topography in the region and the presence of *Typha* pollen suggest extensive shallow lake margins (Drohan et al., 2006). *Typha latifolia* is known to tolerate water to a depth of ~1 m (Grace, 1987) and typically inhabits areas with high phosphorus and nitrogen (Grace and Harrison, 1986). *Pinus* pollen along with *Athyrium filix-femina* spores and those from other Polypodiaceae ferns suggest an open forest with moist or wet well-drained soil (Haeussler et al., 1990). Ferns belonging to Polypodiaceae were likely common in the partial forest shade near the lake margin.

Beginning about 13,300 cal yr BP, organic lake sediments were deposited. The shift to a high-nutrient lacustrine environment is documented by changes in microfossils and an increase in the abundance of pollen from aquatic plants, including *Typha* and *Nuphar*. These organic sediments are characterized by a relatively low carbon content (~30%) compared to later sediments and peat and a similar C:N ratio to most lakes (Meyers and Teranes, 2001). Sediment accumulation rate remained low despite the increasing contribution of organic matter. Abundant freshwater diatoms from 13,300-10,000 cal yr BP (Figure 10) suggest predominantly open water. The increase in carbon and organic matter suggests high primary productivity at the site (Meyers and Lallier-vergés, 1999), which typically increases the abundance of diatoms (Battarbee et al., 2001). Abundant algae and increasing carbon accumulation are characteristic of considerable influx of soil nutrients from the surrounding watershed (Meyers and Lallier-vergés, 1999).

Rotifer eggs including *Filinia*-type are abundant in the organic sediment until ~9900 cal yr BP (Figure 12). Rotifers are found in a variety of aquatic to semi-aquatic

habitats, ranging from lakes to wet soils and mosses (Warner, 1990a), but *Filinia*-type rotifers are most commonly found in lake deposits and brackish water (van Geel, 2001). *Ustulina deusta*, a fungal parasite on the roots of deciduous trees (van Geel, 2001), is also present. Spores from *U. deusta* tend to be transported only several meters from their source and thus suggest the local presence of deciduous trees or shrubs (van Geel and Andersen, 1988). Pollen concentrations from local shrubs and herbaceous plants increase (Figure 10). Overall, there is an increase in vegetation density around the site as soils developed.

The core from Grant's Bog includes approximately 62 cm of limnic peat that accumulated over 1600 cal yr from about 11,500 to 9900 cal yr BP. During this phase, the peat accumulation rate increases. The %C (41%) and %N (2.7%) are similar to average values ( $39.4 \pm 8.2\%$  C,  $1.8 \pm 0.9\%$  N) for limnic peat (Figure 7; Treat et al., 2016). Comparatively high nitrogen is likely related to nutrient influx from the watershed and the abundance of algae.

Herbaceous plant remains form the majority of the limnic peat with a small contribution from *Sphagnum* mosses (Craig, 2016). *Nuphar* and *Typha* pollen increase in relative abundance compared to the lake sediment phase. Algal microfossils remain similar to those found in the lake sediment and suggest the continued presence of standing water. The transition from lake sediment to limnic peat suggests terrestrialization at the coring location, with decreasing lake levels, increasing organic influence and vegetation likely growing on floating mats or in marsh-like shallows.

Terrestrial herbaceous peat gradually replaces limnic peat around 9900 cal yr BP. The start of the terrestrial peat phase is characterized by an increase in the C:N ratios to

>20 as the contribution of algae decreases in the peat, which instead becomes dominated by the remains of land plants (Meyers and Teranes, 2001). The terrestrial peat phase has several periods where the hydrological regime appears to shift between high and low water table depths, a trend most reflected in changes to the NPP assemblages. The consistent herbaceous dominance in the limnic peat gives way to mixtures of sedge, Ericaceae and *Sphagnum* peat (Craig, 2016). *Sphagnum* spores quickly increase to 36% by 8900 cal yr BP; however, *Sphagnum* remains are not a dominant component of the peat until 8500 cal yr BP (Craig, 2016). The increase in *Sphagnum* spores and remains coincides with a decline in *Salix* pollen, and suggests that the bog surface or wetland margins may have become too acidic for *Salix* (Haeussler et al., 1990). The rate of peat accumulation continued to increase to 0.24 cm/yr at ~8900 cal yr BP. The terrestrial peat  $\delta^{13}\text{C}$  (-27.4‰) suggests a dominance of  $\text{C}_3$  plants or algae (Meyers and Lallier-vergés, 1999). The mean C:N ratio (40.6) is intermediate between values typical of *Sphagnum* (81.0), herbaceous (34.4), and woody (45.3) peat (Asada and Warner, 2005).

*Amphitrema flavum* is observed in the sequence from 9700-8300 cal yr BP, which indicates wet conditions and high water table (Charman et al., 2000; Lamarre et al., 2013). Type 124 fungal spores have been found to be correlated with the presence of *Dryopteris* ferns (Pals et al., 1980). Type 124 spores throughout this period, along with the presence of *Dryopteris* fern spores at 9000 cal yr BP, suggest that *Dryopteris* likely had a persistent presence near the site in low abundance. Microthyriaceae fruiting bodies, the reproductive structures of a foliar epiphytic fungi (Wu et al., 2011), are observed only intermittently. The *Closterium* remains common during this time have been found in other studies to inhabit areas with mesotrophic open waters but may also be related to

*Sphagnum* mosses as it is weakly acidophilous (van Geel et al., 1981). Increasing surface acidification by *Sphagnum* mosses (Soudzilovskaia et al., 2010) along with a lower water table likely lead to the decrease in *Closterium* by 8700 cal yr BP. The general change in hydrology is also supported by changes in plant groups (i.e. increase in *Sphagnum* spores). The open waters of the previous zone were likely closing but a high water table remained until about 8700 cal yr BP.

Environmental conditions during the early to middle Holocene lead to a continuation of the transition towards a more terrestrial environment. *Sphagnum fuscum* type spores become abundant (Figure 9). Hummocks and dry areas on nutrient-poor bog surfaces are the preferred locations for *S. fuscum* (Rydin and Jeglum, 2013). It has also been found that *S. fuscum* has increased growth during warm conditions allowing it to outgrow and outcompete vascular plants in nitrogen poor conditions (Keuper et al., 2011). Other *Sphagnum* spores are also common during this period, which, though they are unidentified, do indicate a general shift to an ombrotrophic bog at the coring location. There is a corresponding decrease in Cyperaceae pollen indicating a shift in hydrology and nutrient concentrations at the surface, likely a result of decreasing water table depth. Declines in the pollen from *Menyanthes* and Apiaceae suggest a reduction in nitrogen available to plants on the bog surface, likely resulting from a greater influence of precipitation compared to ground water (Klinka et al., 1989). The mechanism for surface isolation was likely the accumulation of *Sphagnum* peat, which resulted in increased surface height and a resistance to water movement (Soudzilovskaia et al., 2010). High evapotranspiration or a decrease in precipitation could have also been contributing factors to the changing site hydrology. *Drosera* pollen is first observed at 5100 cal yr BP and

suggests an ombrotrophic precipitation regime by at least this time (Figure A2). Type 3A fungal spores are present; they are from an unknown species, but have been documented in other peat records during very dry conditions (van Geel, 1978). The presence of *Gelasinospora* ascospores also indicate dry conditions at the surface (van Geel and Aptroot, 2006). *Assulina muscorum* and *Hyalosphenia subflava* testate amoebae also suggest a declining water table; these species have been documented as requiring a distance of ~15-35 cm between the bog surface and water table (Lamarre et al., 2013).

Between 3500-2300 cal yr BP, the surface of Grant's Bog became inundated, perhaps due to an increase in lake level. An increase in macroscopic charcoal observed during core processing immediately precedes a return of hydric NPPs and increased nitrogen, and suggests a period of increased fires at ~3500 cal yr BP. Wetland fires shift vegetation and plant growth in several ways: altering nutrient availability, local topography, and space for seed germination (Newman et al., 1998). Removing surface vegetation also favours vegetation change by facilitating the invasion of fast growing plants over established species (Newman et al., 1998). A severe fire on the bog surface could have disrupted the surface and nearby vegetation, causing a turnover in local plant community composition, and facilitating a return to wetter conditions at the coring location.

This hydrological change is reflected in the peat composition, the pollen record, and NPP assemblages. Ericaceous roots all but disappear from the record (Craig, 2016). Indeed, there is a marked reduction in Ericaceae pollen and an increase in pollen from *Myrica* and *Sanguisorba*. Increases in these taxa was likely facilitated by the removal of competition and might indicate increased nutrient availability. Vegetation transitioned

from that of a typical ombrotrophic bog to a dominance of sedges, herbs, and shrubs, which are more characteristic of a fen (Rydin and Jeglum, 2013). The increase in *Salix* pollen also supports a change in wetland hydrology and increasing pH to >5.5 if *Salix* was growing on the wetland surface (Haeussler et al., 1990) or the removal of larger trees in the surrounding forests allowing expansion of shade-intolerant *Salix* species. The C:N ratio decreases to <20 near 3000 cal yr BP and marks a shift from the high ratios characteristic of *Sphagnum* peat to that of predominantly herbaceous remains, but is still indicative of a terrestrial environment. The increase in nitrogen to ~2% may be indicative of increased influx to the site, as a result of increased runoff carrying ash produced by the burning of surrounding vegetation (Newman et al., 1998) or an increased contribution of algae.

Pennate diatoms, though present in extremely low abundance during the mid-Holocene, reappear and indicate the return of standing water, possibly from increased lake levels inundating the coring location. Increases in diatom concentration have been found to be related to vegetation composition change (Kokfelt et al., 2009), especially increases in Cyperaceae (Struyf and Conley, 2009). *Closterium* is again observed when the abundance of *Sphagnum* spores decreases and further indicates a decrease in surface acidity and the swamping of hummock species due to higher water levels (Haeussler et al., 1990). A resurgence of Zygnemataceae algae suggests the presence of shallow mesotrophic waters (van Geel, 1978).

The late Holocene (<2000 cal yr BP) is characterized by a return to drier conditions on the surface of Grant's Bog. Cyperaceae pollen remains low while *Sphagnum* spores increase. *Sphagnum* remains and roots from Ericaceous shrubs replace

herbaceous remains as the principal peat component (Craig, 2016). Cooler climate during the late Holocene (Chase et al., 2008; Walker and Pellatt, 2008) likely had little effect on the lowering of the water table. Instead the low decomposability of *Sphagnum* mosses is likely to have raised the surface above lake and ground water influence leading to the re-establishment of an ombrotrophic bog. *Gelasinospora* ascospores increase in combination with fungal spores (Type 3A) and *Entophlyctis lobata*, further suggesting relatively dry surface conditions.

Testate amoebae concentrations and diversity rise in the acrotelmic peat. Until ~400 cal yr BP *Hyalosphenia subflava* dominates. After this point, it is replaced by *Assulina seminulum*, *Hyalosphenia papilio*, *Arcella discoides* type, and *Trignopyxis arcula* type. The conflicting hydrological requirements of these species (Charman et al., 2000; Lamarre et al., 2013) suggest that a variety of moisture conditions were available. *Assulina seminulum* and *T. arcula* type both occur in low water table environments, while *H. papilio* has been found predominantly under very wet conditions (Charman et al., 2000; Lamarre et al., 2013). Surface vegetation remains that of a bog with an ombrotrophic hydrological regime, which continues to the present.

Site development and vegetation succession at Grant's Bog is similar to other south-coastal British Columbia wetlands (Figure 14). As with other low elevation sites (Hebda, 1977, 1983; Hebda and Haggarty, 1997), the wetland formed after sea level lowered. The resulting lake had a gradual increase and expansion of shallow water margins where limnic peat accumulated, similar to East Sooke Fen (Brown and Hebda, 2002b). Hydrosere succession occurred as peat thickness increased and summer

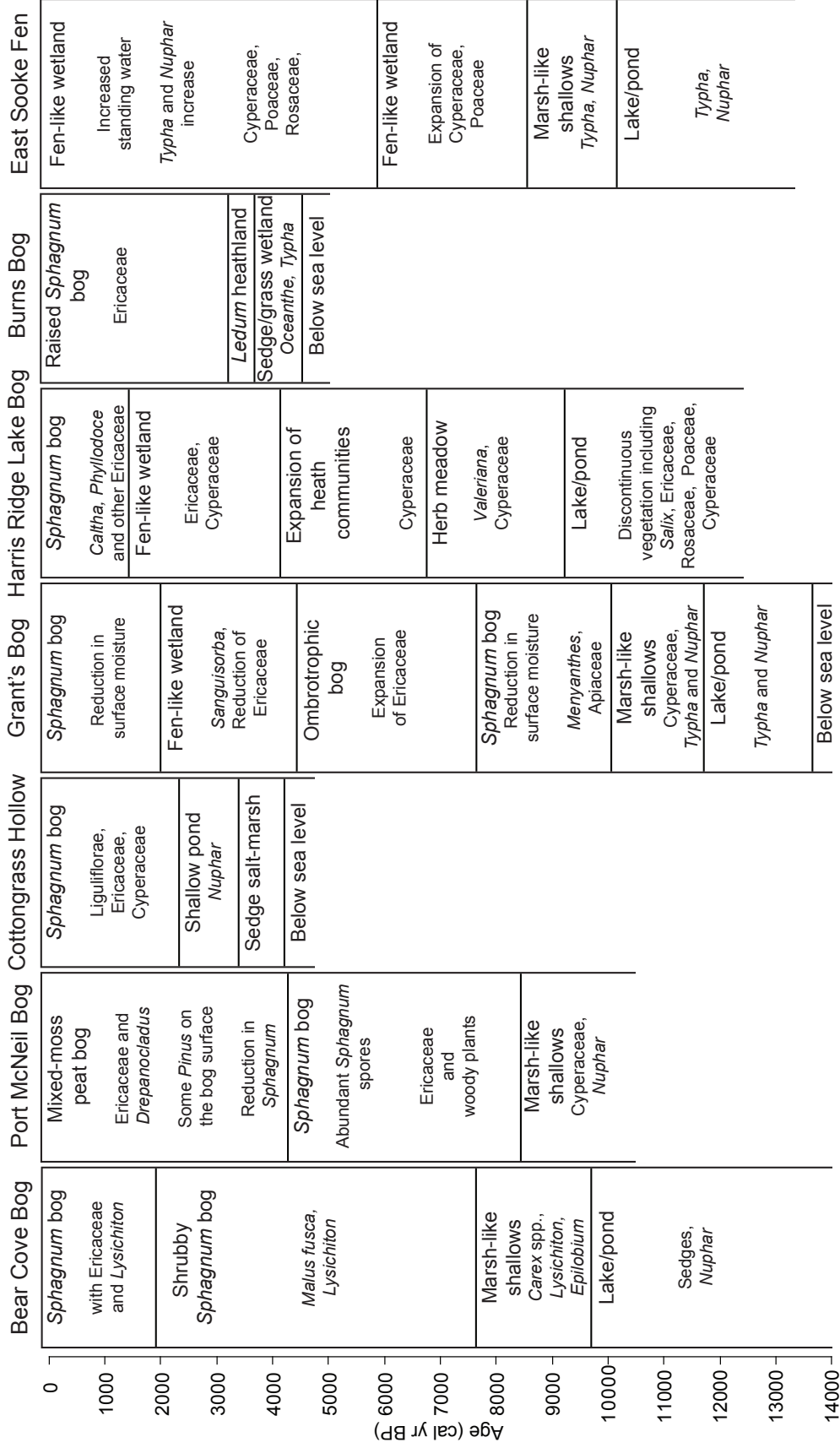


Figure 14. Site development comparison of Grant's Bog to nearby studied coastal British Columbia wetlands arranged from north to south - Bear Cove Bog, site below sea level before ~16,500 cal yr BP (Hebda, 1983), Port McNeill Bog (Lacourse and Davies, 2015), Cottongrass Hollow (Hebda and Haggarty, 1997), Harris Ridge Lake Bog (Fitton, 2003), Burns Bog (Hebda, 1977), and East Sooke Fen (Brown and Hebda, 2002b). Note that divisions and timing are approximate.

temperatures warmed during the early Holocene. Timing of the terrestrialization at Grant's Bog differs from nearby sites, likely due to local topography and climate, but the general developmental pattern towards ombrotrophy is similar among most sites.

Sedge peat underlies *Sphagnum* peat, suggesting that the developmental sequence at Grant's Bog was similar to other bogs in coastal British Columbia (Hebda, 1977; Heusser, 1960). Although pollen from shrubs (e.g. *Salix*, Rosaceae) increased during terrestrialization (Figure 11), there is little indication of a shrub peat phase (Craig, 2016) as was noted in Burns Bog (Hebda, 1977).

Following terrestrialization, natural succession from fen to an ombrotrophic *Sphagnum* bog occurred. *Drosera* was noted in the pollen record, which suggests low nitrogen availability. This sequence of bog development driven by increasing acidity and the reliance on precipitation for surface moisture is often regarded as the final stage of development (Rydin and Jeglum, 2013), though not all sites reach this point. Vegetation at Grant's Bog reached an ombrotrophic state during the middle Holocene; however a retrogressive succession to a fen-like wetland with open pools subsequently occurred, perhaps as a result of disturbance by fire and subsequent flooding.

Recovery from this disturbance and the subsequent expansion of *Sphagnum* lead to progressive succession and the return of an ombrotrophic regime. This is the final stage in the developmental history of Grant's Bog.

### **Long-term carbon and nitrogen accumulation**

The time-weighted mean carbon accumulation rate at Grant's Bog over the last 13,000 years was 18.7 g/m<sup>2</sup>/cal yr. This is higher than the two other peatlands studied in coastal British Columbia. The closest studied peatland in proximity to Grant's Bog is Port McNeill Bog on northern Vancouver Island, which had an overall carbon accumulation rate of 16.1 g/m<sup>2</sup>/cal yr (Lacourse and Davies, 2015). On British Columbia's north coast, carbon accumulation averaged 8.6 g/m<sup>2</sup>/cal yr at Diana Lake Bog, an oceanic slope bog (Turunen and Turunen, 2003; Loisel et al., 2014).

Peatlands with strongly seasonal climates and drier surface conditions, characteristic of northern and continental sites, generally have high long-term carbon accumulation (Gorham et al., 2003). Though primary productivity is greater in coastal sites, given sufficient time the generally more consistent temperature results in greater decomposition and slower long-term accumulation compared to peatlands with more seasonal climates (Asada and Warner, 2005). Mild temperatures and generally high and consistent precipitation throughout the year allows plants, most notably *Sphagnum* mosses, to have almost year-round growth.

Cold winters characteristic of continental climates and high-latitude regions result in a halting of moss photosynthesis, but also reduced decomposition (Buchner and Neuner, 2010; Davidson and Janssens, 2006). Similarly, permafrost peatlands maintain undecomposed organic matter beneath the surface (Treat et al., 2016); however, low year round temperatures result in lower carbon accumulation compared to the sites after permafrost thaw (Camill et al., 2001). Continental fens in western Canada had an average Holocene C accumulation of 32.5 g/m<sup>2</sup>/cal yr (Yu et al., 2014), higher than Grant's Bog,

which is expected. However, the time-weighted average from Grant's Bog is more similar to the mean accumulation of northern peatlands ( $22.9 \pm 2.0 \text{ g/m}^2/\text{cal yr}$ ) (Loisel et al., 2014).

As in other peatlands in the Northern Hemisphere (e.g. Lacourse and Davies, 2015; Loisel et al., 2014; Turunen and Turunen, 2003), Grant's Bog reached its maximum carbon accumulation rate ( $81 \text{ g/m}^2/\text{cal yr}$ ) during the early Holocene. High carbon accumulation during the early Holocene is attributed to high summer insolation and greater seasonality in temperature and insolation coinciding with the Holocene thermal maximum (Loisel et al., 2014; Yu et al., 2010). Interestingly, the maximum rate is nearly double the maximum rate at Port McNeill Bog on northern Vancouver Island ( $48.7 \text{ g/m}^2/\text{cal yr}$ ; Lacourse and Davies, 2015) and several times the rate at Diana Lake Bog on the north coast of BC ( $21 \text{ g/m}^2/\text{cal yr}$ ; Turunen and Turunen, 2003). This may be explained in part through warmer summer temperatures at Grant's Bog compared to these more northern sites.

The highest rate and most rapid increase in C accumulation at Grant's Bog occurred during the early Holocene when herbaceous remains dominated the peat composition (Figures 7 and 9; Craig, 2016). High growth and C content of herbaceous plants coupled with high nitrogen and warmer summer temperatures would have contributed to high primary production resulting in an increase in the CAR. CAR decreases (Figure 8) when *Sphagnum* remains dominate the peat macrofossil remains (Craig, 2016).

During the middle to late Holocene C accumulation reaches its lowest point and generally remains  $\sim 20 \text{ g/m}^2/\text{cal yr}$  from  $\sim 7500 \text{ cal yr BP}$  to the present. The similarity in

trends of peatlands across the Northern Hemisphere (Lacourse and Davies, 2015; Loisel et al., 2014; Turunen and Turunen, 2003; Yu et al., 2010) suggests that C accumulation depends more on regional climate compared to site specific local conditions. Small deviations in this overall trend in the late Holocene likely relate to hydrology or decomposition differences in the surface peat.

Carbon accumulation has been shown to depend on moisture stress and drought (Bu et al., 2013; Skre and Oechel, 1981), which may be reduced in peatlands with a ground water source (Klein et al., 2013). Thus an increase in precipitation might not lead to increased growth if there is a limitation during the growing season (Klein et al., 2013; Yu et al., 2009). Long-term accumulation has been found to be negatively correlated to precipitation (Gorham et al., 2003). Gorham et al. (2003) present precipitation and organic matter accumulation rates for continental North American bogs and fens (n=21) ranging from 450-3000 mm annual precipitation. Grant's Bog, with a mean annual precipitation of 1645 mm, had an average organic matter accumulation of 41 g/m<sup>2</sup>/yr during the Holocene. The rate is consistent with that predicted by the Gorham et al. (2003) model (38.5 g/m<sup>2</sup>/yr) and helps to fill the gap that the authors acknowledge of sites with 1500-3000 mm annual precipitation.

Port McNeill Bog has a lower peat accumulation rate (29.3 g/m<sup>2</sup>/yr; Lacourse and Davies, 2015) compared to that predicted by the model (34.8 g/m<sup>2</sup>/yr; Gorham et al., 2013), but the difference is within the range of the other sites and overall is in support of a negative relationship between precipitation and peat accumulation. The decrease in accumulation with increased precipitation is attributed to lower productivity of wet hollows (Gorham et al., 2003). Lower precipitation at Grant's Bog compared to Port

McNeill Bog (Lacourse and Davies, 2015) and Diana Lake Bog (Turunen and Turunen, 2003) might be a contributing factor to their difference in Holocene carbon accumulation.

Correlation ( $r=0.48$ ,  $P<0.001$ ) between the  $\delta^{13}\text{C}$  and C:N ratio of the Grant's Bog record suggests that the  $^{13}\text{C}$  to  $^{12}\text{C}$  isotopic ratio has been significantly altered from the initial composition by decomposition (Esmeijer-Liu et al., 2012). Surface peat from the last few centuries at Grant's Bog display decreasing  $\delta^{13}\text{C}$  and reflects the anthropogenic alteration of the atmospheric carbon isotope ratio (Esmeijer-Liu et al., 2012; Sharma et al., 2005). Overall,  $\delta^{13}\text{C}$  varies with plant community composition and stratigraphy.

Nitrogen accumulation rates (NAR), and its relation to carbon sequestration, has been a focus of studies using peat cores that span the last few centuries (e.g. León and Oliván, 2014; Olid et al., 2014; Turunen et al., 2004). These studies show the anthropogenic influence on N deposition and provide a prediction of future carbon dynamics in response to climate change. Holocene N accumulation has been the subject of few peat studies, especially in coastal British Columbia. Over long time scales N accumulation depends on precipitation, temperature, atmospheric deposition and other site specific factors (Turunen et al., 2004).

The time-weighted average N accumulation at Grant's Bog was  $0.56 \text{ g/m}^2/\text{cal yr}$  during peat accumulation. This rate is consistent with the mean Holocene N accumulation in northern peatlands ( $0.5 \text{ g/m}^2/\text{cal yr}$ ; Loisel et al., 2014). Port McNeill Bog on northern Vancouver Island has a mean NAR of  $0.4 \text{ g/m}^2/\text{cal yr}$  (Lacourse and Davies, 2015). Comparing values for the terrestrial peat, the rate of N accumulation is similar between the two sites.

Both the C and N accumulation rates are heavily influenced by the age-depth model and lead to similar overall trends through time. The record is characterized by an increase in %N throughout the lake sediment and limnic peat, though the highest rates of nitrogen accumulation are during terrestrial peat formation ( $3.0 \text{ g/m}^2/\text{cal yr}$ ) due to the higher overall rate of peat accumulation. The high %N coincides with the low C:N ratios of the lacustrine sediment, but the accumulation maximum occurs during herbaceous peat formation. Here the relatively high %N is likely the result of algal communities and influx of nutrients from the surrounding watershed, as the C:N is more similar to a lake than a terrestrial environment (Meyers and Teranes, 2001).

Towards the end of the early Holocene the NAR decreases rapidly to generally remain  $<0.5 \text{ g/m}^2/\text{cal yr}$  between 8500-3500 cal yr BP. The decrease in N mirrors a decrease in C accumulation (Figure 8) and a local vegetation change to include *Sphagnum* as a major peat component (Craig, 2016). Low N content of *Sphagnum* mosses in comparison to herbaceous remains helps to explain this accumulation decrease. Wetland surface height and isolation from ground water would also contribute to the N decline, as plants become dependent on atmospheric N deposition. Relative abundance of hummock and hollow microtopography also relate to changing N concentration and accumulation (Turunen et al., 2004). Nitrogen concentration of hummocks and hollows varies based on component plant groups (e.g., those with abundant vascular plants contain more N), but hummocks are on average lower in N (Turunen et al., 2004). Thus, expansion of hummock species over the surface may have been a contributing factor in decreasing N accumulation.

The late Holocene samples (<3500 cal yr BP) have a small increase in N accumulation (time-weighted mean=0.67 g/m<sup>2</sup>/cal yr). This coincides first with the reappearance of hydrophyllic NPP taxa and an inferred inundation of the bog surface. Charcoal immediately preceding this increase suggests that a modification of surface topography may have occurred. The coring location then became inundated, which led to a greater algal contribution to the organic matter and increased N accumulation. N accumulation increases slightly after 2000 cal yr BP compared to middle Holocene samples. This can be attributed to an increase in remains from Ericaceae shrubs (Craig, 2016); their fallen leaves on the surface likely drove this final increase in N accumulation (Turunen et al., 2004).

Interpretation of  $\delta^{15}\text{N}$  values is less clear than N accumulation rates.  $\delta^{15}\text{N}$  values are generally more dependent on microbial remineralization and kinetic fractionation than on plant groups or initial isotopic N ratios in peat (Andersson et al., 2012; Esmeijer-Liu et al., 2012). Hobbie et al. (2017) found that  $\delta^{15}\text{N}$  is correlated with depth. At Grant's Bog,  $\delta^{15}\text{N}$  did not depend on the peat composition or depth and there is only a moderate positive correlation ( $r=0.45$ ,  $P<0.001$ ) with %N. The high variability between samples and lack of correlation to stratigraphic changes exclude meaningful interpretation. There is a need for further studies focusing on N isotopes in deep peat cores in order to better explain the variation in  $\delta^{15}\text{N}$ .

### **Vegetation history of central Vancouver Island**

Lake sediments and peat provide records of British Columbia's vegetation history since the last glaciation (e.g. Brown and Hebda, 2002b, 2003; Brown et al., 2006; Galloway et

al., 2007, 2009; Hebda, 1983; Lacourse, 2005; Lacourse and Davies, 2015; Lucas and Lacourse, 2013) and interglacial period (Hebda et al., 2016). There are, however, spatial gaps throughout the province that necessitate the addition of other sites.

Coastal British Columbia plant communities during and immediately following the last glacial maximum were composed predominantly of shrubs and herbaceous plants (e.g. Warner et al., 1982). During the late-glacial period, tundra-like communities of diverse herbs and shrubs were present north of Vancouver Island (Lacourse et al., 2012). Cyperaceae, Poaceae and *Artemisia* were most common on the landscape along with *Salix* shrubs. As glaciers retreated, exposed terrain on central Vancouver Island would likely have supported similar plant communities due to the continued cold climate. *Pinus contorta* initially grew only as scattered trees across the landscape (Fitton, 2003; Lacourse, 2005).

*Pinus contorta* populations expanded and replaced the shrub and herb dominated tundra once climate became more favourable. Open *Pinus* forests were established by 15,000 cal yr BP on northern Vancouver Island (Lacourse, 2005), and reached northern British Columbia by 10,000 cal yr BP (Strong and Hills, 2013). The pollen record at Grant's Bog begins shortly after the site was isolated from marine waters sometime between 14,000-15,000 cal yr BP (Hutchinson et al., 2004). Isostatic rebound led to a rapid and extreme (~150 m) relative sea level decrease (Hutchinson et al., 2004) and exposure of the Nanaimo Lowlands along the east coast of Vancouver Island. Areas such as these likely provided *P. contorta* with vegetation-free space for colonisation and would have aided in its rapid expansion (Lacourse et al., 2003). By 14,000 cal yr BP, open forests of *P. contorta* were established near Grant's Bog as indicated by *P. contorta*

pollen proportions near 80% and high concentrations (Hebda, 1983; Hebda and Allen, 1993; Heusser, 1978).

The understory vegetation of these *P. contorta* forests included *Salix*, *Alnus viridis* and *Shepherdia canadensis* shrubs, and Polypodiaceae ferns. This community composition is commonly found in the modern environment of British Columbia in areas with immature soils or recent disturbance such as newly exposed shorelines and high elevations (Haeussler et al., 1990; Mathewes, 1973; Stolze et al., 2007). *Salix* was an important component of the late-glacial landscape (Lacourse et al., 2003) and was common in the forest understory around Grant's Bog. *Alnus viridis* is more cold tolerant than *A. rubra* (Furlow, 1979) and thus more abundant in the late-glacial period. The zoophilous nature of *Shepherdia canadensis* pollen results in short dispersal distances; it must therefore have grown in close proximity to Grant's Bog.

Central Vancouver Island forests during the Younger Dryas time period (12,900-11,700 cal yr BP; Rasmussen et al., 2006) were influenced by the return to cooler temperatures that mark this time. Though *Pseudotsuga* had reached central Vancouver Island by 13,300 cal yr BP (Figure 9), low relative pollen abundance (1-2%) suggests it maintained a fairly minor local presence on the landscape. *Picea* and *Abies* become a larger component of the *Pinus* forest and the concentration of all three taxa increase significantly (Figure 10). North of Vancouver Island, pollen records show an inversion in the warming trend through an increase in *Tsuga mertensiana* and replacement of coniferous forest by tundra landscapes (Mathewes et al., 1993). Pollen evidence from Grant's Bog suggests that central Vancouver Island remained sufficiently warm to allow continued presence of forest.

*Pseudotsuga* forests replaced *Pinus*-dominated forests near Grant's Bog by 11,200 cal yr BP. *Pseudotsuga menziesii* was restricted to Washington and Oregon during the height of the last glaciation (Gugger and Sugita, 2010; Tsukada, 1982). Increasing temperatures in the early Holocene allowed for the northward expansion of *P. menziesii* (Gugger and Sugita, 2010; Hebda and Allen, 1993; Klinka et al., 2000). This type of community on southern Vancouver Island dates to >11,500 cal yr BP and is reflective of a suitable climate by this time (Pellatt et al., 2001). Since very little *P. menziesii* pollen was found on northern Vancouver Island even during the periods of driest regional climate (Lacourse, 2005; Lacourse and Davies, 2015), we can infer that *P. menziesii* never dominated the forests of northern Vancouver Island. Of course individual trees would have grown past the continuous range, which accounts for the pollen and cone scales found on northern Vancouver Island and in mainland coastal records (Galloway et al., 2007; Howes, 1981; Lacourse and Davies, 2015).

In the early Holocene, *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Picea*, and *Abies* in the Grant's Bog pollen record suggest the presence of a mixed coniferous forest coincident with climate warming. Increasingly closed canopies likely lead to the exclusion of shade-intolerant *Pinus contorta* (Lacourse, 2005, 2009). Though *Pseudotsuga* pollen accounts for only ~20% of the total assemblage, its low pollen production and low dispersal distance suggest high landscape abundance (Hebda and Allen 1993). About 90% of *Pseudotsuga* pollen falls within a distance of about 800 m from the source, and an even shorter distance when deposited into small lake basins or bogs (Tsukada, 1982). For this reason, *P. menziesii* is commonly interpreted as a component of local vegetation when its pollen accounts for only 1-2% (Heusser, 1978;

Lacourse and Davies, 2015; Tsukada, 1982). Thus the high pollen abundance suggests more than local presence and that by 11,200 cal yr BP *Pseudotsuga* likely replaced *P. contorta* as the most abundant tree in the surrounding area.

The early Holocene fire regime in coastal British Columbia (Brown and Hebda, 2002a) would have benefited *Pseudotsuga* relative to other trees due to its high resistance to ground fires (Klinka et al., 2000). *Pteridium aquilinum* and other Polypodiaceae ferns appear to have been prominent members of the understory of these *P. menziesii* forests around Grant's Bog. Abundant *P. aquilinum* during this time also suggests relatively high fire frequency (Galloway et al., 2009) and open forest canopy (Lucas and Lacourse, 2013).

*Tsuga heterophylla* was less abundant in early Holocene forests near Grant's Bog compared to northern Vancouver Island, likely due to the xeric conditions. High concentration and relative abundance of *Alnus rubra* pollen is unlikely to reflect a high local abundance of *Alnus rubra* due to its prolific pollen production and long distance dispersal. *Alnus* pollen has been found to reach 40% relative abundance despite the nearest tree occurring 2 km from the sampling location (Allen et al., 1999). Furthermore, *Alnus rubra* is common in coastal British Columbia and often overrepresented in Holocene pollen records from the region (e.g. Lacourse and Davies, 2015; Pellatt et al., 2001). Thus the high relative proportion of *A. rubra* pollen at Grant's Bog is likely a reflection of regional pollen transport rather than high local abundance.

*Picea* and *Abies* pollen were of low abundance throughout the Grant's Bog pollen record. Their low pollen contribution is reflective of either low abundance near the site or pollen influx from larger and more distant populations. Cupressaceae, likely *Thuja*

*plicata*, was a minor component of the early Holocene pollen record and notably its pollen was not found in the middle or late Holocene portion of the record, suggesting that Cupressaceae was not abundant immediately around the site. Cupressaceae pollen at Grant's Bog is found only during the accumulation of limnic peat and lake sediment, possibly as a result of increased catchment size as they generally contain higher pollen concentrations than those from terrestrial peat (e.g. Hebda, 1983) or a result of poor preservation in the peat portions of the record. Other nearby sites in coastal British Columbia show that Cupressaceae has been more abundant during the late Holocene when climate was cooler and wetter relative to the early Holocene (Galloway et al., 2007; Hebda, 1983; Lacourse and Davies, 2015; Pellatt et al., 2001).

The composition of the early Holocene mixed forests near Grant's Bog shifts to contain a higher proportion of *Tsuga heterophylla* around 7000 cal yr BP. This coincides with cooler and wetter climate as the peak xerothermic window of the early Holocene closed (Hebda, 1995). The transition from *P. menziesii* to *T. heterophylla* dominated forest occurred over 2600 years from 7800-5200 cal yr BP (Figure 9). Mixed forest of *T. heterophylla* and *P. menziesii* continues until the present, but with *P. menziesii* pollen falling to an average of 14%. Though the decrease in *P. menziesii* is substantial, a continued proportion of this magnitude reflects relatively warm and dry conditions compared to sites on northern Vancouver Island and the mainland coast where *Pseudotsuga* pollen disappears during the middle Holocene (Galloway et al., 2007; Lacourse and Davies, 2015). The change in relative abundance from xeric to hydrophilic species in the mixed coniferous forest varies in time along Vancouver Island. To the north, at Port McNeill Bog, *T. heterophylla* rose to dominate forests around 8200 cal yr

BP coinciding with a decrease in *Pseudotsuga* (Lacourse and Davies, 2015). The Saanich Inlet record from southern Vancouver Island displays this shift as an abrupt increase in Cupressaceae around 5750 cal yr BP (Pellatt et al., 2001). The delayed reduction of xeric tree species in sites to the south is likely driven by a difference in temperature and also dictated by the coastal-inland precipitation gradient on Vancouver Island (Brown et al., 2006).

*Tsuga heterophylla* is the dominant tree species in the region from 5200 cal yr BP to the present where modern vegetation classification characterizes this area as belonging to the Coastal Western Hemlock biogeoclimatic zone (B.C. Ministry of Forests and Lands, 2016; Pojar et al., 1987). The abundance of *P. contorta* continues to decrease, possibly as a result of higher tree density hindering the abundance of this shade-intolerant species (Lacourse, 2009). Though also a shade-intolerant species, *Alnus rubra* pollen further increases and suggests an increase in its abundance in forests regionally, likely in disturbed sites.

The increased concentration of *Tsuga heterophylla* and *Alnus rubra* pollen around 5200 cal yr BP, suggest an increase in their absolute abundance in regional forests. Increased precipitation and continued cooling likely led to an increase in forest density (Lacourse, 2009), however *Alnus* would have persisted regionally in disturbed areas and perhaps even locally on the bog margin. *Myrica* pollen rises in abundance around 3000 cal yr BP. This is likely a local increase resulting from hydrological reversion, but has also been observed in other nearby records (Lacourse, 2005). A regional expansion of boggy lowlands was likely caused by greater moisture and the establishment of modern climate, allowing for an increase in *Myrica* (Lacourse, 2005). Ericaceae pollen and the

relative proportion of *Sphagnum* spores are variable and reflect a very local signal, though they generally increase in samples <3000 cal yr BP. The abrupt increase of *Sphagnum* spores in samples between 1200-500 cal yr BP is perhaps a response to the cool and wet climate or as part of the recovery after a possible surface fire.

Samples from the uppermost 25 cm (<250 cal yr BP) show an increase in *Alnus rubra* pollen at the expense of conifer pollen. Widespread and increased human activity and logging in the region is a likely cause as *Alnus rubra* readily colonizes roadsides and disturbed terrain. This does not indicate widespread *Alnus rubra* forest, but simply more disturbed sites in the region coupled with its high pollen production and dispersal.

The regional pollen record from Grant's Bog meets with the general expectations for central Vancouver Island. Climate forcing and rainshadow effects largely drove Holocene forest composition. During the late glacial, the vegetation of central Vancouver Island consisted of open *Pinus contorta* forest with a well-developed understory of shrubs and ferns. As temperatures warmed during the early Holocene *Pseudotsuga menziesii* became the most abundant species. Higher precipitation and lower temperatures that followed in the middle and late Holocene resulted in a *Tsuga heterophylla*-dominated forest that continues to the present.

## Conclusion

### Summary

A record of the developmental history of Grant's Bog and the surrounding regional vegetation was constructed for the last 14,000 cal yr using carbon, nitrogen, pollen and local microfossil remains. The site was likely exposed by retreating sea level at or by 14,000 cal yr BP, with the lake larger than it is at present. Slowly the site transitioned toward a terrestrial peat-forming ecosystem with vegetation more characteristic of an ombrotrophic bog by 9600 cal yr BP and accumulation of peat consisting of a mixture of herbaceous, woody, and *Sphagnum* remains. Site hydrology as inferred by microfossil remains and testate amoeba indicate a varying water table depth over the Holocene. Carbon accumulation was highest ( $81 \text{ g C/m}^2/\text{cal yr}$ ) during the early Holocene, similar to other Northern Hemisphere records (e.g. Loisel et al., 2014) and suggests a strong climatic influence. CAR decreased during the middle Holocene, likely as a result of climate cooling, but increased in the acrotelmic peat due to insufficient time to reach decay equilibrium. Overall the mean rate of C accumulation ( $18.7 \text{ g C/m}^2/\text{cal yr}$ ) is similar to the mean for northern peatlands. Though %N was highest during the lake sediment and limnic peat phases, the N accumulation rate (mean= $0.64 \text{ g N/m}^2/\text{cal yr}$ ) was highest during terrestrial peat accumulation as a result of rapid organic matter accumulation.

The forests near Grant's Bog were open and *Pinus contorta*-dominated during the late glacial, with a well-developed understory of shrubs and ferns. The Younger Dryas cooling event (12,900-11,700 cal yr BP) led to expansion of *Picea*, *Abies*, and *Pinus contorta* on the landscape and an increase in their pollen concentrations. The warmer and

drier conditions of the early Holocene allowed for the expansion of *Pseudotsuga menziesii*-dominated forest with abundant *Pteridium* in the understory. High relative abundance of *P. menziesii* (mean=28%) between 11,200-7000 cal yr BP reflects the importance of this species on the landscape. *Tsuga heterophylla* forest with continued *Pseudotsuga* and *Alnus rubra* presence occurs in the middle Holocene from 7000 cal yr BP to present due to decreased temperatures and an increase in precipitation compared to the early Holocene. Overall this vegetation history is in line with other studies on Vancouver Island.

### **Study Limitations and Future Research**

Multi-proxy peatland studies, such as the Grant's Bog record, have an advantage over those utilizing a single indicator in terms of inference power by the inclusion of multiple records. The accumulation rates and amounts of bulk N, C and its  $\delta^{13}\text{C}$  isotope have been shown to depend on the vegetation, climate, and hydrology of past environments (Meyers and Teranes, 2001).  $\delta^{15}\text{N}$  however, has been included in few peat studies spanning long time scales (Esmeijer-Liu et al., 2012). Over millennia, differences in N diagenesis and fractionation between core sections with different peat composition likely play as important a role in the final concentration as initial values (Esmeijer-Liu et al., 2012). The lack of long peat sequences in which  $\delta^{15}\text{N}$  was measured limits its power in reconstructing vegetation or environmental conditions. This study adds to the body of  $\delta^{15}\text{N}$  information spanning the Holocene, however interpretation of the Grant's Bog  $\delta^{15}\text{N}$  record was limited. Further studies of  $\delta^{15}\text{N}$  over long timescales and various peat types

would benefit interpretation by separating decomposition from environmental conditions at the time of deposition.

Inferences from paleoecological proxies are limited by knowledge of past ecological optima. Identification of pollen is well established through published keys and works from North America and Europe (e.g. Faegri and Iversen, 1989; McAndrews et al., 1973). However, some microfossils (e.g. fungal spore type 16, 3A) found at Grant's Bog were the remains of unidentified peatland inhabitants (van Geel, 1978). Further documentation of microfossil remains from Canada would be helpful in tying conditions to unidentified remains, which was not within the scope of this project.

This study was limited in its ability to reconstruct water table depth. Testate amoebae were identified only in pollen slides, where not all taxa are preserved, though enough diversity remains to infer general conditions. The generally low counts preclude detailed reconstruction of water table depth over the Holocene.

Since few peat studies in coastal British Columbia include a record of carbon dynamics and site development (e.g. Lacourse and Davies, 2015; Turunen and Turunen, 2003), the published literature would benefit from a higher spatial resolution of study sites and the sampling of additional sites. The complex and diverse physical geography and varying local climate requires a high site density for adequate representation of regional wetland variation. Inclusion of additional peatlands from coastal British Columbia would also aid in modeling peatland response to current and future climate change when integrated into large-scale peatland surveys.

Further study at Grant's Bog could focus on changes in testate amoebae assemblages to better reconstruct the site's hydrology, as there has been little focus on

testate amoebae in British Columbia. This study of Grant's Bog attempts to fill the spatial gap in the peatland record of coastal British Columbia by providing vegetation, hydrology, microfossil identification, and carbon and nitrogen dynamics over the last 14,000 years.

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## **Appendix: Supplemental Figures**

This appendix contains pollen diagrams for shrubs (Figure A1), herbs (Figure A2), ferns, fern allies and aquatics (Figure A3), and fungal and algal spores and remains (Figures A4 and A5). All identified taxa observed in the study of Grant's Bog are presented.

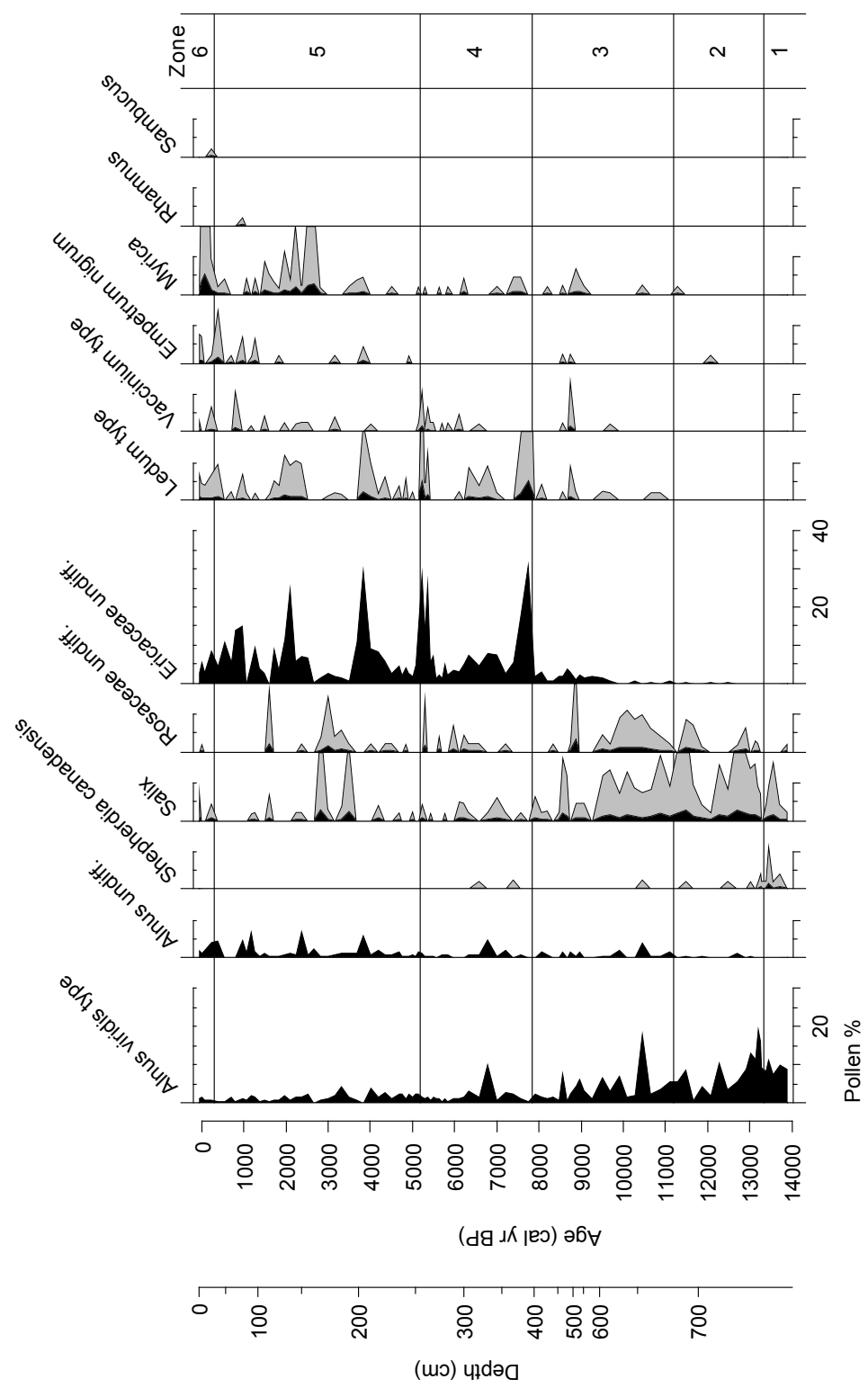


Figure A1. Shrub pollen percentages for Grant's Bog, British Columbia. Light grey represents 10x exaggeration.

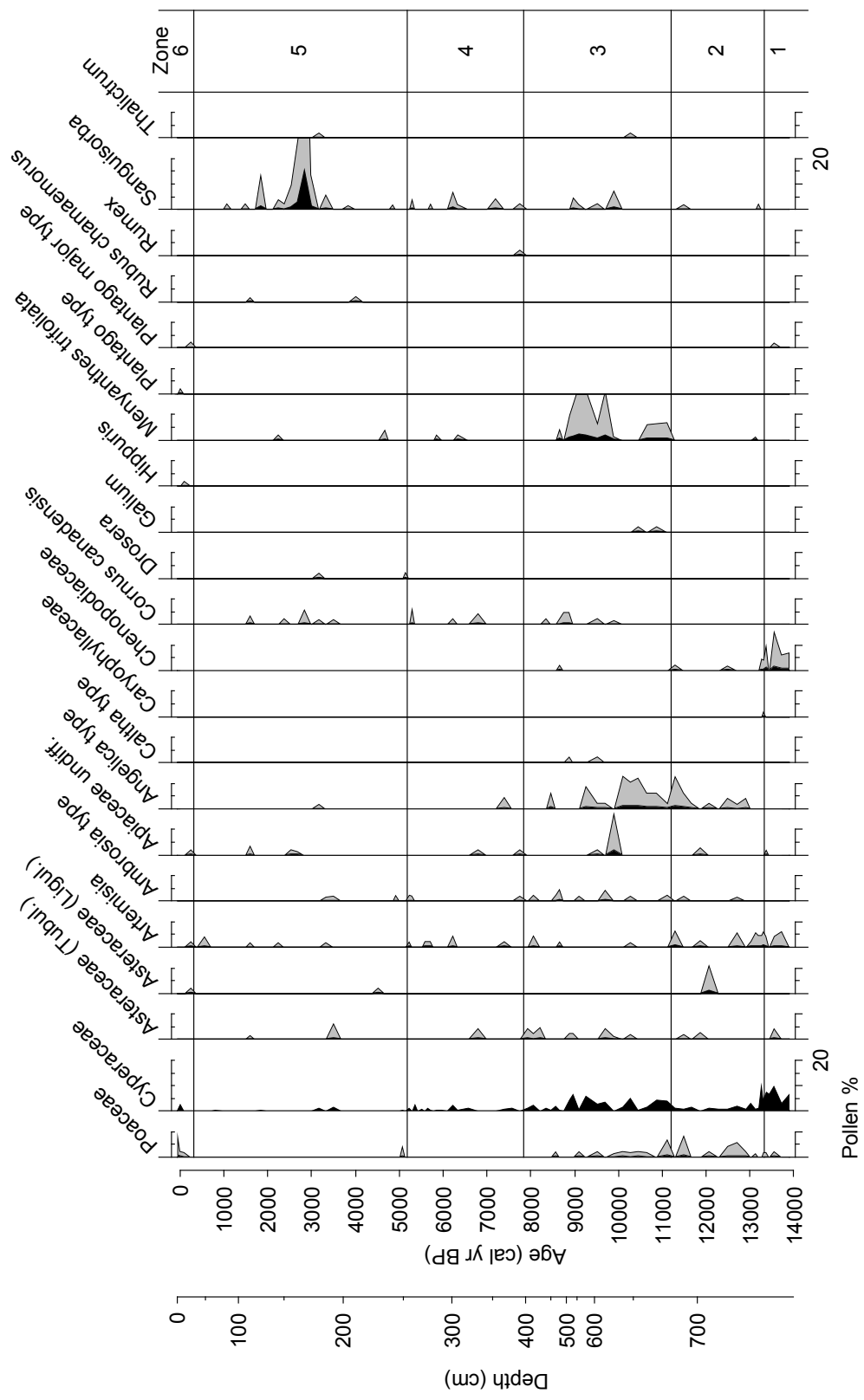


Figure A2. Herb pollen percentages for Grant's Bog, British Columbia. Light grey represents 10x exaggeration.

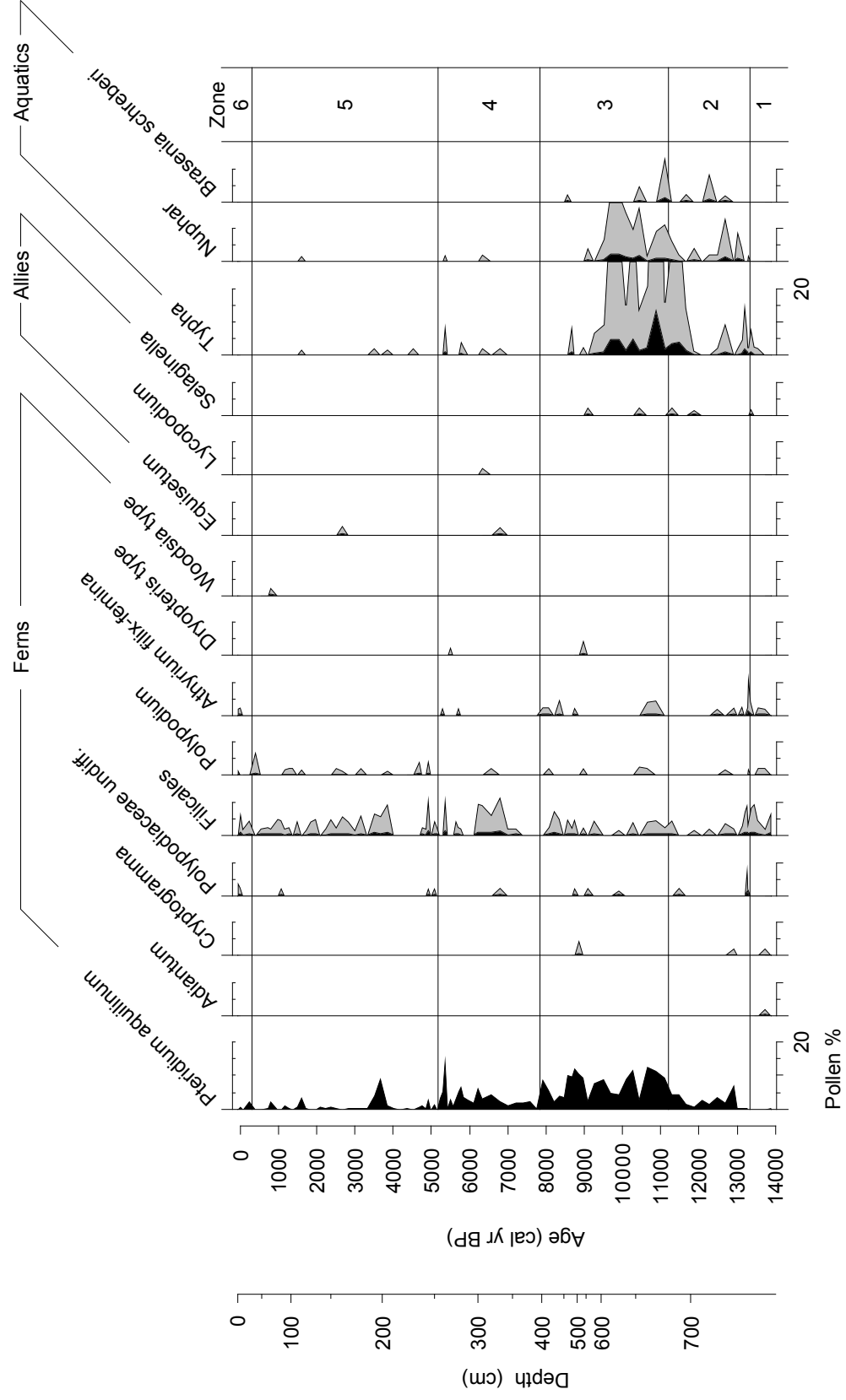


Figure A3. Ferns, fern allies, and aquatic pollen and spore percentages for Grant's Bog, British Columbia. Light grey represents 10× exaggeration.

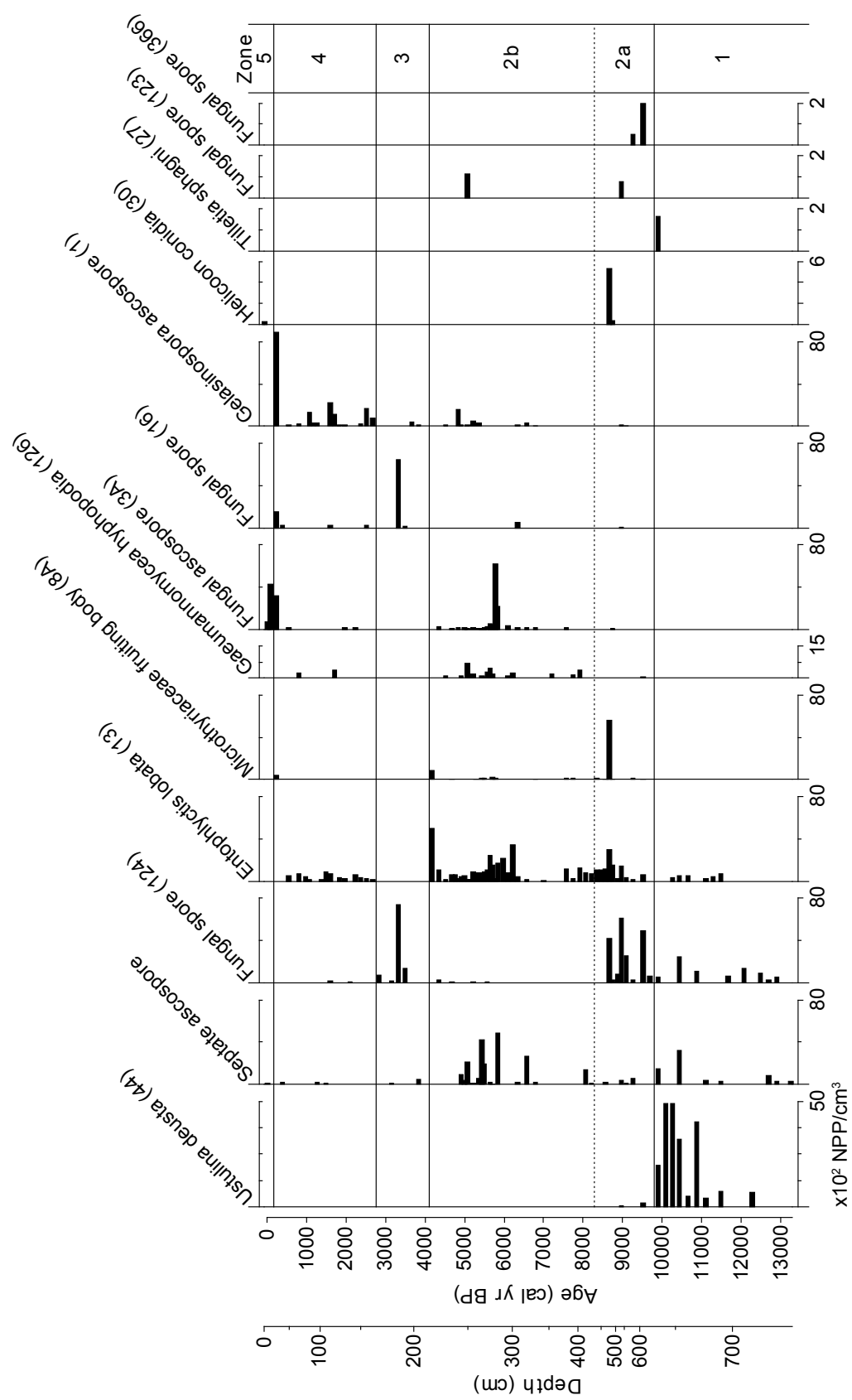


Figure A4. Concentrations of fungal spores and other remains from Grant's Bog, British Columbia. Numbers in parentheses refer to NPP types (Pals et al., 1980; van Geel, 1978). Note changes in scale.

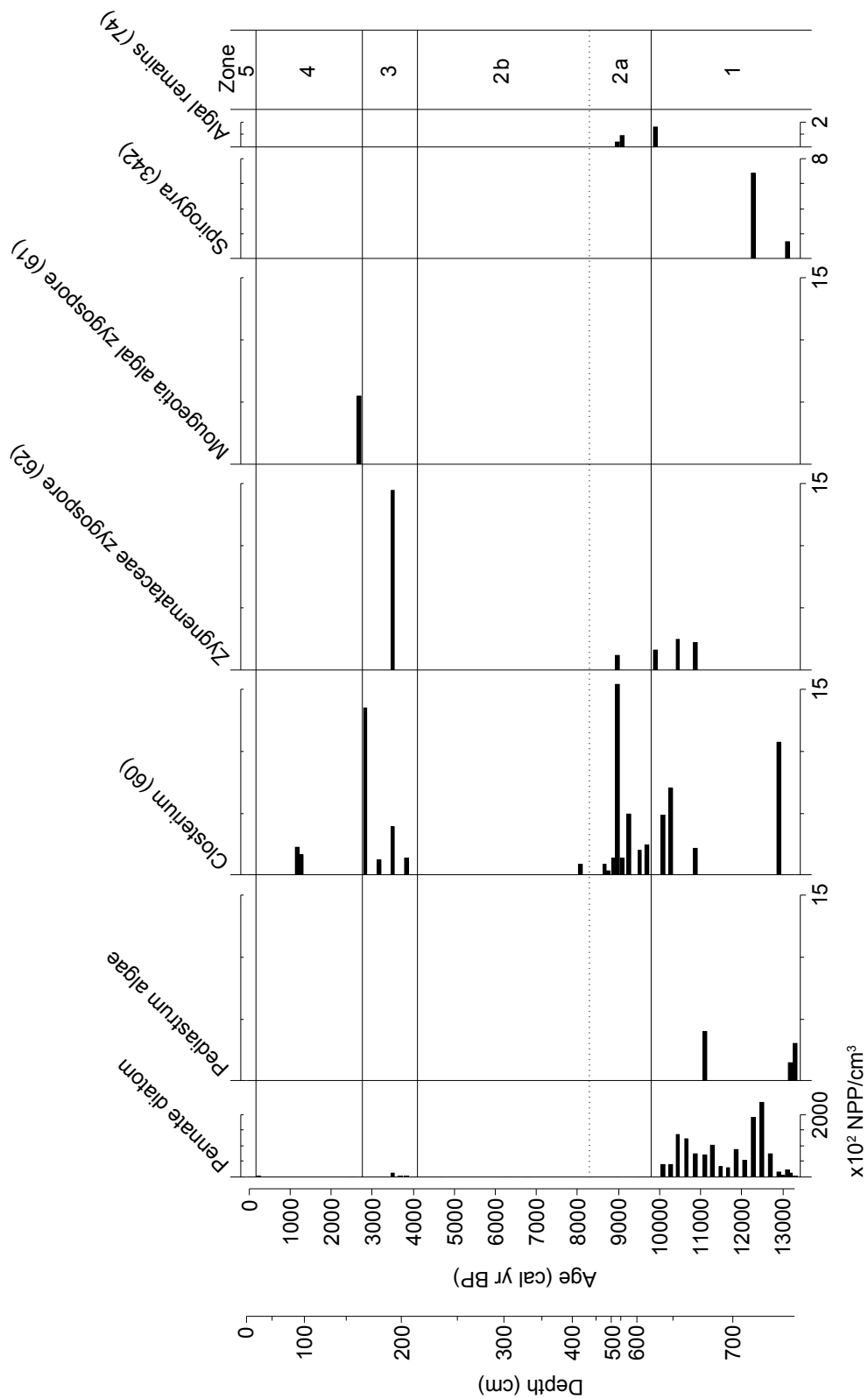


Figure A5. Concentrations of algal spores and other remains from Grant's Bog, British Columbia. Numbers in parentheses refer to NPP types (Pals et al., 1980; van Geel, 1978). Note changes in scale.