LATE QUATERNARY VEGETATION DYNAMICS OF THE QUEEN CHARLOTTE ISLANDS, NORTHERN VANCOUVER ISLAND, AND THE CONTINENTAL SHELF OF BRITISH COLUMBIA, CANADA

by

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ABSTRACT

Paleoecological analyses and radiocarbon dating of late-Quaternary sediments from the Queen Charlotte Islands (QCI), northern Vancouver Island, and the continental shelf along the coast of British Columbia reveal substantial changes in vegetation and climate over the last 14,000 ^{14}C yr (17,000 cal yr). Extensive portions of the shelf were subaerially exposed at the end of the last glaciation due to lowering of relative sea level by as much as 150 m. AMS radiocarbon ages indicate that the shelf in Hecate Strait was exposed between at least 14,330 and 12,860 ^{14}C yr BP. Cyperaceae were locally abundant on the exposed shelf, and fossil *Pediastrum* algae indicate the presence of freshwater. Interpretation of pollen from late-glacial lake sediments in the southern QCI suggest a succession from herb tundra dominated by Cyperaceae to dwarf shrub tundra including *Salix* and *Empetrum* before the development of *Pinus contorta* woodland. Fossil stomata suggest that *Pinus contorta* grew locally by 13,040 ± 305 ^{14}C yr BP, and an *in situ Pinus* stump and associated plant macrofossils demonstrate that forests grew on the adjacent shelf 12,200 ^{14}C yr BP. Submerged lake sediments in Logan Inlet record the transition from *Pinus contorta* woodland to *Picea* forests about 11,200 ^{14}C yr BP.

Northern Vancouver Island also supported *Pinus contorta* woodland during the late-glacial period. Mixed coniferous forests dominated by *Pinus contorta* with *Alnus* and pteridophytes occupied the shelf north of Vancouver Island 10,500 ^{14}C yr BP. Warming in the early Holocene allowed the northward extension of *Pseudotsuga menziesii*, although *Picea*, *Tsuga heterophylla*, and *Alnus rubra* dominated regional forests. By 7500 ^{14}C yr BP, shade-tolerant *Tsuga heterophylla* was the dominant forest tree. A cooler and wetter climate in the late Holocene facilitated development of temperate coniferous rainforest.

This research, in combination with earlier studies, demonstrates that portions of the continental shelf were ice-free and vegetated between 14,300 and 9,500 ^{14}C yr BP; moderate climatic conditions supported diverse and productive vegetation while adjacent mainland areas remained glaciated. Stratigraphic sequences spanning the last glaciation are still required to confirm the existence of continuous late Pleistocene glacial refugia in the QCI region.

— To Matt

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The environmental history of northwestern North America is currently of great interest on several fronts. Concerns about climate change in northern regions and the adjacent Pacific Ocean are spurring research into both short-term and longer term climatic fluctuations and their impacts on fisheries, forests, sea level and other environmental components (e.g., Finney et al. 2002; Moore et al. 2002). Research interest has also increased in the area of environmental dynamics since the end of the last glacial maximum. In particular, the growing debate regarding the peopling of the Americas has shifted to favour a coastal migration route from Asia to North America via the Pacific coast rather than an interior ice-free corridor (Dixon 1999; Koppel 2003). Research on the glacial and climatic history of the Pacific coast is being combined with studies of vegetation dynamics to better define the coastal environment as a migration corridor for plants, animals, and humans at the end of the last glaciation.

Background

The current understanding of late-glacial vegetation dynamics, particularly in the Queen Charlotte Islands (QCI) region, is scattered and incomplete. Numerous late Pleistocene and Holocene palynological and paleobotanical studies have been conducted in coastal British Columbia (Heusser 1955, 1960, 1983b, 1995; Mathewes 1973; Mathewes and Clague 1982; Warner et al. 1982; Banner et al. 1983; Hebda 1983, 1995; Hebda and Mathewes 1984; Warner 1984; Quickfall 1987; Fedje 1993; Pellatt and Mathewes 1994, 1997; Hebda and Haggarty 1997; Pellatt et al. 2001, 2002; Brown and Hebda 2002, 2003; Turunen and Turunen 2003) and along the coast in the adjacent U.S.A. (Heusser 1960, 1972, 1974; Barnosky 1981; Leopold et al. 1982; Petersen et al. 1983; Peteet 1986, 1991; Cwynar 1987, 1990; Worona and Whitlock 1995; Hansen and Engstrom

1996; Peteet and Mann 1994; Grigg and Whitlock 1998; Long and Whitlock 2002). These studies reveal substantial changes in vegetation and climate along the north Pacific coast since the last glacial maximum and provide important insights into natural climate variability in the region. However, only a few pollen records from the QCI (Mathewes and Clague 1982; Warner et al. 1982; Warner 1984; Fedje 1993; Heusser 1995) predate 10,000 ^{14}C yr BP.

The earliest paleoecological records come from the Cape Ball sea cliffs on northeastern Graham Island. Terrestrial and wetland communities dominated by herbs were established at Cape Ball by 15,000 ^{14}C yr BP (Warner et al. 1982; Warner 1984; Mathewes et al. 1985), while the adjacent mainland remained glaciated (Clague 1981). Therefore, the QCI served as a late-glacial center of biotic dispersal earlier than areas to the south and north. By 13,000 ^{14}C yr BP, herb communities were succeeded by dwarf shrub tundra, marked by the presence of *Salix reticulata* (see Appendix for the common names of plants) and other arctic/alpine indicators. The expansion of *Pinus contorta* by 12,000 ^{14}C yr BP, followed by *Picea sitchensis* at 11,300 ^{14}C yr BP and *Tsuga heterophylla* at 10,200 ^{14}C yr BP, suggests that forest development was relatively rapid (Mathewes and Clague 1982).

Due to the combined effects of eustatic sea level changes, isostatic crustal depression and rebound, and tectonism, the north Pacific coast is characterized by spatial and temporal variations in relative sea level that occurred during the late Quaternary (Clague et al. 1982a; Hetherington et al. 2004). During the late-glacial period, relative sea level reached a maximum of 200 m above present sea level along the British Columbia mainland (Clague 1985). A prominent shelf tilt lowered relative sea level by more than 150 m below present sea level in the QCI archipelago (Clague et al. 1982a; Josenhans et al. 1995, 1997; Fedje and Josenhans 2000). Extensive portions of the continental shelf were exposed at the end of the last glaciation and the QCI were intermittently connected to the adjacent mainland (Hetherington et al. 2003, 2004). These broad low-relief plains became ice-free and vegetated during the late-glacial period (Luternauer et al. 1989a; Barrie et al. 1993; Fedje and Josenhans 2000), and may have served as a migration corridor for plants, animals, and possibly humans (Heusser 1960; Fladmark 1979; Josenhans et al. 1997; Mandryk et al. 2001). Around the QCI, shorelines that date between about 12,750 and 9500 ^{14}C yr BP have since been submerged by rising relative sea levels (Josenhans et al. 1997; Fedje and Josenhans 2000; Hetherington et al. 2003). The shoreline history for western and northern Vancouver Island is not well-constrained but portions of the adjacent continental shelf were exposed between 11,500 and 7000 ^{14}C yr BP (Clague et al. 1982a; Luternauer et al. 1989a, 1989b; Friele 1991; Hetherington et al. 2004).

There is only scattered evidence, from both allochthonous and autochthonous plant fossils, of the vegetation that grew on the continental shelf during the latest period of lowered sea levels. Barrie et al. (1993) provided solid evidence for the subaerial exposure of the continental shelf between the QCI and the adjacent mainland in the form of marine cores with terrestrial deposits and *in situ* plant roots dating between 13,790 and 13,190 ^{14}C yr BP. Pollen analysis of a single aggregate sediment sample revealed an assemblage dominated by Cyperaceae, *Equisetum*, *Empetrum*, and Poaceae. Two other sites provide autochthonous evidence of rooted plants from the continental shelf. Fedje and Josenhans (2000) recovered a *Pinus* stump rooted in a peaty soil from Juan Perez Sound in the QCI that dates to 12,240 ± 50 ^{14}C yr BP. The drowned forest appears to have occupied a relatively large area at 145 m below present sea level about 12,200 ^{14}C yr BP. Luternauer et al. (1989a) also report well-developed soils and forests immediately north of Vancouver Island ca. 10,500 ^{14}C yr BP, based on terrestrial soil and *in situ* conifer roots in a marine core collected from Cook Bank in 95 m of water.

Research Objectives

The principal objective of this research is to reconstruct late Quaternary vegetation dynamics at sites on the QCI, northern Vancouver Island, and the adjacent continental shelf. By capturing a wide spatial array of sites, it is possible to develop a regional record of vegetation and climate dynamics between 15,000 and 10,000 ^{14}C yr BP. Emphasis is placed on the late Pleistocene and early Holocene periods on the QCI and the continental shelf, where late-glacial palynological records are scattered and incomplete. Fossil pollen analysis and radiocarbon dating are the main methods of investigation; however, these are supplemented by fossil wood identification, conifer stomata analysis, and plant macrofossil analysis. Lake sediments and the late Pleistocene portions of marine sediment cores collected from the continental shelf that contain submerged lake sediments and terrestrial deposits are analysed. Particular attention is paid to documenting paleobotanical evidence of 1) the Younger Dryas cooling event that occurred 11,000 and 10,000 ^{14}C yr BP using indicator species such as *Tsuga mertensiana* and pollen accumulation rates, and 2) food plants that would have been available to humans migrating along the coast in the late-glacial period. Accurate reconstructions of Pacific coast environments are important for evaluating the ecological context for human populations entering the Americas via a Pacific coastal route.

Thesis Overview

This thesis is organized into four main chapters. Chapter two provides a comprehensive review of all previous late Quaternary pollen and plant macrofossil studies conducted on the QCI and the adjacent continental shelf and summarizes late Quaternary climate change on the north Pacific coast. It also discusses the hypothesis that humans migrated into the Americas along a coastal corridor in the late Pleistocene period and, using paleoecological records, describes the plant resources that would have been available to humans migrating southward along the coast in late-glacial times. Chapter two also includes the results of pollen analysis of sediments from a freshwater lake that existed on the continental shelf between 12,000 and 10,400 ^{14}C yr BP, which is the first record of its kind from the north Pacific coast. This manuscript was written in 2001-2002 (Lacourse and Mathewes *in press*) for inclusion in a peer-reviewed book, which focuses on the human and environmental history of the QCI (Haida Gwaii).

Chapter three focuses on late-glacial terrestrial deposits retrieved from the continental shelf adjacent to the QCI and immediately north of Vancouver Island. To improve our understanding of the plant cover on the continental shelf during the latest period of subaerial exposure, paleoecological analyses were conducted on the radiocarbon-dated terrestrial deposits of Fedje and Josenhans (2000) and Luternauer et al. (1989a), two sites on the continental shelf where *in situ* conifers were preserved. Microscopic identification of fossil wood, and analyses of pollen and plant macrofossils from the associated paleosols and overlying shallow pond sediments indicate that productive *Pinus contorta*-dominated communities with abundant *Alnus crispa* and ferns grew on the shelf adjacent to and on the QCI around 12,200 ^{14}C yr BP. Dwarf shrubs including *Salix* and *Empetrum*, and herbaceous plants such as *Heracleum lanatum* and

Hippuris vulgaris were also important components of the shelf vegetation. Near northern Vancouver Island, mixed coniferous forests dominated by *P. contorta* with *Picea sitchensis*, *Tsuga* spp., *Alnus* spp., and ferns occupied the shelf around 10,500 ^{14}C yr BP. This chapter is published as Lacourse et al. (2003). Plant macrofossils were identified by R.W. Mathewes.

Chapter four reconstructs postglacial dynamics of forest vegetation on northern Vancouver Island including development of coastal temperate rainforests using sediments from Misty Lake originally collected by Walker (1988). Since Misty Lake is a moderate size lake, its sediments provide a regional record (*sensu* Jacobson and Bradshaw 1981) of postglacial vegetation and climate change for coastal British Columbia. Rates of palynological change, taken to represent rates of vegetation change, are used to describe temporal dynamics of forest composition and to determine whether vegetation change was gradual or more rapid during certain periods e.g., the late-glacial. Pollen analysis indicates that *Pinus contorta* dominated late Pleistocene forests on northern Vancouver Island; however, as *P. contorta* decreased in abundance, *Alnus rubra* and more shade-tolerant conifers (i.e., *Picea* and *Tsuga mertensiana*) increased. Orbitally induced warming around 10,000 ^{14}C yr BP allowed the northward extension of *Pseudotsuga menziesii*, although *Picea*, *Tsuga heterophylla*, and *A. rubra* dominated early Holocene forests. By 7500 ^{14}C yr BP, shade-tolerant *T. heterophylla* was the dominant forest tree. Cupressaceae (mostly *Thuja plicata* and *Chamaecyparis nootkatensis*) was present by 7500 ^{14}C yr BP but reached its maximum after 3500 ^{14}C yr BP, when a cooler and wetter regional climate facilitated the development of temperate coniferous rainforest. The highest rates of vegetation change are associated with late-glacial climate change and species with rapid growth rates and short life spans. This manuscript is in press with *Quaternary Science Reviews* (Lacourse *in press*).

Chapter five is an extension of research begun by Fedje (1993) and Barrie et al. (1993) on late Quaternary vegetation in the QCI region. AMS radiocarbon dating and stratigraphic pollen analysis of terrestrial deposits from Hecate Strait collected by Barrie et al. (1993) provide new insight into the vegetation that grew on the exposed continental shelf in Hecate Strait and the duration of its emergence. Pollen analysis of lake sediment from the southern QCI provides a detailed local record of late-glacial successional changes from herb tundra to dwarf shrub tundra before the transition to

Pinus contorta woodland. Fossil stomata confirm the local presence of *Pinus contorta* by 13,000 ^{14}C yr BP, earlier than previously thought. This manuscript will be submitted to *Boreas* for publication in the fall of 2004.

Chapter six summarizes briefly the results of this research, its significance and its limitations, and makes recommendations for future research.

CHAPTER 2

TERRESTRIAL PALEOECOLOGY OF THE QUEEN CHARLOTTE ISLANDS AND CONTINENTAL SHELF: VEGETATION, CLIMATE, AND PLANT RESOURCES OF THE COASTAL MIGRATION ROUTE[1]

Introduction

Since publication of the "Outer Shores" volume (Scudder and Gessler 1989), significant advances have been made regarding the glacial history, sea-level history, archaeology and paleoecology of the western margin of Canada. In order to improve the current state of knowledge about paleoenvironments along the coast of British Columbia, results from pollen and plant macrofossil analyses need to be expanded, synthesized, and integrated with other lines of evidence. Several new paleoecological studies have been published, and they provide intriguing insights into a drowned landscape that played an important role in the biological recolonization of British Columbia since the last glacial maximum.

As Barrie et al. (*in press*) explain, large portions of the continental shelf were exposed during the last glaciation, and were subsequently flooded due to rising relative sea levels. A key element of increasing interest in this drowned landscape is the hypothesis that the earliest migration of humans to the Americas occurred along a coastal corridor during deglaciation, if not earlier (Bryan 1941; Heusser 1960; Fladmark

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[1] Reprinted with permission from Lacourse and Mathewes (*in press*), ©2005 University of British Columbia Press.

1979). By 14,000 ^{14}C yr BP (see Table 2.1 for radiocarbon calibration), the Northwest Coast was a viable route for human movement into the New World with sufficient time depth to allow for pre-Clovis human history such as the 12,500 ^{14}C yr BP occupations at Monte Verde in Chile (Dixon 1999; Fedje and Josenhans 2000; Mandryk et al. 2001). Paleoecological studies that reconstruct the nature and extent of the vegetation during this critical time are important pieces of the puzzle. In addition to determining local and regional vegetation dynamics, these studies describe potential sources of food, medicines, or fibres for early human migrants, and also provide proxy records of past climates.

Intimately linked to the emerging interest in the coast as a biotic migration corridor is the long-standing controversy over whether plants and animals survived during the last glacial maximum in ice-free refugia along the coast (Heusser 1989). This controversy is not yet settled, but new lines of evidence such as molecular data on genetic divergence have recently become available for some of the region's plants, insects, birds, and terrestrial vertebrates (i.e., O'Reilly et al. 1993; Zink and Dittmann 1993; Heaton et al. 1996; Byun et al. 1997; Hamann et al. 1998). Although the search for continuously ice-free refugia on the coast has gone on for more than 40 years, the critical evidence for such a site has not yet been found. Along the central British Columbia coast, radiocarbon-dated evidence of non-glacial environments is restricted to the intervals before 21,000 ^{14}C yr BP and after 16,000 ^{14}C yr BP. In southeastern Alaska, a fossil ringed seal bone dated to 17,565 ± 160 ^{14}C yr BP (AA-18450) hints at a productive marine environment, and possible refugia in the Alexander Archipelago (Heaton et al. 1996; Dixon et al. 1997). Recent research suggests that the best possibility of a continuous refugium around the Queen Charlotte Islands (Haida Gwaii) is on the now-submerged continental shelf in Hecate Strait (Byun et al. 1997; Reimchen and Byun *in press*).

Paleoecological evidence thus far points to expanses of treeless herb and dwarf shrub tundra from the Olympic Peninsula in Washington to southeastern Alaska between at least 15,000 and 13,000 ^{14}C yr BP (Fig. 2.1), marked by the presence of *Salix*, *Empetrum*, Poaceae, Cyperaceae, and a variety of other herbaceous plants (see Appendix for common names of plants) (Warner et al. 1982; Heusser 1985; Mathewes

Table 2.1. Calibrated ages for the last 20,000 ^{14}C years.

Radiocarbon Years (^{14}C yr BP)	Calibrated Age[a] (cal yr BP)
1000	930
2000	1940
3000	3180
4000	4490
5000	5730
6000	6820
7000	7810
8000	8870
9000	10,190
10,000	11,400
11,000	13,000
12,000	14,060
13,000	15,630
14,000	16,790
15,000	17,940
16,000	19,090
17,000	20,240
18,000	21,390
19,000	22,540
20,000	23,690

[a] Calibrated ages are the median age derived from Calib 4.1 (Stuiver et al. 1998).

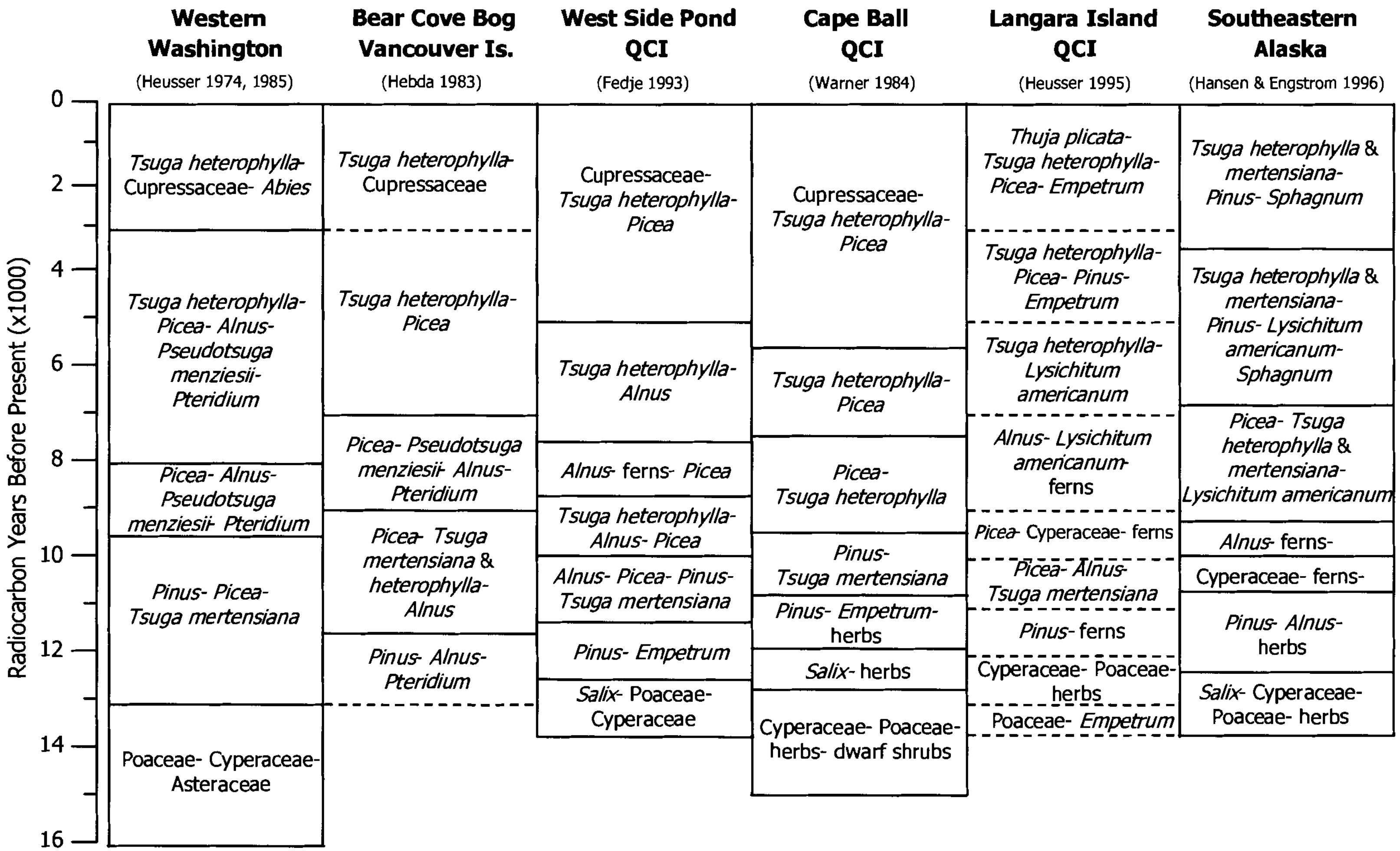

Fig. 2.1. Summary of vegetation histories reconstructed from paleoecological analyses for selected sites along the Pacific coast. Vegetation assemblages are indicated by major species, and are reported as published. Dashed horizontal lines indicate inferred radiocarbon ages.

1989; Barrie et al. 1993). On the Queen Charlotte Islands, this tundra-like plant cover gave way to coniferous forests around 12,500 ^{14}C yr BP with the rapid expansion of *Pinus contorta*, followed by *Picea* at about 11,200 ^{14}C yr BP and then *Tsuga heterophylla* at about 10,000 ^{14}C yr BP. Portions of the continental shelf were ice-free, vegetated, and available to humans between ca. 14,000 and 10,000 ^{14}C yr BP; moderate climatic conditions supported diverse and productive vegetation while adjacent mainland areas remained glaciated.

Review of New Late-Glacial Paleoecological Evidence

Mathewes (1989) summarized the history of vegetation on the Queen Charlotte Islands from the middle Jurassic period to the present. Since then, significant progress has expanded our understanding of the late-glacial paleoecology of the Queen Charlotte Islands and the surrounding areas. This new evidence is presented first, as an update to Mathewes (1989). Botanical nomenclature follows Douglas et al. (1989).

Marine sediment cores from the continental shelf have been particularly useful for investigating the local vegetation of landscapes that were exposed during the regional late Wisconsin deglaciation. Paleoecological analyses of sediments from Dogfish Bank in Hecate Strait (Fig. 2.2) demonstrate that at 13,200 ^{14}C yr BP the landscape was treeless and locally characterized by wet sedge tundra (Barrie et al. 1993). The fossil pollen assemblage includes high frequencies of Cyperaceae pollen and *Equisetum* spores, and relatively high values of *Empetrum* pollen. Total tree pollen frequency is only 4%, a very low value, which suggests a treeless local environment. The few arboreal pollen types found likely arrived by long-distance transport, or were reworked from melting ice or glacial drift. Total pollen and spore concentrations are relatively low, about 5600 grains cm^{-3} of sediment. This may indicate small vegetation populations and/or rapid sediment accumulation rates. Pollen and plant macrofossil studies west of Dogfish Bank at Cape Ball, Graham Island (Fig. 2.2) document the presence of *Salix* shrub tundra with abundant Cyperaceae, Poaceae, and mosses in lowland areas on the Queen Charlotte Islands between 14,000 and 13,000 ^{14}C yr BP (Barrie et al. 1993). Abundant *Salix* macrofossils are from a dwarf species, likely *Salix reticulata* or *S. stolonifera*, but the specific identifications are uncertain. Pollen from other herbs and

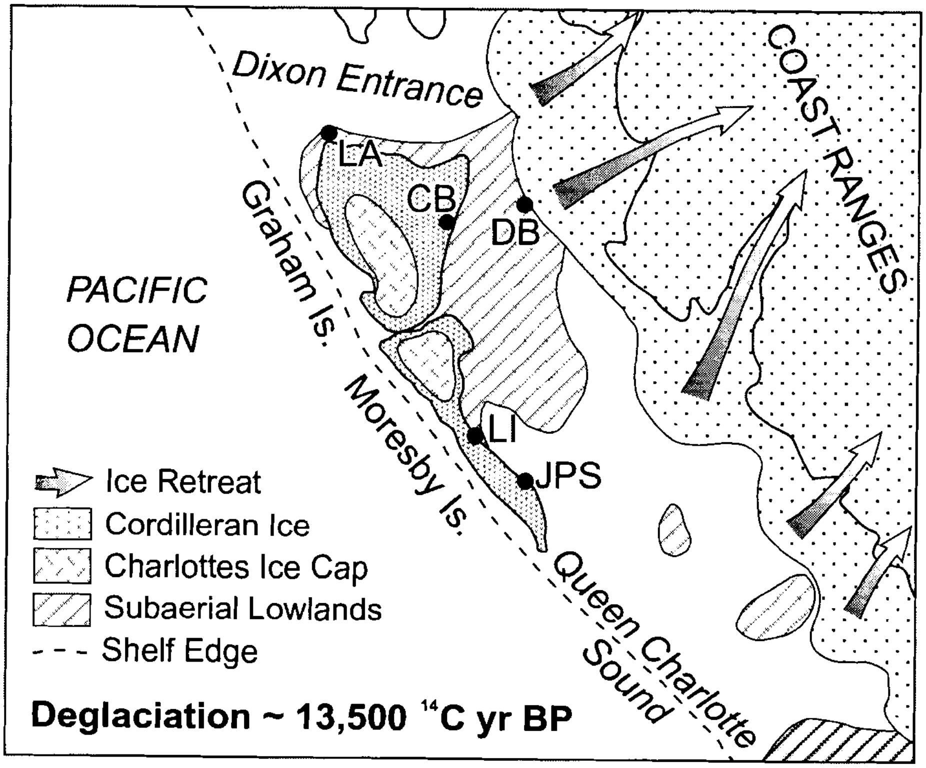

Fig. 2.2. Schematic reconstruction of ice retreat around the Queen Charlotte Islands approximately 13,500 ^{14}C yr BP. As Cordilleran ice retreated eastwards, it exposed large expanses of lowlands in Hecate Strait and elsewhere. Major paleoecological sites are Langara Island (LA), Cape Ball (CB), Dogfish Bank (DB), Logan Inlet (LI), and Juan Perez Sound (JPS).

dwarf shrubs such as *Artemisia*, *Polemonium*, and *Valeriana sitchensis* was also found at Cape Ball.

The most dramatic and incontrovertible evidence for well-developed forests that once occupied the continental shelf comes from a drowned paleosol in Juan Perez Sound (Fig. 2.2) (Fedje and Josenhans 2000). A *Pinus* stump (ca. 20 cm in diameter), still rooted in a peaty soil, was recovered from a drowned fluvial terrace at a present water depth of 145 m and yielded an AMS radiocarbon age of 12,240 ± 50 ^{14}C yr BP (CAMS-59768). This drowned forest site appears to have occupied a relatively large area but was transgressed by marine waters prior to 11,500 ^{14}C yr BP. The recovered sediments also contained abundant *Pinus contorta* cones and needles, and twigs of deciduous wood, one of which dates to 12,190 ± 50 ^{14}C yr BP (CAMS-59769). Fedje and Josenhans (2000) also note that *Picea* tree roots, dating to 10,500 ± 40 ^{14}C yr BP (CAMS-50947), were collected from a fluvial terrace at 51 m water depth and that wood was abundant at several other locations on the shelf.

Further south, on Cook Bank off northern Vancouver Island, Luternauer et al. (1989a) report pollen and plant macrofossil evidence of well-developed soils and colonization by trees, herbs, ferns, and mosses about 10,500 ^{14}C yr BP, when relative sea level at Cook Bank was 95 m lower. Studies of now-submerged terrestrial sediments with *in situ* roots show that *Pinus contorta* is the dominant pollen type but *Picea*, *Alnus* and both *Tsuga heterophylla* and *T. mertensiana* are also present. Total pollen and spore concentrations in a silt bed at this site reach 760,000 grains cm^{-3}, suggesting high productivity from a well-established plant cover, possibly combined with slow sedimentation rates in a shallow freshwater environment. Local wetland conditions are represented by the pollen of Cyperaceae, Apiaceae, and *Caltha*, and spores of various ferns and *Sphagnum* moss. Algal cysts such as those of *Spirogyra* indicate the presence of standing pools of freshwater.

To improve our understanding of the vegetation on the continental shelf during the latest period of subaerial exposure, Lacourse et al. (2003) conducted further paleoecological analyses on the radiocarbon-dated terrestrial deposits of Fedje and Josenhans (2000) and Luternauer et al. (1989a). At both sites on the continental shelf, conifers in growth position are preserved, confirming that terrestrial vegetation was well-established. Microscopic identification of fossil wood, and analyses of pollen and

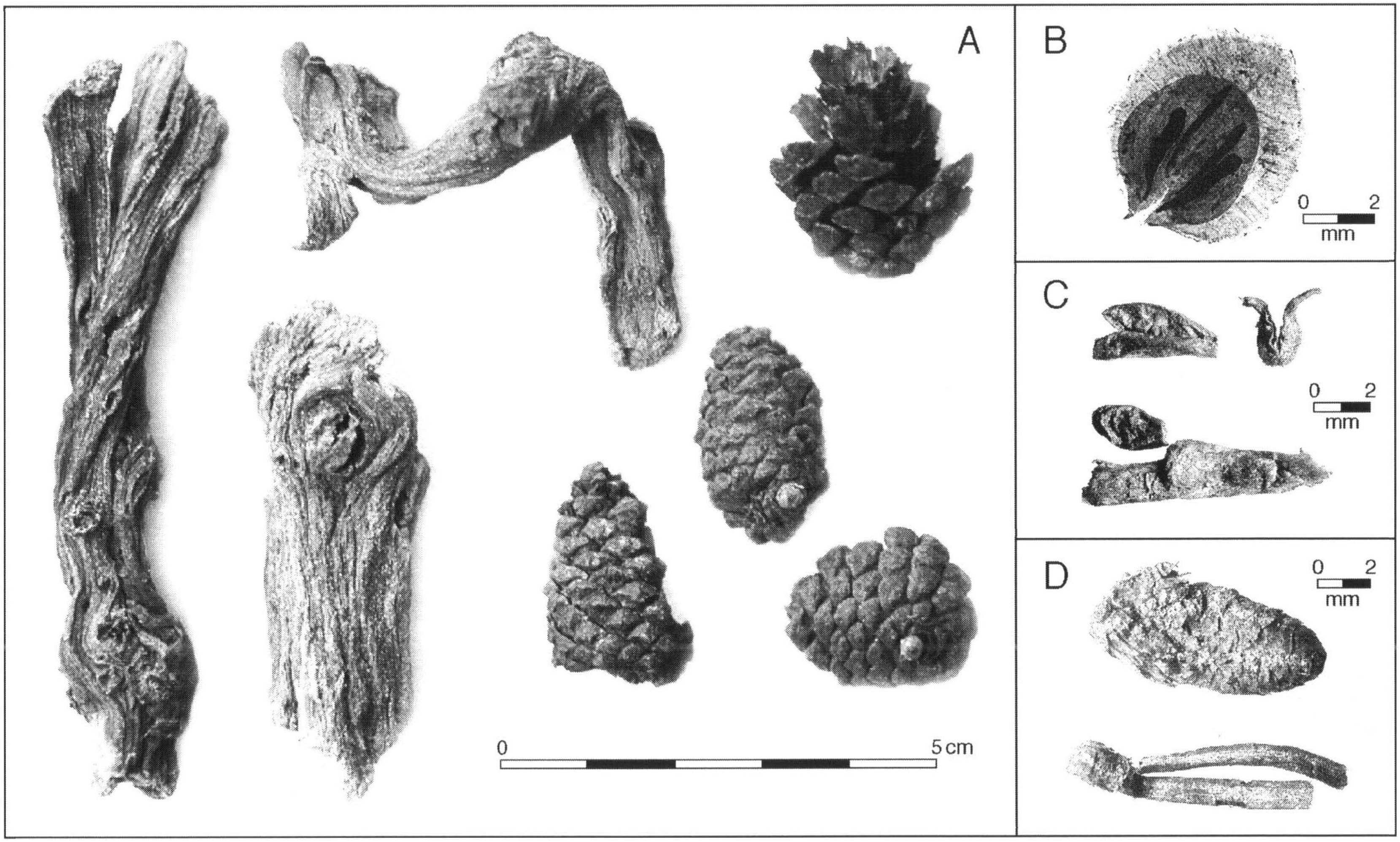

Fig. 2.3. Selected plant macrofossils from Juan Perez Sound. (A) *Salix* twigs (left) and female cones of *Pinus contorta* (right), (B) *Heracleum lanatum* fruit, (C) *Salix* buds and capsules, (D) Male cone and paired needle base of *Pinus contorta*. (Reprinted with permission from Lacourse et al. (2003), © 2003 Elsevier Ltd.)

plant macrofossils (Fig. 2.3) from the associated paleosols and overlying shallow pond sediments indicate that productive *Pinus contorta*-dominated communities with *Alnus crispa*, *Salix* and ferns grew on the shelf adjacent to and on the Queen Charlotte Islands around 12,200 ^{14}C yr BP. The presence of other shade-intolerant species such as *Empetrum*, *Sanguisorba canadensis*, and *Antitrichia curtipendula* moss suggests open gaps in the woodland vegetation. The riparian nature of the landscape is supported by the presence of plants such as *Heracleum lanatum*, *Hippuris vulgaris*, *Adiantum aleuticum*, *Isoëtes*, *Equisetum*, and Cyperaceae. Scattered individuals of *Tsuga mertensiana* accompanied *P. contorta* on more upland sites along with *A. crispa*, *Salix*, and *Empetrum* in open areas. At Cook Bank, mixed coniferous forests dominated by *P. contorta* with *Picea*, *Tsuga heterophylla*, *T. mertensiana*, *Alnus rubra*, *A. crispa*, and ferns occupied the shelf at 10,500 ^{14}C yr BP. Pollen of *Abronia latifolia*, a creeping perennial typical of coastal beaches but infrequent on Vancouver Island today (Douglas et al. 1989), indicates that sandy beach vegetation grew along the ancient shoreline of northern Vancouver Island and that shoreline soils were poorly developed.

In addition to paleoecological studies of sediments from the continental shelf, similar research has been conducted using lake sediments from the Queen Charlotte Islands and Vancouver Island. Heusser (1995) presents an account of past vegetation from analyses of a sediment core taken on Langara Island that, based on regional chronostratigraphy from other sites, spans an estimated 13,500 years (Figs. 2.1 and 2.2). The record commences with a coastal tundra community that is dominated by Poaceae, Cyperaceae, and Ericaceae shrubs including *Empetrum*. This herbaceous tundra also included *Salix*, Apiaceae, *Artemisia*, *Polemonium*, and *Koenigia islandica*, an arctic annual typical of wet sites (Porsild and Cody 1980). By 12,000 ^{14}C yr BP, open *Pinus contorta* communities with *Alnus* and ferns were established. Heusser (1995) attributes the widespread success of *P. contorta* to the absence of competition, its rapid reproductive ability, and its ability to grow on coarse, nutrient-poor soils. As competition with *Alnus* and *Picea* increased, *P. contorta* declined in relative abundance and by 10,000 ^{14}C yr BP was only a minor component of the surrounding vegetation.

Fedje (1993) reconstructed the late-glacial and Holocene vegetation history from West Side Pond, a small basin on South Moresby Island (Fig. 2.1). In this case, basal sediments that date to 13,500 ± 480 ^{14}C yr BP (CAMS-2523) are dominated by herbaceous pollen, including Cyperaceae and Poaceae and other herbs like *Artemisia* and *Heracleum lanatum*. Re-investigation of this site has shown that a variety of other herbs were also present: *Lupinus*, *Epilobium*, *Gentiana douglasiana*, *Rumex*, and *Polemonium* (Chapter 5). These taxa all suggest that local conditions were moist to wet. *Salix* and *Empetrum* shrubs soon became more common and probably occupied drier upland sites while ferns and clubmosses were likely restricted to moist sites. By 12,500 ^{14}C yr BP, *Pinus contorta* dominated the vegetation as it did at most sites along the Pacific coast. The local presence of *P. contorta* is confirmed by abundant macrofossils, including a *P. contorta* needle that dates to 12,190 ± 140 ^{14}C yr BP (CAMS-2525). A sharp decline in the percentage of *P. contorta* pollen concomitant with marked increases in *Alnus* and *Picea* pollen occurs between 11,500 and 10,000 ^{14}C yr BP. *Picea* needles and *Alnus* leaf fragments and seeds demonstrate the local presence of these trees. *Tsuga mertensiana* also arrived ca. 11,000 ^{14}C yr BP. It was a minor yet significant component of the vegetation since its presence indicates cool temperatures and deep snowpacks (Pojar and MacKinnon 1994).

Paleoecological studies have also been conducted on Brooks Peninsula, a reputed glacial refugium on the west coast of Vancouver Island. Hebda and Haggarty (1997) present reconstructed vegetation histories for six sites on Brooks Peninsula. At both high and low elevation sites, the landscape was characterized by *Pinus contorta* forest between 13,000 and 12,000 ^{14}C yr BP that included scattered *Tsuga mertensiana*. *Tsuga mertensiana*, *Picea*, and *Abies amabilis* populations expanded, at the expense of *P. contorta*, between 12,000 and 10,000 ^{14}C yr BP, forming mixed coniferous forests. *Tsuga heterophylla* was abundant on lower slopes. Basal radiocarbon ages from these sites are based on bulk sediments, which typically yield significantly older radiocarbon ages than AMS radiocarbon dating on plant macrofossils at the same depth. Therefore, the radiocarbon ages should be viewed as maximum ages.

Current Studies at Logan Inlet

To further study the terrestrial vegetation and paleoenvironment of Hecate Strait, the late-glacial portions of sediment cores retrieved from submerged lakes on the continental shelf are currently being studied. These studies emphasize the late-glacial interval before 10,000 ^{14}C yr BP, which includes the probable time of human migration from the north. Here, we present the results of pollen analysis from submerged lake sediment in Logan Inlet (52° 47′ N, 131° 41′ W), which is located immediately north of Richardson Island, one of the 150 islands that compose the Queen Charlotte Islands archipelago (Fig. 2.2). Logan Inlet is a formerly subaerial basin with a sill depth of −80 m (Fig. 2.4) (Josenhans et al. 1997). At the end of the Pleistocene, lowered relative sea levels isolated basins such as Logan Inlet, creating sediment-trapping lakes. At that time, as little as 5 km of water may have separated the enlarged archipelago from the mainland (Josenhans et al. 1995). Diatom analysis indicated that marine incursion of the basin occurred about 10,400 ^{14}C yr BP (Josenhans et al. 1997).

Methods

A 12 m piston core (VEC94A-018) was retrieved from Logan Inlet by the Geological Survey of Canada (Josenhans et al. 1997). The core penetrated marine and paleolake sediments (Fig. 2.4), revealing a sharp contact between stratified lake sediment and overlying slumped marine deposits at 4.4 m. Plant macrofossils were removed from the lake sediments, identified and then submitted to Lawrence Livermore Laboratories for AMS radiocarbon dating (Josenhans et al. 1997). The paleolake sediments date between 12,000 and 10,400 ^{14}C yr BP (Table 2.2). Sediment ages were estimated for all depths using linear interpolation between radiocarbon ages.

Sediment subsamples were prepared for pollen analysis following standard methods (Fægri and Iversen 1989; Cwynar et al. 1979). Known quantities of *Eucalyptus* pollen were added to each sample prior to chemical treatment in order to determine pollen and spore accumulation rates (grains cm^{-2} yr^{-1}) (Benninghoff 1962). A minimum sum of 600 pollen and spores, excluding pollen from aquatic plants, was counted for each sample. Pollen and spore identifications were made with the help of reference material at Simon Fraser University and published dichotomous keys. Percentages are based on the sum of all tree, shrub, and herb pollen and fern spores.

Vegetation Reconstruction

At Logan Inlet, there is no evidence of the tundra-like herb assemblage, which predates 12,500 ^{14}C yr BP. The pollen spectra begin during the period of *Pinus contorta* dominance, around 12,000 ^{14}C yr BP, and record the transition from *Pinus* to *Picea*-

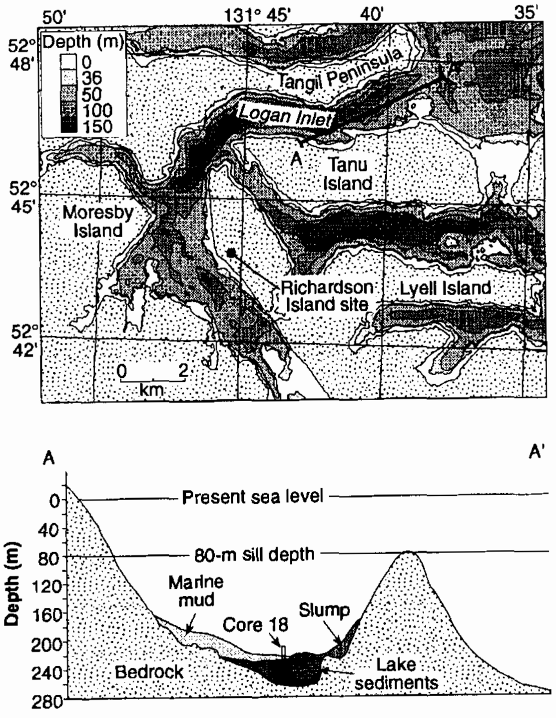

Fig. 2.4. Bathymetric map of Logan Inlet and interpreted geological cross section (A-A') of the fjord and sill. The interpretation is based on 630-cm^3 airgun and 3.5-kHz seismic reflection profile data. (Reprinted with permission from Josenhans et al. (1997), © 1997 AAAS.)

Table 2.2. AMS radiocarbon ages from Logan Inlet paleolake sediments.

Depth (cm)	Material	Laboratory no.	Radiocarbon age (^{14}C yr BP ± 1σ)	Calibrated age[a] (cal yr BP)
444	*Picea* needle	CAMS-18751[b]	10,440 ± 50	12,600; 12,500; 12,350 (12,810 – 12,070)
481	*Picea* branchlet	CAMS-18752[b]	10,560 ± 70	12,790; 12,750; 12,640 (12,920 – 12,310)
510	Unknown twig	CAMS-18753[b]	10,870 ± 60	12,920 (13,130 – 12,810)
639	*Pinus* needle	CAMS-19510	12,020 ± 70	14,070 (14,320 – 13,810)

[a] Intercept ages and age range determined from dendrocalibrated data of Stuiver et al. (1998) using CALIB rev.4.3 (Stuiver and Reimer 1993) and rounded to the nearest 10 yr. Range represents the 95% confidence interval (±2σ).

[b] *Previously published in* Josenhans et al. (1997).

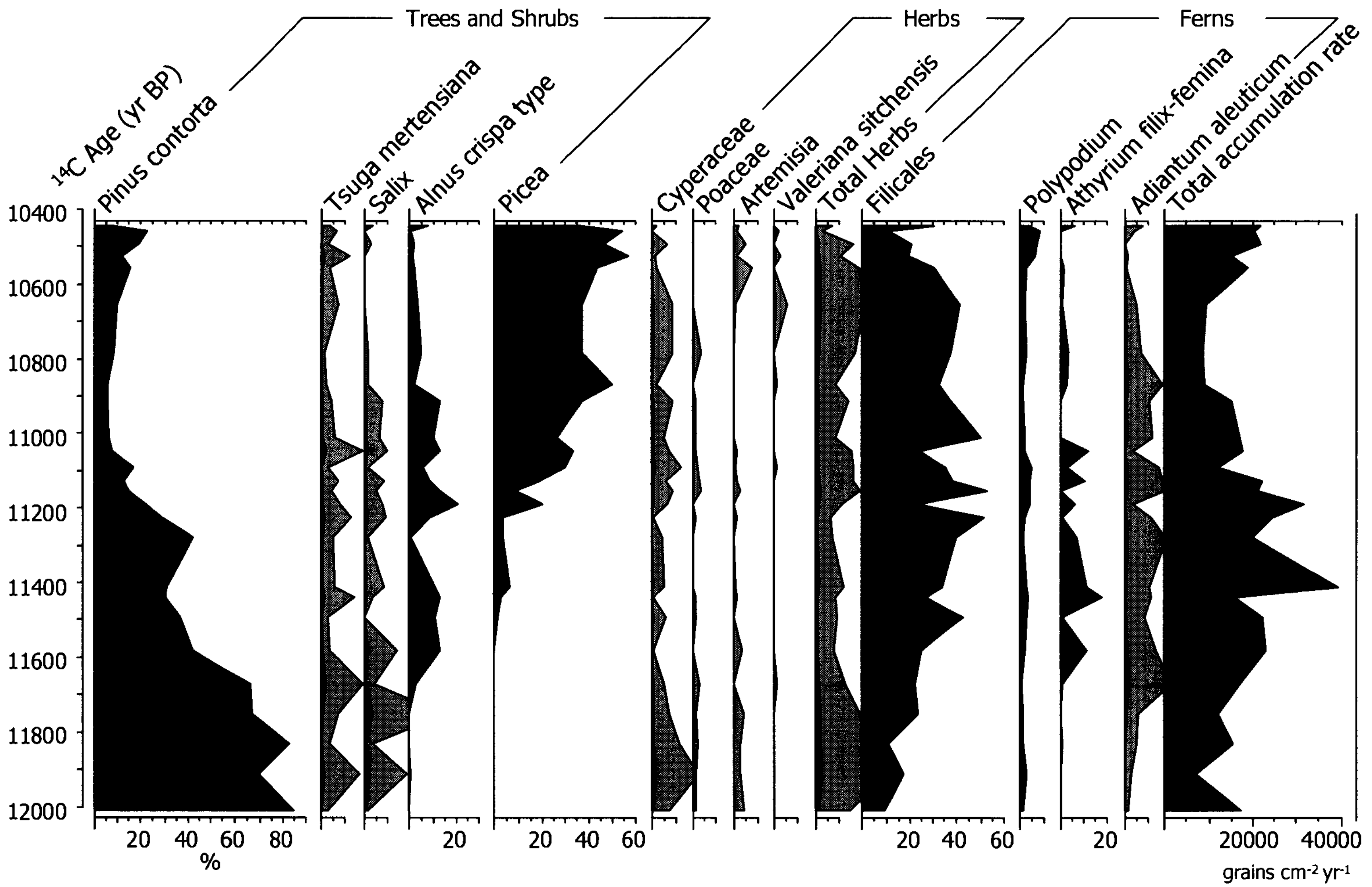

Fig. 2.5. Pollen and spore percentage diagram for late-glacial sediments (VEC94A-018) from a freshwater lake now submerged in Logan Inlet. Only the most abundant pollen and spore types, plus a few selected indicator taxa, are shown. Grey curves represent 10x exaggeration. Total accumulation rates include pollen and spores from all taxa with the exception of aquatics.

dominated forests (Fig. 2.5). Evidence for *P. contorta* abundance is strong here: *Pinus* pollen concentrations are high (up to 135,000 grains cm^{-3}), as are relative frequencies, which account for 85% of all terrestrial pollen and spores at the base of the sequence (Fig. 2.5). *Pinus contorta* needles, one of which dates to 12,020 ^{14}C yr BP, were recovered from the lake sediments at this location and confirm its local presence (Table 2.2). *Pinus* stomata are present in the pollen preparations and also suggest its nearby presence. *Pinus* is a prolific producer of pollen, which have low susceptibility to corrosion and oxidation relative to other pollen types such as *Salix* (Havinga 1984). It is likely then that *Pinus* did not cover the landscape to the extent that the pollen spectra suggest but rather that its pollen is over-represented in the Logan Inlet sediments. This may explain why taxa such as *Salix* appear to be only minor components of the vegetation at a time when there is abundant plant macrofossil evidence from nearby sites for its presence (Lacourse et al. 2003; Chapter 3). Similarly, there is limited pollen evidence of *Empetrum nigrum*; however, an AMS radiocarbon age of 11,990 ± 50 ^{14}C yr BP on *Empetrum* seeds (CAMS-61255) from a small pond on Richardson Island confirms its local presence.

Although *Pinus contorta* dominates the Logan Inlet record between 12,000 and about 11,200 ^{14}C yr BP, fern spores are also consistently abundant (Fig. 2.5), including *Polypodium*, *Adiantum pedatum*, and *Athyrium filix-femina* as well as numerous undifferentiated Polypodiaceae fern spores (Filicales), which may be *A. filix-femina* and *Dryopteris expansa* spores that have lost their diagnostic outer perines. *Adiantum pedatum* and *A. filix-femina* are strong indicators of moist to wet, nitrogen-rich soils (Klinka et al. 1989); ferns probably dominated the understory vegetation. It appears that the only other upland tree that accompanied *P. contorta* before 11,000 ^{14}C yr BP was *Tsuga mertensiana*; though its frequencies are low, they are sufficient to infer its local presence (Hebda 1983).

The major palynological change in the Logan Inlet core occurs about 11,200 ^{14}C yr BP, when *Pinus contorta* pollen decreased to less than 20% and *Picea* pollen increased to more than 30%. This increase in *Picea* pollen has also been recorded near Cape Ball on Graham Island (Mathewes et al. 1993). It has been attributed to the expansion of *Picea sitchensis*, although this is uncertain in light of the analysis by Warner and Chmielewski (1987) at Cape Ball, which indicates that late-glacial *Picea* cones probably represent hybrids of *P. sitchensis* and *P. glauca*. Total pollen and spore accumulation rates are highest during the transition from *Pinus* to *Picea* forests. *Alnus crispa* and ferns, vegetation typical of moist soils such as riparian fringes or floodplains, increased in relative abundance during this transitional period. Meadow vegetation is represented by Poaceae, *Artemisia* and other Asteraceae, *Epilobium*, and *Heracleum lanatum* pollen. Pollen from *Valeriana sitchensis*, which is common in open, coniferous forests at montane to subalpine elevations (Klinka et al. 1989), suggests moist, nitrogen-rich soil. In general, however, there is little change in the relative frequencies of pollen from herbaceous plants (Fig. 2.5). The presence of *Pediastrum* algae and pollen from the aquatic perrenial *Myriophyllum* (*M. spicatum* type) confirm that Logan Inlet was a freshwater lake between 12,000 and 10,400 ^{14}C yr BP.

Discussion

Paleovegetation between 15,000 and 10,000 ^{14}C yr BP

Sea-cliff exposures at Cape Ball on Graham Island (Figs. 2.1 and 2.2) provide the earliest radiocarbon-dated record of plants from the late Wisconsin glaciation on the British Columbia coast. AMS radiocarbon dating of a twig from basal ponded sediments indicate an age of 14,700 ± 700 ^{14}C yr BP (RIDDL-3) (Mathewes et al. 1985); as expected, conventional radiocarbon dating on mixed plant macrofossils indicate older ages of 15,400 ± 190 (GSC-3319) and 16,000 ± 570 ^{14}C yr BP (GSC-3370) (Warner et al. 1982). These ^{14}C ages, combined with pollen and plant macrofossil analyses, suggest that terrestrial vegetation was established by 15,000 ^{14}C yr BP at Cape Ball, beginning with early successional herbaceous plants such as *Juncus*, *Rumex*, Caryophyllaceae, and *Polemonium* as well as Poaceae, Cyperaceae, and mosses. Poaceae, *Polygonum viviparum* and *Artemisia* pollen suggest the presence of drier meadows while *Plantago macrocarpa* and Cyperaceae pollen indicate locally wet conditions. Mineral-rich sediments with low pollen concentrations suggest that areas of open, poorly vegetated soil were common and available for erosion. The shallow ponds and drainage systems that formed during deglaciation were inhabited by aquatic plants such as *Ranunculus* and *Potamogeton*, as well as green algae. Hence, a mosaic of different habitats and plant communities characterized the area, and the richness of the flora at this time, when adjacent areas were glaciated, suggests the presence of nearby refugia. It is unclear, however, how widespread such early communities were, since no other localities are available for comparison prior to 13,500 ^{14}C yr BP.

By 13,500 ^{14}C yr BP, paleoecological evidence from other sites becomes available for comparison to Cape Ball. The pollen record from Pleasant Island in the Panhandle of southeastern Alaska is instructive, since it begins around 13,500 ^{14}C yr BP with herb and dwarf shrub tundra that includes Poaceae, Cyperaceae, *Salix*, Ericaceae shrubs and a variety of herbs (Hansen and Engstrom 1996). This is similar to Cape Ball after 13,000 ^{14}C yr BP, where the vegetation can also be described as tundra-like, with pollen and leaf remains of dwarf *Salix*, *Empetrum*, and an abundance of Poaceae, Cyperaceae and other herbs. A similar pollen assemblage is found on Kodiak Island in southwestern Alaska in sediment that dates to 13,420 ± 20 ^{14}C yr BP (Beta-26607) (Peteet and Mann 1994). There, Poaceae, Cyperaceae and *Empetrum* shrubs dominate a landscape that is also characterized by a diverse array of herbaceous plants. A non-arboreal community is also recorded in a core from Dogfish Bank around 13,200 ^{14}C yr BP (Fig. 2.2), where a wet tundra community dominated by Cyperaceae, *Equisetum*, and *Empetrum* was described by Barrie et al. (1993) from terrestrial sediment deposited when the bank was exposed due to low relative sea level. Low *Empetrum* shrubs probably grew on drier, exposed hummocks within the sedge tundra that likely would have been subject to strong winds. *Empetrum* and other Ericaceae shrubs are a prominent element of many late-glacial sites along the Pacific coast. On Langara Island (Fig. 2.2), Heusser (1995) also identified an early plant community ca. 13,000 ^{14}C yr BP where *Empetrum*, along with Poaceae, Cyperaceae, and Apiaceae, defined the tundra communities. A relatively cool climate and moist but poorly-developed soils are indicated by pollen of the arctic-alpine annual *Koenigia islandica*. On the west coast of South Moresby Island, this tundra assemblage was present as early as 13,500 ^{14}C yr BP (Fedje 1993). *Salix*, Ericaceae shrubs, Poaceae, and especially Cyperaceae dominated the lowland environment. There is ample evidence to conclude that herb-dominated plant communities with dwarf *Salix* and *Empetrum* shrubs were widespread along the Pacific coast before 12,500 ^{14}C yr BP.

At most of these early sites, some tree pollen, mostly that of *Pinus contorta*, is typically recorded: *Pinus* commonly accounts for up to 5% of the pollen sum. The abundance of tree pollen is sufficiently low, however, that treeless tundra is still the most appropriate interpretation for the vegetation cover. Occasional tree pollen is most likely a product of long-distance transport, and/or reworking from melting glacier ice or other surficial deposits. Wood or other tree macrofossils are absent in the largely inorganic sediments deposited during this time. Based on the high pollen frequencies of Poaceae, Cyperaceae, *Salix*, Ericaceae shrubs, and Apiaceae, the closest match between these herb and shrub-dominated fossil pollen spectra and modern vegetation communities appears to be with sites in the Gulf of Alaska region, from Kodiak Island to the Aleutian Islands (Heusser 1985, 1990). This similarity and the presence of indicator taxa such as *Koenigia islandica* and *Bistorta* suggest a cold, arctic-like aspect to the vegetation and landscape in general, which accords well with the interpretation of tundra. In general, the vegetation is indicative of cool, wet, and probably windy conditions that were locally controlled by topography, soils, and disturbance.

Reconstructed climate records from the region also corroborate a cold late-glacial climate (e.g., Heusser et al. 1985; Bartlein et al. 1998). Climate in the late-glacial period was characterized by an anticyclonal high pressure system centered on the continental ice sheet, which generated subcontinental katabatic easterly winds and increased seasonality (COHMAP 1988; Bartlein et al. 1998). Before 12,000 ^{14}C yr BP, the ice sheet shifted the jet stream south, caused cooling in mid-latitudes, intensified cold dry easterly winds and reduced available winter moisture (Bartlein et al. 1998).

A rapid expansion of coniferous forest began around 12,500 ^{14}C yr BP. *Pinus contorta* was the first tree species to colonize the coast following deglaciation. Abrupt increases in *P. contorta* pollen percentages and accumulation rates, and the rooted *Pinus* stump (Fedje and Josenhans 2000) with associated forest litter document its rapid colonization and the formation of open *Pinus* communities. Its local presence is also demonstrated by needles and their stomata, cones, and other *P. contorta* macrofossils (Fig. 2.3) (Lacourse et al. 2003; Chapter 3). It appears that by 12,000 ^{14}C yr BP, *Tsuga mertensiana* was also present, probably as scattered upland trees. *Alnus crispa* and ferns were important components of the understory and edge communities of these early forests. Much of the landscape would have been characterized by fluvial features such as extensive fan and delta complexes (Fedje and Josenhans 2000). Free of competing tall vegetation, *P. contorta* would have colonized the moist but well-drained sands and gravels quickly, due to its efficient seed dispersal, rapid growth and maturation, and wide edaphic tolerance.

Around 11,200 ^{14}C yr BP, *Picea* joined the *Pinus* forests on the Queen Charlotte Islands and soon dominated forests along much of the coast. *Alnus crispa* and ferns expanded during the transition from *Pinus* to *Picea*-dominated forests. Due to greater shade tolerance, *Picea* forests were denser than earlier forests, and soils were moist with increasing humus accumulation. Global climate model simulations suggest that the climate was likely characterized by the northward shift of the jet stream that resulted from the decreasing size of the continental ice sheet and increased seasonality due to changes in the seasonal cycle of insolation (Berger 1978; Whitlock and Bartlein 1997; COHMAP 1988; Bartlein et al. 1998). Summer conditions were progressively warmer and drier, and winters were cooler than at present. As the continental ice sheet receded, moist westerly winds may have become more important in the region (COHMAP 1988). After rapid initial expansion, *Picea* declined in abundance at Cape Ball (Figs. 2.1 and 2.2) (Mathewes et al. 1993), and herbaceous plants expanded their cover. The *Pinus* and *Picea* forests appear to open up into conifer parkland around 10,700 ^{14}C yr BP, with meadows of Cyperaceae, Poaceae, Apiaceae, and other herbs. *Tsuga heterophylla* expansion was delayed until after 10,500 ^{14}C yr BP. Rising sea levels began to flood the lower elevations of the continental shelf around the same time (Josenhans et al. 1997; Fedje and Josenhans 2000), submerging the late-glacial landscapes and their vegetation (Lacourse et al. 2003; Chapter 3). The vegetation history after this time is recorded in lakes, fens, and bogs above the limit of marine inundation.

The Coastal Migration Route

The dramatic sea-level changes at the end of the last glaciation, which resulted in the exposure of large banks in Hecate Strait, caused a near two-fold increase in land area for Haida Gwaii compared to today (Fedje and Christensen 1999). These broad low-relief plains were therefore available during deglaciation to plants, animals, and humans. It has been proposed that the entry of humans into North America was by a marine-adapted people travelling down the coast in the late-glacial period both on land and by simple watercraft (Bryan 1941; Heusser 1960; Fladmark 1979). If early human populations were moving south from Beringia along the Pacific coast, then these emergent landmasses would have been important surfaces along that route.

The Northwest Coast was deglaciated and available for human migration and habitation by 13,500 ^{14}C yr BP (Barrie et al. 1993; Mann and Hamilton 1995; Josenhans et al. 1997; Mandryk et al. 2001) while the hypothesized ice-free corridor would not have been passable until after 11,000 ^{14}C yr BP (Arnold 2002). It is likely that a coastal route was available well before 13,500 ^{14}C yr BP as coastal glaciers were retreating and could have been easily bypassed. The initial Paleoindian migration from Beringia probably occurred ca. 13,500 ^{14}C yr BP, when temperatures rose in the northern hemisphere (Hoffecker et al. 1993; Goebel 1999; Mandryk et al. 2001). Intertidal fauna were an abundant source of food available to marine-adapted peoples by 13,200 ^{14}C yr BP (Hetherington and Reid 2003; Fedje and Christensen 1999). However, archaeological evidence to support the coastal migration hypothesis is inconclusive because known archaeological sites along the Northwest Coast do not predate 10,000 ^{14}C yr BP (Dixon et al. 1997; Josenhans et al. 1997; Dixon 1999; Cannon 2000). Fedje and Josenhans (2000) recovered a stone tool, almost 10 cm in length, from a drowned fluvial terrace 53 m below sea level in Juan Perez Sound (Fig. 2.2). The stone tool was recovered from lag sediments and is encrusted with modern subtidal barnacles; however, on the basis of reconstructed sea-level history, an age of ca. 10,000 ^{14}C yr BP is suggested for the site (Fedje and Josenhans 2000). With a well-defined striking platform and a shallow bulb of percussion, both diagnostic features of humanly fractured stones (Andrefsky 1998), it is clearly the product of human workmanship. However, by 10,000 ^{14}C yr BP, humans could have taken an inland route and then travelled north up the coast. Older archaeological sites would have been rapidly transgressed by rising sea levels (Fedje and Josenhans 2000). Such sites may be preserved on drowned landscapes but will be difficult to locate and may have been exposed to significant erosion and/or subsequent sedimentation. Additional underwater archaeology is desperately needed to further evaluate the possibility of pre-Holocene human occupation of the outer shelf region (Easton 1992).

Paleoecological records provide considerable information as to the food plants that would have been available to humans migrating southward along the coast in late-glacial times (Table 2.3). Animal products probably dominated the total food intake of early migrants. Rick et al. (2001) provide evidence that early New World peoples in coastal California fished intensively and suggest that fish and shellfish provided 50% and 30%, respectively, of their edible meat. Plant products, however, would have provided nutritional diversity and dietary support when yields from fishing and hunting were low. Food plants would have been predictable seasonal resources, requiring minimal searching and little effort and technology to gather. For example, *Heracleum lanatum* and *Epilobium* pollen and plant macrofossils have been identified in late-glacial sediments at several locations in coastal British Columbia, and many aboriginal groups in British Columbia have used the leaves of these plants as green vegetables (Compton 1993; Turner 1995). The Haida have been known to eat the young leaves and red-coloured stems of *Rumex*, which was growing on the shelf around 13,000 ^{14}C yr BP. The roots of *Potentilla* may have also been harvested; when steam-cooked, they apparently taste like sweet potato (Turner 1995). Early migrants could also have eaten cambium cakes, a mixture of berries such as crowberries (*Empetrum*) or bunchberries (*Cornus canadensis*) and the nutrient-rich cambium of *Pinus*, *Picea* or *Alnus* (Turner 1995). The leaves and rhizomes of *Polygonum viviparum* are still eaten by the Inuit of Alaska and Siberia (MacKinnon et al. 1992) and could have been used as a food plant by humans on the coast in the late-glacial period. The presence of *Fritillaria camschatcensis* pollen at Cape Ball suggests that the starch-rich bulb of this plant, which was widely eaten by coastal peoples in British Columbia, was already available in the late-glacial period. Finally, fern spores are abundant at all late-glacial sites; the young shoots and rhizomes of various ferns could have been steamed and eaten as coastal peoples in British Columbia have done for centuries (Turner 1995).

Plants also would have provided materials for fuel, manufacture, dyes, and medicinal purposes. Fern fronds, bark, stems, leaves, and root fibres could have been used to make twine, nets, baskets, mats, and clothing (Turner 1979). The large leaves of plants such as *Heracleum lanatum* are ideal surfaces for drying berries and as liners for baskets or other containers (Turner 1979). Other examples of useful plant materials include silica-rich *Equisetum*, which has been used as sandpaper, and *Epilobium* and *Salix* seed fluff and *Sphagnum* mosses which, due to their absorbent properties, could have been used for a variety of purposes.

Table 2.3. Selected food plants available on the Pacific coast during the late-glacial period, based on fossil evidence.

Latin Name	Common Name	Known Aboriginal Foods[a]
Alnus rubra	red alder	cambium and phloem
Conioselinum pacificum	Pacific hemlock parsley	taproots
Cornus canadensis	bunchberry	fruit
Empetrum nigrum	crowberry	fruit
Epilobium angustifolium	fireweed	young stems and leaves
Equisetum	horsetail	young stems
Fritillaria camschatcensis	rice-root	bulbs
Heracleum lanatum	cow parsnip	young stems and leaf stems
Lupinus	lupine	rhizomes
Nuphar luteum	yellow pond lily	seeds and rootstocks
Picea sitchensis	sitka spruce	cambium and phloem
Pinus contorta	lodgepole pine	cambium and phloem
Polygonum viviparum	bistort	leaves and rhizomes
Polypodiaceae	ferns (various)	young stems (fiddleheads) and rhizomes
Potentilla	cinquefoil	roots
Rumex	dock	young stems and leaves
Sanguisorba canadensis	burnet	leaves (for tea)
Shepherdia canadensis	soapberry	fruit

[a] Sources: Turner (1995), MacKinnon et al. (1992), and Compton (1993).

Evidence for Younger Dryas-like Cooling

Several paleoecological studies from coastal British Columbia and Alaska record a reversion to a cooler climate between 11,000 and 10,000 ^{14}C yr BP, similar in timing and extent to the Younger Dryas cooling documented first in Europe and then eastern North America (Mangerud et al. 1974; Watts 1980; Mott et al. 1986; Peteet et al. 1990). Based on peaks in cold-water benthic foraminifera in marine sediment cores, Mathewes et al.

(1993) document the cooling of ocean waters on the British Columbia coast between 11,000 and 10,200 ^{14}C yr BP. Similarly, most temperate-water bivalves disappeared from waters around the Queen Charlotte Islands between 11,000 and 10,000 ^{14}C yr BP and were replaced by only a few cold-tolerant species (Hetherington and Reid 2003). Using pollen-climate transfer functions, Mathewes et al. (1993) estimate a drop of 2-3°C in summer temperature as well as increasing precipitation during this interval. In particular, late-glacial peaks in *Tsuga mertensiana* pollen suggest a cooling event on the Pacific coast between 10,700 and 10,000 ^{14}C yr BP (Mathewes 1993). *Tsuga mertensiana* is a good indicator of cool and moist conditions; it requires cool temperatures and substantial snow for insulation during winter months (Pojar and MacKinnon 1994). *Tsuga mertensiana* pollen is severely under-represented in modern pollen assemblages, even in areas where it accounts for 40% of the tree cover. In the subalpine zone of Brooks Peninsula on Vancouver Island, where it is a co-dominant in the forest, *T. mertensiana* accounts for only 9% of the pollen sum (Hebda 1983; Hebda and Haggarty 1997). Therefore, even minor increases in *T. mertensiana* pollen are good indicators of climatic cooling and increased moisture. *Tsuga mertensiana* pollen is abundant in sediments from Cook Bank off northern Vancouver Island that date to this critical time period (Luternauer et al. 1989a; Lacourse et al. 2003; Chapter 3). Similar peaks in *T. mertensiana* pollen occur in sediments from the Queen Charlotte Islands (Warner 1984; Fedje 1993; Heusser 1995) including preliminary evidence from Hippa Island on the west coast of the archipelago (R.W. Mathewes, unpublished data), and elsewhere along the Pacific coast (Mathewes 1993; Heusser 1960, 1985).

At Cape Ball, a cooler climate during the Younger Dryas chronozone is suggested not by increases in *Tsuga mertensiana* pollen but by a reversion from forest to open, herb-rich parkland vegetation (Mathewes et al. 1993). In southeastern Alaska, pollen analysis revealed a similar reversion: open *Pinus contorta* forest, which had established sometime after 12,500 ^{14}C yr BP, was replaced by shrub and herb-dominated tundra between 10,800 and 9800 ^{14}C yr BP (Engstrom et al. 1990; Hansen and Engstrom 1996). Late-glacial cooling also appears to have caused dramatic vegetation changes on nearby Kodiak Island (Peteet and Mann 1994). A shift from forest to herb-rich vegetation is also a common feature of Younger Dryas landscapes around the North Atlantic (e.g., Mott et al. 1986; Williams et al. 2002).

Trends in Holocene Vegetation and Climate

Several paleoecological records from the Queen Charlotte Islands and southeastern Alaska demonstrate significant changes in vegetation and climate after 10,000 ^{14}C yr BP (Fig. 2.1). In general, the early Holocene climate along the Northwest Coast was marked by relatively high summer temperatures, low winter temperatures and low mean annual precipitation (Heusser et al. 1985; Bartlein et al. 1998). The mid-Holocene was characterized by a gradual trend toward cooler and wetter conditions, resulting in relatively low temperatures and high annual precipitation in the late Holocene. The typically cool and moist modern climate was established between 4000 and 3000 ^{14}C yr BP (Heusser 1985; Pellatt and Mathewes 1997).

Two sites on eastern Graham Island, Serendipity Bog and Boulton Lake, have detailed and well-dated records of vegetation change with basal sediments that are early Holocene in age (Warner 1984). Mixed coniferous forests of *Pinus contorta*, *Picea* and *Tsuga mertensiana* with abundant *Alnus* and ferns characterized this area and much of the region at the beginning of the Holocene. After 9400 ^{14}C yr BP, *Picea* populations expanded at the expense of *P. contorta* and formed forests with *Tsuga heterophylla*. *Picea* and *T. heterophylla* forests dominated the area until 5500 ^{14}C yr BP when decreasing temperature and increasing precipitation promoted the development of forest-bog complexes throughout the Queen Charlotte Islands, but particularly in poorly drained lowlands (Quickfall 1987). As a result, Cupressaceae, *P. contorta*, and Ericaceae shrubs became more common. The modern *T. heterophylla* and Cupressaceae forest was established by 3000 ^{14}C yr BP, although the relative contributions of *Thuja plicata* and *Chamaecyparis nootkatensis* are unknown due to indistinguishable pollen morphologies.

At the northwestern tip of the Queen Charlotte Islands, on Langara Island, Heusser (1995) found a similar record of Holocene vegetation change (Figs. 2.1 and 2.2). There, *Pinus contorta* was a minor component of the vegetation by 10,000 ^{14}C yr BP, due to the expansion of *Alnus*, *Picea* and, later, *Tsuga heterophylla*. The high proportion of fern spores in early Holocene sediments suggests, however, that local forests remained partially open, providing good habitat for light-demanding ferns. Between 9000 and 5000 ^{14}C yr BP, the pollen record on Langara Island records the local development of an open *Alnus* and *Lysichiton americanum* community. The abrupt increase in *L. americanum* pollen suggests local paludification, a process in which sites become waterlogged through the accumulation of organic matter, had commenced ca. 9000 ^{14}C yr BP. Around 5000 ^{14}C yr BP, Ericaceae shrubs and Cyperaceae replaced *L. americanum.* The climate cooled in the mid-Holocene but humidity increased, allowing *T. heterophylla*, *Picea*, and *Pinus* populations to expand once again. Cupressaceae pollen increased after 3000 ^{14}C yr BP, suggesting establishment of present day coastal forest with *Thuja plicata*, *T. heterophylla* and *Picea*.

Several other sites further to the south on the Queen Charlotte Islands have been studied. Fedje (1993) conducted pollen analysis on lake sediments from two lowland sites, Skittagetan Pond and West Side Pond (Fig. 2.1). There, *Tsuga heterophylla*, *Picea*, and *Alnus* dominated the early Holocene landscape. Ferns were the dominant understory vegetation and *Equisetum* was locally abundant. *Picea*, *Alnus*, and *Lysichiton americanum* expanded around 8700 ^{14}C yr BP as *T. heterophylla* declined in importance. *Tsuga heterophylla* re-expanded after 7500 ^{14}C yr BP, reflecting an increase in precipitation. Vegetation assemblages similar to modern communities were established around 5000 ^{14}C yr BP, with the addition of Cupressaceae. It is interesting to note that the expansion of *Thuja plicata* in coastal forests between 5000 and 2500 ^{14}C yr BP is strongly correlated with the development of massive woodworking technology (Hebda and Mathewes 1984). A similar vegetation history was reconstructed from sediments on Anthony Island, a small island located at the southern tip of the archipelago (see Hebda et al. *in press*). Human activities in the last few thousand years have promoted increases in *Pinus contorta* populations and, more recently, the expansion of *T. heterophylla*. Forest clearing, fire, and harvesting of *T. plicata* for building purposes exposed the soil, allowing other conifers like *P. contorta* to increase in abundance.

Pollen and plant macrofossil records from three subalpine ponds on Moresby Island provide a unique alpine perspective on Holocene vegetation change (Pellatt and Mathewes 1994, 1997). *Tsuga mertensiana*, along with *Picea*, *Alnus* and *Tsuga heterophylla*, characterized the late-glacial upland vegetation. The relatively warm climate of the early Holocene allowed *T. heterophylla* to expand and resulted in a tree line higher in elevation than present-day tree line. Around 7000 ^{14}C yr BP, temperatures began to decrease, forest productivity declined and tree line decreased in elevation. By

6000 ^{14}C yr BP, lower temperatures allowed *T. mertensiana* to dominate subalpine forests, and higher precipitation allowed *Chamaecyparis nootkatensis* to expand soon after. Open *T. mertensiana* and *C. nootkatensis* forests were established by 3500 ^{14}C yr BP. Reconstructed vegetation histories from subalpine ponds (Pellatt and Mathewes 1994, 1997) and lowland sites (Fedje 1993) on the Queen Charlotte Islands suggest that a relatively short-lived cooling occurred ca. 3500 ^{14}C yr BP. This corresponds with glacial advances in the Coast Mountains of British Columbia, in the Rocky Mountains, and climatic cooling documented along the Pacific coast (Pellatt and Mathewes 1997).

Given their proximity, paleoecological records from southern Alaska (Heusser 1960, 1985; Cwynar 1990; Hansen and Engstrom 1996) are both relevant and interesting (Fig. 2.1). Trees consistently arrived later at more northwesterly sites, suggesting that the migration of the major trees was primarily northward and that local refugia did not support trees during the last glacial maximum (Cwynar 1990). *Pinus contorta* may be an exception to this because its dominance at late-glacial coastal sites must be explained by either refugia in Alaska or British Columbia or exceptionally high migration rates (Peteet 1991). *Picea sitchensis* arrived in the Glacier Bay region by 9,500 ^{14}C yr BP (Hansen and Engstrom 1996), forming productive forests with *Alnus crispa* and various ferns about 1500 years after similar vegetation had developed on the Queen Charlotte Islands. *Alnus* was an important component of the vegetation since 12,000 ^{14}C yr BP but, like the Logan Inlet record, it reached its peak abundance during the transition from *Pinus* to *Picea*-dominated forests. *Picea* forests were subsequently replaced when increased summer temperatures and annual precipitation allowed *Tsuga heterophylla* and *T. mertensiana* to form closed forests between 8500 and 8000 ^{14}C yr BP. *Pinus contorta* re-expanded about 7000 ^{14}C yr BP due to widespread paludification. Local edaphic conditions at this time were also favourable for *Sphagnum* moss, *Lysichiton americanum*, and Ericaceae shrubs. Due to a late Holocene increase in precipitation, *Tsuga heterophylla*, *P. contorta* and other bog vegetation became more abundant about 3400 ^{14}C yr BP.

CHAPTER 3

PALEOECOLOGY OF LATE-GLACIAL TERRESTRIAL DEPOSITS WITH *IN SITU* CONIFERS FROM THE CONTINENTAL SHELF OF WESTERN CANADA[1]

Abstract

Extensive portions of the continental shelf off the coast of British Columbia were subaerially exposed during late Wisconsin deglaciation due to lowering of relative sea level by as much as 150 m. Paleoecological analyses were conducted at two sites on the emergent continental shelf where terrestrial surfaces with *in situ* conifers are preserved. The woody plant remains confirm that, during the latest period of subaerial exposure, terrestrial vegetation was established on the continental shelf. Microscopic identification of fossil wood, and analyses of pollen and plant macrofossils from the associated paleosols and overlying shallow pond sediments indicate that productive *Pinus contorta*-dominated communities with abundant *Alnus crispa* and ferns grew on the shelf adjacent to and on the Queen Charlotte Islands around 12,200 ^{14}C yr BP. Dwarf shrubs including *Salix* and *Empetrum nigrum*, and herbaceous plants such as *Heracleum lanatum* and *Hippuris vulgaris* were also important components of the shelf vegetation. Near northern Vancouver Island, mixed coniferous forests dominated by *Pinus contorta* with *Picea*, *Tsuga* spp., *Alnus* spp., and ferns occupied the shelf at 10,500 ^{14}C yr BP.

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Introduction

Due to the combined effects of eustatic sea level changes, isostatic crustal depression and rebound, and tectonism, the Pacific coast of Canada is characterized by a series of marine transgressions and regressions during the Quaternary (Clague et al. 1982a, Clague 1993). Extensive portions of the continental shelf along the coast of British Columbia were emergent at the end of the last glaciation. These broad low-relief plains became ice-free and vegetated during the late-glacial (Luternauer et al. 1989a, 1989b; Barrie et al. 1993; Fedje and Josenhans 2000), and likely served as a migration corridor for plants, animals, and possibly humans (Josenhans et al. 1997; Mandryk et al. 2001). In the Queen Charlotte Islands area, shorelines that date between 9400 and 12,500 ^{14}C yr BP have since been submerged by rising sea levels to depths as great as 150 m (Josenhans et al. 1997; Fedje and Josenhans 2000). The shoreline history of west and north Vancouver Island is not well-constrained but portions of the adjacent continental shelf were exposed between 11,500 and 7000 ^{14}C yr BP (Clague et al. 1982a; Luternauer et al. 1989a; Friele 1991).

There is only scattered evidence from allochthonous plant fossils of the vegetation that grew on the continental shelf during the latest period of lowered sea levels (Barrie et al. 1993). However, two sites provide autochthonous evidence of rooted plants from the continental shelf. Fedje and Josenhans (2000) provided evidence of drowned forests from a *Pinus* stump rooted in a peaty soil in Juan Perez Sound (52° 30′ N, 131° 24′ W) in the Queen Charlotte Islands (Fig. 3.1) (see Appendix for common names of plants). The drowned forest appears to have occupied a relatively large area at 145 m below sea level about 12,200 ^{14}C yr BP and was transgressed by marine waters prior to 11,500 ^{14}C yr BP. On Cook Bank (51° 00′ N, 128° 27′ W), just north of Vancouver Island (Fig. 3.1), Luternauer et al. (1989a) described well-developed soils and forests at 10,500 ^{14}C yr BP when sea level was 95 m lower. This site was transgressed by marine waters after 10,400 ^{14}C yr BP. To improve our understanding of the plant cover on the continental shelf during the latest period of subaerial exposure, we conducted paleoecological analyses on the radiocarbon-dated terrestrial surfaces of Fedje and Josenhans (2000) and Luternauer et al. (1989a).

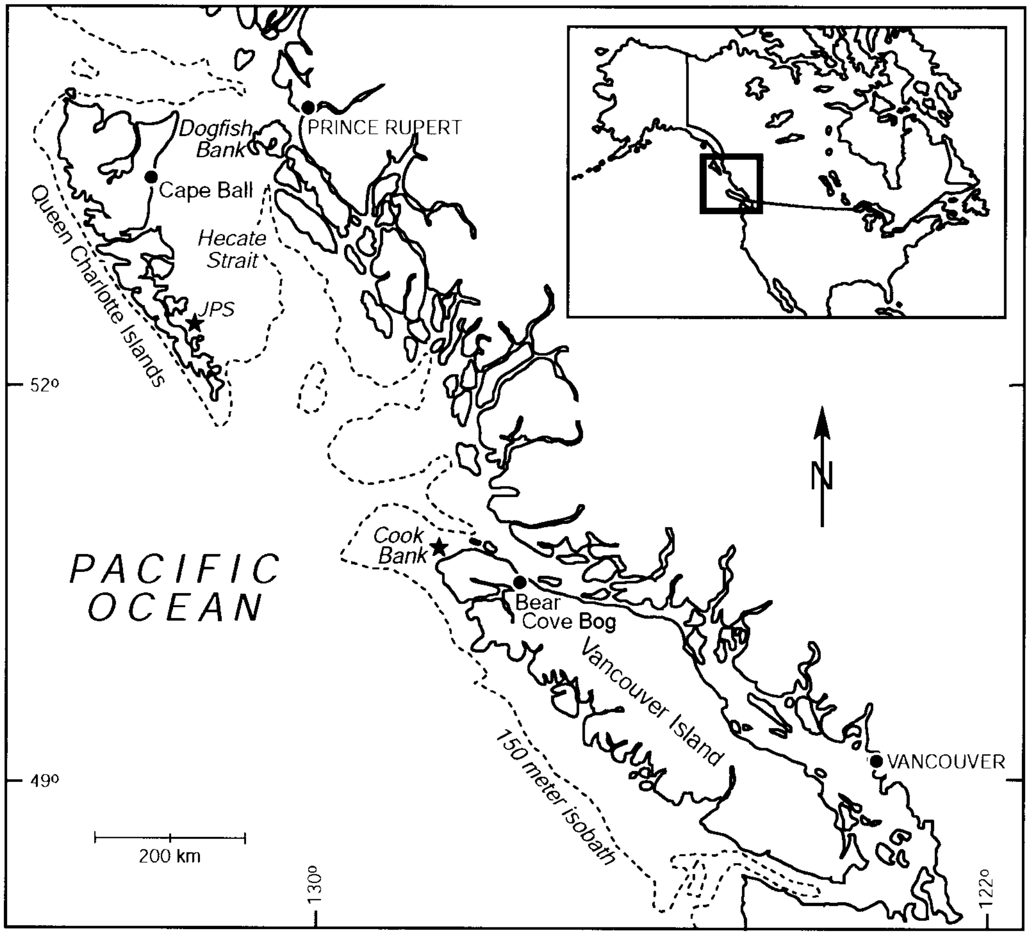

Fig. 3.1. Location of the study sites (★) and other sites mentioned in the text. The 150 m isobath shows the approximate location of the emergent continental shelf; however, the glacioisostatic forebulge would have resulted in considerable spatial and temporal variation in relative sea level. JPS = Juan Perez Sound.

Environmental Setting

Late Quaternary glaciation on the Queen Charlotte Islands was of short duration and limited extent compared to mainland British Columbia (Clague et al. 1982a; Clague 1983). Ice was primarily restricted to the Queen Charlotte Ranges with localized piedmont lobes coalescing in places with ice from mainland British Columbia. Maximum ice extent was reached sometime after 21,000 ^{14}C yr BP (Barrie and Conway 1999). The coastal lowlands were deglaciated about 15,000 ^{14}C yr BP (Mathewes et al. 1985). During deglaciation, relative sea level was as much as 150 m below present, leaving significant portions of the continental shelf exposed (Barrie et al. 1993; Josenhans et al. 1997). Josenhans et al. (1995) and Fedje and Josenhans (2000) provide evidence of relatively slow sea-level rise (<2 cm yr^{-1}) between 12,200 and 10,800 ^{14}C yr BP, and rapid rise (>5 cm yr^{-1}) over the subsequent 2000 years. Marine geological studies of the drowned landscape reveal terrain dominated by alluvial fans, delta plains, and meandering and migrating river systems (Fedje and Josenhans 2000).

Paleoenvironmental conditions during the late Wisconsin glaciation were substantially different on northern Vancouver Island. Ice flowed west from the Coast Mountains across northern Vancouver Island, overrode Vancouver Island ice and coalesced with ice in Queen Charlotte Strait, covering Cook Bank with grounded ice at the glacial maximum (Howes 1983). Deglaciation began around 15,000 ^{14}C yr BP (Blaise et al. 1990) and portions of northern Vancouver Island became ice-free as early as 13,600 ^{14}C yr BP (Hebda 1983). Unlike the Queen Charlotte Islands, northern Vancouver Island and the inner shelf were isostatically depressed at least 125 m due to ice-loading (Josenhans et al. 1995). As ice thinned and retreated, ocean waters flooded the isostatically depressed lowlands about 13,000 ^{14}C yr BP, leaving marine deposits 90 m above present marine limit (Howes 1983). However, rapid isostatic rebound resulted in local sea-level lowering and exposure of large areas of the shelf. Maximum lowstand occurred between 11,700 and 11,000 ^{14}C yr BP (Patterson 1993).

Materials and Methods

A *Pinus* stump ca. 20 cm in diameter and rooted in a 10-cm-thick peaty soil was recovered from a submerged fluvial terrace at 145-m water depth in Juan Perez Sound

(Fig. 3.1) by Fedje and Josenhans (2000). The stump and peat were retrieved from a ship using a 0.5 m^3 clamshell grab sampler. The *Pinus* stump was dated at 12,240 ± 50 ^{14}C yr BP and an associated fragment of angiosperm wood at 12,190 ± 50 ^{14}C yr BP (Table 3.1). The terrestrial peat is poorly compacted and is overlain by marine sediments deposited after transgression.

At Cook Bank (Fig. 3.1), a 180-cm-long submarine vibrocore (END97A-23) containing a late-glacial paleosol with rooted plant remains (Fig. 3.2) was collected at a water depth of 95 m from a submarine valley (Luternauer et al. 1989a). The *in situ* conifer root yielded a radiocarbon age of 10,470 ± 75 ^{14}C yr BP (Table 3.1). Three other radiocarbon ages are from detrital wood, likely derived from vegetation growing on Cook Bank while these sediments were accumulating. The paleosol at 88 cm is sharply overlain by lagoonal or shallow pond sediments (54-88 cm), which are in turn overlain by marine sediments (0-54 cm). The pond sediments were transgressed by rising sea levels and submerged between 10,400 and 10,000 ^{14}C yr BP (Luternauer et al. 1989a).

Sediment samples (1-2 cm^3) were prepared for pollen analysis following standard methods (Fægri and Iversen 1989; Cwynar et al. 1979). To determine pollen concentrations, *Eucalyptus* pollen (Batch #903722; 16,180 ± 1460 grains) was added to each sample prior to chemical treatment (Benninghoff 1962). Average pollen and spore percentages for the Juan Perez Sound peat and the pond sediments at Cook Bank are presented in Table 3.2. Due to the abundance of *Pinus contorta* pollen in the Juan Perez Sound samples, additional slides were scanned for other pollen types not encountered during counting (Table 3.2). For plant macrofossil analysis, 100 mL of sediment was dispersed by soaking in water and then wet-sieved through 2 mm, 500 µm, and 250 µm mesh. Plant macrofossils were identified through comparison with reference material at Simon Fraser University, and aided by Dunwiddie (1985). Friedman (1978) and Panshin et al. (1964) were used for microscopic wood identification. Botanical nomenclature follows Douglas et al. (1989).

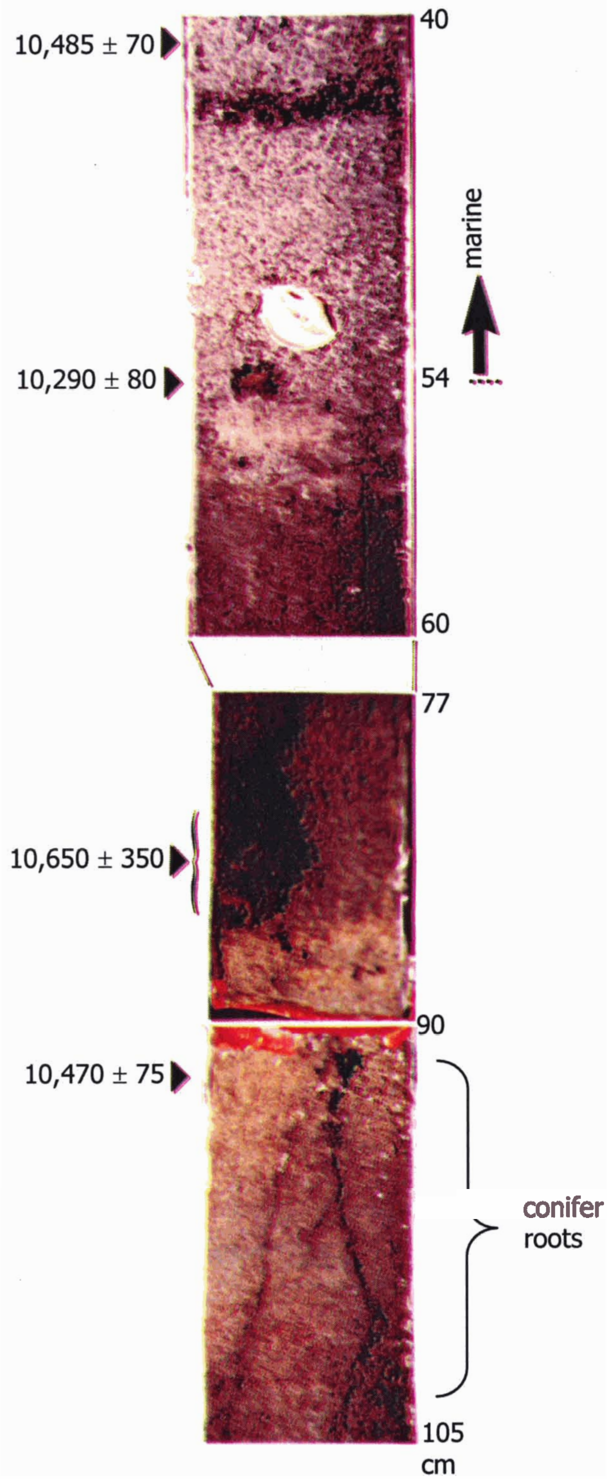

Fig. 3.2. Cook Bank core (END87A-23), showing *in situ* conifer roots and oxidation due to pedogenesis below 88 cm. Radiocarbon ages (^{14}C yr BP ± 1σ) are shown at left.

Table 3.1. AMS radiocarbon ages from Juan Perez Sound and Cook Bank.

Site	Depth in core (cm)	Material	Laboratory no.	Radiocarbon age (^{14}C yr BP ± 1σ)	Calibrated age[a] (cal yr BP)
JPS	—	Angiosperm wood	CAMS-59769[b]	12,190 ± 50	14,130 (15,410-13,840)
JPS	—	*In situ Pinus* stump	CAMS-59768[b]	12,240 ± 50	14,160 (15,430-13,850)
Cook Bank	41	Wood	RIDDL-981[c]	10,485 ± 70	12,620; 12,480; 12,380 (12,900-11,960)
Cook Bank	54 - 55	*Picea* wood	RIDDL-983[c]	10,290 ± 80	12,100; 12,000; 11,980 (12,770-11,690)
Cook Bank	83 - 86	*Picea* wood	RIDDL-984[c]	10,650 ± 350	12,820; 12,710; 12,670 (13,380-11,260)
Cook Bank	93	*In situ* conifer root	RIDDL-985[c]	10,470 ± 75	12,610; 12,490; 12,370 (12,900-11,950)

[a] Intercept ages and age range determined from dendrocalibrated data of Stuiver et al. (1998) using CALIB rev.4.3 (Stuiver and Reimer 1993) and rounded to the nearest 10 yr. Range represents the 95% confidence interval (±2σ).

[b] Previously published in Fedje and Josenhans (2000).

[c] Previously published in Luternauer et al. (1989a).

Results

Juan Perez Sound

Analysis of the Juan Perez Sound peat reveals pollen and spore concentrations between 1 and 3 million grains cm^{-3}. The pollen spectra are dominated by *Pinus contorta*; it accounts for 66% of the total pollen and spore sum (Table 3.2) and 99% of the tree, shrub, and herb pollen. Low amounts of pollen from *Tsuga mertensiana*, *Salix*, *Empetrum nigrum*, and herbaceous plants such as *Heracleum lanatum* are also present. Spores from ferns and fern allies are abundant but range between 8 and 50% of the total pollen and spore sum. The majority of the monolete spores (Polypodiaceae, Filicales) could not be identified beyond the family level due to the loss of their diagnostic outer perine but most are likely from common ferns such as *Athyrium filix-femina* and *Dryopteris expansa*.

Plant macrofossils from the Juan Perez Sound peat (Fig. 3.3) correspond well with the pollen record. *Pinus contorta* needles and cones (Fig. 3.4A, 3.4D) are the most abundant plant macrofossils. *Salix* twigs (Fig. 3.4A), bud scales and capsules (Fig. 3.4C) are common and *Heracleum lanatum* fruit (Fig. 3.4B) are also present. The presence of fungal sclerotia (cf. *Cenococcum geophilum*) is consistent with a terrestrial soil deposit (Fig. 3.3). In two instances, plant macrofossils indicate the presence of taxa not detected by pollen analysis: Cyperaceae and *Hippuris vulgaris*. *Hippuris vulgaris* is an aquatic that grows in standing water, along streams or on mudflats (Pojar and MacKinnon 1994). A single needle tip has been tentatively identified as *Abies lasiocarpa*. *Abies* is not found on the Queen Charlotte Islands today but was among the first tree species to colonize deglaciated surfaces elsewhere in British Columbia (Heinrichs et al. 2002) and seems to be associated with glacial refugia on Vancouver Island and in southeastern Alaska (Heusser 1989).

The Juan Perez Sound grab sample contained abundant terrestrial plant fragments, primarily branches. Microscopic anatomical features were used to identify 25 random wood specimens to three taxa: *Salix* (15), *Alnus* (6), and *Pinus contorta* (3). One specimen was tentatively identified as cf. *Chamaecyparis*. The grab sample also contained abundant *Antitrichia curtipendula* moss remains and a winged aphid, identified

Table 3.2. Juan Perez Sound and Cook Bank pollen and spore percentages.

Pollen / Spore Type	Juan Perez Sound 12,200 ^{14}C yr BP (n = 4)	Cook Bank 10,500 ^{14}C yr BP (n = 3)
Trees		
Pinus contorta	66	60
Picea	-	7
Tsuga mertensiana	-[a]	3
Tsuga heterophylla	-	3
Cupressaceae	-	≤1
Abies	-	≤1
Taxus brevifolia	-	≤1
Alnus rubra type	-	5
Shrubs		
Salix	≤1	-
Empetrum nigrum	≤1	-
Ericaceae undiff.	-[a]	≤1
Alnus crispa type	-[a]	4
Rosaceae	-	≤1
Betula	-	≤1
Herbs		
Apiaceae	≤1	≤1
Heracleum lanatum	≤1	-
Asteraceae (Tubuliflorae)	-[a]	≤1
Artemisia	-[a]	-
Sanguisorba canadensis	-[a]	-
Cyperaceae	-	2
Onagraceae	-	≤1
Poaceae	-	≤1

Pollen / Spore Type	Juan Perez Sound 12,200 ^{14}C yr BP (n = 4)	Cook Bank 10,500 ^{14}C yr BP (n = 3)
Abronia latifolia	-	≤1
Caltha type	-	≤1
Ferns and Allies		
Polypodiaceae (Filicales)	32	9
Adiantum pedatum	≤1	-
Athyrium filix-femina	≤1	-
Cryptogramma crispa	-[a]	-
Polypodium	≤1	≤1
Pteridium aquilinum	-	≤1
Equisetum	≤1	-
Isoëtes	≤1	-
Huperzia selago	≤1	-
Lycopodium annotinum	≤1	≤1
Lycopodium clavatum	-[a]	-
Lycopodium undiff.	-	≤1
Mosses		
Sphagnum	-	≤1
Range of Total Pollen and Spore Concentration (grains cm^{-3})	1,359,900 – 3,098,500	1,260 – 763,700

Note: All values are the average percentage of the total pollen and spore sum. Hyphens denote taxa that were not detected.

[a] Pollen types that were not encountered during counting but only through additional scanning of slides.

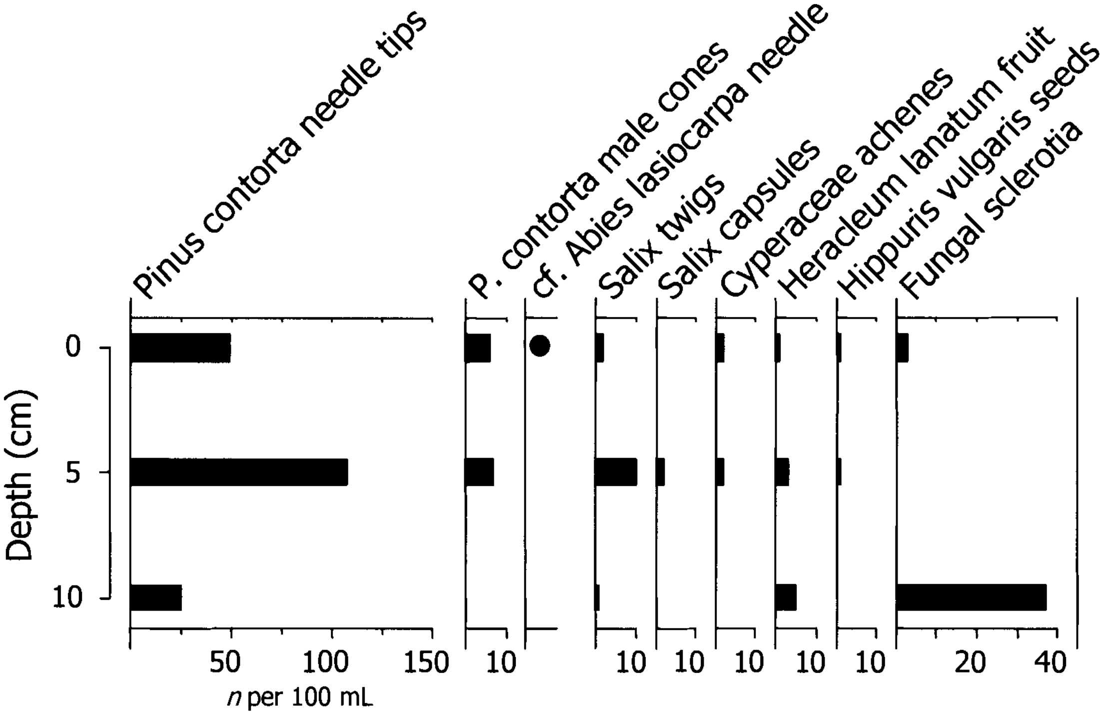

Fig. 3.3. Plant macrofossils from the Juan Perez Sound peat. Note changes in scale.

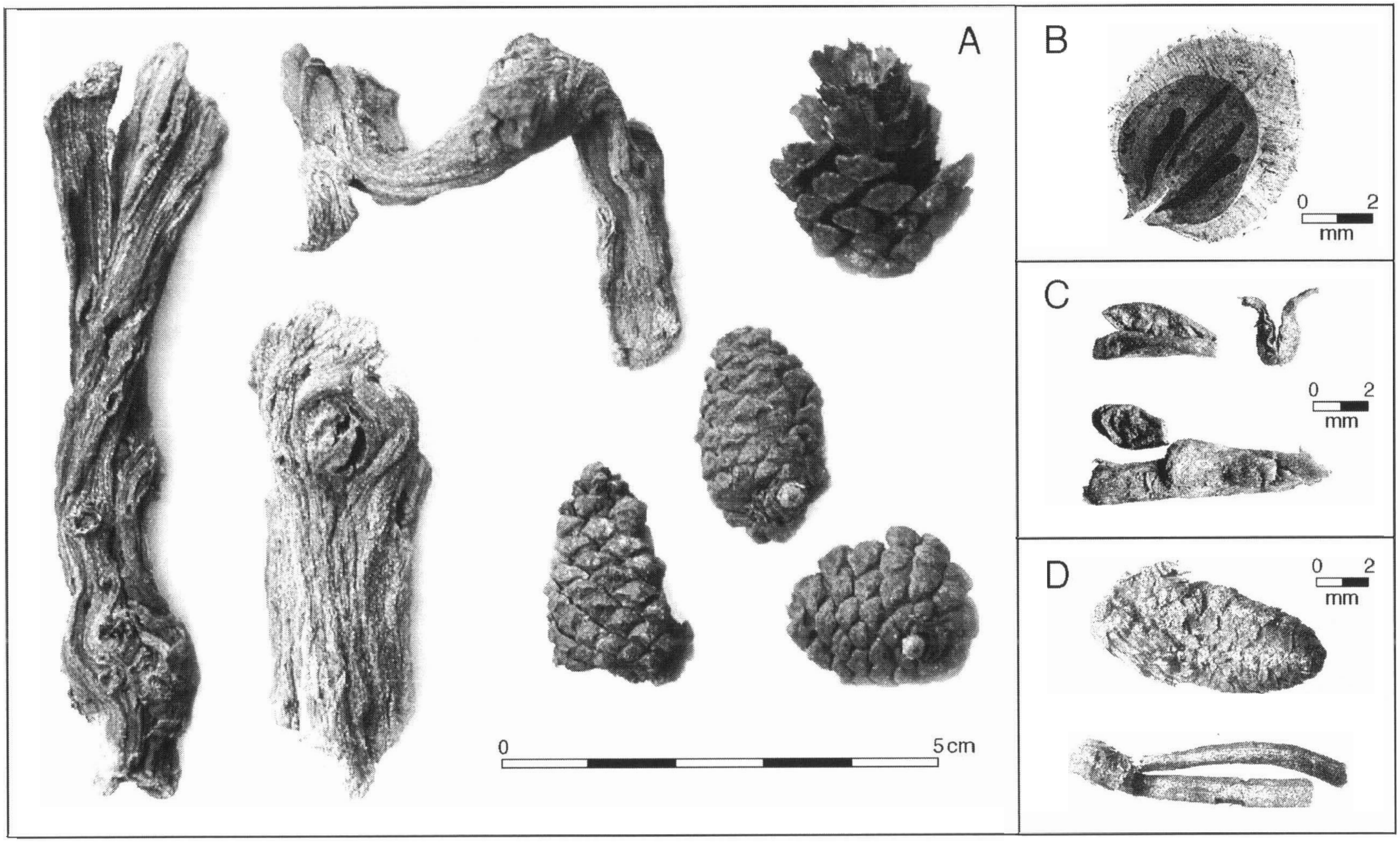

Fig. 3.4. **Selected plant macrofossils from Juan Perez Sound. (A) *Salix* twigs (left) and female cones of *Pinus contorta* (right), (B) *Heracleum lanatum* fruit, (C) *Salix* buds and capsules, (D) Male cone and paired needle base of *Pinus contorta*.**

as *Anoecia* cf. *corni* (Fabricius) or dogwood aphid. A definitive identification is not possible because the body cavity is filled with fungal hyphae, which obscures the diagnostic setal characters, but suggests that the aphid is not a contaminant. *Anoecia corni* hosts alternate between species of *Cornus* in winter and the roots of various herbaceous plants in summer (R. Foottit, personal communication, 2000).

Cook Bank

In situ plant roots extend 18 cm down from a thin soil profile that sits on top of a slopewash unit that accumulated when sea level was lower (Fig. 3.2). The upper portion of the mineral unit appears oxidized (10YR7/4), likely the result of pedogenesis. The thickest *in situ* root consists of a periderm enclosing a vascular cylinder that has been largely replaced by fungal hyphae. Microscopic analysis of partially decayed woody tissue shows tracheids with bordered pits, which indicates that the plant is a gymnosperm. The fungal hyphae are typical of those found in wood decayed in a terrestrial environment by brown rot fungi (Basidiomycetes), suggesting that the plant's root system began to decay before marine inundation. Wood fragments from the overlying pond sediments were identified as *Picea*.

The overlying pond sediments contain pollen and spore concentrations of up to 760,000 grains cm^{-3} (Table 3.2). The pollen assemblages are dominated by arboreal species, mostly *Pinus contorta*. *Picea*, *Tsuga* spp., and *Alnus rubra* are also common while *Abies*, *Taxus brevifolia* and Cupressaceae pollen are uncommon. Pollen from herbaceous plants accounts for less than 5% of the total pollen and spore sum at Cook Bank (Table 3.2). Fern spores are abundant in Cook Bank sediments. However, most monolete fern spores had lost their diagnostic perine and could only be identified to the family level. Algal cysts, *Pediastrum* colonies and *Spirogyra* zygospores indicate a freshwater depositional environment.

Discussion

Juan Perez Sound, ~12,200 ^{14}C yr BP

Our analyses of the Juan Perez Sound peat with the *in situ Pinus* stump indicate that *Pinus contorta* woodland vegetation grew on the exposed continental shelf 12,200 ^{14}C yr

BP. *Pinus contorta* is a shade-intolerant species with wide climatic and edaphic tolerance, capable of rapid invasion of disturbed sites and recently deglaciated terrain (Klinka et al. 1989). *Pinus contorta* was the first tree species to colonize the coast following deglaciation. Its late-glacial dominance on the coast suggests either nearby late Wisconsin refugia or exceptionally rapid late-glacial coastal migration from the south (Peteet 1991). Free of competing tall vegetation, *P. contorta* would have grown quickly on the moist but well-drained sands and gravels. Other shade-intolerant species such as *Empetrum nigrum* and *Sanguisorba canadensis* occupied the continental shelf, suggesting that the vegetation was patchy or open-canopy. The presence of *Antitrichia curtipendula*, a mat-forming coastal moss, also suggests open gaps in the woodland vegetation (Pojar and MacKinnon 1994). Polypodiaceae ferns were an important understory component of this late-glacial landscape. The abundance of fern spores may be the result of fluvial transport and would be expected in an environment dominated by fluvial processes. The riparian nature of the landscape is supported by the presence of plants such as *Heracleum lanatum*, *Sanguisorba canadensis*, *Alnus crispa*, *Salix*, and *Adiantum pedatum*, which are commonly abundant on water-receiving sites such as alluvial fans, deltas and floodplains (Klinka et al. 1989). Although there is no pollen or plant macrofossil evidence of *Cornus*, the dogwood aphid suggests it was also present. Plants of marshy environments were also locally prominent, including Cyperaceae, *Hippuris vulgaris*, *Equisetum* and *Isoëtes*. Scattered individuals of *Tsuga mertensiana* and possibly *Abies lasiocarpa* accompanied *P. contorta* on more upland sites, along with shrubs such as *A. crispa*, *Salix* and *E. nigrum* in open areas.

Pollen and spore preservation is good in the Juan Perez Sound peat, although the exine of some pollen grains is corroded, suggesting oxidation. *Pinus* is a prolific pollen producer (Critchfield 1985) and its pollen is well-preserved, whereas *Salix* pollen is highly susceptible to corrosion and oxidation (Havinga 1964). The relative fragility of *Salix* pollen explains, at least in part, why *Salix* is well-represented by plant macrofossils and fossil wood but poorly represented in the pollen assemblages.

The abundant *Salix* macrofossils are likely from a dwarf species, *Salix reticulata* or *S. stolonifera*, but specific identification is uncertain. Warner et al. (1982) found leaves from the alpine *S. reticulata* in late-glacial sediments near sea level at Cape Ball. On Dogfish Bank and at Cape Ball (Fig. 3.1), Barrie et al. (1993) found dwarf willow remains similar to *S. stolonifera*, including leaves, twigs and buds that date to between 13,700 and 13,200 ^{14}C yr BP. Argus (1973) argues that *S. stolonifera* survived the last glaciation in the Pacific coastal region; it has also been reported in coastal Alaska in the Kodiak Island refugium and on the Kenai Peninsula (Argus 1973). *Salix* was clearly an important component of the late-glacial landscape and more widespread than previously thought. *Salix* species occupy a wide variety of habitats but are typically associated with habitat instability (Argus 1973).

The 12,200 ^{14}C yr BP *in situ Pinus* stump and the paleoecological analyses of its associated peat and forest litter compare well with other paleoecological records. In general, these records demonstrate that *Pinus contorta* dominated the British Columbia coast between approximately 12,500 and 11,200 ^{14}C yr BP (Hebda 1983; Warner 1984; Mathewes 1989; Heusser 1995). *Alnus*, *Empetrum*, and *Salix* shrubs and various ferns are also found at most fossil sites of similar age. The period of *Pinus contorta* dominance was time-transgressive, with more southerly sites showing earlier population expansion.

Paleoecological evidence prior to the arrival of *Pinus contorta* points to expanses of treeless herb and dwarf shrub tundra from the Olympic Peninsula in Washington to southeastern Alaska between at least 15,000 and 13,000 ^{14}C yr BP, marked by the presence of *Salix*, *Empetrum*, Cyperaceae, Poaceae, and a variety of other plants including *Sanguisorba canadensis, Heracleum lanatum,* and *Equisetum* (Warner 1984; Mathewes 1989). At Cape Ball, a terrestrial and wetland herbaceous plant community was present by at least 15,000 ^{14}C yr BP (Mathewes et al. 1985). The Cape Ball area was characterized by patchy tundra-like meadows composed of grasses, sedges, other herbs such as *Sagina maxima*, and wetland plants such as *Juncus*, and *Potamogeton filiformis* (Warner et al. 1982). The richness of the flora at this time, when adjacent areas were glaciated, suggests the presence of nearby refugia (Heusser 1989). At about 13,000 ^{14}C yr BP, this vegetation was replaced by dwarf-shrub tundra that included *Salix reticulata*. The arrival of *Pinus contorta* by 12,200 ^{14}C yr BP, followed by *Picea* at 11,200 ^{14}C yr BP, and *Tsuga heterophylla* at 10,200 ^{14}C yr BP suggests that forest development was relatively rapid at Cape Ball. Pollen analysis of a single sample from a sediment core recovered from Dogfish Bank (Fig. 3.1) suggests that herb tundra grew on the shelf 13,200 ^{14}C yr BP when it was exposed due to low relative sea level (Barrie et al. 1993).

The local environment was dominated by wet sedge tundra that included *Equisetum* and Poaceae. *Empetrum nigrum* and *Salix* were also present and probably grew on drier, exposed hummocks within the sedge tundra.

Cook Bank, ~10,500 ^{14}C yr BP

Our analysis of the Cook Bank sediments indicates that a productive mixed coniferous forest grew on the continental shelf north of Vancouver Island at 10,500 ^{14}C yr BP. *Pinus contorta* dominates the pollen assemblages, accounting on average for 60% of the total pollen and spore sum (Table 3.2). The pioneering phase of *Pinus contorta* ended on northern Vancouver Island at Bear Cove Bog (Fig. 3.1) by ~11,500 ^{14}C yr BP with the establishment of *Picea sitchensis* and *Tsuga mertensiana* forests (Hebda 1983). However, it is likely that *Pinus contorta* continued to dominate the recently exposed continental shelf for a longer period of time than it did further inland. The pollen assemblage suggests that *Pinus* populations were declining as other conifers invaded or expanded their already established populations. *Picea* appears to have been an important secondary component of the lowland forests. *Picea* pollen is likely derived from *Picea sitchensis*, although this is uncertain in light of the analysis by Warner and Chmielewski (1987), which indicates that late-glacial *Picea* cones from Cape Ball probably represent hybrids of *P. sitchensis* and *P. glauca*. Today, *P. sitchensis* commonly forms open-canopy stands along the outer coast where it readily tolerates ocean spray and brackish water (Klinka et al. 1989). *Tsuga mertensiana* and *T. heterophylla*, both species that favour humid conditions, were also present in nearby forests. Cupressaceae, *Abies*, and *Taxus brevifolia* were of minor importance. The presence of *Alnus rubra* and *A. crispa* suggests that, as sea level was rising, edaphic conditions were unstable. Both species of *Alnus* regenerate readily on exposed mineral soil (Klinka et al. 1989). Polypodiaceae ferns likely dominated the understory of the coniferous forests. Cyperaceae, Poaceae, Apiaceae, and *Caltha* pollen, and *Sphagnum* moss spores suggest that wetlands were nearby. Pollen from *Abronia latifolia*, a creeping perennial typical of coastal beaches and sand dunes, but infrequent on Vancouver Island beaches today (Douglas et al. 1989), is a strong indicator of sandy beach habitat and suggests that shoreline soils were poorly developed.

The relative abundance of *Tsuga mertensiana* pollen suggests that this species was important in nearby forests. *Tsuga mertensiana* is a good indicator of cool and moist conditions; it requires cool temperatures and substantial snow for insulation during winter months (Pojar and MacKinnon 1994). *Tsuga mertensiana* pollen is commonly under-represented in modern pollen assemblages (Minckley and Whitlock 2000). In the subalpine zone of Brooks Peninsula on Vancouver Island, where it is a co-dominant of the forest, *Tsuga mertensiana* accounts for only 9% of the pollen sum (Hebda 1983). Late-glacial peaks in *Tsuga mertensiana* pollen provide evidence of cooling and increased moisture between 11,000 and 10,000 ^{14}C yr BP on the Pacific coast (Hebda 1983; Warner 1984; Mathewes 1993; Mathewes et al. 1993; Heusser 1995), similar in timing and extent to the Younger Dryas cooling documented in Europe and eastern North America (Mangerud et al. 1974; Mott et al. 1986; Peteet et al. 1990). Based on peaks in cold-water foraminifera, Mathewes et al. (1993) document the cooling of ocean waters between 11,000 and 10,200 ^{14}C yr BP and suggest a drop of 2-3°C in summer temperatures for the Pacific coast during this time.

Conclusion

Due to significant sea level changes, extensive portions of the continental shelf were exposed during the late Pleistocene and earliest Holocene. Until now, our understanding of the paleovegetation that grew on the emergent shelf was based on just a few allochthonous samples. Rooted plant remains demonstrate that terrestrial vegetation grew on the continental shelf between at least 12,200 and 10,400 ^{14}C yr BP. Our paleoecological analyses indicate that *Pinus contorta*-dominated communities with abundant ferns occupied portions of the continental shelf adjacent to the Queen Charlotte Islands at 12,200 ^{14}C yr BP. Shrubs including *Alnus crispa*, *Salix*, and *Empetrum nigrum* and herbaceous plants such as *Heracleum lanatum* and *Hippuris vulgaris* were also important components of the shelf vegetation. Scattered individuals of *Tsuga mertensiana* were likely present on upland sites with *Pinus contorta* and various shrubs. Near northern Vancouver Island, mixed coniferous forests dominated by *Pinus contorta* with *Alnus* spp. and ferns occupied the shelf on Cook Bank at 10,500 ^{14}C yr BP. Fossil pollen of *Abronia latifolia* indicates that beach vegetation grew along the ancient shoreline. Marine inundation of the vegetated shelf was complete by 7000 ^{14}C yr BP (Friele 1991; Clague et al. 1982a).

Our analyses also demonstrate the importance of examining a variety of biological fossils for paleoenvironmental reconstruction. Pollen analysis alone may be insufficient and should be accompanied by plant macrofossil analysis and fossil wood identification when possible since both provide valuable and complementary paleoecological information (Birks and Birks 2000).

It has been suggested that some ice-free areas between the Aleutian Islands in Alaska and the northwestern United States served as biotic refugia during the last glaciation (Heusser 1989). Late Wisconsin biotic refugia on the north Pacific coast, perhaps with small colonies of trees such as *Pinus contorta*, would have been major centers of dispersal as early as 16,000 ^{14}C yr BP (Warner et al. 1982; Warner 1984) and would have preceded dispersal from refugia in interior Alaska or Yukon and in Washington. There is ample evidence in support of biotic refugia on the north Pacific coast. However, conclusive proof in the form of continuous stratigraphic sequences spanning the last glaciation is still lacking.

CHAPTER 4

LATE QUATERNARY DYNAMICS OF FOREST VEGETATION ON NORTHERN VANCOUVER ISLAND, BRITISH COLUMBIA[1]

Abstract

Pollen analysis of radiocarbon-dated lake sediment from northern Vancouver Island, southwest British Columbia reveals regional changes in forest vegetation over the last 12,200 ^{14}C yr (14,900 cal yr). Between at least 12,200 and 11,700 ^{14}C yr BP (14,900–13,930 cal yr BP), open woodlands were dominated by *Pinus contorta, Alnus crispa*, and various ferns. As *P. contorta* decreased in abundance, *Alnus rubra* and more shade-tolerant conifers (i.e., *Picea* and *Tsuga mertensiana*) increased. Increases in *T. mertensiana*, *P. contorta*, and *A. crispa* pollen accumulation rates (PARs) between 10,600 and 10,400 ^{14}C yr BP (11,660–11,480 cal yr BP) reflect a cool and moist climate during the Younger Dryas chronozone. Orbitally induced warming around 10,000 ^{14}C yr BP (11,090 cal yr BP) allowed the northward extension of *Pseudotsuga menziesii*, although *Picea*, *Tsuga heterophylla*, and *A. rubra* dominated early Holocene forests. By 7500 ^{14}C yr BP (8215 cal yr BP), shade-tolerant *T. heterophylla* was the dominant forest tree. Cupressaceae (*Thuja plicata* and *Chamaecyparis nootkatensis*) was present by 7500 ^{14}C yr BP but reached its maximum after 3500 ^{14}C yr BP (3600 cal yr BP), when a cooler and wetter regional climate facilitated the development of temperate rainforest. The highest rates of vegetation change are associated with late-glacial climate change and species with rapid growth rates and short life spans.

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Introduction

The modern coastal temperate rainforests of western North America form a narrow band along the Pacific coast that extends from Alaska to northern California, and are characterized by high annual precipitation, moderate annual temperatures, and infrequent fire, particularly north of 50°N (Schoonmaker et al. 1997). These coastal temperate rainforests are among the most productive forests worldwide with biomass accumulation far exceeding those of other north temperate forests (Waring and Franklin 1979; Schoonmaker et al. 1997). Conifers have a distinct competitive advantage over deciduous trees in this region because most photosynthesis occurs during the wet and relatively warm fall and winter months as opposed to the relatively dry summer months when high evaporative demand causes stomata to close (Waring and Franklin 1979). In coastal British Columbia, these rainforests are defined by the dominance of *Tsuga heterophylla* (see Appendix for common names of plants) and relatively large areas of undeveloped old-growth forest (Meidinger and Pojar 1991; MacKinnon and Vold 1998).

Modern forest ecology is limited by a lack of long-term community records i.e., records that exceed either decades or centuries. Understandably, there are no long-term modern successional studies for coastal British Columbia; due to the long life spans (400–1000 yr) and large size (1–3 m dia; 30–80 m ht) of the region's dominant tree species (Waring and Franklin 1979), direct observation of succession is extremely limited. Paleoecological analyses offer an indirect approach to study vegetation change and community response at long time scales (Bennett and Lamb 1988; Foster et al. 1990) that is particularly useful in regions with extended seres such as coastal British Columbia. Paleoecological records of vegetation provide an integrated perspective of vegetation dynamics over many millennia and permit identification of species interactions, macroscale vegetation dynamics, and climate change responsible for the composition of modern forests. Pollen data provide a less precise record of vegetation than can be obtained from direct sampling (Webb et al. 1981) but are the primary sources of quantitative information on vegetation dynamics on long time scales. By temporally extending our perspectives, paleoecological studies can provide essential insights into vegetation dynamics at local and regional scales that are vital to our understanding of fundamental ecological processes and managing the biosphere

(Ricklefs 1987; Bennett and Lamb 1988; Foster et al. 1990; Birks 1993; Franklin et al. 2002).

Previous paleoecological studies on northern Vancouver Island used low pollen counts (i.e., 50-300 pollen grains) and did not differentiate *Alnus crispa* and *Alnus rubra* pollen (Heusser 1960; Hebda 1983; Hebda and Haggarty 1997). Some of these studies did not include counts of Cupressaceae pollen or radiocarbon dating (Heusser 1960) and others were based on records from non-uniform sedimentary environments with unconformities (Heusser 1960; Hebda 1983; Hebda and Haggarty 1997). This paper presents the results of pollen analysis of radiocarbon-dated lake sediment from Misty Lake (Fig. 4.1) on northern Vancouver Island. The analyses include complete pollen counts, distinguish *Alnus* types, and are based on a minimum sum of 500 pollen grains. The Misty Lake sediment core was originally collected as part of a north-south transect for a postglacial chironomid study in British Columbia (Walker 1988). Walker and Mathewes (1989) analysed fossil chironomids at 13 levels in the Misty Lake core and detected important differences between late-glacial and Holocene assemblages; however, paleotemperatures were not inferred.

The purpose of this study was to reconstruct the dynamics of postglacial forest composition including development of coastal temperate rainforests and to assess the relative importance of *Alnus crispa* and *Alnus rubra* in forest development. Pollen analyses reveal substantial local and regional changes in late-glacial and Holocene vegetation i.e., over the last 12,200 ^{14}C yr (14,900 cal yr) at the landscape level rather than the history of individual plant communities (Birks 1993). Pollen accumulation rates (PARs) are used as an index of population size to evaluate trends in population growth, since they avoid the statistical interdependence of percentage data (Davis et al. 1984). Rates of palynological change, taken to represent rates of vegetation change, are used to describe temporal dynamics of forest composition and to determine whether vegetation change was gradual or more rapid during certain periods e.g., the late-glacial. In the context of this study, the paper provides a review of the region's postglacial vegetation and climate history.

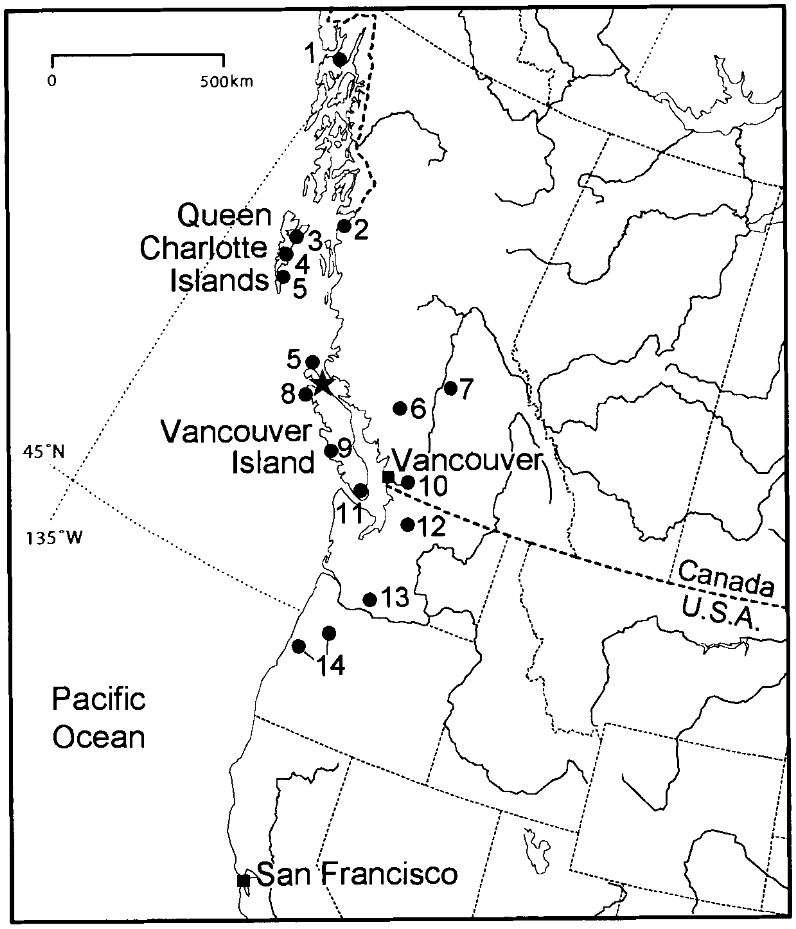

Fig. 4.1. Location of Misty Lake (★) on Vancouver Island, British Columbia, and sites of other paleoecological studies (●) mentioned in the text. 1. Engstrom et al. (1990), Hansen and Engstrom (1996); 2. Turunen and Turunen (2003); 3. Mathewes (1989); 4. Pellatt and Mathewes (1997); 5. Lacourse et al. (2003); 6. Clague and Mathewes (1989); 7. Cumming et al. (2002); 8. Brooks Peninsula; Hebda and Haggarty (1997); 9. Gavin et al. (2003); 10. Mathewes (1973), Mathewes and Heusser (1981), Pellatt et al. (2002); 11. Pellatt et al. (2001), Brown and Hebda (2002, 2003); 12. Cwynar (1987); 13. Whitlock and Bartlein (1997); 14. Grigg and Whitlock (1998).

Environmental Setting

Northern Vancouver Island (Fig. 4.1) is a physiographically and ecologically distinct region with a complex paleoenvironmental history, including dramatic sea level changes and local isostatic complications (Luternauer et al. 1989a; Hebda and Haggarty 1997; Hetherington et al. 2004). The Wisconsin glaciation was well advanced by 25,000 ^{14}C yr BP (ca. 30,000 cal yr BP) and reached its maximum 15,000 ^{14}C yr BP (ca. 18,000 cal yr BP) (Blaise et al. 1990; Clague and James 2002). Ice flowed west from the adjacent British Columbia mainland across northern Vancouver Island and coalesced with ice to the north in Queen Charlotte Strait, covering the exposed continental shelf with grounded ice (Howes 1983). Deglaciation commenced prior to 13,600 ^{14}C yr BP (ca. 16,500 cal yr BP) (Hebda 1983; Howes 1983). As ice thinned and retreated, marine waters flooded the isostatically depressed lowlands, leaving marine deposits up to 90 m above present sea level (Howes 1983). Before modern relative sea levels were reached in the early Holocene, rapid isostatic rebound resulted in local sea-level lowering to at least 95 m below present marine limit, despite rising eustatic sea levels, exposing large areas of the continental shelf (Luternauer et al. 1989a, 1989b).

Misty Lake (50° 36.5′ N, 127° 15.8′ W; 70 m a.s.l.) is located within the Misty Lake Ecological Reserve, 20 km southeast of Port Hardy on northeastern Vancouver Island under the prevailing influence of the Pacific Ocean (Fig. 4.1). It is located within the Nahwitti Lowland of the Hecate Depression, on the windward side of the Coast Mountains of the adjacent mainland, with the Vancouver Island Ranges to the south (Holland 1976). Misty Lake is situated within the Coastal Western Hemlock biogeoclimatic zone (very wet maritime variant), which occurs at low to middle elevations and is characterized by cool summers and wet, mild winters (Meidinger and Pojar 1991). Mean annual temperature is about 8°C and mean annual precipitation is about 2225 mm. Forests in this zone are dominated by *Tsuga heterophylla*, *Thuja plicata*, and to a lesser extent *Abies amabilis*. *Picea sitchensis* is largely restricted to floodplain forests and open-canopy stands along the coast, where it readily tolerates ocean spray and brackish water (Klinka et al. 1989). *Pseudotsuga menziesii* is uncommon and restricted to dry sites, while *Chamaecyparis nootkatensis* is locally common on wet sites and at higher elevations. *Pinus contorta* var. *contorta* is common on both wet and dry sites; it has cones that release seeds upon maturity, unlike the cones of the inland subspecies, *P. contorta* var. *latifolia*, which commonly remain closed until opened by fire. *Tsuga mertensiana* occurs only occasionally, mainly on exposed ridges. *Alnus rubra* and *Populus balsamifera* are locally common on disturbed sites and along rivers. An abundance of ericaceous shrubs (e.g., *Gaultheria shallon* and *Vaccinium alaskaense*), a poorly-developed herb layer dominated mostly by pteridophytes, a well-developed moss layer, and regeneration of *T. heterophylla* characterize the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991). Peatlands are widespread throughout the region due to low relief, cool summer temperatures, and humid conditions.

Misty Lake is a moderate size, humic lake with a surface area of 35.6 ha and a maximum depth of 6.1 m (Lavin and McPhail 1993). Its catchment is approximately 10 km^2 (Walker and Mathewes 1989). A small stream enters the southeastern corner of the lake, flowing through 500 m of wetland before reaching the lake. The vegetation surrounding the lake consists of a bog-forest complex composed of *Tsuga heterophylla*, *Thuja plicata*, *Pinus contorta* var. *contorta*, and *Picea sitchensis* with abundant *Rubus spectabilis*, *Myrica gale*, and *Spiraea douglasii* around the margins of the lake. The littoral zone supports beds of *Brasenia schreberi*, *Nuphar luteum*, *Nymphaea odorata*, *Potamogeton* sp., and *Sparganium angustifolium*.

Materials and Methods

Walker and Mathewes (1989) collected a 7.53 m sediment core from the center of Misty Lake, distant from the inflowing stream, using a Livingstone piston corer (Wright et al. 1984). The sediment-water interface was recovered using a Brown piston sampler (Brown 1956). The uppermost 7 m of sediment was cut into 10 cm sections, and sediment from 7.00 to 7.53 m was cut into 5 cm sections. The 10 and 5 cm sampling intervals of Walker and Mathewes (1989) constrained the temporal resolution of study.

Conventional radiocarbon ages were obtained from six organic-rich sediment samples (Table 4.1). Radiocarbon ages (^{14}C yr BP) were calibrated to calendar ages (cal yr BP) using the BCal calibration system (http://bcal.shef.ac.uk) and CALIB 4.3 (Stuiver and Reimer 1993). BCal uses the same dendrocalibrated data of Stuiver et al. (1998) as

Table 4.1. Radiocarbon ages of organic-rich Misty Lake sediments.

Depth (cm)	Laboratory no.	Radiocarbon age[a] (^{14}C yr BP ± 1σ)	BCal Calibrated age[b] (cal yr BP)	CALIB 4.3 Calibrated age[c] (cal yr BP)
90–100	BETA-16582	1760 ± 80	1644	1690; 1650; 1630 (1870–1520)
290–300	BETA-16583	2860 ± 80	2988	2950 (3240–2780)
490–500	BETA-16584	5720 ± 90	6473	6490 (6730–6310)
590–600	BETA-16585	6960 ± 110	7767	7790; 7770; 7760 (7970–7590)
705–710	BETA-16586	10,180 ± 130	11,660	11,920; 11,810; 11,760 (12,710–11,260)
735–740	GSC-4029	12,100 ± 130[d]	14,090	14,100 (15,390–13,660)

[a] All radiocarbon ages previously published in Walker and Mathewes (1989).

[b] Calendar year with the highest probability.

[c] Intercept ages and age range rounded to the nearest 10 yr. Range represents the 95% confidence interval (±2σ).

[d] Reported as ±2σ.

CALIB 4.3 but employs a Bayesian statistical approach and Markov chain Monte Carlo methods that take other ages from the same sequence into account during the calibration of individual ages. Radiocarbon ages were assigned the calendar age with the highest probability (i.e., the mode) as determined by BCal, but calendar ages from CALIB are also provided (Table 4.1).

Sediment subsamples (1 cm^3) were prepared for pollen analysis following standard methods (Fægri and Iversen 1989). To calculate pollen concentrations and pollen accumulation rates (PARs), known quantities of *Eucalyptus* pollen (Batch #903722; 16,180 ± 1460 grains) were added to each subsample prior to chemical treatment (Benninghoff 1962). A minimum sum of 500 pollen grains, excluding pollen from aquatic plants and Pteridophyte and *Sphagnum* spores, was counted for each subsample since pollen sums of less than 500 have high associated errors (Birks and Birks 1980). The error associated with each pollen percentage depends on the size of the pollen sum and the proportion of the sum accounted for by that pollen type (Maher 1972); 95% confidence intervals for this dataset average between ±0.1 and 3.7%. Pollen and spore identifications were made with reference to published dichotomous keys and the modern pollen and spore reference collection at Simon Fraser University. Diploxylon type *Pinus* pollen was assigned to *Pinus contorta* based on pollen morphology and modern phytogeography. *Abies* pollen could derive from *A. amabilis*, *A. grandis*, or *A. lasiocarpa*, although *A. amabilis* is the most common in regional forests today. *Alnus crispa* and *Alnus rubra* types were differentiated following the criteria of Richard (1970) and Mayle et al. (1993); *Alnus rubra* is similar to *A. rugosa*. Botanical nomenclature follows Douglas et al. (1989).

Percentages were calculated using the sum of all tree, shrub, and herb pollen and Pteridophyte spores. The unconventional taxon order in the pollen diagrams is based on weighted averages since this facilitates identifying the chronological order of arrival of taxa. Pollen and spore accumulation rates (grains cm^{-2} yr^{-1}) were calculated from the pollen concentration (grains cm^{-3}) of each sample and the sedimentation rate (cm cal yr^{-1}). Pollen accumulation rates are often referred to incorrectly as 'pollen influx', which is simply the number of pollen grains in a sample, not an accumulation rate per unit area (Thompson 1980). Due to temporal variations in ^{14}C production, accumulation rates were calculated using calendar years as opposed to radiocarbon years. Phases of constant radiocarbon age particularly during the late-glacial period prevent reliable estimates of rates on the basis of uncalibrated radiocarbon ages (Lotter et al. 1992). Due to the variable sedimentation rate, variations in calculated accumulation rates may partially reflect changes in sedimentation and therefore are interpreted conservatively.

The pollen percentage data were subjected to numerical zonation, using optimal splitting by information content (Bennett 1996). Agglomeration using constrained cluster analysis (CONISS) developed by Grimm (1987), which is based on Ward's sum-of-squares method, was not used as it tends to produce zones of equal size (Birks and Gordon 1985); however, in this case, CONISS produced similar results to optimal splitting. Zonations with variances that exceeded values generated by a broken-stick model of the distribution of variance were deemed statistically significant (Jackson 1993; Bennett 1996). Principal components analysis (PCA) was used to display the major trends in the dataset in only a few dimensions, since gradient lengths of the ordination axes determined by detrended correspondence analysis are less than 2 standard deviations (ter Braak 1995). PCA was carried out on a covariance matrix after the square-root transformation of the dataset, which was done to stabilize the variance. A broken-stick model was used to test the significance of the eigenvalues for each axis (Jackson 1993). For zonation and PCA, the dataset was limited to those pollen types that reached a threshold value of 1% somewhere within the sequence, and then recalculated for analysis to proportions of the sum of pollen types included. To calculate rates of palynological change between adjacent pollen samples, the information statistic, a symmetric measure designed to maximize the signal-to-noise ratio (Prentice 1980), was used as a dissimilarity coefficient and was standardized to calendar time (cf. Jacobson and Grimm 1986). Chord distance is commonly used to measure palynological dissimilarity, but it tends to produce peaks of similar magnitude in rates of change (Bennett and Humphry 1995). *Sphagnum* and obligate aquatic taxa were excluded from all numerical analyses.

Results

Stratigraphy and Radiocarbon Dating

The Misty Lake core begins in grey clay (7.53–7.40 m) that includes minor amounts of sand and pebbles and less than 5% organic matter (Walker and Mathewes 1989). The uppermost 7.4 m of sediment is uniform, dark brown gyttja with an average organic content of 40% (Walker and Mathewes 1989).

An age-depth model, based on radiocarbon ages and their errors (Table 4.1) and an age of –34 ± 20 ^{14}C yr BP for the top of the sediment core, was constructed using a four-term polynomial (Fig. 4.2). Confidence intervals for sediment age estimates were obtained by simulation (n = 100) from the radiocarbon ages and their associated errors (Bennett 1994). This predicted an age of 12,210 ± 112 ^{14}C yr BP (ca. 14,900 cal yr BP) for the base of the sediment core. The four-term polynomial model returned the best fit with the fewest number of terms. Spline models, which are based on a polynomial fitted between adjacent ^{14}C dates (usually a cubic polynomial), are commonly used in age-depth models because the fit is forced through each ^{14}C date. These functions generally behave well when there are many dates in a sequence (Telford et al. 2004). As with linear interpolation, spline models assume that each ^{14}C date is a 'true' date of the sample and do not consider their associated errors. Spline functions can return negative sedimentation rates when ages change rapidly over short depth intervals, particularly at the beginning and end of sequences (Maher 1992; Bennett 1994). In this instance, spline models returned negative sedimentation rates and a large plateau i.e., more than 1 m of sediment was given the same effective age.

Pollen Analysis

The first nine splits or 10 groups of the numerical zonation were examined, but only the first five splits were significant based on a broken-stick model (Fig. 4.3). PCA and numerical zonation of the dataset revealed similar subdivisions; however, PCA highlighted the similarity of samples from 405–0 cm (4160–0 ^{14}C yr BP; 4995–0 cal yr BP). The pollen data (Figs. 4.3 and 4.4) were subdivided into six pollen zones.

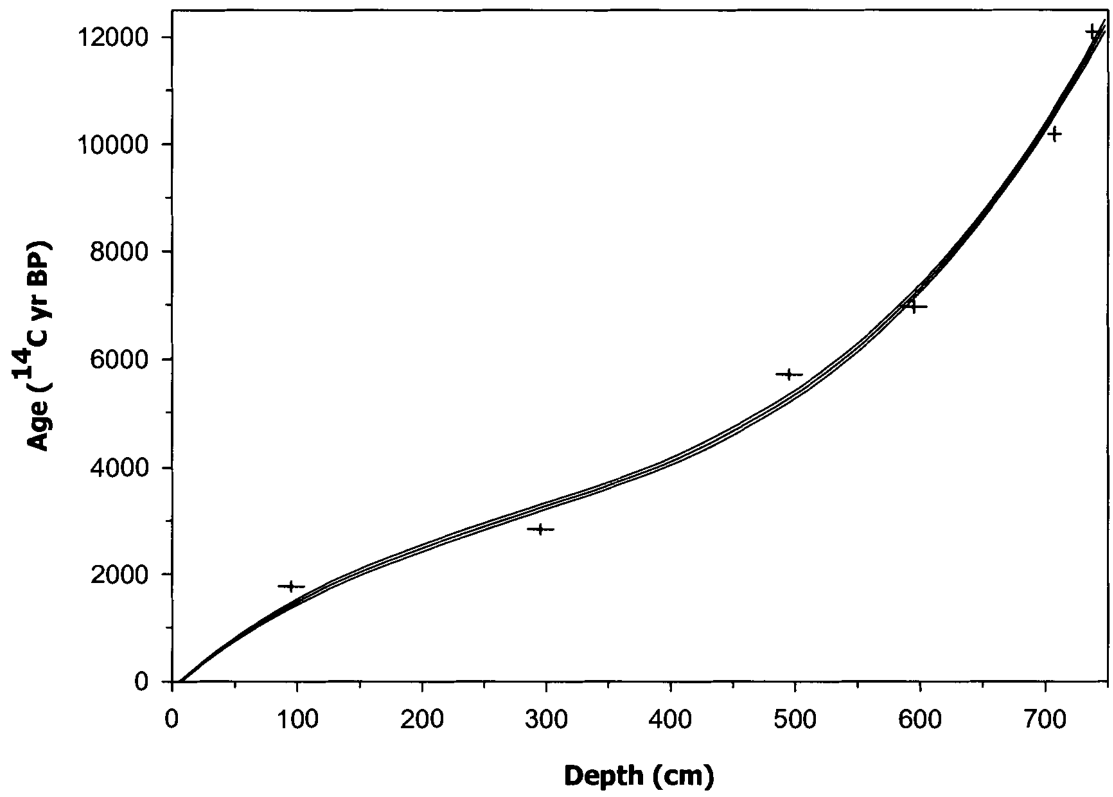

Fig. 4.2. Radiocarbon ages and associated errors from Misty Lake on Vancouver Island plotted against sediment depth. The age-depth model is a four-term polynomial and includes 95% confidence intervals obtained by simulation (*n* = 100) from the radiocarbon ages and their associated errors (Table 4.1).

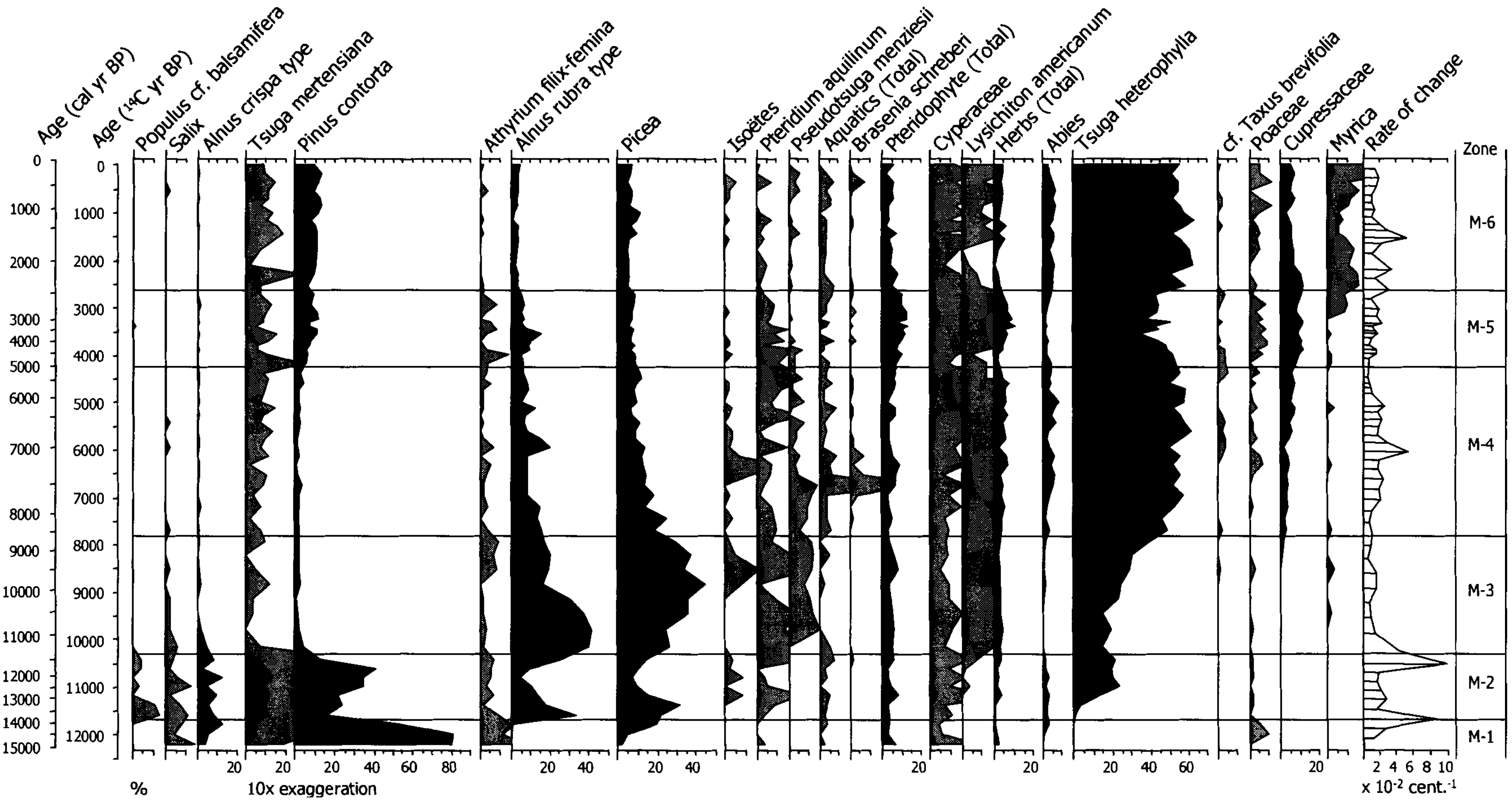

Fig. 4.3. Selected pollen and spore percentages and rates of change from Misty Lake on Vancouver Island. Grey curves represent 10x exaggeration. Taxon order is based on weighted averages of the pollen percentages.

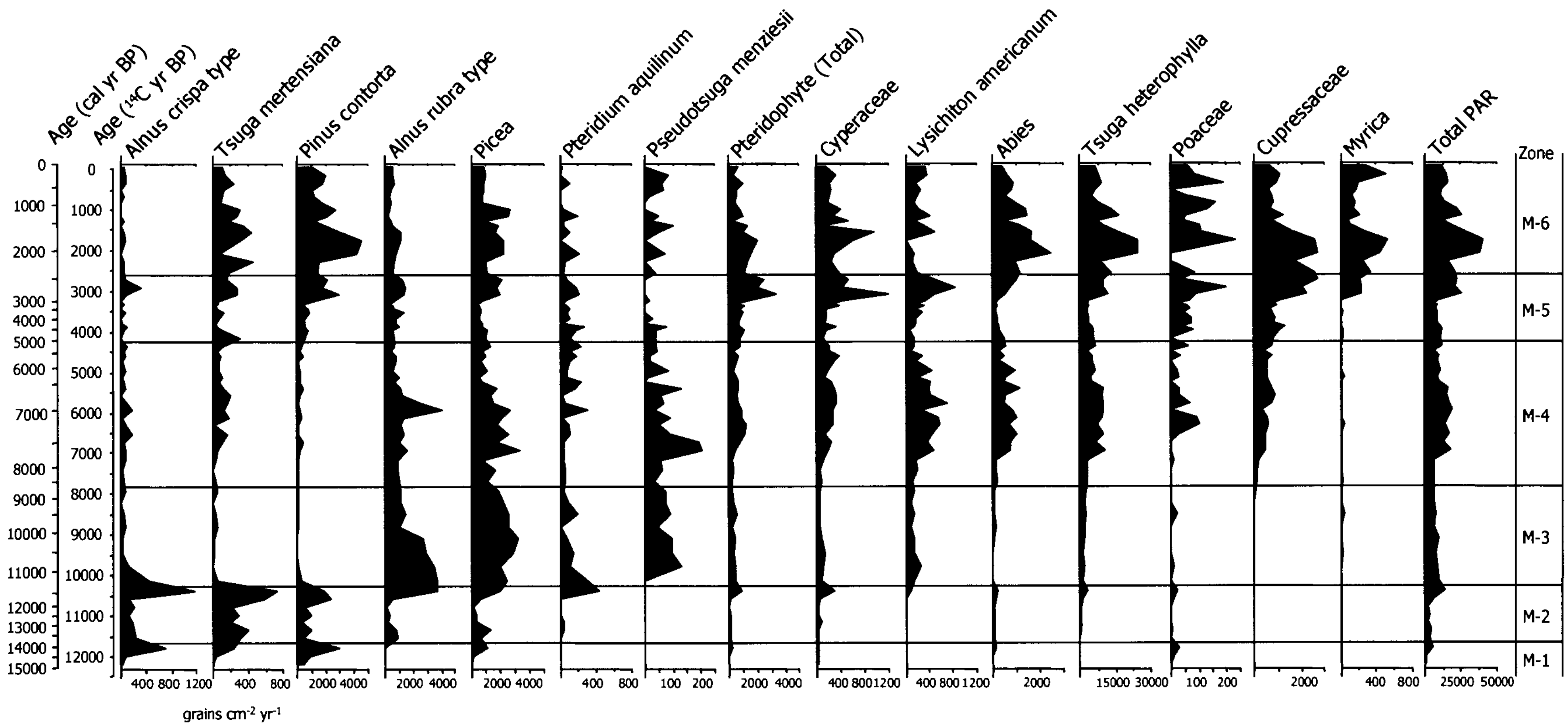

Fig. 4.4. Accumulation rates of important pollen and spore taxa from Misty Lake on Vancouver Island. Note changes in scale. Zonation from the pollen percentage diagram is superimposed. Taxon order is based on weighted averages of the pollen percentages.

Zone M-1: 12,210–11,680 ^{14}C yr BP, 14,900–13,890 cal yr BP (750–735 cm)

The basal zone is dominated by high values of *Pinus contorta* pollen, reaching its maximum (81%) for the period of record. Pollen from other trees and shrubs include *Picea*, *Tsuga mertensiana*, *Abies*, *Alnus crispa*, *Salix*, and *Shepherdia canadensis*. pteridophytes (including *Athyrium filix-femina*, *Cryptogramma acrostichoides* type, *Polypodium*, and *Pteridium aquilinum*) and herbs (*Artemisia*, Poaceae, and Cyperaceae) account for less than 7 and 3%, respectively. *Potamogeton* pollen is present in trace amounts. Total PARs are low at the base of the record (635 grains cm^{-2} yr^{-1}) but rise to 5470 grains cm^{-2} yr^{-1}. *Pinus contorta* PARs are between 500 and 3000 grains cm^{-2} yr^{-1}. Rates of change are moderate with a substantial peak at the transition to the next zone. Organic sedimentation begins at 11,890 ^{14}C yr BP (14,295 cal yr BP).

Zone M-2: 11,680–10,285 ^{14}C yr BP, 13,890–11,365 cal yr BP (735–699 cm)

An increase in *Tsuga mertensiana* pollen to 13.5% and a similar increase in *A. crispa* pollen to 12.5% characterize this zone. *Picea* pollen increases to 31% before decreasing to 7% in the middle of the zone. The *Picea* peak is immediately preceded by a rapid increase in *Alnus rubra* pollen to 34%. *Tsuga heterophylla* pollen first appears in this zone and rises to 24%. *Pinus contorta* pollen decreases dramatically to 15% at the base of the zone but gradually increases to 42% before tapering off to trace levels. *Abies*, *Populus* cf. *balsamifera*, and Cyperaceae pollen and *Adiantum aleuticum*, *Athyrium filix-femina*, *Equisetum*, *Isoëtes*, and *Pteridium aquilinum* spores are also present. Total PARs are about 3000 grains cm^{-2} yr^{-1} but increase to 14,560 grains cm^{-2} yr^{-1} at the top of the zone. *Tsuga mertensiana* PARs peak between 10,600 and 10,400 ^{14}C yr BP (11,660–11,480 cal yr BP). Rates of change are moderate but are highest for the period of record at 10,600 ^{14}C yr BP.

Zone M-3: 10,285–7820 ^{14}C yr BP, 11,365–8630 cal yr BP (699–620 cm)

Picea and *Alnus rubra* pollen reach their maxima during this zone, 45% and 41% respectively, while pollen from *Pinus contorta*, *Tsuga mertensiana*, and *Alnus crispa* decrease to trace amounts. *Tsuga heterophylla* pollen increases from 15 to 40%. *Pseudotsuga menziesii* and *Lysichiton americanum* pollen and *Pteridium aquilinum* spores each account for 2–3% of the sum. *Polypodium*, *Athyrium filix-femina*, and

Dryopteris spores and *Arceuthobium* pollen are also present. Cupressaceae pollen first occurs at the top of this zone. *Rhamnus purshiana* pollen is present in sediments that date to 8815 ^{14}C yr BP (9840 cal yr BP) and does not occur at any other time in the record. Total PARs are about 7500 grains cm^{-2} yr^{-1}. PARs for *Picea*, *T. heterophylla*, *A. rubra*, *P. menziesii*, and *L. americanum* increase within this zone. Rates of change are consistently low.

Zone M-4: 7820–4265 ^{14}C yr BP, 8630–5080 cal yr BP (620–415 cm)

This zone is marked by the dominance of *Tsuga heterophylla* pollen. Cupressaceae pollen gradually increases to 8%. *Picea* and *Alnus rubra* pollen both decrease to about 10%. *Abies* pollen increases but remains less than 10%. *Lysichiton americanum* pollen increases to 5%. *Sphagnum* spores are consistently present from 5760 ^{14}C yr BP (6860 cal yr BP) to the present. *Arceuthobium* pollen is present between 5275 and 4485 ^{14}C yr BP (6475–5430 cal yr BP). There are isolated peaks in *Brasenia schreberi* pollen at 6735 ^{14}C yr BP (7510 cal yr BP) and *Isoëtes* spores at 6315 ^{14}C yr BP (7250 cal yr BP). Total PARs range between 6000 and 20,000 grains cm^{-2} yr^{-1}. Several taxa including *T. heterophylla*, *Abies*, and cf. *Taxus brevifolia* show a marked increase in PARs after 7000 ^{14}C yr BP (7660 cal yr BP). Rates of change are higher than in the previous zone with a peak at 6000 ^{14}C yr BP (7030 cal yr BP).

Zone M-5: 4265–2625 ^{14}C yr BP, 5080–2450 cal yr BP (415–215 cm)

Tsuga heterophylla pollen continues to dominate the pollen spectra but is marked by a minor decrease from about 50 to 40%, corresponding to increases in Cupressaceae and *Pinus contorta* pollen percentages and PARs. Total herb pollen and Pteridophyte spores account for 10 and 13%, respectively. *Myrica* pollen is consistently present by 3000 ^{14}C yr BP (2775 cal yr BP). Total PARs are typically less than 10,000 grains cm^{-2} yr^{-1} but increase to more than 20,000 grains cm^{-2} yr^{-1} at the top of the zone. Pteridophyte accumulation rates reach a maximum of 3425 spores cm^{-2} cal yr^{-1}. Rates of change are higher than during the previous zone but are variable and show a trend of gradual increase.

Zone M-6: 2625–0 ^{14}C yr BP, 2450–0 cal yr BP (215–0 cm)

The uppermost zone is characterized by high percentages of *Tsuga heterophylla* pollen (50–63%), with percentages of *Pinus contorta* pollen up to 14%. Percentages of Cupressaceae pollen and pteridophytes spores are lower than the preceding zone. Percentages of *Picea*, *Abies*, *Alnus rubra*, and *Myrica* pollen are more or less constant at levels less than 10%. Total PARs are highest for the period of record (40,600 grains cm^{-2} yr^{-1}) due mainly to increases in *T. heterophylla* PARs. *Pinus contorta* PARs are higher between 2095 and 1545 ^{14}C yr BP (2045–1710 cal yr BP) than in the late-glacial period, when *P. contorta* reached its maximum percentage. PARs for most taxa show marked decreases over the last 1500 years. Notable exceptions are *Pseudotsuga menziesii* and Poaceae. Rates of change are moderate with an increase at 1500 ^{14}C yr BP (1690 cal yr BP), similar in magnitude to the peak at 6000 ^{14}C yr BP (7030 cal yr BP).

Principal Components Analysis

PCA axes 1 and 2 account for 50.2 and 29.3% of the total variation, respectively, and are the only significant axes according to a broken-stick model. In the ordination of pollen types, axis 1 separates *Pinus contorta*, *Alnus crispa*, and *Tsuga mertensiana* from *T. heterophylla* and Cupressaceae, which have high positive and negative loadings, respectively (Fig. 4.5). Species loadings on axis 1 (Table 4.2) correspond closely to the order in which tree species become dominant and/or reach their highest abundance, separating late-glacial and Holocene taxa, and may reflect interspecific differences in life history traits that are important in competition among trees (i.e., dispersal, shade tolerance, growth rate, longevity, size, and rate of sapling establishment; Huston and Smith 1987; Krajina 1969). Axis 2 separates *Alnus rubra* and *Picea* from all other taxa, most notably *P. contorta* and Cupressaceae, and is interpreted as reflecting postglacial changes in temperature (Figs. 4.5 and 4.6). These hypotheses require testing with independent paleoclimate reconstructions and life history trait data.

The ordination of pollen samples (Fig. 4.6) is directly related to the ordination of pollen types (Fig. 4.5). Pollen types with high loadings (Table 4.2) on one axis dominate samples with high scores on that axis. Samples that are similar in species composition are close together, and species-poor samples are far from the origin while species-rich

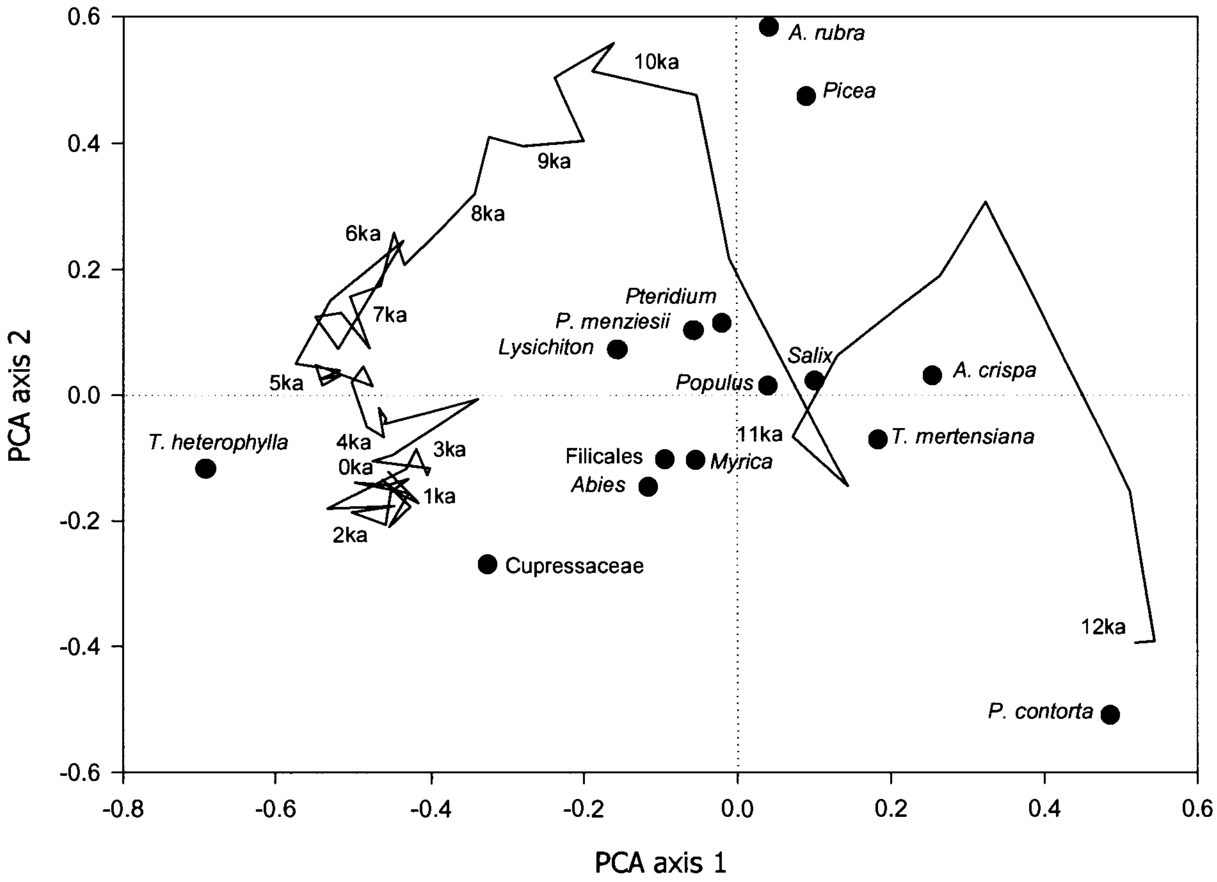

Fig. 4.5. **Principal components analysis (PCA) biplot, following ter Braak (1983), of species loadings (circles) for important pollen and spore taxa from Misty Lake on Vancouver Island, with sample scores (line) in stratigraphic order. PCA axes 1 and 2 account for 50.2 and 29.3% of the total variation, respectively. Radiocarbon age is shown for each 1000 ^{14}C yr (ka).**

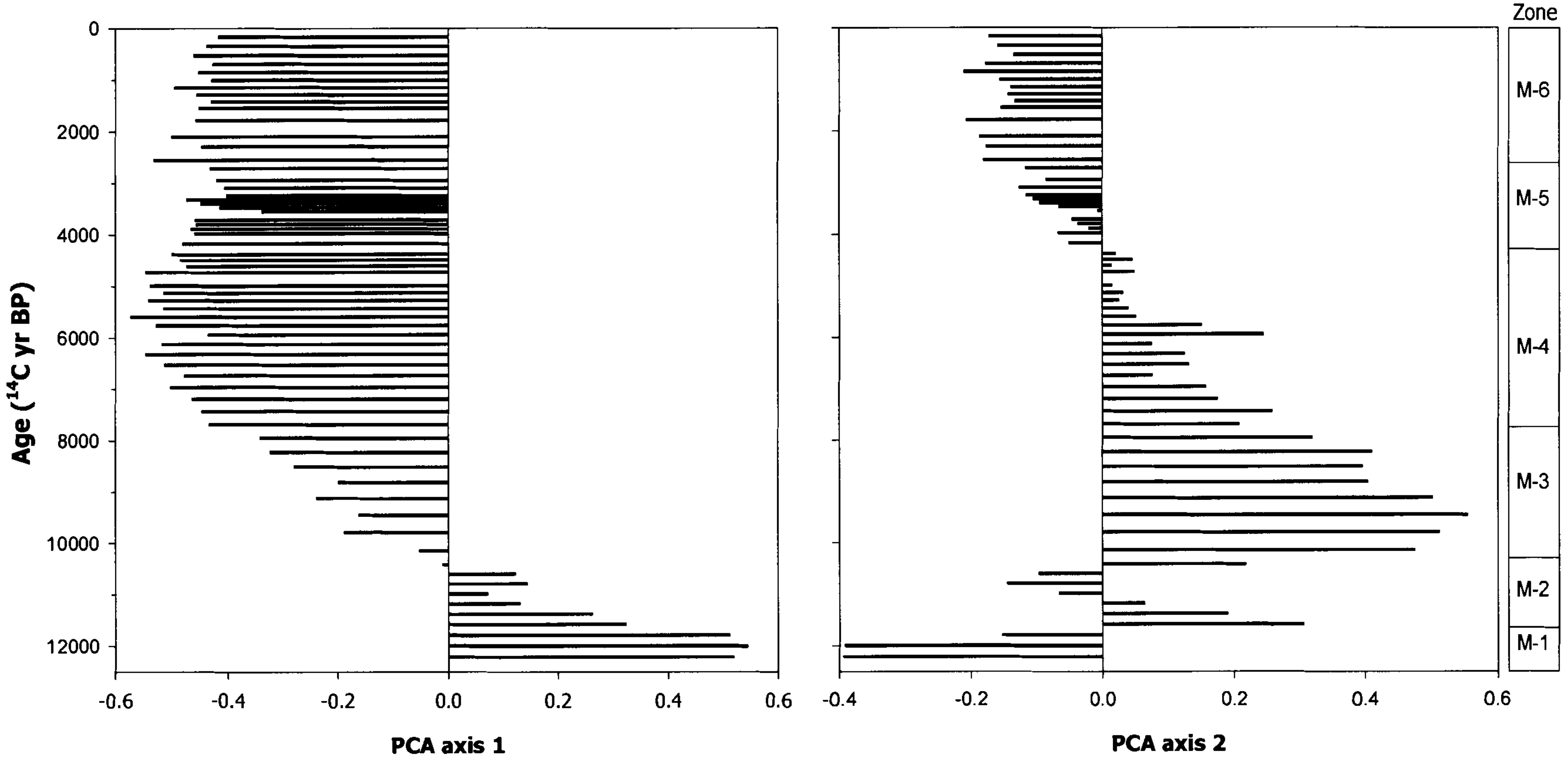

Fig. 4.6. Sample scores for principal components analysis (PCA) of pollen and spore data from Misty Lake on Vancouver Island. PCA axes 1 and 2 account for 50.2 and 29.3% of the total variation, respectively.

samples are closer to the origin. Axis 1 (Fig. 4.6) separates late-glacial assemblages (zones M-1 and M-2) on the positive end from all Holocene assemblages (zones M-3, M-4, M-5, and M-6). Axis 2 (Fig. 4.6) separates late-glacial and early Holocene *Alnus rubra* and *Picea* assemblages from middle and late Holocene samples, and *Pinus contorta*-dominated late-glacial samples. There are three clear trajectory reversals that separate four broad climatic periods (Fig. 4.5): late-glacial or Allerød and earlier (zone M-1), Younger Dryas (zone M-2), early Holocene (zone M-3), and middle and late Holocene (zones M-4, M-5, and M-6). Samples dominated by *Tsuga heterophylla* (zones M-4, M-5, and M-6) are tightly clustered compared to late-glacial (zones M-1 and M-2) and early Holocene (zone M-3) samples (Fig. 4.5).

Table 4.2. Principal component loadings of Misty Lake pollen data for PCA axes 1 and 2, accounting for 50.2 and 29.3% of the total variation, respectively.

Pollen / Spore Type	Axis 1	Axis 2
Pinus contorta	0.486	-0.509
Alnus crispa type	0.254	0.030
Tsuga mertensiana	0.183	-0.071
Salix	0.100	0.023
Picea	0.089	0.474
Athyrium filix-femina	0.070	0.012
Alnus rubra type	0.041	0.583
Populus cf. *balsamifera*	0.040	0.015
Polypodium	0.018	-0.019
Poaceae	-0.014	-0.081
Isoëtes	-0.015	0.043
Pteridium aquilinum	-0.021	0.114
Cyperaceae	-0.035	-0.055
Myrica	-0.054	-0.104
Pseudotsuga menziesii	-0.057	0.103
Filicales	-0.094	-0.102
Abies	-0.115	-0.146
Lysichiton americanum	-0.156	0.073
Cupressaceae	-0.326	-0.269
Tsuga heterophylla	-0.692	-0.116

Discussion

Late-glacial

Between 12,200 and 11,700 ^{14}C yr BP (14,900–13,930 cal yr BP), pollen assemblages (Fig. 4.3) in clay-rich basal sediments at Misty Lake were dominated by *Pinus contorta*, indicating that *Pinus contorta* woodlands characterized the landscape on northern Vancouver Island at this time. Inorganic sediment and low total PARs (Fig. 4.4) suggest that the vegetation was open. Since *P. contorta* PARs were lower in the late-glacial period than in the late Holocene, *P. contorta* likely grew as scattered trees. *Pinus*-dominated vegetation is found at most paleoecological sites of comparable age in British Columbia (Hebda 1983, 1995; Heusser 1985; Mathewes 1989; Hebda and Haggarty 1997; Brown and Hebda, 2002, 2003), in the adjacent U.S.A. (Heusser 1985; Cwynar 1987; Grigg and Whitlock 1998), and in southeastern Alaska (Hansen and Engstrom 1996). *Pinus contorta* may have been present as early as 13,600 ^{14}C yr BP at Bear Cove Bog (Hebda 1983), 20 km northwest of Misty Lake. However, several other studies indicate that treeless herb and shrub vegetation was widespread along the coast before 13,000 ^{14}C yr BP (e.g., Heusser 1985; Mathewes 1989). Given that other taxa were well-established along with *P. contorta* at 12,200 ^{14}C yr BP, it is unlikely that *P. contorta* formed pioneering vegetation on northern Vancouver Island as suggested by Hebda (1983) but rather that a non-arboreal assemblage was the pioneer vegetation. *Pinus contorta* may have colonized the immediate coastline as falling sea levels exposed immature soils (Lacourse et al. 2003; Chapter 3) but early successional communities further inland were likely dominated by herbs and shrubs.

Pinus contorta is a shade-intolerant pioneer tree with wide climatic and edaphic tolerance including high drought and frost tolerance, and is capable of rapid invasion of disturbed sites and recently deglaciated terrain due to efficient seed dispersal and rapid growth and maturation (Klinka et al. 1989; Peteet 1991). Its late-glacial dominance on the coast is commonly interpreted as representing cold and relatively dry climate, and suggests either nearby late Wisconsin refugia e.g., Brooks Peninsula (Fig. 4.1) or exceptionally rapid late-glacial coastal migration from the south (Peteet 1991). Basal sediments from the Misty Lake core contain chironomids typical of cold, well-oxygenated, oligotrophic environments (Walker and Mathewes 1989), and reconstructed climate records from the region also corroborate a cold late-glacial climate (Heusser et al. 1985; Palmer et al. 2002).

Late-glacial climate was characterized by an anticyclonal high pressure system centered on the continental ice sheet that generated subcontinental katabatic easterly winds and increased seasonality (COHMAP 1988; Bartlein et al. 1998). Before 12,000 ^{14}C yr BP, the ice sheet shifted the jet-stream south, caused cooling in mid-latitudes, intensified cold dry easterly winds, and reduced available winter moisture (Bartlein et al. 1998). Fires were absent during this cold and relatively dry climate (Brown and Hebda, 2002, 2003).

Small amounts of pollen from other conifers (i.e., *Picea*, *Abies*, and *Tsuga mertensiana*) suggest that these taxa were also present on northern Vancouver Island in the late-glacial period (Figs. 4.3 and 4.4). Shrubs in the open *Pinus contorta* woodlands included *Alnus crispa* and *Salix*, which suggest that edaphic conditions were unstable. Small amounts of *Shepherdia canadensis* pollen are also present in basal sediments, which is noteworthy since few entomophilous shrubs are recorded in fossil pollen data, suggesting that it grew locally. *Alnus* spp. and *S. canadensis* are often found on open unstable sites and contain nitrogen-fixing bacteria in their roots. Poaceae, Cyperaceae, and pteridophytes including *Athyrium filix-femina*, *Cryptogramma acrostichoides*, and *Pteridium aquilinum* were also important components of the late-glacial landscape.

By approximately 11,700 ^{14}C yr BP (13,930 cal yr BP), *Pinus contorta* decreased in abundance and existing populations of more shade-tolerant *Picea* and *Tsuga mertensiana* expanded (Figs. 4.3 and 4.4). This rapid change in vegetation type is reflected in the rate of palynological change (Fig. 4.3). *Picea* pollen is likely derived from *P. sitchensis*, although this is uncertain in light of the analysis by Warner and Chmielewski (1987), which indicates that late-glacial *Picea* cones from the Queen Charlotte Islands (Fig. 4.1) probably represent hybrids of *P. sitchensis* and *P. glauca*. The mixed conifer forests that replaced the *Pinus*-dominated woodlands also included *Abies* (likely *A. amabilis*), *Alnus* spp., *Populus* cf. *balsamifera*, and later *Tsuga heterophylla*. Trace amounts of *Nuphar* pollen suggest it grew in Misty Lake from 11,575 ^{14}C yr BP (13,685 cal yr BP) to the present. Minor increases in PARs indicate that forests were more dense and productive than the earlier shade-intolerant *P. contorta* woodlands (Fig. 4.4). However, the presence of *Alnus* spp. and *Pteridium aquilinum* suggests that the vegetation was still somewhat open. The increase in the overall forest cover corresponds to a lithological change in Misty Lake sediments from inorganic to organic, which suggests that edaphic parameters that affected sediment deposition also changed at this time. With more continuous vegetative cover due to conifer expansion, the landscape stabilized and mineral input to Misty Lake decreased. Although the humus-enriched soils would have favoured *P. sitchensis* over *Pinus*, *P. contorta* still occupied favourable sites on northern Vancouver Island and may have grown on the exposed continental shelf immediately north of Vancouver Island at 10,500 ^{14}C yr BP (Lacourse et al. 2003; Chapter 3).

More shade-tolerant conifers succeeded *Pinus contorta*, but the expansion of mixed conifer forests was also facilitated by late-glacial changes in climate. Paleoclimate model simulations suggest the northward shift of the jet stream due to the decreasing size of the continental ice sheet and increased seasonality due to changes in the seasonal cycle of insolation resulted in progressively warmer and drier summers (Berger 1978; COHMAP 1988; Whitlock and Bartlein 1997; Bartlein et al. 1998) with more frequent fires (Brown and Hebda, 2002). Winters were cooler than at present, and as the continental ice sheet receded, moist westerly winds would have become more important in the region (COHMAP 1988; Bartlein et al. 1998).

The relative abundance of *Tsuga mertensiana* pollen in late-glacial sediments indicates that this species was important in nearby forests. *Tsuga mertensiana* PARs (Fig. 4.4) suggest that following an initial expansion at about 11,500 ^{14}C yr BP (13,525 cal yr BP), *T. mertensiana* expanded more dramatically between 10,600 and 10,400 ^{14}C yr BP (11,660–11,480 cal yr BP). The PAR increase for *T. mertensiana* is accompanied by contemporaneous PAR increases in *Pinus contorta*, *Alnus crispa*, *Populus*. cf. *balsamifera*, and *Athyrium filix-femina*, and decreases in *Picea* and *Alnus rubra*. These changes are reflected in PCA sample scores, which show a trajectory reversal likely related to climatic cooling at this time (Figs. 4.5 and 4.6). *Tsuga mertensiana* is a robust indicator of a cool and humid growing season; it is characteristic of maritime subalpine forests and requires substantial snow for insulation during winter months (Mathewes 1993; Gedalof and Smith, 2001). *Tsuga mertensiana* pollen is often severely under-represented in modern pollen assemblages (e.g., Peteet 1986; Dunwiddie 1987) but not always (Heusser 1983a). In the subalpine zone of Brooks Peninsula (Fig. 4.1), where it is co-dominant in the forest, *T. mertensiana* accounts for only 9% of the pollen sum (Hebda 1983; Hebda and Haggarty 1997). The increase in *T. mertensiana* to 13.5% at Misty Lake suggests that it was an important component of the surrounding forests particularly at higher elevations, reflecting a cool and moist climate during this time. A number of sites in the region record a similar peak in *T. mertensiana* in the late-glacial portions of their records (Heusser 1985; Mathewes et al. 1993; Pellatt et al. 2002). Mathewes (1993) suggests that increases in *T. mertensiana* pollen between 10,700 and 10,000 ^{14}C yr BP are a regional manifestation of the Younger Dryas cooling event, similar in timing and extent to that first documented around the North Atlantic rim (e.g., Mangerud et al. 1974; Watts 1980; Mott et al. 1986; Peteet et al. 1990). Several studies have identified Younger Dryas cooling outside the North Atlantic region (e.g., Engstrom et al. 1990; Kennett and Ingram 1995; Porter and An 1995), and it now seems likely that the Younger Dryas cooling was a global event (Peteet 1995). Increases in cold-water benthic foraminifera indicate cooling of ocean waters off the coast of British Columbia between 11,000 and 10,200 ^{14}C yr BP and a decrease of 2-3°C in summer temperature during this interval (Mathewes et al. 1993). The Younger Dryas cooling event appears to have arrested successional trends in *A. rubra* and *Picea*, allowing *P. contorta*, *T. mertensiana*, *A. crispa*, and *P.* cf. *balsamifera* populations to expand at their expense (Figs. 4.3 and 4.4). Brown and Hebda (2002) suggest that increases in *Alnus* pollen, as opposed to *T. mertensiana*, record Younger Dryas cooling more accurately on southern Vancouver Island. Unfortunately, *Alnus* pollen types were not differentiated, so it is unclear which of the two species increased during this time in their records.

Alnus spp. were abundant in late-glacial and early Holocene forests and appear to have played an important role in forest succession. The Misty Lake pollen data indicate that populations of *Alnus crispa* and *A. rubra* expanded immediately prior to increases in *Tsuga mertensiana* and *Picea*, respectively (Fig. 4.3), and are consistent with successional trends in *A. rubra* and *P. sitchensis* identified by Chapin et al. (1994). The strong associations between *A. crispa* and *T. mertensiana*, and *A. rubra* and *Picea* are also reflected in the PCA biplot (Fig. 4.5). Facilitation by *Alnus* was likely important in conifer establishment and in early community development by rapidly expanding on immature and disturbed soils due to rapid growth rates and by increasing soil nitrogen content and organic matter (Chapin et al. 1994). *Alnus rubra* can form dense stands in the initial stages of primary succession, and both species of *Alnus* regenerate readily on exposed mineral soil and disturbed sites (Klinka et al. 1989). In contrast to *Pinus contorta*, species such as *P. sitchensis* and *T. mertensiana* are able to succeed *Alnus* spp. due to greater shade tolerance, longer life spans, and larger size. *Pteridium aquilinum* percentages and PARs are highest during the early Holocene; based on the requirements of *P. aquilinum* (Klinka et al. 1989), this likely reflects a greater amount of light in low canopy density forests. It is likely that *A. rubra* was strongly inhibited in subsequent *Tsuga heterophylla* forests due to decreasing light availability and a low-intensity, small scale disturbance regime.

Early Holocene

In the early Holocene, mixed conifer forests with *Alnus rubra* dominated the lowlands of northern Vancouver Island. *Picea*, likely *P. sitchensis*, spread rapidly and was the dominant forest tree by 10,000 ^{14}C yr BP (11,090 cal yr BP), as indicated by increases in percentages and PARs (Figs. 4.3 and 4.4). Pollen percentages resemble those of modern *P. sitchensis* forests on the north coast of British Columbia and in southeastern Alaska (Heusser 1985). *Tsuga heterophylla* was also a prominent component of the vegetation by 10,000 ^{14}C yr BP. It did not experience a migration lag as in the Fraser Lowland, which was likely due to low availability of favourable sites with high organic matter (Mathewes 1973).

Increasing total PARs and increases in pollen from shade-tolerant taxa indicate that early Holocene forests were increasingly closed, but abundant *Alnus rubra* pollen suggests that some canopy openings remained, perhaps in response to disturbance. *Alnus* pollen is commonly over-represented in modern sediments relative to its extent on the landscape (e.g., Heusser 1983a; Peteet 1986; Lacourse 1998; Allen et al. 1999), suggesting that the early Holocene abundance of *A. rubra* pollen may represent regional transport. *Lysichiton americanum* pollen percentages and PARs suggest that it was a common understory plant (Figs. 4.3 and 4.4). Today, *L. americanum* commonly occurs in the understories of wet open-canopy *Picea sitchensis* and *A. rubra* forests (Klinka et al. 1989). The late-glacial decline of chironomids that favour oligotrophic conditions suggests that the productivity of Misty Lake increased in the early Holocene (Walker and

Mathewes 1989), which may be linked to increased *A. rubra* nitrogen fixation in watershed soils and the associated nitrogen flux to the lake (Hu et al. 2001).

A substantial peak in the rate of palynological change at 10,500 ^{14}C yr BP (11,570 cal yr BP) reflects the abrupt disappearance of shade-intolerant *Pinus contorta* and the expansion of *Picea*, *Tsuga heterophylla*, and *Alnus rubra*-dominated forests (Fig. 4.3). Subsequently, low rates of change between about 10,000 and 7000 ^{14}C yr BP (11,090–7660 cal yr BP) suggest that vegetation assemblages were stable at the century-scale.

Pseudotsuga menziesii pollen is present in low relative amounts between 9790 and 6735 ^{14}C yr BP (10,880–7510 cal yr BP), with a notable decrease to trace levels for the remainder of the record (Fig. 4.3). Given the short dispersal distance of *P. menziesii* pollen (Tsukada 1982) and its under-representation in modern pollen assemblages due to low production (Heusser 1985), values of more than 1-2% imply that *P. menziesii* is an important local forest tree (Hebda 1983). Therefore, *P. menziesii* was likely growing locally after 9790 ^{14}C yr BP. Hebda (1983) found that *P. menziesii* accounted for 10% of the pollen sum at nearby Bear Cove Bog at this time and concluded that it was a major component of the forests during the early Holocene. *Pseudotsuga menziesii* cones that date to 8300 ± 70 ^{14}C yr BP confirm its nearby presence (Howes 1981). *Pseudotsuga menziesii* is characteristic of the warmer and drier climate of southern Vancouver Island, where it grows abundantly today and summer drought and fire are more important; it is shade-intolerant and fire-adapted. Its presence near Misty Lake in the early Holocene indicates that conditions were drier than present, and provides further evidence of a thermal maximum in the early Holocene (Clague and Mathewes 1989). Pollen and plant macrofossil evidence from sites in southern British Columbia and the northwestern U.S.A. indicate that early Holocene summers were warmer and drier than present (Heusser et al. 1985; Heusser 1985; Peteet 1986, 1991; Cwynar 1987; Whitlock and Bartlein 1997; Brown and Hebda, 2002, 2003). Based on early Holocene chironomid communities, Palmer et al. (2002) infer that mean July air temperatures were about 3°C warmer in southern British Columbia compared to today. The range extension of *P. menziesii* occurred rapidly in response to early Holocene warming, likely due to fairly rapid growth rates and increased forest fires.

The displacement of *Pinus contorta*, *Tsuga mertensiana*, and *Alnus crispa* by *Picea sitchensis*, *Tsuga heterophylla*, and *Alnus rubra* also signals climatic warming in the early Holocene. Paleotemperature reconstructions based on the original chironomid study at Misty Lake (Walker and Mathewes 1989) suggest that summer temperatures increase from about 12°C at 12,000 ^{14}C yr BP to 15°C at 10,000 ^{14}C yr BP (I.R. Walker, personal communication, 2004). While this paleotemperature reconstruction reveals trends for the past 12,000 ^{14}C yr, it is not able to resolve significant temperature changes due to large associated errors (±2.3°C). Around 9000 ^{14}C yr BP incoming solar radiation was about 8% higher in summer and 10% lower in winter than at present (Berger 1978; COHMAP 1988). Paleoclimate simulations suggest that this amplified seasonality in solar radiation would have resulted in higher summer temperature and less effective moisture, and would have indirectly strengthened the Pacific subtropical high pressure system, causing more intense summer drought (Thompson et al. 1993; Bartlein et al. 1998). Increased drought led to more frequent fires and the expansion of xerophytic species such as *P. menziesii* (Cwynar 1987; Brown and Hebda, 2002; Gavin et al. 2003). However, effective moisture in the lowlands of northern Vancouver Island must have been sufficient to allow the expansion of *P. sitchensis* and *T. heterophylla*, which require abundant moisture for germination, and *Lysichiton americanum*, which favours wet to very wet, nitrogen-rich soils (Klinka et al. 1989).

Middle Holocene

Picea and *Alnus rubra* decreased in relative abundance by 7500 ^{14}C yr BP (8215 cal yr BP) and were gradually replaced by increasing populations of *Tsuga heterophylla*. Since *T. heterophylla* is very shade-tolerant and slow growing, the general successional tendency is toward more *T. heterophylla*, especially as soil organic matter increases. The shade tolerance of *Picea sitchensis* is low and its seedlings often cannot establish on the thick carpet of moss typical of *T. heterophylla* forest, turning instead to dead and down wood substrates (Franklin et al. 2002). After about 5250 ^{14}C yr BP (6450 cal yr BP), *P. sitchensis* was likely relegated to sites affected by ocean spray and brackish water, where its salt tolerance gives it a strong competitive advantage over all other tree species. The dominance of shade-tolerant *T. heterophylla* and the increase in total PARs and PARs for shade-tolerant taxa (i.e., *T. heterophylla*, *Abies*, *Taxus brevifolia*, and

Lysichiton americanum) after 7000 ^{14}C yr BP (7660 cal yr BP) suggests that the forest canopy was closed. Ferns spores show slight increases in the mid-Holocene that are likely attributable to an increase in more suitable sites with rich soils and abundant moisture (Figs. 4.3 and 4.4). A moderate peak in rates of change at 6000 ^{14}C yr BP (7030 cal yr BP) reflects an increase in *Alnus rubra* percentages and PARs (Figs. 4.3 and 4.4). Otherwise, relatively low rates of change suggest that vegetation on northern Vancouver Island was more or less stable at the century-scale.

The middle to late Holocene is also characterized by an increase in Cupressaceae pollen (Figs. 4.3 and 4.4). The relative contributions of *Thuja plicata* and *Chamaecyparis nootkatensis* are unknown due to indistinguishable pollen morphologies. While both species are often associated with wet boggy sites along the coast of British Columbia and are moderately shade-tolerant, *T. plicata* grows mostly on moist to wet soils at low to medium elevations while *C. nootkatensis* is primarily a subalpine to montane species (Klinka et al. 1989). Therefore, *T. plicata* is likely the principal contributor of Cupressaceae pollen in the lowlands of northern Vancouver Island. Hebda and Mathewes (1984) argue that *T. plicata* expanded in most coastal forests between 5000 and 2500 ^{14}C yr BP in response to moistening and cooling trends in the mid-Holocene, and note that between 10,000 and 6000 ^{14}C yr BP Cupressaceae pollen is rare or low in frequency. Cupressaceae, likely *T. plicata*, was present on northern Vancouver Island by 7500 ^{14}C yr BP (8215 cal yr BP). Hebda and Haggarty (1997) report small amounts of Cupressaceae pollen and plant macrofossils of *T. plicata* and *C. nootkatensis* between 10,000 and 8000 ^{14}C yr BP (11,090–8870 cal yr BP) from sites on northwestern Vancouver Island. However, Cupressaceae PARs from Misty Lake indicate that Cupressaceae did not reach its maximum abundance until after 3500 ^{14}C yr BP (3600 cal yr BP), when effective moisture increased (Cumming et al. 2002).

Mid-Holocene forests around Misty Lake were similar to other fossil *Tsuga heterophylla*-dominated communities on Vancouver Island (Hebda 1983, 1995; Hebda and Haggarty 1997; Brown and Hebda, 2002, 2003) and modern pollen samples from the Coastal Western Hemlock biogeoclimatic zone (Pellatt et al. 1997). Some sites on southern Vancouver Island (Brown and Hebda, 2002) and in the Fraser Lowland (Mathewes 1973) were dominated by *Pseudotsuga menziesii* in the mid-Holocene. The mid-Holocene expansion of *Quercus garryana* on southern Vancouver Island (Pellatt et al. 2001; Brown and Hebda, 2002) is not recorded in Misty Lake sediments, suggesting that *Q. garryana* did not reach northern Vancouver Island.

The dominance of *Tsuga heterophylla* represents a trend towards a cooler climate and increasing effective moisture in the mid-Holocene (Heusser et al. 1980, 1985). Temperatures inferred from the original chironomid study at Misty Lake suggest a gradual decrease from about 15°C to 13.5°C over the Holocene period (I.R. Walker, personal communication, 2004). Solar insolation at 6000 ^{14}C yr BP was still greater than at present in summer and less than at present in winter (Berger 1978; COHMAP 1988; Thompson et al. 1993). Heusser et al. (1985) demonstrate that there was a mid-Holocene increase in precipitation along the Pacific coast from Washington to Alaska. Fire frequency declined in the middle and late Holocene due to increased effective moisture (Cwynar 1987; Brown and Hebda, 2002). Climate change in the mid-Holocene reflects a reduction in the intensity of the subtropical Pacific high pressure system, which would have increased the importance of westerly winds and their associated moisture, and decreasing levels of solar radiation in summer and increasing levels in winter. The cool and wet climate would have slowed decomposition on the forest floor, increasing the water-holding capacity of the soils, decreasing nutrient availability and, in turn, favouring the regeneration and growth of *T. heterophylla* and *Thuja plicata*.

Late Holocene

Late Holocene forests are marked by the continued dominance of *Tsuga heterophylla*. Shade tolerance provides *T. heterophylla* with an important competitive advantage because, as light under the canopy is reduced through successional time, the ability to regenerate and grow in shade allows more shade-tolerant types to dominate (Huston and Smith 1987). *Pinus contorta* and Cupressaceae expanded in the late Holocene, likely colonising bog-forest complexes; *P. contorta* is often abundant in the open scrubby bog woodlands along the coast where it regenerates but grows very slowly. *Picea*, *Abies*, and *Tsuga mertensiana* PARs increase in the late Holocene, reflecting their expansion on wetter sites (Fig. 4.4). Several paleoecological records from the region document the late Holocene development of peatlands, which favoured the growth of *Thuja plicata*, *Chamaecyparis nootkatensis*, and *P. contorta* as well as other wetland species (e.g., Cwynar 1987; Turunen and Turunen, 2003). Regional paludification would have restricted tree growth, reducing competition from *Picea* and *T. heterophylla*. *Tsuga heterophylla*-dominated forests with *Abies*, Cupressaceae, and *P. contorta* suggest that a wet mesothermal climate similar to today's was in place by 3500 ^{14}C yr BP (3600 cal yr BP). The expansion of *Myrica gale*, a wetland shrub, after 3000 ^{14}C yr BP (2775 cal yr BP) attests to increased effective moisture, as do late Holocene increases in pteridophytes and *Sanguisorba* (Figs. 4.3 and 4.4). Total PARs are highest for the period of record between 3200 and 1000 ^{14}C yr BP (2955–1120 cal yr BP), suggesting high productivity in the rainforests around Misty Lake (Fig. 4.4). Modern temperate rainforests also have higher productivity and biomass accumulation compared to other temperate forest types (Waring and Franklin 1979; Schoonmaker et al. 1997). The late Holocene peak in productivity corresponds with Neoglacial advances, climatic cooling, lowering of alpine tree line, and increased effective moisture in the region (e.g., Heusser 1985; Peteet 1986; Clague and Mathewes 1996; Pellatt and Mathewes 1997; Cumming et al. 2002). Increased effective moisture, in particular, would have favoured the mesothermal *T. heterophylla* rainforests. It is possible, however, that the late Holocene increase in PARs is an artefact of poor chronological control for this portion of the record.

Decreased fire activity in the late Holocene supported the development of *T. heterophylla*-dominated rainforest; small-scale, low intensity disturbance such as gap-phase processes played a significant role in late Holocene forests, maintaining their late-successional character (Lertzman et al. 1996; Gavin et al. 2003). The late Holocene increase in rates of vegetation change cannot be attributed to changes in a single species but rather reflects subtle changes in the abundance of numerous species in the last few thousand years. Low rates of change for much of the Holocene suggest that vegetation types were stable at the century-scale.

PARs for most taxa including *Tsuga heterophylla* and *Pinus contorta* decreased over the last 1500 years while *Pseudotsuga menziesii* and Poaceae PARs show minor increases (Fig. 4.4). Similar trends are found in other records from the region (Heusser 1985; Hebda and Haggarty 1997), and are likely linked to a regional decrease in precipitation (Mathewes and Heusser 1981; Heusser et al. 1985; Cumming et al. 2002). It is possible that the decline in Cupressaceae is associated with human activity (Hebda and Mathewes 1984), but contemporaneous increases in PARs of xerophytic species such as *P. menziesii* suggest that effective moisture has declined over the last 1500 years.

Conclusion

Pollen analysis of radiocarbon-dated lake sediment from northern Vancouver Island was used to reconstruct postglacial changes in forest composition and species abundance. Between at least 12,200 and 11,700 ^{14}C yr BP (14,900–13,930 cal yr BP), the regional vegetation was dominated by *Pinus contorta*, *Alnus crispa*, and various ferns when more continental conditions (i.e., colder and drier than present) prevailed. As *P. contorta* decreased in abundance, *Alnus rubra* and more shade-tolerant conifers (i.e., *Picea sitchensis* and *Tsuga mertensiana*) increased. Increases in *T. mertensiana*, *P. contorta*, and *A. crispa* PARs between 10,600 and 10,400 ^{14}C yr BP (11,660–11,480 cal yr BP) reflect a cool and moist climate during the Younger Dryas chronozone. Due to orbitally induced changes in solar radiation and the decreased height and extent of the ice sheets, summers were warmer and drier than present between 10,000 and 7000 ^{14}C yr BP, as indicated by the northward extension of *Pseudotsuga menziesii* beyond its modern range. *Picea sitchensis*, *Tsuga heterophylla*, and *A. rubra* dominated early Holocene forests on northern Vancouver Island. *Alnus crispa* and *A. rubra* increased soil nitrogen and reduced the degree of nutrient limitation on conifer growth (Chapin et al. 1994), and likely facilitated the succession to *Picea* and *T. heterophylla*-dominated forests as these and other species with greater shade tolerance and larger size replaced them. The successional role of *A. rubra* was underestimated in previous studies on northern Vancouver Island because *Alnus* pollen types were not differentiated and most *Alnus* pollen was incorrectly assumed to belong to *A. crispa*. By 7500 ^{14}C yr BP (8215 cal yr BP), shade-tolerant *T. heterophylla* was the dominant forest tree, and increases in effective moisture promoted regional paludification. The relatively cool and moist climate of the middle to late Holocene facilitated the development of *T. heterophylla*-dominated rainforest that includes Cupressaceae (*Thuja plicata* and *Chamaecyparis nootkatensis*), *Abies*, and *Picea sitchensis*. Total PARs suggest that forests were most productive between 3200 and 1000 ^{14}C yr BP (2955–1120 cal yr BP). Decreases in PARs for most taxa and minor increases in *P. menziesii* and Poaceae PARs suggest a trend towards decreased effective moisture in the last 1500 years.

Numerical analyses of fossil pollen data provide valuable insights into postglacial forest dynamics. PCA provides a useful summary of the major trends in compositional change, and rates of change offer the potential for detecting changes in temporal stability and structure of major forest types and highlight the importance of regional and historical processes on forest diversity and succession (Ricklefs 1987). High rates of vegetation change are associated with macroscale changes in climate during the late-glacial period, species with relatively rapid growth rates and short life spans, and important regional ecological events such as the near disappearance of *Pinus contorta* in the early Holocene. Rates of vegetation change show that Holocene forest composition is more or less stable at the century-scale and that major shifts in forest type require several generations. High-resolution pollen analysis is required for determinations of rates of change at the decadal-scale due to vegetation changes that can occur over short time periods (e.g., Williams et al. 2002).

Postglacial vegetation dynamics on northern Vancouver Island are similar to those reconstructed at other paleoecological sites in the region, suggesting regional-scale climate change as the ultimate cause of vegetation change. Climate is likely the driving mechanism for species migration (e.g., *Pseudotsuga menziesii*) and can have direct effects on successional trends (i.e., during the Younger Dryas chronozone). However, given that Holocene climate change was minor compared to changes that occurred at the end of the last glaciation, other factors such as competition and disturbance may have been more important in determining species abundances and vegetation dynamics in Holocene forests. Future work should clarify the importance of life history traits in determining postglacial vegetation change. Life history traits associated with dispersal, growth rate, and longevity may have been most important in determining initial forest composition and in determining overall successional response times whereas shade tolerance, resource competition, sapling survival, and relative facilitation by *Alnus* were probably more important in subsequent stages of forest development.

CHAPTER 5

LATE-GLACIAL VEGETATION DYNAMICS OF THE QUEEN CHARLOTTE ISLANDS AND NORTHERN HECATE STRAIT

Abstract

Paleoecological analyses of late-glacial sediments from the southern Queen Charlotte Islands demonstrate succession from herb tundra dominated by Cyperaceae at 13,750 ^{14}C yr BP (16,890 cal yr BP) to dwarf shrub tundra with *Salix* and *Empetrum nigrum* after 13,500 ^{14}C yr BP (15,900 cal yr BP). Pteridophytes increased in abundance during the transition to *Pinus contorta* woodland ca. 13,000 ^{14}C yr BP (15,600 cal yr BP). *Alnus crispa* was co-dominant by 11,500 ^{14}C yr BP (13,500 cal yr BP), and *Picea sitchensis* may have been present after 11,200 ^{14}C yr BP (13,200 cal yr BP). Fossil conifer stomata indicate that *Pinus contorta* grew locally as early as 13,040 ± 305 ^{14}C yr BP. AMS radiocarbon dating indicates that the continental shelf in Hecate Strait was subaerially exposed between at least 14,330 and 12,860 ^{14}C yr BP (17,370–14,570 cal yr BP). Pollen analysis suggests that Cyperaceae formed the dominant plant cover on the exposed shelf, and fossil *Pediastrum* algae indicate the presence of freshwater. Pollen accumulation rates suggest low plant density on the exposed shelf, although this is uncertain due to over- and under-representation of some pollen types in relation to vegetation abundance on the landscape.

Introduction

Researchers from various disciplines have hypothesized that full-glacial refugia existed on the Queen Charlotte Islands (QCI) or on presently submerged portions of the adjacent continental shelf during the late Wisconsin glaciation. The idea of north Pacific coastal refugia during late Wisconsin glaciation was initially based on the presence of several endemic and disjunct taxa and isolated areas of ice-free terrain (Hultén 1937; Heusser 1960, 1989; Foster 1965). In the early 1980s, fossil plant communities on the QCI were dated to ca. 15,000 ^{14}C yr BP (ca. 18,000 cal yr BP), a time when the adjacent mainland remained glaciated (Clague 1981), indicating that the QCI likely served as a late-glacial center of biotic dispersal earlier than areas to the south and north (Warner 1984; Mathewes et al. 1985). Pollen and plant macrofossils of several plant taxa that no longer occur on the QCI were also found in late Quaternary sediments (Mathewes 1980; Mathewes and Clague 1982; Warner 1984; Warner et al. 1984). Most recently, genetic data suggest north Pacific coastal refugia as possible origins of populations for some of the region's fish (O'Reilly et al. 1993; Ortí et al. 1994; Kondzela et al. 1994; but see Deagle et al. 1996), birds (Zink and Dittmann 1993), and mammals (Fleming and Cook 2002; Heaton et al. 1996; Byun et al. 1997; Barnes et al. 2002; but see Stone and Cook 2000). A continuous sedimentary record spanning the last glaciation remains to be found. However, it has been conclusively shown that low relative sea levels around the QCI permitted the establishment of plant communities on the exposed continental shelf (Barrie et al. 1993). It is possible that these ice-free portions of the shelf served as part of a migration corridor for humans travelling along the coast from Beringia into the Americas during the late Pleistocene (Dixon 1999, 2001; Mandryk et al. 2001). Accurate reconstructions of Pacific coast environments are important for evaluating the ecological context for human populations entering the Americas via a Pacific coastal route.

The present study provides new insight into the vegetation that grew on the exposed continental shelf, the duration of the emergence of the shelf, and late-glacial vegetation dynamics on the QCI. Barrie et al. (1993) provided solid evidence for the subaerial exposure of the continental shelf in Hecate Strait (Fig. 5.1) in the form of marine cores with terrestrial deposits and *in situ* plant roots and rhizomes dating between at least 13,790 and 13,190 ^{14}C yr BP (16,650–15,900 cal yr BP). Pollen analysis was conducted on a single aggregate sediment sample and revealed an assemblage

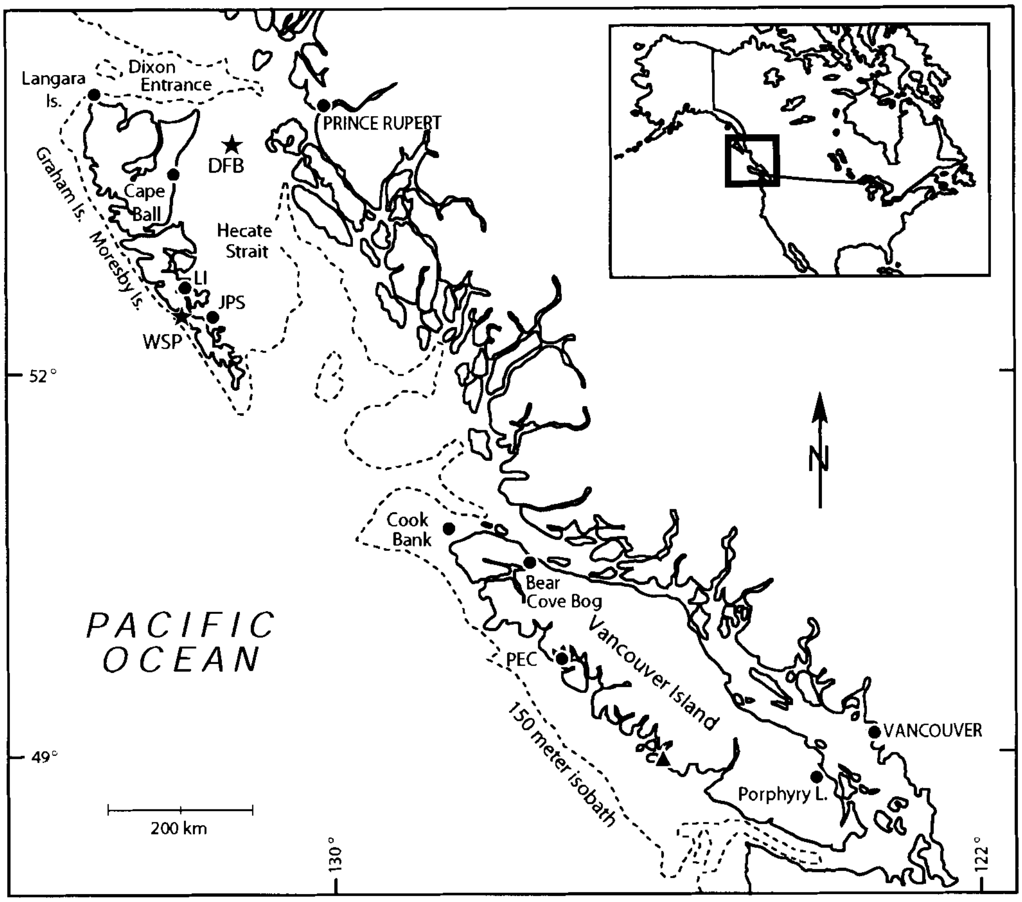

Fig. 5.1. Location of the study sites (★) in the Queen Charlotte Islands region and other sites (●) mentioned in the text. The location of *Pinus* cf. *contorta* wood (▲) dated to 16,700 ± 70 ^{14}C yr BP by Clague et al. (1980) is also shown. The 150 m isobath shows the approximate location of the emergent continental shelf; however, the glacioisostatic forebulge would have resulted in considerable spatial and temporal variation in relative sea level. DFB = Dogfish Bank, LI = Logan Inlet, JPS = Juan Perez Sound, WSP = West Side Pond, PEC = Port Eliza Cave.

dominated by Cyperaceae, *Equisetum*, *Empetrum*, and Poaceae (see Appendix for common names of plants), suggesting an ice-free tundra environment. In the present study, new AMS radiocarbon dating and stratigraphic pollen analysis of the same terrestrial deposits are presented. Fedje (1993) described the vegetation history near West Side Pond (Fig. 5.1) on the southern tip of the QCI for the last 13,500 ^{14}C yr BP (ca. 16,500 cal yr). For the late-glacial period, Fedje (1993) analysed ten sediment samples based on pollen sums of about 300 pollen and spores. The present study presents the results of pollen analysis based on sums greater than 500, pollen accumulation rates (PARs), and the results of fossil stomata analysis of 25 late-glacial samples from the same lake sediment core as well as multivariate statistical analysis of the pollen data.

The research objectives were to reconstruct the late-glacial vegetation history at two sites in the QCI region and to compare these records with published vegetation and climate data from adjacent areas. Specifically, what was the composition of the late-glacial flora on the QCI and the exposed continental shelf? Was the initial vegetation treeless? What was the nature and timing of vegetation change in the late-glacial period, and were vegetation changes simply changes in abundance or did composition also change? Modern pollen spectra from arctic sites, particularly those from coastal Alaska and the Aleutian Islands (e.g., Heusser 1983a; Peteet 1986; Peteet and Mann 1994) serve as important comparisons for the late-glacial herb and shrub assemblages on the QCI.

In this study, fossil conifer stomata are used to confirm the local presence of conifers in the QCI region during the late-glacial period. The presence of stomata on pollen slides provides a useful alternative to plant macrofossil analysis for determining local presence and treeline dynamics, especially for lake sediments where macrofossils are poorly represented (Ammann and Wick 1993; Hansen et al. 1996; Hansen and Engstrom 1996; Pisaric et al. 2000, 2003; Gervais and MacDonald 2001). Like plant macrofossils, stomata are important for documenting the local presence of trees, since conifer stomata are not generally transported far from their source i.e., less than 1-2 km (Hansen 1995; MacDonald 2001).

Environmental Setting

The QCI consist of about 150 islands off the northwest coast of British Columbia on the western edge of the continental shelf (Fig. 5.1). Hecate Strait, which is generally less than 50 m deep, separates the QCI from the adjacent mainland. Dogfish Bank extends 70 km into Hecate Strait and was exposed during the late-glacial period due to low relative sea levels (Barrie et al. 1993; Barrie and Conway 1999; Hetherington et al. 2004).

The QCI are divided into three physiographic units: Queen Charlotte Ranges, Skidegate Plateau, and Queen Charlotte Lowlands (Sutherland Brown 1960). The Queen Charlotte Ranges or San Christoval Mountains reach peaks of more than 1100 m. The Skidegate Plateau slopes northeastward from the San Christoval Mountains to the extensive, boggy Queen Charlotte Lowlands on northeastern Graham Island. The QCI are under the moderating influence of the Pacific Ocean, resulting in cool, moist summers and mild, wet winters. At present, the North Pacific high pressure system is dominant in summer but during colder intervals (e.g., during late Wisconsin glaciation), the Aleutian low was likely stronger (COHMAP 1988; Patterson et al. 1995; Bartlein et al. 1998). Under the North Pacific high, storms are fewer, precipitation is less, and temperatures are generally higher.

Much of the QCI are situated within the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991). Modern coniferous forests on the QCI are dominated by *Tsuga heterophylla*, *Picea sitchensis*, and *Thuja plicata* with variable amounts of *Chamaecyparis nootkatensis* and *Tsuga mertensiana*, particularly at higher elevations (Calder and Taylor 1968). Understory communities are dominated by mosses and ferns. *Abies* species are absent from the QCI and are rare in southeastern Alaska but occur on the British Columbia mainland. Peatlands, often with abundant *Pinus contorta* var. *contorta*, are widespread particularly on the coastal lowlands.

Late Quaternary glaciation of the QCI was of short duration and limited extent compared to mainland British Columbia (Clague et al. 1982a; Barrie et al. 1993; Barrie and Conway 1999). Ice was primarily restricted to the Queen Charlotte Ranges, with localized piedmont lobes coalescing with mainland ice on the eastern and northern shores of Graham Island (Fig 5.1) during the glacial maximum (Barrie and Conway 1999). Maximum ice extent was achieved sometime after 21,000 ^{14}C yr BP (24,500 cal yr

BP) (Blaise et al. 1990). A glacier also extended from the mainland into Dixon Entrance to the shelf edge, effectively separating southeastern Alaska and the QCI until after 16,000 ^{14}C yr BP (19,000 cal yr BP) (Barrie and Conway 1999). A glacioisostatic forebulge developed as a result of the lateral transfer of mantle material away from the centre of ice accumulation during maximum ice loading (Clague et al. 1982a; Clague 1983). The mainland subsided due to a heavy ice load (i.e., 2 km thick), while peripheral shelf areas with less or no ice like the QCI were uplifted (Clague et al. 1982a; Hetherington et al. 2004). The forebulge persisted in northern Hecate Strait from ca. 12,200 until after 9700 ^{14}C yr BP (ca. 14,200–11,150 cal yr BP), suggesting glacial ice persisted on the adjacent mainland until ca. 10,000 ^{14}C yr BP (11,300 cal yr BP) (Hetherington et al. 2004). As ice thinned, the forebulge migrated towards the mainland causing submergence in peripheral areas. Northeastern Graham Island was deglaciated about 15,000 ^{14}C yr BP (18,000 cal yr BP) (Clague et al. 1982b; Warner et al. 1982; Mathewes et al. 1985), and ice had retreated to mainland fjords by 14,300 ^{14}C yr BP (17,300 cal yr BP) (Barrie et al. 1993; this study). Dixon Entrance was ice-free by 13,500 ^{14}C yr BP (16,500 cal yr BP) (Barrie and Conway 1999). As ice retreated to the east and into the Queen Charlotte Ranges, an outwash plain developed across northern Hecate Strait and in Dixon Entrance (Barrie and Conway 1999).

Regional sea-level transgression began soon after the late Wisconsin glacial maximum and continued throughout deglaciation (Barrie and Conway 2002); however, the prominent shelf tilt resulted in spatial and temporal variation in relative sea level change (Clague et al. 1982a; Barrie and Conway 2002; Hetherington et al. 2004). Relative sea level reached a maximum of 200 m above present on the British Columbia mainland (Clague 1985). At the same time, relative sea level was as much as 150 m below present on the outer coast, exposing large portions of the continental shelf and intermittently connecting the QCI to the mainland (Josenhans et al. 1995, 1997; Fedje and Josenhans 2000; Hetherington et al. 2003, 2004). Due to isostatic rebound, maximum lowering occurred after 13,000 ^{14}C yr BP (15,600 cal yr BP) (Barrie and Conway 1999). Marine geological studies of the drowned landscape immediately adjacent to the QCI reveal terrain dominated by alluvial fans, delta plains, and meandering rivers (Fedje and Josenhans 2000; Barrie and Conway 2002). Eustatic sea-level rise and the collapse of the glacioisostatic forebulge resulted in rapid relative sea-level rise (up to 5 cm yr^{-1}) for some areas in the QCI region (Josenhans et al. 1997). Modern sea level was reached about 9100 ^{14}C yr BP (10,200 cal yr BP), before a maximum of 15 m above present was reached at 8900 ^{14}C yr BP (10,000 cal yr BP) (Clague et al. 1982a; Josenhans et al. 1995; Fedje and Josenhans 2000).

West Side Pond (52° 32.5′ N, 131° 47.5′ W; 15.5 m a.s.l.) is located within the Gwaii Haanas National Park Reserve on Moresby Island, southern QCI (Fig. 5.1). It was chosen for study by Fedje (1993) due to its low elevation, protection from wave action and ocean spray, and small basin and watershed size. It is about 300 m inland from the modern shore on the west side of Moresby Island, and is flanked by high granite ridges to the west and south. It is a small pond (0.2 ha) situated within a granitic depression, and is about 4 m deep with a drainage basin of about 6 ha (Fedje 1993). The local vegetation represents an edaphic climax of *Pinus contorta* var. *contorta* and *Chamaecyparis nootkatensis* bog woodland (Fedje 1993). *Tsuga heterophylla*, *Alnus crispa*, *Gaultheria shallon*, *Vaccinium* spp., *Empetrum nigrum*, and Cyperaceae are locally common. Bare ground due to erosion by heavy rain and strong wind is widespread and most conifers are stunted. *Picea sitchensis*, *T. heterophylla*, and *C. nootkatensis* form forests within a few hundred meters of the pond.

Materials and Methods

A 370-cm sediment core was recovered from West Side Pond by Fedje (1993) using a Livingstone piston corer. The uppermost sediment was not collected; sediment depths are depths below the sediment surface. A 129-cm sediment core (TUL91C034) was retrieved from Dogfish Bank (53° 52.2′ N, 131° 18′ W) from aboard the *CSS John P. Tully* in 31 m of water, using the Pacific Geoscience Centre's vibrocorer (Barrie et al. 1993).

AMS radiocarbon ages were obtained from terrestrial plant macrofossils and aggregate plant material removed from the sediment cores (Table 5.1). Radiocarbon ages (^{14}C yr BP) were calibrated to calendar ages (cal yr BP) using the BCal calibration system (http://bcal.shef.ac.uk) and CALIB 4.3 (Stuiver and Reimer 1993). BCal uses the same dendrocalibrated data of Stuiver et al. (1998) as CALIB 4.3 but employs a Bayesian statistical approach that takes other dates from the same sequence into account during the calibration of individual dates. Radiocarbon ages were assigned the

Table 5.1. AMS radiocarbon ages from West Side Pond and Dogfish Bank sediments.

Depth (cm)	Material	Laboratory no.	Radiocarbon age (^{14}C yr BP $\pm 1\sigma$)	BCal Calibrated age[a] (cal yr BP)	CALIB 4.3 Calibrated age[b] (cal yr BP)
West Side Pond					
140	*Picea* seed	CAMS-2322	3820 ± 130	4156	3830 – 4530
225	unidentified wood	CAMS-4107	7110 ± 70	7885	7790 – 8040
265	*Picea* needle	CAMS-4409	8530 ± 70	9526	9420 – 9630
310	*Pinus* needle	CAMS-4108	9980 ± 70	11,320	11,200 – 11,700
345	*Pinus* needle	CAMS-2323	10,890 ± 110	12,960	12,800 – 13,150
358	*Pinus* needle	CAMS-2525	12,190 ± 140	14,143	13,820 – 14,430
368	insect fragments	CAMS-2523	13,550 ± 480	16,491	14,790 – 17,410
368	plant fragments	CAMS-2524	9460 ± 610[c]	–	–
Dogfish Bank					
86 – 87	plant fragments	BETA-159983	12,860 ± 80	14,566	14,430 – 15,890
104 – 113	plant fragments	TO-3492[d]	13,190 ± 100	15,903	14,920 – 16,400
119 – 122	plant fragments	TO-3738[d]	13,790 ± 150	16,646	15,990 – 17,150
127 – 129	plant fragments	BETA-166544	14,330 ± 50	17,365	16,700 – 17,670

[a] Year with the highest probability.

[b] Age range with the highest relative area under the probability distribution, rounded to the nearest 10 yr. Range represents the 95% confidence interval ($\pm 2\sigma$).

[c] Rejected.

[d] Previously published in Barrie et al. (1993).

calendar age with the highest probability (i.e., the mode) as determined by BCal, but calendar age ranges from CALIB 4.3 are also provided (Table 5.1).

Sediment subsamples (1 cm^3) from West Side Pond were prepared for pollen analysis following standard methods (Fægri and Iversen 1989): 10% HCl, 10% KOH, 48% HF, acetolysis, and sieving through 6 μm mesh to remove clay-sized particles (Cwynar et al. 1979). Coarse sieving was not performed to retain epidermal tissue with conifer stomata. Subsampling was constrained by the initial subsampling strategy used by Fedje (1993), which consisted of varying intervals i.e., 0.5–9 cm. To calculate pollen concentrations and accumulation rates, known quantities of *Lycopodium* spores (11,300 ± 400; Batch #201890) were added to each sample prior to chemical treatment (Benninghoff 1962). A minimum sum of 500 terrestrial pollen and spores, excluding pollen from obligate aquatic plants and *Sphagnum* spores, was counted for each sample since pollen sums of less than 500 have high associated errors (Maher 1972; Birks and Birks 1980). Pollen sums for West Side Pond samples range from 506 to 800.

Due to high sand fractions in Dogfish Bank sediments, sediment subsamples (2–5 cm^3) were prepared using heavy liquid separation with ZnBr (Fægri and Iversen 1989), 48% HF, and acetolysis. *Lycopodium* spores (13,911 ± 311; Batch #710961) were added to each sample prior to treatment to calculate pollen concentrations and accumulation rates. At least 300 terrestrial pollen and spores were counted for each sample, which often involved counting four slides of pollen residue. Pollen sums of only 225 and 218 were reached for samples at 112 and 123 cm, respectively, despite counting the entire pollen residue.

Pollen and spore identifications were made with reference to published dichotomous keys including Mathewes (1979), Hebda (1985), Warner and Chinnappa (1986), Heusser and Peteet (1988), and a modern reference collection at Simon Fraser University. Diploxylon type *Pinus* pollen was assigned to *P. contorta* based on pollen morphology and modern phytogeography. *Alnus crispa* and *A. rubra* types were differentiated following Richard (1970) and Mayle et al. (1993). Conifer stomata were counted and identified during routine pollen counting. Where stomata were still attached to epidermal tissue, each stoma was counted. Stomata identifications were made using Hansen (1995) and modern reference material from western North America; however, only *P. contorta* stomata were encountered. Botanical nomenclature follows Calder and Taylor (1968).

Pollen and spore percentages were calculated using the sum of all terrestrial pollen and spores. Pteridophyte spores were included in the main sum because of their importance in vegetation communities on the Pacific coast. Pollen and spore accumulation rates (PARs) (grains cm^{-2} yr^{-1}) were calculated from the pollen concentration (grains cm^{-3}) of each sample and the sedimentation rate (cm cal yr^{-1}). Due to temporal variations in ^{14}C production, PARs were calculated using calendar years as opposed to radiocarbon years. Phases of constant radiocarbon age prevent reliable estimates of rates on the basis of uncalibrated radiocarbon ages (Lotter et al. 1992). Pollen accumulation rates are used as a measure of plant density on the landscape. Due to variable sedimentation rates, variations in calculated accumulation rates may partially reflect changes in sedimentation and therefore are interpreted conservatively.

The pollen percentage data were subjected to numerical zonation, using optimal splitting by information content (Bennett 1996). Zonations with variances that exceeded values generated by a broken-stick model of the distribution of variance were deemed statistically significant (Jackson 1993; Bennett 1996). Agglomeration using constrained cluster analysis (CONISS) developed by Grimm (1987), which is based on Ward's sum-of-squares method, was not used as it tends to produce zones of equal size (Birks and Gordon 1985). Principal components analysis (PCA) was used to display the major trends in the West Side Pond dataset in only a few dimensions; gradient lengths of the ordination axes determined by Detrended Correspondence Analysis were less than 2 s.d. (ter Braak 1995). PCA was carried out on the covariance matrix after square-root transformation of the data, which was done to stabilize the variance. A broken-stick model was used to test the significance of the eigenvalues for each axis (Jackson 1993). For zonation and PCA, the dataset was limited to those pollen types that reached a threshold value of 1% somewhere within the sequence, and then recalculated for analysis to proportions of the sum of pollen types included. *Sphagnum* and obligate aquatic taxa were excluded from all numerical analyses.

Results

West Side Pond, QCI

Stratigraphy and Chronology

The West Side Pond sediment core consists of two lithological units (Fedje 1993). From 370 to 345 cm, the sediment is composed of silt and coarse granitic sand, grading from coarse to fine with few organic layers, and capped by a fine sand-rich gyttja. The remainder of the core is organic-rich, grey-brown gyttja with occasional sand-sized clasts.

An age-depth model was constructed using linear interpolation (Fig. 5.2) between seven AMS radiocarbon ages (Table 5.1). The date of 9460 ± 610 ^{14}C yr BP (CAMS-2524) at 368 cm on plant fragments is stratigraphically inconsistent with dates above and considerably younger than a date on insect fragments obtained from the same depth (13,550 ± 480 ^{14}C yr BP; CAMS-2523). This date was therefore rejected as too young, likely due to insufficient datable carbon or possibly due to intrusive, younger organics such as roots. In any case, the date can be rejected since microfossils at that depth are clearly reflective of tundra, which based on other sites is older than 12,500 ^{14}C yr BP.

Pollen Analysis

Based on numerical zonation by optimal splitting and a broken-stick model, West Side Pond pollen percentages (Fig. 5.3) were divided into three pollen zones.

Zone WSP-1: 13,780 – 13,240 ^{14}C yr BP, 16,890 – 15,950 cal yr BP (370 – 366 cm)

The basal zone is characterized by high relative frequencies of Cyperaceae and *Salix* pollen, reaching their maximums, 65 and 28% respectively, for the period of record. Poaceae and *Empetrum nigrum* also contribute significantly to the pollen sum. Herbaceous taxa account for 52 to 87%, and also include *Artemisia*, *Lupinus*, *Epilobium*, *Angelica/Glehnia littoralis*, *Ligusticum calderi* type (mostly belonging to *L. calderi*, not *L. canbyi*; Hebda 1985), *Saxifraga oppositifolia*, *Sanguisorba canadensis* type, *Caltha*, *Polemonium caeruleum* type, *Rumex/Oxyria*, *Viola*, and *Cornus unalaschkensis*. *Pinus*

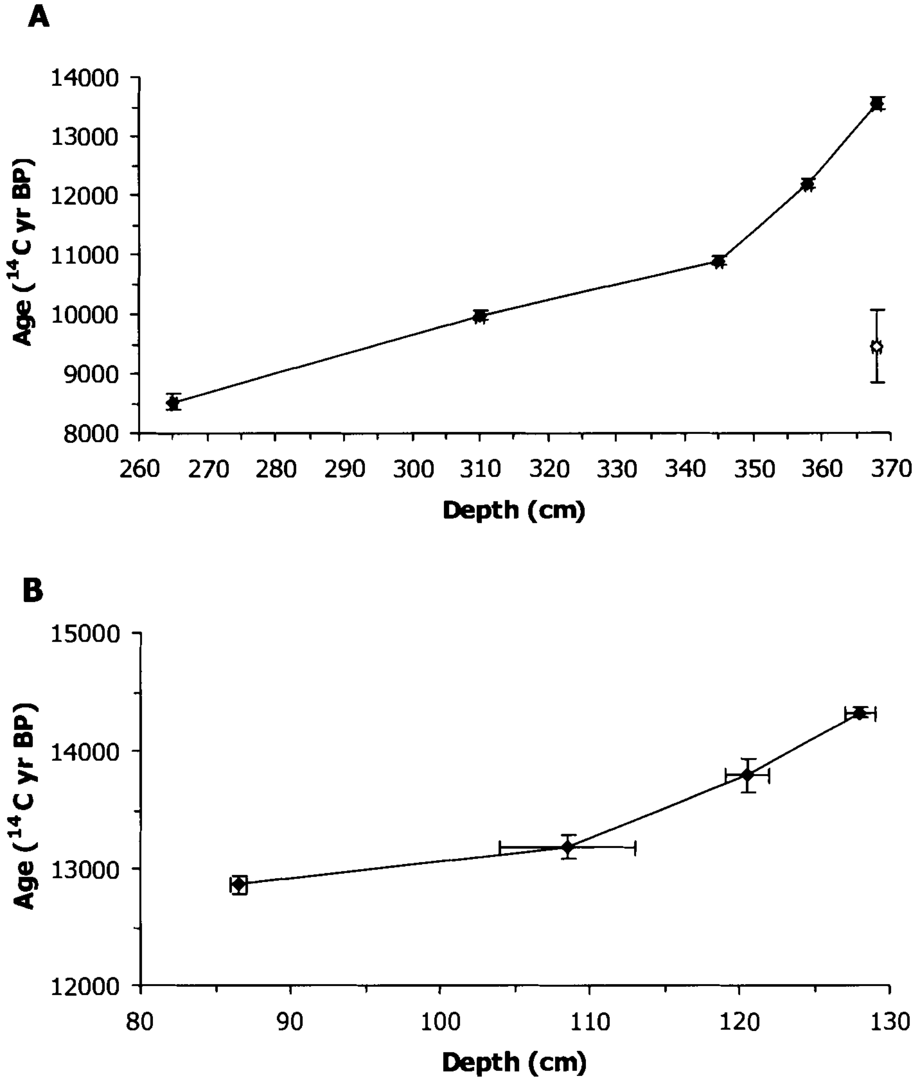

Fig. 5.2. Radiocarbon ages (◆) and associated errors from A) West Side Pond (QCI) and B) Dogfish Bank (Hecate Strait) plotted against sediment depth. The age-depth models were constructed using linear interpolation between adjacent radiocarbon ages (Table 5.1). The rejected West Side Pond date (◇) is also shown.

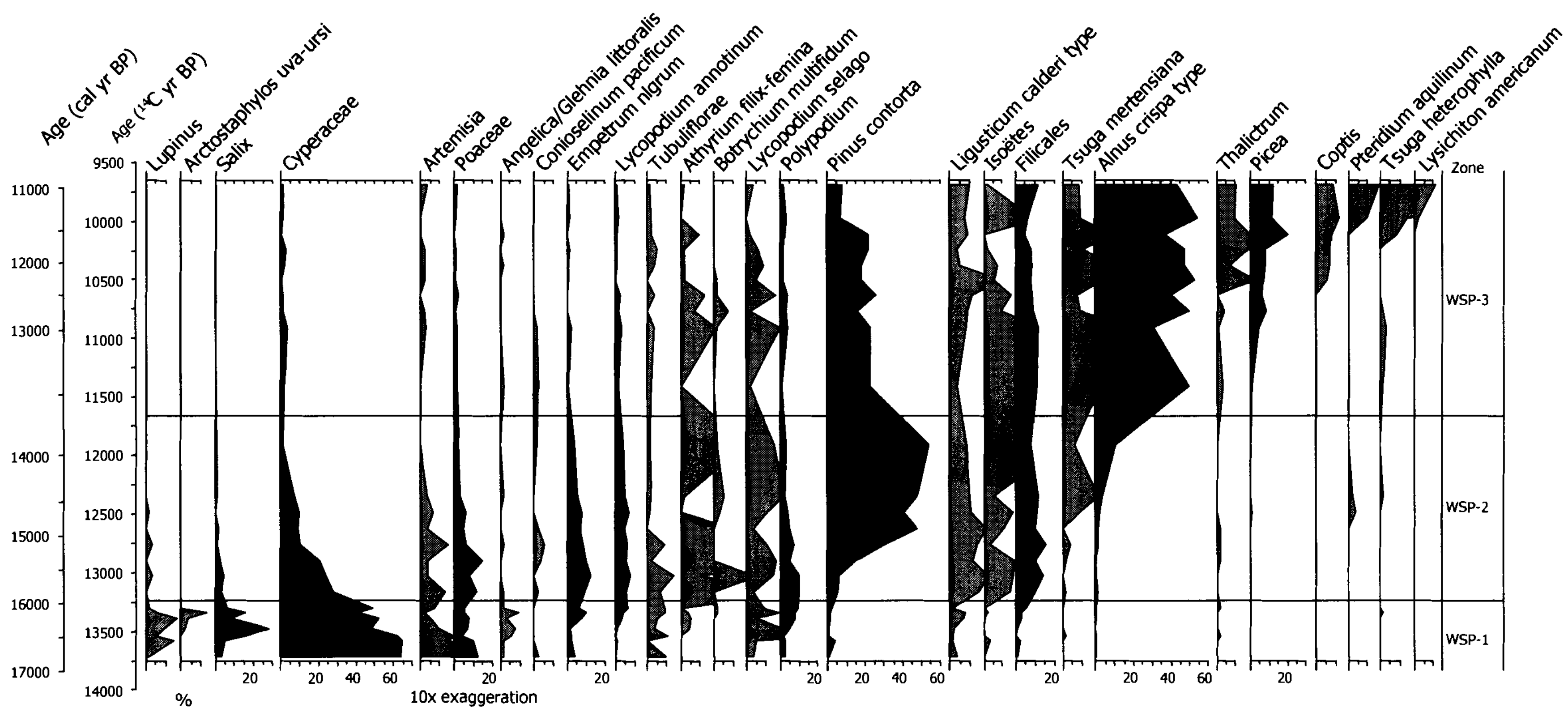

Fig. 5.3. **Selected pollen and spore percentages from West Side Pond (QCI). Grey curves represent 10x exaggeration. Taxon order is based on weighted-averages of the pollen percentages.**

contorta pollen does not exceed 4%. Pteridophytes, particularly *Polypodium* and *Lycopodium annotinum*, gradually increase from 3 to 25%. Total PARs are extremely low, increasing from 28 grains cm^{-2} yr^{-1} at the base of the core to 890 grains cm^{-2} yr^{-1} at the top of the zone (Fig. 5.4), mostly due to a greater abundance of Cyperaceae, *Salix*, Poaceae, and *E. nigrum* pollen and *Polypodium* spores.

Zone WSP-2: 13,240 – 11,660 ^{14}C yr BP, 15,950 – 13,660 cal yr BP (366 – 353 cm)

This zone is characterized by increasing and high percentages of *P. contorta* (up to 54%) and decreasing percentages of Cyperaceae, Poaceae, and *Salix*. *Empetrum nigrum* reaches its maximum (12%) for the period of record. *Alnus crispa* type increases to 10% at the top of the zone. Trace amounts of *Tsuga mertensiana* (2%) and *Picea* (1%) pollen occur in this zone. Herbaceous taxa, including *Artemisia*, *Ligusticum calderi* type, *Angelica/Glehnia littoralis*, *Conioselinum pacificum*, *Heracleum lanatum*, and *Ranunculus*, decrease from 45 to 4% of the pollen sum. Pteridophytes account for up to 40% but gradually decrease to 25%. Total PARs gradually increase to 3980 grains cm^{-2} yr^{-1}, and are dominated primarily by *P. contorta*, Filicales (Polypodiaceae), and *E. nigrum* (Fig. 5.4).

Zone WSP-3: 11,660 – 9680 ^{14}C yr BP, 13,660 – 10,950 cal yr BP (353 – 301 cm)

Increases in *Alnus crispa* type and *Picea* pollen, up to 55 and 20% respectively, characterize this zone. *Pinus contorta* pollen decreases to about 20% initially and then to less than 10%. Pollen from other trees and shrubs include *Tsuga heterophylla* (<7%) and *T. mertensiana* (<4%). Herbaceous taxa include *Thalictrum*, *Coptis*, *Lysichiton americanum*, *Menyanthes/Fauria*, and *Gentiana douglasiana*, but collectively contribute less than 10%. Pteridophytes account for 16% on average. Trace amounts of *Sphagnum* spores and *Nuphar* pollen are also present. This zone has a maximum total PAR (13,210 grains cm^{-2} yr^{-1}) for the late-glacial portion of the core but PARs are typically less than 10,000 grains cm^{-2} yr^{-1} (Fig. 5.4). PARs are dominated by *A. crispa* type. Other important types include *P. contorta*, *Picea*, and Filicales. Maximum Poaceae PARs occur in this zone. Organic sedimentation begins at 345 cm (10,920 ^{14}C yr BP; 12,980 cal yr BP).

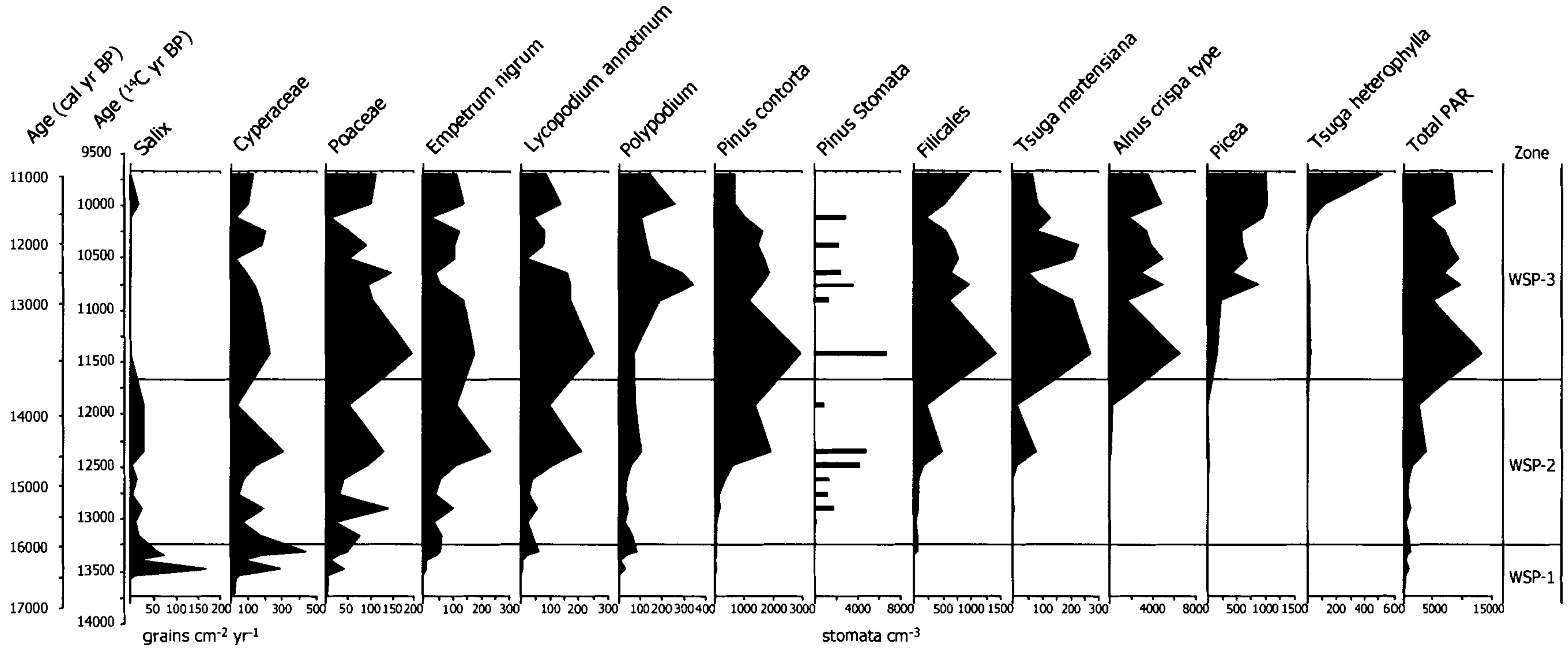

Fig. 5.4. Accumulation rates for important pollen and spore taxa, and *Pinus contorta* stomata concentrations from West Side Pond (QCI). Note changes in scale. Zonation from the pollen percentage diagram is superimposed. Taxon order is based on weighted-averages of the pollen percentages.

Many of the trends in pollen percentages (Fig. 5.3) are not reflected in PARs (Fig. 5.4). Although there is general agreement for some taxa (e.g., *Salix*, Cyperaceae, *Alnus crispa*, *Picea*), there are important differences for other prominent taxa. Poaceae percentages are low after 12,500 ^{14}C yr BP (14,700 cal yr BP) yet PARs demonstrate that Poaceae abundance on the landscape increases ca. 13,250 ^{14}C yr BP (15,900 cal yr BP) and remains more or less consistent for the remainder of the record. In fact, herb PARs are highest in Zone WSP-3 not the herb-dominated basal zone (WSP-1). Assuming pollen production remained constant, this suggests more herbs on the landscape later. *Empetrum nigrum* and *Lycopodium annotinum* show similar patterns. *Pinus contorta* percentages decrease after 11,500 ^{14}C yr BP (13,500 cal yr BP) but PARs reveal that *P. contorta* remains an important component of the vegetation until 10,000 ^{14}C yr BP (11,300 cal yr BP). These differences highlight the importance of using PARs in conjunction with percentage data to reconstruct paleovegetation, whenever possible; however, PARs should be used conservatively given variation in sedimentation rates and when chronological control is poor e.g., at the base of the West Side Pond record.

Principal Components Analysis

PCA axes 1 and 2 account for 69.5 and 17.1% of the total variation, respectively, and were the only significant axes according to a broken-stick model. In the ordination of pollen types, axis 1 separates *Alnus crispa* type, *Pinus contorta*, and *Picea* from Cyperaceae and *Salix*, which have high positive and negative loadings, respectively (Fig. 5.5). Species loadings on axis 1 correspond closely to the order in which species become dominant and/or reach their highest abundance, separating early and later taxa, and may reflect differences in life history traits and/or increasing temperatures. Axis 2 separates *Pinus* from most other taxa, most notably *A. crispa* type, *Picea*, and Cyperaceae (Fig. 5.5). Although axis 2 appears similar to the arch effect (ter Braak 1995), it is not simply the first axis folded; axis 2 corresponds to real structure in the data i.e., the dominance of *P. contorta* during the transition from Cyperaceae-dominated assemblages to *Alnus*-dominated assemblages.

The ordination of pollen samples (Fig. 5.5) is directly related to the ordination of pollen types: pollen types with high loadings on one axis dominate samples with high scores on that axis, and samples that are similar in species composition are close

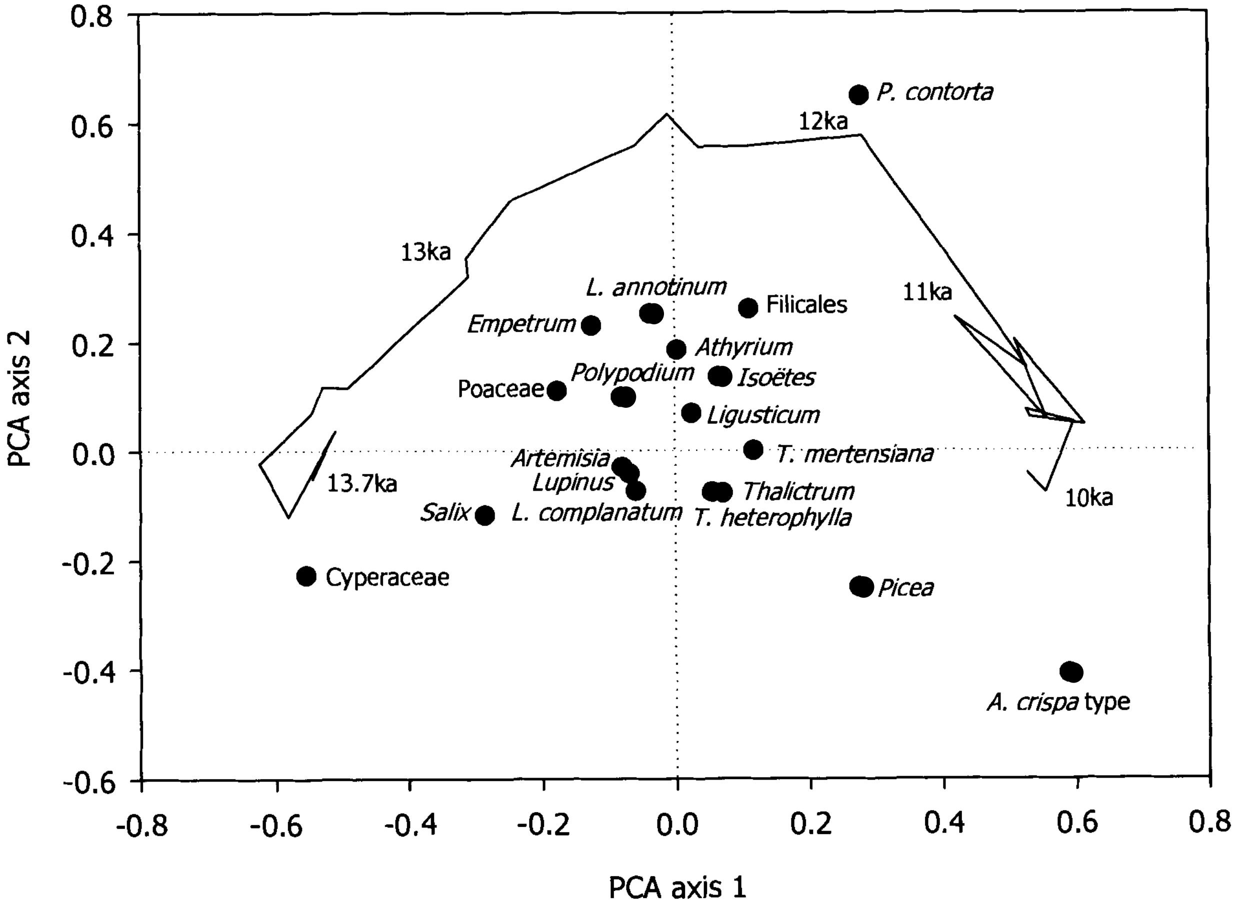

Fig. 5.5. Principal components analysis (PCA) biplot of species loadings (circles) for important pollen and spore taxa from West Side Pond (QCI) with sample scores (line) in stratigraphic order. Axes 1 and 2 account for 69.5 and 17.1% of the total variation, respectively. Radiocarbon age is shown for each 1000 ^{14}C yr (ka).

together. Axis 1 separates *Alnus*-dominated assemblages (Zone WSP-3) on the positive end from Cyperaceae-dominated assemblages (Zone WSP-1) on the negative end. Axis 2 separates *Pinus*-dominated assemblages (Zone WSP-2) from all other samples. PCA and numerical zonation of the dataset revealed similar subdivisions.

Pinus *Stomata*

Pinus stomata first appear at 364 cm (13,040 ± 305 ^{14}C yr BP; ca. 15,600 cal yr BP) and are consistently present until 335 cm (10,635 ^{14}C yr BP; ca. 12,500 cal yr BP). Stomata then occur sporadically between 335 and 315 cm (10,635–10,115 ^{14}C yr BP; 12,500–11,560 cal yr BP) and are subsequently absent from the fossil record. Stomata concentrations range from 0 to 6780 stomata cm^{-3} (Fig. 5.4), peaking in Zone WSP-2 at 350 cm (11,410 ^{14}C yr BP; 13,430 cal yr BP) and corresponding with maximum *P. contorta* PARs. *Pinus* stomata and PARs are positively correlated ($r = 0.70$, $p = 0.01$), as are *Pinus* stomata and pollen percentages ($r = 0.54$, $p = 0.01$).

Dogfish Bank, Hecate Strait

Stratigraphy and Chronology

The Dogfish Bank core (TUL91C034) is composed of two main units (Fig. 5.6), separated by an sharp erosional contact, that characterize the postglacial stratigraphy of much of the British Columbia shelf (Barrie et al. 1993). The upper unit (0-30 cm) is composed of gravelly coarse marine sand with abundant shell fragments, foraminifera, and ostracods, and represents the entire Holocene epoch. The lower unit (30-129 cm) is late-glacial in age and is composed of alternating interbedded and trough-cross-bedded sand and stiff silty-sand. From 30 to 58 cm, sediments coarsen upwards with evidence of bioturbation of overlying marine sediments. Shell fragments are rare between 50 and 75 cm and absent below this depth, suggesting marine inundation at 75 cm. A single marine bivalve fragment at 121 cm is likely the result of contamination. Plant remains, including *in situ* roots and rhizomes, are abundant below 75 cm. Barrie et al. (1993) conclude that the silty-sand (58-129 cm) was probably deposited on a terrestrial surface through fluvial processes and in shallow freshwater ponds. Sand interbeds may be the result of deposition during periodic runoff events (Barrie et al. 1993).

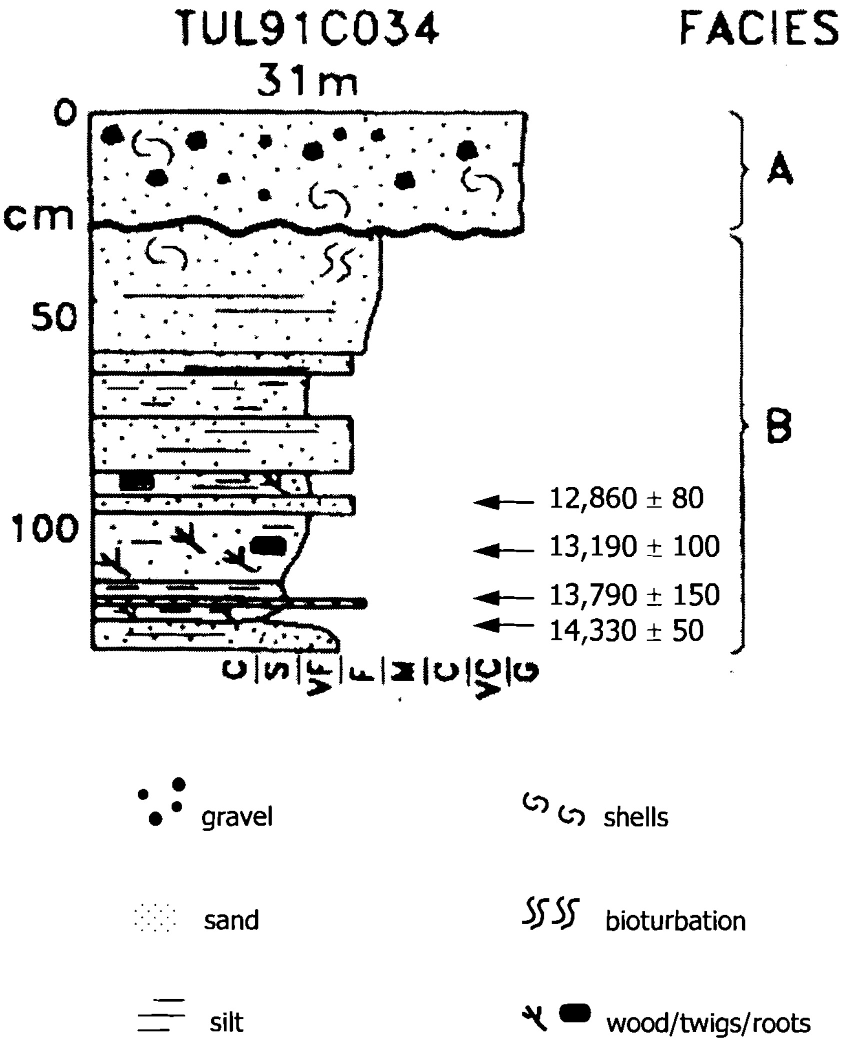

Fig. 5.6. Stratigraphy, facies and AMS radiocarbon ages of TUL91C034 from Dogfish Bank in Hecate Strait. (Reprinted with permission from Barrie et al. (1993), © 1993 Elsevier Ltd.)

An age-depth model was constructed using linear interpolation (Fig. 5.2) between four AMS radiocarbon ages (Table 5.1) and shows that the core site was exposed between at least 14,330 and 12,860 ^{14}C yr BP (17,365–14,570 cal yr BP). Linear extrapolation to a depth of 75 cm suggests marine inundation occurred sometime after 12,700 ^{14}C yr BP (13,900 cal yr BP). The AMS date of 14,330 ± 50 ^{14}C yr BP provides a minimum age for deglaciation of Dogfish Bank.

Pollen Analysis

Given the lack of marine indicators below 75 cm, pollen analysis was conducted on available sediments between 75 and 129 cm. There was little or no pollen in some samples, particularly between 75 and 92 cm, and therefore, the results of pollen analysis are only presented for samples below 92 cm. Some of the variability in pollen percentages and PARs may be due to low pollen sums (Birks and Birks 1980). Conifer stomata were not present in Dogfish Bank sediments.

Dogfish Bank pollen percentages (Fig. 5.7) were divided into three zones based on numerical zonation by optimal splitting and a broken-stick model. The zonation follows the presence or absence of *Pediastrum* algal colonies.

Zone DFB-1: 14,100 – 13,780 ^{14}C yr BP, 17,080 – 16,630 cal yr BP (125 – 120 cm)

Pollen assemblages are dominated by Cyperaceae. Poaceae and *Equisetum* account for 35 and 17%, respectively, in the basal sample. *Pinus contorta* and *Picea* contribute up to 8 and 3% to the pollen sum. Other important taxa include Filicales (Polypodiaceae), *Empetrum nigrum*, *Salix*, *Artemisia*, and *Alnus crispa* type. Total PARs (Fig. 5.8) are very low (<10 grains cm^{-2} yr^{-1}). *Pediastrum* algal colonies are uncommon but present, indicating the presence of freshwater.

Zone DFB-2: 13,780 – 13,215 ^{14}C yr BP, 16,630 – 15,930 cal yr BP (120 – 109 cm)

Although pollen assemblages continue to be dominated by Cyperaceae, there are increases in *Empetrum nigrum*, *Salix*, and *Equisetum*, and a decrease in *Pinus contorta*. Other important taxa include *Ranunculus*, Asteraceae (Tubuliflorae), *Myrica*, and Ericaceae. Total PARs (Fig. 5.8) increase to between 14 and 30 grains cm^{-2} yr^{-1}. *Pediastrum* algal colonies are absent.

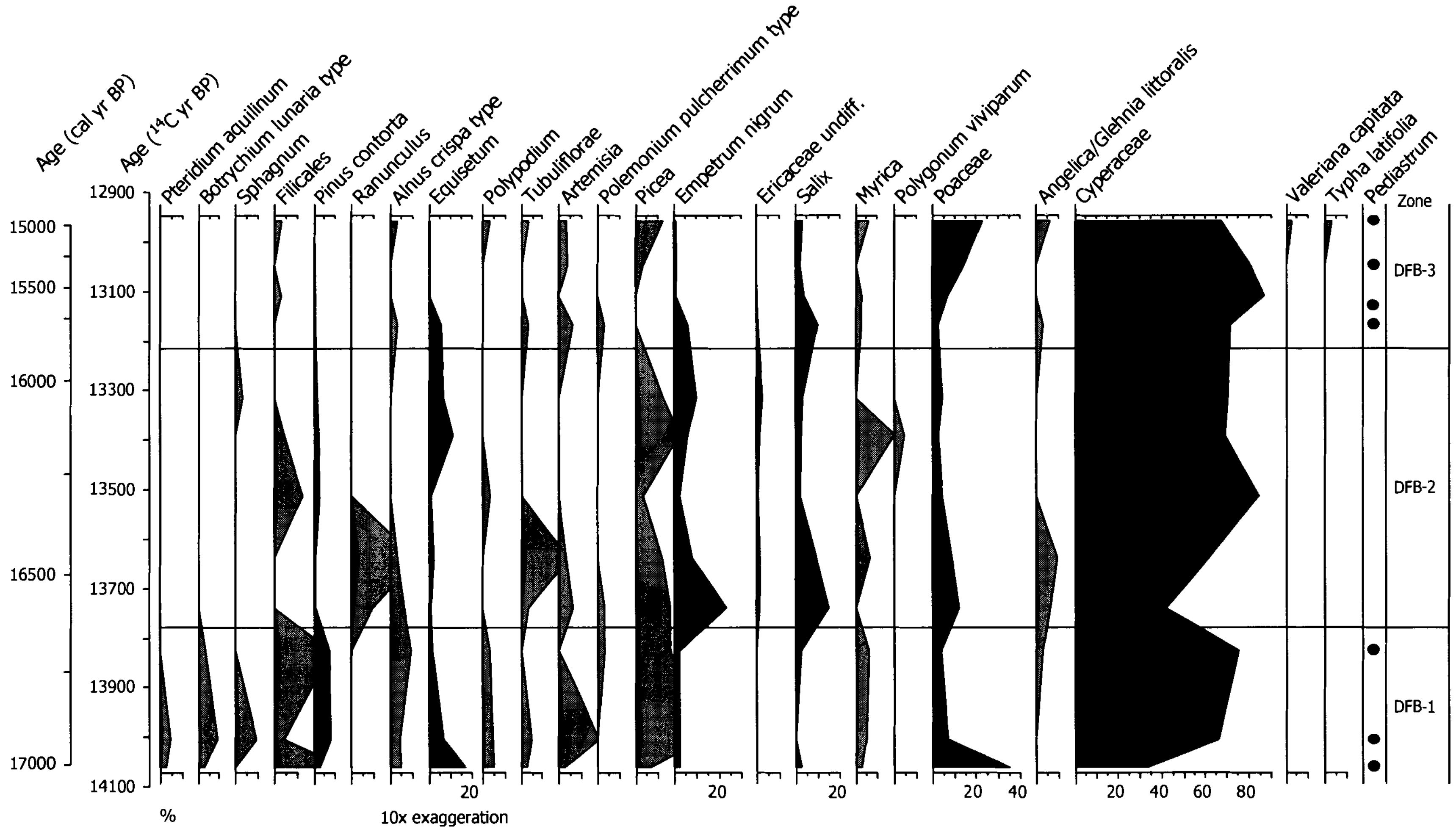

Fig. 5.7. Selected pollen and spore percentages from Dogfish Bank (Hecate Strait). Grey curves represent 10x exaggeration. Taxon order is based on weighted-averages of the pollen percentages.

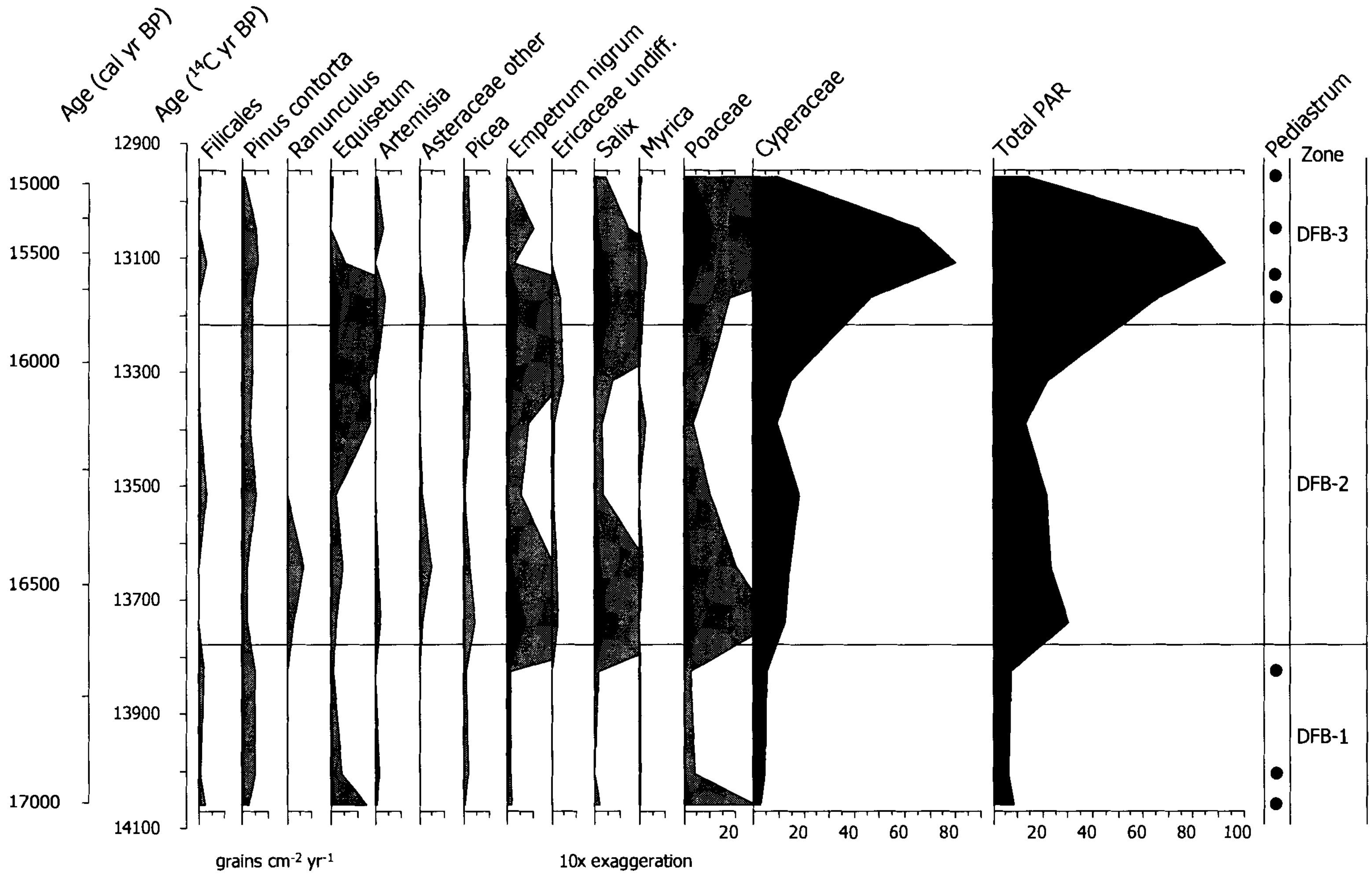

Fig. 5.8. Accumulation rates for important pollen and spore taxa from Dogfish Bank (Hecate Strait). Grey curves represent 10x exaggeration. Note changes in scale. Zonation from the pollen percentage diagram is superimposed. Taxon order is based on weighted-averages of the pollen percentages.

Zone DFB-3: 13,215 – 12,940 ^{14}C yr BP, 15,930 – 14,900 cal yr BP (109 – 92 cm)

Cyperaceae continues to dominate pollen assemblages. Poaceae increases towards the top of the zone, whereas *Empetrum nigrum*, *Salix*, and *Equisetum* decline. Trace amounts of *Valeriana capitata* and *Typha latifolia* are present. *Typha latifolia*, an aquatic of shallow freshwater, is wind-dispersed over short distances (Krattinger 1975), suggesting that even a few *T. latifolia* tetrads record its local presence. Total PARs (Fig. 5.8) increase dramatically to a maximum of 93 grains cm^{-2} yr^{-1} before decreasing to 15 grains cm^{-2} yr^{-1}. Cyperaceae dominates total PARs; however, Poaceae also increases. *Equisetum* and *Salix* PARs are highest at the beginning of this zone. *Pediastrum* algal colonies are present and more abundant than in Zone DFB-1.

Discussion

West Side Pond, QCI

At West Side Pond, basal sediments are characterized by high percentages of herb and shrub pollen, and suggest that mesic tundra dominated by Cyperaceae and, to a lesser extent, Poaceae and *Salix*, was established by 13,750 ^{14}C yr BP (16,890 cal yr BP). A variety of other herbs and shrubs such as *Artemisia*, *Empetrum nigrum*, *Lupinus*, *Angelica/Glehnia littoralis*, Tubuliflorae (Asteraceae), *Ligusticum calderi*, *Conioselinum pacificum*, *Sanguisorba canadensis* type, *Epilobium*, and Rosaceae were also present. Several taxa only appear in the basal sample at West Side Pond: *Viola*, *Rumex/Oxyria*, *Franseria* type, *Caltha*, *Polemonium caeruleum* type, and Lamiaceae. This diversity of herbs indicates that a variety of habitats existed around the lake and on adjacent uplands. Dominance by Cyperaceae and the presence of plants such as *Salix*, *Caltha*, *S. canadensis* type, and members of the Apiaceae family including *Angelica/Glehnia littoralis*, *L. calderi*, and *C. pacificum* suggest moist herb tundra with dwarf *Salix*. *Empetrum nigrum* and *Artemisia* likely occupied drier, upland areas. *Polemonium caeruleum* type is likely derived from *P. caeruleum* subsp. *villosum* (Mathewes 1979), an insect-pollinated wetland species that is currently found on the adjacent mainland and in southeastern Alaska but not on the QCI. Fossil grains of *P. caeruleum* type were also recorded in late-glacial sediments at sites on the east coast of Graham Island (Fig. 5.1) (Mathewes 1980; Mathewes and Clague 1982).

The total PAR is extremely low (28 grains cm^{-2} yr^{-1}) at 13,750 ^{14}C yr BP (16,800 cal yr BP), which is typical for tundra assemblages (e.g., Heusser 1990; Gajewski 1995). PARs in modern tundra communities in Alaska (Heusser 1983a, 1990; Oswald et al. 2003) and in fossil records from arctic sites (e.g., Cwynar 1982; Lozhkin et al. 1993) are often less than 500 grains cm^{-2} yr^{-1}. Low total PARs and low sediment organic content suggest that the vegetation cover was sparse and perhaps marked by large areas of exposed soil. After 13,500 ^{14}C yr BP (16,400 cal yr BP), PARs increase, suggesting that plant cover, particularly Cyperaceae and *Salix* populations, expanded. The increase in plant cover after 13,500 ^{14}C yr BP was likely favoured by enhanced soil development and climatic amelioration. After 13,500 ^{14}C yr BP, the vegetation also included *Arctostaphylos uva-ursi*, a dwarf shrub typical of well-drained exposed sites, and *Saxifraga oppositifolia*, an arctic/alpine cushion plant commonly associated with recently deglaciated terrain (Pojar and Mackinnon 1994).

Tundra dominated by Cyperaceae apparently gave way to more productive and more diverse herb-shrub tundra with pteridophytes after 13,250 ^{14}C yr BP (15,900 cal yr BP). Cyperaceae and *Salix* PARs and percentages decline after 13,250 ^{14}C yr BP while several other taxa including *Empetrum nigrum*, Poaceae, *Athyrium filix-femina*, and *Lycopodium annotinum* increase (Figs. 5.3 and 5.4). These changes suggest increased summer warmth (Chapin et al. 1995). *Empetrum nigrum* is a shade-intolerant evergreen shrub that, in coastal British Columbia, most often grows in peat bogs where it prefers topographic prominences (Klinka et al. 1989). However, *E. nigrum* also dominates dry, wind-swept ridges in coastal Alaska (Heusser 1960; Peteet and Mann 1994), where its tolerance for exposed, cold and windy conditions gives it a competitive advantage. *Empetrum nigrum* likely dominated local topographic prominences in a similar fashion on the late-glacial landscape of the QCI. The abundance of Cyperaceae pollen and Pteridophyte spores indicates that moist habitats were widespread.

Pinus stomata first appear in West Side Pond sediments 13,040 ± 305 ^{14}C yr BP (15,600 cal yr BP), when *Pinus contorta* pollen is only 6% of the sum (Fig. 5.3) and *Pinus* PARs are 17 grains cm^{-2} yr^{-1} (Fig. 5.4). These results are consistent with those of Peteet (1991), who found *P. contorta* needles in late-glacial sediment in southeastern Alaska with less than 2% *Pinus* pollen. The generally short dispersal distance of conifer stomata suggests that *P. contorta* grew locally by 13,000 ^{14}C yr BP. This is the earliest reported presence of *P. contorta* on the QCI and adjacent areas. The local presence of *Pinus* at 12,190 ± 140 ^{14}C yr BP is confirmed by a radiocarbon-dated *Pinus* needle (Table 5.1) as well as *Pinus* seeds identified by Fedje (1993). *Pinus* stomata disappear from the fossil record after 10,115 ^{14}C yr BP (11,560 cal yr BP), simultaneous with decreases in *P. contorta* pollen percentages and PARs. However, a single *Pinus* needle indicates that isolated populations of *P. contorta* were still present at 9980 ± 70 ^{14}C yr BP (11,320 cal yr BP) (Table 5.1).

Pollen assemblages between ca. 12,500 and 10,000 ^{14}C yr BP (ca. 14,700–11,300 cal yr BP) imply open *Pinus contorta* woodland vegetation with abundant non-arboreal vegetation, including Cyperaceae, *Empetrum nigrum*, and various ferns (Figs. 5.3 and 5.4). These assemblages are similar to those recovered from terrestrial sediment on the continental shelf in Juan Perez Sound and Queen Charlotte Sound that were deposited 12,240 ± 50 and 10,470 ± 75 ^{14}C yr BP, respectively (Lacourse et al. 2003; Chapter 3). *Pinus contorta* percentages decline after 11,500 ^{14}C yr BP (13,500 cal yr BP) as *Alnus crispa* percentages increase; however, *P. contorta* PARs remain high until 10,000 ^{14}C yr BP, indicating that *Pinus* populations did not decrease in abundance. *Pinus contorta* is a shade-intolerant pioneer tree with wide climatic and edaphic tolerance including high drought and frost tolerance (Krajina 1969; Klinka et al. 1989). It is capable of rapid invasion of disturbed sites and recently deglaciated terrain (Peteet 1991) due to efficient seed dispersal and rapid growth and maturation (Krajina 1969; Klinka et al. 1989). *Pinus contorta* was the first tree to colonize the coast following deglaciation, and its late-glacial dominance suggests either nearby late Wisconsin refugia or exceptionally rapid late-glacial coastal migration from the south (Peteet 1991).

PARs increase after 12,500 ^{14}C yr BP, due primarily to increases in *Pinus contorta*, and reflect the increased plant cover relative to the preceding tundra vegetation. *Polypodium*, *Athyrium filix-femina*, and other Polypodiaceae ferns (Filicales) and *Lycopodium annotinum* and *L. selago* clubmosses likely dominated the understory vegetation and edge communities. The disappearance of *Lupinus* pollen, a nitrogen-fixing legume and soil stabilizer common in early-seral communities and disturbed sites with exposed mineral soil (Gadgil 1971; Klinka et al. 1989), suggests that suitable open and/or disturbed sites were less common. *Isoëtes*, a shallow water indicator, was present at the lake margins since 13,250 ^{14}C yr BP (15,900 cal yr BP). *Isoëtes* PARs are highest at ca. 11,500 ^{14}C yr BP (ca. 13,500 cal yr BP), likely reflecting an expansion of shallow water areas around the lake.

Stomata from other conifers i.e., *Picea sitchensis*, *Tsuga mertensiana*, and *T. heterophylla* are absent, and pollen of these species is low. These results are consistent with an absence of these species immediately adjacent to the site and suggest regional pollen transport. However, Fedje (1993) concludes that *Picea* and *T. heterophylla* were present near West Side Pond from 11,200 to 9900 ^{14}C yr BP, and from 9900 to 8700 ^{14}C yr BP, respectively, based on the presence of needles in West Side Pond sediments. Fedje (1993) does not present a complete macrofossil analysis and specific arrival dates are not suggested. The species identifications of the conifer needles require verification (D.W. Fedje, personal communication, 2004). Fedje (1993) infers the local presence of *T. mertensiana* based on pollen percentages that exceed 2%, which is common practice (e.g., Hebda 1983; Peteet 1986; Hebda and Allen 1993; Mathewes 1993 but see Heusser 1983a); however, because *T. mertensiana* pollen percentages do not exceed 4% in these late-glacial sediments and *T. mertensiana* stomata are absent, it is possible that *T. mertensiana* trees did not grow immediately adjacent to the site. At most other late-glacial sites on the QCI, forests were dominated by *Picea* by about 11,200 ^{14}C yr BP (ca. 13,200 cal yr BP) (Lacourse and Mathewes *in press*; Chapter 2). *Picea* pollen is likely derived from *P. sitchensis*, although this is uncertain in light of the analysis by Warner and Chmielewski (1987), which indicates that late-glacial *Picea* cones from the QCI probably represent hybrids of *P. sitchensis* and *P. glauca*.

After 11,500 ^{14}C yr BP (ca. 13,500 cal yr BP), *Alnus crispa* type pollen increases dramatically (Figs. 5.3 and 5.4). *Alnus* pollen is commonly greatly over-represented relative to its abundance on the landscape (e.g., Heusser 1973, 1983a, 1990, 1995; Peteet 1986; Hebda and Allen 1993; Lacourse 1998). However, its local presence is confirmed by *Alnus* leaf fragments and seeds (Fedje 1993). Facilitation by *A. crispa* was likely important in conifer establishment and community development by rapidly expanding on immature and disturbed soils due to rapid growth rates and by increasing soil nitrogen content and organic matter (Chapin et al. 1994). *Alnus crispa* regenerates abundantly on exposed mineral soil and disturbed sites (Klinka et al. 1989).

Polypodium and other Polypodiaceae ferns (Filicales) also expand after 11,500 ^{14}C yr BP. Peteet (1986) identified an *Alnus*-Polypodiaceae analogue in modern treeline pollen and spore assemblages from coastal Alaska, which suggests open terrain. Organic sedimentation began 10,910 ^{14}C yr BP (12,980 cal yr BP); with more continuous vegetative cover, the landscape stabilized and mineral input to West Side Pond decreased. PARs are highest after 11,500 ^{14}C yr BP (13,500 cal yr BP), reaching levels that are consistent with modern coastal rainforests in British Columbia i.e., >10,000 grains cm^{-2} yr^{-1} (Lacourse *in press*; Chapter 4). Pollen assemblages also include large amounts of *Pinus contorta* and some *Picea* at this time. The presence of *Pinus* stomata indicates that it remained an important component of the local vegetation around West Side Pond. *Thalictrum*, *Coptis*, and *Lysichiton americanum*, which are common in the herbaceous understory of wet open canopy forests (Klinka et al. 1989), are important additions to the local vegetation after 10,500 ^{14}C yr BP (12,250 cal yr BP). *Picea* and *Tsuga heterophylla* populations expanded in the early Holocene (Fedje 1993). The increase in *Alnus crispa* type pollen during the transition to *Picea*-dominated forests is clearly recorded in Logan Inlet sediments (Lacourse and Mathewes *in press*; Chapter 2).

Dogfish Bank, Hecate Strait

Barrie et al. (1993) concluded that the silty-sand unit was deposited at Dogfish Bank in a terrestrial to freshwater pond environment and that Dogfish Bank was subaerially exposed and vegetated between at least 13,790 and 13,190 ^{14}C yr BP (16,650–15,900 cal yr BP), concurrent with glaciomarine sedimentation in Dixon Entrance, just north of Dogfish Bank (Barrie and Conway 1999). Two new AMS radiocarbon ages (Table 5.1) indicate that the bank was exposed between at least 14,330 ± 50 and 12,860 ± 80 ^{14}C yr BP (17,370–14,570 cal yr BP). A relative sea-level curve for northern Hecate Strait suggests that grounded ice caused relative sea level to fall to -77 m by 13,000 ^{14}C yr BP (15,600 cal yr BP) (Hetherington et al. 2004). A low of -89 m was reached at 11,500 ^{14}C yr BP (ca. 13,500 cal yr BP) and rising sea levels inundated the shelf after 9,700 ^{14}C yr BP (ca. 11,000 cal yr BP), when the glacioisostatic forebulge collapsed (Hetherington et al. 2004). Molluscan evidence suggests that portions of the shelf in Hecate Strait may have been exposed as late as 9130 ± 50 ^{14}C yr BP (10,325 cal yr BP) (Hetherington et al. 2003). This suggests that during the late-glacial period portions of the shelf may have been exposed for as much as 7000 cal yr. It is unlikely, however, that the core site on Dogfish Bank was exposed and vegetated much after 12,860 ± 80 ^{14}C yr BP, since shell fragments were found in the sediment core 9 cm above the level of this date and there is no evidence of an erosional contact (Barrie et al. 1993). Paleogeographic maps based on a digital elevation model, reconstructed sea level curves, and geostatistical interpolation show the core site on Dogfish Bank submerged by 12,700 ^{14}C yr BP and then was re-exposed between 11,700 and 11,200 ^{14}C yr BP (Hetherington et al. 2004).

It is likely that marine conditions existed immediately north of the core site at more or less the same time as tundra vegetation. Barrie and Conway (1999) present an age of 14,980 ± 110 ^{14}C yr BP (TO-4888) on *Cassidulina reniforme*, an indicator of a cold and shallow depositional environment (Patterson et al. 1995), from a marine core retrieved just 9 km northeast on Dogfish Bank. Correcting the depths of these two samples to reflect a more accurate depositional elevation suggests a difference of about 25 m between these sites (Hetherington et al. 2004). The *C. reniforme* date requires marine reservoir correction (Hutchinson et al. 2004), but depending on which marine reservoir correction is used i.e., -600 yr (Barrie and Conway 2002), -800 yr (Southon et al. 1990; Hetherington et al. 2003, 2004) or -950 to -1200 yr (Kovanen and Easterbrook 2002), the *C. reniforme* date may be equivalent to or several hundred ^{14}C years younger than the basal age of 14,330 ^{14}C yr BP for the Dogfish Bank core.

Pollen assemblages from Dogfish Bank (Figs. 5.7 and 5.8) suggest the continental shelf supported wet sedge tundra with dwarf shrubs (i.e., *Salix* and *Empetrum nigrum*) and *Equisetum* between at least 14,100 and 12,940 ^{14}C yr BP (17,080–14,900 cal yr BP). The local presence of Cyperaceae, *Salix*, and *Empetrum* is confirmed by plant macrofossils (Barrie et al. 1993). The dominance by Cyperaceae indicates abundant soil moisture. PARs (Fig. 5.8) are exceptionally low (<30 grains cm^{-2} yr^{-1}) before about 13,200 ^{14}C yr BP (15,850 cal yr BP), suggesting very sparse vegetation on Dogfish Bank. After 13,200 ^{14}C yr BP, PARs increase to about 80 grains cm^{-2} yr^{-1}. The increase in PARs may be due to increased plant cover and/or may reflect deposition and sediment focusing in a small freshwater basin. The abundance of *Pediastrum* colonies after 13,200 ^{14}C yr BP supports the latter interpretation. PAR values correspond closely with other tundra assemblages e.g., modern rates in the Canadian high to mid-arctic (Ritchie and Lichti-Federovich 1967; Gajewski 1995) and late Quaternary rates in Alaska (Brubaker et al. 1983; Heusser 1990), and are not surprising given the proximity of the sea and glaciers. A maximum estimated PAR of 93 grains cm^{-2}

yr^{-1} contrasts with values of about 1000 and 5000 grains cm^{-2} yr^{-1} for forest-tundra and northern coniferous forests (Ritchie and Lichti-Federovich 1967). Although the shelf at Dogfish Bank supported wet sedge tundra, its suitability for human habitation was likely marginal (cf. Barrie et al. 1993; Mandryk et al. 2001). Although some marine resources were available (Hetherington and Reid 2003), human migrants would have found more productive landscapes in the southern Moresby Island region and further south along the coast.

Salix pollen is likely derived from a dwarf species such as *Salix reticulata* or *S. stolonifera*, but specific identification is uncertain. Due to low pollen production and dispersal, *Salix* is typically under-represented by its pollen in modern tundra communities (e.g., Heusser 1983a) and in comparison to macrofossil assemblages (Lacourse et al. 2003; Chapter 3). Warner et al. (1982) identified leaves from the alpine *S. reticulata* in late-glacial sediments near sea level at Cape Ball (Fig. 5.1). On Dogfish Bank and at Cape Ball, Barrie et al. (1993) found *Salix* remains similar to *S. stolonifera*, including leaves, twigs, and buds. Argus (1973) argues that *S. stolonifera* survived the last glaciation in the Pacific coastal region. It has also been reported in coastal Alaska on Kodiak Island and the Kenai Peninsula (Argus 1973). *Salix* was clearly an important component of the late-glacial landscape of coastal British Columbia; *Salix* species occupy a wide variety of habitats but are typically associated with habitat instability (Argus 1973).

Colonies of the green alga *Pediastrum* indicate the presence of standing or perhaps slow-flowing freshwater on Dogfish Bank at the beginning and end of deposition of the terrestrial/freshwater unit (Figs. 5.7 and 5.8). Although *Pediastrum* colonies are most common in shallow water, their presence may reflect a variety of aquatic conditions since *Pediastrum* species differ in their ecological affinities and most species have wide ecological tolerance (Komárek and Jankovská 2001). *Pediastrum* disappears between approximately 13,780 and 13,215 ^{14}C yr BP (16,630–15,930 cal yr BP), at the same time as pollen of *Empetrum nigrum* and *Salix* increase (Figs. 5.7 and 5.8). The disappearance of *Pediastrum* and concurrent rise in shrubs suggest a decrease in available moisture or standing water; however, the abundance of *Equisetum* spores suggests otherwise. The disappearance of *Pediastrum* colonies may instead reflect changes in trophic or taphonomic conditions (Komárek and Jankovská 2001).

Six pollen types found in Dogfish Bank sediments i.e., *Valeriana capitata, Polygonum viviparum, Typha latifolia, Polemonium pulcherrimum* type, *Myrica*, and Liliaceae, were not encountered in West Side Pond sediments and show interesting phytogeographic patterns. *Valeriana capitata*, an alpine plant found mostly north of 60°N (Hultén 1968), is noteworthy since it is not known to occur on the QCI today. The wetland plant *T. latifolia* is also absent from much of the north Pacific coast including the QCI. *Polygonum viviparum* and *Polemonium pulcherrimum*, common in alpine and periglacial habitats, are both rare on the QCI today.

Coastal and wetland taxa, including various Polypodiaceae ferns, *Ranunculus, Valeriana capitata, Typha latifolia, Angelica/Glehnia littoralis, Franseria* type, and *Myrica*, support the interpretation that the exposed Dogfish Bank was a wet environment. The presence of *Myrica*, likely *Myrica gale*, a common nitrogen-fixing wetland shrub (Klinka et al. 1989), suggests that summer temperatures were mild (Ritchie et al. 1983). Modern coastal meadows in southeastern Alaska and their associated pollen assemblages include *M. gale* (Peteet 1986). *Typha latifolia* suggests local ponded environments and a temperate growing season. Other taxa including *Empetrum nigrum, Polemonium pulcherrimum* type, *Polygonum viviparum*, and *Artemisia* and other Asteraceae suggest the availability of drier sites within the sedge tundra. There is some evidence of regional and/or long-distance transport of pollen; small amounts of pollen from *Pinus contorta, Picea*, and *Alnus* spp., and single grains of *Quercus garryana* and *Sarcobatus vermiculatus* (cf. Maher 1964) were found in Dogfish Bank sediments.

The vegetation on Dogfish Bank was likely controlled by local topography and soils with wet Cyperaceae tundra with other herbs, *Equisetum*, and perhaps *Myrica gale* grading into Cyperaceae-*Empetrum*-*Salix* tundra in areas where drainage was slightly improved. This mosaic of vegetation communities closely resembles modern coastal meadows and tundra on the Shumagin Islands (Heusser 1983a) and Aleutian Islands (Heusser 1990) in southwestern Alaska, where Cyperaceae, Poaceae, *Artemisia, Epilobium, Angelica, Polygonum viviparum*, and *Equisetum* dominate lower elevations, and exposed hilltops and well-drained prominences are covered by *Empetrum*-dominated heath communities.

Late-glacial Vegetation and Climate in a Regional Context

Paleoclimate model simulations suggest that late-glacial climate was characterized by an anticyclonal high pressure system centred on the continental ice sheet that generated katabatic easterly winds and increased seasonality (COHMAP 1988; Thompson et al. 1993; Bartlein et al. 1998). Before 12,000 ^{14}C yr BP (14,000 cal yr BP), the ice sheet likely shifted the jet-stream south, caused cooling in mid-latitudes, and reduced winter moisture (Thompson et al. 1993; Bartlein et al. 1998). However, conditions were sufficiently temperate and moist during the growing season to support *Abies* and *Picea* forest in southwestern British Columbia ca. 18,000 ^{14}C yr BP (21,000 cal yr BP) (Hicock et al. 1982; Lian et al. 2001). Simulated late-glacial climates suggest that glacial anticyclonic circulation at the ice sheet margins would have resulted in cold and relatively dry climate around the QCI, particularly in winter (Bartlein et al. 1998). Reconstructed climate records from the region corroborate a cold late-glacial climate (Heusser et al. 1980, 1985; Palmer et al. 2002). Using pollen-climate transfer functions, Heusser et al. (1980, 1985) predict that between 16,000 and 13,000 ^{14}C yr BP (ca. 18,750–15,600 cal yr BP) conditions were colder and drier in coastal Washington compared to today: summer temperatures were about 11°C and annual precipitation about 1500 mm, compared to 14°C and 1800 mm for today. After 12,000 ^{14}C yr BP, increased summer solar insolation and deeper penetration of storm systems from the north Pacific would have resulted in a warmer and wetter summer climate (Berger 1978; Bartlein et al. 1998). Paleoclimate model simulations suggest that as the continental ice sheet receded and the associated glacial anticyclone weakened, moist westerly winds would have become more important and the summer Pacific high pressure system would have strengthened (Thompson et al. 1993; Bartlein et al. 1998). Simulated late-glacial climates suggest that a northward shift of the jet stream due to the decreasing size of the continental ice sheet and increased seasonality due to changes in the seasonal cycle of insolation resulted in progressively warmer and drier summers and colder winters in the early Holocene (Berger 1978; Whitlock and Bartlein 1997; Bartlein et al. 1998).

The fossil pollen assemblages from West Side Pond and Dogfish Bank are similar to other late-glacial vegetation communities on the QCI (Mathewes and Clague 1982; Warner et al. 1982; Warner 1984; Mathewes et al. 1985; Hann and Warner 1987; Heusser 1995), in coastal Alaska (Engstrom et al. 1990; Cwynar 1990; Peteet and Mann

1994; Hansen and Engstrom 1996), and to the south in coastal British Columbia (Pellatt et al. 2002; Brown and Hebda 2003). The earliest paleoecological records come from the Cape Ball sea cliffs on northeastern Graham Island (Fig. 5.1). Terrestrial and wetland communities were established at Cape Ball, approximately 40 km east of Dogfish Bank, by 15,000 ^{14}C yr BP (Warner et al. 1982; Warner 1984; Mathewes et al. 1985). At this time, the Cape Ball area was characterized by sparse tundra composed of Poaceae, Cyperaceae, and other herbs such as *Rumex*, *Sagina maxima*, and wetland plants such as *Equisetum*, *Juncus*, and *Potamogeton filiformis* (Warner et al. 1982; Warner 1984). By 13,000 ^{14}C yr BP, herb communities were succeeded by dwarf shrub tundra that included *Salix reticulata* and various herbs including *Polemonium* spp. and *Polygonum viviparum*. A dwarf *Salix* twig associated with Cape Ball sediments rich in Cyperaceae and *Salix* pollen was AMS-dated at 13,350 ± 200 ^{14}C yr BP (RIDDL-517) (Barrie et al. 1993). A single *Picea sitchensis* needle suggests it may have been present at Cape Ball ca. 12,400 ^{14}C yr BP (Warner 1984). By 11,800 ^{14}C yr BP, *Empetrum nigrum* became abundant, open *Pinus contorta* woodland developed, and PARs increased dramatically. *Pinus contorta*, *Picea sitchensis*, *Tsuga mertensiana*, and *Alnus* formed productive forests after 11,200 ^{14}C yr BP, and *Tsuga heterophylla* was present by 10,700 ^{14}C yr BP (Warner 1984).

Mathewes and Clague (1982) found similar assemblages in a nearby peat bed at Cape Ball. Sediments contain abundant Poaceae pollen with varying amounts of Cyperaceae, Apiaceae, *Pinus contorta*, *Empetrum*/Ericaceae, *Plantago macrocarpa*, *Polemonium caeruleum* type, *Fritillaria*, *Caltha*, *Ranunculus*, and *Claytonia sibirica* as well as large amounts of Cyperaceae seeds, indicating open floodplain vegetation at 12,400 ^{14}C yr BP (Mathewes and Clague 1982). This assemblage is followed by *Pinus contorta*-dominated spectra with abundant ferns around 12,000 ^{14}C yr BP. At 11,300 ± 110 ^{14}C yr BP (GSC-2879), the local arrival of *Picea* is reflected by dramatic increases in *Picea* pollen and radiocarbon-dated *Picea* wood. *Picea* pollen and fern spores decrease about 10,800 ^{14}C yr BP, simultaneous with increases in *P. contorta* and Cyperaceae pollen, and the Younger Dryas cooling event of the North Atlantic.

Heusser (1995) presents a bog record of local conditions from Langara Island (Fig. 5.1) that is dated through stratigraphic correlation with the records from Cape Ball. Basal clay and sand-rich sediments from 13,000 ^{14}C yr BP are dominated by Poaceae, Cyperaceae, *Empetrum*, Apiaceae, and *Salix* pollen but also include *Artemisia*, *Polemonium*, and *Ranunculus*. *Pinus*, *Alnus*, and ferns increase ca. 12,000 ^{14}C yr BP, followed by *Picea sitchensis* and *Tsuga mertensiana* ca. 11,000 ^{14}C yr BP.

Similar pollen assemblages are also found in sediments of comparable age in southeastern Alaska, immediately north of the QCI (Engstrom et al. 1990; Cwynar 1990; Hansen and Engstrom 1996). Between 13,000 and 12,300 ^{14}C yr BP, Pleasant Island supported *Salix* shrub tundra with abundant Cyperaceae and Poaceae, and some Apiaceae, *Alnus crispa*, and Ericaceae (Hansen and Engstrom 1996). *Pinus contorta* contributes about 20% to the pollen sum; however, the lack of *Pinus* stomata suggests a regional source for the pollen. *Pinus contorta*, *A. crispa*, and *Dryopteris* ferns dominate the fossil sequence after 12,300 ^{14}C yr BP. The local presence of *P. contorta* and *Tsuga mertensiana* is confirmed by stomata at 11,900 and 11,200 ^{14}C yr BP, respectively. Herb tundra with abundant *Artemisia* largely replace *Pinus* woodland between 10,600 and 9900 ^{14}C yr BP, coeval with the Younger Dryas chronozone (Engstrom et al. 1990). During this cold interval, PARs and organic matter content decrease. This is followed by *Alnus* and fern shrubland between 9900 and 9200 ^{14}C yr BP. *Picea sitchensis* did not arrive in southeastern Alaska until ca. 9500 ^{14}C yr BP (Cwynar 1990; Hansen and Engstrom 1996), which is about 1800 ^{14}C yr (2500 cal yr) later than at Cape Ball and Logan Inlet on the QCI (Lacourse and Mathewes *in press*; Chapter 2). This may reflect more suitable habitat on the QCI due to earlier deglaciation or the existence of glacial refugia.

Pioneering vegetation following deglaciation of Kodiak Island in southwestern Alaska ca. 14,000 ^{14}C yr BP is similarly composed of a variety of moist herbaceous species with *Empetrum nigrum*, *Artemisia*, and ferns (Peteet and Mann 1994). After 13,000 ^{14}C yr BP, fern populations expand until 10,800 ^{14}C yr BP, when conditions became colder and drier, causing ferns to decline dramatically. This is followed by warming at 10,000 ^{14}C yr BP, increases in ferns, Poaceae, and Apiaceae, and organic sedimentation.

Late-glacial vegetation on the former Bering land bridge was primarily graminoid-herb tundra during full glacial time; increasingly mesic shrub-herb vegetation with dwarf *Betula* expanded after 15,000 ^{14}C yr BP (Ager 1982, 2003). Pollen assemblages from the south coast of the Bering land bridge (Colinvaux 1981) indicate shrubless herb tundra dominated by Poaceae, Cyperaceae, and *Artemisia* under a cold, arid climate before marine inundation ca. 11,000 ^{14}C yr BP (Elias et al. 1997). This pollen record also includes *Picea* in full-glacial and late-glacial sediments. Small, scattered *Picea* populations may have survived on the southeastern land bridge in more mesic environments.

Pinus-dominated vegetation is found at most paleoecological sites ca. 12,000 ^{14}C yr BP in coastal British Columbia (Heusser 1960, 1985; Hebda 1983; Mathewes 1989; Hebda and Haggarty 1997; Brown and Hebda 2002, 2003; Pellatt et al. 2002) and the adjacent U.S.A. (Heusser 1960, 1985; Cwynar 1987, 1990; Hansen and Engstrom 1996; Grigg and Whitlock 1998). The late-glacial dominance of *P. contorta* on the coast is commonly interpreted as representing a cold and relatively dry climate, and suggests either nearby late Wisconsin refugia or exceptionally rapid late-glacial coastal migration from the south following deglaciation (Peteet 1991). Small populations of *P. contorta* may have been present in refugia on the QCI or the adjacent continental shelf. Indeed, genetic data suggest that *P. contorta* var. *contorta* found refuge along the north Pacific coast during the last glacial maximum, as opposed to establishing its present coastal range from a large refugium south of the ice sheet (Wheeler and Guries 1982).

Given the well-known, long-distance dispersal of *Pinus contorta* pollen, it is premature to interpret all *Pinus* pollen as evidence of its presence on the landscape (cf. Peteet 1991). The local presence of conifers should be confirmed through plant macrofossils or stomata. *Pinus* stomata confirm its local presence on the QCI ca. 13,000 ^{14}C yr BP (15,600 cal yr BP), earlier than at most other sites along the Pacific coast, north of the southern late Wisconsin ice limit. A rooted *Pinus* tree stump from the continental shelf in Juan Perez Sound (Fig. 5.1) that dates to 12,240 ± 50 ^{14}C yr BP (CAMS-59768) also confirms its early presence in the QCI region (Fedje and Josenhans 2000; Lacourse et al. 2003; Chapter 3). Silty peat rich in *Pinus* pollen at Bear Cove Bog (Fig. 5.1) that dates to 13,630 ± 310 ^{14}C yr BP (WAT-721) (Hebda 1983) suggests local *Pinus* presence, but does not confirm it. Plant macrofossil evidence confirms that *P. contorta* was present in coastal Oregon (44°N) and Washington (47-48°N) by 13,000 ^{14}C yr BP (Barnosky 1981; Cwynar 1987; Worona and Whitlock 1995; Grigg and Whitlock 1998) and in southwestern British Columbia including southern Vancouver Island (49°N) by 12,000 ^{14}C yr BP (Terasmae and Fyles 1959; Wainman and Mathewes 1987; Friele and Clague 2002). It was likely absent from the Fraser Lowland 18,500 ^{14}C yr BP (Hicock et al. 1982) but was present in coastal Oregon and Washington as early as 20,000 ^{14}C yr BP (Barnosky 1985) and 25,000 ^{14}C yr BP (Worona and Whitlock 1995), respectively. *Pinus* cf. *contorta* wood collected from glaciofluvial sediments underlying till suggests *P. contorta* was present on the west coast of Vancouver Island (49°N; Fig. 5.1) at 16,700 ± 70 ^{14}C yr BP (GSC-2768) (Clague et al. 1980; GSC Wood Identification Report 78-46). A diverse faunal record from Port Eliza Cave (Fig. 5.1) suggests that this area was glaciated sometime after 16,000 ^{14}C yr BP (Ward et al. 2003).

Brown and Hebda (2003) describe a pollen assemblage consisting of *Artemisia*, Poaceae, and ferns with abundant *Pinus* (up to 40%) and *Alnus* (13%) pollen, deposited before 12,540 ± 200 ^{14}C yr BP (BETA-111741) at Porphyry Lake on southern Vancouver Island (Fig. 5.1). This assemblage is similar to the *Pinus*-dominated zone at West Side Pond (WSP-2) both in composition and PARs. Due to the high elevation (1100 m a.s.l) of the site and because plant macrofossils were not identified, it is unclear whether this assemblage represents open parkland vegetation with abundant herbs and some trees and shrubs or open tundra vegetation with upslope transport of arboreal pollen. Brown and Hebda (2003) also suggest that this assemblage may be a remnant of a full-glacial refugium, although direct evidence of this is lacking.

Several paleoecological sites along the Pacific coast reveal vegetation changes, sometimes dramatic reversals, between ca. 11,000 and 10,000 ^{14}C yr BP that have been interpreted as manifestations of the Younger Dryas cooling event, similar in timing and extent to that first documented around the North Atlantic rim (e.g., Mangerud et al. 1974; Mott et al. 1986; Peteet et al. 1990; Levesque et al. 1996). Increases in *Tsuga mertensiana* pollen at sites in coastal British Columbia (Mathewes 1993; Mathewes et al. 1993; Pellatt et al. 2002; Brown and Hebda 2003; Lacourse *in press*; Chapter 4) suggest a cooler and moister climate during this interval. *Tsuga mertensiana* is a robust indicator of a cool and humid growing season; it is characteristic of maritime subalpine forests and requires substantial snow for insulation during winter months (Mathewes 1993; Gedalof and Smith 2001). Increases in cold-water benthic foraminifera indicate cooling of ocean waters off the coast of British Columbia between 11,000 and 10,200 ^{14}C yr BP and a decrease of 2-3°C in summer temperature during this interval (Mathewes et al. 1993). There is also strong molluscan evidence for a cooling event in the QCI region.

Most bivalves disappeared between 10,890 and 10,250 ^{14}C yr BP, leaving only coldwater species and suggesting low sea-surface temperatures, perhaps under an intensified Aleutian low pressure system (Hetherington and Reid 2003). At West Side Pond, there is little evidence for the Younger Dryas cooling event. Increases in *T. mertensiana*, *Polyopodium*, and *Ligusticum calderi* PARs at this time may reflect increases in moisture, although increases in total PARs (Fig. 5.4) contradict notions of cooler temperatures.

Conclusion

Low relative sea levels around the QCI at the end of the last glaciation, resulting from lowered eustatic sea level and glacially induced crustal displacement (Hetherington et al. 2004), permitted establishment of plant communities on the exposed continental shelf. Dogfish Bank was exposed between at least 14,330 and 12,860 ^{14}C yr BP (17,370–14,570 cal yr BP). Total PARs suggest low plant density and/or pollen production on the exposed shelf. Late-glacial plant communities are similar to modern coastal tundra in southwestern Alaska. The earliest communities were dominated by Cyperaceae but also contained a diverse array of herb and dwarf shrubs. The fossil assemblages represent both true physiognomic tundra with an absence of trees and floristic tundra (*sensu* Richard 1994). The abundance of Cyperaceae, *Salix*, *Equisetum*, ferns, and other species of wet habitats such as *Ranunculus* indicates warm, moist habitats, whereas *Empetrum nigrum*, *Arctostaphylos uva-ursi*, *Artemisia*, and *Polemonium* suggest that cold, drier habitats may have also been available. Heusser (1989) argues that the richness of the flora at this time, when adjacent areas were still glaciated, suggests the presence of nearby refugia.

After 13,000 ^{14}C yr BP (15,600 cal yr BP), tundra communities dominated by Cyperaceae, *Empetrum nigrum*, and *Salix* were succeeded by *Pinus contorta* woodlands with abundant ferns. It is likely that colder conditions favoured *P. contorta* over *Alnus crispa*, but other contributing factors for the earlier expansion of *P. contorta* may include more efficient dispersal, closer seed sources, different migration paths, interspecific competition for light, and the possible presence of *P. contorta* and absence of *A. crispa* in nearby refugia. *Alnus crispa* expanded before *Picea* and *Tsuga heterophylla*, likely playing an important facilitative role in conifer establishment. Greater shade tolerance by

Picea and orbitally-induced warming account for the succession to *Picea*-dominated forests and the decline of *Pinus*.

Pollen analysis of late-glacial sediments from the QCI exhibits many of the same problems associated with arctic paleoecology (Gajewski et al. 1995), including low density of plants on the landscape, low local pollen production, under-representation of insect-pollinated plants (e.g., *Polygonum viviparum* and *Valeriana capitata*), and long-distance transport of pollen. Since important herb pollen, including Cyperaceae and Poaceae, can only be identified to the family level and many taxa have wide ecological and environmental tolerances and distributions, the paleoenvironmental inferences that can be drawn are limited.

Like plant macrofossils, conifer stomata offer confirmation of local presence (Hansen 1995; Birks and Birks 2000). Unlike previous pollen–stomata studies (e.g., Ammann and Wick 1993; Clayden et al. 1997; Gervais and MacDonald 2001), there is strong positive correlation between *Pinus* stomata concentration and *Pinus* PARs as well as *Pinus* pollen percentages in West Side Pond sediments. In the case of *Pinus*, stomata appear to reflect not only local presence but also abundance; however, the absence of *Picea* and *Tsuga heterophylla* stomata in sediments that reportedly contain needles requires further attention. Stomata record the local presence of *Pinus* by 13,000 ^{14}C yr BP (15,600 cal yr BP), earlier than at any other site in the QCI region. This early presence may reflect the nearby presence of refugia on the southern QCI and/or the adjacent continental shelf. Conditions suitable for plant growth were available on the QCI by at least 15,000 ^{14}C yr BP (Warner et al. 1982; Mathewes et al. 1985) when the adjacent mainland coast remained glaciated (Clague 1981). Late-glacial sediments from Dogfish Bank and West Side Pond contain fossil pollen of three taxa not known to occur on the QCI today i.e., *Valeriana capitata*, *Typha latifolia*, and *Polemonium caeruleum* type. Conclusive proof in the form of continuous stratigraphic sequences spanning the last glaciation is required to confirm the existence of continuous late Pleistocene glacial refugia in the QCI region.

CHAPTER 6

SYNTHESIS

Late Quaternary Vegetation Dynamics

Sea-cliff exposures at Cape Ball on the northeastern Queen Charlotte Islands (QCI) provide the earliest radiocarbon-dated record of vegetation following the last glacial maximum on the British Columbia coast. AMS radiocarbon ages, combined with pollen and plant macrofossil analyses, suggest that terrestrial vegetation was established there by 14,700 ± 700 ^{14}C yr BP (Mathewes et al. 1985). The Cape Ball area supported terrestrial and wetland plant communities composed primarily of Poaceae, Cyperaceae, and various other herbs including *Rumex*, *Plantago macrocarpa*, *Polemonium*, and *Juncus* (see Appendix for common names of plants) as well as various mosses (Warner et al. 1982; Warner 1984). Mineral-rich sediments with low pollen concentrations suggest that areas of open, poorly vegetated soil were common. A mosaic of different habitats and plant communities characterized the area, and the richness of the flora at this time, when adjacent mainland areas remained glaciated, suggests the presence of nearby refugia. Low relative sea levels in the QCI region allowed plant communities to establish on the subaerially exposed continental shelf (Barrie et al. 1993). Cyperaceae likely formed the dominant plant cover on Dogfish Bank (Fig. 6.1), approximately 40 km west of Cape Ball, between at least 14,100 and 12,900 ^{14}C yr BP, indicating high effective moisture. Pollen and plant macrofossils indicate that Poaceae, *Salix*, *Empetrum nigrum*, and *Equisetum* were also present in the area and locally abundant (Chapter 5).

Mesic herb-dominated tundra was present as early as 13,750 ^{14}C yr BP near West Side Pond (Fig. 6.1) on Moresby Island, southwestern QCI (Chapter 5). Poaceae, *Artemisia*, *Salix*, *Empetrum nigrum*, and especially Cyperaceae characterized the lowland

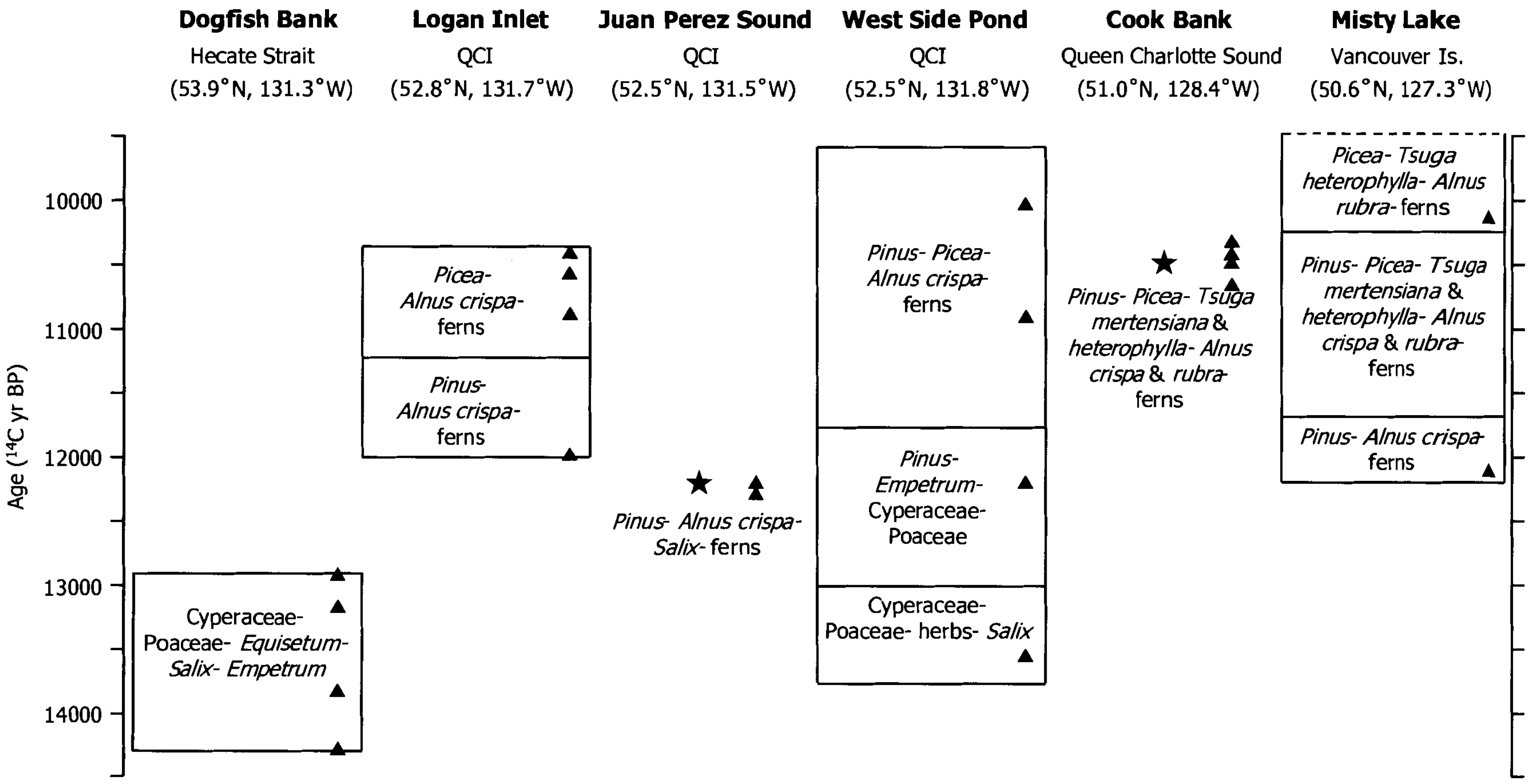

Fig. 6.1. Generalized vegetation histories for 14,500 to 9500 ^{14}C yr BP from Chapters 2 to 5, including terrestrial deposits with *in situ* conifers from the continental shelf (★). Vegetation assemblages are indicated by major species. Radiocarbon dates (▲) are also shown.

environment. A variety of other herbs and shrubs including *Lupinus*, *Ligusticum calderi*, *Epilobium*, *Polemonium*, *Saxifraga oppositifolia*, and *Arctostaphylos uva-ursi* were also present based on the pollen record. Cyperaceae-dominated tundra gave way to more productive and more diverse herb-shrub tundra with various pteridophytes after 13,250 ^{14}C yr BP, suggesting increased summer warmth (Chapin et al. 1995). *Empetrum nigrum*, in particular, increased in abundance at that time. The continued abundance of Cyperaceae pollen and the increase in pteridophyte spores indicate that moist habitats remained widespread.

Tree pollen, particularly *Pinus*, is recorded at most of these early sites. *Pinus* commonly accounts for up to 5% of the pollen sum. The abundance of tree pollen is sufficiently low, however, that treeless tundra is the most appropriate interpretation for the vegetation cover, at least before 13,000 ^{14}C yr BP. High pollen frequencies of Cyperaceae, Poaceae, *Salix*, *Empetrum*, and various herbs including Apiaceae and *Polemonium* indicate similarity to modern coastal tundra in the Gulf of Alaska region, from Kodiak Island to the Aleutian Islands (Heusser 1983a, 1985, 1990). In general, the vegetation is indicative of cool, moist, and probably windy conditions that were locally controlled by topography, soils, and disturbance. Modern coastal tundra can have high plant cover values (Bliss et al. 1981), but late-glacial pollen accumulation rates (PARs), particularly on the exposed continental shelf, commonly do not exceed 100 grains cm^{-2} yr^{-1}, which suggests discontinuous plant cover and/or low pollen production (Chapter 5).

Paleoclimate simulations suggest cold, relatively dry late-glacial climate, particularly in winter (Bartlein et al. 1998). The continental ice sheet would have displaced the jet-stream to the south, causing cooling in mid-latitudes and an intensification of cold dry easterly winds (Thompson et al. 1993; Bartlein et al. 1998). Heusser et al. (1980, 1985) used pollen-climate transfer functions to predict that conditions between 16,000 and 13,000 ^{14}C yr BP were colder and drier in coastal Washington than today. Summer temperatures were about 11°C and annual precipitation about 1500 mm, compared to 14°C and 1800 mm for today. Paleoclimate simulations suggest that as the continental ice sheet receded and the associated glacial anticyclone weakened, moist westerly winds would have become more important and the summer Pacific high pressure system would have strengthened (Thompson et al. 1993; Bartlein et al. 1998).

Fossil *Pinus* stomata from West Side Pond suggest that *Pinus contorta* grew locally in the southern QCI as early as 13,040 ± 305 ^{14}C yr BP, when *P. contorta* type accounts for less than 10% of the pollen sum and *Pinus* PARs are about 20 grains cm^{-2} yr^{-1} (Chapter 5). This is the earliest reported presence of *P. contorta* in the QCI region. It is important to note that the *Pinus* stomata are not directly radiocarbon-dated; rather, the age is based on linear interpolation from a basal date of 13,550 ± 480 ^{14}C yr BP. A rapid expansion of coniferous forest began by 12,500 ^{14}C yr BP. Abrupt increases in *P. contorta* pollen percentages and accumulation rates, and most notably a rooted *Pinus* stump dated at 12,240 ± 50 ^{14}C yr BP in Juan Perez Sound (Fedje and Josenhans 2000) with associated forest litter, document the rapid formation of open pine communities. Its local presence is demonstrated by needles and their stomata, cones, and other *P. contorta* macrofossils (Lacourse et al. 2003; Chapter 3). *Pinus contorta* was the first tree species to colonize the Pacific coast. Free of competing tall vegetation, *P. contorta* would have expanded early and quickly due to efficient seed dispersal, rapid growth and maturation, and wide edaphic tolerance, as well as a possible source of *P. contorta* in nearby glacial refugia.

Paleoclimate simulations suggest that about 12,000 ^{14}C yr BP, increased summer solar insolation and deeper penetration of storm systems from the North Pacific Ocean likely resulted in a warmer and wetter summer climate (Berger 1978; Bartlein et al. 1998). In the early Holocene, increased seasonality due to changes in the seasonal cycle of insolation and the northward shift of the jet stream due to the decreasing size of the continental ice sheet resulted in progressively warmer and drier summers and colder winters (Berger 1978; Whitlock and Bartlein 1997; Bartlein et al. 1998).

Alnus crispa populations expanded before conifers except *Pinus contorta*, and likely facilitated the transition from *Pinus contorta* woodland to *Picea*-dominated forests. The succession to *Picea* forests occurred on a regional scale and appears to have been a time-transgressive event, with more southerly sites recording the transition earlier. The transition is most clearly recorded in submerged lake sediments from the continental shelf in Logan Inlet (Fig. 6.1), occurring at about 11,200 ^{14}C yr BP (Lacourse and Mathewes *in press*; Chapter 2). Greater shade tolerance of *Picea* and orbitally induced warming account for the succession to *Picea*-dominated forests and the decline of *Pinus*. *Picea sitchensis* and *Tsuga mertensiana* may have been present by 12,000 ^{14}C yr BP, probably as scattered trees (Warner 1984; Lacourse et al. 2003; Chapter 3). *Alnus crispa* and various ferns were important components of the understory and edge communities of these early forests. In the southern QCI near West Side Pond, pollen assemblages imply open *P. contorta* woodland with abundant *A. crispa*, *Empetrum nigrum*, and pteridophytes between about 12,500 and 10,000 ^{14}C yr BP (Chapter 5). Based on the presence of *Picea* needles in West Side Pond sediments (Fedje 1993), *Picea* was likely present after 11,200 ^{14}C yr BP. The expansion of *Tsuga heterophylla* was delayed until after 10,500 ^{14}C yr BP. Rising sea levels began to flood the lower elevations of the continental shelf around the same time, submerging late-glacial landscapes and vegetation (Josenhans et al. 1997; Fedje and Josenhans 2000; Lacourse et al. 2003; Chapter 3). The vegetation history after this time is recorded in lakes, fens, and bogs above the limit of marine inundation.

On northern Vancouver Island, Misty Lake sediments provide a regional record (*sensu* Jacobson and Bradshaw 1981) of postglacial dynamics of forest vegetation for coastal British Columbia, including development of coastal temperate rainforests (Lacourse *in press*; Chapter 4). Pollen analysis indicates that between at least 12,200 and 11,700 ^{14}C yr BP, open woodlands were dominated by *Pinus contorta,* with *Alnus crispa*, and various ferns (Fig. 6.1). As *P. contorta* decreased in abundance, *Alnus rubra* and shade-tolerant conifers (i.e., *Picea sitchensis* and *Tsuga mertensiana*) increased in abundance. On Cook Bank, immediately north of Vancouver Island, *in situ* woody plant remains and abundant fossil pollen suggest that mixed coniferous forests dominated by *P. contorta* with *Alnus* spp. and ferns occupied the shelf 10,500 ^{14}C yr BP (Lacourse et al. 2003; Chapter 3). Fossil pollen of *Abronia latifolia*, a creeping perennial typical of coastal beaches and sand dunes but infrequent on Vancouver Island beaches today (Douglas et al. 1989), is a strong indicator of sandy beach habitat and indicates that beach vegetation grew along the ancient shoreline. Orbitally induced warming around 10,000 ^{14}C yr BP allowed the northward extension of *Pseudotsuga menziesii*, although *Picea*, *Tsuga heterophylla*, and *A. rubra* dominated early Holocene forests on northern Vancouver Island (Lacourse *in press*; Chapter 4). By 7500 ^{14}C yr BP, shade-tolerant *T. heterophylla* was the dominant forest tree. Cupressaceae pollen was present by 7500 ^{14}C yr BP and reached its maximum after 3500 ^{14}C yr BP, when a cooler and wetter regional climate facilitated the development of temperate coniferous rainforest with abundant *T. heterophylla*, *T. plicata*, *P. sitchensis*, and *Abies*.

The Holocene development of forests on northern Vancouver Island is similar to the progression of forest types on the QCI. Pollen and plant macrofossils indicate the presence of *Picea sitchensis* and *Tsuga heterophylla* forests with abundant *Alnus* and ferns on the QCI during the early Holocene (Warner 1984; Fedje 1993; Pellatt and Mathewes 1994, 1997) and suggest that regional climatic changes drove macro-scale vegetation dynamics. *Picea* and *T. heterophylla* dominated forests of the northeastern QCI until 5500 ^{14}C yr BP when decreasing temperature and increasing precipitation promoted the development of forest-bog complexes, particularly in poorly drained lowlands, and the expansion of Cupressaceae, *Pinus contorta* and Ericaceae shrubs (Quickfall 1987). Vegetation assemblages similar to modern *Tsuga heterophylla* rainforest were established after 5000 ^{14}C yr BP.

Late Quaternary vegetation dynamics in the QCI region and on northern Vancouver Island are similar to those reconstructed at other paleoecological sites along the Pacific coast, suggesting regional-scale climate change as the ultimate cause of vegetation change. Climate is likely the driving mechanism for species migration and can have direct effects on successional trends (Lacourse *in press*; Chapter 4). Given that Holocene climate change was minor compared to changes that occurred at the end of the last glaciation, other factors such as competition and disturbance may have been more important in determining species abundances and vegetation dynamics in Holocene forests. The importance of life history traits in directing postglacial vegetation change requires clarification. Life history traits associated with dispersal, growth rate, and longevity may have been most important in determining initial vegetation composition and overall successional response times, whereas shade tolerance, sapling survival, size, and resource competition may have been more important in subsequent stages of vegetation change.

Concluding Remarks

The principal objective of this research was to reconstruct late Quaternary vegetation dynamics in the QCI region including the adjacent continental shelf, with emphasis on the late Pleistocene period i.e., between 15,000 and 10,000 ^{14}C yr BP. In combination with geological studies and geo-spatial modelling (e.g., Hetherington et al. 2003, 2004), pollen and plant macrofossil analyses of various types of sedimentary deposits and from different paleoenvironmental settings have permitted detailed paleoecological reconstruction for the late Pleistocene period. Lake sediments from the QCI and northern Vancouver Island, and the late Pleistocene portions of sediment cores from the adjacent continental shelf were analysed, revealing substantial changes in vegetation. The palynological research presented in this thesis has clarified late Quaternary vegetation dynamics for this region, particularly for the late Pleistocene period, since few previous studies predate 10,000 ^{14}C yr BP. The Misty Lake pollen record (Lacourse *in press*; Chapter 4) is the first well-dated postglacial record obtained from a lake on northern Vancouver Island. The addition of these sites to the existing paleoecological record for the north Pacific coast will facilitate future research on postglacial migration patterns of the major tree species such as *Pinus contorta* and *Picea sitchensis*.

Attention was paid to documenting paleobotanical evidence of the Younger Dryas cooling event that occurred between 11,000 and 10,000 ^{14}C yr BP. Pollen analysis of lake sediment from northern Vancouver Island identified relative and absolute increases in *T. mertensiana*, *Pinus contorta*, and *Alnus crispa* between 10,600 and 10,400 ^{14}C yr BP, which may reflect a cool and moist climate during the Younger Dryas chronozone. The West Side Pond record from the southern QCI also spans this critical time period but provides little evidence of the Younger Dryas cooling event (Chapter 5). Increases in *T. mertensiana*, *Polyopodium*, and *Ligusticum calderi* PARs at this time may reflect increases in moisture. However, increases in total PARs contradict notions of cooler temperatures. Other paleoecological records from the north Pacific coast appear to document decreases in temperature during this critical interval (e.g., Engstrom et al. 1990; Mathewes 1993; Mathewes et al. 1993; Hetherington and Reid 2003). Pellatt et al. (2002) conclude that vegetation communities in southwestern British Columbia during most of the Younger Dryas chronozone indicate an increasingly warm climate with a cool interval between 10,400 and 10,000 ^{14}C yr BP. It remains unclear whether there was in fact a Younger Dryas cooling event in coastal British Columbia. Most relevant paleoecological records from the region including those presented in this thesis (Chapter 4 and 5) are low in temporal resolution. Direct comparisons between high-resolution pollen records and independent climate data, as opposed to pollen-based paleoclimate reconstructions, are required to determine the degree of correlation between vegetation dynamics on the north Pacific coast and macroscale climate change during the late Quaternary.

Accurate reconstructions of Pacific coast environments are important for evaluating the ecological context for human populations entering the Americas via a Pacific coastal route. Paleobotanical evidence of plant resources that would have been available to humans migrating along the coast in the late Pleistocene period was documented (Lacourse and Mathewes *in press*; Chapter 2). Although animal products, particularly intertidal fauna, may have dominated the total food intake of early migrants (Rick et al. 2001; Hetherington and Reid 2003), plant products would have provided nutritional diversity and dietary support when yields from fishing and hunting were low. Food plants would have been predictable seasonal sources of food as well as fuel, manufacture, and medicine, requiring minimal searching and little effort and technology to gather. The QCI region was deglaciated and available for human migration and habitation by about 14,000 ^{14}C yr BP (Barrie et al. 1993; Josenhans et al. 1997; Mandryk et al. 2001; Chapter 5). However, archaeological evidence to support the coastal migration hypothesis is inconclusive since known archaeological sites along the north Pacific coast are no older than 10,000 ^{14}C yr BP (Dixon et al. 1997; Josenhans et al. 1997; Dixon 1999; Cannon 2000). Recent paleogeographic reconstructions indicate that late Pleistocene coastlines of potential archaeological significance occur along the west coast of the QCI (Hetherington et al. 2003).

Future research will focus on assessing whether the north Pacific coast was a viable environment for humans at the end of the last glaciation. Paleoecological data including pollen accumulation rates from this thesis and marine biomass estimates from Hetherington et al. (2003) will be used to estimate primary productivity, prey biomass, and total available calories along the coast and determine if values exceed levels capable of supporting human populations (*sensu* Hassan 1981; Mandryk 1992).

Pollen analysis of late-glacial sediments from the QCI region exhibits many of the same problems associated with arctic paleoecology (Gajewski 1995; Gajewski et al. 1995), including the low density of plants on the landscape, low local pollen production, under-representation of insect-pollinated plants, and long-distance transported pollen. Since important herb pollen i.e., Cyperaceae and Poaceae can only be identified to the family level and many taxa have wide ecological and environmental tolerances and distributions, the paleoenvironmental inferences that can be drawn are limited. This research demonstrates the importance of examining a variety of biological fossils for paleoenvironmental reconstruction. Pollen analysis alone may be insufficient and should be accompanied by plant macrofossil analysis and fossil wood identification where possible, because both provide valuable and complementary paleoecological information (Birks and Birks 2000).

Like plant macrofossils, conifer stomata offer confirmation of local presence and, in some instances, greater taxonomic detail compared to pollen (Hansen 1995; Birks and Birks 2000). Future research will include conifer stomata analysis of Misty Lake sediments from northern Vancouver Island, specifically to clarify the roles of *Thuja plicata*, *Chamaecyparis nootkatensis*, and *Juniperus* in postglacial forest development, since their pollen is largely indistinguishable. At West Side Pond in the southern QCI, conifer stomata appear to reflect not only local presence but also abundance, at least in the case of *Pinus contorta* (Chapter 5). Stomata record local *Pinus* presence by 13,000 ^{14}C yr BP, earlier than any other site in the QCI region. This early presence may reflect the nearby presence of glacial refugia on the QCI and/or the adjacent continental shelf.

It has been suggested that some ice-free areas between the Aleutian Islands in Alaska and the northwestern United States served as biotic refugia during the last glaciation (Heusser 1989). In fact, there is radiocarbon-dated evidence of arctic and red foxes (*Alopex lagopus* and *Vulpes vulpes*) having survived the last glacial maximum in isolated refugia in southeastern Alaska (Heaton and Grady 2003). Conditions suitable for plant growth were available on the QCI by at least 15,000 ^{14}C yr BP (Warner et al. 1982; Mathewes et al. 1985) when the adjacent mainland coast remained glaciated (Clague 1981). These refugia, perhaps with small colonies of trees such as *Pinus contorta*, would have been major centers of dispersal, which would have preceded dispersal from refugia in interior Alaska or Yukon and in Washington. Conclusive proof in the form of continuous stratigraphic sequences spanning the last glaciation is still required to confirm the existence of continuous late Pleistocene glacial refugia in the QCI region.

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APPENDIX

Table A.1. Latin and common names of plant taxa.[a]

Latin Name	*Common Name*
Abies amabilis	Pacific silver fir
Abies grandis	grand fir
Abies lasiocarpa	subalpine fir
Abronia latifolia	yellow sand-verbena
Adiantum aleuticum	northern maidenhair fern
Adiantum pedatum	northern maidenhair fern
Alnus crispa	green alder
Alnus rubra	red alder
Angelica	angelica
Antitrichia curtipendula	hanging moss
Apiaceae	parsley / carrot family
Arceuthobium	dwarf mistletoe
Arctostaphylos uva-ursi	common bearberry / kinnikinnick
Artemisia	sage / wormwood
Asteraceae	composite / daisy family
Athyrium filix-femina	lady fern
Betula	birch
Botrychium lunaria	common moonwort
Botrychium multifidum	leathery grape fern
Botrychium simplex	least moonwort
Brasenia schreberi	watershield
Caltha	marsh marigold
Caryophyllaceae	pink / chickweed family

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[a] Botanical nomenclature follows Douglas et al. (1989) and Calder and Taylor (1968).

Latin Name	***Common Name***
Chamaecyparis nootkatensis	yellow cedar
Claytonia sibirica	Siberian miner's-lettuce
Conioselinum pacificum	Pacific hemlock parsley
Coptis	goldthread
Cornus canadensis	bunchberry
Cornus unalaschkensis	bunchberry
Cryptogramma acrostichoides	parsley fern
Cryptogramma crispa	parsley fern
Cupressaceae	cedar family
Cyperaceae	sedge family
Dryopteris expansa	spiny wood fern
Empetrum nigrum	crowberry
Epilobium angustifolium	fireweed
Equisetum	horsetail
Ericaceae	heath family
Eucalyptus	eucalyptus
Fauria	deer cabbage
Franseria	burweed / ragweed
Fritillaria camschatcensis	rice-root
Gaultheria shallon	salal
Gentiana douglasiana	swamp gentian
Glehnia littoralis	beach carrot
Heracleum lanatum	cow parsnip
Hippuris vulgaris	common mare's tail
Huperzia selago (=*Lycopodium selago*)	fir clubmoss
Isoëtes	quillwort
Juncus	rush
Koenigia islandica	Iceland koenigia
Lamiaceae	mint family
Ligusticum calderi	Calder's lovage
Ligusticum canbyi	Canby's lovage

Latin Name	***Common Name***
Liliaceae	lily family
Lupinus	lupine
Lycopodium annotinum	stiff clubmoss
Lycopodium clavatum	running clubmoss
Lycopodium selago (=*Huperzia selago*)	fir clubmoss
Lysichiton americanum	skunk cabbage
Menyanthes	buckbean
Myrica gale	sweet gale
Myriophyllum spicatum	water-milfoil
Nuphar luteum	yellow pond-lily
Nymphaea odorata	fragrant water-lily
Onagraceae	evening primose family
Oxyria	sorrel
Picea glauca	white spruce
Picea sitchensis	sitka spruce
Pinus contorta var. *contorta*	shore pine
Pinus contorta var. *latifolia*	lodgepole pine
Plantago macrocarpa	Alaska plantain
Poaceae	grass family
Polemonium caeruleum	tall Jacob's-ladder
Polemonium pulcherrimum	showy Jacob's-ladder
Polygonum viviparum	alpine bistort
Polypodiaceae	common fern family
Polypodium	polypody fern
Populus balsamifera	balsam poplar
Potamogeton filiformis	slender-leaved pondweed
Potentilla	cinquefoil
Pseudotsuga menziesii	Douglas-fir
Pteridium aquilinum	bracken fern
Quercus garryana	Garry oak
Ranunculus	buttercup

Latin Name	***Common Name***
Rhamnus purshiana	cascara
Rosaceae	rose family
Rubus spectabilis	salmonberry
Rumex	dock
Sagina maxima	coastal pearlwort
Salix reticulata	net-veined willow
Salix stolonifera	stoloniferous willow
Sanguisorba canadensis	Canada burnet
Sarcobatus vermiculatus	greasewood
Saxifraga oppositifolia	purple saxifrage
Shepherdia canadensis	soapberry
Sparganium angustifolium	narrow-leaved bur-reed
Sphagnum	sphagnum moss
Spiraea douglasii	hardhack
Taxus brevifolia	western yew
Thalictrum	meadow-rue
Thuja plicata	western redcedar
Tsuga heterophylla	western hemlock
Tsuga mertensiana	mountain hemlock
Typha latifolia	broad-leaved cattail
Vaccinium alaskaense	Alaskan blueberry
Valeriana capitata	capitate valerian
Valeriana sitchensis	sitka valerian
Viola	violet