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The Northern Inland Temperate Rainforest of British Columbia: Old Forests With a Young History?

Abstract

The inland temperate rainforest (ITR) in east-central British Columbia is marked by superlative examples of old-growth cedar-hemlock forest. How long has this old-growth forest structure been a major component of this landscape? What is the biological and conservation significance of the history of this forest type? Here we present paleoecological evidence from a study in the Robson Valley of the Upper Fraser River. Sediment cores from Gerry Lake and Redmountain Lake show that western hemlock and western redcedar increased in abundance only within the last 2000 years. Thus, the old-growth forests of the northern ITR may have been present for only a few generations of trees. It is even possible, based on our preliminary evidence, that the oldest western redcedar in these stands may be the first colonizing individuals at these sites. Further paleoecological studies, including a combination of stand-age structure and pollen analysis from small lakes and forest hollows, are needed in order to understand the historical significance of these stands. A recent establishment of the ITR has implications for understanding the assembly of the modern diverse biota of the region as well as how the biota will respond to future climate change.

Introduction

The occurrence of disjunct populations of mesic-adapted biota in the Columbia Mountains of British Columbia, ranging from 160 to 320 km from their main coastal distributions, is a pattern that has long been of interest to biogeographers (Daubenmire 1952, 1975; Detling 1968). This region of mesic disjunctions typically is defined by the range of *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western redcedar). Especially towards their northern limit, these forests display ecologically significant old-growth structure and a highly diverse flora of epiphytic macrolichens and bryophytes, supporting their characterization as an "inland temperate rainforest" (Newmaster et al. 2003, Goward and Spribille 2005). Only recently have rigorous approaches been applied to unravel the history of these disjunctions (Brunsfeld et al. 2001, Gavin et al. 2006). Pollen records from the central and southern end of interior *Thuja-Tsuga* forests show that these stands have been present for less than 4000 years (Mehringer 1996, Rosenberg et al. 2003, Chase et al. 2008). However, no pollen records exist from the northern limit of the ITR, and thus their antiquity on the landscape is poorly understood (Sanborn et al. 2006).

The establishment of the disjunct biota that comprises the ITR is an intriguing problem when considering that the region was glaciated until ca. 12,000 years ago. Species that comprise the northern ITR must have migrated there from either ice-free refugia south of the ice-sheet in Idaho, or dispersed across dry rainshadow climates of eastern Oregon, Washington, or British Columbia. How important were these historical events in the formation of the current ITR biota? For example, if the mesic-adapted species had to disperse from the coastal region over a barrier where warm and dry growing conditions would not support these species, then the rare probability of these dispersal events may have delayed the establishment of the ITR biota for millennia after suitable climatic conditions were present. Such a scenario would stand in contrast with a general view that vegetation is in equilibrium with climate (e.g., Shuman et al. 2004).

In this paper we present a summary of the pollen records from two lakes in the Robson Valley in order to assess the timing of *Thuja-Tsuga*

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establishment. The first lake was chosen for its potential for climate reconstruction using carbonate-rich sediments, and also because it is ca. 2 km from *Thuja-Tsuga* forest. The second lake is located in subalpine forest just above the *Thuja-Tsuga* forest. This site was selected to serve the dual purpose of providing a paleoclimate reconstruction from fossil midges (requiring the subalpine location) as well as a vegetation reconstruction from regionally dispersed pollen. The midge-based climate reconstruction proved to be unreliable, probably due to the unusual geomorphic (inorganic sediments) and microclimatic (persistent snow banks) setting, as described in Chase et al. (2008). Here, we focus on the pollen records and additional evidence of past climate inferred from the sediment stratigraphy.

Methods

Study Sites and Field Methods

Gerry Lake (informal name; 53°38′50″N, 121°30′20″W) is a 5.1 ha lake located 893 m above sea level near the head of Slim Creek (Figure 1). The bedrock in the watershed is mainly Upper Proterozoic to Cambrian quartzite and quartz arenite, with sandy dolomite and limestone further up-valley (Massey et al. 1995). The vegetation is a dense forest of *Abies lasiocarpa* (subalpine fir) and *Picea glauca* x *engelmannii* (hybrid white spruce), with minor amounts of *Pseudotsuga menziesii* (Douglas-fir) in the region. The lake is fringed by a wide (10-20 m) sedge fen and a submerged bench of marl sediments. The maximum water depth of Gerry Lake is 14 m.

Redmountain Lake (informal name; 53°55′20″N, 121°17′40″W) is a 6.3 ha cirque lake located at 1595 m above sea level at the head of Redmountain Creek near the town site of Penny (Figure 1). The bedrock in the watershed is Silurian dolomite and limestone, calcareous shale, greenschist, and quartzite (Massey et al. 1995). The vegetation is a lush diverse meadow parkland (e.g., *Caltha*, *Veratrum*, *Valerian*, *Ranunculus*, *Erythronium*) and tree clumps of *Abies lasiocarpa*. The maximum water depth of Redmountain Lake is 2.8 m.

Field and Laboratory Methods

We accessed Gerry Lake by road and Redmountain Lake by helicopter. At each lake, two parallel sediment cores were obtained using a modified Livingstone corer operated by hand from a platform anchored over the deepest portion of each lake. The soft sediments in the upper-most 60 cm were recovered using a clear plastic tube fitted with a piston, and then subsampled in the field at 1-cm intervals.

Sediment cores were split lengthwise and photographed. Loss-on-ignition at 550 °C (LOI), a measure of sediment organic content, was determined by combusting dried 1 cm^3 subsamples. The carbonate content of Gerry Lake sediment was estimated by an additional combustion of the LOI samples at 950 °C and scaling the percent mass loss (from CO_2) by 2.27 (Heiri et al. 2001). Radiocarbon dates were obtained on terrestrial macrofossils at key depths in each core (n = 12 at Gerry; n = 4 at Redmountain). Dates were determined at the Lawrence Livermore Center for Accelerator Mass Spectrometry (Berkeley, CA). All ages were calibrated to the calendar age scale using CALIB 5.0 (Stuiver and Reimer 1993; Reimer et al. 2004). Age-depth relationships were interpolated between age determinations using a monotonic spline, though the Gerry Lake chronology required special consideration of hiatuses and redeposited sediment.

Pollen identification was made from 69 and 62 depths in the Gerry and Redmountain cores, respectively. Pollen samples were processed from 1 cm^3 subsamples following a standard protocol (Faegri and Iverson 1992). The sediment at Redmountain Lake required removal of fine particulates by sieving with a 7 µm Nitex screen (Cwynar et al. 1979). At least 350 terrestrial pollen grains were identified in each level. Pollen concentration and accumulation rates were calculated by spiking each sample with tablets containing a known quantity of exotic *Lycopodium* spores (Faegri and Iverson 1992).

Results

Chronology and Sediment Characteristics

At Gerry Lake, 830 cm of sediment was recovered before reaching coarse sands and gravel (Figure 2). The lower 150 cm contained inorganic silts and clays alternating with organic sediment and segments of fibrous marl containing *Chara*. From 680 to 400 cm the sediment contained angled beds 30°-60° from horizontal, with carbonates comprising the majority (ca. 80%) of the sediment. This

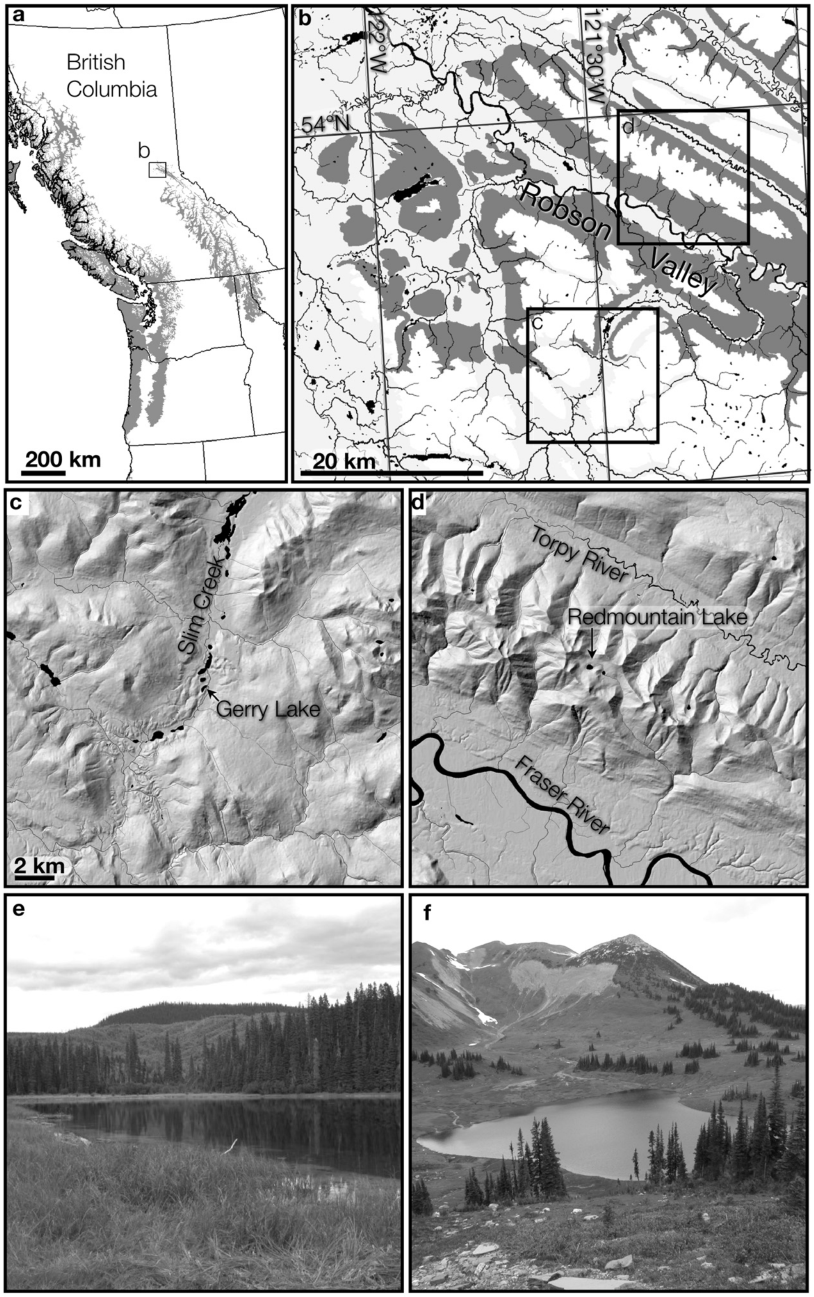

Figure 1. (a) The distribution of western hemlock (Gavin and Hu 2006). Square indicates enlarged map in (b). (b) The distribution of interior cedar hemlock zone in the Robson Valley (gray) as mapped by the biogeoclimatic ecosystem classification (http://www.for.gov.bc.ca/hre/becweb/resources/maps/index.html). Squares indicate enlarged maps in (c) and (d). (c) Shaded relief map showing the location of Gerry Lake in the Slim Creek drainage. (d) Shaded relief map showing the location of Redmountain Lake in a subalpine basin between the Fraser and Torpy Rivers. (d) Photograph of Gerry Lake, showing a marginal fen. (e) Photograph of Redmountain Lake, showing subalpine meadows and shale cliffs (photos by Karlyn Westover).

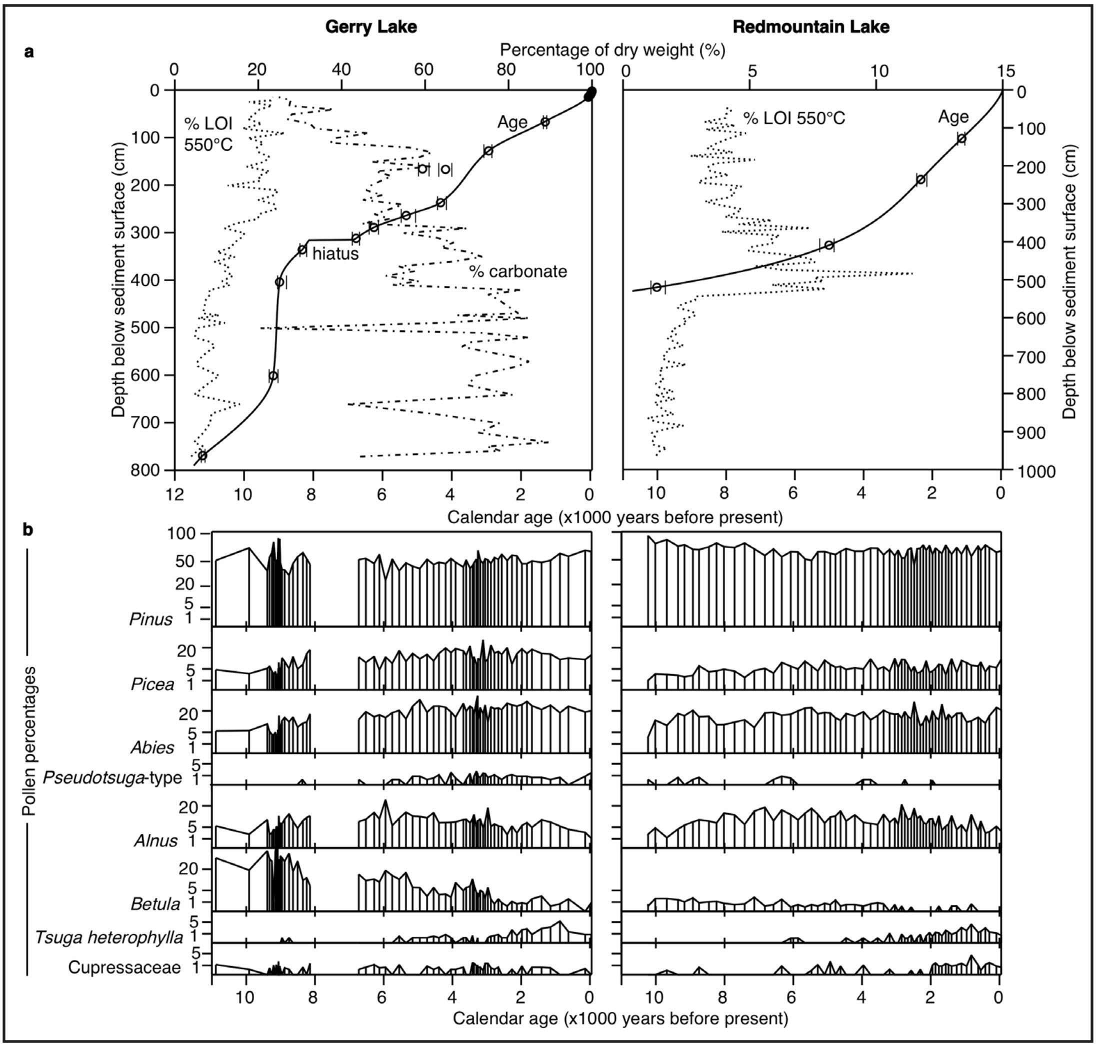

Figure 2. (a) The interpolated relationship between depth in the sediment and sediment age (solid line), the percent organic content estimated by loss-on-ignition at 550°C and, at Gerry Lake, the percent carbonate content (dashed lines). Circles show the median calibrated radiocarbon age and vertical lines demark the 2σ range of the calibrated age. The upper-most sediment at Gerry Lake was dated using ^{210}Pb concentrations. (b) Eight common pollen types (percentages of total identified terrestrial pollen in each depth). Note that the y-axes are on a square-root-transformed scale in order to emphasize variability of low pollen percentages.

portion of the core, occurring at ca. 9000 calendar years before present (yr BP), has very fast sedimentation and may indicate the presence of a shallow marl bench at the core site. Above 400 cm, the sediment was dark brown, contained occasional detrital layers, and was marked by progressively increasing organic content (20%) and decreasing carbonate content (to < 40%). Radiocarbon dating revealed that one such detrital layer at 318 cm corresponds to a hiatus in sedimentation (8130 to 6830 yr BP). Above this hiatus, a sequence of four radiocarbon dates indicates 2440 years of a relatively constant sedimentation rate. However, the next two dates at 166 and 167 cm, in a zone of uniform dark brown sediment, were out of sequence. The older date was from the parallel core that was not sampled. Accepting the younger date would require a 20-fold change in sedimentation rate, but no change in lithology suggests this was the case. It is likely that these dates are from redeposited material during a low lake stand, and should be rejected (Table 1). Therefore, the results from this segment of the chronology (3500-3300 yr BP) may be contaminated with older material and should be interpreted with caution.

At Redmountain Lake, 966 cm of sediment was recovered before reaching impenetrable rock (Figure 2). Below 535 cm, the sediment was low in organic content (3%); no pollen was found at these depths. At 535 cm, organic matter rose sharply (organic content peaking at 11%) and at 520 cm a radiocarbon date indicated an age of ca. 10,020 yr BP. Sediment accumulated slowly after the increase in organic content, at an average deposition time of 4700 yr/m before 5000 yr BP. After 5000 yr BP, organic content decreased to less than 5% and the sedimentation rate steadily increased to an average deposition time of 1200 yr m^{-1}.

Pollen Record

The pollen records are dominated by *Pinus* (averaging 50% and 65% at Gerry and Redmountain, respectively). At both sites, the pollen of *Picea* (spruce), *Abies* (subalpine fir), and *Alnus* (alders) is fairly constant through the Holocene (averaging 15%, 6%, and 9%, respectively). Birch declines steadily from ca. 30% to ca. 2% over the Holocene at Gerry Lake, and from ca. 1% to intermittent occurrences by 3000 yr BP at Redmountain Lake. The first grains of *Tsuga* pollen appear around 6000 yr BP at both sites, but *Tsuga* pollen does not become consistently >1% until 2800 yr BP (2000 yr BP at Gerry Lake). At Gerry Lake, Cupressaceae (cedar-family) pollen is intermittent and rarely represented by more than 2 grains per sample. At Redmountain Lake, Cupressaceae is also intermittent throughout the record but increases abruptly to levels consistently >1% at ca. 2000 yr BP.

At Redmountain Lake the slowly varying sedimentation rate and more robust chronology supported the calculation of pollen accumulation rates (PAR; Figure 3). PAR revealed a general increase in *Picea* and *Abies* over the Holocene that was less distinct as pollen percentages. The abrupt increases in *Tsuga* and Cupressaceae are distinctly more synchronous in the PAR records

TABLE 1. AMS radiocarbon dates from sediment cores from Gerry Lake and Redmountain Lake, British Columbia.

Lake and depth below sediment surface (cm)	Laboratory number[a]	Radiocarbon age ± 1 S.D.	Calibrated 2σ age range (years before 1950 AD)[b]	Material dated
Gerry Lake				
66-68	125242	1385 ± 35	1260 - 1350	*Betula* seed; needle fragments
128	101690	2830 ± 80	2850 - 3070	Wood
166[c]	114120	4275 ± 80	4660 - 4960	1 *Picea* needle
167[cd]	114858	3795 ± 80	4000 - 4380	2 *Abies* needle fragments; 1 conifer seed wing
237	114121	3885 ± 70	4160 - 4420	1 *Abies* seed wing; 0.5 seed wing; 1 *Alnus* seed (no wings)
264	114859	4600 ± 100	5050 - 5470	2 *Picea* needle fragments
289	114860	5455 ± 90	6130 - 6390	2 *Picea* needles
312	114861	5940 ± 90	6670 - 6880	1 *Picea* needle
336	101691	7495 ± 90	8200 - 8390	*Abies* needle
404	114122	8050 ± 70	8780 - 9030	*Picea* needle fragments
601	114123	8200 ± 80	9030 - 9280	2 *Alnus* seeds; *Picea* needle fragments; 1 cone bract
769	101692	9755 ± 80	11130 - 11240	Wood
Redmountain Lake				
128	114126	1215 ± 70	1060 - 1260	*Abies* needle
236	101694	2315 ± 80	2160 - 2460	*Abies* needle
409	101695	4420 ± 80	4870 - 5280	Cone scale
520	114127	8885 ± 100	9780 - 10190	*Abies* needle

[a] Laboratory numbers from the Center for Accelerator Mass Spectrometry (CAMS), Lawrence Livermore National Laboratory.

[b] Minimum and maximum of 2σ age ranges only. Calibration follows Reimer et al. (2004).

[c] Date rejected (see text).

[d] Date from a parallel core, correlated by depth measurement only.

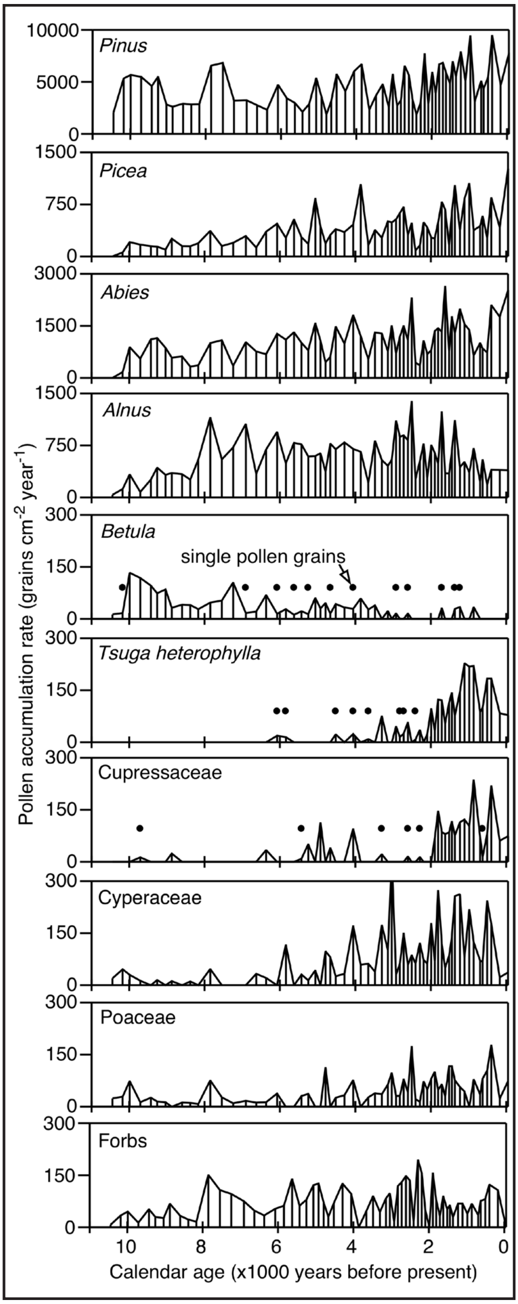

Figure 3. Accumulation rates of the common pollen types at Redmountain Lake. Instances of a taxon represented by a single pollen grain in any given sample are shown with symbols. The forbs category includes Apiaceae, Asteraceae, Fabaceae, *Polemonium*, Polygonaceae, Ranunculaceae, Scrophulariaceae, and Valerianaceae.

compared to pollen percentages. Specifically, at ca. 2000 yr BP there was a change from intermittent presence of pollen to values consistently greater than 100 grains cm^{-2} $year^{-1}$.

Discussion

Gerry Lake and Redmountain Lake contain significant amounts of regionally dispersed pollen and thus may record changes in regional forest composition in the Robson Valley. For example, both records are dominated by pine pollen, likely from *Pinus contorta*, which tends to disperse regionally. *Pinus* pollen is more abundant at Redmountain Lake, located in open subalpine meadows with patches of *Abies lasiocarpa* that produce heavy, poorly dispersed pollen. This setting contributes little local pollen and thus aids in the detection of other regionally dispersed pollen, most importantly, the pollen from *Tsuga heterophylla*. In fact, occasional *Tsuga* pollen grains before 4000 yr BP at both sites may be the result of long-distance transport from the Coast Range. Cwynar (1993) and Spooner et al. (1993) noted long-distance transport of *Tsuga* pollen in northwestern British Columbia and attributed it to the strength of the onshore movement of storms, but over much shorter distances than proposed for our sites. However, Minckley and Whitlock (2000) found occasional *Tsuga* pollen in surface sediments of small lakes in eastern Oregon, occurring up to 350 km from the nearest potential source trees. Therefore, occasional grains of *Tsuga* pollen cannot be interpreted as trees locally present. By 2000 yr BP, *Tsuga* pollen is consistently present at near-modern levels at both sites and PAR values increase abruptly at Redmountain Lake (Figure 3). This likely marks the establishment of *Tsuga* in Robson Valley at near-modern abundances.

Cupressaceae pollen, probably representing *Thuja plicata* and *Juniperus communis* in this region, is more difficult to identify due to few diagnostic features that separate it from algal cysts (Faegri and Iverson 1992). Cupressaceae pollen is also notorious for being sporadically present when few cedar-family taxa exist nearby (Gavin et al. 2005). Currently, *Thuja* is abundant in the Robson Valley. *Juniperus* was not seen in the area, but may have been present during warmer and drier periods. Therefore, the occasional presence of Cupressaceae during the middle Holocene may represent either *Thuja* or *Juniperus*. At Redmountain Lake, the abrupt increase in Cupressaceae at 2000 yr BP is strong evidence of the time when *Thuja* began to dominate the lower slopes of the Robson Valley. At Gerry Lake, Cupressaceae values remain <1% and appear unable to record the regional increase of *Thuja* on the landscape.

The fluctuating levels of organic content in the sediments at Redmountain Lake provide tentative information of the past climate. The inorganic sediment is the result of the highly erodible shale bedrock occurring upslope of the lake (Figure 1). Erosion yielding high sedimentation rates and low organic content of the sediment may have occurred during periods of high surface-water flow and/or low vegetation cover. Following glacial retreat, meltwater from the waning glacier within the watershed, combined with low vegetative cover, resulted in the 380 cm of inorganic basal sediment. The sharp increase in organic content occurred 15 cm below the lowest radiocarbon age (10,020 yr BP), likely reflecting increased temperature and vegetation cover, loss of the proximal glacier, and increased aquatic productivity. These changes at Redmountain Lake coincide with a period of inferred lower lake levels as the result of warmer and drier conditions at Gerry Lake. The slow sedimentation rate at Redmountain Lake continued until an increase in moisture during the middle Holocene increased the delivery of inorganic sediment to the lake. This increased inorganic sedimentation may be the result of increased persistence of snow, which lowered vegetation cover and increased erosion by nivation, or the direct effect of rainfall. Elevated effective moisture during the middle Holocene has been documented from pollen records throughout British Columbia (Hebda 1995; Walker and Pellatt 2003, 2008) and from alpine glacier advances at 4200 yr BP and several times thereafter (Menounos et al. 2008). The increase in sedimentation rate during the late Holocene provided us with a high-resolution record for examining vegetation change.

The initial increase in *Tsuga* pollen (ca. 2800 yr BP) occurred shortly after the increase in sedimentation rate (and by inference, moisture levels), as would be expected for this mesic-adapted species. However, the lagged increase in *Thuja* is perplexing, considering the similar ecological requirements of these species. Mehringer (1996) also noted that, in northern Idaho, the increase in *Thuja* occurred significantly after *Tsuga*. Perhaps the wet toe-slope microhabitat conditions preferred by *Thuja* were only present within the last 2000 years. Sanborn et al. (2006) also noted a period of low fire activity in the Robson Valley around 2000 yr BP, which may reflect increased moisture and a reduction of the extent of post-fire competitive environments. Alternatively, *Thuja* arrival may have lagged behind the onset of suitable conditions due to limited dispersal across large dispersal barriers. A study of molecular markers showed that *Thuja plicata* survived the glacial maximum in small populations in southern Oregon, requiring it to disperse >1200 km to the Robson Valley (O'Connell et al. 2008). Regardless of the reason, the establishment of this forest type within the last 2000 years is unusually recent for forests in the Pacific Northwest, most of which have experienced only minor changes in relative abundances through this period (Brubaker 1991, Whitlock 1992).

The relatively recent increase in *Thuja* is even more surprising when considering the great size, and possibly age, of the old-growth forests in this region. In the Robson Valley most *Thuja* trees have severe heart rot, precluding dendrochronological aging. Similarly sized *Thuja* (>200 cm diameter) from the coast have ages of 400 to 1000 years (Daniels et al. 2005). This raises the possibility that few generations of *Thuja* have existed in this region, and even the possibility that in some stands the oldest *Thuja* today are the first colonizing individuals. The general lack of large coarse woody debris in the understory of some *Thuja* stands in the Robson Valley (D.G. Gavin, personal observation) is consistent with few generations of trees preceding the current stand.

The issue of long-distance pollen dispersal increases the uncertainty of our estimate of the timing of the major increases of *Tsuga* and especially *Thuja*. Optimally, records from several sites are needed, including small ponds proximal to old *Thuja* stands. For example, the wet toe slope positions that support the largest, and presumably oldest, *Thuja* stands also contain small wet depressions that most likely contain records thousands of years in length of local forest composition. Using these "small hollow" sediment records (*sensu* Sugimura et al. 2008) may be a means of overcoming the difficulty of aging large trees with rotten centers. Small hollow sites receive a large proportion of their pollen from the local forest stand. Such a study would reveal the local ecological history and whether indeed these old forest stands have a young history on the landscape.

Two conservation implications emerge from these results. First, the high biodiversity in *Thuja*-associated canopy lichens in this region is even more remarkable when considering that the large *Thuja* may have been present for only 2000 years. This suggests that high local biodiversity may assemble rapidly from a regional pool. This is consistent with the recent finding that the region-wide pattern in lichen biodiversity closely follows environmental conditions, with the greatest diversity in the northern ITR (Goward and Spribille 2005). A rapidly assembled diverse ITR biota dependent on *Thuja*-dominated forests presents a challenge to the common insight from paleoecology that modern communities have assembled over a long history of individualistic responses to past climate change (Flessa and Jackson 2005). Unfortunately, until paleorecords can reveal a greater complement of the flora, long-term associations of taxonomic groups, such as lichens, will prevent a direct assessment of this hypothesis. Knowledge of when old *Thuja* stands first established is a necessary first step toward understanding the assembly of the modern biota.

Second, the establishment of these stands, probably a result of recent climatic fluctuations, would suggest that a less persistent snow pack in the future could result in drier toe slope soils and jeopardize *Thuja* regeneration. A similar influence of climate change on *Thuja* regeneration was recognized decades ago at the southern limit of interior *Thuja* in Idaho (Habeck 1978). In contrast, a statistical model of the climatically controlled distribution of *Thuja* predicts little loss of the current range and a large expansion to the north and northwest into sub-boreal spruce forest as an eventual result of 100 years of projected climate change (Hamann and Wang 2006). This prediction likely reflects the projected increase in winter temperature, a variable that bioclimatic models show is an important control of the northern limit of the ITR (Gavin and Hu 2006). However, bioclimatic model predictions do not involve a simulation of the hydrological conditions that support *Thuja* stands (i.e., toe slopes that receive spring snowmelt). While we are unaware of a soil water balance simulation in this area, a simple increase in winter temperature would most likely both degrade conditions for *Thuja* in the Robson Valley (by reducing snowmelt contribution to growing-season soil moisture) and improve conditions on toe slope positions further north (by lengthening the growing-season during periods of high soil moisture).

Future warming will likely yield different seasonal climates than those that occurred during previous warm periods when *Thuja* was absent or rare in the region. Nevertheless, it is reasonable to assume that if the relatively minor climatic changes of the last 2000 years were sufficient to establish *Thuja*-*Tsuga* forests in the region, then it would not require a major climatic change to stress these stands. Therefore, there remains an urgent need to identify mechanisms, including the hydrological regime, that affect the large-scale distribution of these forests.

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