Quaternary Science Reviews 30 (2011) 2124–2133

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Pre-glacial and interglacial pollen records over the last 3 Ma from northwest Canada: Why do Holocene forests differ from those of previous interglaciations?

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ARTICLE INFO

Article history:
Received 17 September 2009
Received in revised form
11 June 2010
Accepted 22 January 2011
Available online 8 March 2011

Keywords:
Yukon
Interglacials
Forest history
Pollen analysis
Anthropogenic fire
Pliocene
Pleistocene
Holocene
Pinus
Abies

ABSTRACT

We synthesize pollen spectra from eleven dated stratigraphic sections from central and northern Yukon. Palaeomagnetic and tephra dating indicates the earliest assemblages, representing closed canopy *Pinus* and *Picea* forest, are middle-late Pliocene age. More open forest conditions, indicated by increased Poaceae and with evidence of permafrost, are dated at ca 3 Ma. While *Pinus* pollen is abundant at 3 Ma, it is reduced in records after 2.6 Ma, and subsequent Pleistocene interglacial forest records are repeatedly dominated by *Picea*, along with *Alnus* and small but significant amounts of *Abies*. Surface sample comparisons indicate that *Abies* was more widespread and abundant in past interglaciations than at present and that Middle-Pleistocene *Picea*–*Abies* forest grew in the northern Yukon Porcupine Basin, 500 km beyond modern *Abies* limits. In contrast, *Pinus*, which occurs today in southern and central Yukon, was not a significant component of these Pleistocene interglacial forests. Late-Holocene pollen assemblages with rare *Abies* and high *Pinus* are the most distinct in the past 2.6 Ma. Possible factors driving Holocene difference are paleoclimate, paludification, changes in megafaunal herbivory and an unusual fire regime. Anthropogenic burning is a factor unique to the Holocene, and if it is shown to be important in this case, it would challenge our notion of what constitutes boreal wilderness.

1. Introduction

North American studies of Pliocene and interglacial chronology and paleoecology have lagged behind those for Northwestern Europe. The pre-glacial Pliocene is well known from North Sea marine cores and at least eight distinct interglaciations are recognized from classic study areas in the Rhine Valley and East Anglia (West, 1980; Gibbard et al., 1991). North American interglacial records are geographically concentrated in the midwestern United States and, temporally, on the last interglaciation (Heusser and King, 1988). The Yukon Territory, northwestern Canada, is an exception. Here, detailed stratigraphic research, application of palaeomagnetic chronologies, recognition and dating of distal tephras, pollen and plant macrofossil analysis of organic-rich sediment, vertebrate remains and ancient DNA have all contributed to a growing understanding of Pliocene and Pleistocene paleoecology (*e.g.* Westgate et al., 2001; Zazula et al., 2007; Froese et al., 2009). Long term changes such as the tectonic history of the Alaska and St. Elias Ranges, and opening of the Bering Strait have had a great influence on regional climate and in turn on late-Neogene vegetation (White et al., 1997). In contrast, rapid oscillations between glacial and interglacial conditions saw dramatic vegetation changes from steppe-tundra to closed canopy boreal forest (Schweger, 1997).

Here we present pollen records from dated Yukon sites and discuss their stratigraphic and paleoecological significance. The focus is mostly on forest tree and shrub taxa: *Picea*, *Pinus*, *Abies* and *Alnus*, in order to document the composition of Yukon forests over the past 3 Ma. These records fall within the pre-glacial Pliocene, spanning ca 5–2.6 Ma—although there is evidence of extensive Northern Hemispheric glaciation in the late Pliocene (>2.6 Ma), prior to the newly established Pliocene/Pleistocene boundary (Gibbard et al., 2008, 2010)—and within the Pleistocene, spanning ca 2.6–0.09 Ma.

The Yukon is a terrain of mountain ranges and plateaus with numerous large river valleys and basins. Because of topographic variability the vegetation is a complex of alpine and coastal tundra, woodlands and forests (Scudder, 1997) with four tree species reaching their northern or western limits within the territory. *Picea*

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doi:10.1016/j.quascirev.2011.01.020

glauca and *P. mariana*, white and black spruce, respectively, are distributed throughout the Yukon limited by elevation, permafrost, aridity and the colder climate of northern Yukon. Both species do however approach the arctic coast along the Firth River valley (Cody, 1996; Oswald and Senyk, 1977). *Pinus contorta* ssp. *latifolia*, lodgepole pine, reaches its continental northwestern limit in south central Yukon, where it reproduces and spreads successfully following fire (Rowe and Scotter, 1973; Hughes et al., 1987). *Abies lasiocarpa*, alpine fir, is widespread within south and central Yukon at treeline or within subalpine zones. Climate is cold continental, with January mean temperatures −31.1 and −24.2 °C at Old Crow and Watson Lake, respectively (Fig. 1); July mean temperatures at these stations are 14.6 and 15.1 °C, and mean annual precipitation is 265 and 404 mm (1971–2000 normal period WO Canada, 2010).

2. Methods

Sediment samples for pollen analysis were collected from stratigraphic sections exposed as river bluffs or placer mine cuts in northern and central Yukon. Two slightly different sample preparation procedures were employed: (1: White) standard HCl and HF digestion, with the resulting residue screened through a 7 or 10 μm mesh, assisted by an ultrasound probe. Further preparation included heavy liquid separation and Javex bleach oxidation (Geological Survey of Canada, Calgary, Palynology Lab.) or acetolysis depending upon sample requirements (Moore et al., 1991); (2: Schweger) heavy liquid separation followed by HF, HCl and acetolysis treatments. Modern surface samples were treated with NaOH, HF and acetolysis (Moore et al., 1991). Only polleniferous samples are reported here.

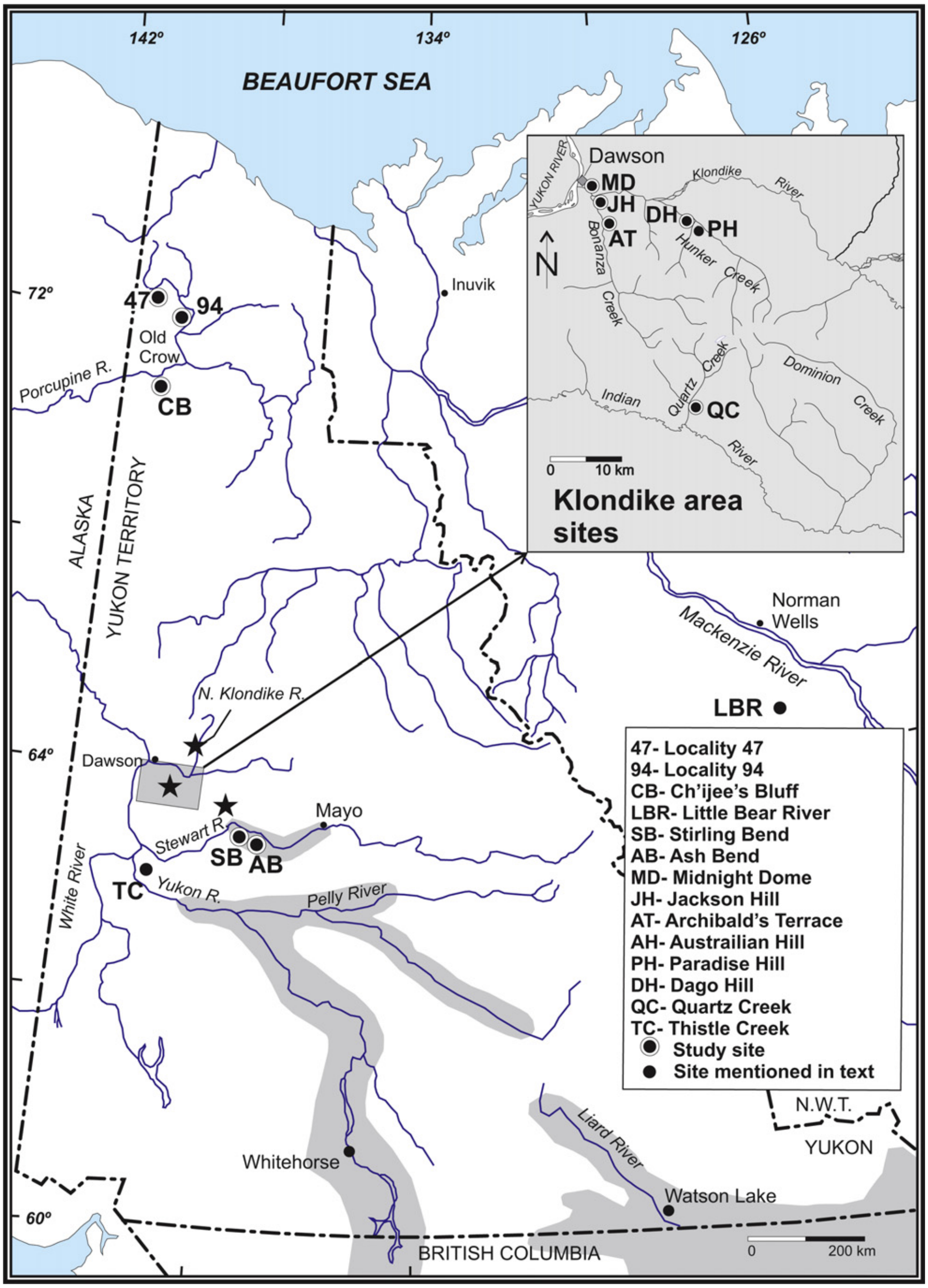

Fig. 1. Location of sites mentioned in text, with inset map of Klondike area locations. Gray shaded area toward center of map covers the known distribution of *Pinus contorta* (lodgepole pine) in Yukon (after Cody, 1996 and authors' observations); stars represent isolated stands of lodgepole pine.

Pollen sums for calculating percentages include all taxa except indeterminable pollen with most sums exceeding 250–300 grains, 500 for modern surface samples. The results are presented in a relative percent diagram for either all taxa or for the four major forest taxa. Since the sampled sediments varied greatly and the temporal resolution is poor, compared with dated Holocene lake sediments (see Honeymoon Pond, Cwynar and Spear, 1991), no attempt was made to determine the amount of charcoal particulates in sediment samples. Modern pollen rain was sampled with Tauber traps placed at 3 m height in the mixed-coniferous, 0.25-ha SEADYN research stands, north central Alberta (Department of Botany, University of Alberta). Percent areal cover was used to estimate plant species importance (La Roi et al., 1983). Moss polsters and pond sediments were also collected at locations in the south, central and northern Yukon.

3. Stratigraphy and pollen results

Insight into the forest history of the Pliocene and Pleistocene in central and northern Yukon is provided by stratigraphic and pollen analytical work in the Klondike area of central Yukon and the Old Crow-Porcupine River basins (Fig. 1), and by comparisons with other pollen stratigraphies in northern Canada and Alaska. The sites (all are located on Fig. 1) are presented by locality with a discussion based on our best understanding of the respective ages. Many sediment samples were sterile and some had little pollen, so multiple samples or slides were examined in order to establish a pollen record for some sites.

3.1. Jackson Hill, Klondike River

The Jackson Hill section exposes 35 m of pre-glacial lower White Channel (LWC) gravel, overlain by a thin (2–5 m) upper White Channel (UWC) gravel (with some of the earliest evidence of periglacial conditions in the northern hemisphere) and this in turn overlain by 40 m of glaciofluvial Klondike gravel, (marking the earliest Cordilleran Ice Sheet glaciation of central Yukon) (Froese et al., 2000). The LWC gravel has mixed polarity (reversed and normal magnetizations) representing either the mid-Gauss (Kaena-Mammoth) sub-chrons or Gilbert Chron suggesting an age >3 Ma (Froese et al., 2000). Palynostratigraphy indicates an age younger than Miocene, <5.3 Ma (see below). This section yielded two productive pollen samples: one (C-248449) from the LWC, polarity unknown, 18 m above bedrock, and the second (C-248453), midway through the normally magnetized Klondike gravel, is associated with the late Gauss Chron, >2.6 Ma (Froese et al., 2000). C-248449 is dominated by *Picea* and *Pinus* pollen, 33 and 48%, respectively, with *Abies*, 1.3%, and traces of *Corylus*-type and Poaceae (Fig. 2). The much younger C-248453 contains only 1% *Picea* and is dominated by *Betula*, 23%, and Cyperaceae, 59%, with 6% *Larix*/*Pseudotsuga* pollen.

3.2. Dago Hill

Dago Hill exposes 15 m of altered LWC gravel overlain by 12 m of well-preserved UWC gravel. Magnetization at the site is normal and correlated with the late Gauss Chron (2.6–3.0 Ma). The occurrence of the Dago Hill tephra at this site (3.18 ± 0.41 Ma) within the UWC supports this correlation (Westgate et al., 2003). Ice wedge casts are present in the UWC gravel immediately up-valley at Paradise Hill (Fig. 1) (Froese, 1997). Dago Hill yielded seven productive samples. Sample C-248526 was collected at the base of the UWC gravel, within a colluvial diamict reworked from the LWC gravel to which it is assigned (>3 Ma). Sample C-248523 was collected 1 m above the base of the UWC gravel and C-248524 was collected 1 m above the latter, within a 2-m thick gleyed organic silt interpreted as a paleogleysol. Samples C-401240 to C-401244 were collected in a vertical sequence from the base through the top of the paleogleysol. Samples C-401244 and C-248524 are laterally equivalent. The Dago Hill samples are similar in their pollen composition, with Poaceae (15–45%) dominating along with *Picea* (4–20%) and *Pinus*, (11–44%; Fig. 2). Small amounts of *Larix*/*Pseudotsuga* occur in six of the samples, a trace of *Abies* occurs in one, while *Polemonium*, <3%, occurs in three.

3.3. Quartz Creek

The Quartz Creek site is located 35 km southeast of Dawson City (Fig. 1). The Quartz Creek tephra (QCt) is preserved in an ice wedge cast developed in a colluvial facies of the UWC gravel (Froese et al., 2000; Sandhu et al., 2001; Westgate et al., 2003). The age of the QCt includes an ^{40}Ar/^{39}Ar age from 2.64 to 3.01 Ma (Kunk, 1995) and an isothermal plateau fission-track age of 2.97 ± 0.24 Ma (Sandhu et al., 2001; Westgate et al., 2003) consistent with its normal polarity (Froese et al., 2000). One productive pollen sample (C-201063) was collected from the QCt and it is dominated by *Picea* and *Pinus*, 41 and 15%, respectively (Fig. 2).

3.4. Mosquito Gulch (Archibald's Terrace), Bonanza Creek

The Mosquito Gulch tephra (MGt) is found on an intermediate terrace incised into the White Channel and Klondike gravels (Naeser et al., 1982; Preece et al., 2000). The tephra, dated at 1.45 ± 0.14 Ma (Westgate et al., 2001), is correlated by glass chemistry with tephra in the Midnight Dome terrace, 8 km down valley (Westgate et al., 2001). At the Midnight Dome site, MGt occurs at the base of the reversely magnetized loess, at the top of a 20–30 cm thick organic silt (Froese et al., 2000; Westgate et al., 2001). At Archibald's Terrace, two palynological samples (C-201059 and C-201058) were taken from a bed of fine silt to clay, 30–45 cm and 46–60 cm below the MGt, respectively. *Corylus*-type, *Alnus* and *Betula* dominate these samples reaching maximum values of 51, 35 and 16%, respectively (Fig. 2). *Salix*, Cyperaceae and Poaceae at 8, 11 and 4%, respectively, are also significant.

3.5. Midnight Dome Terrace

The Midnight Dome (MD) site is located on an intermediate terrace above the Klondike River at Dawson City (Fig. 1). The site consists of massive and retransported loess units 1–4 m thick including three laterally continuous organic horizons, which were palynologically productive. The loessal sediments have a mixed polarity (reverse-normal–reverse-normal) spanning the late Matuyama to early Brunhes Chron, including the Jaramillo subchron, (Froese et al., 2000; Westgate et al., 2001). The presence of the MGt near the base of the exposure and the Midnight Dome tephra (1.09 ± 0.18 Ma) confirm the magnetochronology (Westgate et al., 2001).

MD Organic 1 is magnetically reversed and contains retransported pods of the MGt dated 1.45 ± 0.14 Ma (Froese et al., 2000; Westgate et al., 2001) in the upper few centimeters, indicating an Early Pleistocene age. Only one sample yielded sufficient pollen (211 grains) and it is dominated by *Picea* at 86%; *Pinus* is absent, while *Abies* reaches 2.4% and *Alnus* <2% (Fig. 3).

MD Organic 2 consists of organic lenses occurring within a normally magnetized diamict 5 m above MD Organic 1. The diamict unit and normal MD Organic 2 are correlated with the Jaramillo subchron (0.99–1.07 Ma) on the basis of the reversed polarity above and below (Froese et al., 2000). This suggests a late-Early Pleistocene age, likely representing MIS 31. Six of eighteen samples had sufficient pollen to count. *Picea* pollen dominates, ranging from 92

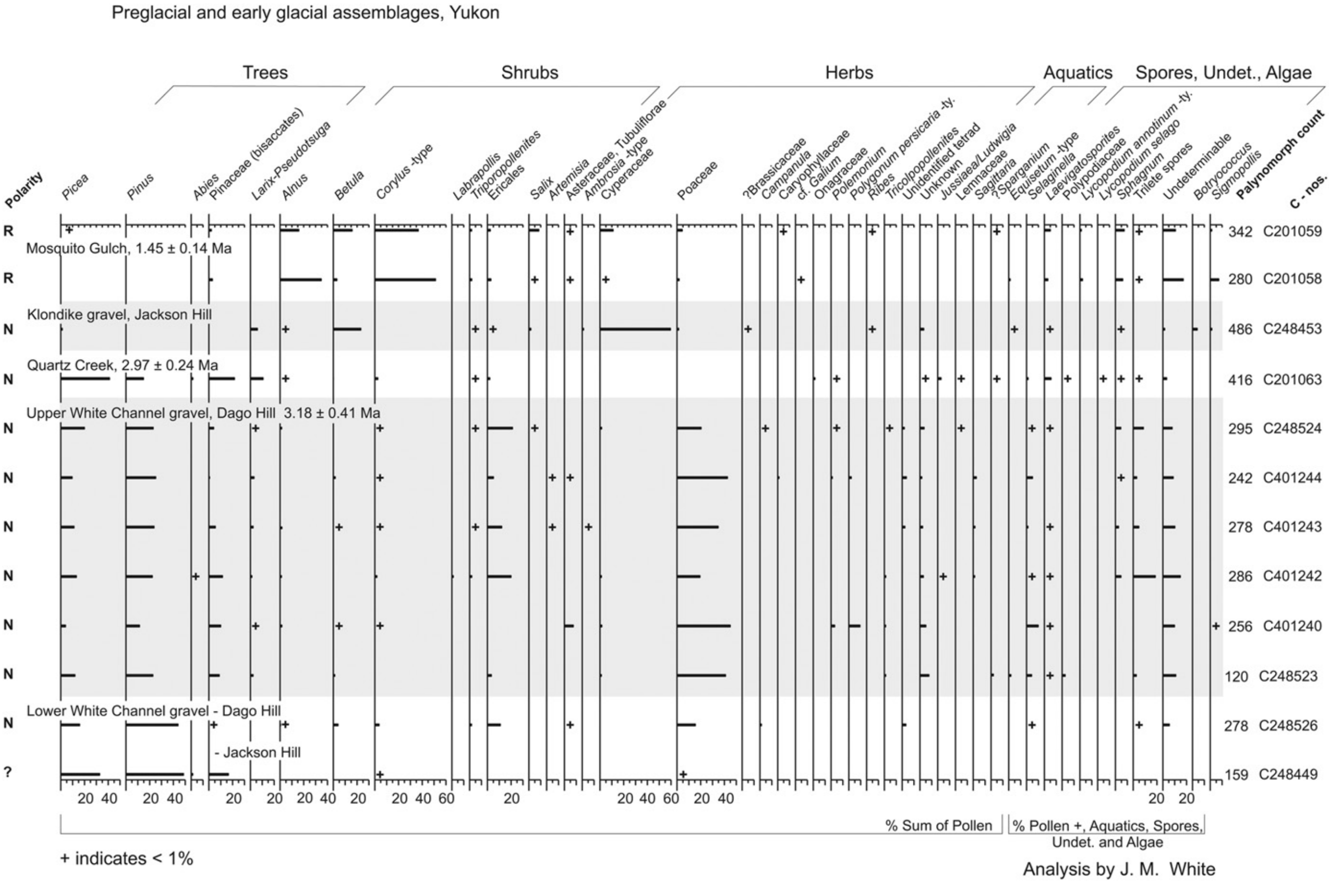

Fig. 2. Pre-glacial Pliocene and early Pleistocene palynological assemblages from stratigraphic sections in the Klondike Mining District, Yukon. Samples are ordered by age; C-numbers are Geological Survey of Canada sample curation numbers. Comparisons can be made with the modern surface sample data from Table 2.

to 78%, *Pinus* occurs at <1% and *Alnus* reaches only 4% (Fig. 3). *Abies* pollen occurs in all samples from 1 to 11%.

MD Organic 3 sediments occur 1.5 m above MD Organic 2 and consist of 10 cm of normally magnetized organic silt with 50 cm of reversely magnetized silt below. On the basis of MD Organic 3 occurring at the late Matayama–Bruhnes transition, which occurred during an interglaciation (Shackleton et al., 1990), MD Organic 3 likely represents an early Brunhes, or early-Middle Pleistocene age. One of seven samples yielded 59 grains of which 70% were *Picea*, 3% *Pinus*, and 3% *Abies*; no *Alnus* was recorded (Fig. 3).

3.6. Locality 94, Old Crow River

Organic-rich, lacustrine and alluvial sediments exposed near the base of the down stream end of Old Crow River section Loc. 94 enclose the Little Timber tephra (LTt). Sediments above and below the LTt were collected and examined for fossil pollen. *Picea* pollen frequencies range up to 14% and *Alnus* reaches a maximum value of 15% (Fig. 3). *Pinus* and *Abies* pollen frequencies reach 1.5 and 2.2%, respectively. The reverse polarity of the sediments and a glass fission-track age of 1.26 ± 0.11 Ma (Westgate et al., 2005) indicate the pollen record is from the late-Early Pleistocene, intermediate to the MD Organic 1 and 2 pollen records (Fig. 3).

3.7. Locality 47 D, Old Crow River

Organic-rich alluvial silts and sands found near the base of this river exposure yielded *Picea* frequencies from 26 to 36%; *Pinus* reaches <2% and *Abies* <1%, while *Alnus* ranges from 2 to 12% (Fig. 3). These sediments are magnetically normal and contain a fossil small mammal record that is early-Middle Pleistocene in age (Storer, 2003). Mammoth molars from Loc. 47 are very similar to the early to middle Pleistocene Olyor mammoth (Sher, 1986; Morlan, 2003).

3.8. Locality 47 B Old Crow River

Organic-rich alluvial silts and fine sands have yielded a pollen record with up to 12% *Picea* pollen, 1.6% *Pinus*, <1% *Abies* and 26% *Alnus* (Fig. 3). This record is associated with the Surprise Creek tephra (SpCt) exposed at several points along the section and dated to 180 ± 0.08 ka (Westgate et al., 1995). The host sediments are normally magnetized. Correlation to MIS 7 is likely.

3.9. Stirling Bend section, Stewart River

Pre-Reid glaciation alluvial sands and silts, and a paleosol are exposed along the base of this river exposure. The pollen stratigraphy of the normally magnetized paleosol and underlying silt records forest development from a tundra environment (Tarnocai and Schweger, 1991). *Picea* pollen frequencies range from 48 to 78%, *Pinus* and *Abies* frequencies are <1% and *Alnus* reaches 8% (Fig. 3). A second section (CS, unpublished data.) yielded up to 84% *Picea*, 1.4% *Pinus* and <1% *Abies* and *Alnus*. *Picea* logs are found in alluvium overlying the paleosol. This record of forest development is stratigraphically below outwash of the Reid glaciation, which is likely equivalent to MIS 6 (Westgate et al., 2008; Ward et al., 2008), suggesting a late-Middle Pleistocene age.

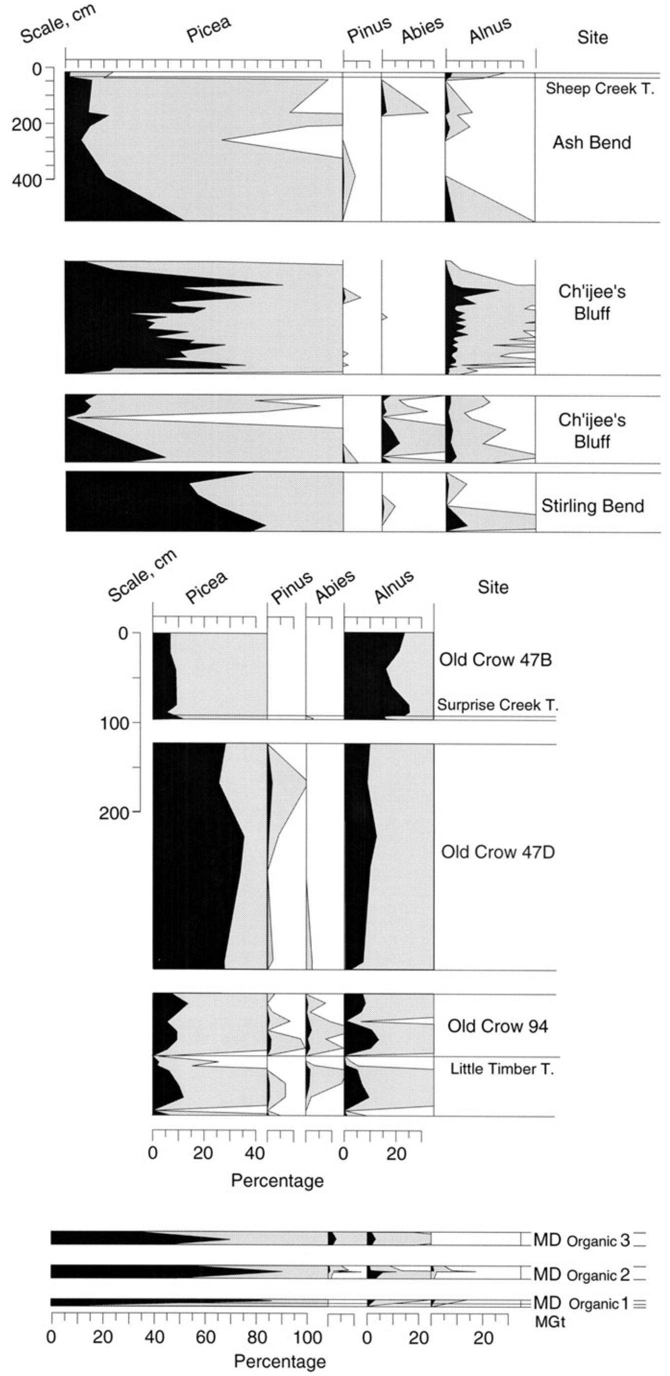

Fig. 3. Pleistocene interglacial pollen frequencies for the four dominant forest taxa, *Picea*, *Pinus*, *Abies* and *Alnus*, from stratigraphic sections, central and northern Yukon. Comparisons can be made with modern surface sample data from Table 2.

3.10. Ch'ijee's Bluff, Porcupine River, Yukon

This 35-m high section exposes Pliocene to Holocene age unconsolidated sediments subdivided into six units. Unit 4 consists mostly of organic-rich silts and sands further subdivided into three subunits (Matthews et al., 1990). Pollen analysis documents *Picea* frequencies up to 39% at the base of Subunit 4a, decreasing upward (Fig. 3). *Pinus* occurrences are rare and no more than 1%, while *Abies* occurs in most samples and reaches a maximum of 7%. *Alnus* reaches a maximum of 4%. This pollen record is stratigraphically below Old Crow tephra, with a glass fission-track age of 124 ± 10 ka (Westgate et al., this volume) and the Biwa 1 Event, a paleomagnetic reversal dated about 180 ka (Evans and Wang, 1994), and spans the interval of late MIS 7 and early MIS 6.

Also at Ch'ijee's Bluff, subunit 4c has yielded well-preserved macrofossils (Matthews et al., 1990). The pollen record is dominated by *Picea* which reaches a maximum of 86% although it is only 2.5 and 6% at the top and bottom of the record, respectively (Fig. 3). *Pinus* ($<$1%) occurs in only three of 35 samples, *Abies* in only one sample at $<$ 1%, while *Alnus* ranges from $<$1 to 20% (CS unpublished data). The presence of Old Crow tephra underlying this record, in addition to the presence of thermophilous plant and insect fossils (Matthews et al., 1990), supports correlation to MIS 5e, or the last interglaciation.

3.11. Ash Bend section, Stewart River

The section consists of 10 m of organic-rich silt deposited in a gulley cut through outwash of the Reid glaciations (Hughes et al., 1987; Westgate et al., 2001). The sediments are organic-rich near the base of the gulley, and include logs, while the section grades to sterile silts and sands with pebbles near the top. Even though the sediments are organic-rich, most of the samples are sterile or if pollen is abundant it is poorly preserved. *Picea* pollen frequencies are 48% at the base and $<$2% near the top of the section (Fig. 3). *Pinus* and *Abies* are rare with a single sample occurrence of $<$2% and *Alnus* reaches a maximum of 4%. Three tephra beds are present within the gulley-fill sediments, including Sheep Creek tephra (SCt) C, K, and A (Westgate et al., 2008). SCt-C is within organic-rich silts near the base associated with woody macrofossils, while SCt-K and A occur midway through the exposure associated with the transition to tundra–steppe conditions (Westgate et al., 2001, 2008). The age of the SCt-K is about 80 ka based on bracketing luminescence ages and a fission-track age on the overlying Dominion Creek tephra of 82 ± 9 ka in the Klondike area (Westgate et al., 2008). Taken together these constraints suggest a late MIS 5 age for the interglacial record at Ash Bend, probably representing MIS 5a.

4. Discussion

4.1. Pliocene forests

Pollen spectra from the LWC gravel at Jackson Hill, the earliest assemblages presented in this paper, are dominated by *Pinus* and *Picea*, with rare *Abies*, (Fig. 2), while shrub and herbaceous taxa are rare, indicating that this was a closed canopy coniferous forest. In contrast, pollen from LWC gravel at Dago Hill includes a number of shrub taxa: *Alnus*, *Betula*, *Corylus*-type and Ericales. Poaceae dominates the non-arboreal pollen (NAP), herbs being rare. A more open coniferous forest with an understory is suggested.

Pinus and *Picea* are also dominant in the UWC gravel at Dago Hill, while *Abies* and *Alnus* are rare or absent (Fig. 3). The abundant Poaceae pollen in the UWC gravel suggests an open-canopy forest. Pollen assemblages from UWC gravels contain *Polemonium*, which is recorded in the Poaceae and *Artemisia* Zones of the Pliocene and Pleistocene (White et al., 1999). Significantly, *Tsuga* and the thermophilous hardwoods *Ulmus*/*Zelkova* and *Pterocarya* are absent. These taxa are characteristic of the Miocene and perhaps earliest Pliocene, as they are present in Loc. A Unit 1 of the Circle Terrace gravel, Alaska (Ager et al., 1994), a unit that lacks independent age constraints and may well extend into the late Miocene. The UWC gravel at Dago Hill includes several tephra beds with fission-track ages around 3 Ma (Westgate et al., 2003), indicating that the underling LWC gravel is at least early Pliocene in age. The vegetation at this time was a warm mixed boreal forest with *Pinus*, *Picea*, *Abies* and Larix/Pseudotsuga. *Betula*, *Alnus*, *Salix* and Ericales were trees or shrubs and there was a variety of herbs, including Cyperaceae, Poaceae, *Campanula*, Asteraceae and *Polemonium*.

The single Quartz Creek pollen assemblage, associated with the Quartz Creek tephra, has more abundant *Picea*, *Abies* and *Larix/Pseudotsuga* with less *Pinus* and rare *Alnus*. *Polemonium* is present but Cyperaceae and Poaceae are absent. Based on the absence of the latter a closed-canopy boreal forest is suggested for this younger site dated at ca 3 Ma (Sandhu et al., 2001; Westgate et al., 2003). However, the presence of an ice wedge cast developed in a colluvial facies of the UWC gravel indicates permafrost conditions prior to the deposition of the QCt.

Pinus is a common element in high-latitude late-Neogene pollen and macrofossil assemblages. Both two- and five-needle pines occur in assemblages on Meighen Island, 80°N latitude (J. Matthews, personal communication 1997). Cones of *Pinus matthewsii* sp. nov., most similar to *P. contorta* (McKown et al., 2002), and *P. monticola* (Schwab et al., 2000) have been described from Unit 1 at Ch'ijee's Bluff, northern Yukon. *Pinus* pollen is also abundant through Unit 1 and overlying Units 2 and 3 (Lichti-Federovich, 1974; R. Hart, personal communication 2010). These units are believed to be of late Pliocene age based on the tephra date discussed below. *Pinus* occurs with herbs at the Lost Chicken II site in Alaska, associated with a tephra unit dated 2.9 ± 0.2 Ma (J. Matthews, personal communication, 1993; White et al., 1999; Matthews et al., 2003). Although most samples from Lost Chicken II contain $<$ 10% *Pinus* pollen, one sample records approximately 30% (White et al., 1999). However, the presence of *Pinus* needles indicates that the genus grew locally, sharing dominance with *Larix*, *Picea*, *Abies* and Poaceae. These records demonstrate that *Pinus* was a significant arboreal component in the Yukon and east-central Alaskan forests during early Pliocene (ca 5–3 Ma).

4.2. Early shrub Tundra

The single pollen assemblage from the Klondike gravel at Jackson Hill (C-248453), dated to the late Gauss Chron (ca 2.6 Ma), differs significantly from those associated with the LWC and UWC gravels. *Pinus* and *Abies* are absent, and *Picea* is rare (Fig. 2). *Betula* and Cyperaceae pollen dominate, which suggests shrub tundra vegetation. The pollen assemblages from Mosquito Gulch are similar in that *Pinus* and *Abies* are absent and *Picea* is absent or rare; however, *Alnus* is abundant. *Alnus* and *Betula* suggest the presence of shrub tundra. The Mosquito Gulch assemblages are associated with the MGt dated 1.45 ± 0.14 Ma, well within the early Pleistocene.

The presence of MGt also dates Midnight Dome Organic 1. However, the MD Organic 1 pollen assemblage is dominated by *Picea* with trace amounts of *Alnus*, and, significantly, while *Abies* reaches 2.4% *Pinus* is absent. Thus pollen associated with MGt at Midnight Dome provides evidence of a closed canopy *Picea–Abies* forest. Given the higher stratigraphic position of the MD sample, which is directly related to the tephra (whereas the Mosquito Gulch samples are located below the MGt), we conclude the forest developed later than the shrub tundra recorded at MG.

In summary, *Pinus* and *Picea* were the dominant forest taxa from mid Pliocene until ca 2.6 Ma. The early Pleistocene records demonstrate increases in non-arboreal pollen at the expense of forest taxa, which points to climatic cooling. From this point on, *Pinus* does not appear in any records as an important component of the interglacial forests of the Yukon–until the Holocene.

4.3. Interglaciations

Interglacial and interstadial intervals are differentiated in marine oxygen isotope records with the former approaching modern ice volumes and the latter larger ice volumes; however, terrestrial sequences of multiple interglacial deposits are uncommon. West (1980) identified eight interglaciations in East Anglia (UK) based on the different successional sequences of temperate forest pollen types, plus interstadials which have a more boreal character, and in the Netherlands and Germany a similar pattern of interglacial and interstadial assemblages is evident (Zagwijn, 1989; Behre, 1989). In the Yukon ten interglaciations have been recognized to date (Duk-Rodkin et al., 2004).

Full-glacial pollen records from the Yukon are typically dominated by non-arboreal pollen with low *Betula* and no *Picea* or *Alnus* and represent herbaceous or steppe–tundra vegetation. Records radiocarbon-dated between 29.6 and $>$43 ka are dominated by pollen of *Betula*, Cyperaceae, Poaceae and *Artemisia* with $<$20% *Picea* pollen (Schweger and Matthews, 1991). These records date to the last interstadial, MIS 3, and record open boreal, shrub tundra or subarctic vegetation. In contrast, the pollen records discussed below have abundant *Picea* pollen (up to 92%), and, for the northern Yukon Old Crow Basin, close to modern frequencies, ca 20%. These high values suggest palaeoclimates warmer than or as warm as present and permit identification of these sites as interglacial in nature.

While they co-occur in areas of the southern Yukon boreal forest today, the four dominant conifer species in the Yukon (*Picea glauca*, *P. mariana*, *Abies lasiocarpa* and *Pinus contorta*) have different Holocene histories. *Picea* appears in Yukon pollen records between ca 9–8 ka with *P. mariana* expanding during the mid Holocene (Cwynar and Spear, 1991, 1995). Pollen records indicate that *Pinus* appeared in southern Yukon between one and two thousand years ago, or perhaps earlier (Cwynar and MacDonald, 1987), and it appears to be expanding under the influence of fire (Johnstone and Chapin, 2003). Little is known about the Holocene history of *Abies* in the Yukon, although limited information indicates its presence in southern Yukon by ca 4 ka (Cwynar and Spear, 1995).

4.3.1. Pollen representation of boreal tree taxa

The four taxa are represented variably in modern pollen assemblages. *Pinus* is a prolific pollen producer whose pollen is able to disperse widely from sources (Webb and McAndrews, 1976; Bradshaw and Webb, 1985). This makes fossil *Pinus* pollen difficult to interpret as it is not clear what frequencies indicate its presence in local forest stands; however, rare occurrence or absence of *Pinus* pollen strongly suggests that *Pinus* was not present in the regional forests. *Picea* pollen frequencies approximate the proportions of *Picea* within forest communities (Webb and McAndrews, 1976). *Abies* is not a prolific pollen producer, nor does its pollen readily disperse, which results in *Abies* being underrepresented in pollen records (Webb and McAndrews, 1976). In eastern North America, *Abies balsamea* so is poorly represented in Holocene pollen records that it is in effect what Ritchie (1987) calls "a silent taxon".

Tauber-trap samples from two 0.25-ha boreal forest stands, north central Alberta, Canada, demonstrate these differences (Table 1). *Picea* pollen frequencies most closely approximate spruce cover area

Table 1
Comparisons of 1989 Tauber trap pollen frequencies and percent cover, north central Alberta.

	Picea	*Pinus*	*Abies*	*Alnus*
Stand 4				
% Pollen	33.1	32.9	5.8	5.2
% Cover	22.1	0.8	22.2	
Stand 6				
% Pollen	25.2	26.8	6.9	15.1
% Cover	13.2		12.3	

percentages in stands; *Pinus* and *Alnus* are greatly over-represented; and *Abies* is significantly underrepresented. East of Whitehorse, Yukon, *Abies lasiocarpa* forms the treeline and sub alpine forest on Sima Mountain. *Picea* and *Pinus* forests are found at lower elevations. A modern pollen surface sample transect from this locality demonstrates the restricted dispersal pattern of *Abies* pollen. Only samples from the floor of pure closed canopy *Abies* stands (Table 2, samples 5–8) have high *Abies* pollen frequencies (32–42%). Its frequencies sharply decline up slope into the alpine zone (<2–11%) and down slope into contiguous *Picea* and mixed *Picea–Pinus–Abies* stands (2.7–16.6%). *Abies* pollen frequencies of only 1–2% are recorded in modern lake surface samples from central Yukon, well within the present distribution of *Abies*, and it is not recorded in surface samples from northern Yukon (Table 2; Esdale et al., 2001).

4.4. Pinus–Picea–Abies forest history

4.4.1. Pinus

Pinus, although not specifically identified as *P. contorta*, was a significant component in the Pliocene forests of the Yukon. However, by 1.4 Ma (Loc. 94) and in subsequent interglacial records *Pinus* is poorly represented in fossil pollen assemblages. The maximum *Pinus* frequency from a Yukon Pleistocene interglacial site is 3.4% from MD Organic 3, otherwise *Pinus* is absent or occurs at <1–2%. Last Interglacial pollen assemblages from Thistle Creek Mine, central Yukon (Fig. 1), are dominated by *Picea* and *Alnus*, while *Pinus* is absent (CS, unpublished data). Thus *Pinus* probably did not occur in northern Yukon during the last interglaciation, and it appears not to have migrated to or established itself in central Yukon either. *Pinus*, then, has not been a significant component of the Yukon forests over the past 3 Ma.

In the late-Holocene *Pinus contorta* migrated into the southern part of the Yukon from British Columbia (Cwynar and MacDonald, 1987). Assuming it has not reached its climatic limit, it may still be expanding its range at the expense of *Picea* (MacDonald and Cwynar, 1991; Johnstone and Chapin, 2003). *P. contorta* exhibits reproductive success over wide climate and substrate types (Beckingham et al., 1996; Thompson et al., 1999) and following fire (Scudder, 1997). Rowe (1983) ranks it as one of the most fire adapted species in the boreal forest, able to replace white and black spruce and *Abies* on most substrates following fire.

Table 2
Transect of modern pollen surface sample from Yukon. Sample source, P = pond sediment, all other moss polsters.

Sample	Vegetation	*Picea*	*Pinus*	*Abies*	*Alnus*
Sima Mountain, southern Yukon					
1P	shrub tundra	6.4	56.1	1.7	6.2
2	fir treeline	15	42	5.5	7.3
3	fir treeline	13.8	48.9	11.2	4.9
4	fir treeline	13.3	43.6	5.1	8
5	fir	13	41.4	32.2	4.3
6	fir	11	34.2	39.1	4.3
7	fir	15.7	33.8	42.1	2.9
8	fir	13.8	37.3	41	2.7
9	spruce-fir	28.6	46	8.8	2.9
10	spruce-fir	45.8	30.5	16.6	2.9
11	spruce-pine	33.1	58.3	2.7	3.7
12	spruce-pine	35.6	53.8	4.2	3
Reid Lake, central Yukon (Hughes et al., 1987)					
P1		49.5	6.8	1.2	12.5
P2		52.1	9.6	1.2	13.3
Old Crow Flats, northern Yukon (Schweger and Matthews, 1985)					
1		23.7	0.2		26.7
P2		23.9			10.7
3		14.3			32.8
P4		2.9			20.8
5		20.6			20.6

4.4.2. Picea

Picea has been a major component in Yukon forests over the past 3 Ma. For the northern Yukon, *Picea* pollen frequencies from localities 94, 47B and Ch'ijee's Bluff Stage 7 approximate or are higher than present surface sample values (Table 2), and significantly higher at Loc. 47D. At Ch'ijee's Bluff, MIS 5e *Picea* pollen frequencies reach a maximum of 86%, one of the highest for any Yukon interglacial record. These data indicate that closed canopy, productive *Picea*-dominated boreal forest grew in a region now characterized by subarctic woodland and shrub tundra. For central Yukon, maximum interglacial *Picea* pollen frequencies range from 47 to 92%, again indicating dense and productive spruce-dominated boreal forest. There is, however, a need for more documentation of the modern pollen rain within the boreal forest before we really understand the significance of the very high *Picea* pollen frequencies.

4.4.3. Abies

Abies pollen is recorded in assemblages of each interglaciation at frequencies that suggest *Abies* was a significant component in the forests over at least the past 1.4 Ma. The presence of *Abies* pollen, even at 2% in the northern Yukon, strongly suggests that it was growing in the region, perhaps forming treeline on Old Crow Mountain. The Ch'ijee's Bluff MIS 7 record includes a maximum of 7% *Abies* pollen, and for central Yukon 11% *Abies* pollen is recorded in Midnight Dome Organic 2 assemblages. In the past, *Abies* may have formed stands at lower elevations in both central and northern Yukon.

4.5. Comparisons with other interglaciations—how different is the Holocene?

Our data indicate that the Holocene is the most unusual of the known Yukon interglaciations, and the late-Holocene Yukon boreal forest is unique in the past 3 million years. A range of factors may be implicated: paleoclimate, temporal duration of interglacial conditions, paludification, megafaunal extinction, fire, and human activity.

During Yukon interglaciations, *Abies* was more widespread and abundant than now, extending its range into northern Yukon perhaps as much as 500 km beyond its present limits, which suggests a climate significantly warmer than at present. At the same time *Pinus* was absent or rare, although it may have been present at Little Bear River, on the eastern slopes of the Mackenzie Mts. (Hughes et al., 1993) (Fig. 1). This is a reversal of the late-Holocene forest composition with abundant *Pinus* and a restricted *Abies* distribution. The pollen records of Europe (see above) also document increases in *Abies* during interglaciations. This has been attributed to rising sea levels and a reduction in continentality (Zagwijn, 1989). Given the Yukon's plateau topography and southern mountain barriers, it is unlikely that a higher sea level would significantly decrease continentality, even with changes to the larger atmospheric circulation. For North America, the current distribution and climate requirements of *Abies lasiocarpa* and *Pinus contorta* are nearly identical (Ritchie, 1987; Thompson et al., 1999). It is not clear how the climate of earlier interglaciations differed from that of the Holocene. Based on *Picea* pollen frequencies, they were warmer than the Holocene, at least for northern Yukon as evidenced at Ch'ijee's Bluff, and for parts of central Yukon where soil properties suggest above 0 °C mean annual temperature for a mid Pleistocene interglaciation (Jackson et al., 1999). Thus, there is little to support climatic explanations for the observed *Pinus–Abies* patterns.

Alnus, most likely *A. crispa*, is a common taxon in Yukon Holocene pollen records but far less common in previous interglaciations.

Maximum Holocene values frequently vary from 20 to 40% (Ritchie, 1984). In surface samples *Alnus* reaches frequencies >30% for northern Yukon (Table 2), and >40% in northwestern Alaska (Anderson and Brubaker, 1986) and the Mackenzie River valley (Ritchie, 1984). A transect from interior Alaska to the north coast recorded 10–77% *Alnus* (Short et al., 1986). In contrast, maximum *Alnus* frequencies in the interglacial records range from <1% to 20% (average 7.6%), considerably lower than Holocene and modern values. Short et al. (1986) document significant over-representation of *Alnus* pollen; less than 10% *Alnus* plant cover yielded 20–77% *Alnus* pollen. Ritchie (1984) also points out that *Alnus* is a prolific pollen producer in far northwestern Canada, and its pollen values greatly over-represent its abundance in the vegetation. Low *Alnus* frequencies he attributes to long distance transport, where 30–65% *Alnus* pollen indicates total *Alnus* plant cover of not more than 5%. Also, pollen production for many species drops off northwards, possibly inflating *Alnus* pollen frequencies further. Nevertheless, even with these caveats, *Alnus* pollen values suggest more abundant alder in the Holocene than in any other interglaciation. The Holocene abundance of *Alnus* may be the result of a more open spruce forest due to slow climatic cooling, the cumulative effect of natural fires and reduced competition due to paludification (Ritchie, 1984; Schweger and Matthews, 1991). If this were the case, the lack of *Alnus* in past interglacials might imply that fires were less frequent and/or that paludification was less widespread. Paludification is frequently linked with the presence of permafrost, which may have been absent or restricted during past interglaciations, compared with the Holocene (Schweger, 1997). Local permafrost degradation influences other landscape and vegetation patterns, for example, *Alnus* groves frequently develop along newly formed local drainages linked to degrading permafrost.

It is also unclear how different interglacial time spans may have affected forest development (see West, 1980). During the Holocene, all four major forest taxa appear within 10 ka of deglaciation (10 ka being the apparent duration of most interglaciations, Kukla et al., 2002). However, *Pinus* arrives late, and its near-absence in interior Yukon during past interglaciations may conceivably reflect time limitation.

The Pleistocene megafauna have been identified as an important factor in the development of the full-glacial vegetation in Beringia (Redmann, 1982; Schweger, 1997). For other regions, Johnson (2009) concludes that the herbifauna broadly maintained vegetation openness and woodland mosaics of different structural types of vegetation. Megafauna collapse at the end of the Pleistocene may have resulted in restructured ecosystems and fuel accumulation in parts of the United States leading to enhanced fire regimes during the Lateglacial-early Holocene transition (Gill et al., 2009). While much is known about glacial faunas of the Yukon [Elsevier staff can we cross reference to Harington this issue?-Ed], very little is known about the interglacial vertebrate record. One can only speculate as to its composition and impact on boreal forest development. Bordes (1972) documented faunal assemblages that alternated between steppe and temperate forest species and which correlated well with a pollen record of stadials and interstadials in southwest France. It seems imprudent, therefore, to assume that the interglacial fauna of the Yukon would be identical to the glacial steppe–tundra adapted species. Assuming interglacial megafauna browsed in forest openings on *Salix*, *Alnus*, and *Populus* and grazed on graminoid and herbaceous taxa, their activities may account for the low amount of *Alnus* pollen; however, it is uncertain how herbifauna might have promoted the growth of *Abies* and suppressed that of *Pinus*. The complex relationships among climate, vegetation development, megafauna extinction, and human colonization during the Lateglacial-early Holocene are well-documented (Guthrie, 2006; Gill et al., 2009). However, the unique Holocene forest did not develop until the late Holocene, many thousands of years after megafaunal extinction, and thus megafaunal dynamics seem an unlikely factor determining the uniqueness of Yukon Holocene forests.

The role of fire in the boreal forest is well studied, and so increasingly is the relationship of fire to past vegetation development via charcoal records from dated lake-sediment cores. A North American study linked fire frequencies during the late Pleistocene–Holocene transition to abrupt climate changes and fuel accumulation under favorable climate conditions (Marlon et al., 2009). For Alaska, shifts in fire frequencies have been linked to changes in vegetation and therefore fuel in response to millennial-scale climate change (Higuera et al., 2009; Brubaker et al., 2009). Because fire favors *Pinus* over *Abies*, data presented here on these two taxa, and also abundance patterns of *Alnus*, suggest that fire frequencies may have significantly increased during the Holocene along the dispersal route of *Pinus* into the Yukon (MacDonald and Cwynar, 1991). If climate were the single significant variable it is difficult to explain why *Pinus* was not present in earlier, warmer interglacials, or earlier in the Holocene when warmer conditions might have increased convection leading to more lightening fires. Unfortunately, detailed charcoal studies are not yet available for the Yukon to test the relationship between fire and climate.

There is, however, one ecological factor that is completely unique to the Holocene. Humans were present in the Yukon as early as 15 ka ago (Cinq-Mars and Morlan, 1999; Hoffecker and Elias, 2007), before forests invaded the Lateglacial tundra, and over time they seemingly occupied all parts of the Territory. Controlled fire has always been an integral part of aboriginal technology anywhere, for cooking and smoking, processing, illumination and protection; larger fires were set to promote browse for game, facilitate hunting, signal activities or presence, and promote the regrowth of specific plants. There is a substantial literature on aboriginal burning that includes burning in the boreal forest (see Scharf, 2010). Aboriginal activities leading to deliberate or accidental fire in the boreal forest were initially treated in a negative manner (Lutz, 1956, 1959). It was not until the work of ethnographers (Lewis, 1982; Lewis and Ferguson, 1988; Bonnicksen et al., 1999) that the full significance of aboriginal fire in the northern boreal forest was documented and appreciated as an appropriate and innovative technology. Lloyd et al. (2006) note that climate and anthropogenic influence are the two factors likely to figure prominently in changing fire regimes in the boreal forest of Alaska. In contrast, conclusions reached by paleoecologists documenting fire history either preclude any substantial impacts caused by prehistoric human activity or treat it only as a possible contributing factor. However, human impact through fire may be significant, as charcoal records for north central Washington demonstrate. Scharf (2010) investigated the relative influences of climate, vegetation and prehistoric population and showed a strong relationship between *Pinus* and human population abundances. Human-caused fires can only be a factor in the Holocene forest, not in any earlier Yukon interglacial, and therefore should be considered as a possible cause of the uniqueness of the Holocene boreal forest over the past 3 Ma in the Yukon. If human impact on vegetation composition can be demonstrated, it will be significant for forest management and it will challenge our notion of what is “natural wilderness” in the Yukon.

5. Conclusions

The earliest pollen assemblages presented here do not contain the deciduous elements recorded for the Miocene and are demonstrably of Pliocene age, dated ca 5–3 Ma. *Pinus* is an important component of these assemblages, indicating a mixed *Picea*–*Pinus* boreal forest. However, by 2.6 Ma *Pinus* drops out of the records.

Since then, successive Pleistocene interglacial records show little change in composition except for *Abies*, which was more widespread and abundant than it is now in the Yukon. A mixed *Picea–Abies* boreal forest appeared repeatedly following glaciations during the Pleistocene. The Holocene is the most unusual of the interglaciations vegetationally, with *Pinus* established as an important component in the Yukon forests while *Abies* is less evident in the pollen assemblages. Although a number of factors have been implicated, increased fire frequencies would have advantaged *Pinus* over *Abies* and stimulated *Alnus* growth. Anthropogenic burning is a factor unique to the Holocene, but to date it has received little consideration in relation to fire patterns; this points to the need for further studies of long-term human disturbance of the boreal forest and for charcoal studies of interglacial deposits.

Acknowledgments

The authors had the pleasure at various times of socializing and doing field work with Andrei Sher, visiting and discussing some of the sites presented here as well as life away from science. He was an inspiring colleague and friend. Schweger's and Froese's research has been supported by the Natural Science and Engineering Research Council of Canada. Many thanks must be given to Harvey Friebe, Department of Anthropology, University of Alberta, for his skilled assistance, from pollen processing to computer troubles. T. Ager (United States Geological Survey) and J.V. Matthews, Jr. (Geological Survey of Canada, retired) are acknowledged for their roles as principal organizers of joint fieldwork, undertaken by both surveys, on Neogene and Quaternary paleoclimatology and biostratigraphy in Yukon and Alaska, 1990–1993, by the United States Geological Survey and the Geological Survey of Canada. B. Davies (Geological Survey of Canada-Calgary, retired) is thanked for careful pollen preparations. We greatly appreciate the very helpful comments of the reviewers and editor, Mary Edwards. They checked our enthusiasm, resulting in a more thoughtful paper.

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