ORIGINAL ARTICLE

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Postglacial vegetational and fire history: pollen, plant macrofossil and charcoal records from two Alaskan lakes

Abstract   Pollen, plant macrofossil and charcoal analyses of sediments from two Alaskan lakes provide new data for inferring Lateglacial and Holocene environmental change. The records span the past 14,700 years at Lost Lake, 240 m a.s.l., central Alaska, north of the Alaska Range and 9600 years at Grizzly Lake, 720 m a.s.l., Copper River Plateau, south of the Alaska Range. *Salix* shrubs expanded in the herb tundra about 14,400 cal B.P., and *Betula* shrub tundra became established at ca. 13,200 cal B.P. Diminished *Betula* shrub cover in association with the increased abundance of herbaceous taxa occurred at 12,500–11,600 cal B.P., although the timing of these changes is not well constrained. *Populus* expanded at 11,200 cal B.P. and formed dense stands until 9600–9400 cal B.P. when *Picea glauca* forests or woodlands became established at both sites. The abundance of *Alnus viridis* increased markedly around 8500 cal B.P. at both sites, marking the development of alder shrub thickets around the lakes and on mountain slopes in these areas. Boreal forests dominated by *Picea mariana* became established around 7200 cal B.P. at Grizzly Lake and 5700 cal B.P. at Lost Lake. At Grizzly Lake, marked vegetational oscillations occurred within the past 8500 years; for example, *A. viridis* expanded at 2750 cal B.P. and 450 cal B.P. and declined at 150 cal B.P. Some of these oscillations coincide with large-scale climatic events,

such as the Little Ice Age cooling (LIA), and they probably reflect vegetational sensitivity to climatic change at this high site. Microscopic charcoal at Lost Lake suggests that fire was important in the lateglacial birch tundra, probably because of severe moisture deficits of the regional climate and/or high abundance of fine fuels. On the basis of the Grizzly Lake microscopic charcoal record, regional fires were common between 8500 and 6800 cal B.P. and between 450 and 150 cal B.P. Around Grizzly Lake, the mean return intervals of local fires estimated from macroscopic charcoal were ~ 386 years between 6800 and 5500 cal B.P. when *Picea glauca* dominated over *P. mariana*, ~ 254 years between 5500 and 3900 cal B.P. when *P. mariana* was more abundant than *P. glauca*, and ~ 200 years after 3900 cal B.P. in both *P. glauca* and *P. mariana* dominated forests. Correlation analysis of pollen and microscopic charcoal at Grizzly Lake reveals that increased fire activity led to the reductions of *P. glauca*, *P. mariana*, and tree *Betula* in association with the expansions of *A. viridis, Epilobium, Lycopodium clavatum,* and *L. annotinum.*

Keywords   Microscopic charcoal · Macroscopic charcoal · Holocene · Lateglacial · *Picea mariana* · *Picea glauca*

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Introduction

During the past decades palynological studies have resulted in a large pollen database from Alaska (e.g. Ager 1975; Anderson et al. 1990; Hu et al. 1993; Anderson and Brubaker 1994). These studies offer important information on late Quaternary vegetational and climatic histories of the region. However, a number of palaeoecological issues remains unresolved. For example, new pollen records with chronologies based on AMS ^{14}C dating of plant macrofossils reveal that vegetational transitions occurred later than previously thought (Bigelow and Edwards 2001). In addition, new palaeoclimatic studies (Hu et al. 2001, 2003; Lynch et al. 2004a) provide compelling evidence of marked climatic change during the middle and late
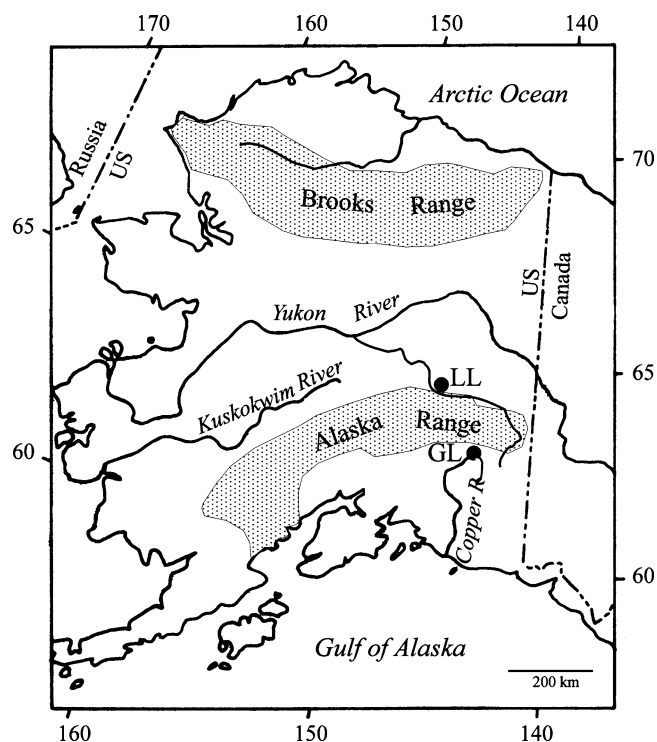
Fig. 1 Map showing the location of the study sites: LL: Lost Lake, GL: Grizzly Lake

Holocene, but existing pollen data do not have the chronological resolution to capture potential vegetational response to this climatic change. Furthermore, it is well known that in the modern landscape, forest fire greatly influences species composition and ecosystem processes, such as energy fluxes and elemental cycles. Although palaeoecologists have speculated that fires were important in shaping Holocene vegetation, only a few fire history records are available from Alaska (Lynch et al. 2002, 2004a; Hu et al. in press). These previous studies of fire history concentrated on the effects of climatic and vegetational change on fire regimes, and the long-term effects of fire on vegetation have not been addressed.

In this paper we first describe vegetational changes during the Lateglacial and the Holocene on the basis of pollen and macrofossil records from Grizzly Lake (62°42′35″ N, 144°11′50″W) and Lost Lake (64°18′00″ N, 146°41′30″W) in Alaska (Fig. 1). We then reconstruct the fire history on the basis of microscopic and macroscopic charcoal records from the same sites. Finally, we attempt to address climate-vegetation-fire linkages at our sites.

Study areas

Grizzly Lake lies at the northeastern edge of the Copper River Basin, on the southern slope of the Alaska Range at 720 m a.s.l. It has a surface area of ca. 11 ha and a watershed area of ca. 125 ha. The maximum water depth of the lake was 8.20 m in July 2000. Today the lake is a topographically closed basin with no major inlet and outlet. The Grizzly Lake area has a boreal continental climate with

marked seasonal temperature variations. In Slana (730 m a.s.l., ~ 10 km east of Grizzly Lake), the mean July and January temperatures are 13.7 and − 19.1 °C (period 1961–1990, WorldClimate 2005). The mean annual temperature is − 2.5 °C, and mean annual precipitation 391 mm. On the moraine ridges around the lake and on the mountain slope north of the lake, boreal forests are dominated by *Picea glauca* (white spruce), with *Betula neoalaskana* (Alaska birch) and *Populus tremuloides* (aspen) as common constituents. *B. kenaica* (Kenai birch) is also found in the region. Plant communities dominated by *Picea mariana* (black spruce) and *Sphagnum* species are prevalent in the extensive lowlands of the Copper River Basin. *P. mariana* forms nearly pure stands on the wet soils of the lowlands south of the lake. Within the region, *P. glauca* forms timberline stands, and this species can reach maximum elevations of 1100–1300 m a.s.l. Locally near Grizzly Lake, the *P. glauca* treeline is at about 900–1000 m a.s.l., and *Alnus viridis* (green alder) thickets grow up to about 1100 m a.s.l. On gentle slopes with wet soils, *P. mariana* extends to the treeline (Viereck and Little 1994). The altitudinal limits of *P. mariana* and *Betula* trees (mainly *B. neoalaskana*, Alaska birch) are at ca. 800–900 m in the study area (Hultén 1968); hence the elevation of Grizzly Lake at 720 m is not far below the altitudinal limits of these two tree species.

Lost Lake (also known as Chisholm Lake) is located in the Tanana valley north of the Alaska Range at 240 m a.s.l. The lake has a surface area of ca. 31 ha and a watershed area of ca. 780 ha. Today the lake has an inlet on the east, but no major surface outlet. The Lost Lake area experiences a boreal continental climate, with warmer summers and slightly cooler winters than in the Grizzly Lake area, but with comparable precipitation. At Big Delta (305 m a.s.l., ~ 5 km south of Lost Lake), the mean July and January temperatures are 15.6 and − 20.0 °C (period 1961–1990, WorldClimate, 2005). The mean annual temperature is − 2.3 °C, and mean annual precipitation 304 mm. Lost Lake is surrounded by bedrock ridges to the south, east and north, whereas the west end is formed by a dam of outwash sand and gravel deposited by the Tanana River during the late Pleistocene (Ager 1975). Local boreal forests around Lost Lake are dominated by *Picea glauca*. Other important forest species are *Betula neoalaskana* and *Populus tremuloides*. Closed *Picea glauca* and *Populus balsamifera* (balsam poplar) forests occur in the floodplains of the Tanana River, ca. 2 km southwest of the lake (Ager 1975). In the flatlands south of the Tanana River, where permafrost is usually close to the soil surface, *P. mariana* and *Larix laricina* (tamarack) are the most common trees. The uppermost treeline positions in the area are at ca. 1000–1200 m a.s.l., and the treeline is formed by *P. glauca*.

Material and methods

Coring

Two parallel short cores (GYG and GYH, 1 m apart) were taken with plexiglass tubes from the deepest

Table 1 ^{210}Pb and ^{14}C dates from Grizzly Lake

Lab code	Core	Depth (cm)	Material	^{210}Pb (yrs A.D.)	^{14}C dates (yrs B.P.)	Cal ages (2 σ[a]) A.D. or B.P.	Age in diagram (before A.D. 1950)
Bern	GYG	0–1	Bulk	1993 ± 0.3		A.D. 1994–1992	-44
Bern	GYG	1–2	Bulk	1980 ± 2.1		A.D. 1984–1976	-30
Bern	GYG	2–3	Bulk	1972 ± 2.3		A.D. 1977–1967	-22
Bern	GYG	3–4	Bulk	1963 ± 2.3		A.D. 1968–1958	-13
Bern	GYG	4–5	Bulk	1937 ± 6.1		A.D. 1949–1925	13
Bern	GYG	5–6	Bulk	1899 ± 12.9		A.D. 1925–1873	51
Ua-19438[b]	GYG	14–15	P, *Picea* N		485 ± 45[b]	465–631[b]	241
Ua-19439	GYG	18–19	P, *Picea* N, *Betula* F, *Ledum* L		330 ± 35	307–479	325
Ua-19440	GYG	19–20	*Picea* N, *Betula* F, P		290 ± 40	155–467	347
CAMS-84953	GYG	21–22	P, T, W		305 ± 40	292–476	364
CAMS-66875	GYA	33–35	W		360 ± 50	311–501	422
CAMS-84955	GYH	43–47	P, C, T, W *Betula* F		385 ± 40	316–511	492
CAMS-66876	GYA	73–75	T		1770 ± 50	1564–1819	1672
Ua-20497	GYE	75–79	P, L, *Alnus* FS, F,		1865 ± 45	1701–1917	1821
Poz-6496	GYF	91			2520 ± 30	2488–2741	2651
Ua-20498	GYE	118–125	P, *Betula* F, *Picea* N		3815 ± 70	3990–4417	4187
CAMS-59343	GYA	131–132	*Picea* T		4170 ± 40	4577–4835	4713
CAMS-82320	GYE	133–134	*Picea* N		4225 ± 40	4626–4858	4792
CAMS-82321	GYE	133–134	wood		4800 ± 45[b]	5331–5609[b]	4792
CAMS-82322	GYE	133–134	*Picea* CS		4125 ± 35	4528–4820	4792
CAMS-82323	GYE	133–134	C		4955 ± 40[b]	5598–5853[b]	4792
CAMS-82324	GYE	133–134	P		4180 ± 40	4581–4769	4792
CAMS-82325	GYE	133–134	P		4190 ± 40	4583–4843	4792
CAMS-82326	GYE	133–134	M		4160 ± 40	4571–4831	4792
CAMS-59342	GYA	193–194	L, *Vaccinium* L, *Picea* N, CS, *Populus* L,		6070 ± 50	6788–7156	6864
CAMS-59339	GYA	292–293	W		7100 ± 50	7835–8013	7806
CAMS-59340	GYA	292–293	W		6910 ± 40	7671–7833	7806
CAMS-59341	GYA	292–293	C		7430 ± 50[b]	8171–8367[b]	7806
CAMS-66877	GYB	351–353	T		7710 ± 40	8415–8581	8459
CAMS-59338	GYA	381	*Picea* CS		8150 ± 50	9004–9257	9061

[a]calibration of radiocarbon dates: Calib 5.01 (Stuiver and Reimer 1993; Reimer et al. 2004)

[b]Rejected date; C: charcoal, CS: cone scales, F: fruits, FS: fruit scales, L: leaves, M: mosses, N: needles, P: periderm, T: twig, W: wood

part of Grizzly Lake. Core GYG contained an intact sediment-water interface. For older sediments, long cores (including GYA, GYB, GYE, and GYF, see Table 1) were taken with a modified Livingstone piston corer (Wright et al. 1984). The cores were correlated according to lithostratigraphy, and the correlation precision among the different cores of Grizzly Lake is ca. ± 1 cm of depth. The core of Lost Lake (LL97B) was retrieved with a modified Livingstone piston corer from the deepest part of the lake.

Dating

The age of the surface sediments of Grizzly Lake (core GYG) was estimated with ^{210}Pb-dating. Bulk-sediment samples for ^{210}Pb dating (Table 1), each containing about 2 g of dry material, were measured with an HPGe detector for several days. From the measured count-rates the corresponding absolute activities and their errors were reduced in order to correct for the absolute decay-branch of the 46.5 keV γ-line of 4%, the detector efficiency, and counting statistics (Gäggeler et al. 1976). The decreasing specific ^{210}Pb activities (in Bq/g) with increasing depth permitted estimates of the absolute age relative to the surface of the core.

AMS (Accelerated Mass Spectrometry) ^{14}C ages were obtained from 24 and five terrestrial plant macrofossils from the sediments of Grizzly and Lost Lakes, respectively (Tables 1 and 2). Macrofossils from the Grizzly Lake sediments were used in a study into the effects of the types and amounts of plant macrofossils on ^{14}C chronologies
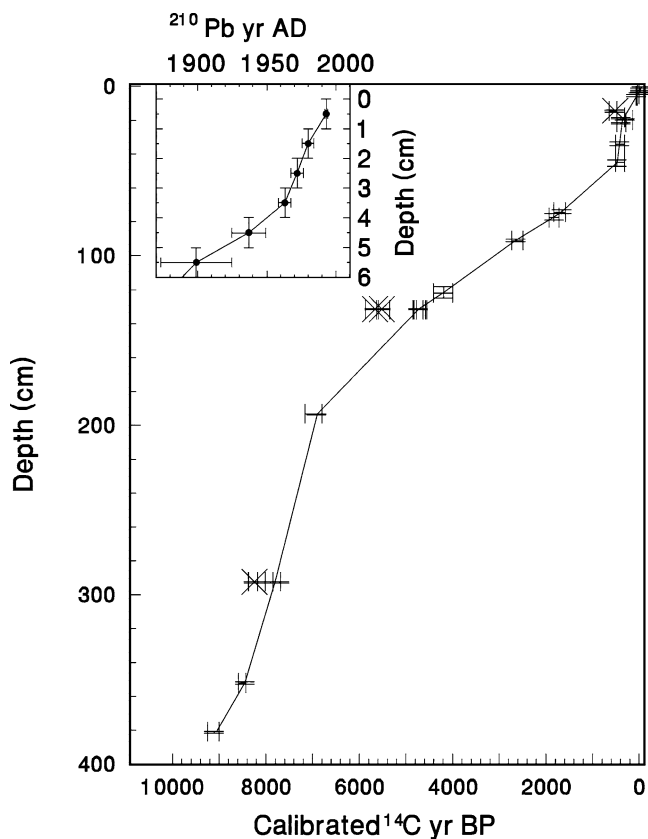
Fig. 2 Depth-age model of Grizzly Lake

(Oswald et al. 2005). The ^{14}C dates were converted to calibrated ages (cal B.P.) with the program Calib version 5.0.1 (Stuiver and Reimer 1993; Reimer et al. 2004). The age-depth models were based on linear interpolation of the mean values of calibrated ^{14}C dates. Three neighbouring ages of core GYG (Table 1, 18–19, 19–20, 21–22 cm) were amalgamated (OxCal 3.5, Ramsey 2001) and connected with linear interpolation to the oldest ^{210}Pb date and the subjacent A.D. ages (Fig. 2). Similarly we pooled groups of ages for the same depths (e.g. GYE 133–134 cm, Table 1).

Pollen and microscopic charcoal analysis

Pollen preparation followed standard procedures for glycerine samples (Moore et al. 1991). *Lycopodium* tablets (Stockmarr 1971) were added to subsamples of 1 cm^3 for estimating pollen concentrations (grains cm^{-3}) and accumulation rates (grains cm^{-2} yr^{-1}). Nomenclature of plant taxa follows that of the Flora of North America (FNA, 2005). Pollen type separation followed Clegg et al. (2005) for *Betula*, Hansen (unpublished) for *Picea*, and Punt et al. (2005) for *Alnus*. A minimum of 600 pollen grains, excluding aquatic pollen and spores, were counted at each level except at several levels where pollen concentrations were extremely low. The pollen diagrams were subdivided into local pollen assemblage zones (LPAZ) by us-

ing the zonation method of optimal partitioning (Birks and Gordon 1985) as implemented in the program ZONE, version 1.2, written by Steve Juggins. To determine the number of statistically significant zones in diagrams, we used the program BSTICK (Bennett 1996). At both sites the divisions of subzones (GY-1a, GY1b, GY-3a, GY-3b, and GY-3c for Grizzly Lake, and LL5a, LL5b, LL4a, LL4b, and LL4c for Lost Lake) are based on the results of ZONE analysis, but they are statistically insignificant.

Microscopic charcoal particles longer than 10 μm (or area >75 μm^2) were counted in pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005). Charcoal number concentration (particles cm^{-3}) and influx (particles cm^{-2} yr^{-1}) were estimated by using the same approach as for pollen (Stockmarr 1971). Mean sampling resolution for pollen and microscopic charcoal was 3 cm (corresponding to 70 yr) at Grizzly Lake and 7 cm (corresponding to 215 yr) at Lost Lake. Unfortunately, it is not possible to quantitatively estimate regional fire frequencies without contiguous sampling and without a calibration set comparing modern regional fire frequencies and the microscopic charcoal influx in surface sediments (Tinner et al. 1998).

Macrofossil analysis and MFI estimation

For the analyses of macroscopic charcoal and terrestrial macrofossils at Grizzly Lake, sediment samples of 18 cm^3 (0–50 cm) or 36 cm^3 (50–190 cm) were washed on a 200 μm mesh sieve, and macrofossils were identified following standard keys, for example Lévesque et al. (1988), and reference specimens. We distinguished tree versus shrub types of *Betula* macrofossils, but did not attempt to identify them to species level with the exception of *B. nana*. The macrofossil diagram shows numbers, for example, of needles, seeds, fruits, leaves, and areas, for example, of bark, wood, and charcoal, of macrofossils per volume of sediment (standardized to 20 cm^3). Areas were measured by fine-grid graph paper under a microscope. Macrofossil and macro-charcoal analyses were done on contiguous 1 cm subsamples, equivalent to 36 years on average. These analyses were restricted to the depths 0–190 cm (6800 cal B.P. to A.D. 2000) because it was not possible to penetrate through the silt layers with the large-diameter coring tubes used to retrieve the cores for macrofossil analysis (GYE and GYF).

In order to eliminate the effect of secondary charcoal, the raw data of macroscopic charcoal influx (mm^2 cm^{-2} yr^{-1}) was smoothed with a bandwidth of 100 years, using a weighted average function. This smoothed background was subtracted from the raw data to derive residual peaks. We then examined the statistical distribution of residuals and estimated the proportion of peak accumulation values above a threshold value P (Lynch et al. 2002). A sensitivity analysis was used to identify how the proportion of peak accumulation rates changes with P. This analysis was used to identify an intermediate range of charcoal accumulation rates between background and the largest peak values

(Clark et al. 1996; Lynch et al. 2002). We assumed that local fire events were represented by the range of charcoal accumulation rates within which the mean intervals in years between peak values were relatively insensitive to changes in P. This analysis identified the upper 14% of residual distribution, with charcoal peaks >0.003 mm^2 cm^{-2} yr^{-1}, as local fire events. The fire return interval is the time between two adjacent events, and the mean fire return interval (MFI) within a period was the average of all fire return intervals of that period. Explorative analyses showed that MFI estimates were similar when a smoother of 600-yr bandwidth (Whitlock and Larsen 2001) was used instead of a 100-yr bandwidth, if all residual peaks identified by the stronger smoother were considered for MFI estimation.

Correlation analysis

To investigate whether microscopic charcoal and pollen are significantly related to each other, we calculated correlation coefficients (r values) and applied a t-test to determine whether the r values were significantly different from 0 ($r \neq 0$, $\alpha = 5\%$, two-sided, Bahrenberg et al. 1985). The period 9000 cal B.P.-A.D. 2000) was selected for this analysis because boreal vegetation existed at both sites. Before 9500–9000 cal. B.P. the vegetation differed from that of modern Alaskan taiga in both areas, with *Populus, Betula* shrubs, and *Salix* as the most important constituents.

Results

Chronology and lithology

At Grizzly Lake, three ^{14}C dates appeared too old when compared with neighbouring dates and were rejected (Table 1, Fig. 2). At Lost Lake all dates were accepted (Table 2, Fig. 3). The sediments are gyttja from 0 to ca. 190 cm (0–6900 cal B.P.) at Grizzly Lake and 0 to ca. 320 cm (0–12,400 cal B.P.) at Lost Lake (Figs. 4 and 5). The lower sediments at Grizzly Lake are mainly silty material with minor gyttja layers (Fig. 4).

Pollen

Pollen percentage, concentration, and influx values are comparable at each of the two sites, and we therefore use the percentage results. The Lateglacial and early Holocene period before 9600 cal B.P. is recorded only at Lost Lake. Pollen assemblages in the oldest section (LPAZ LL-1 and LL-2; ca. 14,600–14,400 cal B.P.) are dominated by herbaceous taxa such as Poaceae, Cyperaceae and *Artemisia*. In zone LL-3 (14,400–13,200 cal B.P.) *Salix* pollen percentages increase (Fig. 5) to reach a peak at ca. 13,400 cal B.P.

LL-4 (13,200–8500 cal B.P.) is a rather long and heterogeneous pollen zone. It is therefore subdivided into three subzones. In LL-4a (13,200–11,200 cal B.P.), a prominent rise of shrub *Betula* pollen is accompanied by a decline of pollen of many herbaceous taxa such as *Artemisia,* Asteroideae and *Bupleurum*). Pollen of shrub *Betula* decreases at 12,500–11,600 cal B.P., when pollen of herbaceous taxa such as *Artemisia* and Poaceae increases. The first tree taxon to reach high pollen values is *Populus* at the beginning of the Holocene (LL-4b, ca. 11,200–9700 cal B.P.). The end of this *Populus* period, which is accompanied by the rise of *P. glauca* t., is also documented at Grizzly Lake near the base of the sediment core (LPAZ GY-1a, ca. 9600–9400 cal B.P.).
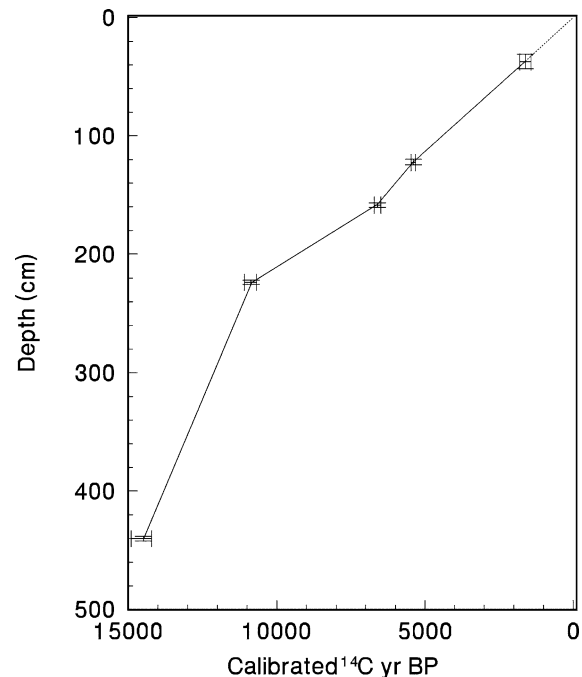

Fig. 3 Depth-age model of Lost Lake

Table 2 ^{14}C dates from Lost Lake; further explanations see Table 1

| Lab code	Core	Depth (cm)	Material	^{14}C dates (yrs B.P.)	Cal B.P. (2 σ∗)	Age in diagram (before A.D. 1950)
CAMS-68678	LL97B	31–43	P, L, *Betula* (tree) F, *Alnus*	1710 ± 60	1422–1812	1621
CAMS-68677	LL97B	120–124	W, T	4670 ± 40	5312–5475	5395
CAMS-68676	LL97B	156–160	T, P	5800 ± 40	6492–6717	6607
CAMS-68675	LL97B	222–226	W, P	9530 ± 50	10682–11091	10845
CAMS-68674	LL97B	438–442	*Potentilla* S	12460 ± 50	14204–14893	14482

284
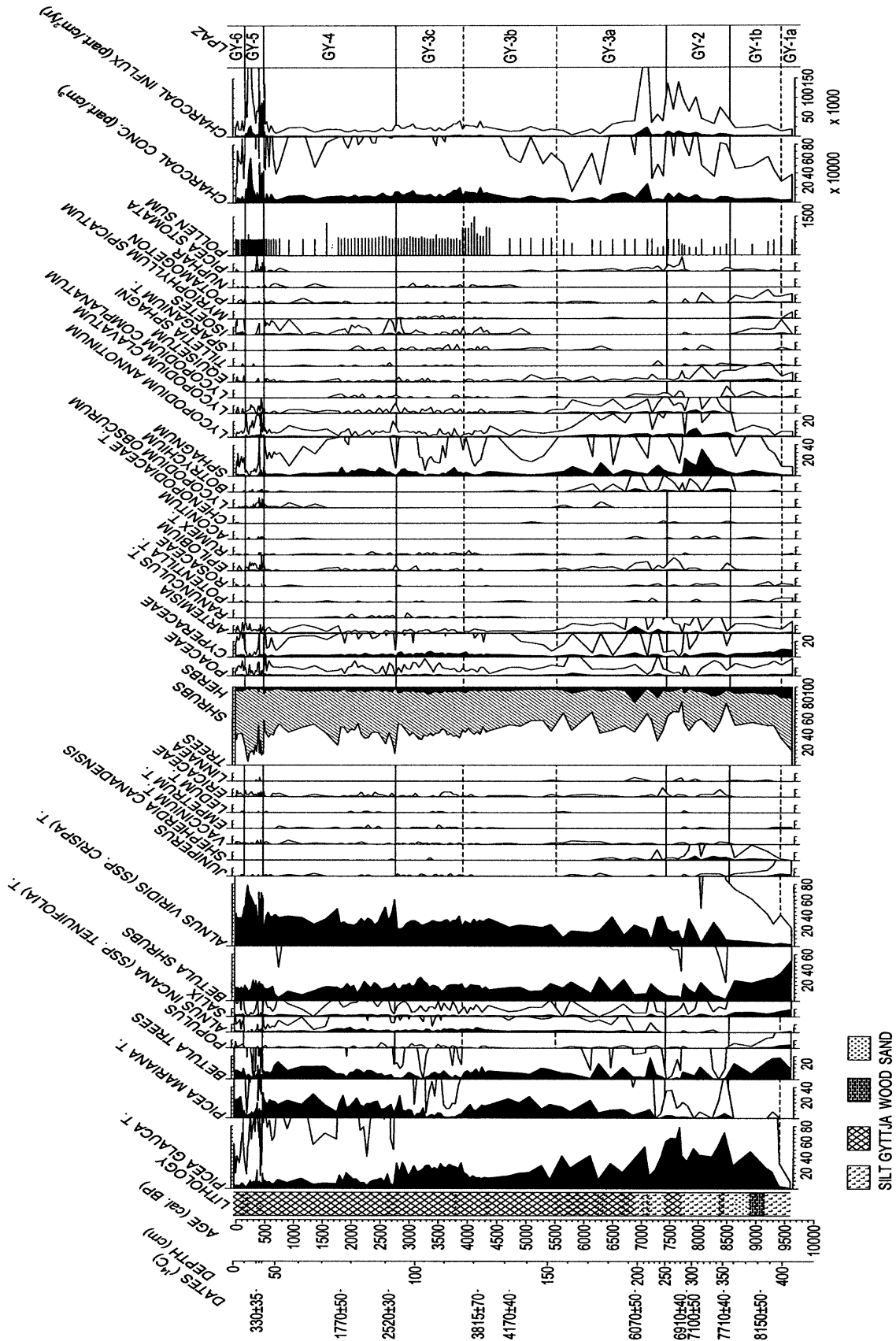
Fig. 4 Pollen percentage and microscopic charcoal diagram of Grizzly Lake. Empty curves show 10x exaggerations. Pollen and microscopic charcoal at Grizzly Lake were analyzed by W. Tinner for the depths 0–71 cm and 131–406 cm and by R. Beer for the depths 75.5–124.5 cm
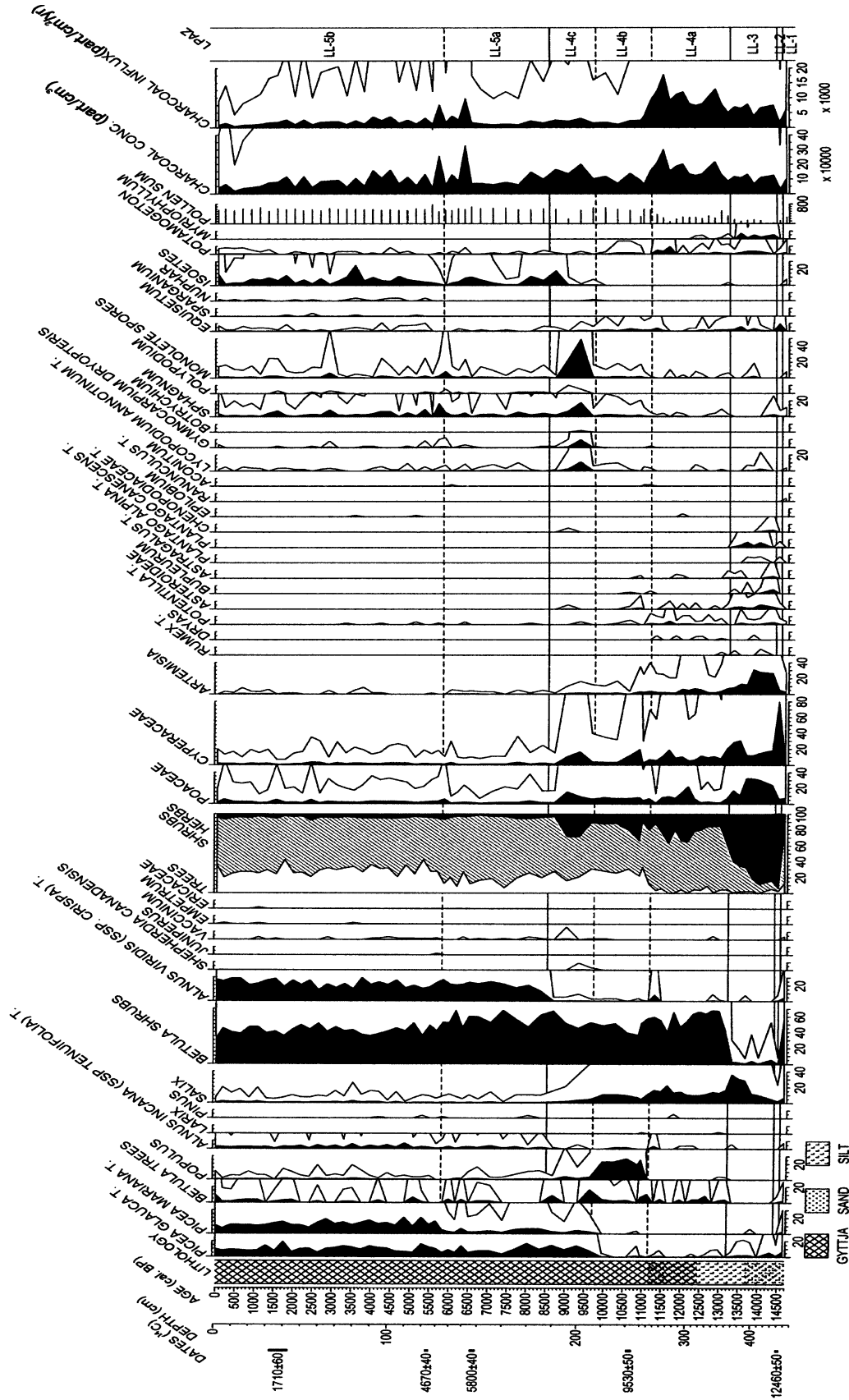
Fig. 5 Pollen percentage and microscopic charcoal diagram of Lost Lake. Empty curves show 10 × exaggerations. Pollen and microscopic charcoal were analysed by B. Scheurer

The subsequent pollen stratigraphies have similar characteristics between Grizzly and Lost Lakes. Between 9500 and 8400 cal B.P. (GY1b and LL-4c) the dominant pollen types are *Picea glauca* t. and *Betula*. Pollen of *Betula* shrubs is more abundant at Lost Lake than at Grizzly Lake throughout the entire Holocene. Statistically, the most marked change after 9700–9400 cal B.P. (*Populus* decline) occurs at ca. 8500 cal B.P. (GY-1 to 2; LL-4 to 5, Figs. 4 and 5) when pollen percentages of *Alnus viridis* increase at both sites. This change is accompanied by a more gradual increase of *Picea mariana* t., reaching maximum values at both sites (zone boundaries GY-3a to GY-3b and LL-5a to LL-5b, Figs. 4 and 5) around 5500 cal. B.P. when *P. glauca* t. declines at Grizzly Lake but not at Lost Lake. The pollen spectra do not vary greatly after 8500 cal B.P. at Lost Lake, with the co-dominance of shrub *Betula*, *P. mariana* t., *P. glauca* t., and *Alnus viridis* (LL-5). In contrast, major pollen assemblage changes occur at Grizzly Lake during the same period, as suggested by four statistically significant pollen zone boundaries at 7400, 2750, 450, and 150 cal B.P. These zone boundaries all coincide with marked variations in *Alnus viridis* pollen percentages.

In GY-2 (8500–7400 cal B.P.) pollen percentages of *Alnus viridis* increase and *P. glauca* t. pollen is abundant at Grizzly Lake, reaching maximum values of ca. 80%. During the same period, *P. glauca* t. pollen reaches maximum percentages also at Lost Lake, but there it never exceeds 20%. This high abundance of *P. glauca* t. at Grizzly Lake is associated with a maximum of *Shepherdia canadensis* and a major decrease in the pollen percentages of shrub *Betula* and *Salix* (Fig. 4, GY-2). Pollen percentages of *Picea mariana* t. are low (with a mean of 2%) in this zone, but they increase substantially at the beginning of LPAZ GY-3 (7400–2750 cal B.P.). The pollen spectra of GY-3 are dominated by *P. glauca* t., *P. mariana* t., *A. viridis*, and *Betula* (trees and shrubs). These spectra are similar to those of the same period at Lost Lake, although greater variations occur at Grizzly Lake. These variations define the three subzones GY-3a, GY-3b, and GY-3c, which are characterized mainly by the opposite stratigraphic patterns of *P. glauca* t. and *P. mariana* t. In GY-3a (7400–5500 cal B.P.) and GY-3c (3900–2750 cal B.P.) *P. glauca* t. is more abundant than *P. mariana* t., whereas between these two zones (GY-3b, 5500–3900 cal B.P.) the latter taxon is more prominent.

Pollen percentages of *A. viridis* increase abruptly at Grizzly Lake at the beginning of zone GY-4 (2750–450 cal B.P.). This change is accompanied by an increase of *P. mariana* t. and *Betula* tree type as well as a decrease of *P. glauca* t. A further increase of *A. viridis* occurs at the transition to GY-5 (450 cal B.P.), when all other tree and shrub pollen types with the exception of *Betula* shrub type decline (Fig. 4). In GY-6 (150 cal B.P. to present), pollen assemblages of Grizzly Lake are similar to those before 450 cal B.P.

Macrofossils, macroscopic charcoal, and MFI

High plant debris accumulation occurs at 4800–4400 cal B.P. and 450–300 cal B.P. (Fig. 6). In the macrofossil record, *Picea* is important throughout the period (many needle and periderm finds, Fig. 6). Fruit scales and fruits of *Betula* trees and shrubs are occasionally present. In one case it was possible to determine the presence of *B. nana* fruits. Fruit scales and fruits of *Alnus viridis* (ssp. *crispa*), as well as seeds of herbs such as *Rubus* and the aquatic plants *Nuphar polysepalum* and *Potamogeton* occur regularly throughout the record. *Sphagnum* reaches conspicuous mean concentrations of 10 leaves 20 cm^{-3} (Fig. 6), which is in good agreement with the microscopic spore record in the pollen diagram (Fig. 4).

Macroscopic charcoal and plant macrofossil concentrations display moderate correlation. For instance, the curves of charred and uncharred *Picea* needles resemble each other, and the two periods of high plant debris accumulation (4800–4400 cal B.P. and 450–300 cal B.P.) are also mirrored in the total macroscopic charcoal concentration and influx record (Fig. 6). The smoothing of the charcoal curve reduces the influence of these high background values, which probably resulted from increased secondary (charcoal) deposition. The residual macroscopic charcoal peaks show a rather even distribution over the past ca. 7000 years (Fig. 7), with no pronounced increasing or decreasing trends. The MFI is 261 yr for the period 6800 cal B.P. to A.D. 2000. To assess the potential effects of vegetational composition on fire occurrence (Hu et al. 1993; Lynch et al. 2002), we divided the macro-charcoal record into four periods based on the relative abundance of *P. glauca* and *P. mariana* and calculated the MFI value of each period (Table 3). The longest MFI of the entire record is ∼386 years between 6800 and 5500 cal B.P. when *P. glauca* dominated over *P. mariana*. MFI then decreased to 254 ± 170 years between 5500 and 3900 cal B.P. when *P. mariana* was more abundant than *P. glauca*. MFI was the lowest (ca. 200 ± 50–100 years) after 3900 cal B.P., and no change in MFI was detected when pollen indicates a dominance shift from *P. glauca* to *P. mariana* around 2750 cal B.P.

Microscopic charcoal

At Lost Lake the microscopic charcoal concentrations reach a maximum of 328,727 particles cm^{-3} (or 87.5 mm^2 cm^{-3} using the equation of Tinner and Hu 2003) at ca. 6300 cal B.P. High levels of microscopic

Table 3 MFI (mean fire return interval) and vegetation type at Grizzly Lake; NA: non applicable, too low numbers

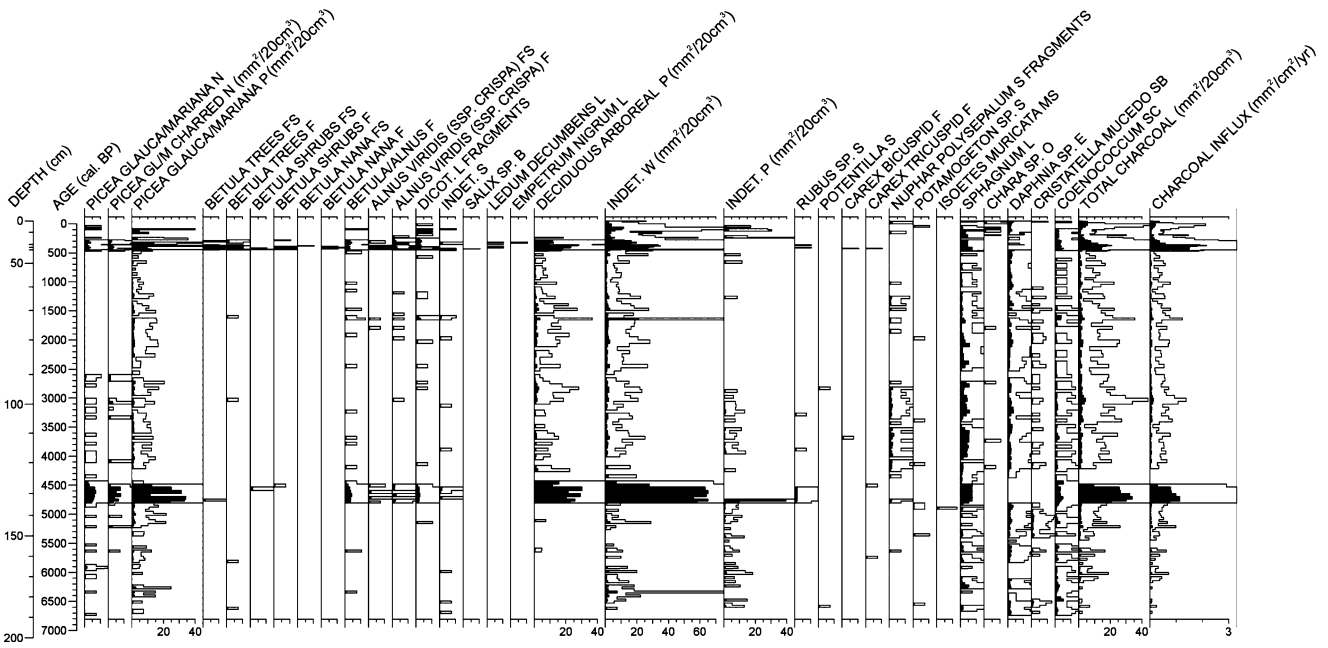| Vegetation type: dominant *Picea* species in pollen record	Period (cal yr B.P.)	MFI (yr)	MFI std. dev
Picea mariana	− 50 to 2750	203	91
Picea glauca	2750 to 3900	201	41
Picea mariana	3900 to 5500	254	170
Picea glauca	5500 to 6800	386	NA
Complete record	− 50 to 6800	261	161

Fig. 6 Macrofossil concentration diagram of Grizzly Lake. All values are square root transformed for better depiction of minor fluctuations. Empty curves show 10x exaggerations. B: buds, E: ephippia, F: fruit, FS: fruit scales, L: leaves, MS: macrospores, N: needles,

O: oogonia, P: periderm, S: seeds, SB: statoblasts, SC: sclerotia, W: wood. Macrofossils and macroscopic charcoal was analysed by P. Kaltenrieder

charcoal concentrations also occur around 5700 (256,295 particles cm^{-3} or 69.3 mm^2 cm^{-3}), 9300 (201,375 particles cm^{-3} or 55.3 mm^2 cm^{-3}), and 11,450 cal B.P. (300,720 particles cm^{-3} or 80.5 mm^2 cm^{-3}). Before 10,700 cal B.P. the microscopic charcoal influx curve of Lost Lake is tentative because of major sedimentological changes that are not well ^{14}C dated. It is conceivable that the charcoal influx peaks between ca. 12,500 and 11,300 cal B.P. are inflated by (undated) slower sediment accumulation rates (gyttja instead of silt). During the Holocene, microscopic charcoal influx reaches maximum values of 9764 particles cm^{-2} yr^{-1} or 3.3 mm^2 cm^{-2} yr^{-1} around 6300 cal B.P.

At Grizzly Lake, microscopic charcoal concentrations reach maximum values at 200 cal B.P. (614,296 particles cm^{-3} or 157.1 mm^2 cm^{-3}) and 7050 cal B.P. (258,365 particles cm^{-3} or 69.8 mm^2 cm^{-3}). These peak values fall into periods with generally high microscopic charcoal values from 150 to 450 cal B.P. and from 7100 to 6300 cal B.P. (Fig. 4). The corresponding microscopic charcoal influx peaks attain 93,762 particles cm^{-2} yr^{-1} (or 27.1 mm^2 cm^{-2} yr^{-1}) at 400 cal B.P. and 24,507 particles cm^{-2} yr^{-1} (or 7.7 mm^2 cm^{-2} yr^{-1}) at 7050 cal B.P. In addition, moderately high microscopic charcoal accumulation rates occur between 8400 and 7400 cal B.P. (corresponding to LPAZ GY-2 with the dominance of *P. glauca* t.; Fig. 4). On average, charcoal influx values for the period 9500-0 cal B.P. are more variable and about five times higher at Grizzly Lake (mean = 12,188, SD = 22,670 particles cm^{-2} yr^{-1} or mean = 4.0, SD = 7.2 mm^2 cm^{-2} yr^{-1}) than at Lost Lake (mean = 2190, SD = 1728 particles cm^{-2} yr^{-1} or mean = 0.8, SD = 0.6 mm^2 cm^{-2} yr^{-1}).

Correlation analysis

Several pollen types are significantly correlated with microscopic charcoal influx at Grizzly Lake between 9000 cal B.P. and A.D. 2000 (Fig. 8). The correlation coefficients are significantly positive for *Alnus viridis*, *Epilobium*, *Lycopodium clavatum*, and *L. annotinum*, and negative for Cyperaceae, Poaceae, *Salix*, *Populus*, *Picea mariana* t., and *P. glauca* t. In agreement, the sum of shrubs (which is dominated by *A. viridis* and *Betula*) is positively correlated with charcoal, whereas the sums of trees and herbs show significant negative correlation coefficients (Fig. 8). At Lost Lake the positive correlation coefficient for *P. glauca* slightly exceeds the significance limit, and none of the other pollen types shows significant correlation with microscopic charcoal.

Discussion

Vegetational and climatic changes

In the Lost Lake area, herb tundra with Poaceae, Cyperaceae, and *Artemisia* as dominant taxa prevailed on the landscape before ca. 14,400 cal B.P. *Salix* became a dominant component of the herb tundra at ca. 14,400 cal B.P. When *Betula* shrubs expanded on the tundra around 13,200 cal B.P., many herbaceous taxa such as *Artemisia* and Asteroideae decreased in abundance. These patterns are broadly consistent with previous studies in central Alaska (Ager 1975; Anderson et al. 1990; Hu et al. 1993; Bigelow and
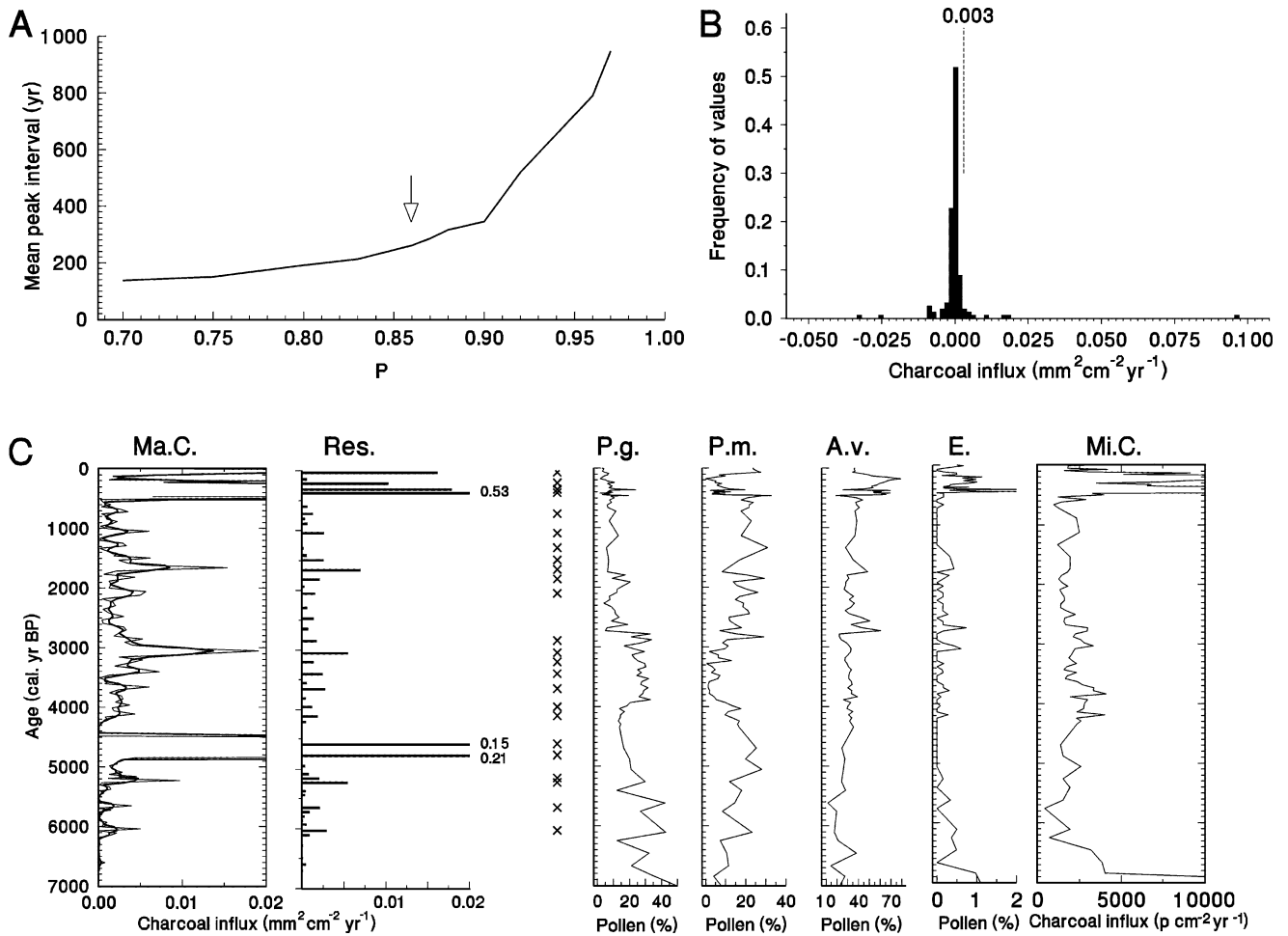
Fig. 7 Summary charcoal influx and pollen percentage diagram. **A** Sensitivity analysis of macroscopic charcoal results for Grizzly Lake. The arrow indicates the point (0.86) where P is less sensitive to mean fire return interval (MFI) (Lynch et al. 2002). Fires were estimated to be 14% of the residual distribution using a 100 yr bandwidth smoother, with charcoal peaks >0.003 mm^2 cm^{-2} yr^{-1}. **B** Distribution of residuals, x-axis was truncated at -0.05 and 0.1 mm^2 cm^{-2} yr^{-1}. **C** Smoothed charcoal accumulation rates using a 100-yr win-

dow and residual peaks. The $\times$ indicate the residual peaks used for MFI estimation (charcoal peaks >0.003 mm^2 cm^{-2} yr^{-1}). Selected pollen types (percentages) and microscopic charcoal influx (<10,000 particles cm^{-2} yr^{-1} or <3.3 mm^2 cm^{-2} yr^{-1}) are given for comparison with macroscopic charcoal influx. Ma.C.: macroscopic charcoal, Res.: residual peaks, P.g.: *Picea glauca* t., P.m.: *Picea mariana* t., A.v.: *Alnus viridis*, E.: *Epilobium*, Mi.C.: microscopic charcoal

Fig. 8 Correlograms showing correlation coefficients between microscopic charcoal influx and selected pollen types for the past 9000 years. Correlation coefficients outside the lines are significant at $P = 0.05$
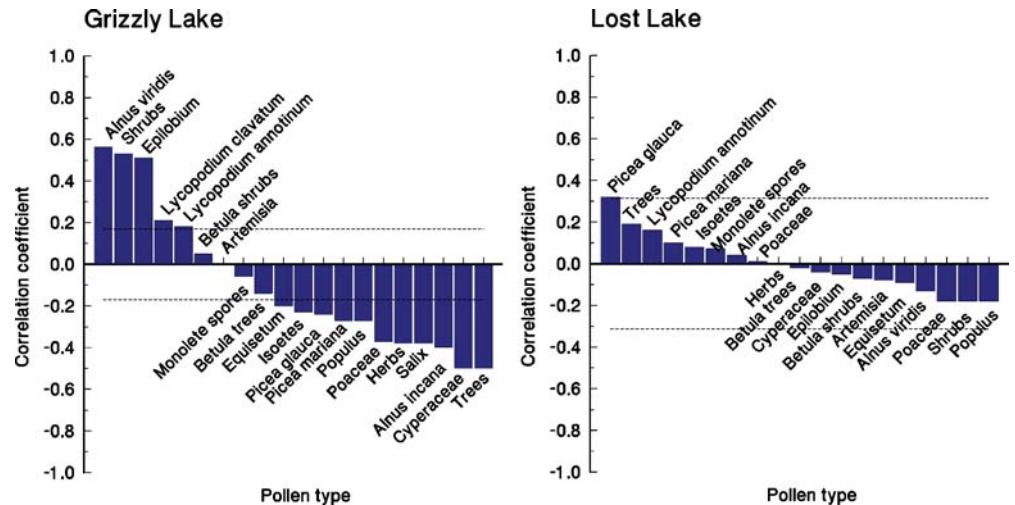
Edwards 2001). However, because the chronologies of most published pollen records from Alaska are based on bulk-sediment radiocarbon dates, they are probably compromised by hard-water effects and/or old carbon washed in from soils of the watershed area, resulting in erroneously old age estimates. Our new record supports the speculation that at many sites across north-central Alaska, the expansion of *Betula* occurred later than previously estimated (Bigelow and Edwards 2001; Carlson and Finney 2004). At Windmill Lake, 120 km southwest of Lost Lake, *Salix* and *Betula* expansions in the lateglacial tundra occurred at ca. 14,500 and 13,500 cal B.P. respectively, which is in general agreement with the Lost Lake record (ca. 14,400 and 13,200 cal B.P.). However, only one radiocarbon date is available for the period of interest at each of these two sites.

The *Salix* expansion in the herb tundra at Lost Lake probably reflects climatic warming at the beginning of the Lateglacial. Around 14,500 cal. B.P. temperatures increased markedly at many areas in the northern hemisphere, by about 8–12 °C in Greenland and 4–6 °C in Europe (Björck et al. 1998; von Grafenstein et al. 1999; Lowe and Hoek 2001; Heiri and Millet 2005), leading to pronounced changes in the biosphere such as an establishment of woodland for instance in central Europe at ca. 14,500 cal B.P., the beginning of the Bølling period (Lotter 1999; Litt et al. 2001, 2003). Similarly, the replacement of herb tundra by *Betula* shrub tundra probably resulted from climatic warming and increased moisture at 13,500 cal B.P. (Bigelow and Edwards 2001; Hu et al. 2002). Rapid responses of *Salix* and *Betula* to climatic amelioration were possible because these shrubs probably grew in scattered localities in the herb tundra prior to 14,500 cal. B.P.

The diminished *Betula* shrub cover in association with the increased abundance of herbaceous taxa at 12,500–11,600 cal B.P. possibly reflects the environmental effects of the Younger Dryas, a climatic reversal characterized by cooling and/or decreased effective moisture in at least some areas of Alaska (Engstrom et al. 1990; Peteet and Mann 1994; Hu et al. 1995, 2002; Hu and Shemesh 2003). Similar patterns of vegetational change suggesting a transient opening of the *Betula* shrub tundra during the YD chronozone were recorded at other Alaskan sites (Hu et al. 1995, 2002; Bigelow and Edwards 2001).

Between ∼ 11,200 and ∼ 9600 cal B.P. *Populus* probably formed dense stands around Lost Lake and along rivers. *Betula* shrubs remained abundant, but herbaceous taxa such as *Artemisia* and *Potentilla* t. continued to decline. *Populus* stands disappeared rather abruptly at ca. 9600 cal B.P. around Lost Lake and at ca. 9600–9400 cal B.P. around Grizzly Lake. The *Populus* period probably reflects the Holocene thermal maximum (HTM; Kaufman et al. 2004) and/or more alluviation (e.g. Hu et al. 1993; Bigelow and Edwards 2001) in the region, although little non-pollen evidence of the HTM exists in Alaska (Kaufman et al. 2004) and the interpretation of *Populus* as a temperature indicator itself is confounded by ecological processes (Hu et al. 1993; Anderson and Brubaker 1994). Nonetheless, preliminary chironomid data show that summer temperatures were higher than today's during the *Populus* period (B. Clegg, I. Walker and F.S. Hu, pers. comm.). In addition, the onset of this period at ca. 11,200 cal B.P. corresponds to increased temperatures at 11,600–11,200 cal B.P. (Dansgaard et al. 1993; Grootes et al. 1993; Lowe and Hoek 2001) in the North Atlantic region.

In the pollen records of Lost Lake, Windmill Lake (Bigelow and Edwards 2001) and Jan Lake, 180 km southeast of Lost Lake (Carlson and Finney 2004), the beginning of the *Populus* period clearly occurred after the termination of the YD (ca. 11,600 cal B.P.). In contrast, many pollen records from Alaska with bulk sediment ^{14}C chronologies show older ages for the *Populus* expansion, many of which fall within the YD chronozone. Thus despite the existence of a dense network of pollen records from Alaska, well dated pollen profiles coupled with temperature-sensitive proxy data, such as chironomid assemblages, are much needed to test whether the early Post-glacial *Populus* communities were related to higher temperatures in Alaska.

Among the common constituents of contemporary boreal forests in Alaska are tree species of *Betula*, whose histories are largely unknown because previous pollen studies did not distinguish tree *versus* shrub *Betula* and because few macrofossil studies have been attempted (Hu et al. 1993). Our pollen record from Grizzly Lake suggests that *Betula* trees were rather common from the onset of the record at 9500 cal B.P. *Betula* seeds provide independent and unambiguous evidence that *Betula* trees grew near this site no later than ca. 6800 cal B.P. (Fig. 6). However, it is more difficult to assess the history of tree *Betula* at Lost Lake, where *Betula* tree type pollen rarely exceeds 10%. In the surface-sediment pollen assemblage of Lost Lake, *Betula* trees attained 10% and *Betula* shrubs 32%, even though *Betula* trees are more common in the modern boreal vegetation around the lake (Ager 1975). A plausible explanation for the under-representation of *Betula* tree pollen is that *B. neoalaskana* was the only tree species in that area, whereas several *Betula* tree species including *B. kenaica* or *B. kenaica* hybrids (Hultén 1968) existed at Grizzly Lake as at present. As concluded by Clegg et al. (2005), among the Alaskan tree birches, *Betula neoalaskana* is the only species of which the pollen cannot be separated quantitatively from those of shrub birches by using the ratio of grain diameter to pore depth. Thus it is likely that the tree *Betula* pollen profile at Lost Lake probably does not faithfully reflect the abundance of *Betula* trees around this lake.

Accompanying the decline of *Populus* at Lost and Grizzly Lakes was the expansion of *Picea glauca*, which probably co-dominated the landscape with tree species of birch during the middle Holocene (Hu et al. 1993). By 9000 cal B.P., *P. glauca* had become a dominant species in the landscape at these sites (Figs. 4 and 5). *Shepherdia canadensis* (buffaloberry) occurred in the early Holocene spruce forests or woodlands around Grizzly Lake. As at present, *S. canadensis* probably occurred on nutrient-poor sandy, gravely, or rocky soils, or in recently burned areas of closed spruce-hardwood forests (Viereck and Little 1994). Before 7200 cal B.P. *Picea mariana* occurred in small amounts at Grizzly Lake and Lost Lake. This taxon increased to reach maxi-

mum abundance at ca. 5500 cal B.P. at Grizzly Lake and at ca. 5000 cal B.P. at Lost Lake. At Grizzly Lake the increase of *P. mariana* at 7200 cal B.P. was accompanied by the decline of *S. canadensis*, suggesting either diminished fire activity and/or the development of organic soils around this site.

Alnus viridis expanded ca. 8500–8400 cal B.P. in the regions of both Lost and Grizzly Lakes. As at present, this species probably formed shrub thickets along rivers, on mountain slopes, and above the treeline. The expansion of *Alnus* has often been interpreted as indicating elevated effective moisture, especially through increased snow, and/or climatic cooling (Anderson and Brubaker 1994; Hu et al. 1995, 1998, 2001). In most of the pollen records from central Alaska, *Alnus* expanded after *Picea glauca* (Ager 1975; Anderson et al. 1990; Hu et al. 1993; Lynch et al. 2002). Only at Windmill Lake did the *Alnus* and *Picea glauca* expansions occur approximately at the same time (Bigelow and Edwards 2001).

At Grizzly Lake, the abundance of *Picea*, *Betula*, and *A. viridis* fluctuated markedly after 8400 cal B.P. (Fig. 4). For example, *P. glauca* expanded at the expense of *P. mariana* from 3900 to 2750 cal B.P. (pollen zone GY-3c). In addition, transient declines of tree *Betula* and *P. mariana* occurred at 450–150 cal B.P. in association with the increases of *A. viridis* and *Betula* shrubs. Although the climatic significance of some of these pollen shifts cannot be deciphered with confidence, the vegetational changes between 450 and 150 cal B.P. correspond to the Little Ice Age. These vegetational changes probably reflect a decrease in growing season temperature (Forester et al. 1989; Hu et al. 2001). However, *Alnus viridis* is also a sprouter well adapted to fire disturbance (Viereck and Little 1994), and thus its increase may have resulted from increased fire activity.

Most of the vegetational fluctuations of the past 8400 years did not occur at Lost Lake, and they seemed rather unusual compared to previously published pollen diagrams, which typically did not exhibit major changes during the mid and late Holocene after the initial mass expansion of *Alnus* (Hu et al. 1998). Although some fluctuations in the abundance of *Picea*, *Betula*, and *Alnus* were observed at Windmill Lake, they were mostly represented by one sample only, so that random noise could not be excluded as a possible explanation (Bigelow and Edwards 2001). In contrast, the pollen assemblage fluctuations at Grizzly Lake are each defined by multiple samples with high pollen counts, and they probably reflect meaningful vegetational shifts, as suggested by the statistical significance of the pollen zone boundaries. We attribute these fluctuations to the greater vegetational sensitivity of the area around Grizzly Lake than at the previously studied sites because of its ecotone position. Located at 720 m above sea level, Grizzly Lake is near the altitudinal limits of tree *Betula* and *Picea mariana*. Thus the site is ideal for detecting the effects of climatic change on these taxa. We assume that Holocene climate cooling caused these trees to decline and that the resulting gaps were invaded by taxa more adapted to cold, such as *A. viridis* and shrub *Betula*. Indeed, such a vegetational response to climatic cooling would generate the pollen patterns observed during the LIA-period. In our pollen record from Grizzly Lake, marked increases of *A. viridis* and declines of trees (*Picea*, tree *Betula*) are also recorded around 2800 and 8500–8200 cal B.P., when transient temperature declines occurred in Alaska and over the northern hemisphere (van Geel et al. 1998; Bond et al. 2001; Hu et al. 2003; Heiri et al. 2004).

For the past 7000 years the macrofossil record confirms the local presence of the most important constituents of pollen-inferred vegetation such as *Picea, Betula* trees, *Betula* shrubs, and *Alnus viridis* around Grizzly Lake. One distinct pattern is the increased abundance of periderms of deciduous woody taxa around 4500 cal B.P., suggesting population expansions of taxa such as *Alnus viridis* and shrub *Betula*. This vegetational change is not clearly discernable in the pollen record, although it may be related to the gradual increase in the abundance of *A. viridis* after ca. 5500–4500 cal B.P. The macrofossil record also reveals that *Sphagnum* bogs existed near the lake throughout the past 7000 years, as suggested by a large amount of *Sphagnum* leaves in the sediment. The presence of macrofossils such as *Nuphar polysepalum, Potamogeton, Isoëtes muricata,* and *Chara* suggests that these taxa were common aquatic plants in Grizzly Lake.

Fire-vegetation-climate relationships

At Lost Lake, regional fires might have been particularly important during the lateglacial tundra period, as suggested by the maximum microscopic charcoal influx values of the entire record. However, because of the chronological uncertainties that may have affected our estimates of charcoal accumulation, it is difficult to determine if fire activity indeed exceeded that of the Holocene epoch. At Sithylemenkat Lake in north-central Alaska, the highest charcoal abundance prior to the establishment of boreal forests also occurred during the Lateglacial (Earle et al. 1996), although this study applied an unusual method to quantify sediment charcoal. In addition, recent macroscopic charcoal studies in the southern Brooks Range found abundant charcoal in the lateglacial sediments, suggesting that fire frequencies during this period were probably among the highest of the Post-glacial periods (Higuera et al 2005; Hu et al. in press). Despite the fact that it is difficult to compare these studies because of their methodological differences, together they raise the possibility that in some areas in Alaska, the lateglacial tundra probably burned as frequently as the late Holocene spruce forests. This inference differs drastically from the modern fire regimes of Alaska where boreal forests generally burn much more frequently than shrub tundra. Fire was probably more important in the Lateglacial than in the modern birch shrub tundra possibly because of (1) much drier climatic conditions of the Lateglacial and (2) high availability of fine fuels in the rather dense birch-tundra communities of the Lateglacial (Hu et al. in press).

During the Holocene, regional scale fire activity did not seem to have varied greatly based on the Lost Lake microscopic charcoal data, with the exception of two periods of

markedly higher charcoal accumulation rates around 6300 and 5300 cal B.P. In the Grizzly Lake area, microscopic charcoal suggests that the Holocene fire regime was more variable. Fires were particularly important during the periods 8500 to 6800 and 450 to 150 cal B.P., as suggested by high micro-charcoal influx values. Regional fire activity was significantly higher in the Grizzly Lake region than around Lost Lake. The striking difference in micro-charcoal influx between the regions possibly reflects the topographic situations of the sites, for fires are especially intensive on steep (south-facing) mountain slopes such as in the area around Grizzly Lake, whereas in flat areas fire intensity and rapidity of fire spread tend to be less pronounced.

The macro-charcoal record from Grizzly Lake offers fire history information that differs greatly from the microscopic charcoal inferences from the same site. Because macro charcoal has short dispersal ranges (Clark et al. 1996; Lynch et al. 2004a), its record indicates local fire events that may or may not be comparable with regional fire activity. In addition, we do not have macro charcoal data for the period before 6800 cal B.P. for comparison. However, consistent with the micro charcoal results, the macro charcoal record shows peak accumulation rates with multiple fire events 450–150 cal B.P.

The estimated MFI of ~200 years for the past 3900 years at Grizzly Lake is strikingly similar to results of local fire reconstructions at two other sites in the Copper River basin (Lynch et al. 2004a). On the basis of lithological and macrofossil data, Lynch et al. (2004a) inferred that the region became wetter during the past ~4000 years than before, and they speculated that increased lightning frequency might have increased fire frequency during the late Holocene. However, the effect of *P. mariana* on fire occurrence appears more equivocal at Grizzly Lake. Although the *P. glauca* dominated period before 5500 cal B.P. indeed had a lower fire frequency than during the two subsequent periods when *P. mariana* dominated the regional vegetation, *P. mariana* dominated vegetation did not burn more frequently than *P. glauca* dominated forests within the past 3900 B.P. Because of the local nature of macroscopic charcoal records (Clark et al. 1996; Lynch et al. 2004b), differences in reconstructed fire histories among these sites are not surprising, macroscopic and/or multiple macroscopic charcoal records are needed to discern patterns of vegetation-fire-climate interaction representative of each region (Hu et al. in press).

While vegetation as a control of fires has been a focus of discussion in previous fire studies in Alaska (Lynch et al. 2002, 2004a; Hu et al. in press), the effects of fire on Holocene vegetational change remain largely unknown in Alaska. We conducted correlation analyses of pollen and microscopic charcoal to assess whether fires affected vegetation at the regional scales for the past 9000 cal B.P. At Lost Lake no significant relationship exists between microscopic charcoal and pollen (Fig. 8), suggesting that fires probably did not cause major vegetational shifts (or *vice versa*) detectable with pollen and microscopic charcoal at these resolutions. However, at Grizzly Lake, some of the regional variations in the fire regime were accompanied by conspicuous vegetational changes. For instance, fire was important during the periods between 8500 and 6300 B.P. and between 450 to 150 cal B.P. when *Epilobium* (fireweed) and *A. viridis* increased abruptly or reached maximum abundance (Figs. 4 and 7). The significant correlation coefficients confirm that the expansions of *A. viridis, Epilobium, Lycopodium clavatum*, and *L. annotinum*, and the reduction of trees such as *P. glauca* and *P. mariana* were linked to increased fire activity (Fig. 8). This inference agrees with observed vegetational changes after stand-replacing fires in the modern boreal forests of Alaska (Viereck and Little 1994).

However, it is more difficult to explain the negative correlation between charcoal influx and several fire adapted taxa, including *Salix, Alnus incana*, and several herbaceous taxa such as Poaceae, Cyperaceae, and *Equisetum* (Fig. 8). Fire occurrence was probably not directly related to the decline of these taxa. Rather, these plants were abundant on wet soils near the lake shore, and drier climatic conditions that might have increased fire activity probably reduced the extent of their wet habitats. Similarly, the significant negative correlation between the aquatic plant *Isoëtes* and microscopic charcoal probably reflects the decline of *Isoëtes* populations because of lower lake levels under drier climatic conditions. This explanation is inconsistent with the millennial-scale fire-climate relationship characterized by an increase in fire frequency with the Holocene trend of decreasing temperature and increasing effective moisture, as documented at a number of sites in Alaska (Lynch et al. 2002, 2004a; Hu et al. in press). It is conceivable that superimposed on this millennial-scale pattern, fire occurrence at multi-decadal to multi-centennial scales increased with decreased effective moisture and the resultant increase in vegetational flammability. For example, regional fire activity increased substantially around Grizzly Lake during the Little Ice Age when the climate of south-central Alaska became drier and cooler (Forester et al. 1989). Conversely, wetter/warmer climatic conditions probably reduced biomass flammability and fire occurrence after the LIA in the Grizzly Lake area.

Similar to the Holocene millennial fire frequency pattern based on macroscopic charcoal records from Alaska, Carcaillet et al. (2001) found that fire frequency increased in eastern Canada during the late Holocene when the regional (annual) climate became wetter. The authors attributed it to greater fire season moisture deficits in dry summers under a generally wetter climatic regime of the late Holocene. In contrast, such a fire-climate relationship probably resulted from increased vegetational flammability with the development of *P. mariana* as a dominant species (Hu et al. 1993; Rupp et al. 2002; Lynch et al. 2002) and/or increased lightning frequency (Lynch et al. 2004a) in Alaska. Our macroscopic charcoal results from Grizzly Lake also showed increased fire frequency around 5500 cal B.P. when *P. mariana* replaced *P. glauca* as the dominant tree species. However, this relationship is ambiguous after 5500 B.P. At the centennial scales, Bergeron and Archambault (1993) reported higher fire frequency in eastern Canada during the LIA when the climate was overall drier than after the

LIA, similar to our LIA interpretations at Grizzly Lake. These results imply that projecting the effects of future climatic changes is not straightforward for the boreal biome. This inference is broadly consistent with recent modelling studies. Simulations using general atmospheric circulation models suggest that with future climatic warming, fire frequencies will increase in some boreal regions and decrease in others in North America (Flannigan et al. 1998, 2001). Thus the relationships among fire, vegetation, and climate in the boreal forest biome are complex and dependent on time and place.

Dedication This study is dedicated to Brigitta Ammann. She bore this and many other projects by her steady support, encouragement, and innovative ideas. One of her most characteristic scientific attitudes is to address new questions in new landscapes with a broad set of palaeoecological tools. For instance she initiated W.T. to investigate palaeofire issues in the Alps in 1993. In 1998 she supported the idea of F.S.H. and W.T. to investigate the fire history of the Copper River Basin by offering a post-doctoral position to W.T. in Bern. Among other things this led to a Swiss NSF post-doc fellowship for W.T. to visit F.S.H. in Urbana-Champaign. This visit in 1999/2000 allowed the start of the Alaskan investigations presented in this study. During the following years Brigitta - who had joined the expedition to Alaska in 1999 - always supported our Alaskan investigations, for instance by encouraging students (R.B. and B.S.) to take over master theses on the Grizzly and Lost Lake cores or by offering laboratory assistance and financing radiocarbon dates. Thus it is difficult to express how deeply indebted we are to Brigitta for her generous, tolerant and congenial attitude during all these years!

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