A 700-YEAR PALEOECOLOGICAL RECORD OF BOREAL ECOSYSTEM RESPONSES TO CLIMATIC VARIATION FROM ALASKA

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Abstract. Recent observations and model simulations have highlighted the sensitivity of the forest–tundra ecotone to climatic forcing. In contrast, paleoecological studies have not provided evidence of tree-line fluctuations in response to Holocene climatic changes in Alaska, suggesting that the forest–tundra boundary in certain areas may be relatively stable at multicentennial to millennial time scales. We conducted a multiproxy study of sediment cores from an Alaskan lake near the altitudinal limits of key boreal-forest species. Paleoecological data were compared with independent climatic reconstructions to assess ecosystem responses of the forest–tundra boundary to Little Ice Age (LIA) climatic fluctuations. Pollen, diatom, charcoal, macrofossil, and magnetic analyses provide the first continuous record of vegetation–fire–climate interactions at decadal to centennial time scales during the past 700 years from southern Alaska. Boreal-forest diebacks characterized by declines of *Picea mariana, P. glauca,* and tree *Betula* occurred during the LIA (AD 1500–1800), whereas shrubs (*Alnus viridis, Betula glandulosa/nana*) and herbaceous taxa (*Epilobium, Aconitum*) expanded. Marked increases in charcoal abundance and changes in magnetic properties suggest increases in fire importance and soil erosion during the same period. In addition, the conspicuous reduction or disappearance of certain aquatic (e.g., *Isoetes, Nuphar, Pediastrum*) and wetland (*Sphagnum*) plants and major shifts in diatom assemblages suggest pronounced lake-level fluctuations and rapid ecosystem reorganization in response to LIA climatic deterioration. Our results imply that temperature shifts of 1–2°C, when accompanied by major changes in moisture balance, can greatly alter high-altitudinal terrestrial, wetland, and aquatic ecosystems, including conversion between boreal-forest tree line and tundra. The climatic and ecosystem variations in our study area appear to be coherent with changes in solar irradiance, suggesting that changes in solar activity contributed to the environmental instability of the past 700 years.

Key words: boreal forest; climatic warming; fire disturbance; Little Ice Age; paleoecology; peatlands; tundra; vegetation response; wetlands.

INTRODUCTION

Boreal ecosystems are highly sensitive to natural and anthropogenic climatic change (e.g., MacDonald et al. 1993, Chapin et al. 2004). Recent studies (e.g., Chapin and Starfield 1997, Alm et al. 1999, Weltzin et al. 2000, Smith et al. 2005) provide strong evidence that greenhouse warming will lead to pronounced alterations of the forest–tundra ecotone and wetland/lake ecosystems in boreal regions. For example, numerical modeling of boreal-forest dynamics indicates that climatic warming

as little as 2°C may result in the conversion from tundra to boreal forest within 70–290 years near the forest–tundra ecotone (Rupp et al. 2000). These projections are in agreement with tree ring and comparative studies showing that tundra communities have been invaded by boreal trees in response to post–Little Ice Age climatic warming (Suarez et al. 1999, Kullman 2002, Lloyd 2005). The effects of climatic change on boreal ecosystems may be exacerbated by the behavior of disturbance regimes (Suffling 1995). In particular, forest fire interacts with climatic change in a complex manner to exert great influences on species composition and ecosystem processes (e.g., energy fluxes and elemental cycles) on the modern boreal landscape (Aber and Melillo 1991, Chapin et al. 2004, Hu et al. 2006).
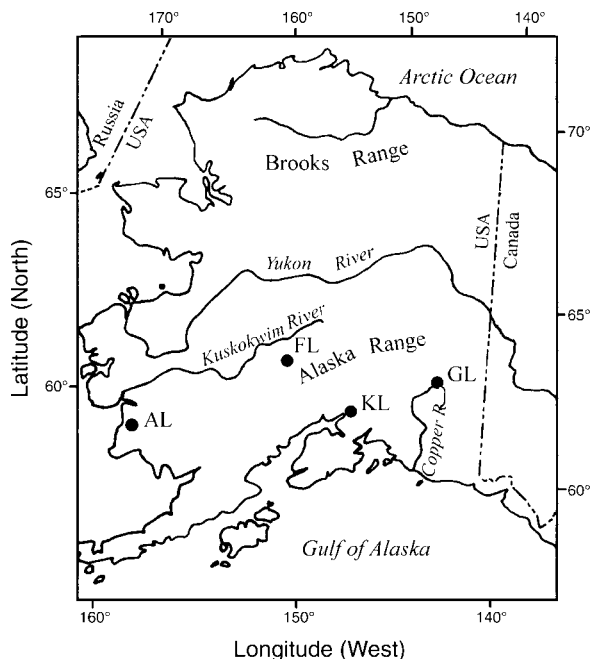
FIG. 1. Map showing the locations of Grizzly Lake (GL), Arolik Lake (AL), Farewell Lake (FL), and Kepler Lake (KL) in Alaska, USA.

High-resolution paleoecological analyses of lake sediments using multiple proxy indicators offer an opportunity to examine how ecosystems responded to past climatic change at local to regional scales. Such studies provide a means to evaluate simulation results and help understand how ecosystems may respond to climatic forcing (Heiri et al. 2006). However, high-resolution paleorecords remain rare, and most existing data do not provide quantitative information on past climate and ecosystems. For instance, pollen records from the boreal regions of northwestern America typically have multicentennial sample resolutions, and only recently have quantitative climatic reconstructions been attempted (e.g., Hu et al. 2001, Palmer et al. 2002). Although numerous paleoecological reconstructions exist from the Alaskan boreal biome (e.g., Anderson and Brubaker 1993, 1994, Tinner et al. 2006), the sensitivity of the regional boreal forests to Holocene climatic variations remains ambiguous. For example, spruce tree line is not known to have extended farther north in Alaska during the early Holocene when summer temperatures were presumably 1–2°C warmer than today (Kaufman et al. 2004). Such paleoecological data stand in contrast with simulated boreal-forest sensitivity to future changes and imply the complexity of predicting ecological response to climatic forcing in certain regions.

In this paper, we present a high-resolution multiproxy data set from sediment analyses at Grizzly Lake (62°43′ N, 144°12′ W, 720 m above sea level [asl]) in the Copper River Basin, south of the Alaska Range. We focus on the past 700 years, a period of marked climatic

oscillations in Alaska including the Little Ice Age (LIA; e.g., Forester et al. 1989, Hu et al. 2001, Wiles et al. 2002, Wiles et al. 2004). We use magnetic and diatom-assemblage data to reconstruct soil/shoreline erosion and lake-level changes. These results are coupled with other paleoclimatic and paleoenvironmental series from Alaska and elsewhere to disentangle temperature and precipitation variations. The paleoclimatic information is then compared with our high-resolution pollen, macrofossil, and charcoal series to address the magnitude and direction of ecological changes during and after the LIA.

STUDY SITE

Grizzly Lake is located in the northeastern edge of the Copper River Basin, south of the Alaska Range (Fig. 1). Human activity around the site was negligible until ~50 years ago when the Tok Cut-Off highway was constructed 200 m north of the lake. The lake has a surface area of ~11 ha and a watershed area of ~125 ha. The maximum water depth was 8.20 m in July 1999 and 2000. Today the lake is a topographically closed basin with no major inlet and outlet. Aquatic macrophytes (*Isoetes muricata* and *Nuphar polysepalum*) are present in shallow areas of the lake.

On the moraine ridges around the lake, boreal forests are dominated by *Picea glauca* (white spruce) with *Betula neoalaskana* (Alaska tree birch) and *Populus tremuloides* (aspen) as common constituents. Plant communities dominated by *Picea mariana* (black spruce) and *Sphagnum* spp. are prevalent in the extensive lowlands of the Copper River Basin. *P. mariana* forms nearly pure stands on the wet soils of lowlands south of the lake. Within the region, *P. glauca* forms timberline stands, and this species can reach maximum elevations of 1000–1300 m asl. Locally near Grizzly Lake, *P. glauca* timberline is at about 900–1000 m asl, and *Alnus viridis* (green alder) thickets grow up to about 1100 m asl. On gentle slopes with wet soils, *P. mariana* extends to timberline (Viereck and Little 1994). The altitudinal limits of *P. mariana* and *Betula* trees (mainly *B. neoalaskana*, Alaska birch) are at ~800–900 m in the study area (Hultén 1968); the elevation of Grizzly Lake at 720 m asl is not far below the distribution limits of these two tree species.

The study area has a boreal continental climate with marked seasonal temperature variation. In Slana, ~10 km east of Grizzly Lake, the mean July and January temperatures are 13.4°C and −20.2°C, respectively (Western Regional Climate Center 2006). The mean annual temperature is −3.3°C, and the mean annual precipitation 390 mm.

MATERIAL AND METHODS

Two parallel short cores (GYG and GYH, 1 m apart) were taken with plexiglass tubes from the deepest part of the lake. Core GYG contained an intact sediment–water interface. For older sediments, long cores (including

TABLE 1. ^{210}Pb and ^{14}C dates of Grizzly Lake, Alaska, USA.

Lab number	Core	Depth (cm)	Material	^{210}Pb, years AD (mean ± SD)	^{14}C dates, years BP, uncalibrated (mean ± SD)	AD 95% CI†
Bern	GYG	0–1	bulk	1993 ± 0.3		1992–1994
Bern	GYG	1–2	bulk	1980 ± 2.1		1976–1984
Bern	GYG	2–3	bulk	1972 ± 2.3		1967–1977
Bern	GYG	3–4	bulk	1963 ± 2.3		1958–1968
Bern	GYG	4–5	bulk	1937 ± 6.1		1925–1949
Bern	GYG	5–6	bulk	1899 ± 12.9		1873–1925
Ua-19438‡	GYG	14–15	P, *Picea* N		485 ± 45‡	1319–1485‡
Ua-19439	GYG	18–19	P, *Picea* N, *Betula* F, *Ledum* L		330 ± 35	1471–1643
Ua-19440	GYG	19–20	P, *Picea* N, *Betula* F		290 ± 40	1483–1795
CAMS-84953	GYG	21–22	P, T, W		305 ± 40	1474–1658
CAMS-66875	GYA	33–35	W		360 ± 50	1449–1639
CAMS-84955	GYH	43–47	P, C, T, W, *Betula* F		385 ± 40	1439–1634
CAMS-66876	GYA	73–75	T		1770 ± 50	131–386

Notes: Abbreviations for Material column: C, charcoal; F, fruits; L, leaves; N, needles; P, periderm; T, twig; W, wood. The labs are at the University of Bern, Bern, Switzerland (Bern); Tandem Laboratory, University of Uppsala, Uppsala, Sweden (Ua); and Lawrence Livermore National Laboratory, Livermore, California, USA (CAMS). Two parallel short cores (GYG and GYH, 1 m apart) were taken from the deepest part of the lake; core GYG contained an intact sediment–water interface. For older sediments, long cores (including GYA) were taken.
† Calibration of radiocarbon dates is by Calib 5.01 (Stuiver et al. 1998).
‡ Rejected date.

GYA) were taken with a modified Livingstone piston corer (Wright et al. 1984). The cores were correlated according to lithostratigraphy and sectioned into continuous 1-cm slices for the analyses of pollen, macrofossils, charcoal, diatoms, and magnetic properties.

The chronology of the record is based on the linear interpolation of six ^{210}Pb ages (0–6 cm) on bulk sediments and five accelerator-mass-spectrometry (AMS) ^{14}C ages on terrestrial macrofossils (Table 1, Fig. 2). As with other studies of the latest Holocene, the quality of our chronology is compromised by the difficulties of dating samples >150 years old and <500 years old. The ^{14}C date at 14–15 cm was rejected because its probability of being correct was very low (2.9%, OxCal 3.5, Ramsey 1995; Fig. 2). Three neighboring AD ages were amalgamated (OxCal 3.5) and connected with linear interpolation to the oldest ^{210}Pb date and the subjacent AD ages (Fig. 2). A date from GYA (33–35 cm) verifies the stratigraphic correlation but is not integrated into the chronology (Table 1, Fig. 2). We used CALIB 5.01 (Stuiver et al. 1998, Reimer et al. 2004) to convert ^{14}C ages to ages in years AD. The mean sample resolution is 14 years for all proxies.

For mineral-magnetic analysis, contiguous 1-cm samples were freeze-dried and packed into prescreened 10-mL polystyrene pots. The samples were measured for low- and high-field magnetic susceptibility (χlf and χhf), from which frequency-dependent susceptibility (χfd) was calculated (Fig. 3). We also measured anhysteretic remanent magnetization (χARM) and saturation isothermal remanent magnetization (SIRM) of 1 T (tesla; magnetic flux density) and backfield IRM ratios (IRM$_{-20}$, IRM$_{-40}$, IRM$_{-100}$, and IRM$_{-300}$). From these results the interparametric ratio χfd/χARM was calculated, which has been shown to be sensitive to the
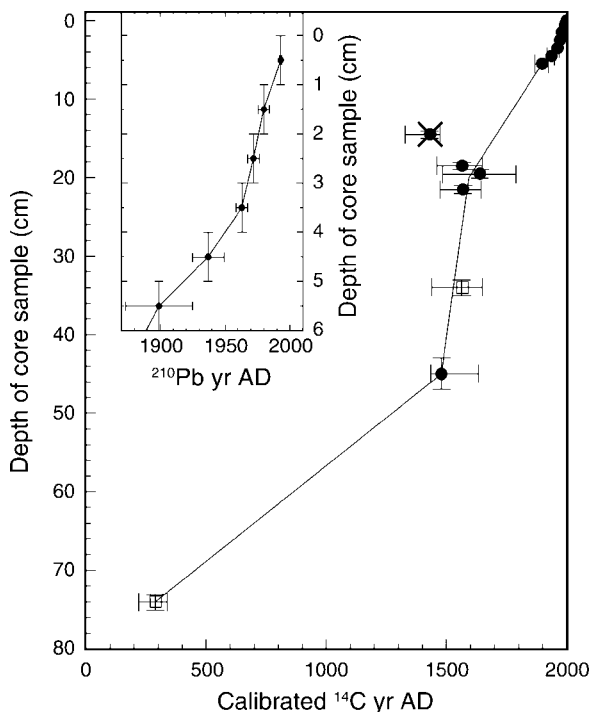

FIG. 2. Age–depth plot of the Grizzly Lake cores. The inset shows the age–depth model for the period after AD 1850 based on ^{210}Pb dating analysis of sediment. Those before AD 1850 are based on calibrated radiocarbon dates of terrestrial plant macrofossils. Solid circles show the dates of the analyzed cores (parallel short cores 1 m apart, taken from the deepest part of the lake: GYG [0–36 cm depth] and GYH [37–50 cm depth]), and open squares show dates for the additional core GYA (long core for older sediments). Data are presented as mean ± 2 SD. The heavy × is a rejected date. For further information see *Material and Methods*.
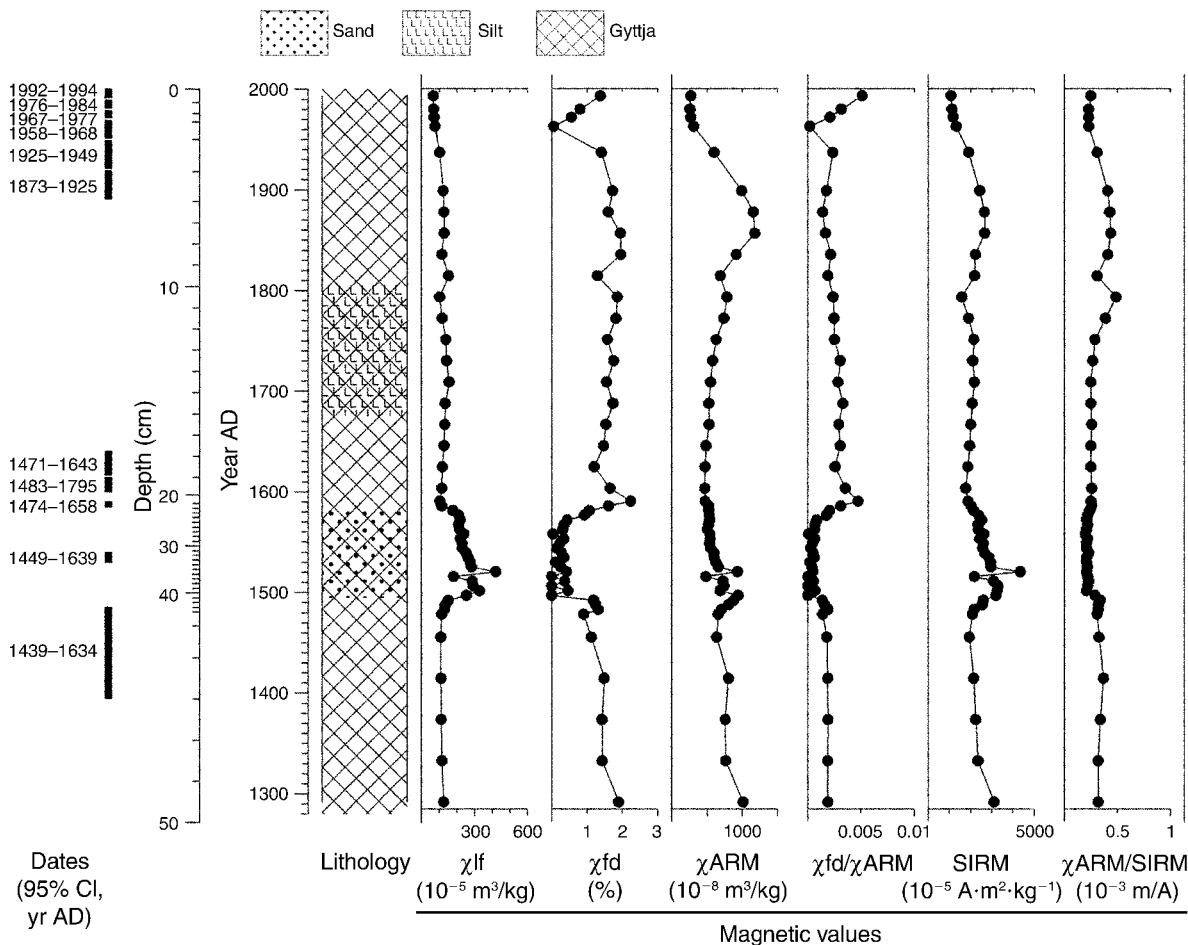
FIG. 3. Magnetic properties of the Grizzly Lake sediments. Low-frequency magnetic susceptibility (χlf) is a parameter indicating the concentration of ferrimagnets (magnetite); frequency-dependent magnetic susceptibility (χfd) reflects the abundance of ultrafine superparamagnetic (SP; 0–0.02 μm) grains. Anhysteretic remanent susceptibility (χARM) is a magnetic grain size parameter sensitive to material slightly more coarse than the χfd parameter; SIRM is saturation isothermal remanent magnetization. Abbreviations and methodology follow Gedye et al. (2000). For the core depth axis, the scale is uneven because of changing sedimentation rates as indicated by the age–depth model (Fig. 2).

presence of pyrogenically derived magnetic material within burned soils (Gedye et al. 2000).

Diatom samples were prepared using standard techniques involving 30% H_2O_2 and 10% HCl (Battarbee 1986). The taxonomy was primarily based on Krammer and Lange-Bertalot (1986–1991; e.g., Krammer and Lange-Bertalot 1986). In general, a minimum of 400 diatom valves were identified and enumerated using 1000× magnification and phase contrast optics. Some samples (e.g., 40–25 cm; Fig. 4) contained extremely low diatom concentrations, and therefore their counting sums were lower. The diatom diagram was subdivided into local assemblage zones by using the method of optimal partitioning (Birks and Gordon 1985) as implemented in the program ZONE (version 1.2; Lotter and Juggins 1991). To determine the number of statistically significant zones in the diagram, we used the program BSTICK (Bennett 1996). The diatom-

inferred quantitative lake-level reconstruction is based on a regional calibration set including 51 lakes, using log-transferred lake depth data (Gregory-Eaves et al. 1999). All diatom data were square-root transformed prior to the numerical analyses in order to stabilize the variances (Birks 1998). Transfer functions were developed using weighted averaging partial least square (WA-PLS) regression and calibration (ter Braak and Juggins 1993). After taxonomical harmonization between calibration and fossil diatom data, our model for log-transformed lake depth yielded a bootstrapped coefficient of determination (r^2_{boot}) of 0.54 and a root mean square error of prediction ($RMSEP_{boot}$) of 0.28, including one WA-PLS component. The summary statistics of our WA-PLS model are almost identical to the original log-transformed lake depth transfer function (WA with classical deshrinking) that had $r^2 = 0.53$ and $RMSEP_{boot} = 0.31$, respectively (Gregory-Eaves et al.
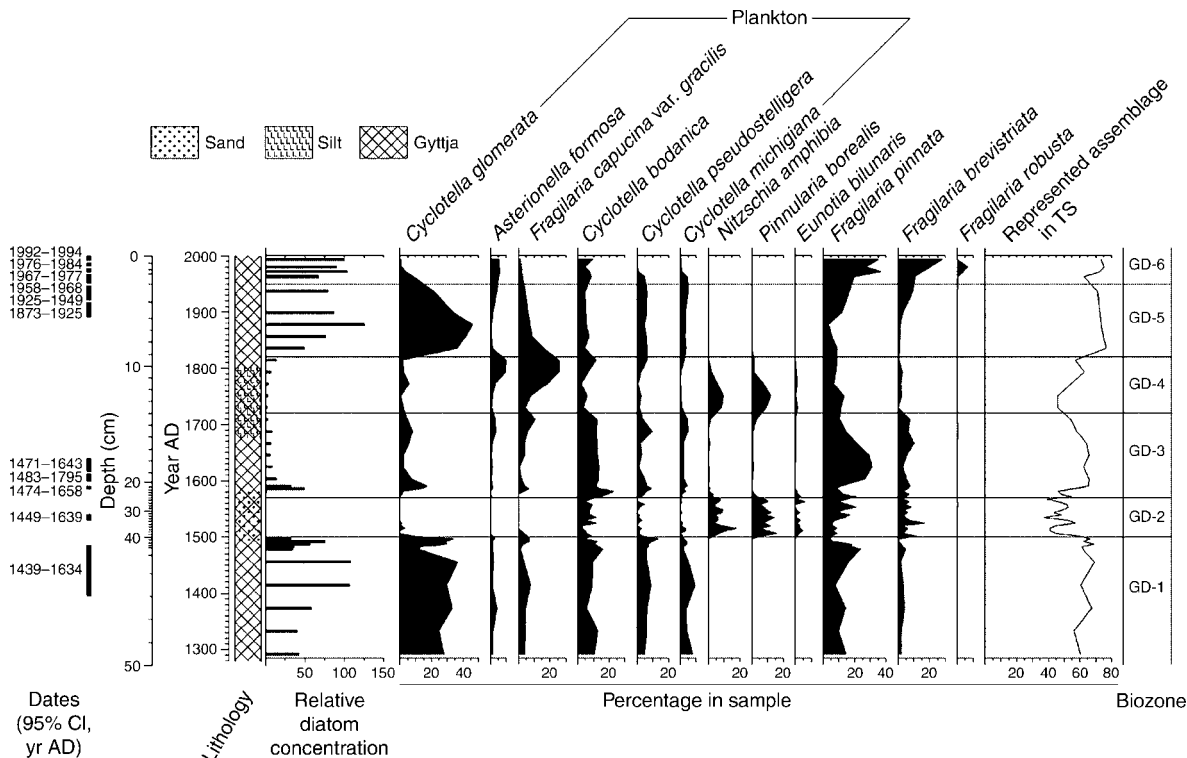
FIG. 4. Diatom assemblages in the Grizzly Lake sediment, as percentage in sample. Relative diatom concentrations are expressed (as percentages) per sediment dry mass and with reference to the uppermost sample (=100%). All biozones are statistically significant (Bennett 1996; see also *Material and Methods*). Abbreviations are as follows: TS, training set; GD, Grizzly Lake diatoms.

1999). The reconstructed log-transformed lake depth values, including their errors, were retransformed for display.

Pollen preparation followed standard procedures (Moore et al. 1991). *Lycopodium* tablets (Stockmarr 1971) were added to subsamples of 1 cm^3 for estimating pollen concentrations (pollen grains/cm^3) and accumulation rates (pollen grains·cm^{-2}·yr^{-1}). Nomenclature of plant taxa followed the Flora of North America (2007). Pollen type separation followed Clegg et al. (2005) for *Betula*, Hansen and Engstrom (1985) for *Picea*, and Punt et al. (2003) for *Alnus*. A minimum of 600 pollen grains, excluding aquatic pollen and spores, were counted at each level. Rarefaction analysis (Birks and Line 1992) was performed on pollen–spore assemblages (terrestrial and wetland types included). Zonation was made using the same technique as for diatom analysis (optimal partitioning, broken-stick model). Three pollen subzones were also delimited but they were not statistically significant (subzones GP-2a, 2b, 2c, Figs. 5 and 6). Preliminary detrended correspondence analysis (DCA) was performed on the pollen and spore data set to estimate the gradient lengths of the DCA axes. Given the resulting gradient length of the first DCA axis of 1.236 standard deviation units, principal components analysis (PCA) was selected to summarize the original

data set (Kovach 1995, Ammann et al. 2000). Pollen percentages and concentrations show comparable stratigraphic variations, suggesting that percentage values were not affected by proportional problems (Fig. 7).

Microscopic charcoal particles >10 μm (or area >75 $μm^2$) were counted in pollen slides (Tinner and Hu 2003, Finsinger and Tinner 2005). For the analyses of macroscopic charcoal and terrestrial macrofossils, sediment samples of 15 cm^3 were washed through a 200-μm mesh screen, and macrofossils were identified following standard keys (e.g., Lévesque et al. 1988) and reference specimens.

RESULTS AND INTERPRETATION

Soil and lakeshore erosion

The sediment of the past 700 years is mainly fine-detritus gyttja (Fig. 3). However, the intervals between 41 and 23 cm (AD 1490–1580) and between 16 and 10 cm (AD 1680–1805) contain conspicuously greater amounts of silt and sand than the remainder of the core. These silty and sandy gyttja layers are unsorted; the silt, sand, and coarse organic debris are homogenously admixed with the fine organic and inorganic particles. This lithological texture argues against the formation of the silty and sandy layers as a result of a turbidite or a single short-lived subaquatic event (Fig.
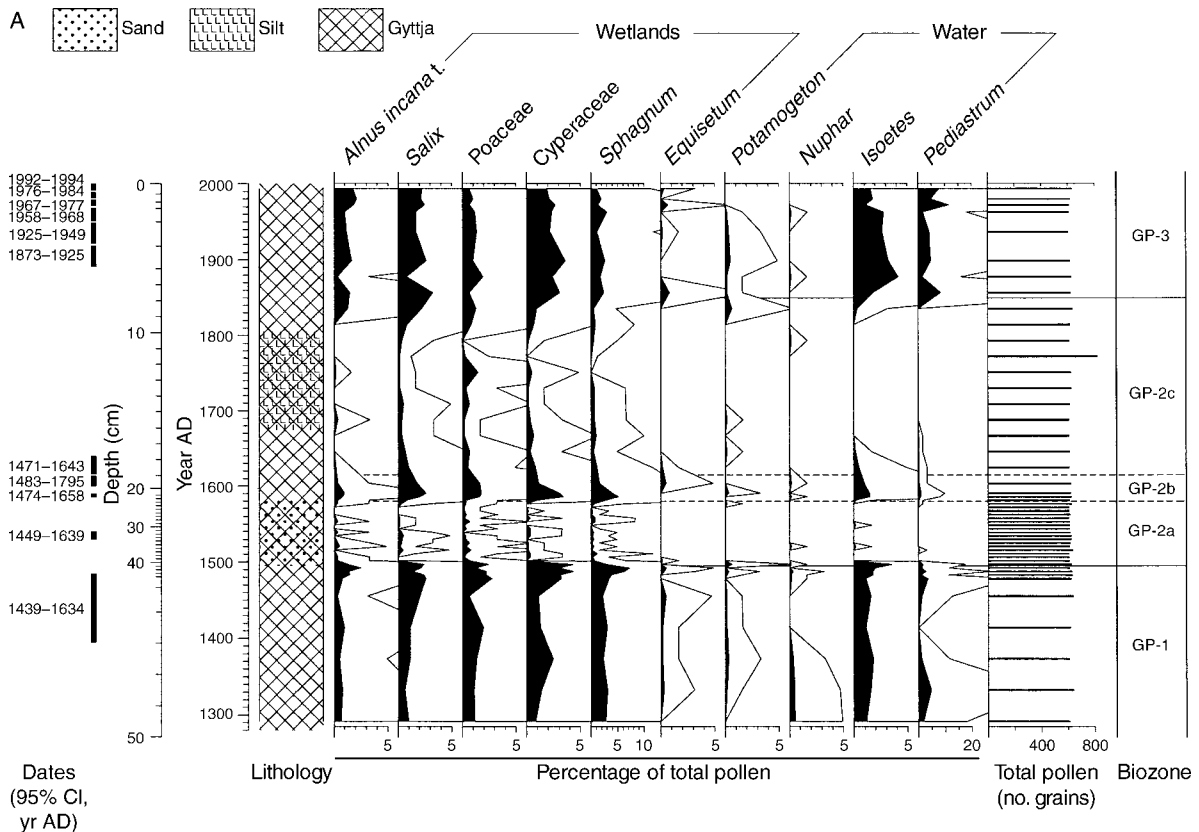
FIG. 5. Aquatic pollen, spores, and macrofossils in the Grizzly Lake sediment. (A) Selected wetland and aquatic pollen and spores as percentage of the total pollen sum (number of pollen grains counted). Pollen of aquatic plants and spores of pteridophytes and bryophytes were excluded from the pollen sum. Statistically significant zone boundaries are depicted as solid lines (Bennett 1996; see also *Material and Methods*). (B) Macrofossil concentrations in number per 15 cm³. Lines above solid curves indicate 10-fold exaggeration so that low values are visible; solid curves show the true values. Abbreviations are as follows: GP, Grizzly Lake pollen; SC, sclerotia; L, leaves; E, ephippia; SF, seed fragments; S, seeds; O, oogonia; "t." following a taxon name indicates type.

3); instead it points to long-lasting erosional input from the lakeshore or from soils.

The mineral-magnetic record to a degree is related to the lithological changes. A sharp increase in χlf, which reflects an overall increase in the concentration of magnetic material, corresponds to the sandy gyttja layer (Fig. 3). The silty gyttja layer is less well defined in the magnetic record, although a gradual rise in χARM/SIRM points to a change in magnetic grain size, possibly because of a change in sediment source. Of particular interest is the χfd% record, which is sensitive to the presence of superparametric grains (SP) produced through pedogenic processes (e.g., Dearing 1999). High values of χfd% (>3–10%) are indicative of soil-derived material, eroded from the catchment. The low values of χfd% recorded here (i.e., <2%) suggest that the lithological changes cannot be attributed to the inwash of mineral topsoil material. In contrast, the consistent deviation between 20–40 cm likely reflects the input of mineral material from exposed lakeshores (e.g., after lake-level drops) and raw, un-weathered soils in the lake catchment.

Although a series of catchment fires have been identified within the charcoal record (Tinner et al. 2006), there is no clear fire signal (χfd/χARM) in the magnetic record that would indicate pyrogenically derived magnetic material in the sediment. This may simply reflect that the majority of fire events was restricted to the forest biomass, leaving the topsoil unaffected, or that no burned mineral soil material made its way into the lake.

The record of *Cenococcum* sclerotia (Fig. 5B) provides unambiguous evidence that organic matter in the surface soil (i.e., litter horizon) has been eroded and deposited into the lake (Wick et al. 2003). The *Cenococcum* sclerotia are most probably from *Cenococcum geophilum,* a ubiquitous ectomycorrhizal fungus living on, in, or just below the litter horizon in both wetland and upland sites (Thormann et al. 1999, Wurzburger et al. 2004). *C. geophilum* is associated with transient or chronic environmental stress of trees in greenhouse seedling studies and under natural field conditions (e.g., winter frost injuries; Webb et al. 1993), and its colonization can be negatively correlated with the
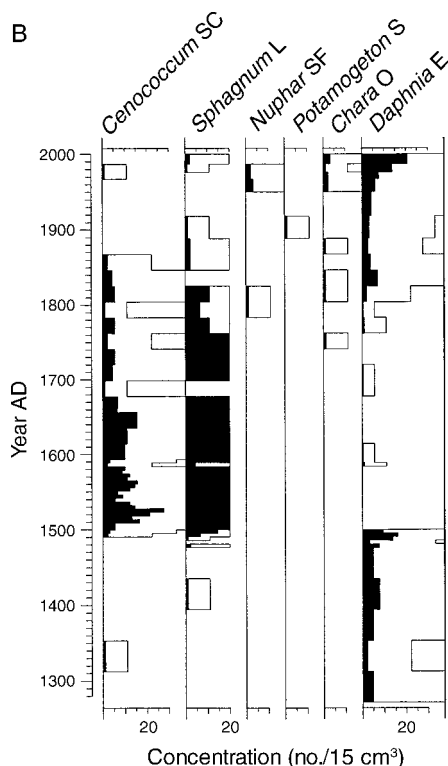
FIG. 5. Continued.

diversity of other mycorrhizal fungi (Glenn et al. 1991). Thus the abundance of *Cenococcum* between AD 1490 and 1870 in our macrofossil diagram probably reflects both physiological stress and erosion.

In summary, the magnetic and macrofossil records reveal the erosion of soil organic litter but not the upper, weathered soil horizons (A, B) between AD 1490 and 1870. Thus the composition of the inwashed organic debris (e.g., *Picea* needles, *Alnus viridis*, tree *Betula*, and *B. nana* remains; see Tinner et al. 2006) dated to AD 1490–1870 probably reflects that of the soil litter horizon near the lakeshore. The associated silts and sands must have derived primarily from exposed lakeshores, given that the lake does not have a major inlet that could have exposed and transported the C horizon of soils.

Lake and wetland ecosystems

Between AD 1280 and 1490, diatom assemblages were dominated by planktonic taxa (e.g., *Cyclotella glomerata, C. pseudostelligera, C. michigiana*; Fig. 4; zone GD-1). Simultaneously with the lithostratigraphic change from AD 1490–1580, an overall decrease in diatom concentrations and major shifts in species composition occurred (zone GD-2). *C. glomerata* and *Fragilaria pinnata* decreased in abundance, whereas *Pinnularia borealis* increased. *P. borealis* often grows in soils and as moss epiphyte with airborne dispersal (Marshall and Chalmers 1997), and *Nitzschia amphibia* can tolerate a broad range of ecological conditions. Some of the

diatom species in zone GD-1 recovered after AD 1580 (e.g., *F. pinnata*, zone GD-3), but most of them were not abundant again until AD 1830 (zone GD-4). Around AD 1830, *C. glomerata*, a planktonic species that often blooms during late summer (Sorvari et al. 2002), became reestablished (GD-5). During the second half of the 20th century, this species was gradually replaced by *Fragilaria brevistriata* and *F. pinnata* (zone GD-6). The most recent diatom-assemblage change (Fig. 4; zone GD-6) was possibly caused by an increased influx of nutrients from human activity in the lake catchment during the past several decades (e.g., by the camping facilities on the northern portion of the lakeshore).

Pollen, spores, and microscopic algae suggest the abundance of aquatic plants, such as *Potamogeton, Nuphar, Isoetes*, and *Pediastrum* between AD 1280 and 1490 in Grizzly Lake (Fig. 5; zone GP-1). Between AD 1490 and 1580 (zone GP-2a) and between AD 1620 and 1850 (zone GP-2c), microscopic remains of aquatic plants (*Nuphar, Isoetes, Pediastrum*) were less abundant or even disappeared, and pollen and spores of wetland and lakeshore plants (*Alnus incana, Salix*, Cyperaceae, Poaceae, *Sphagnum, Equisetum*; Fig. 5) decreased greatly. These data suggest that most aquatic macrophytes either stopped reproducing sexually or died out. The conspicuous amounts of *Sphagnum* leaves in the sediment of AD 1490 and 1870 (Fig. 5B) probably reflect inwash of coarser organic debris from the soil litter horizon. Macrofossil increases associated with pollen decreases have been found for other important taxa, such as *Picea* and tree *Betula* (Tinner et al. 2006) and are interpreted in a similar way, with pollen reflecting tree declines (see Fig. 6) and macrofossils suggesting increased local inwash. Similar to *Sphagnum* spores, *Daphnia* ephippia were absent or in very low abundances from AD 1490 to ~AD 1890, probably reflecting major population collapses or dilution by mineral matter (Fig. 5B). A transient and partial recovery of wetland and aquatic vegetation occurred at AD 1580–1620 AD (zone GP-2b; Fig. 5). Aquatic and wetland vegetation fully recovered between AD 1810 and 1870 (around the zone boundary GP-2/GP-3), and it remained relatively stable until today (zone GP-3).

The diatom record of Grizzly Lake helps us understand the causes of the wetland and aquatic changes. Diatom concentrations and assemblages suggest low lake levels between AD 1490 and 1830 (Fig. 4) when planktonic species decreased and allochthonous input (species related to moist-soil habitats) partly increased. Although the magnitude of the lake-level variations at Grizzly Lake is rather uncertain because of the considerable sample-specific errors of the lake depth reconstruction, lake levels might have been lower by several meters during the period AD 1490–1830 than before and after (Fig. 8). Such significant lake-level fluctuations would have considerably affected the aquatic macrophyte populations (as revealed by pollen, spores, and macrofossils). Furthermore, if they reflect
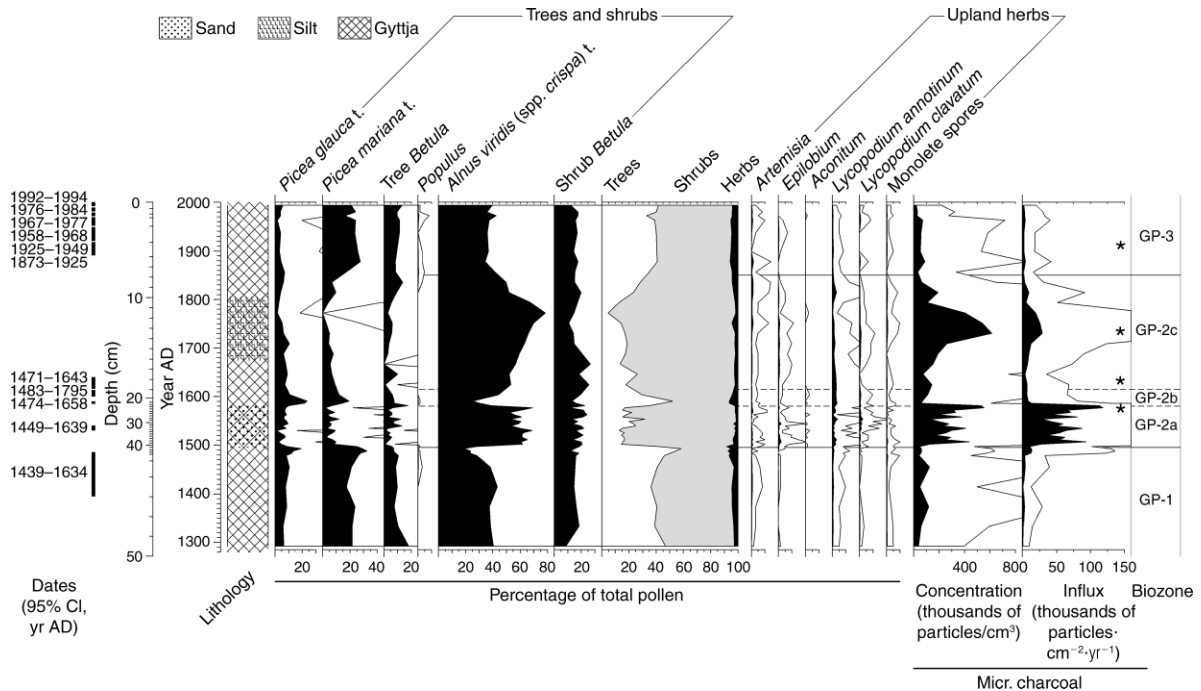
FIG. 6. Terrestrial pollen, spores, and charcoal in the Grizzly Lake sediment; "t." following a taxon name indicates type. Statistically significant biozone boundaries are depicted as solid lines. Stars on the right show the occurrence of local fires (Tinner et al. 2006). Lines above solid curves indicate 10-fold exaggeration so that low values are visible; solid curves show the true values. Microscopic (micr.) charcoal concentrations and influx are also given.

ground water table oscillations around the lake, these fluctuations provide a plausible explanation for diminished wetland communities.

Taken together the diatom, pollen, spore, and macrofossil records suggest that aquatic and wetland habitats (e.g., fens, bogs, floodplains) were reduced because of low water levels. Grizzly Lake has no major inlet and outlet streams. In such a basin, the lake level is primarily influenced by groundwater through precipitation and (temperature-controlled) evapotranspiration. We therefore assume that the lake-level drops primarily reflect precipitation decreases in the Grizzly Lake area during the LIA.

Terrestrial vegetation and fire

Terrestrial ecosystems covaried with the aquatic and wetland changes. The pollen data suggest boreal forests with *Picea mariana* as the dominant tree between AD 1280 and 1490 (Fig. 6 zone GP-1), likely in the lowland area south of the lake. Other important tree taxa were *Betula* and *P. glauca*, which probably occupied dry moraine ramparts and south-facing slopes near the lake together with isolated *Populus* trees. The pollen of *Alnus viridis* probably originated from thickets growing on disturbed soils (e.g., avalanche couloirs, landslides, lakeshores, floodplains) and near timberline. *Betula* shrubs were prevalent in open boggy areas and/or above tree line, as indicated by the abundance of shrub birch pollen at Grizzly Lake. *P. mariana, P. glauca,* and tree

Betula pollen decreased in abundance around AD 1490 (beginning of zone GP-2a). Corresponding to these changes are marked increases in the pollen values of *Alnus viridis* t., *Epilobium, Lycopodium annotinum*, and *L. clavatum*, as well as moderate rises in shrub *Betula, Artemisia, Aconitum,* and monolete spores (ferns). These changes suggest the expansion of cold-adapted or disturbance-adapted vegetation dominated by shrub and herbaceous taxa (e.g., *A. viridis, Epilobium, Aconitum*) at the expense of *Picea* forests. Between AD 1580 and 1620 (zone GP-2b), pollen assemblages are similar to those before AD 1500, pointing to a transient recovery of forest communities. Forest communities collapsed again after AD 1620 (zone GP-2c), giving way to a repeated expansion of shrubs, tall herbs, and club mosses. This phase was interrupted ~150 years ago, when pollen assemblages suggest the reestablishment of boreal forests (zone GP-3). Apparently boreal communities were resilient enough to adjust rapidly to climatic changes during and after the LIA. The period from AD 1580–1620 seems too short for a full recovery of boreal forests, and it is possible that the pollen signal (Fig. 6) reflects productivity changes (e.g., increased bloom of surviving trees). However, forest expansion on glacier forefields in response to glacier retreats at AD 1550–1670 has been unambiguously documented in the tree ring records of the Wrangell Mountains, close to Grizzly Lake (Wiles et al. 2002). Within the limits of chronological reliability, the rapidity of the vegetational change
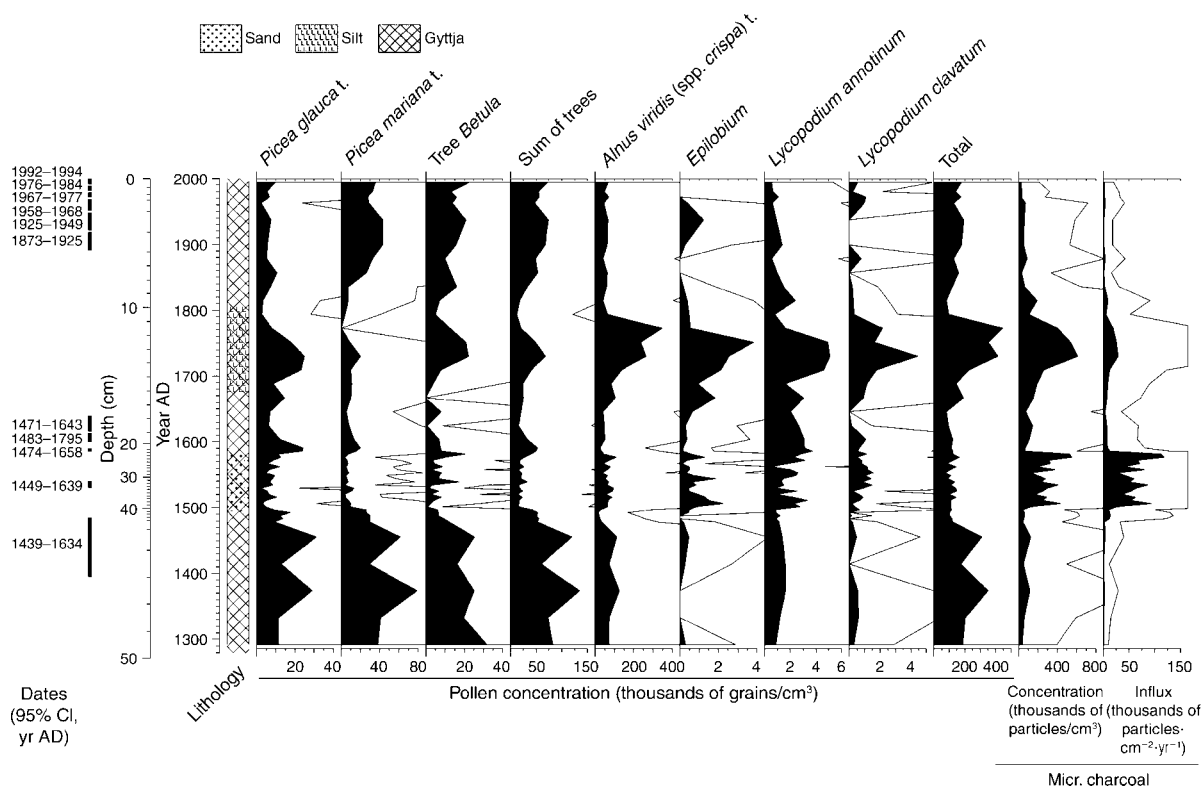
FIG. 7. Pollen and spore concentrations (selected types), along with microscopic charcoal concentration and influx; "t." following a taxon name indicates type. Lines above solid curves indicate 10-fold exaggeration so that low values are visible; solid curves show the true values.

is remarkable: pollen-inferred collapses and recoveries of boreal vegetation during the period AD 1500–1900 occurred within ~20–100 years (Fig. 6).

In addition to pronounced vegetational changes, the fire regime varied substantially in the Grizzly Lake region over the last 700 years, as suggested by stratigraphic changes in microscopic charcoal concentration and influx values (Fig. 6). These values are particularly high between AD 1500–1580 and AD 1700–1780, indicating increased occurrence of forest fires within the region (20–50 km; see MacDonald et al. 1991, Tinner et al. 1998, Whitlock and Larsen 2001). Macroscopic charcoal analysis and estimation of mean fire intervals (MFI) suggest the occurrence of four fire episodes dated to AD 1580, 1640, 1740, and 1920 around Grizzly Lake (Fig. 6; for details about MFI calculation and identification of local fires see Tinner et al. 2006).

DISCUSSION

Little Ice Age climatic fluctuations

Our results provide evidence for climatic and ecosystem fluctuations during the past 700 years in the Grizzly Lake area, and these fluctuations were probably related to the LIA. During the LIA between AD 1500 and 1850, summer temperatures decreased by about 0.3–0.5°C on average over the Northern Hemisphere (Mann 2000, Jones et al. 2001, Briffa and Osborn 2002). The magnitudes of the LIA climatic fluctuations in Alaska (Hu et al. 2001, Davi et al. 2003) were greater than the averaged estimates for the Northern Hemisphere. For example, $\delta^{18}O$ data from Farewell Lake in the northwestern Alaska Range (Fig. 8) suggest that LIA culminated around AD 1700 when summer temperature was up to 1.7°C lower than at present (Hu et al. 2001). Additional evidence of climatic change during the past 700 years in Alaska includes glacier advances during the coldest episodes of the LIA, burying forest stands in front of glaciers (Fig. 8; Wiles et al. 1999, 2002, Calkin et al. 2001).

Although LIA climatic cooling appeared to have occurred across various areas of Alaska (Jacoby and D'Arrigo 1989, Wiles et al. 1999, 2002, Calkin et al. 2001, Hu et al. 2001, Davi et al. 2003), evidence is more complicated for changes in moisture availability. At Farewell Lake, $\delta^{18}O$ and trace-element composition suggest increased moisture availability during the LIA (Hu et al. 2001). In contrast, our diatom results from Grizzly Lake show lower lake levels during the LIA, suggesting decreased moisture availability. This diatom-based inference is consistent with an LIA precipitation reconstruction on the basis of ostracode assemblages at
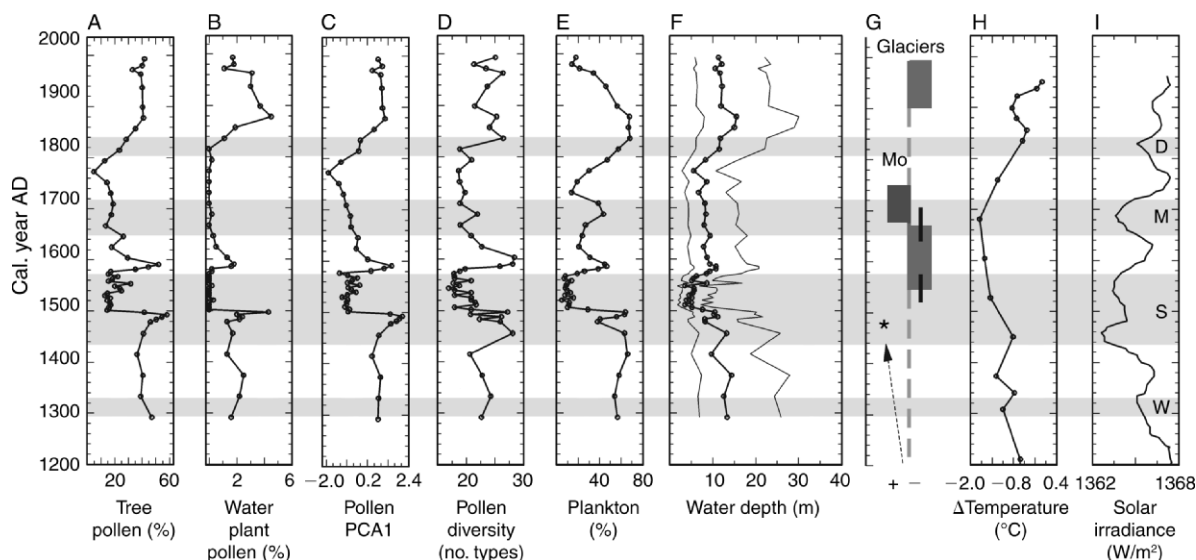
Fig. 8. Comparison of selected summary curves from Grizzly Lake with glacial oscillations (Calkin et al. 2001, Wiles et al. 2002), δ^{18}O-based temperature estimates from Farewell Lake (Hu et al. 2001), and reconstructed total solar irradiance (Bard et al. 2000). (A) The percentage of pollen attributed to trees reflects the relevance of boreal forests during the past 700 years. (B) The percentage of pollen and spores attributed to water plants; *Pediastrum* algae remains are not included. (C) Axis 1 of principal components analysis (PCA) accounts for 83% of the data variance. (D) Pollen diversity (number of pollen types represented in the pollen sample) was estimated by rarefaction analysis with a minimum sum of 618. (E) The percentage of diatoms attributed to planktonic taxa preferring deep water conditions. (F) Reconstruction of water depth at Grizzly Lake is based on diatom transfer functions from Alaskan lakes (Gregory-Eaves et al. 1999). The thin lines delimit the 95% confidence interval. (G) The bars on the left and right sides represent glacial advances and retreats, respectively. The glacier retreat between AD 1544 and 1676 is defined by 12 age ranges of tree growth obtained from 48 tree ring dates of logs overrun by ice in the Wrangell Mountains, Alaska (Wiles et al. 2002). The fine bars represent the standard deviations of the 12 age ranges (1544 ± 32 and 1676 ± 38). One age range of tree growth from Kuskulana (AD 1387–1716) was excluded since it is not in agreement with other records from Chisana, Nizina, Barnard, Kennicott, and Kuskulana (see Wiles et al. 2002). The arrow marks the progressive advance, and the star the attainment of maximum LIA (Little Ice Age) advance positions at important glaciers of the coastal area (Bering glacier, McCarty Fiord, Aialik Bay, Northwestern Fiord; see Calkin et al. 2001). Moraines (Mo) document maximum glacier advances in the coastal area and south-central Alaska at around AD 1800–1900 (minimum ages; Calkin et al 2001). (H) The temperature reconstruction from Farewell Lake primarily relies on oxygen isotope measurements on abiotic carbonates and benthic ostracodes. The Δ temperature values show departures of past surface water temperature during the growing season from the present (Hu et al. 2001). (I) The reconstruction of solar irradiance is based on smoothed cosmonuclide (^{14}C and ^{10}Be) production rates (Bard et al. 2000; 0.25% Maunder minimum irradiance reduction curve). LIA sunspot minima: D, Dalton; M, Maunder; S, Spörer; W, Wolf. Shaded intervals are times of low solar irradiance.

Kepler Lake near Anchorage, ~300 km southwest of Grizzly Lake (Fig. 1, Forester et al. 1989). Although these results should be verified with additional paleoclimatic studies, spatial variations of precipitation within this vast region were evident for the last 50 years (Hess et al. 2001) and should be expected for the late Holocene.

Glaciers are sensitive to climatic change, including both temperature and precipitation oscillations. Past glacier fluctuations have therefore been used to reconstruct climatic changes, but considerable uncertainties exist about the relative contributions of precipitation and temperature changes to glacier growth. Glacier advances such as those recorded in the geomorphic and tree ring data of Alaska (e.g., Calkin et al. 2001, Wiles et al. 2002) mainly reflect decreased summer temperatures and/or increased winter precipitation (Dowdeswell et al. 1997, Nesje and Dahl 2003), and summer precipitation and winter temperature are less important. A recent synthesis of data from 130 Alaskan glaciers shows that

mountain glacier fluctuations during the past millennium were primarily caused by summer cooling, probably as a consequence of decreased solar activity (Wiles et al. 2004).

This interpretation of solar-induced glacial fluctuations agrees with that of Hu et al. (2003), who show connections among solar irradiance, Alaskan climate, and tundra ecosystems during the Holocene. Biogenic-silica, isotopic, and pollen records from the sediments of Arolik Lake in comparison with cosmonuclide (^{10}Be, ^{14}C) time series suggest increased temperatures and precipitation during periods of increased solar irradiance. At this site, effects on tundra ecosystems included higher lake (and especially diatom) productivity and the expansion of *Betula* shrubs in tundra communities. Conversely, periods of diminished solar radiation resulted in colder and drier environments with the reductions of lake productivity and *Betula* shrub density (Hu et al. 2003). Similarly, pollen assemblages from Grizzly Lake suggest the reduction of boreal-forest trees

PLATE 1. A burned spruce forest near Tok in central-east Alaska two years after fire. The vegetation is dominated by herbaceous species such as fireweed (*Epilobium angustifolium*, flowering). The spruce forest will become established after some decades, following an intermediate successional phase with deciduous shrubs such as scrub birch (*Betula glandulosa*) or Alaska birch (*B. neoalaskana*) and quaking aspen (*Populus tremuloides*). Photo credit: W. Tinner.

along with the expansion of *A. viridis* and *B. nana* during the colder and drier LIA (Fig. 6), and within ^{14}C dating uncertainties, the two most pronounced minima of solar radiation (AD 1450–1580, AD 1660–1720 AD; Fig. 8) corresponded to the disruptions of wetland and boreal habitats. Together, the data from Arolik and Grizzly Lakes suggest that boreal and tundra ecosystems may have been quite sensitive to Holocene climatic changes in relation to subtle fluctuations of solar irradiance.

Responses of terrestrial and aquatic ecosystems to Little Ice Age climatic shifts

Our paleoecological data from Grizzly Lake show dramatic and rapid changes of boreal ecosystems in response to the LIA climatic fluctuations. These changes included the decline of *Picea–Betula* forests and the expansion of tundra, and they were probably driven by variations in temperature, precipitation, and fire regime. Pollen PCA indicates that the principal taxa involved were *Picea mariana*, *Alnus viridis*, *Epilobium* (see Plate 1), and *Betula* trees (cumulative fit per taxon [CFIT] as a fraction of variance of species taxa for axis one: 0.988, 0.882, 0.277, and 0.269, respectively; for interpretation of CFIT see Legendre and Gallagher 2001). At Grizzly Lake, *P. mariana* and *Betula* trees are 100–200 m below their altitudinal limits today (Hultén 1968). By assuming a lapse rate of 7°C/km, temperature changes of >0.7–1.4°C as estimated for the LIA may have resulted in

lethal (frost) damages on these tree species. As suggested by ecological observations and model simulations, lethal frost damages can lead to abrupt declines of ecotone or boreal vegetation within a few years (Kullman 1991, Bugmann and Pfister 2000), whereas recoveries involving population buildups require more time (decades to centuries). Thus during the LIA, *P. mariana* and *Betula* trees probably occurred at altitudes 600–700 m asl and disappeared almost completely around Grizzly Lake. Physiological stresses induced by severe frost and increased erosion of surface soils would explain the high abundance of *Cenococcum* remains in the sediments of Grizzly Lake. Compared with *P. mariana* and tree *Betula*, *A. viridis* and *Betula glandulosa/nana* are more adapted to cold conditions and disturbance, so that these species could have benefited from the forest collapse. In agreement, *Alnus viridis* and *Betula glandulosa/nana* form thickets beyond altitudinal and latitudinal tree line today (e.g., in the tundra north of the Brooks Range; Viereck and Little 1994, Gallant et al. 1995).

Since summer precipitation deficits are not the primary limiting factor for the occurrence of forests in Alaska near altitudinal tree line (Arno and Hammerly 1993), it seems unlikely that a precipitation decrease could have directly contributed to the expansion of tundra at the expense of boreal forests. Instead, it is plausible that the reduction of precipitation increased

fuel flammability and thus fire frequency and/or severity. In addition, the high mortality of trees during the LIA (low-temperature driven) probably increased fuel flammability and abundance (increase of dead biomass) and thus promoted fire occurrence. These changes in turn would have resulted in the expansion of disturbance-adapted taxa (e.g., *Epilobium, A. viridis*), as evident in our pollen record (see Fig. 6). This interpretation is consistent with the observation in interior Alaska that recent burned areas were initially colonized by *Epilobium angustifolium* (Viereck and Little 1994, Gallant et al. 1995). This vegetation is usually replaced by shrub communities, broadleaf forests, and ultimately *Picea* forests decades to centuries after fire (Viereck and Little 1994, Gallant et al. 1995). Our data suggest that fire frequency and/or severity decreased and fire-adapted taxa declined in response to climatic amelioration (warmer, moisture conditions) at the end of the LIA. Similar linkages among climate, fire disturbance, and vegetation response occurred during other periods of the Holocene at Grizzly Lake (Tinner et al. 2006).

Other factors may have contributed to changes in fire importance at Grizzly Lake over the past 700 years. For example, evidence exists that native people in adjacent Canada intentionally set fires to enhance moose browse (Workman 1978). However, the close connections among fire, climatic, aquatic, and vegetation changes imply that pre-European human activities at most amplified climatic impact on fire regimes. In the Pacific Northwest, Whitlock and Knox (2002) reached a similar conclusion and emphasized that the close correlation among vegetation, fire regime, and climate variability as inferred from paleorecords is a convincing measure of the prevalence of climate relative to other potential causes of vegetation and fire regime variability.

Additional studies are needed to verify our inference that fire importance decreased during the warmer time intervals of the past 700 years. This inference implies that moisture changes were a more important control for fire occurrence than temperature variations. Such a climate–fire relationship has also been documented in other areas of the North American boreal biome (Bergeron and Archambault 1993, Johnson et al. 1999, Bergeron et al. 2001). Together, these data suggest that future climatic warming may not necessarily result in increased fire occurrence and that predictions for boreal ecosystems in regard to climatic change should assess moisture effects (see Flannigan et al. 1998, 2001).

Effects of LIA cooling on aquatic and wetland ecosystems were most likely exacerbated by drier climatic conditions in the Grizzly Lake region. Our data suggest that lake-level and groundwater drops led to reduced abundance or dieback of aquatic organisms (e.g., *Pediastrum* algae, *Isoetes, Daphnia*; Fig. 5) as well as diminished shoreline and wetland habitats. The complete disappearance of many microfossils of wetland organisms during periods of low water level contributed substantially to the diversity reduction (Fig. 8). Experimental studies (e.g., methane measurements from peat incubation, manipulations of water table elevation in soil monoliths from bogs and fens) suggest that wetland changes are often triggered by water table variations (Brown 1998, Weltzin et al. 2000). Ecological studies document irreversible degradation of *Sphagnum* lawns in response to summer drought (Alm et al. 1999) and decomposition of peat in fens and bogs under dry summer conditions (Shurpali et al. 1995, Wieder 2001, Bubier et al. 2003, Lafleur et al. 2003). Thus persistent droughts can lead to large-scale contraction of wetland habitats within a few decades (Moore 2002). At Grizzly Lake, the negative impacts of water balance changes on wetland ecosystems were probably reinforced by shorter growing seasons during the LIA and by enhanced erosional input into the lake (Figs. 3 and 5).

Implications for the sensitivity of boreal ecosystems to climatic change

Almost all existing pollen records from Alaska suggest that the boreal forests have remained relatively stable since they became established ~7000 years ago (6000 ^{14}C yr BP; see Hu et al. 1998). Moreover, *Picea* tree line is not known to have extended farther north than today in Alaska during the early Holocene (Anderson and Brubaker 1994), when summer temperature was probably about 1–2°C higher than at present because of high summer solar irradiance (Kaufman et al. 2004). Such a vegetational inertia in Alaska seems striking, especially in the context of paleoecological evidence showing that early Holocene *Picea* tree line was farther north than at present in far northwestern Canada (Ritchie et al. 1983) and that warm climatic conditions during the middle Holocene also resulted in rapid invasion of tundra by *Picea* in central Canada (MacDonald et al. 1993). Our LIA data from Grizzly Lake do not directly contribute to understanding the lack of evidence for Holocene latitudinal tree line shifts in Alaska. Nonetheless, these new data and those reported in Tinner et al. (2006) suggest that boreal ecosystems near altitudinal tree line can be highly sensitive to climatic change. Marked vegetational shifts at Grizzly Lake over the past seven centuries can be attributed to the sensitivity of two important tree taxa (*P. mariana* and *Betula*) near their uppermost altitudinal limit and to feedback processes that may have amplified climatic impacts (e.g., forest recovery in response to combined effects of climatic warming and decreased fire disturbance). These results concur with tree ring and comparative studies showing that boreal trees invaded tundra communities in response to climatic warming after the LIA (Suarez et al. 1999, Kullman 2002, Lloyd 2005). In agreement, computer simulations also indicate the conversion of tundra to boreal forests as a result of temperature changes comparable to those at the end of the LIA (e.g., 2°C; Rupp et al. 2000).

The magnitudes of LIA temperature fluctuations are at the lower end of those projected for the future (Intergovernmental Panel on Climate Change 2001). Thus the pronounced shifts in aquatic and terrestrial ecosystems related to the LIA, as revealed by our paleorecord, imply that future warming may result in major shifts in the altitudinal forest–tundra boundary in the Copper River Basin. This interpretation supports model simulations suggesting heightened sensitivity of high-latitude and high-altitude environments to climatic forcing (e.g., Starfield and Chapin 1996, Chapin and Starfield 1997, Flannigan et al. 1998, 2001, Bugmann and Pfister 2000, Rupp et al. 2002, Heiri et al. 2006). Our data also highlight that ecosystem responses to temperature shifts can be amplified by associated moisture balance changes and fire regime feedbacks. Projections of future changes will therefore require consideration of a number of interactive factors, including those discussed here, and landscape domination by humans (Overpeck et al. 2003). Recent studies (Hu et al. 1998, 2001, Wiles et al. 2004, Anderson et al. 2005) provide strong evidence for climatic fluctuations in Alaska during the late Holocene when climatic boundary conditions were similar to those of today. Additional high-resolution studies of ecological responses to these climatic fluctuations using the multiproxy approach are important for verifying our results from Grizzly Lake and for validating model simulations of future changes.

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