

# Boreal Ecosystem Development in the Northwestern Alaska Range since 11,000 yr B.P.

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**Analyses of pollen, plant macrofossils, macroscopic charcoal, mollusks, magnetic susceptibility, and geochemical content of a sediment core from Farewell Lake yield a 11,000-yr record of terrestrial and aquatic ecosystem changes in the northwestern foothills of the Alaska Range. Between 11,000 and 8500 yr B.P., the regional landscape was dominated by a *Betula* shrub tundra, in which *Populus-Salix* communities were common. Abundant charcoal in sediments indicates that fires were common in the lake catchment during this period, and high mineral accumulation rates, allogenic elemental content, and magnetic susceptibility suggest intense soil erosion. In addition, mollusks, pollen and macrofossils of aquatic macrophytes, and biogenic silica provide evidence that the lake was substantially shallower and more productive 11,000–8500 yr B.P. than later. Low lake level and high aquatic productivity might have been caused by warm and dry summers associated with early postglacial insolation maximum in northern high latitudes. About 8000 yr B.P., *Picea glauca* arrived within the lake catchment, forming a forest tundra association until ca. 6000 yr B.P. *Alnus* shrub thickets established in the region ca. 6500 yr B.P., and *Betula papyrifera* arrived ca. 6000 yr B.P. Closed *P. glauca* forests developed ca. 6000 yr B.P. *Picea mariana* became important subsequently and replaced *P. glauca* as the dominant tree species in the region ca. 4000 yr B.P. An increase in authigenic Fe/Mn ratios suggests that the development of waterlogged soils accompanied this vegetation change. Fires increased in importance at this time and might have accelerated soil erosion. The establishment of *P. mariana* forests probably reflected complex responses of forest ecosystems to the onset of cooler and wetter climate conditions during the late Holocene.** © 1996 University of Washington.

## INTRODUCTION

Recent investigations of boreal forests emphasize the importance of complex interactions between climate, ecosys-

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tem processes, and topography in determining vegetation composition, landscape patterns, and ecosystem function (Van Cleve *et al.*, 1983, 1986, 1991; Wien and MacLean, 1983; Bonan and Shugart, 1989; Shugart *et al.*, 1993). Forest fires and soil processes affecting permafrost, forest floor organic layer, and soil temperature and moisture have been identified as the primary controls of forest dynamics. Ecosystem modeling in interior Alaska suggests that these factors could greatly alter boreal forest responses to climatic forcing (Bonan *et al.*, 1990). The roles of fire and soil-forming processes in the postglacial development of boreal forests have also attracted the attention of paleoecologists working in Alaska and adjacent Canada (Ritchie, 1985, 1987; MacDonald, 1987; Hu *et al.*, 1993; Anderson and Brubaker, 1994; Earle *et al.*, in press). Ritchie (1985, 1987), in particular, has stressed the need to examine charcoal and sediment geochemistry along with fossil pollen to elucidate the postglacial history of fire and soil regimes in relation to vegetation and climate changes. However, evidence for evaluating ecosystem processes had been unavailable from this region until two recent studies (Hu *et al.*, 1993; Earle *et al.*, in press). Hu *et al.* (1993) investigated pollen, macroscopic-charcoal, and geochemical content of a sediment core from Wien Lake to infer the relation of soil processes and fire to the associated vegetation changes during the past 12,000 years. Earle *et al.* (in press) presented a 14,000-yr charcoal record from Sityhlemenkat Lake and discussed potential importance of fires in major pollen zones. These studies provide evidence that changes in soil and fire regimes might have exerted proximate controls over vegetation responses to climatic changes during postglacial time.

In addition to the scarcity of information on terrestrial ecosystem processes, postglacial lacustrine environments are poorly documented in Alaska and adjacent Canada (Ritchie and Harrison, 1993; Anderson and Brubaker, 1994). In this

region, the response of aquatic systems to the climatic conditions associated with early postglacial summer insolation maximum (Bartlein *et al.*, 1991) is of particular interest. Ritchie *et al.* (1983) provided palynological evidence in the Yukon, Canada that the ranges of aquatic plant taxa (*Typha*, *Myriophyllum*) extended farther north during this period than at present. However, there is little evidence for range extension of these taxa in Alaska, and limnological evidence for early-postglacial summer warmth remains equivocal in this region.

We undertook this study to (1) describe the postglacial vegetation history at Farewell Lake (62°33'N 153°38' W, 320 m altitude), located on the northwestern foothills of the Alaska Range (Fig. 1a); (2) assess the influence of fires and soil changes on the development of boreal forests in its catchment; and (3) document major features of the limnological environment. The discussion of vegetation history and vegetation–fire–soil interactions is based on a stratigraphic record of pollen, plant macrofossils, macroscopic charcoal, magnetic susceptibility, and geochemical composition. Changes in aquatic environments are inferred from mollusks, pollen and macrofossils of aquatic plants, biogenic silica, and sediment characteristics. This multiproxy record provides insights into the responses of terrestrial and aquatic ecosystems to climatic changes.

#### SITE DESCRIPTIONS

Farewell Lake is located within the limits of Late Wisconsin glacier expansion from the Alaska Range (Fernald, 1960). It lies on a large, gently north-sloping piedmont covered with moraines and outwash. Farewell Lake is about 3 km west of the South Fork of the Kuskokwim River and 3 km east of the west lateral moraine of an ice tongue. Total relief near the lake is less than 61 m in all directions. Bedrock in the area is primarily limestone, slate, phyllite, and chert, all of Paleozoic age (Fernald, 1960). The vegetation is typical of closed boreal forests in Alaska (Van Cleve *et al.*, 1986; Viereck *et al.*, 1992). *Picea mariana* muskegs dominate poorly drained lowland sites, whereas mixed coniferous–deciduous forests of *P. glauca*, *Betula papyrifera*, and *Populus tremuloides* occupy well-drained upland sites. *P. glauca* and *Populus balsamifera* are also common in riparian zones. Shrub tundra communities dominated by *B. glandulosa/nana* and *Alnus crispa* occur above treeline (ca. 600 m) and on high morainal areas. The major soil types are Histic Pergelic Cryaquepts on poorly drained sites and Typic Cryorthods on well-drained sites (Rieger *et al.*, 1979). Permafrost is discontinuous in the region. Hilltops and sideslopes are generally permafrost-free, but permafrost tables are typically shallow on level and gently sloping sites.

Farewell Lake is large (surface area ca. 4 km<sup>2</sup>) and has

three sub-basins (Fig. 1b). The sediment core for this study was retrieved from the deepest part (10 m) of the smallest basin. At present, the lake does not have inlets or outlets and is highly oligotrophic, with a Secchi depth of 16 m in June 1990.

#### METHODS

A 4.40-m sediment core was recovered with a modified Livingstone corer (Wright *et al.*, 1984). The core was described for major stratigraphic changes immediately after extrusion in the field. Subsamples were taken in the laboratory for the following analyses.

##### *Pollen*

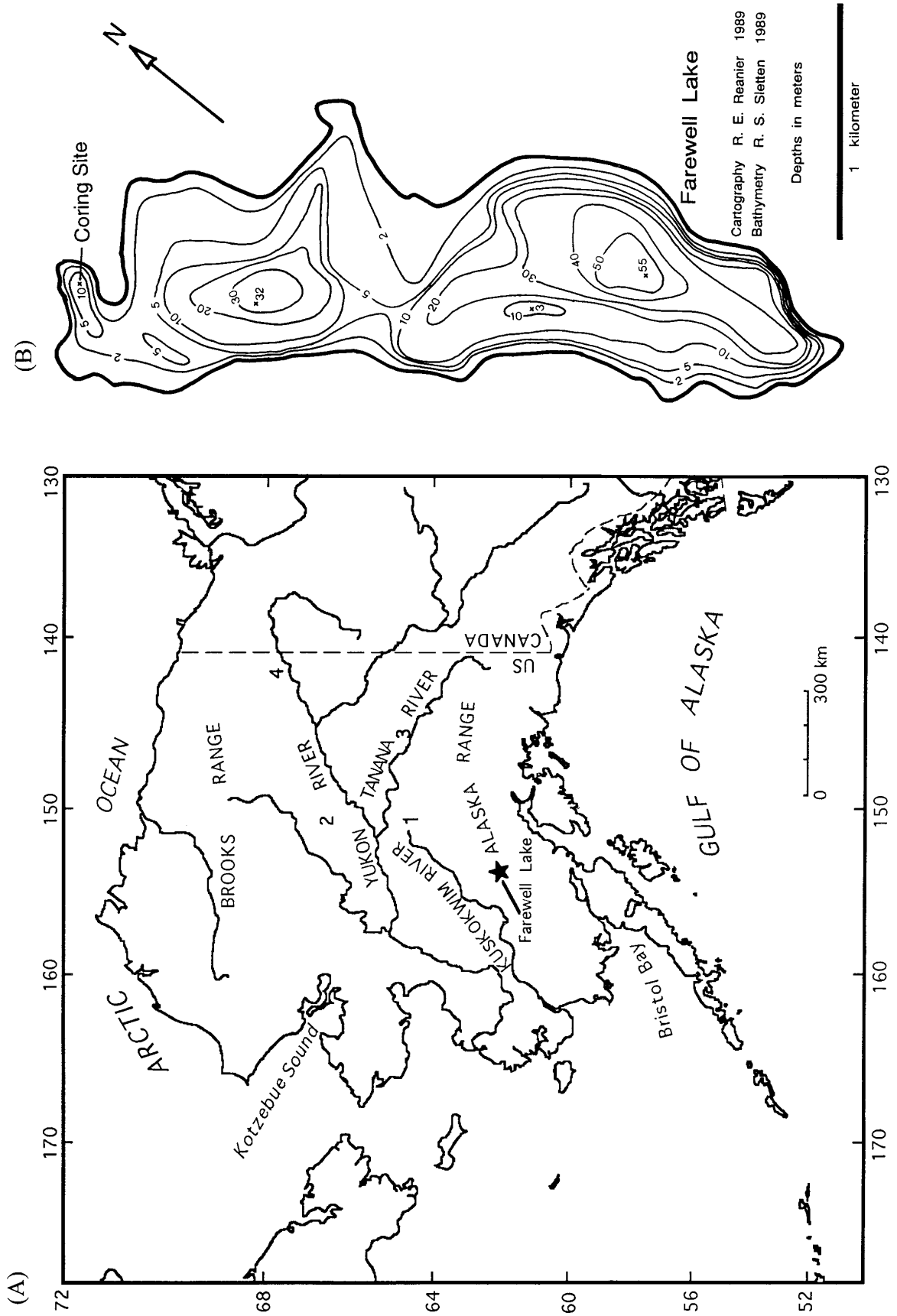
One-cubic-centimeter subsamples were prepared according to standard techniques (Faegri and Iversen, 1992) and by sieving through 7- $\mu$ m mesh screens to remove fine particles (Cwynar *et al.*, 1979). *Lycopodium* spore tablets (Stockmarr, 1972) were added to each sample prior to preparation. *Picea* pollen grains (25 to 50 per sample) were measured to separate *P. glauca* and *P. mariana* using a maximum likelihood computer program (Brubaker *et al.*, 1987). Three pollen zones were delineated by visual examination. All diagrams were plotted using the TILIA computer program (Grimm, 1992).

##### *Macrofossils and Macroscopic Charcoal*

After samples were taken for other analyses, the sediment core was cut into 10-cm continuous sections for the analyses of macrofossils and macroscopic charcoal. Samples from each 10-cm interval were soaked in 10% NaOH and washed through 1.18-mm and 0.425-mm (U.S.A. standard testing sieves 16 and 40) mesh sieves. Identifiable macrofossils were removed and examined at 10X using a dissecting microscope. All identifications were verified by modern reference materials collected from the University of Washington herbarium. Mollusks were identified by Dr. Terrence J. Frest. Identifications are primarily based on comparisons with Taylor (1981) and a modern reference collection from western North America (T. J. Frest, personal communication, 1994). The presence/absence of large charcoal particles (>0.425 mm) was recorded for each of the continuous sediment sections for the entire core. Charcoal fragments of this size are generally considered to indicate the occurrence of fires within or near the lake watershed (Clark, 1988; MacDonald *et al.*, 1991).

##### *Geochemistry and Magnetic Susceptibility*

Gross sediment composition, including organic matter (OM), carbonate, biogenic silica (BSi), and mineral matter



**FIG. 1.** (a) Map of Alaska showing locations of Farewell Lake and other sites discussed in the paper: (1) Wien Lake; (2) Sythylemenkat Lake; (3) Birch Lake; (4) Ped Pond. (b) Bathymetry of Farewell Lake and coring location.

other than carbonate and biogenic silica (MMO), was determined using the following procedures. OM concentration was measured by drying at 90°C and ashing at 550°C, and was calculated as  $100 \times (\text{dry mass} - \text{ash mass})/\text{dry mass}$ . Carbonate concentration was then determined by ashing the same sample at 950°C and was calculated as  $f \times [100 \times (\text{ash mass } 950^\circ\text{C} - \text{ash mass } 550^\circ\text{C})/\text{dry mass}]$ , where  $f = 100/44$  (molecular weight of  $\text{CaCO}_3$ /molecular weight of  $\text{CO}_2$ ). We assumed that loss-on-ignition at 950°C all resulted from loss of  $\text{CO}_2$  from  $\text{CaCO}_3$ , as carbonate concentration determined using this method is highly correlated with that calculated from Ca concentration ( $R^2 = 0.985$ ,  $p < 0.001$ ), with the difference averaging less than 2%. Biogenic silica was extracted from a separate sample using 2 M  $\text{Na}_2\text{CO}_3$  and was determined with a spectrophotometer (Perkin-Elmer 55E) following Mortlock and Froelich (1989). MMO concentration was calculated as  $100 - (\% \text{ OM} + \% \text{ carbonate} + \% \text{ BSi})$ .

Sediment preparation for elemental composition analysis (except for BSi as described above) follows the protocol of D.R. Engstrom (personal communication, 1993) modified from Engstrom and Wright (1984). An "authigenic fraction" was obtained by filtering the sample through a 0.45- $\mu\text{m}$  Millipore filter after oxidation with 30%  $\text{H}_2\text{O}_2$  and extraction with hot 0.3 M HCl. An "allogenic fraction" was prepared by the complete fusion of the remaining clastic residue in lithium metaborate followed by dissolution of the molten bead in 1 M HCl/1% citric acid. Elemental composition was determined by inductively coupled argon plasma/atomic emission spectroscopy (Thermo Jarrel Ash ICAP61E). Concentration of Si in the allogenic fraction is the difference between the borate fusion and the  $\text{Na}_2\text{CO}_3$  extract. Concentrations of all elements except for authigenic Ca are reported on the basis of carbonate-free-ash mass. Authigenic Ca concentrations are reported on the basis of total ash mass (550°C). The rationale for fractionation and interpretation of elemental composition in each fraction is discussed in detail by Engstrom and Wright (1984).

Magnetic susceptibility (MS) was measured on the whole core using a Bartington Instruments M.S. 1 meter and a 7-cm diameter, 2-cm-wide loop. Measurements were taken at 5-cm intervals for the upper 15 cm and continuously for the rest of the core. MS is a function of a number of factors including mineralogy, grain size, and the amount of magnetic material (Thompson and Oldfield, 1986). Thus, the interpretation of its stratigraphic variation is complicated. We do not discriminate among these factors and use MS primarily to supplement other sediment properties (e.g., gross sediment composition) to infer watershed soil erosion.

#### Radiocarbon Dating

Seven conventional  $^{14}\text{C}$  dates of bulk organic matter and five AMS dates of terrestrial plant macrofossils were ob-

**TABLE 1**  
**Radiocarbon Dates, Farewell Lake**

Depth (cm)	Date (yr B.P.)	Laboratory number	Dated material
80–90	2290 $\pm$ 60	Beta-50945	Bulk sediment
95–100	1550 $\pm$ 60	NSRL-1692 CAMS-12816 <sup>a</sup>	<i>Picea mariana</i> cone
145–150	3330 $\pm$ 50	Beta-50946	Bulk sediment
210–220	5190 $\pm$ 70	Beta-50947	Bulk sediment
225–235	3880 $\pm$ 60	NSRL-1584 CAMS-11705 <sup>a</sup>	<i>Picea</i> needles and seeds
250–260	4910 $\pm$ 60	NSRL-1693 CAMS-12590 <sup>a</sup>	<i>Picea</i> needles and <i>Betula</i> seeds
290–300	9180 $\pm$ 80	Beta-48235	Bulk sediment
310–315	7010 $\pm$ 70	NSRL-1585 CAMS-11703 <sup>a</sup>	Unidentified wood
325–335	7860 $\pm$ 60	NSRL-1694 CAMS-12817 <sup>a</sup>	<i>Picea</i> needles and <i>Betula</i> seeds
350–360	11,330 $\pm$ 130	Beta-50948	Bulk sediment
400–410	10,960 $\pm$ 90	Beta-50949	Bulk sediment
430–440	11,200 $\pm$ 100	Beta-48236	Bulk sediment

<sup>a</sup> AMS dates.

tained for the core (Table 1). The upper six bulk dates are 1000–2500 yr older than adjacent AMS dates when differences in sample depths are taken into account. The carbonate-rich bedrock in the watershed and high carbonate concentration of the sediments suggest that the bulk dates are too old due to "the hard water effect" (Deevey *et al.*, 1954). These six dates are excluded from the chronological analysis of the sediment core. Although the basal bulk date of 11,200  $\pm$  100 yr may also be too old, the high *Populus* percentages in these sediments suggest that this age assignment is reasonable, as it corresponds to dates for a relatively synchronous period of increased *Populus* pollen percentages found at sites throughout central Alaska (Anderson *et al.*, 1988). In addition, this interval is characterized by low carbonate concentration (Fig. 5) and terrestrial organic remains (e.g., large charred particles and small twigs) are relatively abundant, suggesting minimal contamination of old carbon. This basal bulk date is therefore used along with the five AMS dates to establish the sediment chronology and to estimate sedimentation rates (using linear interpolation) for calculating accumulation rates of pollen (PARs) and other sediment constituents.

## RESULTS

### *Pollen, Macrofossils, and Charcoal*

*Zone I (11,000–8000 yr B.P.).* Pollen assemblages are dominated by *Betula* (31–75%), *Populus* cf. *balsamifera* (2–29%), *Salix* (4–14%), and Poaceae (6–16%) (Fig. 2).

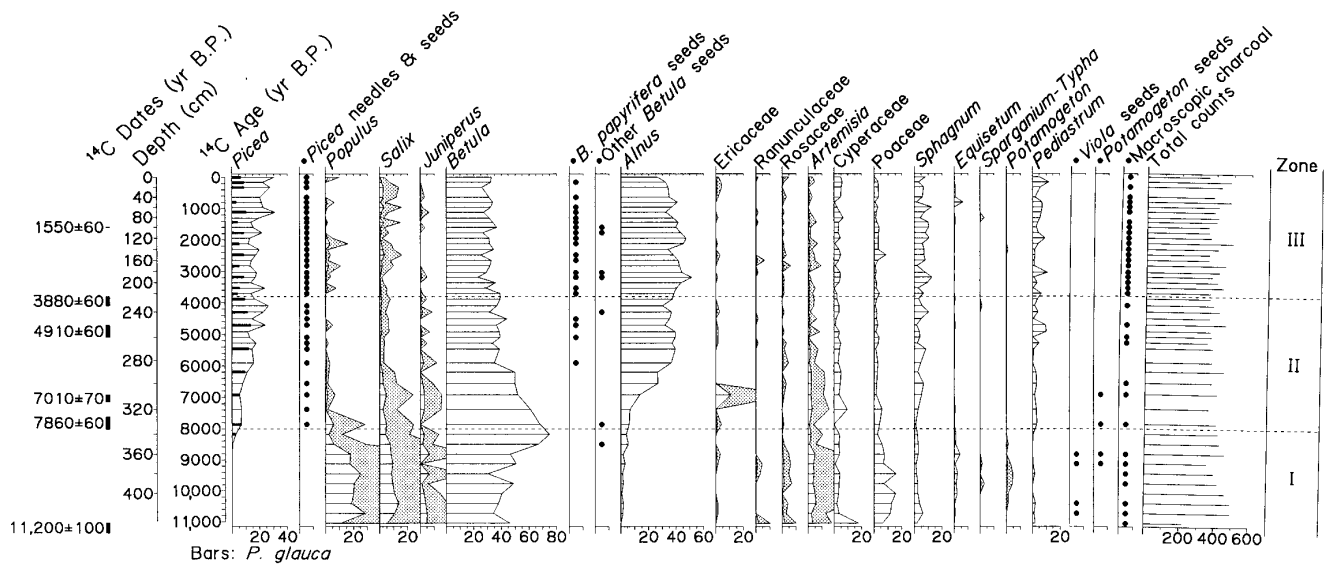


FIG. 2. Pollen percentage diagram of Farewell Lake. Stippled curves represent 10× exaggeration. Dots indicate presence of plant macrofossils, and macroscopic charcoal.

*Artemisia*, *Juniperus*, *Rosaceae*, and *Equisetum* percentages are relatively high. *Populus* and *Poaceae* percentages decrease and *Betula* percentages increase beginning ca. 9500 yr B.P. Total PARs are lower than in other zones (Fig. 3). *Potamogeton* and *Viola* seeds and *Chara* oogonia are present. Mollusks are most abundant and diverse in this zone (Fig. 4). The mollusk assemblages are dominated by *Valvata helicoidea* and *Psidium idahoense*, but contain a variety of other gastropod and bivalve species. All gastropod species except for *V. helicoidea* and *Lymnaeidae* indet. disappeared after 8500 yr B.P. Charcoal is abundant until 8500 yr B.P.

**Zone II (8000–4000 yr B.P.).** This zone is marked by a continuous increase in *Picea* pollen (predominantly *P. glauca*, Fig. 2, Table 2). *Picea* pollen percentages and PARs are low (5–10% and 44–60 grains/cm<sup>2</sup>/yr, respectively) between 8000 and 6000 yr B.P., but *Picea* needles are consistently present after 8000 yr B.P. *P. mariana* pollen increases in relative abundance 6500–5500 yr B.P., reaching 36% of total *Picea* pollen by the end of the zone. *Betula* percentages reach maximum values (50–75%) between 8500 and 6500 yr B.P., although *Betula* PARs are not consistently high during this period. *B. papyrifera*

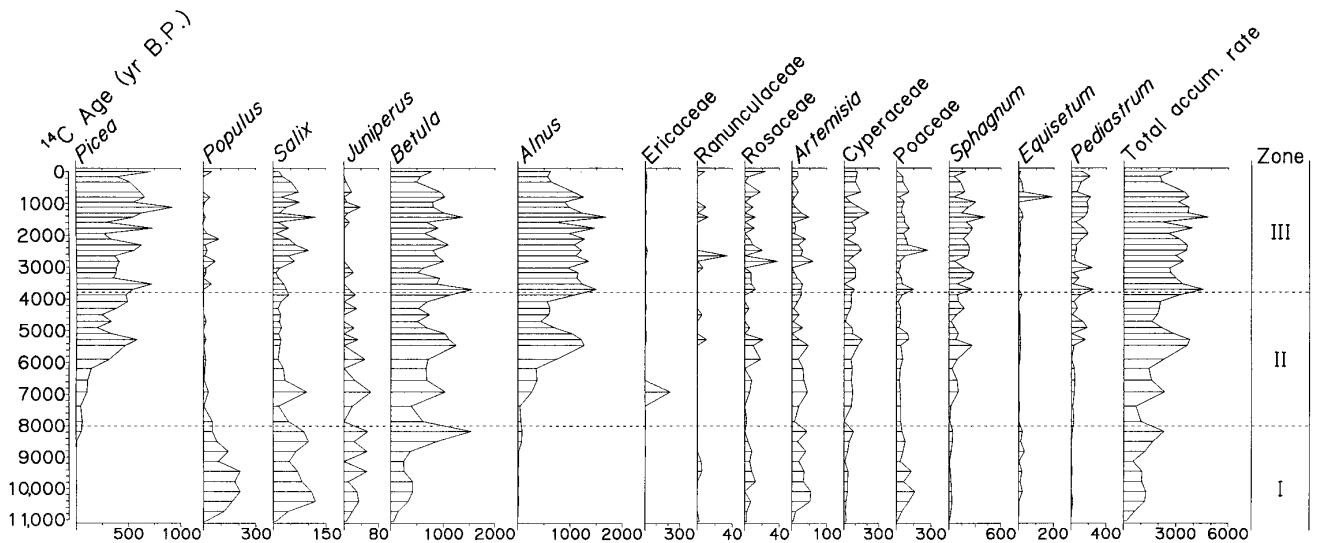


FIG. 3. Pollen accumulation rate (grains/cm<sup>2</sup>/yr) diagram of Farewell Lake.

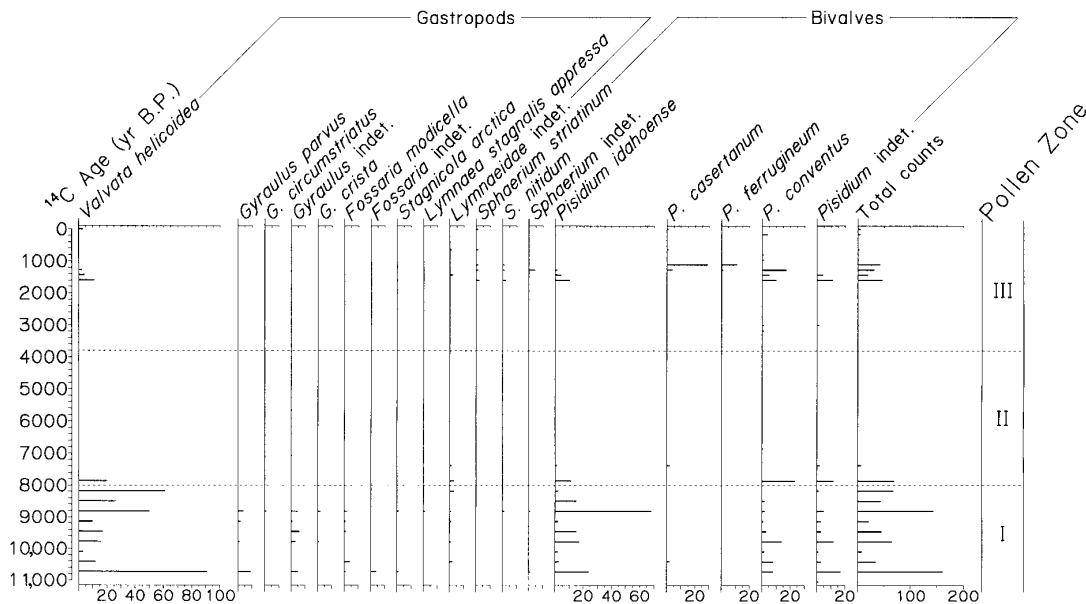


FIG. 4. Mollusk stratigraphy of Farewell Lake. Numbers at each level represent counts in ca. 200 ml sediment.

seeds first appear ca. 6000 yr B.P. *Alnus* pollen increases to 20% ca. 6500 yr B.P., reaching ca. 40% by 5500 yr B.P. Percentages and accumulation rates of *Pediastrum* cell nets are substantially higher than those in zone I.

TABLE 2

Theta ( $\theta$ ) Values and Standard Errors (SE) for *Picea*, Maximum Likelihood Discrimination, Farewell Lake

Depth (cm)	Estimated age (yr B.P.)	$\theta$	SE
0	0	0.2089	0.0855
10	159	0.3979	0.0972
20	318	0.3856	0.1354
50	795	0.1389	0.0766
70	1113	0.3315	0.1322
90	1431	0.2756	0.1274
110	1770	0.3954	0.1358
130	2122	0.4399	0.1373
150	2474	0.4870	0.0984
170	2824	0.4014	0.1361
190	3177	0.4913	0.1379
210	3528	0.2269	0.1217
220	3704	0.2899	0.1288
230	3880	0.5665	0.1368
240	4292	0.5246	0.0973
250	4704	0.7491	0.1237
270	5458	0.8313	0.1113
290	6188	0.8657	0.1043
310	6918	1.0000	—
330	7860	1.0000	—
340	8178	0.9245	0.0882

Except for the presence of two gastropod and four bivalve taxa at the lowest two levels, mollusks are absent. Charcoal fragments are present irregularly.

*Zone III (4000–0 yr B.P.)*. This zone is distinguished primarily by the consistently higher percentages of *P. maritima* than *P. glauca* pollen. *Sphagnum* spore percentages are also generally higher than those in other zones. *Betula* pollen percentages decrease slightly, and *Populus*, *Salix*, and *Alnus* pollen are somewhat more common than those in upper portions of zone II. Total PARs are highest in this zone. Bivalves reappear after ca. 1600 yr B.P. but are less abundant and diverse than those in zone I. Except for *V. helicoidea* and *Lymnaeidae*, gastropod species are absent. Charcoal is present at every sampling interval.

#### Sediment Magnetic and Chemical Properties

*Magnetic susceptibility*. MS is relatively high but gradually decreases between 10,000 and 8500 yr B.P. (Fig. 5). It reaches lowest values 8500–5000 yr B.P., begins to increase at 5000 yr B.P., and remains consistently high after 4000 yr B.P.

*Gross sediment composition*. Three-point running averages of percentages and accumulation rates are used to highlight major stratigraphic patterns of gross sediment components (Fig. 5). MMO (60–80%) is the dominant sediment constituent from 11,000 to 9000 yr B.P. in pollen zone I. BSi is also more abundant in this zone than in other zones. MMO concentration decreases to <30% and carbonate concentration increases to >50% by 8000 yr B.P. Carbonate

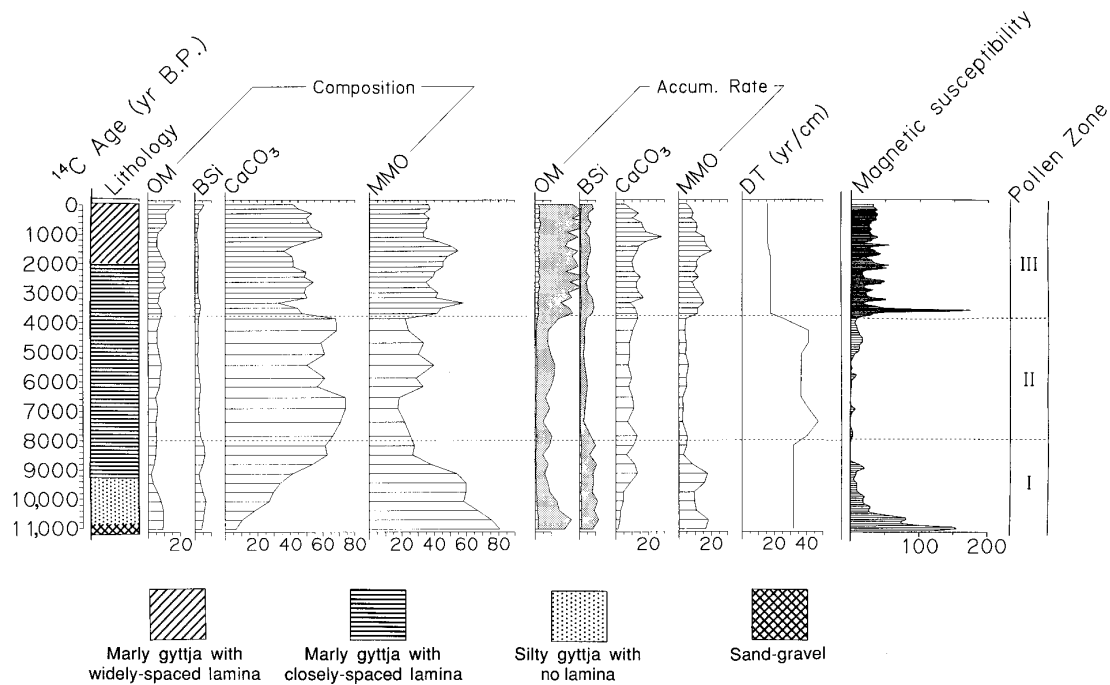


FIG. 5. Lithostratigraphy, composition (%) and accumulation rates ( $\text{mg}/\text{cm}^2/\text{yr}$ ) of gross sediment components, and magnetic susceptibility (S.I. unit) of Farewell Lake. Stipple curves represent  $10\times$  exaggeration. Data are three-point running averages. DT = deposition time.

(50–75%) is the dominant sediment fraction in pollen zone II. Carbonate concentration decreases to 35–50% and MMO concentration increases to 20–45% after 4000 yr B.P. Stratigraphic patterns of the accumulation rates are similar to those of percentages in pollen zones I and II. However, unlike percentages values, the accumulation rates of all gross components are higher in zone III than in zone II. MMO accumulation rates increase to a greater extent than any other components, particularly carbonate, suggesting that the decrease in carbonate content in zone III is due to the dilution of MMO.

**Elemental composition.** Concentrations of most elements in both the authigenic and allogenic fractions fluctuate throughout the core. Stratigraphic patterns, particularly those of the allogenic fraction, are relatively subtle (Fig. 6). The authigenic fraction is dominated by Ca followed by Fe, Mg, and Al. The major stratigraphic features in this fraction are highest concentrations of Ca, Mg, and Na in pollen zone II and highest Fe/Mn ratios in zone III. The allogenic chemistry is dominated by Si, Al, and Na. Most elements have highest but decreasing concentrations in pollen zone I. Concentrations of Si, Al, and Fe are somewhat higher in zone III than in zone II.

#### INTERPRETATION OF PROXY DATA: ECOSYSTEM HISTORY

##### Pollen Zone I (11,000–8000 yr B.P.)

A *Betula* shrub tundra with prominent populations of *Populus balsamifera* probably dominated the regional land-

scape during this period. Similar vegetation has been inferred throughout much of north-central Alaska (Anderson *et al.*, 1988; Anderson and Brubaker, 1994). The widespread occurrence of *P. balsamifera* and range extensions of aquatic species (*Typha*, *Myriophyllum*) has been interpreted to indicate warmer-than-present summer temperatures (Ritchie, *et al.*, 1983; Barnosky *et al.*, 1987; Anderson and Brubaker, 1994). At Farewell Lake, *Populus*-dominated communities probably occupied the lake shore as well as extensive riparian habitats in river drainages from the Alaska Range. The association of *Populus* pollen with relative high percentages of *Salix*, Rosaceae, and Poaceae pollen suggests that these communities might have been similar to modern *Populus* stands on floodplains in interior Alaska (Van Cleve *et al.*, 1986, 1991; Viereck *et al.*, 1992), where *Salix* and Rosaceae are common in the shrub layer and Poaceae (predominantly *Calamagrostis canadensis*) form a dense herb cover. Similarly, *Artemisia*–*Juniperus* shrub communities resembling modern communities on warm, dry south-facing bluffs in interior and south-central Alaska (Viereck *et al.*, 1992) might have dominated south-facing mountain slopes in the Farewell region. Both types of community appeared to have declined in abundance near the end of this period.

The abundance of charcoal in sediments suggests that fires were common within the Farewell Lake watershed. Fires might have been favored by warm and/or dry summer conditions, which would have dried fine fuels of trees, shrubs, and grasses. Common fire occurrence might have resulted

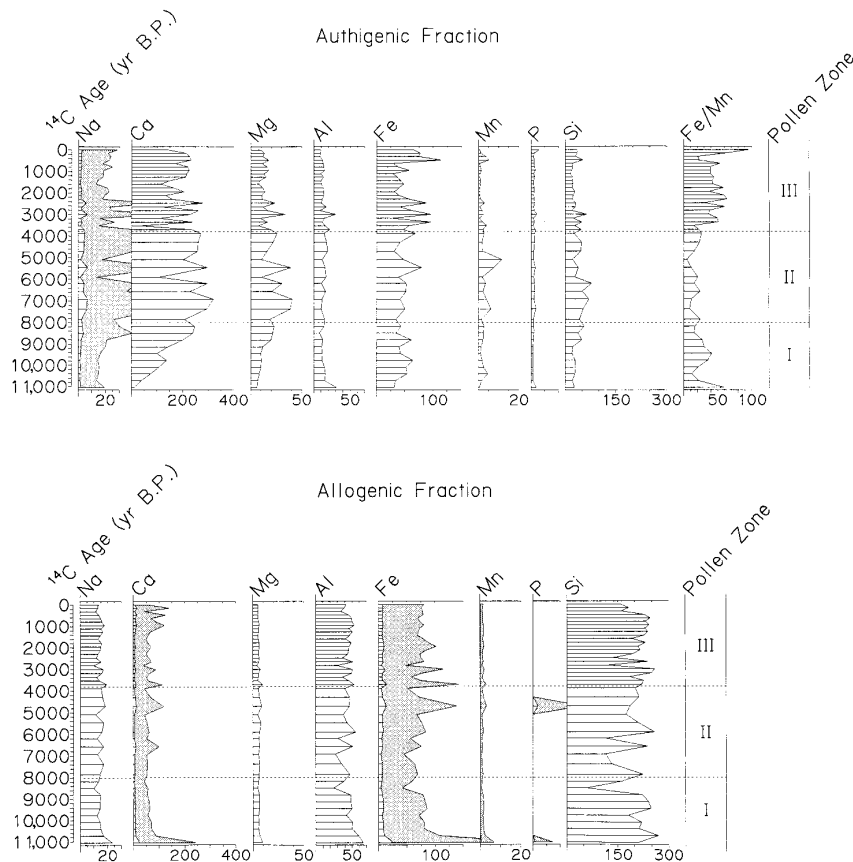


FIG. 6. Sediment elemental composition diagram of Farewell Lake. Stippled curves represent 10× exaggeration. Concentrations of all elements except for authigenic Ca are in milligrams per gram carbonate-free ash. Concentrations of authigenic Ca are in milligrams per gram total ash.

in unstable soils, and intense soil erosion within the lake catchment as indicated by high values of mineral accumulation rates (MAR), allogenic concentrations of most elements, and MS (Engstrom and Wright, 1984; Thompson and Oldfield, 1986). These values may also in part reflect the deposition of coarse-grain mineral matter in a shallow lakeshore environment.

The early limnological conditions of Farewell Lake probably differed substantially from those of later periods. A variety of indicators suggest that Farewell Lake was much shallower and more productive than today. For example, *Fossaria modicella* typically lives at sites with water depth <1 m, and *Gyraulus parvus*, *G. circumstriatus*, and *G. crista* are all common in very shallow, fluctuating water bodies (Clarke, 1979). In addition, lake sediments are not laminated (Fig. 5) during this period, suggesting a shallow depositional environment in which sediments were well mixed by water turbulence and/or bioturbation. The coring basin was probably the center of a small pond, which was separated from the two large sub-basins of Farewell Lake during this period. The pond was likely much more productive than at present

as most of the gastropod taxa present (e.g., *G. parvus*, *F. modicella*, *S. arctica*) are thought to be indicators of eutrophic lakes (Clarke, 1979). Furthermore, the presence of *G. parvus*, *G. crista*, and *L. stagnalis appressa*, which commonly feed on aquatic macrophytes such as *Typha* and *Potamogeton* (Clarke, 1979), indicates that rooted aquatic plants were abundant. The presence of *Potamogeton* and *Viola* seeds and *Potamogeton* and *Sparganium-Typha* pollen confirms this interpretation. The productivity of diatom communities might also have been relatively high, as suggested by relatively high percentages and accumulation rates of biogenic silica.

The interpretation of low water level and high trophic status, however, is not corroborated by the records of carbonate concentration and *Pediastrum* cell nets. Carbonate concentration is lowest during this period, even though high aquatic productivity and warm summer temperatures should have increased carbonate precipitation from the lake water (Kelts and Hsu, 1978). Manny *et al.* (1978) and Dustin *et al.* (1986) suggest that low carbonate percentages of early postglacial sediments in other marl lakes resulted from dilu-

tion by high terrigenous input before stabilization of watershed soils. Although this explanation may apply to the Farewell core, for MMO concentration is highest during the early postglacial period, carbonate accumulation rates are low during this period, arguing against a dilution effect. A more likely cause is that carbonate deposition in sediments was reduced by relatively high dissolved CO<sub>2</sub> concentration and low pH of the water due to organic matter decomposition in the eutrophic lake system. Percentages and accumulation rates of *Pediastrum* cell nets, which tend to be common in surface sediments of shallow lakes in Alaska (Anderson and Brubaker, 1986), are also lowest in this zone. However, the genus *Pediastrum* includes many species with diverse aquatic ecological affiliations. Thus, it should not be used as an indicator of water depths or productivities unless identified to species or corroborated by independent sediment proxies.

#### *Pollen Zone II (8500–4000 yr B.P.)*

This period is characterized by the arrival of several species common in the regional vegetation today. The first appearance of *Picea* needles suggests that *Picea* invaded the Farewell watershed ca. 8000 yr B.P. Results of maximum likelihood analysis suggest that *P. glauca* was the only *Picea* species in the region until ca. 6000 yr B.P. The ranges of *Picea* pollen percentages (5–10%) and PARs (44–60 grains/cm<sup>2</sup>/yr) 8000–6000 yr B.P. fall below values in surface sediments from modern forest tundra in Alaska and Yukon (cf. Cywnar and Spear, 1991), suggesting that tree densities in the Farewell region were low during this period. A forest-tundra ecotone probably persisted in the region until 6000 yr B.P., although *P. glauca* populations gradually increased 7000–6000 yr B.P. About 6000 yr B.P., increases in *Picea* pollen percentages and PARs suggest a conversion from forest tundra to forest. *B. papyrifera* arrived at Farewell Lake ca. 6000 yr B.P. and likely became codominant with *P. glauca* in upland sites. Although the arrival time of *P. mariana* is difficult to judge, this species apparently gained importance in the regional vegetation 6000–5000 yr B.P. *Alnus* probably arrived in the Farewell region ca. 6500 yr B.P., and, as at present, formed dense thickets on mountain slopes and floodplains.

Terrestrial ecosystems differed greatly from the preceding period. The rare occurrences of charcoal suggest that fires were uncommon in the lake catchment. Fluctuations of sediment concentrations of most elements in both authigenic and allogenic fractions become more pronounced after 8500 yr B.P., possibly reflecting the occurrence of isolated erosional events and the laminated nature of sediments. Overall, however, soil erosion was probably less intense than pollen zones I and III since MAR, allogenic elemental concentrations, and MS are generally lowest in this zone.

Changes in several sediment constituents suggest that aquatic productivity decreased and water depth increased from the previous period. For example, all gastropod taxa disappeared except for *V. helicoidea*, a eurytopic species (Clarke, 1979), and *Lymnaeidae* indet. of unknown ecological affiliation. Bivalves were also absent except in the lowest portion of this zone. In addition, the sediment concentrations and accumulation rates of biogenic silica decreased, suggesting a decline in diatom productivity. The pond had probably become substantially deeper by this time, as all gastropod species indicative of shallow water bodies are absent and sediments are finely laminated in zone II. These limnological changes may reflect a general cooling of the regional climate following the early-postglacial summer insolation maximum (Barnosky *et al.*, 1987; COHMAP Members, 1988; Bartlein *et al.*, 1991).

#### *Pollen Zone III (4000–0 yr B.P.)*

The shift in dominance from *P. glauca* to *P. mariana* suggests that the modern mosaic of boreal forest communities developed ca. 4000 yr B.P., with *P. mariana* muskegs occupying poorly drained lowland sites, and mixed conifer–hardwood stands dominated by *P. glauca* and *B. papyrifera* occupying well-drained upland sites. *Populus*, *Salix*, and *Alnus* appear to have increased after 4000 yr B.P., suggesting an expansion of early successional riparian communities. The continuous presence of charcoal in zone III samples suggests that fires became more important in the watershed than during zone II. *Picea* population densities probably increased to present levels ca. 1200 yr B.P. when *Picea* pollen percentages and PARs reach values similar to those in surficial sediments.

Sedimentation rates increased substantially after 4000 yr B.P. Although this change could have been caused by increased sediment focusing (Davis *et al.*, 1984), this explanation is unlikely since sediment focusing should have been more severe during the previous period when the basin was deeper. In addition, sediment focusing would not have caused changes in elemental composition (Engstrom *et al.*, 1991) and MS values. Accelerated soil erosion, as suggested by increases in MAR, allogenic concentrations of several elements, and MS, is a more likely cause of increased sedimentation rates. Increased soil erosion might have been caused by frequent disturbances of forest cover by fires during this period (as discussed above) as well as by climatic changes. Glaciers advanced throughout Alaska, including the northern Alaska Range during the late Holocene (Calkin, 1988), suggesting that the Farewell region might have been cooler and wetter during pollen zone III. These changes would have increased the transport of clastic material from the watershed to the lake. They may have also increased alluvial activity, contributing to the expansion of riparian

communities as indicated by increases in *Populus*, *Salix*, and *Alnus* pollen.

The consistently higher authigenic Fe/Mn ratios in pollen zone III than previously suggest that the extensive lowlands in the northern portion of the Farewell catchment became paludified since ca. 4000 yr B.P. Ratios of Fe and Mn in lake sediments have been used to infer changes in soil redox conditions related to watershed paludification (Mackereth, 1966; Engstrom and Wright, 1984), because the solubility of these elements differs with respect to redox values. For example, Engstrom and Hansen (1985) interpret an increase in the Fe/Mn ratio in sediment cores from Labrador as a signal of the development of peaty, waterlogged soils. Similar soil changes in the lowlands at Farewell Lake might have been induced by cooler climatic conditions that caused permafrost to rise, retarding drainage of lowland sites and leading to the development of waterlogged soils. Decreased soil redox levels under such conditions should have increased the solubilization of Fe over Mn in watershed soils, resulting in increased deposition of Fe relative to Mn in the authigenic fraction of the sediments.

Alternative explanations for elevated Fe/Mn ratios should also be considered, however, because Fe and Mn are vulnerable to sediment diagenesis. In particular, the development of moderately anaerobic bottom water may lower redox levels enough to solubilize manganic oxyhydroxides but not ferric oxyhydroxides in the surface sediments (Mortimer, 1941, 1942; Mackereth, 1966), resulting in the preferential loss of Mn relative to Fe. Hypolimnetic anaerobic conditions could develop with an increase in aquatic productivity. However, the coring basin was likely oligotrophic and never became anaerobic after 8500 yr B.P. The deposition of abundant carbonate from lake water, as indicated by the high carbonate concentration of sediments after 8500 yr B.P., probably resulted in nutrient deficiency for aquatic production, since particulate carbonate adsorbs and complexes essential metallic and organic compounds, suppressing microbial nutrient regeneration and photosynthetic efficiency (Wetzel, 1970). Another possible reason for higher Fe/Mn ratios in zone III is differential coprecipitation of Fe and Mn with carbonates and possible decrease of carbonate precipitation ca. 4000 yr B.P. However, because Fe coprecipitates with carbonates to a greater extent than Mn (Wetzel and Manny, 1978), a decrease in carbonate concentration should have resulted in a decrease rather than an increase in Fe/Mn ratios.

There are some indications that aquatic productivity increased slightly in pollen zone III, although it was probably oligotrophic throughout this period, as at present. For example, elevated BSi accumulation rates ca. 4000 yr B.P. suggest that the productivity of diatom communities increased, possibly due to nutrient inputs from watershed soil erosion. Some bivalve taxa also reappear in this zone ca. 1600 yr B.P., but

most gastropod species found in pollen zone I are absent during this period.

## DISCUSSION

### *Lacustrine Environments during the Early Postglacial*

A variety of paleoenvironmental records from Alaska and adjacent Canada suggest that the region experienced a period of relatively warm summers between 11,000 and 8000 yr B.P., presumably caused by a pronounced maximum in summer insolation in northern high latitudes (Ritchie *et al.*, 1983; Barnosky *et al.*, 1987; Bartlein *et al.*, 1991; Ritchie and Harrison, 1993). Primary evidence includes range extensions of *Picea* and *Populus*, increased eolian activity, accelerated melting of ice wedges, and peaks in *Populus* and *Juniperus* pollen (McCulloch and Hopkins, 1966; Hopkins *et al.*, 1981; Ritchie *et al.*, 1983; Ritchie, 1984, 1987; Anderson and Brubaker, 1993, 1994). In addition, *Typha* and *Myriophyllum* also extended further north and were probably more abundant in lakes than at present (Hopkins *et al.*, 1981; Ritchie *et al.*, 1983; Ritchie, 1984), suggesting a regional lowering of lake levels and/or warmer water temperatures (Anderson and Brubaker, 1994). However, information on lacustrine responses to the early postglacial thermal maximum remains scarce (Ritchie and Harrison, 1993; Anderson and Brubaker, 1994) because little work has been done to investigate limnic indicators of warmth in sediment cores from the region. The Farewell record of mollusks, pollen and macrofossils of aquatic plants, and biogenic silica provides relatively detailed evidence that the lake was shallower and more productive than at present during early postglacial time. Such limnic conditions likely reflected warmer and drier summer conditions than those of today. Our results are in part supported by the abundance of mollusks in early postglacial sediments from other sites in Alaska (Ped Pond, Edwards and Brubaker, 1986; Birch Lake, Edwards and Finney, personal communication, 1994), although mollusks in these cores have not been identified. Detailed investigations of sediment proxies of aquatic productivity and lake water levels are needed to test whether paleolimnological and paleoclimate information derived from the limnological indicators at Farewell is representative of the region during the early postglacial interval.

### *Implications for the Postglacial History of Picea and Betula*

Pollen and macrofossil data from Farewell Lake provide the first paleovegetation record from the vast area of southwestern Alaska currently occupied by closed boreal forests. As such, this record significantly expands current knowledge of the postglacial development of Alaskan boreal forests. In particular, it aids in refining the geographic patterns and

timing of the spread of *P. glauca* and *P. papyrifera* to their present ranges.

*P. glauca* spread throughout northeastern and much of north-central Alaska between 10,000 and 9000 yr B.P. (Anderson and Brubaker, 1993, 1994), continuing its extremely rapid movement from southern Alberta to northwestern Canada (Ritchie and MacDonald, 1986; MacDonald, 1993). In Alaska, *P. glauca* experienced a marked population decline between 8500 and 7500 yr B.P., probably in response to a climatic cooling (Hu *et al.*, 1993; Anderson and Brubaker, 1994). Hopkins *et al.* (1981) and Anderson and Brubaker (1994) speculate that the westward expansion of *P. glauca* also halted during this period. However, pollen and macrofossil data marking the arrival of *P. glauca* at Farewell Lake 8000 yr B.P. imply that its westward migration continued when populations declined in other parts of Alaska.

In the context of other pollen records from Alaska and northwestern Canada (Ritchie, 1987; Anderson and Brubaker, 1994), the Farewell pollen diagram also suggests that both the rates of migration and initial population growth of *P. glauca* differed substantially between the times of its initial arrival in Canada and northeastern Alaska and its subsequent spread to southwestern Alaska. For example, between 10,000 and 9000 yr B.P., *P. glauca* arrived at sites separated by as much as 1000 km in eastern Alaska and Canada, but its arrival at Farewell Lake lagged 1500 yr behind its arrival at Wien Lake, the closest well-dated site ca. 200 km to the northeast (Hu *et al.*, 1993). In addition, new pollen records (Hu *et al.*, 1995; Short *et al.*, 1992) show that *Picea* did not arrive in the Bristol Bay region until ca. 4000 yr B.P. Based on the data from Wien Lake, Farewell Lake, and the northern Bristol Bay region, the rate of *P. glauca* spread across southwestern Alaska averaged less than 0.2 km/yr, more than 10 times slower than the 2 km/yr estimate for its migration rate across the Western Interior Canada (Ritchie and MacDonald, 1986). In addition, pollen records from Farewell Lake and the Bristol Bay region (Hu *et al.*, 1995) are all characterized by a long period of low percentages of *P. glauca*, suggesting that population sizes remained small after its arrival. At Farewell Lake, for example, *P. glauca* population densities probably did not increase substantially between 8000 and 6000 yr B.P., after its initial colonization. This contrasts with the relatively rapid initial rise in percentages of *P. glauca* pollen at sites in northeastern Alaska (e.g., Ager, 1975; Anderson *et al.*, 1988) and Canada (MacDonald, 1993), which suggests much greater rates of population growth in those regions. Reasons for the differences in the rates of spread and population growth between northeastern and southwestern Alaska deserve further study. We speculate, however, that such differences may have resulted from the generally cooler growing seasons during the late Holocene in contrast to those of the early Holocene, and

the greater expanse of fine-texture lowland soils unfavorable for *P. glauca* expansion in southwestern Alaska than in northeastern Alaska.

The history of *B. papyrifera* in Alaska is poorly understood because of the difficulty of distinguishing its pollen from that of other *Betula* species (Edwards *et al.*, 1991) and the scarcity of *B. papyrifera* macrofossil data. A continuous plant macrofossil record from Wien Lake (Hu *et al.*, 1993) indicates that the arrival of *B. papyrifera* coincides with that of *P. glauca* 9500 yr B.P., suggesting that the current ecological association of these species might have developed during the early Holocene. However, the only other published macrofossil information of *B. papyrifera* is from Seward Peninsula, where buried wood indicates that this species was present ca. 8300 yr B.P. and preceded the arrival of *P. glauca* and establishment of forest tundra by several millennia (McCulloch and Hopkins, 1966; Hopkins *et al.*, 1981). In contrast to both these records, the Farewell Lake data indicate that the establishment of *B. papyrifera* followed that of *P. glauca* by 2000 yr. Although a grid of macrofossil records is needed to document the history of *B. papyrifera* in Alaska, the data from these three sites clearly indicate that, despite the similarity of their modern ecological preferences, *B. papyrifera* and *P. glauca* had different postglacial dispersal patterns.

The spreading patterns of *P. glauca* and *B. papyrifera* illustrate the complexity in the shifts of species ranges and population sizes during the postglacial development of boreal forest communities. In particular, the history of *P. glauca* shows that rates of migration and population growth may vary greatly under changing climatic and other environmental conditions, and the difference in the histories of *P. glauca* and *B. papyrifera* suggests that currently co-occurring species may have had contrasting migration patterns during the postglacial. Such individualistic behavior of plant species has been commonly observed in pollen records of late-Quaternary vegetation changes from Alaska (Anderson and Brubaker, 1994; Brubaker *et al.*, in press) and other regions (Davis, 1986; Prentice, 1992).

#### *An Ecosystem Perspective of Modern Boreal Forest Development*

The Farewell sediment record suggests that the establishment of modern boreal forests was associated with complex changes in ecosystem processes. As discussed above, these vegetation and ecosystem shifts were probably caused by regional climatic cooling. On the basis of the Farewell record, we propose a framework for the development of *P. mariana* forest ecosystems in the boreal region in relation to climatic controls in light of relevant paleoecological data from other sites.

A climatic shift to cooler/wetter conditions probably in-

duced permafrost aggradation, impeding drainage in lowland areas and leading to the development of waterlogged soils with low nutrient availability. Such a climatic change would also accelerate soil erosion from surrounding uplands and increase transport of clastic mineral matter into Farewell Lake. Waterlogged soils would have favored the dominance of *P. mariana* over *P. glauca*, because *P. glauca* prefers well-drained, nutrient-rich soils and *P. mariana* occupies acidic, nutrient-poor substrates with poor drainage (Van Cleve *et al.*, 1986; Viereck *et al.*, 1992). Studies of modern forest succession in interior Alaska have also indicated that the shift from *P. glauca*- to *P. mariana*-dominated stands is commonly accompanied by a rise of permafrost and the development of waterlogged soil conditions (Van Cleve *et al.*, 1983, 1986, 1991). Although a cooler/wetter climate should not directly favor the occurrence of fires, the establishment of *P. mariana* forests would have increased the probability that fires, once ignited, would spread across the landscape. *P. mariana* is a strongly fire-adapted species. Its resinous wood and foliage, deep crowns, abundant fine branches commonly covered with lichens, and dense population structures make *P. mariana* stands highly flammable and prone to stand-replacing fires (Dyrness *et al.*, 1986). In addition, the semi-serotinous cones of this species promote self-regeneration after catastrophic burns. Thus, the widespread establishment of *P. mariana* stands would have resulted in a general increase in fires in the region which, in turn, would have favored the dominance of *P. mariana*. The establishment of *P. mariana* forests, therefore, was probably ultimately driven by climate, but complex vegetation–soil–fire interactions likely provided positive feedbacks within the system, sustaining *P. mariana* dominance over *P. glauca*.

Relatively few data are available from other sites for evaluating ecosystem changes described in the framework. A sediment geochemical record from Wien Lake, central Alaska, contrasts with the Farewell evidence that soil waterlogging accompanied the establishment of *P. mariana* dominance. At Wien, no consistent stratigraphic patterns were found in the concentrations and ratios of redox elements at the time fossil pollen indicates that *P. mariana* forests were established in the region. The discrepancy of the Farewell and Wien geochemical records is somewhat difficult to reconcile, but may be related to differences in watershed characteristics and associated vegetation patterns between these sites. A large portion of the Wien Lake watershed is surrounded by rolling hills with well-drained soils dominated by *P. glauca* and *B. papyrifera*. Poorly drained soils occupied by *P. mariana* communities are most common in a relatively restricted area near an outlet stream far from the coring locality. The formation of waterlogged soils in this portion of the watershed would not likely be recorded in the geochemical contents of the sediment core. In contrast, the

coring basin of Farewell Lake is adjacent to an extensive, gently sloping area dominated by *P. mariana* muskeg, and surface runoff and groundwater from this area appear to drain into the lake at present. Changes in soil chemistry associated with the development of waterlogged soils near Farewell are thus more likely to leave signals in the Farewell lake sediments.

Consistent with the Farewell record, charcoal data from other sites in Alaska suggest increased importance of fires associated with the dominance of *P. mariana*. For example, macroscopic charcoal at Wien Lake (Hu *et al.*, 1993) and microscopic charcoal at Sithylemenkat Lake (Earle *et al.*, in press) increase in abundance with the shift from predominantly *P. glauca* to *P. mariana* pollen. This consistency among sites is striking considering methodological differences in charcoal analysis of these studies and the asynchrony of the shift from *P. glauca* to *P. mariana* at the three sites (6500 yr B.P. at Wien, 5000 yr B.P. at Sithylemenkat, 4000 yr B.P. at Farewell). Although these charcoal stratigraphies do not provide information on absolute fire frequency and intensity, they all support the proposition that the establishment of modern fire regime in Alaska developed contemporaneously with the establishment of *P. mariana* forests (Hu *et al.*, 1993).

Our inferences of vegetation–fire–soil interactions in the Farewell region also generally agree with those for eastern Canadian boreal forests. Payette (1992), for example, suggests that a progressive change toward cooler conditions during the mid-Holocene resulted in frequent fires and an increase in *P. mariana*. In addition, several paleoecologists (Lamb, 1980; Engstrom and Hansen, 1985; Liu, 1990) have inferred from pollen or geochemical records that the Holocene development of *P. mariana* forests was accompanied by the initiation of waterlogged soils. These authors, however, emphasized the importance of autogenic soil processes, specifically that *P. mariana* dominance resulted from autogenic soil paludification under stable climatic conditions. In this interpretation, successional processes resulted in the buildup of soil organic layers under coniferous stands, insulating underlying soils from summer heat and leading to poor soil drainage. This contrasts with our proposition that climatic change, based on inferences from regional glacial history, initiated ecosystem changes in the Farewell region. Disagreement between the conclusions of these studies may reflect regional differences in the importance of autogenic soil changes as well as inadequate knowledge of regional climate history. Assessing the role of autogenic soil processes vs climate in the development of boreal forests is difficult without a relatively detailed understanding of climatic history in each region. Ultimately required are proxy climate records that are independent of the data used to infer ecosystem changes and have temporal and spatial resolutions comparable to those of the ecosystem changes.

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