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ORIGINAL PAPER

The pollen record from El'gygytgyn Lake: implications for vegetation and climate histories of northern Chukotka since the late middle Pleistocene

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Abstract Three types of pollen assemblages (shrub-dominated, mixed herb- and shrub-dominated, and herb-dominated) characterize the ~300,000 year palynological record from El'gygytgyn Lake. Despite major changes in global climatic forcings, all pollen spectra, with a few isolated exceptions, have strong to possible analogs in the modern plant communities of Northeast Siberia and Alaska. Paleoclimatic reconstructions based on squared chord-distance analog analyses indicate two periods (~8600–10,700 ^{14}C year B.P. and OIS 5e) when summers were perhaps ~2 to 4°C warmer than modern. January temperatures were also warmer than present, and both July and January were wetter than today. Palynological data remain inconclusive as to the establishment of forests near El'gygytgyn Lake at these times. The wettest Julys occurred during OIS 5d. July temperatures were near modern, and Januarys were colder and drier than now. January temperatures, even into the Middle Pleistocene, generally show little variability, suggesting that the suppression of arboreal taxa during glaciations was likely caused by cool summers with low effective moisture and not by frigid winters. Because age schemes that correlate magnetic susceptibility to variations in summer insolation or ∂^{18}O have cool plant taxa persisting in warm times (and vice versa), we propose an alternative age model based on the palynological data.

Keywords Paleoclimate · Paleovegetation · Pollen · Analog reconstruction · Late Quaternary · Northeast Siberia

This is the *tenth* in a series of eleven papers published in this special issue dedicated to initial studies of El'gygytgyn Crater Lake and its catchment in NE Russia. Julie Brigham-Grette, Martin Melles, Pavel Minyuk were guest editors of this special issue.

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Introduction

The palynological record from El'gygytgyn Lake (Lake E; Fig. 1), whose antiquity rivals that of the Greenland ice sheet, documents striking changes in vegetation and climate from the Middle Pleistocene to the present. The Quaternary

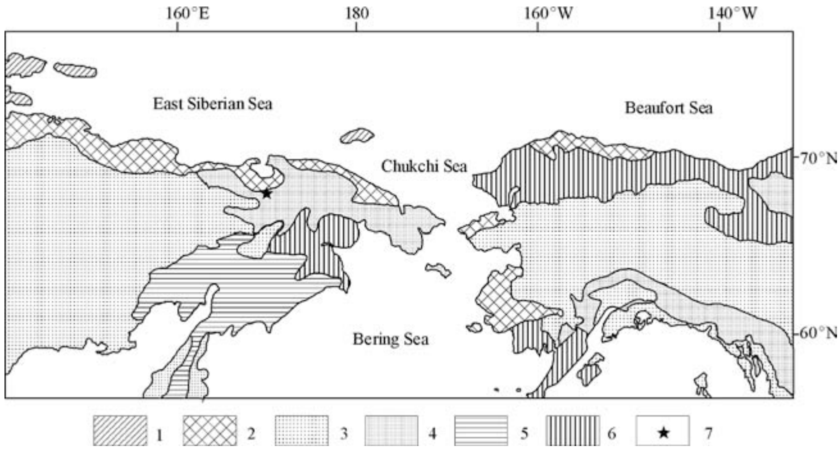

Fig. 1 Generalized map of modern vegetation adapted from Kolosova (1980) and Viereck and Little (1975). Chukotka extends westward from the Bering and Chukchi seas to ~160° E, excluding the Kamchatka Peninsula. The key to the map is: (1) polar desert with discontinuous herb-dominated vegetation; (2) wet arctic tundra dominated by *Eriophorum* species; shrubs generally limited to low growth forms; (3) boreal forest dominated by *Larix dahurica* in Northeast Siberia, by *Picea mariana* and *P. glauca* in northern and central Alaska and northwest Canada, and by *Picea sitchensis, Tsuga heterophylla, T. mertensia*, and *Pinus contorta* in coastal southern Alaska; (4) upland and mesic tundra; (5) high shrub tundra of *P. pumila* and *Duschekia fruticosa* (formerly classified as *Alnaster/A. fruticosa*); (6) moist tundra often with low to mid-sized shrubs (except along streams where shrub growth is taller) and tussock-forming Cyperaceae; and (7) location of El'gygytgyn Lake. Ice-covered areas and alpine tundra within the boreal forest are not illustrated. Note that much of southern Alaska illustrated as tundra, is covered by glaciers

paleoenvironmental history of northern and eastern Chukotka is based largely on cores taken in tectonic depressions bordering the East Siberian and Chukchi seas and on materials extracted from fluvial, glaciofluvial, and floodplain sediments exposed in river valleys (Shilo 1987; Glushkova and Smirnov 2007). Not surprisingly, current interpretations have temporal gaps and become more tentative as the deposits increase in age (Table 1). The Lake E data, which comprise the oldest record of continuous vegetational change in the Arctic, provide a critical cornerstone for clarifying postulated changes in vegetation and climate for this region since the last interglaciation and for documenting a basic environmental history for the poorly understood mid- to late Middle Pleistocene (Lozhkin and Anderson 1995; Anderson and Lozhkin 2002).

Palynological results from Lake E were first reported by Shilo et al. (2001), but continued analyses have provided more detailed documentation, specifically near pollen-zone boundaries, within the last interglacial interval, and for the Late Pleistocene–Holocene transition. As will be evident from discussions in this paper, portions of the Lake E record still warrant additional work. However, the data in hand are sufficient to trace the broad vegetational and associated climatic changes, to explore implications of these paleoenvironmental variations, and to raise questions related to core chronology. Basic descriptions of the lake, core sedimentology, etc. are provided elsewhere in this volume and will not be repeated here (see Brigham-Grette et al. 2007).

Methods

Core PG1351 was raised from the ice surface near the lake's geographic center (water depth 175 m) using gravity (uppermost sediments only) and percussion piston corers. Core sections of 2 to 3-m length overlapped to insure continuity of sediment recovery. These sections were kept in the original core liners to be opened, photographed, described, and subsampled at the Alfred Wegener Institute-Potsdam (see Melles et al. 2007 for further details). One to two cm^3 of sediment were taken from paleomagnetic samples that had been removed previously from the core sections. Pollen preparations followed standard techniques used for organic-poor sediments (PALE 1994). Tablets

Table 1 Stratigraphic schemes and paleoenvironments of Chukotka[a]

Region	Stratigraphic name/OIS equivalent age	Horizon/layer	Paleoenvironment
Northwest Chukotka		*Local name*	
	Holocene interglaciation	Amguemskii	0–4,500 ^{14}C year B.P.: Vegetation was subshrub-herb tundra. Climate was similar to present. 4,500–10,000 ^{14}C year B.P.: Mosaic of subshrub-graminoid tundra and *Betula* forest-tundra. Warm water diatoms present. Climate was warmer than present.
	Late Pleistocene	Local name	
	Sartanskaya stade (OIS 2)	Iskaten'skii	Available ^{14}C dates are between 10,900 and 11,700 B.P. Vegetation was herb-dominated tundra, and herb–shrub tundra; abundant steppe communities. Climate was cooler than present.
	Karginskii interstade (OIS 3)	Longovskii	Available ^{14}C dates are between 28,900 and 33,700 B.P. Vegetation was a mix of shrub and herb-shrub tundra that occasionally included tree *Betula* and *Pinus pumila*. River valleys supported forest-tundra with *Betula, Chosenia*, and *Larix*. Climate was variable throughout this interval, with conditions that were both cooler and warmer than present.
	Zyrianskaya stade (OIS 4)	Kitepskii	Vegetation was predominantly herb tundra, sometimes with steppe elements; occasional boggy areas and thickets of *Alnus fruticosa* and shrub *Betula*. Diatom assemblages include freshwater and brackish taxa that favor cool conditions. Climate was cooler than present.
	Kazantsevskii interglaciation (OIS 5)	El'veneiveemskii	Infinite ^{14}C dates. Vegetation was a mix of *Betula* forest-tundra, open forest with *Larix, Betula, Salix*, and *Pinus pumila*. Diatoms are lake and bog species indicative of moderately warm conditions. Climate was warmer than present.
	Middle Pleistocene	Regional (1) Siberian names (no local names)	
	OIS 6 (?)	Tazovskii	Vegetation was *Betula–Larix* forest. Climate was warmer than present. Note: this stratigraphic association is very questionable given that OIS 6 is a glacial period.
	OIS 7 (?)	Shirtinskii	No vegetation or climate information, although deposits are glacial and glaciofluvial.
	OIS 8 (?)	Samarovskii	Vegetation was tundra with green mosses, *Betula nana*, *Salix*, and subshrubs. Thickets of *Alnus fruticosa* and *Salix* occurred in river valleys. Climate was perhaps similar to present.
	OIS 9 (?) Also includes late Early Pleistocene	Tobol'skii	Vegetation was a mix of open *Betula–Larix* forest with *Pinus* species, shrub *Alnus*-tree *Alnus–Betula* forest with coniferous species, and moss–herb–shrub tundra. Climate was warmer than present.
Eastern Chukotka		*Local name*	
	Late Holocene interglaciation	Unnamed	Available ^{14}C dates are from modern to 4,000 B.P. Vegetation was herb tundra, and climate was similar to present.
	Mid-Holocene interglaciation	Unnamed	Available ^{14}C dates are between 4,000 and 7,000 B.P. Vegetation was shrub tundra. Climate was slightly warmer than present.
	Early Holocene interglaciation	Unnamed	Available ^{14}C dates are between 8,000 and 9,000 B.P. Vegetation was shrub tundra, and climate was slightly warmer than present.

Table 1 continued

Region	Stratigraphic name/OIS equivalent age	Horizon/layer	Paleoenvironment
	Late Pleistocene	Local name	
	Sartanskaya stade (OIS 2)	Iskaten'skii	Vegetation was dominated by herb tundra but shrub tundra occurred in protected areas.
	Karginskii interstade (OIS 3)	Ust'-Lorinskii	Available ^{14}C date of 27,000 B.P. Vegetation was shrub tundra with *Betula*, *Alnus fruticosa*, and *Salix*. *Betula*-forest tundra occasionally occurred. Climate was warmer than present.
	Zyrianskaya stade (OIS 4)	Vankaremskii	Vegetation was herb-dominated tundra or shrub tundra with abundant graminoids and *Artemisia*. Climate was cooler than present.
	Kazantsevskii interglaciation (OIS 5)	Valkatlenskii	Sediments include many marine deposits reflecting rising sea levels associated with the last interglaciation. Vegetation was *Betula* forest-tundra or forest-tundra with *Betula*, *Larix*, and shrub *Alnus*. Climate was much warmer than present.
	Middle Pleistocene	Local name	
	OIS 6	Enmelenskii	No vegetation or climate information available, although deposits are glacial and glaciofluvial.
	OIS 7 (?)	Mechigmenskii	Vegetation was tundra dominated by shoreline communities. Deposits include marine sediments.
	OIS 8 (?)	Olyaionskii	Vegetation was herb–shrub and herb–moss tundra. Climate was similar or cooler than present.
	OIS 9 (?)	Yanrakinotskii	Vegetation was open forest with tree *Betula*, *Alnus*, and *Picea*. Climate was warmer than present.

[a] Information adapted from Shilo (1987)

containing exotic markers were added to the samples so pollen concentrations and accumulation rates (PARs) could be calculated (Davis 1966). Except for levels with low pollen concentrations (84 cm = 184 grain sum; 90 cm = 126; 107 cm = 176; 262.5 cm = 118; 380.7 cm = 248; 1196 cm = 195; 1255.4 cm = 193), pollen sums of identified arboreal and nonarboreal taxa are >300, and often exceed 500 grains. Pollen zonation was done subjectively based on percentage changes of the major taxa. The model used to calculate PARs was based on simple linear interpolation between assigned ages (Table 2). Pollen concentrations are not illustrated, because their trends parallel those of the PARs.

Statistical comparisons of the Lake E palynological data to 310 modern lacustrine samples from Northeast Siberia and Alaska (Anderson and Brubaker 1993; Lozhkin et al. 2001, 2002; Lozhkin 2002; Anderson et al. 2002a, b) assess the likeness of fossil and present-day pollen spectra using a squared chord-distance (SCD) dissimilarity measurement (Overpeck et al. 1985). Because 19 fossil samples were added after the SCD analysis was completed, we present here a subset of the data shown in the pollen percentage and PAR diagrams. Cut-off values for strong (< 0.095), good (0.96–0.185), possible (0.186–0.4) and no (>0.41) analogs follow Anderson et al. (1989). Modern climatic values for each surface-sample site were assigned based on modification of a modern, global climate data set with a 0.5° grid (Climatic Research Unit CRU CL 1.0; New et al. 1999). Lapse rates for every grid point were calculated using a locally weighted trend-surface regression model, which has elevation as a covariate. The lapse rate and elevation of each sample point were used to adjust the values at the adjacent CRU grid points. Bilinear interpolation of the adjusted values provided the assigned climatic parameters for the modern sites.

Table 2 Correlation of oxygen isotope stages and pollen zones, El'gygytgyn Lake

Oxygen isotope stage	Approximate age (year BP)[a]	Depth (cm) and pollen zone
1	0–13,000	0–47 Zone13
		47–75 Zone 12
2	13,000–32,000	75–267 Zone 11
3	32,000–64,000	267–390 Zone 10
4	64,000–75,000	390–448 Zone 9
5	75,000–128,000	448–525 Zone 8
		525–559 Zone 7
		559–593 Zone 6
6	128,000–195,000	593–745 Zone 5
7	195,000–251,000	745–954 Zone 4
		954–1085 Zone 3
		1085–1193 Zone 2
8	251,000–297,000	1193–1283 Zone 1

[a] Based on Shackleton and Opdyke (1973)

In the paleoclimatic reconstructions, we compared single-best and average analog plots and found their trends generally to be similar, although level-to-level changes are more pronounced using the single-best analog approach. Consequently, we present simple averages for mean July and January temperatures and precipitation, because they provide the more conservative estimates of past climatic fluctuations (specific analog data are provided as Electronic Supplemental Material). Samples with only the smallest SCDs were included in the paleoclimatic averages. We note that averaged values for 0 cm underestimate mean January temperature and mean July precipitation and overestimate mean January precipitation as compared to assigned climatic values for Lake E. Consequently, the quantitative paleoclimatic estimates we discuss, possibly with the exception of mean July temperature, must be considered as indicative of general trends and not necessarily as representing actual paleoclimatic values.

Modern vegetation

We provide a brief description of the present-day vegetation of Northeast Siberia, because most fossil analogs are drawn from this region. Due to space constraints, we refer readers to Viereck et al. (1992) and Viereck and Little (1975) for information on Alaskan plant communities (see Fig. 1).

The vegetation of the Lake E basin is dominated by lichen and herbaceous taxa and is often discontinuous, especially on the higher slopes (Kozhevnikov 1993). Shrubs include low-growth forms of *Salix krylovii* and *S. alaxensis*, located in protected microsites ‘‘near the opening of the mountain valleys towards the lake or in valleys that join the ancient Enmyvaam River valley, which flows from the lake'' (*Op. cit*. pg. 64; our English translation). *Betula exilis* is restricted to areas of organic accumulation within alpine valleys, terraces, and saddles both regionally and near the lake. The Chukchi upland, which surrounds the Lake E crater, is a mosaic of low-shrub and herb-dominated tundra, with small populations of *Pinus pumila* and *Duschekia fruticosa* (Anderson and Lozhkin 2002. Note: to reduce confusion, we will follow traditional palynological nomenclature and refer to *D. fruticosa* as *Alnus fruticosa* or shrub *Alnus*). *Salix* and Poaceae species comprise the dominant woody and non-woody taxa, respectively.

Some of the most forbidding landscapes of Northeast Siberia are found on Wrangel Island, located ~600 km to the northeast of Lake E. Vegetation here is discontinuous, herb-dominated tundra and polar desert (Lozhkin et al. 2001; Anderson and Lozhkin 2001). *Salix* is the only shrub species on the island, and while typically found in prostrate form, it can grow to ~1 m height in protected valley settings. The northern coastal plain of Chukotka, located between the Chukchi upland and Wrangel Island, is dominated by graminoid (Cyperaceae and Poaceae) tundra with occasional *B. exilis* and prostrate shrub *Salix*. To the south of Lake E, shrub abundances increase, culminating in the high growth (~2 to 3 m) forms of *P. pumila* and *A. fruticosa* of southernmost Chukotka. The Anadyr lowland, which separates the Chukchi upland from this high-shrub tundra, is characterized by tussock tundra, dominated by Cyperaceae and Ericales. Dense thickets of high-shrub *P. pumila*, *Alnus*, and *Salix* grow along rivers and lake shores. Low to mid-sized shrubs of *Betula, Alnus*, and *P. pumila* also occur in better-drained lowlands and on gentle slopes, the latter two taxa most often as scattered individuals. Light coniferous forest begins ~150 km to the south and west of Lake E, although the main body of the forest is ~300 km distant. *Larix dahurica* is the most widespread tree, but *Populus suaveolens*, tree *Betula*, and/or *Chosenia macrolepis* are common in many river valleys. Shrubs of the Chukotkan tundra are found within the forest understory and in high-shrub tundra beyond altitudinal treeline.

Chronology

Establishing a reliable chronology for lacustrine sediments that are beyond radiocarbon control is difficult. Lake E is no exception, as luminescence dates are few (reduced further by the statistical overlap of dates between 244 and 271 cm) and counting errors are large (Table 3; see also Forman et al. 2007). To improve chronological control, Nowaczyk et al. (2002) and Minyuk et al. (2003) correlated paleomagnetic patterns in the lake core with δ^{18}O records from Greenland and the North Atlantic, obtaining a basal age of ~300,000 years. This chronology was later revised by tuning variations in magnetic susceptibility (MS) at Lake E to Northern Hemisphere insolation, which resulted in a core age of ~250,000 years (Nowaczyk and Melles 2007). Both magnetic-based chronologies use high MS as indicating warm conditions. At least through the upper ~300 cm, these high values also are associated with massive, bioturbated sediments (Asikainen et al. 2007). Conversely, intervals of low MS, typically corresponding to finely laminated sediments, are thought to indicate cool climates. Anoxic conditions, due to a perennial ice-cover on the lake, are postulated as the cause for the formation of the laminae and for the dissolution of magnetic minerals.

The paleomagnetic-based chronologies provide ages for past climatic changes that, with the exception of the boundaries between oxygen isotope stages 1 and 2 (OIS 1–OIS 2) and OIS 5–OIS 6, are inconsistent with the paleoclimatic reconstructions inferred from the palynological data (Fig. 2). For example, an herb-dominated pollen zone that typifies the last glacial maximum (approximate age equivalent of OIS 2; Lozhkin et al. 1993) encompasses both cool and warm events as described in the paleomagnetic and diatom paleoclimatic reconstructions (Minyuk et al. (2003); Nowaczyk and Melles 2007; Cherepanova et al. 2007). The OIS 3–OIS 4, OIS 4–OIS 5, and OIS 6–OIS 7 boundaries as defined in the MS and diatom models also are out of phase with the palynological record.

We do not understand the apparent discrepancy in climatic history for times other than those representing the most dramatic shifts from glacial

Table 3 Radiocarbon and luminescence dates and paleomagnetic events, El'gygytgyn Lake

Absolute age (^{14}C year BP)	Core depth (cm)	Absolute age (IRSL year)	Core depth (cm)	Absolute age (year BP)	Core depth (cm)
Radiocarbon AMS		*Infrared stimulated luminescence*[a]		*Magnetic events*[b]	
6780 ± 55	21–23	11,500 ± 800	66–70	Laschamps ~40,000	180
12,250 ± 70	64–66	17,500 ± 1,300	116–120	Blake ~110,000	500
19,000 ± 110	88–90	48,200 ± 3,900	244–247	Jamaica ~190,000 ~210,000 or Pringle falls ~223,000	920
20,500 ± 130	118–120	61,600 ± 4,300	271–275		
24,600 ± 220	134–136	63,500 ± 4,500	321–327		
26,300 ± 170	142–144	104,200 ± 7,500	459–474		
		159,500 ± 11,800	678–693		
		212,300 ± 16,100	878–895		

[a] From Forman et al. 2007

[b] From Minyuk et al. 2003

to interglacial environments, especially if the proxies are responding to global-scale climatic forcings. Ages of inferred paleoclimatic change in the MS chronologies require warm plant taxa to persist under cool conditions (and vice versa), a conclusion that contradicts the strong vegetation–climate relationships established in modern studies (e.g., Anderson et al. 1991). Two factors that can cause the pollen record to appear in ''disequilibrium'' with climate are delayed plant migration and over representation of palynomorphs that are not indicative of the regional vegetation. The post-glacial vegetation history of Beringia demonstrates that the major taxa represented in the Lake E record responded quickly to climatic amelioration (Anderson and Brubaker 1994). Increasing evidence further suggests that glacial refugia for these plant types were likely found in many areas of Beringia, thereby enhancing the rapid repopulation of the landscape during warm intervals (Brubaker et al. 2005; Lozhkin 2002). Although the vegetation surrounding Lake E is anomalous as compared to plant communities of the Chukchi upland (see Modern vegetation), modern pollen data from Chukotka indicate that the Lake E samples are excellent representatives of the regional pollen rain (see Results). Consequently, we see no clear reason to view the palynological data as unreliable paleoclimatic indicators. If sediment parameters are linked to the annual persistence (cool times) or seasonal absence (warm times) of ice, we find it curious that sedimentation rates in both MS models show no consistent evidence for decreases in deposition that might be expected during times when the lake had a permanent ice cover. Furthermore, we are unsure of any mechanism that allows pollen deposition in a lake where ice is perennially present. Although we can offer no definitive mechanistic explanation, it appears that the lake system and the surrounding vegetation are sensing climatic change in different ways, perhaps with the sediment proxies, such as MS, reflecting more complex responses to climatic shifts as compared to the regional vegetation (see also Asikainen et al. 2007; Nowacyzk and Melles 2007).

The above reservations with the magnetic-based chronologies lead us to offer a third age model, which yields a basal age of ~300,000 years. Because shifts in regional vegetation are widely accepted as reflecting broader scale climatic changes (e.g., Bartlein 1988), we have correlated major shifts in the Lake E pollen zones with ages of the main climatic shifts inferred from North Atlantic oxygen isotope records (Table 2). Our model presumes synchronous climatic fluctuations between the North Atlantic and North

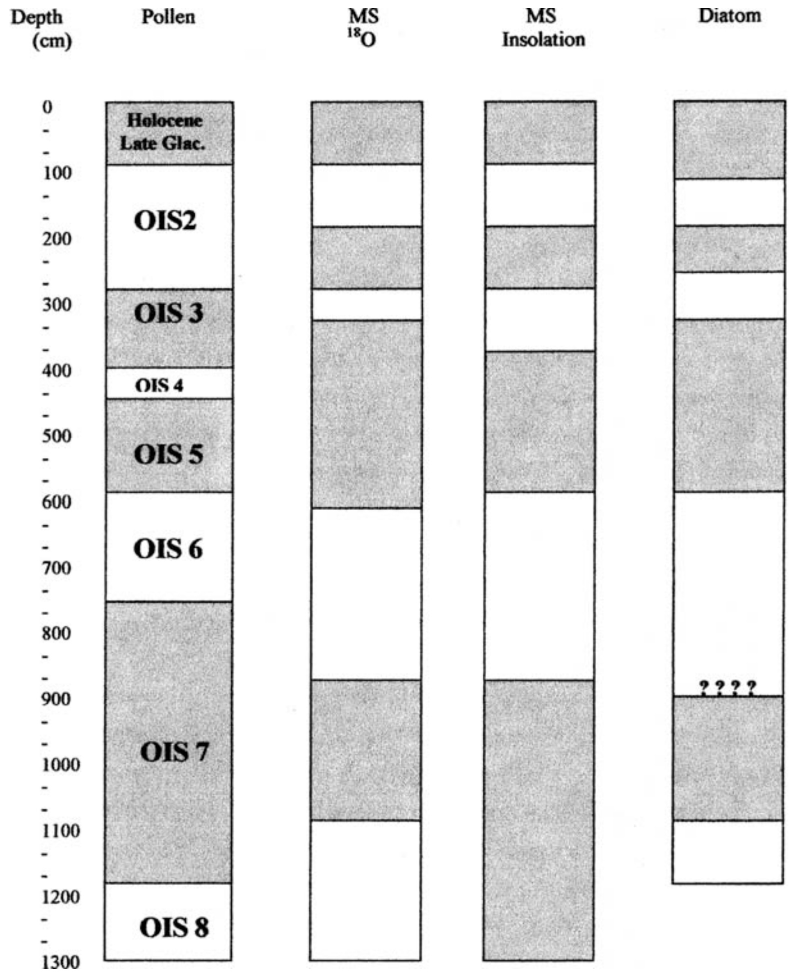

Fig. 2 Comparison of paleoclimatic reconstructions plotted by depth from El'gygytgyn Lake based on palynological, MS-^{18}O (Minyuk et al. 2003), MS-insolation (Nowaczyk and Melles 2007), and diatom (Cherepanova et al. 2007) data. Cool, glacial intervals are indicated by white boxes, with gray shading representing times of relative warmth. Oxygen isotope (OIS) age assignments are shown for the pollen-based scheme. Question marks indicate uncertain boundary placement because of sparse data

Pacific and similar regional responses to the climatic forcings.

Results

The Lake E percentage diagram (Fig. 3) has been divided into 13 zones based on changes in percentages of key palynological taxa. Pollen concentrations (maximum 66,000 grains cm^{-3}; generally <3000 grains cm^{-3}) and PARs (maximum 181 grains cm^{-2} year^{-1}; generally <40 grains cm^{-2} year^{-1}; Fig. 4) are extremely low throughout the entire core. Zone E1 (OIS 8), zone E5 (OIS 6), zone E9 (OIS 4), and zone E11 (OIS 2) are characterized by high pollen percentages of Poaceae, *Artemisia*, and Cyperaceae, low percentages of shrub pollen, a relative abundance of minor herb taxa, generally high percentages of *Selaginella rupestris* spores, and little variability within or between zones. Total pollen concentrations in these herb zones reach a maximum of 3900 grains cm^{-3}, with a maximum PAR of 21 grains cm^{-2} year^{-1}. High pollen percentages of *Betula*, *Alnus*, and *Pinus* and relatively low values for herbs and spores typify zones E6–E8 (OIS 5) and zones E12–13 (OIS 1). Total pollen concentrations (maximum 66,000 grains cm^{-3}) and PARs (maximum 181 grains cm^{-2} year^{-1}) are highest for the core. The remaining zones (E2–E4 [OIS 7], E10 [OIS 3]) have high pollen percentages of Poaceae, variable percentages of other herb and spore taxa, and moderate percentages of shrubs, particularly *Betula*. Total pollen concentrations (3700 maximum grains cm^{-3}) and PARs (maximum 30 grains cm^{-2} year^{-1}) are low.

Of the subset of samples for which SCD were calculated, all fossil spectra except 84, 199,

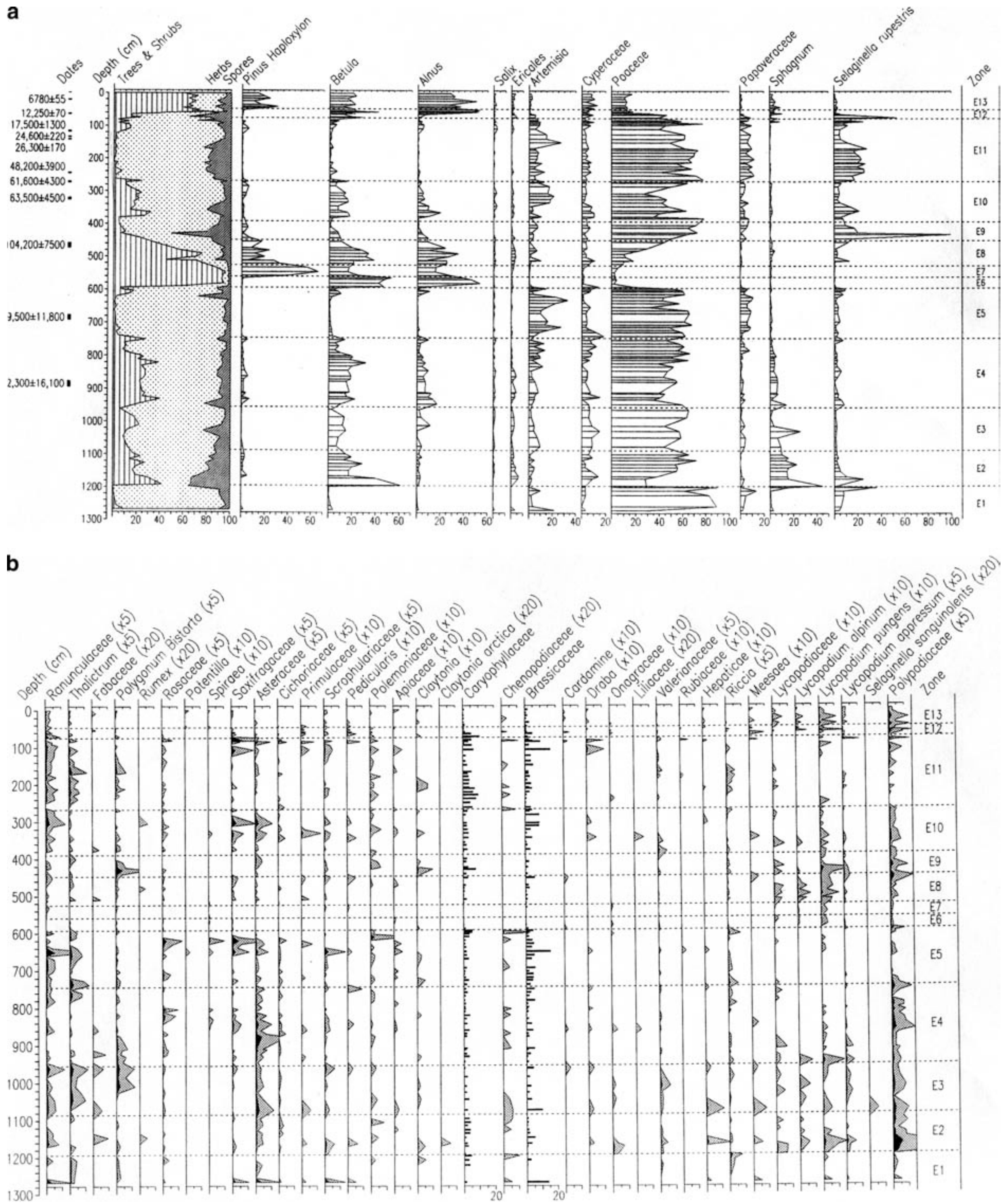

Fig. 3 Pollen percentage diagram from El'gygytgyn Lake: (**a**) major taxa, (**b**) minor taxa. Percentages of individual pollen and spore taxa were based on a sum of all terrestrial trees, shrubs, and herbs. Percentages of the subsums (trees and shrubs, herbs, and spores) were determined from a total of pollen and spores, excepting aquatic taxa. Following Russian protocols, Ericales is considered herbaceous. Because of closely spaced dates, the following are not included in the diagram: 11,500 ± 800 (66–70 cm, luminescence date); 19,000 ± 110 (88–90 cm; ^{14}C date); 20,500 ± 130 (118–120 cm,^{14}C date)

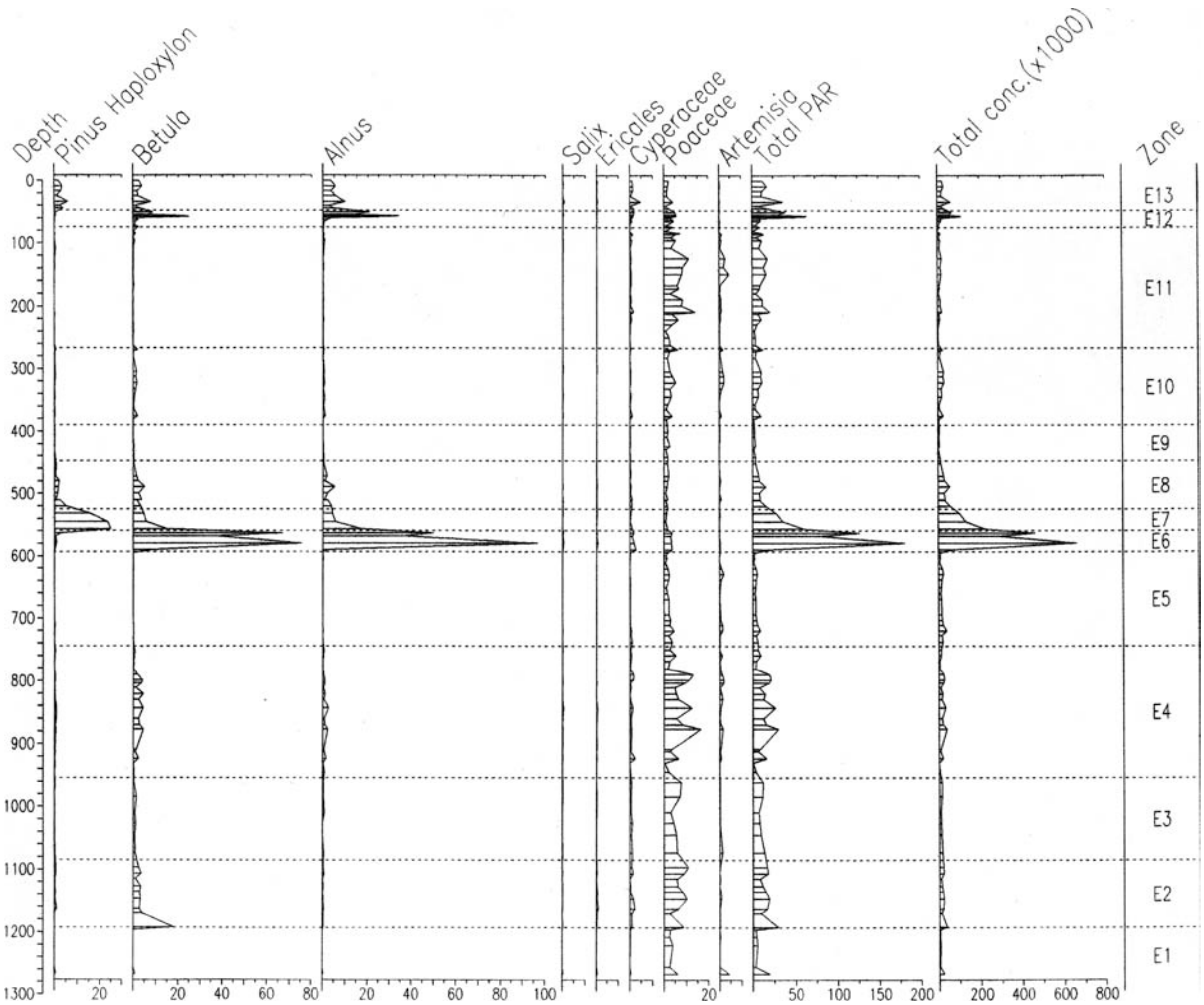

Fig. 4 Pollen accumulation rate (PAR; grains cm^{-2} $year^{-1}$) diagram from El'gygytgyn Lake. The pollen-OIS age model was used to calculate PARs. Pollen concentrations, although not illustrated, show similar trends

211.5, 221.4 and 228.9 cm have analogs (i.e., SCD < 0.4). However, zones E1–E5, upper E8, and E9–E11 are dominated by relatively weak analogs (Fig. 5). Strong analogs characterize zones E7, lower E8, and E13. Good analogs dominate upper zone E4, E6, and upper E12. Paleoclimatic reconstructions for strong to good analogs (i.e., SCD < 0.186) should be trustworthy, whereas weak to possible analogs provide more questionable results.

The large size of the lake (diameter ~12 km) and the barren nature of much of its catchment initially were cause for concern regarding over-representation of exotic taxa in the Lake E record (e.g., conifer pollen from distant boreal forests of Northeast and central Siberia). A study of modern pollen samples from mud–water interfaces of Chukotkan lakes forms a vegetational transect from Wrangel Island (herb-dominated tundra) in the north to the high shrub *P. pumila–A. fruticosa* tundra of southern Chukotka, including three samples from differing depths in Lake E (Lozhkin et al. 2001). The modern samples from Lake E display moderate over-representation of shrub species (*P. pumila* ~10–15%; *Betula* ~10–15%; *Alnus* 20–25%), as compared to the local vegetation. They also contain a significant herbaceous component (35–45%) and no exotic conifer taxa (e.g., *Picea* species, *Pinus* subgen. Diploxylon). When examined

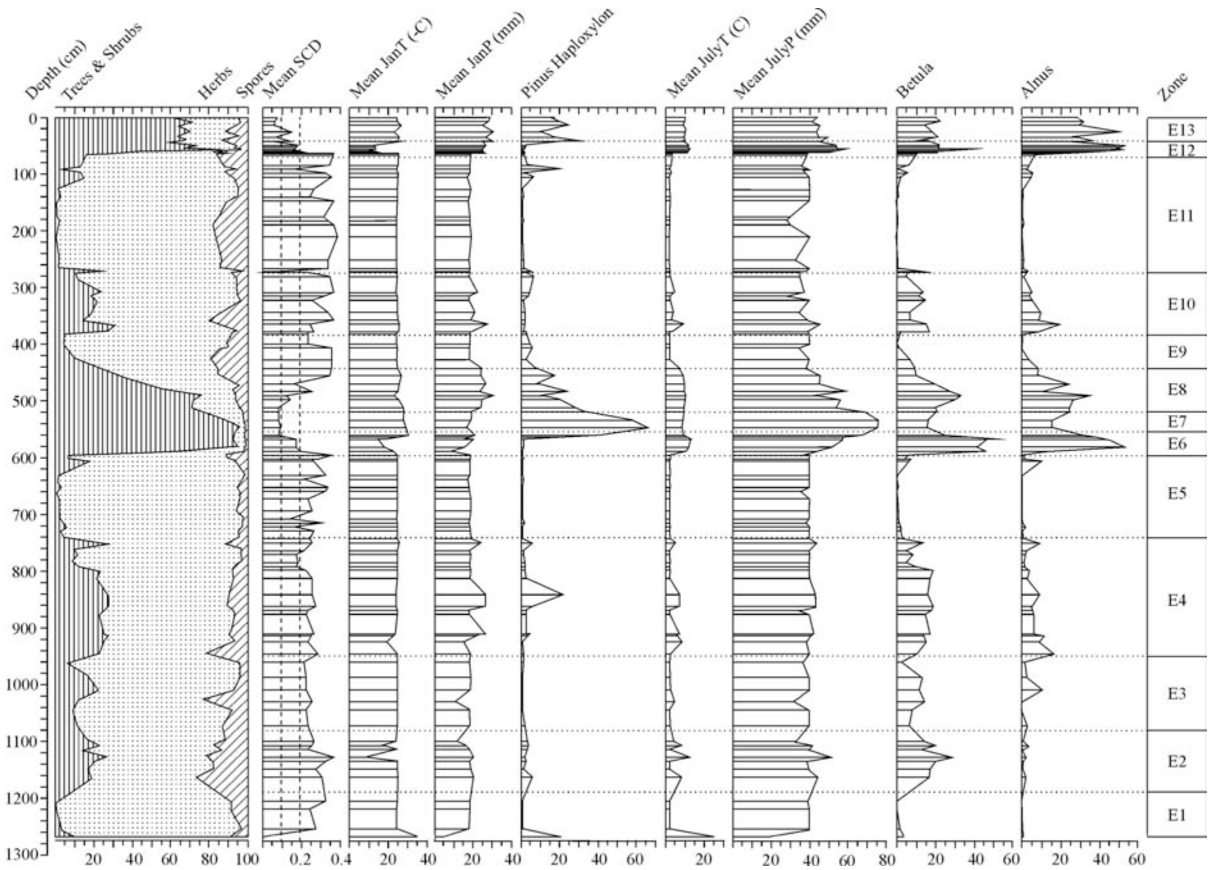

Fig. 5 Diagram of analog-based climate reconstructions and *Pinus*, *Betula*, and *Alnus* pollen percentages from El'gygytgyn Lake. Squared chord-distance dissimilarity (SCD) coefficients were calculated following Overpeck et al. (1985). Paleoclimatic reconstructions are based on the average of best-analog sites. Cut-off values for strong (< 0.095), good (0.960–0.185), possible (0.186–0.400) and no (>0.410) analogs follow Anderson et al. (1989); the various cut-off are shown as vertical lines in the mean SCD graph. The plots of the absolute values of past temperature and precipitation are meant primarily to show trends in past climate, with magnitude of variation being more problematic as SCDs exceed 0.185. Note that the *x*-axis for mean January temperature is in negative °C

in the broader transect of modern sites, the Lake E samples are consistent with spatial trends defined by the Chukotkan data set, indicating that the present-day pollen spectra are more characteristic of the bordering upland than they are of the immediate vegetation surrounding the lake. Unlike many studies, the importance of an extra-local component in the Lake E record is a benefit, because the vegetation in the Lake E catchment is anomalous to the region and determined in large part by the unusual bedrock. In that a major goal of the project is to describe past climates, the regional nature of the pollen record will allow a more realistic evaluation of past changes than would a record that was more faithful to variations in the local plant communities.

Vegetation history

Pollen percentages document a vegetation history for Lake E that is an alternation of three general types of vegetation defined by shrub-dominated, herb-dominated, and mixed herb- and shrub-dominated assemblages. Because of similarities among zones, we present them as groups rather than providing a more repetitive zone by zone reconstruction.

Shrub-dominated assemblages (zones E13, E12, E8, E7, E6)

Zone E13 represents the establishment of the modern regional vegetation associated with the current interglaciation (Figs. 4 and 5). Our age-model places the establishment of *P. pumila*, the last major component of the contemporary regional vegetation, at ~9600^{14}C year BP. Strong modern analogs to the fossil spectra (Fig. 5) are from Lake E itself and sites of the Anadyr basin (Lozhkin et al. 2001), indicating a mixed vegetation of herb-dominated and low- to mid-sized shrub tundra within the basin and surrounding upland. *Betula* was probably the most common shrub, with varying abundances of *Alnus* and *P. pumila* depending on microhabitats.

Zone E12, encompassing the late glaciation and Early Holocene, marks the postglacial establishment of shrub tundra. Increases in pollen percentages of *Betula* suggest a regional presence by ~12,800^{14}C year BP, but PARs indicate this shrub probably was uncommon until ~9900^{14}C year BP. *Alnus* shows a smaller temporal discrepancy, with percentages implying establishment ~10,700^{14}C year BP and PARs indicating abundance by ~9900^{14}C year BP. Modest percentages of *Sphagnum* spores near the zone E12–E11 boundary suggest the early appearance of "peaty landscapes" described in the modern vegetation (Kozhevnikov 1993). Low percentages, concentrations, and PARs of taxa associated with dry and/or disturbed landscapes (e.g., *Selaginella rupestris, Artemisia*) also imply a relatively mesic landscape. The regional stratigraphic scheme (Table 1) indicates that a postglacial thermal maximum (PGTM) began in the Early Holocene, as indicated by the establishment of *Betula* forest-tundra in northern Chukotka. Macrofossil remains of *Salix* and *Alnus* dating to the same period have stems of sufficient diameter to suggest that tall shrubs, many perhaps achieving tree heights, were established in what is now near-coastal tundra of Northeast Siberia (Lozhkin 1993; Edwards et al. 2005). These conclusions when combined with the analog-based climatic reconstructions from Lake E (Fig. 5; see section on Climatic history) strongly suggest that conditions during the Early Holocene were sufficient to support a forest-tundra mosaic or perhaps gallery forests in the river valleys of northern Chukotka.

Zone E8 marks the latter stages of the last interglaciation and probably encompasses OIS 5a, 5b, and 5c. While there is variability in the percentages of major taxa and to a certain extent the PARs in this zone, the sampling intervals are insufficient to definitively associate possible vegetational changes with particular oxygen isotope substages. Plant communities throughout this time were similar to those of the Mid- to Late Holocene. Percentage data indicate the widespread presence of *Betula–Alnus* shrub tundra with scattered populations of *P. pumila*. Analogs, while variable in quality, suggest that upper zone E8 was shrub *Betula* tundra with local importance of *Alnus* and *P. pumila*, whereas the earlier portion of the zone was high-shrub tundra of *P. pumila*, *Alnus*, and *Betula*.

Zone E7 (OIS 5d) contains the highest pollen percentages and PARs of *Pinus* in the Lake E diagram. *P. pumila* likely formed dense high-shrub tundra within the basin and also dominated the regional landscape. Shrubs of *Betula* and *Alnus* were present but formed a secondary component of the vegetation. The relative abundance of *P. pumila* is based largely on both qualitative and statistical comparisons with two modern spectra from southern Chukotka, where the modern vegetation is high-shrub *P. pumila–A. fruticosa* tundra. However, the more prevalent and statistically strong analogs are drawn from boreal regions of the upper Kolyma and the northern Okhotsk coast, implying the presence of *Larix* forest. Although *Larix* pollen is absent in the OIS 5d spectra, the lack of this taxon does not necessarily indicate that the tree was not present. *Larix* produces large pollen grains that tend to be deposited near the tree, and the palynomorphs readily degrade. Given the size of Lake E, it may be physically impossible for *Larix* pollen to be carried to the lake center, where the core was taken, even if small populations were present in the catchment. For the same reasons, *Larix* would remain invisible in the Lake E record if forests established in the surrounding uplands.

Spectra of the last interglacial maximum (zone E6; OIS 5e) are dominated by *Betula* and *Alnus* pollen. Although the pollen taxonomy is inconclusive and plant macrofossils are absent, we postulate that *Betula, Alnus*, and possibly *Salix* occurred in large growth forms (trees or tree-sized shrubs), reminiscent of the Boreal period, the

PGTM for northern Northeast Siberia (Lozhkin 1993). Other studies have suggested that during OIS 5e there was extensive northward displacement of boreal taxa, with open *Betula* forest-tundra and *Larix–P. pumila* forest established in northeastern Chukotka (Table 1: Lozhkin and Anderson 1995). Such vegetation reconstructions require modern range extensions of ~600 km for *L. dahurica* and ~600–1000 km for tree *Betula*. As in zone E7, *Larix* pollen is absent, but analog-based temperature reconstructions (see Climatic history) for warmest intervals in zone E6 indicate sufficient July temperatures to support *Larix*. The relatively high PARs for Poaceae and Cyperaceae suggest that if *Larix* or broad-leaf deciduous forests were present in the catchment, they were likely open, with many areas having a significant graminoid component. Zone analogs are dominated by shrub-tundra sites of western Alaska (particularly southwestern Alaska), reflecting the contemporary dominance of *Betula* and *Alnus* shrubs in association with graminoid tundra in this region. Unfortunately, we lack modern samples from *Betula–Alnus* woodlands to assess the probability that the landscape was forested.

Herb-dominated assemblages (zones E11, E9, E5, E1)

The glacial/stadial vegetation near Lake E was herb-dominated tundra (Figs. 3, 5), similar to that found in other regions of Chukotka (Table 1). *Salix*, likely occurring in prostrate form, was the only significant shrubby taxa. *Betula, Alnus*, and *P. pumila* were not present in the basin, with the pollen representing wind-blown input from distant and likely scattered populations. The low pollen concentrations and PARs suggest a more sparse vegetation cover than present and hence a largely barren landscape. Modern analogs for all zones, with few exceptions, are located on Wrangel Island, further indication of vegetation that varied from graminoid tundra to polar desert. During the Late Pleistocene (zones E11 and E9), high percentages of *S. rupestris* spores, indicative of dry, barren, stony slopes, imply that vegetated surfaces probably were restricted to protected lower elevations. *S. rupestris* percentages are relatively low during the Middle Pleistocene (zones E5, E1), perhaps evidence for greater vegetation cover on lower slopes as compared to the subsequent glaciations. Xeric communities (e.g., *Artemisia* and other Compositae) were likely common during all stadial times. Cyperaceae percentages in zone E11 generally are not as high as those found in many OIS 2 assemblages from Beringia (Brubaker et al. 2005). Possibly this difference reflects the presence of Cyperaceae species (*Carex argunensis*, *C. obtusata*, *C. rupestris*) associated with near-steppe communities, growing today in alpine zones (Berman 1990), rather than of Cyperaceae types associated with more mesic settings.

Mixed herb- and shrub-dominated assemblages (zones E10, E4, E3, E2)

Pollen data assigned to the Late Pleistocene interstade (zone E10) and OIS 7 of the Middle Pleistocene (zones E2–E4) share characteristics with both glacial and interglacial spectra. Percentages of shrub taxa (particularly *Betula*) in these intermediate pollen assemblages are clearly greater than found in the stadial spectra, but shifts in concentrations and PARs are relatively subtle, suggesting that the extent of vegetation change may not be as great as implied by the percentages.

The zone E10 (OIS 3) pollen assemblage indicates that the local vegetation was likely dominated by xeric Poaceae-*Artemisia* tundra, with *Salix* being the primary woody species. Pollen concentrations and PARs for *Betula* and *Alnus* are marginally higher than in stadial zones E11 (OIS 2) and E9 (OIS 4), but neither taxon was likely present in the Lake E drainage. Analogs, while including some more southerly mainland Chukotkan sites, are dominated by those from Wrangel Island, further indication of little difference between the glacial and interstadial vegetation. Data from other OIS 3 age sites suggest that the regional Chukotkan vegetation, while variable, included the establishment of *Betula* forest-tundra during the warmest times of the Karginskii interstade (Table 1; Anderson and Lozhkin 2001).

Little is known about OIS 7 (Table 1), but pollen percentages in zones E2, E3, and E4 share some of the same ‘‘interstadial’’ characteristics as seen in zone E10. However, *Betula* pollen spikes at higher values, *Artemisia* percentages are somewhat lower, and Poaceae percentages are generally greater in the Middle Pleistocene samples. OIS 7 analogs, especially for zone E3, are mixed with sites drawn from Wrangel Island, the Alaskan North Slope, and southwestern Alaska. Although shrubs were likely present in the Lake E basin, the geographic disparity of the analogs suggests that the SCD results should be used with caution.

Among the OIS 7 assemblages, the zone E3 vegetation is most similar to that of zone E10 (OIS 3). Graminoid tundra characterized the landscape, although the setting was perhaps more mesic than during zone E10, as indicated by slightly lower *Artemisia* pollen percentages. *Salix* was the most common shrub, with *Betula* likely restricted to scattered, small populations. Percentages of *Betula* in zones E4 and E2 are generally similar or exceed modern values, although other aspects of the assemblage differ greatly (e.g., high versus low Poaceae, low versus high *Pinus*, respectively). For these zones, *Betula* and *Salix* are the only significant woody taxa, the former most likely occurring within the uplands beyond the Lake E crater. Ericales at times may have been more common than in zone E10. *Pinus* and *Alnus* percentages are sufficiently low to indicate that these shrubs were not an important component of the local landscape, although conditions during zone E4 times may have ameliorated sufficiently to allow pollen production by small and isolated populations in the region.

The relatively high percentages of *Sphagnum* spores in zone E2 suggest an increased presence of mesic habitats. High percentages of *Betula* pollen at the base of this zone in conjunction with more Alaskan analogs as compared to zones E3 and E4 also argue that moderate conditions existed, at least for a portion of zone E2 times. The dominance of *Betula* pollen in lowermost zone E2 is reminiscent of late-glacial spectra from northern Alaska that have been interpreted as productive, high-shrub *Betula* tundra (Anderson and Brubaker 1994). *Betula* and total PARs for zones E4 and E2 match or exceed Late Holocene rates. However, the Holocene samples include a large component of *Alnus* and *Pinus* pollen, which is absent in the OIS 7 assemblages. This pattern suggests that in these zones shrub *Betula* was at least as important regionally as today. Because of the lack of *Alnus* and *Pinus* input, the vegetation may have been relatively dense shrub *Betula* tundra during early zone E2. Although summer insolation was greater than during the latest Holocene (Bartlein et al. 1991), analog-based climatic reconstructions do not support the presence of conditions sufficiently warm to allow an abundance of shrub *Betula*.

Climatic history

Unlike the paleovegetational interpretations, paleoclimatic patterns are best discussed chronologically even though similarities exist between and among pollen zones. As noted previously (see Methods), modern climate parameters assigned to Lake E (mean January temperature (JanT) –28.4°C; mean January precipitation (JanP) 21.5 mm, mean July temperature (JulT) 8.3° C; mean July precipitation (JulP) 47.4 mm) differ from the SCD-averaged analog values, with the averages giving warmer, wetter winters and slight warmer, drier summers. Absolute values are included in the reconstructions to help clarify possible magnitudes of change, but general temperature/precipitation trends are likely more accurate than the absolute values, particularly when SCDs exceed 0.186 (Fig. 5).

Holocene and late glaciation (zones E13–E12)

Modern climatic conditions appear within zone E13, ~6000–7000^{14}C year B.P. JulT (~11 to 12.4°C) and JanT (~ –12 to –18°C) were at their warmest between ~8600 and 10,700^{14}C year B.P., a period that includes the Early Holocene thermal maximum (Lozhkin 1993) and part of the Younger Dryas. In zone E13, JulT cooled slightly, and JanT decreased to values near those of the last glacial maximum (LGM). Both zones E13 and E12 show an increase in general precipitation as compared to the LGM. JulP (~49–60 mm) was at its post-glacial maximum in zone E12, whereas, wettest post-glacial Januarys occurred in zone E13.

Late Pleistocene (zones E11–E9)

The Late Pleistocene is characterized by JulT and seasonal precipitation that were considerably less than modern. JanT (~ –24 to –25°C) show little variation between stadial and interstadial times, and are generally similar to those of the Middle to Late Holocene. During the Late Pleistocene stades (zones E11 and E9), JulT were frigid, reconstructed as ~2 to 3°C. During OIS 3, JulT, while variable (2 to 9°C), mostly fall between 2.5 and 4°C, suggesting conditions that were only slightly warmer than those of OIS 2 and OIS 4. Some of the lowest winter precipitation (~17 to 19 mm) for the entire Lake E record occurred during the Late Pleistocene. Julys were also relatively dry, varying between ~28 to 40 mm, with driest conditions between ~22,600 and 24,300 ^{14}C year B.P.

Last interglaciation sensu lato (zones E8–E6)

Climatic conditions vary considerably during this interval as all climatic parameters achieve maximum values and several others record minima. Zone E8 (OIS 5a–OIS 5c), with cool, wet winters and warm, wet summers, is transitional between the glacial climates of the Late Pleistocene and the more moderate conditions of the last interglacial maximum. JanT (~ –23.4 to –27.4°C) were slightly cooler than at any time during the Late Pleistocene, particularly at the top and bottom of the zone. JulT (~9 to 10°C) were similar to those of the Mid- to Late Holocene, resulting in an interval with relatively great seasonality. JanP was variable (~19 to 25 mm), showing a general, increasing trend from the bottom to the top of the zone. In contrast, JulP (~43 to 69 mm) decreased through time, but was wetter than modern.

The cool winter temperatures of zone E8 are depressed further in zone E7 (OIS 5d; ~ –27.2 to –29.4°C). This cooling is accompanied by decreased JanP (~16 to 21 mm). Zone E7 summers (~9°C) were slightly cooler than during late OIS 5, but JulP (~73 to 75 mm) increased by ~25 mm, representing the wettest conditions in the Lake E record. The establishment and dominance of *P. pumila* in zone E7 implies that winter precipitation would have increased significantly (Andreev 1980). However, the *Pinus* pollen maximum in zone E7 is associated with JanP that was less than modern. In contrast, the high percentages of *Pinus* pollen in the Holocene resulted in reconstructed JanP that were similar to modern. The successful winter survival of *P. pumila*, which is a non-deciduous conifer, depends on the insulating effects of a sufficiently deep snowcover. However, this snow cover must be in place by early to mid-autumn when daily temperatures begin to decrease. Possibly the high precipitation inferred for summer was carried through the fall, so that relatively "dry" Januarys did not have an adverse impact on *P. pumila* growth.

The seasonal precipitation patterns inferred from the Lake E data have important implications for glacial history. During OIS 5d, mountain glaciers expanded in Beringia (Kaufman and Hopkins 1986; Brigham-Grette et al. 2001). While the cooler than present JanT of zone E7 would enhance glacier growth, the relatively warm (i.e., near modern) JulT should increase ablation. Here again the solution may lay with climatic conditions during autumn and spring, when warm summers might be offset by greater snowfall during the transitional seasons.

Some of the warmest temperatures for the entire Lake E record are reconstructed for the last interglacial climatic optimum (zone E6). Inferred JanT (~ –16 to –24.7°C) exceeded and JulT (~10.6 to 12.7°C) approximated values of the PGTM. SCD-inferred OIS 5e temperatures were ~2 to 4°C warmer than those reconstructed at core top. JanP (~7.5 to 20 mm) was generally drier than during other OIS 5 substages, with lowest values approaching those of glaciations. JulP (~36.5 to 57.5 mm) was not as great as during zone E7, but the analog analysis indicates an increase from zone bottom to top, with highest values exceeding modern. Paleoclimatic reconstructions based on proposed range extension of plant taxa suggest JulT may have been 4–8°C warmer than present in areas of Northeast Siberia (Velichko et al. 1991; Lozhkin and Anderson 1995). Furthermore, winter temperatures near the coast are postulated as 12°C cooler than modern. The analog-based reconstructions agree that summer conditions were warm but suggest this warming was only half that proposed by range extensions. In contrast, the two methods disagree on the direction of change for winter temperatures.

Middle Pleistocene (zones E5–E1)

Although the Middle Pleistocene data encompass an interglaciation (zones E4–E2/OIS 7) and two glaciations (zone E5/OIS 6 and zone E1/OIS 8), the analogs indicate that pollen assemblages, and thus vegetation communities, have only weak analogs to the contemporary Beringian landscape. The paleoclimatic reconstructions are equally problematic.

Glacial climates (zones E5, E1) of the Middle Pleistocene had JanT (~–24 to –25°C), JulT (~2 to 3°C), and JanP (~17 to 19 mm) similar to those of the Late Pleistocene stades. Unlike these more recent stades, which had variable JulP (particularly zone E11), Middle Pleistocene cool intervals experienced more consistent JulP.

The Middle Pleistocene interglaciation (zones E4–E2) differed greatly from the Holocene and OIS 5 warm periods. JulT, with the exception of three levels in zone E2 (1106.1, 1126.3, 1163 cm), were all ~1 to 6°C cooler than core top values. Temperature maxima in zone E2 varied between 8.1 and 10.3°C or ~2.4 to 2.1°C cooler than the last interglacial and Holocene thermal maxima, respectfully. Additionally, these warm temperatures occurred as isolated peaks and may likely be overly influenced by small anomalies in the pollen percentages (e.g., 1126 cm has a peak in both *Betula* pollen percentages and JulT). The coolest JulT in zones E4-E2 fall between 2.3 and 2.5°C, values that are similar to those of modern Wrangel Island. Not only were summers cool, but they were also drier (~32 to 44 mm) than present.

In zones E4-E2, JanT were generally between –23.7 and –24.8°C. The only noticeable deviations occurred in zone E2 with JanT of –16.2°C (1126.3 cm) and –18.5°C (1106.1 cm), levels that also showed unusually warm JulT. However, such atypical winter conditions (~10 to 12°C warmer than core top) are questionable, because results are based on a single datum. Reconstructed JanP (~10 to 27 mm) indicates variable conditions characterized the warm portions of the Middle Pleistocene. Wettest values (24.3–26.8 mm) occurred in zone E4, but JanP remained lower than present.

Discussion

While the Lake E palynological record is distinguished by three general types of pollen assemblages (shrub-dominated, herb-dominated, mixed herb- and shrub-dominated), repetitive pollen trends for individual taxa are also evident, suggesting that generally similar patterns of climatic change and/or vegetational succession happened over the last ~300,000 years. Shifts from glaciations to interglaciations are marked always by a rise in *Betula* pollen percentages. Beginning with OIS 6–OIS 5, these cool-to-warm transitions are characterized by an equally pronounced rise in *Alnus* pollen, occurring soon after the initial increase in *Betula* pollen, followed by a peak in *Pinus* pollen. The pollen-stratigraphic sequence for the Middle Pleistocene differs somewhat, in that the *Betula* zone seemingly persists longer, *Alnus* pollen percentages are modest (<20%), and *P. pumila* (<10%) is essentially a minor taxon. To a lesser extent the Middle Pleistocene pattern is mirrored in the OIS 3 interstade, except in the latter interval, the increases in *Betula* and *Alnus* pollen are more nearly synchronous.

The Lake E record encompasses times of extreme changes in global climates and of significant reorganization of vegetational communities worldwide. Nonetheless, possible analogs to the modern vegetation of Beringia exist for all but a few fossil pollen samples at Lake E. This result suggests that contemporary communities and/or taxa persisted in northern Chukotka since the Middle Pleistocene, changing abundances and spatial distributions certainly, but providing arctoboreal landscapes that are not unfamiliar to us today. Even under the warmest of conditions, northern Chukotka remained sufficiently cool and dry to prevent the encroachment of "warmer" boreal conifers, such as *Picea obovata* and *Pinus sylvestris*, presently found in the Lena drainage of eastern Siberia and regions of the Far East.

Edwards et al. (2005) suggested that the PGTM in Alaska and Northeast Siberia was characterized by a widespread deciduous-forest that, while no longer having a significant geographic occurrence in Beringia, was composed of trees found in the region today (e.g., *Populus balsamifera, P. suaveolens, Betula platyphylla, B. papyrifera*). A similar vegetation type was postulated to have occupied the Anadyr drainage during OIS 5e (Table 1; Lozhkin and Anderson 1995) and by extension possibly areas near Lake E. The reconstructed climatic changes for OIS 5e and the PGTM at Lake E suggest that JulT were ~2 to 4°C warmer than core-top during both intervals. These values are consistent with results of Harrison et al. (1995), who simulated OIS 5e climate based on variations in solar insolation. A biome model using the warm-climate simulations indicated Lake E was near the ecotone of cool, deciduous-forest and tundra, lending some indirect support for the presence of *Betula* (or perhaps *Betula–Larix*) forest at or near the lake. If JulT during OIS 5e were indeed at the high end of the reconstructed range, then summer temperatures would have been sufficient (12°C) to support both *Larix* and *P. pumila*.

Of the three interglaciations represented in the Lake E record, the Holocene and warmest portions of OIS 5 have strong analogs, but those of the Middle Pleistocene (OIS 7) are weak statistically. Additionally, no clear thermal maximum is evident in the oldest interglacial period. In OIS 7, pollen spectra have fewer analogs, with the warmest ones scattered across northern Chukotka, southwestern Alaska, and the Alaskan North Slope. The disparities in vegetation type and climatic characteristics among these three regions strongly suggest that the paleo-results border more closely to no-analogs than suggested by the SCDs. Although OIS 7 plant taxa are similar to those found in OIS 5 and the Holocene, paleovegetation interpretations are not as straightforward (e.g., zone E2), with OIS 7 assemblages sharing more characteristics with the Late Pleistocene interstade (zone E10) than with other interglacial spectra. The climatic mechanisms responsible for such a ‘‘cool’’ interglacial signal are unclear. For example, OIS 7 experienced three insolation maxima, one that approximated that of the PGTM, one similar to OIS 5c, and a third that exceeded all insolation peaks of the last ~350,000 years (see Bartlein et al. 1991). The lack of parallel responses in the pollen record indicates the important influence of other boundary conditions in dampening an insolation-driven warming. For example, using 9000 ^{14}C B.P. model runs, residual continental ice has been shown to decrease the temperature effect of summer insolation maxima by ~2°C in the North (Kutzbach and Guetter 1984; Mitchell et al. 1988). This residual ice-effect may have been compounded by relatively cool sea-surface temperatures in the North Pacific. The positive or negative feedbacks associated with other factors, such as extent and duration of sea ice, and their ultimate impact on the vegetation are unknown for this ancient interglaciation. Nonetheless, the Lake E data suggest that there may be fundamental differences in the warm climate-systems of the Middle Pleistocene as compared to the present and previous interglaciations.

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