



Vegetation responses to interglacial warming in the Arctic: examples from Lake El'gygytgyn, Far East Russian Arctic

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Abstract. Preliminary analyses of Lake El'gygytgyn sediment indicate a wide range of ecosystem responses to warmer than present climates. While palynological work describing all interglacial vegetation is ongoing, sufficient data exist to compare recent warm events (the postglacial thermal maximum, PGTM, and marine isotope stage, MIS5) with “super” interglaciations (MIS11, MIS31). Palynological assemblages associated with these climatic optima suggest two types of vegetation responses: one dominated by deciduous taxa (PGTM, MIS5) and the second by evergreen conifers (MIS11, MIS31). MIS11 forests show a similarity to modern *Picea–Larix–Betula–Alnus* forests of Siberia. While dark coniferous forest also characterizes MIS31, the pollen taxa show an affinity to the boreal forest of the lower Amur valley (southern Russian Far East). Despite vegetation differences during these thermal maxima, all glacial–interglacial transitions are alike, being dominated by deciduous woody taxa. Initially *Betula* shrub tundra established and was replaced by tundra with tree-sized shrubs (PGTM), *Betula* woodland (MIS5), or *Betula–Larix* (MIS11, MIS31) forest. The consistent occurrence of deciduous forest and/or high shrub tundra before the incidence of maximum warmth underscores the importance of this biome for modeling efforts. The El'gygytgyn data also suggest a possible elimination or massive reduction of Arctic plant communities under extreme warm-earth scenarios.

1 Introduction

Marine and ice cores contain vital data that document fluctuations in past climate and provide insight into the possible causes of the observed paleoclimatic variability. However, such records cannot provide information on the responses of biotic systems to those changes. Most paleo-biotic records do not have the longevity, continuity, or temporal resolution of ocean and ice cores, which limits the comparison of long-term trends in biological and climatic data. Lake El'gygytgyn (Lake E), whose basin was created following a meteor impact 3.58 ± 0.04 Ma ago (Layer, 2000), presents a rare exception having yielded a continuous sedimentary record dating back ~ 2.8 Ma (Melles et al., 2012). The location of the lake in Arctic Chukotka (Fig. 1) provides a unique look into the response of terrestrial ecosystems at northern high latitudes to a broad range of warm and cold conditions.

Several biological proxies have been examined in cores from Lake E (Brigham-Grette et al., 2007; Melles et al., 2012); we present here interpretations of past vegetation based on palynological data. Previous research has shown that cool, dry intervals are clearly marked in the Lake E record by a dominance of herb pollen (particularly Poaceae) and usually higher values of *Selaginella rupestris* spores (Lozhkin et al., 2007; Matrosova, 2009). These spectra contrast with interglacial assemblages where arboreal pollen is at a maximum, herbaceous taxa are low, and spores are often dominated by *Sphagnum*. Continued research on a newly raised core shows that interglacial assemblages display vegetation and climatic variability both within and between isotope stages. For example, marine isotope stage (MIS) 11.3

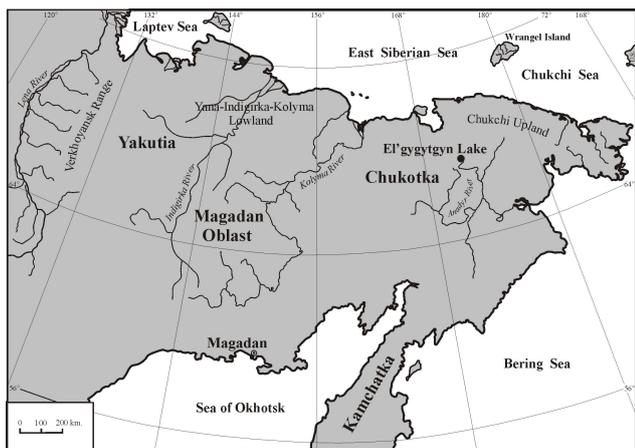


Fig. 1. Map of northeast Siberia showing location of Lake El'gygytyn.

and MIS31 have been described as “super interglaciations” with maximum summer temperatures ~ 4 to 5°C warmer than either MIS5.5 or the postglacial thermal maximum (PGTM; Melles et al., 2012).

These warmer-than-present intervals are of particular interest for understanding possible responses and feedbacks related to increasing global temperatures (e.g., Harrison et al., 1995; Kaplan et al., 2003). Both conceptual and quantitative models have considered two types of vegetation responses at northern high latitudes: one suggests the expansion of evergreen conifer forest northward across North America and much of Eurasia (e.g., Claussen, 1996; Kaplan et al., 2003), whereas the second postulates a dominance of broadleaf deciduous forest in current areas of tundra (e.g., Bonan et al., 1990; Chapin III and Starfield, 1997). Paleobotanical data are one means by which these alternative scenarios may be evaluated. Although analysis continues on Lake E, sufficient palynological data are available to compare the vegetation responses during the “super interglaciations” and the more moderate warming represented in MIS5.5 and the PGTM.

2 Methods

One to two cm^3 sediment samples were processed for palynological analysis following standard procedures used in preparing organic-poor samples (PALE, 1994). Samples for MIS1 and MIS2 and MIS4 to MIS6 are from core PG-1352 (Lozhkin et al., 2007), whereas core ICDP 5011 provided samples from MIS11 and MIS12, and MIS31 (Melles et al., 2012). Pollen sums for interglacial spectra generally exceed 500 identified pollen grains. Percentages of individual taxa are based on a sum of all arboreal, nonarboreal, and unidentified pollen grains. Subsumed percentages on the left of the diagrams (Figs. 2–4) are calculated from a total of pollen and spores. Pollen zonation was done subjectively using changes

in percentages of major taxa. Although many palynologists have differentiated tree and shrub *Betula* based on morphology and/or size, blind tests in our laboratories of modern reference materials suggest that these criteria are inconsistent and unreliable; thus we do not separate the *Betula* pollen. *Picea obovata* pollen is classified within *Picea* sect. *Eupicea*, *Picea ajanensis* within *Picea* sect. *Omorica*, *Pinus sylvestris* within *Pinus* subg. *Diploxylon*, and *Pinus pumila* and *Pinus sibirica* within *Pinus* subg. *Haploxylon*. Following traditional palynological usage, *Duschekia fruticosa* is referred to as shrub *Alnus*. All other plant taxonomy follows Czerepanov (1995).

The age model for the El'gygytyn record is based on paleomagnetic stratigraphy and tuning of additional proxy data to the marine isotope stratigraphy and to variations in regional insolation (see Melles et al., 2012). Because pollen zones do not always correspond to isotope substages, the zones are identified by isotope stage (number) and as a pollen assemblage (letter). Following palynological format the lowest zone is indicated by “a” the next youngest by “b”, etc., in contrast to the order of isotope substages.

Modern analogs to the fossil samples were based on a squared chord-distance measure (Overpeck et al., 1985) using palynological surface samples from Beringia (MIS5e and younger; Lozhkin et al., 2007) or a geographically unrestricted modern dataset (Melles et al., 2012; MIS1, MIS5, MIS11, MIS31). Modern climate values assigned to each surface sample were calculated based on interpolated values from a high-resolution surface-climate dataset (see supplement in Melles et al., 2012, and Lozhkin et al., 2007, for more detail).

3 Modern setting

Lake E ($67^\circ 30' \text{N}$, $172^\circ 5' \text{E}$; $\sim 500 \text{ m a.s.l.}$) has a diameter of 12 km and a maximum depth of 175 m (Melles et al., 2012). The local vegetation is a mix of discontinuous and continuous herb-lichen tundra (Kozhevnikov, 1993). Shrubs (*Salix krylovii*, *S. alaxensis*, *Betula exilis*) are not abundant and limited to protected sites in valleys and saddles within the crater walls and along the outlet valley. The vegetation in the Lake E catchment is sparser than in the surrounding Chukchi Uplands because of unusual soil qualities associated with the meteor impact crater. The uplands are dominated by shrub tundra that includes *Betula exilis*, *Duschekia fruticosa* (shrub *Alnus*), *Pinus pumila*, *Salix*, and *Ericales*. *Larix gmelinii* tree line is located ~ 150 to the southwest of the lake, but the main body of the forest is found at $\sim 300 \text{ km}$ distance. Modern pollen studies indicate that the pollen rain in Lake E is more indicative of regional than local vegetation with up to 60 % of the pollen (*Alnus*, *Betula*, *Pinus pumila*) being blown in from the Chukchi Uplands (Lozhkin et al., 2001). The over-representation of upland vegetation, which reflects regional conditions, strengthens the use of the Lake E pollen

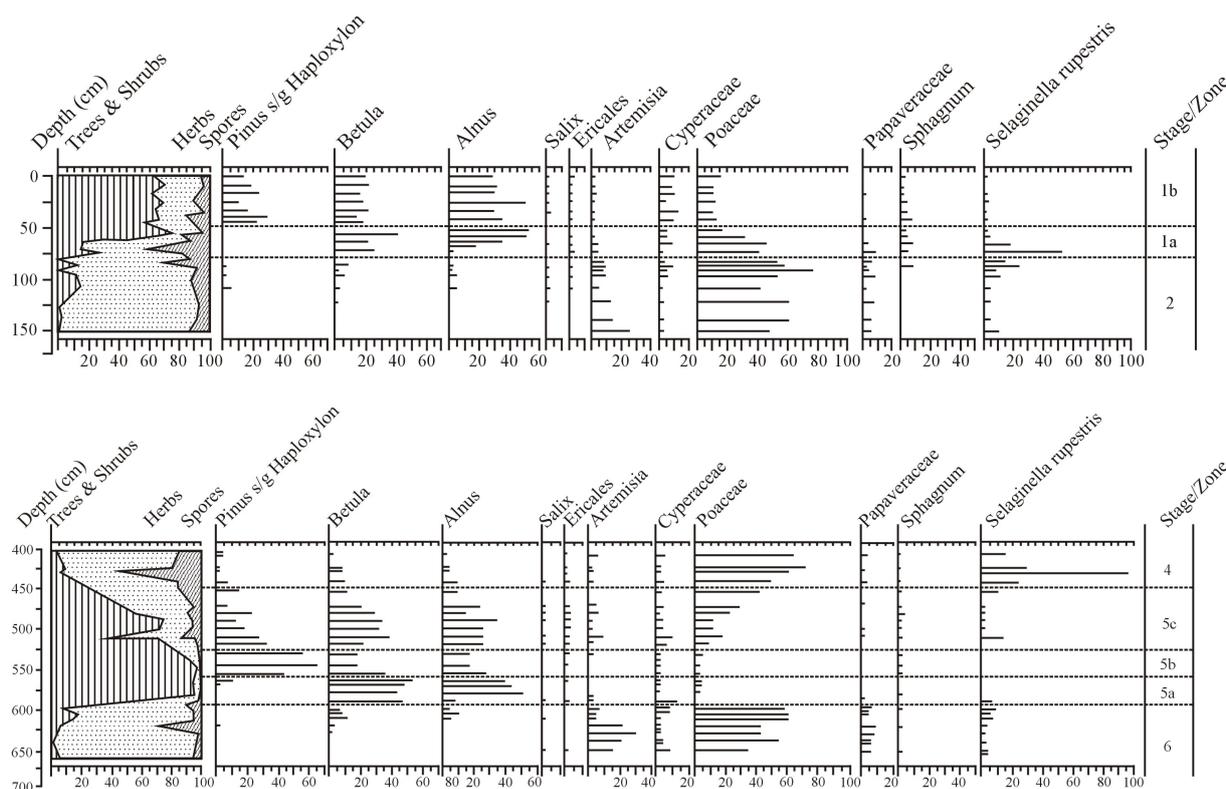


Fig. 2. Percentage diagram of select taxa from MIS1 and MIS2 and MIS4 to MIS6. Results are from core PG-1352. Note that labels for the pollen assemblages include both a number, indicating the isotope stage, and a letter, indicative of the pollen zone. Climatic optima are represented by zones 1a and 5a.

record for paleoclimatic interpretations. Estimated mean climatic values are as follows: annual temperature -13.5 to -14°C ; July temperature 8.8 to 9°C ; January temperature -31 to -32°C ; annual precipitation 255 mm (Melles et al., 2012).

4 Interglacial vegetation of Lake E and the Chukchi Uplands

While interglaciations share similarities in boundary conditions (e.g., high summer insolation, warm sea surface temperatures, minimal terrestrial ice cover), variations in the climatic forcings and strengths of feedback mechanisms add a uniqueness to each warm interval (see Melles et al., 2012). The following sections describe the variability of vegetation responses to climates of the PGTM, MIS5, MIS11, and MIS31.

4.1 PGTM

High percentages of *Betula* and *Alnus* characterize the late glacial and early Holocene pollen assemblages at Lake E (Fig. 2; pollen zone 1a), an assemblage that is common across northern sectors of the Russian Far East (Lozhkin et al., 1993). Statistical comparisons to modern pollen and

related climatic parameters reveal mean July temperatures were perhaps 2 – 4°C warmer than present between ~ 8600 and $10\,700$ ^{14}C yr BP (Lozhkin et al., 2007). Analog analysis also indicates warm January temperatures and increased July precipitation as compared to modern. These conclusions are based on “possible pollen analogs” to southern Beringia shrub tundra (Ibid.). Macrofossil evidence from the Yana–Indigirka–Kolyma lowlands (Fig. 1) and northern Chukotka documents the occurrence of tree or tree-sized shrubs of *Salix* and *Alnus* beyond present-day tree line (Lozhkin, 1993). Using both pollen and plant macrofossils to enhance understanding of plant functional types, Edwards et al. (2005) concluded that an unusual biome of deciduous forest and forest-tundra characterized Beringia during the PGTM. In the Chukchi Uplands, vegetation was probably a mosaic of forest and tundra communities including gallery forests of tree *Betula* and perhaps *Salix*, and possibly stands of deciduous trees in protected sites within the interfluvies. Other areas likely supported high shrub tundra.

4.2 MIS5

Because MIS5 vegetation has been described elsewhere (Lozhkin et al., 2007), we focus here on MIS5.5. Like the PGTM, the MIS5 climatic optimum (Fig. 2; pollen zone 5a)

is characterized by high percentages of *Betula* and *Alnus* pollen. The dominance of these woody taxa suggests that the regional vegetation during MIS5.5 was also a mix of deciduous forest and high shrub tundra. The reduced herb percentages as compared to the PGTm indicate a more extensive and/or denser population of *Betula*, *Alnus*, and possibly *Salix* in the regional vegetation. The spectra may also indicate a greater establishment of trees/high shrubs within the Lake E catchment as compared to the PGTm.

Plant macrofossils of last interglacial age have been found throughout northern sectors of the Far East (Lozhkin and Anderson, 1995). Although chronological control is insufficient to assign sites specifically to MIS5.5, current understanding of the valley stratigraphies suggests they are from MIS5. The reconstructions vary from open *Betula* forest (Anadyr basin; Fig. 1), to *Larix* forest with tree *Betula*, tree *Alnus*, and *Pinus pumila* (northern Chukotka, upper Kolyma and Indigirka basins, Yana–Indigirka–Kolyma lowlands) to *Larix* forest with *Picea* (upper Kolyma and Indigirka basins, northern lowlands, northern Okhotsk sea coast). Although *Picea* may have extended almost to the coast of the East Siberian Sea, the Lake E record raises the possibility that these sites may actually be from MIS11 (see below). Nonetheless, the preponderance of woody remains and nature of the MIS5.5 pollen spectra at Lake E strongly indicate the extensive presence of forest in northern areas of the Russian Far East and likely establishment of deciduous forest in the Chukchi Uplands. Analog-based analyses of the pollen data indicate the prevalence of warmer and wetter conditions as compared to modern (Lozhkin et al., 2007; Melles et al., 2012).

4.3 MIS11

Three vegetation types characterize MIS11 (Fig. 3), and all types indicate greater summer warmth and annual precipitation as compared to modern (Melles et al., 2012). However, the history of MIS11 diverges dramatically from the vegetation succession seen in MIS5 and MIS1 (i.e., *Betula*–*Alnus*–*Pinus pumila*).

The earliest climatic amelioration in MIS11 is indicated by high percentages of *Betula* and decreasing percentages of Poaceae pollen (pollen zone 11a). In contrast to the MIS6/MIS5 and MIS2/MIS1 transitions, *Betula*-dominated vegetation appears to persist for a longer time in MIS11 prior to the arrival of *Alnus*. Lower zone 11a, representing the earliest effects of warming, was likely characterized by *Betula* shrub tundra with *Salix* and Ericales. Possibly shrubs achieved large growth forms as occurred in the PGTm. *Betula* pollen increases to 45–60% in the mid-to-upper levels of zone 11a, percentages that generally exceed modern values from shrub tundra environments in the northern Far East (Anderson et al., 2002; Lozhkin et al., 2002). These values more closely approximate modern surface samples from Kamchatka (Lozhkin and Anderson, unpublished data)

where forests of *Betula ermanii* are common. In Alaska, highest *Betula* percentages (> 40%) also occur in interior forests, where *Betula papyrifera* is found in valleys and lower mountain slopes (Anderson and Brubaker, 1993). Inasmuch as we can draw from modern analogs, these data suggest that *Betula* shrub tundra probably was replaced by *Betula* woodland. The presence of *Larix* pollen, even in only a single sample, further suggests the establishment of deciduous woodland. The decreasing percentages of graminoids and Ericales and increases in *Betula* pollen likely indicate a greater presence of wooded landscapes by upper zone 11a.

Zone 11b, representing the climatic optimum and corresponding to MIS11.3, includes some variation within the pollen assemblage. The pollen spectra between 1855–1905 cm (1) are dominated by *Picea* sect. Eupicea, *Alnus*, and *Betula*; (2) show a consistent appearance of *Larix*; and (3) have decreased percentages of herb taxa, particularly Poaceae. *Pinus* subg. Haploxylon pollen appears initially in low amounts but increases in later spectra (1827–1855 cm). This pollen type may represent either *Pinus pumila* or *Pinus sibirica* (see below). The increase in *Pinus* pollen is associated with a slight decline in *Betula* and *Alnus* pollen.

The abrupt increase in *Picea* pollen at the zone 11a–11b boundary suggests a rapid replacement of deciduous woodland by *Picea obovata*–*Larix*–*Betula*–*Alnus* forest. The expansion of *Picea obovata* to Lake E represents a range extension northeastward of ~2000 km (Kolossova, 1980). *Chosenia macrolepis* possibly was present in this forest (see below), but its pollen can not be differentiated from shrub *Salix*. Herb pollen is virtually absent, which is characteristic of modern spectra from closed dark coniferous forest. Although other coniferous taxa (e.g., *Picea* sect. Omorica, *Pinus* subg. Diploxylon) and *Corylus* appear, these grains likely represent long-distance transport, and the pollen is not indicative of a local presence. Shrub communities of *Betula*, *Alnus*, and *Salix* grew along streams and on moist sites near the lake shore. Shrub tundra perhaps occupied higher elevations, but the regional vegetation was dominated by dark coniferous forest.

The inferred vegetation for early MIS11.3 (1855–1905 cm) is reminiscent of that found today in the middle reaches of the Yama and Maimandzha rivers, which are located ~150 km to the east of Magadan (Fig. 1) and thought to be a relict forest from a previous warm interval (Rheutt, 1970). Its plant communities contrast to the regional vegetation of light coniferous forest dominated by *Larix gmelinii* and *Pinus pumila*. In the Yama–Maimandzha lowlands, the forest is a mix of *Picea obovata*, *Larix*, tree *Alnus* (*Alnus hirsuta*), and tree *Betula* (*B. platyphylla*, *B. lanata*). *Populus suaveolens* and *Chosenia macrolepis* are limited to floodplains. *Picea* grows to 20+ m heights, and *Larix* and *Alnus hirsuta* have diameters of 30–50 cm (Lozhkin, personal observation). The percentages of *Pinus* pollen occurring between 1855 and 1905 cm are sufficiently low to suggest *Pinus* shrubs or trees were likely absent or at best minor

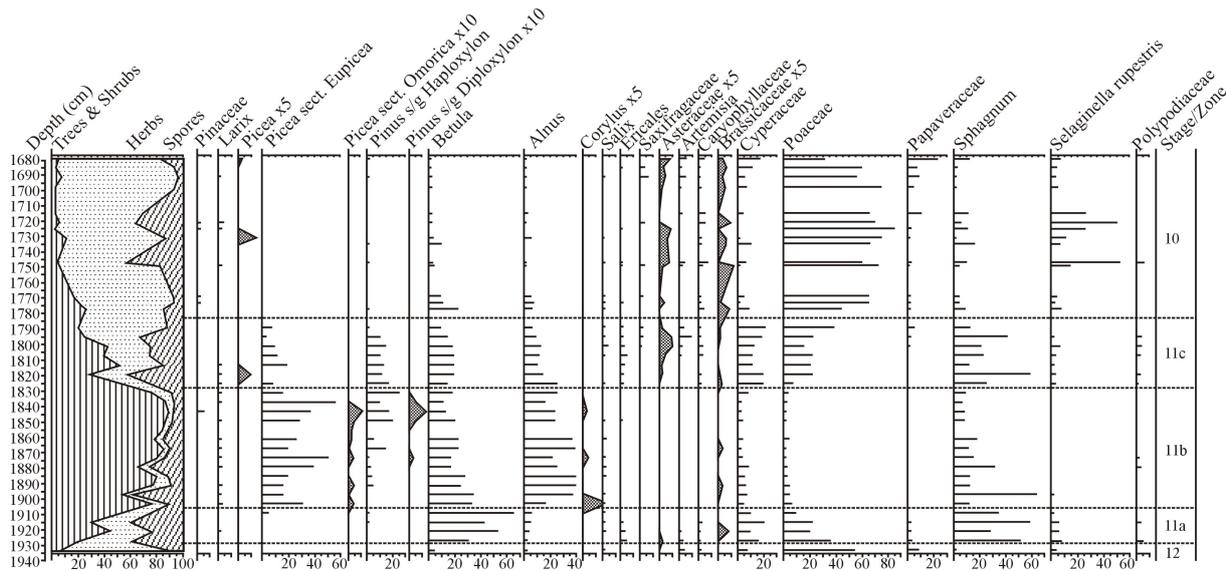


Fig. 3. Percentage diagram of select taxa from MIS10 to MIS12. The climatic optimum is represented by zone 11b. Results are from core ICDP 5011.

components of the ancient vegetation. This pattern is consistent with the modern Yama–Maimandzha *Picea* forest, where *Pinus sibirica* is absent and *Pinus pumila* is restricted to other areas of the drainage.

Dark coniferous forest continues to dominate the landscape during later MIS11.3 (1827–1855 cm). Pollen percentages indicate that *Picea obovata*, *Alnus hirsuta*, and *Betula* remain important elements in the forest communities, although the abundance of the latter two species perhaps decreased from earlier in the zone. The most significant shift in the pollen assemblage of late MIS11.3 is the rise in *Pinus* subg. Haploxyton pollen. As mentioned above, this pollen type represents both *Pinus pumila* and *Pinus sibirica*. Modern range distributions of *Picea obovata* and *Pinus pumila* do not overlap in the northern Far East (*Pinus pumila* only) or to the west of the Lena drainage (*Picea obovata* only; Kolosova, 1980). However, the two conifers do co-occur in the middle and upper reaches of the Lena catchment, extending southward to the Amur drainage. Here mean July temperatures are usually $\leq 12^\circ\text{C}$ (Mock, 2002). In contrast, *Pinus sibirica* is found from southeastern Siberia to northern sectors of the Western Siberian Plain, a distribution it shares with *Picea obovata*. In some of this region, mean July temperatures can be as high as 20°C . The three species ranges overlap in the area of Lake Baikal, where their distribution reflects altitudinal gradients. *Larix–Picea–Pinus* forest is found along large flat areas between ~ 1100 – 1900 m, and *Pinus pumila* is part of a subalpine tundra zone beyond 1900 m (Suslov, 1961).

These modern distributions suggest three alternative paleovegetation interpretations. If the pollen is exclusively from *Pinus pumila*, its increase suggests that the *Picea* forest became sufficiently open to allow for the establishment of

Pinus shrubs in the understory and/or the shrubs formed a mid-elevation shrub zone beyond altitudinal tree line. As compared to early MIS11, this vegetation change would perhaps suggest a slight summer cooling (to open the forest or lower tree line) and/or increased depth/duration of snow fall (required to protect *Pinus pumila* from winter desiccation; Khokhyrakov, 1985). However, the persistence of low percentages of herb pollen does not suggest a significant opening of the forests or decrease in *Picea* cover on mountain slopes. If the pollen represents *Pinus sibirica*, then the Lake E record marks a range extension of ~ 2500 km (Kolosova, 1980) and an extensive forest cover across northern Chukotka. The addition of *Pinus sibirica* would not require changes in summer conditions as it shares similar requirements with *Picea obovata*, raising questions as to why *Pinus sibirica* was absent in early MIS11.3. If both *Pinus* species are present, then the regional and/or local vegetation probably had a strong altitudinal component with increased snow fall to aid establishment of *Pinus pumila*.

Quantitative paleoclimatic reconstructions indicate little systematic change in summer temperatures (ranging from ~ 12 – 16°C) between early and late MIS11.3 (Melles et al., 2012). The absence of *Pinus sibirica* during early MIS11.3 probably was not caused by insufficient summer temperatures, especially given the establishment of *Picea obovata* at the time. Possibly delayed migration from an unknown but distant population may account for the tree's absence. Mean annual precipitation is estimated to be at its highest during late MIS11.3 (> 600 mm yr^{-1} vs. ~ 350 mm yr^{-1} during early MIS11.3). If this trend reflects greater seasonal and/or annual snow fall, then this shift in climate would provide a reasonable mechanism for the expansion of *Pinus*

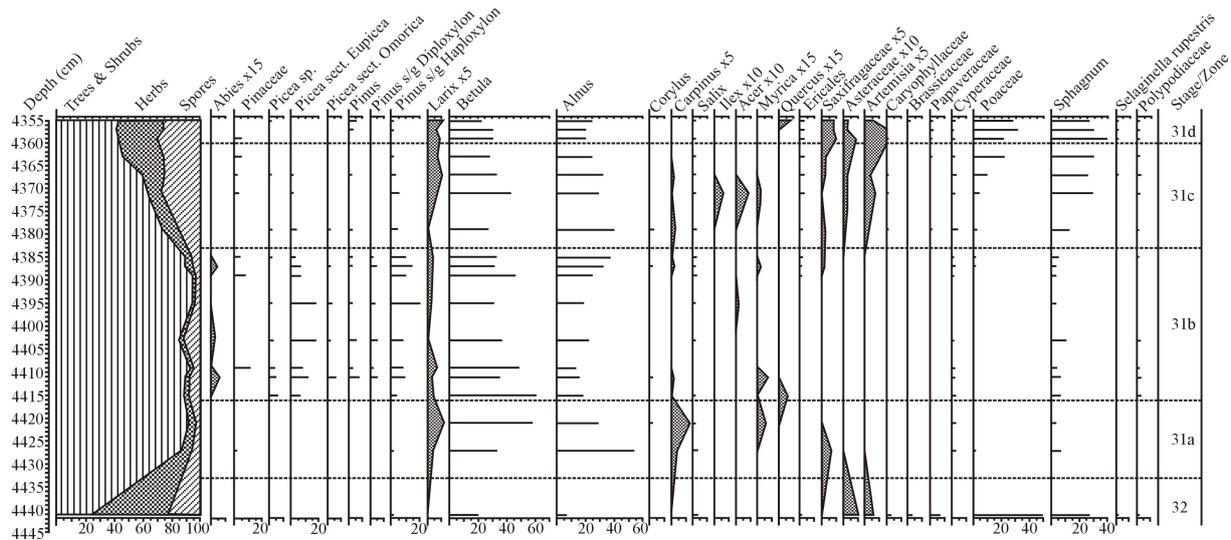


Fig. 4. Percentage diagram of select taxa from MIS31. The climatic optimum is represented by zone 31b. Results are from core ICDP 5011.

pumila. This conclusion, if correct, would indicate that early MIS11.3 experienced drier cool seasons or seasonal transitions as compared to late MIS11.3. This interpretation would also suggest that *Pinus pumila* was the main *Pinus* species present during late MIS11.3.

Pollen zone 11c represents the final stages of MIS11 and is marked by the decrease in *Picea* pollen, a more gradual decline in *Alnus* pollen, and increases in herb pollen (primarily from Cyperaceae and Poaceae). Areas of graminoid meadows or tundra were more common than previously suggested by the higher percentages of herb pollen, slightly greater amounts of Ericales and *Salix* pollen, and to a lesser extent the occurrence of higher *Sphagnum* values. Trees were limited on both local and regional landscapes. The loss of *Larix* pollen late in the zone suggests that tundra dominated in the latter part of MIS11.

The forest-tundra of zone 11c perhaps was similar to areas found today in eastern Siberia (e.g., lower Lena River valley), where *Picea* and *Larix* form latitudinal tree line with isolated stands of *Larix* scattered northward across the tundra. *Pinus pumila* may have persisted from zone 11b, having a similar role as seen in the contemporary vegetation. However, paleoclimatic reconstructions show a sharp decline in mean annual precipitation (Melles et al., 2012), a potentially adverse factor in the survival of *Pinus pumila*. Decreased summer temperatures as indicated by the quantitative climate estimates would have been sufficiently severe to eliminate *Pinus sibirica*, if it was present on the zone 11b landscapes.

4.4 MIS 31

Of all warm periods discussed in this paper, MIS31 presents the most unusual pollen spectra (Fig. 4). While dominated by typical boreal taxa (*Picea*, *Larix*, *Abies*, *Betula*, *Alnus*), the MIS31 assemblages also contain small numbers of more

temperate deciduous taxa (e.g., *Corylus*, *Carpinus*, *Acer*, *Quercus*). Not surprisingly given the 1.1 Ma age, these assemblages seem to lack exact analogs in the modern landscapes. Although the pollen diagram is somewhat skeletal, the data are sufficient to determine general characteristics of the MIS31 vegetation.

The MIS32/MIS31 transition (pollen zone 31a) is similar to that of MIS6/MIS5 (pollen zone 5a) with spectra dominated by *Betula* and *Alnus* pollen and with very low numbers of herb types. However, differences do exist between the two transitions, including the minor presence of *Larix* pollen and occasional occurrence of the warm taxa *Corylus*, *Carpinus*, and *Myrica* in zone 31a. As during pollen zone 5a, the regional vegetation during early MIS31 probably was dominated by deciduous trees possibly with tree-sized shrubs including *Betula*, *Alnus*, and *Salix*. Unlike MIS5, *Larix* was established in the Lake E watershed and likely across the upland. The low percentages of herb pollen suggest that a relatively dense deciduous forest rather than open woodland was established at this time. Although pollen from other deciduous trees is the result of long-distance wind transport, occurrence of these taxa suggests that temperate forests were in closer proximity to north-central Chukotka as compared with today.

The zone 31b assemblage represents the thermal maximum within MIS31 and is characterized by several *Picea* and *Pinus* species, *Larix*, *Abies*, *Betula*, *Alnus*, and <5% herb pollen. Several partial analogs to this assemblage can be found in Asiatic Russia. The northernmost is the dark coniferous forest of the lower Yenisei valley (northern sector of the Western Siberia Plain), where today *Picea obovata*, *Pinus sibirica*, and *Pinus sylvestris* are found. A southern variant of this forest occurs in the upper Yenisei drainage between ~ 51 to 54° N, an area that is transitional between

the Siberian dark coniferous taiga and Mongolian steppes. In this region, taiga dominates in the mountains and forests between ~1000 and 2000 m and includes *Larix sibirica*, *Picea obovata*, *Abies sibirica*, *Pinus sibirica*, and occasional *Pinus sylvestris*. A third possible analog is from the western shores of the Sea of Okhotsk (from ~51° N southward to the lower Amur valley), where the taiga is a mix of *Picea glehnii*, *Abies nephrolepis*, *Larix gmelinii*, and *Betula ermanii*. *Pinus pumila* is limited to protected sites where it can grow in dense thickets achieving over 2 m height (Suslov, 1961). The more temperate taxa *Corylus mandshurica*, *Quercus mongolica*, *Carpinus cordata*, and *Acer mandshuricum* are present in the Sikhote-Alin Mountains, which border the Amur drainage. Possibly the zone MIS31b vegetation represented a mix of plant communities from the Siberian dark coniferous forest and the Okhotsk taiga, as no modern vegetation type totally corresponds to taxa represented in the pollen assemblage.

The combined percentages of *Betula* and *Alnus* pollen, as in zone 31a, dominate the MIS31b spectra and demonstrate that deciduous forest remained an important landscape component. The presence of *Corylus* in two samples in minor but significant amounts (2–3 %) suggests that the plant was probably present within the region. Today the nearest *Corylus* population (*Corylus mandshurica*) is found in the lower reaches of the Amur drainage, and its establishment near Lake E would represent a ~2400 km range extension (Kolosova, 1980). Inasmuch as we can draw on the Okhotsk taiga as analog, it is likely that during zone 31b the vegetation in the Lake E crater and neighboring uplands was characterized by a marked altitudinal zonation. *Betula*–*Larix*–*Alnus* forest likely dominated river valleys and lower slopes. Possibly the *Salix* pollen represents *Chosenia macrolepis*, a common floodplain tree in modern landscapes. Transitioning to mountain slopes, deciduous forest was replaced by conifer communities of *Picea*, *Pinus*, and *Abies*. *Betula ermanii* is common today in *Picea*–*Abies* forest, sometimes forming pure stands. This *Betula* species occupies rockier and steeper slopes. *Corylus* was likely an understory shrub that grew on warmer, south-facing slopes. Other temperate taxa (e.g., *Acer*, *Carpinus*), if present, would be restricted to the warmest sites. *Pinus sylvestris*, if the *Pinus* subg. Diploxylon pollen is not the result of long-distance transport, was not abundant. As in the case of MIS11, the *Pinus* subg. Haploxylon pollen may be interpreted in two ways. If from *Pinus pumila*, the species likely grew in protected, open areas within the forest and possibly formed high shrub tundra beyond altitudinal tree line. As in zone 11b, low percentages of herb taxa suggest closed forests that extended far up mountain slopes, making the occurrence of a *Pinus pumila* belt less likely. If the pollen represents *Pinus sibirica*, then the taxon would be a member of the coniferous forest.

Within pollen zones 31c and 31d, the pollen spectra indicate steady vegetation changes implying gradual climatic cooling and increasing aridity. Pollen from evergreen conifers decreases, whereas *Betula* and *Alnus* continue as

dominant taxa with a consistent appearance of *Larix* pollen. Deciduous forest probably became the most extensive vegetation type both locally and regionally. The increase in Ericales, Poaceae, and total herb pollen and *Sphagnum* spores indicates an opening of the forest and establishment of tundra communities by late zone 31c and zone 31d.

5 Discussion and conclusions

The palynological data presented here and in previous papers (Lozhkin et al., 2007; Matrosova, 2009) are in many senses a preview of the exciting paleoenvironmental information contained within the Lake E archive. For example, a focus on only a small part of the vegetation history has revealed interglaciations with an unexpected magnitude of warming (Melles et al., 2012). The pollen data described herein further indicate that there are at least two types of vegetation responses to interglacial conditions. The vegetation in the first type of thermal optimum is dominated by deciduous tree and shrub species and corresponds to the two most recent warming events (PGTM, MIS5.5): the second type, or “super” interglaciation (MIS11.3, MIS31), indicates climax vegetation dominated by evergreen conifers, particularly *Picea*. These exceptional climatic events experienced warmer summers (+4.5 °C) and greater annual precipitation (~300 mm) as compared to the PGTM and MIS5.5 (Melles et al., 2012), which themselves are characterized by summers that are warmer and wetter than present (increases of ~2 °C and up to 20 mm for mean July temperature and precipitation, respectively; Lozhkin et al., 2007).

Despite the classification into types, the interglaciations share some commonalities. One characteristic of interglacial intervals at Lake E is that they show greater heterogeneity in vegetation types as compared to glaciations. These latter periods display a general uniformity in their pollen assemblages both through time as in the Lake E record (Lozhkin et al., 2007) and also in space, at least in the cases of the latest glaciation when the most paleobotanical data are available (Brigham-Grette et al., 2004). This observation implies that once a “threshold” of coolness and/or dryness was surpassed, the vegetation response during glaciations is limited to herb-dominated tundra or steppe tundra. Of course, the establishment of climatic “thresholds” affected interglacial as well as glacial vegetation. Although a level of summer warmth is required for the expansion of boreal tree species, modeling by Kaplan et al. (2003) illustrated the importance of relatively mild winters for the spread of *Picea*. The Lake E data suggest that once temperature “thresholds” have been achieved, the importance of seasonal precipitation (particularly the duration and volume of snow cover) and/or effective moisture may have been the greatest determinant of interglacial forest composition and distribution.

Another shared trait of the interglaciations is the rapid establishment of plant communities dominated by woody

taxa during the glacial to interglacial transition. The earliest interglacial vegetation was *Betula* shrub tundra (note that this is not evident in early MIS31, but we expect additional pollen counts will show a parallel trend to the other interglaciations) that quickly was replaced by deciduous forest or woodland. For the PGTM and MIS5, the establishment of *Betula* woodland/high shrub tundra and *Betula*–*Larix* forest/high shrub tundra during the PGTM and MIS5, respectively, represents maximum summer warming. However, during the older warm periods, *Betula*–*Larix* (MIS11) or *Betula*–*Alnus*–*Larix* (MIS31) forests were transitional as interglacial climates continued to become warmer and wetter. Edwards et al. (2005) noted that the widespread establishment of deciduous forest in Beringia during the PGTM represented a novel biome that differed structurally and functionally from evergreen coniferous forest and tundra that dominate arctic boreal settings today. They also commented that deciduous boreal forest should be included in modeling efforts that explore likely biosphere–atmosphere feedbacks and possible impacts caused by global warming. The new Lake E data underscore the importance of this proposition, as deciduous forest seems to play an essential role in interglacial vegetation history, whether it was as transitional or as climax vegetation.

The different interglacial vs. “super” interglacial modes suggest the need to explore the potential impact of a range of forcing mechanisms and feedbacks involved in “warm” and “warmer” scenarios. Melles et al. (2012), for example, suggested that the melting of the West Antarctic Ice Sheet, with consequent changes in ocean and atmospheric circulation, was possibly a major factor contributing to the magnitude of temperature and precipitation increases reconstructed for the “super” interglaciations of MIS11 and MIS31. The cryosphere and biosphere perhaps exerted additional influences as interactions among sea ice and snow albedo, and forest extent can provide a further positive feedback to climate change (Foley et al., 1994). Moreover, modeling and modern observations indicate the magnitude and direction of change associated with biosphere and atmosphere feedbacks are sensitive to the composition and distribution of plant communities. For example, positive feedbacks to high latitude warming, including such factors as increasing sensible heat flux and reducing albedo (e.g., Foley et al., 1994; Levis et al., 1999; Eugster et al., 2000; Chapin et al., 2000), would be enhanced by the shift from deciduous to evergreen conifer forest. If Lake E is indicative of vegetation responses across northern high latitudes during these “warmer” intervals, then Arctic plant communities during “super” interglaciations constricted to such an extent that they no longer existed as a major biome with consequent feedbacks related to shifts in albedo, sensible heat flux, surface roughness, etc. Such an effect was noted during MIS5 when a 5–10% decrease in albedo was estimated for northeastern Asia in response to the northern expansion of forest (Velichko, 2009).

In summary, the Lake E record provides a set of natural experiments within which scientists might gauge the range of

vegetation responses, the degree to which the distribution and composition of arctic-boreal communities may alter, and the scope of expansion or contraction of contemporary biomes as means to further improve predictions of possible biotic responses in Arctic regions to projected global warming. The palynological data from Lake E highlight the merits of existing models that predict the northward expansion of either conifer or deciduous forests under warmer-than-present climate scenarios. However, the Lake E record also demonstrates that idiosyncrasies of climatic forcings and associated atmosphere–biosphere–cryosphere feedbacks may cause more complex vegetation responses than anticipated by current modeling efforts.

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