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Forest or no forest: implications of the vegetation record for climatic stability in Western Beringia during Oxygen Isotope Stage 3

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ABSTRACT

Two conflicting stratigraphic schemes describe the Siberian Karginskii interstade (Oxygen Isotope Stage 3 equivalent) as having: 1) relatively stable climate with environments more similar to the full glaciation; or 2) variable climate with landscapes that more closely approximate contemporary ones. New data from continuous lake cores and a nearly continuous section from western Beringia (WB) suggest that both schemes are valid. Herb-dominated communities, possibly with isolated populations of *Larix*, characterized northern WB with only a slight shift from relatively warm to cool summers during the mid-interstade. In contrast, herb and shrub tundra, steppe, forest-tundra, and modern Larix forest occurred at various times in areas of southern WB, suggesting greater climatic instability. A thermal optimum is evident in the south during the mid-interstade, with modern vegetation in southeastern WB and *Larix* forest-tundra in the southwest. Variations in *Pinus pumila* pollen indicate summer warm/winter dry and summer warm/winter wet conditions in southeastern WB. These fluctuations contrast to other areas of WB, where summers and probably winters were consistently arid. Although the interstade presents a unique interval within the Late Pleistocene, paleodata and paleoclimatic models suggest that changes in marine conditions, including sea level, were likely key drivers in the regional climate history.

1. Introduction

While Andrei Sher is perhaps most identified with the "mammoth-steppe paradox", which focused on the biota of the last glacial maximum (LGM; Hopkins et al., 1982), he was also a central figure in investigations of the Karginskii interstade (Oxygen Isotope Stage (OIS) 3 equivalent). Like the LGM, this period of the Late Pleistocene has presented its own set of mysteries. Two contradictory paleoenvironmental schemes currently exist for Siberia, one which suggests fluctuating vegetation and climate (Kind, 1974) and a second, championed by Sher, which portrays more monolithic conditions. Controversy has marked the study of OIS-3 from the first, when Baskovich (1959) and Kartashov (1966) came to opposing conclusions based on data collected from the Upper Kolyma region of Northeast Siberia. Baskovich proposed that this interval was cooler than present, whereas Kartashov inferred a uniformly warm environment with a greater affinity to an interglaciation than an interstade. It was not until Kind (1974) that some resolution was achieved when she proposed a dated stratigraphy for the Karginskii interval, at the time thought to be ~50–22 ka (note: all ages are reported as radiocarbon years BP times 1000). Her work was based on material from the Yenisei drainage (Eastern Siberia), where she defined a series of alternating warm and cool intervals: 50–45 ka warm; 45–43 ka cool; 43–33 ka warm (optimum), 33–30 ka cool; 30–22 ka warm. Although various terminologies have arisen (see Anderson and Lozhkin, 2001), the general characteristic of fluctuating interstadial climates and vegetation was accepted and applied across Siberia. Equally accepted was the widespread establishment of forest or forest-tundra during warm intervals, possibly with latitudinal treeline extending farther north than present (Arslanov et al., 1980).

Sher was one of the first to question the validity of Kind's conclusions (Sher and Plakht, 1988; Sher, 1991; see also Sher et al., 2005). He stressed that her climatostratigraphic sequence was not drawn from a single section, leaving open possible questions about the true sequencing and continuity of the proposed scheme. Furthermore, application to other regions was not without problem, as absolute dating was weak or absent. Many of these latter studies presumed a correspondence with Kind's scheme and relied on the topographic relationships of fluvial terraces within and between valleys to make those correlations. Sher and Plakht

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(1988) in a detailed stratigraphic examination of radiocarbon-dated material used by Kind and others demonstrated the potential errors in the chronostratigraphy and suggested that contamination of samples from "warm" horizons yielded erroneously finite dates. More recent work by Astakhov (2001) apparently confirmed Sher's suspicions, when he re-dated the lower Yenisei material and found that units Kind had assigned to OIS-3 had infinite radiocarbon dates, making the supposed "Karginskii" deposits most probably from the last interglaciation. If most or all of the samples indicative of warming are more correctly assigned to OIS-5, then the overlying deposits of OIS-3 and OIS-2 show evidence for relatively uniform and cool conditions (Sher et al., 2005). Thus, Sher envisioned an interstade in Siberia, where: 1) vegetation differed little from that of the LGM; 2) climatic variation was subtle at best; and 3) northernmost areas remained essentially treeless with no extensive encroachment of forest boundary into the present-day coastal lowlands.

Sher's interest in OIS-3 resurfaced with the publication of the Icy Complex section from the Mamontovy Khayata site to the south of the Lena delta (Sher et al., 2005; Fig. 1). In this paper, he again questioned the fluctuating nature of the Karginskii interstade. The subject of OIS-3 climate "instability," of course, is of broader geographic interest (e.g., Grimm et al., 1993; Watts et al., 1996; Heusser et al., 1999; Grigg and Whitlock, 2001; Coope, 2002; Voelker and Workshop participants, 2002; van Andel, 2002), particularly as scientists seek to understand the impact of the short-term, Dansgaard-Oeschger (DO) climatic oscillations on terrestrial environments (e.g., Barron and Pollard, 2002; Pollard and Barron, 2002; Alfano et al., 2003; Huntley et al., 2003). Two mechanisms that were of particular interest to Sher et al. (2005) were: 1) seasonality; and 2) paleogeography. The latter is an often overlooked factor in regions where shifting sea-levels resulted in only modest changes in land surface area, in contrast to northern Asia, where the coastal plain widened by ~700 km during the last glaciation (Lozhkin, 2002).

Questions of basic stratigraphy, however, still need answering prior to exploring the magnitude and nature of ecosystem responses to interstadial climates. We focus on three of our own lake records from Western Beringia (WB, extending from the Lena River eastward to Bering Strait) as means for re-examining the Kind-Sher stratigraphic dispute. Unlike section materials, which act as "snapshots" of past interstadial environments (see Anderson and Lozhkin, 2001), these lacustrine cores present continuous vegetation and climate histories that include all or much of OIS-3. Published data from El'gygytgyn Lake (Lozhkin et al., 2007; Fig. 1), located in northeastern WB (Fig. 1), encompass the last 8 Oxygen Isotope Stages. The southeastern tier of WB is represented by the ~60 ka Elikchan-4 (Lozhkin et al., 1995, 2002a) and ~45 ka Alut (Anderson et al. 1998; Lozhkin et al., 2002a) sites. We supplement this material with other records, one of the most important being the recently published Lake Billyakh site (Müller et al., 2010) from WB's southwestern border. Although the available data can not possibly represent a detailed paleogeography of the vast WB subcontinent, their locations do provide a representative sampling of OIS-3 paleoenvironments and as such, at least offer a preliminary means for exploring spatio-temporal patterns of change. We

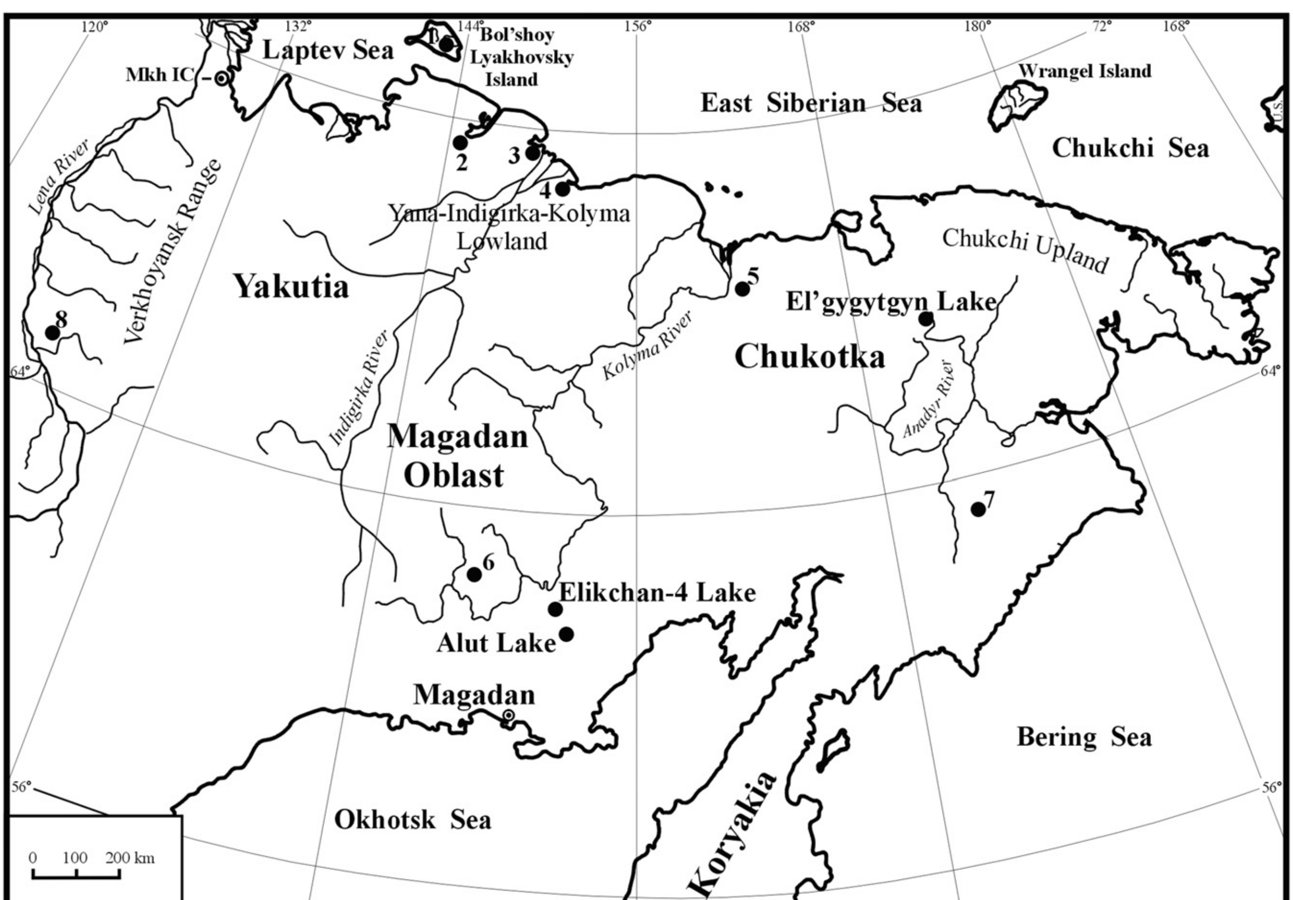

Fig. 1. Map of Western Beringia. Primary sites are fully labeled. Secondary site identification is: 1) Bol'shoy Lyakhovsky mammoth; 2) Khroma-Keremesit; 3) Shandrin mammoth; 3) Berelekh mammoth (lower Indigirka); 4) Bol'shoy Khomus-Yuryakh; 5) Molotkovskiy Kamen; 6) Kirgirlyakh mammoth; 7) Ledovy Obryv, Main River; and 8) Lake Billyakh.

specifically will focus on the stability or instability of interstadial paleoenvironments as presented through the stratigraphic schemes and their implications for issues of biogeography and seasonality raised by Sher and colleagues.

2. Western Beringia – modern setting, paleogeography and the study sites

2.1. Modern setting

WB, while topographically diverse, can be viewed most simply as a suite of mountain and upland complexes (elevations ~600–2500 m) and large tectonic depressions ringed by coastal lowlands. The latter are extensive in the north (~150–500 km wide) but are more modest in eastern Chukotka and along the OkhotskSea (<100 km wide). The heartland of WB is characterized by numerous mountain ranges dominated by the north-south trending Verkhoyansk Range (Fig. 1) that separates *Larix dahurica* dominated forest to the east from *Larix dahurica–Pinus sylvestris* and *Larix dahurica–Pinus sylvestris–Picea obovata* forests to the west. Coastal and alpine tundra, with a predominance of graminoids and low- to mid-sized shrubs of *Betula*, *Salix*, *Duschekia fruticosa* and/or *Pinus pumila*, are generally similar between these regions. Northern and central Chukotka consists of uplands with shrub- and herb-dominated tundra. In southern Chukotka, high-shrub *Pinus pumila–Duschekia fruticosa* tundra characterizes the vegetation. Major river systems (e.g., Lena, Kolyma, Indigirka, Yana; Fig. 1) flow northward from the deep interior to the Laptev and East Siberian Seas. With the exception of the Anadyr system, which drains into the Bering Sea, rivers of Chukotka and the Okhotsk Sea drainage are more modest in size and catchment. Climate near the Laptev coast is cooler and drier than locales in the Chukchi Uplands or the southern mountains (Table 1).

2.2. Paleogeography, glaciation, and sea level

Despite suggestions that a large ice-sheet covered much of WB during at least part of the Late Pleistocene, field evidence does not support such a conclusion (see Brigham-Grette et al., 2004, for discussion of this debate). Known morainal systems are associated with OIS-2 and OIS-4, the latter being the more extensive glaciation, and indicate coastal lowlands and most river valleys were ice-free (Glushkova, 2001; Brigham-Grette et al., 2004). Positions of OIS-3 glaciers are uncertain. If interstadial ice retreated significantly into the mountains, as would be likely under ameliorated conditions, such evidence was subsequently destroyed by advancing OIS-2 glaciers.

Beringia experienced one of earth's greatest changes in land mass during the Late Pleistocene caused by the growth of continental glaciers and consequent reduction in sea level (see Brigham-Grette et al., 2004). At the height of the LGM, the East Siberian coastline extended to ~78°N, a widening of ~700 km, thus incorporating the current arctic islands into the mainland (Lozhkin, 2002; Manley, 2002; Fig. 2). Lowered sea-levels also created a massive land bridge connecting Asia and North America. Addition of dry land in the south was predominantly on the Alaskan side of Bering Strait, as changes in coastline along southern Chukotka and the Okhotsk Sea were modest (Lozhkin, 2002). Ice volume equivalent sea-levels (ESL) indicate a maximum decrease of ~ −80 m in OIS 3 as compared to the ~ −100 to −120 m ESL during the LGM (Lambeck et al., 2002; Fig. 3). Even at −80 to −60 m ESL, WB would still retain a northern shelf of up to ~500–400 km width. Global sea-levels were not constant during the interstade. Highest stands were between ~57–45 ka with lowest levels occurring after ~39 ka. Within the former interval, comparatively lowered ESL is noted at ~53–51 ka and ~45–43 ka. In a recent modeling exercise that used a relative sea-level curve for Bering Strait, Hu et al. (2010) suggested that Bering Strait may have been opened for much of the early to mid-interstade. Field results from the Laptev and East Siberian seas support the occurrence of near-modern sea levels at times during the interstade (Saks, 1948; Alekseev, 1997).

2.3. Study sites

As mentioned above, the study sites represent northern and southern locales in WB: the Mamontovy Khayata Ice Complex exposure occupies a coastal cliff to the south of the Lena Delta, El'gygytgyn Lake is in the northern Chukotkan uplands, and Elikchan and Alut lakes lie in the mountainous southern Magadan Oblast. Following is a brief description of each of these important sites.

2.3.1. Laptev coast – Mamontovy Khayata Ice Complex

The Mamontovy Khayata (MKH) cliff is located on Bykovsky Peninsula, a spit of land that juts into the Laptev Sea (Fig. 1). The peninsula, the remnants of a Late Pleistocene accumulation plain (Siegert et al., 2002), consists of "ice-complex" sediments, which are "ice-rich and perennially frozen fine-grained deposits, penetrated by thick polygonal ice-wedge systems…and formed under extremely continental climate…mainly in the lowlands and river

Table 1
Characteristics of Study Sites.

	Mamontovy Khataya IC	El'gygytgyn Lake	Elikchan Lake	Alut Lake
Latitude (°N)	71° 60′	67° 30′	65° 45′	60° 08′
Longitude (°E)	129° 25′	172° 05′	151° 53′	152° 20′
Elevation (m)	40	495	810	480
Site origin	Ice complex developed in accumulation plain	Meteor impact crater	Tectonic lake	Tectonic lake
Setting	Coastal lowlands	Uplands	Mountain valley	Mountain valley
Modern vegetation	Graminoid-moss tundra with dwarf shrubs	Discontinuous lichen-herb tundra (local); graminoid-shrub tundra (low to mid-growth forms; regional)	*Larix dahurica–Pinus pumila* forest	*Larix dahurica–Pinus pumila* forest
Mean Annual Temperature (°C)	−13.2	−9.9	−12.2	−12.2
Mean July Temperature (°C)	8.9	13	11.9	11.9
Mean January Temperature (°C)	−34	−29.4	−35.7	−35.7
Mean Annual Precipitation (mm)	212	256	293	293
Mean July Precipitation (mm)	21	53	50	50
Mean January Precipitation (mm)	9	16	13	13
Nearest Meteorological Station	Stolb[a]	Stalino[b]	Atka[b]	Atka[b]

[a] From Anonymous, 1968.
[b] From Anonymous, 1960.

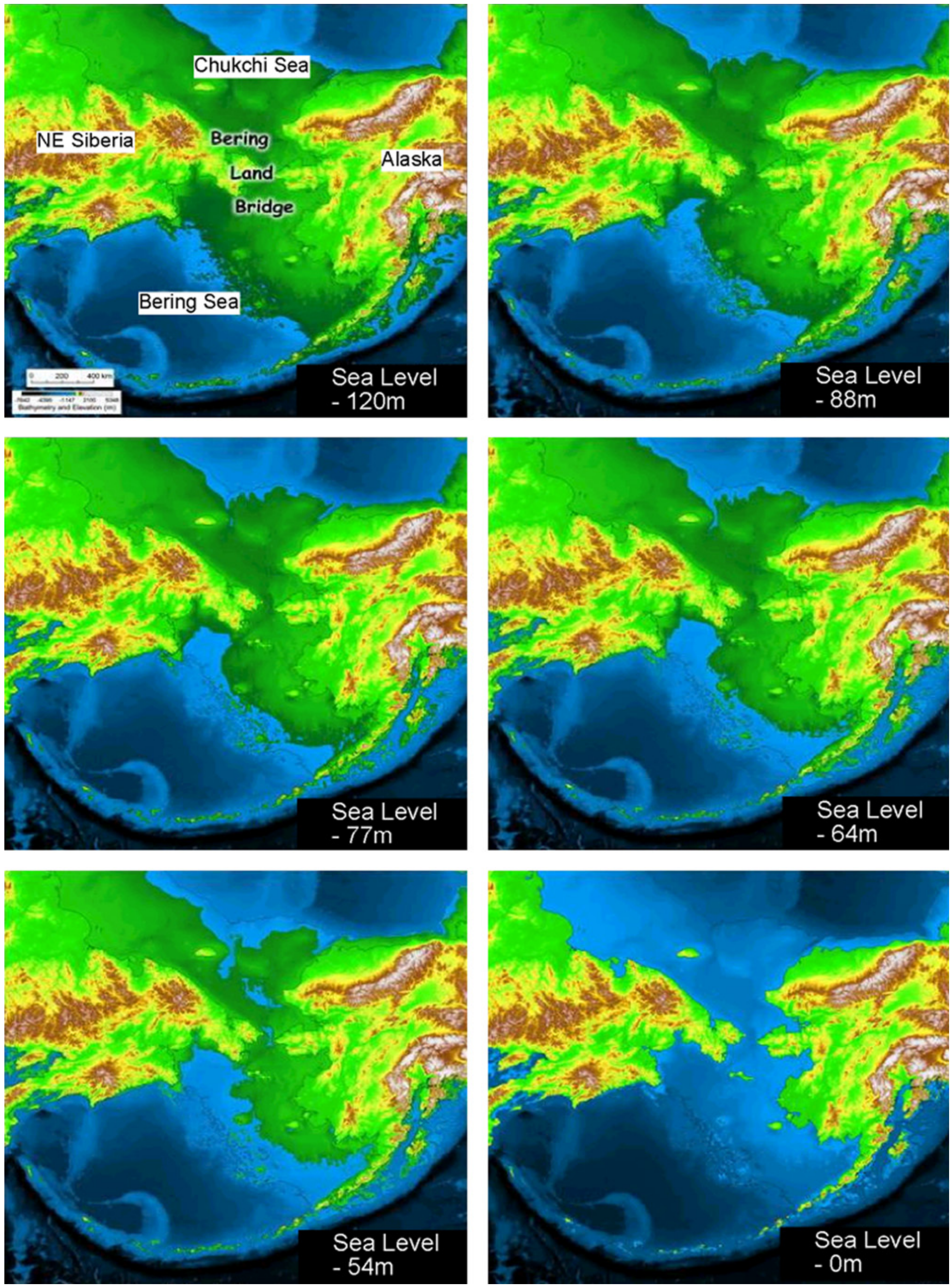

Fig. 2. Sea-level reconstruction based on Manley (2002). The −120 m figure illustrates maximum expansion of Beringia during the LGM. OIS-3 sea-levels are uncertain for this region but likely were between −80 and −50 ESL m, as approximated in the middle and lower left panels. Permission to reproduce the figure from Brigham-Grette et al. (2004) was provided by The University of Utah Press.

valleys of north Siberia during cold stages of the late Pleistocene" (Kienast et al., 2005, p. 285). The complicated geomorphic histories of ice-complex sediments generally do not permit tracing continuous records of change. However, careful stratigraphic description and detailed radiocarbon dating (Schirrmeister et al., 2002; Siegert et al., 2002) allowed 2 to 6-m-high profiles to be correlated, thereby providing a near continuous history at least over the past ~46 ka (Sher et al., 2005) to ~60 ka (Andreev et al., 2002; Kienast et al., 2005). No evidence exists to indicate any local glaciation during either OIS-2 or OIS-3.

The modern vegetation of Bykovsky Peninsula is graminoid and moss tundra with dwarf shrubs, such as *Betula exilis* and *Salix glauca*, and ericads (e.g., *Ledum decumbens*, *Vaccinium vitis-idaea*, *Vaccinium uliginosum*). *Salix* and *Betula* spp. can grow to 50 cm height in protected sites. Locally wet areas associated with thermokarst or polygonal depressions support abundant *Eriophorum* and *Carex* spp. (Kienast et al., 2005; Sher et al., 2005). Today the forest boundary lies ~70 km to the south of the peninsula.

2.3.2. Northern Chukotka – El'gygytgyn Lake

El'gygytgyn Lake is a meteor impact crater formed ~3.6 million years ago (Brigham-Grette et al., 2007a) in the north Chukchi Upland (Fig. 1). Today the lake is roughly circular in shape with a ~15 km diameter. Bedrock is Late Cretaceous ignimbrites, pyroclastics, and lavas. Sides of the lake basin are steep, deepening to a 150 m water depth, where the lake floor forms a gradual slope

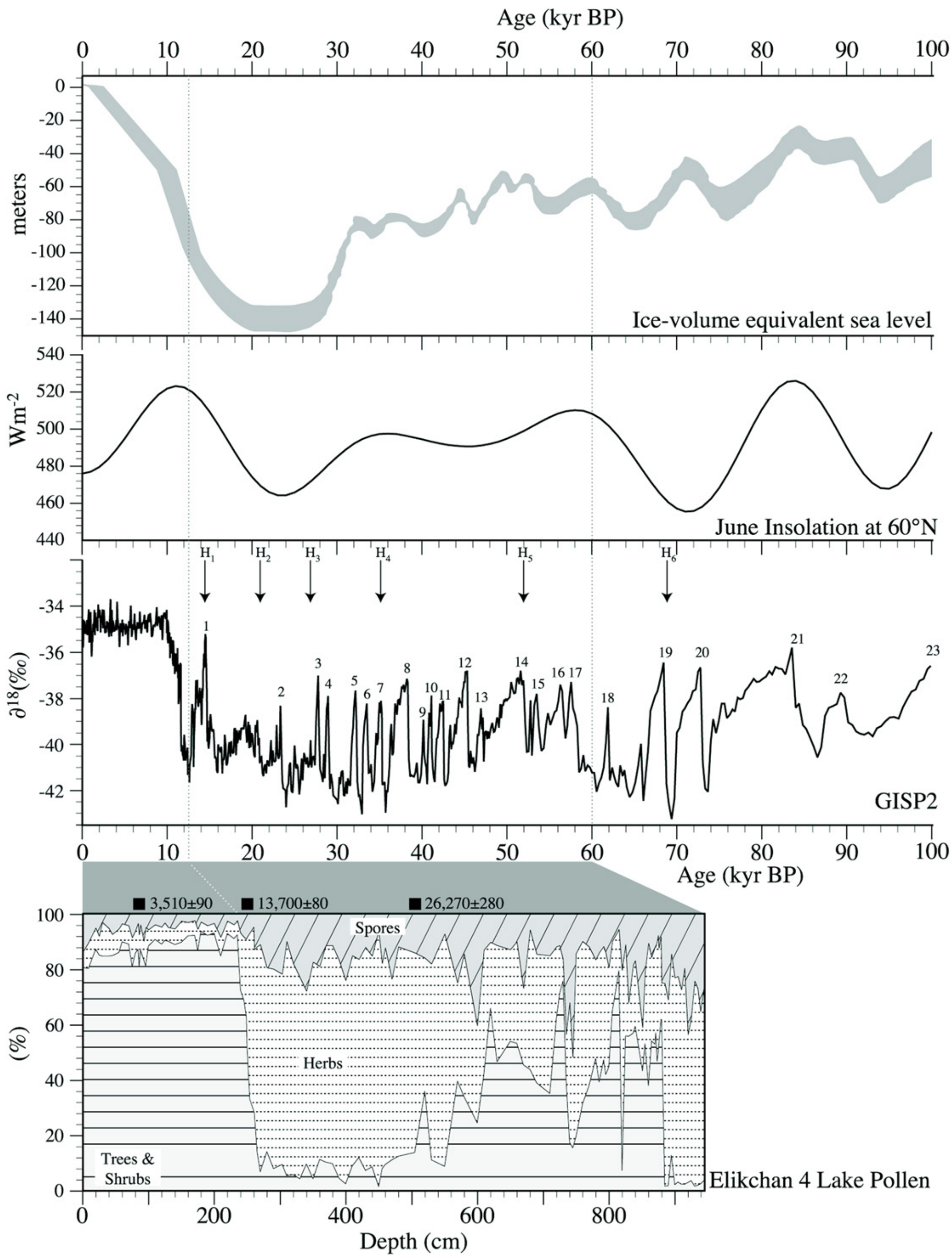

Fig. 3. Illustration of global sea-level curve, June insolation for the northern hemisphere, the $\delta^{18}O$ record from the GISP2 core including Dansgaard/Oeschger and Heinrich events, and summary pollen diagram from Elikchan Lake. Note that ages are given in cal ka. Permission to reproduce the figure from Brigham-Grette et al. (2004) was provided by The University of Utah Press.

to a 175 m deep central basin. The lake is surrounded by hills of ~850–950 m altitude. Streams drain from these hills to the lake with the Enmyvaam River flowing southward to the Bering Sea. The El'gygytgyn area has never been glaciated. The pollen record discussed here extends back ~300 ka (Lozhkin et al., 2007).

Lichen and herbaceous taxa characterize the El'gygytgyn basin, with vegetation often being absent on the crater's slopes (Kozhevnikov, 1993). Shrubs are few, the most common being low-growth forms of *Salix krylovii* and *Salix alaxensis*, found only in the most protected sites. *Betula exilis* is more rare and restricted to areas of organic accumulation. The El'gygytgyn vegetation differs from the surrounding Chukchi Upland, caused by atypical soils associated with the crater's unusual substrate. The Upland is a mosaic of low-shrub and herb tundra. Dominant woody taxa are *Salix* spp., although small populations of *Pinus pumila* and *Duschekia fruticosa* occur. Poaceae is the most regionally abundant herb, and many hilltops are barren. Modern treeline is located ~150 km to the south of the lake.

2.3.3. Magadan sites – Elikchan and Alut lakes

Both Elikchan-4 (~3900 m long, 900–1300 m wide) and Alut lakes (~2000 m long, 400 m wide) are elongate basins that drain to the Okhotsk Sea. Bathymetric transects indicate Alut consists of two basins, with a maximum water depth of 18 m in the eastern basin and 8 m in the western basin. Elikchan-4 (herein referred to as Elikchan Lake) is one of four lakes that occupies a saddle that separates the Upper Kolyma and Okhotsk drainages. Elikchan also consists of two basins (~22 and 19 m water depth) bordered by broad shelves to the north (~10 m water depth) and east (~1.5 m water depth). Although lake origins are uncertain, earthquake-triggered landslides may have blocked ancient rivers in both valleys. Extrapolated ages based on radiocarbon dates suggest that Alut and Elikchan cores have basal ages of ~65.6 and ~45 ka, respectively.

Alut Lake is located ~70 km to the southeast of Elikchan Lake in a narrow valley on the northern flanks of the Bilibin Range (heights of ~900 m asl) within the tectonically active Okhotsk-Chukchi volcanic belt (Anderson et al., 1998; Lozhkin et al., 2002a). Granite or granodiorite with gabbro inclusions characterize the local bedrock. Glacial features are absent, indicating the region has been ice-free throughout the Late Pleistocene (Glushkova, 2001). *L. dahurica* forest, with occasional *Betula platyphylla*, covers the slopes that border the lake. Understory communities include *Betula middendorffii*, *D. fruticosa*, *P. pumila*, *Salix* spp., and Ericales (e.g., *Rhododendron* spp., *Ledum* spp., *Vaccinium* spp.). Altitudinal treeline lies between 600–700 m, but isolated individuals or small groups occur up to 900 m. Continuous, dense thickets of *P. pumila* (up to 3 m height) are found beyond the upper forest limit.

Elikchan Lake also occupies a narrow tectonic valley but with bedrock of late Triassic claystone and sandstone and early Cretaceous granodiorite (Lozhkin et al., 1995, 2002a). The Elikchan area was also ice-free during the Late Pleistocene. *L. dahurica*-lichen forest occupies low-lying areas near the lake. The forest understory is similar to that at Alut Lake, although *D. fruticosa* is generally less common near Elikchan Lake. The decreased numbers of *Duschekia* at higher as compared to mid- to low-elevation sites is typical in southern WB. Shrub tundra, dominated by *P. pumila*, occurs beyond altitudinal treeline (~850–900 m), although many of the upper slopes bordering the lake are sparsely vegetated scree.

3. Age models

With the exception of MKH, radiocarbon control is inadequate to provide definitive time series for the long-term, continuous paleobotanical records from WB. We provide preliminary age-models based on OIS-age transitions and/or reliable ^{14}C dates as a first-level examination of temporal trends. These models are provisional and offered as a means to further understand temporal patterns during the last interstade. Ages of zone boundaries for the various sites are given in Table 2. Because the original data are given as radiocarbon dates (see Andreev et al., 2002 for list of ^{14}C ages for MKH; ^{14}C dates for other sites are included in Figs. 7–9), all ages presented here are in ^{14}C kyr BP (ka). In the few cases where necessary, we have recalibrated calendar yr to ^{14}C yr by subtracting 3 kyr, following Bard et al. (1993). We also refer to the early, middle, and late OIS-3, approximately 60–48 ka, 48–36 ka, and 36–25 ka, respectively.

Although over 70 samples (note: these samples include OIS-2 and Holocene materials) were taken at MKH and adjacent exposures, Sher et al. (2005) used results only from the main section to avoid contamination problems common in highly active ice-complexes where sediments are often disturbed due to thermokarst activity. Thus, the Sher et al. time series ends at ~46 ka. In contrast, Kienast et al. (2005) plotted 70 AMS and 20 conventional dates to construct an alternative age-model, concluding a basal age for the section of ~60 ka. In a third treatment, Andreev et al. (2002) compiled a ~57 kyr-old composite pollen diagram using only radiocarbon-dated samples. In actuality the latter two models differ little from Sher et al., who did not include the lower 11 m in their analysis, and depth-age relationships are similar in both models for the 11–27 m section.

Two different chronologies have been proposed for El'gygytgyn Lake, one based on paleomagnetic parameters tuned to Northern Hemisphere insolation (Nowaczyk et al., 2002, 2007) and the second on pollen-inferred climatic changes correlated with ages of major climate fluctuations in North Atlantic oxygen-isotope records (Lozhkin et al., 2007). We have disputed the former chronology, which was used as standard for other El'gygytgyn analyses (Brigham-Grette et al., 2007b), because climatostratigraphic boundaries in the magnetic-based age model(s) are inconsistent with reconstructed vegetation (e.g., OIS-2 includes both cool and warm pollen spectra). In our re-examination here of the OIS-3 pollen assemblage, we have further modified the chronology, assigning a ~25 ka upper interstade boundary following Sher et al. (2001) and using a basal age of 60 ka based on oxygen isotope records (Schackleton and Opdyke, 1973).

Anderson and Lozhkin (2001) suggested a mid- to late-interstadial climatostratigraphic scheme for the southern Magadan region consisting of two warm (~39–33 ka; ~30–26 ka) and two cool periods (~45–39 ka; ~33–30 ka) based primarily on section data. The sequence of climatic events parallels Kind (1974), but the timing differs. This sequence also does not span the entire interstade. Rather than using the previously published scheme to establish chronologies for Elikchan and Alut lakes, we determined the sedimentation rate closest to the undated portions of OIS-3 and then applied that rate to assign ages to zone boundaries. For Alut Lake, we used the ~25 and ~13.7 ^{14}C dates to extrapolate downcore, receiving a basal age of ~45 ka. In the case of Elikchan Lake, the rate was determined by using the ~26 ka ^{14}C age and an OIS-based age of 60 ka age for the OIS3/OIS4 boundary with a basal age of ~65.6 ka for the core. Where the records overlap, the

Table 2
Zone Boundaries and Preliminary Age Assignments.

Site	Zone	Age range (ka)
MKh IC	Cool summer	34–25
	Warm summer	46–34
El'gygytgyn	10c	46.2–25
	10b	54.1–46.2
	10a	60–54.1
Elikchan	560–510 cm	30.8–26.3
	EL2j	34.9–30.8
	EL2i	41.2–34.9
	EL2h	44.8–41.2
	EL2g	46.8–44.8
	EL2f	48.4–46.8
	EL2e	53.4–48.4
	EL2d	55.6–53.4
	EL2c	56.5–55.6
	EL2b	57.6–56.5
	EL2a	60–57.6
Alut	AT5	30.2–25.6
	AT4	34.4–30.2
	AT3b	39.4–34.4
	AT3a	41.3–39.4
	AT2	43.8–41.3
	AT1	45–43.8
Kind (1974)	warm	30–22
	cool	33–30
	optimum	43–33
	cool	45–43
	warm	50–45

chronostratigraphy differs between the two sites, although the general paleoclimatic trends are similar and are also similar to those of Kind (1974); (see section 4). Given the proximity of Elikchan and Alut lakes, such temporal variations seem unlikely, suggesting one or both age models are in error. As stated above, they are offered as preliminary chronologies and meant for use in discussing general trends in the data so we made no attempt in this paper to arbitrarily make the two sites time-equivalent.

4. The paleorecords – variations in past vegetation

The following is a brief summary of the interstadial vegetation history reconstructed from four of the most robust records in WB, with reference to other sites as relevant. It is important to remember that the depositional environments at these sites vary in terms of their landscape representation (Jacobson and Bradshaw, 1981). The MKH section documents local environments (area sampled: $\sim 10^{-2}$ to 10^{-4} km^2), Elikchan and Alut are extra-local ($\sim 10^1$–10^2 km^2), and the large-basined El'gygytgyn Lake is regional ($>10^3$ km^2). However, for the sake of discussion in this paper, we presume that all records are indicative of conditions across a broad region. Note that by convention pollen of *D. fruticosa* (shrub alder) is labeled as *Alnus* in the diagrams.

4.1. The northern records

4.1.1. Mamontovy Khataya ice complex (MKH)

The MKH site has been studied repeatedly (see Sher et al., 2005, for summary) with the most recent, interdisciplinary investigations focused on the 40-m-high section (pollen Andreev et al., 2002; ground ice, Meyer et al., 2002; mammals, Kuznetsova et al., 2003; testate amoebae Bobrov et al., 2004; plant macrofossils, Kienast et al., 2005; insects and mammals, Sher et al., 2005; ostracodes, Wetterich et al., 2005). We focus here on the insect and paleobotanical analyses.

Sher et al. (2005) inferred two main intervals within OIS-3 based primarily on variations in insect fauna (Fig. 4). The early part of OIS-3 (11–19 m; between 46 ka, or possibly older, and 35–34 ka) is characterized by dry tundra and steppe insect species (average 28% and 22%, respectively) with minor occurrences of forest-tundra taxa (2–9%). These latter taxa, which include members of the Chrysomelidae (leaf beetle) and Curculionidae (weevil or snout beetle), are mostly associated with shrubs (e.g., *Phatora polaris*, *Lepyrus* spp.) or meadows (e.g., *Phyllobius* spp., *Phaedon concinnus*) within the forest zone. However, the true taiga species *Pterostichus magus* (Carabidae, ground beetle) appears in three samples. These assemblages contrast to late OIS-3 (19–27 m; 34–24 ka) where mesic (average 39%; e.g., *Chrysolina septentrionalis*, *Tachinus arcticus*, *Cholevinus sibiricus*) and dry (average 21%; e.g., *Curtonotus alpinus*, *Sitona borealis*, *Hypera diversipunctata*, *Hemitrichapion tschernov*) tundra insects predominate. Forest-tundra taxa in general are reduced (average 4%) with only one sample containing an obligate forest species (*P. magus*). Steppe insects (e.g., *Chrysolina perforate Stephanocleonus eruditus*) while appearing in many samples occur in fewer numbers ($\sim$2%).

Although the OIS-3 vegetation reconstructed by Sher et al. (2005) is generally similar between early and late portions of the record, differences do exist. Between $\sim$46–34 ka, insect data suggest the presence of a "warm" or "warm summer" tundra-steppe. The landscape was dominated by graminoids, but forbs were relatively abundant and diverse. Shrubs were rare, probably with dwarf *Salix* being most predominant. The presence of forest or

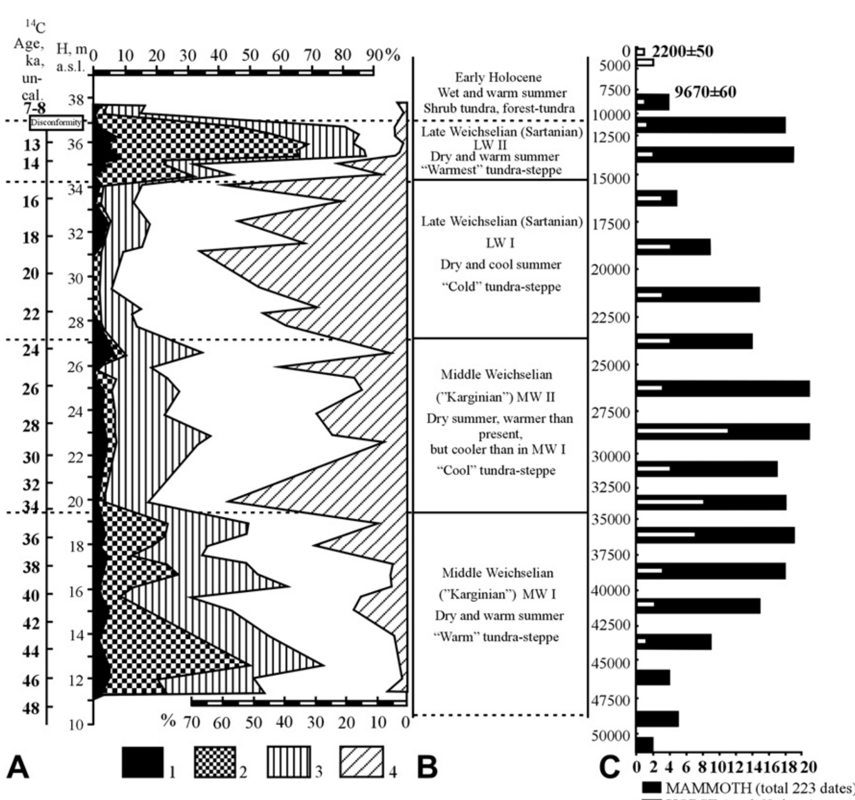

Fig. 4. Summary of insect and mammal data from the Laptev Sea region showing: a) fossil insects; b) climatic and environmental reconstruction, and c) remains of radiocarbon-dated mammals (number of dates within a 2.5 ka interval). The insect key is: 1) steppe species; 2) other xerophilous insects (excluding tundra species); 3) dry tundra species from warmer sites; and 4) arctic species. Permission to reproduce the modified figure from Sher et al. (2005) was provided by Elsevier.

forest-tundra beetles suggests that isolated individuals or small stands of *Larix* established in more mesic habitats. Later portions of the interstade (∼34–24 ka) also were characterized by Poaceae-Cyperaceae dominated vegetation. The reduction in forest-tundra insects may reflect a decline of woody taxa on the landscape. Vegetation cover was likely more discontinuous. Sher et al. termed this an interval of “cold” or “cool summer” tundra-steppe.

Plant macrofossil analysis at MKH primarily emphasized the difference between Holocene and Late Pleistocene vegetation (Kienast et al., 2005). A diverse landscape represented by arctic (e.g., *Minuartia arctica*, *Draba*, *Kobresia myosuroides*), steppe (e.g., *Alyssum obovatum*, *Silene repens*, *Linum perenne*), meadow (e.g., *Hordeum brevisubulatum*, *Puccinellia tenuiflora*), littoral (e.g., *Ranunculus reptans*, *Rumex maritimus*), and aquatic (e.g., *Potamogeton vaginatus*, *Calliitriche hermaphroditica*) species characterized both OIS-3 and OIS-2 intervals (Fig. 5). Although representing a variety of microhabitats, community composition is most similar to relict steppe found today in areas of Yakutia and WB (Yurtsev, 1982). The interstadial and stadial assemblages contrast to those of the Holocene, which are uniform by comparison and generally lack Late Pleistocene species. As with the insect data, the plant macrofossils imply slight variations within OIS-3. Between ∼48–35 ka, increased numbers of macrofossils from wet habitats suggest somewhat ameliorated conditions during the middle as compared to the late interstade. Greater pioneer species and lesser floristic diversity indicating the presence of disturbed landscapes centered on ∼58 and 28 ka, implying brief periods of severe environments.

Andreev et al. (2002) compiled a composite pollen diagram (Fig. 6) based on radiocarbon-dated samples taken from various sections within the MKH site. OIS-3 encompasses pollen zones I–III (radiocarbon ages from ∼28 to >52.9 ka) with pollen assemblages that: 1) are dominated by graminoids; 2) include a variety of minor herb taxa with the greatest numbers in zone II; and 3) show consistent albeit minor amounts of shrub pollen in zone II. An open landscape likely with little vegetation cover characterized earliest OIS-3 (∼60–53 ka; zone I), the result of a cold, dry climate. Between ∼48–42.5 ka (lower zone II), tundra and steppe-like vegetation predominated. Shrub *Salix*, *Betula*, and *Duschekia* may have grown at or near the site. High percentages of reworked Pinaceae pollen suggest denuded areas persisted from earlier times. Climate was likely dry but warmer than previously. The warmest interstadial period (∼42.5–33 ka; upper zone II) is inferred from increases in forb pollen, implying enhanced plant diversity, and the reduction in Pinaceae pollen, suggestive of a more continuous vegetation. Conditions became cold and dry by ∼28.5–28 ka (zone III) associated with tundra and steppe-like communities and increases in disturbed ground indicators. The general climate trends based on the palynological data parallel those from the insect and plant macrofossil evidence; i.e., relatively warm but dry conditions from ∼48 ka to 35–33 ka with cold, dry climates in the later interstade.

4.1.2. El’gygytgyn Lake

Like MKH, El’gygytgyn sediments have been the focus of multidisciplinary investigations (see Brigham-Grette et al., 2007b).

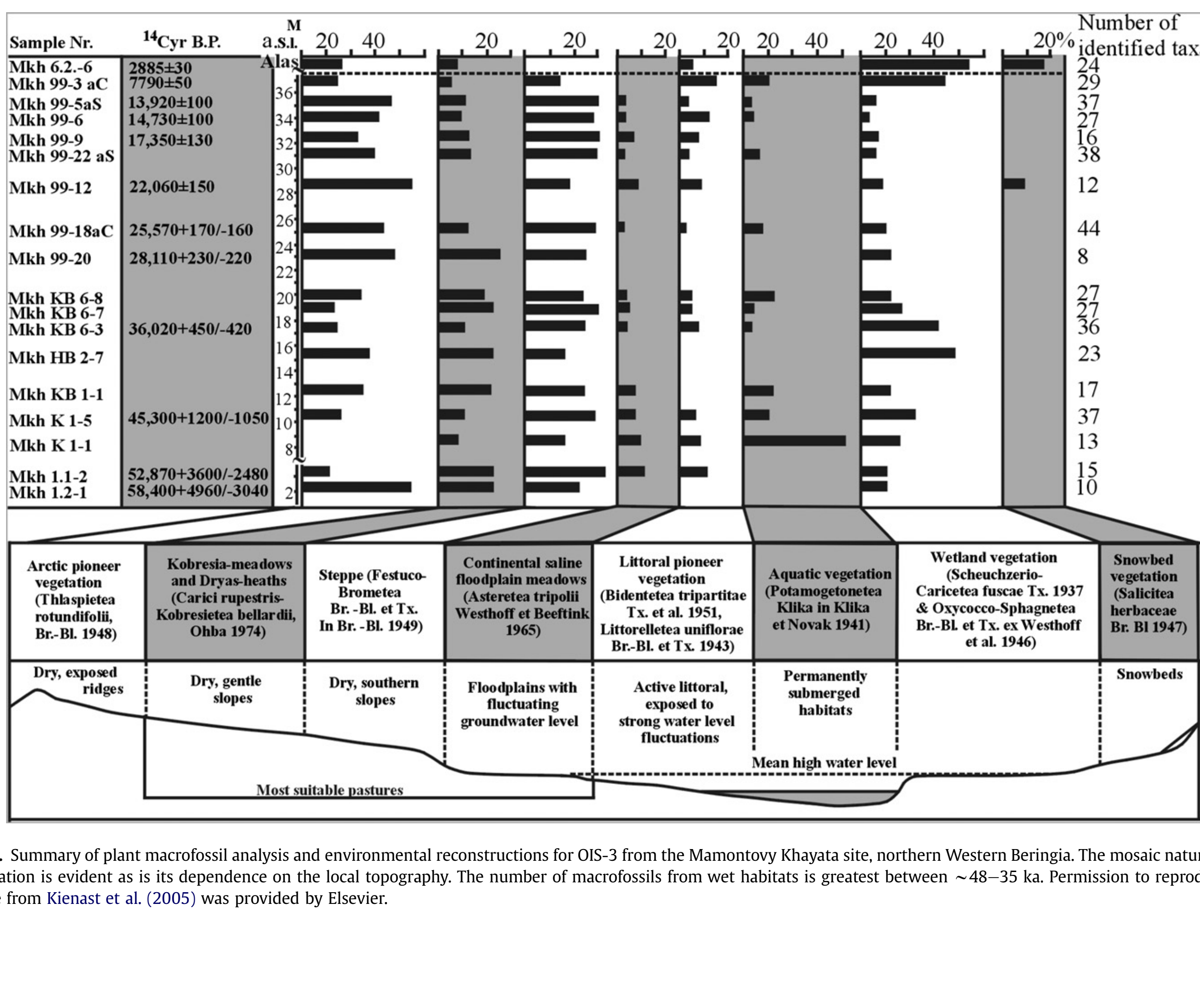

Fig. 5. Summary of plant macrofossil analysis and environmental reconstructions for OIS-3 from the Mamontovy Khayata site, northern Western Beringia. The mosaic nature of the vegetation is evident as is its dependence on the local topography. The number of macrofossils from wet habitats is greatest between ∼48–35 ka. Permission to reproduce the figure from Kienast et al. (2005) was provided by Elsevier.

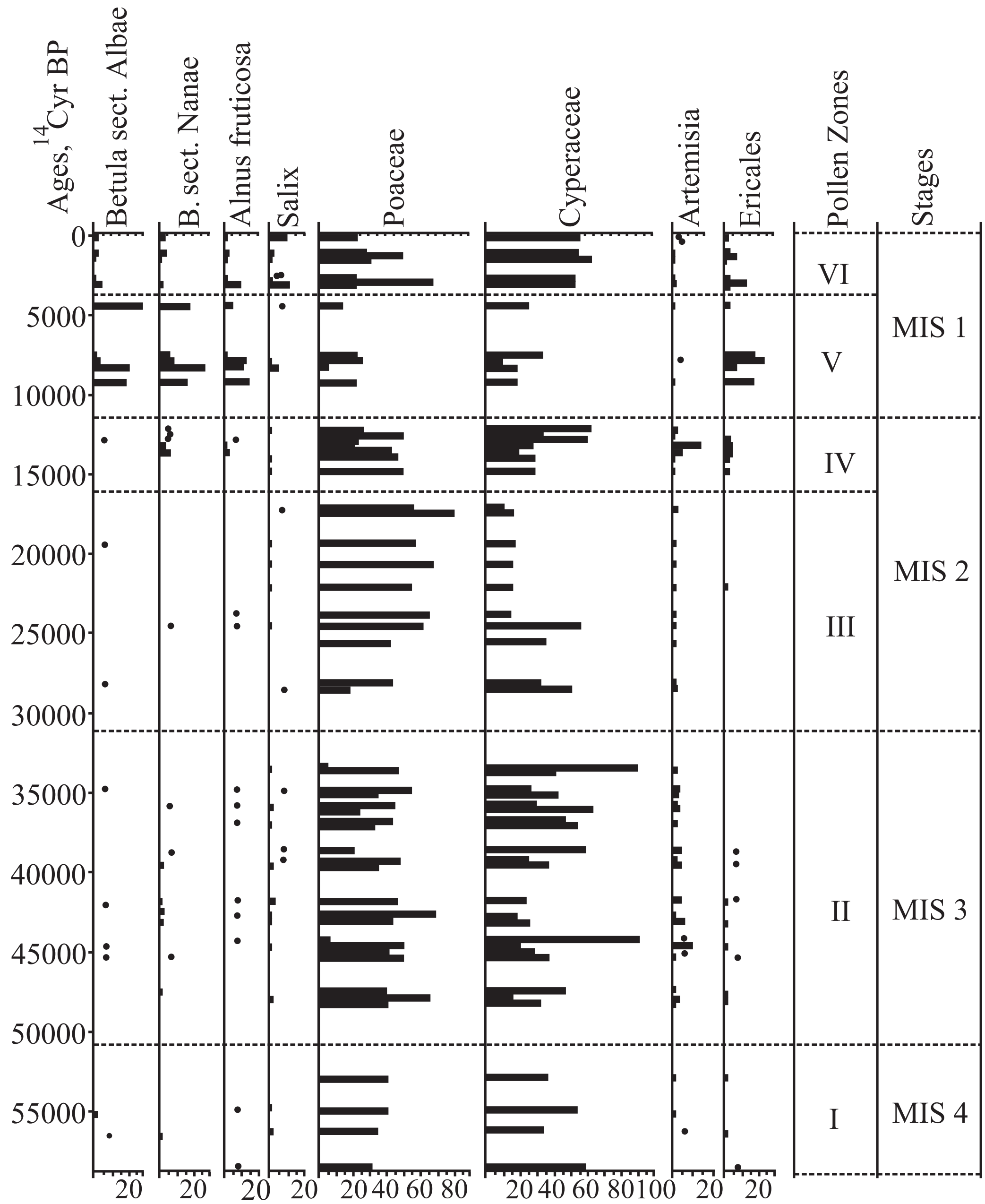

Fig. 6. Composite percentage pollen diagram from Mamontovy Khayata site modified from Andreev et al., (2002). MIS stages in the diagram are equivalent to OIS stages in the text.

Palynological analysis of OIS-3 sediments from El'gygytgyn (Shilo et al., 2001; Lozhkin et al., 2007) is not as detailed as from Elikchan and Alut lakes (cf Figs. 7b, 8b, and 9b). Nonetheless, the OIS-3 assemblage clearly differs from the shrub-dominated spectra of OIS-5 (zones EG6-EG8; Fig. 7), and while sharing high herb percentages with OIS-4 and OIS-2 (zone EG9, zone EG11), it contains greater frequencies of shrub pollen as compared to the stadial samples (Fig. 7a).

Little attention was given to the OIS-3 assemblage (zone EG10) by Lozhkin et al. (2007) except to note that the spectra are more similar to those from OIS-7 (zone EG4) of the Middle Pleistocene than to other Late Pleistocene spectra. Zone EG10 is characterized by high percentages of Poaceae pollen and modest percentages of shrub *Betula* and *Alnus* (generally <15%). Modern analogs are dominated by ones from Wrangel Island (~600 km to the north of El'gygytgyn), which today is a mix of discontinuous herb tundra with rare shrub *Salix* and polar desert (Lozhkin et al., 2001, 2007). Pollen concentrations and accumulation rates, while showing small increases in zone EG10, indicate little difference between vegetation of OIS-3 and OIS-2.

Re-plotting the percentage data to focus on OIS-3 through OIS-5 better illustrates possible albeit subtle variations within the interstade (Fig. 7b), although the paucity of samples restricts us to working hypotheses only. The total shrub pollen curve, dominated by *Betula* and *Alnus*, indicates higher values in the lower part of the zone (zone EG10a; ~60–54.1 ka), suggesting that woody taxa, although never abundant, may have formed scattered thickets during the earliest interstade in an otherwise herb-dominated landscape. Zone EG10b (~54.1–46.2 ka) is marked by increases in Poaceae pollen and *Selaginella* spores and a small decrease in shrub pollen. This zone is transitional to zone EG10c (~46.2–25 ka), where increases in *Artemisia* pollen and high Poaceae pollen suggest an expansion of herb-dominated communities that were nearly full-glacial in character. Percentages of *Betula* pollen, while variable, are

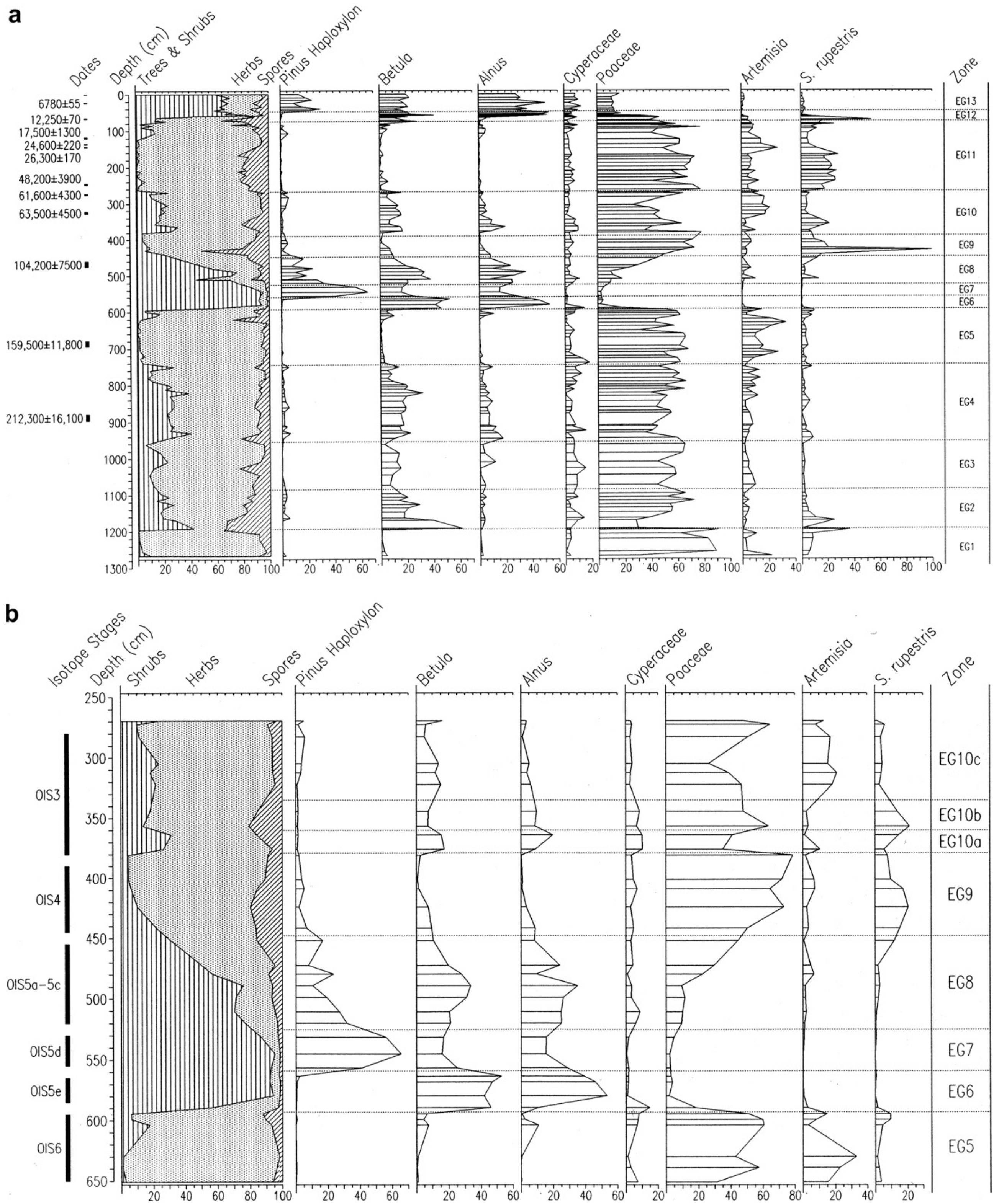

Fig. 7. Pollen percentage diagram from El'gygytgyn Lake showing the main taxa from (a) the complete record and (b) OIS-3, 4 and 5. Percentages of individual taxa are based on a sum of all arboreal and nonarboreal pollen. Subsums presented in the left column of the diagram are based on a sum of all pollen and spores. Pollen analysis by T.V. Matrosova.

somewhat higher than in zone EG10b, perhaps indicating the persistence of dwarf shrubs in protected microsites. Organic and isotope geochemistry also suggest a difference from early to later OIS-3, shifting from warm to cool-moist climate modes at ~54 ka (i.e., zone EG10a–EG10b boundary; Melles et al., 2007). Diatom data indicate that a warm-climate mode, perhaps associated with longer ice-free periods, was present in El'gygytgyn Lake during zones EG10a and EG10b, whereas cold conditions, marked by low diatom abundances and possibly extended ice-cover on the lake, prevailed in zone EG10c (Cherepanova et al., 2007).

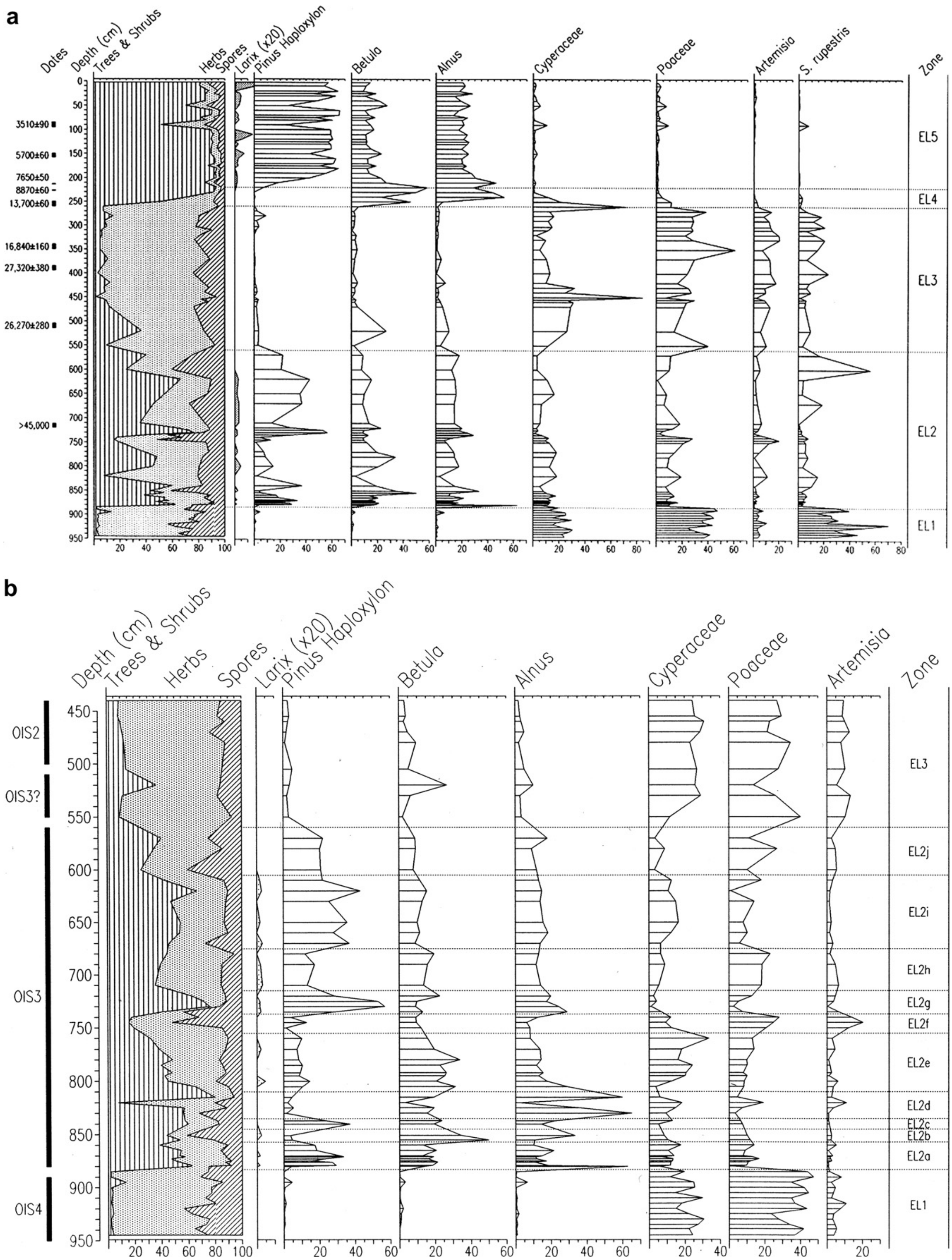

Fig. 8. Pollen percentage diagram from Elikchan Lake showing the main taxa from (a) the complete record and (b) lower OIS-2, 3 and 4. The OIS-2/OIS-3 boundary is questionable, as marked in the diagram. Percentages of individual taxa are based on a sum of all arboreal and nonarboreal pollen. Subsums presented in the left column of the diagram are based on a sum of all pollen and spores. Pollen analysis by B.V. Belaya.

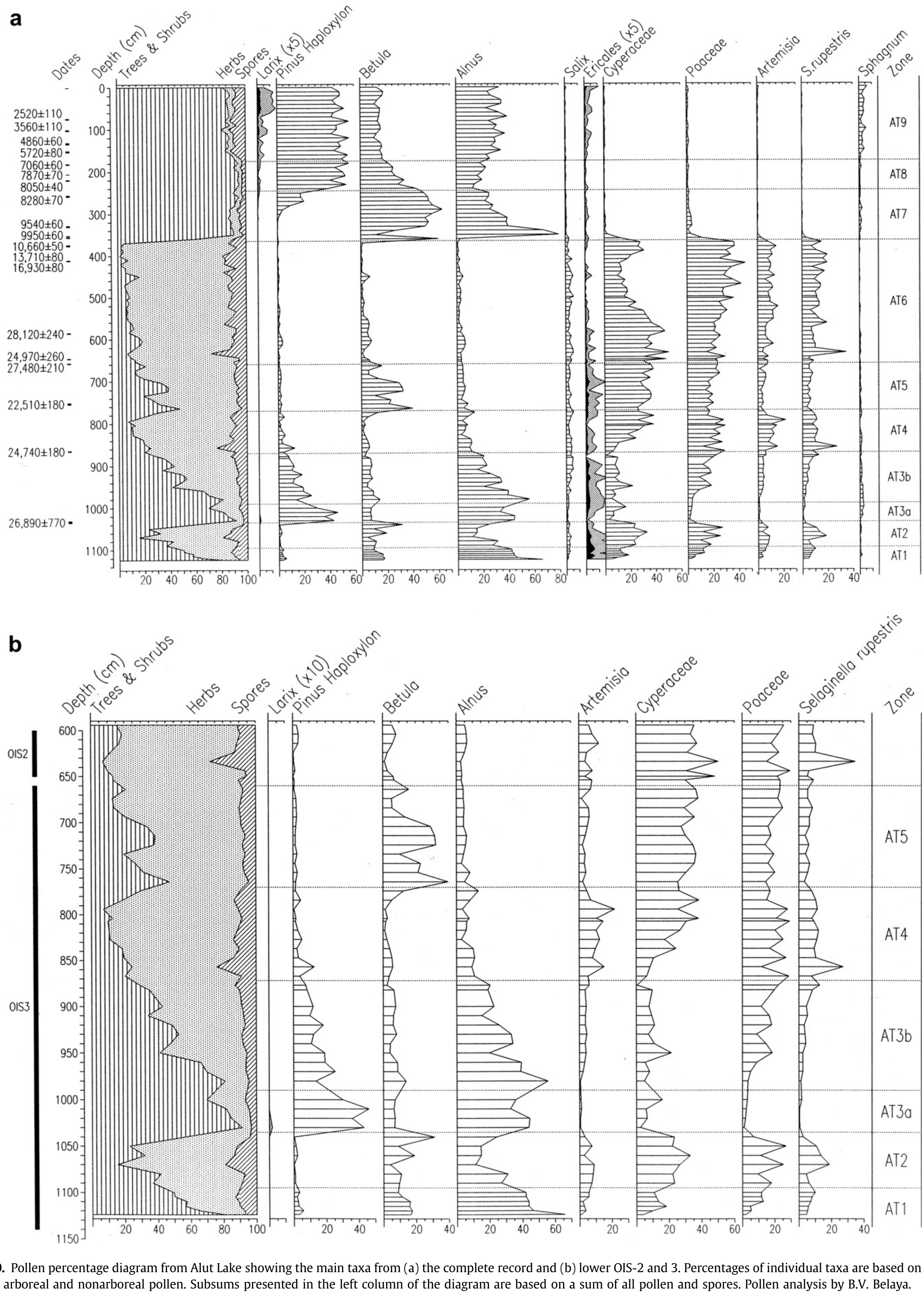

Fig. 9. Pollen percentage diagram from Alut Lake showing the main taxa from (a) the complete record and (b) lower OIS-2 and 3. Percentages of individual taxa are based on a sum of all arboreal and nonarboreal pollen. Subsums presented in the left column of the diagram are based on a sum of all pollen and spores. Pollen analysis by B.V. Belaya.

Assessing the extent of landscape changes from the El'gygytgyn palynological data is difficult, because the major OIS-3 taxa represent broad ecological ranges. However, the El'gygytgyn pollen record is generally consistent with a shift from "warm" to "cool" tundra or tundra-steppe as inferred by Sher et al. (2005) and Kienast et al. (2005). Other lake proxies provide additional support for this paleoclimatic trend. The El'gygytgyn data, within the limits of samples available, are more in agreement with MKH and not with Kind's (1974) interstadial scheme of fluctuating conditions. However the timing of a "warm" to "cool" shift between the upland (~46 ka) and lowland sites (~34 ka) is inconsistent. This inconsistency is almost certainly a function of inadequate dating control at El'gygytgyn Lake.

4.1.3. Comparison with other northern sites

Floral and faunal evidence from MKH indicate the persistence of tundra-steppe throughout OIS-3 and OIS-2. Sher et al. (2005) and Kienast et al. (2005) argued, primarily on the basis of large mammal and plant macrofossil data, that this biome was sufficiently productive and extensive to support significant numbers of Pleistocene megafauna. The OIS-3 pollen data from El'gygytgyn Lake suggest the adjacent northern uplands also supported herb-dominated plant communities, although modern analogs from interior Wrangel Island would indicate a rather depauperate landscape. Confirming either interpretation from other sites is difficult, because palynological data prior to the LGM are rare from northern WB. In the Yana-Indigirka-Kolyma lowlands, results from the Berelekh mammoth (Indigirka lowland; Lozhkin, 1990; Fig. 1), Khroma and Keremesit basins (Yana-Kolyma lowland; Ovander et al., 1987), and Bolshoii Lyakhovskii mammoth (Bolshoii Lyakhovskii Island; Lozhkin, 1990) parallel those from MKH. Scattered radiocarbon-dated horizons from sections farther east indicate tundra-steppe extended into northern Chukotka ~34–29 ka (Anderson and Lozhkin, 2001). Such similarity in interpretations suggests that a huge area of northern WB was tundra-steppe, occupying the contemporary coastal plain, adjacent uplands, and most likely the exposed continental shelf.

While the biological data agree that the predominant interstadial vegetation in northern WB was tundra-steppe or tundra, a question remains as to whether trees, particularly *Larix*, survived in small populations during all or part of the interstade. Prior to resampling by Sher and W.R. Eisner (reported in Sher et al., 2005), the Molotkhovsky Kamen site was considered the regional type-section for the Karginskii interval (Shilo et al., 1987). The initial vegetation reconstruction included *Larix*-tree *Betula* forest-tundra from 28–24.5 ka, tundra-steppe from 34–28 ka, and *Larix*-tree *Betula* forest from 48–34 ka. New radiocarbon dates disputed this chronology, resulting in the rejection of all previous dates in the 28–24.5 ka range. These latter were deemed to be too young, indicating that the most recent forest-tundra or forest was established in this area some time prior to ~40 ka with the "warm" horizons most likely dating to the last interglaciation.

Yet other evidence exists that suggests the interstadial landscape may not have been totally treeless. For example, two sites from the Indigirka Lowland, which are today in shrub tundra, suggest trees were present in northern WB. The Bol'shoy Khomus-Yuryakh site yielded pieces of *Larix* roots and cones radiocarbon-dated to ~41 ka, and the stomach contents of the Shandrin River mammoth attest to the presence of the deciduous conifer ~42–40 ka (Anderson and Lozhkin, 2001; Fig. 1). A recent study by Zazina et al. (2011) from the lower KoymaRiver also documents the presence of *Larix* during OIS-3. [ed].

Evidence is more ambiguous from MKH. Sher et al. (2005) concluded from insect and pollen data that *Larix* occurred as isolated individuals or small stands on Bykovsky Peninsula, perhaps establishing in greatest numbers from ~46 (or earlier)–35 ka. Andreev et al. (2002) argued for the absence of trees, saying that poor preservation indicated the *Larix* pollen was redeposited from older sediments and did not represent contemporary populations. However, Andreev et al. also noted the presence of rhizopods between ~42.5–33.5 ka from species that are found today in forest and forest-steppe of northeastern Asia (e.g., *Cyclopyxix puteus*, *Cyclopyxix kahli*). No *Larix* macrofossils appeared in the MKH samples, but aquatic remains indicate summer temperatures were at least 12 °C (Kienast et al., 2005), sufficient for *Larix* growth as suggested by the insect fauna

Kienast et al. (2005) discussed possible mechanisms that might account for the absence or scarcity of trees despite the warm summers. Increased continentality caused by lowered sea-levels would result in generally arid conditions in northern WB. The presence of steppic species and indicators of salty substrates and disturbed-ground at MKH provide strong evidence of such aridity. *Larix* like other conifers requires relatively mesic settings, and low effective moisture would have limited the tree to only the most favorable habitats (e.g., north-facing slopes; moist depressions as seen today in relict steppes of Yakutia). Low snow-cover could also have adversely affected *Larix* seedlings, exposing them to severe winter temperatures. Grazers, whose populations were likely significant on Bukovsky Peninsula, would have benefited from easier access to fodder during the relatively dry winters. However, the impact of the Pleistocene megafauna would likely have occurred through much of the year. For example, the presence in the fossil assemblage of *Carex duriuscula* at MKH suggests over-grazing and flattening of meadow plants, behavior that would harm young *Larix*. The importance of aridity and grazing for forest development is underscored by comparison to the early to mid-Holocene, another time of warm summers in northern Asia. Unlike OIS-3, a significant northern shift in Siberian treeline occurred with macrofossils of extralimital *Larix* dated to ~10–5 ka (Kremenetski et al., 1998). The effects of increased continentality/aridity related to lowered sea-levels were greatly reduced by this time (Lozhkin, 2002), resulting in mesic conditions more amenable for extensive tree establishment (Kienast et al., 2005). Furthermore, herds of large grazing mammals were diminished significantly by this time (Sher et al., 2005; Fig. 4).

Previously we argued that treeline was likely to have moved northward into the lowlands during OIS-3 (Anderson and Lozhkin, 2001), a conclusion based largely on the Molotkhovskiy Kamen site. This is contradicted by the re-analysis of Sher and Eisner in Sher et al. (2005), which finds that the data do not indicate a significant northward movement of forest or the forest-tundra boundary into the lowlands; however, the evidence from the sites discussed above and the new results of Zazina et al. (2011) is sufficient to argue that *Larix* did survive in the far north, at least as scattered stands, during much or some of OIS-3.

These cryptic refugia possibly acted as source areas for Holocene reforestation of northern river valleys, meaning *Larix* followed both northerly and southerly postglacial migration routes (Anderson et al., 2002a; Edwards et al., 2005; Binney et al., 2009).

4.2. The southern records

4.2.1. Elikchan Lake

Elikchan Lake provided the first long-term, continuous record of vegetation change in WB (Lozhkin and Anderson, 1995; Lozhkin et al., 1995; Anderson and Lozhkin, 2001; Fig. 8a). The Elikchan diagram shows variable but generally "warm" pollen assemblages that have a more moderate climatic signal compared to a stadial but generally cooler pollen spectra (except zone EL2g; Fig. 8b) than in an interglaciation. At the time of publication, dating the lower portion of the Elikchan core was problematic due to contamination problems within the University of Washington lab, and it was not possible to dispute Sher's (1991; Sher and Plakht, 1988) general claim that all pre-LGM "warm" deposits in Late Pleistocene sites from WB represent OIS-5. In Sher's interpretive framework, zones EL3 would correspond to OIS-2, OIS-3, and OIS-4, showing little variation between stadial and interstadial periods, and zone EL2 would represent OIS-5. Subsequent analysis of El'gygytgyn sediments, where a last interglacial record is confirmed, showed that the warmest pollen spectra occur at the beginning of the last interglaciation (i.e., OIS-5e; zone EG6, EG7; Fig. 7), in contrast to Elikchan where a climatic optimum is apparent during middle portions of the "warm" pollen assemblages. Although a strong absolute chronology is still lacking for Elikchan, the Alut record (see below), which spans the mid- to late OIS-3, strengthens the conclusion that Elikchan Lake is not of interglacial age. Furthermore, the Alut results confirm that fluctuations in vegetation and inferred climate in the Elikchan data are regionally robust and not simply idiosyncratic to the site.

The OIS-3 portion of the Elikchan diagram has been described in detail in Anderson and Lozhkin (2001), but we have modified the zonation to emphasize the fluctuating nature of the lower portion of the interstadial record (Fig. 8b). Establishing the existence of forest or forest-tundra near Elikchan Lake based solely on the presence of *Larix* pollen is problematic, because its extreme underrepresentation makes this taxon the interpretive equivalent of a macrofossil. To aid vegetation reconstructions, we have added percentages of *P. pumila* pollen that exceed 10% as a secondary criterion for inferring the presence of forested landscapes, based on modern pollen studies (Anderson et al., 2002b, 2002c; Lozhkin et al., 2002b). Even with these inferences, OIS-3 forest was likely more open than present, because herb pollen percentages are higher than in modern shrub tundra or forest-tundra. The Elikchan record can be divided into three intervals. Early OIS-3 (zones EL2a–EL2f; ~60–46.8 ka) is characterized with highly variable vegetation and climate. The middle portion (zones EL2g–EL2i; ~46.8–34.9 ka) is less variable with generally warm temperatures, including the interstadial optimum and establishment of present-day vegetation (zone EL2g; ~46.8–44.8 ka). Late OIS-2 (zone EL2j; ~34.9–30.8 ka) is characterized by a transitional vegetation leading to the full-glacial conditions of OIS-2 (zone EL3).

The earliest OIS-3 pollen data (EL2a ~60–57.6 ka; excepting samples with >40% *Alnus* pollen), although not having perfect analogs, approximate modern spectra from the coastal region of the Okhotsk Sea, indicating a mix of *Larix* forest and shrub tundra. *Larix* populated the valley bottom near Elikchan and likely extended up the nearby mountain slopes. Summer climate was perhaps slightly cooler than present, but still sufficiently warm to support significant conifer growth. *Larix* persisted into zone EL2b (~57.6–56.5 ka), implying a continuation of warm summers. However, *P. pumila* was reduced and deciduous shrubs increased near the lake. The zone EL2b fossil spectra are reminiscent of modern samples from *Larix*-graminoid meadows of tectonic depressions along the coast and from Elikchan-1 and Elikchan-2 lakes, which occupy a boggier substrate with more open vegetation than found near Elikchan-4 Lake. The absence or severe reduction of *P. pumila* is brief, as the evergreen shrub is once more common in zone EL2c (~56.5–55.6 ka). Although *Larix* pollen is absent in this zone, the high *Pinus* pollen percentages suggest the tree still grew near the lake. However, altitudinal treeline may have declined with forest or forest-tundra limited to the valley floor, suggesting a cooling of summer temperatures. Zone EL2d (~55.6–53.4 ka) represents an unusual pollen assemblage, lacking modern analogs. However, the absence of *Larix* and low percentages of *Pinus* pollen indicate conditions too severe to support taiga communities. Deciduous shrub tundra dominated the valley, perhaps with thickets of *D. fruticosa* near the lake shore. Conditions ameliorated in zone EL2e (~53.4–48.4 ka), and *Larix* re-established near the lake. The moderate percentages of *Pinus* and relatively high percentages of graminoid pollen suggest conditions may have been marginal for *Larix* growth. Deciduous shrub tundra probably dominated the landscape with restricted growth of the conifers. Conditions again deteriorated in zone EL2f (~48.4–46.8 ka), such that *Larix* and *P. pumila* were no longer present near the lake and vegetation probably was herb-dominated tundra.

In the middle interstade, the consistent appearance of *Larix* pollen in zones EL2g–EL2i (~44.8–34.9 ka) suggests a long-term presence of forest and warm summer temperatures in the Elikchan region. The zone EL2g (~46.8–44.8 ka) pollen assemblage mirrors that of modern pollen from Elikchan-4 and marks the interstadial thermal optimum and the onset of present-day conditions. *P. pumila* was likely reduced during zone EL2h (~44.8–41.2 ka), perhaps with the shrub retreating from the mountain slopes. The increase in *Pinus* pollen in zone EL2i suggests the presence of near-modern climate. This assemblage is similar to that of zone EL2a with a mix of *Larix* forest and shrub tundra.

Larix pollen disappears in late OIS-3 (zone EL2j, ~34.9–30.8 ka), although *P. pumila* pollen is >10%, suggesting summer temperatures that could support *Larix* growth. However, given the increase in Poaceae pollen and *Selaginella rupestris* spores and slight decreases in *Betula* and *Alnus* pollen, the landscape at best was forest-tundra and perhaps shrub tundra. In previous discussions, zone EL3 was considered as OIS-2, with a single sample suggesting a slight warming interval. The analysis of Alut Lake (see below) indicates a well-developed late OIS-3 *Betula* interval. Unfortunately, it was not possible to resample the Elikchan core to verify the high *Betula* percentage, but given other similarities of the cores and material from other sites in the region (see section 5.1), we think it likely that a final, moderate warming occurred prior to the occurrence of full-glacial conditions.

4.2.2. Alut Lake

Like in the Elikchan record, the OIS-3 assemblages (zones AT1–AT5) at Alut Lake are dominated by shrub taxa with a significant component of herb pollen (Anderson et al., 1998; Lozhkin et al., 2002a; Fig. 9a,b). As discussed above, the lack of *Larix* pollen, while making forest establishment less definitive, does not necessarily mean the trees were absent near the lake. Consequently, as compared to the Elikchan record, we rely more heavily on the >10% *P. pumila* pollen threshold for inferring the presence of forest.

Zone AT1 (~45–43.8 ka) represents a deciduous shrub tundra, probably dominated by *D. fruticosa* growing in dense thickets near the lake and possibly in shrub tundra on bordering slopes. This assemblage represents conditions that were sufficiently warm and wet to support *Duschekia*–*Betula* shrub tundra but were inadequate for the survival of *P. pumila* or *Larix*. Conditions likely worsened in zone AT2 (~43.8–41.3 ka) with the up-core decrease in pollen from deciduous shrubs and increases in graminoids and *Artemisia* pollen.

Relatively high percentages of *P. pumila* pollen characterize zone AT3 (~41.3–34.4 ka), which represents the warmest interval within OIS-3. Curiously, only one sample within this assemblage contains *Larix* pollen, although the taxon is consistently present in Holocene pollen spectra of zones AT7–AT9. The appearance of *Larix* pollen in zone AT3a (~41.3–39.4 ka), when combined with the maximum interstadial percentages of *Pinus* pollen, marks the OIS-3 climatic optimum. Vegetation was probably like modern. Zone AT3b shows a generally steady decline in *Pinus* and *Alnus* pollen with increases in Poaceae and *Artemisia* pollen. Because *Pinus* pollen >10%, the persistence of *Larix* forest is a reasonable inference. If present, the trees were almost certainly restricted to the valley bottom, with *Pinus pumila–Duschekia* tundra on mid-elevation slopes. The decrease in shrub pollen throughout zone AT3 reflects the likely compaction of an altitudinal shrub-tundra zone and a gradual climatic deterioration.

The cooling trend climaxed in zone AT4 (~34.4–30.2 ka), when pollen spectra approximate those of the LGM. *Larix* was probably absent from the valley, and shrubs were greatly restricted. The end of the interstade is marked with moderate summer warming (Zone AT5, ~30.2–25.6 ka). *Betula* shrub tundra or herb tundra with *Betula* thickets (*yerniki*) perhaps occupied much of the valley bottom. High pollen percentages of graminoids and forbs suggest non-woody plants were important in the vegetation probably at all elevations.

4.2.3. Comparison of Elikchan, Alut and other southern records

Although chronologies for the Alut and Elikchan diagrams do not totally concur (Fig. 10), biostratigraphic comparison of Alut and Elikchan diagrams indicates that the Alut record is younger, beginning during the mid-interstade. The high percentages of *Alnus* and Tree & Shrub pollen in zone AT1 correlates to the *Alnus*-dominated deciduous shrub tundra of late zone EL2d (high *Alnus* pollen) and lower EL2e. Prior to the interstadial optimum (zones AT3a, EL2g), herb-dominated and near-glacial conditions are registered at both sites (zones AT2, EL2f). The modern conditions of the thermal maximum are followed by forested landscapes and warm but generally declining conditions (zones AT3b, EL2h–j). The Elikchan record shows more marked variability in this interval, related to changes in *Pinus* pollen, as compared to the Alut record but minor peaks in *Pinus* in zone AT3b suggest a subdued parallel to those in the Elikchan record. The decline in *P. pumila* is followed by the establishment of stadial-like herb tundra (zones AT4, EL3 560–530 cm). The Alut diagram shows a well-defined *Betula* shrub tundra assemblage (zone AT5) that is only hinted at in the Elikchan record (520 cm). Although a single sample is not definitive, other palynological evidence from the Magadan region indicates that a slight warming occurred prior to the onset of OIS-2 (Anderson and Lozhkin, 2001), suggesting the rise in *Betula* pollen at Alut Lake is not necessarily an anomaly.

The fluctuating nature of OIS-3 vegetation and climate evident in these lake records is confirmed by data from exposures in southern WB (Anderson and Lozhkin, 2001). Valley settings in the southern interior have provided the greatest insight into interstadial conditions. The most detailed analysis is from the Kirgirlyakh mammoth site, Upper Kolyma, which is the type section for the Kirgilyakhsky cool interval, ~45–43 ka (Shilo et al., 1983; Lozhkin, 1991; Fig. 1). Three buried river terraces showed a range of microenvironments, as indicated by *Larix* megafossils, which were found in growth positions, to plant macrofossils from the mammoth's digestive tract, which have associations with contemporary subarctic and arctic communities. The vegetation was a mix of *Larix* woodland in the valley bottoms with *Betula* shrub and herb tundra on mid-elevation slopes. *P. pumila* and *D. fruticosa*, important elements in the modern vegetation, were likely absent. In coastal areas of the Okhotsk Sea, *Larix* forest probably was established from ~37–24 ka (see Anderson and Lozhkin, 2001), while high-shrub tundra occupied regions of southern Chukotka from ~42–27 ka (Lozhkin et al., 2000).

A newly analyzed pollen record from Lake Billyakh in the western foothills of the Verkhoyansk Range provides the strongest documentation of interstadial vegetation and climate changes for southwestern WB (Müller et al., 2010; Fig. 1). Biome-based vegetation reconstructions suggest that tundra and steppe communities were prevalent throughout the interstade. Müller et al. noted *Larix* likely grew near the lake based on the consistent amounts of its pollen and on the presence of macrofossils. However, establishment of extensive forest is not indicated by biome analyses until the Holocene, the latter including both *P. sylvestris* and *Picea obovata*. Pollen from these evergreens is rare during the interstade, but percentages of *Larix* and tree *Betula* pollen are similar between OIS-3 and the Holocene, suggesting these deciduous trees were not uncommon. Scarcity of *Pinus* and *Picea* would be reasonable under arid conditions. However, the absence of *Larix* and tree *Betula* would be harder to explain if summers exceeded 12 °C, which is likely given inferred temperatures for northeastern WB. If conditions were extremely arid (e.g., due to increased continentality), reconstructions of a steppe biome would be expected for all of OIS-3, although prior to ~30 ka the reconstructions are dominated by tundra biomes. We suggest as an alternative interpretation that *Larix* forest or woodland with occasional tree *Betula* probably grew along river valleys and protected lowland sites in southwestern Beringia during the mid- to late-interstade.

Müller et al. (2010) concluded that greater pollen concentrations, pollen diversity and numbers of tree and shrub taxa suggested conditions were somewhat warmer and/or moister ~47–28 ka as compared to latter parts of the interstade (note: they place the OIS-3/OIS-2 boundary at ~22 ka). However, they viewed OIS-3 as being generally cool and arid compared to the present-day, perhaps with slight amelioration at ~44, 34, and 30 ka.

While we agree that there is no evidence for warmer or similar to present climates during OIS-3 in this area of WB (see Kind, 1974; Anderson and Lozhkin, 2001), we think the Billyakh record indicates more variable conditions than suggested by Müller et al. For example, examination of total tree and shrub pollen shows periods of increase from ~35 to 33.5 ka and from 31.5 to 28 ka, with periods of decreased arboreal pollen from ~47 to 35 ka, 33.5–31.5 ka, and from 28 to 22 ka. Such palynological changes could indicate shifts in summer temperature making the Billyakh sequence of cool–warm–cool–warm–transition into OIS-2, similar to that described in other parts of Siberia (Kind, 1974; Anderson and Lozhkin, 2001). However, the chronologies are not equivalent, and we think that these changes are more likely related to shifts in aridity not only temperature, with low arboreal pollen marking times of decreased effective moisture. The Billyakh pattern does not approach the magnitude of change seen at Elikchan and Alut lakes, where precipitation and temperatures were adequate at times during OIS-3 to support modern or near-modern vegetation communities.

5. Discussion

Patching together an understanding of past spatial patterns and temporal trends for the WB interstade is challenging, because of the general paucity of sites, their uneven geographic distribution, and issues of dating control. However, the differences between the MKH-El'gygytgyn and the Elikchan-Alut records (Fig. 10) are striking and not necessarily inconsistent with data from less continuous OIS-3 records (Anderson and Lozhkin, 2001; Sher et al., 2005). Much in the paleoenvironmental history of necessity remains speculative and what we offer below is a framework for further study. In this discussion, we first consider the patterns within the paleodata and then explore their paleoclimatic implications.

5.1. Chronological limitations

General trends for the early, middle, and late interstade are described below, but chronologies, even in the strongest WB records, are insufficient to present an exact temporal scheme for OIS-3. Thus, we will use the more general time divisions of the early (~60–48 ka), middle (~48–36 ka) and late (~36–25 ka)

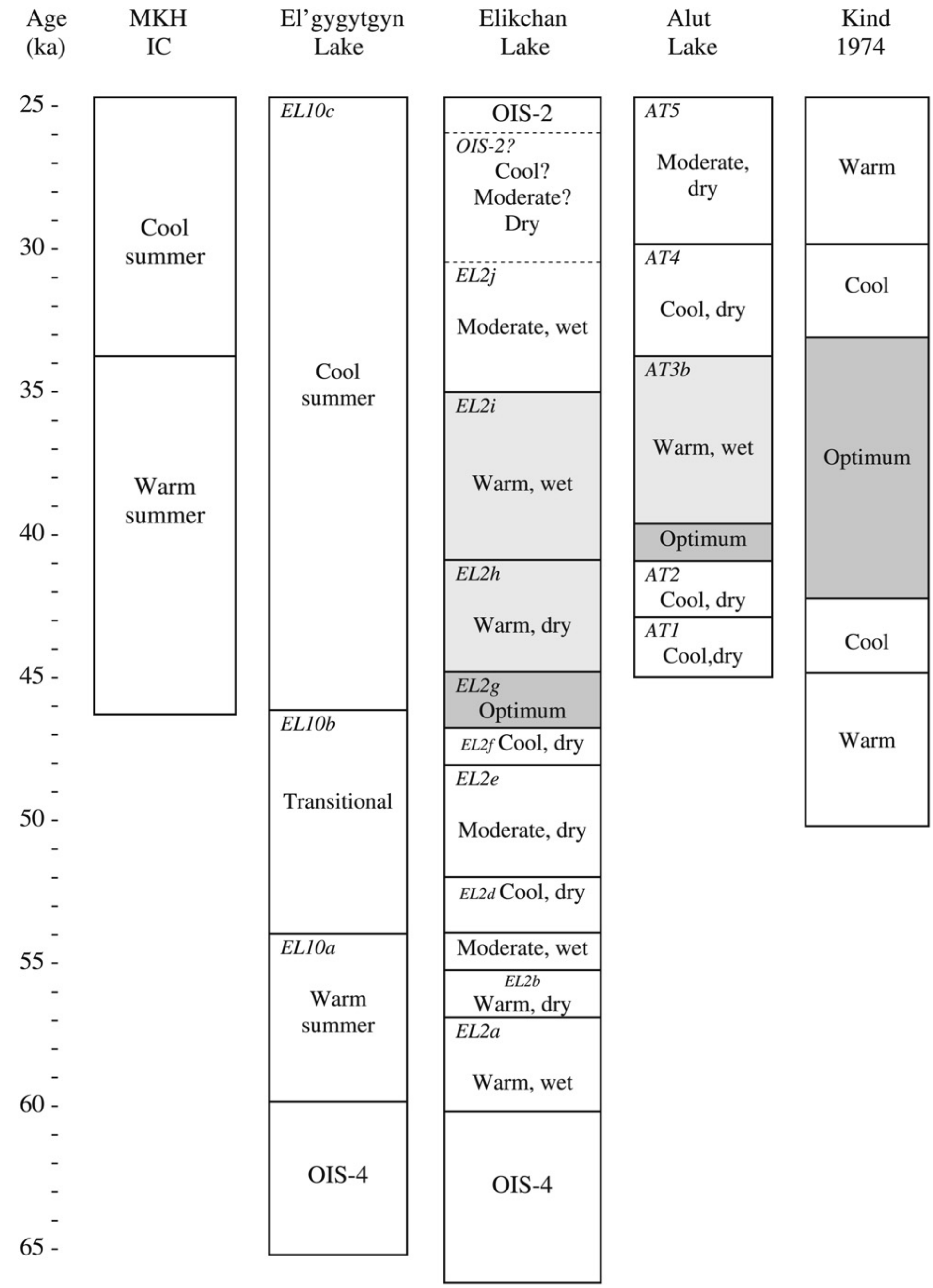

Fig. 10. Comparison of paleoclimatic trends from Mamontovy Khayata Ice Complex (MKH), El'gygytgyn Lake, Elikchan Lake, and Alut Lake. Kind's (1974) scheme from Eastern Siberia is given as reference. Dark gray shading indicates modern conditions of the climatic optimum, whereas light gray denotes times, which while warm were likely slightly cooler than present.

interstade. Even with the application of what certainly are too simplified age-models (see section 3), some broad consistencies are evident. For example, times of relatively moderate vegetation and warmest climates occurred during the mid-interstade in both lacustrine and nonlacustrine sites (see section 4). Yet the specific timing of vegetation and climatic changes differs within the south (e.g., between Elikchan and Alut lakes), within the north (e.g., between MKH and El'gygytgyn Lake) and between northern and southern WB (Fig. 10). Somewhat surprisingly, especially given the compelling critique of Sher (Sher and Plakht, 1988; Sher, 1991; Sher et al., 2005), the composite chronology presented by Kind and the chronostratigraphy of the Alut site are remarkably similar, as is the general climatostratigraphy (warm–cool-optimum-cool–warm) between southern WB and the Yenisei valley. However, the climatic variability of early OIS-3 represented at Elikchan Lake is absent from Alut Lake and within the Yenisei records, suggesting that Kind's scheme may more accurately represent the mid- to late-interstade rather than all of OIS-3. Even with these caveats, temporal patterns clearly vary between northern and southern WB with greater frequency of change in the south.

5.2. Interstadial vegetation change in WB

During OIS-3, the northern tundra comprised a greater portion of WB than occurs today. This herb-dominated vegetation extended significantly northward, due to lowered sea-levels, and expanded southward, probably because of drought stress that prevented or greatly limited forest establishment. This widespread tundra-or tundra-steppe biome is reduced today to small relict populations found throughout WB (Yurtsev, 1982), but during the Late Pleistocene this plant community is postulated to be a much more productive vegetation than is present in the contemporary tundra (see Sher et al., 2005). *Larix* possibly occurred in scattered stands in northern WB, but the main latitudinal forest-tundra boundary likely lay to the south of its modern position for all of OIS-3.

In contrast to the rather monolithic nature of the northern vegetation, the paleobotanical records from southern WB suggest a much more dynamic vegetation history. *Larix* forests, perhaps with tree *Betula*, occupied mountain valleys in the south. Modern or near-modern distributions were probably achieved in the Magadan region during the OIS-4–OIS-3 transition and the mid-interstade. However, at other times treed landscapes were limited to protected habitats. Deciduous shrub tundra, herb tundra or steppe (southwestern areas only) dominated in the severest periods. The greatest magnitude of change occurred in southeastern Beringia at the end of the early interstade, with a shift from nearly full-glacial tundra to modern forests of the interstadial optimum. The general variability in the south suggests environmental conditions were such that only slight changes altered the vegetation system either toward tundra/steppe or forest. The sensitivity of such communities was also evident during the Holocene when similarly rapid changes occurred near treeline (e.g., MacDonald et al., 1993). In the Magadan region, mid- to late OIS-3 was characterized by more stable vegetation with a gradual deterioration of forest to herb tundra. The establishment of *Betula* shrub tundra and forest-tundra in the southeast signals a last stage of somewhat moderate conditions prior to the onset of OIS-2. In southwestern WB, the vegetation changes were not as dramatic with the most stable period occurring during the mid-interstade.

The interstade of southeastern WB is unusual in the nature of its transitions. For example, the LGM-Holocene transition is characterized across WB by a consistent, sharp, and rapid change from herb- to *Betula*-dominated pollen assemblages (Lozhkin et al., 1993). The OIS-4–OIS-3 transition appears no different in its rapidity, but it is dissimilar in the nature of the vegetation changes. During the most recent shift from cool to warm climates (i.e., late glaciation to mid-Holocene), the biostratigraphy indicates the order of establishment as *Betula*–*Alnus*–*Larix*–*Pinus pumila*. In contrast, the earliest OIS-3 (zone EL2a) is marked by an apparently simultaneous appearance of *Larix* and all three of the major shrub taxa. For establishment of all these taxa, it would require that summer temperatures shifted from <10 °C (required by shrub *Betula*) to >12 °C (required by *Larix* and *P. pumila*) and/or effective moisture and winter snow depths increased from drier glacial times. Such a pattern suggests that the magnitude of change during the OIS4-OIS-3 transition was greater than the temperature and precipitation shifts that occurred during the OIS-2–OIS-1 transition.

Although *Larix* forest or forest-tundra was present in southern WB at various times during OIS-3, herb-dominated communities were an important component of interstadial environments. Percentages of graminoid pollen are high as compared to modern samples (Lozhkin et al., 2001, 2002b; Anderson et al., 2002b, 2002c), suggesting the southern tundra, like in the north, was not the exact equivalent of any seen today. However, the pollen assemblages, particularly in the Magadan region, include significant percentages of shrubby taxa. Such spectra suggest the presence of either shrub thickets or shrub tundra, in contrast to the herb-dominated landscapes inferred for northern WB. Unlike OIS-3, the tundra pollen assemblages from OIS-2 and OIS-4 vary little across WB, indicating a uniformity of stadial landscapes and climate over this vast region. The spatial complexity of OIS-3 marks it as unique within the Late Pleistocene, suggesting an equally complex set of mechanisms and feedbacks responsible for the observed spatio-temporal patterns.

5.3. Climatic implications of the paleodata

As with the vegetation, climatic histories appear to differ between northern and southern WB (Fig. 10). While such differences may be expected over such a vast subcontinent, the extent that these histories diverge is much greater than anything experienced in the LGM, late glaciation, or Holocene of Beringia. After describing paleoclimatic patterns inferred from the paleobotanical data, we explore some possible paleoclimatic forcings, but improving knowledge about the mechanisms and feedbacks responsible for shaping the WB paleoclimates will likely require modeling applications as was done for Europe (van Andel, 2002).

5.3.1. General paleoclimatic patterns

Climate in northern WB appears relatively stable during OIS-3 with only a subtle shift in summer conditions occurring during the late interstade. Southern areas experienced more variable conditions in terms of frequency of climatic events, with the magnitude of the climatic changes greatest in southeastern WB. The Elikchan record indicates that this variability peaked during the early interstade, with climates fluctuating from warm–wet (i.e., near interglacial conditions) to cool–dry (i.e., near full-glacial conditions). Preliminary age-schemes for the southeast suggest these climatic events lasted from 0.9 to 5 kyr. Conditions appear to stabilize during the mid-interstade, in the sense that the Magadan forests persisted in the region for perhaps ~16 kyr, beginning with the thermal optimum.

The presence or absence of full-interglacial conditions during OIS-3 has been a point of consistent disagreement in the Karginskii debate (e.g., Kartashov and Baskovich; Kind and Sher). With the exception of the Shandrin mammoth and Bol'shoy Khomus Yuriyakh sites, support for a period as warm or warmer than modern is missing in northern WB. However, evidence of an interstadial climate similar to the present day is strong in southeastern WB. The Elikchan record, in particular, confirms Kind's proposal that conditions in this region were similar to modern during at least a portion of the interstade. The Magadan lake records, conversely, do not support Sher's idea that all pre-LGM "warm" horizons should be assigned to OIS-5. Radiometric ages aside, the sequence or timing of maximum warmth differed between OIS-3 and OIS-5. That is, the warmest OIS-5 climates occurred during the early interglaciation, but the OIS-3 thermal optimum appeared in the middle portion of the interstade (cf Figs. 7 and 8). This "late" occurrence of a climatic maximum also contrasts with the late glaciation-early Holocene, when the thermal maximum happened early in the climatic transition (see Edwards et al., 2005).

5.3.2. Seasonality

Sher and colleagues were influenced greatly by working in an area where the northern extent of exposed shelf turned sites that currently are located near the coast to ones that existed well in the interior of the Beringian subcontinent. Under this scenario, a more continental climate would be expected, with greater seasonal temperature variability (i.e., relatively cooler winters and warmer summers) and decreased effective moisture. Multiple lines of evidence from MKH indicate OIS-3 summers in northern WB were slightly warmer than present, but winters were much cooler than today. The presence of boreal aquatics suggests summer temperatures of at least 12 °C and possibly exceeding 15 °C (Kienast et al., 2005). Occurrences of steppe insects also indicate warmer than modern summers and marked aridity (Sher et al., 2005). Plant and insect remains associated with the MKH steppe communities are capable of surviving relatively severe winters. Low values for ^{18}O and ^{2}H extracted from nearby ice wedges provide additional evidence of severe winter temperatures (Meyer et al., 2002). Plant macrofossils associated with pioneering plant communities and from *Kobresia* meadows, in addition to being cold-resistant, indicate areas of thin or no snow-cover in the north (Kienast et al., 2005). Tree seedlings and dwarf shrubs need sufficiently deep snows to protect their buds from low temperatures and snow abrasion, so their rarity on the northern landscape provide indirect evidence of dry winters.

Steppe species of plants and insects, halophytic species, and other indicators of fluctuating ground water found at MKH suggest effective moisture was low during the warm season as well (Kienast et al., 2005; Sher et al., 2005). Despite temperatures that could sustain coniferous taiga (i.e., >12 °C), summers were likely too dry for the widespread establishment of forest species. In areas of relict steppe in modern Yakutia, trees are found in limited numbers on north-facing slopes or in depressions where water has accumulated (Yurtsev, 2001). It is not unreasonable to think similar settings in northern WB supported isolated stands of *Larix* during the interstade (Sher et al., 2005).

The impact of lowered sea levels would have been more variable in southern WB. Certainly, the present-day continental climate of southwestern WB would have been exacerbated by the northern extension of the arctic coast. Only a small area of continental shelf was exposed in southeastern WB, making increased continentality a negligible factor affecting interstadial climates (Lozhkin, 2002; Brigham-Grette et al., 2004; Fig. 2). The presence of *Larix* in southern WB implies mean July and January temperatures as warm or warmer than 12 °C and −11.6 °C, respectively (Andreev, 1980; Kozhevnikov, 1981). Seasonal or annual arid conditions in the interior likely limited the trees to only the moistest sites (see section 4.1.3). Establishment of *Larix* and *P. pumila* require a minimum mean annual precipitation of 150 mm (Andreev, 1980; Kozhevnikov, 1981), but the seasonal distribution of that precipitation is crucial for the survival of *P. pumila*. The evergreen shrub, which today grows to heights of 3–4 m in some areas of WB, requires a sufficient snow-depth to protect its leaves from winter desiccation. To aid in its protection, *P. pumila* takes a prostrate form in autumn, increasing the chances that its branches will be completely snow-covered during the frigid months.

Even during many of the "warm" interstadial intervals, the high percentages of graminoid pollen in the southern records suggest that warm-season conditions remained too cool and/or too dry to support extensive forest or shrub-tundra growth in the lowlands or on lower mountain slopes. During those times when *Betula* shrub tundra was the dominant vegetation, summer temperatures were at least 10 °C but <12 °C and growing season moisture decreased from forested conditions (Berg, 1950). When herb-dominated tundra prevailed, summer temperatures were <10 °C and/or effective moisture was so low that growth of woody species was severely limited. Steppe communities inferred at times in southwestern WB could survive under warm summers but here, too, drought would limit the extent of woody taxa.

Although summer temperatures perhaps were near modern during the warm interstadial events documented in the southeastern sites, cool-season precipitation, as indicated by *P. pumila* pollen, was not constant during OIS-3. The Elikchan record suggests that intervals of both summer warm–winter wet (e.g., zones EL2a, El2i) and summer warm–winter dry (e.g., zones EL2b, EL2h) occurred during the interstade, although cool intervals (e.g., zones EL2d, EL2f) were consistently dry (Fig. 10). Furthermore, these data suggest that early OIS-3 may have been generally drier than the mid- to late interstade. Multiple proxies from MKH indicate that effective moisture was at its highest from ~34–46 ka, with drier summers characterizing late OIS-3.

5.3.3. Mechanisms of paleoclimatic change in Beringia

Sher appreciated the fact that understanding Late Pleistocene environments of Beringia required new approaches and the shedding of old schemes that spoke of general warming and cooling and of mean annual conditions (Sher et al., 2005). In his conceptual paleoclimate model, Sher envisioned seasonal variability, as related to changes in sea level, as key for unraveling WB paleoclimatic patterns. In another conceptual model, Bartlein et al. (1991, 1998) explored the importance of seasonal insolation, marine conditions, and sea level on Eastern Beringian (Alaska to northwestern Canada) climates focusing on the last 18 ka. Based on the interaction of these forcing factors, they postulated that OIS-3 in Eastern Beringia would have been characterized by "very cold, continental conditions year round, and…variability through time probably was low as well" (Bartlein et al., 1991, p. 80), a conclusion more in line with Sher's thinking than with Kind's. However, the data from southern WB do not support such stability, suggesting a certain distinctiveness to the climates of OIS-3 as compared to other times during the Late Pleistocene.

Computer models have shown the importance of SSTs for affecting various aspects of the climate system (e.g., Kutzbach et al., 1993). During OIS-3, generally lower than present SSTs at northern high latitudes (Morley et al., 1987) should have aided regional cooling and offset insolation-driven warming (Bartlein et al., 1991). However, waters of the northwestern Pacific and marginal seas did not all remain uniformly cool throughout the interstade (Voelker and Workshop participants, 2002). For example, Gorbarenko et al. (2004) noted fluctuating conditions in the Okhotsk Sea during OIS-3 that suggested intervals of relatively warmer and cooler waters. Such variation would likely have greatest impact in coastal areas of southern WB, with little or no effect to the north or in the southern interior. Currently, the chronological control of the terrestrial records is inadequate to make rigorous comparisons to the marine records and requires additional dating. Despite this limitation, it is interesting to note that the duration (albeit not the actual timing) of the marine events are of similar length as seen in the vegetation.

Other models illustrate the importance of sea ice in the paleoclimate system. In these simulations, increased summer radiation during the late glaciation and early Holocene resulted in warming of SSTs from autumn to spring (Gallimore and Kutzbach, 1995). Relatively warm seas reduced the thickness and extent of sea ice, which subsequently led to warming over land during fall and winter (Kutzbach and Gallimore, 1988; Mitchell et al., 1988; Kutzbach et al., 1991). The impact of such seasonal shifts is potentially great in WB. For example, Anderson et al. (2010) postulated that variations in timing of autumn snowfall associated with these changing insolation and marine conditions explain the persistence of *P. pumila* during the LGM in southwestern Beringia and its disappearance during the postglacial thermal maximum. A similar mechanism might have played some role in southeastern WB. However, the frequency of vegetation change is greater as compared to insolation variability (Fig. 3), suggesting regional climate was not driven simply by insolation and/or its effects on sea ice.

Sher et al. (2005) postulated that characteristics of both summer and winter seasons were the primary determinants of interstadial vegetation. For Sher, this seasonality was driven by lowering of sea level, which resulted in increased continentality for sites in northern and central WB. Global ESL curves indicate that while lower than modern, interstadial seas were considerably higher than during OIS-2, roughly −60 m during early OIS-3 and −80 m for the mid- to late-interstade as opposed to the −120 m of the LGM (Lambeck et al., 2002; Brigham-Grette et al., 2004; Fig. 3). Even at these relatively higher lowered levels, vast areas of shelf remained exposed. As with insolation, fluctuations in sea levels do not correspond to times of climatic change in either northern or southern sites. However, in southeastern WB the interval of variable climates during early OIS-3 approximates the period of relatively high seas and insolation; lowered sea-levels and insolation are associated with both the interstadial optimum and an interval of more stable climate during the mid- to late-interstade. The exposed shelf along the northern Okhotsk Sea was minimal as compared to other areas of Beringia (Fig. 2), but the influence on regional environments of a closed Bering Strait must have been great. The existence during OIS-3 of such a megacontinent, with the joining of Asia and North America, in combination with changes in other global forcings, would certainly alter synoptic patterns as we understand them over the late glaciation and Holocene, evidently leading to the relative climate stability of northern WB, highly variable conditions of the southeast, and environments of the southwest with lesser magnitude variability than near the southern coast.

The instability of interstadial environments in southern WB occurs on suborbital scales and bring to mind DO and Heinrich events documented in the Greenland ice cores and North Atlantic marine records (Heinrich, 1988; Johnsen et al., 1992; Dansgaard et al., 1993). Model simulations and paleodata indicate that DO or Heinrich-related climatic cycles have far-reaching implications (e.g., Gonapolski and Rahmstorf, 2001; Voelker and Workshop participants, 2002; Claussen et al., 2003). For example, CLIMBER-2, an Earth system model, indicated an increase in precipitation in northern high latitudes during warm phases of OIS-3 related to the northward shift of the intertropical convergence zone (Claussen et al., 2003). Conversely, regional precipitation decreased during cool phases. The fluctuations in the Elikchan pollen diagram particularly are reminiscent of the instability seen in the North Atlantic records. While preliminary comparisons of DO events and the pollen time series (Fig. 3) are suggestive, analysis of the Elikchan core is currently insufficient to hypothesize mechanistic links between the North Atlantic and WB (Brigham-Grette et al., 2004).

As mentioned above, understanding the influences of various forcing factors on WB climate will require experiments with a regional paleoclimate model. Interestingly, an OIS-3 mesoscale model suggest that SSTs and/or sea ice were dominating influences on interstadial conditions in Europe (STAGE 3 project; Barron and Pollard, 2002; Huntley et al., 2003; Alfano et al., 2003), factors that are likely of equal import in Beringia. Huntley et al. (2003) suggested that such conditions resulted in a climate system that hovered between "warm" and "cool," a situation that is reminiscent of southeastern Beringia. The STAGE 3 Project concluded, as did Sher, that vegetation characteristics are determined by both summer and winter climates, rather than predominantly by summer conditions. The paleodata from WB indicate that OIS-3 climatic patterns were unlike others of the past 125 ka, and the conceptual and computer models suggest that marine conditions, including sea level, may have been primary determinants in those patterns in Beringia and beyond.

6. Summary

The puzzle that has been the Karginskii interval is perhaps closer to resolution with the recent analyses of records from MKH and El'gygytgyn Lake (northern WB) and from Elikchan and Alut lakes (southern WB). A reassessment of the data suggests that both Kind (1974) and Sher (Sher et al., 2005) were correct in their evaluations of the last interstade. In WB, the generally stable climate and vegetation proposed by Sher typifies northern areas, whereas the more variable conditions documented by Kind in Eastern Siberia are more similar to observed changes in southern WB. Interstadial landscapes of northern WB were characterized by a variety of tundra or tundra-steppe communities, although small populations of *Larix* probably survived in well protected sites. In contrast, steppe (southwest only) herb and shrub tundra, *Larix* forest-tundra, and modern *Larix* forest (southeast only) occurred at various times in southern WB. The southern records further indicate the presence of a thermal maximum during mid-OIS-3, although this evidence is weaker in southwest WB. Indication for a similar event is lacking in the north. The Elikchan pollen diagram suggests that climates were more unstable with greater magnitude of change during early OIS-3 as compared to later in the interstade. Across WB, the paleobotanical data indicate that vegetation was sensitive to shifts in seasonal precipitation and not summer temperature alone. In the southeast, this sensitivity is evidenced by shifts from forest to tundra and from *Larix* to *Larix*–*Pinus pumila* forest. In the interior, increased continentality and low effective moisture limited plant communities to only those most adapted to droughty conditions. Both computer and conceptual models suggest that changes in marine conditions, including sea level, were likely key drivers in the regional climate history.

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