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Last glacial vegetation reconstructions in the extreme-continental eastern Asia: Potentials of pollen and *n*-alkane biomarker analyses

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ABSTRACT

The current study presents quantitative reconstructions of tree cover, annual precipitation and mean July temperature derived from the pollen record from Lake Billyakh (65°17′N, 126°47′E, 340 m above sea level) spanning the last ca. 50 ka (ca. 50,000 cal yrs). The reconstruction of tree cover suggests presence of woody plants through the entire analyzed time interval, although trees played only a minor role in the vegetation around Lake Billyakh prior to 14 ka BP (<5%). This result corroborates low percentages of tree pollen and low scores of the cold deciduous forest biome in the PG1755 record from Lake Billyakh. The reconstructed values of the mean temperature of the warmest month ~8–10 °C do not support larch forest or woodland around Lake Billyakh during the coldest phase of the last glacial between ~32 and ~15 ka BP. However, modern cases from northern Siberia, ca. 750 km north of Lake Billyakh, demonstrate that individual larch plants can grow within shrub and grass tundra landscape in very low mean July temperatures of about 8 °C. This makes plausible the hypothesis that the western and southern foreland of the Verkhoyansk Mountains could provide enough moist and warm microhabitats and allow individual larch specimens to survive climatic extremes of the last glacial. Reconstructed mean values of annual precipitation are about 270 mm during the last glacial interval. This value is almost 100 mm higher than modern averages reported for the extreme-continental north-eastern Siberia east of Lake Billyakh, where larch-dominated cold deciduous forest grows at present. This suggests that last glacial environments around Lake Billyakh were never too dry for larch to grow and that the insufficient summer warmth was the main factor, which limited tree growth during the last glacial interval. The *n*-alkane analysis of the Siberian plants presented in this study demonstrates rather complex alkane distribution patterns, which challenge the interpretation of the fossil records. In particular, extremely low *n*-alkane concentrations in the leaves of local coniferous trees and shrubs suggest that their contribution to the litter and therefore to the fossil lake sediments might be not high enough for tracing the Quaternary history of the needleleaved taxa using the *n*-alkane biomarker method.

1. Introduction

Knowledge of past changes in vegetation serves for a better understanding of archaeological data (e.g. Dolukhanov et al., 2002; Tarasov et al., 2007a), the earth climate system and carbon cycle (e.g. Prentice et al., 1992; Kleinen et al., 2011) and genetic diversity (Semerikov et al., 1999; Petit et al., 2008), and can help to build up current predictions and conservation strategies. The need for accurate vegetation cover datasets is particularly acute for the last glacial–interglacial interval, given the critical role of surface-atmosphere feedbacks on regional climate dynamics and global biogeochemical cycles (Williams et al., 2011). However, the current knowledge about last glacial vegetation in many regions of the world is limited due to the lack or scarcity of palaeobotanical records (e.g. Prentice et al., 2000). The poor spatial coverage and dating control of the available records may lead to contradicting interpretations of the composition and density of glacial vegetation cover, and of the last glacial climate and environments. All mentioned problems are well pronounced in continental Asia (including vast areas of Siberia), which was not covered with ice

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during the last glacial (e.g. see Tarasov et al., 2000, 2007b; Müller et al., 2010; Lozhkin and Anderson, 2011 for discussion and references).

Abundant woody macrofossils from northern Asia confirm the advance of boreal trees almost to the current arctic coastline between 9 and 7 ka (MacDonald et al., 2000; Binney et al., 2009). However, the frequently discussed question, whether trees could continuously grow there during the coldest intervals of the last glacial, remains without an answer. Some authors (e.g. Ray and Adams, 2001) have doubted the existence of discontinuous vegetation cover in most parts of northern Asia and suggested desert environments with less than 2% of the ground covered by vascular plants during the last glacial maximum interval (LGM: ~25–17 ka BP). Others argue for a continuous forest belt (e.g. Crowley, 1995; Kaplan et al., 2003) or scattered boreal trees and shrubs refugia (Grichuk, 1984; Frenzel et al., 1992) in Siberia between 55 and 60°N during the LGM. The more recent syntheses and re-analyses of the available pollen and archaeological charcoal data (Vasil'ev et al., 2002; Brubaker et al., 2005; Tarasov et al., 2007b; Williams et al., 2011) from Siberia also conclude that (i) small populations of boreal trees and shrubs were capable of surviving long periods of harsh climate; and suggest (ii) a mosaic pattern of the LGM vegetation in the Asian mid-latitudes with a substantially reduced and likely discontinuous forest belt.

The recently published last glacial–interglacial pollen (Müller et al., 2009, 2010) and plant macrofossil records from Lake Billyakh (65°17′N, 126°47′E; 340 m a.s.l.) and nearby Dyanushka Peat section K7/P2 (Tarasov et al., 2009; Werner et al., 2010) provided the first unequivocal evidence of uninterrupted growth of larch in the extreme-continental eastern Asia ~50–26 ka and ~15–0 ka BP, but left open the question 'whether larch could survive the much colder and drier LGM interval ~140–170 km south of the Arctic Circle or its postglacial expansion occurred from more southern refugia'. Müller et al. (2010) suggested that application of the alkane biomarker analysis of the lake sediments may help to answer this question and verify the presence of trees.

Alkane biomarkers in soils, peat and lake sediments have been successfully used to reconstruct changes in vegetation cover (e.g. Cranwell, 1973; Schwark et al., 2002; Ishiwatari et al., 2009; Zech, 2006; Zech et al., 2008, 2009, in press). The long-chain alkanes originate from the leaf epicuticular waxes of land plants (Eglinton and Hamilton, 1967; Kolattukudy, 1976), with the homologues n-C_{27} and n-C_{29} alkanes dominating in most trees and shrubs, and n-C_{31} and n-C_{33} dominating in most grasses and herbs (e.g. Maffei, 1996). This approach was applied to the fossil sediment samples from extreme-continental Siberia in order to reconstruct relative changes in wood coverage during the late Quaternary (Werner et al., 2010; Zech et al., 2010). Comparison of the pollen and n-alkane records from the Tumara palaeosol sequence southeast of Lake Billyakh gave grounds for the hypothesis (Zech et al., 2010) that the pollen-based reconstruction might underestimate the wood coverage of glacial landscapes, mainly due to the poor preservation and dispersion of larch pollen (Müller et al., 2010 and references therein). A similar hypothesis was proposed by Malaeva (1989), who suggested that during the last glacial, forestation in Mongolia was greater than today as a result of cooler summers and lower evaporation. Larch is indeed the most abundant and often the only tree growing in both regions (Gerasimov, 1964). It tolerates extremely low winter and moderately low summer temperatures (CAVM-Team, 2003; MacDonald et al., 2008). Therefore, underrepresentation of larch in the pollen records can substantially affect the reconstructions of past vegetation and climate. On the other hand, the n-alkane biomarker approach also needs to be tested using characteristic plants representative of modern and past vegetation communities in the study region.

The current study (i) applied the n-alkane analysis to the sediment from Lake Billyakh and to a representative collection of modern plants from the region; (ii) performed woody cover and climate reconstructions using the recently published Lake Billyakh pollen record (Müller et al., 2010) and the quantitative approaches presented in Tarasov et al. (2007b, 2009) in order to discuss the presence/absence of woody plants in extreme-continental eastern Asia during the last glacial interval.

2. Data and methods

2.1. Site setting and modern environments

Fossil sediment samples analyzed for pollen and n-alkanes and used in this study came from Lake Billyakh (Fig. 1). The lake (65°17′N, 126°47′E) occupies an intermountain depression on the western macroslope of the Verkhoyansk Mountain Range, which rises up to 2389 m a.s.l. in its central part. Lake Billyakh has an area of ~23 km^2, an average water depth of 8 m and a maximum depth of about 25 m (Müller et al., 2009). The lake is situated at about 340 m a.s.l., but the mountain ridges surrounding the lake reach 700–950 m in elevation. A small stream flows from the southern part of the lake and reaches the Lena River ~90 km southwest. The lake is situated within an area of continuous permafrost, several hundred meters thick (Gavrilova, 1993), and experiences an extreme-continental climate with very cold, long winters (mean January temperatures around −40 °C) and short but relatively warm summers (mean July temperatures ~15–19 °C). Annual precipitation sums reach 300–400 mm (Alpat'ev et al., 1976; Climatic Atlas of Asia, 1981). Today cold deciduous forests and woodlands with larch (*Larix*) occupy low-elevation plains, mountain slopes and river valleys; while tundra vegetation occurs above 400–500 m (Gerasimov, 1964) and in the arctic plains, where mean July temperatures do not exceed 10 °C (MacDonald et al., 2000). Other woody taxa well represented in the regional vegetation include birch (*Betula*) trees and shrubs, and shrubs of alder (*Alnus fruticosa*), pine (*Pinus pumila*), heath (Ericales) and rose family (Rosaceae). Scots pines (*Pinus sylvestris*) are widespread on the sandy terraces in the Lena River valley, and spruce (*Picea obovata*) and alder (*Alnus hirsuta*) grow in the locally moister and warmer riparian environments (Alpat'ev et al., 1976). Grasses (Poaceae), sedges (Cyperaceae), and mosses including *Sphagnum* are well represented in all vegetation types (Walter, 1974).

The distribution patterns of modern tree cover (expressed in percent per 1 × 1 km pixel) reflect local topography and climate (Fig. 1B). The satellite-based Advanced Very High Resolution Radiometer (AVHRR) dataset (DeFries et al., 1999, 2000a, 2000b) used to construct the map (Fig. 1B) demonstrates that tree cover percentages vary significantly from 0 to 61% per pixel in the study area around Lake Billyakh. The average values are between 25 and 45%. Treeless vegetation predominates in the higher elevated north–east and the highest tree cover values (up to 71%) are registered in the valley of the Lena River.

2.2. Fossil pollen data

The 936 cm long sediment core PG1755 was recovered in spring 2005 and analyzed for pollen, spores and other non-pollen palynomorphs (see Müller et al., 2010 for details of coring, pollen extraction, identification and counting). This study used original pollen data generated by Müller et al. (2010) and stored in the PANGAEA data information system (doi:10.1594/pangaea.729891). The age-depth model for the PG1755 pollen record presented in Müller et al. (2010) has been used in the current study without change. It is then applied to the pollen-based vegetation cover and

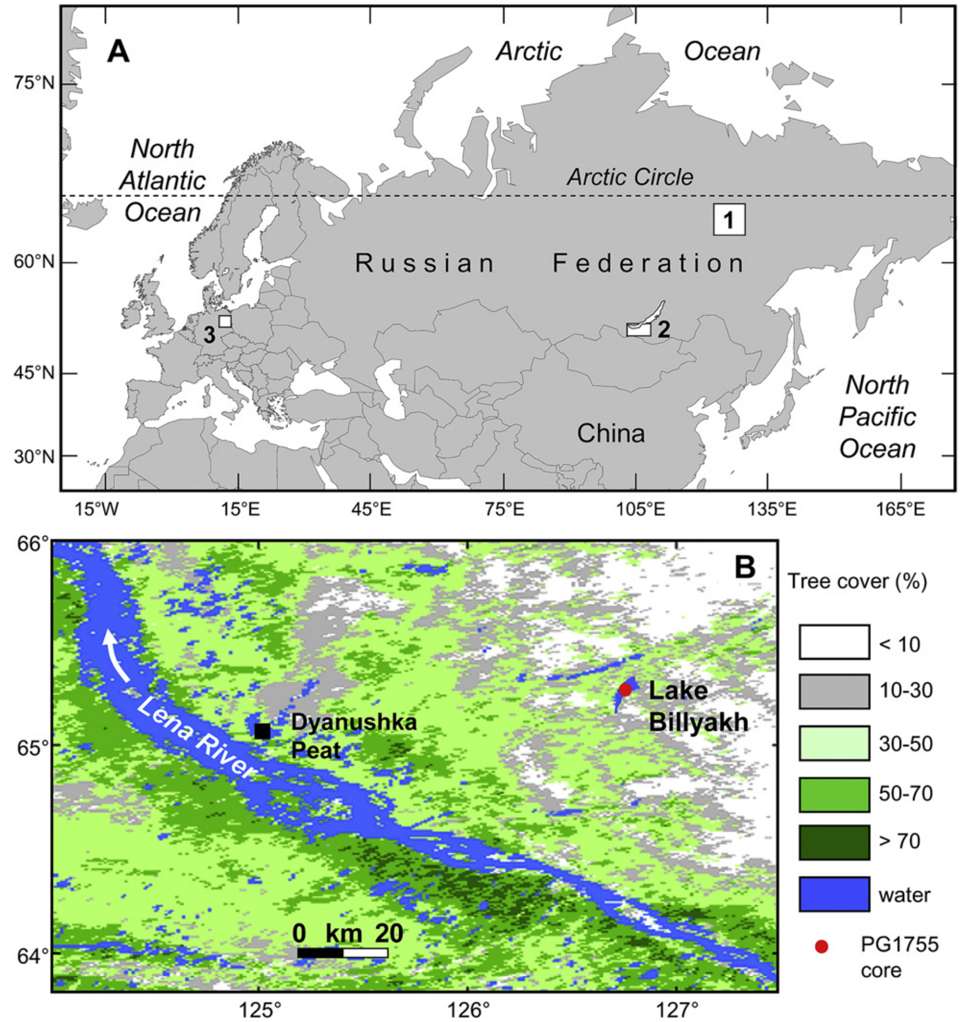

Fig. 1. Simplified maps showing (A) location of the areas with pollen and alkane biomarker data discussed in this paper, and (B) AVHRR-derived percentage values of modern tree cover (based on DeFries et al., 1999, 2000a, 2000b dataset) in the study area around Lake Billyakh and Dyanushka Peat (each pixel represents a 1 × 1 km window).

climate reconstructions to discuss the temporal changes of vegetation and climate. Calibrated ages expressed as ka BP (1 ka = 1000 cal yrs) are used throughout the text.

2.3. Pollen-based vegetation cover and climate reconstruction methods

Müller et al. (2010) refined the quantitative method of biome reconstruction (Prentice et al., 1996; Tarasov et al., 1998) for reconstruction of major vegetation types in the study region during the past ~50 ka. The refined method was successfully tested using a representative surface pollen dataset from eastern Siberia collected between 56–73°N and 111–133°E and then applied to the fossil pollen records from Lake Billyakh (Müller et al., 2010).

However, the biome reconstruction provides no quantitative information about vegetation cover structure and can mask temporal variations in the internal composition of regional vegetation (Williams et al., 2004). To obtain this information from the fossil pollen record and to reconstruct changes in woody cover, another quantitative approach described in Tarasov et al. (2007b) was used. The approach combines extensive modern surface pollen and satellite-based Advanced Very High Resolution Radiometer (AVHRR) datasets from northern Eurasia (DeFries et al., 1999; Tarasov et al., 2007b) with the best modern analogue (BMA) approach (Overpeck et al., 1985; Guiot, 1990), allowing fossil pollen samples to be attributed to the vegetation characteristics associated with their closest modern pollen analogues.

This method was recently applied to the late Quaternary pollen records from the Lake Baikal region (Bezrukova et al., 2010), northern Asia (Tarasov et al., 2007b; Kleinen et al., 2011) and middle and high latitudes of the Northern Hemisphere (Williams et al., 2011) in order to reconstruct spatial and temporal patterns of forest expansion in response to short-term episodes and long-term trends in climate amelioration. In the current study the AVHRR-based estimates of woody cover percentages within a 21 × 21 km window around pollen sampling sites were attributed to the PG1755 pollen spectra (see Tarasov et al., 2007b; Williams et al., 2011 for the method evaluation and design).

The BMA approach is also frequently employed to reconstruct past climates from fossil pollen data (e.g. Guiot, 1990; Nakagawa et al., 2002; Brewer et al., 2007; Bartlein et al., 2011). In eastern Asia it was successfully applied to the late Quaternary records south and north of Lake Billyakh, including the Lake Baikal region (Tarasov et al., 2005, 2007a, 2009), northwestern Mongolia (Rudaya et al., 2009), Taymyr Peninsula (Andreev et al., 2003, 2004a) and the Laptev Sea region (Andreev et al., 2004b, 2009; Kienast et al., 2008, 2011). The present study used the reference pollen dataset from the large area of the former Soviet Union and Mongolia with all main bioclimatic regions well represented (see Tarasov et al., 2005 for details) to reconstruct changes in annual precipitation (PANN) and in mean temperature of the warmest month (MTWA), representing July. These two climatic variables are commonly used to discuss the late Quaternary vegetation dynamics in the study region.

2.4. Alkane biomarker analysis

The recent plant material used for testing the *n*-alkane biomarker approach was collected in the central part of eastern Siberia south of Lake Billyakh (region 1 in Fig. 1A) in summer 2007. All collected plant specimens were dried and identified using botanical literature and reference plant collections at the Free University Berlin. For comparison leaves from the characteristic Siberian plants collected in the southern part of eastern Siberia south of Lake Baikal (region 2 in Fig. 1A) and in the Botanical Garden of the Free University in Berlin (region 3 in Fig. 1A) were added. All plant species used for *n*-alkane analysis and the analytical results obtained are available in the open-access PANGAEA data information system (doi:10.1594/PANGAEA.777016).

In total 53 recent plant samples and 18 fossil samples representing interglacial, glacial and interstadial sediments of the PG1755 core from Lake Billyakh were analysed for *n*-alkanes using the method described by Zech and Glaser (2008). The method was applied to the fossil samples from the study region of eastern Siberia (Werner et al., 2010; Zech et al., 2010). Free lipids were extracted with methanol/toluene (7/3) using an accelerated solvent extractor (ASE) and subsequently concentrated using rotary evaporation. Lipid extracts were purified on silica-alox columns (2 g of each, 5% deactivated). Alkanes were eluted with 30 ml hexane/toluene (85/15). Measurements were carried out on an HP 6890 gas chromatograph equipped with a flame ionization detector (FID).

3. Results

3.1. The n-alkane analysis of recent plant material

The results of the alkane biomarker analysis of the recent samples are summarized in Figs. 2–5. Fig. 2 shows concentrations of the long-chain (n-C_{25} to n-C_{33}) alkanes derived from the leaves of the recent plants, which were collected in the central and southern parts of eastern Siberia (regions 1 and 2 in Fig. 1A). The alkane concentrations are extremely low (0.01–0.04 mg/g dry plant material) for all needleleaved trees and shrubs. Although *Juniperus* reveals a slightly higher value (0.3 mg/g), it is still much lower than in all analyzed samples representing broadleaved trees and shrubs (Fig. 2). The highest *n*-alkane concentrations appear in the samples from tree and shrub *Betula* (4.9–5.7 mg/g) and in some representatives of the heath order, i.e. *Empetrum nigrum* (7.04 mg/g), *Ledum palustre* (4.91 mg/g) and *Vaccinium vitis-idaea* (4.07 mg/g). Among the grass and herb taxa analyzed *Comarum palustre*, *Dryas octopetala* and *Rumex* show moderately high alkane concentrations (2.18, 1.79 and 0.97 mg/g, respectively), while some others, i.e. *Rubus* and *Caltha palustris* reveal very low values comparable to those in coniferous trees and shrubs. Plants representing ferns and mosses show substantial difference, i.e. the *Sphagnum* contribution is very low (0.04 mg/g) and the contribution of *Cystopteris* is moderately high (2.98 mg/g).

The percentage distribution of the *n*-alkanes in plant samples from eastern Siberia are shown in Figs. 3 and 4. The plants from central eastern Siberia (region 1 in Fig. 1A) reveal rather complex alkane patterns (Fig. 3). The predominance of n-C_{27} is obvious

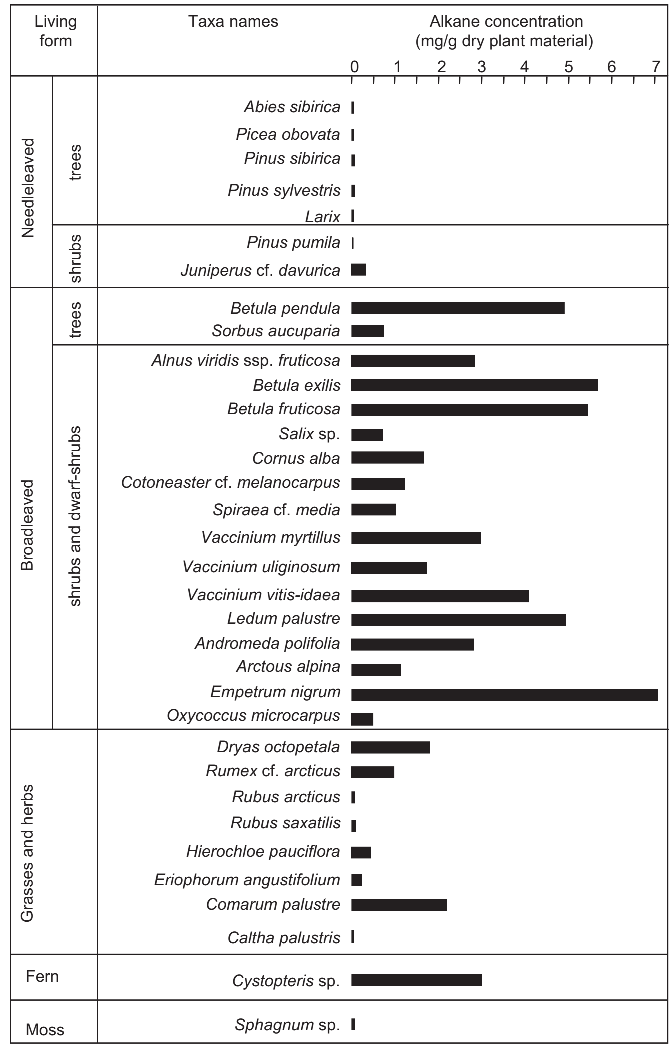

Fig. 2. Long-chain *n*-alkane concentrations (mg/g dry plant material) in the leaf epicuticular waxes of land plants from eastern Siberia (regions 1 and 2 in Fig. 1A).

in alder, birch and willow shrubs and dwarf shrubs, but relatively high percentage values occur also in some herbaceous taxa, including *Dryas*, *Rubus* (Rosaceae), *Eriophorum* (Cyperaceae), *Hierochloe* (Poaceae), *Rumex* (Polygonaceae), *Caltha* (Ranunculaceae) and in *Sphagnum* moss. High percentages of n-C_{29} appear in most of the analyzed heath shrubs, however some others, i.e. *Arctous*, *Vaccinium* show a predominance of n-C_{31}. Results based on the recent samples collected in southern Siberia (Fig. 4) and in the Botanical Garden of Berlin (Fig. 5) support the rather complex pattern of *n*-alkane distribution in the living plants representing Siberian vegetation revealed by Fig. 3. Moreover, comparison of the results shown in Figs. 3–5 demonstrates that the *n*-alkane distribution pattern may vary among plants belonging to the same genus and even species (e.g. *Andromeda polifolia*).

3.2. The n-alkane analysis of fossil lake sediment samples

In total 18 samples from the PG1755 core were analyzed for *n*-alkanes. In all samples, concentration of long-chain *n*-alkanes was relatively low and varied between 0.021 and 0.038 mg/g dry sediment. The percentage values calculated from the total sum of n-C_{25} to n-C_{33} alkanes taken as 100% (Fig. 6) demonstrate that the n-C_{25}, n-C_{27}, n-C_{29} and n-C_{31} contribution is most significant, while

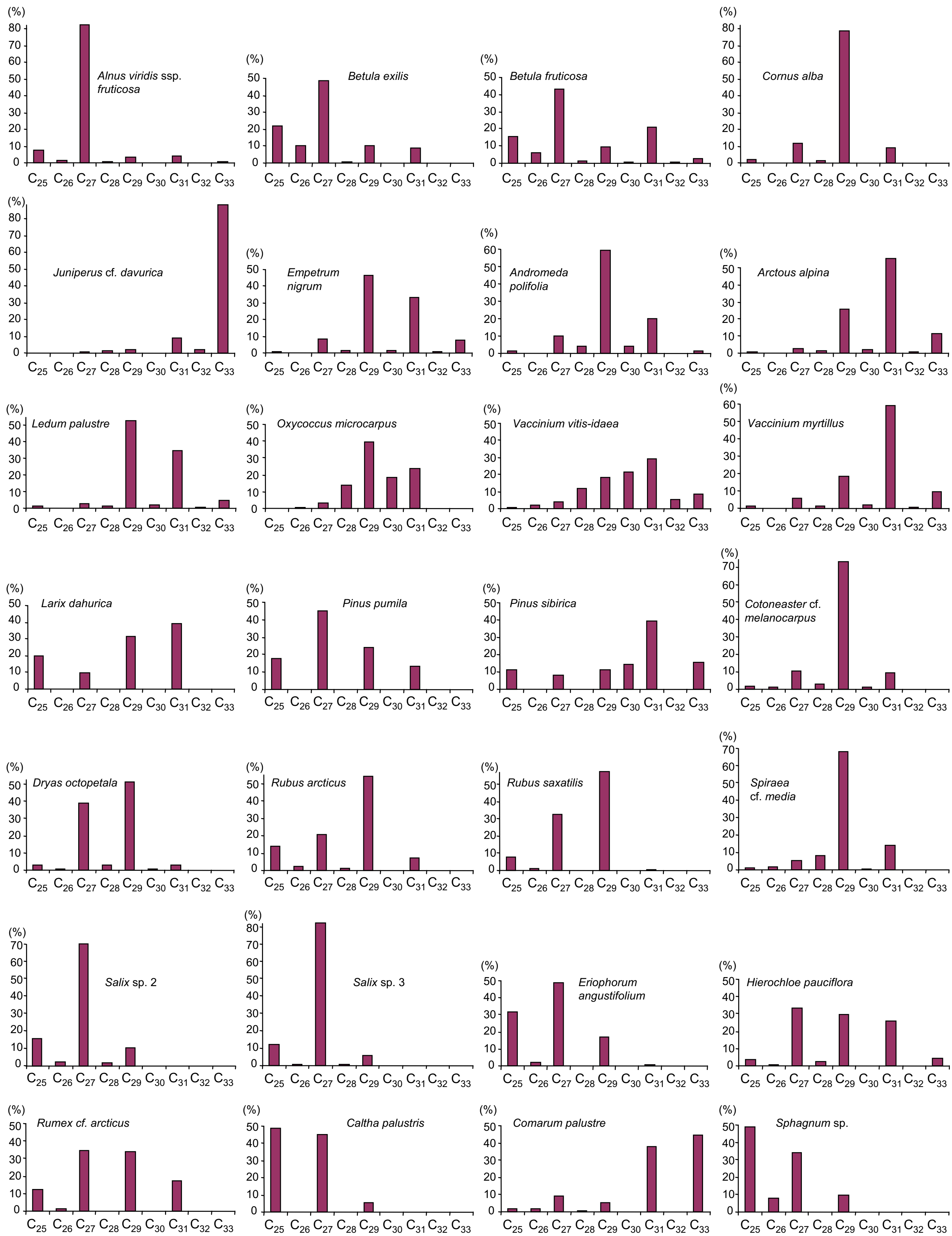

Fig. 3. Long-chain *n*-alkane percentage distribution patterns of plant samples from the central part of eastern Siberia (region 1 in Fig. 1A).

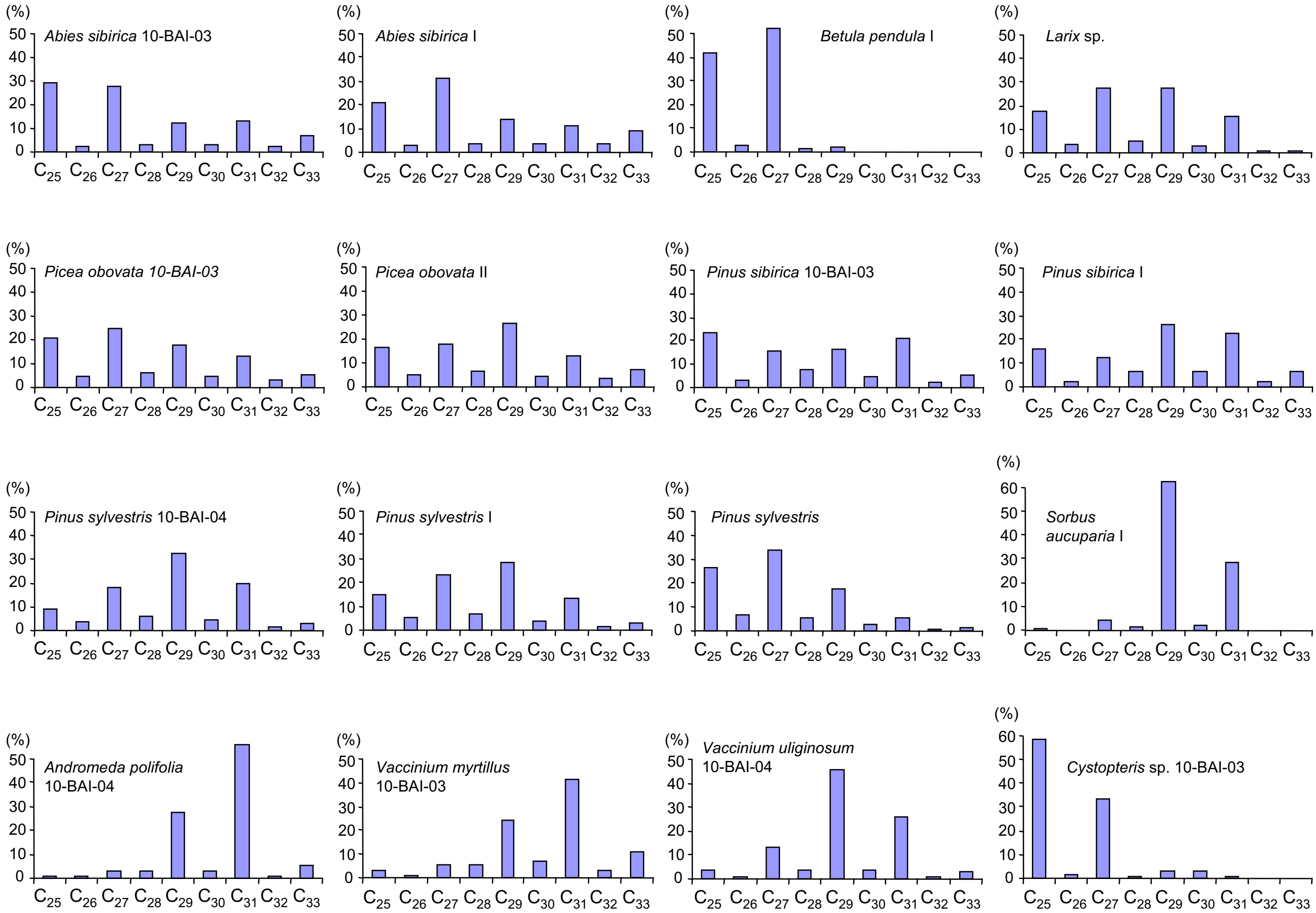

Fig. 4. Long-chain *n*-alkane percentage distribution patterns of plant samples from the Lake Baikal region in eastern Siberia (region 2 in Fig. 1A).

n-C_{33} is relatively stable and does not exceed 5–6%. The observed trends allow three zones to be distinguished. The lower zone (~37–35 ka BP) is characterized by moderate percentages of *n*-C_{25}, *n*-C_{27}, and *n*-C_{31} and low *n*-C_{29}. The middle part of the record (~27–13 ka BP) shows lowest percentage values of *n*-C_{25} and *n*-C_{27}, but highest values of *n*-C_{29} and *n*-C_{31}. The upper zone (~11.7–5 ka BP) reveals the reverse, with highest values of *n*-C_{25} and *n*-C_{27}, but lowest values of *n*-C_{29} and *n*-C_{31}.

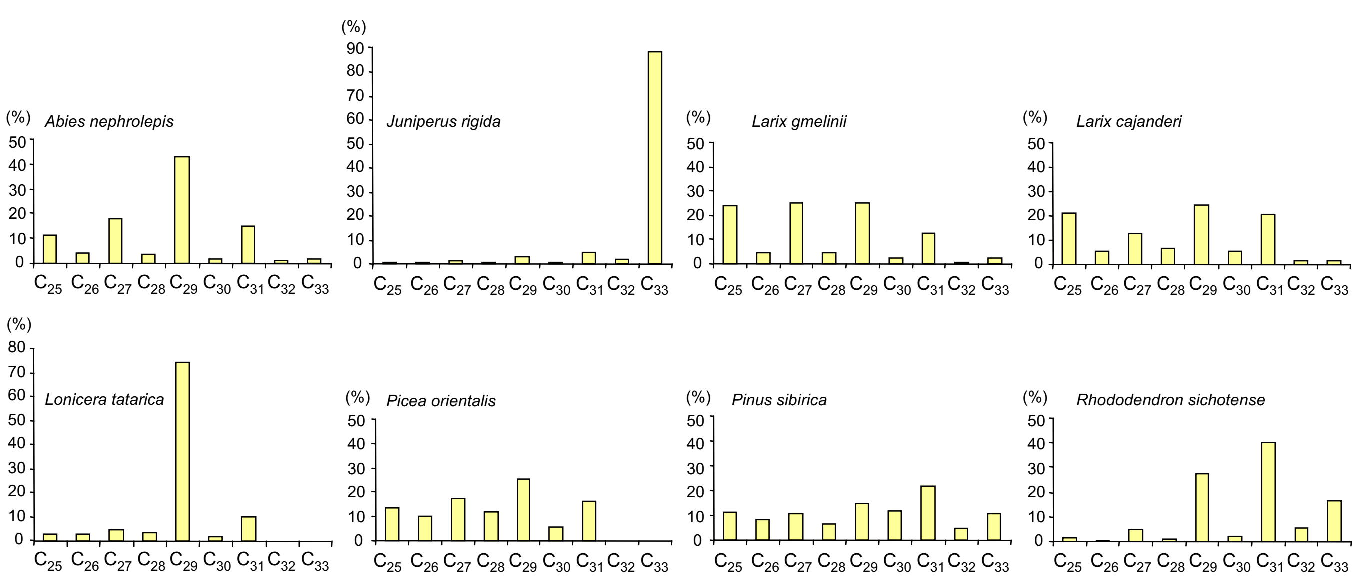

Fig. 5. Long-chain *n*-alkane percentage distribution patterns in samples representing Siberian plants growing in the Botanical Garden of the Free University in Berlin (region 3 in Fig. 1A).

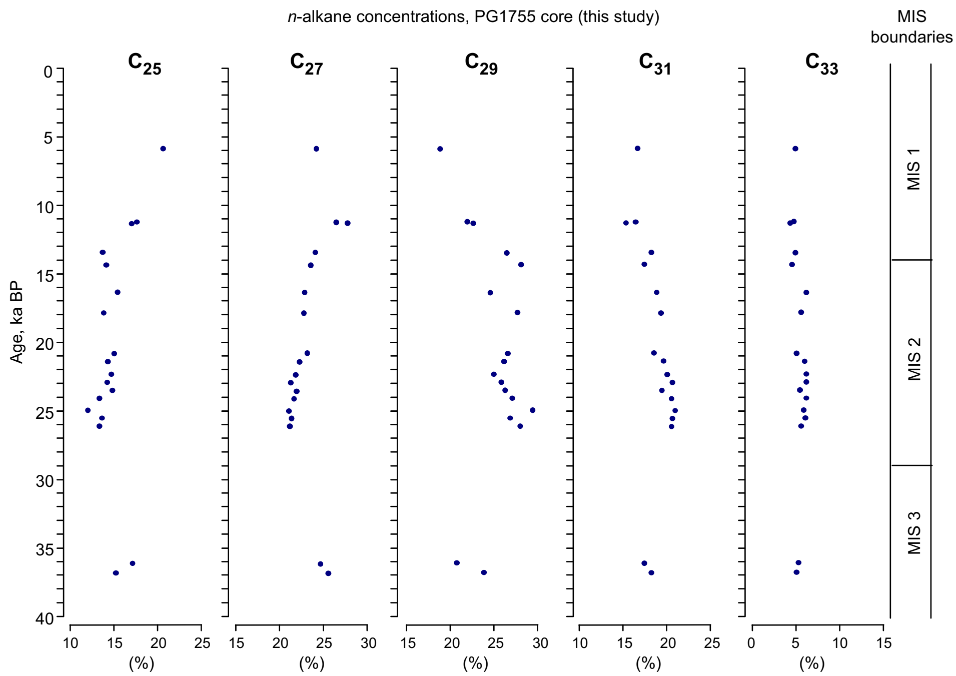

Fig. 6. Long-chain *n*-alkane percentage distribution patterns in the fossil samples from the PG1755 core of Lake Billyakh plotted along the age axis. The numbers and boundaries of marine isotope stages (MIS) after Lisiecki and Raymo (2005).

3.3. Pollen-based tree cover reconstruction

The results of pollen-based tree cover reconstruction are shown in Fig. 7C. The reconstructed values are very low (<5%) during the last glacial interval, including marine isotope stages (MIS) 3 and 2, but increase abruptly to ~10% during the late glacial. One sample representing the Younger Dryas (Greenland Stadial 1) demonstrates a slight decrease in tree cover to ~8%. However, the onset of the Holocene once again experienced an increase in regional tree cover up to ~25% at ~10.5 ka BP. Moderately high tree cover remains a feature of the early part of the Holocene interglacial and the reconstruction shows two minima at about 9.2 and between 8.2 and 7.5 ka BP. The middle and late Holocene experienced an increase in tree cover and the reconstructed values remained high (~35–45%) from ~7.2 ka BP until the present.

3.4. Pollen-based climate reconstruction

The results of pollen-derived PANN (Fig. 7D) and MTWA (Fig. 7E) reconstruction demonstrate that the last glacial climate at and around Lake Billyakh was significantly colder and drier than at present. The mean temperatures of the warmest month were generally between 10° and 11 °C prior to ~36 ka BP, fluctuated around 10 °C between 36 and 32 ka BP, and decreased to 8–10 °C during 32–14 ka BP. A significant increase in temperature to ~12–13 °C occurred at ~13.5 ka BP, indicating the onset of the late glacial interstadial (Greenland Interstadial 1). The following temperature rise was interrupted by three oscillations towards slightly lower MTWA values around 12, ~9.2 and ~8.2 ka BP (Fig. 7E). The temperatures were about 16 °C during the past 8 ka. The reconstructed PANN curve (Fig. 7D) shows that precipitation values were between 240 and 290 mm during the entire interval prior to ~7.5 ka BP. Slightly higher values are reconstructed during MIS 3, and the lowest occurred during MIS 2. A shift to the PANN values representing similar to present-day climate is reconstructed after ~7.5 ka BP. Since then the reconstructed PANN values have been between 320 and 410 mm, with a slightly lower value around ~5 ka BP.

4. Interpretations and discussion

4.1. The n-alkane analysis and vegetation cover reconstruction

The results of the *n*-alkane analysis of the Siberian plants presented in this study are challenging for the interpretation of the fossil records. In particular, extremely low *n*-alkane concentrations in the leaves of local coniferous trees and shrubs suggest that their contribution to the litter and therefore to the fossil lake sediments might be not high enough for tracing the Quaternary history of the needleleaved taxa using the *n*-alkane biomarker method. Bearing in mind the great role which coniferous taxa, particularly larches and pines, play in the vegetation and tree cover of eastern Siberia, this is a major shortcoming of the *n*-alkane biomarker approach. Similar results are reported in a case study on reconstructing vegetation history using *n*-alkane biomarkers in loess-paleosol sequences from the Saxonian region in Germany (Zech et al., in press). One exception to the rule seems to be *Juniperus*, which reveals ~10-times higher concentrations of *n*-alkanes (Fig. 2) and a predominance of *n*-C_{33} in the *n*-alkane composition, which distinguishes it from other analyzed plants (Figs. 3 and 5). Unfortunately, junipers play a minor role in the vegetation cover of the study region (Alpat'ev et al., 1976). The fossil alkane biomarker record from Lake Billyakh (Fig. 6) obtained in this study also shows consistently low percentages of *n*-C_{33}, suggesting that juniper was not significantly present in the vegetation cover around the lake during the past 37 ka. This is in agreement with the results of the pollen analysis of PG1755 and PG1756 cores from Lake Billyakh reporting only rare occurrence of single *Juniperus* pollen grains (Müller et al., 2009, 2010). However, it is widely distributed and often a dominant tree or shrub in other regions, e.g. in the mountains of Inner Asia (Walter, 1974), where *n*-alkane biomarker analysis may provide a more valuable contribution to the discussion on vegetation history, climatic changes and prehistoric human migrations during the late Quaternary in combination with other proxies (Sheppard et al., 2004; Miehe et al., 2006; Dambricourt Malassé and Gaillard, 2011).

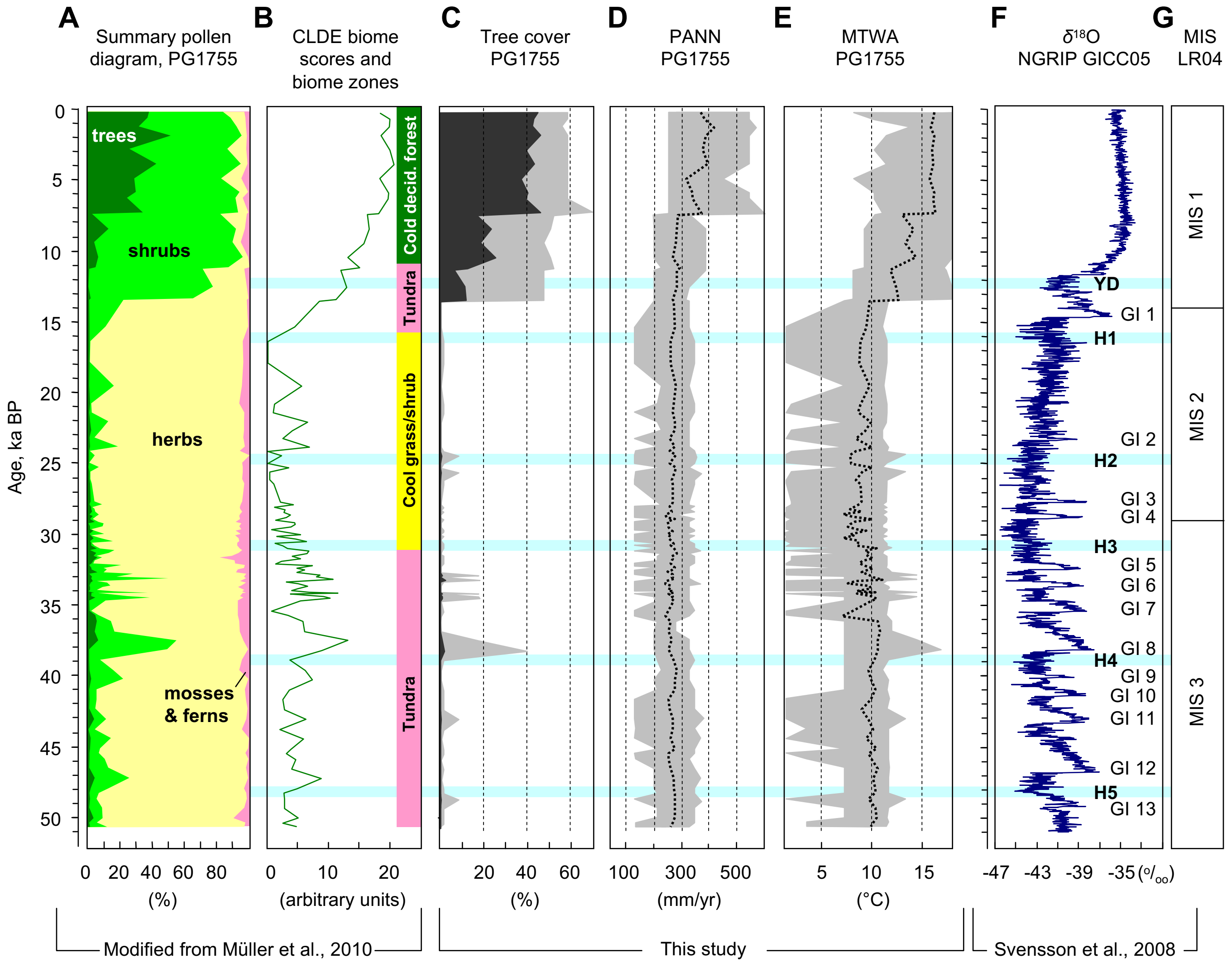

Fig. 7. (A) Summary pollen diagram (percentages are based on total sum of pollen and spores identified at each level) and (B) cold deciduous biome scores and biome zones derived from the PG1755 core record (based on Müller et al., 2010) compared with the pollen-based reconstructions of (C) tree cover, (D) annual precipitation, and (E) mean temperature of the warmest month (this study, dashed lines (D–E) indicate most probable values and grey bands (C–E) show range of the best modern analogues for each reconstructed variable), along with (F) the NorthGRIP $\delta^{18}O$ profile and the Greenland Interstadials (GI) 1 to 13 (after Svensson et al., 2008) and (G) the marine isotope stages (MIS) stratigraphy (after Lisiecki and Raymo, 2005). Blue bars indicate approximate positions of the Younger Dryas (YD) and Heinrich events H1 to H5 (after Tierney et al., 2008). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The *n*-alkane distribution observed across the late Pleistocene glacial and Holocene interglacial sediment of the PG1755 core demonstrates relatively high percentages of *n*-C_{27} followed by *n*-C_{25} during the interglacial and low percentages during the full glacial interval. Based on the alkane composition of the analyzed modern plants, this pattern might indicate a higher contribution of deciduous trees and shrubs (mainly *Betula*, *Alnus* and *Salix*), but also herbaceous plants growing in moist environments, i.e. *Caltha*, *Eriophorum*, *Sphagnum*, etc. contributing to the local vegetation during warmer and more humid intervals. The relative increase in *n*-C_{29} followed by *n*-C_{31} can be interpreted in terms of a greater contribution of herbaceous plants, but also heath semi-shrubs, to the vegetation cover around Lake Billyakh during the colder and drier glacial interval. This interpretation finds further support in the PG1755 pollen record (Fig. 7A) and in the pollen-based biome reconstruction (Fig. 7B), which show the predominance of herbaceous pollen and cool grass/shrub (or 'tundra-steppe') vegetation during the last glacial maximum phase, and the predominance of arboreal pollen and cold deciduous forest vegetation during the Holocene interglacial (Müller et al., 2010). The detailed pollen diagram presented in the latter study also demonstrates the more frequent appearance of Rosaceae and Ericales pollen in the late Pleistocene and *Sphagnum* spores in the Holocene part of the record, in line with the alkane-based interpretation. However, the most pronounced features of the Lake Billyakh glacial pollen assemblages are high percentages of *Artemisia*, Cyperaceae (presumably *Carex*), Poaceae and spores of *Selaginella rupestris*. Alkane composition of recent *Carex* plants from eastern Siberia shows a predominance of *n*-C_{29} and that of a mixed grass-herb sample is dominated by *n*-C_{31} (Zech et al., 2010). Other authors (Ficken et al., 1998, 2000; Andersson et al., 2011) have also noted that the *n*-alkane distribution in *Carex* may vary between the species and maximize at *n*-C_{27}, *n*-C_{29} or *n*-C_{31}. The other members of Cyperaceae family also show a non-uniform *n*-alkane distribution pattern. For example, the typical tundra plant *Eriophorum angustifolium* shows maximum values of *n*-C_{27} (Fig. 3). Notably, the alkane concentrations observed for three *Carex* species (Ficken et al., 1998) are similar to those of *Sphagnum*. *Eriophorum* also reveals low concentrations (Fig. 2). A study on the alkane composition of aerial parts of two *Artemisia* species (*Artemisia ludoviciana* and *Artemisia frigida*) widespread in the Canadian prairies and one species (*Artemisia cana*) restricted to dry saline areas (Bachelor et al., 1972) demonstrates highest values for n-C_{29} (~41%, 45% and 53%, respectively) followed by n-C_{31} (~41%, 19% and 23%, respectively) within the long-chain alkane sequences. There is apparently no available data on the alkane composition of *Selaginella* species. However, it should not strongly affect the general pattern, as the contribution of club moss to the total sum of pollen and spores (Fig. 7A), and therefore to the vegetation cover, is relatively small (~3–4% on average).

The n-alkane-based reconstruction of late Quaternary environments in the southern part of eastern Siberia based on the core from Lake Baikal spanning the last 20 ka (Brincat et al., 2000) interprets a shift in the abundance of n-C_{27} alkane relative to n-C_{31} homologue across the late Quaternary glacial–interglacial transition as indicative of the climate-induced change in vegetation deduced from pollen records. Ishiwatari et al. (2009) present a 35 ka record of n-alkanes from peat bog sediments of the Lake Baikal region and show a similar trend in n-C_{27} and n-C_{31} alkane distributions, suggesting the dominance of herbaceous vegetation during the last glacial and the spread of broadleaved tree and shrub vegetation during the early part of the Holocene interglacial. These results are in good agreement with the pollen records from Cheremushka Peat (Shichi et al., 2009) and from the neighbouring Lake Kotokel (Bezrukova et al., 2010) showing highest values of *Artemisia* and Poaceae pollen prior to ~14.5 ka BP and highest percentages of birch and alder pollen between 14.5 and 7 ka BP.

4.2. Trees or no trees: the pollen-based reconstruction

'Trees or no trees?' remains a key research question when discussing the location and survival of trees in the coldest stages of the last glacial in temperate and boreal zones of Eurasia from central (Willis and van Andel, 2004) and eastern Europe (Tarasov et al., 2000) to eastern (Tarasov et al., 2009; Müller et al., 2010) and north-eastern Siberia (Lozhkin and Anderson, 2011). The recent research in Europe brought significant progress in identifying the location and character of the glacial refugia of many coniferous and broadleaved tree species. However, in the vast regions of Siberia direct evidence is still unavailable, encouraging further research and stimulating discussion on the likelihood of tree presence in these extreme-continental Siberian environments.

The quantitative reconstruction of tree cover presented in Fig. 7C suggests that trees played a minor role in the vegetation around Lake Billyakh during the last glacial prior to 13.5 ka BP. This result corroborates low percentages of tree pollen (Fig. 7A) and low scores of cold deciduous forest biome (Fig. 7B) in the PG1755 record, as well as the majority of earlier reconstructions summarized in the most up-to-date synthesis (i.e. Lozhkin and Anderson, 2011). The latter work, based on the new data from lake cores from north-eastern Siberia (also called western Beringia), suggests the rather complex composition of the vegetation cover during the second part of the last glacial, with only isolated populations of larch within herb-dominated communities in the northern part of the region and herb/shrub tundra, steppe, forest-tundra, and larch forest growing in its southern part, more sensitive to the short-term episodes of climate amelioration/deterioration.

It is suggested that too cool and/or too dry warm-season conditions are responsible for the limited presence (or even total absence) of woody plants and the spread of herbaceous vegetation even during many of the "warm" interstadial intervals (Lozhkin and Anderson, 2011). In particular, summer temperatures between 10 and 12 °C and decreased growing season moisture are suggested for the intervals when birch shrub tundra was the dominant vegetation, and summer temperatures below 10 °C accompanied by very low effective moisture for the intervals when herbaceous tundra prevailed (Lozhkin and Anderson, 2011). Quantitative pollen-based reconstructions of biomes (Fig. 7B), warmest month temperature (Fig. 7E) and annual precipitation (Fig. 7D) performed for the Lake Billyakh area accord well with the above scenario. Reconstructed mean values of PANN (~270 mm) are almost 100 mm higher than modern averages reported for Verkhoyansk (67°33′N, 133°23′E), where cold deciduous larch-dominated forest grows at present (Kolbek et al., 2003) in relatively high summer temperatures (MTWA = 16 °C). The present-day extension of larch in the Arctic is limited mainly by the mean July isotherm of 10–12 °C (MacDonald et al., 2000). Mean MTWA values derived from the Lake Billyakh pollen record (Fig. 7E) are mostly below 10 °C during the interval from ~32 to ~15 ka BP, which corresponds to the coldest part of the Greenland ice record (Fig. 7F). Comparing the reconstruction results with the present-day climate and vegetation distribution of the region (Müller et al., 2010), low summer temperatures were most likely the main factor which limited tree growth in the study area during the last glacial interval.

The pollen-derived reconstruction of MTWA below 10 °C (Fig. 7E) does not support larch woodland around Lake Billyakh during the coldest phase of the last glacial, in line with the pollen spectra composition (Fig. 7A) and quantitative vegetation cover reconstructions (Fig. 7B,C). It has been suggested, however, that individual larch plants could survive cold and dry intervals in the western and southern foreland of the Verkhoyansk Mountains, which provided enough moisture and warm microhabitats to buffer larch specimen against climatic extremes (Tarasov et al., 2009; Müller et al., 2010). The presence of larch populations during the last glacial and late glacial termination likely explains the quick reforestation of eastern Siberia by the early Holocene as indicated by the wood macrofossil records (MacDonald et al., 2000; Binney et al., 2009), and supports the molecular-based hypothesis suggesting the existence of high-latitude refugia during the last glaciation (Semerikov et al., 1999; Abbott et al., 2000). Living larch trees (*Larix dahurica*) were found in the tundra near Dolgoe Lake (71°52′N, 127°04′E), ca. 750 km north of Lake Billyakh, where the mean July temperature is about 8 °C and total annual precipitation is below 300 mm (Pisaric et al., 2001), suggesting that scattered individuals of larch can survive July temperatures below 10 °C limit. Along with a strong resistance to cold and relatively dry environments, Siberian larch is also known for its longevity. Dendrochronological investigation on the *Larix cajanderi* population growing in the Indigirka River valley (69°24′N, 148°25′E) showed that ca. 15% of analyzed individuals were older than 700 years, reaching maximal ages of about 900 years (Vaganov et al., 1999). Another important feature of larch in Siberia is its ability to survive as a prostrate shrub or 'krummholz' at or beyond the subalpine and subarctic tree lines. This form is particularly helpful against strong winds, freezing temperatures and thin snow cover and has been found as far north as ca. 74°30′N on Taymyr Peninsula and on the northern Anabar Plateau (Andreev et al., 2003).

5. Conclusions

The current study presents quantitative results of tree cover and atmospheric precipitation and temperature reconstructions based on the recently published pollen record from Lake Billyakh spanning the last ca. 50 ka. The work contributes to the ongoing debate on the presence/absence of trees in the extreme-continental regions of Siberia during the coldest phases of the last glacial.

The quantitative reconstruction of tree cover suggests that trees were present, although played only a minor role in the vegetation around Lake Billyakh during the time interval prior to 14 ka BP, with slightly higher values representing MIS 3. This result corroborates low percentages of tree pollen and low scores of the cold deciduous forest biome in the PG1755 record from Lake Billyakh.

The reconstructed values of the mean temperature of the warmest month ~8–10 °C do not support larch forest or woodland around Lake Billyakh during the coldest phase of the last glacial between ~32 and ~15 ka BP. However, modern cases from northern Siberia, ca. 750 km north of Lake Billyakh, demonstrate that individual larch plants can grow within shrub and grass tundra landscape in very low mean July temperatures of about 8 °C. This makes plausible the hypothesis that the western and southern foreland of the Verkhoyansk Mountains could provide enough moist and warm microhabitats and allow individual larch specimens to survive climatic extremes of the last glacial.

Reconstructed mean values of annual precipitation are about 270 mm, almost 100 mm higher than modern averages reported for Verkhoyansk, where cold deciduous larch-dominated forest grows at present. This suggests that last glacial environments around Lake Billyakh were never too dry for larch to grow and that the insufficient summer warmth was the main factor, which limited tree growth during the last glacial interval.

The *n*-alkane analysis of the Siberian plants presented in this study demonstrates rather complex alkane distribution patterns, which challenge the interpretation of the fossil records. In particular, extremely low *n*-alkane concentrations in the leaves of local coniferous trees and shrubs suggest that their contribution to the litter and therefore to the fossil lake sediments might be not high enough for tracing the Quaternary history of the needleleaved taxa using the *n*-alkane biomarker method.

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