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Post-glacial vegetation and environment of the Labanoras Region, East Lithuania: implications for regional history

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Multiproxy data (pollen, plant macrofossils, ^{14}C dates and loss-on-ignition measurements) obtained from the Bevardis and Verpstinis lakes in the Labanoras area (East Lithuania) were used to reconstruct a vegetation history and to reveal major environmental features during post-glacial time. Biostratigraphical data indicates ongoing sedimentation in Verpstinis Lake since the final stages of the Allerød. The pollen data shows that *Pinus*-dominated forest flourished during the Allerød, while the Younger Dryas was characterized by open shrub/herb/grass vegetation with highly abundant *Juniperus*. These are evidences of severe climatic conditions in the area. The ^{14}C data suggests that sedimentation started in Bevardis Lake with the onset of the Holocene. *Picea* immigrated into the Verpstinis Lake surroundings in the Late Glacial, just before 11 500 cal yr BP according to the palynological evidence. The expanding deciduous taxa, e.g., *Corylus* (*ca*. 10 200–10 000 cal yr BP), *Alnus* (8200–8000 cal yr BP), and broad-leaved species with *Ulmus* (*ca*. 10 000 cal yr BP), *Tilia* (7700–7400 cal yr BP) and *Quercus* (5200 cal yr BP), formed a dense mixed forest where *Picea* appeared at 7300–6800 cal yr BP. Both diagrams show only negligible human impact. It seems that natural factors were responsible for the formation of vegetation cover and environment in the study area throughout the post-glacial.

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INTRODUCTION

Recent palaeoenvironmental studies combining pollen, plant macrofossil and diatom data with the results of ^{14}C and ^{10}Be isotope investigations, optically stimulated luminescence (OSL) measurements as well as geochemical and lithological data have provided a detailed Late Glacial and early Holocene environmental history of Lithuania (Bitinas, 2004; Molodkov and Bitinas, 2006; Šeirienė *et al.*, 2006; Rinterknecht *et al.*, 2008; Stančikaitė *et al.*, 2008, 2009*b*). The vegetation history was better understood after the discovery of *Pinus sylvestris* L. macrofossils dated back to *ca*. 13 700 cal yr BP (Stančikaitė *et al.*, 2008), and *Picea* sp. seeds in deposits of Allerød age in southeastern Lithuania (Stančikaitė *et al.*, 1998). Moreover, an early Holocene (*ca*. 10 600 cal yr BP) immigration of the latter taxa to northeastern Lithuania was recently indicated on the basis of plant macrofossil data (Stančikaitė *et al.*, 2004, 2009*b*), and the main stages of the Late Glacial environmental history have been discussed in the context of North Atlantic climatic events of the Last Termination (Stančikaitė *et al.*, 2008).

Relatively few studies have been lately devoted to the Holocene environment and vegetation in Lithuania (Balakauskas, 2003; Kabailienė *et al.*, 2009; Mažeika *et al.*, 2009; Šeirienė *et al.*, 2009). Most of the data for this time-interval was obtained from archaeological sites where environmental changes have been examined in the context of human activity (Stančikaitė *et al.*, 2006, 2009*a, b*). The Holocene vegetation history has been studied mostly using biostratigraphical data obtained a few decades ago, or from even earlier when numerous sediment profiles were examined throughout the country (Kabailienė, 2006). The existing sparse radiocarbon data for these pollen records was insufficient for a detailed regional correlation of the vegetation history. In order to shed more light on the Holocene environmental history and to improve the chronology of vegetation development, sediment cores representing different parts of Lithuania were selected for a multiproxy study.

As the eastern part of Lithuania is situated close to the margin of the Late Weichselian (Vistulian) Glaciation, the area was liberated from ice relatively early, providing new land for immigration of the Late Glacial vegetation. During the Holocene when deciduous trees expanded from refuges situated in south-eastern and southern Europe (Bennett *et al*., 1991; Willis *et al.*, 2000), this part of Lithuania served as a key area for the further establishment of taxa in the region. Moreover, a new data suggests that isolated patches of trees existed between the Scandinavian ice sheet and the Ural Mountains during the Late Glacial and early Holocene. These small populations acted as initial nuclei for population expansion and forest development in the early Holocene (Väliranta *et al*., 2010). These refuge areas may also have influenced immigration of particular species to Eastern Lithuania.

The aim of this study is to describe patterns of the post-glacial vegetation with a particular emphasis on Holocene vegetation dynamics in the Labanoras Region, East Lithuania, and to discuss this in the context of the regional vegetation history. Immigration, flourishing and extinction of distinct taxa, as well as the main stages of environmental variation are discussed in this paper. The multiproxy data of pollen, plant macrofossil, ^{14}C and loss-on-ignition (LOI) measurements from the two sediment sequences obtained from Bevardis and Versptinis lakes were used to achieve this goal and to improve our knowledge of Late Glacial and Holocene forest dynamics in this part of the Baltic Region.

STUDY AREA

The first study locality (55°11′30″N, 25°52′26″E) is situated at Verpstinis Lake (11 ha, 156 m a.s.l.) within the Beržalotas Highmoor (Fig. 1B) in Eastern Lithuania. The partly overgrown lake, up to 4 m deep, is predominantly surrounded by highmoor vegetation. The highmoor is in a centre of the Žeimena Plain that is a part of a glaciofluvial outwash plain stretching beyond the marginal deposits of the Late Weichselian (Vistulian) Glaciation (Guobytė, 2002). Depressions of this slightly undulating plain were filled with lakes, which later transformed into bogs and highmoors.

Another sediment sequence was taken in the eastern part (55°10′55″N, 25°44′42″E, 167 m a.s.l.) of Bevardis Lake (Fig. 1A) situated in the western part of the Žeimena Plain. This small (*ca*. 0.4 ha) lake is surrounded by a 0.7 ha bog of transitional type.

This part of Lithuania is characterized by a continental climatic regime. The average annual precipitation varies from 650 to 700 mm, the major part of which falls during the warm season. The mean temperature varies from –6.3°C in January to 16.8°C in June. The mean temperature of the year is about 5.5°C.

METHODS

CORING AND SAMPLING

Multiple sediment cores were obtained from Bevardis and Verpstinis lakes using a Russian corer (1 m long chamber with a 5 cm inner diameter). After visual description of the sediments (Fig. 2), the cores obtained were sub-sampled at 2 cm resolution for pollen (the Bevardis and Verpstinis cores) investigations and at 5 cm resolution for plant macrofossil (the Bevardis core) and loss-on-ignition (the Bevardis core) studies. Bulk samples of 4–5 cm were taken for conventional ^{14}C dating from both cores.

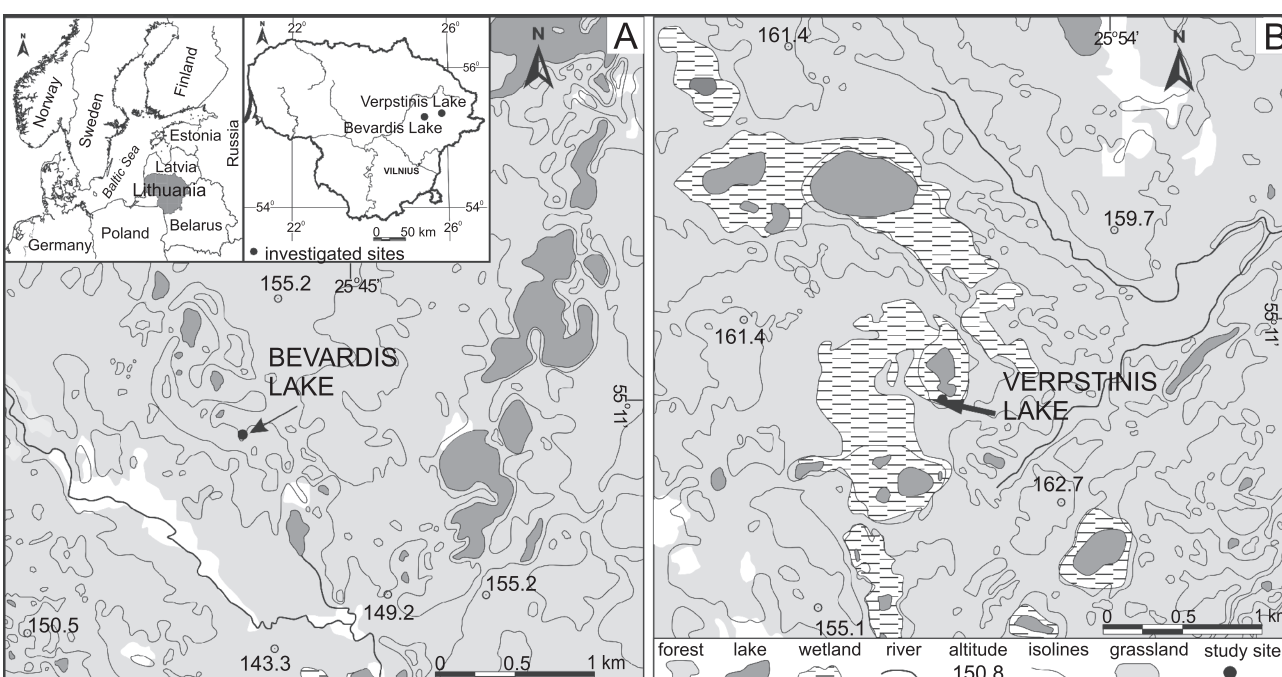

Fig. 1. Location of the study sites

A – Bevardis Lake in the thermocarst lakes complex; **B** – Verpstinis Lake in Beržalotas Highmoor

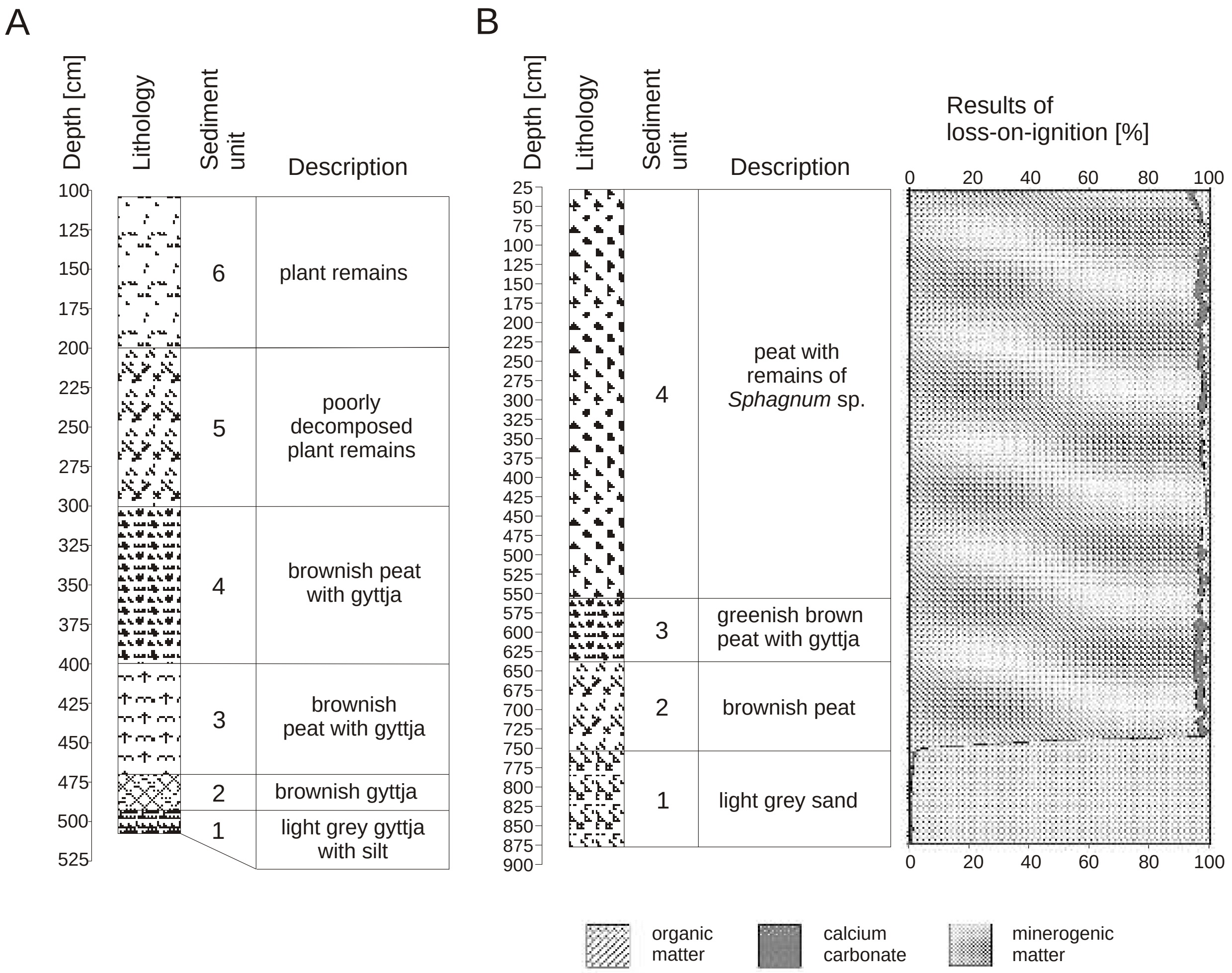

Fig. 2. Lithological descriptions of the Verpstinis and Bevardis lake cores with results of LOI for the Bevardis Lake sequence

A – lithology of Verpstinis Lake; **B** – lithology and results of loss-on-ignition performed on the sediments from Bevardis Lake

POLLEN ANALYSIS

The sub-samples of 1–3 cm^3 for pollen analysis were prepared using a standard chemical procedure (Erdtman, 1936; Grichiuk, 1940), including treatment of the sediments with a heavy liquid (CdI_2 + KI). A known amount of *Lycopodium* spores was added in order to calculate pollen concentrations (Stockmarr, 1971). 500 terrestrial pollen grains were counted from each sample using a light *NIKON* microscope. Pollen identification was based on Moore *et al*. (1991). Taxa are presented as percentages of the sum of arboreal (ΣAP) plus non-arboreal (ΣNAP) taxa (ΣAP + ΣNAP = ΣP). For calculation and presentation of pollen, diatom and plant macrofossil data the programs *TILIA* and *TILIA-graph* (Grimm, 2000) were applied.

Along with the visual inspection, a stratigraphically constrained cluster analysis (CONISS – Constrained Incremental Sums of Squares cluster analysis; Grimm, 1987) was used for the subdivision of the pollen and plant macrofossil diagrams into local zones.

PLANT MACROFOSSIL SURVEY

80 samples were individually analysed by means of a plant macrofossil survey. The collected remains, which had been extracted from the sediment samples (390 cm^3 in volume) by wet sieving (screens with mesh sizes of 0.2 and 0.5 mm) were analysed using *NIKON SMZ 1500* microscope, at a magnification of ×20–60. Identification of the material collected was based on Berggren (1969, 1981), Grigas (1986) and Cappers *et al.* (2006) in combination with the reference collection at the Institute of Geology and Geography (Vilnius). The plant macrofossils are presented as various identified specimens/sediment volumes and classified into groups (trees and shrubs, wa-

ter plants, plants of wetland and xeromesophytes) to aid in the interpretation of vegetation history. Botanical nomenclature follows Gudžinskas (1999).

RADIOCARBON (^{14}C) DATING

Samples representing the Verpstinis and Bevardis cores were selected for the determination of ^{14}C age in the Radioisotope Research Laboratory, Institute of Geology and Geography, Vilnius and the Kiev Radiocarbon Laboratory, the Ukraine. All together 11 bulk samples from the Bevardis and 3 from the Verpstinis cores were investigated. All dates used in the manuscript were calibrated to calendar years BP using the calibration curve of Reimer *et al.* (2004) within the calibration software *OxCal v3.10* (Bronk Ramsey, 2001).

Time scales were constructed on the basis of two-order polynomial interpolation between available conventional ^{14}C dates (the midpoint of the ±1σ) and biostratigraphical data in case of the Verpstinis core. All ages are given as calibrated years before 1950 AD (cal yr BP).

LOSS-ON-IGNITION (LOI)

In order to improve the lithological description, calcium carbonate ($CaCO_3$) and organic matter contents were determined for the Bevardis Lake core. The sediments were dried at 500°C for 4 h to obtain the loss-on-ignition (LOI). The determination of calcium carbonate content followed Gedda (2001), and the amount of mineral matter was calculated by eliminating organic matter and carbonate contents from the total dry matter. In total, 133 samples were investigated.

RESULTS

LITHOLOGY AND LOI RESULTS

Lithological subdivision is based on visual sediment inspection of the Bevardis and Verpstinis sections supplemented with the LOI results in the case of the Bevardis core. The lower part (755–885 cm) of the 885 cm long Bevardis section consists of a 30 cm long interval of mineral material (>95%; Fig. 2). The upper part of the core (15–755 cm) mainly consists of organic matter (up to 98%) with admixtures of $CaCO_3$ (*ca*. 2–3%) at certain intervals.

Similarly, the 510 cm long Verpstinis core sequence is made up of terrigenous material at the bottom (493–510 cm) and organogenic sediments with admixtures of gyttja (300–470 cm) from a depth of 470 cm upwards (Fig. 2). A thin interlayer of gyttja was discovered at a depth of 470–493 cm.

PALYNOLOGICAL RESULTS

The pollen data have been described in terms of local pollen assemblage zones (LPAZ) based on visual and statistical evaluations of the pollen spectra. Eight LPAZ were established for the Verpstinis (Table 1 and Fig. 3) and six for the Bevardis pollen diagrams (Table 2 and Fig. 4) respectively.

PLANT MACROFOSSIL SURVEY

Four plant macrofossil zones (LMAZ) were determined in the diagram of the Bevardis core (Table 3). The selected taxa

Table 1

Local pollen assemblage zones in Verpstinis Lake

LPAZ	Depth [cm]	Description
V_P-8	100–140	*Betula* has a peak of 56.2% and AP sum stays high in this zone. *Artemisia* and *Calluna* form continuous curves. Number of broad-leaved trees decreased upwards.
V_P-7	140–247	*Alnus* (17.5%) culminates in this zone and *Betula* increases showing 42.5%. The total AP sum reaches 95.7% and is the highest throughout the diagram. Number of broad-leaved pollen decreases approaching the upper boundary of the zone.
V_P-6	247–327	*Quercus* (6%) culminates in this zone and number of *Picea* increases showing up to 10%. Number of NAP decreased down to 3–4%. Representation of *Alnus* and *Betula* is the lowest throughout the diagram. Sum of NAP reaches up to 9%.
V_P-5	327–418	Deciduous species e.g., *Corylus* (up to 10.4%), *Alnus* (up to 11.1%) and *Tilia* (up to 4.2%), established in this zone. Number of *Picea* increases upwards (up to 9.7%) and *Ulmus* (up to 6.8%) culminates in this zone. The total amount of NAP as well as the number of identified species is the low throughout the zone.
V_P-4	418–455	Poaceae culminates in this zone and shows 31.8%. Number of AP pollen increases upwards including *Corylus*, *Alnus* and *Ulmus* forming continuous curves.
V_P-3	455–477	This zone is characterized by *Picea* culmination (up to 15%) along with remarkable rise of *Betula* curve (up to 37.2%). Number of NAP decreased showing about 14.6%.
V_P-2	477–497	Determination of this zone is based on the culmination of NAP (up to 26.2%) with *Artemisia* predominating (11.4%). Simultaneously *Juniperus* increased up to 15.2%. The total value of AP species decreased when compared with V_P-1 and is about 73%.
V_P-1	497–502.5	*Pinus* culminates in this zone showing up to 82.6%. *Betula* reaches up to 18% and number of *Alnus* and *Corylus* is negligible. The total amount of NAP reaches 5.6% and that of AP – 94.1%.

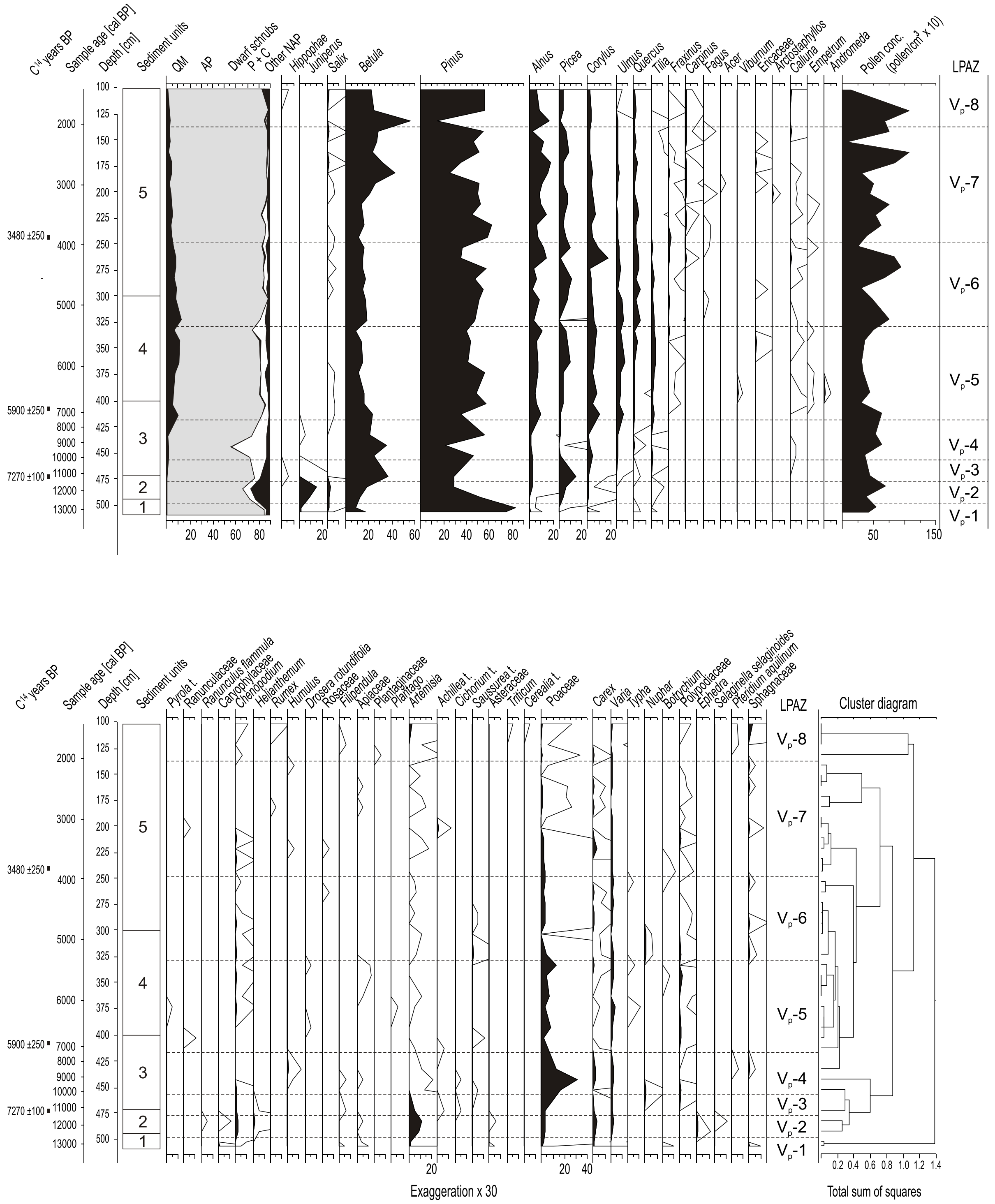

Fig. 3. Percentage pollen diagram for the Verpstinis Lake sediment sequence

AP – arboreal pollen, P + C – Poaceae and Cyperaceae, QM – quercetum mixtum, t. – type; analysed by Stančikaitė and Gaidamavičius (2007)

Table 2

Local pollen assemblage zones in Bevardis Lake

LPAZ	Depth [cm]	Description
B_P-5	25–320	*Corylus* shows some rise of the curve approaching the upper limit of the zone (up to 12.4%) as well as *Alnus* (6.7%). Number of *Pinus* pollen increase up to 80.3% in this zone. *Picea* curve lowered to 3.2% with some rise in the upper part of the zone. Number of broad-leaved trees decreased even more and NAP number is negligible.
B_P-4b	320–384	*Picea* (22.3%) culminates in this zone and number of *Betula* (up to 17%), *Corylus* (up to 7.4%), *Alnus* (up to 10%) and broad-leaved species (up to 17.2%) increases. Mostly of NAP taxa occurred sporadically.
B_P-4a	384–515	Number of the broad-leaved species decreased in this zone while representation of *Pinus* (up to 71.6%) and *Picea* (up to 13.9%) increased in comparison with the previous one. Amount of *Betula* and *Alnus* decreased as well. NAP sum is negligible in this zone.
B_P-3	515–625	Broad-leaved species e.g., *Ulmus* (up to 10%), *Quercus* (up to 5.5%) and *Tilia* (up to 5.7%) culminates in this zone alongside with *Corylus* (up to 12.4%) and *Alnus* (up to 13.5%). Number of *Picea* increases upwards (up to 9%). The total amount of NAP as well as the number of identified species is the low throughout the zone.
B_P-2	625–755	*Betula* culminates in this zone showing 24.1%. Amount of *Corylus* and *Ulmus* pollen increases upward reaching 9.7% and 3.3% respectively. Number of NAP pollen decreased in comparison with the previous zone.
B_P-1	755–879	Determination of this zone is based on the high *Pinus* representation (up to 80.2%). *Betula* reaches 22.9% in the uppermost part of the zone. *Alnus*, *Picea*, *Corylus* and *Ulmus* are represented continuously while the rest AP taxa occur sporadically. Chenopodiaceae has a peak of 3.8% while other NAP species are registered in a separated spectra only. Total sum of NAP reaches up to 13.4%.

are shown on the diagram (Fig. 5). The plant macrofossil taxa (fruits, seeds, oospores, needles and leaves) were grouped according to their habitats, e.g., water plants, plants of wetland, xeromesophytes and particular group of trees and shrubs.

CHRONO- AND BIOSTRATIGRAPHY

The chronology of the indicated environmental variations is based on the results of ^{14}C dating (Table 4 and Fig. 6) and biostratigraphical information obtained both on the regional and local scales.

According to the biostratigraphical data, the oldest sediments are recorded in the bottom part of the Verpstinis Lake core, where abundance of *Pinus* pollen (V_P-1, Fig. 3) changed to shrub/herb/grass communities with a high amount of *Juniperus* (V_P-2, Fig. 3), suggesting initial deposition during a relatively warm climate stage followed by rapid climatic deterioration. This palaeobotanical record correlates well with the Allerød/Younger Dryas biostratigraphical boundary (Kabailienė, 1993) dated back to *ca*. 12 600 cal yr BP in Lithuania (Stančikaitė *et al.*, 2008, 2009*b*).

The development of pollen spectra in the Verpstinis Lake core shows an increase in *Picea* and *Betula* pollen and concomitant decrease in NAP (V_P-3, Fig. 3). The earliest post-glacial immigration of spruce to eastern and northeastern Lithuania was dated back to 10 798–10 491 cal yr BP according to the conventional ^{14}C date or to 11 507–9739 cal yr BP according to accelerator mass spectrometry (AMS) information (Stančikaitė *et al.*, 2004, 2009*b*), thus suggesting a similar age for the *Picea* peak recorded in the Verpstinis Lake core (V_P-3, Fig. 3). Since the ^{14}C data obtained (8180–7980 cal yr BP; Table 4) is not in agreement with this chronological information, it was rejected from the age-depth model (Fig. 6).

According to the ^{14}C data (10 160–9980 cal yr BP, Ki-10954; Table 4), sedimentation in Bevardis Lake started before 10 000 cal yr BP. Organogenic strata started to form after 10 000 cal yr BP, together with the sudden rise in pollen concentration. The rise was likely related to growing vegetation cover due to immigration of new deciduous species such as *Corylus* at *ca*. 10 200–10 000 cal yr BP (B_P-2, Fig. 4 and V_P-4, Fig. 3).

The next stage of forest formation coincided with *Ulmus* immigration (*ca*. 10 000 cal yr BP; V_P-3, Fig. 3 and B_P-2, Fig. 4) followed by *Alnus* (8200–8000 cal yr BP; B_M-2, Fig. 5) and other broad-leaved species. Although sparse, broad-leaved species were present among the forest vegetation until *ca*. 4000 cal yr BP (end of V_P-6, Fig. 3). In the Bevardis Lake pollen diagram (B_P-4a, Fig. 4), a low number of deciduous trees between 6200 and 4000 cal yr BP was followed by a small peak dated to *ca*. 3800 cal yr BP (B_P-4b, Fig. 4).

Picea appeared in the region at 7300–6800 cal yr BP (Fig. 6) as seen in the Bevardis Lake pollen spectra (B_P-3, Fig. 4). However, *Picea* seeds (B_M-3, Fig. 5) were not discovered in the sediments until *ca*. 5000 cal yr BP (Fig. 6). In the Verpstinis Lake environment, the amount of *Picea* pollen started to increase at *ca*. 6800 cal yr BP (V_P-5, Fig. 3). According to the ^{14}C data obtained, *Picea* flourished in the Labanoras area until *ca*. 2500–2000 cal yr BP (onset of B_P-5, Fig. 4 and B_M-4, Fig. 5).

The uppermost parts of both cores consist of sediments deposited during the last few thousand years (Fig. 6). The pollen and plant macrofossil data (V_P-8, Fig. 3; B_P-5, Fig. 4 and B_M-4, Fig. 5) shows that *Pinus*, *Betula*, *Alnus* and *Corylus* vegetation covered the entire area near the lake rim. This indicates no trace of human activity.

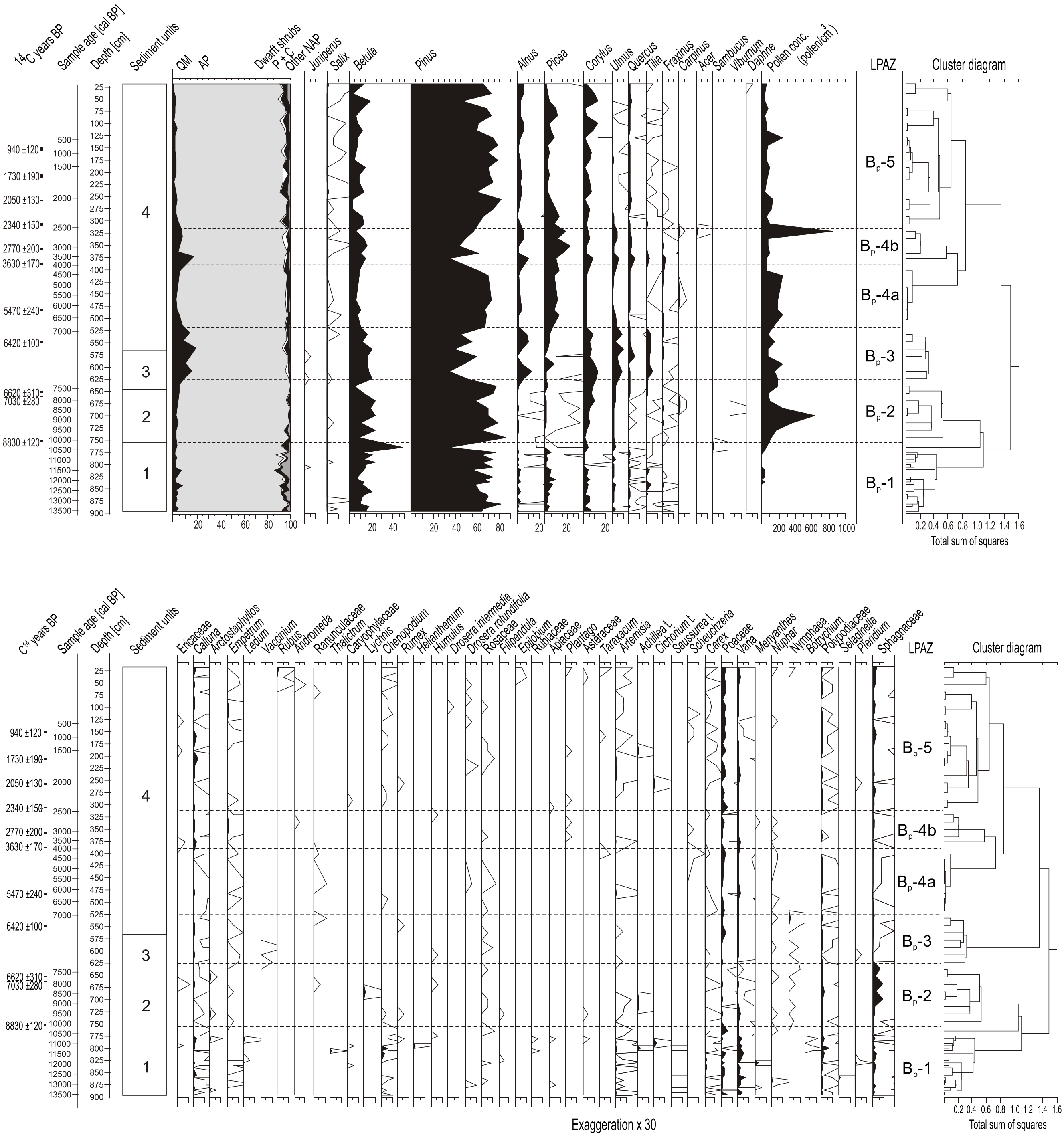

Fig. 4. Percentage pollen diagram for the Bevardis Lake sediment sequence

For explanations see Figure 3; analysed by Stančikaitė and Gaidamavičius (2007)

DISCUSSION

The results obtained provide information on the post-glacial vegetation and environmental history of the Labanoras Region, East Lithuania, and allowed the interpretation of regional vegetation dynamics.

According to the Verpstinis Lake pollen data, sedimentation started here shortly before 12 600 cal yr BP or during the latest Allerød Interstadial (Walker *et al.*, 1999). The climate regime, with high mean temperature and humidity, was favourable for pine-dominated forest. The appearance of *Pinus* suggests that the mean July temperature was higher than +12°C (Kultti *et al.*, 2006). The flourishing of pine may indicate se-

Table 3

Plant macrofossil zones in Bevardis Lake

LMAZ	Depth [cm]	Description
B_M-4	45–330	Dominant of this zone is *Pinus*. It together with scattered remains of *Picea* and *Betula* reach from 40 up to 100% of all finds. Water plant taxa occur sporadically and their remains are negligible. *Carex* species are main component of group of wetland plants and *Carex nigra* predominate among them.
B_M-3	330–515	Trees predominate in this zone. *Pinus* culminates there alongside with *Betula* sect. *Albae*. Finds of *Picea* are registered in the upper part of zone. Water plants are represented by continuous finds of *Chara, Nymphaea alba* and several remains of other species (e.g., *Nuphar lutea, Najas flexilis, Sparganium erectum, S. natans, Potamogeton*). Different species of *Carex* represent group of wetland plants in this zone.
B_M-2	515–690	Remains of water plants culminate in this zone and finds of *Chara* predominate among them. Big amount of plant macroflora compose of tree remains. *Pinus* dominates in this zone. Scatered fruits of *Betula* sect. *Albae* and *Alnus glutinosa* are registered too. *Sphagnum, Bryales and Carex* are represented continuously while the rest taxa of wetland (e.g., *Comarum palustre, Eupatorium cannabinum*) occur sporadically.
B_M-1	690–845	Determination of this zone is based on the high *Sphagnum* representation (it composed mine part of sediments). Remains of other plants are scattered. *Menyanthes trifoliata* and some species of *Carex* are registered in the lower most and upper most part of this zone.

vere conditions, particularly in winter, *i.e.* increasing continentality (Walker, 1995). The formation of open, pine or pine-birch dominated forest was recorded in areas along the eastern margin of the Late Weichselian ice sheet during the Allerød (Zernitskaya, 1995; Veinbergs and Jakubovska, 1999; Ralska-Jasiewiczowa *et al.*, 2004; Stančikaitė *et al.*, 2004, 2009*a*; Saarse *et al.*, 2009; Heikkilä *et al.*, 2009; Wacnik, 2009; Amon *et al.*, 2010; Novik *et al.*, 2010). In some areas of southeastern Lithuania (Stančikaitė *et al.*, 1998) and Eastern Latvia (Heikkilä *et al.*, 2009), growing spruce was forming a denser vegetation cover. At the same time the distribution of the light-demanding species *Juniperus*, *Artemisia* and *Chenopodium* indicated the existence of open areas. The latter provided a source for terrigenous material transported into lake basins, as it was recorded in the Verpstinis Lake core where light grey gyttja with silt accumulated (Fig. 2).

Vegetation changed considerably in the area after *ca*. 12 600 cal yr BP. Representatives of light-demanding species *Juniperus* and *Selaginella selaginoides* as well as pioneer taxa *Chenopodium* and *Helianthemum* flourished here. The vegetation pattern indicated a climatic situation similar to the GS-1d event (Lowe *et al.*, 2008) or Younger Dryas cooling. The amount spruce (*Picea*) pollen increased and reached 5.8% in the late Younger Dryas, while the amount of two major representatives of the Allerød forest, birch and pine, decreased considerably. The post-glacial chronology as well as the migration pattern of spruce has been long discussed (Moe, 1970; Hafsten, 1992; Giesecke and Bennett, 2004; Giesecke, 2005; Latałowa and van der Knaap, 2006), however, new information on its history in the eastern Baltic and neighbouring regions was obtained recently. In SE Lithuania, *Picea* sp. seeds were found in deposits of Allerød age (Stančikaitė *et al.*, 1998), and became established in Western Lithuania in the late Younger Dryas, (Stančikaitė *et al.*, 2008). The pollen and plant macrofossils show an early Holocene, *ca*. 11 507–10 790 cal yr BP, immigration of this tree into northern and northeastern Lithuania (Stančikaitė *et al.*, 2004, 2009*b*). Similarly, the stomatal and plant macrofossils showed spruce expansion at *ca*. 12 900–11 700 cal yr BP into eastern (Heikkilä *et al.*, 2009) and briefly before 10 200 cal yr BP into Central (Kangur *et al.*, 2009) Latvia. Spruce had already arrived in the Late Glacial and early Holocene even in Scandinavia (Kullman, 2000, 2002; Segerström and Stedingk, 2003; Giesecke, 2005). However, in Northern Estonia where spruce pollen were discovered in Allerød deposits, "*Picea* macroremains have not been found in the Haljala sequence, the presence of *Picea* at the end of the Allerød still remains open..." (Saarse *et al.*, 2009). A fact that spruce arrived into the Labanoras environs shortly before 11 500 cal yr BP correlates very well with the regional pattern (Fig. 7). The presence of *Picea* suggests that a continental climate with warm summers (about 10–13°C) and moist soil conditions (Giesecke and Bennett, 2004) predominated in the region during the final stages of the Younger Dryas.

Pollen data suggest remarkable vegetation changes in the area during the initial stages of the Holocene. The birch and spruce forest development culminated at *ca*. 11 200–10 800 cal yr BP. The peak was followed by birch, pine and deciduous *Ulmus* and *Corylus* expansion. As suggested by Giesecke *et al.* (2008) "...the disappearance of *Picea* pollen in the beginning of the Holocene and the readvance of *Betula*–*Pinus* forest may indicate that the shift from the Younger Dryas was foremost a shift in winter temperatures and from a continental climate during the Younger Dryas to a more oceanic climate in the early Holocene". Simultaneously the number and variety of herbs, shrubs and grasses gradually decreased indicating consolidation of the vegetation cover. This climatic amelioration caused the deposition of peat with gyttja in Verpstinis Lake. The biological productivity increased, and the lake became partly overgrown. Similarly, Bevardis Lake started to convert into a bog with the deposition of peat after 10 000 cal yr BP.

Early Holocene climatic warming was followed by the introduction of new deciduous species. The earliest recorded pollen peaks of *Corylus*, *Ulmus* and *Alnus* reflected the regional rather than a local distribution pattern. *Corylus* was the first to appear in the area at *ca*. 10 200–10 000 cal yr BP. Italy and Western France were major refuge areas for this faxon during the Last Glaciation, although there are also indications of this plant on the Hungarian Plain (Bennett *et al.*, 1991). Hazel

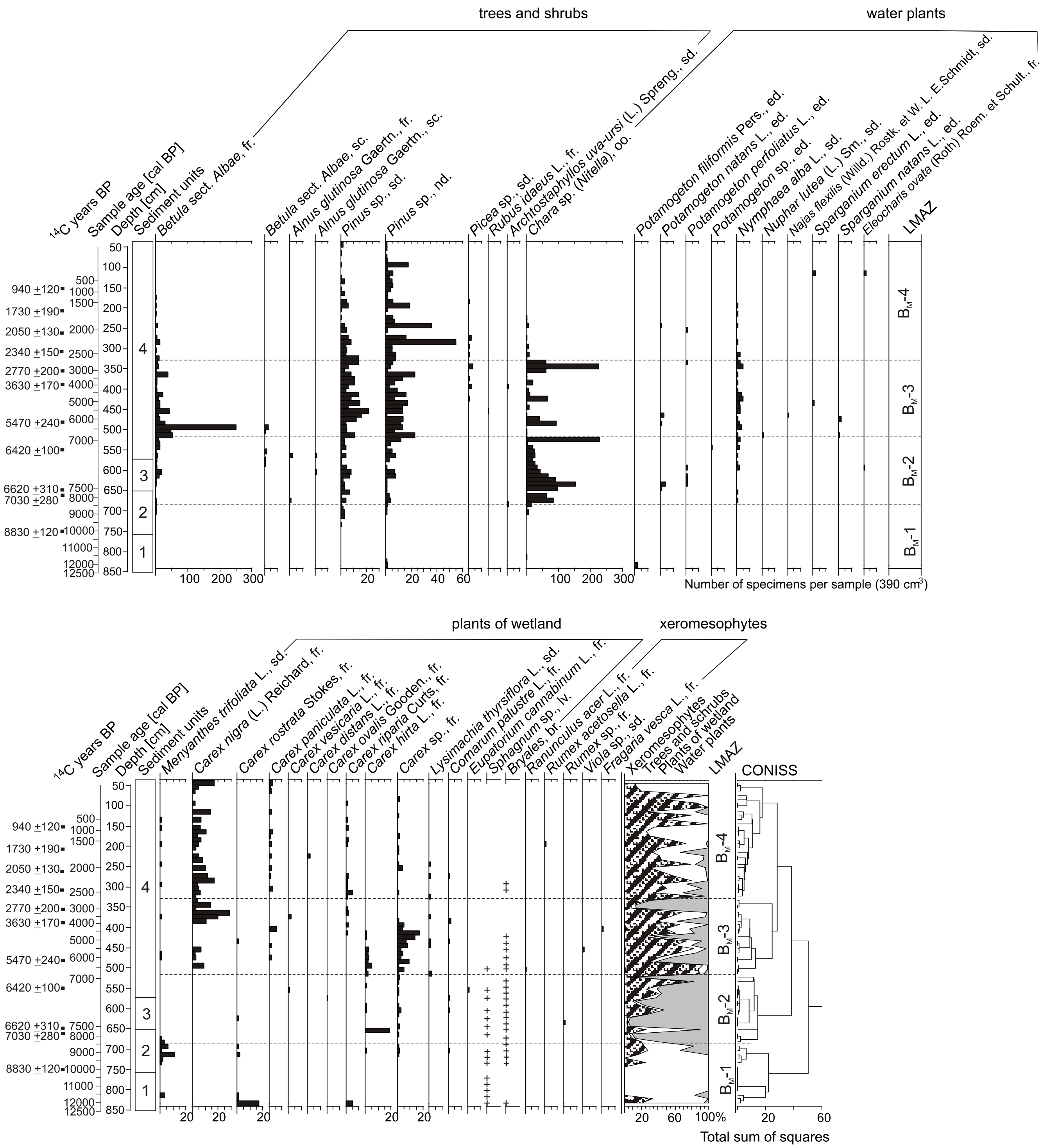

Fig. 5. Plant macrofossil diagram for the Bevardis Lake sediment sequence

br. – branch, ed. – endocarp, fr. – fruit, lv. – leaf, nd. – needle, oo. – oospore, sc. – scale, sd. – seed; analysed by Kisielienė (2010)

which is very common in early forest development may grow on different soils as compared to thermophylous taxa (Huntley and Prentice, 1993). Therefore *Corylus* could spread easily in the study area where sandy habitats predominated. The early Holocene immigration of this tree to northeastern Poland was dated to *ca*. 9450 cal yr BP (Wacnik, 2009), while it arrived to Estonia before 10 000 cal yr BP (Saarse, 2004). In central and northwestern Belarus *Corylus* appeared at *ca*. 9700 cal yr BP (Zernitskaya and Kolkovskij, 2003; Novik *et al.*, 2010). Possible migration routes for this tree to the eastern Baltic region from the south-west and west (Miotk-Szpiganowicz *et al.*, 2004; Saarse, 2004) explain the recorded differences of the immigration chronology (Fig. 7).

Table 4

^{14}C uncalibrated (BP) and calibrated (cal yr BP) dates from Bevardis and Verpstinis

No.	Depth [cm]	^{14}C [yr BP]	Calibrated age [cal yr BP] (68.2%)	Laboratory code	Dated material
Bevardis Lake					
1	150–155	940 ±120	960–730	Vs-1430	bulk organic
2	205–210	1730 ±190	1870–1410	Vs-1448	
3	255–260	2050 ±130	2160–1870	Vs-1431	
4	305–310	2340 ±150	2700–2150	Vs-1428	
5	355–360	2770 ±200	3250–2700	Vs-1434	
6	385–390	3630 ±170	4250–3700	Vs-1429	
7	480–485	5470 ±240	6500–5900	Vs-1435	
8	540–550	6420 ±100	7430–7250	Vs-1959	
9	650–655	6620 ±310	7850–7150	Vs-1968	
10	660–665	7030 ±280	8200–7600	Vs-1951	
11	750–755	8830 ±120	10.160–9980	Ki-10954	
Verpstinis Lake					
1	240–245	3480 ±250	4100–3450	Vs-1449	bulk organic
2	405–410	5900 ±250	7050–6400	Vs-1450	
3	470–475	7270 ±100	8180–7980	Ki-11400	

Ash trees followed hazel in the area investigated. Even though *Ulmus* appeared as one of the first deciduous trees during the initial stages of the Holocene in Lithuania (Kabailienė, 2006) and neighbouring countries (Ralska-Jasiewiczowa and Latałowa, 1996), this plant immigrated to the Labanoras area not earlier than *ca.* 10 000 cal yr BP. The latter fact can be explained by predominance of poor sandy soils in the study area while this taxon is very vulnerable to drought and requires moist and fertile soil (Grime *et al.*, 1986). *Ulmus* expanded from southeastern Europe suggesting its refuge had been in Southern and Central Europe (Rudner and Sümegi, 2001; Willis and Tjeerd, 2004) including the Hungarian Plain (Willis *et al.*, 2000) and the Eastern Carpathians (Björkman *et al.*, 2002, 2003). In NE Poland the arrival of *Ulmus* is dated at *ca.* 94 50 cal yr BP (Wacnik, 2009), in northwestern Belarus at *ca.* 10 200–9700 cal yr BP (Novik *et al.*, 2010), and in Latvia at *ca.* 10 000–9500 cal yr BP (Ilves and Medne, 1979), indicating overall climatic amelioration, formation of fertile soils and increasing humidity. However, in Western Estonia the earliest records of *Ulmus* were dated at 10 700–10 800 cal yr BP suggesting a western immigration pathway (Veski, 1998).

Alnus was the last deciduous tree which immigrated to the Labanoras Region during the early Holocene. It is still widely accepted that in this part of Europe *Alnus* was established in the early Holocene; however, recent publications on pollen and plant macrofossil data suggest a Late Glacial age of this tree in Western Lithuania (Stančikaitė *et al.*, 2008) and Northern Poland (Latałowa and Borówka, 2006). Such early establishment of *Alnus* in the western part of the Baltic region may imply a migration route from the west. The western migration route sheds light on the history of *Alnus* in Estonia where alder was established at *ca*. 9500 cal yr BP, or even earlier depending on the site and region (Veski, 1998; Saarse *et al.*, 1999). Furthermore this chronology fits very well with the history of *Alnus* in northwestern Lithuania where alder was dated at *ca*. 9000–8800 cal yr BP (Stančikaitė *et al.*, 2006). Evidently, the western route of alder expansion as well as its post-glacial chronological framework has to be studied more carefully in the Baltic region.

Alnus appeared in the Labanoras area and all of Eastern Lithuania at *ca*. 8200–8000 cal yr BP, almost at the same time as in northeastern Poland where the earliest pollen peaks were dated back to 8160 cal yr BP (Wacnik, 2009). Alder was established somewhat earlier in Latvia, i.e. at *ca*. 8800–8600 cal yr BP (Ilves and Medne, 1979), and even earlier in Belarus. In southwestern Belarus, the earliest peak of the *Alnus* pollen curve was dated back to *ca*. 9400–9300 cal yr BP, while in the northwestern part the amount of alder pollen increased considerably at *ca*. 8600 cal yr BP (Novik *et al.*, 2010). Since the results of DNA analysis show that the majority of north and central European areas were occupied by alder derived from the Carpathian refugia (Środoń, 1981; King and Ferris, 1998), its immigration to Baltic countries *via* Belarus is easily explicable. In our opinion, the *Alnus* history was mainly influenced by local factors such as the quality of soil, number of suitable habitats and hydrological conditions in the Labanoras area. Poor sandy soils, typical for the marginal area of the Weichselian Glaciation, of the Labanoras Region were highly unsuitable for the early immigration and prosperity of this tree.

The expansion of *Alnus*, *Corylus* and *Ulmus* was followed by the time-transgressive immigration of *Tilia* which was recorded in the Labanoras area between 7700 and 7400 cal yr BP. This tree prefers habitats with rich, mineral-humic soils, quite different from those in the study area, which is why the amount of *Tilia* pollen is rather low in the both diagrams (Figs. 3 and 4). Moreover is highly possible that the earliest pollen grains dated back to *ca*. 8000 cal yr BP originated at quite a long distance. The southern part of Romania and the Hungarian Plain

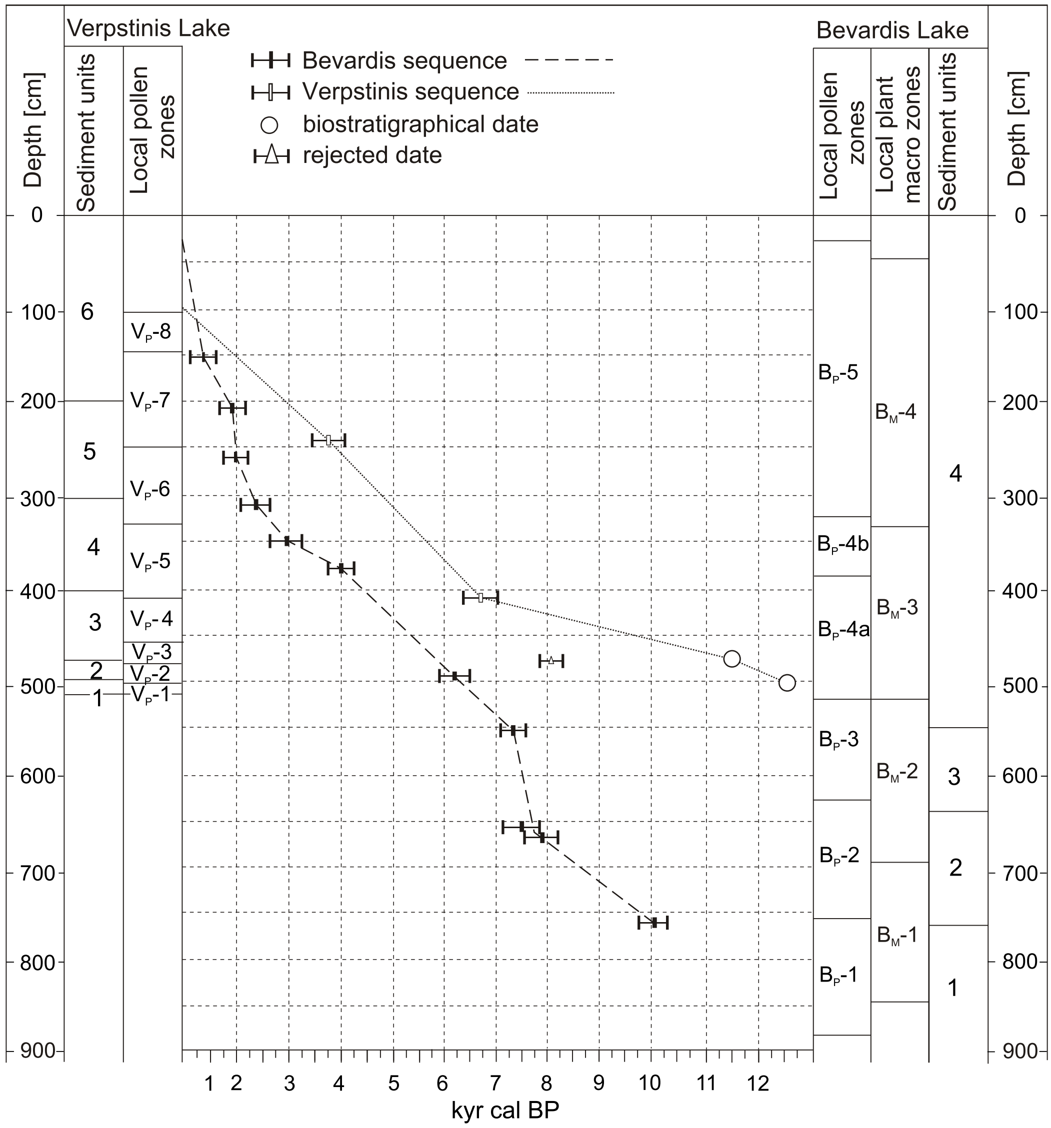

Fig. 6. Age-depth curves for the sediments of the Bevardis and Verpstinis lakes

(Björkman *et al.*, 2003) have been indicated as possible refugia areas of this taxon during the Last Glaciation. The earliest immigration of lime, dated back to 9200–9600 cal yr BP, was recorded in northwestern Belarus (Novik *et al.*, 2010) and shortly later, at 8500–8000 cal yr BP, *Tilia* started to expand into southeastern Estonia (Niinemets and Saarse, 2009) and Eastern Latvia (Ilves and Medne, 1979). Nearly at the same time, i.e. at *ca*. 8160 cal yr BP, this plant reached northeastern Poland (Wacnik, 2009). Such a relatively late immigration of lime to northeastern Poland and the delayed arrival of this taxon to the Labanoras area were determined by local conditions, e.g., lack of the proper habitats, rather than by the regional features. The distribution of lime depends very much on the degree of climate continentality (Kupryjanowicz *et al.*, 2004) which may have increased due to the 8200 cal yr BP climatic reversal caused by cold winters, humid summers and strong seasonal contrasts (Seppä *et al.*, 2005).

Quercus and *Fraxinus* were the last broad-leaved species established in the area investigated. In the Verpstinis pollen diagram (Fig. 3), the rational limit of the *Quercus* pollen curve was recorded at *ca*. 5200 cal yr BP. At that time the proportion of *Quercus* pollen exceeded 2% indicating its local origin (Huntley and Birks, 1983). In addition, the low level of ash pollen confirms the fact that both trees were insignificant in the local forest community. The empirical limit of ash was dated at *ca*. 5500 cal yr BP. However, the palaeobotanical data shows that *Quercus* and *Fraxinus* were established much earlier elsewhere in the region. For example, in northeastern Poland they were established at *ca*. 8160 cal yr BP (Wacnik, 2009), in southeastern Estonia at *ca*. 8500–8000 cal yr BP (Niinemets and Saarse, 2009), whereas in Northern Estonia oak did not appear until *ca*. 6700 cal yr BP (Saarse and Veski, 2001). Oak immigrated to Eastern Latvia at *ca*. 8100–8000 cal yr BP (Ilves and Medne, 1979). The earliest finds of *Quercus* pollen were

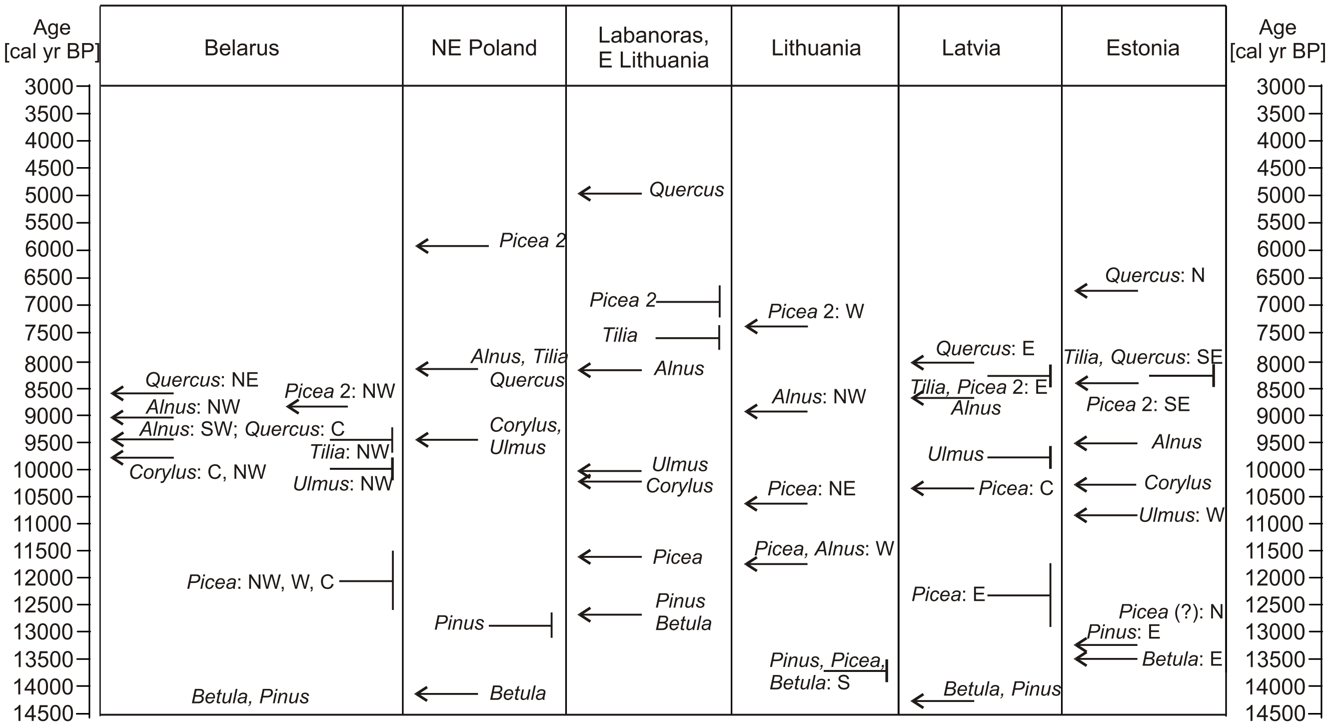

Fig. 7. Summary chart of tree immigration to the region

C – central part, E – eastern, W – western, NW – northwestern, NE – northeastern, S – southern, SW – southwestern parts of the countries

dated back to 9500–9400 cal yr BP in the central part of Belarus (Elovicheva and Bogdel, 1987) and back to *ca*. 8600 cal yr BP in the northeastern part of the country (Novik *et al*., 2010). Presumably both trees immigrated from the south-east or south that coincides with the two migration routes established on a European scale (Milecka *et al.*, 2004). It should be pointed out that the expansion of these trees to Northern Europe has mainly been controlled by the climatic factors during the initial stages of the colonization; however, the importance of secondary factors including local topography, hydrology, quality of soil cover and so on increased later. The Holocene thermal maximum, which started at *ca*. 8000 cal yr BP (Seppä and Poska, 2004), was generally responsible for the expansion of these trees to the eastern Baltic region, while the delayed expansion of oak to the Labanoras area may have been determined more by secondary factors, e.g., scarcity of soil cover and lack of suitable habitats.

Flourishing of broad-leaved forest is the next important factor which characterizes the vegetation history in the region throughout the Holocene. Undoubtedly the Holocene thermal maximum distinguished at 8000–4500 cal yr BP (Seppä and Poska, 2004) played a leading role in this process. The pollen-stratigraphical data reflect progressively warmer and drier summers at that time that may be interpreted as indications of increasing climatic continentality (Seppä and Poska, 2004). The broad-leaved forest reached its development maximum at *ca*. 7400–5100 cal yr BP in Estonia (Saarse and Veski, 2001). In the northeastern part of Poland, the thermophilous trees attained the optimum of their Holocene development between 7300 and 6000 cal yr BP (Kupryjanowicz, 2007). The *Quercetum mixtum* pollen sum shows that these trees were present in the Labanoras area from 7400 to 4200 cal yr BP. Evidently, the prospering of the broad-leaved forest started nearly simultaneously throughout the region while its decline differs in time and may have been caused by both natural and anthropogenic factors. In case of Labanoras, this recession was coincident with the cooling that followed the Holocene thermal maximum briefly after 4500 cal yr BP. In northwestern Belarus, the first elm decline was dated back to *ca*. 5700 cal yr BP followed by the lime and oak recession between 4700 and 4500 cal yr BP (Novik *et al*., 2010). In Estonia, the gradual retreat of broad-leaved trees caused by climatic and anthropogenic factors as well as by fungal diseases started even earlier at *ca*. 6300–5700 cal yr BP (Saarse and Veski, 2001).

The decline of broad-leaved species was followed by the prospering of shady forest where *Picea* gained a renewed importance. The amount of *Picea* pollen is low in the Bevardis and Verpstinis diagrams (Figs. 3 and 4), while the amount of spruce increased from *ca*. 7300–6800 cal yr BP onwards. The chronological framework is similar to that in Western Lithuania where the pollen data suggests a negligible input of spruce by 7400–7300 cal yr BP (Stančikaitė *et al*., 2006). Spruce re-appeared somewhat earlier in the neighbouring areas, i.e. at *ca*. 8800 cal yr BP in northwestern Belarus (Novik *et al*., 2010) and at *ca*. 8400 cal yr BP in southeastern Estonia (Saarse, 2004) and Eastern Latvia (Ilves and Medne, 1979). This early appearance of spruce in the eastern part of the region fits well with the E–W and NE–SW immigration routes of this tree indicated in Latałowa and van der Knaap (2006). However, the appearance of *Picea* in the Suwałki Lake District, northeastern Poland, at *ca*. 5700–5900 cal yr BP indicates a remarkable delay (Obidowicz *et al*., 2004; Kupryjanowicz, 2007). We assume that *Picea* immigrated later there because of local factors such as soil conditions and lack of favourable sites in the marginal area of Weichselian Glaciation. Generally the re-establishment of *Picea* in the region is close in time with the so-called "8.2" climatic event dated back to 8600–8000 cal yr BP (Seppä and Poska, 2004). This short-lasted climatic deterioration may have limited the expansion of deciduous trees, providing space for the spruce. Furthermore, the development of spruce forest may possibly be a response to a wet and cool climate with colder and snowier winters (Seppä and Poska, 2004). Spruce dominated woodland in the Labanoras area until *ca*. 2400–2200 cal yr BP. The area was covered with dense shady forest and experienced a generally stable climatic regime. The prospering of spruce ended somewhat earlier in the neighbouring regions, i.e. at *ca*. 3000 cal yr BP in southeastern Estonia (Niinemets and Saarse, 2009) and northeastern Poland (Obidowicz *et al.*, 2004). This widespread late Holocene spruce decline caused by the increasing human impact and climate change was recorded in western areas of Central and Eastern Europe (Latałowa and van der Knaap, 2006).

During the last two thousand years, the earlier dominance of spruce and broad-leaved species ended, and the diversity of the local forest increased considerably. The pollen data indicate that *Betula*, *Pinus*, *Corylus* and *Salix* as well as herbs and grasses gained more ground in the area. The distribution of the cereals *Cerealia* and *Triticum* and ruderals such as *Artemisia* and Chenopodiaceae points towards a human presence in the area even though this impact was negligible, and the development of vegetation was driven mostly by natural factors.

CONCLUSIONS

The results of multiproxy (pollen, plant macrofossils, ^{14}C and LOI) studies has revealed the pattern of evolution of the palaeoenvironment in the Labanoras area (Eastern Lithuania) during the post-glacial interval.

During the Allerød Interstadial, the development of forest cover started with *Pinus* and *Betula* stands in the area. Despite the fact that tundra-dominated vegetation existed in the area throughout the Younger Dryas cooling, an influx of *Picea* was recorded shortly before 11 500 cal yr BP suggesting a rise in the mean temperature accompanied by increasing humidity. Spruce declined shortly after the onset of the Holocene, and hazel was the first newly established deciduous tree in the area. *Corylus* arrived at *ca*. 10 200–10 000 cal yr BP and was followed by *Ulmus* at *ca*. 10 000 cal yr BP. They were established here later than in the rest of Lithuania, this being likely determined by local factors such as poor sandy soils typical for marginal areas of the Late Weichselian Glaciation. *Alnus* arrived and started to expand along with the above-mentioned species at *ca*. 8200–8000 cal yr BP, though its representation was rather low in the area throughout the Holocene. *Tilia* appeared at *ca*. 7700–7400 cal yr BP, while *Fraxinus* with *Quercus* were established even later at *ca*. 5500 and *ca*. 5200 cal yr BP respectively. The time-transgresive, delayed immigration and low abundances of these broad-leaved taxa were caused by scarse soil cover and lack of suitable habitats. Nevertheless, broad-leaved trees were present in the Labanoras forests until *ca*. 4000 cal yr BP, likely because of generally warm and humid conditions. However, some climatic instabilities at *ca*. 7300–6800 cal yr BP may have favoured *Picea* expansion in the region. Spruce dominated the woodland until *ca*. 2400–2200 cal yr BP in the Labanoras surroundings. During the last few thousand years, both the decline of spruce and subsequent formation of a *Betula*- and *Pinus*-dominated forest were driven by natural factors because the minor traces of human impact on the both diagrams show only negligible human activity in the area.

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