Estonian Journal of Ecology, 2010, **59**, 4, 259–280 doi: 10.3176/eco.2010.4.02

Linking diatom community dynamics to changes in terrestrial vegetation: a palaeolimnological case study of Lake Ķūži, Vidzeme Heights (Central Latvia)

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Received 26 April 2010, revised 13 September 2010

Abstract. Diatom and pollen records from the deepest part of Lake Ķūži (Vidzeme Heights, Central Latvia) show the history of the lake and its ecosystem responses to changes in the surrounding vegetation during the Holocene. Principal Component Analysis (PCA) was used to compare the timing of the changes in the diatom and pollen assemblages. We found that major changes in the diatom record were contemporaneous with those in the pollen records. At the beginning of the Early Holocene, when the lake was receiving high inputs of mineral matter, no diatoms were found. Around 11 000 cal. BP, when the upland vegetation became established, periphytic diatom taxa (mostly *Fragilaria* species) prevailed. The Mid-Holocene period (9000–2000 cal. BP) was characterized by *Cyclotella* spp. and *Tabellaria flocculosa*, indicating long ice-free seasons and a rather high water level. *Picea* was a major tree species around the lake 5300–2500 cal. BP and it facilitated acidification of the lake water via the acidification of the soil, indicated by the increase in the acidophilous diatoms *Eunotia* spp. and *T. flocculosa*. The Late Holocene (2000–0 cal. BP) is characterized by anthropogenic impacts on both the upland vegetation and lake ecosystem, depicted by the simultaneous increase in *Aulacoseira* spp., herbaceous pollen such as Poaceae, *Secale*, and *Rumex*, and charcoal fragments. With pollen taxa used as predictor and diatom taxa as response variables, Redundancy Analysis (RDA) provided a statistically significant model that explains the variation in the diatom data. Our results show that the diatoms responded strongly to the catchment-driven changes around Lake Ķūži during the entire Holocene.

Key words: diatoms, pollen, palaeolimnology, Holocene, Lake Ķūži, Vidzeme Heights, Latvia.

INTRODUCTION

Palaeolimnological studies offer an opportunity to improve our knowledge about the past environmental conditions as the physical, chemical, and biological information preserved in lake sediments provides an insight into past events that have occurred within the catchment and their effects on the lake environment.

Due to their ability to colonize new habitats quickly and their sensitivity to environmental factors, diatoms (Bacillariophyceae) can be used to trace changes in a lake, such as water depth, aquatic pH, nutrient availability, salinity, and current conditions. They are preserved well in many types of sediment because of the siliceous composition of their cell walls (Stoermer & Smol, 1999; Battarbee et al., 2001). These features make diatoms ideal for reconstructing environmental changes in lake ecosystems.

As diatoms primarily reflect conditions in a waterbody, palynological analysis is needed to describe the development of its surroundings. Pollen-based palaeoecological studies can provide an essential long-term perspective, not available from the instrumental record or modern ecological studies, on the development of vegetation and its response to past climate change and human impact (Moore et al., 1991; Galloway et al., 2007).

Although palaeoecological records of terrestrial (pollen) and aquatic (diatoms) biota are important in assessing past environmental conditions in a lake and its surroundings, these proxies are frequently observed separately. Palaeolimnological studies quite often focus solely on a lake and its changes while the catchment of the lake is just a background. The reason for this is that the interpretation of patterns in proxy records can be challenging because different components of an ecosystem responding to different aspects of environmental variability have different sensitivities and thresholds to the environmental changes influencing the lake and its catchment system.

The general assumption is that diatoms reflect the development of an aquatic ecosystem and the pollen profile indicates the dynamics of vegetation on the catchment. At the same time processes inside a lake are closely related to the changes in the terrestrial ecosystem, especially to those taking place on the lake catchment. Using pollen and macrofossil data, Kangur et al. (2009) described the Holocene stratigraphy and palaeogeography of a paludified near-shore area of Lake Ķūži (Vidzeme Heights, Central Latvia). They distinguished two terrestrial periods (first from ca. 11 400 cal. BP up to 10 900 cal. BP and the second from 700 cal. BP until present) when the water level was below or around the sediment limit and a lacustrine period between these two when the water level was mainly above the sediment surface. The relatively stable water level after 10 900 cal. BP suggests that the changes in diatom and pollen profiles were mainly caused by other factors than lake-level fluctuations. Therefore we find that this lake is a suitable object for examining lake–catchment interactions and for comparing the dynamics of diatom and pollen sequences, which was the first aim of this study. The overall purpose was to improve the reconstruction of the environmental history of the small Lake Ķūži and the vegetation in its surroundings during the Holocene based on diatom and pollen data.

STUDY SITE

Lake Ķūži (57°2′ N, 25°20′ E; altitude 191.5 m a.s.l.) is situated in the western part of the Vidzeme Heights, Central Latvia (Fig. 1a). The Vidzeme Heights is located distally from the ice marginal formations of the Luga (North Lithuanian) stage. The most impressive formations of this ice advance were formed about

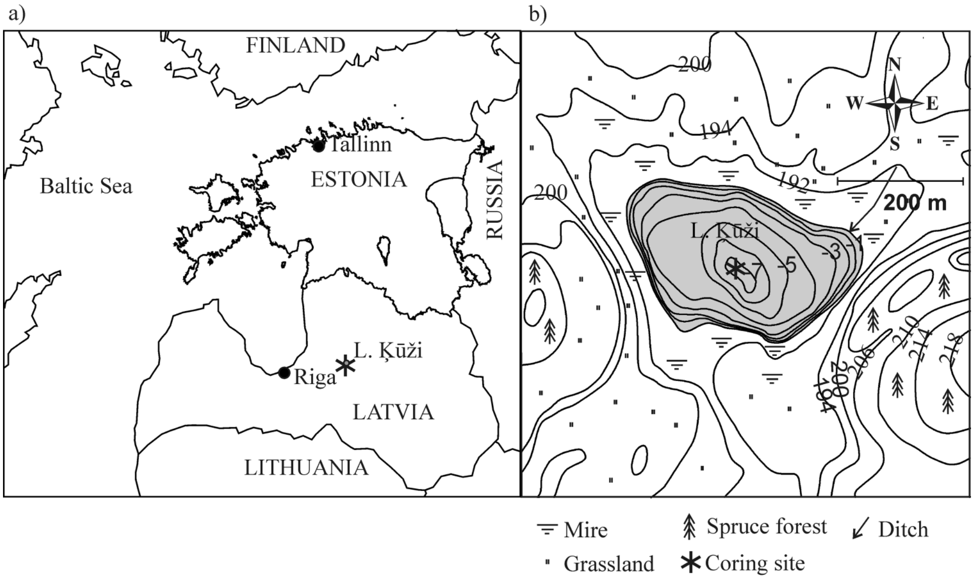

Fig. 1. Location (a) and bathymetry (b) of Lake Ķūži.

13 200–13 000 BP (Raukas et al., 1995). The topography of the Vidzeme Heights is varied and complex, with the dominance of subglacial landforms. The elevations of the area vary from 180 to 240 m. Small depressions between hillocks were formed following the withdrawal of glaciers. Many basins, such as Lake Ķūži, are of glaciokarstic origin.

The mean annual precipitation is about 800 mm, of which 550 mm falls in summer and 250 mm during the cold season. The mean summer and winter temperatures are 16.5 °C and –7.5 °C, respectively. The frost-free period lasts for 120 days and the vegetation period for 175–185 days. The area is usually covered with snow from November to April. The soils are varied in the region because of the hilly topography. Podzols dominate on the hills and cultivated slopes are intensively eroded (Āboltiņš, 1997).

The Vidzeme Heights belongs to the Central Vidzeme geobotanical region. Only 25% of the heights is covered with forests; the rest of the area is mainly cultivated. The most common are mixed spruce forests, which make up 50.4% of all the forests in the area (Kabucis, 1994).

Lake Ķūži has a surface area of 6.5 ha. Its maximum depth is 8 m, maximum length 380 m, and maximum width 250 m. The lake is fed by four artificial inflows and has no active outflow. It is situated in the hilly landscape and is surrounded in the north-west by an up to 100 m wide peaty area (Fig. 1b). The hydrological catchment has an area of 155 ha and is covered with forests to the east and west of the lake. Meadows and agricultural land are situated to the north and south of the lake.

METHODS

Fieldwork, dating, and lithology of the sediment

A 9.2 m long sediment core (KC081) was taken close to the deepest part of the lake (Fig. 1b) in June 2008. The unconsolidated sediments in the upper layers (from surface to 100 cm depth) were sampled using a modified Livingstone–Vallentyne piston corer (diameter 7 cm). The lower, more consolidated sediments were sampled with a Belarus (Russian) peat sampler (chamber length 1 m, inside diameter 7 cm). The lithological description of the cores was recorded in the field. The top 100 cm was contiguously sub-sampled at 2 cm intervals. The sediment core taken with the peat sampler was photographed and wrapped in plastic. The samples remained refrigerated in dark before sub-sampling in the laboratory prior to analysis.

The chronology of the sediment core is based on five AMS ^{14}C dates of terrestrial macrofossils (Table 1). Samples were sent for dating to the Poznan Radiocarbon Dating Laboratory, Poland. The radiocarbon calibration program OxCal v4.1.3 (Bronk Ramsey, 2009) was used for the calibration.

The lithological analyses were performed by the standard loss-on-ignition (LOI) method. To determine the water content the samples were contiguously taken at 2 cm intervals and dried at 105 °C for 24 h. The content of organic matter

Table 1. Radiocarbon dates from Lake Ķūži. The dates were calibrated using IntCal09 (Reimer et al., 2009) in OxCal v4.1.3 (Bronk Ramsey, 2009)

Depth, cm	Dated material	Laboratory number	^{14}C date, yr BP	Calibrated year range (1σ; 68.2%), cal. BP	Calibrated year range (2σ; 95.4%), cal. BP	Calibrated age (mid intercept), cal. BP
260–265	*Picea* seeds	Poz-26181	2 508±30	2 695–2 717 (10.8%) 2 614–2 637 (11.5%) 2 501–2 595 (45.9%)	2 487–2 736 (95.4%)	2 610
365–370	*Picea* needle, *Betula* seeds, *Salix* remains	Poz-26182	4 553±35	5 276–5 315 (25.9%) 5 125–5 167 (22.5%) 5 070–5 109 (19.8%)	5 213–5 320 (38.2%) 5 052–5 191 (56.3%)	5 120
460–465	*Betula* seeds, *Picea* seeds	Poz-26184	5 257±40	6 155–6 174 (9.3%) 6 080–6 112 (16.0%) 5 938–6 021 (42.9%)	6 143–6 180 (13.6%) 5 925–6 125 (81.8%)	6 030
660–665	*Betula* seeds, *Alnus* seeds	Poz-26185	7 123±60	7 928–8 006 (55.3%) 7 872–7 895 (12.9%)	7 820–8 050 (94.4%) 7 794–7 814 (1.0%)	7 940
860–865	Wood remains	Poz-26186	9 891±60	11 377–11 388 (3.5%) 11 227–11 355 (64.7%)	11 529–11 603 (6.3%) 11 428–11 496 (5.4%) 11 201–11 413 (83.7%)	11 310

was measured by LOI after 3.5 h of combustion at 550 °C and expressed as the percentage of dry matter. The carbonate content was calculated from the loss of weight after burning the LOI residue at 950 °C for 2.5 h (Heiri et al., 2001). The siliclastic (minerogenic) component was calculated by subtracting the amounts of LOI_{550} and LOI_{950} from the dry mass.

Diatom and pollen analyses

Samples of diatoms and pollen were taken from the same stratigraphic levels to allow sample-by-sample comparison between proxies. Diatom samples were prepared using standard methods based on Battarbee et al. (2001). Diatom samples at 10 cm intervals were prepared with 33% H_2O_2 and 10% HCl. Aliquot evaporated suspensions were embedded in Naphrax. At least 500 valves were counted per sample using a 1000× oil immersion objective (N.A. 1.5) on an Olympus BX41 light microscope equipped with DIC optics. Abundance of diatom species was expressed as the percentage of the sum total of all diatoms counted in each sample. Diatom concentrations, expressed as frustules per mass of oven-dried sediment (DW), were calculated by adding a known quantity of microspheres to samples (Battarbee & Kneen, 1982). Diatoms were classified according to their habitat into two groups: planktonic and periphytic. Periphytic taxa in this study include all epilithic, epipelic, epiphytic, and shallow-water benthic life forms. The planktonic taxa designations include euplanktonic, tychoplanktonic, and meroplanktonic taxa. Diatom identifications and nomenclature are based on Krammer & Lange-Bertalot (1988–1991; 1999–2004).

For pollen analysis 1 cm^3 block samples from every 10 cm were treated with a 10% KOH solution followed by standard acetolysis according to Moore et al. (1991). Three tablets containing a known number of *Lycopodium* spores were added to each sample at the beginning of the treatment, thus enabling the calculation of pollen concentrations and accumulation rates (Stockmarr, 1971). Generally all pollen grains and spores were counted to at least 500 arboreal pollen (AP) grains per sample. Pollen and spore nomenclature follows Moore et al. (1991). Besides the pollen grains also non-pollen palynomorphs (NPP) were counted from the same slides.

Numerical analysis

Stratigraphic pollen and diatom zones were determined with CONISS (constrained incremental sum of square cluster analysis) in the TILIA program (Grimm, 1990). Diagrams were also constructed using TILIA and TILIA GRAPH (Grimm, 1990). The percentage pollen diagrams are based on total terrestrial pollen sums. Concentrations of charcoal pieces and NPP (number of pieces in cm^{-3} sediment) were calculated using the ratio of counted and added *Lycopodium* spores.

In order to investigate the dynamic changes in the diatom and pollen composition, detrended correspondence analysis (DCA) was applied. The percentage data were transformed to their square roots in an attempt to stabilize the variance in each data set. All gradient lengths were shorter than 2 standard deviation units; therefore, linear ordination techniques (Principal Component Analysis (PCA)) were employed. Direct gradient ordination by Redundancy Analysis (RDA) was used to identify correlations between diatom and pollen data. RDA is a constrained form of PCA, where the ordination axes are constrained to be linear (Birks, 1995). The explanatory variables used for RDA were main pollen types or groups (*Picea*, *Pinus*, *Betula*, *Alnus*, herbs, broad-leaved trees) and charcoal. In the present study the term *broad-leaved trees* is used for *Alnaster, Corylus*, *Ulmus*, *Quercus*, *Tilia*, *Fraxinus*, *Carpinus*, and *Fagus*. RDA was performed using Monte Carlo tests with 999 permutations to determine variables that explained significant ($p < 0.05$) amounts of variation in the diatom data. Diatom taxa were retained in the statistical analyses if they were present in at least four samples and their relative abundance in at least one of these samples was ≥2%. All ordinations were performed with the program CANOCO version 4.52 (ter Braak & Šmilauer, 2002).

RESULTS

Lithology, chronology, and the content of organic matter and carbonates

Details of the five samples from the Lake Ķūži sediment core dated by the AMS ^{14}C technique are shown in Table 1. In order to compare results obtained in this study and in an already published paper (Kangur et al., 2009), the uncalibrated and calibrated dates were plotted against depth (Fig. 2). Lithological descriptions and the content of carbonates, organic matter, and mineral matter are given in percentages in Fig. 3. The organic matter content is very low from the base of the core to 865 cm (ca. 11 400 cal. BP), not reaching more than 8%. Subsequently it increases sharply to over 60%. A decrease in the organic matter content can be observed starting at 650 cm (7800 cal. BP). The average content is 33% between 650 and 240 cm (7800–2400 cal. BP). Above 240 cm, the organic matter content increases (maximum 45%) until 80 cm (800 cal. BP). From 80 cm, it steadily decreases to 30%. The content of carbonaceous matter is relatively low throughout the record (mean value 7%); only the lowermost part of the sediment sequence contains more than 10% carbonates.

The sediment stratigraphy is described in Table 2. The sediment sequence was subdivided into six lithological units on the basis of the visual description and photographic documentation applied directly after coring in field. In general it indicates that gravel and sand with silt and clay fractions (920–870 cm) are covered by unstructured gyttja with silty clay and a thin peat layer (865–859 cm; ca. 11 400 cal. BP). The central part of the sediment sequence consists of partially

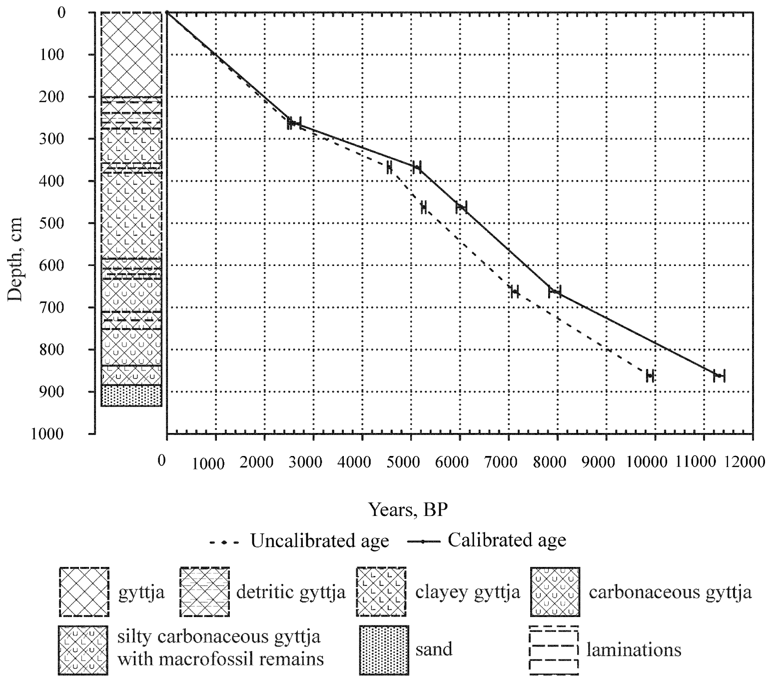

Fig. 2. Age–depth curve of Lake Ķūži sediment core KC081 based on five AMS ^{14}C dates shown in Table 1.

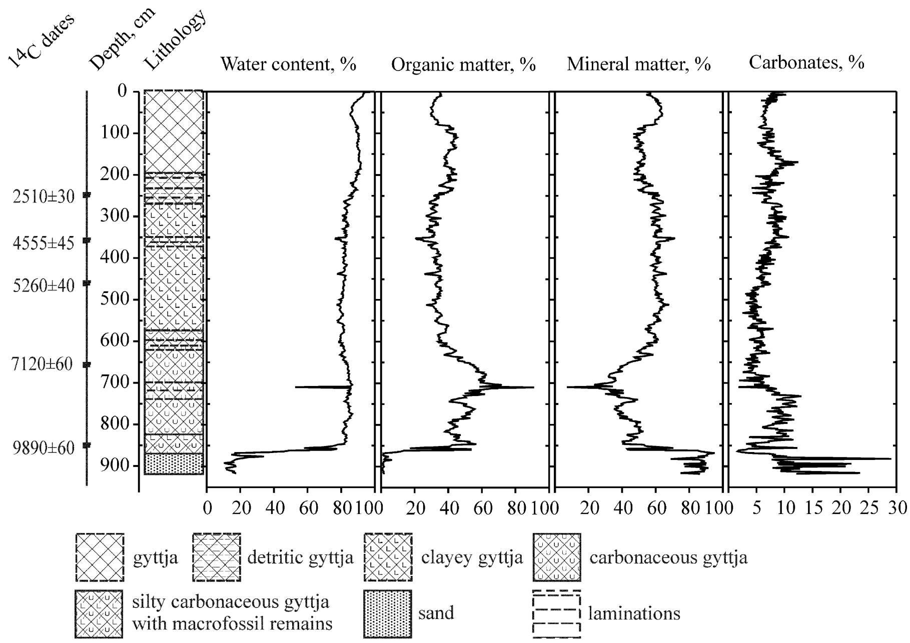

Fig. 3. Lithostratigraphy and the content of water, organic matter (LOI_{550}), carbonaceous matter (LOI_{950}), and minerogenic component in Lake Ķūži sediment core KC081.

Table 2. The sediment lithology of core KC081 from Lake Ķūži

Depth from the sediment surface, cm	Lithological description
0–200	Gyttja
200–270	Dark brown detritic gyttja with laminations
270–570	Clayey gyttja with laminations
570–840	Dark brown carbonaceous gyttja with lighter interlayers
840–870	Silty carbonaceous gyttja with macrofossils and thin peat layer (859–865 cm)
870–920	Sand with silt and clay fractions

laminated carbonaceous, clayey dark brown detritic gyttja (840–200 cm; ca. 11 000–2000 BP). More regular and undisturbed laminations appear between 370 and 200 cm sediment depth (5100–2000 cal. BP). The upper part (200–0 cm) of the sediment core is homogeneous gyttja with no abrupt transitions.

Diatom stratigraphy

All samples in the Holocene sediment sequence from Lake Ķūži were generally rich in well-preserved diatoms except the samples from the deepest part of the sediment core (920–860 cm), which contained only a few valves. Altogether over 230 diatom taxa representing 32 genera were recorded in the sediment sequence. The diatom profile was divided into seven local diatom assemblage zones (D-K81 (1–7)), which are briefly described in chronological order (Fig. 4).

The lowest zone D-K81-1 (up to 11 100 cal. BP, up to 850 cm) contains only a few diatom valves. These belong mainly to the genus *Fragilaria*.

Diatoms first appear abundantly at 850 cm in zone D-K81-2 (11 100–9000 cal. BP, 850–725 cm). Then the lake was dominated mainly by periphytic taxa (over 80%) such as *Fragilaria construens* var. *venter*, *F. leptostauron*, *F. pinnata*, *F. brevistriata*, and *Achnanthes* spp. Small quantities of planktonic *Cyclotella* spp. (*C. ocellata*, *C. radiosa*) were found. The dominants in this zone are meso-eutrophic species. Diatoms are absent in samples from the depth 740 to 730 cm (9200–9100 cal. BP) but reappear at 720 cm depth.

At a depth of 720 cm in zone D-K81-3 (9000–7400 cal. BP, 725–605 cm) planktonic taxa become dominant, mainly caused by the increase of *Cyclotella ocellata*, *C. radiosa*, and other small *Cyclotella* species. This zone is characterized by the first significant occurrence of *Tabellaria flocculosa*. The percentage of planktonic taxa rises to 80%. Of periphytic taxa, many *Fragilaria*, *Achnanthes*, and *Navicula* species occur.

The dominance of planktonic diatoms continues in zone D-K81-4 (7400–5600 cal. BP, 605–415 cm). The percentages of *Tabellaria flocculosa* and also of

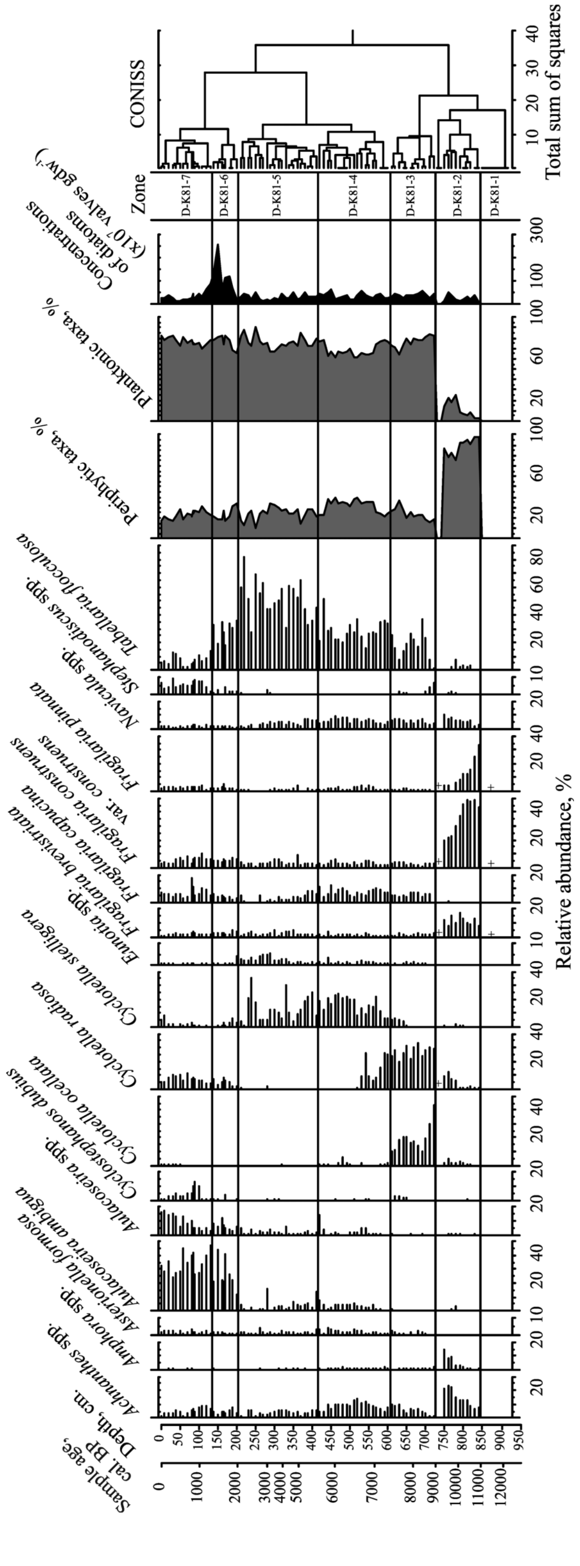

Fig. 4. Relative abundance of the most common diatom taxa of Lake Ķūži sediment core KC081. Zone boundaries were delimited using CONISS.

the oligotrophic *Cyclotella stelligera* rise. Important periphytic taxa in this zone include *Fragilaria*, *Achnanthes*, and *Navicula* spp. (mainly *N. pupula*).

Zone D-K81-5 (5600–2000 cal. BP, 415–205 cm) is continuously characterized by *Tabellaria flocculosa* and *Cyclotella stelligera*, the former increasing to 50%. At the same time also the percentage of acidophilic periphytic *Eunotia* taxa increases.

The proportion of *Tabellaria* spp. starts to decrease in zone D-K81-6 (2000–1300 cal. BP, 205–135 cm) and the more eutrophic *Aulacoseira ambigua* dominates and rises up to 30%.

In zone D-K81-7 (1300–0 cal. BP, 135–0 cm) the eutrophic *Cyclostephanos dubius* begins to increase. Small *Stephanodiscus* spp. (*S. hantzschii*, *S. parvus*, *S. rotula*) appear but do not rise to more than 10%. Also the percentage of *Cyclotella radiosa* is relatively high (12%).

The concentration of diatom valves per gram of dry sediment is quite stable from the depth of 800 to 200 cm (mean value 33×10^7 valves per gram sediment), rises up to 120×10^7 in zone D-K81-6, and decreases in zone D-K81-7 having the mean value of 24×10^7 (Fig. 4).

Pollen stratigraphy

A summary of the most frequent pollen types is presented in Fig. 5. The sediment sequence was divided into seven local pollen assemblage zones (P-K81 (1–7)). The lowermost part of the sediment sequence did not contain pollen and therefore the results cannot be shown in a diagram.

The lowest zone P-K81-1 (11 100–10 000 cal. BP, 850–785 cm) is dominated by *Betula* (80%) and *Pinus* (15%). These lowermost levels in the core were distinguished also by high percentages of pollen of herbs (8%) and spores of Bryophyta.

The percentage of *Betula* decreases to 45% in zone P-K81-2 (10 000–9000 cal. BP, 785–725 cm). At the same time first appearance of *Corylus* and *Ulmus* pollen grains occurs with about 9% and 18% shares, respectively. *Picea* and *Alnus* pollen grains are found in small numbers.

The transition between zones P-K81-2 and P-K81-3 (9000–7500 cal. BP, 725–625 cm) is defined by a decline in the proportions of *Pinus* pollen and Bryophyta spores. There is a notable temporary increase of *Betula*. The percentage of *Picea* pollen increases in the zone and the share of *Ulmus* is continuously about 10%.

The pollen spectrum of zone P-K81-4 (7500–5300 cal. BP, 625–385 cm) is characterized by high relative abundances of *Alnus*, *Betula*, and *Corylus* pollen. Small quantities of *Fraxinus*, *Tilia*, and *Quercus* pollen are found. *Picea*, *Pinus*, and *Ulmus* pollen grains are present in the whole zone.

An important change in zone P-K81-5 (5300–2500 cal. BP, 385–255 cm) is the increase of *Picea* pollen, which reaches its maximum postglacial abundance (32%). The proportions of *Alnus*, *Corylus*, *Ulmus*, and *Tilia* pollen grains decrease slightly. The amount of *Quercus* pollen has its maximum (15%) and the percentages of *Betula* and *Pinus* increase all over the zone.

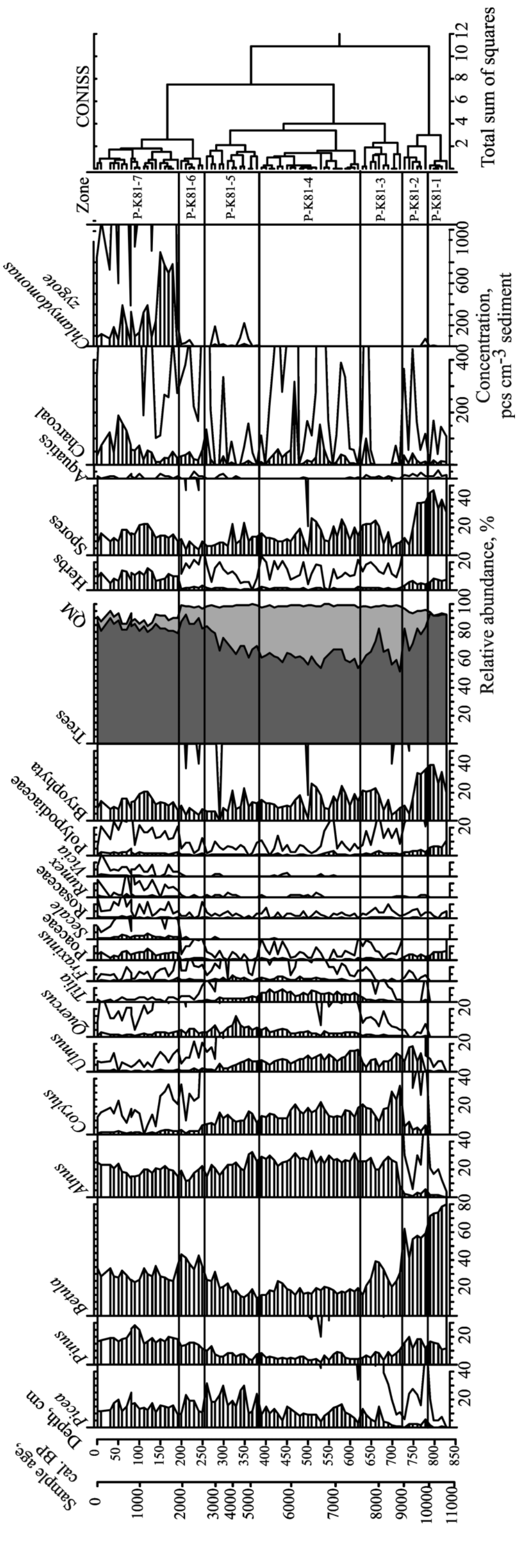

Fig. 5. Relative abundance of the most common pollen types of Lake Ķūži sediment core KC081. The sum of *Quercetum mixtum* (*QM*) includes *Alnaster*, *Carpinus*, *Corylus*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia*, and *Ulmus*. Zone boundaries were delimited using CONISS.

Zone P-K81-6 (2500–1900 cal. BP, 255–195 cm) is dominated by *Betula* and is characterized by a decline in *Picea* pollen and an increase in *Pinus* pollen. A decrease was recorded in the percentage of *Corylus* pollen.

In the uppermost zone P-K81-7 (1900–0 cal. BP, 195–0 cm) the occurrence of terrestrial herbs, mainly Poaceae and *Secale*, increases. A sharp increase can be seen in the NPP *Chlamydomonas zygote* (identified by Dr J. N. Haas and G. Gärtner from the University of Innsbruck). The zone is also characterized by a rather large number of charcoal fragments.

Numerical analyses

The diatom and pollen sample scores of Principal Component Analysis (PCA) are shown in Fig. 6. Diatom PCA axes 1 and 2 explain 30.2% and 23.6% of the total variance in the diatom record, respectively. PCA axis 1 is driven primarily by planktonic *Cyclotella radiosa* and *C. ocellata* and periphytic *Fragilaria* spp. on the positive end, and by *Tabellaria flocculosa* and *C. stelligera*, characteristic of oligotrophic waterbodies, and acidophilous *Eunotia* spp. on the negative end. PCA axis 2 separates the planktonic *C. ocellata* and several periphytic *Navicula* and *Achnanthes* spp. on the negative end from several *Aulacoseira* spp. (*A. ambigua*, *A. granulate*, *A. italica*) and *Stephanodiscus* spp. (*S. hantzschii*, *S. parvus*, *S. rotula*) on the positive end.

PCA axis 1 accounts for 56.4% of the variance in the data set and axis 2 explains 23.6%. Pollen taxa with positive scores of PCA axis 1 are produced by

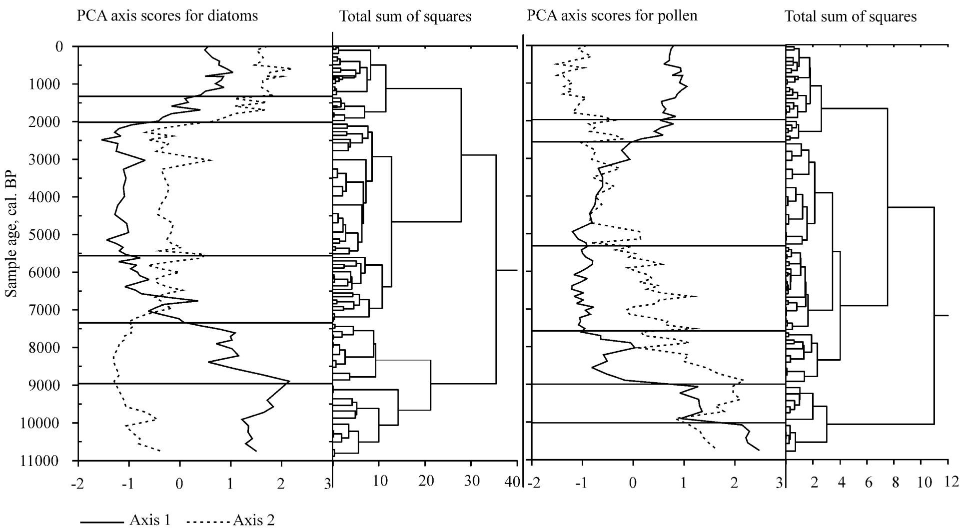

Fig. 6. Principal Component Analysis (PCA) sample scores of the first two axes for diatoms and pollen throughout the Holocene and the results of diatom and pollen CONISS analysis.

Table 3. Results of redundancy analysis of diatoms with pollen data used as predictor variables

Variable	*p*-value	Variance in diatom data explained by the first two RDA axes, %
Betula, *Pinus*, *Picea*, *Alnus*, broad-leaved trees, herbs, and charcoal	0.001	78.8
Betula	0.12	40.2
Pinus	0.35	47.0
Alnus	0.16	39.1
Picea	0.04	40.9
Broad-leaved trees	0.43	45.2
Herbs	0.001	30.4
Charcoal	0.02	39.2

Betula, *Pinus*, and Poaceae and those with negative scores are *Alnus* and broad-leaved trees. The positive side of PCA axis 2 is influenced by *Ulmus* and the negative scores are associated with *Picea* and herbs.

The changes in the diatom assemblages were correlated with the changes in the pollen assemblages. Redundancy analysis of the data set of diatoms gave us a statistically significant model (Table 3) with the variables (*Betula*, *Pinus*, *Picea*, *Alnus*, broad-leaved trees, herbs, and charcoal) explaining together 78.8% of the variation in the diatom data. Figure 7 illustrates the major directions of variation in the pollen data in relation to the diatom assemblage. Independently significant ($p \leq 0.05$) variables are *Picea*, herbs, and charcoal, which explain 40.9%, 30.4%, and 39.2%, respectively, of the variation (Table 3).

DISCUSSION

Seven clearly distinguishable zones (Figs 4, 5) give evidence of long-term changes in the diatom and pollen compositions of Lake Ķūži during the Holocene. There are similarities in the timing of compositional shifts between proxies but also differences occur in the response time (Fig. 6). Considering the large number of species, most diatoms probably have narrower ecological niches than terrestrial plants and are thus more sensitive to changes in the aquatic environment caused by different physical and chemical factors and mechanisms. Therefore, greater turnover in a period of time may be expected in diatom assemblages than in terrestrial palynological assemblages. The following discussion, however, focuses on similarities and positive correlations between the two proxies rather than on differences.

The diatom and pollen data show a consistent change in composition as evidenced by a synchronous zone boundary at 9000 cal. BP and 2000 cal. BP (Fig. 6). Therefore, on the basis of the diatom and pollen stratigraphies and their

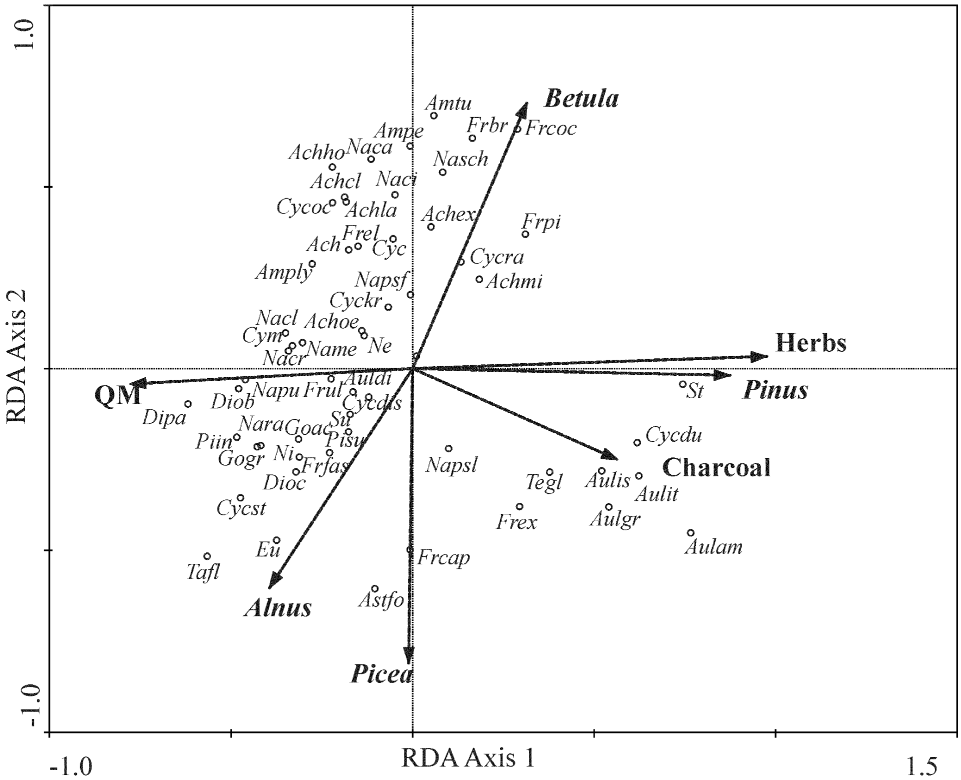

Fig. 7. Redundancy Analysis (RDA) biplot showing the correlations between diatom taxa and pollen types and charcoal.

Codes used: *Achnanthes clevei – Achcl*, *Achnanthes exigua – Achex*, *Achnanthes holsatica – Achho*, *Achnanthes lanceolata – Achla*, *Achnanthes minutissima – Achmi*, *Achnanthes oestrupii – Achoe*, *Achnanthes* spp. *– Ach*, *Amphora libyca – Amply*, *Amphora pediculus – Ampe*, *Amphora thumensis – Amtu*, *Asterionella formosa – Astfo*, *Aulacoseira ambigua – Aulam*, *Aulacoseira distans – Auldi*, *Aulacoseira granulata – Aulgr*, *Aulacoseira islandica – Aulis*, *Aulacoseira italica – Aulit*, *Cyclostephanos dubius – Cycdu*, *Cyclotella distinguenda – Cycdis*, *Cyclotella krammmeri – Cyckr*, *Cyclotella ocellata – Cycoc*, *Cyclotella radiosa – Cycra*, *Cyclotella* spp. *– Cyc*, *Cyclotella stelligera – Cycst*, *Cymbella* spp. *– Cym*, *Diploneis oblongella – Diob*, *Diploneis oculata – Dioc*, *Diploneis parma – Dipa*, *Eunotia* spp. *– Eu*, *Fragilaria brevistriata – Frbr*, *Fragilaria capucina – Frcap*, *Fragilaria construens* var. *construens – Frcoc*, *Fragilaria elliptica – Frel*, *Fragilaria exigua – Frex*, *Fragilaria fasciculate – Frfas*, *Fragilaria pinnata – Frpi*, *Fragilaria ulna – Frul*, *Gomphonema acuminatum – Goac*, *Gomphonema gracile – Gogr*, *Navicula cari – Naca*, *Navicula cincta – Naci*, *Navicula clementis – Nacl*, *Navicula cryptocephala – Nacr*, *Navicula menisculus – Name*, *Navicula pseudo-scutiformis – Napsf*, *Navicula pseudolanceolata – Napsl*, *Navicula pupula – Napu*, *Navicula radiosa – Nara*, *Navicula schoenfeldii – Nasch*, *Neidium* spp. *– Ne*, *Nitzschia* spp. *– Ni*, *Pinnularia interrupta – Piin*, *Pinnularia subcapitata – Pisu*, *Quercetum mixtum – QM*, *Stephanodiscus* spp. *– St*, *Surirella* spp. *– Su*, *Tabellaria flocculosa – Tafl*, *Tetracyclus glans – Tegl*.

contribution to the PCA axes, calibrated ^{14}C dates (Figs 2, 6), and already published results (Kangur et al., 2009), three general stages in the development of the lake and its catchment were defined: the Early Holocene (11 400–9000 cal. BP; 920–725 cm), the Mid-Holocene (9000–2000 cal. BP; 725–200 cm), and the Late Holocene (2000–0 cal. BP; 200–0 cm). Redundancy analyses between diatoms and some pollen types provide further details of the relationship between the aquatic ecosystem and catchment vegetation.

Early Holocene zones (11 400–9000 cal. BP; 920–725 cm)

The sediment content of the studied core (KC081) described here (Fig. 3; Table 2) and the sediment profile from a paludified near-shore area of the lake (KM071; Kangur et al., 2009) suggest changeable conditions in the lake before 9000 cal. BP. The complex lithology (layers of peat, macrofossils, sand, and gyttja) and variations in the organic matter of both sediment cores (KM071 and KC081) indicate that the water level has probably fluctuated within a large range.

The less than 7% LOI suggests that aquatic productivity was low. The high minerogenic matter content may reflect erosional input from soils, which had a scanty vegetation cover. The mineral matter has its highest values up to 11 200 cal. BP. Diatoms are absent from the mineral-rich period. Extended ice-cover (Smol, 1988) and/or high rates of minerogenic sediment flux (Anderson, 2000) may have inhibited the development of the diatom community during this period by reducing light penetration and thereby inhibiting photosynthesis and also limiting habitats.

After 11 200 cal. BP organic matter increases substantially (Fig. 3) as the surrounding terrestrial vegetation gradually started to develop as shown by Kangur et al. (2009). Also diatoms increased in abundance. Zones P-K81-1 and P-K81-2 are dominated by *Betula* and *Pinus* pollen in association with high shares of Poaceae pollen and Polypodiaceae and Bryophyta spores, which suggests semi-open landcover with sparse vegetation. Probably the developing terrestrial plant cover became gradually denser and reduced the inflow of minerogenic matter as seen in Fig. 3.

Following the increase in organic matter 11 200 cal. BP, the diatom assemblages are dominated by *Fragilaria* spp., suggesting that sedimentation during that phase of lake development was typical of oxygen-rich and alkaline water (Marciniak, 1979). This phenomenon is also interpreted as the effect of nutrient availability, for example through soil erosion in the catchment. In addition, *Fragilaria* spp. are widely regarded as pioneering taxa that are commonly associated with early post-glacial periods (Stabell, 1985; Denys, 1990; Bigler et al., 2002) and as dominating when water levels have fallen significantly (Hickman et al., 1984; Hickman & White, 1989; Hickman & Schweger, 1991). The dominance of these species in the lowermost zone may represent an early successional stage in the lake history. A study from Lake Väike Juusa in the southern part of Estonia (Punning & Puusepp,

2007) describes a similar diatom composition at the beginning of the Holocene as characteristic of a newly formed lake. According to Bradshaw et al. (2000), the reason for the domination of periphytic diatom taxa could be seasonally not high enough nutrient levels for plankton growth. Moreover, the nutrient balance was unfavourable, or their growth may have been inhibited by the turbidity created by the inwash of terrestrial minerogenic and organic material in spring at the critical time for diatom blooms. Also the shorter ice-free season could have caused a low abundance of planktonic taxa (Lotter & Bigler, 2000).

There are only a few diatom valves in the sediment samples from 9300–9000 cal. BP. The reason might be dissolution and/or breaking of frustules during sinking or within sediments or the absence of nutrients. Water depth may play a role where surface sediments are subject to physical resuspension from wind (Flower & Nicholson, 1987). In addition, significant changes in the sedimentation took place at the same time (J. Terasmaa et al., pers. comm.) with coarse silt dominating. Therefore, the physical degradation and breaking of frustules during the sedimentation process because of interaction with coarse-grained minerogenic matter occurred. At the same time the carbonate content, which is relatively low throughout the records, increases in the analysed sediment sequence and also in core KM071 from a paludified near-shore area (Kangur et al., 2009). This could have given an impulse for the dissolution and breaking of diatom valves (Flower, 1993).

Mid-Holocene zones (9000–2000 cal. BP; 725–200 cm)

Evidence from physical properties of sediment suggests that the primary stabilization of the water level occurred 10 200 cal. BP when carbonaceous gyttja started to deposit (Fig. 3). The sediment sequence from the near-shore area (Kangur et al., 2009) supported by lithological, macrofossil, and pollen data also confirms a stable water level.

A major shift in both the diatom and pollen stratigraphy occurred 9000 cal. BP at a depth of 725 cm. The high relative abundances of *Alnus*, *Ulmus*, and *Corylus* pollen and consistent representation of *Tilia* suggest warm and moist climatic conditions.

The abundance of *Fragilaria* spp. in zone D-K81-3 decreased simultaneously with changes in the terrestrial vegetation and lithology. Probably, the erosion of and nutrient input from the surroundings of the lake decreased because the vegetation around the lake had become denser and the proportion of broad-leaved trees and *Picea* had increased and that of *Betula* had decreased. The gradual immigration of trees most certainly resulted in soil stabilization. Similar stabilization has been noted in other Early Holocene studies (Punning et al., 2003; Wick et al., 2003; Dalton et al., 2005).

The dominance of *Cyclotella* and *Tabellaria* species indicates oligo-mesotrophic conditions. The scores on PCA axis 1 also point to a lower nutrient level in the lake as the variation in the species composition along PCA axis 1 is most probably linked to changes in the trophic state of the lake. The changes in life forms (periphytic *Fragilaria* spp. versus planktonic *Cyclotella* spp. and *Tabellaria flocculosa*) probably reflect a lengthened open-water period and a longer growing season (Bradshaw et al., 2000; Lotter & Bigler, 2000; Bigler et al., 2002; Sorvari et al., 2002; Ampel et al., 2009). The increase in the proportion of planktonic diatoms may be evidence of a substantial rising of the water level in the lake. However, the occurrence of planktonic diatoms is also substantially affected by the amount of light, stratification, and the stability of the water depth.

In zone P-K81-5 we can see an increase of *Picea* pollen content in the sediment. During the same period the increase of *Picea* pollen content was even larger in core KM071 (Kangur et al., 2009) where *Picea* pollen made up more than 50%. The differences in the amounts of *Picea* pollen in the two cores can be explained by species-specific pollen accumulation patterns (Kangur, 2009). The large amounts of *Picea* pollen in sediment suggest dominance of spruce among the terrestrial vegetation. During the same period the diatom record undergoes a notable change. Periphytic acidophilous taxa (*Eunotia* spp.) appear with a relative abundance over 5% 3600 cal. BP. The dominance of *Tabellaria flocculosa*, an acidophilous taxon, also shows a low pH (van Dam et al., 1994; Bigler et al., 2000; Köster et al., 2005; Leira, 2005; Bennion & Simpson, 2010). A low pH could be expected due to the production of humic acids by *Picea*. For example, in a Finnish study, a rapid expansion of acidobiontic diatom taxa coincided with the appearance and increase in the pollen of *Picea* (Salomaa & Alhonen, 1983). Korsman et al. (1994) found correlations between diatom composition and *Picea* but not acidification associated with the immigration of *Picea* into lake catchments. However, in our study an RDA biplot shows that acidophilous diatom taxa are positively correlated with the proportion of *Picea* (Fig. 7).

The Late Holocene period (2000–0 cal. BP; 200–0 cm)

Results of the PCA analysis (Fig. 6) reveal that great changes occurred in the diatom and pollen assemblages 2000 cal. BP and that the last stage of the history of Lake Ķūži and its surroundings differs clearly from the previous ones. Changes in the terrestrial vegetation and diatom flora are contemporaneous with an increase in the organic content. The homogeneous gyttja of the upper part (200 cm) of the sediment core and the high concentration of diatom valves in it might be explained by the increase of primary production in the lake. After 2000 cal. BP a further decrease is seen in tree pollen, while an increase occurs in herbs such as Poaceae, *Secale*, and *Rumex*. This suggests an increase of human impact. Archaeological material from Vidzeme Heights from the Bronze Age (3800–2500 cal. BP) and the Early Iron Age (2500–1550 cal. BP) is scarce. The beginning of agrarian activities in other places of Latvia occurred during the archaeological late Bronze Age, when farming became the main form of human economy in the Baltic region (Vasks et al., 1999).

The change in the pollen record also coincides with changes in the aquatic assemblages. The rapid shifts in the species composition and concentration of diatom valves marked a limnological change. The dominant diatom species along PCA axis 2 suggest that this axis reflects human activity, and variations in pollen composition along PCA axis 1 may also be linked to it. Characteristic diatom taxa in this phase are *Aulacoseira* spp. (mostly *A. ambigua*, *A. granulate*, *A. italica*), which prefer high light conditions and bloom in spring and early summer in many temperate lakes (Brugam, 1983; Leira, 2005). *Cyclotella stelligera* and *Tabellaria flocculosa* decline in an apparent response to increased nutrient loadings as those taxa live in oligo-mesotrophic lakes. The dominance of *A. ambigua* during the Late Holocene suggests a prevalence of turbulent conditions in Lake Ķūži. These diatoms rely on mixing and turbulence to remain suspended in the water column. Bradbury et al. (2002) reported increases of *A. ambigua* after deforestation. It is likely that the lack of tree cover and increasing cultivated area around the lake led to higher wind exposure of the open-water area, thus inducing a better mixing of the water column.

Additionally, the decrease in the sediment organic matter during the last 1000 cal. BP suggests higher mineral inputs through soil erosion caused by cultivation and logging activities. During the same period the proportions of *Cyclostephanos dubius* and *Stpehanodiscus* spp. increase. These taxa are known as centric species that are commonly found in highly eutrophic waters influenced by human activity (Bennion, 1995). The abundance of pollen of herbs is positively correlated with *C. dubius* and *Stephanodiscus* spp. (*S. hantzschii*, *S. parvus*, *S. rotula*) (Fig. 7). The correlation supports the idea of nutrient enrichment of the lake as a result of intensified agricultural activities.

Based on the results of the sediment core taken from the near-shore area of Lake Ķūži, Kangur et al. (2009) concluded that the period from 700 cal. BP up to the present, when the water level close to the near-shore area was below or around the sediment surface, can be clearly seen in the lithological composition of the sequence. The fossil diatom flora from this period from core KC081 consists mainly of planktonic species, which can be expected in a core taken from the deepest part of the lake. As the coring site is located at 7 m depth, there is likely a large area around it that does not receive enough light and has low habitat diversity to support a periphytic diatom population. We could not see any changes in the diatom composition caused by large-scale water-level fluctuations during the Late Holocene period.

CONCLUSION

Fossil pollen assemblages in Lake Ķūži follow the general pattern of forest development and provide evidence about changes related to climate oscillation. Changes in diatom assemblages during the Holocene indicate fluctuating limnological conditions. Besides the change of the trophic state of the lake, natural acidification and human impact are reflected in the diatom response. In our study, it was possible to observe a certain degree of synchronicity among proxy responses in the sediments. Principal component analysis and redundancy analysis provide a summary of major compositional changes in the assemblages of diatoms and pollen.

The correlations between diatom and pollen data are complex but still reveal some general patterns in the diatom and pollen profiles. The results suggest that diatoms respond most strongly to catchment-driven changes due to the expansion of *Picea* forests and the impact of human intervention on terrestrial vegetation. The expansion of *Picea* forests led to natural acidification of the lake water causing changes in the diatom assemblages, in particular an increase of acidophilous taxa such as *Eunotia* spp. and *Tabellaria flocculosa*. The pollen profile reflects human impact through the occurrence of various herbs (including Poaceae and *Secale*) and a rise of the charcoal concentration, which in turn is correlated with changes in the composition of diatoms: *Aulacoseira* spp. (*A. ambigua*, *A. granulate*, *A. italica*) and *Stephanodiscus* spp. (*S. hantzschii*, *S. parvus*, *S. rotula*) appear.

The information obtained in this study on the history of Lake Ķūži and its catchment vegetation during the Holocene helps to establish a linkage between aquatic and terrestrial systems.

ACKNOWLEDGEMENTS

The study was supported by the Estonian Ministry of Education and Research (target-financed project SF0280016s07) and the Estonian Science Foundation (MTT3). We express our sincere thanks to colleagues from the Institute of Ecology at Tallinn University for assisting in the field. Particular thanks to Jan Risberg, Shinya Sugita, Tiiu Koff, and Eve Niinemets for their helpful comments on an earlier version of this manuscript.

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Diatomee- ja õietolmuprofiilide dünaamika ning nende omavahelised korrelatsioonid Holotseenis Ķūži järve (Vidzeme kõrgustikul Lätis) näitel

Liisa Puusepp ja Mihkel Kangur

Käesoleva uurimuse eesmärkideks on kirjeldada Ķūži järve (Vidzeme kõrgustikul Lätis) ökosüsteemi arengut diatomeeanalüüsi tulemuste põhjal ja järve ümbritseva taimkatte arengut, tuginedes õietolmuanalüüsi tulemustele, ning leida omavahelisi korrelatsioone kahe erineva paleomarkeri dünaamika vahel Holotseenis.

Uurimus tugineb lisaks diatomee- ja õietolmuanalüüsi tulemustele sette litoloogilisele analüüsile ning viiele kalibreeritud AMS ^{14}C dateeringule ja statistilisele andmetöötlusele (CONISS, PCA, RDA).

Tulemused näitavad, et uuritud järve ja seda ümbritseva ala arengu võib jaotada kolmeks suuremaks perioodiks. Vara-Holotseeni algul diatomeesid ei leitud, alates ajast 11 100 aastat tagasi (850 cm) domineerivad madalale veele omased perifüütsed diatomeeliigid (*Fragilaria* spp.) ja preboreaalsele ning boreaalsele kliimaperioodile omased taimeliigid (rohttaimed, kask, mänd). Kesk-Holotseeni (9000–2000 aastat tagasi; 725–200 cm) iseloomustavad sügavale ja oligo- ning mesotroofsele veekogule omased diatomeed (*Cyclotella* spp. ja *Tabellaria flocculosa*) ning atlantilise ja subboreaalse kliimastaadiumi tüüpilised taimekooslused (laialehised puud, kuusk). Hilis-Holotseenis (2000–0 aastat tagasi; 200–0 cm) on nii diatomee- kui ka õietolmuprofiilidel näha selgeid inimmõju ilminguid. Diatomeekooslused viitavad selgelt järve toitelisuse suurenemisele ja ümbritseva maastiku avatusele (*Aulacoseira* spp. ning *Stephanodiscus* spp.). Inimtegevuse intensiivistumisele viitavad ka rohttaimede õietolmu ja söeosakeste osakaalu suurenemine õietolmuprofiilil.

Statistilisele andmetöötlusele tuginedes saab väita, et Holotseeni vältel toimunud muutused õietolmuprofiilis korreleeruvad muutusega diatomeekooslustes. Statistiliselt olulisim korrelatsioon esineb diatomeekoosluste ja kuuse ning rohttaimede õietolmu osakaalu ja söeosakeste kontsentratsiooni dünaamikate vahel. Perioodil, mil suureneb kuuse õietolmu osakaal settes (5300–2500 aastat tagasi) on jälgitav ka happelistele veekogudele omaste diatomeekoosluste (*Eunotia* spp. ja *Tabellaria flocculosa*) esinemine. Söeosakeste kontsentratsiooni ja rohttaimede õietolmu osakaalu dünaamika on positiivses korrelatsioonis diatomeedega, mida seostatakse järve ümbruse avatumaks muutumisega ning inimtegevuse intensiivistumisega.