

Coexistence of *Lobelia dortmanna* and *Cladium mariscus*, an ecological and paleobotanical study

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ABSTRACT. *Lobelia dortmanna* L. (Lobeliaceae family) is an indicator species that is predominantly found in oligotrophic and acidic lakes. They are mainly distributed in northwestern Europe. Their occurrence in Poland is highly threatened by the increasing grade of human activity and environmental eutrophication; however, new sites of *Lobelia* were discovered in the last few decades, for example, in Lake Krzywce Wielkie situated in Bory Tucholskie National Park (BTNP), Poland. The existence of *Lobelia* in this lake was unexpected because *Cladium mariscus* was also found in the lake. *Cladium* has different ecological demands and is regarded as a species typical of calcareous habitats where calcium is found in abundance in the substrate. To explain the coexistence of both species in Krzywce Wielkie, pollen analysis of organic sediments was performed for four short cores collected from the littoral zone of the lake and for one long deep-water core. Additionally, macrofossil analysis was done for all the short cores. Pollen analysis revealed the existence of *Cladium* from the early Holocene period up to the present time. Pollen and seeds of *Lobelia* were found to be present since the beginning of the 20th century. Development of *L. dortmanna* and *Myriophyllum alterniflorum* populations and a decrease in the number of aquatic macrophytes in the eutrophic water indicate oligotrophication of water. This process started following the construction of drainage canal and the consequent water level decrease. This situation can be attributed to the abandonment of the agricultural areas adjoining the lake, which causes a decrease in the inflow of nutrients into the lake. Development of pine forest and establishment of BTNP enabled the protection and conservation of the surrounding catchment areas, thus restricting the potential eutrophication of the habitats.

KEYWORDS: *Lobelia dortmanna*, *Cladium mariscus*, Late Holocene, land use, trophy changes, Tuchola Forest

INTRODUCTION

Ongoing climate and environmental changes result in the shift of the geographical distribution of numerous plant and animal species (Pecl et al., 2017). However, various environmental factors, such as temperature, nutrient availability and humidity, and interactions among them (e.g., feedback effects) affect the

nature of habitat. Therefore, the resulting response of a species to an ecological habitat may be highly variable. For instance, it was found that in lake environments an increase in water temperature may favor the growth of an ecologically dominant invasive species (Dziuba et al., 2020), whereas in other conditions, local but so far endangered species may be predominant (Kowalewski et al., 2013; Brzozowski

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et al., 2021). Several features of the habitat contribute to the type of species living in it. For instance, in a lake environment, factors like an increase in water temperature, a drop in water level (Kornijów et al., 2016), a reduction in the period of ice cover, or changes in catchment management (Poraj-Górska, 2017) may play a crucial role in determining the nature of the species living in the lake. To interpret the future response of a particular species to the ecological changes, it is beneficial to obtain the information provided in sedimentary paleorecords (Davidson et al., 2013).

Lake environments are in constant danger of undergoing rapid changes in the near future, and this situation is particularly expected to be observed in the case of lakes dominated by species that have reached the limits of their modern distribution range. A good example of such lakes is the so-called Lobelian lakes that are characterized by the presence of *Lobelia dortmanna* L. (Lobeliaceae family), which is an indicator species and predominantly found in oligotrophic and acidic lakes with low conductivity (Szmeja, 1997). Other species that commonly inhabit these lakes are *Isoëtes lacustris*, *I. echinospora*, *Littorella uniflora* and *Myriophyllum alterniflorum*, and these plants have similar environmental demands (Szmeja, 1992; Hannon and Gaillard, 1997; Heegaard et al., 2001). The geographical distribution of these lakes correlates with the spatial limits of the above-mentioned species. They are distributed mainly in the boreal zone of north-western Europe (Sculthorpe, 1985; Szmeja, 2014a, b), extending further to the northern boreal zone (Moen, 1999) and eastern Lithuania (Gostyńska-Jakuszczyńska and Lekavičius, 1994). Thus, they occur in regions with cool and wet temperate climates, with catchments frequently dominated by pine forests (Szmeja, 2014a). In Poland, 155 Lobelian lakes were identified (Szmeja, 1997); however, only 131 of them were inhabited by populations of *L. dortmanna*, which grow in the northwestern part of the country (Szmeja et al., 1998).

Extensive studies focusing on Lobelian lakes were conducted during the second half of the 20th century (Sand-Jensen, 1978; Sand-Jensen and Borum, 1984; Rørslett, 1991; Szmeja et al., 1998). Hence, the environmental conditions that influence the development of isoetids (*Lobelia*, *Isoëtes*, and *Littorella*) are well known. In addition, the structure of these

specific populations was analyzed (Szmeja, 1987; Chmara et al., 2014, 2015a; Ronowski et al., 2020). However, their responses to modern land use and human activities are poorly understood, especially in the context of political changes in Central and Eastern Europe at the end of the 20th century and following the development of nature conservation measures. It turns out, in spite of many threats related to anthropogenic pressure, that many of these lake ecosystems are in good condition due to the protection provided by law and stable environmental conditions in the catchments dominated by pine forest, acidic beech forest, and peatlands (Kraska et al., 2013; Szmeja, 2014a).

Lobelian lakes constitute the most precious resource of Bory Tucholskie National Park (BTNP), which is also inhabited by lichen-rich Scotts pine forests and mires. There are six Lobelian lakes in the park (Fig. 1): Gacno Wielkie, Gacno Małe, Nierybno, Głuche, Krzywce Wielkie and Krzywce Małe, but *L. dortmanna* was not noticed in the last lake in recent years (Królikowska et al., 2012). The Lobelian lakes are often surrounded by patches of mires along the shore, which provide additional protection against eutrophication, as they restrict the transfer of nutrients from the catchment area (Tobolski, 2003; Szmeja, 2014a).

Krzywce Wielkie Lake has been recently included in the group of Lobelian lakes. Information regarding the development of *L. dortmanna* population in this lake was first published by Kochanowski and Tobolski (2010) and further confirmed by Kochanowska et al. (2013). This occurrence seems to be interesting because a few clusters of *Cladium mariscus* L. Pohl (Cyperaceae family) were also found in this lake (Herbichowa and Wolejko, 2004; Mróz, 2010). This species has quite different ecological demands and usually grows in fertile, calcareous habitats. Both *L. dortmanna* and *C. mariscus* are used as indicator species in Habitats Directive's Natura 2000 network (Council Directive 92/43/EEC). However, they are characterized by different types of habitats: code 3110 includes *Lobelia* lakes with *Littorelletalia uniflorae* and code 7210 includes calcareous fens with *Cladietum marisci*, *Carexetum buxbaumi* and *Schoenetum nigricantis*.

The phenomenon of the coexistence of *L. dortmanna* and *C. mariscus* in the same lake was studied by adopting a paleoecological

approach, which provided useful information in a preliminary investigation carried out by Milecka and Tobolski (2015). In this study, pollen and macrofossil analyses were performed for the upper 314 cm of the deep-water core of sediments rich in organic matter (KW/2014) accumulated since about 2300 cal yr BP. These analyses revealed the presence of pollen grains of *Cladium* but the absence of *Cladium* fruits and also the absence of pollen and seeds of *Lobelia*. *Lobelia* species produce small amounts of pollen that are poorly transported through the lake bottom (Milecka and Obremska, 2002), which could be the likely reason for the lack of *Lobelia* fossils. The quantity of *Cladium* pollen increased at ~350 cal yr BP and was concurrent with the occurrence of high trophicity indicators (e.g., *Rumex acetosella*, *Plantago lanceolata*, *Pediastrum boryanum*, *P. duplex*); however, at ~200 cal yr BP, water trophicity decreased resulting in the development of *Chara* population in the lake (Milecka and Tobolski, 2015). All these findings help to draw clear conclusions regarding the emergence of the *Lobelia* population and the duration of the coexistence between *Lobelia* and *Cladium*. Moreover, some questions also arise: (1) From

when did *Lobelia* and *Cladium* start to occur together in the lake? (2) What conditions influenced their presence and what was the reason for the recent spread of *Lobelia*? (3) How did land use, human pressure and protection by law influence this recent spread? (4) What are the general conditions for the modern existence of Lobelian lakes and what may be their future?

To trace the development of the recent population of *Lobelia* in Lake Krzywce Wielkie, a detailed paleoecological analysis of the lake's sediments was conducted. The evaluation was based mainly on high-resolution pollen records and macrofossil analyses of ^{14}C -, ^{210}Pb - and ^{137}Cs -dated sediment cores, and was supplemented with the analysis of old maps that show the hydrological and land-use changes during the last 200 years, prepared by Nienartowicz (2012). To determine the initial existence of *Lobelia* populations in Lake Krzywce Wielkie, four cores of sediments from the littoral zone of the lake were taken. To trace the development of *Cladium* and *Lobelia* populations, the pollen analysis of the older part of the long core from the central part of the lake (KW/2014) was done.

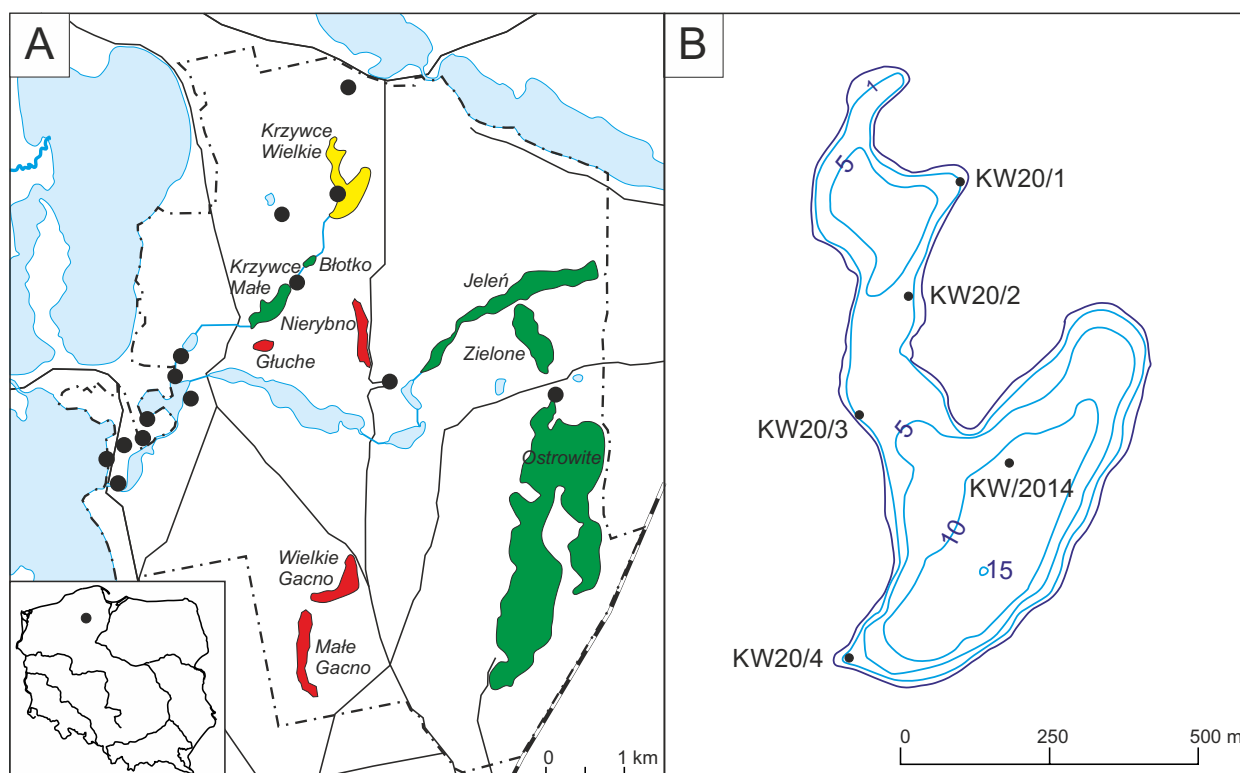


Fig. 1. Study area. **A** – location of lake Krzywce Wielkie in BTNP. Inset map shows location in Poland. Dot-dashed line – border of BTNP, black circle – fossil site of *Cladium mariscus* according to Gałka and Tobolski (2006), yellow lake – sites of *Lobelia dortmanna* and *C. mariscus*, red lakes – sites of *L. dortmanna*, green lakes – site of *C. mariscus*; **B** – locations of sediment cores in Lake Krzywce Wielkie. Isobaths after Błoniarz et al. (2016) in metres

STUDY AREA

Tuchola Forest is a large forest located on an outwash plain formed during the last glaciation (Dysarz, 1998; Kowalewski, 2002). Woś (1999) defined the modern climate of the region as temperate, cool and wet. The mean temperature in January is -3.2°C and in July it is 19°C , the annual average rainfall is 573 mm, and the vegetative period lasts of 180–200 days.

BTNP (Fig. 1), established in 1996, is located adjacent to the previously established five landscape parks covering the entire area of Tuchola Forest. The area of BTNP is about 5000 ha, which comprises only a small portion of the whole complex. The park is almost completely covered by dry and fresh pine forest communities with many lakes (Tobolski, 1998; Matuszkiewicz et al., 2012). Lake Krzywce Wielkie is located in the northern part of BTNP. Its surface area is 25 ha, has a maximum depth of 15.1 m and a mean depth of 9.0 m (Błoniarczyk et al., 2016). Direct catchment of this endorheic lake is 1624 km² (Bajkiewicz-Grabowska, 2004). The poor sandy soils and prevailing pine forest cover of the catchment limit the supply of nutrients to the lake (Bajkiewicz-Grabowska, 2004).

In BTNP, two water courses connect some lakes (Fig. 1): the stream Struga Siedmiu Jezior and an artificial canal called Krzywce-Błotko. *C. mariscus* is found in three lakes located along the upper course of Struga Siedmiu Jezior (Solon and Matuszkiewicz, 2012); however, fossil macroremains were found in recent sediments along the whole course of this stream (Gałka and Tobolski, 2006). The growth of *Lobelia* was detected in some endorheic lakes of the central part of BTNP and in the Krzywce-Błotko canal. Both species co-occur only in Krzywce Wielkie, along the western and eastern shores of the lake. The coexistence of *C. mariscus* and *L. dortmanna* was also documented in three lakes of Tuchola Forest (outside of BTNP): Nawionek, Głuche and an unnamed one in West Pomerania (Milecka, 2005; Kochanowska et al., 2013).

L. dortmanna, *M. alterniflorum*, and *Juncus bulbosus* were identified in Krzywce Wielkie during the botanical analysis of two cross-sections traversing the eastern part of the lake (Bociąg, 2011). *Polygonum amphibium* and *Potamogeton natans* were also recorded. That research was conducted to monitor the protection efficiency

of the park in retaining the natural ecosystem. *Lobelia* occurred down to 1 m of water depth. The patches of *M. alterniflorum* were abundant and clear down to 4 m of water depth. *C. mariscus*, *Typha angustifolia*, and *Carex* species developed along the lake shores.

METHODS

FIELD WORK AND SAMPLING

On May 18, 2020, four cores (KW20/1, KW20/2, KW20/3 and KW20/4) of sediments rich in organic matter were collected from the littoral zone of Lake Krzywce Wielkie using a gravity corer (UWITEC Co., Austria). The inner diameter of the corer liner was 86 mm. The cores were sampled in the laboratory of the Faculty of Geographical and Geological Sciences, Adam Mickiewicz University, Poznań. The uppermost layers of the sediments (1–10 cm), characterized by high water content, were sectioned in 2-cm-thick intervals in order to ensure that sufficient volume of the sediment is sampled for macrofossil analysis and dating. The deeper parts (10–35 cm) were sliced into 1-cm-thick samples. Each sediment sample was further subsampled for pollen analysis (1 cm³), macrofossil analysis and radiometric dating. The long core (624 cm, KW/2014) was drilled in 2014 from a deeper central part of the lake for paleobotanical analysis (Fig. 1). The upper half (314 cm) of the sediment was analyzed and discussed by Milecka and Tobolski (2015), while the lower half (310 cm) was investigated in this work. The samples were taken at 4-cm-thick intervals.

CHRONOLOGY

¹⁴C dating

Fifteen organic samples, each taken at 20 cm intervals in 1 cm slices from the lower part of the core KW/2014, were transported to Poznań Radiocarbon Laboratory for ¹⁴C dating using the AMS technique (Goslar et al., 2004). Most of the samples were macrofossils of terrestrial plants (*Pinus* needles, bud scales and *Betula* fruits, bud scales), but sediments from the deepest part contained few terrestrial macrofossils, and hence bulk sediment sample was taken from this area.

²¹⁰Pb and ¹³⁷Cs dating

The age models for the cores collected from the recently formed lake sediments (deposited during the past century) of the littoral zone were constructed using ²¹⁰Pb and ¹³⁷Cs radioisotopes. ²¹⁰Pb is a natural radioisotope formed in the course of the decay of ²³⁸U and has a half-life of 22.3 years. In sediments, total ²¹⁰Pb is the sum of the so-called supported ²¹⁰Pb (²¹⁰Pb_{sup}), which is continuously produced by the decay of parent isotopes, and excess ²¹⁰Pb (²¹⁰Pb_{ex}), delivered to the sediment surface mainly by atmospheric

deposition. Along with the continuous accumulation of the deposits, the activity of $^{210}\text{Pb}_{\text{ex}}$ decreases with depth due to its decay and provides a tool for the assessment of sediment age using models based on various assumptions (Appleby and Oldfield, 1992; Sanchez-Cabeza and Ruiz-Fernández, 2012). The artificial ^{137}Cs was first introduced into the environment in measurable amounts in the early 1950s. It showed maximum activity in 1963 in relation to numerous nuclear bomb tests and also in 1986 related to the Chernobyl event (Ritchie and McHenry, 1990).

The ^{137}Cs and ^{210}Pb activities were measured using gamma spectrometry at the Institute of Geology, Adam Mickiewicz University, Poznań, Poland (Szczuciński et al., submitted). The 2-cm-thick sediment core samples were dried and homogenized. The activities of ^{137}Cs , ^{210}Pb , ^{214}Pb and ^{214}Bi were measured for ~50–70 hours using a high-purity coaxial wide-energy germanium detector (Canberra BE3830) with a remote detector chamber option set for low-energy background reduction. The average of ^{214}Pb and ^{214}Bi activities, which are in radioactive equilibrium with ^{226}Ra , was used as a measure to determine the concentration of $^{210}\text{Pb}_{\text{sup}}$. The $^{210}\text{Pb}_{\text{ex}}$ value was calculated as the difference between the measured total ^{210}Pb and $^{210}\text{Pb}_{\text{sup}}$. The obtained analytical results were used to develop an age model for the sediments deposited during the last century using the *serac* package (Brueel and Sabatier, 2020). Constant flux constant sedimentation rate (CFCS) and constant initial concentration models were established and verified based on ^{137}Cs activity profiles. The results revealing very low $^{210}\text{Pb}_{\text{ex}}$ activities, much smaller than the activity obtained using 2-sigma accuracy tests, were not taken into consideration for the age model computation.

POLLEN ANALYSIS

Pollen analysis was done for every sample collected from four short cores, that is, 30 samples per core, and for 78 samples obtained from the long core KW/2014. The procedure for laboratory preparation followed that described by Berglund and Ralska-Jasiewiczowa (1986). Mineral particles were removed by HF, and organic compounds by KOH. Acetolysis was performed for 3 minutes. Prior to the preparation of pollen slides, samples were stained with safranin. Samples taken from core KW/2014 were counted to at least 700 pollen grains of trees and shrubs. The analysis of the sediments of the littoral cores revealed lower pollen frequencies than observed in more consolidated sediments from the deeper part of the lake. Hence, the sum of the pollen grains was not very high, exceeding 400 pollen grains of trees and shrubs in almost all spectra. The sum of AP (trees and shrubs) and herbs (NAP) was the basis for percentage calculations (calculation sum). Aquatics, telmatophytes, and selected nonpollen palynomorphs (NPPs) were also counted; however, they were not included in the calculation sum. The pollen diagrams were initially compiled using Tilia and Tilia Graph programs (Grimm, 1992) and later improved using CorelDraw X16 software.

Particular attention was given to the identification of the pollen of *Lobelia* and *Cladium*, which is the main objective of our research. Every pollen slide was

examined in detail, regardless of the pollen sum, to find their grains. The pollen types of both species were identified according to Beug (2004). Every pollen grain type of *Lobelia* species was carefully examined, because there are some similar types of pollen, for example, *Linaria*, *Digitalis* and *Verbascum*. The determination of *Cladium* pollen was not simple either because some of them do not have an elongated ending, which is a critical feature for reliable classification. However, regular presence of *Cladium* in the samples allowed for the detailed observation and recognition of some additional indicator features, which include regular conical shape, relatively big size, very gentle, circular perforations at 1/3 of the grain length, and very clear perforation at the base of the cone. Pollen grains “cf. *Cladium*” were not classified as “*Cladium*” if the analyzed grains were partially destroyed or crushed and the perfect observation of all the indicator features was not possible.

MACROFOSSIL ANALYSIS

Macrofossil analysis was conducted for sediment slices with a volume of 60 cm³ and collected from a depth of 1–10 cm and also for slices with a volume of 30 cm³ taken from 11–35 cm. The samples were washed with water and sieved using a mesh size of 0.125 mm. The residue was examined under a stereomicroscope (Nikon, Japan) at 10×, 40×, and 100× magnifications. The results were presented in the diagrams of absolute frequency prepared in R (R Core Team, 2020) in “rioja” package (Juggins, 2020) and modified in CorelDraw X16.

RESULTS

The results showed that the long core KW/2014, drilled at the water depth of 546 cm, is composed of gray and fine detritus gyttja (314–604 cm of sediment depth) with increased content of mineral particles in the bottom part (604–624 cm).

The four short sediment cores collected from the littoral zone of Lake Krzywe Wielkie showed very similar lithological features at the depth of 40–50 cm from the water surface (Fig. 1, Table 1). The samples are composed of dark brown detritus gyttja with decreasing content of mineral particles toward the upper part.

Table 1. The location of coring sites (Fig. 1)

Name of core	Longitude	Latitude
KW/2014	17°33'40.18"E	53°50'21.55"N
KW20/1	17°33'35.86"E	53°50'37.36"N
KW20/2	17°33'30.85"E	53°50'30.91"N
KW20/3	17°33'26.22"E	53°50'24.29"N
KW20/4	17°33'25.18"E	53°50'10.55"N

¹⁴C DATING

The ¹⁴C ages of samples taken from the core KW/2014 (Table 2) were calibrated against the curve INTCAL20 (Reimer et al., 2020), and were used to build an age–depth model using a free shape algorithm (Goslar et al., 2009). For the development of models, the set of calibrated ¹⁴C dates was supplemented with the calendar date that marked the beginning of Holocene (11,550 cal BP, according to the increase of birch and decrease of juniper trees

Table 2. ¹⁴C ages of samples from the core KW/2014

Depth [cm]	Material	Lab no. Poz-	Age ¹⁴ C (BP)	Modeled date (68.2% conf. interval, cal BP)
314	Plant remains	126617	2415±35	2490–2375
334	Plant remains	126618	2570±40	2760–2705
354	Plant remains	126619	2875±35	3060–2960
374	Plant remains	126621	3055±30	3340–3230
394	Plant remains	126622	3385±35	3680–3575
414	Plant remains	126623	3565±35	3920–3835
434	Plant remains	126624	3770±35	4220–4090
456	Plant remains	126625	3925±30	4420–4310
476	Plant remains	126626	4165±35	4825–4650
494	Plant remains	126627	4520±40	5175–5055
514	Plant remains	126628	4610±35	5450–5315
538	Plant remains	126629	5570±40	6385–6310
562	Plant remains	126631	6480±35	7400–7335
586	Plant remains	126632	9090±50	10270–10200
620	Bulk sediment	126633	11110±60	13095–12935

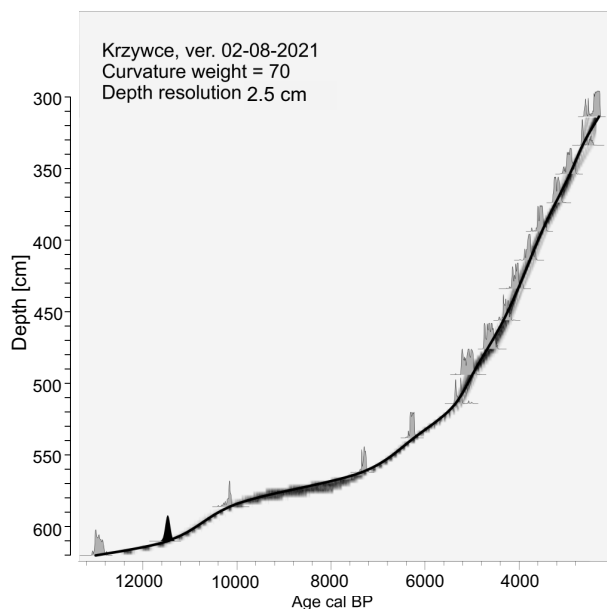


Fig. 2. Age–depth model of the lower part of profile KW/2014. Gray silhouettes represent calibrated dates of the samples analyzed with ¹⁴C. Black silhouette represents the date of the beginning of Holocene

(Milecka, 2005; Filbrandt-Czaja, 2009), which has been clearly indicated in the pollen profile at the depth of 610 cm. The age–depth model (Fig. 2) indicates a rather slow (and variable) accumulation rate in the lower part of the profile (until ~6000 BP) and a distinctly faster (and almost constant) accumulation rate in the upper part (until ~2500 BP). It has to be considered, however, that the ¹⁴C age of the lowermost sample (at 620 cm) might be influenced by the reservoir effect of unknown magnitude, therefore the uncertainty of dates at the lowest 30 cm of the profile may be greater than that calculated using the algorithm.

²¹⁰Pb AND ¹³⁷Cs DATING

The vertical distribution of ²¹⁰Pb_{ex} and ¹³⁷Cs activities is presented in Fig. 3, while the complete dataset is available in the supplementary material (Supplementary file 1¹). The total ²¹⁰Pb and ²¹⁰Pb_{ex} content was generally characterized by a downward decrease, although with some irregularities. The latter was likely due to sediment mixing. The sediment accumulation rates for the last century according to the CFCS model (Fig. 3) were as follows: 1.64 ± 0.36 mm/yr in core KW20/1, 1.05 ± 0.19 mm/yr in core KW20/2, 1.06 ± 0.09 mm/yr in core KW20/3, and 1.38 ± 0.30 mm/yr in core KW20/4.

The ¹³⁷Cs activity profiles (Fig. 3) showed maximum values in the near-surface sediments, decreasing with the sediment depth and reaching very low activities in the lower parts of the investigated cores. Such ¹³⁷Cs profiles often result from postdepositional remobilization of the isotope, both upward and downward, as previously documented in the littoral zones of other lakes and lagoons (Foster et al., 2006; Woszczyk et al., 2017; Brzozowski et al., 2021). However, taking into account the ²¹⁰Pb-based sediment accumulation rates, the calculated sediment depths, dated to the early 1950s AD (Fig. 3), correspond to a decrease in ¹³⁷Cs activities to values below 20 mBq/g. As a consequence, generally, the presence of moderate-to-high ¹³⁷Cs activities in the sediments dated post-1950s AD suggests that the

¹ Supplementary file radionuclides in KW20 cores. Results of the radionuclide analysis of sediment cores. The tables include the analytical data (lab no, sampling depth intervals, ¹³⁷Cs, total ²¹⁰Pb, supported ²¹⁰Pb, excess ²¹⁰Pb, ⁴⁰K, ²³²Th, ²³⁸U activities, and the respective 2-sigma measurement uncertainties) and metadata (coring year, geographical coordinates, laboratory name, instrument type, measurement start and end dates)

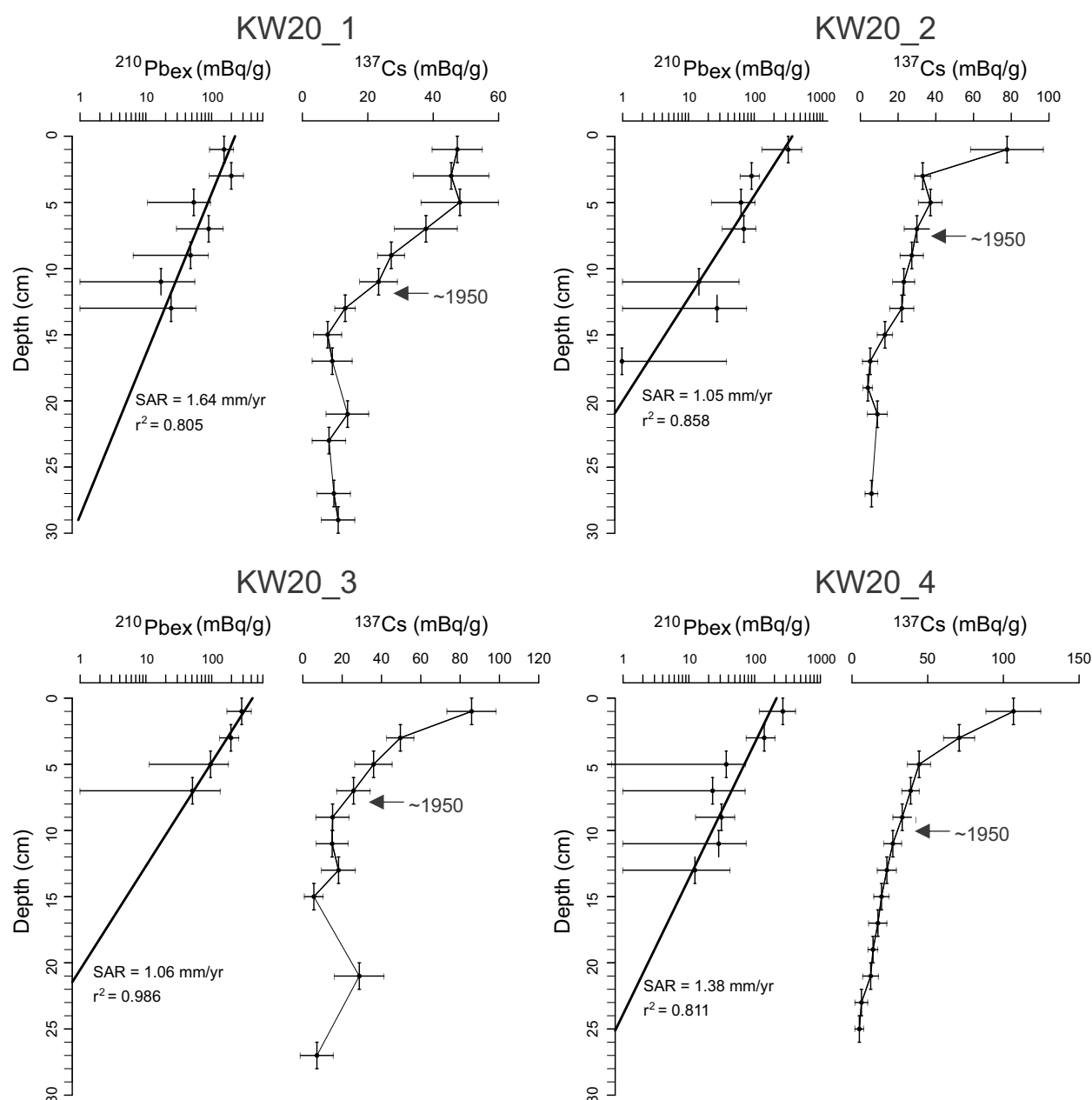


Fig. 3. Short-lived radionuclide ($^{210}\text{Pb}_{\text{ex}}$ and ^{137}Cs) measurements in cores KW20_1, KW20_2, KW20_3 and KW20_4. $^{210}\text{Pb}_{\text{ex}}$ activities are presented as semilogarithmic plots, the trend line was used for sediment accumulation rate (SAR) calculation using constant flux constant sedimentation rate model. The sediment depth of ^{210}Pb -based age of 1950 AD is marked on ^{137}Cs activity profile. The vertical error bars refer to analyzed sediment sample thickness, while the horizontal bars depict 2-sigma uncertainty. The plots were obtained using *serac* (Bruehl and Sabatier, 2020)

^{210}Pb -based age model is generally accurate. The comparison of the CFCS and CIC models with ^{137}Cs profiles is presented in supplementary files (Supplementary file 2²). Since the cores show the evidence of sediment mixing, the sediment accumulation rates and consequently the calculated ages indicate approximate values only.

² Supplementary file 2. Age scale to the CFCS and CIC models KW20_1–KW20_4

POLLEN AND MACROFOSSIL ANALYSES

Core KW/2014

The sediment core from the deepest part of the lake demonstrates the occurrence of vegetation changes from the end of the Late Glacial period to ~2300 cal yr BP (Fig. 4). The upper part of this core (2300 BP to the present) was studied by Milecka and Tobolski (2015). As the main objective of this paper was to trace the history and development of *Cladium* and *Lobelia* populations, only selected results relevant

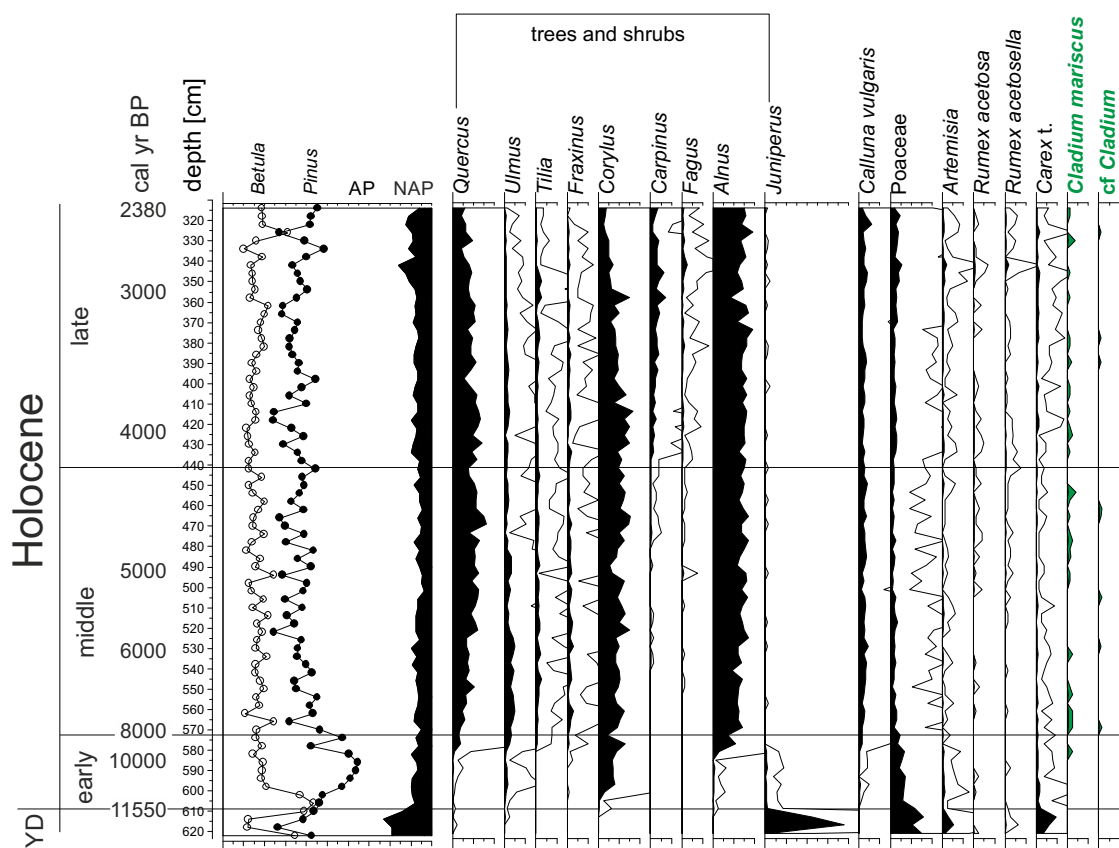


Fig. 4. Pollen diagram of core KW/2014, selected percentage curves (in black). Exaggerations $\times 10$ are given for better observation of rare types. Division of the Holocene after Walker et al. (2012)

for the reconstruction of the local environment are presented.

The oldest part, deposited during the Late Glacial period, contains pollen typical for open tundra and steppe-like vegetation with clusters of *Juniperus*. The beginning of the Holocene (11,550 cal yrs BP, Fig. 4) was marked by the disappearance of cold-demanding tundra species (*Juniperus*) and an increase of *Betula*. The phase of birch-pine forest lasted to 11,000 cal yrs BP, and was subsequently overtaken by the pine-birch forest, until the spread of deciduous forest (*Quercus*, *Ulmus*, *Tilia*, *Fraxinus*) at ~9850 cal yrs BP. During the middle part of the Holocene, approximately between 8200 and 4150 cal yrs BP, deciduous forest prevailed, as suggested by the presence of numerous pollen grains of *Quercus*, *Ulmus*, and *Corylus*. The record of the older part of the late Holocene approximately between 4150 and 2380 cal yrs BP, showed the presence of a forest cover, but the proportion of *Ulmus*, *Tilia*, and *Fraxinus* decreased, paving the way for the development of *Carpinus*. Pine forests with juniper and heather continued to be present. In the youngest layers of

the sediments, the proportion of the pollen of light-demanding plants increased, which included members of the *Poaceae* family, *Artemisia* sp., *Rumex* sp. and *Carex* sp. This could be the result of occasional human activity in the Tuchola Forest.

The investigation of younger sediments of the late Holocene, as reported by Milecka and Tobolski (2015), revealed continued forest cover in the areas adjacent to Lake Krzywce Wielkie. Pine trees with a minor proportion of deciduous trees were found, and *Carpinus* played an important role from 1800 to 750 BP. Later, *Pinus* became dominant, and some human activity indicators appeared (Milecka and Tobolski, 2015).

L. dortmanna and *C. mariscus* in the core KW/2014

The pollen of *Lobelia* was not found in this core. Pollen grains of *C. mariscus* were found regularly from the depth of 579 cm (~9560 cal yr BP) to the uppermost layers (2380 cal yr BP), except for the climatic optimum period (5740–5235 cal yr BP). The pollen was also regularly identified in the youngest part of this

core, analyzed earlier by Milecka and Tobolski (2015). Stable and consistent occurrence of the pollen of *C. mariscus* through the entire Holocene indicates that this plant was present continuously in the reed beds of Lake Krzywe Wielkie.

Littoral cores (KW20/1–KW20/4)

The cores KW20/1 – KW20/4 (Figs 5A, B and 6) show ~200 years of sediment accumulation and development of vegetation in the lake and in the catchment. This is confirmed by similar time and pattern of the accumulation of sediments indicated by isotope dates and the general picture of vegetation succession in Tuchola Forest during the last centuries. Regional plant communities were dominated by pine forest and a low proportion of deciduous species, such as *Quercus*, *Carpinus*, *Corylus*, *Alnus* and *Populus*. They likely occurred as mixtures in some patches of forest and reflect the complex mosaic of habitats at these sites. The dominance of *Pinus* decreased slowly with time (Fig. 5A, B). In contrast, the proportion of herbs, especially grasses, increased. During the last 100 years, higher proportion of *Juniperus* was also documented, accompanied by a declining contribution of deciduous species like *Quercus*, *Carpinus* and *Corylus*. Percentages below 1% of the calculation sum for these species indicate their possible disappearance in the areas directly adjacent to the lake; pollen grains were blown from distant places (Milecka et al., 2004; Miotk-Szpiganowicz et al., 2004; Ralska-Jasiewiczowa et al., 2004).

KW20/1

Cladium pollen was present in almost all the spectra of the entire core. Moreover, single fruits were found in the middle part of the core, which indicate that *Cladium* was likely present in this part of the lake for over 200 years. It was a regular constituent of reed bed communities, along with *Carex*, *Schoenoplectus*, *Typha latifolia* and probably *Phragmites australis* (common species at present). The presence of *Schoenoplectus* and *Typha* is confirmed by the presence of their fruits revealed by the macrofossil analysis (not identified to species level). The investigations also revealed the presence of another species that is predominantly found in high reed bed, *Eleocharis palustris*. Frequent occurrence of pollen grains and fruits of *Carex* species suggests that they

are common inhabitants of low reed bed communities.

Pollen grains of *Lobelia* were found in samples taken from the depth of 14 cm in the sediment toward the upper layers. There were singular grains in a few samples, despite the fact that the core was collected from the area right next to the location where the modern population of *Lobelia* was found. Seeds of *Lobelia* were found in the samples at the sediment depth of 8 and 10 cm. The presence of *Lobelia* pollen in the sample at the depth of 14 cm indicates that the population must have developed before 1935 AD.

Myriophyllum alterniflorum is a common component of aquatic plants in the upper part of the core. Its pollen grains were found in all the samples taken from the depth of 11 cm upward, with the maximum content being 2%. Moreover, single pollen grains were found at the depth of 14 and 23 cm. Fruits of *Myriophyllum* sp. were found at the depths of 10, 12 and 14 cm in the sediment. Taking into account the exact identification of pollen and the modern presence of *M. alterniflorum* in the lake, the fruits very likely belong to this species. Fruits of *Potamogeton* (6–28 cm, up to 9 specimens) and *Chara* oospores (2–29 cm, up to 219 specimens) were the most abundant in the macrofossil group. The relatively high numbers of subfossil *Potamogeton* fruits and *Chara* oospores suggest their local occurrence.

KW20/2

Pollen of *Cladium* were found in many samples throughout the core; however, they occurred mostly as single grains. Subfossil fruits of *Cladium* were found at the depths of 2, 6 and 12 cm. Few fruits of other reed bed plants were also identified, for example, *Typha* sp. (at the depth of 6–22 cm) and *E. palustris* (32 cm). Low reed bed plants were relatively abundant, which comprised *Carex* fruits, *P. amphibium*, *Ranunculus sceleratus*, and *J. bulbosus*.

A single pollen grain of *L. dortmanna* was found at the depth of 14 cm. The seeds were found at 10–13 cm. Thus, according to the fossil record, *Lobelia* was present in this part from the turn of the 19th and 20th centuries.

Among the aquatic macrophytes, *Potamogeton* (3–33 cm, 1–4 specimens) and *Chara* sp. (2–31 cm, 1–1090 specimens) were the most abundant. Pollen of *M. alterniflorum* occurred

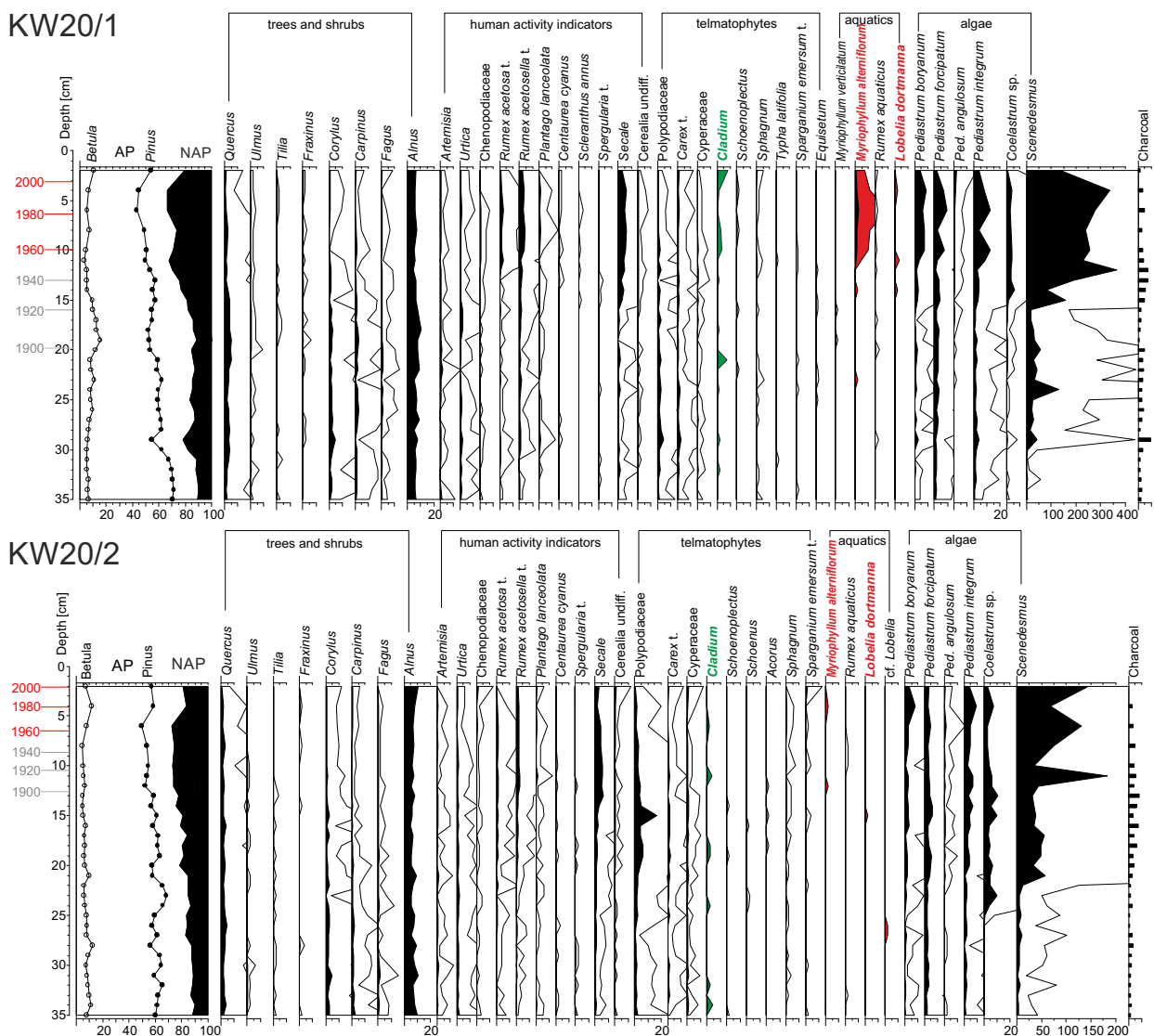


Fig. 5A. Pollen diagrams of cores KW20/1 – KW20/2. Selected percentage curves of trees and shrubs, human indicators and pollen of local plant communities. Curve units – 10% unless otherwise stated. Red dates – dates derived from the ^{210}Pb -based age model, gray dates – linear approximation of the model assuming constant accumulation rate

at the depths of 4 and 12 cm. The existence of *Myriophyllum* fruits (at 4, 6 and 17 cm), despite low fruit production by this plant, suggests the in situ presence of this species (*M. alterniflorum*).

KW20/3

Pollen grains of *Cladium* and cf. *Cladium* were found in the lower part of the core, up to 18 cm, and in the uppermost layers of the sediments. Singular seeds of this species were identified at the depths of 10, 14 and 25 cm, and more numerous, up to 12 specimens per sample, were found at the depths of 2 and 4 cm. Thus, the fossil records suggest almost continuous presence of this species. They were accompanied by other species of high reed beds as indicated by the seeds and pollen of

Schoenoplectus lacustris, and seeds of *Typha* sp. and *Elocharis*. Low reed beds are represented by pollen of the Cyperaceae family, *Carex* sp., *Thelypteris palustris*, *Hottonia*, *Iris pseudoacorus*, and seeds of *J. bulbosus*, *P. amphibium* and *R. scleratus*.

Pollen of *Lobelia* was not found in the core KW20/3. However, singular seeds of *Lobelia* occurred at sediment depths of 6, 8, 10, 12 and 22 cm. During the macrofossil analysis, numerous seeds of *Potamogeton* (3–33 cm, 1–12 specimens) and some seeds of *Myriophyllum* sp. (6, 8, 20 and 22 cm, singular specimen) and *Najas marina* were identified. Singular pollen of *Potamogeton* and *M. alterniflorum* were identified at 12 cm. *Utricularia* (8 cm) and *Rumex aquaticus* (4 cm) were also found as single pollen. At the depth interval of 1–13 cm, *Chara*

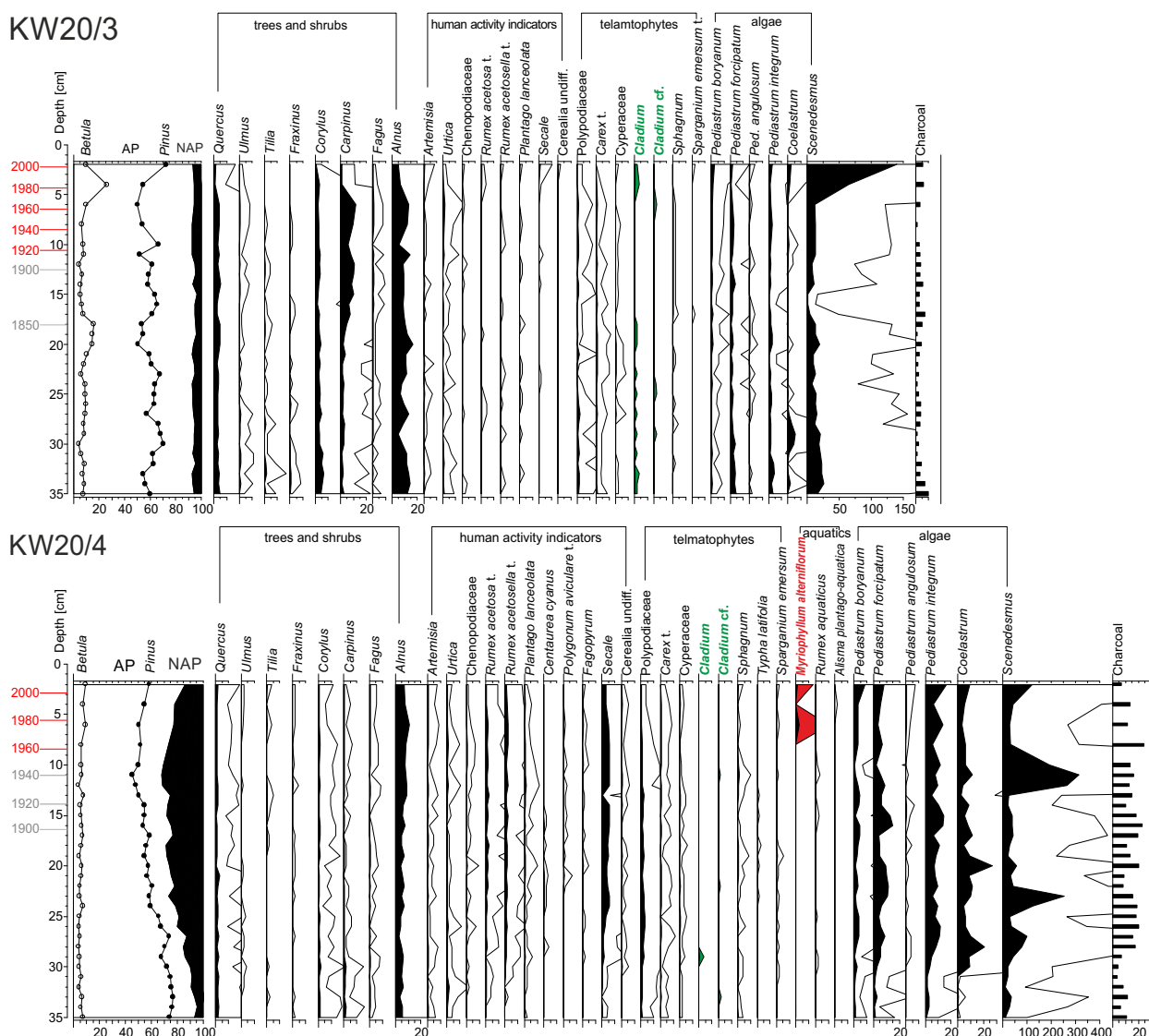


Fig. 5B. Pollen diagrams of cores KW20/3 – KW20/4. Selected percentage curves of trees and shrubs, human indicators and pollen of local plant communities. Curve units – 10% unless otherwise stated. Red dates – dates derived from the ^{210}Pb -based age model, gray dates – linear approximation of the model assuming constant accumulation rate

oospores (1–35) were found in the sediments. The consistent presence of *Potamogeton* fruits in most of the samples suggests the stable existence of a pondweed population in the western part of the lake.

KW20/4

Few pollen grains of *Cladium* were noted in the lower and middle parts of the core, but their seeds were not found. Today, fen-sedge does not exist in the southern part of the lake. Singular grains could come from long-distance transportation or from temporarily developed small plant communities. The flora of high reed bed was represented by pollen and seeds of *T. latifolia*, probably *T. angustifolia* (*Sparganium emersum* type, *Typha* sp.) and *Schoenoplectus*. Low reed bed included *Carex*

(pollen and seeds), ferns (spores) and seeds of *J. bulbosus*, *R. sceleratus* and *P. amphibium*.

Neither pollen nor seeds of *L. dortmanna* were found in this core. According to the information provided by the manager of BTNP, Mr. Wojciech Błoniarz, during the last few years, few specimens of flowering *Lobelia* were observed in this place, which prompted us to select this site for coring. However, this fact was not confirmed during the field observation conducted in July 2020.

Pollen of *M. alterniflorum* occurred abundantly in the sediments above 6 cm, and fruits were also found in the samples taken at depths of 2 and 4 cm (up to 6 specimens). Pollen grains of numerous other aquatic macrophytes were present in this core: *R. aquaticus* (30–10 cm), *Utricularia* (4 cm), *Alisma*

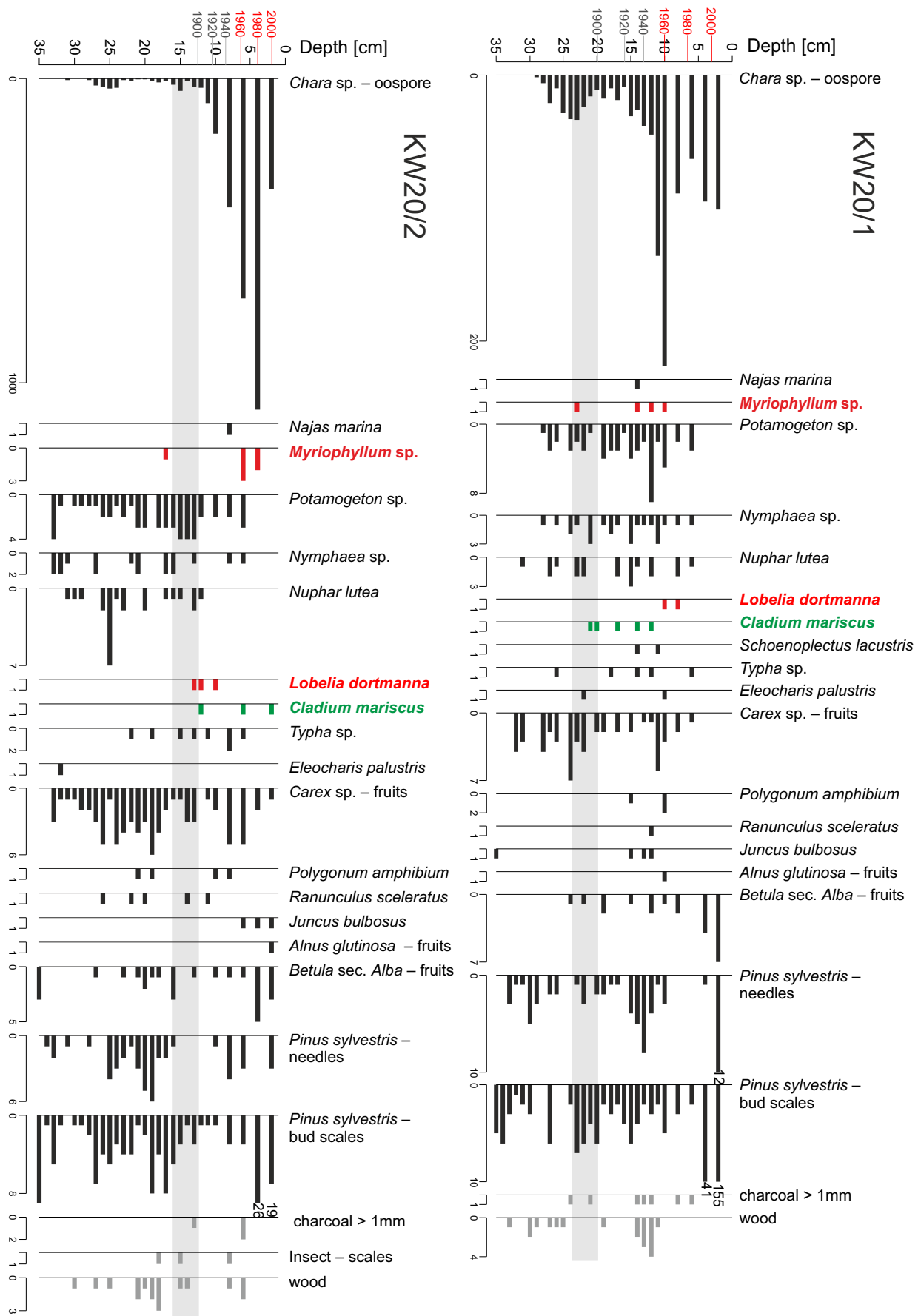


Fig. 6A. Macrofossil diagrams of cores KW20/1–KW20/2. Red dates – ^{210}Pb -based age dates derived from the model, gray dates – linear approximation of the model assuming constant accumulation rate. Scales represent numbers in sample volume. Out of scale values are given next to the bars. Gray bar indicates approximate age of water level drop

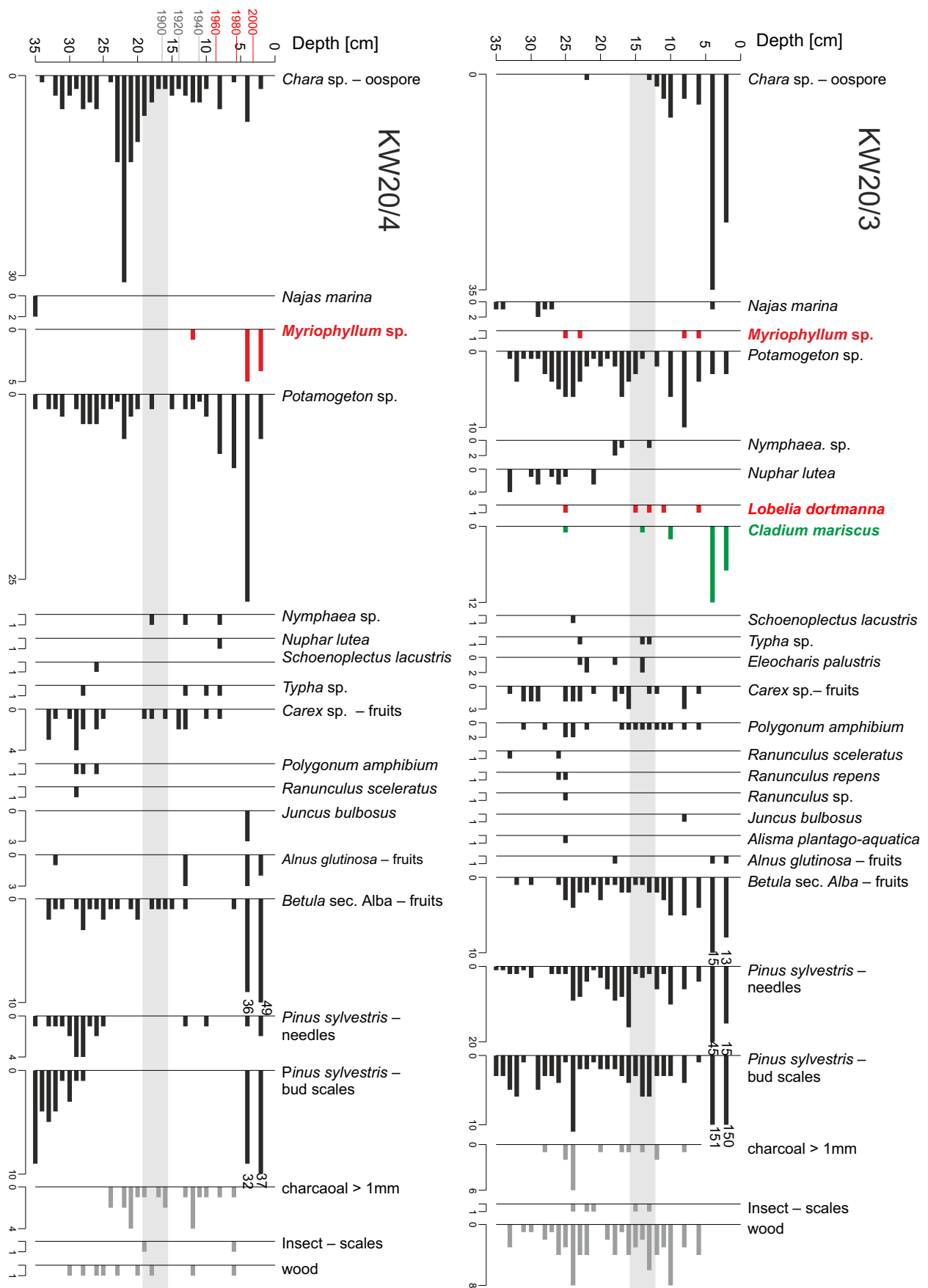


Fig. 6B. Macrofossil diagrams of cores KW20/3–KW20/4. Red dates – ^{210}Pb -based age dates derived from the model, gray dates – linear approximation of the model assuming constant accumulation rate. Scales represent numbers in sample volume. Out of scale values are given next to the bars. Gray bar indicates approximate age of water level drop

plantago-aquatica (4 cm), and *Myriophyllum spicatum* (2 cm). Fruits of *N. marina* (35 cm), *Nymphaea* (8–18 cm), and *Nuphar lutea* (8 cm) were found during macrofossil analysis. *Potamogeton* fossils were the most abundant (up to 28 fruits).

DISCUSSION

EVIDENCE AND TIMING OF LOBELIA AND CLADIUM CO-OCCURRENCE IN THE LAKE

The investigations revealed a low representation of both pollen and seeds of *L. dortmanna*. The results are in agreement with the conclusions of earlier studies (Moeller, 1978; Milecka and Obremska, 2002; Milecka, 2005). *Lobelia* is an aquatic plant, but the flowering shoot grows above the water surface and is pollinated by insects. Dąmbska (1965) and Moeller (1978) found that the deeper the depth of water is, the smaller the number of flowering plants will be. Plants growing below 1.7–2 m do not flower at all. It has also been proved that some specimens do not open their flowers and undergo self-pollination (Faegri and Van der Pijl, 1979). Spence (1982) reported that the process of seed production requires a large amount of light. The significance of adequate light conditions was also stressed by Szmeja and Bociąg (2004), Banaś et al. (2012) and Ronowski et al. (2020). Consequently, low frequency of micro- and macrofossils is observed in lacustrine sediments rich in organic matter. This observation was confirmed in the present study. Although two cores (KW20/1 and KW20/2) were collected from the direct neighborhood of flowering *Lobelia* patches, the frequency of occurrence of micro- and macrofossils was low. This proves that this species occurs along with other macrophytic plants in the lake. The lack of *Lobelia* pollen in the long sections of cores, confirmed by the lack of fruits, suggest that *Lobelia* was absent in the studied periods. The complete lack of *Lobelia* fossils in the older parts of four cores of sediments rich in organic matter and also in the long deep-water core (Milecka and Tobolski, 2015, and this research) suggests that *Lobelia* is a very recent component of aquatic vegetation in Lake Krzywce Wielkie. It likely appeared by the end of the 19th century.

Studies that aimed to determine the presence of *Lobelia* in the temperate climate zone based on pollen analysis of organic sediments

were previously carried out in Europe. According to Hjelmroos-Ericsson (1981) and Milecka (2005), *L. dortmanna* developed in Tuchola Forest lakes in the late Holocene period, at ~3800 yrs BP in Gacno Wielkie and at ~2000 yrs BP in Nierybno, Lake Linowskie and Moczadło. On Wolin Island (NW Poland), *Lobelia* was found since ~1700 yrs BP (Latałowa, 1992). Odgaard (1994) identified *Lobelia* pollen occurring from ~4000 yrs BP in northern West Jutland. In Lake Krzywce Wielkie, *Lobelia* was documented only in the youngest sediments and it constitutes very recent floral species of this lake. The spread of *Lobelia* to the temperate zone of Central Europe during the late Holocene (decline of interglacial cooling) can be explained by its climatic demands and ecological optimum related to the cold climate of the boreal zone (Odgaard, 1994; Birks, 2000). The middle Holocene climatic optimum did not favor the existence of this boreal species. According to Farmer (1989), the temperature of 17°C in the month of July is a limiting factor for its expansion. Therefore, the occurrence of *Lobelia* was documented in many works mainly during the late Holocene cooling. However, it is not the case of Krzywce Wielkie, where *Lobelia* presence was documented during warming after the Little Ice Age (20th and 21st centuries). Thus, it is likely that environmental conditions (e.g., land use) and human activity as well significantly influence the development of *Lobelia* populations.

The pollen profile of Krzywce Wielkie demonstrated the consistent presence of *C. mariscus* from the beginning of the Holocene period (core KW/2014; Milecka and Tobolski, 2015) and in all cores of the littoral zone. However, relatively high content of fruits was found only in core KW20/3.

DISTRIBUTION AND CONSERVATION IN POLAND AND EUROPE

The existence of both species in BTNP is considered to be of environmental value because it is within the geographical limits of Poland and hence is under strict jurisdiction (Regulation of the Ministry of Environment of 9 October 2014). *Lobelia* reaches the southern border of occurrence in Poland (Sculthorpe, 1985; Szmeja, 2014a). However, there are some sites in western Europe that are situated farther south (e.g., in France). Many authors (Czubiński, 1950; Kucharczyk, 2000; Herbichowa and Wołejko, 2004) assumed that the eastern European

border of the range of *C. mariscus* is in Poland. Considering the fact that the species is found in scattered locations south and east of the study area, for example, in Latvia (Salmina, 2004) and Czechia (Pokorný et al., 2010), it would be better to assume that it shows a “scattered distribution” and avoid the determination of an accurate border. As these species predominantly occur within the borders of their occurrence in Poland, their IUCN status in Poland differs from their global and European status. According to Maiz-Tome (2016), *L. dortmanna* globally (or in Europe) is not likely to meet the threshold for being included in the “Vulnerable” IUCN category and is assessed as “Least Concern.” But locally, in Poland, the status of this species was changed from vulnerable (Zarzycki and Szeląg, 2006) to endangered (Kaźmierczakowa et al., 2016). Similar status has been given to *C. mariscus* in Europe and the world (Lansdown et al., 2017), but in Poland it is placed under the category “Near Threatened” (Kaźmierczakowa et al., 2016).

The reasons for the disappearance of *Lobelia* sites were widely discussed, and considered to be related to eutrophication and changes in land use over time (Farmer, 1989; Szmeja, 1997, 1998; Kraska et al., 2013). The causes for the disappearance of *Cladium* sites can be attributed to both natural (vegetation succession) and anthropogenic changes of habitats, such as changes in water level and trophy (Herbichowa and Wołójko, 2004; Karcz, 2008). Report under Article 17 of the Habitats Directive Period 2007–2012 indicated the factors that pose a threat to their existing habitat, which include physical and chemical changes in water bodies (29%), vegetation succession/biocenotic evolution (16%) and other changes related to human activities (55%). Despite many known threats, new modern localities of both *Lobelia* (Chmara, 2007; Chmara et al., 2015b) and *Cladium* (Namura-Ochalska, 2004; Gałka, 2007; Karcz, 2008; Towpasz and Stachurska-Swakoń, 2009; Krajewski, 2011) are still being identified in Poland.

DIFFERENCES IN CONTEMPORARY ECOLOGICAL REQUIREMENTS OF *LOBELIA* AND *CLADIUM*

Lobelia dortmanna and *Cladium mariscus* differ in their spatial ranges. Contrary to the boreal range of *Lobelia*, *C. mariscus* is an evergreen reed bed plant widely spread across all

the continents except Antarctica (Pawłowska, 1972) and is considered to be an indicator of temperate warm climate (Tobolski, 2006; Brande, 2008). Both species are found in the areas subjected to a strong oceanic influence (Czubiński, 1950; Szmeja, 2014a). In Poland, *Cladium* tend to spread toward the north (Kłosowski, 1986–87) and separate sites are found in calcareous mires of eastern Poland (Fijałkowski, 1959; Buczek, 2005), whereas the present occurrence of *Lobelia* species is limited to northwestern Poland.

Both species differ in their ecological demands. Podbielkowski and Tomaszewicz (1994) reported that *Cladium* is an expansive plant inhabiting eutrophic or dystrophic lakes. On the contrary, Zarzycki et al. (2002) classified it as a species of oligotrophic habitat. Ellenberg et al. (1991) present medium requirements with regard to nitrogen content. *Cladium* species represent group 3 (“indicator of more or less infertile sites”), while *Lobelia* is included in group 1 (“indicator of extremely infertile sites”). The biggest difference in their demands relates, however, to pH. According to Ellenberg et al. (1991), *C. mariscus* is an indicator of basic conditions prevalent in calcareous or other high-pH soils where the maximum pH is found to be 9. In contrast, *Lobelia* is an indicator of acidic conditions, where pH decreases to 2, and it exceptionally occurs in sediments with nearly neutral pH. Herbichowa and Wołójko (2004) and Mróz (2010) regarded *C. mariscus* as a calciphilous plant. Rothmaler (1994) reported that it can grow on basic and lime-rich substrates. However, it is also known that saw-sedge is capable of growing on habitats poor in calcium carbonate (Grosse-Brauckmann, 1964; Marek, 1991; Sawilska and Dąbrowska, 1995; Brande, 2008; Tobolski and Gałka, 2008). According to Gałka (2007), appropriate climatic conditions, especially temperature and air moisture, are the main factors that contribute to the development of a *Cladium* population instead of the abundance of calcium carbonate. Calcium plays a key role only at the sites located adjacent to the border of the range of the population. In these regions, calcium compensates for the heat shortage due to the exothermic reaction of calcium oxide and water. This means that the calcareous soil is important, but only in the case of the eastern and northern sites of the range. The lack of the necessity of calciphilous

Table 3. Ranges of calcium content, acidity and conductivity of water documented in Lobelian lakes and other lakes in BTNP

Locality and references	Ca mg/l	pH	conductivity
7 Lobelian lakes in Pomerania, NW Poland, some of them are degraded (Kraska and Piotrowicz, 1994)	1.45–23.6	4.6–8.77	42–170
16 lakes with <i>Isoëto-Lobelieta</i> community from Pomerania (Kłosowski, 1994)	6–17.6	6.4–8	–
18 lakes with <i>Myriophylletum alterniflori</i> community from Łęczyńsko-Włodawskie Lakeland, E Poland (Kłosowski, 1994)	8.2–17.6	6.5–7.6	–
9 Lobelian lakes in Zaborski Landscape Park, Tuchola Forest (including lakes in BTNP) (Gonet et al., 1994)	4–13	4.2–6.9	38–81
Lakes of Krzywce-Błotko channel (Zdanowski, 2004)	6.4–10.4	6.9–7.7	39.8–69.3
Lakes of Struga Siedmiu Jezior (Zdanowski, 2004)	43.3–48.9	8–8.5	215–232

sediments was also reported by Pokorny et al. (2010) in relation to fens.

Lobelia occurs in acidic to neutral water, that is, pH 4–7 (Zarzycki et al., 2002). Hanon and Gaillard (1997) reported its presence in waters with pH 5.0–6.7. There is a wide range of calcium content in Lobelian lakes and the lakes with *Cladium* (Table 3). The lakes of the Krzywce-Błotko canal (including Krzywce Wielkie) have Ca contents similar to that of Lobelian lakes, while the concentration of Ca is found to be much higher in other lakes with *Cladium* in BTNP (Fig. 1). Thus, from this point of view, the presence of *Cladium* in Lake Krzywce Wielkie is exceptional. On the other hand, it presents a wide ecological scale in terms of pH because *Cladium* occurs in both the calcium-rich Struga Siedmiu Jezior stream and the calcium-poor Krzywce-Błotko canal.

LAND-USE, HYDROLOGICAL AND TROPHY CHANGES

Presently, Krzywce Wielkie is considered to be an endorheic lake. However, a topographic map from 1874 AD shows a drainage canal connecting it with Lake Krzywce Małe. On the younger maps, the drainage canal is clearly marked, which indicates that it existed at least before 1900 AD. According to Mr. Błoniarz, manager of BTNP, this drainage canal has been dry for many years. The altitude of the drainage threshold is about 124.4 m a.s.l., and the water level of the lake as shown on topographic maps (1965, 1992, 1:10,000, see Nienartowicz 2012) is 123.5 m a.s.l. In the years 2000–2004, the water level was found to be 123.44 m a.s.l., which slightly increased in the following years; however, it has not exceeded 123.8 m a.s.l. (Marszelewski et al., 2016). When the threshold was dug in the 19th century, the water level was the same as or higher than the altitude of the threshold (124.4 m a.s.l.). Thus,

the outflow through the drainage canal caused a decrease in the water level of the lake by at least 60–90 cm, and strongly influenced the littoral zone of the lake and the plant communities living therein. The above is reflected in macrofossil diagrams, and the gray bar roughly separate the two periods of higher and lower lake water levels (Figs 6A, B and 7).

Exposure of the littoral areas of the lake as a consequence of the decreasing water level created conditions favorable for the development of *Lobelia* populations. Most of their fruits were found in sediments deposited at the time of the digging of the drainage canal or later. Pollen of *Lobelia* in core KW20/1 appeared likely at the time of drainage construction, and in core KW20/2 a singular grain was found shortly before the decrease of the water level. One seed of *Lobelia* in core KW20/3 at the depth of 22 cm was found probably due to disturbing the sediments in the course of the drilling (reposition from the upper layers by the corer). Hence, a *Lobelia* succession at the end of the 19th century would be possibly supported by the decrease of the water level. New habitats in shallow waters enabled the potential development of new-coming species.

The analyses of old maps provide additional supporting evidence explaining the development of conditions favorable for *Lobelia*. At the turn of the 18th and 19th centuries, Schröter's map showed open spaces on the eastern and western sides of the lake (Nienartowicz, 2012). They were suitable for rye cultivation or pastures. Riemann's map, prepared in 1860 AD, showed a similar distribution. There was no drainage canal during that time, but fields existed in the west and southeast of the lake. Thus, only the areas adjacent to the northeastern part of the lake (cores KW20/1 and KW20/2) were covered by forests. The presence of cultivated fields or pastures undoubtedly influenced

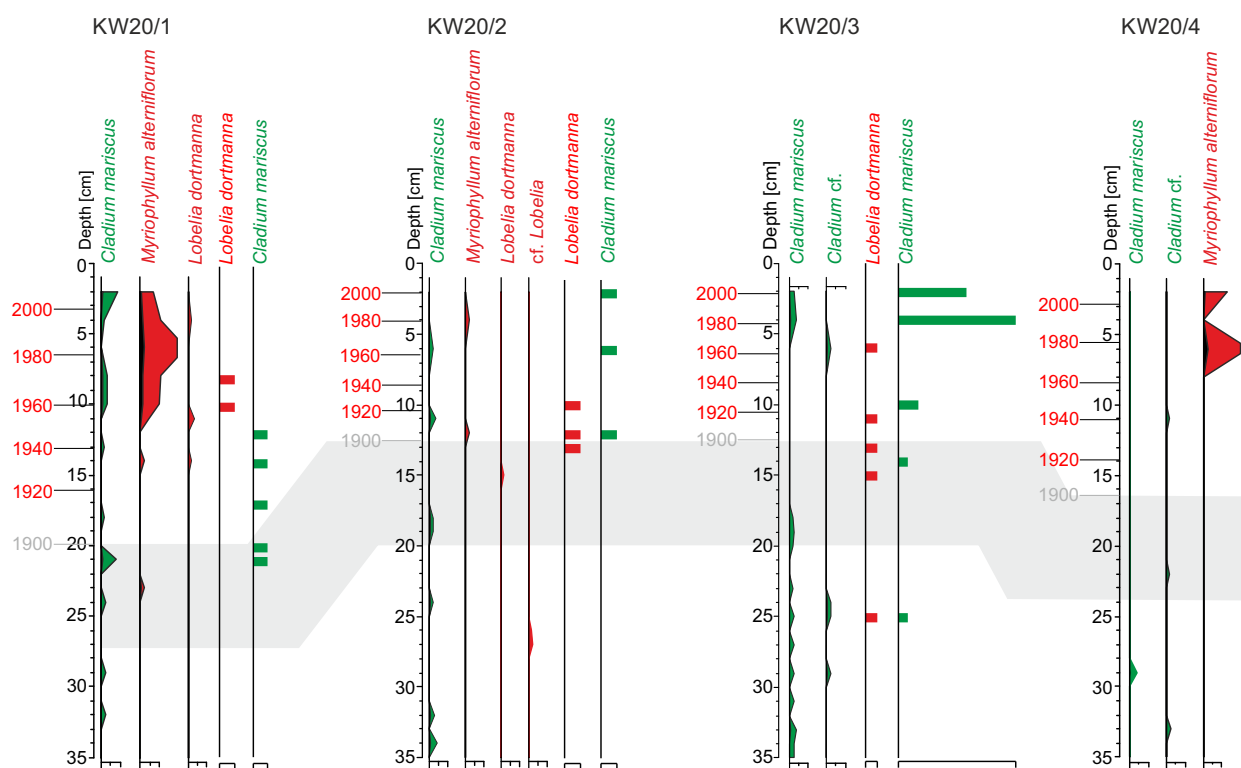


Fig. 7. Summary diagram of the content of pollen and macrofossils of the indicative species discussed in the article. For explanations of scale, dates and gray bar see Figs 4–6

the trophy of the lake by the surface discharge of nutrients. The occurrence of *Rumex* and *P. lanceolata* and only a few pollen grains of weeds indicates that the neighborhood areas around the lake shore were used as pastures rather than as cultivation sites in the 19th century. Agricultural activity was abandoned and forest communities developed at the end of the 19th century, which is confirmed by the presence of a unit of Prussian Forestry Academy in 1894 AD. According to the map created in 1920 AD, the whole area of presently existing BTNP is covered by forests (Nienartowicz, 2012). The development of forests restricted the supply of nutrients and resulted in a decrease of the trophy of the lake. Additionally, pine forests and boggy patches protected the lake and contributed to decreasing pH and oligotrophy (Kraska et al., 1998; Zdanowski, 2004).

The decrease of trophy at the turn of the 19th and 20th centuries is manifested by an increase in the *Lobelia* population, as well as by the growth of *M. alterniflorum*, *J. bulbosus* and *Chara* sp. Three species of *Myriophyllum* are found in Europe, and all of them are present in BTNP (Wróbel and Hutorowicz, 2012). Among them, *M. alterniflorum* adapted to the low nutrient content and constitutes the typical component and indicator of oligotrophic

lakes (Rutkowski, 2004). According to Zarzycki et al. (2002), trophy of *M. alterniflorum* is classified as level 2–3 (oligotrophy to mesotrophy), while the other species are classified as level 4 (eutrophy). *Juncus bulbosus* grows in oligotrophic habitats (Zarzycki et al., 2002) and appeared not earlier than the second half of the 20th century. *Chara* oospores were not identified to species level; however, species of Characeae exist in the clear waters of oligotrophic or mesotrophic lakes (Pełechaty et al., 2007; Schubert et al., 2018), and may be associated with rare plants such as *L. dortmanna*, *L. uniflora* and *Isoëtes* (Bertrin et al., 2013). The decrease of trophy during the 20th century is also indicated by the lower content of macrofossils of eutrophic species, such as *P. amphibium*, *R. sceleratus*, *Nuphar* and *Nymphaea*, in the younger parts of all the cores. A decreasing trend was observed with regard to the contamination and concentration of P, K and Ca in the selected lakes of BTNP (Wielkie Gacno, Zmarle, Czarne i Ostrowite), as reported by Chmara (2006). This trend is favorable for the Lobelian lakes situated within the Park, and is considered to be the result of land-use changes and the establishment of BTNP.

The near-surface layers of sediments were characterized by a lower diversity of herbs due

to the unification of the vegetation cover and the development of a pine forest around Lake Krzywce Wielkie. However, in cores KW20/1, KW20/2 and KW20/4 the increased presence of indicators related to human activities was noted (Fig. 5A, B), mainly *Rumex* and *Secale*, which are wind-pollinated plants and release large amounts of pollen (Meese and Morris, 1984; Subba-Reddi and Reddi, 1986; Sugita et al., 1999). Their presence in the upper part of the sediments in the study area is the result of the regional transport. Thus, the increased occurrence of *Rumex* and *Secale* is the consequence of a huge production of pollen and the common presence of these species in the 20th century under the strong human activity.

CONCLUSION

Paleobotanical analysis of the sediments revealed that a *C. mariscus* population developed during the early Holocene and has almost continuously existed in Lake Krzywce Wielkie since then. While *L. dortmanna* is a new species that appeared in this lake at the end of the 19th century.

In the younger part of the cores, higher frequencies of oligotrophic species, other than *L. dortmanna*, such as *M. alterniflorum*, *J. bulbosus* and Charophytes, were noted. There was a concurrent decrease in the population of aquatic macrophytes typical for eutrophic water, namely *P. amphibium*, *R. sceleratus*, *Nuphar* and *Nymphaea*. The spread of *L. dortmanna* and other oligotrophic species was possible due to the artificial lowering of the lake water level and the changes in the land use of adjacent areas, which mainly included the abandonment of agricultural activities, grazing and the development of a pine forest. The drainage canal dug by the end of the 19th century resulted in a decrease of water level, which caused changes in the littoral zone of the lake and enabled the rebuilding of the plant communities and the development of new species. The changes in the surroundings of the lake favored the filtering of water from the catchment areas and resulted in the smaller supply of nutrients, which enabled the development of oligotrophic species communities. The establishment of BTNP at the end of the 20th century contributed to the complex protection and conservation of the catchment area, which

further limited the potential eutrophication of habitats.

The recent development of *L. dortmanna* population proves that the presence of this oligotrophic species is generally possible under the present environmental conditions in the temperate zone, despite a continuous supply of nutrients to the lakes in the industrial countries as a result of agricultural activities and synanthropic changes of flora and vegetation. The necessary conditions are related to the catchment. Forest cover, especially pine forest, is an important factor because of the low pH of the soil and infertile habitat. It is essential for such lakes that the adjacent areas would be protected by law so that changing the land use would be impossible.

Potentially, a gradual and slow decline of *Cladium* could be expected due to the oligotrophication of the water of a lake. However, the often contradictorily defined ecological demands of *Cladium* and its presence in various habitats prevent us from drawing such a conclusion. Perhaps, its ability to adapt to different habitats contributes to its persistence in Lake Krzywce Wielkie for a longer period of time.

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