

Late Glacial development of lakes and wetland vegetation in a dune area in Central Poland

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ABSTRACT. This study investigated the history of the development of six, paleo-lakes, which are at present filled with sediments, in a dune area in Central Poland, based on multiproxy paleoecological analyses and accelerator mass spectrometry radiocarbon dating. The aims of the paleoecological studies were: i) to determine the initial age of lakes development, ii) to reconstruct the local and regional plant succession, as well as iii) to reconstruct the environmental conditions during the initial stage of the development of lakes and peatlands. The obtained results indicated that: the former lakes in dune depressions were developed during the Bølling and Allerød when sparse vegetation allowed strong aeolian activity. Climate warming in Bølling led to the development of a denser plant cover, inhibition of sand transportation and the formation of mid-dune reservoirs with the accumulation of organic sediments. As indicated by ¹⁴C dating, mid-dunes basins were formed between 14 686 ± 60 cal. yr BP and 13 421 ± 60 cal. yr BP.

The results of the paleobotanical analysis suggested that the reservoirs were shallow, oligo-mesotrophic, inhabited by pioneer calcicole vascular plant species such as: *Chara* sp., *Hippuris vulgaris*, *Potamogeton natans*, *Potamogeton fresii*, *Potamogeton alpinus* and *Potamogeton filiformis*, and mosses such as: *Pseudocalliergon trifarium*, *Calliergon* sp. and *Calliergonella cordifolium*. The area next to the reservoirs was covered with sparse pine forests combined with birch, which is typical of the Late Glacial period. The open areas were dominated by psammophilic and steppe vegetation, including Poaceae, *Artemisia* and *Hippophae rhamnoides*.

Geochemical analysis revealed that Ca²⁺ and Fe³⁺ were in high concentrations, which could have influenced the presence of taxa preferring soil with high Ca²⁺ content. The accumulation of calcium in sediments confirms that the reservoirs were fed by groundwater originating from the progressive degradation of permafrost associated with thermal changes.

KEYWORDS: plant succession, mid-dune reservoirs, paleoecology, climate change, Late Glacial

INTRODUCTION

A wide belt stretches across almost the whole of Europe, known as the European sand belt, on which aeolian sands and inland dunes can be found (Kobojeck and Kobojeck, 2021).

It covers the areas that have been released from the ice sheet stretching from the Netherlands in the west to Ukraine and Russia in the east. These belts are most numerous in hollows associated with river valleys in inland dunes in Poland (Galon, 1958; Manikowska,

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1985; Nowaczyk, 2009). Clusters of dunes are present in the Płock Basin and Warciańsko-Notecki Interfluve (Pilarczyk, 1976), Warsaw Hollow (Forest of Kampinoska) (Konecka-Betley et al., 1996), Toruń-Bydgoszcz Hollow, Bory Dolnośląskie, and Sandomierz Hollow (Rurek, 2013). They can also be found on moraine plateaus (Nowaczyk, 1967), at the bottom of river valleys (Izmailow, 2001), in subglacial gutters (Nowaczyk, 1967) and within the plains of postglacial uplands and valley dens in the Łódź voivodeship (Dylikowa, 1958; Galon, 1959; Rotnicki and Tobolski, 1969; Dzieduszyńska, 2013; Kobojeck and Kobojeck, 2021).

Dunes are unique landforms. These structures are built of sands blown by wind, and are of various shapes with considerable heights. They were formed in the late Vistulian under cold periglacial climatic conditions as a result of deflation, transport and accumulation by wind (Dylikowa, 1958; Kobojeck and Kobojeck, 2021). Dunes were accompanied by a variety of drainless melting or deflation bowls of different sizes and depths. In the Late Glacial period, they mainly underwent changes due to climate warming. Small recesses transformed into peat bogs due to the accumulation of mineral and organic sediments during the Late Glacial period (Niewiarowski and Kot, 2010).

Based on the internal structure of dunes, especially the presence of fossil soils, aeolian series formed in successive dune-forming phases can be distinguished (Dylikowa, 1969; Nowaczyk, 1976; Manikowska, 1985). Lithogenic soils, which formed from deep aeolian sands, favoured the development of psammophilic vegetation and few trees that are the most resistant to high temperatures and droughts (Mocek, 1997), leading to temporary immobilization of dunes in Bølling. Due to their high dynamics, the quick response of dunes to external factors may provide data about paleoenvironmental changes, including climate changes. Therefore, dunes can be considered forms of the earth's surface that are particularly sensitive to current climate changes and human activities that lead to the partial or often complete destruction of their original structure (Kobojeck and Kobojeck, 2021).

The origin, age, phases of development, typology, climatic conditions and vegetation succession of inland dunes have been widely explored as elements of lowland areas in Poland (Galon, 1958, 1959; Krygowski, 1958; Kozarski,

1962; Nowaczyk, 1986; Izmailow, 2001). However, there is a scarcity of studies on mid-dune areas, as well as fossil lakes and peatlands developed in depressions, which were crucial for the survival of many protected and rare plant species. Dunes were often accompanied by several shallow, peat-covered depressions of irregular shapes (e.g. Wasylkowa, 1964, 1999; Rotnicki and Tobolski, 1969). These reservoirs formed as a result of climate changes, geochemical conditions and trophy. Accumulation of organic sediments allows the development of a record of vegetation succession which can be revealed using paleobotanical methods (Wasylkowa, 1964; Tobolski, 1966; Kobendzina, 1969; Nowaczyk, 1986; Birks, 2000).

One of the dune areas, which are poorly studied in terms of the development of lakes and peat bogs, is the dune area located near the village of Płęsy, Przedborów forest inspectorate. Rotnicki and Tobolski (1969) carried out geomorphological and paleobotanical studies (pollen analysis) of dunes and peat bogs near Węglewice (~4 km from our study site). However, their research was not based on radiocarbon dating.

In the present study, a comprehensive and detailed analysis in the interdune area in Central Poland is presented. This is the first multiproxy study in this area in which plant macrofossil analysis, pollen analysis and geochemical analysis were carried out along with ^{14}C radiocarbon dating of the bottom layers of the sediment cores.

The aims of the study were to: i) record the time and evolution of the mid-dune area and plant development in the Late Glacial period, ii) understand the impact of climate changes on local vegetation, iii) determine the paleohydrological changes in the Late Glacial period, and iv) assess the variability of physicochemical parameters and their influence on the local plant succession.

STUDY AREA

In this study the results of the analysis of six mid-dune peat bogs located in Łódź Province in Central Poland (Fig. 1) are presented. The study area is situated within the Central European Lowlands (the highest elevation of the sampling site is 160 m a.s.l.), in the following subregions (Kondracki, 2013): South-Baltic

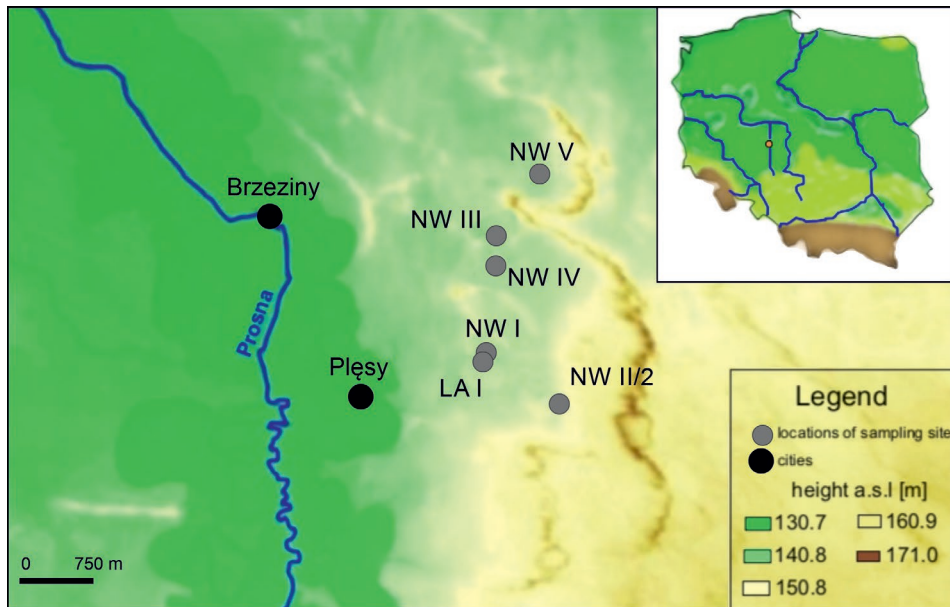


Figure 1. Location of the study sites

Lake District and Central Polish Lowland (mesoregion: Grabowska Valley). The present land relief occurred at the end of the Neogene (Kondracki, 2013). At present, the site is covered with pine forest along with spruce and oak. The Prosna River is the lowest point of the terrain (~130 m a.s.l.). The study area has a temperate climate and is influenced by both maritime and continental climate (Woś, 1999; Kondracki, 2013). The average annual temperature in the region is around 8.5°C. The highest temperature fluctuations occur in winter and range from -8.1°C to 2.2°C. Strong frosts occur rarely. The annual rainfall is estimated at 500–550 mm (Woś, 1999). Western winds prevail in the study area (Woś, 1999), which is one of the factors determining the shape of the dunes.

MATERIALS AND METHODS

Drilling was done using a manual Instorf corer with a diameter of 5 cm and a length of 50 cm. At all investigated sites, drilling reached mineral sediments, indicating the bottom of biogenic sediments and the beginning of water bodies in the area. The oldest sediments of six cores (each with a length of 50 cm) in the central parts of the depressions were sampled for paleoecological analyses (Table 1). The study material was placed in PVC pipes and stored in a cold room (4°C) in Adam Mickiewicz University, Poznań.

Six Accelerator Mass Spectrometry radiocarbon dates were measured on hand-picked plant macrofossils, and the starting date of the accumulation of organic sediment was determined (Table 2). Radiocarbon dating was undertaken at Poznań Radiocarbon Laboratory.

The radiocarbon dates were calibrated with OxCal 4.4.4 software (Bronk Ramsey, 2020). The modeled ages are expressed as calendar years (cal. yr BP).

Geochemical analysis was performed for all cores with a resolution of 3 cm, with the exception of NW I, for which the analysis was performed with a resolution of 4 cm (in five cores – 17 samples, NW I – 12 samples). In total 97 samples were analyzed. The analysis of the sediments was performed for 21 chemical elements. In the NW cores and in the LA core – zones were not distinguished.

To determine the selected elements, a 5110 ICP-OES (inductively coupled plasma with optical emission spectrometry) system (Agilent, USA) was used. The common conditions used for multielemental determination were as follows: radiofrequency (RF) power, 1.2 kW; nebulizer gas flow, 0.7 L min⁻¹; auxiliary gas flow, 1.0 L min⁻¹; plasma gas flow, 12.0 L min⁻¹; viewing height for radial plasma observation, 8 mm; charge-coupled device detector temperature, -40°C; and signal acquisition time, 5 s for 3 repeats. The detection limits for all elements were 0.01 mg kg⁻¹ dry weight 3-sigma criterion). The uncertainty of the total analytical procedure (including sample preparation) was 20%. Traceability was verified using the following reference materials: CRM S-1-loess soil; CRM NCSDC (73349)-bush branches and leaves; CRM 2709-soil; CRM 405-estuarine sediments; and CRM 667-estuarine sediments. Recovery (80–120%) was acceptable for most of the elements. For uncertified elements, recovery was defined using the standard addition method.

Analysis of plant macrofossils was carried out for all cores with a resolution of 1 cm. The macrofossils were selected under a stream of warm, running water on a sieve with a mesh size of 0.2 cm. Plant macroremains were identified using a Nikon SMA 800 stereoscopic microscope with the help of keys (Velichkevich and Zastawniak, 2006, 2008). A total of 300 samples were analyzed.

Pollen analysis was carried out with 18 samples (volume: 2 cm³) taken from six profiles.

The samples were taken from the bottom parts of cores. The purpose was to date the beginning of sedimentation.

Briefly, the samples were treated with 10% HCl to dissolve carbonates, heated in 10% KOH to remove humic compounds, and soaked in 40% HF for at least 24 h to remove the mineral fraction, followed by acetolysis (Berglund and Ralska-Jasiewiczowa, 1986). The prepared pollen slides were examined under a Nikon ECLIPSE 50i upright microscope until at least 500 arboreal pollen grains were reached. Pollen taxa were identified as described by Beug (2004) and Moore et al. (1991) and using the reference slide collection of modern pollen grains, owned by the Climate Change Ecology Research Unit, Adam Mickiewicz University, Poznań.

RESULTS

LITHOLOGY AND CHRONOLOGY

The main components of sediment cores were peat and gyttja with layers of sand.

The details of sediment lithostratigraphy are presented in Table 1.

The results of radiocarbon dating indicated that organic sediments were accumulated during the Bølling–Allerød period (Table 2).

GEOCHEMICAL ANALYSIS

In the NW I core (224–175 cm) in the bottom part there is a high concentration of Al^{3+} and much higher Ca^{2+} , Fe^{3+} , Ba^{2+} , Mg^{2+} , Na^+ . In the middle part of the core, there was a significant decrease in Ca^{2+} concentration with an increase in the values of Al^{3+} , Fe^{3+} , K^+ , Mg^{2+} . High values of Na^+ , Ti^{4+} also occurred. In the depth of 196–200 cm Al^{3+} dominated. There was also an increased level of Fe^{3+} , K^+ , Mg^{2+} , Mn^{2+} , Na^+ , Nd^{3+} , Ti^{4+} .

In the core of NW II/2 (400–350 cm) Ca^{2+} dominated, high values of Fe^{3+} , K^+ , Mg^{2+} were recorded in the bottom part. In the rest of the core, the elements had low concentration values.

In the NW III core (79–30 cm), the bottom part was characterized by low values of elemental concentration values. In the central part of the core at a depth of 45–33 cm, Fe^{3+}

Table 1. Lithology description of sediment sequences

Site	Coordinates	Depth [cm]	Description of sediments
NW I	51°25'33.3"N 18°14'27.4"E	175–210	Decomposed herbaceous peat
		210–214	Gyttja with sand
		214–224	Gyttja
NW II/2	51°25'09.2"N 18°14'38.3"E	350–397	Brown moss peat
		397–400	Decomposed herbaceous peat with sand
NW III	51°25'58.8"N 18°14'04.5"E	30–42	Very decomposed herbaceous peat
		42–62	Decomposed herbaceous peat
		62–67	Peat/coarse detritus gyttja
		67–80	Sand
NW IV	51°25'49.9"N 18°14'05.3"E	110–155	Decomposed herbaceous peat
		155–159	Gyttja without sand
		159–160	Gyttja with sand
NW V	51°26'17.4"N 18°14'26.5"E	500–519	Poorly decomposed herbaceous peat
		519–525	Strongly decomposed herbaceous peat
		525–550	Sand
LA I	51°25'20.4"N 18°13'59.8"E	50–65	Decomposed herbaceous peat
		65–93	Poorly decomposed herbaceous peat
		93–99	Gyttja
		99–100	Gray sand

Table 2. Results of radiocarbon dating

Site	Depth [cm]	Material	Lab. No.	^{14}C date	Age cal. yr BP (95.4%)
LA I	96–100	<i>Carex</i> sp. fruits, <i>Betula</i> sp. fruits	Poz-104882	12 140 ± 60 BP	14 174–13 796
NW I	218–220	<i>Carex</i> cf. <i>flava</i> fruits, <i>Betula</i> sect. <i>Albae</i> fruits and fruit scales, <i>Menyanthes trifoliata</i> seeds, <i>Pinus sylvestris</i> needles + bud scale	Poz-104885	12 320 ± 60 BP	14 686–14 070
NW II/2	399–400	<i>Pinus sylvestris</i> needles	Poz-104881	12 180 ± 50 BP	14 230–13 864
NW III	63–66	<i>Carex rostrata</i> fruits, <i>Betula</i> sp. fruits	Poz-104872	11 870 ± 60 BP	13 815–13 546
NW IV	155–160	<i>Carex rostrata</i> and <i>Carex</i> cf. <i>flava</i> fruits, <i>Betula</i> sect. <i>Albae</i> fruits, <i>Menyanthes trifoliata</i> seeds	Poz-104871	11 710 ± 60 BP	13 715–13 430
NW V	490–530	<i>Carex</i> sp. fruits, <i>Pinus sylvestris</i> needles, brown moss stems	Poz-104870	11 440 ± 60 BP	13 421–13 142

dominated. At a depth of 39–42 cm, there was an increased level of K^+ , Na^+ , Mn^{2+} , Mg^{2+} , Ti^{4+} .

In the NW IV (157–110 cm), high concentration of Ca^{2+} and Fe^{3+} occurs throughout the core. In the bottom part (depth of 157–152 cm), an increase in the values of K^+ , Mg^{2+} , Nd^{3+} and Ti^{4+} was recorded. In the top part of the core the Fe^{3+} concentration increased significantly.

In the core NW V (550–500 cm), Ca^{2+} reached relatively low values. A high concentration was found for Ba^{2+} and Al^{3+} , however, the latter occurred only at a depth of 539–536 cm. In the bottom part of the core, increased Fe^{3+} concentrations were found together with high K^+ , Na^+ , Ti^{4+} concentrations.

In the LA I core (100–50 cm), Ca^{2+} dominated in the entire core with high concentrations of Fe^{3+} , Zn^{2+} . Significant concentrations of K^+ , Mg^{2+} , Mn^{2+} , Na^+ , Ti^{4+} were in the bottom part of the core. High concentrations of Fe^{3+} , Mn^{2+} were measured in the topmost part.

Detailed results of the geochemical analysis of the sediments are presented in Supplementary File 1¹.

PLANT MACROREMAINS

Presence and proportion of macrofossils allowed for the differentiation of two or three zones in all of the cores except LA I.

NW I (Fig. 2)

NW I-1 zone (224.5–215.5 cm) was characterized by the presence of aquatic vegetation, including *Chara* sp., *Myriophyllum spicatum*, *Potamogeton* sp. and *Najas marina*, as well as peatland plant species such as *Carex flava* and *C. rostrata*. The fruits of *Betula* sect. *Albae*, *B. nana* and *B. pubescens* were also recorded.

NW I-2 zone (214.5–174.5 cm) showed the presence of *Menyanthes trifoliata* and *Potamogeton filiformis*, *Potamogeton* sp. and *C. rostrata*. The abundance of *Betula* sect. *Albae* decreased. The needles of *Pinus sylvestris* were also found.

NW II/2 (Fig. 2)

NW II/2-1 zone (400.5–374.5 cm) was very poor regarding the macroremains of aquatic plants except for *Typha latifolia*. Seeds of

P. sylvestris and *Betula* sect. *Albae* and fruits of *B. pubescens* were recorded.

NW II/2-2 zone (374.5–350.5 cm) was characterized by the presence of aquatic and rush species: *C. rostrata*, *T. latifolia*, *Potamogeton natans* and *M. trifoliata*. *N. marina* appeared at a depth of 356.5 cm. *Caltha palustris* and *Betula* sect. *Albae* appeared in the uppermost part of this zone next to *Epilobium* sp.

NW III (Fig. 3)

NW III-1 zone (79.5–60.5 cm) was dominated by trees. The remains of *Betula* sect. *Albae* and *B. pubescens* were found at a depth of 63.5 cm and 68.5 cm, respectively. *M. trifoliata* and *C. rostrata* were also present.

NW III-2 zone (60.5–30.5 cm) was represented mainly by *M. trifoliata*. For the first time, the fruits of *Nymphaea alba* and *Typha* sp. appeared.

NW IV (Fig. 3)

NW IV-1 zone (159.5–150.5 cm) was dominated by brown mosses and Cyperaceae macrofossils. Among brown mosses, the remains of *Pseudocalliergon trifarium*, *Calliergonella cuspidata* and *Calliergonella cordifolium* were documented. The remains of *H. vulgaris*, *Chara* sp., *Potamogeton alpinus*, *P. fresii*, *Carex flava*, and *C. rostrata* were found.

NW IV-2 zone (150.5–135.5 cm), documented the remains of *P. natans*, *P. fresii*, *N. alba*, *C. rostrata*, *C. flava* and *M. trifoliata*.

NW IV-3 zone (135.5–110.5 cm), the remains of brown mosses, Cyperaceae, as well as significant amounts of *Warnstorfia exannulata* were recorded. In the upper part, the remains of *Pseudocalliergon trifarium* were found followed by single fruits of aquatic *Potamogeton alpinus* and *P. fresii* (120.5 cm). The presence of *M. trifoliata* was also recorded. Fruits of *B. pubescens* and *Betula* sect. *Albae* were found at a depth of 132.5 cm.

NW V (Fig. 4)

NW V-1 (550.5–532.5 cm) was poor in plants and had a few remains of *P. natans*, *Potamogeton* sp. and *C. rostrata*.

NW V-2 zone (532.5–500.5 cm), *Betula* sect. *Albae*, *B. pubescens* and *P. sylvestris* clearly dominated among the tree species. The presence of *Carex elongata* and *C. flava*, as well as the abundance of *C. rostrata*, was noticed.

¹ Supplementary File 1: Results of geochemical analysis

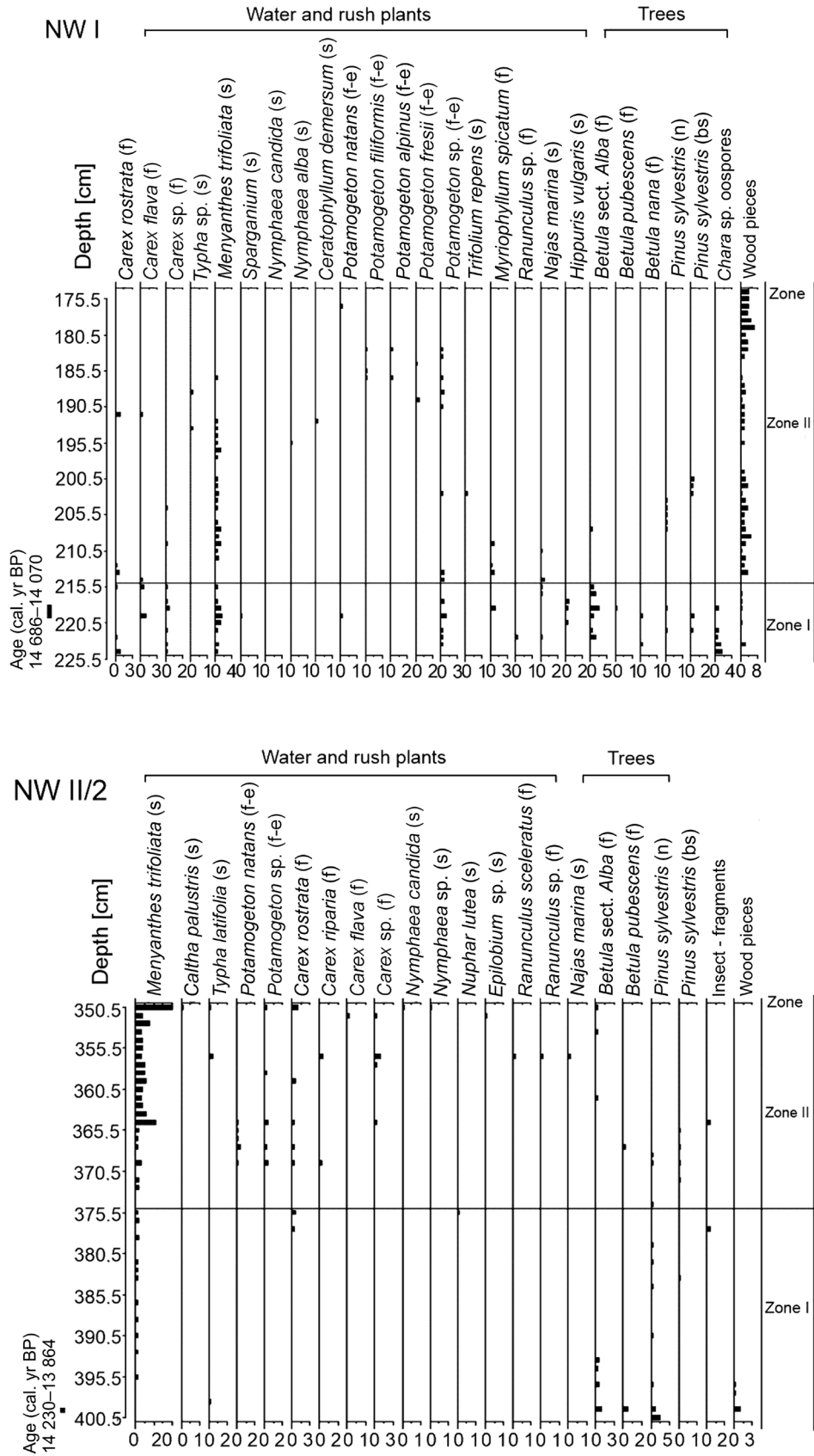


Figure 2. Macrofossil diagrams of NW I and NW II/2 cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

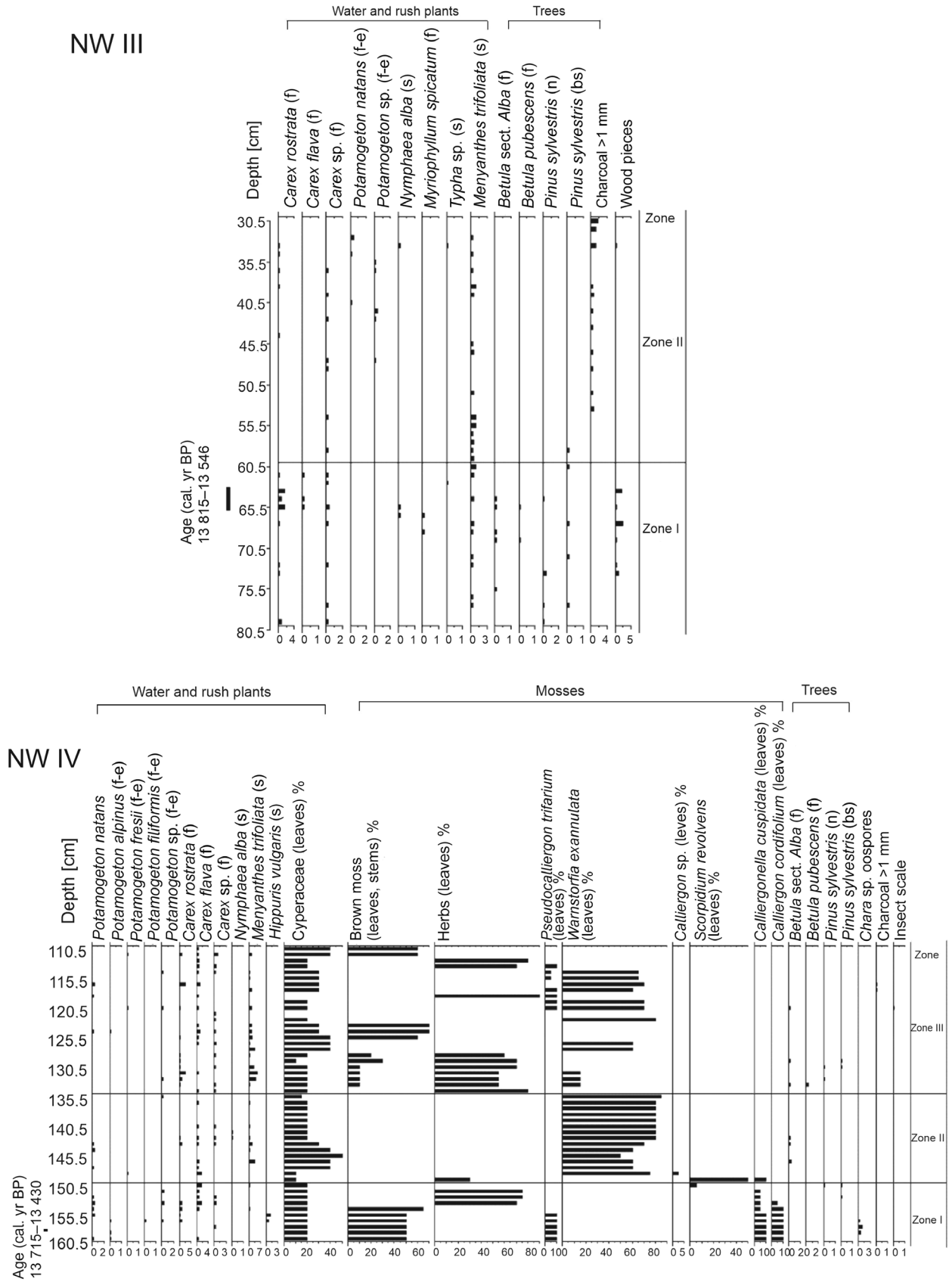


Figure 3. Macrofossil diagrams of NW III and NW IV cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

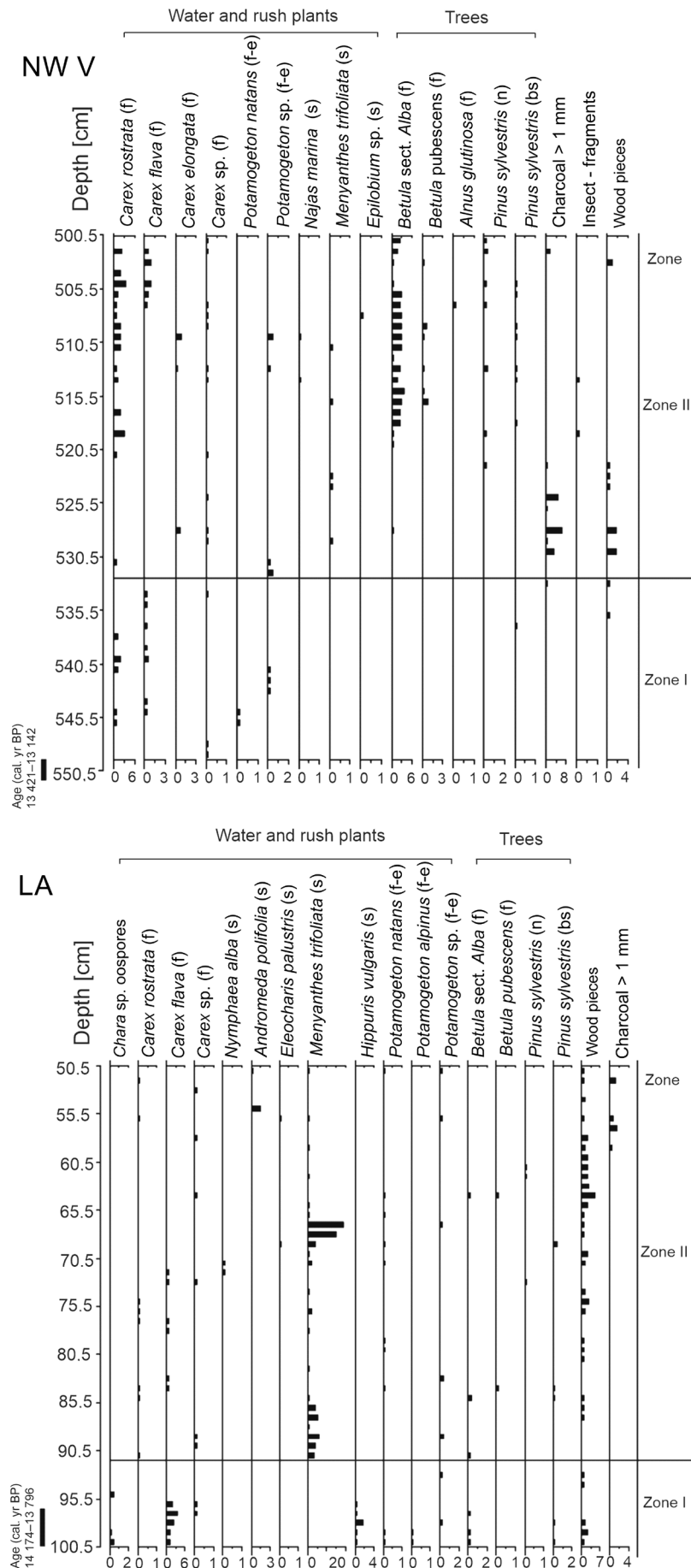


Figure 4. Macrofossil diagrams of NW V and LA I cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

The seeds of *Najas marina* were found at depths of 513.5 and 509.5 cm.

LA I (Fig. 4)

LA I (99.5–91.5 cm) – zones were not distinguished.

The lower part revealed macrofossils of *P. alpinus*, *P. natans*, *Chara* sp. and *Carex* sp. At a depth of 96.5 cm, *Eleocharis palustris* and *C. flava* were found. The aquatic plants were represented by *Chara* sp., *H. vulgaris* and *P. alpinus*.

POLLEN ANALYSIS

Pollen analyses were done only for the bottom parts of the studied cores (Fig. 5). Therefore, the pollen record revealed regional plant communities and local vegetation of the lakes and adjacent areas only at the beginning of the accumulation of organic sediments.

NW I

A high percentage of *P. sylvestris* pollen indicates the presence of sparse pine stands with a significant proportion of *Betula* (Ralska-Jasiewiczowa et al., 2004). The species *B. nana* was also probably present. *Salix* was most likely found near the basin shoreline. The telmatic part of the reservoir was covered by relatively big clusters of Cyperaceae and a low proportion of *M. trifoliata* and *T. latifolia*. Aquatic macrophytes were represented by *Sparganium* type and *Lemna* type. A minor occurrence of coprophilous fungi (e.g. HdV-55 A *Sordaria* type, HdV-205 Sordariaceae, *Sporormiella*) indicated the possible presence of mega herbivores (Gill et al., 2013; Rey et al., 2020).

NW II/2

During the Bølling period (14 050 cal. yr BP), the vegetation cover was dominated by *P. sylvestris* and *Betula* along with *Salix* in wet areas. At a depth of 399.5 cm, the relatively high presence of Poaceae (10%) corresponded with the abundance of coprophilous fungi (HdV-55 A type *Sordaria*, HdV-205 Sordariaceae). At lower depths, the proportion of Poaceae pollen decreased to about 3% and 4%. The progressive terrestrialization of the reservoir was indicated mainly by the abundance of Cyperaceae (more than 45% at 397.5–392.5 cm).

NW III

The bottom sediments dated 13 700 cal. yr BP, i.e. the turn of Bølling and older dryas, showed the dominance of *Pinus* and *Betula*. At the beginning of the sedimentation process, the dunes adjacent to the peatland were overgrown by *Hippophae rhamnoides*. This was evidenced by the relative abundance of pollen of this species (~9%) at the depth of 66.5 cm. The presence of Poaceae at 66.5 cm corresponded with a high proportion of Cyperaceae, as well as HdV-55 A *Sordaria* type and HdV-205 Sordariaceae. At greater depths the above-mentioned taxa showed a decrease or even disappeared.

NW IV

Accumulation in this reservoir began at 13 500 cal. yr BP, i.e. the Bølling period. At the early stage (159.5 cm), the vegetation was mainly composed of birch (most likely *B. pubescens* and *B. nana*), as well as willow on damp soils. Buckthorn was the main constituent of the dune habitat. In younger samples, a transition from birch to pine-dominated forests was seen. Open vegetation was represented by Poaceae and *Artemisia*. The main species in the mire vegetation was probably *B. nana*; however, due to poor preservation of pollen grains, its pollen could not be identified in all of the profiles. The high presence of Cyperaceae was recorded in this profile. At the depth of 159.5 cm, the slight presence of *Lemna* and *Spirogyra* indicated stagnant water. At higher levels, these species disappeared corresponding with the emergence of *M. trifoliata* and *Sparganium* type. In this profile, similar to others, the presence of coprophilous fungi (mainly HdV-368 *Podospora* type) corresponded with a high value of charcoal particles, as well as the indicators of open areas (depth 159.5 cm), followed by a sharp decrease of these taxa (157.5–151.5 cm).

NW V

The pollen spectra were dominated by *P. sylvestris* (>80% of pollen sum in all of the samples). This finding is in line with the results of radiocarbon dating. A marginal proportion of birch, willow and sea buckthorn was observed during that time. Among the herbaceous plants, the most important were Poaceae, *Artemisia*.

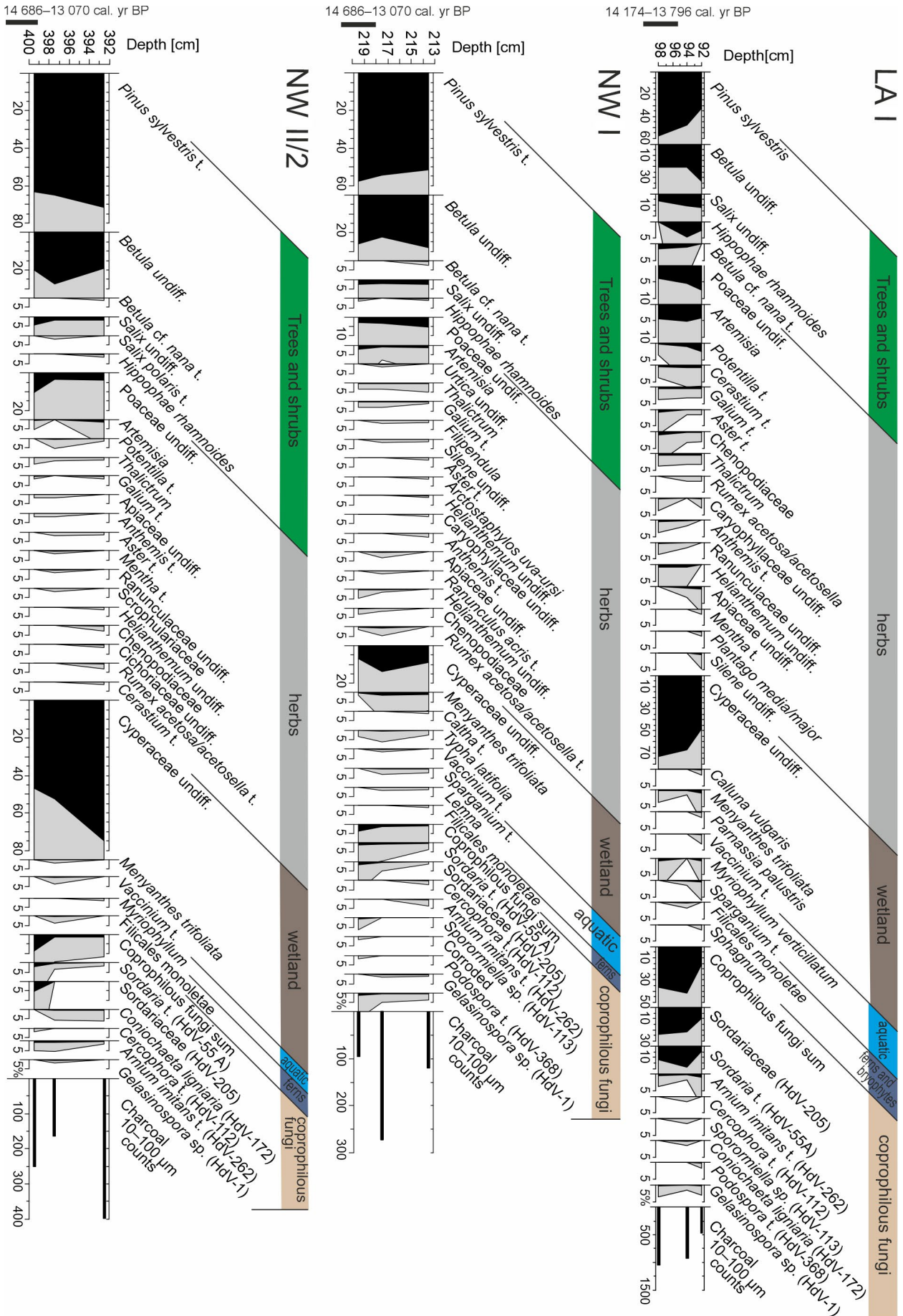


Figure 5. Pollen diagrams of LA I, NW I, and NW II/2, NW III, NW IV, and NW V cores

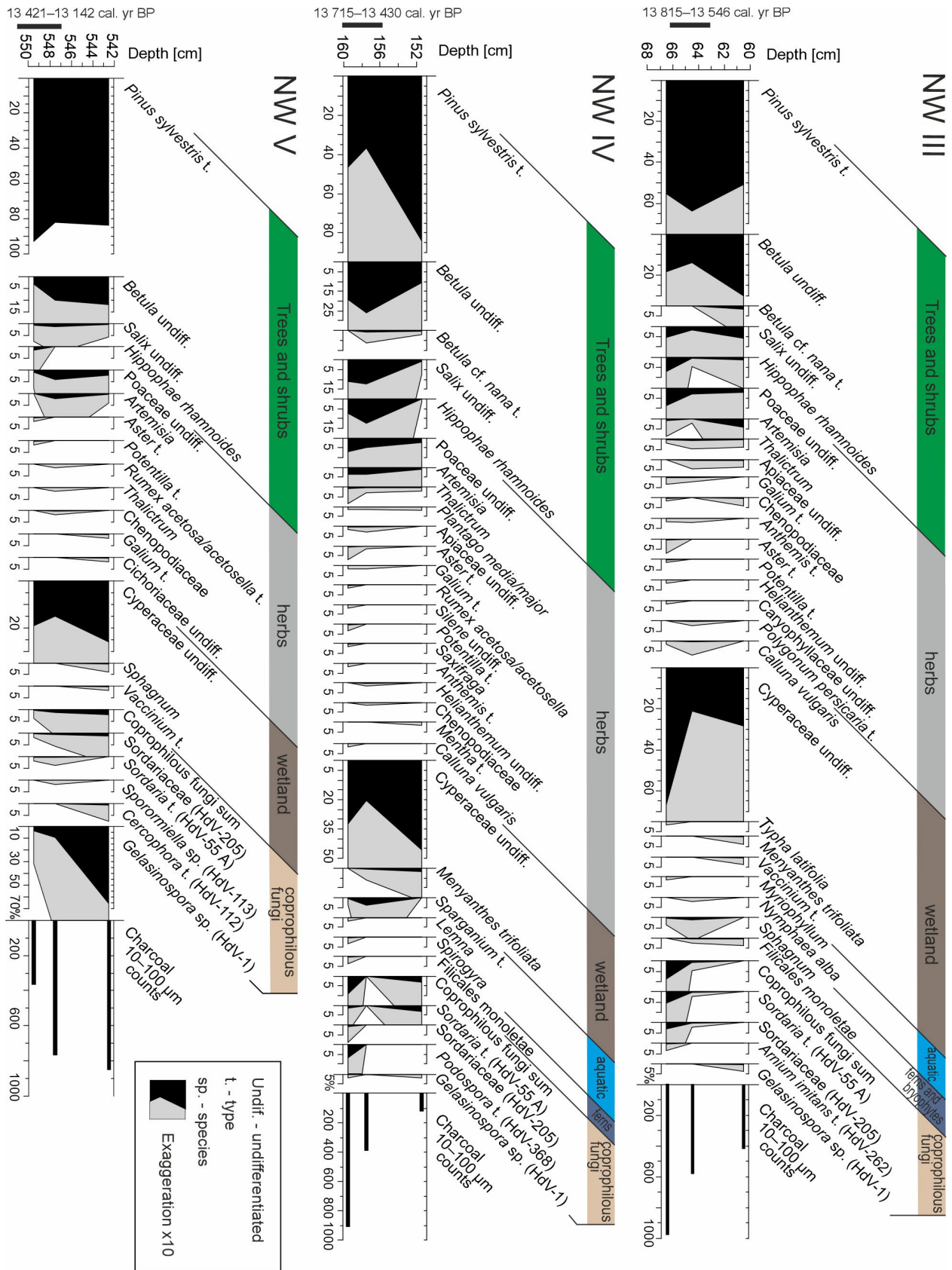


Figure 5. Continued

LA I

According to the radiocarbon dates (~14 000 cal. yr BP), sediment accumulation began during the Bølling period. Similar to the adjacent profile (NW I), the vegetation constituted mostly pine, birch and willow. However, this profile was distinguished by the high proportion of *H. rhamnoides* (up to 18.5%) at a depth of 60.5 cm. A decline in *Hippophae* was observed. *Betula* sp. pollen value increased. The presence of open area indicators, such as Poaceae, *Artemisia*, *Potentilla* t. or *Cerastium* t., was constant throughout the profile.

DISCUSSION

BEGINNING OF THE ORGANIC SEDIMENT ACCUMULATION AND CLIMATIC CONDITIONS

The results of this study suggest that the reservoirs between dunes developed at the turn of the Oldest Dryas and Bølling period (before 14 700 cal. yr BP). In the subarctic climate of Oldest Dryas, aeolian sand carried by the wind accumulated, favoring the formation of dunes (Dylikowa, 1969; Konecka-Betley, 2012). At the foot of the dunes, land depressions and basins formed (Rotnicki and Tobolski, 1969; Kulesza and Bałaga, 2015). Aeolian processes of the Oldest Dryas have also been recorded in Węglewice (Tobolski, 1966), which is situated approximately 4 km south of Płęsy village. The materials forming the dunes, with quartz and silicon being dominant, were poor in nutrients (Prusinkiewicz, 1969). The area was covered by open, tundra plant communities and *Hippophae* shrubs, a pioneer and light-demanding species of raw, mineral soil (Krupiński et al., 2004). The aeolian processes and dune formation ended with the warming of the Bølling interstadial (Konecka-Betley, 2012), partly due to the development of a denser vegetation cover. During the Bølling period, average annual air temperatures in Europe were ~12–15°C (Wasylikowa, 1964; Maruszczak, 1974; Klimanov, 1984, 1997; Ralska-Jasiewiczowa et al., 1998; Velichko et al., 2002; Bos et al., 2006), while air temperature in Central Poland was ~13–15°C (Pawłowski et al., 2016).

Stopped sand transportation resulted in the development of wetlands and water bodies in mid-dune areas. Damp habitats were covered by shallow-water vegetation such as *Carex* and

Cyperaceae, suggesting a minimum June temperature of 13°C (Isarin and Bohncke, 1999), and *Typha* sp., indicating a mean July temperature of 15°C (Iversen, 1954; Wasylikowa, 1964) or 13–16°C depending on the species (Kolstrup, 1979). A similar pattern of vegetation succession in Bølling/Allerød has been reported for the Czech Republic (Pokorný and Jankovská, 2000), western Lithuania (Kisieliene et al., 2005) and western Ukraine (Kołaczek et al., 2018).

The oldest sediments analyzed in the present study are dated to early Bølling (14 686 to ~14 070 cal. yr BP), as revealed by ¹⁴C ages of the bottom sediments of the NW I, NW II/2 and LA I cores. During that period, the initial soil made of dune sand gradually developed (Łącka et al., 1998; Konecka-Betley, 2012), which led to the emergence of *Betula* forest/shrubs and sparse population of *P. sylvestris* trees as indicated by pine needles and bud scales (NW I, Fig. 2). It was the initial soil formed due to the accumulation of mineral material as a result of aeolian processes (Dylikowa, 1969). In this soil there is a thin layer of organic matter only in the uppermost layer (Konecka-Betley, 2012). The pollen spectra showed a significant share of pine in all sites (Fig. 5); however, most of them are related to transportation from a long distance. The landscape during this period was open and pine pollen could be transported over long distances. This is reflected in the diagram. Similar results were obtained by Wasylikowa (1964), Tobolski (1966), Krajewski and Balwierz (1984), and Balwierz and Goździk (1997). The period of transition to the Bølling interstadial was characterized by the migration of deciduous, pioneer trees such as *Salix* and *Populus tremula* (Łącka et al., 1998; Wacnik, 2009; Mortensen et al., 2011; Forysiak, 2012). At the end of Bølling (~13 815 cal. yr BP), birch-pine forest was an integral part of the environment based on the presence of macroremains and the proportion of *Pinus* pollen exceeding 50% of the total sum recorded in the sediments (Fig. 5). These results agree with the observations of Huntley and Birks (1983), which showed that >50% of *Pinus* pollen with less than 25% of *Betula* pollen indicates the local existence of pine. *Salix* inhabited more humid areas at the shores of the basins.

The lack of sand inflow and the stabilization of dunes favored the diversity of taxa, as suggested by the development of forest and a relatively dense vegetation cover on dunes.

Age (cal. yr BP) of the bottom part	LG periods	Migration series +	Minimum mean July temperatures	Indicative species	Dominant vegetation		Beginning of organic accumulation
					Regional	Local wetlands	
13 421–13 142	Allerød	Ca ²⁺ ↑ Al ³⁺ ↑ Fe ³⁺ ↑ Ba ²⁺ ↑ K ⁺ ↑ Mg ²⁺ ↑ Mn ²⁺ ↑	> 12°C	<i>Pinus sylvestris</i> (plant macrofossil)	sparse birch- pine forest	<i>M. trifoliata</i> <i>C. rostrata</i> <i>C. flava</i> <i>N. marina</i>	NW V
13 715–13 430	Older Dryas	Ca ²⁺ ↑ Al ³⁺ ↓ Fe ³⁺ ↑ Ba ²⁺ ↑ K ⁺ ↑ Mg ²⁺ ↑	10–13°C	<i>Hippophae rhamnoides</i> (pollen)		<i>M. trifoliata</i> <i>C. rostrata</i> <i>C. flava</i> <i>P. natans</i>	NW IV
13 815–13 546		Ca ²⁺ ↓ Al ³⁺ ↑ Fe ³⁺ ↓ Ba ²⁺ ↓ K ⁺ ↑ Mg ²⁺ ↓	13°C	<i>Typha latifolia</i> (pollen)	park tundra	<i>M. trifoliata</i> <i>P. natans</i> <i>C. rostrata</i> <i>C. flava</i> <i>N. alba</i> <i>M. spicatum</i>	NW III
14 174–13 796		Ca ²⁺ ↑ Al ³⁺ ↓ Fe ³⁺ ↓ Ba ²⁺ ↑ K ⁺ ↑ Mg ²⁺ ↑ Mn ²⁺ ↑	> 12°C	<i>Pinus sylvestris</i> (plant macrofossil)		<i>M. trifoliata</i> <i>A. polifolia</i> <i>C. rostrata</i> <i>E. palustris</i>	LA I
14 230–13 864	Bølling	Ca ²⁺ ↑ Al ³⁺ ↑ Fe ³⁺ ↓ Ba ²⁺ ↓ K ⁺ ↑ Mg ²⁺ ↑ Mn ²⁺ ↑			sparse birch- pine forest	<i>N. alba</i> <i>P. natans</i> <i>M. trifoliata</i> <i>P. natans</i> <i>C. rostrata</i> <i>N. lutea</i> <i>C. palustris</i> <i>N. marina</i>	NW II/2
14 686–14 070		Ca ²⁺ ↓ Al ³⁺ ↑ Fe ²⁺ ↓ Ba ²⁺ ↑ K ⁺ ↑ Mg ²⁺ ↑	13°C	<i>Typha latifolia</i> (pollen)		<i>M. spicatum</i> <i>M. trifoliata</i> <i>P. friesii</i> <i>N. marina</i> <i>C. flava</i> <i>C. rostrata</i>	NW I

Figure 6. Comparison of vegetation development at the analyzed sites. Arrows indicate increase or decrease of elements in migration series. Temperatures given after Bos et al., 2006 and authors cited in the text

Paleobotanical analyses revealed the presence of psammophilic vegetation at ~13 800 cal. yr BP (*Helianthemum* and *Artemisia*). The constantly present *H. rhamnoides* belongs to the group of heliophytes, which prefers dry sites rich in Ca²⁺ and is eminently light-demanding forming the highest level of vegetation (Kobenzina, 1969; Tobolski, 2003). Dunes were the proper habitat for *Hippophae* because this species can grow even on nondurable dunes and on irrigated soils due to its extensive root system (Li and Schroeder, 1996). The peatland was overgrown with *B. nana*, while its shores were occupied by *Salix* undiff.

Similar to the Oldest Dryas, Bølling was characterized by a high groundwater level, resulting from the melting of dead ice blocks (Drzymulska, 2010), which allowed the depressions formed at the foot of the dunes to be further filled with water (Rotnicki and Tobolski, 1969; Kloss and Wilpiszewska, 1994; Balwierz and Goździk, 1997). The sediments accumulated in the reservoirs. This led to the decrease of the depth and surface of the reservoirs.

The location of reservoirs at a distance of a few or several kilometers from each other would suggest that they developed in an analogous manner despite the fact that they

formed at different times. They were created successively, which is confirmed by the dates of the lower part of the cores (Table 2). However, small but significant differences could occur in plant succession, mainly due to the intensity of groundwater supply affecting the depth and shape of the reservoir, the degree of sunlight, or geochemical features (Kulesza and Bałaga, 2015). In all the reservoirs, Ca^{2+} was the major element in the migration series, which indicates the advantage of ground supply (Borówka, 1992). However, the functioning of these reservoirs was closely influenced by the hydrological regime of the Prosna River (cf. Gałka et al., 2019). The influx of river waters was likely suggested by a high concentration of Al^{3+} , Ti^{4+} , K^+ and Na^+ in the bottom parts of LA I and NW II/2 (~14 000 cal. yr BP) and NW IV, as well as NW III (level 39–42 cm, ~13 700 cal. yr BP) and NW V (level 536–539 cm, ~13 400 cal. yr BP) and the unidentified remains of plants and wood.

SUCCESSION OF LOCAL PLANT COMMUNITIES IN THE RESERVOIRS

The local flora (NW I: ~14 600, LA I: ~14 100 cal. yr BP) included species such as *Chara* sp., *Hippuris vulgaris*, *Potamogeton* sp. including *P. filiformis* and *Myriophyllum spicatum*. These species prefer water reservoirs to a depth of 5–6 m (Podbielkowski and Tomaszewicz, 1996; Pawłowski et al., 2016). The communities of *Chara* sp. were the first to colonize the lower layers of reservoirs, and recorded as pioneering plants in sediments in the early stage of lake development in the Late Glacial period (Birks, 2000; Matuszkiewicz, 2001; Schubert, 2003; Kisieliene et al., 2005; Lamentowicz and Mitchell, 2005; Mortensen et al., 2011; Gałka and Sznal, 2013). The presence of these species indicates oligo-mesotrophic environment (Pełchaty et al., 2007; Schubert et al., 2018) rich in Ca^{2+} , due to the slow disappearance of permafrost and groundwater circulation (Borówka, 2007; Drzymulska, 2010; Żurek and Kloss, 2012). Palynological and geochemical analyses revealed that a similar process took place in NW II/2 in ~14 200 cal. yr BP. A high concentration of Ca^{2+} , Fe^{3+} and Mn^{2+} in the sediments confirms the high level of groundwater, and Mn^{2+} accumulation is typical for oligo-mesotrophic reservoirs (Pawłowski et al., 2016).

The presence of Co^{2+} , Cr^{3+} and Ni^{2+} was influenced by the geological structure of the

area (postglacial formations), weathering of postglacial material and migration of activated components along with surface runoff (Bojarska and Sokołowska, 1997).

A pattern similar to the early developmental stages of NW I and LA I was recorded for NW IV at ~13 700 cal. yr BP, when the communities of *Chara* sp. developed first followed by the appearance of *H. vulgaris*, brown mosses and *Potamogeton* species such as *P. natans*, *P. alpinus* and *P. filiformis*, which colonized the reservoir. The disappearance of *Chara* sp. in NW IV (156.5 cm) and the simultaneous development of the *Carex* group, along with a large proportion of *Cyperaceae* pollen, indicate the gradual decrease in water levels in the bottom part of the profile (Fig. 3). The persistent high concentration of Ca^{2+} , Al^{3+} and Fe^{3+} in NW IV, as well as in NW I and LA I cores influenced the concentration of the mineral forms of phosphorus (Graca and Bolalek, 1998), which could indirectly affect the disappearance of *Chara* sp. characterized by low phosphorus tolerance (Crawford, 1977). Pollen analysis revealed the presence of other microfossils of various origins (van Geel, 2001). The presence of *Spirogyra* palinomorphs in NW IV (Fig. 3) indicates good water oxygenation and gradual transition to mesotrophic environment. It also suggested the development of fungi, or Cyanobacteria, which is probably limited the light supply into the reservoir, affecting the productivity of submerged macrophytes (Dong et al., 2014). Calciphilic mosses (cf. Hedenäs, 2003) including *Pseudocalliergon trifarium*, *Calliergonella cuspidata* and *C. cordifolium* were undoubtedly pioneering plants of NW IV. *Scorpidium revolvens* is a glacial relic flora currently found in Poland (Hedenäs, 2003; Krajewski, 2012). The finding of its macroremains in NW IV (Fig. 3) is of significance, due to the fact that it is not present in Ca^{2+} -rich places, unlike *S. scorpioides* and *S. cossonii*, which prefer a calcareous environment (Hedenäs, 2003; Graham et al., 2019).

An open water surface existed within the reservoirs during Bølling, as indicated by the presence of *Ceratophyllum demersum*, *M. spicatum*, *P. natans* and *N. alba*. Endocarps of *P. filiformis* and *P. alpinus* were also found in the bottom layers of NW I and NW IV. Their presence in the sediments indicates a cool climate, and the macrofossils of both species are commonly found in the sediments accumulated

in Europe in the Late Glacial period (Szafer, 1954; Mortensen et al., 2011; Gałka and Sznal, 2013; Gałka et al., 2020). *Potamogeton natans* is a cosmopolitan plant that can resist changing conditions, and its endocarps can be found in the deposits accumulated during the Late Glacial and Holocene (Kisieliene et al., 2005; Żurek and Kloss, 2012; Gałka et al., 2017, 2020).

In ~13 800–13 400 cal. yr BP, NW III and NW V showed some changes. The concentration of Al^{3+} , K^+ , Mg^{2+} , Ti^{4+} , Fe^{3+} and Cr^{3+} clearly decreased in NW III (depth 78–80 cm) and NW V (depth 500–503 cm), which indicates that both reservoirs were shallowing. Soil erosion occurred in NW V, as evidenced by an increase in Al^{3+} , Ti^{4+} , Zn^{2+} , Fe^{3+} and Mn^{2+} (Łącka et al., 1998). A slight and short-lived water space occurred in the middle part of NW III (Fig. 3), which allowed the development of aquatic macrophytes such as *M. spicatum* and *N. alba*; however, plant macrofossil data and low pollen percentages (<1%) confirm their limited importance. A sharp decline in Ca^{2+} and a low content of Mn^{2+} in NW III (depth 63.5–66.5 cm) and NW V (depth 550.5–545.5 cm) suggest a minor supply of groundwater and insufficient inflow of surface waters. The very high percentages of ascospores of *Gelasinospora carboniculus* fungi together with a high concentration of microcharcoal confirm the occurrence of local fires in the vicinity of the reservoir during this period (Shumilovskikh and Van Geel, 2020).

A short-lived local episode related to an extreme phenomenon, perhaps a period of aeolian activity (Wasylikowa, 1964; Dylikowa, 1969; Tobolski, 1969; Konecka-Betley, 2012) or a change in local hydrological conditions, is indicated by disturbances in the plant cover system in NW III (63.5 cm), NW IV (157.5 cm) and NW V (49.5 cm). In ~13 600 cal. yr BP, a decrease in the pollen curve of *P. sylvestris* occurred (Fig. 5), while the proportion of *Salix* and *B. nana* pollens increased (Fig. 5). A number of herbaceous plants, such as *Potentilla* and *Rumex*, disappeared (NW IV – 158.5 cm, NW III – 63.5 cm, NW V – 49.5 cm).

The cooling of the climate in the Old Dryas was characterized by a decrease of the average temperature of July to 10–13°C (Wasylikowa, 1964; Ralska-Jasiewiczowa et al., 1998; Płóciennik et al., 2011) which resulted in the decrease of humidity and water level in the reservoirs. Concurrently the increase

of dune-forming activity and sandy backfilling of the initial soil was observed, which later resulted in the disappearance of an open water table in the reservoirs (Dzieduszyńska and Forysiak, 2015) and the formation of peat bogs.

These changes preceded the beginning of Allerød interstadial which was dated in the record of oxygen isotopes in Greenland's ice cores between 13 610 and 13 550 cal. yr BP (Rasmussen et al., 2014).

CONCLUSIONS

The paleoecological analysis of sediments in a dune area in Central Poland allowed the reconstruction of the paleoenvironmental changes in the Late Glacial period. Based on the results, the following conclusions were drawn:

1. Dunes were formed during the Oldest Dryas, when sparse vegetation favored strong aeolian activity. Climate warming in Bølling led to the development of a denser plant cover, ceasing sand transportation and the formation of mid-dune reservoirs with the accumulation of organic sediments.

2. The first element in the migration series to be recorded in the sediments was Ca^{2+} . Its presence indicates the ongoing process of permafrost degradation and the slow release of groundwater. Calcium accumulation in sediments confirms that the reservoirs are fed with groundwater originating from the progressive degradation of permafrost associated with thermal changes.

3. Palynological data confirmed that the area around the reservoirs was covered with sparse pine forests along with birch, which is typical of warm periods of the Late Glacial. The open areas were dominated by Poaceae, *H. rhamnoides* and *B. nana*.

4. Paleobotanical analysis showed the reservoirs to be shallow, oligo-mesotrophic and inhabited by pioneer calciphilic vascular plant species, such as *Chara* sp., *H. vulgaris*, *P. natans*, *P. fresii*, *P. alpinus*, and *P. filiformis* and mosses such as *P. trifarium*, *Calliergon* sp. and *C. cordifolium*.

5. The short period between Bølling and Allerød characterized by a decrease in the *P. sylvestris* curve, an increase in the proportion of *Salix* pollen, the presence of *B. nana* in the NW IV profile (depth 157.5 cm,

~13 600 cal. yr BP) and a clear decrease in Cyperaceae suggests climate cooling related to the episode of Older Dryas.

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