

# Pattern of plant succession from eutrophic lake to ombrotrophic bog in NE Poland over the last 9400 years based on high-resolution macrofossil analysis

Mariusz Gałka

Adam Mickiewicz University, Department of Biogeography and Palaeoecology, Dziegielowa 27, PL-61-680 Poznań, Poland (e-mail: galka@amu.edu.pl)

Received 31 May 2013, final version received 30 Sep. 2013, accepted 18 Oct. 2013

Gałka, M. 2014: Pattern of plant succession from eutrophic lake to ombrotrophic bog in NE Poland over the last 9400 years based on high-resolution macrofossil analysis. — *Ann. Bot. Fennici* 51: 1–21.

This article describes vegetation history and plant succession in Lakes Kojle and Perty (NE Poland) and in the surrounding peatlands during the last 9400 cal. BP. Vegetation changes were reconstructed based on high-resolution plant macrofossil analysis of three sediment cores. The changes in vegetation and the course of succession found in the studied lakes and peatlands resulted largely from regional climate changes. Climate cooling that took place approximately 5000 cal. BP resulted in an increase in *Picea abies* cover in the vicinity of the lakes, as well as in the appearance of *Nuphar pumila* and *Potamogeton alpinus* in the lakes. A further increase in *Picea abies* approximately 3500 cal. BP coincided with the development of an ombrotrophic bog at one site. During the period under study, the aquatic plant species that persisted for the longest time at one site were *Najas marina* and *Nymphaea alba*, and the shortest-term residents were *Potamogeton* spp.

## Introduction

Significant changes in vegetation have occurred in Europe over the last several millennia, primarily resulting from changes in climate and soil. The mechanism of vegetation transformations as a result of climate changes is clearly accounted for by the climate-edaphic cycles in glacial-interglacial periods (Birks 1986, Lang 1994). The historic course and rate of vegetation succession in lake-peatland areas were affected not only by climate changes but also by the surroundings of a given lake; its physical parameters, i.e., surface area, depth, and nutrient supply; and also by human activity. Vegetation development in peat-

lands is frequently related to the development of forests in their vicinity (Gałka *et al.* 2013a). In instances of vegetation succession in large-area ombrotrophic bogs, such changes are often autogenic (Swindles *et al.* 2012).

Palaeoecological studies in Europe, primarily based on analyses of plant macrofossils, have permitted the reconstruction of the general migration routes of trees and selected herbaceous plants (Lang 1994, Ralska-Jasiewiczowa *et al.* 2004). A number of works have also been published on the reconstruction of the development of local vegetation in lakes (Bennike 2000, Birks 2000, Bešta *et al.* 2009, Väiliranta *et al.* 2011, Rütina *et al.* 2012, Gałka & Sznel 2013, Gałka & Apoli-

narska 2014) and peatlands (Barber *et al.* 2004, Sillasoo *et al.* 2007, Mauquoy & Yeloff 2008, Gałka *et al.* 2013b). Plant macrofossil analysis plays a very important role in the reconstruction of local vegetation succession, as well as in the determination of the time of appearance of various plant species in lake-peatland areas and their vicinity (Hannon & Gaillard 1997, Allen & Huntley 1999, Tobolski 2000, Birks & Birks 2006, Velichkevich & Zastawniak 2006). The application of such analyses in palaeoecological studies allows for the identification of plant remains to species level, but is dependent on the presence of the plant. Identification of plant macrofossils is mostly not possible in palynological analyses (Birks 2000, Tobolski 2000, Feurdean & Bennike 2008). This is particularly the case with plants of Cyperaceae and Juncaceae and with the genus *Potamogeton*, which occur frequently in lake-peatland areas. With well-preserved generative or vegetative plant macrofossils in sediments, it is possible to identify plant species and also estimate their contributions in plant assemblages growing in lakes and peatlands.

Previous studies in Europe focusing on the analysis of vegetation succession from lake to peatland, with plant macrofossil analysis as one of the research methods, attempted to reconstruct habitat conditions, e.g., water depth, pH, and age and duration of appearance of various plant species at a site (Bradshaw *et al.* 2005, Mortensen *et al.* 2011, Fajer *et al.* 2011, Gałka *et al.* 2014, Karpińska-Kończak *et al.* 2013). The reconstruction of fossil plant assemblages in lakes and peatlands has involved the development of succession models (Hannon & Gaillard 1997, Drzymulska 2008, Tuittila *et al.* 2007).

In spite of the expansion of knowledge on vegetation succession in lake-peatland areas in Europe, high-resolution (e.g., 1 cm) palaeobotanical works are still scarce. The application of such high-resolution sample analysis permits a detailed reconstruction of changes in the vegetation at a given site and the contributions of individual species, even at intervals of a dozen years or so (Gałka *et al.* 2014).

The research presented in this paper was conducted in NE Poland, an area heavily influenced by its boreal climate. Due to this influence, this part of Europe includes plant species adapted to

an oceanic climate, e.g., *Cladium mariscus*, as well as those that require a continental climate, e.g., *Picea abies* and *Nymphaea candida*.

The objectives of the study were (1) to reconstruct the development and changes in vegetation in the area of Lakes Kojle and Perty and their surrounding peatlands, and (2) to determine the effects of climate changes on the course of succession at these localities.

The results of the plant macrofossil analyses presented in this article constitute part of a more extensive palaeoecological study conducted in NE Poland by the author. Thus far, palaeoecological research has focused on palaeoecological and palaeoclimatic reconstructions, with an emphasis on the reconstruction of vegetation development in lakes and peatlands in the Late Glacial and Holocene (Gałka & Sznal 2013, Gałka *et al.* 2013b, 2014, Gałka & Apolinarska 2014). Due to the biogeographic significance and palaeoecological importance of the area, the Holocene history of the local occurrence of several plant species was determined, namely *Juncus subnodulosus* (Gałka 2009), *Sphagnum wulfianum* (Gałka 2010), *Epipactis palustris* (Gałka & Kasper 2011), *Najas flexilis* (Gałka *et al.* 2012), *Cladium mariscus* (Gałka & Tobolski 2012), and *Picea abies* (Gałka & Tobolski 2013).

## Material and methods

### Study area

Eutrophic Lakes Kojle and Perty are located in NE Poland in the Suwalski Landscape Park (SLP; Fig. 1). The development of the lakes was related to the local occurrence of the Scandinavian Ice Sheet, which retreated from the area approximately 14 600 cal. BP (Rinterknecht *et al.* 2006). Bottom sediments in Kojle date to approximately 13 730–13 380 cal. BP (Gałka & Sznal 2013), but the presence of older sediments cannot be excluded. The studied lakes are located in an area of terminal moraines and are surrounded by terrain whose height reaches approximately 200 m a.s.l. In the past, Kojle and Perty were connected (Gałka & Tobolski 2013) but today they are separated from each other by a peatland. Hence, the name (Lake) Kojle–Perty

shall be frequently used in this article. According to measurements from 2010, the surface area of Kojle is 17.13 ha and that of Perty is 19.69 ha (Gałka 2012). The water level in both lakes is approximately 148.3 m a.s.l. Currently, the deepest point in Kojle is 33 m and in Perty 32 m.

The climate in this part of Poland is transitional, with a clear influence of continentalism. The study area has the lowest number of vegetative days in lowland Poland, i.e., 180–190. The mean annual precipitation amounts to 650 mm. The mean monthly temperatures in the area range from 17 °C in July to –5 °C in January (Woś 1999).

SLP is dominated by boreal plant assemblages. Morainic and kame hills and eskers are primarily overgrown with coniferous forests dominated by *Picea abies*. Among deciduous trees, *Carpinus betulus* and *Corylus avellana* are dominant. In humid areas, forests dominated by *Alnus glutinosa* and *Fraxinus excelsior* occur. The littoral zone of the studied lakes is inhabited primarily by *Phragmites australis*, *Typha latifolia*, and *Cladium mariscus*. In deeper parts of the lakes, among other taxa, *Chara* spp., *Potamogeton lucens*, and *Nymphaea alba* occur. *Pinus sylvestris* and *Picea abies* grow in the peatland between Kojle and Perty and along the southwestern bay of Kojle. Occurrences of plants associated with oligotrophic habitats have also been recorded, particularly species of *Sphagnum*, including among others *S. magellanicum*, *S. palustre*, and *S. russowii*, as well as *Andromeda polifolia* and *Oxycoccus palustris*.

Geological drilling and sampling of cores for laboratory analyses was performed using a Russian peat corer, 7 cm in diameter and 100 cm in length. The locations of the core sampling sites are presented in Fig. 1.

## Laboratory work

Sediments from the three sites were sampled for further analyses. The limnic-peat sediment was placed in PVC tubes. In the laboratory, the sediment was unpacked, cleaned, and sliced into 1-cm thick slices with a surgical scalpel.

The plant macrofossil analysis covered 1935 samples. The three cores were analysed

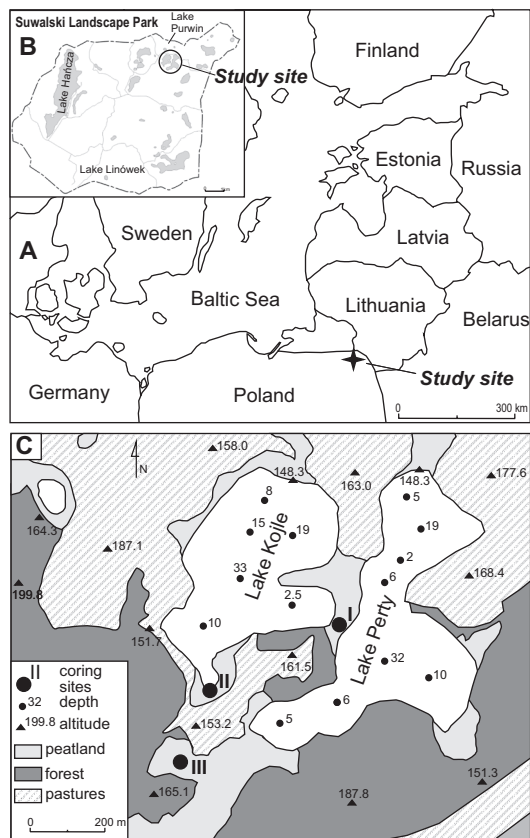


Fig. 1. Location of the study site. — A: Part of Europe. — B: Suwalski Landscape Park. — C: Lake Kojle–Perty; The sampling sites coordinates are: I: 54°16'26.8''N, 22°53'43.4''E; II: 54°16'21.36''N, 22°53'21.80''E; III: 54°16'15.45''N, 22°53'17.77''E.

at a resolution of 1 cm. The volume per sample was approximately 25 cm<sup>3</sup>. The samples were sieved under warm running water on sieves with 0.25 mm mesh size. The selected plant macrofossils were studied under a stereoscopic microscope (Nikon SMZ800 under 10–200× magnification) and a light microscope. The determination of vascular plant fossil species was performed with the help of Grosse-Brauckmann (1974), Grosse-Brauckmann and Streitz (1992), Tobolski (2000), and Velichkevich and Zastawniak (2006, 2009). Brown mosses were identified using Hedenäs (2003) and Smith (2004), and the *Sphagnum* species by using Hölzer (2010) and Laine *et al.* (2011). The plant macrofossil diagrams were prepared with the C2 graphic software (Juggins 2003).

Zones and phases of the vegetation development were distinguished visually from the diagrams. Fossil fruits and seeds are given in absolute numbers, and contributions of mosses, e.g., *Calliergon giganteum* and *Sphagnum magellanicum* and vegetative parts of vascular plants, are expressed as percentages of the total volume of a sieved sediment sample. The names of the plant species were adopted from Mirek *et al.* (2002) and Ochyra *et al.* (2003).

Plant macrofossils in nine samples from three cores were selected for the determination of radiocarbon age (Table 1). The age analysis was conducted at the Radiocarbon Laboratory in Poznań. The resulting conventional radiocarbon dates were calibrated by means of OxCal 4.2 software (Bronk Ramsey 2009). An age–depth model for site III was developed using the OxCal 4.2 application (Bronk Ramsey 2009).

This article presents the results for the period from 9400 cal. BP to present. Late Glacial and Early Holocene vegetation history and lake level changes will be published in a separate article. This division is due to a key event in the development of vegetation and lakes, i.e., a significant climate change around 9400 in NE Poland (Lauterbach *et al.* 2011, Gałka *et al.* 2014).

## Results and discussion

### Lithology and chronology

Due to the limited number of radiocarbon dates,

an age–depth model was only performed for site III (Fig. 2). The age of the dated sediment at particular depths, and its type, i.e., weakly decomposed peats in the upper part, suggest that at site III, the accumulation of organic sediments occurred continuously for 9100 years, with no hiatuses. Sediment accumulation took a different course at sites I and II, where it is probable that sediment accumulation was interrupted. This is suggested by the sediment age at particular depths, the presence of strongly decomposed peats, and fire horizons at site I (Fig. 3).

Calcareous gyttja occurs in the lower part of the sediments sampled at sites I and II, while at site III, calcareous gyttja with detritus gyttja are present (Table 2). Gyttja covers a layer of peat that developed during a period of low water levels in Kojle–Perty during the Early Holocene (Gałka & Sznal 2013). The beginning of the calcareous-gyttja accumulation at sites I, II and III was dated to 9533–9308, 9473–9142 and 9262–8819 cal. BP, respectively (Table 2). The thinnest layer of calcareous gyttja (240 cm thick) was found at site I.

A layer of detritus gyttja accumulated on calcareous gyttja. The thickest layer of detritus gyttja, 196 cm, was recorded at site II. At site III, above the layer of calcareous-detritus gyttja from approximately 7500 cal. BP, a layer of brown moss-herbaceous peat with detritus gyttja was accumulated. From 7500 to 6500 cal. BP, the main component of the sediment was *Drepanocladus* sp. Next, a layer of *Phragmites* peat developed that includes numerous oospores

**Table 1.** Radiocarbon dates. Numbers I–III refer to the study sites.

Site/depth (cm)	Dated material	Lab. no.	Age <sup>14</sup> C date (BP)	Cal. BP range (95%)
I/219–220	Needles of <i>Picea abies</i>	Poz-43865	4260 ± 40	4959–4646
I/340–341	Fruits and fruit scales of <i>Betula</i> sp.	Poz-37192	6130 ± 40	7160–6910
I/614.5–615.5	Bud scales of tree	Poz-37191	8430 ± 50	9533–9308
II/241–242	Needles of <i>Picea abies</i>	Poz-44774	6960 ± 35	7921–7694
II/444–446	Fruits and fruit scales of <i>Betula</i> sp.	Poz-38822	8330 ± 50	9473–9142
III/153–154	Stems of <i>Sphagnum magellanicum</i>	Poz-44906	1885 ± 30	1890–1730
III/297–298	Seed, bud scale, needles of <i>Picea abies</i> and fruit scales of <i>Betula pubescens</i>	Poz-44907	3175 ± 35	3464–3345
III/452–453	Needles of <i>Picea abies</i>	Poz-44773	4390 ± 35	5211–4859
III/872–873	Needles and periderm of <i>Pinus sylvestris</i>	Poz-39558	8120 ± 50	9262–8819

of *Chara* sp. and seeds of *Nymphaea alba* and *Cladium mariscus*. This finding suggests the presence of a shallow lake or an inundated peatland.

From approximately 5850 to 4000 cal. BP, a layer of sediment dominated by *Hamatocaulis vernicosus* developed. The environment of accumulation of this sediment is difficult to determine. On the one hand, the presence of macrofossils of five aquatic plants in this sediment layer suggests lake conditions; on the other, *Hamatocaulis vernicosus* grows in very humid peatlands and fens and is sometimes found submerged in shallow lakes (Hedenäs 2003). It is possible that *H. vernicosus* grew on the periphery of a peatland, and its leaves and stems, detached by waves, settled in large numbers on the lake bottom. This situation occurs frequently in lakes where a floating mat of *Sphagnum* mosses develops (author's pers. obs.). Mosses developed on limnic sediments. The thickest peat deposit, 346 cm, was found at site III. This layer was composed of *Pseudocalliergon trifarium* mosses in its lowest part, and more than 300 cm of *Sphagnum* peat, primarily made up of *S. magellanicum*. The beginning of accumulation of the *S. magellanicum* peat was dated to approximately 3500 cal. BP.

At site I, peat accumulation began approximately 6000 cal. BP, with a contribution of roots of Cyperaceae and *Menyanthes trifoliata*. From a depth of 138 cm, the peat was composed of *Sphagnum* leaves, *Eriophorum vaginatum*, and Ericaceae roots. At site II, from a depth of 86 cm, peat composed of roots of herbaceous plants, primarily Cyperaceae, and the brown moss *Calliergon giganteum* occurred: the contribution of those taxa reaching 80%.

## Palaeobotanical analyses

### Site I

I distinguished four phases in the history of development of local vegetation at site I (Fig. 3). The first phase (I/I, 615–450 cm) is the lake period. It is dominated by *Nymphaea alba*, *Nuphar* sp., and, clearly in the second half of the period, *Najas marina*. At the beginning of this

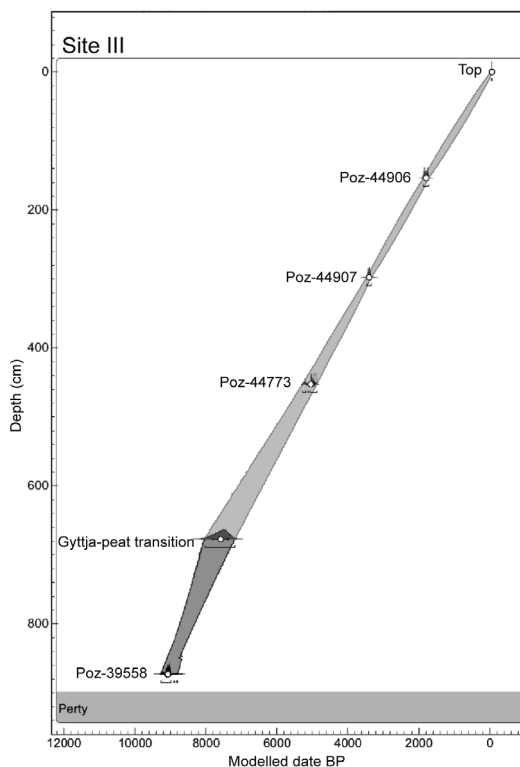


Fig. 2. Age–depth model of the profile at site III (prepared by Piotr Kołaczek).

phase, *Typha* sp., *Cladium mariscus*, and *Menyanthes trifoliata* occurred, i.e., plants that can grow in shallow waters of a lake's littoral zone. Among trees, *Pinus sylvestris*, *Betula pubescens*, and *Alnus glutinosa* were present.

Table 2. Lithostratigraphy of the sediment sequence at the three studied sites in Lake Kojle–Perty.

Site	Description of sediments
I	614–374 cm calcareous gytija
	374–277 cm detritus gytija
	277–138 cm herbaceous peat
	138–48 cm <i>Sphagnum</i> -herbaceous peat
	48–0 cm herbaceous-brown moss peat
II	445–282 cm calcareous gytija
	282–86 cm detritus gytija
	86–0 cm herbaceous-brown moss peat
III	875–677 cm calcareous-detritus gytija
	677–346 cm brown moss-herbaceous with detritus gytija
	346–308 cm brown moss peat
	308–0 cm <i>Sphagnum</i> -herbaceous peat





The second phase (I/II, 450–277 cm) is distinguished by a clear increase in the number of species of aquatic plants. In the first half, *Najas marina* and *Chara* sp. were dominant. In the second half, four species of *Potamogeton* appeared: *P. natans*, *P. trichoides*, *P. lucens*, and *P. gramineus*. Also in the second half, *Schoenoplectus lacustris* occurred regularly, and *Cladium mariscus* and *Typha* sp. appeared. The contribution of trees increased substantially, with *Alnus glutinosa* as the most abundant species. New species appeared: *Tilia* sp., *Populus tremula* and *Acer* sp.

In the third phase (I/III, 277–138 cm), the contribution of peatland plants, particularly that of sedges, increased. *Cladium mariscus* occurred, then disappeared at a depth of 211 cm. *Menyanthes trifoliata* was also present. Phase I/III is also distinguished by the occurrence of *Potentilla* sp. and *Rubus* sp. In the middle of this period, *Thelypteris palustris* was dominant, and the dominant trees were *Betula pubescens* and *Alnus glutinosa*. *Picea abies* appeared, with the highest contribution at a depth of 220–227 cm.

Phase four (I/IV, 138–0 cm) is distinguished by the appearance of *Sphagnum* sect. *Acutifolia* and sect. *Sphagnum*. In the upper part of this phase, *S. teres* appeared. Along with *Sphagnum*, *Eriophorum vaginatum* and *Andromeda polifolia* occurred. In the second half of the phase, *Menyanthes trifoliata*, *Comarum palustre*, and *Juncus articulatus* appeared. The contributions of *Carex paniculata* and brown mosses increased and the contribution of trees decreased substantially. Phase four was the only phase with visible macroscopic charcoal fragments.

## Site II

I distinguished five phases in the history of development of local vegetation at site II (Fig. 4). Phase one (II/I, 445–366 cm) is distinguished by the presence of five species of aquatic plants: *Najas marina* and *Nymphaea alba* were dominant, and *Nuphar lutea*, *Chara* sp., and *Potamogeton gramineus* occurred more sporadically. Macrofossils of *Cladium mariscus*, *Schoenoplectus lacustris* and *Typha* sp. were rare. In this phase, five species of trees occurred:

*Pinus sylvestris*, *Betula pubescens*, and *Tilia* sp. were the most numerous, and *Alnus glutinosa* and *Picea abies* occurred sporadically.

At the beginning of phase two (II/II, 366–282 cm), the contributions of *Najas marina* and *Chara* sp. increased substantially. In the middle of this phase, *Schoenoplectus lacustris* occurred. In the second half of phase two, *Urtica dioica* appeared. *Tilia* sp. and *Alnus glutinosa* occurred regularly throughout the phase.

Phase three (II/III, 282–200) is distinguished by a decrease in the contribution of aquatic plants, particularly *Najas marina*, and trees. Among trees, only *Alnus glutinosa* occurred regularly. Phase three is also distinguished by the co-occurrence of *Urtica dioica* and *Rubus idaeus*.

During phase four (II/IV, 200–86 cm), a substantial increase of aquatic species and trees occurred. *Najas marina* occurred regularly. *Nymphaea alba* and *Chara* sp. were numerous. *Potamogeton natans* appeared for the first time. Among Cyperaceae, *Schoenoplectus lacustris* and *Cladium mariscus* occurred. In the second half of the phase, among others, *Carex rostrata* and *Stellaria palustris* appeared. In this phase, the highest increase among trees occurred for *Picea abies*. *Acer* sp. also appeared. *Alnus glutinosa* and *Betula pubescens* occurred regularly.

Phase five (II/V, 86–0 cm) is distinguished by the disappearance of aquatic plants, a decrease in the contribution of trees, and an increase in the contribution of peatland plants. *Carex paniculata* occurred regularly throughout this phase. In the first half of the phase, *Stellaria palustris* and brown mosses were dominant, with sporadic occurrences of *Bidens tripartita*, *Juncus articulatus*, and *Lychnis flos-cuculi*. In the second half, the contributions of *Menyanthes trifoliata* and *Calliergon giganteum* increased considerably.

## Site III

I distinguished five phases in the history of development of local vegetation at site III (Fig. 5). In phase one (III/I, 875–792 cm), the site was a lake, with regular occurrences of *Nymphaea alba* in the sediment. *Najas marina*, *Nuphar lutea*, and *Chara* sp. occurred sporadically.

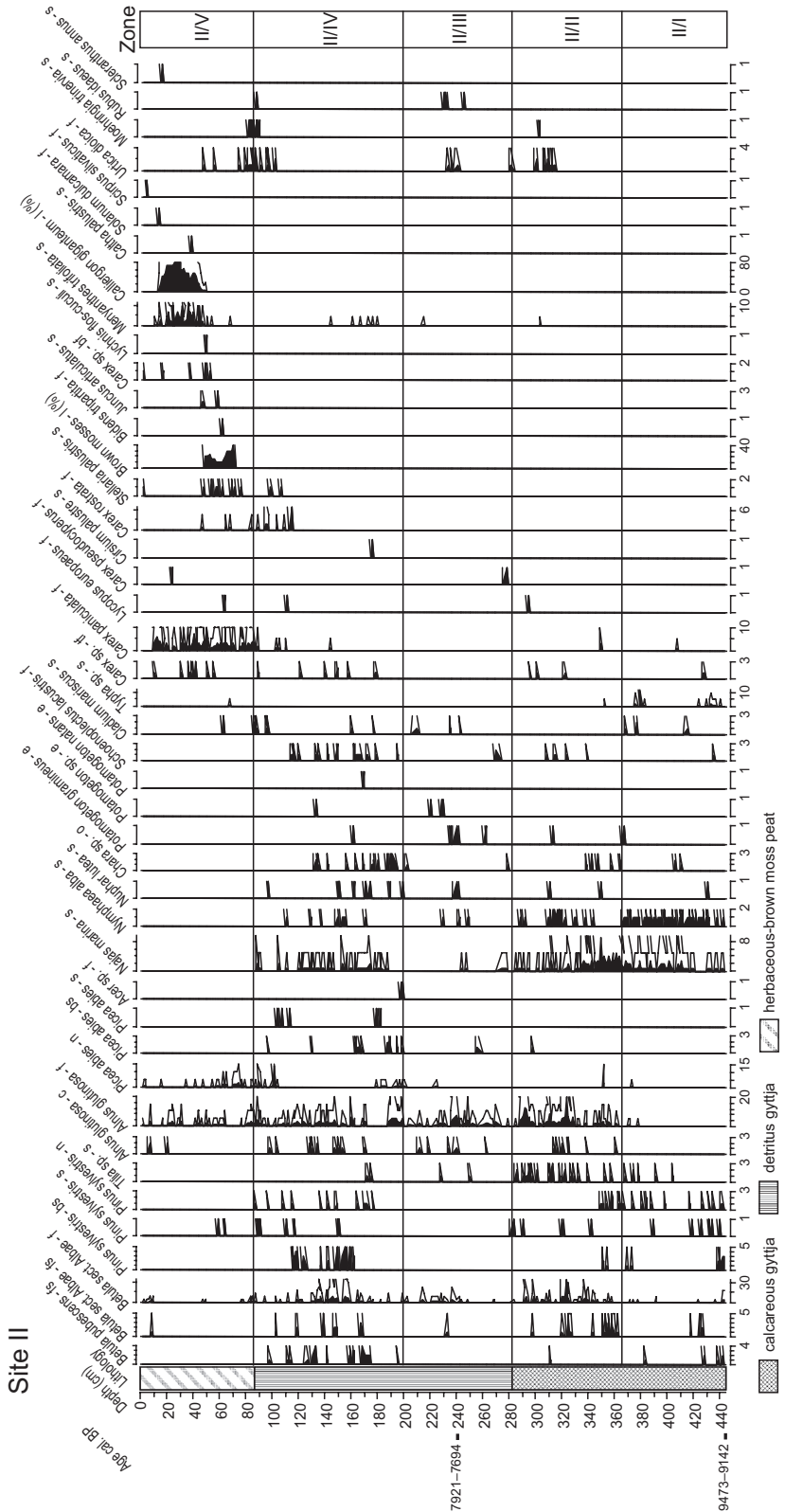


Fig. 4. Plant macrofossil diagram presenting local vegetation changes in site II. Description of plant macroremains, see legend of Fig. 3.





cally. Cyperaceae, including *Cladium mariscus* and *Schoenoplectus lacustris*, were present. The following trees occurred regularly: *Alnus glutinosa*, *Tilia* sp., and *Betula* sect. *Alba*.

Phase two (III/II, 792–584 cm) is distinguished by the appearance of *Drepanocladus* sp. (up to 90% of the total sediment volume) and *Potamogeton natans*. Among aquatic plants, *Nymphaea alba* occurred regularly. *Carex pseudocyperus* and *Menyanthes trifoliata* also appeared. During this phase, *Betula pubescens* was dominant, *Tilia* sp. was numerous, and *Picea abies* and *Acer* sp. appeared.

During phase three (III/III, 584–526 cm), *Phragmites australis*, *Chara* sp., and *Nymphaea alba* were dominant. *Potamogeton obtusifolius* was present. *Cladium mariscus* appeared again. Among trees, the most abundant were birches and alders.

Phase four (III/IV, 526–308 cm) is distinguished by the dominance of *Hamatocaulis vernicosus*. In the lower part, *Nuphar pumila* and *Potamogeton alpinus* appeared. In the middle part, *Nymphaea alba* and *Nuphar lutea* occurred. In the upper part, *Pseudocalliergon trifarium* appeared. The frequency of occurrence of various trees in the middle part of the phase is characteristic, with a clear dominance of *Picea abies*.

In phase five (III/V, 308–0 cm), no aquatic plants occurred. Plants typical of acidic habitats were dominant, primarily *Sphagnum magellanicum* with short periodical appearances of *Scheuchzeria palustris*, *Sphagnum* sect. *Cuspidata*, and *Eriophorum vaginatum*. In the second half of the period, *Andromeda polifolia*, *Oxycoccus palustris*, and *Carex echinata* were present. After the disappearance of *S. magellanicum* in the upper part of this phase, *S. palustre*, *Potentilla erecta*, and *Rubus* sp. appeared.

### Plant succession in Lake Kojle–Perty

Considering the duration of existence of aquatic plants at a given site, I distinguished three groups of plants. The first group includes plants that occurred quite regularly at one site in the lake over several thousand years. These include, among others e.g., *Najas marina* which occurred at site I for approximately 2500 years (Fig. 3)

and at site II for approximately 5000 years (Fig. 4). At site III, *N. marina* was only present at the beginning of the second phase (Fig. 4). At the beginning of the Holocene, the water level decreased substantially in Kojle and Perty. In the shallow parts of the lakes, on Late Glacial limnic sediments, peats were accumulated, and overlaying the peats, again calcareous gyttja (Gałka & Tobolski 2013). During the period of occurrence of *N. marina*, Kojle and Perty were eutrophic lakes. Currently, *N. marina* grows primarily in eutrophic lakes, but it is also encountered in brackish waters (Bennike et al. 2001). In the past in western and northern Europe it also occurred in eutrophic and brackish waters (Backmann 1941, Godwin 1975, Bennike et al. 2001). In Poland, *N. marina* mainly occurred in eutrophic lakes (Gałka 2007).

Other Holocene sites in Poland where *Najas marina* was present suggest that it also grew for several thousand years in a number of other lakes. In Lake Purwin, located approximately 1 km north of the studied lakes, *N. marina* seeds, and periodically also vegetative fragments of stems and leaves, were recorded on a regular basis in sediments that developed between 5000 and 2000 cal. BP (Gałka & Apolinarska 2014). However, *N. marina* was already present in Lake Purwin approximately 8300 cal. BP. The constant presence of *N. marina* over a period of several thousand years was also determined in other lakes in N Poland (Gałka 2007, Konieczna & Kowalewski 2009, Gałka & Tobolski 2011, Stachowicz-Rybka & Obidowicz 2013). The stability of occurrence of *N. marina* over several thousand years has also been confirmed in lakes in Latvia (Rūtina et al. 2012).

The group of plants that occurred quite regularly over several thousand years in Kojle–Perty also includes *Nymphaea alba*. It occurred at site I for approximately 2500 years, at site II during four periods over approximately 5000 years, and at site III for approximately 5000 years (Fig. 6). The modern and fossil environments of *N. alba* suggest that its environmental preferences are quite flexible. In general, *N. alba* inhabits meso- to eutrophic waters (Kłosowski & Kłosowski 2007), but it is also encountered in dystrophic and oligotrophic waters. It grows at depths down to approximately 3 m (Hannon

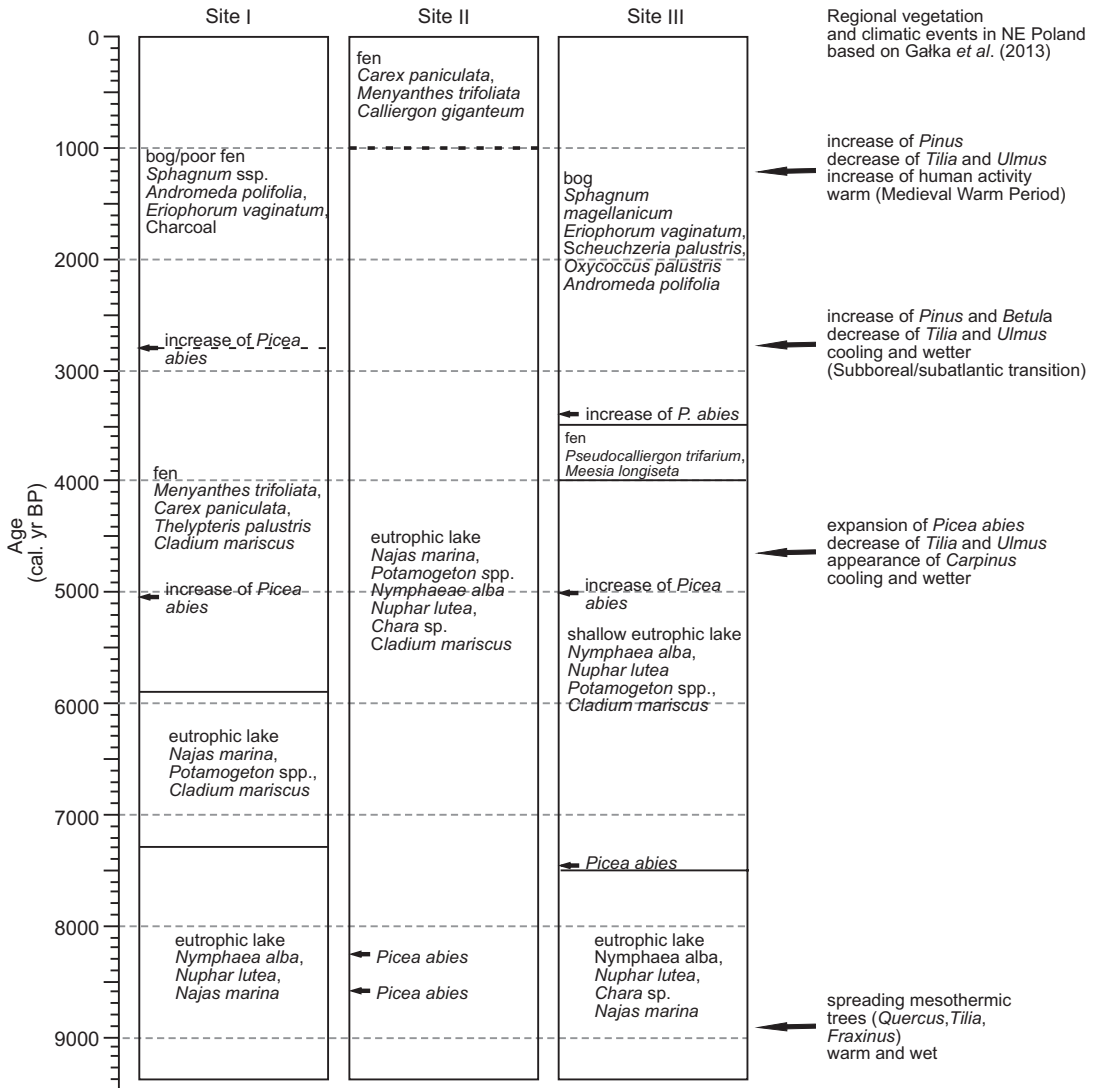


Fig. 6. Comparison of the vegetation development at the analysed sites of Lake Kojle–Perty.

& Gaillard 1997). The regular occurrence of *N. alba* in lakes over several thousand years has been confirmed, among other locations, in NE Poland: Linówek (Gałka *et al.* 2014), Purwin (Gałka & Apolinarska 2014; north-central Poland (Gałka 2007), and S Poland (Fajer *et al.* 2012). *Nymphaea alba* also remained present at a given site for long periods in other parts of Europe: in Lithuania (Gaidamavičius *et al.* 2011), Latvia (Rūtina *et al.* 2012), and Denmark (Bradshaw *et al.* 2005). The second group of plants includes *Nuphar lutea* and *Chara* sp., which occurred

at each of the studied peatlands less regularly and for shorter periods than *N. marina* and *N. alba*. At sites II and III, macrofossils of *N. lutea* and *Chara* sp. were found occasionally. At site I, *Chara* appeared in the second phase of the existence of the lake (Fig. 3). The number of oospores in some samples, up to 150 items, suggests that in certain periods, *Chara* was the dominant species. The consistent presence of *N. marina* seeds suggests that *Chara* sp. and *N. marina* co-existed in Kojle–Perty. In the past, *N. marina* co-occurred with *Chara* in Latvian

(Rütina et al. 2012) and Danish lakes (Bradshaw et al. 2005), among others. The situation was different in Lake Purwin, where a decrease of *N. marina* occurred in a period of substantially growing numbers of *Chara* sp. oospores (Gałka & Apolinarska 2014). This finding may indicate that the development of assemblages with *Chara* sp. caused the disappearance of *N. marina*, i.e., that the species were not able to coexist. Such an interpretation is supported by the fact that the reappearance of *N. marina* in Lake Purwin was accompanied by a rapid decrease in the number of *Chara* sp. oospores. However, the disappearance of *N. marina* in Lake Purwin can be related not only to the competition between those species but also to a water level increase. The optimal habitat for *N. marina* is a lake environment with a depth of approximately 1 m and a maximum depth of approximately 2 m (Hannon & Gaillard 1997). *Chara* spp. can grow at depths of up to 30 metres (Haas 1994). Therefore, after the water level increase, the area of the lake with conditions favourable for the growth of *N. marina* decreased, and it most likely withdrew to the shallower parts of the lake. The disappearance of *N. marina* in Lake Purwin corresponds with the disappearance of *Cladium mariscus* and *Schoenoplectus lacustris*, plants that grow in shallow waters in the rush zone. This fact can additionally confirm the withdrawal of *N. marina* and expansion of *Chara* sp. due to a water level increase. In the case of stable conditions, i.e., an appropriate water depth, *N. marina* and *Chara* sp. can grow next to each other. The phenomenon of *N. marina* growing next to stoneworts is currently described in various parts of Europe (Eriksson et al. 2004, Landucci et al. 2011, Wolf et al. 2013).

### Palaeoecology of *Potamogeton*

The third group of plants present in the limnic phase in the Lake Kojle–Perty includes *Potamogeton*. Considering the low frequency of endocarps of given *Potamogeton* species, their presence at the three analysed sites can generally be considered short-term. The past occurrence of *Potamogeton* in Kojle–Perty is only demonstrated by the presence of single endocarps in the sediment. At site I, *Potamogeton natans*, *P.*

*trichoides*, *P. gramineus*, and *P. lucens* occurred in the last phase (Fig. 2). The appearance of *P. natans* and *P. trichoides* corresponds with a change of sediment. Calcareous gyttja that had previously accumulated was replaced by detritus gyttja with no recorded presence of calcium carbonate. The presence of *P. natans* and *P. trichoides* also corresponds with a gradual decrease in the number of oospores of *Chara* sp. and *Najas marina*. Moreover, the appearance of *P. gramineum* and *P. lucens* is accompanied by the disappearance of *Chara* and a further decrease in the occurrence of *Najas marina*.

*Potamogeton natans* is a species very frequently found as fossils (Godwin 1975, Velichkevich & Zastawniak 2006). At present, it grows in shallow parts of lakes, usually down to 3 m (Kłosowski & Kłosowski 2007) or to a maximum depth of 6 m (Hannon & Gaillard 1997). It inhabits waters with various trophic statuses, from oligo- to eutrophic, and grows on various substrata (Kłosowski & Kłosowski 2007). Due to this flexibility, its fossil presence is not a very good palaeoenvironmental indicator. In Poland, it is recorded in Holocene sediments in both calcareous gyttja and detritus gyttja, and the duration of its existence is very variable. *Potamogeton natans* can indicate a lower lake level. It is most frequently encountered in sediments of the final period of a lake's existence (Miotk-Szpiganowicz & Gałka 2009, Fajer et al. 2012, Żurek & Kloss 2012, Gałka & Sznel 2013, Stachowicz-Rybka & Obidowicz 2013).

In Poland, *Potamogeton trichoides* is usually encountered in the south, growing in eutrophic waters with organic sediments (Zalewska-Gałosz 2008). It is only rarely present in the fossil record and is considered an indicator of warm periods (Velichkevich & Zastawniak 2006). At site I, I found three endocarps of *P. trichoides* in three samples in sediments dated approximately 7000 cal. BP, i.e., during the climatic optimum (9000 to 5500 cal. BP.; Kalis et al. 2003). A single endocarp of *P. trichoides* was also found in the uppermost layer of detritus gyttja under peats on peatland Gązwa near Mrągowo (NE Poland). The age of the sediments with *P. trichoides* was dated approximately to 6300 cal. BP (Gałka & Lamentowicz 2014). At site Kobylnica Wołoska, located in NE Poland, *P. trichoides*

endocarps were recorded in a sediment accumulated approximately 14 700 cal. BP (pers. obs.). It grew on calcareous gyttja substrate for approximately 100 years, together with *P. alpinus*, *P. pusillus*, and *P. natans*.

In the area of Kojle–Perty, *Potamogeton lucens* was only recorded in one sample in sediments from site I, accumulated approximately 7000 cal. BP. Currently, *P. lucens* occurs primarily in eutrophic waters and is encountered at depths of greater than 3 m (Kłosowski & Kłosowski 2006). Considering the other fossil sites of *P. lucens* in Poland, it appears to persist quite a short period at a given site. Its endocarps are usually only recorded in one to several samples. This situation occurred in Lake Linówek, where *P. lucens* occurred episodically approximately 11 200 cal. BP (Gałka *et al.* 2014). In Lake Purwin, *P. lucens* was present occasionally at three points over a period of approximately 3500 years. The periods of its occurrence were more than 1000 years apart (Gałka & Apolinaraska 2014). Several endocarps of *P. lucens* were found in single samples of the medieval sediments from Gdańsk (N Poland) (Święta-Musznicka *et al.* 2011). *Potamogeton lucens* occurred for a little longer in the fossil lake in SE Poland near Pakośćawice. There it was very abundant in fine detritus gyttja (30 cm thick) accumulated in the Alleröd, and co-occurred with *P. obtusifolius*, *P. natans*, and *P. acutifolius* (Maj & Gałka 2012).

At site II, two species of *Potamogeton* were recorded (Fig. 4). *Potamogeton natans* was only present in one sample, and grew in the environment of detritus gyttja. *Potamogeton gramineus* was found in six samples, in both calcareous and detritus gyttja. It is a circumboreal species (Hulten & Fries 1986). In Poland, it usually occurs in the north and east and grows in meso- and eutrophic waters on calcareous organic and mineral substrates (Zalewska-Gałosz 2008). According to Godwin (1975), in England, *P. gramineus* prefers non-calcareous waters. It is noteworthy that the occurrence of *P. gramineus* at site II coincides in two periods with the occurrence of *Urtica dioica* fruits and in one period with the presence of *Rubus idaeus* seeds in the sediment. This correlation suggests the appearance of *P. gramineus* in the lake during periods of low water levels. *Urtica dioica* and *Rubus idaeus* often grow on

decomposed peat in peatlands adjacent to lakes. The appearance of *P. gramineus* during a water level drop is also suggested by the simultaneous occurrence of *Cladium mariscus* and *Schoenoplectus lacustris*. Considering other fossil sites of *P. gramineus*, it seems to have no clear substrate preference. In Lake Linówek, I found a single *P. gramineus* endocarp in one sample of sediment accumulated approximately 8500 cal. BP (Gałka *et al.* 2014). It was accompanied in this lake by, among others, *Chara* sp. and *Potamogeton natans*. In another sample, 1 cm higher, *P. obtusifolius* appeared. In Lake Mielnica in the Tuchola Forest, *P. gramineus* appeared in the final phase of the lake's existence, after a change in the sediment from calcareous gyttja to detritus gyttja, and grew together with *N. marina* and *Nuphar lutea* (Gałka 2007). In Lake Pilcines (E Latvia), *P. gramineus* appeared in a shallow lake (the deepest location being 1.9 m) in sediments younger than 800 cal. BP (Rütina *et al.* 2012). It was accompanied by *P. natans*, *P. perfoliatus* and others. In Kråkenes Lake (SW Norway), *P. gramineus* occurred sporadically approximately 10 900 cal. BP and was accompanied by, among others, *Batrachium* sp. and *Myriophyllum alterniflorum*. This find suggests that pH oscillated around approximately 6–7 (Birks 2000). An abundant occurrence of endocarps of *P. gramineus* was determined in the former mesoeutrophic Lake Velanská Cesta (S Czech Republic) in the period from 14 000 to 13 500 cal. BP, with a less frequent occurrence from 13 500 to 11 500 cal. BP (Bešta *et al.* 2009). There it grew on algal gyttja, accompanied by *P. praelongus* and *P. perfoliatus*, and in the final phase of its presence in the lake also by *P. obtusifolius*. Considering the above examples in palaeoecological reconstructions, the appearance in a given lake of *P. gramineus* suggests either shallow water or a decrease in water depth.

At site III, three *Potamogeton* species appeared in the lake after a change in the type of accumulated sediment. *Potamogeton natans* appeared after a change from calcareous gyttja to detritus gyttja with abundant *Drepanocladus* sp. The accumulation of this sediment layer in the environment of the shallow lake is probable because certain species of *Drepanocladus* moss, e.g., *D. aduncus*, can grow on the bottom of shallow water bodies (Smith 2004, Suško 2010).



Sediment accumulation in the lake is also suggested by the presence of macrofossils of four aquatic taxa: *Nymphaea alba*, *Nuphar lutea*, *Chara* sp., and *Potamogeton natans*. *Potamogeton obtusifolius* and *P. alpinus* also occurred in the environment with no calcareous gyttja, but they appeared only after the disappearance of *Phragmites australis*. During that time, an open space most likely appeared in the shallow lake, which permitted colonisation of the site by *P. obtusifolius* and *P. alpinus*. It should be taken into account, however, that *P. alpinus* endocarps were found in the sediment where the main component was *Hamatocaulis vernicosus*. This brown moss can exist in a peatland even when it is submerged in shallow water (Hedenäs 2003). The presence of seeds of *Nymphaea alba* or accompanying *P. alpinus* in the sediment is noteworthy. Based on this, it can be assumed that the numerous *Hamatocaulis vernicosus* leaves in the sediment resulted from the presence of a shallow lake inhabited by *H. vernicosus*. Alternatively, leaves of *H. vernicosus* could have accumulated on the lake bottom after falling along the periphery of the peatland, as mentioned earlier.

The time of appearance of *P. alpinus* and the accompanying *Nuphar pumila* in the lake at site III is very significant. At the time of appearance of those plants in the lake, the contribution of *Picea abies* increased in the nearby forests. *Picea abies* was already recorded on the shores of Kojle and Perty in the Early Holocene (Gałka & Tobolski 2013). Sporadic macrofossils were found in the analysed sediments dating to approximately 9500 cal. BP from its expansion in the vicinity of Kojle and Perty, i.e., until approximately 5000 cal. BP. A clear increase in *P. abies* beginning approximately 5000 cal. BP is visible at two sites (I and III), as confirmed by radiocarbon dates (Figs. 2 and 4). In the sediments of Lake Purwin, the first macrofossils of *P. abies* were found approximately 4700 cal. BP (Gałka & Apolinarska 2014), and in the sediments of Lake Linówek approximately 4300 cal. BP (Gałka et al. 2014).

The appearance of *Nuphar pumila* and *Potamogeton alpinus* with a simultaneous increase of *Picea abies* could be related to the climate cooling that occurred around 5800 cal. BP in this part of Europe (Heikkilä & Seppä 2003).

The migration to these areas of *N. pumila* and *P. alpinus* could be caused by an increase in the influence of the continental climate. This migration accounts for the modern distributions of those plants. Modern *N. pumila* is concentrated in eastern and northern Europe (Piękoś-Mirkowa & Mirek 2003), and *P. alpinus* is a species with a circumboreal range (Hulten & Fries 1986). *Potamogeton alpinus* and *N. pumila* also appeared together at a similar time in Lake Linówek approximately 3900 cal. BP (Gałka et al. 2014), and grew in an environment of accumulating detritus gyttja. Also in the area of the former lake near Kobylnica Wołoska (SE Poland), those two species co-occurred approximately 14 600 cal. BP (pers. obs.), but at that site, their macrofossils were found in calcareous gyttja. The co-occurrence of *P. alpinus* and *N. pumila* in the past suggests their similar ecological requirements.

*Potamogeton obtusifolius* was found only in one sample from site III, which suggests that this species occurred in that location only sporadically. Currently, the species prefers meso- and eutrophic waters with alkaline reaction (Zalewska-Gałosz 2008). It usually grows at water depths of approximately 1–1.5 m on substrates with a thick layer of organic sediments (Kłosowski & Kłosowski 2007). In SW Poland, it was recorded in one sample (Maj & Gałka 2012). Also in SE Poland, it grew for a relatively short time, i.e., approximately 100 years (pers. obs.). Considering other fossil occurrences of this plant, however, it can be concluded that the duration of its persistence at one site varies, unlike in Lake Kojle. In Lake Linówek, *P. obtusifolius* appeared during two periods: 8500–8000 cal. BP and 4300–2200 cal. BP (Gałka et al. 2014). In Gdańsk, *P. obtusifolius* endocarps were found in medieval deposits (Święta-Musznicka et al. 2011). In N Romania, it occurred regularly during the period 10 300–8600 cal. BP (Feurdean & Bennike 2004). In England, it was present almost throughout the Holocene (Godwin 1975).

### Plant succession on the mires

The gradual filling of the basins of Lakes Kojle and Perty with sediments resulted in the coloni-

sation of the shallow parts of the lakes by rush vegetation. This included *Schoenoplectus lacustris*, *Cladium mariscus*, and *Typha* sp. The last one occurred first in the studied lakes. Its seeds were already recorded approximately 11 000 cal. BP (Gałka & Sznel 2013). Next, *C. mariscus* appeared. Its seeds and fruits were found in the sediments of the lakes approximately from 9500 cal. BP (Gałka & Tobolski 2012). In this study, the first fruits of *S. lacustris* were found in sediments accumulated approximately 9200 cal. BP at site II. The plants occurred at each of the sites analysed, although they were not always present at the same time.

### Development of vegetation from lake to poor fen/bog at site I

Colonisation of the shallow parts of the lake and initiation of the development of a peatland was dominated by *Cladium mariscus* and *Menyanthes trifoliata* (Fig. 3). *Carex* also occurred, including among others, *C. pseudocyperus* and *C. lasiocarpa*. These plants formed most of the peat until approximately 4800 cal. BP, when a substantial change occurred. *Picea abies* appeared in the vicinity of the sediment sampling site, as suggested by its numerous macrofossils (seeds, needles, bud scales). The occurrence of spruce coincided with the disappearance of *Cladium mariscus* and appearance of *Thelypteris palustris*, *Carex paniculata*, and *Cirsium palustre*. The presence of *Thelypteris palustris* and *Carex paniculata* lasted for approximately 200 years. These two species disappeared most likely as a result of a decrease in the water level on the peatland, as evidenced by a decrease in the degree of decomposition of peat and the appearance of fruits of *Rubus* sp. and *Potentilla* sp. In N Poland, *Thelypteris palustris* and *Cladium mariscus* frequently overgrow shallow lakes, often developing several-centimetre-thick floating mats (Kłosowski 1986/87, Namura-Ochalska 2005, Karcz 2008, Gałka & Tobolski 2012) or belt-like assemblages (Jasnowska & Jasnowski 1991a, Karcz 2008). A peat layer with *T. palustris* roots as its main component is usually from several (Jasnowska & Jasnowski 1991b, Gałka 2007, Gałka & Tobolski 2013) to

approx. 200 cm thick (Forysiak *et al.* 2012). The disappearance of *Cladium mariscus* from site I may have been caused by a shift towards open water, which resulted in a lack of seeds in the sediment at the sampling site. In N Poland, *C. mariscus* is usually encountered on lake shores (Gałka & Tobolski 2006). However, the disappearance or decrease of the *C. mariscus* population at site I could be related to substantial climate cooling that occurred in this part of Europe approximately 4500 cal. BP (Heikkilä & Seppä 2003). *Cladium mariscus* clearly favours warmer climatic conditions, as confirmed by its modern distribution in Latvia (Salmina 2004).

After a period of domination of sedges and *Menyanthes trifoliata* on the peatland at site I, *Sphagnum*, *Eriophorum vaginatum*, and Ericaceae with *Andromeda polifolia* and *Calluna vulgaris* appeared. This suggests habitat acidification, which may have resulted from the presence of *Picea abies*. Numerous *Picea abies* needles were found in the sediment from that period (Fig. 6). An association between the appearance of *P. abies* in the vicinity of the peatland and the development of peatlands with *Sphagnum* was found for the peatlands surrounding Lake Linówek (Gałka *et al.* 2014). The presence of numerous macroscopic charcoals in the uppermost peat layer is noteworthy, as they provide evidence of repeated fires in the peatland and its vicinity. These fires may have been either of natural origin or initiated by the local tribes (primarily Yotvingians) burning forests to clear land for cultivation. Unfortunately, due to the lack of radiocarbon dates from this part of the core, it is difficult to determine the age of the layer. Nonetheless, cereal cultivation in the area was determined to occur approx. 2300 cal. BP (Gałka *et al.* 2014).

In the uppermost part of the sediments from site I, *Menyanthes trifoliata*, *Carex paniculata*, *Juncus articulatus*, as well as *Cladium mariscus* appeared. This finding provides evidence of an increase in the trophic status and development of a meso-eutrophic habitat.

### Development of vegetation from lake to fen at site I

At site II, with the thinnest peat layer among all

of the sites analysed, the succession of plants from lake to fen was similar to that at site I (Fig. 4). After the infilling of the lake, and even after the decrease in the water level evidenced by numerous *Urtica dioica* fruits, one *Rubus idaeus* seed, and several *Moehringia trinervia* seeds, plants appeared that could grow even in shallow water, i.e., *Cladium mariscus* and *Carex rostrata* (Fig. 4). The presence of seeds of *Moehringia trinervia* suggests that the water level on the peatland surrounding the lake substantially decreased, because that species is typical of humid habitats in deciduous forests or on stream banks. A substantial decrease in the water level is also suggested by the appearance of needles of *Picea abies* in the sediment. A decrease in habitat humidity on the peatland most likely permitted the growth of *Picea abies*. In the initial phase of the development of the peatland, *Carex paniculata* was present. It strongly prefers wet surfaces and often grows on lake shores (Zarzycki et al. 2002, Kłosowski & Kłosowski 2007). In the uppermost part of the peat, macrofossils of *Menyanthes trifoliata* and *Calliergon giganteum* were found, which is evidence of increased humidity. An increase in the water level is also suggested by the presence of *Caltha palustris*. Similarly to the two former plants, this species grows even in habitats with standing water (Zarzycki et al. 2002). Due to its quite wide habitat amplitude in terms of pH and humidity, *M. trifoliata* is not a very precise palaeoecological indicator. However, its presence suggests a humid or even inundated habitat. *Menyanthes trifoliata* can even grow in the littoral zone of lakes at water depths down to 1 m (Hannon & Gaillard 1997). A better indicator of an increase in habitat humidity in this case is *C. giganteum*, which primarily prefers very humid surfaces (Smith 2004) and grows even on submerged peatlands (Hölzer & Hölzer 1994, Hedenäs 2003). *Calliergon giganteum* is often found as subfossils (Gałka & Kasper 2011, Lamentowicz et al. 2013).

### Development of vegetation from lake to bog at site III

Vegetation succession at site III (Fig. 5) was the most complex, considering the individual

phases of plant succession in the shallow lake and peatland. In this case, similarly to site I, a raised bog developed in place of the eutrophic lake over thousands of years. The development of the ombrotrophic peatland was preceded by the presence of first *Hamatocaulis vernicosus* and then *Pseudocalliergon trifarium*, which was the dominant species at the site from approximately 3850 to 3550 cal. BP. Peat from that period did not contain macrofossils of vascular plants. The presence of *H. vernicosus* suggests a very humid surface and a pH of approximately 6.7–7.2 (Štechová & Kučera 2007). Currently, the species grows on moderately rich fens with local flushes (Hugonnot 2003). In Estonia, *H. vernicosus* occurs primarily in spring fens and quagmires (Vellak & Ingerpuu 2012). A modern occurrence of *H. vernicosus* in NE Poland was found in the Rospuda River valley, where it was accompanied by *Tomentypnum nitens* and *Carex diandra* (Jabłońska et al. 2011). However, it can also occur at less acidic sites. In the Czech Republic, *H. vernicosus* grew together with *Sphagnum warnstorffii*, *S. teres*, and *S. contortum* (Hájek et al. 2006, Štechová & Kučera 2007) and also accompanied *Sphagnum magellanicum* and *Andromeda polifolia* (Štechová et al. 2010). At a fossil site in NE Poland (peatland Mechacz Wielki), *H. vernicosus* grew approximately 1800 cal. BP together with *Carex rostrata*, *C. paniculata*, *Comarum palustre*, and *Oxycoccus palustris* (Gałka et al. 2013d). It disappeared after the expansions of *Scheuchzeria palustris* and then of *Sphagnum obtusum*. The fossil presence of *H. vernicosus* was also determined at the northern shore of Lake Balaton (Hungary) in Late Glacial sediments (Sümegei et al. 2008). At this site, *H. vernicosus* co-occurred with, among others, *Scorpidium scorpioides*, *Calliergon giganteum*, *Drepanocladus aduncus*, and *Tomentypnum nitens*.

At site III, *H. vernicosus* disappeared at approximately 3850 cal. BP. This was most likely related to the appearance of *Pseudocalliergon trifarium*. The modern occurrence of *P. trifarium* suggests that the disappearance of *H. vernicosus* could have resulted from a decrease in pH, because *P. trifarium* requires pH values of 5.6–7.6 (Bisang et al. 2006). *Pseudocalliergon trifarium* was present in the peatland until approximately 3500 cal. BP.

After that, *Meesia longiseta*, *Oxycoccus palustris*, and species of *Sphagnum* sect. *Cuspidata* appeared for a short time. Then, *S. magellanicum* appeared in the peatland (Fig. 6), a species typical of ombrotrophic bogs that grows in habitats with an average pH of 3.8 (Hölzer 2010). The appearance of *S. magellanicum* was related to a change in the water alimentation of the peatland. Since that time, precipitation alimentation has increased in the vicinity of the site. It is worth emphasising that the rapid colonisation of the habitat by *S. magellanicum* was also influenced by the presence of *Picea abies*. The occurrence of *P. abies* in the peatland or on mineral margins in its direct vicinity, as well as the falling of spruce needles, may have helped to acidify the habitat. *Sphagnum magellanicum* was consistently present at site III for approximately 3000 years. Only the proportion of the plant in some samples changed. The fossil presence of *S. magellanicum* within the last several thousand years in NE Poland has also been observed at, among other sites, the peatland Kładkowe Bagno (Drzymulska 2008) and the peatland Mechacz Wielki (Żurek & Kloss 2012).

Approximately 2800 cal. BP, *Scheuchzeria palustris* and *Carex rostrata* appeared in the peatland for approximately 100 years. These plants grow in wetter habitats (Ellenberg *et al.* 1991, Zarzycki *et al.* 2002). This finding suggests an increase in the water level in the peatland at that time. An increase in humidity at a given peatland coincides well with an increase in climatic humidity observed during that time at a number of sites in Europe (van Geel *et al.* 1996, Barber *et al.* 2004, Andersson & Schoning 2010, Gałka *et al.* 2013a). During the presence of *S. magellanicum* on the peatland, *Eriophorum vaginatum* also appeared four times. The appearance of *E. vaginatum* on peatlands suggests instability and fluctuations of the water level (Silvan *et al.* 2004, Tuittila *et al.* 2007, Gałka *et al.* 2013b). Approximately 600 cal. BP., *Picea abies* appeared on the bog. A rapid dispersal of this species during the same time was also found on the peatland surrounding Lake Linówek (Gałka *et al.* 2014). The appearance of *Picea abies* at site III coincides with the presence of numerous *Carex echinata* fruits in the peat. The sudden and abundant appearance of *C. echinata* fruits

in the bottom layer of *Sphagnum-Eriophorum* peat was recorded in S Poland (Dukla Mts, the lowest central part of the Low Beskidy Mts.) by Szczepanek (2001). In that location, however, the appearance of *C. echinata* coincided with an increase in the contribution of *Salix* pollen. Currently, in this part of Europe, *C. echinata* quite frequently grows in marshy coniferous forests with spruce and pine. The appearance of *C. echinata* in the peatland suggests water level disturbances. Considering an increase in the presence of *Sphagnum* sect. *Cuspidata* during the expansion of *C. echinata* at site III, the water level most likely increased. The disappearance of *S. magellanicum* at site III and appearance of more eutrophic species such as *S. palustre* or *Potentilla erecta* is related to the attempt to meliorate the peatland in the second half of the 20th century. *Sphagnum magellanicum* currently occurs in the peatland at the southwestern lake shore, although it is not common. The dominant *Sphagnum* is *S. palustre*.

## Conclusions

The high-resolution palaeobotanical studies conducted in Lake Kojle–Perty suggest that the changes in vegetation and the course of succession in the lake and peatland have largely resulted from regional climate changes. Cooling caused an increase in the abundance of *Picea abies* in the forests in the vicinity of the lake and the appearance of species related to boreal climate, such as *Nuphar pumila*, within the lake. The deposition of *P. abies* needles on the surface of the peatland resulted in acidification and a retreat of species that prefer eutrophic habitats, such as *Cladium mariscus*, as well as the appearance of species preferring acidic habitats, such as *Sphagnum magellanicum*. Substantial changes in the vegetation of the lake also resulted from changes in the accumulated sediment. I found that the appearance of *Potamogeton* species in the lake coincided with the beginning of the accumulation of detritus gyttja in place of calcareous gyttja. Note, however, that this change in the accumulated sediment may have been accompanied by a shallowing of the lake, which favoured the appearance of *Potamogeton*. I



found a certain division in the development of vegetation in Lake Kojle–Perty resulting from the duration of the occurrence of aquatic plants at one site. *Najas marina* and *Nymphaea alba* occurred for the longest times at one site, and the shortest-term residents were species of *Potamogeton*.

## Acknowledgements

The study was financed through a grant from the Ministry of Science and Higher Education as a research project N N305 3259 33 and the Polish Science Centre awarded for the following projects NN305 0622 40. I thank the employees of the Suwalski Landscape Park, especially Marcin Sznel and Łukasz Halik (UAM Poznan) for assistance in the field work and sediment sampling. I'm very thankful to Petra Hajkova for help in the identification of brown moss species, Piotr Kołaczek for constructing age–depth model of the site III and, and editors from *American Journal Experts* for improving the English. I express my gratitude to anonymous reviewers for their comprehensive reading of the manuscript and constructive suggestions for its improvement.

## References

- Allen J.R.M. & Huntley B. 1999: Estimating past floristic diversity in montane regions from macrofossil assemblages. — *Journal of Biogeography* 26: 55–73.
- Andersson S. & Schoning K. 2010: Surface wetness and mire development during the late Holocene in central Sweden. — *Boreas* 39: 749–776.
- Arie J., Kalis A.J., Merkt J. & Wunderlich J. 2003: Environmental changes during the Holocene climatic optimum in central Europe — human impact and natural causes. — *Quaternary Science Reviews* 22: 33–79.
- Backman A.L. 1941: *Najas marina* in Finland während der Postglazialzeit. — *Acta Botanica Fennica* 30: 1–38.
- Barber K.E., Chambers F.M. & Maddy D. 2004: Late Holocene climatic history of northern Germany and Denmark: peat macrofossil investigations at Dosenmoor, Schleswig-Holstein, and Svanemose, Jutland. — *Boreas* 33: 132–144.
- Bennike O. 2000: Palaeoecological studies of Holocene lake sediments from west Greenland. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 155: 285–304.
- Bennike O., Jensen J.B. & Lemke W. 2001: Late Quaternary records of *Najas* spp. (Najadaceae) from the southwestern Baltic region. — *Review of Palaeobotany and Palynology* 114: 259–267.
- Bešta T., Šafránková J., Pouzar M., Novák J. & Nováková K. 2009: Late Pleistocene–early Holocene transition recorded in the sediments of a former shallow lake in the Czech Republic. — *Hydrobiologia* 631: 107–120.
- Birks H.J.B. 1986: Late-Quaternary biotic changes in terrestrial and lacustrine environments, with particular reference to north-west Europe. — In: Berglund B.E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*: 3–65. John Wiley & Sons Ltd., Chichester.
- Birks H.H. 2000: Aquatic macrophyte vegetation development in Kråkenes Lake, western Norway, during the lateglacial and early-Holocene. — *Journal of Paleolimnology* 23: 7–19.
- Birks H.H. & Birks H.J.B. 2006: Multi-proxy studies in palaeolimnology. — *Vegetation History and Archaeobotany* 15: 235–251.
- Bisang I., Ehrlen J. & Hedenäs L. 2006: Reproductive effort and costs of reproduction do not explain female-biased sex ratios in the moss *Pseudocalliergon trifarium* (Amblystegiaceae). — *American Journal of Botany* 93: 1313–1319.
- Bradshaw E.G., Rasmussen P., Nielsen H. & Anderson N.J. 2005: Mid- to late-Holocene land-use change and lake development at Dallund Sø, Denmark: trends in lake primary production as reflected by algal and macrophyte remains. — *Holocene* 15: 1130–1142.
- Bronk-Ramsey C. 2009: Dealing with outliers and offsets in radiocarbon dating. — *Radiocarbon* 51: 1023–1045.
- Drzymulska D. 2008: Development of the Kładkowie Bagno peat-bog in the Late Glacial and Holocene: diversified history of two deposit basins studied with use of macrofossil remains analysis. — *Studia Quaternaria* 25: 23–32.
- Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W. & Paulißen D. 1991: Zeigewerte von Pflanzen in Mitteleuropa. — *Scripta Geobotanica* 18: 1–248.
- Eriksson B.K., Sandström A., Isæus M., Schreiber H. & Karås P. 2004: Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. — *Estuarine, Coastal and Shelf Science* 61: 339–349.
- Fajer M., Waga J.M., Rzetala M., Szymczyk A., Nita M., Machowski R., Rzetala M.A. & Ruman M. 2012: The Late Vistulian and Holocene evolution of Jezioro Lake: a record of environmental change in southern Poland found in deposits and landforms. — *Journal of Paleolimnology* 48: 651–667.
- Feurdean A. & Bennike O. 2004: Late Quaternary palaeoecological and palaeoclimatological reconstruction in the Gutaiului Mountains, northwest Romania. — *Journal of Quaternary Science* 19: 809–827.
- Feurdean A. & Bennike O. 2008: Plant macrofossils analysis from Steregoiu, NW Romania: taphonomy, representation, and comparison with pollen analysis. — *Studia Universitatis Babeş-Bolyai, Geologia* 53: 5–10.
- Forysiak J., Kloss M. & Żurek S. 2012: Wstępna charakterystyka geologiczna i paleobotaniczna torfowiska Wilczków [Preliminary geological and palaeobotanical description of the Wilczków mire]. — *Studia Limnologica et Telmatologica* 6: 95–101. [In Polish with English summary].
- Gaidamavičius A., Stančikaite M., Kisieliene D., Mažeika J., Gryguc G. 2011: Post-glacial vegetation and environment of the Labanoras Region, East Lithuania: implications for regional history. — *Geological Quarterly* 55: 269–284.
- Gałka M. 2007: *Zmiany jeziorno-torfowiskowe w ujściowym*



- odcinku Strugi Siedmiu Jezior. — Bogucki Wydawnictwo Naukowe, Poznań.
- Gałka M. 2009: A *Juncus subnodulosus* Schrank fossil site in Holocene biogenic sediments of Lake Kojle. — *Studia Limnologica et Telmatologica* 3: 55–59.
- Gałka M. 2010: *Sphagnum wulfianum* Girgens. in the Suwałki Landscape Park (NE Poland). — *Studia Limnologica et Telmatologica* 4: 51–56.
- Gałka M. 2012: Paleoeologiczne badania torfowisk i kopalnych jezior w Suwalskim Parku Krajobrazowym jako podstawa do ich ochrony [Palaeoecological studies of peat bogs and fossil lakes in Suwałki Landscape Park as the basis for their protection]. — In: Świerubska T. (ed.), XXXV lat Suwalskiego Parku Krajobrazowego [XXXV years Suwałki Landscape Park]: 11–25. Suwałki Park Krajobrazowy, Turtul. [In Polish with English summary].
- Gałka M. & Apolinarska K. 2014: Climate change, vegetation development, and lake level fluctuations in Lake Purwin (NE Poland) during the last 8600 cal. yr BP based on a high-resolution plant macrofossil record and stable isotope data ( $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$ ). — *Quaternary International*. [In press, doi:10.1016/j.quaint.2013.12.030].
- Gałka M. & Kasper P. 2011: Palaeobotanical peat analysis on contemporary *Epipactis palustris* (L.) Crontz. (Marsh Helleborine) sites in northeastern part of Poland. — *Studia Limnologica et Telmatologica* 5: 67–75.
- Gałka M. & Lamentowicz M. 2014: *Sphagnum* succession in a Baltic bog in central-eastern Europe over the last 6200 years and paleoecology of *Sphagnum contortum*. — *Bryologist* 117. [In press].
- Gałka M. & Tobolski K. 2006: Materiały do rozmieszczenia subfossylnych i współczesnych stanowisk kłoci wiechowatej *Cladium mariscus* (L.) Pohl. w Parku Narodowym „Bory Tucholskie”. — In: Banaszak J. & Tobolski K. (eds.), *Park Narodowy Bory Tucholskie u progu nowej dekady*: 71–85. Wydawnictwo Uniwersytetu Kazimierza Wielkiego, Bydgoszcz.
- Gałka M. & Tobolski K. 2011: The history of *Cladium mariscus* (L.) Pohl. in the “Kłocie Ostrowieckie” reserve (Drawieński National Park). Part I. — *Studia Quaternaria* 28: 53–59.
- Gałka M. & Tobolski K. 2012: Palaeoecological studies on the decline of *Cladium mariscus* in NE Poland. — *Annales Botanici Fennici* 49: 305–318.
- Gałka M. & Tobolski K. 2013: Macrofossil evidence of the early Holocene presence of *Picea abies* (Norway spruce) in NE Poland. — *Annales Botanici Fennici* 50: 129–141.
- Gałka M. & Sznel M. 2013: Late Glacial and Early Holocene development of lakes in northeastern Poland in view of plant macrofossil analyses. — *Quaternary International* 292: 124–135.
- Gałka M., Lamentowicz Ł. & Lamentowicz M. 2013d: Palaeoecology of *Sphagnum obtusum* in NE Poland. — *Bryologist* 116: 238–247.
- Gałka M., Tobolski K. & Kończak P. 2012: The Holocene decline of slender naiad (*Najas flexilis* (Willd.) Rostk. & Schmidt) in NE Poland in the light of new palaeobotanical data. — *Acta Palaeobotanica* 52: 127–138.
- Gałka M., Tobolski K., Zawisza E. & Goslar T. 2014: Post-glacial history of vegetation, human activity, and lake-level changes at Jezioro Linówek in northeast Poland, based on multi-proxy data. — *Vegetation History and Archaeobotany* 23: 123–152.
- Gałka M., Miotk-Szpiganowicz G., Goslar T., Jęsko M., Van der Knaap W.O. & Lamentowicz M. 2013a: Palaeohydrology, fires and vegetation succession in the southern Baltic during the last 7500 years reconstructed from a raised bog based on multi-proxy data. — *Palaeogeography Palaeoclimatology Palaeoecology* 370: 209–221.
- Gałka M., Miotk-Szpiganowicz G., Goslar T., Jęsko M., Van der Knaap W.O. & Lamentowicz M. 2013a: Palaeohydrology, fires and vegetation succession in the southern Baltic during the last 7500 years reconstructed from a raised bog based on multi-proxy data. — *Palaeogeography Palaeoclimatology Palaeoecology* 370: 209–221.
- Gałka M., Tobolski K., Górská A., Milecka K., Fiałkiewicz-Kozieł B. & Lamentowicz M. 2013b: Disentangling the drivers for the development of a Baltic bog during the Little Ice Age in northern Poland. — *Quaternary International*. [In press, doi:10.1016/j.quaint.2013.02.026].
- Godwin H. 1975: *The history of the British flora: A factual basis for phytogeography*. — Cambridge University Press, Cambridge.
- Grosse-Brauckmann G. 1974: Über pflanzliche makrofossilen mitteleuropäischer Torfe, II. Weitere Reste (Früchte und Samen, Moose u.a.) und ihre Bestimmungsmöglichkeiten. — *Telma* 4: 51–117.
- Grosse-Brauckmann G. & Streitz B. 1992: Über pflanzliche Makrofossilen mitteleuropäischer Torfe, III. Früchte und Samen, Moose und einige Gewerbe (Fotos von fossilen Pflanzenresten). — *Telma* 22: 53–102.
- Haas J.N. 1994: First identification key charophyte oospore from central Europe. — *European Journal of Phycology* 29: 227–235.
- Hájek M., Horsák M., Hájková P. & Dítě D. 2006: Habitat diversity of central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. — *Perspectives in Plant Ecology, Evolution and Systematics* 8: 97–114.
- Hannon G.E. & Gaillard M.-J. 1997: The plant-macrofossil record of past lake-level changes. — *Journal of Paleolimnology* 18: 15–28.
- Hedenäs L. 2003: The European species of the *Calliergon-Scorpidium-Drepanocladus* complex, including some related or similar species. — *Meylania* 28: 1–116.
- Heikkilä M. & Seppä H. 2003: A 11000 yr palaeotemperature reconstruction from the southern boreal zone in Finland. — *Quaternary Science Review* 22: 541–554.
- Hölzer A. 2010: *Die Torfmoose Südwestdeutschlands und der Nachbargebiete*. — Weissdorn-Verlag Jena, Jena.
- Hölzer A. & Hölzer A. 1994: Studies on the vegetation history of the Lautermeer in the Upper Rhine valley (SW Germany) by means of pollen, macrofossils, and geochemistry. — *Dissertationes Botanicae* 234: 309–336.
- Hugonnot V. 2003: *Rapport sur la présence de Hamatocaulis vernicosus (espèce de l'annexe II de la Directive Habitats) dans le Parc National des Pyrénées, zone éphémère*. Convention no. 2003-15S. — Association Loisirs Botaniques, Parc National des Pyrénées.

- Jabłońska E., Pawlikowski P., Jarzombkowski F., Chormański J., Okruszko T. & Kłosowski S. 2011: Importance of water level dynamics for vegetation patterns in a natural percolation mire (Rospuda fen, NE Poland). — *Hydrobiologia* 674: 105–117.
- Jasnowska J. & Jasnowski M. 1991a: Dynamika rozwojowa roślinności torfotwórczej w rezerwacie „Kłocie Ostrowickie”, Cz. I: Szata roślinna [Development dynamics of peat-forming vegetation in the “Kłocie Ostrowickie” reserve, Part I: Vegetation]. — *Zeszyty Naukowe Akademii Rolniczej w Szczecinie, Rolnictwo* 149: 11–24. [In Polish with English summary].
- Jasnowska J. & Jasnowski M. 1991b: Dynamika rozwojowa roślinności torfotwórczej w rezerwacie „Kłocie Ostrowickie”, Cz. III: Sukcesja roślinności w procesie torfotwórczym, historii złoża i obecnej szacie roślinnej [Development dynamics of peat-forming vegetation in The “Kłocie Ostrowickie” reserve, Part III: Vegetation succession in the peat-forming process, history of the deposit, and current vegetation]. — *Zeszyty Naukowe Akademii Rolniczej w Szczecinie, Rolnictwo* 149: 37–52. [In Polish with English summary].
- Juggins S. 2003: *C2 User guide. Software for ecological and palaeoecological data analysis and visualisation*. — University of Newcastle, Newcastle upon Tyne.
- Karcz, G. 2008: Kłoc wiewiórkowy *Cladium mariscus* (L.) i torfowiska nakredowe jako siedlisko priorytetowe Natura 2000 w Pszczewskim Parku Krajobrazowym [The Great Fen Sedge (*Cladium mariscus*) and mires on chalk substratum as a priority habitat of Natura 2000 in Pszczew Landscape Park]. — *Studia Limnologica et Telmatologica* 2(2): 47–53. [In Polish with English summary].
- Karpińska-Kończak M., Kończak P., Stachowicz-Rybka R. & Obidowicz A. 2013: Palaeobotanical studies on Late Glacial and Holocene vegetation development and transformations of the ‘Wielkie Błoto’ mire near Gołdap (north-eastern Poland). — *Acta Palaeobotanica* 53: 53–67.
- Kłosowski S. 1986/87: *Cladietum marisci* (All. 1922) Zobrist 1935 w północno-wschodniej Polsce na tle warunków siedliskowych [Das *Cladietum marisci* (All. 1922) Zobrist 1935 in nord-östlichen Teil Polens und seine Standortverhältnisse]. — *Fragmenta Floristica et Geobotanica* 31–32: 207–223. [In Polish with German summary].
- Kłosowski S. & Kłosowski G. 2007: *Flora Polski. Rośliny wodne i bagienne*. — Multico Oficyna Wydawnicza, Warszawa.
- Konieczna N. & Kowalewski G. 2009: Sukcesja jeziora Drażynek w świetle analizy osadów i szczątków makroskopowych [Sedimentary and macrofossil records of lake succession in Lake Drażynek]. — *Studia Limnologica et Telmatologica* 3: 61–70. [In Polish with English summary].
- Lamentowicz M., Gałka M., Milecka K., Tobolski K., Lamentowicz Ł., Fiałkiewicz-Kozieł B. & Blaauw M. 2013: A 1300 years multi-proxy, high-resolution record from a rich fen in northern Poland: reconstructing hydrology, land-use and climate change. — *Journal of Quaternary Science* 28: 582–594.
- Landucci F., Gigante G. & Venanzoni R. 2011: An application of the Cocktail method for the classification of the hydrophytic vegetation at Lake Trasimeno (Central Italy). — *Fitosociologia* 48: 3–22.
- Lang G. 1994: *Quartäre Vegetationsgeschichte Europa*. — Gustav Fischer Verlag, Jena, Stuttgart, New York.
- Laine J., Harju P., Timonen T., Laine A., Tuittila E.-S., Minkinen K. & Vasander H. 2011: The intricate beauty of *Sphagnum* mosses — a Finnish guide to identification. — *University of Helsinki Department of Forest Sciences Publications* 39: 1–190..
- Lauterbach S., Brauer A., Andersen N., Danielopol D.L., Dulski P., Hüls M., Milecka K., Namiotko T., Plessen B. von Grafenstein U. & DecLakes participants 2011: Multi-proxy evidence for early to mid-Holocene environmental and climatic changes in northeastern Poland. — *Boreas* 40: 57–72.
- Maj J. & Gałka M. 2012: Wiek i historia rozwoju torfowiska w Pakoślawicach (południowo-zachodnia Opolszczyzna) na podstawie badań paleobotanicznych [The age and development history of biogenic accumulation basin in Pakoślawice (south-western Opole Province) in the light of palaeobotanical research]. — *Przegląd Geologiczny* 60: 110–116. [In Polish with English summary].
- Mauquoy D. & Yeloff D. 2008: Raised peat bog development and possible responses to environmental changes during the mid- to late-Holocene. Can the palaeoecological record be used to predict the nature and response of raised peat bogs to future climate change? — *Biodiversity & Conservation* 17: 2139–2151.
- Miotk-Szpiganiowicz G. & Gałka M. 2009: A new site of Holocene fossil *Trapa natans* L. at the Kaszuby Lakeland (Poland). — *Limnological Review* 9: 165–173.
- Mirek Z., Piękoś-Mirkowa H., Zajac A. & Zajac M. 2002: *Flowering plants and pteridophytes of Poland. A checklist*. — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- Mortensen M.F., Birks H.H., Christensen C., Holm J., Nanna Noe-Nygaard N., Odgaard B., Olsen J. & Rasmussen K.L. 2011: Lateglacial vegetation development in Denmark. New evidence based on macrofossils and pollen from Slotseng, a small-scale site in southern Jutland. — *Quaternary Science Review* 30: 2534–2550.
- Namura-Ochalska A. 2005: Contribution to the characteristic of *Cladium mariscus* (L.) Pohl population in the initial zone of floating mat on an oligo-humotrophic lake in north-eastern Poland. — *Acta Societatis Botanicorum Poloniae* 74: 167–173.
- Ochyra R., Żarnowiec J. & Bednarek-Ochyra H. 2003: *Census catalogue of Polish mosses*. — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- Piękoś-Mirkowa H. & Mirek Z. 2003: *Flora Polski. Atlas roślin chronionych*. — Multico Oficyna Wydawnicza, Warszawa.
- Ralska-Jasiewiczowa M., Latałowa M., Wasylkowa K., Tobolski K., Madeyska E., Wright H.E. & Turner C. (eds.) 2004: *Late Glacial and Holocene history of vegetation in Poland based on isopollen maps*. — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.

- Rinterknecht V.R., Clark P.U., Raisbeck G.M., Yiou F., Bitinas A., Brook E.J., Marks L., Zelas V., Lunkka J.P., Pavlovskaya I.E., Piotrowski J.A. & Raukas A. 2006: The last deglaciation of the southeastern sector of the Scandinavian Ice Sheet. — *Science* 311: 1449–1452.
- Rütiņa L., Ceriņa A., Stankeviča K. & Kļaviņš M. 2012: Character of paleovegetation change in lakes Pilcines, Pilveļu and Padēlis. — *Acta Biologica Universitatis Daugavpiliensis*, Suppl. 3: 94–107.
- Salmina L. 2004: Factors influencing distribution of *Cladium mariscus* in Latvia. — *Annales Botanici Fennici* 41: 367–371.
- Sillasoo Ü., Mauquoy D., Blundell A., Charman D., Blaauw M., Daniell J.R.G., Toms P., Newberry J., Chambers F.M. & Karofeld E. 2007: Peat multi-proxy data from Männikjärve bog as indicators of late Holocene climate changes in Estonia. — *Boreas* 36: 20–37.
- Silvan N., Tuittila E.-S., Vasander H. & Laine J. 2004: *Eriophorum vaginatum* plays a major role in nutrient retention in boreal peatlands. — *Annales Botanici Fennici* 4: 189–199.
- Smith A.J.E. 2004: *The moss flora of Britain and Ireland*, 2nd ed. — Cambridge University Press, Cambridge.
- Stachowicz-Rybka R. & Obidowicz A. 2013: The development and genesis of a small thaw lake filling the Skalska Basin during the Late Glacial and Holocene. — *Acta Palaeobotanica* 53: 69–91.
- Štechová T. & Kučera J. 2007: The requirements of the rare moss, *Hamatocaulis vernicosus* (Calliergonaceae, Musci), in the Czech Republic in relation to vegetation, water chemistry and management. — *Biological Conservation* 135: 443–449.
- Štechová T., Holá E., Manukjanová A. & Mikulášková E. 2010: Distribution and habitat requirements of the moss *Hamatocaulis vernicosus* (Mitt.) Hedenäs in the Bohemian Forest. — *Silva Gabreta* 16: 1–11.
- Sümeği P., Gulyás S. & Jakab G. 2008: Holocene paleoclimatic and paleohydrological changes in Lake Balaton as inferred from a complex quantitative environmental historical study of a lacustrine sequence of the Szigliget embayment. — *Documenta Praehistorica* 25: 33–43.
- Suško U. 2010: Macrophyte flora and vegetation of Lake Riču. — *Acta Biologica Universitatis Daugavpiliensis*, Suppl. 2: 79–96.
- Swindles G.T., Morris P.J., Baird A.J., Blaauw M., Plunkett G. 2012: Ecohydrological feedbacks confound peat-based climate reconstructions. — *Geophysical Research Letters* 39, L11401, doi:10.1029/2012GL051500.
- Szczepanek K. 2001: Late Holocene vegetation history in the Dukla Pass region (Low Beskidy, Carpatians) based on pollen and macrofossil analyses. — *Acta Palaeobotanica* 41: 341–353.
- Święta-Musznicka J., Latałowa M., Szmęja J. & Badura M. 2011: *Salvinia natans* in medieval wetland deposits in Gdańsk, northern Poland: evidence for the early medieval climate warming. — *Journal of Paleolimnology* 45: 369–383.
- Tobolski K. 2000: *Przewodnik do oznaczania torfów i osadów jeziornych*. — Vademecum Geobotanicum, Wydawnictwo Naukowe PWN, Warszawa.
- Tuittila E.-S., Väliaranta M., Laine J. & Korhola A. 2007: Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. — *Journal of Vegetation Science* 18: 891–902.
- Väliaranta M., Korhola A., Seppä H., Tuittila E.-S., Sarmaja-Korjonen K., Laine J. & Alm J. 2007: High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: a quantitative approach. — *Holocene* 17: 1093–1107.
- Väliaranta M., Weckström J., Siitonen S., Seppä H., Alkio J., Juutinen S. & Tuittila E.-S. 2011: Holocene aquatic ecosystem change in the boreal vegetation zone of northern Finland. — *Journal of Paleolimnology* 45: 339–352.
- Van Geel B., Buurman J. & Waterbolk H.T. 1996: Archeological and paleoecological indications of an abrupt climate change in The Netherlands, and evidence for climatological teleconnections around 2650 BP. — *Journal of Quaternary Science* 11: 451–460.
- Velichkevich F.U. & Zastawniak E. 2006: *Atlas of the Pleistocene vascular plant macrofossils of Central and Eastern Europe*, Part 1: *Pteridophytes and monocotyledons*. — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- Velichkevich F.U. & Zastawniak E. 2009: *Atlas of the Pleistocene vascular plant macrofossils of Central and Eastern Europe*, Part 2: *Pteridophytes and monocotyledons*. — W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków.
- Vellak K. & Ingerpuu N. 2012: The state of bryophyte conservation in Estonia. — *Studia Botanica Hungarica* 43: 59–68.
- Wolf P., Rößler S., Schneider T. & Melzer A. 2013: Collecting in situ remote sensing reflectances of submersed macrophytes to build up a spectral library for lake monitoring. — *European Journal of Remote Sensing* 46: 401–416.
- Woś A. 1999: *Klimat Polski*. — Wydawnictwo Naukowe PWN, Warszawa.
- Zalewska-Gałosz J. 2008: *Rodzaj Potamogeton L. w Polsce – taksonomia i rozmieszczenie*. — Instytut Botaniki Uniwersytetu Jagiellońskiego, Kraków.
- Zarzycki K., Trzcińska-Tacik H., Rózański W., Szeląg Z., Wołek J. & Korzeniak U. 2002: *Ecological indicator values of vascular plants of Poland*. — Biodiversity of Poland, Kraków.
- Żurek S. & Kloss M. 2012: Torfowiska zachodniej części Puszczy Rominckiej ze szczególnym uwzględnieniem rezerwatu Mechacz Wielki. — *Studia Limnologica et Telmatologica* 6: 73–86.