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Rozprawa doktorska

**Wykorzystanie walorów bioindykacyjnych roślin
w interpretacjach paleoklimatycznych
i paleoekologicznych**

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Spis treści

Lista publikacji	5
Abstrakt	8
Streszczenie	9
Wstęp.....	10
Cele i metody badań	12
Wyniki badań	14
Podsumowanie i wnioski.....	17
Literatura	20
Kopie artykułów naukowych	25
Deklaracje współautorów	86

Lista artykułów naukowych składających się na rozprawę doktorską

Na rozprawę doktorską składają się trzy artykuły opublikowane w międzynarodowych czasopismach naukowych.

1.Lewandowska A., Niedzielski P., Gałka M. 2019. The late Holocene decline of *Trapa natans* L. in Northern Poland in the light of new palaeobotanical and geochemical data. *Limnological Review* 19(2):77-91, doi.10.2478/limre-2019-0007.

2.Milecka K., Kowalewski G., Lewandowska A., Szczuciński W., Goslar T. 2021. Coexistence of *Lobelia dortmanna* and *Cladium mariscus*, an ecological and paleobotanical study. *Acta Palaeobotanica* 61(2), 195–217, doi.org/10.35535/acpa-2021-0012.

3.Lewandowska A., Milecka K., Niedzielski P., Czerwiński S., Gałka M. 2023. Late Glacial development of lakes and wetland vegetation in a dune area in Central Poland. *Acta Palaeobotanica*, <https://doi.org/10.35535/acpa-2023-0001>.

Pozostałe publikacje współautorskie:

1. Siepak M., **Lewandowska A.**, Sojka M. 2022. Variability in the Chemical Composition of Spring Waters in the Postomia River Catchment (Northwest Poland). *Water*, Vol. 15(1), 157. <https://doi.org/10.3390/w15010157>.

2. Gałka M., Kołaczek P., Sim T.G., Knorr K.H., Niedzielski P., **Lewandowska A.**, Szczurek G. 2021. Palaeoenvironmental conditions and human activity in the vicinity of the Grodzisko fortified settlement (central Europe, Poland) from the late-Neolithic to the Roman period. *Geoarchaeology An International Journal*. <https://doi.org/10.1002/gea.21896>.

3. Gałka M., **Lewandowska A.**, Niedzielski P., Sim T.G., Swindles G.T., Szczurek G. 2020. Late Glacial and early Holocene development of an oxbow lake in Central Europe (Poland) based on plant macrofossil and geochemical data. *The Holocene* vol. 30(I), 178-189. DOI: 10.1177/0959683619875803.

4. Ewertowski W., Latos B., **Lewandowska A.**, Miszczak A., Piniarska D. 2019. Przestrzenne i czasowe zróżnicowanie natężenia hałasu na odcinku strefy brzegowej Morza Bałtyckiego: Biała Góra-Międzyzdroje z uwzględnieniem wpływu morza oraz oddziaływań antropogenicznych (w:) Kostrzewski A., Abramowicz D. (red.). *Miasto i gmina Międzyzdroje – wybrane problemy*. Geoprzestrzeń 2. Bogucki Wydawnictwo Naukowe Poznań. ISBN 978-83-79861-281-8.



Ryc. 1.1 Zróźnicowanie stanowisk badawczych: 1/ torfowisko śródmowowe (fot. Lewandowska 2019), 2/ Bagno Kusowo (fot. Gałka 2017), 3/ Mechacz Wielki (fot. Gałka 2017), 4/jezioro Krzywce Wielkie (opracowanie: Nowacka-Grześkowiak).

Abstract

The first article focuses on identifying the interaction of environmental/climate factors affecting the disappearance of the *Trapa natans* plant (kotewka orzech wodny) in north-eastern Poland in the context of its ecological requirements. The main aim of the research was to determine the interaction of paleoenvironmental factors based on the bioindicative values of plants identified in biogenic sediments in the late glacial and holocene periods. The work focused on tracking climatic changes affecting the evolution of reservoirs in the regional and local context and reconstructing the succession of vegetation based on bioindicating species. Macroremain analyses were used for the research high-resolution and palynological and geochemical analyses of organic sediment cores, supported by radiocarbon dating by accelerator mass spectrometry.

The first article focuses on determining the causes of the disappearance of the *Trapa natans* plant (kotewka orzech wodny) in north-eastern Poland. A high-resolution analysis of plant macroremains was carried out, supported by geochemical analysis. On this basis, the paleoecological conditions of the development of the *T. natans* population were reconstructed and the reasons for its decline in the late Holocene were investigated. In the second article, the research focused on determining the environmental conditions indicated by the appearance of *Lobelia dortmann* (lobelia jeziorna) in it, as well as the causes and time of coexistence with *Cladium mariscus* (kłóc wiechowata), a different species in terms of ecological requirements. In the third article, the initial age of lake development was determined and, based on the presence of bioindicating taxa, local and regional plant succession, as well as environmental conditions at the initial stage of lake and peat bog development, were reconstructed.

Streszczenie

W niniejszej pracy zaprezentowano wyniki badań paleoekologicznych prowadzonych na dziewięciu stanowiskach w północnej i środkowej Polsce. Głównym celem badań było ustalenie interakcji czynników paleośrodowiskowych na podstawie bioindykacyjnych walorów roślin identyfikowanych w osadach biogenicznych w okresie późno glacialnym i holoceniście. W pracy koncentrowano się na prześledzeniu zmian klimatycznych wpływających na ewolucję zbiorników w kontekście regionalnym i lokalnym oraz odtworzeniu sukcesji roślinności w oparciu o bioindykacyjne gatunki. Do badań wykorzystano analizy makroszczątkowe w wysokiej rozdzielczości i analizy palinologiczne i geochemiczne rdzeni osadów organicznych, wsparte datowaniem radiowęglowym metodą akceleratorowej spektrometrii mas.

W artykule pierwszym skoncentrowano się na rozpoznaniu interakcji czynników środowisko/klimat mający wpływ na zanik rośliny *Trapa natans* (kotewka orzech wodny) w północno-wschodniej Polsce, w kontekście jej wymagań ekologicznych. Przeprowadzono analizę makroszczątków roślin w wysokiej rozdzielczości popartą analizą geochemiczną. Na tej podstawie zrekonstruowano paleoekologiczne uwarunkowania rozwoju populacji *T. natans* i zbadano przyczyny jej spadku w późnym holocenie. W artykule drugim badania koncentrowały się na ustaleniu warunków środowiskowych wskazywanych przez pojawienie się w nim *Lobelia dortmanna* (lobelia jeziorna) oraz przyczyn i czasu współistnienia z odmiennym co do wymagań ekologicznych gatunkiem *Cladium mariscus* (kłóć wiechowata). W artykule trzecim określono początkowy wiek rozwoju jezior oraz, na podstawie obecności taksonów bioindykacyjnych, zrekonstruowano lokalną i regionalną sukcesję roślinną, a także warunki środowiskowe w początkowej fazie rozwoju jezior i torfowisk.

Wstęp

Roślinność definiowana jest jako „ogół zbiorowisk roślinnych występujących na danym obszarze, w danym ekosystemie lub w danym okresie geologicznym” (Falińska 1997). „Poszczególne zbiorowiska natomiast, składają się ze specyficznej kompozycji różnych, współwystępujących ze sobą gatunków, które w znacznym stopniu wpływają na środowisko swojego występowania” (Pełechaty, Pronin 2015).

Jeziora słodkowodne dynamicznie reagują na wszelkie zmiany środowiskowe i klimatyczne. Dzięki badaniom nagromadzonych w zbiornikach osadów możliwa jest rekonstrukcja zmian zachodzących w jeziorach i w ich otoczeniu, a także zmian klimatycznych (Szeroczyńska, Zawisza 2007). Na przełomie tysiącleci to klimat był głównym czynnikiem kształtującym zmiany w środowisku naturalnym. Dzięki cyklicznym wahaniom fal globalnego ochłodzenia i ocieplenia przez tysiąclecia kształtowała się powierzchnia Ziemi (Bradley 1999; Dzieduszyńska 2013). Zmiany klimatyczne w okresie późno glacialnym i wczesno holoceniowym zostały szeroko omówione na podstawie licznych badań w zachodniej i środkowej Europie (m.in. Iversen 1973; Haas i in. 1998; Wick 2000, Ralska-Jasiewiczowa i in. 2003; Tuner i in. 2013).

Większość polskich jezior powstała w okresie późnego glaciału, a ich charakter warunkowało położenie geograficzne oraz powierzchnia i głębokość, zaś kształt biocenoz uzależniony był przede wszystkim od wahań temperatury (Choiński 2007; Szeroczyńska, Zawisza 2007). Zdeponowane w osadach makroszczątki roślinne posiadają istotne walory bioindykacyjne jako wskaźniki zmian klimatycznych i hydrologicznych zachodzących w ekosystemie.

Definicję bioindykacji sformułował Górny (1996) wskazując, że „bioindykacja to metoda za pomocą której, dzięki stosowanym żywym organizmom, na różnych poziomach ich organizacji, określa się kierunek i stopień nasilenia zmian w środowisku ich życia”.

Zimny (2006) uważa, że „bioindykacja jest to proces, w którym na podstawie ilościowych i jakościowych zmian jednego obiektu indykatora, określa się stan innego obiektu lub całego systemu ekologicznego, włączając substancje i oddziaływania antropogeniczne”.

Falińska (1997) zaproponowała definicję bioindykatora wskazując, że „są to organizmy roślinne i zwierzęce cechujące się zróżnicowaną wrażliwością i charakterystyczną reakcją na działanie czynników środowiska”. Najczęściej stosuje się gatunki o wąskim zakresie tolerancji

na określone czynniki lub zmiany zachodzące w ich środowisku (Pełechaty, Pronin 2015) i na tej podstawie możliwe jest dokonanie oceny dynamiki rozwoju badanego układu (Sadowska 2012).

Teoretyczne podstawy bioindykacji opierają się na prawie minimum Liebiga stwierdzającego, że rozwój rośliny ograniczony jest przez jeden czynnik siedliskowy (ciepło, światło, klimat, składniki odżywcze), którego jest najmniej w środowisku czyli stanowiącego minimum potrzeb danego organizmu, poza którymi funkcje życiowe ustają. Dla prawidłowego rozwoju rośliny niezbędne jest zachowanie równowagi wszystkich czynników. Według zasady tolerancji sformułowanej przez Shelforda, nadmiar jednego ze składników pokarmowych jak i jego niedostatek skutkuje ograniczeniem wzrostu, sukces populacji jest więc uzależniony od dostępnych czynników limitujących (Sadowska 2012; Biesiadka 2013).

Czynniki wpływające na rozwój populacji roślin są zróżnicowane, zakres tolerancji dla wielu z nich jest szeroki, w przypadku innych ograniczony do konkretnych zasobów, obejmujących fizyko-chemiczne właściwości wody i podłoża (Kłosowski, Kłosowski 2006; Szmeja 2006).

Do bioidentyfikacji środowisk wodnych chętnie wykorzystywane są makrofity. Przydatne są do ustalenia zmian zachodzących w ekosystemie i oddziaływania na inne gatunki, a także z uwagi na ich zdolność do wchłaniania mikroelementów ze środowiska (Rabajczyk, Józwiak 2008). Ilościowa, jakościowa i mieszana charakterystyka bioindykatorów umożliwia ocenę zmiennych środowiskowych. Bioindykatory jakościowe określają ogólny stan jakości środowiska. Są to organizmy wskazujące na określonej wyjątkowej jakości czynniki występujące w środowisku lub na czynniki, które mimo że występują powszechnie, to w danym momencie przyjmują natężenie inne niż w panujących zazwyczaj warunkach (Biesiadka 2013). Bioindykatory ilościowe informują o ilości osobników, biomasy lub zajmowanej powierzchni. Bioindykatory mieszane, łączące cechy obu poprzednich, wskazują na określone zjawisko, a następnie umożliwiają określenie jego natężenia (Nagórska-Socha 2021).

Bioindykacyjne właściwości roślin umożliwiają stwierdzenie wpływu różnych czynników środowiskowych na rodzaj i wielkość populacji zasiedlającej jezioro. Na ich podstawie możliwe jest m.in. ustalenie typu troficznego jeziora (Sadowska 2012). Dla jezior oligotroficznych, ubogich w składniki biogenne charakterystycznymi gatunkami są lobelia jeziorna (*Lobelia dortmanna*), poryblin jeziorny (*Isoëtes lacustris* L.) oraz brzeżyca jednokwiatowa (*Littorella uniflora* L.). Są to bioindykatory ilościowe (Podbielkowski, Tomaszewicz 1996; Kłosowski 2006.). Na typ jeziora eutroficznego wskazuje obecność

zbiorowiska kotewki orzecha wodnego (*Trapa natans*), a także rogatka sztywnego (*Ceratophyllum demersum* L.), klasyfikowanego jako bioindykator ilościowy. Rdestnice (*Potamogeton* L.) tolerują różne typy jezior, zasiedlają również środowisko eutroficzne. Ważnym bioindykatorem są ramienice (*Characeae*) zasiedlające jeziora oligo- i mezotroficzne. Zaliczane są do bioindykatorów mieszanych. Wywłócznik okółkowy (*Myriophyllum verticillatum* L.) występujący w niewielkich grupach lub pojedynczo wskazuje na środowisko mezotroficzne, zaś wywłócznik kłosowy (*Myriophyllum spicatum* L.) tworzy zwarte jednogatunkowe zbiorowiska w zbiornikach eutroficznych. Odnotowuje się też jego obecność w jeziorach mezotroficznych jako gatunek współistniejący z innymi zbiorowiskami roślinności zanurzonej (Podbielkowski, Tomaszewicz 1996; Pelechaty, Pronin 2015).

Roślinność jest bardzo istotnym elementem środowiska. Badając gatunki wskaźnikowe uzyskujemy informacje o zachodzących w ekosystemie powiązaniach i zależnościach mających miejsce w przeszłości.

Cel i metody badań

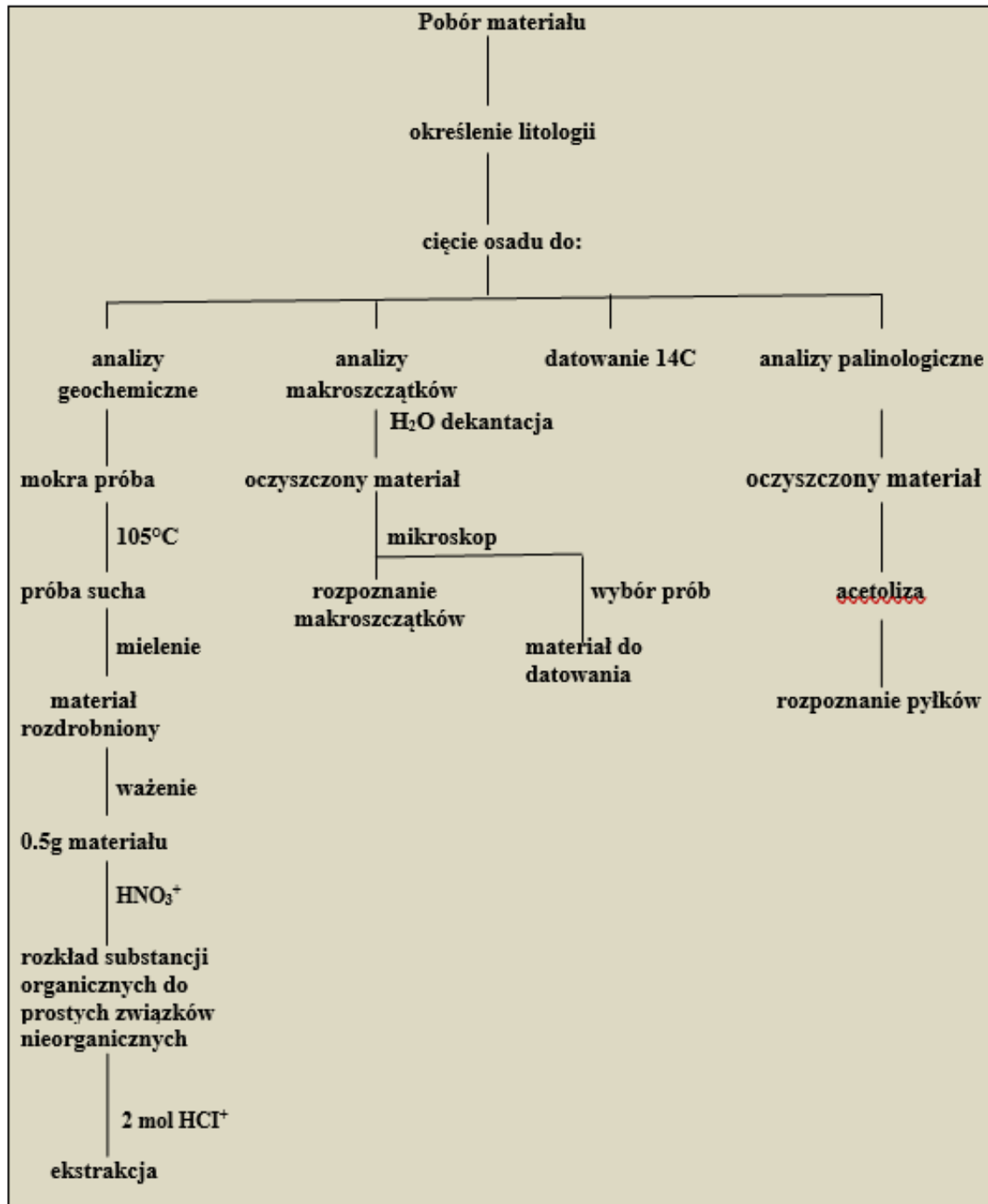
Głównym celem badań było ustalenie interakcji czynników paleośrodowiskowych na podstawie bioindykacyjnych walorów roślin identyfikowanych w osadach biogenicznych w okresie późno glacialnym i holoceniście.

W ramach celu głównego określono cele szczegółowe:

- prześledzenie sukcesji roślinności w oparciu o bioindykacyjne gatunki;
- odtworzenie historii jezior i zmian hydrologicznych na poszczególnych etapach ich rozwoju;
- rekonstrukcja zmian klimatu w kontekście regionalnym i lokalnym;
- rekonstrukcja paleohydrologicznych i geochemicznych zmian wpływających na rozwój gatunkowy flory.

Wyniki badań przedstawione w artykułach stanowiących podstawę rozprawy doktorskiej oparte zostały na badaniach makroszczątków roślinnych w rozdzielczości 1 cm., analizie palinologicznej i geochemicznej oraz datowań radiowęglowych prowadzonych na dziewięciu stanowiskach w północno-wschodniej i środkowej Polsce. Badania uzupełnione zostały (w artykule 2) analizą map sporządzonych przez Nienartowicza (2012) w celu porównania zmian hydrologicznych i użytkowania gruntów na przestrzeni ostatnich 200 lat.

Ryc. 2. Metody badawcze



Wielowskażnikowa strategia badań pozwoliła na zrozumienie ewolucji ekosystemów, skutków cyklicznie zachodzących zmian klimatycznych i określenie elementów wpływających na jego funkcjonowanie w określonej skali czasowej.

Wyniki badań

Artykuł 1.

W artykule przedstawiono charakterystykę dwóch nowych stanowisk *Trapa natans*, położonych w północnej Polsce, obecnie zajmowanych przez bałtyckie torfowiska wysokie Mechacz Wielki (MW) i Bagno Kusowo (BK). Stanowiska te zlokalizowane są poza jej teraźniejszym występowaniem.

W artykule skoncentrowano się na ustaleniu przyczyn zaniku rośliny *Trapa natans* (kotewka orzech wodny) w północno-wschodniej Polsce. *Trapa natans* jest rośliną wodną, ciepłolubną, której wymieranie obserwuje się na wielu stanowiskach w centralnej Europie w ostatnich dziesięcioleciach (Zetter, Ferguson 2001; Piękoś-Mirkowa, Mirek 2003; Olszewski, Markowski 2014; Bryl i in. 2016). Przeprowadzono analizę makroszczątków roślin w wysokiej rozdzielczości popartą analizą geochemiczną. Na tej podstawie zrekonstruowano paleoekologiczne siedliska i zbadano przyczyny spadku populacji *T. natans* w późnym holocenie.

Badania wykazały, że wymieranie populacji *T. natans* nastąpiło ok. 3440–3240 cal. yr BP w Mechaczu Wielkim i ok. 4090–3890 cal. yr BP w Bagnie Kusowo. Przyczyną zaniku *T. natans* w Mechaczu Wielkim mogło być ochłodzenie klimatu pod koniec okresu subborealnego, ponieważ rozwój tego gatunku jest ściśle uzależniony od czynników ekologicznych, zwłaszcza od temperatury.

Obecność roślin szuwarowych, np. *Eleocharis* sp., *Carex rostrata* i *Carex pseudocyperus* dokumentują spłylenie jeziora w Bagnie Kusowo zaś szybkie rozprzestrzenianie się *Nuphar* sp. i *Nymphaea candida* wyeliminowały *T. natans* w Mechaczu Wielkim. Dodatkowo, masowe pojawienie się *Potamogeton natans* przyczyniło się do produkcji dużych ilości biomasy osiadłej na dnie, powodując spłylenie jeziora i rozwój roślinności szuwarowej.

Analizy geochemiczne prowadzone w MW I, BK I i BK II wykazały dominującą rolę Ca^{2+} , Al^{3+} i Fe^{3+} we wszystkich osadach. Najwyższe stężenia Ca^{2+} i Fe^{3+} odnotowano w MW I. Jednak nie było możliwe skorelowanie wysokich wartości tych pierwiastków z rozwojem

T. natans, ponieważ poziom ich koncentracji nie zbiegał się z maksymalnym rozwojem jej populacji.

Analiza paleobotaniczna wskazuje, że oba jeziora były płytkimi, eutroficznymi zbiornikami porośniętymi przez różne makrofity. W obu jeziorach, w okresie swojego występowania, dominował *T. natans* w towarzystwie kilku gatunków *Nymphaea candida*, *Potamogeton obtusifolius*, *Stratiotes aloides* (MW II), *Potamogeton crispus* (BK I) i *Nymphaea alba* (BK II). Odnotowano współwystępowanie *T. natans* z *Nuphar pumila* (BK II), co jest rzadkim zjawiskiem, ponieważ rośliny te mają odmienne wymagania ekologiczne (Piękoś-Mirkowa i Mirek 2003).

Artykuł 2.

W artykule drugim badaniami objęto jezioro Krzywce Wielkie, położone w północnej części Borów Tucholskich (Park Narodowy Bory Tucholskie PNBT) koncentrując się na ustaleniu warunków środowiskowych przeszłych i obecnych, panujących w jeziorze, sprzyjających pojawienia się w nim *Lobelia dortmanna* oraz przyczyn i czasu współistnienia z odmiennym co do wymagań ekologicznych *Cladium mariscus*.

Lobelia dortmanna L. (rodzina *Lobeliaceae*) jest gatunkiem wskaźnikowym jezior oligotroficznych i kwaśnych (Szmeja 1997). Występuje głównie w północno-zachodniej Europie (Sculthorpe 1985; Szmeja 2014a,b). Jej występowanie w Polsce jest zagrożone czynnikami antropogenicznymi i eutrofizacją środowiska. W ostatnich kilkudziesięciu latach odkryto nowe stanowiska *L. dortmanna*, np. w położonym w Borach jeziorze Krzywce Wielkie w Parku Narodowym Bory Tucholskie. Istnienie *L. dortmanna* w tym jeziorze było nieoczekiwane, ponieważ w jeziorze tym stwierdzono obecność *Cladium mariscus*, który ma odmienne wymagania ekologiczne i przez niektórych autorów jest uważany za gatunek typowy dla siedlisk wapiennych (Kłosowski 1986; Brande 2008; Karcz 2008).

Aby wyjaśnić współistnienie obu gatunków w Krzywcach Wielkich przeprowadzono analizę pyłkową osadów organicznych dla czterech pobranych krótkich rdzeni ze strefy litoralnej jeziora i jednego długiego rdzenia głębokowodnego. Dodatkowo przeprowadzono analizę makroszczątków dla wszystkich krótkich rdzeni.

Wyniki badań wykazały występowanie w jeziorze *C. mariscus* od wczesnego holocenu do chwili obecnej. Natomiast obecność pyłku i nasion *L. dortmanna* stwierdzono od początku XX wieku. Rozwój populacji *L. dortmanna* i *Myriophyllum alterniflorum* oraz spadek udziału makrofitów preferujących siedlisko eutroficzne, wskazują na oligotrofizację wody. Analiza

starych map wskazała zmianę zagospodarowania okolic jeziora w drugiej połowie XIX wieku, mianowicie zanik pól uprawnych i wprowadzenie zbiorowisk leśnych. W konsekwencji doprowadziło to do ograniczenia dopływu substancji biogennej do jeziora. Budowa kanału odwadniającego spowodowała obniżenie poziomu wody, poszerzenie strefy litoralnej co ułatwiło rozwój populacji lobelii. Zagospodarowanie okolic jeziora lasem sosnowym oraz utrzymanie torfowisk zaowocowało spadkiem dopływu substancji biogennej i oligotrofizacją jeziora (Tobolski 2003; Szymeja 2014a). Od końca XX wieku taki stan jest wspomagany utworzeniem parku narodowego.

Artykuł 3.

Artykuł prezentuje historię rozwoju sześciu paleo-jezior, obecnie wypełnionych osadami, na obszarze wydmowym w centralnej Polsce. Badania przeprowadzono w oparciu o analizy makroszczątków roślinnych, analizę pyłkową osadów i datowanie radiowęglowe metodą akceleratorowej spektrometrii mas. Celem badań paleoekologicznych było określenie początku funkcjonowania jezior oraz odtworzenie lokalnej i regionalnej sukcesji roślinnej, a także warunków środowiskowych w początkowej fazie rozwoju jezior i torfowisk.

Uzyskane wyniki, wsparte datowaniem ^{14}C wskazują, że zbiorniki powstały między 14686 ± 60 cal. yr BP i 13421 ± 60 cal. yr BP. Ocieplenie klimatu w Bølling doprowadziło do rozwoju gęstszej szaty roślinnej, zahamowania transportu piasku i powstania zbiorników śródwydmowych z akumulacją osadów organicznych (Niewiarowski, Kot 2010). Wyniki analizy paleobotanicznej sugerowały, że zbiorniki były płytkie, oligo-mezotroficzne i zasiedlane przez pionierskie wapniolubne gatunki roślin naczyniowych, takie jak: *Chara* sp., *Hippuris vulgaris*, *Potamogeton natans*, *Potamogeton friesii*, *Potamogeton alpinus*, *Potamogeton filiformis* oraz mchy takie jak: *Pseudocalliergon trifarium*, *Calliergon* sp. i *Calliergonella cordifolium*. Okolice zbiorników porastały rzadkie bory sosnowe połączone z brzozą, co jest charakterystyczne dla cieplejszych faz późnego glacjału. Na terenach otwartych dominowała roślinność psammofilna i stepowa, w tym *Poaceae*, *Artemisia* sp. i *Hippophae rhamnoides*.

Analiza geochemiczna wykazała, że Ca^{2+} i Fe^{3+} występowały w wysokich stężeniach, co mogło mieć wpływ na występowanie taksonów preferujących gleby o wysokiej zawartości Ca^{2+} . Nagromadzenie wapnia w osadach potwierdza, że zbiorniki były zasilane wodami podziemnymi pochodzącymi z postępującej degradacji wiecznej zmarzliny związanej ze

zmianami termicznymi (Rotnicki, Tobolski 1969; Kloss, Wilpiszewska 1994; Balwierz, Goździk, 1997).

Podsumowanie i wnioski

Głównym celem rozprawy doktorskiej było wykazanie wysokich walorów bioindykacyjnych szczątków roślin zdeponowanych w osadach biogenicznych oraz odtworzenie na ich podstawie historii zbiorników w okresie późno glacialnym i holoceńskim. Do badań wybrano grupę roślin o dużej wartości wskaźnikowej, zasiedlające stanowiska o różnym charakterze. Zastosowanie analizy makroszczątków i analizy pyłkowej wspartej badaniami geochemicznymi i datowaniem ^{14}C pozwoliło na dokonanie rekonstrukcji środowiska przyrodniczego zarówno w samych zbiornikach jak i w ich bezpośrednim otoczeniu. Umożliwiły określenie składu gatunkowego zbiorowisk roślinnych, zmian i kierunków w dostawie materii i wahań poziomu wody w jeziorach. Prześlędzono fazy wilgotne i suche skorelowane z okresami ochłodzenia i ocieplenia klimatu. Określenie tych czynników pozwoliło na wyciągnięcie wniosków dotyczących funkcjonowania całych ekosystemów w przeszłości i zagrożeń wynikających z działalności człowieka obecnie.

Badania wykazały, że istnieje związek między cyklicznie zachodzącymi zmianami klimatu (Iversen 1973; Bradley 1999) a właściwościami geochemicznymi badanych jezior co pośrednio i bezpośrednio wpływało na sukcesję roślin (Cedro 2012). Brak dostępu do optymalnych czynników warunkujących przetrwanie (m.in. temperatura, światło, składniki odżywcze) prowadziło do wytworzenia się konkurencji pomiędzy gatunkami (Jusik, Szoszkiewicz 2009). Gatunki eurytopowe posiadające szeroką amplitudę ekologiczną opanowały zbiorniki wypierając rośliny stenotopowe, nie radzące sobie w zmieniających się warunkach (Biesiadka 2013). Niektóre rośliny posiadają jednak duże zdolności adaptacyjne, m.in. współwystępowanie *L. dortmanna* jednocześnie z *C. mariscus* (artykuł 2.) czy *T. natans* z *Nuphar pumila* (artykuł 1), co jest zjawiskiem rzadkim, gdyż rośliny te mają odmienne wymagania ekologiczne.

Rozwój roślinności ekspansywnej, np. masowe pojawienie się *Potamogeton natans* przyczyniło się do powstania dużych ilości biomasy odkładanej na dnie, co powodowało

spłylenie jeziora i rozwój roślinności szuwarowej (np. *Eleocharis* sp., *Carex rostrata* i *Carex pseudocyperus*) i w konsekwencji zarastanie jezior, co zostało opisane w artykułach 1. i 3.

Nie mniej ważne w procesie kształtowania siedlisk są czynniki wynikające z dostaw materii organicznej związanej z rolnictwem wpływające na eutrofizację jezior czy nadmierna eksploatacja zbiornika prowadząca do jego spłylenia. Nie zawsze jednak czynniki antropogeniczne mają niekorzystny wpływ na stan ekosystemu. W artykule 2. przedstawiono taki przykład. Prace hydrotechniczne (budowa rowu melioracyjnego) doprowadziły do zmian w poziomie jeziora, obniżenia stanu wody, co umożliwiło rozwój populacji *L. dortmanna* w XX w. Jest to o tyle ważne, że jest to roślina kwitnąca, której kwiat rozwija się ponad powierzchnią wody gdzie dochodzi do zapylenia przez owady, toteż im większa głębokość wody, tym kwitnienie uboższe (Dąbska, 1965; Moeller, 1978).

Rozwój strefy litoralnej umożliwia zatem rozmnażanie generatywne populacji. Nadto rezygnacja z rolnictwa, zatrzymanie dopływu substancji biogennych i rozwój lasów sosnowych w okolicy jeziora oraz utworzenie PNBT pozwoliły na powstrzymanie eutrofizacji, pojawienie się gatunków o niewielkich wymaganiach troficznych i zachowanie jeziora o charakterze oligotroficznym.

Tab.1. Przykładowe rośliny wskaźnikowe rozpoznane w badanych zbiornikach.

		
 <p style="text-align: center;">seed</p> <p>Lobelia dortmanna</p> <p>jest rośliną wodną, światłolubną, jej kwiat wyrasta ponad powierzchnię wody i jest zapylany przez owady. W głębszej wodzie kwitnienie jest uboższe. Liście zanurzonej części łodygi nieliczne, drobne. Występuje w strefie przybrzeżnej jezior oligotroficznych ubogich w składniki odżywcze, o czystych, stojących wodach, z małą zawartością związków mineralnych .</p> <p>Jest gatunkiem wskaźnikowym dla jezior oligotroficznych.</p>	 <p style="text-align: center;">oospore</p> <p>Chara sp.</p> <p>jest rośliną wodną, światłolubną. Występuje głównie w płytkich, niedużych zbiornikach ale dobrze toleruje zmienny poziom wody. Często jest zbiorowiskiem pionierskim w osadach we wczesnej fazie rozwoju jezior, jego obecność notowana jest często w okresie późnego glacjału. Wykorzystywane są jako bioindykatory, obecność tych gatunków świadczy o środowisku oligo-mezotroficznym.</p>	 <p style="text-align: center;">chestnut</p> <p>Trapa natans</p> <p>jest rośliną wodną zakorzenioną na dnie zbiornika, z liśćmi unoszącymi się nad powierzchnią zaliczaną do gatunków światłolubnych i ciepłolubnych. Rośnie głównie w płytkich, eutroficznych zbiornikach wodnych oraz w wodach stojących i wolno płynących, o dnie gliniasto-mułowym lub mułowym, o odczynie obojętnym lub lekko zasadowym i znacznej zawartości azotu. Jest gatunkiem wskaźnikowym cieplejszych stadiów klimatycznych.</p>

Wyniki badań opisane w prezentowanych publikacjach, potwierdzają wartość bioindykacyjną roślin zdeponowanych w osadach biogenicznych. Stanowią wiarygodne źródło wiedzy w rekonstrukcjach paleoklimatycznych i paleośrodowiskowych.

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**Oryginalne artykuły naukowe wchodzące w skład
rozprawy doktorskiej**

Pierwszy artykuł

Lewandowska A., Niedzielski P., Gałka M. 2019. The late Holocene decline of *Trapa natans* L. in Northern Poland in the light of new palaeobotanical and geochemical data. *Limnological Review* 19, 2: - DOI 10.2478/limre-2019-0007.

The late Holocene decline of *Trapa natans* L. in Northern Poland in the light of new palaeobotanical and geochemical data

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Abstract: *Trapa natans* (water chestnut) is an aquatic, thermophilic plant whose decline has been observed in many localities in central Europe during the last decades. In this paper, we present a description of two new *T. natans* subfossil sites located outside its present northern distribution in Poland. High-resolution analysis of plant macrofossils supported by geochemical analysis were undertaken to reconstruct the palaeoecological habitat and examine the cause of the late Holocene decline of *T. natans* that took place ca. 4000 calibrated years before AD 1950 (cal. yr BP) in a paleolake, presently the Bagno Kusowo bog. Its disappearance was a consequence of terrestrialisation and the development of peatland. In paleolake sediments covered by the peat layer in the Mechacz Wielki bog, *T. natans* macrofossils were found from before ca. 3300 cal. yr BP. The decline of *T. natans* could have resulted from the changes and development of other plant communities where the dominant role was played by *Stratiotes aloides* and *Nymphaea* sp. In our study sites, *T. natans* occurred together with *Potamogeton crispus*, *Potamogeton obtusifolius*, *Nymphaea alba*, and *Nuphar* sp. in eutrophic water dominated by Ca²⁺, Fe²⁺, and Al³⁺ ions. Our palaeobotanical and geochemical results align with the contemporary conditions of *T. natans* habitat.

Key words: water chestnut, plant macrofossils, palaeoecology, geochemical sediment analysis

Introduction

Over the last several thousand years, many aquatic plants have changed their range of distribution in Europe due to climate change and human activity, e.g., the inflow of pollutants into water reservoirs causing changes in the water quality and eutrophication (Piórecki 1980; Bradshaw and McNeilly 1991; Zajac and Zajac 2001; Nienhuis et al. 2002; Berglund et al. 2008; Yang 2008; Martín-Closas 2013; Väliiranta et al. 2015; Marquer et al. 2017). Moreover, for several centuries, with the increase in human migration and the development of communication routes, the number of invasive alien aquatic plant species such as, *Elodea canadensis*, has increased in European freshwater ecosystems, with an ecological and economic impact (Hussner et al. 2017). Autogenous processes such as natural succession and competition among plants are also important factors in aquatic ecosystems (Zetter and Ferguson 2001; Kamiński 2012). All these factors contribute to a decreasing natural macro-

phyte community and a withdrawal of rare and valuable aquatic species (Zetter and Ferguson 2001; Kamiński 2012; Hussner et al. 2017). In many cases, changes in the plant communities are so advanced that it is difficult to determine what is native for some ecosystems. For this reason, it is important to know the time of the appearance and disappearance of various plants and the impact of autogenous and allogenic factors that have triggered changes in aquatic ecosystems. Palaeoecological studies and many methods used in this research, e.g., plant macrofossils, pollen and geochemical analysis, provide an overview of plant cover changes and their migration routes, and they help determine past environmental conditions (Lang 1994; Davidson et al. 2005; Normand et al. 2011; Martín-Closas 2013; Galka et al. 2014; Kołaczek et al. 2017). Apart from this approach, detailed studies of accumulated lake deposits are important sources of professional knowledge that can be applied during management and environmental protection and restoration of highly changed and damaged aquatic ecosystems (Tor-

nadore et al. 2000; Baldantoni et al. 2004; Staniszewski and Zielnica 2006; Herbichowa et al. 2007; Smieja and Ledwoń 2013; Petrović et al. 2016; Ławicki et al. 2017).

At present, many rare aquatic species are endangered or declining and are protected by law. One of these plants is *Trapa natans* L. (water chestnut), for which a decline has been recorded over several decades in Northern and Central Europe (Kaźmierczakowa and Zarzycki 2001; Dżigurski et al. 2012). *T. natans* is an aquatic plant that is considered a thermophilic species, and its distribution area in the past was much larger (Zetter and Ferguson 2001; Piękoś-Mirkowa and Mirek 2003; Olszewski and Markowski 2014; Bryl et al. 2016). In palaeoecological reconstructions *T. natans* plays an important role as an indicator of warmer climatic stages because its fossil presence (nut remains and pollen) is usually recorded during the Holocene Climate Optimum (ca. 9000–5000 cal. yr BP) in Europe (Samuelson 1934; Szafer 1954; Godwin 1975; Flenley et al. 1975; Lang 1994; Korhola and Tikkanen 1997; Magyari et al. 2008; Miotk-Szpi-

ganowicz and Gałka 2009). Presently, *T. natans* occurs in southern, central and eastern Europe, and its range in the north covers northern France and stretches to 57°N in Central Russia (Fig. 1) (Zajac and Zajac 2001; Olszewski and Markowski 2014). In Poland, *T. natans* is found in the upper and central stretches of the Vistula, Oder and San rivers (Piękoś-Mirkowa and Mirek 2003; Jakubowska and Kazuń 2005; Krechowski et al. 2009; Bryl et al. 2016). In the XIX and XX centuries, the northern limit of distribution of *T. natans* moved significantly south in Poland (Piórecki 1980). It is estimated that approximately 180 plant sites disappeared during this period (Piękoś-Mirkowa and Mirek 2003).

T. natans belongs to the *Trapaceae* family. It is an annual aquatic plant, rooted at the bottom of a water body, with leaves floating over the surface (Piórecki 1980; Zetter and Ferguson 2001; Krechowski et al. 2009). The plant predominantly grows in shallow, eutrophic water bodies as well as in stagnant and slow-moving water, usually 120–200 cm deep, with clay-silt or mud bottoms, neutral or slightly alkaline pH, and significant nitrogen content (Kłosowski and Tomaszewicz 1996). *T. natans* is a photophilic and thermophilic species (Piórecki 1980; Kostrakiewicz and Kozak 2009). Because of their high nutrient content, *T. natans* nuts have been used as food by both humans and animals for centuries (Kuneš et al. 2008; Łuczaj 2008; Karg 2013). In folk medicine, it is considered a medicinal plant (Arima et al. 1999; Ali and Javed 2014; Bharthi et al. 2015).

It is typical for *T. natans* to form monospecies communities. It can also be found with other plants, e.g., *Potamogeton* sp., *Ceratophyllum* spp., *Myriophyllum spicatum*, *Nuphar lutea*, *Nymphaea alba*, *Salvinia natans*, *Spirodela polyrrhiza*, and *Lemna* sp. These plants develop rapidly in shallow water and compete with *T. natans*, pushing them into deeper water unfavourable for development above 200 cm (Zetter and Ferguson 2001). However, in smaller and shallower reservoirs, *T. natans* may become the dominant plant (Piórecki 1980; Perzanowska 2012).

In this paper we present the results of high-resolution, contiguous plant macrofossil analysis of four cores and geochemical analysis of three cores taken from paleolakes located in northern Poland with the following aims: (i) to determine the age and reasons for the decline of *T. natans*; and (ii) to reconstruct the palaeoecological habitat of *T. natans*.

Material and methods

Coring and subsampling, chronology of the core

Coring and sampling were undertaken in 2011 using a Russian peat corer (Instorf type), with a 7 cm diameter and 100 cm length. The sediments including

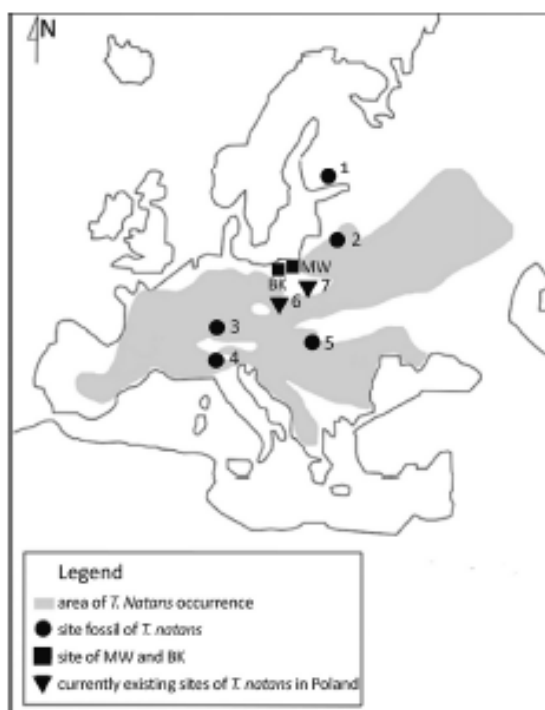


Fig. 1. Setting of the study site and the location of palaeoecological and contemporary records of *T. natans* presence mentioned in the text: BK – Bagno Kusowo (Poland), MW – Mechacz Wielki (Poland). Location of the sites mentioned in the text: 1 – Pyysuo Lake (Finland), 2 – Burtņieks Lake (Latvia), 3 – Federsee Lake (Germany), 4 – Molino Casarotto (Italy), 5 – plain Bereg (Hungary), 6 – Szumirad Lake (Poland), 7 – Opatkowskie Lake (Poland)

Table 1. Radiocarbon dates from Mechacz Wielki (MW) and Bagno Kusowo (BK) bogs (after Lamentowicz et al. 2015; Gałka et al. 2017)

Depth [cm]	Material	Laboratory Nr.	AMS date	Age [cal. yr BP]
MWII 518	10 fruits of <i>Carex pseudocyperus</i> , 2 fruits of <i>Betula pubescens</i>	Poz-44490	1875 ± 35 BP	1885–1720
MWII 475	5 fruits of <i>Carex rostrata</i> , 1 fruit of <i>Carex pseudocyperus</i> , 2 fruits of <i>Betula pubescens</i> , 1 fruits of <i>Sparganium</i>	Poz-44491	2005 ± 30 BP	2038–1883
MWII 571	<i>Picea abies</i> seed wings and periderm	Poz-52364	3125 ± 35 BP	3443–3238
BKII 795	25 fruits of <i>Carex rostrata</i>	Poz-44492	3665 ± 35 BP	4090–3891
BKII 795	<i>Sphagnum</i> stems	Poz-48361	3010 ± 30 BP	3335–3077

peat and gyttja layers were placed in PVC tubes and wrapped in plastic foil. In the laboratory, the sediment was unpacked, cleaned and sliced into 1 cm slices using a scalpel. The core chronology was based on AMS (accelerator mass spectrometry). Radiocarbon dating was carried out at the Poznan Radiocarbon Laboratory. The calibration of the radiocarbon dates and the construction of the age-depth models was performed with OxCal 4.1 software (Bronk-Ramsey 2009) and the IntCal13 curve (Reimer et al. 2013). Five samples from four cores were used to determine the time of deposit accumulation (Lamentowicz et al. 2015; Gałka et al. 2017).

In this paper, we present the results of the analysis of the bottom parts of the cores covering lake deposits. The tests of cores in MW were investigated at a depth of 470 cm to 600 cm and in BK at a depth of 790–900 cm. The results of the detailed multi-proxy palaeoecological studies covering the entire peat layer sand sequence and most of the upper part of the lake sediments in MW as well as the peat layers in BK, have already been published: MW (Gałka et al. 2017) and BK (Lamentowicz et al. 2015).

Study sites

The studied paleolakes are located in northern Poland where the Mechacz Wielki (MW) and Bagno Kusowo (BK) Baltic raised bogs are presently developed (Fig. 1).

The MW bog is situated in north-eastern Poland in the Romnicka Forest (54°19'57"N; 22°26'46"E) (Fig. 1). This bog is situated in a basin with a surface area of 174 ha and is dewatered through a small river, the Czarna Struga. The eastern part of the peat bog is frequently flooded by water from the upper regions and the catchment. The central part is characterized by lower fertility and higher acidification (Zurek and Kloss 2012).

The present-day vegetation covering the peat bog has varied character. The central part (markedly uplifted) is characterized by lower nutrient concentration habitat overgrown with dwarf pine. Communities of *Sphagnum magellanicum*, *S. rubellum* and *S. fuscum* predominate in the peat bog. *Empetrum nigrum* and *Rubus chamaemorus* occur less frequently, and in the hollows, *S. cuspidatum* and *S. balticum* (Gałka et al. 2017).

During summer, the temperature system is influenced by the proximity of the Baltic Sea (average July

temperature of 16–17°C). In winter, the influence of the continental system (meaning January –5°C) is noticeable in MW. The average annual temperature is +6.4°C. The vegetation period is 190 days, and annual rainfall reaches 700 mm. The winters are relatively long and frosty (Woś 1993).

The Baltic raised bog BK, located in north-central Poland (53°48'41"N; 16°34'59"E) (Fig. 1), is part of the Bagno Kusowo nature reserve. *Sphagnum* spp. and *Eriophorum vaginatum* play a dominant role (Lamentowicz et al. 2015). On the edge of the raised bog there is a swampy pine forest of *Vaccinio uliginosi-Pinetum* (Ciaciura and Wilhelm 2005).

The BK bog lies at the intersection of the Atlantic and continental climates. The climate is characterized by a relatively cool summer (average temperature in July 17–18°C) and a rather mild winter (average temperature in January 0–2°C) (Kondracki 2009; Cedro and Sotek 2016). The climatic conditions are temperate and mostly conditioned by the influence of polar and polar-continental air masses (Woś 1993).

The average annual air temperature is approximately +8°C. The growing season is approximately 200 days, and rainfall reaches 700 mm.

Palaeoecological analysis

Plant macrofossils were analysed for 1 cm intervals in contiguous samples in four cores. The number of macroremains was calculated on the basis of the same sample volume, which was 25 cm³. The samples were rinsed under a warm-water current over 0.20 mesh screens. The vascular plant composition was determined on the basis of carpological remains and vegetative fragments (leaves, rootlets, epidermis) using the available identification keys (Tobolski 2000; Velichkevich and Zastawniak 2006, 2008). The macrofossils were identified with a Nikon SMA 800 stereoscopic microscope under 10–200A and an Olympus CX 41 light microscope. A total of 197 samples were analysed. The names of the plant species were adopted following Mirek et al. (2002).

Geochemical analysis

For the determination of selected elements, a 5110 ICP-OES (Agilent, USA) inductively coupled plasma

with optical emission spectrometry was used. For multi-elemental determination, the common conditions were as follows: radio frequency (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, detector CCD (charge coupled device) temperature, -40°C, and signal acquisition time, 5 s for 3 replicates. The detection limits were 0.01 mg kg⁻¹ dry weight (DW) for all elements (as 3-sigma criteria). The uncertainty for the total analytical procedure (including sample preparation) was 20%. The traceability was checked using 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. The recovery (80–120%) was acceptable for most elements. For uncertified elements, recovery with the standard addition method was defined.

Plant macrofossils and geochemical data are presented in diagrams and plotted using C2 software (Juggins 2003).

Results

Lithology and chronology

Fine detritus olive gyttja was analysed in cores MW I, MW II and BK I. The core BK II lake sediment consisted of fine detritus olive gyttja at a depth of 800.5–809.5 cm and fine detritus brown gyttja at 809.5–849.5 cm. Olive gyttja with visible *T. natans* chestnuts occurred at 819.5 cm, 828.5 cm and 838.5 cm.

Based on the radiocarbon dates and the age-depth model, the analysed sediments containing *T. natans* macrofossils accumulated before ca. 3440–3240 cal. yr BP for MW and 4090–3890 cal. yr BP for BK.

Macrofossil analysis

1. Mechacz Wielki

Two zones of local vegetation development at MW I (Fig. 2A) and four zones at MW II were visually delimited (Fig. 2B). The core of MW I was analysed for *T. natans* macroremains (comparison of species of plants MW I with plants in MW II core). In the MW I core, *T. natans* remains were not recorded.

In zone MWI-ma-1 (599.5–586.5 cm), *Nitella* sp. oospores occurred most numerous and the individual remains of *Nuphar* sp. seeds.

The zone MWI-ma-2 (586.5–550.5 cm) was characterized by dominant aquatic plants, e.g., *Potamogeton natans* and *Nymphaea alba*, at a depth from 582.5 to 551.5 cm. At the depth of 576.5–550.5 cm, the remains of trees *Alnus glutinosa*, *Populus tremula*, *Betula pubescens* (maximum of amount), *Pinus sylvestris* and *Picea abies* were also found.

In zone MWII-ma-1 (600–587.5 cm), macroremains of aquatic plants e.g. *T. natans*, *Stratiotes aloides*, *Nitella* sp., *Potamogeton obtusifolius* and *Nymphaea candida* were recorded.

In zone MWII-ma-2 (587.5–550.5 cm), the dominant aquatic plants were *Nitella* sp., *Nymphaea* sp., and *Stratiotes aloides* also occurred.

The third zone MWII-ma-3 (550.5–485 cm) was characterized by the lack of *T. natans* and abundant species of aquatic plants: *Nuphar* sp., *Cicuta virosa*, *Nymphaea candida* and *Potamogeton natans* (numerous).

In zone MWII-ma-4 (485–470 cm), there was a lack of *T. natans* remains and the presence of *Comarum palustre*, *Calliargon cordifolium* (numerous), *Carex pseudocyperus*, *Carex rostrata* (numerous), *Sparganium minimum* and *Scheuchzeria palustris*. The remains of trees were found all over the analysed gyttja sequence: *Pinus sylvestris*, *Picea abies* and *Betula pubescens*.

2. Bagno Kusowo

Three zones at BK I (Fig. 3A) and two zones at BK II (Fig. 3B) in local vegetation development were visually delimited.

In the first zone, BKI-ma-1 (899.5–837.5 cm), aquatic plants such as *T. natans*, *Nuphar* sp., *Nymphaea alba*, *Potamogeton crispus*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, and *Nuphar lutea* were recorded.

The second zone, BKI-ma-2 (837.5–802.5 cm), was characterized by an abundance of *T. natans* and single seeds of *Nymphaea alba*.

In zone BKI-ma-3 (802.5–790.5 cm), macrofossils of *Carex pseudocyperus* (numerous), *Eleocharis palustris*, *Bidens tripartita*, *Scheuchzeria palustris*, *Carex rostrata*, and *Cicuta virosa* were documented.

In the first zone, BKII-ma-1 (850–808.5 cm), *T. natans* was the dominant species. Twenty pieces of chestnuts and 66 pieces of harpoons were found (Fig. 3B). At the same depth, single remains of *Nymphaea alba*, *Nuphar pumila* and *Nuphar* sp. were identified.

In zone BKII-ma-2 (808.5–795 cm), *T. natans* and other aquatic plants disappeared. At a depth of 804.5 cm, the remains of *Andromeda polifolia* seeds were found. The remains of the trees occurred throughout the entire core, most numerous was *Pinus sylvestris*.

Geochemical analyses

1. Mechacz Wielki

Five zones at MW I were visually delimited for present chemical elements (Fig. 4).

In zone MWI-gm-1 (600–577.5 cm), the dominance of Ca²⁺ (14010 mg kg⁻¹), Fe³⁺ (8516 mg kg⁻¹) and Al³⁺ (2074 mg kg⁻¹) was recorded. Other elements had low and medium values. The depth (585.5–551.5 cm) considerably elevated Ca²⁺ concentrations (13289 mg kg⁻¹),

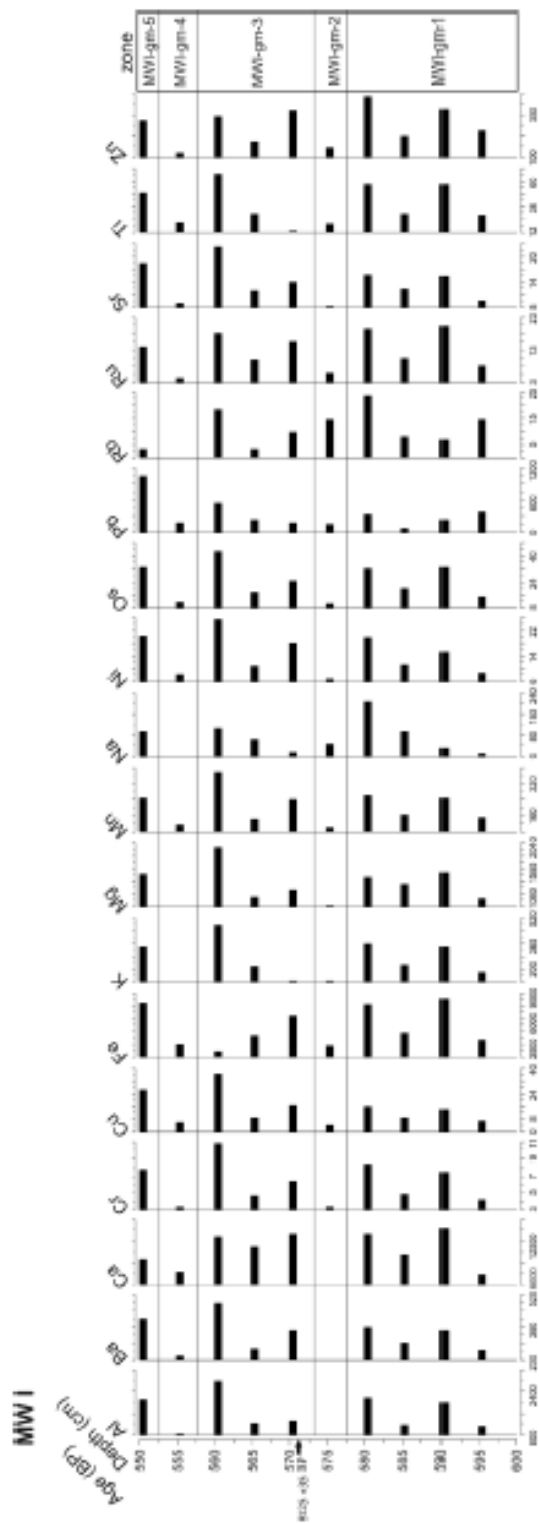


Fig. 4. Results of the geochemical analysis of the core MWI (values at X-axis are given in mg kg⁻¹)

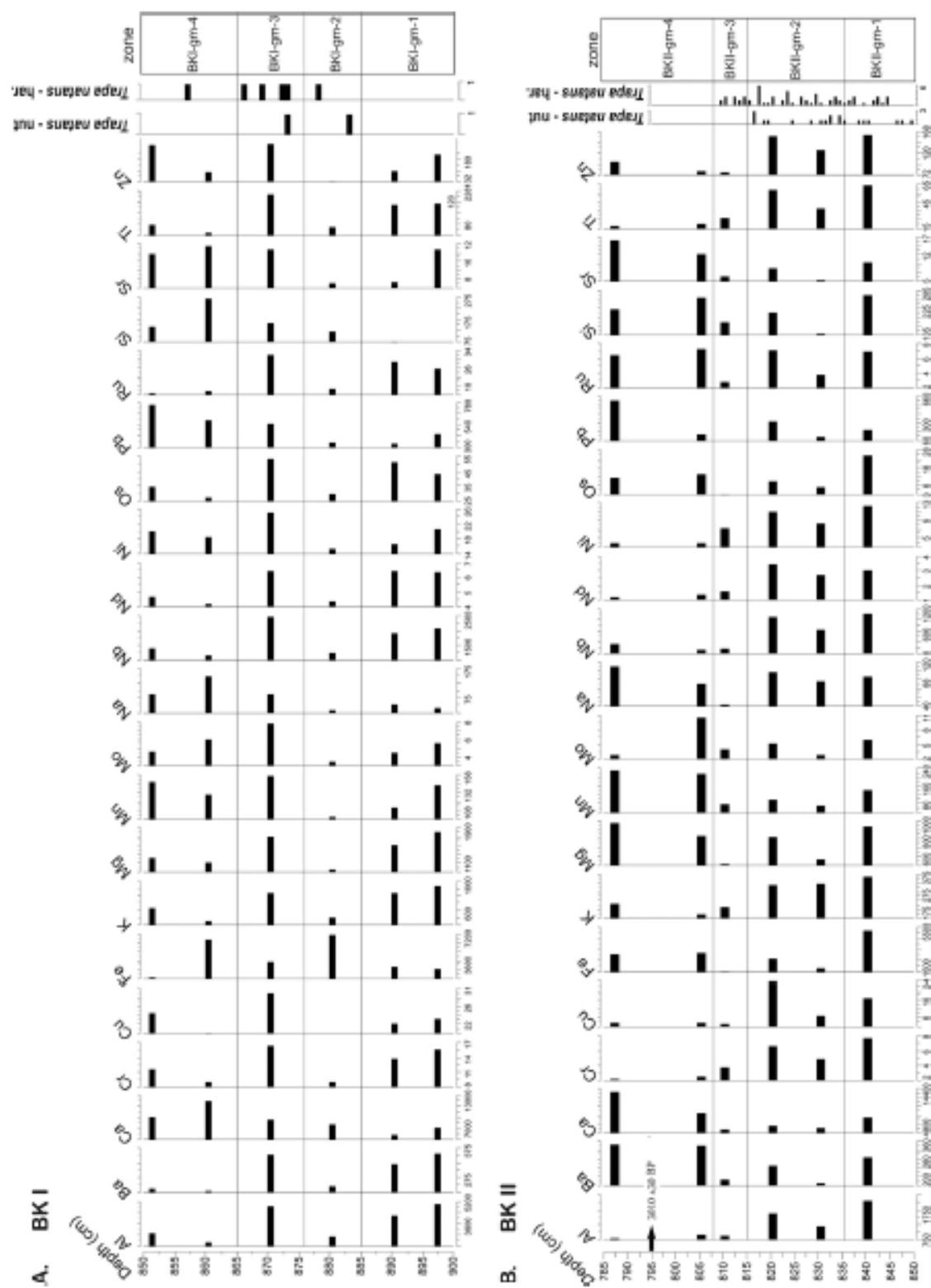


Fig. 5. Results of the geochemical analysis of cores from from Bagno Kusowo bog
A - core BK I., and B - core BK II (values at X-axis are given in mg kg⁻¹)

very high Fe^{3+} (7773 mg kg^{-1}) and Al^{3+} (2228 mg kg^{-1}) levels, and fairly high values of other elements.

The zone MWI-gm-2 (577.5–572.5 cm) had the lowest concentrations, including a layer in which Ca^{2+} and Al^{3+} were not recorded, and the remaining were only trace elements.

In zone MWI-gm-3 (572.5–557.5 cm), the elements were arranged in layers. At a depth of 570.5 cm, they reached the highest concentration values: Ca^{2+} (13201 mg kg^{-1}), Fe^{3+} (6451 mg kg^{-1}), and Al^{3+} (1373 mg kg^{-1}). Slightly lower values were found at 560.5 cm: Ca^{2+} (12921 mg kg^{-1}), Al^{3+} (2835 mg kg^{-1}), and Fe^{3+} (2385 mg kg^{-1}). The highest Mg^{2+} (1982 mg kg^{-1}) and K^+ (486 mg kg^{-1}) levels in the entire core were noted.

Zone MWI-gm-4 (557.5–552.5 cm) was a layer with lower concentration values: Ca^{2+} (8010 mg kg^{-1}), Fe^{3+} 3101 (mg kg^{-1}), a sharp decline of Al^{3+} (918 mg kg^{-1}), and the lowest Mg^{2+} level in the entire core (847 mg kg^{-1}).

Zone MWI-gm-5 (552.5–550 cm) was dominated by Ca^{2+} (9642 mg kg^{-1}), Fe^{3+} (8002 mg kg^{-1}) and Al^{3+} (2147 mg kg^{-1}). Attention was drawn to a high concentration of Pb^{2+} (1075 mg kg^{-1}). This layer was characterized by periodic increases in most elements. Their highest concentration values were recorded at depths of 550.5 cm and 560.5 cm.

It follows that the dominant roles in MW I sediments at all levels were played by Ca^{2+} , Fe^{3+} and Al^{3+} . In the vertical arrangement, Ca^{2+} was 52.42% of all the elements contained in the sediment, followed by the others: Fe^{3+} , 25.42%; Al^{3+} , 7.89%; Mg^{2+} , 6.298%; Pb^{2+} , 1.8%; Ba^{2+} , 1.58%; K^+ , 1.28%; Zn^{2+} , 1.25%; Mn^{2+} , 1.05%; and the remaining elements < 1.00%.

2. Bagno Kusowo

Geochemical analysis for BK I sediments was performed for 21 chemical elements. Four zones at BK I and BK II were visually delimited for elements present (Figs 5A and 5B).

In the first zone, BKI-gm-1 (899.5–885.5 cm), the chemical concentrations in the upper part were low, but in the bottom, these values increased significantly. Ca^{2+} (7370 mg kg^{-1}), Al^{3+} (5170 mg kg^{-1}) and Fe^{3+} (2699 mg kg^{-1}) predominated. There was also increased Mg^{2+} (1827 mg kg^{-1}) and Mn^{2+} (144 mg kg^{-1}) (Fig. 5A).

Zone BKI-gm-2 (885.5–875.5 cm) was characterized by the dominance of Ca^{2+} (7991 mg kg^{-1}), Fe^{3+} (7151 mg kg^{-1}) and Al^{3+} (2734 mg kg^{-1}). The concentration of other elements was low.

In zone BKI-gm-3 (875.5–865.5 cm), the concentrations of all elements were clearly increased in the middle part of the layer, dominated by Ca^{2+} (8813 mg kg^{-1}), Al^{3+} (4913 mg kg^{-1}) and Fe^{3+} (3586 mg kg^{-1}).

In zone BKI-gm-4 (865.5–851.5 cm), very high concentrations of Ca^{2+} (12250 mg kg^{-1}), Fe^{3+} (6602 mg

kg^{-1}), Pb^{2+} (605 mg kg^{-1}), Si^{4+} (273 mg kg^{-1}) and Na^+ (153 mg kg^{-1}) were recorded at a depth of 860.5 cm. In the upper layer, Ca^{2+} (9205 mg kg^{-1}) and Al^{3+} (3024 mg kg^{-1}) predominated. There was a clear reduction in Fe^{3+} concentration (1540 mg kg^{-1}), with relatively high Pb^{2+} (764 mg kg^{-1}) and Mn^{2+} (149 mg kg^{-1}) levels.

Based on our results, the dominant elements in the BK I sediments at all levels were Ca^{2+} , Fe^{3+} and Al^{3+} . In the vertical arrangement, Ca^{2+} represents 44.05% of the composition, followed by all the elements contained in the sediment: Fe^{3+} , 19.84%; Al^{3+} , 14.04%; Nb^{5+} , 6.44%; Mg^{2+} , 6.14%; K^+ , 2.73%; Pb^{2+} , 2.15%; Ba^{2+} , 1.57%; Si^{4+} , 1.01%; and the remaining elements < 1.00%.

In zone BKII-gm-1 (850–835 cm), all the elements reached very high concentrations, especially Ca^{2+} (6768 mg kg^{-1}), Fe^{3+} (5262 mg kg^{-1}), and Al^{3+} (2096 mg kg^{-1}), as well as Nb^{5+} (1120 mg kg^{-1}) and Mg^{2+} (950 mg kg^{-1}) (Fig. 5B).

In zone BKII-gm-2 (835–815 cm) in the lower layer, the elements did not reach high concentrations: Ca^{2+} (3961 mg kg^{-1}), Fe^{3+} (1947 mg kg^{-1}), and Al^{3+} (1231 mg kg^{-1}). In the upper layer at a depth of 820 cm, we found Ca^{2+} (4564 mg kg^{-1}), Fe^{3+} (2714 mg kg^{-1}), and Al^{3+} (1674 mg kg^{-1}). An increased Nb^{5+} (1025 mg kg^{-1}) concentration was noteworthy.

In zone BKII-gm-3 (815–808.5 cm), the elements had small concentration values: Ca^{2+} (3591 mg kg^{-1}), Fe^{3+} (1581 mg kg^{-1}), and Al^{3+} (912 mg kg^{-1}). *T. natans* harpoons were found in this layer.

The fourth zone BKII-gm-4 (808.5–785.5 cm) was characterized by the highest Ca^{2+} concentration. In the bottom part, Ca^{2+} (8152 mg kg^{-1}), Fe^{3+} (3333 mg kg^{-1}) and Mg^{2+} (848 mg kg^{-1}) prevailed. The ceiling was dominated by Ca^{2+} (13622 mg kg^{-1}), Fe^{3+} (3142 mg kg^{-1}), and Mg^{2+} (986 mg kg^{-1}), with a relatively high Pb^{2+} (615 mg kg^{-1}) level. Other elements occurred in small amounts in this zone.

This result indicates a dominant role in the BK II sediments (similarly to BK I) at all levels for Ca^{2+} , Fe^{3+} and Al^{3+} in the vertical system. Ca^{2+} represented 48.85% of all chemical elements in the sediments, followed by the others: Fe^{3+} , 21.60%; Al^{3+} , 9.23%; Ba^{2+} , 1.93%; K^+ , 1.88%; Pb^{2+} , 1.81%; Si^{4+} , 1.56%; Mg^{2+} , 1.03% and the remaining elements < 1.00%.

Discussion

Reasons for the disappearance of *Trapa natans*

1. Climate change

Our palaeoecological studies carried out for MW and BK confirmed the occurrence of *T. natans* in these paleolakes during the Subboreal period. An interesting finding in BK II is the occurrence of *Nuphar pumila* together with *T. natans* macroremains. The com-

mon presence of these two plants is very rare because *Nuphar pumila*, in contrast to *T. natans*, prefers cool and calcium-free waters (Piękoś-Mirkowa and Mirek 2003). A periodic presence of *Nuphar pumila* may indicate short-term climate cooling. However, *T. natans* still occurred and declined later than *Nuphar pumila*. Based on radiocarbon dating, *T. natans* disappeared before 4000 years ago on both sites (MW & BK), in what might be partly linked to the climate cooling documented after ca. 4500 cal. yr BP in this part of Europe (Seppä and Poska 2004; Gałka et al. 2014). Moreover, in the case of MWII, *T. natans* disappeared long before the disappearance of the lake, so one can exclude the cause of lake terrestrialisation.

The fossil presence of *T. natans* has been documented in Holocene deposits in many European countries (e.g., Samuelson 1934; Szafer 1954; Godwin 1975; Lang 1994 and papers cited there). In Germany, *T. natans* fruits have been identified in a few archaeological sites around Lake Federsee. The fossil fruits of *T. natans* were found in sediment at the bottom of the old lake and along its shoreline. *T. natans* macrofossils occurred in the layer accumulated from 6019 to 3000 BP. The presence of charred fruits may indicate that they were used for food (Karg 2013). The charred remains of *T. natans* nuts dated to the beginning of the Subatlantic (approximately 2500 cal. yr BP) were found in Lake Burtnieki in northern Latvia (Ozola et al. 2010). Excavations at a study site in Molino Casarotto in subalpine Italy revealed remnants of water chestnut fruits that date their consumption as far back as ca. 5900 BP (Hummel and Kiviat 2004).

T. natans remains have been found in Holocene deposits in Poland: (e.g., Piórecki 1980; Miotk-Szpiganowicz and Gałka 2009; Krechowski et al. 2009; Olszewski and Markowski 2014; Bryl et al. 2014). *T. natans* came to Poland through the Morawska Gate from southern Europe in the Early Holocene and its distribution was connected to a warmer climate (Kostuch and Misztal 2007; Kowalczyk 2009).

Many authors suggest that the main reason for the disappearance of *T. natans* coincides with cold climatic stages. Deteriorating climatic conditions at the end of the Subboreal and beginning of Subatlantic periods caused the gradual disappearance of water chestnuts from Finland, northern Russia, and the east Baltic (Hummel and Kiviat 2004; Ozola et al. 2010; Thompson 2014). Climate changes and temperature reduction also had an impact on *T. natans* germination. The optimal temperature to start germination is 15–23°C (Cozza et al. 1994; Bryl et al. 2014).

2. Terrestrialisation in the lake

Based on our results at the BK site, we suggest that the decline of *T. natans* is a consequence of peatland de-

velopment. The results of the plant macrofossil analysis proved that *T. natans* was a dominant plant in the paleolake at the BK sites and that its disappearance coincided with the appearance of *Carex pseudocyperus*, *Eleocharis palustris* and *Bidens tripartita* macrofossils. These three plants are common in the transitional zone between lakes and peatland. The development of the peatland with *Sphagnum* species can lead to gradual acidification and further aggravate the *T. natans* growth conditions. This phenomenon led to the disappearance of *Najas flexilis* in the Romincka Forest (Gałka et al. 2012). Currently, these processes are ongoing. Szumirad reservoir (SSW Polska) is decreasing as a result of being filled with sediments deposited by the River Bystrzyzna and as a result of natural succession of vegetation, leading to shallowing and overgrowing (Bryl et al. 2014), and this effect could have influenced the periodic reduction of *T. natans* in this reservoir. In Lake Opatkowskie (central Poland), due to a reduction in water depth and overgrowing, *T. natans* is at risk. *T. natans* coexists with *Stratiotes aloides* and *Spirodela polyrhiza* (Krechowski et al. 2009). Small populations of the water chestnut occur in Lake Kozienickie (central Poland). The main danger for *T. natans* is a strong shallowing of the bay in which the population occurs and competition from other plant species, such as *Ceratophyllum demersum* and *Stratiotes aloides* (Krechowski et al. 2009).

Other authors indicate the natural process of lake disappearance as one reason for *T. natans* decline (Alhonen 1964; Korhola and Tikkanen 1997). For instance, in SW Finland, *T. natans* macroremains were found in deposits accumulated ca. 3500 cal. yr BP in Pyysuo Lake, a small, shallow, eutrophic lake (Korhola and Tikkanen 1997). The lake, rich in vegetation, turned into a peat bog approximately 2500 cal. yr BP as a consequence of overgrowing (Alhonen 1964). In Hungary's Bereg plain, the presence of remains of *T. natans* in sediments in the period from 6900 to approximately 4550 cal. yr BP was recorded (Magyari et al. 2008). The gradual shallowing of the reservoir and development of vegetation such as *Polygonum persicaria* and *Carex pseudocyperus* led to the gradual formation of peatland in the period from 2000 to 1000 cal. yr BP.

3. Competition with other plants

The optimal conditions for water chestnut development are warm, shallow, eutrophic reservoirs (Kowalczyk 2009). Average annual temperatures, excessively low water temperatures and flow rates may cause *T. natans* to retreat and encourage the development of other macrophytes. The reduction in the *T. natans* population is also observed as a consequence of organic sediment deposition in eutrophic reservoirs, in which water exchange takes place every few years. (Piórecki 1980;

Staniszewski and Zielnica 2006). *T. natans* can cover the surface of the water reservoir for several vegetation seasons, hindering the heating water. The plant also contributes to shallowing by the production of large quantities of biomass falling to the bottom (Kowalczyk 2009).

T. natans requires an open water reservoir for development and is not able to compete with heliophytes (Zetter and Ferguson 2001). Adverse species for the development of *T. natans* are *Stratiotes aloides*, *Nymphaea alba*, and *Nuphar* sp., characterized by strong growth and competition with *T. natans* (Kłosowski and Tomaszewicz 1996), pushing it to deeper places (Zetter and Ferguson 2001; Kamiński 2012).

In BK I, at a depth of 883.5–857.5 cm, the remains of a single *T. natans* were found with other water species such as *Nuphar* sp. and *Nymphaea alba* that frequently co-occur and species such as *Potamogeton crispus* and *Ceratophyllum demersum* that compete with *T. natans*.

In the zone from 838.5–801.5 cm, *T. natans* dominated the aquatic flora. Only single remains of *Nymphaea alba* survived. The rapid development of rush plants *Carex pseudocyperus*, *Eleocharis palustris*, and *Carex rostrata* at approximately 3670 cal. yr BP led to a superseding of *T. natans*.

The remains of plants in the sediments of MW II also confirm the coexistence of *T. natans* with other plants such as *Nitella* sp. and *Nymphaea candida*. The decline of *T. natans* falls in the period of *Stratiotes aloides* development, a very expansive thermophilic plant. In the MW I reservoir, we observe the initial development of *Nitella* sp. and *Nuphar* sp. followed by *Nymphaea alba* and *Potamogeton natans* preventing the development of *T. natans*.

4. Other reasons for the *Trapa natans* decline in Poland in the last two centuries

In the vicinity of Szczecin (53°26'17"N; 14°32'32"E), *T. natans* was present until AD 1870, in Gdańsk Pomerania until 1862, and it disappeared from north-eastern Poland after 1872 (Piórecki 1980; Olszewski and Markowski 2014). In the northern part of the country, the vicinity of Szczecin was the last place of *T. natans* occurrence in the 19th century (Olszewski and Markowski 2014). In the same period, *T. natans* also occurred in Gdańsk Pomerania (Olszewski and Markowski 2014). Until 1862, *T. natans* was present in Lake Mirachowskie (54°24'40"N, 17°59'11"E) (Olszewski and Markowski 2014). The work of draining water from the lake led to the disappearance of the species at the above mentioned sites. The presence of *T. natans* in the vicinity of Mirachów is evidence of the species occurrence throughout the northern part of the country until the mid-19th century.

The first information about the occurrence of *T. natans* was in Szumirad reservoir (50°50'14"N; 18°14'59"E) dating back to 1887 (Bryl et al. 2016). In this lake, the species disappearance has been recorded since 1950, despite the fact that its population could have as many as 20 000 rosettes. In the years 1976–1977, there were no more rosettes. The reason for the disappearance of *T. natans* was the shallowing and excessive exploitation of the reservoir by a local, now non-existent recreational centre (Bryl et al. 2014). A catastrophic consequence of the disappearance of *T. natans* in some lakes is also related to the herbivorous white amur fish introduced in the 20th century (Piórecki 1980; Piękoś-Mirkowa and Mirek 2003; Walusiak et al. 2011; Bryl et al. 2014).

Floods can wash off *T. natans* fruits located at the bottom of the research area and remove them to an area not very favourable for the development of the plant (Kamiński 2012).

Water chestnut does not tolerate salinity and does not exist in reservoirs where the sodium chloride concentration exceeds 0.1%. Changes in nutrient content, dehumidification of wetlands and dredging of reservoirs contribute to its extinction. From the analysed literature, *T. natans* has a high tendency to fluctuate. This observation confirms the extinction of many stations in the San River basin and the Upper Oder, Vistula and the Lusatian Neisse. In the 19th century, *T. natans* survived in the vicinity of Gdansk and Greater Poland. Between 1970 and 1980, 82% of the *T. natans* known in Poland disappeared.

Geochemical parameters of the fossil habitat of *Trapa natans*

T. natans is a plant that requires a specific habitat and chemical conditions (Kłosowski and Tomaszewicz 1996). Ecological studies indicate that optimal development occurs in shallow water with high organic matter content that is rich in Ca²⁺, total Fe²⁺, and PO₄³⁻ and low in NH₄⁺ and Mg²⁺ concentrations (Kłosowski and Tomaszewicz 1996; Szańkowski and Kłosowski 1999).

Geochemical analysis conducted in MW I, BK I and BK II show the dominant role of Ca²⁺, Al³⁺ and Fe²⁺ in all sediments. In MW I, the highest concentrations of Ca²⁺ and Fe²⁺ were recorded, preventing *T. natans* development.

In BK I sediments, Ca²⁺, Fe²⁺ and Al³⁺ sustained a high level. There was also significantly elevated Mg²⁺ and Na⁺ content. Slight traces of *T. natans* were found in layers with a reduced level of these elements at a depth of 883.5–855.5 cm. *Nuphar* sp. *Nymphaea alba* and *Potamogeton crispus* were better adapted to the environmental changes (Kłosowski and Tomaszewicz 1996). Rapid development of *T. natans* took place at depth 836.5–802.5 cm, dominating the vegetation and

almost completely displacing other aquatic species. BK II has similar geochemical parameters to those of BK I. *T. natans* occurred in the layer with the lowest levels of Ca^{2+} , Mg^{2+} and Na^+ without high Al^{3+} and K^+ . In relation to MW I and BK I, the lowest level was also reached by Fe^{2+} . *T. natans* was accompanied by only a few *Nymphaea alba* and *Nuphar* sp. having a wider ecological amplitude of occurrence (Kłosowski and Tomaszewicz 1996).

Present ecological studies also confirm that *T. natans* populations are well developed in areas with elevated calcium levels (Piórecki 1980; Kłosowski and Tomaszewicz 1996; Szańkowski and Kłosowski 1999; Piękoś-Mirkowa and Mirek 2003). Our research confirms the dominance of calcium in sediments, although its maximum incidence does not coincide with the maximum development of *T. natans*. In the investigated sediments, Zn^{2+} occurs at different levels. In BK II, Zn^{2+} is predominantly located at greater depths as well as in MW I and BK I in higher layers. A very low content of heavy metals such as Cr^{2+} , Ni^{2+} , and Cu^{2+} indicates that anthropogenic factors did not play a role in the analysed lakes. This result, however, leads to a high level of Pb^{2+} , reaching 1050 mg kg^{-1} in MW I and 780 mg kg^{-1} in BK I. Pb^{2+} is a heavy metal, poorly migrating, therefore its natural content in the soil reflects its content in content in host rocks. *T. natans* in the BK II core occurs at depths of 808.5–849.5 cm. The highest values of practically all the elements were observed in this core; however, they cannot be correlated with the occurrence of *T. natans* because the layers with elevated values are beyond the reach of *T. natans* macroremains (805.5 cm).

Conclusions

Our palaeoecological studies (plant macrofossils and geochemical analysis) allowed us to determine the age and causes of *T. natans* decline as well as to reconstruct its subfossil habitat in two formed lakes in northern Poland presently occupied by the Baltic raised bogs Mechacz Wielki (MW) and Bagno Kusowo (BK).

1. The decline of *T. natans* took place approximately 3440–3240 cal. yr BP at MW and approximately 4090–3890 cal. yr BP at BK.
2. The climate cooling at the end of the Subboreal period could be the reason for the disappearance of *T. natans* at MW.
3. In BK I and MW, lake transformation took place. The presence of rush plants, e.g., *Eleocharis* sp., *Carex rostrata*, and *Carex pseudocyperus*, documents the shallowing of the lake at Bagno Kusowo. A rapid spread of *Nuphar* sp. and *Nymphaea candida* eliminated *T. natans* in MW. Additionally, the

massive appearance of *Potamogeton natans* contributed to the production of large amounts of biomass deposited to the bottom, resulting in a shallowing of the lake and the development of rush vegetation.

4. Geochemical analyses conducted in MW I, BK I and BK II showed the dominant role of Ca^{2+} , Al^{3+} and Fe^{2+} in all sediments. The highest concentrations of Ca^{2+} and Fe^{2+} were recorded in MW I. However, it is not possible to correlate the high values of these chemical elements with the development of *T. natans* because the level of their concentration does not coincide with its maximum development. In BK II, *T. natans* reached the peak of development at a Ca^{2+} concentration of $4000\text{--}5000 \text{ mg kg}^{-1}$. At a very large Ca^{2+} concentration, *T. natans* did not occur as it did in the case of high Fe^{2+} , Al^{3+} and Mg^{2+} , and, what is interesting, almost all the aquatic plants died.
5. Palaeobotanical analysis indicates that both lakes were shallow, eutrophic reservoirs overgrown by various macrophytes. *T. natans* was the dominant plant in both lakes during its prevalence accompanied by a few *Nymphaea candida*, *Potamogeton obtusifolius*, *Stratiotes aloides* (MW II), *Potamogeton crispus* (BK I) and *Nymphaea alba* (BK II). The common occurrence of *T. natans* with *Nuphar pumila* (BK II) was also recorded, which is a rare phenomenon because these plants have different ecological requirements.

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

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

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

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

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

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

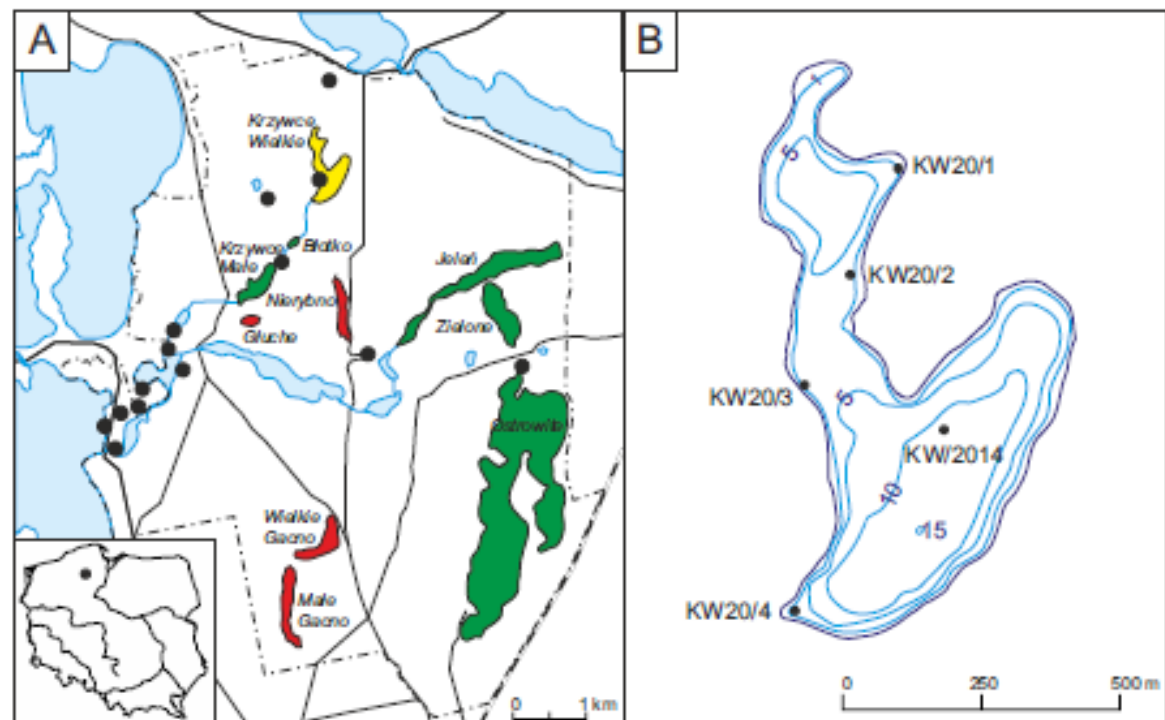


Fig. 1. Study area. A – location of lake Krzywec Wielkie in BTNP. Inset map shows location in Poland. Dot-dashed line – border of BTNP, black circle – fossil site of *Cladium mariscus* according to Galica and Tobolski (2006), yellow lake – sites of *Lobelia dortmanna* and *C. mariscus*, red lakes – sites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

STUDY AREA

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

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

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

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

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

METHODS

FIELD WORK AND SAMPLING

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

CHRONOLOGY

¹⁴C dating

Fifteen organic samples, each taken at 20 cm intervals in 1 cm slices from the lower part of the core KW20/4, were transported to Poznań Radiocarbon Laboratory for ¹⁴C dating using the AMS technique (Goslar et al., 2004). Most of the samples were macrofossils of terrestrial plants (*Pinus* needles, bud scales and *Betula* fruits, bud scales), but sediments from the deepest part contained few terrestrial macrofossils, and hence bulk sediment sample was taken from this area.

²¹⁰Pb and ¹³⁷Cs dating

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

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

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

POLLEN ANALYSIS

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

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

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

MACROFOSSIL ANALYSIS

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

RESULTS

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

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

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

Name of core	Longitude	Latitude
KW/2014	17°33'40.16"E	53°50'21.55"N
KW20/1	17°33'35.86"E	53°50'37.26"N
KW20/2	17°33'30.85"E	53°50'30.91"N
KW20/3	17°33'26.22"E	53°50'24.29"N
KW20/4	17°33'25.16"E	53°50'10.55"N

¹⁴C DATING

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

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

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

Depth [cm]	Material	Lab no. Poz.	Age ¹⁴ C (BP)	Modeled date (68.2% conf. interval, cal BP)
314	Plant remains	126617	2415±35	2490–2375
334	Plant remains	126618	2570±40	2760–2705
354	Plant remains	126619	2675±35	3060–2960
374	Plant remains	126621	3055±30	3340–3230
394	Plant remains	126622	3385±35	3680–3575
414	Plant remains	126623	3565±35	3920–3835
434	Plant remains	126624	3770±35	4220–4090
456	Plant remains	126625	3925±30	4420–4310
476	Plant remains	126626	4165±35	4825–4650
494	Plant remains	126627	4520±40	5175–5055
514	Plant remains	126628	4610±35	5450–5315
538	Plant remains	126629	5570±40	6385–6310
562	Plant remains	126631	6480±35	7400–7335
586	Plant remains	126632	9090±50	10270–10200
620	Bulk sediment	126633	11110±60	13095–12935

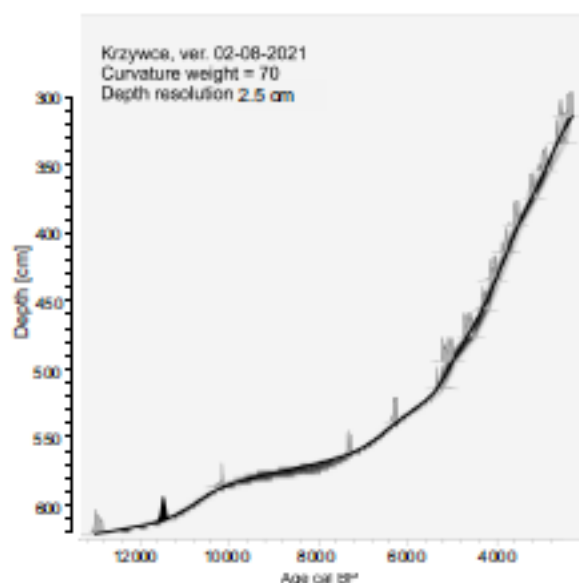


Fig. 2. Age–depth model of the lower part of profile KW/2014. Gray silhouettes represent calibrated dates of the samples analyzed with ¹⁴C. Black silhouette represents the date of the beginning of Holocene

²¹⁰Pb AND ¹³⁷Cs DATING

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

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

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

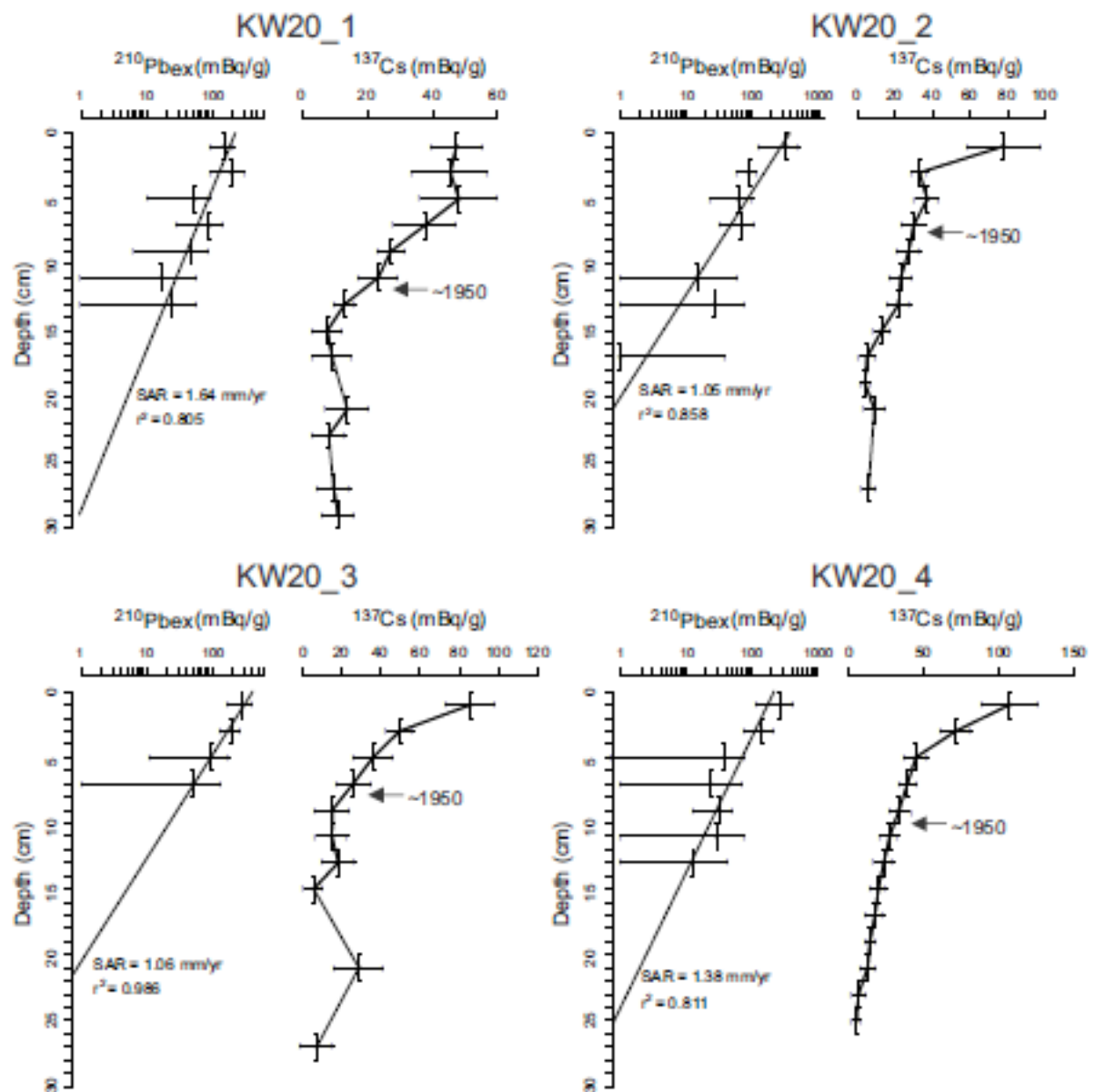


Fig. 3. Short-lived radionuclide ($^{210}\text{Pb}_{\text{ex}}$ and ^{137}Cs) measurements in cores KW20_1, KW20_2, KW20_3 and KW20_4. $^{210}\text{Pb}_{\text{ex}}$ activities are presented as semilogarithmic plots, the trend line was used for sediment accumulation rate (SAR) calculation using constant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

^{210}Pb -based age model is generally accurate. The comparison of the CFCS and CIC models with ^{137}Cs profiles is presented in supplementary files (Supplementary file 2³). Since the cores show the evidence of sediment mixing, the sediment accumulation rates and consequently the calculated ages indicate approximate values only.

POLLEN AND MACROFOSSIL ANALYSES

Core KW/2014

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

³ Supplementary file 2. Age scale to the CFCS and CIC models KW20_1–KW20_4

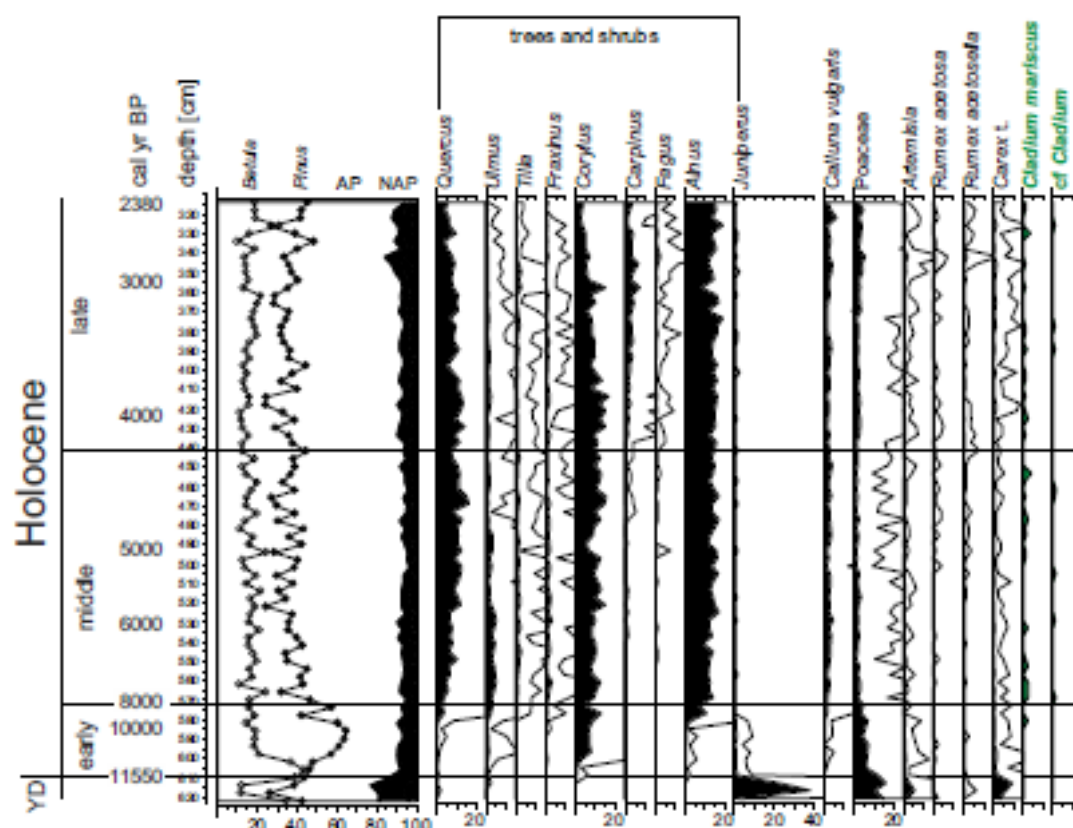


Fig. 4. Pollen diagram of core KW/2014, selected percentage curves (in black). Enaggarations $\times 10$ are given for better observation of rare types. Division of the Holocene after Walker et al. (2012)

for the reconstruction of the local environment are presented.

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

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

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

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

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

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

Littoral cores (KW20/1–KW20/4)

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

KW20/1

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

are common inhabitants of low reed bed communities.

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

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

KW20/2

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

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

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

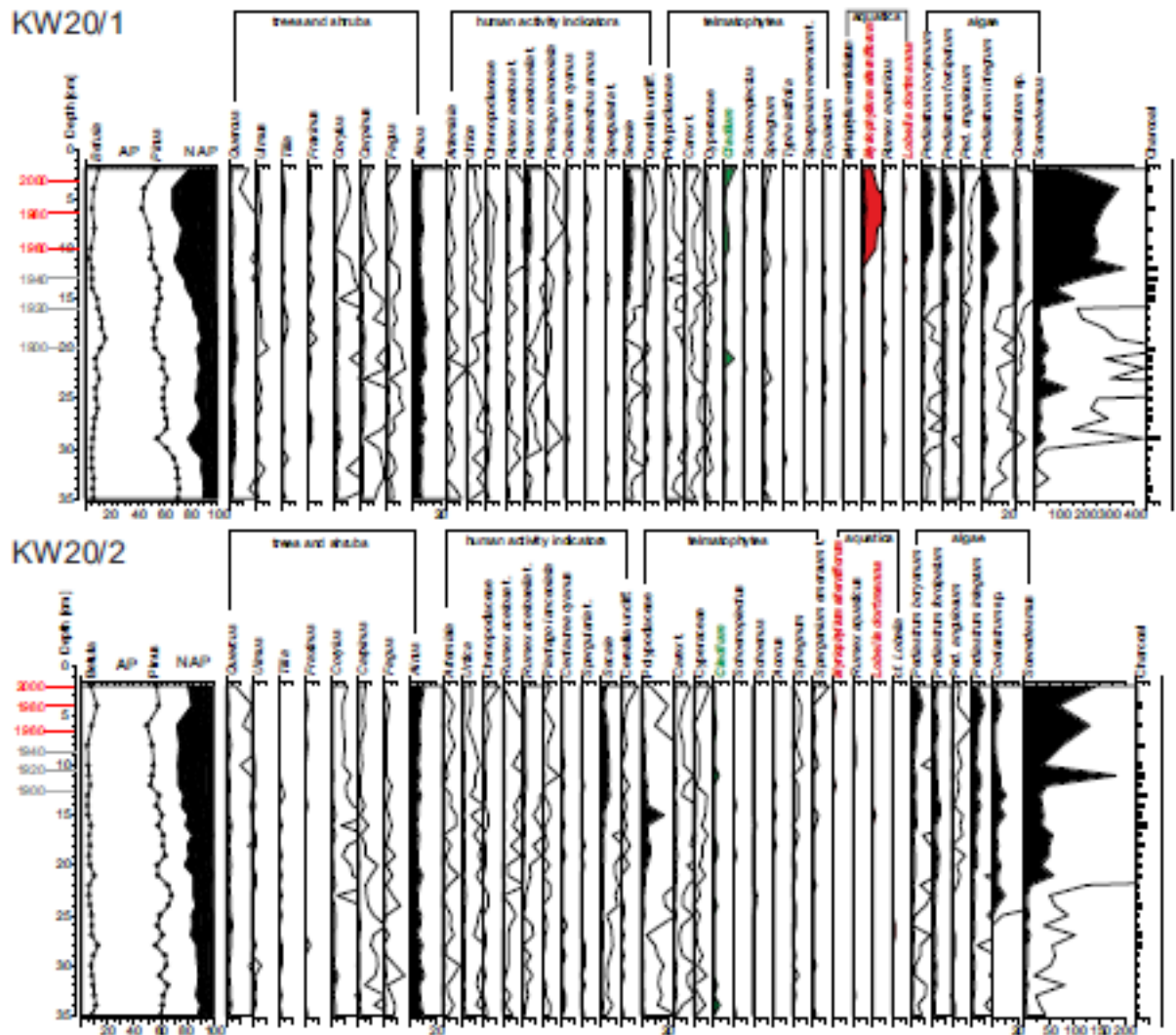


Fig. 5A. Pollen diagrams of cores KW20/1 – KW20/2. Selected percentage curves of trees and shrubs, human indicators and pollen of local plant communities. Curve units – 10% unless otherwise stated. Red dates – dates derived from the ^{210}Pb -based age model, gray dates – linear approximation of the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

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

KW20/3

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

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

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

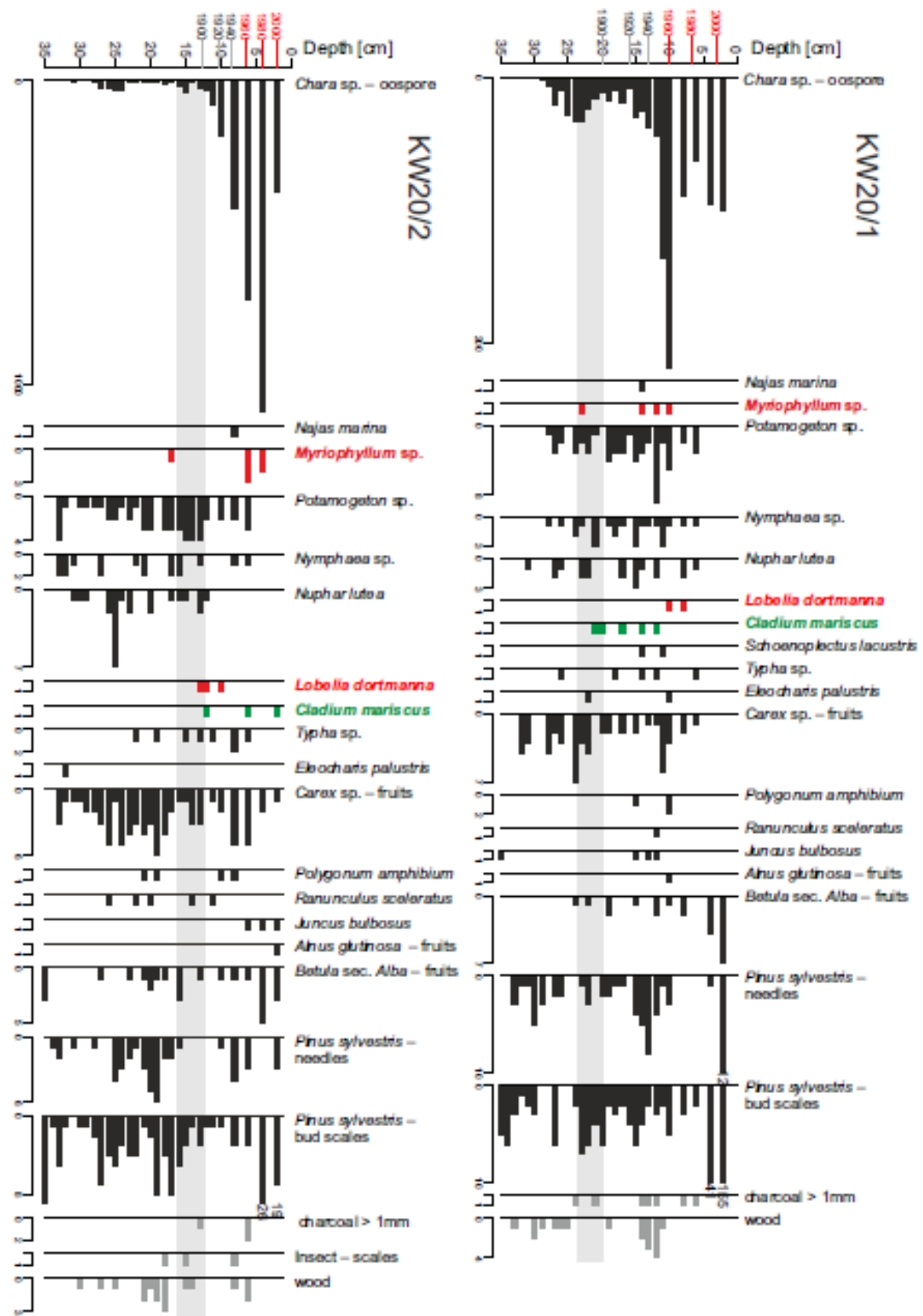


Fig. 6A. Macrofossil diagrams of cores KW20/1–KW20/2. Red dates – ^{210}Pb -based age dates derived from the model, gray dates – linear approximation of the model assuming constant accumulation rate. Scales represent numbers in sample volume. Out of scale values are given next to the bars. Gray bar indicates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

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

DISCUSSION

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

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

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

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

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

DISTRIBUTION AND CONSERVATION IN POLAND AND EUROPE

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

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

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

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

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

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

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

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

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

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

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

LAND-USE, HYDROLOGICAL AND TROPHY CHANGES

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

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

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

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

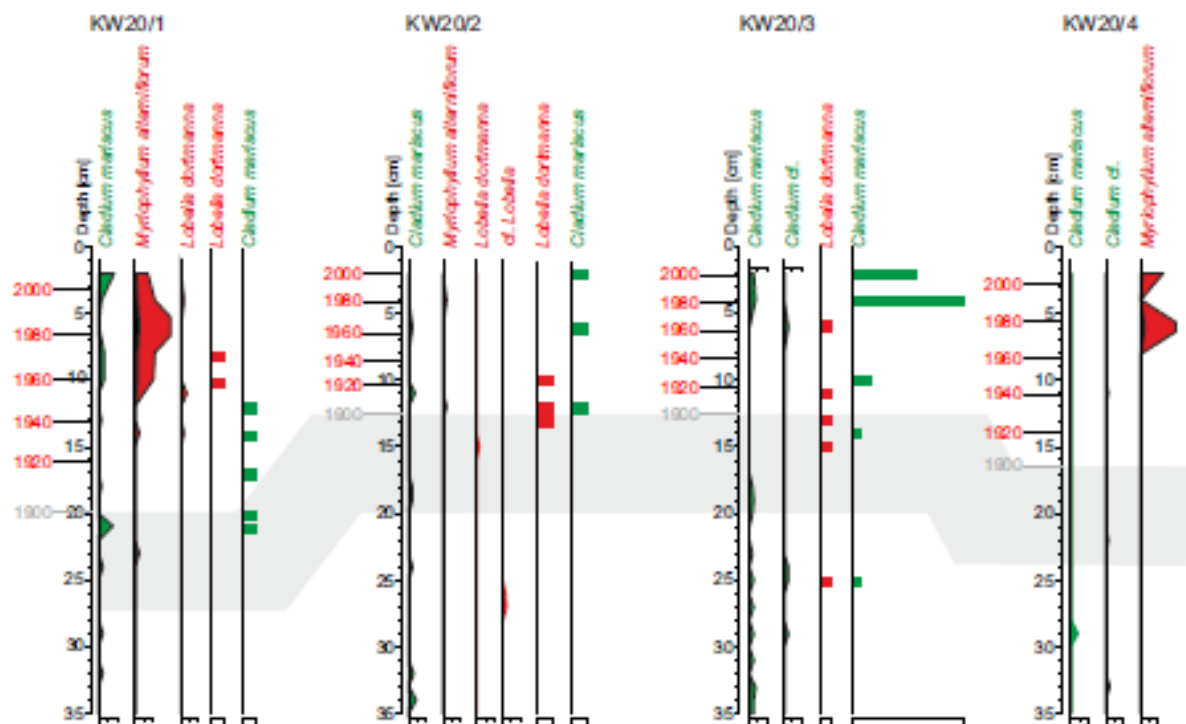


Fig. 7. Summary diagram of the content of pollen and macrofossils of the indicative species discussed in the article. For explanations of scale, dates and gray bar see Figs 4–6

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

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

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

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

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

CONCLUSION

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

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

further limited the potential eutrophication of habitats.

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

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

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Trzeci artykuł

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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. Wasylikowa, 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 (Wasylikowa, 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

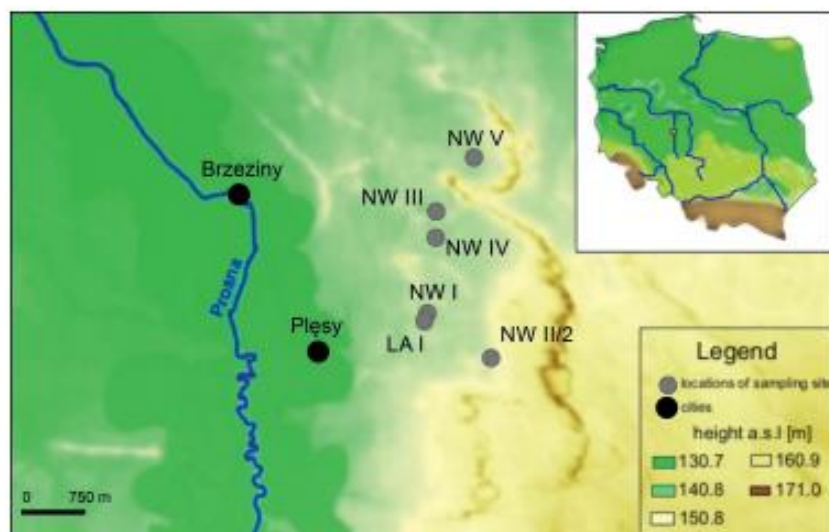


Figure 1. Location of the study sites

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

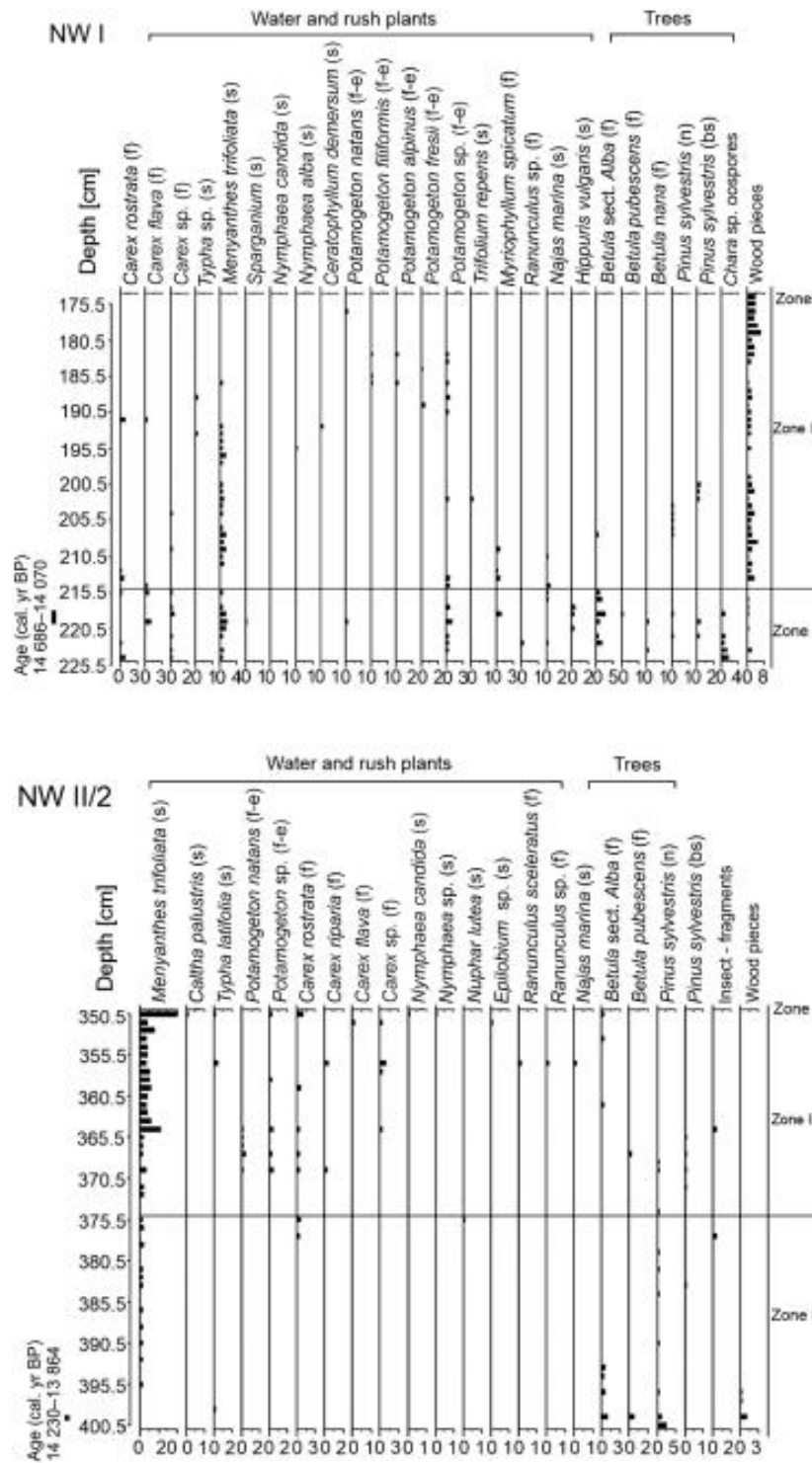


Figure 2. Macrofossil diagrams of NW I and NW II/2 cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

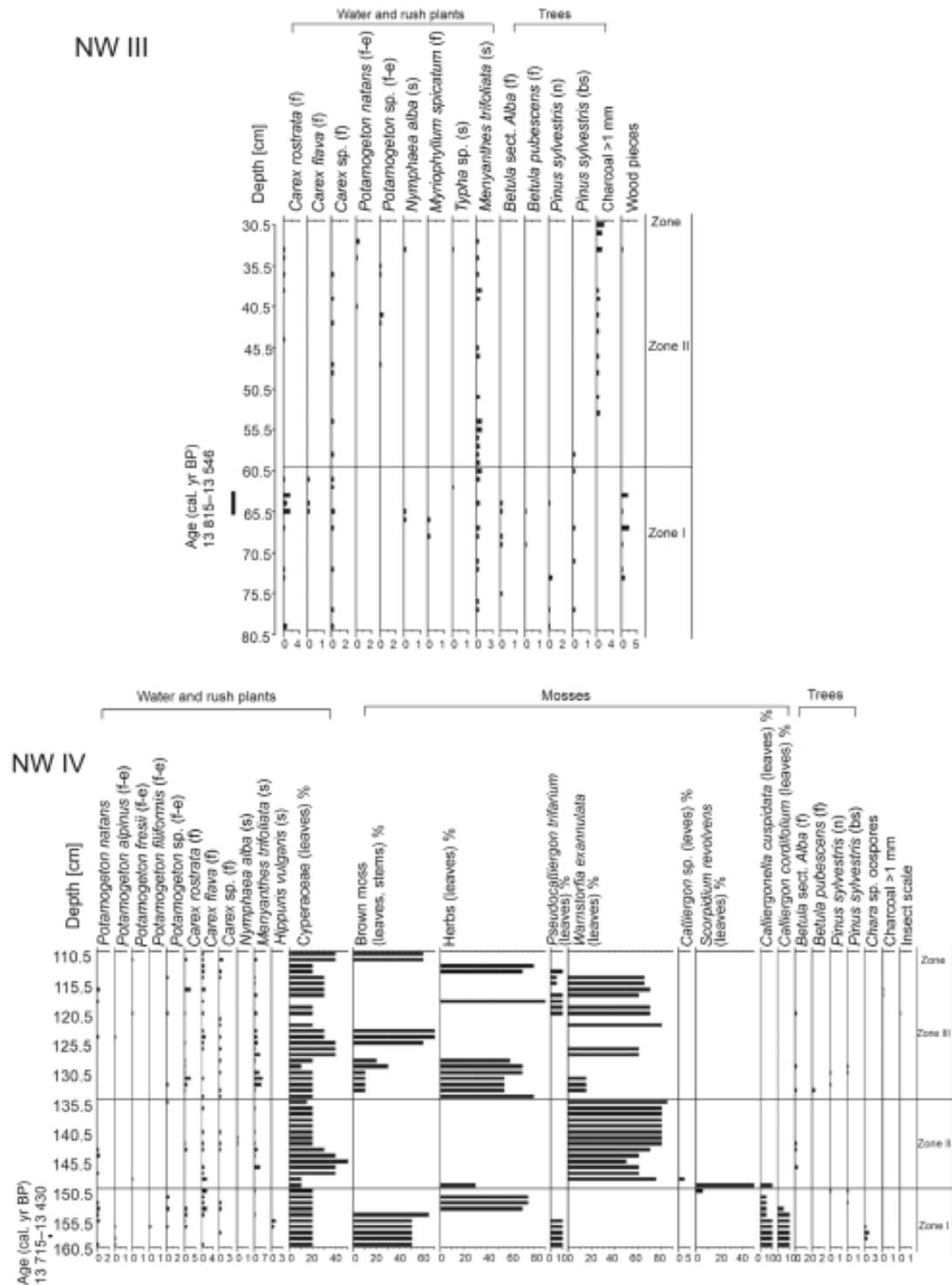


Figure 3. Macrofossil diagrams of NW III and NW IV cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

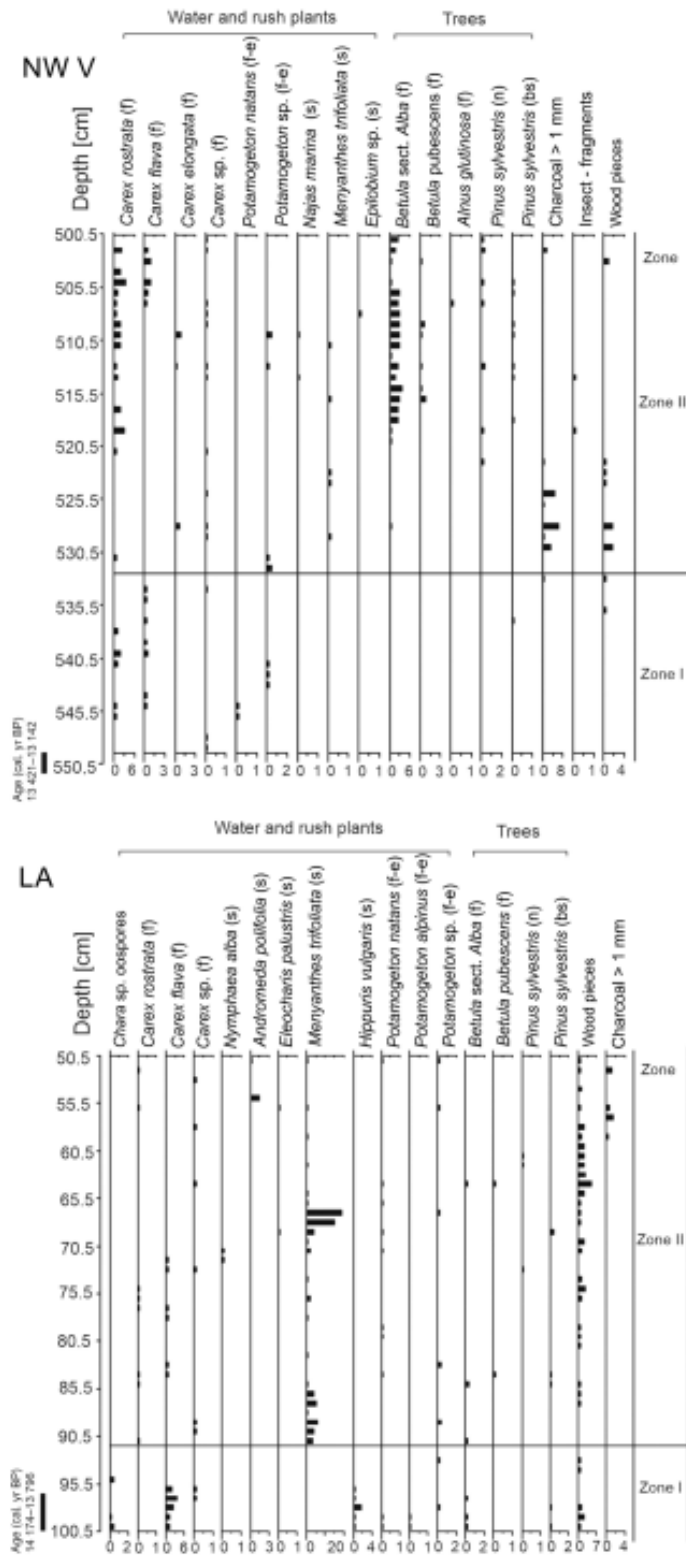


Figure 4. Macrofossil diagrams of NW V and LA I cores (f – fruits, s – seeds, f-e – fruits (endocarps), n – needles, bs – bud scales)

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-55A *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-55A 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-55A *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*.

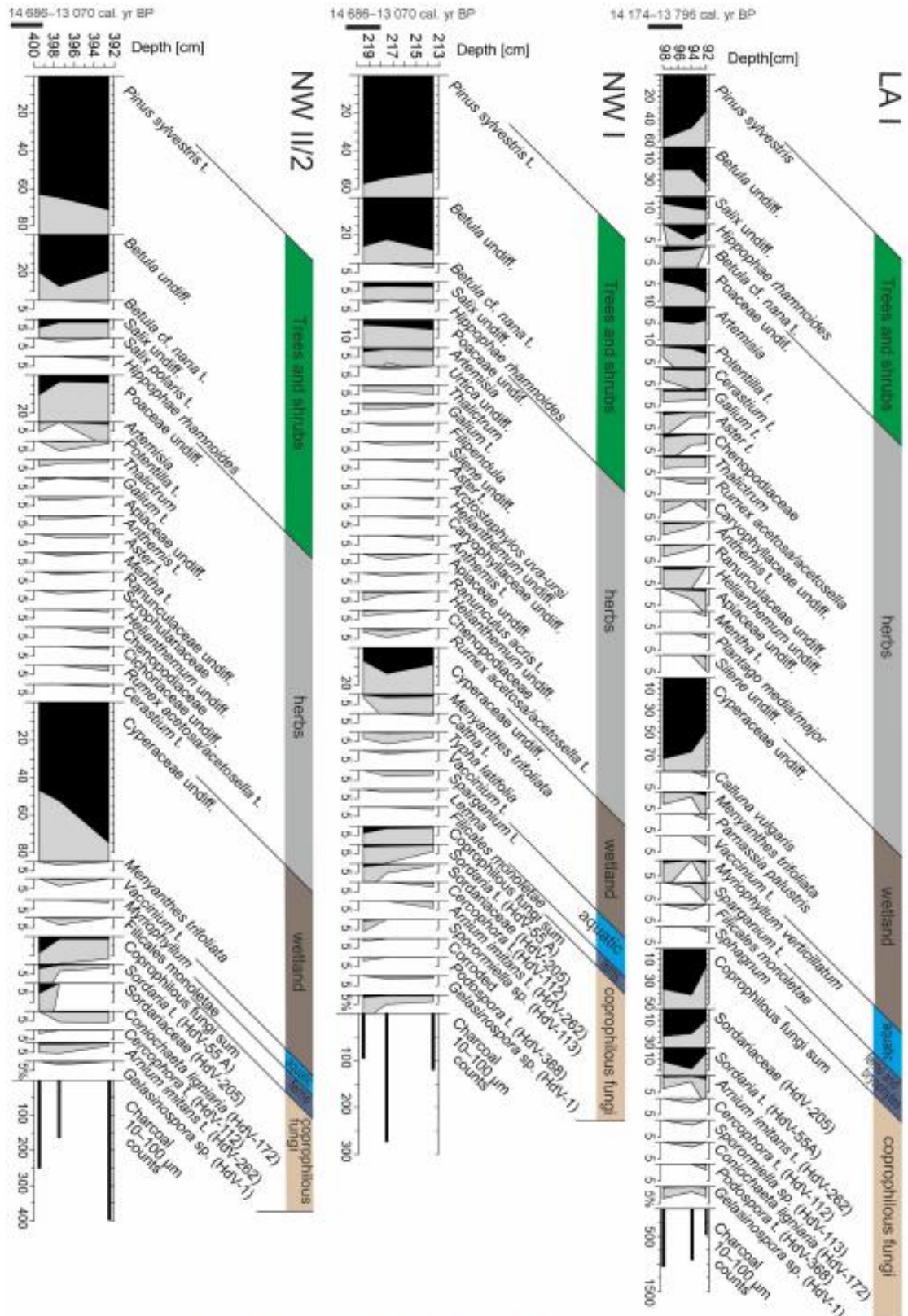


Figure 5. Pollen diagrams of LA I, NW I, and NW II/2, NW III, NW IV, and NW V cores

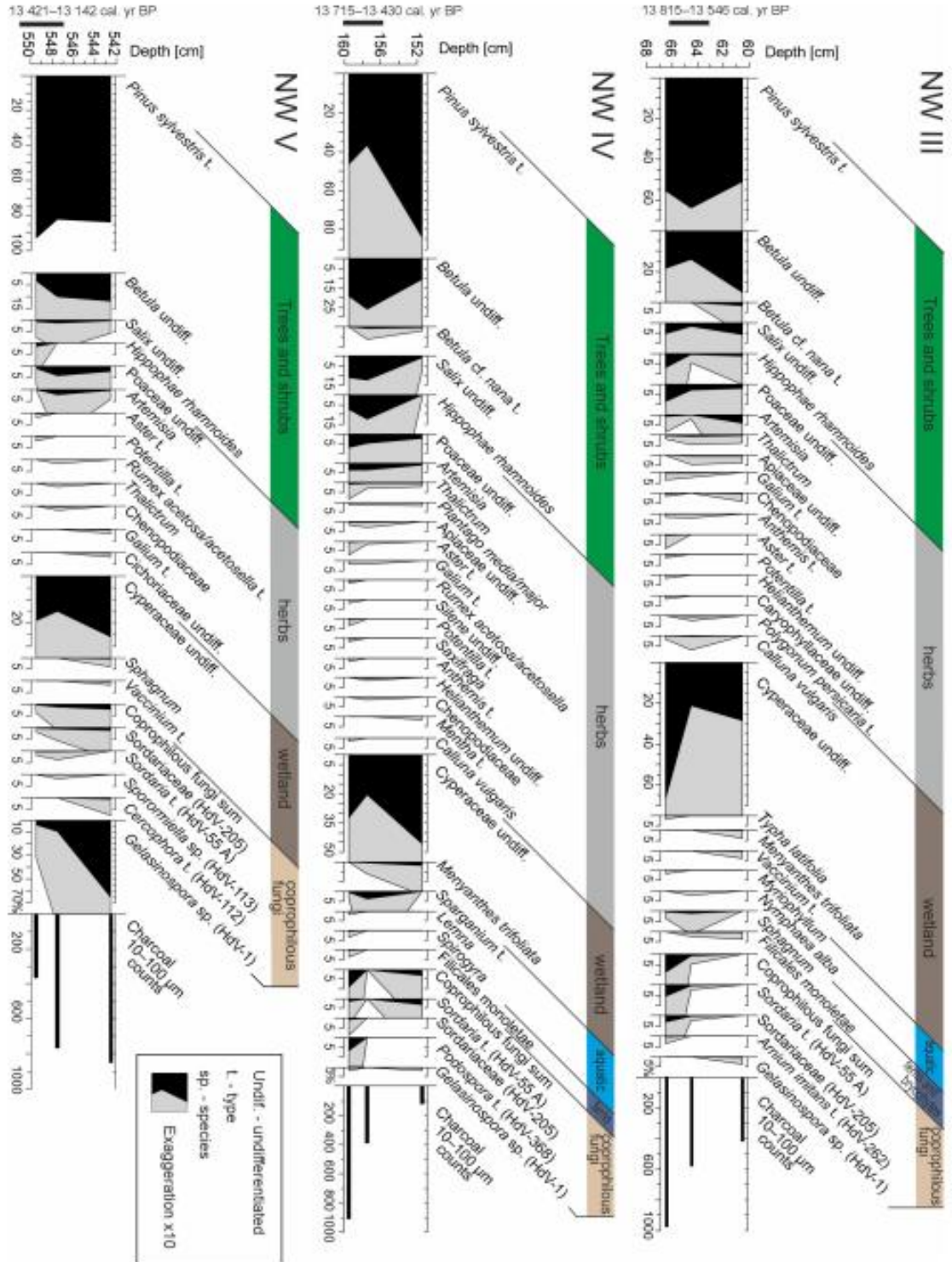


Figure 5. Continued

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 (Pawlowski 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; Forsytek, 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)	park tundra	<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)		<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	Bölling	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>A. polifolia</i> <i>C. rostrata</i> <i>E. palustris</i>	LA I
14 230–13 864		Ca ²⁺ ↑ Al ³⁺ ↑ Fe ³⁺ ↓ Ba ²⁺ ↓ K ⁺ ↑ Mg ²⁺ ↑ Mn ²⁺ ↑				<i>N. alba</i> <i>P. natans</i>	NW II/2
14 886–14 070		Ca ²⁺ ↓ Al ³⁺ ↑ Fe ³⁺ ↓ 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, Bölling 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 Balaga, 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 Proсна 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 (Pelechaty 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 (Bojakowska 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; Galka and Sznal, 2013; Galka 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; Galka 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; Dylkowa, 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; Plóciennik 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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