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Palaeoecological studies on the decline of *Cladium mariscus* (Cyperaceae) in NE Poland

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The history of the occurrence of *Cladium mariscus* (Cyperaceae) in NE Poland at the north-eastern limit of its distribution in Europe is discussed. The decline of the species may be related to gradual oligotrophication of its habitats, caused by the isolation of calcareous deposits and the decline of calcium carbonate in the substratum. The presence of *C. mariscus* in Kojle and Perty, lakes in NE Poland, is related to the occurrence of calcareous sediments, which may compensate for the lack of sufficient warmth. The occurrence of calcium carbonate in the substratum allows for the growth of *C. mariscus* in areas that are influenced significantly by a continental climate. The abundance of Ca^{2+} cations in the substratum compensates for that climatic factor.

Introduction

Cladium mariscus (Cyperaceae) is a thermophilous species (Szafer 1954, Berglund 1968, Walter & Straka 1970) very useful as an indicator of palaeoclimate. Because of its habitat requirements and biogeographical significance, it has been the subject of many palaeoecological studies carried out in various parts of Europe (von Post 1925, Conway 1937, Jalas & Okko 1950, Valovirta 1962, Hafsten 1965, Berglund 1968, Balátová-Tuláčková 1991, Gałka & Tobolski 2006, 2011, Gałka 2007, Pokorný *et al.* 2010). Phytosociological characteristics of assemblages with *C. mariscus* and the habitat requirements of such assemblages were studied by Fiałkowski (1959), Kępczyński and Ceynowa (1968), Staniewska-Zątek (1977), Kłosowski (1986/87), Jasnowska and Jasnowski (1991, 1991a, 1991b, 1991c), Eggers (1994), Pott (1995), Salmina (2003, 2004), Buczek (2005), Theocharopoulos *et al.* (2006), Karcz (2008), and Šumberová *et al.* (2011).

A study of the ecological amplitude of an assemblage with *C. mariscus* in NW Poland by Jasnowski (1962) distinguished four variants in the *Mariscetum* assemblage (= *Cladietum marisci*): (1) typical, consisting of dense *Cladium* agglomerations (sometimes the extreme one-species variant), (2) calciphilous, (3) acidophilous, and (4) halophilous. Jasnowski (1962) presented the phytocoenotic relationships of the four variants in a phytosociological table. Pott (1995) suggested a wide ecological amplitude for patches of the *Cladietum marisci* assemblage. Close relationships with substrates rich in calcium (calcareous peatlands "Kalkflachmoore", calcareous gyttja, and lacustrine chalk) are noticeable in more continental regions, for example in the Dolne Łużyce region, where *C. mariscus* can develop even on submerged peat deposits. In the Atlantic climate, the species occurs on sandy deposits poor in calcium, and on peaty soils. Pott (1995) emphasised the relic character of the species from the postglacial warm (Atlantic) period. In the vicinity of Lake Constance, *Cladium* is a typical component of assemblages of lakes subject to terrestrialisation ("Verlandungsgesellschaften"; Lang 1990). It prefers sites within the range of headwaters with a high content of calcium and oxygen. However, it also grows on substrates poor in calcium, such as detritus gyttja and peats.

Currently *C. mariscus* is rare in Poland (Zając & Zając 2001), and it is subject to strict species protection in this country (Piękoś-Mirkowa & Mirek 2006) and in the European Union (Herbichowa & Wołejko 2004). The current distribution of *C. mariscus* in NE Poland was analysed by Polakowski (1969) and Kłosowski (1986/1987). Those studies included descriptions of the habitats and floristic composition, and an analysis of the surface layer of the deposits on which *Cladium* grows. However, no palaeobotanical studies focusing on the postglacial history of this species have been undertaken in NE Poland.

We carried out studies on the current distribution and history of *C. mariscus* in NE Poland. We believe that this area is important because of its location at the boundary of the species' range in northern Europe (Meusel *et al.* 1965), and because of the need for protection within the Natura 2000 protected area.

The primary objectives of the study were to determine the duration of the occurrence of *Cladium mariscus* at Kojle and Perty (lakes in northeastern Poland), and to determine its past habitat requirements. We attempted to establish whether the species has grown at these lakes for thousands of years, or if it has appeared there recently. The stability of the occurrence of *C. mariscus* was examined in terms of its presence at the lakes in general, and also at one specific site at which it is currently most abundant. Another objective was to reconstruct the vegetation type in which *C. mariscus* occurred, particularly during the lake–peatland transition.

The palaeobotanical analyses within the area of the current occurrence of *C. mariscus* in the Suwalski Landscape Park form a part of a wider study, conducted in various parts of Poland, including the Tuchola Forest, the Lublin Region, the Drawieński National Park and the Pszczewski Landscape Park. The study is concerned with the postglacial history of *C. mariscus*, its fossil habitat preferences, and its peat-forming capacity.

Our hypothesis is that the decline of *C. mariscus* in NE Poland has a causal link with the gradual oligotrophication of habitats, which is taking place together with the disappearance of habitats rich in calcium carbonate. Such disappearance occurs through the loss of calcium carbonate in the aquatic environment after deposition in sediments, and the gradual decline of habitats through the development of Ca-poor layers on top of calcareous deposits. The lack of access to calcareous deposits probably results in a decrease in the occurrence of *C. mariscus*.

Material and methods

Study site

The study site is located in NE Poland, within the Suwalski Landscape Park (Fig. 1). Kojle and Perty, on the shores of which *C. mariscus* grows, are lakes located in the northern part of the park. The lakes, together with the surrounding peatlands, fill an extensive depression in the young-moraine landscape that developed during the retreat of the Scandinavian icesheet at the end of the last glaciation (Ber 1987, Krzywicki 2002). The soil in the area consists of ground moraine and has numerous kame hills. Variation in the land elevation in the vicinity of the lakes is about 50 m. In the past, Kojle and Perty constituted one lake, but now they are separated by a peatland. Their areas, according to the measurements in 2010, are 17.127 ha and 19.688 ha for Kojle and Perty, respectively. The surrounding area is occupied mainly by pastures to the north, and by mixed forests dominated by *Pinus sylvestris* and *Betula pubescens* to the south. The slopes of the hills include numerous springs with *Alnus glutinosa* stands. Along the lake borders *C. mariscus* is accompanied by *Schoenoplectus lacustris*, *Phragmites australis*, *Carex paniculata* and *Thelypteris palustris*.

For the study of the current distribution of *C. mariscus* in the Suwalski Landscape Park,

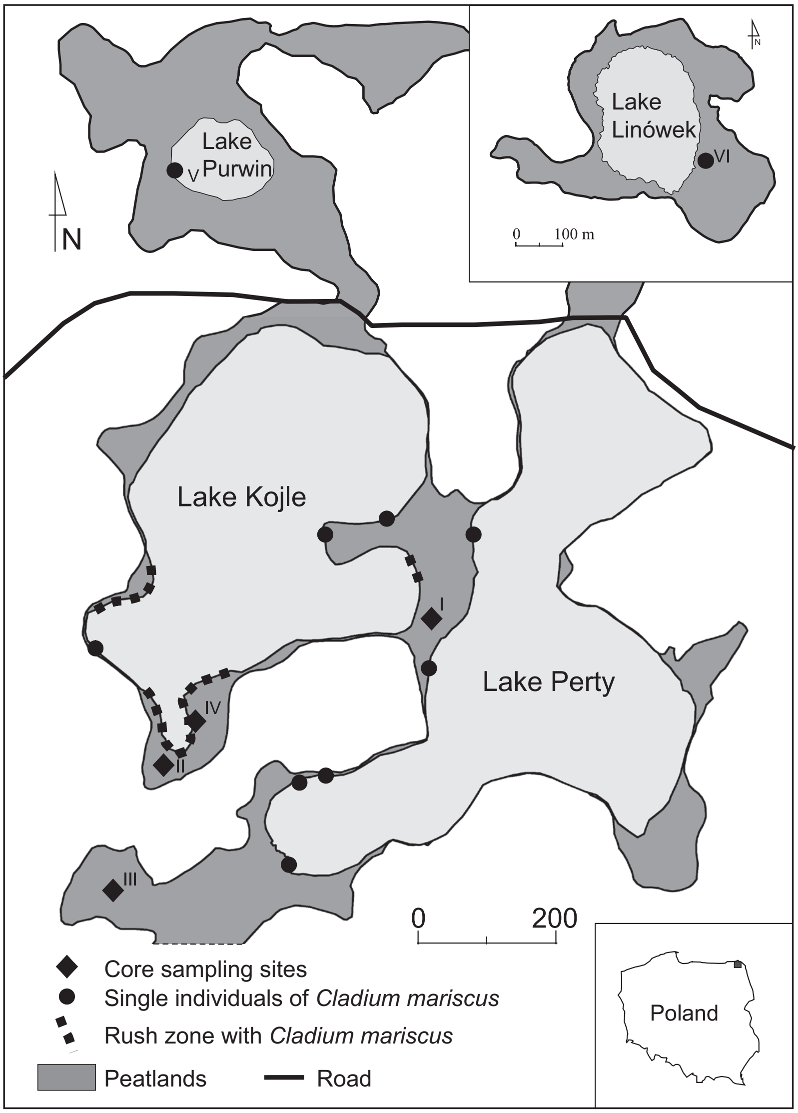

Fig. 1. Setting of the study area.

we examined the coastal zones of all twenty-seven lakes in the park. We cored material for the laboratory analyses. Peat deposits and gyttja were sampled using an Instorf manual corer. For the field research, we used a Russian corer with a length of 100 cm and a diameter of 7 cm. The sediment samples were inserted into PVC tubes and wrapped in plastic foil. We sampled the organic sediments from various parts of the peatlands surrounding Kojle and Perty, from Lake Purwin (Fig. 1), and from a peatland located at the eastern shore of Lake Linówek, in the southern part of the park. The geographic co-ordinates of the coring sites were as follows:

I 54°16´26.08´´N, 22°53´43.04´´E,
II 54°16´21.36´´N, 22°53´21.80´´E,
III 54°16´15.45´´N, 22°53´17.77´´E,
IV 54°16´23.01´´N, 22°53´24.03´´E,
V 54°16´49.60´´N, 22°53´24.29´´E,
VI 54°13´24.30´´N, 22°50´29.99´´E.

We also sampled the deposits, including the uppermost part of the lacustrine sediments and the overlying peat (200 cm in total), from the southern shore of Kojle, at a distance of 3 m from the *C. mariscus* zone (Fig. 1, site IV). The purpose of that sampling was to determine whether *C. mariscus* grew in this location in the rush zone of Kojle in the past, and whether the site of the occurrence has changed along with terrestrialisation during the succession process.

Laboratory studies

The sampled sediments were analysed for micro- and macrofossils. We conducted a palynological analysis, allowing us to estimate the duration and characteristics of the transformations in the plant assemblages, with variable sample distances but not exceeding 10 cm. For the palynological sample preparation, we followed the methodology described by Faegri and Iversen (1975). Samples were counted until we reached at least 500 tree and herb pollen taxa. Percentage values of sporomorphs in the individual spectra were calculated on the basis of values for particular taxa in relation to the total pollen number (pollen sum of AP + NAP), excluding local taxa (cryptogams, limnophytes, telmatophytes, and Cyperaceae). Percentages of local pollen taxa and cryptogams were also calculated in relation to the pollen sum. We used the TILIA software (Grimm 1991) to present the pollen records in a percentage diagram.

Analysis of the plant macrofossils was conducted every 1 cm (the volume per sample was approximately 20 cm^3), except for site IV (Fig. 1), for which the resolution applied was 2.5 cm (the volume per sample was approximately 50 cm^3).

The sampled sediments were strained under warm, running water through a sieve with 0.25 mm mesh. A stereoscopic microscope and an optical microscope were used to identify the plant remains. Published keys for identification of plant macrofossils were used (Grosse-Brauckmann 1974, Tobolski 2000, Velichkevich & Zastawniak 2006, 2009). The graphic presentation of the results was prepared using the C2 software (Juggins 2003).

In order to determine the age of appearance of *C. mariscus* in the area, we selected macrofossils of trees for the C^{14} AMS dating. The macrofossils were stored following the recommendations of Walanus and Goslar (2009). The C^{14} dating was performed in the Poznań Radiocarbon Laboratory. The resulting conventional radiocarbon dates were calibrated with the OxCal 4.1 software (Bronk-Ramsey 2009).

Results

Lithostratigraphy

Stratigraphical data of the analysed cores were collected during the fieldwork and in the laboratory. We sampled the lowermost sediments, using variable core lengths, including peats and gyttja, from the peatlands that currently separate the waters of Kojle and Perty (site I). We also took samples from the area adjacent to the southern shore of Kojle (site II), and from the area adjacent to the southwestern shore of Perty (site III). The palaeobotanical analyses at site III were performed mainly in order to determine the history of vegetation that grew in the area during abrupt changes in the water level of the lakes. Our findings regarding the Early Holocene water level variations in the lakes that resulted in the disappearance of open water, the development of peatlands, and the subsequent flooding of peatlands will be presented in a separate paper. The sediments from site I consisted of calcareous gyttja (700–660 cm), peat (660–613 cm), calcareous gyttja (613–327 cm), detritus gyttja (327–274 cm), and peat (274–0 cm). The sediments from site II consisted of calcareous gyttja (520–493 cm), peat (493–444), calcareous gyttja (444–327 cm), detritus gyttja (327–73 cm) and peat (73–0 cm). The sediments from site III consisted of peat (1052–874 cm) and calcareous gyttja (874–800 cm). The sediments from site IV consisted of calcareous gyttja (200–110 cm) and peat (110–0 cm). The sediments from Purwin (site V) had a total thickness of 1100 cm and consisted of fine and coarse detritus gyttja containing calcium carbonate, except for the uppermost part (105 cm) that was devoid of calcium carbonate. The sediments sampled from the peatland by the eastern shore of Linówek (site VI) were 800 cm thick and included calcareous silts in the lowermost part (800–680 cm), non-calcareous fine detritus gyttja (680–190 cm), and moss-herbaceous peats in the uppermost part (190–0 cm).

Radiocarbon data

Nine AMS radiocarbon datings were performed (Table 1), mostly for the lowermost sections of the analysed cores where the oldest *Cladium* seeds were found. The time of appearance of *C. mariscus* in various parts of Kojle and Perty was essentially simultaneous, around 9500 cal. BP.

Current occurrence of *Cladium mariscus*

Our search for current occurrences of *C. mariscus* within the Suwalski Landscape Park included the helophyte zones of 27 lakes. We found *Cladium* only in the coastal zones of Kojle and Perty (Fig. 1). *Cladium mariscus* grows in the littoral zone in two forms: as dense stands (found only at Kojle) and as single individuals (found at both lakes). Only a few individuals were found on the southwestern shore of Perty. Detailed mapping of the current distribution of *C. mariscus* within Kojle and Perty will facilitate future studies to determine whether the populations at these lakes are regressing or expanding. We recorded the occurrence of *Schoenoplectus lacustris*, *Phragmites australis*, *Carex paniculata* and *Thelypteris palustris*, along with *C. mariscus*.

Palaeobotanical analyses

For sites I–V and Linówek, we included selected plant taxa whose fossils were found in the sediments next to the seeds and fruits of *C. mariscus*. Our objective was to elucidate the co-distribution of *C. mariscus* and other plants whose macrofossils were found.

Sites within Kojle and Perty

At site I, *C. mariscus* seeds were found in calcareous gyttja at depths of 616–617, 563–564, 365–212, and 36–35 cm (Fig. 2). Among the other helophyte taxa, we found seeds of *Typha* sp. and fruits of *Schoenoplectus lacustris*.

At site II, located at the southern shore of Kojle, we found *C. mariscus* seeds in calcareous gyttja at depths of 415–368, 243–160, and 97–62 cm (Fig. 2).

We recorded *C. mariscus* seeds in the lowermost section of the sediments at site III, which is located within the peatland adjacent to the southwestern shore of Perty. The fruits and seeds of *C. mariscus* were deposited in the peat containing remnants of *Sphagnum warnstorfii, Paludella squarrosa*, *Polytrichum strictum* and *Thelypteris palustris*, and in calcareous gyttja overlying the peat. *Cladium* seeds and fruits were found at a depth of 1031–863 cm (Fig. 3).

At site IV, for which the uppermost section (200 cm) of the sediment core was analysed, we found *C. mariscus* seeds and fruits at a depth of 162–16 cm (Fig. 3). Based on the results of the plant macrofossil analysis and palynological analysis, we distinguished three stages of development of the local vegetation:

1. KL I, 200–112 cm. Lake phase, with the occurrence of *Najas marina*, *Chara* sp., *Nuphar lutea*, and *Nymphaea alba*. At a depth

Table 1. Radiocarbon datings. For site description *see* text.

Site, depth (cm)	Lab. no.	Dated material	AMS ^{14}C age BP	Calibrated age BP (95%)
I, 340–341	Poz-37192	Fruits and fruits scales of *Betula* sp.	6130 ± 40	7160–6910
I, 614.5–615.5	Poz-37191	Bud scales of tree	8430 ± 50	9533–9308
II, 219–220	Poz-43865	Needles of *Picea abies*	4260 ± 40	4959–4646
II, 444–446	Poz-38822	Fruits and fruits scales of *Betula* sp.	8330 ± 50	9473–9142
III, 872–873	Poz-39558	Needles and peryderm of *Pinus sylvestris*	8120 ± 50	9262–8819
III, 1057–1058	Poz-39559	Needles and seed of *Pinus sylvestris*	8600 ± 50	9680–9495
V, 453–455	Poz-35960	Needles of *Picea abies*	2940 ± 35	3214–2971
V, 1099–1100	Poz-37190	Bud scales of tree	7769 ± 50	8628–8425
VI, 214–215	Poz-35957	Fruits and fruits scales of *Betula* sp.	1025 ± 30	1051–803
VI, 381–382	Poz-39023	Needle and fruits scales *Picea abies*	3860 ± 50	4420–4102

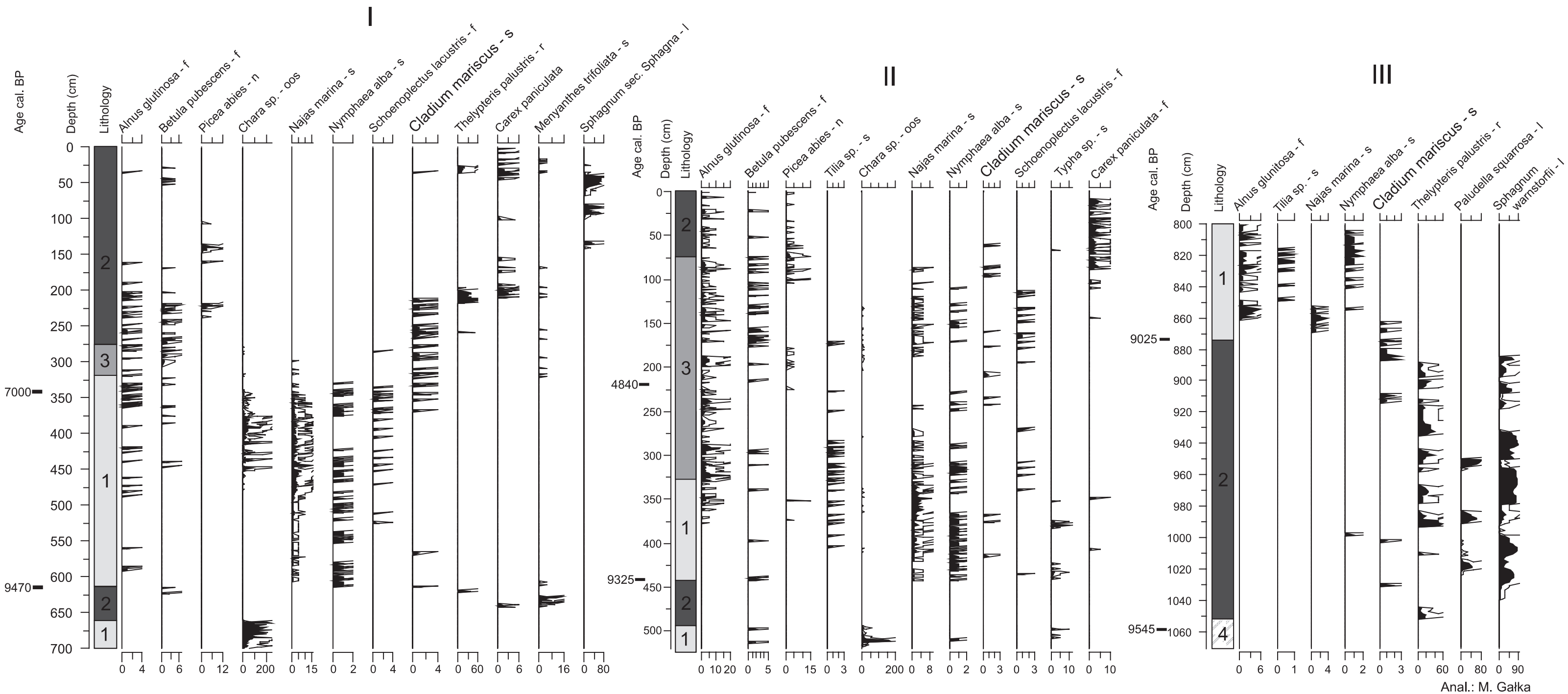

Fig. 2. Diagram of plant macrofossils illustrating local vegetation changes in the lakes and peatland adjacent to sites I–III (lakes Kolje and Perty). — 1: Calcareous gyttja. — 2: Peat. — 3: Detritus gyttja. — 4: Sand. Description of plant remains: f = fruit, s = seed, oos = oospore, e = endocarp, r = rootlets, n = needle, fs = fruits scale, bs = bud scale, p = pollen, l = leaf.

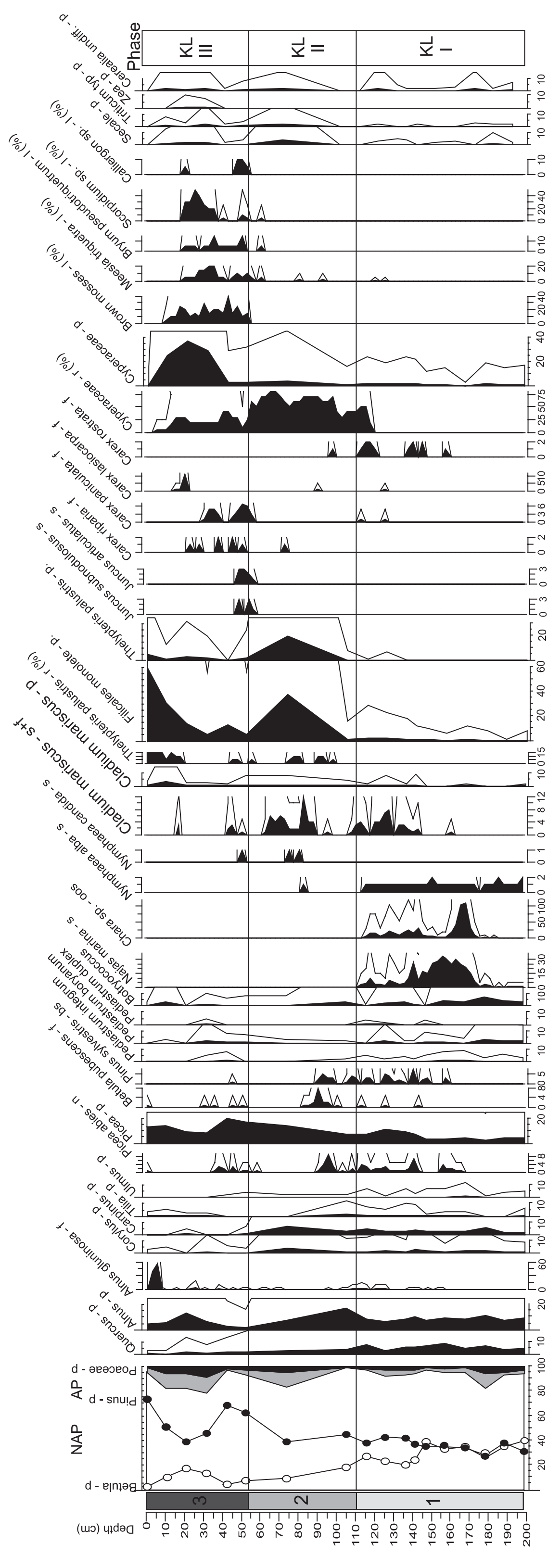

Fig. 3. Composite diagram of macrofossils and pollen diagram illustrating regional vegetation changes in the peatland adjacent to site IV. — 1: Calcareous gyttja. — 2: Herbaceous peat. — 3: Herbaceous–brown-moss peat. Description of plant remains as in Fig. 2

of 174 cm, a clear increase in the abundance of *Najas marina* and *Chara* sp. occurred. The number of oospores of *Chara* sp. decreased at a depth of 160 cm, with a simultaneous maximum abundance of *N. marina*. In the second part of the interval, the number of *Betula pubescens* remains increased, and the fruits of *Alnus glutinosa* as well as the needles of *Picea abies* appeared. The sediment also included seeds of *C. mariscus*.

2. KL II, 112–54 cm. Lower peatland phase. The number *Picea abies* needles was highest at a depth of 98–83 cm. The abundance of *C. mariscus* reached a maximum at a depth of 92–64 cm. *Nymphaea alba*, *N. candida*, and the roots of *Thelypteris palustris* were also present.
3. KL III, 54–0 cm. Upper peatland phase. The observed number of species was highest in this period. The proportion of brown mosses increased, including the occurrence of *Meesia triquetra*, *Bryum pseudotriquetrum, Calliergon* sp., and *Scorpidium* sp. *Juncus subnodulosus* and *J. articulatus* occurred in this period. *Menyanthes trifoliata* and *Carex paniculata* were at their maximum abundance. Seeds of *C. mariscus* occurred at the beginning and the end of the period. In the upper part, the brown mosses decreased and the amount of roots of *Thelypteris palustris, Carex* sp., and *Alnus glutinosa* increased.

Site V, Purwin

We found seeds of *Cladium mariscus* in calcareous fine detritus gyttja at depths of 981–980 and 490–263 cm (Fig. 4). The lowermost sediment layer did not include *Cladium* seeds. Hypothetically, the seeds should occur in higher numbers due to the shallowing of the lake, which would promote development of the rush zone. The concentration of fruits of *Carex paniculata*, seeds of *Menyanthes trifoliata*, and leaves of brown mosses in the uppermost layer suggests that these plants occurred in the helophyte zone. Following the disappearance of *Alnus glutinosa* and *Picea abies* and an increase in *Betula pubescens*, an increase of *Chara* sp. occurred in the lake along with a decline of *Potamogeton natans*.

Site VI, Linówek

Seeds of *C. mariscus* were deposited in the sediment of this lake at a depth of 261–218 cm (Fig. 4). The site was distinguished by the absence of macrofossils of other typical taxa of the helophyte zone during the occurrence of *C. mariscus*. According to the palaeobotanical analysis, *Schoenoplectus lacustris* and *Typha* sp. occurred earlier than *C. mariscus*. Among other plants that prefer a marshy substratum, we recorded *Carex paniculata*, *C. pseudocyperus*, and *Menyanthes trifoliata*. Between 4250–1010 cal. BP *Chara* sp., *Potamogeton natans*, and *Nymphaea alba* grew in the lake.

Discussion

Climate changes occurring at the turn of the late Glacial and Holocene resulted in the migration of plants with differing habitat and temperature requirements to areas of northeastern Poland (Szafer 1977, Kupryjanowicz 2007). The development of favourable climatic conditions in the early Holocene allowed *Cladium mariscus* to occur in NE Poland. *Cladium* is a thermophilous helophyte (Szafer 1954, Berglund 1968, Walter & Straka 1970). Expansion of this species in various parts of Kojle and Perty occurred approximately 9500 cal. BP, as confirmed by the radiocarbon dates 8600 ± 50 BP and 8430 ± 50 BP. In the Suwałki region during this time, the mean temperature in July was at least 16 °C and the mean temperature in January was approximately –4 °C. These temperature regimes restricted the range of *C. mariscus* (Wasylikowa 1964). A similar dependence on favourable climatic conditions was demonstrated by Salmina (2004) in Latvia, where the occurrence of *C. mariscus* is concentrated at the Baltic Sea coast. *Cladium mariscus* expanded rapidly in Poland during the early Holocene, as evidenced by the presence of its fossils in the Tuchola Forest (Milecka 2005), at the coast of the Baltic Sea (Tobolski *et al.* 1997), and in Scandinavia (Valovirta 1962, Berglund 1968).

In view of the plant macrofossil analyses and palynological analyses described here, the occurrence of *C. mariscus* at Kojle and Perty since

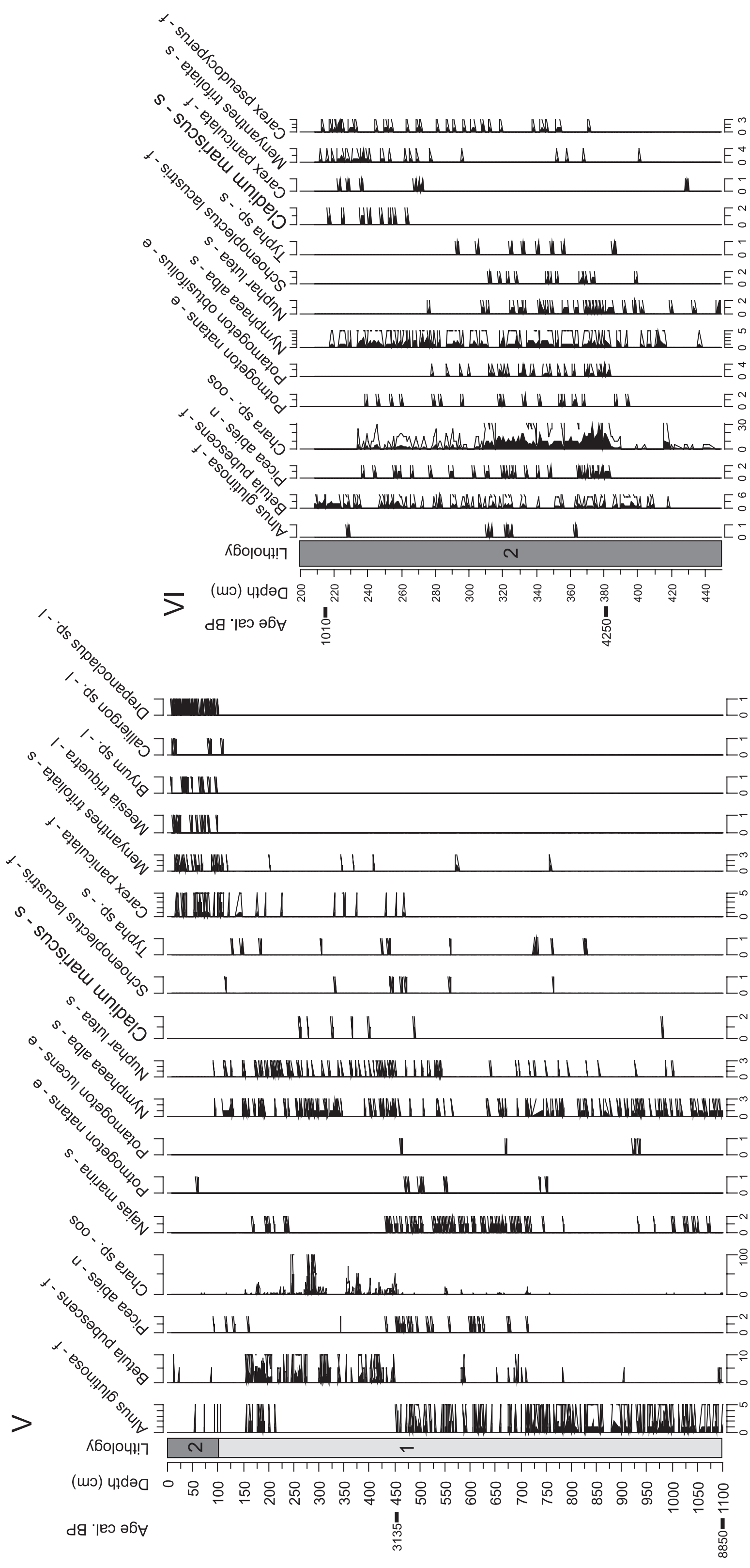

Fig. 4. Diagram of plant macrofossils illustrating local vegetation changes in the lakes adjacent to the lakes Purwin (site V) and Linówek (site VI). — 1: Calcareous gyttja. 2: Detritus gyttja. Description of plant remains as in Fig. 2.

approximately 9500 cal. BP can be considered to be continuous. This conclusion is supported by the finding of fossil seeds and pollen at various depths in the sediments sampled from various parts of the lakes. The macrofossil analysis for site I showed that *C. mariscus* retreated from this area following an increase of the water level 9470 cal. BP (Fig. 2). It returned into the area again when the water depth of the lake decreased significantly, as reflected by the gradual decline of the macrophytes *Najas marina*, *Chara* sp., and *Nymphaea alba*. The species retreated from the area again concurrently with the acidification of the habitat and the appearance of transitional bog plants, which were preceded by a phase with the occurrence of *Thelypteris palustris* (depth 215 cm). The acidification of the habitat may be connected with the appearance of *Picea abies*, as evidenced by the presence of its needles in the sediment. The third appearance of *C. mariscus* at the site (depth 35–36 cm) occurred simultaneously with another change in the environment, as reflected by the decline of *Sphagnum* mosses and the appearance of *Thelypteris palustris* and *Carex paniculata*. Thus, *C. mariscus* was not permanently present at this single site throughout the millenia.

The analysis of the occurrence of *Cladium mariscus* at site IV, where we studied the uppermost section of 200 cm of the core, including lake sediments in the form of gyttja and the overlying peat, revealed that the presence of *Cladium* was related to the occurrence of aquatic macrophytes (*Nymphaea alba, N. candida*) and algae (Fig. 3), which suggests that the surface was permanently flooded. The disappearance of the carpological fossils of *C. mariscus* was concurrent with the appearance in the area of *Juncus subnodulosus* and *J. articulatus* and of brown mosses including *Meesia triquetra* and *Bryum pseudotriquetrum* (Fig. 3: phase KL III). Some sedge species (*Carex riparia*, *C. paniculata*) were strongly competitive with *C. mariscus*. The occurrences of *C. mariscus* and *Thelypteris palustris* were strongly correlated (Figs. 2 and 3, phases II and I). Examples of the current co-occurrence of these two species in eastern Poland were provided by Polakowski (1969), Kłosowski (1986/1987), and Namura-Ochalska (2005).

The occurrence of *C. mariscus* at Kojle and Perty is currently restricted to the lake border zone. However, the species is present in various parts of these lakes. Considering the historical and current habitat requirements of *C. mariscus* and its capability for rapid migration in combination with a succession of other plant species, we can assume that it has existed continuously within the area, but in different parts of the lakes.

Considering the distribution of *C. mariscus* in the past, in different parts of the lake, identified by the presence of its fruit and seeds in the sediment, it is worth noting that its fruits, owing to their peculiar structure, can readily float on water. What should be taken into account in palaeoecological reconstruction is that often *Cladium*'s allocation in the samples did not grow simultaneously and steadily, and its fruits appeared in the sediment due to fluctuations in the water level. The occurence of this plant should therefore be carefully interpreted, especially regarding single findings. Our results as well as the amount of the seeds and fruits of *Cladium* found in the sediment suggest that it grew at the same time in different parts of the lake, just as today.

The stability of the occurrence of *C. mariscus* at Kojle and Perty throughout more than 9000 years demonstrates that the site is favourable for the species. The palaeobotanical studies conducted in other parts of the Suwalski Landscape Park have shown that *C. mariscus* occurred in the past at Purwin and Linówek, where it does not occur at present. In the case of Linówek, the disappearance of this species occurred fairly recently. Its seeds have also been found in the surface sediments (M. Gałka unpubl. data). The disappearance of *Cladium* was caused by a change in the trophic status of the lake water. A peatland developed around the lake with assemblages including *Sphagnum magellanicum*, *S. fuscum*, *Scheuchzeria palustris*, and *Oxyccocus palustris*. A contrasting situation has occurred recently. During the past two years, the predominant plant assemblages included *Sphagnum teres* and *Thelypteris palustris* as their main components. In Purwin, which is located in the vicinity of Kojle and Perty, *C. mariscus* ceased to grow much earlier (ca. 1700 cal. BP). We found the most recent seeds of this species in the lake sediment at a depth of 262 cm (Fig. 4).

The permanent occurrence of *C. mariscus* at Kojle and Perty throughout several millenia is connected with the occurrence of calcareous deposits in the substratum. During geological drillings in various parts of these lakes, we recorded the occurrence of calcareous deposits, usually in the form of lacustrine chalk. The accumulation of calcareous deposits within the lakes is still taking place. Several reports on the ecological requirements of *C. mariscus* in Poland have emphasised the calciphilic character of this species (e.g., Świeboda 1968, Herbichowa & Wołejko 2004). We believe that the occurrence of *C. mariscus* at Kojle and Perty is related to the presence of calcareous deposits that have a compensatory, "warming" effect, which may be a decisive factor for a sub-atlantic species such as *C. mariscus*. This hypothesis is consistent with the situation at Purwin, where *C. mariscus* no longer occurs. Its disappearance from Purwin may be related to the gradual decrease in the deposition of calcareous sediments within the lake. The uppermost layer of the sediments, which has a thickness of approximately 110 cm, was devoid of calcium carbonate continuously to a depth of 1100 cm (the age of the lowermost sampled sediments was 8545 cal. BP). A different situation occurs in Linówek, where *C. mariscus* grew in a non-calcareous environment as evidenced by the findings that small amounts of calcium carbonate are present only in the late Glacial sediments and that non-calcareous deposits were accumulated in the Holocene.

It is worth emphasizing that the rhizomes and roots of *C. mariscus* reach maximum sizes of 40–50 cm and penetrate vertically or diagonally to a depth of 20–50 cm, but mostly to about 20 cm (Chlewińska-Karpowicz, 1929, Conway 1936 in Buczek 2004, Staniewska-Zątek 1977, Taranta 1991, Eggers 1994, Namura-Ochalska 2005). Due to the wet conditions in the bog, the rhizomes and roots penetrate only to the surface layers of the substrate (Taranta 1991).

Considering the increasingly restricted occurrence of *C. mariscus* in the Suwalski Landscape Park, which marks the eastern limit of the occurrence of the species in this part of Europe, we assume that the presence of the species in the calcareous environment at Kojle and Perty is related to the compensatory function of calcium carbonate. Plants preferring a milder climate can also grow at sites located in more northern parts of Europe, where there are calcareous sediments. For example *Stratiotes aloides* and *Ceratophyllum demersum* grow in northern Finland (67°40´N) in calcareous environments (Kotilainen 1955). The occurrence of *C. mariscus* in the border zone of Saarijärvi (central Finland), which is the northernmost site of this plant, is connected with calcareous sediments (Jalas & Okko 1951). In Latvia, *C. mariscus* grows in calcareous environments and mainly in the coastal region (Salmina 2003, 2004). In the south of Sweden *Cladium* grew by 1851 in a spring fen (von Post 1916, 1925). There was a high abundance of *Cladium* in Gotland in the second half of Atlantic period, which Valovirta (1962) connected with the presence of limestone.

The gradual borealisation of the climate in NE Poland has resulted in the retreat of Atlantic species and their replacement by taxa typical of the boreal zone (Szafer 1972, Kupryjanowicz 2007, Gałka 2009, 2010, Gałka *et al.* 2012). The presence of calcium carbonate in the substratum allows the growth of *C. mariscus* in areas that are significantly influenced by continental climate. Such a calcium-rich environment compensates for the climatic factor, i.e., a harsher climate at the boundary of the species' distribution. If the contact with calcareous deposits is lost, *C. mariscus* will disappear.

Studies conducted in the Tuchola Forest (Gałka & Tobolski 2006, Tobolski & Gałka 2008) and Pszczewski Landscape Park (Karcz 2008) revealed the wide current and historical habitat preferences of *C. mariscus*, as also emphasised by Pott (1996) for other parts of western Europe, and by Theocharopoulos *et al.* (2006) for Greece. In those areas, *C. mariscus* also grows on sandy substrates and non-calcareous gyttja. The species is sometimes found accompanied by *Lobelia dortmanna*, e.g., in the Tuchola Forest at Lake Krzywce Wielkie (Kochanowska 2005, Gałka & Tobolski 2006, Kochanowski & Tobolski 2010) and at Lake Nawionek (Kępczyński & Ceynowa 1968). The difference between the climates in eastern Poland (more continental) and western Poland (more Atlantic, or oceanic) is reflected in the environmental preferences of *C. mariscus*. In western Poland, the species has a wider ecological tolerance than in eastern Poland (Polakowski 1969, Staniewska-Zątek 1977). In eastern Poland, at the eastern limit of its distribution, the species almost always occurs at sites containing calcium carbonate (Fiałkowski 1959, Kłosowski 1986/1987, Buczek 2004). In western Poland, Germany and the Netherlands, where the climate is milder, the species occurs in various habitats, and also grows on a sandy substratum or even in a halophilic environment (Jasnowski 1962, Eggers 1994, Pott 1995).

During the present study, we did not observe any *Cladium* peat as described in previous reports by Overbeck (1975), Jasnowska and Jasnowski (1991b), and Tobolski (2000). We found only layers of peat several centimetres thick containing radicelles of *C. mariscus* as one of several components. The lack of peat development may be related to the occurrence of the species at the limit of its distribution and the associated loss of its peat-forming capability. That was suggested for the Tuchola Forest area, where *Cladium* peat is also absent, by Gałka and Tobolski (2006).

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