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The Holocene decline of slender naiad (*Najas flexilis* (Willd.) Rostk. & W.L.E. Schmidt) in NE Poland in the light of new palaeobotanical data

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ABSTRACT. The article presents a potential explanation of disappearance of *Najas flexilis* in two lakes during the Atlantic and Subboreal chronozones in Romincka Forest and Lake Linówek in northeastern Poland. Palaeobotanical (palynological and macrofossil) analyses revealed the disappearence of *N. flexilis* that was possibly connected with the trophic state change. Those changes of water trophic state in the lake in Romincka Forest were probably triggered by *Picea abies* expansion stimulated by climate change at the beginning of the Subboreal. The appearance of spruce in the area of the lake led to acidification of the water body where *N. flexilis* grew, which caused the decline of its population. The Lake Linówek site revealed a possible connection of the disappearence of *N. flexilis* (as well as other submerged plants) with *Botryococcus* blooms (probably caused by increasing trophy) that led to depletion of light availability on the bottom of the water body. Slender naiad, in both cases, grew on non-calcareous sediments, which reveals its broader pH ecological amplitude, despite the opinion that this species is an indicator of calcareous ground. The simultaneous occurrence of *N. flexilis* and *Potamogeton pusillus* suggests that also in the past, these species built together submerged aquatic plant vegetation.

KEYWORDS: *Najas flexilis*, macrofossil analysis, pollen analysis, Holocene, NE Poland

INTRODUCTION

The study of lake sediments in terms of their contents of plant fossils belongs to the main research methods used in palaeoecology (Birks 1986, Tobolski 2000). Due to the use of palaeobotanical research it is possible to reconstruct the history of changes in distribution of individual plants and their environmental requirements in a particular area (Wasylikowa 1964, Pokorný & Jankovská 2000, Tobolski & Ammann 2000, Milecka 2005, Mortensen et al. 2011). Climate changes, which have occurred over thousands years of the Holocene resulted in characteristic patterns of vegetation and development of edaphic conditions. Those processes are well-explained by the model of glacial/interglacial cycles (Iversen 1964, Tobolski 1976, Birks 1986, Lang 1994). Among the vascular plants of the Europaean flora, slender naiad (*Najas flexilis*) – an annual submersed macrophyte, seems to be very susceptible to this cycles and closely linked to the Holocene as well. This fact is well illustrated by the number of Holocene sites of this plant in Europe, which at the end of the first half of the 20th century, consisted of more than 200 (Lang 1994). Their distribution covered the area throughout northern and Central Europe from Lake Garda (on the Swiss-Italian border) to the western fringe of the Varanger Peninsula in NE Norway (Lang 1994). From the territory of Poland this species has been identified at 13 palaeobotanical sites (Stasiak 1963, Borówko-Dłużakowa 1970, Bałaga 1990, Marek 2000, Zalewska-Gałosz 2001, Gałka

2006, Kowalewski & Żurek 2011). Recently, Szubert (2012) found seeds of *Najas flexilis* in the surface sediments of Lake Szarcz (western Poland), however, this site has not been examined for its present-day occurrence yet. Seeds of *Najas flexilis* were also found in numerous sites dating from the late Pleistocene in Central and Eastern Europe, so this species is considered characteristic of the Eemian interglacial (Velichkevich & Zastawniak 2006). Palaeoecological studies, which showed the largest distribution of this naiad species in the climatic optimum, enable categorization of *Najas flexilis* as an indicator of warm climate (Backmann 1948, Czubiński 1950, Godwin 1975, Lang 1994).

Nowadays *Najas flexilis* occurs in northern Europe (British Isles, Germany, Russia), the Alps and in central Asia and North America (Hulten & Fries 1986, Piękoś-Mirkowa & Mirek 2003). In the area of Poland, *Najas flexilis* was reported from the northern part in the early 20th century, but the present occurrence is still not confirmed. Hence this taxon was finally included in the category of extinct taxa (Sudnik-Wójcikowska 2004). Recently *Najas flexilis* has been disappearing rapidly in Europe and this led to its qualification for the special protection, and to its entry in Annex 2 and 4 of the EU Habitats and Appendix I of the Bern Convention (Zaleska-Gałosz 2001, Wingfield et al. 2006). The modern difficulties connected with the protection of slender naiad encourage incorporating of conclusions from palaeoecological data into nature conservation programs.

The reason for the regression of *Najas flexilis*, often mentioned in the literature, is related to gradual cooling of the climate (Backman 1935, 1948, Godwin 1975, Lang 1994, Bennike et al. 2001), and therefore worsening of habitat conditions – acidification or eutrophication of water (Samuelsson 1934, Lang 1994, Wingfield et al. 2006). Other reason of decline of *N. flexilis* is connected with transforming process lake into peat land (Backman 1948).

In our article we present palaeoecological reconstructions of two different cases of *Najas flexilis* disappearance driven by natural factors. Moreover, we contribute new information about habitat requirements of slender najad from the area where this species was observed for the last time in Poland. The main aim of this article is a palaeoecological reconstruction of the fossil environment of *Najas flexilis* and identifying the reasons of the decline of this plant in two sites in the northeastern part of Poland.

MATERIAL AND METHODS

STUDY SITES

Both analysed fossil sites of *Najas flexilis* are located in NE Poland. The first is a few-acre forest pond situated in the Romincka Forest Landscape Park (54°19′46.8″N, 22°37′47.28″E). Around this water body developed a peat bog with features of a kettle-hole bog, overgrown by oligotrophic vegetation composed mainly of numerous species of *Sphagnum*, *Ledum palustre*, *Oxyccocus palustris*, and *Carex limosa*. The second site is the Lake Linówek (54°13′24.35″N, 22°50′29.55″E) within the Suwalski Landscape Park, which is an eutrophic lake of a size of 2.74 ha, currently surrounded by a transitional peat bog in which grow *Sphagnum teres*, *Oxyccocus palustris*, *Scheuchzeria palustris* (Fig. 1).

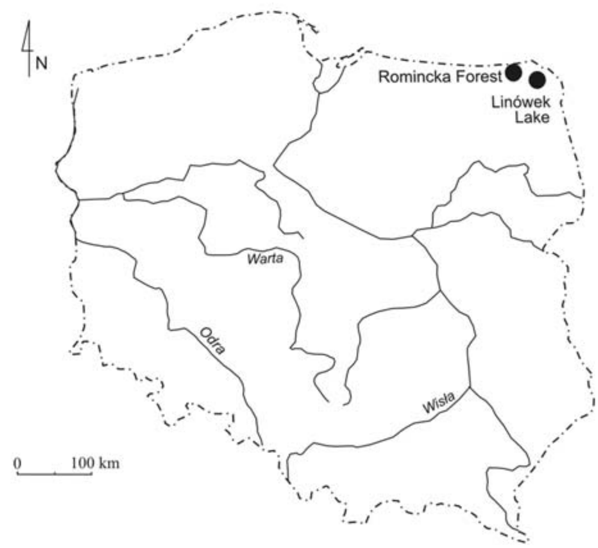

Fig. 1. Location of study site in Poland. ● – sites of *Najas flexilis* subfossil seeds

FIELD WORKS AND PROFILES DESCRIPTION

Limnic sediments were collected using a manual Instorf type corer. In the case of the Romincka Forest, the core had a the length of 50 cm and a diameter of 5 cm, whereas the corer from the Lake Linówek had a length of 100 cm, and a diameter of 7 cm. The paper describes only fragments of both cores, with lengths about 100 cm each, which contained *Najas flexilis* macroscopic remains. Results of analyses of complete cores from both sites is the subject of a separate publication.

The lithology of analysed core fragments were described according to Troels-Smith method (Troels-Smith 1955, Tobolski 2000). The sediments were described in Tab. 1.

Table 1. Lithology from Romincka Forest and Lake Linówek

Site	Description of sediments
Romincka Forest	515–540 cm: Ld3, Dh1 (leaves of *Sphagnum* sec. *Sphagna*), Dd+; fine detritus gyttja 540–620 cm: Ld4, Dg+ (leaves of brown mosses cf. *Drepanocladus* sp.), Dh+; fine detritus gyttja
Linówek Lake	450–550 cm: Ld4, Dg+, Dh+; fine detritus gyttja

LABORATORY TREATMENT

Twenty six samples of 1 cm^3 were selected for palynological analysis, six from the Romincka Forest, and twenty from Lake Linówek. Each sample was acetolysed following the Erdtman's method (1960) with pretreatment of HCl, KOH and HF (Faegri & Iversen 1989). Pollen taxa were identified and counted with the application of Zeiss AMPLIVAL light microscope under 400x and 1000x magnification. Pollen was identified with the use of specialist keys and atlases (Moore et al. 1991, Beug 2004) and the reference slide collection of the W. Szafer Institute of Botany, Polish Academy of Sciences as well. Samples were counted until the minimum number of 500 tree and herb pollen grains was reached. Percentage values of sporomorphs in individual spectra were calculated on the basis of particular taxa values in relation to the total pollen sum (AP+NAP), excluding local taxa (cryptogams, limnophytes, telmatophytes, and Cyperaceae).

Material designated to the macrofossils analysis was sifted under a stream of warm water through sieves with mesh size of 0.25 mm and 0.50 mm. The volume of an individual sample was approximately 40 cm^3 in both cases, however, the resolution of samples differed depending on the core. The sediment from Lake Linówek was analysed every 1 cm, whereas that from the Romincka Forest – every 2 cm. Macrofossils were identified with the application of a stereoscopic microscope with the magnification of 10–100×. The selected plant fossils, mainly their generative organs, were determined with the application of keys and atlases (Grosse Brauckmann 1974, Tobolski 2000, Velichkevich & Zastawniak 2006, 2009).

Results of the macrofossil analysis are presented as 1:1 diagrams prepared in the C2 programme (Juggins 2003) whereas results of the palynological analysis are presented as pollen percentage diagrams, drawn using the TILIA software (Grimm 1991).

RADIOCARBON DATING

Two radiocarbon datings from sections where macrofossils of *Najas flexilis* reached their highest values, were carried out in the Poznań Radiocarbon Laboratory (laboratory code – Poz). Both dates were calibrated using the OxCal v 4.10 programme (Bronk Ramsey 2009) with the IntCal09 calibration curve (Reimer et al. 2009; Tab. 2).

RESULTS

VEGETATION HISTORY AND CHRONOLOGY OF SEDIMENTS

To facilitate the description of results and discussion we used the division of the Holocene provided by Starkel et al. (1998).

Palynological analysis

Pollen diagrams are divided into local pollen assemblage zones (L PAZ) on principles given by Birks (1986) and Janczyk-Kopikowa (1987). Results of the pollen analysis are presented in Figs. 2, 3 and Tab. 3.

Romincka Forest (Fig. 2)

During the period reflected by the PR-1 L PAZ the pond was surrounded by forest dominated by pine and birch, with hazel thickets overgrown their understorey (Fig. 2). The important component of mixed and deciduous woodland was small-leaved lime (*Tilia cordata*). Damp and periodically inundated habitats were dominated by alder (*Alnus*), and where the water level was lower riparian forest with elm (*Ulmus*) and ash (*Fraxinus*) constituted. The assemblages were typical of the climatic optimum for the area of NE Poland (Kupryjanowicz 2007, Wacnik 2009, Lauterbach et al. 2011). At the beginning of the PR-2 L PAZ, hornbeam (*Carpinus*) and spruce (*Picea*) started to spread, especially the expansion of the latter taxon can be related to the early phase of the Subboreal chronozone, which was observed in the Lake Hańcza deposits, in which this phenomenon was dated at approx. 4900 cal. BP (Lauterbach et al. 2011). So then, the radiocarbon dating obtained from the depth below this episode, which revealed the age 5930–5746 cal. BP seems to be reliable.

Table 2. Radiocarbon datings

Site	Sample/Lab. code	Depth (cm)	Dated material	AMS ^{14}C age	Calib. age BP (2σ range)
Lake Linówek	Poz-35949	491–492	Fruits of *Betula* sp.	6100±70 BP	7166–6791
Romincka Forest	Poz-35950	604–606	Fruits of *Betula* sp.	5110±40 BP	5930–5746

Table 3. Romincka Forest and Lake Linówek. Description of local pollen assemblage zones (L PAZ)

Number and name of L PAZ	Depth (cm)	Description
Romincka Forest		
PR-2.	575–570	Rise in *Carpinus* (max. 1%) and *Picea* (max. 5%). Maximum in *Phragmites australis* t. values (0.5%).
PR-1.	620–575	The highest percentages *Alnus* (26%), *Ulmus* (10%), *Corylus* (20%), *Quercus* (11%), and *Tilia* (5.5%). *Pinus* (14.0–23.5%), *Betula* (11–17.5%). Low percentage curve of herbs, stable occurence of Poaceae, Cyperaceae and *Calluna vulgaris*. Gradual increase in *Potamogeton* subgen. *Eupotamogeton* (max. 1.2%). Filicales monolete and *Pteridium aquilinum* are almost in every spectrum.
Lake Linówek		
LL-2.	527.5–440	Increase in values trees and maximum in *Corylus avellana* (22.1%), *Alnus* (16.4%), *Ulmus* (19.4%), *Tilia* (12.6%), *Quercus* (9.6%) and *Fraxinus*. Constant occurrence of limnophytes among them pollen grains of *Nuphar*, *Nymphaea alba* (also idioblasts), *Potamogeton* subgen. *Eupotamogeton* occur. Presence of leaf spines of *Ceratophyllum* in bottom and middle part of phase. From 470 cm *Botryococcus* sharply increases. Decline in herbs, the most visible fall in Poaceae values. Decrease in Filicales monolete and *Thelypteris palustris* spores and rise the frequency of *Pteridium aquilinum*.
LL-1.	527.5–555	The highest values of *Pinus* (51.4%) and *Betula* (28.8%). High percentages of *Corylus avellana*. Continuous curves of *Alnus*, *Ulmus* and *Tilia*. Maximum in values of spores of Filicales monolete (11.4%) and *Thelypteris palustris* (4.6%). Stable presence of *Botryococcus* and *Pediastrum boryanum* var. *boryanum*.

On the base of the isopollen maps the presence of spruce in north-eastern Poland clearly had increased since 4000 ± 100 BP (Obidowicz et al. 2004). It is worth emphasizing that the isolated populations of spruce in the Suwalki region had existed during the Boreal chronozone, which was confirmed by the presence of its macroremains (needles, bud scales and seeds) near Lake Kojle and Perty (Gałka, unpublished data).

Lake Linówek (Fig. 3)

During the LL-1 zone, an important forest-forming element in the vicinity of the lake was pine (*Pinus*) and birch (*Betula*) while in the understorey probably dominated hazel (*Corylus*). The beginning of the LL-2 L PAZ brought the expansion of small-leaved lime (*Tilia cordata*) which displaced pine and birch from the part of well-drained habitats; however, this shift did not influenced hazel population. *Tilia* probably played a more important role in the site vicinity in comparison to the PR-1 L PAZ. In the moister areas, but not inundated, expanded woodlands similar to modern riparian forest in which elm (*Ulmus*), ash (*Fraxinus*) and oak (*Quercus*) dominated. On the other hand the alder carrs were slightly less represented among woodlands in comparison to the PR-1 L PAZ whereas elm seems that it was more widespread in damp habitats. The transition between LL-1 and LL-2 L PAZ is very similar to the episode visible in the deposits of Lake Hańcza situated in the Suwalski Lanscape Park in which the age of this phenomenon was dated at approx. 9000 cal. BP (Lauterbach et al. 2011). However, this episode recorded in the south-westerly situated Lake Miłkowskie was dated at approx. 8600 cal BP (Wacnik 2009). Hence, the radiocarbon dating obtained from the LL-2 L PAZ (in the layer above the aforementioned episode), which points to 7166–6791 cal. BP, might be recognized as matching to regional chronology. However, single radiocarbon date prevents from the establishment of more detailed assessment of the age in this case.

MACROFOSSILS ANALYSIS

Romincka Forest (Fig. 4, Tab. 4)

The presence of seeds of *Najas flexilis* was determined at a depth of 620–554 cm (Fig. 4, phase RF 1). The occurrence of seeds between those depths was not even. The largest accumulation of seeds, in the number of almost 40 seeds, was found at a depth of 620–604 cm. It is followed by almost entire lack of seeds. Only at a depth of 576 cm, their number increases again. At that site, no vegetative parts of *Najas flexilis* were found. During the existence of *Najas flexilis* in the lake, it was also inhabited by *Potamogeton natans*, *P. pusillus*, and *Nymphaea alba*. It is worth noting that a decrease in the number of *Najas flexilis* seeds in the sediment is accompanied by a clear increase in fruits of *Potamogeton natans* (at a depth of 604 cm).

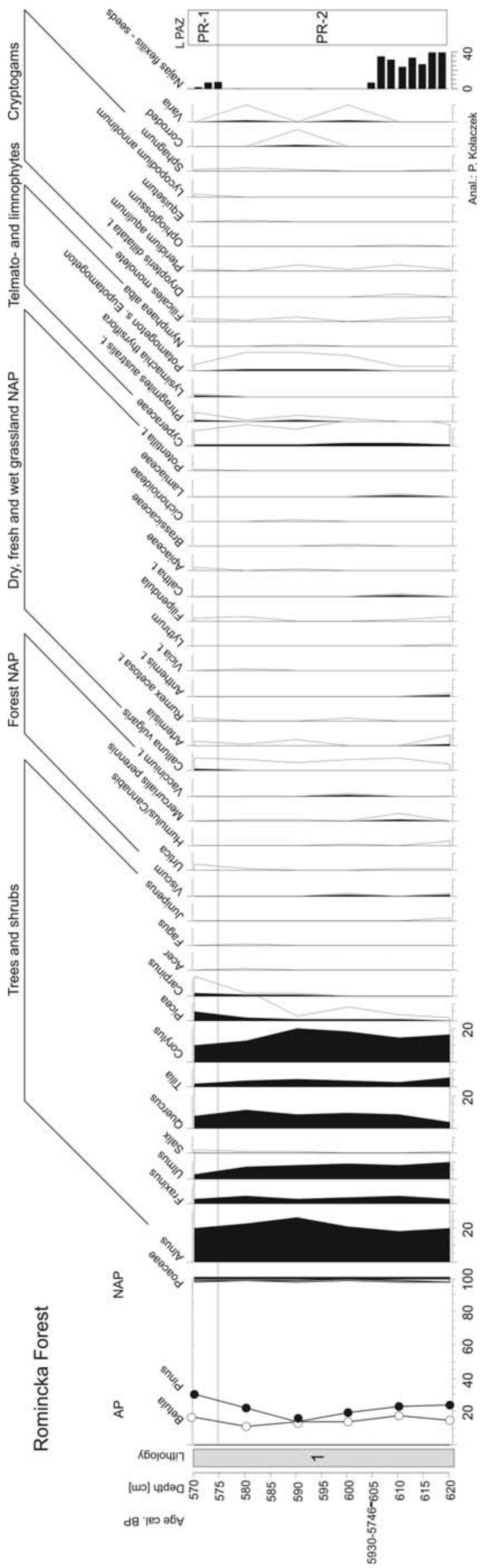

Fig 2. Percentage pollen diagram from Romincka Forest. Lithology: **1** – fine detritus gyttja, **2** – fine detritus gyttja with *Sphagnum* leaves

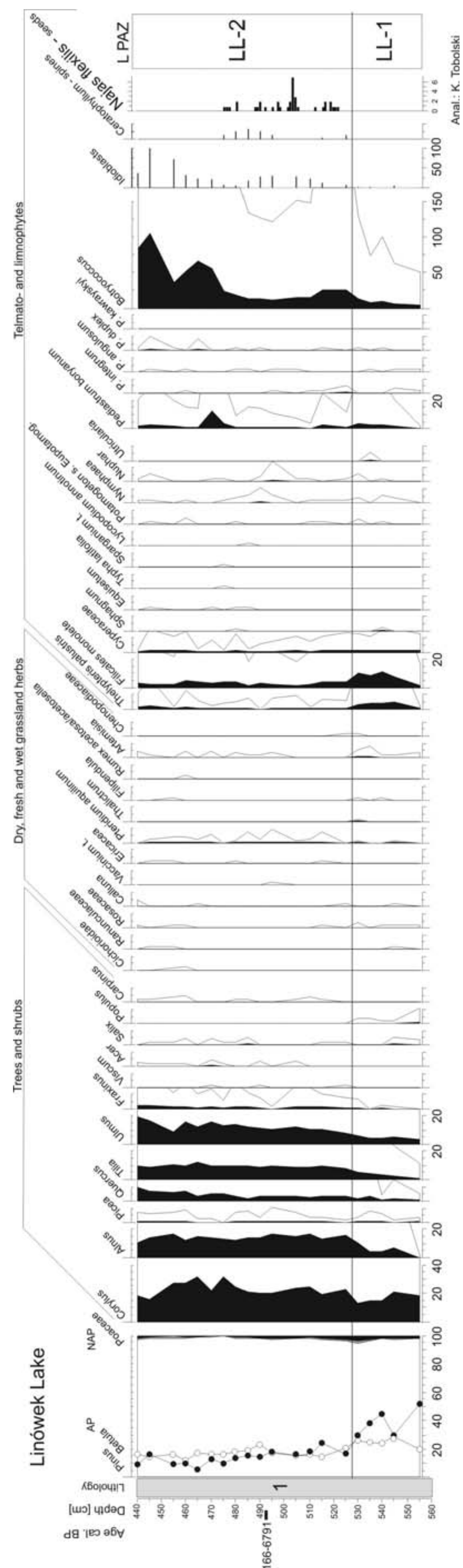

Fig. 3. Percentage pollen diagram from Lake Linówek. Lithology: **1** – fine detritus gyttja

Tab. 4. Romincka Forest and Lake Linówek. Description of macrofossil assemblage zones (L MAZ)

Number and name of LMAZ	Depth (cm)	Description
Romincka Forest		
RF 2	553–515	Complete disappearance of aquatic plants. Numerous leaves of *Sphagnum* sp. and several leaves of *Oxyccocus palustris.* Presence of *Betula pubescens* and *Pinus sylvestris.*
RF 1	620–553	Presence of *Najas flexilis*. The highest concentration seeds of *N. flexilis* in the bottom part of this phase. In the middle part only one seeds of *N. flexlis* at the depth 593 cm. Two species of *Potamogeton*: *P. natans* (max. 603 and 596 cm) and *P. pusillus* (max. 614 cm). Presence of trees: *Betula pubescens*, *Pinus sylvestris* and *Picea abies.*
Linówek Lake		
LL 3	475–450	Almost complete disappearance of submerged vegetation. Presence of *Nymphaea alba* and *Nuphar lutea*. In the bottom part of this phase presence of *Typha* sp.
LL 2	524–475	*Najas flexilis* (max. 7 seeds at the depth 503 cm). Three species of *Potamogeton*, most endocarps of *Potamogeton pussilus*. Next to *Pinus syvestis* and *Betula pubescens* is also *Tilia* sp. (508 cm). Almost constant presence of *Nymphaea alba* and *Nuphar lutea*.
LL 1	550–524	Numerous oospores of *Chara* sp. Four species of *Potamogeton*: *P. natans*, *P. pussilus. P. obtusifolius*, *P. gramineus.* At the depth 527 cm fruit of *Ceratophyllum demersum*. Among trees presence of *Pinus sylvestis* and *Betula pubescens*. Presence of *Carex pseudocyperus*, *Typha* sp. and *Rubus idaeus*.

At a depth from 574 to 515 cm, no macrofossils of macrophytes were found (Fig. 5, phase RF 2). In the upper part of the core analysed, in the sediment, fossils of peat bog plants were determined in the form of leaves of *Sphagnum* sec. *Sphagna*, leaves of *Oxycoccus palustris*, and a seed of *Andromeda polifolia*.

Lake Linówek (Fig. 5, Tab. 4)

Seeds of *Najas flexilis* were found in the sediment at a depth of 521–476 cm (Fig. 5, phase LL 2). Their highest concentration, i.e. 7 seeds, was determined in a sample from a depth of 503–502 cm. During the analysis, also fruits of

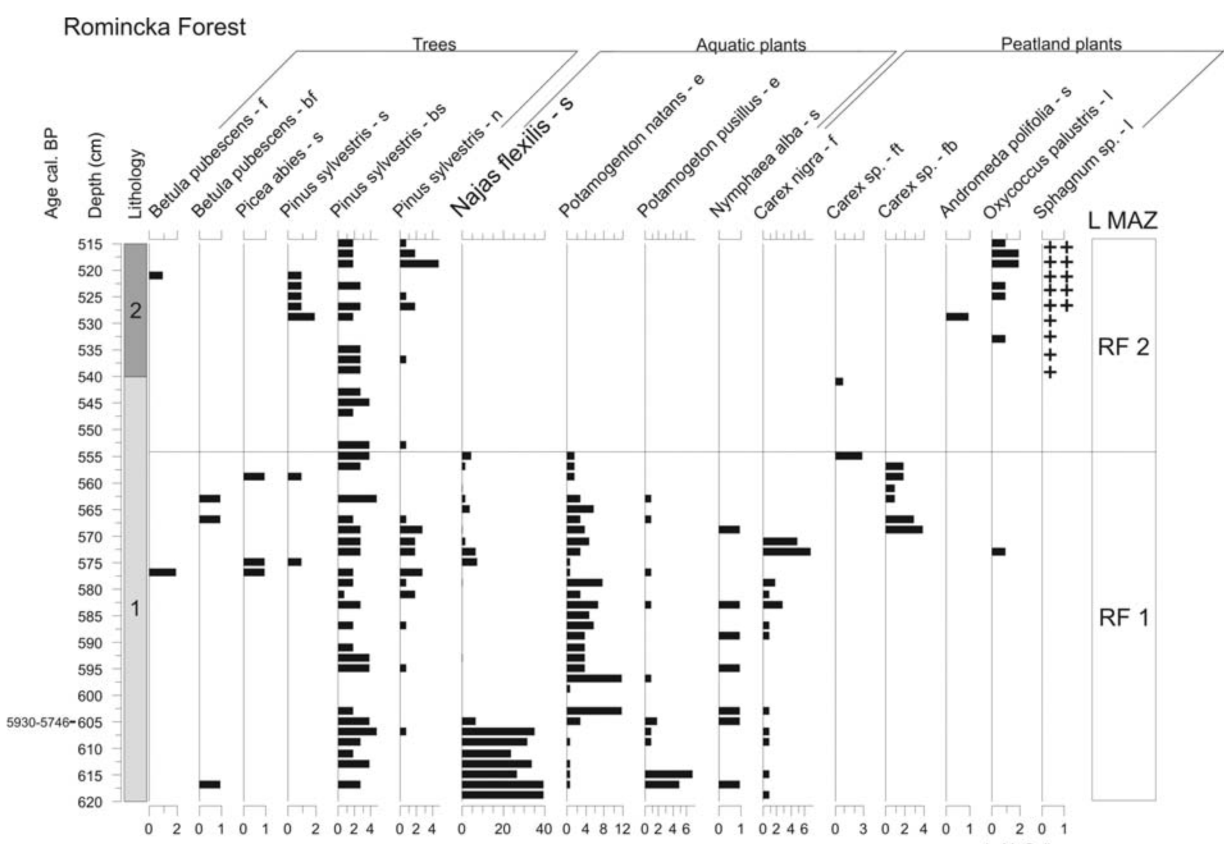

Fig 4. Plant macrofossils diagram of the section of profile from the Romincka Forest site. Description of plant remains: **s** – seed, **f** – fruit, **fb** – fruit biconvex, **ft** – fruit trigonous, **fs** – fruit scale, **o** – oospore, **e** – endocarp, **l** – leaf

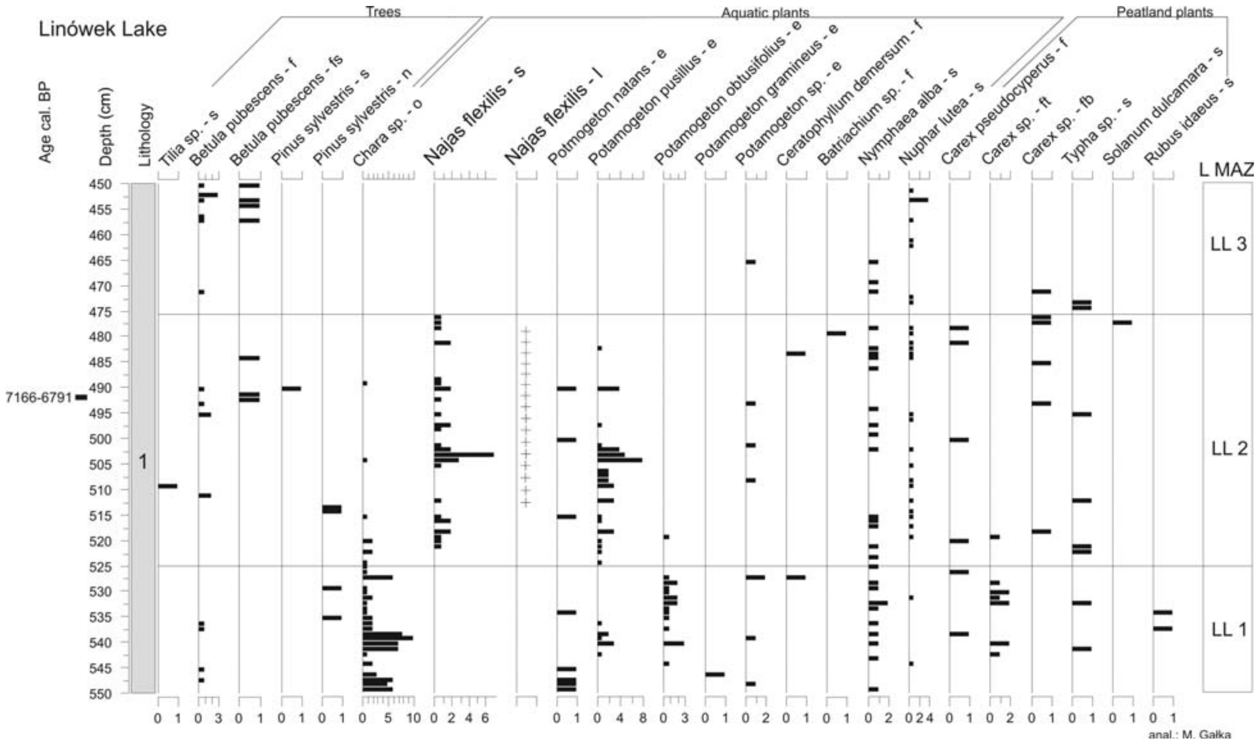

Fig. 5. Plant macrofossils diagram of the section of the Lake Linówek deposits. Description as in Fig. 4

Potamogeton were found, represented mainly by *P. pusillus*. In addition to pondweed, in the period of the occurrence of *Najas flexilis* in the lake, also the following species occurred: *Nymphaea alba*, *Nuphar lutea*, and *Ceratophyllum* sp. It is typical that the appearance of *Najas flexilis* in the lake is accompanied by a clear decrease in the participation of oospores of *Chara* sp. and endocarps of *Potamogeton obtusifolius* in the sediment (Fig. 5, phase LL 1). Attention is drawn by very numerous occurrence of vegetative organs (steams and leaves) of *Najas flexilis* at that site. Some samples did not include seeds, but only vegetative fragments of the plant.

DISCUSSION

TAPHONOMIC REMARKS

Only macroscopic findings, narrow-lanceolate seeds with hard shells (Fig. 6) and less-frequently vegetative parts of plants, are indicative of *Najas flexilis* occurrence in the past. Pollen grains of *Najas flexilis* are difficult to identify due to thin exine and indistinguishable sculpture (Sun et al. 2001), or even its complete lack as claims Lang (1994). In addition to the fact that such exine prevents their grains from long-term preservation, this species, as the hydrophilous pollinated plant, is a low pollen producer (Szczepanek 2003); therefore, it is hardly represented among pollen deposits. To sum up, these features make its pollen regularly skipped by authors of atlases (see e.g. Moore et al. 1991, Beug 2004).

WHY DID *NAJAS FLEXILIS* DISAPPEAR IN BOTH WATER BODIES?

The extensive expansion of the plant in Europe occurred in the Early Holocene, and even already in the Late Glacial, at sites on the British Isles (Godwin 1975) and in Finland (Mölder et al. 1957, Vasari et al. 2007).

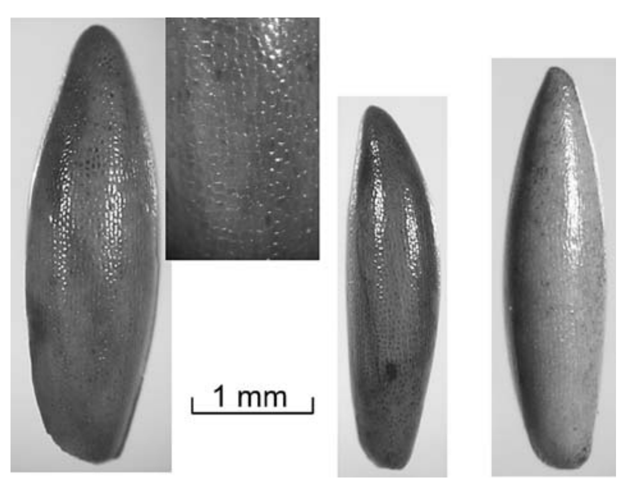

Fig 6. Seeds of *Najas flexilis* from Lake Linówek

The reason for the regression of *Najas flexilis*, often mentioned in the literature (Lang 1994), is related to gradual cooling of the climate, and therefore worsening of habitat conditions – water acidification. Based on a review of fossil sites, it can be determined that already in the Boreal chronozone *Najas flexilis* reached its maximum distribution (Samuelsson 1934, Backmann 1935, 1948, Godwin 1975, Lang 1994, Bennike et al. 2001).

In Poland *Najas flexilis* grew during different periods of the Holocene. Fossil seeds of *Najas flexilis* were found in the Boreal chronozone (Stasiak 1963, Bałaga 1990, Gałka 2006), from the Boreal to Atlantic chronozones (Marek 2000), in the Atlantic chronozone (Kowalewski & Żurek 2011), the Subatlantic chronozone (reappearance in Lake Łukcze; Bałaga 1990) and at other sites *Najas flexilis* was confirmed in the early 20th century (Zalewska 1999, Zalewska-Gałosz 2001). Since the Atlantic chronozone, the number of European sites decrease, subsequently continued in following periods (Lang 1994). However, a fall in temperature was probably an indirect cause of slender naiad disappearance, because the minimum mean July temperature required for *Najas flexilis* occurrence is 15°C (Aalbersberg & Litt 1998) and the mean July temperature after the Holocene Climatic Optimum has not fell below this value up to nowadays in north-eastern Poland (comp. Davis et al. 2003).

The intense terrestrialisation of both water bodies, simultaneous with climate worsening, probably resulted in the decrease in the number of plants. Lang (1994) points to the gradual transformation of water bodies into acidic habitats, as one of the mechanisms of the modern glacial-interglacial cycle. The disappearance of *Najas flexilis* in the water body in the Romincka Forest (Fig. 4, RF 2 L MAZ) can be related to a change in the trophic state which occurred as a result of the appearance of *Sphagnum* mosses in the close vicinity. The sediment layer located above the layer with determined *Najas flexilis* seeds includes numerous leaves of *Sphagnum* sec. *Sphagna.* The co-occurrence of macrofossils of *Sphagnum* and other plants of oligotrophic habitats such as *Andromeda polifolia* and *Oxycoccus palustris* in the sediment proves that a transitional peat bog started to develop around (Fig. 4, RF 2 L MAZ). Those processes were simultaneous to the expansion of spruce, which was a response to the fall in temperature and the rise in humidity during the Atlantic/Subboreal transition (Birks 1986). A consequent acidification of habitats might have triggered the development of the peat bog, and the retreat of submersed macrophytes. The disappearance of *Najas flexilis* corresponding to the *Picea* spread was recorded in Lithuania as well (Gaidamavičius et al. 2011). In the eastern part of Poland, in the Knyszyńska Forest, the time of decline of *Najas flexilis* was simultaneous to appearing of *Picea abies* (Marek 2000). But on this site – Stare Biele since the expansion of *Picea abies* had started, the lake level was lowering and the development of fen started, which was probably the direct cause of decline of *N. flexilis*. On the site in Tuchola Forest *Najas flexilis* disappeared in Atlantic (Kowalewski & Żurek 2011), which is connected with development of peat bog around the lake and acidification of the water. The development of fen and restriction of water surface was also the cause of disapperence of *N. flexilis* on the site in northern Poland – Mirowice (Gałka, unpublished data).

Samuelsson (1934) pointed to the habitat as the reason for the disappearance of *Najas flexilis* in Scandinavia. Moreover, Wingfield et al. (2006) claim that acidification next to eutrophication of the habitats of slender naiad is the main cause of its extinction, because the ability of seed production of *Najas flexilis* reduces after acidification. The other cause of slender naiad decline in the Romincka Forest site might be the spread of *Potamogeton natans* at the beginning of the Subboreal chronozone, which certainly restricted the light availability in the bottom of the water body. However, these processes are definitive cause of the slender naiad population disappearance, because afterward it occurred in sparse number. It is worth emphasizing that the largest accumulation of seeds (about 40 seeds/sample) was found before *P. natans* appeared (at a depth of 620–606 cm – RF 1 L MAZ, Fig. 4). The seeds of *N. flexilis* are usually detected singly or by a few occurrences (Bennike et al. 2001). Such a numerous deposition is a rare phenomenon and might be indicative of the decrease in the water table in the lake, taking into account Haas (1996) and Haas et al. (1998) who proved that shallowing of the water body induces the rise in the seed production of *N. flexilis*.

In the period of the disappearance of *Najas flexilis* within Lake Linówek (Fig. 5), a change of trophic state occurred as well. However, it was not related to a lowering of the lake level and the development of the a transitional peat bog, because after the *Najas flexilis* disappearance, detritus gyttja still accumulated and reached a thickness of 270 cm. In this case trophic changes are revealed by *Botryococcus* expansion convergent with *Najas flexilis* disappearance. Kawecka and Eloranta (1994) show that the blooms of *B. braunii* (a widespread species from this genus) occur in the surface layers of water in water bodies and they have an orange colour. These processes might have cut-off light availability which caused *Najas flexilis* retreat. The observation of Backman (1948) and Wingfield et al. (2004) clearly suggest that the optimum depth for slender naiad occurrence is about 2 m. However, in an extreme case, in which water transparency was sufficient, this species was found at a depth of 12–14 m (Lake Shoal, Manitoba-Ontario; Pip & Simmons 1986). Even though light availability might have been reduced by *Nuphar lutea* and *Nymphaea alba* that occurred simultaneously with slender naiad, there are no visible traces of the competition between naiad and these species in macrofossil deposition. Moreover, together with the final decline of *N. flexilis*, other submersed macrophytes retreated as well. Hence, the appearance of *Botryococcus* seems to be the crucial factor for the disappearance of *N. flexilis* in Lake Linówek.

ECOLOGICAL REMARKS

The literature often emphasises the fact of the present occurrence of *Najas flexilis* in waters rich in calcium carbonate (Piękoś-Mirkowa & Mirek 2003, Zalewska-Gałosz 2001, Sudnik-Wójcikowska 2004). On the other hand, Backman (1948) states that in Finland most sites are related to areas with little calcium content. A similar situation was observed in Great Britain, where *Najas flexilis* grows in non-calcareous environment as well (Wingfield et al. 2004). A wider ecological preferences of *Najas flexilis* is also evidenced by the fact of its simultaneous occurrence in Scandinavia with *Isoëtes lacustris* (Luther 1945, Backmann 1948), which is a well known indicator of oligotrophic environment (Ellenberg et al. 1991, Zarzycki et al. 2002). Also Bennike et al. (2001) note that *Najas flexilis* can grow in more oligotrophic and acid water in comparison to other two species of *Najas* (*N. marina* and *N. minor*). Hence, the results of the review of subfossil Holocene sites of *Najas flexilis* in the Polish sites, suggesting a growth on grounds poor in $CaCO_3$, are not an exception. In those sites, the seeds of slender naiad were found in detritus gyttja (e.g. Tuchola Pineforest – Gałka 2006, Kowalewski & Żurek 2011, Mirowice k. Świecia – Gałka unpublished data), similarly to the sites described in this article.

The interesting fact seems to be a coexistence of *Potamogeton pusillus* and *Najas flexilis* (endocarps of *P. pusillus* and seeds of *Najas flexilis* are simultaneously found in the samples of LL 2 L MAZ and RF 1 L MAZ, see Fig. 4 and 5). The sites show the lack of competition between both species, therefore, *P. pusillus* and *N. flexilis* probably formed vegetation assemblages in the past. Sites where these two plants grow together quoted Backman (1948) and Lang (1994). Lang (1994) observed, that *Najas flexilis* had been disappearing together with *Potamogeton pusillus* since the Atlantic period in the Schwarzwald. Given the contemporary presence of *Najas flexilis* and *P. pusillus*, Matuszkiewicz (2007) included them to the *Potamion* alliance, however, this author has not distinguished any special association for both taxa occuring together.

CONCLUSION

Based on the results obtained from the palaeobotanical studies, the reasons for the disappearance of *Najas flexilis* in the examined sites is connected with the change trophic state in the lakes. The disappearance of *Najas flexilis* in the site situated in the Romincka Forest can be related to a change of the trophy state in the water body, connected with the development of the transitional peat bog around the water body. This process started at the beginning of the Subboreal chronozone and was probably triggered by the development of forest communities with spruce. In the case of the disappearance of *Najas flexilis* in Lake Linówek, which was detected in the Atlantic chronozone, also trophic changes of water are suggested. It is significant that with the disappearance of *Najas flexilis* in Lake Linówek other submerged plants disappear as well, while *Botryococcus* increases sharply, and its blooms might have caused the deterioration of the water transparency.

The seeds of *Najas flexilis* were found in detritus gyttja, which proves that there is no close connection of this species with the calcareous ground. Both lakes reflected simultaneous optima of macrofossils deposition of *Najas flexilis* and *Potamogeton pusillus* which clearly suggest that both taxa built the plant community in former limnic environments.

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