Aquatic vegetation as an indicator of littoral habitats and various stages of lake aging in north-eastern Poland

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Abstract – The habitats of 356 phytocoenoses dominated by 15 species of aquatic plants were investigated. Among the properties of water, Na^+ , pH, total Fe, Ca^{2+} , NO_3^- , SO_4^{2-} , hardness and COD-KMnO₄ were the most important in differentiating the habitats of the phytocoenoses studied. Considerable physicochemical differences were found between the waters of the phytocoenoses of *Ranunculus circinatus* (hard waters rich in Na^+), *Nuphar pumila* (soft waters with high levels of total Fe), *Elodea canadensis*, *Ceratophyllum demersum* (alkaline waters) and *Stratiotes aloides* (waters containing high concentrations of Ca^{2+} and SO_4^{2-}). The substrate properties that best differentiated the habitats compared were PO_4^{3-} , hydration, organic matter content, total N, dissolved SiO₂, Ca^{2+} , Na^+ and pH. Patches of *R. circinatus* inhabited substrates containing the highest levels of PO_4^{3-} . Those of *S. aloides* were associated with substrates poor in PO_4^{3-} . Patches of *C. demersum* were confined to substrates rich in total N. Phytocoenoses of *R. circinatus* were associated with large lakes, whereas those of *N. pumila* were restricted mostly to smaller lakes. The deepest parts of lakes were inhabited by *Potamogeton lucens*. Phytocoenoses of *S. aloides* occurred mostly in shallow waters, on thick sediments. The investigated phytocoenoses also represent different stages of succession. The phytocoenoses of *Potamogeton perfoliatus*, *R. circinatus*, *Myriophyllum spicatum* and *Polygonum amphibium*, which develop on mineral substrates, initiate the process of succession, whereas those of *Myriophyllum verticillatum*, *Nymphaea candida*, *Nymphaea alba*, *N. pumila* and *S. aloides*, which inhabit highly hydrated organic substrates, are characteristic of the late stages of succession.

Key words: Submerged and floating-leaved phytocoenoses / habitat indicators / water and substrate analyses / process of succession / Water Framework Directive

Introduction

Aquatic plants and their communities are an important component of water ecosystems. They often occupy a large part of the littoral zone and as such constitute a land–water ecotone (e.g., Melzer, 1999; Lorens *et al.*, 2003). The allochthonous material derived from elsewhere that enters a body of water passes through the land–water interface and often undergoes changes (e.g., Misztal *et al.*, 2003). The aquatic vegetation also plays an important role in a number of natural and anthropogenic processes that occur within a body of water, such as circulation of nutrients (e.g., Carpenter and Lodge, 1986), eutrophication (e.g., Lind and Cottam, 1969; Blindow, 1992; Sand-Jensen *et al.*, 2000; Egerston *et al.*, 2004; Mäemets *et al.*, 2010), acidification (Roelofs, 1983; Arts *et al.*, 1990; Arts, 2002) and aging of bodies of water (e.g., Barko *et al.*, 1991; Marek, 1992; Van Groenendael *et al.*, 1996). Consequently, studies of

the relationships between macrophytes, the communities they form and their habitats have been conducted worldwide for many years (e.g., Pietsch, 1972; Wiegand, 1978; Papastergiadou and Babalonas, 1993a, 1993b; Toivonen and Huttunen, 1995; Nurminen, 2003; Lacoul and Freedman, 2006; Lumbreras *et al.*, 2008; Lukács *et al.*, 2009). These studies have been aimed at understanding the role that macrophytes play as indicators of change taking place in water ecosystems.

In connection with the formulation and implementation of the EU Water Framework Directive (European Commission, 2000), in recent years attempts have been made to develop standardized methods of assessing the ecological status of rivers and lakes based on aquatic plant and vegetation sampling (e.g., Schamburg *et al.*, 2004; Schneider, 2007; Penning *et al.*, 2008a, 2008b; Tóth *et al.*, 2008; McElarney and Rippey, 2009).

In Poland, studies on the ecology of aquatic vegetation have been conducted for several decades (e.g., Kłosowski, 1985, 1990; Szańkowski and Kłosowski, 2001). Data on

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the ecology of submerged lake vegetation (Kłosowski, 2006; Szańkowski and Kłosowski, 2006) and the bioindicator value of the plant communities occurring in astatic water bodies (Kłosowski and Jabłońska, 2009) were assessed.

The present work aims at summarizing the results of ecological studies conducted among the submerged and floating-leaved plant communities of the class Potametea occurring in the lakes of north-eastern Poland. The main objectives of the study were to determine the main environmental factors that best differentiate the habitats of the plant communities studied and the connection between plant communities and various stages of succession, establish the (bio)indicator value of plant communities, and discuss the results obtained and their relevance to the Water Framework Directive.

Material and methods

Phytosociological and habitat data were collected during the peak growing season (July–August) from 1978 to 2005. Due to the distinct character of the littoral zone of lakes (Pieczyńska, 1972; Planter, 1973) and hydrochemical differences even between neighbouring patches of vegetation within the various bodies of water (Úlehlová and Pribil, 1978; Gaudet and Muthuri, 1981; Kłosowski, 1992), the investigations were carried out on particular phytocoenoses, regardless of the trophic state of the lake. The patches were selected on the basis of floristic dominance. A total of 356 phytocoenoses of the class Potametea from 128 lakes were investigated (Fig. 1). The phytocoenoses dominated by the following 15 species were considered in the study (in brackets number of investigated phytocoenoses): *Hydrilla verticillata* (L. f.) Royle (14), *Ceratophyllum demersum* L. (25), *Ranunculus circinatus* Sibth. (20), *Elodea canadensis* Michx. (20), *Myriophyllum verticillatum* L. (24), *Myriophyllum spicatum* L. (26), *Potamogeton perfoliatus* L. (28), *Potamogeton lucens* L. (32), *Potamogeton natans* L. (33), *Nuphar lutea* (L.) Sibth. et Sm. (17), *Nuphar pumila* (Timm) DC (18), *Nymphaea alba* L. (21), *Nymphaea candida* C. Presl (30), *Polygonum amphibium* L. (18) and *Stratiotes aloides* L. (30).

In each phytocoenosis one phytosociological relevé (10–25 m² plot) was recorded, and water depth was measured at the deepest and shallowest point of the phytocoenosis taking into account the slope of lake bottom. The abundance of each species within the relevé area was counted according to a modified Braun–Blanquet scale in which + = a few scattered specimens, mean coverage 0.1%; 1 = 1–10% coverage, mean 5%; 2 = 10–25% coverage, mean 17.5%; 3 = 25–50% coverage, mean 37.5%; 4 = 50–75% coverage, mean 62.5%; 5 = 75–100% coverage, mean 87.5%. All the relevés recorded in the investigated phytocoenoses were aggregated into one synoptic phytosociological table. In addition, the constancy of each species was counted according to the following

scale: I = species present in 1–20% of relevés; II = 21–40%; III = 41–60%; IV = 61–80%; V = 81–100%.

In each phytocoenosis (within the relevé area) one water and one substrate sample were taken for physical and chemical analyses (356 water and 356 substrate samples in total). Both water and substrate samples were collected at the same time as the relevés were assessed (July–August). Water samples were taken from an intermediate depth at which a given phytocoenosis occurred and transferred to two 1000 mL plastic containers. Half of the water samples were preserved by the addition of 1 mL concentrated H₂SO₄ for PO₄^{3−}, NH₄⁺, NO₃[−], total Fe and COD-KMnO₄ analyses. Substrate samples were taken from the rhizome-root layer with a tubular bottom sampler and transferred to plastic bags. Each sample was a mixture of three random subsamples taken within a phytocoenosis. Both water and substrate samples were transported to the laboratory within 3–5 h of collection and the determinations were carried out immediately. Prior to the analyses, the samples were filtered and stored at 4 °C until all analyses were performed. Altogether 14 physical and chemical parameters of water, 12 of the substrate, mean water depth in which the phytocoenoses occurred and lake surface area were determined.

The following analyses were carried out on water samples: pH using pH-meter; total hardness using Warthy–Pfeifer sodium mixture and by titration with EDTA reagent and Man Ver 2 as indicator; carbonate hardness by titration with 0.01 N HCl using methyl orange as an indicator; chemical oxygen demand (COD) as consumption of KMnO₄ in acid medium; PO₄^{3−} spectrophotometrically by the molybdate method; NO₃[−] spectrophotometrically with phenoldisulphonic acid; NH₄⁺ by distillation and spectrophotometrically by Nessler's method; total Fe spectrophotometrically by the rhodanate method; dissolved SiO₂ spectrophotometrically by the molybdate method; SO₄^{2−} spectrophotometrically by the nephelometric method; colour spectrophotometrically according to the platinum–cobalt scale; Ca²⁺, Na⁺ and K⁺ with a flame spectrophotometer Flapho 4. Concentrations of K⁺ and Na⁺ were determined in 100 mL solutions extracted with 2 mL HCl 1 + 1 (mixture of one part of concentrated acid to one part of demineralized water from evaporated and ignited 100 mL samples of water).

In the substrate samples, pH was assessed in pore water. Concentrations of dissolved SiO₂ and NO₃[−] were determined in solutions extracted by the addition of 100 mL of demineralized water to a substrate sample containing 1 g of dry matter (water extracts). In the case of solutions used for determinations of total Fe, PO₄^{3−}, Ca²⁺ and SO₄^{2−}, each substrate sample containing 1 g of dry matter was first digested in 20 mL HCl 1 + 1 for 2 h and then 100 mL of demineralized water was added (acid extracts). After 24 h all the extracted solutions (water and acid) were filtered, rinsed with small amounts of demineralized water and the final quantities of the extracted solutions were adjusted to 250 mL. Hydration (water content) was determined by drying substrate samples at 105 °C to constant weight, organic matter content by

Fig. 1. The study area in north-eastern Poland. The dots represent the lakes that have been sampled.

ignition of dry samples at 550 °C for 1.5 h and total N by Kjeldahl's method. The concentrations of K^+ and Na^+ in substrate were determined in 100 mL solutions extracted with 2 mL HCl 1 + 1 from dried and ignited samples. The analyses from water and acid extracts, and the determinations of Na^+ , K^+ and pH were conducted by the methods described above.

Most of the determinations of water and substrate properties were carried out by methods described by Hermanowicz *et al.* (1999). Determinations of total hardness were performed according to the procedures described by Hermanowicz *et al.* (1999) and Hach Company (1992).

Data processing

The relationships between species composition of vegetation types were analysed by indirect ordination in CANOCO for Windows Version 4.0 (Ter Braak and Šmilauer, 1998). Indirect ordination methods were also used to choose between unimodal or linear ordination methods based on the lengths of gradient (DCA) and in search of arch-effect and outliers (CA).

The relationships between habitat factors and vegetation were analysed by direct ordination in CANOCO for Windows v. 4.0 (Ter Braak and Šmilauer, 1998). As the length of gradient in DCA exceeded 3 SD – CCA was used (Jongman *et al.*, 1987). To avoid using strongly correlated variables in CCA, a variance inflation factor was analysed – no habitat variable showed a high correlation with the other variables ($VIF > 20$, cf. Ter Braak, 1986), so there

was no need to remove any variable from the analysis on the basis of VIF values. A forward selection was performed to determine which variables have the greatest effect on macrophyte ecology. Only variables that were significant ($p < 0.05$) and explained more than 0.5% of the overall species diversity were used in the final CCA analysis. The significance of CCA (first canonical axis and all canonical axes) was tested with the Monte-Carlo permutation test, using unrestricted permutations.

The habitat conditions of the 15 types of phytocoenoses investigated were compared with respect to each property using quartiles. The significance of differences in water and substrate properties between the plant communities studied was determined by the Kruskal–Wallis test and non-parametric multiple comparisons (Zar, 1984).

Results

Characteristics of the phytocoenoses studied

The phytocoenoses studied were characterized by a strong dominance of one species, *i.e.*, species with high constancy (class V) and cover (3–5 according to the Braun–Blanquet scale) (Table 1). Patches of *R. circinatus*, *E. canadensis*, *P. perfoliatus*, *M. spicatum* and *P. amphibium* had a higher frequency of species with submerged leaves than floating-leaved species among the Potametea species. Phytocoenoses of *E. canadensis* and *P. perfoliatus* were characterized by a higher proportion of *Lemna trisulca* L. Patches with *M. verticillatum*, *C. demersum*,

Table 1. Continued.

Phytocoenose type Number of relevés Number of lakes	RC	EC	PP	PL	MS	MV	HV	CD	PA	PN	NL	NA	NP	NC	SA
<i>Glyceria maxima</i> (Hartm.) Holmb.	20	14	18	23	20	15	7	19	11	26	16	16	5	11	23
<i>Sparganium erectum</i> L.	5								I ⁺	I ⁺					
<i>Chara rudis</i> A. Br.				I ²											I ⁺
<i>Sagittaria sagittifolia</i> L.							I ⁺								
<i>Riccia fluitans</i> L.								I ⁺	I ⁺						
<i>Lysimachia thyrsiflora</i> L.															
<i>Chara</i> sp.															
<i>Thelypteris palustris</i> Schott										I ⁺			I ⁺		I ⁺
<i>Menyanthes trifoliata</i> L.															
<i>Cicuta virosa</i> L.															
<i>Rumex hydrolapathum</i> Huds.															I ⁺
<i>Mentha aquatica</i> L.															I ⁺
<i>Calla palustris</i> L.															I ⁺
<i>Salix pentandra</i> L.															I ⁺

RC, *Ranunculus circinatus*; EC, *Elodea canadensis*; PP, *Potamogeton perfoliatus*; PL, *P. lucens*; MS, *Myriophyllum spicatum*; MV, *M. verticillatum*; HV, *Hydrilla verticillata*; CD, *Ceratophyllum demersum*; PA, *Polygonum amphibium*; PN, *Potamogeton natans*; NL, *Nuphar lutea*; NA, *Nymphaea alba*; NP, *Nuphar pumila*; NC, *Nymphaea candida*; SA, *Stratiotes aloides*. I, II, ..., V, constancy; +, 1, 2, ..., 5-abundance.

P. natans, *P. lucens*, *N. alba*, *N. candida* and *N. lutea* typically included more floating-leaved species. Both submerged and floating-leaved species were noted frequently in the phytocoenoses dominated by *H. verticillata* and *N. pumila*. The *S. aloides* phytocoenoses had the highest proportion of free-floating species such as *Lemna minor* L., *L. trisulca* and *Hydrocharis morsus-ranae* L. Reed swamp species did not play an important role in the structure of the communities studied, with the exception of *Equisetum fluviatile* L. in the phytocoenoses of *N. pumila*, *Typha latifolia* L. in the phytocoenoses of *S. aloides* and *Phragmites australis* (Cav.) Trin. ex Steud. in the patches of *P. amphibium*, *N. lutea*, *N. alba* and *S. aloides*.

Environmental properties

The differentiation of the 15 types of phytocoenoses in relation to environmental properties (amplitude, inter-quartile ranges of values and medians) is shown in Figure 2 (see Appendix 1 online supporting material at www.limnology-journal.org for the significances of differences). In CCA we took into account 24 variables (Table 2). The four main ordination axes showed high eigenvalues (λ): I- $\lambda_1 = 0.655$, II- $\lambda_2 = 0.527$, III- $\lambda_3 = 0.473$, IV- $\lambda_4 = 0.543$, respectively. Therefore, we analysed the phytocoenosis-habitat relationships along a gradient of all four axes (Figs. 3–5). Here we focus on discussing those variables that were most strongly correlated with the ordination axes.

The analysis of the first and second ordination axes (Fig. 3) revealed that the properties that best differentiated the habitats of the communities studied were hydration, organic matter, total N, PO_4^{3-} , dissolved SiO_2 (in the case of substrates), Na^+ (in the case of water) as well as lake surface area. All the above-mentioned variables were correlated with the first ordination axis. Water variables correlated with the second ordination axis, such as pH, Ca^{2+} , NO_3^- and COD-KMnO₄, also played an important role in differentiating the habitats. Hydration, organic matter and total N content differentiated the substrates of the communities studied into two groups. Low values of these parameters were found for *P. amphibium*, *M. spicatum*, *P. perfoliatus* and *R. circinatus* phytocoenoses, whereas *C. demersum*, *N. candida*, *N. alba*, *M. verticillatum*, *N. pumila*, *H. verticillata* and *S. aloides* were distinguished by high values. *P. lucens*, *E. canadensis* and *N. lutea* occupied an intermediate position. The first four types of phytocoenoses were restricted mainly to large lakes, whereas the remaining communities were usually found in smaller lakes. The PO_4^{3-} content and dissolved SiO_2 differentiated the substrates of the communities studied in a different manner. The highest values of PO_4^{3-} were recorded in the substrates of *R. circinatus*, with lower levels for *C. demersum*, and the lowest values in the case of *S. aloides*, *N. pumila* and *N. lutea*. The concentration of dissolved SiO_2 showed the opposite trend compared to that of PO_4^{3-} . Na^+ concentration and pH in water differentiated the communities studied in the same

Fig. 2. Differentiation of the 15 types of water plant phytocoenoses studied in relation to (a) 14 physicochemical properties of water and mean water depth in which the phytocoenoses occurred and (b) 12 physicochemical properties of substrate and lake surface area. Black boxes indicate 25–75% interquartile ranges of values and white boxes show the medians. Abbreviations of phytocoenoses (dominant species): RC, *Ranunculus circinatus*; EC, *Elodea canadensis*; PP, *Potamogeton perfoliatus*; PL, *P. lucens*; MS, *Myriophyllum spicatum*; MV, *M. verticillatum*; HV, *Hydrilla verticillata*; CD, *Ceratophyllum demersum*; PA, *Polygonum amphibium*; PN, *Potamogeton natans*; NL, *Nuphar lutea*; NA, *Nymphaea alba*; NP, *Nuphar pumila*; NC, *Nymphaea candida*; SA, *Stratiotes aloides*.

Fig. 2. Continued.

Table 2. Correlation coefficient of environmental variables with CCA axes.

Axes	I	II	III	IV
S-pH	0.2061	0.1425	0.2936	–0.1839
S-hydration	–0.6995	–0.2610	–0.0262	–0.2121
S-organic matter	–0.5235	–0.1878	–0.0234	–0.1399
S-total N	–0.3728	–0.2466	–0.1068	–0.0637
S-Ca ²⁺	–0.1671	–0.0277	0.2815	–0.2124
S-Na ⁺	–0.1772	0.1200	0.1143	–0.3140
S-total Fe	–0.1777	–0.1060	0.0199	0.0721
S-NO ₃ [–]	–0.1917	0.1621	–0.2025	–0.2428
S-PO ₄ ^{3–}	0.4369	–0.2741	–0.1729	–0.1406
S-dissolved SiO ₂	–0.3277	0.1847	–0.1496	–0.2408
W-pH	0.2128	–0.3597	–0.0367	0.0734
W-total hardness	0.1679	–0.2679	0.0627	–0.3115
W-carbonate hardness	0.0730	–0.1844	0.1646	–0.3724
W-colour	–0.2324	0.0543	–0.1947	–0.1993
W-COD-KMnO ₄	–0.1208	–0.2584	–0.2257	–0.0943
W-Ca ²⁺	0.1204	0.3214	0.0470	–0.3342
W-Na ⁺	0.5370	–0.2090	–0.0448	–0.3228
W-total Fe	–0.2857	–0.1350	–0.1546	0.2749
W-NO ₃ [–]	–0.0959	0.3249	–0.1063	–0.1360
W-PO ₄ ^{3–}	–0.1288	0.0844	–0.1489	0.0347
W-SO ₄ ^{2–}	0.0864	0.2832	0.3421	–0.2377
W-dissolved SiO ₂	–0.2368	0.0686	–0.0190	–0.3839
Average water depth	0.0523	–0.1985	0.4482	0.1869
Lake area	0.3059	0.1415	–0.0866	–0.0761

S, substrate; W, water.

way as PO₄^{3–} in substrates. Levels of Ca²⁺ in waters of the communities studied differed considerably. The highest values of Ca²⁺ were detected in the waters of *P. perfoliatus* and *N. lutea*, and the lowest in those of *N. candida*, *M. verticillatum*, *N. pumila*, *H. verticillata* and *C. demersum* (Fig. 2). Communities of *S. aloides*, *P. perfoliatus*, *N. lutea* and *N. pumila* were distinguished from those of *C. demersum*, *E. canadensis* and *N. candida* by much higher values of NO₃[–]. COD-KMnO₄ is used to estimate the amount of dissolved organic matter in water. This parameter differentiated the habitats of the communities studied into two groups. The phytocoenoses of *P. perfoliatus*, *P. amphibium*, *P. lucens* and *S. aloides* were associated with waters containing low amounts of dissolved organic matter, whereas those of *C. demersum*, *E. canadensis* and *N. candida* developed in waters rich in dissolved organic matter.

The third ordination axis (Fig. 4) represents most of the variance resulting from differentiation of the plant communities in relation to water depth, SO₄^{2–} concentration in the water, substrate pH and substrate Ca²⁺ content. These four parameters were most strongly correlated with the third ordination axis (Table 2). The deepest parts of lakes were inhabited by phytocoenoses of *P. lucens*, *M. verticillatum* and *N. candida*. The *S. aloides* and *E. canadensis* phytocoenoses were associated with the shallowest waters (Fig. 2). SO₄^{2–} concentration differentiated waters of the communities studied into two groups. The first group included phytocoenoses of *P. lucens* and *N. lutea* developed in waters with the highest

concentration of SO₄^{2–} (Fig. 2). The second group included *N. pumila*, *C. demersum*, *E. canadensis* and *H. verticillata* and formed in waters poor in SO₄^{2–}. The substrates of the communities studied differed considerably with respect to pH. The *N. pumila* phytocoenoses were associated with the most highly acidic substrates, whereas *P. perfoliatus*, *M. spicatum* and *R. circinatus* inhabited alkaline substrates (Fig. 2). Substrates of *P. natans*, *N. alba*, *H. verticillata* and *S. aloides* communities had the highest content of Ca²⁺, whereas *N. pumila*, *P. amphibium*, *P. perfoliatus* and *E. canadensis* inhabited substrates poorer in Ca²⁺.

The fourth axis (Fig. 5) represents most of the variance resulting from habitat differentiation in relation to Ca²⁺ concentration in water, total hardness and carbonate hardness, as well as Na⁺ content in the substrates. Particularly noteworthy were patches of *N. pumila* that developed in soft waters poor in Ca²⁺, and those of *R. circinatus* associated with hardest waters. The *H. verticillata* phytocoenoses were also found in relatively soft waters containing low amounts of Ca²⁺, whereas *N. lutea* showed preference for harder waters having higher concentrations of Ca²⁺ (Fig. 2).

Among the remaining properties, the total Fe concentration in water is worthy of note. This parameter was correlated to a similar degree with the first and fourth ordination axes (Table 2). The highest values of total Fe were noted in the waters of *N. pumila*, and lowest values in those of *P. amphibium* (Fig. 2).

Discussion

The results obtained in this study indicate that in spite of the highly unstable habitat and biotope conditions in the littoral zone dominated by macrophyte communities and the high degree of plasticity of aquatic plants (Hinneri, 1976; Willby *et al.*, 2000, Chambers *et al.*, 2008), clear relationships exist between particular types of phytocoenoses and their habitats. In addition to the depth in which the phytocoenoses occurred and the lake surface area, these vegetation–habitat relationships include both water and substrate properties. The water properties that best differentiated the habitats of the aquatic plant associations studied were Na⁺, SO₄^{2–}, dissolved SiO₂, total Fe, Ca²⁺ and water hardness, pH, dissolved organic matter (COD-KMnO₄) and NO₃[–]. The substrates compared were best differentiated by the following properties: hydration, organic matter, total N, PO₄^{3–}, dissolved SiO₂, Ca²⁺, Na⁺ and pH.

The greatest differences between the habitats of the associations studied were found in the case of *R. circinatus* (larger lakes, hard, alkaline waters that are particularly rich in Na⁺, and mineral substrates with high PO₄^{3–} content) and *N. pumila* (small lakes, soft waters that are particularly poor in Na⁺ and SO₄^{2–}, but rich in total Fe, and acidic substrates containing low amounts of Ca²⁺). The remaining plant communities compared in this study were usually distinguished by several properties,

Fig. 3. CCA ordination diagram of I and II axes obtained from 356 relevés and 12 water properties, mean water depth in which the phytocoenoses occurred, lake surface area and 10 substrate properties. The dominant species of the 15 types of water plant phytocoenoses studied were plotted. Eigenvalues: $\lambda_1 = 0.655$, $\lambda_2 = 0.527$, $\lambda_3 = 0.473$, $\lambda_4 = 0.453$. The significance of first canonical axis and all canonical axes tested with Monte-Carlo permutation test; $p < 0.01$. See Figure 2 for the abbreviations of phytocoenoses.

e.g., *C. demersum* and *E. canadensis* (small lakes, alkaline waters rich in dissolved organic matter), and *S. aloides* (very shallow waters, strongly hydrated substrates, both water and substrate rich in dissolved SiO_2).

How do our findings compare with those of other authors, aimed at developing universal methods of assessing the ecological status of lakes and rivers based on macrophyte composition (European Commission, 2000). The majority of these other studies are concerned with the relationships between macrophytes and water quality in bodies of water (Pietsch, 1972; Wiegand, 1978; Papastergiadou and Babalonas, 1993a, 1993b; Lukács *et al.*, 2009; Lumbreras *et al.*, 2008). Many authors take into account the general limnological conditions in a lake, such as its morphometry (size and shape of the lake basin) and/or geographical coordinates, when investigating the occurrence of aquatic plants and their communities (Vestergaard and Sand-Jensen, 2000; Heegaard *et al.*, 2001; Mäkelä *et al.*, 2004; McElarney and Rippey, 2009; Free *et al.*, 2009; Del Pozo *et al.*, 2010; Sass *et al.*, 2010). The present studies were consistently conducted within dense stands of macrophytes from which the water and substrate samples were taken for analysis and the particular properties were determined. It seems, therefore, difficult to compare such data. However, in the case of

water, the results of our study confirmed the findings of other authors, who point to the important role of properties associated with the carbonate system in differentiating the habitats of aquatic plant communities (Wiegand, 1978; Kadono, 1982; Kunii, 1991; Papastergiadou and Babalonas, 1993a, 1993b; Toivonen and Huttunen, 1995; Vestergaard and Sand-Jensen, 2000). Changes in the carbonate system affect the amount of available inorganic carbon as well as such properties as water hardness, pH, and Ca^{2+} and Na^+ concentrations. The properties indicating water richness, such as COD-KMnO_4 , NO_3^- and PO_4^{3-} , appear to be important as well, but not as important as the factors associated with the carbonate system, which may be attributed to the small differences in the trophic state of the lakes studied (from slightly eutrophic to eutrophic lakes). Similar observations were also made by others (Jackson and Charles, 1988; Kunii, 1991; Mäkelä *et al.*, 2004).

Our results are in agreement with the data reported from works of other authors for most of the investigated plant communities. For example, the relationship of *C. demersum* to hard, alkaline waters was indicated by Moyle (1945), Kadono (1982), Pietsch (1982), De Lyon and Roelofs (1986a, 1986b), Pip (1988), Papastergiadou and Babalonas (1993a, 1993b) and Vestergaard and

Fig. 4. CCA ordination diagram of I and II axes obtained from 356 relevés and 12 water properties, average water depth in the phytocoenoses, lake surface area and 10 substrate properties. The dominant species of the 15 types of water plant phytocoenoses studied were plotted. Eigenvalues: $\lambda_1 = 0.655$, $\lambda_2 = 0.527$, $\lambda_3 = 0.473$, $\lambda_4 = 0.453$. The significance of first canonical axis and all canonical axes tested with Monte-Carlo permutation test: $p < 0.01$. See Figure 2 for the abbreviations of phytocoenoses.

Sand-Jensen (2000). Similar observations were made with regard to *R. circinatus* (e.g., Wiegleb, 1978; Pietsch, 1982; De Lyon and Roelofs, 1986a, 1986b). Lumberras *et al.* (2008) pointed to the great variety of habitats of plant communities dominated by various aquatic *Ranunculus* species. In their recent publication, Lukács *et al.* (2009) reported that the phytocoenoses of *P. lucens* occurred in waters rich in Ca^{2+} . Pietsch (1982) indicated that *P. perfoliatus* was also associated with waters with high Ca^{2+} concentrations, whereas *M. verticillatum* developed best in waters containing low levels of PO_4^{3-} . Relatively low concentrations of P in waters of the latter community were also confirmed by Wiegleb (1978), De Lyon and Roelofs (1986a, 1986b) and Mäkelä *et al.* (2004). De Lyon and Roelofs (1986a, 1986b) and Heegaard *et al.* (2001) demonstrated that the phytocoenoses of *M. spicatum* have a broad ecological amplitude with respect to properties of water, and developed best in waters relatively rich in SO_4^{2-} .

Our results also confirm the distinct character of the habitats of some floating-leaved plant communities, particularly the phytocoenoses of *N. pumila*, which are found in mostly nutrient-rich (Roweck, 1988; Kozłowski and Eggenberg, 2005) soft waters, poor in Ca^{2+} (Kadono, 1982; Roweck, 1988; Kłosowski and Tomaszewicz, 1990; Doll, 1991). The results obtained by some authors confirm our findings for *N. lutea* (waters rich in Ca^{2+}

and NO_3^- – Wiegleb, 1978; hard alkaline waters – De Lyon and Roelofs, 1986a, 1986b; Smits *et al.*, 1988), *N. candida* (mesotrophic or slightly eutrophic waters – Pietsch, 1982; narrow ecological amplitude with respect to Ca^{2+} – Van der Velde *et al.*, 1986) and *P. amphibium* (waters relatively poor in NH_4^+ – Wiegleb, 1978). Some authors, however, present different results regarding the phytocoenoses dominated by a particular species. For example, Wiegleb (1978) and Pietsch (1982) indicated the relationship of *C. demersum* to waters rich in NO_3^- , which was not confirmed by our study. Perhaps NH_4^+ plays a more important role in influencing the distribution of *C. demersum*. These differences may result from regional differences between the habitats, changes in a number of complex factors and ecological plasticity of aquatic plants.

Despite many methodological differences that exist between studies, our findings concerning the relationship between macrophytes and properties of water agree to a large extent with the results of many other studies. Since the size of the dataset being analysed is large (15 types of phytocoenoses from 128 lakes), it could be used to implement the Water Framework Directive (European Commission, 2000). The data may prove particularly useful in determining specific groups of aquatic macrophytes that can be used as indicators of water quality (sensitive, tolerant and indifferent

Fig. 5. CCA ordination diagram of I and IV axes obtained from 356 relevés and 12 water properties, average water depth in the phytocoenoses, lake surface area and 10 substrate properties. The dominant species of the 15 types of water plant phytocoenoses studied were plotted. Eigenvalues: $\lambda_1 = 0.655$, $\lambda_2 = 0.527$, $\lambda_3 = 0.473$, $\lambda_4 = 0.453$. The significance of first canonical axis and all canonical axes tested with Monte-Carlo permutation test: $p < 0.01$. See Figure 2 for the abbreviations of phytocoenoses.

species – Penning *et al.*, 2008a). Moreover, these data could help increase our knowledge about the ecology and habitat requirements of many species. This is a particularly important task since the data of Penning *et al.* (2008a) show that in the REBECCA macrophyte database, established to provide scientific support for the implementation of the EU Water Framework Directive, the number of lakes from different countries is not comparable (e.g., Poland – 5 lakes, Romania – 19 lakes, Sweden 254 lakes, Finland – 527 lakes).

The situation is completely different for substrates. Although the role of substrates as an anchorage for roots of aquatic vegetation and nutrient source as well as the place where the decomposition, sedimentation and accretion processes occur has been well recognized (Barko *et al.*, 1991 and literature cited therein), the relationships between plant communities and substrates have been less frequently studied. Hence, there are only a few studies with which to compare our findings. De Lyon and Roelofs (1986a, 1986b) indicated that *P. perfoliatus* and *E. canadensis* occurred frequently on mineral substrates, whereas *C. demersum*, *N. alba*, *N. candida* and *S. aloides* were associated mostly with organic substrates, which is in agreement with the results of our study. In some phytosociological works, the relationship of *C. demersum* to organic substrates was also demonstrated (e.g., Doll,

1991), and in the case of *N. alba* confirmed by Rejewski (1981). Roweck (1988) and Kozłowski and Eggenberg (2005) indicated that the phytocoenoses of *N. pumila* were confined to organic substrates. The data obtained by other authors (e.g., De Lyon and Roelofs, 1986a, 1986b; Van Katwijk and Roelofs, 1988) show that the phytocoenoses dominated by species such as *P. natans*, *P. lucens*, *N. lutea*, *M. spicatum* and *M. verticillatum* have a wide ecological amplitude with respect to substrate properties.

It should be noted that substrate data (as opposed to water) have not been used in aquatic macrophyte community indices defining the ecological status of lakes (e.g., trophic indices – TI; lake trophic ranking index – LTR, see Penning *et al.*, 2008b). It is undoubtedly much easier to use water properties (e.g., total P, Secchi depth, chlorophyll-*a* concentration) to determine the indices. The averaged hydrochemical data can be representative for the lake due to mixing of all the water in the lake. It is difficult to calculate the average values for the properties of substrates from mixed samples taken within the aquatic vegetation growth zone due to the high degree of spatial heterogeneity of the littoral sediments (Spence, 1967, 1982; Nôges and Kisand, 1999; Schmieder and Lehmann, 2004) and the presence of dense stands of macrophytes that differentiate and stabilize the bottom sediments (James and Barko, 1990; Barko *et al.*, 1991). As a result, there is

Fig. 6. Mean values of the organic matter content and water content in substrate in the 15 types of water plant phytocoenoses compared.

limited mixing of sediment. Despite many methodological problems, substrate properties should also be considered when assessing the ecological status of lakes, as indicated by Penning *et al.* (2008b). Therefore the new data on the relationships between aquatic plant communities and substrate properties from the 128 lakes included in our study may prove to be significant.

Our study showed that the substrate properties that best differentiated the habitats of the plant communities were primarily hydration and organic matter content. These parameters could be used in assessing the ecological condition of a lake. Changes in organic matter content and quality in substrates not only affect the vegetation structure but also lead to changes in the species composition of plant communities in the littoral zone (Barko and Smart, 1983, 1986). Since it is generally recognized that sediment deposition and an increase in organic matter content take place during the aging process of lakes (e.g., Misra, 1938; Wilcox and Simonin, 1987; Barko *et al.*, 1991; Van Groenendael *et al.*, 1996), plant communities associated with substrates containing different amounts of organic matter could serve as indicators of the succession process.

Some plant communities are associated with mineral substrates in the early stages of succession, whereas others are confined to organic substrates in the late stages of this process. This is clearly evident when the substrates of all the plant communities investigated in this study (data from several tens of lakes) are arranged in order of increasing organic matter content and degree of hydration (Fig. 6). Sediments in the late stages of succession are highly hydrated in the upper layers (Kłosowski, 1990). Therefore, many plant communities are not able to develop as their dominant species need a firm substrate for anchorage. This eventually leads to the formation of floating mats of vegetation composed of the phytocoenoses of *Thelypteris palustris* Schott, *Cicuta virosa* L. or *Carex acutiformis* Ehrh., which encroach from the lake

edges toward the centre. From the open water these communities adjoin the patches of *S. aloides*, which in turn occur beside the phytocoenoses of *N. alba*, *M. verticillatum* or *C. demersum*. A similar spatial distribution of plant communities has been observed in a number of very shallow bays of lakes in north-eastern Poland (Tomaszewicz, 1979; Kłosowski, 1990). The phytocoenoses of *R. circinatus*, *P. perfoliatus*, *M. spicatum* and *P. amphibium* dominate in deeper waters of lakes. In places where the sediments are more highly hydrated (less firm) and contain greater amounts of organic matter, the phytocoenoses of *P. lucens*, *P. natans* and *N. lutea* occupy larger areas of the lake.

Among the plant communities studied, at least two contrasting groups of phytocoenoses can be distinguished: a group of phytocoenoses associated with mineral substrates, representing early stages of succession (the phytocoenoses of *R. circinatus*, *P. perfoliatus*, *M. spicatum* and *P. amphibium*), and a group of communities restricted to highly hydrated organic substrates, which are characteristic of late stages of lake aging (the phytocoenoses of *M. verticillatum*, *C. demersum*, *S. aloides* and *N. alba*, and in some lakes – patches of *N. candida* and *N. pumila*).

The present study has demonstrated habitat differentiation of the plant communities dominated by various aquatic species with submerged and floating leaves (Potamion and Nymphaeion). In addition, many aquatic plant communities are good indicators of the habitat conditions (water and substrates) within lakes. Based on the presence of plant communities, it is possible to determine the degree of advancement of the aging process and identify the particular stages of succession in water ecosystems. Our data obtained for the 356 phytocoenoses from 128 lakes will prove a useful basis for developing universal methods of assessing the ecological state of lakes based on macrophyte composition (EU Water Framework Directive).

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