

HABITAT DIFFERENTIATION OF THE *MYRIOPHYLLUM ALTERNIFLORUM* AND *LITTORELLA UNIFLORA* PHYTOCOENOSES IN POLAND

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ABSTRACT

The present study showed the ecological differentiation of phytocoenoses dominated either by *Myriophyllum alterniflorum* or by *Littorella uniflora*, which in Poland are classified within the Myriophylletum alterniflori or Myriophyllo-Littorelletum association. The properties which best differentiated the waters of the above types of phytocoenoses were calcium and factors associated with the carbonate complex (pH, electrolytic conductivity, total and carbonate hardness), and pH in the case of substrates. The most distinct differences in the habitats were found between the phytocoenoses dominated by *L. uniflora* from the Pomeranian *Lobelia* lakes and those dominated by *M. alterniflorum* from the Łęczna-Włodawa Lake District, in which other species from the Littorelletea uniflorae class were absent. The *L. uniflora* phytocoenoses are associated with soft waters poor in Ca^{2+} and with the lowest values of pH, electrolytic conductivity, dissolved organic matter (COD-KMnO₄) and dissolved SiO₂. The substrates they inhabit are mineral and more acidic. By contrast, the values of the above-mentioned properties are considerably higher in the case of the phytocoenoses from the Łęczna-Włodawa Lake District. The habitats of the *M. alterniflorum* phytocoenoses from the Pomeranian *Lobelia* lakes occupy an intermediate position and are more similar to those of *M. alterniflorum* from the Łęczna-Włodawa Lake District. The results obtained in this study suggest that the phytocoenoses of *L. uniflora* and *M. alterniflorum* should not be included in the same association. Further studies are, therefore, necessary to resolve this problem. The comparative analysis of the present ecological findings and data obtained from other regions of Europe show that in Poland the phytocoenoses dominated either by *L. uniflora* or by *M. alterniflorum*, in which the contribution of Littorelletea uniflorae species is appreciable, are clearly associated with soft waters and their habitats are representative of the Littorelletea uniflorae class. The massive development of the phytocoenoses with both *L. uniflora* and *M. alterniflorum* in the *Lobelia* lakes is not always indicative of the increase in water hardness and eutrophication of waters typical of the communities of the Littorelletea uniflorae class. The *M. alterniflorum* dominated phytocoenoses without other Littorelletea species could be good indicators of the above processes taking place in such water ecosystems.

KEY WORDS: *Myriophyllum alterniflorum* and *Littorella uniflora* phytocoenoses, Littorelletea uniflorae, habitat differentiation, properties of water and substrate, Myriophylletum alterniflori and Myriophyllo-Littorelletum.

INTRODUCTION

In Poland most of the plant communities of the Littorelletea uniflorae Br.-Bl. et R.Tx. 1943 class are known to occur in the western part of the country (Matuszkiewicz 2001). They are confined mainly to soft waters of *Lobelia* lakes in the Pomeranian Lake District (Dąbska 1965; Rejewski 1981; Boiński and Boińska 1988; Szymeja and Clément 1990; Kłosowski 1994; Szańkowski and Kłosowski 1996, 2001, 2002; Matuszkiewicz 2001). Among the communities of Littorelletea uniflorae, the phytocoenoses dominated either by *Myriophyllum alterniflorum* or by *Littorella uniflora* are highly interesting since:

– the two types of phytocoenoses show a considerable tolerance of the increase in the fertility of soft oligotrophic waters; the spread of *M. alterniflorum* in *Lobelia* lakes could be indicative of the progressive eutrophication of the waters (Matuszkiewicz 2001),

– *M. alterniflorum* phytocoenoses have been found in other types of waters as well (their localities have also been reported from the Łęczna-Włodawa Lake District); their ecological amplitude should, therefore, be well-defined,

– in Poland the phytocoenoses of *M. alterniflorum* have been identified with various associations, e.g. Myriophylletum alterniflori Westhoff mscr. 1944 (Dąbska 1965; Kreńska 1971; Michna 1976; Podbielkowski and Tomasz-

wicz 1979), Myriophylletum alterniflori Lemée 1937 em. Siss. 1943 (Rejewski 1981; Kłosowski and Tomaszewicz 1989; Kłosowski 1994) or Myriophyllo-Littorelletum Jeschke 1959 (Szmeja 1994; Szańkowski 1998 mscr; Matuszkiewicz 2001), and only either *M. alterniflorum* (Fijałkowski 1959; Rejewski 1981) or *L. uniflora* (Dąbska 1965; Kreńska 1971; Michna 1976; Podbielkowski and Tomaszewicz 1979; Kłosowski 1994; Matuszkiewicz 2001) are recognized as the character species of the above syntaxa.

The above findings show that knowledge on the phytosociology and ecology of the *M. alterniflorum* and *L. uniflora* phytocoenoses is insufficient and should, therefore, be supplemented by more data. It is also necessary to evaluate whether these phytocoenoses should be classified as belonging to one association. With regard to all this, detailed phytosociological and habitat studies of the communities of *M. alterniflorum* and *L. uniflora* were performed within wider research on the ecology of plant communities of the class Littorelletea uniflorae in Poland.

Therefore, the main objectives of this study were:

- to compare the phytocoenoses of *M. alterniflorum* and *L. uniflora* from the Pomeranian *Lobelia* lakes and those of *M. alterniflorum* from the Łęczna-Włodawa Lake District with respect to phytosociology and habitat conditions,
- to evaluate whether it is justifiable to include the phytocoenoses of *M. alterniflorum* and *L. uniflora* in one association,
- to compare the habitats of the above phytocoenoses from Poland with those reported from other regions of Europe.

MATERIAL AND METHODS

The survey was carried out in the years 1986-1997 within the Pomeranian and Łęczna-Włodawa Lake Districts. All sites were sampled during the height of the growing season (July-August). Altogether the habitats of 46 phytocoenoses (13 with *M. alterniflorum* in 8 *Lobelia* lakes and 16 with *L. uniflora* in 12 *Lobelia* lakes from the Pomeranian Lake District, and 17 dominated by *M. alterniflorum* in 7 lakes from the Łęczna-Włodawa Lake District) were investigated. In each phytocoenosis one phytosociological relevé was recorded by Braun-Blanquet's method. In addition one water and one substrate sample were taken for physical and chemical analyses. 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 of H₂SO₄ for NO₃⁻, PO₄³⁻, 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 a few random subsamples taken within a phytocoenosis.

The following determinations were carried out in water samples: pH (using pH-meter), electrolytic conductivity (EC) by means of a conductivity meter, total and carbonate hardness using Warthy-Pfeifer sodium mixture and by titration with EDTA reagent and ManVer 2 as an indicator, chemical oxygen demand (COD) as consumption of KMnO₄ in acid medium, PO₄³⁻ spectrophotometrically by molybdate method, NO₃⁻ spectrophotometrically with phenoldisulphonic acid and by the cadmium reduction method, total Fe

spectrophotometrically by the rhodanate method, dissolved SiO₂ spectrophotometrically by the molybdate method, Ca²⁺, Na⁺ and K⁺ with a flame spectrophotometer.

In the substrate samples, the following properties were assessed directly; pH, hydration and organic matter content. Concentrations of dissolved SiO₂ were determined in solutions extracted by addition of 100 ml of demineralized water to a substrate sample containing 1g of dry matter (water extracts). In the case of solutions used for determi-

TABLE 1. Synoptic phytosociological data of the phytocoenoses studied. L – phytocoenoses dominated by *L. uniflora* (Pomeranian *Lobelia* lakes); M1 – phytocoenoses dominated by *M. alterniflorum* (Pomeranian *Lobelia* lakes); M2 – phytocoenoses dominated by *M. alterniflorum* (Łęczna-Włodawa Lake District).

Constancy: I, II...V; Abundance: +, 1, 2...5.

Types of phytocoenoses	L	M1	M2
Number of relevés	16	13	17
<i>Littorella uniflora</i>	V ⁴⁻⁵	II ⁺³	
<i>Myriophyllum alterniflorum</i>	III ⁺³	V ⁴⁻⁵	V ⁴⁻⁵
Ch. Littorelletea uniflorae			
<i>Lobelia dortmanna</i>	IV ⁺²	II ⁺¹	
<i>Isoetes lacustris</i>	IV ⁺¹	I ⁺	
<i>Eleocharis acicularis</i>	I ⁺¹	I ⁺	
<i>Luronium natans</i>	I ⁺	II ⁺	
<i>Nitella flexilis</i>	I ⁺		
<i>Elatine hydropiper</i>	I ⁺		
<i>Juncus bulbosus</i>		I ¹	
<i>Ranunculus reptans</i>		I ⁺	
<i>Chara delicatula</i>		I ⁺	
Ch. Potametea			
<i>Polygonum amphibium</i>	II ⁺		
<i>Elodea canadensis</i>	I ⁺²	III ⁺²	II ⁺
<i>Nuphar lutea</i>	I ⁺		I ⁺
<i>Potamogeton obtusifolius</i>	I ⁺		
<i>Myriophyllum spicatum</i>		II ⁺	V ⁺¹
<i>Potamogeton natans</i>		I ⁺	II ⁺²
<i>Ceratophyllum demersum</i>		I ⁺	I ⁺
<i>Nuphar pumila</i>		I ⁺	
<i>Myriophyllum verticillatum</i>		I ⁺	
<i>Potamogeton sp.</i>		I ⁺	
<i>Stratiotes aloides</i>			II ⁺
<i>Nymphaea alba</i>			I ⁺
<i>Potamogeton lucens</i>			I ⁺
<i>Potamogeton perfoliatus</i>			I ⁺
<i>Potamogeton friesii</i>			I ⁺
<i>Nymphaea candida</i>			I ⁺
Ch. Phragmitetea			
<i>Eleocharis palustris</i>	III ⁺¹	I ⁺	I ⁺
<i>Equisetum fluviatile</i>	I ⁺	I ⁺	I ⁺
<i>Carex rostrata</i>	I ⁺		
<i>Phragmites australis</i>		I ⁺	III ⁺¹
<i>Schoenoplectus lacustris</i>		I ⁺	I ⁺
<i>Acorus calamus</i>			I ⁺
Accompanying species			
<i>Fontinalis antipyretica</i>	I ⁺		I ⁺
<i>Drepanocladus tenuinervis</i>	I ¹		
<i>Lemna trisulca</i>		I ⁺¹	I ⁺
<i>Chara fragilis</i>		I ⁺	
<i>Callitriche hamulata</i>		I ⁺	
<i>Chara sp.</i>			II ⁺²
<i>Nitellopsis obtusa</i>			I ¹

nations of Ca^{2+} , total Fe and PO_4^{3-} each substrate sample containing 1 g of dry matter was first digested in 20 ml 1:1 HCl within 2 hours and then 100 ml of demineralized water were added (acid extracts). After 24 hours all the extracted solutions were filtered with 3 m-paper, rinsed with small amounts of demineralized water and the final quantities of the solutions were adjusted to 250 ml. Concentrations of K^+ and Na^+ in substrate were determined in 100 ml water solutions extracted with 2 ml 1:1 HCl from ignited samples. The analyses from water and acid extracts, the determinations of Na^+ K^+ and pH were conducted by the methods described above. Hydration was determined by drying substrate samples at 105°C to constant weight. Organic matter content was assessed by ignition of dry samples at 550°C for 1.5 h.

Numerical data were evaluated statistically. The vegetation-habitat relationships were analysed by means of Canonical Correspondence Analysis (CCA) using CANOCO for Windows Version 4.0 (Ter Braak and Šmilauer 1998). Two sets of data were analysed separately: phytocoenoses-water properties and phytocoenoses-substrate properties. Moreover the habitat conditions of the three types of phytocoenoses investigated were compared with respect to each property using quartiles (Kendal and Buckland 1986). The significance of differences in water and substrate properties between the phytocoenoses investigated were determined by one-way analysis of variance and the Tukey test (Zar 1984). The pH values were recalculated so as to obtain specific acidity according to Wherry (1922).

RESULTS

Phytosociological characteristics of the phytocoenoses and their distribution within the lakes

On the basis of phytosociological data (Table 1) it was demonstrated that the three types of phytocoenoses analysed were distinct with respect to their floristic composition. The phytocoenoses dominated by *M. alterniflorum* from the Łęczna-Włodawa Lake District differed most considerably from the other phytocoenoses studied. Species from the Littorelletea uniflorae class, with the exception of *M. alterniflorum*, were absent. The following species from the Potametea class played an important role in the community structure: *Myriophyllum spicatum* (V constancy class), *Potamogeton natans*, *Stratiotes aloides* and *Elodea canadensis* (II constancy class). There was also a high contribution of such species as *Phragmites australis* (III constancy class) from the Phragmitetea class. In both types of the phytocoenoses investigated from the Pomeranian *Lobelia* lakes, species of the Littorelletea uniflorae class were most abundant. In addition to *M. alterniflorum*, a high proportion of *Lobelia dortmanna* and *Isoetes lacustris* (IV constancy class) was noted in the phytocoenoses with *L. uniflora*. They were also characterised by a high proportion among companions of *Eleocharis palustris* from the Phragmitetea (III constancy class) and *Polygonum amphibium* (Potametea) – II constancy class. In the Pomeranian lakes *M. alterniflorum* dominated phytocoenoses had a lower proportion of Littorelletea uniflorae species. *L. dortmanna*, *Luronium natans* and *L. uniflora* were fairly constant (II constancy class), whereas *I. lacustris* was noted only in two patches

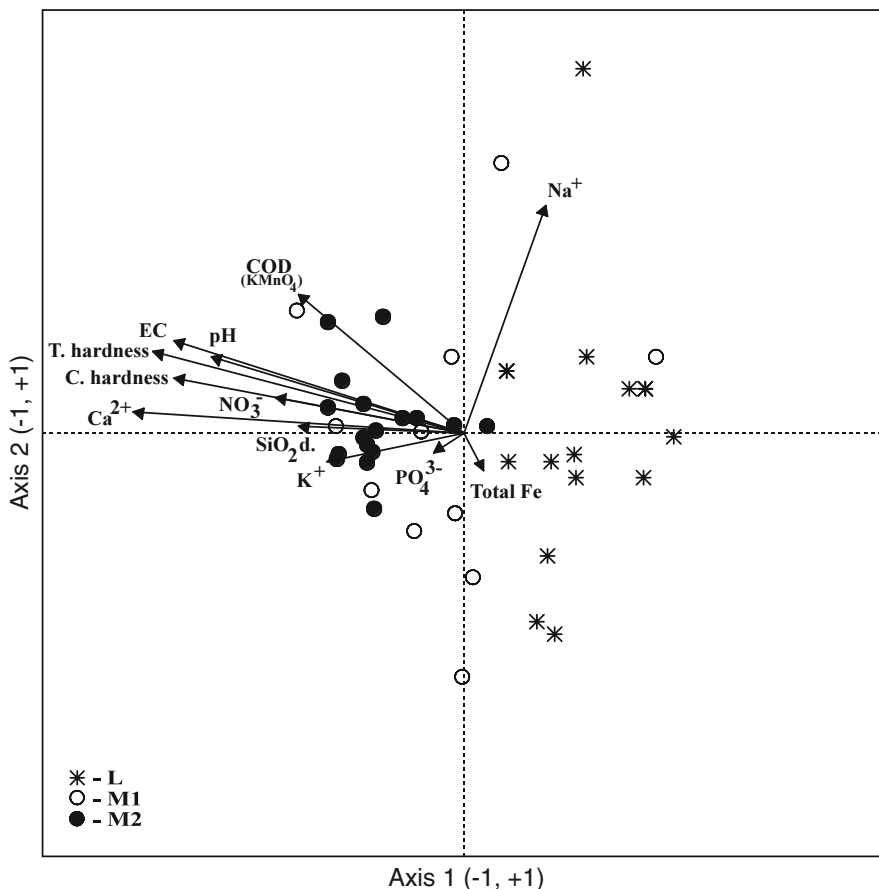


Fig. 1. An ordination diagram of CCA performed on 12 properties of water and 46 relevés. Eigenvalues: $\lambda_1=0.59$ (horizontal axis), $\lambda_2=0.09$ (vertical axis), $\lambda_3=0.05$, $\lambda_4=0.03$, $\Sigma \lambda=1.98$. 1st and 2nd axes. L – phytocoenoses of *Littorella uniflora* (n=16), M1 – phytocoenoses of *Myriophyllum alterniflorum* from *Lobelia* lakes (n=13), M2 – phytocoenoses of *Myriophyllum alterniflorum* from the Łęczna-Włodawa Lake District (n=17). The overlapping points could not be displayed.

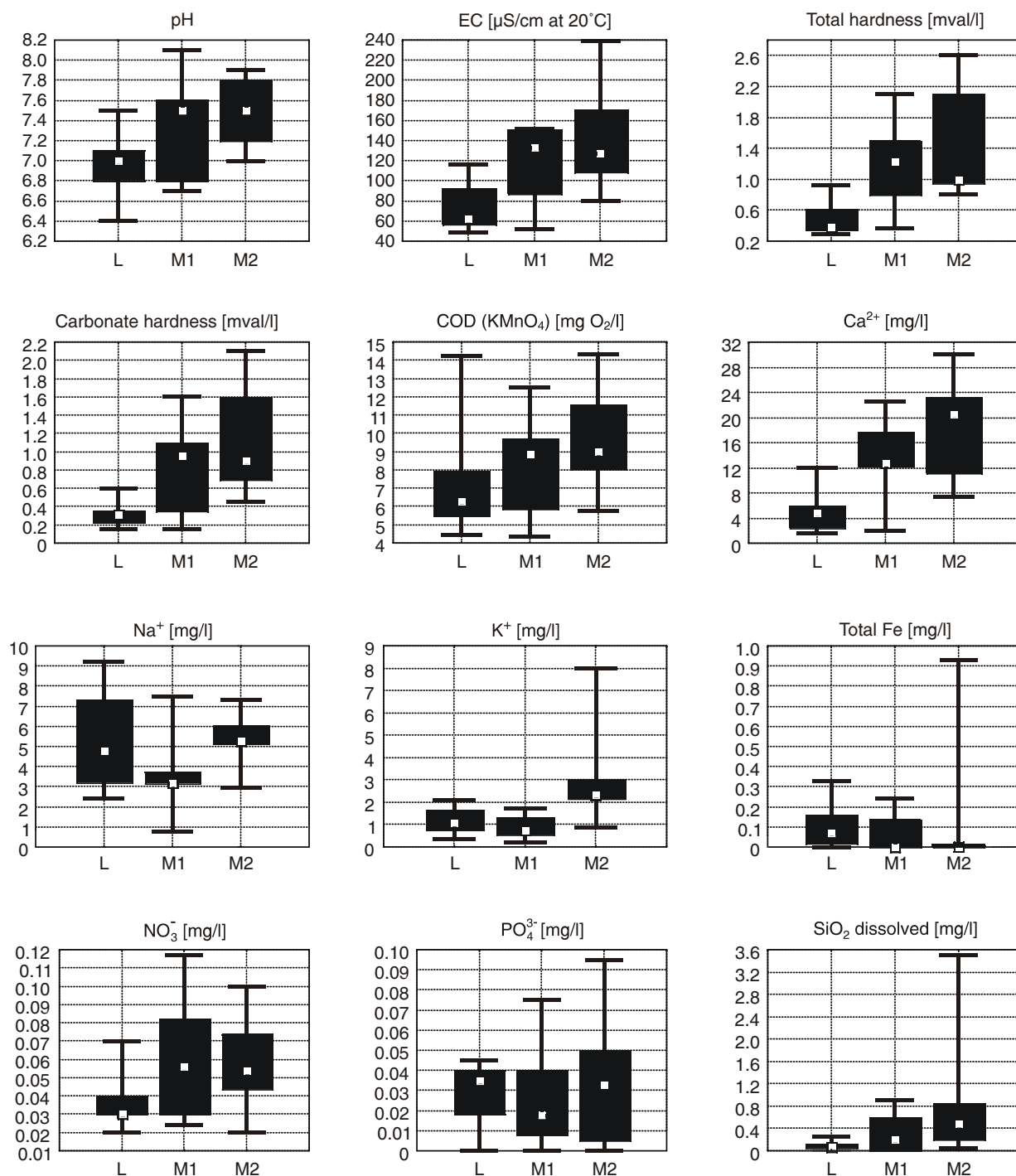


Fig. 2. Differentiation of the three types of phytoceenoses studied in relation to 12 properties of water. Black boxes show 25-75% interquartile ranges of values and white boxes show medians. L – phytoceenoses of *Littorella uniflora* (n=16), M1 – phytoceenoses of *Myriophyllum alterniflorum* from Lobelia lakes (n=13), M2 – phytoceenoses of *Myriophyllum alterniflorum* from the Łęczna-Włodawa Lake District (n=17).

(I constancy class). There was a relatively high incidence of the Potametea species (*E. canadensis* – III constancy class and *M. spicatum* – II constancy class).

Considerable differences in the spatial distribution of the three types of phytoceenoses investigated within the lake littoral were also found. In the Pomeranian lakes the phytoceenoses dominated by *L. uniflora* were restricted to the most shallow parts of the littoral zone. They occurred at a depth of 0-1.1 m. The patches dominated by *M. alterniflorum* developed at a depth ranging from 0.2 to 2.1 m. The *M. alterniflorum* phytoceenoses from the Łęczna-Włodawa

Lake District displayed the widest range of depth (0.3-2.5 m). Both types of the phytoceenoses from the Pomeranian lakes were associated with mineral-sandy bottoms. Most of the phytoceenoses from the Łęczna-Włodawa Lake District showed also preference for mineral substrates. However, some of them were found to occur abundantly on organic substrates as well.

Physical and chemical properties of water

It appears that such properties as calcium and factors associated with carbonate complex (carbonate and total hard-

TABLE 2. The significance of differences in water properties between the three types of phytocoenoses compared. += significant at $P < 0.05$, ns = not significant. Symbols of phytocoenoses – see Table 1.

Properties	L-M1	L-M2	M1-M2
pH	+	+	ns
Electrolytic conductivity (EC)	+	+	+
Total hardness	+	+	ns
Carbonate hardness	+	+	ns
COD-KMnO ₄	ns	+	ns
Ca ²⁺	+	+	ns
Na ⁺	+	ns	+
K ⁺	ns	+	+
NO ₃ ⁻	ns	ns	ns
PO ₄ ³⁻	ns	ns	ns
SiO ₂ dissolved	ns	+	ns

ness, electrolytic conductivity and pH) differentiate the phytocoenoses investigated much better than the other components (Figs 1 and 2). These variables are strongly correlated with the first ordination axis (Fig. 1) and clearly separate the water habitats of the phytocoenoses dominated by *L. uniflora* in the Pomeranian lakes from those dominated by *M. alterniflorum* in the Łęczna-Włodawa Lake District. The former are characterized by significantly lower values of the above mentioned properties (see Table 2). They inhabit very soft waters, considerably poor in Ca²⁺ and with the lowest values of pH and electrolytic conductivity. The phytocoenoses with *M. alterniflorum* from the Łęczna-Włodawa Lake District show preference for harder alkaline waters, richer in Ca²⁺ (see Fig. 2). The habitats of the phytocoenoses dominated by *M. alterniflorum* from the Pomeranian *Lobelia* lakes occupy an intermediate position

with respect to the above properties of water (Fig. 2). Other variables such as K⁺, dissolved SiO₂, NO₃⁻ and COD-KMnO₄ (Fig. 1) differentiate the water habitats in a similar way. Phosphates and total iron play the least significant role in the CCA model (the shortest arrows). With regard to these two properties and NO₃⁻, there are no significant differences between the water habitats studied (Table 2). In the case of Na⁺, which is correlated with the second ordination axis (Fig. 1), there are no significant differences between the water habitats of the phytocoenoses with *L. uniflora* and those of *M. alterniflorum* from the Łęczna-Włodawa Lake District (Table 2). From Fig. 2 and Table 2 it is clear that considerable differences between the *M. alterniflorum* phytocoenoses from the Pomeranian *Lobelia* lakes and those dominated by *M. alterniflorum* from the Łęczna-Włodawa Lake District are detected regarding their Na⁺ concentration.

Physical and chemical properties of substrate

The analysis of the data given in Figs 3 and 4 showed that the substrates of the studied phytocoenoses differed most distinctly with respect to pH, which was correlated with the first and second ordination axis to the same degree. The *L. uniflora* dominated phytocoenoses (Pomerania) inhabit the most acidic substrates (mainly with pH 5.1-6.1), whereas the patches with *M. alterniflorum* from the Łęczna-Włodawa Lake District occur on slightly acidic substrates (pH 6.2-6.8). The *M. alterniflorum* dominated phytocoenoses from Pomerania are confined to substrates with pH ranging from 5.8 to 6.3 (see Fig. 4). The other 8 properties (except for PO₄³⁻) are correlated with pH (Fig. 3) and they differentiate the habitats in a similar way (Figs

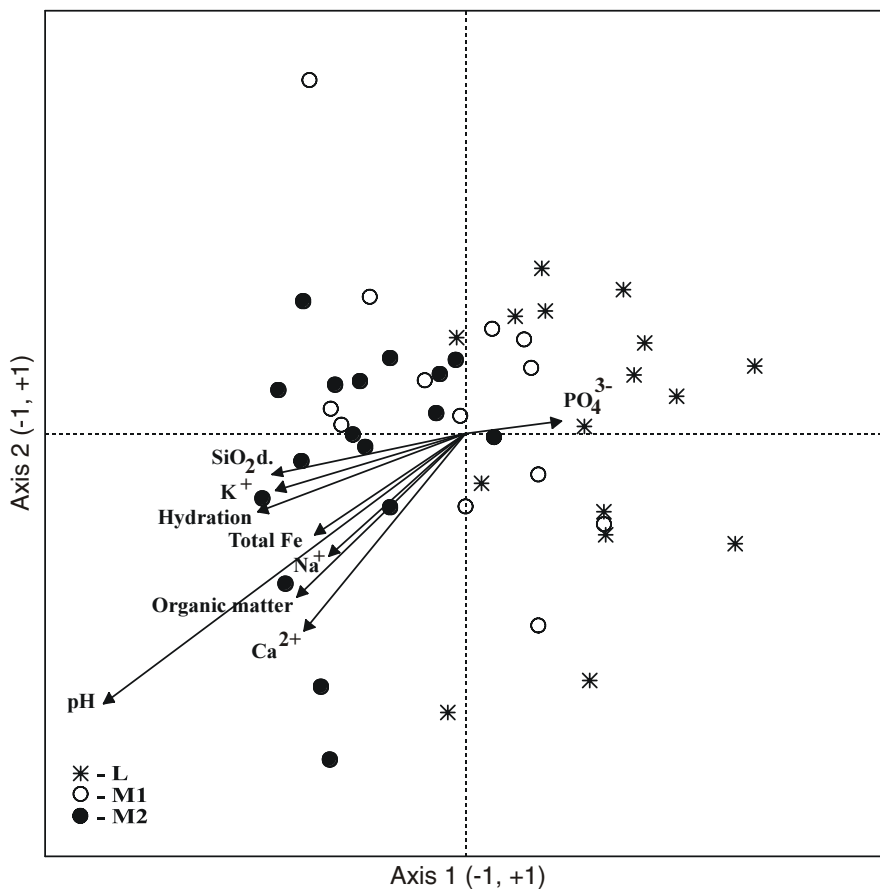


Fig. 3. An ordination diagram of CCA performed on 9 properties of substrate and 46 relevés. Eigenvalues: $\lambda_1=0.46$ (horizontal axis), $\lambda_2=0.06$ (vertical axis), $\lambda_3=0.05$, $\lambda_4=0.04$, $\Sigma \lambda=1.98$. 1st and 2nd axes. The overlapping points could not be displayed. For symbols and number of phytocoenoses see Figure 1.

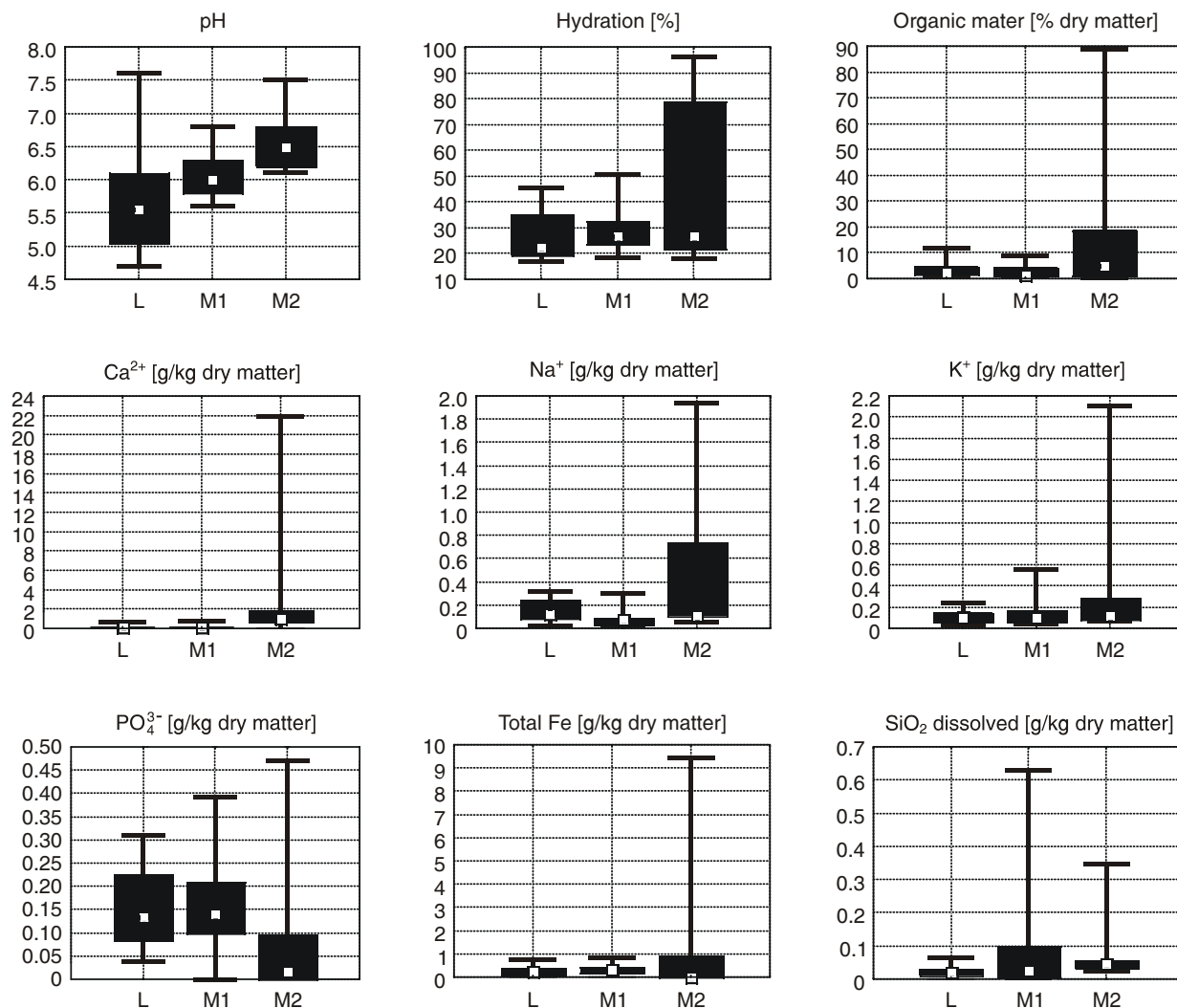


Fig. 4. Differentiation of the three types of phytocoenoses studied in relation to 9 properties of substrate. Black boxes show 25-75% interquartile ranges of values and white boxes show the medians. For symbols and number of phytocoenoses see Figure 2.

TABLE 3. The significance of differences in substrate properties between the three types of phytocoenoses compared. += significant at $P < 0.05$, ns = not significant.

Symbols of phytocoenoses – see Table 1.

Properties	L-M1	L-M2	M1-M2
pH	+	+	ns
Hydration	ns	+	ns
Organic matter	ns	+	ns
Ca ²⁺	ns	ns	ns
Na ⁺	+	ns	+
K ⁺	ns	+	ns
PO ₄ ³⁻	ns	ns	ns
Total Fe	ns	ns	ns
SiO ₂ dissolved	ns	ns	ns

3 and 4). This mainly applies to such properties as hydration, organic matter content, K⁺, Ca²⁺ and dissolved SiO₂. As in the case of pH, the above properties differentiate the substrates of the *L. uniflora* dominated phytocoenoses in the Pomeranian *Lobelia* lakes (lower values of the above-mentioned properties) from those dominated by *M. alterniflorum* in the Łęczna-Włodawa Lake District (higher values of properties). Significant differences were, however, found

only in the case of hydration, organic matter content and K⁺ (Table 3). The substrates of the phytocoenoses with *M. alterniflorum* from Pomerania have intermediate values of the above properties analysed. In addition, they contain the lowest amount of Na⁺ (Fig. 4, Table 3). A reverse trend was determined in the case of PO₄³⁻ (Figs 3 and 4). It was demonstrated that the substrates inhabited by the phytocoenoses from the Łęczna-Włodawa Lake District were poorer in PO₄³⁻ than those from the Pomeranian Lake District.

DISCUSSION

Myriophylletum alterniflori or *Myriophyllo-Littorelletum*?

The present results confirm that like other plant communities of the Littorelletea uniflorae class in Poland (Szańkowski and Kłosowski 2001, 2002), the three types of phytocoenoses analysed in this study are associated with waters poor in Ca²⁺ and mostly with acidic substrates containing a low amount of calcium. The current findings, however, indicate that the investigated phytocoenoses are distinct with respect to habitat conditions, which is ascribed to the regional differences between the waters and dominance of different species. It was demonstrated that the phytocoeno-

ses of *L. uniflora* differed considerably from the two types of phytocoenoses of *M. alterniflorum*. In addition the habitats of *M. alterniflorum* phytocoenoses with *L. uniflora* in the Pomeranian *Lobelia* lakes were more similar to those of *M. alterniflorum* in the Łęczna-Włodawa Lake District than to the phytocoenoses of *L. uniflora* with *M. alterniflorum* in the Pomeranian *Lobelia* lakes. Therefore floristic dominance plays an important role in distinguishing these communities. This suggested that the phytocoenoses of *L. uniflora* and those of *M. alterniflorum* should be treated separately. The separation of the *L. uniflora* phytocoenoses in Pomerania from those of *M. alterniflorum* in the Łęczna-Włodawa Lake District is fully justified (the lack of similarities in their floristic composition is confirmed by their habitat distinctness). In the case of *M. alterniflorum* phytocoenoses from the Pomeranian *Lobelia* lakes the problem is much more complicated. Earlier phytosociological data (Dąbska 1965; Kreńska 1971; Michna 1976; Szmeja and Clément 1990) showed that *L. uniflora* and *M. alterniflorum* occurred jointly in the same patches and thus were recognized as the character species of one association (Myriophylletum alterniflori or Myriophyllo-Littorelletum) which was associated with *Lobelia* lakes. The above findings are in agreement with the present results, which point to a fairly high contribution of *M. alterniflorum* to the *L. uniflora* dominated phytocoenoses and vice versa. In addition both types of phytocoenoses were similar with respect to their floristic composition (a considerable contribution of Littorelletea uniflorae species). As significant differences between the habitats of the above two types of phytocoenoses in the *Lobelia* lakes have been found therefore the following question needs to be answered: Do the phytocoenoses differ to such an extent that they could be considered as distinct communities or do the differences simply manifest the internal ecological variability within the association? If the principles of phytosociology are considered, the latter assumption seems justified. Such an ecological differentiation of phytocoenoses was indicated in the case of other water and reedswamp plant communities, e.g. Elodeetum canadensis (Kłosowski and Tomaszewicz 1997) and Phragmitetum australis (Pełechaty 1997). The above studies should also include the phytocoenoses of *M. alterniflorum* from the Pomeranian non-*Lobelia* lakes and those in which *M. alterniflorum* and *L. uniflora* are the codominant species. At present only the phytocoenoses from the Łęczna-Włodawa Lake District can be considered as a distinct association (Myriophylletum alterniflori). Perhaps the patches with *M. alterniflorum* which occur in the non-*Lobelia* lakes within the Pomerania in the region of Laska (Rejewski 1981), should be included in the above association as well. This is supported by data obtained by the present authors from Lake Zmarłe near Laska. In this lake the patches with *M. alterniflorum* developed in waters with total hardness of 1.7 mval/l and calcium concentration 33.6 mg/l. Thus their habitats are similar to those reported from the Łęczna-Włodawa Lake District. Perhaps these phytocoenoses should not be included in the Littorelletea uniflorae class (see Den Hartog 1981, Rejewski 1981). There is no doubt that the phytocoenoses dominated by *L. uniflora* and/or *M. alterniflorum* from the *Lobelia* lakes, in which the contribution of Littorelletea uniflorae species is appreciable, belong to this class. Therefore if the association Myriophyllo-Littorelletum is recognized, only these phytocoenoses should be included in this association.

The above findings are supported by the present results concerning the properties which are of major importance in differentiating the waters of the investigated phytocoenoses (calcium, total hardness, electrolytic conductivity – see Fig. 2), and by earlier data obtained for some communities of the Littorelletea uniflorae class, namely Lobelietum dortmannae, Isoëtetum lacustris and Luronietum natantis (Szańkowski and Kłosowski 2001). The maximum values of these properties for the above communities were as follows: Lobelietum dortmannae – 17.6 mg/l (Ca^{2+}); 1.50 mval/l (total hardness); 154 $\mu\text{S}/\text{cm}$ (electrolytic conductivity), Isoëtetum lacustris – 12.0 mg/l; 0.80 mval/l; 72 $\mu\text{S}/\text{cm}$, Luronietum natantis – 3.1 mg/l; 0.62 mval/l; 94 $\mu\text{S}/\text{cm}$. From these data and Figure 2, it is clear that the maximum values of the above properties are much higher in the case of *M. alterniflorum* phytocoenoses from the Łęczna-Włodawa Lake District (Ca^{2+} – 30 mg/l; total hardness – 2.60 mval/l; electrolytic conductivity 239 $\mu\text{S}/\text{cm}$). Thus the ecological amplitude of these phytocoenoses is wider than that of the typical communities of Littorelletea uniflorae. The waters of the phytocoenoses of *L. uniflora* appeared to be similar to those of Isoëtetum lacustris and Luronietum natantis with low values of Ca^{2+} and total hardness, whereas those of *M. alterniflorum* from the *Lobelia* lakes were similar to those of Lobelietum dortmannae.

The comparison of the habitats of Myriophyllum alterniflorum and Littorella uniflora phytocoenoses in Europe and Poland

The phytocoenoses dominated by either *M. alterniflorum* or *L. uniflora* have been included in the Isoëto-Lobelietum (Koch 1926) Tx. 1937 association by European phytosociologists (e.g. Szmeja and Clément 1990), or assigned different names depending on the co-occurrence of other species. Such communities as Myriophyllo-Littorelletum Jeschke 1959, Myriophylletum alterniflori Lemée 1937 em. Siss. 1943, Myriophylletum alterniflori Westhoff mscr. 1944, Callitricho hamulatae-Myriophylletum alterniflori (Steusloff 1939) Weber-Oldecop 1967 and Myriophyllo alterniflori-Potametum praelongi (Pietsch 1984) ass. now. (see Vöge 1993) have been described. The following communities which have no fixed syntaxonomic rank have also been recognized, e.g. *Littorella uniflora* und *Baldellia ranunculoides*-Gesellschaft (Pott 1982), *Littorella uniflora*-Gesellschaft (Dierssen 1975, 1996), *Littorella*-Potamogeton filiformis-Soz. Schoof van Pelt and Westhoff 1969 (Dierssen 1975), *Myriophyllum alterniflorum* – Gesellschaft (Dierssen 1996), groupment à *Littorella uniflora* et *M. alterniflorum* (Szmeja and Clément 1990), Potamogeton perfoliatus-Myriophyllum alterniflorum community (Rodwell 1995).

The names of the aforementioned communities which point to the presence of species belonging to other classes than Littorelletea uniflorae reflect the wide coenological amplitude of these communities. This is confirmed by habitat data obtained for *M. alterniflorum*, *L. uniflora* and their phytocoenoses which are characterized by various floristic composition (Pietsch 1982, 1984; Vöge 1993). According to Pietsch (1982) both *M. alterniflorum* and *L. uniflora* develop in waters with a wide range of hardness: from soft (minimum values of total hardness: *L. uniflora* – 0.036 mval/l; *M. alterniflorum* – 1.46 mval/l) to hard waters (maximum values: *L. uniflora* – 6.42 mval/l; *M. alterniflorum* – 4.28 mval/l). Hence *L. uniflora* can be found in much har-

der waters than *M. alterniflorum*. However this does not apply to the species reported from Poland. In the case of *L. uniflora* Pietsch (1982) also indicated wider ranges of pH: 4.6-9.0 (*M. alterniflorum*: 4.6-7.5) and higher maximum values of Ca²⁺ (*L. uniflora* – 80 mg/l; *M. alterniflorum* – 60 mg/l). In the Mecklemburg Lake District in Germany the maximum values of total hardness for *L. uniflora* (2.42 mval/l) are lower (Pietsch 1982) than those for *M. alterniflorum* (3.96 mval/l). Vöge (1993) investigated the habitats of *M. alterniflorum* in 70 lakes in central and northern Europe with regard to pH, total hardness, alkalinity, electrolytic conductivity. The author indicated the presence of *M. alterniflorum* and the phytocoenoses formed by it (with *L. uniflora* as well) in oligotrophic waters with total hardness of 0.14-0.54 mval/l, as well as in oligo-mesotrophic lakes (range of water hardness: 1.71-3.21 mval/l). The proportion of species characteristic of Littorelletea uniflorae declined considerably while passing from oligotrophic to oligo-mesotrophic lakes. *L. uniflora* was found in some meso-eutrophic lakes.

It appears that in Poland the phytocoenoses dominated by either *L. uniflora* or by *M. alterniflorum* in which the contribution of Littorelletea uniflorae species is appreciable are clearly associated with soft waters and their habitats are representative of the Littorelletea uniflorae class when the data from other regions of Europe are considered. The massive development of the phytocoenoses with both *L. uniflora* and *M. alterniflorum* in the *Lobelia* lakes is not always indicative of the increase in water hardness and eutrophication of waters typical of the communities of the Littorelletea uniflorae class. The *M. alterniflorum* dominated phytocoenoses in which other Littorelletea species are absent, could be good indicators of the above processes taking place in such water ecosystems.

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