DISTRIBUTION AND HABITAT CONDITIONS OF THE PHYTOCOENOSES OF SPHAGNUM DENTICULATUM BRIDEL AND WARNSTORFIA EXANNULATA (B., S. & G.) LOESKE IN POLISH LOBELIA LAKES

MARCIN SZAŃKOWSKI. STANISŁAW KŁOSOWSKI

Department of Environmental Botany Institute of Botany, University of Warsaw Al. Ujazdowskie 4, 00-478 Warszawa, Poland e-mail: m.szankowski@uw.edu.pl e-mail: s.klosowski@uw.edu.pl

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ABSTRACT

Phytosociological and habitat studies of Sphagnum denticulatum and Warnstorfia exannulata phytocoenoses from Polish Lobelia lakes have been conducted. The present results were compared with data on Isoëtes lacustris community. It is demonstrated that both communities of mosses are distinct with respect to their floristic composition. Moreover, they differ significantly from the patches of *I. lacustris* with regard to many properties of water and substrates. The phytocoenoses of S. denticulatum are associated with softer waters, poorer in Ca²⁺, Na⁺, NH₄⁺ and dissolved organic matter, but richer in total Fe than those of *I. lacustris*. They are also distinguished by lower values of electrolytic conductivity. The substrates they inhabit are more strongly hydrated and richer in organic matter, total N, dissolved SiO₂, Ca²⁺ and Na⁺, but poorer in PO₄³⁻. The W. exannulata phytocoenoses are also confined to softer waters with lower Ca²⁺, NH₄+ and dissolved organic matter contents than those of *I. lacustris*. Their substrates are more strongly hydrated and have higher contents of organic matter, total N and Na+ but lower amounts of PO₄3-. In addition the waters of W. exannulata phytocoenoses are characterized by higher pH values and lower concentration of dissolved SiO2. The substrates are less acidic and richer in NO3-, but poorer in total Fe. The differences between the habitats of the S. denticulatum and W. exannulata phytocoenoses are also distinct. The former inhabit more acidic waters, richer in dissolved SiO₂ and total Fe, but with lower values of electrolytic conductivity and concentration of Na+. Their substrates are distinguished by higher contents of organic matter and Ca²⁺, as well as by lower amount of NO₃. In view of the fact that the above phytocoenoses of mosses are distinct with respect to their floristic composition and are associated with specific habitats in which they form dense mats close to the bottom of the lake, they should be classified as distinct associations (Sphagnetum denticulati and Warnstorfietum exannulatae) in the system of aquatic communities (Class: Utricularietea intermedio-minoris).

KEY WORDS: Sphagnum denticulatum, Warnstorfia exannulata, Isoëtes lacustris, phytocoenoses, habitat conditions, Lobelia lakes, acidification.

INTRODUCTION

In most of the *Lobelia* lakes within the Pomeranian Lake District species considered as being typical of these lakes (mainly *Lobelia dortmanna*, *Isoètes lacustris*, *Littorella uniflora*, *Luronium natans*, *Juncus bulbosus*, *Myriophyllum alterniflorum*) and forming in them plant communities of the class Littorelletea uniflorae are accompanied by communities of mosses which occupy the deepest waters of the littoral zone (Kraska and Piotrowicz 1994; Szmeja 1994). The latter communities were not dealt with in the classical Polish phytosociological works on *Lobelia* lakes (Dambska 1965; Ceynowa and Rejewski 1969; Kreńska 1971; Rejew-

ski 1981; Boiński and Boińska 1988). Most of the authors, however, indicated the presence of various species of mosses in some of the littoral communities of these lakes. It was not until the work of Szmeja and Clément (1990) that the role of mosses in the phytocoenose structure of the associations of the class Littorelletea uniflorae in the Pomeranian Lake District was appreciated. The aforementioned authors distinguished the communities of L. uniflora-Sphagnum cuspidatum and variants with *S. auriculatum* var. *auriculatum* (= *S. denticulatum*) within the Isoëto-Lobelietum association. In recent years, as the number of studies on the flora and vegetation of Polish *Lobelia* lakes increased, more and more papers have been published which deal with

aquatic mosses and their phytocoenoses in Lobelia and non-Lobelia lakes in the Pomerania (Gos et al. 1998; Kraska and Rusińska 1998; Szańkowski 1998 mscr; Kraska et al.1999; Gos and Banaś 1999; Banaś 2002). As a result of these investigations the following associations were recognized: Drepanocladetum tenuinervi (Kraska and Rusińska 1998) and Warnstorfietum exannulatae Szańkowski 1998 n.n. (Matuszkiewicz 2001). In spite of the fact that there was increasing interest in the massive development of moss communities, very little was known about their floristic, phytosociological and ecological differentiation, especially in Lobelia lakes. Studies on the ecology of moss communities were, therefore, initiated as a result of investigations carried out on vegetation of Polish *Lobelia* lakes (Szańkowski 1998 mscr). The necessity to undertake such studies was due to the fact that the massive development of mosses in Lobelia lakes is associated frequently with anthropogenic changes in the water habitats, among others acidification (Roelofs 1983; Vöge 1988; Arts et al. 1990; Arts and Buskens 1998; Dierssen 1998; Gos and Banaś 1999; Arts 2002), which leads to the disappearance of communities of the class Littorelletea uniflorae.

In 1994 detailed phytosociological studies were initiated which showed that the following species of mosses dominated in many of the *Lobelia* lakes: *S. denticulatum* and *W. exannulata* (=*Drepanocladus exannulatus*). The aforementioned species formed dense mats close to the bottom of the lake. Thus they could be recognized as the main communities of mosses in Polish *Lobelia* lakes. These communities were considered in the study. The main objectives of the present paper were to:

- determine the floristic composition, structure and distribution of the phytocoenoses dominated by *S. denticulatum* and *W. exannulata*,
- determine the properties of water and substrate in both moss communities studied and compare them with the data available for *Isoëtes lacustris*, which they often adjoin,
- compare the current findings with the data regarding the distribution and ecology of S. denticulatum and W. Exannulata, which were reported by other authors from different regions of Europe.

MATERIAL AND METHODS

The survey was carried out within the Pomeranian Lake District in the years 1994-1997 at the height of the growing season (July, August). Altogether 20 phytocoenoses of W. exannulata from 9 Lobelia lakes and 21 phytocoenoses of S. denticulatum from 14 Lobelia lakes were investigated. In each phytocoenose one phytosociological relevé was recorded by Braun-Blanquet method. In addition one water and one substrate sample were taken for physical and chemical analyses. Water samples were taken above the bottom within the phytocoenoses and transferred to two 1000 ml plastic containers. Half of the samples were preserved by the addition of 1 ml of H₂SO₄ for NH₄⁺, PO₄³⁻, NO₃⁻ total Fe and COD 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 samples taken within a phytocoenose. Both substrate and water samples were stored at 4°C and analysed within a few days.

The following determinations were carried out in both water and substrate samples: pH (using pH-meter), NO_3^- – spectrophotometrically by cadmium reduction method, PO_4^{3-} – spectrophotometrically by the molybdate method, SO_4^{2-} – spectrophotometrically with SulfaVer 4 reagent, dissolved SiO_2 – spectrophotometrically by the heteropoly method, total Fe – spectrophotometrically by the rhodanate method. The concentrations of Ca^{2+} , Na^+ and K^+ were estimated with a flame spectrophotometer.

Water samples were analysed for electrolytic conductivity (EC), total hardness by titration with EDTA reagent and carbonate hardness by titration with 0.01 m HCl, chemical oxygen demand as consumption of KMnO₄ in acid medium (COD), NH₄⁺ by Nessler's method, Cl⁻ by mercuric thiocyanate method. Colour was assessed spectrophotometrically according to the platinum-cobalt scale. Concentrations of Na⁺ and K⁺ in water were analysed in 100 ml solutions extracted with 2 ml 1:1 HCl from evaporated and ignited samples. Substrate samples were analysed for hydration by drying them at 105°C to constant weight, total N by Kjeldahl's method, organic matter content by ignition of dry samples at 550°C for 1.5 h. The ion concentrations were

TABLE 1. A synoptic table of the vegetation data studied. IL – community of *Isoëtes lacustris*; WE – community of *Warnstorfia exannulata*; SD – community of *Sphagnum denticulatum*. Constancy: r - 0-5%; + 5-10%; I - 10-20%; II - 20-40%; III - 40-60%; IV - 60-80%; V - 80-100%. Accompanying species are not displayed.

Community type	IL	WE	SD
Number of relevés	22	20	21
Number of lakes	17	9	14
Character or dominant species:			
Isoëtes lacustris	V ³⁻⁵	II+-2	+1-2
Warnstorfia exannulata	\mathbf{r}^1	V^{4-5}	Π^{+-3}
Sphagnum deenticulatum	II+-2	II+-2	V4-5
Character species of the class <i>Littorelletea</i>	!		
Myriophyllum alterniflorum	III+-3	Π^{+-1}	
Nitella flexilis	II+-1	++-3	I+-1
Littorella uniflora	II^{+-1}		
Lobelia dortmanna	II+		
Luronium natans	++-1		
Chara delicatula	++		
Sparganium x diversifolium	r+		
Sparganium angustifolium	r ⁺		
Character species of the class <i>Potametea</i>			
Callitriche hamulata	r^2	r+	
Elodea canadensis	r ⁺	I^{+-1}	
Potamogeton obtusifolius		I^{+-1}	
Ceratophyllum demersum		I^+	
Potamogeton acutifolius		+1	
Nymphaea candida		r ⁺	
Potamogeton crispus		r+	
Potamogeton praelongus		r ⁺	
Potamogeton bertholdi	r ⁺		
Bryophytes			
Fontinalis antipyretica (sensu lato)	II ¹⁻²	II+-3	\mathbf{r}^2
Warnstorfia fluitans	II+-3	r ³	I ¹⁻⁴
Chiloscyphos polyanthos	r^3	-	r^1
Riccardia multifida	r^3		-
Fontinalis dalecarlica	r ¹		
Drepanocladus tenuinervis	-	++	
Warnstorfia trichophylla		•	r+

determined in solutions extracted from the substrate samples. The solutions were obtained from fresh samples containing 1 g of dry matter by addition of 100 ml of demineralized water. In the case of solutions used for determinations of Ca²⁺ SO₄²⁻, PO₄³⁻ and total Fe each sample was first dissolved in 20 ml 1:1 HCl within 2 h. After 24 h the dissolved samples were 3 m-paper filtered, rinsed with small amounts of demineralized water and the quantity of the extracted solutions was adjusted to 250 ml. Contents of Na⁺ and K⁺ in substrate were assessed in 100 ml solutions extracted with 2 ml 1:1 HCl from dried and ignited samples.

The phytocoenoses of S. denticulatum and W. exannulata were compared with 22 phytocoenoses of Isoëtes lacustris previously investigated in the Pomeranian Lake District (Szańkowski and Kłosowski 1996). The multivariate 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 communities studied were compared with respect to each property using quartiles. The significance of differences between the water and substrate properties of the phytocoenoses investigated was determined by one-way analysis of variance and the Newman-Keuls test (Zar 1984). The pH values were recalculated so as to obtain H⁺ concentration.

RESULTS

Phytosociological characteristics of the phytocoenoses studied and their distribution within the lakes

Phytosociological analysis of the phytocoenoses of *S. denticulatum* and *W. exannulata* (Table 1) showed that they occurred in dense stands. The floristic poverty of the aforementioned phytocoenoses was attributed to the floristic dominance of the species forming these phytocoenoses. This mainly applied to the patches with *S. denticulatum*, in which only *W. exannulata* played an important role in the community structure (II constancy class) and where the mean number of species in a relevé was 2. Among the representatives of the class Littorelletea uniflorae, the following species were found to occur rarely in the *S. denticulatum* phytocoenoses: *I. lacustris* and *Nitella flexilis*. The contribution of *Warnstorfia. fluitans* was much higher in 3 patches only.

The phytocoenoses of *W. exannulata* were richer in species (on average 4 species in a relevé). They were characterized by a higher proportion of species representing the class Littorelletea uniflorae, e.g. *M. alterniflorum* and *I. lacustris* (II constancy class). Such species as *N. flexilis* and *Sparganium angustifolium* were noted occasionally. Among mosses *Fontinalis antipyretica* and *S. denticulatum* were also encountered (II constancy class). The presence of Potametea species (e.g. *Potamogeton obtusifolius, Elodea canadensis* and *Ceratophyllum demersum*) was recorded in some of the phytocoenoses studied.

The *I. lacustris* phytocoenoses had a higher frequency of the following Littorelletea species: *M. alterniflorum* (III constancy class), *L. dortmanna*, *L. uniflora* and *N. flexilis* (II constancy class). *Luronium natans*, *Chara delicatula* and *Sparganium* x *diversifolium* were recorded more rarely. Among mosses *S. denticulatum*, *W. fluitans*, and *F. antipyretica*, were encountered (II constancy class). In the individual phytocoenoses the following species of liverworts

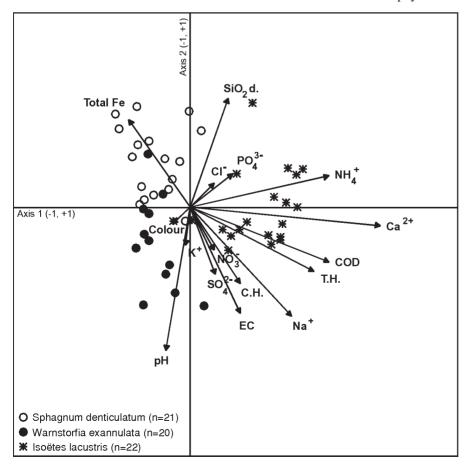


Fig. 1. CCA ordination diagram of 1^{st} and 2^{nd} axes based on 16 properties of water and 63 relevés. Eigenvalues: $\lambda 1$ =0.72, $\lambda 2$ =0.44, $\lambda 3$ =0.16, $\lambda 4$ =0.11, $\Sigma \lambda$ =3.94. The overlapping relevés could not be displayed. EC – electrolytic conductivity; T.H. – total hardness; C.H. – carbonate hardness; SiO₂ d. – SiO₂ dissolved; COD – chemical oxygen demand.

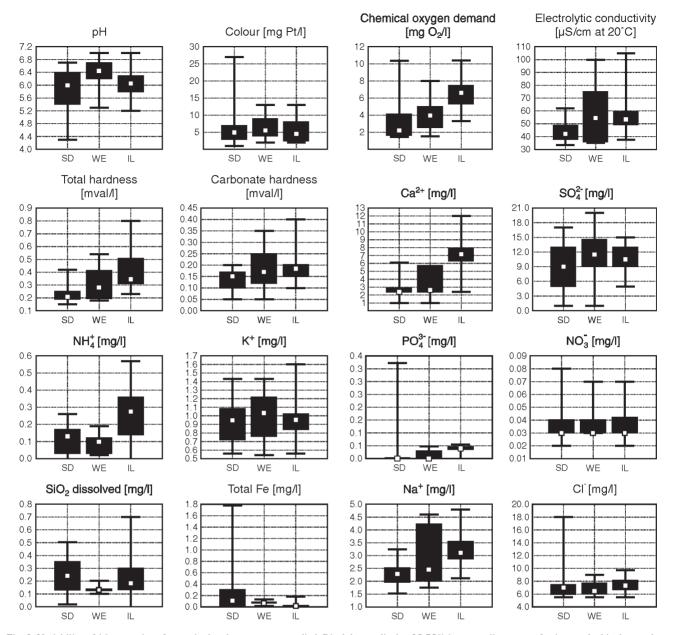


Fig. 2. Variability of 16 properties of water in the phytocoenoses studied. Black boxes display 25-75% interquartile ranges of values and white boxes show the medians. Groups of phytocoenoses dominated by: SD – *Sphagnum denticulatum* (n=21), WE – *Warnstorfia exannulata* (n=20), IL – *Isoëtes lacustris* (n=22).

played an important role: Chiloscyphos polyanthos and Riccardia multifida.

The above floristic composition of the phytocoenoses analysed reflects their spatial distribution in the *Lobelia* lakes studied. The patches with *S. denticulatum*, being the poorest in species, occur in the deepest layers (about 7 m) of the lake, which receive less light. They usually develop at a depth of 2.5-4.5 m, inhabiting the upper, highly hydrated layers of the organic substrates. The phytocoenoses of *W. exannulata* are found at 5.5 m. They attain their optimum development at the depth range of 2.8-3.9 m on mineral-organic and organic bottoms. The patches of *I. lacustris* occur in waters down to 5 m. They usually develop at a depth ranging from 1.0 m to 2.5 m. In most cases the phytocoenoses of *I. lacustris* adjoin those of mosses at the lower limit of their vertical range of distribution. In some lakes they border the *W. exannulata* phytocoenoses, in others

the *I. lacustris* phytocoenoses adjoin the patches of *S. denticulatum*. The above phytocoenoses of mosses rarely neighbour one another in the same lake.

Habitat properties of the phytocoenoses studied

Considerable differences between the water habitats of the phytocoenoses studied were found regarding Ca²⁺ concentration. This variable is strongly correlated with the first ordination axis which separates the water habitats of the *I. lacustris* phytocoenoses from those of the communities of mosses (Fig. 1). The lowest concentration of Ca²⁺ (mainly 2.5-2.9 mg/l) was found in the water of the *S. denticulatum* phytocoenoses (Fig. 2) with higher levels in that of *W. exannulata* (2.2-5.8 mg/l) and the highest in that of *I. lacustris* phytocoenoses (6.2-8.0 mg/l). A similar trend was observed in the case of other properties of water which are correlated with the first ordination axis: chemical oxygen

TABLE 2. Significance of differences in water and substrate properties between the three communities studied. + - significant at P≤0.05; ns - non-significant at P≤0.05. Symbols of communities - see Table 1.

Properties of water	IL-WE	IL-SD	WE-SD
Ca ²⁺	+	+	ns
Total hardness	+	+	ns
COD-KMnO₄	+	+	ns
NH ₄ ⁺	+	+	ns
pH	+	ns	+
SiO ₂ dissolved	+	ns	+
Na ⁺	ns	+	+
Electrolytic conductivity	ns	+	+
Total Fe	ns	+	+
Carbonate hardness	ns	+	ns
Colour	ns	ns	ns
SO ₄ ²⁻	ns	ns	ns
PO_4^{3}	ns	ns	ns
Cl-	ns	ns	ns
K+	ns	ns	ns
NO ₃ -	ns	ns	ns
Properties of substrate	IL-WE	IL-SD	WE-SD
Hydration	+	+	ns
Organic matter	+	+	+
Total N	+	+	ns
PO_4^{3-}	+	+	ns
Na ⁺	+	+	ns
NO ₃ -	+	ns	+
Ca ²⁺	ns	+	+
рН	+	ns	ns
Total Fe	+	ns	ns
SiO ₂ -dissolved	ns	+	ns
$SO_4^{\frac{2}{2}}$	ns	ns	ns
K+	ns	ns	ns

demand (COD) and total hardness. Similar results were also obtained for NH₄⁺ (Figs 1 and 2) in waters inhabited by the *I. lacustris* phytocoenoses.

The second ordination axis clearly separates the water habitats of S. denticulatum from those of W. exannulata and is correlated with pH, electrolytic conductivity (EC), dissolved SiO₂, total Fe and Na⁺ concentration (Fig. 1). The three communities analysed in this study are associated with acidic waters (Fig. 2). The phytocoenoses of S. denticulatum developed best in the most acidic waters (mostly at pH 5.3-6.3), whereas those of W. exannulata showed preference for slightly acid waters (mainly pH 6.2-6.7) and differed significantly from the other phytocoenoses in the case of pH (Table 2). With regard to this property the I. lacustris phytocoenoses occupy an intermediate position (5.8-6.3 pH). The highest concentration of total Fe was recorded in the S. denticulatum dominated phytocoenoses. The latter community (like the patches of *I. lacustris*) developed in waters rich in dissolved SiO₂ (Figs 1 and 2) but with significantly lower concentration of Na⁺ and lower value of electrolytic conductivity than the other types of phytocoenoses studied (see Table 2). The patches with W. exannulata were associated with waters having the lowest concentration of dissolved SiO₂ (significantly different values from those obtained for the other types of phytocoenoses studied – see Table 2) and relatively poor in total Fe, but rich in Na⁺ (Figs 1 and 2). The remaining properties (colour, Cl⁻, SO₄²⁻ and those indicating water richness: PO₄³⁻, NO₃⁻, K⁺) appeared to be less important in differentiating the water habitats of the phytocoenoses studied.

The substrates differentiated the habitats of the three types of phytocoenoses studied to a similar degree as water. The first ordination axis clearly separates the substrates of I. lacustris from those of the phytocoenoses of mosses and is strongly correlated with hydration, organic matter content, total N and PO₄³⁻ (Fig. 3). These properties are most important in differentiating the habitats compared. In the case of the first three properties, the highest values were recorded for the substrates inhabited by the S. denticulatum phytocoenoses, lower for the patches with W. exannulata and the lowest for those of *I. lacustris* (Fig. 4). With regard to these three properties, the differences between the substrates of *I. lacustris* phytocoenoses and the two moss communities are significant (Table 2). A reverse tendency was observed in the case of PO₄³-. From Figures 3 and 4, it is clear that the substrates of the moss communities are markedly poorer in PO₄³⁻ than those of *I. lacustris* (see Table 2). A similar trend as in the case of hydration, total N, and organic matter content was noted for dissolved SiO2 and Ca²⁺ (Fig. 3). The highest levels of the above properties were noted in the substrates of S. denticulatum and the lowest levels in that of *I. lacustris* (significant differences were marked – Table 2). The substrates of W. exannulata occupy an intermediate position with regard to the aforementioned properties (Fig. 4).

Other properties, such as Na⁺ and total Fe, which are correlated with the first ordination axis (Fig. 3), differentiated the substrates of the phytocoenoses studied as well. The highest content of Na+ was observed in the substrates of the W. exannulata phytocoenoses and the lowest in that of I. lacustris. A reverse tendency was observed in the case of total Fe content. The highest content of total Fe was noted in the substrates of *I. lacustris* phytocoenoses and the lowest in that of W. exannulata (Fig. 4). Significant differences between the above types of phytocoenoses were found regarding these two properties (Table 2). The substrates of S. denticulatum patches occupy an intermediate position (Fig. 4). In the case of Na+ significant differences were marked between the phytocoenoses of *I. lacustris* and those of mosses (with regard to total Fe the differences are significant only between the phytocoenoses of I. lacustris and those of W. exannulata – see Table 2).

DISCUSSION

The results obtained in the present study indicated that the phytocoenoses of mosses analysed in this study differed significantly from I. lacustris phytocoenoses with respect to many properties of water (e.g. Ca²⁺, total hardness, COD, NH₄+), and substrate (e.g. organic matter, total N, hydration, PO₄³⁻, Na⁺). Considerable differences between the habitats of S. denticulatum and W. exannulata phytocoenoses were also found. The properties which sharply differentiated the water habitat of S. denticulatum from that of W. exannulata were pH, dissolved SiO₂, Na⁺, electrolytic conductivity and total Fe, and in the case of substrates organic matter content, Ca²⁺ and NO₃⁻. In addition (although the differences were not statistically significant) the waters of S. denticulatum phytocoenoses were softer and poorer in Ca²⁺ and dissolved organic matter than those of W. exannulata. In many cases the substrates inhabited by S. denticulatum were more acidic and strongly hydrated.

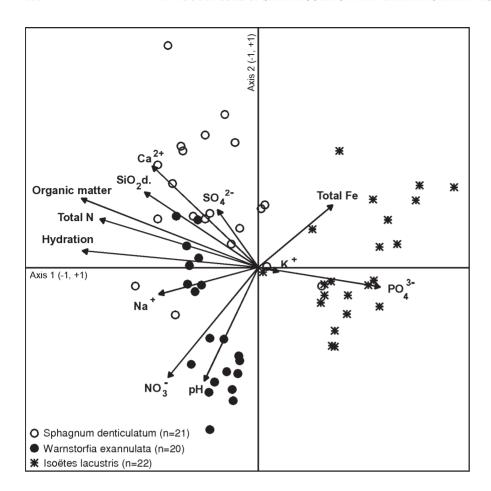


Fig. 3. CCA ordination diagram of 1^{st} and 2^{nd} axes based on 12 properties of substrate and 63 relevés. Eigenvalues: $\lambda 1$ =0.71, $\lambda 2$ =0.39, $\lambda 3$ =0.11, $\lambda 4$ =0.09, $\Sigma \lambda$ =3.94. The overlapping relevés could not be displayed. SiO₂ d. – SiO₂ dissolved.

They were also distinguished by a higher total N content. It appears that both communities of the studied mosses could be good indicators of the littoral habitat conditions. The importance of mosses as limnological indicators, especially in lakes undergoing acidification, was pointed out by various authors, e.g. Grahn (1977), Arts (1990). The invasion of lakes by various *Sphagnum* species, including *S. denticulatum* (=*S. auriculatum*), was observed with increasing acidification of their waters (e.g. Roelofs 1983; Roberts et al. 1985; Raven 1988; Arts 1990, 2002; Arts and Buskens 1998; Dierssen 1998).

The present study revealed the association of S. denticulatum phytocoenoses with acidic habitats, which is in agreement with the findings of the aforementioned authors. However the range of pH values most frequently noted in the water of the S. denticulatum phytocoenoses from Lobelia lakes analysed in this study lies within higher values (5.4--6.4) compared to that of the waters from other regions of Europe, which are subject to acidification as well. In the case of 4 phytocoenoses, the pH of water was, however, below 5.4 and within the pH range of 4.3-5.3. In Denmark S. denticulatum occurred mainly at pH 4.5-5.5 (Soerensen 1948). In other West European countries, e.g. Holland and Scotland, the lakes affected by acidification were inhabited by the S. denticulatum phytocoenoses developing in the pH range of 4.4-5.0, (Arts 1990) and 4.5-5.0 (Raven 1988), respectively. In Poland such low values of pH in the S. denticulatum habitat have been recorded mainly in acidic waters of non-Lobelia lakes (Banaś 2002). These differences may have been attributed to the fact that many of the Polish Lobelia lakes inhabited by S. denticulatum are subject to natural acidification, which is related to the nature of the

catchment area and dominance of pine forests and acidophilic deciduous forests developing beside the lakes. Compared with the rapidly proceeding process of acidification of lakes in Western Europe caused mainly by human activities e.g. acid rains (Grahn 1977; Evans 1984; Arts et al. 1990; Arts and Buskens 1998), the acidification process taking place in many of the Polish Lobelia lakes has been reported to proceed at a slower rate and leads gradually to the dystrophy of the lakes (Szmeja 1997; Gos et al. 1998; Gos and Banas 1999; Kraska et al. 1999). Under natural conditions the slow process of dystrophy is favourable for the coexistence of typical isoetid species with the phytocoenoses of mosses, which occupy the deepest layers of the littoral zone. This mainly applies to *I. lacustris*, of which the phytocoenoses often adjoin those of S. denticulatum and W. exannulata. These observations were made in most of the Lobelia lakes investigated by the authors. The data obtained by various authors (e.g. Kohler and Schoen 1984; Raven 1988; Arts et al. 1990; Kraska et al. 1998) indicate that I. lacustris is highly tolerant of acid waters. The present findings are in agreement with the data of the aforementioned authors and those relating to substrate properties. It was found that the substrates of most I. lacustris phytocoenoses were more acidic than those of S. denticulatum and W. exannulata. At present the phytocoenoses of I. lacustris are not endangered by the natural process of dystrophy taking place in many of the Lobelia lakes as the process is not in its final stage. Some authors (Szmeja et al. 2001; Banaś 2002) indicate that humic substances, which are released into the lakes due to human activities in the catchment area, can threaten the vegetation of Lobelia lakes, including the S. denticulatum phytocoenoses. The in-

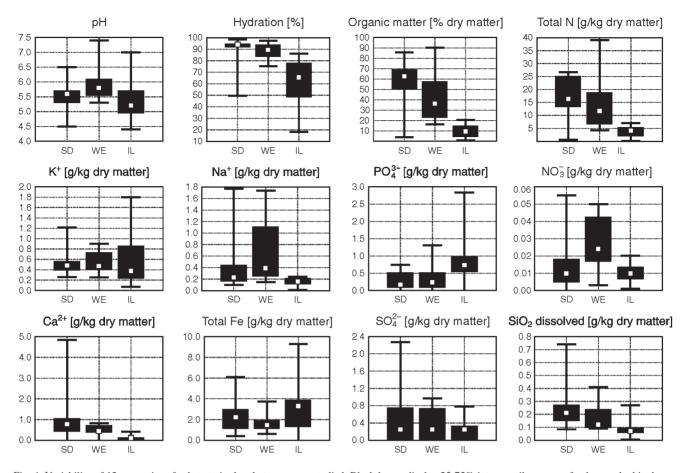


Fig. 4. Variability of 12 properties of substrate in the phytocoenoses studied. Black boxes display 25-75% interquartile ranges of values and white boxes show the medians. Groups of phytocoenoses dominated by: SD – Sphagnum denticulatum (n=21), WE – Warnstorfia exannulata (n=20), IL – Isoëtes lacustris (n=22).

flow of humic substances leads to an increase in the colour of water and results in the retreat and, subsequently, elimination of the plant communities from the deeper parts of the lake littoral.

Most data obtained from different regions of Europe point to a relatively wide ecological amplitude of *W. exannulata* (especially in the case of pH of water). Sörensen (1948) demonstrated that *W. exannulata* occurred mainly in water with pH 4.5-6.5, Malme (1978): 5.6-7.2 pH, and Karttunen and Toivonen (1995): 5.5-8.1. The above findings indicate that *W. exannulata* is associated with less acidic habitats than *S. denticulatum*. The present study confirms these observations made in the case of both water and substrate. It appears, therefore, that the phytocoenoses of *W. exannulata* cannot be regarded as indicators of the progressing dystrophy of the *Lobelia* lakes, as opposed to those of *S. denticulatum*.

It is interesting to note that the three studied communities differed from each other with respect to their substrate and water properties to a similar degree. This fact is of great importance, as in the case of moss communities the chemistry of water is usually analysed, which is considered to be their main source of nutrients (Malme 1978; Brandrud and Johansen 1994). The present study showed that the phytocoenoses of the mosses analysed, particularly those dominated by *S. denticulatum*, were associated mainly with substrates rich in organic matter. Some authors, however, claim that most aquatic mosses avoid highly organic sub-

strates (e.g. Sörensen 1948). Malme (1978) suggested that mosses developed best on mineral-organic bottoms and that the thick layer of slightly decomposed organic substrate (more than 50 cm thick) restricts their occurrence. The current findings showed that in the case of the phytocoenoses of *S. denticulatum* and *W. exannulata* the layer of organic substrate did not exceed 50 cm. The substrates were, however, highly decomposed and hydrated. Thus strongly hydrated substrates just like water could constitute the source of nutrients for such species as *S. denticulatum* and *W. exannulata*.

The differences between the substrates of the phytocoenoses of *I. lacustris* and the phytocoenoses of mosses could be associated with the fact that the patches with *I. lacustris* occupy shallower and more mineral parts of the lake littoral. The differences between the phytocoenoses of *S. denticulatum* and *W. exannulata* may be due to the interaction of floating mats formed by various species of mosses with their substrates, particularly the deposition of a specific phytomass by the two dominating species of mosses. The interaction of mosses and their substrates was described by Jaynes and Carpentier (1986) and Dierssen (1998).

The results obtained in the present study indicate that the phytocoenoses of the studied mosses are distinct with respect to their floristic composition and occupy a specific position in the littoral of the *Lobelia* lakes (deep waters of the littoral zone), where they form dense meadows. The above phytocoenoses should, therefore, be classified as dis-

tinct associations (Sphagnetum denticulati and Warnstorfietum exannulatae) in the system of aquatic communities (Class: Utricularietea intermedio-minoris). In addition they could be good indicators of habitat conditions in deep waters of the littoral zone of *Lobelia* lakes.

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