

## Ecology of rare water plant communities in lakes of north-eastern Poland

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### Abstract

Habitat studies were conducted on three rare plant communities dominated by *Nuphar pumila*, *Nymphaea candida* and *Hydrilla verticillata* in lakes of north-eastern Poland. The comparison of habitat properties of these three types of phytocoenoses with those of *Nuphar lutea* common in the area under study was also performed. It was demonstrated that the plant communities studied were ecologically distinct. The habitats of the phytocoenoses of *N. pumila* differed most significantly from those of the other phytocoenoses. They often inhabited softer waters poor in  $Mg^{2+}$ , dissolved  $SiO_2$ , but rich in total Fe,  $PO_4^{3-}$ ,  $NO_3^-$ , and were associated with acidic substrates containing lower levels of  $Ca^{2+}$  and  $Na^+$ , but greater amounts of total Fe and  $NO_3^-$ . The differences in the habitats of *H. verticillata* and *N. candida* phytocoenoses were most pronounced in the case of four properties of water:  $Na^+$ ,  $K^+$ ,  $Cl^-$ , and  $Mg^+$ . Their values were lower in waters of the *H. verticillata* phytocoenoses. The habitats of all the three types of rare phytocoenoses differed considerably from those of *N. lutea*. The most significant differences were found between the *N. lutea* and *N. pumila* phytocoenoses and the smallest differences were between the patches of *N. lutea* and *N. candida*. The properties of water were more important in differentiating the habitats of the phytocoenoses studied than the substrate properties. Due to alkalization and increase in water hardness in the lakes studied the stands of *N. pumila* are among the most threatened. The patches of *N. candida* and *H. verticillata*, which occur in waters with a wider range of hardness and tolerating a slight increase in trophy, can still continue to persist in the lakes for a long time.

**Keywords:** rare plants, floating leaved and submerged phytocoenoses, properties of water and substrate, comparative analysis

### Introduction

The north-eastern area of Poland (Lithuanian Lake District) is dominated by a postglacial landscape with diverse geological landforms (terminal moraines, sanders and eskers) left behind by retreating glaciers. These are accompanied by forests and numerous lakes supporting a rich vegetation [1]. There are no larger industrial plants or urban agglomerations in this area, which is less populated than the other regions of Poland. As a result the lakes remain in good condition and the vegetation has preserved to a considerable extent its original natural character. Therefore some rare plant communities dominated by such species as *Hydrilla verticillata* or *Nymphaea candida* are found to occur more frequently in this region of Poland than in other parts of the country [2-4]. Moreover, the analysed area hosts the only rich population of the glacial relict *Nuphar pumila* isolated from the main Polish area of occurrence in the Pomerania Lake District [5,6]. Data regarding the ecology of these plant communities were published in other papers

as a result of continued phytosociological and habitat studies conducted in north-eastern Poland (e.g. [4,7-11]). The investigations performed in the years 2002-2005 in 66 lakes within Lithuanian Lake District revealed new localities of *N. candida* and *H. verticillata* phytocoenoses in Poland. As in the case of the plant communities surveyed earlier they were examined with respect to their species composition, structure and habitat conditions. The numerous phytosociological data available for these three rare plant communities enabled the comparative analysis of the above types of phytocoenoses. The objective of this study, among others, was to define the ecological amplitude and the optimum growth conditions for these three rare plant communities. The present work also aimed at determining the degree to which they differed with respect to their ecology from the phytocoenoses of *N. lutea*, which are common in Poland. In addition an attempt has been made to predict the chances of survival of the phytocoenoses of *N. pumila*, *N. candida* and *H. verticillata* in lakes of the area under study.

### Material and methods

The phytosociological and habitat data were collected at the height of the growing season (from the end of June to the end of August) in the years 1978-2004. Due to the distinct character of the littoral zone of lakes (e.g. [12,13]) as well as hydrochemical differences even between neighbouring patches of vegetation within the various bodies of water [14,15], the

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investigations were carried out on particular phytocoenoses, irrespective of the lake's trophic status. Studies were conducted on 18 phytocoenoses of *N. pumila* from 5 lakes, 14 phytocoenoses of *H. verticillata* from 7 lakes, 30 phytocoenoses of *N. candida* from 11 lakes and 17 phytocoenoses of *N. lutea* from 16 lakes. From a phytosociological point of view these phytocoenoses belong to the alliance Nymphaeion within the class Potametea [16].

In each phytocoenose one phytosociological relevé (10-25 m<sup>2</sup> plots) was recorded and water depth was measured in the deepest and the shallowest point of each phytocoenose taking into account the slope of the 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 in 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 phytocoenose one water and one substrate sample were taken for physical and chemical analyses (79 water and 79 substrate samples together). Both types of samples were collected at the same time as the relevés were performed. Water samples were taken from an intermediate depth at which a given phytocoenose occurred and transferred to two 1000 ml plastic containers. Half of the water samples were preserved by the addition of 1 ml concentrated H<sub>2</sub>SO<sub>4</sub> for PO<sub>4</sub><sup>3-</sup>, NO<sub>3</sub><sup>-</sup> and total Fe 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 phytocoenose. Both water and substrate samples were transported to the laboratory within several hours (3-5) and the determinations were carried out immediately. Prior the analyses the samples were filtered and stored in refrigerators at 4°C until all the analyses were performed. Altogether 14 properties of water (including water depth) and 12 properties of substrate were determined.

The following analyses were carried out in water samples: pH, total and carbonate hardness, PO<sub>4</sub><sup>3-</sup>, NO<sub>3</sub><sup>-</sup>, total Fe, dissolved SiO<sub>2</sub>, SO<sub>4</sub><sup>2-</sup>, Cl<sup>-</sup>, Mg<sup>2+</sup>, Ca<sup>2+</sup>, K<sup>+</sup> and Na<sup>+</sup>.

In the substrate samples, pH was assessed in pore water. Hydration was determined by drying substrate samples at 105°C to constant weight and organic matter content was assessed by ignition of dry samples at 550°C for 1.5 h. Concentrations of dissolved SiO<sub>2</sub>, NO<sub>3</sub><sup>-</sup> and Cl<sup>-</sup> were determined from water extracts, total Fe, Ca<sup>2+</sup>, Mg<sup>2+</sup>, PO<sub>4</sub><sup>3-</sup> and SO<sub>4</sub><sup>2-</sup> from (1:1 v/v) HCl extracts (see [17]). The concentrations of K<sup>+</sup> and Na<sup>+</sup> in substrate were determined from dried and ignited samples. Most of the determinations were carried out by methods described by Hermanowicz et al. [18]. Determinations of total hardness were performed according to procedures described by Hermanowicz et al. [18] and Hach Company [19].

The vegetation-habitat relationships were determined by means of Canonical Correspondence Analysis (CCA) using CANOCO for Windows Version 4.0 [20]. Water and substrate data were analysed separately. Moreover the habitat conditions of the four 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 were determined by the Kruskal-Wallis test and the nonparametric multiple comparisons [21].

## Results

### Phytosociological characteristics of the phytocoenoses studied and their range of depth in the lake littoral

The analysis of Tab. 1 showed that the phytocoenoses studied formed dense stands and were characterized by a strong dominance of one species. The patches of *H. verticillata* were highly represented by species from the class Potametea, e.g. *N. lutea*, *Myriophyllum verticillatum*, *Ceratophyllum demersum*

Tab. 1 Synoptic table of the four types of phytocoenoses studied.

Phytocoenose type	HV	NC	NP	NL
Numer of relevés	14	30	18	17
Number of lakes	7	11	5	16
<b>Potametea</b>				
<i>Hydrilla verticillata</i>	V <sup>4-5</sup>			
<i>Nymphaea candida</i>		V <sup>3-5</sup>		I <sup>+</sup>
<i>Nuphar pumila</i>			V <sup>3-5</sup>	
<i>Nuphar lutea</i>	III <sup>+</sup>	III <sup>+1</sup>	V <sup>+1</sup>	V <sup>4-5</sup>
<i>Nymphaea alba</i>				I <sup>+</sup>
<i>Potamogeton natans</i>		III <sup>+2</sup>	II <sup>+1</sup>	II <sup>+1</sup>
<i>Myriophyllum verticillatum</i>	III <sup>+2</sup>	I <sup>+1</sup>		I <sup>+</sup>
<i>Ceratophyllum demersum</i>	III <sup>+1</sup>	II <sup>+2</sup>		I <sup>+</sup>
<i>Stratiotes aloides</i>	II <sup>+1</sup>		II <sup>+1</sup>	I <sup>+</sup>
<i>Utricularia vulgaris</i>	II <sup>+</sup>	I <sup>+2</sup>		I <sup>-1</sup>
<i>Myriophyllum spicatum</i>	I <sup>1</sup>	I <sup>+</sup>	I <sup>+</sup>	
<i>Potamogeton lucens</i>	I <sup>+</sup>	I <sup>+</sup>	II <sup>+1</sup>	I <sup>+</sup>
<i>Potamogeton compressus</i>	I <sup>+</sup>		I <sup>+</sup>	I <sup>+</sup>
<i>Potamogeton friesii</i>		I <sup>+</sup>	I <sup>+</sup>	
<i>Batrachium circinatum</i>		I <sup>+</sup>		I <sup>+</sup>
<i>Elodea canadensis</i>		I <sup>+</sup>	III <sup>+2</sup>	I <sup>+</sup>
<i>Hydrocharis morsus-ranae</i>		I <sup>+</sup>		
<i>Potamogeton perfoliatus</i>		I <sup>+</sup>		I <sup>+</sup>
<i>Potamogeton crispus</i>		I <sup>+</sup>		
<b>Others</b>				
<i>Equisetum fluviatile</i>	I <sup>+</sup>	I <sup>+</sup>	III <sup>+2</sup>	I <sup>+</sup>
<i>Sagittaria sagittifolia</i>	I <sup>+</sup>			
<i>Lemna trisulca</i>		II <sup>+2</sup>	II <sup>+</sup>	I <sup>+</sup>
<i>Spirodela polyrhiza</i>		I <sup>+3</sup>	I <sup>+</sup>	I <sup>+</sup>
<i>Lemna minor</i>		I <sup>+1</sup>	I <sup>+</sup>	I <sup>+</sup>
<i>Fontinalis antipyretica</i>		I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
<i>Phragmites australis</i>		I <sup>+</sup>	I <sup>+</sup>	II <sup>+</sup>
<i>Schoenoplectus lacustris</i>		I <sup>+</sup>		I <sup>+</sup>
<i>Typha angustifolia</i>		I <sup>+</sup>		I <sup>+</sup>
<i>Sparganium emersum</i>		I <sup>+</sup>	I <sup>+</sup>	
<i>Chara tomentosa</i>		I <sup>2</sup>	I <sup>+</sup>	
<i>Chara</i> sp.			I <sup>+</sup>	I <sup>+</sup>
<i>Typha latifolia</i>				I <sup>+</sup>

I, II... V – constancy; +, 1, 2... 5 – abundance; HV – *Hydrilla verticillata*; NC – *Nymphaea candida*; NP – *Nuphar pumila*; NL – *N. lutea*.

(constancy class III), *Stratiotes aloides* and *Utricularia vulgaris* (constancy class II). In the phytocoenoses of *N. candida* there was a high contribution of floating-leaved species such as *N. lutea*, *Potamogeton natans* (constancy class III) and *C. demersum* (constancy class II). The most frequent accompanying species was *Lemna trisulca* (constancy class II). The patches with *N. pumila* were characterized by a high proportion of *N. lutea* (constancy class V). Other frequently occurring species of the class Potametea included: *Elodea canadensis* (constancy class III), *Potamogeton lucens*, *P. natans* and *S. aloides* (constancy class II). Frequent accompanying species were: *Equisetum fluviatile* (constancy class III) and *L. trisulca* (constancy class II).

The analysis of the phytocoenoses of *N. lutea* showed that in addition to *N. lutea*, which dominated in the patches, *P. natans* and, among accompanying species, *Phragmites australis* (constancy class II) also played an important role in the community structure. It should be noted that among the dominant species *N. lutea* was the only species which occurred with high constancy in all the (four) types of phytocoenoses compared in the study.

The phytocoenoses studied developed at the following depths: *H. verticillata* (0.6-3.5 m; mainly 1.5-1.75 m), *N. pumila* (0.6-1.8 m; mainly 1.1-1.3 m), *N. candida* (0.1-2.8 m; mainly 1.5-1.7 m), *N. lutea* (0.4-2.0 m; mainly 0.9-1.3 m).

#### Water properties

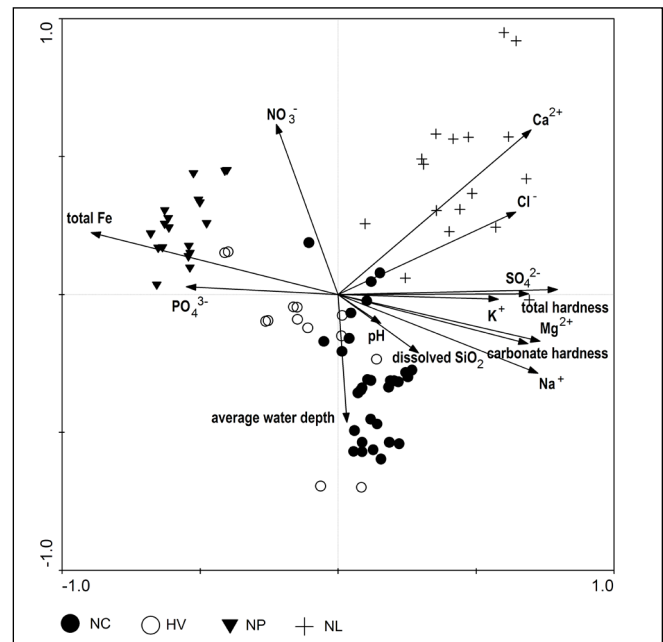
The analysis of Fig. 1 showed that among the properties of water analysed the factors associated mainly with the carbonate complex, such as total hardness,  $\text{SO}_4^{2-}$ ,  $\text{K}^+$ , carbonate hardness,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{Ca}^{2+}$  and dissolved  $\text{SiO}_2$ , as well as total Fe and  $\text{PO}_4^{3-}$  were most important in differentiating the waters of the vegetation types studied. These properties were correlated with the first ordination axis, which clearly separated the waters of *N. pumila* (left side of the diagram) from those of *N. lutea* (right side). The habitats of *N. candida* and *H. verticillata* phytocoenoses occupied an intermediate position.

The properties related to water hardness and correlated with the first ordination axis had significantly lower values in the waters of *N. pumila* than in those of *N. candida* (except for  $\text{Ca}^{2+}$ ) and *N. lutea* (Fig. 2, Tab. 2). Compared to *H. verticillata*, the waters of *N. pumila* contained lower levels of total and carbonate hardness, dissolved  $\text{SiO}_2$  and  $\text{Mg}^{2+}$  (Tab. 2). With regard to these properties the smallest differences were detected between the waters of *N. candida* and *N. lutea*, as well as between *N. candida* and *H. verticillata* (Fig. 2, Tab. 2). The waters of *N. lutea*, which are distinctly different from those of *N. pumila*, can be distinguished from the habitat of *H. verticillata* by higher total hardness,  $\text{Ca}^{2+}$ ,  $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{SO}_4^{2-}$  and  $\text{Cl}^-$  concentrations (Fig. 2, Tab. 2). A reverse trend was demonstrated for total Fe and  $\text{PO}_4^{3-}$ , which were also correlated with the first ordination axis. The waters of *N. pumila* were characterized by the highest values of these two parameters (significant differences between *N. pumila* and the other three types of phytocoenoses were found – Tab. 2). The waters of *H. verticillata* were also richer in total Fe than those of *N. lutea* (the differences between *H. verticillata* and *N. lutea* were significant – Tab. 2).

From Fig. 1 it is clear that such properties as  $\text{NO}_3^-$  and mean water depth also played an important role in differentiating the waters of the phytocoenoses studied. These properties were negatively related to each other, but were both correlated with the second ordination axis, which clearly separated the waters of *N. pumila* and *N. lutea* (the upper part of the diagram) from

those of *N. candida* and *H. verticillata* (the lower part of the diagram). The waters inhabited by *N. pumila* and *N. lutea* were rich in  $\text{NO}_3^-$ , whereas those of *N. candida* and *H. verticillata* were distinguished by lower values of this parameter (see Tab. 2 for significant differences). In the case of mean water depth, the phytocoenoses of *N. candida* and *H. verticillata* developed in deeper waters, whereas those of *N. pumila* and *N. lutea* were associated with shallower parts of the lakes. Although significant differences were found only between the *N. candida* and *N. lutea* phytocoenoses, the observed trends in water depth were clearly marked (Fig. 2).

Among the 14 properties of water analysed only pH did not significantly differentiate the waters of the phytocoenoses studied.

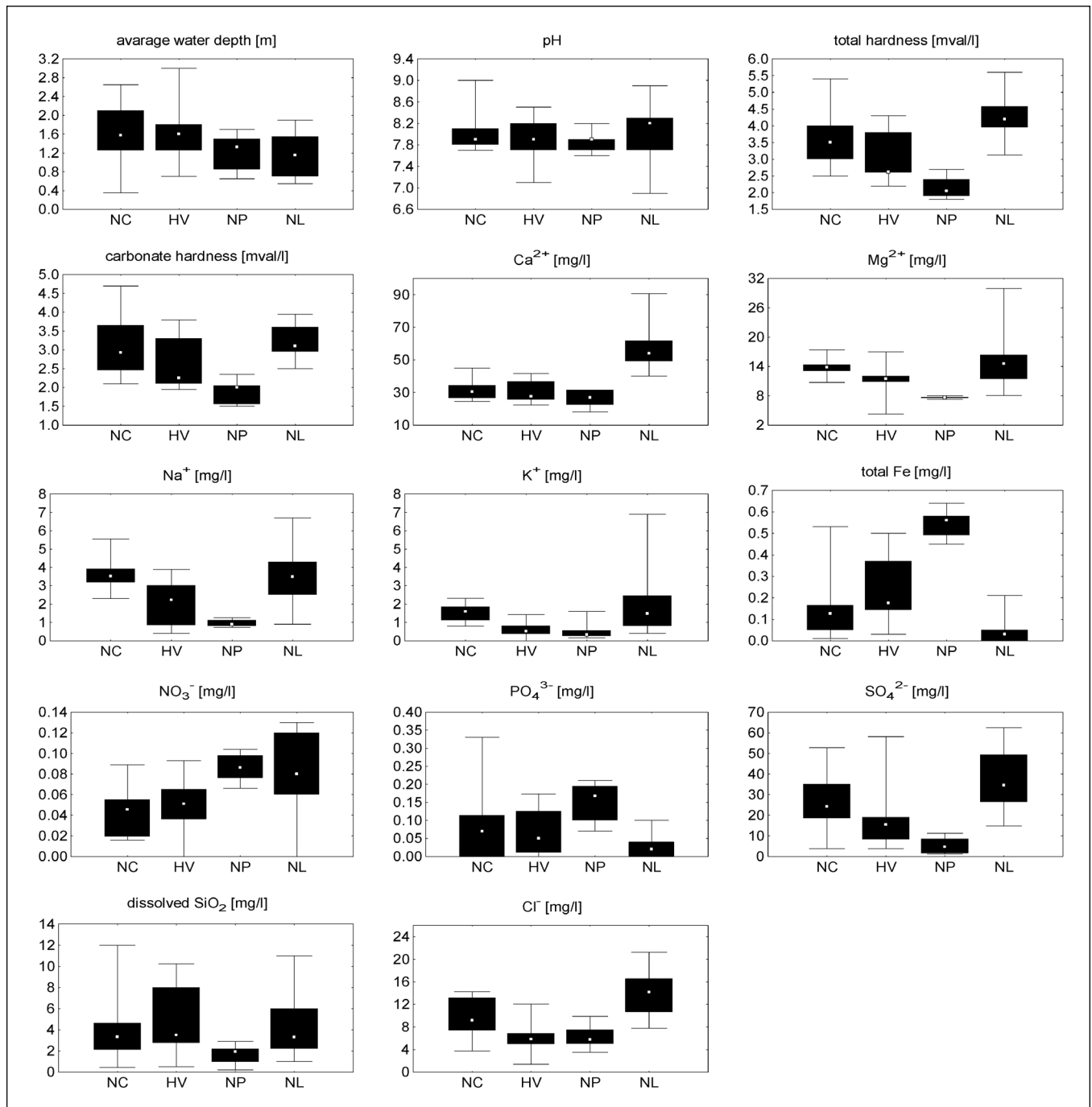


**Fig. 1** CCA ordination diagram of 1st and 2nd axes obtained for water properties and relevés of four plant communities, dominated by: NC – *Nymphaea candida*; HV – *Hydrilla verticillata*; NP – *Nuphar pumila*; NL – *Nuphar lutea*. Eigenvalues:  $\lambda_1 = 0.787$ ;  $\lambda_2 = 0.595$ ;  $\lambda_3 = 0.216$ ;  $\lambda_4 = 0.108$ . Monte Carlo permutation test of significance of all canonical axes:  $p = 0.002$ .

#### Substrate properties

The substrate properties which best differentiated the habitats of the plant communities studied were pH,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$  and  $\text{Na}^+$ , which were correlated with the first ordination axis (Fig. 3). As in the case of water properties, the axis clearly separated the substrates of *N. pumila* from those of *N. lutea*, whereas the habitats of *N. candida* and *H. verticillata* occupied an intermediate position. Total Fe, which was also correlated with the first ordination axis but negatively related to the five properties mentioned above (Fig. 3), appeared to play a significant role in differentiating the substrates of the plant communities studied as well.

The lowest values of pH,  $\text{Ca}^{2+}$ ,  $\text{Na}^+$  and  $\text{Mg}^{2+}$  were detected in the substrates of *N. pumila* (Fig. 4; significant differences between *N. pumila* and the other types of phytocoenoses were found regarding pH,  $\text{Ca}^{2+}$  and  $\text{Na}^+$ , and between *N. pumila* and *N. lutea* with regard to  $\text{Mg}^{2+}$  – Tab. 2). High values of pH,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$  and  $\text{Ca}^{2+}$  were recorded in the case of substrates of *N. lutea* (Fig. 4), which differed significantly from those of *N.*



**Fig. 2** Differentiation of the four communities studied in relation to water properties. Black boxes show 25–75% interquartile ranges of values and white boxes show the medians. NC – plant communities dominated by *Nymphaea candida*; HV – by *Hydrilla verticillata*, NP – by *Nuphar pumila*, NL – by *Nuphar lutea*.

*pumila* and (except for  $\text{Na}^+$ ) *N. candida* (Tab. 2). It should be noted that no significant differences were detected between the substrates inhabited by *N. candida* and those of *H. verticillata*, whereas only slight differences were noted between the substrates of *H. verticillata* and *N. lutea* ( $\text{Mg}^{2+}$  content). As in the case of water, the substrates of *N. pumila* were distinguished from those of the other types of phytocoenoses by significantly higher values of total Fe (Fig. 3, Fig. 4, Tab. 2).

Fig. 3 shows that such properties as  $\text{PO}_4^{3-}$ ,  $\text{Cl}^-$  and, to a smaller degree, dissolved  $\text{SiO}_2$  also played an important role in differentiating the substrates of the phytocoenoses studied. These properties were correlated with the second ordination axis, which clearly separated the substrates inhabited by *N. pumila* and *N. lutea* from those of *N. candida*

and *H. verticillata*. The substrates of *N. pumila* and *N. lutea* were generally poorer in  $\text{PO}_4^{3-}$  but richer in  $\text{Cl}^-$  (significance of differences – see Tab. 2). It is interesting to note that the highest content of  $\text{NO}_3^-$  was detected in the substrates of *N. pumila* (the differences between *N. pumila* and the other types of phytocoenoses were significant). Such properties as organic matter,  $\text{K}^+$  and  $\text{SO}_4^{2-}$  did not significantly differentiate the substrates of the plant communities studied.

## Discussion

The comparative analysis showed that in north-eastern Poland the three rare water plant communities examined in

**Tab. 2** Significance of differences in water and substrate properties between the four types of phytocoenoses studied.

Properties of water	NP-NC	NP-HV	NP-NL	NC-HV	NC-NL	HV-NL
Depth	ns	ns	ns	ns	+	ns
pH	ns	ns	ns	ns	ns	ns
Ca <sup>2+</sup>	ns	ns	+	ns	+	+
Mg <sup>2+</sup>	+	+	+	+	ns	ns
Total hardness	+	+	+	ns	ns	+
Carbonate hardness	+	+	+	ns	ns	ns
Na <sup>+</sup>	+	ns	+	+	ns	+
K <sup>+</sup>	+	ns	+	+	ns	+
Cl <sup>-</sup>	+	ns	+	+	+	+
SO <sub>4</sub> <sup>2-</sup>	+	ns	+	ns	ns	+
SiO <sub>2</sub> dissolved	+	+	+	ns	ns	ns
Total Fe	+	+	+	ns	ns	+
PO <sub>4</sub> <sup>3-</sup>	+	+	+	ns	ns	ns
NO <sub>3</sub> <sup>-</sup>	+	+	ns	ns	+	ns

Properties of substrate	NP-NC	NP-HV	NP-NL	NC-HV	NC-NL	HV-NL
Organic matter	ns	ns	ns	ns	ns	ns
K <sup>+</sup>	ns	ns	ns	ns	ns	ns
SO <sub>4</sub> <sup>2-</sup>	ns	ns	ns	ns	ns	ns
SiO <sub>2</sub> dissolved	+	ns	ns	ns	ns	ns
Cl <sup>-</sup>	+	+	ns	ns	ns	+
Ca <sup>2+</sup>	+	+	+	ns	+	ns
Mg <sup>2+</sup>	ns	ns	+	ns	+	+
Na <sup>+</sup>	+	+	+	ns	ns	ns
Total Fe	+	+	+	ns	ns	ns
pH	+	+	+	ns	+	ns
NO <sub>3</sub> <sup>-</sup>	+	+	+	ns	ns	ns
PO <sub>4</sub> <sup>3-</sup>	ns	ns	ns	ns	+	+

Symbols of phytocoenoses – see Tab. 1. “+” – significant at  $p < 0.05$ ; ns: non-significant.

this study were distinct with respect to water and substrate chemistry preferences. The phytocoenoses of *N. pumila* were found to be ecologically most distinct among the phytocoenoses compared (acidic substrates, rich in total Fe and NO<sub>3</sub><sup>-</sup> and soft waters, containing greater amounts of total Fe, PO<sub>4</sub><sup>3-</sup> and NO<sub>3</sub><sup>-</sup>).

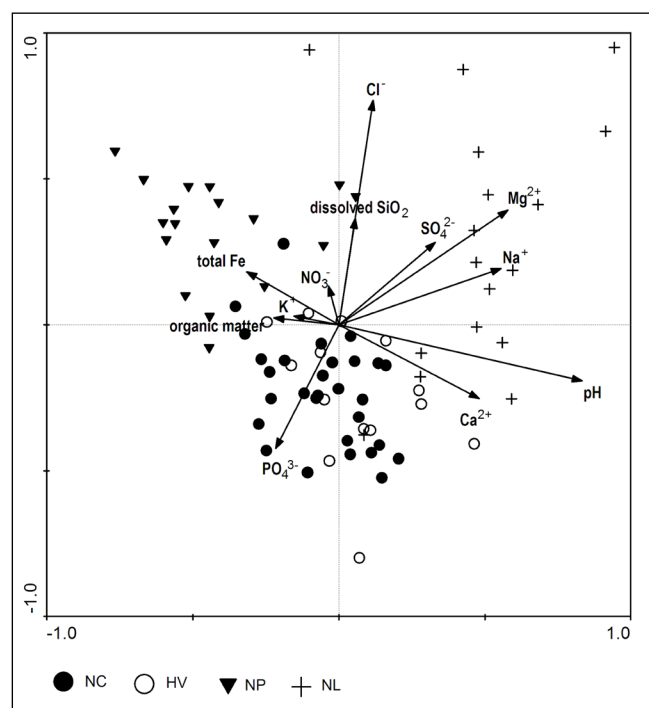
The relationship of *N. pumila* to soft waters was indicated by various authors (e.g. [8,9,11,22-24]). The specific character of the substrates (mostly organic and frequently peat bottoms) inhabited massively by this species was also emphasized [8,9,11,23,25]. Moreover the findings of some authors [9,26] showed that the phytocoenoses formed by *N. pumila* were ecologically distinct from those of *N. lutea* and *N. candida*. The results of this study demonstrated the distinct character of each of the habitats of *N. pumila* and *H. verticillata*.

The habitats of the phytocoenoses dominated by *H. verticillata* were also distinct from those of *N. lutea*, especially with regard to properties of water (lower values of most of the parameters analysed). Their substrates contained lower levels of Mg<sup>2+</sup> and Cl<sup>-</sup>, and greater amounts of PO<sub>4</sub><sup>3-</sup> compared to those of *N. lutea*, which may be ascribed to a higher proportion of well decomposed organic matter in the substrates of

*H. verticillata*.

The ecological distinctness of the *H. verticillata* phytocoenoses in relation to the patches of *Elodea canadensis* was already indicated earlier [10]. Moreover recent study showed the distinct character of the habitats of the phytocoenoses with *H. verticillata* in relation to some submerged plant communities of the alliance Potamion [27], especially with regard to waters which were poorer in Na<sup>+</sup>, K<sup>+</sup> and Cl<sup>-</sup>. The data obtained by other authors revealed that *H. verticillata* had a wide ecological amplitude with respect to properties of water [4,22,28] and the species was very tolerant to organic pollution [29]. The persistence of *H. verticillata* in north-eastern Poland in dense, often large phytocoenoses and the establishment of new stands of the species may indicate that *H. verticillata* finds optimal growth conditions in this region of Poland.

The presented data referring to all the known localities of *N. candida* in north-eastern Poland confirmed the ecological distinctness of the phytocoenoses dominated by this species in relation to the phytocoenoses of *N. pumila* [9] and *N. lutea* [9,30,31]. It is interesting to note that the habitats of *N. candida* are very similar to those of *H. verticillata*, especially with regard to substrate properties (no significant differences between these two communities were found). These two types of phytocoenoses inhabit more frequently organic substrates than other types of phytocoenoses. These findings confirm the results of several other studies concerning *N. candida* [31-33]. Earlier data indicated that *N. candida* phytocoenoses were associated mostly with mesotrophic waters [9,34]. The supplemented wider study conducted in north-eastern Poland shows that at present the phytocoenoses of *N. candida* inhabit more fertile eutrophic waters, as evidenced by a wide range of PO<sub>4</sub><sup>3-</sup> concentration in water. It appears that both *N. candida*



**Fig. 3** CCA ordination diagram of 1st and 2nd axes obtained for substrate properties and relevés of four plant communities, dominated by: NC – *Nymphaea candida*; HV – *Hydrilla verticillata*; NP – *Nuphar pumila*; NL – *Nuphar lutea*. Eigenvalues:  $\lambda_1 = 0.628$ ;  $\lambda_2 = 0.472$ ;  $\lambda_3 = 0.153$ ;  $\lambda_4 = 0.029$ . Monte Carlo permutation test of significance of all canonical axes:  $p = 0.002$ .

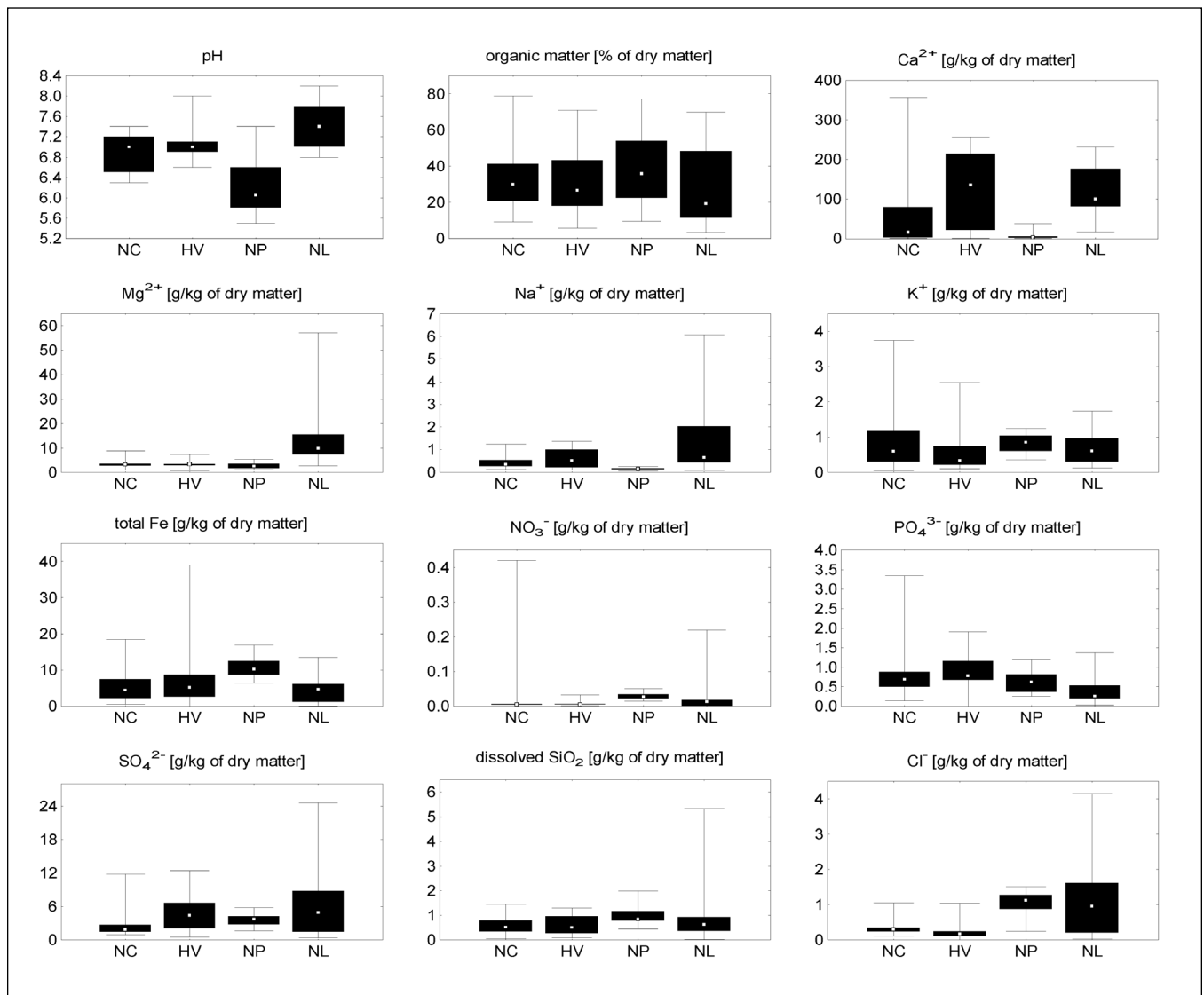
and *H. verticillata* attain their optimum development in lakes of north-eastern Poland.

The following question should also be considered: What might happen to the three types of phytocoenoses studied in the future? Recent studies conducted in several tens of lakes within north-eastern Poland (2002-2005) indicate that twenty-five years after the first habitat investigations (1978-1980) there has been a slight increase in the trophic level of the lakes [27]. In addition alkalization proceeds gradually and an increase in water hardness is observed. It appears, therefore, that the phytocoenoses of *N. pumila* are among the most threatened communities in the lakes. The increase in water trophy does not seem to affect these phytocoenoses as *N. pumila* tolerates a wide range of trophic conditions [8], which was also indicated by some other authors [23,25]. However, changes in water hardness appear to play an important role. The phytocoenoses of *N. pumila* are associated mostly with soft waters. The data obtained hitherto from Poland [8,9,35] indicate that the stands of this species in north-eastern Poland are established outside of their ecological optimum, which are very soft waters, i.e. they are rather closer to the tolerance limits of the species for water hardness. It may be assumed, therefore, that the

phytocoenoses of *N. pumila* will retreat from the lakes even when there is a slight increase in water hardness. By contrast, the *N. candida* and *H. verticillata* phytocoenoses, which inhabit waters with a wider range of hardness (slightly soft to moderately hard waters) and tolerate a moderate increase in trophic level, will probably continue to persist in lakes of north-eastern Poland for a long time provided that they are not subject to stronger anthropogenic impact.

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**Fig. 4** Differentiation of the four communities studied in relation to substrate properties. Black boxes show 25-75% interquartile ranges of values and white boxes show the medians. NC – plant communities dominated by *Nymphaea candida*; HV – by *Hydrilla verticillata*; NP – by *Nuphar pumila*; NL – by *Nuphar lutea*.

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