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Species richness and vegetation structure in different morphogenetic types of river lakes in the San River valley

Bogactwo gatunkowe i struktura roślinności w zróżnicowanych morfogenetycznie starorzeczach Sanu

SUMMARY

The aim of the conducted research was to check in what way the genetic diversity of the old river beds of the San River influences species richness as well as the structure of aquatic and rush vegetation in those water basins. The investigation was carried out during the period of 2003–2007 in the San River valley from Ulanów to the river's mouth.

Three main types of old river beds were distinguished: two at the meadow (*rendzina*) terrace (meander river lakes, irregular river lakes) and one on the floodplain (braided river lakes). The flora of 28 river lakes in the San valley was analyzed by statistical methods.

The study shows some differences in species richness and vegetation structure (species composition and abundance) connected with the morphogenetic variability of lakes in the study area. Essential relationships were observed in the case of some of the species richness indices. The irregular river lakes of the meadow terrace turned out to be the richest group of all; 72 species, i.e. 86.8% of the flora of all the explored old river beds, have been found there. The average number of species for this group amounted to 44.5, whereas for the meander and braided ones the value of this index was 30.9 and 25.9, respectively.

The differences between the two main groups of the old river beds, connected with the two main terraces (active floodplain and meadow terrace outside the embankments) can be marked on the level of the average number of all considered species and the average number of helophytes and floating-leaved macrophytes per river lake. However, small richness of floodplain lakes resulted mainly from their small size. The differences become statistically irrelevant after levelling the influence of the surface area of the lakes.

The interpretation of the results of PCA analysis indicates that the location of old river beds in the valley and their connectivity to the river, as well as the stage of terrestralization can be regarded as the main drivers behind the vegetation structure.

Key words: river lakes, morphogenetic differentiation, species richness, species composition, disturbance, the San River, SE Poland

STRESZCZENIE

Przeprowadzone badania miały na celu sprawdzenie, w jaki sposób genetyczne zróżnicowanie starorzeczy Sanu wpływa na bogactwo gatunkowe oraz strukturę roślinności wodnej i szuwarowej występującej w tych zbiornikach. Badania florystyczne zostały przeprowadzone w latach 2003–2007 w dolinie dolnego Sanu na odcinku od Ulanowa do ujścia do Wisły.

Na podstawie prac z zakresu geomorfologii wyróżnione zostały trzy główne typy starorzeczy na badanym terenie. Dwa na terasie rędzinnej (zakolowe i nieregularne) i jeden na terasie łęgowej (łachy). Flora 28 wytypowanych starorzeczy została przeanalizowana metodami statystycznymi w celu znalezienia różnic w jej strukturze.

Morfogenetyczne zróżnicowanie starorzeczy miało swoje odbicie w kompozycji i bogactwie makrofitów. Najbogatszą grupą starorzeczy okazały się starorzecza nieregularne terasy rędzinnej, znaleziono tam łącznie 72 gatunki, czyli 86.8% flory wszystkich badanych starorzeczy. Średnio w jednym zbiorniku z tej grupy występowało 44.5 gatunków. Dla starorzeczy zakolowych i roztokowych wartość ta wyniosła odpowiednio 30.9 i 25.9.

Różnice w bogactwie gatunkowym pomiędzy dwiema głównymi grupami starorzeczy (terasy łęgowej w międzywalu i rędzinnej poza obwałowaniem) zaznaczają się na poziomie średniej liczby wszystkich rozpatrywanych gatunków oraz średniej liczby helofitów i nymfeidów w starorzeczu. Głównym powodem takiego stanu rzeczy są jednak różnice w wielkości zbiorników. Po wprowadzeniu wskaźnika niwelującego ten czynnik różnice w bogactwie stają się nieistotne statystycznie.

Interpretacja wyniku analizy PCA wskazuje, że jako główne czynniki wpływające pośrednio lub bezpośrednio na strukturę roślinności wodnej i szuwarowej można uznać położenie w obrębie doliny i związaną z tym hydrologiczną łączność z rzeką oraz stadium lądowacenia zbiornika, które jest najczęściej funkcją jego wieku.

INTRODUCTION

River lakes (old river beds, oxbow lakes, cut-off channels) are natural ecosystems which are formed in the dynamic system of a river valley. The level of exploration of these environmental elements in Poland is insufficient, especially when we take into consideration their rapid declining.

River lakes are not uniform formations. The diversity results from many factors, such as their origin, age, location in the valley, morphometric features, the way of water supply, physicochemical properties of water and sediments, the connection with the river and the stage of terrestralization (2, 4, 6, 7, 10, 11, 14, 26, 28). To a large extent the way and time of forming determine other factors, directly or indirectly. From among the listed factors, one of the most important as regards shaping phytocoenosis, is river connectivity – a complex factor which may be described as the hydrological connection between river lake and active river channel. This phenomenon significantly influences species richness, vegetation structure and succession (5, 6, 30, 31, 32).

The additional factor is human activity which, in general, may accelerate the process of the disappearing of old river beds (eutrophication), as well as the reverse process connected with artificial excavation and removing the vegetation in order to exploit the water basins economically. Moreover, many young river lakes were formed as a result of river regulation works – shortening and narrowing of the river bed (13, 18, 24, 25, 26). The constructing of embankments isolates the old river beds from the river, making the direct hydrological connection between these elements impossible.

The subject of the influence of morphogenetic changeability of old river beds upon flora and vegetation is a matter which is discussed very rarely and the majority of up-to-date research being conducted in Poland concerns phytosociological characteristics of these water bodies (12, 17, 20, 27, 29). The references to species richness and vegetation structure in river lakes, as well as the factors that influence them can be found in the works of Bornette and co-workers (4, 5, 6), Van Geest and co-workers (30, 32) and Lorens (19).

There is no uniform and detailed classification of old river beds which takes into account morphogenetic criteria. Such classification was made in Poland for the Bug River; the authors distinguished six genetic types of river lakes (7).

In the valley of the lower section of the San River at least two main groups of old river beds can be identified; these are connected with the two different terrace levels of the contemporary bottom of the valley – meadow (*rendzina*) terrace and floodplain.

According to Szumański (25), on the meadow terrace exist 4 types of paleomeanders whose location, size and the state of preservation depend upon the time of creation. They were formed in the period of the meander pattern of the river channel, from late Pleistocene to the 18th century. At present, very few of them, mainly the young ones, are constantly or periodically filled with water. In addition, there exist a number of old river beds of irregular shape on this level in the mouth section of the river. Their origin is connected with numerous natural alternations of the river channel, as well as intensified river regulation works (23, 26). However, little documentary evidence has been provided as regards the forming of these old river beds, which is difficult to reconstruct; most probably they were formed from 150 to 300 years ago. All water bodies of this terrace are located outside the embankment and, therefore, are isolated from the influence of the river. Only some kind of catastrophic flood can result in the direct connection with the river.

Old river beds of the floodplain are in the form of narrow lengthy water bodies with the course almost parallel to the river bed. They are connected with the period of the past 150 years, when the San River changed the channel pattern from meandering to a braided one due to intensification of the activity in the catchment (24). It is this group of water basins of rather small surfaces area that retain a periodical link with the river. They can undergo the processes of terrestralization and fragmentation at a fast rate.

The conducted study was meant to specify in what way the genetic differentiation of river lakes of the San River influences species richness and the structure of water and rush vegetation (species composition and abundance) which can be found in these water bodies. Much attention has been paid to the phenomenon of river connectivity.

STUDY AREA

The San River is the largest Carpathian tributary of the Vistula. In its lowland section the river flows through the belt of sub-mountain basins and joins the Vistula at the boundary of an upland area near Sandomierz. In this section the river flows from the south east to the west north and is 160 km long (3, 34). The bottom of the present (Holocene) valley is 1–8 km wide and is filled with mud and used as an agricultural land. The channel width is 80–200 m. At the turn of the 19th century the main river-control works were conducted and embankments were built (3, 24, 33).

The mentioned section of the river valley is a separate unit in the physical-geographical and geobotanical division (16, 21).

MATERIAL AND METHODS

Floristic investigation of river lakes was carried out in the years 2003–2007 in the 45-km long section between Ulanów and the mouth of the San River (Fig. 1). Each river lake was examined in the summer (June–September) at least two times in two different years. Vegetation of the whole lake area was surveyed, by wading in shallow water and using the grapnel, until no new species were found. The abundance of species present were expressed in a 5-rank ordinal scale (1 – sporadic, 2 – rare, 3 – moderately frequent, 4 – frequent, 5 – dominant). Water and rush species were included in the study. Apart from a few exceptions (*Calla palustris*, *Scirpus radicans*, *Glyceria declinata*), these are the taxa which are, according to the system adopted by Matuszkiewicz (22), characteristic of the class of *Charetea*, *Lemnetea minoris*, *Potametea* and *Phragmitetea*.

For each river lake the surface area was determined. Furthermore, the proportion of open water surface in the total surface area of river lake was presented (Tab. 1). Open water surface was defined as an area covered with water communities or lacking vegetation and indicate the level of overgrowing of water basin. The surfaces were calculated by planimetering of air photos.

On the basis of the works on geomorphology (24, 25, 26) and detailed geological maps, the following morphogenetic types of river lakes were distinguished:

type I – on the floodplain (19th – 20th c.)

1 – braided river lakes – inside the embankments (with the exception of the old river bed 19 – outside the embankment)

- 1a – at the low level of the terrace, with regular flooding
- 1b – at the high and middle level of the terrace, with occasional flooding

type II – on the meadow (*rendzina*) terrace outside the embankments

2 – meander river lakes (according to Szumański (25, 26); modified)

- 2a – young age (17th – 18th c.), middle size, situated in the interior parts of the terrace in contact with floodplain
- 2b – middle age, formed mainly in the Atlantic and Subboreal period, small and narrow in the middle of the terrace
- 2c – old age, of large size, situated in the marginal zone of the terrace, dominated by swamp vegetation

3 – irregular river lakes, connected with the mouth section of the river (17th – 18th c.)

Twenty-eight river lakes of the San River, diverse in terms of their origin, size and the level of overgrowing have been chosen for the research (Fig. 1, Tab. 1).

On the basis of the data collected during the field study, the following indices of the species richness were defined for river lakes: (1) *N* – the number of species occurring in the lake, (2) *R* – the species richness defined as *N/logA,* where *A* marks the surface area of the old river bed in square meters (this index was applied to make, at least partly, species richness measure independent of the influence of the surface area). In addition, the total richness value was calculated for particular types of river lakes: (1) N_t – the number of species occurring in river lakes of one type, (2) N_t% – the percentage of species in the river lakes of particular type with relation to the whole of the investigated flora, (3) the average values of *N* and *R* indices for particular types of lakes, (4) *U* – uniqueness defined as the number of species that were found only in river lakes of one type.

A comparison of the richness indices has been made in two ways: for three main genetic types (meander, braided, irregular) and for two groups which differ as regard the river connectivity. The first group is still under the influence of river (type I), the second one is separated from river activity (type II). The old river bed 19 (located outside the embankments, subject to heavy anthropopressure) was excluded from the comparison. The indices mentioned above, as well as the differences in the number of species of particular life forms of macrophytes (pleustonic, submerged, floating-leaved, helophytes) have been taken into account.

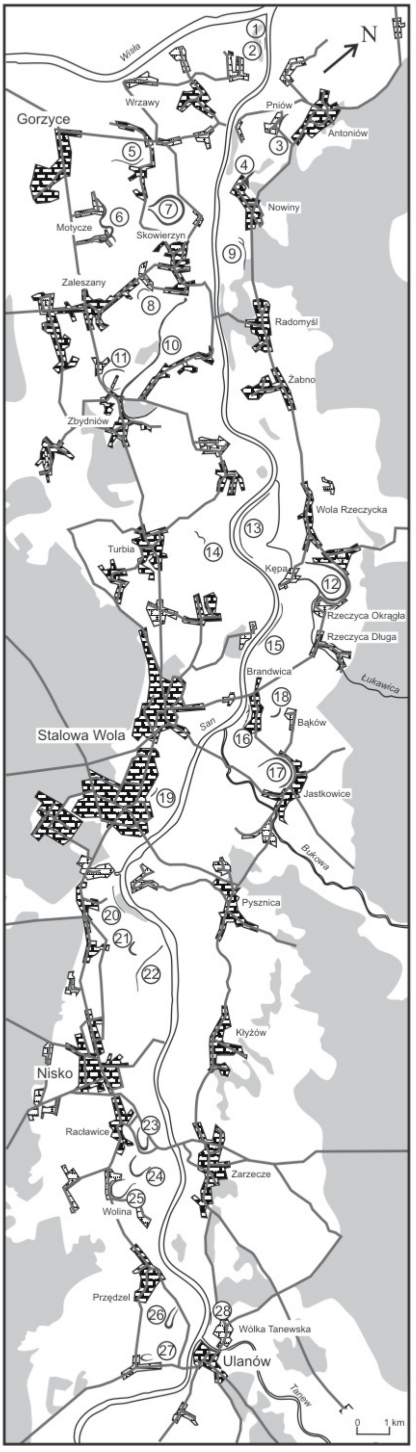

Fig. 1. The location of the studied river lakes

Table 1. Characteristics of the studied river lakes

Location	River lake type*	Surface area [ha]	Share of open water surface**	Location	River lake type*	Surface area [ha]	Share of open water surface**
1 – Wrzawy 1	1a	0.3	0.4	15 – Kępa	1b	0.54	0.3
2 – Wrzawy 2	1b	0.1	0.4	16 – Brandwica	1b	1.7	0.6
3 – Pniów	3	5.2	0.9	17 – Jastkowice	2c	20.0	0.05
4 – Nowiny	3	4.5	0.7	18 – Bąków	2b	2.1	0.4
5 – Gorzyce	3	1.0	0.6	19 – Stalowa Wola 1	1b	0.24	0.7
6 – Motycze	3	15.3	0.65	20 – Stalowa Wola 2	1a	0.29	0.1
7 – Skowierzyn	2c	19.0	0.05	21 – Nisko 1	2b	3.5	0.1
8 – Zaleszany	2b	0.6	0.1	22 – Nisko 2	1b	0.4	0.5
9 – Radomyśl	3	4.4	0.1	23 – Racławice	2a	11.8	0.2
10 – Zbydniów 1	3	65.8	0.5	24 – Wolina 1	2a	12.9	0.7
11 – Zbydniów 2	2c	7.1	0.05	25 – Wolina 2	2c	14.1	0.05
12 – Rzeczyca Okrągła	2c	47.7	0.15	26 – Przędzel 1	2a	10.0	0.1
13 – Wola Rzeczycka	1a	.9	0.2	27 – Przędzel 2	2b	4.50	0.15
14 – Turbia	2b	1.6	0.3	28 – Wólka Tanewska	1a	1.6	0.5

* see Material and Methods, ** proportion of open water surface (water communities or lack of vegetation) to total surface area of a river lake

In the statistical analyses the Mann-Whitney U test was used to examine data regarding species richness. Relationships between environmental variables and richness indices were evaluated with Spearman rank correlation coefficient. Statistical analysis was made with the help of Statistica software.

In order to reveal the similarities in the vegetation structure of the explored river lakes the ordination method was applied. Small value of the gradient length (<2 SD) was the reason that the principal components analysis (PCA) was chosen. All the examined species were used in this analysis (except the ones occurring only in one lake). The abundance of each species has been described in the 5-rank ordinal scale. To made the ordination diagram more legible only the crucial species were presented. The analysis was conducted by means of Canoco software.

RESULTS

In 28 of the explored river lakes, 83 species of water and rush plants were recorded. Most of them are vascular plants, while lower plants are represented by 4 species (Tab. 2).

The number of species which can be found in one old river bed was from 9 to 62, which constitutes respectively 10.8% and 74.7% of the whole flora of the explored river lakes. The same lakes show extreme values of *R* index,

Table 2. Abundance of species and species richness in particular river lakes

Number of river lake	1	13	20	28	2	15	16	19	22	23	24	26	8	14	18	21	27	7	11	12	17	25	3	4	5	6	9	10
Type of river lake*	1a	1a	1a	1a	1b	1b	1b	1b	1b	2a	2a	2a	2b	2b	2b	2b	2b	2c	2c	2c	2c	2c	3	3	3	3	3	3
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Acorus calamus									3	3	2		2		2			3	2	4	3	2	3	2	4	3	3	2
Alisma plantago-aquatica	3	3	3	4	3	4	3	3	4	3	4	2	3	3	2	3	3	2	2	3	2	2	3	3	4	3	3	3
Batrachium aquatile																				2								2
Batrachium circinatum							3																	2	2			
Batrachium peltatum																								2				
Batrachium trichophyllum	2	1																										
Berula erecta																								2		2		2
Bulboschoenus maritimus			3			4			2																			
Butomus umbellatus			2	2			2		2		2			1			1										1	2
Calla palustris										3	2							2		2	2	2					2	3
Callitriche cophocarpa					2															2								
Callitriche verna				2						2	2									2			2			2	2	2
Carex acutiformis		1							2	3	3		2			2		3	2	2	3	2			4	2	2	2
Carex diandra			1								2	2	1		1			2		1	2					2		2
Carex elata																					1	1	1					
Carex gracilis	4	3	2	2	3	4	3		4	3	3	3	4	3	3	3	2	4	4	4	4	4	3	2	4	3	3	4
Carex paniculata																					2					1		
Carex pseudocyperus									3	3	3	2	2		3	2		3	2	3	3		2	2	3	3		3
Carex riparia	2								2					2						1			3			1		2
Carex rostrata											2											2						
Carex vesicaria									2	2	2	2	2		2		1	3	2	3	3	3	2	1			2	2
Ceratophyllum demersum		3		4		3	4	2	3	3	3			3		2				1			2	3	4	4	3	4
Ceratophyllum submersum							2																					
Chara globularis		2		2																								
Cicuta virosa									2	2	2	3	1		3	2	2	3	3	2		2	2			2		2
Eleocharis palustris	2					2		2			2	1					2	2		2	2		2	2	2	2		2
Elodea canadensis		3		3		4	2		2											1			2					2
Equisetum fluviatile	2	3		2		1	2		3	3	3		2	2	2		2	3	3	3	3	3				2		3
Galium palustre	3	4	2	2	4	3	4		4	4	3	3	3	4	4	4	3	4	4	4	4	4	4	3	4	4	4	4
Glyceria declinata																				2				2	1			1
Glyceria fluitans	2		2	2		2			2	2	2		2			2				2	1	2	2	2	3	2	2	2
Glyceria maxima	3	4	3	4		4	4	3	4	4	4	2	3	3	3	3	3	3	3	2	3	3	3	3	3	3	3	3
Glyceria plicata										2										1				1	2			2
Hottonia palustris									2										1					2		1		2
Hydrocharis morsus-ranae				2			3		4	3	4	2	2	4	4	3	2	2		2	2		2	3	2	3	3	4
Iris pseudacorus	3	2	3	3	3	2	3		3	4	3	3	3	3	4	3	3	4	4	3	4	4	3	2	4	3	4	4
Leersia oryzoides										2													1					2
Lemna minor	2	3	2	2	4	2	3	3	4	3	3	2	3	3	3	4	2	2	2	2	2	2	3	3	3	3	2	3
Lemna trisulca		2	3			3	2		3	3	3	2	3	3	3	3		2		2	2		3	3		3		3
Lycopus europaeus	3	1	3	3	3	1	3	3	4	3	3	3	3	4	2	3	3	3	3	3	2	2	3	3	4	3	3	3
Lysimachia thyrsiflora									2		2									2	2		2	2		3		2
Myriophyllum spicatum				3		3	2				2	2												3		2	3	3
Myriophyllum verticillatum							1				1																	2
Najas minor																							2	1				

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Nitella capillaris																							2					
Nitella flexilis																					2							
Nuphar lutea	3	3				3	3	2	3	3	4					3							3	2		3	2	3
Nymphaea alba										2	4													1		1	2	1
Nymphoides peltata																				2								
Oenanthe aquatica	4	3	3	3	4	3	3		3	3	3	2	2	3	2	2	3	3	2	2	3		2	2	4	1	3	2
Peucedanum palustre										3	3						2			2	3	3	2	2	2		3	2
Phalaris arundinacea	3	3	2	3	2	2	2		2	2	2	2	2	3		2		2	2	2	2		3	1	1	2	2	2
Phragmites australis	2	1			2	1	3		3	4	4	5	5	5	4	5	5	5	4	3	4	5	3	4	4	3	4	4
Poa palustris	4	3		3	3	3	3	3	3	3	3	3	2	3	3	3	3	4	3	4	3	3	3	3	3	4	3	4
Polygonum amphibium f. natans																							2					1
Potamogeton crispus		2		2						2	2	2											4	2	3	2		1
Potamogeton lucens		2																										
Potamogeton natans				2																	1		2				3	2
Potamogeton pectinatus																								2		2	2	1
Potamogeton perfoliatus																								1				
Potamogeton pusillus									2																			
Potamogeton trichoides	3	2			3				2																2		2	
Ranunculus lingua										2	3							2	1		2					2		2
Riccia fluitans											2												2		2			2
Rorippa amphibia	2	2	3	3	2	2	3		2	3	3	3	2		2	3	4	2	3	2	2			2	3	2	2	2
Rumex hydrolaphatum					2		2		3	4	4	3	2	3	3	3	3	4	4	4	4	3	2	3	4	4	2	4
Sagittaria sagittifolia		2		3		1	2		2	2		1								1							1	2
Salvinia natans							3		2	2	3				2	1	2						3			3	3	3
Schoenoplectus lacustris					1						2															1		
Scirpus radicans																				3								
Scutellaria galericulata				2		2	2		2	3	3	3	2	4	3		3	3	4	3	3	3	2	2	2	3	2	3
Sium latifolium			3	2	3		2		3	4	3	3	2	3	3	3	3	3	3	3	3	3	2	3	3	3	3	4
Sparganium emersum				3			2																				1	2
Sparganium erectum						2				3							2							2			1	2
Spirodela polyrrhiza	2	2	2		1	2	2		3	3	3	2	2	3	3	2	3			2	2		2	3	3	2	2	2
Stratiotes aloides							3		2		3			3	2	3	2			3						2	2	4
Trapa natans											1												3				2	1
Typha angustifolia											2												2			4	1	2
Typha latifolia	3			2				3	3	4	2	2	3	3	2		3	3	2	3	3	3	2	2	4	3	2	3
Utricularia vulgaris				2			2										2			2				2				2
Veronica anagallis-aquatica	2	2																	1		2				2	2		2
Veronica beccabunga							1			2											2			2		2		2
Wolffia arrhiza													2										2					
Number of species *N*	22	26	17	28	17	25	33	9	39	40	47	27	28	23	26	25	27	28	25	46	37	23	43	43	32	47	40	62
Species richness *R*	6.33	6.58	4.91	6.62	5.67	6.7	7.8	2.66	9.17	7.89	9.2	5.4	7.41	5.47	6.02	5.5	5.8	5.3	5.15	8.1	6.98	4.47	9.12	9.24	8.0	9.07	8.61	10.7

Quantitative index of species within the investigation site: 1 – sporadic, 2 – rare, 3 – occasional (moderately frequent), 4 – frequent, 5 – dominant; * – see Material and Methods equal to 2.66 and 10.66 (Tab. 3). The irregular river lakes of the meadow terrace turned out to be the richest group; 72 species were found there, which constitutes 86.8% of the flora of all the explored old river beds (Tab. 3). The average species richness *R* for this group amounted to 9.12 ± 0.88 and was significantly higher than average value of this index for both meander (Mann-Whitney U test: Z = -2.98, p<0.005) and braided (Mann-Whitney U test: Z = -2.58, p<0.01) river lakes. The differences among meander and braided lakes for this index were insignificant.

Table 3. A comparison of species richness indices in different types of river lakes

Index	Type I	Type II	
	braided (n=8)	meander (n=13)	irregular (n=6)
N_t	58	68	72
N_t%	69.9%	81.9%	86.8%
N	25.9±7.6 (r: 17–39)	30.9±8.5 (r: 23–47)	44.5±9.9 (r: 32–62)
R	6.72±1.20 (r: 4.91–9.17)	6.36±1.41 (r: 4.47–9.20)	9.12±0.88 (r: 8.00–10.66)
U	6	4	7

N_t – the number of species occurring in river lakes of one type, N_t% – the percentage of species in the river lakes of particular type with relation to the whole of the investigated flora, *N* – the average number of species per river lake, *R* – the average species richness, *U* – the number of species found only in river lakes of one type

When comparing two main types of river lakes (type I and type II) differing with respect to river connectivity, variability in the species richness is marked on the level of the average number of species per lake (*N*). The differences of values for N_t and *U* indices among these groups are also clearly visible (Tab. 4). It is the number of helophytes and floating-leaved macrophytes that decides about it. However, after having ruled out the influence that surface area of a lake had on the real value of richness, by implementing the *R* index, the differences become statistically insignificant (Tab. 4). The braided river lakes are characterized by relatively high species richness, taking into consideration their small size. Almost 70% of all species of the explored lakes were found in them. The considerable age differentiation of river lakes of the meadow terrace (type II) is the cause of their being in different stages of overgrowing, which in turn causes – with the applied methodology (only water and rush species) – a wide range of the species richness value. Species richness is positively correlated with the share of an open water surface (Spearman rank correlation coefficient R=0.542, p<0.005).

Table 4. A comparison of species richness indices in two main types of river lakes

Life form	Index	Type I (n=8)	Type II (n=19)	Statistical significance*
All species	N_t	58	77	-
	N	25.9	32.2	p<0.05
	R	6.72	7.23	n.s.
	U	6	25	-
Pleustonic	N_t	4	6	-
	N	2.75	3.37	n.s.
	R	0.75	0.71	n.s.
	U	0	2	-
Submerged	N_t	16	16	-
	N	4.13	3.11	n.s.
	R	1.07	0.63	n.s.
	U	5	5	-
Floating-leaved	N_t	4	10	-
	N	1.38	2.84	p<0.1
	R	0.35	0.58	n.s.
	U	0	6	-
Helophytes	N_t	34	45	-
	N	17.6	25.9	p<0.05
	R	4.77	5.32	n.s.
	U	1	12	-

N_t – the number of species occurring in river lakes of one type, N – the average number of species per river lake, R – the average species richness, U – number of species found only in river lakes of one type; * – Mann-Whitney U test

The result of the PCA analysis, despite the low eigenvalues of the axes, is to a large extent convergent with the applied classification of river lakes (Fig. 2). The first two ordination axes contributed 25.9% and 15.4% of total variation, respectively. Axis I divides samples into two main groups, that is the water bodies of the floodplain on the left and the meadow terrace on the right. The second group is then differentiated by axis II separating irregular river lakes from the meander ones, the former being grouped in the lower part of the diagram.

The greatest differences in the structure of species composition are marked in the group of helophytes. Species such as *Acorus calamus*, *Calla palustris*, *Carex diandra*, *Carex pseudocyperus*, *C. vesicaria*, *Cicuta virosa*, *Peucedanum palustre* or *Ranunculus lingua* can only be found in the group of river lakes of the meadow terrace, whereas *Bulboschoenus maritimus* is connected mainly with braided river lakes. Taking into consideration the abundance of particular species, in braided river lakes more *Glyceria maxima* could be found, while in river lakes of the meadow terrace *Phragmites australis* was often dominant. In the case of rooted aquatic plants in old river beds of type I, the distinguished ones were *Nymphaea alba*, *Potamogeton pectinatus*, *P. crispus*, *P. natans*, *Hottonia palustris*, *Callitriche verna*. The species which could be found more frequently were also *Stratiotes aloides* and *Hydrocharis morsus-ranae* (Tab. 2). The braided river lakes were characterized by greater frequency of species such as *Potamogeton trichoides*,

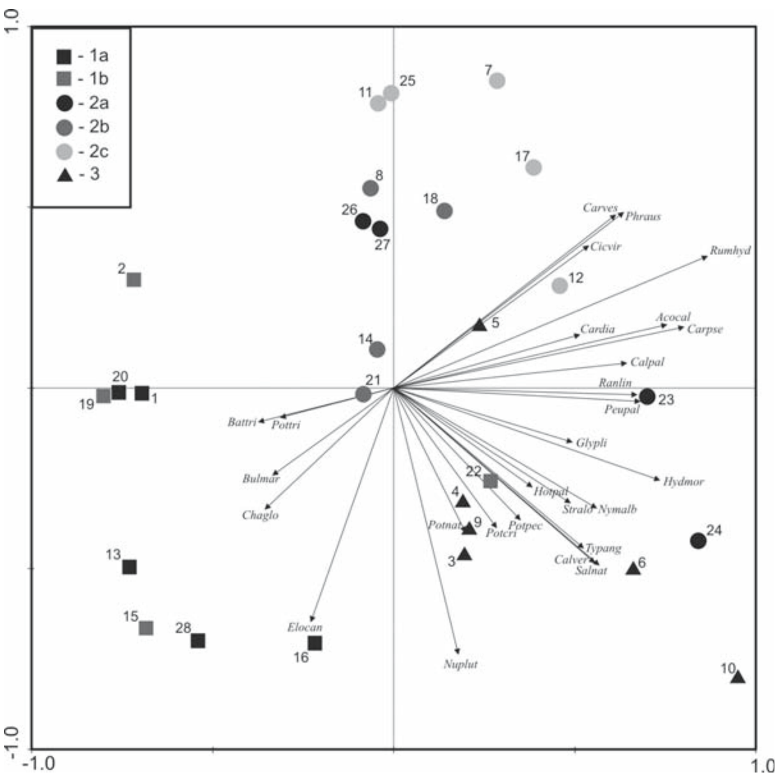

Fig. 2. Principal components analysis (PCA) ordination of the examined river lakes (Eigenvalues: Axis 1 = 0.259, Axis 2 = 0.154). Explanations: 1 – braided river lakes (a/b at the low/high level of floodplain), 2 – meander river lakes (a/b/c young/middle/old age), 3 – irregular river lakes

Chara globularis and *Elodea canadensis*. River lakes of the meadow terrace were distinguished by the presence of two pleustonic species which were not found in the lakes of the second type; these were *Wolffia arrhiza* and *Riccia fluitans*. In the group of lakes of type II, 25 species whose presence was not noted in lakes of type I can be found. The group of type I lakes has only 6 unique taxa.

DISCUSSION

The results of the study show that morphogenetic type of old river beds and conditions of the habitat which result from it have an influence on the vegetation structure. The variability of lakes influences species richness to a smaller extent, but differences are more visible in species composition and the structure of various life forms.

The value of species richness in particular types of river lakes was different, however, in the case of the two main groups, the differences were mostly a result of significant differences in the surface area of lakes, the braided river lakes are small or very small objects. If this factor is partly eliminated – by applying the *R* index – they become indistinct and statistically insignificant. Only the irregular river lakes can be regarded as significantly richer. The values of species richness are more often connected with the level of overgrowing of the water body, rather than the genetic type. There is a clear correlation between species richness (*R* index) and the share of the open water surface in total lake surface area (Spearman rank correlation coefficient $R=0.542$, $p<0.005$). Almost all irregular river lakes are characterized by a large open water surface and diversified zonational vegetation structure, whereas many of the meander river lakes are water bodies in their terminal stage of overgrowing, with hardly any water species. It seems that the stage of terrestralization will be a derivative of the age of the water basin, but in reality this is not always true. The rate and time of terrestralization are dependent upon many natural factors, as well as anthropogenic transformations of the environment.

The precise comparison of the species richness indices with the studies conducted by other authors is often impossible owing to the differences in the methodology used. In seven old river beds of the Bug River explored by Lorens (19) the number of species in aquatic and rush communities, noted in phytosociological relevés, ranges from 30 to 61 (on average 45) and, therefore, was similar to those from the river lakes of the San River.

Structure of vegetation in riverine wetlands are the result of operating many factors. Some studies emphasize the role of a nutrient content and morphometric features of river lakes (6, 19), other point out river connectivity as the main complex driver shaping species and vegetation diversity (5, 6, 30, 32). The connection between river lake and main channel water happens in two ways. Firstly, during the overbank flow, the connection and exchange of water between the river channel and its lake occurs. This hydrological connectivity has a significant impact on the physicochemical conditions of water, it improves oxygen conditions and causes the decrease in the concentration of all chemical compounds. For instance, the amount of total phosphorus can be reduced 13 times after the flooding (15). The second possibility consists in the exchange with the contribution of the groundwater aquiler. It can occur in both directions depending on the water level in the river bed. The distance away from the river and more pervious sand substratum of young lakes make such exchanges easier (32).

The two ways of hydrological connection mentioned above are accompanied by the phenomenon of periodical disturbance of the habitat. In the first case the floodwater, depending on the speed of the flow, can be a destructive force for vegetation and the bottom sediment stratum (*flood scouring*). The speed of the flow is dependent on the morphometric features of a river lake. It is negatively correlated with sinuosity and positively correlated with the rake of a slope (1, 6). The close link with the contribution of underground water causes fluctuations of the water level in an old river bed, the magnitude of which is dependent on the hydrologic regime in the river bed (15, 32). This evokes a temporal exposure of the water basin bottom (*drawdown*).

Through limiting the competition, the two phenomena contribute to the increase of species richness when their intensity and frequency are temperate. In other cases (long periods of drawdown or flooding, frequent and intensive overbank flows) they usually act reversely (1, 5, 32). This relationship is consistent with *The Intermediate Disturbance Hypothesis* (8). Periodical exposing of the bottom also activates the germination of diasporas and growth of the seedlings of some plants connected with the littoral zone (9). River lakes, which are located on those river sections with regulated regime (with no low-water flow periods), show small richness and invasive species are often dominant (31).

In reference to the processes of disturbance, the results of the study from the river lakes of the San River valley do not present such regularities. There are no significant differences in richness between the two main groups of old river beds or on the contrary, the old river beds under the influence of the river are poorer. The comparison of the *R* index for irregular river lakes and braided river lakes clearly indicates higher values of species richness of the former group, the difference is significant (Mann-Whitney U test: $Z = -2.58$, $p<0.01$). There are two possible reasons for the presented situation. Braided river lakes are straight water basins; they run parallel to the river bed and, therefore, they may be subject to high flood scouring, especially when they are located on the lowest terrace level. In addition, as a result of narrowing, the San River is strongly incised in the bottom of the valley and, therefore, during the low-water flow periods, the floodplain is heavily drained and dried (33). The maximum occurrence of flood scouring and drawdown mentioned above can cause the impoverishment of the water basins' flora. Furthermore, in lakes outside the embankments moderate human activity (fish breeding, preventing the water bodies from overgrowing, watering places, nearby location of pastures and farm animals) can be regarded as an intermediate disturbance. Also the phenomenon of bottom exposure occurs here even with minor fluctuations of the water level thanks to shallow and wide littoral zones.

The layout of samples in the ordination space, gained by the PCA method, suggests the activity of two factors which determine the composition of plant species of the river lake of the San River. The layout of the samples along the axis I could be, at least partly, identified with the gradient of the habitat's stability/disturbance, which is, to a large extent, the consequence of the hydrological connectivity between the lakes and the river channel described above. The size of the water body must have influence on the stability of conditions. The largest lakes, isolated from the impact of the river, are grouped on the right side of the diagram, whereas the small ones, braided river lakes influenced by the river, occupy its left side (Fig. 2). It can be also assumed that the location of samples along axis II illustrates the stage of overgrowing of the old river bed, which is most often connected with its age. This regularity is visible in the group of meadow terrace river lakes which are diversified in terms of age. The lower part of the diagram is occupied by relatively young lakes with large open water surface. Old river beds with advanced staged of overgrowing, mainly the oldest ones, located in the marginal zone of the valley, are placed at the reverse pole (Fig. 2).

The comparisons of river lakes, in which the genetic type of water basin was taken into consideration, were conducted by Bornette and co-authors (4). The authors took into account two genetic types (braided and meander rivers), as well as the dominant processes in the river bed (incision and aggradation) and supplying by groundwater connected with the location in the valley. The comparison of species composition with the use of ordination analysis did not bring any unequivocal results; as the reason for this outcome the authors point out the complexity of factors and processes, thanks to which each water basin has its distinctiveness. They also highlight the interactions between the geomorphological and biological processes which occur in different time scales. Some differences in the flora structure of the old river beds of the Bug River, by the use of the ordination method, were found by Lorens (19); however, the number of basins taken into account was rather small and the author did not refer to the genetic type of the old river bed.

The differences in species presence and abundance in river lake of the San River result from different contribution of particular life forms, as well as the presence of certain species which – according to various studies (1, 31) – can be used as indicators of the presence of phenomena connected with the influence of the river upon river lakes. Unlike other river lakes, the basic feature of braided river lakes is a small percentage of helophytes, which is often connected with the absence of well developed littoral zone and the lack of thicker bed of mineral-organic sediments, on which the species such as *Calla palustris*, *Peucedanum palustre* or *Carex diandra* could grow. The differences are visible both on the level of the average richness per river lake and in the total number of species occurring in both types of old river beds (Tab. 4). In the case of floating-leaved macrophytes which prefer more stable habitats, the difference to the advantage of lakes of the *rendzina* terrace can be marked; it can be more properly expressed in the values of indices N_t and U than the average value of N index. No differences have been found in the group of submerged macrophytes. All indices applied are similar or identical; however, taking into consideration major differences in the surface area of both types river lakes, it can be said that the flora of submerged macrophytes is relatively richer in the braided river lakes. It is consistent with Van Geest's (32) observations, who showed a clear positive correlation between the intensity of the drawdown and the number of species representing this life form. The smaller amount of pleustonic species occurring in the braided river lakes (N_t) can be the result of this group's susceptibility to both carrying away by flood water and – as

Wołek (35) pointed out – the sensitivity to desiccation. No significant differences in richness have been affirmed in this group of plants, which is consistent with the results of the study conducted by Wołek (36).

The results from the San River valley are to a large extent convergent with Van Geest's et al. (30) observations, who stated that the probability of the occurrence of helophytes was increasing with the age and decreasing with the surface, the probability of the domination of submerged macrophytes was decreasing with the increase of the surface area, depth and age and floating-leaved macrophytes could hardly be found in shallow reservoirs.

According to established patterns, young river lakes which are influenced by the river are characterized by a smaller contribution of species connected with stable habitats, which include *Nymphaea alba*, *Hydrocharis morsus-ranae*, *Carex pseudocyperus*, *Phragmites australis*, *Riccia fluitans* and they were observed in the San River valley more frequently or exclusively in the old river beds of the meadow terrace. The opposite are the taxa which tolerate the destructive activity of flood water, such as *Elodea canadensis*, *Potamogeton natans*, *Sparganium emersum*, *Phalaris arundinacea*, *Berula erecta* and *Glyceria fluitans* (1, 4). In reference to the conducted study, only waterweed and, rather weakly, Bur-reed reflected this regularity. We can observe the reverse situation in the case of *Potamogeton natans*, which could be found almost exclusively in the water basins outside the embankment.

The *Chara* species, desiccation tolerant plants, observed in young reservoirs in the neigbourhood of the river bed, are considered as indicators of major fluctuations of the water level in the water bodies and the exposure of the bottom (32). In the river lakes of the San River *Chara globularis* has been observed only in the braided river lakes. *Nuphar lutea* is claimed to be desiccation sensitive plant, which cannot be confirmed by the research from the San River. This species can be equally often found in all types of river lakes.

As Bornette et al. (4) pointed out, apart from the flood resistant species, braided river lakes are also distinguishable by greater contribution of mesotrophic species, which could not be confirmed unambiguously for the lakes of the San River. According to my own research, *Potamogeton trichoides* and *Bulboschoenus maritimus* can be considered the species which characterize braided river lakes.

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