Changes of aquatic-riparian bryophyte vegetation between 1991–1992 and 2004 in the Szigetköz branch-system after the diversion of the Danube

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CHANGES OF AQUATIC-RIPARIAN BRYOPHYTE VEGETATION BETWEEN 1991–92 AND 2004 IN THE SZIGETKÖZ BRANCH-SYSTEM AFTER THE DIVERSION OF THE DANUBE

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In 1992 a 120 km long section of the Danube river, part of the border line between Hungary and Slovakia, was diverted into a new riverbed to put into operation the Gabčikovo (Bős–Nagymaros) Hydropower Plant. To follow up the environmental changes a monitoring system in the Szigetköz region, seriously affected by the diversion of the river, was established by the Hungarian Academy of Sciences. Results of the bryological monitoring work, conducted in the river branches are presented in this article. Today, the species composition of the aquatic-riparian bryophyte vegetation living in the various sections of the Szigetköz branch-system is different from that of 1991–1992. The abundance-frequency values of aquatic species have decreased, while the proportions of mesophilous long-lived species and short-lived bryophytes have increased. The changes of water requirement spectra of bryophyte vegetation and the growing importance of certain species groups indicate that the ecological conditions became drier. Apparently, the water supply system operated from 1995 provides insufficient amount of water and is inadequate to stop (and even less so to reverse) the environmental changes that took place in the branch-systems.

Key words: bryophyte vegetation changes, Danube river, Hungary, hydropower plant

INTRODUCTION

A 120 km long section of Danube, the largest river of Central Europe, forms the official boundary line between Hungary and Slovakia (formerly, Czechoslovakia) (Fig. 1). Its flow velocity at Rajka, where the Danube reaches Hungary and at the same time the Carpathian Basin, slows down and ramifies to several branches (Fig. 2). The Hungarian part of the branch-systems is the

Szigetköz region (527 km^2) and the Slovakian side is the Žitný ostrov (Csallóköz) region (1,800 km^2). The network of branches was in continuous change due to the fluvial dynamics, from year to year islands were destroyed, branches were altered, removed or blocked and new islands were built in other places. This spatial and temporal heterogeneity of the landscape has maintained high biodiversity, but for centuries it was disadvantageous for the navigation on the river. This and the threat of floods have led to its regulation by building an artificial bed (main branch) at the end of the 19th century to aid the increasing water traffic.

Afterwards, this artificial riverbed had been systematically altered for almost 50 years in order to provide adequate water level for navigation by damming the entrances of the branches and narrowing the bed wherever it was necessary. This way the previously always changing network of smaller and larger branches and arms had been changed to a system containing a main branch and several side branches. Consequently, at low water level, the water of the main branch and that of the rest of the branch system was disconnected (normally, the water of the side-branches and that of the main branch was in natural connection, especially during high water level and floods).

As a unilateral step towards putting into operation the Gabčikovo (Bős–Nagymaros) Hydropower Plant, in October 1992 the Czechoslovak water management authority has diverted the Danube onto their own territory into a new riverbed (Fig. 2). Originally, the utilisation of the river for hydropower production was a joint project of the two countries. Hungary cancelled the contract in 1989 citing the potential (and foreseen) environmental impacts, but Slovakia was determined to finish the construction of the hydropower plant alone (Hajósy and Vargha 1997).

Fig. 1. Location of the Szigetköz region

After the diversion the water output of the Danube had been reduced to one tenth of the original one. Before the diversion the average yearly flow rate at the inflow section (the town of Rajka) was about 2,000 m^3s^{-1}. After the diversion about 250 m^3s^{-1} was let into the former riverbed. The water level in this main branch (the so-called Old Danube) has dropped by approximately 4 m. After 1995, thanks to an agreement between the two governments the water income increased to 300–400 m^3s^{-1}. In 1995 a water supply system was also built on the Hungarian side to provide water to the critically dried out tributaries. The system was constructed by digging new channels, dredging the old ones and building new gates (Smith *et al.* 2000).

To follow up on the environmental changes a monitoring system was established by the Hungarian Academy of Sciences involving hydrological, forestry, vegetational and zoological investigations in the Szigetköz region. Results of long-term bryological monitoring conducted in the branches are presented in this paper.

Bryophytes, which react to varying environmental conditions rapidly, are good indicators. Bryophytes of running waters are typically used to detect heavy metal pollution (e. g. Elisa *et al.* 1992, Mouvet *et al.* 1986, Nimis *et al.* 2002, Samecka-Cymerman *et al.* 2002). Data on water quality (saprobity) indications of bryophytes are widely available (e. g. Frahm 1974, Empain 1973, 1978, Peñuelas and Sabater 1987, Vanderpoorten 1999, Vanderpoorten *et al.* 1999, Vrhovšek *et al.* 1984, 1985). Correlation between the bryophyte vegetation and water quality along the Danube are presented in Papp and Rajczy (1995, 1998*b*). According to these papers the bryophyte vegetation living on

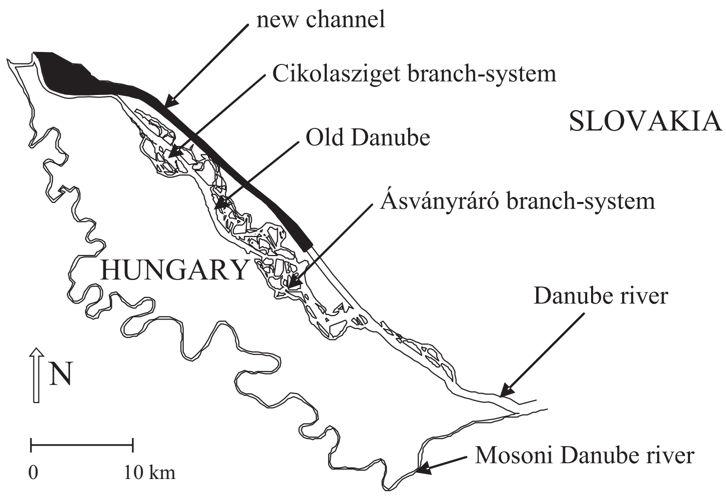

Fig. 2. Map of the Szigetköz region

the stony embankments of the Danube section at Szigetköz reflects β–α meso-saprobic water quality. This section is less polluted than the downstream parts of the river. Studies dealing with changes in species composition of the bryophyte vegetation of running waters in connection with environmental changes, especially water regime, water supply changes, and conclusions based on observations of a longer time period are rare. Whitton *et al*. (1998) reports on long-term (30-year period) changes in macrophytes in a British river. The changes occurred are associated with the slower flow and greater nutrient richness of the river. Several bryophytes were recorded during these surveys, but more apparent changes have occurred in the distribution of higher plants rather than in that of bryophytes. Effects of river regulation to aquatic bryophytes are discussed in Vanderpoorten and Klein (1999) and Englund *et al*. (1997).

The aquatic-riparian bryophyte vegetation is influenced strongly by the water supply; hence the study of these bryophyte assemblages is an adequate tool for the monitoring of the changes of surface water in Szigetköz. The aquatic-riparian bryophyte vegetation is quite well developed on the banks of the branches in the branch-system. This bryophyte vegetation consists of mainly terricolous species, hence only a few members of the saxicolous bryophyte assemblages living on the stony embankments of the main riverbed (Old Danube) are present on the banks of the branches (Papp and Rajczy 1998*a*). According to the survey carried out before the installation of the Gabčikovo Hydropower Plant (in 1991–92) the bryophyte vegetation of the banks of the branches represented natural conservation values of various level. Several bryophyte rarities were still living on the banks, although forestry operations even at that time have seriously threatened these habitats. This activity causes the destruction of natural banks by cutting the *Salix* and *Alnus* trees, which formerly protected the banks from erosion, and planting *Populus* trees, which cannot prevent this process.

METHODS

In 1991–1992, before the diversion of the Danube, a complete survey was carried out in the two biggest branch-systems of the Hungarian side (Cikolasziget and Ásványráró branch-systems), which included almost all the branches of these branch-systems. In the Cikolasziget branch-system 16 branches, while in the Ásványráró branch-system 10 branches were sampled. Beginning in 1995, the aquatic-riparian bryophyte vegetation had been yearly investigated in 6 selected branches (four in the Cikolasziget and two in the Ásványráró branch-system). In the year 2001 the complete survey, concerning all branches, was repeated.

The same method was applied in each study. In a *ca* 100 m long section of the branches the species composition and species abundance-frequency values were recorded in the bank bryophyte vegetation (it includes an about 2 m wide strip from the water level until the point where the bank begins to level out). The abundance-frequency values for each species in each branch were estimated using a scale of 1–4. During the data analysis, the relative water requirement ecological indicator values (Zólyomi and Précsényi 1964, Orbán 1984) and life strategy types (During 1972, 1992, Orbán 1984) were used. For the comparison of samples taken in 1991–92 and 2001 principal component analysis (standardised PCA) was used from the program package SYN-TAX (Podani 2001). Wilcoxon paired-sample test (Zar 1999) was carried out to reveal the significance of the difference in occurrence and abundance-frequency of characteristic species in bryophyte assemblages and summarised abundance-frequency of species groups in different sampling years and periods. Nomenclature of bryophyte species follows Erzberger and Papp (2004).

RESULTS

Table 1 shows the changes in the species composition of aquatic-riparian bryophyte vegetation of the branch-systems. Occurrence and summarised abundance-frequency values of characteristic species are shown in 1991–92, before the diversion of the Danube and ten years later, in 2001, respectively. Of all species recorded in the mentioned two years only those are included, which occur at least in half of the branches in at least one of the branch-systems and in at least one year of the investigation.

Species are grouped according to their water requirement and life strategy types. The occurrence and abundance-frequency values of the formerly characteristic aquatic species as *Amblystegium humile*, *A. riparium* and *Bryum pseudotriquetrum* have decreased. The change of abundance-frequency of the latter species is significant (Table 2). The occurrence and abundance-frequency values of a number of mesophilous, perennial species like *Brachythecium mildeanum*, *B. rutabulum*, *Eurhynchium hians* and those of long-lived shuttle species as *Mnium marginatum*, *Plagiomnium undulatum* have increased. Except for *Mnium marginatum*, the changes of abundance-frequency of these above-mentioned species are significant. Several short-lived species (colonists, annual shuttle species) show expansion with increasing abundance-frequency values in the branches, examples include *Pohlia melanodon*, *Dicranella schreberiana*, *Didymodon fallax*, and *Bryum* species. The changes of abundance-frequency of these

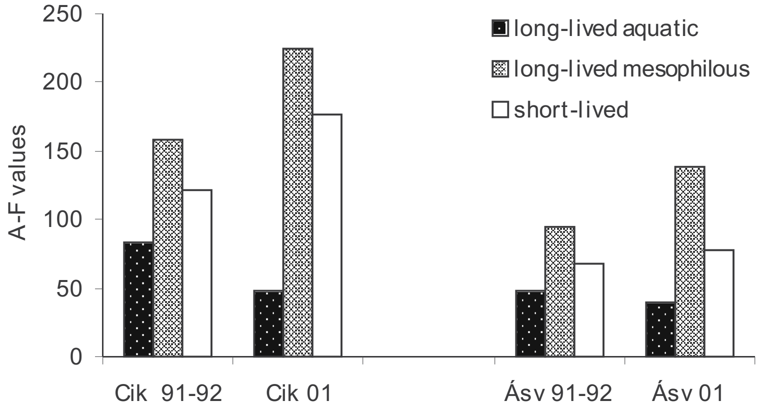

Fig. 3. Changes of summarised abundance-frequency values as illustrated in three different species groups in two branch-systems in 1991–1992 and 2001, respectively. (Cik = Cikolasziget branch-system, Ásv = Ásványráró branch-system)

species are significant. *Physcomitrium pyriforme* has spread within the Cikolasziget branch-system, but is retreating in the Ásványráró branch-system. *Pohlia wahlenbergii* was a characteristic species in 1991–1992 in the study area. It has almost completely disappeared from the branches. This species seems to be very sensitive to the environmental changes that took place in the branch-systems.

Changes of total abundance-frequency values of the various species groups in the two branch-systems in 1991–1992 and 2001 are presented on Figure 3. The summarised abundance-frequency values of aquatic species are decreased, while those of long-lived mesophilous and short-lived species are increased in both branch-systems. The changes are significant according to the Wilcoxon paired-sample test (Table 3). The differences appear to be greater in the Cikolasziget than in the Ásványráró branch-system. The changes of abundance-frequency values of all species groups are significant in the Cikolasziget branch-system, while in the Ásványráró branch-system only the long-lived mesophilous species showed significant change in the summarised abundance-frequency values (Table 4).

Results of the principal component analysis (1 axis – Eigenvalue 12.09; 2 axis – Eigenvalue 6.29) based on the data series (59 species; 52 branches) of the two surveyed years show that the samples of 1991–1992 are mainly situated on the right side of the figure and they differ from the samples of 2001, which are located mostly on the left side (Fig. 4).

Table 5 exhibits the species composition change in a characteristic branch (Cikolasziget branch-system: N branch) sampled yearly beginning from 1995. Similar events can be recognised as on the basis of comparison of all branches

Table 1

Occurrence and summarised abundance-frequency values of characteristic species in 1991–92 and 2001. (Cik = Cikolasziget branch-system, Ásv = Ásványráró branch-system); species names printed in boldface are characteristic members of the bank bryophyte vegetation in 1991–92; for explanation of abbreviations of species names see Table 5)

		No. of branches		Sum A-F values		Diff. of sum A-F	No. of branches		Sum A-F values		Diff. of sum A-F
		Cik 91–92	Cik 01	Cik 91–92	Cik 01	91/92–01	Ásv 91–92	Ásv 01	Ásv 91–92	Ásv 01	91/92–01
Long-lived aquatic	AMBHUM	10	10	22	13	–9	5	4	11	6	–5
	AMBRIP	13	16	42	31	–11	9	9	21	22	1
	BRYPSE	9	4	20	4	–16	6	9	16	12	–4
Long-lived mesophilous	AMBSER	14	16	39	34	–5	9	10	28	27	–1
	AMBVAR	9	8	18	13	–5	6	5	13	9	–4
	BRAMIL	5	12	8	25	17	6	10	15	19	4
	BRARUT	14	16	41	51	10	6	10	14	33	19
	EURHIA	12	16	32	61	29	7	9	23	36	13
	MNIMAR	7	11	18	25	8	1	5	2	7	5
	PLAUND	2	9	2	16	14	0	5	0	8	8
Short-lived	BARUNG	13	15	36	34	–2	6	8	17	14	–3
	BRYSPP	0	10	0	17	17	1	6	1	11	10
	DICSCH	1	10	1	11	10	0	0	0	0	0
	DIDFAL	6	11	6	14	8	1	5	1	6	5
	FISTAX	8	11	15	17	2	1	7	3	12	9
	LEPPYR	4	11	6	17	11	4	5	13	7	–6
	PHYPYR	7	14	14	21	7	6	2	13	3	–10
	POHMEL	12	16	26	46	20	6	8	16	24	8
	POHWAH	8	0	17	0	–17	2	0	4	0	–4

Table 2

Significance of the changes of abundance-frequency values of characteristic species summarised for all samples in 1991–1992 and 2001 using Wilcoxon paired-sample test at $p < 0.05$; for explanation of abbreviations of species names see Table 5

	Sum A-F 1991–92	Sum A-F 2001	Diff. of sum A-F	Wilcoxon test
AMBHUM	33	19	–14	n. s.
AMBRIP	63	53	–10	n. s.
BRYPSE	36	16	–20	s.
AMBSER	67	61	–6	n. s.
AMBVAR	31	22	–9	n. s.
BRAMIL	23	44	21	s.
BRARUT	55	84	29	s.
EURHIA	55	97	42	s.
MNIMAR	20	32	12	n. s.
PLAUND	2	24	22	s.
BARUNG	53	48	–5	n. s.
BRYSP	1	28	27	s.
DICSCH	1	11	10	s.
DIDFAL	7	20	13	s.
FISTAX	18	29	11	n. s.
LEPPYR	19	24	5	n. s.
PHYPYR	27	24	–3	n. s.
POHMEL	42	70	28	s.
POHWAH	21	0	–21	s.

sampled in 1991–1992 and 2001. Aquatic *Amblystegium* species e. g. *A. humile*, *A. riparium* were predominant elements in the bank bryophyte vegetation in 1991–1992. *A. humile* disappeared after the diversion, nowadays it has medium abundance-frequency. *A. riparium* after its initial loss of its abundance-frequency reached again the earlier values. The aquatic *Bryum pseudotriquet-*

Table 3

Significance of the changes of abundance-frequency values of different species groups summarised for all samples in 1991–1992 and 2001 using Wilcoxon paired-sample test at $p < 0.05$

	Sum A-F 1991–92	Sum A-F 2001	Diff. of sum A-F	Wilcoxon test	p-level
Long-lived aquatic	132	88	–44	s.	0.018417
Long-lived mesophilous	253	364	111	s.	0.00140
Short-lived	189	254	65	s.	0.008147

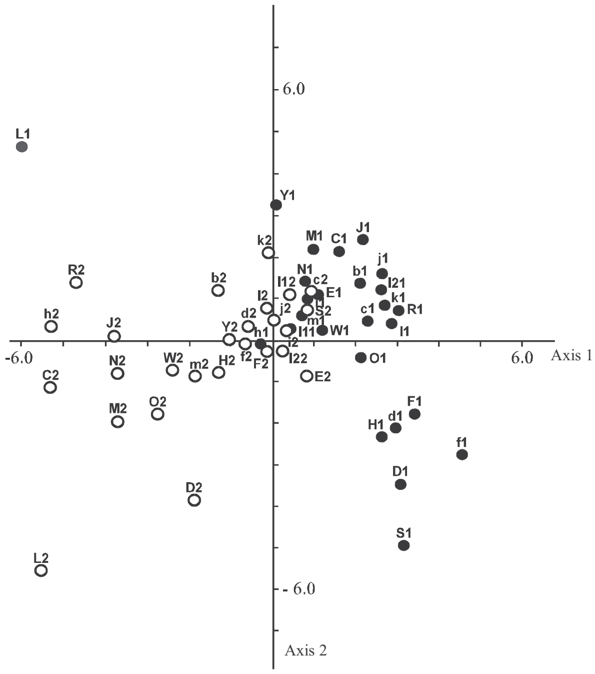

Fig. 4. Results of PCA made on the basis of bryophyte vegetation samples of the branches in 1991–1992 and 2001. (Black dots marked by 1 = samples of 1991–1992; white dots marked by 2 = samples of 2001; capital letters = branches of Cikolaszigeti branch-system; lower-case letters = branches of Ásványráró branch-system)

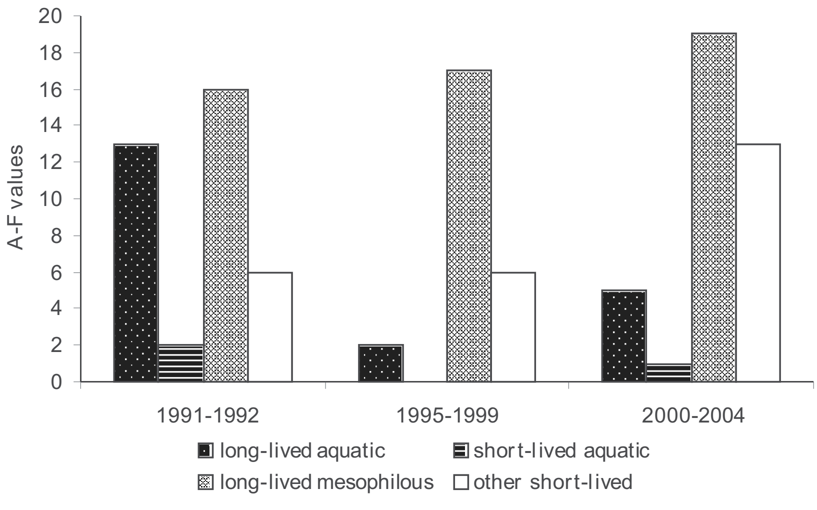

Fig. 5. Changes of total abundance-frequency values of four species groups in 1991–1992, between 1995–1999 and 2000–2004 in N branch of the Cikolasziget branch-system

Table 4

Significance of the changes of abundance-frequency values of different species groups summarised for the two branch-systems in 1991–1992 and 2001 using Wilcoxon paired-sample test at $p < 0.05$

	Cikolasziget branch-system				Ásványráró branch-system			
	Sum A-F		Diff. of sum A-F	Wilcoxon	Sum A-F		Diff. of sum A-F	Wilcoxon
	91–92	01		test	91–92	01		test
Long-lived aquatic	84	48	–36	s.	48	40	–8	n. s.
Long-lived mesophilous	158	225	67	s.	95	139	44	s.
Short-lived	121	177	56	s.	68	77	9	n. s.

rum was a characteristic species in 1991–1992, after the diversion it almost completely disappeared, with some individuals sporadically detected in a few years. A mesophilous *Amblystegium* species, *A. varium* seemed to be also sensitive. It was an important element in this branch in 1991–1992, but afterwards it

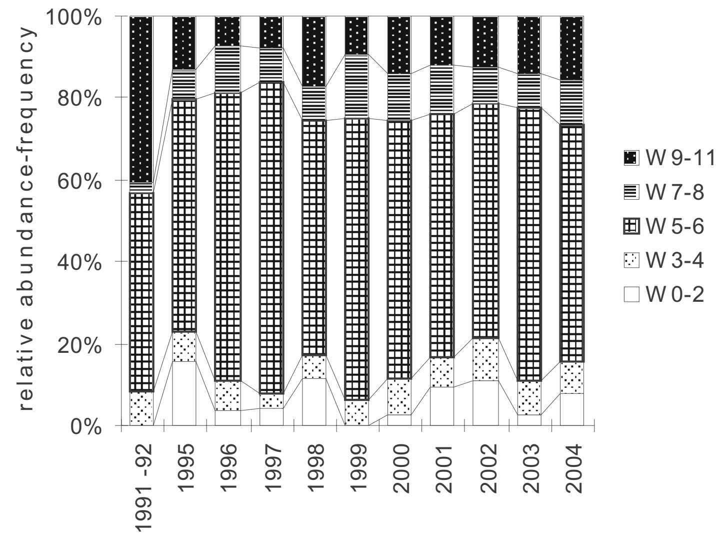

Fig. 6. Water requirement spectra weighted by the abundance-frequency of species in different years in N branch of the Cikolasziget branch-system. (Water requirement (W): 11–0: ordinal scaled range between the species adapted to aquatic and extreme dry conditions; wet = 9–11, moist = 7–8, mesophilous = 5–6, med. dry = 3–4, dry = 0–2)

almost entirely disappeared. In the same branch some mesophilous perennials, e. g. *Brachythecium rutabulum* and *Eurhynchium hians* were predominant before the diversion; they remained predominant during the whole period of investigation. Several mesophilous members of the Mniaceae family have appeared in the branch. *Mnium marginatum* and *Plagiomnium undulatum* became quite abundant after the diversion, but presently they show medium or low abundance-frequency. Others as *P. affine*, *P. cuspidatum*, *P. rostratum* appear occasionally: in some years they reach medium abundance-frequency, in other years they are absent. An aquatic *Plagiomnium*, *P. elatum* was an important element in the branch in 1991–92. After the diversion it disappeared and it was not recorded again during the investigated period. Several short-lived species have appeared, especially in the past few years, in the branch. Some of them are mesophilous species such as *Dicranella schreberiana*, *Leptobryum pyriforme*, *Physcomitrium pyriforme*, but some others are drought tolerant colonisers, like *Didymodon fallax*, *Barbula unguiculata*, *Bryum* species. The mesophilous *Pohlia melanodon* became also very abundant in recent years. The sensitive *Pohlia wahlenbergii* had medium abundance-frequency values in 1991–1992; by now it has vanished from the branch.

Habitat alteration is clearly shown by the transformation of aquatic-riparian bryophyte vegetation following the diversion. Figure 5 expresses the changes in the summarised abundance-frequency values of the various species groups in 1991–1992 and afterwards within 5–5-year periods. For each species the most frequent abundance-frequency value occurring during the 5–5-year periods was taken into consideration.

Decrease of the summarised abundance-frequency values of aquatic species was very sharp after the diversion, with some increase detected in subsequent years. Certain amount of increase of the summarised abundance-frequency of mesophilous species can also be recognised. Increase of the summarised abundance-frequency values of short-lived species is rather strong in the past years.

According to the water requirement spectra of N branch in different years investigated (Fig. 6), it is obvious that the proportion of aquatic species has decreased after the diversion and although there are better years (e. g. 1998, 2000, 2004), its proportion remained much lower than in 1991–1992. Species adapted to moist conditions (W = 7–8) became important elements of the vegetation. The ratio of mesophilous species has increased. Drought tolerant species (W = 0–2) appeared in the branch and their abundance-frequency fluctuates from year to year. They had high ratio in 1995, directly after the diversion, but in some years (1998, 2001, 2002) they show again expansion in the branch.

Table 5

List of the species, their life strategy types, water requirement values and abundance-frequency values in subsequent years of the monitoring in N branch of Cikolasziget branch-system. (life strategy types; P = perennial, LS = long-lived shuttle, SL = short-lived shuttle, C = colonist, AS = annual shuttle, F = fugitive; water requirement values (W): 11–0: ordinal scaled range between the species adapted to aquatic and extreme dry conditions; species are arranged according to their water requirement values and life strategies)

	Species	Species code	1991–92	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
LS10	*Plagiomnium elatum* (B. et S.) T. Kop.	PLAELA	3										
P10	*Amblystegium riparium* (Hedw.) B., S. et G.	AMBRIP	3	2	1	2	2	2	1	2	3	3	3
P10	*Cratoneuron filicinum* (Hedw.) Spruce	CRAFIL	1	1	1								
P9	*Amblystegium humile* (P. Beauv.) Crundwell	AMBHUM	4				1	1	2	2	2	1	2
P9	*Bryum pseudotriquetrum* (Hedw.) Gaertn., Meyer et Scherb.	BRYPSE	2	1			1				1		
P9	*Calliergonella cuspidata* (Hedw.) Loeske	CALCUS		1			1						
AS11	*Riccia fluitans* L. emend. Lorbeer	RICFLU							1				
SL9	*Pellia endiviifolia* (Dicks.) Dum.	PELEND	2				1		1	1	1	1	1
P7	*Brachythecium mildeanum* (Schimp.) Schimp. ex Milde	BRAMIL	1	1			1	1	2	2	1	1	1
P6	*Amblystegium varium* (Hedw.) Lindb.	AMBVAR	3	1					1				
P6	*Brachythecium rutabulum* (Hedw.) B., S. et G.	BRARUT	4	4	4	4	4	4	4	4	3	3	4
P5	*Brachythecium velutinum* (Hedw.) B., S. et G.	BRAVEL				1			1				
P5	*Eurhynchium hians* (Hedw.) Sande Lac.	EURHIA	4	4	4	4	4	4	4	4	4	4	4
P5	*Eurhynchium pumilum* (Wils.) Schimp.	EURPUM								1	2		
P5	*Leskea polycarpa* Hedw.	LESPOL		2								1	
P5	*Lophocolea bidentata* (L.) Dum.	LOPBID						1					
P4	*Amblystegium serpens* (Hedw.) B., S. et G.	AMBSER	3	2	2		2	2	3	3	2	2	2
LS5	*Mnium marginatum* (With.) Brid. ex P. Beauv.	MNIMAR		3	3	2	3	3	1	2	2	2	2
LS5	*Mnium stellare* Hedw.	MNISTE		1		1			1	1	1		
LS5	*Plagiomnium affine* (Bland.) T. Kop.	PLAAFF		1	2		1	2	1	2	2		

Table 5 (continued)

	Species	Species code	1991–92	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
LS5	*Plagiomnium cuspidatum* (Hedw.) T. Kop.	PLACUS			1		1		1	1	1		1
LS5	*Plagiomnium rostratum* (Schrad.) T. Kop.	PLAROS					1	2	1		2	1	1
LS5	*Plagiomnium undulatum* (Hedw.) T. Kop.	PLAUND	1	2	2	3	2	3	2	2	2	1	1
F3	*Funaria hygrometrica* Hedw.	FUNHYG				1					2	1	1
AS6	*Physcomitrium pyriforme* (Hedw.) Brid.	PHYPYR					1	1		2	2	1	1
AS5	*Aphanorhegma patens* (Hedw.) Lindb.	APHPAT							1			3	2
C8	*Marchantia polymorpha* L.	MARPOL									1	2	1
C7	*Lunularia cruciata* (L.) Lindb.	LUNCRU		2	2	2	2	2	2	2	2		2
C6	*Dicranella rufescens* (With.) Schimp.	DICRUF								1			1
C6	*Pohlia melanodon* (Brid.) J. Shaw	POHMEL	2		1	1	2	2	3	3	4	4	3
C6	*Pohlia wahlenbergii* (Web. et Mohr) Andr.	POHWAH	2										
C5	*Bryum bicolor* Dicks.	BRYBIC		1									
C5	*Bryum capillare* Hedw.	BRYCAP				1							1
C5	*Bryum flaccidum* Brid.	BRYFLA		1					1		1		
C5	*Dicranella schreberiana* (Hedw.) Hilp. ex Crum et Anders.	DICSCH								1	2	1	
C5	*Dicranella varia* (Hedw.) Schimp.	DICVAR					1					1	
C5	*Fissidens taxifolius* Hedw.	FISTAX	2	1	1	1				1	2	1	1
C5	*Leptobryum pyriforme* (Hedw.) Wils.	LEPPYR				1					1	1	
C4	*Bryum caespiticium* Hedw. var. *caespiticum*	BRYCAE		1									
C3	*Bryum argenteum* Hedw.	BRYARG									2		
C2	*Barbula unguiculata* Hedw.	BARUNG		2		1	1		1	2	3	1	2
C2	*Ceratodon purpureus* (Hedw.) Brid.	CERPUR		2									
C2	*Didymodon fallax* (Hedw.) Zander	DIDFAL		1			1			1	1		1
C	*Bryum* spp.	BRYSPP		1	1		2			1	2		
SL8	*Conocephalum conicum* (L.) Lindb.	CONCON								1	1		
SL6	*Pseudephemerum nitidum* (Hedw.) Reim	PSMNIT									1		

DISCUSSION

Today, the species composition of the aquatic-riparian bryophyte vegetation living in the banks of branches of the Szigetköz branch-system is different from that of 1991–1992. The abundance-frequency values of aquatic species have decreased, while the proportion of mesophilous long-lived species and short-lived bryophytes have increased. According to the water requirement spectra, species adapted to dry conditions have appeared and spread in the area. The changes of water requirement spectra of bryophyte vegetation and the growing importance of certain species groups indicate that the ecological conditions became drier.

To improve the water regime of the branch-system, from 1995 a water supply system has been operated. Thanks to this system, the branches have been refilled with water, but the water level is almost constant. The natural dynamics of water level fluctuation has changed, floods are extremely rare events, taking place only in some years. The constant water level is highly favourable for the colonisation of certain higher plants; e. g. the distribution of *Rubus caesius* and *Impatiens glandulifera* had expanded down to the water surface. Thus, the suitable habitat – the water fluctuation zone – for aquatic bryophytes has decreased greatly.

The reduced area of water level variations causes apparent decrease in aquatic bryophyte diversity and changes the species abundance patterns in regulated rivers (Englund *et al.* 1997). As a consequence of water regulation, several species characteristic of variable water levels have almost entirely disappeared from large European rivers (Philippi 1961, 1968). Natural disturbance caused by flood, and high flow are important factors in maintaining high species diversity by opening up space for less competitive species (Muotka and Virtanen 1995, Vitt *et al.* 1986). Stable conditions allow strong competitors to monopolise the suitable habitats. In our case mesophilous species (*Brachythecium rutabulum*, *Eurhynchium hians*) became very abundant. *Eurhynchium hians* spreads down to the water surface. At the same time, the formerly predominant aquatic *Amblystegium riparium* has lost from its earlier importance. The decrease of abundance-frequency of this species was sharp after the diversion. Later on, it regained some level of abundance-frequency. Another aquatic species, *Bryum pseudotriquetrum* is growing mainly in habitats that are submerged only for shorter period (Glime and Vitt 1987). This periodically submerged zone became very narrow due to the constant water level, and consequently, the abundance-frequency of this species has decreased considerably. In the past years the constant water level has underwashed the steep banks making open, muddy surfaces, which are shadowed by the overhanging canes of *Rubus*. Presently, these are favourite habitats for the mesophilous, colonist

Pohlia melanodon, which appears abundantly in such places along with *Eurhynchium hians*. The erosion of the bank has fastened due to the effects of underwashing, especially at those places where *Salix* trees were cut previously and *Populus* were planted directly on the bank. Willows can stabilise and protect the banks from erosion thanks to the dense network of their roots. The open and exposed muddy surfaces on the eroded banks, somewhat higher than the water surface, provide adequate habitat for a short time for colonist species adapted to drier conditions (e. g. *Dicranella schreberiana*, *Didymodon fallax*, *Bryum* spp.). Usually, after a year or so, these openings are occupied by invasive higher plants. Hence the turnover of colonist bryophyte species in the branches is high; they can establish stable populations only at a few sites, especially where tracks used by game lead to the water. But the accelerated bank erosion makes more and more open surfaces for mesophilous and drought tolerant colonists, which indeed have spread intensively during the past years.

In the 20th century Europe, the regulation of rivers and industrialisation of surrounding areas caused major changes in water regime and water quality of running waters, which manifested in the reduction of diversity of riparian habitats and hydrophytes. Along large floodplain rivers islands and secondary channels are important elements of the ecosystem maintaining habitat diversity and providing refugia for sensitive hydrophytes (Gurnell and Petts 2002, Vanderpoorten and Klein 1999). Hence more attention should be paid for the protection of the presently existing side arm systems. The Szigetköz branch-system is one of the largest remnants and a unique example of this riverine landscape in Europe.

The changes in the aquatic-riparian bryophyte vegetation of the branches at Szigetköz branch-system exhibit considerable changes in its overall environmental conditions. The results of the bryological monitoring suggest that the recent water supply is insufficient and unable to stop (and even more so to reverse) the environmental changes that took place in the branch-systems.

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