Determinants of floating island vegetation and succession in a recently flooded shallow lake, Kis-Balaton (Hungary)

Imelda Somodi [a,*], Zoltán Botta-Dukát [b]

[a] *Department of Plant Taxonomy and Ecology, Eötvös Loránd University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary*
[b] *Institute for Ecology and Botany, Hungarian Academy of Sciences, Alkotmány út 2-4, 2163 Vácrátót, Hungary*

Abstract

Floristic composition and vegetation succession were studied in relation to abiotic factors on secondarily developed young floating islands. These had formed after the reflooding of a drained wetland where mature floating fens had been present. We selected two floating fen Kis-Balaton Hungary complexes with similar physiognomy as references and performed stratified sampling with strata distinguished according to species dominance in all three sites. Species cover was estimated in 5 m × 5 m quadrats and the resulting data set was analysed with correspondence analysis. Interstitial (ground)water and soil parameters were measured and vegetation composition were recorded subsequently on the site in Kis-Balaton. Results were evaluated with canonical correspondence analysis including forward selection to test for significant abiotic variables: plots formed three main groups in the ordination space. One group contained ruderal vegetation, while the other ones were characterised by sedges and willows respectively. According to the forward selection, available nitrogen content of the soil was responsible for the segregation of the ruderal group from willow scrubs.
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1. Introduction

Floating islands are widespread vegetation formations (e.g. Pallis, 1916; Junk, 1970; Van Diggelen et al., 1996; Clark and Reddy, 1998; Azza et al., 2000; Van Duzer, 2002) and many

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* Corresponding author.
E-mail addresses: somodiimelda@freemail.hu (I. Somodi), bdz@botanika.hu (Z. Botta-Dukát).

of the well-known fens and bogs of Northern Europe (Steffen, 1931; Eurola, 1962) have a floating character, in the sense that they are located on a column of water, even if they are very rarely mentioned as floating fens or bogs. According to Clark and Reddy (1998) there are three main natural ways in which floating wetlands develop. The first formation type is characterised by the delamination of unvegetated, floating organic substrates from the deeper sediment reaching the surface of water. Here germination of plants only occurs in a second phase, i.e. after emergence. This process is considered to be due to shallow-water conditions and subsequent rewetting during summer. The second type of formation occurs when the rhizomes of aquatic plants begin to colonise the water surface from a nucleus formed by floating aquatic vegetation that is either unattached or expanding from the shore line. This is well-known in Hungary and its neighbouring countries (Pallis, 1916; Balogh, 2000), and similar processes may have contributed to the formation of some of the bogs in Northern Europe as well (Steffen, 1931; Balogh, 2000). The third formation type occurs when units of rooted vegetation and substrate split simultaneously from the bed, usually as a result of flooding as well.

In Hungary only the second of these types had been witnessed hitherto and considered to be an important way of floating fen formation (Balogh, 2000). The origin of the young floating islands studied here may be in fact characterised by a mixture of the first and the third formation type. These islands were formed following the artificial flooding of a former fen complex, resulting in the delamination of dead organic substrate possibly containing viable rhizomes.

The aim of our survey was to characterise the vegetation on these newly established floating islands and to determine the main abiotic factors which are responsible for its distribution:

- First, in order to compare vegetation of the young floating islands with that of the older, longer-established floating fens we analysed floristic composition at the three sites.
- Second, since our goal also was to reveal the factors that determine what vegetation appears on the individual young islands, we analysed interstitial water and soil samples. In selecting environmental parameters we relied on our results obtained in the course of the comparison of the three sites and also included some parameters that are generally considered to be important in mire succession (Mitsch and Gosselink, 1993).

2. Study area

The shallow lake Kis-Balaton (47°30′N, 17°10′E) is situated on the south-western edge of Lake Balaton in Hungary. Originally, the depression of Kis-Balaton was part of Lake Balaton. The depression has been drained partially, and later disconnected from the lake, leaving only a narrow channel for the Zala River to pass from Kis-Balaton into Lake Balaton. In the 1970s construction work began on the "Kis-Balaton Reservoir System" (KBRS) in the Kis-Balaton depression, with the aim of producing a natural filter of macrophytes for the water reaching Lake Balaton (Somlyódy, 1998). Two adjoining areas of the depression were flooded to create reservoirs, the first with a surface area of 18 km^2 in 1985, and the second with a surface of 16 km^2 in 1992 (Tátrai et al., 2000). The original vegetation of the

second reservoir consisted mainly of reed beds (Kárpáti et al., 1983) and floating vegetation was also present (Balogh, pers. commun.), while at the time of the rewetting only reed beds occurred. As a consequence of the flooding, the reed-beds were damaged in a certain part (Ingó) of the second reservoir, which had been subject to strong flooding. The KBRS receives its water from the river Zala. The water is directed into the first reservoir, which is shallow and is covered with blue-green algae in the summer. The water then flows from the first reservoir into the second one, first entering the Ingó area. The main cause of reed decay in Ingó is presumably the increase of water depth and the inflow of algal-rich water (Somlyódy, 1998).

Following the damage to the reed-beds at Ingó, the dead reed rhizomes that were covered with water filled with gas, which made them buoyant, and so some fragments of the reed-bed rose to the surface of the water as a floating mat which also contained mud and in a few cases mature willows (*Salix cinerea*). These mats formed a matrix for secondary succession.

Our study site, which had an area of about 1 km^2, was located in the centre of the area with damaged reed-beds in Ingó and thus within the second reservoir of the KBRS. The buoyancy status of floating islands is dynamic. They may be in physical contact with the sediment in extremely shallow water conditions, as some of our objects were in the summer of 2001, but the vertical position is influenced by the season, water level, and physical buoyancy components (e.g. gas content, rhizome content, below-water shoots; not studied here, see also Clark and Reddy, 1998; Sasser et al., 1996). Consequently, we included all sites where secondary succession had commenced on a floating mud surface (with or without willows) to be objects of our study, and accordingly will refer to them as floating islands, even if they were not floating at the time of sampling. These floating islands are partly attached to the still-living fragments of reed beds rooted in the sediment, and have an approximate diameter of about 15 m. The approximate rhizome mat thickness of the floating islands was 0.5 m in 2001.

For the evaluation of the floating vegetation situated in Ingó, we selected two older floating fen complexes (cf. Clymo, 1983; or floating marsh-fen complexes *sensu* Polunin and Walters, 1985) as reference sites: fens of Lake Velencei and an oxbow system of the Danube. At each site we included several floating islands in our survey. Before the start of water management operations, Ingó is considered to have been similar (Balogh, pers. commun.) to these. An important feature of the three sites is that unlike other fens in Hungary, they are all located on a considerably large and continuous body of water. The two older fens also share their origin, i.e. their succession departed from the shoreline (Balogh, 2000). The water supply is continuous at both reference sites and water level is maintained artificially.

Lake Velencei (47°10′N, 18°32′E) is a large (26 km^2) shallow lake with an average depth of 1.1 m. Two-third of its surface is covered by reed beds, partly of floating character. The eastern basin of the lake is alkaline (the water is grey or green), while the western basin is slightly acidic (dark brown water; Lakatos et al., 1991) and covered by floating fens. The centres of the floating units are covered by reed beds or willow scrub, while the edges possess special edge vegetation consisting of reed-bed species with higher light demand.

The second reference floating fen complex is located in several adjoining oxbows of the smaller branch of the Danube south of Budapest (48°45′N, 19°E). Some samples of reedy vegetation were also taken from a not directly adjoining oxbow with similar conditions, north of the former, because the reed beds had been damaged or drained in the first oxbow complex.

Both sites have a direct contact with the smaller branch of the Danube and agricultural pressure is considerable. The physiognomy of the vegetation of these sites is similar to that of Lake Velencei, but possibly due to water pollution, edge vegetation has become sparse and the mat thickness of the islands is only about 30 cm.

3. Methods

To support the comparison of the three sites, percentage cover of species was estimated in 31 plots of 5 m × 5 m at Ingó, 41 plots at Lake Velencei, and 29 plots at the Danube oxbows in early August of 2000. Our sampling was non random on purpose in the sense that we stratified our effort over the variation in dominant vegetation groups present at the floating fens, to cover most potentially available gradients (as in Podani, 1994; Sheldon et al., 2002). Several facies of dominant species or species groups were present in the area and we used five strata presented in Table 1 that were based on these species dominance patterns. Plots were selected so as to represent these strata. Differences of species number of the strata were evaluated with Kruskal–Wallis test and Dunn's posthoc test (Sokal and Rohlf, 1981).

Both binary and abundance data were analysed using correspondence analysis (CA; Podani, 1994) without detrending (c.f. Wartenberg et al., 1987) to ordinate samples in terms of their species composition. The SYN-TAX program package was used (Podani, 2000). Our detailed vegetation data are available upon request from the Hungarian phytosociological database: CoenoDAT (contact person: Ferenc Horváth, Institute for Ecology and Botany of the Hungarian Academy of Sciences, Vácrátót, e-mail: horvfe@botanika.hu).

In late July of 2001 samples were taken of the vegetation, soil, and interstitial water at 18 plots on several floating islands at Ingó. Samples were taken with regards to the strata used in 2000, with open mud surfaces added to estimate conditions in the very first step of secondary succession. The location of these plots was completely independent of those examined in 2000. At each plot percentage cover was estimated in a 2 m × 2 m quadrat. We collected 1–2 kg samples of the whole depth of the soil in each plot using an Eikelkamp soil sampler, and about 1 dl interstitial (ground) water that had seeped into the holes made during the soil sampling. Conductivity and pH of the interstitial water was measured, in addition to the amount of water, phosphorus, sulphur, and available nitrogen in the soil. To measure the total amount of phosphorus and sulphur, microwave digestion was performed, with a digestion mixture of 65% nitric acid and 30% hydrogen-peroxide. The amount of these two elements was then determined using an inductively coupled plasma emission spectrometer (ICP-AES; Spiers et al., 1983). For available nitrogen, 20 g of the formerly dried soil samples were extracted in 1 mol/l potassium-chloride at a soil:solution ratio of 1:5 in the course of a 1 h shaking treatment. Available nitrogen content was measured by steam distillation after the reduction of samples with Dewarda alloy (Moore and Chapman, 1986). Relationships among strata and each environmental parameter were investigated with one-way ANOVAs (Sokal and Rohlf, 1981).

Plant–soil relationships were evaluated with canonical correspondence analysis (CCA; Ter Braak, 1986). Significance tests of these relationships were also done using the Monte-Carlo method (Cade and Richards, 1996; Ter Braak and Šmilauer, 1998) in two ways:

Table 1
Sampling strata used in vegetation sampling

No. of stratum	Name	Dominant species	Discriminating species	Average number of species per quadrats	Standard error	No. of plots
1	*Sphagnum*–willow scrub	*Sphagnum fimbriatum, Salix cinerea*	*Sphagnum fallax, Sphagnum squarrosum, Thelypteris palustris*	14.9	1.0	7
2	Willow scrubs and lesser reedmace beds	*S. cinerea* and/or *Typha angustifolia* and *Theylpteris palustris*	No *Sphagnum* species present	7.1	0.6	29
3	Reeds	*Phragmites australis*	*Solanum dulcamara, Eupatorium cannabinum*	6.5	0.8	36
4	Large *Carex* beds	*Carex pseudocyperus, Carex elata, Carex riparia*	Ruderal species (*Bidens cernuus* and *Rumex maritimus*) also present	9	0.5	10
5	Ruderal vegetation	*B. cernuus, R. maritimus, Cyperus fuscus*	*Chenopodium ficifolium* and *Epilobium hirsutum, Veronica anagallis-aquatica*	6.5	2.2	19

Average number of species per quadrats was calculated from the data collected in 2000.

in the first case all environmental variables were involved the test, while in the second case forward selection (Montgomery and Peck, 1982) was used to select the significant environmental variables. In forward selection variables are added to the model in order to achieve maximum extra fit. Significance levels were obtained using the unrestricted permutation test. The SYN-TAX (Podani, 2000) and CANOCO (Ter Braak and Šmilauer, 1998) packages were used. We followed the International Code of Botanical Nomenclature in our plant names.

4. Results

4.1. Comparisons based on species composition and abundance

The Kruskal–Wallis test showed significant differences in the mean species numbers among our sampling strata. This, however was solely due to the high species number of the *Sphagnum*–willow scrub vegetation, whilst according to Dunn's posthoc test, there were no significant differences among the other strata. Analysis of the abundance data resulted in the sampling strata appearing in distinct, only slight overlapping ranges along a continuum and so in the separation of plots dominated by different species (the first two axes explained the 8% and 7% of the variance, Fig. 1a). On the two-dimensional projection of the ordination space a horseshoe pattern is discernable, which has been interpreted (Podani, 1994) as indicating the presence of a background gradient. Correspondence analysis of presence/absence led to similar results with a more pronounced separation of samples from different sites (figure not shown).
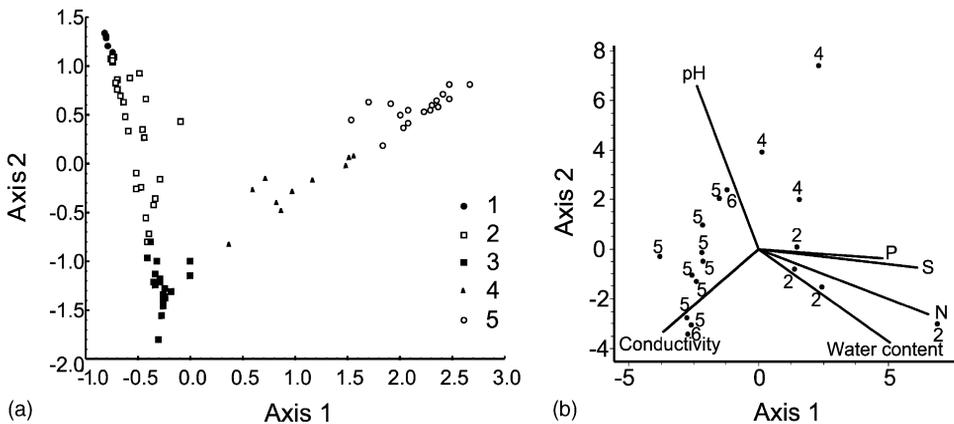

Fig. 1. Results of multivariate analyses. (a) Result of the correspondence analysis of abundance data: plots corresponding to sampling strata occupied a characteristic range along the gradient discernable in the ordination space. The shown first two dimensions explained 15% (8% and 7%) of the variance in the data set. Numbers refer to sampling strata (see also Table 1). (b) Segregation of vegetation types of Ingó according to soil and interstitial water parameters by canonical correspondence analysis. Numbers refer to vegetation strata except for number 6, which refers to samples from open mud surfaces; N: available nitrogen, P: phosphorus, S: sulphur. The first two dimensions explained 59% of the explainable inertia (35% and 24%).

Table 2
Sediment and interstitial water characteristics of strata used in vegetation sampling

Name	Interstitial water		Soil core			
	pH	Conductivity (μS cm^{-1})	Water content (%)	Available nitrogen (mg kg^{-1})	Total phosphorus (g kg^{-1})	Total sulphur (g kg^{-1})
Willow scrubs and lesser *T. angustifolia*	6.83 ± 0.06	1140 ± 66	84.0 ± 1.2	63 ± 13	1.7 ± 0.1	9.9 ± 0.4
Large *Carex* beds	7.15 ± 0.11	903 ± 138	79.8 ± 2.0	46 ± 18	1.7 ± 0.2	10.4 ± 1.3
Ruderal vegetation	6.94 ± 0.07	1317 ± 107	80.4 ± 1.4	36 ± 3	1.4 ± 0.1	9.1 ± 0.2
Open mud surface	6.97 ± 0.15	991 ± 33	77.9 ± 3.6	53 ± 13	1.6 ± 0.3	10.0 ± 2.0

Data originate form Kis-Balaton only and from the year 2001. *Note*: one-way ANOVAs among strata were not significant.

4.2. Environmental parameters

The means and standard error of our measurement of environmental parameters in the sampling strata are shown in Table 2. One-way ANOVAs among the strata based on environmental parameters were not significant.

According to the simultaneous analysis of soil and vegetation samples from Ingó by canonical correspondence analysis, samples formed three main groups (Fig. 1b). The first group contained samples from willow scrubs (stratum 2), which correlated positively with the amount of nutrients, sulphur, and water in the soil; and negatively with pH. The second group contained floating large *Carex* beds (str. 4), which, in contrast with the former, correlated positively with pH. The third group included samples of ruderal vegetation (str. 5) and open mud surfaces. These samples correlated positively with conductivity, but negatively with the amount of nutrients, sulphur, and water. Because of the restricted number of samples (which reduced the possibility of detecting significant relationships), the first two axes of the canonical correspondence analysis of the whole data set did not prove to be significant, but they explained 14% and 9% of the total variation and 35% and 24% of the variance of species-environment relations (explainable inertia), so we consider these results informative. Sulphur, phosphorus, available nitrogen and relative water content were significantly ($P < 0.05$) correlated to axis 1, while pH was significantly correlated to axis 2 (Table 3). According to the forward selection, available nitrogen content of the soil was responsible (on a significance level of $P = 0.0539$) for the following results: the most nitrogen-poor communities were those belonging to ruderal vegetation (str. 5); floating *Carex* beds (str. 4) had

Table 3
Correlation coefficients between environmental variables and canonical correspondence axes (see Fig. 1)

	pH	Conductivity	Available nitrogen (N)	Total phosphorus (P)	Total sulphur (S)	Relative water content
Axis 1	-0.10	-0.28	0.59^*	0.62^*	0.41^*	0.59^*
Axis 2	0.70^*	-0.28	-0.26	0.09	0.2	-0.06

* $P < 0.05$.

transitional characters; whilst willow scrubs (str. 2) proved to be relatively nitrogen-rich. This variable explained 10% of the total variance and a considerable part, 26% of the explainable inertia.

5. Discussion

Although there were no distinct differences in the species number of the different sampling strata they spread along a continuum in the ordination space with only slight overlaps when abundance patterns were taken into account. Samples from willow scrubs and reeds in Ingó appeared in the same range as plots from older sites belonging to the same stratum, showing that these represent similar successional stages on both sites, in contrast to the floating large *Carex* beds and ruderal vegetation, which were absent from the older sites. The horseshoe pattern in the ordination space implied a background gradient that may be associated with some kind of soil nutrient status. Canonical correspondence analysis of vegetation together with environmental data from Ingó confirmed that compositional differences of plots correlate with differences in sediment geochemistry, although geochemistry only did not differentiate significantly among strata. According to the CCA with forward selection available nitrogen amount in the soil was a major factor determining vegetation dominance at a certain location. Since this parameter strongly correlated with sulphur and phosphorus content as well, general nutrient availability appeared to be important.

Correlation between vegetation and environmental parameters gave implications on succession routes in Ingó as well. Presence of ruderal vegetation correlated with high conductivity values. These high values are probably due to the subsequent oxidization of the peat during the drainage period and thus suggest the early successional status of this pioneer vegetation. The other two groups of samples point to two possible pathways of vegetation development from this initial stage. As floating large *Carex* beds were correlated with higher pH conditions and where insensitive to nutrient availability these may represent a possible route towards neutral fens. At the same time plots with willow scrubs had lower pH and higher nutrient availability. Although both lower pH and the species composition of this vegetation suggest conditions that may develop towards *Sphagnum*–willow scrubs, the increased nutrient availability appears to contradict this view.

Availability of nutrients in the soil was found to be an important determining factor in several other wetlands as well (Walker and Wehrhahn, 1971; Hemond, 1983; Day et al., 1988; Van Diggelen et al., 1996). In primary successions available nutrient amount in the soil is known to increase with maturation (Crawley, 1997), although the opposite has been proposed and accepted generally to occur during mire succession (Van Diggelen et al., 1996). Nevertheless, there is evidence that nitrogen availability may increase during the early steps (Wind-Mulder et al., 1996), and even in general (Waugham and Bellamy, 1980; Van Breemen, 1995) during mire succession. Furthermore, contradiction between our and traditional findings may also be due to the fact that traditionally surface water has been analysed (Vitt and Bayley, 1984; Vitt and Chee, 1990). Consequently, nitrogen accumulation is not necessarily a contradiction in mire succession, when a supply of nitrogen is available; in our case the source of nitrogen was the eutrophic water originating from the first reservoir

of Kis-Balaton. As a result, higher available nitrogen amounts associated with willow scrub may not preclude further succession towards *Sphagnum*–willow scrubs.

In conclusion, we underline that vegetation composition on the young floating islands separated out well according to sediment and soil conditions, and these also imply successional trends. These trends show that secondary floating islands may develop into very similar vegetation stands as those formed primarily, departing from the shoreline.

Acknowledgements

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