

Floodplain forest communities along the Mura River (NE Slovenia)

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Abstract – Ecological gradients along river banks of the Mura River influence forest species composition. On the basis of 58 relevés of floodplain forests along the Mura River, the classification of vegetation plots was performed with the Pc-Ord program. The diagnostic species combination for three clusters revealed after classification was calculated by fidelity measure (phi-coefficient) and presented in an analytic table. Average Ellenberg indicator values, stream distances and relative elevations of the relevés were passively projected onto PCA to show ecological relationships among them. Correlations of plant functional type and stream distance gradients were calculated with regression analysis. For the main edifiers response curves to the stream distance gradients were made. The classification of the Mura floodplain forests has revealed three ecologically interpretable vegetation types: *Salicetum albae* (most humid and nutrient-rich sites), *Fraxino-Ulmetum allietosum ursini* (ecologically intermediate sites), *F.-U. quercetosum robori* (the driest and the least nutrient-rich sites). Zonation of vegetation is connected to distance from the closest stream which influences species distribution through ecological gradients of moisture and nutrient. The proportion of therophytes is significantly negatively correlated with the distance from the closest stream and the proportion of neophytes is significantly negatively correlated with distance from the main stream.

Key words: Floodplain, gradient, hardwood, neophytes, riparian, vegetation, softwood, zonation, Mura River

Abbreviations: DCS – distance from the closest stream, DMS – distance from the main stream.

Introduction

Floodplain forests are subject to periodic over/the-bank flooding and cycles of erosion and deposition of nutrient-rich sediment. Well drained and nutrient-rich soils of floodplain

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forests distinguish these forests from the floodplain swamp forests on stagnant water sites with gleyic soils, which are periodically flooded predominately by ground water. Floodplain forests are characterized by the highest species richness and diversity, density and productivity (DEILLER et al. 2001, MITSCH and GOSSELINK 2000, SCHNITZLER 1994). They include several microhabitats harbouring numerous plant and invertebrate species unable to survive elsewhere (MACHAR 2001). Therefore floodplain forests, according to the Habitat Directive, belong among the habitats of the greatest importance for nature protection on the European scale.

Historically, natural floodplain forests have been fragmented and heavily impacted by watercourse regulations, timber harvesting and other human activities (KLIMO and HAGER 2001).

Like other large European rivers, the Mura has undergone several hydraulic management phases since the 19th century. These regulation works and other human impacts, such as plantation and felling, have modified the floodplain forest ecosystem. Therefore identification of vegetation types along the Mura River is very difficult, undistinct and has not been done yet. Despite many an intervention into the river and its current, the Mura has still preserved so many natural treasures that it is treated as a nationally important value (GORŠAK and BAKAN 2003).

Flooded forests have already been thoroughly studied in many parts of Europe (MÜLLER 1992, SCHNITZLER 1994, VICHEREK et al. 2000, PAAL et al. 2007, WILLNER and GRABHERR 2007, KEVEY 2008, KLIMO et al. 2008, POLDINI et al. 2011) and also in the southeastern part of Europe in the area of large rivers, such as the Sava, Drava and Danube (HORVAT et al. 1974, VUKELIĆ and BARIČEVIĆ 2004, 2005).

Two types of forests have usually been identified in the area of floodplain forests: softwood and hardwood forests. Softwood forests are mainly composed of early successional and light-demanding species such as *Salix alba*, *Salix fragilis*, *Populus nigra* and *Populus alba*. Hardwood forests are dominated by long-living species, with *Fraxinus excelsior*/*Fraxinus angustifolia*, *Quercus robur* and *Ulmus minor*/*Ulmus laevis*. Alluvial hardwood forests are found on flooded but well-drained and fertile soils of large European floodplain (SCHNITZLER 1994)

In Slovenia there were some surveys of vegetation of river banks, about all white willow stands *Salicetum albae*, along some other rivers, such as the Drava (PETRINEC 1999), Soča (DAKSKOBLER et al. 2004), Krka and Mirna (ŠILC 2003), mostly with a relatively narrow belt of riverine forest vegetation. The Mura River has the best preserved floodplain in Slovenia, but floodplain forests of river banks of the Mura River remain so far unresearched.

The main research questions of the study were:

- Which are the main forest vegetation types on the banks of the Mura River and the main ecological gradients that influence species composition of these forests?
- Despite the big changes in flooding regime and human impact (plantation, cutting down) does zonation of vegetation along the Mura River still exist? Is zonation connected to distance from the main stream of the river (DMS) or distance from the closest stream (DCS)?
- What is the distribution of plant functional types (life forms, plant ecological strategies, origin and residence time status) along stream distance gradient?

Material and methods

Study area

The study took place along the Mura River in the eastern part of Slovenia, on the banks of the Mura River and Holocene terraces. This part of Slovenia has a continental climate: the annual mean precipitation is 800 mm and annual mean temperature is 9.2 °C.

The study area belongs to the sub-Pannonian region, as we can find some Pannonian features; flooded and swamp forests, some very rare Pannonian elements. Since the area is composed mainly of sandstone, the flora shows a mainly central European floristic character.

The Mura (Mur) river is a Central European river, springing at 1898 m a.s.l. in the Eastern Alps in Austria. The Mura River is the largest tributary of the Drava river, that is the fourth largest tributary of the Danube River. When reaching Slovenia, the Mura river forms a 34-km long state border line between Austria and Slovenia, flows through Slovenian territory for 29 km and then becomes a state border again: first between Slovenia and Croatia (33 km), and then between Croatia and Hungary (GLOBEVNIK and MIKOŠ 2009). In Slovenia it has riverbed in lowland with a small gradient. The level of the Mura River increases in spring because of the melting snow in the high mountains and in autumn because of higher precipitation.

Regulation works on the Mura River started in 19th century. Before regulation, 40% of water flowed through main channel, but today almost all the water flows in the main channel. There are still some side channels in the forests along the Mura River with connection to the main stream of the Mura. Flood protection dikes were constructed in the 1972–1990 period using a 100 year flood design to protect cultivated areas. The Mura River corridor between the dikes is up to 1 km wide (GLOBEVNIK and MIKOŠ 2009). Most of the forests range inside these dikes.

Sampling and measurements

Vegetation of floodplain forests was investigated according to the standard Central European method (BRAUN-BLANQUET 1964). We made 58 relevés of floodplain forests along the Mura River. All the relevés were made inside levees in the area of periodic floods. We did not include floodplain swamp forests (class *Alnetea glutinosae*) in our research as they have already been investigated (ACCETTO 1994, NEMESSZEGHY 1986, GLAVAC 1975). For each plot, GPS coordinates were collected and later on, distances from main stream of Mura (DMS) and distances from the closest stream (DCS), which may be the main or a side stream, were measured from the map in Arc-Gis program. In 14% of relevés (8 of 58) DCS value equalled DMS value. This means that in 86% of the relevés the closest stream was a side stream. We also measured the relative elevation of each plot (elevation relative to average river level) with DMR of the area as it is known that elevation as well as distance from the river affects hydroperiod (flood frequency and duration) and thus influences species distribution and abundance (TURNER et al. 2004).

Data analysis

58 relevés made on flooded sites of the Mura River were entered into the TURBOVEG (HENNEKENS and SCHAMINÉE 2001) database.

The numerical classification of vegetation plots, based on their species composition, was performed with PC-ORD 5.0 program (McCUNE and MEFFORD 2005). The data was square root transformed. Euclidean (Pythagorean) distance as the distance measure and Flexible Beta method for group linkage were used. We made several classifications with different numbers of clusters of relevés. We subjectively accepted classification with three clusters being most ecologically sound.

58 relevés are presented in the analytic table. The nomenclature of taxa is according to Flora Europaea (TUTIN et al. 1964–1980). Diagnostic species for the clusters (corresponding associations and subassociations) were determined in the JUICE program (TICHÝ 2002) by their fidelity values. Fidelity was calculated using the phi coefficient, applied to the classified data set with cluster sizes equalized to 1/3 or 1/2 respectively (in the case of searching for species diagnostic for two clusters together) of the size of the entire data set, of the total data set size according to TICHÝ and CHYTRÝ (2006). Species with $\phi > 30$ were considered as diagnostic for individual clusters, but species whose occurrence concentration in the plots of a particular cluster was not significant at $p < 0.05$ (Fisher's exact test) were excluded.

Unweighted average Ellenberg indicator values of relevés made on flooded sites, distances of the relevés from the streams (DMS, DCS) and relative elevation were passively projected onto a Principal Components Analysis biplot (PCA from CANOCO 4.5; TER BRAAK and ŠMILAUER 2002) to show ecological relationship among these relevés and to explain environmental gradients underlying the main ordination axes. Square root transformed cover data were used as the input data.

For further interpretation of the three clusters of flooded forests of the Mura River, unweighted average Ellenberg indicator values of 3 clusters of flooded forests, moisture and nutrient, which indicate the biggest correlations with axis 1 of the PC-ORD diagram, calculated in the JUICE program, and stream distances (DMS, DCS) were presented with Box-whiskers diagrams made in STATISTICA program (STATSOFT 2007). Boxes present mean and standard errors (SE), whiskers indicate standard deviations (SD).

Correlations of plant ecological strategies, life forms and origin and residence time status (native, archaephyte, neophyte) and stream distance gradient were calculated with regression analysis, also in STATISTICA program. Each of the patterns was fitted with a linear regression model. The plant ecological strategies, life forms and plant status have been defined using the BIOLFLOR database (KLOTZ et al. 2002), that considers Grime's classification (GRIME 1979).

For the five most important tree species of the forests in the area, responses to the environmental variables (DCS, DMS) were fitted using the Huisman-Olff-Fresco models (HOF; HUISMAN et al. 1993). HOF is a hierarchical set of five species response models with increasing complexity: model I-flat with no response, II-monotonously increasing or decreasing, III-monotonously increasing or decreasing with a »plateau«, IV-symmetric unimodal and V-asymmetric unimodal response. Four parameters of these models were estimated using a non-linear maximum likelihood estimation procedure (OKSANEN and MINCHIN 2002), available in Jari Oksanen's »gravy« library (<http://cc.oulu.fi/%7Ejraioksa/softhelp/softalist.html>) for the R program (<http://www.r-project.org>). This routine was run externally with R program (<http://www.r-project.org>) from the JUICE program (TICHÝ 2002), using a procedure developed by ZELENÝ and TICHÝ (2007)

Results

The classification of the flooded forests of the Mura River is presented in the dendrogram (Fig. 1), and in the analytic table (Tab. 1). Classification into three clusters was accepted as it represents three ecologically interpretable vegetation types; 1. *Salix alba* and *Populus nigra* stands, 2. *Fraxinus angustifolia* subsp. *oxycarpa* stands and 3. *Quercus robur* and *Carpinus betulus* stands. The three clusters correspond to three communities; *Salicetum albae* Issler 1926, *Fraxino-Ulmetum effusae* Slavnić 1952 *allietosum ursini* subass. nova hoc loco, *Fraxino-Ulmetum effusae* Slavnić 1952 *quercetosum robori* subass. nova hoc loco.

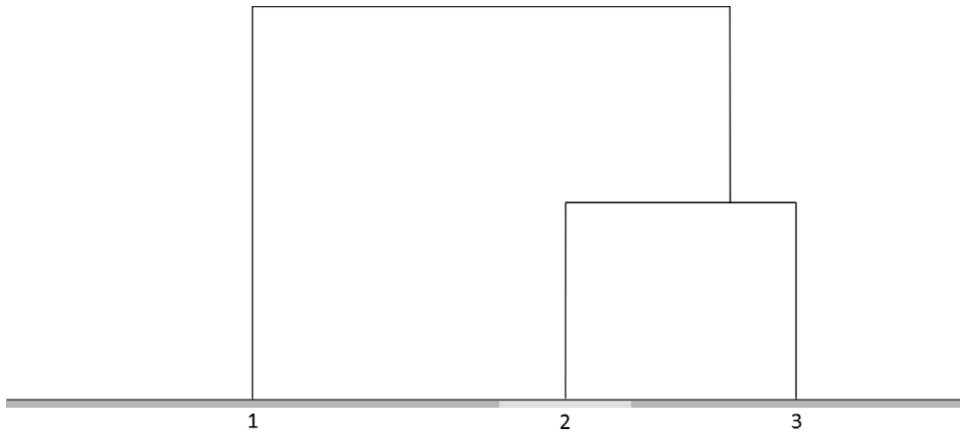


Fig. 1. Dendrogram of classification. Cluster 1: *Salix alba* and *Populus nigra* stands, cluster 2: *Fraxinus angustifolia* subsp. *oxycarpa* stands and cluster 3: *Quercus robur* and *Carpinus betulus* stands. For simplicity, the bottom part is not shown.

PCA is presented of the 58 relevés of flooded sites of the Mura River with Ellenberg indicator values (Fig. 2). Eigenvalues of the first two axes are 0.161 and 0.114. The three communities (three clusters) thrive along a moisture and nutrient gradient. Moisture and nutrient indicator values are negatively correlated with DCS (with moisture -0.308 , with nutrients -0.341) and DMS (with moisture -0.224 , with nutrients -0.209). The association *Salicetum albae* (cluster one) occurs on the most moist and nutrient-rich sites, the subassociation *Fraxino-Ulmetum effusae quercetosum robori* (cluster three), on the other hand, occurs on the least moist and the least nutrient-rich sites (Fig 2, Fig. 3).

DCS is the lowest in cluster one (*Salicetum albae*) and the highest in cluster three (*Fraxino-Ulmetum effusae quercetosum robori*). DMS is also the highest in cluster three and lower in clusters one and two (*Fraxino-Ulmetum effusae allietosum ursini*). Cluster three shows the highest range of DMS indicating that the main stream of the Mura has the lowest effect on the distribution of *Quercus robur* stands, which can be also found relatively far (up to 3080 m far) from the main stream of Mura.

The proportion of neophytes is strongly significantly negatively correlated with DMS (Fig. 5), and not significantly correlated with DCS. The most abundant neophytes in our relevés are *Robinia pseudacacia*, *Impatiens glandulifera*, *Solidago gigantea* and *Rudbeckia laciniata*.

Tab. 1. – continued

Number of relevé	1			2			3			
	1	2	3	1	2	3	1	2	3	
Cluster number										
F <i>Athyrium filix-femina</i>	h
SM <i>Aristolochia clematitis</i>	h
QF <i>Campanula persicifolia</i>	h
F <i>Corydalis solida</i>	h	+	+
SA <i>Salicetea purpureae</i>	tl
<i>Salix fragilis</i>	t2
<i>Salix fragilis</i>	s
AI <i>Alnion incanae</i>	h	1 + 2 + 3	1 . + 2	1 + 1 + 1 + 2	1 + 2	1 + 2	1 + 2	1 + 2	1 + 2	1 + 2
AI <i>Ranunculus ficaria</i>	h	1 + + +	2 + 1 + 2	1 + 2 +
AI <i>Arenemone ranunculoides</i>	h	+	+	+	+	+	+	+	+	+
AI <i>Stachys sylvatica</i>	t2	3	1 . +	1
AI <i>Prunus padus</i>	s	2 + . + 3	1 + 2 .	1 . 1 +
AI <i>Prunus padus</i>	h	+	+
AI <i>Circaea lutetiana</i>	h	+	+
AI <i>Omphalodes scorpioides</i>	h	+	+
AI <i>Carex remota</i>	h
AI <i>Acer negundo</i>	t2
AI <i>Acer negundo</i>	s
AI <i>Acer negundo</i>	h
AI <i>Chrysosplenium alternifolium</i>	h
AI <i>Populus alba</i>	tl
AI <i>Populus alba</i>	s
AI <i>Populus alba</i>	h
AI <i>Impatiens noli-tangere</i>	h
AI <i>Carex brizoides</i>	h
AI <i>Dryopteris carthusiana</i>	h
AI <i>Stellaria nemorum</i>	h

Tab. 1. – continued

	1	2	3	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Number of relevé																								
Cluster number																								
AI <i>Ulmus minor</i>	t2	+																						
AI <i>Ulmus minor</i>	s	+																						
AI <i>Ulmus minor</i>	h																							
F <i>Fagetalia sylvaticae</i>																								
<i>Sambucus nigra</i>	t2	1 2																						
<i>Sambucus nigra</i>	s	2 3 2 1 + 2 2 1	1																					
<i>Sambucus nigra</i>	h																							
<i>Adoxa moschatellina</i>	h	1 + +	1 + +																					
<i>Lamium strum galeobdolon</i> subsp. <i>montanum</i>	h	+ + 1	+ + + +																					
<i>Symphylum tuberosum</i>	h	+	+																					
<i>Ranunculus lanuginosus</i>	h																							
<i>Milium effusum</i>	h																							
<i>Oxalis acetosella</i>	h																							
QF <i>Quercus-Fagetia</i>																								
<i>Anemone nemorosa</i>	h																							
<i>Cerastium sylvaticum</i>	h																							
<i>Hedera helix</i>	h																							
<i>Corylus avellana</i>	t2																							
<i>Corylus avellana</i>	s																							
<i>Corylus avellana</i>	h																							
AG <i>Alnetea glutinosae</i>																								
<i>Humulus lupulus</i>	s																							
<i>Humulus lupulus</i>	h																							
<i>Caltha palustris</i>	h																							
<i>Carex vesicaria</i>	h																							
RP <i>Rhamno-Prunetea</i>																								
<i>Eonymus europaeus</i>	t2																							

Tab. 1. – continued

Number of relevé	Cluster number																																			
	1										2										3															
<i>Euonymus europaeus</i>	s	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Euonymus europaeus</i>	h	
<i>Cornus sanguinea</i>	t2	+	
<i>Cornus sanguinea</i>	s	.	1	
<i>Cornus sanguinea</i>	h	
<i>Viburnum opulus</i>	s	
<i>Viburnum opulus</i>	h	
<i>Crataegus laevigata</i>	t2	
<i>Crataegus laevigata</i>	s	
<i>Crataegus laevigata</i>	h	
GU <i>Galio-Urticetea</i>	h	3	3	2	4	3	1	1	4	3	2	2	2	+	1	2	3	4	3	1	3	3	2	3	3	3	1	1	2	+	2	3	1	1		
<i>Gallium aparine</i>	h	1
<i>Stellaria neglecta</i>	s
<i>Rubus caesius</i>	h	1
<i>Rubus caesius</i>	h	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Lamium maculatum</i>	h	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
<i>Galeopsis pubescens</i>	h	+
<i>Duchesnea indica</i>	h	+
<i>Myosotis sparsiflora</i>	h
<i>Anthriscus sylvestris</i>	h
<i>Calystegia sepium</i>	h
<i>Chelidonium majus</i>	h
<i>Echinocystis lobata</i>	h
<i>Chaerophyllum aureum</i>	h
PM <i>Phragmiti-Magnocaricetea</i>	h
<i>Iris pseudacorus</i>	h
<i>Carex acutiformis</i>	h
<i>Phragmites australis</i>	h
<i>Carex elata</i>	h

Tab. 1. – continued

5162377; tl 80%, t2 20%, s 50%, h 100%; **20**, 400 m²; 4. 5. 2005; 586046, 5162437; tl 80%, t2 10%, s 10%, h 100%; **21**, 400 m²; 25. 5. 2005; 586980, 5161401; tl 80%, t2 40%, s 20%, h 100%; **22**, 400 m²; 25. 5. 2005; 587259, 5161466; tl 70%, t2 50%, s 40%, h 100%; **23**, 400 m²; 5. 5. 2005; 582258, 5165222; tl 40%, t2 30%, s 5%, h 100%; **24**, 400 m²; 13. 5. 2005; 593539, 5156656; tl 75%, t2 20%, s 20%, h 100%; **25**, 400 m²; 14. 5. 2005; 589937, 5160369; tl 50%, t2 40%, s 40%, h 100%; **26**, 200 m²; 13. 5. 2005; 593711, 5158107; tl 50%, t2 40%, s 30%, h 100%; **27**, 400 m²; 17. 5. 2005; 594748, 5156679; tl 60%, t2 20%, s 40%, h 100%; **28**, 400 m²; 25. 5. 2005; 587483, 5161303; tl 60%, t2 50%, s 20%, h 100%; **29**, 400 m²; 25. 5. 2005; 587293, 5161424; tl 70%, t2 40%, s 20%, h 100%; **30**, 400 m²; 25. 5. 2005; 587442, 5161442; tl 60%, t2 40%, s 30%, h 100%; **31**, 400 m²; 5. 5. 2005; 582311, 5165133; tl 70%, t2 30%, s 20%, h 100%; **32**, 400 m²; 20. 5. 2005; 593571, 5157963; tl 75%, t2 20%, s 30%, h 100%; **33**, 400 m²; 20. 5. 2005; 581012, 5166218; tl 70%, t2 30%, s 20%, h 100%; **34**, 400 m²; 20. 5. 2005; 580950, 5166310; tl 80%, t2 50%, s 30%, h 100%; **35**, 200 m²; 13. 5. 2005; 593628, 5158082; tl 60%, t2 30%, s 40%, h 100%; **36**, 200 m²; 13. 5. 2005; 593451, 5157897; tl 80%, t2 40%, s 30%, h 100%; **37**, 300 m²; 6. 5. 2005; 588255, 5161921; tl 80%, t2 40%, s 20%, h 100%; **38**, 200 m²; 17. 5. 2005; 594752, 5156956; tl 75%, t2 35%, s 50%, h 100%; **39**, 200 m²; 19. 6. 2005; 602051, 5155522; tl 80%, t2 40%, s 40%, h 100%; **40**, 400 m²; 21. 4. 2005; 588212, 5162249; tl 80%, t2 50%, s 30%, h 100%; **41**, 400 m²; 4. 5. 2005; 586049, 5163087; tl 60%, t2 70%, s 30%, h 100%; **42**, 400 m²; 5. 5. 2005; 582250, 5165396; tl 80%, t2 20%, s 10%, h 100%; **43**, 400 m²; 5. 5. 2005; 582209, 5165005; tl 60%, t2 30%, s 30%, h 100%; **44**, 400 m²; 17. 5. 2005; 594701, 5157131; tl 80%, t2 20%, s 35%, h 100%; **45**, 400 m²; 20. 5. 2005; 580901, 5166063; tl 70%, t2 40%, s 30%, h 100%; **46**, 400 m²; 20. 5. 2005; 581073, 5166202; tl 60%, t2 60%, s 40%, h 90%; **47**, 400 m²; 6. 5. 2005; 585135, 5163546; tl 60%, t2 60%, s 20%, h 100%; **48**, 400 m²; 13. 5. 2005; 593401, 5156838; tl 70%, t2 30%, s 40%, h 100%; **49**, 400 m²; 17. 5. 2005; 596965, 5155629; tl 80%, t2 50%, s 40%, h 100%; **50**, 400 m²; 17. 5. 2005; 597330, 5155558; tl 90%, t2 40%, s 40%, h 90%; **51**, 400 m²; 20. 5. 2005; 580966, 5166382; tl 60%, t2 50%, s 40%, h 100%; **52**, 300 m²; 26. 5. 2005; 588641, 5161673; tl 70%, t2 50%, s 30%, h 90%; **53**, 400 m²; 26. 5. 2005; 588590, 5161629; tl 60%, t2 40%, s 20%, h 100%; **54**, 400 m²; 26. 5. 2005; 602533, 5154003; tl 75%, t2 50%, s 20%, h 100%; **55**, 400 m²; 26. 5. 2005; 602562, 5154001; tl 80%, t2 40%, s 30%, h 90%; **56**, 400 m²; 6. 5. 2005; 588247, 5161957; tl 90%, t2 60%, s 10%, h 100%; **57**, 400 m²; 6. 5. 2005; 584521, 5163341; tl 80%, t2 40%, s 70%, h 90%; **58**, 400 m²; 6. 5. 2005; 584494, 5162788; tl 80%, t2 40%, s 50%, h 90%.

Taxa occurring only once in the table 1

Crocus vernus, h, 44 (+), 46 (+), *Geranium robertianum*, h, 45 (+), 47 (+), *Cardamine amara*, h, 8 (+), *Cirsium erisithales*, h, 31 (+), *Ulmus glabra*, t2, 50 (+), *Lonicera caprifolium*, h, 45 (+), 50 (+), *Scrophularia nodosa*, h, 46 (r), 50 (+), *Clematis vitalba*, h, 45 (+), 57 (+), *Prunus avium*, t1, 45 (l), *Knaulia drymeia*, h, 45 (+), *Euphorbia dulcis*, h, 53 (r), *Acer platanoides*, t2, 54 (+), *Acer platanoides*, h, 54 (+), *Helleborus odoratus*, h, 45 (r), *Matanthenum bifolium*, h, 56 (+), *Veronica officinalis*, h, 44 (+), *Cardamine pratensis*, h, 16 (+), 18 (+), *Peucedanum palustre*, h, 40 (+), *Ranunculus repens*, h, 8 (+), *Glechoma hirsuta*, h, 4 (l), *Stachys palustris*, h, 17 (+), *Cirsium oleraceum*, h, 17 (+), 44 (+), *Valeriana dioica*, h, 18 (+), *Angelica sylvestris*, h, 17 (+), *Carex divulska*, h, 44 (+), 47 (+), *Cruciata glabra*, h, 40 (+), 45 (+), *Dipsacus* species, h, 32 (+), 36 (+), *Elymus repens*, h, 8 (+), 26 (+), *Lysimachia punctata*, h, 15 (l), 17 (+), *Piptatherum virescens*, h, 23 (+), 27 (+), *Polygonum mite*, h, 18 (4), 27 (+), *Rumex acetosa*, h, 40 (+), 56 (+), *Rumex crispus*, h, 5 (+), 10 (+), *Senecio nemorensis*, h, 27 (+), 44 (+), *Aesculus hippocastanum*, h, 35 (+), *Aesculus hippocastanum*, t2, 7 (l), *Alisma plantago-aquatica*, h, 15 (+), *Allium scorodoprasum*, h, 34 (+), *Alnus incana*, t2, 10 (+), *Alnus* species, t2, 12 (l), *Arctium lappa*, h, 27 (+), *Artemisia vulgaris*, h, 27 (+), *Bromus sterilis*, h, 27 (+), *Cardamine flexuosa*, h, 26 (+), *Carex muricata* agg., h, 44 (+), *Chenopodium* species, h, 21 (+), *Cruciata laevis*, h, 58 (+), *Dipsacus pilosus*, h, 29 (+), *Euonymus verrucosus*, h, 1 (+), *Fragaria vesca*, h, 45 (+), *Fraxinus pennsylvanica*, h, 49 (+), *Fraxinus pennsylvanica*, t1, 44 (+), *Gagea spathulata*, h, 55 (+), *Holcus lanatus*, h, 10 (+), *Impatiens parviflora*, h, 1 (+), *Juglans regia*, s, 5 (+), *Lapsana communis*, h, 54 (+), *Leeersia oryzoides*, h, 46 (+), *Lithospermum officinale*, h, 17 (+), *Lonicera caerulea*, h, 43 (r), *Mentha aquatica*, h, 15 (+), *Morus alba*, t2, 12 (+), *Ornithogalum nutans*, h, 52 (+), *Oxalis stricta*, h, 6 (+), 56 (+), *Parthenocissus inserta*, h, 30 (+), *Polygonum lapathifolium*, h, 18 (+), *Poa palustris*, h, 8 (+), *Populus* species, t1, 23 (+), *Potentilla reptans*, h, 15 (+), *Pulmonaria mollis* ssp. *mollis*, h, 24 (+), *Reynoutria japonica*, h, 26 (+), *Succisa* species, h, 8 (+), *Thalictrum aquilegifolium*, h, 45 (r), *Ulmus* species, t2, 7 (+), *Verbascum* species, h, 18 (+), *Viburnum lantana*, h, 87 (+), *Viburnum lantana*, s, 17 (+).

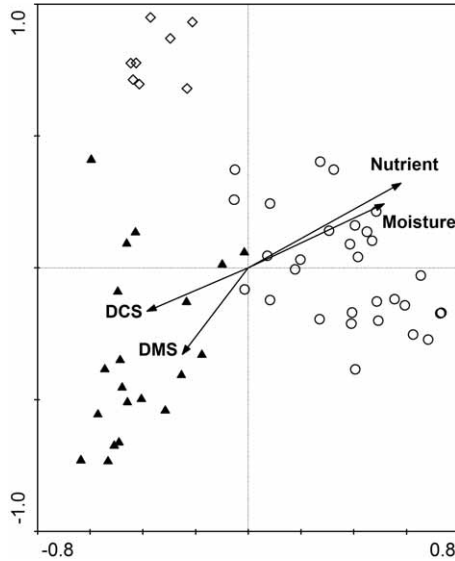


Fig. 2. Passive projection of Ellenberg indicator values and values of DCS and DMS onto the PCA diagram of relevés and species of flooded sites of the Mura River. Only indicator values with the highest correlations with the first two PCA axes are shown. The highest correlations with the first axis are shown by the indicator values for nutrients (0.579), moisture (0.515) and DCS (−0.384), with the second axis the values for DMS (−0.328). Legend: ○ *Salix alba* and *Populus nigra* stands (*Salicetum albae* Issler 1926), ◇ *Fraxinus angustifolia* subsp. *oxycarpa* stands (*Fraxino-Ulmetum effusae* Slavnić 1952 *allietosum ursini* subass. nova hoc loco), ▲ *Quercus robur* and *Carpinus betulus* stands (*Fraxino-Ulmetum effusae* Slavnić 1952 *quercetosum robori* subass. nova hoc loco)

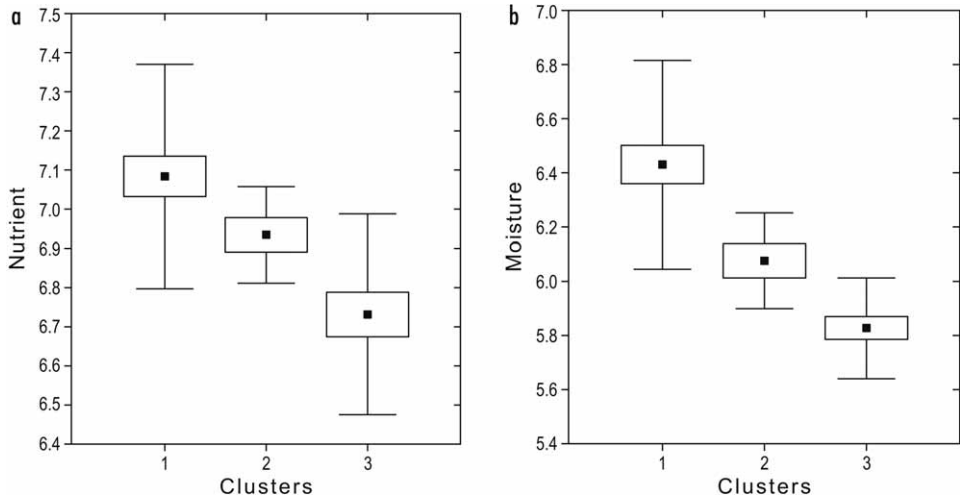


Fig. 3. Mean, standard error (box) and standard deviation (whiskers) of Ellenberg indicator values for nutrients (a) and moisture (b) of the three communities of the flooded forests. Communities (clusters) are numbered as in Fig.1.

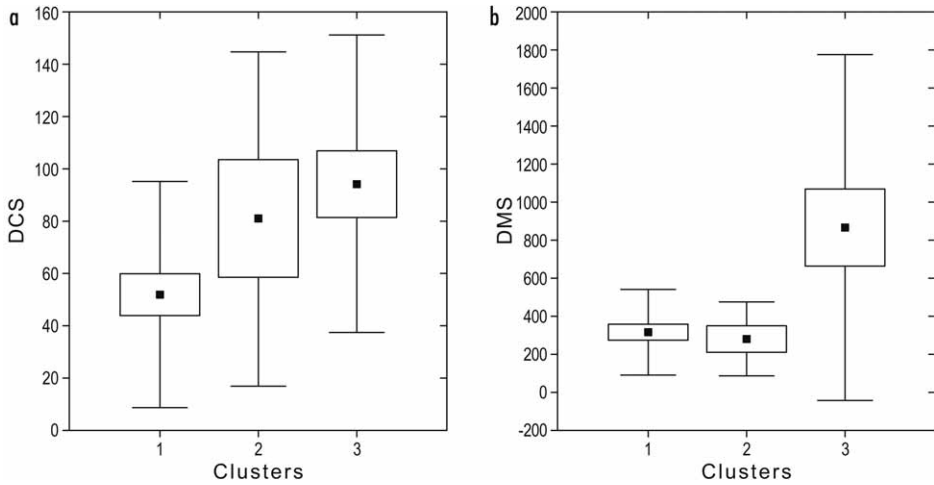


Fig. 4. Mean, standard error (box) and standard deviation (whiskers) of distance from the closest stream (DCS) (a) and distance from the main stream (DMS) (b) of the three clusters. Clusters are numbered as in Fig. 1.

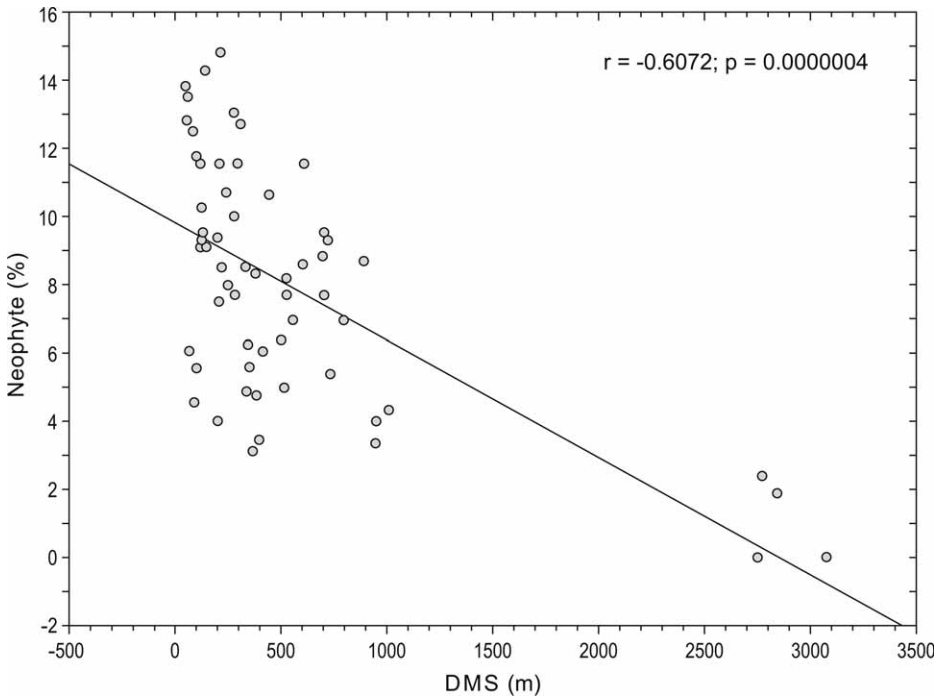


Fig. 5. Relation between the proportion of neophytes and increasing distance from the main stream (DMS).

In the case of life forms, correlation with DCS was very highly significant only in the case of therophytes (Fig. 6). Correlation with DMS was not significant in any case of life form.

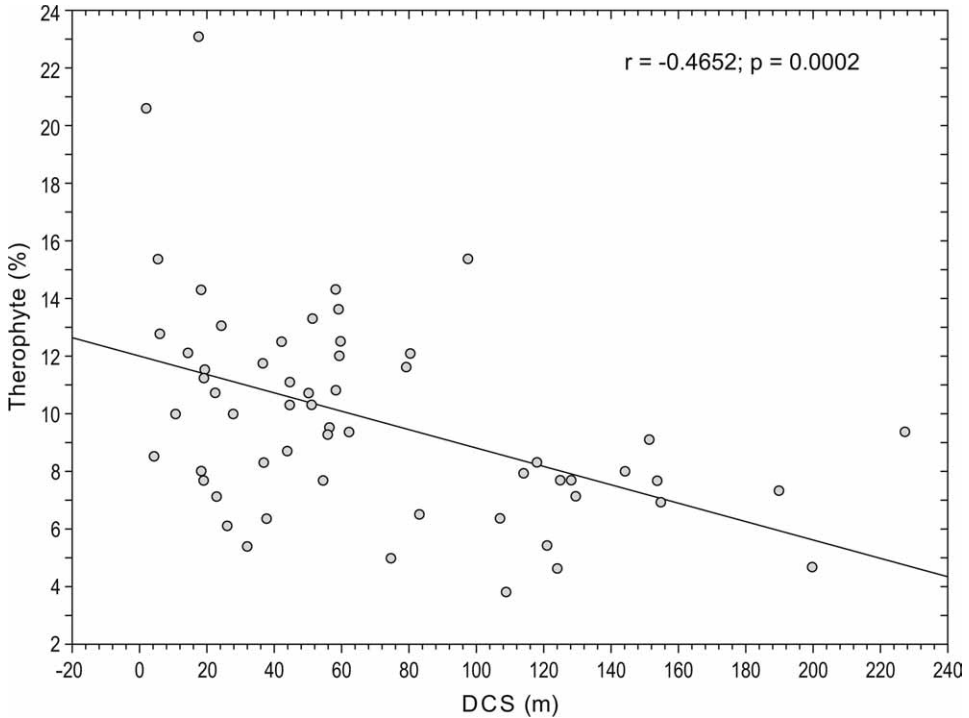


Fig. 6. Relation between the proportion of therophytes and increasing distance from the closest stream (DCS).

Correlations of ecological strategists and DCS and DMS was calculated with regression analysis. No analysis show statistical significant correlation.

In all three clusters hemicryptophytes represent the biggest proportion of species, geophytes and phanerophytes follow. Therophytes represent the smallest proportion of species in the relevés of three clusters (Tab. 2).

Tab. 2. Mean value of the share (%) of life forms with standard deviations (SD) of the three clusters.

life form	cluster 1	cluster 2	cluster 3
Hemicryptophytes	37.6 ± 8.96	48.37 ± 6.88	41.67 ± 6.87
Geophytes	22.16 ± 7.74	21.62 ± 2.94	22.79 ± 6.05
Phanerophytes	20.95 ± 5.4	13.17 ± 3.61	20.47 ± 5.62
Therophytes	11.8 ± 3.66	7.68 ± 1.57	7.55 ± 2.48

All three clusters consist of a mixture of different strategists (C-S-R, C, C-S, C-R and R). The proportions of CSR and C species were the highest in all three clusters (Tab. 3).

Species response curves fitted using HOF models (Fig. 7) describe the relationships among the main tree species of flooded forests of the Mura River and environmental variables DCS (Fig. 7a) and DMS (Fig. 7b).

Tab. 3. Mean value of the share (%) of C-S-R strategies with standard deviations (SD) of three clusters.

strategy type	cluster 1	cluster 2	cluster 3
C-S-R	36.25 ± 8.07	41.09 ± 3.79	41.14 ± 5.5
C	33.54 ± 6.87	27.07 ± 3.18	31.28 ± 5.35
C-S	10.8 ± 5.15	13.66 ± 3.98	11.81 ± 2.28
C-R	9.81 ± 4.06	6.81 ± 1.55	6.82 ± 2.45
R	4.25 ± 1.5	3.71 ± 1.59	3.67 ± 2.22

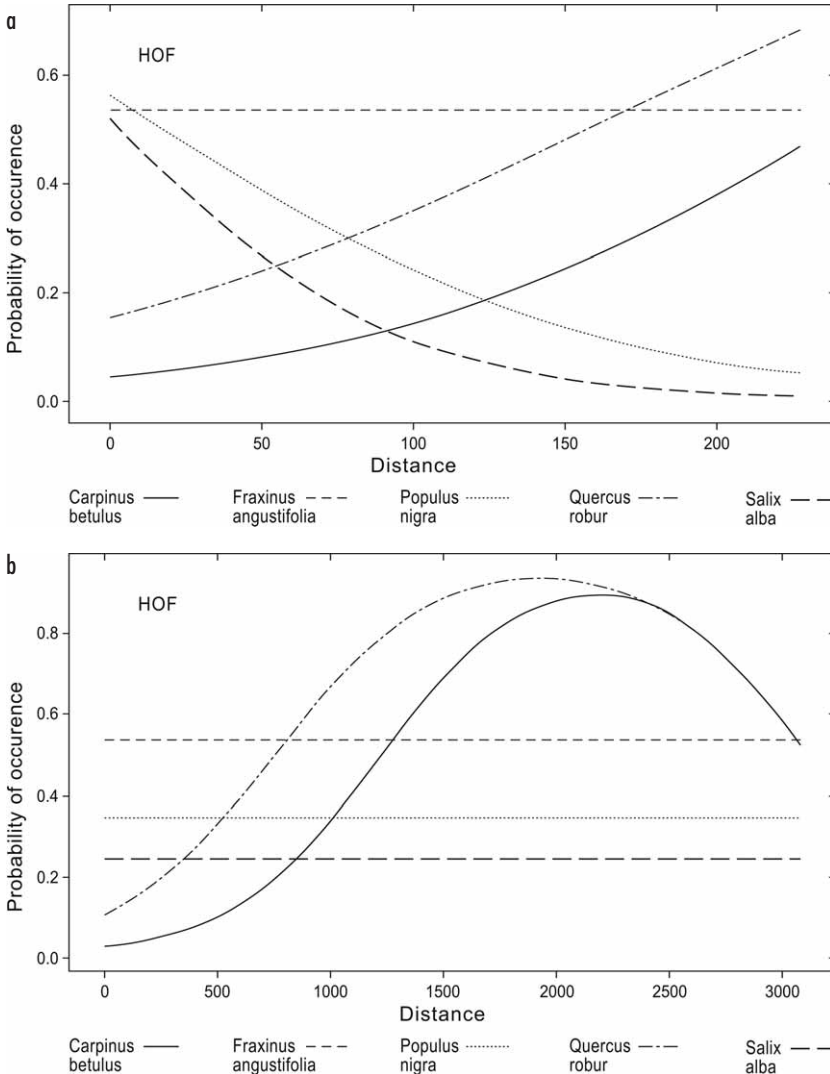


Fig. 7. Probability of occurrence of the main tree species of the area of the Mura River on the gradients of DCS (a) and DMS (b), modelled with the Huisman-Olff-Fresco models. Only species occurrences in the tree layer were considered for modelling.

Carpinus betulus and *Quercus robur* respond to both DCS and DMS. They are found in areas distant from streams. *Fraxinus angustifolia* subsp. *oxycarpa* does not respond to either DCS or DMS. *Salix alba* and *Populus nigra* respond only to DCS and do not respond to DMS. Their response is the opposite of the response of *Carpinus betulus* and *Quercus robur* as they are found close to the stream.

Discussion

Zonation of plant communities and ecological gradients

The three forest vegetation types that appear on river banks were detected with numerical analysis (Fig. 1). The main ecological gradients that influence the species composition of these forests are nutrients and moisture, and they are negatively correlated with distance from the stream (DCS, DMS) (Fig. 2). Moisture- and nutrient-rich plots are closer to the stream. Distance from the first closest stream (DCS) shows bigger correlation to species composition than DMS and it is the underlying gradient of vegetation zonation, which can be also seen from the DCS values of the three forest vegetation types (Fig. 4a). Three forest vegetation types are also ecologically delimited (Fig. 3a,b) as there is a distinction between the ecological values of the three groups of relevés. The values of relative elevation of the plots were much equalized, (as forests in depressions – floodplain swamp forests – were not included), and therefore do not influence species composition.

The three communities have been classified into syntaxa, as follows.

Syntaxonomical scheme:

Salicetea purpureae Moor 1958

Salicetalia purpureae Moor 1958

Salicion albae Soó 1930

***Salicetum albae* Issler 1926**

Quercio-Fagetea Br.-Bl. et Vlieger 1937

Fagetalia sylvaticae Pawlowski in Pawlowski et al. 1928

Alnion incanae Lüdi 1921

***Fraxino-Ulmetum effusae* Slavnić 1952 subass. *allietosum ursini* subass. nova hoc loco**

Holotypus: relevé number 31 in Tab. 1 *holotypus hoc loco*

***Fraxino-Ulmetum effusae* Slavnić 1952 subass. *quercetosum robori* subass. nova hoc loco**

Holotypus: relevé number 48 in Tab. 1 *holotypus hoc loco*

In the central part of Europe along big rivers the hardwood association *Quercio-Ulmetum minoris* Issler 1926 (syn. *Fraxino-Ulmetum* Tx. ex Oberd. 1953) is distinguished by the dominant species *Quercus robur*, *Ulmus minor/laevis*, *Fraxinus excelsior*. In central eastern and south eastern Europe a hardwood association with different *Fraxinus* species *Fraxinus angustifolia* subsp. *oxycarpa* (*Fraxino-Ulmetum effusae* Slavnić 1952 (syn. *Fraxino pannonicae-Ulmetum* Soó 1936 corr. 1963)) is the one that occupies the highest positions in floodplain areas along large rivers (WILLNER and GRABHERR 2007, NEUHÁUSLOVÁ et al. 2001, BORHIDI and KEVEY 1996, VICHEREK et al. 2000, VUKELIĆ and BARIČEVIĆ 2004, 2005, RAUŠ 1976, 1992, SLAVNIĆ 1952). That association was first correctly described by Slavnić in 1952 in the floodplain area of Vojvodina (Serbia) along rivers Drava and

Danube. The reference of SLAVNIĆ (1952) was overlooked by most European researchers who recognized the name *Fraxino pannonicae-Ulmetum* Soó 1936 corr. 1963 given by Soó (1963) as the correct one.

Description of the syntaxa (Tab. 1, Fig. 3a, b)

Salicetum albae Issler 1926

This community occurs along streams, on floodplains and along gravel pits. Along the Mura the white willow (*Salix alba*) and poplar tree (*Populus nigra*) form a relatively wide belt of riparian vegetation. These tree species dominate the stands and are also diagnostic species of the association. In the tree layer there are also *Alnus glutinosa*, *Salix fragilis*, *Ulmus laevis*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Prunus padus* and *Robinia pseudacacia*. The stands are often inundated and the ground water is high. The soil is structureless. Sedimentation is the result of inundation and alluvium deposits and its layers are clearly defined. Diagnostic species (Tab. 1) such as *Impatiens glandulifera*, *Agrostis stolonifera*, *Elymus caninus*, *Urtica dioica* etc. indicate moist and nutrient-rich, regularly disturbed sites. The large surfaces of the sites of this community were reclaimed in the past and planted with different cultivars of hybrid poplar and alder. The association is widely accepted and described all over Europe.

Fraxino-Ulmetum effusae Slavnić 1952

The community occurs in a wide belt along the Mura above the belt formed by white willow forests. In the area of Mura river we detected two subassociations of this association (subass. *allietosum ursini* and subass. *quercetosum robori*);

Fraxino-Ulmetum effusae Slavnić 1952 subass. *allietosum ursini* subass. nova. It occurs fragmentarily on finely structured alluvial soil. The sites are only occasionally flooded. The community is confined to the association *Salicetum albae*. In the tree layer species *Fraxinus angustifolia* subsp. *oxycarpa* dominates the stands, while *Ulmus laevis*, *Robinia pseudacacia* and *Prunus padus* also frequently occur. The diagnostic species are characteristic for moist, fresh, nutrient rich sites: *Geranium phaeum*, *Allium ursinum* (dominates the herb layer), *Festuca gigantea*, etc. In the vegetation map of forest communities of the area of Murska Sobota (ČARNI et al. 2008) forests of this subassociation were treated as a variant of *Fraxino-Ulmetum effusae* Slavnić 1952 var. *Prunus padus* Vukelić et Baričević 2004.

Fraxino-Ulmetum effusae Slavnić 1952 subass. *quercetosum robori* subass. nova. In terms of development, this forest type is the most mature and stable in the inundated region, it is the least nutrient rich and the least moist of the three vegetation types (Fig. 3). The dominant tree species in the tree layer is *Quercus robur*, sometimes also *Carpinus betulus*, *Fraxinus angustifolia* subsp. *oxycarpa*, *Robinia pseudacacia* and *Ulmus laevis*. The group of diagnostic species is large, and most species are of ordo *Fagetalia* (alliance *Alnion incanae*) and classes *Rhamno-Prunetea* and *Galio-Urticetea*. In the vegetation map of forest communities of the area of Murska Sobota (ČARNI et al. 2008) forests of this subassociation were treated as the association *Genisto elatae-Quercetum roboris* Horvat 1938. Later on, recent analysis showed that this vegetation type was more related to the association *Fraxino-Ulmetum* than to the association *Genisto elatae-Quercetum*. SLAVNIĆ (1952) was among the first to point out that the community *Fraxino-Ulmetum* displays a significant floristic affiliation with the Slavonian forest of pedunculate oak *Genisto elatae-*

-*Quercetum roboris*; however these are two separate systematic units. The community *Fraxino-Ulmetum effusae* inhabits the highest position of floodplain areas along large rivers, all these areas being exposed to periodical flooding. On the other hand, the community of *Genisto elatae-Quercetum* occurs in swamps along boggy backwaters, where mollic gleysol is formed (VUKELIĆ and BARIČEVIĆ 2004).

Both the above described subassociations of association *Fraxino-Ulmetum effusae* correspond well to forests along the upper course of the river Drava (around Varaždin) in Croatia near to Slovenia described by VUKELIĆ and BARIČEVIĆ (2004) as *Fraxino-Ulmetum* variant *Prunus padus* (drier variant). As the difference between the variant *Prunus padus* and variant *typicum* (more humid variant along the Danube River and lower part of the Sava River) described by the same authors, is significant, we propose a description of subassociations.

Zonation of forest vegetation can also be evidenced in a response curve of the main edifiers of plant communities (Fig. 7a) on the gradient of DCS. *Salix alba* and *Populus nigra*, edifiers of association *Salicetum albae*, are found close to streams and their occurrence decreases with the distance from the stream. The probability of occurrence for the tree species *Quercus robur* and *Carpinus betulus*, edifiers of the variant *Fraxino-Ulmetum* subass. *quercetosum robori*, increases with distance from the stream. The tree species *Fraxinus angustifolia* does not respond to DCS, its probability of occurrence is equalized on the gradient of distances, and therefore gets a chance to become dominant in stands in the middle of the distance gradient (*Fraxino-Ulmetum* subass. *allietosum ursini*), where the occurrence of *Salix* and *Populus* falls and the increasing occurrence of *Quercus* and *Carpinus* is still low. Response curve of main edifiers of plant communities in the gradient of DMS on the other hand proved the already established fact that DMS is not an underlying gradient for the zonation of forest vegetation.

Distribution of plant functional types along stream distance gradient

The group of life forms is a good indicator of disturbance. Short-living species (like therophytes) are favoured by continual disturbance, therefore cover value of therophytes is higher in flooded stand compared to unflooded stands. Long-living species (geophytes, phanerophytes) on the other hand, benefit from the interruption of inundation or from long habitat continuity (GLAESER and WULF 2009). In our case too, the proportion of therophytes in the relevés close to the stream is bigger and decreases with distance from it (Fig. 6). That is because the stands close to the stream are more disturbed by floods, deposition and removal of nutrient material. Other life forms show no statistical significant correlation with DCS as has been already found out also for some other plant communities along the moisture gradient (ZELNIK and ČARNI 2008).

Riparian habitats are considered to be particularly prone to invasion by alien plant species (TICKNER et al. 2001). The expansion of neophytes (alien species introduced to the region after the year 1500 A.D.) in river-floodplain systems characterized the 20th century as human alterations to these systems, such as channel modifications, flow regulation, and floodplain drainage, intensified (SCHNITZLER et al. 2007, TABACCHI et al. 1996). Many alien species are typically wetland species (ZEDLER and KERCHER 2004, SKAÁLOVA and PYŠEK 2009), and some of them have also high nutrient demands (SCHNITZLER et al. 2007). Close to the river the abundant supply of water and the high nutrient content of freshly deposited

sediments combine with the typically plentiful light availability to promote the successful germination and establishment of alien species (SANCHEZ-PEREZ et al. 1993, SCHNITZLER et al. 2003).

As we tested the proportion of neophytes in the stands and their correlation to DCS and DMS, surprisingly there were no significant correlations with DCS, but there was a significant correlation with DMS (Fig. 5). This means that bigger occurrence of neophytes is not connected to certain type of vegetation (willow stands because of their community architecture promote light in the understoreys) as has been reported (SCHNITZLER and AUMAITRE 2008). Also in the area of Mura the best preserved willow stands are along side streams (and not along the main stream) as vegetation close to main stream is much more affected by different human impacts. A more important factor is the proximity of the main stream alone, which beside promotion of light (there are many open and disturbed areas near the main stream) assures active dispersal of rhizomes or stems (vegetative matter and seeds) deposited during floods and thereby encourages propagation (SCHNITZLER et al. 2007, RICHARDSON et al. 2007). The flow of the main stream is quick and never drains up, in contrast to side streams.

Both groups of species (neophytes and therophytes) are characteristic of disturbed sites. The proportion of therophytes is significantly negatively correlated with the distance from the closest stream (DCS), which can be easily understood and has been observed and explained already by other authors. More surprising is that neophytes do not respond to environmental factors in the same way as therophytes. A proportion of neophytes does not correlate with the same distance – distance from the closest stream (DCS), but with distance from the main stream (DMS). It seems that for establishment of neophytes, the propagation assured with the flow of the main stream is one of the most important factors beside disturbance itself.

Strong correlations of ecological strategy and moisture gradient have already been detected for some other vegetation types (ZELNIK and ČARNI 2008, TURNER et al. 2004, GLAESER and WULF 2009). Relative elevation and distance from main channel, as indicators of flooding regime, were reported to be consistently important in predicting occurrence, community composition and abundance of species (TURNER et al. 2004, MENGES and WALLER 1983). In our case the distribution of plant ecological strategies indicates similar habitat conditions along transect from the streams, as there is no statistical significant correlation of plant ecological strategies with DMS and DCS. All relevés were made inside the area of frequent floods (inside dikes) on quite equalized elevations. In our study all three types of vegetation show similar proportions of plant ecological strategies in their compositions.

Conclusion

The present study contributes basic data on the floristic composition and structure of floodplain forests of Mura river. The zonation of floodplain forests is connected to distance from the closest stream (DCS) and not from the main stream (DMS). Distance from the closest stream influences species distribution through ecological gradients of moisture and nutrient. Three types of forests have been detected along these gradients. The proportion of therophytes is significantly negatively correlated with the distance from the closest stream and the proportion of neophytes is significantly negatively correlated with distance from the

main stream. The correlation of proportion of neophytes with DMS can be explained by the importance of their effective propagation ensured by flow of the main stream.

Acknowledgements

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