THE EFFECTS OF RIVER EMBANKMENT AND FOREST FRAGMENTATION ON THE PLANT SPECIES RICHNESS AND COMPOSITION OF FLOODPLAIN FORESTS IN THE MEUSE VALLEY, BELGIUM

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ABSTRACT. — We studied the effect of disruption of alluvial forests from natural river flooding on their vascular plant diversity in the river Meuse floodplain in Belgium. The river Meuse is a rain-fed river, originating at an altitude of 409 m above sea level and discharging into the North Sea some 900 km further downstream. The Meuse river was channelized for most of its course in Belgium and The Netherlands during the last two centuries. In the study area a continuous embankment was gradually realised with a system of winter dykes. This enabled us to sample forests along a gradient of isolation from the river and flooding frequency. Flooding frequency was the most important correlate of community composition of the forests. Forests still under influence of the river were significantly richer in river species and significantly poorer in woody species than forests disconnected from the river. They also had a higher *beta* species diversity and tended to have a higher *alpha* diversity. Disconnected forests seem to loose species but they do not gain species at the same rate. We suggest that the two most important ecological processes behind this are 1) the poor colonisation capacity of typical forest plant species, which is mainly due to dispersal limitation and 2) the absence of natural disturbance events, which stimulates the dominance of certain competitive species in these forests. Only the re-establishment of lateral river connectivity and natural dynamics can stop this process.

KEY WORDS. — River embankment, river connectivity, forest fragmentation, intermediate disturbance hypothesis, floodplain forests, dispersal limitation.

INTRODUCTION

Due to their extremely high spatio-temporal habitat heterogeneity and habitat connectivity, river systems belong to the most species rich ecosystems in temperate regions (NILSSON *et al.* 1989, GREGORY *et al.* 1991, ZWICK 1992, POLLOCK *et al.* 1998, WARD 1998, WARD *et al.* 1999, TOCKNER *et al.* 1999). SCHNITZLER (1996) refers to river ecosystems as natural non-steady state systems characterized by short-term cyclic changes. Research on biodiversity gradients within river

systems can be categorized into studies of longitudinal diversity patterns (*i.e.* along the river course) and lateral diversity patterns (*i.e.* perpendicular to the river course) (WARD 1998). Most research until now dealt with along-stream changes in biodiversity and used the River Continuum Concept as a useful theoretical framework for hypothesis testing, especially for North American rivers (VANNOTE *et al.* 1980, and see *e.g.* STATZNER & HIGLER 1985, OBERDORFF *et al.* 1993, GRUBAUGH *et al.* 1996). Lateral biodiversity gradients in the floodplain of natural flowing rivers have also been documented (*e.g.* WARD & STANFORD 1995, TOCKNER *et al.* 1999, LYON & SAGERS 1998).

During the last century, almost all large European rivers have been subjected to hydraulic management in order to facilitate navigation and to control flooding. Hydraulic management may affect both lateral and longitudinal biodiversity gradients (BRAVARD *et al.* 1986). Dam construction for example, mainly affects longitudinal connectivity and hampers the migration and dispersal of species (*e.g.* ENGLUND *et al.* 1997, ANDERSSON *et al.* 2000, JAGER *et al.* 2001) although it may also affect indirectly lateral biodiversity gradients by preventing downstream floodplain flooding (NILSSON *et al.* 1997). River channelization and dyke construction on the other hand mainly affect lateral biodiversity gradients by disrupting the connection of the river with its floodplain. Much less research documenting this process is available so far, as it is only recently that aquatic ecologists appreciated the extent of it (WARD 1998).

Here, we deal with the effects of river embankment on lateral plant diversity gradients in a river floodplain. In unmodified river systems, the riparian vegetation is expected to exhibit a zonation from the river channel to the uplands along an elevation gradient (LYON & SAGERS 1998, SIEBEL & BOUWMA 1998). In the lower parts of the floodplain, regular flooding creates disturbance and opens space for recruitment of plants that are transported by the river. Along the upward elevation gradient, disturbance and connectivity with the river channel gradually decrease resulting in a characteristic plant diversity gradient. Some authors have compared the plant diversity of

riparian zones with the surrounding area free from any river influence and concluded that diversity may be more than two times higher in the floodplain zone (BROWN & LUGO 1982, GREGORY *et al.* 1991). Hence it can be expected that disrupting floodplains from their river channel may have a serious impact on biodiversity.

Some attention has already been paid to the effects of flood disruption on species richness and species composition of floodplain forests (TRÉMOLIÈRES *et al.* 1998, DEILLER *et al.* 2001). These authors concluded that forests in the former floodplain of the Rhine River lost their alluvial specificity but did not suffer from a loss in species richness. These studies, however, lacked a statistical comparison of species richness between locations subjected to different flooding regimes and only dealt with woody plants and fungi.

We studied the total plant species richness of forests in the floodplain of the river Meuse in Eastern Belgium. The Meuse river was channelized for most of its course in Belgium and The Netherlands during the last two centuries. For the study area of the border Meuse stretch with The Netherlands, a continuous embankment was gradually realised with a system of winter dykes (Fig. 1). This enabled us to sample forests along a gradient of isolation from the river and flooding frequency. The main questions were : (1) What is the effect of complete disruption of the forests from river flooding on their plant diversity compared to the diversity of forests in the winter bed, which are still under river influence ? (2) Can the plant species diversity and species composition gradient in the floodplain forests (if present) be explained by their flooding frequency ?
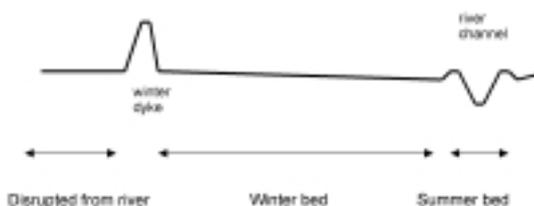

FIG. 1. — System of winter and summer dikes in the border Meuse stretch under study.

MATERIAL AND METHODS

The river system

The river Meuse is a rain-fed river, originating at an altitude of 409 m above sea level at the Plateau of Langres in the Northeast of France and discharging into the North Sea some 900 km further downstream. The catchment area of the river is c. 33,000 km² and is situated in France (9,000 km²), Belgium (13,500 km²), Germany (4,000 km²), Luxembourg (600 km²) and The Netherlands (6,000 km²) (van Leussen *et al*. 2000). The Meuse can be divided in 5 reaches based on geomorphological and hydrological characteristics (Fig. 2) (Pedroli & de Leeuw 1997). The Common Meuse is a typical gravel river with a strong longitudinal gradient (0.45 m km^{-1}). The discharge of the Meuse shows great fluctuations. Discharge levels for the Common Meuse range from 10 m³ s^{-1} during dry periods to 3.000 m³ s^{-1} in periods of heavy rainfall in the catchment area. The study area is the unregulated middle course section (50 km) of the Meuse between Maastricht and Maaseik on the Flemish-Dutch border. For this river section, a large-scale nature development project is defined in a master plan for the complete Common Meuse valley. Restoration projects in general aim at mitigating the effects of the regulation works by rehabilitating geomorphological diversity, to promote the recovery of degraded biota and the floodplain benefits from the river (Tockner & Schiemer 1997). However, the hydrological, geomorphological and biological heterogeneity and variability of river-floodplain systems, both temporally and spatially, complicate the restoration schemes (Amoros *et al*. 1987).

Communities, sampling and species diversity

Floodplain woodland communities in the study area show considerable variation but can be divided in three groups. The first community is the most frequent one and may be considered as a willow woodland with *Salix alba* and *S. viminalis* as the most common woody species. But also other woody species may occur (*e.g. Fraxinus excelsior*, *Crataegus monogyna*, *C. laevigata*, *Alnus glutinosa*). Syntaxonomically this community relates to the Salicion albae and at least part of the plots may be described as the Artemisio-Salicetum albae (cf. Hommel *et al*. 1999 :167). *Alnus glutinosa* dominates the second community. It is differentiated by a considerable number of Alnion glutinosae-species, *e.g. Lycopus europaeus, Solanum dulcamara, Iris pseudacorus*. It therefore belongs to the Alnion glutinosae and probably to the Carici elongatae-Alnetum (cf.
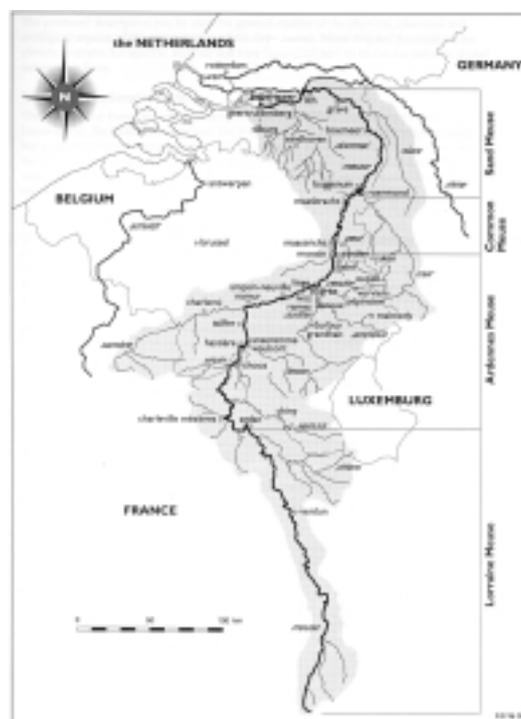

Fig. 2. — Location of the common Meuse or border Meuse between Belgium and The Netherlands. (Pedroli & de Leeuw 1997).

Stortelder *et al*. 1999). The last community is dominated by hardwood species, mainly *Fraxinus excelsior*, but *Quercus robur* and *Acer pseudoplatanus* also occur regularly. It clearly belongs to the Alno-Padion, but typical forest plant species often are absent (*e.g. Lamium galeobdolon*, *Adoxa moschatellina*, *Primula elatior*, *Paris quadrifolia*). In general all observed communities are relatively heterogeneous and usually not fully developed. This clearly relates to the highly dynamic nature of these habitats with regular disturbances (flooding, erosion and sedimentation).

Fifty-five forest fragments were sampled using 69 plots of 3 x 3 m in size. The forests ranged from hardwood to softwood forests (although it is not always possible to attribute them unequivocally to one of these categories, and understorey layers between these forests do not really differ). Four samples (all softwood) were lying in the summer bed, 48 samples (29 softwood and 19 hardwood) were lying in the winter bed and 17 samples (5 softwood and 12 hardwood) were lying in forests completely disrupted from any river influence. Disruption occurred 20-30 years ago for 9 of these disconnected forests and 160-180 years ago
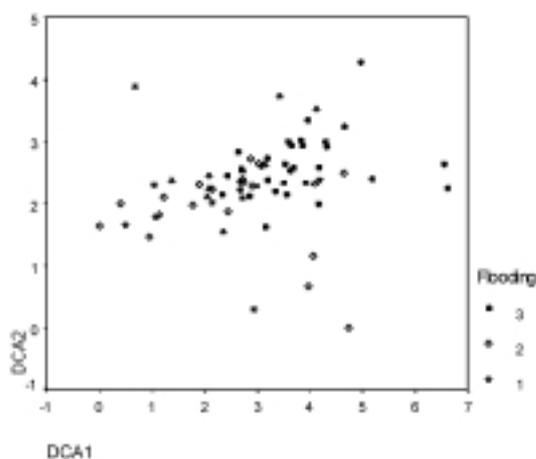
F IG . 3. — DCA sample scores of the sample plots marked by their flooding frequency. 1 : never to less than once in a decade ; 2 : between once a year and once in a decade ; 3 : more or equal to once a year.

for 8 of these forests. Flooding frequency of the samples ranges from more than once a year to less than once within a decade. Flooding frequency was summarised in three categories : 'never to less than once in a decade', 'more or equal to once a year' and 'between once a year and once in a decade'. We also determined for each plot the distance in bird's-eye view to the river channel (m). Also, soil texture in each sample plot was manually analysed using a scale that ranged from gravel (9) over clay-sand (5) to clay (1).

All taxa of vascular plants within the sample plots were recorded using the Tansley scale (T ANSLEY 1935) between 1996 and 1999. The full data matrix is available from the authors upon request. Species were attributed to different functional ecological groups. We distinguished between woody species, typical forest species (*sensu* H ONNAY *et al.* 1999a) and typical river species (*sensu* M ALANSON 1996 and B ERTEN & L ETEN 1995). We also calculated the Shanon-Wiener diversity index and a dominance index for each sample plot using the EcoSim software (G OTELLI & E NTSMINGER 2001). The Shannon-Wiener diversity index includes both species richness and evenness in one index, while the dominance index simply reflects the fraction of the sample plot represented by the most abundant species (M AGURRAN 1988). Finally, *beta* species diversities of the winter bed and the isolated floodplain zone were calculated together with the *beta* diversities of the sample plots grouped by flooding frequency. *Beta* diversity was defined as *gamma* diversity divided by *alpha* diversity (S CHLUTER & R ICKLEFS 1993). *Gamma* diversity is the total species richness of the group of sample plots under consideration. *Alpha* diversity is the mean number of species in this group of sample plots. We report the results as the reciproque of *beta* diversity as this measure expresses the mean number of sample plots where a species occurs. We used a jackknife method (M ANLY 1997) to generate a variance for each calculated *beta* diversity value in order to be able to compare the *beta* diversity between groups of sample plots.

D ATA ANALYSES

In a first stage we performed a data exploratory Detrended Correspondence Analysis (DCA) using the CANOCO 4.0 software (H ILL & G AUCH 1980, TER B RAAK & S MILAUER 1997). In order to identify the abiotic drivers of the species composition gradients, DCA sample scores of the 69 sample plots were related with flooding frequency and river channel connectivity (summer bed, winter bed or disrupted from the river) using a one way Analysis of Variance (ANOVA) and with distance to river and soil texture using a Spearman rank correlation coefficient. DCA sample scores were normally distributed (Kolmogorov-Smirnov test) and exhibited equal variances across examined class variables.

Next, to investigate whether the construction of winter dykes and the associated disruption of forests from the river affected the species diversity of these forests we compared their community composition and species richness with the forests situated in the winter bed using independent two sample t-test tests. Because there were only four summer bed samples these were omitted from this analysis.

Finally, we aimed at revealing the ecological mechanism behind the differences in species diversity and we related species richness and diversity of the sample plots with their flooding frequency. We used a one-way ANOVA with Tukey pairwise comparisons between the three levels of flooding frequency.

All statistical analyses were performed with SPSS 10.0.5. The jackknife procedure was performed using the S-Plus software.

RESULTS

We found a total of 209 plant species. Species and the species subgroups are listed in the appendix, with species ranked according to their sore on the first DCA axis (representing increasing flooding frequency and disturbance). The first two axes of the DCA only explained a cumulative percentage of the variance of the species data of

TABLE 1

Relation between the DCA sample plot scores and three variables measuring river dynamics in each sample plot (n=69)

	Flooding frequency[1]	River connectivity[1]	Soil texture[2]	Distance river[2]
DCA1	11.54***	11.48***	-0.16	-0.05
DCA2	6.97**	0.04	-0.38**	0.15

[1] F-values (ANOVA, k = 3)
[2] Spearman rank correlation coefficient
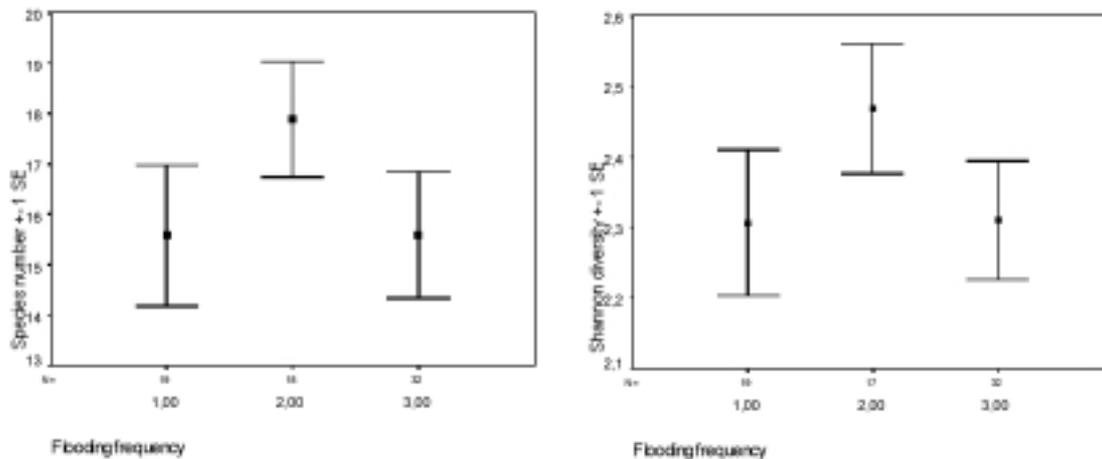*** : P ≤ 0.001; ** : 0.001 < P ≤ 0.01 (2-tailed P-values)

FIG. 4a and b. — Relation between species richness (a) and the Shannon diversity index (b) and the flooding frequency. 1 : never to less than once in a decade ; 2 : between once a year and once in a decade ; 3 : more or equal to once a year.

10%, expressing the very heterogeneous character of the vegetation in the sample plots. There was a significant relation between DCA1 sample scores and flooding frequency and river connectivity. DCA2 sample scores were significantly correlated with flooding frequency and with soil texture. We found no correlations with the distance to the river (Table 1, Fig. 4).

Forests in the winter bed were significantly richer in river species and marginally significantly poorer in woody species than forests disconnected from the river (Table 2). This resulted in a tendency for winter bed forests to be more species rich than disconnected forests, although the difference is not significant. Disconnected forests were also more homogeneous in species composition : they had a higher dominance value and a lower *beta* diversity (*i.e.* species were, on average, occurring in more sample plots than in the winter bed forests).

TABLE 2

Average species number and species diversity of the sample plots in the winter bed and in the zone which is completely disrupted from river influence. Comparison of means using an independent sample t-test (n=65)

	Disconnected	Winterbed	t-value
All species	15.4	17.4	1.14
Forest plant species	10.4	9.4	0.78
Woody species	4.9	3.9	1.75(*)
River species	1.4	3.2	3.30**
Dominance	0.22	0.18	1.78(*)
Shannon Diversity	2.27	2.43	1.44
1/Beta diversity (samples/species)	4.64	2.49	1.99*

** : 0.001 < P ≤ 0.01; *: 0.01 < P ≤ 0.05; (*) : 0.05 < P ≤ 0.1 (2-tailed P-values).

TABLE 3

Effects of flooding frequency on average species richness and diversity (n=69).
Different letters represent significant differences (P<0.1) according to Tukey pairwise comparisons

	1 (≤once /10y)	2 (2-9 /10y)	3 (≥once /y)	Overall F value
All species	15.6	17.9	15.8	0.81
Forest plant species	10.2ab	10.6a	7.8b	2.81(*)
Woody species	4.8b	4.2ab	3.4a	2.65(*)
River species	1.4a	3.0b	3.4b	6.17**
Dominance	0.21	0.19	0.21	0.58
Shannon Diversity	2.31	2.47	2.31	0.81
1/Beta diversity (samples/species)	3.61a	2.40b	3.55a	4.36*

** : $0.001 < P \leq 0.01$; *: $0.01 < P \leq 0.05$; (*) : $0.05 < P \leq 0.1$ (2-tailed P-values)

Frequently flooded forests contained marginally significantly less forest plant species, less woody species and significantly more river species (Table 3). This resulted in maximal species richness and species diversity in the forests with an intermediate flooding regime, although the differences with the higher and lower flooding regime forests were not significant (Fig. 4a and b). *Beta* diversity is significantly higher in the forests with the intermediate flooding regime (Table 3).

DISCUSSION

As appeared from the DCA analysis, flooding frequency is the major driving force behind the plant community composition of forests in the Meuse river floodplain. Other variables like river connectivity, distance to river channel and soil texture are less effective in explaining community composition. Soil texture is a secondary and complex variable that is the result of the interaction between flooding frequency and the presence, dimension and shape of geomorpholoical features in the landscape (BORNETTE & AMOROS 1996). River connectivity and bird's-eye distance to the river channel are moderate to very poor correlates of flooding frequency, which is also due to the geomorphological heterogeneity of the floodplain.

Forests in the winter bed tend to be more species rich than forests disconnected from the river although the difference is not statistically significant. River species in particular disappear from the forests when they are disconnected from river influence. Most of these river species are dependent on free space generating disturbance events for their germination and recruitment on the one hand and on flowing water for their dispersal on the other hand (BORNETTE & AMOROS 1996, WARD *et al.* 1999). Both processes (*i.e.* recurrent disturbance and habitat connectivity through flowing water) are lacking in the forests that became disconnected from river influence. The importance of disturbance events in structuring the plant communities is confirmed also by the (on average) higher dominance index and the lower *beta* diversity of the disconnected forests. In the absence of disturbance some plant species tend to become dominant on the sample plot scale and between sample plots. This results in a higher dominance of certain species and in the relatively high number of sample plots where individual species occur (*i.e.* in a low *beta* diversity). Regular disturbance events in the winter bed due to flooding leaves less opportunities for certain plant species to become dominant. It is known that, especially in highly productive ecosystems like most river systems, species diversity can be maintained only when some species are eliminated regularly. This corresponds to Huston's so called general hypothesis of species diversity (HUSTON 1979, WARD *et al.* 1999). Generally, flood-created disturbances provoke rejuvenation of floodplain zones with patches of different degrees of maturity, resulting in a meta-stability

of plant and animal communities (BRETSCHKO 1995).

This conclusion is also in accordance with the homeorhesis (from the Greek "preserving the flow") concept as an important issue in dynamic systems. The analysis of the system in motion, incorporating the processes and the meta-stability of the dynamic system, is the challenge for the planning of restoration schemes. The ecological restoration focusses on enabling the river dynamic processes that maintain the floodplain habitat heterogeneity. For the restoration, *i.e.* regeneration of floodplain woodlands, flooding events are documented as an essential feature (SCHNITZLER 1997).

Besides their loss of river species, disconnected forests tend to become enriched with forest plant species, although the latter is not as explicit as the first. The habitat of the disconnected forests slowly changes and becomes more and more suitable for the establishment of typical forest plant species. Three interconnected processes may be responsible for this process : (1) Lowering of the ground water table. (2) Gradual colonisation of understorey woody shrub species which decrease light transmission to the soil and hence the cover of very competitive tall herb species (SIEBEL & BOUWMA 1998, DEILLER *et al.* 2001). It is known from other forest ecosystems that tall species like *Urtica dioica* and *Rubus fruticosus* coll. may prohibit forest plant species colonisation (HONNAY *et al.* 1999b, VERHEYEN AND HERMY 2001). (3) Decrease in soil phosphate level, which also has a negative impact on the presence of the tall herb vegetation and hence a positive on forest plant species colonisation (TRÉMOLIÈRES *et al.* 1998, HONNAY *et al.* 1999b). The biodiversity lost by the disappearance of river species, however, did not seem to be completely compensated by enrichment in typical forest species. Most forest plants species have no special seed adaptations for long distance dispersal (HERMY *et al.* 1999, BUTAYE *et al.*, 2001). Hence it is very difficult for these species to reach these fragmented forest patches although they seem suitable for colonisation after the termination of the flooding events. In other words, the loss of river species is hardly compensated by the colonisation of typical forest plant species due to the fragmentation of the forests. In the winter bed, forest fragmentation is no problem as the connectivity between forest species is guaranteed due to regular flooding events. The impoverishment process of the disconnected forests is confirmed when the recently (20-30 yrs) and long time ago (160-180 yrs) disconnected forests are compared (results not shown). The latter contain significantly less river species than the former and only marginally significantly more forest plant species.

TRÉMOLIÈRES *et al.* (1998) and DEILLER *et al.* (2001), in contrast, found an accumulation of species in Rhine alluvial hardwood forests along a gradient going from still flooded to unflooded for 30 years and unflooded for 130 years. These authors, however, only studied woody plants and found an accumulation of species like *e.g. Viburnum* spp., *Ligustrum vulgare*, *Prunus spinosa*, *Berberis vulgaris*, *Acer campestre*, and *A. pseudoplatanus*. These tree and shrub species are ornithochorous or anemochorous and hence are dispersed relatively easily over long distances. The forests that we studied became also significantly richer in woody species after disconnection from the river. However, the dispersal and establishment process of most herbaceous forest plant species seems much more problematic.

In order to get an insight into the basic ecological process responsible for differences in species richness between disconnected and winter bed forests, we also directly focused on the effects of flooding frequency on species richness. As already mentioned when discussing the DCA results, flooding frequency is a more precise exploratory variable than river connectivity because even within one connectivity class (the winter bed) there is a flooding frequency gradient which is associated with the presence of large geomorphological features, rather than with the distance to the river channel (cf. Table 1). Species richness and species diversity (the latter expressed as Shannon diversity) tend to peak at intermediate flooding frequency (Fig. 4a and b). At low flooding frequency, certain species tend to become dominant as already discussed in a previous paragraph. When flooding frequency becomes too high, only a small number of specialist pioneer

species can survive. This is completely in accordance with the intermediate disturbance hypothesis, which again proves to be a very powerful theoretical framework (CONNELL 1978, HUSTON 1979, BARTHA *et al.* 1997). WARD *et al.* (1999) recently confirmed the relevance of general biodiversity concepts derived from terrestrial and marine environments to river systems.

CONCLUSION

Forests disconnected from river influence lose typical river species and do not gain forest plant species at the same rate. Disconnected forests tend to become less species-rich and have a lower *beta* diversity due to the increasing dominance of certain plant species. The ecological rationale behind this species loss is (1) dispersal limitation of typical forest plant species in reaching the fragmented disconnected forests, and (2) the intermediate disturbance hypothesis that predicts a decrease in species richness in the absence of disturbance events prohibiting dominance of certain competitive species.

ACKNOWLEDGEMENTS

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Appendix

List of the surveyed species (n=209). 1 : typical river species ; 2 : typical forest species ; 3: woody species ; 4 : highest frequency in summer bed (S), winter bed (W) or disconnected (D) sites. Species are ranked ascending according to their DCA scores on the first axis, *i.e.* with increasing tolerance against flooding.

	1	2	3	4		1	2	3	4
Allium schoenoprasum	x			W	*Rumex sanguineus*	x	x		W
Carpinus betulus			x	W	*Lysimachia vulgaris*				W
Acer platanoides			x	D	*Populus sp.*			x	D
Allium vineale				W	*Geum urbanum*		x		D
Anemone nemorosa		x		W	*Valeriana officinalis*				DW
Corydalis solida	x	x		D	*Lysimachia nummularia*				DW
Alisma plantago-aquatica				W	*Cirsium vulgare*				W
Myosotis laxa				W	*Ranunculus lingua*		x		D
Arum maculatum		x		D	*Humulus lupulus*		x		D
Carex sylvatica		x		D	*Carex riparia*				W
Ribes nigrum	x	x	x	D	*Crepis capillaris*				W
Polygonatum multiflorum		x		D	*Senecio jacobaea*				W
Viola riviniana		x		W	*Glechoma hederacea*				DW
Hedera helix		x		D	*Sonchus arvensis*				D
Ranunculus ficaria		x		D	*Populus tremula*			x	D
Veronica hederifolia		x		W	*Parietaria officinalis*		x		DW
Ulmus minor	x		x	D	*Poa nemoralis*		x		D
Arum italicum				D	*Angelica sylvestris*				D
Corylus avellana		x	x	D	*Myosotis palustris*				W
Milium effusum		x		D	*Malus sylvestris*		x	x	W
Tilia sp.			x	D	*Mentha suaveolens*	x			W
Ornithogalum umbellatum		x		D	*Carex acutiformis*				W
Ribes rubrum		x	x	W	*Populus nigra*	x		x	D
Acer pseudoplatanus			x	D	*Lycopus europaeus*				S
Evonymus europaeus	x	x	x	DW	*Cardamine hirsuta*				W
Circaea lutetiana		x		D	*Filipendula ulmaria*				W
Ulmus glabra			x	W	*Crataegus laevigata*	x	x	x	W
Sorbus aucuparia		x	x	D	*Crepis biennis*	x	x		W
Lamium maculatum	x			W	*Stellaria holostea*		x		D
Geranium robertianum				D	*Alopecurus pratensis*				D
Solanum dulcamara				S	*Cornus sanguinea*	x	x	x	D
Vaccinium vitis-idaea			x	D	*Eupatorium cannabinum*				W
Iris pseudacorus				D	*Epipactis helleborine*		x		W

	1	2	3	4		1	2	3	4
Cardamine amara	x	x		W	*Cardamine impatiens*		x		W
Impatiens parviflora		x		W	*Myosotis sylvatica*				D
Stellaria nemorum	x	x		D	*Rosa rubiginosa*	x		x	W
Stachys sylvatica		x		D	*Veronica officinalis*				W
Brachypodium sylvaticum		x		D	*Urtica dioica*				W
Caltha palustris				W	*Dryopteris filix-mas*			x	D
Athyrium filix-femina		x		D	*Salix aurita*			x	W
Ligustrum vulgare		x	x	W	*Poa palustris*				W
Thelypteris palustris				D	*Lythrum salicaria*				W
Mycelis muralis	x	x		W	*Ranunculus repens*				W
Sambucus nigra		x	x	D	*Carex vesicaria*				W
Impatiens glandulifera	x			W	*Eleocharis palustris*				W
Viburnum opulus		x	x	D	*Rorippa amphibia*				W
Juglans nigra			x	W	*Chaerophyllum temulum*				W
Alliaria petiolata				W	*Symphytum officinale*				D
Alnus glutinosa		x	x	W	*Silene dioica*				W
Carex remota		x		D	*Salix alba*	x			W
Fraxinus excelsior			x	W	*Cardamine flexuosa*			x	W
Aegopodium podagraria				W	*Sisymbrium altissimum*				W
Calystegia sepium				W	*Euphorbia esula ssp. esula*		x		S
Salix triandra	x		x	S	*Brassica nigra*				W
Salix x multinervis			x	S	*Silene vulgaris*				W
Arctium lappa				W	*Verbascum nigrum*	x			W
Salix viminalis	x		x	S	*Lactuca serriola*				W
Convolvulus arvensis				W	*Carex hirta*				W
Primula veris				W	*Heracleum sphondylium*				W
Galeopsis tetrahit				W	*Stellaria media*				D
Potentilla anserina				D	*Geranium molle*				W
Campanula rapunculus				W	*Quercus robur*			x	D
Juncus compressus				W	*Matricaria maritima*				W
Plantago major				W	*Saponaria officinalis*		x		W
Salix x rubens			x	S	*Dactylis glomerata*				W
Clematis vitalba				W	*Rorippa sylvestris*				W
Epilobium hirsutum				W	*Ajuga reptans*		x		D
Galium aparine				D	*Capsella bursa-pastoris*				W
Polygonum amphibium				D	*Reseda lutea*	x			W
Mentha aquatica				W	*Sisymbrium officinale*				W
Quercus rubra			x	D	*Stellaria aquatica*				W
Festuca arundinacea				S	*Melilotus altissima*		x		W
Thalictrum flavum	x			W	*Bryonia cretica ssp. dioica*		x		W
Prunus spinosa		x	x	D	*Tanacetum vulgare*				S
Agrostis canina				W	*Chelidonium majus*				W
Viola odorata		x		W	*Torilis japonica*		x		W
Rubus caesius		x	x	W	*Potentilla reptans*				W
Poa pratensis				D	*Crataegus monogyna*		x	x	D
Vicia sp.				D	*Cardamine pratensis*				W
Juncus effusus				D	*Vicia cracca*				W
Scrophularia nodosa		x		W	*Cruciata laevipes*		x		W
Salix caprea		x	x	W	*Lathyrus pratensis*				W
Epilobium tetragonum				DW	*Prunus avium*		x	x	D
Phalaris arundinacea	x			S	*Anthriscus sylvestris*				W
Ranunculus acris				D	*Cirsium arvense*				W
Rubus fruticosus agg.		x	x	W	*Galium mollugo*	x			W
Senecio inaequidens	x			W	*Stellaria graminea*				W
Salix purpurea	x		x	S	*Deschampsia cespitosa*			x	W
Sinapis arvensis				S	*Vicia sepium*		x		D

	1	2	3	4		1	2	3	4
Salix cinerea		x	x	D	*Pimpinella major*				D
Helianthus tuberosus	x			S	*Geranium dissectum*				W
Scrophularia auriculata	x			W	*Lotus corniculatus*				W
Stachys palustris				D	*Poa trivialis*				D
Elymus repens				D	*Agrimonia eupatoria*			x	D
Prunella vulgaris				W	*Arrhenatherum elatius*				W
Carex cuprina				WD	*Carex spicata*				W
Chenopodium album				W	*Veronica chamaedrys*				W
Rumex crispus				W	*Holcus lanatus*				DW
Euphorbia esula	x			S	*Hypericum perforatum*				W
Geranium rotundifolium	x			W	*Prunus serotina*			x	D
Barbarea vulgaris				W	*Rosa canina*		x	x	D
Juncus inflexus				W	*Plantago lanceolata*				W
Artemisia vulgaris				S	*Equisetum arvense*				W
Lolium perenne				W	*Cerastium fontanum ssp. vulgare*				W
					Origanum vulgare				W