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# Regeneration strategies in a temperate hardwood floodplain forest of the Upper Rhine: sexual versus vegetative reproduction of woody species

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## Abstract

The regeneration mechanisms of woody species in the hardwood floodplain forest of the Upper Rhine are not well known, although they are of primary importance for future forest development. To gain a better understanding of the balance between sexual and asexual regeneration strategies and to assess the role of the seed bank in regeneration, the similarities in species composition and abundance of four fundamental compartments involved in regeneration (the seed rain, the seed bank, the recruits and the canopy) were compared in three hardwood forest stands with different flooding conditions. The results show that the floristic composition of the recruits is very similar to that of the canopy, whereas the composition of the seed bank is very dissimilar to the latter and comprises very few hardwood species. However, some species such as *Fraxinus excelsior*, *Carpinus betulus* and *Acer pseudoplatanus* which are very rare in the seed bank release a high number of diaspores, and seedlings of these species germinate abundantly in the field in the year following seed release. Moreover, the germinating seeds originate from the litter layer and not from the soil itself. This shows that most woody species regenerating by seed in the hardwood Rhine forest build transient seed banks and that the role of persistent seed banks for regeneration is very limited. Furthermore, it appears that many woody species have developed strategies favouring vegetative propagation for their regeneration, particularly understorey species, such as *Cornus sanguinea* and *Prunus padus*. As vegetatively grown individuals better withstand prolonged inundation in their early life stages than seedlings, species relying on vegetative regeneration strategies might be advantaged by regular and prolonged flooding of the Rhine forest over species regenerating only by seeds.

*Keywords:* Regeneration; Flooding; Similarity; Floristic composition; Seed rain; Seed bank

## 1. Introduction

Forest regeneration mechanisms are often considered primarily from the point of view of sexual reproduction, i.e. regeneration by seeds of surroundings trees or seeds being present in the soil, while little attention is given to vegetative reproduction processes (Barik et al., 1996; Harmer et al., 1997; Guariguata and Pinard, 1998; Matic et al., 1999). However, as pointed out by Grubb (1977) very diverse mechanisms are involved in regeneration, the relative importance of both seed and vegetative organs varying according

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to the community concerned. Main characteristics of seed-based reproduction include potential long-distance dispersal, delayed germination from a persistent seed bank and genetic adaptation to new ecological conditions (Krebs, 1994; Raven et al., 2000). On germination, seedlings are vulnerable to high predation, require appropriate conditions for establishment and are very sensitive to environmental stress. In their early life stages, seedlings exclusively rely on limited seed reserves. By contrast, vegetatively grown trees show a better resistance to stress in their first years as they develop with a continuous supply of resources from the parent plant (Watkinson, 1997) and can easier re-sprout when damaged. However, their dispersal is limited by the physical extension of the roots and branches of the parent plant (Ozenda, 2000). Reproduction strategies are therefore of major concern regarding the spreading and demography of plant communities, especially under conditions in which strong ecological constraints such as flooding exist. Do these differences result in plants developing strategies to allow their establishment and their growth despite strongly limiting conditions?

In the hardwood floodplain forest of the Upper Rhine (northeastern France), the interruption of flooding for several decades has led to a progressive change of the floristic composition and structure of the forest. Replacement of alluvial trees by flood-intolerant species has been shown in mature communities (Trémolières et al., 1998) and in regeneration units (Deiller et al., 2001). In recent years, interest in the protection and restoration of the Rhine hardwood forest has strongly increased, leading to several large-scale restoration projects. The most spectacular of these aims at the re-flooding of former alluvial forests stands. Although the dynamics and structure of the Rhine forest have been widely documented (Carbiener, 1970; Schnitzler, 1994a,b), little is known about its regeneration mechanisms, the balance between sexual and vegetative reproduction of understorey and overstorey trees and the role of seed bank in regeneration. However, these issues are of crucial importance to restoration projects, as the responses of young trees to re-flooding may will vary according to their regeneration strategies. A better understanding of the regeneration mechanisms of these species is needed to provide effective support for conservation and restoration projects.

The aim of this paper is to assess the relative importance of sexual and vegetative reproduction and to explore the potential role of seed banks in maintaining or restoring woody floristic composition of hardwood forest in the Rhine floodplain. The species composition of four so-called “compartments” involved into the regeneration phase of hardwood forests are compared by quantifying the similarities differences between the seed rain, the seed bank, the recruits and the canopy of three forest stands with different hydrological status. The regeneration strategies that affect a plants’ ability to adapt to flooding are discussed.

## 2. Study sites

The study area (Fig. 1) is situated on the French border of the Upper Rhine, in the Alsace floodplain forest, northeastern France (48°05′–48°35′N, 7°30′–7°46′E), at ca. 140–150 m a.s.l. The climate of the Rhine rift valley is continental with oceanic influence, the mean annual temperature is 10 °C (mean minimum 5.6 °C, mean maximum 14.4 °C), and the annual rainfall ranges from 500 to 600 mm. The soils of the Rhine forest are very calcareous, silty or silty clayey at surface and coarser (sand and gravel) in the deeper layers (Jeanmaire, 2000).

The Rhine hardwood floodplain forest in the Alsace, which is considered as one of the most rich and diverse woody ecosystem of West Europe (Carbiener, 1970), belongs to the *Querco-Ulmetum minoris* association (Issler, 1924) and includes *Quercus robur* (pedunculate oak), *Fraxinus excelsior* (ash), *Ulmus laevis* (European white elm) and *U. minor* (smooth-leaved elm), *Populus alba* (white poplar) in the overstorey, *Prunus padus* (bird cherry), *Cornus sanguinea* (dogwood), *Corylus avellana* (hazel), *Sambucus nigra* (elder) and *Crataegus monogyna* (hawthorn) in the understorey. It also typically comprises two liana species, *Clematis vitalba* (old man’s beard) and *Hedera helix* (ivy), which can reach up to the canopy. From the middle of the 19th century until the 1970s, the Upper Rhine floodplain ecosystem has suffered considerably from three successive hydraulic management stages, which were aimed at protecting the riverine population from floods, allowing shipping all-year long and producing hydroelectricity. As a consequence, the major part of the

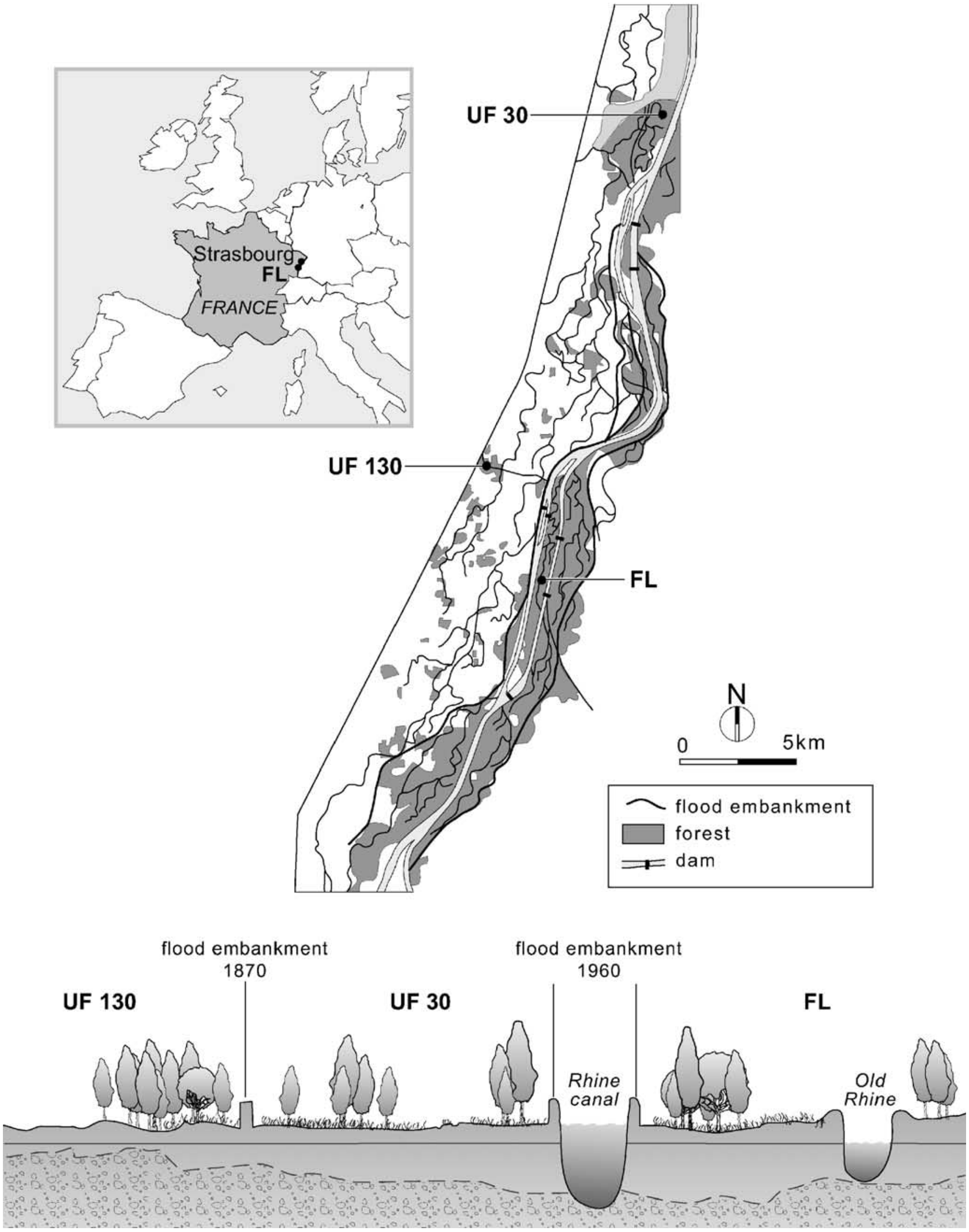

Fig. 1. Sites location.

Rhine forest in the Alsace has been lost to agricultural and urban land use, or is now disconnected from the river. Consequently the forest area that can still be flooded is less than 400 ha, down from 17 000 ha prior to the management interventions. Thanks to a growing interest in restoration of functional zones, re-flooding of a hardwood forest stand will occur in 2002. This project, the "Erstein polder", will combine retention of flood water during peak discharge, with so-called "ecological" flooding of a formerly alluvial forest.

Table 1
Main characteristics of the three study sites

| | FL | UF 30 | UF 130 |
|---|---|---|---|
| Site name | Nature Reserve of the Rhinau Island | Nature Reserve of Erstein | Dachsenkopf forest |
| Flooding status | Floodable, 2 days per year on average, against 15 days per year before management works | Non-flooded for 30 years | Non-flooded for 130 years |
| Current protection measures and forestry practices | Nature Reserve (311 ha) since 1991. No logging | Nature Reserve (180 ha) since 1989. No logging | Logging (high forest system) |
| Planned restoration measures | Increase of the number of flooding days. Increase of flood discharge | Re-flooding 600 ha of forest, starting in 2002 | – |

For this study, three hardwood forest stands were selected in 1997 in the braided and anastomosed geomorphological sector of the Upper Rhine, between 20 and 40 km south of Strasbourg. Flooding conditions and hydrological history differ between these sites following hydraulic management of the Upper Rhine since the 19th century (Table 1). Regular flooding still occurs in one of the sites (FL), while it has been suppressed in the second site (UF 30) for 30 years, and for 130 years in the third site (UF 130). FL is one of the most natural remnants of the Rhine hardwood forest and has been the subject of ecological and hydrological studies for several years (Trémolières et al., 1991, 1998; Sánchez-Pérez et al., 1993). The three forest stands are characterised by a closed canopy with some small gaps.

## 3. Materials and methods

### 3.1. Field sampling

In the three study sites, four so-called "compartments" relevant for forest regeneration were monitored from 1997 to 2000, but varied depending on the compartment for the seed rain (SR), the seed bank (SB), the recruits (RE) and the extent of the canopy (CA). The "compartments" represent spatial–temporal steps in the regeneration process. A similar data sampling was applied to the three sites: in each forest stand, seven circular plots (20 m in diameter) were randomly established within a 100 m × 500 m rectangle. Ten microsites were randomly selected within each of these circles, yielding a total of 70 microsites per site, i.e. 210 sampling points for the three stands (Deiller et al., 2001).

### 3.2. Seed rain

The seed rain was monitored at 2-week intervals from 1997 to 1999 during periods of seed dispersal, in seed traps made of shallow plastic dishes (7 cm in depth, 17 cm in diameter, 227 $cm^2$) covered by a thin-meshed net. Each site contained 35 seed traps equally distributed through the seven circles. The traps were placed 1 m above ground to avoid predation by rodents and to keep them above the inundations at the flooded site. No protection was used against seed predation by birds, since possible loss caused by protection was considered to be greater than that by birds. Counting and identifying the seeds was usually done in the field, but samples were sometimes brought to the laboratory to complete the identification.

### 3.3. Seed bank

One soil core was taken annually within each microsite with a gauge (5.5 cm in diameter, 14 cm in depth, 333 $cm^3$), yielding a total of 70 samples per site and 210 samples for the three sites. Sampling was carried out at the start of the field campaign (summer 1997) and repeated in the springtime of 1998 and 1999, before the germination of most plants occurred. In the laboratory, the soil cores were hand-crumbled and all vegetative parts, stones and coarse debris were removed. The samples were mixed together by groups of five and spread on a thin layer (1 cm) in polystyrene trays (ca. 20 cm × 35 cm), above a 1 cm thick layer of fine sand. The germination experiment was conducted in the greenhouse. The woody seedlings were identified, counted and eliminated from the trays at intervals depending on germination rates. At the end of the first growing season, the samples were cold-stratified during the winter to encourage germination of species requiring vernalization, and germination was followed for one more year.

### *3.4. Recruits*

In summer 1998 and spring 1999, an inventory of the recruits was carried out within 1 $m^2$ plots located at each microsite, yielding a total of 210 quadrats for the three sites. All the woody individuals <1.5 m tall were identified and counted. No distinction was made between sexual and vegetative origin of the recruits, unless the seedlings' cotyledons were clearly identifiable.

### *3.5. Canopy*

A census of the adult trees situated within a distance of 15 m from the centre of each circle was carried out in 2000 (Cassifour, 2000) to establish the presence of potential sources of vegetative spread and potential seed sources. All woody individuals, including woody lianas, with a dbh (diameter at breast height) exceeding 5 cm were identified and mapped.

### *3.6. Data analysis*

Data were analysed to assess the total species richness per compartment and per site. For each compartment, the mean number of individuals per year and per unit area ($m^2$) was calculated. A computer program was written to compute the similarity indices from the distribution data and to calculate the observed species richness of all compartments. Two similarity indices were used for the analysis: the similarity index of Sørensen (Sørensen, 1948), based on presence–absence data, i.e. the floristic composition of the samples, and the cosine similarity index (or Ochiai coefficient) based on species abundance. The Sørensen index, also known as community coefficient (CC) is widely used in ecology to compare the ratio of the number of species shared by two sites (or compartments) to the number of species belonging to only one of these sites and is given by

$$\mathrm{CC} = \frac{2c}{A + B}$$

where $c$ is the number of species shared by the two sites, $A$ and $B$ are the total numbers of species for each site. A value of $\mathrm{CC} = 1$ indicates a perfect similarity between the two samples (all species found in the two sites) whereas $\mathrm{CC} = 0$ means that no species are shared.

The cosine similarity index (cos) is a quantitative index which is moderately sensitive to species richness and dominant species, but is not affected by the sample total. This is in contrast to other quantitative indices, such as the *Euclidean distance and squared Euclidean distance* indices (Jongman et al., 1995), which are heavily influenced by one dominant species.

The cosine index is given by

$$\cos = \sum_k y_{ki} y_{kj} \sqrt{\sum_k y_{ki}^2 \sum_k y_{kj}^2}$$

where $y_{ki}$ is the abundance of the $k$th species in sample $i$ and $y_{kj}$ the abundance of the $k$th species in sample $j$.

The similarity matrices resulting from the calculations were interpreted graphically using a hierarchical clustering method: dendrograms were produced in which the similarity between two compartments is inversely related to the distance between these compartments. Therefore, the higher the similarity the shorter the horizontal distance ($d$) between the compartments on the dendrogram. The graphical representation was based on the Euclidean distance and the distances between clusters were calculated using the average linkage method (SPSS, 1998).

## 4. Results

### *4.1. Species richness and floristic composition*

A total of 29 woody taxa was found over all compartments and sites, 25 of which were identified to species, two to genus and one to family (Table 2). One woody species that occurred in the seed bank remained unidentified. All 29 taxa were present in UF 130, whereas the observed species richness did not exceed 20 in both FL and UF 30 (Fig. 2). The mean species richness per compartment was highest in the recruits compartment (13.7 species per site on average) and lowest in the seed bank (6.7 species per site). The canopy and the seed rain compartments came close to the number of species found in the recruits

Table 2
Mean number of individuals per year and per m$^2$ by compartment and by site, over the period of measurements given in the methods section[a]

| Species | FL | | | | UF 30 | | | | UF 130 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SR | SB | RE | CA | SR | SB | RE | CA | SR | SB | RE | CA |
| *A. campestre* | – | – | 0.02 | 0.0004 | 27.27 | – | 0.72 | 0.0042 | – | 21.05 | 0.32 | 0.0012 |
| *A. pseudoplatanus* | 1.26 | – | – | – | 1.26 | – | 0.03 | 0.0002 | 52.87 | – | 11.92 | 0.0020 |
| *Alnus glutinosa* | 1.26 | – | – | – | 0.42 | – | – | – | 8.81 | – | – | – |
| *A. incana* | – | – | – | – | – | – | – | – | – | – | – | 0.0016 |
| *B. vulgaris* | – | – | – | – | – | – | – | – | – | – | 0.02 | – |
| *Betula* sp. | 96.92 | – | – | – | 20.98 | – | – | – | 196.37 | – | – | – |
| *C. betulus* | 0.42 | – | – | – | – | – | – | – | 460.71 | – | 5.81 | 0.0101 |
| *C. sanguinea* | 3.36 | – | 0.49 | – | 3.78 | 4.01 | 0.51 | 0.0014 | 1.89 | 6.01 | 0.42 | – |
| *C. avellana* | 1.26 | – | – | 0.0016 | 4.20 | – | 0.08 | 0.0071 | 8.18 | – | 0.06 | 0.0323 |
| *C. monogyna* | 2.52 | – | 0.03 | 0.0026 | 2.94 | – | 0.16 | 0.0053 | – | – | 1.67 | 0.0053 |
| *Euonymus europaeus* | – | – | 0.20 | 0.0008 | – | – | 0.29 | – | – | – | 0.38 | 0.0002 |
| *F. excelsior* | 821.13 | 4.01 | 2.54 | 0.0323 | 355.39 | 8.02 | 5.34 | 0.0220 | 334.20 | – | 11.22 | 0.0123 |
| *J. regia* | – | – | – | – | – | – | – | – | – | – | – | 0.0002 |
| *L. vulgare* | – | – | – | – | – | – | 0.01 | – | – | – | 1.09 | – |
| *Lonicera xylosteum* | – | – | 0.05 | – | – | – | 0.01 | – | – | – | 0.29 | – |
| *P. alba* | 0.42 | 6.01 | 0.11 | 0.0038 | 0.42 | 18.04 | – | – | 6.92 | 3.01 | 0.06 | 0.0008 |
| *P. nigra* | – | – | – | – | – | – | – | – | – | – | – | 0.0002 |
| *P. avium* | – | – | – | – | – | – | – | – | – | – | – | 0.0004 |
| *P. padus* | – | – | 0.35 | 0.0226 | 8.8 | – | 0.26 | 0.0073 | – | – | 0.32 | 0.0006 |
| *Prunus spinosa* | – | – | 0.04 | 0.0002 | – | – | – | – | – | – | 0.16 | – |
| *Q. robur* | – | – | – | 0.0004 | 5.04 | – | 0.01 | 0.0049 | 8.18 | – | 0.06 | 0.0006 |
| *Salicaceae* | – | – | – | – | 2.52 | – | – | – | 6.92 | – | – | – |
| *S. caprea* | – | 16.03 | – | – | – | 54.12 | – | – | – | 9.02 | – | – |
| *Salix* sp. | – | 44.09 | – | – | 0.84 | 52.11 | – | – | 15.73 | 99.21 | – | – |
| *S. nigra* | 101.96 | 12.03 | 0.69 | 0.0036 | 91.05 | 10.02 | 0.57 | 0.0026 | – | 9.02 | – | – |
| *U. laevis* | 64.20 | – | 0.12 | 0.0065 | 1.26 | – | 0.01 | 0.0006 | 36.50 | – | – | 0.0008 |
| *V. lantana* | – | – | – | – | – | – | – | – | – | – | 0.01 | – |
| *Viburnum opulus* | – | – | – | – | – | – | – | – | – | – | 0.02 | – |
| *Sp.*1 | – | 54.12 | – | – | – | 60.13 | – | – | – | 93.20 | – | – |

[a] "*Salicaceae*" stands for undistinguished diaspores of both *Populus* and *Salix* genera.

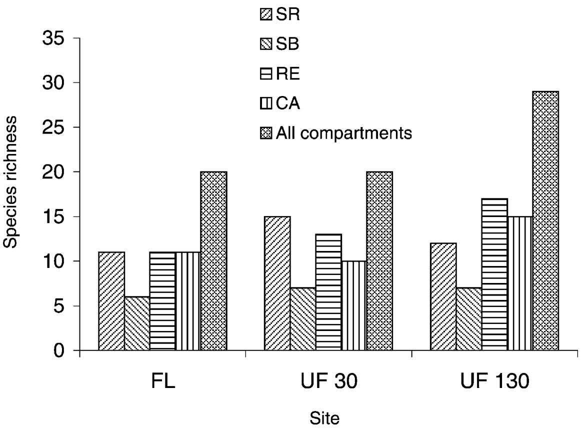

Fig. 2. Species richness by compartment and by site.

compartment with 12 and 12.7 species, respectively. In addition to the trees species listed in Table 2, *C. vitalba* and *H. helix*, two woody lianas typical of the Rhine floodplain forest were found in all three sites and compartments. However, these species were not included in the similarity indices calculations because the local abundance of seedlings of *H. helix* would have dominated the results of the cosine index calculations.

None of the woody species listed in Table 2 occurred within all compartments and sites, but three species were found in nine or more compartments: the dominant canopy species was *F. excelsior*, which occurred in all compartments and all sites except in the seed bank of UF 130, *P. alba*, which was only absent from the recruits and the canopy of UF 30 and *S. nigra* which was present in all compartments of FL and UF 30 but occurred only in the seed bank of UF 130. In contrast, the species *Alnus incana*, *Berberis vulgaris*, *Juglans regia*, *Populus nigra*, *Prunus avium*, *Viburnum lantana* and *V. opulus* occurred only once, either in the recruits or the canopy compartment. Two species which were found only in the seed bank may result from contamination of the culture trays during the seed germination experiment: firstly the pioneer tree *Salix caprea*, which germinated several months after sample collection, although the viability of *Salix* sp. seeds is known not to exceed a few weeks after dispersal, and secondly, the unidentified woody species *Sp.* 1, which germinated during the seed bank experiment, although is not known as a species of Rhine floodplain forest.

Most of the diaspores found in the seed rain were provided with wind-dispersal mechanisms, such as key fruits (*Carpinus betulus* and *C. vitalba*), samaras (*Acer pseudoplatanus*, *A. campestre*, *F. excelsior*, *Betula* sp., *U. laevis*) and capsules (*Populus* sp.).

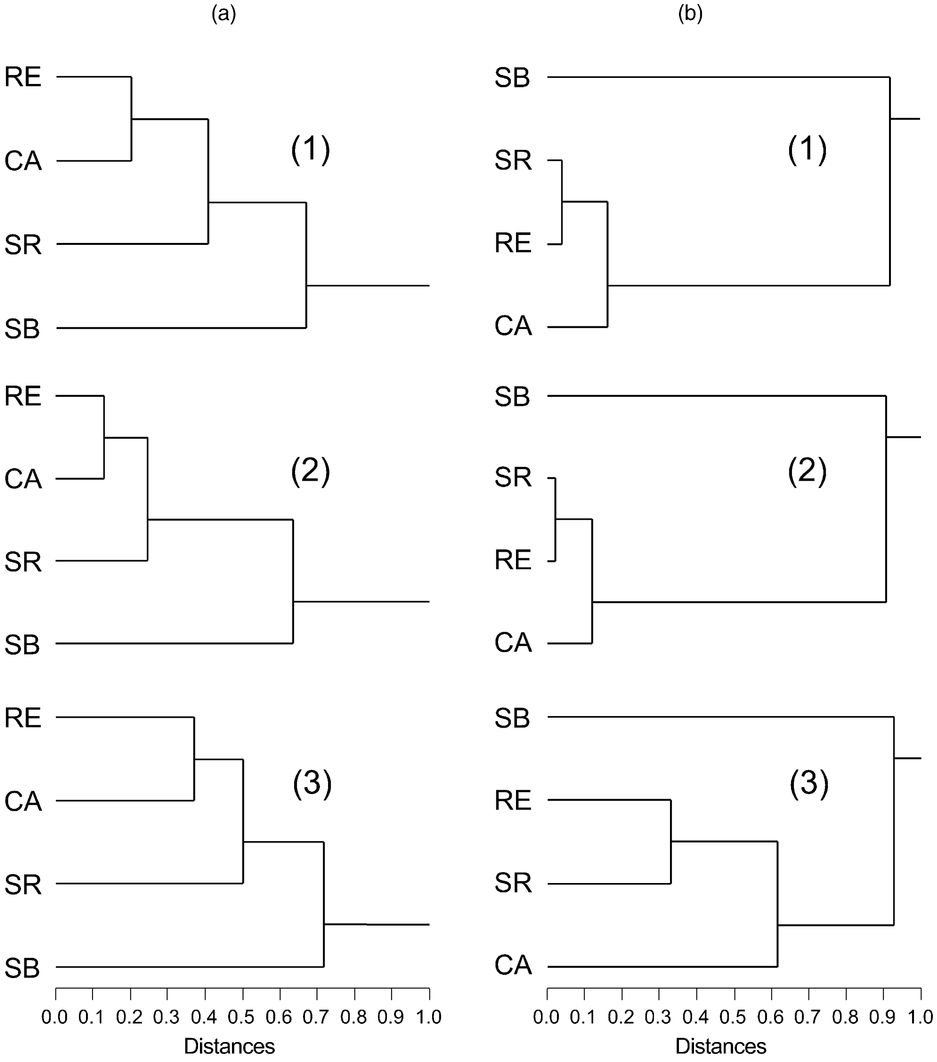

Fig. 3. Dendrograms showing similarities between SR, SB, RE and CA in FL (1), UF 30 (2) and UF 130 (3). The similarities are based on the Sørensen (a) and the cosine indices (b).

Avian-dispersed fruits were also locally collected in abundance, such as *S. nigra* and *H. helix*. In most cases, the exocarp of these fruits was removed, indicating ingestion by birds prior to deposition in the seed-traps. Two species, *A. glutinosa* and *Betula* sp. occurred only in the seed rain of the three sites.

### 4.2. Similarity between compartments

The clustering patterns found with the Sørensen and cosine indices were remarkably similar within the three forests stands (Fig. 3). With the Sørensen index (Fig. 3a) the greatest similarity was always found between the recruits and the canopy, the seed rain clustering next with the two former compartments, and the seed bank being strongly dissimilar from those compartments. Amongst the three sites, the highest similarity between floristic composition of the recruits and the canopy was found in UF 30 ($CC = 0.87$, $d = 0.13$), followed by FL ($CC = 0.80$, $d = 0.20$) and UF 130 ($CC = 0.63$, $d = 0.37$). The floristic composition similarity between the seed rain and the cluster “recruits–canopy” was highest in UF 30 ($d = 0.11$) and UF 130 ($d = 0.13$) and lowest in FL ($d = 0.20$). The dissimilarity of the seed bank with the other compartments was highest in UF 30 ($d = 0.39$) and lower in the two other sites ($d = 0.26$ and 0.22 in FL and in UF 130, respectively). Finally, the overall similarity between all compartments, i.e. the similarity between the first and the last compartment clustered, was clearly higher in UF 130 ($d = 0.35$) compared to FL and UF 30 ($d = 0.47$ and 0.50, respectively).

The cosine index yielded maximum similarity between the seed rain and the recruits for the three sites, the former then clustering with the canopy (Fig. 3b). As observed with the Sørensen index, the seed bank was very dissimilar from the three other compartments. The overall shape of the cosine index dendrograms was very similar in FL and UF 30 compared to UF 130, as the similarity between recruits and seed rain was extremely high in UF 30 ($\cos = 0.98$, $d = 0.02$) and FL ($\cos = 0.96$, $d = 0.04$) but lower in UF 130 ($\cos = 0.67$, $d = 0.33$). This pattern also applied to the similarity of the canopy with the two former compartments: in UF 30 and FL the distance between the cluster recruits–seed rain and the canopy was 0.10 and 0.12, respectively, and reached 0.28 in UF 130. As a consequence, the overall similarity between all compartments was low in FL and UF 30 ($d = 0.88$ and 0.89, respectively) compared to UF 130 ($d = 0.60$).

## 5. Discussion

### 5.1. Regeneration strategies

#### 5.1.1. Sexual reproduction

One of the most striking patterns revealed by the similarity indices is the great dissimilarity of the seed bank to any other compartment, whatever the site and the similarity index. Most species present in either the canopy, recruits or seed rain compartment were absent from the seed bank, both qualitatively (Sørensen index) and quantitatively (cosine index). The fact that no seeds were stored in the soil indicates that most of the hardwood species of the Rhine forest are not able to build a persistent seed bank. However, some seeds were found in the fresh soil litter and numerous seedlings were observed in the field, which suggests that most of their sexual reproduction is achieved through transient seed banks, i.e. seeds that persist in the soil for less than 1 year, according to the definition of Thompson et al. (1997). This view is supported by seed bank longevity studies, which have shown that many woody species present in the study sites build transient seed banks, e.g. *F. excelsior*, *Acer campestre*, *A. pseudoplatanus*, *C. betulus*, *C. sanguinea*, *C. avellana*, *C. monogyna*, *Ligustrum vulgare* and *Q. robur* (Thompson et al., 1997). According to Brown and Oosterhuis (1981), this is due to the fact that shade-tolerant species did not need to develop seed dormancy mechanisms, thanks to their ability to survive under closed vegetation.

Releasing large amounts of seeds seems to increase the chance of regenerating, as indicated by the high similarity between the seed rain and the recruits for the cosine index. This mainly applies to *F. excelsior*, which yielded by far the largest number of seeds over the 3 years of seed rain monitoring (43% of the total seed number in the three sites and 70% of FL), and to *C. betulus*, which dominated the seed rain, canopy and RE compartments of UF 130. Great interannual differences in the timing of seed dispersal were observed for both species, the seeds being released either in the fall for most of them, or progressively until the next springtime. Gradual seed release may increase regeneration chance by allowing vernalization of the fruits that have reached physical ripeness, while protecting them against predation by rodents and small animals in the winter when food resources are scarce. Germination can then occur in the following springtime shortly after seed release (Osumi and Sakurai, 1997).

### 5.1.2. Vegetative reproduction

The highest similarity was found between the REs and the CA for the Sørensen index, and between the REs and the SR for the cosine index, whereas the SB compartment was very dissimilar from any other compartment in both cases. For the Sørensen index, this indicates that the CA and the REs contain the same species but that these species are absent from the SB, which suggests that they rely on vegetative mechanisms for their regeneration. These results are supported by field observations, as various strategies of vegetative spread were met, such as aerial layering (*P. padus*, *Ligustrum vulgare*), production of root-suckers (*C. sanguinea*, *U. laevis*, *P. alba*), and by the literature (Table 3). Comparable lack of similarity between SB and above-ground vegetation has been previously reported for a wide range of environments including woodlands (Drake, 1998), wet meadows (Jensen, 1998) and grasslands (Peco et al., 1998; Perez et al., 1998), and stress the importance of vegetative strategies in regeneration of plant communities.

Table 3
Known vegetative regeneration strategies of the main woody species of the Rhine hardwood forest and dispersal agents (Rameau et al., 1989; Siebel, 1998)

| Species | Vegetative reproduction | Pollination | Dispersal |
|---|---|---|---|
| *Alnus glutinosa* | Shoots | Wind | Wind |
| *C. betulus* | Abundant shoots | Wind | Wind |
| *C. vitalba* | Shoots, twining stems | Insects | Wind |
| *C. sanguinea* | Shoots, layering, root-suckers | Wind | Birds |
| *C. avellana* | Shoots, root-suckers | Wind | Mammals |
| *C. monogyna* | Shoots | Insects | Birds |
| *Euonymus europaeus* | Shoots | Insects | – |
| *F. excelsior* | Shoots | Wind | Wind |
| *H. helix* | Adventitious roots | Insects | Birds |
| *P. alba* | Shoots, root-suckers, cuttings | Wind | Wind |
| *P. padus* | Shoots, root-suckers, layering | Insects | Birds |
| *Prunus spinosa* | Abundant root-suckers | Insects | Birds |
| *Q. robur* | Shoots | Insects | Mammals, birds |
| *U. laevis* | Shoots, root-suckers | Insects | Wind, water |

### 5.2. Sexual versus vegetative strategies in an alluvial environment

Environmentally restrictive conditions such as flooding, fire or drought limit the establishment and growth of plants to those who are able to develop strategies ensuring successful regeneration in spite of the constraint. The consequences of flooding are particularly dramatic for seedlings because their sensitivity to prolonged anoxic conditions is very high (Siebel and Blom, 1998), while individuals relying on vegetative regeneration mechanisms generally resist better to submersion (Barsoum and Hugues, 1998; Johnson, 2000).

In the Upper Rhine forest, the germination of most tree seeds occurs in March–April while the maximal Rhine discharge is reached between May and July, following snowmelt in the Swiss Alps. Hence, prolonged flooding in the year of germination may be fatal to seedlings while shoots may show higher survival rates. Consequently, long-lasting annual flooding could favour the species that rely on asexual regeneration mechanisms. However, seedlings can escape flooding by postponing seed release until the end of the inundation, like elm species (*Ulmus minor*, *U. laevis*) whose seeds are released in the beginning of the summer. In this case, springtime flooding might even favour germination by eliminating competitive herbaceous species. Therefore, timing of seed release and germination, i.e. flowering and fruiting phenology, versus period, duration and level of flooding seems to be critical for sexual regeneration of woody species in floodplains.

## 6. Conclusion

This study shows that vegetative mechanisms dominate the regeneration of woody species in the alluvial hardwood forest of the Upper Rhine. Sexual regeneration is limited to a small number of species, which are able to release a large number of seeds to increase their germination chance (i.e. *F. excelsior* and *C. betulus*). Germination occurs generally in the year following seed dispersal, thus relying on transient seed banks. Only very few seeds of woody species were found in the soil, which indicates the absence of persistent seed banks. Survival of seedlings during the first years is strongly linked to height and duration of flooding. Contrarily, species reproducing vegetatively are less sensitive to submersion and can produce new shoots within a short time. These considerations should not be overlooked in restoration projects of flooding areas, as regular long flooding during the growing season might favour species relying on vegetative mechanisms for their regeneration.

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