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# Impact of river management history on the community structure, species composition and nutrient status in the Rhine alluvial hardwood forest

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## Abstract

The present-day Rhine alluvial hardwood forest (*Querco-Ulmetum minoris*, Issler 24) in the upper Rhine valley (France/Germany) is comprised of three vegetation units, one still flooded by calm waters (F) and the two others unflooded, one for 30 years (UF30) (after the river canalisation) and the other for about 130 years (UF130) (after river straightening and embankment work in the middle nineteenth century). In the three stands, species composition, structure and diversity of vegetation and nutrient content of mature leaf, leaf litter and soil have been studied. Fungi (*Macromycetae*) were only studied in two stands (F and UF130). The intensity of nutrient recycling was exemplified by comparing the chemical composition of rainwater, flood, throughfall, mature leaf, leaf litter, soil and groundwater in two of these stands (F and UF30).

The elimination of floods has caused a change in floristic composition, tree density and plant diversity. Tree density was higher in the two unflooded stands and was related to a large increase in sapling (< 6 cm dbh) density more than to a change of stem (> 6 cm dbh) density. Sapling density increased 2 times and three times in the UF30 and the UF130 respectively, whereas the stem density increased only 12% in the first stand and decreased 29% in the second one. The saprophytic macromycete communities have been supplemented with mycorrhizal species. Leaf litter production was slightly greater in the flooded (4.44 T ha$^{-1}$ yr$^{-1}$) than in the two unflooded stands ($\leq$ 3.72 T ha$^{-1}$ yr$^{-1}$). Foliar N level is twice as high in the flooded stands in spite of an opposite soil status. P level decreased in soil and leaves with the duration of isolation and was at the same level in the groundwater in two stands (F and UF30). K, Mg and Ca contents of green leaf and leaf litter were high due to the geochemistry of the Rhine substrate (calcareous gravels and pebbles) and similar in all the stands studied, even though there are large inputs of these three elements by floods. Moreover we showed that the groundwater chemistry reflected the variations of nutrient inputs and thus could be a good indicator of the functioning of an alluvial ecosystem and of its change as a result of human activities. The restoration of floods in hardwood forest contributes to the preservation of alluvial vegetational structure and composition, the stimulation of biological processes and a better plant mineral nutrition and water supply.

## Introduction

General features of alluvial hardwood communities such as structural complexity, species richness, primary productivity are linked to floods. The literature is unanimous on the relationships between hydrology (flooding duration and frequency, annual groundwater level fluctuations) and ecosystem functioning (groundwater chemistry, biogeochemical cycle, productivity, species richness and diversity) (e.g., Carbiener 1970; Johnson et al. 1976; Robertson et al. 1978; Whittaker et al. 1979; Mitsch et al. 1979; Klinge et al. 1983; Mitsch & Rust 1984; Carbiener 1984; Klimo 1985; Grubb 1987; Décamps et al. 1988; Adams 1989; Mitsch et

al. 1991; Sánchez-Pérez et al. 1991a; Sánchez Pérez & Trémolières 1997). Elimination of floods as a result of river management therefore modifies the forest ecosystem functioning (Pautou & Girel 1994). Examples of negative effects such as decrease of biomass, lower landscape diversity have been developed in studies in the Missouri and other river floodplains (Johnson et al. 1976; Lugo et al. 1990). The relationships between hydrological and vegetation characteristics have been quantified in some interesting models in order to predict changes in floodplain forest characteristics following dam construction and forestry (Phipps 1979; Brody & Pendelton, 1987); however it still remains difficult to make such predictions as shown by Pautou et al. (1992). The estimation of these changes, given the modifications in hydrological and nutritional conditions, are important for conservation and restoration of these complex forest systems, which have the highest species richness and productivity, and the most complex horizontal and vertical structure of the temperate forest ecosystems (e.g., Carbiener 1970, 1984; Walter 1979; Hügins 1981; Bravard et al. 1986; Trémolières et al. 1988; Schnitzler et al. 1991, 1992; Schnitzler & Carbiener 1991; Schnitzler 1994).

The objective of our study was to determine the impact of the elimination of floods on the hardwood alluvial forest by comparing the species composition, structure and diversity of vegetation and fungi, soil and foliar nutrient levels and leaf litter production in three forested wetlands of the Rhine valley, one still subjected to periodic flooding and high groundwater oscillations (2–3 m), the two others deprived of flooding, the one as a result of straightening and embankment works in 1870 and the other by canalisation about 30 years ago. Consequently both of the latter areas have low groundwater oscillations (0.6 m). Additional data regarding external inputs by rainfall, throughfall and outputs by groundwater in the flooded forest were compared with those found in the forest unflooded for 30 years. We shall use different methodologies (Table 1), which consist in a synthesis of different studies carried out between 1980–1995 in the Rhine rift valley (Carbiener 1981; Carbiener & Schnitzler 1990; Carbiener et al. 1975; Sánchez-Pérez et al. 1991a, b, 1993; Sánchez-Pérez & Trémolières 1997; Schnitzler 1988, 1994; Weiss et al. 1991), for predicting change in the functioning of the ecosystem after the elimination of floods. It will be interesting also to observe the rapidity of change in order to be able to make proposals for the management and/or restoration of these unflooded areas.

## Study area description

The studies were carried out in the Upper Rhine valley, on the French side of the river (48°05′–48°35′ N, 7°30′–7°46′ E).

*Historical account of the vegetation in this area before and during the river management*
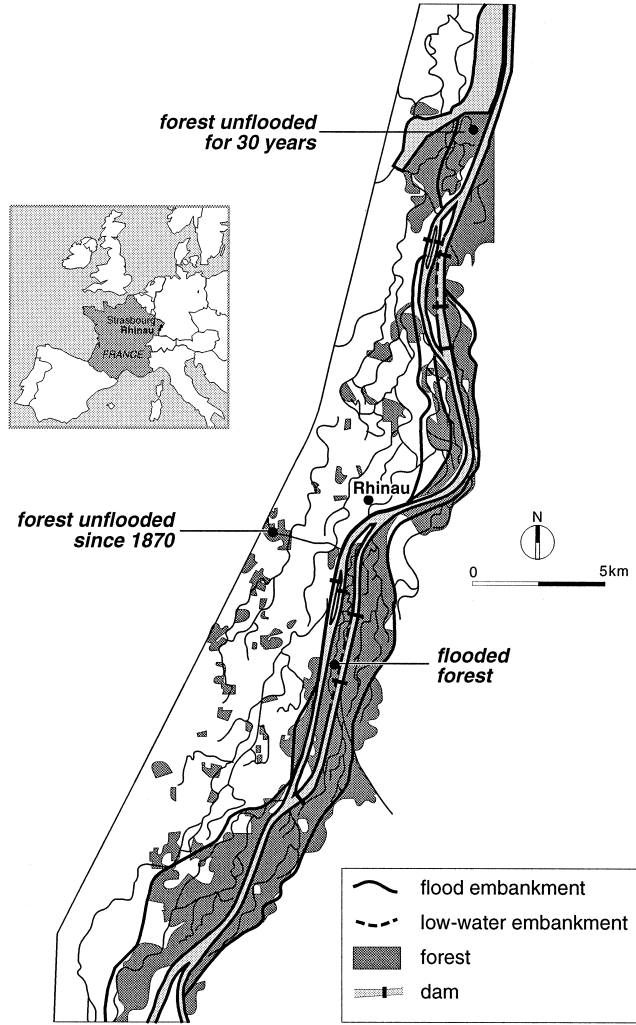
Before river straightening at the beginning of the 19th century, the annual highwater bed of the Rhine was 2–3 km wide. This area was characterized by a large number of migrational braided and anastomosed arms (Carbiener 1970, 1984). Primeval Rhine forests covered a large surface on both banks of the river, with variable proportion of softwoods and hardwoods (Schnitzler 1994). In fact this flooded area was characterized by the development of a successionnal vegetation type depending on the dynamics of river flood. Herbaceous communities were located on sites well exposed to flood, and pioneer and mature stages of ligneous communities on sites less exposed to flood. The distribution of pioneer and mature stages could vary on the banks of the river, a post-pioneer stage then a mature stage occurring after a pioneer forest if there is no catastrophic flood. The original alluvial forest was preserved due to low forestry logging.

Natural extension of Rhine floods and consequently the natural evolution of the alluvial forest was stopped by various large scale hydraulic works. Since river straightening in 1850, the hardwood community (*Querco-Ulmetum minoris*, Issler 24) has been disappearing at an alarming rate as a result of logging and river management. The major forested surface has not been flooded, except within dykes 2 to 3 km apart. Then the canalisation of the Rhine between 1928–1932 and 1950–1970 disconnected the remaining forests from the main channel. The flooded areas are now restricted to four small islands, enclosed between the old Rhine and the canal to the south of Strasbourg (Figure 1) and within the dykes built in 1870 to the north of Iffezheim (north of Strasbourg). Due to the suppression of floods or, if still flooded, to a high reduction of flood dynamics, the vegetation has evolved to a dominance of hardwood forests.

*Physical characteristics*

The annual groundwater oscillations, which reached 2 to 3 m in the flooded areas, decreased after canalisation to 40 to 60 cm outside the dykes. On the islands,

A

forest unflooded
for 30 years

forest unflooded
since 1870

Rhinau

N

0          5km

flooded
forest

⌒  flood embankment
--⋅-⋅  low-water embankment
▓  forest
▓▬  dam

B

West

flood embankment
1870

flood embankment
1960

East

forest unflooded
since 1870

forest unflooded
for 30 years

flooded forest

Rhine
canal

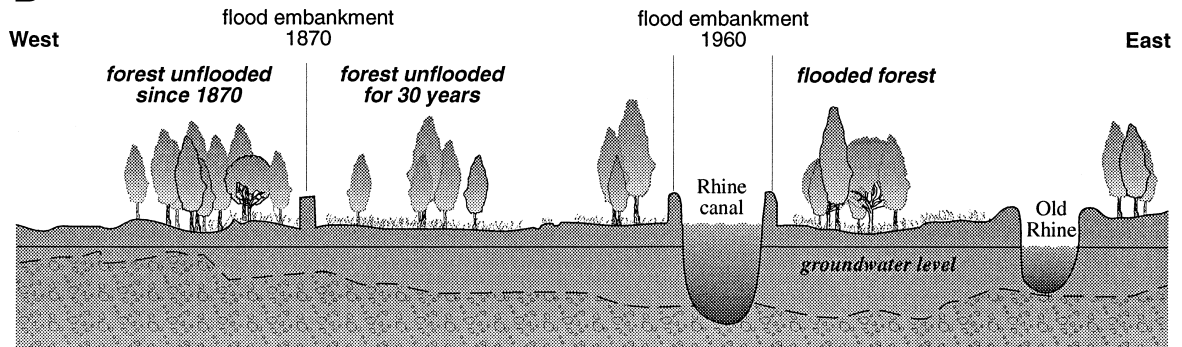Old
Rhine

groundwater level

Figure 1. Location of the study site in the upper Rhine floodplain (Eastern France), A and sectorisation of the three forest stands along a cross section east-west according to the Rhine hydraulic management works, B.

| | Flooded hardwood | Unflooded hardwood for 30 years | Unflooded hardwood for 130 years |
|---|---|---|---|
| Vegetation analysis | | | |
| – floristic composition | ∗ | ∗ | ∗ |
| – diversity | ∗ | ∗ | ∗ |
| – tree density | ∗ | ∗ | ∗ |
| – litter biomass | ∗ | ∗ | ∗ |
| Fungi (Macromycetes) | ∗ | – | ∗ |
| Soil nutrient level | ∗ | ∗ | ∗ |
| Foliar nutrient level | | | |
| – mature leaf | ∗ | ∗ | ∗ |
| – leaf litter | ∗ | ∗ | ∗ |
| Nutrient level | | | |
| – groundwater | ∗ | ∗ | – |
| – rainfall | ∗ | ∗ | – |
| – throughfall | ∗ | ∗ | – |
| – flood | ∗ | ∗ | – |

floods occur when the flow exceeds 2500 m$^3$ s$^{-1}$, generally in summer (June–July). The natural, very active morphogenesis of the Rhine already slowed with the straightening of the main channel 130 years ago and the flowing waters, which essentially carried sand and gravel, have been enriched in silt and clay during this period. The upper horizons are therefore silty or silty clayey, but the lower sediments (1–2 m lower down), laid when the Rhine had a natural course in the valley, are coarse-textured (sand and gravel). The soils are very calcareous (25% total carbonate, pH > 7.5) and young (Fluvent A/C type, USDA). In the study area, the Rhine forest elevation is about 140 m above mean sea level. The annual precipitation for the region ranges from 500 to 600 mm, increasing from south to north. The mean annual temperature is 10 °C (mean min. 5.6 °C and mean max. 14.4 °C).

The global species richness, the forest structure, dynamics and ecology, the definition of the discriminate species are well-known along the whole Rhine axis from a series of monographic papers (Hailer 1965; Kunze 1970; Carbiener 1974, 1984; Krause 1974; Walter 1979; Dister 1980, 1985; Schnitzler 1988; Carbiener et al. 1988).

*Study sites*

We chose three adjacent forested stands in the same alluvial sector (braids and anastomoses) between Rhinau and Erstein (30–50 km south of Strasbourg), with similar ecological conditions, i.e., calcareous substrate, floristic composition (hardwood forests with oak, ash and elm). These forests were originally in early successional stages as a result of natural disturbances without dykes. The flooded area (F) is constituted by three of the four islands and are used as the reference. The unflooded areas extend outside the dykes of 1870 (UF130) and between these dykes and those resulting from canalisation in 1963–1967 (UF30), but form part of the original alluvial forest. For studying nutrient inputs and outputs of the alluvial system, we selected two sites, the Rhinau island still subject to flood and the Erstein forest unflooded for 30 years (Figure 1).

**Methods**

*Vegetation and fungal flora*

Botanical data relating to the Rhine forests were analysed with the phytosociological method of Braun-Blanquet (1964). Nomenclature followed Oberdorfer (1983).

Six transect areas ranging from 1500 to 2000 m$^2$ (which corresponds to the mean surface area of a phytosociological forest survey in the Rhine environment) were chosen in the relatively undisturbed forests

of the *Querco-Ulmetum*, the hardwood forest with the dominant species oak, ash and elm. We selected wet communities of lower levees or old channels because the high, mesic terraces, which were rarely flooded when the Rhine had a natural course, did not show any disturbances in species richness and structure after the elimination of floods. Within each transect, stems (diameter > 6 cm) and sapling (i.e., young trees and shrubs < 6 cm diameter and 1 m high) were counted. Vegetation data were summarized by calculating sapling and stem densities for the three stands. Basal areas (in $m^2$ $ha^{-1}$) were calculated for trees and shrubs. We quantified the woody diversity of the three vegetation units using the Shannon index (Shannon and Weaver 1949) as: $H' = \Sigma p_i \log_2 p_i$ where $i$ is one species and $p_i$ represents its proportion of the community. The equitability index $J'$ (Pielou 1966) is a measure of evenness and is calculated by $J' = H'/\ln S$, where $H'$ is the value as calculated above and $S$ the number of species. As the response measure becomes more evenly distributed among the species, $J'$ approaches 1.

The macromycetes in only two stands, flooded (F) and unflooded for 130 years (UF130) were estimated from regular visits to the two vegetation units between 1980 and 1991. The data probably are an underestimate because of the rapidity of the fructification cycle of many species. Nomenclature follows Moser (1983) and for lignicolous species Breitenbach & Kränzlin (1986).

### Soil nutrients

Twelve soil samples per vegetation unit were taken in the three stands (F, UF30 and UF130). We extracted the upper layer to a depth of 15–20 cm, which comprises the humus zone and mixed 3 samples for the same site. The biogenic elements (N, P, K, Mg and Ca) of the upper layer were analysed. Extractable soil $NO_3^-$ and $NH_4^+$ were determined by extraction with 1N KCl, coupled with colorimetric methods. Available phosphorus was determined by extraction with 0.2 N ammonium oxalate according to the Joret-Hébert method for calcareous soils (Joret & Hébert 1955). Exchangeable cations ($Ca^{2+}$, $Mg^{2+}$, $Na^+$ and $K^+$) were analysed by flame AAS after extraction with 1N ammonium molybdate at pH 7.

### Water chemistry

Groundwater samples were collected in a network of 9 piezometers in the flooded stand and 7 piezometers in the UF30. The 9 piezometers were pumped every month during 16 months between April 1989 and July 1990 and only 4 times (representative of the groundwater in the mature stage of the alluvial forest) between December 1993 and July 1995 for the flooded stand. In the unflooded stand, samples were collected in a network of 7 wells during 20 months (December 1993 to July 1995). The water samples were collected in polyethylene bottles after pumping, filtered in the laboratory and stored in the dark at 4 °C until chemical analyses were performed. Surface water was collected in the Rhine at the same times. More details regarding water sampling methods are given in Sánchez-Pérez (1992).

Samples of throughfall were collected twice a month between May 1994 and July 1996 for F and UF30. Three collectors each of 1 $m^2$ surface were randomly installed in the two stands. The collector was drained and rinsed after each collection.

Concentrations of $N-NO_3^-$, $N-NH_4^+$ and $P-PO_4^{3-}$ were measured by an automated microflux analyzer (Alliance Instruments) according to analytical procedures described in APHA (1985). Analytical detection limits were 5 $\mu g\,l^{-1}$ for each element. $Ca^{2+}$ and $Mg^{2+}$ have been analysed by atomic absorption spectroscopy (Varian), $Na^+$ and $K^+$ by flame emission spectroscopy (Varian).

### Foliar nutrient level in summer and autumn

#### Nutrient status of mature and senescent foliage
Five leaves of 10 individuals of the most common species of the hardwood forest (i.e., *Fraxinus excelsior, Quercus robur, Ulmus minor, Acer campestre, Carpinus betulus, Corylus avellana, Cornus sanguinea, Clematis vitalba, Hedera helix*) were collected at a height 1.5–2 m between 1987 and 1991 in the three forested stands. One set was collected when mature and the other one when senescent (from September to December). N, P, K, Mg and Ca were analysed after drying (24 h at 105 °C) and grinding to a diameter less than 500 $\mu$m. The detailed method is given in Weiss et al. (1991). The results were expressed in kg $ha^{-1}\,yr^{-1}$, on the basis of litter biomass and taking into account the mass loss to estimate the mature leaf content.

#### Biomass of the leaf litter
Ten tubs (1 $m^2$ per tub) were randomly installed in the hardwood forest within and outside the dykes from September to early December between 1987 and 1990. Litter was harvested every week during the period of

litterfall and dried at the temperature of the laboratory. The leaves of the different species were sorted and weighed separately for the F and UF130. The production of litter was measured globally in Autumn 1994 in the third stand.

### Leaf analyses

The leaves were ground for chemical analysis, digested in a sulphuric acid-hydrogen peroxide-mercuric oxide mixture and, after neutralisation, analysed for nitrogen by an automated method involving the formation of a blue indophenol-like compound, and for phosphorus by an automated phosphomolybdate blue method. Potassium was determined by flame emission spectrophotometry and calcium and magnesium by atomic absorption spectrophotometry.

### Statistical comparisons

Results were compared by means of the Student-$t$ test using StatView SE+ (Abacus Concept, Inc., USA). In the reported results we considered differences significant at $p < 0.05$.

## Results

### Community structure and species diversity

### Woody flora

The elimination of floods and subsequent development of forest management caused an increase in diversity: the Shannon index ranged from 2.92 in the islands (flooded stand) to 3.52 and 3.28 in the unflooded stands (Tables 2 and 3), and in tree density. However this last difference was the result of a high development of saplings (< 6 cm dbh), 12% more in the UF30 site and three times more in the UF130, whereas the stem density was lower in this last site, compared with the flooded stand. The percentage of woody lianas in the canopy and total canopy density (with lianas) decreased with the elimination of floods. In the same way the total canopy basal area strongly decreased in the UF130.

In flooded sites, the total number of lianas (*Clematis* and *Hedera*) of more than 2 cm dbh is 141 lianas ha$^{-1}$, which represents a proportion of 4.8% of the total woody population (Table 3). The presence and abundance of giant lianas in the canopy is also a striking characteristic of flooded stands, with 28.6% lianas

of more than 6 cm dbh per ha and 30 m high, which represents 20.2% of the canopy population.

In unflooded stands, these data change dramatically. The total liana population increases up to 439 and 491 individuals of more than 2 cm dbh per ha, but the number of giant lianas decreases from 28.6 to 6.3% per ha, which represents 1.2% of the canopy woody population in the stand unflooded for 130 years.

### Fungal flora

Whether flooded or not, the hardwood ecosystem forest is rich in lignicolous species (32 and 31 species respectively, Table 4). The flooded stand is relatively poor in saprophytic species with only 17 species whereas outside the dykes, common species appear such as *Clitocybe phyllophila, Collybia confluens, Collybia dryophila, Marasmius wynnei*, and the flora reaches the total number of 30 species.

The number of mycorrhizal species is moderate (6 species) in the flooded stands. Mycorrhizal fungi include *Inocybe* and *Hebeloma* genera, and the very typical thermophilic *Amanita strobiliformis.* Outside the dykes, we observe an extraordinary development of the mycorrhizal flora (up to 19 species) with a great number of rare calcareous species of the genera *Boletus, Tricholoma, Cortinarius* and *Russula.*

### Leaf litter biomass

Autumn litter biomass reflects the differences in species composition of the two vegetation units with a dominance of *Fraxinus excelsior* and *Quercus robur* leaves (Table 5). The litter of the two species is higher in flooded stands. Data from 1990 indicated a litter biomass of 4.44 T ha$^{-1}$ yr$^{-1}$ in the flooded stand, and of 3.72 and 3.41 T ha$^{-1}$ yr$^{-1}$ in the UF30 and UF130 respectively. Mean litter production from 1987 to 1990 was 4.28 T ha$^{-1}$ yr$^{-1}$ in the flooded stand and 4.04 T ha$^{-1}$ yr$^{-1}$ in the stand unflooded for 130 years, observed for one year. Outside the dykes, extension of *Acer pseudoplatanus* and other mesic, flood-intolerant species (*Carpinus betulus, Prunus avium, Corylus avellana*) compensates for the decrease in softwoods (*Alnus incana, Populus alba* and *Prunus padus*) and in woody lianas.

### Nutrient budget (N, P, K, Mg, Ca)

Information on inputs, circulation and outputs of nutrients is given for the Rhinau flooded forest ecosystem and the Erstein forest, a stand unflooded for 30 years.

Table 2. Composition and structure of the Rhine hardwood forest in three vegetation units (one stand still flooded by calm waters, one unflooded for 30 years and one unflooded for 130 years). Density is given in stems per hectare and basal area in $m^2$ $ha^{-1}$. Blanks denote values $<0.5$ $m^2$ $ha^{-1}$. dbh=diameter at breast height.

| | Flooded hardwood | | | Unflooded hardwood for 30 years | | | Unflooded hardwood for 130 years | | |
|---|---|---|---|---|---|---|---|---|---|
| | Density <6 cm dbh | Density >6 cm dbh | Basal area >6 cm dbh | Density <6 cm dbh | Density >6 cm dbh | Basal area >6 cm dbh | Density <6 cm dbh | Density >6 cm dbh | Basal area >6 cm dbh |
| *Acer campestre* | | | | 14 | 7 | 0.63 | 82.5 | 16.6 | 1.16 |
| *Acer negundo* | 2.2 | | | | | | | | |
| *Acer platanoides* | | | | | | | | 6.3 | 0.11 |
| *Acer pseudoplatanus* | 33 | 13 | 0.17 | 282.7 | 24 | 1.21 | 1893 | 19.1 | 1.37 |
| *Alnus glutinosa* | | 13.1 | 0.4 | | 1 | | | 3.8 | 0.57 |
| *Alnus incana* | 30.6 | 13.1 | 0.19 | 54 | 44 | 0.55 | 54.1 | 15.4 | 0.11 |
| *Berberi vulgaris* | | | | | | | 9 | | |
| *Betula pendula* | | | | | 2 | 0.11 | | 2.5 | 0.5 |
| *Carpinus betulus* | | | | | | | 2.5 | | |
| *Clematis vitalba* | 88 | 4.4 | | 317 | 8 | 0.02 | 237.2 | 6.3 | 0.04 |
| *Cornus mas* | | | | | 5 | 0.01 | 41.2 | 17.9 | 0.36 |
| *Cornus sanguinea* | 584 | 17.4 | 0.05 | 1253 | 30 | 0.11 | 1084.4 | 3.8 | 0.01 |
| *Corylus avellana* | | 8.7 | 0.27 | 116 | 90 | 2.57 | 248.8 | 144.3 | 5.8 |
| *Crataegus monogyna* | 41.5 | 17.4 | 0.11 | 449 | 130 | 1.4 | 250 | 29.6 | 0.9 |
| *Daphne mezereum* | | | | 55 | | | 9 | | |
| *Evonymus europeaus* | 2 | 2 | 0.01 | 46 | 10 | 0.06 | 20.6 | 7.6 | 0.06 |
| *Frangula alnus* | | | | 1 | | | 7.7 | 1.2 | |
| *Fraxinus excelsior* | 78.7 | 286.5 | 11.81 | 196 | 196 | 19.42 | 453.9 | 145.5 | 9.68 |
| *Hedera helix* | 24.2 | 24.2 | 0.03 | 66 | 48 | 0.36 | 247.5 | | |
| *Juglans regia* | | | | | | | 18 | 4.5 | 0.17 |
| *Ligustrum vulgare* | 24 | | | 446 | | | 455 | | |
| *Lonicera xylosteum* | 41.5 | | | 16 | | | 652.4 | | |
| *Malus sylvestris* | 12.7 | | | 2 | 7 | 0.56 | 2.5 | 1.2 | |
| *Populus alba* | 15.3 | 12.4 | 8.51 | | 6 | 1.65 | | 3.7 | 0.47 |
| *Populus nigra* | | 6.3 | 2.08 | | 11 | 6.37 | | 6.3 | 1.03 |
| *Populus tremula* | | | | | 2 | 0.03 | | 1.2 | 0.02 |
| *Prunus avium* | | | | | | | 1.2 | 1.2 | 0.1 |
| *Prunus padus* | 790 | 155.1 | 1.35 | 440 | 110 | 1.25 | 120 | 14.1 | 0.12 |
| *Prunus spinosa* | 236.2 | 50.2 | 0.29 | 276 | 19 | 0.11 | 225.6 | 1.2 | |
| *Quercus robur* | | 13.1 | 5.8 | | 39 | 1.41 | | 30.8 | 7.24 |
| *Rhamnus catharticus* | | | | 1 | | | | | |
| *Ribes rubrum* | | | | 14 | | | | | |
| *Rosa arvensis* | | | | 1 | | | 1.2 | | |
| *Salix alba* | | 2 | 0.01 | | 3 | 0.37 | | | |
| *Sambucus nigra* | 21.8 | 6.5 | 0.01 | 4 | | | | | |
| *Ulmus laevis* | 6.5 | 10.9 | 0.63 | | 2 | 0.29 | 1.2 | 3.7 | 0.04 |
| *Ulmus minor* | 123.6 | 78.6 | 0.58 | 88 | 22 | | 105.7 | 30.2 | 0.17 |
| *Viburnum lantana* | 28.4 | | | | 6 | 0.01 | 61.8 | 1.2 | |
| *Viburnum opulus* | | | | 123 | | | 24.5 | | |
| Total | 2184.2 | 734.9 | 32.3 | 4259.7 | 823.0 | 38.5 | 6310.5 | 519.2 | 30.03 |
| Total density | 2919.1 | | | 5082.7 | | | 6829.7 | | |

*Table 3.* Biotic diversity in the three vegetation units of the Rhine valley (data modified from Schnitzler, 1994). $H' = $ Shannon index, $H' = -\sum(Ni/N)^* Log_2 (Ni/N)$, ($N$ is the total density of woody species and $Ni$ the individual number of each woody species, $J' = $ Pielou index, $J' = H'/\ln S$ ($S$ is the total species richness). Mean total species richness and mean woody species richness are calculated on the basis of all the subunits for one association.

| | Flooded hardwood | Unflooded hardwood for 30 years | Unflooded hardwood for 130 years |
|---|---|---|---|
| Total density of woody species (stems/ha) | 2919.1 | 5082.7 | 6829.7 |
| Basal area ($m^2 ha^{-1}$) | 32.3 | 38.5 | 30 |
| Total species richness | 63 | 121 | 95 |
| Mean total species richness | 31.2 | 33.7 | 34.8 |
| Woody species richness | 25 | 45 | 47 |
| Mean woody species richness | 17.8 | 15.7 | 16.7 |
| Woody lianas of the total density (%) | 4.8 | 8.0 | 5.5 |
| Woody lianas in the canopy (%) | 20.0 | 12.7 | 1.2 |
| Total canopy density with lianas (stems/ha) | 56.4 | 48.5 | 19.0 |
| Total canopy basal area ($m^2 ha^{-1}$) | 17.3 | 16.5 | 5.3 |
| Shannon Index $H'$ | 2.92 | 3.52 | 3.28 |
| Pielou Index $J'$ | 0.70 | 0.73 | 0.72 |

These two sites are now reference sites for studies on the functioning of alluvial forest ecosystems in the Rhine floodplain, in the context of national research programs. Inputs correspond to rainfall, throughfall and flooding, outputs to groundwater recharge (Table 6, Figure 2). Circulation of nutrients is visualised in different compartments including mature leaves, leaf litter, soils and throughfall (Table 7, Figure 2) .

Chemistry of the surface and flooding waters compared to the groundwater varies considerably, particularly for potassium, nitrogen and phosphorus (ten times less K in the groundwater than in the surface water up to 40 times less P, Figure 2).

*Phosphorus*
In the flooded stand, inputs of P come mainly from surface waters (0.63 kg ha$^{-1}$ mean of six flood events, calculated on the basis of the height of infiltrated flood water), from sediment deposits (6.2 kg ha$^{-1}$ mean of four flood events) and from rainfall (1.03 kg ha$^{-1}$ yr$^{-1}$). Restitution of P is made by throughfall (1.68 kg ha$^{-1}$ yr$^{-1}$) and leaf litter (5.6 kg ha$^{-1}$ yr$^{-1}$), which shows the high level of internal phosphorus and the importance of recycling. In the unflooded stand (UF30), inputs of P come only from rainfall (0.74 kg ha$^{-1}$ yr$^{-1}$). Restitution of P is made by throughfall (1.08 kg ha$^{-1}$ year$^{-1}$) and litter (3.2 kg ha$^{-1}$ yr$^{-1}$), amounts which are significantly lower than in the flooded stand. Elimination of floods also causes a decrease of the P stock in soils and leaves (36.3 kg ha$^{-1}$ in the flooded soils against

only 17.3 kg ha$^{-1}$ in the unflooded soils for 130 years, Table 6). In groundwater the concentrations of P are low and similar in flooded and unflooded stands.

*Nitrogen*
Inputs from rainfall reach 9.1 to 17.6 kg ha$^{-1}$ yr$^{-1}$. In the flooded stand, restitution of N is made by throughfall, i.e., 12.7 kg ha$^{-1}$ yr$^{-1}$ and more extensively by leaf litter (69 kg ha$^{-1}$ yr$^{-1}$). Floods brings twice as much as throughfall with 25.3 kg ha$^{-1}$ yr$^{-1}$. In the unflooded stand, the N budget is a little less, restitution of N by throughfall being 12.2 kg ha$^{-1}$ yr$^{-1}$ and 66.4 kg ha$^{-1}$ yr$^{-1}$ by litter. In the mature leaf, the N content is significantly higher in the flooded hardwood than in the unflooded ones, but there is no not difference in the leaf litter content between the three stands. Nitrogen (N-NO$_3^-$ + N-NH$_4^+$) mean content in groundwater was higher (1.03 mg l$^{-1}$) in the flooded stand than that in the unflooded stand (0.59 mg l$^{-1}$).

*Calcium, magnesium and potassium*
Inputs of calcium and magnesium by throughfall are similar in both stands whereas that of potassium was higher in the unflooded stand. These three elements were at the same level in leaves and soil whatever the stand, flooded or unflooded F and UF130 (Table 7) even though the floods (water and sediments) contribute to a high input of these elements in the flooded stand. In groundwater, the concentrations of Ca and K were similar in both stands, F and UF30, Mg being more

Table 4. Fungal flora (mycorrhiza, saprophytes and lignicolous species) in two Rhine vegetation units (flooded hardwood and unflooded hardwood for 130 years). * = indicates common species. ** = indicates very common species. Data obtained from R. Carbiener unpublished and Carbiener et al. (1975).

| | Period of fructification | Flooded hardwood | Unflooded hardwood for 130 years |
|---|---|---|---|
| Mycorrhizal species | | | |
| *Amanita echinocephala* | Aug–Sept | | ** |
| *Amanita strobiliformis* | June–Sept | * | ** |
| *Boletus luridus* | June–Sept | | * |
| *Boletus radicans* | June–Sept | | * |
| *Boletus rhodopurpureus* | Sept | | * |
| *Boletus satanas* | Aug–Sept | | * |
| *Gyrodon lividus* | Sept–Oct | * | ** |
| *Hebeloma sacchariolens* | Sept–Oct | * | * |
| *Hebeloma sinuosum* | Sept–Oct | | ** |
| *Inocybe fastigiata* | Sept–Oct | | * |
| *Inocybe maculata* | Aug–Oct | ** | * |
| *Lactarius acerimus* | Aug–Oct | * | * |
| *Lactarius pubescens* | Aug–Oct | | * |
| *Russula delica* | June–Feb | | * |
| *Russula maculata* | July–Sept | | * |
| *Russula pulchella* | Sept–Oct | | * |
| *Russula vitellina* | Oct–Nov | | * |
| *Scleroderma verrucosum* | Aug–Oct | * | * |
| *Tricholoma scalpturatum* | Nov–Dec | | ** |
| Saprophytic species | | | |
| *Agaricus campestre* | Sept–Oct | ** | * |
| *Agaricus gennadii* | June–Oct | * | * |
| *Agaricus subfloccosus* | June–Sept | | * |
| *Calocybe ionides* | Aug–Oct | | * |
| *Calvatia excipuliformis* | July–Oct | | * |
| *Candidus albutiscorticus* | Aug–Nov | ** | * |
| *Chamaemyces fracidus* | Aug–Sept | * | ** |
| *Clitocybe candidans* | Aug–Oct | * | ** |
| *Clitocybe phyllophila* | Oct–Nov | | * |
| *Clitocybe suaveolens* | Oct–Nov | | * |
| *Collybia confluens* | Oct–Nov | | * |
| *Collybia dryophila* | Oct–Nov | | * |
| *Cystolepiota sistrata* | Aug–Oct | * | * |
| *Disciotis venosa* | March–April | ** | * |
| *Entoloma aprilis* | April | * | |
| *Entoloma saundersii* | March–April | | * |
| *Helvella crispa* | | | * |
| *Hemimycena candida* | | * | |
| *Lepiota acutesquamosa* | July–Oct | * | ** |
| *Lepiota cristata* | Sept–Nov | ** | ** |
| *Lepista sordida* | Sept–Nov | | * |

*Table 4 continued.*

| | Period of fructification | Flooded hardwood | Unflooded hardwood for 130 years |
|---|---|---|---|
| *Lycopordon perlatum* | | | * |
| *Marasmius wynnei* | Sept–Oct | | * |
| *Mitrophora semilibera* | April–May | ** | * |
| *Morchella esculenta* | Nov | | * |
| *Morchella rotunda* | Nov | ** | * |
| *Mycena roseipallens* | July–Oct | ** | |
| *Paxina acetabulum* | April | | * |
| *Pholiotina foetidus* | | ** | * |
| *Psathyrella melanthina* | Sept–Oct | * | * |
| *Psathyrella vernalis* | April–May | * | * |
| *Verpa bohemica* | April–May | | * |
| *Verpa digitaliformis* | April–May | | * |
| Lignicolous species | | | |
| *Armillaria bulbosa* | | * | ** |
| *Aurantioporus fissilis* | Sept–Oct | * | * |
| *Auricularia auricula judae* | Oct–March | ** | * |
| *Auricularia mesenterica* | | ** | * |
| *Chondrostereum purpureum* | | * | * |
| *Coprinus domesticus* | April–May | * | |
| *Coprinus radians* | April–May | * | |
| *Daedaleopsis confragosa* | | ** | * |
| *Daedaleopsis confragosa var. tricolor* | | * | ** |
| *Funalia gailica* | | * | * |
| *Funalia trogii* | | * | * |
| *Laetiporus sulfureus* | | ** | * |
| *Lentinus tigrinus* | May–Sept | ** | * |
| *Lyophyllum ulmarium* | | * | * |
| *Marasmius candidus* | | ** | * |
| *Marasmius rotula* | | * | ** |
| *Micromphale foetidum* | | ** | ** |
| *Mycena haematopoda* | | * | * |
| *Phellinus conchatus* | | ** | * |
| *Phellinus pomaceus* | | * | * |
| *Phellinus ribi* | | | * |
| *Pleurotus cornucopiae* | June–Sept | ** | * |
| *Pluteus salicinus* | | * | * |
| *Polyporus badius* | April–Oct | * | * |
| *Polyporus brumalis* | | * | * |
| *Polyporus ciliatus* | April–June | * | * |
| *Polyporus mori* | | * | * |
| *Polyporus squamosus* | May–Sept | * | ** |
| *Polyporus tuberaster* | | * | * |
| *Postia subcaesia* | | * | * |
| *Stereum subtomentosum* | | ** | * |
| *Trametes suaveolens* | | ** | * |
| *Tubaria hiemalis* | Oct–March | ** | * |

*Table 5.* Mean values of litter (in T ha$^{-1}$ for the main components of the tree and shrubs layers in two Rhine vegetation units (flooded hardwood, unflooded hardwood for 30 years and unflooded hardwood for 130 years). The other species bring less than 0.01 t.ha$^{-1}$. Blanks denote biomass values <0.01 t.ha$^{-1}$

| Species | Flooded hardwood | Unflooded hardwood for 30 years (T ha$^{-1}$ yr$^{-1}$) | Unflooded hardwood for 130 years |
|---|---|---|---|
| *Quercus robur* | 0.94 ± 0.52 | | 0.80 ± 0.58 |
| *Fraxinus excelsior* | 2.12 ± 1.52 | | 1.13 ± 1.13 |
| *Cornus sanguinea* | 0.03 ± 0.06 | | 0.02 ± 0.03 |
| *Hedera helix* | 0.09 ± 0.12 | | 0.06 ± 0.10 |
| *Prunus padus* | 0.08 ± 0.08 | | |
| *Corylus avellana* | 0.02 ± 0.06 | | 0.43 ± 0.39 |
| *Crataegus sp.* | 0.01 ± 0.01 | | 0.06 ± 0.17 |
| *Populus alba* | 0.98 ± 1.31 | | |
| *Alnus incana* | 0.06 ± 0.10 | | |
| *Ulmus sp.* | 0.01 ± 0.03 | | 0.05 ± 0.10 |
| *Acer sp.* | 0.06 ± 0.18 | | 0.22 ± 0.45 |
| *Prunus spinosa* | 0.01 ± 0.03 | | |
| *Carpinus betulus* | | | 0.53 ± 0.49 |
| Other leaves | 0.11 ± 0.08 | | 0.14 ± 0.09 |
| Total leaves | 4.44 ± 1.58 | 3.72 ± 0.69 | 3.41 ± 0.99 |

concentrated in the unflooded site. The litter has a Ca high content, which is similar to leaf mature content.

## Discussion

*Changes in community structure and species diversity*

*Woody flora*

In the three stands, the canopy is dominated by *Fraxinus excelsior*, which is favoured by the recent silty soil coverage and the bad health of its direct competitors, *Quercus robur* and *Ulmus minor*. *Quercus robur*, one of the previously codominant trees, is not regenerating within the hardwood community for unknown reasons (cessation of the morphogenesis, competition with *Fraxinus excelsior*, importance of the game). *Ulmus* species regenerate better but the young trees still die because of Dutch Elm disease. In the flooded stands, the canopy still includes some remnant softwoods (*Populus alba, Salix alba, Populus nigra*) as a result of either the previous successional stages or the youth phase of the hardwood ecosystem (Schnitzler 1995b).

In the UF130, flood intolerant and/or mesic species, naturally relegated to high terraces, were, such as *Acer campestre, Acer pseudoplatanus, Carpinus betulus, Prunus avium, Juglans regia, Corylus avellana, Frangula alnus* (a calcicolous mesic phenotype), *Lonicera xylosteum, Daphne mezereum, Cornus mas, Berberis vulgaris, Viburnum lantana* higher in density and basal area. Conversely, the hydrophilic species which are tolerant to summer floods, such as *Prunus padus, Fraxinus excelsior, Quercus robur, Ulmus minor, Malus sylvestris, Hedera helix, Clematis vitalba, Cornus sanguinea, Sambucus nigra, Viburnum opulus, Evonymus europaeus, Rubus caesius*, decrease in stem density and basal area, as shown also by Pautou et al. (1992). The number of giant shrubs such as *Crataegus monogyna, Evonymus europaeus, Prunus spinosa ssp fruticans, Cornus sanguinea* decreases. The stand unflooded for 30 years is an intermediate case, already showing significant modifications compared with the flooded stand. Among trees which cannot tolerate summer floods, only *Acer campestre* and *A. pseudoplatanus* are present in abundance. The other species are rare. The total species richness is the highest of the three stands. This could be due to the still cohabiting species, hydrophilic and intolerant to flood, whereas the hydrophilic species have decreased in the stand unflooded for a longer period.
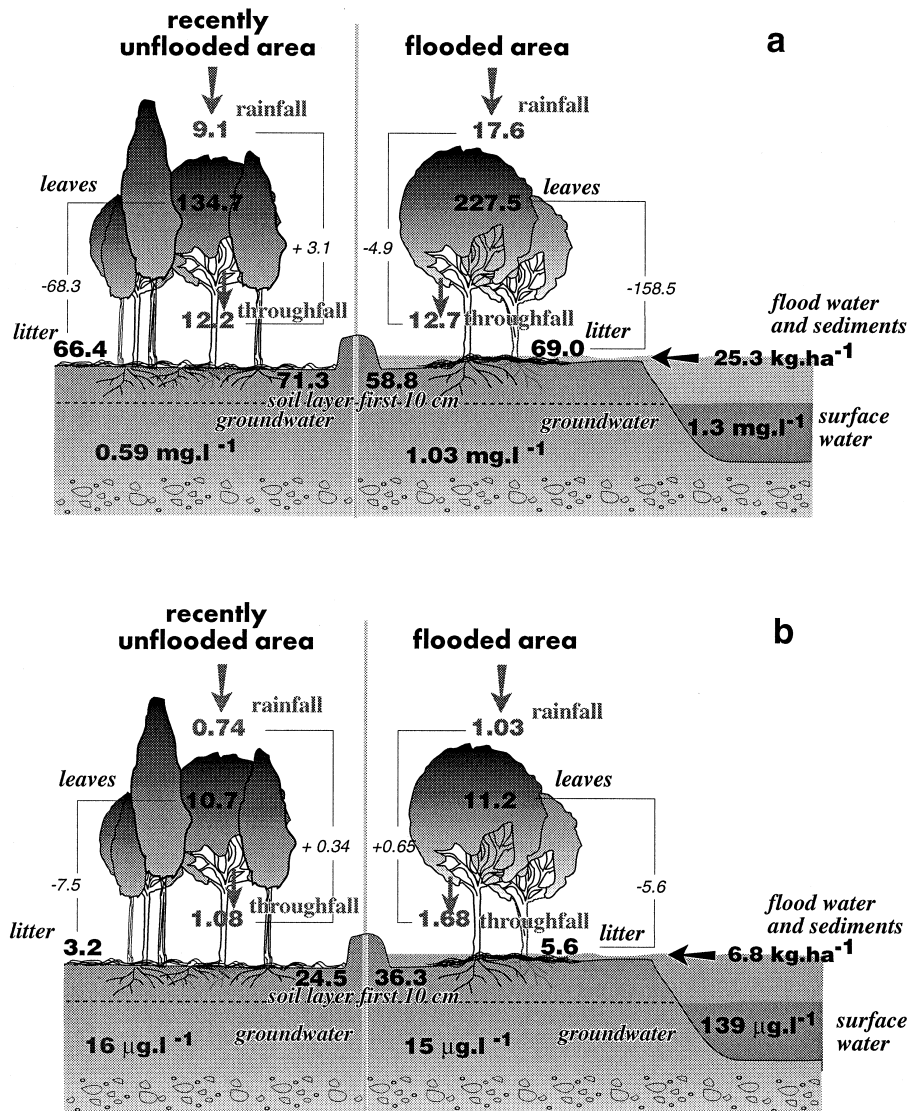
*Figure 2*. Nitrogen (a) and phosphorus (b) budgets in the two stands, flooded and unflooded for 30 years. Inputs expressed in kg ha$^{-1}$ yr$^{-1}$ and outputs in concentration, mg l$^{-1}$.

The Rhine forests, when flooded, are liana-rich communities, for two reasons: (1) the absence of an anoxic horizon to which liana roots are very sensitive, (2) the mechanisms of forest successions, which involve successive waves of species of low shade tolerance and competitiveness (*Salix, Populus*). These species favour rapid colonisation by lianas and prepare their future integration in the mid-successional stages (Schnitzler 1995a).

These results indicate that flooding periods are crucial for the establishment of typical alluvial species and also giant lianas, because of regular water and nutrient inputs coupled with absence of hydromorphy. However, after several years without flooding, the lianas are first favoured by the elimination of periodic anoxia, and increase significantly in density and basal area (Schnitzler 1995a). After more than a century, the total density of woody elements has doubled, which has increased the competition for light and nutrients, and may explain the decrease in giant lianas.

Changes in species composition emphasize the difficulty for many plants of growing in flooded areas.

| Inputs by floods (kg ha$^{-1}$ yr$^{-1}$) | | |
|---|---|---|
| | Water ($n = 22$) | Soil deposit ($n = 18$) |
| N | 20.4 $\pm$ 6.7 | 4.9 $\pm$ 2.5 |
| P | 0.63 $\pm$ 0.39 | 6.2 $\pm$ 1.4 |
| K | 40.4 $\pm$ 9.8 | 10.6 $\pm$ 2.0 |
| Mg | 64.2 $\pm$ 11.7 | 13.4 $\pm$ 0.6 |
| Ca | 443.4 $\pm$ 76.7 | 469.4 $\pm$ 8.1 |

| Inputs by throughfall (kg ha$^{-1}$ yr$^{-1}$) | | | |
|---|---|---|---|
| | flooded stand ($n = 108$) | Unflooded hardwood for 30 years ($n = 91$) | |
| N | 12.7 $\pm$ 1.3 | 12.2 $\pm$ 1.5 | |
| P | 1.68 $\pm$ 0.29 | 1.08 $\pm$ 0.06 | ($*$) |
| K | 27.6 $\pm$ 8.5 | 50.4 $\pm$ 7.8 | ($*$) |
| Mg | 3.6 $\pm$ 1.1 | 3.8 $\pm$ 1.6 | |
| Ca | 29.3 $\pm$ 9.5 | 25.2 $\pm$ 4.4 | |

| Outputs by shallow groundwater quality (mg l$^{-1}$) | | | |
|---|---|---|---|
| | flooded stand ($n = 131$) | Unflooded hardwood for 30 years ($n = 76$) | |
| N | 1.03 $\pm$ 0.42 | 0.59 $\pm$ 0.21 | ($*$) |
| P | 0.015 $\pm$ 0.005 | 0.016 $\pm$ 0.007 | |
| K | 3.9 $\pm$ 0.9 | 3.0 $\pm$ 1.0 | |
| Mg | 11.9 $\pm$ 3.8 | 17.5 $\pm$ 3.3 | ($*$) |
| Ca | 99.8 $\pm$ 37.1 | 105.8 $\pm$ 26.6 | |

Flood periods are known to be harmful because of the reduction of soil oxygen (enhanced in summer and in poorly drained soils) (Kovlowski 1982). Many species cannot tolerate periods of waterlogging and grow sparsely in well-drained flooded forests with high pulsing hydroperiods and coarse textures (Gill 1970; Dister 1983). That is the case of the *Acer* genus (*pseudoplatanus, campestre, platanoides* species in Europe, *saccharum* species in North America), the genus *Cornus* (*mas* in Europe, *florida* in North America), *Quercus* (*pubescens* in Europe, *alba* in North America) (Carbiener 1970; Robertson et al. 1978). These trees extend their range immediately at the end of inundation periods. But when plants are adapted to floods, their growth is greatly favoured by regular supplies of nutrients, which explains their high productivity. In the Dakota floodplain, peak growth was observed just after flood recession when the groundwater was still within the root zone (Johnson et al. 1976) because of immediate passage of nutrients through the soil. That is why general decrease in basal area outside the dykes probably results more from the elimination of floods than from intensive forestry, however it is difficult to separate the effect of flood suppression from the logging effect.

In the unflooded areas, the increasing density of *Fraxinus excelsior* in the canopy and of *Acer pseudoplatanus* in the second and third woody layers suggests an enhancement of the process of dominance. The stopping of the disturbance normally caused by flooding, under conditions of high nutrient availability, allows rapid growth of the best competitors and competitive exclusion. This fact was predicted in the Huston model (Huston 1979) and observed in the Costa Rican forests

Table 7. Nutrient levels in soil, mature leaves (August) and leaf litter for the two vegetation units (flooded hardwood and unflooded hardwood for 30 years). Data expressed in kg ha$^{-1}$ yr$^{-1}$. The species analysed are the most frequent species of the hardwood forest, i.e. *Fraxinus excelsior, Quercus robur, Ulmus minor, Acer campestre, Carpinus betulus, Corylus avellana, Cornus sanguinea, Clematis vitalba, Hedera helix*. $*$ = significant at the 0.05 level.

| | Flooded hardwood | Unflooded hardwood for 30 years | Unflooded hardwood for 130 years |
|---|---|---|---|
| Nutrient level in the mature leaves (kg ha$^{-1}$ yr$^{-1}$) | | | |
| N | $227.5 \pm 58.7$ | $134.7 \pm 33.5$ ($*$) | $151.9 \pm 28.6$ ($*$) |
| P | $11.2 \pm 2.7$ | $10.7 \pm 1.4$ | $8.3 \pm 1.4$ ($*$) |
| K | $106.7 \pm 20.8$ | | $105.6 \pm 32.7$ |
| Mg | $26.2 \pm 9.0$ | | $25.7 \pm 14.7$ |
| Ca | $198.7 \pm 51.2$ | | $211.6 \pm 52.6$ |
| Nutrient level in the leaf litter (kg ha$^{-1}$ yr$^{-1}$) | | | |
| N | $69.0 \pm 15.2$ | $66.4 \pm 14.9$ | $68.5 \pm 14.2$ |
| P | $5.6 \pm 1.7$ | $3.2 \pm 1.0$ ($*$) | $3.6 \pm 1.2$ ($*$) |
| K | $53.0 \pm 15.6$ | $62.2 \pm 9.9$ | $55.1 \pm 23.0$ |
| Mg | $14.7 \pm 6.8$ | $8.6 \pm 1.1$ | $13.3 \pm 6.8$ |
| Ca | $172.8 \pm 43.9$ | | $181.3 \pm 48.7$ |
| Nutrient level in the upper soil layer, 10 cm (kg ha$^{-1}$) | | | |
| N | $58.8 \pm 11.0$ | $71.3 \pm 6.2$ ($*$) | $67.8 \pm 7.4$ ($*$) |
| P | $36.3 \pm 15.2$ | $24.5 \pm 7.2$ ($*$) | $17.3 \pm 7.2$ ($*$) |
| K | $97.8 \pm 16.3$ | $142.5 \pm 11.6$ ($*$) | $124.2 \pm 57.3$ |
| Mg | $169.7 \pm 27.7$ | $192.5 \pm 21.9$ | $150.0 \pm 18.0$ |
| Ca | $8957 \pm 1264$ | $8709 \pm 383$ | $6971 \pm 109$ ($*$) |

(Huston 1980), in the Missouri floodplain and elsewhere (Johnson et al. 1976; Brinson 1990) and now in the Rhine floodplain.

*Fungal flora*
Like the Angiosperm flora, the peculiarity of the Rhine fungal flora (high species richness, with a particular abundance in calcareous and thermophilic species) is a direct response to the particular alluvial environment of the Upper Rhine valley (Carbiener, 1969, 1970, 1981; Carbiener & Schnitzler, 1990). The paucity of saprophytic species in the flooded stands (17 species) is related to the rapid decomposition of the dead leaves – the half life decomposition of ivy litter requires six months (Trémolières et al. 1988) and 80% mass loss of the oak litter occurs after 18 months (Badre et al. 1996). The low number of mycorrhizal species is probably due to the considerable allochthonous supply of phosphorus and nitrogen. Many experiments suggest that the level of mycorrhizal establishment decreases with progressive enrichment of P and N (Le Tacon 1985). Increase in mycorrhizal species outside the dykes improves the turn-over of the nutrients and the P uptake by plants (Hudson 1986), thus partly compensates for the loss in allochthonous nutrients.

*Changes in the nutrient budget (N, P, K, Mg, Ca)*

Fluxes of energy, sediment and nutrient passing through the hardwood forest are therefore mainly retained in the biomass and the soil (Sánchez-Pérez et al. 1991a, b). Several studies have demonstrated the high potential for removal of nitrogen in riparian areas. Denitrification represents a net loss of N from the terrestrial ecosystem to the atmosphere (Patrick & Reddy 1976; Pinay & Décamps 1988; Cooper 1990; Groffman et al. 1992), although riparian vegetation may also be involved in nitrogen retention via uptake (Garten 1993).

*Phosphorus*
This element is a vital and limiting nutrient for plants, and directly related to primary productivity in forested wetlands (Schlesinger 1978; Mitsch et al. 1979). The

litter contributes considerably to the internal recycling of phosphorus. The data are close to those measured, in December 1972 in a floodplain ecosystem of Southern Moravia (5.3 kg ha$^{-1}$ yr$^{-1}$, Klimo 1985), and more generally in the range of those observed in riverine forested wetlands (Lugo et al. 1990). In calcareous soils, P precipitates as insoluble hydroxyapatite and accumulates on the colloids. Now, after many years of regular inundation by polluted and eutrophicated floods, the soil concentration of P reaches 181 kg ha$^{-1}$ (Sánchez-Pérez et al. 1993), but Klimo (1985) found only about 4–18 kg ha$^{-1}$ in the A horizon of soil in the Moravian floodplain, indicating that this type of soil is not rich in P but confirming the accumulation of P in the surface horizon in a system subjected to regular flooding. During flood periods, waterlogging creates reducing conditions which allows phosphorus to be solubilized as ferrous phosphate. P becomes more available to plants for a short time, during and after flooding (Patrick & Mahapatra 1968). There is a better uptake of phosphate when P is supplied by floods to calcareous soils where phosphorus is less available, as was also shown by Morel & Fardeau (1990). These authors demonstrated in an experiment in which fertilizer was applied in both cases of soil poor in available P and soil rich in available P, that the plants used phosphate fertilizer more readily in the case of the soil poor in available P. Weiss et al. (1991) and Weiss & Trémolières (1993) showed that flooding was the main factor which controlled the bioavailability of phosphorus.

In the unflooded stand, the decrease in P stock in the soil could be partly compensated by the P uptake with help of the mycorrhizal fungi, which increases the absorption surface and transforms insoluble into soluble phosphate due to phosphatases. However, as a consequence of this decrease in soil, there is also a decrease in foliar P content. The decrease in abundance and basal area of many eutrophic, often phosphatophilous plants (*Ulmus minor, Fraxinus excelsior, Clematis vitalba, Hedera helix* in the canopy and giant shrubs in the overstorey) could be the result of decreasing P (and N) content.

In groundwater, the very low level of phosphate in both stands is due to the high retention of phosphate by soils, accentuated by precipitation as tricalcic phosphate. Therefore the concentration in groundwater is the result of several processes which occur during the vertical transfer of flood waters, i.e., adsorption and/or precipitation in soils and also absorption by plants.

*Nitrogen*

Rhine waters and consequently flood waters are not very rich in N (only 1.97 mg l$^{-1}$ N-NO$_3^-$ during the floods, mean of six flood events from the period 1990–1995, compared with about 3 mg l$^{-1}$ in the Ill river, the main tributary of the Rhine in the upper Rhine floodplain (Trémolières et al. 1994) and 0.5 mg l$^{-1}$ in a stream of acidic geochemistry (Probst et al. 1995a). Inputs from rainfall reach a level, due to air pollution, which is rather similar to that measured in a Norway spruce forested catchment in Eastern France close to our study area (Probst et al. 1995b). Restitution of N is made by throughfall, which is also close to that measured by Probst et al. (1995b) in the same area mentioned above, and to the 16 kg ha$^{-1}$ yr$^{-1}$ in a mixed conifer stand measured on the 1990 summer season (Bytnerowicz & Riechers 1995). Leaf litter content is in the same order of this measured by Klimo (1985), i.e., 85.1 kg ha$^{-1}$ yr$^{-1}$.

Soluble N content in the soil is different in the three stands and is the highest in the stand unflooded for 30 years, probably because of the persistence of a very active microbiological cycle, stimulated by the basicity, the porosity and good oxygenation of the alluvial deposits (Carbiener 1970). Even after several decades without inundation, the total production of nitrogen outside the dykes remains high (984 mg inorganic N per 100 g organic matter after six weeks in an incubator, Schnitzler 1988). Furthermore, the regular rising of the groundwater in summer makes available high quantities of nitrate, possibly taken up by plants. In the flooded sites, despite the lower content of N in soils, we observe a very significantly large foliar N level, which emphasises the major role of autogenous N production stimulated by high variations of groundwater level. The higher N level in leaves may also be related to higher basal area in the flooded sites and to a better productivity than in unflooded sites (more giant shrubs and lianas, higher litter production). Duvigneaud & Denaeyer-De Smet (1969) stressed the direct relationships between N level in leaves and the humus N level: the more available N in soils, the higher the N foliar level, the greater growth and productivity. Retranslocation (transfer of nutrients to the perennial organs during the senescence) was observed in several oak communities in Belgium, classified over a gradient of productivity (Duvigneaud & Denaeyer-De Smet 1969). N retention in woody parts of the oak was found to be higher in the best productive oak communities, but restitution of litter was identical. In these studies, the

herb productivity, higher in less productive oak communities, compensated for the lower N in the biomass. That could be the case in the unflooded stands.

Nitrate concentrations in groundwater are directly influenced by hydrological functioning, i.e., presence or absence of floods and this duration which influence the variations of groundwater level. There is a higher $N-NO_3^-$-$N-NH_4^+$ mean content in groundwater in the flooded stand than in the unflooded stand. In the flooded Rhine forest, where the alluvial soils are loamy, very porous and well oxygenated (mean 3.5 mg $l^{-1}$ dissolved oxygen), the nitrification-denitrification or dissimilatory reduction processes can occur alternately during the phases of desiccation-oxygenation of soils (leading to the nitrification) and hydric saturation-deoxygenation (leading to a denitrification). In fact, we measured up to 29 mg $l^{-1}$ $N-NO_3^-$ in soil solution of sandy terraces in the flooded area. In the unflooded forests, the lower nitrate concentrations in the superficial groundwater (2.5 m below ground) are probably the result of the hydrological stability, nitrification process being more limited than in the flooded stands.

*Potassium, calcium and magnesium*
Calcium and magnesium are abundant in the soils due to the geochemistry of the deposits (table 6). They are brought in larger quantities by floods than by throughfall or by litter. However in the unflooded stand, the litter contribution to the total input is around 60% for K and 72% for Mg, which is in agreement with the results of Parker (1983). Despite the large input by floods, K, Ca and Mg contents in all the compartments (leaf, litter, soil) are not significantly different in the three stands; they remain at a high level (mean 180 kg ha$^{-1}$ Ca, mean 14 kg ha$^{-1}$ Mg in the litter) by comparison for example with the litter contents (93.6 kg ha$^{-1}$ Ca, 7.8 kg ha$^{-1}$ Mg) measured in a forest of *Quercus ilex* despite a similar soil status (Rapp 1969). Uptake of Ca and Mg by plants is very high in calcimagnesic soils, which probably decreases uptake in K (Duvigneaud & Denaeyer-De Smet 1969). In fact K availability is relatively weak in calcareous environment because of antagonism Ca/K: K absorption is 106.7 kg ha$^{-1}$ yr$^{-1}$ whereas Ca absorption reaches 198.7 kg ha$^{-1}$ yr$^{-1}$.

Calcium concentrations in groundwater are very high, and not significantly different in the two stands F and UF30 (around 100 mg $l^{-1}$), which is explained by the calcareous substrate; in comparison, Probst et al. (1995b) measured 0.93 mg $l^{-1}$ Ca in an acidic stream water of a Norway spruce forested catchment

and Likens et al. (1977) only 0.2 mg $l^{-1}$ in the Hubbard Brook Experimental Forest. In comparison, potassium in both stands is at a low concentration despite the large inputs by floods and throughfall or by throughfall only, which shows the retention capacity of argilo-humic colloids. Magnesium is at a significantly higher level in the groundwater of unflooded stand.

## Conclusion

*Long-term evolution of the alluvial hardwood ecosystem*

The study sought to determine what were the main short term effects produced by the elimination of floods upon the alluvial forest ecosystem. Some changes in composition structure, species richness and nutrient status in the soil and in the biomass demonstrate that the ecosystem may be altered in its functioning, even if the nutrients accumulated in the active upper layer soil before dam correction, and then regularly recycled, remain the basis of continuous soil fertility with the help of the summer rising of the groundwater. The isolation from floods lead more to a change of succession, i.e., change in the ratios between alluvial communities, disappearance of pioneer stages with willows and poplars and appearance of new communities related to new conditions of water supply than change of ligneous species in the mature hardwood forests. In fact, Pautou et al. (1992) indicate that these forests persist after some decades of isolation, with some change of floristic composition only in the shrub and herbaceous strata, the dominant characteristic species, oak, elm and ash being preserved. The change in vegetation is more marked after more than a century, due to the increased lowering of the water table which causes the disappearance of hydrophilous plants, and probably also to change in the nutrient status. The change of this nutrient status leads to a decrease of nutrients because of absence of inputs by water and sediment floods and of productivity despite change of floristic composition and compensation by new species biomass.

Soil nutrient level in the upper layer of the hardwood forests unflooded for several decades show some differences from the flooded Rhine forests, with a significant decrease in P and increase in N. However in the output compartment (groundwater), P remains at the same level whereas N is at a lower level in the shallow groundwater (root layer), showing that the system has preserved its efficiency in retaining biogenic nutrients.

However the bioavailability of nutrients changes with the suppression of floods. In fact leaf and litter nutrient level follows the soil content with a lower foliar P content by comparison with flooded forests. Nitrogen is also at a lower level in leaf despite a higher content in soil. Litter production is quite similar in the three stands, varying with the ligneous species; the appearance of intolerant-flood species compensates for the disappearance of others. These results suggest that only P and N cycles are modified by suppression of floods for a relatively short period (30 years), whereas K, Mg and Ca contents are not modified, due to the geochemistry of the Rhine valley. This change might be expected to be more accentuated in areas deprived of floodwaters after more than a century.

*Ecological engineering of the Rhine system*

Since the nineteenth century, the hardwood alluvial ecosystem has lost immense surface areas through engineering works, cuttings for industries and gravel-pits and inappropriate forestry management. Industrialised countries now realise the errors of the past, the scientific and economical importance of the large floodplains (Wenger et al. 1990; Moorhead 1991) but too many short-term interests still prevent effective planning. In the Rhine rift valley, a programme (Integriertes Rheinprogramm) was proposed in 1988 by the Baden Württemberg Land (Germany) to restore the vast surface areas of the natural high-water bed of the Rhine on both parts of the main channel, with protection and re-creation of the natural forest for the new millennium. Even though these projects will not be able to restore the natural morphogenesis of the Rhine, they may prevent possible industrial and forestry damage. At present, restoration programs are in progress along the French bank of the Rhine by the creation of four nature reserves corresponding to 700 ha of the Rhine riverine landscape (Klein et al. 1996). The objective is to re-inundate these areas, to propose ecological forestry management and to re-establish connections between floodplain and river in order to restore the buffer role of forests between agricultural area and river and to restore the purifying function for eutrophicants (P, N). Given the present state of stands unflooded for 30 years (little change of ligneous species and nutrient in soils, preservation of hygrophilous species), alluvial hardwood forest could probably be restored with great efficiency as regard the vegetational aspect and the biogeochemical functioning. Thus Lowrance et al. (1995) show that the restoration of the water quality of a forested wetland is successful and rapid when the hydrologic and soil changes are limited. The functions of purifying were preserved, especially for the nitrate removal via denitrification but it was not due to the reforestation in this case, as shown also by Leonardsson et al. (1994), who measure nitrogen retention in artificially flooded meadows as well as in a farmland stream (Jansson et al. 1994). Discharge, retention time and charge of nitrate are factors which control the elimination of nitrogen. It appears also that nitrogen uptake by plants was stimulated by flooding (Leonardsson et al. 1994). Consequently these authors recommend 'the creation of artificially flooded meadows provided that long irrigation period are applied and subsurface flow and high supply of nitrate can be maintained'.

However to re-establish the former ratios between the different communities of the succession could be more difficult, without human intervention. The restoration of floods in hardwood forests is desirable and necessary for mineral nutrition of plants and also for productivity related to water and nutrient supply, and the stimulation of biological processes, especially in the case of nitrogen and phosphorus.

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