

## Evolution of major pattern models and processes of alluvial forest of the Rhine in the rift valley (France/Germany)

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### Abstract

In the rift valley (North-East of France/South-West of Germany), the Rhine runs freely for 300 km from South to North. The absence of natural obstacles allows the development of a very regular profile of the river. We have therefore an opportunity to study very gradual modifications of the alluvial forest communities of the fluvial corridor from upstream to downstream, according to the gradual evolution of the ecological factors, related to slope decrease and hydrological modifications.

We describe, from Basel to Mainz:

- 1) modification of dynamic processes in the forest communities such as successional sequences or sylvigenetic mosaics of the terminal stages.
- 2) modification of species richness.
- 3) reduction of species diversity.
- 4) simplification of the forest stratification.
- 5) modification of efficiency of the biogeochemical cycling.
- 6) ecological vicariances.
- 7) modification in species behaviour.

### Introduction

In the alluvial forests of great rivers, the characteristics of the plant communities change with the gradual modifications in geomorphology and hydrology from upstream to downstream.

In the case of the Rhine rift valley, the river runs freely (without any obstacle). A remarkable causal correlation is therefore observed between the evolution of alluvial forest-models (sylvigenetic patterns, dynamic processes), their functional aspects (the nutrient cycling, the resistance to hydromorphy), and the evolution of the

geomorphological and hydrological features of the rift valley. Thus, this rift can be considered as an ecological model for studying the direct effects of geomorphological and hydrological parameters upon structure and dynamics of alluvial forests.

### Material

*The site: the Rhine flood plain in the Rhine rift valley (North-East France/South-West Germany)*

Thanks to the very regular course of the Rhine along the rift (300 km long), this great river is

homogeneous lengthwise and the geomorphological and hydrological parameters throughout its length evolve very regularly from upstream to downstream (Fig. 1).

Four main sectors follow each other from Basel to Mainz.

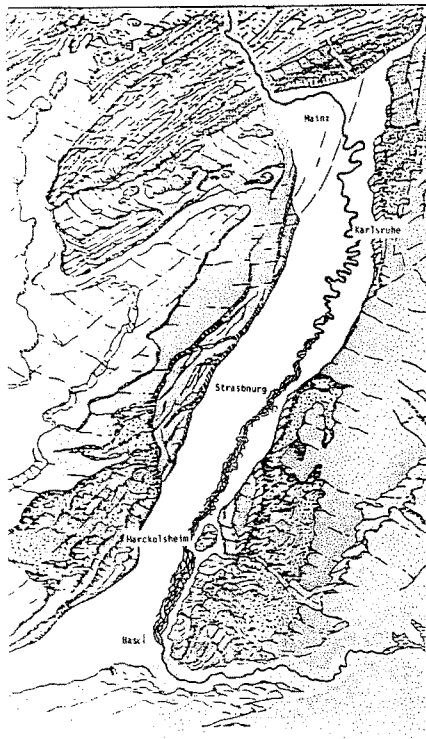
Their characteristics evolve according to the slope, nature of the deposits and hydrology (though the hydrological regime is dependent on the dominant alpine catchment of the basin, with summer floods and low waters in winter and spring: it is a typically nival and nivo-glacial regime) (Carbiener 1984; Pautou & Decamps 1985).

- the braided sector (slope 1‰) occupies the southern area from Basel to Marckolsheim. It is characterized by strong dynamics and dominant ablation. The substrates are sandy/gravelly and very calcareous.
- the braided and anastomosed sector (slope 0,7‰) follows the former sector northwards (from Marckolsheim to Strasbourg). It is char-

acterized by strong dynamics, light texture and very calcareous deposits too. But, owing to the exceptional width of the high-water bed of the Rhine (250 km<sup>2</sup> on the left bank partially for tectonic reasons, Vogt 1978, 1980), two kinds of channels (braids and anastomoses Bravard 1982) are observed: the braids are fast-running, shallow channels located very near the river and often reworked by the flood (braided channels). The anastomoses are low-velocity channels, further from the river (1–2 km away), and only in operation during great floods (anastomosed channels).

In this sector, tributaries from the Hercynian mountains are rare, occurring only on the right bank (Carbiener 1983).

- the anastomosed sector with incipient meanders (slope 0,4‰), stretches between Strasbourg and Karlsruhe. In this area, the dynamics of the Rhine are still strong, but less so than in the southern sectors. That is why the deposits become finer (enrichment in clay). The



MEANDER SECTOR  
Slope: 0,1 - 0,3 ‰

ANASTOMOSED SECTOR WITH INCIPIENT MEANDERS  
Slope (average): 0,4‰

BRAIDED AND ANASTOMOSED SECTOR  
Slope (average): 0,7‰

BRAIDED SECTOR  
Slope (average): 1‰

HYDROLOGY	GRAIN-SIZE DISTRIBUTION	GEOCHEMISTRY OF THE DEPOSITS
Summer floods, but floods can occur in winter and in spring (snow-melting and rains in the Hercynian mountains)	Fine-grained deposits (60% clay) Clay-humus complexes	Calcareous, but mixed with acid deposits from Hercynian mountains CaCO <sub>3</sub> = 15%
Intermediate, between the meander sector and the braided and anastomosed sector		
Only summer floods	Rolled pebbles, sand and silt 20% clay in a few sites	Very calcareous: CaCO <sub>3</sub> = 20-25%
Only summer floods	Rolled pebbles, sand	Very calcareous: CaCO <sub>3</sub> = 20-25%

Fig. 1. Evolution of the ecological parameters along the length profile of the Rhine in the rift valley.

deposits are calcareous but slightly mixed with acid deposits from Hercynian tributaries.

The channels are deeper and with a low current velocity.

- the meander sector spreads through the German Rhine flood plain between Karlsruhe and Mainz. The decreasing slope reaches less than 0,03‰ in Mainz. This sector is characterized by weaker dynamics of the river, with dominant silting up and frequent floods in the winter and spring, thanks to the tributaries. The meanders have a very low down-valley migration (Musall 1969). The alluvial deposits become less calcareous and richer in clay than in the former sector (60% clay, Dister 1980).

#### *Characteristics of the alluvial forest communities in the flood plains of great rivers*

All alluvial ecosystems, owing to regular supplies of energy, water and mineral nutrients stemming from floods, are relatively open.

Flood energy is responsible for regular changes in the deposits by morphogenesis. It emphasizes

the successional sequences of forest communities, quickens mineral and organic turn-over and sylvigenetic cycles.

But this energy varies in terms of longitudinal and tranverse sectors of the flood plain: the energy is greatest near the main channel and in the upper and middle water-courses. So, in the upper course of the Rhine, the constant supply of water and biogenic minerals by summer floods on aerobic, porous and eutrophic substrates is directly responsible for the diversity in forest communities and in species, for a very complex pattern and for a tremendous primary woody productivity (15–20 m<sup>3</sup>/year/ha in pioneer stages and on the best types of the terminal hardwood stages of the braided and anastomosed sector of the Rhine).

With the decrease in energy downstream, the regular renovation of substrates and forest communities slows down.

Our results (Carbiener *et al.* 1987; Schnitzler 1988) stress that the successional sequences and sylvigenetic pattern of alluvial forests become simpler with the increase in hydromorphy, the enrichment in clay and the longer flooding

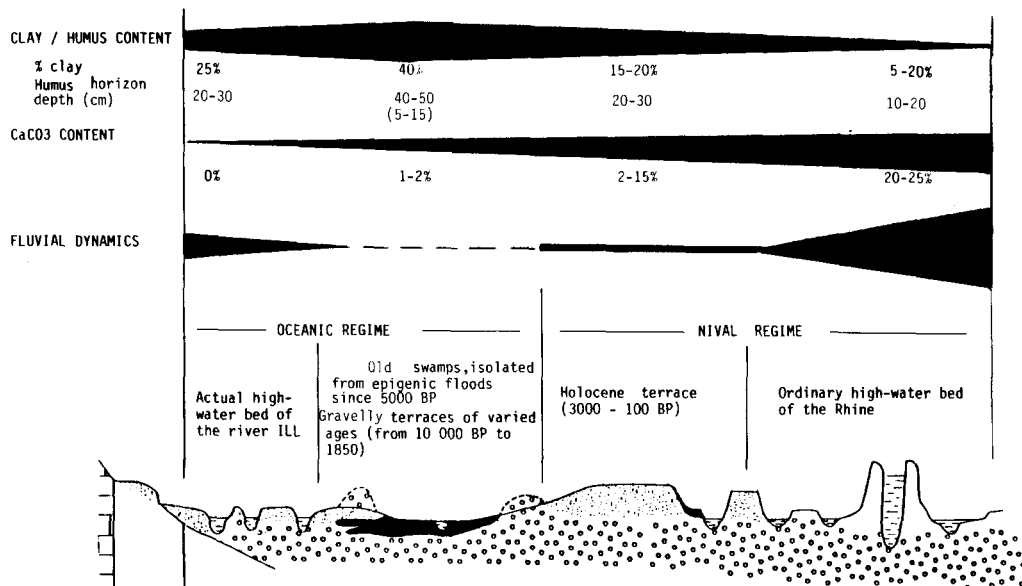


Fig. 2. Evolution of the ecological parameters along the tranverse profile of the Rhine in the braided and anastomosed sector of the Rhine.

periods. Alluviation (essentially clay and silt) in forests predominates over ablation.

This evolution from upstream to downstream is observed along the transverse profile too, in the braided and anastomosed sector (Carbiener 1984; Carbiener *et al.* 1988) (Fig. 2). The homology between longitudinal and transverse profiles of the great European rivers was first emphasized by Wendelberger (1973) in the Danube flood plain.

#### *Typology of the alluvial forest communities of the Rhine fluvial axis*

There are many forest communities in the high-water bed of the Rhine, because of the complexity of the topography, the grain-size distribution and the influence of the distance from the main channels (which defines the impact of the flood upon the woody successions) (Margl 1973; Ellenberg 1963; Carbiener *et al.* 1988). But the building of dykes (1830–1850) along the Rhine, at a constant distance of 2–3 km, has altered the natural order of the forest communities over the past century or so.

We therefore distinguish 6 main forest communities (Carbiener 1974; Schnitzler 1988). They include

- the Rhine succession-catena with 3 flooded associations: *Salici albae-Populetum nigrae*, *Fraxino-Populetum albae*, *Querco-Ulmetum minoris*,
- the non-flooded associations: *Ulmo-Carpinetum*, *Carici albae-Tilietum*, *Pruno padi-Quercetum*.

#### *The succession-catena of alluvial forest communities within the dykes*

Near the Rhine, the strong dynamics are responsible for a complex successional sequence with 3 main stages: Willows Poplars communities, Ash Poplars communities, Oak Elm Ash communities.

- 1) A pioneer stage of soft-wood trees (*Salici albae-Populetum nigrae*), constituted by early-successional and light-demanding species, mainly *Salix alba* and *Populus nigra*.

This stage lasts on average about 50 years (30–80).

On silty-clayey deposits, *Acer negundo*, a neophyte species avoiding limestone, can participate in the pioneer stage.

- 2) A post-pioneer stage of mixed trees (soft and hard-woods: *Fraxino excelsiori-Populetum albae*), constituted by intermediate-successional species: *Populus alba*, *Ulmus minor*, *Alnus incana*, *Prunus padus*, *Fraxinus excelsior*, *Betula pendula*.

This stage follows the pioneer stage and lasts 100 to 150 years on average. Its structure becomes more complex than the former (3–4 layers) and woody lianas (*Hedera helix* and *Clematis vitalba*) appear, thanks to the enrichment of fine deposits (silt) (Margl 1973; Schnitzler 1988), but the sylvigenetic cycle remains linear.

This succession (pioneer/post-pioneer stages) is not however seen in all the cases. A succession may start with a white Poplar-Elm (or white Alder) forest community when the alluvial deposits are mainly silty after a flood (Carbiener D. 1989).

- 3) A terminal stage of hard-wood trees (*Querco-Ulmetum minoris*), essentially constituted by long-living successional species belonging to the terminal stage. *Quercus robur*, *Fraxinus excelsior* and *Ulmus minor* are the main species of the canopy. But this forest community is characterized by a remarkable richness in phanerophytes and a great species diversity (i.e., a remarkable spatial distribution of the woody species) (Carbiener 1970, 1974). The sylvigenetic cycle also includes softwoods of the former stages, which are dominated by small-tree species such as *Malus sylvestris*, *Pyrus pyraeaster*, *Crataegus monogyna*, *Prunus fruticans*, *Evonymus europaeus* (in tree form).

Thus, species of the zonal European forests (Carpinion, Fagetalia) such as *Acer campestre*, *Acer pseudoplatanus*, *Acer platanoides*, *Carpinus betulus*, *Tilia cordata*, *Fagus sylvatica* can also reach the terminal community, but they are strongly selected according to the abiotic environ-

ment and to the synecological selective pressure acting on the juvenile phase of these phanerophytes (Carbiener 1974).

Other isolated woody species such as *Ulmus laevis* and *Alnus glutinosa* (both in moist sites) occur locally in the canopy.

The smaller trees such as *Pyrus pyraister*, *Malus sylvestris*, *Juglans regia*, *Betula pendula*, all low competitive species, can grow in this kind of forest community because the leaves of the dominant trees of the canopy allow a high-flux radiance to reach the ground. But all these species are strongly selected by the substrate conditions and thus characteristic of only one or two geomorphological sectors of the fluvial corridor. For example, *Pyrus pyraister*, a subacidophilic species, increases with the enrichment in clay content downstream. This enrichment in clay compensates for the basicity of the substrates and allows a relative abundance of this species in the meander sector.

The behaviour of *Malus sylvestris* (a basiphilic species) and *Juglans regia* (intolerant of soil hydromorphy), is the opposite.

They occur in the intermediate sectors (braided and anastomosed sector and anastomosed sector with incipient meanders).

Finally, because of the complexity of the sylvi-genetic cycle, which includes internal phases of youth, maturity and senescence, isolated big soft-wood trees such as *Salix alba*, *Populus alba*, *Populus x canescens*, *Populus nigra* belonging to former stages can reach the canopy and a height of 35–48 m.

The high species diversity allows the development of an irregular canopy pattern and the presence of many gaps in which woody lianas (*Clematis vitalba*, *Hedera helix*, *Vitis sylvestris* till 1900) occur. These lianas, which can reach 30–35 m in height, are very sensitive to hydromorphy (especially if there is summer flooding). They are therefore restricted to the upstream sectors, between Basel and Karlsruhe, and to the coarse-grained islands downwards.

The irregular canopy mosaic is responsible too for the complexity of the vertical structure with 7 layers (Carbiener 1970, 1974; Walter 1979, Dister

1985) (Fig. 3), as well as the complexity of the horizontal pattern (dispersed species distribution, giving high species-diversity indexes).

The structure complexity is greater in the non-hydromorphic, braided and anastomosed sector (Carbiener 1974; Carbiener *et al.* 1987).

In the herbaceous layer, we observe an increase in geophytes (Table 1) and a decrease in helophytes.

Thus, trees in the mature phase of this terminal forest community may reach an age of 200–400 years (the ages of the longest-living trees such as *Quercus robur*, *Populus nigra*, in the alluvial sites), according to the dendrochronological results (Becker 1982), who, when studying fossil trees in Alsatian gravel-pits, never found any Oak more than 400 years old (rather young for this species!). This fact might be explained, on one hand, by the mean periodicity of great floods in all sites of the high-water bed of the Rhine from the Subboreal era to 1850. On the other hand, this period might correspond to the senescence of Oaks in eutrophic-hydrophilic conditions.

#### *The non-flooded forest communities*

These communities are situated far from the Rhine, or on high terraces, or resulting from the 1850 correction of the river.

*A) Oak-Hornbeam alluvial communities (Ulmo-Carpinetum), beyond the dykes established between 1830–1860.* Beyond the dykes, the Querco-Ulmetum has evolved into another forest community through the withdrawal of the flood waters (from epigenic waters) since 1860. This forest community is alluvial too because it remains linked with the ground waters, rich in dissolved oxygen. It still contains characteristic alluvial forest trees (*Salicetea*, *Alno-Ulmion* and *Ulmenion*) such as *Populus alba*, *Populus x canescens*, *Salix alba*, *Alnus incana*, *Prunus padus* and woody lianas. But these species are less abundant than within the dykes because of the arrival of shade-tolerant and competitive species such as *Carpinus betulus* belonging to the zonal chalky wing of the Carpinion (*Daphno-Carpinenion sensu Rameau 1987*) and intolerant of soil hydromorphy (*Prunus*



Table 1. Enrichment in geophytes in the herbaceous layer from the pioneer stage to the terminal stage.

Forest communities (10–30 samples)	Salici- populetum nigrae	Fraxino- populetum albae	Quercu- ulmetum minoris	Ulmo- carpinetum	Pruno padi- quercetum
Geophyt					
Allium ursinum	II <sup>+</sup>	II <sup>+</sup>	(V <sup>4</sup> )	(V <sup>4</sup> )	(V <sup>4</sup> )
Arum maculatum	II <sup>+</sup>	II <sup>+</sup>	III <sup>1</sup>	III <sup>1</sup>	IV <sup>2</sup>
Paris quadrifolia	II <sup>+</sup>	IV <sup>+</sup>	IV <sup>1</sup>	IV <sup>1</sup>	II <sup>1</sup>
Polygonatum multiflorum	II <sup>+</sup>	III <sup>+</sup>	IV <sup>1</sup>	IV <sup>1</sup>	V <sup>2</sup>
Anemone nemorosa	II <sup>+</sup>	II <sup>+</sup>	III <sup>2</sup>	V <sup>2</sup>	V <sup>2</sup>
Convallaria maialis	II <sup>+</sup>	III <sup>+</sup>	IV <sup>2</sup>	I <sup>+</sup>	IV <sup>2</sup>
Ficaria verna	(III <sup>3</sup> )	(III <sup>2</sup> )	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
Neottia nidus avis		I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
Listera ovata		I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
Orchis purpurea		I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
Platanthera bifolia		I <sup>+</sup>	I <sup>+</sup>	II <sup>1</sup>	I <sup>+</sup>
Asarum europaeum		I <sup>+</sup>	I <sup>1</sup>	(II <sup>2</sup> )	(III <sup>2</sup> )
Scilla bifolia					(IV <sup>2</sup> )
Mercurialis perennis					I <sup>1</sup>

( ): locally.

avium, Juglans regia, Asarum europaeum, Orchidaceae).

The species richness is still high but the species diversity and the structural complexity decrease.

*B) Lime-Hornbeam alluvial communities (Carici albae-Tilietum cordatae) on high sandy terraces.* This forest community is established on high sandy terraces not often flooded (every 10 years) inside or outside the dykes. The canopy is dominated by Tilia cordata and Acer campestre, and includes Oak, Elms and Ash. Sometimes, relics of the Ulmenion with reduced vitality such as Populus alba, Populus x canescens, Alnus incana, Prunus padus, Ulmus laevis, Ulmus minor, occur in the canopy.

The main shrubs are basophilic and thermophilic species, such as Berberis vulgaris, Ligustrum vulgare, Daphne mezereum and Viburnum lantana. The herbaceous layer is characterized by facies of meso-xerophilic species such as tussocks of Carex alba, Euphorbia amygdaloides, Carex flacca, Helleborus foetidus.

*C) Oak-Maple alluvial communities (Pruno padi-Quercetum) of the Holocene terrace (5–6 km from the Rhine) (Carbiener 1983, Striedter 1988).* This

forest community stems from the Ulmo-Carpinetum, after some 2000 years of pedological evolution. The soils become less calcareous (only 4–10%) and richer in clay (20% in the upper horizon).

The species richness decreases, as does the species diversity. But, despite the increase in the zonal species (Carpinion, Fagetalia) such as Carpinus betulus, Prunus avium, Acer pseudoplatanus, the alluvial species (Ulmenion), such as Prunus padus, Ulmus minor, Ulmus laevis, are still present, sometimes even abundant.

Table 2 shows the evolution of trees in the canopy from pioneer to terminal stages (flooded, non-flooded). There is a gradual change from soft-wood to hard-wood from the pioneer to the terminal stages (a well-known fact), but also a decrease in species richness from the flooded forest communities to the non-flooded communities. The species diversity is not shown in this table. In table 1, we have an example of the changes in the spring flower patterns between the 3 terminal stages. There is an enrichment in argilophytes (Mercurialis perennis, Scilla bifolia) in the Pruno-Quercetum, by enrichment in clay (pedological evolution).

## Results

### *A new conception of river-side zonation*

In spite of appearances, the spatial pattern of the major flood plain forest communities does not depend on the topography (Moor 1958; Tchou-Yen-Tcheng 1948...) but on temporal processes and secondarily (but linked with the dynamics) on the grain-size distribution of the substrates (Margl 1973; Carbiener *et al.* 1988; Schnitzler 1988).

These temporal processes depend on:

- the energy-load of flooding
- the frequency and periodicity of great floods (mean time-span of the frequency of floods for each element of the mosaic of natural units forming the dynamic flood-plain sequence).

Consequently, the temporal processes vary along the Rhine, with the decrease in the slope, as well with the transverse profile. In both cases, there is a gradual reduction in reworked deposits.

### *Spatial evolution of the alluvial pattern along the Rhine*

*A) The braided sector.* Before the canalization of the Rhine, there was an absolute spatial dominance of pioneer and post-pioneer stages, linked

with the instability of the braided channels, leading to pluridecennial substrate reworking.

Nowadays, after the correction in the 19th century, canalization, followed by a severe fall in the ground-water table, the xeric wing of the alluvial forest complex (Carici-Tilietum, typical of young and calcareous substrates) dominates, with Ulmo-Carpinetum, in silty-clayey terraces.

*B) The braided and anastomosed sector.* This sector is the most complex and diverse in its alluvial pattern. Within the Rhine axis itself, we observe a great number of sub-associations and variants in the 3 successional dynamic stages. These 3 stages (pioneer, post-pioneer and terminal stages) are almost equally extensive, but the pattern comprises Carici-Tilietum and Ulmo-Carpinetum too.

The braided and anastomosed sector also presents a maximum geomorphological differentiation in the transverse profile, including the Holocene terraces and depressions, particularly developed on the left bank. The great extent of this left-bank depression (the marginal depression, Carbiener 1969) allows the development of 10 major forest communities (Carbiener 1983, Schnitzler 1988) (Fig. 4).

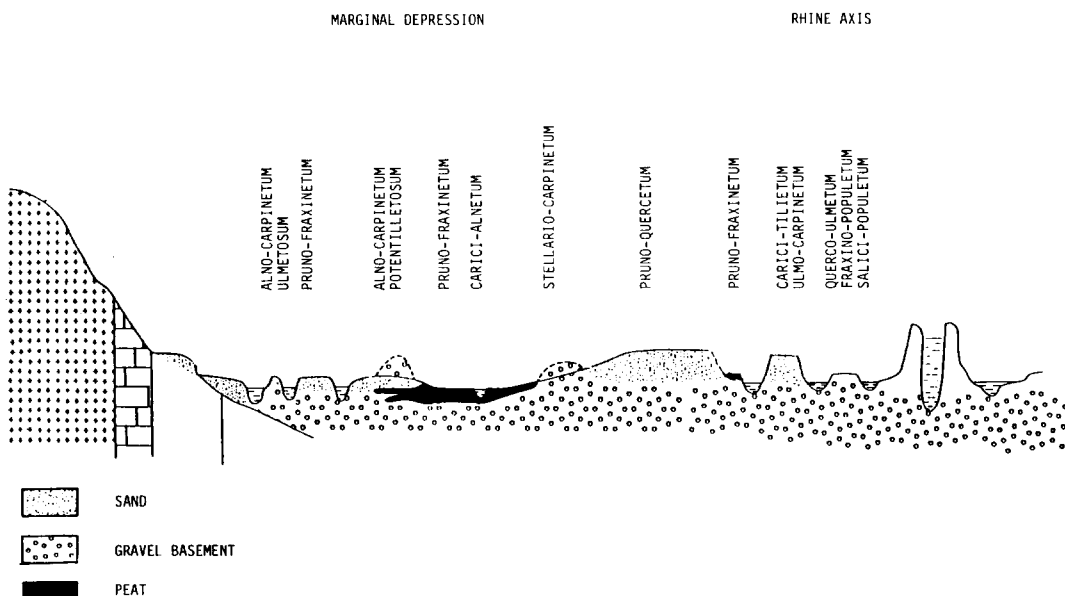


Fig. 4. The ten main forest communities of the braided and anastomosed sector.



Table 2. Modifications in the canopy pattern in the three main stages of the Rhine successional sequence.

SP: Salici albae-Populetum; FP: Fraxino excelsiori-Populetum albae; QU: Quercu-Ulmetum; UC: Ulmo-Carpinetum; CT: Carici albae-Tilietum; PQ: Pruno padi-Quercetum.

Forest communities	SP	FP	QU	UC	CT	PQ
<i>Pioneer species</i>						
Salix alba	V <sup>3</sup>	V <sup>+</sup>	II <sup>+</sup>	I <sup>+</sup>		
Salix eleagnos	II <sup>+</sup>	II <sup>+</sup>	I <sup>+</sup>	+		
Populus nigra	V <sup>2</sup>	IV <sup>2</sup>	II <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	
Robinia pseudacacia	III <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	
<i>Intermediate species</i>						
Populus alba	IV <sup>1</sup>	V <sup>2</sup>	III <sup>1</sup>	II <sup>1</sup>	II <sup>+</sup>	I <sup>+</sup>
Alnus incana	I <sup>1</sup>	V <sup>2</sup>	III <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>	I <sup>+</sup>
Betula verrucosa	I <sup>+</sup>	II <sup>2</sup>	II <sup>+</sup>	II <sup>+</sup>	III <sup>+</sup>	
<i>Intermediate and mature species</i>						
Prunus padus	I <sup>+</sup>	II <sup>1</sup>	III <sup>1</sup>	III <sup>1</sup>	I <sup>+</sup>	IV <sup>2</sup>
Ulmus minor	I <sup>+</sup>	IV <sup>2</sup>	IV <sup>3</sup>	IV <sup>3</sup>	IV <sup>1</sup>	V <sup>2</sup>
Fraxinus excelsior	I <sup>+</sup>	V <sup>3</sup>	V <sup>3</sup>	V <sup>3</sup>	V <sup>3</sup>	V <sup>2</sup>
Quercus robur	I <sup>+</sup>	V <sup>2</sup>	V <sup>2</sup>	V <sup>3</sup>	V <sup>2</sup>	V <sup>3</sup>
Ulmus laevis	I <sup>+</sup>	II <sup>1</sup>	III <sup>1</sup>	II <sup>+</sup>	II <sup>+</sup>	I <sup>+</sup>
Populus canescens		I <sup>+</sup>	III <sup>1</sup>	II <sup>1</sup>	II <sup>+</sup>	I <sup>1</sup>
Malus sylvestris		I <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>	II <sup>+</sup>
<i>Mature species</i>						
Acer campestre		I <sup>2</sup>	III <sup>2</sup>	IV <sup>2</sup>	V <sup>2</sup>	III <sup>1</sup>
Acer pseudoplatanus	I <sup>+</sup>	III <sup>2</sup>	II <sup>1</sup>	II <sup>+</sup>	II <sup>2</sup>	V <sup>3</sup>
Acer platanoides		+	I <sup>+</sup>	+	+	I <sup>1</sup>
Tilia cordata		III <sup>+</sup>	II <sup>1</sup>	II <sup>+</sup>	V <sup>2</sup>	II <sup>+</sup>
Alnus glutinosa	+	+	I <sup>1</sup>	+		+
Ulmus glabra			I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>
Pyrus pyrastrer			+			I <sup>+</sup>
Prunus avium			I <sup>+</sup>	II <sup>+</sup>	I <sup>+</sup>	III <sup>+</sup>
Juglans regia		I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	I <sup>+</sup>	III <sup>1</sup>
Carpinus betulus			II <sup>1</sup>	II <sup>2</sup>	IV <sup>2</sup>	III <sup>3</sup>
<i>Woody lianas</i>						
Clematis vitalba		III <sup>+</sup>	V <sup>3</sup>	V <sup>2</sup>	IV <sup>1</sup>	III <sup>2</sup>
Hedera helix	+	+	IV <sup>2</sup>	IV <sup>2</sup>	IV <sup>2</sup>	IV <sup>1</sup>

C) *The anastomosed sector, with incipient meanders.* This sector has roughly the same pattern as the former sector, but with a general decrease in species richness and species diversity in most of the communities concerned, especially along the Rhine itself (Ulmenion and the foregoing pioneer stages). Some boreo alpine species, such as *Prunus padus*, *Alnus incana*, *Salix eleagnos*, *Salix daphnoides*, *Salix nigricans*, gradually disappear. The thermophilic, intolerant of soil hydromorphy species such as *Tamus communis* and *Juglans regia* disappear too.

According to Becker (1982), Ash was present during Holocene era, but very rare (about 0,7% of the reconstituted fossil canopy pattern) (Table 4).

Table 4. Rates of genera among the fossil trunks found in the Alsatian gravel-pits (Becker 1982).

Genera	Number of trees
<i>Quercus</i>	180
<i>Ulmus</i>	138
<i>Populus</i>	67
<i>Salix</i>	9
<i>Acer</i>	8
<i>Pinus</i>	6
<i>Fagus</i>	4
<i>Fraxinus</i>	3
<i>Alnus</i>	3
<i>Abies</i>	1
<i>Castanea</i>	2
<i>Picea</i>	1

Table 3. Changes in floristic composition in the Querco-Ulmetum from upstream to downstream.

Braided and anastomosed sector	Meander sector
Great development of the stratification (5–6 layers)	Simplification of the stratification (3–4 layers)
Complexity of the sylvigenetic processes and the spatial pattern	Simplification of the silvigenetic processes and the spatial pattern
High species diversity	Low species diversity
Great species richness (60 woody species)	Decrease in species richness (30 woody species)
Enrichment in light-demanding, mostly basiphilic species of the pioneer and post-pioneer stages such as <i>Prunus padus</i> , <i>Alnus incana</i> , <i>Populus alba</i> , <i>Populus × canescens</i> , <i>Salix alba</i>	Disappearance of light-demanding species, partly replaced by neutrophilic and subacidophilic species and favoured by the high clay-content of the deposits such as <i>Acer pseudoplatanus</i> , <i>Acer negundo</i> , <i>Sambucus nigra</i>
Enrichment in species intolerant of soil hydromorphy such as <i>Juglans regia</i> , <i>Malus sylvestris</i> , <i>Tamus communis</i> , woody lianas	Enrichment in species intolerant of soil hydromorphy, such as <i>Pyrus pyraeaster</i> , <i>Scilla bifolia</i> , <i>Viola elatior</i> , <i>Primula elatior</i>
Enrichment in boreo-alpine species, such as <i>Salix eleagnos</i> , <i>Salix daphnoïdes</i> , <i>Daphne mezereum</i> , <i>Prunus padus</i> , <i>Alnus incana</i> , <i>Equisetum hyemale</i> , <i>Carex alba</i> , <i>Carex ornithopoda</i> , <i>Hippophae rhamnoides</i> , <i>Pinus sylvestris</i> (gravel terraces)	Disappearance of boreo-alpine species
Enrichment in calcicollic and thermophilic species, such as <i>Populus alba</i> , <i>Populus × canescens</i> , <i>Euphorbia amygdaloïdes</i> , <i>Helleborus foetidus</i> , <i>Orchidaceae</i>	Impoverishment in calcicollic and thermophilic species and enrichment in neutrophilic, subacidophilic species, such as <i>Fagus sylvatica</i> , <i>Populus tremula</i> , <i>Acer platanoides</i> , <i>Salix viminalis</i> , <i>Impatiens parviflora</i> , <i>Maianthemum bifolium</i>
Luxuriance of woody lianas ( <i>Clematis vitalba</i> , <i>Hedera helix</i> , <i>Vitis sylvestris</i> till 1900). Presence in gaps of herbaceous lianas, such as <i>Tamus communis</i> , <i>Humulus lupulus</i>	Quasi-disappearance of woody lianas

On the contrary, Ash was absent from the braided and anastomosed sector till the 19th century. But, since then, with the general enrichment in silt after this correction, *Fraxinus excelsior* has developed widely in this sector. It is nowadays favoured by the Elm disease and often supplants *Ulmus minor*, *Ulmus laevis* and their hybrids in the post-pioneer and the terminal stages.

*D) The meander sector.* In this sector, the internal diversity of the stages is greatly reduced, as the relevés tables published by Dister (Dister 1980) show. The intermediate stage almost disappears, due to the reduction in the hydrological dynamics, correlated with the sharp decrease in the slope and the disappearance of the species of boreo-alpin origin playing an important role in this stage (Table 3).

The terminal forests dominate here, and are poorer in species and in habitat diversity. The pioneer stages are restricted to the banks of the meanders and the islands of the main channels. They correspond to the dampest wing of the *Salicetum albae* and tend to evolve towards a quasi-permanent stage on lower levels flooded for a long time every year.

#### *Evolution of the terminal stage of Quercu-Ulmetum from upstream to downstream*

The characteristics of the *Quercu-Ulmetum* along the length change gradually with the decrease in substrate-porosity and the correlative increase in hydromorphy (Tables 3 and 5).

#### *Vicariance upstream/downstream*

##### *Ecological vicariances*

Vicariances are numerous between the extreme sectors of the Rhine (Table 6). They are numerous too along the tranverse profile, essentially in the

Table 6. Ecological vicariances along the length profile of the Rhine (South/North).

Upstream	Downstream
<i>Alnus incana</i>	→ <i>Alnus glutinosa</i>
<i>Populus alba</i>	→ <i>Populus tremula</i> , <i>Populus × canescens</i>
<i>Salix eleagnos</i>	→ <i>Salix viminalis</i>
<i>Salix nigricans</i>	→ <i>Salix triandra</i>
<i>Salix alba</i>	→ <i>Salix fragilis</i> , <i>Salix × rubens</i>
<i>Anemone nemorosa</i>	→ ( <i>Anemone ranunculoides</i> )
<i>Carex acutiformis</i>	→ <i>Carex gracilis</i>

Table 5. Decrease of lianas in the *Quercu-Ulmetum* from upstream to downstream.

Geomorphological sectors along the longitudinal profile of the Rhine	Braided and anastomosed sector	Anastomosed sector with small meanders	Meander sector
Number of observations	200	14	13
<i>Woody lianas</i>			
<i>Hedera helix</i> (25–30 m high)	V <sup>2</sup>	II <sup>2</sup>	I <sup>2</sup>
<i>Clematis vitalba</i> (25–30 m high)	V <sup>2</sup>	IV <sup>1</sup>	III <sup>1</sup>
<i>Rubus caesius</i> (0,50 m high)	IV <sup>1</sup>	IV <sup>1</sup>	III <sup>1</sup>
<i>Herbaceous lianas</i>			
<i>Tamus communis</i>	II <sup>1</sup>	–	–
<i>Solanum dulcamara</i>	(III <sup>+</sup> )	(II <sup>+</sup> )	(I <sup>+</sup> )
<i>Humulus lupulus</i>	I <sup>+</sup>	–	–
<i>Galium aparine</i>	(III <sup>2</sup> )	–	–

( ): locally

Table 6'. Ecological vicariances along the tranverse profile of the Rhine (East/West) in the braided and anastomosed sector.

Rhine axis	Marginal depression
<i>Alnus incana</i>	→ <i>Alnus glutinosa</i>
<i>Populus alba</i>	→ <i>Populus tremula</i>
<i>Salix alba</i>	→ <i>Salix fragilis</i> , <i>Salix</i> × <i>rubens</i>
<i>Salix eleagnos</i>	→ <i>Salix viminalis</i>
<i>Salix nigricans</i>	→ <i>Salix triandra</i>
<i>Crataegus monogyna</i>	→ <i>Crataegus laevigata</i>
<i>Prunus fruticans</i>	→ <i>Prunus spinosa</i>
<i>Rubus caesius</i>	→ <i>Rubus fruticosus</i>
<i>Melica nutans</i>	→ <i>Melica uniflora</i>
<i>Anemone nemorosa</i>	→ ( <i>Anemone ranunculoides</i> )

( ): locally

braided and anastomosed sector (Table 6'), because of the decrease in basicity, the increase in fine textures, and the winter and spring floods.

#### Modifications of species behaviour

Radical differences in behaviour in a same species appear from upstream to downstream, due to changes in synecology. Thus, several species become more tolerant to flooding (Carbiener *et al.* 1987) (Table 7').

In the tranverse profile, there are modifications in species too (Table 7), partially the same as those in the longitudinal profile, and which are due to the changes in ecological factors.

### The biogeochemical cycling

#### General features

The general features of the alluvial Rhine ecosystem are as follows:

- 1) Rapid turn-over of litter, by intense fungal, bacterial and detritus-consuming activity, stimulated by the soil richness in mineral and the low fungal-inhibitor content of the leaves in most alluvial species. Litter therefore decays within a few weeks.
- 2) Regular fertilization both organic and mineral, by summer floods
- 3) Base-rich fertile soil (mull soil) with dominant biological humification
- 4) At least 2 seasonal cycles: in the spring (with the vernal species) and in the autumn
- 5) No problem of drought thanks to the summer floods (of the Rhine) and the nearness of the ground-water (in the marginal depression).
- 6) As a result: timber productivity can reach 20 m<sup>3</sup>/ha/year.

#### Evolution of the biogeochemical cycling from upstream to downstream.

The availability of nutrients (K +, Mg + +, P -) evolves along the Rhine, because fertilization due to flooding comes at 2 different periods: upstream in the summer and, downstream in the summer

Table 7. Modification of species behaviour along the length profile of the Rhine (South/North).

Rhine flood plain	Upstream	Downstream
Species		
<i>Tilia cordata</i>	Only on higher and non-flooded terraces	Extended on lower and flooded terraces
<i>Acer campestre</i>		
<i>Scilla bifolia</i> <i>Convallaria maialis</i>		
<i>Allium ursinum</i> <i>Arum maculatum</i> <i>Hedera helix</i> <i>Clematis vitalba</i>	Extended on lower and flooded terraces, with coarse texture of the deposits	Only on higher and non-flooded terraces, with fine-grained texture of the deposits
<i>Prunus padus</i>	Extended along the Rhine axis	Pushed away to marginal damp areas

Table 7'. Modification of species behaviour along the tranverse profile of the Rhine (East/West) in the braided and anastomosed sector.

Braided and Anastomosed sector	Rhine axis	Marginal depression
Species		
Tilia cordata Acer campestre Scilla bifolia	Only on higher and non-flooded terraces	Extended on lower and flooded terraces
Convallaria maialis	Only on higher and non-flooded terraces Very abundant	Sparse
Allium ursinum Arum maculatum	Extended on lower and flooded terraces	
Hedera helix Clematis vitalba	Very abundant. Extended on flooded, but non-hydromorphic terraces	Rare within the forest communities
Prunus padus	Extended along the Rhine axis	Extended along the Ill axis

and spring. The availability is enhanced downstream by the enrichment in clay of the substrates.

The activity of aerobic bacteria decreases downstream due to the appearance of hydromorphy.

In upstream forest communities, the presence of symbiotic nitrogen fixation by *Alnus incana* and the presence of species whose leaves disappear very quickly (*Prunus padus*, *Cornus sanguinea* and others, such as *Populus alba*, with specific ectomycorrhizal symbionts and mineral-rich litter) improve the efficiency of the global mineral cycling and quickens the turn-over. With the disappearance of these species downstream, dwindles this contribution to better mineral cycling also.

In upstream forest communities, the presence of complementary cycles (spring cycle with spring ephemerals and summer cycle with *Hedera helix*) (Trémolières *et al.* 1988) quickens the turn-over too. Downstream, the near-disappearance of woody lianas, the changes in the behaviour of geophytes (because of enrichment in clay and increase in hydromorphy) and reduction in their abundance, are responsible for a slower turn-over.

The complexity of successional stages, linked (as shown on p. 118) with the sylvigenetic patterns upstream is another factor of better biogeochemical cycling efficiency. Downstream, the disappearance of the boreo-alpine and thermophilic alluvial species is responsible for the reduced complexity in successional sequences and in sylvigenetic patterns and, probably suggests a reduced efficiency of biogeochemical cycling.

As a result, we propose the following hypothesis: the closure of the biogeochemical cycle is most efficient in the mosaic complex of the braided and anastomosed sector.

In this sector, thanks to the richness in phanerophytes the complementarities in the supply and in the cycling of mineral resources reach maximum efficiency.

Thus, the most developed alluvial community (*Querco-Ulmetum*) of this complex is close to the working model proposed for the intertropical moist forests (Edwards & Grubb 1982; see also Grubb 1987).

In connexion with the foregoing hypothesis, it may be stated that in the braided and anastomosed sector, the better closure of the mineral cycling tends to compensate for the reduced

cation-exchange capacity due to the shortage of colloids and the dominance of coarse substrates.

On the contrary, in the meander sector, the fine-grained substrates, rich in colloids tend to compensate for the less efficient mineral cycling.

In both cases, the ground-waters are protected against eutrophication and remain very clean in alluvial forests (Carbiener *et al.* 1988). This fact also suggests that the mineral inputs through the floods are balanced by outputs (ablation, release of organic matter). This fact tallies with the theory of the spiral metabolism of the alluvial river corridor (Decamps & Naiman 1989).

## Conclusion

This short survey bears out our introductory statements.

The alluvial forest ecosystem complexes of the Rhine in the rift valley, thanks to its very regular lengthwise profile, provides a remarkable opportunity to study the close relationships between the progressive changes in the dynamic physical processes (such as alluvial morphogenesis) and the correlative changes in dynamic biological processes such as successional sequences and pattern of the forest ecosystems (mosaics of forest communities, sylvigenetic mosaics of the terminal stages).

Thus, all the physical gradations in hydrology, geomorphology and geochemistry create immediate biological reactions in the forest communities.

From upstream to downstream, we observe:

- 1) A simplification of succession processes by the reduction in boreo-alpine species, intolerant of soil hydromorphy, thermophilic, calcareous species such as *Alnus incana*, *Populus alba*, *Prunus padus*, *Daphne mezereum*, *Cornus mas*, *Carex alba*, woody lianas.
- 2) A simplification in pattern, which appears at 2 levels:
  - on a small scale: the spatial pattern of phytosociological units (through the disappearance of the post-pioneer stages).
  - on a large scale: the reduction in the diver-

sity of the woody species in each phytosociological unit, particularly in the very complex mature stage (and, closely connected with this fact: the simplification of the stratification, of the internal sylvigenetic process sequence and of the resulting pattern mosaic).

- 3) A tendency towards less efficient biogeochemical cycling:
  - the reduction in the activity of aerobic bacteria downstream, caused by the appearance of hydromorphy.
  - the reduction in the number of species and populations with nutrient-rich litters
  - the reduction in, or near-disappearance of, the spring cycle (reduction of spring flowers) and the summer cycle (disappearance of *Hedera helix*).
  - but the availability in nutrients increases inversely (reduction in alkalinity, increase in colloids downstream) and balances out the first 3 effects.
- 4) Ecological vicariances of species and changes in species behaviour, another aspect of these physical changes, are also observed between the different sectors of the flood plain.

The interest of the Rhine site is enhanced by the enormous diversity in natural habitat, resulting from the geomorphological complexity of major flood plains.

These flood plains can be considered as one of the most elaborated ecosystem complexes in the temperate area.

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