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# River Dynamics as a Forest Process: Interaction between Fluvial Systems and Alluvial Forests in Large European River Plains

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## I. Abstract

This paper corresponds to an overview of the impacts of the inundations on gallery forest processes, with examples of the upper Rhine valley, France. The geomorphic pattern of big river plains, the particularities of the nutrient cycle, the adaptations of the flora, the specificities of the sylvigenetic cycles are detailed, with examples of the upper Rhine valley.

## Résumé

Cet article se propose de passer en revue les impacts majeurs des rivières sur les forêts riveraines, en s'appuyant sur les écosystèmes alluviaux de la vallée du Rhin, en France. Les adaptations de la flore et les spécificités des cycles sylvigénétiques sont mis en

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relation avec les particularités géomorphologiques et celles des cycles biogéochimiques particuliers au milieu alluvial tempéré.

## II. Introduction

In alluvial plains, river dynamics is recognized as the major force for landscape patterning and ecosystem distribution. Very often the nomenclature for forests is restricted to detailed aspects of species composition, vegetation type, biogeochemical cycles, or forest management. There are fewer comprehensive works concerning the long-term natural forest dynamics (i.e., gap dynamics, successional processes or cycles of mature stands). Understanding the complex relationships between river dynamics and forest processes is critical in both applied and basic ecology. A thorough knowledge is necessary for the correct interpretation both of forest landscapes in big river plains and of the multiple roles that rivers play in maintaining them.

This paper, an overview of the multiple impacts of the recurrence of disturbance dynamics on the functioning of gallery forests, is based on scientific works published in European and North American reviews and on data and figures from more than 10 years of studies carried out in the upper Rhine valley, France.

## III. The Geomorphic Pattern of Big River Plains

A floodplain is an accumulation of deposits carried and then set down by flowing water. Water is hence the dynamic component of the alluvial landscape that distributes energy, material, and information across and through the plain. Fluxes of water, sediments, and energy are both longitudinal (from upstream to downstream) and transversal (from the river to the edges of the plain and vice versa). Water movements are also vertical, with infiltration within the sediments of the plain and circulation through them (Amoros & Petts, 1993).

Water kinetic energy decreases with the decreasing slope of the valley. Along their courses from the high valleys to the coastal lowland, rivers present a wide diversity of geomorphological and hydrological patterns, in relation to the decreasing slope and various other factors such as subsidence, diversity of the geological structure of valleys, and effects of Pleistocene and Holocene history. Moor (1958) distinguished at least five sections characteristic of a river that has its source in the high mountains:

1. Near its source, a narrow stream including small channels into the rock
2. An upstream, erosive river sector with a wandering gravel-bed river split into small fast-flowing channels (braids)
3. A wide middle sector with a river divided into braids and anastomosed side-arms. Sedimentation and erosion alternate in space and time. Sediments are mainly sand and silt. Erosion, migration, and sedimentation constantly rework the landscape, which explains the complex sedimentological pattern with terraces, hollows, backwater depressions, wetlands, secondary arms, and old channels periodically connected with the river. Exchanges with groundwaters are highly active. In the Rhine valley, for example, the river permanently feeds the water table with about 3 $m^3 s^{-1}$, and abandoned channels form a cold, oligotrophic running network of groundwater streams (Carbiener & Trémolières, 1990).

4. A wide low sector characterized by a gradient of less than 0.3%. The river presents large-sized meanders, and sedimentation is predominant. Deposits are fine-textured (clay).
5. Estuaries, with special conditions due to the influence of the tide.

Flooding periods vary according to the longitudinal sector. In sectors 1 and 2, flooding occurs in summer after the melting of snow and glaciers. In sector 3, floods occur in early summer but also in winter, and the influence of tributaries becomes important. Downstream, flood periods occur increasingly later in spring and winter (Ellenberg, 1988).

In middle and downstream sectors, tributaries entering through the valley create new ecological gradients, from very wet sites (swamps) to low-altitude terraces. In these two sectors, a transversal section of the floodplain from the main river to its edges shows increase of hydromorphy and enrichment in clay, due to the increasing influence of tributaries. These gradients are similar to those of the longitudinal profile. This homology between longitudinal and transversal profiles was emphasized for large river plains in Europe by Wendelberger (1952), for the Danube by Wendelberger (1984), and for the Rhine by Carbiener (1984) and Carbiener and Schnitzler (1990).

Floodplain pattern depends also on vegetation (Tricart, 1977; Pautou et al., 1986). It is well known that bare soil, newly deposited by rivers, very quickly becomes invaded by plants. Bushes of therophytes or woody species (essentially *Salix* and *Populus*) contribute, by their rapid growth, to raising the level of the ground by retaining sand, gravel [up to 60 cm in one season according to observations of Grelon (1971) in the middle Loire], woody debris, and leaves. A new sand layer covers these organic deposits during the next flood. Except in the case of a great flood, the island in formation grows regularly in width and height, with continuing accumulation of coarse debris and trapped sediment on its head and an encroachment of willow thickets. When the extension of the islands is lowered, the extension of the islands and the spread of plant cover can be dramatic: in the Loire valley the islands have doubled in the last century (Bomer, 1971). Coarse debris (dead trunks, large branches or roots) therefore play a major role in stream channel geomorphology (Tricart, 1977; Sedell & Frogatt, 1984; Triska, 1984; Harmon et al., 1986), by accumulating at sites such as heads of islands and mouths of secondary channels and bridges, causing local movements of colluvium and sediments. Coarse debris also creates backwaters, stores inorganic sediments, and maintains complex aquatic habitats. Dead trees originate from the river banks; they are frequently pulled down by the river when it undercuts the ground of the edges. Large portions of trees can also be swept away when big channels migrate laterally during great floods. In large rivers, coarse debris is transported downstream and out of channels onto floodplains. This transfer can reach high volumes: up to 5.2 $m^3$ $ha^{-1}$ $year^{-1}$ for five streams of different sizes in Oregon (Harmon et al.,1986).

## IV. Particularities of the Nutrient Cycle

Exceptionally fertile conditions occur in floodplains more than in any other type of habitat, because of favorable temperature, favorable air and soil moisture, and regular input of nutrients and water through flooding. Temperatures are often higher in floodplains than in upland adjacent sites for various reasons, particularly because of protection by nearby mountains against cold winds and influence of warm-air masses when valleys are oriented north-south (e.g., in the case of the Rhine and the Rhône). Air moisture is also constantly higher than upland adjacent sites [up to 20% more (Wendelberger, 1952; Corillion, 1995)] because of the permanence of wide surfaces of evaporating water, particularly during flooding periods. High air moisture coupled with thermophilic mesoclimate enhance evapotranspiration, which probably reaches potential values (Carbiener, 1970). In large floodplains subject to summer floods, soil moisture is provided in hot months by the rising of groundwater coupled with floodings. In upstream sectors, high soil moisture does not induce below-hydromorphic horizons such as gley, thanks to the permeability of the sediments and the high amplitude of groundwater levels, which ventilate the soil and bring an immediate renewal of soil to flooded surfaces. If natural drainage quickly removes flood waters, flooding is hence an energy source bringing sediments and nutrients. Surface water is rich in nutrient salts, fine-particulated sediments [20–25μm (Décamps & Naiman, 1989)], and litter or coarse debris. One major effect of the floodwaters when invading the plain is therefore to manure soils in communities. Along the Garonne, it was assessed that a willow community gave to the river up to five tons per year and per kilometer (Tabacchi & Planty-Tabacchi, 1990). In February 1990, inputs of a Rhine inundation 1 m high and with 2 cm of sediment deposit were 27 kg $ha^{-1}$ phosphorus, 8.9 kg $ha^{-1}$ nitrogen, 86 kg $ha^{-1}$ sulphur, 51 kg $ha^{-1}$ magnesium, and 34 kg $ha^{-1}$ potassium (Sanchez-Perez et al.,1993). Ions and gases are transported within the sediments by vertical movements of flowing waters.

Manuring conditions, however, are not similar all over the floodplain. When the soil level is high above the average water level, inundations are rarer and plants therefore evolve in a less nutrient-rich environment Besides, they may have to cope with temporary dry periods, particularly when they grow on high terraces. When the soil level is barely above the average water level (essentially, old channels), soils are waterlogged and plants suffer from excess of hydromorphy and slowing of the nutrient cycle. The most productive zone is found around the center of the floodplain, where inundations are regular and calm, the soils coarse-textured, and the amplitudes of the groundwaters high.

Chemical transfers between the river and the plain present a spiraling dynamics from upstream to downstream (Amoros & Petts, 1993). In the upper sectors, C, N, and P are assimilated under organic form by invertebrates, then degraded, mineralized, transported, and reassimilated downstream with resilience times that vary according to the size of the debris. Storage in water of big dead trunks can be very long [up to several years (Franklin et al., 1981)], leading to a considerable slowing down of nutrient flux toward downstream, in spite of physical fragmentation by erosive effects of current and activity of aquatic invertebrates and bacteria. However, the importance of forested systems to consumer metabolism is very high. It was estimated that over 50% of the carbon consumed in estuarine waters originated in upstream forests. In conditions of high moisture, warmth, and richness in aerobic bacteria and mushroom populations, decomposition rate of organic matter is rapid—e.g., leaves of *Fraxinus excelsior*, *Cornus sanguinea*, *Ulmus minor*, *Clematis vitalba*, and *Prunus padus* (decomposition within 7 months, according to Penka et al., 1985). Nutrient supplies from litter are therefore available at the beginning of spring. In early summer there exists another source of nutrients, from ivy litter and the geophyte leaves of *Allium ursinum*. These species, abundant in flooded forests, decompose easily and rapidly (Trémolières & Carbiener, 1985; Trémolières et al.,1988).

The specificity of the Rhine fungi flora [high species richness, with a particular abundance in calciphilous and thermophilous species, (Carbiener, 1981)] is a direct response to the particular environment of the floodplain. When flooded, the forests are rich in lignicolous species (32 species). But the number of mycorrhiza is moderate (only 6 species, essentially Cortinariaceae), because of the importance of phosphorous and nitrogen inputs from floodwaters. Noteworthy is the absence of the Russulaceae (Table I). The relative poverty of the saprophyte population is another particularity of the flooded sites (17), due to the very rapid decomposition of the dead leaves. In unflooded sites, the mycorrhizal flora increases to 19 species with a great number of rare, basic species of *Boletus*, *Tricholoma*, and *Russula* genera. Common saprophytes (29 species) of the litter, humus, and buried dead wood appear. Lignicolous, highly specialized species are nearly as numerous as in flooded sites (31 species). Increase in mycorrhiza and saprophyte fungi in unflooded sites improves the nutrient turnover and the P uptake by plants, which partly compensates the loss in nutrient inputs from floodwaters.

For many microbes, invertebrates, vertebrates, and plants, coarse debris represents a habitat and food source. Vascular plants may send their roots into rotting wood to extract water and nutrients. In the Rhine valley, logs are frequently colonized by shrubs and even trees (*Rosa canina*, *Prunus padus*)—which may emerge from rotting hearts of old, senescent trees, particularly in forests prone to long flooding (willow or alder forests)—because rotting trees are the only site on which mesophytic species can grow. Seedlings of some woody species (*Hedera helix*, *Fraxinus excelsior*, *Acer pseudoplatanus*) and grasses (*Impatiens noli-tangere*, *Glechoma hederacea*, *Carex remota*) are found on logs when they rot in full light of wide gaps, but they generally die after one year (pers. obs. along the Rhine).

Nutrient inputs are partly stored in the surface humus and partly taken up by plants. Very few nutrients reach the groundwaters, particularly under highly complex and species-rich forest communities (Sanchez-Perez et al., 1991). Topsoil of floodplain forests is an important and dynamic component, characterized by marked temporal and spatial changes in nutrient concentrations, due to the heterogeneous species composition and the periodic inundations (Penka et al., 1985; Sanchez-Perez et al.,1993). In basic environments, the soil retains phosphorus, potassium, and ammonium. When they are not taken up by plants, magnesium, sodium, sulfate, and nitrate are leached into the groundwaters. Phosphorus may be available to plants during flooding in the form of soluble ferrous phosphate. The regularly flooded sites therefore offer good conditions for P nutrition, in spite of calcareous substrates (Weiss et al., 1991). Concentrations and reserves of nutrients were estimated in woody components of the floodplain forest ecosystem of South Moravia. From this study, Penka et al. (1985) concluded that the highest supplies of nutrients were accumulated in tree stems, and the order of elements was as follows: Ca, N, K, Mg, and P. Leaves are also rich in N and P, as shown by a comparative foliar analysis of dominant woody species between sites prone to eutrophic floods and sites where floods were eliminated by dykes (Schnitzler et al., submitted).

The litter was also nutrient-rich: a total of about 5.6 kg ha yr in south Moravia. For some species, floods influence nutrient retention via the phloem during senescence in autumn, as proved in experiments carried out in the Rhine forests (Table II). The study (Schnitzler et al., submitted) indicates a higher N nutrient retention in flooded sites for *Fraxinus excelsior*, *Clematis vitalba*, and *Ulmus minor*, in spite of a high N nutrient supply in soils. This behavior does not concern P translocation, which may be either higher or similar in flooded sites and unflooded sites (Weiss et al., 1991).

The high organic productivity of floodplains explains the high primary productivity and the high wood productivity. Many trees, shrubs, and woody lianas reach optimum

*(continued on p. 47)*

## Table I

Mushroom species richness in flooded and unflooded stands of the Rhine forests (data from Carbiener, 1981; flora from Michael & Hennig, 1964–1970)

| Species | Period of fructification | Flooded stand | Unflooded stand |
|---|---|---|---|
| | Mycorrhizal species | | |
| *Amanita echinocephala* | Aug–Sep | | ** |
| *Amanita strobiliformis* | Jun–Sep | * | ** |
| *Boletus luridus* | Jun–Sep | | * |
| *Boletus radicans* | Jun–Sep | | * |
| *Boletus rhodopurpureus* | Sep | | * |
| *Boletus satanas* | Aug–Sep | | * |
| *Gyrodon lividus* | Sep–Oct | * | ** |
| *Hebeloma sacchariolens* | Sep–Oct | * | * |
| *Hebeloma sinuosum* | Sep–Oct | | ** |
| *Inocybe fastigiata* | Sep–Oct | | * |
| *Inocybe maculata* | Aug–Oct | ** | * |
| *Lactarius acerimus* | Aug–Oct | * | * |
| *Lactarius pubescens* | Aug–Oct | | * |
| *Russula delica* | Jun–Feb | | * |
| *Russula maculata* | Jul–Sep | | * |
| *Russula pulchella* | Sep–Oct | | * |
| *Russula vitellina* | Oct–Nov | | * |
| *Scleroderma verrucosum* | Aug–Oct | * | * |
| *Tricholoma scalpturatum* | Nov–Dec | | ** |
| Total number of species | | 6 | 19 |
| | Saprophytic species of litter, humus and buried dead wood | | |
| *Agaricus campestre* | Sep–Oct | ** | * |
| *Agaricus gennadii* | Jun–Oct | * | * |
| *Agaricus subfloccusus* | Jun–Sep | | * |
| *Calocybe ionides* | Aug–Oct | | * |
| *Calvatia exepuliformis* | Jul–Oct | | * |
| *Candidus albutiscorticus* | Aug–Nov | ** | * |
| *Chamaemyces fracidus* | Aug–Sep | * | ** |
| *Clitocybe candidans* | Aug–Oct | * | ** |
| *Clitocybe phyllophila* | Oct–Nov | | * |
| *Clitocybe suaveolens* | Oct–Nov | | * |
| *Collybia confluens* | Oct–Nov | | * |
| *Collybia dryophylla* | Oct–Nov | | * |
| *Cystolepiota sistrata* | Aug–Oct | * | * |
| *Disciotis venosa* | Mar–Apr | ** | * |
| *Entoloma aprilis* | Apr | * | |
| *Entoloma saundersii* | Mar–Apr | | * |
| *Helvella crispa* | | | * |
| *Hemimycena candida* | | * | |
| *Lepiota acutesquamosa* | Jul–Oct | * | ** |
| *Lepiota cristata* | Sep–Nov | ** | ** |
| *Lepiota sordida* | Sep–Nov | | * |
| *Lycopordon perlatum* | | | * |
| *Marasmius wynnei* | Sep–Oct | | * |
| *Mitrophora semilibera* | Apr–May | ** | * |

**Table I *(continued)***

Mushroom species richness in flooded and unflooded stands of the Rhine forests (data from Carbiener, 1981; flora from Michael & Hennig, 1964–1970)

| Species | Period of fructification | Flooded stand | Unflooded stand |
|---|---|---|---|
| *Morchella esculenta* | Nov | | * |
| *Morchella rotunda* | Nov | ** | * |
| *Mycena roseipalleus* | Jul–Oct | ** | |
| *Paxina acetabulum* | Apr | | * |
| *Pholiotina foetidus* | | ** | * |
| *Psathyrella melanthina* | Sep–Oct | * | * |
| *Psathyrella vernalis* | Apr–May | * | * |
| *Verpa bohemica* | Apr–May | | * |
| *Verpa digitaliformis* | Apr–May | | * |
| Total number of species | | 17 | 29 |
| | Lignicolous species | | |
| *Armillaria bulbosa* | | * | ** |
| *Auricularia auricula judae* | Oct–Mar | ** | * |
| *Airocimara mesenterica* | | ** | * |
| *Chondrostereum purpureum* | | * | * |
| *Coprinus domesticus* | Apr–May | * | |
| *Coprinus radians* | Apr–May | * | |
| *Funalia gallica* | | * | * |
| *Funalia trogii* | | * | * |
| *Laetiporus sultureus* | | ** | * |
| *Lentinus tigrinus* | May–Sep | ** | * |
| *Lyophyllum ulmarium* | | * | * |
| *Marasmius candidus* | | ** | * |
| *Marasmius rotula* | | * | ** |
| *Micromphala foetidum* | | ** | ** |
| *Mycena haematopoda* | | * | * |
| *Phellinus conchatus* | | ** | * |
| *Phellinus pomaceus* | | * | * |
| *Phellinus ribi* | | | * |
| *Pleurotus cornucopiae* | Jun–Sep | ** | * |
| *Pluteus selicinus* | | * | * |
| *Polyporus brumalis* | | * | * |
| *Polyporus lentus* | | * | * |
| *Polyporus lepideus* | Apr–Jun | * | * |
| *Polyporus mori* | | * | * |
| *Polyporus picipes* | Apr–Oct | * | * |
| *Polyporus squamosus* | May–Sep | * | ** |
| *Stereum subtomentosum* | | ** | * |
| *Trametes confragora* | | ** | * |
| *Trametes suaveolens* | | ** | * |
| *Trametes tricolor* | | * | ** |
| *Tubaria hiemalis* | Oct–Mar | ** | * |
| *Tyromyces fissilis* | Sep–Oct | * | * |
| *Tyromyces subcaesius* | | * | * |
| Total number of species | | 32 | 31 |

* Present; ** abundant.

### Table II

Mean values for concentrations (mg $g^{-1}$ on a dry weight basis of major nutrients in mature and dead leaves of three species in the Rhine valley; data from Schnitzler et al., submitted)

| | Nitrogen | Phosphorus | Potassium | Magnesium |
|---|---|---|---|---|
| *Fraxinus excelsior* | | | | |
| *Summer leaves* | | | | |
| Flooded stands | 36.0 | 1.53 | 15.2 | 5.6 |
| Unflooded stands | 24.0 | 1.25 | 12.3 | 6.8 |
| Significance | ** | *** | * | * |
| *Autumn leaves* | | | | |
| Flooded stands | 14.0 | 0.70 | 7.1 | 3.7 |
| Unflooded stands | 13.4 | 0.50 | 4.2 | 3.9 |
| Significance | ** | *** | | |
| *Ulmus minor* | | | | |
| *Summer leaves* | | | | |
| Flooded stands | 36.7 | 1.90 | 19.8 | 3.2 |
| Unflooded stands | 26.5 | 1.40 | 19.6 | 2.9 |
| Significance | ** | *** | | |
| *Autumn leaves* | | | | |
| Flooded stands | 9.9 | 0.73 | 10.5 | 2.3 |
| Unflooded stands | 9.5 | 0.56 | 8.7 | 2.2 |
| Significance | | *** | | |
| *Clematis vitalba* | | | | |
| *Summer leaves* | | | | |
| Flooded stands | 42.8 | 2.1 | 19.1 | 4.1 |
| Unflooded stands | 23.4 | 1.4 | 23.5 | 2.4 |
| Significance | ** | ** | | ** |
| *Autumn leaves* | | | | |
| Flooded stands | 18.2 | 1.1 | 9.6 | 3.2 |
| Unflooded stands | 12.9 | 0.76 | 12.3 | |
| Significance | ** | ** | | ** |

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

sizes. Along the Danube valley, *Salix alba* and *Populus nigra* can reach up to 40 m in height and 5–6 m in circumference in less than 100 years. In the Rhine valley, *Ulmus minor* reaches 36–40 m. Understory trees or shrubs are often giant: 24 m for *Prunus padus*, 17 m for *Crataegus monogyna*. In Lanzhot Natural Park in Moravia, Korpel (1995) quoted about 907 $m^3$ pro ha in the optimum stage of oak–elm forest with ashes (*Fraxinus excelsior*) 47.5 m high and 139 cm dbh (diameter at breast height). From 1958 to 1987, the wood productivity increased from 600 $m^3$ to 728 $m^3$ per hectare.

Rapid growth and rapid decomposition explain why the forests have high nutrient recycling capacity, which in turn is why generation changes take less time than upland adjacent areas, the successional processes from bush pioneer communities to young mature hardwoods take less than 100 years (Koop, 1989), and the regeneration units are fragmented much more quickly (Frye & Quinn, 1979; Koop, 1989).

## V. Specific Particularities

The flow of water in terrestrial ecosystems has many effects on plants and animals. Water acts as a resource because floods act as migration routes for hydrochorous seeds. Schwabe (1991) estimated the persistent seed bank in the soils of a forest community dominated by young *Alnus incana* trees at 935 viable seeds per $m^2$. After a high-flood winter, new sediments downstream of the forest included about 38 viable seeds per $m^2$. Transported seeds are also of allochtonous origin (exotic plants, e.g., those along the Loire as described in Loiseau & Felzines, 1992).

Floods also favor vegetative propagation through the transport of broken but living trunks of pioneer trees or bushes, which can anchor downstream (Grelon, 1971; Koop, 1987; Amoros & Petts, 1993). But flood water is also a constraint. It can damage plants when water speed slows rapidly. Accumulation of sediment frequently covers low vegetation. Plants react against physical damage by high reiteration capacity. *Salix* and *Populus* species, as well as *Alnus, Tilia, Ulmus,* and *Fraxinus* can build reiterative sprouts that can replace the vertical axis of a broken or fallen tree. When buried under sediments, species can develop lateral sprouts which allow them to survive. Another constraint is the temporal anoxia caused by standing waters during flooding. At the plant level, many morphological and anatomical adaptations have been described (Lugo et al., 1990). Flood tolerance of trees was investigated by direct observations of scientists when particularly long floodings occurred [i.e., along the Tennessee River, by Hall and Smith (1955); along the Rhine, by Dister (1983)] but also by experiments [along the Mississippi River, by Hosner (1960)]. Adaptations to anoxia include rapid seedling growth enabling them to emerge above the inundation level (this is the case for all tree species from regularly inundated forests), a rough and thick bark for keeping air (e.g., *Quercus robur, Fraxinus excelsior,* and *Ulmus minor*), and aerial roots (e.g., *Alnus glutinosa, Salix* species).

Alluvial species present a gradient in flood tolerance. In Europe, *Salix alba* shows a particularly high flood tolerance because its seedlings can survive up to 30 days of total submersion. *Salix alba* adults can tolerate up to 300 days of inundation; *Quercus robur, Ulmus minor,* and *Ulmus laevis,* up to 151 days. *Fraxinus excelsior* dies after 102 days; *Acer campestre, Carpinus betulus,* and *Tilia cordata,* after 13 days. *Acer pseudoplatanus* and *Fagus sylvatica* are not tolerant at all, particularly when floods occur in summer. These species are relegated to high-elevated terraces or are eliminated. In North America, the decreasing tolerance to complete inundation begins with *Salix nigra, Fraxinus pennsylvanica, Liquidambar styraciflua, Populus deltoides,* and *Acer saccharinum* (Hosner, 1960).

Resource availability and trees' adaptations to disturbance constraints play a part in the development of different life-strategies, which include the quantity and seasonality of propagule production, propagule dispersal, growth rates, vulnerability to death or injury from enemies or disturbances, the viability of recruitment from dormant propagules, and the potential for vegetative regrowth from damaged tissues. The model of Grime (1977), analyzed by Brzeziecki and Kienast (1994) using multivariate statistical methods, distinguishes three major groups and intermediates: the ruderal (R), the stress tolerant (S), and the competitive (C) strategies. Ruderal strategy is the strategy of species adapted to colonize intensively disturbed sites. In alluvial environments, the dominant pioneer species are *Salix* and *Populus.* They have short lifespan (100–150 years), high potential growth rate, low wood density (330–410 kg $m^{-3}$), and early reproduction through wind and water dispersion (February to April) to allow reestablishment in bare sediments. The costs paid for these abilities involve a lack of seed reserves, which causes their vulnerability to shade or drought, and vulnerability of wood to attacks by insects and fungi. *Alnus glutinosa*, *Alnus incana*, and *Betula pendula*, also ruderal strategists, are present in the floodplains as scattered small populations because of less competitivity with *Salix* and *Populus* species.

Pure stress-tolerant species [mainly conifers, according to Bzreziecki and Kienast (1994)], are not very rare in the alluvial forests. *Pinus sylvestris* can germinate from seedlings coming from plantations on dry, coarse terraces along the Rhine valley. *Juniperus* exists naturally in situations of air and soil drought under the Mediterranean climate, on sandy dunes 3–5 m above the mean water level (dunes of the quaternary Danube river bed, Hungary, or dunes in the Rhône delta in Camargue, France). In the Rhône delta, *Juniperus phonicea* reaches large sizes: 6–8 m high, 30 cm dbh).

But the intermediate group, stress-tolerant ruderals (S-R), is represented by *Acer campestre*, *Malus sylvestris*, *Pyrus communis*, *Prunus padus*, and *Prunus avium*. These species, like ruderals, have short life-span (50–150 years), relatively high potential growth rate, and low age of sexual maturity; but they are stress-tolerant and have high wood density (500–700 kg $m^{-3}$), small stature (15–25 m), large seeds dispersed by birds and small mammals, and a dominated position which explains why these species are scattered in end-successional stages.

Another intermediate group, competitive stress tolerators (C-S), is here represented by *Quercus robur*. In its establishment phase, this species is tolerant of low availability of water and mineral nutrients. That is why oaks are found along a wide range of moisture gradient, as long as floodwaters are not too frequent or too violent. Oak is able to grow rapidly, can attain large sizes at maturity (42 m, 160 cm dbh), and can reach great age (400–500 years). It is resistant to biotic and abiotic agents and plays the major role among end-successional species.

The third group, of pure competitive strategy, is composed of *Ulmus minor* and *Fraxinus excelsior*, which are most successful on the productive sites under conditions of high resource availability and low disturbance, in well-drained, silty, and fertile low floodplain terraces. *Fraxinus excelsior* and *Ulmus minor* can attain large sizes and can live to about 300 years. They, along with oak, form the canopy of the end-successional stage in the most fertile sites. *Fraxinus excelsior*, which is of neutrophilous tendency, is not dominant in all floodplains of central Europe. On subacidic sediments (e.g., along the Loire), it is easily dominated by elm and oak.

Dutch elm disease (vehiculated by *Ceratocystus ulmi*) and phloem necrosis have contributed to low biomass by eliminating all the large trees of *Ulmus minor* in Europe and *Ulmus americana* in the United States which dominated the canopy of fertile forested sites prior to 1960. However, the elm has not disappeared from the alluvial forests, remaining abundant in underlayers, thanks to an active vegetative regeneration.

The alluvial forests include other European tree species defined as competitive in upland forests, such as *Acer pseudoplatanus*, *Tilia cordata*, *Carpinus betulus*, *Acer platanoides*, and *Tilia cordata*. In an alluvial environment these species are rarely dominant (except *Tilia cordata* on high, gravelly terraces), essentially because of intolerance to summer floods.

## A. SPECIES ABUNDANCE AND DIVERSITY

Alluvial forests of large river plains have a large array of species, particularly in sectors of high fluvial dynamics, when the plain becomes large and multiplies landforms and gradients: up to 157 species, including 56 woody elements (trees, shrubs, and lianas), in the upper Rhine valley (Schnitzler, 1988). Alpha diversity in the warm temperate floodplain forests is higher, with 59 woody species in the end-successional forests of the Mississippi alluvial plain (Robertson et al., 1978). Species richness decreases from upstream to downstream with changes in channel slope, topography, and fluvial forms. As an example, woody species richness is only 34 species of hardwoods in the downstream sectors of the Rhine (Dister, 1980), 19 in the Danube delta (Simon, 1960), and 19 in the Pô delta (Piccoli & Gerdol, 1984). In the lower sectors of the Rhine, increasing hydromorphy and acidity of the substrates account for the fact that some species are progressively disappearing (*Alnus incana, Cornus mas, Daphne mezereum, Populus nigra, Tilia platyphyllos, Euphorbia amygdaloides,* and *Helleborus foetidus*) while others are appearing (*Salix viminalis, Allium scorodoprasum, Asperula odorata,* and *Maianthemum bifolium*).

Similar species and genera recur in the different alluvial forest communities of Europe. This confirms the importance of common edaphic conditions and physiological stresses that plants of riverine ecosystems share regardless of climatic differences (Brinson, 1990). On a broader scale, similar genera recur throughout the temperate area (Table III). The reference to the fossil species lists established by Geissert (1984) for the Pliocene Rhine alluvial forests shows their specific analogies with present-day alluvial forests of Europe, Asia Minor, and North America.

The species richness allows the coexistence of many species of relatively few genera (Schnitzler et al., 1992). In the Rhine valley, the 157 species occur within 113 genera. In the Mississippi valley, the genus *Quercus* includes 12 species; *Acer*, 3; *Fraxinus*, 2; and *Ulmus*, 2 in the end-successional stage (Robertson et al., 1978).

In complex land-forms in upstream and middle sectors of large river plains, the spatial segregation of closely related species becomes particularly fine-grained. In the upper Rhine valley, spatial segregation of the genus *Salix* (9 species without hybrids) provides an excellent opportunity to visualize the environmental gradients (Schnitzler et al.,1992). For *Salix*, selection between species occurs during germination (Ellenberg, 1988). All seeds brought to a new open environment by wind or floods can germinate, but they are quickly selected according to the geochemistry: the basic deposits favor *Salix elaeagnos, S. daphnoides,* and *S. alba*, and the subacidic deposits favor *Salix triandra, S. viminalis,* and *S. fragilis*. On the same deposit, then, species segregate along a textural gradient: bushes of narrow-leaved *S. daphnoides* and *S. elaeagnos* grow on gravels and face the current, whereas bushes of broad-leaved *S. alba* grow on the opposite face of the same deposit, where texture is enriched in sand or silt. In subacidic deposits, *S. viminalis* and *S. triandra* segregate from *S. fragilis* in the same way. Moreover, geochemistry and groundwater levels segregate the species close to the main river channel from those of stabilized areas. Along the main river, the distribution of *Salix* species gradually changes downstream because of the increasing hydromorphy and decreasing amount of limestone. Subacidic species replace basiphilous species. Hybrids of *S. alba* and *S. fragilis* (*S.* × *rubens*) are found in a broader range of sites, both in calcareous and subacidic sites.

In the same valley, *Alnus glutinosa* and *A. incana* and their hybrid *A.* × *pubescens*, and *Populus alba* and *P. tremula* and their hybrid *P.* × *canescens*, segregate mainly on the basis of geochemistry (Schalin, 1967). *Acer* and *Ulmus* genera, which both have three species in the Rhine valley, have strongly marked biogeographical characters. *Acer campestre* and *Ulmus minor* are thermophilous species, frequent in forests along the Rhine. *Acer pseudoplatanus* and *Ulmus glabra* are subatlantic, submontaneous species, sparse in all

## Table III

Common genera of the alluvial forests in North America, Asia Minor, and Europe, in comparison with the alluvial flora of the Rhine during the Pliocene

| | North America[a] | Asia Minor[b] | Europe[c] | Fossil genera in the Rhine valley (Pliocene)[d] |
|---|---|---|---|---|
| Trees and shrubs | | | | |
| Acer | negundo, rubrum, saccharinum | laetum, rubra, insigna | campestre, negundo,** tataricum, monspessulanum, pseudoplatanus | campestre, platanoides, monspessulanum |
| Aesculus | discolor, glabra | | hippocastaneum | spinosissimo |
| Alnus | serrulata, rhombifolia, tenuifolia | glutinosa, subcordata | glutinosa, incana | viridis, glutinosa |
| Betula | nigra | | pendula | |
| Carpinus | caroliana | betulus | betulus | betulus, minima |
| Carya | aquatica, cordiformis, glabra, laciniosa, ovalis, ovata, tomentosa | | | angulata, moenana |
| Celtis | occidentalis, laevigata, canadensis | australis | | |
| Cornus | amomum, florida, foemina, racemosa | australis | mas, sanguinea | mas, sanguinea |
| Corylus | | avellana | avellana | |
| Crataegus | | monogyna, ambigua | monogyna, nigra, laevigata, degenii | sp. |
| Diospyros | virginiana | lotus | | |
| Euonymus | atropurpurea | | europaeus, latifolia | |
| Fagus | grandifolia* | | sylvatica* | decurrens |
| Fraxinus | americana, caroliana, latifolia, pennsylvtica, tomentosa | angustifolia, excelsior, ornus | | excelsior |
| Ilex | decidua, opaca | | aquifolium | aquifolium, cornuta |
| Juglans | capsica, hindsii | | regia | bergomensis |
| Liquidambar | styraciflua | | | europaea |
| Liriodendron | tulipifera | | | germinata |
| Morus | nigra | alba | | |
| Nyssa | aquatica, sylvatica | | | disseminata |
| Parrotia | | persica | | persica, fagifolia, reidiana |
| Pinus | taeda | | sylvestris | |

## Table III *(continued)*

Common genera of the alluvial forests in North America, Asia Minor, and Europe, in comparison with the alluvial flora of the Rhine during the Pliocene

| | North America[a] | Asia Minor[b] | Europe[c] | Fossil genera in the Rhine valley (Pliocene)[d] |
|---|---|---|---|---|
| *Platanus* | *occidentalis, racemosa* | | *occidentalis* | |
| *Populus* | *angustifolia, deltoides, fremontii, heterophylla, sargentii* | *capsica* | *alba, nigra, tremula* | 7 species |
| *Prunus* | *occidentalis, heterophylla, deltoides* | *capsica, laurocerasus* | *avium, spinosa, mahaleb, padus* | *girardii, spinosa, lansdorfii, laurocerasus* |
| *Pterocarya* | *serotina* | *fraxinifolia* | | *limburgensis* |
| *Quercus* | *alba, lobata, lyrata, pagodaefolia, phellos, michauxii, bergii, mulhenbergi, nigra, palustris, shumardi, bicolor, imbricaria, velutina, macrocarpa, virginiana, rubra* | *castaneifolia* | *robur, pubescens* | *hickelii, pubescens* |
| *Rhamnus* | | *grandifolia, frangula* | *catharticus, frangula, alaternus* | |
| *Robinia* | *pseudacacia* | | *pseudacacia*** | |
| *Rubus* | | *ulmifolius* | *ulmifolius, caesius, fruticosus* | *laticostatus* |
| *Salix* | *nigra, interior* | *fragilis, micans, aegyptica* | *alba, eleagnos, daphnoides, triandra, purpurea, viminalis, nigricans, cinerea* | 2–3 species |
| *Sambucus* | *canadensis* | *ebulus* | *nigra, ebulus* | *pulchella* |
| *Sassafras* | *albidum* | | | 1 species |
| *Staphylea* | | | *pinnata* | *pliocaenica* |
| *Tamarix* | | *pentandra* | *gallica** | *ramossisima, laxa* |
| *Taxodium* | *distichum* | | | *dubium* |
| *Tilia* | *americana* | *rubra, caucasica* | *cordata, platyphyllos* | *platyphyllos* |
| *Ulmus* | *americana, rubra* | *minor* | *minor, laevis, glabra* | *minor, longifolia* |
| *Zelkova* | | *crenata* | | *ungeri* |

**Table III** ***(continued)***

Common genera of the alluvial forests in North America, Asia Minor, and Europe, in comparison with the alluvial flora of the Rhine during the Pliocene

| | North America[a] | Asia Minor[b] | Europe[c] | Fossil genera in the Rhine valley (Pliocene)[d] |
|---|---|---|---|---|
| Woody lianas | | | | |
| *Hedera* | | *colchica* | *helix* | *helix* |
| *Vitis* | *aestivalis, riparia, cinerea, rupestris* | *hissarica, silvestris* | *silvestris* | *parasilvestris, teutonica, ludwigii* |

[a] Brinson, 1990.

[b] Emberger & Sabeti, 1962.

[c] Schnitzler, 1988; Karpati & Toth, 1961.

[d] Geissert, 1984.

* Not regenerating.

** Introduced.

alluvial phytocoenoses. *Acer platanoides* and *Ulmus laevis* are both continental and central European species, which also are sparse in the Rhine forest communities. The six species coexist in the Rhine rift thanks to its climatic particularities (subatlantic with a continental tendency), segregating in the same genera according to a double gradient of fertility and texture (Schnitzler et al.,1992).

High total diversity is closely coupled with the river system. First, on a large scale, alluvial landscape presents a continuum from flooding-prone sites to particularly protected ones. Both extremes act on refuges and seed sources when the conditions change (White, 1979). That is why there is no regional species extinction but, rather, local elimination of species, either pioneer or climax; and additional allochtonous species are also brought by floods. Second, the instability of the landscape is a factor eliminating intense interspecific competition, because the temporal dynamics of spatial environmental gradients, plus chance events, maintain population variability. Third, the high fertility occurring in most habitats of the plain due to recurrent flooding is a positive factor for high species diversity and productivity as well as high coexistence potential.

### B. COMMUNITY PATTERN AND FOREST DYNAMICS

The majority of forest communities described in large European plains occur in geographically separated forested basin wetlands, with minor floristic differences. Many detailed phytosociological and floristic descriptions of the alluvial forests of the large European rivers are found for the Danube forests in Wendelberger (1952) and Karpati and Toth (1961), for the Pô in Sartori (1984), for the Rhine in Dister (1980), Carbiener (1983), and Schnitzler (1988, 1994a), and for the Loire in Schnitzler (1995a). Landscape diversity is high in large river plains such as the upper Rhine (Tables IV, V).

The particularities of the microrelief and the local distribution of protected and unprotected sites, as well as the kinetic energy level of floods, generate patches of forest units. Vegetation varies from communities adapted to long hydroperiods, in swales and old channels, to communities located in relatively high terraces on the floodplain, some

## Table IV

Patterns of landscape diversity and community richness in the Rhine and Loire valleys

| | Community richness | Family richness | Genera richness | Total species richness | Total woody species richness | Beta (1)[a] diversity | Beta (2)[b] diversity |
|---|---|---|---|---|---|---|---|
| RHINE VALLEY | 12 | 56 | 113 | 157 | 56 | 1.07 | 0.66 |
| Rhine floodplain | 8 | 53 | 107 | 143 | 52 | 0.26 | 0.26 |
| Ill floodplain | 4 | 29 | 83 | 106 | 37 | 0.98 | 0.98 |
| LOIRE VALLEY | 8 | 47 | 98 | 110 | 46 | 0.49 | 0.41 |
| Loire floodplain | 7 | 47 | 98 | 110 | 46 | 0.48 | 0.41 |
| Allier floodplain | 7 | 47 | 98 | 110 | 46 | 0.47 | 0.41 |

[a] Beta 1 = s/a-1 where s = total number of species and a = number of species in each of the samples.

[b] Beta 2 = g(H) + I(H)/2a where g is the gain of species and I is loss.

of which are not regularly flooded. In both extremes of the moisture gradient, forest communities have low structural development and relatively low species richness, attributed to water stress. This is the case for the swamp forests (*Alnetum glutinosae*) and the hardwoods of the gravelly, unflooded terraces of the center of the plain (*Stellario–Carpinetum*) defined in the Rhine valley (Table V).

Each of these communities shows a specific sylvatic mosaic, composed of a variable spatial pattern of the different stages of the successions. Oldeman (1990) defined five different steps:

1. The innovation stage develops on a large, empty site caused by a severe disturbance. In alluvial plains, disturbance consists mainly in floods of high kinetic energy. This stage is characterized by patches of pioneer herbs, shrubs, or tree saplings.
2. The pre-equilibrium stage appears with the closure of the canopy, after about 50–100 years in upland, stable environments. In alluvial plains, the closure of the canopy may be shortened to 10–15 years.
3. The equilibrium stage is the "climax" stage, which represents ecosystem maturity. Internal functioning is complex and highly structured, fragmented in complex mosaic units (units of regeneration or gaps, units of maturity, units of decay or death) that are of small dimension and structurally dynamic. The internal organization of the equilibrium stage is clearly separated from the environment. In temperate, stable forests, the average time to reach this level is about 250–300 years (Jones, 1945). This stage may persist a long time (several thousand years) if no severe accident occurs.
4. The elimination stage appears after a stress that eliminates many units at the same time. Rather severe floods, when frequent after a change in the course of the river, may be another common stress in the alluvial plains. The stress can also be of biotic origin, such as the present-day extension of Dutch elm disease, which has caused since the beginning of the century the death of many *Ulmus* species in alluvial forests [e.g., 8 elms per ha for a total surface of about 40 ha in alluvial forests of the Morava (Korpel, 1995)].
5. The collapse stage, during which nothing is left but bare soil, leads to a new installation stage. Paleogeomorphological studies of the Rhine valley (Striedter, 1988) proved that

## Table V

Ecology (physiography and hydrology) and species diversity per vegetation type in the upper Rhine valley (Rhine and its tributary the Ill)

| Phytosociology | Physiography | Flooding regime | Total species richness | Mean species richness in 0.1 ha | Total woody species richness | Mean woody species richness in 0.1 ha | Shannon index H′ |
|---|---|---|---|---|---|---|---|
| RHINE | | | | | | | |
| Salici-Populetum nigrae | river bank of low elevation | 3–8 days several times a year in summer | 81 | 18.4 | 31 | 4.1 | 1.8–2.9* |
| Ligustro-Populetum nigrae | gravelly terraces of high elevation | 1–2 days every 3–5 years in May–June | 63 | 28.6 | 35 | 10.6 | 2.1–2.7* |
| Fraxino-Populetum albae | silty terraces | 1–3 days every 3–5 years in May–June | 111 | 28.9 | 47 | 15.9 | 1.9–2.1* |
| Querco-Ulmetum populetosum | silty-sandy low terraces | 1–3 days every 3–5 years in May–June | 99 | 31.2 | 44 | 17.8 | 3.4 |
| Querco-Ulmetum typicum | silty-sandy low terraces | unflooded for 30 years | 92 | 33.7 | 43 | 15.7 | 3.4 |
| Querco-Ulmetu tilietosum | sandy high terraces | every 10 years in May–June | 90 | 34.4 | 44 | 17.6 | 2.6 |
| Querco-Ulmetum carpinetosum | sandy low terraces | unflooded for 150 years | 84 | 34.8 | 41 | 16.7 | 3.1 |
| Pruno-Quercetum | silty Holocene terraces | major floods in summer | 77 | 37.1 | 39 | 16.1 | 3.2 |
| ILL | | | | | | | |
| Carici elongatae-Alnetum | clayey swamps | 5–6 months every year in spring/winter | 51 | 18 | 14 | 4.1 | 0.8 |
| Pruno-Fraxinetum | old channels | 1–2 weeks in spring/winter | 85 | 27.1 | 32 | 10 | 2.7 |
| Alno-Carpinetum | clayey-silty low terraces | 3–8 days in spring/winter | 87 | 35 | 32 | 13.7 | 2.8 |
| Stellario-Carpinetum | gravelly Würmian terraces | major floods in summer | 41 | 16.6 | 12 | 4.3 | 0.8 |

* Range of values for young and old forest communities.

great floods, which destroyed all the forest formations of the entire valley, occurred about every 500–800 years during the Holocene. This could explain why the oldest trees of fossil trunks of *Quercus* found in the Rhine valley never exceed 500 years. This relatively short periodicity of destructive floods was still higher along the main river (every century for the big European river plains).

In alluvial environments, the forests present several particularities. First, the forest-environment separation is not very clear, since floodwaters regularly pass through the system, bringing new propagules, sediments, water, and nutrients and transporting organic matter and seeds elsewhere. Secondly this stage may be reached in less than 150 years.

In alluvial forests, self-perpetuation through gap dynamics is promoted by flood action (transport of trees or destabilization and uprooting) as well as by biotic causes (disease, senescence). However, patterns of tree mortality vary regionally in the plain because the relative importance of catastrophic agents varies widely with forest type and the situation in the floodplain (influence of river energy). Unfortunately, the paucity of undisturbed bottomland hardwood stands now existing in Europe have made it difficult for researchers to deduce the relative impacts of uprooting and piecemeal disintegration by physiological factors.

Gap dynamics were studied in alluvial forests of the Rhine valley by Walter (1982), Beekman (1984), and Koop (1989). When small, gaps are rapidly colonized by pioneer trees and shrubs, often extending through vegetative reproduction. Clonal structures are numerous in gaps, with stands of *Populus*, *Ulmus*, *Alnus*, *Prunus*, *Crataegus*, *Viburnum*, *Ligustrum*, *Cornus*, and *Salix*. When larger, gaps are colonized by dense blankets of *Clematis vitalba* (and *Vitis sylvestris* before phylloxera) which covers the ground and remnant shrubs and climbs to the edges and into the trees. Regeneration is slowed by the blankets of lianas, which prevent the closure of the canopy for decades.

### C. THE PARTICULAR CASE OF RIVERINE ECOSYSTEMS OF HIGH-DYNAMICS RIVERS

Along a big river, vegetation must cope with flooding severity (i.e., frequency and kinetic energy of flowing waters), a factor that depends essentially on distance from the river channel and elevation. In this zone there are two major units: softwoods and hardwoods. This denomination is a direct translation from the German *Weichholz* and *Hartholz* (terms related to wood density) as softwoods (for the first steps of the successions: Salici–Populetum, Ligustro–Populetum) and hardwoods (for the equilibrium stage: Querco–Ulmetum).

The installation stage near the river is composed of various patterns of shrubs (*Salix viminalis*, *S. triandra*, *S. eleagnos*, *S. purpurea*, or tree saplings of *Populus nigra* and *Salix alba* or *S. fragilis*). The pre-equilibrium stage occurs with the establishment of two forest units: Salici–Populetum in moist, low sites, and Ligustro–Populetum nigrae in dry, elevated terraces.

Salici–Populetum and Ligustro–Populetum have similar features, the only difference being the dominance of *Salix* or *Populus* in the canopy (Schnitzler, 1988, 1995b). These units are characterized by two main strata: the canopy (about 20 m high) and the grass layer (up to 2 m high). The Shannon index varies from 2 to 2.7. Shrubs are relatively rare on wet sites and in young stands. The canopy is even-aged and composed of pioneer species: *Salix alba* and *Populus nigra*, sometimes *Populus alba* or *Alnus incana*. Trees never exceed 60 cm dbh. The ratios of *Salix alba* and *Populus nigra* depend on the degree of moisture. The shrubs are mainly remnant individuals of the previous bush stage (*Salix eleagnos* or *Salix viminalis*). In gaps, *Humulus lupulus* and *Convolvulus sepium* form small veils. The grass layer is composed of high clones of *Urtica dioica*, *Impatiens glandulifera*, *Phalaris arundinacea*, and other nitratophilous, heliophilous species. The total density of this association varies with flooding conditions. In the Rhine valley, the total density varies from 1212 stems per $ha^{-1}$ when regularly inundated and dominated by *Salix alba* to 4900 stems per $ha^{-1}$ in terraces that are rarely flooded and are dominated by *Populus nigra*. Average basal area is 20 $m^3$ $ha^{-1}$. When old, moist Salici–Populetum (dominated by *Salix alba*) keeps similar total woody densities, with some giant old willows (up to 160 cm dbh). High grasses are still abundant and surround small patches of *Rosa canina*, *Salix purpurea*, *S. viminalis*, or *S. eleagnos*. In Salici–Populetum dominated by *Populus nigra*, total density decreases to less than 2000 stems per $ha^{-1}$ and the woody species richness increases. In both stands, the presence of giant old trees explains the high basal area: from 80 to 90 $m^2$ $ha^{-1}$.

Querco–Ulmetum is characterized by five well-defined strata. The Shannon index varies from 3 to 3.4. The total density is 5400 stems per $ha^{-1}$, which corresponds to an average along a gradient of flooding recurrence. In regularly flooded sites, the average density is 2919 stems per $ha^{-1}$. When flooded every 30 years, seedlings are less often killed by floods, and the density increases to as much as 5081 stems per $ha^{-1}$. After a long period without flooding (about 150 years), the density reaches 6830 stems per $ha^{-1}$ (Schnitzler, 1994b). The average basal area of the Querco–Ulmetum is 32 $m^2$ $ha^{-1}$. The canopy is uneven and relatively open (about 38 stems per $ha^{-1}$), with trees ranging from 25 to 30 m in height and some emergent individuals of 35 m height and up to 120 cm dbh (Fig. 1). The dominant trees are *Quercus robur* and *Fraxinus excelsior*, with 51% and 26% of the forest canopy, respectively. *Ulmus minor*, the third component of the canopy, is being progressively eliminated because of elm disease. *Populus alba* and *Populus nigra*, with a scattered distribution, are often relicts of earlier successional episodes. Unevenness of the canopy, coupled with small leaf size, favors penetration of light along trunks and the ground and accounts for the abundance of giant lianas (*Clematis vitalba*, *Hedera helix*, *Vitis sylvestris* before phylloxera) in the upper tree layers, the higher proportion of giant shrubs in the secondary tree layer (*Cornus mas*, *Cornus sanguinea*, *Corylus avellana*, *Crataegus monogyna*, *Evonymus europaeus*, *Prunus spinosa*, *Sambucus nigra*, and *Viburnum lantana*), and high underlayer densities (average of 5000 stems per $ha^{-1}$). In the Loire valley, *Humulus lupulus* and *Evonymus europaeus* reach large sizes in Querco–Ulmetum, whereas all the calcicolous species cited above are rare or absent.

The high species richness and complexity of Querco–Ulmetum explain its strong phenological individuality. This forest community flowers in an interrupted phenological sequence over a period of 9 months, from early January to early September (Schnitzler & Carbiener, submitted), which is a long time in comparison with other forest systems of temperate regions [no more than 7 months, according to Ellenberg (1988)]. Aerial surveys of hardwood forests during flowering and fruiting peaks in April–June and October could provide a crucial overall view of canopy structure from contrasting foliage coloring and irregularity in this degree of openness with species population patchiness.

Another originality of gallery forests is liana richness. Giant lianas are particularly abundant in Querco–Ulmetum mature stands, when regularly flooded (20% of the total individuals of the canopy in the Rhine valley). Old softwoods, when dominated by *Populus nigra*, are liana-rich as well. In tributaries, the proportion of giant lianas is low because of the presence of below-hydromorphic horizons, to which liana roots are very sensitive, and the abundance of shade species such as *Carpinus betulus* (Table VI; Schnitzler, 1995c).

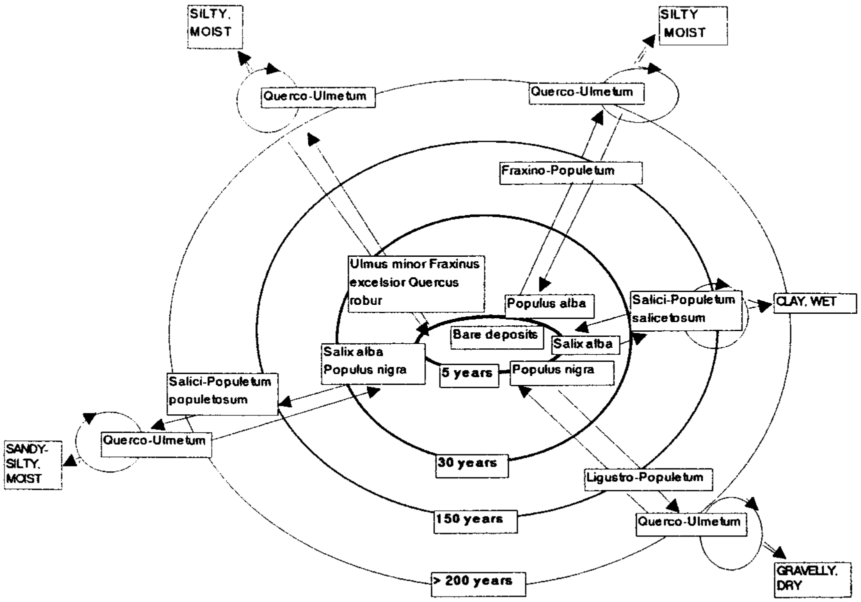

**Fig. 1.** A model of successional sequences in the Rhine valley (from Schnitzler, 1995b).

The Querco–Ulmetum area is vast, covering three big climatic areas in Europe: west Mediterranean Europe, continental Europe, and central Europe (for a phytosociological synthesis of central Europe, see Seibert, 1987). Vicariant alluvial hardwood forests evolving in a warmer and moister climate exist in Asia Minor [extending around the Black Sea, the Caspian Sea, and the Aral Sea (Emberger & Sabeti, 1962)] and in North America [e.g., along the Mississippi River (Hosner & Minckler, 1963; Carter-Johnson et al., 1976; Robertson et al., 1978). These forests are more species-rich (including Tertiary relics such as *Parrotia*, *Zelkova*, *Pterocarya*, *Celtis*, *Gleditsia*, *Diospyros*, *Liquidambar*, *Liriodendron*, and *Nyssa* genera, as well as more species per genera) than the European alluvial hardwoods for two main reasons: the presence of refuge sites during the Quaternary glaciations, which did not occur in Europe, and the present-day warmer climate (with annual temperatures of 14°C and mean annual rainfall of 1000 mm in the Mississippi valley, e.g.). European, Asian, and American alluvial hardwoods all originate from the warm temperate, dense forests of the end of the Pliocene (Table III).

The forested pattern of softwood/hardwood in big river plains has been variously interpreted. For some authors (e.g., Wendelberger, 1952; Moor, 1958; Passarge, 1985), the softwood/hardwood mosaic is guided mainly by textural and moisture gradients (linked to river dynamics) and by flooding frequency (linked to floodplain elevation and distance from the main channel). For others, the pattern depends essentially on temporal processes, and softwoods and hardwoods are interpreted as different steps in the same succession. The basis of this interpretation was the frequent observation that *Populus* and *Salix* species predominate in young stands and then are replaced by *Ulmus*, *Acer*, and *Quercus* species over time (for the Missouri River, see Hosner & Minckler, 1963; Wilson,

### Table VI

Structural characteristics of canopy lianas in the old stands of the Rhine valley

| Forest type | Number of giant lianas (ha$^{-1}$) | Giant lianas (%) in the canopy | Basal area (m$^2$ ha$^{-1}$) | Dominant species |
|---|---|---|---|---|
| Flooded Querco-Ulmetum populetosum | 28.6 | 30 | 0.03 | *Hedera helix* |
| Salici-Populetum populetosum | 24.9 | 6.6 | 0.78 | *Clematis vitalba* |
| Unflooded Querco-Ulmetum populetosum | 56 | 42.7 | 0.38 | *Hedera helix* |
| Alno-Carpinetum | 4.4 | 4.2 | 0.02 | *Hedera helix* |
| Ligustro-Populetum | 120 | 11.4 | 1.13 | *Hedera helix* |
| Pruno-Quercetum | 18.9 | 17.7 | 0.1 | *Hedera helix* |
| Querco-Ulmetum tilietosum | 20.8 | 24 | 0.12 | *Clematis vitalba* |
| Fraxino-Populetum albae | 33.3 | 15.3 | 0.1 | *Hedera helix* |
| Querco-Populetum carpinetosum | 6.3 | 7.3 | 0.04 | *Clematis vitalba* |

1970; and Robertson et al., 1978; for the Danube, see Margl, 1973; for the Rhine, see Carbiener et al., 1988; Koop, 1989; and Schnitzler, 1995c) (Fig. 1).

The causes of these different interpretations are due to the fact that there exist old softwood communities in the alluvial floodplains, particularly in downstream sectors. For the proponents of the succession hypothesis, old softwoods are the result of extreme conditions that have disturbed the progress of succession, arresting it at different stages of development. Another cause was that species composition and structure are so dramatically different between the steps of the succession. In Europe, phytosociologists classify them in different associations and even in different higher phytosociological ranks (up to class level).

However, the temporal links between forest units are the key to understanding the forest pattern along the longitudinal profile of large rivers. If inundations are frequent and severe, the time required for developing the succession is too short and forest communities are perpetually in a state of effective non-equilibrium. That is why softwoods predominate the forested landscape in upstream sectors. With the increasing possibilities of protected sites developing downstream, perpetually young softwoods are relegated to the active braids (where they occupy only 10% of the total forested landscape), whereas hardwoods dominate the landscape. In lower sectors, softwoods survive only in extreme conditions of wetness or drought where they can age and become permanent communities. The proportion of old softwoods is about 20–40%.

The successional softwood/hardwood links explain also why the forest pattern of the big valleys has changed during prehistoric times with the changes in climatic conditions. The history of fluvial dynamics with identification of high-disturbance periods has been studied in the upper Rhine, Main, and Danube through geomorphological profiles of terraces and tree-ring analyses of fossil trunks (Becker, 1982; Striedter, 1988). In the upper Rhine, Striedter (1988) determines six major periods of widespread flooding increase and maximum extension of gravel deposition, from 9000 years b.p. to the beginning of the 20th century, during which a maximum of trees were pulled out and sedimented. The maximum stages of flooding and lateral-changing river courses occur in the middle of Subatlantic times. These periods of intensive disturbance have favored the extension of pioneer communities in a great part of the plain, which explains the high number of fossil trunks of *Populus*, *Salix*, and *Alnus* found in gravel pits. In periods of relatively low disturbance, the main fossil trunks found in the gravel pits were *Ulmus*, *Quercus*, and *Fraxinus* in the Rhine valley.

## VI. Conclusion

The role of river dynamics on forest functioning was described through some characteristic elements of the nutrient cycle, species composition, and forest structure and dynamics. The recognition of these fundamental features makes it difficult to apply here the concept of climax, considered traditionally as the presumed result of autogenesis within a stable physical environment. But if we consider the high level reached by hardwood forests, we can admit that this particular forest has reached a climax level.

The problem of separation between strictly endogenous and exogenous categories of disturbance factors was discussed in depth by White (1979), who posited that physical events, when recurrent and predictable, lead to selection of species and communities for adaptation and must hence be considered an intrinsic part of forest dynamics. According to this concept, Querco–Ulmetum is a climax state, reached after deep transformations in its species composition and structure. For White (1979), truly exogenous disturbances are those of very low frequency or those that create new, irreversible situations to which species are not adapted. Human disturbance in alluvial landscape corresponds to the latter case. Man has separated the forests from the river, physically destroyed them, and interfered with the successional and maturation processes. Nowadays all temperate alluvial plains are altered to varying degrees, especially in wealthy countries. As a result, many forests have reached the absolute biological limit of adaptation and have lost many of their original and aesthetic characteristics. Old-growth alluvial stands are nowadays very rare: in Europe, the only primeval alluvial hardwood is situated in the Lanzhot Reserve, situated at the confluence between the Dyje and the Morava Rivers in the Slovak Republic (Korpel, 1995). We are now becoming conscious of this immense loss, and some scientific programs propose restoration measures. Unfortunately, it is rare that we see proposals for conservation, restoration, extension, and re-inundation over wide areas (at least 1000 ha: Schnitzler, 1994b) of complex alluvial ecosystems, evolving in a natural environment with a free course of the river in the floodplain, in order to reconstitute the complete sylvigenesis, with all forest successional steps and all sylvigenetic phases. In France, the best site for creating such a natural forested reserve is the Loire valley, because the river still has a quite natural course, and many alluvial lands are nowadays abandoned by agriculture (Schnitzler, 1995a). But there are probably other adequate sites in Europe and North America.

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