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Special paper

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## RIPARIAN ZONES: WHERE BIOGEOCHEMISTRY MEETS BIODIVERSITY IN MANAGEMENT PRACTICE

*About paper and project:*

*The ecotone project began in 1991, after a period of preparation of three years. It was launched in the framework of the Man and Biosphere Program (MAB) and the International Hydrological Program (IHP) of UNESCO, and concluded by a seminar held in Toulouse, France, 1997.*

*The present text is a result of this seminar*

*and further work with the text until 1998. Clearly, new research and publications have advanced our knowledge of riparian systems since that time. However, thanks to the convincing energy and determination of one of us – Anna Hillbricht-Ilkowska – it was felt that our text still holds some interest, and may be useful to read at the present time. Therefore, selected recent literature was added into the last text in order to illustrate our ideas with new data.*

*In addition, during the program, several influential seminars led participants in Poland, and this publication in the Polish Journal of Ecology is symbolic of exceptional opportunities of links developed between researchers from the 24 participating countries. On the whole, 22 research projects were organised, and about 20 seminars were attended by more than 2,000 researchers.*

*In this perspective, the ecotone project of UNESCO may appear as a joint venture similar to what we urgently need today if ecological research is to contribute to the edification of a more sustainable world.*

Henri Décamps

**ABSTRACT:** Riparian zones are well known for their inherent ecological properties related to biogeochemical cycles, biodiversity, and catchment management. The international MAB/UNESCO programme which was running between 1988 and 1998 was related to the land/water ecotones, mainly riparian zones. This article, inspired by this programme – seeks to highlight the role of riparian processes on biogeochemical cycles and biodiversity under different climatic conditions. Their role is investigated by focusing on: i) the lateral ecotone between land and water systems, ii) their longitudinal corridor structure and, iii) the dry-wet cycles. This information is then used to suggest the value of riparian zones in landscape management. We emphasize the key roles of the ecotonal structure, longitudinal connectivity and timing of the occurrence of wet-dry cycles for riparian zones to process nitrate fluxes and to maintain high levels of biodiversity at the landscape scale. In the context of the worldwide transformations of flow regimes, the deterioration of water quality and loss of biodiversity, restoring riparian zones is both a key objective and a formidable challenge that implies envisioning the consequences of management actions on the long term, considering entire river basins, and paying attention to other environmental, regional and global changes.

**KEY WORDS:** riparian zones, ecotones, biogeochemistry, biodiversity, management

## 1. INTRODUCTION

Riparian zones along river networks possess important ecological properties, far in excess of their spatial extent. They are now regarded as one of the biosphere's most complex ecological systems but also one of the most important for maintaining the vitality of landscapes (Naiman and Décamps 1997). These important ecologi-

cal characteristics relate to terrestrial aquatic ecotonal properties specifically the seasonal changes of dry-wet cycles, i.e. aerobic, anaerobic conditions. Typically they form highly productive and biodiverse corridors. As such riparian zones control the flows and characteristics of nutrients and other materials across the landscape, they harbor rich assemblages of flora and fauna, and they have proven applications for watershed and wildlife management. They also manifest early indications of global environmental change, particularly because of their sensitivity to variation in the hydrological cycle.

In 90's several compilations have focused on general characteristics of riparian zones (Naiman and Décamps 1990, Holland *et al.* 1991, Décamps and Décamps 2001), biogeochemistry (Hillbricht-Ilkowska and Pieczyńska 1993), fish communities (Schiemer *et al.* 1995), groundwater interactions (Gibert *et al.* 1997), forest renewal (Décamps 1996), biodiversity (Lachavanne and Juge 1997), and aspects of management (Haycock *et al.* 1997). These compilations and the other land/water ecotone publications were related or inspired by the international programme MAB/UNESCO founded in 1988 and lasted almost ten years (Naiman *et al.* 1989, Décamps *et al.* 1990). In this period many case studies as well the generalizations on the land/water ecotone both lacustrine and riverine were enhanced. The final conference organized in Toulouse in 1997 made the effort to summarise the main findings and perspectives of the programme. However, this article does not attempt to provide another summary of the large literature that has appeared on riparian zones in last decade. More specifically, it seeks to highlight the role of riparian processes on biogeochemical cycles and biodiversity under different climatic conditions. Their role will be investigated by focusing on: i) the lateral ecotone between land and water systems, ii) their longitudinal corridor structure and, iii) the dry-wet cycles. This information is then used to suggest the value of riparian zones in landscape management.

## 2. BIOGEOCHEMISTRY

We know from the beginning of the last decade that riparian zones can act as buffers for sediment and nutrient (nitrogen and

phosphorus) fluxes (Schlosser and Karr 1981). Since these years, the use of natural buffer zones to protect fresh water from pollution has attracted considerable interest. Yet, factors accounting for the pollution retention capacity are diverse, and the performance of a buffer zone within a catchment is difficult to predict (Haycock *et al.* 1997). For example, we need to know the extent and rate at which nitrogen and phosphorus are transported through the landscape before being deposited on surface of soil and plants in riparian zones.

Indeed, the transfer of nitrogen and phosphorus within the drainage basin and their transformation within riparian zones vary widely in response to local environmental conditions. For example, phosphorus is mainly transported in association with fine sediment in surface flow and its removal from the riparian zones can only be accomplished through harvest since it is not present in any gaseous form. Moreover, riparian zones may become a source of labile P for the adjacent stream under flooded conditions, thus limiting their sustainable role in phosphorus flux control. On the contrary, nitrogen is transported mainly in a dissolved form (nitrate) through both surface and subsurface routes, and there is a gaseous pathway in the nitrogen cycle (denitrification) which is prevalent in wetlands in general. The existence of this microbial process transforming a dissolved form of nitrogen ( $\text{NO}_3$ ) to a gaseous form ( $\text{N}_2$ ) in riparian zones (Fig. 1) has led to the discovery that these zones can contribute to the regulation of non-point source pollution from upland agricultural areas (Peterjohn and Correll 1984).

### 2.1. Temperate riparian zone model

The non-point source regulation function of riparian zones has been confirmed under temperate climatic conditions. Two major biological processes are involved in regulating the nitrogen fluxes through riparian ecosystems: vegetative uptake and microbial denitrification (Haycock *et al.* 1993). In short, plant uptake retains nitrogen during the vegetative growth period corresponding to a low water table and a limited spatial occurrence of anaerobic sites. During the high water period, gener-

ally winter and early spring seasons under temperate climate, denitrification takes over, reducing nitrate inputs to a reduced gaseous form ( $\text{N}_2$ ) using organic carbon from root exudates and vegetative litter as a source of energy. The effective absorption of nitrate within the riparian zone depends upon the establishment of conditions conducive to a high denitrification potential, in addition to the maintenance of a stable vegetative community. Over the long term, there is no sign of microbially-mediated nitrogen saturation (Hanson *et al.* 1994).

Paradoxically, nitrogen retention efficiency of riparian zones depends on a slow nitrogen inflow that entails a long contact time for further biological uptake and

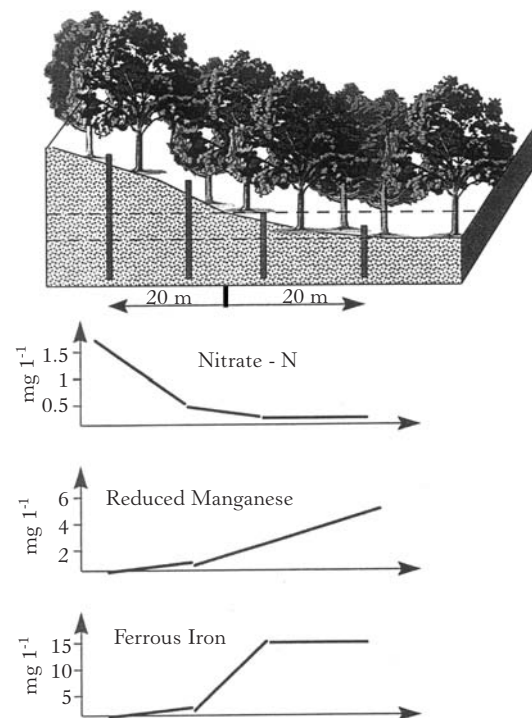


Fig. 1. Along a tributary of the Garonne River, in southern France, nitrate concentration decreases along the groundwater flow path and totally disappears after 20 meters. The permanent presence of reduced manganese and ferrous iron in the groundwater under the lower sites suggests that microbiological demand for electron acceptors is higher than that provided by nitrate through denitrification. Thus, oxidized forms of manganese and iron are used as electron acceptors and, in turn, are reduced to dissolved forms (from Pinay *et al.* 1993 modified, with primary author and editor permission).

transformation. In contrast, nitrogen retention at the drainage basin scale is proportional to total nitrogen flux (Haycock *et al.* 1997). At the scale of the riparian zone, the spatial extent of nitrogen regulation is most often situated at the inland boundary representing a few meters in width, leaving the remaining part of the riparian zone free of allochthonous nitrogen input from upland origins (Haycock and Pinay 1993). At the scale of the drainage basin, the most efficient placement of riparian zones along the river continuum is to be found along the margins of small streams where a high ratio of land-riparian zone interaction is conducive to higher nitrogen retention potential (Haycock *et al.* 1993).

The Temperate Riparian Zone Model (Fig. 2A) has been developed under temperate oceanic conditions (Bailey 1996), mostly along small streams receiving high nutrient loads. Large uncertainties concerning the application of the model under other conditions remain. Here, we analyze the control of nitrogen fluxes in riparian zones under temperate, continental, tropical, and arid climatic conditions, as well as along large river systems under temperate climatic conditions to test the robustness of the Temperate Riparian Zone Model.

## 2.2. Continental climatic conditions

The seasonal pattern found in the temperate model is exacerbated under more continental conditions (Fig. 2B), where three distinct periods can be found. In early spring, snow melt and soil thaw encourage the movement of water and nutrients through the landscape (Renman 1993), as well as through riparian zones. A combination of high nitrogen flux and low temperature may limit nitrogen retention during this phase (Hillbricht-Ilkowska *et al.* 1995). Later, during the vegetative growth period, the low water table limits the spatial development of anaerobic zones, as well as nitrogen fluxes. Nitrogen retention is then mainly due to vegetative uptake if the groundwater is in contact with the root system (Vought *et al.* 1994). Finally, in autumn, the pulse of available organic carbon via litter fall, combined with rainfall events, promotes suitable conditions for denitrification to occur

but only for a limited time period (Hillbricht-Ilkowska 1993, Bechtold *et al.* 2003).

On an annual basis, under continental climatic conditions, denitrification removal represents only 30 to 40% of the total N regulation taking place in riparian zones (Jansson *et al.* 1994), as compared to 80–100% in temperate oceanic zones. Moreover, during flood events, riparian zones can become a source of organic nitrogen to the stream through riparian soil erosion (Leonardson *et al.* 1994).

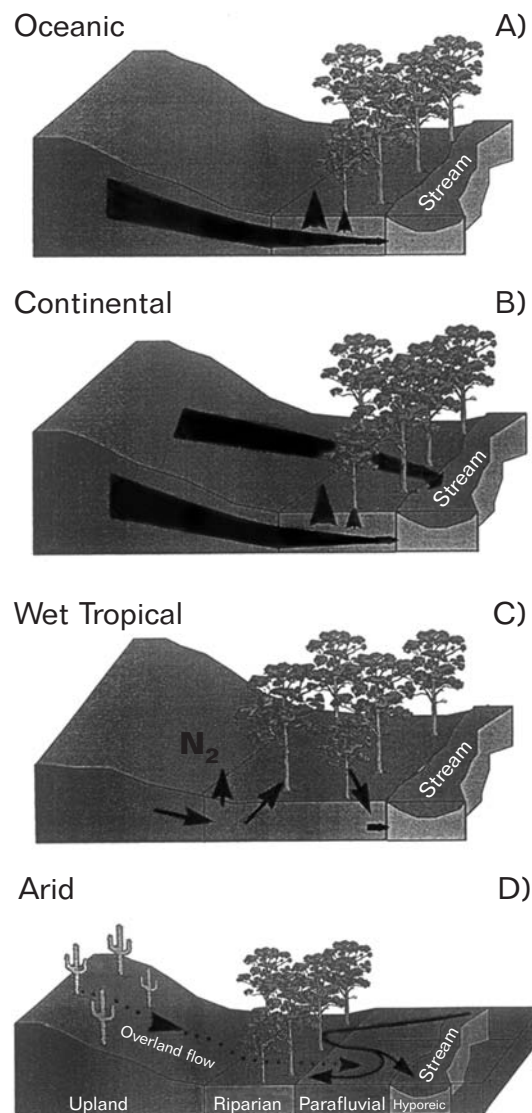


Fig. 2. The Temperate Riparian Zone Model developed under temperate oceanic conditions (A) and its possible applications under cold continental (B), wet tropical (C), and arid (D) climatic conditions.

### 2.3. Wet tropical conditions

Fundamentally, the temperate riparian zone model of nitrogen cycling seems to hold in humid tropical regions (Fig. 2C). Studies from Puerto Rico (McDowell *et al.* 1992) and the central Amazon Basin of Brazil (McClain *et al.* 1994, Williams *et al.* 1997) identify the riparian zones of small streams as a sink for nitrogen input from the surrounding uplands. Furthermore, denitrification is identified as a prime controlling factor. However, the humid tropics differ from the temperate regions in several ways that alter processes of nitrogen cycling, and thus limit the direct applicability of the temperate model.

Whereas temperate and continental riparian zones have been shown to undergo strong seasonal shifts in the predominance of plant uptake *versus* denitrification, biogeochemists working in humid tropical areas speculate that denitrification occurs during all seasons of the year (McDowell *et al.* 1992, McClain *et al.* 1994, Williams *et al.* 1997). In the central Amazon, nitrate entering the riparian zone from surrounding uplands via groundwater flow is consumed within a few meters. The respective roles of denitrification, dissimilation and plant uptake on the reduction of nitrate are yet to be determined.

A distinct feature of nitrogen cycling in undisturbed catchments of both Puerto Rico and the central Amazon is that total inorganic nitrogen concentrations of riparian groundwater are not dramatically different from upland groundwater concentrations (McDowell *et al.* 1992, McClain *et al.* 1994). Instead, there is a pronounced shift in the speciation of nitrogen: whereas nitrate dominates upland groundwater, ammonium dominates groundwater beneath the riparian zone, reflecting differences in oxidation-reduction potential. Significant reductions in total inorganic nitrogen do not occur until groundwater crosses the boundary of the riparian zone and the stream channel. Coupled nitrification/denitrification may account for this decrease. In that case, the denitrification rate would be controlled by the nitrification rate.

The scenario described here is more complex than the temperate oceanic and continental examples. However, rather than necessarily reflecting a more complex

ecosystem, the complexities described above may result from researchers ability to perceive finer details in the lower overall N concentrations characterizing undisturbed humid tropical systems. A similar scenario of inorganic nitrogen replacement in riparian zones may operate in temperate regions, but it may be largely masked by the more pronounced gradients and features associated with the reduction of high upland nitrogen loads (Williams *et al.* 1997).

### 2.4. Arid climatic conditions

Upland-riparian-stream interactions in arid catchments differ substantially from what has been described for both temperate and tropical regions (Fig. 2D). These differences ultimately are related to precipitation regime, but are mediated through differences in soil characteristics and hydrology. Since research on nitrogen cycling in riparian zones of arid catchments is limited, we will focus on research that has been done in central Arizona (USA) as an example.

In an arid catchment, precipitation is infrequent, but comes in intense, short-lived storms. Between runoff events, which may be more than 200 days in locations such as the Sonoran Desert in Arizona, the upland is disconnected from the riparian zone and stream (Fisher *et al.* 1998). This is in sharp contrast to the temperate model where lateral groundwater transport is continuous. During runoff events, infiltration is minimal, arid soils being hydrophobic and including a continuous, nearly impermeable caliche layer, near the soil surface. Consequently, storms induce surface runoff that rapidly moves from the upland and reaches directly the stream channel through rills on the surface of the riparian zone. As a result of this rapid transport and limited contact between incoming water and plant roots, little processing occurs during initial flows through the riparian zone. Most nitrogen retention by riparian vegetation can only occur after water enters the stream channel and has moved back into the riparian zone.

Another contrast between riparian zones in arid and humid climates is the extent to which tributaries support riparian vegetation. In temperate and tropical regions (i.e. well-vegetated systems), small tributaries buffer hillslope runoff

before it gets to streams. By contrast, arid small streams lack the vegetation and soil structure necessary to influence runoff and, in any case, such runoff is too rapid to be effectively intercepted. Therefore, any nutrient retention by riparian vegetation, or denitrification associated with riparian vegetation, probably occurs after runoff has entered the stream channel (Holmes *et al.* 1996). It is suspected that substantial nitrogen retention may occur in the riparian zone as water moves longitudinally down the stream channel. However, the retention of nitrogen in flooded riparian zones or by transmission losses from the channel into the riparian zone in arid basins needs clarification.

#### 2.5. Large river riparian zones in temperate climatic conditions

Do riparian zones along large rivers behave the same way as along small streams? A recent study along the Garonne River in France (stream order 6) has shown that the nitrate concentration decrease observed along the groundwater flow path through the riparian zone was due mainly to the mixing of two different types of water. Surface water with low nitrate concentration ( $3 \text{ mg l}^{-1} \text{ N-NO}_3$ ) intrudes into the alluvial aquifer with groundwater heavily loaded with nitrate ( $25 \text{ mg l}^{-1} \text{ N-NO}_3$ ), and this physical mixing accounted for about 50% of the observed nitrate concentration reduction along the flow paths (Pinay *et al.* 1998). Such a pattern has yet to be observed along other large river floodplains, but the geomorphologic settings and interactions between large rivers and their floodplains suggests that this pattern may occur in many situations. These findings also stress that the nitrogen buffering capacity of a given riparian zone cannot be evaluated without a careful assessment of groundwater flow paths.

#### 2.6. Lacustrine versus riverine (riparian) ecotones in temperate regions

The land/water ecotones associated with lakes and reservoirs in temperate regions are mostly covered with wetland vegetation similar in composition to typi-

cal riparian vegetation. Additionally, the supply of nutrients (like nitrate) and organic matter generally follow the flow-paths presented in Fig. 2A and 2B (Hillbricht-Ilkowska and Pieczyńska 1993). However, there is some difference between the functioning of riverine and lacustrine ecotones in temperate regions. The primary reason is the amplitude of seasonal water table fluctuations, which in the case of rivers is generally much greater. In rivers, over-bank flooding takes place during the highest discharge and the riparian zone close to the bank is "washed-through" by flowing water. In this period, the stream-borne nutrients may be filtered and retained in the riparian zone but in most cases (depending on the velocity of water) the nitrogen compounds present in riparian zone before flooding – are released and supply the nitrogen pool in the stream. This is why some authors state that the riparian sites, at least in these hydrological conditions – are the donors of organic matter and the organic nitrogen to the stream (e.g., Malanson 1995). Leonardson *et al.* (1994) found that after the flooding the wet meadows, the water is strongly enriched with organic nitrogen. Almost the same was found by Stachurski and Zimka (1994); there was almost four times more dissolved organic nitrogen in water passing through a wetland patch.

The above situation does not occur in lacustrine ecotones due to much smaller vertical movements of water table and the presence of wide littoral zone. The lake littoral zone functions as an "additional" riparian-like system effective in N-uptake and partly in denitrification (anoxic patches in highly organic littoral sediments).

In general, the lacustrine ecotones in temperate regions are sustained mainly by surface and ground water from uplands. Therefore the movement of nitrogen load inside the system is mainly "perpendicular" in respect to the aquatic ecosystem. The efficiency of nitrate nitrogen removal in the lacustrine land/water ecotones is similar to analogous riparian systems with the maximal removing rate usually occurring on the upland-wetland edge (Rzepecki 2000).

### 3. BIODIVERSITY

The dynamic character of natural flow regimes creates a mosaic of non-equilibrium habitats in riparian zones along rivers (Salo *et al.* 1986). These non-equilibrium habitats are covered with a remarkable diversity of plant communities, including trees, shrubs and herbs. The shelter and food thus provided enhances animal diversity in the riparian zone as well as promotes diversity in adjacent aquatic and terrestrial habitats. Whence the basic hypothesis that riparian zones are key landscape components in maintaining alpha and gamma biological diversity (Naiman *et al.* 1993, Pollock *et al.* 1998, Hanley and Barnard 1999, Naiman *et al.* 2004).

#### 3.1. Factors promoting biodiversity in riparian zones

Riparian zones serve as habitat for resident flora and fauna as in most linear patches (Rosenberg *et al.* 1997). Many species found are not just transient species but are true inhabitants that survive and reproduce in riparian zones. This habitat function is probably a primary cause of the high biodiversity (Naiman *et al.* 1993, Pollock *et al.* 1998). However, riparian corridors clearly favor plant displacement and colonization rates that are influenced by environmental features such as cold or dry climatic conditions and local microtopography. Even so, connectivity of riparian zones is a fundamental characteristic for maintaining biodiversity. Firstly, movement is necessary for a species living within a linear patch, as in any other habitat patch. Secondly, the habitat function of riparian zones depends on a corridor function that is likely to take place parallel to these zones: along the nearby river (waterborne seeds), along the upland boundary (displacement of mammals), and in the air (wind or birds transporting propagules). Therefore, both functions – habitat and corridor – of riparian zones and their accompanying environments need connectivity along river networks, a characteristic threatened worldwide by fragmentation and flow regulation of river systems (Dynesius and Nilsson 1994).

Riparian corridors are also well-established routes for invasions by exotic plants across landscape patch types. Specific well-

documented examples are *Tamarix* spp in western USA (Brock 1994), *Impatiens glandulifera* in central Europe (Pysek and Prach 1995), and *Mimosa nigra* in northern Australia (Lonsdale 1993). However, the nature and consequences of interactions between exotics and native plant species within riparian zones along rivers remains unclear. It has been suggested that in riparian corridors, the richest communities may be the most invadable by exotic species (Planty-Tabacchi *et al.* 1996). Nevertheless, exotic species such as *Heracleum mantegazzianum* and *Tamarix* spp are expected to locally reduce native plant species diversity, although there is no clear evidence of this effect at the scale of river corridors. Advances on these issues are needed to understand the role of riparian corridors in the human induced homogenization of flora through expansion of exotic species, which appear as a major threat to plant biodiversity at the global scale.

Flow variability is the principal process in structuring the riparian zones. For example, flood pulses facilitate the establishment of rejuvenated habitats (Junk *et al.* 1989), the coexistence of potentially competitive species (Duncan 1993), and the development of rich species assemblages through local accumulation of litter and silt (Nilsson and Grelsson 1990, Langlade and Décamps 1995). There are five critical components of flood pulses that affect the biodiversity of riparian communities: magnitude, frequency, duration, timing and the rate of change (Poff *et al.* 1997). Under the natural conditions that occur along riparian zones (Pollock *et al.* 1998) concluded that mean flood frequency (number per year) and spatial variation in flood frequency (coefficient of variation) explained much of the variation in plant species richness and local scale variations in plant species richness microtopography (Fig. 3). Small-scale spatial variation in topography affects the disturbance regime by creating mean disturbance frequencies that vary from patch to patch.

At a larger scale, along transects perpendicular to river banks, plant species diversity follows a pattern roughly predicted by the intermediate disturbance hypothesis. There is low biodiversity on highly disturbed depositional bars near the river, highest biodiversity on active channel shelves moderately disturbed by floods,

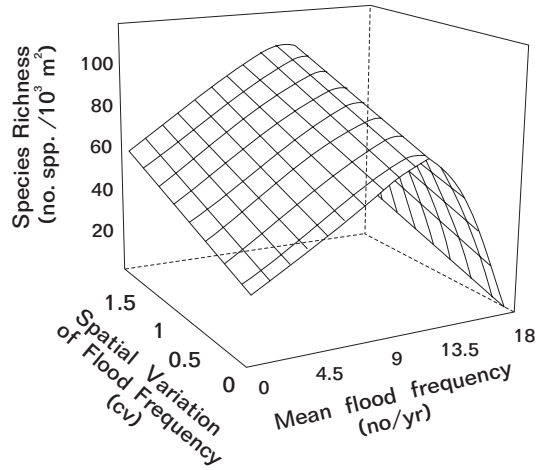


Fig. 3. Relations among species richness, flood frequency, and the spatial variation in flood frequency (from Pollock *et al.* 1998, with permission of primary author and editor).

and decreasing biodiversity in the floodplain, terrace and upland communities where floods are progressively less frequent (Gregory *et al.* 1991) (Fig. 4). Destructive less frequent floods destroy ancient vegetative patches and create new ones, thus enhancing habitat turn-over rates and heterogeneity. This allows the development of a patch age distribution favorable to the juxtaposition of early, mid and late successional species along rivers as described for lowland forests from the Amazon (Salo *et al.* 1986) and North America (Naiman *et al.* 2004). Thus, plant diversity within riparian zones largely depends on the spatio-temporal variability of hydrogeomorphic conditions over a range of landforms including terraces, floodplains, active channel shelves, depositional bars, abandoned channels, overflow channels, backwater, oxbow lakes, meander scrolls, alluvial fans, and mid-channel islands. Lateral channel migrations regularly change one of these landforms to another, resulting in a dynamic mosaic of plant communities along rivers (Décamps 1996).

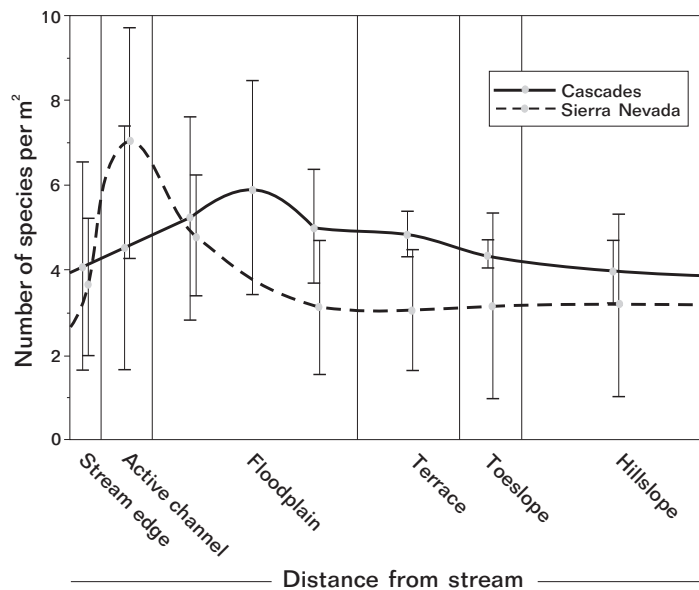


Fig. 4. Gradients in riparian plant species richness. Plant species diversity was found to decrease from the active channel and floodplain to the hill slope along streams on the west slope of Oregon's Cascade Mountains (USA) and three streams in California's Sierra Nevada Mountains (from Gregory *et al.* 1991 with permission of copyright holder: American Institute of Biological Sciences). The peak in plant diversity found in the active channel and floodplain is associated with the large variety of vegetative age classes and landforms created by erosion and depositional processes. Furthermore, large wood accumulations on the floodplain are significant sites for colonization by coniferous species within an otherwise deciduous tree matrix, as well as sites for the retention of numerous plant propagules in a favorable microclimate (Gregory *et al.* 1991, Fetherston *et al.* 1995, McKee *et al.* 1982).

### 3.2. Role in promoting surrounding aquatic and terrestrial diversity

Since the first observations by Egglisshaw (1964), freshwater ecologists have frequently reported high correlation between the amounts of riparian detritus in streams during autumn and the density of benthic macroinvertebrates, especially leaf-shredder detritivores. A closer look reveals that it may be difficult to generalize. Densities of benthic detritivores are positively correlated with the amount of organic matter in riffles but not in pools in intermittent streams in Australia (Boulton and Lake 1992). Moreover, typical shredders may not be the only or even the major users of organic matter accumulations. For example, leaves provide large surface areas that promote a rich development of microorganisms. Hence, there is abundant food for fine particle feeders such as oligochaetes, regularly encountered on the surface but also inside the leaf matrix, enhancing leaf breakdown by their activity (Chauvet *et al.* 1993).

Nevertheless, increased prey (insects and fish) attracts terrestrial and semi-aquatic vertebrates. Thus, insects that feed of the species-rich terrestrial vegetation and aquatic insects that emerge from the stream provide abundant and diverse food. Similarly, many species of mammals and birds prey on fish that are resident in the stream (Dollof 1993, Ben David *et al.* 1997). When fish populations exhibit pronounced seasonal peaks in their abundance (e.g., returns of anadromous salmon to their freshwater spawning habitat), large and very important temporal pulses of food availability are introduced to riparian systems. Pacific salmon (*Oncorhynchus* spp.), for example, are a major food resource for many species of terrestrial carnivores in their region of occurrence (Willson *et al.* 1998) and shape the characteristics of riparian system (Naiman *et al.* 2002).

The shade provided by riparian vegetation exerts strong influence over fundamental aspects of stream habitat and energy flow that influence biodiversity. Riparian shade can influence thermal regime (Rutherford *et al.* 1997), primary production (Hill *et al.* 1995), and input of harmful UV-B radiation. Lighting in narrow streams (<3.5 m wide channels) with forested riparian areas may be as little as 1% of ambient, but this increases sharply

as the gap in the canopy widens with increasing stream width (Davies-Colley and Quinn 1998). Removal of shading riparian vegetation by forest clearcutting or pasture development results in high light exposure, which is expected to reduce stream biodiversity at the regional scale (Quinn *et al.* 1992).

Riparian characteristics such as slope and microtopography are important factors to consider in relation to this ecological functioning. They influence the proportions of litter entering streams either directly or transported laterally from the forest floor. These proportions influence significantly in-stream community dynamics as a consequence of input quality and timing. Laterally transported litter may be qualitatively important as a source of nourishment, even if not exceeding 10% of the total litter input, because of a higher nitrogen concentration than that of leaves falling directly into the stream (Benson and Pearson 1993).

Further, where accumulations of large woody debris exist, there is a higher degree of spatial heterogeneity in river channels with a higher habitat diversity, both within and between accumulated debris (Angermeier and Karr 1984). These piles may be both dense and durable: woody piles of more than 300 years old (Abbe and Montgomery 1996, Bilby and Bisson 1998) have been reported from streams of the Pacific coastal rain forest in the USA. Some of these piles exceed 10 meters in height and trap more than 10,000 m<sup>3</sup> of sediments. Among the biophysical function of woody debris piles, habitat formation within stream channels is especially important for maintaining fish and macroinvertebrate diversity (Anderson and Sedell 1979). Densities of macroinvertebrates can largely exceed 20,000/m<sup>2</sup> for areas covered with woody debris dams in coastal plain streams in the United States (Benke *et al.* 1984), confirming (along with many other studies) the relevance of riparian derived woody debris as habitat for macroinvertebrates in stream systems.

The influence of riparian derived leaf litter on aquatic food webs was experimentally tested by a large scale, 3-year exclusion of leaf litter inputs to a forest stream in western North Carolina (Wallace *et al.* 1997). This exclusion had a strong bottom-up effect that propagated through detritivores to predators, with significant declines

in either abundance, biomass or both for most invertebrate taxa, providing evidence of the importance of riparian litter for the development of diverse aquatic food webs. Riparian zones may also influence aquatic insect biodiversity by providing necessary habitat conditions for adult phases for aquatic insects. Collier and Smith (1998) found that the main area of activity for adult Trichoptera in forested riparian zones was within 30 m of the edge of three New Zealand streams.

Litter quality significantly influences rates of litter breakdown (Aber and Melillo 1982), much of this influence being mediated through trophic interactions between microbes and invertebrate shredders feeding on the litter (Suberkrop 1998). Mechanisms contributing to litter breakdown (i.e. leaching, microbial colonization, fragmentation by physical force and invertebrate feeding) lead to the production of fungal, bacterial, and animal biomass, as well as the formation of carbon fractions such as carbon dioxide, and dissolved and particulate organic matter. The resulting microbial diversity appears as a basic property of the ecological functioning of riparian zones.

Riparian zones exert an attraction to a variety of animal and plants. Many examples could be mentioned of the attractiveness of riparian zones for birds and mammals (Naiman and Décamps 1997, Naiman and Rogers 1997). The reasons are many and interrelated: drinking water, quality of vegetation, anti-predation strategy, migration routes, and so forth. It is now recognized that animal assemblages developing in riparian zones are interdependent with those living in adjacent uplands, particularly at intermediate elevations along river profiles, as suggested for birds (Lock and Naiman 1998).

Finally, the diversity of inhabitants of riparian zones can modify habitat structure and function. Among such modifiers are the well known beaver (Naiman *et al.* 1986) but also larger mammals such as moose and brown bear in North America, and hippopotamus and warthog in South Africa. Browsing can result in long term consequences such as reported for moose in North America (Pastor *et al.* 1993), and for elephant, kudu, giraffe and bushbuck in South Africa (Naiman and Rogers 1997).

#### 4. MANAGEMENT

In this paper we highlight that the maintenance of a natural hydrological regime is critical for sustaining the key structural and functional characteristics of riparian systems. Many examples clearly demonstrate that the regulation of natural hydrological regimes is a key factor in the deterioration of riparian communities along rivers (Poff *et al.* 2003). Consider the drainage of velvet mesquite (*Prosopis velutina*) forests of many arid riparian ecosystems (Stromberg *et al.* 1993). There the invasion of non native species of *Tamarix ramosissima* is eliminating native species (Busch and Smith 1995), and there is an excessive increase in water consumption (Sala *et al.* 1996). Similar deterioration is also frequently demonstrated in various parts of the world. At the same time, about 70% of the earth's freshwater flow was regulated by dams at the beginning of the 1980s (Petts 1984), and fragmentation and flow regulation of river systems have extensively altered the natural conditions of hydrological regimes (Gregory *et al.* 1991).

Riparian zones have been used successfully to control diffuse pollution mainly under temperate climatic conditions. From the point of view of riparian zones as buffers against stream or lake or river contamination, even narrow riparian zones (< 10 m) could prove effective as long as agricultural practices remain at relatively low intensity and at the intermediate flow rate of water passage through the ecotones. But the riparian zones will not buffer all the pollutants in the same way and with the same efficiency. This requires different management procedures. For instance, if riparian zones serve as storage sites for conservative pollutants such as sediments, phosphorus or heavy metals, they will eventually become saturated. Hence they need constant or periodical active management procedures such as sediment removal or plant harvest. Somewhat in contrast, nitrate is effectively removed via microbial denitrification and requires that the bulk of the water move either across the surface or as shallow groundwater through biologically active soil zones.

The integrated effects of riparian zones on water quality will differ according to stream order, smaller streams having

a greater potential than larger ones to buffer against diffuse pollution (Lowrance *et al.* 1995). In the long term, it will also depend on the variability of the hydrologic regime – the only way to regenerate a diversified riparian vegetation, which itself is a key factor for maximal interception of groundwater flows and, therefore, long-term vitality of the buffer function of a riparian zone.

These groundwater flows follow intricate routes, which complicates predicting how water-borne nitrate and other nutrients encounter roots and soil microbes. Moreover, hydrological pathways are naturally highly dynamic, changing widely in space and time (Lowrance *et al.* 1995), and forest growth or weather variations may affect the degree of saturation of the riparian zone as well as the proximity of the water table to the soil surface (Haycock *et al.* 1997). Also, the traveling distance of subsurface flow and drainage to the river affects the duration of contact and therefore the efficiency of a given riparian zone regarding N flux regulation. This large diversity of conditions forces one to consider local factors when designing a riparian zone for buffering diffuse pollution.

Appraisal tools at the landscape levels also need to be developed. The control of water quality in headwater catchments is indeed an effective management strategy since, once a river is contaminated, few inexpensive possibilities remain for improvement, except maybe in arid zones where the longitudinal connections are exacerbated. Yet, riparian zones should not be regarded as inexhaustible sinks for high nutrient inputs. The use of riparian zone as a nitrogen buffer needs to be accompanied by appropriate land practices over the broader landscape to control nutrient inputs within levels that can be assimilated.

Wooded river corridors are also recognized as having a crucial role in conserving the biological diversity of rivers and their surroundings. This role is linked with the other goods and services that river corridors can deliver: flow regulation, water quality, fish production, wildlife habitats, landscape amenities, timber production (Petts 1990, Naiman *et al.* 2000). All these benefits require that biodiversity of riparian zones be considered by those charged with management, restoring and protecting the world's rivers. As for maintaining their buffer capacity, maintaining

biodiversity of riparian zones implies paying attention on two basic features (Peterken and Hughes 1995). Firstly, hydrological processes in order to allow artificially constrained rivers to move freely about their floodplains. Secondly, vegetation in order to maintain wooded communities that develop naturally along riparian corridors (Zalewski *et al.* 1998). But the issue is not only ecological; the response of riparian vegetation to hydrological and geomorphological processes must be coupled to public-policy consideration of social, economical and cultural issues.

Sustainable management of riparian zones, either to conserve or restore, implies that biogeochemistry and biodiversity are linked under natural regimes of hydrologic disturbances (Poff *et al.* 1997, 2003). Such a link is at the basis of the services provided by riparian zones. The Riparian Ecosystem Management Model (REMM) developed in the USA suggests that multi-species buffer strips provide the best protection of streams against agricultural impacts (Lowrance *et al.* 1995). This model uses three interactive zones that are in consecutive up-slope order from the stream: (i) A permanent forested zone to influence the stream environment (e.g., temperature, light, habitat diversity, channel morphology, food webs and species richness). (ii) A zone of managed shrubs and trees to maximize biomass production, as well as biological and chemical transformations, storage in woody vegetation, infiltration, and deposited sediments. (iii) A herbaceous zone next to cropland, to provide spreading of overland flow, thus facilitating deposition of coarse sediments. Clearly this basic model must be adapted to various catchment geomorphologies, climatic conditions and stream orders to provide effective management.

In the context of the worldwide transformations of flow regimes, the deterioration of water quality and loss of biodiversity, restoring riparian zones is both a key objective and a formidable challenge.

Decision makers need to envision the consequences of management actions on the long term. How many years are necessary for riparian vegetation to adjust to dam construction? And what will be the new dynamic equilibrium? Contrasting answers may occur depending on the type of river studied as well as on the type of water level regulation. For example, water

development produced a decline in the establishment of *Populus-Salix* woodlands along the meandering Missouri River, but an expansion of the same woodlands along the nearby braided, sand-bed Platte River in the USA (Johnson 1997). In the first case, the effects were slow to appear, two centuries being estimated for the riparian vegetation to reach a new post-dam steady state. In the second case, the response to stream regulation was both rapid and extensive, evolving to a new equilibrium after some decades. Species richness in riparian plant communities also varied with the type of water level regulation in central and northern Sweden (Nilsson *et al.* 1997). After some thirty years, storage reservoirs were found to maintain an impoverished riparian vegetation with an index of species richness of about one half compared to adjacent free-flowing rivers, whereas some community characteristics deteriorated and others recovered in run-of-river impoundments. These results argue for the restoration of natural attributes of flow regimes, eventually by removing some ancient dams.

We need to consider entire river basins when managing riparian zones for maintaining biodiversity. Differences characterize hydrological networks – between a river and its tributaries or between various sections of the same river – when considering hydrological conditions, geomorphologic background or the structure of riparian plant communities. For example, aquifer recharge conditions may differ dramatically over short distances and short periods of time. Also, ecological effects of dam construction depend on location of the impoundment in the upper, middle or lower reach of river networks (Ward and Stanford 1983). On the other hand, river systems may act as corridors for displacement of plants and animals along riparian zones, allowing some communities to recover their species richness after a catastrophic event or, on the contrary, facilitating invasions by non-native species with possible deleterious effects on species richness of native communities.

## 5. CONCLUSIONS

1. Testing the robustness of the Temperate Riparian Zone Model in other

climatic conditions reveals both similarities and differences in the nitrogen retention capacities of riparian zones. Their retention is controlled by i) vegetation uptake and denitrification, ii) corridor structure. Moreover, the retention of allochthonous nitrate coming from the terrestrial inland is a function of its travel duration and timing of input through the riparian zone.

2. The review emphasizes the key role of wet-dry cycles but most specifically points out the importance of the timing of their occurrence. In temperate and wet tropical areas nitrate fluxes are rather constant. Under such conditions allochthonous nitrate seems to be processed to such an extent that it is totally removed within a few meters of travel flow in the riparian zone. Under harsher continental conditions, the high nitrate fluxes occurring during spring thaw pass through the riparian zone largely unprocessed, because cold temperatures limit both denitrification and plant uptake. Similarly little nitrogen processing occurs during transport from upland through riparian zones in arid areas. Thus the riparian zone is rather ineffective in initial retention of upland nitrogen inputs in cold continental and in arid climates, in part because overland flow rapidly transports water and nitrogen across the riparian surface during storm events. This hydrologic connectivity between the surface stream and the riparian zones allows for longitudinal processing of upland derived nitrogen.

3. However, in the periods when the groundwater transport of upland nitrogen load is rather long the effective removal of nitrate nitrogen at the land/water ecotones is observed in both oceanic and continental temperate regions. There is a similarity in this respect between lacustrine and riparian ecotones.

4. Riparian zones maintain high levels of biodiversity at the landscape scale reflecting their ecotonal properties. This is supported by studies conducted in various parts of the world which again highlight the importance of i) longitudinal connectivity and ii) wet-dry cycles. As a result, while advances in biogeochemistry depend on our knowledge of how well known cycling processes are modified by climatic conditions occurring in different ecoregions, advances in biodiversity depends

rather on our ability to improve basic understanding of dynamic processes. On the other hand, we need to understand the physical-chemical mechanisms influencing these processes within accretional sedimentary environments subjected to seasonal aerobic-anaerobic cycles.

5. A better understanding of the role that riparian zones play in maintaining biodiversity is likely to come from a new examination of two main characteristics. First, would be studies of the effects of hydrologic variability, which are focused on timing or predictability of disturbance in various geomorphic conditions. Second, would be studies of connectivity, which concentrate on the habitat, rather than on the corridor, characteristics of riparian zones.

6. Restoring the biodiversity of riparian zones implies attention to other goods and services that riparian systems can bring to human societies. Location and pattern of remedial measures must be planned on the basis of socioeconomic as well as ecological consequences. As stated by Peterken and Hughes (1995), restoration of floodplain forests does not imply forests everywhere, but careful consideration of the other potential benefits of riparian systems. Clearly, locational principles are needed in order to combine at best public-policy utilization with conservation of biodiversity in riparian systems (Nilsson 1996, Dale *et al.* 2000). But this should include careful consideration of local environments: urban, arable or pasture areas, flood risk sites, and so forth. Riparian zones along rivers appear as one of the best examples of the necessity of adaptive management, that is the ongoing interactions between scientists, managers and the public.

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