

Development, maintenance and role of riparian vegetation in the river landscape

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SUMMARY

1. Riparian structure and function were considered from a longitudinal perspective in order to identify multiscale couplings with adjacent ecosystems and to identify research needs.
2. We characterized functional zones (with respect to vegetation development in association with various biogeochemical processes) within geomorphological settings using a delineation based upon erosional, transitional and depositional properties.
3. Vegetation dynamics within the riparian corridor are clearly influenced substantially by hydrological disturbance regimes. In turn, we suggest that vegetation productivity and diversity may widely influence riverine biogeochemical processes, especially as related to the consequences of changing redox conditions occurring from upstream to downstream.
4. However, surface and groundwater linkages are the predominant controls of landscape connectivity within riparian systems.
5. The importance of riparian zones as sources and sinks of matter and energy was examined in context of structural and functional attributes, such as sequestering or cycling of nutrients in sediments, retention of water in vegetation, and retention, diffusion or dispersal of biota.
6. The consequences of interactions between different communities (e.g. animals and plants, micro-organisms and plants) on biogeochemical processes are notably in need of research, especially with respect to control of landscape features. Multiscale approaches, coupling regional and local factors in all three spatial dimensions, are needed in order

to understand more synthetically and to model biogeochemical and community processes within the river-riparian-upland landscape of catchments.

Keywords riparian zone, plant ecology, rivers, streams, ecosystems, groundwater

Introduction

Geomorphology as a template

For the last two decades tremendous research activity has focused on the role of riparian vegetation as a source of energy and matter for the aquatic ecosystem (Hynes, 1975; Décamps, 1984; Naiman & Décamps, 1997). The ability of riparian vegetation to control and recycle allochthonous inputs from the upland drainage basin and the river itself is a fundamental aspect of river ecology (Brinson *et al.*, 1984; Schlosser & Karr, 1981; Peterjohn & Correll, 1984). The role of stream functioning on vegetation has most often been studied with respect to the physical injury that hydrological disturbance causes to riparian woodlands and plant communities at a local scale. Very few studies have been devoted to the consequences of the riparian vegetation on the system functioning at broader scales (i.e. the entire river corridor or drainage basin). Until recently, the role of riparian vegetation for upland systems (and, conversely, of upland systems for riparian vegetation), has received little attention.

We assume that the myriad of factors controlling the health and functioning of stream ecosystems can be grouped into two categories, internal (or endogenous to the riparian system) and external (or exogenous, involving adjacent systems linked to the riparian ecotone). Hence, we can delimit them spatially in order to consider the relationship of the riparian vegetation to the stream and the stream to the riparian vegetation. We also assume that since every type of river system has its own character (e.g. geological and climatic traits), so does its geomorphological structure, and hence the reciprocal control between hydrology and vegetation may be analysed overall from a geomorphological template. It is clear, however, that such a template can not substitute for a particular system-specific study explaining stream-vegetation relationships, particularly if regional constraints on streams (e.g. desert climate) are strong (Malanson, 1993; Naiman & Décamps, 1997). Moreover, the importance of the character of a given river system for the relationship between stream and riparian vegetation should increase following altera-

tion of the natural regime by human activities (Poff *et al.*, 1997). Our view of the problem is landscape oriented, assuming that spatial structures interplay with ecological processes at different scales (i.e. from the drainage basin to the microhabitat scale), including the complex interactions between surface and subsurface compartments.

Since the River Continuum Concept (Vannote *et al.*, 1980) and the Nutrient Spiralling Concept (Webster, 1975; Minshall *et al.*, 1983; Newbold *et al.*, 1981), riparian zones have been fully integrated as major compartments for stream ecosystem functioning. Hence, river systems and their accompanying riparian zones can be viewed as open ecosystems dynamically linked longitudinally, laterally and vertically by hydrological and geomorphic processes occurring within a temporal hierarchy (Ward, 1989). These hydrological and geomorphic processes act as primary ecosystem drivers, whereas chemical and biological factors act as secondary response variables. This should not be interpreted as suggesting that chemical or biological factors do not affect river and riparian structures or processes, but rather that hydrogeomorphic variables establish the physical template and provide constraints under which chemical and biological processes must operate. This view is consistent with the current concept of the interface between the riparian and the stream channel, in which valley floor landforms and associated riparian vegetation form a mosaic of bio-physical habitats across and beneath the surface of the floodplain (Stanford & Ward, 1988, 1993; Gregory *et al.*, 1991). Geomorphic factors may be internal (soil physics and chemistry, slope within the riparian zone) or external (catchment area and gradient, soil mineralogy and texture, bedrock type and depth, volume and composition of groundwater inputs, channel morphology). Catchment area and gradient are major determinants of the volume and kinetics of external inputs to riparian zones. Soil mineralogy is a very important determinant of the chemical composition of external imputes, whereas soil texture to a large extent determines the relative proportions of surface water and groundwater inputs. The characteristics of the

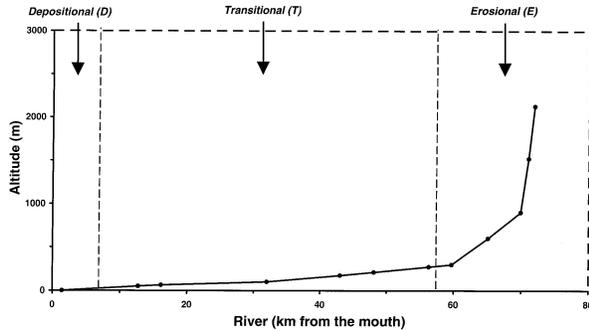


Fig. 1 Delineation of Erosional, Transitional and Depositional (ETD) provinces along the longitudinal profile of a stream.

surface soil control water movement and retention and, secondarily, control the main water supply for riparian plant and animal communities. This is particularly important during dry periods when river and groundwater levels are low. Therefore, our approach to this analysis, like most of the contemporary ecological theory of rivers and streams, is based on a geomorphic, longitudinal delineation of the stream ecosystem. This delineation also includes explicitly the transverse zonation of the riparian ecotone based on similar patterns and processes, but expressed at a different spatial scale.

The aim of this paper is to give some insight to the development, maintenance and the role of riparian vegetation in the riverine landscape. We emphasize a 'riparian vegetation approach' wherein surface and groundwater controls are considered in context of stream ecosystem ecology from local (internal) to catchment (regional) spatial scales.

Geomorphological settings: pattern and scale

Erosional, transitional, and depositional (ETD) provinces

Stream channel and floodplain morphology are governed by the volume and timing of discharge, the volume, timing and character of sediment delivery and transport, and the large-scale geological history and geomorphology of the drainage basin. The size of the stream channel is largely determined by flood-peak flows, particularly those that affect sediment erosion and transport. Rosgen (1994) suggested that bankfull flows with a recurrence interval of ≈ 1.5 –2.5 years are largely responsible for channel formation. However, Calow & Petts (1992) maintained that no

consistent correlation between flood frequency and channel formation could be universally demonstrated across biotopes. Rather, channel morphology is shaped by the interaction between stream power (i.e. erosive capacity) and the grain size of the bed material. For example, channels and associated floodplains of large, low gradient rivers may be shaped by frequently recurring flows, while small headwaters with a cobble/gravel substratum may see major reshaping of the channel only during infrequent, extreme events.

Studies of alluvial channels and the type, supply and dominant textures of sediments demonstrate predictable relationships in form and structure (Leopold *et al.*, 1964; Shelby, 1985; Swanson *et al.*, 1988; Church, 1992). Furthermore, fluvial processes acting on geomorphic surfaces create physical patterns that are reflected in spatial and temporal development of riparian plant communities as well as in the soil nutrient cycling. Indeed, it is reasonable to assume that soil grain size affects the rates of microbiological processes involved in the nitrogen cycle through the effect of grain size on water holding capacity. For instance Pinay *et al.* (1995) found that *in situ* denitrification rates measured in loamy riparian forest soils were three times greater than those measured in the sandy soils. These fluvial processes are significantly affected by drainage basin gradient, bed-material grain size, characteristics of stream discharge, and the volume of stored alluvium.

The major physical factors of river catchments that influence the development of riparian corridors are the bedrock geology, geomorphic features (e.g. surface landforms such as erosional features, and deposits created by fluvial, landslide and wind storm events), soil character, climate, and hydrological regimes. These physical factors operate in three large geomorphic provinces of a river catchment: the erosional (E), transitional (T) and depositional (D) provinces (Sullivan *et al.*, 1987).

The erosional province (E) begins in the steep headwaters then proceeds downstream to the transitional province (T, Fig. 1). It corresponds to the most upstream reach in most cases. This province is characterized by a high gradient channel ($> 4\%$) that is structurally controlled (constrained) by a V-shaped valley which permits only minor shifting (lateral adjustment). The increase in kinetic energy through channel constriction or accelerated run-off creates a

Table 1 Spatial and temporal scales associated with a river catchment. Modified from Wissmar (1998) and Sear (1994).

Geomorphic structure	Geomorphic function	Temporal scale (years)	Spatial scale (m)
River basin network	Water and sediment transfer	10^1 – 10^6	$> 10^4$
Valley floor	Water and sediment storage	10^2 – 10^4	10^3 – 10^4
Floodplain	Water and sediment storage	10^1 – 10^3	10^2 – 10^3
Riparian corridor	Water and sediment storage, wildlife habitat	10^0 – 10^3	10^1 – 10^2
Channel meander	Water and sediment transfer+storage	10^1 – 10^2	10^1 – 10^2
Pools and riffles	Water and sediment transfer+storage	10^1 – 10^2	10^1 – 10^2
Depositional bars	Sediment transfer	10^0 – 10^2	10^0 – 10^2
Dunes and ripples	Water and sediment storage	< 1	< 1
Particles	Erosion product	< 10	1 – 10^2

greater ability to transport bedload of a variety of substratum particle sizes. These physical conditions usually limit the spatial development of the riparian corridor.

The transitional province (T) occurs in the river valley and is characterized by a channel gradient commonly ranging from 1 to 4% and with enough kinetic energy for considerable transport of suspended sediments of small size (approximately 0.2–250 mm diameter). It corresponds generally to the middle course of a river. The channel is generally more stable than in the E province and exhibits slow rates of meandering as well as having multiple channels with islands. These physical conditions, coupled with longer residence times of surface and subsurface waters, often permit the establishment of a wide riparian corridor. Complex spatial heterogeneity is expected in this province, and diverse plant assemblages develop there in response to habitat diversity.

The deposition province (D), downstream from the transitional province, has a channel that is low gradient ($> 1\%$), unconstrained and shallow. It visually corresponds to lower courses of streams. The channel is commonly unstable or braided and exhibits a high rate of deposition of fine sediments (< 0.2 mm diameter). The riparian corridor here is often fragmented or dispersed.

However, it must be kept in mind that channel type, slope and length throughout the river continuum is predominately influenced by terrestrial factors, such as bedrock formations and geomorphic changes relating to soil character, hillslope gradient and area and land use history. Climate and associated meteorology and the location and size of tributaries within the drainage

network are also important in channel form and function.

Spatial and temporal scales

Viewing the catchment as a hierarchy of cross-scale dynamics can expand the landscape perspective of riparian corridors and their river catchments. The hierarchy of scales describes structures (e.g. landforms) and processes (e.g. natural disturbance regimes) that influence the development of riparian ecosystems and interactions between channel and upland components of the catchment (Wissmar, 1998). The largest temporal and spatial scale includes the river catchment (10–10 years, km) and the smallest is the particle scale (< 10 years, $> 10^{-8}$ m²) (Table 1). The scales within the river catchment include valley and channel reaches which in turn contain smaller sized riparian and channel habitats. Riparian, channel and floodplain habitats lie within river and tributary valleys whose channel widths range from being narrow (constrained) to wide (unconstrained reaches) depending on the bedrock geology and geomorphological features. Changes in these physical features, and the structure and function of the riparian system, commonly depend on hydrological regimes, sediment routing dynamics, natural disturbances (e.g. tectonic events, floods and fires) and anthropogenic modifications.

The effects of environmental factors on vegetation across riparian landscapes may differ in relation to scale. For example, floods of frequent recurrence may be viewed as moderate events at the scale of pioneer vegetation patches on sandbars; whereas, at the scale of the riparian corridor, these floods may

significantly influence development of mid-term vegetation (Tabacchi, 1992; Auble *et al.*, 1994).

Both the riparian and channel areas can contain a wide variety of wildlife and aquatic habitats (e.g. forest canopies, floodplain ponds, side channels, pools and riffles). The scale of these habitats and their diversity can be controlled by local factors such as channel geometry, discharge and edaphic conditions. Subsurface flow systems and habitats, or hyporheic zones (Stanford & Ward, 1988), also can form important components at both the reach and local scale, depending on influences of the geomorphology and bedrock formations. The smallest scale, which exists within local habitats, includes the boundary layer between water and substratum, fine particles and individual organisms.

Disturbance events and the development of riparian corridors

Studies of the environmental history of river catchments can be used to define different spatial and temporal scales. A common research method is to develop a chronology that describes the history of climatic change and other natural disturbance events. Such a chronology provides a perspective on how various types of disturbance operate over different temporal and spatial scales in the landscape. Retrospective studies also provide essential knowledge for predicting how interactions between natural disturbance events and human modifications cause long-term cumulative effects in both aquatic and terrestrial ecosystems (Wissmar & Beschta, *in press*).

Examples of natural disturbances in recent times (0–6000 BP) include floods, avalanches, debris flows in channels, fire, wind, glacial activity, tectonic and volcanic events. The frequencies of large-sized natural fires and floods are of considerable interest because they recur on a decadal basis (Wissmar & Swanson, 1990; Covington *et al.*, 1994). The frequencies of large-sized natural fires and floods can also overlap with the frequencies of tectonic disturbances (Wissmar *et al.*, 1982; Wissmar & Swanson, 1990). All these disturbances act to reshape earth surface landforms, riparian and channel features. The flood events, along with the accompanying erosion and deposition of materials, also contribute to the formation of different riverine habitats (Benda *et al.*, 1992).

Several studies of riparian ecosystems point to the importance of the frequency of natural disturbances and biological processes in influencing successional stages of riparian ecosystems (Wissmar & Swanson, 1990; Gregory *et al.*, 1991; Auble *et al.*, 1994). In riparian forests along mountain streams, where disturbances can be chronic and frequent (e.g. beavers constructing dams on streams, flash floods), the succession of forest patches may be interrupted by events that occur periodically on a year to several decades time scale, maintaining a young succession stage of the forest community. In such cases, the stand initiation and exclusion stages during recovery tend to be continually reset by disturbance (Fig. 2).

Where disturbances are less frequent (e.g. large flood events and wind storms with 100-year recurrence periods), such as in riparian areas of lowlands rivers with unconstrained channels, the succession might have the opportunity to proceed beyond the stand initiation and understory exclusion stages and persist as understory reinitiation and old growth stages. Predictive tools for these successional changes could have considerable significance to the design of long-term restoration plans. Long-term data sets on the temporal regime of disturbance permits objectives to be based on the expected recovery time or system resilience (Wissmar, 1998), providing a basis for assessing how and when human actions might interact with these processes.

Hydrological controls

An adequate understanding of the hydrology of a riparian zone is fundamental to the understanding of the riparian zone dynamics (Brinson, 1990; Ward & Stanford, 1995). All components of the hydrological cycle in a catchment (i.e. precipitation, runoff and evapotranspiration) exert an important control on the riparian (Correll & Weller, 1989). Evapotranspiration is, in turn, governed primarily by such factors as vegetation, humidity, temperature, wind and sunlight. Thus, to some extent the riparian vegetation has a feedback effect on the hydrological cycle. Water yield (runoff) of the catchment equals precipitation minus evapotranspiration minus infiltration to disconnected, deep aquifers. Depending upon the situation, some upslope runoff will proceed directly into the riparian zone. Channel waters may enter the

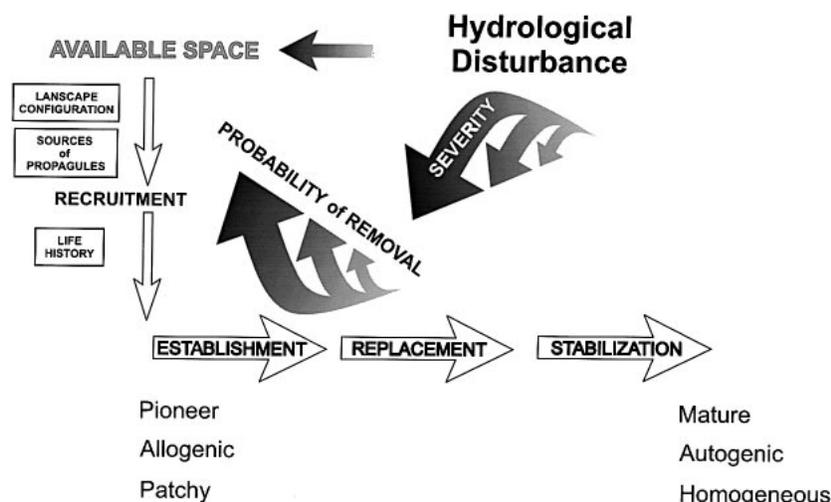


Fig. 2 General scheme of plant succession in the riparian zone. Hydrological disturbance creates space available for recruitment of new individuals or species. The recruitment phase depends on the landscape configuration and on the proximity (or accessibility) of a source of propagules. Life history controls the establishment phase, where pioneer species dominate following allogenic processes in patchy environments. At the opposite end, the stabilization of the succession tends to produce mature stands following autogenic changes in homogeneous environments. According to disturbance frequency, size and severity, the replacement phase is highly conditioned by the removal probability, which creates available space and locally re-initializes the succession.

riparian zone via interstitial flow paths or via surface flooding, depending upon substratum characteristics and stream discharge. Water flux through the riparian zone equals precipitation plus surface and groundwater inputs minus evapotranspiration minus infiltration to deeper layers.

Riparian corridors and landscape connectivity

The high level of connectivity recognized in the riparian corridor mainly results from their location at the interface between the stream and its valley (Hynes, 1975; Naiman *et al.*, 1988). This lateral linkage is increased at the regional scale by the river network within the drainage basin (Forman & Godron, 1986; Malanson, 1993) and at the local scale by the mosaic structure of both geomorphology and vegetation (Kalliola & Puhakka, 1988).

The riparian corridor can be viewed as a major vector propagating matter, energy and organisms longitudinally (Tabacchi *et al.*, 1990; Saunders and Hobbs, 1991). An example of this role is given by plant-animal interactions that facilitates dispersal of both 'partners.' For example, many birds use riparian corridors as migration pathways, thereby connecting vastly different areas (Décamps *et al.*, 1987). As a result, many plants (especially Rosaceae) are dispersed by birds migrating along the riparian zone (especially Turdidae) (Van Dorp & Kalkhoven, 1988; Metzger, 1995). Plant movements

or exchanges may increase at nodes where riparian and other corridors, such as roads, railways and edgerows) intersect (Riffel & Gutzwiller, 1996).

Internal connectivity is highly dependent on the hydraulic conductivity within the corridor, but also on the complexity of surficial and subsurface structures. The importance of surficial structures for sediment, energy and propagule transport has been widely documented, although the role of vegetation in modifying this transport remains poorly understood. Little information is available on the consequences of subsurface flows on the vegetation structure and its dynamics. However, we know that abandoned channels buried by alluvium (palaeochannels) on flood plains frequently maintain exceptionally high rates of hydraulic conductivity and close affinity with surface flow. They are zones of preferential flow in the flood plain aquifer systems and thereby function as an efficient pathway for interstitial biota moving between channel, hyporheic and phreatic habitats (Stanford & Gaufin, 1974; Stanford & Ward, 1988). Likewise, near-surface palaeochannels may enhance hydric conditions in flood plain soils and sustain hydrophilic vegetation (Bornette *et al.*, 1994a; Bornette *et al.*, 1994b).

On the whole, connectivity between the stream and its basin is an interrelated function of (i) the position within the altitudinal gradient (ii) the intrinsic hydraulic power of the stream and (iii) of the development and stability of the riparian zone (Fig. 3). The dynamics as well as the symmetry of

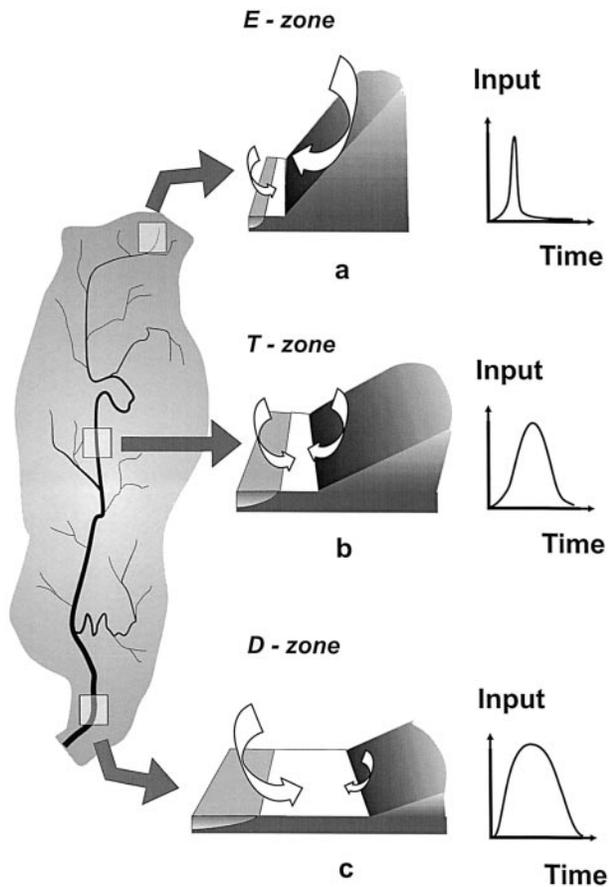


Fig. 3 Variations in input dynamics (right diagrams) and relationships between the stream and its basin (arrows) within the riparian zone (white strip) in Erosional (a), Transitional (b) and Depositional (c) zones along a major stream within a fluvial basin.

the inputs (matter, energy, species) vary from upstream to downstream. In the upper zone (zone E; Fig. 3a), inputs from basin to stream dominate, with very sharp and narrow input peaks. In the middle course (zone T; Fig. 3b) influences coming both from the stream and from the basin tend to be similar in size and dynamics become more smoothed. In the lower part (zone D; Fig. 3c), most of inputs come from the stream, while external inputs from the basin are less important in size and tend to be spatially dissociated from internal inputs from the stream which dominate. The sharpness of the input profile is also reduced in zone D.

The conclusion is that biophysical connectivity associated with the riparian zone is closely related to the hydrology and geomorphology of the landscape. Moreover, the role of riparian vegetation in the

landscape can be viewed from three different perspectives: (i) internal biogeochemical controls on vegetation dynamics; (ii) riparian vegetation as a sink of matter and energy from adjacent systems; and (iii) riparian vegetation as a source of matter and energy for adjacent ecosystems.

Vegetation dynamics and spatial delineation

Plant succession in the riparian context

Perhaps more than any other ecosystem, river ecosystems are intimately connected to and interact with their surrounding landforms (*sensu* Hynes, 1975). Owing to geomorphic, hydraulic and human-induced events, the linkage between the stream and its valley is subject to frequent change. The internal structure of the riparian corridor plays a fundamental role in controlling those changes. Therefore, vegetation dynamics appears as a major actor in the control of linkages between stream and floodplain, and also between the riparian corridor and the uplands. Plant succession induces great changes in the general structure of the corridor, and therefore changes in the physical and biological properties of this structure. The successional process is essentially reset by hydrological disturbance, the intensity and frequency of which varies not only from upstream to downstream, but also from the river to the floodplain. For this reason, riparian vegetation structure has been used as an indicator of hydrological and geomorphological events (Osterkamp & Hupp, 1984; Nilsson, 1987; Hupp, 1990, 1992; Tabacchi, 1992, 1995; Gurnell, 1995).

Plant succession has been widely documented by general studies (Glenn-Lewin & van der Maarel, 1992; see also McCook's (1994) review of concepts and models). Detailed studies devoted to the role of vegetation succession in fluvial processes (Bellah & Hulbert, 1974; McBride & Strahan, 1984; Pautou & Décamps, 1985; Kalliola & Puhakka, 1988; Décamps, 1997) lead to the conclusion that frequency and duration of disturbance events (e.g. flooding) determines the probability of removal of old vegetation and establishment of new riparian plant communities. Quantifying disturbance is key to understanding the plant succession process in riparian systems. From a plant ecology perspective, Grime (1979) defines disturbance as 'the mechanism which limits the plant

biomass by causing its partial or total destruction'. From a landscape ecology perspective, Forman & Godron (1986) give a very similar definition: 'an event that causes a significant change from the normal pattern in an ecological system'. In the riparian context, however, the landscape corresponds to a permanently shifting mosaic, as defined by Whittaker & Levin (1977). So, one might wonder if a 'normal pattern' is not the heterogeneous, irregular, dynamic mosaic resulting from 'normal' hydrological disturbance. As suggested by Glenn-Lewin & van der Maarel (1992), a better approach to the concept of disturbance would lay in the response of organisms according to their use of the resources remaining after the disturbant event.

The role of disturbance in riparian plant succession

In all cases, establishment is a critical stage for succession. The importance of the initial conditions has recently been pointed out from the viewpoint of chaos theory (Ston & Ezrati, 1996). The success of the initialization of the sequence in riparian vegetation succession depends on (i) the availability of the seeds (or of other propagules) (ii) the availability of colonizable habitat (iii) the possibility of seedlings to develop enough before the next disturbance and (iv) the resilience of established populations to the next disturbance. The availability of seeds depends on the presence of genitors, although in the riparian context water flow helps the dispersal of most species (Johansson *et al.*, 1996). However, two factors appear to be critical for a seed to germinate in proper conditions at the right site. The first one is the landscape structure that might facilitate (or not) the dispersal of the seed. The spatial pattern of the landscape may determine species access, though there have been no tests of this hypothesis. The efficiency of species dispersal is supposed to vary from one reach to another in response to the physical integrity and the mosaic structure of the corridor, as well as to the adjacent landscape structure. The second factor is the seedling period, that might coincide (or not) with the availability of appropriate habitat and resources (bare ground, sediment texture, groundwater level). Moreover, most vegetation stages, from mature, seldom flooded hardwoods to ephemeral hygrophilic vegetation, appear to be highly influenced by the interaction between river discharge and groundwater

dynamics. This interaction may result from a coupling in the rise of both water levels, but usually a rise in groundwater may compensate for a lowering of surface water, or simply maintain sustainable hydric conditions for semiterrestrial vegetation (Bernhardt, 1993; Müller & Bürger, 1990). Examples of the importance of such interaction have been found in *Limosella* or *Marsilea* communities, developing rapidly in a very narrow window of time on the muddy banks of a falling river.

Although competition is the main driving force of plant succession, disturbance may often affect any successional stage in the riparian corridor. Van der Maarel (1988) defined this secondary succession as a 'regeneration succession,' in contrast to the primary succession that occurs on a recently exposed substratum. Therefore, another critical step in the process is the recovery stage that can occur with different modalities. At this point, we should consider two kinds of constraints that induce the partial or complete deletion of the riparian vegetation. The first one is stress, due to biotic (grazing, nutrient uptake) or abiotic (water and nutrient availability) factors. In some cases, the activity of large animals can significantly modify riparian vegetation (Naiman & Rodgers, 1997). Animals may also substantively affect vegetation by providing organic matter (carcasses, faeces) and effecting seed banks. The second constraint is the physical disturbance due to floods and human influence (Müller, 1997).

Fig. 2 illustrates a general scheme of plant succession in the riparian context. The recently created available space is colonized by pioneer vegetation. At this stage, the recruitment of new individuals and new species depends on the habitat accessibility for the propagules (Kellman, 1970). Generally, this property is controlled by the landscape configuration and by the presence of propagule providers. Landscape configuration facilitates the access of propagules when corridor and/or edge effects are maximized. This is often the case in the riparian zone in the middle course of rivers, where the disturbance regime allows high levels of patchiness. The distance which separates the source of propagules from the colonizable habitat does not seem to be limiting at the local scale. Indeed, the spreading of most riparian species is highly facilitated by water flows. Hence, patch connectivity during permanent or temporary flooding reduces the importance of the dispersal

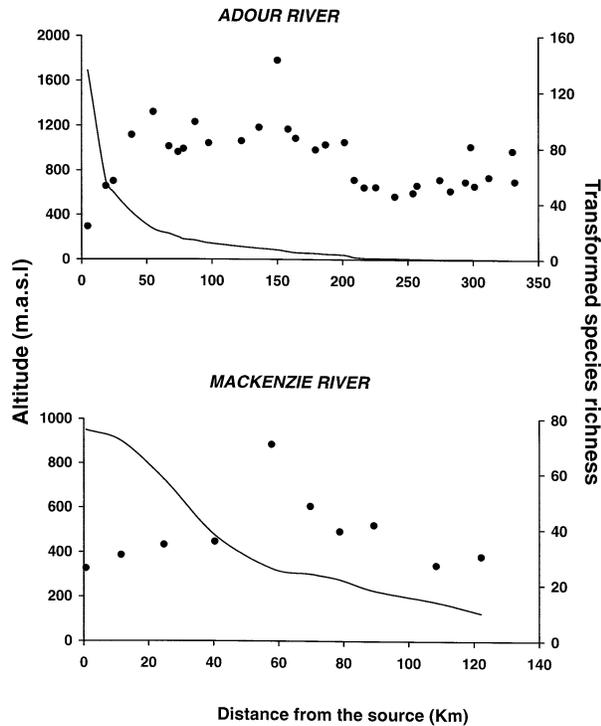


Fig. 4 Changes in species richness of the riparian plant community along two temperate streams. Top: Adour River, SW France. Bottom: MacKenzie River, Oregon, U.S.A. Altitude (left axis, line) and standardized species richness (right axis, dots) are plotted vs. the distance from the source. Modified from Planty-Tabacchi *et al.* (1996).

spectrum (Luftsteinsteine, 1979) of riparian plant communities (Sauer, 1988). The corridor structure is probably strongly involved in the regional connectivity along the upstream-downstream continuum. Hence, a 'metapopulation-type' functioning of the riparian plant communities is expected, although not yet demonstrated (Hanski & Gilpin, 1997). Species life history patterns are also fundamental. For instance, in ruderal and exotic species we have found some evidence of downward and upward linkages between reaches (Planty-Tabacchi, 1993; Tabacchi, 1995; Tabacchi *et al.*, 1996; Müller, 1997; Bureau *et al.*, 1997). These species tend to invade naturally and artificially disturbed streamside systems. The process of invasion has been shown to occur both in the longitudinal and in the transverse dimension of the riparian system, and to be particularly sensitive to the landscape structure.

Following the establishment of species, the replacement process mainly involves competition, which may facilitate, inhibit or tolerate the invasion of new

species. As the root and stem density increases, and the spatial heterogeneity decreases, the community becomes less and less vulnerable to low intensity disturbance. Autogenic processes predominate and community structure tends to stabilize until no higher level disturbance occurs. As suggested in Fig. 2, the probability of removal is expected to decrease from pioneer to mature stages. However, the recovery dynamics following dramatic changes is expected to be greater in young stages, except if the spatial configuration of the gaps created by disturbance enhances dispersal from propagule providers. Another fundamental actor in the recovery of riparian plant communities is the seed bank, that may remain after disturbance or even be created by the disturbance. Then, as suggested by Wissmar & Swanson (1990), the disturbance frequency becomes the main controlling factor for the recovery success of mature stages.

Community species richness and ETD delineation

Patterns of plant community structure along rivers are expected as a direct consequence of the spatial distribution of disturbance events. Many recent observations on plant species richness distribution along streams (Nilsson *et al.*, 1989; Tabacchi *et al.*, 1990; Tabacchi *et al.*, 1996) support the Intermediate Disturbance Hypothesis (Connell, 1978) as the determinant of species richness and sustained biodiversity. Indeed, maximum species richness has been observed in most cases in the middle course of rivers (the T province) where intermediate hydrological disturbance occurs and, as a consequence, where maximum habitat diversity can be found (Fig. 4). The upper reaches (the E province) usually have a lower species richness of riparian plants and this increases downstream. In the lower course (the D province) the low frequency but high duration of inundations supposedly induces a higher degree of specialization of the flora, which therefore has a lower regional species richness. The increase of specialized organisms is further enhanced in the estuary, where salinity mostly restricts riparian vegetation to halophytic species. However, those general patterns observed under temperate climates may be inconsistent in some cases. For example, drastic climates (e.g. semiarid ones, cf. Tabacchi *et al.*, 1996) or natural physical disruptions of the geomorphic upstream/downstream continuum

can induce an irregular, non structured pattern. Climatic factors may also affect the longitudinal pattern. For instance along the Adour River in SW France, the mild climate originating from the Atlantic Ocean increased the riparian community species richness by adding native and exotic thermophilous species to the lower course (Planty-Tabacchi *et al.*, 1996). Further, human-induced disturbance (stream-flow regulation, corridor fragmentation, land use) affects the longitudinal patterns of species richness through loss of habitat or through species introductions (Planty-Tabacchi, 1993).

Community composition and ETD delineation

Plant species attributes have been recognized as potential indicators of the disturbance regime (Grubb, 1977; Noble & Slatyer, 1980; McIntyre *et al.*, 1995) and of the landscape connectivity (Martin & Bouchard, 1993; Tabacchi *et al.*, 1996). The composition of riparian communities based on the life span, the morphology or the habitat/origin of the species may characterize each geomorphic province of the stream. Some plant groups clearly indicate external influences on the riparian corridor. Other groups indicate internal influences induced by endogenous processes.

Some examples of the existing relationship between ETD delineation and plant community composition can be found in the comparison of plant groups proportions (i.e. exotics, ruderals, trees, etc.) between the Adour River and the Mackenzie River (Fig. 5). Exotic species are riparian or non riparian species originating from other countries and invading riparian corridors following human activities. Those species are not expected to be specifically adapted to riparian conditions, and occur in other disturbed systems. Similarly, ruderals are species that are adapted to low stress/high disturbance environments. They usually benefit from human-induced disturbance, and widely colonize crop fields and waste grounds. However, some of them may be usual or specific inhabitants of riparian corridors. Annual species, with the shortest life-span of any plants in the riparian community, are expected to be more adapted to disturbed reaches. On the contrary, trees represent the most stable component of the community, although some of them (mainly poplars and willows) are pioneer species adapted to disturbance. Finally, we called 'externals' the species which are neither

exotics nor ruderals, but which can not be included within the usual riparian flora. Those species mainly occur at the edge of the uplands and the riparian corridor, and colonize accidentally the riparian zone because of the high accessibility of available habitat for propagules (Tabacchi, 1992). As indicated by Fig. 5, exotics clearly colonize more the lower part (the D province) of both streams. The mildness of the climate in the lower valley favours the exotic species which are mainly thermophilous. However, the increase of human influence on the lower part of the basin induces fragmentation in the riparian zone and higher connectivity between riparian corridor and cultivated or urbanized ground and is the main factor responsible for the observed pattern.

Finally, one major consequence of the interaction between natural (hydrological) and human induced disturbance in riparian temperate zones is the increase of the number of endogenous and/or exogenous stress tolerant species.

Internal biogeochemical processes and riparian vegetation

Importance of redox derived processes

Many characteristics of the riparian zone, such as the species composition of the vegetation and processes such as denitrification, require that the soils be anaerobic or of low oxidation/reduction potential (Eh), at least for part of the year. The below ground processes which result in this low Eh are composed of a series of biogeochemical reactions that occur in a defined order (Billen, 1976). These reactions transfer electrons from organic matter, released from the plants, to various terminal electron acceptors. The vegetation of the riparian zone is of fundamental importance in maintaining this low Eh, since it represents the main source of organic carbon. Hence, for the riparian zone to maintain a low Eh it is therefore essential that the plants have a high primary productivity and that enough of the resulting photosynthate is released below-ground to provide enough electrons to drive these reactions at high rates. The availability of terminal electron acceptors determines which level in the series will dominate below-ground processes at any one time and place in the riparian zone.

ADOUR RIVER

MACKENZIE RIVER

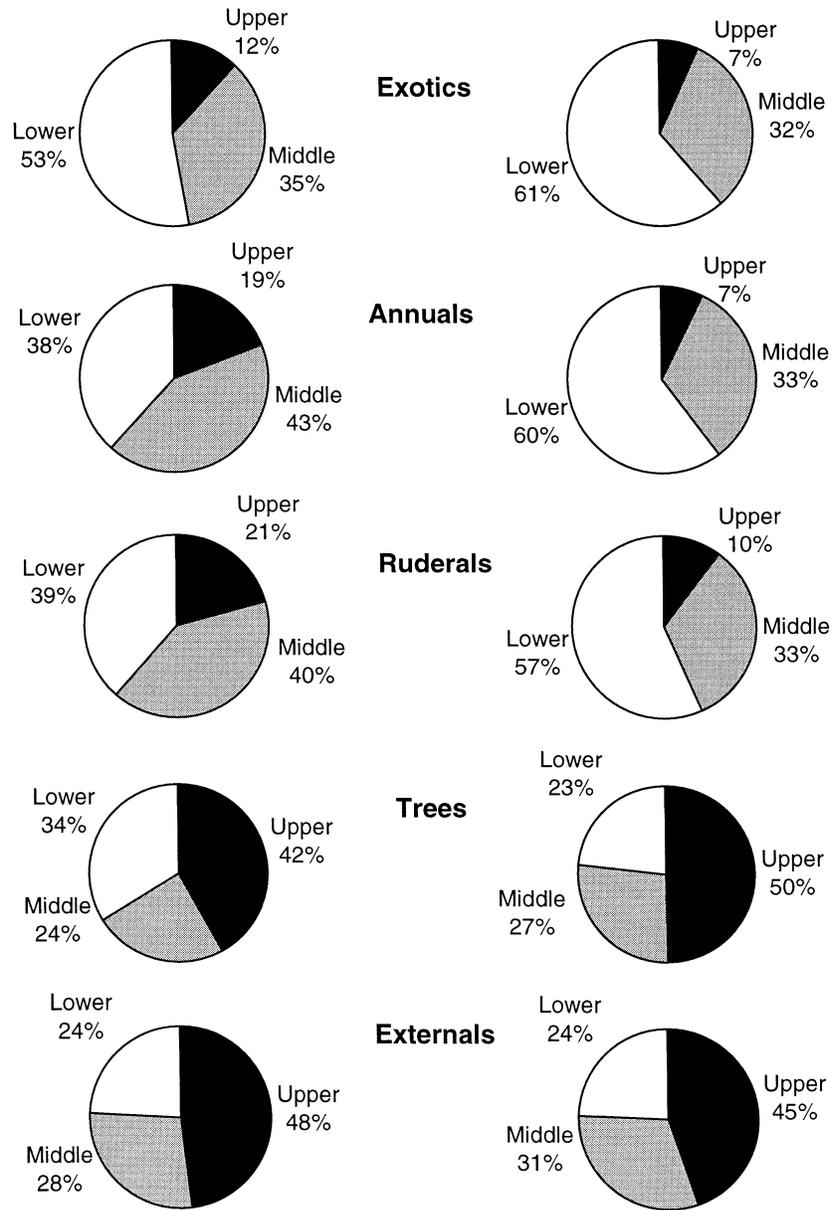


Fig. 5 Changes in plant groups proportions in riparian communities of the Adour River (left) and of the MacKenzie River (right). Each diagram shows the relative importance of each group for the E province (black) for the Middle reaches (grey, T province) and for the Lower reaches (white, D province). See text for the definition of external species.

Some of the more commonly important reactions are manganate ion reduction, denitrification, ferric iron reduction, sulphate reduction and methanogenesis. They occur in this order as a result of thermodynamic considerations. None of these reactions can proceed in the presence of molecular oxygen. Once oxygen has been consumed by processes such as respiration, and sulphide and ammonium ion oxidation, then manganate reduc-

tion may proceed. Once all manganate is reduced or if none occurs at the site, then denitrification can proceed, etc. The reversibility of many of the reactions is limited by the production of volatile end products or changing pH. These factors and others produce a series of negative feedback mechanisms which tend to limit the further progress of a below-ground process (Correll & Weller, 1989).

For example, in the case of sulphate reduction, as the ratio of electron acceptor to product decreases (e.g. $\text{SO}_4^{2-}/\text{S}^{2-}$), the equilibrium Eh required for the reaction to proceed declines. As the absolute concentration of sulphate declines, Eh must also decline for the reaction to proceed. As the pH rises, due to consumption of hydronium ions in the reaction, the Eh must decline for the reaction to proceed. At the same time the rates of entry of oxygen and other more easily reduced electron acceptors, such as nitrate, continue at previous rates, which will raise the Eh if sulphate reduction rates begin to slow down. Another example is denitrification. As the reaction proceeds, pH rises due to hydronium ion consumption in the reaction, and nitrate is converted to dinitrogen and nitrous oxide gases which evolve from the system, and the rate of denitrification slows while the rates of other processes, such as nitrification, may increase.

We can hypothesize that reduced conditions are more marked both in terms of spatial occurrence and intensity of reduction in riparian zones situated along larger streams (Fig. 6). In such areas, the finer sediment deposits and longer flood periods both contribute to the maintenance of reduced conditions in the floodplain soils (Pinay *et al.*, 1994). Moreover, the active hydrological processes maintain a mosaic of geomorphic areas having various sediment texture which influence soil oxido-reduction conditions and, in turn, the spatial pattern of riparian forests (Pinay *et al.*, 1995).

Nutrient cycling and productivity

Wetland productivity is mainly a function of the importance of energy and matter supplied by the drainage basin as well as the alternation of reduced and oxidized conditions of its soils and sediments. Due to their location along rivers, riparian forests receive large amounts of dissolved and particulate organic matter and nutrients from upstream. In agricultural headwaters, riparian zones are subject to large subsurface nitrate inputs from the uplands (Peterjohn & Correll, 1984), while in larger rivers, significant amounts of sediments, organic matter and nutrients are deposited during flood events (Brinson *et al.*, 1984; Schlosser & Karr, 1981; Lowrance *et al.*, 1986; Grubaugh & Anderson, 1989). Moreover, riparian forest soils present rapid successions of reduced and oxidized conditions which are governed by flood

events, and soil grain size (Pinay *et al.*, 1995). This alternation in redox favours soil microbiological processes and increases the soil nutrient cycling and availability for plant growth (Reddy & Patrick, 1975). These large allochthonous nutrient inputs and the alternation in soil redox, sustain a high productivity in riparian forests compared to other natural ecosystems. For instance Chauvet (1989) measured up to 5 tons of dry litter per hectare in a riparian forest of the Garonne River in South-west France. Little is known about the effects of production in the herbaceous layer, although similar values of necromass have been observed. For example, *Urtica/Impatiens glandulifera* community stands produce up to 20 tons/ha (A.-M. Planty-Tabacchi and E. Tabacchi, unpublished).

Riparian vegetation as a sink of energy and matter

Sediment and nutrient trapping on the surface of the riparian zone

Riparian vegetation facilitates the removal of suspended sediment, along with its nutrient contents, from two types of surface water: (a) overland storm water entering laterally (Peterjohn & Correll, 1984; Chescheir *et al.*, 1991; Klarer & Millie, 1989; Lowrance *et al.*, 1988; Mitsch *et al.*, 1979; Parsons *et al.*, 1994) and (b) flood waters entering from the stream channel (Brunet *et al.*, 1994; Hart *et al.*, 1987; Hupp & Morris, 1990; Hupp *et al.*, 1993; Johnston, 1993; Kleiss *et al.*, 1989). In both cases, riparian vegetation plays an important role in removing and retaining particulates. Increased friction with the soil surface can cause reduced velocity and consequent sedimentation of particulates, but riparian vegetation and the layer of litter it deposits on the soil surface are much more effective at slowing the velocity of the surface waters. The fine roots of the plants, which are concentrated on or near the surface, and the microbial communities on the surfaces of the soil, litter and above ground plant organs also are able to assimilate dissolved nutrients from the surface waters (Peterjohn & Correll, 1984). In agricultural areas phosphorus is mainly exported with sediments to which it is chemically bounded. Several studies have focussed on the effectiveness of the riparian zones controlling phosphorus loss from agricultural land to the streams (Omernik *et al.*, 1981; Peterjohn & Correll, 1984; Cooper & Gilliam, 1987)

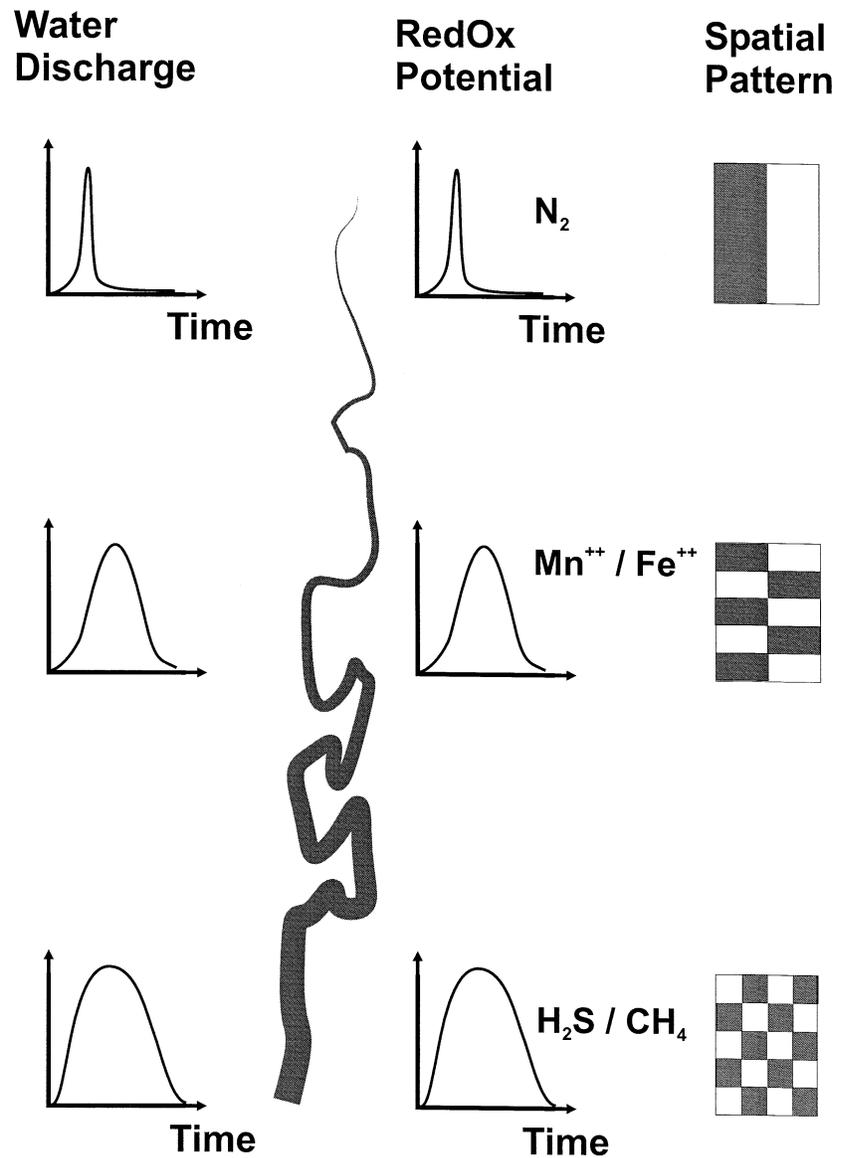


Fig. 6 Changes in redox patterns along a temperate stream. Redox dynamics parallel water inputs, which become more uniform downstream. Spatial pattern is symbolized by reduced zones in black and oxidized zones in white. This pattern becomes more heterogeneous or patchy downstream (see text).

and produced equivocal results. Hence, depending on the soil texture and the form of phosphorus taken into account, one might consider riparian forest soil either as a source or a sink of phosphorus (Fabre *et al.*, 1996).

Nitrogen trapping by the riparian zone

Over the last 15 years, research has focused on the role of riparian zones as regulators of diffuse, subsurface pollution, especially nitrogen (Peterjohn & Correll, 1984). Several studies have pointed out that nitrogen buffering in the riparian zone was due to combined effect of plant uptake and microbial denitrification (see Haycock *et al.*, 1993

for a review). Buffering capacity is most efficient along low order streams where the surface contact between riparian wetland and the adjacent agricultural land is maximized (Brinson, 1990). However, efficiency of riparian biota in regulating subsurface fluxes of nitrogen is often limited by the geomorphic features of the riparian zone, which determine the groundwater flow path and thus influence allochthonous nitrate availability (e.g. draining from adjacent agricultural land). Hence, the riparian zone may exist as a mosaic of hydrogeomorphic units, which can be hydrologically disconnected from each other and more or less disconnected from the upland subsurface flow.

As a result, the efficiency of a given riparian zone in regulating subsurface nitrogen fluxes cannot be a simple function of the surface area covered by riparian vegetation. Rather, nitrogen and the attenuation of other pollutants is a function of the length of the hydrological contact zone as the pollutant plume moves through the riparian zone from upland drainage areas toward the stream channel.

Riparian vegetation as a source of energy and matter

Most stream channels are partially heterotrophic ecosystems that rely on inputs of organic matter from the riparian zone and catchment for much of the energy needed to drive the stream food web (Connors & Naiman, 1984; Cuffney, 1988; Fisher & Likens, 1973; Kleiss *et al.*, 1989; Minshall, 1978; Triska *et al.*, 1982). Many studies have shown that most of the particulate organic matter and much of the dissolved organic matter derives from areas immediately adjacent to the stream channel (Sedell *et al.*, 1974; McDowell & Fisher, 1976; Winterbourn, 1976; Sidle, 1986; King *et al.*, 1987; Chauvet & Jean-Louis, 1988; Cushing, 1988; Gurtz *et al.*, 1988; Benson & Pearson, 1993; Sweeney, 1993; Triska *et al.*, 1984).

Stream channels benefit from a steady input of woody branches and tree trunks. The resulting debris dams increase complexity in channel morphology and produce more useful habitats for stream biota (Minshall, 1978). In some cases, this effect is enhanced by secondary factors, like a high frequency of storms or the presence of beavers. The necessary woody debris originates almost entirely in the riparian zone (Webster, 1977; Sedell & Frogart, 1984; Harmon *et al.*, 1986; Maser & Sedell, 1994; Keller & MacDonald, 1995). In some cases, woody debris can be essential for the establishment or the survival of plant and animal riparian communities. For example, Müller & Bürger (1990) have shown the importance of coarse debris and an interaction with groundwater level on the establishment of the *Salici-Myricarietum* community on sandbars. The importance of large woody debris has been shown to have major ecological consequences not only for the stream itself (Hering & Reich, 1997), but also for oceanic ecosystems (Maser & Sedell, 1994).

The role of riparian vegetation in controlling stream temperature and flow

Stream temperature

Riparian forests reduce solar heating of stream water by shading, especially in low order streams (Brown & Krygier, 1970). Riparian vegetation also provides cooling by evapotranspiration of soil water and shallow groundwater (Beschta, 1984; heuer *et al.*, 1984; Sinokrot & Stefan, 1993). The evapotranspiration cooling is greatest when the vegetation is forest, since forest has the highest leaf area index and consequently the highest evapotranspiration rates. Hardwood deciduous riparian forest in temperate climates has an evapotranspiration rate up to 118 cm per year (Peterjohn & Correll, 1986). Stream temperature also may be moderated by groundwater flowing laterally into the stream as a consequence either of upwelling from deep phreatic sources or of upwelling from the hyporheic zone (Stanford, Ward & Ellis, 1994).

Stream flow

Whereas the role of riparian vegetation in controlling channel and bank stability is well documented, little is known about natural control of stream flow by riparian vegetation. Most studies concerning this topic are devoted to local scales and to vegetation dominated by grasses or sedges (Kadler, 1990). Within the channel, aquatic macrophytes may be impeded and otherwise influence flow (Madsen & Warncke, 1983; Sand-Jensen & Mebus, 1996). Pioneer vegetation on point bars may influence the flow, even outside the period of flood occurrence (Monteith, 1973). During high water and floods, riparian vegetation usually has significant effects on flow by increasing roughness. Channel separations are often mediated by woody debris. Water abstraction from the channel and/or alluvial aquifer may reduce the height of the water table, killing riparian vegetation and increasing erosion potential of the stream banks (Kondolf & Curry, 1984). Conversely, flow regulation by dams and diversions may allow encroachment of riparian vegetation into the channel which, in some cases, can cause increasing velocity and associated channel degradation (Johnson, 1994).

Linking stream, groundwater and landscape concepts to riparian plant ecology

Contemporary stream ecology is multidisciplinary and includes regional characterization of the drainage basin (Martin & Bouchard, 1993), including longitudinal, lateral and vertical analyses of the ecology of the riparian zone and its subsurface components (Stanford & Ward, 1993). Synthetic understanding of riparian plant biodiversity and processes, like competition, colonization and nutrient and water uptake, require thorough grounding in geomorphology, landscape ecology and biogeochemistry of the stream and its valley. Many, perhaps most, studies in stream ecology (*sensu lato*) are still devoted to studies of the various ecological compartments *per se*, instead of trying to take into account the interactive effects of the structures and processes from one compartment to another and at different places within the stream network.

We suggest that regional settings should be more rigorously included in freshwater ecosystem studies as input parameters. Using regional frameworks as templates allows better understanding of upland and instream controls on riparian vegetation and the influences of riparian vegetation on stream ecology. Site-specific studies of biodiversity and ecosystem processes are important and commonly performed (Schultze & Mooney, 1994; Mooney *et al.*, 1996), but cascading effects between adjacent compartments or systems may be expected when ecological continua are examined (Forman, 1995; Mooney *et al.*, 1996). Moreover, many of the processes examined in this paper are scale-dependent and similar analyses could lead to very different conclusions when scale is properly considered.

Anthropogenic stream regulation elicits many edaphic, biogeochemical and biological problems that are seldom considered from a total system perspective. Assessing the consequences of water abstraction on stream ecosystem functioning should be restricted to considering instream effects, but also to the dynamics and linkages of the channel and riparian compartments. For example, as noted above, riparian soils develop and are sustained by linkages and dynamics of channel flooding, sediment transport, riparian vegetation and groundwater supply or permanence, among a host of other potential controls,

all of which are likely to be dramatically influenced by stream regulation.

We believe that riparian vegetation can buffer pollutant loading to streams from upland sources. The evidence of riparian plant controls on stream chemistry is very sparse, however, and this subject is very clearly in need of innovative research from both localized (stream reach) and catchment perspectives, especially with respect to interactions between rooted plants, groundwater and soil microbiology and nutrient allocation.

Qualitative changes accompany quantitative changes in riparian vegetation. We focused on exotic species because they represent good case studies of such changes. As a consequence of human activities along temperate streams, as well as over entire drainage basins, exotic species tend to invade the riparian zone where they can find appropriate ecological niches. Exotic species may be expected to change the plant patch dynamics and associated biogeochemical cycling of ecotones such as riparian zones (Forman, 1995). Moreover, riparian and channel corridors are efficient vectors for spreading of many exotic plants and probably accelerate regional changes. Vegetation changes may stimulate other biota in other unexpected ways (e.g. by providing habitats that were not present before exotic plants established). Finally, a better understanding of control of riparian vegetation by animals is needed, such as large herbivore influences on the riparian corridor (see Naiman & Rodgers, 1997).

The perspective in this paper is clearly ecosystem and landscape oriented. This does not mean that other approaches are not useful or appropriate. Our main point is that a spatially explicit theory explaining the occurrence and abundance of riparian vegetation remains elusive and is one of the great challenges for sustaining the integrity of stream ecosystems worldwide (*sensu* Meyer & Swank, 1996). We believe this challenge requires a synthetic view of the biophysical linkages between instream, groundwater and terrestrial components of the riparian corridor in a regional landscape (catchment) context.

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